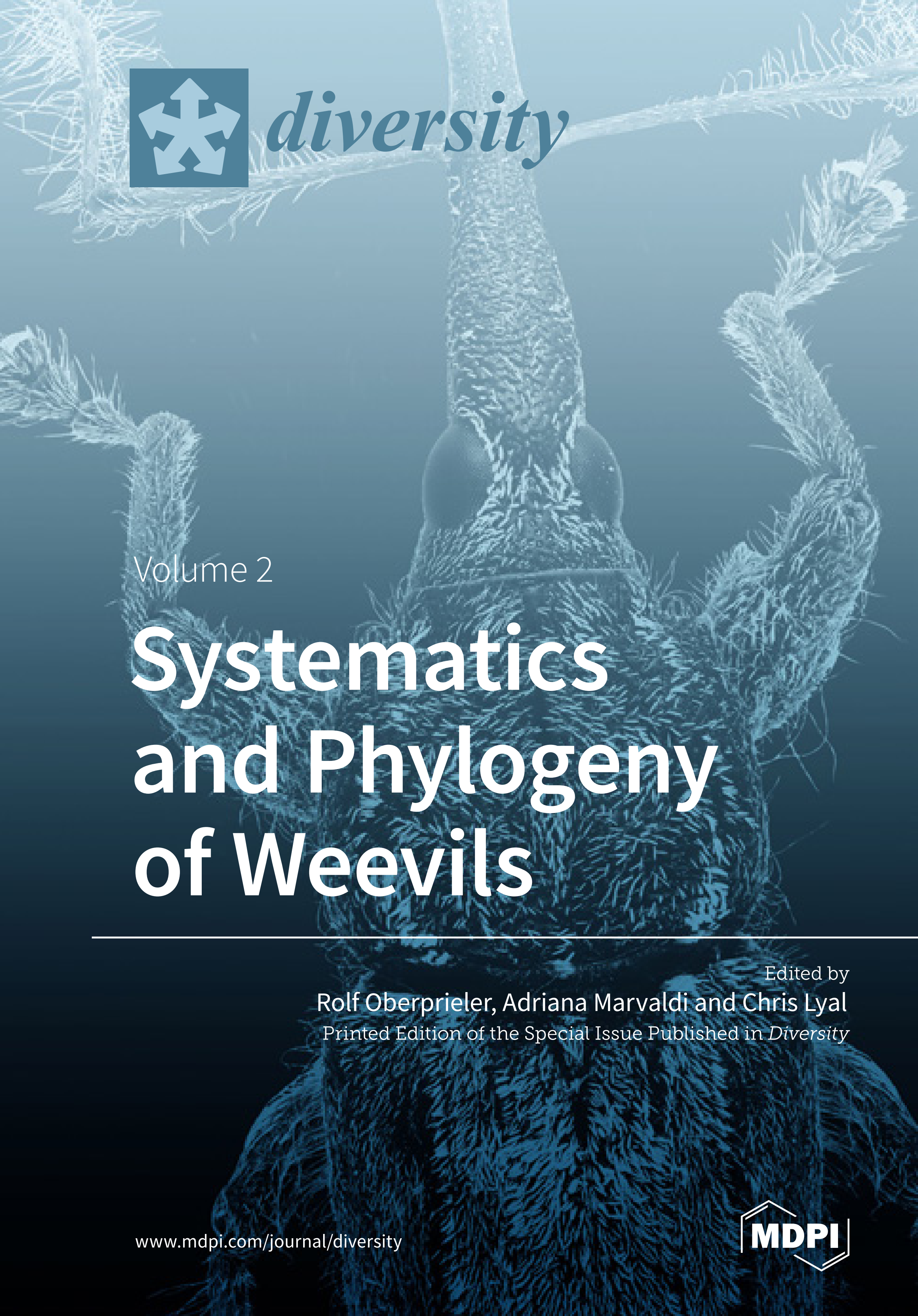

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Systematics and Phylogeny of Weevils

Edited by

Rolf Oberprieler, Adriana Marvaldi and Chris Lyal

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Special Issue Editors

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About the Special Issue Editors

Rolf Oberprieler is a senior research scientist at the Australian National Insect Collection of the Commonwealth Scientific and Industrial Research Organisation (CSIRO) in Canberra, Australia. He worked on weevils at the National Insect Collection of the Plant Protection Research Institute in Pretoria, South Africa, for 17 years, mainly on the subfamily Entiminae but also on several other groups. For his Ph.D. degree he studied the systematics and biology of the African cycad-associated weevils, an interest that followed him to Australia in 1997. There he continued taxonomic research on broad-nosed weevils (Entiminae and Cyclominae) but also on some taxa of economic importance. He authored and co-authored a comprehensive catalogue of Australian weevils and several chapters on weevils in the Handbook of Zoology, as well as papers on weevil fossils and phylogeny. With almost 40 years of experience in weevil systematics, he has a broad knowledge of the weevil fauna of the Southern Hemisphere.

Adriana E. Marvaldi is as a research scientist of The National Scientific and Technical Research Council (CONICET) based at the Museum of Natural Sciences in La Plata, Argentina. Insects, especially beetles, have always fascinated her. She studied biology and earned her Doctorate degree in 1995 at the Faculty of Natural Sciences and Museum of the National University of La Plata. Adriana has focused her research on weevil systematics, starting her career at the Argentine Dryland Research Institute (IADIZA) in Mendoza, where she contributed to the foundation of an active entomology group and worked for 20 years. During this period she also spent time at the Museum of Comparative Zoology of Harvard University as a postdoctoral researcher. Her research work initially centred on the comparative morphology of the immature stages of weevils and the use of their characters in phylogenetic reconstruction, but she later also became interested in the morphology of adult weevils and in using molecular data in phylogenetic and evolutionary studies. Since 2015 Adriana has worked at the Entomology Division of the Museum of La Plata, where she continues pursuing her research interests in Coleoptera systematics, in particular of the weevil fauna of South America. Adriana's publications include several articles and book chapters spanning various taxonomic levels, including phylogenetic hypotheses on Curculionoidea, Belidae and curculionid groups such as Entiminae.

Chris Lyal is a scientific associate at the Natural History Museum in London, where he worked as a research scientist for more than 45 years. After research on the morphology and evolution of Heteroptera and Phthiraptera, he moved on to study weevil taxonomy, morphology, nomenclature and systematics. In the 1980s, he spent a year in New Zealand working with Willy Kuschel and preparing a handbook to New Zealand Cryptorhynchinae. He co-authored a global catalogue of weevil genus and family group names and with others is building a global species catalogue. Chris has published on key morphological features, in particular stridulation, sclerolepidia and the rectal system, on weevil seed predators, particularly of the South-East Asian tree family Dipterocarpaceae, and on a variety of other weevil groups. He is currently reviewing all of the tribes and subtribes of the subfamily Molytinae with the intent of creating a firm basis for further systematic research on this subfamily.

Preface to ”Systematics and Phylogeny of Weevils”

Weevils (Curculionoidea) are one of the largest superfamilies of animals on Earth, comprising about 62000 described species in 5800 genera, but it has been estimated that about three times as many exist. Their tremendous diversity has been attributed to their close associations and co-radiation with angiosperm plants, but weevils have also evolved intimate relationships with gymnosperms (especially conifers and cycads) and other plant groups. As a consequence of their often highly specialized associations with plants, many weevils are regarded as pests of human agriculture and silviculture, whereas others are used as biological control agents of noxious weeds or as pollinators of crops such as oil palms. Weevils also play critical roles in native ecosystems, from herbivores and seed predators to pollinators to decomposers of dead and dying plants.

Weevil systematics and phylogeny have come a long way since the first comprehensive phylogenetic analysis of the group, published by Willy Kuschel in 1995, and the phylogenetic backbone of the superfamily (its family classification) outlined in that paper has been confirmed several times by later studies and is quite robust. However, intrafamilial relationships and natural groups (subfamilies and tribes) remain much less clear, particularly in the largest family, Curculionidae. Further study is also needed in fields such as comparative morphology, biogeography and patterns of host associations.

Not surprisingly for such a huge and diverse taxonomic group, advances in the systematics and phylogeny of weevils have largely occurred on regional levels and in treatments of genera and other groups scattered across the superfamily, with large-scale studies still needed to address big-picture questions about the evolution of the group effectively. Some collaborative efforts have recently begun to ameliorate this, notably the international cooperation to cover the weevils in the recent Handbook of Zoology and the weevil symposium and follow-up meeting at the 2016 International Congress of Entomology in Orlando, Florida. This Special Issue aims to continue this process and promote collaboration between weevil systematists as well as the dissemination of systematic information on these fascinating beetles. At the same time, it provides an apt forum to recognize and commemorate the significant contributions to the discipline made by the recently deceased Guillermo (“Willy”) Kuschel, whose work on especially the phylogeny and higher classification of weevils has shaped our understanding of their evolutionary history like that of no-one else. This Special Issue therefore also serves as a memorial issue for him.

We are thrilled that our call to contribute papers to this Special Issue has been taken up so widely and enthusiastically that it can collate 31 papers spanning over 900 pages, both advancing our knowledge of weevil systematics and phylogeny on a broad front and also paying homage to Kuschel's impact on the field. The papers comprise 24 systematic studies, including seven phylogenetic ones, and five on host associations, diversity, distribution and biocontrol, as well as a summary of the proceedings of the weevil meeting in Orlando and a tribute to Willy Kuschel containing a biography and a summary of his contributions to weevil systematics, including also lists of all his publications and the taxa named after him. We extend our warmest thanks to *Diversity* for inviting this Special Issue, to all the colleagues who contributed their time and research results to this issue, to all the anonymous reviewers who ensured the quality of the papers and to the Editorial Staff of the journal for their sterling efforts in dealing so speedily and efficiently with all the manuscripts, reviewers' comments and various unforeseen problems. We hope that this Special Issue will form another milestone on the road to comprehending and appreciating the evolutionary success of these special beetles.

Rolf Oberprieler, Adriana E. Marvaldi, Chris Lyal
Special Issue Editors

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Article

A Combined Molecular and Morphological Approach to Explore the Higher Phylogeny of Entimine Weevils (Coleoptera: Curculionidae), with Special Reference to South American Taxa

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Abstract: The Entiminae are broad-nosed weevils constituting the most diverse subfamily of Curculionidae, with over 50 tribes. We performed Bayesian and Maximum Parsimony combined phylogenetic analyses with the main objective of testing higher-level relationships and the naturalness of the major Neotropical and Southern South American (Patagonia and Andes) tribes, including some members from other regions. We compiled a data matrix of 67 terminal units with 63 Entiminae species, as well as four outgroup taxa from Cyclominae, by 3522 molecular (from nuclear 18S rDNA and 28S rDNA, and mitochondrial 16S rDNA and COI gene sequences) and 70 morphological characters. The resulting trees recover a clade Entiminae with a monophyletic Cylydrorhinini and *Premnotrypes* branching off early. The tree resulting from parsimony analysis shows a clade of Leptopiini from the Australian region and another clade including taxa mainly distributed in the Palaearctic and Neotropical regions, but in the Bayesian tree the South American and Australian Leptopiini are grouped together. The mainly Palaearctic Entiminae (e.g., Brachyderini, Laparocerini, Otiorhynchini, Peritelini, Polydrusini, Phyllobiini and Sciaphylini) form a subclade separated from Southern Hemisphere taxa. Among the latter, the well-supported Naupactini are the sister group of the South American Tanymecini, excluding *Platyaspistes*, herein transferred to Leptopiini (new placement). Another well-justified clade is Eustylini–Geonemini, which also includes the enigmatic *Galapagonotus*, and the genus *Artipus*, thus corroborating its recent exclusion from Naupactini.

Keywords: Broad-nosed weevils; Entiminae; tribal relationships; combined evidence; ribosomal markers; structural alignment; mitochondrial COI; adults; larvae

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1. Introduction

Entiminae constitute the most species-rich subfamily of Curculionoidea, with about 12,000 described species worldwide, classified into ca. 1370 genera and 54 tribes [1–3]. This subfamily includes mainly taxa that were grouped in the section Adelognatha of older Curculionidae classifications. With few exceptions, most entimine species have soil-dwelling larvae, many of them polyphagous. Monophyly of Entiminae is suggested by some synapomorphic characters in the adult (e.g., mandibles with deciduous mandibular processes or their corresponding scar) [1] as well as the larva (e.g., cushion-like antennal sensorium) [4]. Molecular analyses consistently show the Entiminae as being part of a larger clade of broad-nosed weevils that also includes taxa classified in the Cyclominae and Hyperinae [5–10]. Such molecular studies, however, do not provide evidence supporting a clade Entiminae distinct from Cyclominae, except for a shared gene order rearrangement in the mitogenome [7,11]. The entimines and allied taxa have in common a relatively short, broad rostrum that is not used in oviposition site preparation; and their larvae are mostly ectophytic, feeding on roots in the soil or on aerial plant parts (some species with endophytic or semi-endophytic larvae, especially in Cyclominae) [3,12]. Among the structural features that would support the monophyly of "broad-nosed weevils" are the bilobed, largely sclerotized basal part of male sternite IX, the meso- and metatibiae apically either unarmed or mucronate (not uncinate) and the occurrence of iridescent scales with a particular nanostructure [3].

During recent decades, several specialists worldwide have done a considerable revisionary work on different tribes of Entiminae, providing useful morphological features to contribute to tribal diagnoses, to recognize genera and species, and to analyze their relationships. Most of the studies include taxa from a restricted biogeographic region, e.g., Entimini [13–15]; Eustylini and Geonemini [16–20]; Tanymecini [21–25]; Naupactini [26–29]; Sitonini [30]; Cyphicerini, Phyllobiini and Polydrusini [31,32]; Laparocerini [33–36]; Otiorhynchini [37–40]; Tanyrhynchini [41,42]; Leptopiini (as Tropiphorini in recent studies) [43–46]; and Trachyphloeini [47]. However, the generic classification of the entimines into tribes, as in the last worldwide weevil catalogue [2], remains unsatisfactory, with many tribes probably not representing natural groups.

For historical reasons, weevil generic and suprageneric classifications remain essentially based on the Holarctic fauna. The relatively less studied entimines from other regions have been often classified in already well-known genera and tribes from the Holarctic region, but based on similar observed features which do not necessarily reflect unique common ancestry. A more detailed examination of the morphological features, however, suggests a deep divergence of the austral faunas relative to the Holarctic fauna, and a probable closer relationship between some Australian Entiminae and Cyclominae with those from southern Argentina and Chile [48–52].

In this contribution, we present results of a phylogenetic study focused on South American tribes of Entiminae. The study was based on nuclear and mitochondrial molecular markers combined with morphological data for a sample of species representing the Neotropical and Patagonian-Andean faunas as well as entimines from other regions in both southern and northern hemispheres, including some South American Cyclominae used as outgroups.

The main hypotheses to be tested are as follows: that the Neotropical and Patagonian-Andean members of the tribes Cylydrorhinini, Entimini, Eudiagogini, Eustylini, Geonemini, Leptopiini, Naupactini, Premnotrypini and Tanymecini form a clade separated from the mainly Palaearctic tribes (e.g., Brachyderini, Laparocerini, Otiorhynchini, Peritelini, Polydrusini, Phyllobiini and Sciaphylini) and Oriental Entiminae (e.g., Celeuthetini); and that the South American species of Leptopiini are related to genera of this tribe occurring in the Australian region. In addition, we are interested to address the phylogenetic positions of *Platyaspistes* Schoenherr and *Galapagonotus* Anderson & Lanteri, two South American genera with unclear affinities but currently classified in Tanymecini and Eustylini, respectively.

2. Materials and Methods

2.1. Specimens and Taxon Sampling

Table 1 lists the specimens and taxa used in the phylogenetic analyses, corresponding to 67 terminal species of Entiminae and Cyclominae, including valid names, acronyms, geographic data and GenBank accession numbers of DNA sequences for the four markers used.

The tribal classification used in this paper is based primarily on the world generic catalogue by Alonso-Zarazaga and Lyal [2], but incorporating some changes made subsequent to this publication. *Artipus* Sahlberg was classified in Geonemini and not in Naupactini [28]. The names of the Palaearctic species, genera and subgenera, and their assignment to tribes were updated according to Alonso-Zarazaga et al. [53]. Since the concept of Tropiphorini is very controversial (e.g., [53,54]), for the moment, we prefer to classify the genera from the southern hemisphere in the tribe Leptopiini, as suggested by Pullen et al. [55].

The classification of geographic regions follows Morrone [56] except for the Andean region in which case we recognized four biogeographic units: High Andes, Central Chile, Patagonia and Subantarctic.

We selected 63 species of Entiminae in 42 genera representing 17 tribes, as well as four species of Cyclominae in three genera from two tribes used as outgroups. The taxon sampling includes the tribes of Entiminae best representing the Neotropical and Patagonian-Andean faunas (Cylydrorhinini, Entimini, Eudiagogini, Eustylini, Geonemini, Leptopiini, Naupactini, Premonotrypini and Tanymecini), as well as some tribes typical of the Palaearctic fauna (Brachyderini, Laparacerini, Otiorhynchini, Peritelini, Phyllobiini, Polydrusini, and Sciaphilini) and some representatives of the dominant element of the Australian fauna in tribe Leptopiini [55] and Celeuthetini, corresponding to the Australian and Oriental regions. In Southern Chile and Argentina three species of *Polydrusus* Germar are associated with *Nothofagus* spp. trees [57,58]. In our study, the *Polydrusus* specimens from this area were not preserved for DNA extraction, and consequently we only analyzed Polydrusini species from Europe.

Samples of adult specimens assayed for molecular analyses were collected in different areas of Argentina and Brazil, using a beating sheet or a sweep net, or were provided by colleagues (see Acknowledgements). The material was stored in 96–100% ethanol at −20 °C freezer until DNA extraction. Voucher specimens were deposited at the entomological collection of the Museo de La Plata, Argentina.

Table 1. Studied taxa, geographical sources and GenBank accession numbers. Codes in boldface indicate the new sequences produced for this study. * Tribes of Outgroups, in Cyclominae.

Tribe	Species	Acronyms	Locality	Accesion Codes			
				18S	28S	16S	COI-5P
***Aterpini**	*Aegorhinus silvicola* Kuschel	*CYC_Aegorhinus_sil*	Argentina, Neuquén, San Martín de los Andes	**MH746278**	**MH746328**	**MH746378**	**MH734198**
	Aegorhinus vitulus (Fabricius)	*CYC_Aegorhinus_vit*	Argentina, Tierra del Fuego, Ushuaia	**MH746279**	-	**MH746379**	**MH734199**
***Listroderini**	*Listroderes victus* Germain	*CYC_Listroderes_vic*	Chile, Cartagena, El Tabo, coastal dunes	**MH746280**	**MH746329**	**MH746380**	**MH734200**
	Rhigopsidius piercei Heller	*CYC_Rhigopsidius_pie*	Argentina, Jujuy	**MH746281**	**MH746330**	**MH746381**	**MH734201**
Cylydrorhinini	*Caneorhinus biangulatus* (Champion)	*CYL_Caneorhinus_bia*	GenBank source (Arg. Falklands Is.)	-	-	EF213994	-
	Cylydrorhinus caudiculatus (Fairmaire)	*CYL_Cylydrorhinus_cau*	GenBank source (Arg. Falklans Is.)	-	-	EF214094	-
	Cylydrorhinus chilensis (Blanchard)	*CYL_Cylydrorhinus_chi*	Argentina, La Rioja, Dto. Vinchina	**MH746286**	**MH746335**	-	**MH734202**
	Cylydrorhinus aff. patagonicus (Kuschel)	*CYL_Cylydrorhinus_pat*	Argentina, Jujuy, Dto. Susques	**MH746287**	**MH746336**	**MH746385**	**MH734203**
Premnotrypini	*Premnotrypes latithorax* (Pierce)	*PRE_Premnotrypes_lat*	Perú, Cuzco	**MH746316**	**MH746365**	**MH746416**	**MH734204**
Leptopiini	*Catasarcus impresipennis* (Boisduval)	*LEP_Catasarcus_imp*	GenBank source (Australia)	-	KF016401	KF016266	-
	Catasarcus sp.	*LEP_Catasarcus_sp*	GenBank source (Australia)	FJ867744	FJ867671	AJ495489	FJ867847
	Cecyropa sp.	*LEP_Cecyropa_sp*	New Zealand, Waikuku Beach, Surf Club	**MH746322**	**MH746371**	-	**MH734205**
	Irenimus sp.	*LEP_Irenimus_sp*	New Zealand, Ahuriri Scenic Reserve, Port Hills, Christchurch	**MH746324**	**MH746373**	**MH746422**	**MH734206**
	Strangaliodes deserticola Kuschel	*LEP_Strangaliodes_des*	Chile, Atacama	**MH746325**	**MH746374**	-	**MH734207**
	Strangaliodes sp. *(aff. deserticola)*	*LEP_Strangaliodes_sp*	Chile, Pichilemos	-	**MH746375**	**MH746423**	**MH734208**
	Strangaliodes niger (Blanchard)	*LEP_Strangaliodes_nig*	Argentina, San Juan	**MH746326**	**MH746376**	**MH746424**	**MH734209**
	Vossius nebulosus (Gyllenhal)	*LEP_Vossius_neb*	Argentina, Misiones, on way to Salto Tabai, close to Jardín America	**MH746323**	**MH746372**	-	**MH734210**
Entimini	*Entimus* sp.	*ENT_Entimus_sp*	Brazil, Rio de Janeiro, Coastal Restingas	**MH746327**	**MH746377**	**MH746425**	**MH734211**
Eudiagogini	*Eudiagogus rosenschoeldi* Fahraeus	*EUD_Eudiagogus_ros*	GenBank source (United States of America)	AF250081	-	-	-
	Pororhynchus aff. albolateralis Hustache	*EUD_Pororhynchus_alb*	Argentina, San Juan, near Telteca	**MH746288**	**MH746337**	**MH746387**	**MH734212**
Eustylini	*Compsus* sp.	*EUS_Compsus_sp*	GenBank source (South America)	-	KT350862	-	KT350650
	Diaprepes abbreviatus (Linnaeus)	*EUS_Diaprepes_abb*	GenBank source (Central America)	AY157729	KT350865	CN475651	HQ891432
	Galapagonotus cuneiformis Waterhouse	*Galapagonotus_cun*	Ecuador, Islas Galápagos, San Cristóbal, El Junco	**MH746282**	**MH746331**	**MH746386**	-
	Oxyderces bimaculatus (Hustache)	*EUS_Oxyderces_bim*	Argentina, Corrientes, Empedrado	**MH746289**	**MH746338**	**MH746388**	**MH734213**
Geonemini	*Artipus* sp.	*GEO_Artipus sp.*	GenBank source (Caribbean)	-	KT350859	KP253881	HQ891428
	Epicaerus sp	*GEO_Epicaerus_sp*	United States of America	**MH746290**	**MH746339**	**MH746389**	**MH734214**
	Lachnopus sp.	*GEO_Lachnopus_sp*	GenBank source (Caribbean)	AF389052	KT350910	-	HQ891465

Table 1. *Cont.*

Tribe	Species	Acronyms	Locality	Accesion Codes			
				18S	28S	16S	COI-5P
Naupactini	*Atrichonotus taeniatulus* (Berg)	*NAU_Atrichonotus_tae*	Argentina, Mendoza, Guaymallén	**MH746296**	**MH746345**	**MH746395**	**MH537919**
	Hoplopactus lateralis Arrow	*NAU_Hoplopactus_lat*	Brazil, San Pablo	**MH746297**	**MH746346**	**MH746396**	**MH537920**
	Litostylus sp.	*NAU_Litostylus_sp*	GenBank source (Caribbean)	-	KT350916	-	HQ891470
	Naupactus auricinctus Boheman	*NAU_Naupactus_ aur*	Brazil, San Pablo	**MH746298**	**MH746347**	**MH746397**	**MH537921**
	Naupactus aff chloraspis Erichson	*NAU_Naupactus_chl*	Brazil, Bahia	**MH746299**	**MH746348**	**MH746398**	**MH734215**
	Naupactus aff faldermanni Boheman	*NAU_Naupactus_ fald*	Brazil, Mato Grosso	**MH746300**	**MH746350**	**MH746399**	-
	Naupactus leucoloma Boheman	*NAU_Naupactus_leu*	Argentina, Mendoza	**MH746301**	**MH746349**	**MH746400**	**MH537922**
	Naupactus aff peruvianus Hustache	*NAU_Naupactus_ per*	Perú, Cuzco, Dto. Machu Pichu, Puerta Ciudad Antigua	**MH746302**	**MH746351**	**MH746401**	-
	Naupactus sulphurifer Pascoe	*NAU_Naupactus_sul*	Argentina, Mendoza, Reserva Divisadero Largo	**MH746303**	**MH746352**	**MH746402**	-
	Naupactus tarsalis Boheman	*NAU_Naupactus_tar*	Argentina, Formosa, Dto. Matacos, 20 Km Ing. Juárez	**MH746304**	**MH746353**	**MH746403**	-
	Naupactus viridisquamosus Boheman	*NAU_Naupactus_vir*	Brazil, Mato Grosso	**MH746305**	**MH746354**	**MH746404**	
	Naupactus xanthographus (Germar)	*NAU_Naupactus_xan*	Argentina, Mendoza [except 16S, Buenos Aires, La Plata]	FJ867775	FJ867695	**MH746405**	NC0180354
	Pantomorus ruizi (Brèthes)	*NAU_Pantomorus_rui*	Argentina, Chubut, Trelew INTA	**MH746306**	**MH746355**	**MH746407**	**MH537925**
	Symmathetes setarius (Boheman)	*NAU_Symmathetes_seta*	Brazil, Mato Grosso	**MH746308**	**MH746357**	**MH746408**	**MH537923**
	Symmathetes setulosus Hustache	*NAU_Symmathetes_setu*	Argentina, Catamarca, Las Esquinas, Dpto. Valle Viejo	**MH746307**	**MH746356**	**MH746406**	**MH537924**
Tanymecini	*Airosimus jacobi* (Hustache)	*TAN_Airosimus_jac*	Argentina, Misiones, Urugua-i	**MH746318**	**MH746367**	**MH746418**	**MH734216**
	Hadromeropsis aff. pallida Howden	*TAN_Hadromeropsis_pal*	Argentina, Entre Ríos, Cerrito	**MH746319**	**MH746368**	**MH746419**	**MH734217**
	Pandeleteius platensis Brèthes	*TAN_Pandeleteius_pla*	Argentina, Mendoza, Reserva Ñacuñán	**MH746320**	**MH746369**	**MH746420**	**MH734218**
	Pandeleteius sp.	*TAN_Pandeleteius_sp*	GenBank source (United States of America)	-	HQ891475	-	HQ891475
	Platyaspistes argentinensis Kuschel	*TAN_Platyaspistes_arg*	Argentina, San Juan, Dto. Sarmiento-Pedernal, Camino de los Berros	**MH746321**	**MH746370**	**MH746421**	**MH734219**
Brachyderini	*Brachyderes incanus* Linnaeus	*BRA_Brachyderes_inc*	GenBank source (Europe)	-	KX551463	AJ495503	KJ962877
	Caulostrophus subsulcatus (Boheman)	*BRA_Caulostrophus_sub*	Italy, Genova, Voltri, Fiorino	**MH746283**	**MH746332**	**MH746382**	**MH734220**
	Strophosoma (Strophosoma) melanogrammum (Forster)	*BRA_Strophosoma_ mel*	Italy, Vercelli, Val Sesia, Monte Tovo	**MH746284**	**MH746333**	**MH746383**	**MH734221**

Table 1. *Cont.*

Tribe	Species	Acronyms	Locality	Accesion Codes			
				18S	28S	16S	COI-5P
Laparocerini	*Laparocerus (Atlantis) noctivagans* Wollaston	*LAP_Laparocerus_noc*	Portugal, Madeira, Rabaçal	**MH746293**	**MH746341**	**MH746391**	**MH734222**
	Laparocerus (Fernandezius) subcalvus Wollaston	*LAP_Laparocerus_sub*	Spain, Islas Canarias, Isla El Hierro, NE San Andrés	**MH746292**	**MH746344**	**MH746394**	-
	Laparocerus (Guanchotrox) canariensis Boheman	*LAP_Laparocerus_can*	Spain, Islas Canarias, Isla de Tenerife, El Portillo	**MH746294**	**MH746342**	**MH746392**	**MH734223**
	Laparocerus (Laparocerus) morio Boheman	*LAP_Laparocerus_mor*	Portugal, Madeira, Encumeada,	**MH746295**	**MH746343**	**MH746393**	**MH734224**
Otiorhynchini	*Dodecastichus mastix* Olivier	*OTI_Dodecastichus_mas*	Italy, Pescara, La Maielletta	**MH746309**	**MH746358**	**MH746409**	**MH734225**
	Otiorhynchus (Dorymerus) sulcatus Fabricius	*OTI_Otiorhynchus_sul*	GenBank source (Europe)	AF250084	KU041875	AJ495482/ JN163969	KJ962464
	Otiorhynchus (Metopiorrhynchus) teretirostris Stierling	*OTI_Otiorhynchus_ter*	Italy, Vercelli, Val Sesia, Monte Tovo	**MH746310**	**MH746359**	**MH746410**	**MH734226**
	Otiorhynchus (Provadilus) alpicola Boheman	*OTI_Otiorhynchus_alp*	Italy, Pescara, La Maielletta	**MH746311**	**MH746360**	**MH746411**	**MH734227**
Peritelini	*Drouetius azoricus parallelirostris* Machado	*PER_Drouetius_azo*	Portugal, Islas Azores, Isla Terceira, Angra, Monte Brazil	**MH746291**	**MH746340**	**MH746390**	**MH734228**
	Simo hirticornis Herbst	*PER_Simo_hir*	Italy, Lecco, Lombardia, Lagi di Annone	**MH746312**	**MH746361**	**MH746412**	**MH734229**
Phyllobiini	*Phyllobius (Parnemoicus) viridicollis* Fabricius	*PHY_Phyllobius_vir*	Italy, Verona, Monti Lessini, Monte Castelberto	**MH746313**	**MH746362**	**MH746413**	**MH734230**
Polydrusini	*Liophloeus (Liophloeus) tessulatus* O.F. Müller	*POL_Liophloeus_tes*	Italy, Como, Lombardia, Piano del Tivano	**MH746314**	**MH746363**	**MH746414**	**MH734231**
	Polydrusus (Eurodrusus) cervinus Linnaeus	*POL_Polydrusus_cer*	GenBank source (Europe)	-	HQ883568	AJ495494	HQ883653
	Polydrusus (Eurodrusus) confluens Stephens	*POL_Polydrusus_con*	Italy, Como, Lombardia, Piano del Tivano	**MH746315**	**MH746364**	**MH746415**	**MH734232**
Sciaphilini	*Eusomus ovulum* Germar	*SCI_Eusomus_ovu*	Italy, Milan, Zelo Buon Persico, Fiume Adda [except COI, GenBank source]	**MH746317**	**MH746366**	**MH746417**	**MH734233**
	Sciaphilus asperatus Bonsdorff	*SCI_Sciaphilus_asp*	GenBank source (Europe)	JN619105	-	AJ495502	KJ962310
Celeuthetini	*Celeuthetes* sp.	*CEL_Celeuthetes*_sp	Vanuatu, Efate, Tagabe, Agr. Research Stn, Port Vila	**MH746285**	**MH746334**	**MH746384**	**MH734234**

- means "unavailable".

2.2. Molecular Data

2.2.1. DNA Isolation, PCR Amplification and Sequencing

The experiments of DNA extraction and PCR amplification of genetic material were performed at the molecular laboratories of IADIZA-CONICET (Mendoza, Argentina) and IMBIV-CONICET-UNC (Córdoba, Argentina).

Total genomic DNA was extracted from adult voucher specimens using an adapted "salting out" protocol [59] or, alternatively, the DNeasy Blood and Tissue Kit (QIAGEN, MD, USA.). Tissue was processed from 1–2 legs or part of the thorax. Extracted DNA was stored at −20 °C. Four molecular markers (two nuclear and two mitochondrial) were used in this study: 18S rDNA (entire), 28S rDNA (regions D2, D3), 16S rDNA (regions IV, V) and COI ("barcode" or 5´region).

Amplification and sequencing of the targeted loci was performed using primers listed in Table 2. Polymerase chain reaction (PCR) was performed in a 50 µL volume: 10 pmol for each primer, 0.8 mM dNTPs (Genbiotech SRL, Buenos Aires, Argentina), $MgCl_2$ 50 mM to a final concentration of 2–4 mM, 5 µL 10 × Buffer, and 1.25 units of Taq DNA Polymerase (Invitrogen SA, Buenos Aires, Argentina). The 18S (~2000 bp) was amplified in two parts with the primer pairs E and F1094, and R1138 and P, with PCR conditions as in McKenna et al. [6]: 3 min at 95 °C; then 30 cycles of 1 min at 94 °C, 1 min at 60 °C, 1 min at 72 °C; final extension of 5 min at 72 °C; kept at 4 °C. In few instances, another combination of primers was used to obtain two smaller 18S fragments of ~500 bp each that contain the variable regions V4 and V7–V9 of 18S [60]: 18S a07 and 18S b25, and V7V9up and V7V9dwn, with PCR conditions: 3 min at 95 °C; then 10 cycles of 30 s at 95 °C, 30 s at 46 °C, 30 s at 72 °C; then 30 cycles of 30 s at 95 °C, 40 s at 48 °C, 40 s at 72 °C; final extension of 10 min at 72 °C. The fragment used of 28S (~700 bp spanning regions D2 and D3) was amplified with primers S3660 and A335, with PCR reactions as in Brown et al. [61]: 2 min at 94 °C; 40 cycles of 15 s at 94 °C, 30 s at 54 °C, 75 s at 72 °C; final extension of 7 min at 72 °C. The 16S (~600 bp spanning regions IV and V) was amplified with primers N13398 and J12887, with PCR conditions as in Hundsdoerfer et al. [5]: 4 min at 94 °C; 5 cycles of 45 s at 93 °C, 90 s at 40 °C, 90 s at 72 °C; then 26 cycles of 45 s 93 °C, 90 s at 50 °C, 90 s at 72 °C; final extension of 10 min at 72 °C. The COI gene was amplified with the primer pair LCO and HCO that produce the standard barcode fragment of 658 bp, but sometimes with the primers LCO and A3014 that allow a longer fragment of 1000–1300 bp; using in both cases the PCR conditions as in McKenna et al. [6]: 3 min at 94 °C; then 5 cycles of 30 s at 94 °C, 30 s at 42 °C, 90 s at 72 °C; then 34 cycles of 1 min at 94 °C, 30 s at 45 °C, 90 s at 72 °C; final extension of 5 min at 72 °C. The PCR products were purified and bi-directionally sequenced with the Sanger method, by means of the Sequencing Service of "Unidad de Genómica de INTA-Castelar" (Buenos Aires, Argentina) or by Macrogen Inc. (Seul, South Korea). Electropherograms were edited and contig assembled using ProSeq v.2.91 [62] or Sequencher v.5 (GeneCodes Corp.). All sequences were deposited in GenBank under accession numbers provided in Table 1.

2.2.2. Alignment of Sequences

The sequences of the ribosomal markers (nuclear 18S and 28S and mitochondrial 16S) were aligned using information on secondary structure of the rRNA genes to identify homologous positions [63]. The alignment was constructed manually using as reference the structural model of arthropod rRNA [64,65]. The program PAUP [66] was used for editing the annotated alignment as text file and for exporting the data in other formats for analyses. Regions identified as being of ambiguous alignment were bracketed to be excluded from phylogenetic analyses.

Table 2. List of primers used for PCR amplification and sequencing of the markers used in the phylogenetic analyses of Entiminae.

Marker	Primer	Sequence (5′ > 3′)	Sense	Reference
18S	E	CTG GTT GAT CCT GCC ACG T	F	[67]
	R1138	CGC CTT CGA ACC TCT AAC	R	[68]
	F1094	GGA TCG TCG CAA GAC GGA CAG AAG	F	[68]
	P	TAA TGA TCC TTC CGC AGG TTC ACC T	R	[67]
	18S a07	ATT AAA GTT GTT GCG GTT	F	[60]
	18S b25	TCT TTG GCA AAT GCT TTC GC	R	[60]
	V7V9up	TCC GAT AAC GAA CGA GAC TC	F	[60]
	V7V9dwn	GTT ACG ACT TTT ACT TCC TC	R	[60]
28S	S3660	GAG AGT TMA ASA GTA CGT GAA AC	F	[69]
	A335	TCG GAR GGA ACC AGC TAC TA	R	[70]
16S	N13398	CGC CTG TTT AWC AAA AAC AT	F	[5]
	J12887	CTC CGG TYT GAA CTC AGA TCA AGT	R	[5]
COI	LCO	GGT CAA CAA ATC ATA AAG ATA TTG G	F	[71]
	HCO	TAA ACT TCA GGG TGA CCA AAA ATC A	R	[71]
	A3014	TCC AAT GCA CTA ATC TGC CAT ATT A	R	[72]

2.3. Morphological Characters

External and internal (dissected) adult structures were observed with a Nikon SMZ1000 stereomicroscope (Tokyo, Japan), Leica S6D and MZ16 stereomicroscopes (Wetzlar, Germany); line drawings were done with a camera lucida attached to the former scope. Digital photographs were taken with cameras attached to the S6D and MZ16 steromicroscopes. For dissections, we used standard entomological techniques [73]. The terminology used for morphological characters follows Marvaldi et al. [3], and Lanteri and del Rio [28]. Some characters have been illustrated to facilitate recognition of different character states (Figures 1–4).

For each terminal, we scored 70 discrete morphological characters, of which 62 correspond to the morphology of adults and 8 to larvae. The list of morphological characters is given in Table 3 and the data matrix is shown in Table S1. When larval specimen or genitalia from adult could not be examined, character states were scored with "?" and treated as missing data. For some taxa (e.g., *Aegorhinus* Erichson, *Listroderes* Schoenherr, *Cylydrorhinus* Guérin-Méneville, and *Entimus* Germar), larval information was available from specimens belonging to different, but clearly co-generic species of those included in the analysis (see [4,74,75]).

Table 3. List of the 70 morphological characters, character states and codes.

1	Rostrum, length: more than 1.25 × as long as wide (minimum width, measured across apex without scrobes) (0) (Figure 1a); about as long as wide (slightly longer to slightly shorter) (1) (Figure 1b).
2	Rostrum, anterior portion of epistome: not raised and not projecting beyond anterior margin of rostrum (0); raised and projecting beyond anterior margin of rostrum (1) (Figure 1c).
3	Rostrum, outline of apex: slightly emarginated (0) (Figure 1a); V-shaped (1) (Figure 1b).
4	Rostrum, posterior part of epistome: denuded (0); covered with vestiture different from that of posterior part of rostrum (1) (Figure 5 in [28]).
5	Rostrum, expansion at apex (including pterigia): rostrum distinctly expanded at apex, ahead of antennal insertion (0) (Figure 1b); not to slightly expanded apex (sides subparallel or convergent towards apex) (1) (Figure 1d).
6	Rostrum, dorsal surface: impressed or flat (0) (Figure 1e); convex (1) (Figure 1c).
7	Rostrum, groove along midline: absent or indistinct (0); present (1) (Figure 1d).
8	Rostrum unicarinate or tricarinate (with central and lateral longitudinal carinae): not unicarinate or tricarinate (0); unicarinate or tricarinate (1) (Figure 1f).
9	Rostrum bicarinate (with pair of dorso-lateral carinae): not bicarinate (0); bicarinate (1) (Figure 1d).
10	Rostrum, scrobes in dorsal view: completely exposed, visible along their whole length (0) (Figure 3b); not completely exposed, only apical part partially visible (1) (Figure 3a).

Table 3. *Cont.*

11	Rostrum, sulcus along pterigia in lateral view: absent to slight (0); deep (1).
12	Rostrum, curvature of scrobes in lateral view: strongly curved ventrad of head (0) (Figure 1e); curved downwards and passing below eyes (1) (Figure 2a); slightly curved and orientated towards eyes (2) (Figure 2b).
13	Rostrum, scrobes in lateral view: well-defined and slightly widened posteriad (0) (Figure 2a); vaguely defined, shallow and very widened posteriad (1) (Figure 2b).
14	Rostrum, anteocular impression: longitudinal, latero-dorsal (0) (Figure 1 in [14]); triangular, lateral (1) (Figure 5 in [14]); indistinct (2).
15	Rostrum, transversal sulcus between rostrum and head (ventral view): present (0); indistinct (1).
16	Rostrum, occipital sutures (ventral view): longitudinal, curved, usually connected with lower edge of eye (0) (Figure 4a); transversal relative to longitudinal axis of rostrum, not connected with lower edge of eye (1) (Figure 4b); reduced to a fovea (2) (Figure 4c).
17	Mouthparts, inner side on mandibles: with two or more teeth (0) (Figures 1 and 2 [76]); with a single tooth on distal end or lacking tooth (1) (Figures 7 and 8 in [18])
18	Mouthparts, scar or lasting appendage on apical surface of mandibles: absent (0); present (1) (Figures 1b and 2e).
19	Mouthparts, prementum relative to maxillae: prementum incompletely concealing maxillae (phanerognathous condition) (0); prementum completely concealing maxillae (adelognathous condition) (1) (Figure 2f) (Figure 4d,e in [77]).
20	Mouthparts, long setae on prementum: absent (0) (Figure 2f); present (1) (Figures 9 and 10 in [18]).
21	Head, transversal furrow or impression between rostrum and forehead (dorsal view): present (0) (Figure 1c); absent (1).
22	Head, width of forehead relative to minimum width of rostrum (without pterigia): forehead wider than rostrum (0); forehead about same width to narrower than rostrum (1).
23	Head, orientation of setae behind forehead (vertex): setae anteriorly oriented (0); posteriorly oriented (1).
24	Head, superciliar arches: absent (0); present (1) (Figure 1e).
25	Head, circumocular sulcus: absent (0); present (1) (Figure 1e).
26	Head, large fovea on forehead: present (0); absent or very small (1).
27	Head, shape and position of eyes: rounded to slightly oval, oriented antero-posteriad (Figure 2b) (0); oval, oriented dorso-ventrad (1) (Figure 1f).
28	Head, convexity of eyes: flat (slightly protruding) (0) (Figure 1b); convex (protruding) (1) (Figure 1d); conical (strongly protruding) (2) (Figure 3a).
29	Eyes, position relative to anterior margin of pronotum: slightly separated from pronotum (by 1× or less than 1X the diameter of eyes) (0) (Figure 3c); largely separated from pronotum (by 1× of more than 1× the diameter of eyes) (1) (Figure 3b).
30	Antennae, shape and width of scape: clavate to spatulate, broad (0) (Figure 2b); clavate to capitate, slender (1) (Figure 3c).
31	Antennae, curvature of scape: straight (0) (Figure 1a); curved (1) (Figure 3b).
32	Antennae, scape in resting position: passing below eyes (0); passing across dorsal half of eyes or over eyes (1) (Figure 2c).
33	Antennae, length of scape: not reaching anterior margin of eyes (0); exceeding anterior margin of eye, but not exceeding anterior margin of pronotum (1); largely exceeding anterior margin of pronotum (2).
34	Antennae, relative length of funicle antennomeres 1 and 2: funicle antennomere 2 slightly shorter than 1 or both subequal (0); funicle antennomer 2 longer than 1 (1).
35	Antennae, length/ width ratio of funicle antennomeres 4–7: wider than long (0); about as long as wide (1); distinctly longer than wide (2).
36	Pronotum, postocular lobes: absent (0); present, not covering eyes (1) (Figure 1e); present, covering eyes (2) (Figure 1c).
37	Pronotum, long vibrissae on lateral margins: absent (0); present (1) (Figure 2d).
38	Pronotum, shape: subcylindrical to subconical, not impressed behind anterior margin (0); subhexagonal, impressed behind anterior margin (1) (Figure 3d).
39	Pronotum, basal margin: not constricted (0); strongly constricted (1) (Figure 3d in [28]).
40	Prosternum, channel to accommodate the rostrum in repose: absent (0); present (1).
41	Scutellum, shape: subtriangular (0); quadrate to rounded (1); suboval to subrectangular (longitudinal) (2) (Figure 3d); subcircular (3).
42	Elytra, striae 9 and 10: closer to each other on posterior 2/3 (0) (Figure 3f); equally separated along their extension (1) (Figure 3e); closer to each other on anterior 1/3 (2).
43	Elytra, outline of apex: entire (0); bifid (1) (Figure 3a,d in [28]).
44	Procoxae, position relative to anterior and posterior margins of prosternum: about equally close to both margins of prosternum (0); distinctly closer to anterior margin (1).
45	Femora, large tooth on ventral edge: absent (0); present on all femora (1) (Figure 3c).
46	Femora, width of profemora relative to width of metafemora: profemora about as wide as metafemora (0); 1.25–1.5× as wide as metafemora (1); more than 1.5× as wide as metafemora (2); narrower than metafemora (3) (Figures 2a and 3a,d,e in [28]).
47	Tibiae, mucro on protibiae: reduce to indistinct (0) (Figure 3b); moderate to large, not forming forceps with tuft of stiff setae (1) (Figure 3a); large, forming forceps with tuft of stiff setae (2).
48	Tibiae, line of denticles along inner edge: absent in all tibiae (0); present at least on protibiae (1) (Figure 3a).

Table 3. *Cont.*

49	Tibiae, spurs at metatibial apex: present (0); absent (1).
50	Tibiae, true corbel at metatibial apex: absent (metatibial apex simple or corbel open); present (1) (Figures 5A, 5B–D in [3]).
51	Tibiae, false corbel (inner flange or corbel semi-enclosed): absent (0); present (1) (Figure 5E,F in [3]).
52	Tibiae, dorsal comb at metatibial apex (corbel ascending): absent (0); present (1) (Figures A–B and E–J in [78]).
53	Tarsal claws: free, widely separated (0) (Figure 4d); free, moderately separated (1) (Figure 4e); connate (2) (Figure 4f–g).
54	Metepisternum and metepisteral-metasternal suture: metepisternum wide, suture complete (0) (Figure 3f); metepisternum narrow, suture complete (1); metepisternum indistinct, suture incomplete, partially fused with metasternum (2) (Figure 3e).
55	Metasternum, length relative to metacoxae: about 2X as long as metacoxae (0); 1–2× as long as metacoxae (1) (Figure 3f); less than 1× as long as metacoxae (2) (Figure 3e).
56	Venter, convexity of ventrites: flat to slightly convex (0); ventrites 1 and 2 more convex than remaining ventrites (Figure 3e) (1); ventrites 1–4 very convex (2).
57	Venter, separation between metacoxae: equal to slightly narrower than width of each metacoxa (0); much wider than width of each metacoxae (1).
58	Venter, length of ventrite 2 relative to ventrites 3 + 4 (female): longer than 3+ 4 (0); about as long as to slightly shorter than 3 + 4 (1).
59	Female genitalia, shape of plate of sternite VIII: subtriangular (0); not subtriangular (1). (Figure 6a–g in [28])
60	Female genitalia, length of apodeme of sternite VIII: about as long as plate (0); distinctly longer than plate (1).
61	Female genitalia, distal gonocoxites and styli: gonocoxites membranous to slightly sclerotized, styli present (0); gonocoxites strongly sclerotized, styli absent (1) (Figure 7c,d in [28])
62	Female genitalia, pair of baculi along ovipositor: absent (0); present (1) (Figure 7b–e in [28]).
63	Larva, length and shape of antennal sensorium: longer than wide, subconical (0) (Figure 53 [75]; wider than long, cushion like (1) (Figure 2 in [74]).
64	Larva, shape of antennal sensorium in apical view: subcircular (0) (Figure 10 in [4]); elliptical (1) (Figure 13 in [4]).
65	Larva, number of ventral setae on maxillary mala: five (0) (Figure 56 in [75]); four (1) (Figures 7, 52, and 74 in [74]).
66	Larva, shape of posterior extension of premental sclerite of labium: acute at apex (0) (Figure 28 in [4]); truncate at apex (1) (Figures 33 and 34 in [4]).
67	Larva, accessory teeth on intermediate portion of mandibular cutting-edge: present (0) (Figure 20 in [4]); absent (1) (Figure 6 in [79]).
68	Larva, mandibular scrobe: sclerotized, similar to the rest of mandible (0) (Figure 55 in [75]); slightly sclerotized, paler than the rest of mandible (1) (Figure 6 in [79]).
69	Larva, labral rods: subparallel (0)(Figures 3–5 in [79]); divergent in their distal half (1) (Figures 1 and 2 in [79]); U-shaped (2) (Figures 50 and 60 in [74]).
70	Larva, number of setae on alar area: two (0) (Figure 9 in [74]); one (1) (Figure 7 in [79]).

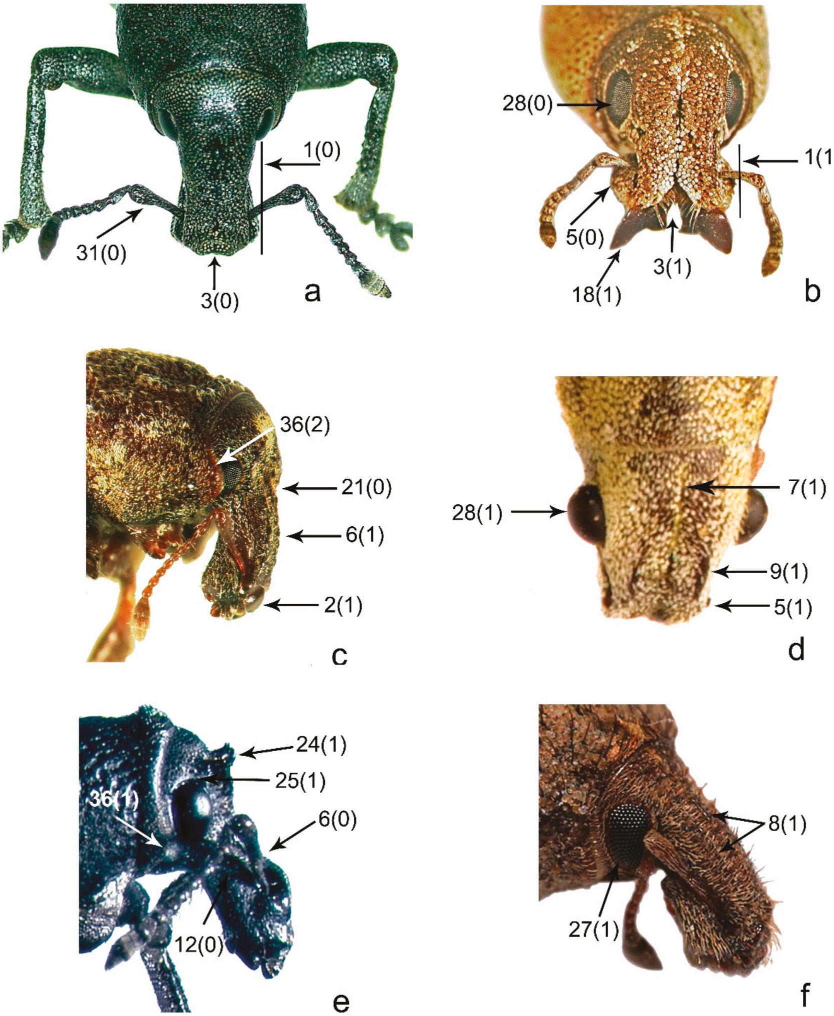

Figure 1. Morphology of adults, head and rostrum: (**a**) *Strangaliodes niger*, frontal view; (**b**) *Pororhynchus labeonis*, frontal view; (**c**) *Premnotrypes latithorax*, lateral view; (**d**) *Hoplopactus lateralis*, frontal view; (**e**) *Aegorhinus vitulus*, lateral view; and (**f**) *Listroderes costirostris*, lateral view. Arrows indicate characters and character states (between parentheses).

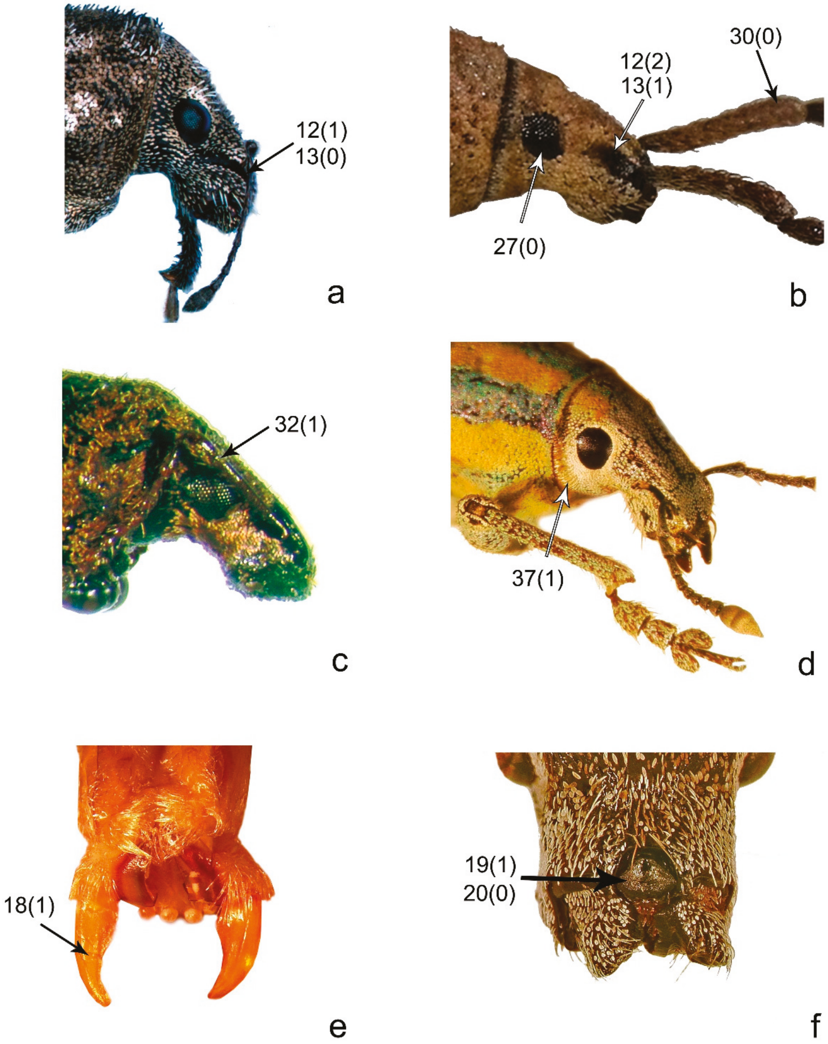

Figure 2. Morphology of adults, head and rostrum: (**a**) *Pantomorus postfasciatus*, lateral view; (**b**) *Simo hirticornis*, lateral view; (**c**) *Galapagonotus cuneiformis*, lateral view; (**d**) *Platyaspistes argentinensis*, lateral view; (**e**) *Entimus sastrei* (teneral adult), frontal view; and (**f**) *Naupactus xanthographus*, ventral view. Arrows indicate characters and character states (between parentheses).

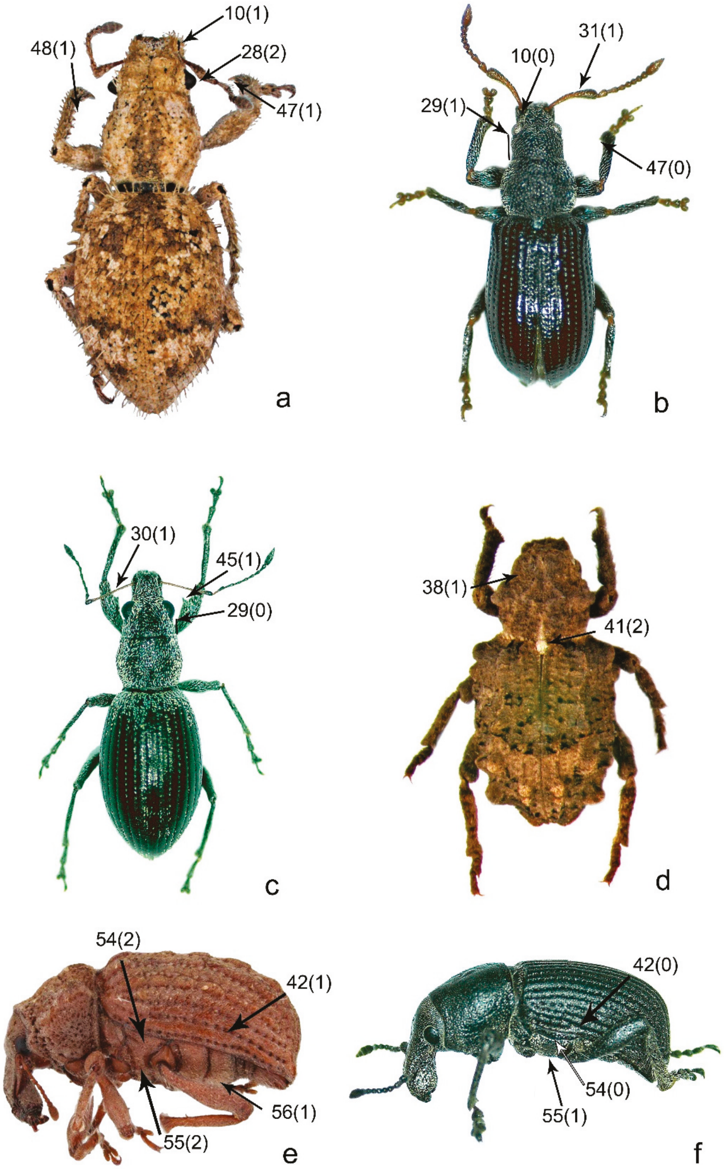

Figure 3. Morphology of adults, habitus: (**a**) *Symmathetes setulosus*, dorsal view; (**b**) *Phyllobius viridicollis*, dorsal view; (**c**) *Eusomus ovulum*, dorsal view; (**d**) *Rhigopsidius piercei*, dorsal view; (**e**) *Premnotrypes latithorax*, lateral view; and (**f**) *Strangaliodes niger*, lateral view. Arrows indicate characters and character states (between parentheses).

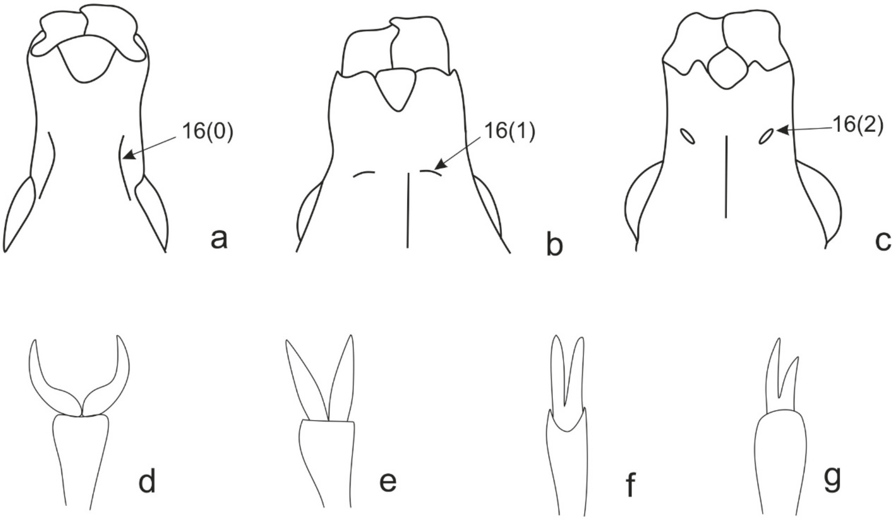

Figure 4. Morphology of adults, occipital sutures and tarsal claws. Head and rostrum, ventral view, position of occipital sutures (character 16): (**a**) longitudinal (16.0); (**b**) transversal (16.1); (**c**) reduced to a fovea (16.2). Tarsal claws (character 53): (**d**) free, widely separated (53.0); (**e**) free, moderately separated (53.1); (**f**) connate, claws of equal length (53.2); and (**g**) connate, claws of different length (53.2).

2.4. Phylogenetic Analyses

The molecular and combined data sets were analyzed using Bayesian Inference (BI) and Maximum Parsimony (MP) approaches.

The Bayesian analysis was performed using BEAST 2 v2.4.8 [80] on the Cipres Science Gateway (http://www.phylo.org) [81] with random starting trees without constraints. Each individual gene was treated as a separate partition in the analyses, resulting in a dataset comprising 3522 aligned nucleotide positions. The optimal substitution model for each partition was selected using the jModeltest software v.2.0 [82], on the basis of the corrected Akaike Information Criterion, as suggested by Burnham and Anderson [83]. We applied the following substitution models: TVM + I + G (16S, 28S), SYM + I + G (18S), TIM2 + I + G (COI) and Lewis MK for morphological data. We assumed a Yule speciation model and strict molecular clock. Clock and tree parameters were linked across partitions. All priors were left as the default values in BEAUti [80]. The analyses were run for a total of 30 million generations with sampling every 20,000 generations. The convergence of the runs was evaluated by accessing log files in TRACER v1.6 [84]. We generated a maximum clade credibility tree in TreeAnnotator v2.4.8 [80], using a burn-in of 10% (1500 trees) and visualized in FigTree v1.4.3 [85].

Parsimony analysis was conducted using TNT v1.5 [86], excluding third codon positions of COI and considering all other characters as un-weighted and non-additive. Gaps were treated as a fifth state (default in TNT). A heuristic search with TBR branch swapping was applied to a series of 500 random addition sequences, retaining 30 trees per replicate. A strict consensus tree was calculated when more than one most parsimonious tree (MPT) was obtained. Clade stability was evaluated by 1000 parsimony bootstrap replications [87]. For the MPTs we provided the basic parameters as total length (L), consistency index (CI) [88] and retention index (RI) [89].The program WinClada [90] was used for character mapping (under unambiguous, fast and slow optimization options) and to prepare MP tree figures.

The outgroup *Aegorhinus silvicola* Kuschel (Cyclominae, Aterpini) was used to root the trees in both analyses. Posterior probability values (under BI) were considered as follows in the Results and Discussion: 0.95–1, strong to maximal clade support; 0.70–0.94, low to moderate clade support; and <0.70, not supported.

3. Results

3.1. Annotated Structural Alignment

The annotated structural alignments of the entire 18S rRNA gene, the D2 and D3 expansion segments of the 28S rRNA gene and domains IV and V of the 16S rRNA gene performed for 63 entimine taxa and four cyclomine outgroups, are available online as Supplementary Materials (Table S2).

3.2. Phylogenetic Trees

3.2.1. Bayesian Analysis

The tree obtained from the Bayesian analysis is shown in Figure 5. Entiminae are monophyletic (PP 0.92), with the tribes Cylydrorhynini–Premnotrypini (Andes, Patagonia) (Clade I) retrieved as a sister group of the remaining members of this subfamily, which form a quite well-supported clade (Clade II). The latter contains four main groups (A–D) of which the first three include taxa from the Southern Hemisphere and the fourth from the Palaearctic and Oriental regions. Group A shows three subclades: the pair *Entimus*–Eudiagogini, the sampled Leptopiini from South America (*Strangaliodes* Schoenherr and *Vossius* Kuschel) with *Platyaspistes* (Tanymecini) as a sister group of *Vossius* (PP = 1), and the sampled Leptopiini from the Australian region (*Catasarcus* Schoenherr, *Cecyropa* Pascoe and *Irenimu*s Pascoe); Group B includes the sister tribes Naupactini–Tanymecini; Group C includes the Eustylini–Geonemini tribes, even though they may not be reciprocally monophyletic; and Group D consists of entimines mainly from the Palaearctic and Oriental regions. Within Group D, there are three subgroups, one corresponding to Bachyderini, Phyllobiini, Sciaphilini and Polydrusini; another to Otiorhynchini; and a third to Laparocerini with *Simo* Dejean (Peritelini), sister of the strongly supported pair *Drouetius* Méquignon (Peritelini) and *Celeuthetes* Schoenherr.

The following entimine tribes are recovered as monophyletic, with either maximal or almost maximal support: Cylydrorhinini, Eudiagogini, Naupactini, Tanymecini (except for *Platyaspistes*), Brachyderini, Polydrusini, Sciaphilini, Otiorhynchini, and Laparocerini. Conversely, the relationships among tribes are moderate, weakly or not supported, except for the sister groups Tanymecini–Naupactini, Geonemini–Eustylini (not reciprocally monophyletic) and Phyllobiini–Brachyderini (among the Palaearctic taxa).

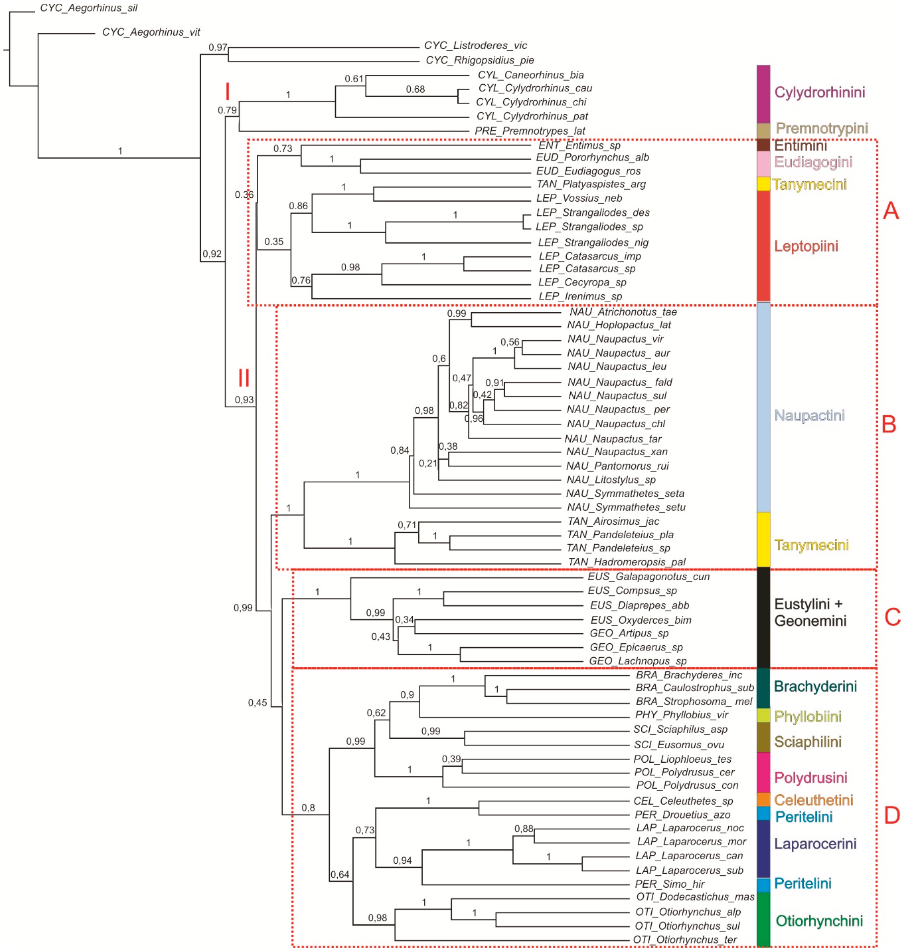

Figure 5. Phylogenetic tree of Entiminae resulting from partitioned Bayesian analysis (MCC) of DNA sequences from four markers and morphological data (see Section 2 Material and Methods). Posterior probability values indicated above branches. Clades discussed in the text are indicated in red (I, II, and A–D).

3.2.2. Combined Maximum-Parsimony Analysis and Synapomorphies

The Maximum Parsimony (MP) analysis yielded four most parsimonious trees (L = 3325 steps; CI = 0.35; RI = 0.53), the strict consensus of which is shown in Figure 6. Bootstrap values over 40% are indicated above the branches of the tree. The main differences from the Bayesian (BI) tree are as follows: (1) The Leptopiini from the Australian region (*Catasarcus*, *Cecyropa* and *Irenimus*) are separated from those of South America (*Vossius* and *Strangaliodes*) (Group A of the BI tree is broken up). (2) The remaining entimines are grouped into two main clades, one including tribes mainly distributed in the Palaearctic and Oriental regions, and the other including those from the Neotropics, Andes and Patagonia. (3) The latter clade includes Groups B and C and the Neotropical members of Group A of the BI, *Strangaliodes–Entimus*, the pair *Platyaspistes–Vossius*, and the Eudiagogini. (4) Within the Palaearctic and Oriental Group D, the consensus tree shows that the basal relationships are not resolved, resulting in a polytomy of *Simo* (Peritelini), Otiorhynchini, *Laparocerus* Schoenherr and *Celeuthetes–Droetius*, and a clade of the remaining tribes, within which Polydrusini are closer to Brachyderini and Phyllobiini than Sciaphilini.

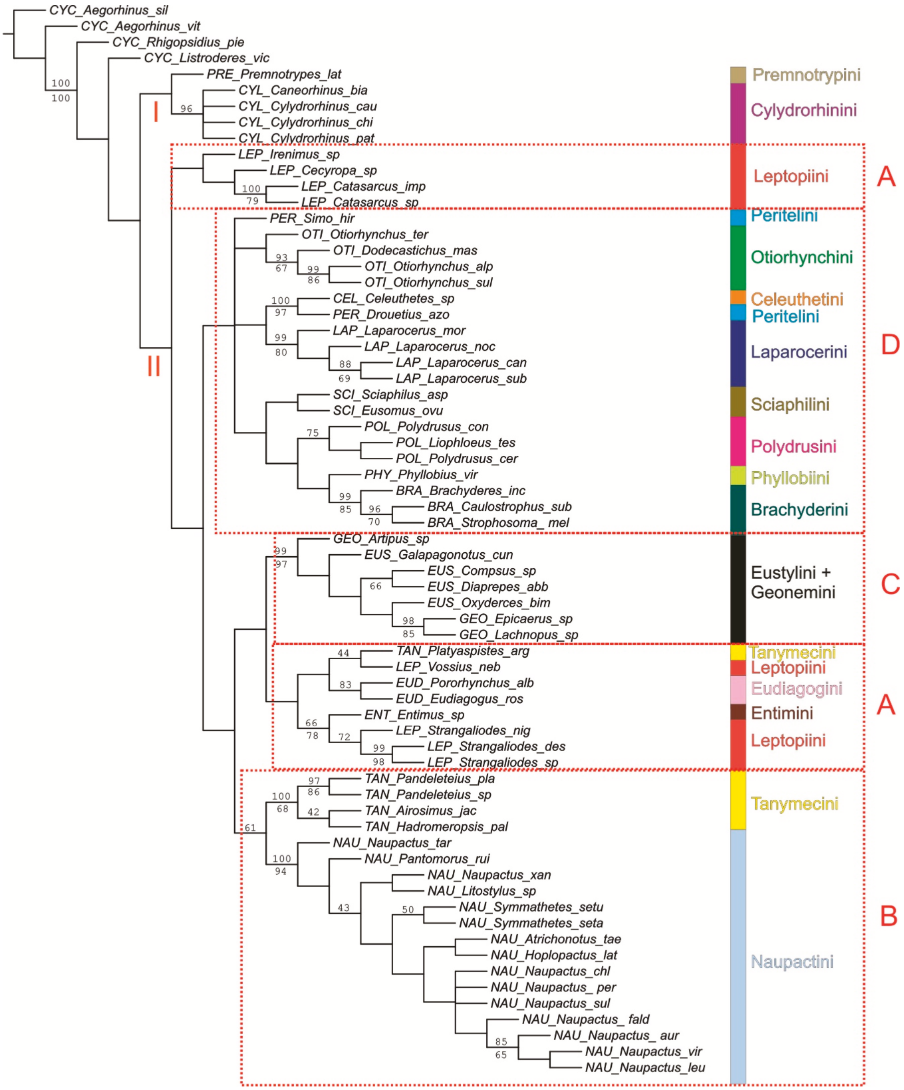

Figure 6. Strict consensus tree of four most parsimonious trees of Entiminae resulting from Maximum Parsimony analysis of DNA sequences from four markers and morphological data (see Material and Methods). Bootstrap values from the combined molecular and morphological data are indicated above branches and Bootstrap values from the separate molecular data are indicated below branches. Tribes are indicated in different colors. Clades recovered in the Bayesian tree are indicated in red.

The selected MP tree (Figure 7) shows unambiguous optimization of morphological characters (see Figures S1 and S2 for character changes under fast and slow optimization options), with unique and homoplastic changes in black and white, respectively. It suggests that the monophyly of Entiminae is mainly justified by the presence of a scar or lasting appendage in the mandibles (18.1) and several larval synapomorphies: antennal sensorium wider than long, cushion-like (63.1) and elliptical in apical view (64.1), maxillary mala with four setae (65.1), mandibles without accessory teeth on the intermediate portion of the cutting edge (67.1) and slightly sclerotized mandibular scrobes, which are paler than the rest of the mandible (68.1). The monophyly of entimines is also supported by two other adult mouthpart characters using the fast optimization (Figure S1): absence of two or more teeth on the inner margin of mandibles (17.1) and prementum completely concealing the maxillae (19.1); however, in Cylydrorhinini, these characters appear to have reversed to the primitive condition and the mandibular scar is sometimes markedly reduced.

Most Entiminae, except for Cylydrorhinini and Premnotrypini, share the synapomorphies of tibiae lacking spurs (49.1) and moderately separated tarsal claws (53.1), although this character shows further change. Some European groups such as Otiorhynchini have tibial spurs but these are usually more slender and shorter than those of Cyclominae (Aterpini and Listroderini) and Cylydrorhinini. Other characters supporting the monophyly of this group under fast optimization (Figure S1) are: epistome not projecting beyond the anterior margin of the rostrum (2.0) and rostrum not separated from the forehead by a deep impression (21.1). However, rostrum and forehead are separated by a deep impression in several Leptopiini from Australia, mainly *Catasarcus*.

Except for the Australian Leptopiini, the remaining entimines form a clade supported by characters of the rostrum, which is usually less than 1.25 × as long as wide at the apex (1.1), has an impressed or flat dorsum (6.0) and is neither unicarinate nor tricarinate (8.0); eyes usually rounded (27.0); absence of postocular lobes (36.0); and a truncate-conical or subcylindrical pronotum (38.0), in contrast to the subhexagonal pronotum of most South American Listroderini, Cylydrorhinini, and Premnotrypini. This clade split into two major subclades, one including the Palaearctic and Oriental tribes and the other the mainly Neotropical tribes. The Palaearctic and Oriental subclade is justified by the following characters: slightly defined scrobes widening backwards (13.1), occipital sutures transversal relative to the longitudinal axis of the rostrum and usually not connected with eyes (16.1), setae behind eyes directed posteriad (23.1), reduced to indistinct mucro of protibiae (47.0), narrow metepisternum and complete metepisteral-metasternal suture (54.1), larvae with labral rods diverging in their distal half (69.1) and larvae with a single seta on the alar area (70.1). The Neotropical subclade is justified by a usually present rostral groove (7.1), scrobes partially visible in dorsal view (10.1) and strongly curved towards the ventral side of the head or passing below the eyes in lateral view (12.0–1), and a scape passing below the eyes (32.0).

The intertribal relationships within both Palaearctic and Oriental and Neotropical subclades are weakly supported by synapomorphies. Within the Palaearctic and Oriental subclade, the group that includes most of the tribes (i.e., all except Laparocerini, Peritelini and Celeuthetini) is mainly justified by the presence of teeth on the three pairs of femora (45.1). Within the Neotropical subclade, the relationship between Tanymecini and Naupactini is the best supported based on the following characters: rostrum with subparallel or convergent sides toward the apex (5.1), and usually bicarinate (9.1); occipital sutures reduced to a small fovea (16.2), a usually slender and capitate scape (30.1), inner margin of protibiae with a line of denticles (48.1), presence of dorsal comb at metatibial apex (52.1) and presence of baculi along the ovipositor (62.1). Most of these characters are also present in other tribes, e.g., Eustylini–Geonemini. Although baculi are also found along the ovipositor of Australian and South American Cylydrorhinini and Leptopiini, in these groups, they are more laterally placed and usually curved at the distal end.

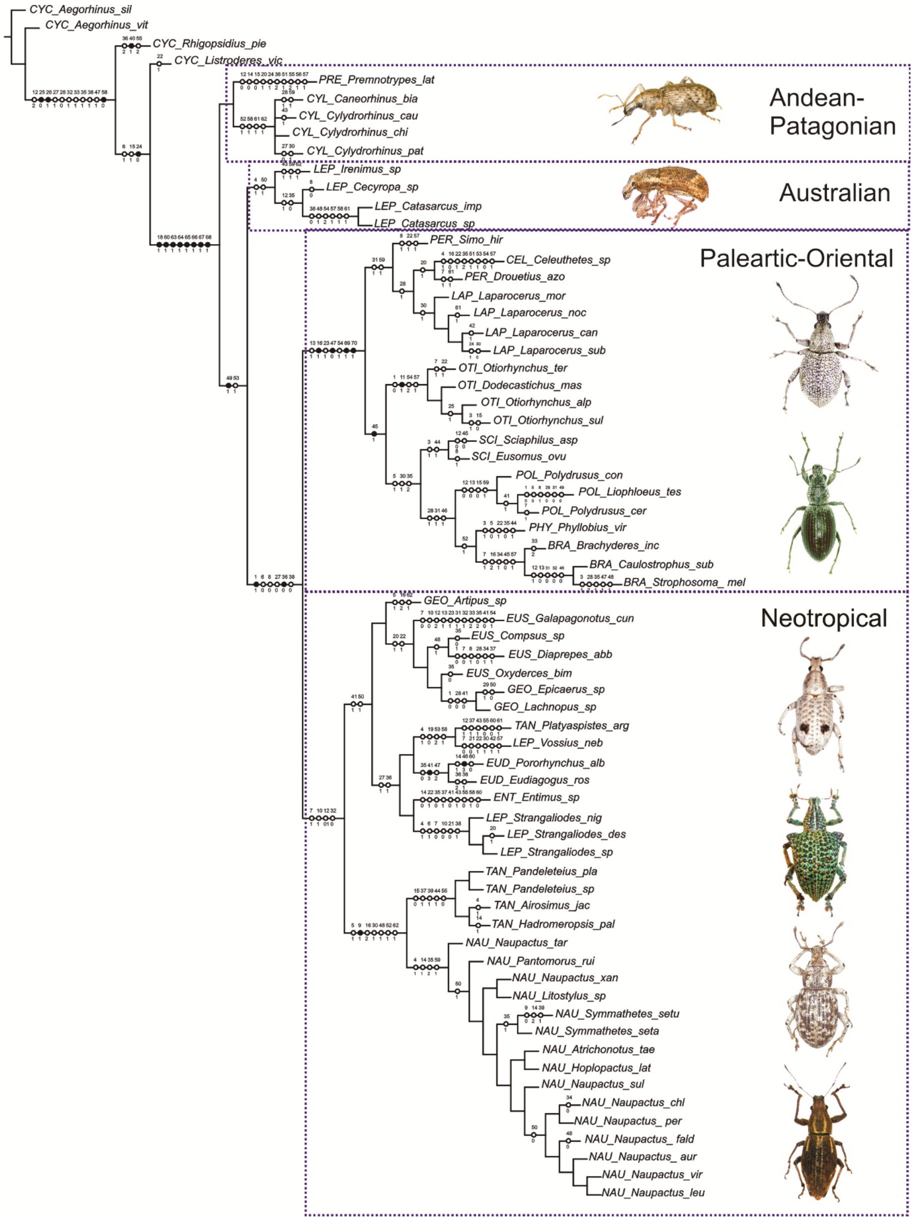

Figure 7. Most parsimonious tree of Entiminae, selected from the four MPTs obtained after combined parsimony analysis. Morphological unambiguous character changes are indicated at branches, with numbers above and below corresponding to character and state, respectively; unique changes are in black and homoplastic changes in white. The most important clades are illustrated and highlighted with boxes and their main biogeographic areas are indicated.

3.2.3. Separate Molecular Analyses (Bayesian and Parsimony)

The monophyly of Entiminae was supported by the BI and MP trees derived from combined molecular and morphological data, but not by those obtained from molecular data only (Figures S3 and S4), because *Listroderes* and *Rhigopsidius* Heller were included in the ingroup. In addition, several suprageneric groups (e.g., tribes) were resolved as monophyletic independently of morphological evidence (e.g., Cylydrorhinini, Naupactini, Tanymecini (except for *Platyaspistes*), Eudiagogini, Brachyderini, Otiorhynchini (except for *Otiorhynchus* subgenus *Metopiorrhynchus*) and Laparocerini). Moreover, both the BI and MP molecular trees justify the relationships Geonemini–Euslylini (including *Artipus* and *Galapagonotus*) and *Celeuthetes*–*Drouetius*, while the relationship *Entimus*–*Strangaliodes* was supported by the BI molecular tree as well as the combined and molecular MP trees.

4. Discussion

4.1. Southern South American Entiminae and Cyclominae

The Cyclominae are widely distributed in the Southern Hemisphere [12,91,92], with some fossils being found in Antarctica [93], suggesting a Gondwanan ancestry [52]. The tribe Aterpini, used as outgroup in our analyses, is distributed in the Australian region (Australia, Tasmania, New Guinea, New Caledonia and New Zealand) and southern Argentina and Chile [94], along the southern Andes from 37° S to the Cape Horn, including the archipelago of southern Chile, Tierra del Fuego, South Georgia, and the Falkland Islands, an area mainly corresponding to the Subantarctic subregion [51,95,96].

Listroderini, Cylydrorhinini and Leptopiini are other tribes of Cyclominae and Entiminae with South American elements that would have close relatives in the Australian region [49,58,97–102]. However, they are not mainly associated to the Subantarctic and have diversified in northern and eastern areas, mainly Central Chile, Patagonia and the Andes. In comparison with Aterpini, these tribes are less clearly related to the Australian groups, probably because the latter areas have been subjected to more drastic geological and environmental changes after the separation of the southern continents [99]. It is worth mentioning that *Rhigopsidius* Heller and *Listroderes* Schoenherr are sister taxa in the Bayesian tree, consistent with the hypothesis of Oberprieler [91] that Rhythirrinini are confined to the African region and *Rhigopsidius* is assumed to belong to the tribe Listroderini. Morrone [52], who recovered the relationship of *Rhythirrinus* Schoenherr with *Rhigopsidius* based on a morphological cladistic analysis of Listroderini using other cyclomines as outgroups, considered that this inference required further confirmation. From a biogeographical point of view, it seems more plausible that *Rhigopsidius* is more closely related to other Andean genera of Listroderini than to any African Rhytirrhinini. The morphology of *Rhygopsidius*, including that of the female genitalia [91,103], suggests that it is a Listroderini which has acquired new characters in response to a new environment. Indeed, the species of this genus inhabit the Andean region from southern Peru to Argentina at higher altitudes than do most other listroderines (mainly highland plateau of Puna), and their larvae bore into potato tubers [103], unlike the aerial and ectophytic larvae of most members of this tribe.

Several authors have classified Listroderini and Cylydrorhinini in the same subfamily Cylydrorhininae [104–107]. Their distribution ranges overlap but Cylydrorhinini mostly occur from 36° to 48° S, while Listroderini are mainly distributed from 48° S southward [48,52], including the Tristan da Cunha-Gough Islands [49]. Both tribes are phanerognathous, with a subcylindrical rostrum which is frequently unicarinate or tricarinate and has a transversal impression separating it from the forehead. In addition, they show well-developed postocular lobes and oval, dorso-ventrally oriented eyes; a typical subhexagonal pronotum which is transversally impressed behind the anterior margin; tibiae with spurs and widely separated tarsal claws (Figure 4d). The latter two characters are most likely plesiomorphic and have not been found in other South American Entiminae. These tribes mainly differ in larval morphology [49,74], and the adults show the following differences: Listroderini lack mandibular scars and their ovipositor is reduced to a pair of distal gonocoxites, whereas Cylydrorhinini have mandibular appendages or scar (though sometimes extremely reduced) and a long ovipositor with baculi.

The monophyly of Entiminae was recovered by our analyses based on molecular and morphological data (including Cylydrorhinini and excluding Listroderini), but not by the trees obtained from molecular data only. A more accurate analysis of the relationship between Cyclominae and Entiminae—with a particular focus on Listroderini and Cylydrorhinini—would be achieved by a modern taxonomic revision involving diverse, yet poorly studied, genera such as *Cylydrorhinus.* Moreover, such phylogenetic analysis should include increased taxon and character sampling of both groups and allied taxa.

The Clade I, Cylydrorhinini–Premnotrypini in trees from BI and MP analyses based on combined evidence, is rather weakly supported. Under slow optimization (Figure S2), this relationship is justified by having the anterior part of the epistome usually raised and projecting beyond the anterior margin of the rostrum (2.1). The Premnotrypini occur in the high Central Andes, from Colombia to northern Chile, within 2800–4500 masl. The adults show some particular features (e.g., presence of false corbels) and external similarities with *Rhigopsidius* (see Figure 3d) probably because adults and larvae share habits associated with development in potato tubers [108,109]. Interestingly, the geographic distributions of the South American groups that attack potatoes in the Andes (*Rhigopsidius* and *Premnotrypes* Pierce) are partially sympatric with those of their putative related taxa (Listroderini and Cylydrorhinini, respectively).

The Leptopiini (type genus *Leptopius* Oke endemic to Australia) sensu Kuschel [58,97] basically correspond to the entimines from the Southern Hemisphere, which are listed in Tropiphorini by Alonso-Zarazaga and Lyal [2]. They share some characters with Cylydrorhinini, particularly those of the rostrum and the hexagonal pronotum. However, they are adelognathous, as are most Entiminae, their tibiae lack spurs, their tarsal claws are less separated than in Cylydrorhinini, and their metatibial apex usually has true corbels (also referred to as close corbels). The leptopiines are particularly well-represented in extreme environments such as deserts, mountain areas and Subantarctic islands [58,97,101,102] although some also occur in temperate forests [110]. The external expansion of the protibiae in Leptopiini from deserts may represent an adaptation to this environment [45].

Kuschel [97] described several genera and species of leptopiines from arid and semiarid environments in Chile, Argentina and Peru [58,107]. More recently, new synonymies, new species and a new genus have been established [45,110,111]. Thompson [43] revised the Australian genus *Catasarcus* and Brown [46] studied some genera endemic to New Zealand, such as *Irenimus* and *Cecyropa*.

The South American Leptopiini, *Strangaliodes* and *Vossius* form a monophyletic group with those from the Australian region in the Bayesian tree (Figure 5), but not in the MP tree (Figures 6 and 7). The former result could be interpreted as a phylogenetic signal of an ancient southern connection, whereas the MP tree suggests that *Strangaliodes* is related to some typical Neotropical entimines. In fact, *Strangaliodes* is distributed in the Transition Zone sensu Morrone [56] between the Brazilian and Patagonian biotas, the latter being more related to the Southern Hemisphere fauna. The relationship *Strangaliodes–Entimus* is mostly justified by molecular evidence, recovered in both combined and molecular MP trees and in the BI molecular tree. According to previous phylogenetic analyses based on morphology, *Strangaliodes* would be closer to other southern South American letopiines, e.g., *Geniocremnu*s Kuschel and *Megalometis* Schoenherr, and less related to *Leptopius* and some genera from the Australian region [44]. Conversely, Entimini would be related to the Neotropical Lordopini [14]. Unfortunately, no samples of these groups were available in our study.

Although it is beyond the scope of our analyses, we consider that the wide concept of Tropiphorini (type genus *Tropiphorus* Schoenherr from the Palaearctic) as in Alonso-Zarazaga and Lyal [2] is not appropriate for the South American fauna, because the Palaearctic Tropiphorini exhibit a different combination of characters, such as mandibles without an obvious scar, absence of postocular lobes and connate tarsal claws. Therefore, we prefer to use the name Leptopiini as originally used by Kuschel [97] and more recently by Pullen et al. [55], at least until a more comprehensive study is carried out. According to molecular analyses based on mitogenome data, the Palaearctic Tropiphorini would be related to Otiorhynchini [7,8]. Moreover, we disagree with the placement of *Strangaliodes* in the Palaearctic tribe Alophini (as a synonym of Tropiphorini) as proposed by Alonso-Zarazaga et al. [112], because of the synonymy of the monotypic genus *Ctenolobus* Debrochers based on a single specimen from Morocco, which was probably mislabeled.

4.2. Neotropical Entiminae

Entimini, Eudiagogini, Naupactini and Eustylini have been based on Neotropical genera and are highly diversified in this region, particularly in tropical and subtropical forests, although some derived lineages have colonized other areas and a few genera or species occur in the Nearctic [28,113].

Entimini include 13 genera [14], most of which have been revised taxonomically [13,15,114,115]. They are composed of large species (about 20 mm long) with iridescent scaly vestiture and well-developed humeri and hind wings; their rostrum usually shows a median sulcus and the postocular lobes are always present. Females have a subtriangular sternite VIII, with a slightly longer than plate apodeme—as in most entimines—and a short ovipositor (about one-third the length of the abdomen) bearing styli and sclerotized proximal and distal gonocoxites [15]. The phylogenetic position of Entimini is doubtful because our analyses included a single species of *Entimus* and lacked representatives of other allied taxa, such as Lordopini [14].

Eudiagogini are probably close to Entimini (in the BI, Figure 5), as suggested by shared larval features [74], but their adults are differentiated by having several apomorphic characters: a very short rostrum with broad pterigia; very pronounced postocular lobes covering more than half of the eyes; laterally expanded mandibular lasting appendages in some species (see Figure 1b); protibiae bearing a hook-like mucro, which forms a forceps with a tuft of stiff setae; metafemora being usually wider than the profemora; and metatibial apex showing a very broad, squamose corbel. The type genus *Eudiagogus* Schoenherr was taxonomically revised by Warner [116] and studied by O'Brien and Kovarik [117].

The results of both combined analyses indicated that Naupactini are monophyletic and closely related to Tanymecini, but this relationship was not recovered in the separate molecular analyses. Most species in our sampling belong to the *Pantomorus*–*Naupactus* complex [29], but other genera outside this complex (e.g., *Cyrtomon* Schoenherr, *Stenocyphus* Marshall, *Hadropus* Schoenherr, *Ericydeus* Pascoe, *Briarius* Fischer de Waldheim) are more similar to some Eustylini (e.g., *Compsus* Schoenherr, *Exoderces* Schoenherr) [28], probably by convergence.

The Eustylini *sensu* Franz [18] are an exclusively Neotropical assemblage with 20 genera and approximately 325 species, *Compsus* being the most diverse genus (104 species). This tribe is the subject of ongoing studies by Franz and colleagues [20,118,119], who suggested that Geonemini are paraphyletic relative to Eustylini [18]. According to our analyses, Eustylini become monophyletic when the Neotropical Geonemini are included. Moreover, we corroborated that *Artipus* belongs to the clade Eustylini–Geonemini, and is not a Naupactini (see [28]), while *Galapagonotus* Anderson & Lanteri and probably also *Coconotus* Anderson & Lanteri (not included) belong to Eustylini [120].

On the other hand, *Geonemus* Schoenherr as well as other genera currently assigned to Geonemini occur in the Palaearctic region (e.g., *Barynotus*) and we are doubtful about their close relationship with Neotropical Geonemini. This uncertainty is supported by results based on mitogenome data [8]. We think that Geonemini are probably valid for some genera outside the Neotropics, but this issue must be addressed by specialists.

Something similar occurs with Tanymecini, whose type genus *Tanymecus* Germar is from the Holarctic region. The Neotropical tanymecines have been extensively studied by Howden [21–25], particularly *Pandeleteius* Schoenherr, *Hadromeropsis* Pierce and *Airosimus* Howden, which were included in our analyses and constitute a well-supported monophyletic group. Conversely, *Platyaspistes* Schoenherr, currently classified in the Tanymecini subtribe Piazomiina (type genus *Piazomias* Schoenherr from Africa and Asia) has never been found to be related to the remaining Tanymecini but rather to *Vossius* (Leptopiini). The larval characters of *Platyaspistes* studied by Marvaldi [74] concur with those of the leptopiine larvae (e.g., two alar setae) but not with those of the larvae of Piazomiina, as in *Piazomias* and *Leptomias* Faust, and other Tanymecini as in *Pachnaeus* Schoenherr, described by van Emden [121].

Platyaspistes includes five Chilean species distributed from the Atacama desert to Valparaiso (with one present in Argentina), and differs from the sampled Tanymecini and other Neotropical Entiminae in its tarsal claws, which are connate –as in most of the Holarctic entimines studied herein– but unequal in length. Moreover, the distal coxites of the ovipositor are strongly sclerotized and bifurcated and females show a particular type of oviposition, as observed in *Platyaspistes glaucus* Farhaeus [122] and in *P. argentinensis* Kuschel [123]. The eggs are laid between, and glued to, two adjacent surfaces of a host plant leaf which was previously folded by the female, in the same way as does *Cyphometopus marmoratus* (Blanchard) (currently classified in Leptopiini). The larvae emerge through a hole made by gnawing the meristem and complete their development in the soil as do other entimines [122].

Although there was not complete agreement between the results of the Bayesian and the Parsimony analyses regarding the Leptopiini, we propose to transfer *Platyaspistes* from Tanymecini to Leptopiini.

4.3. Palaearctic, and Australian and Oriental Entiminae

Both analyses recovered the entimine tribes mainly distributed in the Palaearctic region as a monophyletic group. In our study, every tribe represented by more than one species/genus is monophyletic, although no definite conclusions can be drawn due to insufficient taxon sampling. In general terms, we conclude that Brachyderini, Phyllobiini, Polydrusini and Sciaphylini might be closer to each other than to Otiorhynchini, Laparocerini and Peritelini.

The phylogenetic position of *Drouetius* is controversial. It was formerly treated as a subgenus of *Laparocerus* [35] and later as a separate genus [33] and was assigned to Peritelini [33,53]. *Laparocerus* includes about 240 flightless species and subspecies endemic to the Atlantic islands of Macaronesia (Madeira, Selvagens, and Canary Islands), except for one species from northern Africa, Morocco [36], whereas *Drouetius* is endemic to the Azores Islands (northern Macaronesia), thus more distant geographically.

In a Bayesian analysis based on 16SrRNA, *Drouetius* was closer to *Peritelus* Germar than to *Laparocerus* [33] and probably for this reason it was transferred to Peritelini. In our analyses, *Drouetius* is the most closely related to *Celeuthetes* sp. and the pair *Droetius–Celeuthetes* is within the same group as *Laparocerus* (Figures 6 and 7) or as *Laparocerus–Simo* (Peritelini) (Figure 5). The Celeuthetini are distributed in the Oriental or Indo-Australian region, mainly diversified across islands of the Pacific (New Guinea, Molucas, Sulawesi and Lesser Sunda Islands) [124]. According to a recent phylogenetic analysis, this tribe is most likely related to other Indo-Australian entimines, e.g., Pachyrhynchini [125] and, therefore, we believe that the close relationship *Droetius–Celeuthetes* may not be recovered in further studies expanding the taxon sampling.

Our results support the hypothesis that the genus *Drouetius* is independent from *Laparocerus*, but reject the hypothesis that it belongs to Peritelini. Indeed, the BI tree (Figure 5) shows that the only Peritelini included in our analysis (*Simo*) is close to *Laparocerus* and not to *Drouetius*, and in the MP trees *Simo* is in an unstable position (Figure 6). A more complete taxon sampling is necessary to elucidate the correct tribal placement of *Drouetius.*

4.4. General Remarks

Our study provides evidence for the monophyly of several Neotropical tribes, however, the relationships among the large clades are in general weakly supported by both analyses, preventing us from drawing firm conclusions. Notwithstanding this, results suggest that the Palaearctic entimines evolved independently from the typical Neotropical ones, e.g., Entimini, Eudiagogini, Eustylini, Naupactini, Tanymecini and other tribes not included in our analysis, such as Lordopini and Anypotactini. Future research should be aimed at expanding the geographic representation of tribes/genera with disjoint distributions in both hemispheres or in different continents, as is the case highlighted by Kuschel [48] for the mainly Holarctic Polydrusini/*Polydrusus* occurring in southern South America. This information would be helpful to discriminate between old clades widely distributed in the past and artificial taxa defined on the basis of convergences.

The striking similarity between some derived lineages of Palaearctic and Neotropical entimines, attributed to the subfamily Brachyderinae in older classifications, e.g., *Strophosoma* Billberg (Brachyderini) and some species currently assigned to *Symmathetes* Schoenherr or *Pantomorus* Schoenherr (Naupactini) is most likely due to convergent evolution.

As already suggested by Kuschel [48,50,94], some South American entimines (Leptopiini and Cylydrorhinini) as well as some cyclomines (Listroderini and Aterpini) are probably closely related to those of the Australian region. These groups are expected to be ancient and to occupy a relatively basal position with respect to the typical Neotropical tribes (e.g., Entimini, Eudiagogini, Eustylini and Naupactini).

Further investigation with more complete taxon and character samplings is needed to clarify all the tribal relationships within the Entiminae–Cyclominae clade. To achieve a natural tribal classification of the Entiminae, we propose considering not only morphological and molecular evidence, but also important biological features and information on the historical biogeography of the areas they inhabit.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/10/3/95/s1: Table S1: Morphological data matrix. Table S2: Annotated structure alignment of the ribosomal markers. Figure S1: Selected Most Parsimonious tree with morphological character changes under fast optimization. Figure S2: Selected Most Parsimonious tree with morphological character changes under slow optimization. Figure S3: Bayesian tree based on molecular data only. Figure S4: Strict consensus tree of 395 MPTs from parsimony analysis of molecular data only.

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References

1. Thompson, R.T. Observations on the morphology and classification of weevils (Coleoptera, Curculionoidea) with a key to major groups. *J. Nat. Hist.* **1992**, *26*, 835–891. [CrossRef]
2. Alonso-Zarazaga, M.A.; Lyal, C.H.C. *A World Catalogue of Families and Genera of Curculionoidea: (Insecta: Coleoptera) Excepting Scolytidae and Platypodidae*; Entomopraxis. D.C.P.: Barcelona, Spain, 1999; pp. 1–315, ISBN 978-84-605-9994-4.
3. Marvaldi, A.E.; Lanteri, A.A.; del Río, M.G.; Oberprieler, R.G. 3.7.5. Entiminae Schoenherr, 1823. In *Handbook of Zoology. Coleoptera, Beetles. Morphology and Systematics*; Leschen, R.A., Beutel, R.G., Eds.; De Gruyter: Berlin, Germany; Boston, MI, USA, 2014; Volume 3, pp. 503–522.
4. Marvaldi, A.E. Higher Level Phylogeny of Curculionidae (Coleoptera: Curculionoidea) based mainly on Larval Characters, with Special Reference to Broad-Nosed Weevils. *Cladistics* **1997**, *13*, 285–312. [CrossRef]

5. Hundsdoerfer, A.K.; Rheinheimer, J.; Wink, M. Towards the phylogeny of the Curculionoidea (Coleoptera): Reconstructions from mitochondrial and nuclear ribosomal DNA sequences. *Zool. Anz.* **2009**, *248*, 9–31. [CrossRef]
6. McKenna, D.D.; Sequeira, A.S.; Marvaldi, A.E.; Farrell, B.D. Temporal lags and overlap in the diversification of weevils and flowering plants. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 7083–7088. [CrossRef] [PubMed]
7. Gillett, C.P.; Crampton-Platt, A.; Timmermans, M.J.; Jordal, B.H.; Emerson, B.C.; Vogler, A.P. Bulk de novo mitogenome assembly from pooled total DNA elucidates the phylogeny of weevils (Coleoptera: Curculionoidea). *Mol. Biol. Evol.* **2014**, *31*, 2223–2237. [CrossRef] [PubMed]
8. Gillett, C.P.; Lyal, C.H.; Vogler, A.P.; Emerson, B.C. Statistical Evaluation of Monophyly in the 'Broad-Nosed Weevils' through Molecular Phylogenetic Analysis Combining Mitochondrial Genome and Single-Locus Sequences (Curculionidae: Entiminae, Cyclominae, and Hyperinae). *Diversity* **2018**, *10*, 21. [CrossRef]
9. Gunter, N.L.; Oberprieler, R.G.; Cameron, S.L. Molecular phylogenetics of Australian weevils (Coleoptera: Curculionoidea): Exploring relationships in a hyperdiverse lineage through comparison of independent analyses. *Austral Entomol.* **2016**, *55*, 217–233. [CrossRef]
10. Shin, S.; Clarke, D.J.; Lemmon, A.R.; Moriarty Lemmon, E.; Aitken, A.L.; Haddad, S.; Farrell, B.D.; Marvaldi, A.E.; Oberprieler, R.G.; McKenna, D.D. Phylogenomic Data Yield New and Robust Insights into the Phylogeny and Evolution of Weevils. *Mol. Biol. Evol.* **2018**, *35*, 823–836. [CrossRef] [PubMed]
11. Haran, J.; Timmermans, M.J.; Vogler, A.P. Mitogenome sequences stabilize the phylogenetics of weevils (Curculionoidea) and establish the monophyly of larval ectophagy. *Mol. Phylogenet. Evol.* **2013**, *67*, 156–166. [CrossRef] [PubMed]
12. Oberprieler, R.G. 3.7.4 Cyclominae Schoenherr, 1826. In *Handbook of Zoology. Coleoptera, Beetles. Morphology and Systematics*; Leschen, R.A., Beutel, R.G., Eds.; De Gruyter: Berlin, Germany; Boston, MI, USA, 2014; Volume 3, pp. 483–502.
13. Gaiger, F. Systematic revision and cladistic analysis of the genus *Rhigus* Schoenherr, 1823 (Coleoptera, Curculionidae). *Rev. Bras. Entomol.* **2001**, *45*, 43–85.
14. Vanin, S.A.; Gaiger, F. A cladistic analysis of the genera of the tribe Entimini (Coleoptera, Curculionidae), with description of a new genus and species from the Amazonian region. *Zootaxa* **2005**, *1053*, 1–21.
15. Gaiger, F.; Vanin, S.A. On the utility of female genitalia in the systematics of Curculionidae: Examples from Entimini and Hylobiina (Coleoptera: Curculionidae). *Ann. Soc. Entomol. Fr.* **2008**, *44*, 47–57. [CrossRef]
16. Franz, N.M. Redescriptions of critical type species in the Eustylini Lacordaire (Coleoptera: Curculionidae: Entiminae). *J. Nat. Hist.* **2010**, *44*, 41–80. [CrossRef]
17. Franz, N.M. Revision and phylogeny of the Caribbean weevil genus *Apotomoderes* Dejean, 1834 (Coleoptera, Curculionidae, Entiminae). *ZooKeys* **2010**, *49*, 33–75. [CrossRef]
18. Franz, N.M. Phylogenetic reassessment of the *Exophthalmus* genus complex (Curculionidae: Entiminae: Eustylini, Geonemini). *Zool. J. Linn. Soc.* **2012**, *164*, 510–557. [CrossRef]
19. Girón, J.C.; Franz, N.M. Revision, phylogeny and historical biogeography of the genus *Apodrosus* Marshall, 1922 (Coleoptera: Curculionidae: Entiminae). *Insect Syst. Evol.* **2010**, *41*, 339–414. [CrossRef]
20. Girón, J.C.; Franz, N.M. Phylogenetic assessment of the Caribbean weevil genus *Lachnopus* Schoenherr (Coleoptera: Curculionidae: Entiminae). *Invertebr. Syst.* **2012**, *26*, 67–82. [CrossRef]
21. Howden, A.T. The *Pandeleteius* subgenus *Exmenetypus* Voss in Central America (Coleoptera: Curculionidae, Tanymecini). *Coleopt. Bull.* **1974**, *28*, 7–16.
22. Howden, A.T. Revision of the New World genus *Hadromeropsis* Pierce (Coleoptera, Curculionidae, Tanymecini). *Contrib. Am. Entomol. Inst.* **1982**, *19*, 1–180.
23. Howden, A.T. Revision of the Mesoamerican species of *Airosimus* Howden (Coleoptera: Curculionidae). *Coleopt. Bull.* **1993**, *47*, 249–267.
24. Howden, A.T. The species of *Pandeleteius* Schoenherr of coastal Chile and Peru (Coleoptera, Curculionidae). *Zootaxa* **2008**, *1773*, 55–62.
25. Howden, A.T. On some species of *Pandeleteius* Schoenherr, 1834, in South America south of the tenth parallel (Coleoptera, Curculionidae: Entiminae: Tanymecini). *Zootaxa* **2011**, *2977*, 50–60.
26. Scataglini, M.A.; Lanteri, A.A.; Confalonieri, V.A. Phylogeny of the *Pantomorus–Naupactus* complex based on morphological and molecular data (Coleoptera: Curculionidae). *Cladistics* **2005**, *21*, 131–142. [CrossRef]
27. Rosas, M.V.; Morrone, J.J.; del Río, M.G.; Lanteri, A.A. Phylogenetic analysis of the *Pantomorus-Naupactus* complex (Coleoptera: Curculionidae: Entiminae) from North and Central America. *Zootaxa* **2011**, *2780*, 1–19.

28. Lanteri, A.A.; del Río, M.G. Phylogeny of the tribe Naupactini (Coleoptera: Curculionidae) based on morphological characters. *Syst. Entomol.* **2017**, *42*, 429–447. [CrossRef]
29. del Río, M.G.; Rodriguero, M.S.; Confalonieri, V.A.; Lanteri, A.A. Molecular and Morphological Phylogenetic Analysis of *Naupactus* Dejean (Curculionidae: Entiminae) and Allied Genera: The Dilemma of Classification. *Diversity* **2018**, *10*, 59. [CrossRef]
30. Velazquez De Castro, A.J.; Alonso-Zarazaga, M.Á.; Outerelo, R. Systematics of Sitonini (Coleoptera: Curculionidae: Entiminae), with a hypothesis on the evolution of feeding habits. *Syst. Entomol.* **2007**, *32*, 312–331. [CrossRef]
31. Korotyaev, B.A.; Meleshko, J.Y. On the systematics of the weevil genus *Polydrusus* (Coleoptera: Curculionidae). *Zoosyst. Ross.* **1997**, *6*, 275–286.
32. Morimoto, K.; Kojima, H.; Miyakawa, S. *The Insects of Japan. Vol. 3. Curculionoidea: General Introduction and Curculionidae: Entiminae (Part 1), Phyllobiini, Polydrusini and Cuphicerini (Coleoptera)*; Entomological Society of Japan, Touka Shobo Co. Ltd.: Fukuoka, Japan, 2006.
33. Machado, A. El género *Drouetius* Méquignon, 1942 *stat. prom.*, de las islas Azores (Coleoptera, Curculionidae, Entiminae). *Graellsia* **2009**, *65*, 19–46. [CrossRef]
34. Machado, A. Revisión de los antiguos *Lichenophagus* (= *Laparocerus*) de la Macaronesia (Coleoptera, Curculionidae, Entiminae). *Bol. SEA* **2015**, *57*, 93–141.
35. Machado, A.; Lopez, M.; Almeida, T.; Hernandez, M. Mitochondrial DNA phylogenetic analysis of the genus *Laparocerus* (Coleoptera, Curculionidae, Entiminae). I. The Madeiran clade. *Zool. Scr.* **2008**, *37*, 415–427. [CrossRef]
36. Machado, A.; Rodríguez-Expósito, E.; López, M.; Hernández, M. Phylogenetic analysis of the genus *Laparocerus*, with comments on colonisation and diversification in Macaronesia (Coleoptera, Curculionidae, Entiminae). *ZooKeys* **2017**, *1651*, 1–77. [CrossRef] [PubMed]
37. Yunakov, N.N. Species of the Subgenus *Pseudocryphiphorus*, Genus *Otiorhynchus* (Coleoptera, Curculionidae), in the Fauna of the Crimea. *Entomol. Rev.* **2003**, *83*, 221–229.
38. Yunakov, N.N. On the taxonomy of the weevil genus *Parameira* Seidl. (Coleoptera, Curculionidae, Entiminae). *Zool. Zhurnal* **2004**, *83*, 1284–1289.
39. Yunakov, N.N.; Korotyaev, B.A. On the systematics of the weevil genus *Araxia* Khnzorian with descriptions of new taxa from Transcaucasia, Turkey, and Turkmenistan (Coleoptera: Curculionidae: Entiminae). *Insect Syst. Evol.* **2008**, *39*, 39–54. [CrossRef]
40. Yunakov, N.N.; Klass, K.D. Contribution to the taxonomy and nomenclature of Entiminae from the Palearctic region and South Africa (Coleoptera: Curculionidae). *Beitr. Entomol.* **2012**, *62*, 427–445. [CrossRef]
41. Oberprieler, R. Revision of the Tanyrhynchini of continental Africa (Coleoptera, Curculionidae) I. Introduction and review of the genera, revision of the genus *Brachytrachelus* Schönherr and description of *Afroleptops* gen. nov. *Entomol. Mem. Dep. Agric. Water Supply Repub. S. Afr.* **1988**, *71*, 1–50.
42. Oberprieler, R.G. Systematic position and composition of the tribes Tanyrhynchini and Myorhinini (Coleoptera: Curculionidae). *Mem. Entomol. Soc. Wash.* **1995**, *14*, 155–167.
43. Thompson, R.T. Revision of the genus *Catasarcus* Schonherr (Coleoptera: Curculionidae). *Bull. Br. Mus. (Nat. Hist.) Entomol.* **1968**, *22*, 357–454.
44. Posadas, P.E. Los Curculionoidea (Insecta: Coleoptera) de la Tierra del Fuego e Islas Malvinas. Ph.D. Thesis, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina, 2002.
45. Elgueta, M. *Geosphaeropterus*, nuevo género de Tropiphorini (Coleoptera: Curculionidae) de Chile, con descripción de tres nuevas especies. *Bol. Mus. Nac. Hist. Nat. Chile* **2013**, *62*, 203–217.
46. Brown, S.D.J. Taxonomy and Evolution of Endemic New Zealand Broad-Nosed Weevils (Coleoptera: Curculionidae: Entiminae). Ph.D. Thesis, Lincoln University, Christchurch, New Zealand, 2016.
47. Borovec, R. Revision of the Palaearctic supraspecific taxa of the tribe Trachyphloeini (Coleoptera: Curculionidae: Entiminae). *Klapalekiana* **2009**, *45*, 1–97.
48. Kuschel, G. Terrestrial zoology in southern Chile. *Proc. R. Soc. Lond. B* **1960**, *152*, 540–550. [CrossRef]
49. Kuschel, G. The Curculionidae of Gough Island and the relationships of the weevil fauna of the Tristan da Cunha group. *Proc. Linn. Soc. Lond.* **1962**, *173*, 69–78. [CrossRef]
50. Kuschel, G. Biogeography and ecology of South American Coleoptera. In *Biogeography and Ecology of South America*; Fittkau, E.J., Illies, J., Klinge, H., Schwabe, G.H., Eds.; Monographiae Biologicae; Springer: The Hague, Switzerland, 1969; pp. 709–722.

51. Morrone, J.J.; Roig-Juñent, S. Synopsis and cladistics of the American Aterpini (Coleoptera: Curculionidae, Cyclominae). *Insect Syst. Evol.* **2000**, *30*, 417–434. [CrossRef]
52. Morrone, J.J. The subtribes and genera of the tribe Listroderini (Coleoptera, Curculionidae, Cyclominae): Phylogenetic analysis with systematic and biogeographical accounts. *ZooKeys* **2013**, *273*, 15–71. [CrossRef] [PubMed]
53. Alonso-Zarazaga, M.A.; Barrios, H.; Borovec, R.; Bouchard, P.; Caldara, R.; Colonnelli, E.; Gültekin, L.; Hlaváč, P.; Korotyaev, B.; Lyal, C.H. Cooperative catalogue of Palaearctic Coleoptera Curculionoidea. *Monogr. Electrón. SEA* **2017**, *8*, 1–729.
54. Grebennikov, V.V. Neglected *Trichalophus* (Coleoptera: Curculionidae): DNA barcode and phylogeography of high-altitude flightless weevils rediscovered in Southwest China. *Bonn. Zool. Bull.* **2016**, *64*, 59–76.
55. Pullen, K.R.; Jennings, D.; Oberprieler, R.G. Annotated catalogue of Australian weevils (Coleoptera: Curculionoidea). *Zootaxa* **2014**, *3896*, 1–481. [CrossRef] [PubMed]
56. Morrone, J.J. Biogeographical regionalisation of the world: A reappraisal. *Aust. Syst. Bot.* **2015**, *28*, 81–90. [CrossRef]
57. Kuschel, G. Nuevos Brachyderinae y Magdalinae chilenos (Coleoptera Curculionidae). *Arthropoda* **1950**, *1*, 181–195.
58. Kuschel, G. The Curculionidae of the Cordillera Chileno-Argentina (1a. parte) (Aporte 13 Coleoptera Curculionidae). *Rev. Chil. Entomol.* **1952**, *2*, 271–273.
59. Sunnucks, P.; Hales, D.F. Numerous transposed sequences of mitochondrial cytochrome oxidase I-II in aphids of the genus *Sitobion* (Hemiptera: Aphididae). *Mol. Biol. Evol.* **1996**, *13*, 510–524. [CrossRef] [PubMed]
60. Duckett, C.N.; Gillespie, J.J.; Kjer, K.M. Relationships among the subfamilies of Chrysomelidae inferred from small subunit ribosomal DNA and morphology with special emphasis on the relationship among the flea beetles and the Galerucinae. In *New Developments in the Biology of Chrysomelidae*; Jolivet, P., Santiago-Blay, J.A., Schmitt, M., Eds.; SPB Academic Publishing BV.: The Hague, The Netherlands, 2004; pp. 3–18.
61. Brown, S.D.J.; Armstrong, K.F.; Cruickshank, R.H. Molecular phylogenetics of a South Pacific sap beetle species complex (*Carpophilus* spp., Coleoptera: Nitidulidae). *Mol. Phylogenet. Evol.* **2012**, *64*, 428–440. [CrossRef] [PubMed]
62. Filatov, D.A. ProSeq: A software for preparation and evolutionary analysis of DNA sequence data sets. *Mol. Ecol. Notes* **2002**, *2*, 621–624. [CrossRef]
63. Kjer, K.M.; Roshan, U.; Gillespie, J.J. Structural and evolutionary considerations for multiple sequence alignment of RNA, and the challenges for algorithms that ignore them. In *Sequence Alignment: Methods, Models, Concepts, and Strategies*; Rosenberg, M.S., Ed.; University of California Press: Berkeley, CA, USA, 2009; 337p.
64. Gillespie, J.J.; Johnston, J.S.; Cannone, J.J.; Gutell, R.R. Characteristics of the nuclear (18S, 58 S, 28S and 5S) and mitochondrial (12S and 16S) rRNA genes of *Apis mellifera* (Insecta: Hymenoptera): Structure, organization, and retrotransposable elements. *Insect Mol. Biol.* **2006**, *15*, 657–686. [CrossRef] [PubMed]
65. Marvaldi, A.E.; Duckett, C.N.; Kjer, K.M.; Gillespie, J.J. Structural alignment of 18S and 28S rDNA sequences provides insights into phylogeny of Phytophaga (Coleoptera: Curculionoidea and Chrysomeloidea). *Zool. Scr.* **2009**, *38*, 63–77. [CrossRef]
66. Swofford, D.L. *PAUP* Phylogeny Analysis Using Parsimony (* and Other Methods)*; Version 40b10; Sinauer Assoc. Inc.: Sunderland, MA, USA, 2002.
67. Halanych, K.M.; Lutz, R.A.; Vrijenhoek, R.C. Evolutionary origins and age of vestimentiferan tube-worms. *Cah. Biol. Mar.* **1998**, *39*, 355–358.
68. Sequeira, A.S.; Lanteri, A.A.; Scataglini, M.A.; Confalonieri, V.A.; Farrell, B.D. Are flightless *Galapaganus* weevils older than the Galápagos Islands they inhabit? *Heredity* **2000**, *85*, 20–29. [CrossRef] [PubMed]
69. Dowton, M.; Austin, A.D. Phylogenetic relationships among the microgastroid wasps (Hymenoptera: Braconidae): Combined analysis of 16S and 28S rDNA genes and morphological data. *Mol. Phylogenet. Evol.* **1998**, *10*, 354–366. [CrossRef] [PubMed]
70. Whiting, M.F.; Carpenter, J.C.; Wheeler, Q.D.; Wheeler, W.C. The Strepsiptera problem: Phylogeny of the holometabolous insect orders inferred from 18S and 28S ribosomal DNA sequences and morphology. *Syst. Biol.* **1997**, *46*, 1–68. [CrossRef] [PubMed]

71. Folmer, O.; Black, M.; Hoeh, W.; Lutz, R.; Vrijenhoek, R. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol.* **1994**, *3*, 294–299. [PubMed]
72. Simon, C.; Frati, F.; Beckenbach, A.; Crespi, B.; Liu, H.; Flook, P. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Ann. Entomol. Soc. Am.* **1994**, *87*, 651–701. [CrossRef]
73. Lanteri, A.A.; O'Brien, C.W. Taxonomic revision and cladistic analysis of Atrichonotus Buchanan (Coleoptera: Curculionidae). *Trans. Am. Entomol. Soc.* **1990**, *116*, 697–725.
74. Marvaldi, A.E. Larvae of South American Entimini (Coleoptera: Curculionidae), and phylogenetics implications of certain characters. *Rev. Chil. Entomol.* **1998**, *25*, 21–44.
75. Marvaldi, A.E. Larvae of South American Rhytirrhininae (Coleoptera: Curculionidae). *Coleopt. Bull.* **1998**, *52*, 71–89.
76. Morrone, J.J.; Diaz, N.B.; Loiacono, M.S. Comparative morphology of mouthparts in the tribe Listroderini (Coleoptera: Curculionidae). *Elytron* **1992**, *6*, 47–59.
77. Marvaldi, A.E.; Lanteri, A.A. Key to higher taxa of South American weevils based on adult characters (Coleoptera: Curculionoidea). *Rev. Chil. Hist. Nat.* **2005**, *78*, 65–87. [CrossRef]
78. Buchanan, L.L.F. *The Species of Pantomorus of America North of Mexico*; U.S. Department Agriculture: Washinton, DC, USA, 1939; Volume 341, pp. 1–39.
79. Marvaldi, A.E. Larvae of Entiminae (Coleoptera: Curculionidae): Tribal diagnoses and phylogenetic key, with a proposal about natural groups within Entimini. *Insect Syst. Evol.* **1998**, *29*, 89–98. [CrossRef]
80. Bouckaert, R.; Heled, J.; Kühnert, D.; Vaughan, T.; Wu, C.H.; Xie, D.; Suchard, M.A.; Drummond, A.J. BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. *PLoS Comput. Biol.* **2014**, *10*, e1002537. [CrossRef] [PubMed]
81. Miller, M.A.; Pfeiffe, W.; Schwartz, T. Creating the CIPRES Science Gate way for inference of large phylogenetic trees. In Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, LA, USA, 14 November 2010.
82. Darriba, D.; Taboada, G.L.; Doallo, R.; Posada, D. jModelTest 2: More models, new heuristics and parallel computing. *Nat. Methods* **2012**, *9*, 772. [CrossRef] [PubMed]
83. Burnham, K.P.; Anderson, D.R. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*; Springer Science & Business Media: New York, NY, USA, 2002.
84. Drumond, A.J.; Rambaut, A. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* **2007**, *7*, 214. [CrossRef] [PubMed]
85. Rambaut, A. FigTree v. 1.3.1. Computer Program and Documentation Distributed by the Author, 2006–2012. Available online: http://tree.bio.ed.ac.uk/software/ (accessed on 21 December 2017).
86. Goloboff, P.A.; Catalano, S. TNT version 1.5, including full implementation of phylogenetic morphometrics. *Cladistics* **2016**, *32*, 221–238. [CrossRef]
87. Felsenstein, J. Confidence Limits on Phylogenies: An Approach Using the Bootstrap. *Evolution* **1985**, *39*, 783–791. [CrossRef] [PubMed]
88. Kluge, A.G.; Farris, J.S. Quantitative phyletics and the evolution of anurans. *Syst. Biol.* **1969**, *18*, 1–32. [CrossRef]
89. Farris, J.S. The retention index and the rescaled consistency index. *Cladistics* **1989**, *5*, 417–419. [CrossRef]
90. Nixon, K.C. *WinClada, ver. 1.00.08*; Nixon, K.C.: Ithaca, NY, USA, 2002.
91. Oberprieler, R. A reclassification of the weevil subfamily Cyclominae (Coleoptera: Curculionidae). *Zootaxa* **2010**, *2515*, 1–35.
92. Meregalli, M.; Germann, C.; Bernasconi, M.V.; Cervella, P. Phylogeny of the Genus *Dichotrachelus* (Coleoptera: Curculionidae: Cyclominae). *Diversity* **2018**, *10*, 66. [CrossRef]
93. Ashworth, A.C.; Kuschel, G. Fossil weevils (Coleoptera: Curculionidae) from latitude 85° S Antarctica. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2003**, *191*, 191–202. [CrossRef]
94. Kuschel, G. La subfamilia Aterpinae en América. *Rev Chil. Entomol.* **1951**, *1*, 205–244.
95. Morrone, J.J. Distributional pattern of South American Aterpini (Coleoptera: Curculionidae). *Rev. Soc. Entomol. Argent.* **1996**, *55*, 131–141.
96. Posadas, P.; Morrone, J.J. Biogeografía histórica de la familia Curculionidae (Coleoptera) en las subregiones Subantártica y Chilena Central. *Rev. Soc. Entomol. Argent.* **2003**, *62*, 75–84.

97. Kuschel, G. Los "Curculionidae" del extremo Norte de Chile (Coleoptera, Curcul. Ap. 6). *Acta Zool. Lilloana* **1949**, *8*, 5–54.
98. Kuschel, G. Entomology of the Aucklands and other islands south of New Zealand: (Coleoptera: Curculionidae). *Pac. Insects Monogr.* **1971**, *27*, 225–259.
99. Morrone, J.J. Distributional patterns of species of Rhytirrhinini (Coleoptera: Curculionidae) and the historical relationships of the Andean provinces. *Glob. Ecol. Biogeogr. Lett.* **1994**, *4*, 188–194. [CrossRef]
100. Morrone, J.J. Cladistics of the new world genera of Listroderina (Coleoptera: Curculionidae: Rhytirrhinini). *Cladistics* **1997**, *13*, 247–266. [CrossRef]
101. Posadas, P. A preliminar overview of species composition and geographical distribution of Malvinian weevils (Insecta: Coleoptera: Curculionidae). *Zootaxa* **2008**, *1704*, 1–26.
102. Posadas, P. Species composition and geographic distribution of Fuegian Curculionidae (Coleoptera: Curculionoidea). *Zootaxa* **2012**, *3303*, 1–36.
103. Morrone, J.J.; Loiácono, M.S. Revision of the genus *Rhigopsidius* Heller (Insecta, Coleoptera, Curculionidae: Rhytirrhininae). *Entomol. Abh* **1992**, *54*, 129–139.
104. Hustache, A. Contribution à l'étude des Curculionides de la République Argentine. *An. Mus. Nac. Hist. Nat. Bernard. Rivadavia* **1926**, *34*, 155–261.
105. Schenkling, S.; Marshall, G.A.K. *Coleopterorum Catalogus*; Schenkling, S., Ed.; W. Junk: Berlín, Germany, 1931; Volume 28, Pars 114. Curculionidae: Eremninae, pp. 3–39; Leptopinae, pp. 1–83; Tanyrrhinchinae, pp. 1–10; Cylydrorrhininae, pp. 1–23; Thecesterninae (Suppl.), p. 1; Rhytitthininae (Suppl.), pp. 1–4; Ryparosominae (Suppl.) p. 4.
106. Voss, E. Curculionidae (Col.). In *Beiträge zur Fauna Perus*; Titschack, E., Ed.; Gustav Fischer Verlag: Jena, Germany, 1954; Volume 4, pp. 163–376.
107. Kuschel, G. Nuevos Cylydrorhininae de la Patagonia (Col. Curculionoidea, Aporte 18). *Investig. Zool. Chil.* **1958**, *4*, 231–252.
108. Kuschel, G. Revisión de los Premnotrypini y adiciones a los Bagoini (Aporte 17 sobre Coleoptera Curculionoidea). *Bol. Mus. Nac. Hist. Nat. Chile* **1956**, *26*, 187–235.
109. Alcázar, J.; Cisneros, F. Taxonomy and bionomics of the Andean potato weevil complex: *Premnotrypes* spp. and related genera. *CIP Program Rep.* **1997**, *98*, 141–151.
110. Elgueta, M. Descripción de una nueva especie de *Hybreoleptops* Kuschel 1949 y comentarios sobre otros representantes del género (Insecta: Coleoptera: Curculionidae). *Bol. Mus. Nac. Hist. Nat. Chile* **2012**, *61*, 29–42.
111. Pérez, M.E.; Posadas, P. Cladistics and redescription of *Hybreoleptops* Kuschel (Coleoptera: Curculionidae: Entiminae) with the description of two new species from the Central Chilean subregion. *J. Nat. Hist.* **2006**, *40*, 1775–1791. [CrossRef]
112. Alonso-Zarazaga, M.A.; Perrin, H.; Sanchez-Ruiz, M. Sur l'identité du genre *Ctenolobus* Desbrochers des Loges, 1892 (Coleoptera, Curculionidae). *Bull. Société Entomol. Fr.* **2010**, *115*, 479–483.
113. del Río, M.G.; Morrone, J.J.; Lanteri, A.A. Evolutionary biogeography of South American weevils of the tribe Naupactini (Coleoptera: Curculionidae). *J. Biogeogr.* **2015**, *42*, 1293–1304. [CrossRef]
114. Vaurie, P. Revision of the genus *Entimus* with notes on other genera of Entimini (Coleoptera Curculionidae). *Rev. Chil. Entomol.* **1952**, *1*, 147–171.
115. Vanin, S.A. Revision of *Phaedropus* Schoenherr with notes on the male genitalia of Entimini (Coleoptera: Curculionidae: Leptopiinae). *Coleopt. Bull.* **1983**, *37*, 283–298.
116. Warner, R.E. The genus *Eudiagogus* (Coleoptera: Curculionidae: Leptopiinae), with two new species on the weed *Sesbania* (Leguminosae). *Proc. Entomol. Soc. Wash.* **1979**, *81*, 304–320.
117. O'Brien, C.W.; Kovarik, P.W. A new species of *Eudiagogus* Schoenherr from South America (Coleoptera: Curculionidae). *Coleopt. Bull.* **2000**, *54*, 313–317. [CrossRef]
118. Girón, J.C.; O'Brien, C.W.; Rose-Smyth, M.C. On the West Indian weevil genus *Lachnopus* Schönherr, 1840 (Coleoptera: Curculionidae: Entiminae): Descriptions of six new species, a proposal for species-groups, and an annotated checklist. *Zootaxa* **2018**, *4423*, 1–85. [CrossRef]
119. Zhang, G.; Basharat, U.; Matzke, N.; Franz, N.M. Model selection in statistical historical biogeography of Neotropical insects—The *Exophthalmus* genus complex (Curculionidae: Entiminae). *Mol. Phylogenet. Evol.* **2017**, *109*, 226–239. [CrossRef] [PubMed]

120. Anderson, R.S.; Lanteri, A.A. New genera and species of weevils from the Galapagos Islands, Ecuador, and Cocos Island, Costa Rica (Coleoptera; Curculionidae; Entiminae; Entimini). *Am. Mus. Novit.* **2000**, *3299*, 1–15. [CrossRef]
121. Van Emden, F.I. On the taxonomy of Rhynchophora larvae: Adelognatha and Alophinae (Insecta: Coleoptera). *Proc. Zool. Soc. Lond.* **1952**, *122*, 651–795. [CrossRef]
122. Jackson, S.D. Observaciones sobre la biologia de *Platyaspistes glaucus* Fahraeus, 1840 (Coleoptera: Curculionidae). *Rev. Chil. Entomol.* **1987**, *15*, 85–87.
123. Marvaldi, A.E. Eggs and oviposition habits in Entimini (Coleoptera: Curculionidae). *Coleopt. Bull.* **1999**, *53*, 115–126.
124. Marshall, G.A.K. *The Otiorrhynchine Curculionidae of the Tribe Celeuthetini (Col.)*; Trustees of the British Museum: London, UK, 1956; pp. 1–134.
125. Toussaint, E.F.; Tänzler, R.; Rahmadi, C.; Balke, M.; Riedel, A. Biogeography of Australasian flightless weevils (Curculionidae, Celeuthetini) suggests permeability of Lydekker's and Wallace's Lines. *Zool. Scr.* **2015**, *44*, 632–644. [CrossRef]

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Statistical Evaluation of Monophyly in the 'Broad-Nosed Weevils' through Molecular Phylogenetic Analysis Combining Mitochondrial Genome and Single-Locus Sequences (Curculionidae: Entiminae, Cyclominae, and Hyperinae)

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Abstract: Establishing well-supported monophyletic groups is a key requirement for producing a natural classification that reflects evolutionary descent. In a phylogenetic framework this is best achieved through dense taxon sampling and the analysis of a robust character dataset, combined with statistical testing of topological hypotheses. This study assesses the monophyly of tribes and subfamilies within the diverse 'broad-nosed weevils' (Curculionidae: Entiminae, Cyclominae and Hyperinae) through analysis of single-locus sequence data for mitochondrial *cox1* and *rrnL* genes, in combination with a 'backbone' of complete and near-complete mitochondrial genome sequences. Maximum likelihood phylogenetic analyses incorporating topological constraints for various higher-taxa were statistically tested using the AU, SH, and KH tests, which indicated that three tribes within Entiminae, as presently classified, are not monophyletic. Moderate and high bootstrap support was also consistent with two entimine tribes (Peritelini and Cylydrorhinini) being each recovered as monophyletic in an unconstrained analysis. Furthermore, one genus of cyclomine weevils (*Aphela*) is recovered outside the clade of 'broad-nosed weevils', although its taxonomic placement remains uncertain. It is apparent that the present approach may be hampered by limited taxon sampling in the 'backbone' dataset, rendering it difficult for divergent taxa to robustly match to their closest lineages. However, with improved taxon sampling of the mitogenome tree, the general approach can be a useful taxonomic tool for weevils.

Keywords: constraint analysis; AU test; SH test; KH test; mitochondrial genomes; Curculionoidea

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1. Introduction

The fundamental aim of phylogeny reconstruction is to summarise genealogically determined evolutionary relationships as phylogenetic trees, visually tracing the historical course of speciation, organised through the relative recency of common ancestry [1,2]. Together with other data, such as geographic distributions and ecological traits for species under consideration, phylogenies can be powerful tools for explaining observed patterns, and for testing hypothesised processes of speciation.

Of paramount importance when inferring biological and systematic meaning from trees is the formulation of a sound basis for identifying natural groups of taxa, from which broader conclusions and predictions can be made regarding the biology of the included species. Such predictions might include the identification of lineage-specific host-plant use, breeding behavior, or even geographic distribution. Deciphering which groups of organisms are natural (or monophyletic) is a prerequisite for constructing a hierarchical classification system that reflects their underlying evolutionary history. A well sampled dataset, containing taxa of as many potential lineages of the taxon of interest as possible, is crucial for the meaningful testing of monophyletic groups in order to increase confidence in the resulting topologies. However, because comprehensive taxon sampling in very diverse groups containing thousands of species, such as the weevils (Coleoptera: Curculionoidea), is very difficult in practice [3], alternative sources of data other than specifically collected specimens should be investigated to enhance taxon coverage. Such data can be obtained from public repositories of DNA sequence data held in freely accessible online databases such as the National Center for Biotechnology Information's GenBank [4]. Other databases also exist, for example The Barcode of Life Data System (BOLD) [5] but GenBank is by far the most comprehensive, at present holding more than 206 million sequences belonging to almost 260,000 described species, submitted by research laboratories across the world (NCBI GenBank Flat File release 223.0, 15 December 2017) [4].

Statistical tests available to undertake hypothesis testing between competing ML tree topologies generally utilise the likelihood values (for each tree this is the product of all per-site likelihoods in the input alignment) for calculation of test statistics. Such tests include the Shimodaira–Hasegawa (SH) test [6] and the Kishino–Hasegawa (KH) test [7] which both compare the log-likelihoods of two trees to produce a probability statistic for each of them. In the SH test, the trees tested are selected a posteriori, whereas in the KH test, the trees are selected a priori [8]. Both these tests have biases and limitations, including a correlation between the SH test results with the number of trees being tested (rendering the test conservative in rejecting trees) and the inability of the KH test to control for type 1 errors [9]. An alternative test that is able to correct for the tree selection bias is the approximately unbiased (AU) test [9]. The AU test is based upon bootstrap resampling of the per-site log-likelihoods of the input alignment, which allows for the alignment length to be altered and the newly bootstrapped probabilities being scaled to the original alignment length [8]. The AU test statistic is calculated from the change in BS probabilities for each bootstrapped set of replicates. This test is able to control for type 1 errors and is currently one of the most widely employed methods to assess topologies under the ML optimality criterion. To statistically test whether monophyly of any of the higher taxa constrained as described below could be rejected, the AU test was implemented to obtain the confidence set of trees. This was achieved through resampling the per-site log-likelihood of the input alignment by changing the alignment length and drawing new BS samples from these lengths. The number of times the hypothesis is supported by the BS replicates is used to calculate the BS support for different sequence lengths; the AU test then calculates a *p*-value from the change in bootstrap values along the changing sequence length [9].

We concur with recent opinion promoting the modern classification of weevils as a data-driven science [10], and the present study therefore aims to contribute to this by testing the monophyly of tribes and subfamilies within the diverse group of weevil subfamilies known as the 'broad-nosed weevils' (Curculionidae subfamilies Entiminae, Cyclominae, and Hyperinae) using sequences obtained from GenBank to enhance the taxon coverage of these groups in a phylogeny of Curculionoidea previously constructed from complete and near-complete mitochondrial genomes (mitogenomes) [11]. The approach used is analogous to that employed in a study which obtained short (<100 bp) phylogenetically informative amplicons (SPIAs) of the mitochondrial 16S ribosomal large subunit gene (*rrnL*) from DNA-degraded specimens of weevils and incorporated them into a 'backbone' phylogeny built from a concatenation of longer sequences from five loci (including *rrnL*) [12]. The process tested here differs in that, instead of SPIAs, longer 'complete' sequences of mitochondrial *cox1* and *rrnL* genes obtained from GenBank are added to the mitogenome 'backbone' phylogeny, containing sequences of both those loci and 13 other genes, in order to identify the lineages to which the database sequences are most closely related under a maximum likelihood (ML) optimality criterion.

The concept of 'broad-nosed weevils' dates back to an 1863 work of Lacordaire [13], who divided his family 'Curculionides' into two groups: the Adelognatha and the Phanerognatha. The former of these represents the broad-nosed weevils, defined morphologically by having the prementum covering the maxillae and by the possession of deciduous processes on the adult mandibles [14,15], in addition to bearing the distinctive relatively short rostrum that eventually gave rise to their popular name. Interpretation of precisely which taxonomic groups are characterised as broad-nosed weevils has varied according to the opinion of different authors [14,16]. One widely used definition [17], which was tested in assessing the monophyly of broad-nosed weevils based upon larval and adult morphological characters [18], contained the following higher taxa sensu the family-level catalogue of Bouchard et al. [19]: Brachyceridae, Ithycerinae, and Microcerinae (subfamilies of Brentidae); Gonipterini (tribe of Curculioninae); Entiminae, Cyclominae, and Hyperinae (subfamilies of Curculionidae). That study concluded that broad-nosed weevils are not monophyletic, with the Ithycerinae, Microcerinae, and Brachyceridae recovered as forming three stepwise basal lineages (Ithycerinae most basal) and the Entiminae + Cyclominae forming an apical clade (Hyperinae was not analysed) [18]. This result, together with the results in the mitogenome phylogeny [11] and those based on other molecular data [20–24] represent strong independent evidence that Brachyceridae, Ithycerinae, and Microcerinae form separate basal lineages to those 'broad-nosed' weevils classified within Curculionidae sensu Bouchard et al. [19] except Platypodinae (i.e., Entiminae + Cyclominae + Hyperinae). For the purposes of this study, only the latter group is defined and henceforth referred to as the 'broad-nosed weevils', within which the monophyly of various taxa is tested. Throughout this article we employ an existing definition and terminology in naming the other large true weevil clade, containing the subfamilies Curculioninae + Conoderinae + Cossoninae + Molytinae + Scolytinae, as the 'CCCMS clade' [23].

Selection of the *cox1* 5′ region and *rrnL* as the short loci to be added to the mitogenome data was made based upon the fact that a large number of sequences for these genes are available on GenBank owing to their wide use in phylogenetics research, and in the case of *cox1*, its ubiquitous use as the 'barcode' region of choice for molecular-based species identifications [25]. The 'backbone' phylogeny of Curculionoidea, constructed with mitogenome data from 120 weevil taxa (in seven families, including 67 tribes of Curculionidae) [11] is highly congruent with other molecular hypotheses of weevil relationships [20–24] and clearly demonstrates the well supported division of the Curculionidae *s.str.* into two large clades, one of which represents the monophyletic 'broad-nosed weevils' as defined below, and recovered with 100% bootstrap (BS) support in that analysis. The 'broad-nosed weevils' are selected for further investigation of tribal relationships because of their unambiguous monophyly and the comparatively large number of taxa represented in the mitogenome phylogeny (33 species in 19 tribes), maximising the number of lineages available for study. Additionally, one of its component subfamilies, the Entiminae, is the most speciose subfamily-level taxon in Curculionidae, containing an estimated 12,000 described species globally [16]. Although Entiminae has generally been recovered as monophyletic [17] or paraphyletic [20–24] with respect to the other broad-nosed weevil subfamilies, Hyperinae and/or Cyclominae, in molecular analyses, its internal tribal structure is not well understood, with as many as 55, and as few as 5 tribes proposed [18,26]. Consequently, these relationships are in need of further investigation. General life-history in the Entiminae consists of adult feeding on leaves and shoots, and larval development in underground roots, with apparently low host-plant specificity [16]. Identification of lineage specific life-history traits is also a desirable goal of phylogenetic analyses combined with biological observations.

This study is therefore both an exploration of the phylogenetic utility of incorporating shorter sections of sequence data into a longer alignment, and a test of monophyly of the tribes and subfamilies for which sequences of more than one taxon are available, undertaken in a real-world scenario of combining newly generated sequences with publicly available ones.

2. Materials and Methods

2.1. 'Backbone' Phylogeny

The mitogenome sequences for 120 curculionid taxa analysed in a previous phylogeny [11], (Supplementary Figure S1 and File S1) were used in the phylogenetic reconstructions in this study, acting as a comprehensive phylogenetic framework insofar as they provided the 'backbone' in the resulting trees. Shorter single loci sequences for *cox1* 5′ and *rrnL* obtained from GenBank (as described below) were added to the data-matrix for a combined analysis.

2.2. Public Database Sequences

Automated extraction of sequence data from GenBank was achieved through the use of a series of Perl scripts originally developed as part of a custom-built bioinformatics pipeline for analysing public database sequence data [27,28]. These greatly facilitate the selection of both taxa and loci of interest from amongst all the sequences available, in addition to expediting the process of sequence retrieval. Similar scripts were successfully used to reconstruct a very large phylogeny of >8000 Coleoptera species from analysis of four nuclear and mitochondrial loci obtained from GenBank, indicating the importance of such databases as a source of freely available data [29]. The pipeline was used here only for the selection and retrieval of sequences; subsequent sequence alignment and phylogenetic analyses were undertaken separately. All scripts were run on the Natural History Museum 'ctag' Linux-based bioinformatics server.

The GenBank dataset was further reduced to a maximum of five species per genus following a preliminary ML analysis containing all downloaded GenBank broad-nosed weevil *cox1* and *rrnL* sequences (180 and 175 sequences respectively, representing 278 species-level taxa), combined with the mitogenome data from 120 taxa in Gillett et al. [11]. The alignment step and analysis was otherwise identical to that described below for the unconstrained analysis. The results of this allowed for objective selection of divergent species (sometimes recovered in clearly different lineages) within each genus to ensure that no bias for closely related species was made when choosing taxa to retain for further analysis. Wherever possible, taxa represented by both *cox1* and *rrnL* loci were preferentially selected to reduce missing data. Additionally, all taxonomic names were corrected for any mistakes and to ensure that genera had been assigned to tribes and subfamilies according to the generic catalogue of Alonso-Zarazaga and Lyal [26], except the genera *Aphela* and *Bronchus*, which are now classified in the cyclomine tribes Notiomimetini and Hipporhinini respectively, according to a recent review of the Cyclominae [30].

2.3. Multiple Sequence Alignment and Dataset Concatenation

Prior to alignment, the *cox1* 5′ and *rrnL* GenBank sequences were added to the corresponding whole mitogenome *cox1* and *rrnL* sequences to construct the combined GenBank + whole mitogenome dataset. Whole mitogenome sequences for the genes *nad5*, *nad4*, *nad4L*, and *nad1*, which are transcribed on the reverse strand of the mitogenome, were reverse complemented prior to alignment. Sequences for each of the 13 protein-coding and 2 ribosomal RNA genes were individually aligned using the MAFFT version 7 online server, incorporating the FFT-NS-i slow iterative refinement strategy [31], with the following parameter values: nucleotide scoring matrix 200PAM/k = 2, gap open penalty = 1.53, offset value = 0 [31]. Alignments were thereafter checked manually in Geneious 5.4 [32] for quality and to ensure that protein-coding genes were in the correct reading frame. The resulting individual gene alignments were concatenated together in mitogenome gene order to create the final dataset in Phylip format for phylogenetic analysis.

2.4. Monophyly Constraints

In order to test whether monophyly of any of the subfamilies Entiminae, Cyclominae, and Hyperinae, and any of the tribes within the subfamily Entiminae were consistent with the combined dataset, a series of 20 constraint tree files in Newick format were constructed, each topologically constraining one subfamily or tribe within the broad-nosed weevils, as summarised and described in the results. Only groups with two or more species, and which were not recovered as monophyletic in the initial unconstrained ML analysis (an initial test of monophyly), were selected for constraint analysis.

2.5. Phylogenetic Analyses

Both an unconstrained and 20 constrained (as outlined above and in the results) ML analyses were undertaken using RAxML 7.6.6 [33] run on the CIPRES web-based server [34]. To assess nodal support, a rapid BS analysis with 1000 iterations was run simultaneously with tree-building. The dataset was analysed and partitioned by gene because previous analysis of the mitogenome dataset indicated that a partitioned analysis outperforms an unpartitioned one [11]. Therefore, separate estimated models of nucleotide substitution were specified for each gene region in the alignment. A GTRCAT model was implemented for the bootstrapping phase and a GTRGAMMA model was used for final tree inference (GTR + optimisation of substitution rates + optimisation of site-specific evolutionary rates). All trees were visualised in Dendroscope 3 [35] and were rooted with a divergent outgroup within Polyphaga (Chrysomelidae: *Crioceris duodecimpunctata*).

2.6. Statistical Hypothesis Testing

To undertake the AU test, the per-site log-likelihood was computed for each of the unconstrained and 20 constraint trees in RAxML using the —f g algorithm, and written to a Treepuzzle formatted file [8]. These values were then used in the program CONSEL [36] to perform the bootstrap resampling (100,000 replicates per tree) and to calculate the p-values for the AU, SH, and KH tests.

3. Results

3.1. Public Database Sequences

The GenBank-derived dataset obtained via the bioinformatics pipeline contained 107 species of Entiminae, Cyclominae, and Hyperinae. Within Entiminae, 22 tribes, 62 genera, and 92 species were represented. Within Cyclominae, 4 tribes, 10 genera, and 13 species were represented. The Hyperinae was represented by one genus and two species. A total of 68 *rrnL* and 63 *cox1* sequences were obtained and 24 species were represented by sequences from both loci, with 44 species only represented by *rrnL* and 39 species only by *cox1*. Sequence lengths varied between 113–558 bp for *rrnL* and 262–748 bp for *cox1*. Supplementary Table S1 summarises the GenBank-obtained sequence data matrix.

3.2. Phylogenetic Analyses

The GenBank-obtained sequences were combined with the existing mitogenome data (Supplementary Table S2) to yield an aligned matrix of 229 taxa, 15 genes and 13912 positions. The mitogenome sequence data is available in Supplementary File S1. The final dataset contained the following broad-nosed weevil taxa: 27 tribes, 74 genera, and 119 species (121 terminals) of Entiminae; 5 tribes, 14 genera and 18 species of Cyclominae; 1 genus and 3 species of Hyperinae. The following 18 tribes of Entiminae contained more than one species and therefore could be tested for monophyly, initially through the unconstrained ML analysis (as analysed by topology and BS support), and then through the individual constraint analyses: Brachyderini, Celeuthetini, Cylydrorhinini, Cyphicerini, Elytrurini, Eustylini, Geonemini, Laparocerini, Naupactini, Otiorhynchini, Peritelini, Polydrusini, Rhyncogonini, Sciaphilini, Sitonini, Tanymecini, Trachyphloeini, and Tropiphorini. Additionally, the subfamilies Entiminae, Cyclominae, and Hyperinae separately, and the three of them combined as the ‘broad-nosed weevils’, were each also tested for monophyly using constraint analyses.

The topology of weevil families and subfamilies recovered in the unconstrained ML tree (final ML optimisation likelihood: −789,416.469537) shown in Figure 1 (and Supplementary Figure S2) is highly congruent with that in the tree generated using the mitogenome data alone [11], (Supplementary Figure S1). Only the position of *Ocladius* (Brachyceridae: Ocladiinae) differs in being placed within the Dryophthoridae + Platypodinae clade in the present analysis, and outside of it in the mitogenome analysis. One other intriguing disparity is the sister relationship recovered between *Aphela* (Cyclominae) and *Bagous* (Bagoinae) in a clade sister to all other Curculionidae *s.str. sensu* Bouchard et al. [19] except Platypodinae. Cyclominae is, in fact, recovered here in six separate lineages, whereas analysis of the mitogenomie data alone (containing much more restricted taxon coverage) resulted in a monophyletic Cyclominae [11], in contrast to most other molecular studies [20,21,23,24]. The division of the remainder of Curculionidae *s.str.* into two large clades is also recovered, although support for the dividing node is reduced to 31% BS from 100% BS in the mitogenome tree alone (Figure 1).

Relationships within the CCCMS clade are similarly highly congruent with the previous mitogenome analyses [11], (Supplementary Figure S1), consisting of a sister relationship between the Scolytini (Scolytinae) and the remaining taxa that are split into two clades, one containing the moderately well supported (70% BS) remaining Scolytinae (except *Coptonotus*) and the other containing the rest of the subfamilies with little support for the monophyly of any of them except Lixinae (100% BS).

Within the clade of focal interest, composed of the broad-nosed weevils, there is generally very low nodal support for the deeper nodes, although some of the more apical nodes are well supported, with 26 of them having support values of 80% BS or higher (Figure 1). Two tribes of Entiminae are recovered as a clade with moderate nodal support in this analysis: the Peritelini (88% BS) and the Cylydrorhinini (69% BS), each represented by two genera and two species.

Because of their monophyly as evaluated through bootstrap analysis, these last two tribes are therefore not considered for further constraint analyses. The remaining 16 tribes of Entiminae were recovered as paraphyletic or polyphyletic and were consequently each constrained as monophyletic (Table 1) in separate RAxML analyses (identical to the unconstrained analyses other than enforcing the topological constraint). The resulting per-site log likelihoods of these trees, estimated separately in RAxML, were used to calculate the AU test statistic as detailed below.

Table 1. Higher-taxa constrained as monophyletic for ML analysis and the AU test of monophyly.

Constrained Taxon	Generic Diversity (No. Genera) *	No. of Genera in Constraint	No. of Terminals in Constraint
Broad-nosed weevils	1585	89	142
Entiminae	1370	74	121
Cyclominae	180	14	18
Hyperinae	35	1	3
Brachyderini	24	2	6
Celeuthetini	75	8	8
Cyphicerini	120	1	2
Elytrurini	6	2	3
Eustylini	17	6	9
Geonemini	39	5	7
Laparocerini	9	3	9
Naupactini	65	9	19
Otiorhynchini	27	1	6
Polydrusini	14	3	6
Rhyncogonini	3	1	3
Sciaphilini	46	4	4
Sitonini	8	1	4
Tanymecini	42	5	6
Trachyphloeini	23	1	2
Tropiphorini	115	6	9
UNCONSTRAINED		147	229

* approximate count, data taken from [26].

3.3. Statistical Hypothesis Testing

Results of the statistical tests carried out in CONSEL indicate that at a significance level $\alpha = 0.05$, the confidence sets are the same across the AU, SH, and KH tests (Table 2), with only trees constraining Otiorhynchini, Brachyderini, and Tropiphorini as monophyletic rejecting the null hypothesis that there is no difference between the trees (i.e., that all unconstrained and constrained trees are equally good explanations of the data). Consequently, for these three tribes, the alternative hypothesis is accepted that their likelihoods are significantly different and therefore their monophyly is rejected.

Table 2. Results of the AU, KH, and SH tests of constrained monophyly of 20 higher taxa and the unconstrained analysis, ranked by likelihood. Log likelihood difference to the best tree is shown, except for the best tree, which shows the negative distance of the second best. The three *p*-values below a significance level $\alpha = 0.05$ are ranked 19–21, and represent the three tribes whose monophyly is rejected (Otiorhynchini, Brachycerini, and Tropiphorini).

Rank (By Likelihood)	Taxon Constrained in ML Tree	ΔLog Likelihood to Best Tree	AU Test *p*-Value	KH Test *p*-Value	SH Test *p*-Value
1	Sitonini	−4.1	0.621	0.526	0.971
2	UNCONSTRAINED	4.1	0.605	0.474	0.948
3	Hyperinae	8.7	0.527	0.396	0.968
4	Laparocerini	11.7	0.573	0.430	0.961
5	Rhyncogonini	18.0	0.513	0.409	0.921
6	Broad-nosed weevils	21.4	0.442	0.378	0.913
7	Polydrusini	23.7	0.431	0.357	0.942
8	Cyphicerini	24.1	0.425	0.362	0.865
9	Geonemini	26.7	0.411	0.355	0.873
10	Elytrurini	29.2	0.395	0.340	0.876
11	Celeuthetini	55.6	0.202	0.213	0.719
12	Naupactini	56.4	0.206	0.185	0.726
13	Cyclominae	70.6	0.132	0.174	0.627
14	Eustylini	72.6	0.176	0.125	0.619
15	Sciaphilini	78.0	0.119	0.153	0.573
16	Entiminae	88.0	0.080	0.100	0.505
17	Trachyphloeini	94.3	0.083	0.059	0.463
18	Tanymecini	99.3	0.054	0.059	0.426
19	Otiorhynchini	204.2	2×10^{-4}	0.006	0.048
20	Brachyderini	241.0	6×10^{-51}	3×10^{-5}	0.007
21	Tropiphorini	483.0	0.001	0	0

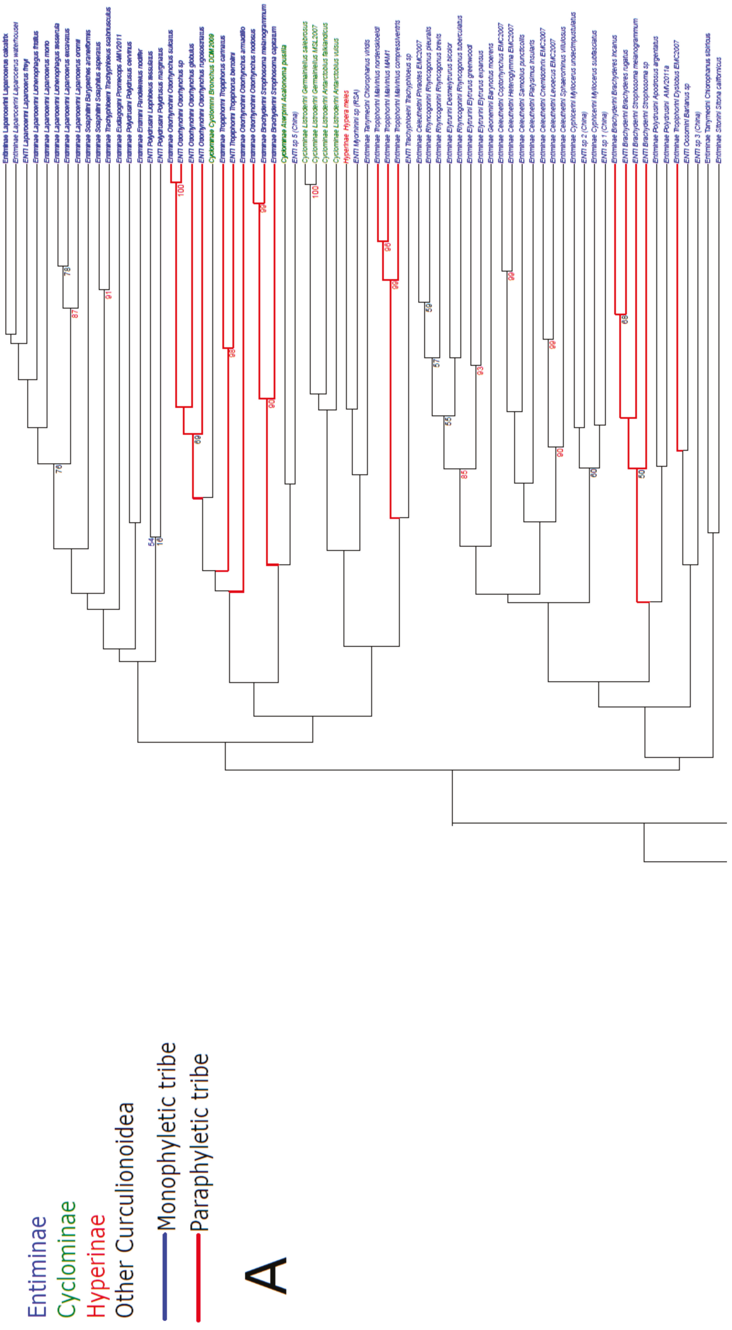

Figure 1. *Cont.*

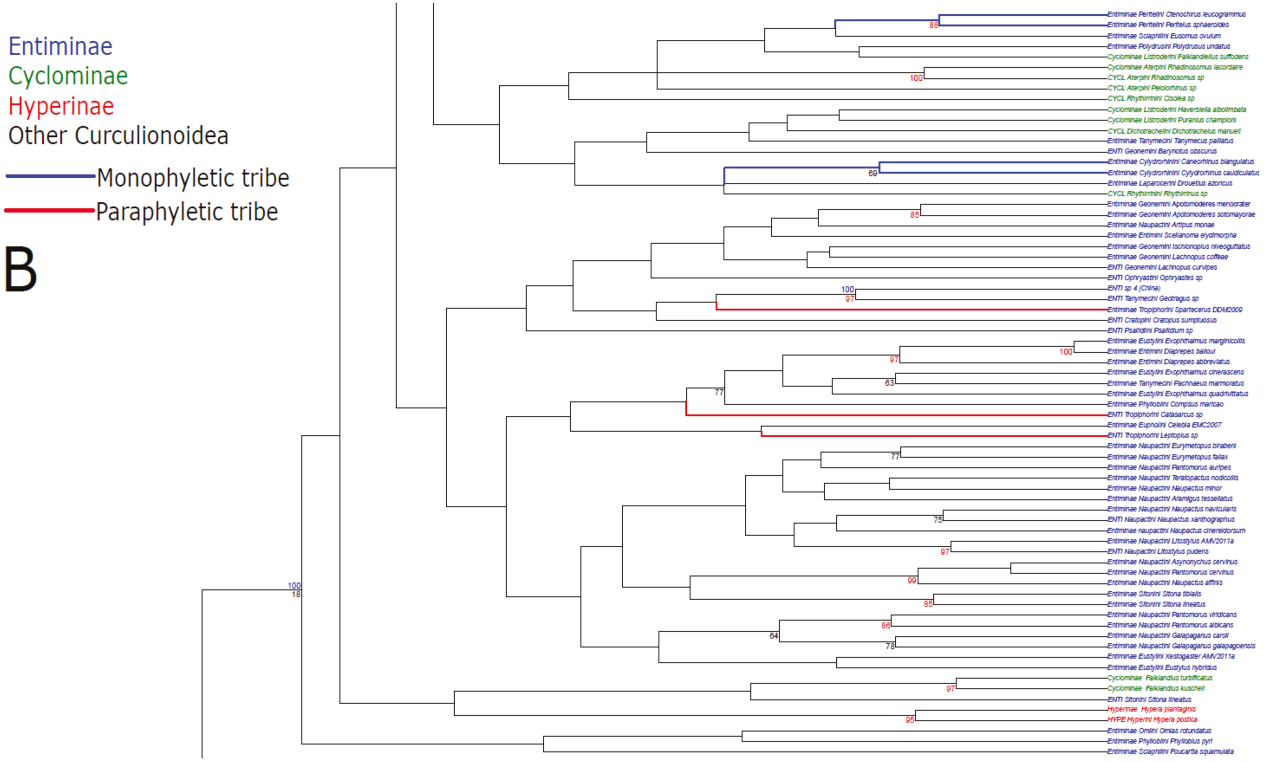

Figure 1. *Cont.*

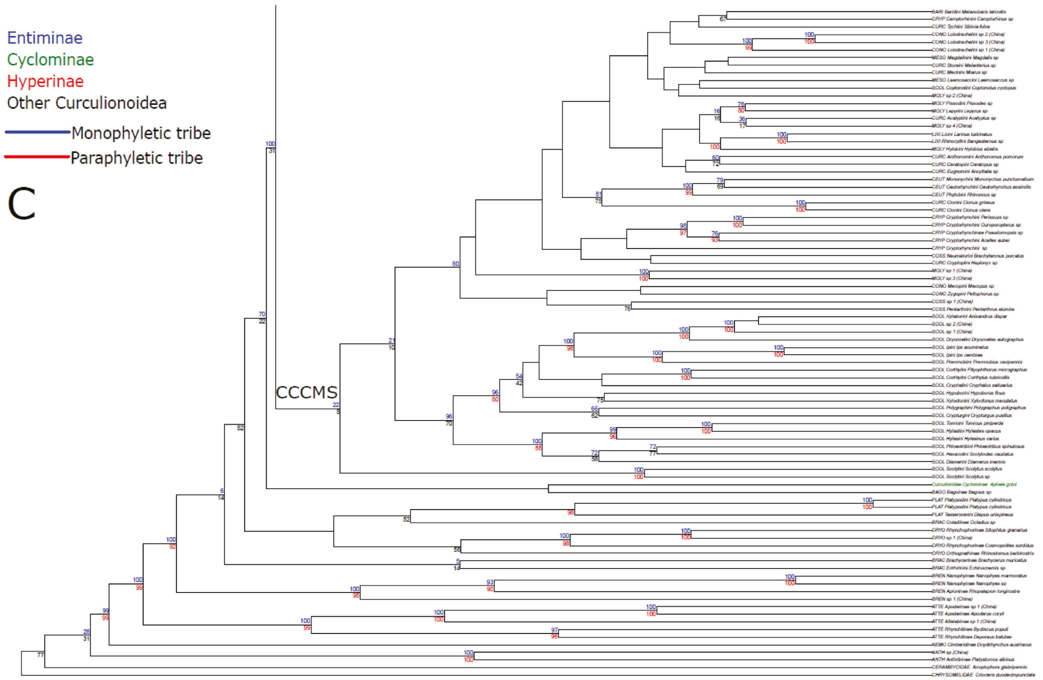

Figure 1. Unconstrained maximum likelihood tree of combined mitogenome and single-locus sequences, rooted at *Crioceris duodecimpunctata* (Chrysomelidae). Shown in three sequential sections (A–C). Bootstrap nodal supports are indicated below nodes, with those of 80% and higher indicated in red. Bootstrap values above nodes (in blue) are shown for consistent nodes in the 'backbone' mitogenome-only data ML tree [11]. Node labelled 'broad-nosed weevils' represents the clade consisting of subfamilies Entiminae + Hyperinae + Cyclominae (with exception of *Aphela*); node labelled CCCMS represents the clade consisting of subfamilies Curculioninae + Conoderinae + Cossoninae + Molytinae + Scolytinae [23]. In green is highlighted the aberrant position of *Aphela gotoi*, currently classified in Cyclominae, but recovered in the CCCMS clade. Taxa represented by mitogenome sequences have family and subfamily codes prefixes as follows: Anthribidae (ANTH), Attelabidae (ATTE), Brachyceridae (BRAC), Brentidae (BREN), Dryophthoridae (DRYO), Nemonychidae (NEMO), Bagoinae (BAGO), Baridinae (BARI), Ceutorhynchinae (CEUT), Conoderinae (CONO), Cossoninae (COSS), Cryptorhynchinae (CRYP), Curculioninae (CURC), Lixinae (LIXI), Mesoptiliinae, (MESO), Molytinae (MOLY), Platypodinae (PLAT), and Scolytinae (SCOL).

4. Discussion

4.1. Unconstrained Analysis

Augmenting the mitogenome dataset with the GenBank sequence data did not strongly affect the main topology with regards to family- and subfamily-level relationships compared to the mitogenome data alone. This was expected because the bulk of phylogenetic signal is present in the full mitogenome alignment and no additional taxa in the deeper portion of the tree were incorporated into this analysis. The single aberrant placement of *Aphela gotoi*, currently classified in the Cyclominae [30], outside the broad-nosed weevil clade, and together with Bagoinae, was the only inconsistency. Although the *Aphela* + *Bagous* relationship has only very weak nodal support (47% BS), it is nevertheless striking that *Aphela*, an apparent broad-nosed weevil, is recovered outside the large Entiminae + Cyclominae + Hyperinae clade, which is otherwise monophyletic in the mitogenome phylogeny of Gillett et al. [11].

When *Aphela* was separately constrained within the Cyclominae and within the broad-nosed weevils, neither of the resulting ML trees was rejected by the AU, SH or KH test, prohibiting a definitive systematic placement. *Aphela* was previously classified within the cyclomine tribe Minyopini, now considered synonymous with the molytine subtribe Plinthina on morphological grounds [26], although *Aphela* itself is presently classified in the cyclomine tribe Notiomimetini [30] and clearly this fact, together with the present molecular findings, indicate that this taxon warrants further investigation with additional sequence data (ideally a full mitogenome sequence). The Cyclominae have been considered a "'subfamily of convenience' for now, sharing no obvious synapomorphic characters" [16], and has consistently been shown to be a paraphyletic taxon in recent molecular studies [20,21,23,24]. The uncertain placement of *Aphela* in our analyses supports these previous results.

The unconstrained analysis indicated that the tribes Peritelini and Cylydrorhinini are each monophyletic in our dataset, although due to the limited taxon sampling of each, interpretation of monophyly beyond the included genera remains putative. Nevertheless, inclusion of the type genera of both these tribes (*Peritelus* and *Cylyndrorhinus* respectively) in the dataset increases objectivity and confidence in at least establishing that each of the other genera included per tribe is correctly classified at present (*Ctenochirus* in Peritelini and *Caneorhinus* in Cylydrorhini), which would not have been the case had the type genera not been analysed.

The tribe Peritelini is large, containing 76 genera with a wide distribution in the Holarctic, Afrotropical, and Australian regions, with new species being continuously discovered even in the relatively well studied European fauna [37,38]. However, morphologically it has not been well defined, and in particular, lacks apomorphies enabling a clear separation from Otiorhynchini [39]. Additionally, at least one genus, *Caenopsis*, has been recently transferred to the tribe Trachyphloeini [39], further highlighting the uncertain monophyly of the group.

In contrast, the tribe Cylydrorhinini is much smaller, containing only six genera, and is of restricted distribution, occurring only in the Australian and southern Neotropical regions. It had previously been classified as a subfamily (Cylyndrorhininae) consisting of two tribes: the Cylyndrorhinini and Listroderini [40]. However, study of larval characters led to the conclusion that the Cylyndrorhinini (in particular the genera *Caneorhinus* and *Cylydrorhinus*, also evaluated here with molecular data) belong in the Entiminae, and the Listroderini belong in the 'Rhytirrhininae', i.e., within the current subfamily Cyclominae [40]. The molecular data indicate that Listroderini is paraphyletic, consisting of three lineages, only one of which, *Germainiellus* + *Antarctobius*, has low support (56% BS), with the two included *Germainiellus* species being well supported as monophletic (100% BS). Whilst the limited taxon sampling in the present study suggests that Cylydrorhinini is monophyletic, no firm conclusions can be drawn with regards to its relationship with Listroderini because of low nodal support in the intervening parts of the tree. This specific relationship was not investigated further with constraint analyses although constraining the Cyclominae as a whole did not lead to the resulting tree being rejected by the AU test statistic, suggesting that the molecular data is consistent with larval morphology and that Listroderini is distinct from Cylydrorhinini.

Although the unconstrained analysis failed to recover any of the remaining 16 tribes of Entiminae as monophyletic, some of these were recovered in two or more well supported clades. Therefore, within the Tropiphorini, *Tropiphorus carinatus*, and *T. bertolini* form one clade (98% BS), *Malvinius* (three species) forms another (99% BS), with the remaining four genera (and species) of Tropiphorini distributed across the tree with low support. In the Celeuthetini, *Cnemidothrix*, *Levoecus*, and *Sphaerorhinus* form a clade (90% BS), as do *Coptorhynchus* and *Heteroglymma* (99% BS). With the addition of *Samobius* and *Platysimus*, all seven aforementioned genera form a clade, but with low support (14% BS); the remaining genus of Celeuthetini, *Phraotes*, is recovered away from this last clade with one moderately supported (85% BS) intervening node that groups it with members of the tribes Rhyncogonini and Elytrurini. Whilst such clades with moderate and high nodal support appear to offer evidence for the paraphyly of several tribes, the generally low nodal supports in the intermediate nodes between such clades preclude conclusions to be drawn based on bootstrap values alone.

4.2. Constraint Analyses and Statistical Tests of Monophyly

In supplement to the bootstrap support results, the AU tests rejecting the three ML trees respectively containing the constrained monophyly of the tribes—Otiorhynchini, Brachyderini, and Tropiphorini—provide further evidence for the paraphyly of these higher taxa.

Otiorhynchini is a particularly species-rich tribe containing 10 genera, of which the *Otiorhynchus* 'complex' contains about 1500 species exclusive to the Palaearctic region (except for a few introduced species in the Nearctic) which have been divided into 105 subgenera [41]. No detailed phylogenetic analysis has been undertaken within this group, although a karyotype analysis of three genera was in accordance with the current classification [41]. The taxa analysed in this study belong to five subgenera: *O.* (*Otiorhynchus*) *armadillo*, *O.* (*Postaremus*) *nodosus*, *O.* (*Dorymerus*) *sulcatus*, *O.* (*Nihus*) *globulus*, and *O.* (*Zustalestus*) *rugosostriatus* [39]. Four of these species (*O. globulus*, *O. sulcatus*, *O. rugosostriatus*, and *Otiorhynchus* sp.) were retrieved in a clade in the unconstrained ML analysis (69% BS), with a high support for the sister relationship between *O. sulcatus* and *Otiorhynchus* sp. (100% BS). Of the two remaining species, *O. nodosus* was retrieved with high support as sister to *Strophosoma melanogrammum*, belonging to the tribe Brachyderini (98% BS), and *O. armadillo* was weakly supported as a lineage sister to a clade containing the first group of four *Otiorhynchus* + two members of Tropiphorini (two *Tropiphorus* spp.) and one Hipporhinini (*Bronchus* sp.). It is difficult to be confident about the relationships amongst these Otiorhynchini, and the retrieval of *O. nodosus* sister to *S. melanogrammum* is particularly surprising. Sequences for *cox1* for these last two species were obtained from GenBank, and both originated from the same study investigating clonality and polyploidy in *Otiorhynchus* [40]. A BLAST search against the GenBank database revealed that the *S. melanogrammum cox1* sequence very closely matches sequences from four *Otiorhynchus* species in the same study (98–99% identity over 100% of the 552 bp sequence; E = 0.0) indicating a close relationship between these two genera. It is unlikely that the sample was mislabelled on GenBank, although this cannot be ruled out with certainty. *Strophosoma melanogrammum* is also represented in the present data matrix by a partial mitogenome sequence, lacking both *cox1* and *rrnL* [11], and not recovered together with the GenBank sequence represented *S. melanogrammum*, but in another clade containing three other Brachyderini taxa (*Brachyderes* spp.), most likely explaining the relationship with *Otiorhynchus* described above being driven by the closest-matching *cox1* sequence. A previous molecular analysis, based on a smaller dataset than the present, resulted in the recovery of monophyletic Otiorhynchini and Brachyderini [20].

5. Conclusions

The approach used here has confirmed the utility of combining shorter sequences into a longer alignment insofar as several interesting relationships were identified, both supporting and rejecting monophyly of currently classified higher taxa. The extent to which meaningful conclusions can be made regarding how accurately shorter sequences are able to match to their correct lineages is undoubtedly a function of the depth of taxon coverage in the backbone mitogenome alignment, from which most of the phylogenetic signal is derived. The mitogenome dataset contained members of less than a third (19 out of 63) of the tribes within the broad-nosed weevils, so it is hardly surprising that nodal BS support for many internal nodes within this group were poorly supported with the addition of taxa represented by single mitochondrial genes from GenBank. This is a direct result of the small amount of shared comparative data for calculating BS support between taxa with long mitogenome sequences and the taxa solely represented by short sequences.

The inability to reject several of the apparently paraphyletic clades through constraint analyses highlights the presence of conflicting or insufficient data, and demonstrates the complex systematics of the Curculionoidea, wherein particular genera cannot confidently be ascribed to even a particular subfamily. Other limitations in this study included the use of taxa incompletely identified only to the level of subfamily, therefore not allowing for possible further scrutiny of tribal- or generic-level relationships. Additionally, several sequences from the mitogenome dataset lacked the *cox1* and *rrnL* genes [12], confounding their utility here to act as 'backbone' sequences due to the missing data for the critical loci. Alternative or additional mitochondrial loci, such as *cytB* and *cox2* that have been used in the phylogeny of Coleoptera, could have been also incorporated in the alignment which may have increased the number of taxa available for study. Another potential limitation with this approach is that taxonomic coverage within the public databases is currently rather patchy, being dependent upon a multitude of sources such that in many cases certain higher taxa are represented by a small number of potentially highly aberrant or localised species e.g., most of the Cyclominae obtained from GenBank stemmed from a single study based on the fauna of the Falkland Islands [42]. Additionally, a potential general criticism of mitogenome data, despite its consistency with bifurcating phylogenetic trees [43] owing to its maternal inheritance and its unambiguous orthology [44], is that phylogenetic analyses may be confounded by inconsistencies of the coalescent history.

Whilst some results obtained here are cautionary in highlighting the necessity for the careful use of publicly available sequences, it has been demonstrated that it is possible to both single out interesting relationships that warrant further investigation and to test for monophyly, whilst attempting to maximise taxon sampling. One avenue of possible investigation for reconstructing supra-specific phylogenies may involve the use or concatenation of several congeneric GenBank-obtained sequences to represent genus-level or higher taxa, rather than relying only on conspecific sequences, as used here. This may be particularly useful where inter-generic limits may already be well established a priori for such taxa.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/10/2/21/s1. Figure S1: Mitogenome-derived 'backbone' ML tree. Figure S2: Unconstrained ML tree of combined mitogenome and single-locus sequences. Table S1: List of single-locus sequences analysed; Table S2: List of mitogenome sequences analysed. File S1: Mitogenome DNA sequence data analysed [11].

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References

1. Harrison, C.J.; Langdale, J.A. A step by step guide to phylogeny reconstruction. *Plant J.* **2006**, *45*, 561–572. [CrossRef] [PubMed]
2. Wiley, E.O.; Lieberman, B.S. *Phylogenetics: Theory and Practice of Phylogenetic Systematics*, 2nd ed.; Wiley-Blackwell: Hoboken, NY, USA, 2011; pp. 1–432, ISBN 978-0-470-90596-8.
3. Franz, N.M.; Engel, M.S. Can higher-level phylogenies of weevils explain their evolutionary success? A critical review. *Syst. Entoml.* **2010**, *35*, 597–606. [CrossRef]

4. Benson, D.A.; Cavanaugh, M.; Clark, K.; Karsch-Mizrachi, I.; Lipman, D.J.; Ostell, J.; Sayers, E.W. GenBank. *Nucleic Acids Res.* **2013**, *41*, D36–D42. [CrossRef] [PubMed]
5. Ratnasingham, S.; Hebert, P.D.N. BOLD: The Barcode of Life Data System (www.barcodinglife.org). *Mol. Ecol. Notes* **2007**, *7*, 355–364. [CrossRef] [PubMed]
6. Shimodaira, H.; Hasegawa, M. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Mol. Biol. Evol.* **1999**, *16*, 1114–1116. [CrossRef]
7. Kishino, H.; Hasegawa, M. Evaluation of the maximum-likelihood estimate of the evolutionary tree topologies from DNA-sequence data, and the branching order in Hominoidea. *J. Mol. Evol.* **1989**, *29*, 170–179. [CrossRef] [PubMed]
8. Schmidt, H.A. Testing tree topologies. In *The Phylogenetic Handbook: A Practical Approach to Phylogenetic Analysis and Hypothesis Testing*, 2nd ed.; Lemey, P., Salemi, M., Vandamme, A.M., Eds.; Cambridge University Press: Cambridge, UK, 2009; pp. 381–404. ISBN 9780521730716.
9. Shimodaira, H. An approximately unbiased test of phylogenetic tree selection. *Syst. Biol.* **2002**, *51*, 492–508. [CrossRef] [PubMed]
10. Jordal, B.H.; Smith, S.M.; Cognato, A.I. Classification of weevils as a data-driven science: Leaving opinion behind. *Zookeys* **2014**, *439*, 1–18. [CrossRef] [PubMed]
11. Gillett, C.P.D.T.; Crampton-Platt, A.; Timmermans, M.J.; Jordal, B.H.; Emerson, B.C.; Vogler, A.P. Bulk *de novo* mitogenome assembly from pooled total DNA elucidates the phylogeny of weevils (Coleoptera: Curculionoidea). *Mol. Biol. Evol.* **2014**, *31*, 2223–2237. [CrossRef] [PubMed]
12. Hernández-Vera, G.; Caldara, R.; Tosevski, I.; Emerson, B.C. Molecular phylogenetic analysis of archival tissue reveals the origin of a disjunct southern African-Palaearctic weevil radiation. *J. Biogeogr.* **2013**, *40*, 1348–1359. [CrossRef]
13. Lacordaire, T. *Histoire Naturelle des Insectes. Genera des Coléoptères, ou Exposé Méthodique et Critique de Tous Les Genres Proposés Jusqu'ici Dans cet Ordre D'insectes*; pp Tome sixième contenant la famille des curculionides; Librairie Encyclopédique de Roret: Paris, France, 1863; pp. 1–637.
14. Thompson, R.T. Observations on the morphology and classification of weevils (Coleoptera, Curculionoidea) with a key to major groups. *J. Nat. Hist.* **1992**, *26*, 835–891. [CrossRef]
15. Velazquez De Castro, A.J.; Alonso-Zarazaga, M.A.; Outerelo, R. Systematics of Sitonini (Coleoptera: Curculionidae: Entiminae), with a hypothesis on the evolution of feeding habits. *Syst. Entomol.* **2007**, *32*, 312–331. [CrossRef]
16. Oberprieler, R.G.; Marvaldi, A.E.; Anderson, R.S. Weevils, weevils, weevils everywhere. *Zootaxa* **2007**, *1668*, 491–520. [CrossRef]
17. Kuschel, G. A phylogenetic classification of Curculionoidea to families and subfamilies. *Mem. Entomol. Soc. Wash.* **1995**, *14*, 5–33.
18. Marvaldi, A.E. Higher level phylogeny of Curculionidae (Coleoptera: Curculionoidea) based mainly on larval characters, with special reference to broad-nosed weevils. *Cladistics* **1997**, *13*, 285–312. [CrossRef]
19. Bouchard, P.; Bousquet, Y.; Davies, A.E.; Alonso-Zarazaga, M.A.; Lawrence, J.F.; Lyal, C.H.C.; Newton, A.F.; Reid, C.A.M.; Schmitt, M.; Ślipiński, S.A.; et al. Family-group names in Coleoptera (Insecta). *Zookeys* **2011**, *88*, 1–972. [CrossRef] [PubMed]
20. Hundsdoerfer, A.K.; Rheinheimer, J.; Wink, M. Towards the phylogeny of the Curculionoidea (Coleoptera): Reconstructions from mitochondrial and nuclear ribosomal DNA sequences. *Zool. Anz.* **2009**, *248*, 9–31. [CrossRef]
21. McKenna, D.D.; Sequeira, A.S.; Marvaldi, A.E.; Farrell, B.D. Temporal lags and overlap in the diversification of weevils and flowering plants. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 7083–7088. [CrossRef] [PubMed]
22. Haran, J.; Timmermans, M.J.T.N.; Vogler, A.P. Mitogenome sequences stabilize the phylogenetics of weevils (Curculionoidea) and establish the monophyly of larval ectophagy. *Mol. Phylogenet. Evol.* **2013**, *67*, 156–166. [CrossRef] [PubMed]
23. Gunter, N.L.; Oberprieler, R.G.; Cameron, S.L. Molecular phylogenetics of Australian weevils (Coleoptera: Curculionoidea): Exploring relationships in a hyperdiverse lineage through comparison of independent analyses. *Austral Entomol.* **2015**, *55*, 217–233. [CrossRef]
24. Shin, S.; Clarke, D.J.; Lemmon, A.R.; Aitken, A.L.; Haddad, S.; Farrell, B.D.; Marvaldi, A.E.; Oberprieler, R.G.; McKenna, D.D. Phylogenomic data yield new and robust insights into the phylogeny and evolution of weevils. *Mol. Biol. Evol.* **2017**. [CrossRef] [PubMed]

25. Hebert, P.D.N.; Cywinska, A.; Ball, S.L.; DeWaard, J.R. Biological identifications through DNA barcodes. *Proc. Biol. Sci.* **2003**, *270*, 313–321. [CrossRef] [PubMed]
26. Alonso-Zarazaga, M.A.; Lyal, C.H.C. *A World Catalogue of Families and Genera of Curculionoidea (Insecta: Coleoptera) (Excepting Scolytidae and Platypodidae)*; Entomopraxis: Barcelona, Spain, 1999; pp. 1–315, ISBN 84-605-9994-9.
27. Hunt, T.; Bergsten, J.; Levkanicova, Z.; Papadopoulou, A.; John, O.S.; Wild, R.; Hammond, P.M.; Ahrens, D.; Balke, M.; Caterino, M.S.; et al. A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science* **2007**, *318*, 1913–1916. [CrossRef] [PubMed]
28. Hunt, T.; Vogler, A.P. A protocol for large-scale rRNA sequence analysis: Towards a detailed phylogeny of Coleoptera. *Mol. Phylogenet. Evol.* **2008**, *47*, 289–301. [CrossRef] [PubMed]
29. Bocak, L.; Barton, C.; Crampton-Platt, A.; Chesters, D.; Ahrens, D.; Vogler, A.P.V. Building the Coleoptera tree-of-life for >8000 species: Composition of public DNA data and fit with Linnaean classification. *Syst. Entomol.* **2013**, *39*, 97–110. [CrossRef]
30. Oberprieler, R.G. A reclassification of the weevil subfamily Cyclominae (Coleoptera: Curculionidae). *Zootaxa* **2010**, *2515*, 1–35. [CrossRef]
31. Katoh, K.; Misawa, K.; Kuma, K.; Miyata, T. MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Res.* **2002**, *30*, 3059–3066. [CrossRef] [PubMed]
32. Kearse, M.; Moir, R.; Wilson, A.; Stones-Havas, S.; Cheung, M.; Sturrock, S.; Buxton, S.; Cooper, A.; Markowitz, S.; Duran, C.; et al. Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **2012**, *28*, 1647–1649. [CrossRef] [PubMed]
33. Stamatakis, A. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **2006**, *22*, 2688–2690. [CrossRef] [PubMed]
34. Miller, M.A.; Pfeiffer, W.; Schwartz, T. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, LA, USA, 14 November 2010; pp. 1–8.
35. Huson, D.H.; Scornavacca, C. Dendroscope 3: An Interactive Tool for Rooted Phylogenetic Trees and Networks. *Syst. Biol.* **2012**, *61*, 1061–1067. [CrossRef] [PubMed]
36. Shimodaira, H.; Hasegawa, M. CONSEL: For assessing the confidence of phylogenetic tree selection. *Bioinformatics* **2001**, *17*, 1246–1247. [CrossRef] [PubMed]
37. Pierotti, H.; Fink, T. New and interesting Peritelini of the Western Mediterranean fauna. XX. A novel *Meira* (Jacquelin du Val, 1852) species from the Ligurian Alps. *Zootaxa* **2013**, *3716*, 595–598. [CrossRef] [PubMed]
38. Pierotti, H.; Germann, C.; Braunert, C. New or interesting Peritelini of the West-Mediterranean fauna. XXIV. Two new Simmeiropsis Pierotti & Bello, 2013 from Portugal (Coleoptera, Curculionidae, Entiminae). *Zootaxa* **2013**, *3734*, 273–280. [CrossRef] [PubMed]
39. Pierotti, H.; Bello, C.; Alonso-Zarazaga, M.A. Contribution to the systematic rearrangement of the Palaearctic Peritelini. VI. A synthesis of the Spanish Peritelini (Coleoptera: Curculionidae: Entiminae). *Zootaxa* **2010**, *2376*, 1–96.
40. Marvaldi, A.E. Larvae of South American Entimini (Coleoptera: Curculionidae), and phylogenetic implications of certain characters. *Rev. Chil. Entomol.* **1998**, *25*, 21–44.
41. Lachowska, D.; Rozek, M.; Holecova, M. Cytotaxonomy and karyology of the tribe Otiorhynchini (Coleoptera: Curculionidae). *Eur. J. Entomol.* **2008**, *105*, 175–184. [CrossRef]
42. Papadopoulou, A.; Jones, A.G.; Hammond, P.M.; Vogler, A.P. DNA taxonomy and phylogeography of beetles of the Falkland Islands (Islas Malvinas). *Mol. Phylogenet. Evol.* **2009**, *53*, 935–947. [CrossRef] [PubMed]
43. Curole, J.P.; Kocher, T.D. Mitogenomics: Digging deeper with complete mitochondrial genomes. *Trends Ecol. Evol.* **1999**, *14*, 394–398. [CrossRef]
44. Botero-Castro, F.; Tilak, M.K.; Justy, F.; Catzeflis, F.; Delsuc, F.; Douzery, E.J.P. Next-generation sequencing and phylogenetic signal of complete mitochondrial genomes for resolving the evolutionary history of leaf-nosed bats (Phyllostomidae). *Mol. Phylogenet. Evol.* **2013**, *69*, 728–739. [CrossRef] [PubMed]

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The Enigmatic Weevil Genus *Philetaerobius* from Southern Africa: Definition, Affinities and Description of Three New Species (Coleoptera: Curculionidae: Entiminae)

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Abstract: The small entimine genus *Philetaerobius* Marshall, 1923 is revised, entailing a redescription of the genus and the only hitherto described species, *P. nidicola* Marshall, as well as the description of three new species, *P. endroedyi* sp. n., *P. garibebi* sp. n. and *P. louwi* sp. n. A lectotype is designated for *P. nidicola* Marshall. The habitus and taxonomically important structures of all species are illustrated, including the previously unrecorded male and female genitalia. A key to the four species is provided, as well as a map of their known distributions in southern Namibia and the Northern and Western Cape provinces of South Africa. The habits of the genus, as known, are summarized, and its taxonomic position and indicated relationship with the taxonomically equally isolated genus *Spartecerus* are discussed. The habitus and genitalia of some *Spartecerus* species are also illustrated, and the available information on the life-history of the genus is summarized.

Keywords: taxonomy; South Africa; Namibia; weevils; new taxa; spermatheca; *Mimaulus*; *Spartecerus*

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1. Introduction

Philetaerobius Marshall, 1923 is a very unusual genus of Entiminae, as its flat body and rostrum distinguish it from all other Entiminae in southern Africa. It was described by Marshall [1] for a single species, *P. nidicola* Marshall, which was found in a communal nest of the Sociable Weaver, *Philetairus socius* (Latham, 1790), in South Africa. In the literature, *Philetaerobius* remained known from only the five type specimens of *P. nidicola* for more than 60 years, until Louw [2] recorded collecting 150 specimens during a 1976 ecological study in southern Namibia. Oberprieler [3] later reported finding an undescribed species on grasses in central Namibia in 1987. However, substantial additional material of the genus was also collected in the 1970s and 1980s by the late Sebastian Endrödy-Younga, a coleopterist at the former Transvaal Museum in Pretoria, and some more specimens had accumulated in other collections in South Africa. Field work in 2011, 2013 and 2016 by two of the authors of the present paper (R.B., M.M.) in the Namaqualand and Richtersveld regions of the Northern Cape province of South Africa yielded a large number of further specimens and localities, which prompted us to revise the genus and describe the new species represented among the material collected after Marshall's description of *P. nidicola*.

Marshall [1] assigned *Philetaerobius* to the then subfamily Rhythirrininae as a "very aberrant form allied to *Gronops*", and it was also listed in this group by Schenkling & Marshall [4] and by

Louw [5] (classified as Brachycerinae: Rhythirrinini), whereas Alonso-Zarazaga & Lyal [6] placed it as *incertae sedis* in the subfamily Cyclominae, which includes Rhythirrinini as a tribe. Oberprieler [3] noted that *Philetaerobius* has adelognathous mouthparts and the scars of deciduous mandibular cusps, and he consequently transferred the genus to the subfamily Entiminae, suggesting an affinity with the South African genera *Mimaulus* Schoenherr, 1847 and *Protostrophus* Jekel, 1875, which are currently classified in the tribe Cneorhinini. However, the taxonomic affinities of the genus have never been properly investigated. With much more material in hand now, we discuss its significant characters and taxonomic position in more detail, as far as is possible in the context of the present (unsatisfactory) tribal classification of the Entiminae, globally and specifically in southern Africa.

2. Materials and Methods

Body length was measured in profile, from the anterior border of the eyes to the apex of the elytra. Ratios of the width and length of the rostrum, pronotum and elytra are between the maximum width and length of the respective parts in dorsal view. Dissected genitalia are preserved in glycerol in microvials pinned with the specimens or embedded in Solakryl BMX mounted on the same card as the respective specimen. The photographs were taken using a Leica DFC500 digital camera mounted on a Leica M205C microscope, combining ("montaging") image stacks in Leica Application Suite 4.4.0., and using a Nikon P 6000 digital camera mounted on a Wild MDG17 microscope, combining image stacks with the software program Zerene Stacker. All images were slightly enhanced for contrast and brightness, as necessary, in Adobe Photoshop CS3.

Sequences of the mitochondrial gene *COX1* were obtained for *P. nidicola* using the method described by Meregalli et al. [7] but using the primers of Folmer et al. [8] as modified by Astrin & Stüben [9].

Label data were generally recorded *verbatim*, with a slash (/) indicating separate lines on a label and a double slash (//) indicating different labels on a pin, except for those wrong coordinates of localities that were corrected where needed. This applied in particular to labels of specimens collected by Endrödy-Younga, which use a decimal-degree format but actually indicate minutes (and seconds). We checked and verified all given coordinates during compilation of the distribution map. Additional data were inserted where relevant and placed in square brackets.

The material examined (175 specimens) is housed in the following collections, identified by the following codens:

ANIC	Australian National Insect Collection, Canberra, Australia
BMNH	The Natural History Museum, London, United Kingdom
MMTI	Collection Massimo Meregalli, Torino, Italy
RBSC	Collection Roman Borovec, Sloupno, Czech Republic
SAMC	Iziko Museums of South Africa (formerly South African Museum), Cape Town, South Africa
SANC	South African National Insect Collection, Pretoria, South Africa
TMSA	Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa

3. Descriptions

Genus ***Philetaerobius*** Marshall, 1923

Philetaerobius Marshall, 1923: 546 [1]; Schenkling & Marshall, 1929: 20 [4]; Louw, 1998: 24 [5]; Alonso-Zarazaga & Lyal, 1999: 144 [6]; Oberprieler, 2010: 11 [3].

Type species: *Philetaerobius nidicola* Marshall, 1923, by original designation.

Diagnosis. Small Entiminae, with rostrum distinctly enlarged apicad, at apex broader than at base; frons large, indistinctly triangular, apically tectate, with 6–8 pairs of long setae; mandibles with spoon-shaped, vertical deciduous cusps; antennal scrobes narrow, straight, usually confluent on venter of rostrum; eyes in lateral view subtriangular to flatly reniform; antennal scapes significantly shorter than funicles; procoxal cavities nearer to posterior than anterior border of prothorax; metatibiae without corbels; tarsal claws single or inner one (outer one on protibiae) reduced to minute tooth at the base of other; tergite VII in both sexes with sclerotised margin, deeply V-shaped concave with straight sides and a row of coarse punctures; ventrite 1 in middle about as long as ventrite 2, ventrite 2 slightly shorter than 3–5 combined; gonocoxites small, flat, placed at angle to each other, without styli; sternite VIII of female with basal plate broadly triangular, its basal margin sclerotised, apodeme with apex transformed into a long transverse bar; spermatheca with collum longer than cornu, irregularly distorted, apically usually bulbous and curled over.

Redescription. Body length 2.7–4.2 mm. Integument of body black, legs and antennae blackish or reddish brown with apical parts of femora, basal parts of tibiae and clubs blackish, claws black, apical tibial spines yellowish brown. Vestiture of body consisting of very dense, tessellate, appressed scales, completely hiding integument; scales on elytra large and flat, 3 across one elytral interstria, irregularly angular, leaving only very slender spaces between them, sometimes concave and with irregular puncture in centre; scales on pronotum, head and rostrum, legs, antennae except clubs and underside slightly smaller than elytral ones, imbricate, with a distinct puncture in centre. Raised setae on whole body inconspicuous, very sparse and very short, pale to dark brownish, hardly visible in lateral view, shorter than diameter of one adherent scale; pronotum dorsally with anterior fringe of short semi-erect setae; antennal funicle, tibiae and tarsi with short, suberect to recumbent, subspatulate greyish setae. Color pattern of body various, in fresh specimens basic colour of pronotum and elytra brown, often with small irregular blackish spots on dorsal part of elytra and greyish on outer interstriae and two slender blackish longitudinal stripes on pronotum; in some specimens predominant color of pronotum and elytra dark brown to blackish, with irregular small spots of pale brownish and whitish scales, in others creamy with few scattered white scales; head and rostrum blackish, frons greyish, sometimes with pearly sheen; antennae and legs greyish; only vestiture of *P. garibebi* paler, grey with admixed blackish and greenish or bronze scales; underside white greyish, legs and underside in some specimens opalescent.

Rostrum 1.13× broader than long to 1.14× longer than broad, ventral part in dorsal view not visible below epifrons, in apical half to two-thirds distinctly widened apicad, at apex broader than at base and slightly narrower than head including eyes; in lateral view flat, at same level as head, anteriorly more or less abruptly declivous beyond antennal insertions. Epifrons broad, flat or longitudinally depressed, tapering anteriad with straight or weakly concave sides, at base as wide as interocular space, with slender median longitudinal stria along the whole length. Frons (Figures 1d, 2d, 4d, 6d, 8d) large, vaguely triangular to trapezoidal but not raised, reaching antennal insertions, squamose, border with epifrons indicated by lines between 2–4 pairs of long, stout setae; epistome distincty tectate, squamose, border with frons indicated by 2–3 pairs of setae, one anteriorly and more widely spaced and the others further back. Mandibles very small, not projecting, base squamose; deciduous mandibular processes (Figure 4e,f) vertical, flatly, bluntly asymmetrically spoon-shaped, with concavity on the outside and base, there thickened and strongly protruding, situated just inside of squamose base of mandible and leaving a narrow, vertical, subtriangular scar when broken off. Prementum with two setae. Antennal scrobes (Figures 1e, 2e, 4e, 6e, 8e) in dorsal view invisible; in lateral view slender, sharp, curved obliquely downwards in front of eyes, mostly (except in *P. garibebi*) shallowly to deeply confluent at back of venter of rostrum, creating a small flat median projection of venter (Figure 6e). Head broad, flat to slightly concave, with slender longitudinal stria continuing into median stria on epifrons; laterally with prominent, rounded projection partly covering eyes in dorsal view. Eyes moderately large, kidney-shaped to subtriangular in outline, flat to slightly convex, placed in about middle of head height in lateral view, in dorsal view hardly to distinctly prominent from outline of head. Antennal scapes short, hardly reaching anterior border of eyes when folded back, at apex distinctly narrower than clubs, weakly curved, faintly regularly enlarged apicad. Funicles 7-segmented, 1.2–1.3× longer than scape, with segment 1 longer than broad, 2 isodiametric to transverse and 3–7 cupular to transverse, progressively shorter and broader towards club. Clubs oval with segment 1 conspicuously largest.

Pronotum flat, narrow, 1.08× longer than broad to 1.10× broader than long, sides strongly rounded, broadest near the midlength, strongly tapered anteriad and more gradually posteriad, anteriorly slightly broader than posteriorly, anteriorly constricted. Disc finely and densely punctate, flat or slightly vaulted with faint, shallow, curved depressions next to faint median longitudinal elevation, sometimes concealed below appressed scales. Base faintly to strongly arched. Anterior border in lateral view straight, without ocular lobes or setae. Procoxal cavities contiguous, round, nearer to posterior than to anterior border but not reaching it; procoxae subglobular. Scutellar shield indistinct.

Elytra very flat or slightly convex, subrectangular, together 1.48–1.71× longer than wide, subparallel-sided or weakly and regularly curved, bases jointly strongly arched and embracing posterior part of pronotum, sides straight or moderately curved, at apex shortly elongated and rounded, with regularly rounded shoulders; 9-striate, striae distinctly narrowly punctate; interstriae flat to slightly convex, with single row of sparse, short, blunt, semi-erect setae but these often largely or totally absent on even interstriae, in all species except *P. garibebi* interstriae 1 and 3 raised at base and transversely connected, 5–8 also raised at base into shallow humeral callus, in *P. garibebi* all interstriae equally wide and even ones also with complete row of sparse but small, translucent setae. Mesocoxae semiglobular, mesoventral process narrow, about as wide as third of mesocoxal width, not reaching posterior margin of mesocoxae, prominently raised in *P. garibebi* but not in other species. Metacoxae semiglobular, not reaching elytra (cavities laterally closed by metaventrite), metaventral process arched, about twice as wide as metacoxa. Tergite VII short and broad, translucent, with well sclerotised narrow margins, deeply V-shaped concave with straight sides and row of coarse punctures; tergite VIII rounded, well sclerotised, coarsely punctate. Tergite VII and VIII identical in both sexes. Femora faintly swollen, unarmed. Tibiae moderately long and slender, straight, apical surface (surrounding tarsal socket) densely squamose; protibiae apically rounded, mucronate, with 6–7 short, fine, yellowish, sparse, well separate spines, with lateral margin straight and mesal margin faintly bisinuate, at apex enlarged; mesotibiae apically with 6, metatibiae with 8 subequal spines, mesotibiae also mucronate but metatibiae amucronate; metatibiae without corbels. Tarsi slender and long, underside with several sparse long setae, with segment 2 slightly broader than long, 3 faintly broader than 2, bilobed, segment 5 slightly shorter than 3; claws single or with minute remnant of second claw (on outside in protibiae, on inside in meso- and metatibiae), about 0.3× as long as major claw.

Abdomen ventrally stretched subtriangular, about 1.3–1.4× longer than broad; ventrite 1 in middle about as long as 2, 2 slightly longer than 3 + 4 combined, 5 short, apically rounded; suture between 1 and 2 faintly sinuate, very fine and inconspicuous, other sutures somewhat arched towards apex, fine and narrow; all ventrites regularly, finely and densely punctate but obscured by dense cover of scales; ventrites 1, 2 and 5 with irregularly scattered, semierect to recumbent, moderately long, subspatulate setae, ventrites 3 and 4 each with single transverse row of the same setae; ventrites 1 and 2 in male longitudinally shallowly concave, in female convex.

Genitalia. Penis moderately short, well sclerotised, tubular, curved, apex ventrally attenuate, dorsally below ostium with a tuft of two or more long subapical setae; inside in basal half with thick, single but complex sclerite about 0.5× as long as body (Figures 3a, 5a, 7a), in *P. garibebi* with tubular sclerite as long as body and protruding from base of penis (Figure 9a); temones 1.4–1.7× longer than body of penis and 4× longer than tegminal manubrium. Tegmen with slender ring without parameres, manubrium slightly shorter than diameter of ring. Sternite IX of male with spiculum gastrale moderately long, anteriorly curved and tapered, posteriorly with short, transverse basal plate; sternite VIII consisting of two sickle-shaped, sclerotised hemisternites. Gonocoxites lightly sclerotised, flat, short and broad, roundly subtriangular (in *P. garibebi* longer and laterally curved outwards), at about right angle to each other, apex with a row of 3–7 stout setae, stylus absent. Sternite VIII of female (Figures 3c, 5c, 7c, 9d) short and broad, basal plate broadly triangular, wider than long, in centre weakly sclerotised, often forming a round fenestra, basal margin thickened and sclerotised, apical margin thin, arcuate, medially usually with 1 pair of long stiff setae (sometimes 2 pairs, and 4 in *P. garibebi*) and some smaller setae, sometimes medially notched; apodeme about as long as basal plate, conspicuously T-shaped, caput forming a slender transverse rod as long as or longer than stem of apodeme. Spermatheca (Figures 3d, 5d, 7d, 9c) extraordinarily large and conspicuous, well sclerotised; cornu long, variously curved or bent, apically pointed or bluntly inflated; ramus short, subglobular, faintly longer than wide, sessile or on short stem, gland stalked, globular or elongate (in *P. garibebi*); nodulus not differentiated; collum distinctly longer than cornu, variously curved and twisted, apex usually bulbous and curled so that duct arises next to collum (in *P. garibebi* not curled and duct arising apically); spermathecal duct stiff, more or less straight, about as long as or shorter than spermatheca, inserted in middle of underside of bursa.

Distribution. *Philetaerobius* as known is endemic to the southern half of Namibia (the Erongo, Hardap and Karas regions) and the north-western parts of South Africa (the Northern and Western Cape provinces) (Figure 10).

Habitat and life-history. Marshall described *P. nidicola* from specimens found in a nest of the Sociable Weaver, a bird species endemic to southern Africa and occurring from central and south-eastern Namibia southwards through south-western Botswana into the Northern, North-West and Free State provinces of South Africa [10]. Two additional short series of specimens have been collected from such nests, at least one evidently representing the same collecting event (see under *P. nidicola* below). However, all newer specimens have been collected in pitfall traps [2,11], sifted from plant debris beneath shrubs or collected from grasses [3]. Given also that the adults are wingless, it seems that the specimens collected from Sociable Weaver nests were carried into the nests with plant material collected by the birds to construct their nests. The flat body and cryptic coloration of all species except *P. garibebi* suggest a specialized lifestyle on the ground, under leaf litter or stones or in crevices in the soil, but *P. garibebi* appears to lead a more exposed way of life on plants, as other entimines generally do. The weevils have invariably been collected in xeric habitats, such as dry grassy plains adjacent to dunes [11], but little further is known about their habitats and nothing about the larvae and their hostplants and feeding sites. The deciduous mandibular cusps of teneral adults indicate that the weevils pupate in the ground and have soil-dwelling, root-feeding larvae like other entimines do. The peculiar, shovel-like shape of the deciduous cusps suggests a specialized mode of pupation, perhaps in loose sand rather than in firm soil as it occurs in other entimines, and possibly the larvae of *Philetaerobius* also lead a specialized way of life. Closer observation of the weevils in their habitats is required to properly assess their habits and life-history.

Remarks. *Philetaerobius* is a unique genus among the entimine fauna of southern Africa, differing most significantly from all other genera in the unusual shape of its spermatheca and sternite VIII of the female and, as far as known, of its deciduous mandibular cusps. Other characteristic features are the flat body shape, squamose epistome and frons, ventrally confluent or almost confluent scrobes, single or almost single tarsal claws, tubular internal sclerite of the penis, apical tuft of setae on the penis and tessellate scales arranged on the elytra in rosettes around the interstrial setae. The only entimine genus in southern Africa with a similar spermatheca is *Spartecerus* Schoenherr, 1834, to which *Philetaerobius* appears to be related on this account, although *Spartecerus* is very different in shape and other external features. A tubular internal sclerite of the penis also occurs in *Spartecerus* and, to a lesser degree, in *Mimaulus*, which furthermore has a similar rosette-like arrangement of scales on its pronotum and elytra. The likely relationships of *Philetaerobius* to these genera are explored in more detail below (see Discussion).

Philetaerobius can be regarded as a monophyletic taxon mainly on the shape of the apodeme of sternite VIII of the female, featuring a conspicuous transverse bar at its apex, and, as far as known, on the shovel-like mandibular processes, the squamose epistome and the apical tuft of setae on the penis. The structure of its spermatheca is also rather unique, differing from the similar one of *Spartecerus* in not having a nodulus differentiated at all. In *Philetaerobius*, *P. garibebi* occupies an isolated position, differing in several characters from all the other species (see description and key). Some of these characters appear to be more derived, e.g., the single claws and absence of humeri, whereas others seem more plesiomorphic, e.g., the shape of the elytra (especially at the base) and eyes, the long tubular penis sclerite and the development and setation of the gonocoxites and sternite VIII of the female. While these numerous differences may warrant placing *P. garibebi* in a separate genus, we prefer to assign it to *Philetaerobius* as it shares all the critical genital characters of the other species and evidently belongs to the same monophyletic taxon. When or if additional species of *Philetaerobius* are discovered and perhaps accentuate these differences, the taxonomic position of *P. garibebi* may be revised.

Key to the species of *Philetaerobius*

1. Body in lateral view dorsally gently convex, elytral declivity in apical third; eyes vertically aligned on head in lateral view; scrobes not confluent on underside of rostrum; body dorsally covered with greyish-white scales, partly with a pearl to coppery sheen; tarsal claws single; penis with long, thick, straight, simple, cylindrical internal sclerite..***P. garibebi* sp. n.**

\- Body in lateral view dorsally flat, elytral declivity in apical fifth; eyes obliquely to horizontally aligned on head in lateral view; scrobes confluent on underside of rostrum; body dorsally covered with mainly brown scales, admixed with some black and white scales arranged in rosettes; tarsal claws unequal, tiny remnant of second one present; penis with short, thick, dorsally open, apically double internal sclerite..2

2. Eyes in lateral view subtriangular, regularly tapered posteriad, with ventroposterior margin straight, in dorsal view almost flat, hardly protruding from outline of head; epifrons flat; pronotum slightly longer than broad; internal sclerite of penis with dorsal apical arm as long and about as thick as ventral arm; spermatheca with cornu thickened apicad, apex globular...***P. endroedyi* sp. n.**

\- Eyes in lateral view kidney-shaped, in posterior half abruptly tapered posteriad, with ventroposterior margin distinctly concave, in dorsal view faintly vaulted, protruding from outline of head; epifrons longitudinally depressed; pronotum slightly broader than long; internal sclerite of penis with dorsal apical arm shorter and thinner than ventral arm; spermatheca with cornu tapered apicad, apex acute...3

3. Rostrum shorter, 1.1× broader than long; elytra broader, 1.45–1.55× longer than broad, laterally at apex beak-shaped elongate; odd elytral interstriae more elevated than even ones on disc; funicle segments moniliform, well separated; internal sclerite of penis broad, dorsal arm divided into two laterally projecting teeth..***P. nidicola*** Marshall

\- Rostrum longer, 1.05× longer than broad; elytra slender, 1.6–1.7× longer than broad, laterally at apex regularly convex; elytral interstriae flat on disc; funicle segments cylindrical, closely approximated; internal sclerite of penis narrow, dorsal arm not divided into laterally projecting prongs..***P. louwi* sp. n.**

***Philetaerobius nidicola* Marshall, 1923** (Figures 1–3)

Philetaerobius nidicola Marshall, 1923: 547 [1]; Schenkling & Marshall, 1929: 20 [4]; Alonso-Zarazaga & Lyal, 1999: 144 [6]; Oberprieler, 2010: 11 [3].

Redescription. Body length 3.16–4.25 mm, lectotype 4.06 mm. Color pale brownish, elytra with only several dark brownish or blackish and whitish spots, whitish spots sometimes forming irregular lateral stripes on interstriae 6 and 7, blackish spots dominant sometimes in posterior declivity. Pronotum with two irregular dark brownish longitudinal stripes. Rostrum 1.05–1.13× broader than long, in basal half faintly tapering anteriad, in apical half distinctly enlarged anteriad, with straight sides; in lateral view short and robust. Epifrons evenly tapered anteriad along whole length, with straight to slightly convex sides, longitudinally shallowly regularly deepened along the median longitudinal stria. Scrobes shallowly confluent at back of venter of rostrum. Eyes in dorsal view vaulted, weakly prominent from outline of head; in lateral view slender, horizontal, kidney-shaped, tapered posteriad, with ventral margin concave. Antennae with funicle with segments well separated, bead-shaped; segment 1 conical, 1.1–1.2× longer than broad and 1.1–1.2× longer than segment 2; segment 2 1.1–1.3× broader than long to isodiametric; segments 3–5 1.1–1.5× broader than long; segment 6 1.2–1.6× broader than long; segment 7 1.4–1.7× broader than long. Clubs 1.6–2.1× longer than broad. Pronotum 1.07–1.18× broader than long, broadest at midlength, in lateral view flat to slightly convex, with swollen anterior margin. Elytra 1.45–1.57× longer than broad, parallel-sided, apically broadly rounded, evenly tapered posteriad; interstriae flat, only 1, 3 and 6 behind base more elevated than others, 1 also on declivity slightly elevated. Tarsi with segment 2 isodiametric to 1.3× broader than long, segment 3 1.1–1.3× broader than long and 1.1–1.2× broader than segment 2, onychium 1.1–1.2× longer than segment 3. Genitalia. Penis parallel-sided, in apical fifth regularly tapered with slightly convex sides, with apex truncate, in lateral view regularly curved, equal in width, in apical third regularly tapered with lengthened apex; internal sclerite with dorsal arm apically divided into 2 stout short teeth directed lateroposteriad but not reaching apex of ventral part (giving the appearance of a clove), ventral part dorsoapically raised into narrow spout. Gonocoxites flat to shallowly convex, spatulate, broader in apical half; apex broadly rounded, with 1–2 stiff setae; orientated at about 90–135° to each other. Spermatheca with cornu abruptly bent at basal third of its length, apically slightly narrowed and bluntly pointed, often slightly bent; ramus globular, shortly stalked; gland ovoid, ca. 2× broader than ramus, on narrow stalk of same length; collum long, more or less straight but with slight irregular bends along the length, apex bulbous and curled over; duct stiff, straight to faintly twisted, shorter than spermatheca.

Material examined (60 exx.). Types. Lectotype (here designated), ♂: Type [printed, rounded with red margin] / Philetaerobius nidicola, Mshl. TYPE [handwritten] / S. Africa [printed] / In nest of Social Weaver Bird (Philetaerus socius) [handwritten] / Pres. by Imp. Bur. Ent. Brit. Mus. 1923-253. [printed] / LECTOTYPUS *Philetaerobius nidicola* Marshall // Borovec, Oberprieler & Meregalli desig. 2018 [printed, red] (BMNH). Paralectotypes: 1 ♀: SYNTYPE [printed, rounded with blue margin] / Philetaerobius nidicola, Mshl. COTYPE [handwritten] / S. Africa, fr. nest of Sociable Weaver bird [handwritten] / G.A.K. Marshall Coll. B.M. 1950-255 [printed] / PARALECTOTYPUS *Philetaerobius nidicola* Marshall // Borovec, Oberprieler & Meregalli desig. 2018 [printed, red] (BMNH); 1 ♂, 1 ♀?: from nest of / Social Weaver / bird [handwritten] // Philetaerobius / nidicola, Mshl. / COTYPES. [in Marshall's hand] // Type / SAM/Ent / 3706 [on green card] / PARALECTOTYPUS *Philetaerobius nidicola* Marshall // Borovec, Oberprieler & Meregalli desig. 2018 [printed, red] (SAMC). Other specimens: 1 ♂, 8 exx.: TransKei / A. L. du Toit / 1910 [handwritten] // from nest of / Social Weaver / bird [handwritten] // *Philetaerobius / nidicola Mshl* [handwritten] // SAM-COL- / A048230 (SAMC); 6 exx.: [no locality], from thorn tree / bearing nest of / social weaver / bird [handwritten] // *Philetaerobius / nidicola Mshl* [handwritten] // SAM-COL- / A048229 (SAMC); 1 ♂: Hanover [31°4.100′ S 24°26.383′ E] / C. C. / Cronr. Schrein. / 1901 [handwritten] // *Philetaerobius nidicola Mshl* // SAM-COL- / A048227 (SAMC); 1 ♀, 5 exx.: Kenhardt [29°22.909′ S 21°11.211′ E] / 1911 // *Philetaerobius / nidicola Mshl* [handwritten] // SAM-COL- / A063585 (SAMC); 1 ♂: Kakamas [28°47.339′ S 20°38.214′ E] / Kenhardt Div. [typed] // R. F. Lawrence / May 1934 [underside of label] // SAM-COL- / A048228 (SAMC); 1 ♀: S. Afr. [Northern Cape], Richtersveld / Buffelsriv. Valley/29°33′ S 17°27′ E // 31.8.1976, E-Y: 1193 / groundtraps, 35 days / leg. Endrödy-Younga // groundtraps with / banana bait (TMSA); 1 ♂: [South Africa, Northern Cape], S.Afr., Namaqualand / Onseepkans–Kakamas / 28°52′ S 19°37′ E // 9.9.1976; E-Y:1244 / groundtraps, 24days / leg. Endrödy-Younga // groundtrap / with faeces bait (TMSA); 2 ♂, 5 exx.: [South Africa, Northern Cape], S.Afr., Namaqualand / Onseepkans–Kakamas / 28°52′ S 19°37′ E // 2.10.1976; E-Y:1280 / groundtraps, 12days / leg. Endrödy&Breyten. (TMSA, ANIC); 1 ♀: [South Africa, Northern Cape], S. Afr., Richtersveld / farm Haramoep / 29°06′ S 18°40′ E // 13.10.1976, E-Y: 1276 / cattle dung / Endrödy & Breytenb. (TMSA); 1 ♀: S. Afr. Cape [Northern Cape], Karroo / Struisputs farm / 30°02′ S 20°55′ E // 1.5.1985, E-Y: 2202 / under stones, plants / leg. M.-L. Penrith (TMSA); 1 ♀: SOUTH AFRICA, C. P. / 24 km W Springbok / 29°42′ S 17°44′ E / 10.ix.1986 / R. Oberprieler // collected off / *Zygophyllum / morgsana* (SANC); 1 ♂, 1 ♀: Gannapo[o]rt farm /

29°16′ S, 19°39′ E / 17.iii.[1988] // S. Afr. Cape // W. Wittmer (SANC); 1 ♀: RSA, Western Cape, 811 m / R 358 12 km S Kliprand / 30°40.169′ S, 18°42.597′ E / 30.x.2011, R. Borovec lgt. // sifted detritus and dead / leaves below / *Euphorbia dregeana* shrubs (RBSC); 1 ♂: RSA, Northern Cape, 541 m / 40 km S Springbok, Die Drif / 1 km from Koringhuis, sifting / 29°59.139′ S 17°51.875′ E / 31.x.2011, R. Borovec legit (MMTI); 1 ♂, 2 ♀, 4 exx.: **RSA Northern Cape** 757 m / Ca 2 km NE Nigramoep / 29°27.147′ S 17°37.968′ E / R. Borovec lgt. 15.xi.2016 / Sifting below *Euphorbia dregeana* (TMSA, RBSC, ANIC); 1 ♀, 1 ex.: **RSA Northern Cape** 545 m / W Anenous Pass / 29°14.475′ S 17°35.922′ E / R. Borovec lgt. 16.xi.2016 // Sifting of detritus died / leaves and branches / below shrubby *Euphorbia dregeana* (RBSC, ANIC); 2 ♀, 7 exx.: **RSA Northern Cape** 908 m / R355 SE Springbok / 29°43.641′ S 18°01.413′ E / Sifting below *Euphorbia dregeana* / R. Borovec lgt. 20.xi.2016 (RBSC, ANIC).

Distribution (Figure 10). The species occurs in the Northern Cape province of South Africa, from Namaqualand eastwards into the Great Karoo, apparently as far east as Hanover (near De Aar). It does not seem to occur north of the Orange River and also not in the Richtersveld; the two localities so-labelled (Buffelsrivier Valley and Haramoep) lie further south, the former west of Springbok and the latter near Goodhouse in the Riemvasmaak Community Conservancy. The distribution range of *P. nidicola* thus apparently does not overlap with those of *P. endroedyi* and *P. louwi*. The implied type locality of the species (“Transkei”, see below) is evidently erroneous as the Sociable Weaver does not occur in this region.

Habitat and life-history. The type and two other series of specimens in the SAMC were found in the communal nest of the Sociable Weaver (*Philetairus socius*, Ploceidae), but the species also occurs outside the range of this bird and more recently collected specimens have been taken on the ground in pitfall traps, among detritus under plants and under stones. A single specimen was beaten off a *Zygophyllum* bush, but this plant is unlikely to represent a host for the species. It remains to be seen whether *P. nidicola* may occur in Sociable Weaver nests (or other bird nests) more regularly and how the flightless specimens end up in such nests.

Derivation of name. Marshall [1] did not state how he derived the name of the species, but it is obviously formed from the Latin noun *nidus*, a nest, and the verb *colere*, to live or inhabit. A *nidícola* is a nest-dweller, and the species name is a masculine noun in apposition.

Remarks. Marshall [1] based his description of *P. nidicola* on five specimens. Two are housed in the BMNH, a male labelled “TYPE” and a female labelled “COTYPE”, and another two specimens are in the SAMC, glued in the top corners of a large card and labelled “COTYPES”. The space between these two specimens, with the remains of a ring of glue there, indicates that the card originally held a third specimen between the outer two, thus accounting for Marshall’s remaining fifth syntype. Although Marshall labelled the male in the BMNH as type, he did not designate a holotype in his description of *P. nidicola*, and we therefore here designate the male in the BMNH as lectotype and the other three existing syntypes as paralectotypes.

The lectotype is glued on a triangular card and lacks the protarsi and several segments of the other tarsi. It was dissected by someone (not by Marshall or us) as its ventrites are glued on a card, and a second triangular card holds a blob of glue but without any genitalia. A search by one of us (M.M.) in the drawer in which the specimen is housed failed to find the aedeagus, which is apparently lost. The paralectotype female in the BMNH, glued on a rectangular card, is missing the entire right front leg. It has also been dissected and the ventrites, tergites VII and VIII, spermatheca and slightly damaged sternite VIII are glued on another rectangular card placed beneath it. The two paralectotypes in the SAMC were not dissected; the one on the right of the card, glued on its back, appears to be a male and the other is possibly a female. Although study of the genitalia of at least one type specimen is desirable for unequivocal assignment of other specimens to *P. nidicola*, we chose not to attempt dissection of the only two remaining intact types due to the insufficient dissecting facilities in the SAMC during our (R.G.O.) visit there, instead dissecting a male from the longer series of specimens (SAM-COL-A048230) bearing the same host label as the paralectotypes and evidently representing the same collecting event and a female from the series of six specimens from Kenhardt (SAM-COL-A048229). The internal sclerite of the dissected male has the characteristic clove-type shape and the spermatheca of the dissected female is consistent with that of other specimens assigned to *P. nidicola* here.

Marshall (1923) provided no locality for *P. nidicola* in his description, and none of the types have such attached to their pins. However, a series of nine specimens in the SAMC (SAM-COL-A048230) with an identical host label (handwritten "from nest of Social Weaver bird"), thus apparently representing the same collecting event, is labelled as being from the Transkei, the former region in the Eastern Cape province of South Africa lying northeast of the Great Kei River. This region is far removed from the Northern Cape province as well as from the range of the Sociable Weaver and therefore cannot be regarded as representing a conceivable type locality for *P. nidicola*. The date on the label, 1910, is plausible, but it appears that a wrong locality label has been attached to this series.

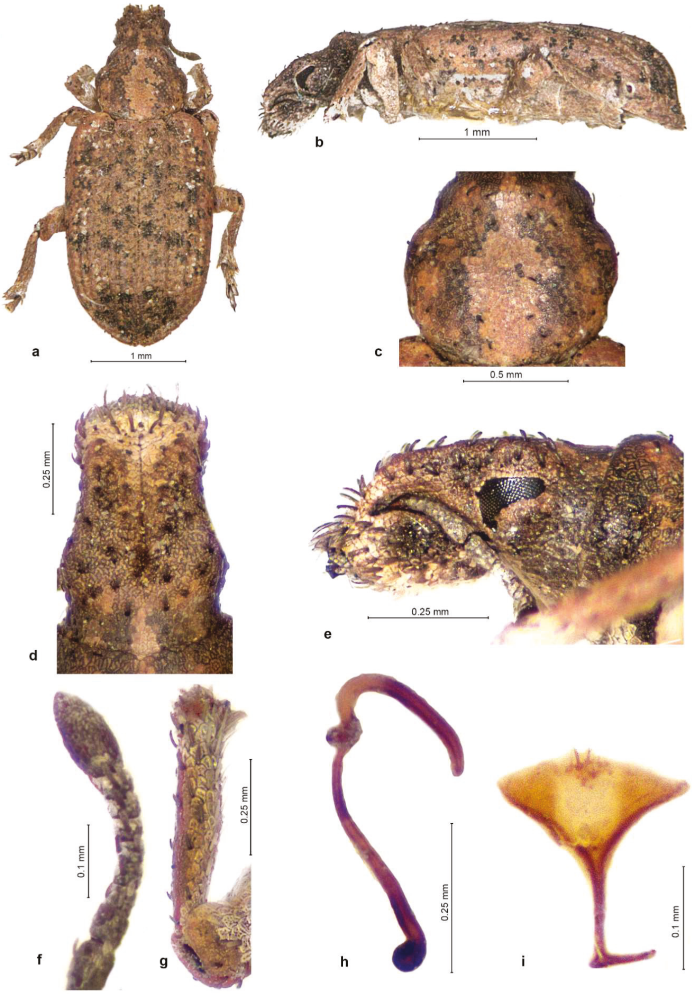

Figure 1. *Philetaerobius nidicola* Marshall. Lectotype ♂—dorsal habitus (**a**); left lateral habitus (**b**); pronotum, dorsal view (**c**); head, dorsal view (**d**); head, lateral view (**e**); right antenna, dorsal view (**f**); left protibia, dorsal view (**g**). Paralectotype ♀—spermatheca (**h**); sternite VIII (**i**).

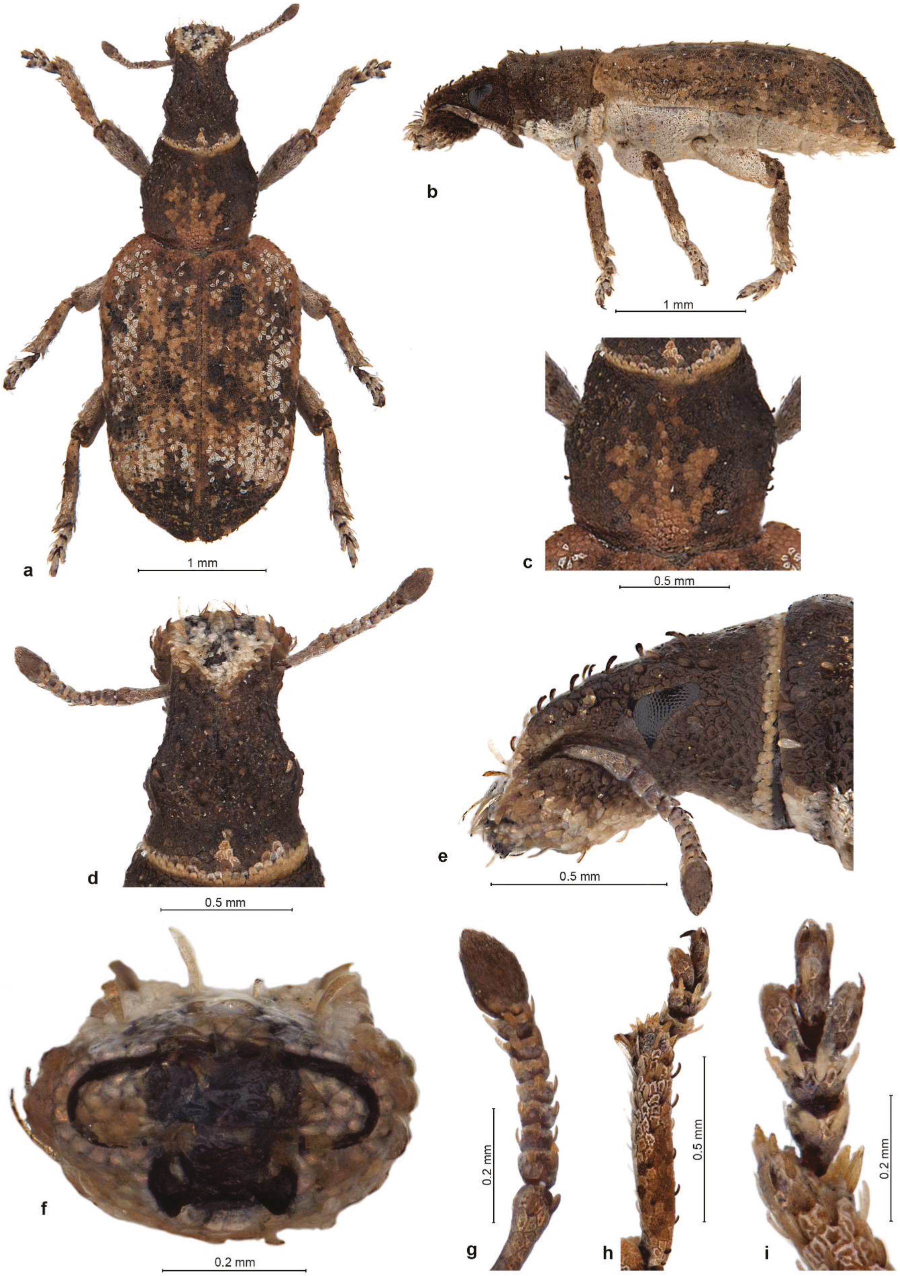

Figure 2. *Philetaerobius nidicola* Marshall (Gannapoort), ♂—dorsal habitus (**a**); left lateral habitus (**b**); pronotum, dorsal view (**c**); head, dorsal view (**d**); head, lateral view (**e**); rostrum, frontal view (**f**); right antenna, dorsal view (**g**); right protibia and -tarsus, dorsal view (**h**); right protarsus, dorsal view (**i**).

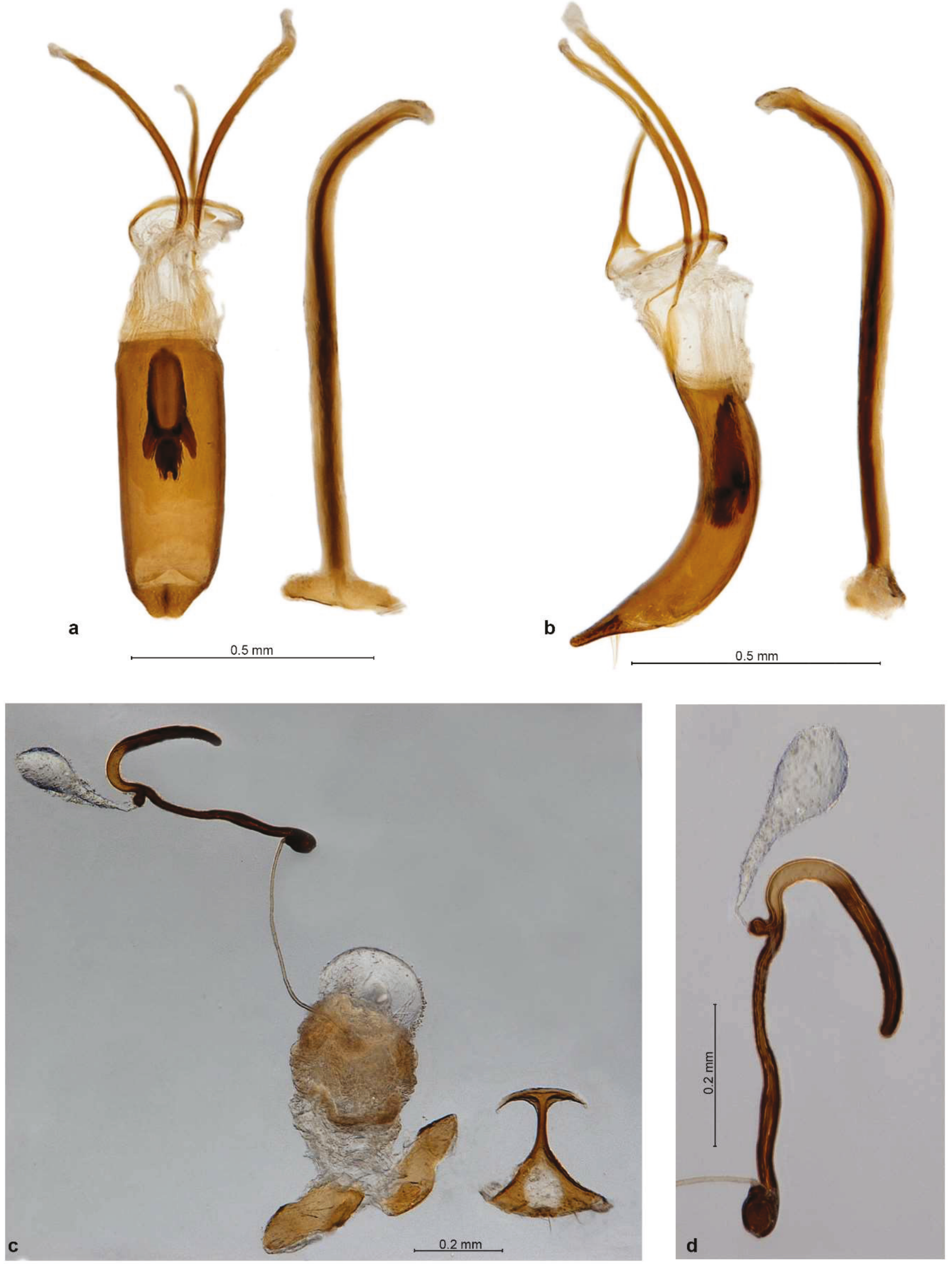

Figure 3. *Philetaerobius nidicola* Marshall, genitalia. ♂(Gannapoort), aedeagus and sternite IX, dorsal view (**a**); ditto, left lateral view (**b**); ♀(Springbok), ovipositor and sternite VIII, dorsal view (**c**); spermatheca, dorsal view (**d**).

Philetaerobius nidicola differs from the other species most conspicuously in the characteristic clove-type internal sclerite of its penis. Its spermatheca differs from that of *P. endroedyi* in having an acute cornu and from those of *P. louwi* and *P. garibebi* in having the collum more or less straight, not widely curved. Externally *P. nidicola* differs from the former two species (the other flat ones of the genus) mainly by its shorter and more robust rostrum, which is broader than long in dorsal view. In other characters it is somewhat variable. The elytra and pronotum vary from being slender to broader and in lateral view from flat to slightly convex, and the range of the length-width ratio of the antennal clubs is larger than in the other species, the shape varying from slender and spindle-shaped to oval.

The *COX1* sequence of a male from Nigramoep has been deposited on GenBank.

***Philetaerobius louwi* sp. n.** (Figures 4 and 5)

Philetaerobius nidicola: Louw, 1986: 310 [2].

Description. Body length 3.16–4.50 mm, holotype 4.05 mm. Integument black but densely covered with tessellate scales, these mostly pale orange-brown or greyish in color but on pronotum and elytra also irregularly scattered black and whitish scales, arranged in partial or complete rosettes around strial punctures on lateral and posterior parts of elytra, and white scales sometimes forming a large drop-shaped macula on pronotal disc. Rostrum 1.04–1.06× longer than broad, in basal half faintly narrowing anteriad, in apical half distinctly widening anteriad; in lateral view moderately short and robust, abruptly declivous in front of antennal insertions. Epifrons inflated, sides straight but slightly converging anteriad, disc longitudinally deeply trough-shaped impressed towards a narrow median stria. Scrobes shallowly confluent at back of venter of rostrum. Eyes flat but slightly curved, in dorsal view barely visible below broad and raised forehead; in lateral view narrowly elongate, horizontal, anteroventrally extended into acute angle, ventral margin concave and raised on blunt canthus from posterior and ventral part of head. Antennae with funicle segments cupular, closely approximated; segment 1 more cylindrical, 1.1–1.2× longer than broad and 1.1–1.2× longer than segment 2, segment 2 1.1× broader than long, segments 3–5 1.2–1.3× broader than long, segment 6 1.4–1.5× broader than long, segment 7 1.6–1.7× broader than long. Clubs 1.6–1.7× longer than broad, very compact. Pronotum 1.06–1.16× broader than long, broadest at midlength, sides rounded; in lateral view flat with swollen anterior margin. Elytra long and slender, together 1.61–1.71× longer than broad, broadest at basal part and slightly, regularly tapered posteriad, base deeply emarginate and embracing base of pronotum, broadly rounded at apex; interstriae mostly flat, 3, 5 and 7 slightly roundly raised, 1 also raised on declivity, only just behind basal margin odd interstriae more elevated than even ones. Tarsi with segment 2 1.2× broader than long, segment 3 1.2–1.3× broader than long and 1.1–1.2× broader than segment 2, onychium 1.1× longer than segment 3. Genitalia. Penis parallel-sided, posteriorly abruptly truncate with narrow, attenuated, truncate apex, in lateral view regularly curved, basally slightly thicker than apically, posteriorly sharply tapered to narrow, flat ventral apex; internal sclerite narrowly navicular in dorsal view, in lateral view cleft in apical third, with dorsal arm shorter than ventral one and only about half as thick. Gonocoxites flat to shallowly convex, sublenticular, about equally broad throughout or slightly broader in apical half; apex broadly rounded, with 2–3 stiff setae; orientated at about 90–120° to each other. Spermatheca with cornu sharply curved into right angle at basal third of its length, nearly straight, apically usually shortly bent, blunt but not inflated; ramus small, globular, sessile or shortly stalked; gland elongate, without distinct stalk; collum very long (longer than spermathecal duct), strongly variously bent and coiled, often faintly hook-shaped, apex bulbous but not curled (insertion of duct rotated at most 90°); duct stiff, straight to slightly twisted, only about half as long as spermatheca.

Material examined (54 exx.). Types. Holotype, ♂: [Namibia, Erongo], S.W.Afr., Namib / Us Pass, Park Gate / 23°04′ S 15°35′ E // 15.11.1974, E-Y: 468 / groundtraps 70 days / leg. Endrödy-Younga // ground traps with / ferm.banana bait (TMSA). Paratypes. 3 ♀, 13 exx.: same data as holotype (TMSA, ANIC); 1 ♂, 1 ♀: South West Africa / ??? [obtained in 1973 from old school collection in Windhoek, probably collected on the Khomas Hochland] (ANIC); 2 exx.: [Namibia, Hardap], Bullspoort S.W.A. [24°8.943′ S 16°21.783′ E] / R. G. Strey (TMSA); 2 exx.: [Namibia, Hardap], S.W.Afr., Naukluft / Felseneck farm / 24°21′ S 16°00′ E // 25.10.1974, E-Y: 417 / groundtraps, 136 day / leg.

Endrödy-Younga (TMSA); 1 ♀: [Namibia, Hardap], S.W.Afr., Nauwkluft / Nauwkluft Park / 24°16′ S 16°15′ E // 26.10.1974, E-Y: 425 / groundtraps, 88 day / leg. Endrödy-Younga // groundtrap with / banana bait (TMSA); 1 ex.: [Namibia, Hardap], S.W.Afr., Nauwkluft / Naukluft Park / 24°16′ S 16°15′ E // 26.10.1974, E-Y: 428 / groundtraps, 88 day / leg. Endrödy-Younga // ground traps / unbaited (TMSA); 3 exx.: [Namibia, Erongo], S.W.Afr., Namib / Ganab water / 23°06′ S 15°32′ E // 1.11.1974, E-Y: 437 / groundtraps, 17 day / leg. Endrödy-Younga // ground traps with / ferm. banana bait (TMSA); 1 ex.: [Namibia, Erongo], S.W.Afr., Namib / Ganab NE range / 23°08′ S 15°36′ E // 18.11.1974, E-Y: 483 / groundtraps, 65 day / leg. Endrödy-Younga // ground traps with / ferm. banana bait (TMSA); 1 ♂: [Namibia, Hardap], S.Afr., Kalah. Park / Farm Mara / 25°25′ S 19°30′ E // 19.12.1974, E-Y: 513 / ground traps, 73 d / leg. Endrödy-Younga // ground traps / with meat bait (TMSA); 3 exx.: [Namibia, Erongo], S.W.Afr., Namib / Ganab NE range / 23°08′ S 15°36′ E // 1.3.1975, E-Y: 711 / groundtrap: 90 day / leg. Endrödy-Younga (TMSA); 2 exx.: [Namibia, Erongo], S.W.Afr., Namib / Us Pass, 10 km Park / 23°03′ S 15°40′ E // 5.6.1975, E-Y: 852 / groundtraps 88 days / leg. Endrödy-Younga // ground traps / with faeces bait (TMSA); 1 ♂, 2 ♀, 1 exx.: [Namibia, Erongo], S.W.Afr., Namib / Us Pass, 10 km Park / 23°03′ S 15°40′ E // 1.9.1975, E-Y: 900 / groundtraps, 75 day / leg. Endrödy-Younga (TMSA); 1 ♂, 2 ♀, 8 exx.: [Namibia, Erongo], S.W.Afr. KhomasHl. / Us Pass, 10 km Park / 23°03′ S 15°40′ E // 7.7.1978; E-Y:1472 / groundtraps, 3years / leg. Endrödy-Younga (TMSA); 3 exx.: [Namibia, Erongo], S.W.Afr., c. Namib / Ganab, N. E. Hillgap / 23°08′ S 15°35′ E // 7.7.1978, E-Y: 1470 / groundtraps, 3 years / leg. Endrödy-Younga (TMSA); 1 ♀: [Namibia], Wildheim Ost 384 / SE 2619 Bc [26°28′ S 19°34′ E] / KEETMANSHOOP / 26–29 October 1976 / S. Louw, M.-L. Penrith // H33608 (SANC).

Distribution (Figure 10). The species as known occurs in south-central Namibia, in the west along the edge of the Namib Desert from the Khomas-Hochland west of Windhoek southwards to the Naukluft, but also in the east along the western edge of the Kalahari Desert. It is probably distributed throughout south-central Namibia and may also occur in south-western Botswana and the Northern Cape province along the eastern border of Namibia, but its distribution range does not seem to overlap with that of *P. endroedyi* in the south-west and with that of *P. nidicola* in the south-east.

Habitat and life-history. Most specimens examined were collected in pitfall traps, some of which had been baited with fermented bananas or faeces, but it is unlikely that the weevils were attracted by the bait. Louw [2] recorded the species (as *P. nidicola*) to be common in the Kalahari in spring, occurring in large numbers on plains dominated by grasses and *Rhigozum trichotomum* (in 1976 at Wildheim Ost) [11]. It appears that the species is associated with grasses, but its larva and life-history remain unknown.

Derivation of name. *Philetaerobius louwi* is cordially named after the late Schalk van der Merwe Louw, Professor of Zoology and Entomology at the University of the Free State in Bloemfontein, South Africa, who collected 150 specimens of this species during an ecological study of ground-living Coleoptera in the Namib and Kalahari Deserts and who also made significant contributions to the taxonomy of other taxa of terricolous weevils in southern Africa. Schalk sadly and unexpectedly passed away while this paper was in the proof stage.

Remarks. This species is distinguishable from *P. nidicola* by its slender rostrum and elytra and from *P. endroedyi* by its kidney-shaped and vaulted eyes and longitudinally depressed epifrons. Its internal penis sclerite is also distinctive, being deeply cleft and with the dorsal arm shorter and narrower than the ventral one, and its spermatheca is characteristic in having a long, curved to twisted collum. It is one of three *Philetaerobius* species known from Namibia and apparently the most widespread and common one, *P. garibebi* and *P. endroedyi* being known from only a few specimens and occurring to the north and south of it, respectively.

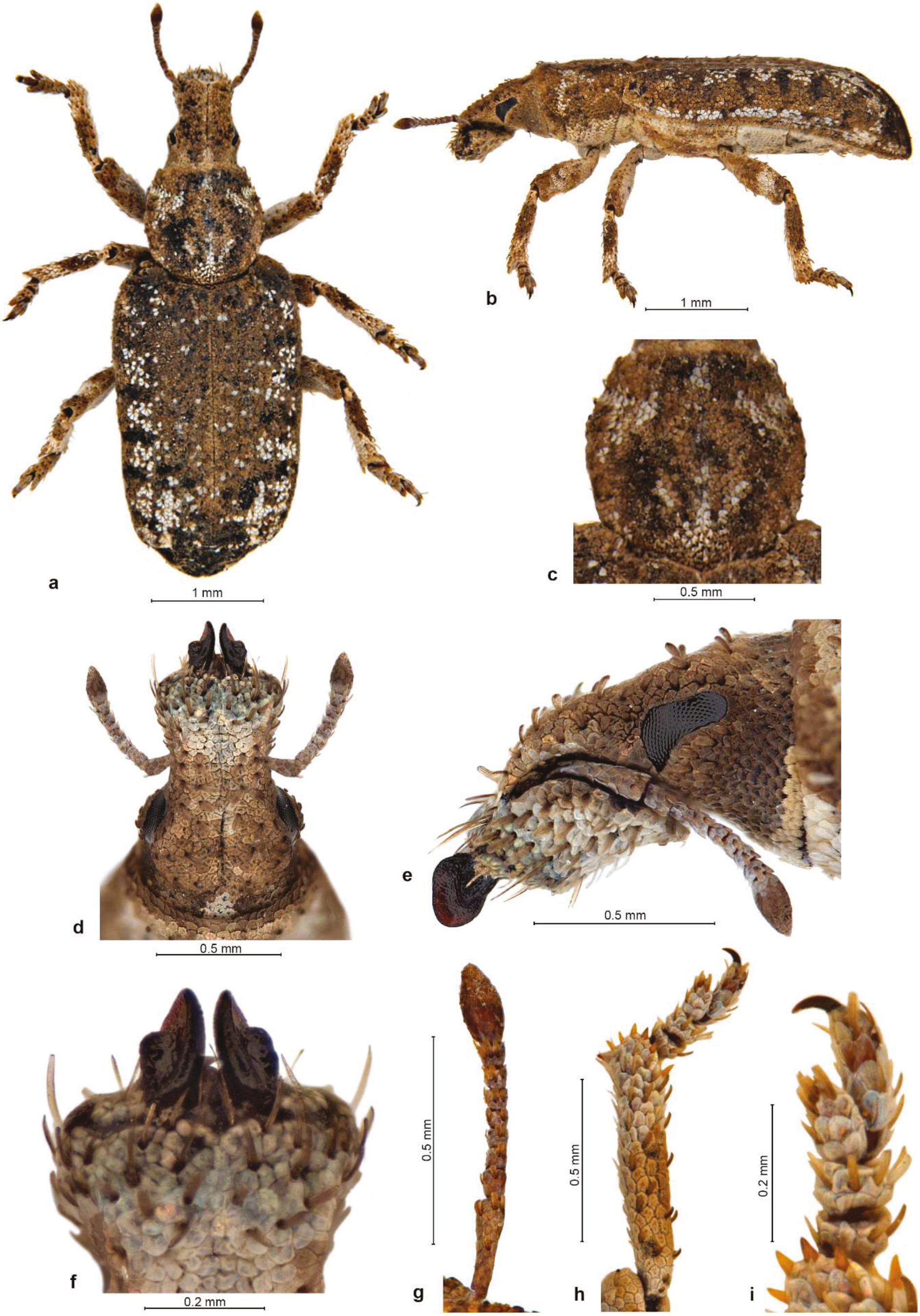

Figure 4. *Philetaerobius louwi* sp. n. (Us Pass), ♂—dorsal habitus (**a**); left lateral habitus (**b**); pronotum, dorsal view (**c**); head, dorsal view (**d**); head, lateral view (**e**); rostrum and mandibular cusps, dorsal view (**f**); right antenna, dorsal view (**g**); right protibia and -tarsus, dorsal view (**h**); right protarsus, lateral view (**i**).

Figure 5. *Philetaerobius louwi* sp. n., genitalia. ♂(SWA [Namibia]), aedeagus and sternite IX, dorsal view (**a**); ditto, left lateral view (**b**); ♀(Us Pass), ovipositor and sternite VIII, dorsal view (**c**); ♀(Us Pass), spermatheca, dorsal view (**d**).

***Philetaerobius endroedyi* sp. n.** (Figures 6 and 7)

Description. Body length 2.66–4.38 mm, holotype 4.38 mm. Integument black on body, dark testaceous on antennae and tarsi, densely covered with tessellate variegated golden brown and black scales, laterally and posteriorly on elytra admixed with a few white scales arranged in complete or partial rosettes around strial punctures. Rostrum 1.09–1.14× longer than broad, in basal third slightly tapering anteriad, in apical two-thirds widening anteriad; in lateral view moderately long and slender, abruptly declivous in front of antennal insertions. Epifrons dorsally tapering anteriad, sides almost straight, at declivity widening again, with faintly concave sides; disc flat, not impressed but with thin median stria along whole length. Scrobes deeply confluent at back of venter of rostrum. Eyes flat, in dorsal view narrowly visible below broad and raised forehead; in lateral view obliquely subtriangular, with ventroposterior margin straight, slightly raised on weak canthus from posterior and ventral part of head. Antennae with funicle segments subcylindrical to frustocone-shaped, closely approximated; segment 1 almost parallel-sided, 1.2× longer than broad and 1.5–1.6× longer than segment 2; segment 2 isodiametric to 1.1× longer than broad; segments 3–5 1.1–1.2× broader than long; segment 6 1.3–1.4× broader than long; segment 7 1.5× broader than long. Clubs oval, 1.4–1.6× longer than broad. Pronotum 1.03–1.08× longer than broad, broadest before midlength to anterior third, distinctly constricted behind anterior margin, in dorso-lateral view flat or faintly depressed on disc. Elytra together 1.56–1.67× longer than wide, parallel-sided, base deeply emarginate and embracing base of pronotum, broadly rounded at apex; interstriae flat to faintly convex, odd ones only in very short basal part somewhat more elevated than even ones and sutural ones elevated on declivity. Tarsi with segment 2 1.1× broader than long, segment 3 1.3–1.4× broader than long and 1.3–1.4× broader than previous segment, onychium 0.9× as long as segment 3. Genitalia. Penis subparallel-sided, posteriorly weakly attenuate, apex truncate, in lateral view regularly curved, equal in width, in apical third regularly tapered to ventrally placed apex; internal sclerite narrowly to broadly navicular in dorsal view, in lateral view cleft in apical quarter, with dorsal arm as long as ventral one and almost as thick. Gonocoxites flat to shallowly convex, subspatulate, broader in apical half; apex subrectangular, with 1–2 stiff setae; orientated at about 90–135° to each other. Spermatheca with cornu abruptly curved at basal third of its length, then evenly weakly C-shaped, apically inflated (twice thicker than at base) and broadly globular; ramus globular, broadly sessile to shortly stalked; gland elongate, medially constricted, not stalked; collum long but shorter than spermathecal duct, more or less straight but with slight irregular bends along the length, apex bulbous and tightly curled over (insertion of duct rotated 180°); duct stiff, straight to slightly twisted, shorter than spermatheca.

Material examined (59 exx.). Types. Holotype, ♂: **RSA Northern Cape** / Richtersveld 19.ix.2013 / rd to Akkedis pass 450 m / 28°09.880′ S 17°01.497′ E // Sifting of detritus, died / leaves and branches / below shrubby *Euphorbia* sp. / R. Borovec, M. Meregalli lgt. (TMSA). Paratypes: 1 ♂, 1 ♀, 7 exx.: same data as holotype (RBSC, MMTI, ANIC); 1 ♂, 1 ♀, 6 exx.: S. Afr. Richtersveld / Rooiberg Valley / 28°12′ S 17°07′ E // 4. 9. 1976; E-Y: 1217 / groundtraps, 30day / leg. Endrödy-Younga // ground traps with banana bait (TMSA); 3 ♀, 7 exx.: S. Afr., Richtersveld / GanakomRiv. Valley / 28°15′ S 17°07′ E // 5.9.1976; E-Y: 1223 / groundtraps, 35 days / leg. Endrödy-Younga // groundtrap / with banana bait (TMSA); 1 ♂, 8 exx.: **RSA Northern Cape** / Richtersveld 465 m / Koeroegab 19.ix.2013/28°17.298′ S 17°02.606′ E // Sifting of detritus, died / leaves and branches / below shrubby *Euphorbia* sp. / R. Borovec, M. Meregalli lgt. (RBSC, MMTI, ANIC); 1 ♀, **RSA, Northern Cape** / NE Eksteenfontein, 640 m // Pass E Jenkinskopf, 17.ix.2013 // 28°41.612′ S 17°16.559′ E (RBSC); 1 ♀, 3 exx., **RSA, Northern Cape** / S Eksteenfontein, 612 m / dir. Vioolsdrift, 23.ix.2013 / 28°51.957′ S 17°21.503′ E // Sifting of detritus, died / leaves and branches / below shrubby *Euphorbia* / R. Borovec, M. Meregalli lgt. (RBSC, MMTI); 1 ♂: **RSA Northern Cape** 463 m / Richtersveld NP 18.xi.2016 / Pass 2km S X RT 14 / 28°17.309′ S, 17°02.657′ E [R. Borovec lgt.] (ANIC); 1 ♂, 2 exx.: **RSA Northern Cape** 359 m / Richtersveld NP 19.xi.2016 / Gannakouriep / 28°23.558′ S 17°09.285′ E / R. Borovec lgt. sifting *Euphorbia* sp. (RBSC, ANIC); 1 ♀, 11 exx.: **South Namibia Karas** / 7 km N Rosh Pinah / 22.ix.2013 470 m / 27°53.711′ S 16°42.627′ E // Sifting of detritus, died / leaves and branches / below shrubby *Euphorbia dregeana* / R. Borovec, M. Meregalli lgt. (RBSC, MMTI, ANIC).

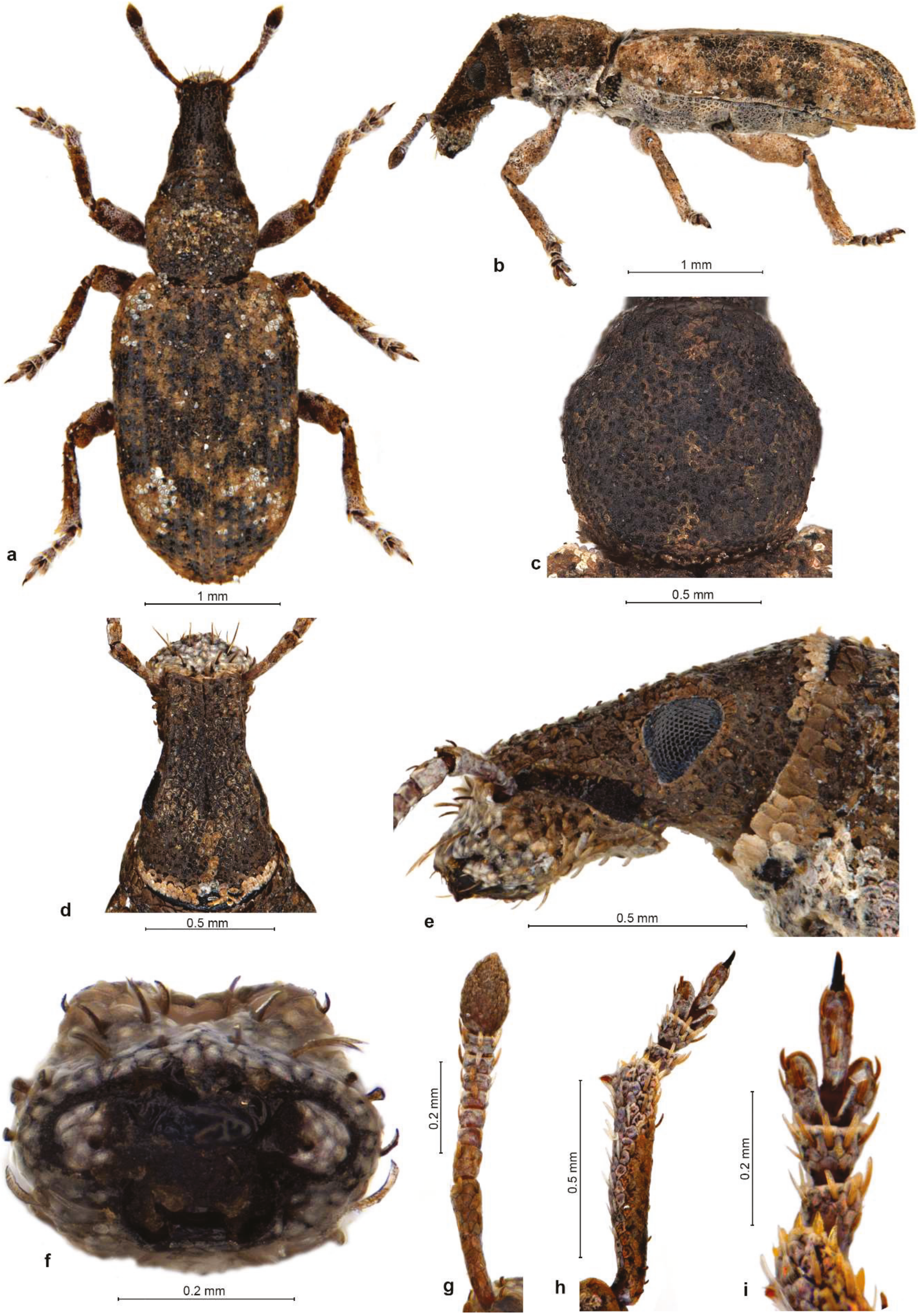

Figure 6. *Philetaerobius endroedyi* sp. n. (Koeroegap), ♂—dorsal habitus (**a**); left lateral habitus (**b**); pronotum, dorsal view (**c**); head, dorsal view (**d**); head, lateral view (**e**); rostrum and mandibles, frontal view (**f**); right antenna, dorsal view (**g**); right protibia and -tarsus, dorsal view (**h**); right protarsus, lateral view (**i**).

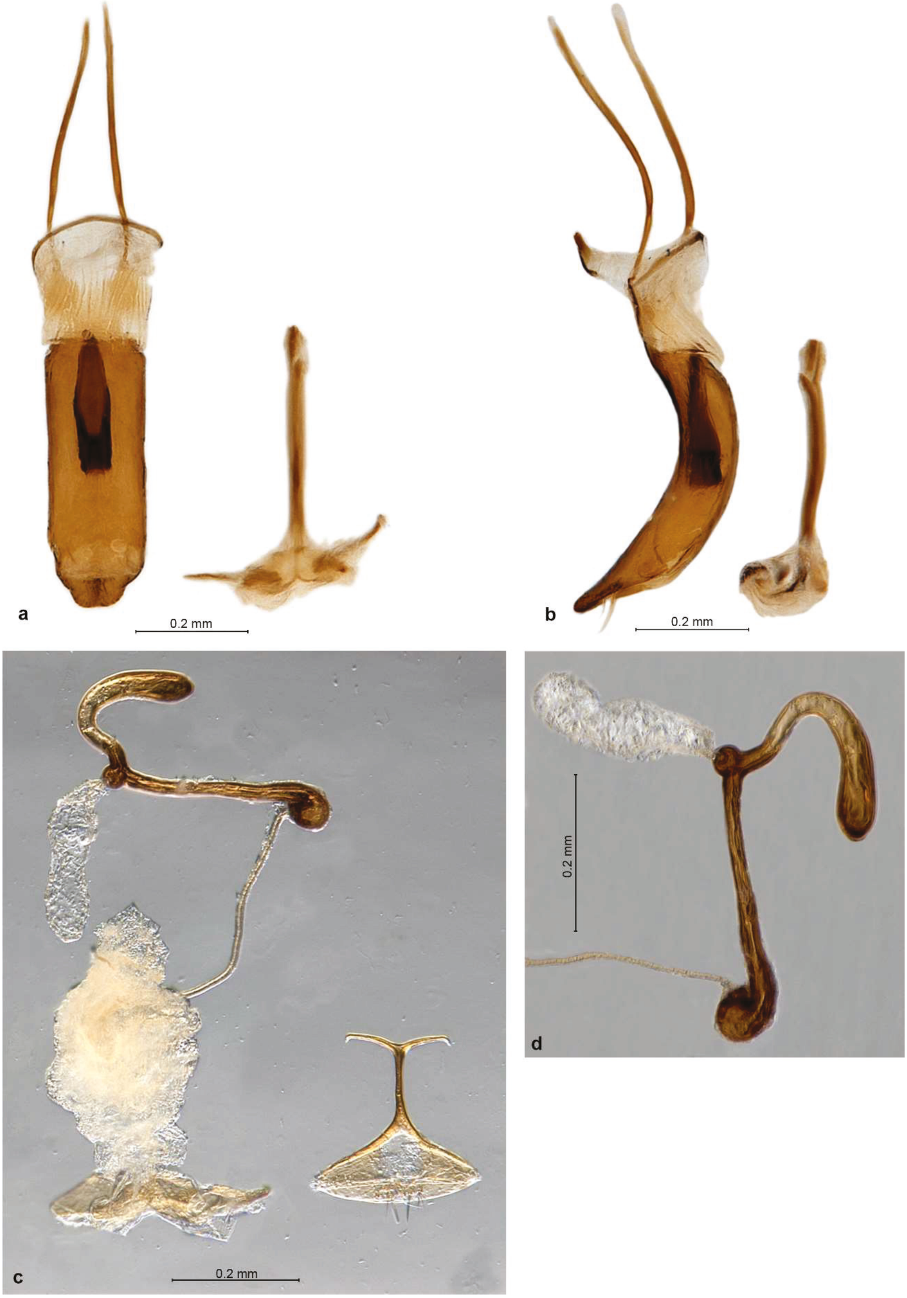

Figure 7. *Philetaerobius endroedyi* sp. n., genitalia. ♂(Rooiberg), aedeagus and sternite IX, dorsal view (**a**); ditto, left lateral view (**b**); ♀(Ganakom), ovipositor and sternite VIII, dorsal view (**c**); ♀(Ganakom), spermatheca, dorsal view (**d**).

Distribution (Figure 10). The species is known only from the Richtersveld area, from Eksteenfontein in the north-western part of the Northern Cape province of South Africa northwards across the Orange River to Rosh Pinah in the south-western part of Namibia. It appears not to overlap in distribution with *P. nidicola*, which occurs in Namaqualand slightly further south, nor with *P. louwi*, which occurs further north in Namibia.

Habitat and life-history. Most of the recently collected specimens were obtained by sifting detritus and dead branches under shrubby *Euphorbia* plants, *E. dregeana* and other species of similar appearance. This suggests that the weevils live among plant debris and walk around on the ground (perhaps at night). This probably accounts for them having been collected in pitfall traps, rather than being attracted to any bait placed in these.

Derivation of name. *Philetaerobius endroedyi* is named in memory of the late Sebestyén (Sebastian) Endrődy-Younga (1934–1999), erstwhile coleopterist at the former Transvaal Museum in Pretoria (now Ditsong Museum), who extensively collected beetles throughout South Africa and Namibia, mainly terricolous taxa such as Tenebrionidae but also many weevils, including several *Philetaerobius* specimens. In the formation of the species name *endroedyi*, we adopt the spelling of his surname as he used it in South Africa both in his publications and on his specimen labels, Endrödi-Younga, and as used in the names of many other species named after him.

Remarks. This species is readily distinguishable from the other three flat species by its subtriangular, dorsally flat eyes, flat epifrons, longer pronotum and spermatheca with an apically enlarged, blunt cornu. The sclerite in the penis is also characteristic, similar to that of *P. louwi* but posteriorly only cleft in the apical quarter, and the dorsal arm as long and about as thick as the ventral one.

***Philetaerobius garibebi* sp. n.** (Figures 8 and 9)

Philetaerobius undescribed species: Oberprieler, 2010: 11 [3].

Description. Body length 3.52–4.36 mm. Integument black on body, testaceous on antennae and tarsi, uniformly covered with tessellate scales, scales on dorsum, venter and legs pale grey with slight greenish (in males) or stronger bronze to coppery (in females) tinge, admixed with white scales and sparser black ones, these not forming distinct pattern but white scales often clustered around interstrial setae. Rostrum slightly (1.1×) longer than wide at base and apex, narrower in middle of length (at antennal insertions); in lateral view dorsal outline mostly flat, continuous with that of head, but more or less abruptly but only slightly declivous in anterior third. Epifrons broadly shallowly impressed in middle, with deep broad median sulcus from base to frons but largely obscured (closed) by scales. Scrobes not confluent at back of venter of rostrum. Eyes in dorsal view flat, not raised from outline of head, barely visible; in lateral view inversely ovate, with sharp ventral point. Funicle with all 7 segments distinct, segments 1 and 5–7 obconical, 2–4 subcylindrical; segment 1 1.4× longer than broad and 1.4× longer than segment 2, segment 2 1.4× longer than broad, segments 3–7 about as long as broad. Clubs 1.8× longer than broad. Pronotum 1.1× broader than long, broadest at midlength, in lateral view flat (males) to slightly convex (females), with swollen anterior margin. Elytra together 1.57× (males)–1.42× (females) longer than broad, laterally gently rounded, widest in apical third (males) to middle (females), base straight (male) to slightly emarginate (female) but not embracing base of pronotum. All interstriae very slightly convex, none raised above others, all with single row of sparse, short, translucent, recumbent setae. Tarsi with segment 2 1.18× broader than long, segment 3 about as long but broader (1.4×), onychium 1.16× longer than segment 3; claws single, without remnant of second claw. Genitalia. Penis stout, cylindrical, in dorsal view broadest at base, then narrowing fairly abruptly, middle portion subparallel-sided, apical part slightly flaring out, apex ventrally shortly, roundedly attenuate; in lateral view slightly arcuate, with base curved up and apex curved down, subparallel-sided except tapering down at apex and ending in narrow tip; internal sclerite thickly tubular, straight, longer than body of penis; temones very slender, about as long as body of penis. Tegmen very slender, without parameres, apodeme about half as long as temones. Gonocoxites longer, sinuately sclerotised with proximal end curved outwards, placed at >90 angle to each other, apex blunt, with a row of 7 stout setae. Spermatheca very long and slender, S-shaped; cornu sharply bent into acute angle just after junction with ramus, then straight before gently bent in apical third and tapering to blunt point; ramus small, globular, sessile, gland as long as cornu, with narrow stalk and elongate body; collum evenly curved, thicker near duct insertion, apex narrow, not bulbous or curled; duct stiff, straight, shorter than collum.

Material examined (2 exx.). Types. Holotype, ♂: "S.W.Africa/Namibia / 10 km E Karibib / 21°57′ S 15°57′ E / 10.iii.1987 / R. Oberprieler // collected / on grass" (SANC). Paratype, 1 ♀: same data as holotype (SANC).

Distribution (Figure 10)**.** The species is thus far known from a single locality in the western part of central Namibia.

Habitat and life-history. The only known specimens were collected clinging to the stems of green grasses.

Derivation of name. This species is named after its type locality, Karibib, in central Namibia, but using the original Nama name *‡garibeb*, which apparently means a place of preparing an edible plant (seemingly the fruits of the nara, *Acanthosicyos horridus*). The epithet *garibebi* is a latinized genitive singular noun derived from the Nama name.

Remarks. This species is quite different from all other *Philetaerobius* species, most obviously in its convex body, vertically aligned eyes, and predominantly greyish scales. It also differs in many additional features from the other three species (see description), but it shares the distinctive female genitalia and several other characters with these and we therefore place it in the same genus. In many of its features, such as the shape of its elytra, eyes, scrobes, spermatheca and internal sclerite of the penis, it appears to be less derived than the other species, but its single claws and total absence of humeri are evidently more apomorphic characters.

4. Discussion

Philetaerobius is a very unusual and enigmatic entimine genus. Its original placement in Rhythirrinini (as "Rhytirrhininae") as "allied to *Gronops*" [1] is evidently incorrect, not only because of its adelognathous mouthparts and deciduous mandibular cusps but also because its ovipositor does not conform with the "clawed" type (with large, curved, pointed styli) characteristic of the tribe Hipporhinini, in which *Gronops* is now placed [3]. Oberprieler [3] suggested an affinity of *Philetaerobius* with the southern African genera *Mimaulus* and *Protostrophus*, which have similarly squamose mandibles, connate tarsal claws and, at least in some species (e.g., *P. memorabilis* van Schalkwyk, 1968), also similarly flat and asymmetrical eyes. *Mimaulus* and *Protostrophus* are currently placed in the tribe Cneorhinini due to possessing metatibial corbels but no elytral humeri [12], but some *Protostrophus* species have only very faint or no corbels and this character alone is unsuitable both to determine the placement of a genus and to define a tribe in Entiminae, as it varies widely in the subfamily. The development of elytral humeri is an equally problematical character, in all weevils, as the reduction or absence of humeri is associated with the loss of wings, which has evolved many times in weevils. In *Philetaerobius* this character furthermore varies among the species, *P. garibebi* having no humeri but the other species broadly rounded ones (Figure 8a vs. Figures 1a, 2a, 4a, 6a). In van Emden's [12] key to the tribes of "Brachyderinae", *P. garibebi* therefore runs to Brachyderini but the other species run to Polydrusini. Both these tribes, however, differ in numerous other features from *Philetaerobius* and cannot feasibly accommodate it. The concepts of these and most other "brachyderine" tribes (as encapsulated in van Emden's key) are largely based on Palaearctic genera and generally compromised by the suites of characters exhibited by genera of other regions, such as southern Africa. In addition, no other "brachyderine" genus with a similar ovipositor and spermatheca is known to us. Comparison of *mt* cytochrome-oxydase-I sequences of *Philetaerobius nidicola* with those of genera from several entimine tribes from the Palaearctic region (retrieved from GenBank and BOLD) showed no supported relationships. Sequences of South African Entiminae were only available for a few as yet undescribed species of *Oosomus*, *Cycliscus*, *Phaylomerinthus* and *Nama* (Meregalli, unpublished data); also in analyses with these genera *Philetaerobius* clustered in a separate lineage.

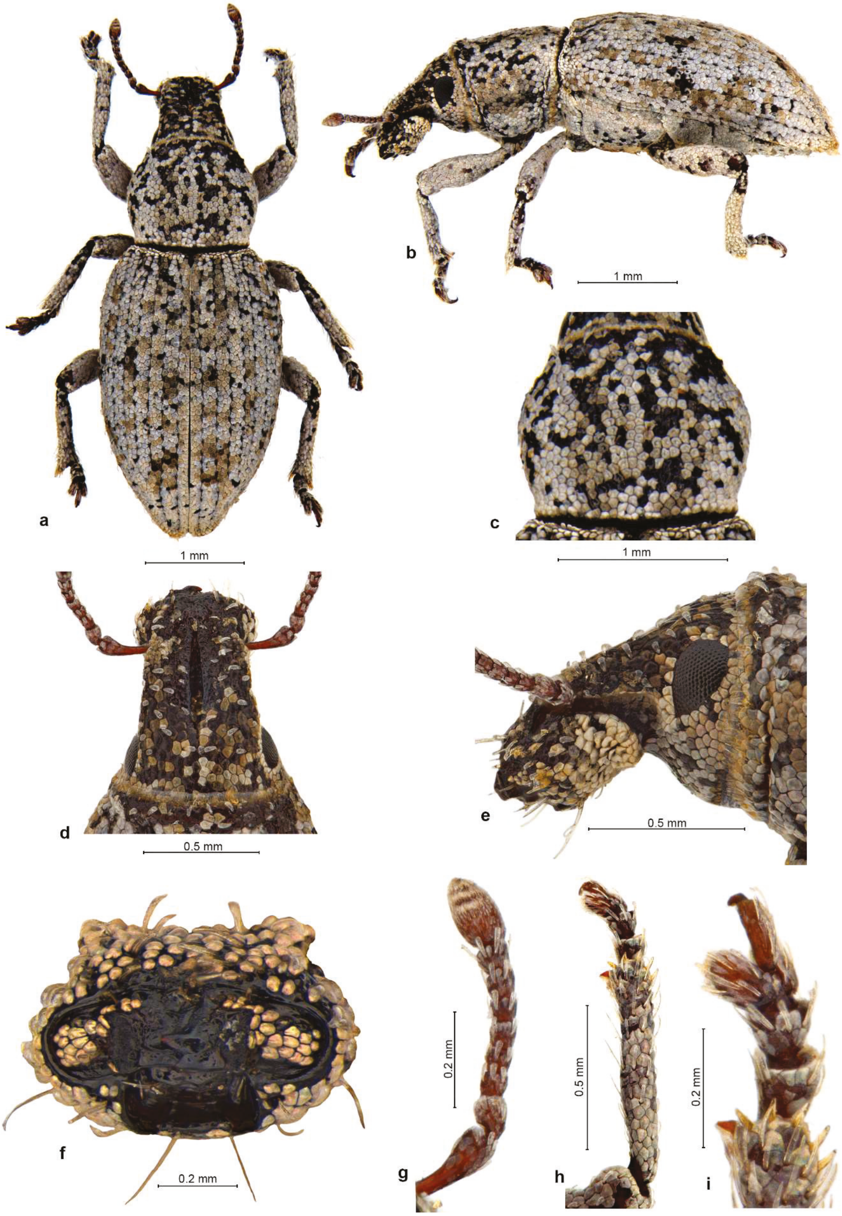

Figure 8. *Philetaerobius garibebi* sp. n. (Karibib), ♂—dorsal habitus (**a**); left lateral habitus (**b**); pronotum, dorsal view (**c**); head, dorsal view (**d**); head, lateral view (**e**); rostrum and mandibles, frontal view (f); right antenna, dorsal view (**g**); right protibia and -tarsus, dorsal view (**h**); right protarsus, lateral view (**i**).

Figure 9. *Philetaerobius garibebi* sp. n. (Karibib), genitalia. ♂, aedeagus and sternite IX, dorsal view (**a**); ditto, left lateral view (**b**); ♀, ovipositor and spermatheca, dorsal view (**c**); ♀, sternite VIII, dorsal view (**d**).

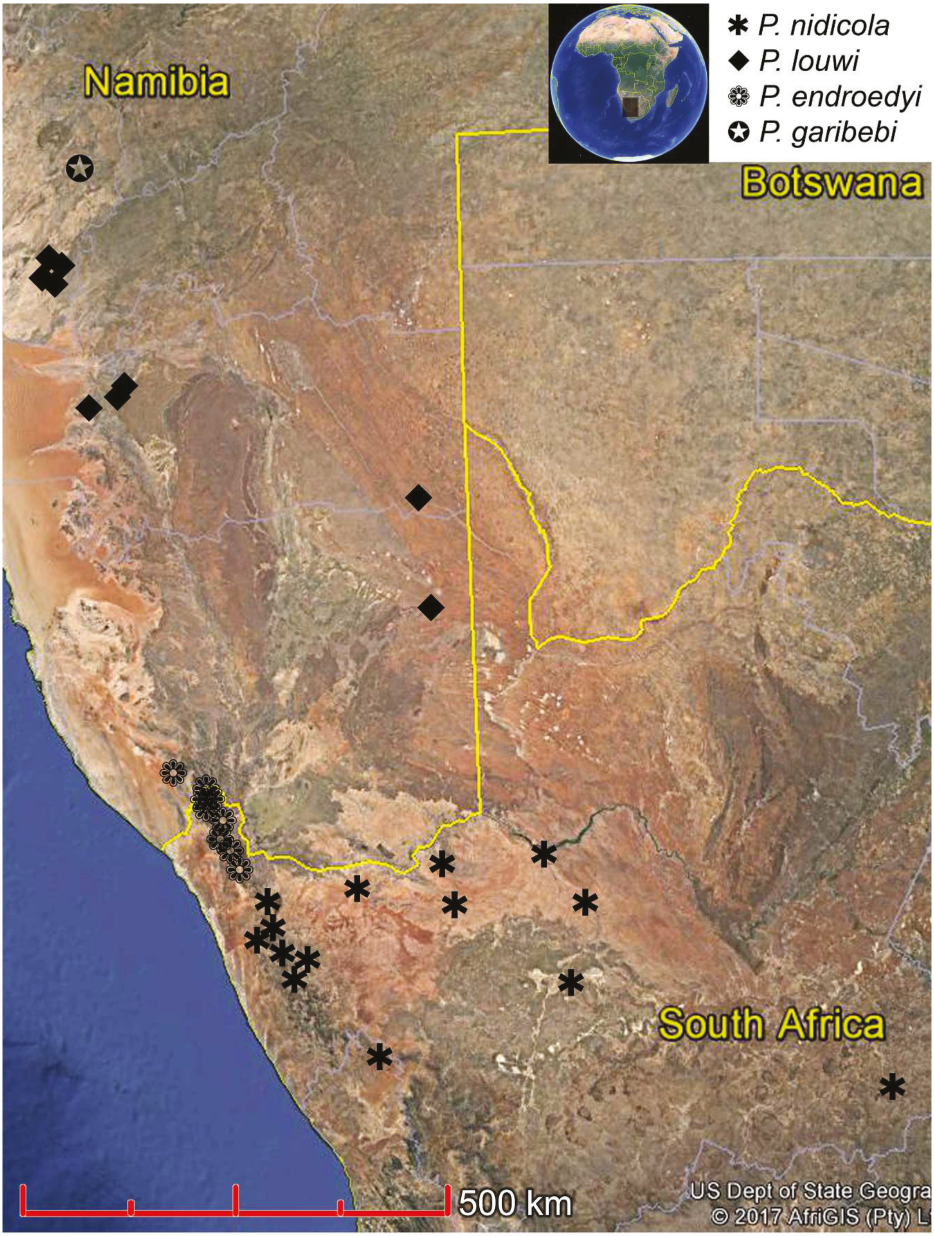

Figure 10. Recorded distribution of *Philetaerobius* in southern Namibia and north-western South Africa.

Of the southern African genera currently classified in Cneorhinini, *Mimaulus* (*M. papulosus* Fåhraeus, 1871) shares the most characters with *Philetaerobius*. It also has squamose, paucisetose mandibles, the rostrum dorsally separated from the head by a transverse sulcus, flat eyes situated under a distinct ridge ("eyebrow") and posteriorly raised on a canthus protruding from the head, white tessellate scales arranged in rosettes around short setae (on the pronotum), the apical surface of the tibiae (around the tarsal socket) squamose, a short thick penis with a large, strongly sclerotised, bow-shaped, tubular internal sclerite and the basal plate of sternite VIII of the female with a distinct basal margin. However, it differs from *Philetaerobius* foremost in having long, slender, pointed gonocoxites, a normal spermatheca, the basal plate of sternite VIII of the female without a central fenestra, a glabrous epistome and frons, narrow squamose metatibial corbels, basally connate claws, the penis without an apical tuft of setae and the temones short (third of penis body length), broad and flatly compressed. The similarities of the rostrum, mandibles and eyes between these two genera occur in other entimine genera too, whereas the differences in the genitalia, especially the different structures of the ovipositor and spermatheca, argue against a close relationship between *Mimaulus* and *Philetaerobius*.

To our knowledge, there is only one entimine genus in southern Africa that shares the peculiar genital structures of *Philetaerobius*, namely *Spartecerus*. This flightless, terricolous genus (Figures 11 and 12) has been classified in Leptopiinae in the past [13,14] and more recently in Tropiphorini [6], but it shares no significant characters either with the northern-hemisphere Tropiphorini (in the narrow sense; "Alophini") or with the mainly southern-hemisphere Leptopiini (though these are currently not properly delimited and defined), and its relationships among the Entiminae remain obscure. *Spartecerus* has never been properly studied, apart from a review of the 19 described species by Marshall [13] and a later description of another species from Namibia [14].

The most important character agreements between *Spartecerus* and *Philetaerobius* occur in the female genitalia. The spermatheca of *Spartecerus* is similarly slender and elongate, the collum up to ca. 4 × longer than the cornu and strongly S-shaped (Figure 12d) to doubly folded (Figure 11f) to compactly coiled (Figure 12g,i), the ramus large, broad and sessile with an elongated or bulbous gland, and a slight nodulus is differentiated. The gonocoxites (Figures 11e, 12c, 12e, 12f) are short and broad, jointly triangular, internally open, well to poorly differentiated into a proximal and a distal part and apically with a fringe of setae along the outside of the socket of the stylus (Figure 12c). The styli are large and broad, situated apically or ventro-apically, with an apical field or tuft of setae (numerous, short and dense to three long ones), and sometimes with a number of short, stout pegs laterally (Figure 12h), and their sockets are internally open. Sternite VIII of the female (Figures 11e, 12c, 12e, 12f) is short and broadly triangular, the basal plate with a large median fenestra and the short apodeme straight and symmetrical with an unmodified apex. The extremely elongate and twisted collum of the spermatheca and the fenestra of sternite VIII are clear character agreements with *Philetaerobius*, and the simpler gonocoxites of *Philetaerobius* are readily derivable from those of *Spartecerus* by a reduction of the sclerites and styli.

In the male genitalia, the penis of *Spartecerus* (Figures 11d, 12a,b) is short and thick, dorsally open (membranous) or not, apically extended into a flat ventral point without a median tuft of setae, the temones are slightly longer or shorter than the body of the penis, and inside there is a long, thick, straight, tubular sclerite. The tegmen has a pair of long, slim dorsal parameres. The character agreement with *Philetaerobius* lies foremost in the shape of the internal sclerite, which is near-identical to that of *P. garibebi*.

Agreement in external characters between *Spartecerus* and *Philetaerobius* occurs in the apically broadened rostrum (Figure 11c), squamose mandibles, dorsal sulcus separating rostrum from head, flattened eyes situated under a distinct "eyebrow", tessellate scales, squamose tibial apices and absence of metatibial corbels, but *Spartecerus* differs from *Philetaerobius* in a more globose shape, tuberculate sculpture, the frons elevated and posteriorly sharply carinate, often glabrous, the prementum squamose, the pronotum with ocular lobes and the prosternum impressed before the procoxae, and the claws long and free. While these differences suggest that the two genera are not very closely related and/or have evolved separately for some time, the similarity in especially the spermatheca indicates that a closer relationship exists between them than with any other southern African entimine genus.

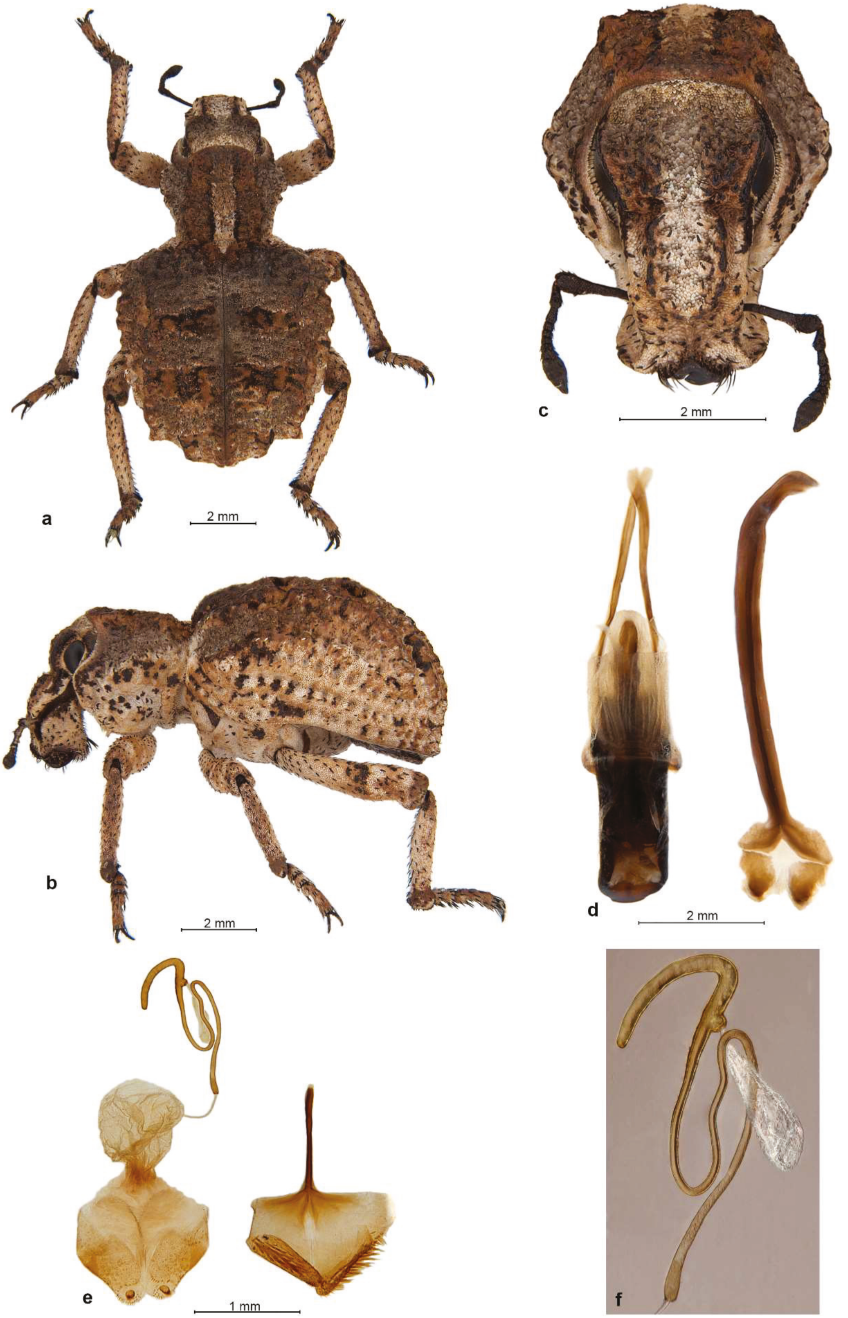

Figure 11. *Spartecerus umbrinus* Fåhraeus (South Africa, 5 km S Barkley West, 02.ii.1985, *ab larva* feeding on underground stem of *Bulbine* cf. *narcissifolia*, R. Oberprieler), habitus and genitalia. ♀, dorsal habitus (**a**); ♀, lateral habitus (**b**); ♀, head, frontal view (**c**); ♂, aedeagus and sternite IX, dorsal view (**d**); ♀, terminalia, dorsal view (**e**); spermatheca with gland, ventral view (**f**).

Figure 12. *Spartecerus* species, genitalia. *Spartecerus rudis* Fåhraeus (South Africa, Krugersdrift Dam, xii.1984, R. Oberprieler) (**a**–**d**). ♂, aedeagus, dorsal view (a), ditto, left lateral view (b); ♀, terminalia, dorsal view (c), spermatheca (d). *Spartecerus mendax* Péringuey (South Africa, Stanspruitfontein, 05.viii.1948, C. Koch) (**e**,**g**,**h**). ♀, terminalia, dorsal view (e); spermatheca (g); apex of gonocoxites with styli, dorsal view (h). *Spartecerus* sp. (Namibia, Etosha N. P., Okaukuejo, 20.xii.1977, R. Oberprieler) (**f**,**i**). ♀, terminalia, dorsal view (f); spermatheca (i).

Spartecerus is a taxonomically equally isolated genus in Africa as *Philetaerobius*. The only other somewhat similar genera (with traditional "leptopiine" characters, namely lateral scrobes and ocular lobes) are *Leptostethus* Waterhouse, 1853 and *Afroleptops* Oberprieler, 1988. The former was comprehensively revised by Thompson [15] and not regarded as particularly closely related to *Spartecerus*, differing especially in its female genitalia, and it is generally classified in its own tribe, Leptostethini [6]. *Afroleptops*, although described in the tribe Tanyrhynchini [16], differs from *Tanyrhynchus* Schoenherr and allies in numerous features, again particularly in the female genitalia, and appears more closely related to Australian leptopiines such as *Prypnus* Schoenherr, 1823 [16,17]. It shares no significant characters with *Spartecerus*. *Spartecerus* further differs from most other Entiminae in its larva having a subglobular antennal sensorium [18], not the flat, cushion-like one typical of the subfamily [19]. Neither *Spartecerus* nor *Philetaerobius* can thus be related to any other entimine genus in southern Africa or be satisfactorily accommodated in any entimine tribe as presently constituted, and we therefore treat them both as *incertae sedis* in the subfamily.

The life-history and hosts of *Spartecerus* are poorly known, but it appears that the larvae consistently feed on the underground bulbs of small geophytic monocotyledons. Voss [14] recorded *S. mendax* Péringuey, 1888 having been collected on bulbs (*an Zwiebeln*) in Namibia, and Louw [18] mentioned that the larvae feed semi-endophytically on bulbs of smaller monocotyledons. One of the authors of the present paper (R.G.O.) reared *S. umbrinus* (Fåhraeus, 1871) in 1984 from larvae found feeding on bulbs of *Bulbine* cf. *narcissifolia* (Asphodelaceae) just below the soil surface. The antenna of this larva was illustrated by Louw [18]. The adults are long-lived and overwinter under selected stones [20], but it is not known for how many years they may live. The association of *Spartecerus* with monocotyledonous hosts further supports the presumed association of *Philetaerobius* with this plant group, although it appears unlikely that the latter genus is also associated with geophytic Asparagales or similar monocotyledan orders rather than with grasses.

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Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Marshall, G.A.K. On new Curculionidae from South Africa. *Ann. Mag. Nat. Hist.* **1923**, *11*, 531–552. [CrossRef]
2. Louw, S. Periodicity in and ecological equivalence between the ground-living Tenebrionidae (Coleoptera) in the southern Namib and Kalahari ecosystems with notes on phylogenetic relationships. *Navors. Nas. Mus. Bloemfontein* **1986**, *5*, 301–324.
3. Oberprieler, R.G. A reclassification of the weevil subfamily Cyclominae (Coleoptera: Curculionidae). *Zootaxa* **2010**, *2515*, 1–35.
4. Schenkling, S.; Marshall, G.A.K. Curculionidae: Byrsopinae, Rhytirrhininae, Thecesterninae, Hipporhininae, Rhyparosominae. In *Coleopterorum Catalogus, Pars 106*; Junk, W., Schenkling, S., Eds.; W. Junk: Berlin, Germany, 1929; p. 62.
5. Louw, S. Solving the riddle: Combining life-history analysis and morphological comparison in weevil systematics. In *Taxonomy, Ecology and Distribution of Curculionoidea (Coleoptera: Polyphaga), Proceedings of the XX. International Congress of Entomology, Florenze, Italy, 28 August 1996*; Colonnelli, E., Louw, S., Osella, G., Eds.; Museo Regionale de Scienze Naturali: Torino, Italy, 1998; pp. 19–26.
6. Alonso-Zarazaga, M.A.; Lyal, C.H.C. *A World Catalogue of Families and Genera of Curculionoidea (Insecta: Coleoptera) (Excepting Scolytidae and Platypodidae)*; Entomopraxis: Barcelona, Spain, 1999; p. 315.

7. Meregalli, M.; Menardo, F.; Klass, K.D.; Cervella, P. Phylogeny of the *Saxifraga*-associated species of *Dichotrachelus* (Insecta: Coleoptera: Curculionidae), with remarks on their radiation in the Alps. *Arthropod Syst. Phylogeny* **2013**, *71*, 43–68.
8. Folmer, O.; Black, M.; Hoeh, W.; Lutz, R.; Vrijenhoek, R. DNA primers for amplification of mitochondrial cytochrome c ochridase subunit I from diverse metasoan invertebrates. *Mol. Mar. Biol. Biotechnol.* **1994**, *3*, 294–299. [PubMed]
9. Astrin, J.J.; Stüben, P.E. Phylogeny in cryptic weevils: Molecules, morphology and new genera of Western Palaearctic Cryptorhynchinae (Coleoptera: Curculionidae). *Invertebr. Syst.* **2008**, *22*, 503–522. [CrossRef]
10. Sinclair, I.; Hockey, P.; Tarboton, W. *Birds of Southern Africa*; Princeton University Press: Princeton, NJ, USA, 2002; p. 448.
11. Louw, S. The diversity and daily and seasonal activity of ground-living Tenebrionidae (Coleoptera) in the southern Namib and Kalahari ecosystems. *Cimbebasia* **1983**, *7*, 35–56.
12. Van Emden, F. A key to the genera of Brachyderinae of the world. *Ann. Mag. Nat. Hist.* **1944**, *11*, 503–532, 559–586. [CrossRef]
13. Marshall, G.A.K. On the curculionid genus *Spartecerus* Schönherr (Col.). *Proc. R. Entomol. Soc. Lond.* **1948**, *17*, 137–141.
14. Voss, E. Coleoptera Curculionidae partim. In *South African Animal Life*; Hanström, B., Brinck, P., Rudebeck, G., Eds.; Results of the Lund University Expedition in 1950–1951; Almqvist and Wiksell: Stockholm, Sweden, 1974; Volume 15, Chapter VI; pp. 395–479.
15. Thompson, R.T. Revision of the weevil genus *Leptostethus* Waterhouse, 1853 (Coleoptera: Curculionidae: Entiminae). *Cimbebasia Memoir* **1988**, *7*, 80.
16. Oberprieler, R.G. Revision of the Tanyrhynchini of continental Africa (Coleoptera: Curculionidae). I. Introduction and review of the genera, revision of the genus *Brachytrachelus* Schönherr and description of *Afroleptops* gen. nov. *Entomol. Mem. Dep. Agric. Water Supply Repub. S. Afr.* **1988**, *71*, 50.
17. Oberprieler, R.G. Systematic position and composition of the tribes Tanyrhynchini and Myorhinini (Coleoptera: Curculionidae). *Mem. Entomol. Soc. Wash.* **1995**, *14*, 155–167.
18. Louw, S. Systematics and biogeography of the subfamily Microcerinae (Coleoptera: Curculionidae): A re-evaluation based on larval morphology. *Mem. Entomol. Soc. Wash.* **1995**, *14*, 169–174.
19. Marvaldi, A.E. Higher level phylogeny of Curculionidae (Coleoptera: Curculionoidea) based mainly on larval characters, with special reference to broad-nosed weevils. *Cladistics* **1997**, *13*, 285–312. [CrossRef]
20. Louw, S. Notes on adult overwintering of Microcerinae and Entiminae (Coleoptera: Curculionidae) in southern Africa. *Coleopt. Bull.* **1988**, *42*, 155–156.

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Validation of the Names of Three Weevil Species Described by Borovec et al., The Enigmatic Weevil Genus *Philetaerobius* from Southern Africa: Definition, Affinities and Description of Three New Species (Coleoptera: Curculionidae: Entiminae); *Diversity*, 2018, *10*, 30

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Abstract: Three new species of the small entimine genus *Philetaerobius* Marshall, 1923 from southern Africa are described, *P. endroedyi* sp. n., *P. garibebi* sp. n. and *P. louwi* sp. n., with bibliographic reference to fuller descriptions and illustrations in the recent paper by Borovec et al. (2018) published in the journal *Diversity* 10 (2), 30, in which the names were not made available under the rules of the International Code of Zoological Nomenclature dealing with electronic publication. A lectotype is also here designated for *P. nidicola* Marshall, 1923.

Keywords: taxonomy; South Africa; Namibia; weevils; new taxa

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1. Introduction

The recent paper by Borovec et al. published in *Diversity* 10 (2) [1] was not in full compliance with the International Code of Zoological Nomenclature [2] regarding publication of online taxonomic papers. Article 8.5. states that, to be considered published [within the meaning of the code], "a work issued and distributed electronically must be registered in the Official Register of Zoological Nomenclature (ZooBank) (see Article 78.2.4) and contain evidence in the work itself that such registration has occurred" (Article 8.5.3.). Because the paper by Borovec et al. (2018) was not registered in ZooBank prior to publication and therefore evidence of registration was not included in it, the new taxonomic names proposed in the paper are not available under the code [3]. The purpose of this paper is to make those names available.

To fulfill the requirements of Article 8.5. of the code, this paper has been registered in ZooBank, with the LSID above, and the names of the species described below have also been registered, following recommendation 10B of the Code. Their LSIDs are given under each name. Nomenclatural acts other than new taxon names cannot presently be registered in ZooBank, but we also here validate the lectotype designation of *Philetaerobius nidicola* that was proposed by Borovec et al. [1].

To meet the requirements of Article 13.1.2. of the Code, the names listed below are accompanied by a bibliographic reference to their full descriptions and are thereby made available from the publication of this paper. The wording of Article 13.1.2. is somewhat ambiguous as to the status of descriptions based on bibliographic reference, so to avoid any further problems we have added below a brief description differentiating each taxon and a holotype designation with the repository identified; these are repeated from the original paper [1].

All label data are recorded *verbatim*, with a slash (/) indicating separate lines on a label and a double slash (//) indicating different labels on a pin.

2. New Nomenclatural Acts

Philetaerobius nidicola Marshall, 1923

Lectotype designation. Lectotype (here designated), ♂: "Type [printed on circular label with red border] // Philetaerobius nidicola, Mshl. / TYPE [handwritten] // S. Africa [printed] // from nest of / Social Weaver / bird / (Philetaerus socius) [handwritten] // Pres. by / Imp. Bur. Ent. / Brit. Mus. / 1923–253. [printed] // LECTOTYPUS / *Philetaerobius nidicola* Marshall / Borovec, Oberprieler & Meregalli / desig. 2018 [printed, red]" (Repository: The Natural History Museum, London, United Kingdom). See Borovec, Oberprieler & Meregalli, 2018: 7 [1] for further details of the specimen.

Philetaerobius louwi Borovec, Oberprieler & Meregalli, **sp. n.**

Philetaerobius louwi Borovec, Oberprieler & Meregalli, 2018: 12 [1] (not available)

http://zoobank.org/urn:lsid:zoobank.org:act:38D7D44A-4B8D-4ACC-8D85-608F3D749936

Description. This species is distinguishable from *P. nidicola* by its slender rostrum and elytra, from *P. endroedyi* sp. n. by its kidney-shaped, vaulted eyes and longitudinally depressed epifrons and from *P. garibebi* sp. n. by its flat shape, horizontal eyes and variegated brown, black and white scales. Its internal penis sclerite is also distinctive, being deeply cleft and with the dorsal arm shorter and narrower than the ventral one, and its spermatheca is characteristic in having a long, curved to twisted collum. See Borovec, Oberprieler & Meregalli, 2018: 12, Figures 4, 5 and 10 [1] for full description.

Holotype, ♂: "[Namibia, Erongo], S.W.Afr., Namib / Us Pass, Park Gate / 23 040 S 15 350 E // 15.11.1974, E-Y: 468 / groundtraps 70 days / leg. Endrödy-Younga // ground traps with / ferm.banana bait// HOLOTYPE / *Philetaerobius louwi* / sp. nov. Borovec, / Oberprieler, Meregalli / 2018 [on red card]" (Repository: Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa). Paratypes listed in [1].

Distribution. Namibia.

Philetaerobius endroedyi Borovec, Oberprieler & Meregalli, **sp. n.**

Philetaerobius endroedyi Borovec, Oberprieler & Meregalli, 2018: 15 [1] (not available)

http://zoobank.org/urn:lsid:zoobank.org:act:AE538A19-DD3C-4AC9-BB21-AEA3E1357824

Description. This species is distinguishable from *P. nidicola*, *P. louwi* and *P. garibebi* by its subtriangular, dorsally flat eyes, flat epifrons, longer pronotum and spermatheca with an apically enlarged, blunt cornu. From *P. garibebi* it also differs in its flat shape and variegated colour pattern. The sclerite in the penis is characteristic, similar to that of *P. louwi* but posteriorly only cleft in the apical quarter and the dorsal arm as long and about as thick as the ventral one. See Borovec, Oberprieler & Meregalli, 2018: 15–16, Figures 6, 7 and 10 [1] for full description.

Holotype, ♂: "RSA Northern Cape / Richtersveld 19.ix.2013 / rd to Akkedis pass 450 m / 28°09.880′ S 17°01.497′ E // Sifting of detritus, died / leaves and branches / below shrubby *Euphorbia* sp. / R. Borovec, M. Meregalli lgt. // HOLOTYPE / *Philetaerobius endroedyi* / sp. nov. Borovec, / Oberprieler, Meregalli / 2018 [on red card]" (Repository: Ditsong National Museum of Natural History (formerly Transvaal Museum), Pretoria, South Africa). Paratypes listed in [1].

Distribution. South Africa, Namibia.

Philetaerobius garibebi Borovec, Oberprieler & Meregalli, **sp. n.**

Philetaerobius garibebi Borovec, Oberprieler & Meregalli, 2018: 19 [1] (not available)

http://zoobank.org/urn:lsid:zoobank.org:act:8D5B9A05-D033-4CED-8DFC-7E3CADA92D94

Description. This species differs from all other *Philetaerobius* species most obviously in its convex body, vertically aligned eyes, predominantly greyish scales, single claws and genitalia, especially in the long tubular internal sclerite of the penis and the S-shaped spermatheca. See Borovec, Oberprieler & Meregalli, 2018: 19–20, Figures 8, 9 and 10 [1] for full description.

Holotype, ♂: "S.W.Africa/Namibia / 10 km E Karibib / 21°57′ S 15°57′ E / 10.iii.1987 / R. Oberprieler // collected / on grass // HOLOTYPE / *Philetaerobius garibebi* / sp. nov. Borovec, / Oberprieler, Meregalli / 2018 [on red card]" (Repository: South African National Insect Collection, Pretoria, South Africa). Paratype listed in [1].

Distribution. Namibia.

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Conflicts of Interest: The authors declare no conflict of interest.

References

1. Borovec, R.; Oberprieler, R.G.; Meregalli, M. The enigmatic weevil genus *Philetaerobius* from southern Africa: definition, affinities and description of three new species (Coleoptera: Curculionidae: Entiminae). *Diversity* **2018**, *10*, 30. [CrossRef]
2. International Commission on Zoological Nomenclature. INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE Fourth Edition [Incorporating Declaration 44, Amendments of Article 74.7.3, with Effect from 31 December 1999 and the Amendment on e-Publication, Amendments to Articles 8, 9, 10, 21 and 78, with Effect from 1 January 2012]. 2012. Available online: http://www.iczn.org/iczn/index.jsp (accessed on 26 July 2018).
3. International Commission on Zoological Nomenclature. Amendment of Articles 8, 9, 10, 21 and 78 of the International Code of Zoological Nomenclature to expand and refine methods of publication. *Zookeys* **2012**, *219*, 1–10. [CrossRef]

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Article

Molecular and Morphological Phylogenetic Analysis of *Naupactus* Dejean (Curculionidae: Entiminae) and Allied Genera: The Dilemma of Classification

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Abstract: *Naupactus* (Curculionidae: Entiminae) is the most speciose weevil genus of the tribe Naupactini. The main objective of this work is to recognize species groups within *Naupactus* and to analyze the relationships between this and other Neotropical genera. For this purpose, we compiled a combined data matrix of 60 terminal units corresponding to 40 species for which we recorded 812 molecular and morphological characters (763 and 49 respectively), which were analyzed by Maximum Parsimony and Bayesian analyses. The single tree obtained from each analysis was rooted with *Cyrtomon inhalatus*. The species of *Naupactus* were recovered as different monophyletic groups, some of them closer to other genera of Naupactini (*Lanterius*, *Teratopactus*, *Pantomorus* and *Parapantomorus*) than to species of the same genus. We conclude that *Naupactus* is non-monophyletic, even though most species can be recognized based on a particular combination of morphological characters, which are probably symplesiomorphic. To be consistent with the cladistic principles, some genera diversified in marginal areas of the *Pantomorus-Naupactus* complex should be synonymized with *Naupactus*; however, these nomenclatural changes may not ensure a generic definition based on synapomorphies. We prefer to be conservative about the current classification until more evidence is available. The only nomenclatural amendments proposed herein are the transference of *Naupactus inermis* Hustache to *Lanterius* and of *N. setarius* to *Symmathetes.*

Keywords: Neotropical region; broad-nosed weevils; Naupactini; *Pantomorus-Naupactus* complex; phylogeny; COI; combined evidence

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1. Introduction

Naupactini is one of the most diverse tribes of broad-nosed weevils in the Neotropical Region [1,2]. It includes about 500 described species, several of them with agricultural importance, that probably represent half of its real diversity. This tribe may not be monophyletic in its present definition because it includes some genera from Africa, New Guinea, North America and an extinct genus from the Baltic Amber [3], which probably do not belong to this tribe. However, all the Neotropical genera and a few ranging also in the Nearctic region (e.g., *Phacepholis* Horn, *Ericydeus* Pascoe) [4,5] are likely to have a more recent common ancestor, as suggested by previous phylogenetic analyses based on morphological and combined data [2].

The generic definition of *Naupactus* has varied according to different authors [6–11]. For example, Morrone [12] includes in *Naupactus* most of the South American species traditionally placed in *Pantomorus* Schoenherr [13]. The actual number of species is uncertain due to the lack of a comprehensive revision. According to the last checklists of American weevils [12–14], there are more than 200 nominal species of *Naupactus*. However, it is possible that some of them should be synonymized because they are morphotypes, geographic races or males and females of the same species, others should be transferred to other genera of Naupactini, while many new species still remain to be described.

A preliminary phylogeny of 54 genera of Naupactini based on 69 terminal units (type species or species representative of these genera) and a set of 100 morphological characters suggests that there are three main clades (I, II and III), the latter being the most diversified in species and genera and divided into three major subclades (A, B and C) [2]. The analysis revealed that *Naupactus* belonged to clade III and the fact that the three species analyzed (types of genera considered synonyms of *Naupactus*) were distributed in subclades B and C would indicate that the genus is not monophyletic [2]. Likewise, phylogenetic analyses of a small set of *Naupactus* from South America [15] and from Central and North America [16] showed that the genus is not monophyletic, with species being placed close to the root of the tree.

In this study, we increased the sample size by adding more species of *Naupactus* and other genera of the *Pantomorus-Naupactus* complex [2,4,15–18] to recognize well-supported groups in an attempt to gain further insight into a natural generic classification of the naupactines. The recognition of natural groups (either genera or species groups) is essential to understand the evolution of certain characters, e.g., oviposition habits and parthenogenetic reproduction [15,19] and for testing hypotheses about historical biogeography [1,20].

The specific objectives of this contribution are as follows:

1. To recognize different groups of *Naupactus* and to analyze the relationships among them and with other genera of the *Pantomorus-Naupactus* complex: *Aramigus* Horn, *Atrichonotus* Buchanan, *Eurymetopus* Schoenherr, *Floresianus* Hustache, *Galapaganus* Lanteri, *Hoplopactus* Chevrolat, *Lanterius* Alonso-Zarazaga and Lyal, *Pantomorus* Schoenherr, *Parapantomorus* Emden, *Phacepholis* Horn, *Symmathetes* Schoenherr and *Teratopactus* Heller.
2. To test the monophyly of *N. leucoloma* Boheman species group [10] and *N. xanthographus* (Germar) species group [21].

2. Materials and Methods

2.1. Taxon Sampling and Morphological Characters

Samples of adult specimens were obtained from Argentina, Brazil, Ecuador, Uruguay, Mexico and Central America (Dominica Island). The new specimens included in this paper were collected from different areas of Argentina and Brazil; they were captured on wild and cultivated plants using a beating sheet or a sweeping net. The material was stored at −80 °C or in 100% ethanol at 4 °C for molecular analysis. One leg of each specimen was removed for DNA sequencing. Most voucher specimens were deposited at the entomological collection of the Museo de La Plata, Argentina.

Externally visible and dissected structures were observed with a Nikon SMZ1000 stereomicroscope (Japan). For dissections we used standard entomological techniques [18]. The terminology used for morphological characters follows Marvaldi et al. [22], and Lanteri and del Rio [2].

We selected 58 specimens corresponding to 40 species and 12 genera of Naupactini recovered in Clade III, subclades B and C *sensu* Lanteri and del Río [2], plus species representative of two genera placed outside this clade, *Cyrtomon* Schoenherr and *Litostylus* Faust, which were used as outgroups. The taxon sampling includes almost all genera of the *Pantomorus-Naupactus* complex (except *Alceis* Billberg) and species of the main groups of *Naupactus.* For the phylogenetic analyses we consider only terminals for which COI sequences were available. Unfortunately, we were not able to get molecular sequences for the type species of *Naupactus*, *N. rivulosus* (Olivier) from South America.

The complete valid names, acronyms, geographic data and accession numbers for the terminal units are given in Table 1. Some species are represented by more than one specimen because they show different morphotypes and/or haplotypes.

Table 1. List of the 60 terminal taxa included in the phylogenetic analysis of the tribe Naupactini, valid names, acronyms used in the analysis, geographic data and genbank accession numbers and source for the terminal units. * The acronyms of *Lanterius inermis* and *Symmathetes setarius* correspond to the species names previous to the nomenclatural actions taken in this work.

Species	Acronyms	Location	Accession Numbers	Source
Cyrtomon inhalatus (Germar)	*Cyrtomon_inh*	AR, Entre Ríos, Victoria	MH537926	
Litostylus sp.	*Litostylus_sp*	Dominica Island, Warner, Caribbean	HQ891471.1	
Aramigus tessellatus Say, morph. *tessellatus*	*Aramigus_tes_tes*	AR, Buenos Aires, Otamendi	MH537929	
Aramigus tessellatus Say, morph. *pallidus*	*Aramigus_tes_pal*	AR, Buenos Aires, Punta Lara	MH537928	
Aramigus tessellatus Say, morph. *santafecinus*	*Aramigus_tes_san*	AR, Buenos Aires, La Plata	MH537927	
Aramigus conirostris (Hustache)	*Aramigus_con1*	UR, San José, Libertad	MH537930	
	Aramigus_con2	AR, Entre Ríos, Paraná	U25295	[23]
Atrichonotus taeniatulus (Berg), morph. *taeniatulus*	*Atrichonotus_tae_tae*	AR, Mendoza, Guaymallén	MH537919	[23]
Atrichonotus taeniatulus (Berg), morph. *pictipennis*	*Atrichonotus_tae_pic*	AR, Buenos Aires, Arrecifes	MH537931	
Eurymetopus birabeni Kuschel	*Eurymetopus_bir*	AR, Buenos Aires	AY790877	[23]
Eurymetopus fallax Boheman	*Eurymetopus_fal*	AR, Buenos Aires	AY790878	[23]
Floresianus sordidus Hustache	*Floresianus_sor1*	AR, Misiones	MH537932	
	Floresianus_sor2	BR, RG do Sul, Santa María	MH537933	
Galapaganus galapagoensis (Linell)	*Galapaganus_gal*	EC, Galápagos, San Cristobal	AF015914	[23]
Hoplopactus lateralis Arrow	*Hoplopactus_lat*	BR, São Paulo	MH537920	[23]
* *Lanterius inermis* (Hustache)	*N_inermis1*	AR, Misiones, Urugua-í	MH537908	IBOL MLPCU0411
	N_inermis2	AR, Misiones, Urugua-í	MH537909	IBOL MLPCU0412
	N_inermis3	AR, Misiones, PP Moconá	MH537910	IBOL MLPCU0407
Lanterius micaceus (Hustache), morph. *micaceus*	*Lanterius_mic_mic1*	AR, Misiones, Urugua-í	MH537911	IBOL MLPCU0420
	Lanterius_mic_mic2	AR, Misiones, Urugua-í	MH537912	IBOL MLPCU0418
Lanterius micaceus (Hustache), morph. *villosipennis*	*Lanterius_mic_vil*	AR, Misiones, Urugua-í	MH537913	IBOL MLPCU0427
Naupactus auricinctus Boheman	*N_auricinctus*	BR, São Paulo	MH537921	[23]
Naupactus cervinus Boheman	*N_cervinus1*	AR, Misiones, Cerro Azul	JX440490.1	[23]
	N_cervinus2	BR, Misiones, Oberá	GQ406843.1	[23]
	N_cervinus3	AR, Córdoba, Río Cuarto	GQ406828.1	[23]
Naupactus cinereidorsum Hustache	*N_cinereidorsum*	AR, Córdoba	AY770388	[23]
Naupactus condecoratus Boheman	*N_condecoratus*	AR, Misiones, PP Moconá	MH537914	IBOL MLPCU00406
Naupactus cyphoides (Heller)	*N_cyphoides*	AR, Misiones, San Ignacio	MH537942	
Naupactus dissimilis Hustache	*N_dissimilis*	AR, Misiones, Yacutinga	MH537940	
Naupactus dissimulator Boheman	*N_dissimulator1*	AR, Misiones, PP Las Araucarias	MH537915	IBOL MLPCU0041
	N_dissimulator2	AR, Buenos Aires, Punta Lara	JX440494	[23]
Naupactus leucoloma Boheman	*N_leucoloma1*	AR, Mendoza	MH537922	[23]
	N_leucoloma2	AR, Entre Ríos, Victoria	MH537934	
Naupactus minor (Buchanan)	*N_minor1*	AR, Entre Ríos	AY790881	[23]
	N_minor2	AR, Buenos Aires	EU264960	[23]
Naupactus navicularis Boheman	*N_navicularis*	BR, São Paulo	AY790882	[23]

Table 1. *Cont.*

Species	Acronyms	Location	Accession Numbers	Source
Naupactus peregrinus (Boheman)	*N_peregrinus*	AR, Entre Ríos, Concordia	MH537935	
Naupactus purpureoviolaceus Hustache	*N_purpureoviolaceus*	AR, Entre Ríos, Concordia	MH537936	
Naupactus stupidus Boheman	*N_stupidus*	ME, Oaxaca, Salina Cruz	GU565274	[23]
Naupactus sulfuratus Champion	*N_sulfuratus*	ME, Oaxaca, Salina Cruz	GU565270	[23]
Naupactus tremolerasi Hustache	*N_tremolerasi*	BR, RG do Sul, Santa María	MH537937	
Naupactus tucumanensis Hustache	*N_tucumanensis*	AR, Tucumán	MH537938	
Naupactus verecundus Hustache	*N_verecundus*	AR, La Pampa, Santa Rosa	AF211490	[23]
Naupactus versatilis Hustache	*N_versatilis1*	AR, CABA	MH537939	
	N_versatilis2	AR, Misiones, Teyú Cuaré	MH537916	IBOL MLPCU0117
Naupactus xanthographus (Germar)	*N_xanthographus*	AR, Buenos Aires, Punta Lara	AY790880.1	[23]
Pantomorus auripes Hustache	*Pantomorus_aur*	AR, Córdoba	AY770383	[23]
Pantomorus cinerosus (Boheman)	*Pantomorus_cin*	AR, Córdoba	AY770384	[23]
Pantomorus postfasciatus (Hustache) (misidentified as *N. ambiguus* [23])	*Pantomorus_pos1*	AR, Chaco, Resistencia	MH537917	
	Pantomorus_pos2	BR, RG de Sul, Santa Maria	MH537918	
Pantomorus ruizi (Brèthes)	*Pantomorus_rui1*	AR, Chubut, Trelew	MH537925	[23]
	Pantomorus_rui2	AR, La Pampa	AY770385	[23]
Pantomorus viridisquamosus (Boheman)	*Pantomorus_vir*	AR, Buenos Aires	AY770386	[23]
Parapantomorus fluctuosus (Boheman)	*Parapantomorus_flu*	BR, São Paulo	MH537941	
Phacepholis albicans (Sharp)	*Phacepholis_alb*	ME, Gerrero, Tecpan	GU565278	[23]
Phacepholis globicollis (Pascoe)	*Phacepholis_glo*	ME, Oaxaca, Salina Cruz	GU565273	[23]
Phacepholis viridicans (Sharp)	*Phacepholis_vir*	ME, Jalisco, Chamela	GU565277	[23]
**Symmathetes setarius* (Boheman)	*N_setarius*	BR, Mato Grosso	MH537923	[24]
Symmathetes setulosus Hustache	*Symmathetes_setu*	AR, Catamarca, Las Esquinas	MH537924	[24]
Teratopactus nodicollis (Boheman)	*Teratopactus_nod*	BR, São Paulo	AY770387	[15]

For each terminal, we recorded data for 49 discrete morphological characters, of which 37 correspond to external morphology and 12 to female and male genitalia; 35 characters are coded as double state (binary) and 14 as multistate. The list of morphological characters is given in Table 2 and the data matrix is shown in Table S1. When genitalia could not be examined (mainly because males are unknown), character states were scored with '?' and treated as missing data. For the illustrations of several characters, particularly those of male and female genitalia, see Lanteri and del Rio [2]. The acronyms used to describe the shape of the rostrum are as follows: WF, maximum width of forehead; WR, width of rostrum at apex excluding borders of scrobes.

The combined data matrix includes 60 terminal units by 812 characters (49 morphological and 763 molecular).

Table 2. List of the 49 morphological characters, character states and codes.

0. Rostrum, lateral margins: subparallel to slightly convergent anteriad (WF/WR less than 1.25×) (0); moderately convergent anteriad (WF/WR 1.25–1.50×) (1); strongly convergent anteriad (WF/WR more than 1.50×) (2).
1. Rostrum, lateral carinae: absent (0); present (1).
2. Mouthparts, prementum, long setae on external face: present (0); absent (1).
3. Rostrum, anteocular impression: distinct (0); indistinct (1).
4. Head, eyes: flat (0); convex (1); strongly convex (2); conical (3).
5. Head, post-ocular constriction: absent to very slight (0); present (1).
6. Antennae, shape of scape: clavate, broad (0); slightly capitate, slender (1).
7. Antennae, length of scape: not reaching hind margin of eye (0); reaching to exceeding hind margin of eye (1).
8. Antennae, relative length of funicle antennomeres 1 and 2: funicle antennomere 2 about as long as antennomere 1 (0); funicle antennomere 2 more than 1.5× longer than antennomere 1 (1).
9. Antennae, length of funicle antennomeres 4 to 7: distinctly longer than wide (0); about as long as to slightly longer than wide (1).
10. Pronotum, shape: subconical (0); subcylindrical (1).
11. Pronotum, convexity of disc (males): flat to slightly convex (0); strongly convex (1).
12. Pronotum, lateral longitudinal impressions: present (0); absent (1).
13. Pronotum, lateral tubercles: absent (0); present (1).
14. Pronotum, macrosculpture of surface: irregularly shaped and connected fovae (0); granulose (1); slightly granulose to smooth (2).
15. Scutellum, vestiture: present (0); absent (1).
16. Elytra, shape of scales: rounded (0); oval (1); piliform (2).
17. Elytra, setae: recumbent (0); erect (1).
18. Elytra, white, obliquely ascending stripes, on sides on posterior third: absent (0); present (1).
19. Elytra, white stripes along intervals 6 to 8: absent (0); present (1).
20. Elytra, brown, rectangular maculae on middle length of interval 3: absent (0); present (1).
21. Elytra, outline of base: strongly bisinuate (0); slightly bisinuate (1); straight (2).
22. Elytra, development of humeri: well-developed (0); reduced (1); absent (2).
23. Elytra, humeral tubercle: absent (0); present (1).
24. Elytra, declivity of disc: slightly to strongly ascending towards declivity (0); elytral disc not ascending towards declivity (1).
25. Elytra, height in lateral view: high (0); flat (1).
26. Elytra, proximity of striae 9 and 10: striae 9 and 10 confluent along posterior 2/3 (0) striae 9 and 10 slightly closer to each other along posterior 2/3 (1).
27. Elytra, presence of apical tubercles: absent (0); present (1).
28. Legs, separation of front coxae from each other (females): contiguous (0); separated from each other (1).
29. Legs, width of front femora less than 1.5× as wide as hind femora (0); more than 1.5× as wide as hind femora (1).
30. Legs, denticle on front femora: absent (0); present (1).
31. Legs, row of denticles on inner edge of tibiae: absent to indistinct in all tibiae (0); present in front tibiae only (1); present in the three pairs of tibiae (2).
32. Legs, mucro of tibiae: present only on front tibiae (0); present on front and middle tibiae (1).
33. Legs, metatibial apex: not to slightly widened (0); distinctly widened (apex about 1.5–2× as wide as minimum width of tibia) (1).
34. Legs, corbel at metatibial apex: well-developed (0); indistinct, metatibial apex thickened (1); absent (=metatibial apex simple) (2).
35. Legs, relative length of combs at metatibial apex: dorsal comb distinctly longer than distal comb (0); dorsal and distal comb about same length (1); dorsal comb shorter than distal comb (2).
36. Venter, denticles on ventrite 2 of male: absent (0); present (1).
37. Female terminalia, shape of sternite VIII (plate): subrhomboidal, not elongate (0); subrhomboidal, very elongate (1); suboval (2); subpentagonal (3).
38. Female terminalia, length of ovipositor (distal plus proximal gonocoxites): ovipositor shorter than abdominal length (0); equal to slightly longer than abdominal length (1).

Table 2. *Cont*.

39. Female terminalia, setae along each side of baculi, in their posterior half: absent (0); with three pairs of long setae (1); with rows of several setae (2).
40. Female terminalia, sclerotization of distal coxites: slightly sclerotized (0); strongly sclerotized, projected in a short nail-shaped piece (1); strongly sclerotized, projected in a long nail-shaped piece (2).
41. Female terminalia, styli: present (0); absent (1).
42. Spermathecal duct: straight (0); undulate to spiraled (1); curled (2).
43. Spermatheca, shape of corpus: subcylindrical (0); rounded (1).
44. Spermatheca, walls of corpus: slightly thickened at proximal portion (0); strongly thickened at proximal portion (1).
45. Spermatheca, shape and length of collum (=duct lobe): conical, short (0); subcylindrical, long (1); subcylindrical, long and with basal prominence (2).
46. Aedeagus, length of median lobe relative to its apodemes (=temones): median lobe about as long as its apodemes (0); about twice as long as its apodemes (1).
47. Aedeagus, shape of apex of median lobe: acute to rounded (0); arrow-shaped (1).
48. Aedeagus, sclerites of internal sac: absent or not *Cyrtomon* type (0); sclerites consisted of a pair of lateral struts on each side of a pyriform piece connected with ejaculatory duct = *Cyrtomon* type (1).

2.2. Molecular Data: DNA Assay and Sequencing

Cytochrome Oxidase I (COI) was chosen as molecular marker because is the most commonly used in Naupactini for analyses at species level. COI sequences derived from different sources. Most of them were obtained at the Instituto de Ecología, Genética y Evolución, Buenos Aires (IEGEBA-CONICET/UBA), or at the Biodiversity Institute of Ontario, University of Guelph, Canada, and they are available at the Barcode of Life Data Systems (BOLD) [23], Invertebrates from Argentina project, with the participation of A. Lanteri and M.G. del Río. Other sequences have already been published by some of us [15,16,24–27], and one sequence was downloaded from GenBank (see Table S1).

The DNA assayed at the IEGEBA-CONICET/UBA was extracted following the protocol of Sunnucks and Hales [28]. The COI mitochondrial gene was amplified using the following primers designed by Normark [29]: S1718 (5′-GGA GGA TTT GGA AAT TGA TTA GTT CC-3′) and A2442 (5′-GCT AAT CAT CTA AAA ATT TTA ATT CCT GTT GG-3′).

Amplification was carried out in a total volume of 50 uL with 50–100 ng of DNA used as template, 0.5 uM of each primer (Thermo Scientific, Rockford, IL, USA), 0.1 mM of each dNTP (Promega, Madison, WI, USA), 1.0 unit of Taq polymerase, 3.0 mM $MgCl_2$ and 1× reaction buffer (Thermo Scientific, Rockford, IL, USA). Amplifications were performed in a thermal cycler GeneAmp PCR System 2700 (Applied Biosystems, Inc., Gaithersburg, MD, USA) under the following conditions: 94 °C for 1 min, 35 cycles at 94 °C for 1 min, 46 °C for 1.5 min, and 72 °C for 1.5 min, and a final extension at 72 °C for 5 min. Each series of amplifications included a negative control with no template DNA. Double—stranded PCR products were separated by electrophoresis on a 1% agarose gel with TAE buffer containing GelRed TM (GenBiotech, Buenos Aires, Argentina). The PCR products were purified using an AccuPrep purification kit (Bioneer, Daejeon, Korea). DNA was sequenced using a 3130-XL Automatic Sequencer (Applied Biosystems, Inc., Foster City, CA, USA) at the Unidad de Secuenciación y Genotipificado (FCEyN, UBA, Buenos Aires, Argentina). The sequences obtained have been entered into GenBank under the accession numbers MH537908–42.

To avoid amplification of COI pseudogenes [30], sequences were translated according to the invertebrate mitochondrial genetic code in MEGA v. 5 [31] and examined using as reference amino acid sequences obtained for several insect orders [32]. A copy containing no frame-shifts or stop codons was assumed to be mitochondrial [33,34]. Sequence alignment was done using CLUSTAL W [35].

The molecular data matrix included 763 bp of the mtDNA COI gene corresponding to positions 210–973.

2.3. Phylogenetic Analyses

The combined and molecular data sets were analyzed using Maximum Parsimony (MP) and Bayesian approaches. For the MP method, a heuristic search with TBR branch swapping was applied to a series of 500 random addition sequences, retaining 30 trees per replicate, using TNT v1.5 [36]. Clade stability was evaluated by 1000 parsimony bootstrap replications [37] and support values over 40% were mapped onto internal nodes of the tree. All characters were considered as un-weighted and non-additive. For the MP trees we provided the total length (L), consistency index (CI) [38] and retention index (RI) [39].

The Bayesian analysis was performed using BEAST2 v2.4.8 [40] on Cipres Science Gateway (http://www.phylo.org) [41] with random starting trees without constraints. The optimal substitution model was selected using the jModeltest software v2.0 [42], on the basis of the corrected Akaike Information Criterion, as suggested by Burnham and Anderson [43]. We applied the substitution models GTR + I + G and Lewis MK for COI and morphological data, respectively. We assumed a Yule speciation model and strict molecular clock. Clock and tree parameters were linked across partitions. All priors were left as the default values in BEAUTI [40]. The analyses were run for a total of 30 million generations with sampling every 10,000 generations. The convergence of the runs was evaluated by accessing log files in TRACER v1.6 [44]. We generated a maximum clade credibility tree in TreeAnnotator v2.4.8 [40], using a burn-in of 10% (3000 trees) and visualized in FigTree v1.4.3 [45].

The trees obtained from both analyses were rooted with *Cyrtomon inhalatus* (Germar) (Naupactini clade II sensu Lanteri and del Rio [2]).

3. Results

3.1. Bayesian Analysis

The tree obtained from the Bayesian analysis is shown in Figure 1. Clades with posterior probabilities $\geq$0.95 are indicated in boldface. *Litostylus* was recovered as the sister genus of the remaining taxa (PP 0.8). The species groups of *Naupactus* are spread into four main clades of the tree, with PP values $\geq$0.50: clade A includes the pair *N. stupidus*–*N. sulfuratus* (PP 1); clade B includes the majority of species, with *N. tucumanensis* to *N. versatilis* (PP 1) as sister group of *Hoplopactus–anterius-N. inermis*; clade C includes the pair *N. cinereidorsum*–*N. cyphoides* related to *Teratopactus*; and clade D includes the species usually classified as belonging to genera other than *Naupactus*, except for the group ((*N. dissimilis*–*N. xanthographus*) *N. navicularis*) (PP 1), *N. cervinus*–*N. dissimulator* (PP 1), and *N. setarius*.

The combined approach provided strong evidence for the monophyly of the genera *Aramigus, Eurymetopus* and *Phacepholis*, but this would not the case for *Pantomorus*. In addition, well-supported nodes proved intergeneric relationships for *Galapaganus*–*Phacepholis*, and *Eurymetopus*–*Floresianus* to be robust. The best supported group within *Pantomorus* is *P. auripes*–*P. ruizi* (PP 0.98).

The terminal units regarded as the same species are recovered in the same groups, despite their different geographic origins, sex or morphotypic variation. For example, the two females of *Lanterius micaceus* belonging to the *micaceus* morphotype (originally described as *Mimographus micaceus*) are grouped with the male of *villosipennis* morphotype (originally described as *M. villosipennis*) (synonymy by Lanteri, 1985 [46]). Similarly, the two morphotypes of *Atrichonotus taeniatulus* (*taeniatulus* and *pictipennis*) [18], originally described as different species, are recovered as conspecific.

The length of the branches of the Bayesian tree indicate a very high infraspecific variation in the parthenogenetic species *Aramigus tessellatus*, *A. conirostris* and *N. cervinus*, which show several divergent lineages and/or cryptic species [26,47].

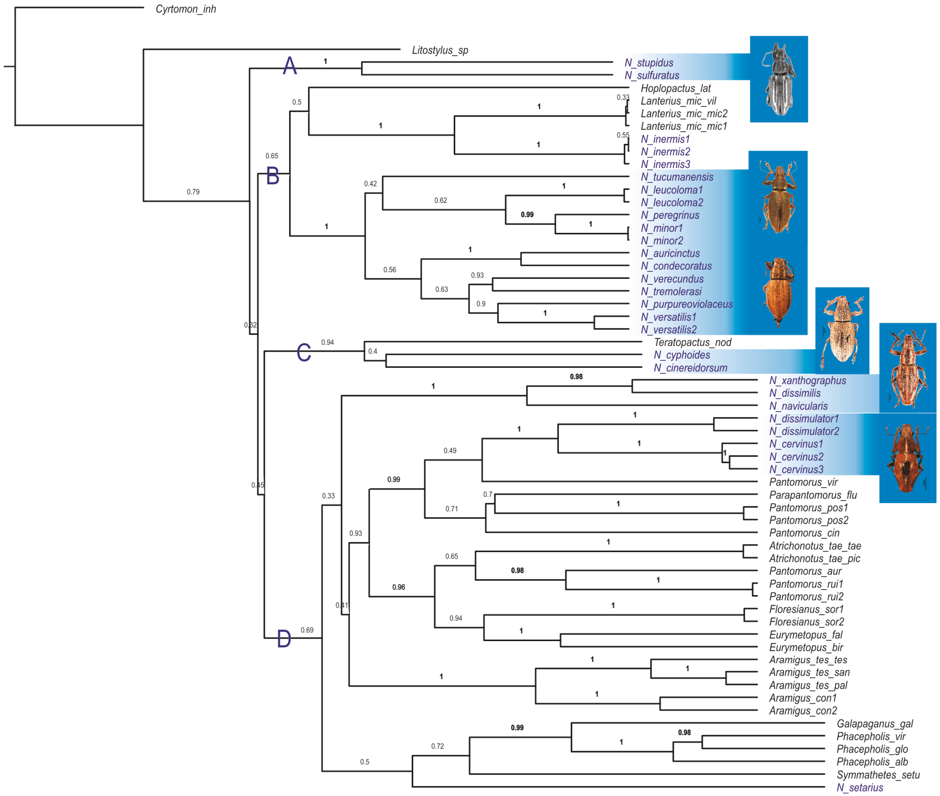

Figure 1. Tree obtained by Bayesian analysis (MCC) from a data matrix of 60 terminal units of Naupactini by 812 characters. Posterior probabilities ≥ 0.95 are indicated in boldface. The groups of *Naupactus* are highlighted in blue and illustrated.

3.2. Parsimony Analysis

The Parsimony analysis of the combined data set yielded four most parsimonious trees (L = 2457 steps; CI = 0.52; RI = 0.27) (Figure 2), which best support the same monophyletic groups as the Bayesian tree. There are changes in the relationships among some weakly supported groups and unstable species: (1) the pair *N. sulfutatus*–*N. stupidus* is recovered in the same clade as *Galapaganus*–*Phacepholis*; (2) the group *N. auricinctus* to *N. tucumanensis* is strongly supported, but the interspecies relationships within it are slightly different from those in the Bayesian tree; (3) *N. cinereidorsum*, *N. cyphoides* and *Teratopactus* are recovered in the same clade as *N. navicularis* (*N. xanthographus*–*N. dissimilis*), and *Aramigus*; (4) *Naupactus setarius* + *S. setulosus* are sister species within a large clade that includes the pair *N. dissimulator*–*N. cervinus* and species of other genera (*Pantomorus*, *Parapantomus*, *Atrichonotus, Floresianus* and *Eurymetopus*).

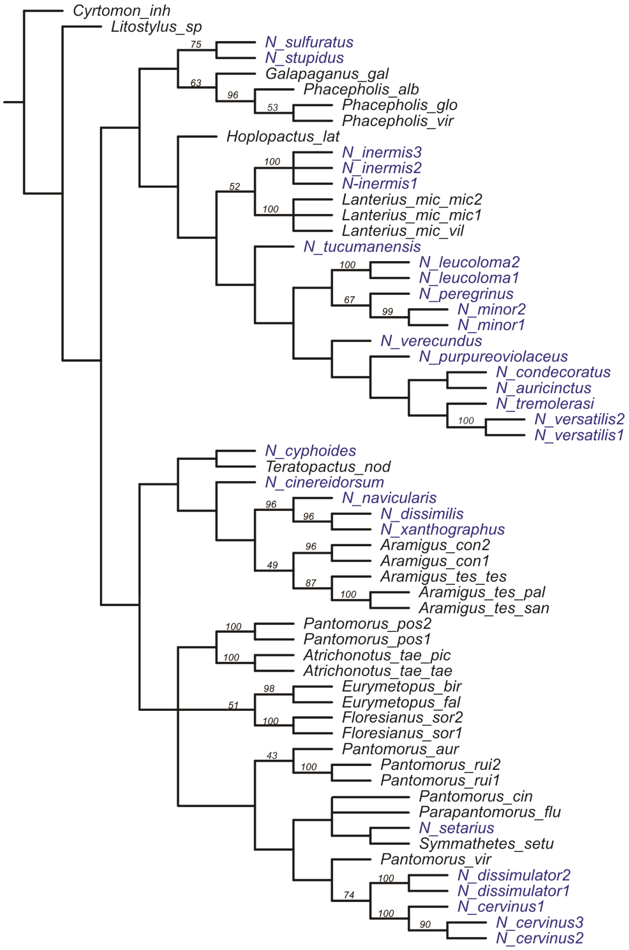

Figure 2. Strict consensus tree obtained by parsimony analysis from a data matrix of 60 terminal units of Naupactini by 812 characters. Bootstrap values ≥40 are indicated onto branches. The species of *Naupactus* are highlighted in blue.

4. Discussion

Naupactus is recognized by a particular combination of characters, which is useful for the generic identification but misses out exclusive synapomorphies, e.g., the presence of rows of setae along the ovipositor is a derived character for Naupactini, but also occurs in other genera such as *Lanterius.* Moreover, this feature is lacking in some species of the same genus, e.g., the Central American *N. sulfuratus* and *N. stupidus*. The most diagnostic characters of *Naupactus* are: parallel-sided rostrum, orientated anteriad and with strong lateral carinae; long antennae with funicular antennomere 2 distinctly longer than antennomere 1; wide pronotum, elevated over the mesothoracic peduncle, lacking tubercles; squamose scutellum; moderately bisinuate to straight elytral base; well-developed to reduce humeri, lacking tubercles; fully-developed to reduce hind wings; slightly separate to contiguous front coxae; front femora distinctly wider than hind femora, lacking large denticles or spines; mucro and row of denticles usually present on inner margin of front tibiae; metatibial apex having broad to slender squamose corbel or lacking corbel; penis without flagellum; proximal half of spermatheca with strongly thickened walls, collum (=duct lobe) usually short and ramus indistinct; ovipositor usually not exceeding length of abdomen, bearing styli and rows of long setae along its posterior two-thirds.

Clade A corresponds to the sister species *N. sulfuratus* and *N. stupidus,* which are the only *Naupactus* from Central America included in our taxon sampling. In the MP tree these species are closer to other Central American or Northern South American naupactines (e.g., *Phacepholis* and *Galapaganus*). Additional information suggests that they might be related to some *Naupactus* from northern South America not included in our analyses, e.g., *N. instabilis* Boheman (from Colombia and Venezuela) and *N. litoris* Bordón (from Venezuela).

Naupactus of clade B are more closely related to *Lanterius* and *Hoplopactus* than to other *Naupactus* in both analyses. Indeed, *N. inermis* was recovered as a sister species of *Lanterius micaceus.* Consequently, we decided to transfer *N. inermis* to *Lanterius*, a genus that mainly differs from *Naupactus* in its smaller body size, slender pronotum, not elevated over the thoracic peduncle, and the 9 and 10 elytral striae separated along their posterior two-thirds. *Hoplopactus* differs from *Lanterius* and *Naupactus* by a distinct apomorphic character, namely the presence of one to three spines on the inner margin of front femora. Neither *Lanterius* nor *Hoplopactus* have yet been taxonomically revised.

The group *N. tucumanensis to N. versatilis* is well supported by the combined evidence and includes two weakly supported subgroups: *N. auricintus* to *N. versatilis* is mainly characterized by the undulate to spiraled spermathecal duct, and *N. tucumanensis* to *N. minor* is recognized by a particular color pattern of white stripes along sides of pronotum and elytra, and the penis about $\frac{1}{2}$ longer than its apodemes. The second subgroup corresponds to *N. leucoloma* species group *sensu* Lanteri and Marvaldi [10] described for the white-fringed weevils *N. leucoloma*, *N. minor*, *N. peregrinus*, *N. tucumanensis* and *N. albolateralis*. The relationship *N. peregrinus*–*N. minor* is strongly justified (PP 0.99). Scataglini et al. [15] recovered the sister relationship *N. leucoloma*–*N. minor*, but the species *N. peregrinus* and *N. tucumanensis* were not available for that analysis.

Clade C includes the sister species *N. cinereidorsum*–*N. cyphoides* and *Teratopactus*. The type species of *Naupactus*, *N. rivulosus*, would belong to this group [48]. *Teratopactus* occurs in similar environments (woodlands and savannas) and mainly differentiates from the typical *Naupactus* by the apomorphies of the tubercles at the humeri and, in some cases, on the sides of pronotum; the front coxae separated from each other; the styli of the ovipositor usually lacking, and the distal coxites transformed into strong nail-like pieces adapted to oviposition of isolated eggs in the soil [49].

Clade D includes the species of *Naupactus* assigned to the *N. xanthographus* species group, mainly characterized by the presence of one pair of tubercles at the apex of the elytra [21], *N. cervinus* and *N. setarius*, plus those of some genera other than *Naupactus* (*Aramigus*, *Atrichonotus*, *Pantomorus*, *Parapantomorus*, *Floresianus*, *Eurymetopus*, *Galapaganus*, *Phacepholis* and *Symmathetes*). Within the *N. xanthographus* species group Lanteri & del Río [21] recognized two subgroups: one comprising *N. xanthographus*, *N. navicularis*, *N. dissimilis* and *N. mimicus*, having well-developed, squamose corbels at the metatibial apex, and the other composed of *N. dissimulator* and *N. marvaldiae*, without corbels.

In our trees, these subgroups are recovered as independent lineages. The former subgroup shows unstable relationships, as evidenced by the different results from the Bayesian and MP trees. *Naupactus dissimulator* is always recovered as sister species of *N. cervinus* based on molecular data and some synapomorphies of the female and male genitalia (e.g., shape of spermatheca and sclerites of the internal sac of the penis). The latter species lacks the pair of tubercles at the apex of the elytra, typical of the *N. xanthographus* species group, suggesting that these tubercles evolved independently at least twice in the genus *Naupactus* and were lost in *N. cervinus.*

Naupactus cervinus is a species complex containing divergent parthenogenetic lineages and cryptic species [26]. It has been classified in *Naupactus* [3], *Pantomorus* [13,14] and *Asynonychus* (type species *A. godmanni* Crotch, junior synonym of *N. cervinus*) [12,50] and according to previous analyses its phylogenetic position is uncertain. It was placed close to *Aramigus* when only morphological characters were used [2], while it was recovered as the sister species of *N. dissimulator* when molecular information was added [15]. In this work we confirm its relationship with *N. dissimulator*, although additional taxonomic information suggests that might be closer to some species not included in our analysis, such as *N. marvaldiae* [21] and other undescribed naupactines close to *Alceis*, considered as a synonym of *Naupactus* in some old classifications [51].

The South American *Pantomorus* herein analyzed (classified as *Naupactus* in Morrone [12]) do not form a monophyletic group. The pair *P. auripes* + *P. ruizi* is recovered in the same group as *Atrichonotus*, *Floresianus* and *Eurymetopus*, and the remaining *Pantomorus* and *Parapantomorus*, in the group that includes *N. cervinus–N. dissimulator.* As in the case of *N. cervinus*, we guess that several naupactines from South America alternatively classified in *Pantomorus*, *Parapantomorus* or *Naupactus*, belong to or are more closely related to *Alceis*. Unfortunately, the available molecular information and the taxon sampling are insufficient to take a definite decision about the correct placement of these taxa.

Aramigus (South America) and *Phacepholis* (Central and North America), considered subjective synonyms of *Pantomorus* in some classifications (e.g., [13,51] and later revalidated [4,52], are monophyletic genera, which is in agreement with previous phylogenetic analyses [16,47]. They are grouped neither together nor with other *Pantomorus*, thus supporting the hypothesis that *Pantomorus sensu* Wibmer and O'Brien [13] is not monophyletic. *Aramigus* is not close to any particular group of South American *Pantomorus* or *Naupactus*, included in our analysis, whereas *Phacepholis* is related to *Galapaganus* [53,54]; however, in previous analysis [2,16], *Phacepholis* is more related to the Central American *Pantomorus* (the type species *P. albosignatus* Boheman from Mexico). We believe that the latter hypothesis is more plausible and that it was retrieved closer to *Galapaganus* because of the absence of species from that area.

Symmathetes was also considered as a synonym of *Pantomorus* in earlier classifications [13,51] and latter revalidated [12]. In our MP tree and in the MP tree using four molecular markers [24], *N. setarius* was recovered as sister species of *Symmathetes setulosus*, consequently we propose to transfer the former species to *Symmathetes* and to establish the new combination *Symmathetes setarius* (Boheman). This species is very similar to the type species *S. kollari* Schoenherr except for its flat eyes. *Symmathetes* mainly characterizes by the expanded metatibial apex, split off in *S. kollari* and *S. setarius*.

Eurymetopus is monophyletic and related to *Floresianus*, based on several morphological synapomorphies and also supported by molecular evidence [15]. Although grouped within the same clade, *Atrichonotus* is not recovered as sister taxon of the pair *Eurymetopus–Floresianus* as in Lanteri and del Río [2]. The fact that some species show intermediate characters between *Atrichonotus* and *Eurymetopus*, e.g., *Atrichonotus whiteheadi* Lanteri [55], suggests that the three genera are related.

4.1. Taxonomic Implications of Phylogenetic Analyses

The *Pantomorus-Naupactus* complex includes several lineages with derived characters, such as shorter and more conical rostrum, shorter antennae, reduced to absent hind wings and parthenogenetic reproduction, which might have evolved several times, thus obscuring phylogenetic signal and leading to high degrees of homoplasy [2,15,56]. *Pantomorus sensu lato* (including species from different areas of North, Central and South America) is an example of a non-monophyletic genus diversified in new adaptive zones or marginal areas within the range of this complex. Other groups undergoing diversification in marginal areas would have acquired exclusive synapomorphies, allowing the recognition of monophyletic genera, e.g., *Phacepholis* would have diversified along the western coast of Central America and the Great Plains of North America, and it is recognized by the particular shape of the spermatheca and the presence of a series of small denticles on the second ventrite of the male [4,16,20]; *Aramigus* and *Eurymetopus* have acquired several synapomophies in the female genitalia (particular shape of spermatheca, sternite VIII or ovipositor) and would have diversified in grasslands and steppes of South America [18,52,57]; and *Galapaganus*, which displays synapomorphies in the male genitalia (setae around the ostium), would have diversified along the western coast of South America and the Galapagos Islands [24,53,54,58,59].

The result obtained herein raises the dilemma that the recognition of several genera within the *Pantomorus-Naupactus* complex leads *Naupactus* to be non-monophyletic. Morrone [12] made an attempt to solve this problem by transferring all the South American species of *Pantomorus* to *Naupactus*, in a checklist based on neither revisionary nor phylogenetic studies. However, these nomenclatural changes did not solve the problem of the monophyly of *Naupactus*, but instead they created a large genus very difficult to circumscribe. According to our analysis, if *Naupactus is* monophyletic, it may include not only the South American *Pantomorus* but also *Hoplopactus*, *Lanterius*, *Teratopactus*, *Aramigus*, *Eurymetopus*, *Floresianus*, *Parapantomorus*, *Galapaganus*, *Phacepholis* and *Symmathetes.* Moreover, the phylogeny of Naupactini [2] suggests that the naupactine genera diversified in the High Andes, Paramos and Puna (*Amitrus* Schoenherr, *Amphideritus* Schoenherr, *Asymmathetes* Wibmer and O'Brien, *Leschenius* del Río, *Melanocyphus* Jekel, *Obrieniolus* del Río and *Trichocyphus* Heller) also belong to the *Pantomorus-Naupactus* complex, and might be classified in *Naupactus*.

We conclude that so far there is no satisfactory solution for the classification of the highly diversified weevil genus *Naupactus* and its relatives. One more comprehensive taxon sampling and new molecular evidence will contribute to essential information for a more definite conclusion. Until then, we prefer to maintain *Naupactus* as non-monophyletic and to accommodate the remaining species in species groups, subgroups or genera useful for further evolutionary or biogeographic studies (see [1]), thereby avoiding the creation of unnecessary generic names.

Classification should serve as a general reference system, endowed with explanatory, predictive and heuristic properties providing foundation for all comparative studies in biology [60]. The field of Phylogenetic Systematics [61] has greatly benefited from the use of molecular markers and, more recently, of genomic data, all of which have given rise to novel hypotheses on the evolution of animals and plants [62–65]. However, there is an increasing gap between phylogenetic analyses and classifications based on Linnaean nomenclature, probably because of the difficulties in translating monophyletic groups inferred from molecular phylogenetic signals into words [66]. In addition, there are many other issues affecting final results, such as the poorly known morphology of several taxa that are yet to be revised, genealogies resulting from insufficient taxon samplings, and the effect that the absence of some terminal taxa may have on phylogenetic hypotheses; the fact that a single tree may result in more than one classification, even if it represents a robust phylogenetic hypothesis; and a potential conflict between the dynamic nature of phylogenetic analysis and the desirable stability of the Linnaean Classification and Nomenclature. In the case of hyperdiverse groups of animals, such as weevils, the reduction of the gap between Phylogeny and Classification will take a time. Meanwhile, we attempt to shed light on the evolution of particularly complex taxa, such as the genus *Naupactus*, while being conscious of nomenclatural decisions.

4.2. Taxonomic Amendments

In order to address the taxonomic implications of our phylogenetic results, we propose the following nomenclatural changes, relative to Wibmer and O'Brien [13] and Alonso-Zarazaga and

Lyal [3]: (i) to transfer the species *Naupactus inermis* to the genus *Lanterius*; (ii) to transfer the species *Naupactus setarius* to the genus *Symmathetes.*

Lanterius inermis (Hustache), new combination.

Symmathetes setarius (Boheman) new combination.

Supplementary Materials: The following data is available online at http://www.mdpi.com/1424-2818/10/3/59/s1, Table S1: Morphological data matrix.

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References

1. Del Río, M.G.; Morrone, J.J.; Lanteri, A.A. Evolutionary biogeography of South American weevils of the tribe Naupactini (Coleoptera: Curculionidae). *J. Biogeogr.* **2015**, *42*, 1293–1304. [CrossRef]
2. Lanteri, A.A.; del Río, M.G. Phylogeny of the tribe Naupactini (Coleoptera: Curculionidae) based on morphological characters. *Syst. Entomol.* **2017**, *42*, 429–447. [CrossRef]
3. Alonso-Zarazaga, M.A.; Lyal, C.H.C. *A World Catalogue of Families and Genera of Curculionoidea: (Insecta: Coleoptera) Excepting Scolytidae and Platypodidae*; Entomopraxis, D.C.P.: Barcelona, Spain, 1999; ISBN 978-84-605-9994-4.
4. Lanteri, A.A. Systematic revision and cladistic analysis of *Phacepholis* Horn (Coleoptera: Curculionidae). *Southwest. Entomol.* **1990**, *15*, 179–204.
5. Lanteri, A.A. Systematic revision of *Ericydeus* Pascoe (Coleoptera: Curculionidae). *Entomol. Scand.* **1995**, *26*, 393–424. [CrossRef]
6. Schoenherr, C.J. *Genera et Species Curculionidum, cum Synonymia hujus Famili*; Roret: Paris, France, 1833; Volume 1, pp. I–XV, 1–381, 383–681.
7. Schoenherr, C.J. *Genera et Species Curculionidum, cum Synonymia hujus Famili*; Roret: Paris, France, 1840; Volume 6, pp. I, 1–474.
8. Sharp, D.; Champion, G.C. *Biologia Centrali-Americana*; Taylor & Francis: London, UK, 1889–1911; Volume IV, part 3; p. vi-354.
9. Hustache, A. Naupactini de l'Argentine et des régions limitrophes (Col. Curculion.). *Rev. Soc. Entomol. Argent.* **1947**, *13*, 3–146.
10. Lanteri, A.A.; Marvaldi, A.E. *Graphognathus* Buchanan, a new synonym of *Naupactus* Dejean, and systematics of the *N. leucoloma* species group (Coleoptera: Curculionidae). *Coleopt. Bull.* **1995**, *49*, 206–228.
11. Bordón, C. El género *Naupactus* Dejean (Coleoptera: Curculionidae) en Venezuela. *Acta Biológica Venezuelica* **1997**, *17*, 11–51.
12. Morrone, J.J. The species of Entiminae ranged in America south of the United States. *Anales del Instituto de Biología Serie Zoología* **1999**, *70*, 99–168.
13. Wibmer, G.J.; O'Brien, C.W. Annotated checklist of the weevils (Curculionidae sensu lato) of South America (Coleoptera: Curculionoidea). *Mem. Am. Entomol. Inst.* **1986**, *39*, 1–563.
14. O'Brien, C.W.; Wibmer, G.J. Annotated checklist of the weevils (Curculionidae sensu lato) of North America, Central America and the West Indies (Coleoptera: Curculionoidea). *Mem. Am. Entomol. Inst.* **1982**, *34*, 1–382.
15. Scataglini, M.A.; Lanteri, A.A.; Confalonieri, V.A. Phylogeny of the *Pantomorus-Naupactus* complex based on morphological and molecular data (Coleoptera: Curculionidae). *Cladistics* **2005**, *21*, 131–142. [CrossRef]

16. Rosas-Echeverría, M.V.; Morrone, J.J.; del Río, M.G.; Lanteri, A.A. Phylogenetic analysis of the *Pantomorus-Naupactus* complex (Coleoptera: Curculionidae: Entiminae) from North and Central America. *Zootaxa* **2011**, *2780*, 1–19.
17. Buchanan, L.L. *The Species of Pantomorus of America North of Mexico*; United States Department of Agriculture: Washington, DC, USA, 1939; Volume 34, pp. 1–39.
18. Lanteri, A.A.; O'Brien, C.W. Taxonomic revision and cladistic analysis of *Atrichonotus* Buchanan (Coleoptera: Curculionidae). *Trans. Am. Entomol. Soc.* **1990**, *116*, 697–725.
19. Lanteri, A.A.; del Río, M.G. Caracteres genitales de la hembra en la clasificación y filogenia de la tribu Naupactini (Coleoptera: Curculionidae). In *Contribuciones Taxonómicas en Órdenes de Insectos Hiperdiversos*; Llorente Bousquets, J., Lanteri, A.A., Eds.; UNAM-RIBES-CYTED: Mexico city, Mexico, 2008; pp. 159–176.
20. Rosas, M.V.; del Río, M.G.; Lanteri, A.A.; Morrone, J.J. Track analysis of the North and Central American species of the *Pantomorus-Naupactus* complex (Coleoptera: Curculionidae). *J. Zool. Syst. Evol. Res.* **2011**, *49*, 309–314. [CrossRef]
21. Lanteri, A.A.; del Río, M.G. *Naupactus xanthographus* (Germar) species group (Curculionidae: Entiminae: Naupactini): A comprehensive taxonomic treatment. *J. Nat. Hist.* **2017**, *51*, 1557–1587.
22. Marvaldi, A.E.; Lanteri, A.A.; del Río, M.G.; Oberprieler, R.G. 3.7.5. Entiminae Schoenherr, 1823. In *Handbook of Zoology. Coleoptera, Beetles. Morphology and Systematics, Vol. 3*; Leschen, R.A., Beutel, R.G., Eds.; De Gruyter: Berlin, Germany; Boston, MI, USA, 2014; Volume 3, pp. 503–522.
23. Bold Systems v4. Available online: http://www.boldsystems.org/ (accessed on 4 May 2018).
24. Marvaldi, A.E.; del Río, M.G.; Pereyra, V.A.; Rocamundi, N.; Lanteri, A.A. A combined molecular and morphological approach to explore higher phylogenetics of entimine weevils with special reference to South American taxa. *Diversity* **2018**. under review.
25. Sequeira, A.; Lanteri, A.A.; Scataglini, M.A.; Confalonieri, V.A.; Farrell, B. Are flightless *Galapaganus* weevils older than the Galápagos Islands they inhabit? *Heredity* **2000**, *85*, 20–29. [CrossRef] [PubMed]
26. Rodriguero, M.S.; Lanteri, A.A.; Confalonieri, V.A. Speciation in the asexual realm: Is the parthenogenetic weevil *Naupactus cervinus* a complex of species in *statu nascendi*? *Mol. Phylogenet. Evol.* **2013**, *68*, 644–656. [CrossRef] [PubMed]
27. Elias-Costa, A.J.; Confalonieri, V.A.; Lanteri, A.A.; Rodriguero, M.S. Game of Clones: Is *Wolbachia* inducing speciation in a weevil with a mixed reproductive mode? *Mol. Phylogenet. Evol.* **2018**. under review.
28. Sunnucks, P.; Hales, D.F. Numerous transposed sequences of mitochondrial cytochrome oxidase I-II in aphids of the genus *Sitobion* (Hemiptera: Aphididae). *Mol. Biol. Evol.* **1996**, *13*, 510–524. [CrossRef] [PubMed]
29. Normark, B.B. Phylogeny and Evolution of Parthenogenesis in the *Aramigus tessellatus* Complex (Coleoptera: Curculionidae). Ph.D. Thesis, Cornell University, Ithaca, NY, USA, 1994.
30. Bensansson, D.; Zhang, D.; Hewitt, G.M. Frequent assimilation of mitochondrial DNA by grasshopper nuclear genomes. *Mol. Biol. Evol.* **2000**, *17*, 406–415. [CrossRef] [PubMed]
31. Tamura, K.; Peterson, D.; Peterson, N.; Stecher, G.; Nei, M.; Kumar, S. MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol. Biol. Evol.* **2011**, *28*, 2731–2739. [CrossRef] [PubMed]
32. Lunt, D.H.; Zhand, D.X.; Szymura, J.M.; Hewitt, G.M. The insect cytochrome oxidase I gene evolutionary patterns and conserved primers for phylogenetic studies. *Insect Mol. Biol.* **1996**, *5*, 153–165. [CrossRef] [PubMed]
33. Sorenson, M.D.; Fleischer, R.C. Multiple independent transposition of mitochondrial DNA control region sequences to the nucleus. *Proc. Natl. Acad. Sci. USA* **1996**, *93*, 15239–15243. [CrossRef] [PubMed]
34. Zhang, D.X.; Hewitt, G.M. Nuclear integrations: Challenges for mitochondrial DNA markers. *Trends Ecol. Evol. (Amst.)* **1996**, *11*, 247–251. [CrossRef]
35. Thompson, J.D.; Higgins, D.G.; Gibson, T.J. CLUSTAL W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position specific gap penalties and weight matrix choice. *Nucleic Acids Res.* **1994**, *22*, 4673–4680. [CrossRef] [PubMed]
36. Goloboff, P.A.; Catalano, S. TNT version 1.5, including full implementation of phylogenetic morphometrics. *Cladistics* **2016**, *32*, 221–238. [CrossRef]
37. Felsenstein, J. Confidence Limits on Phylogenies: An Approach Using the Bootstrap. *Evolution* **1985**, *39*, 783–791. [CrossRef] [PubMed]

38. Kluge, A.G.; Farris, J.S. Quantitative phyletics and the evolution of anurans. *Syst. Biol.* **1969**, *18*, 1–32. [CrossRef]
39. Farris, J.S. The retention index and the rescaled consistency index. *Cladistics* **1989**, *5*, 417–419. [CrossRef]
40. Bouckaert, R.; Heled, J.; Kühnert, D.; Vaughan, T.; Wu, C.H.; Xie, D.; Suchard, M.A.; Drummond, A.J. BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. *PLoS Comput. Biol.* **2014**, *10*, e1002537. [CrossRef] [PubMed]
41. Miller, M.A.; Pfeiffe, W.; Schwartz, T. Creating the CIPRES Science Gate way for inference of large phylogenetic trees. In Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, LA, USA, 14 November 2010; Towns, J., Ed.; IEEE: New Orleans, LA, USA, 2010.
42. Darriba, D.; Taboada, G.L.; Doallo, R.; Posada, D. jModelTest 2: More models, new heuristics and parallel computing. *Nat. Methods* **2012**, *9*, 772. [CrossRef] [PubMed]
43. Burnham, K.P.; Anderson, D.R. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*; Springer Science & Business Media: New York, NY, USA, 2002.
44. Drumond, A.J.; Rambaut, A. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evol. Biol.* **2007**, *7*, 214. [CrossRef] [PubMed]
45. Rambaut, A. FigTree v. 1.3.1. Computer Program and Documentation Distributed by the Author, 2006–2012. Available online: http://tree.bio.ed.ac.uk/software/ (accessed on 21 December 2017).
46. Lanteri, A.A. Revisión de las especies argentinas del género *Macrostylus* Boheman, subgénero *Mimographus* Schoenherr (Coleoptera: Curculionidae). *CIPFE-CED Orione Contribuciones en Biología* **1985**, *12*, 1–6.
47. Normark, B.B.; Lanteri, A.A. Incongruence between morphological and mitochondrial DNA characters suggests hybrid origins of parthenogenetic weevil lineages (genus *Aramigus*). *Syst. Biol.* **1998**, *47*, 475–494. [CrossRef] [PubMed]
48. Lanteri, A.A.; del Río, M.G.; Rodriguero, M.; Confalonieri, V. Weevils of the *Pantomorus-Naupactus* complex: Cladistics and generic classification. *Cladistics* **2010**, *26*, 214.
49. Del Río, M.G.; Lanteri, A.A.; Guedes, J.V.C. Taxonomic revision and cladistic analysis of *Teratopactus* Heller (Coleoptera: Curculionidae). *Invertebr. Syst.* **2006**, *20*, 585–602. [CrossRef]
50. Lanteri, A.A. Revisión del género Asynonychus Crotch (Coleoptera: Curculionidae). *Rev. Asoc. Cs. Nat. Litoral.* **1986**, *2*, 161–174. [CrossRef]
51. Blackwelder, R.E. Checklist of the Coleopterous insects of Mexico, Central America, the West Indies and South America. Part 5. *Bull. U. S. Natl. Mus.* **1947**, *185*, 765–925. [CrossRef]
52. Lanteri, A.A.; Díaz, N.B. Systematic study and cladistic analysis of the genus *Aramigus* Horn (Coleoptera: Curculionidae). *Trans. Am. Entomol. Soc.* **1994**, *120*, 113–144.
53. Lanteri, A.A. Systematics, cladistics and biogeography of a new weevil genus *Galapaganus* (Coleoptera: Curculionidae) from the Galápagos Islands, and coasts of Ecuador and Perú. *Trans. Am. Entomol. Soc.* **1992**, *118*, 227–267.
54. Lanteri, A.A. New Taxonomic and Biogeographic Information on *Galapaganus femoratus* species group (Coleoptera: Curculionidae: Entiminae). *Trans. Am. Entomol. Soc.* **2004**, *130*, 177–192.
55. Lanteri, A.A.; Morrone, J.J. Cladistics of the *Naupactus leucoloma* species group, *Atrichonotus*, and *Eurymetopus* (Coleoptera: Curculionidae). *Revista de la Sociedad Entomológica Argentina* **1995**, *54*, 99–112.
56. Lanteri, A.A.; Normark, B.B. Parthenogenesis in the tribe Naupactini (Coleoptera: Curculionidae). *Ann. Entomol. Soc. Am.* **1995**, *88*, 722–731. [CrossRef]
57. Lanteri, A.A. Revisión sistemática del género *Eurymetopus* Schoenherr (Coleoptera: Curculionidae) mediante la aplicación de técnicas numéricas. *Revista de la Sociedad Entomológica Argentina* **1984**, *43*, 247–281.
58. Sequeira, A.; Sijapati, M.; Lanteri, A.; Roque Albelo, L. Nuclear and mitochondrial sequences confirm complex colonization patterns and clear species boundaries for flightless weevils in the Galapagos archipelago. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **2008**, *363*, 3439–3451. [CrossRef] [PubMed]
59. Sequeira, A.S.; Lanteri, A.A.; Albelo, L.R.; Bhattacharya, S.; Sijapati, M. Colonization history, ecological shifts and diversification in the evolution of endemic Galápagos weevils: Colonization and diversification of Galápagos weevils. *Mol. Ecol.* **2008**, *17*, 1089–1107. [CrossRef] [PubMed]
60. Mayr, E. *Principles of Systematic Zoology*; McGraw-Hill: New York, NY, USA, 1969.
61. Hennig, W. *Phylogenetic Systematics*; University of Illinois Press: Urbana, IL, USA, 1966.

62. Marvaldi, A.E.; Sequeira, A.S.; O'Brien, C.W.; Farrell, B.D. Molecular and Morphological Phylogenetics of Weevils (Coleoptera, Curculionoidea): Do Niche Shifts Accompany Diversification? *Syst. Biol.* **2002**, *51*, 761–785. [CrossRef] [PubMed]
63. Jordal, B.H.; Sequeira, A.S.; Cognato, A.I. The age and phylogeny of wood boring weevils and the origin of subsociality. *Mol. Phylogenet. Evol.* **2011**, *59*, 708–724. [CrossRef] [PubMed]
64. Gunter, N.L.; Oberprieler, R.G.; Cameron, S.L. Molecular phylogenetics of Australian weevils (Coleoptera: Curculionoidea): Exploring relationships in a hyperdiverse lineage through comparison of independent analyses. *Austral Entomol.* **2016**, *55*, 217–233. [CrossRef]
65. Shin, S.; Clarke, D.J.; Lemmon, A.R.; Moriarty Lemmon, E.; Aitken, A.L.; Haddad, S.; Farrell, B.D.; Marvaldi, A.E.; Oberprieler, R.G.; McKenna, D.D. Phylogenomic Data Yield New and Robust Insights into the Phylogeny and Evolution of Weevils. *Mol. Biol. Evol.* **2018**, *35*, 823–836. [CrossRef] [PubMed]
66. Franz, N.M. On the lack of good scientific reasons for the growing phylogeny/classification gap. *Cladistics* **2005**, *21*, 495–500. [CrossRef]

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Phylogeny of the Genus *Dichotrachelus* (Coleoptera: Curculionidae: Cyclominae)

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Abstract: A phylogenetic analysis of the genus *Dichotrachelus* (Curculionidae: Cyclominae) was carried out, based on a morphological matrix and, for some species, on mitochondrial cytochrome oxidase I sequences. Bayesian Inference, Maximum Likelihood and Maximum Parsimony were implemented and the results were compared. The genus is found to be isolated in the subfamily, not related to the only other Palaearctic tribe (Hipporhinini) and possibly nearer to the south-American genera of Cyclominae of the tribe Listroderini. Among these, *Macrostyphlus* is also equally associated to mosses as the host plant. In *Dichotrachelus*, two main clades were recognized, one distributed in the western part of the Mediterranean region (Iberian Peninsula, northern Africa and southern France) and the second distributed in the Alps and Apennines. Within each clade, some differentiated monophyletic subgroups could be identified. An evaluation of the most important characters that led to the phylogenetic reconstruction indicated the male genital sclerite as the most useful structure to characterize the different clades.

Keywords: Dichotrachelini; systematics; morphology; evolution; *mt-Cox1*

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1. Introduction

The genus *Dichotrachelus* Stierlin, 1853 includes 59 species from southern Europe and North Africa [1]. The genus belongs to the subfamily Cyclominae, tribe Dichotrachelini Hoffmann, 1957. Within the subfamily, its relationships are largely unknown [2] and no sister group to Dichotrachelini has been recognized. All species of *Dichotrachelus* are wingless, with a very low mobility, and are either associated with the forest environment, or-more often-with the alpine zone above the timberline. Each species usually has a restricted (or very restricted) range, and, in some cases, only one or very few populations are known. The genus has raised much interest since its description, and after a sequence of new species being named, a first revision was proposed in 1878 [3]. Since then, other than descriptions of new species, taxonomic revisions of local faunas have been provided for Switzerland [4], for the Iberian Peninsula [5–7], for France [8,9], and for Italy [10–12]. A complete revision of the genus was proposed in 1971 [13]. In the latter paper, the author recognized some species-groups and suggested a biogeographical scenario. Some remarks on relationships among the Iberian and north-African species and their historical biogeography were provided in 1987 [7], based on a discussion of the most important morphological characters, but without a cladistic analysis. More recently, several remarks on the Swiss species were given [14–16], and a checklist for Switzerland was provided [17,18]. A first attempt to reconstruct the phylogeny and phylogeography of the genus, limited to the *Saxifraga*-associated alpine species, was given based on a Bayesian analysis of morphological characters and mitochondrial cytochrome oxidase I (*mt-Cox1* hereafter) sequences [19], updated in 2015 [20]. Some additional species of the genus were also included in a more generic Barcode-approach on Swiss Alpine weevils [21].

Herein, we propose a phylogenetic analysis for the entire genus *Dichotrachelus*, based on a morphological database matrix, as well as on *mt-Cox1* sequences available for some species, in order to support the main clades (or species groups) and recognize the synapomorphies that define these groups. Available sequences of other Cyclominae were used in a first attempt at recognizing the affinities of *Dichotrachelus* within Cyclominae.

2. Material and Methods

2.1. Samples Origin

See Table I in the supplementary materials for a list of the species and specimens used, and for authorship and year of publication of the names. Specimens for molecular analyses were sampled by the authors. The weevils were hand-collected, immediately killed in 95% ethanol and preserved at −20 °C. Attempts to recover complete sequences of other species from dry collection specimens were seldom successful, and usually did not provide any reliable data. For the morphological analysis, samples from Meregalli's collection were used. Almost all species were included in the morphological matrix, except for *D. elongatus* and *D. ulbrichi*, species only known from the types, or, for the former, from very few specimens which could not be analysed, and the descriptions of which are insufficiently detailed to permit the scoring of the character states used for the study. Different subspecies of the same species were united with the nominal species, with the exception of *D. knechti*. This species was classified as a subspecies of *D. stierlini* in [1], but in the morphological analysis some of the character-states were distinct from those of *D. stierlini*, hence we have included it in the study. Sequences of the other species of *Cyclominae* were retrieved from GenBank.

2.2. Outgroup Selection

The selection of an outgroup proved particularly complex, since, as previously reported, there are no suggested sister groups of the tribe Dichotrachelini. The only other taxa of the subfamily Cyclominae present in the Palaearctic region belong to the tribe Hipporhinini, but only *mt-Cox1* sequences of *Gronops lunatus* are available for this tribe. However, Hipporhinini do not seem to share any close relationships based on either external or genital morphology. One of the authors (CG) discovered Cyclominae associated with mosses in high elevation habitats of Ecuador. These belong to the genus *Macrostyphlus* Kirsch, 1889 (Listroderini LeConte, 1876, a tribe distributed in the Americas, Australia, New Zealand and Tristan da Cunha [22]). These *Macrostyphlus* specimens have some morphological resemblance to *Dichotrachelus*, and *mt-Cox1* sequences showed that *Dichotrachelus* shares more sites in common with *Macrostyphlus* than with *Gronops*: *D. rudeni*, for example, has 667/775 sites in common with *Macrostyphlus* and 625/775 in common with *Gronops*, and the translated sequences have 226/258 sites of amino acids in common with *Macrostyphlus* and 207/258 in common with *Gronops*. A similar situation also occurred for the other species of the genus. Furthermore, when other taxa of Cyclominae, for which sequences are available, were tested, *Dichotrachelus* showed more differences from *Gronops* than from any of the other species of Cyclominae. *Macrostyphlus* was used as the nearest outgroup for the analyses, since it was also possible to use it for the morphological matrix; *Gronops lunatus* was used as a more distant outgroup. *Otiorhynchus pseudonothus* (Entiminae) was used as the outgroup for the Cyclominae analysis.

2.3. Morphological Data

Coding was conducted in a quantitative way and all characters were treated as non-additive. Scores were assigned based on the analysis of the various species, without any a-priori evaluation. Therefore, the state in the outgroups was not necessarily scored as 0. Morphological characters were selected in part according to the literature [7,19], with some more characters added for this study. Their selection had to consider the extreme morphological uniformity among species of the genus, particularly those associated with mosses. Many of the characters generally used in the morphological analyses showed either a limited amount of variation, or variation that seems to appear by parallelism in various species, or even occurs among different specimens of the same species. These traits, which seemed to be independent of the phylogenetic affinities, were therefore excluded from the analysis. Genitalia were cleared in hot 10% KOH and carefully dissected. Aedeagi were observed dry, female terminalia and the sclerite of the internal sac of the penis were placed in histology resin (Mounting Medium Leica CV Ultra) after dehydration in ethanol 95% and passage through xylene. Photographs were taken with a Nikon Coolpix P6000 mounted on a Leica S6E stereomicroscope. A series of photographs at different focal planes were taken and stacking was performed with Zerene Stacker 1.04 (Zerene Systems LCC). We identified 59 discrete characters, 38 based on external morphology and 21 based on genitalia, with special attention given to the sclerite of the internal sac of the penis (Table II, Supplementary Material). The biology (mosses or *Saxifraga*) was added since host-plant associations in weevils are considered to reflect phylogenetic lineages [23].

2.4. Molecular Data

Total DNA was extracted non-destructively from the entire specimen by placing the whole animal body in 400 µL of 5M guanidine–isothiocyanate, after separating the combined head + pronotum from the rest of the body to maximize DNA extraction [24]. Extraction and PCR were performed for a proportion of the species in the molecular laboratory of the Department of Life Sciences of the University of Turin, Italy, and for the remaining species in the molecular laboratory of the University of Geneva, Switzerland, within the frame of SwissBOL (Swiss Barcoding of Life: www.swissbol.ch). In both laboratories an 829 bp fragment of *mt-Cox1* was amplified with the following primers: forward C1–J–2183 (Jerry), 5′–CAACATTTATTTTGATTTTTTGG–3′ and reverse L2–N–3014 (Pat), 5′–TCCAATGCACTAATCTGCCATATTA–3′ [25]. In Turin, reactions were performed in a volume of 20 µL with HotStarTaq Master Mix (Qiagen, Hilden, Germany); the PCR program comprised an initial denaturation at 95 °C for 15 min, followed by 10 cycles of 30 s at 94 °C, 45 s at 60 $\geq$ 50 °C (lowering the annealing temperature each cycle 1 °C), 2 min at 72 °C followed by 30 cycles of 30 s at 94 °C, 45 s at 50 °C, 2 min at 72 °C, and a final extension cycle of 15 min at 72 °C. The reaction products were visualized by agarose gel electrophoresis, with successive purification from the gel. Sequencing was performed by an external service (Genechron, Roma, Italy). In Geneva, reactions were performed in a 20 µL total volume with 0.60U Taq (Roche, Basel, Switzerland), 2 µL of 10X buffer containing 20 mM $MgCl_2$, 0.8 µL of each primer (10 mM), 0.4 µL of a mix containing 10 mM of each dNTP (Roche) and 0.8 µL template DNA of an unknown concentration. The PCR program comprised an initial denaturation at 95 °C for 5 min, followed by 35 cycles of 95 °C for 40 s, annealing at 42 °C for 45 s and 72 °C for 1 min, with a final elongation step at 72 °C for 8 min. PCR products were then directly sequenced bi-directionally on an ABI 3031 automated sequencer (Applied Biosystems, Foster City, CA, USA).

Forward and reverse chromatograms were examined with Chromas (https://technelysium.com.au/wp/chromas). Multiple sequence alignment was performed with Mega6 (http://www.megasoftware.net) using default parameters and manually correcting ambiguities. After alignment, sequences were trimmed at the ends, reducing the length to a segment of 775 bp. All sequences were deposited in GenBank.

2.5. Phylogenetic Analysis: Morphology

Bayesian inference (BI) was performed using MrBayes 3.2 [26]. We ran two runs with four MCMC chains, each for two million generations under a binary MarkovK + Γ model, sampling every 500 generations. The first 25% generations were discarded (burn-in) and convergence was evaluated with the average standard deviation of split frequencies. Goodness of mixing was assessed by looking at the acceptance rate of swaps between adjacent chains [27].

Parsimony analysis (MP) was performed with TNT 1.1 [28] with the New Technology Search option, selecting all four search methods (Sectorial Search, Drift, Ratchet and Tree Fusing), using default parameters, and independently finding the optimal score 100 times. Trees were TBR-collapsed and the consensus tree was calculated with Majority Rule. Tree statistics were calculated using a TNT script (stats.run) included with the package. Character-states and synapomorphies common to all trees were mapped onto the resulting consensus tree.

Maximum likelihood (ML) was performed with raxmlGUI1.1 [29] using a MarkovK + Γ model. Support values were computed with 1000 bootstrap replications.

2.6. Phylogenetic Analyses: mt-Cox1

We obtained 84 sequences from 27 species. Sequences of other species, used as outgroups, were retrieved from GenBank (see supplementary material, Table I). Some of the *Dichotrachelus* sequences were identical and were only computed once in the alignments. All the sequences are 775 bp except that of *D. rossettoi*, which has a gap in position 137–178. It could not be determined whether this gap is true or due to artefacts that may have occurred during the sequencing procedure. The overall quality of the sequence of *D. rossettoi* was, however, relatively low.

Pairwise distance was calculated with MEGA6, implementing the p-distance model.

BI was performed using MrBayes 3.2 [26]. The nuclear substitution model was set to the “codon” evolutionary model [30] implemented in MrBayes, also according to [31]. To recognize the codons, the aligned sequences were translated to the respective amino acids with Mega6 and checked for congruity among the species. This was accomplished by deleting the first nucleotide in the sequence, thus obtaining 774 bp long sequences. We ran two runs with four chains, each for two million generations, sampling every 500 generations, using reversible jump Monte Carlo Markov Chain (MCMC) [32]. The heterogeneity of substitution rates among different sites was modelled with a four categories discretized Γ distribution and with a proportion of invariable sites. The first 25% of generations were discarded (burn-in) and convergence was evaluated with the average standard deviation of split frequencies. Goodness of mixing was assessed by looking at the acceptance rate of swaps between adjacent chains [27].

Morphological matrix

See Figures 1–3 for some of the morphological characters used. See also illustrations in [7,19], in particular for other detailed drawings and photographs of the male genital sclerite ([7], Figures 245–301; [19], Figures 28–53).

1. Size. 0 = small, length less than 5 mm; 1 = large, length more than 5 mm.

2. Rostrum, dorsal margins. 0 = subparallel; 1 = distinctly convergent anteriad; 2 = broadened at midlength; 3 = broadened at base.

3. Rostrum, width at antennal insertion. 0 = almost half as wide as at base; 1 = almost as wide as at base.

4. rostrum, vestiture on median part. 0 = almost completely covered with scales; 1 = almost completely lacking scales.

5. Rostrum, vestiture of scales on median part. 0 = scales adherent to integument; 1 = scales distinctly raised.

6. Rostrum length 0 = short, about 1.5× as long as wide; 1 = slender, almost twice as long as wide; 2 = very slender, more than twice as long as wide

7. Apex of rostrum. 0 = roughly punctured; 1 = striate; 2 = smooth, punctures or striae absent.

8. Vestiture of body, shape of scales: 0 = round or elliptical; 1 = narrow, long hair-like.

9. Vestiture of body, shape of setae. 0 = long hair-like; 1 = elliptical; 2 = spatulate, broadened apicad; 3 = very shortly oval, almost rounded; 4 = polygonal.

10. Shape of setae above eyes. 0 = as long as or slightly longer than setae on rostrum; 1 = much longer than setae on rostrum; 2 = setae almost indistinct, not raised; 3 setae absent.

11. Scrobe, dorsal view. 0 = expanded outside of rostrum; 1 = not expanded outside of rostrum.

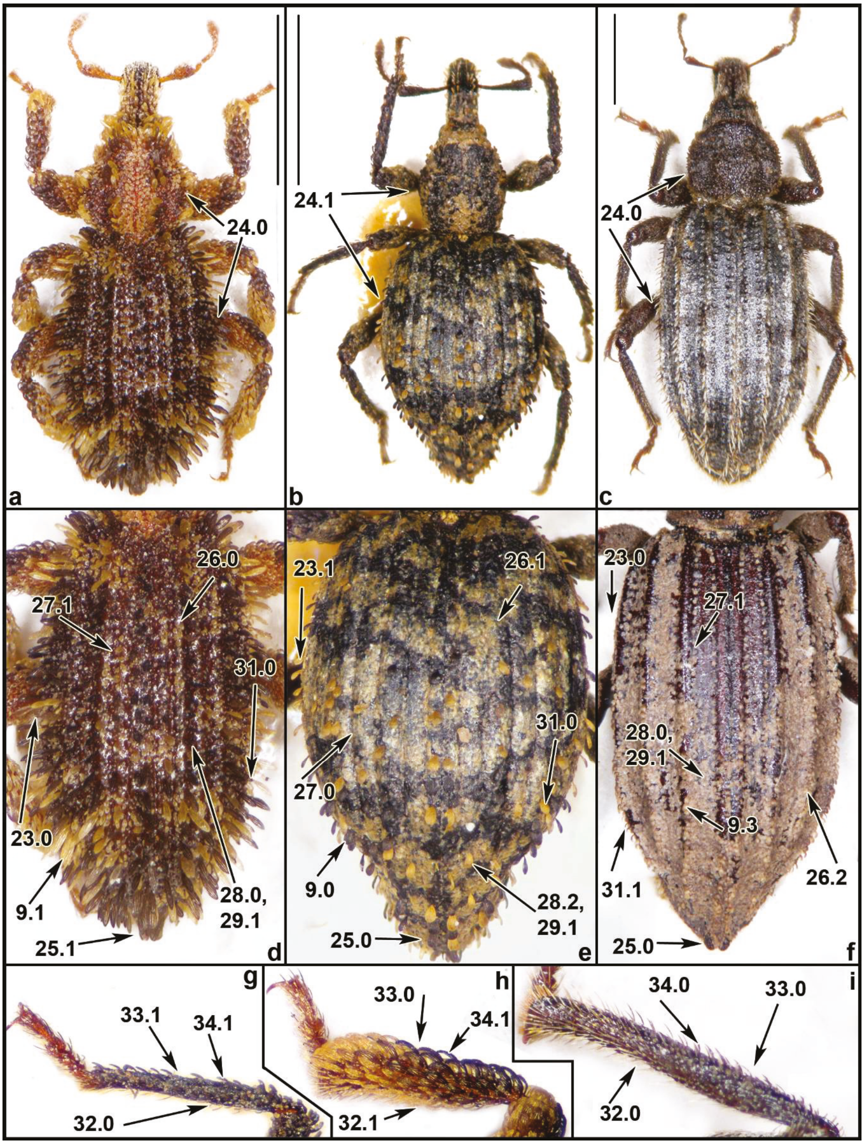

Figure 1. Body of *Dichotrachelus baldensis* Barajon (**a**); *D. afer* Peyerimhoff (**b**); *D. manueli* Marseul (**c**). Elytra of *D. baldensis* (**d**); *D. afer* (**e**); *D. linderi* (Fairmaire) (**f**). Protibia of *D. afer* (**g**); *D. baldensis* (**h**); *D. manueli* (**i**). Not in scale. Bars for body size. 2 mm.

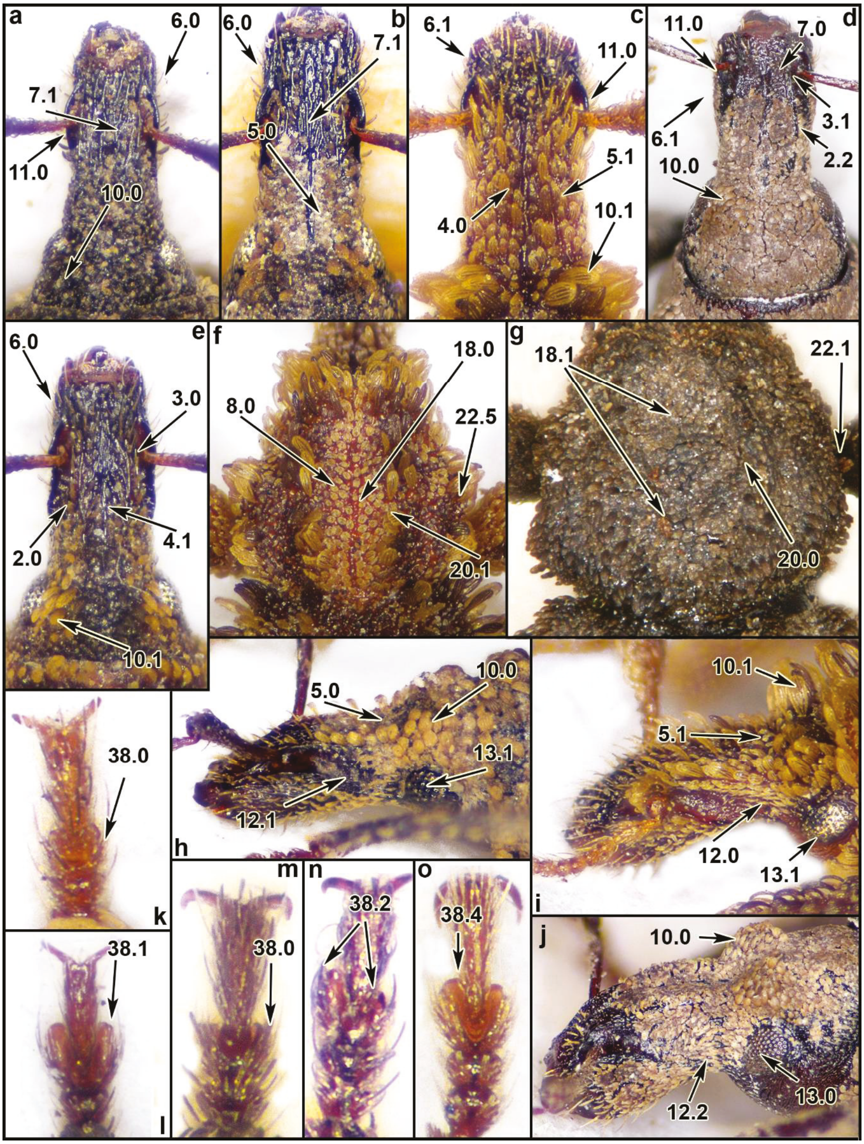

Figure 2. Rostrum, dorsal side, of *Dichotrachelus augusti* F. Solari (**a**); *D. laurae* Meregalli (**b**); *D. baldensis* Barajon (**c**); *D. linderi* (Fairmaire) (**d**); *D.pericarti* Osella (**e**). Rostrum, lateral side of *D. rifensis* Meregalli (**h**); *D. baldensis* (**i**); *D. linderi* (**j**). Pronotum of *D. baldensis* (**f**); *D. sulcipennis* Stierlin (**g**). Protarsus of *D. baldensis* (**k**); *D. meregallii* Osella (**l**); *D. augusti* F. Solari (**m**); *D, negrei* Gonzalez (**n**); *D. rifensis* (**o**). Not in scale.

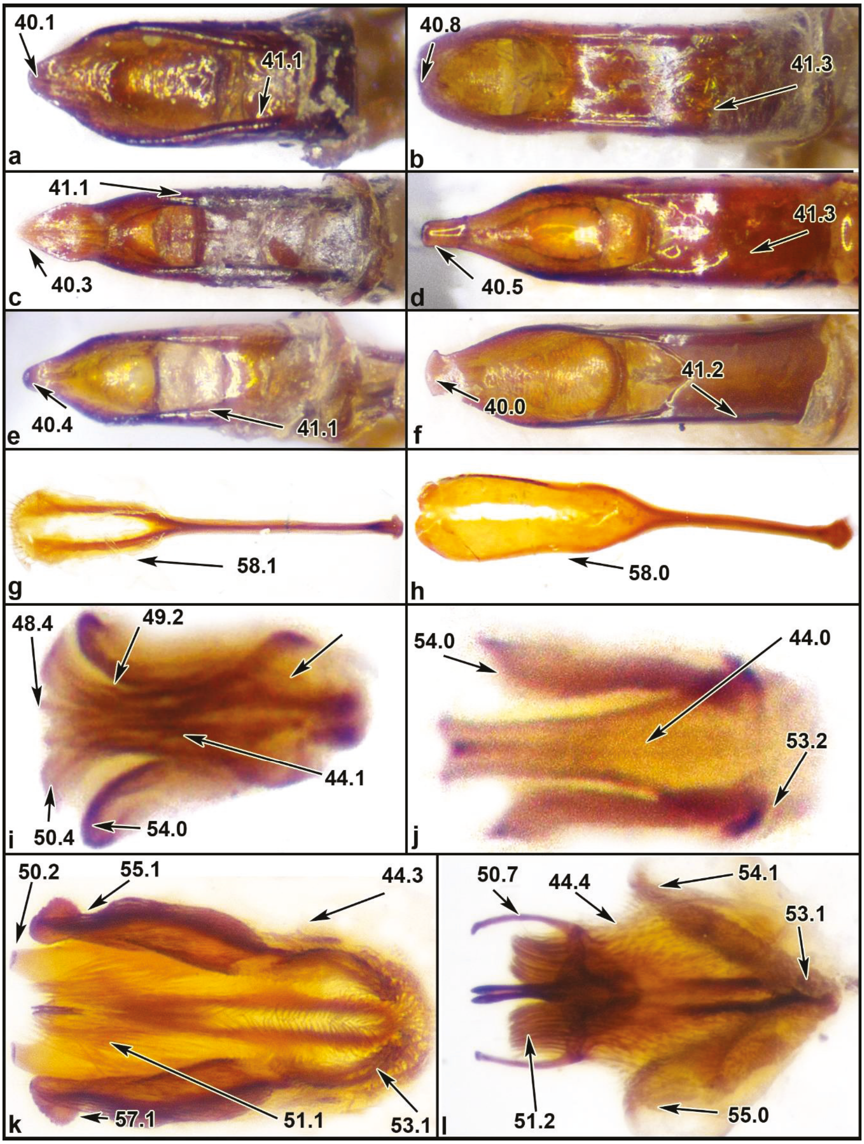

Figure 3. Penis of *Dichotrachelus baldensis* Barajon (**a**); *D. cantabricus* Franz, 1954 (**b**); *D. meregallii* Osella (**c**); *D. devillei* Osella (**d**); *D. negrei* Gonzanez (**e**); *D. augusti* F. Solari (**f**). Sternum VIII of female of *D. sterlini* Gredler (**g**); *D. sulcipennis* Stierlin (**h**). Male genital sclerite of *D. baldensis* (**i**); *D. graellsii* Perris (**j**); *D. baudii* (Seidlitz) (**l**); *D. sulcipennis* (**k**).

12. Shape of setae at base of scrobe, in front of eyes. 0 = elliptical; 1 = hair-like; 2 = oval; 3 = absent.
13. Eyes, number of ommatidia. $0 \geq 50$; $1 \leq 30$; 2 = about 40.
14. Shape of setae on antennal scape. 0 = slender; 1 = spatulate; 2 = hair-like.
15. Shape of antennomere 1 of funicle. 0 = longer than wide; 1 = globose.
16. Shape of antennomere 2 of funicle: 0 = very slender; 1 = moderately longer than wide.

17. Pronotum, ratio length/width. 0 = transverse; 1 = subquadrate; 2 = longer than wide.

18. Pronotum, shape of median groove. 0 = not distinctly separated in anterior and posterior groove; 1 = distinctly divided into two grooves separated by a median relief.

19. Pronotum, deepness of median groove. 0 = deep; 1 = weakly impressed; 2 = groove flat, margins not raised.

20. If 19 $\neq$ 2, shape of median groove. 0 = very broad; 1 = broad; 2 = narrow.

21. Pronotum, shape of dorso-lateral grooves. 0 = weakly impressed longitudinally; 1 = isolate, round and deeply impressed; 2 = undifferentiated.

22. Pronotum, shape of lateral margins of pronotum in dorsal view. 0 = narrowed anteriad and basad and parallel in median part; 1 = converging anteriad almost from base; 2 = regularly and slightly broadened medially; 3 = distinctly incised medially; 4 = linearly broadened to apical third; 5 = distinctly broadened at midlength.

23. Elytra, sides. 0 = subparallel for most of length; 1 = regularly broadened laterally.

24. Elytra, shape. 0 = not much broader than pronotum at maximum width; 1 = almost twice as broad as pronotum, particularly in female.

25. Elytra, apex. 0 = prominent in female; 1 = regularly rounded also in female.

26. Elytra, intervals convexity. 0 = odd intervals convex on dorsal part; 1 = all intervals flat; 2 = odd intervals convex from base to apex.

27. Elytra, shape of punctures on striae. 0 = punctures fuse, striae linear and deep, narrow; 1 = punctures distinct, spaced, as broad as intervals.

28. Elytra, distribution of setae. 0 = present also on even intervals; 1 = absent from even intervals; 2 = absent on dorsum of even intervals and present on their declivity.

29. if 28 $\neq$ 1, shape of elytral setae on even intervals. 0 = distinctly shorter than setae on odd intervals; 1 = almost identical to setae on odd intervals.

30. Setae on declivity part of suture. 0 = not distinctly more dense than setae on dorsum; 1 = setae much more dense than on dorsum.

31. Setae on odd intervals of elytra. 0 = dense; 1 = spaced.

32. Tibiae. 0 = slender, more than 5× as long as wide; 1 = robust, at most 4× as long as wide.

33. Vestiture of setae on tibiae. 0 = dense; 1 = sparse.

34. Shape of setae on tibiae. 0 = very slender, almost hair-like; 1 = thicker, spatulate.

35. Apex of foretibiae. 0 = almost straight; 1 = distinctly curved inwards.

36. Ventrites, vestiture. 0 = scales dense; 1 = scales sparse.

37. Shape of scales on ventrites. 0 = slender; 1 = oval.

38. Shape of segment 3 of tarsus. 0 = as wide as 2, lobes not broadened; 1 = broader than segment 2, as long as wide, both lobes equally broadened; 2 = broader than segment 2, only internal lobe broadened; 3, broader than segment 2 in male, not broadened in female; 4 = weakly lobed, only slightly broader than segment 2, slightly asymmetrical.

39. Penis, shape. 0 = very long and narrow, tube more than 5× as long as wide; 1 = regular, not very slender, tube less than 5× as long as wide.

40. If 39 = 1 penis, apical lamella. 0 = subtruncated, angularly broadened at sides; 1 = regularly shortly narrowed, subacute, not curved upwards; 2 = scarcely narrowed, apex round; 3 = with a flat, triangularly acute apex; 4 = as 1, curved upwards; 5 = elongated lamella, rounded at apex, upwards directed; 6 = very slender, regularly narrowed; 7 = long regularly narrowed, subacute, upwards directed; 8 = short, curved downwards, acute; 9 = scarcely narrowed, long upwards directed.

41. If 39 = 1 penis, sclerotization of dorsum: 0 = sides sclerotized to centre, basal part of ostium sharply delimited, margins of sclerotization sharply delimited; 1 = sides sclerotized to half of width; 2 = sides sclerotized only marginally, basal part of ostium not clearly delimited; 3 = dorsum strongly sclerotized; 4 = dorsum membranous.

42. If 39 = 1, shape in lateral view. 0 = scarcely curved; 1 = curved.

43. Length of internal sac: 0 = long, genital sclerite placed in correspondence of apex of temones; 1 = moderately long, sclerite placed in correspondence of midlength of temones; 2 = short, sclerite placed at base of temones; 3 = sclerite absent.

44. If 43 $\neq$ 3, shape of shield of sclerite. 0 = broadened basad and strongly narrow apicad, with downward curved apical plate; 1 = broadened basad, moderately narrowed at midlength, slightly broadened apicad; 2 = subquadrate, very broad basad and apicad; 3 = rectangular, almost not restricted medially; 4 = short, broadened at midlength; 5 = oblong, bifurcate apicad, not curved; 6 = linearly converging from very broad base to apex; 7 = same as 6, triangularly curved downwards at apex.

45. If 44 = 0, shape of lateral arms at apex of tectum. 0 = almost undifferentiated; 1 = developed, shorter than median plate; 2 = very short and thick; 3 = thick and highly developed, as long as median plate.

46. If 44 = 0, presence of setae on underside of apex of shield. 0 = present; 1 = absent.

47. If 44 = 0, apex of downward curved apex of shield. 0 = bifurcate; 1 = narrowed apicad; 2 = sides broadened, apex broadly rounded; 3 = sides parallel, apex barely rounded.

48. If 44 = 1, horn at apex of tectum. 0 = absent; 1 = longer than arms, slightly bifurcate at apex; 2 = obtuse, barely developed; 3 = as long as arms, broadened apicad; 4 = very minute, shorter than arms

49. If 44 = 1, width of shield at first third of length. 0 = half as wide as at base; 1 = scarcely narrower than at base; 2 = uniformly narrowed.

50. if 44 $\neq$ 0, anterior arms of genital sclerite. Anterior arms of genital sclerite: 0 = absent; 1 = very minute at side of apical plate; 2 = short, thick, with nearly the same thickness from base to apex, sharply curved downwards, only base of arm visible from above; 3 = short (much shorter than apical horn), thick at base and narrowed apicad, not or barely curved downwards, entire arm visible from above; 4 = moderately elongated, thick, distinctly and evenly curved downwards, the proximal half of its length visible from above; 5 = very long, narrow, sharply curved in its proximal part, reaching underside of sclerite; 6 = very long and narrow, prominent forwards beyond margin of tectum, not tapered apicad; 7 = same as 6 but distinctly tapered apicad.

51. if 44 $\neq$ 0, presence of setae on underside of tectum near apex. 0 = absent; 1 = scarce; 2 = dense and prominent beyond anterior margin of sclerite.

52. Ratio between length and width of tectum of genital sclerite. 0 = very long, ratio length/width > 4; 1 = long, ratio length/width 3–4; 2 = ratio l/w 2–3; 3 = ratio l/w 1.5–2; 4 = subquadrate, ratio l/w 1.1–1.3.

53. Position of base of valves of genital sclerite. 0 = at basal third of sclerite; 1 = at base of sclerite; 2 = valves joined basad behind base of sclerite; 3 = valves reaching base but not joined

54. Distal extension of valves of genital sclerite. 0 = almost reaching apex of tectum; 1 = distant from apex of tectum

55. Lower margin of valves of genital sclerite. 0 = entire; 1 = bilobate.

56. Thickness of anterior part of valves. 0 = not thickened; 1 = distinctly thicker than the basal part

57. Structure of distal part of valves of genital sclerite. 0 = without an apical lobe or a subapical process; 1 = with an apical lobe; 2 = with a subapical process.

58. Female sternite VIII, side of plate. 0 = sublinearly convergent from near base to apodeme (plate shape subtriangular); 1 = subparallel for most of length (plate shape subrectangular); 2 = curved with maximum width at basal third (plate shape oval); 3 = as 2, but plate much longer (plate shape elliptical); 4 = slightly curved inwards near apodeme.

59. Food plant. 0 = moss; 1 = Saxifraga; 2 = other Phanerogams.

3. Results

The results and discussion are primarily based on the data obtained from the Bayesian Inference. Topology and supports of the BI consensus tree were checked for congruence with topologies obtained with ML and MP. Usually, the terminal clades were uniformly present in all analyses, with various supports, whereas deep phylogeny, i.e., relationships among the large monophyletic groups, was not always clearly defined and in part differed among the analyses.

3.1. Morphological Analysis

Dichotrachelus always resulted in a monophyletic unit (BI: 92% posterior probability (pp); ML: 74% bootstrap (bs); MP: 70% symmetric resampling (sr), Bremer support 3; Figure 4). In ML and MP *Macrostyphlus* and *Dichotrachelus* clustered in the same clade, whereas in BI the two genera resulted in a polytomy (Figures 5 and 6).

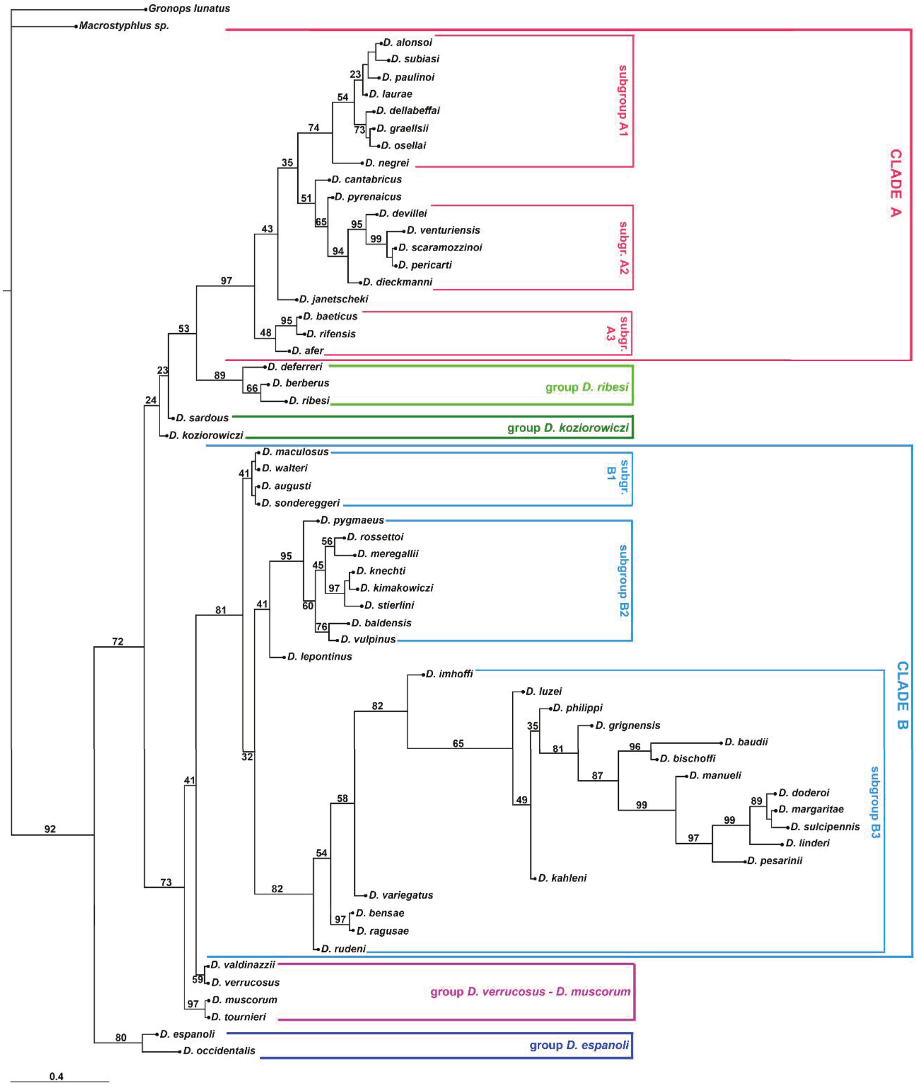

Figure 4. Morphological analysis. Bayesian Inference consensus tree. Numbers above branches indicate posterior probability. Scale bar unit: expected changes of state per character. See discussion for remarks on the clades and species group.

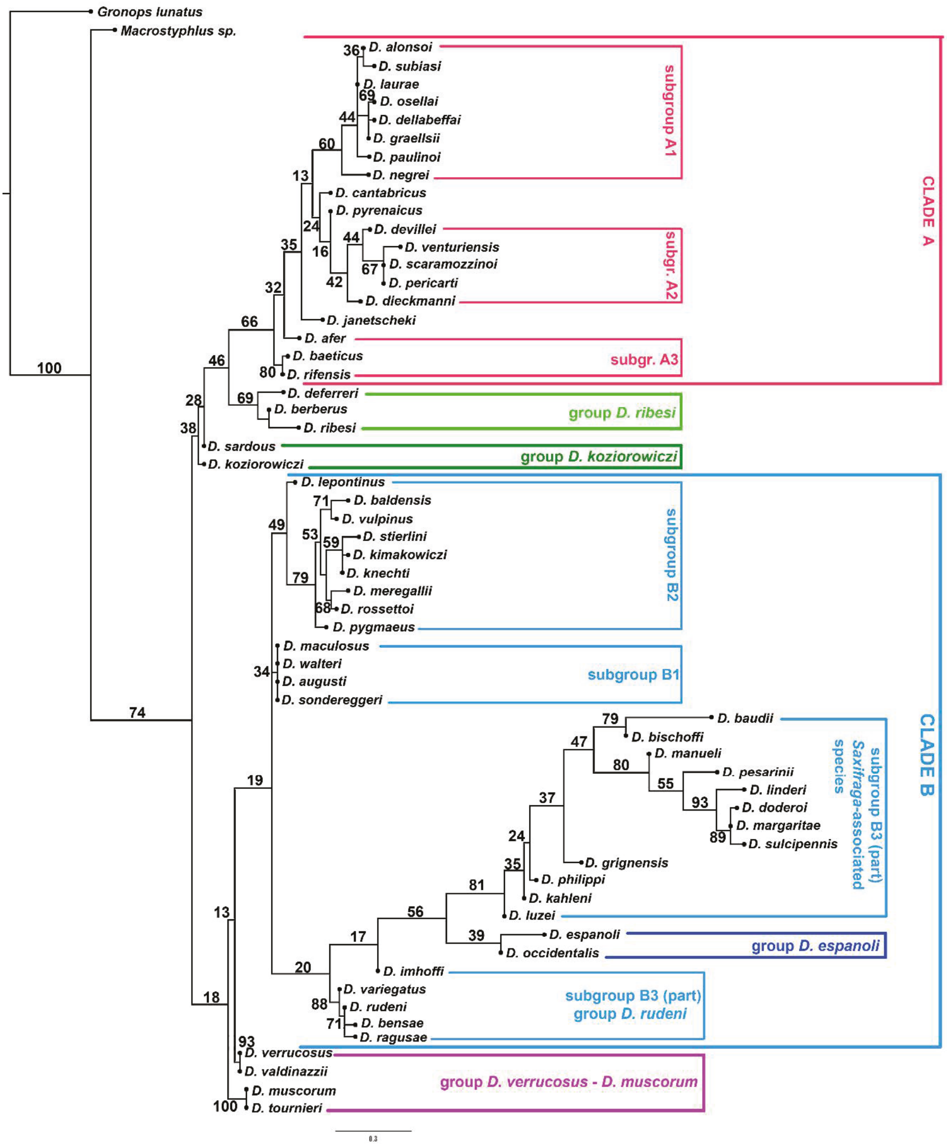

Figure 5. Morphological analysis. Maximum Likelihood consensus tree. Numbers above branches indicate bootstrap value. Scale bar unit: expected changes of state per character. Clades and species group are indicated as shown by the Bayesian analysis.

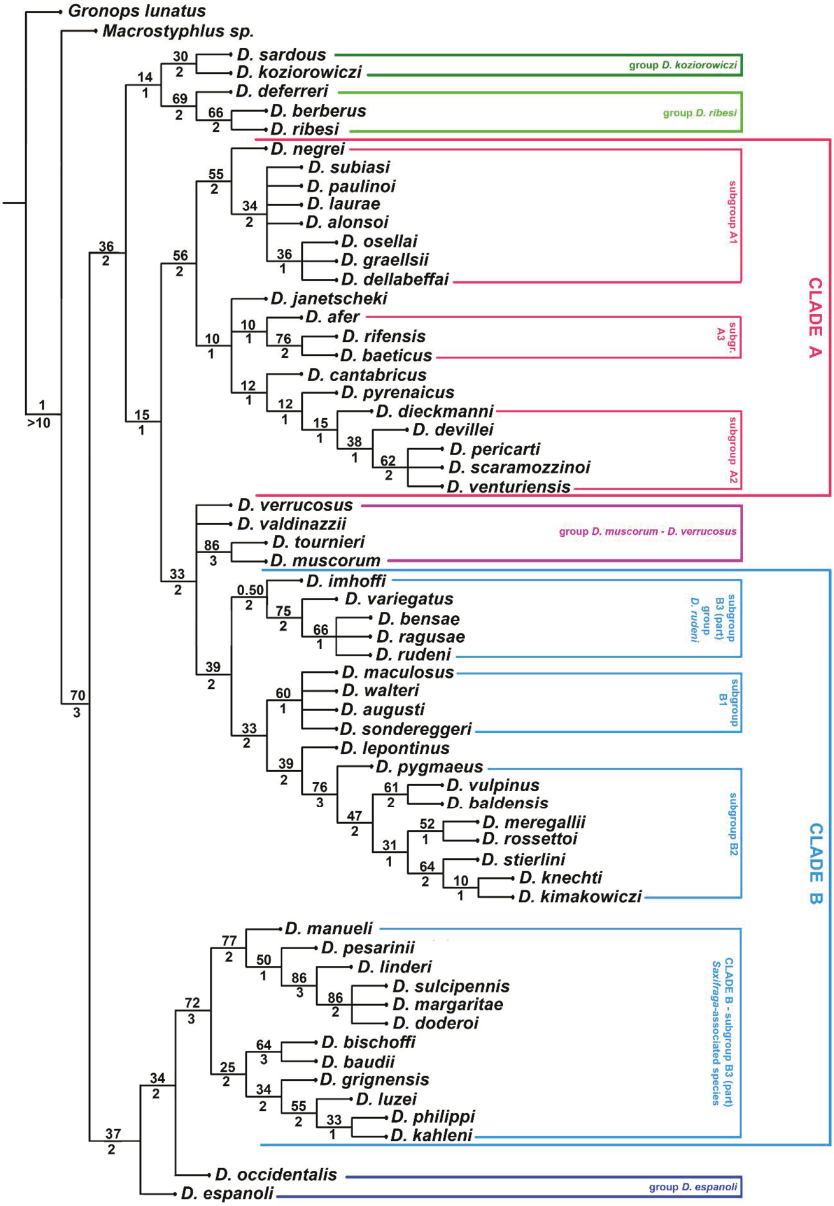

Figure 6. Morphological analysis. Maximum Parsimony consensus tree. Numbers above branches indicate symmetric resampling; numbers below branches indicate Bremer support. Length 281, consistency index = 0.45, retention index = 0.82. Clades and species group are indicated as shown by the Bayesian analysis.

Within *Dichotrachelus*, some relatively well-supported groups were differentiated. A first group (Clade A, BI: 97% pp; ML: 66% bs; MP: 56% sr, Bremer 2) includes the majority of the species present in the Iberian peninsula and the massifs of central-southern France and northern Africa. Within this clade, some subgroups correspond to reciprocally closely related species, which are distributed in the same region. Subgroup A1 (BI: 74% pp; ML: 60% bs; MP: 55% sr, Bremer 2) encompasses species that are present in central and northern Spain, excluding the Pyrenean region, and Portugal: *D. graellsii*, *D. dellabeffai* and *D. osellai*, that form a monophyletic species complex, present in all analyses, and with 73% support in BI, plus *D. alonsoi*, *D. laurae*, *D. paulinoi* and *D. subiasi*, the reciprocal placement of which was not univocally defined. *D. negrei* was the sister to the previous species. Another subgroup in Clade A delimited species from north-eastern Spain and the massifs of central-southern France: *D. dieckmanni*, *D. devillei*, *D. scaramozzinoi*, *D. pericarti* and *D. venturiensis* (Subgroup A2, 94% pp in BI). Among these species, the Spanish *D. dieckmanni* clustered as the sister taxon to the other species, and the last three taxa always formed a well-supported monophyletic complex. Two species from the Pyrenees and the Cantabrians (*D. pyrenaicus* and *D. cantabricus*) were weakly associated with Subgroup A2. Clade A also includes some *Dichotrachelus* from southern Spain and northern Africa: *D. afer* from the Algerian Djurdjura and the two vicariant species living on the two sides of the Gibraltar strait, *D. baeticus* from Mount Mulhacen in Sierra Nevada, southern Spain and *D. rifensis* from Mount Tidiquin, in the Rif chain, northern Morocco (Subgroup A3). A further species from southern Spain, Sierra Nevada, *D. janetscheki*, clustered in an "intermediate" position between Subgroups A3 and Subgroups A1 and A2 (as sister to A1–A2). Three very peculiar species from, respectively, north-western Spain (*D. ribesi*), southern Spain (*D. deferreri*) and the Djbel Tazzeka in northern Morocco (*D. berberus*), the reciprocal relationships of which appeared to be quite strong (BI: 89% pp; ML: 69% bs; MP: 69% sr, Bremer 2), were together weakly supported as the sister group to Clade A under BI and ML analyses (BI: 53%; ML: 46% bs). Under MP, however, these three species clustered in a different clade, together with *D. sardous* and *D. koziorowiczi* from Sardinia and Corsica, respectively. These two latter species clustered as sister to Clade A in both BI and ML, but this placement lacked any support.

A second major clade (Clade B, 81% pp in BI) included all the species from the Alps and Apennines. Inside this unit, three large subgroups were differentiated. One subgroup (Subgroup B1), not statistically supported in BI and ML (respectively, 41% pp and 34% bs in ML), and weakly supported in MP (60% sr, Bremer 1), is exclusive to the western Alps, and includes four very similar species: *D. maculosus*, *D. walteri*, *D. augusti* and *D. sondereggeri*. A second subgroup (Subgroup B2, BI: 95% pp; ML: 79% bs; MP: 76% sr, Bremer 3) includes many of the "small sized" species present in the entire Alpine chain and expanded to the Carpathians: *D. meregallii*, *D. rossettoi*, *D. pygmaeus*, *D. kimakowiczi*, *D. stierlini*, *D. knechti*, *D. baldensis* and *D. vulpinus*. A further species, *D. lepontinus*, from the mountains north-west of Lake Maggiore, in central-western Alps, clustered as sister to the taxa of Subgroup B2, in all the analyses, even though this placement was scarcely supported (BI: 41% pp, ML: 49% bs; MP: 39% sr, Bremer 2). The last group in Clade B (Subgroup B3) encompasses the remaining moss-associated Alpine species, and those from the Apennines: *D. rudeni*, *D. bensae*, *D. variegatus*, *D. ragusae* and *D. imhoffi*. These last species clustered in BI as sister to the species associated with *Saxifraga*, already discussed in [19,20], with a high support in BI (82%). The same topology also resulted in the ML analysis, except for the placement within Subgroup B3 of *D. espanoli* and *D. occidentalis* (see below for further comments). In MP, however, the *D. imhoffi*-*D. rudeni* complex clustered as sister to the other small-sized, moss-associated Alpine species of Subgroups B1 and B2, whereas the *Saxifraga*-associated species formed a separate clade, as sister to the clade of the small-sized, moss-associated species.

Two Pyrenean taxa, *D. muscorum* and *D. verrucosus*, and its vicariant *D. valdinazzii* (originally described, probably correctly, as a subspecies of *D. verrucosus*), plus the enigmatic *D. tournieri* from the surroundings of Geneva (Switzerland), clustered in two groups, as sister to the Alpine-Apennine taxa in all analyses.

Two more *Dichotrachelus* from the Pyrenees, *D. espanoli* and *D. occidentalis*, clustered as sister to the remaining *Dichotrachelus* in BI, but were instead correlated with the *Saxifraga*-associated species in MP and ML, as sister to the alpine species, even though without statistical support.

3.2. Molecular Analyses

The *mt-Cox1* analysis was relatively congruent with the results of the morphological analysis, with some exceptions. Since only a few species were available, our results cannot be conclusive at present. A first Clade (Clade A) corresponds to Clade A in the morphological analysis, with a minor difference in the suggested relationships of *D. venturiensis*, which was here associated with the Spanish species rather than with *D. devillei*.

More differences between the morphological and the *mt-Cox1* analyses are apparent for some of the alpine and apennine species (Clade B), with particular regard to the subgroup B2 as circumscribed by the morphological analysis. In the molecular analysis the *D. imhoffi*-*D. rudeni* complex was not directly related to the *Saxifraga*-associated taxa, but rather it clustered as a sister clade to the group of *D. kimakowiczi*, *D. kraussi* and *D. vulpinus*. A further species that was part of Subgroup B2, *D. knechti*, in the molecular analysis was placed as sister to the *Saxifraga*-associated species, even though the support was quite low (56% pp). *D. meregallii* and *D. rossettoi* clustered in separate lineages, whereas *D. lepontinus*, a species placed as sister to Subgroup B2 in the morphological analysis, was here associated with Subgroup B1, i.e., the *D. maculosus* complex, even though with low support (51% pp). The complex of species feeding on *Saxifraga* also clustered in a strongly supported clade (93% pp) in the *mt-Cox1* analysis. The relationships among these last species were almost identical in the morphological and the molecular analyses.

In the Cyclominae BI analysis *Dichotrachelus* formed a fully supported clade, distinct from the other Cyclominae (Figures 7 and 8). Weak possible relationships with Listroderini, in particular the genera *Puranius Macrostyphlus* and *Listronotus*, were suggested, but without statistical support.

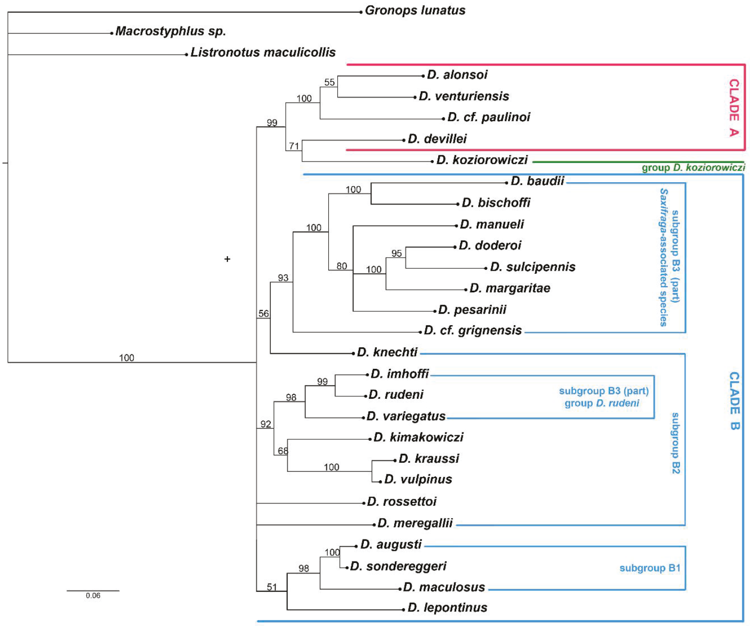

Figure 7. Mitochondrial cytochrome oxidase I analysis, *Dichotrachelus*. Bayesian Inference consensus tree (50% majority rule). Numbers above branches indicate posterior probability. Scale bar unit: expected substitutions per site. Clades and species group are indicated as shown by the Bayesian analysis based on morphology.

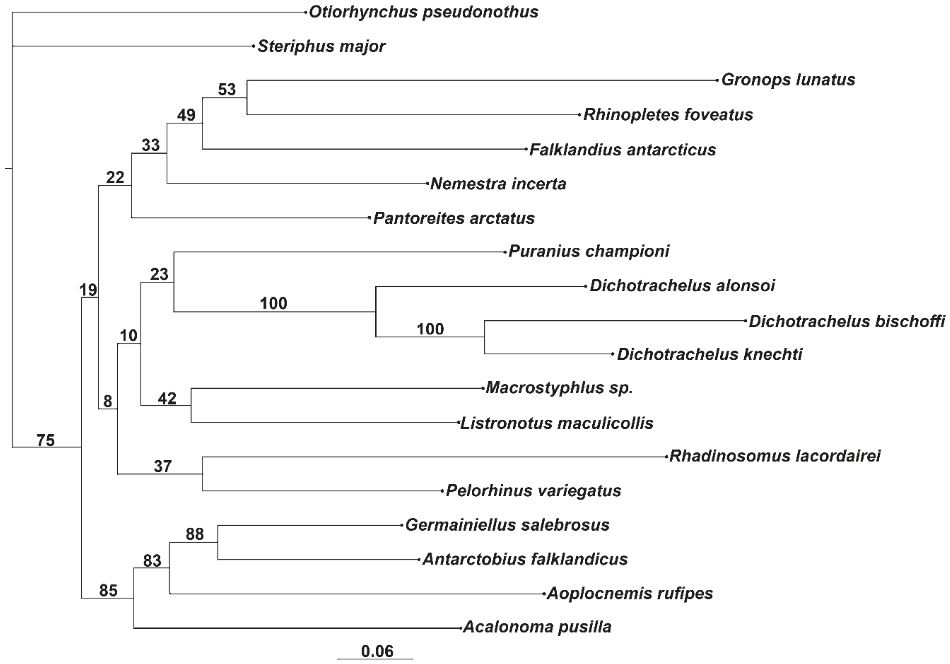

Figure 8. Mitochondrial cytochrome oxidase I analysis, Cyclominae. Bayesian Inference consensus tree. Numbers above branches indicate posterior probability. Scale bar unit: expected substitutions per site.

3.3. Pairwise Distance

In the aligned sequences of the *Dichotrachelus*, 458 out of 775 sites (59%) were conserved. When translated to amino acids, 195 out of 258 (75.6%) sites were conserved. Hence, a large part of the variable sites regarded the third position of the codon, in cases when the third nucleotide of the codon does not result in a different amino acid.

Dichotrachelus* vs. *Macrostyphlus, Listronotus* and *Gronops. Median pairwise distance in base sequences of *Dichotrachelus* vs. *Macrostyphlus* sp. was 0.1667, with a mean distance of 0.1659 (Tables III and IV). The lowest distance was found in *D. rudeni*, with a value of about 0.14, and the highest was in the *Saxifraga*-associated species, with a value of 0.17–0.19. The median pairwise distance vs. *Gronops lunatus* was 0.1925, the mean distance was 0.1937, and it was quite constant in all species. The median distance of *Dichotrachelus* vs. *Listronotus maculicollis* was 0.1743, and the mean distance was 0.1780. When the sequences were translated to amino acids, the distance of *Dichotrachelus* vs. *Macrostyphlus* sp. was quite low (median pairwise distance 0.1026, mean distance 0.1076), and only slightly lower than the distance vs. *Listronotus maculicollis* (respectively 0.1106 and 0.1108), whereas the distance vs. *Gronops* was about twice as great (median distance 0.2000, mean 0.1980).

Interspecific distance. The distance between different species in the base sequence varied from about 8 to 18%, depending on the reciprocal affinities, with the lower values being found among species belonging to the same clade. Distance between closely related sister species was between 7–8% and 12%: *D. alonsoi* and *D. paulinoi* differed by 11.5–12% in base sequences, and 4% in amino acids; *D. margaritae* differed by 11% from *D. sulcipennis* and 7–8% from *D. doderoi*, corresponding to, respectively, 5.7% and 3.6–4% in amino acids.

Intraspecific distance. Specimens of different populations of the same species, or more specimens of the same population, were available for some taxa. Variation was usually quite limited, and often it did not result in different amino acids, or at most, in the replacement of three to four amino acids. In *D. maculosus* variation was between 0 and 2.8%, and this variation was related to the different populations: specimens from Switzerland differed up to 2.8% from those from the southern and western part of the range, in south–western Piedmont and in south-eastern France. This variation resulted in a maximal substitution of 0.16% of the transcribed amino acids (four amino acids out of 258). All *D. rudeni* specimens examined came from southern Switzerland and bordering areas of northern Italy; interpopulation variation among them in base sequences was between 0.5 and 1.7%, with a variation in the amino acid sequence of 0 to 1.2%. In *D. koziorowiczi*, however, the two specimens that were sequenced, found in two different localities in Corsica, one at high altitude and one in a forest habitat, differed by 6.2% in base sequences and 1.2% in amino acids.

Intrapopulation distance. It was possible to obtain some data on intrapopulation variation in *D. bischoffi*: six of the eight specimens from Col de Bardoney, in the Aosta Valley, that were sequenced did not show any variation, and the other two differed by only a single site, not resulting in a different amino acid. In *D. knechti* no variation was detected among the five specimens, again all from Col de Bardoney. The two specimens sequenced of *D. pesarinii* differed by seven sites, but again this did not result in different amino acids.

No synapomorphy in amino acids or base sites was seen for any clade, even though some variation apparently characteristic of a single species, or of closely related species, could be detected when many specimens of the same taxon were available. For example, all specimens of *D. maculosus* examined (16) have a Glycine replacing an Alanine in position 83 and a Serine replacing a Methionine or a Leucine in position 244. The related *D. doderoi* and *D. margaritae*, apparently vicariant species distributed in the western Alps, south of the Susa Valley, share a Threonine replacing an Alanine in position 88 and a Threonine replacing an Isoleucine in position 229 in the eight specimens examined; these can be considered as synapomorphies for the two sister species.

4. Discussion

The discussion is mainly based on the results of the morphological analyses, since *mt-Cox1* was only available for a part of the species, which, moreover, were not uniformly representative of all the distinct clades that resulted from the morphological analysis. The topology taken into account was the one obtained by the BI analysis, since it is considered to outperform parsimony [33]. Nevertheless, cases of incongruence among the results of the other methods of analysis implemented are considered and further discussed.

4.1. Relationships of *Dichotrachelus* within Cyclominae

Cyclominae, in phylogenetic analyses based on a variety of datasets, has been shown to be a paraphyletic taxon [34]. The classification within the subfamily was recently revised [2], and considered to include eight tribes, mostly restricted to the southern hemisphere. However, the composition of the tribes is also uncertain, and some appear to be paraphyletic, or even polyphyletic [2,34]. Palaearctic species are only found in the Cyclominae tribe Hipporhinini, which is mainly composed of African and Australian taxa, and Dichotrachelini, comprising the Palaearctic genus *Dichotrachelus* [1,2] and, doubtfully, the African genus *Adichotrachelus* Hoffmann, 1965 [35] (Figure 8). To date, phylogenetic relationships of *Dichotrachelus* within the Cyclominae are unclear [2]. We are aware that the use of the single *mt-Cox1* marker does not allow the inference of deep phylogenies with confidence, because of its high variability and subsequent saturation effect for taxa separated for a long time [36,37], particularly regarding the third nucleotide of the codon, which has the highest substitution rate [38]. However, *mt-Cox1* gave good information on relationships in Curculionidae Cryptorhynchinae [39] and in surveys on Curculionoidea [40], and particularly on the "Broad-nosed weevils" (Entiminae and Cyclominae), the mitogenome helped in reconstructing phylogenies [34]. Hence, we will now shortly discuss some indications that can be drawn from our analyses about possible relationships of the genus within the subfamily. We emphasise that these data are intrinsically incomplete and therefore must only be considered as simple hypotheses to be tested when a more complete set of molecular markers and Cyclominae taxa is available.

The most interesting remark regards the rather evident absence of any close relationship between *Dichotrachelus* and the other Palaearctic Cyclominae, members of the tribe Hipporhinini, neither regarding their external and genital morphology, nor based on the *mt-Cox1* sequences. Indeed, among the few species of Cyclominae for which sequences were available, *Gronops* had the highest *p*-distance from *Dichotrachelus*, a distance similar to that of non-Cyclominae taxa (around 0.20, that is, saturation of *mt-Cox1*). Furthermore, in the Cyclominae BI analysis it did not show any relationship with *Dichotrachelus*.

If the absence of close relationships between *Dichotrachelus* and the Palaearctic Hipporhinini seems to be well supported, the present data do not clarify with equal reliability the true affinities of the genus. In the *mt-Cox1* analysis *Macrostyphlus* (Cyclominae: Listroderini, a predominantly south-American tribe, the range of which also includes Australia, New Zealand and Tristan da Cunha Islands [41]) showed a *p*-distance of about 0.16, but also other species of Listroderini and Aterpini had a p-distance varying between 0.16 and 0.18. In BI the genus clustered as a separate, fully supported lineage, part of a (poorly supported) clade also including *Macrostyphlus* and *Puranius*. Additionally, in the recent combined Cyclominae-Entiminae analysis [34], where a more complete set of markers was used, *Dichotrachelus* was weakly associated with *Puranius* ([34], Figure 1), and thus with the Listroderini subtribe Macrostyphlina, as defined in [42]. As previously said, we used *Macrostyphlus* as one of the outgroups in our study because we had specimens available for the morphological matrix. *Macrostyphlus* sp. also shares mosses as the host-plants of both larvae and adults (Germann, pers. obs. on two species of *Macrostyphlus* from Ecuador). Cryptogam herbivory is rare in Curculionoidea [43,44], and it has been considered to be often a secondary, recent strategy response to the harsh habitat conditions that occurred during the Pleistocene glaciations [45]. This explanation cannot be advocated for *Dichotrachelus*, the only Palaearctic weevil taxon associated with cryptogams, or for *Macrostyphlus*. Both taxa appear to be primarily associated with mosses, since the ecosystems of the regions that they colonize were not influenced by, or were largely protected from, quaternary glaciations. However, even if the unusual biology shared between *Dichotrachelus* and *Macrostyphlus* is taken into account, there is so far no conclusive evidence that it derives from a common ancestor. Regarding *Adichotrachelus*, from Kenya, Mount Aberdare, a species never collected again after its description, it has not yet been possible to examine it, since the type specimen is not present in the Paris Natural History Museum (Perrin, pers. comm.). Its similarity was regarded as being due to convergence [12,13], but relationships between these genera may be possible. The presence of a taxon related to *Dichotrachelus* in the mountains of Kenya could in fact indicate a possible route of dispersal of its ancestors northwards from a primary centre of differentiation in tropical or subtropical Africa, even though the exclusive presence of taxa of *Dichotrachelus* in territories derived from the fragmentation of the western Peri-Tethys plates, and their apparent absence from any of the territories derived from the African plate (Atlas of Morocco, for example), does not seem to support this hypothesis. In any case, since the actual distribution of Cyclominae is strongly suggestive of a primary Gondwanian differentiation [2], relationships in the deep phylogeny of Dichotrachelini with taxa from the southern hemisphere are possible, and even likely. Ancestral dispersal towards the Iberian plate via the present day American plate, where many Listroderini live, may have occurred, since Cyclominae apparently differentiated during the mid-Cretaceous [46], more than 100 mya, thus before the split of the American continent from the Afro-European plates, an event dating to about 80 mya [47].

4.2. Phylogenetic Lineages in Dichotrachelus

Our results indicate that the genus is composed of two major lineages, Clade A and Clade B, as presented in Figure 4, with a few additional species, the placement of which is still uncertain. Relationships among the major clades are still poorly disclosed, and the placement of some taxa is not univocally defined in the various analyses.

Clade A. This clade includes the majority of the Iberian species, plus those of the massifs of southern France. All these species share a specific shape of the genital sclerite (Char. 45.0, Figure 3j). Its shield has a broad basal part and the sides are then regularly narrowed, up to the midlength, where it is between half and 1/3 as wide as at the base. From here to the apex, the sides are more or less parallel. The apex has a downwards curved broad plate, rounded or sub-acute apicad, and, laterally, this plate presents two arms, which can be long, reaching the apex of the plate, or shorter, to very short and narrow. The narrow elliptical scales in front of the eyes, which are sometimes not clearly visible, (Char. 12.0) and the scales appressed to the integument on the frons (Char. 5.0) are other synapomorphies for this clade. Within this clade, some species-groups are morphologically more or less well differentiated. Only for a few of them were molecular data available, that confirm the monophyly of the clade.

The Iberian species belonging to Clade A share the very narrow elytral striae, the punctures of which are not clearly distinct, rather they form relatively deep lines, with much broader intervals (Char. 27.0). Among these species, a lineage of closely related taxa lives in the massifs of central and northern Spain (*D. subiasi*, *D. paulinoi*, *D. laurae*, *D. alonsoi*, *D. osellai*, *D. graellsii* and *D. dellabeffai*, Subgroup A1). These species share two additional genital synapomorphies, with the dorsal sclerotization of the penis not being clearly delimited (Char. 43.3) and the absence of setae on the lower part of the genital sclerite (Char. 52.0). *D. negrei*, from north-western Spain and northern Portugal, appears to be related to these species. It mainly differs inbecause the third tarsal segment is slightly, but distinctly, broadened (Char. 38.2, Figure 2n), besides some characters on the rostrum, partly homoplastic (Char. 3.1, 4.1).

The species from southern France of the *D. pericarti* complex (*D. devillei*, *D. pericarti*, *D. scaramozzinoi*, *D. venturiensis*), together with *D. dieckmanni*, from north-eastern Spain, form another apparently monophyletic group (Subgroup A2). These species share the shape of the apical part of the penis (Char. 40.5), with the exception of *D. dieckmanni*, the penis of which, even though with a rather similar shape, has a broader apical lamella, which moreover shows two angular lateral prominences. The species of the *D. pericarti* complex also differ from those of Subgroup A1 by the presence of setae on the lower side of the genital sclerite (Char. 52.1), the elytra being broadly ovate in females (Char. 24.1) and the distribution of setae on the even intervals, usually absent from the dorsum and present on the declivity (Char. 28.2). The elytral striae in these species are distinctly punctured (Char. 27.1). Two species from the Pyrenees and Cantabrians, *D. pyrenaicus* and *D. cantabricus*, are also part of Clade A. They have narrow, linear striae, and the former typically has very slender elytra and thepenis with a downwards curved apex, an autapomorphy not appearing in other taxa of the genus. The correct placement of these two species within the clade is still uncertain.

Another well-defined complex in Clade A, Subgroup A3, includes three species from southern Spain and northern Africa: *D. afer*, *D. rifensis* and *D. baeticus*. The two last species are morphologically extremely similar, sharing almost all of the character-states and thus representing a pair of sister species. This complex is characterized in particular by the odd intervals that are almost flat at their base (Char. 26.1), a state seldom present in the genus, as well as the shape of the apex of the genital sclerite (Char. 48.1) and the broad elytra in females. This last trait, anyway, may be partly homoplastic.

A further species belonging to Clade A is *D. janetscheki*, occurring in Sierra Nevada, mainly on the northern slopes. Although its precise relationships with other species of the clade are still uncertain, it shares several characters with the taxa of Subgroup A1, such as the narrow striae (Char. 27.0), the third tarsal segment not being bilobate, and the scarcely broadened female elytra.

Three taxa of *Dichotrachelus* known from very isolated localities appear to form a sister group to all these species of clade A. These are *D. ribesi*, from Sierra de Obac, in north-eastern Spain, the very similar *D. berberus*, from Djbel Tazzeka, in northern Morocco and possibly *D. deferreri*, found at 50 m a.s.l. in southern Spain. The inclusion of the latter in this group was only based on the morphological characters of the female, the only specimen known, and its position is therefore uncertain, as no information on the shape of the male genital sclerite was available.

Clade B. This clade includes all the species occurring in the Alps and the Apennines, plus apparently a few species from the Pyrenees. The sequences of *mt-Cox1* were available for several of these species. However, the results between morphology and *mt-Cox1* are only partly congruent.

One monophyletic clade, Subgroup B1, was recovered by both the molecular and the morphological analyses. It includes the species from the western and southwestern Alps of the *D. maculosus* complex (*D. maculosus*, *D. walteri*, *D. augusti* and *D. sondereggeri*). This complex is characterized by the very small third segment of tarsi (Char. 38. 0), the shape of the apical lamella of the penis, flattened and with two lateral acute projections (Char. 42.0) and a slightly differentiated structure of the apex of the genital sclerite, with a slightly broadened apex of horns (Char. 49.3), a trait shared with *D. lepontinus*. The latter species, according to the *mt-Cox1* analysis, appears indeed to be sister to the *D. maculosus* complex, from which it mainly differs in the slightly bilobed segment 3 of the tarsi. In all the morphological analyses another complex of species (Subgroup B2) was found to be monophyletic, with strong support (95% pp in BI). This group includes many of the remaining small-sized alpine *Dichotrachelus*. These species share some traits regarding the density of the elytral setae (Char. 32.0) and, with the exception of *D. meregallii*, also the shape of the penis (Char. 42.1). Within this group, some complexes of species seem to be reciprocally more closely related, such as *D. vulpinus*-*D. baldensis* and the complex including *D. stierlini*, *D. knechti* and *D. kimakowiczi*. However, in the *mt-Cox1* consensus tree *D. knechti* was separated from *D. kimakowiczi*, and placed instead in the clade including the *Saxifraga*-associated taxa, near its root and as sister to these (even though with low support). This position appears doubtful, since *D. knechti* shares all its characters with the taxa of Subgroup B, including the shape of the male genital sclerite. Therefore, we do not consider the placement resulted by the molecular analysis to be correct.

The disjunct range of *D. kimakowiczi* from all the other species of the genus, and in particular from its sister taxa distributed in the Eastern Alps, is remarkable. Vicariance between Alps and Carpathians, with a gap corresponding to the Dinarides, is not uncommon in montane flightless species, and it presumably originated during the late Tertiary orogenetic events that affected this region.

Two small-sized species, *D. rossettoi* and *D. meregallii*, had an uncertain classification, quite different between the morphological and the *mt-Cox1* analyses. As indicated by the molecular analysis, these two species could be old relicts, distantly related to the other alpine taxa of the genus. The shape of the genital sclerite clearly confirms that they belong to Clade B, but an isolated position in the clade is also suggested by some of the other morphological traits.

Additionally, the *D. imhoffi*-*D. rudeni* complex had a different placement in the various analyses. In the molecular analysis it formed a sister clade to the clade including some of the species of the morphological group B2, whereas in BI this complex was placed towards the root of the clade of the *Saxifraga*-associated species. In MP it clustered as sister to the small-sized species of the Subgroups B1 and B2. The placement suggested by the Bayesian analysis is supported by some characters that are shared between the *D. imhoffi* complex and the apparently less derived species of the *Saxifraga*-associated group, with particular regard to a somewhat "intermediate" structure of the genital sclerite.

Regarding the *Saxifraga*-associated species, our molecular and morphological analyses are congruent and reflect the classification already discussed [19]. The only difference with respect to the reconstruction proposed in [19] is the placement of *D. baudii* as the sister species to *D. bischoffi* also in the molecular analysis. This position appears to be correct according to the majority of the characters of the two species, with particular emphasis on the shape of the genital sclerite and the biology. In the molecular analysis reported in [19] *D. baudii* had clustered as sister to the whole *Saxifraga*-associated group, near its root. This placement was not considered to be correct, since it would imply a parallelism in the development of some 20 characters, including the very complex structure of the genital sclerite, almost identical between *D. baudii* and *D. bischoffi*, and also a double shift from mosses to *Saxifraga* as the host plants. In [19] the Bayesian analysis was performed by implementing the usual nucleotide substitution model (model "4by4" in MrBayes), whereas in the present study the "codon" model, which considers the codon as the substitution unit, was implemented. This model, according to the results of this study, seems to be less sensitive to the bias due to long-branch attraction and therefore it appears to perform better than the “4by4” substitution model, at least in the case of the codifying gene *mt-Cox1* for these weevils. Always regarding the *Saxifraga*-associated species, it can be noticed that they are not characterized by any synapomorphy, with respect to the other *Dichotrachelus*, in the *mt-Cox1* sequence. There are variations, occasionally typical of one or a few species, but not shared among all species of this subgroup.

D. koziorowiczi and *D. sardous* from Corsica and Sardinia are isolated from the other taxa. They are characterized by a peculiar shape of the genital sclerite, which shares its general structure with the Pyrenean species of the *D. verrucosus*-*D. muscorum* complex, even though in the latter the sclerite is much smaller. In the morphological analysis both groups cluster near the root of the entire genus, but since no molecular data are thus far available for the *D. verrucosus* complex, we prefer not to indicate any definite position for the group. One interesting point is the high pairwise distance (6%) that was observed between the two specimens of *D. koziorowiczi*, one collected at high altitude, above the timberline, and one found in a beech forest of low altitude. Furthermore, from a morphological perspective, small differences between these forms were previously observed by the first author. These data suggest that two different species may be recognized in the *Dichotrachelus* from Corsica, one typical of the alpine habitat and one associated with the forest habitat. More specimens from various other populations from the two habitats are required in order to achieve more detailed information.

The relationships of three species from the Pyrenees, *D. espanoli*, *D. occidentalis* and *D. elongatus*, are particularly uncertain. These clustered in a separate clade, sister to all the other *Dichotrachelus* in BI, but were at the base of the *Saxifraga*-associated clade in MP and ML. This placement is supported by some traits, such as the relatively larger size, the shape of the rostrum and the scrobes, yet the shape of their genital sclerite does not show any similarities with the *Saxifraga*-associated species. Also their biology is not yet certain. *D. occidentalis* and *D. elongatus* were indicated to be living on *Saxifraga* [48], but this information should be confirmed, since very often mosses are found together with *Saxifraga*. Already in the past it was suggested that some species, indeed associated with mosses, could live on *Saxifraga* or both *Saxifraga* and mosses depending on the habitat or locality. This was, for example, reported for *D. rudeni*, *D. alpestris* and *D. verrucosus* [49], or *D. imhoffi* [12,13]. So, for the time being, we prefer to maintain the *D. espanoli*-*D. occidentalis*-*D. elongatus* complex as *incertae sedis* in the genus *Dichotrachelus*.

The distribution of the various clades is shown in Figure 9.

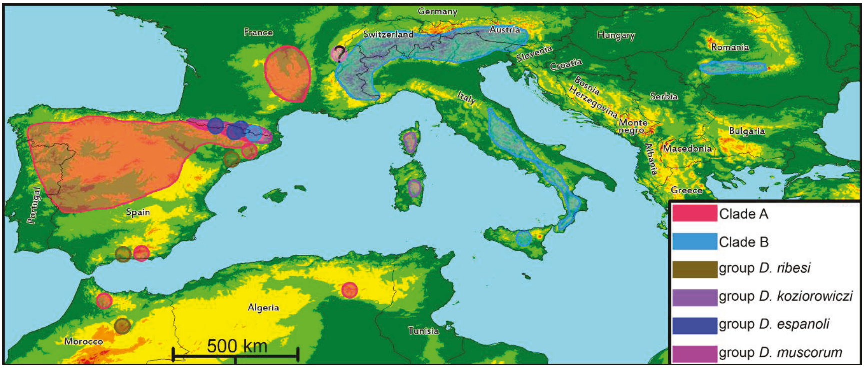

Figure 9. Distribution of the clades and species group of *Dichotrachelus*. Country level data downloaded from DIVA-GIS Free Spatial Data (http://www.diva-gis.org/Data) and processed with DIVA-GIS.

4.3. Species-Groups

Several species-groups in the genus were proposed [12,13]. Some of them are confirmed by our study, but in many cases the new information allows a more precise definition of the monophyletic groups, and placement of the species whose position is still not yet fully disclosed. Species-groups are informal categories and are not covered by the ICZN code, thus we do not necessarily follow the principle of priority for naming them.

a. *Species-groups associated with mosses*.

1. Species-group *D. graellsii*. It includes these reciprocally more closely related species:
    a. *D. graellsii*, *D. dellabeffai* and *D. osellai*.
    b. *D. alonsoi*, *D. subiasi*, *D. paulinoi* and *D. laurae*.
    c. *D. negrei*.

Distribution. Northern and central Spain, Portugal.

2. Species-group *D. pericarti*. It includes these reciprocally more closely related species:
    a. *D. pericarti*, *D. scaramozzinoi*, *D. venturiensis*, *D. devillei* and possibly *D. dieckmanni*
    b. *D. pyrenaicus*.
    c. *D. cantabricus*.

Distribution. Southern France, Pyrenees, north-eastern Spain, Cantabrians.

3. Species-group *D. afer*. It includes *D. afer*, *D. baeticus* and *D. rifensis*.

Distribution. Northern Algeria, northern Morocco, southern Spain.

These three species-groups form a fully supported monophyletic clade.

The relationships of *D. janetscheki*, from southern Spain, apparently sister to all species of clade A, should be confirmed. For this reason, we prefer not to include it in any of the previous groups.

4. Species-group *D. ribesi*. It includes *D. ribesi*, *D. berberus* and possibly *D. deferreri*.

Distribution. North-eastern and southern Spain, northern Morocco.

5. Species-group *D. koziorowiczi*. It includes *D. koziorowiczi* and *D. sardous*.

Distribution. Corsica, Sardinia.

6. Species-group *D. muscorum*. It includes *D. muscorum*, *D. tournieri, D. valdinazzii* and *D. verrucosus*. According to the examination of the holotype, *D. tournieri* might be a mislabelled specimen of *D. muscorum*. However, more research is required at its type locality, the surroundings of Geneva, Switzerland, before the hypothetical synonymy can be confirmed.

Distribution. Pyrenees, surroundings of Geneva, Switzerland (doubtful).

7. Species-group *D. maculosus*. It includes *D. maculosus*, *D. walteri*, *D. augusti* and *D. sondereggeri*.

Distribution. Western Alps.

8. Species-group *D. stierlini*. As for other groups, it is possible to recognize species more closely reciprocally related:
    a. D. *stierlini*, *D. knechti* and *D. kimakowiczi*.
    b. D. *baldensis*, *D. vulpinus* and *D. pygmaeus*.

Distribution. Alps, Carpathians.

D. rossettoi and *D. meregallii* might also be part of this group, even though they are quite isolated, and the *mt-Cox1* data are not congruent with those of the morphological analysis. *D. ulbrichi*, from the eastern Alps, is not included in the present study since it was not possible to examine its type. However, the only specimen known is apparently, morphologically, sister to *D. meregallii*.

Also *D. lepontinus* might be part of this species-group, in a somewhat "intermediate" position linking group 7 to group 8 (more precisely, as the sister to group 8).

9. Species-group *D. rudeni-D. imhoffi*. It includes *D. imhoffi*, *D. rudeni*, *D. variegatus*, *D. bensae*, and *D. ragusae*.

Distribution. North-western to central Alps, Apennines, Sicily.

b. Species groups associated with Saxifraga

10. Species-group *D. luzei*. It includes *D. luzei*, *D. kahleni*, *D. philippi* and *D. grignensis*. Some characters of the genital sclerite of the latter indicate that it is a more derived species, which already shows some of the states present in the species of group 11.

Distribution. Eastern to central Alps.

11. Species-group *D. manueli*. It includes *D. manueli*, *D. bischoffi* and *D. baudii*. The latter species is morphologically strongly differentiated, due to the ovate scales being modified into long, hair-like scales not covering integument, and the possibly consequent smoothness of sculpture, with flat elytral intervals and pronotal grooves not impressed. However, its genital sclerite is almost identical to that of *D. bischoffi*, as is the general structure of the rostrum.

Distribution. Western Alps.

12. Species-group *D. sulcipennis*. It includes

    a. *D. pesarinii*.
    b. *D. linderi*.
    c. *D. sulcipennis*, *D. margaritae* and *D. doderoi*.

Distribution. Central and Western Alps, eastern Pyrenees.

c. Species group with uncertain biology

13. Species-group *D. espanoli*. It includes *D. espanoli*, *D. elongatus* and *D. occidentalis*. As previously indicated, this group has a particularly uncertain position within the *Dichotrachelus* classification. As suggested by some of the characters, it might be closely related to the *Saxifraga*-associated species, possibly as a less derived species, but the shape of the male genital sclerite contradicts this hypothesis. Moreover, confirmed data on their biology remain absent.

Distribution. Central and eastern Pyrenees.

4.4. Inter vs. Intraspecific Distance

Our results show that the species are well characterized, with no intra- and interspecific overlap, with the unique exception of *D. sondereggeri*, which does not show any difference from *D. augusti*. This fact suggests that speciation occurred by vicariance following geographical isolation in these stenotopic and flightless weevils. In species with a broad range, such as *D. maculosus*, which also has a broad altitudinal range, comprised between 700 and more than 2500 m a.s.l., the relatively higher difference between the populations, up to almost 3%, confirms that gene flow in the distance is reduced, so that, in the absence of true geographical barriers, only slow clinal variation occurs. In more localized taxa, the population consistence of which is probably also small, differences–not only for *mt-Cox1*, but also in morphological characters–appear to fix at a faster rate.

4.5. Analysis of the Morphological Characters

As previously mentioned, and demonstrated by the relatively low consistency index in the parsimony analysis, a large number of character-states appear by parallelism in various lineages.

Furthermore, some of the apparent reversals are probably morphologically similar states appearing independently in different lineages. Some of these traits are obviously useful for single species differentiation, but they cannot be used to infer clade-specific relationships. Examples of these traits are, for example, (i) shape and ratios of antennal segments, particularly segments 1 and 2; (ii) shape of the funicle; (iii) density of the scales on ventrites, and more. These traits were used in the first analyses, but were discarded for the subsequent analyses, since they often had more than 15–20 passes in the classification obtained with MP, and were not synapomorphic for single clades (that is, both consistency and retention indexes for these traits were very low). In some cases, a single, broader defined state was used to show variation previously scored into different states. For example, the elytral setae, other than being long elliptical or hair-like, can have a more or less continuous variation between short oblong, ovate to short ovate, and spatulate, independently from the relationships among the species, and sometimes even with some intraspecific variation. Hence, short ovate-spatulate to oblong setae were scored as the same state.

Examination of some of the characters in detail indicates those that bear a stronger phylogenetical signal. Synapomorphies and autapomorphies are traced in Figure 10.

Size (Char. 1) clearly differentiates the *Saxifraga*-associated species, which are always much larger than the others. *D. occidentalis* is also a large species (as the related *D. elongatus*), but, as already discussed, the relationships of these species within the genus are not yet understood.

Rostrum, dorsal margins. All species associated with mosses have rostral sides that are more or less convergent (Char. 2.0), so that the ratio length/width of the rostrum is distinctly higher in these species than in those associated with *Saxifraga*. Those that are associated with *Saxifraga* have almost parallel-sided rostrum, sometimes slightly broadened at midlength, and scrobes are not broadened laterally, possibly following adaptation to the different host plants, habitats colonized, and feeding habits.

Rostral vestiture (Chars 4–5). Almost all species have a dense vestiture on the dorsum of rostrum (Char. 4.0), and only those from southern France of the *D. devillei* group (excluding *D. venturiensis*) differ in almost lacking scales on the median part of the rostrum (Char 4.1). However, the way scales are inserted characterizes the groups: in the species of clade A scales are flat and adherent to integument (Char. 5.0); in the small-sized species of clade B scales are obliquely inserted, suberect (Char 5.1), and in the large *Saxifraga*-associated species they are adherent to the integument again.

Rostral sculpture. The apex of the rostrum is rough, with irregular longitudinal glossy lines in the small species (Char. 7.1), or, alternatively, it is smoother, with irregular punctures (Char. 7.0), as in the *Saxifraga*-associated species. The *D. rudeni* complex differs from the other small-sized species in having the rostrum roughly punctured towards the apex. This character could support its hypothetical placement in the same clade as the *Saxifraga*-associated species, near its root. Species in this group, however, feed on mosses and share many of their characters with the other small-sized species, with *D. imhoffi* being somewhat morphologically intermediate.

Scrobes. The outer margin of the scrobes is dorsally expanded externally in the small species (Char. 11.0), and delimited by the outer margin of the genae in the larger species (Char. 11.1). Other traits correlated with the scrobes, such as length and direction of the lower margin, width of the posterior part, divergence between the upper and lower margin, and others, show considerable variation, apparently not correlated with the phylogenetic affinities. Hence, these traits were excluded from the final analysis. Scales in front of the eyes, in the basal part of the scrobes, are elliptical in the species of clade A (Char. 12.1), generally oval in the species of clade B (Char. 12.0), or even hair-like in a few other species (Char. 12.2).

Ommatidia. The small-sized, moss-associated species have small eyes (Char. 13.1), composed of a limited number of ommatidia, usually less than 30, and about 40 in *D. ribesi* and *D. baeticus*. Only the large-sized species, associated with *Saxifraga*, have larger eyes, with more than 50 ommatidia (Char. 13.0). Also this trait may be associated with the different biology and the more exposed life on the *Saxifraga* clumps.

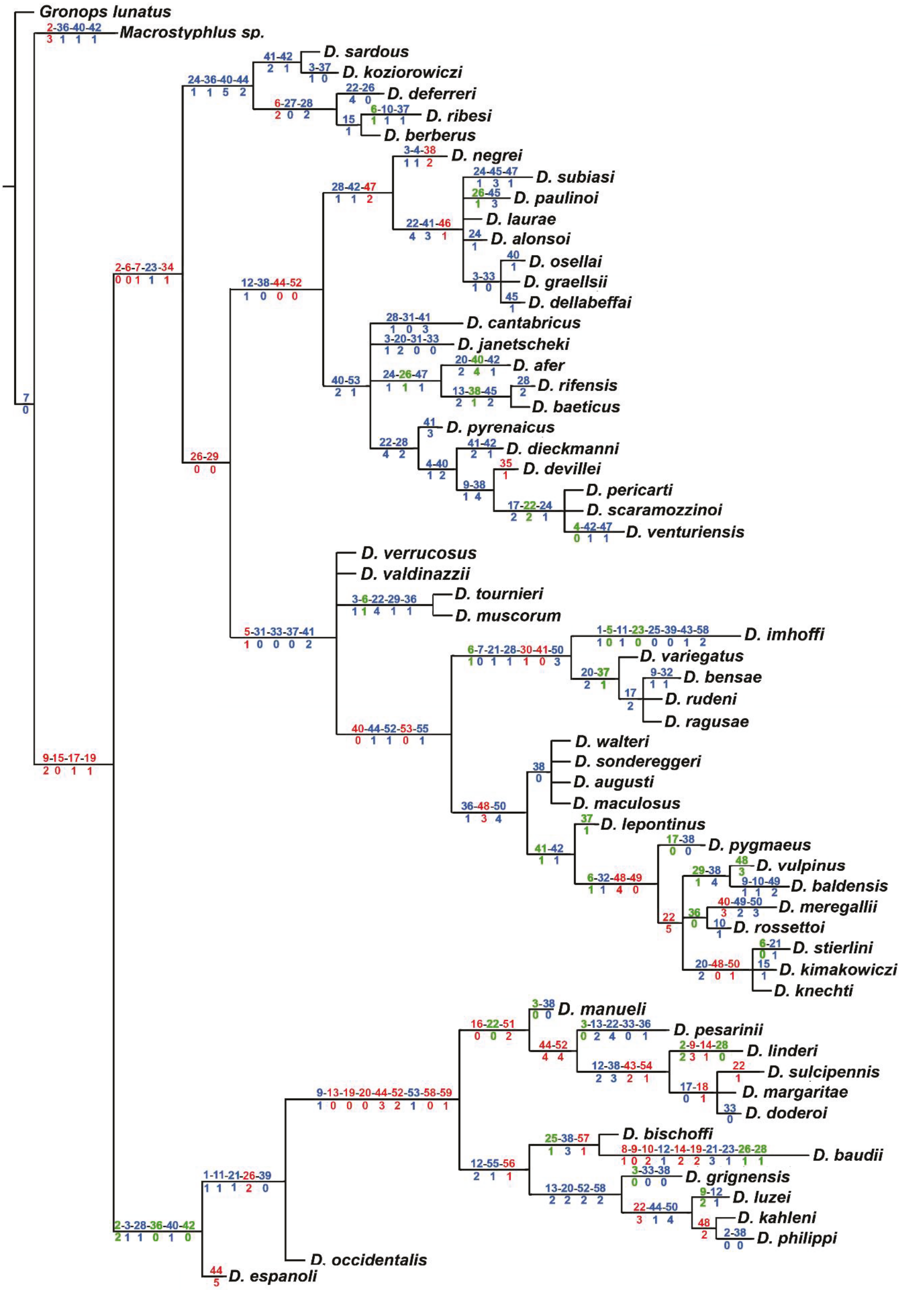

Figure 10. Synapomorphies and autapomorphies plotted on the MP consensus tree. Numbers above branches refer to the character, numbers below branches refer to the state of the character. Characters in red: synapomorphies and autapomorphies unique for the *Dichotrachelus* clade. Characters in blue: synapomorphies and autapomorphies not unique for the clade or the species. Characters in green: apparent reversals.

Pronotum (Chars 17–22). Characters on the pronotum are quite variable, also intraspecifically. Depth and width of the median and dorso-lateral grooves, as well as curvature of the sides and ratio length/width, are more or less typical of each species, or occasionally of a species-complex, but show great polymorphism. Clade-specific states were observed in the ratio length/width and shape of the median groove in the *D. sulcipennis* complex (Char. 17.0; 18.1), depth of the median groove in many of the *Saxifraga*-associated species (Char. 19.0), width of the median groove in some species groups, such as the *D. stierlini* complex (Char. 20.2) and shape of the dorso-lateral grooves, shared by the species in the subgroup B3 (Char. 21.1).

Elytra. Like the pronotum, the width of elytra, their shape, elevation of the intervals, and other traits have strong intra- and interspecific variation, not always related to phylogenetic relationships. Some of the species have flat intervals on elytra, particularly in females (Char. 24.1; 26.1). The *Saxifraga*-associated species have typically highly convex odd intervals from the base to apex (Char. 26.2). One character of high interest is the shape of the striae, which are very narrow, with punctures merged to form a deep narrow furrow in many of the species of clade A (Char. 27.0), excluding those of the *D. devillei* group, that, like the species of clade B, have broad, visible punctures on the striae (Char. 27.1). The vestiture of scales and setae shows quite a high level of parallelism. However, the small-sized species of clade B, excluding the *D. rudeni* complex, have some setae also present on the even intervals (Char. 28.1), whereas these are usually missing in the other species of clade B (Char. 28.0). This character is variable in the species of clade A, but in the subgroup A2 the even intervals have no scales on the dorsum, and a few are present on declivity (Char. 28.2).

Legs. The legs are generally rather slender, with the exception of the species of subgroup B2, which have short and robust tibiae (Char. 32.1); their setae are usually relatively broad, except in the *Saxifraga*-associated species. The shape of segment 3 of the tarsi (Char. 38), narrow or with more or less broadened lobes, is typical of some species-groups, but the same state appears homoplastically in distinct lineages, and occasionally even closely related species have differences in the width of the lobes.

Genitalia. Male genitalia proved to be the most important character in inferring phylogenetic relationships in the genus. This was already evidenced for the *Saxifraga*-associated species, and is now confirmed for the entire genus, even though not all characters used bear the same phylogenetic signal. The penis is generally relatively short in the majority of the small-sized species (Char. 39.0), and more slender in the *Saxifraga*-associated taxa (Char. 39.1). The shape of its apex varies to a great extent (Char. 40), but the different states are usually shared between closely related species, as well as its dorsal sclerotization (Char. 41). The length of the internal sac (Char. 44) and the position of the genital sclerite, however, closely reflect taxonomic affinities. The most useful structure for inferring relationships among the species of the genus proved to be the male genital sclerite (Chars 45–57), as we have extensively discussed. Female genitalia, conversely, made only a limited contribution, and most of them were discarded after the first analyses, since they proved to be generally uniform and occasionally quite variable within the same species.

5. Conclusions and Future Developments

With the present study it was possible to infer the phylogenetic structure of the genus *Dichotrachelus*, supporting its isolated position in Palaearctic fauna and suggesting a very ancient diversification in Cyclominae. The present day species apparently derive from an ancestral split that led to two main lineages, one associated with the Iberian plate and the other with the alpine arch in a wide sense, with an apparently more recent penetration into the Apennines by a single lineage. The relationships of the species from the Sardinian and Corsican plate, and part of those from northern Africa and the Iberian plate (the *D. ribesi* and *D. espanoli* species-groups), are not fully understood. They might be old relicts of the first lineages that differentiated, but this cannot yet be determined with full confidence. Groups of closely related species are rather clearly defined, but thus far the more distant relationships could not be disclosed with sufficient precision. Our study confirms some of the biogeographical hypotheses that were previously proposed [19,20], at least regarding the alpine taxa; however, more data are required to fully define the biogeographic scenario that led to the present day distribution of the separate lineages.

Future research will concentrate on achieving a broader set of molecular data from more species of the genus, also based on nuclear genes, and from a larger number of taxa of Cyclominae. This should hopefully allow the deep phylogeny of the genus to be inferred with more confidence, disclosing its true relationship in the subfamily, and reconstructing its evolution in the territories of the Peri-Tethys.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/10/3/66/s1, Table I. List of the species and specimens examined. For the *mt-Cox1* analysis, specimens sequenced in Turin are indicated with an asterisk; Table II Characters matrix for the morphological analysis; Table III. Pairwise distance of *mt-Cox1*, bases. The number of base differences per site from between sequences are shown. There were a total of 774 positions in the final dataset; Table IV. Pairwise distance of *mt-Cox1*, amino acids. The number of amino acid substitutions per site from between sequences is shown. Analyses were conducted using the Poisson correction model. The rate variation among sites was modelled with a gamma distribution (shape parameter = 1). The coding data was translated assuming a Invertebrate Mitochondrial genetic code table. There were a total of 258 positions in the final dataset.

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References

1. Alonso-Zarazaga, M.A.; Barrios, H.; Borovec, R.; Bouchard, P.; Caldara, R.; Colonnelli, E.; Gültekin, L.; Hlaváč, P.; Korotyaev, B.; Lyal, C.H.C.; et al. Cooperative Catalogue of Palaearctic Coleoptera Curculionoidea. *Monografías Electrónicas SEA* **2017**, *8*, 1–729.
2. Oberprieler, R.G. A reclassification of the weevil subfamily Cyclominae (Coleoptera: Curculionidae). *Zootaxa* **2010**, *2515*, 1–35.
3. Stierlin, G. Revision der Dichotrachelus-Arten. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **1878**, *5*, 392–425.
4. Stierlin, G. *Fauna Coleopterorum Helvetica. Teil II*; Bolli und Boecherer: Schaffhausen, Switzerland, 1898; p. 662.
5. Franz, H. Die südwesteuropäischen Arten der Gattung *Dichotrachelus* (Col. Curc.). *Koleopterol. Rundsch.* **1954**, *23*, 93–96.
6. González, M. Los *Dichotrachelus* ibéricos (Col. Curculionidae). *Publicaciones del Instituto de Biología Aplicada* **1964**, *37*, 5–16.
7. Meregalli, M. Revisione delle specie iberiche del genere *Dichotrachelus* Stierlin, 1853 (Coleoptera, Curculionidae). *MRSN* **1987**, *5*, 335–418.
8. Hustache, A. Curculionides gallo-rhénans (suite). *Ann. Soc. Entomol. Fr.* **1929**, *98*, 1–96.
9. Hoffmann, A. Coléoptères Curculionides. Deuxième Partie. *Faune Fr.* **1954**, *59*, 488–1208.
10. Barajon, M. Le specie Italiane del Gen. *Dichotrachelus* Stierl. (Col. Curculionidae). *Estratto dalle Memorie del Museo Civico di Storia Naturale* **1946**, *85*, 112–129.
11. Barajon, M. Le specie Italiane del Gen. *Dichotrachelus* Stierl. II. *Estratto dalle Memorie del Museo Civico di Storia Naturale Milano* **1947**, *86*, 31–32.
12. Osella, G. Revisione delle specie Italiane del Genere *Dichotrachelus* Stierlin (Coleoptera, Curculionidae). *Estratto dalle Memorie del Museo Civico di Storia Naturale* **1967**, *15*, 349–445.

13. Osella, G. Revisione del genere Dichotrachelus Stierlin. *Estratto dalle Memorie del Museo Civico di Storia Naturale* **1970**, *18*, 449–569.
14. Germann, C. About the enigmatic *Dichotrachelus valesiacus* Stierlin, 1878 (Coleoptera, Curculionidae, Cyclominae). *Zookeys* **2009**, *5*, 81–86. [CrossRef]
15. Germann, C. Review of the *Dichotrachelus alpestris* Stierlin, 1878 species group with evidence for a species complex of *D. augusti* F. Solari, 1946, and *D. sondereggeri* sp. nov. from Switzerland (Coleoptera, Curculionidae). *Contrib. Nat. Hist.* **2011**, *17*, 1–21.
16. Germann, C.; Baur, H. Notes on the taxonomy and biology of *Dichotrachelus imhoffi* Stierlin, 1857 (Coleoptera, Curculionidae) with the observation of a length dimorphism of the aedeagus. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **2010**, *83*, 249–260.
17. Germann, C. Die Rüsselkäfer der Schweiz–Checkliste (Coleoptera, Curculionoidea) mit Verbreitungsangaben nach biogeografischen Regionen. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **2010**, *83*, 41–118.
18. Germann, C. Supplement zur Checkliste der Rüsselkäfer der Schweiz (Coleoptera, Curculionoidea). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **2011**, *84*, 155–169.
19. Meregalli, M.; Menardo, F.; Klass, K.-D.; Cervella, P. Phylogeny of the *Saxifraga*-associated species of *Dichotrachelus* (Insecta: Coleoptera: Curculionidae), with remarks on their radiation in the Alps. *Arthropod Syst. Phylogeny* **2013**, *71*, 43–68.
20. Meregalli, M.; Monguzzi, R.; Klass, K.-D.; Cervella, P.; Kahlen, M. *Dichotrachelus pesarinii* sp.n., a missing link between the species from the central and the western southern Alps (Coleoptera: Curculionidae: Cyclominae). *Arthropod Syst. Phylogeny* **2015**, *73*, 323–332.
21. Germann, C.; Wyler, S.; Bernasconi, M. DNA barcoding of selected alpine beetles with focus on Curculionoidea (Coleoptera). *Rev. Suisse Zool.* **2017**, *124*, 15–38.
22. Morrone, J.J. Annotated checklist of the tribe Listroderini (Coleoptera: Curculionidae: Cyclominae). *Zootaxa* **2011**, *3119*, 1–68.
23. Marvaldi, A.E.; Sequeira, A.S.; O'Brien, C.W.; Farrell, B.D. Molecular and morphological phylogenetics of weevils (Coleoptera, Curculionoidea): Do niche shifts accompany diversification? *Syst. Biol.* **2002**, *51*, 761–785. [CrossRef] [PubMed]
24. Riedel, A.; Daawia, D.; Blake, M. Deep COX1 divergence and hyperdiversity of *Trigonopterus* weevils in a new Guinea mountain range (Coleoptera Curculionidae). *Zool. Scr.* **2009**, *39*, 63–74. [CrossRef]
25. Hughes, J.; Vogler, A.P. The phylogeny of acorn weevils (genus *Curculio*) from mitochondrial and nuclear DNA sequences: The problem of incomplete data. *Mol. Phylogenet. Evol.* **2004**, *32*, 601–615. [CrossRef] [PubMed]
26. Ronquist, F.; Teslenko, M.; Van der Mark, P.; Ayres, D.L.; Darling, A.; Höhna, S.; Larget, B.; Liu, L.; Suchard, M.A.; Huelsenbeck, J.P. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* **2012**, *61*, 539–542. [CrossRef] [PubMed]
27. Ronquist, F.; Van der Mark, P.; Huelsenbeck, J.P. Bayesian phylogenetic analysis using MrBayes. In *The Phylogenetic Handbook: A Practical Approach to Phylogenetic Analysis and Hypothesis Testing*; Lemey, P., Salemi, M., Vandamme, A.M., Eds.; Cambridge University Press: Cambridge, UK, 2009; p. 723.
28. Goloboff, P.A.; Farris, J.S.; Nixon, K.C. TNT, a free program for phylogenetic analysis. *Cladistics* **2008**, *24*, 774–786. [CrossRef]
29. Silvestro, D.; Michalak, I. RAxML GUI: A graphical front-end for RAxML. *Org. Divers. Evol.* **2011**, *12*, 335–337. [CrossRef]
30. Goldman, N.; Yang, Z. A codon-based model of nucleotide substitution for protein-coding DNA sequences. *Mol. Biol. Evol.* **1994**, *11*, 725–736. [PubMed]
31. Baele, G.; Lemey, P. Bayesian evolutionary model testing in the phylogenomics era: Matching model complexity with computational efficiency. *Bioinformatics* **2013**, *29*, 1970–1979. [CrossRef] [PubMed]
32. Huelsenbeck, J.P.; Larget, B.; Alfaro, M.E. Bayesian phylogenetic model selection using reversible jump Markov chain Monte Carlo. *Mol. Biol. Evol.* **2004**, *21*, 1123–1133. [CrossRef] [PubMed]
33. Wright, A.M.; Hillis, D.M. Bayesian Analysis Using a Simple Likelihood Model Outperforms Parsimony for Estimation of Phylogeny from Discrete Morphological Data. *PLoS ONE* **2014**, *9*, e109210. [CrossRef] [PubMed]

34. Gillett, C.P.D.T.; Lyal, C.H.C.; Vogler, A.P.; Emerson, B.C. Statistical Evaluation of Monophyly in the 'Broad-Nosed Weevils' through Molecular Phylogenetic Analysis Combining Mitochondrial Genome and Single-Locus Sequences (Curculionidae: Entiminae, Cyclominae, and Hyperinae). *Diversity* **2018**, *10*, 21. [CrossRef]
35. Alonso-Zarazaga, M.A.; Lyal, C.H.C. *A World Catalogue of Families and Genera of Curculionoidea (Insecta: Coleoptera). (Excepting Scolytidae and Platypodidae)*; Entomopraxis, S.C.P., Ed.; Entomopraxis: Barcelona, Spain, 1999; p. 315.
36. Bik, H.M.; Lambshead, P.J.; Thomas, W.K.; Lunt, D.H. Moving towards a complete molecular framework of the Nematoda: A focus on the Enoplida and early-branching clades. *BMC Evol. Biol.* **2010**, *10*, 353. [CrossRef] [PubMed]
37. Song, N.; Li, H.; Song, F.; Cai, W. Molecular phylogeny of Polyneoptera (Insecta) inferred from expanded mitogenomic data. *Sci. Rep.* **2016**, *6*, 36175. [CrossRef] [PubMed]
38. Wang, M.; Lv, S. Substitution saturation analysis of mitochondrial cytochrome C oxidase subunit 1 (Cox1) gene of *Angiostrongylus cantonensis*. *Chin. J. Parasitol. Parasit. Dis.* **2014**, *32*, 205–209.
39. Stüben, P.E.; André Schütte, A.; Bayer, C.; Astrin, J.J. The Molecular Weevil Identification Project (Coleoptera: Curculionoidea), Part II-Towards an Integrative Taxonomy. *Snudebiller* **2015**, *16*, 1–316.
40. Gillett, C.P.D.T.; Crampton-Platt, A.; Timmermans, M.J.T.N.; Jordal, B.H.; Emerson, B.C.; Vogler, A.P. Bulk de novo mitogenome assembly from pooled total DNA elucidates the phylogeny of Weevils (Coleoptera: Curculionoidea). *Mol. Biol. Evol.* **2014**, *31*, 2223–2237. [CrossRef] [PubMed]
41. Morrone, J.J. Cladistics of the New World genera of Listroderina (Coleoptera: Curculionidae: Rhytirrhinini). *Cladistics* **1997**, *13*, 247–266. [CrossRef]
42. Morrone, J.J. The subtribes and genera of the tribe Listroderini (Coleoptera, Curculionidae, Cyclominae): Phylogenetic analysis with systematic and biogeographical accounts. *Zookeys* **2013**, *273*, 15–71. [CrossRef] [PubMed]
43. Kuschel, G. Insects of Campbell Island Coleoptera: Curculionidae of the Subantarctic islands of New Zealand. *Pac. Insects Monogr.* **1964**, *1*, 416–493.
44. Kuschel, G. Entomology of the Aucklands and other islands south of New Zealand: Coleoptera: Curculionidae. *Pac. Insects Monogr.* **1971**, *27*, 225–259.
45. Chown, S.L.; Scholtz, C.H. Cryptogam herbivory in Curculionidae from the sub-Antarctic Prince Edward Islands. *Coleopt. Bull.* **1989**, *43*, 165–169.
46. McKenna, D.D.; Sequeira, A.S.; Marvaldi, A.E.; Farrell, B.D. Temporal lags and overlap in the diversification of weevils and flowering plants. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 7083–7088. [CrossRef] [PubMed]
47. Frisch, W.; Meschede, M. *Plattentektonik 2*; Wissenschaftliche Buchgesellschaft: Darmstadt, Germany, 2007; p. 196.
48. Péricart, J. Notes sur divers Curculionidae français avec la description d'une espèce et d'une sous-espèce nouvelles (Coleoptera). *Nouv. Rev. Entomol.* **1974**, *4*, 55–70.
49. Meregalli, M. Osservazioni preliminari sulla biologia dei *Dichotrachelus* (Coleoptera, Curculionidae). In Proceedings of the XII Congresso Nazionale Italiano di Entomologia, Roma, Italy, 5–9 November 1980; pp. 125–133.

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Weevils as Targets for Biological Control, and the Importance of Taxonomy and Phylogeny for Efficacy and Biosafety

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Abstract: Curculionidae are a large mainly herbivorous family of beetles, some of which have become crop pests. Classical biological control has been attempted for about 38 species in 19 genera, and at least moderate success has been achieved in 31 % of cases. Only two weevil species have been considered to be completely controlled by a biological control agent. Success depends upon accurately matching natural enemies with their hosts, and hence taxonomy and phylogeny play a critical role. These factors are discussed and illustrated with two case studies: the introduction of the braconid parasitoid *Mictroctonus aethiopoides* into New Zealand for biological control of the lucerne pest *Sitona discoideus*, a case of complex phylogenetic relationships that challenged the prediction of potential non-target hosts, and the use of a mymarid egg parasitoid, *Anaphes nitens*, to control species of the eucalypt weevil genus *Gonipterus*, which involves failure to match up parasitoids with the right target amongst a complex of very closely related species. We discuss the increasing importance of molecular methods to support biological control programmes and the essential role of these emerging technologies for improving our understanding of this very large and complex family.

Keywords: Curculionidae; biological control; target host; non-target host; taxonomy; phylogeny

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1. Introduction

Risk assessment for biological control agent (BCA) introduction has increasingly become standard best practice in recent years, and regulatory legislation has been adopted in many countries [1]. Risks associated with biological control can range from direct impacts of a biocontrol agent on non-target species to indirect impacts, which can sometimes be hard to predict (e.g., [2]). These include impacts resulting from food-web effects [3], hybridization with related natural enemies [4] and apparent competition [5].

Decisions made by regulators considering BCA applications depend heavily on information on a wide range of factors including, where possible, that available from the native range of the proposed BCA and its host(s), from introductions to new areas elsewhere and from data on laboratory host range tests usually carried out under quarantine conditions. The latter is one of the key datasets that regulators have on which to base their assessment of risk to native and non-target species in the new proposed area of introduction [6]. In Europe, a Commission of the International Organisation for Biological Control, established to harmonize regulations, recommended that a list of all known hosts from the natural range and new areas of introduction should be documented [7]. Since then it has become widely accepted that information on host range (natural and novel) should be included in applications to import and release new biological control agents [8–10].

The Curculionoidea are one of the most speciose taxonomic groups of insects, estimated to comprise over 200,000 species [11], with members inhabiting most ecosystems throughout the world. The evolutionary steps that have resulted in the "phenomenal diversification and success of weevils" that we see today have been discussed by Oberprieler, Marvaldi and Anderson [11]. Whereas the diversity of weevils has been studied and progressed extensively over the last 250 years, since the first species was described, the identities and delimitations of natural family-group taxa and their phylogenetic relationships have remained the subject of much debate. Recent molecular techniques in combination with analyses of morphological characters have increasingly helped to clarify some of these quandaries and have mostly confirmed Kuschel's proposed 6–7 main weevil lineages as based only on morphology [12]. In the large family Curculionidae, however, phylogenetic relations still remain largely unresolved [13–16].

As weevils are essentially herbivorous, it is unsurprising that many species have been used for biological control of weeds with significant success [17]. However, by the same token, many species of the Curculionidae have become agricultural and horticultural pests, in particular those in the subfamily Entiminae. Species in this very large and diverse group of more than 12,000 species [11] comprise mainly live-plant-feeding adults with root-feeding larvae, often with a wide plant host range that predisposes them to become crop pests. Consequently, some members of this subfamily, amongst others, have become the target of biological control programs. The large family Curculionidae, therefore, represents a useful taxon for an analysis of biological control deployment and the challenges it presents for practitioners and regulators.

In this contribution we review classical biological control programs for which species of Curculionidae have been the target species and the range of insect biological control agents (predators and parasitoids) that have been used globally to assist in the management of weevil pest species. We emphasize in particular the importance of taxonomy for correct matching of host–parasitoid relationships and understanding phylogenetic relationships within the family in order to more accurately predict non-target hosts and assess other risks of biological control introductions for weevils. Case studies are used to exemplify each of these issues and to highlight the complexities of working with such a speciose and diverse family.

2. Weevils as Targets of Biological Control

With reference to the BIOCAT database [18], as updated by Kenis, et al. [19], 23 genera (approximately 38 species) of Curculionidae have been the subject of a classical biological control programme; of these 24 weevil species (63 %) have BCAs permanently established in at least one of the countries of release (Table A1 in Appendix A). Impact of BCAs on weevil hosts has ranged from complete control (no other control method required) to no impact at all on pest populations (Table A1). Some level of control has been achieved on 12 target species, a success rate of approximately 31 % (Table 1(A)). The most common subfamilies of weevils that have been targets of biocontrol are the Entiminae, Scolytinae and Curculioninae, while most successes have been achieved with biological control of entimines (Table 1(A)).

The biological control agents listed in BIOCAT that have been used for classical biological control of weevil target pests comprise parasitoids and predators from four insect orders, 22 families and 81 species, and 15 species have had some positive impact on pest weevils (Table 1(B)). The most commonly used and successful BCAs have been hymenopteran parasitoids, of which six families and 12 species have had some impact on the target (Table 1(A)). Only two cases of complete control of a pest weevil are listed in BIOCAT (Table A1). One is that of *Lixophaga sphenophori* (Villeneuve) (Diptera: Tachnidae) released in the United States for biocontrol of the Sugar-cane Weevil, *Rhabdoscelus obscurus* (Boisduval); however, no control with this tachinid was reported from Australia or Fiji. The other case is that of the egg parasitoid *Anaphes nitens* (Girault) (Hymenoptera: Mymaridae) used for the control of

Gonipterus scutellatus Gyllenhal defoliating eucalypts in Madagascar, but again such complete control has not been the case for all releases; incomplete control has been reported in New Zealand, South America, Europe and Africa (Table A1).

Table 1. (**A**) Summary of weevil taxa for which biological control agents (BCAs) have been established and those that are having an impact. (**B**) Number of biological control agents that are established and those having an impact on the target host.

(A)	**Target Weevil Taxa**	
Species × Subfamily	**BCA Permanently Established**	**BCAs Having Some Impact**
Entiminae	8	5
Curculioninae	3	1
Cyclominae	2	1
Dryophthorinae	2	2
Molytinae	1	0
Scolytinae	8	3

(B)	**Biological Control Agents**		
Category	**Released**	**Permanently Established**	**Having Some Impact**
No. orders	4	4	3
No. families	22	13	9
No. species	81	37	15

Referring to biological control of the Banana Weevil, *Cosmopolites sordidus* (Germar), with predatory histerids in Fiji, it was noted that "weevils as a group seem to be poor candidates for biological control" [20], although some success was reported in reducing the pest status of the Banana Weevil. However, there have been notable successes, for example with weevil pests of forage crops in Australasia. In New Zealand in particular, species of the wasp genus *Microctonus* Wesmael (Hymenoptera: Braconidae) have provided substantial levels of control of the Lucerne Weevil, *Sitona discoideus* Gyllenhal. These wasps are parasitoids of the adult stage of the host, and although the weevil hosts survive for the duration of the parasitoid larval development inside them, the female weevils become reproductively incapable almost immediately after parasitism [21].

3. Importance of Taxonomy and Phylogeny

For risk assessment for biological control it is vital to have a good understanding of the taxonomy and phylogenetic relationships of the organisms involved (biocontrol agent, target host, potential non-target hosts) for many reasons [22]. Clearly, certainty of the identity of the BCA is paramount, so that the correct and intended organism is selected for release and reliable literature can be accessed on efficacy, host range, climatic and geographical distribution, as well as basic biology and ecology [23]. This is also essential information usually required by regulators (e.g., [24,25]). Furthermore, taxonomic certainty when selecting test species for host range testing in quarantine is paramount so that organisms closely related to the target pest can be identified [8]. Molecular methods have become increasingly important in supporting taxonomic determination [26,27], and they can provide an interim alternative where the taxonomic impediment prevents a name from being available (Cock in preparation).

The identity of potential BCAs determined on morphological grounds alone is no longer sufficient in many taxonomic groups, particularly when working with the less well known tropical faunas. Thus, the inventory of Lepidoptera caterpillars, their food plants and natural enemies in Costa Rica [28] has revealed numerous apparently polyphagous parasitoids, particularly Braconidae and Tachinidae (so far), which on closer examination comprise a species complex of variously monophagous, oligophagous or polyphagous species that can initially be distinguished on their DNA CO1 barcodes [29,30].

Natural enemies and their hosts have usually coevolved together, with a dynamic interplay or even "power struggle" between the two both spatially and temporally. When selected for a biological control program, natural enemies are often transported to a new area, where, for the first time, they may encounter new organisms that are within their host range as might be anticipated based on close phylogenetic relationships. While this is often considered to be a 'host shift', it should more appropriately be seen as host range expansion onto new host species that have always been within the host range of the natural enemy [31]. Understanding of phylogenetic relationships between natural enemy and host taxa in the native range is therefore vital for predicting potentially novel hosts that might be physiologically suitable (or permissive) hosts for the natural enemy, whether for weed targets [9,32] or insect targets [8]. Naturally, a range of other ecological and behavioural factors also comes into play that might preclude hosts in the receiving environment from becoming a suitable host.

As mentioned above, risk assessment for weevils as target hosts can present a particularly challenging task because of the complexity of determining phylogenetic relationships in such a large and imperfectly resolved group of organisms.

3.1. Case Study: Microctonus aethiopoides *(Loan) for Biological Control of* Sitona discoideus

Microctonus aethiopoides Loan (Hymenoptera: Braconidae) is a solitary, koinobiont endoparasitoid of the adult stage of its host. This parasitoid was introduced into Australia in 1977 from the Mediterranean region [33,34] for biological control of the weevil *S. discoideus* (Curculionidae: Entiminae: Sitonini), an introduced pest of lucerne (alfalfa) (*Medicago sativa* L.). Specimens of *M. aethiopoides* sourced from Australia were released in New Zealand in 1982 [35] also to control *S. discoideus*. Later molecular studies suggested that the *M. aethiopoides* population introduced into New Zealand comprised specimens that originated from Morocco [36]. In Australia the parasitoid was released mainly in south-eastern regions between 1977 and 1980 [37], and in New Zealand it was released at 17 lucerne-growing sites in the South Island [35].

The initial exploration research for biocontrol agents for *S. discoideus* in Europe and North Africa involved extensive surveys of potential candidate biocontrol agents for *Sitona* but did not consider their natural host ranges [38]. However, following the identification of *M. aethiopoides* as a potentially suitable BCA, its native host range in Morocco was investigated and found to comprise weevil species in the genera *Sitona* Germar and *Hypera* Germar (Curculionidae: Hyperinae) [39]. Evidence was later presented for the existence of two sympatric biotypes of *M. aethiopoides* associated with *Sitona* and *Hypera* as hosts respectively [40]. As the parasitoids sent from Morocco to Australia and then to New Zealand were in the form of parasitised adult *S. discoideus* weevils [34], it has been assumed that the introduced parasitoids were *Sitona*-associated biotypes.

Despite the knowledge that *M. aethiopoides* was not entirely host-specific in its native range, there was little pre-release risk assessment of it undertaken in Australia. A single weevil species being introduced as a weed biological control agent, *Perapion antiquum* (Gyllenhal) (Brentidae: Apioninae), was tested, and no parasitism was recorded (J. Cullen pers. comm.). In New Zealand, quarantine testing was also carried out with weed biological control agents [41] to identify any adverse impacts on beneficial insects, as required by regulation at the time. In both countries, no native insects were tested, because it was argued that there are no native *Sitona* species present and no members of the tribe Sitonini. In Australia, however, there are several native genera of Hyperini [42]. Post-release recovery rates of the parasitoid from *S. discoideus* (and hence efficacy of parasitism) in Australia during 1977–1979 ranged from 0–22.7 % [33]. A survey of 25 sites in New South Wales, Victoria and South Australia in November 2001 found a mean level of parasitism of *S. discoideus* of 2.6 %, with a range of 0–24.6 % [43]. In New Zealand, *M. aethiopoides* has been considered a successful biological control agent of *S. discoideus*, especially in Canterbury, where parasitism levels of 50–70 % have been reported in summer [44] and similar levels of parasitism are still found currently (S. Goldson, pers. comm.). A survey of 88 lucerne sites in Otago and Southland (southern New Zealand) found mean parasitism levels ranging from 16–67 % with parasitism reaching 100 % at some sites [45].

In Australia, no post-release studies had been carried out to determine whether non-target parasitism was also occurring in that country, until a survey conducted in south-eastern Australia in 2001 discovered a single incidence of parasitism by *M. aethiopoides* of the native species "*Prosayleus*" sp. 2 [43]. This species, now assignable to the genus *Agroicus* Jekel [46], belongs to the subfamily Entiminae (currently placed in the tribe Leptopiini) but is not closely related to Sitona [46]. However, in Australia the Entiminae are the second-largest subfamily of weevils, and Leptopiini comprise about 90 % of the species [46], and so further non-target hosts might be discovered in the future.

The non-target weevils recorded as parasitised in the field by *M. aethiopoides* in New Zealand are shown in Table 2, spanning four subfamilies, five tribes and ten genera. Leptopiini are clearly common hosts, and given the number of species present in New Zealand including in the genera *Irenimus* Pascoe (seven species) and *Chalepistes* Brown (62 species) [47,48] and *Austromonticola* Brown (eight species) [49], it is likely that the actual number of potential hosts is much higher.

Table 2. Genera of Curculionidae known to be hosts of the Moroccan biotype of *Microctonus aethiopoides* in New Zealand and the number of species known to be attacked in the laboratory and in the field. NT = not tested; ND = not determined.

Subfamily: Tribe	Genus	Species Attacked		Status in New Zealand
		Lab	**Field**	
Entiminae: Leptopiini	*Irenimus*	NT	1	endemic
"	*Chalepistes*	5	6	endemic
"	*Nicaeana*	1	4	endemic
"	*Nonnotus*	NT	1	endemic
	Protolobus	1	ND	endemic
Entiminae: Naupactini	*Atrichonotus*	NT	1	adventive
Curculioninae: Eugnomini	*Eugnomus*	NT	1	endemic
Cyclominae: Listroderini	*Listronotus*	1	1	adventive
"	*Listroderes*	0	1	adventive
"	*Steriphus*	1	1	endemic
Lixinae: Cleonini	*Rhinocyllus*	1	1	adventive

As the early exploratory work involving *M. aethiopoides* in Morocco did not aim to determine the extent to which a wider range of possible host species might be present, further research was carried out in Morocco with this goal [50]. Using this retrospective example, we wanted to advise New Zealand regulators on whether information on host breadth in the natural range (Morocco) could have helped predict the greater than expected host range that we had found post-release in New Zealand. This was considered as a model case study to test the value of natural-range research, particularly natural host range in general. Monthly sampling in lucerne crops in three regions of Morocco over a nine-month period collected over 3500 specimens of weevils, of which the majority were *S. discoideus*. However, almost 600 specimens of other weevils (46 species in four families and 11 subfamilies) were found. *Hypera postica* (Gyllenhal) was also commonly collected. In all, 13 weevil species containing parasitoids consistent with *M. aethiopoides* were found by dissection: eight species of *Sitona*, *Charagmus gressorius* (Fabricius) and *C. griseus* (Fabricius) and three species of *Hypera* [51]. This study increased the known number of genera parasitised by *M. aethiopoides* by only the two species of *Charagmus* Schoenherr, but as *Charagmus* had been considered as a subgenus of *Sitona* until 2007 [52], in effect the natural host range had not been expanded at all by this study.

As it was already known in 1977 that *M. aethiopoides* also attacks *Hypera* in its native range [39], the potential for the parasitoid to attack native species, at least in Australia where species of Hyperinae were known to occur, should have been recognised. The phylogenetic relationship between Hyperinae and Sitonini (and Entiminae overall) was poorly understood in the 1970s and is still not resolved. All recent molecular phylogenetic analyses [13–16,53–55] recovered a close relationship between Hyperinae and Entiminae, although taxon sampling was too small and patchy in all of them to properly elucidate this relationship. Both *Hypera* (Hyperini or Hyperinae) and *Sitona* have usually been recovered in basal positions in relation to Entiminae, either separate from each other [55] or in some clade together [14,15,53], although in the analysis of McKenna et al. [54] both genera appeared bedded inside different, mixed clades of Entiminae and Cyclominae and in that of Gunter et al. [13] the three Australian genera of Hyperinae (*Hypera* not included) clustered with the genus *Steriphus* Erichson (Cyclominae: Listroderini) in some analyses, whereas *Sitona* grouped separately on a long branch. Strong support for a position of *Hypera* (Hyperinae) as sister-group of Entiminae + Cyclominae was found by Shin et al. [16], but their analysis did not include *Sitona* nor a sufficient number of other Entiminae, Hyperinae and Cyclominae to resolve the exact relationships between *Sitona* and *Hypera* and between Entiminae and Hyperinae overall.

This uncertainty notwithstanding, it is evident that a deep-level relationship exists between *Hypera* and Entiminae-Cyclominae, estimated to date back ca. 60 million years [16], implying that any parasitoid that develops in both *Hypera* and *Sitona* has the potential to also parasitise most other taxa of Entiminae and Cyclominae. The existence of different biotypes of *M. aethiopoides* seemingly adapted to either *Hypera* or *Sitona* (or even different species of *Sitona*) suggests that its host range is not nearly as wide as encompassing all Entiminae and Cyclominae, but it appears impossible to predict which taxa of these subfamilies from outside the native range of *M. aethiopoides* may be susceptible to parasitism by one or another of its biotypes. In our view, such non-target parasitism stands not only to negatively affect such taxa but also to dilute the intended biocontrol of the target species.

3.2. Case Study: Anaphes nitens *(Girault) for Biological Control of* Gonipterus scutellatus

The mymarid wasp *Anaphes nitens* is a parasitoid of the eggs of weevils in the genus *Gonipterus* Schoenherr and perhaps other genera of the small Australo-Pacific tribe Gonipterini, which, like Hyperinae, is related to the subfamilies Entiminae and Cyclominae but with its precise relationships to these also unclear [16,56]. Both adults and larvae of *Gonipterus* (and of some other Gonipterini) feed on the leaves of *Eucalyptus* and related genera of Myrtaceae. One species of *Gonipterus*, named *G. scutellatus* Gyllenhal, was accidentally introduced into South Africa in 1916 and rapidly became a major defoliator of eucalypt plantations there, spreading in a span of 30 years from the Western Cape province eastwards across the country and then northwards along the eastern side of Africa to Kenya and Uganda, as well as to Mauritius and Madagascar in the Indian Ocean. In 1925 *Gonipterus* weevils also appeared in Argentina and gradually spread northwards along the east coast of South America, reaching Espirito Santo in Brazil in 2018, and from the 1990s they also appeared in Chile, California, Hawaii, the Canary Islands and south-western Europe (Italy, France, Portugal and Spain). In all locations where it established, the weevil caused major defoliation of eucalypt plantations and significant losses for the timber and paper industries based on these trees. In 1925 the South African government embarked on a search for natural enemies of the weevil in Australia, discovering and importing a suitable egg-parasitic wasp (*A. nitens*) and releasing, between 1927 and 1933, about 0.75 million parasitoids in the country [57]. The biocontrol was a huge success, parasitism levels reached 98 % and by 1940 *Gonipterus* was effectively under total control in the country, except for a small region on the Transvaal Highveld and surrounding montane regions. This effort of classical biological control was considered so successful that a monument and plaque was erected for it in 1995 at Cedara in KwaZulu-Natal [58].

Following the success of this biological control, other countries suffering under *Gonipterus* imported the parasitoid species from South Africa, but while it proved equally successful in other African countries, it was far less effective in other parts of the world, particularly in Spain [59,60], Portugal [61] and Chile [62]. Also in Western Australia, where *Gonipterus* weevils had appeared in plantations of *Eucalyptus globulus* in about 1995, control by *A. nitens* was patchy and ineffective [63]. The limited success to failure of the biocontrol efforts in these countries was generally ascribed to climatic factors, in particular low temperatures during winter and at higher altitudes, which were thought to exceed the temperature tolerance of the parasitoid but not that of the weevil. However, Loch [63] raised the possibility that *G. scutellatus* may be a complex of sibling species and that the identity of the weevil species could play a role in the differential successes of the biocontrol efforts.

The identity of the *Gonipterus* weevil in South Africa had been controversial from the start. It was originally identified by the Commonwealth Institute of Entomology in London (G. A. K. Marshall) as *G. reticulatus* Boisduval in 1916 but revised to *G. scutellatus* by Marshall in 1921, whereas in Australia it was identified as *G. rufus* Blackburn by N. Tindale in 1924 and as *G. gibberus* Boisduval by A. M. Lea in 1926 [57]. At the same time, the *Gonipterus* weevils introduced to New Zealand were identified as *G. exaratus* Fåhraeus by H. M. Nicholls in 1924 [57] and those in Argentina were described by C. A. Marelli as *Dacnirotatus bruchi* and *D. platensis* [64], but Marshall changed the names of the latter two species to *Gonipterus gibberus* and *G. platensis* after he examined Marelli's specimens and recognised them as being Australian, not South American [65,66]. Tooke [57] eventually settled on the name *G. scutellatus* for the weevil in South Africa, and this name was accepted in other countries as well, especially after the name *G. platensis* was synonymised with *G. scutellatus* [67] and later also the names *G. gibberus*, *G. exaratus* and *G. notographus* [68]. Only Rosado-Neto and Marques [69] did not agree, drawing attention to differences in the male genitalia of the *Gonipterus* weevils in Argentina (detected and illustrated before by Vidal Sarmiento [70]) and recognising two species in South America, named *G. gibberus* and *G. scutellatus*.

Against this background of uncertainty about the identities of the weevils and the varying success of the biocontrol programs using *A. nitens*, a molecular analysis was conducted in Australia [71] in conjunction with a taxonomic study of the genus *Gonipterus* (Oberprieler, in prep.). Together these studies revealed that *G. "scutellatus"* is indeed a complex of externally similar species, though well distinct in their male genitalia as well as genetically [71]. Specifically, they showed that: (1) none of the invasive *Gonipterus* species outside of Australia represent *G. scutellatus* (which is a comparatively rare species restricted to Tasmania); (2) the species occurring throughout Africa and into Italy is undescribed; (3) the species present in France, Spain, Portugal, California, Hawaii, Chile, Argentina, Brazil, Uruquay, New Zealand and Western Australia is a different one, named *G. platensis* (Marelli), which is native to Tasmania but had not been described from Australia; (4) there is indeed a second species in Argentina, Brazil and Uruquay, described as *G. pulverulentus* Lea from Australia; (5) the *G. scutellatus* complex comprises three further undescribed species (in fact there are more); (6) *G. exaratus*, *G. gibberus* and *G. notographus* are all different species but do not belong in the *G. scutellatus* complex. The COI-based phylogenetic reconstruction of the *G. scutellatus* complex [71] indicates that *G. platensis* and *G. pulverulentus* are not too closely related to the undescribed species (sp. n. 2) in Africa and Italy, which is closer to *G. scutellatus* and also to *G. balteatus* Pascoe. This relationship is also borne out by the male genitalia; the differences in the copulatory sclerite between *G. platensis* and *G. pulverulentus* (as illustrated by Rosado-Neto and Marques [69]) and *Gonipterus* sp. n. 2 are distinct and very consistent.

It is thus evident that the hailed story of the successful biocontrol of *Gonipterus scutellatus* is based on a mistake in identification as well as on a fundamental flaw of the biocontrol program. The *Gonipterus* species in Africa was thought to have originated from Tasmania [57,72], yet the *Anaphes* parasitoid imported into South Africa to control it was collected at Penola in South Australia. Unbeknown to Tooke and his colleagues, the *Gonipterus* species in South Africa (sp. n. 2) is native in South Australia (it occurs throughout south-eastern Australia), so Tooke quite by chance collected the correct parasitoid species for it. In contrast, *G. platensis*, the species introduced into South America, western Europe and the U.S.A., is native in Tasmania and does not occur on the Australian mainland, whereas *A. nitens* does not occur in Tasmania, as far as is known (though other species of *Anaphes* do [73]). By importing *A. nitens* from South Africa, countries such as Argentina, France, Spain, the U.S.A. and Chile released a parasitoid against *G. platensis* that is not ideally equipped to control it. It was recently shown that net reproductive rates of *A. nitens* are higher at temperatures between 20 and 25 °C, whereas those of *A. inexpectatus* Huber & Prinsloo, sourced from the native range of *P. platensis* in Tasmania, are higher at temperatures between 10 and 15 °C, making the latter parasitoid species better equipped to control this weevil in colder conditions (spring and higher altitudes) [60]. The ecologically mismatched *A. nitens* is able to control *G. platensis* adequately in warmer areas of Portugal and has thus provided an economic benefit of 1.8–6.5 billion Euro over 20 years (1996–2016) [74], but the weevil still causes wood loss of up to 86 % in plantations of *Eucalyptus globulus* in some areas [61]. If Tooke had searched for natural enemies of *Gonipterus* sp. n. 2 in Tasmania and imported *A. inexpectatus* into South Africa, the biocontrol program there may have been similarly less effective and far less successful than that achieved with *A. nitens*. He imported the correct parasitoid purely by chance.

4. Discussion

A recent analysis of the entire BIOCAT database of insect biological control agents up to 2010 reported that 32 % of biological control introductions have resulted in establishment and about 10 % have resulted in satisfactory control [18]. The equivalent metrics for weevils as targets of biological control are 63 % established and 31 % providing some control. Those providing complete or substantial control comprise almost 16 % of those established, although this would not necessarily be the case throughout the range where each biological control agent has been introduced. Nevertheless, these data do indicate that biological control of pest weevils has enjoyed a higher level of success than would be expected on average, contrary to the observation of Waterhouse and Norris [20], working in the Pacific region, that weevils are poor candidates for biological control. More research effort has gone into biological control programs in recent years, for example to ensure an appropriate climate match between a BCA and its intended target (e.g., [75]), to assist in the exploration for the best-adapted biotypes or provenance of BCAs [76] and to ensure that the most effective natural enemy biotypes [40] are selected for introduction, and consequently success rates have increased [18].

The two case studies included in this contribution have demonstrated how phylogeny and taxonomy have been important factors in risk assessment and biocontrol efficacy, respectively. It is well accepted that host phylogeny is an important determining factor in most parasitoid/host relationships and hence its importance in risk assessment (e.g., [8]). The close dependence of successful biological control on taxonomy has also been emphasized by many practitioners (e.g., [22]), and the careful alignment of these disciplines is vital for a desirable outcome. These examples demonstrate the challenges of working with target species from such a large, complex and phylogenetically poorly resolved family as the Curculionidae. The importance of accurate taxonomy both for the pest and biological control agent has long been recognised [77,78], and there are well known examples of biological control failure resulting from poor differentiation between species. For example, initial attempts to control California Red Scale (*Aonidiella aurantii* (Maskell)) failed not only because the pest species was not accurately identified, but confusion between species of the natural enemy *Aphytis* Howard (Hymenoptera: Aphelinidae) delayed the selection of effective species for biological control [22]. Nowadays, molecular techniques have become commonplace tools for resolving problems of differentiation between morphologically cryptic or indistinct species [79].

Insects and their natural enemies, parasitoids in particular, have generally coevolved in their natural range, and therefore phylogenetic relationships understandably feature prominently in biological control risk assessment. Host-specific parasitoids are generally selected in preference over generalists (for reasons of biosafety), and so it is expected that closely related hosts are more likely to be at risk from attack of a parasitoid than a more distantly related species. This principle is well accepted and tested in weed biological control [80,81]. Insect biological control is complicated by an extra trophic level (host food plant), not to mention the much larger number of potential non-target hosts, and although studies have shown that host phylogeny is often a strong factor in host selection by parasitoids and indeed parasitoid performance in a host (e.g., [82]), host ecology can also be a determinant of host selection. For example, host use by parasitoids of leaf-mining insects was shown to be capable of spanning several orders of insects [83].

The biosafety record of biological control programs targeting weevils is poorly known, as indeed for most insect biological control programs. Other than the research carried out in Australasia for

M. aethiopoides, there appear to be few records of non-target attack by natural enemies of weevil hosts. For the two examples from the BIOCAT database mentioned above, for which complete control has been reported (*Anaphes nitens* and *Lixophaga sphenophori*), the literature has revealed no example of non-target attack by either BCA. Another species of the tachinid genus *Lixophaga* (*L. diatraeae* (Townsend)), which attacks Crambidae stem borers of Poaceae, has been cultured on alternative Crambidae hosts in the laboratory. However, this tachinid is larviparous, and the rearing technique is based on dissecting the active first-instar larvae from the gravid female *L. diatraeae* and physically transferring them onto other potential hosts. This gives no useful indication of what may happen in the field, from where non-target records are not reported [84].

Undoubtedly more research post-release of biological control agents to verify pre-release predictions would help to provide greater certainty in biosafety risk assessments. Our research in New Zealand, Australia and Morocco on *M. aethiopoides* was carried out with the intention of providing information on the predictive value of natural host range research [51], the expectation at the outset being that a wider range of hosts would be revealed in Morocco, given what we had discovered post-release in New Zealand in particular. However, our findings showed that the taxonomic breadth of the natural host range was actually quite narrow and that host range testing could have been much better informed by the current understanding of phylogenetic relationships within the family Curculionidae. This is clearly a conclusion that can probably be extended more widely across many target groups.

Poor knowledge of the taxonomy, phylogeny and ecology of potential non-target species in the receiving environment is often a severe challenge for predicting non-target impacts as part of a biological control risk assessment (e.g., [85,86]). A risk assessment for the eulophid wasp *Phymastichus coffea* La Salle for biological control of the scolytine weevil *Hypothenemus hampei* (Ferrari) in coffee was carried out [87], and although some non-target attack on scolytines was predicted in genera related to the target, it was argued that so little is known about the scolytine fauna in Colombia that identifying potential non-target hosts for laboratory testing was impossible.

The discovery that *Gonipterus scutellatus* as referred to in the literature comprises a complex of several very similar species with different geographical ranges and host preferences [71,88] illustrates the critical need of accurate identification of both the target (host) and the biocontrol agent. In taxonomically complicated cases the biocontrol program may need to commission specific taxonomic research into the relevant taxa, as occurs in biological control of weeds, e.g., of *Salvinia* by *Cyrtobagous* Hustache weevils [89] and of *Carduus* and *Onopordum* thistles by *Trichosirocalus* Colonnelli weevils [90]. Molecular markers (such as DNA "barcoding") can often help in distinguishing closely related species, but generally morphological assessment (including examination of old type specimens) is needed to assign the correct names to the different species. Further, biocontrol programs of apparently the same target species in different countries need to ensure that this is indeed the case and confirm the identity of the targets in different regions or countries both macroscopically and genetically/biologically (races, biotypes).

In view of the non-target parasitism displayed by *M. aethiopoides* in New Zealand and how this may have been predicted by an understanding of the phylogenetic relationships of its natural hosts, the success of the biocontrol of *Gonipterus* is probably in part ascribable to the fact that the tribe Gonipterini is restricted to the Australo-Pacific region and has no known close relatives in Africa, America and Europe. It does, however, belong in the same clade as the tribe Hyperini (or subfamily Hyperinae), which occurs in Africa as in other areas where *Gonipterus* has become invasive and which also has ectophytic larvae [56]. For egg parasitoids such as *Anaphes nitens* this may not be so relevant as *Gonipterus* lays its eggs in a hard capsule on the surface of leaves, whereas the eggs of Hyperini as known are laid between plant parts. However, for larval parasitoids such as the eulophid *Entedon* Dahlman [62] the nature of the phylogenetic relationship between Gonipterini and Hyperini would be of greater importance if these parasitoids were considered as biocontrol agents.

5. Conclusions

We do not believe that the issues raised by this review of classical biological control of Curculionidae are unusual compared to other groups for which biological control has been used, although the enormous diversity of and the lack of clear phylogenetic relationships in Curculionidae have exacerbated this. The combination of traditional taxonomy and new molecular tools will remain an essential component of the good practice of biological control in the future.

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Appendix A

Table A1. Weevil species that have become targets for biological control programs, their origin and countries where biological control agents have been recorded as established and their impact. Data from BIOCAT2010.1. The BIOCAT database maintained by CABI aims to be comprehensive, but inevitably some relevant publications have been overlooked, and records of introductions focus on what is perceived to be the primary target pest, and may omit or condense data on actual or potential secondary targets.

Target Taxon				Biological Control Agent						
Subfamily	**Genus Species**	**Crop**	**Origin**	**Biocontrol Agent**	**Ord: Family**	**BCA Origin**	**Stage Attacked**	**Release Country**	**Impact ***	**Ref. in BIOCAT**
Curculioninae	*Anthonomus eugenii*	*Piper* spp.	Mexico	*Eupelmus cushmani*	Hymenoptera: Eupelmidae	Guatemala	larva	USA, Mexico, Central America	NC	[91]
Curculioninae	*Anthonomus eugenii*	*Piper* spp.	Mexico	*Pteromalus hunteri*	Hymenoptera: Pteromalidae	Guatemala	larva	USA, Hawaii	NC	[91]
Curculioninae	*Gonipterus* sp.n. 2	eucalypts	Australia	*Anaphes nitens*	Hym: Mymaridae	Australia	egg	NZ, S. America, Europe, Africa, USA, Madagascar	CC Madagascar, PC-SC elsewhere	[92]
Curculionidae	*Gonipterus pulverulentus*?	eucalypts	Australia	*Anaphes nitens*	Hymenoptera: Mymaridae	Australia	egg	Argentina	NC	[93]
Cyclominae	*Listronotus bonariensis*	pasture grasses	South America	*Microctonus hyperodae*	Hymenoptera: Braconidae	Argentina	adult	NZ	SC	[94]
Cyclominae	*Listroderes difficilis "costirostris"*	vegetables	South America	*Stethantyx parkeri*	Hymenoptera: Ichneumonidae	Argentina, Uruguay	larva	Australia	NC	[95]
Dryophthorinae	*Cosmopolites sordidus*	banana	Malaysia	*Dactylosternum abdominale*	Coleoptera: Hydrophilidae		predator	Australia, Jamaica	PC Jamaica, NC Australia	[20,84,96]
Dryophthorinae	*Cosmopolites sordidus*	banana	Malaysia	*Dactylosternum hydrophiloides*	Coleoptera: Hydrophilidae	Malaysia, Pacific	predator	Jamaica, Australia	PC Jamaica, NC Australia	[95]
Dryophthorinae	*Cosmopolites sordidus*	banana	Malaysia	*Plaesius javanus*	Coleoptera: Histeridae	Indonesia	predator	France, Jamaica, Mexico, Palau, Samoa, Tonga, Trinidad and Tobago, USA	PC Jamaica, NC elsewhere	[20]
Dryophthorinae	*Cosmopolites sordidus*	banana	Malaysia	*Plaesius laevigatus*	Coleoptera: Histeridae	Indonesia	predator	Cook Islands, Fiji	PC Fiji, NC Cook Isls.	[20]
Hyperinae	*Hypera postica*	lucerne	Europe	*Bathyplectes anurus*	Hymenoptera: Ichneumonidae	Europe	larva	USA, Canada, Japan	PC Japan, NC elsewhere	[93,97,98]
Hyperinae	*Hypera postica*	lucerne	Europe	*Bathyplectes curculionis*	Hymenoptera: Ichneumonidae	Europe	larva	USA, Canada	PC USA, NC Canada	[93,98]
Hyperinae	*Hypera punctata*	lucerne, clover	Europe	*Bathyplectus infernalis*	Hymenoptera: Ichneumonidae	Italy	larva	USA	SC	[93]
Hyperinae	*Hypera postica*	lucerne	Europe	*Oomyzus (syn Tetrastichus) incertus*	Hymenoptera: Eulophidae	Europe	larva	USA, Canada	NC	[93,98]
Hyperinae	*Hypera postica*	lucerne	Europe	*Microctonus colesi*	Hymenoptera: Braconidae	Iran	adult	USA	NC	[93,98]

Table A1. *Cont.*

Target Taxon				Biological Control Agent						
Subfamily	**Genus Species**	**Crop**	**Origin**	**Biocontrol Agent**	**Ord: Family**	**BCA Origin**	**Stage Attacked**	**Release Country**	**Impact ***	**Ref. in BIOCAT**
Hyperinae	*Hypera postica*	lucerne	Europe	*Bathyplectes stenostigma*	Hymenoptera: Ichneumonidae	Europe	larva	USA	NC	[93]
Hyperinae	*Hypera postica*	lucerne	Europe	*Coelopisthia extenta*	Hymenoptera: Pteromalidae	Europe	larva	USA	NC	[93]
Hyperinae	*Hypera postica*	lucerne	Europe	*Peridesmia discus*	Hymenoptera: Pteromalidae	Europe	egg predator	USA	NC	[99]
Hyperinae	*Hypera brunnipennis*	lucerne	Europe	*Coelopisthia extenta*	Hymenoptera: Pteromalidae	Europe	larva	USA	NC	[93]
Entiminae	*Diaprepes abbreviatus*	citrus	Carribbean	*Aprostocetus vaquitarum*	Hymenoptera: Eulophidae	Dominica	egg	USA (Florida)	PC	[100]
Entiminae	*Diaprepes abbreviatus*	citrus	Carribbean	*Quadrastichus haitiensis*	Hymenoptera: Eulophidae	Puerto Rico	egg	USA	NC	[101]
Entiminae	*Sitona discoideus*	lucerne (*Medicago sativa*)	Mediterranean	*Microctonus aethiopoides*	Hymenoptera: Braconidae	Morocco, Greece	adult	Australia, NZ, USA, Canada	SC NZ, PC elsewhere	[95,102,103]
Entiminae	*Sitona obsoletus*	white clover		*Microctonus aethiopoides*	Hymenoptera: Braconidae	Ireland	adult	NZ	SC	[104]
Entiminae	*Sitona cylindricollis*	Sweet clover		*Pygostolus falcatus*	Hymenoptera: Braconidae	Sweden	adult	Canada	NC	[105]
Entiminae	*Sitona hispidulus*	lucerne		*Anaphes diana*	Hymenoptera: Mymaridae	Europe	egg	USA	NC	[106]
Molytinae	*Syagrius fulvitarsis*	ferns	Australia	*Jarra syagrii*	Hymenoptera: Braconidae	Australia	larva?	USA, Hawaii	NC	[91]
Dryophthorinae	*Rhabdoscelus obscurus*	sugar cane	Papua New Guinea	*Dactylosternum hydrophiloides*	Coleoptera: Hydrophilidae	Philippines	predator	USA, Hawaii	NC	[91]
Dryophthorinae	*Rhabdoscelus obscurus*	sugar cane	Papua New Guinea	*Fulvius brevicornis*	Hemiptera: Miridae	Philippines		USA, Hawaii	NC	[91]
Dryophthorinae	*Rhabdoscelus obscurus*	sugar cane	Papua New Guinea	*Lixophaga sphenophori*	Diptera: Tachinidae	Papua New Guinea	larva	Australia, Fiji, USA, Hawaii	CC USA, NC elsewhere	[91,95]
Scotytinae	*Dendroctonus micans*	spruce	Europe, Asia	*Rhizophagus grandis*	Coleoptera: Monotomidae	Belgium	predator on larva	France, Georgia, UK	PC Georgia and UK, NC France	[107,108]
Scotytinae	*Dendroctonus terebrans*	*Pinus* spp.	USA	*Rhizophagus grandis*	Coleoptera: Monotomidae	Belgium	predator on larva	USA	U	[109]
Scotytinae	*Ips grandicollis*	*Pinus* spp.	USA, Canada	*Dendrosoter sulcatus*	Hymenoptera: Braconidae	USA	adult	Australia	NC	[95]
Scolytinae	*Ips grandicollis*	*Pinus* spp.	USA, Canada	*Roptrocerus xylophagorum*	Hymenoptera: Pteromalidae	USA	larva	Australia	PC	[95]
Scolytinae	*Orthotomicus erosus*	*Pinus* spp.		*Dendrosoter caenopchoides*	Hymenoptera: Braconidae	Israel		South Africa	NC	[110]

Table A1. *Cont.*

Target Taxon				Biological Control Agent						
Subfamily	**Genus Species**	**Crop**	**Origin**	**Biocontrol Agent**	**Ord: Family**	**BCA Origin**	**Stage Attacked**	**Release Country**	**Impact ***	**Ref. in BIOCAT**
Scolytinae	*Scolytus rugulosus*	peach		*Rhaphitelus maculatus*	Hymenoptera: Pteromalidae	USA	larva?	Chile	PC	[111]
Scolytinae	*Scolytus multistriatus*	Elm		*Dendrosoter protruberans*	Hymenoptera: Braconidae	France	larva	USA	NC	[112]
Scolytinae	*Hypothenemus hampei*	coffee	Africa	*Cephalonomia stephanoderis*	Hymenoptera: Bethylidae	Africa	larva/pupa	Central America, India	U	[113,114]
Scolytinae	*Hypothenemus hampei*	coffee	Africa	*Phymastichus coffea*	Hymenoptera: Eulophidae	Africa	adult	Central America, India	U	[115,116]
Scolytinae	*Hypothenemus hampei*	coffee	Africa	*Prorops nasuta*	Hymenoptera: Bethylidae	Africa	larva/pupa	Central America, Brazil, India	U	[113,114]
Scolytinae	*Hylastes ater*	Pinus spp		*Thanasimus formicarius*	Coleoptera: Cleridae	Austria	predator	New Zealand	NC	[102]

* NC = no control, PC = partial control, SC = substantial control, CC = complete control, U = unknown impact.

References

1. Barratt, B.I.P.; Ehlers, G.A.C. Impacts of exotic biological control agents on non-target species and biodiversity: Evidence, policy and implications. In *Environmental Pest Management: Challenges for Agronomists, Ecologists, Economists and Policymakers*; Coll, M., Wajnberg, E., Eds.; John Wiley & Sons Ltd.: Oxford, UK, 2017; pp. 325–346.
2. Kenis, M.; Auger-Rozenberg, M.; Roques, A.; Timms, L.; Péré, C.; Cock, M.J.W.; Settele, J.; Augustin, S.; Lopez-Vaamonde, C. Ecological effects of invasive alien insects. *Biol. Invasions* **2009**, *11*, 21–45. [CrossRef]
3. Tylianakis, J.M.; Binzer, A. Effects of global environmental changes on parasitoid–host food webs and biological control. *Biol. Control* **2013**, *75*, 77–86. [CrossRef]
4. Hopper, K.R.; Wajnberg, E. Risks of interbreeding between species used in biological control and native species, and methods for evaluating their occurrence and impact. In *Environmental Impact of Arthropod Biological Control: Methods and Risk Assessment*; Kuhlmann, U., Bigler, F., Babendreier, D., Eds.; CABI Publishing: Delemont, Switzerland, 2006; pp. 78–97.
5. Van Veen, F.J.; Memmott, J.; Godfray, H.C.J. Indirect effects, apparent competition and biological control. In *Trophic and Guild Interactions in Biological Control*; Brodeur, J., Boivin, G., Eds.; Springer: Dortrect, The Netherlands, 2006; pp. 145–169.
6. Barratt, B.I.P. Assessing safety of biological control introductions. *CAB Rev. Perspect. Agric. Vet. Sci. Nutr. Nat. Resour.* **2011**, *6*, 1–12. [CrossRef]
7. Bigler, F.; Bale, J.S.; Cock, M.J.W.; Dreyer, H.; Greatrex, U.; Kuhlmann, U.; Loomans, A.J.M.; Van Lenteren, J.C. Guidelines on information requirements for import and release of invertebrate biological control agents in European countries. *Biocontrol News Inf.* **2005**, *26*, 115N–123N. [CrossRef]
8. Kuhlmann, U.; Schaffner, U.; Mason, P.G. Selection of non-target species for host specificity testing. In *Environmental Impact of Invertebrates for Biological Control of Arthropods: Methods and Risk Assessment*; Bigler, F., Babendreier, D., Kuhlmann, U., Eds.; CABI Publishing: Wallingford, Oxford, UK, 2006; pp. 15–37.
9. Goolsby, J.A.; Klinken, R.D.V.; Palmer, W.A. Maximizing the contribution of native-range studies towards the identification and prioritization of weed biological control agents. (Special issue: Agent selection in weed biocontrol). *Aust. J. Entomol.* **2006**, *45*, 276–286. [CrossRef]
10. Barratt, B.I.P. BIREA—Biocontrol Information Resource for ERMA New Zealand applicants. *Forest Health News Magazine*, May 2007; 2.
11. Oberprieler, R.G.; Marvaldi, A.E.; Anderson, R.S. Weevils, weevils, weevils everywhere. *Zootaxa* **2007**, *1668*, 491–520.
12. Kuschel, G. A Phylogenetic Classification of Curculionoidea to Family and Subfamily Level, Biology and Phylogeny of Curculionoidea. *Mem. Entomol. Soc. Wash.* **1995**, *14*, 5–33.
13. Gunter, N.L.; Oberprieler, R.G.; Cameron, S.L. Molecular phylogenetics of Australian weevils (Coleoptera: Curculionoidea): Exploring relationships in a hyperdiverse lineage through comparison of independent analyses. *Aust. Entomol.* **2016**, *55*, 217–233. [CrossRef]
14. Gillett, C.P.D.T.; Crampton-Platt, A.; Timmermans, M.J.T.N.; Jordal, B.; Emerson, B.C.; Vogler, A.P. Bulk de novo mitogenome assembly from pooled total DNA elucidates the phylogeny of weevils (Coleoptera: Curculionoidea). *Mol. Biol. Evol.* **2014**, *31*, 2223–2237. [CrossRef] [PubMed]
15. Gillett, C.P.D.T.; Lyal, C.H.C.; Vogler, A.P.; Emerson, B.C. Statistical evaluation of monophyly in the 'broad-nosed weevils' through molecular phylogenetic analysis combining mitochondrial genome and single-locus sequences (Curculionidae: Entiminae, Cyclominae, and Hyperinae). *Diversity* **2018**, *10*, 21. [CrossRef]
16. Shin, S.; Clarke, D.J.; Lemmon, A.R.; Moriarty-Lemmon, E.; Aitken, A.L.; Haddad, S.; Farrell, B.D.; Marvaldi, A.E.; Oberprieler, R.G.; McKenna, D.D. Phylogenomic data yield new and robust insights into the phylogeny and evolution of weevils. *Mol. Biol. Evol.* **2017**, *35*, 823–836. [CrossRef] [PubMed]
17. Clewley, G.D.; Eschen, R.; Shaw, R.H.; Wright, D.J. The effectiveness of classical biological control of invasive plants. *J. Appl. Ecol.* **2012**, *49*, 1287–1295. [CrossRef]
18. Cock, M.J.W.; Murphy, S.T.; Kairo, M.T.K.; Thompson, E.; Murphy, R.J.; Francis, A.W. Trends in the classical biological control of insect pests by insects: An update of the BIOCAT database. *BioControl* **2016**, *61*, 349–363. [CrossRef]

19. Kenis, M.; Hurley, B.P.; Hajek, A.E.; Cock, M.J.W. Classical biological control against insect pests of trees: Facts and figures. *Biol. Invasions* **2017**, *19*, 3401–3417. [CrossRef]
20. Waterhouse, D.F.; Norris, K.R. *Biological Control Pacific Prospects*; Inkata Press: Melbourne, Australia, 1987; p. 454.
21. Barratt, B.I.P.; Evans, A.A.; Johnstone, P.D. Effect of the ratios of *Listronotus bonariensis* and *Sitona discoideus* (Coleoptera: Curculionidae) to their respective parasitoids *Microctonus hyperodae* and *Microctonus aethiopoides* (Hymenoptera: Braconidae), on parasitism, host oviposition and feeding in the laboratory. *Bull. Entomol. Res.* **1996**, *86*, 101–108.
22. Rosen, D. The role of taxonomy in effective biological control programs. *Spec. Issue Invertebr. Biodivers. Bioindic. Sustain. Landsc.* **1986**, *15*, 121–129. [CrossRef]
23. Sands, D.P.A.; van Driesche, R.G. Using the scientific literature to estimate the host range of a biological control agent. In *Assessing Host Ranges for Parasitoids and Predators Use for Classical Biological Control: A Guide to Best Practice*; van Driesche, R.G., Reardon, R., Eds.; Forest Health Technology Enterprise Team, Forest Service, USDA: Morgantown, WV, USA, 2004; pp. 15–23.
24. European and Mediterranean Plant Protection Organization. Import and release of non-indigenous biological control agents. *Bull. OEPP/EPPO Bull.* **2010**, *40*, 335–344.
25. HSNO Act (Hazardous Substances and New Organisms Act). Available online: http://www.chemsafetypro.com/Topics/NZ/HSNO_Act_Hazardous_Substances_and_New_Organisms_Act.html (accessed on 15 June 2018).
26. Sheppard, A.W. Prioritising agents based on predicted efficacy: Beyond the lottery approach. In *Improving the Selection, Testing and Evaluation of Weed Biocontrol Agents*; Spafford-Jacobs, H., Briese, D.T., Eds.; Cooperative Research Centre for Australian Weed Management: Adelaide, Australia, 2003; pp. 11–21.
27. Stouthamer, R. Molecular methods for the identification of biological control agents at the species and strain level. In *Environmental Impact of Invertebrates for Biological Control of Arthropods: Methods and Risk Assessment*; Bigler, F., Babendreier, D., Kuhlmann, U., Eds.; CABI Publishing: Wallingford, Oxon, UK, 2006; pp. 187–201.
28. Janzen, D.H.; Hallwachs, W.; Blandin, P.; Burns, J.M.; Cadiou, J.-M.; Chacon, I.; Dapkey, T.; Deans, A.R.; Epstein, M.E.; Espinoza, B.; et al. Integration of DNA barcoding into an ongoing inventory of complex tropical biodiversity. *Mol. Ecol. Resour.* **2009**, *9*, 1–26. [CrossRef] [PubMed]
29. Smith, M.A.; Wood, D.M.; Janzen, D.H.; Hallwachs, W.; Hebert, P.D.N. DNA barcodes affirm that 16 species of apparently generalist tropical parasitoid flies (Diptera, Tachinidae) are not all generalists. *Proc. Natl. Acad. Sci. USA* **2007**, *104*, 4967–4972. [CrossRef] [PubMed]
30. Smith, M.A.; Rodriguez, J.J.; Whitfield, J.B.; Deans, A.R.; Janzen, D.H.; Hallwachs, W.; Hebert, P.D.N. Extreme diversity of tropical parasitoid wasps exposed by iterative integration of natural history, DNA barcoding, morphology, and collections. *Proc. Natl. Acad. Sci. USA* **2008**, *105*, 12359–12364. [CrossRef] [PubMed]
31. Cory, J.S.; Myers, J.H. Direct and indirect ecological effects of biological control. *Trends Ecol. Evol.* **2000**, *15*, 137–139. [CrossRef]
32. Briese, D.T.; Walker, A. Choosing the right plants to test: The host-specificity of *Longitarsus* sp. (Coleoptera: Chrysomelidae) a potential biological control agent of *Heliotropium amplexicaule*. *Biol. Control* **2008**, *44*, 271–285. [CrossRef]
33. Cullen, J.M.; Hopkins, D.C. Rearing, release and recovery of *Microctonus aethiopoides* Loan (Hymenoptera: Braconidae) imported for the control of *Sitona discoideus* Gyllenhal (Coleoptera: Curculionidae) in south eastern Australia. *J. Austr. Entomol. Soc.* **1982**, *21*, 279–284. [CrossRef]
34. Aeschlimann, J.P. Sources of importation, establishment and spread in Australia of *Microctonus aethiopoides* Loan (Hymenoptera: Braconidae), a parasitoid of *Sitona discoideus* Gyllenhal (Coleoptera: Curculionidae). *J. Austr. Entomol. Soc.* **1983**, *22*, 325–331. [CrossRef]
35. Stufkens, M.W.; Farrell, J.A.; Goldson, S.L. Establishment of Microctonus aethiopoides, a parasitoid of the sitona weevil in New Zealand. In Proceedings of the 40th New Zealand Weed and Pest Control Conference, Quality Inn, Nelson, New Zealand, 11–13 August 1987; Popay, A.J., Ed.; The New Zealand Weed and Pest Control Society: Quality Inn, Nelson, New Zealand, 1987; pp. 31–32.
36. Vink, C.J.; Phillips, C.B.; Mitchell, A.D.; Winder, L.M.; Cane, R.P. Genetic variation in *Microctonus aethiopoides* (Hymenoptera: Braconidae). *Biol. Control* **2003**, *28*, 251–264. [CrossRef]

37. Hopkins, D.C. Establishment and spread of the sitona weevil parasite Microctonus aethiopoides in South Australia. In Proceedings of the 3rd Australasian Conference on Grassland Invertebrate Ecology, Adelaide, Australia, 30 November–4 December 1982; Lee, K.E., Ed.; CSIRO: Adelaide, Australia, 1982; pp. 177–182.
38. Aeschlimann, J.P. The *Sitona* (Col.: Curculionidae) species occurring on *Medicago* and their natural enemies in the Mediterranean region. *Entomophaga* **1980**, *25*, 139–153. [CrossRef]
39. Aeschlimann, J.P. Notes on the variability of *Microctonus aethiopoides* Loan (Hymenoptera: Braconidae: Euphorinae). *Contrib. Am. Entomol. Inst.* **1983**, *20*, 329–335.
40. Phillips, C.B.; Vink, C.J.; Blanchet, A.; Hoelmer, K.A. Hosts are more important than destinations: What genetic variation in *Microctonus aethiopoides* (Hymenoptera: Braconidae) means for foreign exploration for natural enemies. *Mol. Phylogenet. Evol.* **2008**, *49*, 467–476. [CrossRef] [PubMed]
41. Barratt, B.I.P.; Todd, J.; Malone, L.A. Selecting non-target species for arthropod biological control agent host range testing: Evaluation of a novel method. *Biol. Control* **2016**, *93*, 84–92. [CrossRef]
42. Zimmermann, E.C. *Australian Weevils (Coleoptera: Curculionidae). Volume VI—Colour Plates 305-632*; CSIRO: Melbourne, Australia, 1992; p. 707.
43. Barratt, B.I.P.; Oberprieler, R.G.; Ferguson, C.M.; Hardwick, S. Parasitism of the lucerne pest *Sitona discoideus* Gyllenhal (Coleoptera: Curculionidae) and non-target weevils by *Microctonus aethiopoides* Loan (Hymenoptera: Braconidae) in south-eastern Australia, with an assessment of the taxonomic affinities of non-target hosts of *M. aethiopoides* recorded from Australia and New Zealand. *Austr. J. Entomol.* **2005**, *44*, 192–200.
44. Goldson, S.L.; Proffitt, J.R.; McNeill, M.R. Seasonal biology and ecology in New Zealand of *Microctonus aethiopoides* (Hymenoptera: Braconidae), a parasitoid of *Sitona* spp. (Coleoptera: Curculionidae), with special emphasis on atypical behaviour. *J. Appl. Ecol.* **1990**, *27*, 703–722. [CrossRef]
45. Ferguson, C.M.; Roberts, G.M.; Barratt, B.I.P.; Evans, A.A. The distribution of the parasitoid Microctonus aethiopoides Loan (Hymenoptera: Braconidae) in southern South Island Sitona discoideus Gyllenhal (Coleoptera: Curculionidae) populations. In Proceedings of the 47th New Zealand Plant Protection Conference, Waitangi Hotel, Pahia, New Zealand, 9–11 August 1994; Popay, A.J., Ed.; New Zealand Plant Protection Society Inc.: Waitangi Hotel, Pahia, New Zealand, 1994; pp. 261–265.
46. Pullen, K.R.; Jennings, D.; Oberprieler, R.G. Annotated catalogue of Australian weevils (Coleoptera: Curculionoidea). *Zootaxa* **2014**, *3896*, 1–481. [CrossRef] [PubMed]
47. Brown, S.D.J. A revision of the New Zealand weevil genus *Irenimus* Pascoe, 1876 (Coleoptera: Curculionidae: Entiminae). *Zootaxa* **2017**, *4263*, 1–42. [CrossRef] [PubMed]
48. Brown, S.D.J.; Armstrong, K.F.; Barratt, B.I.P.; Cruickshank, R.H.; Phillips, C.B. Taxonomy and evolution of New Zealand broad-nosed weevils (Coleoptera: Curculionidae: Entiminae). In *XXV International Congress of Entomology*; Entomological Society of America: Orlando, FL, USA, 2016.
49. Brown, S.D.J. *Austromonticola*, a new genus of broad-nosed weevil (Coleoptera, Curculionidae, Entiminae) from montane areas of New Zealand. *Zookeys* **2017**, *707*, 73–130. [CrossRef] [PubMed]
50. Barratt, B.I.P.; Oberprieler, R.G.; Barton, D.M.; Mouna, M.; Stevens, M.; Alonso-Zarazaga, M.A.; Vink, C.J.; Ferguson, C.M. Does knowledge of natural host range always help predict host range in new areas of introduction? A case study with the braconid parasitoid *Microctonus aethiopoides* Loan. In Proceedings of the XXIV International Congress of Entomology, Daegu, Korea, 19–25 August 2012.
51. Barratt, B.I.P.; Oberprieler, R.G.; Barton, D.; Mouna, M.; Stevens, M.; Alonso-Zarazaga, M.A.; Vink, C.J.; Ferguson, C.M. Could research in the native range, and non-target host range in Australia, have helped predict host range of the parasitoid *Microctonus aethiopoides* Loan (Hymenoptera: Braconidae), a biological control agent introduced for *Sitona discoideus* Gyllenhal (Coleoptera: Curculionidae) in New Zealand? *BioControl* **2012**, *57*, 735–750.
52. Velazquez De Castro, A.J.; Alonso-Zarazaga, M.A.; Outerelo, R. Systematics of Sitonini (Coleoptera: Curculionidae: Entiminae), with a hypothesis on the evolution of feeding habits. *Syst. Entomol.* **2007**, *32*, 312–331. [CrossRef]
53. Hundsdoerfer, A.K.; Rheinheimer, J.; Wink, M. Towards the phylogeny of the Curculionoidea (Coleoptera): Reconstructions from mitochondrial and nuclear ribosomal DNA sequences. *Zool. Anz.* **2009**, *248*, 9–31. [CrossRef]
54. McKenna, D.M.; Sequeira, A.S.; Marvaldi, A.E.; Farrell, B.D. Temporal lags and overlap in the diversification of weevils and flowering plants. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 7083–7088. [CrossRef] [PubMed]

55. Haran, J.; Timmermans, M.J.T.N.; Vogler, A.P. Mitogenome sequences stabilize the phylogenetics of weevils (Curculionoidea) and establish the monophyly of larval ectophagy. *Mol. Phylogenet. Evol.* **2013**, *67*, 156–166. [CrossRef] [PubMed]
56. Oberprieler, R.G.; Caldara, R.; Skuhrovec, J. Bagoini Thomson, 1859; Gonipterini Lacordaire, 1863; Hyperini Marseul, 1863. In *Handbook of Zoology, Volume 3: Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Eds.; Walter de Gruyter: Berlin, Germany, 2014; pp. 452–476.
57. Tooke, F.G.C. The Eucalyptus Snout-beetle, *Gonipterus scutellatus* Gyll. A study of its ecology and control by biological means. *Entomol. Mem. Union S. Afr.* **1955**, *3*, 1–282.
58. Londt, J. Milestone in biological control. *Antenna (Lond.)* **1996**, *20*, 24.
59. Cordero Rivera, A.; Santolamazza Carbone, S.; Andres, J.A. Life cycle and biological control of the Eucalyptus snout beetle (Coleoptera, Curculionidae) by *Anaphes nitens* (Hymenoptera, Mymaridae) in north-west Spain. *Agric. For. Entomol.* **1999**, *1*, 103–109. [CrossRef]
60. Valente, C.; Gonçalves, C.I.; Reis, A.; Branco, M. Pre-selection and biological potential of the egg parasitoid *Anaphes inexpectatus* for the control of the Eucalyptus snout beetle, *Gonipterus platensis*. *J. Pest Sci.* **2017**, *90*, 911–923. [CrossRef]
61. Reis, A.R.; Ferreira, L.; Tomé, M.; Clara Araujo, C.; Branco, M. Efficiency of biological control of *Gonipterus platensis* (Coleoptera: Curculionidae) by *Anaphes nitens* (Hymenoptera: Mymaridae) in cold areas of the Iberian Peninsula: Implications for defoliation and wood production in *Eucalyptus globulus*. *For. Ecol. Manag.* **2012**, *270*, 216–222. [CrossRef]
62. Gumovsky, A.; De Little, D.; Rothmann, S.; Jaques, L.; Mayorga, S.E.I. Re-description and first host and biology records of *Entedon magnificus* (Girault & Dodd) (Hymenoptera, Eulophidae), a natural enemy of *Gonipterus* weevils (Coleoptera, Curculionidae), a pest of Eucalyptus trees. *Zootaxa* **2015**, *3957*, 577–584. [PubMed]
63. Loch, A.D. Parasitism of the Eucalyptus weevil, *Gonipterus scutellatus* Gyllenhal, by the egg parasitoid, Anaphes nitens Girault, in *Eucalyptus globulus* plantations in southwestern Australia. *Biol. Control* **2008**, *47*, 1–7. [CrossRef]
64. Marelli, C.A. La plaga de los gorgojos de los eucaliptos. *Rev. Soc. Entomol. Argent.* **1926**, *1*, 14–22.
65. Marshall, G.A.K. New injurious Curculionidae (Col.). *Bull. Entomol. Res.* **1927**, *17*, 199–218. [CrossRef]
66. Marshall, G.A.K. New injurious Curculionidae (Col.). *Bull. Entomol. Res.* **1928**, *18*, 257–266. [CrossRef]
67. Wibmer, G.J.; O'Brien, C.W. Annotated checklist of the weevils (Curculionidae sensu lato) of South America (Coleoptera: Curculionoidea). *Mem. Am. Entomol. Inst.* **1986**, *39*, 1–563.
68. Zimmermann, E.C. *Australian Weevils (Coleoptera: Curculionidae). Volume I—Orthoceri. Anthribidae to Attelabidae. The Primitive Weevils*; CSIRO: Melbourne, Australia, 1994; p. 741.
69. Rosado-Neto, G.H.; Marques, M.I. Características do adulto, genitália e formas imaturas de *Gonipterus gibberus* Boisduval and *G. scutellatus* Gyllenhal (Coleoptera, Curculionidae). *Rev. Bras. Zool.* **1996**, *13*, 77–90. [CrossRef]
70. Vidal Sarmiento, J.A. Contribución a la aclaración definitiva del problema existente entre las especies "*Gonipterus gibberus*" Boisd. y "*G. platensis*" Mar. *Notas Mus. La Plata* **1955**, *18*, 31–41.
71. Mapondera, T.S.; Burgess, T.; Matsuki, M.; Oberprieler, R.G. Identification and molecular phylogenetics of the cryptic species of the *Gonipterus scutellatus* complex (Coleoptera: Curculionidae: Gonipterini). *Austr. J. Entomol.* **2012**, *51*, 175–188. [CrossRef]
72. Mally, C.W. The Eucalyptus Snout-beetle (*Gonipterus scutellatus*, Gyll.). *J. Depart. Agric. Union S. Afr.* **1924**, *51*, 1–30.
73. Huber, J.T.; Prinsloo, G.L. Redescription of *Anaphes nitens* (Girault) and description of two new species of *Anaphes* Halliday (Hymenoptera: Mymaridae), parasite of *Gonipterus scutellatus* Gyllenhal (Coleoptera: Curculionidae) in Tasmania. *J. Austr. Entomol. Soc.* **1990**, *29*, 333–341. [CrossRef]
74. Valente, C.; Gonçalves, C.I.; Monteiro, F.; Gaspar, J.; Silva, M.; Sottomayer, M.; Paiva, M.R.; Branco, M. Economic outcome of classical biological control: A case study of the Eucalyptus snout beetle Gonipterus platensis and the parasitoid Anaphes nitens. *Ecol. Econ.* **2018**, *149*, 40–47. [CrossRef]
75. Avila, G.A.; Charles, J.G. Modelling the potential geographic distribution of *Trissolcus japonicus*: A biological control agent of the brown marmorated stink bug, *Halyomorpha halys*. *Biocontrol* **2018**, *63*, 505–518. [CrossRef]
76. Robertson, M.P.; Kriticos, D.J.; Zachariades, C. Climate matching techniques to narrow the search for biological control agents. *Biol. Control* **2008**, *46*, 442–452. [CrossRef]

77. Clausen, C.P. The relation of taxonomy to biological control. *J. Econ. Entomol.* **1942**, *35*, 744–748. [CrossRef]
78. Sabrosky, C.W. The interrelations of biological control and taxonomy. *Econ. Entomol.* **1955**, *48*, 710–714. [CrossRef]
79. Hewitt, G.M.; Johnston, A.W.B.; Young, J.P.W. *Molecular Techniques in Taxonomy*; Springer: Berlin, Germany, 1991; Volume 57, p. 412.
80. Briese, D.T. Phylogeny: Can it help us to understand host choice by biological weed control agents? In *Proceedings of the 9th International Symposium on Biological Control of Weeds, 19–26 January 1996*; Moran, V.C., Hoffmann, J.H., Eds.; University of Cape Town: Stellenbosch, South Africa, 1996; pp. 63–70.
81. Pemberton, R.W. Predictable risk to native plants in weed biological control. *Oecologia* **2000**, *125*, 489–495. [CrossRef] [PubMed]
82. Desneux, N.; Blahnik, R.; Delebecque, C.J.; Heimpel, G.E. Host phylogeny and specialisation in parasitoids. *Ecol. Lett.* **2012**, *5*, 453–460. [CrossRef] [PubMed]
83. Askew, R.R. Parasitoids of leaf-mining Lepidoptera: What determines their host ranges? In *Parasitoid Community Ecology*; Hawkins, B.A., Sheehan, W., Eds.; Oxford University Press: Oxford, UK, 1994; pp. 177–202.
84. Bennett, F.D.; Cock, M.J.W.; Hughes, I.W.; Simmonds, F.J.; Yaseen, M. A Review of Biological Control of Pests in the Commonwealth Caribbean and Bermuda up to 1982. In *Technical Communication No. 9*; Cock, M.J.W., Ed.; Commonwealth Institute of Biological Control: Farnham Royal, UK, 1985; p. 218.
85. Van Driesche, R. Predicting host ranges of parasitoids and predacious insects—What are the issues. In *Assessing Host Ranges for Parasitoids and Predators Used for Classical Biological Control: A Guide to Best Practice*; van Driesche, R., Reardon, R., Eds.; USDA Forest Service: Morgantown, WV, USA, 2004; Volume FHTET, pp. 1–3.
86. Hopper, K.R. Research needs concerning non-target impacts of biological control introductions. In *Evaluating Indirect Ecological Effects of Biological Control*; Wajnberg, E., Scott, J.K., Quimby, P.C., Eds.; CABI Publishing: Wallingford, Oxfordshire, UK, 2001; pp. 39–56.
87. Lopez-Vaamonde, C.; Baker, P.S.; Cock, M.J.W.; Orozco, J. *Dossier on Phymastichus coffea (Hymenoptera: Eulophidae: Tetrastichinae), a Potential Biological Control Agent for Hypothenemus Hampei (Ferrari) (Col.: Scolytidae) in Colombia*; International Institute of Biological Control: Ascot, UK, 1997; p. 26.
88. Newete, S.W.; Byrne, M.J.; Oberprieler, R.G. The host range of the Eucalyptus Weevil, *Gonipterus* "*scutellatus*" Gyllenhal (Coleoptera: Curculionidae), in South Africa. *Ann. For. Sci.* **2011**, *68*, 1005–1013. [CrossRef]
89. Calder, A.; Sands, D.P.A. A new Brazilian *Cyrtobagous* Hustache (Coleoptera: Curculionidae) introduced into Australia to control *Salvinia*. *J. Austr. Entomol. Soc.* **1985**, *24*, 57–64. [CrossRef]
90. Alonso-Zarazaga, M.A.; Sánchez-Ruiz, M. Revision of the *Trichosirocalus horridus* (Panzer) species complex, with description of two new species infesting thistles (Coleoptera: Curculionidae, Ceutorhynchinae). *Austr. J. Entomol.* **2002**, *41*, 199–208. [CrossRef]
91. Lai, P.Y.; Funasaki, G.Y. *List of Biological Control Introductions in Hawaii*; Hawaii Department of Agriculture: Honolulu, USA, 1983.
92. Greathead, D.J. *A Review of Biological Control in the Ethiopian Region*; Commonwealth Institute of Biological Control: Farnham Royal, UK, 1971; p. 162.
93. Clausen, C.P. *Introduced Parasites and Predators of Arthropod Pests and Weeds: A World Review*; Handbook No. 480; United States Department of Agriculture: Washington, DC, USA, 1978.
94. Goldson, S.L.; Proffitt, J.R.; Baird, D.B. Establishment and phenology of the parasitoid *Microctonus hyperodae* (Hymenoptera: Braconidae) in New Zealand. *Environ. Entomol.* **1998**, *27*, 1386–1392. [CrossRef]
95. Waterhouse, D.F.; Sands, D. *Classical Biological Control of Arthropods in Australia*; CSIRO Entomology; Australian Centre for International Agricultural Research: Canberra, Australia, 2001; p. 559.
96. Ooi, P.A.C.; Lim, G.S.; Khoo, S.G. Biological control in Malaysia. In Proceedings of the Plant Protection Seminar, Kuala Lumpur, Malaysia, 1–2 March 1979; pp. 1–35.
97. Shoubu, M.; Okumura, M.; Shiraishi, A.; Kimura, H.; Takagi, M.; Ueno, T. Establishment of *Bathyplectes anurus* (Hymenoptera: Ichneumonidae), a larval parasitoid of the alfalfa weevil, *Hypera postica* (Coleoptera: Curculionidae) in Japan. *Biol. Control* **2005**, *34*, 144–151. [CrossRef]
98. Kelleher, J.S.; Hulme, M.A. *Biological Control Programmes agaist Insects and Weeds in Canada 1969–1980*; Commonwealth Agricultural Bureau: Farnham Royal, UK, 1984; p. 410.

99. Dysart, R.J. Establishment in the United States of *Peridesmia discus* (Hymenoptera: Pteromalidae), an egg predator of the alfalfa weevil (Coleoptera: Curculionidae). *Environ. Entomol.* **1988**, *17*, 409–411. [CrossRef]
100. Jacas, J.A.; Peña, J.E.; Duncan, R.E. Successful oviposition and reproductive biology of *Aprostocetus vaquitarum* (Hymenoptera: Eulophidae): A predator of *Diaprepes abbreviatus* (Coleoptera: Curculionidae). *Biol. Control* **2005**, *33*, 352–359. [CrossRef]
101. Frank, J.H.; McCoy, E.D. The introduction of insects into Florida. *Fla. Entomol.* **1993**, *76*, 1–52. [CrossRef]
102. Cameron, P.J.; Hill, R.L.; Bain, J.; Thomas, W.P. *A Review of Biological Control of Invertebrate Pests and Weeds in New Zealand 1874 to 1987*; Technical Communication No. 10; CAB International and DSIR: Oxford, UK, 1989; p. 424.
103. Carmako, H.; Vankosky, M.A. Sitona spp. Germar, broad nosed weevils (Coleoptera: Curculionidae). In *Biocontrol Programmes in Canada 2001–2012*; Mason, P.G., Gillespie, D.R., Eds.; CABI: Wallingford, UK, 2013; pp. 277–284.
104. Gerard, P.J.; Wilson, D.J.; Eden, T.M. Field release, establishment and initial dispersal of Irish *Microctonus aethiopoides* in *Sitona lepidus* populations in northern New Zealand pastures. *Biocontrol* **2011**, *56*, 861–870. [CrossRef]
105. Commonwealth Agricultural Bureaux. *Biological Control Programmes against Insects and Weeds in Canada 1959–1968*; Commonwealth Institute of Biological Control, Technical Communication: Slough, UK, 1971; Volume 4, p. 266.
106. Dysart, R.J. The introduction and recovery in the United States of *Anaphes diana* [Hym.: Mymaridae], an egg parasite of *Sitona* weevils [Col.: Curculionidae]. *Entomophaga* **1990**, *35*, 307–313. [CrossRef]
107. Evans, H.; Fielding, N.J. Restoring the natural balance: Biological control of *Dendroctonus micans* in Great Britain. In *Proceedings of the British Crop Protection Conference Symposium, 18 November 1996*; Waage, J.K., Ed.; British Crop Protection Council: Farnham, UK, 1996; Volume 67, pp. 47–57.
108. Fielding, N.J.; Evans, H.F. Biological control of *Dendroctonus micans* (Scolytidae) in Great Britain. *Biocontrol News Inf.* **1997**, *18*, 51N–60N.
109. Coulson, J.R.; Vail, P.V.; Dix, M.E.; Nordlund, D.A.; Kauffman, W.C. *110 Years of Biological Control Research and Development in the United States Department of Agriculture, 1883–1993*; U.S. Department of Agriculture, Agricultural Research Service: Washington, DC, USA, 2000; p. 645.
110. Neuenschwander, P.; Borgemeister, C.; Langewald, J. *Biological Control in IPM systems in Africa*; CABI Publishing: Wallinford, UK, 2003; p. 414.
111. Zuñiga, E. Ochenta años de control biologico en Chile. *Agric. Tech.* **1985**, *45*, 175–182.
112. Sailer, R.I. Beneficial Foreign Species of Hymenoptera Known to Be Established in the 48 Contiguous United States. 1983; 10, unpublished typescript.
113. Quintero, H.; Bustillo, P.; Benavides, M.; Chaves, E. Evidencias del establecimiento de *Cephalonomia stephanoderis* y *Prorops nasuta* (Hymenoptera: Bethylidae) en cafetales del departamento de Nariño, Colombia. *Rev. Colomb. Entomol.* **1998**, *24*, 141–147.
114. Murphy, S.T.; Moore, D. Biological control of the coffee berry borer *Hypothenemus hampei* (Ferrari) (Coleoptera, Scolytidae): Previous programmes and possibilities for the future. *Biocontrol News Inf.* **1990**, *11*, 107–117.
115. Baker, P. Managing the coffee berry borer. *Biocontrol News Inf.* **2001**, *21*, 61N–64N.
116. Singh, S.P. Biocontrol progress in India. *Biocontrol News Inf.* **2001**, *21*, 78N–79N.

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A Review of the *Araucaria*-Associated Weevils of the Tribe Orthorhinini (Coleoptera: Curculionidae: Molytinae), with Description of New Species of *Ilacuris* Pascoe, 1865 and *Notopissodes* Zimmerman & Oberprieler, 2014 and a New Genus, *Kuschelorhinus* Anderson & Setliff

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Abstract: The *Araucaria*-associated weevils of the tribe Orthorhinini are reviewed, namely the genera *Eurhamphus* Shuckard, 1838; *Ilacuris* Pascoe, 1865; *Imbilius* Marshall, 1938; *Notopissodes* Zimmerman & Oberprieler, 2014 and *Vanapa* Pouillaude, 1915. The genus *Ilacuris* is revised with three species recognized: *I. laticollis* Pascoe, 1865 and *I. suttoni* Anderson & Setliff, new species from Australia, and *I. papuana* Anderson & Setliff, new species from Papua New Guinea. A second species of *Notopissodes*, *N. variegatus* Oberprieler, new species from Australia, is also described. Lastly, *Kuschelorhinus hirsutus* Anderson & Setliff, new genus and new species, is described from Papua New Guinea. The new genus is a close relative of *Ilacuris* and it is named in honor of our esteemed late colleague, Guillermo 'Willy' Kuschel (1918–2017), recognizing his interest in *Araucaria*-associated Coleoptera. Habitus images, natural history information and a key to the *Araucaria*-associated Orthorhinini are presented.

Keywords: taxonomy; weevil; new species; Araucariaceae; Hoop Pine; Klinki Pine; Australia; Papuan region

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1. Introduction

The Orthorhinini, as currently constituted, are an Australo-Pacific tribe of Molytinae comprising of 12 genera [1,2], seven occurring in Australia [2], five in New Guinea [3], three in New Caledonia [1] and five in the Pacific region north of the Philippines [1]. Recent molecular evidence [4] suggests that the *Tranes* group, comprising six genera in Australia [2,5,6], belongs in this tribe as well. Although the tribe in this expanded sense is not well defined and delineated, it can be broadly divided into three groups of genera, an *Orthorhinus* group, a *Eurhamphus* group and a *Tranes* group. The *Orthorhinus* group includes the genera *Allorthorhinus* Kuschel, 2008, *Coffearhynchus* Risbec, 1936, *Dracophyllius* Kuschel, 2008, *Faustiellus* Kuschel, 2014, *Homorthorhinus* Voss, 1960, *Orthorhinus* Schoenherr, 1825 and *Parorthorhinus* Kuschel, 2008 and was recently taxonomically treated [1,7]. Its species generally develop in dead or dying branches and stems of a large variety of plant species. The *Tranes* group includes the genera

Demyrsus Pascoe, 1872, *Miltotranes* Zimmerman, 1994, *Siraton* Hustache, 1934, *Tranes* Schoenherr, 1843, *Paratranes* Zimmerman, 1994 and *Howeotranes* Zimmerman, 1994, the first four strictly associated with cycads and *Paratranes* with grasstrees (*Xanthorrhoea*) but the host of *Howeotranes* unknown [6]. The *Eurhamphus* group includes the genera *Eurhamphus* Shuckard, 1838, *Ilacuris* Pascoe, 1865, *Imbilius* Marshall, 1938, *Notopissodes* Zimmerman & Oberprieler, 2014 and *Vanapa* Pouillaude, 1915 [2], all associated with conifers of the genus *Araucaria* as known. This group has never been treated taxonomically and is the subject of the current paper, as a number of undescribed taxa have accumulated in collections.

The formerly monotypic genus *Ilacuris* was described for *I. laticollis* Pascoe from Queensland, Australia. Pascoe [8] originally placed the genus in the subfamily Zygopinae, and it has since been variously treated by authors and cataloguers in the Conoderinae [9–12], Pissodinae [13], Molytinae: Pissodini [5,14] and, most recently, in the molytine tribe Orthorhinini [2,15]. In Australia *I. laticollis* has been regarded as a timber pest of economically important Hoop Pine (*Araucaria cunninghamii* D. Don., Araucariaceae) [16]. *Ilacuris laticollis* has also been reported from Hoop Pine stands in Papua New Guinea [3,17]; however, collections of *Ilacuris* specimens made on Hoop Pine by the first author in Papua New Guinea contained no *I. laticollis* but were entirely composed of a heretofore undescribed species. Closer examination of *Ilacuris* specimens in museum collections confirmed that *I. laticollis* is restricted to Australia, that all specimens of *Ilacuris* from Papua New Guinea are this undescribed species and that yet another undescribed species occurs in Australia. Additionally, an undescribed weevil genus and species from Papua New Guinea, closely related to *Ilacuris* and also associated with *Araucaria*, here named *Kuschelorhinus hirsutus*, was discovered among this material. Along with *Vanapa oberthuri* Pouillaude, *Eurhamphus fasciculatus* Shuckard, *Imbilius araucariae* Marshall and *Notopissodes pictus* Zimmerman & Oberprieler, *Ilacuris* and *Kuschelorhinus* appear to represent a distinct group in the tribe Orthorhinini associated with this genus of conifers. Unlike a number of other beetle lineages that maintain ancient associations with *Araucaria* across Gondwana [18], these Orthorhinini are limited to eastern Australia and New Guinea and may have developed this association relatively recently. We have no evidence that the *Araucaria*-associated Orthorhinini (or *Eurhamphus* group, see above) constitute a monophyletic lineage in Qrthorhinini. The somewhat disparate adult morphology would suggest otherwise and point to multiple origins of association with *Araucaria*.

In this contribution, we revise *Ilacuris*, redescribe its type species and describe two new species in the genus. We also describe a second species in the genus *Notopissodes* from Australia as well as a new *Araucaria*-associated genus and species from Papua New Guinea. We name the new genus in honor of Guillermo 'Willy' Kuschel (1918–2017), in recognition of his pioneering contributions to the study of weevil phylogeny and taxonomy. Willy had a long history of interest in *Araucaria*-associated beetles, and we think it is appropriate that this new genus be named for him.

2. Materials and Methods

Standard taxonomic procedures and terminology used follow [19].

2.1. Collections in Which Specimen Are Deposited

ANIC	Australian National Insect Collection, Canberra, Australia; R. Oberprieler
BMNH	The Natural History Museum, London, U.K.; M. Barclay
BPBM	Bernice P. Bishop Museum, Honolulu, HI, U.S.A.; J. Boone
CASC	California Academy of Sciences, San Francisco, CA, U.S.A.; C. Grinter
CMNC	Canadian Museum of Nature, Ottawa, Canada; F. Génier
CWOB	Charles W. O'Brien Collection, Green Valley, AZ, U.S.A.; C. W. O'Brien
FSCA	Florida State Collections of Arthropods, Gainesville, FL, U.S.A.; P. Skelley
GPSC	Gregory P. Setliff collection, Kutztown University, Kutztown, PA, U.S.A.; G. Setliff
MVM	Museum of Victoria, Melbourne, Australia
SAMA	South Australian Museum, Adelaide, Australia
QDPC	Queensland Department of Primary Industries, Queensland, Australia; J. Bartlett, M. Schutze

QMB	Queensland Museum, Brisbane, Australia; S. Wright, G. Monteith
USNM	United States National Museum, Washington D.C., U.S.A.; L. Chamorro

2.2. Note about Localities

The holotype of the new species *I. suttoni* and several of the specimens of *I. laticollis* in the collection of the Canadian Museum of Nature were acquired by Anne Howden from Edmund Sutton of Fletcher, Queensland, and fitted by Anne with two labels reading: "probably Queensland, near Stanthorpe, E. Sutton" and "gift from E. Adams ex. E. Sutton collection". Edmund Sutton (ca. 1887–1981) was an orchardist and amateur beetle collector who lived in Fletcher (near Stanthorpe) in southern Queensland and collected over 30,000 beetles in the vicinity during his life [20]. According to Geoff Monteith, of the Queensland Museum in Brisbane, there is no rainforest or *Araucaria cunninghamii* (Hoop Pine) in Fletcher or Stanthorpe, but Sutton often collected the large *Eurhamphus* weevils on hoop pines at a location in nearby Rivertree (−28.6260, 152.2450, 290 m) in New South Wales. Furthermore, he never drove or owned a car and rarely left the Stanthorpe district. Thus, we assume that the Sutton specimens of *Ilacuris* acquired by Anne were collected in the Rivertree vicinity, and they have been relabeled accordingly.

3. Results

3.1. Key to Species of Araucaria-Associated Orthorhinini

1 Body length (excluding head) more than 20 mm, often more than 30 mm 2

1′ Body length (excluding head) less than 20 mm, often less than 15 mm 3

2 Body cuticle black, generally lacking any distinct dorsal vestiture of scales or hairs (some females with very sparse, white scales on the elytra, faintly arranged in 2 transverse bands in the basal and distal thirds). Elytra with alternate interstriae distinctly raised and rounded-carinate. Rostrum of male densely setose ventrally in apical two-thirds. Procoxae of male with long, anteriorly directed spine-like projection. New Guinea . . . . *Vanapa oberthuri* Pouillaude

2′ Body cuticle black, densely covered with creamy white to medium-brown, appressed, elongate, hair-like scales, some very long and erect in two dorsolateral clumps at about midlength of pronotum and in variously sized and positioned clumps on elytra. Elytra with sutural interstria slightly swollen towards base and at base of interstria 3, otherwise all interstriae flat. Rostrum of male glabrous ventrally but granulate dorsally, with a pair of larger, dorsally directed, triangular projections at point of antennal insertions and a second pair subapically. Procoxae of male lacking projections. Australia (Queensland, New South Wales) . . . . *Eurhamphus fasciculatus* Shuckard

3 Prothorax with ocular lobes. Elytra with all interstriae flat, interstria 5 without declivital callus. Australia (Queensland, New South Wales) . . . . *Notopissodes* Zimmerman & Oberprieler . . . 4

3′ Prothorax without ocular lobes. Elytra with odd interstriae raised, interstria 5 with callus on declivity 5

4 Body length about 7.5 mm. Scales on elytral disc segregated into distinct pattern: yellowish scales on interstriae 1–4, black ones on interstriae 5–7, white ones forming a broad V stretching from humeri posteromesad onto interstriae 4 and a similar, parallel but more irregular V on declivity stretching onto interstriae 4 or 2. Rostrum of female ca. 1.25× longer than pronotum. Scutellar shield longer than wide. Australia (southern Queensland) . . . . *Notopissodes pictus* Zimmerman & Oberprieler

4′ Body length about 4.8 mm. Scales on elytral disc intermixed, yellow and white ones forming a broad, short irregular V stretching from humeri posteromesad onto interstriae 2 and a broad, transverse one on declivity stretching onto interstriae 1. Rostrum of female as long as pronotum. Scutellar shield shorter than wide. Australia (southern Queensland) . . . . *Notopissodes variegatus* Oberprieler n. sp.

5 Body length less than 5 mm. Pronotum without median ridge or carina. Elytra with interstria 3 smoothly raised (subcostate) on disc (from base to middle of length), interstria 5 smoothly subcostate from anterior one-fifth of length to declivity, there subcarinate but carina abruptly ending. Australia (southern Queensland) . . . . *Imbilius araucariae* Marshall

5′ Body length more than 7 mm. Pronotum with median ridge or carina. Elytra with odd interstriae variously raised, usually granulate and sparsely setose to partially glabrous 6

6 Antennae with funicle segment 1 distinctly longer than segment 2. Vestiture of pronotum and elytra composed of flattened, narrow, hair-like scales. Dorsum of both sexes with at least some long erect fine hairs (dense and over almost entire body in male, sparse and limited to dorsum of pronotum in female). Profemora with distinct subapical tooth, large and sharp in male, small in female. New Guinea . . . . *Kuschelorhinus hirsutus* Anderson & Setliff, n. gen., n. sp.

6′ Antennae with funicle segment 1 shorter than 2. Vestiture of pronotum and elytra composed of short, broad scales. Dorsum of both sexes with no long erect vestiture, only appressed or recumbent scales. Profemora with only a small subapical angulation in both sexes. New Guinea and Australia . . . . *Ilacuris* Pascoe . . . 7

7 Elytra with dark brown median fascia transverse, distinctly bounded posteriorly by an area of dense, imbricate, white and pale brown, broad scales. Elytra with only base of interstria 3 slightly swollen. Rostrum in male setose ventrally from point of antennal insertions to base. Australia (New South Wales) . . . . *Ilacuris suttoni* Anderson & Setliff, n. sp.

7′ Elytra with dark brown median fascia V-shaped, bounded posteriorly by an area of intermixed tan to pale brown, broad scales. Elytra with most of interstriae 3, 5 and 7 elevated and granulate. Rostrum in male finely granulate ventrally from point of antennal insertions to base 8

8 Pronotum with area adjacent to median carina variously impressed into a broad, sinuate furrow extending from anterior to posterior margin; scales of furrow dark golden metallic (in clean specimens). Australia (Queensland, New South Wales) . . . . *Ilacuris laticollis* Pascoe

8′ Pronotum with area adjacent to median carina not impressed, evenly convex and densely rugulose. New Guinea . . . . *Ilacuris papuana* Anderson & Setliff, n. sp.

3.2. *Descriptive Taxonomy*

3.2.1. *Vanapa* Pouillaude, 1915

Species included: *Vanapa oberthuri* Pouillaude, 1915 (Figures 1 and 2).

Diagnosis: Body length (exclusive of head and rostrum) 32–40 mm. Body black, generally lacking any distinct dorsal vestiture of scales or hairs (some females with very sparse white scales on elytra, faintly arranged in 2 transverse bands in basal and distal thirds). Rostrum of both sexes longer than pronotum, more so in male; rostrum of male densely setose ventrally in apical two-thirds, point of antennal insertions subapical; rostrum of female very finely setose ventrally, point of antennal insertions at about apical one-third. Elytra with alternate interstriae distinctly raised and rounded-carinate. Procoxae of male each with long, anteriorly directed spine-like projection.

Distribution: The genus is known only from the central highlands of Papua New Guinea. ANIC records, 40 specimens: **PAPUA NEW GUINEA:** Bulolo, Gadsup, Telefomin, Wau, Okapa, Gimi village (Eastern highlands, −6°37′ S 145°58′ E), Aiyura, 5000′ (Central Highlands).

Life history: Adults and larvae of this species are associated with Hoop Pine, *Araucaria cunninghamii* [21–23]. Larvae mine in the wood. The life history and damage caused by this species have been well-documented [24–27].

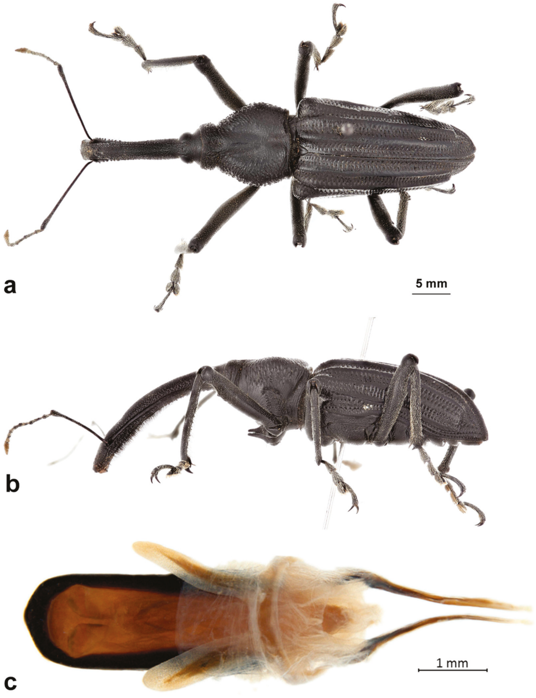

Figure 1. *Vanapa oberthuri*: (**a**) habitus of male, dorsal aspect; (**b**) habitus of male, lateral aspect; (**c**) aedeagus, dorsal aspect.

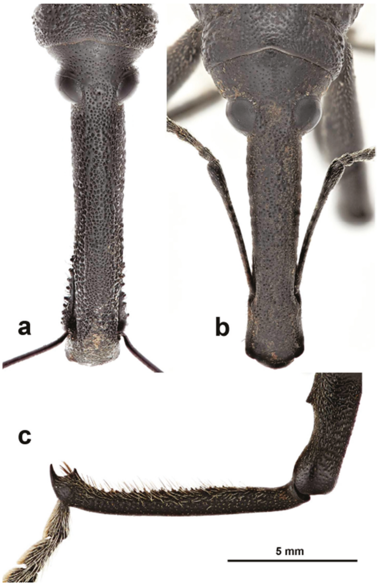

Figure 2. *Vanapa oberthuri*: (**a**) rostrum of male, dorsal aspect; (**b**) rostrum of female, dorsal aspect; (**c**) protibia of male, anterior aspect.

3.2.2. *Eurhamphus* Shuckard, 1838

Species included: *Eurhamphus fasciculatus* Shuckard, 1838 (Figures 3 and 4).

Diagnosis: Body length (exclusive of head and rostrum) 21–33 mm. Body black, densely covered with creamy white to medium brown, appressed, elongate hair-like scales, some very long and erect in two dorsolateral clumps at about midlength of pronotum and in variously sized and positioned clumps on elytra. Elytra with sutural interstria slightly swollen towards base and at base of interstria 3, otherwise all interstriae flat. Rostrum of both sexes slightly longer than pronotum; rostrum of male glabrous ventrally but granulate dorsally, with a pair of larger, dorsally directed triangular projections at point of antennal insertions and a second pair subapically; rostrum of female straight, finely densely punctate, lacking any projections. Procoxae of male lacking projections, mesosternum tuberculate between mesocoxae.

Distribution: The genus is known from northern New South Wales northwards into Queensland in Australia. ANIC records, 28 specimens: **AUSTRALIA:** Queensland—Mt. Glorious, Rivertree, "Fletcher", Canungra, Mt. Goonaneman, Benarkin, Bunya Mountains. New South Wales—Brooklana, Dorrigo.

Life history: No mention of host plants is on the labels of any specimens examined; however, Froggatt's [27] early description of its life history states that he reared a specimen from a pupa found in a snapped-off trunk of Hoop Pine, *Araucaria cunninghamii*, at Brooklana in 1923. Monteith & Baldwin [28] presented a good summary of the life history of the species on *Araucaria cunninghamii*.

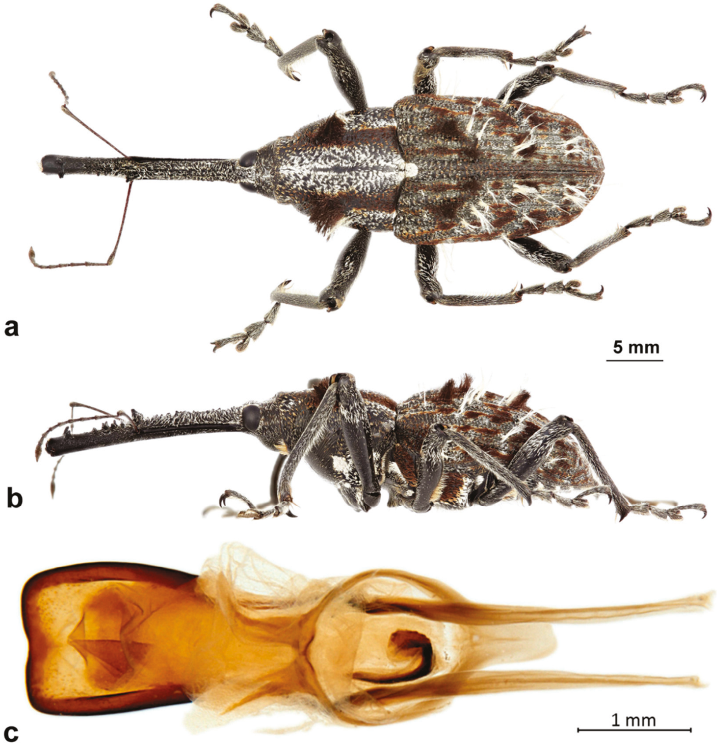

Figure 3. *Eurhamphus fasciculatus*: (**a**) habitus of male, dorsal aspect; (**b**) habitus of male, lateral aspect; (**c**) aedeagus, dorsal aspect.

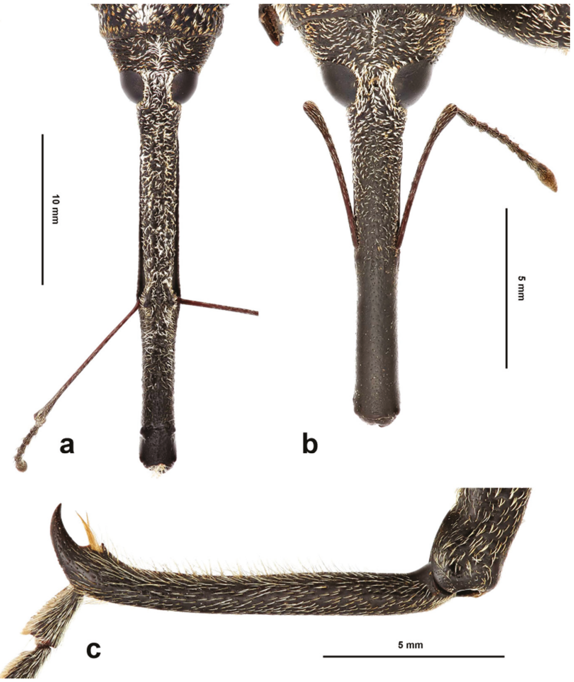

Figure 4. *Eurhamphus fasciculatus*: (**a**) rostrum of male, dorsal aspect; (**b**) rostrum of female, dorsal aspect; (**c**) protibia of male, anterior aspect.

3.2.3. *Ilacuris* Pascoe, 1865

Ilacuris Pascoe, 1865: 425 [8]. Pascoe, 1871: 202 [9] (in key, as Zygopinae); Gemminger, 1871: 2594 [10] (catalog, as Zygopinae); Masters, 1886: 682 [11] (catalog, as Zygopinae); Dalla Torre et al., 1932: 25 [13] (catalog, as Pissodini); Hustache, 1934: 57 [12] (catalog, as Zygopinae); Wiley & Shanahan, 1973: 373 [17] (range extension into Papua New Guinea and natural history); Zimmerman, 1994: 694 [14] (in Molytinae); Alonso-Zarazaga & Lyal, 1999: 207 [5] (catalog, transfer to Molytinae: Pissodini); Setliff, 2007: 296 [3] (catalog); Mecke et al., 2005 [16] (natural history); Lyal, 2014: 529, 556 [15] (natural history and transfer to Molytinae: Orthorhinini); Pullen et al., 2014: 283 [2] (as Molytinae: Orthorhinini).

Jlacuris; Heller, 1893: 47 [29] (incorrect subsequent spelling).

Illacuris; Masters, 1886: 682 [11]; Setliff, 2007: 296 [3]; Lyal, 2014: 556 [15] (incorrect subsequent spelling).

Type species: *Ilacuris laticollis* Pascoe, 1865, by monotypy.

Redescription: Medium-sized (8.5–14.5 mm); elongate oval; prothorax trapezoidal in dorsal view, widest subbasally, base as wide as base of elytra; elytra parallel-sided to declivity in dorsal view, tapering toward apex. Integument dark brown to black; covered with small, appressed to recumbent, tan to brown scales and sparsely distributed, capitate, pale scales; dorsum with various white patches, maculae or vittae and patches of fuscous scales. Scales becoming longer and more hair-like on venter and legs. Eyes large, outline hemispherical, dorsally elevated, separated by slightly less than width of rostrum at base. Rostrum subequal to or longer than pronotum in both sexes; straight to feebly curved, circular in cross-section; tapering slightly to apex; basal half dorsally covered with sparse hair-like scales, apical half bare, venter bare in female, granulate or finely hirsute in male. Antennae inserted at apical one-third to two-fifths of rostrum in males and near middle of rostrum in females; scrobes sharply defined, running towards anteroventral angle of eye; scapes subcylindrical, clavate towards apex, reaching anterior margin of eye in repose in males, not so in females; funicles 7-segmented, segments 1 and 2 each at least twice as long as 3, 3–7 subequal in length, 7 pilose and closely appressed to but distinct from club; clubs elongate, transversely 4-segmented. Pronotum with glabrous dorsomedian carina from apex to slightly past middle, lateral portions of basal margins produced posteriad over elytral bases laterally, anterolateral angles tapered to apex in dorsal view; Elytra with base weakly sinuate, scutellar shield externally visible, large, cordate, densely squamose; 10 complete striae of small, shallow punctures each bearing a single scale similar to those on adjacent interstriae; declivital callus indistinct, low, rounded. Legs elongate, inner margins of femora with small subapical angulation or small tooth; inner margin of protibiae with patch of long golden hairs throughout apical half of length in male, hairs lacking in female. Aedeagus with penis subequal in width throughout length, very slightly emarginate at apex at middle, apex with a number of elongate setae on each side of emargination, body slightly shorter than apodemes, internal sac with fine spicules and vaguely defined apical sclerite complex. Female not dissected.

Comments: Sexual dimorphism in two of the three known species (third species known only from a single male) is most evident in the position of the antennal insertions on the rostrum and in the sculpture and form of the rostrum.

Distribution: The genus is known from northern New South Wales northwards into Queensland in Australia as well as the central highlands of Papua New Guinea.

Natural history: Adults of two species, *I. laticollis* and *I. papuana*, have been collected on, or reared from, species of *Araucaria* (label data, [16]). It is likely that the third species, *I. suttoni*, is similarly associated as it was mixed with a series of *I. laticollis* presumed to have been collected from *Araucaria* at Rivertree, New South Wales.

Ilacuris laticollis Pascoe, 1865
(Figures 5–7)

Ilacuris laticollis Pascoe, 1865: 425 [8]; Pascoe, 1871: 202 [9] (in key, in Zygopinae) and plate XVII (illustrated); Dalla Torre et al., 1932: 25 [13] (catalog, in Pissodini); Hustache, 1934: 57 [12] (catalog, in Zygopinae); Zimmerman, 1994: 694 [14] (in Molytinae) and Figure 371 on page 561 (wing-folding pads illustrated); Alonso-Zarazaga & Lyal, 1999: 207 [5] (catalog, in Molytinae: Pissodini); Mecke et al., 2005 [16] (natural history); Lyal, 2014: 529 [15] (natural history, in Molytinae: Orthorhinini); Pullen et al., 2014: 283 [2] (in Molytinae: Orthorhinini).

Illacuris laticollis (Pascoe): Masters, 1886: 682 [11]; Wiley & Shanahan, 1973: 373 [17]; Setliff, 2007: 296 [3]; Lyal, 2014: 556 [15] (incorrect subsequent spelling). All previously published records of *I. laticollis* from Papua New Guinea likely to refer to *I. papuana* n. sp.; see [3,17].

Redescription. Male. Body length 10.9–14.5 mm. Body width 4.6–6.1 mm. Dorsal surface with dispersed to dense, variously colored, appressed scales; no erect or suberect hairs present. Rostrum with antennal insertions at about apical two-fifths of length, ventral surface of rostrum finely granulate from just before base to antennal insertions; in dorsal view with area behind antennal insertions not dilated or much wider than area before antennal insertions, width greatest near base. Antennae with funicle segment 2 slightly longer than 1. Pronotum with distinct, narrow, sharp median carina in anterior half, culminating in elongate narrow, fusiform callosity at about midlength, then posteriorly continued as a low, less distinct, elevated line to about posterior quarter. Median carina bordered laterally by area of pale brown or white scales contrasting with darker scales of rest of pronotal disk; area laterally of pale median fascia irregularly impressed in a broad sinuate furrow deepest laterally of median raised callosity, shallower anteriorly and posteriorly; scales in furrow distinctly metallic gold in sheen and color (in clean specimens); area laterally of furrow with similarly impressed patch of golden scales just in front of midlength towards lateral margin; anterolateral margins in dorsal view tapered evenly to apex. Elytra with odd interstriae (sutural, 3, 5, 7 and 9) distinctly elevated and variously granulate throughout most of their length, except 3 interrupted at about basal two-fifths. Dorsal fascia of dark brown to black scales "V-shaped"; apical quarter of elytra with dispersed scales somewhat paler. Pro- and mesofemora with inner margin with indistinct slight subapical angulation; inner margin of metafemora with moderately large, distinct subapical tooth. Inner margin of protibiae with short row of sparse but distinct, elongate, golden hairs in apical two-fifths. Abdomen with ventrite 1 concave medially. Aedeagus with penis widest in apical half, apex slightly medially emarginate, with a few setae at outer apical corners, body slightly shorter than apodemes; internal sac with a vague apical armature composed of two faint, inwardly convergent elongate-narrow sclerites. **Female.** Body length 9.5–11.8 mm. Body width 3.8–5.1 mm. As for male, except antennal insertions at about midlength, ventral surface of rostrum smooth from base to antennal insertions; in dorsal view with area behind antennal insertions not dilated or much wider than area before antennal insertions; width is greatest near base. Abdomen with ventrite 1 flat to slightly evenly convex. Genitalia not examined.

Specimens examined. AUSTRALIA: Queensland. Mackay [−21°09′ 149°11′], 1912 (1 male, SAMA). Yeppoon [−23°08′ 150°44′], Dec. 1960 (1 female, ANIC). Barrimoon [−24°40′ 151°19′], 22.i.1944, (2 males, 1 female, ANIC). Wide Bay [−25°52′ 153°07′] (1 male, 1 female, SAMA). Yarraman [−26°51′ 151°59′], 8.xi.1939, A. Hanson (1 male, ANIC). Yarraman State Forest, Forest Drive, 650 m, 26°49′57″ S, 151°57′55″ E, 19.i.2000, R. S. Anderson, beating *Araucaria cunninghamii* (1 female, CMNC). Blackbutt [−26°53′ 152°06′], 9.i.1913 (1 female, ANIC). Brisbane [−27°28′ 153°01′], 17.iii.1913, H. Hacker (1 male SAMA). Brisbane [−27°28′ 153°01′] (1 male, ANIC; 2 males, SAMA). Moreton Bay [Brisbane, −27°28′ 153°01′], 29061 (1 male, ANIC). Pine Mountain [−27°33′ 152°43′] (1 male, ANIC). Stanthorpe [−28°40′ 151°56′], E. Sutton (3 males, ANIC; 2 males, MVM; 8 males, 5 females, SAMA) [probably from Rivertree, N.S.W.; see note above about this locality]. Fletcher [−28°46′ 151°51′], E. Sutton (2 males, 5 females, ANIC; 2 males, 1 female, MVM) [probably from Rivertree, N.S.W.; see note above about this locality]. Queensland (1 male, 1 female, SAMA). Imbil [−26°28′ 152°41′], 28.v.1959, F. McDonald (2 males, MVM, UQB). Imbil State Forest [−26.6185 152.6149], 25–28.v.1959, I. C. Yeo (4 males, QMB). **New South Wales.** Rivertree [−28°38′ 152°18′], E. Sutton (5 males, 1 female, ANIC). Rivertree [−28°38′ 152°18′], 21.vii.1932, E. Sutton (1 male, ANIC). Rivertree [−28.6260 152.2450], 290 m, N. Sutton [no date, likely from *Araucaria* (see note above about this locality)] (23 males, 12 females, CMNC, GPSC). No data, E. Sutton collection [probably from Rivertree, N.S.W.] (2 males, 1 female, ANIC). Alstonville, −28°50′, 153°26′, 10.viii.1971, J. O'Grady (1 male, ANIC). Nana Glen, −30°08′ 153°01′, 14.ii.1925 (1 male, ANIC). Dorrigo [−30°20′ 152°43′] (1 female, SAMA).

Specimen data recorded from other institutions (not examined): AUSTRALIA: Queensland. Yarraman [26°51.001′ S, 151°59.015′ E], 1.xii.1938, L. T. Carron (1, QMB). Yarraman, 21.xi.1936, R. Brimblecombe (1, QDPC). Brisbane [27°28.002′ S, 152°59.985′ E], R. Illidge (1, QMB). Brisbane, 14.x.1968, R. Yule, *Araucaria cunninghamii* (1, QDPC). Brisbane, 17.iii.1913, H. Hacker (1, QMB). Killarney [28°20.002′ S, 152°18.011′ E], 1.xi.1901 (1, QMB). Gatton [−27.566 152.277], 1.x.1937, C. S. Andrew (1, QMB). East Nanango [−26.666 152.039], 14.x.1967, R. Yule, ex hoop pine (2, QMB). Imbil, viii.1936, R. Brimblecombe, *Araucaria cunninghamii* (3, QDP). Imbil, 30.x.1937, R. Brimblecombe (1, QDPC). Imbil, 30.xi.1971, R. Yule, *Araucaria cunninghamii* (4, QDPC). Imbil, 16.xii.1971, R. Yule, *Araucaria cunninghamii* (5, QDPC). Imbil, 8.xi.1972, R. Yule, *Araucaria cunninghamii* (2, QDPC). Imbil State Forest, 24.vi.1969, N. W. Heather (1, QDPC). Imbil State Forest, 18.v.1970, N. W. Heather (1, QDPC). Imbil State Forest, 30.vi.1981, R. Gould, *Araucaria cunninghamii* (1, QDPC). Benarkin, 17.iv.1933, H. Hacker (3, QDPC). Mount Tamborine, no date (3, QDPC). Jimmy's Scrub, 17.ix.1971, R. Yule, *Araucaria cunninghamii* (4, QDPC). Jimmys Scrub, 9.xii.1971, R. Yule, *Araucaria cunninghamii* (4, QDPC). Kandanga, 3.iv.1975, R. J. Rabbits, *Araucaria cunninghamii* (5, QDPC). Gympie, Nut Farm, 13.xi.1968, N. W. Heather, *Araucaria cunninghamii* (1, QDPC). Canungra, 2.xi.1977, DeBaar & Wylie (1, QDPC). Amamoor, 18.x.1974, DeBaar & Wylie, *Araucaria cunninghamii* (1, QDPC). Compartment 6, Mossman Logging Area, Bulburin State Forest, iv.2016, M. Ramsden, *Araucaria cunninghamii* (1, QDPC). Glen Witheren, 28°2′48″ S, 153°7′12″ East, main scrub, 15.iv.2001, G. Monteith, ex hoop pine log (1, QMB). Mt. Ipswich, 1867, W. Hart (4, QMB). **New South Wales.** Rivertree, various dates (23, QMB).

Natural history: Adults have been collected on, and reared from, *Araucaria cunninghamii* (Hoop Pine) (label data, [16]). Geoff Williams reared a number of specimens from *Araucaria* logs collected at Reserve Creek Road, Murwillumbah, Queensland (Figure 5).

Figure 5. *Ilacuris laticollis* reared from *Araucaria* logs collected at Murwillumbah, Queensland, Australia (image used with permission from Geoff Williams).

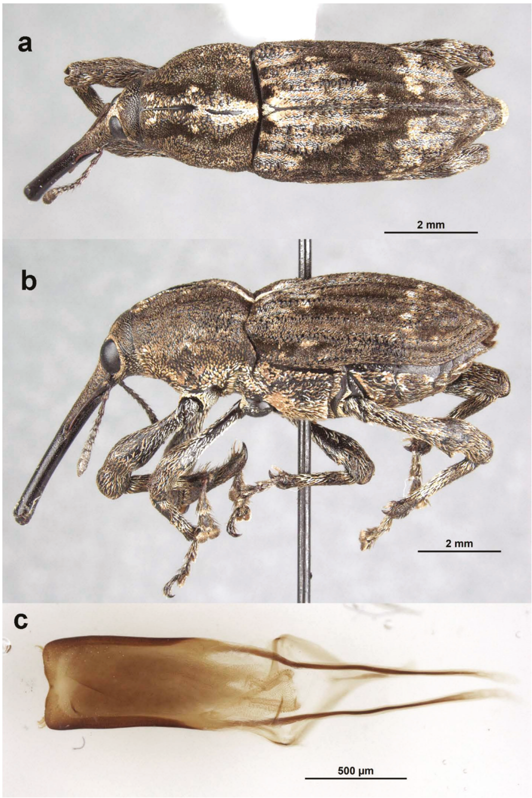

Figure 6. *Ilacuris laticollis*: (**a**) habitus of female, dorsal aspect; (**b**) habitus of female, lateral aspect; (**c**) aedeagus, dorsal aspect.

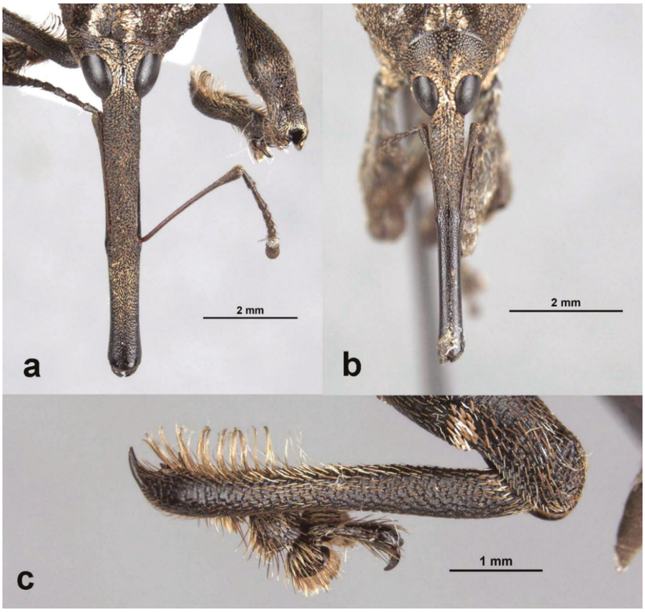

Figure 7. *Ilacuris laticollis*: (**a**) rostrum of male, dorsal aspect; (**b**) rostrum of female, dorsal aspect; (**c**) protibia of male, anterior aspect.

Ilacuris papuana Anderson & Setliff, new species
(Figures 8 and 9)

Ilacuris laticollis Pascoe *sensu* Wylie & Shanahan, 1973 [17], in Papua New Guinea.

Description: Male. Body length 8.5–14.2 mm. Body width 3.1–5.2 mm. Dorsal surface with dispersed to dense, variously colored, appressed scales, no erect or suberect hairs present. Rostrum with antennal insertions at about apical two-fifths of length, ventral surface of rostrum finely granulate from just before base to antennal insertions; in dorsal view with area behind antennal insertions not dilated or much wider than area before antennal insertions, width greatest in front of base. Antennae with funicle segment 2 subequal in length to 1. Pronotum with distinct, narrow, sharp median carina in anterior half, culminating in elongate fusiform callosity at about midlength, then posteriorly continued as a low, less distinct, elevated line to about posterior quarter. Median carina bordered laterally by an area of broad, pale brown or white scales contrasting with much smaller, darker scales of the rest of the pronotal disk. Area laterally of pale median fascia continuing to flanks not impressed (except for at most a small very shallow spot laterally of median callosity); scales small, tan throughout rest of disk; flanks with a very small but distinct spot of larger white scales at about midlength; anterolateral margins in dorsal view tapered evenly to apex. Elytra with alternate interstriae (3, 5 and less so 7) slightly elevated and variously granulate throughout basal three-quarters of their length. Dorsal fascia of dark brown to black scales "V-shaped"; apical portion of elytra with dispersed scales somewhat paler in color. Pro- and mesofemora with inner margin lacking subapical angulation or tooth; inner margin of metafemora with small, distinct subapical tooth. Inner margin of protibiae with a row of dense but distinct elongate, golden hairs in apical half to three-fifths. Abdomen with ventrite 1 concave medially. Aedeagus with penis widest at about midlength, apex slightly medially emarginate, with a few setae across the apical margin laterally of emargination, body slightly shorter than apodemes; internal sac with a vague apical armature composed of two faint, inwardly convergent elongate-narrow sclerites. **Female.** Body length 8.5–14.0 mm. Body width 3.4–5.4 mm. As for male, except antennal insertions at about midlength of rostrum, ventral surface of rostrum smooth from base to antennal insertion; in dorsal view with area behind antennal insertions not dilated or much wider than area before antennal insertions, width greatest near base. Abdomen with ventrite 1 flat to slightly evenly convex. Female genitalia not examined.

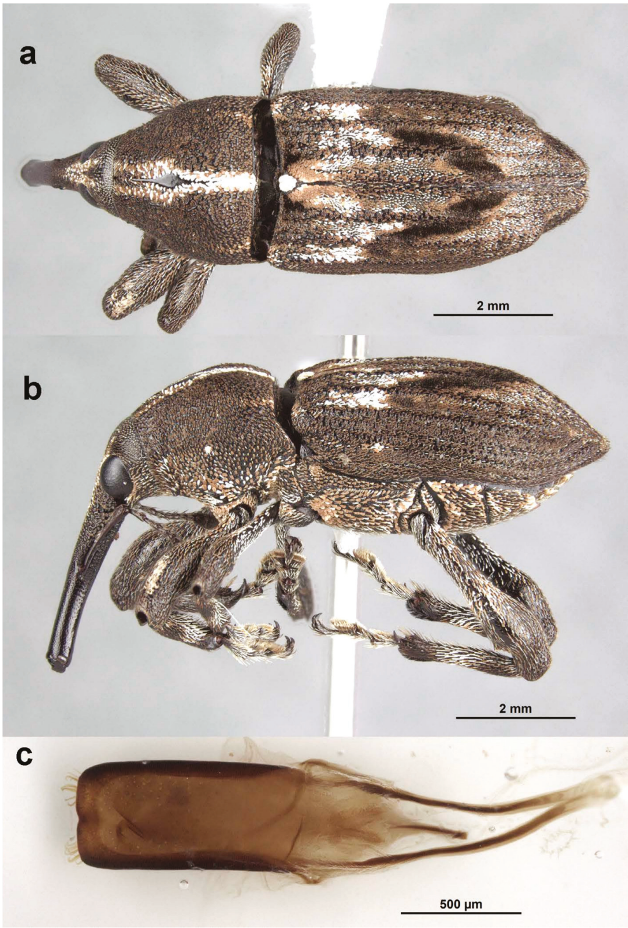

Figure 8. *Ilacuris papuana*: (**a**) habitus of female, dorsal aspect; (**b**) habitus of female, lateral aspect; (**c**) aedeagus, dorsal aspect.

Specimens examined: Holotype, male (CMNC), labelled PAPUA NEW GUINEA: Morobe, Wau (18 km N.W.), 950 m, 11.ii.2000, 7°15′46″ S 146°39′54″ E, R. S. Anderson, *Araucaria cunninghamii* logs, RSA2000-044X. Paratypes, PAPUA NEW GUINEA: Morobe, Wau (18 km N.W.), 950 m, 11.ii.2000, 7°15′46″ S 146°39′54″ E, R. S. Anderson, *Araucaria cunninghamii* logs, RSA2000-044X (1 female, CMNC). 4.ii.2000, RSA2000-031X (2 females, CMNC). Wau Ecology Institute, 1200 m, 7 20′24″ S 146 42′17″ E, 5.ii.2000, R.S. Anderson, on *Araucaria*, RSA2000-034X (1 female, CMNC). Wau, 17.v.1962, J. Sedlacek (3 males, 2 females, BPBM). Wau, 16.x.1961, J. Sedlacek (1 female, BPBM). Wau, 1050 m, 16.ix.1961, J. & M. Sedlacek (1 female, ANIC). Wau, 5.ix.1961, J. Sedlacek, klinki pine (2 males, 5 females, BPBM). Wau, 1050 m, 18.xi.1961, J. Sedlacek (1 female, BPBM). Wau, 1200 m, 15.xi.1961, J. Sedlacek (2 males, BPBM). Wau, 1150 m, 16.ix.1961, J. Sedlacek (3 males, 1 female, BPBM). Wau, 1200 m, 3.xii.1961, J. Sedlacek (1 male, 1 female, BPBM). Wau, 8.v.1973, J. L. Gressitt (2 males, BPBM). Wau, 1200–1250 m, v.1966, J.L. Gressitt (1 male, BPBM). Wau, 2.ix.1966, G.A. Samuelson, *Araucaria* (3 males, BPBM). Wau, Nakata Ridge, 1830 m, 18.xii.1963, J. Sedlacek (1 male, BPBM). Wau, 20.xii.1963 (1 male, BPBM). N.E. Wau, Mount Missim, 1150 m, 21.iii.1964, J. Sedlacek (10 males, BPBM). Mount Missim, 1600 m, 17.iii.1966, J. L. Gressitt (4 males, BPBM). Mount Missim, 1150 m, 11.iv.1964, J. Sedlacek (2 males, 1 female, BPBM). Mount Missim, 1250 m, 14.vii.1971, J. Sedlacek (1 female, BPBM). Bululo, i-ii.1972, J. Sedlacek (2 males, CWOB). Asiki, i-ii.1972, J. Sedlacek (2 males, CWOB). 18 km N.E. Okapa, 1300 m, 2.vi.1967, G. A. Samuelson (1 female, BPBM). Bulldog Road, km 14, south of Edie Creek, 2405 m, 4–10.vii.1964, G. R. Wilkes (1 male, BPBM). S.E. Popondetta, 25 m, v.1956, G. Lippert (1 female, BPBM). N.E. Kainantu, 1560 m, 6.vi.1967, G.A. Samuelson, on *Araucaria cunninghamii* (6 males, 1 female, BPBM). No data (1 male, BPBM). Taun Creek logging area, 920 m, 07°15′06″ S, 146°37′35″ E, 13.vii.1999, P. Bouchard (2 males, QMB). "Papua New Guinea", ii.1963, W. Rosenberg (2 males, FSCA). Bulolo, on log, 6.i.1970, L. Radunz (1 female, ANIC). Gadsup, ix.1972, H. Ohlmus (1 male, 4 females, ANIC). Gadsup, ix.1973, H. Ohlmus (2 males, ANIC).

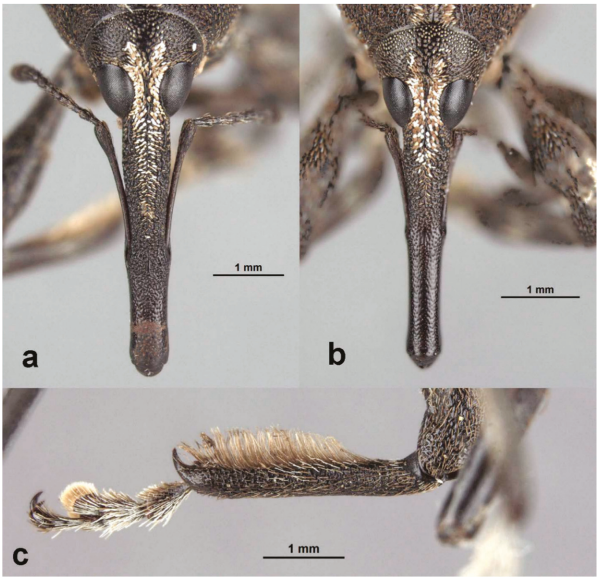

Figure 9. *Ilacuris papuana*: (**a**) rostrum of male, dorsal aspect; (**b**) rostrum of female, dorsal aspect; (**c**) protibia of male, anterior aspect.

Natural history: Adults have been collected on *Araucaria cunninghamii* (Hoop Pine) and *A. hunsteinii* (Klinki Pine) in the vicinity of the Wau Ecology Institute, Papua New Guinea.

Derivation of name: The species name is an adjective formed from part of the name of the country of Papua New Guinea.

Ilacuris suttoni Anderson & Setliff, new species
(Figures 10 and 11)

Description: Male. Body length 9.2 mm. Body width 3.7 mm. Dorsal surface with dispersed to dense, variously colored, broad appressed scales; no erect or suberect hairs present. Rostrum with antennal insertions at about apical one-third, ventral surface finely granulate from just anteriorly of base to antennal insertions and with long fine golden hairs, densest and longest just below antennal insertions; in dorsal view with area behind antennal insertions not dilated, not wider than area before insertions, width greatest at antennal insertions; dorsally carinate from antennal insertions to near base. Antenna with funicle segments 1 and 2 subequal in length. Pronotum with distinct, narrow, sharp median carina in anterior three-quarters; area next to median carina continuing to flanks not impressed; scales mostly white to tan throughout rest of disk except area basally of carina at middle with patch of dense, white to pale brown broad scales in front of scutellar shield; anterolateral angles subapically subquadrate. Elytra with interstria 3 slightly elevated throughout basal half of its length. Mid-dorsal fascia of dark brown to black scales transverse; apical portion of elytra with dense white and pale brown scales immediately behind transverse dark fascia, scales dispersed, somewhat paler towards elytral apex. Pro- and mesofemora with inner margin with small subapical angulation; inner margin of metafemora with small, distinct subapical tooth. Inner margin of protibiae with a row of sparse, elongate, golden hairs in apical three-quarters. Abdomen with ventrite 1 convex medially. Aedeagus with penis widest in apical half, apex somewhat sharply, medially emarginate, with a few setae at middle of apical margin next to emargination, body shorter than apodemes; internal sac with a vague apical sclerite composed of fine dense spicules. **Female.** Not known.

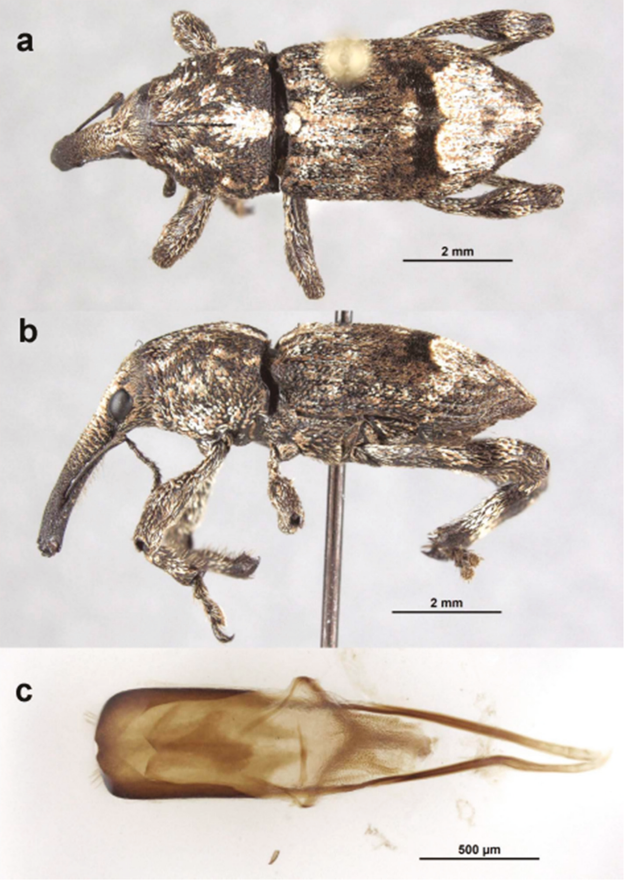

Figure 10. *Ilacuris suttoni*: (**a**) habitus of male, dorsal aspect; (**b**) habitus of male, lateral aspect; (**c**) aedeagus, dorsal aspect.

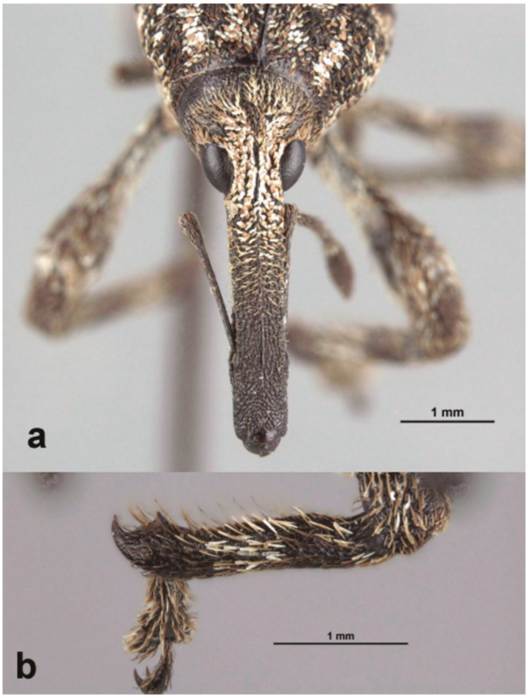

Figure 11. *Ilacuris suttoni*: (**a**) rostrum of male, dorsal aspect; (**b**) protibia of male, anterior aspect.

Specimens examined. Holotype, male: "AUSTRALIA: N.S.W., Rivertree [−28.6260 152.2450], 290 m, N. Sutton" (ANIC). See note above about this locality.

Derivation of name. This species is named after Edmund ("Ned") Sutton of Fletcher, Queensland, Australia, who collected the only known specimen. Mr. Sutton was one of few people successful in collecting numbers of the large pine weevil *Eurhamphus fasciculatus*. Parts of his collection are in some North American museums, but the bulk of his collection is now housed in the Queensland Museum.

Natural history. It is assumed that this unique specimen, which was mixed with a long series of *I. laticollis* labelled the same, was collected at Rivertree, New South Wales, where Sutton is known to have collected beetles associated with *Araucaria*.

3.2.4. *Kuschelorhinus* Anderson & Setliff, New Genus

Type species: *Kuschelorhinus hirsutus* Anderson & Setliff, new species.

Description. Medium-sized (7.9–9.8 mm); elongate oval; prothorax trapezoidal in dorsal view, widest subbasally, maximum width equal to maximum width of elytra, slightly less so in female; elytra subparallel-sided to about apical third, tapering towards apex. Integument dark brown to black; covered with small, appressed to recumbent, tan to brown, elongate-narrow hair-like scales; dorsum with few patches of white or fuscous hair-like scales. Male with dense covering of elongate, very fine, wispy hairs covering almost entirety of surface of body and appendages; female with such hairs limited to pronotum. Eyes large, outline subcircular, slightly elevated, separated by less than width of rostrum at base in male, less so in female. Rostrum longer than pronotum in both sexes; straight (male) to slightly curved (female), circular in cross-section; tapering slightly to apex; basal half dorsally covered with sparse hair-like scales in male, almost bare in female, apical half bare, venter moderately coarsely granulate in basal portion in male, bare in female. Antennae inserted slightly before midlength of rostrum in male, slightly behind midlength in female; scrobes sharply defined, running towards anteroventral angle of eye; scapes subcylindrical, clavate towards apex, reaching posterior margin of eye in repose in male, about middle of eye in female; funicles 7-segmented, segments 1 and 2 each two to three times longer than 3 in male, slightly less so in female, 3 slightly longer than 4, 4–7 subequal in length, 7 with appressed white scales, closely appressed to but distinct from club; clubs elongate, transversely 4-segmented. Pronotum with glabrous dorsomedian elevated ridge from apex to slightly past midlength, lateral portions of basal margins not produced posteriad over elytral bases laterally, anterolateral corners in dorsal view acutely angulate in male, tapered to apex in female. Elytra with base weakly sinuate, scutellar shield externally visible, elongate-triangular, densely squamose; with 10 complete striae of small, shallow punctures; declivital callus distinct, tuberculate, with apical tuft of elongate-narrow scales. Legs elongate; femora with inner margin distinctly toothed, tooth in male large and recurved on profemora, slightly smaller on meso- and metafemora, in female slightly smaller on all femora; inner margin of protibiae expanded and flanged at about midlength, more so in male than female. Aedeagus with penis widest at apex, emarginate at apex at middle, apex lacking setae, body about as long as apodemes, internal sac with distinct apical armature of two elongate, narrow curved sclerites. Female not dissected.

Distribution: The genus is only known from the central highlands of Papua New Guinea (a record from New Britain requires confirmation).

Comments: Sexual dimorphism in the single known specie is extreme and evident in the antennal insertions on the rostrum, the sculpture and form of the rostrum (swollen and granulate basally in the male) and mostly notably in the dense covering of long, fine, wispy hairs over the entire body surface (including appendages) in the male. *Kuschelorhinus* is closely related to *Ilacuris* but is here given generic status because of the extreme sexual dimorphism, the form of the aedeagus, the very different vestiture lacking any broad scales, the lack of long setae along the inner margin of the front tibiae in males and the presence of distinct elytral declivital calli.

Derivation of genus name: This genus is named in honor of Guillermo 'Willy' Kuschel (1918–2017), in recognition of his lifetime of contributions to the study of the Curculionoidea; the name is masculine in gender.

Kuschelorhinus hirsutus Anderson & Setliff, new species
(Figures 12–14)

Description. Male. Body length 7.9–9.3 mm. Body width 3.2–3.8 mm. Dorsal surface with dispersed, mostly tan, appressed to recumbent, elongate, narrow hair-like scales; rather dense, white long, wispy erect hairs on dorsum, legs, antennae (except clubs) and venter. Rostrum with antennal insertions at about apical two-fifths of length, ventral surface coarsely granulate from just before base to antennal insertions; in dorsal view with area behind antennal insertions strongly dilated, much wider than area before insertions; width greatest at or before base. Antennae with funicle segment 2 much shorter than 1; 1 and 2 very long, 1 about as long as combined length of 3–5. Pronotum with distinct, narrow median carina in anterior half, culminating in slightly fusiform callosity at about midlength, then posteriorly continued as a low, less distinct line to about posterior quarter. Median carina bordered laterally by a deeply impressed area in anterior half, less deep in posterior half; areas next to impression raised towards pronotal margins, with scattered denser white scales forming a faint lateral vitta; otherwise scales of pronotum uniformly elongate-narrow, fine, tan except for patch of broad white hair-like scales towards each posterolateral corner; anterolateral corners subapically distinctly angled, quadrate. Prosternum strongly tumescent in front of procoxae. Elytra with interstria 3 slightly elevated and variously granulate throughout basal three-quarters of length; dorsal fascia of dark brown to black scales faint, "V-shaped"; apical portion of elytra with uniformly tan, elongate hair-like scales. Pro-, meso- and metafemora with inner margin distinctly toothed, tooth especially large on profemora. Inner margin of protibiae expanded laterally at midlength opposite profemoral tooth. Abdomen with ventrite 1 concave medially, lacking hair-like scales (which uniformly cover ventrites 2–5), with only very fine hairs. Aedeagus with penis apically abruptly, rather deeply emarginate; internal sac with apical sclerites individually distinct, strongly curved outwards. **Female.** Body length 8.9–9.8 mm. Body width 3.1–3.9 mm. As for male except dorsal and other surfaces lacking long, erect wispy hairs, except for a few scattered long hairs on pronotum. Rostrum with antennal insertions at basal third of length, ventral surface smooth from the base to antennal insertions; in dorsal view with area before antennal insertions not dilated or much wider than area behind insertions, width greatest near base. Pronotum with anterolateral corners subquadrate. Prosternum flat in front of procoxae. Pro-, meso- and metafemora with inner margin only weakly toothed, tooth largest on metafemora. Protibiae with very slight median expansion. Abdomen with ventrite 1 flat to slightly evenly convex, lacking scales, with only fine appressed hairs. Genitalia not examined.

Specimens examined. Holotype, male: "NEW GUINEA: NE / Wau, Morobe Distr. / 1300 m, 1.II.1961 // J. Sedlacek / Collector / BISHOP" (BPBM). Paratypes: Same data (1 male, ANIC). PAPUA NEW GUINEA, Wau, 23.viii.1956, 960 m, E. J. Ford Jr. (4 males, 2 females, BPBM). Wau, 1100–1200 m, i.1966, J. Sedlacek (6 males, 5 females, BPBM, CWOB). Wau, 1200–1300 m, 14–17.i.1963, J. Sedlacek (1 female, BPBM). Wau, 1250 m, 23.i.1963 (1 female, BPBM). Wau, 1300 m, 1.ii.1961, J. Sedlacek (2 males, BPBM). Wau 1200 m, 25–30.ix.1964, J. Sedlacek (1 female, BPBM). Wau 1250 m, 23.i.1964, J. Sedlacek (4 males, 2 females, BPBM). Wau, 1300 m, 1.ii.1961, J. Sedlacek (20 males, 15 females, BMNH, BPBM, CMNC, CWOB, GPSC, USNM). Wau, 1150–1250 m, 1.ii.1963, J. Sedlacek (2 males, 2 females, BPBM). Wau, 1200–1300 m, 14–17.i.1963, J. Sedlacek (19 males, 11 females, BPBM, CMNC). Wau, 23.i.1963, 1250 m, J. Sedlacek (5 females, BPBM). Wau, 1100 m, 30.ix.1961, J. Sedlacek (1 male, BPBM). Wau, 1000–1250 m, 3.iii.1964, J. Sedlacek (7 males, 8 females, BPBM). Wau, 1200 m, 17.viii.1963, J. Sedlacek (1 male, BPBM). Wau, 1200 m, 26–27.ix.1964, J. Sedlacek (1 female, BPBM). Wau, 980–1100 m, 14.viii.1964, J. Sedlacek (1 male, 1 female, BPBM). Wau, 1100 m, 31.i.1963, J. Sedlacek (1 male, BPBM). Wau, 1250 m, 22.vii.1969, J. Sedlacek (1 male, BPBM). Wau, 1200–1300 m, 6–12.iv.1962, J. Sedlacek (1 male, 1 female, BPBM). Wau, 1700–1800 m, 27.ix.1965, J. Sedlacek, malaise trap (1 female, BPBM). Wau, Mount Missim, 11.iv.1964, J. Sedlacek (6 males, 6 females, BPBM). Wau, Hospital Creek, 10.iv.1965, J. Sedlacek (2 females, BPBM). Wau, J. Sedlacek (2 females, BPBM). Bulolo, 900 m, 29.iii.1968, P. Colman (2 males, 2 females, BPBM). Bulolo, 880 m, 14.viii.1956, J. Sedlacek, light trap (1 female, BPBM). Bululo, 1010 m, 28.viii.1956, J. Sedlacek, light trap (1 male, BPBM). Crooked Creek logging area, 920 m, 7°12′56″ S, 146°35′39″ E, 11.vii.1999, P. Bouchard (3 males, 2 females, QMB). Forestry road north of Wau, 21.x.1969, J.E. Tobler (2 male, 2 females, CASC). NEW GUINEA, Bulolo District, 17.xii.1967, B. B. Lowery (1 male, ANIC). NEW GUINEA, Bulolo, 26.xii.1971, H. Ohlmus (1 male, ANIC). Same data but 28.xii.1971 (2 males, ANIC). NEW GUINEA, Wau, Feb. 1973, H. Ohlmus (1 female, ANIC). New Britain: Gazelle Peninsula, Gaulim, 130 m, 28.xi.1962, J. Sedlacek (23 males, 12 females, BPBM, CMNC, CWOB, GPSC). Forest Station Bulolo, 7.x.1976, Ento Crew, ex. *Araucaria hunstenii* log (1 male, BMNH). Hump Logging Area, Bululo, 4.v.1970, B. Gray, under bark upper stem *Araucaria hunstenii* (1 female, BMNH).

Natural history. Two adult specimens were collected from Klinki Pine (*Araucaria hunsteinii*) in Bulolo, Papua New Guinea. The majority of specimens were collected together with *I. papuana* in mixed stands of *Araucaria*; however, a long series of specimens collected on New Britain appears to be from a locality where no *Araucaria* is known to occur [30] and may be mislabeled. Label data on a few specimens indicate that they were collected at a light trap.

Derivation of name. This species is named for its distinct, densely hairy males; the name is an adjective.

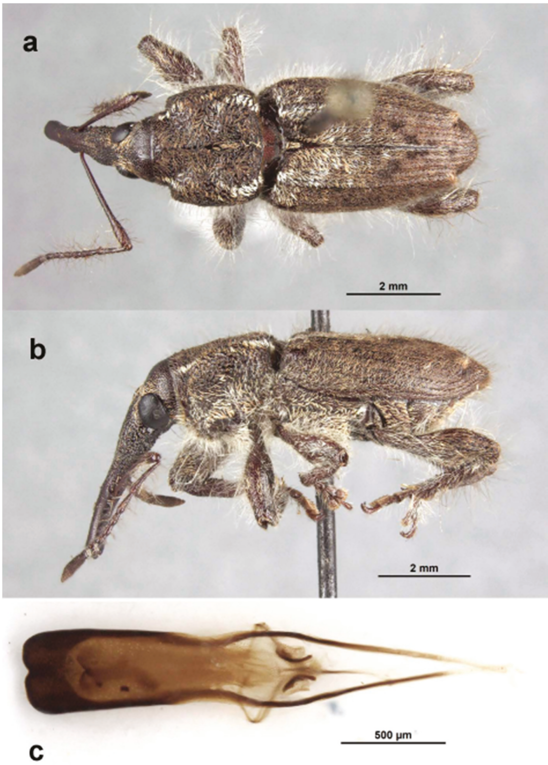

Figure 12. *Kuschelorhinus hirsutus*: (**a**) habitus of male, dorsal aspect; (**b**) habitus of male, lateral aspect; (**c**) aedeagus, dorsal aspect.

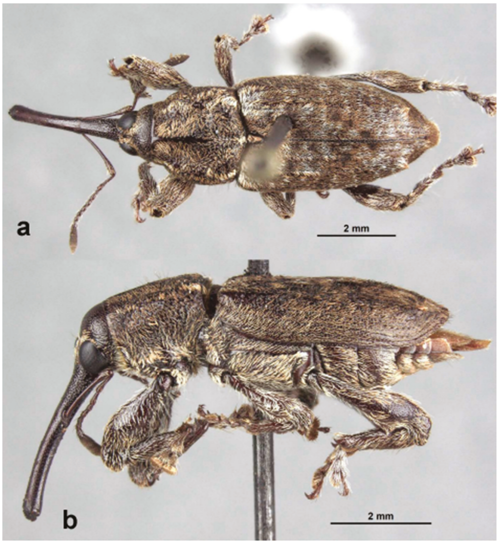

Figure 13. *Kuschelorhinus hirsutus*: (**a**) habitus of female, dorsal aspect; (**b**) habitus of female, lateral aspect.

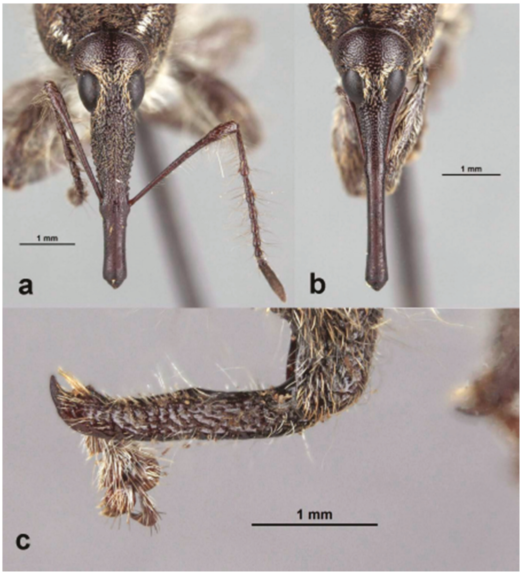

Figure 14. *Kuschelorhinus hirsutus*: (**a**) rostrum of male, dorsal aspect; (**b**) rostrum of female, dorsal aspect; (**c**) protibia of male, anterior aspect.

3.2.5. *Notopissodes* Zimmerman & Oberprieler, 2014

Notopissodes Zimmerman & Oberprieler in Pullen et al., 2014: 469 [2].

Type species: *Notopissodes pictus* Zimmerman & Oberprieler, 2014, by original designation.

Distribution: The genus is known from northern New South Wales northwards to northern Queensland in Australia but appears to be rare.

Natural history. *Notopissodes* is evidently also associated with Araucariaceae, *N. pictus* having been reared from Hoop Pine (*Araucaria cunninghamii*). Its larvae probably develop in the wood or bark of trunks or branches.

Comments. *Notopissodes* was only recently described, except for its genitalia (see under *N. pictus* below). Apart from the type species, one other species is known, as described below. *Notopissodes* differs significantly in its male genitalia from *Eurhamphus*, *Ilacuris*, *Kuschelorhinus* and *Vanapa*, the penis being narrowly elongate and dorsally closed and the tegmen having a long apodeme, and it is not evidently closely related to these genera.

Notopissodes pictus Zimmerman & Oberprieler, 2014
(Figures 15 and 16)

Notopissodes pictus Zimmerman, 1992: 580, plate 594, Figures 7 and 8 [31] (not available, no description)
Notopissodes pictus Zimmerman & Oberprieler in Pullen et al., 2014: 470 [2].

Description of genitalia. Male: aedeagus with body of penis narrow, 5 x longer than wide, subequal in width for four-fifths of length, then slightly narrowing apicad but widening again just before apex, apex broadly, roundly truncate, asetose; temones half as long as body; internal sac with fine spicules, condensed basally into a lyre-shaped field behind a small narrow sclerite with short, flat lateral arms; tegmen dorsally very weakly sclerotized, broad, parameres long and broad, only medially lightly sclerotized; sternite IX very thin (but dissected specimen somewhat teneral), asymmetrical, bladal part consisting of narrow, unequal arms, apodeme long, curved, apically tapered. Female: gonocoxites long, narrow, weakly sclerotized; styli apical, shortly elongate, apically obliquely truncate and with a few long setae; bursa membranous, small; spermatheca crescentic, with globular ramus and elongate collum differentiated, duct short, membranous, inserted on ventral side of bursa, spermathecal gland large, distinctly capitate, with short membranous duct; sternite VIII with bladal part shortly spatulate, broadly truncate, apodeme stout, straight, slightly longer than bladal part.

Specimens examined. See Pullen et al. (2014: 470) [2] for details of the type series. Additional specimens: Queensland: Canungra Creek, 4 miles s. of Canungra, 3.ii.1973, G. B. Monteith (1 male, QMB); Wrattens Camp via Widgee, 28.iii.1974, G. B. Monteith (1 female, QMB).

Comments. The species is known from Dorrigo in northern New South Wales northwards to Widgee and Mt. Goonaneman in southern Queensland, with an isolated record also from the Paluma Range in northern Queensland.

Natural history. A short series of specimens in the ANIC is labelled as having been reared from Hoop Pine (*Araucaria cunninghamii*). The larvae presumably develop in the wood or bark of trunks or branches of this tree species.

Figure 15. *Notopissodes pictus*: (**a**) habitus of male, dorsal aspect; (**b**) habitus of male, lateral aspect.

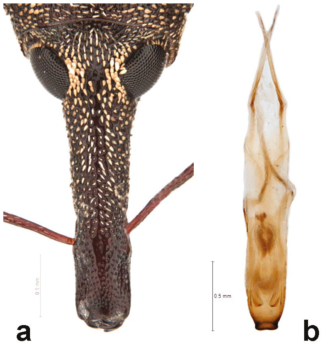

Figure 16. *Notopissodes pictus*: (**a**) rostrum of male, dorsal aspect; (**b)** aedeagus, dorsal aspect.

Notopissodes variegatus Oberprieler, new species
(Figure 17)

Notopissodes sp., Pullen et al., 2014: 470 [2].

Description Female. Body: length 5.15 mm, width 1.8 mm; rostrum: length 1.4 mm, width at base 0.64 mm, width at antennal insertions 0.35 mm; pronotum: length 1.3 mm, width at middle 1.6 mm; elytra: length 3.4 mm, width across humeri 1.8 mm; antennae: scape length 1.82 mm, length of funicle segment 1 0.2 mm, club length 0.4 mm, club width at middle 0.15 mm. Rostrum as long as pronotum, dorsally behind antennal insertions moderately densely covered with broad, creamy scales; forehead with similar scales adjacent to eyes but denuded around deep median fovea. Pronotum densely covered with large, shallow, open punctures arranged in indistinct circles, interstices between circles narrow and slightly raised, giving surface a granulose appearance, each puncture with a pale hair-scale directed to centre of circles (summit of pronotum, at ca. 0.7 of length). Elytra with interstriae mostly covered with short, broad, subappressed, intermixed white, creamy and black scales, forming an irregular pattern except for yellow and white scales condensed into broad, irregular V stretching from humeri posteromesad onto interstriae 2 and a broad, transverse one on top of declivity stretching onto interstriae 1, interstriae 1–3 on declivity with dense creamy scales. Scutellar shield shorter than wide. For other characters see generic description in Pullen et al. [2]. Genitalia not examined. Male unknown but probably similar except for slightly shorter rostrum and longer scapes.

Specimens examined. Holotype, female: “Fletcher [−28°46′ 151°51′] / Queensland / E. Sutton” (ANIC).

Comments. This species is only known from a single female, but we deem it appropriate to describe it in the context of this study of all the *Araucaria*-associated Orthorhinini. It is readily distinguishable from *N. pictus* by its smaller size and by its different, variegated dorsal scale pattern. Although the single specimen bears an exact locality on its label, it is uncertain whether it was actually collected in Fletcher or rather at a nearby locality where Sutton is known to have collected beetles on hoop pines, such as Rivertree across the border in New South Wales.

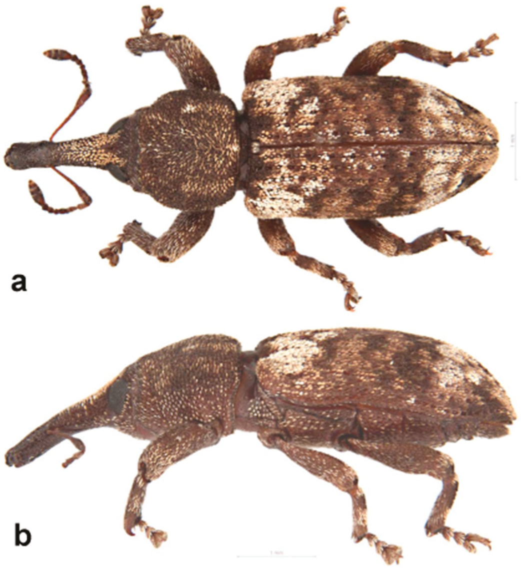

Figure 17. *Notopissodes variegatus*: (**a**) habitus of female, dorsal aspect; (**b**) habitus of female, lateral aspect.

Natural history. The species is likely to also live on Hoop Pine (*Araucaria cunninghamii*) and its larvae to develop in the wood or bark of this tree species.

Derivation of name. The species is named for its variegated color pattern of scales on the elytra; the name is an adjective.

3.2.6. *Imbilius* Marshall, 1938

Imbilius Marshall, 1938: 9 [32] (in Hylobiinae: Hylobiina); Zimmerman, 1994: 694 [14] (transfer to Molytinae); Alonso-Zarazaga & Lyal, 1999: 202 [5] (catalogue, in Molytinae: Hylobiini); Pullen et al., 2014: 283 [2] (catalogue, in Molytinae: Orthorhinini).

Type species: *Imbilius araucariae* Marshall, 1938, by original designation.

Distribution: The genus appears restricted to a small forest area in southern Queensland, Australia, to date known from only two localities and few specimens.

Natural history. *Imbilius* is associated with Hoop Pine (*Araucaria cunninghamii*), several specimens of its single species having been reared from dying or dead trunks of this tree species [32].

Comments. Marshall's description of the genus is apt and comprehensive, except for the genitalia (see *I. araucariae* below).

Imbilius araucariae Marshall, 1938
(Figures 18 and 19)

Imbilius araucariae Marshall, 1938: 9 [32]; Zimmerman, 1992: 578 [31] (illustrated in color); Pullen et al., 2014: 283 [2] (catalogue).

Diagnosis: Body length (exclusive of head and rostrum) 3.8–4.4 mm. Body testaceous, densely covered with small, elongate, truncate, appressed, shiny, greyish-brown (male) to cinnamon-coloured (female) scales (except dorsal anterior two-thirds and venter of rostrum only sparsely setose), lateral side of humeri and posterior pronotal angles with narrow strip of white scales, a few scattered white scales also on elytra, pronotum medially with a pair of small patches of black scales. Rostrum of both sexes slightly shorter than pronotum, weakly downcurved, antennal insertions lateral, in apical third of rostral length. Antennae with funicle 7-segmented, segment 1 as long as 2 + 3, others shorter, slightly transverse; clubs elongate, compact, about 2× wider than funicle. Elytra with interstriae 3 bluntly raised in basal half, interstriae 5 similarly raised from near base to declivity, there forming a blunt flange, 7 and 8 slightly elevated from humeri to declivity; elytral apices produced into separate blunt cones. Femora short, subcylindrical, armed with short tooth on inside at apical third; tibiae stout, shorter than femora, subcylindrical, apically uncinate. Tarsi short and broad; claws divergent, simple but basally swollen. Ventrites 1 and 2 about 3× longer than 3 and 4, at lower level.

Description of genitalia. Male: aedeagus with body of penis narrow, 4.5× longer than wide, subparallel in basal three-quarters of length, at apical quarter slightly constricted, then roundly expanded before strongly tapering to a narrowly acute asetose apex, dorsally closed (sclerotized), ostium flanked by 2 elongate, slanting, sclerotized flanges; temones 0.75× as long as body; internal sac with a pair of elongate, parallel, looped sclerites basally of ostium; tegmen with well sclerotized slanting ring slightly drawn out at parameres, parameres long, narrow, close together, more weakly sclerotized; sternite IX thick, straight, almost symmetrical, bladal part roundly triangular, with thick, forked, sclerotized internal arms, apodeme apically abruptly hooked dorsad. Gonocoxites moderately short, broad, tapering caudad, apically roundly truncate, very weakly sclerotized (specimen teneral); styli apical, moderately long, stout, apically truncate with a few long setae; bursa membranous, large; spermatheca thickly crescentic, basally broad, not differentiated into ramus and collum, duct moderately short, membranous, inserted on ventral side of bursa, spermathecal gland large, shortly elongate, with very short membranous duct; sternite VIII with bladal part spatulate, unsclerotized except for narrow, widely Y-shaped arms, apodeme stout, straight, ca. 1.5× longer than bladal part, apically flared, truncate.

Specimens examined. Imbil State Forest [−25.46° 152.68°], 16.xii.1971, light trap, R. A. Yule (1 male, ANIC); Imbil State Forest, October 1971, ex *Araucaria cunninghamii* killed by *Hyleops glabratus*, R. A. Yule (2 females, ANIC); Imbil State Forest, 22.vi.1972, ex *Araucaria cunninghamii*, R. A. Yule (1 female, ANIC); Amamoor State Forest, 18 km S. Gympie, Dec. 1977, ex *Araucaria cunninghamii*, M. De Baar (2 females, ANIC).

Comments. The sexes are very similar but the male tends to be darker, less vividly cinnamon-colored. The species is only known from a small area of native forests south of Gympie in southern Queensland and has only been collected a few times.

Natural history. The species was described from six specimens reared from *Araucaria cunninghamii* in 1936 by A. Brimblecombe [32] and a few more reared from the same host several decades later (see above). Its larvae appear to develop in the bark or wood of dead or dying (felled) trees, but nothing has been recorded about its life history.

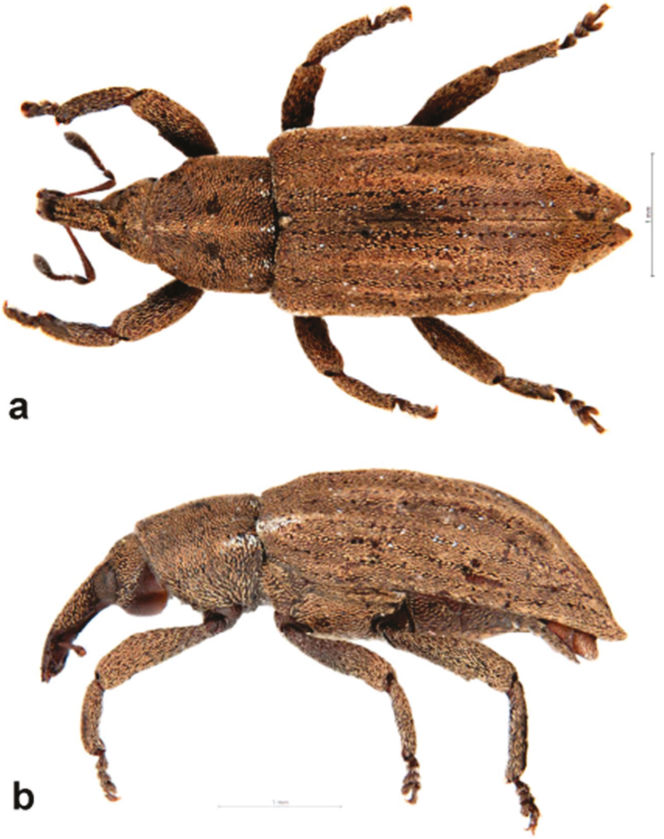

Figure 18. *Imbilius araucariae*: (**a**) habitus of male, dorsal aspect; (**b**) habitus of male, lateral aspect.

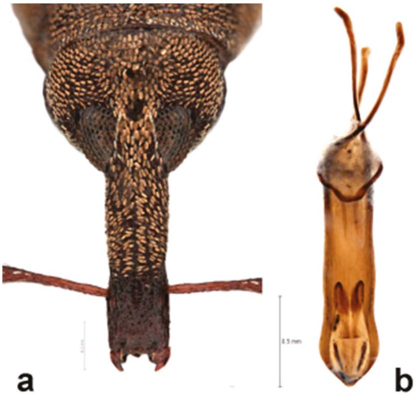

Figure 19. *Imbilius araucariae*: (**a**) head of male, dorsal aspect, (**b**) aedeagus, dorsal aspect.

4. Conclusions

While this contribution has focused on the taxonomy of the *Araucaria*-associated Orthorhinini, there has been no attempt to resolve the phylogenetic relationships among the now 13 genera in the tribe. Future studies should attempt to address this issue as well as diversity in the speciose and morphologically diverse genus *Orthorhinus*. Plant associations also need to be determined for the other taxa in the tribe, such that an evolutionary analysis of host plant-weevil history can be reconstructed.

Author Contributions: R.S.A., R.G.O. and G.P.S. conceived and designed the study, acquired and analyzed the data and wrote the paper.

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Conflicts of Interest: The authors declare no conflict of interest.

References

1. Kuschel, G. Curculionoidea (weevils) of New Caledonia and Vanuatu: Basal families and some Curculionidae. In *Zoologia Neocaledonica 6. Biodiversity Studies in New Caledonia*; Grandcolas, P., Ed.; Mémoires du Muséum National d'Histoire Naturelle: Paris, France, 2008.
2. Pullen, K.R.; Jennings, D.; Oberprieler, R.G. Annotated catalogue of Australian weevils (Coleoptera: Curculionoidea). *Zootaxa* **2014**, *3896*, 1–481. [CrossRef] [PubMed]
3. Setliff, G.P. Annotated checklist of weevils from the Papuan region (Coleoptera, Curculionoidea). *Zootaxa* **2007**, *1536*, 1–296.
4. Shin, S.; Clarke, D.J.; Lemmon, A.R.; Moriarty-Lemmon, E.; Aitken, A.L.; Haddad, S.; Farrell, B.D.; Marvaldi, A.E.; Oberprieler, R.G.; McKenna, D.D. Phylogenomic data yield new and robust insights into the phylogeny and evolution of weevils. *Mol. Biol. Evol.* **2017**, *35*, 823–836. [CrossRef] [PubMed]
5. Alonso–Zarazaga, M.A.; Lyal, C.H.C. *A World Catalogue of Families and Genera of Curculionoidea (Insecta: Coleoptera) (Excepting Scolytidae and Platypodidae)*; Entomopraxis: Barcelona, Spain, 1999.
6. Oberprieler, R.G.; Caldara, R. *Siraton devillei* Hustache (Coleoptera: Curculionidae), the mysterious weevil from the Isle of Elba: Exiled no longer. *Zootaxa* **2012**, *3573*, 55–58.
7. Kuschel, G. The New Caledonian and Fijian species of Aterpini and Gonipterini (Coleoptera: Curculionidae). In *Zoologia Neocaledonica 8. Biodiversity Studies in New Caledonia*; Guilbert, É., Robillard, T., Jourdan, H., Grandcolas, P., Eds.; Mémoires du Muséum National d'Histoire Naturelle: Paris, France, 2014.

8. Pascoe, F.P. On some new genera of Curculionidae. Part I. *J. Entomol.* **1865**, *2*, 413–432.
9. Pascoe, F.P. Catalogue of Zygopinae, a subfamily of Curculionidae, found by Mr. Wallace in the Eastern Archipelago. *Ann. Mag. Nat. Hist.* **1871**, *7*, 198–222. [CrossRef]
10. Gemminger, M. Curculionidae. In *Catalogus Coleopterorum Hucusque Descriptorum Synonymicus et Systematicus*; Gemminger, M., von Harold, E., Eds.; E.H. Gummi: Monachii, Germany, 1871; Volume 8.
11. Masters, G. Catalogue of the described Coleoptera of Australia. Part V. *Proc. Linn. Soc. N. S. W.* **1886**, *1*, 585–686. [CrossRef]
12. Hustache, A. Curculionidae: Subfam. Zygopinae. In *Coleopterorum Catalogus auspicii et auxilio*; Pars 136; Schenkling, S., Ed.; W. Junk: Berlin, Germany, 1934.
13. Von Dalla Torre, K.W.; Schenkling, S.; Marshall, G.A.K. Curculionidae: Subfam. Pissodinae. In *Coleopterorum Catalogus auspicii et Auxilio*; Pars 125; Schenkling, S., Ed.; W. Junk: Berlin, Germany, 1932.
14. Zimmerman, E.C. *Australian Weevils (Coleoptera: Curculionoidea) Volume 1. Orthoceri, Anthribidae to Attelabidae, the Primitive Weevils*; CSIRO: Melbourne, Australia, 1994.
15. Lyal, C.H.C. 3.7.7 Molytinae Schoenherr, 1823. In *Handbook of Zoology, Arthropoda: Insecta: Coleoptera. Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Eds.; Walter de Gruyter: Berlin, Germany, 2014.
16. Mecke, R.; Mille, C.; Engels, W. Araucaria beetles worldwide: Evolution and host adaptations of a multi-genus phytophagous guild of disjunct Gondwana derived biogeographic occurrence. *Pró Araucária Online* **2005**, *1*, 1–18. Available online: http://www.cerambycoidea.com/titles/meckemilleengels2005.pdf (accessed on 28 June 2018).
17. Wylie, F.R.; Shanahan, P.J. Insect attack in fire-damaged plantation trees at Bulolo in Papua New Guinea. *J. Aust. Entomol. Soc.* **1973**, *14*, 371–382. [CrossRef]
18. Sequeira, A.S.; Farrell, B.D. Evolutionary origins of Gondwanan interactions: How old are *Araucaria* beetle herbivores? *Biol. J. Linn. Soc.* **2001**, *74*, 459–474. [CrossRef]
19. Anderson, R.S. A taxonomic monograph of the Middle American leaf-litter inhabiting weevil genus *Theognete* Champion (Coleoptera: Curculionidae; Molytinae; Lymantini). *Zootaxa* **2010**, *2458*, 1–127.
20. Daniels, G. *Bibliography of Australian Entomologists 1687–2000*; Privately Published: Mt. Ommaney, QLD, Australia, 2004; Volumes 1 and 2.
21. Barrett, J.H. The biology, ecology and control of *Vanapa oberthuri* Pouill. (Coleoptera: Curculionidae) in hoop pine *Araucaria* plantations in New Guinea. *P. N. G. Agric. J.* **1967**, *19*, 47–60.
22. Gray, B.; Howcroft, N. Notes on the incidence, attack, associated insects and control of *Vanapa oberthuri* Pouillaude (Coleoptera: Curculionidae), a pest of hoop pine, *Araucaria cunninghamii* D. Don. plantations in New Guinea. *Z. Angew. Entomol.* **1970**, *66*, 248–256.
23. Peters, B. *Vanapa oberthuri*: A pest of hoop pine plantations in PNG. *Entomol. Soc. Qld. News Bull.* **2018**, *45*, 181–182.
24. Gray, B.; Barber, I.A. Studies on *Vanapa oberthuri* Pouillaude (Coleoptera: Curculionidae), a pest of hoop pine plantations in Papua New Guinea. *Pac. Insects* **1974**, *16*, 383–394. [CrossRef]
25. Gray, B.; Wylie, F.R. Forest tree and timber insect pests in Papua New Guinea. II. *Pac. Insects* **1974**, *16*, 67–115.
26. Wylie, F.R. Insect problems of *Araucaria* plantations in Papua New Guinea and Australia. *Aust. For.* **1982**, *45*, 125–131. [CrossRef]
27. Froggatt, W.E. *Forest Insects and Timber Borers*; Alfred James Kent, Government Printer: Sydney, Australia, 1927.
28. Monteith, G.; Baldwin, N. David Behrens and his studies on the giant hoop pine weevil, *Eurhamphus fasciculatus*. *Entomol. Soc. Qld. News Bull.* **2018**, *45*, 177–181.
29. Heller, K.M. Zygopiden-Studien mit besonderer Berücksichtigung der Gattung Mecopus. *Abhandlungen und Berichte des Königlichen Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden* **1893**, *4*, 1–48.
30. Gray, B. Distribution of *Araucaria* in Papua New Guinea. *Res. Bull.* **1973**, *1*, 1–56.
31. Zimmerman, E.C. *Australian Weevils (Coleoptera: Curculionoidea)*; Colour Plates 305–632; CSIRO: Melbourne, Australia, 1992; Volume V1.
32. Marshall, G.A.K. New Australian Curculionidae. *Proc. R. Entomol. Soc. Lond. Ser. B* **1938**, *7*, 8–14.

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MDPI

Communication

Validation of the Names of Five Weevil Taxa Described by Anderson et al., A Review of the *Araucaria*-Associated Weevils of the Tribe Orthorhinini (Coleoptera: Curculionidae: Molytinae), with Description of New Species of *Ilacuris* Pascoe, 1865 and *Notopissodes* Zimmerman & Oberprieler, 2014 and a New Genus, *Kuschelorhinus* Anderson & Setliff; *Diversity*, 2018, *10*, 54

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Abstract: One new genus and four new species of the Orthorhinini from Australia and Papua New Guinea are described, with bibliographic reference to complete descriptions and illustrations in the recent paper by Anderson et al. (2018) published in the journal *Diversity* 10 (3), 54, in which the names were not made available under the rules of the International Code of Zoological Nomenclature dealing with electronic publication, as follows: *Ilacuris papuana* Anderson & Setliff, sp. n., *Ilacuris suttoni* Anderson & Setliff, sp. n., *Notopissodes variegatus* Oberprieler, sp. n., *Kuschelorhinus* Anderson & Setliff, gen. n. and *Kuschelorhinus hirsutus* Anderson & Setliff, sp. n.

Keywords: taxonomy; weevil; new species; Australia; Papuan region

1. Introduction

The recent paper by Anderson et al. published in Diversity 10 (3) [1] was not in full compliance with the International Code of Zoological Nomenclature [2], regarding the publication of online taxonomic papers. Article 8.5 states that, to be considered published [within the meaning of the Code], "a work issued and distributed electronically must be registered in the Official Register of Zoological Nomenclature (ZooBank) (see Article 78.2.4) and contain evidence in the work itself that such registration has occurred" (Article 8.5.3). Because the paper by Anderson et al. (2018) was not registered in ZooBank prior to publication and therefore evidence of registration was not included in it, the new taxonomic names proposed in the paper are not available under the Code [3]. The purpose of this paper is to make those names available.

To fulfill the requirements of Article 8.5, this paper has been registered in ZooBank, under the LSID above, and the names of the species described below have also been registered, following recommendation 10B of the Code. Their LSIDs are given under each name.

To meet the requirements of Article 13.1.2 of the Code, the names listed below are accompanied by a bibliographic reference to their full descriptions and are thereby made available from the publication of this paper. The wording of Article 13.1.2 is somewhat ambiguous as to the status of descriptions based on bibliographic reference, so to avoid any further problems we have added a brief description differentiating each taxon and a holotype designation with the repository identified; these are repeated from the original paper [1].

All label data are recorded *verbatim*, with a slash (/) indicating separate lines on a label and a double slash (//) indicating different labels on a pin.

2. New Nomenclatural Acts

Ilacuris papuana Anderson & Setliff, **sp. n.**

> *Ilacuris papuana* Anderson & Setliff, 2018: 11 [1] (not available)
> http://zoobank.org/urn:lsid:zoobank.org:act:3200BE61-484D-47C5-ADB6-62F54A1F4625

Description. This species is most easily distinguished from the two Australian species of *Ilacuris* by its V-shaped dark brown elytral fascia and evenly convex pronotum (without lateral impressions adjacent to the median carina). See Anderson, Oberprieler & Setliff, 2018: 12, Figures 8 and 9 [1] for full description.

Holotype, ♂: "PAPUA NEW GUINEA: / Morobe, Wau (18 km N.W.), 950 m / 11.ii.2000, 7°15′46″ S 146°39′54″ E / R. S. Anderson / *Araucaria cunninghamii* logs / RSA2000-044X // HOLOTYPE / *Ilacuris* / *papuana* / Anderson & Setliff, 2018 [on red card]" (Repository: Canadian Museum of Nature, Ottawa, Canada). Paratypes listed in [1].

Distribution. Papua New Guinea.

Ilacuris suttoni Anderson & Setliff, **sp. n.**

> *Ilacuris suttoni* Anderson & Setliff, 2018: 13 [1] (not available)
> http://zoobank.org/urn:lsid:zoobank.org:act:2A6EA420-404B-4679-AB75-C6FE268EBE8A

Description. This species is distinguished from its congeners by the transverse dark brown fascia on the elytra and the ventrally setose rostrum of the male. See Anderson, Oberprieler & Setliff, 2018: 15, Figures 10 and 11 [1] for full description.

Holotype, ♂: "AUSTRALIA: N.S.W. / Rivertree, −28.6260, 152.2450 / 290 m, no date, N. Sutton / likely from *Araucaria* / *cunnighamii* // HOLOTYPE / *Ilacuris* / *suttoni* / Anderson & Setliff, 2018 [on red card]" (Repository: Australian National Insect Collection, Canberra, Australia).

Distribution. Australia.

Kuschelorhinus Anderson & Setliff, **gen. n.**

> *Kuschelorhinus* Anderson & Setliff, 2018: 15 [1] (not available)
> http://zoobank.org/urn:lsid:zoobank.org:act:ABC7A1C9-02E6-4EA5-BB5A-550BBADEDD74

Description. This genus differs from the closely related genus *Ilacuris* Pascoe, 1865, by the erect, hair-like scales on the dorsum, the first funicle segment being longer than the second and the profemora armed with a distinct subapical tooth. In *Ilacuris* the dorsal vestiture is composed of small, appressed or recumbent scales, the first funicle segment is shorter than the second and the profemora are not dentate but have a small subapical angulation. See Anderson, Oberprieler & Setliff, 2018: 17–18 [1] for full description.

Type species: *Kuschelorhinus hirsutus* Anderson & Setliff, **sp. n.**

Kuschelorhinus hirsutus Anderson & Setliff, **sp. n.**

> *Kuschelorhinus hirsutus* Anderson & Setliff, 2018: 16 [1] (not available)
> http://zoobank.org/urn:lsid:zoobank.org:act:4E3935F1-43FC-4495-A94D-B998A77A7A45

Description. This species differs from members of the closely related genus *Ilacuris* Pascoe, 1865, by the erect, hair-like scales on the dorsum, first antennal segment being longer than the second and the profemora armed with a distinct subapical tooth. In *Ilacuris* species, the dorsal vestiture is composed of small, appressed or recumbent scales, the first antennal segment is shorter than the second and the profemora are not dentate but have a small subapical angulation. See Anderson, Oberprieler & Setliff, 2018: 17–18, Figures 12–14 [1] for full description.

Holotype, ♂: "NEW GUINEA: NE / Wau, Morobe Distr. / 1300 m, 1.II.1961 // J. Sedlacek / Collector / BISHOP // HOLOTYPE / *Kuschelorhinus* / *hirsutus* Anderson & Setliff, 2018 [on red card]". (Repository: Bernice P. Bishop Museum, Honolulu, HI, U.S.A.). Paratypes listed in [1].

Distribution. Papua New Guinea.

Notopissodes variegatus Oberprieler, **sp. n.**

> *Notopissodes variegatus* Oberprieler, 2018: 21 [1] (not available)
> http://zoobank.org/urn:lsid:zoobank.org:act:B1BC7B94-DED2-43B8-B938-CB1F23965216

Description. This species is readily distinguishable from the only other species of *Notopissodes*, *N. pictus* Zimmerman & Oberprieler, 2014, by its smaller size (4.8 mm body length), variegated colour pattern of scales on the elytra and the shorter rostrum in the female (as long as the pronotum). See Anderson, Oberprieler & Setliff, 2018: 23–24, Figure 17 [1] for full description

Holotype, ♂: "Fletcher [−28°46′ 151°51′] / Queensland / E. Sutton // HOLOTYPE / *Notopissodes* / *variegatus* Oberprieler, 2018 [on red card]" (Repository: Australian National Insect Collection, Canberra, Australia).

Distribution. Australia.

Author Contributions: R.G.O. drafted the paper and R.S.A. and G.P.S. added details of the descriptions and specimens.

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Conflicts of Interest: The authors declare no conflict of interest.

References

1. Anderson, R.; Oberprieler, R.G.; Setliff, G.P. A review of the *Araucaria*-associated weevils of the tribe Orthorhinini (Coleoptera: Curculionidae: Molytinae), with description of new species of *Ilacuris* Pascoe, 1865 and *Notopissodes* Zimmerman & Oberprieler, 2014 and a new genus, *Kuschelorhinus* Anderson & Setliff. *Diversity* **2018**, *10*, 54.
2. International Commission on Zoological Nomenclature. 2012. INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE Fourth Edition [Incorporating Declaration 44, Amendments of Article 74.7.3, with Effect from 31 December 1999 and the Amendment on E-Publication, Amendments to Articles 8, 9, 10, 21 and 78, with Effect from 1 January 2012]. Available online: http://www.iczn.org/iczn/index.jsp (accessed on 26 July 2018).
3. International Commission on Zoological Nomenclature. Amendment of Articles 8, 9, 10, 21 and 78 of the International Code of Zoological Nomenclature to expand and refine methods of publication. *Zookeys* **2012**, *219*, 1–10. [CrossRef]

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Article

The Molecular Phylogeny of the New Zealand Endemic Genus *Hadramphus* and the Revival of the Genus *Karocolens*

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Abstract: The delineation of species is important to the fields of evolution, ecology and conservation. The use of only a single line of evidence, e.g., morphology or a single gene sequence, may underestimate or overestimate the level of diversity within a taxon. This problem often occurs when organisms are morphologically similar but genetically different, i.e., for cryptic species. The *Hadramphus* genus contains four endangered, morphologically similar species of weevils, each endemic to a specific New Zealand region (*Hadramphus spinipennis* Chatham Islands, *H. stilbocarpae* Fiordland, *H. tuberculatus* McKenzie Country, *H. pittospori* Poor Knights Islands). The systematic relationships among these species are unclear. We used samples from these species and a closely related genus, *Lyperobius huttoni*, to obtain data from the mitochondrial gene cytochrome c oxidase subunit I and the nuclear gene internal transcribe spacer 2. In addition to the multi-locus coalescent approach, we modelled morphological characteristics combined with the genetic data. We found that *H. spinipennis*, *H. tuberculatus* and *H. stilbocarpae* were a closely related clade. Despite a strong morphological similarity, *Hadramphus pittospori* was found to be genetically distinct from the other *Hadramphus* species, which supports the resurrection of the monotypic genus *Karocolens* for this species.

Keywords: *Aciphylla*; Chatham Islands; integrative taxonomy; Poor Knights Islands; weevils

1. Introduction

Accurate species delineation is fundamental to the fields of ecology and evolution and is particularly important in conservation. Effective conservation relies on each species being a well-defined taxonomic unit for preservation purposes, or for species diversity in general. As an indicator for biodiversity hotspots, the correct identification of species is fundamental to conservation [1].

Taxonomic units can be determined using multiple types of data. In particular, the use of integrative taxonomy is recognised as a robust method for delimitating species [2]. Integrative taxonomy allows different types of methods and data, such as genetic, morphological, behavioral, and developmental, to be combined in a synergetic way to more completely identify the boundaries among taxa [3].

Although integrative taxonomy is a strong method for identifying species, the approach is limited when dealing with cryptic and allopatric species [4]. Species delimitation that uses morphological characteristics, even when using an integrative approach, can be subjective and based on ambiguous and hard to determine traits [4]. Previously established phylogenies based on strictly morphological characteristics have been found, at times, to be based on questionable synapomorphies [5]. Phenotypic characteristics can vary within a single species, and this can be misleading when building phylogenies based on traits such as colour and size. The New Zealand endemic widow spider was previously separated into two distinct species, *Latrodectus katipo* and *L. atritus*, based on colour morph. Molecular methods determined that the widow spider is a single species, *L. katipo*, and that the colour variation correlated with mean annual temperature [6]. When identifying cryptic or allopatric species, combining genetic data with coalescent theory provides a quantitative assessment of species status [7].

The use of multispecies coalescent models to estimate genetic structure that provide information on species trees from multilocus genetic data has provided researchers with a strong tool to identify species events, understand evolutionary processes and determine relationships among taxa [4,8]. For example, a molecular reconstruction of scorpions using 5025 genes reconstructed a basal topology completely different from traditional morphological taxonomy, changing the understanding of scorpion evolution [9]. Coalescent methods have become increasingly important in conservation. For example, Vuataz et al. [10] used a coalescent approach on freshwater insects from Madagascar and found evidence for considerably more endemic (and threatened) species than expected. Likewise, Rutchsmann et al. [11] found an additional 11 mayfly species when they used a coalescent approach on the Canary Islands. Microendemicity has been detected using a molecular coalescence approach in Balkan trichopterans [12]. All of these approaches suggest that we have often underestimated the level of divergence using past methods.

New Zealand has a high diversity of invertebrate species, many of which have been in decline since the arrival of humans [13]. A large proportion of New Zealand's invertebrates have yet to be described, and even fewer have been genetically analysed. The evolutionary divergence of insects on islands isolated from neighbouring continents results in high levels of endemism [14–16]. As an oceanic island, New Zealand is considered one of the world's biodiversity hotspots, with a large proportion of endemic species [17]. By offering greater insight into the evolutionary history and taxonomic diversity of invertebrates, coalescent methods may help to identify and conserve declining species in New Zealand, inform conservation decisions, and help protect an international biodiversity hotspot.

Hadramphus Broun, 1911 is an endemic genus of weevils (Coleoptera: Curculionidae) in the tribe Molytini that consists of four species: *H. tuberculatus* (Pascoe, 1877), *H. spinipennis* Broun, 1911, *H. stilbocarpae* Kuschel, 1971, and *H. pittospori* (Kuschel, 1987). These weevils are some of the largest in the world for this tribe and are characterized by rounded tubercles on their backs [18]. All four species are of conservation concern due to their limited population numbers or a reduced range compared to their historical distribution.

The Canterbury knobbled weevil, *H. tuberculatus*, is perhaps the rarest beetle species in the genus, consisting of only one known population. Last sighted in the 1922, it was presumed extinct by the late 1990s. However, in 2004 it was rediscovered at Burkes Pass Scenic Reserve, Mackenzie County [19]. *Hadramphus tuberculatus* is the only species in the genus to be found in subalpine grasslands rather than coastal habitats. Based on evidence from Holocene fossils and museum records, *H. tuberculatus* was once distributed throughout the Canterbury Plains and surrounding hills but is now confined to only one small reserve [20]. The host-plants for *H. tuberculatus* were historically thought to be *Aciphylla subflabellata* and *A. glaucescens*, but currently it is found feeding on *A. aurea* [18,21]. Captive rearing studies show that *H. tuberculatus* is somewhat plastic in host-plant choice and can successfully feed on *A. aurea*, *A. subflabellata* and *A. dieffenbachii* [22].

Found in the Chatham Islands, *H. spinipennis* is currently confined to Rangatira (South East) Island, Mangere Island, and Little Mangere Island, although museum records show the species was once present on Pitt Island as well [18]. It is a coastal species and is often found on rocky coastal cliffs on its host-plant *Aciphylla dieffenbachii.* Due to its range restriction and loss of populations in the past, *H. spinipennis* is considered endangered. Although extensive studies on ecology and population dynamics were done by Schöps [23] who suggested that the remaining populations were healthy, a recent study by Fountain [24] suggests the population on Rangatira is declining.

Hadramphus stilbocarpae was once widespread on several islands in Fiordland and the sub-Antarctic, but has undergone population decline, due mainly to the introduction of rats. It is currently found on Resolution Island, Puysegur Point, Bird Island, The Snares (North East Island and Broughton Island) [18] and a small population was translocated to Breaksea Island in 1991 [25]. Population decline and the continual threat from rats have led to this species being classified as endangered. *Hadramphus stilbocarpae* is confined to coastal areas and is found on the host-plants *Anisotome lyalli* and *Stilbocarpa robusta*.

Discovered in 1981, *H. pittospori* is endemic to the Poor Knights Islands [18,26]. The protected status of the island groups means that the weevil was automatically classified as a protected species. The weevil is usually found in coastal lowlands on its host plant, *Pittosporum crassifolium*. *Hadramphus pittospori* was originally placed into its own genus, *Karocolens,* by Kuschel [26]. Kuschel noted that *H. pittospori* was closely related to the genus *Hadramphus* but key morphological differences, such as prothorax and elytra shape, and differing host-plant family, Pittosporacea instead of Apiaceae or Araliaceae, placed the weevil in its own genus. Craw [18] synonymised the genus *Karocolens* with *Hadramphus* as a number of morphological traits defining *Karocolens* were found to be shared with the other *Hadramphus* species.

Few genetic studies have been conducted on the *Hadramphus* genus [24,27]. In this study, we construct the first molecular phylogeny for *Hadramphus* using mitochondrial and nuclear genes. A member of its sister genus, *Lyperobius huttoni* Pascoe, 1876, is used as an outgroup based on its positioning in the morphological phylogenetic tree constructed by Craw [18]. We examine whether *H. pittospori* correctly belongs to the genus *Hadramphus* or if the genus *Karocolens* should be reinstated.

2. Methods and Methods

2.1. Specimen Collection

Hadramphus tuberculatus, *H. spinipennis*, *H. stibocarpae* and *L. huttoni* were collected by pitfall trapping and visual searches of their host-plants. For each captured weevil, we collected a tarsal clip from the mesothoracic leg using ethanol-sterilised scissors. We then returned the weevil to the host-plant it was found on, or in the case of pitfall trapping, to the nearest host-plant. Tarsal clips were stored in 100% ethanol at −20 °C until DNA extraction. For *H. pittospori*, a weevil was collected from Poor Knights Islands and stored in ethanol. We also sampled an additional museum specimen of *H. pittospori* from the New Zealand Arthropod Collection (NZAC) collected on Aorangi Island in 1981. Seventy-one *H. tuberculatus* tarsal clips were collected from Burkes Pass Scenic Reserve between October and February in 2007, 2009, 2010, and 2011; six *L. huttoni* tarsal clips were collected in the Mackenzie Basin in November 2009; 15 *H. spinipennis* tarsal clips were collected from Rangatira (South East) Island in February 2010 and 13 tarsal clips from Mangere Island in February 2011 [24]; two *H. stilbocarpae* tarsal clips were collected from Breaksea Island from in January 2010; and *H. pittospori* was collected 17 December 2009.

2.2. DNA Extraction, Amplification and Sequencing

We cut each tarsal clip into several pieces using a sterile scalpel blade and then transferred them to a sterile 1.7 mL microcentrifuge tube. For *H. pittospori*, we made a pin hole in the thorax, and for the museum specimen we removed the pin from the thorax and the whole body was submerged in lysis buffer (Supplementary Material 1). A Qiagen DNeasy Blood and Tissue Kit (Qiagen, catalogue # 69504) was used for DNA extraction following the manufacturer's spin-column protocol for animal tissues and for the museum specimen a QIAmp Investigator Kit (Qiagen, catalogue # 56504) was used for DNA extraction. We amplified the mitochondrial gene cytochrome *c* oxidase subunit I (COI) and the nuclear gene internal transcribe spacer 2 (ITS2) by PCR. Each PCR reaction consisted of 0.25 mM of dNTPs, 0.02 unit/µL of polymerase (*i*-taq, iNtRON Biotechnologies), 0.2 µM of each primer, 1 × PCR buffer, 2.5 µL DNA extraction, and deionized water to bring the total reaction volume to 25 µL. The PCR reaction for the museum specimen of *H. pittospori* included an additional 1 mM $MgCl_2$, 5 µg/µL BSA and the amount of DNA extraction was increased to 5 µL.

For COI, we used the primer set LCO1490 and HCO2198 (656 base pairs) [28]. The PCR cycle consisted of one step at 94 °C for 3 min followed by 35 cycles of 94 °C for 45 s, 45 °C for 45 s and 72 °C for 1 min 20 s, then with a final step at 72 °C for 5 min. Positive results for *H. pittospori* could not be obtained from the primers LCO and HCO, so we amplified a smaller fragment of COI using MLepF1 and LepR1 (426 base pairs) [29]. The same PCR reagents and parameters were used for this primer set. For ITS2, primers, PCR mix and parameters followed the protocol in Fountain et al. [24]. We sequenced PCR products using 0.8 µM of primer, Big Dye version 3.1 (Applied Biosystems, Warrington, Cheshire, UK) and the following thermal regime: 96 °C for 1 min followed by 25 cycles of 96 °C for 10 s, 50 °C for 5 s and 60 °C for 4 min. Sequence products were resolved in an AVANT 3100 (ABI) capillary sequencer. We BLAST [30] searched the results to confirm sequence identity. All sequences were submitted to GenBank, with accession numbers MH536680–MH536727 and MH537666–MH537735 (Supplementary Material 2).

2.3. Data Analysis

We analysed the chromatograms of 100 COI sequences and 48 ITS2 sequences. An additional 15 COI sequences and 25 ITS2 sequences previously published for *H. spinipennis* sequences [24] were included for a total of 115 COI sequences and 73 ITS2 sequences. We built sequence alignments using MEGA 7.0.26 [31]. All COI sequences were visually aligned and the ITS2 sequences were auto-aligned in WebPrank [32]. For COI and ITS2, we calculated nucleotide composition and pairwise distances in MEGA 7.0.26 and nucleotide diversity for each species in DnaSP 6.10.03 [33]. Maximum likelihood (ML) trees were built in MEGA 7.0.26 [31] with all sites including gaps and an extensive SPR ML heuristic method for tree inference. The best fit evolutionary models for the ML analyses were found using the AIC with jModelTest 2.1.1 [34], which identified the transition (TIM) model as the optimal model for COI and the symmetrical (SYM + G) model [35] with gamma distribution as the optimal model for ITS2. For all Bayesian phylogenetic analyses, we used StarBEAST2 [36] implemented in BEAST 2.4.7 [37]. To assign taxon groups for the species tree, we used current species taxonomy based on morphological characteristics [18], with *L. huttoni* as an outgroup. Evolutionary models were determined through model averaging using a reversible jump MCMC implemented in BModelTest [38] as part of the BEAST2 package. We checked effective sampling sizes and convergence using Tracer 1.6 [39]. Four independent runs of each analysis were conducted and then combined in Log Combiner 2.4.7. We compared the performance of strict and uncorrelated relaxed lognormal clock models using path sampling [40]. For the species tree, we combined the trees from the four independent runs in Log Combiner 2.4.7 using a 20% burn-in for each run. A maximum clade credibility tree was compiled in TreeAnnotator 2.4.7 after discarding the initial 10% burn-in and we visualized the tree in FigTree 1.4.3 [41].

To determine tree topology for each gene tree and the taxonomic placement of each species, we first conducted StarBEAST2 analyses for each gene tree separately using all sequences. For ITS2, we were unable to amplify a fragment for *H. pittospori, and* so this species was not included in the ITS2 analysis. Both Bayesian gene trees converged on the same topology, with the last common ancestor of *H. pittospori* and the other *Hadramphus* species being considerably earlier than the last common ancestor of the remaining three *Hadramphus* species in COI, and *H. tuberculatus* and *H. stilbocarpae* shared a more recent common ancestor than with *H. spinipennis* in both COI and ITS2.

The multi-locus dataset was reduced to 72 individuals that had a sequence for both COI and ITS2. For *H. pittospori*, the ITS2 sequence was replaced by question marks to represent unknown nucleotides. In addition to a species phylogeny based on DNA sequences, we also conducted phylogenetic analysis combining morphological traits and DNA sequences to determine how morphology influenced the placement of *H. pittospori*. We conducted two analyses using the morphological descriptions of Craw [18] and Kuschel [26,42]. For both Craw and Kushel datasets, we included 13 morphological traits

(Supplementary Material 3) and analysed the morphological traits under the Lewis MK model [43]. We then conducted path-sampling analyses and calculated the Bayes factor to determine support for species delimitation. For all final analyses, we used an uncorrelated relaxed lognormal clock prior to the species tree. We estimated the clock rates for COI and ITS2 and used a lognormal prior with the clock rate for COI based on the mutation rate of Polyphaga [44] (M = 0.02 S = 0.8 and M = 0.001 S = 0.9, respectively). The COI and ITS2 gene trees were unlinked, and each run consisted of 100,000,000 generations, sampling every 3500 for analyses of only DNA sequences, and 130,000,000 generations, sampling every 4500 for morphological analyses.

3. Results

In total, 115 extractions for COI and 73 extractions for ITS2 were successfully amplified and sequenced. For COI, all sequences were trimmed to 426 bp and the ITS2 sequences were 419–452 bp. Nucleotide diversity in COI within *H. pittospori* was the highest in comparison to the others' within-species diversity (Table 1). *Hadramphus tuberculatus* had the most individuals sequenced for COI and also the greatest number of haplotypes when compared to the other species (Table 1). Interspecific enetic distances ranged from 0.052–0.289, with the largest divergence between *H. pittospori* and *L. huttoni* (Table 2). The intraspecific genetic distances ranged from 0.001–0.010 (Table 2). The COI ML tree supports the high intraspecific nucleotide diversity in *H. pittospori* (Figure 1A). For *L. huttoni*, *H. spinipennis*, and *H. tuberculatus*, the majority of branch tips were collapsed due to low bootstrap support, and the remaining branches within each species were shorter than 0.01 (Figure 1A). The ITS2 ML consensus tree had higher intraspecific variation compared to the COI ML tree, and the tree was mainly concordant with the COI ML tree, except for paraphyly in *H. stilbocarpae* (Figure 1B).

An examination of log-likelihood in Tracer 1.6 indicated that the MCMC chains reached convergence and all effective sampling size (ESS) values reached above 200. The uncorrelated lognormal clock for the species tree was the best supported clock model and was used in all analyses. The StarBEAST2 analyses (individual genes and multi-coalescent approaches) supported the divergence of *H. pittspori* much earlier than the subsequent divergence of the remaining *Hadramphus* species at 22.76 (1.01–60.68) million years ago (MYA) (Figure 2). *Hadramphus spinipennis* was the sister taxon of the pair *H. tuberculatus* and *H. stilbocarpae* in the analyses (Figure 2).

Table 1. Estimates of diversity in 426 bp fragment of *c* oxidase subunit I (COI) for each species including sample size (N), number (#) of haplotypes, number of polymorphic sites and nucleotide diversity (π) with standard deviation (STD).

Species	N	# Haplotypes	# Polymorphic Sites	Π (STD)
huttoni	10	2	1	0.001 (0.0002)
pittospori	2	2	5	0.012 (0.0059)
spinipennis	28	4	3	0.001 (0.0003)
tuberculatus	71	7	6	0.002 (0.0003)
stilbocarpae	2	2	3	0.007 (0.0035)

Table 2. Mean genetic distances for a 426 bp fragment of COI calculated using the Kimura-2-parameter model are shown along the bottom diagonal. Standard errors, shown above the bold diagonal, were obtained by bootstrapping (10,000 replicates). The mean intraspecific distance is presented along the diagonal in bold.

Species	*huttoni*	*pittospori*	*spinipennis*	*tuberculatus*	*stilbocarpae*
huttoni	**0.001**	0.029	0.024	0.024	0.025
pittospori	0.289	**0.010**	0.027	0.028	0.028
spinipennis	0.210	0.270	**0.007**	0.011	0.013
tuberculatus	0.210	0.270	0.052	**0.002**	0.012
stilbocarpae	0.210	0.287	0.071	0.061	**0.001**

Figure 1. Maximum likelihood bootstrap consensus trees inferred from 1000 replicates for (**A**) cytochrome *c* oxidase subunit I (COI) and (**B**) internal transcribe spacer 2 (ITS2). Nodes with a lower than 50% bootstrap are collapsed. For branches with zero length, the number of samples with identical sequences is listed in parentheses after the species name.

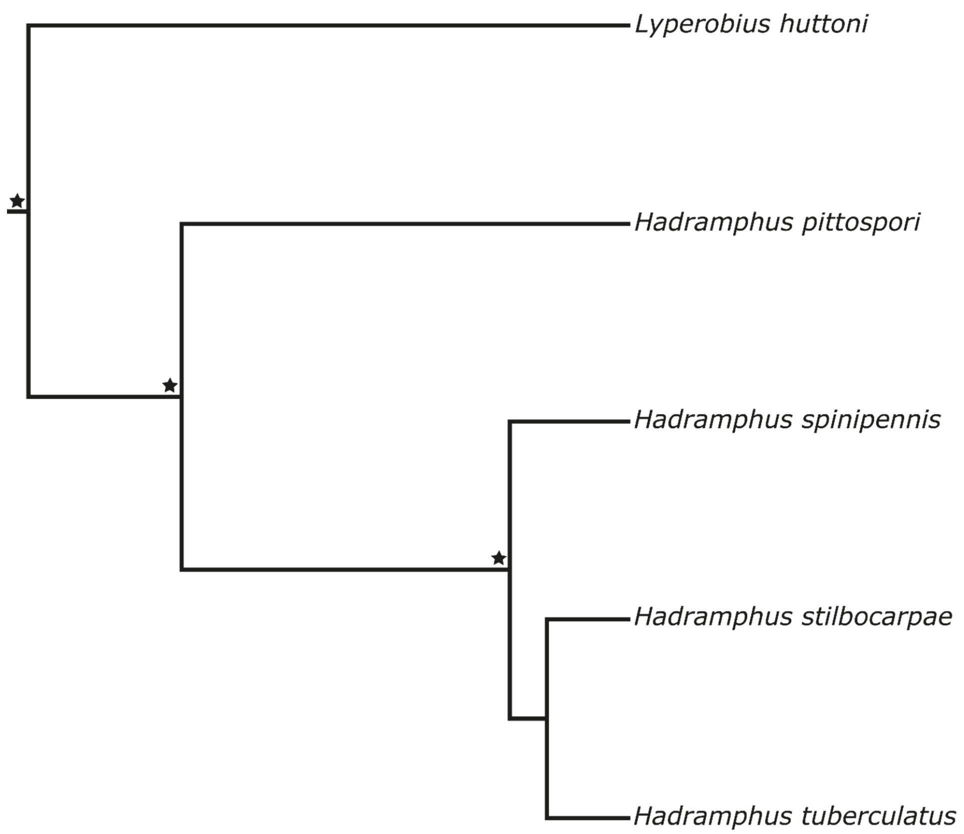

Figure 2. Multi-locus coalescent species tree built from COI and ITS2 gene trees. The stars represent nodes supported with a posterior probability of one.

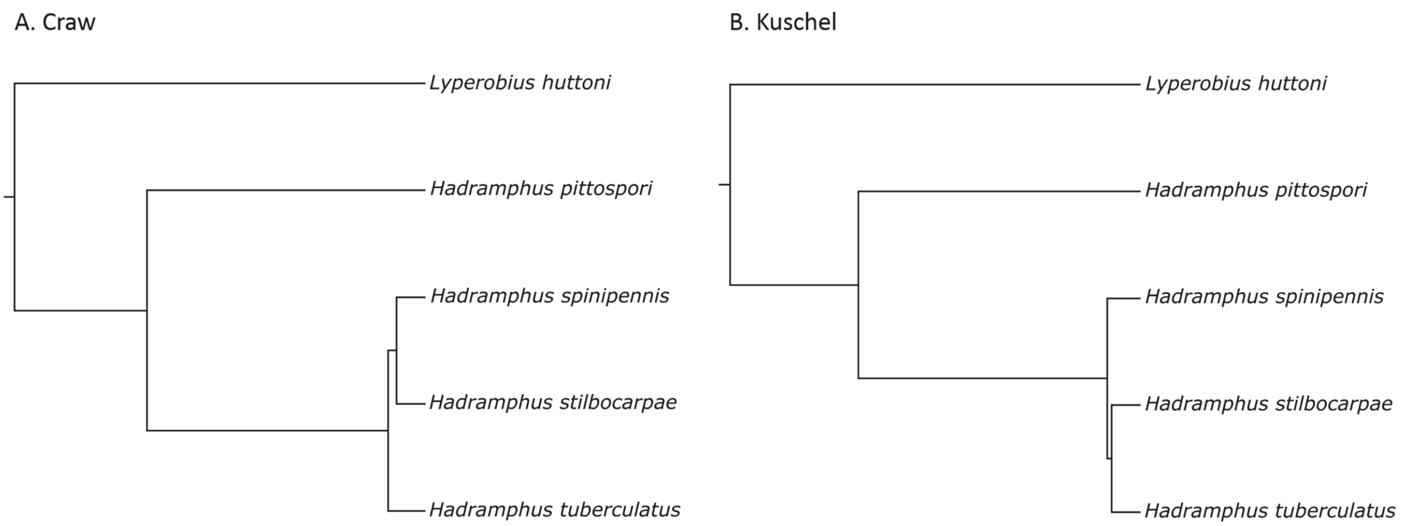

Figure 3. Multi-locus coalescent species trees with morphological characteristics included in the analysis: (**A**) morphological characteristics based on Craw [18], (**B**) morphological characteristics based on Kuschel [26,42]. All nodes except for the most recent, *stilbocarpae* and *spinipennis* (**A**) and *tuberculatus* and *stilbocarpae* (**B**), are supported with posterior probabilities of one.

In the morphological analysis, the species' trees converged on two different topologies (Figure 3). Both the Craw and Kuschel species trees supported the placement of *H. pittospori* as the sister group of the remaining three *Hadramphus* species (posterior probability = 1). The results of the path sampling analysis supported the species delimitations of the Kuschel phylogeny (marginal L estimate = −2990.32 for Kuschel and −2996.07 for Craw).

4. Discussion

We present the first phylogenetic species tree for the endemic genus *Hadramphus* using a multilocus coalescent approach. When combining morphological characteristics, we found support for the taxonomic classification for *H. pittospori* originally suggested by Kuschel [26].

Despite sequencing only two specimens of *H. pittospori*, the nucleotide diversity within the species was greater when compared to the within-species diversity of the other species. The high diversity within the species may be a result of differences in the time of collection. DNA was extracted and amplified from one specimen shortly after collection in 2009, whereas the other specimen was collected in 1981. Captive rearing of *H. pittspori* has shown that the weevil takes over a year from hatching to pupate into an adult and will survive 2–3 years as an adult [45], suggesting a possible generation time of 1 year. Therefore, at least 30 generations passed between the collection of the *H. pittospori* samples, allowing for multiple mutations to occur and possibly resulting in the high genetic diversity between the two samples. Although DNA damage is common in historical samples, we do not feel this contributed to the differences in the sequences. Each sequence returned had an open-reading frame, which is expected for COI, and all samples were amplified and sequenced three times with each replicate returning identical results, suggesting no deamination or oxidative damage [46]. The high nucleotide diversity in *H. pittospori* may also be a result of the fine scale population structure as one specimen was collected from Aorangi Island and the other specimen was collected from the Poor Knights Islands, with no specific island identified. Increasing the sample size in future studies will help to determine if the nucleotide diversity is a result of population structure or a relic of small sample size or historical sampling. Overall, the within-species nucleotide diversity is consistent with other large-bodied, flightless weevils (e.g., Galápagos weevils, [47]).

The COI genetic distance between *H. pittospori* and the other three *Hadramphus* species ranged from 0.27–0.29, which was greater than the distance of *H. stilbocarpae, H. spinipennis,* and *H. tuberculatus* to the outgroup *L. huttoni* (0.20–0.21). The genetic distance amongst these three species ranged from 0.05–0.07, suggesting that *H. pittospori* is as distantly related as another genus to the other *Hadramphus* species. One of the thresholds in DNA barcoding is that the genetic divergence between species should be 10 times greater than the within-species divergence [48]. Given this criterion, the divergence between *H. pittspori* and the other species in *Hadramphus* is at least 20 times greater than the within-species divergence, further supporting the distant relationship of *H. pittospori* to the rest of *Hadramphus*.

The COI and ITS2 ML gene trees were mostly congruent, except for *H. stilbocarpae*, being paraphyletic in ITS2. Nonmonophyly in closely related species is well documented in insects [49] and the slower mutation rates in nuclear genes may result in incomplete lineage sorting in recently diverged species. The COI gene tree from the StarBEAST analysis matches the ML COI tree; however, that in the Bayesian ITS2 tree, *H. stilbocarpae*, was not paraphyletic. The most recent common ancestor for *H. pittospori* and the other three *Hadramphus* species was during the late Oligocene–early Miocene period and the most recent common ancestor for *H. spinipennis*, *H.stilbocarpae* and *H. tuberculatus* was in the late Miocene (6.12 MYA), suggesting that the *H. pittospori* lineage has diverged from the rest of *Hadramphus* for an evolutionary long period. Although we used the molecular rate for COI for polyphaga [44], rates of molecular evolution can differ between lineages and across timescales [50]; therefore, the common ancestor times should be viewed with caution. Although the lack of taxon sampling makes the resolution of taxonomy difficult [51], our study provides insight into the phylogenetic structure of the genus *Hadramphus*, which is currently recognized to contain only four species. Future studies would benefit from wider taxon sampling of Molytini in New Zealand and the use of fossil or geological dating, such as the rise of Poor Knights Islands and the Chatham Islands, for calibration.

The taxonomic tree based on morphological characters presented by Craw [18] placed all four *Hadramphus* species into a well-supported clade; however, the genetic data does not fully support the morphological character tree. Originally, *H. pittospori* was placed into its own genus, *Karocolens* [26], until it was incorporated into *Hadramphus* in 1999 [18]. The genetic phylogeny suggests that *H. pittospori* may not be part of the genus *Hadramphus* due to the large amount of genetic variation between *H. pittospori* and the other *Hadramphus* species. Indeed, the amount of genetic variation between *H. pittospori* and *Hadramphus* is similar to that between *Lyperobius* and *Hadramphus* and suggests that *H. pittospori* may not belong in the *Hadramphus* genus. Depending on which morphological characters are chosen for phylogenetic analysis, the traits may be biased depending on whether the characters of interest are chosen to be included or removed from the data [52]. In Craw [18], he states there are some unique characters remaining that separate *H. pittospori* from other *Hadramphus* species, such as the prothorax being as, or nearly as, long as it is wide and diverging into a straight line. The remaining characteristics separating *H. pittospori* may be more important to the evolutionary history of the species and should be analysed in more detail. Indeed, when modelling the morphological characteristics with the genetic data, those characters considered important by Kuschel [26] are supported over those emphasised by Craw [18].

The phylogenetic relationship between *H. tuberculatus, H. spinipennis* and *H. stilbocarpae* in the genetic trees differs from that of the morphology-based tree in which *H. spinipennis* and *H. stilbocarpae* were considered sister taxa. Morphological characteristics, such as low median rostral carina and a distinctive tubercle on interval 3 of the elytra declivity [18], placed *H. spinipennis* and *H. stilbocarpae* as sister species. Goldberg and Trewick [27] reported *H. spinipennis* and *H. tuberculatus* to be sister taxa based on the results of their COI Bayesian tree. In our study, *H. tuberculatus* is shown to be a sister taxon to *H. stilbocarpae*; however, the relationship is only supported by a posterior probability of 0.71. A difference in phylogenetic trees inferred from morphological and molecular data has been reported for other species in New Zealand. For example, the beetle genus *Prodontria* showed marked differences in its molecular and morphological phylogenetic trees [53]. In particular, the sister-species relationship of the group *P. modesta* and *P. lewisi* to *P. capito* was unsupported.

This study provides clarification on the taxonomic groupings in the genus *Hadramphus*. The phylogeny provides an indication of evolutionary relationships that were not predicted based on morphology alone. Based on the genetic data and the supported morphological description of *H. pittospori* by Kuschel [26], we are reinstating the genus *Karocolens*, consisting of a single species, *K. pittospori*, as originally described by Kuschel [26]. The four species in *Hadramphus* range from protected to critically endangered and are all managed by the Department of Conservation. By combining the evolutionary history of species with their taxonomy rather than relying on morphology alone, more evidence-based decisions can be made regarding their conservation status.

Supplementary Materials: The following are available online at http://www.mdpi.com/1424-2818/10/3/88/s1. Supplementary Material 1: Additional methods used for the extraction of DNA from the museum specimen of *H. pittospori*. Supplementary Material 2: A list of GenBank accession numbers for sequences obtained from GenBank and also the accession numbers for the new sequences from this study. Supplementary Material 3: The morphological characteristics defined by Craw [18] and Kuschel [26] used in the Bayesian analyses.

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References

1. Frankham, R. Challenges and opportunities of genetic approaches to biological conservation. *Biol. Conserv.* **2010**, *143*, 1919–1927. [CrossRef]
2. Yeates, D.K.; Seago, A.; Nelson, L.; Cameron, S.L.; Joseph, L.; Trueman, J.W. Integrative taxonomy, or iterative taxonomy? *Syst. Entomol.* **2011**, *36*, 209–217. [CrossRef]
3. Dayrat, B. Towards integrative taxonomy. *Biol. J. Linn. Soc.* **2005**, *85*, 407–415. [CrossRef]
4. Fujita, M.K.; Leaché, A.D.; Burbrink, F.T.; McGuire, J.A.; Moritz, C. Coalescent-based species delimitation in an integrative taxonomy. *Trends Ecol. Evol.* **2012**, *27*, 480–488. [CrossRef] [PubMed]
5. Scotland, R.W.; Olmstead, R.G.; Bennett, J.R. Phylogeny reconstruction: The role of morphology. *Syst. Biol.* **2003**, *52*, 539–548. [CrossRef] [PubMed]
6. Vink, C.J.; Sirvid, P.J.; Malumbres-Olarte, J.; Griffiths, J.W.; Paquin, P.; Paterson, A.M. Species status and conservation issues of New Zealand's endemic *latrodectus* spider species (Araneae: Theridiidae). *Invertebr. Syst.* **2008**, *22*, 589–604. [CrossRef]
7. Edwards, S.V. Is a new and general theory of molecular systematics emerging? *Evolution* **2009**, *63*, 1–19. [CrossRef] [PubMed]
8. Sukumaran, J.; Knowles, L.L. Multispecies coalescent delimits structure, not species. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, 1607–1612. [CrossRef] [PubMed]
9. Sharma, P.P.; Fernández, R.; Esposito, L.A.; González-Santillán, E.; Monod, L. Phylogenomic resolution of scorpions reveals multilevel discordance with morphological phylogenetic signal. *Proc. R. Soc. Lond. B Biol. Sci.* **2015**, *282*, 20142953. [CrossRef] [PubMed]
10. Vuataz, L.; Sartori, M.; Gattolliat, J.-L.; Monaghan, M.T. Endemism and diversification in freshwater insects of madagascar revealed by coalescent and phylogenetic analysis of museum and field collections. *Mol. Phylogen. Evol.* **2013**, *66*, 979–991. [CrossRef] [PubMed]
11. Rutschmann, S.; Gattolliat, J.L.; Hughes, S.J.; Báez, M.; Sartori, M.; Monaghan, M.T. Evolution and island endemism of morphologically cryptic *baetis* and *cloeon* species (ephemeroptera, baetidae) on the canary islands and madeira. *Fresh. Biol.* **2014**, *59*, 2516–2527. [CrossRef]
12. Vitecek, S.; Kučinić, M.; Previšić, A.; Živić, I.; Stojanović, K.; Keresztes, L.; Bálint, M.; Hoppeler, F.; Waringer, J.; Graf, W. Integrative taxonomy by molecular species delimitation: Multi-locus data corroborate a new species of Balkan Drusinae micro-endemics. *BMC Evol. Biol.* **2017**, *17*, 129. [CrossRef] [PubMed]
13. Winterbourn, M.; Knox, G.; Burrows, C.; Marsden, I. *The Natural History of Canterbury*, 3rd ed.; Canterbury University Press: Christchurch NZ, New Zealand, 2008; p. 923.
14. Cooper, R.A.; Millener, P.R. The New Zealand biota-historical background and new research. *Trends Ecol. Evol.* **1993**, *8*, 429–433. [CrossRef]
15. Caldecott, J.O.; Jenkins, M.D.; Johnson, T.H.; Groombridge, B. Priorities for conserving global species richness and endemism. *Biodivers. Conserv.* **1996**, *5*, 699–727. [CrossRef]
16. Gillespie, R.G.; Roderick, G.K. Arthropods on islands: Colonization, speciation, and conservation. *Annu. Rev. Entomol.* **2002**, *47*, 595–632. [CrossRef] [PubMed]
17. Myers, N.; Mittermeier, R.A.; Mittermeier, C.G.; Da Fonseca, G.A.; Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **2000**, *403*, 853. [CrossRef] [PubMed]
18. Craw, R.C. *Fauna of New Zealand: Molytini Number 39*; Manaaki Whenua Press: Lincoln, Canterbury, New Zealand, 1999; p. 68.
19. Young, L.M.; Marris, J.W.M.; Pawson, S. Back from extinction: Rediscovery of the canterbury knobbled weevil *Hadramphus tuberculatus* (pascoe 1877) (Coleoptera: Curculionidae), with a review of its historical distribution. *N. Z. J. Zool.* **2008**, *35*, 323–330. [CrossRef]
20. Kuschel, G.; Worthy, T.H. Past distribution of large weevils (Coleoptera: Curculionidae) in the South Island, New Zealand, based on holocene fossil remains. *N. Z. Entomol.* **1996**, *19*, 15–22. [CrossRef]
21. Fountain, E.D.; Wiseman, B.H.; Cruickshank, R.H.; Paterson, A.M. The ecology and conservation of *Hadramphus tuberculatus* (pascoe 1877) (Coleoptera: Curculionidae: Molytinae). *J. Insect Conserv.* **2013**, *17*, 737–745. [CrossRef]

22. Fountain, E.D.; Pugh, A.R.; Wiseman, B.H.; Smith, V.R.; Cruickshank, R.H.; Paterson, A.M. Captive rearing of the endangered weevil *Hadramphus tuberculatus* (pascoe, 1877) (Coleoptera: Curculionidae: Molytinae) for ex-situ conservation. *N. Z. Entomol.* **2016**, *39*, 23–32. [CrossRef]
23. Schöps, K.; Wratten, S.D.; Emberson, R.M. Life cycle, behaviour and conservation of the large endemic weevil, *Hadramphus spinipennis* on the Chatham Islands, New Zealand. *N. Z. J. Zool.* **1999**, *26*, 55–66. [CrossRef]
24. Fountain, E.D.; Malumbres-Olarte, J.; Cruickshank, R.H.; Paterson, A.M. The effects of island forest restoration on open habitat specialists: The endangered weevil *hadramphus spinipennis* broun and its host-plant *Aciphylla dieffenbachii* kirk. *PeerJ* **2015**, *3*, e749. [CrossRef] [PubMed]
25. Thomas, B.W.; Meads, M.; Notman, P.R. *A Report on the Restoration of Knobbled Weevils (Hadramphus stilbocarpae) and Flax Weevils (Anagotus fairburni) to Breaksea Island, Breaksea Sound, Fiordland*; DSIR Land Resources: Lower Hutt, New Zealand, 1992; p. 30.
26. Kuschel, G. The subfamily Molytinae (Coleoptera: Curculionidae): General notes and descriptions of new taxa from New Zealand and Chile. *N. Z. Entomol.* **1987**, *9*, 11–29. [CrossRef]
27. Goldberg, J.; Trewick, S.A. Exploring phylogeographic congruence in a continental island system. *Insects* **2011**, *2*, 369–399. [CrossRef] [PubMed]
28. Folmer, O.; Black, M.; Hoeh, W.; Lutz, R.; Vrijenhoek, R. DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol.* **1994**, *3*, 294–299. [PubMed]
29. Hajibabaei, M.; Janzen, D.H.; Burns, J.M.; Hallwachs, W.; Hebert, P.D.N. DNA barcodes distinguish species of tropical lepidoptera. *Proc. Natl. Acad. Sci. USA* **2006**, *103*, 968–971. [CrossRef] [PubMed]
30. Johnson, M.; Zaretskaya, I.; Raytselis, Y.; Merezhuk, Y.; McGinnis, S.; Madden, T. Ncbi blast: A better web interface. *Nucleic Acids Res.* **2008**, *36*, 5–9. [CrossRef] [PubMed]
31. Kumar, S.; Stecher, G.; Tamura, K. Mega7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Mol. Biol. Evol.* **2016**, *33*, 1870–1874. [CrossRef] [PubMed]
32. Löytynoja, A.; Goldman, N. Webprank: A phylogeny-aware multiple sequence aligner with interactive alignment browser. *BMC Bioinform.* **2010**, *11*, 579. [CrossRef] [PubMed]
33. Rozas, J.; Ferrer-Mata, A.; Sánchez-DelBarrio, J.C.; Guirao-Rico, S.; Librado, P.; Ramos-Onsins, S.E.; Sánchez-Gracia, A. Dnasp 6: DNA sequence polymorphism analysis of large data sets. *Mol. Biol. Evol.* **2017**, *34*, 3299–3302. [CrossRef] [PubMed]
34. Darriba, D.; Taboada, G.L.; Doallo, R.; Posada, D. Jmodeltest 2: More models, new heuristics and parallel computing. *Nat. Methods* **2012**, *9*, 772. [CrossRef] [PubMed]
35. Zharkikh, A. Estimation of evolutionary distances between nucleotide sequences. *J. Mol. Evol.* **1994**, *39*, 315–329. [CrossRef] [PubMed]
36. Ogilvie, H.A.; Drummond, A.J. StarBEAST2 brings faster species tree inference and accurate estimates of substitution rates. *Mol. Biol. Evol.* **2017**, *34*, 2101–2114. [CrossRef] [PubMed]
37. Bouckaert, R.; Heled, J.; Kühnert, D.; Vaughan, T.; Wu, C.H.; Xie, D.; Suchard, M.A.; Rambaut, A.; Drummond, A.J. BEAST 2: A software platform for bayesian evolutionary analysis. *PLoS Comput. Biol.* **2014**, *10*, e1003537. [CrossRef] [PubMed]
38. Bouckaert, R.R.; Drummond, A.J. Bmodeltest: Bayesian phylogenetic site model averaging and model comparison. *BMC Evol. Biol.* **2017**, *17*, 42. [CrossRef] [PubMed]
39. Rambaut, A.; Suchard, M.A.; Xie, D.; Drummond, A. Tracer v1.6. 2014. Available online: http://beast.bio.ed.ac.uk/Tracer.
40. Baele, G.; Lemey, P.; Bedford, T.; Rambaut, A.; Suchard, M.A.; Alekseyenko, A.V. Improving the accuracy of demographic and molecular clock model comparison while accommodating phylogenetic uncertainty. *Mol. Biol. Evol.* **2012**, *29*, 2157–2167. [CrossRef] [PubMed]
41. Rambaut, A. *Figtree v1. 4. Molecular Evolution, Phylogenetics and Epidemiology*; University of Edinburgh: Edinburgh, UK, 2012.
42. Kuschel, G. Entomology of the Aucklands and other Islands South of New Zealand: Coleoptera: Cuculionidae. *Pac. Insects Monogr.* **1971**, *27*, 225–259.
43. Lewis, P.O. A likelihood approach to estimating phylogeny from discrete morphological character data. *Syst. Biol.* **2001**, *50*, 913–925. [CrossRef] [PubMed]
44. Papadopoulou, A.; Anastasiou, I.; Vogler, A.P. Revisiting the insect mitochondrial molecular clock: The mid-aegean trench calibration. *Mol. Biol. Evol.* **2010**, *27*, 1659–1672. [CrossRef] [PubMed]

45. Bennett, B.G. Observations on rearing *Karocolens pittospori* (Coleoptera: Curculionidae: Molytinae). *N. Z. Entomol.* **1987**, *9*, 34–37. [CrossRef]
46. Gilbert, M.T.P.; Bandelt, H.-J.; Hofreiter, M.; Barnes, I. Assessing ancient DNA studies. *Trends Ecol. Evol.* **2005**, *20*, 541–544. [CrossRef] [PubMed]
47. Sequeira, A.S.; Stepien, C.C.; Sijapati, M.; Roque Albelo, L. Comparative genetic structure and demographic history in endemic galápagos weevils. *J. Hered.* **2012**, *103*, 206–220. [CrossRef] [PubMed]
48. Hickerson, M.J.; Meyer, C.P.; Moritz, C. DNA barcoding will often fail to discover new animal species over broad parameter space. *Syst. Biol.* **2006**, *55*, 729–739. [CrossRef] [PubMed]
49. Hendrich, L.; Pons, J.; Ribera, I.; Balke, M. Mitochondrial cox1 sequence data reliably uncover patterns of insect diversity but suffer from high lineage-idiosyncratic error rates. *PLoS ONE* **2011**, *5*, e14448. [CrossRef] [PubMed]
50. Ho, S.Y.; Lo, N. The insect molecular clock. *Aust. J. Entomol.* **2013**, *52*, 101–105. [CrossRef]
51. Gunter, N.L.; Oberprieler, R.G.; Cameron, S.L. Molecular phylogenetics of Australian weevils (Coleoptera: Curculionoidea): Exploring relationships in a hyperdiverse lineage through comparison of independent analyses. *Aust. Entomol.* **2016**, *55*, 217–233. [CrossRef]
52. Queiroz, K.D. Including the characters of interest during tree reconstruction and the problems of circularity and bias in studies of character evolution. *Am. Nat.* **1996**, *148*, 700–708. [CrossRef]
53. Emerson, B.C.; Wallis, G.P. Phylogenetic relationships of the *prodontria* (Coleoptera; Scarabaeidae; subfamily Melolonthinae), derived from sequence variation in the mitochondrial cytochrome oxidase II gene. *Mol. Phylogen. Evol.* **1995**, *4*, 433–447. [CrossRef] [PubMed]

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Article

The Problematic Genus *Sclerocardius* (Coleoptera: Curculionidae: Molytinae: Ithyporini)

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Abstract: The genus *Sclerocardius* is revised, using morphological characters. Four species are recognized, including *S. africanus* (Boheman), *S. bohemani* Schoenherr stat.rev., *S. indicus* Hartmann and *S. kuscheli* sp.nov. The species *Sclerocardius madecassus* Ferragu is synonymized with *S. bohemani* syn.nov., and *Charactocnemus hintzi* Hartmann is treated as a junior synonym of *S. bohemani*, not *S. africanus*. A key to species is given. Lectotypes are designated for *Heteramphus africanus* Boheman and *Sclerocardius africanus* Schoenherr. A female elytro-tergal stridulatory system involving the modification of the wing-binding patch of the seventh tergite is reported for the Sclerocardiina for the first time and supports the inclusion of the subtribe within the Ithyporini.

Keywords: *Sclerocardius*; Sclerocardiini; taxonomy; systematics; elytro-tergal stridulation

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1. Introduction

The genus *Sclerocardius* is an odd-looking weevil. With a huge rounded pronotum, elongate flanges on the fore tibiae, and a very narrow rostrum it looks like nothing else. Although it has been placed in the Ithyporini since 1935, this conveyed little about its relationships, since until relatively recently the tribe has been rather a dumping ground for taxa with a prosternal canal but no mesoventrite receptacle. The treatment by Alonso-Zarazaga & Lyal [1] as a subtribe of Ithyporini, followed by that of Lyal [2] as a separate tribe, indicates the continuing uncertainty as to its relationships. That is resolved in this paper.

There is some uncertainty about the names to be applied to the African species of *Sclerocardius*. The earlier-described species, *Heteropus africanus* Boheman, 1845, *Sclerocardius bohemani* Schoenherr, 1847 and *Charactocnemus hintzi* Hartmann, 1896, had all been synonymised and from 1897 have been known as *S. africanus*. Ferragu [3] described a new species, *Sclerocardius madecassus* from Madagascar, distinguishing it from *S. africanus* by external and internal characters. However, examination of a number of specimens from African countries identified as *S. africanus* revealed specimens with the same characters as described for *S. madecassus*, suggesting that this species is much more widely distributed than expected. This leads to a problem regarding which name to apply to which species. None of the descriptions of *S. africanus*, *H. bohemani* and *C. hintzi* provide sufficient information to distinguish between the two species which are hitherto known to occur, and the geographical distribution overlaps, so no name could be assigned with full confidence to any of the species. This problem is addressed below.

In addition to the two known African species a further species has been found in Angola. This is described below.

2. Materials and Methods

Descriptions are made on external and internal characters. Adult specimens were examined using a Zeiss SV11 stereomicroscope with a magnification of up to 6.4 and a ×2 additional objective;

dissected genitalia were examined using this and a Laborlux 12 compound microscope. Drawings were made using a camera lucida on each microscope. To examine the genitalia, specimens were relaxed in de-ionised water and heated on a Tecam Dri-Block DB-1. The abdomen was removed and warmed in 10% KOH solution to macerate the internal tissues. Following maceration, the abdomen was transferred to de-ionised water and the genitalia dissected out of the abdomen. After resting in the water to wash off the KOH the genitalia were transferred to glycerol for imaging and preservation, and the abdomen glued flat on a card pinned beneath the specimen, with the terga and sterna both visible. The genitalia were transferred into glycerol for imaging and preservation. Following examination and imaging, the dissected genitalia are preserved in glass microvials pinned beneath the rest of the specimen. Habitus photographs were taken using a Canon 5 dsR camera with a 100 mm macro lens. Terminalia were placed in a cavity microscope slide with glycerol or KY gel, and photographs were taken using a Canon EOS 55D camera attached to a Leica 125 stereomicroscope. Habitus and terminalia images were stacked using Helicon Focus stacking software. Images were cleaned using GIMP 2.8 software.

Specimen label transcriptions are written verbatim; lines on a label are separated by a slash: "/" (type specimens only) and different labels by the word "and".

Specimen length measurements were taken in lateral view along a straight line between the anterior and posterior of the structures concerned (see Figure 6 of Lyal & Curran [4]); the elytral length was taken from the anterior of the scutellum to the posterior extent of the elytra, the total length from the front of the head capsule to the posterior of the elytra. The pronotal width and elytral width refer to the maximum width of each. The morphological terminology follows Lyal [5].

The material examined is housed in the following collections, identified by the following codens:

BMNH—Natural History Museum, London, United Kingdom
NHRS—Naturhistoriska Riksmuseet, Stockholm, Sweden.
MTD—Museum für Tierkunde, Dresden, Germany

3. Taxonomy

3.1. Genus Sclerocardius Schoenherr, 1847

Sclerocardius Schoenherr, 1847:82 [6]

Type species: *Sclerocardius bohemani* Schoenherr, 1847 (original designation, combined description). Gender: Masculine

= *Heteropus* Schoenherr, 1845: 1 [7] (non Palisot de Beauvois, 1820, nec Fitzinger, 1826, nec Jourdan, 1837, nec Spinola, 1837, nec Germar, 1839, nec Laporte, 1840, nec Hodgson, 1843). (synonymised with *Sclerocardius* by Lacordaire 1865: 317 [8]).

Type species: *Heteropus africanus* Boheman, 1845 (original designation)

= *Charactocnemus* Hartmann, 1896: 185 [9] (synonymised with *Sclerocardius* by Hartmann, 1897 [10])

Type species: *Charactocnemus hintzi* Hartmann, 1896 (monotypy) = *Sclerocardius bohemani* Schoenherr, 1847

= *Charactonemus*: Hustache, 1936: 18 [11] (Unavailable name: Lapsus)

Description

Large (6–14 mm long) weevils (Figure 1A,B, Figure 10A,B, Figure 14A,B and Figure 19A,B), with bulbous pronotum, fore tibiae with dorso-posterior flanges (Figures 6A, 12A, 15A and 20A) and hind tibiae strongly expanded distally (Figures 6C, 12C, 15F and 20D).

Head. Rostrum (Figure 2A,B) longer than prosternum, slender (approximate width of fore tibia omitting tibial teeth) and compressed. Mandibles lacking teeth on internal face, closing anteriorly to rostrum and projecting in a triangle (Figure 2A and Figure 3). Labial palps with three palpomeres. Scrobe not visible dorsally, slanting ventrally from anterior end about halfway along rostrum to underneath rostrum near eyes, scrobes separated by narrow carina under rostrum. Antennae (Figure 2C) with seven antennomeres in funicle, 3–5 quadrate, 6–7 transverse and broadening to club but not joining with club; club oval, slightly flattened, all club antennomeres with short dense pilosity, sutures sinuate. Eyes very large, lateral, extending slightly underneath rostrum but not approaching one another ventrally; ommatidia separately convex.

Figure 1. *Sclerocardius africanus* (Boheman) lectotype: (**A**) habitus, dorsal, (**B**) habitus, lateral. Photographed by Gunvi Lindberg (© 2018 Naturhistoriska riksmuseet). Original photo cropped, light levels and contrast adjusted. Made available by the Swedish Museum of Natural History under Creative Commons Attribution 4.0 International Public License, CC-BY 4.0.

Thorax. Pronotum (Figures 1B, 10B, 14B and 19B) extending over head capsule, more or less convex dorsally in lateral aspect, more shallowly so in anterior aspect (Figure 3); notosternal suture well-marked, curved (Figure 2D). Prosternum (Figure 2D) with anterior margin emarginate; postocular lobes present; prothoracic rostral canal present, with lateral carina; procoxae separate, inner faces sometimes densely covered with long orange setae; sternellum depressed but post-coxal lamellae sometimes present and converging posteriorly immediately behind fore coxae to more or less close the gap between the coxae. Mesoventrite raised abruptly, anterior face weakly concave with weak lateral flanges directed anteriad. Metaventrite not depressed anteriorly; metanepisternal suture complete, sclerolepidia absent; metepimeron not fused to metanepisternum, concealed by elytron. Sclerolepidia absent. Elytra with basal margin concave; humeri developed; interstria III meeting interstria IX but not VI or VIII; submarginal fold pocket not broad; hind wings present, large. Elytro-tergal stridulatory structures present in male but not in females of all species; male elytral stridulatory file elongate and broad, near sutural margin. Femora with ventral tooth present, single, or absent. Fore tibia extended dorso-posteriorly into two large convex flattened lobes, one subapical and another medial, sometimes with a smaller prominence nearer the base (Figures 6A, 12A, 15A,D and 20A); uncus present, flattened; pre-mucro present; adventitious dorsal tooth sometimes present near apex; apical margin not distinct from inner flange, anterior setal comb absent; posterior apical setal comb on fore tibia curved round tarsal insertion. Mid tibia with premucro present or absent, uncus present, one or two dorsal adventitious teeth present apically, inner flange united with anterior apical margin and anterior apical setal comb on distal part of tibia. Hind tibiae with anterior apical setal comb broadened and developed into patch filling apical concavity between anterior apical margin and inner flange or, (*S. kuscheli*) not distinguishable from other setae and anterior apical margin not distinct from inner flange; inner flange where distinct developed into two or more flattened lobes (Figures 6C, 12C, 15F and 20D). Fifth tarsomere with ventral flat projection between and beneath base of claws. Tarsal claws simple, free and divaricate.

Abdomen. Abdominal tergites sclerotized. Pygidium not exposed in female; male apex of TVIII ventrally visible beyond emarginate posterior margin of ventrite 5. Male with elytro-tergal stridulation plectrum on tergite 7 as a pair of ridges on posterior margin (Figure 7A, Figure 12D and Figure 21A) or pair of plectral tubercles (Figure 16C); female wing-binding patches on tergite 7 not organised into file (Figures 7B, 12E and 21B) or with parallel arrangement on inner face (Figure 16A,B). Rectal loop present, weakly sclerotized, comprising six shallowly posteriorly-convex bands joining weak nodes.

Male terminalia. Sternite VIII entire, not separated into two hemisternites. Spiculum gastrale nearly straight, basal arms narrow and symmetrical. Tegmen with apodeme shorter or longer than diameter of ring; ring incomplete; parameroid lobes absent. Penis tubular, dorsally sclerotized, ostium opening posteriorly with apex extending posteriad ventrally (Figure 8D,E) or ostium opening more dorsally (Figure 17D,E), apodemes longer or shorter than body; endophallus lacking flagellum.

Female terminalia. Tergite VIII longer than wide, sides subparallel, posterior margin medially emarginate, convex on either side of emargination. Spiculum ventrale Y-shaped (Figures 9C and 13H) or V-shaped, with basal arms subparallel, converging toward apex (Figures 18C and 23C). Gonocoxites entire or with anterior unpigmented region, with elongate styli present; small tubular accessory gland sometimes present at base of each gonocoxite. Bursa at least as long as vagina, sometimes with large balloon-like anterior portion; membranous tubular extension from bursa to meet common oviduct (Figures 9E and 23D), or oviduct arising on membranous area separated from rest of bursa by sclerite (Figure 18D); spermathecal duct arising near common oviduct. Spermatheca with elongate conical sclerotized duct lobe, smaller conical sclerotized gland lobe.

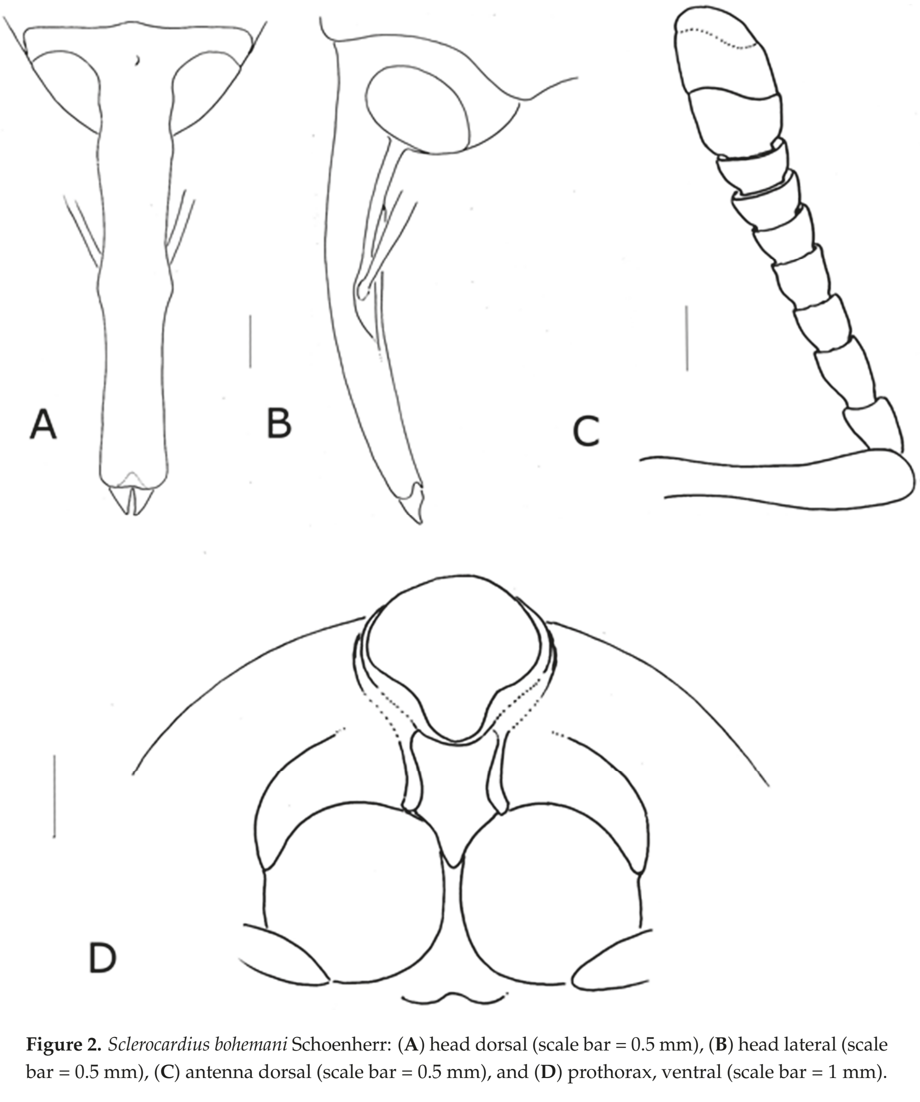

Figure 2. *Sclerocardius bohemani* Schoenherr: (**A**) head dorsal (scale bar = 0.5 mm), (**B**) head lateral (scale bar = 0.5 mm), (**C**) antenna dorsal (scale bar = 0.5 mm), and (**D**) prothorax, ventral (scale bar = 1 mm).

Figure 3. *Sclerocardius bohemani* Schoenherr: head and prothorax, anterior (holotype of *Charactocnemus hintzi* Hartmann). Photograph by Marc Srour (Museum für Tierkunde).

Distribution

Angola, Democratic Republic of Congo, Ethiopia, Malawi, Mozambique, Nigeria, Senegal, Sierra Leone, South Africa, Swaziland, Tanzania, Togo, Zaire, Zambia, Zimbabwe; Madagascar; Sumatra.

Comments

Sclerocardius is the only genus placed in the subtribe Sclerocardiina. As discussed below, there is no other known genus that is morphologically similar, although there are indications that *Ithyporus* may be a close relative. The form of the body and the fore tibiae and the lack of a mesoventrite receptacle serve to distinguish species from any other currently known weevil.

Heteropus Schoenherr, 1845 is a junior homonym of *Heteropus* Palisot de Beauvois, 1805, leading Lacordaire 1865: 318 [8] to use the next available name, *Sclerocardius* Schoenherr, 1847. Schoenherr [7] attributed the genus *Heteropus* to Chevrolat, although there is no evidence that Chevrolat ever published the name. Subsequently, Schoenherr [6] stated that he had not seen *Heteropus*, so he may have taken the 1845 description from an unpublished source. However, authorship of the name rests with Schoenherr 1845.

In species where more extensive series are available for study, the uncus and sometimes premucro were much more acuminate in the younger specimens, suggesting wear with the age of the beetle.

The form of the tibiae in particular suggests digging, and the large prothorax in particular suggests housing for enlarged leg muscles. The biology of adults and larvae is unknown, however.

Key to the species of *Sclerocardius*

1. Striae with large elongate foveae; interstriae lacking regular transverse creases (Figure 4A); hind tibia more than twice as long as maximum width, not strongly curved posteriad, anterior margin revealing internal flange (Figure 6C) 2

\- Striae with no large foveae, interstriae with more or less regular transverse creases, giving an appearance of rectangular blocks (Figure 4B); hind tibia less than twice as long as maximum width, strongly curved posteriad, internal flange concealed by anterior margin (Figure 15B) Angola . . . .***Sclerocardius kuscheli* sp. nov.**

2. Scales on pronotum absent, setiform or, if present and broader, less or only slightly longer than diameter of basal puncture and not or only just projecting above it (Figures 1A and 10A). Male with single small rounded tooth projecting from postero-ventral side of fore tibia (Figure 6A) (none in female). Africa, Madagascar. 3

\- Scales on pronotum and elytra bright orange, many at least twice as long as the diameter of the basal puncture and almost all projecting beyond it (Figure 19A). Male with several small rounded teeth projecting from postero-ventral side of fore tibia (Figure 20B) (none in female). Sumatra . . . . (***Sclerocardius indicus* Hartmann**)

3. Pronotum punctate on disc, posteriorly punctures sometimes confluent and separated by raised irregular transverse ridges (Figure 1); penis body three-quarters the length of its apodemes, penis body length more than 2.6 times its maximum width (Figure 8D) Africa. . . . . ***Sclerocardius africanus* (Boheman)**

\- Pronotum with raised irregular ridges between punctures posteriorly and extending onto disc (Figure 10A); penis body half the length of its apodemes, penis body length not more than 2.1 times its maximum width (Figure 13D) Africa, Madagascar. ***Sclerocardius bohemani* Schoenherr**

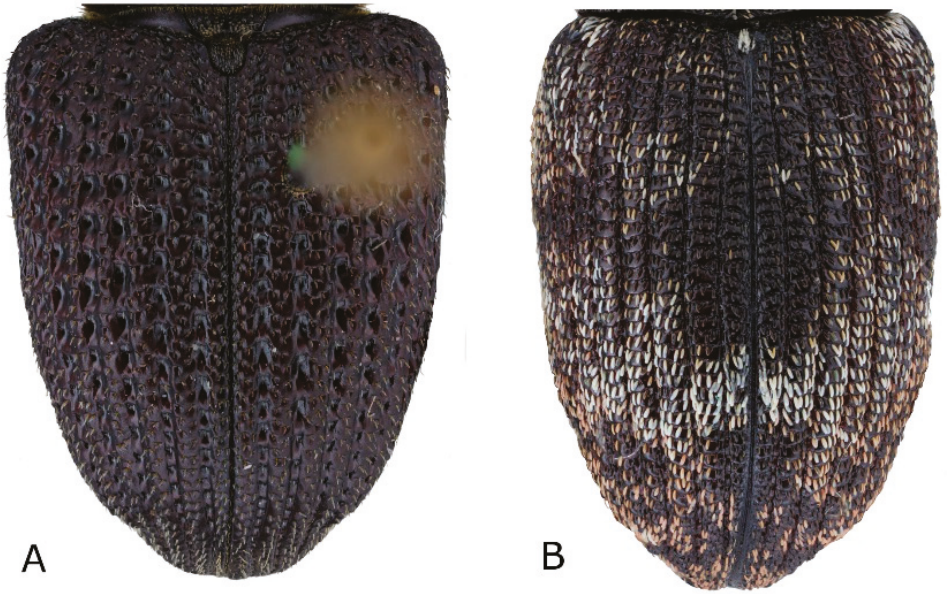

Figure 4. *Sclerocardius* spp., elytra: (**A**) *Sclerocardius africanus*, and (**B**) *Sclerocardius kuscheli*.

3.2. Sclerocardius africanus (Boheman, 1845)

Heteropus africanus Boheman in Schoenherr, 1845: 3 [7] (non *H. africanus* Palisot de Beauvois, 1805 [12])

Description

Figure 1, Figure 4A, Figure 5, Figure 6, Figure 7, Figure 8 and Figure 9.

Figure 5. *Sclerocardius africanus* (Boheman): lectotype, ventral. Photographed by Gunvi Lindberg (© 2018 Naturhistoriska riksmuseet). Original photo cropped, light levels and contrast adjusted. Made available by the Swedish Museum of Natural History under Creative Commons Attribution 4.0 International Public License, CC-BY 4.0.

Length 9.1–12.5 mm (mean 10.7 mm, *n* = 17); Pronotal width 2.9–5.5 mm (mean 4.6 mm, *n* = 17); Elytral width 3.5–6.56 mm (mean 5.6 mm, *n* = 17); males and females not significantly different in size.

Derm black, not developed into prominences or tubercles. Scales small, inconspicuous, pale or orange, rarely longer than the punctures in which they arise, not forming clear patterns. Setae longer and slender laterally on elytra and metathorax, on coxae, and ventrally on tibiae and femora (Figures 5 and 6A).

Head. Rostrum weakly curved, similar in males and females, strongly punctate laterally along most of its length, strongly to sparsely punctate dorsally in basal half and sometimes distal to antenna, dorsal surface basal to antennae smooth between punctures or weakly raised into irregular longitudinal rounded ridges, especially dorso-laterally; each puncture with dark short setiform elongate scale, most visible laterally in dorsal view; abruptly narrowed lateroventrally before eyes to form weak notch. Head capsule densely punctate dorsally, each puncture with a very small setiform scale.

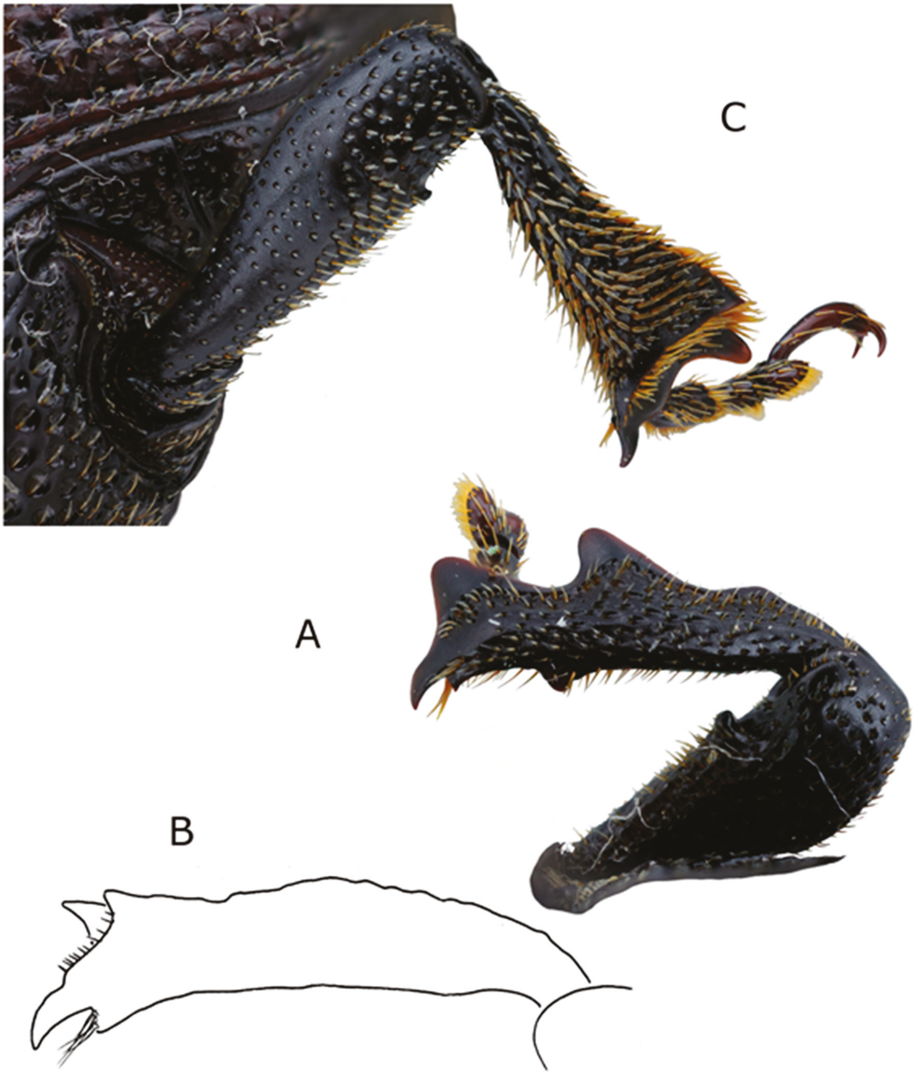

Figure 6. *Sclerocardius africanus* (Boheman): (**A**) fore tibia, male right showing postero-ventral tooth, (**B**) mid tibia, right antero-dorsal, and (**C**) hind tibia left anterior.

Thorax. Pronotum with length:width 0.83–1.00 (mean 0.89, *n* = 17), higher than long when length is taken as axis normal to height, strongly convex dorsally in lateral aspect (Figure 1B), more shallowly so in anterior aspect, punctate on disc with punctures separate, more posteriorly and laterally punctures sometimes confluent, and separated by irregular ridges running transversely on dorsum and more longitudinally laterally; anteriorly extending over head capsule (Figure 1A,B). Prothorax ventrally with deep narrow rostral canal with lateral carinae before fore coxae; fore coxae separate, with strong tuft of elongate orange scales on inner face (Figure 5); post-coxal lamellae present and converging posteriorly immediately behind fore coxae to more or less close the gap between coxae with bilobed wall. Elytra with length:width 1.1–1.40 (mean 1.34, *n* = 17); interstriae sometimes broad, sometimes distorted by very large strial punctures, these more or less rectangular (Figures 1A and 4A). Fore femora with small hooked femoral tooth in distal half (Figure 6A), other femora with smaller hook-like ventral tooth (Figure 6C). Fore tibia with postero-ventral tooth in male (Figure 6A), this absent in female; premucro prominent, uncus ventral on apex, acuminate in newly-emerged specimens, more rounded in older specimens, continuous with distal dorso-posterior lobe on posterior margin, dorso-posteriorly with three laminate asetose lobes, the distal two much larger than the basal one, which may be indistinct (Figure 6A). Mid tibia with dorsal margin somewhat irregular, premucro strong, long acuminate uncus and two dorsal apical teeth (Figure 6B). Hind tibial apex with premucro weak, inner flange bearing ventral acuminate uncus and more dorsal rounded tooth (Figure 6C).

Abdomen. Tergites 1–6 weakly sclerotised; 7 more strongly sclerotised. Male tergite VII fairly evenly sclerotised; plectral tubercles with setae not present, but posterior margin with a pair of small raised ridges which may function as a plectrum (Figure 7A). Female tergite VII with posterior margin biconcave and median abrupt emargination (Figure 7B); spines of wing-binding patches not oriented in parallel along inner margin.

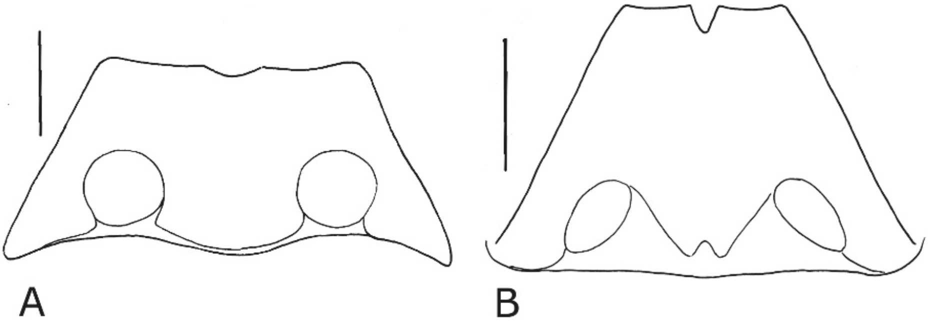

Figure 7. *Sclerocardius africanus* (Boheman): (**A**) tergite VII male, and (**B**) tergite VII female. Scale bars = 1 mm.

Male genitalia. Sternite VIII with two very weakly sclerotised lobes posteriorly, anterior of sclerite smoothly concave (Figure 8A). Spiculum gastrale Y-shaped, simple (Figure 8B). Tegmen with apodeme short, asymmetric (Figure 8C). Penis (Figure 8D–F) with body three-quarters the length of its apodemes, penis body length more than 2.6 times its maximum width; fully sclerotised; dorsally weakly concave; sides weakly convex anteriorly; ostium almost at right angles to long axis of penis body; small ventral projection anteriorly, anterior ventral margin with anteriad lobe, partially sclerotised (Figure 8F); endophallus with small cornet-shaped sclerite near gonopore

Female genitalia. Tergite VIII (Figure 9A) with posterior margin abruptly emarginate medially; approximately one-third as deep as wide (Figure 9B). Spiculum ventrale with posterior arms separate for two-thirds of length, with large membranous pouch between them, apodeme distinct anteriorly; posteriorly with numerous setae (Figure 9C). Gonocoxites entire, lacking median unpigmented area (Figure 9D). Vagina and bursa lacking pigmented area around junction with common oviduct and spermathecal duct; common oviduct and spermathecal duct arising separately from ventral membranous lobe of vagina (Figure 9E).

Distribution

South Africa, Sierra Leone, Ivory Coast, Togo, Zambia, Tanzania, Nigeria, Angola.

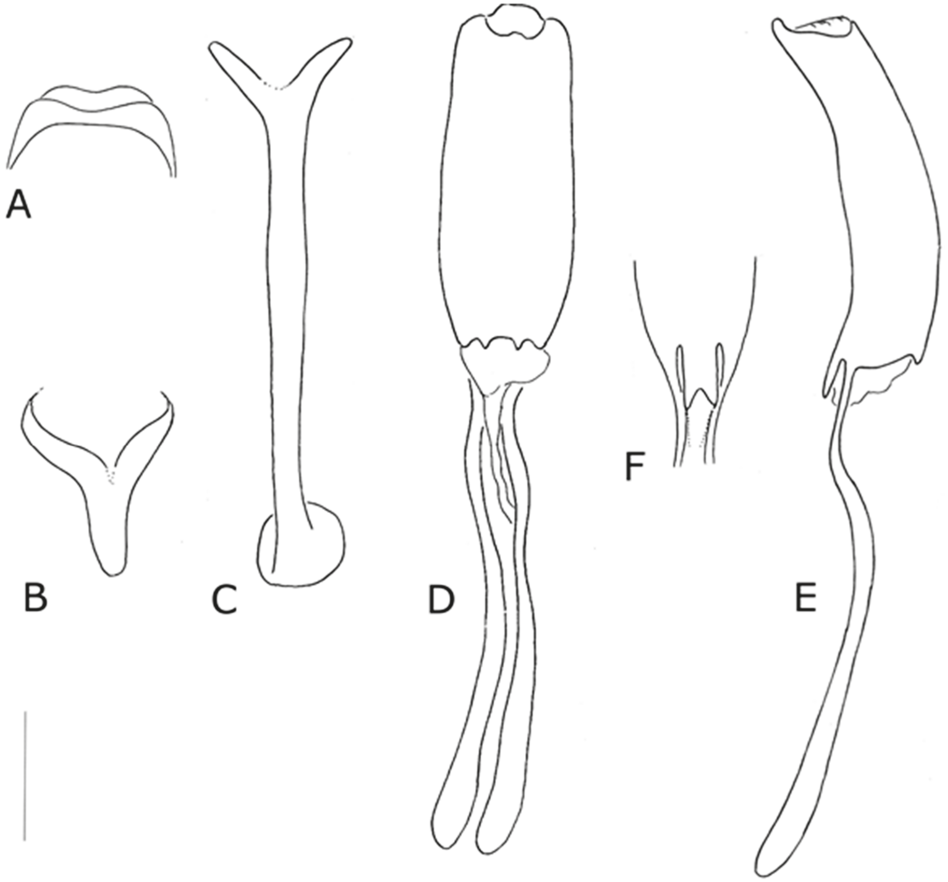

Figure 8. *Sclerocardius africanus* (Boheman), male terminalia: (**A**) sternite VIII, ventral, (**B**) tegmen, dorsal, (**C**) spiculum gastrale, ventral, (**D**) penis, dorsal, (**E**) penis, lateral, and (**F**) penis, anterior ventral margin. Scale bar = 1 mm.

Comments

The characters distinguishing this species from *S. bohemani* are discussed under that species. Both species differ from *S. kuscheli* in having a much more convex pronotal profile, shorter dorsal scales, much broader elytral striae with large punctures, and a separate inner flange on the hind tibia. *Sclerocardius indicus* can be distinguished by the much longer orange scales.

The species was originally described under the homonymic genus name *Heteropus*. Although *Heteropus africanus* Boheman, 1845 has the same name string as *Heteropus africanus* Palisot de Beauvois, 1805, they are not homonyms, since they were not originally established in combination with the same generic name (Articles 53.3 and 57.8.1).

The earlier synonymies of *Sclerocardius bohemani* Schoenherr and *Charactocnemus hintzi* Hartmann are rejected here; this is discussed under *S. bohemani* below.

Boheman did not indicate the original number of specimens seen. Only one specimen has been located with the appropriate data to be in the type series, and it is designated as lectotype here.

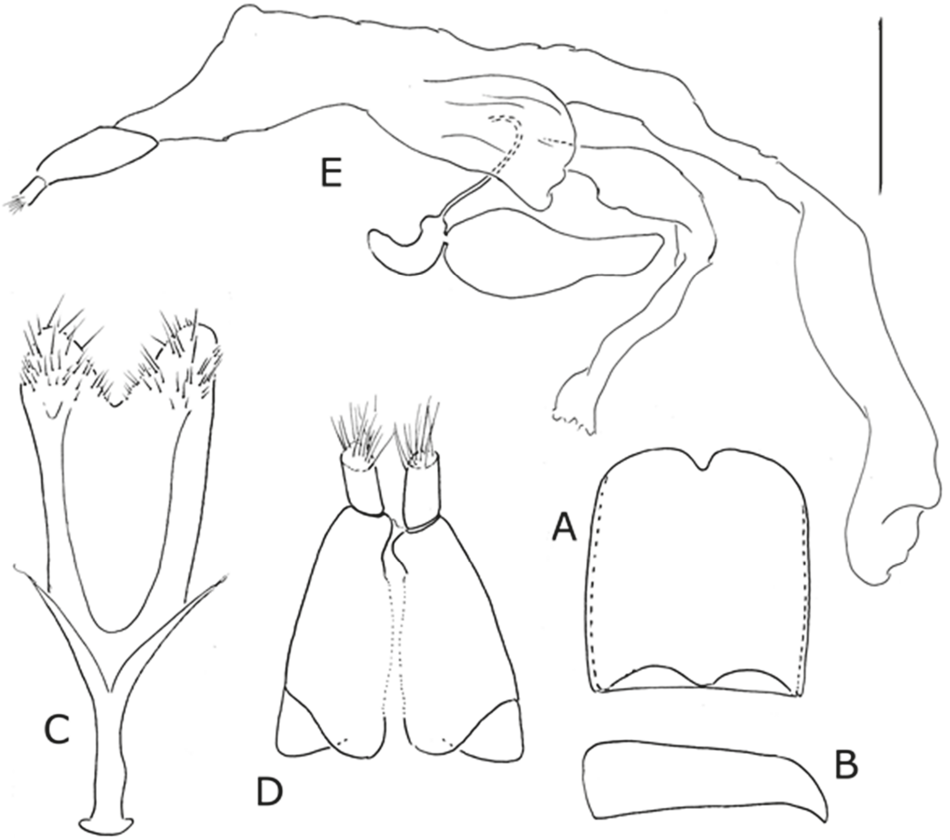

Figure 9. *Sclerocardius africanus* (Boheman), female terminalia: (**A**) tergite VIII, dorsal, (**B**) tergite VII, lateral, (**C**) spiculum ventrale, ventral, (**D**) gonocoxites, ventral, and (**E**) genitalia, lateral. Scale bar = 1 mm.

Specimens examined

LECTOTYPE ♂, here designated, with the labels: "Senegallia/Chevrol." [blue paper, handwritten] and [orange square] and "248." ["148" printed but '1′ with handwritten '2′ superimposed, pink paper] and "♂" [handwritten, white paper] and "7/83" [printed and handwritten, bright pink paper] and "Typus" [printed, red card] and "Riksmuseum / Stockholm" [printed, green paper] and "NHRS-GULI/000054255" [white card, printed] and "LECTOTYPE ♂/ *Heteropus africanus* / Boheman, 1845 / Lyal des. 2018" [printed, white paper] (NHRS). Other Material: South Africa: 1♂with the labels "Natal" and "E. Gowring-Scopes Collection" and "BMNH(E) 2005-4"; 1♂with the labels "Natal"and "23" and "Sclerocard. Bohemanni Sch. (sed Hete-ropi pertin et pot. and sp.)"; 1♀with the labels "[indecipherable] Krantzkloof Natal" and "Distant Coll. 1911-383" and 1 ♂with the labels "Pt. Natal" and "55.96"; 1♂with the labels "Rustenburg, Transvaal" and "Rustenburg [indecipherable]" and "Distant Coll. 1911-383". Angola: 1 ♂with the labels "at light" and "Angola (A36) Chianga 21–24.iii.1972" and "Southern African Exp." and "B.M. 1972-1" and "BMNH(E) 1237657". Zambia: 1 ♂with the labels "Zambia 1340m Jiwundu Swamp S11°51′54" E25°33′20" 21–24.ix.13 Light Trap. leg. Smith, R, & Takano, H. BMNH(E) 2013-71 1458902". Tanzania: 1 ♂with the label "Morogoro Tanganika territory 27.iii.21 N.C.E.Miller". Sierra Leone: 1 ♂with label "S. Leone Hill Station Nr. Freetown Oct. 1908 A. Pearse 1909-269"; 1 ♀with the label "S. Leone 6771"; 2 ♂♂with the labels "Sierra Leone Noala 17.viii.32 E. Hargreaves" and "G.A.K. Marshall Coll. B.M.1950-255". Ivory Coast:

1 ♀with labels “IVORY COAST 415m Telo Village outside Mt Sangbe NP 08°09′06.5″N 07°23′53.5″W” and “10-13.XI.15, Light Trap, Aristophanous, M., Moretto, P., Ruzzier, E. leg., BMNH(E) 2015-177” and “[QR code] 011218873”. Togo: 1 ♀with the labels “Atakpalwé Togo West viii 1981 R.J. Cooter” and “Brit. Mus 1982-259”. Nigeria: 1 ♀with the labels “M/V light White sheet” and “Nigeria Samaru 1–8. ix. 1970 P.H. Ward B.M. 1970-604”; 1 ♂with the labels “M/V light White sheet” and “Nigeria Samaru 13–20. vii. 1970 P.H. Ward B.M. 1970-604”. West Africa: 1 ♂Male: with the labels “W. Afr. Discove” and on the reverse “53 29”. Unknown: 1 ♂with the label “Sclerocardius africanus Boh Nya[indicipherable]a”.

3.3. *Sclerocardius bohemani Schoenherr, 1847*

Sclerocardius bohemani Schoenherr, 1847: 84 [6]

Sclerocardius africanus; Lacordaire, 1865: 317 [8]

= *Charactocnemus hintzi* Hartmann, 1896: 185 [9], synonymised with *S. africanus* by (Hartmann 1897 [10]); here removed from that synonymy and synonymised with *S. bohemani* Schoenherr, 1847 **syn. nov.**

= *Sclerocardius madecassus* Ferragu, 1990: 107 [3] **syn.nov.**

Description

Figure 2, Figure 3, Figure 10, Figure 11, Figure 12 and Figure 13.

Length 8.64–14.16 mm (mean 11.69 mm, $n = 32$); Pronotal width 3.44–6.4 mm (mean 5.02 mm $n = 32$); Elytral width 4.48–7.68 mm (mean 6.18 mm, $n = 32$), males and females not significantly different in size.

Derm black, not developed into prominences or tubercles. Scales small, inconspicuous, pale or orange, rarely longer than the punctures in which they arise, not forming clear patterns. Setae longer and more slender laterally on elytra and metathorax, on coxae, and ventrally on tibiae and femora.

Head. Rostrum weakly curved, similar in males and females, strongly punctate laterally along most of length, strongly punctate dorsally in basal two-thirds, dorsal surface basal to antennae weakly raised into irregular longitudinal rounded carinae especially dorso-laterally, detail differing between specimens; each puncture with dark or pale short setiform scale; rostrum sometimes with weak notch before eyes. Head capsule densely punctate dorsally, each puncture with very small setiform scale.

Thorax. Pronotum with length:width 0.86–0.94 (mean 0.87, $n = 32$), higher than long when length is taken as axis normal to height (Figure 10B), strongly convex dorsally in lateral aspect (Figure 10B), more shallowly so in anterior aspect (Figure 3), punctate on disc with punctures sometimes confluent, and separated by irregular ridges running transversely on dorsum and more longitudinally laterally; anteriorly extending over head capsule. Prothorax ventrally with deep narrow rostral canal with lateral carinae before fore coxae; fore coxae separate, with strong tuft of elongate orange scales on inner face; post-coxal lamellae present and converging posteriorly immediately behind fore coxae to more or less close gap between coxae with bilobed wall. Elytra with length:width 1.22–1.40 (mean 1.32, $n = 32$); interstriae sometimes broad, sometimes distorted by very large strial punctures, these more or less rectangular. Fore femora with small hooked femoral tooth in distal half, other femora with very weak inconspicuous ventral tooth. Fore tibia (Figure 12A) with postero-ventral tooth in male (Figure 6A), this absent in female; premucro not prominent, uncus ventral on apex, acuminate, continuous with distal dorso-posterior lobe, three asetose dorso-posterior lobes, the distal two much larger than the basal one. Mid tibia (Figure 12B) with dorsal margin somewhat irregular, premucro strong, long acuminate uncus and two dorsal apical teeth, more anterior one weaker than in *S. africanus*. Hind tibial apex (Figure 12C) with premucro weak or undeveloped, inner flange bearing ventral acuminate uncus and more dorsal rounded tooth.

Abdomen. Male tergite VII (Figure 12D) fairly evenly sclerotised; plectral tubercles with setae not present, but posterior margin with pair of small raised ridges which may function as a plectrum. Female tergite VII (Figure 12E) with posterior margin medially and laterally emarginate; sometimes an indication of parallel rows of spines in anteromedial margin of wing-binding patch but these not obviously developed into plectrum.

Figure 10. *Sclerocardous bohemani* Schoenherr lectotype: (**A**) dorsal, and (**B**) lateral. Photographed by Gunvi Lindberg (© 2018 Naturhistoriska riksmuseet). Original photo cropped, light levels and contrast adjusted. Made available by the Swedish Museum of Natural History under Creative Commons Attribution 4.0 International Public License, CC-BY 4.0.

Figure 11. *Sclerocardius bohemani* Schoenherr: holotype of *Charactocnemus hintzi* Hartmann, dorsal. Photograph by Marc Srour.

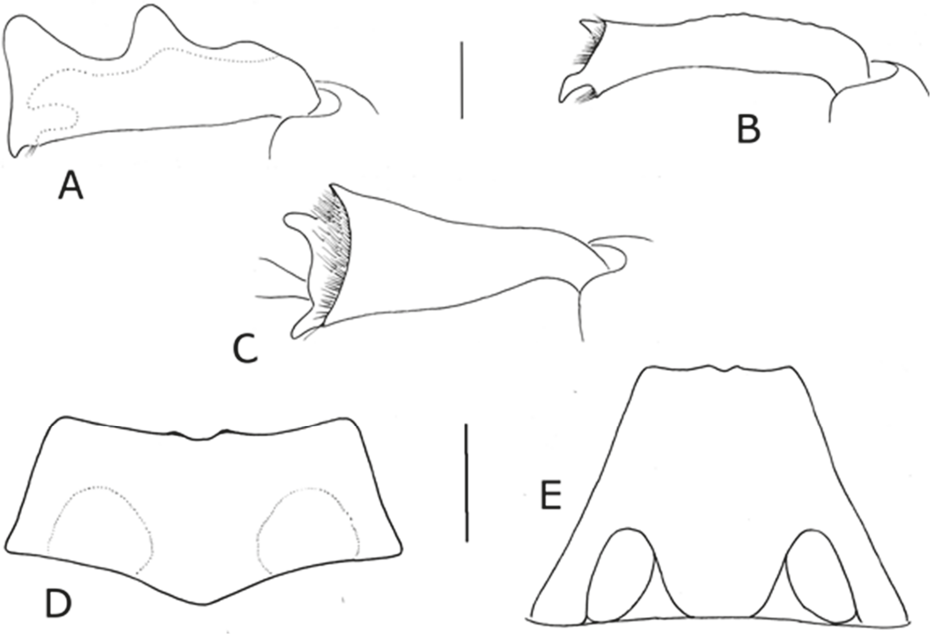

Figure 12. *Sclerocardius bohemani* Schoenherr: (**A**) fore tibia, right (dotted line indicates smooth asetose areas), (**B**) Mid tibia, right anterior (setae omitted other than on premucro and apical comb), (**C**) hind tibia, right anterior, (**D**) tergite VII, male, and (**E**) tergite VII, female. Scale bars = 1 mm.

Male genitalia. Sternite VIII with two very weakly sclerotised lobes posteriorly, anterior margin of sclerite tri-concave (Figure 13A). Spiculum gastrale Y-shaped, simple (Figure 13B). Tegmen with apodeme short, asymmetric (Figure 13C). Penis (Figure 13D,E) body half length of its apodemes, length not more than 2.1 times its maximum width; fully sclerotised; dorsally weakly concave; sides subparallel; ostium almost at right angles to long axis of penis body; small ventral projection anteriorly, anterior ventral margin with anteriad lobe, partially or completely sclerotised (Figure 13F,G); endophallus with pair of irregular small sclerites near gonopore.

Female genitalia. Very similar to those of *Sclerocardius africanus* and not figured separately. Tergite VIII with posterior margin abruptly emarginate medially; approximately one-third as deep as wide. Spiculum ventrale (Figure 13H) with posterior arms separate for two-thirds of length, with large membranous pouch between them, apodeme distinct anteriorly; posteriorly with numerous setae. Gonocoxites entire, lacking median unpigmented area. Vagina and bursa lacking pigmented area around junction with common oviduct and spermathecal duct; common oviduct and spermathecal duct arising separately from ventral membranous lobe of vagina.

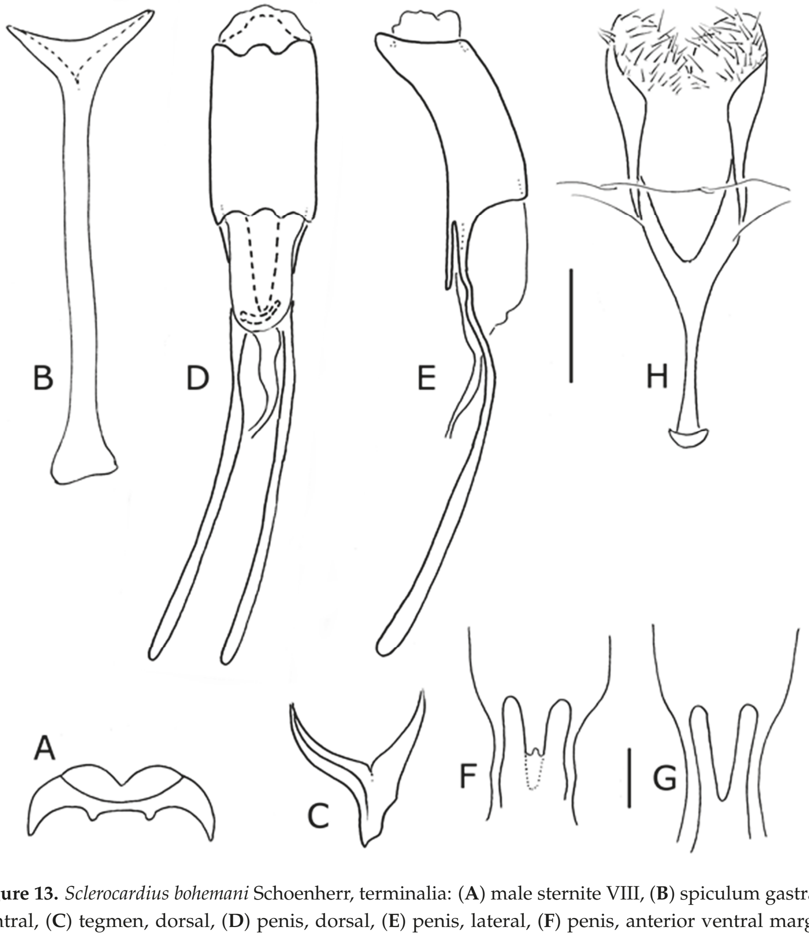

Figure 13. *Sclerocardius bohemani* Schoenherr, terminalia: (**A**) male sternite VIII, (**B**) spiculum gastrale, ventral, (**C**) tegmen, dorsal, (**D**) penis, dorsal, (**E**) penis, lateral, (**F**) penis, anterior ventral margin, showing truncated form of projection, (**G**) penis, anterior ventral margin, showing complete form of projection, and (**H**) female spiculum, ventrale ventral. Scales bars: (**A**–**E**) 1 mm, and (**F**,**G**) 0.5 mm

Distribution

South Africa, Swaziland, Malawi, Angola, Zimbabwe, Ethiopia, Tanzania, Democratic Republic of Congo, Mozambique, N. Nigeria, Madagascar.

Comments

A male specimen from Tanzania differed from the other males dissected in having a slightly smaller penis (although the insect itself was of a similar size to the others) and the ventral anteriad projection of the penis body fully sclerotised and lanceolate (Figure 13F) rather than only sclerotised part-way and with an emarginate anterior margin (Figure 13E). The significance of this difference taxonomically is unclear and will require examination of additional specimens to be resolved.

Boheman [7] described *Heteropus africanus* from Senegal, stating that the type was in "Mus Dom Chevrolat". Schoenherr [6] subsequently described *Sclerocardius bohemani* from "Montes Makkalisenses" in "Africa meridionali orientali" without having seen *Heteropus africanus* (although he was aware of the similarity). Lacordaire [8] subsequently synonymised *S. bohemani* Schoenherr with *S. africanus* (Boheman). Hartmann [9] described *Charactocnemus hintzi*, from "Ponguë bei Tanga, Deutsch-Ostafrika" (presumably the Tanga region, Tanzania) in 1896, but in the following year synonymised it with *Sclerocardius africanus* [10]. Most recently, Ferragu described *Sclerocardius madecassus* from Madagascar, differentiating it from *S. africanus* by the shorter penis and the dorsal sculpture, which is described as "tégument présentant sur les côtés et les bords de la face dorsale une forte rugosité produite par des rides profondes longitudinales, contiguës" (as opposed to "tégument lisse, brillant et pourvu de points petits et espacés") [3].

Review of a number of specimens, and of the type material, has shown that the four names above represent two species, the most senior names for which are *S. africanus* and *S. bohemani. Sclerocardius africanus* has the pronotum punctate on the disc, the punctures posteriorly sometimes confluent and separated by raised irregular transverse ridges (Figure 1A), while the pronotum of *S. bohemani* has raised irregular ridges between the punctures both posteriorly and extending onto the disc (Figures 10A, 11); *S. africanus* has a penis body that is three-quarters the length of its apodemes and more than 2.6 times its maximum width (Figure 8D), while that of *S. bohemani* is half the length of its apodemes and not more than 2.1 times its maximum width (Figure 13D). The apical projections of the inner flange of the hind tibia in *S. bohemani* are less developed than those of *S. africanus*. The pronotal character is unequivocal in most specimens and has served to assign the types of all four species. The characters that separate *S. bohemani* from the other two species in the genus are the same as those already detailed for *S. africanus*.

Schoenherr did not indicate the original number of specimens seen when he described *Sclerocardius bohemani*. Only one specimen has been located with the appropriate data to be in the type series, and this is designated as lectotype here. The precise type locality cannot be identified. Wahlberg passed through the Magaliesberg on two trips: October 1841–August 1842 and June 1843 –December 1844 (Oberprieler, pers com), his routes being provided in his published journals [13].

Hartmann stated that he had only one specimen of *Charactocnemus hintzi*. Although not labeled with the original name, only one specimen has been found in the collection at Dresden that is of the correct genus and with the collection data quoted by Hartmann (Jäger, pers com).

Specimens examined

LECTOTYPE *Sclerocardius bohemani* Schoenherr 1847 ♀, here designated, with the labels: "Mont. Mak / kalisenses / Wahlberg." [cream paper, handwritten] and [orange square] and "♀" [handwritten, white paper] and "140 / 83" [printed and handwritten, bright pink paper] and "Typus" [printed, red card] and "Riksmuseum / Stockholm" [printed, green paper] and, "NHRS-GULI / 000054254" [white card, printed] and "LECTOTYPE ♀/ Sclerocardius / bohemani / Schoenherr, 1847 / Lyal des. 2018" [printed, white paper] (NHRS).

HOLOTYPE *Charactocnemus hintzi* Hartmann 1896, with the labels: “Tauga / ostafrika / E. Hintz” [brown paper, handwritten] and “Sclerocardius / africanus Boh.” [brown paper, handwritten] and “Samm’ K.F. Hartmann / Ankauf 1941.1” [blue paper, printed] and “Staatl. Museum für / Tierkunde, Dresden” [white card, printed] and “HOLOTOTYPE / *Charactocnemus* / *hintzi* / Hartmann 1896 / Lyal vid. 2018” [printed, white paper] and “*Sclerocardius* / *bohemani* / Schoenherr 1847 / Lyal det. 2018” [printed, white paper] (MTD).

Other Material: South Africa: 1♀with the labels “Port Natal” and on the reverse “49; 29”; 1♀with the labels “Grahamstown” and “G.A.K. Marshall Coll. B.M. 1950-255”. Swaziland: 1♀with the labels “Mt Chirunda Swaziland Swynnerton 1906” and “G.A.K. Marshall Coll. B.M. 1950-255” [this could be Mt Chirundu in Zimbabwe; a Mt Chirunda in Swaziland has not been located]. Zimbabwe: 1♀with the label “Chirinda Rhodesia C.F.M.Swynnerton 1908-212”; 1♂with the labels “Salisbury Dec 97 1884” and “Sharp Coll. B.M. 1948-336”; 1♀with the label “Salisbury Mashonaland G.A.K. Marshall 1901-239”; 1♀with the labels “Salisbury Mashonaland Jan 1901 G.A.K Marshall” and “G.A.K. Marshall Coll. B.M. 1950-255”; 1♀with the labels “Salisbury Mashonaland Feb. 1899 G.A.K. Marshall” and “G.A.K. Marshall Coll. B.M. 1950-255”; 1♀with the labels “Salisbury Mashonaland Dec. 1898 G.A.K. Marshall” and “G.A.K. Marshall Coll. B.M. 1950-255”; 1♀with the label “Mashonaland G.A.K. Marshall 1908-212”; 1♀with the label “N.W. Rhodesia Mwengwa 27°40′ E. 13° S 14.i.1914 H.C. Dollman” and on the reverse “on low shrubs about sundown”. Mozambique: 1♀with the labels “Caia, Zambezi H. Swale 1913-117” and “23.2.12 Caia Zambezi H. Swale”; 1♀with the labels “Delgoa H. Junod” and “G.A.K. Marshall Coll. B.M. 1950-255”; 1♀with the label “Delagoa B”. Angola: 1♂with the labels “Angola: Kwanza Norte prov., near N’Dalatando, collected at a petrol station 22.xi.2013, T. Lackner leg.” and “BMNH(E) 2014-40 T. Lackner”; 1♀with the labels “Angola 19278” and “Angola Dundo 22.xii.1953 A.de B. Machado Pres by Com Inst Ent B.M. 1957-100”. Malawi: 2♀♀1♂with the labels “Nyasaland 19 Karonga” and “E. Gowring-Scopes Collection BMNH(E) 2005-4”; 1♀with the label “Nyasaland Mlanje 22.1.13 S.A. Neave 1914-123”. Democratic Republic of the Congo: 1♀with the labels “Belgian Congo Mpala, Katanga 1-vii-1953 H. Bomans” and “E. Gowring-Scopes Collection BMNH(E) 2005-4” and “BMNH(E) # 716136 Digitally Imaged”; 1♀with the labels “Quilu R. Congo” and “Sharp Coll. B.M. 1948-336”. Tanzania: 1♀1♂with the labels “Tanganiyka: Old Shinyanga 1934 E. Burtt” and “Brit. Mus. 1935-257”; 1♂with the labels “at light” and “Tanganyika Tanga Prov. iv–v. 1950 R.C.H.Sweeny B.M.1950-493”. Kenya: 1♀with the labels “at light” and “Kenya Tanga, Ngomeni Mlingano Sisal Research Stn i-iii.1931” and “R.C.H Sweeny B.M. 1951-320”. Senegal: 1♀with the labels “Seneg” and “Heteropus africanus Sch – Seneg” and “Bowring 63.47 *”. Nigeria: 2♀♀with the labels “N. Nigeria Azare Dr. Ll. Lloyd” and “G.A.K. Marshall Coll. B.M. 1950-255”. Ethiopia: 1♀with the label “Abyssinia Raffray” [probably high altitude, since this collector was collecting in the mountains]. Unknown locality: 1♂with no labels; 1♀with the label “G.A.K. Marshall Coll. B.M. 1950-255”; 1♀with the labels “U[r]araga” and “D. Sharp Coll. B.M. 1932-116”.

3.4. *Sclerocardius kuscheli sp. nov.*

http://zoobank.org/urn:lsid:zoobank.org:act:0CA0B46C-CA7E-4BD9-82E3-C8E4602B6E92

Description

Figures 4B and 14–18

Length 5.04–6.72 mm (mean 5.99 mm, $n = 9$); Pronotal width 2.0–2.88 mm (mean 2.54 mm, $n = 9$); Elytral width 2.4–3.28 mm (mean 2.91 mm, $n = 9$); males and females not significantly different in size.

Derm black, not developed into prominences or tubercles. Scales not concealing derm, elongate, white or yellowish- orange, longer than the punctures in which they arise, with white patch on either side of pronotum posteriorly, shading into orange anteriorly, elytral declivity with orange scales, more basally elytral scales pale; femoral scales pale, tibial scales more yellowish-orange.

Head. Rostrum weakly curved, similar in males and females; strongly punctate dorsally and laterally in basal half, each puncture with pale elongate scale, these longest dorsal to eyes; irregular longitudinal carinae sometimes present baso-laterally; abruptly narrowed before eyes lateroventrally to form weak indistinct notch. Head capsule densely punctate dorsally, each puncture with an elongate scale.

Thorax. Pronotum with length:width 0.70–0.77 (mean 0.75, *n* = 9), as high as long when length is taken as axis normal to height (Figure 14A), weakly convex dorsally in lateral aspect (Figure 14B), punctate on disc with punctures separate, without irregular ridges running transversely between them; anteriorly extending over head capsule. Prothorax ventrally with shallow narrow rostral canal with weak lateral carinae before fore coxae; fore coxae weakly separate, lacking tuft of elongate orange scales on inner face; post-coxal lamellae not developed. Elytra with length:width 1.39–1.50 (mean 1.45, *n* = 9); interstriae broad, with transverse rows of punctures, striae very narrow and linear, strial punctures narrow, more or less confluent (Figures 4B and 14A). Femoral teeth absent. Fore tibia lacking postero-ventral tooth in male and female; premucro present, small, uncus very small and forming part of distal posterior lobe although curved ventrad; dorso-posteriorly with two lobes, the distal one larger than the basal one (Figure 15A,D). Mid tibia (Figure 15E) with premucro well developed, uncus ventral, single dorsal adventitious tooth present; anterior apical setal comb on apical margin just dorsal to uncus. Hind tibia (Figure 15B,C,F) strongly broadened distally, anterior face with transverse ridges and apically inclined posteriad so that anterior apical margin with setal comb not distinguishable and inner flange continuous with anterior margin of the tibia; premucro undeveloped, uncus acuminate, apex with two rounded or acuminate teeth; dorsal margin apically with large laminate teeth continuous with apical teeth.

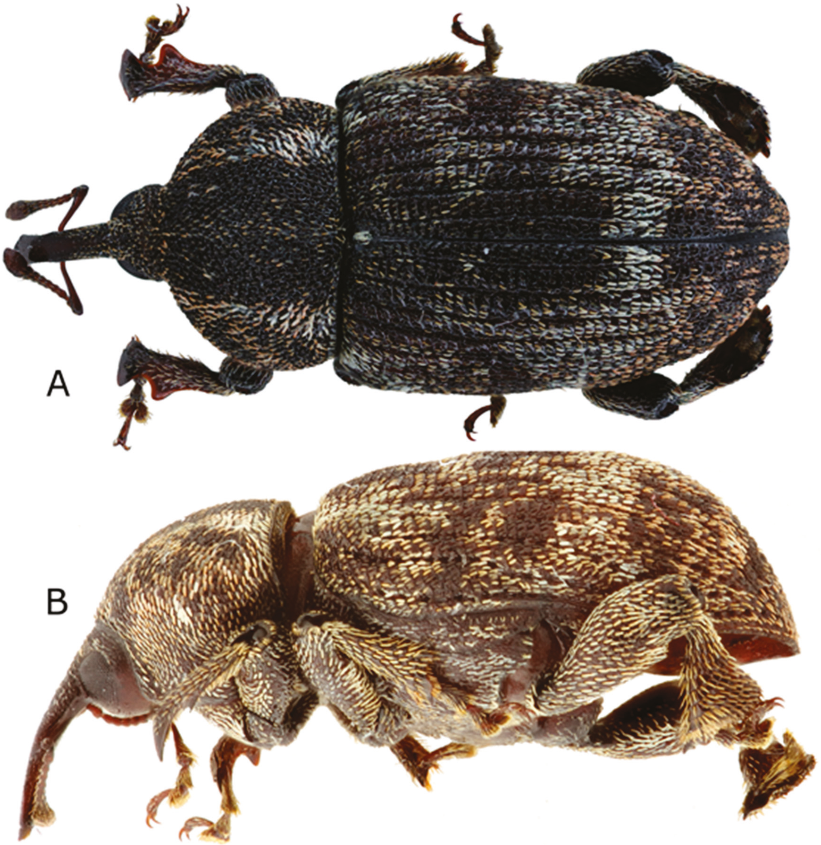

Figure 14. *Sclerocardius kuscheli* sp.nov. habitus: (**A**) dorsal, and (**B**) lateral.

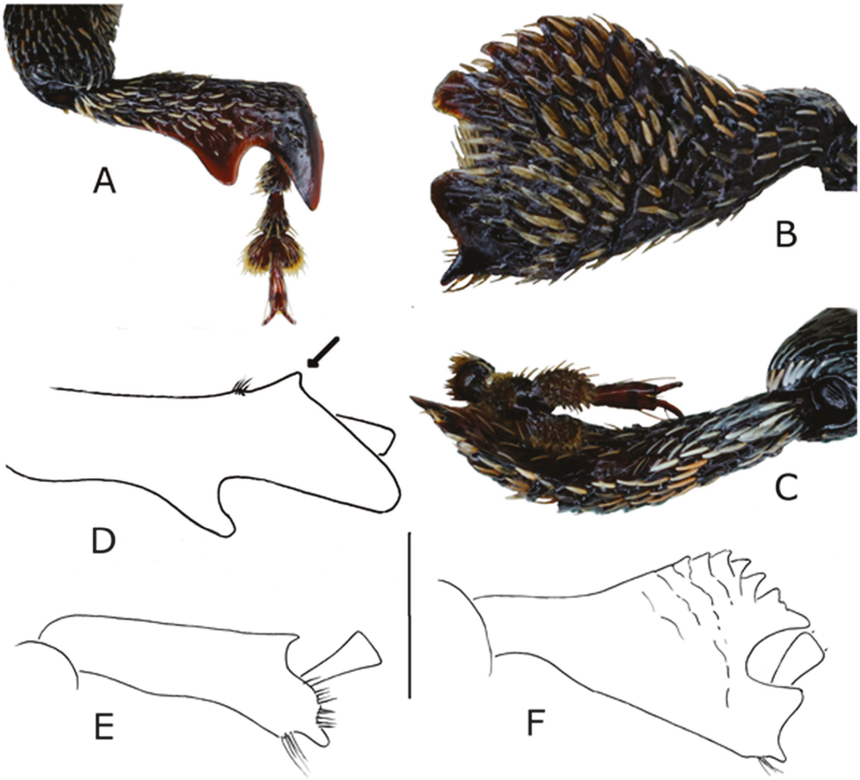

Figure 15. *Sclerocardius kuscheli* sp.nov. tibiae: (**A**) fore tibia, right, (**B**) hind tibia, anterior right, (**C**) hind tibia, dorsal right, (**D**) fore tibia, antero-apical, to show premucro (arrowed), (**E**) mid tibia, anterior left, and (**F**) hind tibia, anterior right. Scale bar (line drawings only) 1 mm.

Abdomen. Tergites I-V weakly sclerotised, VI and VII more strongly sclerotised. Male tergite VII with posterior margin weakly emarginate, sclerotised area projecting anteriad between wing-binding patches bearing a pair of plectral tubercles near anterior margin (Figure 16C). Female tergite VII lacking plectral tubercles but with inner third of wing-binding patches with spines parallel, transverse, forming a series of ridges (Figure 16A,B).

Male terminalia. Sternite VIII narrowly sclerotised along posterior margin (Figure 17A). Spiculum gastrale Y-shaped, simple (Figure 17B). Tegmen (Figure 17C) with apodeme longer than width of 'ring', slender. Penis (Figure 17D,E) body weakly sclerotised dorsally, lack anteriad ventral lobe; ostium diagonal with respect to longitudinal axis of penis; endophallus with pair of oval toothed sclerites not near gonopore.

Female genitalia. Tergite VIII with ventrolateral bulbous lobe on either side directed posteriad and covered with microtrichiae (Figure 18A); dorsal plate with sides narrowing to setose posterior margin, emarginate medially (Figure 18B). Spiculum ventrale (Figure 18C) with no separate apodeme, but basal arms separate for whole length, the space between them being an open pocket opening within the genital chamber; posterior margin truncate. Gonocoxites lacking unsclerotized area. Posterior end of bursa with oval bulbous sclerite, the oviduct and spermathecal duct inserted ventrally in its membranous center (Figure 18D).

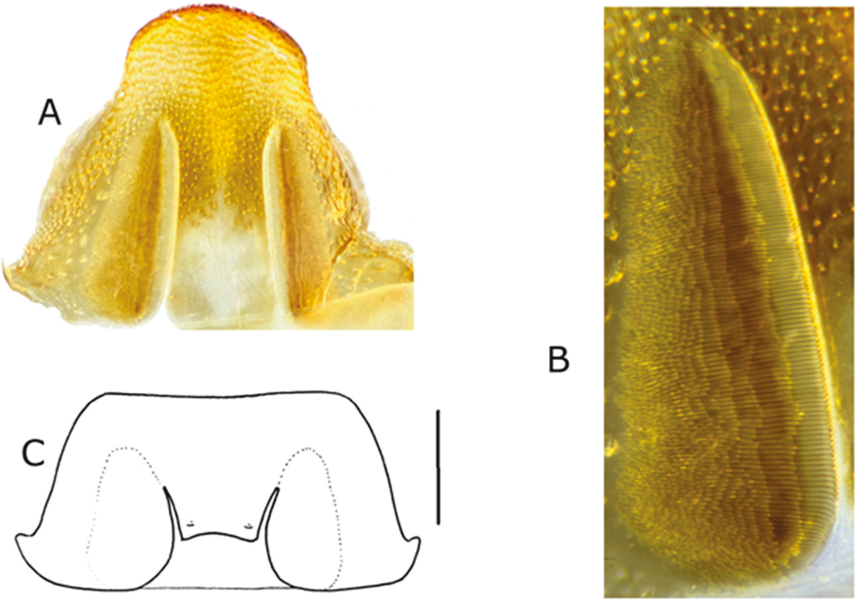

Figure 16. *Sclerocardius kuscheli* sp.nov., tergite VII: (**A**) female, dorsal, (**B**) female showing wing-binding patch, and (**C**) male, dorsal (Scale bar = 0.5 mm).

Distribution

Angola

Etymology

The species is named after my friend and mentor Willy Kuschel, a name particularly apposite since the new species has enabled the resolution of one troubling systematic problem while simultaneously producing a new one.

Comments

The new species *S. kuscheli* is placed in the genus because of the following synapomorphies: fore tibia with dorso-posterior margin produced into two laminate lobes; mid tibia with uncus flattened and with additional laminate projections; hind tibia broadened distally, with laminate projections distad; pronotum rounded in dorsal view. It differs from other members of the genus in the following characters: fore coxae lacking tuft of orange scales on inner face; penis body with ostium oblique (and of a type seen in many other Curculionidae) compared to more or less at right angles to the longitudinal axis of the penis, sometimes terminal and across the full diameter of the penis; female tergite VIII with unique lateroventral lobes; female tergite VII with wing-binding patches modified as a stridulatory file. It shares the form of the female spiculum ventrale with *S. indicus*, which also shows a very small patch of parallel spines on the wing binding patch of SVII in the females.

Sclerocardius kuscheli can be distinguished from all other species so far known in the genus by the form of the hind tibia, which is less than twice as long as deep, as opposed to much more than twice as long as deep, and has no clearly differentiated anterior apical margin and inner flange. It differs from the Oriental species by having pale and dark scales dorsally as opposed to orange ones, and from the other African species in having much longer dorsal scales and a much less convex pronotum. The aligned scales of the female tergite VII differentiate it from all other known species, as does the presence of plectral tubercles on the male tergite VII.

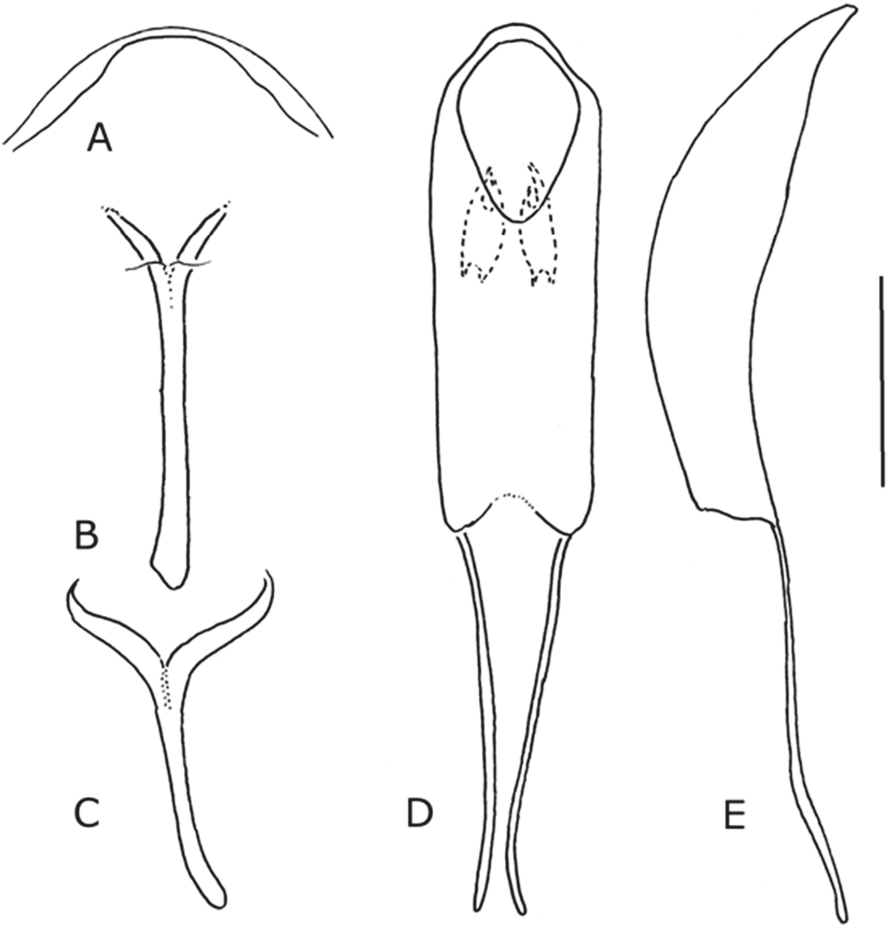

Figure 17. *Sclearocardius kuscheli* sp.nov. male terminalia: (**A**) sternite VIII, ventral, (**B**) spiculum gastrale, ventral, (**C**) tegmen, dorsal, (**D)** penis, dorsal, and (**E**) penis, lateral. Scale bar = 0.5 mm.

As noted, the wing-binding patches of tergite VII in the female *S. kuscheli* are modified as a file in a very similar way to that of Ithyporina, there being a longitudinal patch of spines on the inner margin that are elongate and parallel, although the patch is not as produced dorsad as much as in most species of that group [14]. Such a structure has been seen nowhere else in the Curculionidae, and supports the placement of *Sclerocardius* in the Ithyporini as restricted by Lyal [2]. The female genitalia of *S. kuscheli* resemble those of *Ithyporus setulosus* Hustache: the spiculum ventrale lacks an apodeme but instead the basal arms are separate for almost the entire length, meeting anteriorly and containing between them an open pocket opening into the genital chamber, and the common oviduct and spermathecal duct arise separately from a membranous area in the centre of a bowl-shaped sclerite at the base of the bursa (this area is more expanded than in *S. kuscheli*, and of a slightly different shape). The form of the spiculum ventrale is also shared with *S. indicus*, although that species has the female bursa of a similar form to that found in *S. africanus* and *S. bohemani*.

Specimens examined

HOLOTYPE, ♂with the labels: "Holo- / type" [printed, white disc with red border] and "ANGOLA central / Bié prov., Kuemba env. / 23.xi.2012/T. Lackner leg." [printed] and "BMNH (E) / 2014-48 / T. Lackner" [printed] and "HOLOTYPE / *Sclerocardius* / *kuscheli* Lyal, 2018 / Lyal det. 2018" [printed]. PARATYPES: 8 ♀♀with same data as the holotype, but with "Para- / type" [printed, white disk with yellow border] and "PARATYPE / *Sclerocardius* / *kuscheli* Lyal / Lyal det 2018" [printed].

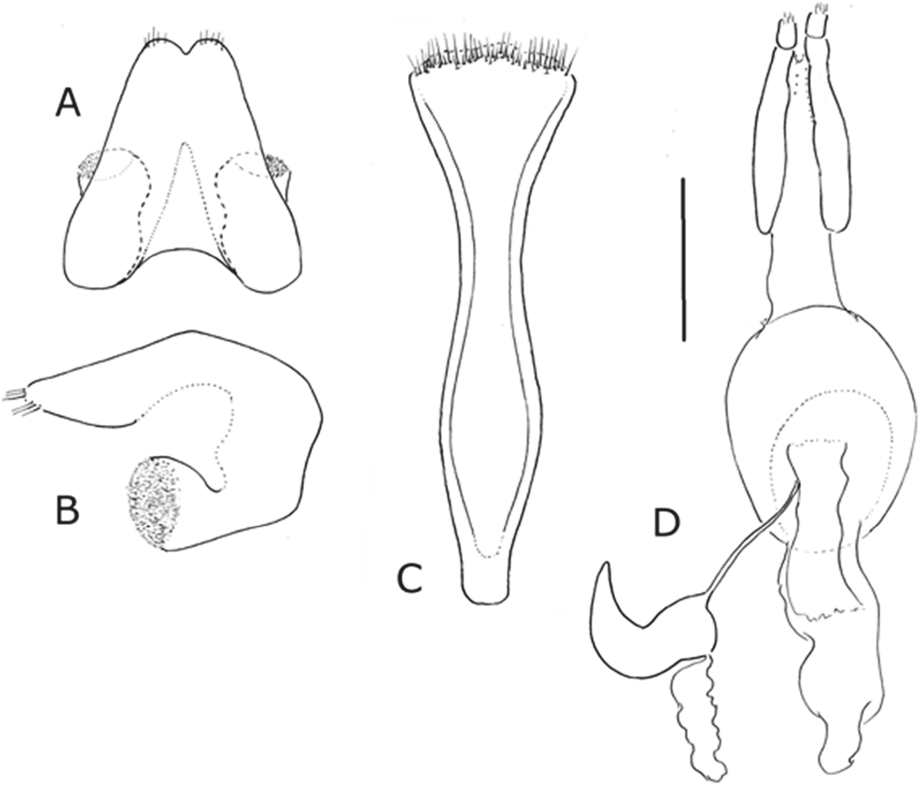

Figure 18. *Sclerocardius kuscheli* sp.nov., female terminalia: (**A**) tergite VIII, dorsal, (**B**) tergite VIII, lateral, (**C**) spiculum ventrale, ventral, and (**D**) genitalia, ventral. Scale bar = 0.5 mm.

3.5. Sclerocardius indicus Hartmann, 1903

Sclerocardius indicus Hartmann, 1903: 29 [15]

Description

Figure 19, Figure 20, Figure 21, Figure 22 and Figure 23.

Length 7.9–11.2 mm (mean 9.94 mm, $n = 10$); Pronotal width 2.88–3.92 mm (mean 3.69 mm, $n = 10$); Elytral width 3.52–5.04 mm (mean 4.50 mm, $n = 10$), males and females not significantly different in size.

Derm black, not developed into prominences or tubercles. Scales not concealing derm, elongate and narrow, orange, longer than the punctures in which they arise (Figure 19A,B).

Figure 19. *Sclerocardius indicus* Hartmann habitus, (**A**) dorsal, and (**B**) lateral.

Head. Rostrum weakly curved, similar in males and females; strongly punctate laterally in basal half above scrobe and distally at same level as scrobe, weakly to strongly punctate dorsally basal to antennal insertion, very weakly punctate more distally, sometimes with rounded longitudinal ridges dorsally basally, each puncture with orange elongate setiform scale, longer than diameter of puncture; abruptly narrowed before eyes lateroventrally to form a notch. Head capsule strongly punctate dorsally, each puncture with an orange elongate setiform scale, longer than diameter of puncture.

Thorax. Pronotum with length:width 0.91–1.0 (mean 0.94, $n = 10$), as high as long when length is taken as axis normal to height (Figure 19B), weakly convex dorsally in lateral aspect (Figure 19B), punctate on disc with punctures separate or confluent, irregular rounded ridges running more or less antero-transversely between them, these ridges most pronounced laterally and posteriorly; anteriorly pronotum extends over head capsule (Figure 19A). Prothorax ventrally with broad rostral canal with lateral carinae before fore coxae; fore coxae separate, with tuft of elongate orange scales on inner face; post-coxal lamellae present and forming two transverse lobes immediately behind fore coxae to more or less close the gap between the coxae. Elytra with length:width 1.30–1.50 (mean 1.45, n = 10); interstriae with irregular transverse rows of punctures or lacking such rows, striae narrow and linear, strial punctures more or less confluent (Figure 19A). Fore femora with small hooked femoral tooth in distal half, other femora with smaller hook-like ventral tooth. Fore tibia (Figure 20A,B) with three rounded postero-ventral teeth in male, these absent in female; premucro prominent, uncus in ventral half of apex, acuminate, curved posteriad (Figure 20B), continuous with distal dorso-posterior lobe, dorso-posteriorly with two lobes, the distal one larger than the basal one. Mid tibia (Figure 20C) with premucro very large, acuminate, uncus acuminate, directed ventrad, two dorsal apical teeth, the more posterior one slightly larger than the more anterior. Hind tibia (Figure 20D) strongly broadened distally; apex with premucro very weak, inner flange bearing acuminate uncus and more dorsal rounded tooth.

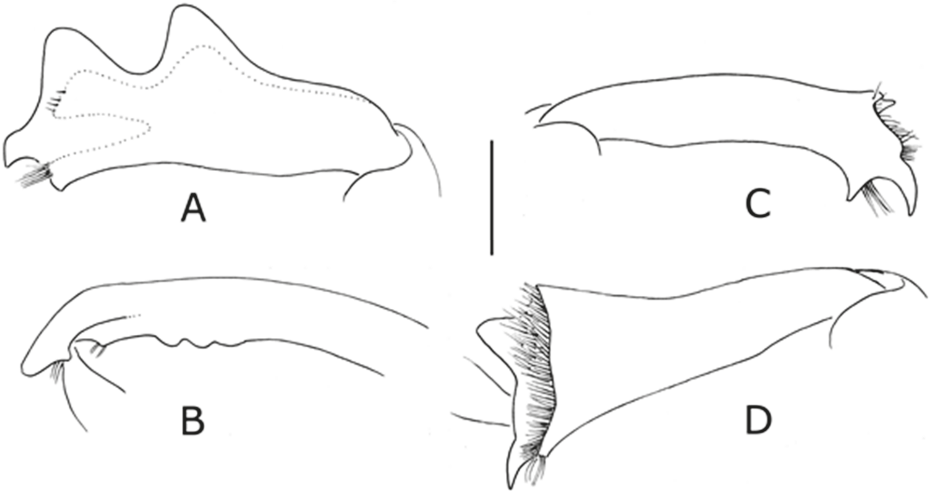

Figure 20. *Sclerocardius indicus* Hartmann, tibiae: (**A**) Fore tibia, right dorso-posterior (dotted line indicates smooth asetose areas), (**B**) fore tibia, anterior, showing postero-ventral teeth of male, (**C**) mid tibia, anterior left, and (**D**) hind tibia, anterior. Scale bar = 1 mm.

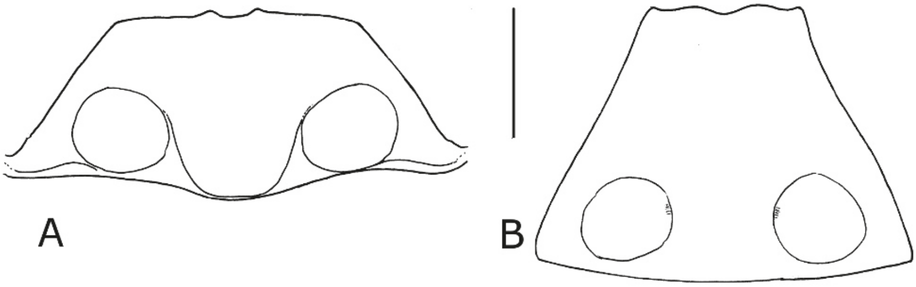

Figure 21. *Sclerocardius indicus* Hartmann, tergite VII, dorsal: (**A**) male, and (**B**) female. Scale bar = 1 mm.

Abdomen. Tergites I to VI weakly sclerotised. Male tergite VII (Figure 21A) lacking plectral tubercles, but with pair of prominences on posterior margin. Female TVII (Figure 21B) with very small patch of parallel transverse spines on inner margin of wing-binding patch.

Male genitalia. Sternite VIII narrow with very weakly sclerotised lobe posteriorly providing convex posterior margin to sternite (Figure 22A). Spiculum gastrale Y-shaped, simple (Figure 22D). Tegmen with apodeme short, asymmetric (Figure 22B). Penis body weakly sclerotised dorsally; sides concave posteriorly, convex anteriorly; ostium almost at right angles to long axis of penis body (Figure 22E,F); small ventral projection anteriorly, anterior ventral margin with long sclerotised anteriad lobe (Figure 22C); endophallus lacking internal sclerite.

Female genitalia. Tergite VIII with posterior margin abruptly and deeply emarginate medially (Figure 23A); approximately 0.4 times as deep as wide (Figure 23B). Spiculum ventrale (Figure 23C) with no separate apodeme, but basal arms separate for whole length, the space between them being an open pocket; posterior margin bilobed. Gonocoxites (Figure 23E) with small separately pigmented area ventrally anteriorly separated from main pigmented area. Common oviduct and spermathecal duct arising separately off a long lobe of the vagina and both distant from the bursa; vagina and bursa lacking internal sclerites (Figure 23D).

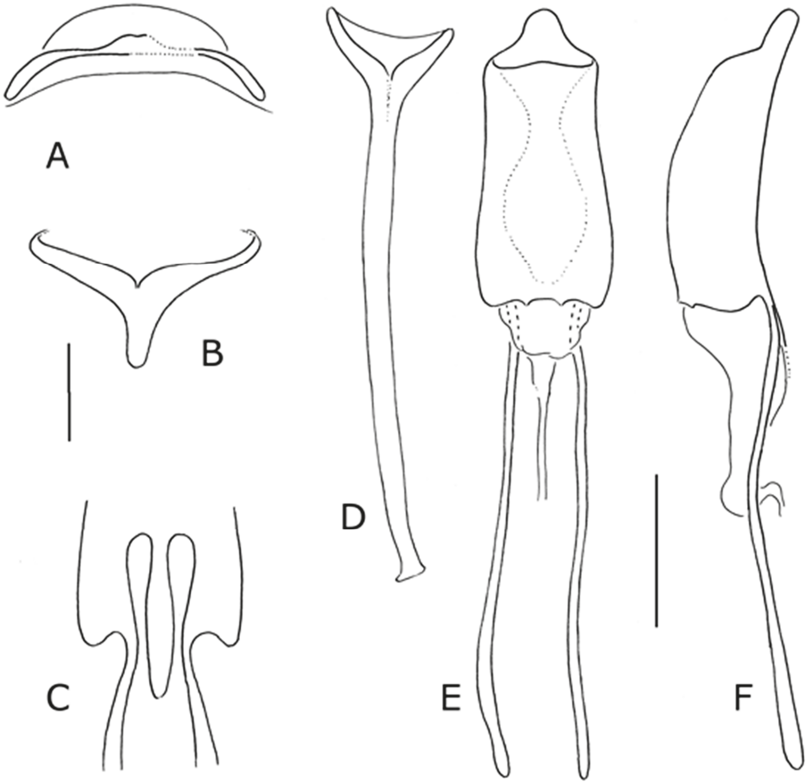

Figure 22. *Sclerocardius indicus* Hartmann, male terminalia: (**A**) sternite VIII, ventral (not fully pigmented in the figured specimen), **(B)** tegmen, dorsal, (**C**) penis, anterior ventral margin, (**D**) spiculum gastrale, ventral, (**E**) penis, dorsal, and (**F**) penis, lateral. Scale bars 1 mm ((**A**–**C**) at the same scale, (**D**–**F**) at the same scale).

Distribution

Malaysia: Peninsular Malaysia, Sarawak.

Comments

Sclerocardius indicus can be distinguished from the other known species by the covering of elongate and sometimes very narrow orange scales; in all other species, scales are pale or dark and sometimes very small. The multiple postero-ventral rounded teeth on the fore tibia in the male are unique in the genus.

The genitalia show a mix between the morphologies shown by *S. kuscheli* and the other African species. The female spiculum ventrale has the same deep V form as *S. kuscheli* (and *Ithyporus setulosus*). However, the female sternite VII and the ovipositor itself are of a similar form to *S. africanus* and *S. bohemani*. The small patch of transverse spines on the wing-binding patch of the female TVII may suggest the loss of this character.

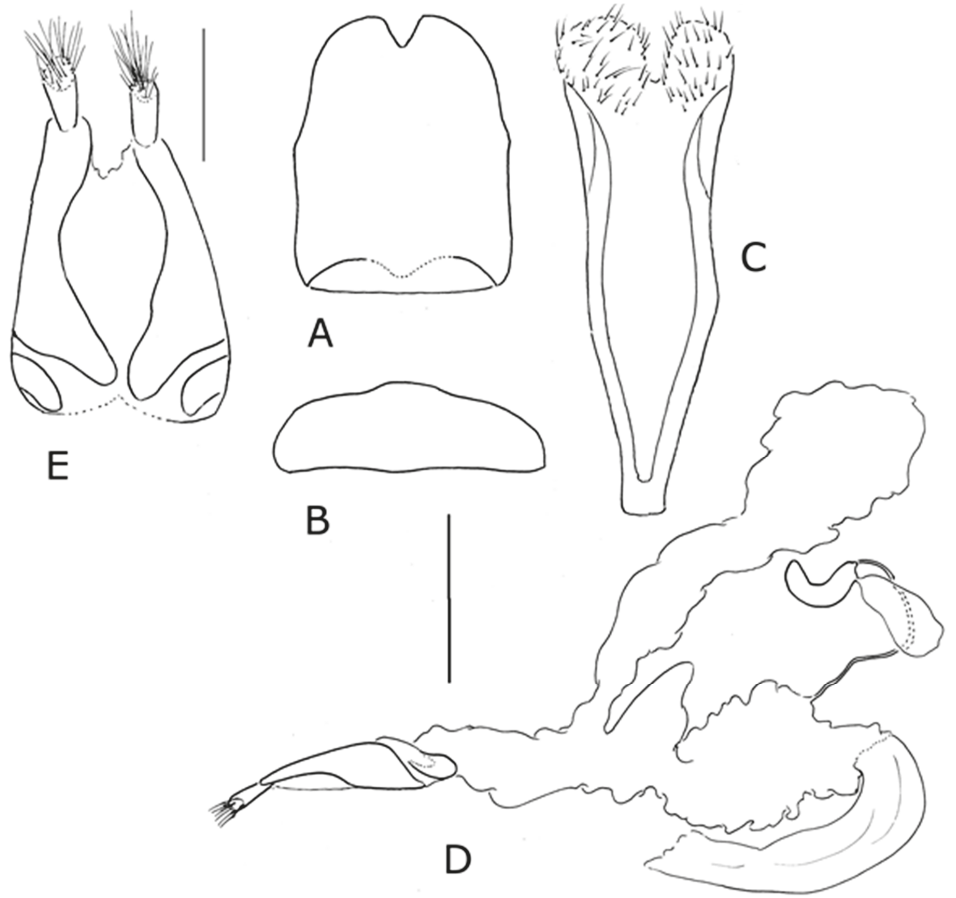

Figure 23. *Sclerocardius indicus* Hartmann, female terminalia: (**A**) tergite VIII, dorsal, (**B**) tergite VIII, lateral, (**C**) spiculum ventrale, ventral, (**D**) genitalia, lateral, and (**E**) gonocoxites, ventral. Scale bar for (**A**–**D**) = 1 mm, for **E** = 0.5 mm.

Specimens examined

PENINSULAR MALYSIA: ♂with the labels “Malay Penin. Selangor. Bukit Kutu at light, 3500 ft. March 16th 1931 H.M. Pendlebury” and “Ex Coll F.M.S. Museum” on the reverse, and “Ex FMS Museum BM 1955-354”; 1♂with the labels “Malay Penin. Ex: Coll. Ag. Dept. Bukit Fraser June 1921” and “ex coll. FMS Museum” on the reverse, and “Pres. By Imp. Inst. Ent. B.M. 1927-355”; 1♂with the labels “Malay Penin. Larat Hills at light 3700ft, 8th Feb 1932 H.M. Pendlebury” and “Ex. Coll. F.M.S. Museum” on the reverse, and “Pres. By Com. Inst. Ent. B.M. 1952-94”; 1♂with the labels “Malaysia, Pahang Tanah Rata, 4700ft. 3.x.-13.xi.1980” and “A. Harman Coll. B.M. 1982-49.”; 1♂with the labels “Malay Penin. Kedah Peak, 3300ft. 22nd March 1928” and “at light H.M. Pendlebury Coll. F.M.S. Museums” on the reverse, and “Ex FMS Museum BM 1955-354”; 1♂with the labels “69775”, “Perak” and “Fry Coll 1905-100”; 1♀with the labels “Malay Penin. Perak F.M.S. ex coll. Perak Mus. C. Warang 19.” and “Ex FMS Museum BM 1955-354”; 1♀with the labels “Malay Penin. Selangor. Bukit Kutu at light, 3500ft. April 18th 1926 H.M. Pendlebury” and “Ex Coll F.M.S. Museum” on the reverse, and “Ex FMS Museum BM 1955-354”; 1♀with the labels “Malaya Tanah Rata 19.5.1939. H.T. Pagden, Agric. Dept. at light” and “G.A.K. Marshall Coll. B.M. 1930-255” and “G.2734”. SARAWAK: 1♂with the labels “Guning Tamabo [indecipherable] Baram River Sarawak 7.11.1920 J. C. Moulton” and “Raffles Museum Singapore” on the reverse, “430” and “Pres. By Imp. Inst. Ent. B.M. 1941-7”.

4. Discussion: The Systematic Position of *Sclerocardius*

The adult insect is highly unusual in shape, with its expanded fore tibiae, strongly convex pronotum and relatively small head, and this has probably caused confusion as to the correct placement of the genus. Lacordaire [8] originally gave it a family-group name and placed it in the Sipalides, and it remained in the Sipalini until Marshall [16] transferred the genus to Ithyporinae (without mentioning the family-group name Sclerocardiini). Alonso-Zarazaga & Lyal [1] formally placed the Sclerocardiina as a subtribe of Ithyporini (although failed to note its earlier transfer by Marshall). Lyal [2] failed to find synapomorphies with the Ithyporini and referred to it both as a separate tribe and as a subtribe of Ithyporini. The examination in this study has revealed putative synapomorphic characters shared with Ithyporini in whole or in part, supporting its placement within this tribe.

Characters supporting the placement of *Sclerocardius* within Ithyporini include: mandibles smoothly convex exteriorly and narrow in lateral aspect, closing medially; antennal club with sutures sinuate; eyes extending under head (although not as far as in Ithyporini); prothoracic rostral canal bordered by strongly developed carinae; tarsal segment 5 extending beneath claws; tegmen unsclerotized dorsally and lacking parameroid lobes; female with wing-binding patch on TVII sometimes modified so that spines on inner edge are parallel and elongate, probably functioning as a stridulatory file. This last character is present in *S. kuscheli* only within the Sclerocardiina but is unique to Ithyporini and suggests homology.

Most species of *Sclerocardius* lack the apomorphic female stridulatory system of the Ithyporina, the female lacking both the modification to the wing binding patch on tergite VII (although there is sometimes an indication of regularity in the spines near the inner margin of the patch) or any indication of a stridulatory file on the elytron and plectral tubercles on tergite VII. However, the presence of the modified wing-binding patch in *S. kuscheli* suggests that the condition in other species of *Sclerocardius* represents a loss state.

Males of most species of *Sclerocardius* lack plectral tubercles on tergite VII, although they do have an elongate stridulatory file on the elytra. Instead, they appear to have a pair of protuberances on the posterior margin of the tergite, which may act as a plectrum. The exception to this is *S. kuscheli*, which has a pair of plectral tubercles medially on the tergite. *Ithyporus setulosus* has five pairs of plectral tubercles arranged in weakly converging lines, the more posterior tubercle lying on the posterior margin of the tergite.

There are some indications of a close relationship with *Ithyporus*, at least with *I. setulosus* Hustache, 1924. This species has the apex of the hind tibia elongate and scoop-shaped, although not as developed as in *Sclerocardius*. Perhaps significantly, the form of the female genitalia, particularly the junction of vagina, bursa, common oviduct and spermathecal duct, and the form of the spiculum ventrale, are very similar to the morphology of *S. kuscheli*, as discussed above.

Further work is required to place *Sclerocardius* more firmly, but for now it is retained as a subtribe of Ithyporini. This potentially creates a paraphyletic Ithyporina, and the placement needs to be examined more closely.

Sclerocardius appears strongly adapted for digging (although no observations have been published to support this assumption): fore tibia broadened with laminar projections; hind tibia with broad apex; fore coxae with trochanteral articulation on posterior face; prothorax very large and convex (suggesting enlarged muscles supporting forelegs); prosternum with prothoracic rostral canal bordered by carinae; rostrum narrow (suggesting that the head can be pulled down and the rostrum concealed while the insect digs). Whether this is in soil or plant material is not known. Other Ithyporini are known to bore as larvae into bark and sometimes into wood, although some species have been observed developing in seeds [2].

Sclerocardius contains four described species, three of which are found in the Afrotropical Region, one also in Madagascar, and the third in the Malaysian Peninsula and Sumatra. There is no doubt that *S. indicus* is congeneric with the other species, and seems to share some apomorphies with the two larger African species (male with ventro-posterior tibial teeth, female wing-binding patch on tergite VII unmodified, male tergite VII lacking plectral tubercles, penis with ostium nearly perpendicular), although this will need to be confirmed by further analysis. No specimens of the genus have been found in India. Within Africa, the broad distribution of both *S. africanus* and *S. bohemani* is surprising; there are some indications of variation within the latter species but research on far more specimens is required to evaluate this.

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Conflicts of Interest: The author declares no conflict of interest.

References

1. Alonso-Zarazaga, M.A.; Lyal, C.H.C. *A World Catalogue of Families and Genera of Curculionoidea (Insecta: Coleoptera) Excluding (Scolytidae and Platypodidae)*; Entomopraxis: Barcelona, Spain, 1999.
2. Lyal, C.H.C. Molytinae Schoenherr, 1832. In *Coleoptera, Beetles. Morphology and Systematics. Volume 3. In Handbook of Zoology. Arthropoda: Insecta*; Leschen, R.A.B., Beutel, R.G., Eds.; De Greuter: Berlin, Germany; Boston, MA, USA, 2014; pp. 529–570.
3. Ferragu, M.; Richard, R. Trois Nouveaux Curculionides de Madagascar et de l'Île de La Réunion [Coleoptera]. *Rev. Fr. Entomol.* **1990**, *12*, 105–110.
4. Lyal, C.H.C.; Curran, L.M. Seed-Feeding Beetles of the Weevil Tribe Mecysolobini (Insecta: Coleoptera: Curculionidae) Developing in Seeds of Trees in the Dipterocarpaceae. *J. Nat. Hist.* **2000**, *34*, 1743–1847. [CrossRef]
5. Lyal, C.H.C. Glossary of Weevil Characters. Available online: http://weevil.info/glossary-weevil-characters (accessed on 25 June 2018).

6. Schoenherr, C.J. *Mantissa Secunda Familiae Curculionidum Seu Descriptiones Novorum Quorundam Generum Curculionidum*; Typis Norstedt et Filii: Holmiae, Sweden, 1847.
7. Schoenherr, C.J. *Genera et Species Curculionidum, Cum Synonymia Hujus Familiae. Species Novae Aut Hactenus Minus Cognitae, Descriptionibus a Dom. Leonardo Gyllenhal, C. H. Boheman, et Entomologis Aliis Illustratae*; Roret: Paris, France, 1845; Volume 8.
8. Lacordaire, T. *Toire Naturelle Des Insectes. Genera Des Coléoptères Ou Exposé Méthodique et Critique de Tous Les Genres Proposés Jusqu'ici Dans Cet Ordre D'insectes*; Librairie Encyclopédique de Roret: Paris, France, 1865; Volume 7.
9. Hartmann, F. Beschreibung Einer Neuen Gattung Der Rüsselkäfer Aus Deutsch-Ostafrika. *Dtsch. Entomol. Z.* **1896**, *1896*, 185–188. [CrossRef]
10. Hartmann, F. Neue Rüssel-Käfer Aus Deutsch-Ostafrika. *Dtsch. Entomol. Z.* **1897**, *1*, 81–96. [CrossRef]
11. Hustache, A. Curculionidae: Cryptorrhynchinae. In *Coleopterorum Catalogus Auspiciis et Auxilio W. Junk. 151*; Schenkling, S., Ed.; Junk: Gravenage, The Netherlands, 1936; 317p.
12. Palisot de Beauvois, A.M. *Insectes Recueillis En Afrique et En Amerique, Dans Les Royaumes d'Oware et de Benin, à Saint-Dominique et Dans Les Etats-Unis, Pendant Les Années 1786–1797*; Levrault: Paris, France, 1805.
13. Wahlberg, J.; Craig, A.; Hummel, C. *Johan August Wahlberg: Travel Journals (and Some Letters) South Africa and Namibia/Botswana, 1838–1856*; Van Riebeck Society: Cape Town, South Africa, 1994.
14. Lyal, C.H.C.; King, T. Elytro-Tergal Stridulation in Weevils (Insecta: Coleoptera: Curculionoidea). *J. Nat. Hist.* **1996**, *30*, 703–773. [CrossRef]
15. Hartmann, F. Neue Exotische Rüsselkäfer. *Wiener Entomol. Zeitung* **1903**, *22*, 23–30.
16. Marshall, G.A.K. New Curculionidae (Col.) from Tropical Africa, with Notes on Synonymy Etc. *Ann. Mag. Nat. Hist.* **1935**, *10*, 497–518. [CrossRef]

diversity

Article

Anchonini in Africa: New Species and Genus Confirming a Transatlantic Distribution (Coleoptera: Curculionidae: Molytinae)

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Abstract: The Anchonini known from Africa are reviewed. The monotypic genus *Aethiopacorep* is redescribed. The new West African genus *Titilayo* gen. nov. is described, with seven new species: four from São Tomé, *T. perrinae* sp. nov., *T. saotomense* sp. nov., *T. barclayi* sp. nov., and *T. turneri* sp. nov.; two from Ivory Coast, *T. geiseri* sp. nov. and *T. garnerae* sp. nov.; and one from Sierra Leone, *T. takanoi* sp. nov. Neither of these genera is known outside West Africa. A neotype is designated for *Anchonus africanus* Hustache 1932. A key to the two African genera, *Aethiopacorep* and *Titilayo*, as well as their corresponding species, is provided. This work provides the first records of Anchonini for mainland Africa; this group is still understudied in the region but shows signs of being very diverse on both the mainland and in the western African islands.

Keywords: Curculionidae; Anchonini; Molytinae; *Aethiopacorep africanus*; neotype; *Titilayo*; *Titilayo barclayi*; *Titilayo garnerae*; *Titilayo geiseri*; *Titilayo takanoi*; *Titilayo perrinae*; *Titilayo saotomense*; *Titilayo turneri*; taxonomy; distribution

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1. Introduction

The tribe Anchonini Imhoff, 1856 is recognised as predominantly Neotropical and Nearctic, with a few problematic genera in the Oriental region [1], which are probably incorrectly placed in the tribe [2–8]. Although three species have been recorded from the Afrotropical and Mascarene regions two are undoubtedly introductions and the other known only from one collection event. This paper demonstrates that the tribe is endemic to West Africa, and reports species from continental Africa for the first time.

While introduced species of Anchonini are known from Réunion and Madagascar (see Discussion below), the only endemic anchonine species so far described from Africa is *Anchonus* (*Aethiopacorep*) *africanus* Hustache (1932) from the island of Annobón, a province of Equatorial Guinea. The syntypes of this species were destroyed in 1943 as a result of a RAF air raid, which led to a catastrophic fire, burning the majority of the Hamburg Museum's dry collections [9,10]. A neotype is designated and the species redescribed here.

Six new species of Anchonini were found during three recent study trips by the African Natural History Research Trust (ANHRT) and The Natural History Museum, London to Mount Nimba in Ivory Coast, the Loma Mountains of Sierra Leone, and São Tomé island.

A total of seven specimens were hand-collected on Mount Nimba, south-west of Richard Molard peak ("Crête de Nion"), on the border between Ivory Coast and Guinea at an altitude of 1250 to 1430 m in May 2016. They were found on a foggy, drizzly morning, sitting on low vegetation, which included vines [11]. The general environment is shown in Figure 1A. Published results from expeditions to Mount Nimba [12,13] record only three Molytinae species: *Aclees senegalensis* Fairmaire, 1891, *Niphades angustus* Faust, 1898, and an unidentified species of *Niphades*.

A single specimen was hand-collected in the Loma Mountains of Sierra Leone at an altitude of 1050 m at around 17:30 in the afternoon on a cloudy day with sunny spells. The specimen was found in June in a closed-canopy, sub-montane forest. The specimen was collected at the base of a white mushroom, which was growing on a rotting piece of wood at less than 1 cm above the leaf-litter-covered ground [14]. The general environment is shown in Figure 1B.

The six specimens collected in São Tomé were collected in banana and carrion pitfall traps. The general environment as well as one of the pitfall traps in which the specimens were collected is shown in Figure 1C. This is presumably a chance occurrence, as explained in the discussion section of this paper.

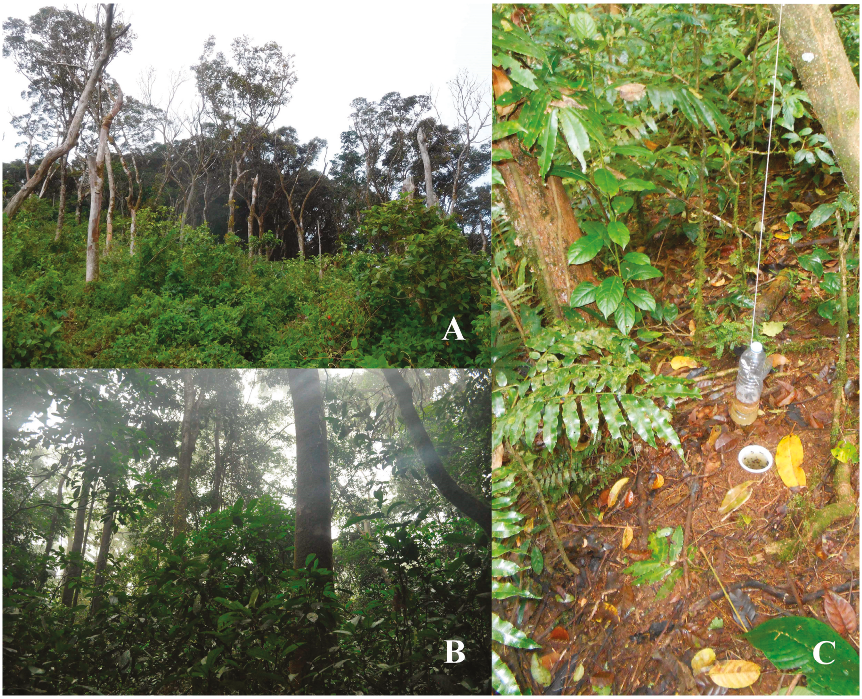

Figure 1. Environments in which *Titilayo geiseri*, *T. garnerae* (**A**); *T. takanoi* (**B**) and *Titilayo saotomense*, *T. turneri*, and *T. barclayi* (**C**) were collected.

2. Materials and Methods

This study was made possible by examining collection materials, both historical and newly collected, deposited at the Natural History Museum, London, UK (BMNH) and at the Muséum national d´Histoire naturelle, Paris, France (MNHN).

Descriptions are based on external and internal characters, including male and female genitalia where possible.

Specimens were relaxed in deionised water and heated on a Tecam Dri-Block DB-1. The abdomen was then removed and placed in a 10% KOH solution to macerate the internal connective tissues and reveal the sclerotised terminalia. Following maceration, the cleaned genitalia and abdomen were transferred into deionised water for cleaning and to wash off the KOH, and thence into glycerol for imaging and preservation. Dissected genitalia are preserved in glass microvials pinned beneath the specimen and the abdomen within in the microvial or glued to a card pinned beneath the rest of the specimen. A Zeiss SV11 dissecting microscope was used to prepare and transfer the genitalia from distilled water onto glycerol.

Habitus photographs were taken using a Canon 5dsR camera with 100 mm macro lens. Terminalia were placed in a cavity microscope slide with glycerol or KY gel and photographs that were taken using a Canon EOS 55D camera attached to a Leica 125 stereomicroscope. Habitus and terminalia images were stacked using Helicon Focus stacking software.

Specimen label transcriptions are written verbatim; lines on a label are separated by a slash "/".

Specimen lengths and widths were measured as in Figure 5 of Lyal & Curran [15]. Total length was taken from the front of the head capsule to the rear of the elytra; all of the length measurements were made in lateral view but in the same plane, not as in Lyal & Curran Figure 6 [15]. The pronotal width and elytral width refer to the maximum width of each. The eye height (vertical measurement) and length (horizontal measurement) were taken laterally and a ratio calculated.

The distribution map for *Aethiopacorep* and *Titilayo* species was made using Quantum GIS [16].

The morphology of anchonine genitalia is very different in some respects to that of other Molytinae. The key apomorphies of the Anchonini s. str. are: male spiculum gastrale frequently with anterior end expanded into broad circular plate; tegmen often largely membranous, with toughened membrane forming a folded sleeve around base of penis body, bearing dense feathery tendons; penis apodemes lacking sclerotised connection to penis body, but instead arising from the membrane folded around the tegmen; female with bulbous, internally folded 'bursal atrium' between vagina and bursa; bursa (if present) with narrow duct connecting it to bursal atrium. The 'bursal atrium' needs a little more explanation; in most weevils, the bursa (bursa copulatrix) is said to arise from the vagina at the junction with the common oviduct; the spermathecal duct inserts most frequently at the meeting point of the bursa and the common oviduct, although in some taxa it inserts ventrally on the bursa away from where it meets the common oviduct. There is generally little if any difference in the membrane of the bursa and the vagina, although there may be a pigmented or sclerotised area around the insertion of the spermathecal duct, so the two areas are effectively differentiated by the landmark of the common oviduct. In Anchonini, there is in most species an expanded and sometimes folded area with a thicker membrane around the junction with the common oviduct, and into which the spermathecal duct inserts and the bursa proper arises (if present). The membrane of the bursa is generally different from that of the bursal atrium. Homologies of these structures are difficult to establish, but the terminology serves to identify the regions. The bursa in most Anchonini (if present) is connected to the bursal atrium by a narrow 'bursal duct'. A labelled diagrammatic representation of male and female *Titilayo* genitalia is given in Figure 2A–D.

The material examined is housed in the following collections, identified by the following codens:

BMNH	Natural History Museum, London, UK
MNHN	Muséum national d'Histoire naturelle, Paris, France

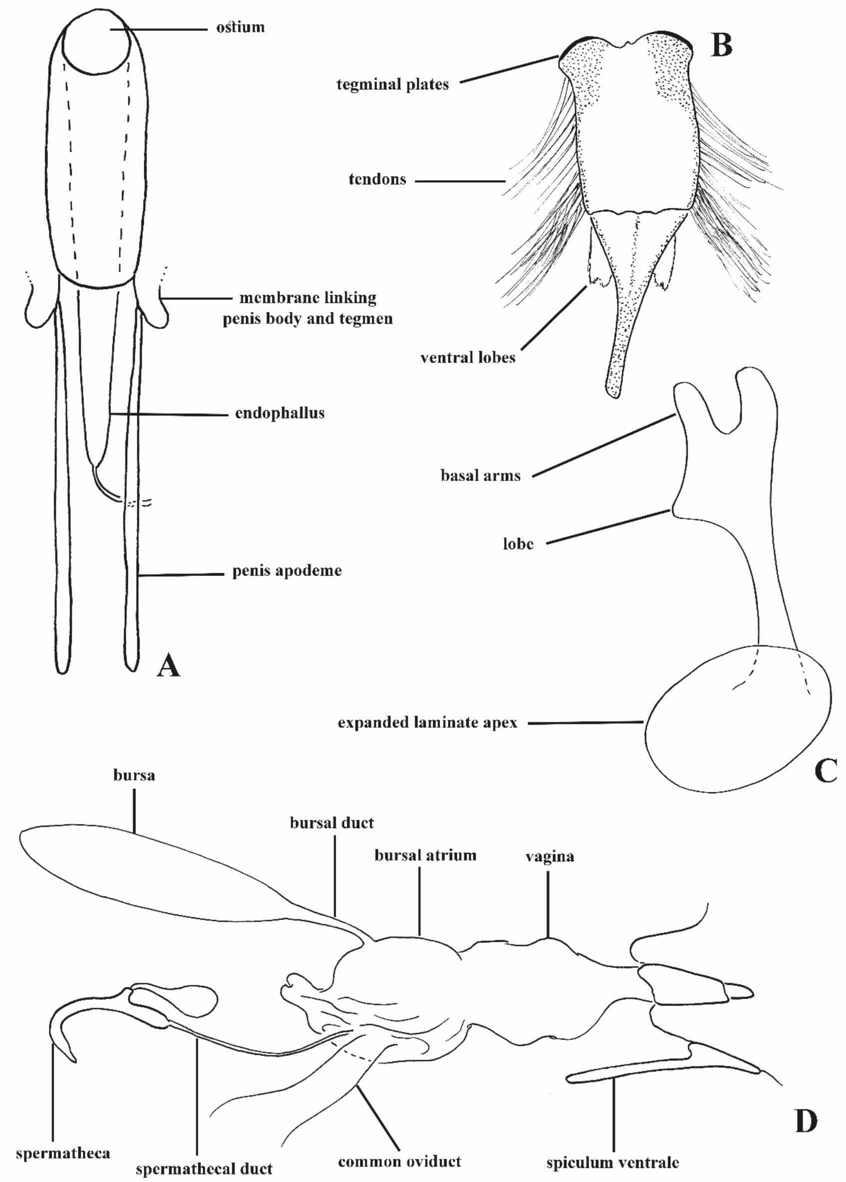

Figure 2. Diagrammatic representation of *Titilayo* male (**A**–**C**) and female (**D**) genitalia showing named areas. (**A**) aedeagus, dorsal; (**B**) tegmen, dorsal; (**C**) spiculum gastrale, dorsal; and, (**D**) female terminalia, lateral.

3. Taxonomy

Tribe **Anchonini** Imhoff 1856

Anchonidae Imhoff 1856-XX [17] (*Anchonus* Schoenherr)
Anchoninae; Faust 1892-19 [18]
Anchonina; Champion, 1902-66 [19]

Anchonini; Blatchley & Leng 1916-518,k [20]

Species of the tribe Anchonini are flightless, apterous, and easily distinguishable from other Molytinae by the following characters: basal club antennomere separate from rest of club and similar in pubescence to other funicle antennomeres; eyes flattened; ommatidia lightly domed to flattened; penis sub-cylindrical to cylindrical, penis apodemes not fused to penis, tegminal ring longitudinally expanded and mostly membranous, tendons generally densely present on tegmen; females with bursa absent, vestigial, or elongate, and with ridges running longitudinally and teeth present within; bursal atrium present, well-developed, and folded within, more so if bursa absent or vestigial. Some of these characters are discussed above; a more comprehensive description of the Anchonini genitalic characters and synapomorphies is being developed for publication by Lyal & Cristóvão [21].

These apomorphic character states are shared by the two African genera described below, placing them unequivocally in the tribe.

Genus ***Aethiopacorep*** Voisin, 1992

Acorep (*Aethiopacorep*) Voisin, 1992: 265 [22]. Type species *Anchonus africanus* Hustache, 1932, by monotypy.

Aethiopacorep; Poinar & Voisin, 2002: 381 [2] stat. nov.

Aethiopacorep Voisin, 1992 was elevated from a subgenus of *Acorep* Voisin, 1992 to genus by Poinar & Voisin [2], together with others that are described by the same author in 1992 and 1994 [22,23]. However, the reasons for this decision were not specified and a clear description of this genus was lacking.

Redescription. Length 3.8–4.2 mm; apterous; rufous.

Head. Head capsule dorsally with fine reticulation, not glossy. Eyes flat, oval; ommatidia separately convex. Scrobes diagonal, opening ventrally for most of length; not punctate internally. Rostrum punctate dorsally, laterally and ventrally, with weak irregular longitudinal carinae; each punctures with short erect scale. Club with basal antennomere separate from the rest of club, its pilosity being similar to that of funicle antennomeres.

Thorax. Pronotum with punctation deep; widest in basal half; anteriorly constricted laterally so collar formed; pair of weak submarginal prominences anteriorly. Scutellum concealed.

Elytra. Broader than the pronotum, longer than wide; weakly convex dorsally, apical declivity steep. Tubercles at base of interstriae 3 and 5 elevated and elongate, extending anterior to base on interstria 5; interstriae otherwise with scattered elongate tubercles of similar height, somewhat asymmetrical.

Legs. Femora weakly setose, pair of longitudinal rows of pale erect scales ventrally; tibiae with pale erect scales in longitudinal rows. Tibiae weakly curving ventrad apically. Tarsomere 3 symmetrical.

Terminalia. Male. Penis cylindrical, curved ventrad basally and apically, well sclerotised and pigmented. Pigmented quadrate patterns present dorso-apically within the ostium. Penis apodemes pigmented, connected to tegminal membrane instead of the base of penis. Tegminal ring expanded, unpigmented, mostly membranous, lacking parameroid lobes or tegminal plates dorsally; tegminal apodeme pigmented; tegmen lacking tendons. Spiculum gastrale slender, with basal arms elongate, sub-parallel for most of length; lateral flange anterior to basal arms absent; apex spatulate, not circular.

Female. Tergite VII with posterior margin broadly emarginate (Figure 4F). Spiculum ventrale with posterior margin convex. Vagina with membrane thin, weakly pigmented. Bursal atrium pigmented with concavity from which common oviduct and spermathecal duct arise. Bursa elongate, constricted at base. Bursal membrane thick, pigmented, lacking longitudinal folds; teeth present within bursa. Spermatheca slender, tubular, curved, with duct lobe weak, lateral.

Distribution. *Aethiopacorep* is known only from the type locality, Annobón Island of Equatorial Guinea (Figure 20).

Remarks. *Aethiopacorep* lacks any clear synapomorphies with the other African genus, *Titilayo* gen. nov. It can be distinguished from almost all other genera of Anchonini by the combination of weakly expanded apex of the male spiculum gastrale and the lack of tendons on the tegmen. The species of the American genus *Gonianchonus* share these characters but the females lack a bursa, while *Aethiopacorep* has a very large, elongate bursa. *Rhyparonotus impar* Voss, from St Helena, also has a very weak apex to the spiculum gastrale and lacks tendons on the tegmen, but in this species the bursa is far more membranous and the ommatidia are much less concave and more united. Relationships of *Aethiopacorep* are unclear but they may lie with *Acorep* and related genera, based on the form of the bursa. Although the genus was originally described as a subgenus of *Acorep*, no synapomorphies were given to justify this, a situation characteristic of most if not all Anchonine genera.

Aethiopacorep africanus (Hustache, 1932) (Figure 3A,B and Figure 4A–F)

Anchonus africanus Hustache, 1932: 50 [24].

Acorep (*Aethiopacorep*) *africanus*; Voisin, 1992: 266 [22].

Aethiopacorep africanus; Poinar & Voisin, 2002: 381 [2].

Diagnostic characters. *Aethiopacorep africanus* can be distinguished from other known African species of Anchonini by the lack of tegminal plates on the male genitalia. It can be distinguished from other known species of Anchonini both in and outside Africa by the combination of: spiculum gastrale with apex weakly expanded; tegmen lacking tendons (Figure 4B); bursa very large, elongate, membrane thick and pigmented (Figure 4D). While there are currently no other known species of *Aethiopacorep* it is expected that the detail of the male and female genitalia, as figured here, will be sufficient to distinguish *A. africanus*.

Redescription. Length 4.1–4.6 mm. Apterous. Completely rufous.

Head. Rufous. Head capsule dorsally with fine reticulation, not glossy. Eyes medium-sized, approximately 0.83 × depth of rostrum where it meets head capsule; dorsal margin lower than top of rostrum basally; flat, oval, just less than twice as long as deep; ommatidia hemispherical and well-defined, lacking dips at the centre of each ommatidium. Rostrum arising abruptly from head capsule with dorsal margin and head capsule forming an obtuse angle; no notch dorsally between head capsule and rostrum, weak notch laterally at base of scrobe. Rostrum curved ventrad, more strongly so distal to antennal insertions; strongly punctate dorsally, laterally and ventrally, punctures sometimes confluent along rostrum, especially laterally, causing irregular longitudinal carinae dorsally; punctation in females shallower and rostrum smoother, especially from antennal insertions to apex; each puncture with short (1/2 puncture length) golden scale. Antennae rufous. First funicle antennomere shorter than second; club with basal antennomere separate from rest of club but broadened to meet rest of club, less setose and more glossy than other club antennomeres, which are obscured by dense golden setae; club oval.

Thorax. Pronotum approximately 0.4 times the length of elytra; pronotal breadth: length ratio 1.22; broadest before middle; collar apparent laterally; dorsally convex in lateral aspect. Punctation coarse, deep; anteriorly submarginally with weak prominence on each side of midline punctures at these protuberances, as well as dorsally across broadest part of pronotum, with scales that are up to 3.5 times longer than those found over rest of pronotum.

Elytra. Elytra broader than pronotum; approximately 1.4 times longer than broad; lightly convex dorsally with steep apical declivity. Interstria 1 lacking tubercles; other interstriae with elevated, elongate tubercles weakly or not symmetrical between elytra, basal tubercle on interstriae 3 and 5, that on 5 projecting anterior to basal elytral margin. Each tubercle with several long golden scales that are identical to those on pronotal protuberances.

Legs. Tibia curving ventrad apically, more strongly in fore tibia than others. Neat rows of sparse setae running longitudinally between base and apex. Ventral longitudinal row of teeth present at apical 1/3 of all tibiae. Single anterior apical setal comb and double posterior apical setal comb on fore tibia. Tarsomere 3 symmetrical, lobes separate for 1/3 length of tarsomere.

Genitalia. Male (Figure 4A–C). Penis cylindrical, curved ventrad basally and apically; thoroughly sclerotised and pigmented brown, including dorsally; pigmented quadrate patterns apically. Endophallus with longitudinal dense bands of very small teeth. Ductus seminalis arising subapically on endophallus. Penis apodemes connected to an unpigmented membrane instead of the base of penis, pigmented dark brown. Tegmen unpigmented with exception of its apodeme, which is fully pigmented; tegminal ring membranous, expanded, apodeme extending beyond rest of tegmen by about 0.2 of total tegmen length; tendons absent. Spiculum gastrale with apex spatulate. Apodemes of spiculum gastrale fused medially.

Female (Figure 4D–F). Tergite VII with posterior margin broadly emarginate. Spiculum ventrale with posterior margin convex. Vagina with membrane thin, unpigmented. Bursal atrium pigmented with concavity from which common oviduct and spermathecal duct arise, slightly separate. Bursa elongate, constricted at base, lacking longitudinal folds; bursal membrane thick, pigmented; teeth present within bursa. Spermatheca slender, curved, of similar diameter throughout.

Type locality: Equatorial Guinea, Annobón Island.

Type material: NEOTYPE, here designated, ♂, with labels: "Neo- / type" (purple-bordered disk) and "ANNOBON IS: / 9.vii.1959-22.vii.1959. / Cambridge Univ. Exped. / B.M.1960-51" and "NEOTYPE / *Anchonus africanus* / Hustache, 1932 / Cristóvão & Lyal 2018". PARANEOTYPES: 2♀♀with same data as Neotype and with labels: "Paraneo- / type" (yellow-bordered disk) and "PARANEOTYPE / *Anchonus africanus* / Hustache, 1932 / Cristóvão & Lyal 2018".

Depository: BMNH.

Neotype designation. A neotype is designated for *Anchonus africanus* Hustache, 1932 in accordance with Article 75.3 of the Code of Zoological Nomenclature. This was the first species of Anchonini to be described from an African locality, Annobón island. Three syntypes were deposited in Hamburg Museum. In 1943, during World War II, Hamburg was bombed; Weidner [10] states that the Museum's Coleoptera collection was burnt, with the exception of the larval spirit collection. The account of some of the lost material [9,10], is partial and it mentions only one Anchonini species (*Anchonus assimilis* Voss, 1954). Professor Thure Dalsgaard has confirmed [25] that no specimens of the species could be found in the collection in Hamburg. Hustache is known to have sometimes kept syntype specimens as desiderata for his collection, currently found in the MNHN [26]. However, Hélène Perrin confirms [27] that no specimen(s) could be found in Hustache's collection or the main collection of Anchonini in the MNHN.

Figure 3. *Aethiopacorep africanus*, habitus. (**A**) *Ae. africanus*, dorsal; and, (**B**) *Ae. africanus*, lateral.

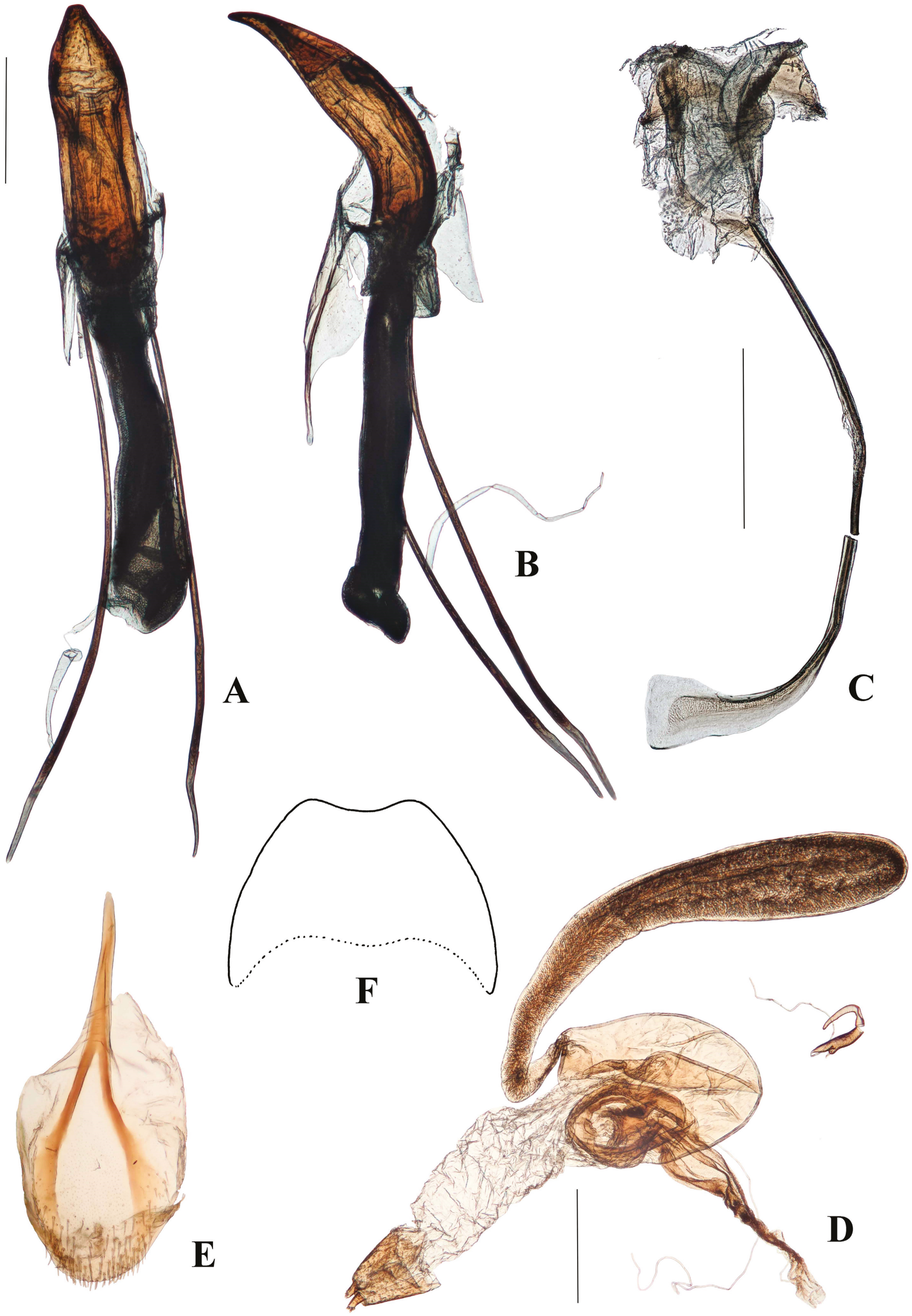

Figure 4. *Aethiopacorep africanus*, genitalia. (**A**) male aedeagus, dorsal; (**B**) male aedeagus, lateral; (**C**) male spiculum, dorsal; (**D**) female terminalia; (**E**) female spiculum, ventral; (**F**) female TVII. All scales 0.5 mm.

The designation of the Neotype is performed here with the express purpose of clarifying the taxonomic status of the species. Anchonini are a very speciose group, and morphological differences between species are often very subtle. Very few of the published descriptions are adequate to distinguish species, and virtually none have images of the male or female genitalia, which appear to hold good diagnostic characters. Hustache's description of *A. africanus* is adequate but it contains no characters that appear at first sight to be obvious apomorphies that might serve to distinguish a species. While currently we have seen only one species from Annobón, the presence of multiple sympatric species of *Titilayo* in Africa, and similar sympatry in congeneric Anchonini species in Central and South America, suggests the likelihood of further species of *Aethiopacorep* being discovered in time. Fixing the identity of the species (and consequently the genus) at this point allows for a description of the new genus *Titilayo*, which might otherwise be confused with *Aethiopacorep*, and will also support current revisionary work on the tribe by Cristóvão & Lyal.

A statement of distinguishing characters is given above (Art. 75.3.2).

The specimens listed above, which form the neotype series, are from the type locality of Annobón Island and fit the description given by Hustache [24].

Genus ***Titilayo*** Cristóvão and Lyal **gen nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:CE3721B4-01CA-4A47-AAC2-DE71116B8A02

Type species. *Titilayo geiseri* **sp. nov.**

Diagnostic characters. Despite its external similarity to *Spinanchonus* Voisin 1992 [22,23], especially *S. galapagoensis*, *Titilayo* gen. nov. can be separated from all other genera of Anchonini by the presence of tegminal plates in the male terminalia (Figures 6E, 12D, 13, 15C and 17C), which is an apomorphy within this tribe (see "remarks").

Description. Length 3.5–5 mm; apterous; black and rufous to completely black. Often with gummy substance coating part of body.

Head. Black to black and rufous; capsule dorsally with fine reticulation, not glossy. Eyes not protruding, oval, ommatidia separately weakly convex. Scrobes lateral for at least first quarter, then running ventrally until base; not punctate internally; antennal insertion closer to apex of rostrum in male than in female. Rostrum punctate dorsally, laterally, and ventrally sometimes shallowly, so, each puncture bearing a short scale that is no longer than the radius of each puncture; weak and generally irregular longitudinal carinae present latero-dorsally; often a dorsal notch present at base of rostrum where it meets head capsule. Club with basal antennomere separate from the rest of the club; other club antennomeres obscured by dense golden setae.

Thorax. Pronotum with punctation deep, strong, sometimes punctures confluent and broad glossy irregular ridges formed between them; widest in basal half, generally fairly abruptly widened behind collar; collar constriction strong laterally and weaker dorsally; pair of sometimes very weak submarginal prominences anteriorly, bearing erect scales. Scutellum concealed.

Elytra. Black, sometimes with rufous patches. Broader than the pronotum, longer than wide; weakly convex dorsally, apical declivity steep. Tubercles at the base of interstria 3 and 5 elevated and elongate, beginning at or just past the base of the elytra. Tubercles small to large and elliptical with some merging together, sometimes extending anterior to base on interstria 5; interstriae otherwise with scattered elongate tubercles that are generally of similar height, being somewhat asymmetrical.

Legs. Black, rufous, or both. Femora with disorganised deep punctation, each puncture bearing a golden seta of approximately the same diameter of the puncture. Tibiae curving apically, with single anterior and double posterior apical setal comb. Tarsi rufous.

Abdomen. Tergites I-VI weakly or not pigmented. Rectal ring present, with posteriorly convex loops between six nodes.

Terminalia. Male. Penis sub-cylindrical to cylindrical, weakly curving basally and apically, well sclerotised and pigmented. Pigmented quadrate patterns present dorso-apically inside ostium. Penis apodemes pigmented dark-brown, connected to tegminal membrane instead of base of penis. Tegminal ring expanded, unpigmented, mostly membranous, with two asymmetrical lobes ventrally and two tegminal plates dorsally (see remarks); tegminal ring and plates bearing tendons. Spiculum gastrale with apex large, concave, laminate; basal arms of similar size, right arm (in dorsal aspect) with crest-like lobe anteriorly.

Female. Vaginal membrane weakly pigmented. Bursal atrium expanded and folded internally, creating a concavity from which common oviduct arises, generally expanded, and membranous between the folded area and the junction with the bursal duct (Figures 10B, 12G, 15F and 19B), the only exception being found in *T. garnerae* (Figure 8F). Bursa elongate with narrow or broad bursal duct; minute teeth present in bursa. Collum of spermatheca expanded or more cylindrical.

Composition. Other than the type species, this genus currently includes *Titilayo takanoi* sp. nov., *T. garnerae* sp. nov., *T. perrinae* sp. nov., *T. saotomense* sp. nov., *T. turneri* sp. nov. and *T. barclayi* sp. nov.

Distribution. Ivory Coast, Mount Nimba; Sierra Leone, Loma Mountains; and São Tomé e Príncipe, Isle of São Tomé (Figure 20).

Etymology. The name "*Titilayo*" comes from the Yoruba language which is spoken in many countries in Western Africa and means "everlasting joy". Despite it being a name that is given to females, it is here considered as neuter.

Remarks. Members of the Anchonini generally lack parameroid lobes, the known exceptions being *Capsonotus smilodon* (Voisin, 2006), *Rhyparonotus libertinus* (Faust, 1892) and *Sulconotus scapha* (Faust, 1893). In *Titilayo*, the tegmen bears a pair of transverse sclerotised, pigmented plates dorsally on the ring, extending weakly posteriad (Figure 13). These "tegminal plates" may join dorsally, as seen in *Titilayo geiseri* (Figure 6A,B,E) or are separated, to various degrees, on the membranous, unpigmented tegminal ring, as seen in *T. perrinae* (Figures 12A,B,D and 13), *T. saotomense* (Figure 15A–C), and *T. turneri* (Figure 17A–C). The plates may also extend apical and basally (e.g., *T. geiseri*) or apically only (e.g., *T. perrinae*) (penis position as reference). The plates bear tendons that are similar to those found throughout the apically-expanded, asymmetrically-lobed tegminal ring, albeit smaller. The tegminal plates are not considered homologous to the parameroid lobes, but a novel apomorphic structure, due to the differences of the structures' position and morphology.

The tegmen is more sclerotised and less membranous in *Titilayo* than in most other Anchonini.

Titilayo gen. nov. can be easily distinguished from *Aethiopacorep*, which lacks tegminal plates, displays no tendons on the expanded, membranous tegmen and it possesses an underdeveloped laminar extension at the apex of the spiculum gastrale, which is not thickened and concave as in *Titilayo* species. The membrane of the bursa copulatrix in *Titilayo* is thinner and bears faint longitudinal ridges (cf. many Central and South American Anchonini species where the females present the same type of elongate bursa with well-marked ridges). In addition, most species of *Titilayo* have a dorsal notch at the base of the rostrum where it meets the head capsule (not *T. perrinae*); *Aethiapocorep* does not have such a notch.

Titilayo geiseri Cristóvão and Lyal **sp. nov.** (Figure 5A,B and Figure 6A–F)
http://zoobank.org/urn:lsid:zoobank.org:act:F80DDC17-B8CB-4D8F-89AB-5928C6C93E7B

Diagnostic characters. *T. geiseri* is most similar to *T. garnerae.* It differs from this species in the following characters: pronotum with widest part approximately 0.4 of length from anterior margin (cf. 0.3 of length); pronotal punctures smaller (ca. one-fifteenth length of pronotum on midline cf. one tenth of length); endophallus with long dorsal pigmented lobe (cf. lacking pigmented lobe); entrance of ductus seminalis pigmented near endophallus; ratio of penis depth at anterior of ostium to penis body length more than 0.31 (cf. less than 0.26). It can be distinguished from *T. takanoi* by the following character: basal tubercle of 5th interstria less than one elytral puncture diameter from the basal margin (cf. more than one puncture diameter).

Figure 5. *Titilayo geiseri*, habitus. (**A**) *T. geiseri*, dorsal; (**B**) *T. geiseri*, lateral.

Description. Length 4.4 mm (n = 1). Apterous. Black.

Head. Eye with height approximately 0.75 of depth of rostrum at base; dorsal margin below dorsal margin of rostrum at base; oval, 0.4 times as wide as high; ommatidia well-defined. Rostrum curved ventrad, more strongly basally than distally; transversely notched dorsally where it meets head capsule, and laterally before eyes; scrobe visible laterally for less than half its length, opening ventrally in basal half, in male visible dorsally at antennal insertion. Rostral punctation deep, large, irregularly distributed; longitudinal carinae not developed; golden scale in each puncture at most same length as puncture diameter, shorter in most areas. Head capsule shallowly concave and rugose dorsally to eyes, rugose areas meeting dorsally behind short medial glossy triangular area. Antennae rufous. 1st and 2nd funicle antennomeres subequal in length.

Thorax. Prothorax approximately 0.42 length of elytra dorsally, 1.8 times wider than long (n = 1); abruptly widening from collar to widest point at approximately 0.4 of length; punctures dorsally large (ca. one-fifteenth length of pronotum on midline), deep, circular, with rugose and sometimes glossy ridges between them; anterior margin of pronotum weakly emarginate; collar punctate dorsally and laterally, with submarginal prominence dorsally either side of midline; dorsal punctures each with erect scale as long as diameter of puncture, scales shorter laterally; weak tuft of erect scales on submarginal prominences.

Elytra. Weakly convex dorsally, apical declivity steep. Approximately 1.3 times longer than wide (n = 1). Tubercles at base of interstria 3 submarginal, at base of interstria 5 very nearly reaching basal margin of elytra and no more than diameter of one interstrial puncture from it; interstrial tubercles elliptical, all of similar height, each with row of yellow erect scales slightly shorter than those found anteriorly on pronotum, but longer than strial scales. Strial punctures small, distinct, separate, each with scale shorter than puncture diameter.

Legs. Tibial punctures confluent longitudinally forming neat rows, each with a row of erect scales, these more hair-like ventrally. Tibiae lacking ventral longitudinal row of teeth. Tarsomere 3 symmetrical.

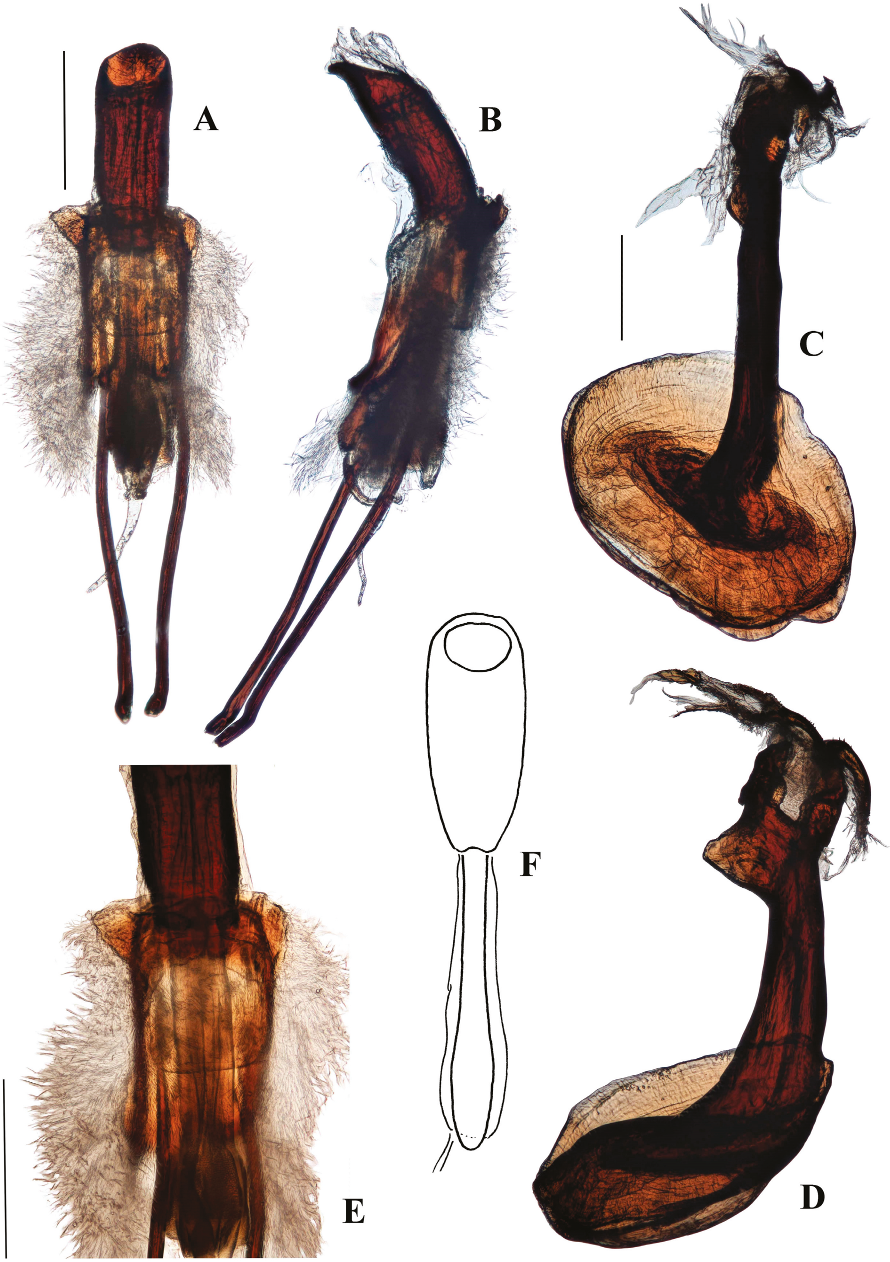

Figure 6. *Titilayo geiseri*, genitalia. (**A**) aedeagus, dorsal; (**B**) aedeagus, lateral; (**C**) spiculum gastrale, dorsal; (**D**) spiculum gastrale, lateral; (**E**) tegminal plates detail, dorsal; and, (**F**) penis and endophallus (penis apodemes and tegmen omitted) showing dorsal lobe in endophallus. All scales 0.5 mm.

Genitalia. Male (Figure 6A–F). Penis cylindrical, sclerotized and pigmented reddish-brown, curved ventrad basally and at apex. Ostium extending to first quarter of penis length; depth of penis at ostium 0.31–0.37 of ventral length of penis body. Endophallus with contiguous small, granular teeth particularly distally (when everted); dorsal elongate pigmented lobe present; ductus seminalis inserted ventro-apically, pigmented near endophallus. Tegmen with ring weakly pigmented reddish-brown; dorsally with two well-developed tegminal plates that are connected dorso-medially (Figure 6E), ventrally with short pigmented lobe asymmetrically on either side of apodeme; tegminal apodeme present, approximately one-quarter of length of tegmen, including apodeme; tendons well-developed. Female not known.

Type locality: Ivory Coast, Mount Nimba.

Type material: HOLOTYPE ♂, with labels: "Holo- / type" (red-bordered disk) and "IVORY COAST 1100–1430m / Mt Nimba. Track and crest 5Km / SW of Richard Molard peak. / From: 7°35′24″N, 08°25″43W / To: 7°35′28″N, 08°26′09″W" and "6.V.2016. General / collecting. Aristophanous, M., Geiser, M., Moretto, P., leg. / BMNH(E)2016-109 / Trip Ref: CI-003(ANHRT 17)" and "[QR code] / "NHMUK010871077" and "HOLOTYPE / *Titilayo* / *geiseri* / Cristóvão & Lyal 2018". PARATYPE ♂, same data as holotype and with labels: "Para- / type" (yellow-bordered disk) and "[QR code] / "NHMUK010871078" and "PARATYPE / *Titilayo* / *geiseri* / Cristóvão & Lyal 2018".

Depository: BMNH.

Etymology. This species is named after our friend and colleague Dr Michael Geiser, who caught the first series of Anchonini from mainland Africa.

Titilayo garnerae Cristóvão and Lyal **sp. nov.** (Figure 7A,B and Figure 8A–F)

http://zoobank.org/urn:lsid:zoobank.org:act:91D3734C-EF3F-41A1-819C-19CF65EF70D9

Diagnostic characters. *T. garnerae* is most similar to *T. geiseri.* It differs from this species in the following characters: pronotum with widest part approximately 0.3 of length from anterior margin (cf. 0.4 of length); pronotal punctures larger (ca. one-tenth length of pronotum on midline cf. one-fifteenth of length); endophallus lacking dorsal longitudinal pigmented lobe (Figure 8A) (cf. with a weakly pigmented longitudinal dorsal lobe (Figure 6A,F); entrance of ductus seminalis not pigmented; ratio of penis depth at anterior of ostium to penis body length less than 0.26 (cf. more than 0.31). It can be distinguished from *T. takanoi* by the following characters: basal tubercle of 5th interstria less than one elytral puncture diameter from basal margin (cf. more than one puncture diameter); female genitalia (Figure 8F) lacking large expansion at apex of bursal atrium, at base of bursal duct (cf. large expansion present, Figure 10B); collum of spermatheca only slightly elongate (cf. longer than cornu).

Description. Length 3.8–5.3 mm (mean 4.91 mm, n = 5). Apterous. Black.

Head. Eye with height approximately 0.75 of depth of rostrum at base; dorsal margin lower than top of rostrum basally; oval, 0.4 times as wide as high; ommatidia well-defined. Rostrum fairly evenly curved ventrad; transversely notched dorsally where it meets head capsule, and laterally before eyes; scrobe visible laterally for less than half its length, opening ventrally in basal half, in male visible dorsally at antennal insertion. Rostral punctation deep, large, irregularly distributed, punctures smaller and shallower in female; longitudinal carinae not developed; golden scale in each puncture approximately same length as puncture diameter, shorter in some areas. In females, rostrum does not broaden apically to antennal insertions. Head capsule shallowly concave and rugose dorsally to eyes, rugose areas meeting dorsally or separated by two weak ridges. Antennae rufous; 2nd funicle antennomere slightly longer than 1st.

Thorax. Prothorax 0.43–0.47 length of elytra dorsally (mean 0.45, n = 5), 1.12–1.19 times wider than long (mean 1.15, n = 5); widening abruptly from collar to widest point at approximately 0.3 of length; punctures dorsally large (ca. one-tenth length of pronotum on midline), deep, circular, sometimes confluent, with glossy ridges between them; anterior margin of pronotum weakly emarginate; collar punctate dorsally and laterally, with sometimes weak submarginal prominence dorsally on either side of midline; dorsal punctures each with erect scale as long as diameter of puncture, scales shorter laterally; weak tuft of erect scales on submarginal prominence.

Elytra. Weakly convex dorsally, apical declivity steep. Approximately 1.3–1.4 times longer than wide (mean 1.38, n = 5). Tubercles at base of interstriae 3 and 5 submarginal, that at base of interstria 5 separated from margin by no more than diameter of one interstrial puncture; interstrial tubercles elliptical, all of similar height, each with row of yellow erect scales of similar length to those of pronotal tufts. Strial punctures small, distinct, separate, and each with scale approximately half as long as puncture diameter.

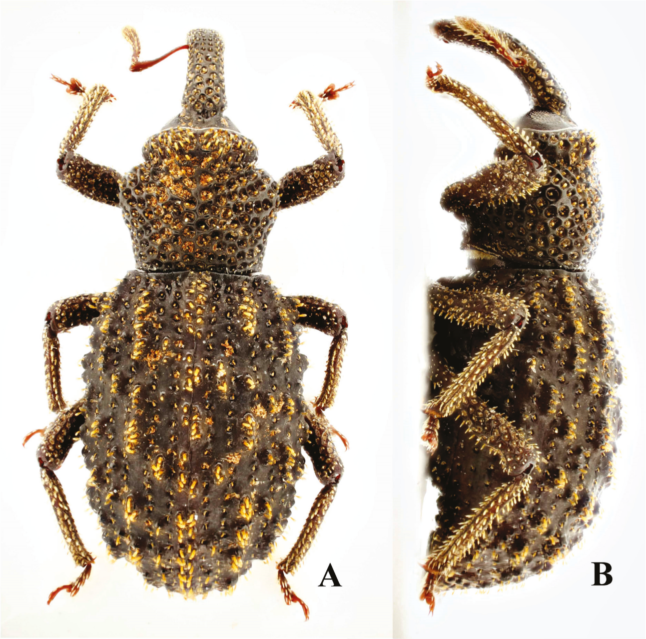

Figure 7. *Titilayo garnerae*, habitus. (**A**) *T. garnerae*, dorsal; and, (**B**) *T. garnerae*, lateral.

Legs. Tibial punctures confluent longitudinally forming neat rows, each with row of erect scales, these slightly narrower ventrally. Tibiae with ventral longitudinal row of teeth present, very inconspicuous. Tarsomere 3 symmetrical.

Genitalia. Male (Figure 8A–D). Penis cylindrical, sclerotized and pigmented reddish-brown, curved ventrad basally and at apex. Ostium extending to first quarter of penis length; depth of penis at ostium 0.25 of ventral length of penis body. Endophallus with contiguous small, granular teeth particularly distally (when everted), but lacking dorsal pigmented lobe; ductus seminalis inserted ventro-apically, not sclerotised near endophallus. Tegmen with ring weakly pigmented reddish-brown; dorsally with tegminal plates lacking pigmented connection, extending laterally anteriad (Figure 8A); ventrally with short unpigmented lobe asymmetrically on either side of apodeme; apodeme present, approximately one quarter total length of tegmen including apodeme; tendons well-developed.

Female (Figure 8E,F). Posterior margin of tergite VII emarginate. Spiculum ventrale with posterior margin convex. Vaginal membrane thin, weakly pigmented. Bursal atrium expanded laterally with few internal folds; bursal membrane thick, pigmented; numerous sharp teeth present within bursa; bursa with indistinct longitudinal folds. Spermathecal duct arising at base of bursa away from common oviduct. Spermatheca with collum bulbous (Figure 8F).

Type locality: Ivory Coast, Mount Nimba.

Type material: HOLOTYPE ♂, with labels: “Holo- / type” (red-bordered disk) and “IVORY COAST 1100–1430m / Mt Nimba. Track and crest 5Km / SW of Richard Molard peak. /

From: 7°35′24″N, 08°25″43W / To: 7°35′28″N, 08°26′09″W" and "6.V.2016. General / collecting. Aristophanous, M., Geiser, M., Moretto, P., leg. / BMNH(E)2016-109 / Trip Ref: CI-003(ANHRT 17)" and "HOLOTYPE / *Titilayo* / *garnerae* / Cristóvão & Lyal 2018". PARATYPES: 4♀♀1♂with same data as Holotype and with labels: "Para- / type" (yellow-bordered disk) and "PARATYPE / *Titilayo* / *garnerae* / Cristóvão & Lyal 2018".

Depository: BMNH.

Etymology. This species is named after our friend and colleague Beulah Garner.

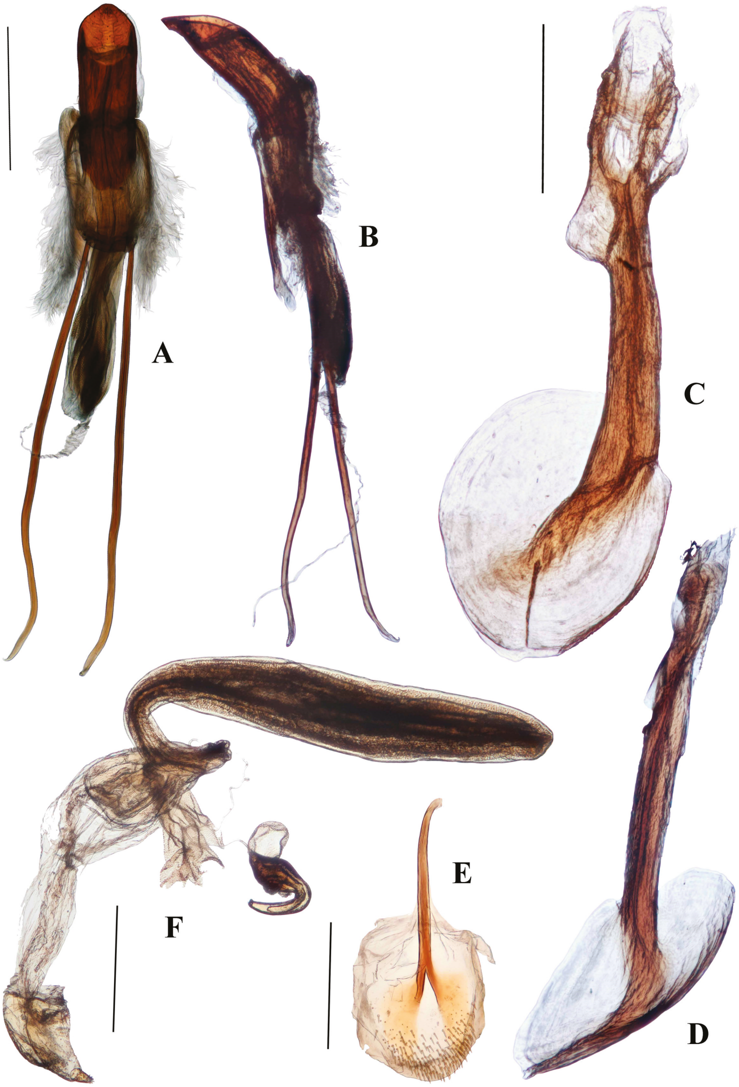

Figure 8. *Titilayo garnerae*, genitalia. (**A**–**D**) *T. garnerae*, male (**A**) aedeagus, dorsal; (**B**) aedeagus, lateral; (**C**) spiculum gastrale, dorsal; (**D**) spiculum gastrale, lateral. (**E**,**F**) *T. garnerae*, female. (**E**) spiculum ventrale; and, (**F**) female terminalia. All scales 0.5 mm.

Titilayo takanoi Cristóvão and Lyal **sp. nov.** (Figure 9A–C and Figure 10A,B)

http://zoobank.org/urn:lsid:zoobank.org:act:3DD7CE83-546A-4EFB-A597-71CEA0169286

Diagnostic characters. *T. takanoi* is morphologically similar to *T. geiseri* and *T. garnerae*. For diagnostic characters see under those species.

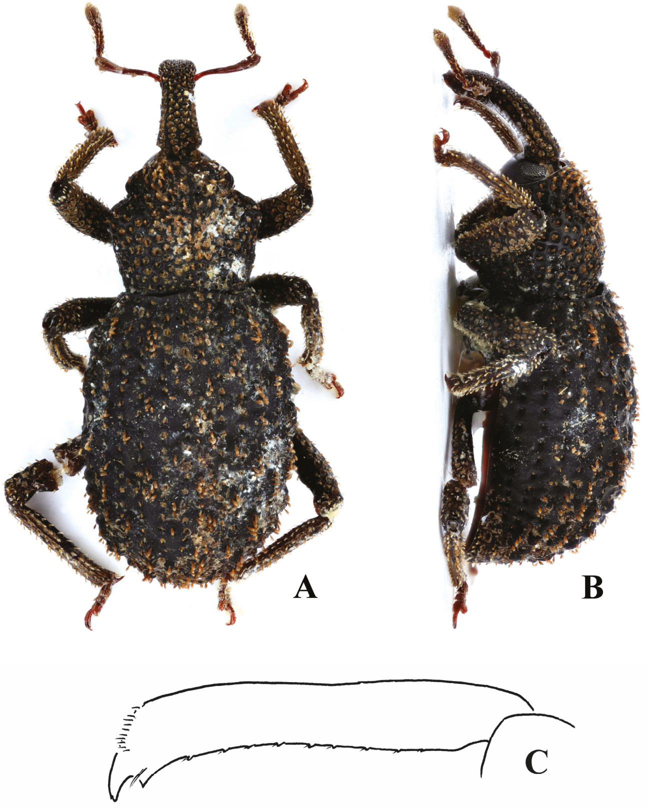

Figure 9. *Titilayo takanoi*, habitus. (**A**) *T. takanoi*, dorsal; (**B**) *T. takanoi*, lateral; and, (**C**) right foretibia, anterior view.

Description. Length 5.35 mm (n = 1). Black.

Head. Eye with height approximately 0.8 × depth of rostrum at base; dorsal margin lower than top of rostrum basally; oval, 0.8 times as wide as high; ommatidia well-defined. Rostrum curved ventrad, more strongly basally than distally; transversely notched dorsally where it meets head capsule, and laterally before eyes, slightly expanded laterally before eyes; scrobe visible laterally for more than half its length, opening ventrally for basal half; punctation deep basally dorsally, punctures more shallow and smaller distal to antennal insertions, arranged in rows basally and laterally; golden erect scale in each puncture approximately as long as the diameter of puncture. Head capsule shallowly concave and rugose dorsally to eyes, rugose areas meeting dorsally. Antennae rufous; first funicle antennomere shorter than second.

Thorax. Prothorax slightly less than 1/2 the length of the elytra dorsally, abruptly widening from collar to widest point at basal 3/5th of length. Punctation dorsally deep, varying in size, sometimes confluent on collar, with matte ridges between them; weak tuft of elongate erect scales submarginally on either side of midline dorsally; scattering of similar scales dorsally anteriorly, otherwise scales shorter, one-third the length of the long scales, and subequal to the diameter of punctures.

Elytra. Weakly convex dorsally, apical declivity steep; 1.35 times longer than wide (n = 1). Tubercles at the base of interstriae 3 and 5 submarginal; interstrial tubercles elongate, rarely rounded, some twice as long as others; dorsal tubercles slightly higher than lateral tubercles; each with row or weak tuft of yellow erect scales slightly shorter than those found anteriorly on pronotum, but longer than strial scales. Strial punctures small, distinct, separate, each with scale approximately as long as puncture diameter.

Legs. Tibial punctures confluent longitudinally, forming neat rows, each with a row of erect scales. Tibiae with ventral longitudinal row of teeth present, inconspicuous (Figure 9C). Tarsomere 3 symmetrical.

Genitalia. Male unknown.

Female (Figure 10A,B). Tergite VII with posterior margin emarginate. Spiculum ventrale with posterior margin weakly convex. Vaginal membrane thin and weakly pigmented. Bursal atrium greatly expanded ventrally, folded, more pigmented than vaginal membrane, and bearing numerous sharp small teeth internally. Bursa with numerous teeth, longer and larger than those of bursal atrium; membrane thick and well pigmented. Spermatheca weakly broadened in middle, collum elongate, cylindrical, curved (Figure 10B).

Type locality: Sierra Leone, Loma Mountains.

Type material: HOLOTYPE ♀, with labels: "Holo- / type" (red-bordered disk) and "SIERRA LEONE 1050m / Loma Mountains / Closed-canopy forest / N09°10′35″, W11°05′25″ / 7-10.vi.16 General Coll. / leg. Takano, Miles & Goff" and "BMNH(E) / 2016-196" and "[QR code] / "NHMUK010871079" and "HOLOTYPE / *Titilayo* / *takanoi* / Cristóvão & Lyal 2018".

Depository: BMNH.

Etymology. This species is named after our friend and colleague Hitoshi Takano, who caught this first recorded Anchonini from Sierra Leone.

Remarks. Despite the male being unknown, this species is being described in *Titilayo* gen. nov. due to its geographical proximity and external similarity to *T. geiseri* sp. nov. as well as to the close similarity of the female genitalia to the other species being described in this genus.

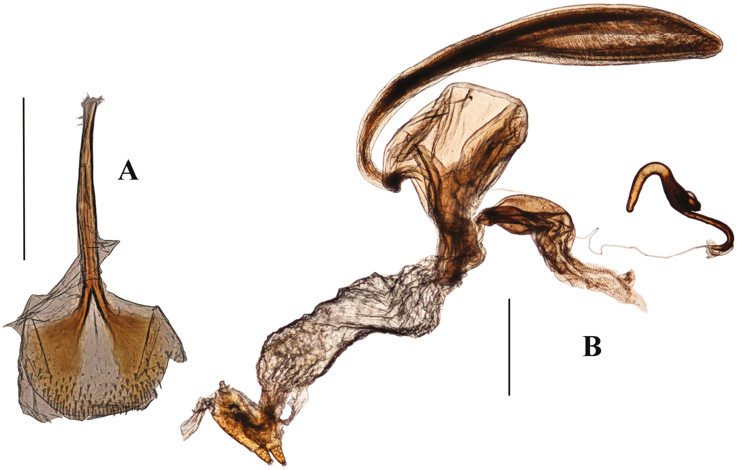

Figure 10. *Titilayo takanoi* female genitalia (**A**) spiculum ventrale; (**B**) *T. takanoi*, female terminalia; All scales 0.5 mm.

Titilayo perrinae Cristóvão and Lyal **sp. nov.** (Figure 11A,B, Figure 12A–H and Figure 13) http://zoobank.org/urn:lsid:zoobank.org:act:9A9B2900-9F58-4365-B6D9-2DD6571895FC

Diagnostic characters. This species can be separated from other *Titilayo* species by its short, weakly defined paired tufts of scales on the collar constriction and by the broad, irregular, very glossy longitudinal raised areas between the deep punctures dorsally on the pronotum.

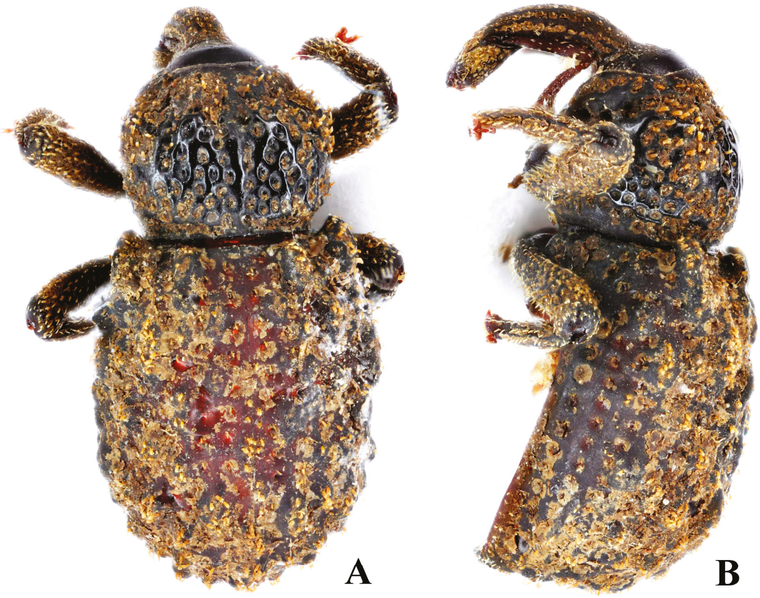

Figure 11. *Titilayo perrinae*, habitus. (**A**) *T. perrinae*, dorsal; (**B**) *T. perrinae*, lateral.

Description. Length 3.3–4.8 mm (mean 4.29mm, n = 8). Black.

Head. Eye with height slightly less than depth of rostrum at base; dorsal margin lower than top of rostrum basally; oval, 0.66 times as wide as high; ommatidia well defined. Rostrum strongly curved ventrad in basal quarter, more weakly curved distally; meeting head capsule at obtuse angle, lacking dorsal transverse notch at the base or before eyes; scrobe visible laterally only in its distal quarter, opening ventrally for most of length. Rostral punctation moderately deep dorsally and laterally, some punctures merging creating short, neat longitudinal rows separated by very weak longitudinal carinae, especially in male; golden scale in each puncture approximately same length as puncture diameter. Antennae rufous; first funicle antennomere shorter than second.

Thorax. Prothorax 0.42–0.5 of length of elytra dorsally (mean 0.45, n = 8); 1.16–1.36 times wider than long (mean 1.29, n = 8), broadest at anterior quarter of length, abruptly widening from collar dorsolaterally only, more ventrally lacking abrupt widening; collar strong dorsolaterally and dorsally; dorsally convex in profile (Figure 11B); collar impunctate, dorsal punctures behind collar large, deep, confluent longitudinally on disc and anteriorly, with broad glossy raised areas between them, these sometimes appearing to be irregular longitudinal flattened carinae; paired weak tufts of long, golden scales either side of pronotum where it is broadest; sparse tuft of long, golden erect scales submarginally on either side of midline anteriorly, scales in tufts up to three times longer than the other pronotal scales.

Elytra. Weakly convex dorsally, apical declivity steep. Approximately 1.2–1.36 times longer than wide (mean 1.29, n = 8). Tubercles at base of interstriae 3 and 5 more elevated and elongate than other elytral tubercles, tubercle on 3 reaching basal margin, that on 5 extending anteriad to base of elytra; other elytral tubercles numerous, elliptical, larger at the apical declivity than elsewhere, only weakly symmetrical between elytra; each tubercle with tuft of golden erect scales of similar length to pronotal tuft scales. Strial punctures weak, separate, each with scale approximately as long as puncture diameter; striae indistinct.

Legs. Femora black with sparse erect golden scales, more numerous distally. Tibiae dark rufous; with punctures confluent longitudinally forming rows, each with row of narrow erect golden scales or setae; ventral longitudinal row of teeth present, weak at apical quarter of all tibiae. Tarsomere 3 asymmetrical, outer lobe slightly broader than inner lobe.

Genitalia. Male (Figure 12A–F and Figure 13). Penis cylindrical, sclerotized, and pigmented reddish-brown; curved ventrad basally and apically; penis apodemes pigmented reddish-brown. Posterior of ostium at approximately 0.4 length of penis from apex of penis body. Endophallus with matrix of small, granular teeth. Ductus seminalis arising ventrally, sub-apically. Tegminal ring lightly pigmented, expanded dorsally and ventrally, with visible tendons and two asymmetrical, short lobes; tegminal plates weakly expanded dorso-posteriorly and sclerotisations not connected dorso-medially (Figures 12D and 13); tegminal apodeme present, pigmented, less than half total length of tegmen, including apodeme.

Female (Figure 12G–H). Tergite VII with posterior margin emarginate. Spiculum ventrale with posterior margin convex. Vaginal membrane thin, unpigmented. Bursal atrium expanded laterally, lobate, internally folded, and pigmented. Common oviduct arising from bursal atrium. Spermathecal duct arising on bursal atrium away from its junction with the common oviduct. Bursa elongate, constricted at base; membrane thick and pigmented; numerous sharp teeth present internally. Spermatheca slightly broadened at base of ramus, collum elongate, curved, more or less of constant diameter (Figure 12G).

Type locality: São Tomé e Príncipe, São Tomé Island.

Type material: HOLOTYPE ♂, with labels: "Holo- / type" (red-bordered disk) and "San Thomè" and "Muséum Paris / ex Coll. / R. Oberthür / 1952" and "HOLOTYPE / *Titilayo* / *perrinae* / Cristóvão & Lyal 2018". PARATYPES 1♂1♀with labels: "Para- / type" (yellow-bordered disk) "San Thomè" and "Muséum Paris / Coll. M. Pic" and "PARATYPE / *Titilayo* / *perrinae* / Cristóvão & Lyal 2018"; 1♂3♀♀with labels: "Para- / type" (yellow-bordered disk) and "San Thomé" and "Museum Paris / Collection Léon Fairmaire / 1906" and "PARATYPE / *Titilayo* / *perrinae* / Cristóvão & Lyal 2018"; 1♀with labels: "Para- / type" (yellow-bordered disk) and "San Thomè" and "Muséum Paris / ex Coll. / R. Oberthür / 1952" and "PARATYPE / *Titilayo* / *perrinae* / Cristóvão & Lyal 2018".

Depository: MNHN.

Etymology. This is one of the first anchonine species described from the island of São Tomé. It is named after Madame Hélène Perrin who brought these specimens to our attention.

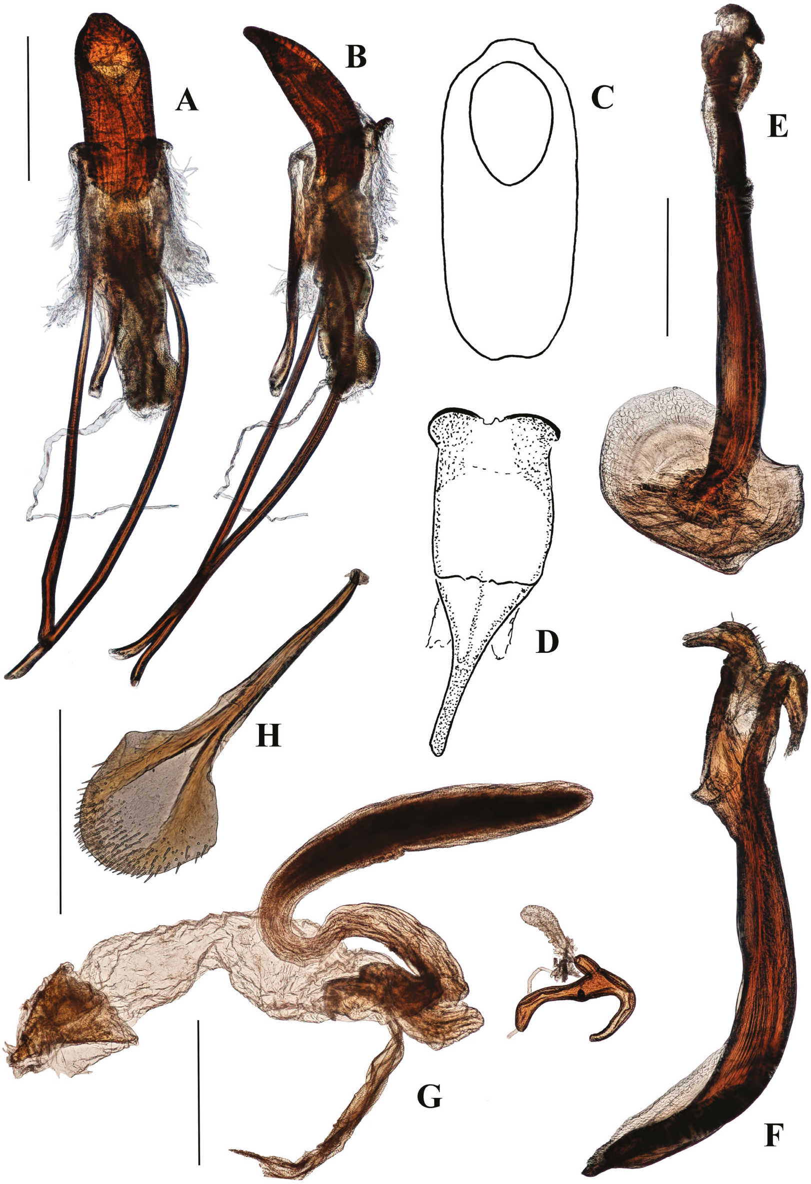

Figure 12. *Titilayo perrinae*, genitalia. (**A**–**F**) *T. perrinae*, male (**A**) aedeagus, dorsal; (**B**) aedeagus, lateral; (**C**) penis body, dorsal; (**D**) tegmen, dorsal, showing tegminal plates; (**E**) spiculum gastrale, lateral; (**F**) spiculum gastrale, dorsal. (**G**,**H**) *T. perrinae*, female (**G**) female terminalia; and, (**H**) spiculum ventrale. All scales 0.5 mm.

Figure 13. *Titilayo perrinae*, male tegminal plates, detail. Scale 0.5 mm.

Titilayo saotomense Cristóvão and Lyal **sp. nov.** (Figure 14A,B and Figure 15A–G)

http://zoobank.org/urn:lsid:zoobank.org:act:1A17524A-7DDC-4317-9E8F-FD635912D7CA

Diagnostic characters. This species can be distinguished from all other *Titilayo* by its smaller size, pronotum less than 1.1 times as wide as long (some specimens of *T. barclayi* have a smaller ratio) with convex shoulders immediately behind the collar, pronotum with inconspicuous setae, as well as erect scales, and by its very small, inconspicuous interstrial tubercles.

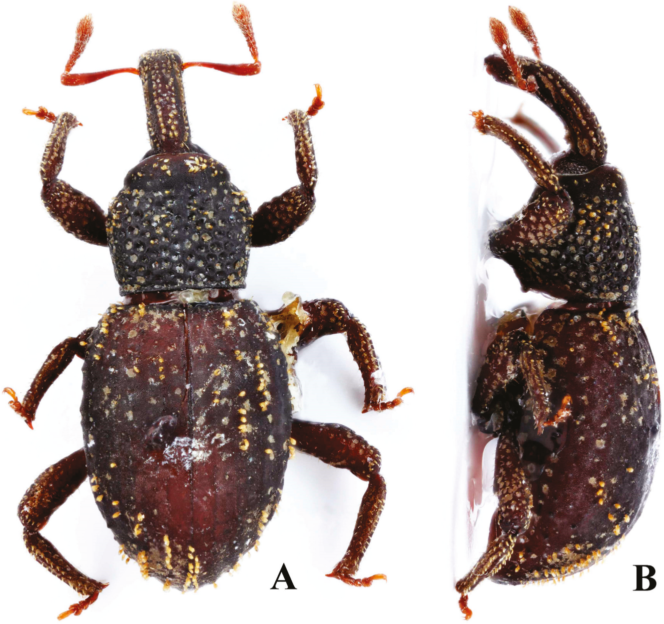

Figure 14. *Titilayo saotomense*, habitus. (**A**) *T. saotomense*, dorsal; (**B**) *T. saotomense*, lateral.

Description. Length 3.03–3.38 mm (mean 3.16mm, n = 3). Black and rufous.

Head. Eye with height approximately 0.85 depth of rostrum at base; dorsal margin lower than top of rostrum basally; oval, 0.64 times as wide as high; ommatidia well defined. Rostrum curved ventrad, more strongly basally than distally; transversely very weakly notched dorsally where it meets head capsule, more strongly so in male than female and notch may not be apparent; baso-lateral part of rostrum weakly expanded, with weak lateral notch before eyes. Scrobe visible laterally for half its length, opening ventrally in its basal half. Rostral punctation shallow, obscure, especially in female, punctures often longitudinally confluent, delimiting longitudinal carinae in male; punctation present distal to antennal insertions, shallower in females. Scales in punctures short, in neat rows, especially laterally. Antennae rufous; first and second funicle antennomeres subequal in length.

Thorax. Prothorax 0.49–0.50 times length of elytra dorsally, 1.03–1.09 (mean 1.07, n = 3) times as wide as long; widest antero-medially (at 0.4 of length), widened from collar, shoulders evenly convex. Anterior margin dorsally weakly emarginate. Punctation deep, circular, punctures not confluent dorsally, reticulation between them not glossy, punctation very weak and shallow on collar; very weak tuft of erect and semi-erect golden scales submaginally on either side of midline anteriorly, sparser tuft on each shoulder, these scales approximately same length as those elsewhere on pronotum.

Elytra. Black, with rufous patches. Weakly convex dorsally, apical declivity not steep. 1.22–1.35 longer than wide (mean 1.28, n = 3). Tubercles at base of interstriae 3 and 5 weak, submarginal although close to margin; other interstrial tubercles very weak, sparse, very weakly symmetrical between elytra; tubercles marked mainly by erect golden setae of a similar size to those in pronotal tufts; strial punctures very shallow, indistinct, mostly lacking short scales or setae.

Legs. Rufous. Femora with longitudinal rows of erect golden setiform scales ventrally, shorter scales present distally dorsally and laterally. Tibial punctures confluent longitudinally, forming neat rows, each with row of erect scales laterally and dorsally, these more setiform ventrally. Ventral longitudinal row of teeth absent. Tarsomere 3 symmetrical.

Genitalia. Male (Figure 15A–E). Penis cylindrical, sclerotised and pigmented brown, including apodemes; curved ventrad strongly in basal third and again apically. Endophallus with band of very small quadrate sclerotised reticulations along ventral side and as band around the endophallus near entrance of ductus seminalis. Ductus seminalis arising apically, slightly ventrally. Tegmen pigmented dark-brown from lateral parts of the tegminal ring through to tegminal lobes, otherwise pigmented light-brown; ring membranous, expanded; tegminal plates (Figure 15C) with weak sclerotised connection dorsally; apodeme present, pigmented dark-brown, approximately one-third total length of tegmen, including apodeme; tendons large and present from tegminal plates to lobes of tegminal ring. Darkly pigmented ring in membrane between tegmen and penis (shown in Figure 15B at same level as junction of penis apodemes and membrane).

Female (Figure 15F–G). Tergite VII with posterior margin deeply concave. Spiculum ventrale with posterior margin weakly smoothly emarginate. Vaginal membrane thin, unpigmented. Bursal atrium expanded laterally, lobate, internally folded, and pigmented. Bursa elongate, constricted at the base; membrane unfolded and unpigmented; internal teeth absent. Spermathecal duct arising next to common oviduct. Spermatheca expanded, bulbous at ramus, collum elongate, cylindrical, curved (Figure 15F).

Type locality: São Tomé, São Tomé e Príncipe.

Type material: HOLOTYPE ♂, with labels: "Holo- / type" (red-bordered disk) and "SÃO TOMÉ, 1324m, / Antenna, Bom Successo, / 00°16′31.6"N 6°36′13.7"E, / (20-29).x.2016" and "Banana trap, / Turner, C.R., Tasane, T., / BMNH(E) 2017-11, / TripRef: ST-001 (ANHRT 21)" and "[QR code] / "NHMUK010599878" and "HOLOTYPE / *Titilayo* / *saotomense* / Cristóvão & Lyal 2018". PARATYPES: 2♀♀, same data as Holotype except "Para- / type" (yellow-bordered disk) and with QR code labels numbering "NHMUK010599879" and "NHMUK010599880" respectively and "PARATYPE / *Titilayo* / *saotomense* / Cristóvão & Lyal 2018".

Depository: BMNH.

Etymology. This species is named after the island on which it was caught.

Remarks. The locality should properly be spelled "Bom Sucesso".

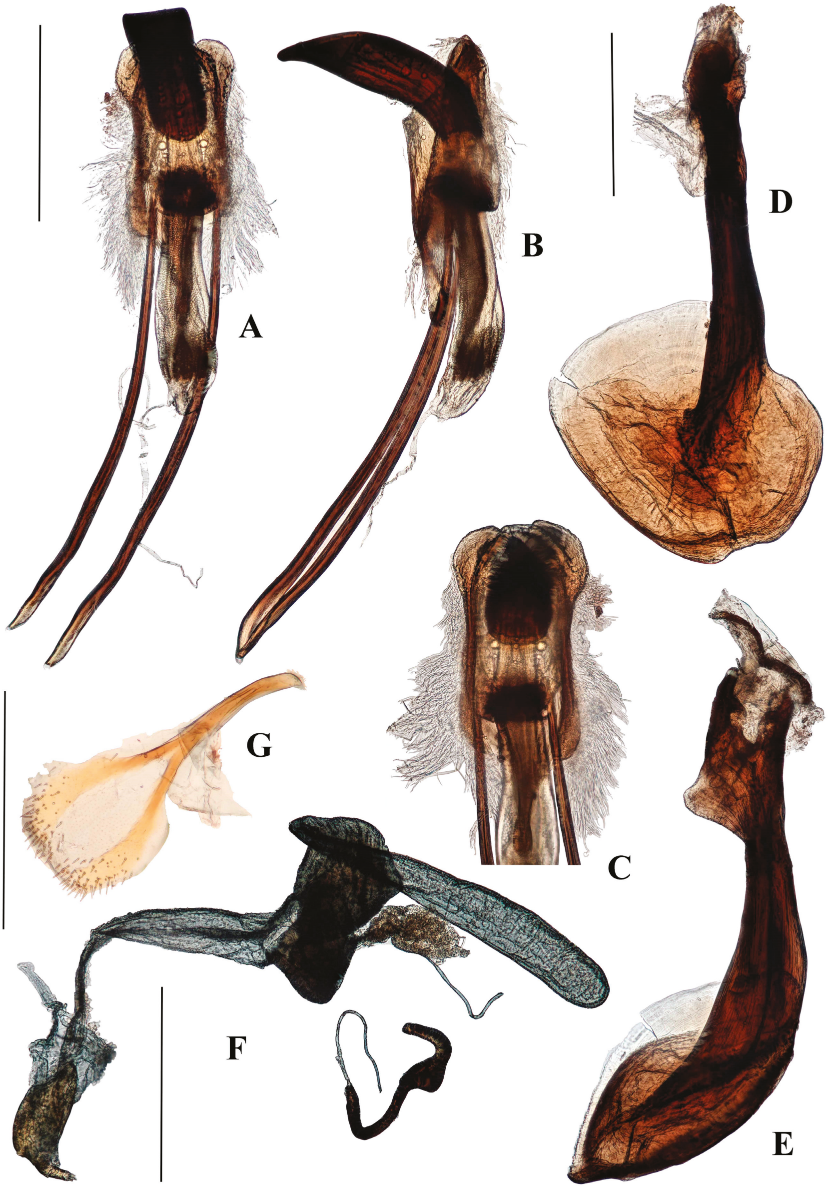

Figure 15. *Titilayo saotomense*, genitalia. (**A**–**E**) *T. saotomense*, male (**A**) aedeagus, dorsal; (**B**) aedeagus, lateral; (**C**) tegminal plates, detail; (**D**) spiculum gastrale, lateral; (**E**) spiculum gastrale, dorsal. (**F**,**G**) *T. saotomense*, female (**F**) female terminalia; and, (**G**) spiculum ventrale. All scales 0.5 mm.

Titilayo turneri Cristóvão and Lyal **sp. nov.** (Figure 16A,B and Figure 17A–E)
http://zoobank.org/urn:lsid:zoobank.org:act:8E7A4EF1-D7F1-4574-9F5B-F880B5E13CBC

Diagnostic characters. In some characters, *T. turneri* ♂is similar to *T. perrinae*: pronotal collar very short, so that pronotum appears convex in outline from close to anterior margin to its widest point in dorsal view; anterior submarginal scale tufts of pronotum weak; basal tubercle on elytral interstria 5 large and projecting anterior to base of elytra. It differs in lacking the broad glossy raised areas on the pronotum, the punctures being more oval and well-defined, and having a weak setal tuft on either side of the midline on the pronotal disc. *Titilayo barclayi* is also similar, but it is a less robust insect (Pronotal width:length 1.23 in *T. turneri*, 1.04–1.16 in *T. barclayi*; elytral length:width 1.24 in *T. turneri*, 1.27–1.33 in *T. barclayi*; in *T. turneri* the basal tubercles of elytral interstria 5 extend strongly over the basal margin of the elytra, which they do not in *T. barclayi.*

Figure 16. *Titilayo turneri*, habitus. (**A**) *T. turneri*, dorsal; and, (**B**) *T. turneri*, lateral.

Description. Length 4.19 mm (n = 1). Black.

Head. Height of eye 0.8 times depth of rostrum where it meets head capsule; dorsal margin lower than top of rostrum basally; oval, width 0.6 times height; ommatidia well-defined, separately convex. Rostrum strongly curved ventrad in basal half, nearly straight ventrally distal to antennal insertion; meeting head capsule at obtuse angle, lacking dorsal transverse notch and with very weak vertical notch before eyes; scrobe visible laterally in distal half, opening ventrally for most of length. Rostral punctures sometimes confluent dorsally and laterally basal to antennal insertions, with five matte longitudinal carinae dorsal to scrobe; more scattered distal to antennal insertions; each puncture with small golden scale subequal in length to puncture diameter. Antennae rufous; first funicle antennomere longer and broader than second.

Thorax. Prothorax 0.47 length of elytra, 1.23 × wider than long, widest at anterior 0.4 of length, abruptly widening from collar only dorsolaterally, more ventrally lacking abrupt widening; collar strong dorsolaterally; dorsally convex; strong convex shoulders present dorsolaterally; pronotum with anterior margin entire; punctures deep except on collar, where shallow, all similar in size, rarely confluent, with weakly raised matte reticulation between them; paired weak tufts of semi-erect golden scales either side of midline where pronotum is broadest, on shoulders and submarginally on either side of midline anteriorly, scales in tufts only slightly longer than other pronotal scales.

Elytra. Very weakly convex dorsally, apical declivity very steep. Length 1.23 times maximum width. Tubercles at base of interstriae 3 and 5 more elevated and elongate than other elytral tubercles, tubercle on 3 reaching basal margin, that on 5 extending strongly anteriad to base of elytra; other elytral tubercles numerous, elliptical, only weakly symmetrical between elytra; each tubercle with tuft of golden semi-erect scales of a similar length to pronotal scales away from tufts. Strial punctures weak, separate, each with scale approximately as long as puncture diameter; striae indistinct.

Legs. Black. Femora with semi-erect scales dorsally and laterally, long slender erect scales ventrally. Tibial punctures confluent longitudinally forming rows, each with row of narrow erect golden scales, these more elongate and hair-like ventrally; ventral teeth absent. Tarsomere 3 symmetrical.

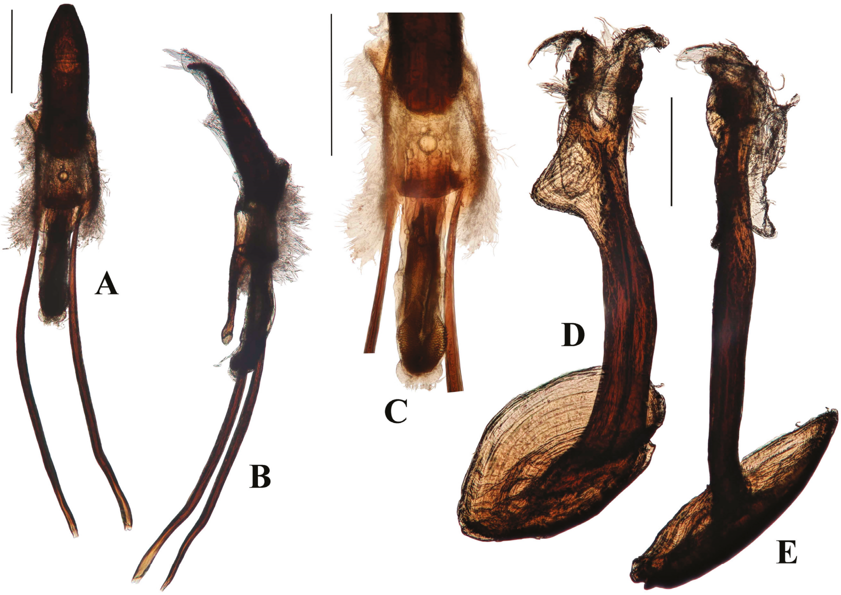

Figure 17. *Titilayo turneri* male genitalia (**A**) aedeagus, dorsal; (**B**) aedeagus, lateral; (**C**) tegminal plates, detail; (**D**) spiculum gastrale, dorsal; and, (**E**) spiculum gastrale, lateral. All scales 0.5 mm.

Genitalia. Male (Figure 17A–E). Penis dorso-ventrally compressed, sclerotised, and pigmented brown; curved abruptly ventrad basally and apically; penis apodemes pigmented dark brown; ostium vertical with respect to long axis of penis, opening into distal U-shaped furrow in penis, which extends nearly half length of penis. Endophallus with longitudinal bands of densely-packed small quadrate teeth distally, these forming broadened pads of teeth dorsally near gonopore; gonopore ventral, subapical. Microtrichiae externally at apex of endophallus.

Tegmen pigmented light brown on the tegminal plates, laterally and ventrally; tegminal plates asymmetrical, not meeting medially; apodeme free for about 0.4 total length of tegmen; membranous collar folds over approximately half way down tegmen, marked by darker band in membrane to which penis apodemes attach; membranous lobes on tegmen not present, although dense patches of tendons give a similar impression; tendons large and present from tegminal plates to level of base of apodeme (Figure 17C).

Spiculum gastrale with large, concave apical laminate extension; basal arms of similar size with one possessing a large triangular sclerotized lobe.

Female not known.

Type locality: São Tomé

Type material: HOLOTYPE ♂, with labels: “Holo- / type” (red-bordered disk) and “SÃO TOMÉ, 1324m / Antenna, Bom Successo / 00°16’31.6“N 6°36’13.7“E / (20-29). x.2016” and “Carrion pitfall / Turner, C.R., Tasane, T. / BMNH(E) 2017-11 / TripRef: ST-001 (ANHRT 21)” and “[QR code] / “NHMUK010599883” and “HOLOTYPE / *Titilayo* / *turneri* / Cristóvão & Lyal 2018”.

Depository: BMNH.

Etymology. This species is named after Dr. Clive Turner who collected this species and several other specimens and species described here from the island of São Tomé.

Remarks. The locality should properly be spelled “Bom Sucesso”.

Titilayo barclayi Cristóvão and Lyal **sp.nov**. (Figure 18A–C and Figure 19A–C)

http://zoobank.org/urn:lsid:zoobank.org:act:342BCA24-A712-478D-BBA0-4E6A8267C731

Diagnostic characters. *T. barclayi* is most similar to *T. saotomense* and to *T. turneri.* It can be distinguished from the latter by: basal tubercles on elytral interstria 5 submarginal to very weakly projecting anteriad to the elytral margin (cf. very strongly projecting, overlapping base of pronotum); no scale tufts on disc of pronotum (cf. weak scale tufts either side of pronotal midline); ratio of pronotal length to maximum width less than 1.17 (cf. more than 1.2); height of eye slightly more than three-quarters of depth of rostrum where it meets head capsule (cf. subequal). It can be distinguished from *T. saotomense* by: elytral tubercles raised, prominent, basal tubercle on interstria 5 submarginal to weakly projecting anteriad to basal margin of elytron (cf. elytral tubercles only very weakly raised, not prominent, basal tubercle on interstria 5 not projecting anteriad); pronotum raised either side of midline (cf. pronotum not raised either side of midline). The form of the tibiae with a ventral projection at the base (Figure 18C) is not known from other species.

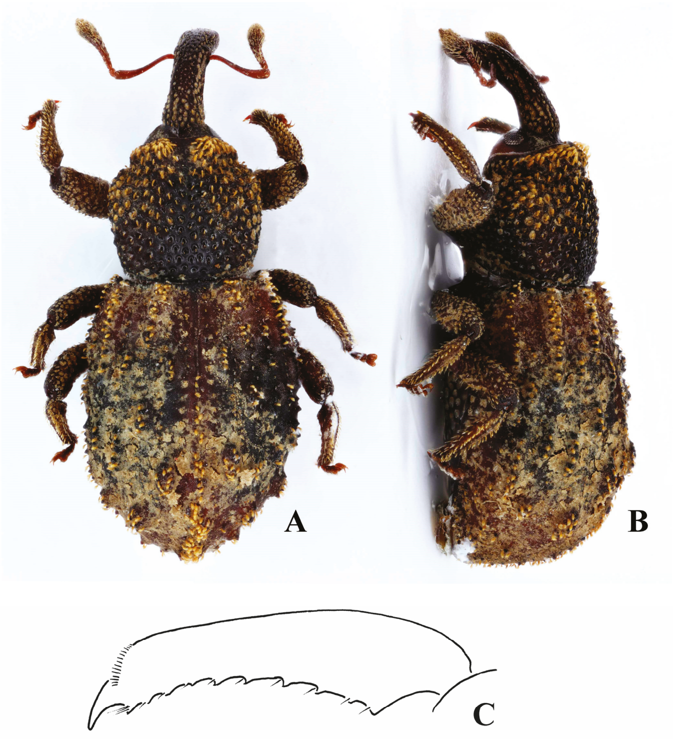

Figure 18. *Titilayo barclayi* habitus and right foretibia. (**A**,**B**) *T. barclayi*, habitus. (**A**) *T. barclayi*, dorsal; (**B**) *T. barclayi*, lateral. (**C**) *T. barclayi* female, right foretibia, anterior view.

Description. Length 3.8–4.1 mm (mean 3.92 mm, n = 3). Black.

Head. Height of eye slightly more than three-quarters depth of rostrum where it meets head capsule, just less than twice width of eye; dorsal margin lower than top of rostrum basally; ommatidia well-defined, separately convex. Rostrum curved ventrad strongly in basal third, more weakly distally; meeting head capsule at obtuse angle, lacking dorsal transverse notch, and with very weak vertical notch before eyes; scrobe visible laterally in distal half, opening ventrally for most of length. Rostrum densely punctate dorsally, more sparsely so distal to antennal insertions, punctures weakly arranged in irregular longitudinal rows, these more apparent laterally where punctures often confluent; each puncture with small golden setiform scale. Antennae rufous; first funicle antennomere longer and broader than second.

Thorax. Prothorax; 0.45–0.52 times length of elytra (mean 0.48, n = 3), 1.04–1.16 wider than long (mean 1.11, n = 3), widest at anterior third of length, abruptly widening from collar; collar visible laterally and dorsally; dorsally with median longitudinal depression behind collar, raised and convex on either side; collar with weak rounded tubercle on either side of midline submarginally; pronotum with anterior margin weakly emarginate; collar with punctures laterally, not dorsally, otherwise pronotum deeply densely punctate, glossy highlights on some reticulation between punctures, otherwise matte; tuft of semi-erect golden scales on prominences on collar, otherwise each puncture with single golden decumbent scale.

Elytra. Very weakly convex dorsally, apical declivity very steep. Length 1.27–1.33 maximum width (mean 1.30, n = 3). Tubercles at base of interstria 3 submarginal, that at base of interstria 5 submarginal or weakly projecting anteriad to base of elytra; other interstrial tubercles numerous, each being crowned with small glossy points, only weakly symmetrical between elytra; each tubercle with sparse tuft of erect or semi-erect golden scales. Strial punctures weak, sparse; striae poorly defined.

Legs. Mainly rufous. Femora with small semi-erect narrow scales, longer and more setiform ventrally. Tibiae with strong ventral projection basally and sparse ventral row of teeth (Figure 18C); tibial punctures confluent longitudinally forming rows, each with row of narrow erect pale scales, more setiform and longer ventrally than dorsally. Tarsomere 3 symmetrical.

Genitalia. Male not known.

Female (Figure 19A–C). Tergite VII posterior margin with deep concave emargination (Figure 19A). Spiculum ventrale with posterior margin weakly convex. Vaginal membrane thin, lightly pigmented. Bursal atrium expanded, with few internal folds; unpigmented externally, pigmented brown in folded area. Common oviduct, bursa, and spermathecal duct arise from bursal atrium, with bursa arising apically, spermathecal duct arising anterior to common oviduct on ventral side of bursal atrium. Bursa arising on dorsal side of bursal atrium, bursal duct narrow, as long as bursa, bursa elongate, with longitudinal folds, thickened and lightly pigmented; fine teeth visible internally. Spermatheca expanded at base of ramus, collum short (Figure 19B).

Type locality: São Tomé (Figure 20)

Type material: HOLOTYPE ♀, with labels: "Holo- / type" (red-bordered disk) and "SÃO TOMÉ, 1324m / Antenna, Bom Successo, / 00°16'31.6"N 6°36'13.7"E / (20-29). x. 2016" and "Carrion pitfall / Turner, C.R., Tasane, T. / BMNH(E) 2017-11 / TripRef: ST-001 (ANHRT 21)" and "[QR code] / "NHMUK010599884" and "HOLOTYPE / *Titilayo* / *barclayi* / Cristóvão & Lyal 2018".

PARATYPES: 2♀♀with same data as Holotype except with QR code labels numbering "NHMUK010599886" and "NHMUK010599885" respectively, and with labels: "Para- / type" (yellow-bordered disk) and "PARATYPE / *Titilayo* / *barclayi* / Cristóvão & Lyal 2018".

Depository: BMNH.

Etymology. This species is named after our friend and colleague Max Barclay in recognition of his assistance to J.P.C.

Remarks. The locality should properly be spelled "Bom Sucesso".

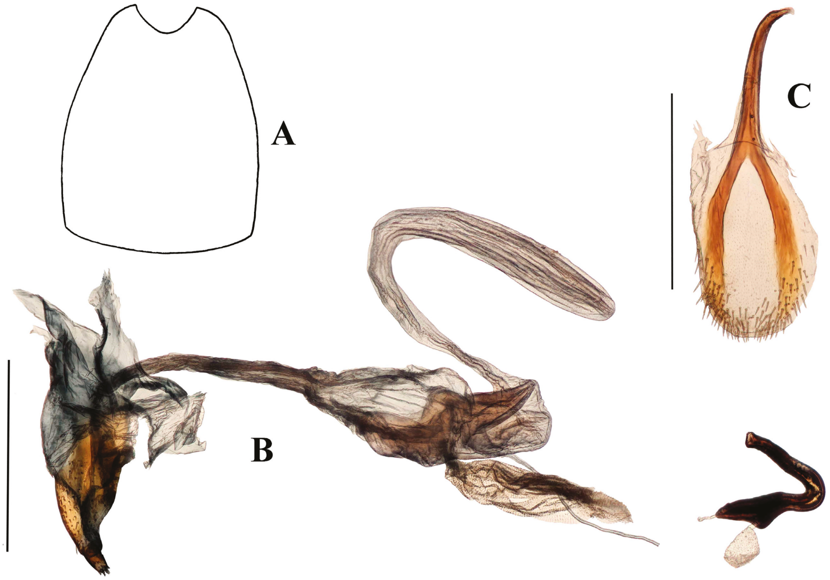

Figure 19. *Titilayo barclayi*, female genitalia. (**A**) tergite VII, dorsal; (**B**) *T. barclayi* female terminalia; and, (**C**) spiculum ventrale. All scales 0.5 mm.

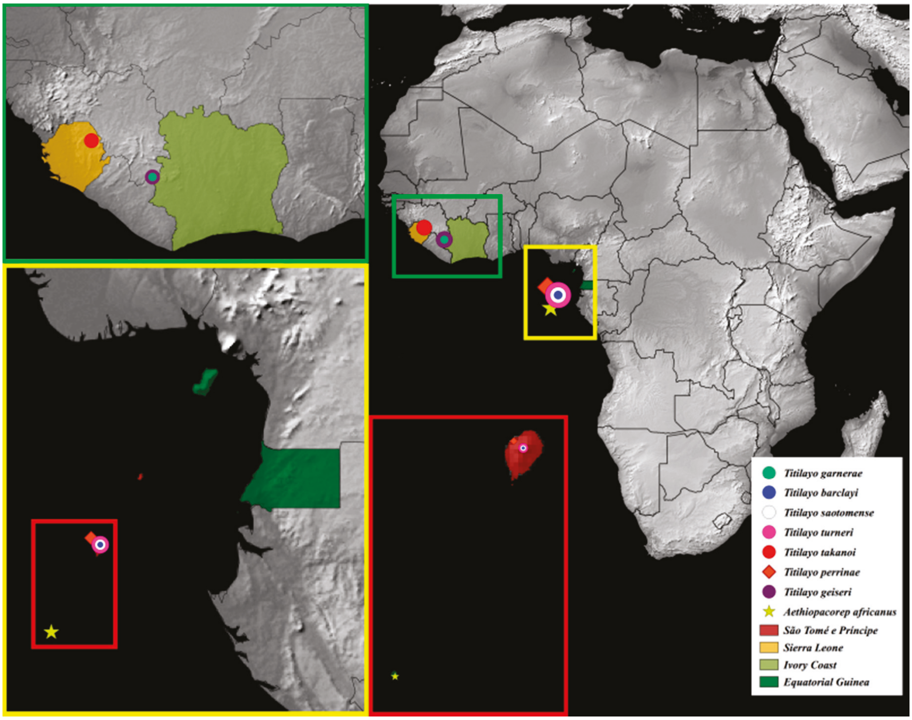

Figure 20. Map showing current distribution of *Aethiopacorep africanus* and *Titilayo* species.

Key to species of *Aethiopacorep* and *Titilayo*

1. Completely rufous. Tegmen completely membranous, unpigmented, lacking tendons, asymmetrical ventral lobes, and tegminal plates. Apex of spiculum gastrale spatulate. Bursa lacking basal-apical folds. Spermatheca of similar diameter throughout (Figure 4D). Annobón Island . . . .*Aethiopacorep africanus* **(Hustache)**

\- Black to black and rufous. Tegmen pigmented, with strongly pigmented dorsal tegminal lobes; tendons present, sometimes densely gathered in asymmetrical ventral membranous lobes. Apex of spiculum gastrale concave, circular, laminar. Bursa bearing basal-apical folds. Spermatheca broadened at least near base of ramus. Ivory Coast, Sierra Leone and São Tomé island 2

2. Pronotum with collar constriction not well-marked, shoulders with convex outline nearly reaching anterior margin of pronotum (Figures 11A and 16A); basal tubercle on elytral interstria 5 strongly projecting over basal elytral margin 3

\- Pronotum with collar constriction well-marked, with clear angle between collar and shoulders of pronotum (Figures 5A, 7A, 9A, 14A and 18A); basal tubercle on elytral interstria 5 submarginal or weakly projecting over basal elytral margin 4

3. Pronotum with broad glossy raised areas between punctures, sometimes giving the impression of longitudinal convex ridges; pronotal disc lacking setal tufts. São Tomé, São Tomé e Príncipe . . . .*Titilayo perrinae* **sp.nov.**

\- Pronotum lacking broad glossy raised areas between punctures; pronotal disc with weak sparse setal tuft on either side of midline. São Tomé . . . . *Titilayo turneri* **sp.nov.**

4. Elytral tubercles conspicuous, occupying at least width of interstriae and sometimes interrupting striae; more than 3.8 mm long 5

\- Elytral tubercles inconspicuous, occupying less than width of interstria and very weakly or not raised, giving elytra smooth (although matte) appearance; striae faint but not interrupted; less than 3.4 mm long. São Tomé . . . . *Titilayo saotomense* **sp.nov.**

5. Pronotum with collar constriction approx. 1/3rd length of pronotum, widest part of pronotum approximately 0.3 of length; endophallus (where known) lacking dorsal pigmented lobe. 6

\- Pronotum with collar constriction approx. 1/5th length of pronotum, widest part of pronotum approximately 0.4 of length; endophallus with dorsal pigmented lobe dorsally (Figure 6F). Ivory Coast . . . .*T. geiseri* **sp.nov.**

6. Tibiae with ventral margin more or less straight or weakly sinuate, lacking ventral projection basally (Figure 9C); pronotal shoulders more angular (Figures 7A and 9A) 7

\- Tibiae deeper basally than apically, with strong ventral projection (Figure 18C); pronotal shoulders more rounded. São Tomé . . . . *Titilayo barclayi* **sp.nov.**

7. Basal tubercle of 5th interstria less than one elytral puncture diameter from basal; female genitalia (Figure 8F) lacking large expansion at apex of bursal atrium, at the base of bursal duct; collum of spermatheca only slightly elongate (Figure 8F). Ivory Coast .. . . *Titilayo garnerae* **sp.nov.**

\- basal tubercle of 5th interstria more than one elytral puncture diameter from basal margin; female genitalia (Figure 10B) with large expansion at apex of bursal atrium, at base of bursal duct; collum of spermatheca. longer than cornu (Figure 10B). Sierra Leone . . . . *Titilayo takanoi* **sp.nov.**

4. Discussion

4.1. Distribution Patterns of Anchonini

The Anchonini are considered here as only including those genera with the suite of characters mentioned in the brief tribal description above. This excludes a number of genera included by Alonso-Zarazaga & Lyal (1999) [1]: *Cycloterinus* Kolbe, *Euthycodes* Pascoe, *Falsanchonus* Zherikhin, *Himalanchonus* Zherikhin, *Leptanchonus* Morimoto, *Nepalanchonus* Zherikhin, *Otibazo* Morimoto, *Stenanchonus* Voss, and *Tanyomus* Champion. Some of these have already been discussed by various authors [2–6]. The placement of others will be discussed in forthcoming papers by Lyal [7] and Cristóvão & Lyal [8]. Anchonini in this concept are almost entirely confined to Central and South America (especially Panama, Colombia, and Ecuador) and the Caribbean, where they are both speciose and morphologically diverse. Outside this area there are a few species recorded from southern North America and Brazil.

There is one species in the Galapagos islands, *Spinanchonus galapagoensis* (Waterhouse, 1845), currently congeneric with Central American species. Another Central American genus, *Rhyparonotus*, is also found on St. Helena, an island in the south Atlantic Ocean, where there is a single endemic species, *Rhyparonotus impar* Decelle & Voss 1972.

Two Anchonine species are known to occur in Eastern African islands. *Anchonus interruptus* Fåhraeus, 1843 is found in Réunion, but it appears to have been introduced from Guadeloupe [28]. *Anchonus cribripennis* (Fairmaire, 1899) (= *Anchonus madecassus* Hustache 1955) has been recorded only from Madagascar, but it appears likely that it is another introduced American species; there is still a great deal of revisionary work to be done on the speciose genus *Anchonus*. Further East, Zimmerman [29] reported the species *Anchonus duryi* (Blatchley, 1916) (thought to have been introduced from Florida, U.S.A.) in Tahiti and Raiatea, islands in southeastern Polynesia; comparison with the descriptions and images in Thomas & O'Brien [30] suggests that the species is in fact *A. floridanus* Schwartz 1894.

Hitherto only one species was known from the Afrotropical Region, *Aethiopacorep africanus* (Hustache) [24] from the West African island of Annobón. The presence of the species in that locality is confirmed in this study. This genus may be related to *Acorep*, though currently no evidence can be provided for this placement; current studies on the phylogeny of the tribe will hopefully illuminate this. This study also reports a clade of Anchonini not represented in the Neotropics or Nearctic on other off-shore islands and the West African mainland itself, with new records from São Tomé island, Ivory Coast, and Sierra Leone. The low numbers of each species obtained, and the number of sympatric species, suggest that the diversity is likely to be higher than reported here; moreover, representatives of several further species are available but not yet suitable for description (one new species close to *T. perrinae* and *T. turneri* on São Tomé, one new species close to *T. saotomense* also on São Tomé, one new species of *Titilayo* in Liberia, and three new species of one or more potentially new genera also from São Tomé). There seems to be no doubt that Anchonini s.str. are established in the Afrotropical Region as well as the Americas.

Although unusual, the disjunct distribution pattern of this tribe is not unique: *Microborus* Blandford (Curculionidae: Scolytinae) is also mainly a Neotropical genus, which includes species occurring in Cameroon, Ghana, Congo, and Madagascar [31]; the seven species of *Rhinostomus* Rafinesque (Curculionidae: Rhyncophorinae) are distributed in South and Central America, Mexico, Cuba, and Haiti, the Afrotropics (including Madagascar) and Australasia [32]; and Bromeliaceae, a chiefly Neotropical tropical and sub-tropical plant family also includes one endemic species, *Pitcairnia feliciana*, in central Guinea [33]. Thorne [34] and Renner [35] each record more than 100 genera of plants with distributions on both sides of the tropical Atlantic.

While anthropogenic factors are responsible for the presence of most other Anchonini outside the Americas, this seems unlikely in this case. *Titlilayo* species are distributed widely both on the African mainland and offshore islands, but the genus has never been found in the New World. *Titilayo geiseri* and *T. garnerae* were collected at an altitude between 1250–1430 m in a transition area between low growing montane forest and montane savannah; *T. takanoi* was collected at an altitude of 105 m in a sub-montane, closed-canopy forest. Given that these closely-related species are small (approx. 4–5 mm), flightless and putatively nocturnal and both environments are located far from any human settlements, ports, or trading routes, it seems improbable that they were introduced due to (earlier or recent) human activities.

If the root of the distribution is older, as seems likely, it is unlikely that it is Gondwanan. Brazil and this part of Africa began to separate ca. 115 mybp, while the diversification of the Curculionidae was probably later. McKenna et al. [36] suggest higher-level diversification of the Curculionidae was taking place throughout the Late Cretaceous (99.6 mybp 65.5 mybp) and Paleocene–Eocene (65.5–33.9 mybp). Shin et al. [37] place diversification later, indicating that the CCCMS clade (the major clade in Curculionidae to which Molytinae belong) probably did not differentiate before 75 mybp. While the age of the Anchonini is not yet known, they are unlikely to antedate the separation of South America and Africa.

Transoceanic dispersal seems to be the most likely hypothesis. Renner [35], considering plants found on both sides of the Atlantic, suggests that both oceanic currents and wind may have played a role in dispersal of plant propagules, nothing that wind is more likely to be associated with West-East movement, but that oceanic currents may have carried propagules in both directions. Ancestral transoceanic dispersal has also been postulated for insects [38], although much more rarely. If this is the case the South or North Equatorial Countercurrent (NECC) may be responsible for the transport. The NECC originates away from the South American Coast, a situation that may not have changed since the breakup of Gondwana [34,39] (although various models of past oceanic circulations have been postulated [40]). However, distance from the coast may not preclude rafting, since floating rafts of plant material carying insects may have been carried from river mouths to the current. Some weevils are known to survive oceanic rafting [41]; Cossoninae of the genera *Pentarthrum* and *Euophryum* have apparently been transported in logs in the Southern Ocean, for example [42]. These are of course wood dwellers, while we know nothing of the biology of *Titilayo*. However, rafting is not impossible. There is little information about wind transport of weevils, especially flightless ones, such as Anchonini, but again, it is possible that winds could have carried them across.

To ascertain when the African taxa diverged from their putative American origins, and whether *Titilayo* and *Aethiapocorep* are more closely related to each other than to American taxa will take additional surveys and specimens and further research, including molecular analysis.

4.2. Diversity and Biology

Anchonines seem to be most diverse in tropical areas, although a monospecific genus can also be found the Andean Páramo region of Venezuela [43]. They are generally said to be nocturnal, flightless, tropical leaf litter dwellers, although records show that some also occur in rotten wood near beach areas [30]. In the latter case, they were observed and collected at dawn on frailejón leaves (*Espeletia* sp.), but were nowhere to be seen during the day, perhaps because they shelter in between the dead leaves around this plant species or under the mosses that surround them during the day [44].

Given the published literature and unpublished data [8,21], it seems that this tribe may be much more diverse than current literature and collections suggest, but, due to their nocturnal, flightless nature, they might not be collected with the frequency or in a manner that reflects this.

Perhaps beating trees and bushes during the night or during overcast days as well as leaf litter sifting and opening deadwood might increase the number of specimens that are caught on collecting trips.

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References

1. Alonso-Zarazaga, M.A.; Lyal, C.H.C. *A World Catalogue of Families and Genera of Curculionoidea (Insecta: Coleoptera) Excluding (Scolytidae and Platypodidae)*; Entomopraxis: Barcelona, Spain, 1999; p. 315.
2. Poinar, G.J.; Voisin, J. A Dominican Amber Weevil, Velatis Dominicana Gen.n., Sp.n. and Key to the Genera of the Anchonini (Molytinae, Curculionidae). *Nouv. Rev. Entomol.* **2003**, *19*, 373–381.
3. Meregalli, M. The Genus Falsanchonus Zherikhin 1987, with Description of Six New Species (Insecta: Coleoptera: Curculionidae: Molytinae). In *Biodiversity and Natural Heritage of the Himalaya*; Hartmann, M., Baumbach, H., Eds.; Naturkundemuseums Erfurt: Erfurt, Germany, 2003; pp. 323–335.
4. Meregalli, M. Stenanchonus Voss 1937, a Junior Synonym of Euthycus Pascoe 1885. *Senckenb. Biol.* **2003**, *82*, 127–133.
5. Meregalli, M.; Osella, G. Studies on Oriental Molytinae. IV. Anonyxmolytes Lilliput New Genus and New Species from Vietnam (Coleoptera, Curculionidae). *Ital. J. Zool.* **2007**, *74*, 381–388. [CrossRef]
6. Lyal, C.H.C. Molytinae Schoenherr, 1832. In *Handbook of Zoology. Arthropoda: Insecta Coleoptera, Beetles, Volume 3: Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Eds.; De Gruyter: Berlin, Germany, 2014; pp. 529–570.
7. Lyal, C.H.C. A Review of the Molytinae (Insecta: Coleoptera: Curculionidae). in preparation.
8. Cristóvão, J.P.; Lyal, C.H.C. Review of the Tribe Anchonini (Coleoptera: Curculionidae: Molytinae). in preparation.
9. Weidner, H. Die Entomologischen Sammlungen Des Zoologischen Instituts Und Zoologischen Museums Der Universität Hamburg, Nachtrag Zum IX. Teil, Insecta VI. *Mitt. Hamb. Zool. Mus. Inst.* **1976**, *73*, 87–264.
10. Weidner, H. Die Entomologischen Sammlungen Des Zoologischen Instituts Und Zoologischen Museums Der Universität Hamburg, Nachtrag Zum IX. Teil, Insecta VI. *Mitt. Hamb. Zool. Mus. Inst.* **1979**, *76*, 395–468.
11. Geiser, M.; Natural History Museum, London, UK. Personal communication, 2017.
12. Marshall, G.A.K. Le Reserve Naturelle Integrate Du Mont Nimba, Fasc. II, Coleoptéres Curculionides. *Mém. Inst. Franç. Afr. Noire* **1954**, *40*, 201–205.
13. Hoffmann, A. La Réserve Naturelle Intégrale Du Mont Nimba. Coleoptera Curculionidae (Deuxième Note). *Mém. Inst. Franç. Afr. Noire* **1963**, *66*, 309–336.
14. Takano, H.; Natural History Museum, London, UK. Personal communication, 2017.
15. Lyal, C.H.C.; Curran, L.M. Seed-Feeding Beetles of the Weevil Tribe Mecysolobini (Insecta: Coleoptera: Curculionidae) Developing in Seeds of Trees in the Dipterocarpaceae. *J. Nat. Hist.* **2000**, *34*, 1743–1847. [CrossRef]
16. QGIS Development Team. QGIS Geographic Information System. Open Source Geospatial Foundation. Available online: https://www.researchgate.net/publication/263441203_QGIS_Geographic_Information_System_Open_Source_Geospatial_Foundation (accessed on 1 January 2018).
17. Imhoff, L. *Versuch Einer Einführung in Das Studium Der Koleopteren*; Schweighauser'sche Buchdruckerei: Basel, Switzerland, 1856; p. 272.
18. Faust, J. Die Anchoniden-Gruppe. *Dtsch. Entomol. Z.* **1892**, *1*, 17–60.
19. Champion, G.C. Coleoptera. Rhynchophora. Curculionidae. Curculioninae. In *Biologia Centrali-Americana. Insecta. Coleoptera. Volume 4 Part 4*; Privately published: London, UK, 1902; pp. 1–144.
20. Blatchley, W.S.; Leng, C.W. *Rhynchophora or Weevils of North Eastern America*; The Nature Publishing Company: Indianopolis, IN, USA, 1916; p. 682.
21. Lyal, C.H.C.; Cristóvão, J.P. Morphology of Genitalia in the Anchonini (Curculionidae: Molytinae). *Zootaxa*. under review.
22. Voisin, J. Notes Sur Les Genres de La Tribu Des Anchonini 1. Généralités, Redefinition Du Genre Anchonus Schönherr et Description de Cinq Genres et de Deux Sous-Genres Nouveaux (Coleoptera, Curculionidae). *Nouv. Rev. Entomol.* **1992**, *9*, 259–271.
23. Voisin, J. Notes Sur La Tribu Des Anchonini: 2. Description de Quatre Genres Nouveaux et Revue de Six Anciens (Coleoptera, Curculionidae). *Nouv. Rev. Entomol.* **1994**, *10*, 327–340.

24. Hustache, A. Curculionides Nouveaux de l'Afrique Équatoriale. II Partie. *Sb. Entomol. Oddělení Nár. Mus. Praze* **1932**, *10*, 28–109.
25. Dalsgaard, T.; Hamburg, Germany. Personal communication, 2017.
26. Maldes, J.-M.; Péricart, J. Pour Un Trentenaire Rétrospective Sur La Biographie et l'oeuvre Entomologique d'Alphonse Hustache (1872–1949). *Ann. Soc. Entomol. Fr.* **1979**, *15*, 194–208.
27. Perrin, H.; Muséum national d'Histoire naturelle, Paris, France. Personal communication, 2017.
28. Poussereau, J.; Voisin, J. Découverte de Anchonus Interruptus Fåhraeus, 1843 à l'île de La Réunion (Coleoptera, Curculionidae). *Bull. Soc. Entomol. Fr.* **2002**, *107*, 281–283.
29. Zimmerman, E.C. Anchonus Duryi in Southeastern Polynesia (Coleoptera: Curculionidae: Hylobiinae: Anchonini). *Psyche J. Entomol.* **1964**, *71*, 53–56. [CrossRef]
30. Thomas, M.C.; O'Brien, C.W. On the Genus Anchonus Schonherr in Florida (Coleoptera: Curculionidae). *Insecta Mundi* **1999**, *13*, 229–233.
31. Jordal, B.H. Ancient Diversity of Afrotropical Microborus: Three Endemic Species–not One Widespread. *Zookeys* **2017**, *710*, 33–42. [CrossRef] [PubMed]
32. Vaurie, P. Weevils of the Tribe Sipalini (Coleoptera, Curculionidae, Rhynchophorinae) Part 1. The Genera Rhinostomus and Yuccaborus. *Am. Mus. Novit.* **1970**, *2419*, 1–57.
33. Jacques-Félix, H. The Discovery of a Bromeliad in Africa: Pitcairnia Feliciana. *Selbyana* **2000**, *21*, 118–124.
34. Thorne, R.F. Floristic Relationships between Tropical Africa and Tropical America. In *Tropical forest Ecosystems in Africa and South America: A Comparative Review.*; Meggers, B.J., Duckworth, W.D., Eds.; Smithsonian Institution: Washington, DC, USA, 1973; pp. 27–47.
35. Renner, S. Plant Dispersal across the Tropical Atlantic by Wind and Sea Currents. *Int. J. Plant Sci.* **2004**, *165*, S23–S33. [CrossRef]
36. McKenna, D.D.; Sequeira, A.S.; Marvaldi, A.E.; Farrell, B.D. Temporal Lags and Overlap in the Diversification of Weevils and Flowering Plants. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 7083–7088. [CrossRef] [PubMed]
37. Shin, S.; Clarke, D.J.; Lemmon, A.R.; Moriarty Lemmon, E.; Aitken, A.L.; Haddad, S.; Farrell, B.D.; Marvaldi, A.E.; Oberprieler, R.G.; Mckenna, D.D. Phylogenomic Data Yield New and Robust Insights into the Phylogeny and Evolution of Weevils. *Mol. Biol. Evol.* **2018**, *35*, 823–836. [CrossRef] [PubMed]
38. Murray, E.A.; Heraty, J.M. Invading Africa: A Novel Transoceanic Dispersal by a New World Ant Parasitoid. *J. Biogeogr.* **2016**, *43*, 1750–1761. [CrossRef]
39. Parrish, J.T. The Paleogeography of the Opening South Atlantic. In *The Africa–South America Connection*; George, W., Lavocat, R., Eds.; Clarendon: Oxford, UK, 1993; pp. 8–41.
40. Hay, W.W. Cretaceous Oceans and Ocean Modeling. In *Cretaceous Oceanic Red Beds: Stratigraphy, Composition, Origins, and Paleoceanographic and Paleoclimatic Significance*; Hu, X., Wang, C., Scott, R.W., Wagreich, M., Jansa, L., Eds.; SEPM Special Publication: Oklahoma, OK, USA, 2009; pp. 243–271.
41. Kuschel, G. Biogeography and Ecology of South American Coleoptera. In *Biogeography and ecology in South America. Monographiae biologicae 19.*; Fittkau, F.J., Illies, J., Klinge, H., Schwabe, G.H., Eds.; Springer: New York, NY, USA, 1968; pp. 709–722.
42. Thompson, R.T. A Preliminary Study of the Weevil Genus Euophryum Broun (Coleoptera: Curculionidae: Cossoninae). *New Zeal. J. Zool.* **1989**, *16*, 65–79. [CrossRef]
43. Voisin, J. Description d'Escalonates Narizensis n. Gen., n. Sp., Du Venezuela (Coleoptera, Curculionidae). *Bull. Soc. Entomol. Fr.* **2004**, *109*, 409–411.
44. Escalona, H.; CSIRO, Canberra, Australia. Personal communication, 2015.

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Article

A Review of *Philenis* Champion, 1906 (Coleoptera: Curculionidae: Conoderinae), with Descriptions of New Species from Central and South America

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Abstract: A brief review of the history of the taxonomic treatment of the genus *Philenis* Champion is presented and characters are discussed. *Philenis flavipes* Champion and *P. fuscofemorata* Champion, and 11 new species are described, including the first records from South America: *P. anzaldoi* **new species** (Costa Rica, Panamá), *P. costaricensis* **new species** (Costa Rica), *P. laselvaensis* **new species** (Costa Rica), *P. auritibiae* **new species** (Costa Rica), *P. brunnea* **new species** (Costa Rica, Panamá), *P. muscamimetica* **new species** (Panamá), *P. chiriquiensis* **new species** (Panamá), *P. guyanensis* **new species** (French Guiana), *P. ferruginea* **new species** (Ecuador), *P. howdeni* **new species** (Ecuador), and *P. kuscheli* **new species** (Colombia, Ecuador). A key is provided to separate the species, and an unusual type of "multifurcate" scale is reported for some species. Two species have been associated with plants of the family Araceae. Most collections of this genus by the Arthropods of La Selva (ALAS) biodiversity project in Costa Rica were made by passive trapping methods during the dry season and at lower to middle elevations along an altitudinal transect on the slopes of Volcan Barva. The coloration of some species in the genus is hypothesized to mimic social Hymenoptera or flies.

Keywords: Araceae; biodiversity; ecology; faunal inventories; mimicry; phenology

1. Introduction

The genus *Philenis* Champion [1] was described for two species from western Panama, *P. flavipes* Champion and *P. fuscofemorata* Champion, each based on a single specimen. Specimens of members of the genus are not common in collections, but have been accumulating, largely by passive sampling (see below, also [2]). The Arthropods of La Selva (ALAS) project collected at least 131 specimens of nine species at the La Selva Biological Station in Costa Rica [3] and on an altitudinal transect above La Selva and has stimulated this review. Anzaldo [4] mentions undescribed species in his review of conoderine genera. I have previously suggested [5] that some species in the genus may participate in mimicry complexes and reported a record of larval ecology. This paper describes 11 new species, describes an unusual new character, reports the genus for the first time from South America, and describes what little is known about the biology of members of the genus. A few specimens could not be assigned with certainty to any of the species treated here and may represent either extreme variants or additional undescribed species.

2. Materials and Methods

Only part of the specimens collected by the ALAS project were available for this study. At the time of the original processing of the ALAS material, only a few specimens of commoner species were retained for study, and the rest were deposited with the Instituto Nacional de Biodiversidad (INBio) collection, now in the care of the National Museum of Costa Rica. These latter specimens are listed here as "other specimens examined" and are not considered to be paratypes. Specimens were measured to the nearest 0.05 mm. Dates have been standardized to day.month.year. In the genus it is difficult to determine the sex of specimens without dissection, and several species are described here without the sex of specimens having been determined. The following acronyms of collections are used:

AMNH, American Museum of Natural History, New York, N.Y.;
BMNH, The Natural History Museum, London, England;
CHAH, Henry A. Hespenheide, University of California, Los Angeles, CA;
CMNC, Canadian Museum of Nature, Ottawa, Canada;
CSCA, California State Collection of Arthropods, Sacramento, CA;
LACM, Los Angeles County Museum of Natural History, Los Angeles, CA;
MNCR, National Museum of Costa Rica, San Jose, Costa Rica;
MUCR, University of Costa Rica, San Pedro, Costa Rica;
USNM, National Museum of Natural History, Smithsonian Institution, Washington, DC.

3. Results

3.1. Taxonomic Treatment

Philenis Champion, 1906

Philenis Champion, 1906: 43 [1]

Type species: *Philenis flavipes* Champion, 1906 by original designation.

Champion [1] described the genus and its two included species from single specimens of each. He compared *Philenis* to the genus *Copturus* Schoenherr, 1825, now *Macrocopturus* Heller, 1895, differentiating it by their slender rostrum, short and slender antennae with a small acuminate club, and having only the metafemora dentate but not carinate. The diagnostic characters, relationships with other genera, and tribal placement of the genus have recently been discussed by Anzaldo [4]. Addition of species to the genus and further study will eventually necessitate a redefinition of the genus as only the antennal characters are shared among the species treated here. Champion does not comment on his choice of the name for the genus, which is feminine. "Philænis" is a diminutive of the feminine form of the Greek word "philos", meaning "love". Philænis of Samos may have been the author of a famous ancient sex manual, and Philænis may also have been a name commonly used by prostitutes in ancient Greece [6], but its connection to this genus of weevils appears to be arbitrary.

3.1.1. Species Descriptions

Philenis flavipes Champion, 1906

Philenis flavipes Champion, 1906: 43 [1]
Figure 1

Redescription: Body size 5.30 mm long, 2.90 mm wide. Moderately robust, oboval, narrower anteriorly, pronotum and head black, otherwise reddish brown, rostrum, legs and abdominal ventrites 1, 2, and 5 paler, abdominal ventrites 3–4 and elytra darker, darkest on posterior 2/3; sparsely to somewhat densely covered with complex pattern of scales: from above, pronotum with pale yellow scales along anterior and basal margins and in undulate transverse facia at middle, the medial and basal bands joining at sides, otherwise scales black; elytra with scales pale yellow in intervals 1 and 2 along suture, interrupted for middle 1/2 of suture, and narrowly along basal margin and in slightly oblique transverse fasciae at 1/3 and 2/3 of length 1/5, scales dark brown otherwise, scales moderately, uniformly dense and pale yellow on base of rostrum, legs, and ventrally, denser on metasternum, episternum, mesepimeron, posterior margins of abdominal ventrites 1 and 2, scales brown on ventrites 3–4.

Figure 1. *Philenis flavipes* Champion, Holotype, dorsal and lateral habitus.

Head 1.00 mm wide, convex in dorsal view, eyes contiguous at upper 1/2; rostrum slender, nearly straight, polished and glabrous below antennal insertions, somewhat flattened dorsoventrally, 1.40 mm long, antennae inserted at basal 1/4.

Pronotum 1.50 mm long, 2.00 mm wide at base, lateral margins weakly rounded from base to apex, in lateral view gibbous at basal 1/4 and declivous anteriorly. vaguely carinate along medial 1/2 of midline. Scutellum narrowly ovate lengthwise.

Elytra 0.5 wider than pronotum, humeri moderately prominent, intervals broad, striae nearly linear.

Mesosternum declivous, flat, posterior margin straight, anterior margin of metasternum declivous. In lateral view abdominal ventrite 1 very convex, 1.4 mm long along midline, ventrite 2 only 0.2 mm long along midline, ventrites 3–5 very narrow, ascending. From front, procoxae broadly rounded-triangular with large tooth on inner margin. Metafemora with suggestion of lateral carina at middle and very weak tooth at distal 2/3.

Specimens examined: Panamá, Bugaba, Champion (Holotype, BMNH). Costa Rica: Heredia: Est. Biol. La Selva., 50–150 m, 10°26′ N 84°01′ W, INBio-OET, 1.02.1996, 15.03.1994, Bosque primerio, M/08/561 (MNCR, INBIOCRI002304056), 11 km ESE La Virgen, 250–350 m, 10°21′ N 84°03′ W, INBio-OET-ALAS transect, 9.03.2004, 03/M/02/022 (MNCR, INB0003613035), 22.02.2004, 03/M/03/003 (MNCR, INB0003611312); Puntarenas Prov., Parque Nacional Corcovado, Est. Sirena, 08°28–31′ N 83°36′ W, 23.01.1981, H.A. Hespenheide, on aroid; flying 1.5 m above ground (CHAH), Sirena, Corcovado N.P., 0–100 m, 270500, 508300, 12.1989, G. Fonseca (MNCR, INBIOCRI000188371), Osa Peninsula, 2.5 mi SW Rincon, 08°42′ N 83°29′ W, 8.08.1968, H. Hespenheide (CHAH), R.F. Golfo Dulce, 3 km S Rincon, 10 m, 06.1991, P. Hanson (MUCR), S. Vito, Las Cruces, 1200 m, 17.08–12.09.1982, B. Gill (CMNC).

Discussion: This species differs most obviously from the following in the distinct pattern of the elytra with the transverse fasciae separating three darker areas, with the posterior one being the darkest. The overall color pattern of yellow and dark reddish brown and black suggests the coloration of social Hymenoptera [5], but the robust body form is unlike the slender habitus of wasps, and no particular model is obvious. The specimen from Heredia Province, Costa Rica, has a significantly longer (2.0 mm) and more slender rostrum, but does not differ appreciably in other ways. Specimens vary only slightly in size (5.15–5.30 mm, x = 5.24, N = 6). The images in Anzaldo's work [4] attributed to *P. flavipes* are those of the next species.

Philenis anzaldoi Hespenheide new species

Figure 2

http://zoobank.org/urn:lsid:zoobank.org:act:C4BC5B10-3C30-4A48-A84C-36BAC36A78F1

Description: Holotype female: body size 5.70 mm long, 3.10 mm wide. Moderately robust, oboval, narrower anteriorly, head, pronotum, mesepimeron, and abdominal ventrites 3–4 black, otherwise reddish brown, rostrum, legs and abdominal ventrites 1 and 2 paler; sparsely to somewhat densely covered with complex pattern of largely pale yellow scales, darker on elytra: from above, pronotum with scales along anterior and basal margins, and in narrow transverse fascia anterior to middle, bands joining at sides for anterior 1/2 of pronotum, otherwise scales black on disc; elytra with scales in intervals 1 and 2 along suture, narrowly interrupted at anterior 1/4 of suture, in narrow transverse fasciae in intervals 1–8, and in broad oblique fascia on posterior 1/2, scales dark brown otherwise; scales sparse on rostrum above antennal insertions, moderately dense on legs, and ventrally, denser on procoxae, metasternum, episternum, mesepimeron, posterior margins of abdominal ventrites 1 and 2, sparser on ventrites 3–4.

Head 1.10 mm wide, convex in dorsal view, eyes narrowly separated; rostrum very slender, nearly straight, polished and glabrous below antennal insertions, somewhat flattened dorsoventrally, 1.90 mm long, antennae inserted at basal 1/5.

Pronotum 1.85 mm long, 2.15 mm wide at base, lateral margins weakly rounded from base to anterior collar, in lateral view gibbous at basal 1/4 and declivous anteriorly. weakly carinate along basal 3/4 of midline, posterior margin extended posteriorly anterior to scutellum. Scutellum narrowly ovate lengthwise.

Elytra 0.5 wider than pronotum, humeri slightly prominent, intervals broader than striae, striae punctate.

Mesosternum declivous, unmodified, weakly emarginate posteriorly, anterior margin of metasternum declivous. In lateral view abdominal ventrite 1 weakly convex, 1.60 mm long along midline, midline linearly impressed, narrowly emarginate at posterior margin, ventrite 2 only 0.25 mm long along midline abruptly, strongly declivous posteriorly, ventrites 3–4 very narrow, ventrite 5 equal to 3 + 4, ascending. From front, procoxae broadly angulate-obovate with large tooth on inner margin. Metafemora with distinct tooth at distal 2/3.

Figure 2. *Philenis anzaldoi*, dorsal and lateral habitus.

Specimens examined: Holotype: Panamá: Canal Zone, Barro Colorado Is., 09°10′ N 79°50′ W, 17.08.1974, H.A. Hespenheide, aroid gall, l[ea]f. vs, vial (USNM). Paratypes: Panamá: Canal Zone, Barro Colorado Is., 12.11.1923, F 4857 OL (AMNH), Madden Forest, 09°05′ N 79°37′ W, 15.03.1984, Stockwell (CMNC); Panamá Prov., (8 km NW Capira), Cerro Campana, 1000 m, 7.05.1981, R.W. Brooks, on *Clethra lanata* (CMNC); Prov. Colón, 'Achiote-PN San Lorenzo', 09°12′ N 79°59′ W, 100 m, Pastizal B Dist, 12–27.05.2004, A. Mercado, Tr. Intercepción (CMNC). Costa Rica: Prov. Guanacaste, Estac. Pitilla, 9 km S Santa Cecilia, 700 m, 330200–380200, 09.1989, GNP Biodiversity Survey (MNCR, INBIOCRI000035371); Heredia Pr., F. La Selva, 3 km S Pto. Viejo, 10°26′ N 84°01′ W, 26.06.1985, H.A. Hespenheide (CHAH), Est. Biol. La Selva., 50–150 m, 10°26′ N 84°01′ W, INBio-OET, 14.06.1993, Bosque primario, M/08/130 (MNCR, INBIOCRI0022718655), 16.10.1995, Parcelas sucessionales, M/01/471 (MNCR, INBIOCRI002300586), 11 km ESE La Virgen, 250–350 m, 10°21′ N 84°03′ W, INBio-OET-ALAS transect, 21.03.2004, 03/M/03/043 (MNCR, INB0003614035), 6.04.2004, 03/M/03/063 (MNCR, INB0003615778); [Limon Prov.], Hamburg Farm, Sta Clara Pr, 27.01.1926, Nevermann Coll. (USNM).

Host: The aroid liana with the gall from which the holotype was cut is probably a species of *Philodendron*.

Derivation of name: This species is named in honor of Salvatore Anzaldo for his review [4] of the conoderine genera of North and Central America.

Discussion: This is the species figured in Anzaldo's review [4] as *Philenis flavipes*. The two species are similar, but differ most obviously in the color and pattern of scales on the elytra. Specimens vary in length from 5.00–6.40 mm, (x = 5.66, N = 12).

Philenis fuscofemorata Champion, 1906

***Philenis fuscofemorata* Champion, 1906:44. [1]**
Figures 3 and 4b

Redescription: Body size 4.50 mm long, 2.40 mm wide. Moderately robust, elliptical, conspicuously narrower anteriorly, pronotum, mesosternum, mesepimera, epimeron, apical 1/4 of elytra, abdominal ventrites 4 and 5, coxae and femora black, otherwise head, metasternum, metepimera, abdominal ventrites 1–3, middle portion of metafemora, and tibiae reddish brown, and basal 3/4 of elytra darker reddish brown; sparsely to somewhat densely covered with complex pattern of scales: scales reddish-brown on reddish brown portion of elytra; scales black on black portion of elytra and in broad longitudinal stripes on pronotum lateral to midline; scales yellowish-white on head, on pronotum in narrow stripe along midline and on anterior portions of broad stripe along lateral margins extending to sides, on elytra in small slightly oblique spot on intervals 2–5 at basal 1/3 of elytra and in broader irregular oblique transverse fascia at apical 2/3 of elytra, along apical 1/2 of elytral suture and narrowly along elytral apices; in dorsal view, scales white in posterior portions of lateral margins of pronotum; ventrally, scales white, and more or less uniformly dense throughout and on femora, denser on metasternum and on metepisterna; scales golden on most of tibiae, except white on posterior margin of metatibiae; sides of pronotum and apical 3/4 of rostrum glabrous (Figure 3).

Figure 3. *Philenis fuscofemorata* Champion, Holotype, dorsal and lateral habitus.

Head 0.80 mm wide, 0.40 mm long, convex in dorsal view, eyes separated by 2 rows of small semi-erect scales; rostrum forming distinct obtuse angle at base with frons, rounded-rectangular in cross section, broadening toward apex, curved, micropunctate below antennal insertions, 1.25 mm long, antennae inserted at basal 1/5.

Pronotum 1.45 mm long, 1.50 mm wide at base, lateral margins weakly convex at base then nearly straight to anterior collar, weakly convex on basal 2/3 in lateral view. weakly carinate along basal 2/3 of midline, posterior margin obliquely convergent from posterior angles and extended in rounded-acute projection anterior to scutellum. Scutellum small, round.

Elytra abruptly 3/5 wider than pronotum at base, widest at basal 1/3; humeri somewhat prominent, intervals rounded, 1.5–2× broader than striae, striae coarsely punctate.

Mesosternum deeply emarginate and concave to receive apex of rostrum, lateral angles narrow, curved and raised interior to mesocoxae; anterior margin of metasternum strongly declivous. In lateral view abdominal ventrite 1 very weakly, broadly convex, slightly depressed along midline, posterior margin slightly narrowly emarginate, 1.10 mm long, ventrite 2 0.50 mm long along midline, strongly declivous at posterior margin, ventrites 3–5 narrow, subequal in length. From front, procoxae broadly rounded-triangular with long tooth on inner margin. Metafemora with tooth at distal 2/3, mesofemora with minute tooth at middle. Genitalia as in Figure 4b.

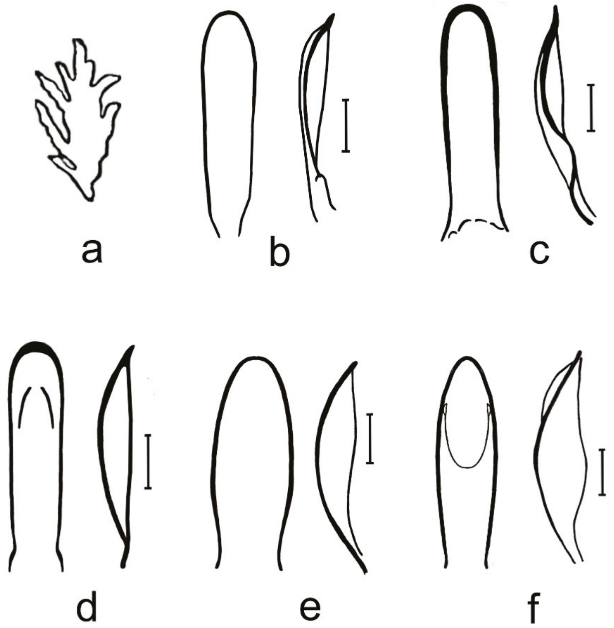

Figure 4. (**a**). Multifurcate scale; **b**–**f**. male genitalia, dorsal and lateral views; (**b**). *Philenis fuscofemorata*; (**c**) *P. costaricensis*; (**d**) *P. laselvaensis*; (**e**) *P. brunnea*; (**f**) *P. chiriquiensis*; scale bars = 0.2 mm.

Specimens examined: Costa Rica: Prov. Guan[acaste], Est. Cacao, Lado suroeste del Volcan Cacao, 1000–1400 m, L-N-323300-375700, II curso Parataxon., 06.1990 (MNCR, INBIOCRI000255075); Heredia: Est. Biol. La Selva., 50–150 m, 10°26′ N 84°01′ W, INBio-OET, 10.1992 (CHAH), 29.09.1995, Bosque secundario, M/02/460 (MNCR, INBIOCRI002300930), 14.04.1999, Bosque secundario, L/17/566 (MNCR, INBIOCRI001284616), La Selva Biol. Sta., 3 km S Pto. Viejo, 10°26′ N 84°01′ W, 3.01.1994, Bosque secundario, M/13/315 (MNCR, INBIOCRI002267491), 13.04.1993, Bosque secundario, L/06/027 (MNCR, INBIOCRI001274880), 14.04.1999, Bosque secundario, L/18/619 (MNCR, INBIOCRI001285095), 11 km ESE La Virgen, 250–350 m, 10°21′ N 84°03′ W, INBio-OET-ALAS transect, 6.04.2004, 03/M/15/075 (6, MNCR, INB0003614609-12, -14-15), 18.04.2004, 03/M/15/095 (2, MNCR, INB0003616876, -77), 11 km SE La Virgen, 450–550m, 10°20′ N 84°04′ W, 8.04.2003, 05/M/06/066 (MNCR, INB0003231453), 05/M/03/033 (MNCR, INB0003243099), 05/M/17/037 (2, MNCR, INB0003243092 [genitalia figured], -3); Prov. Puntarenas, Rancho Quemado, Peninsula de Osa, 200 m, L-N-292500, 511000, 05.1992, F. Quesada y G. Varela (MNCR, INBIOCRI000407983), Est. Sirena, P.N. Corcovado, 0–100m, L-S 270500, 508300, 17.06–4.09.1991, Tp. Malaise (2, CMNC, INBIOCRI000721235, -66), 03–06.1991, Tp. Malaise (MNCR, INBIOCRI000335807), Corcovado National Park, Sirena stn., Rio Pavo trail 5 m, 8°29′5″ N 83°35′33″ W, 25–28.06.2000, Z. H. Falin, ZF2000-37, *ex* f.i.t. (CMNC), Rincon de Osa, 150 m, 8°41.141′ N 83°31.117′ W, 22–26.06.2001, S. & J. Peck, 97–24, S&JP 2001-14, *ex* f.i.t., rain forest (3, CMNC), Pen. Osa., Est. Fund. Neot. Aguas Buenas, 7 km W Rincon de Osa, 80 m, 21–25.06.1997, S. & J. Peck, 97–24, f.i.t., *ex* rain forest (CMNC), R.F. Golfo Dulce, 5 km W Piedras Blancas, 100 m, 08.1992, P. Hanson (MUCR). Panama: Chiriqui, La Fortuna, Hydrological Trail, 1050m, 9–12.06.1995, J. Ashe & R. Brooks, #188, FIT (CMNC), V. de Chiriqui, 4000–6000 ft., Champion (Holotype, BMNH).

Discussion: As treated here, this is a widespread and very variable species but may actually be a complex of sibling species. Initially I had separated out different groups of specimens based partially on geography and morphological characters, but variability within groups and overlaps in both geography and characters recommended this more conservative interpretation. There is also the possibility of significant sexual dimorphism that parallels that in the following species. As a consequence, many other collections from the ALAS transect initially determined as this species are probably this species but are not listed. Further study and collections, including genetic barcoding, is required. The coloration is somewhat suggestive of that of social Hymenoptera, but unspecific in pattern.

This species is similar to the following species, but is smaller in size and differs in other characters given in the key, below, especially the metafemoral teeth which are minute in *P. fuscofemorata* and strong in the following species. Specimens vary in length from 3.75–4.80 mm, (x = 4.17, N = 22).

Philenis costaricensis Hespenheide new species

Figure 4c and Figure 5

http://zoobank.org/urn:lsid:zoobank.org:act:F4AC77DB-3F8B-4740-81C0-14780A0FF156

Description: **Holotype male**: body size 5.20 mm long, 2.70 mm wide. Moderately robust, elliptical, narrower anteriorly, black, except tibiae, head, metasternum, and abdominal ventrites 1 and 2 reddish brown, basal 2/3 of elytra darker reddish brown; sparsely to somewhat densely covered with complex pattern of scales: scales reddish-brown on reddish brown portion of elytra; scales black on black portion of elytra and in broad longitudinal stripes on pronotum lateral to midline; scales yellowish-white on head, on metafemora, in slightly oblique transverse fascia on intervals 2–5 at basal 1/3 of elytra and in broader, irregular oblique transverse fascia at apical 2/3 of elytra, along apical 1/4 of elytral suture and narrowly along elytral apices; in dorsal view, scales white in longitudinal stripes along midline and lateral margins of pronotum, narrowly at base of elytra; ventrally scales white on procoxae and on pronotum just above procoxae, on metasternum, meso and metepisterna, abdominal ventrites, and fore- and mesofemora, denser on lateral portion of metasternum and on metepisterna, abdominal ventrite 5, and lateral margins of ventrites 2–4; scales golden on most of tibiae; sides of pronotum and apical 2/3 of rostrum glabrous.

Head 0.95 mm wide, 0.45 mm long, convex in dorsal view, eyes separated by 4 rows of small semi-erect scales; rostrum rounded-rectangular in cross section, curved, micropunctate below antennal insertions, weakly transversely depressed and weakly carinate along midline above antennal insertions, somewhat flattened dorsoventrally, 1.35 mm long, antennae inserted at basal 1/4.

Pronotum 1.55 mm long, 1.80 mm wide at base, lateral margins weakly convex at base then nearly straight to anterior collar, weakly convex in lateral view. weakly carinate along basal 3/4 of midline, posterior margin extended in acute projection anterior to scutellum. Scutellum small, round.

Elytra abruptly 0.5 wider than pronotum at base, humeri not prominent, intervals relatively flat, 1.5–2× broader than striae, striae narrow, punctate.

Mesosternum emarginate and concave to receive apex of rostrum, lateral angles narrow and raised interior to mesocoxae; anterior margin of metasternum strongly declivous. In lateral view abdominal ventrite 1 nearly flat, very weakly, broadly concave, 1.20 mm long along midline, ventrite 2

0.45 mm long along midline, strongly declivous at posterior margin, ventrites 3–5 narrow, subequal in length. From front, procoxae broadly rounded-triangular with tooth on inner margin. Metafemora with small tooth at distal 3/5, mesofemora with minute tooth at middle. Genitalia as in Figure 4c.

Allotype female: Body size 5.00 mm long, 2.80 mm wide. Robust, elliptical, slightly narrower anteriorly; generally dark reddish brown, head, abdominal ventrites 1–3, and legs paler; pronotum above procoxae, coxae, abdominal ventrites 3–4, and interior surface of metafemora black; sparsely to somewhat densely covered with complex pattern of scales: scales dark-brown or black in broad longitudinal stripes on pronotum lateral to midline; scales yellowish-white on head, on pronotum in narrow stripe along midline and on anterior portions of broad stripes along lateral margins extending to sides; in dorsal view, scales white in posterior portions of lateral margins of pronotum, on elytra in small slightly spots anterior to humeri, narrowly on intervals 2–4 at base of elytra extending on intervals 1–2 to narrow weakly arcuate transverse fascia at basal 1/3, and in broader irregular oblique transverse fascia at apical 2/3, and on intervals 1–2 along apical 2/3 of elytral suture continuing narrowly along elytral apices; ventrally, scales white, and more or less uniformly dense throughout except absent on medial 2/3 of abdominal ventrites 3–4 and sparser on femora; scales pale golden on tibiae; sides of pronotum above procoxae, most of elytra, medial 2/3 of abdominal ventrites 3–4, and apical 3/4 of rostrum glabrous.

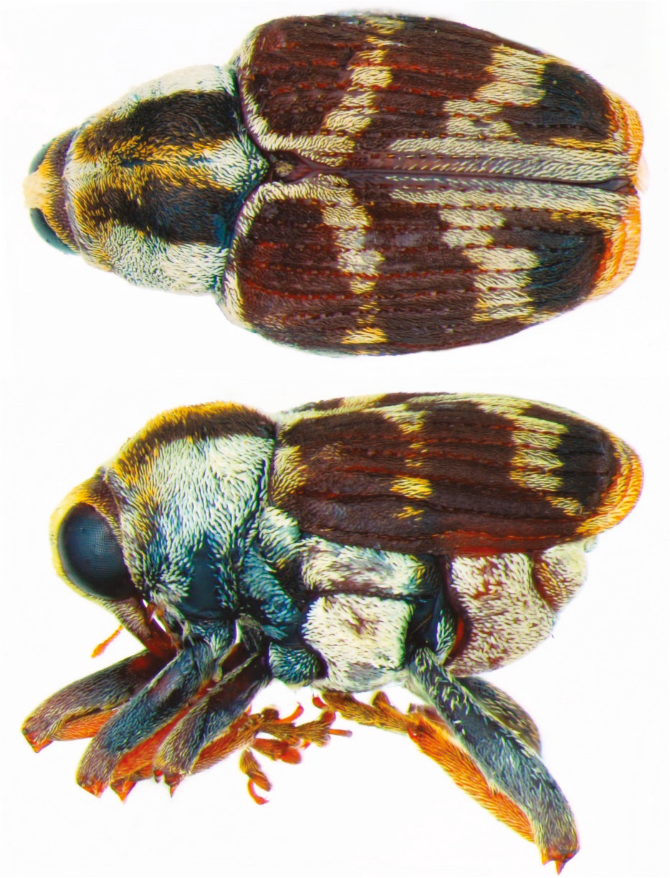

Figure 5. *Philenis costaricensis*, dorsal and lateral habitus.

Head 1.05 mm wide, 0.60 mm long, convex in dorsal view, eyes separated by 4 rows of semi-erect scales; rostrum slender, rounded-rectangular in cross section, broadening slightly at apex, weakly curved, weakly carinate above antennal insertions along midline to just above lower margins of eyes, micropunctate below antennal insertions, 1.25 mm long, antennae inserted at basal 1/5.

Pronotum 1.70 mm long, 1.80 mm wide at base, lateral margins weakly convex to weak anterior collar, in lateral view convex on basal 2/3. very weakly carinate along medial 1/3 of midline, posterior margin obliquely convergent from posterior angles and obtusely angulate anterior to scutellum. Scutellum very small, round.

Elytra 1/2 wider than pronotum at base, widest at basal 1/3. humeri somewhat prominent, intervals rounded, 1.5–2× broader than striae, striae coarsely punctate.

Mesosternum deeply emarginate and concave to receive apex of rostrum, lateral angles narrowly angulate and raised interior to mesocoxae; anterior margin of metasternum strongly declivous. In lateral view abdominal ventrite 1 very convex, slightly depressed along midline, posterior margin broadly rounded, 1.70 mm long, ventrite 2 0.50 mm long along midline, strongly ascending and declivous at posterior margin, ventrites 3–5 narrow, subequal in length. From front, procoxae broadly rounded-triangular with long tooth on inner margin. Metafemora with tooth at distal 2/3, mesofemora with minute tooth just beyond middle.

Specimens examined: Holotype: Costa Rica: Prov. Heredia, 16 km SSE La Virgen, 1050–1150 m, 10°16′ N 84°05′ W, INBio-OET-ALAS transect, 9.04.2001, 11/M/20/080 (MNCR, INB0003202065). Allotype: Costa Rica: Heredia: Est. Biol. La Selva., 50–150 m, 10°26′ N 84°01′ W, INBio-OET, 29.09.1995, Bosque primario, M/07/464 (MNCR, INBIOCRI002300837). Paratypes: Costa Rica: Cart[ago] Prov., Tapanti Nat Pk., Orosi, 1500 m, 3–4.06.1997, S. Peck, FIT, mont. evergr forest (m, CMNC); Prov. Guanacaste, Rio San Lorenzo, Tierras Morenas, 1050m, L_N_287800_427600, 10.1995, G. Rodriguez, Malaise de Cianuro (2m, MNCR, INBCRI002362313, -4); Heredia: Same data as allotype but 1.10.1993, Bosque primario, M/06/235 (f, INBC, INBIOCRI001245081), 16.08.1995, Bosque primario, M/07/440 (f, MNCR, INBIOCRI002301652), 11 km SE La Virgen, 450–550m, 10°20′ N 84°04′ W, 23.03.2003, INBio-OET-ALAS transect, 05/M/16/056 (MNCR, INB0003238453), Prov. Limon, Sector Cerro Corocori, F[in]ca de E. Rojas, 150 m, L–N 286000, 567500, 04.1992, E. Rojas (f, MNCR, INBCRI000879457), Puntarenas [Province], 1 km SE Monte Verde, 1500–1600 m, 10°18′ N 84°48′ W, 16.08.1976, H.A. Hespenheide (m, CHAH), Est. G. Brenes, Res. Biol. Monteverde, 1300 m, L-N-249750,450075,06.1991, E. Bello (m, MNCR, INBIOCRI000601598).

Other Specimens examined: Costa Rica: Heredia: 11 km ESE La Virgen, 250–350 m, 10°21′ N 84°03′ W, INBio-OET-ALAS transect, 12.02.2004, 03/M/09/009 (5, MNCR, INB0003610223, -24, -28, -29, -31), 21.03.2004, 03/M/09/049 (MNCR, INB0003613913), 12.02.2004, 03/M/11/011 (MNCR, INB0003610202), 18.04.2004, 03/M/14/094 (MNCR, INB0003617566), 22.02.2004, 03/M/15/015 (5, MNCR, INB0003610962, 63, 72, -73, -74), 9.03.2004, 03/M/15/035 (MNCR, INB0003612483), 6.04.2004, 03/M/15/075 (3, MNCR, INB0003614607, -08, -13), 18.04.2004, 03/M/15/095 (MNCR, INB0003616879), 11 km SE La Virgen, 450–550 m, 10°20′ N 84°04′ W, 2003, INBio-OET-ALAS transect, 23.03.2003, 05/M/13/053 (MNCR, INB0003236729), 8.04.2003, 05/M/14/074 (MNCR, INB0003231670), 23.03.2003, 05/M/16/056 (MNCR, INB0003238453), 23.02.2003, 05/M/17/017 (MNCR, INB0003237584), 11.03.2003, 05/M/17/037 (MNCR, INB0003239388), 23.03.2003, 05/M/17/057 (MNCR, INB0003238213), 8.04.2003, 05/M/17/077 (MNCR, INB0003231528), 23.02.2003, 05/M/19/019 (MNCR, INB0003238964), 05/R/DB/013 (MNCR, INB0003657435), 16 km SSE La Virgen, 1050–1150 m, 10°16′ N 84°05′ W, INBio-OET-ALAS transect, 9.03.2001, 11/M/13/053 (MNCR, INB0003200184), 21.03.2001, 11/M/14/074 (MNCR, INB0003202146).

Derivation of name This largely black/dark species is named for the country where all specimens have been collected.

Discussion: *Philenis costaricensis* is very similar to *P. fuscofemorata* but is larger, with the pronotum more globose and not conspicuously narrower than the elytra, and differs in the pattern of scales on elytra. The sexual dimorphism of this species led me originally to consider the sexes separate species and parallels that of *P. fuscofemorata*. The distinctive coloration suggests that it is mimetic, but no model is obvious. Specimens have been collected from lowlands to middle and higher elevations, above 1000 m. Males vary in length from 5.15–5.70 mm, (x = 5.36, N = 6); females vary in length from 5.00–5.40 mm, (x = 5.26, N = 5)

Philenis laselvaensis **Hespenheide new species**
Figure 4d and Figure 6

http://zoobank.org/urn:lsid:zoobank.org:act:6D85E6CE-E3A0-49B7-A2DC-6489BFD78F18

Description: Holotype male: body size 5.50 mm long, 2.80 mm wide. Moderately robust, elliptical, somewhat narrower anteriorly, from the side nearly flat above, convex below; black, except elytra, tibiae, antennae and rostrum reddish brown, elytra darker; sparsely to somewhat densely covered with complex pattern of scales, except rostrum below antennal insertions, most of elytra, and broad longitudinal areas lateral to midline of pronotum glabrous: scales reddish brown on most of tibiae; scales pale brownish-yellowish-white on head and in sparse, broad stripe along midline of pronotum; in dorsal view, scales yellow in broad longitudinal stripes along lateral margins of pronotum, on intervals 1 and 2 along suture and along apices of elytra, in weakly indicated transverse fascia at basal 1/4 of elytra and in weakly indicated oblique fascia just beyond middle of elytra; laterally and ventrally scales dense and white or yellowish white throughout; scales sparser on sides of femora (Figure 6).

Figure 6. *Philenis laselvaensis*, dorsal and lateral habitus.

Head 1.15 mm wide, convex in dorsal view, eyes narrowly separated by 2 rows of small scales; rostrum weakly carinate above antennal insertions, polished below antennal insertions, widening from middle toward apex, from side slightly curved and somewhat flattened dorsoventrally, 1.50 mm long, antennae inserted at basal 1/4.

Pronotum 1.80 mm long, 2.10 mm wide at base, lateral margins nearly straight from base to indistinct anterior collar, in lateral view only slightly convex. weakly carinate along midline, posterior margin narrowly convex anterior to scutellum. Scutellum very small, round.

Elytra 1/3 wider than pronotum, humeri not prominent, widest at basal 1/3, intervals slightly broader than striae.

Mesosternum declivous, deeply quadrately emarginate to receive apex of rostrum with slightly elevated, narrowly rounded lateral margins, anterior margin of metasternum declivous. In lateral view abdominal ventrite 1 weakly convex, 1.35 mm long along midline, ventrite 2 0.50 mm long along midline, strongly declivous, ventrites 3–4 narrow, subequal in length, ascending, ventrite 5 longer. From front, procoxae broadly rounded-triangular with large tooth on inner margin. Metafemora with distinct tooth at distal 2/3, mesofemora with indistinct tooth at middle. Genitalia as in Figure 4d.

Specimens examined: Holotype: Costa Rica: Heredia, Est. Biol. La Selva, 50–150m, 10°26′ N 84°01′ W, Mar 1993, INBio-OET, 3.03.1993, Bosque primario, M/10/025 (MNCR, INBIOCRI001262759). Paratypes: Costa Rica: Rio [Bouciano?], 250m, 2.04.1935, F. [Gongora] col., F. Nevermann (USNM); Prov. Alajuel[a], Chiles de Aguas, Zarcas, Café. 300 m, 11.1989–1.1990, R. Céspedes (MUCR); Prov. Heredia, F. La Selva, 3 km S Pto. Viejo, 10°26′ N 84°01′ W, 1.03.1979, T. Ray, 156 (CHAH), 22.03.1987, H.A. Hespenheide (CHAH); La Selva Biol. Sta., 3 km S Pto. Viejo, 10°26′ N 84°01′ W, 20.01.1993, Bosque primario, M/00/009 (MNCR, INBIOCRI002267490), same data as holotype but, INBio-OET-ALAS transect 24.02.2004, Malaise, M/21/763 (MNCR, INB0003663309), 24.02.2004, Malaise, M/22/764 (MNCR, INB0003663364), 24.02.2004, Malaise, M/29/771 (MNCR, INB0003663090), 9.03.2004, Malaise, M/24/776 (MNCR, INB0003663661), 9.03.2004, Malaise, M/29/781 (2, MNCR, INB0003663513, -4), 21.03.2004, Malaise, M/29/791 (MNCR, INB0003664169); 11 km SE La Virgen, 450–550m, 10°20′ N 84°04′ W, 2003, INBio-OET-ALAS transect, 11.03.2003, 05/M/10/030 (MNCR, INB0003236656), 17-21.03.2003, R. Anderson (CMNC); Prov. Limón, Cerro Tortuguero, P.N. Tortuguero,100 m, 285000 588000, 11.1989, J. Solano (MNCR, INBIOCRI000141186), Amburi, 70 m, L_S_385000_578100, 07.1996, G. Gallardo, #7884 (MNCR, INBIOCRI002446633).

Other specimens examined Costa Rica: Prov. Heredia, Est. Biol. La Selva, 50–150 m, 10°26′ N 84°01′ W, INBio-OET-ALAS transect, 1.12.1993, Bosque secondario, M/02/277 (MNCR, INBIOCRI001268174), 14,09.1995, Bosque secondario, M/02/448 (MNCR, INBIOCRI002289496), 15.03.1993, Bosque primario, M/04/035 (MNCR, INBIOCRI001245200), 15.03.1993, Bosque primario, M/05/036 (MNCR, INBIOCRI001262732), 1.04.1993, Bosque primario, M/05/052 (MNCR, INBIOCRI001239872), 31.08.1995, Bosque primario, M/08/441 (MNCR, INBIOCRI002301592), 16.02.1996, Bosque primario, M/08/573 (MNCR, INBIOCRI002304148), 15.03.1996, Bosque primario, M/08/597 (MNCR, INBIOCRI002304277), 29.09.1995, Bosque secondario, M/09/466 (MNCR, INBIOCRI002301108), 3.03.1993, Bosque primario, M/10/025 (MNCR, INBIOCRI001262759), 2.04.1993, Bosque primario, M/10/057 (MNCR, INBIOCRI002276663), 1.09.1993, Bosque primario, M/10/200 (MNCR, INBIOCRI001244971), 1.09.1993, Bosque secondario, M/11/201 (MNCR, INBIOCRI001245099), 1.11.1995, Bosque secondario, M/11/492 (MNCR, INBIOCRI002289671), 29.09.1995, Bosque secondario, M/13/470 (MNCR, INBIOCRI002300875), 16.04.1993, Bosque secondario, M/14/077 (MNCR, INBIOCRI001244670), 23.01.1998, M/18/700 (MNCR, INBIOCRI002289971), 19.02.1998, M/18/702 (2, MNCR, INBIOCRI002284055, -56), 21.01.1999, M/18/726 (MNCR, INBIOCRI002721198), 21.02.2000, M/19/742 (2, MNCR, INBIOCRI002727070, -80), 11 km ESE La Virgen, 250–350 m, 10°21′ N 84°03′ W, INBio-OET-ALAS transect, 9.03.2004, 03/M/01/041 (MNCR, INB0003613693), 18.04.2004, 03/M/01/081 (MNCR, INB0003616968), 9.03.2004, 03/M/02/022 (MNCR, INB0003613033), 22.02.2004, 03/M/03/003 (MNCR, INB0003611310), 22.02.2004, 03/M/05/005 (MNCR, INB0003610322), 18.04.2004, 03/M/15/095 (MNCR, INB0003616857), 9.03.2004, 03/M/16/036 (MNCR, INB0003612319), 11 km SE La Virgen, 450–550m, 10°20′ N 84°04′ W, 2003, INBio-OET-ALAS transect, 23.02.2003, 05/M/13/013 (2, MNCR, INB0003237736, -7), 11.03.2003, 05/M/13/033 (MNCR, INB0003238065), 23.03.2003, 05/M/13/053

(2, MNCR, INB0003236730, -1), 8.04.2003, 05/M/13/073 (MNCR, INB0003231478), 20.04.2003, 05/M/13/093 (MNCR, INB0003231913), 20.04.2003, 05/M/17/097 (MNCR, INB0003231859).

Derivation of name: This species is named for the La Selva Biological Station where this is the most frequently collected species of *Philenis*. See discussion below under ecology.

Discussion: The bright yellow scales of this common species are unique among the species treated here. Specimens varied in size from 4.9–6.5 mm (x = 5.93 mm, N = 17).

Philenis auritibiae **Hespenheide new species**

Figure 4a and Figure 7

http://zoobank.org/urn:lsid:zoobank.org:act:4F1E70FB-1D9A-4268-B8C6-514709681DFB

Description: Holotype: body size 5.55 mm long, 3.00 mm wide. Moderately robust, oboval, narrower anteriorly, black, except tibiae, antennae and apical 2/3 of rostrum reddish brown, intervals 2–8 of elytral disc dark reddish brown; sparsely to somewhat densely covered with complex pattern of scales: scales reddish-brown on reddish brown portion of elytra and in small triangular spots anterior to humeri; scales golden on most of tibiae; scales yellowish-white between eyes, in narrow stripe along midline of pronotum and broad transverse fascia on basal 1/3 of elytra; in dorsal view, scales white in longitudinal stripes along lateral margins of pronotum, in narrow bands at bases and apices of elytra, along apical 1/6 of elytral suture and in broad transverse fascia at apical 2/3 of elytra; ventrally scales white on procoxae and on pronotum just above procoxae, on metasternum, meso and metepisterna, mesepimeron, posterior margins of abdominal ventrites 1 and 5, posterior 1/2 of ventrite 2, and lateral margins of ventrites 3–4; scales sparser and white on femora and posterior margins of meso- and metatibiae, otherwise scales black; sides of pronotum and apical 3/4 of rostrum glabrous (Figure 7).

Figure 7. *Philenis auritibiae*, dorsal and lateral habitus.

Head 1.00 mm wide, convex in dorsal view, eyes separated by 4 rows of small scales; rostrum nearly straight, polished below antennal insertions, somewhat flattened dorsoventrally, 1.25 mm long, antennae inserted at basal 1/4.

Pronotum 1.80 mm long, 2.00 mm wide at base, lateral margins nearly straight from base to indistinct anterior collar, in lateral view gibbous at basal 1/3 and declivous anteriorly. weakly carinate along basal 3/4 of midline, posterior margin extended posteriorly anterior to scutellum. Scutellum small, round.

Elytra 0.5 wider than pronotum, humeri slightly prominent, intervals much broader than striae, striae linear.

Mesosternum declivous, deeply emarginate to receive apex of rostrum, anterior margin of metasternum declivous. In lateral view abdominal ventrite 1 weakly convex, 1.50 mm long along midline, ventrite 2 0.70 mm long along midline, strongly declivous, ventrites 3–5 narrow, subequal in length, ascending. From front, procoxae broadly rounded-triangular with large tooth on inner margin. Meso- and metafemora with distinct tooth at distal 2/3.

Specimens examined: Holotype: Costa Rica: Prov. Heredia, 9 km NE Vara Blanca, 1450–1550 m, 10°14′ N 84°06′ W, INBio-OET-ALAS transect, 17.04.2005, 15/M/04/114, Finca Murillo (MNCR, INB0003672307). Paratypes: Costa Rica: Prov. Guanacaste, Rio San Lorenzo, Tierras Morenas, Z.P. Tenorio, 1050 m, L–N 287800, 427600, 10.1992, G. Rodriguez, Malaise de Cianuro (MNCR INBIOCR000836551); same data as holotype, 17.04.2005, 15/M/04/104, Finca Murillo (MNCR, INB0003670685), 17.04.2005, 15/TN/04/022, Finca Murillo (MNCR, INB0003676106).

Derivation of name: The name refers to the elongate golden scales on the tibiae. Other species share this character, but not as strikingly as on this largely black species.

Discussion: *Philenis auritibiae* is an upper middle elevation (1–2000 m) species and is the only essentially all black Central American species with a design of white scales dorsally. Three of the four individuals show small "multifurcate" scales (Figure 4a) on the pronotum discussed further below. Specimens vary in length from 4.80–5.80 mm, (x = 5.47, N = 4).

Philenis brunnea Hespenheide new species

Figure 4e

http://zoobank.org/urn:lsid:zoobank.org:act:CB39214A-F25E-4400-A3E8-DF115F0EE2EF

Description: Holotype male: body size 4.70 mm long, 2.55 mm wide. Robust, elliptical, narrower anteriorly, pale reddish brown throughout, elytra darker, especially apical 1/4; mesosternum, epimeron, coxae, interior surface of metafemora, abdominal ventrites 3–4, and pronotum above procoxae black; more or less densely and uniformly covered with complex pattern of scales, except rostrum distal to antennal insertions glabrous: scales pale yellow on head; scales pale brownish-yellow dorsally on medial portion of disc and anterior 1/2 of pronotum; scales dark brown and inconspicuous on much of elytra; scales white on elytra along basal and apical margins, on elytral intervals 1–2 lateral to suture, in slightly oblique transverse band at basal 1/3, and in broader, irregular oblique band from middle to apical 2/3; scales white ventrally and on femora; and scales golden yellow on tibiae.

Head 1.00 mm wide, 0.50 mm long, very convex in dorsal view, eyes narrowly separated by 4 rows of semierect scales; rostrum slender, rounded-rectangular in cross section, widening slightly toward apex, from side slightly curved, 1.25 mm long, antennae inserted at basal 1/4. rostrum below antennal insertions micropunctate.

Pronotum 1.60 mm long, 1.70 mm wide at base, lateral margins weakly rounded to anterior collar, in lateral view gibbous at basal 1/3 and declivous anteriorly, posterior margin obliquely convergent, acute and slightly upturned anterior to scutellum. Scutellum small, rounded.

Elytra 1/2 wider than pronotum, humeri moderately prominent, widest at basal 1/3, intervals much broader than striae, somewhat flattened, striae linear.

Mesosternum deeply concave, deeply emarginate at posterior margin to receive apex of rostrum, with blunt, raised teeth at lateral margins interior to mesocoxae, anterior margin of metasternum declivous. In lateral view abdominal ventrite 1 very weakly convex, 1.10 mm long and slightly depressed along midline, ventrite 2 ascending, 0.40 mm long along midline, weakly convex in lateral view, ventrites 3–5 narrow, subequal in length, ascending, From front, procoxae triangular with narrow tooth on inner margin. Metafemora with distinct acute tooth at distal 2/3. Genitalia as in Figure 4e.

Specimens examined: Holotype: Costa Rica, Prov. Heredia: 11 km SE La Virgen, 450–550m, 10°20′ N 84°04′ W, 11.03.2003, INBio-OET-ALAS transect, 05/M/03/033 (MNCR, INB0003243097). Paratype: Costa Rica, same data as Holotype (MNCR, INB0003243098).

Other specimen examined: Panamá: Prov. Colón, Achiote PN San Lorenzo, 09°11′ N 79°58′ W, Cafetal C, Dist 50 m 11–26.01.2008, A Mercado, Tr. Intercepción (CMNC).

Derivation of name: The species name refers to the generally pale brown overall coloration.

Discussion: This is the only completely pale brown species of *Philenis* in Central America. The color pattern of scales is similar to that of *P. costaricensis* (Figure 5). The two Costa Rican specimens are both males and equal in size. The specimen from Panama is probably a female and larger, 5.55 mm long, and has a few differences from the Costa Rican specimens - a stouter rostrum that is carinate at the base along the midline - but has the same distinctive albeit finer pattern of coloration.

Philenis muscamimetica Hespenheide new species

Figure 8

http://zoobank.org/urn:lsid:zoobank.org:act:025E7530-EAB2-4D59-8549-ED2EA6F9A3E1

Description: Holotype: body size 5.75 mm long, 3.00 mm wide. Moderately robust, elliptical, somewhat narrower anteriorly, black throughout, except elytral disc reddish brown; sparsely to somewhat densely covered with scales: scales orange-red on vertex of head posterior to eyes and on anterior 1/2 of pronotum dorsally extending on sides to middle of eyes; scales dense and yellowish on frons and on rostrum to antennal insertions; scales pale sparse brown on disc of pronotum; scales pale yellowish-brown on ventral 1/2 of procoxae, in narrow line on midline of basal 1/4 of pronotum, in narrow line along base of elytra, on interval 2 along suture for length of elytra, in narrow line along apices of elytra and in spots on intervals 9 and 10 at basal 1/4 of elytra and intervals 8–10 at apical 3/4 of elytra; scales white in broad irregular line from posterior angles of pronotum to posterior edge of red scales and along anterior edge of sides of pronotum to procoxae, on mesepisterna, dorsal 1/2 of epimera, middle 2/3 of metepistera, and metasternum; scales white in broadly triangular area on sides of abdominal ventrite, 1, on posterolateral 1/2 of ventrite 2, and on lateral 1/3 of ventrites 3–5, and on basal 1/2 of ventral surfaces of meso- and metafemora; elsewhere scales are dark brown or black or minute and inconspicuous.

Head 1.20 mm wide, 0.45 mm long, very convex in dorsal view, eyes narrowly separated by 2–4 rows of scales; rostrum narrowly carinate at and above antennal insertions, matte black below antennal insertions, widening slightly toward apex, from side slightly curved, 1.60 mm long, antennae inserted at basal 1/4.

Pronotum 1.95 mm long, 2.25 mm wide at base, lateral margins weakly rounded from base to indistinct anterior collar, in lateral view weakly convex at base and declivous anteriorly, posterior margin narrowly acutely rounded and slightly upturned anterior to scutellum. Scutellum small, rounded-triangular.

Elytra 1/2 wider than pronotum, humeri not prominent, widest at basal 1/4, intervals 2–3× broader than striae.

Mesosternum concave, deeply emarginate at posterior margin to receive apex of rostrum with slightly elevated, rounded lateral lobes internal to mesocoxae, prosternum strongly excavate anterior to forecoxae, anterior margin of metasternum declivous. In lateral view abdominal ventrite 1 weakly convex, 1.90 mm long along midline, ventrite 2 0.50 mm long along midline, strongly declivous at posterior margin, ventrites 3–4 narrow, subequal in length, ascending, ventrite 5 longer. From front, procoxae broadly oval with large tooth on inner margin. Metafemora with strong acute tooth at distal 2/3, mesofemora with small, distinct tooth at distal 3/5, profemora angulate at middle.

Figure 8. *Philenis muscamimetica*, dorsal and lateral habitus.

Specimen examined: Holotype: Panamá, Panamá Pr., 6–8 km N El Llano on El Llano-Carti Road, 6.06.1994, F. Andrews & A. Gilbert (CSCA).

Derivation of name: This species is named for its coloration, which is typical of conoderines in the putative fly mimicry complex [5,7] and is probably the same species mentioned by Anzaldo [4] as undescribed.

Discussion: As a putative fly mimic, *Philenis muscamimetica* stands uniquely apart from the other members in the genus treated here in terms of habitus.

Philenis chiriquiensis Hespenheide new species

Figure 4a,f and Figure 9

http://zoobank.org/urn:lsid:zoobank.org:act:F26FA38B-8035-4F2D-BF12-7C2F1FD09C51

Description: Holotype male: body size 5.60 mm long, 2.90 mm wide. Moderately robust, elliptical, somewhat narrower anteriorly, reddish brown throughout, ventral surface and femora nearly black; sparsely to somewhat densely covered with complex pattern of scales: scales dark brown or black on most of elytra and on disc and oblique lateral stripe on pronotum; scales brownish yellow on tibiae, head and antero-medial stripe on midline of pronotum; scales pale brownish-white on femora, in broad longitudinal stripes along lateral margins of pronotum, on interval 1 and along suture and apical margins of elytra, along basal margins of elytra connecting to weakly oblique fascia at basal 1/3 of elytra and in broad oblique fascia just beyond middle of elytra; laterally and ventrally scales moderately dense and white throughout (Figure 9).

Head 1.05 mm wide, 0.40 mm long, very convex in dorsal view, eyes narrowly separated by 2 rows of erect scales; rostrum weakly carinate at antennal insertions, polished below antennal insertions, widening from middle toward apex, from side slightly curved, 1.60 mm long, antennae inserted at basal 1/4.

Pronotum 1.70 mm long, 2.00 mm wide at base, lateral margins weakly rounded′ from base to indistinct anterior collar, in lateral view weakly gibbous at basal 1/4 and declivous anteriorly, disc strongly shining, posterior margin narrowly acutely rounded and slightly upturned anterior to scutellum. Scutellum small, round.

Elytra 1/3 wider than pronotum, humeri not prominent, widest at humeri, intervals 2–3× broader than striae.

Mesosternum somewhat concave, deeply emarginate at posterior margin to receive apex of rostrum with slightly elevated, narrowly rounded lateral margins, prosternum strongly excavate anterior to procoxae, anterior margin of metasternum declivous and weakly concave. In lateral view abdominal ventrite 1 weakly convex, 1.40 mm long along midline, ventrite 2 0.60 mm long along midline, strongly declivous at posterior margin, ventrites 3–4 narrow, subequal in length, ascending, ventrite 5 longer. From front, procoxae broadly rounded-triangular with large tooth on inner margin. Metafemora with distinct tooth at distal 2/3, mesofemora weakly angulate at middle. Genitalia as in Figure 4f.

Specimens examined: Holotype: Panamá: Chiriqui Prov., Reserva Fortuna, Continental Divide Trail, 26.05.1993, F. Andrews & A. Gilbert (CSCA). Paratypes: Costa Rica: Puntarenas Province, Monteverde, John Campbell property, 4.06.1992, F. Andrews & A. Gilbert (CSCA). Panamá: same data as holotype except 1.06.1993, F. Andrews & A. Gilbert (CSCA), La Fortuna, Cont. Divide Trail, 08°47′76″ N 82°14′75″ W, 1370 m, 7.09.2010, L. Sekerka, montane forest, beating (2, BMNH), La Fortuna, Continental Divide Trail, 08°47′07″ N 082°12′49″-14′ W, 1170–1300 m, 20.09.2007, L. Sekerka & D. Windsor, cloudy forest, beating (BMNH), Continental Divide Trail, 3–8.07.1997, J. Huether (CMNC).

Derivation of name: This species is named for the volcano and the Panamanian province on and in which most specimens have been collected.

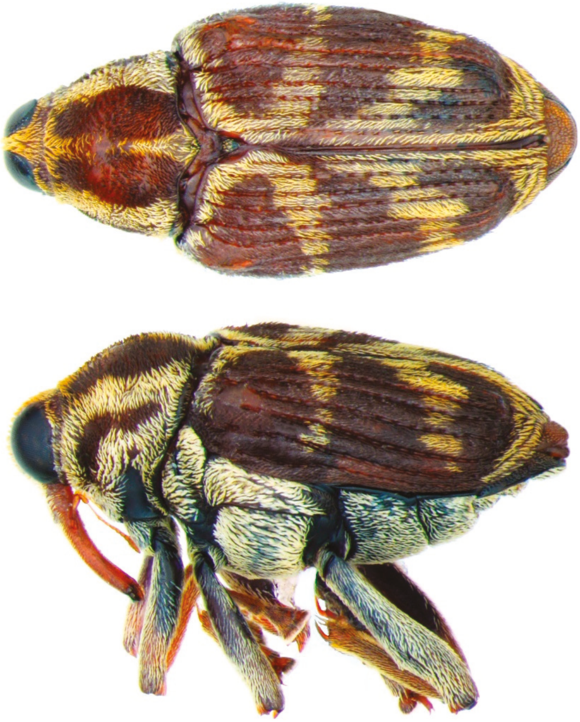

Figure 9. *Philenis chiriquiensis*, dorsal and lateral habitus.

Discussion: *Philenis chiriquiensis* is a relatively large, somewhat flattened, high elevation species, largely dark reddish brown in ground color dorsally and black ventrally, with a bold pattern of scales on the elytra. The Huether specimen is treated as conspecific but shows striking scales on the pronotum not shared by the other specimens. As with *P. auritibiae*, above, I term these scales "multifurcate" in that they branch separately and sequentially along the axis of the scale (Figure 4a), a character that is also shared by two somewhat different specimens from the Monteverde area in Costa Rica that may represent an undescribed species. These scales differ from "multifid" scales of Anzaldo [4] (also termed "pectinate" by Champion [1]; "plumose" by Lyal et al. [8]) in the genera *Philides* Champion and *Philinna* Champion, as well as in *Tachygonus* Schoenherr, where the separate "fingers" of the scales all arise from the base, rather than sequentially along the axis. Specimens vary in length from 4.80–6.10 mm, (x = 5.50, N = 7).

***Philenis guyanensis* Hespenheide new species**
Figure 10b,c

http://zoobank.org/urn:lsid:zoobank.org:act:E7158A1E-15F6-499C-A322-2D275F0F3202

Description: Holotype male: body size 4.40 mm long, 2.50 mm wide. Very robust, elliptical, narrower anteriorly, pale reddish brown throughout, anterior angles of pronotum paler, disc of pronotum and oblique transverse bands just posterior to base and at middle darker; metatibiae and apices of metafemora, and triangular areas at apices of elytra exterior to intervals 1–2 black; sparsely to somewhat densely covered with complex pattern of scales: scales black on metatibiae and in triangular black areas at elytral apices; scales dark brown on darker areas of pronotum and elytra or black on most of elytra and on disc and oblique lateral stripe on pronotum; scales golden yellow elsewhere; rostrum below antennal insertions glabrous, micropunctate (Figure 10b).

Head 0.95 mm wide, 0.55 mm long, very convex in dorsal view, eyes narrowly separated by 2 rows of scales; frons and rostrum carinate from lower 1/3 of eyes to antennal insertions, widening slightly from middle toward apex, from side slightly curved, 1.30 mm long, antennae inserted at basal 1/4.

Pronotum 1.30 mm long, 1.75 mm wide at base, lateral margins weakly rounded to distinct anterior collar, in lateral view gibbous at basal 1/3 and strongly rounded-declivous anteriorly, posterior margin rounded anterior to scutellum. Scutellum small, elliptical.

Elytra 1/3 wider than pronotum, humeri moderately prominent, widest at humeri, intervals broader than striae, intervals 4, 6 and 8 raised, subcarinate, striae linear.

Mesosternum concave, deeply emarginate at posterior margin to receive apex of rostrum with triangular lateral margins, anterior margin of metasternum declivous. In lateral view abdominal ventrite 1 weakly convex, 1.20 mm long and somewhat depressed along midline and weakly emarginate at posterior margin, ventrite 2 0.50 mm long along midline, strongly declivous at posterior margin, ventrites 3–5 narrow, subequal in length, ascending. From front, procoxae broadly rounded-triangular without tooth on inner margin. Metafemora with distinct tooth at distal 2/3, fore- and mesofemora with very small tooth at distal 2/3. Genitalia as in Figure 10c.

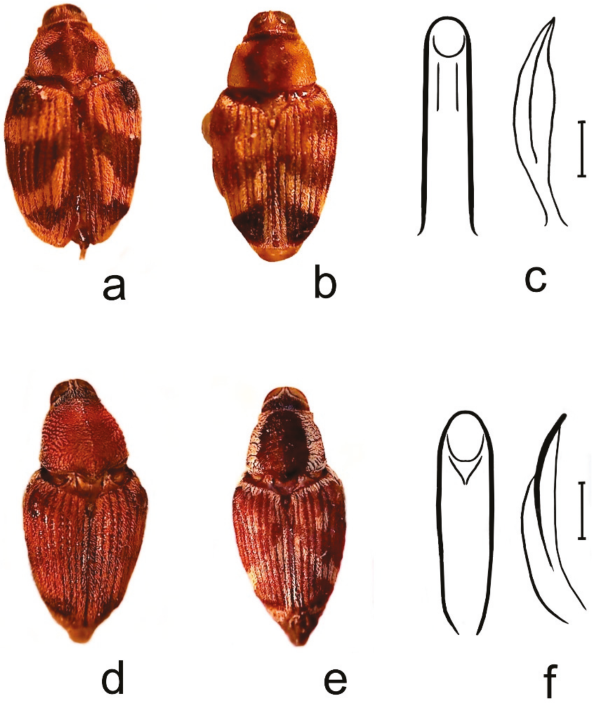

Figure 10. (**a**) *Philenis ferruginea*, dorsal habitus; (**b**) *P. guyanensis*, dorsal habitus; (**c**) *P. guyanensis*, male genitalia, dorsal and lateral views; (**d**) *P. howdeni*, dorsal habitus; (**e**) *P. kuscheli*, dorsal habitus; (**f**) *P. kuscheli*, male genitalia, dorsal and lateral views; scale bars = 0.2 mm.

Specimens examined: Holotype: French Guiana: Nouragues Saut-Pararé, 4°02′16.1″ N, 52°40′21.1″ W, 09.2009, S. Brulé, Window trap (BMNH(E) 2010-62). Paratypes: Same data as holotype (3, BMNH(E) 2010-62).

Derivation of name: This species is named for Guyane, also known as French Guiana, the overseas department of France in which all specimens have been collected.

Discussion: *Philenis guyanensis* has a pattern of scales that is similar to that of many Central American species, but is unusually robust, and generally pale reddish-brown, excpt for black triangular areas at the apices of the elytra and black metatibiae. Specimens vary in length from 4.30–4.70 mm, (x = 4.51, N = 4).

Philenis ferruginea Hespenheide new species

Figure 10a

http://zoobank.org/urn:lsid:zoobank.org:act:E07F6D73-28F6-4AEC-A807-393E136BB4E2

Description: Holotype: body size 4.95 mm long, 3.05 mm wide. Very robust, elliptical, narrower anteriorly, complex pattern of ground color: black on scutellum and elytral humeri above, vertical spot on side of pronotum above procoxae, mesepimra, and epimeron, posterior 4/4 of metepimera, postero-lateral margin of abdominal ventrite 1, meso- and metacoxae, apex of metafemora and basal 1/2 of metatibiae; otherwise reddish brown throughout, hourglass shaped area on disc of pronotum, elytra, and posterior margin of abdominal ventrites 2 and 5 darker; sparsely to somewhat densely covered with brownish yellow scales: scales dark brown on darker area of pronotum or other darker areas, black on elytra in oblique broadening fascia from basal 1/3 to posterior 2/3 and in irregular oblique fascia anterior to elytral apices; rostrum below antennal insertions glabrous, polished.

Head 0.95 mm wide, 0.30 mm long, rounded-truncate in dorsal view, eyes narrowly separated by 1 row of scales; rostrum not carinate, shallowly transversely depressed at base above antennal insertions, widening slightly from middle toward apex, from side strongly curved, 1.45 mm long, antennae inserted at basal 1/4.

Pronotum 1.35 mm long, 1.75 mm wide at base, lateral margins weakly rounded to distinct anterior collar, in lateral view strongly gibbous at basal 1/3 and rounded-declivous anteriorly, posterior margin projecting and rounded-triangular anterior to scutellum. Scutellum small, rounded-rectangular.

Elytra 5/7 wider than pronotum, humeri prominent, widest at basal 1/4, intervals broader than striae, interval 3 broader than others, striae narrow and punctate.

Mesosternum slightly concave posterior margin straight without projecting lateral angles, anterior margin of metasternum weakly declivous. In lateral view abdominal ventrite 1 weakly convex, 1.40 mm long, posterior margin broadly, shallowly rounded, ventrite 2 0.50 mm long along midline, strongly declivous at posterior margin, ventrites 3–4 narrow, subequal to ventrite 5, ascending. From front, forecoxae broadly rounded-triangular with short narrow, incurved tooth on inner margin. All femora with short distinct tooth.

Specimen examined: Holotype: Ecuador: Sucumbios, Sacha Lodge, 270 m, 0.5° S, 76.5° W, 3–13.04.1994, Hibbs, ex malaise (CMNC).

Derivation of name: This species is named for its generally dark reddish-brown ground coloration.

Discussion: *Philenis ferruginea* is one of the more distinct species treated here in being very robust with a reddish-brown ground coloration variegated with black, in the structure of the rostrum, and comparatively simple mesosternum. The type is probably a female.

Philenis howdeni Hespenheide new species

Figure 10d

http://zoobank.org/urn:lsid:zoobank.org:act:214D0D67-3558-4C0D-AA40-13B5C77A76ED

Description: Holotype: body size 5.60 mm long, 2.95 mm wide. Moderately robust and somewhat flattened dorsoventrally, elliptical, somewhat narrower anteriorly, elytra, dorsal portion of pronotum, protibiae, and rostrum below antennal insertions reddish brown, elytral humeri darker and with very dark spots on elytra on elytral intervals 4–9 anterior to elytral apices; head, scutellum, ventral surface and legs black; dorsally more or less uniformly densely covered with reddish scales; scales pale brownish yellow on head; ventrally and on femora more or less uniformly covered with greyish-white scales, denser on ventral portions of femora, metasternum and abdominal ventrite 5; rostrum below antennal insertions, elytral humeri and apical spots glabrous.

Head 1.15 mm wide, 0.45 mm long, rounded-truncate in dorsal view, eyes narrowly separated by 2 rows of small semi-erect scales; midline of head from lower 1/4 of eyes to antennal insertions rostrum carinate, polished below antennal insertions, widening slightly at apex, from side slightly curved, 1.55 mm long, antennae inserted at basal 1/3.

Pronotum 1.90 mm long, 2.10 mm wide at base, lateral margins weakly rounded' from base to indistinct anterior collar, in lateral view lightly gibbous at base and declivous anteriorly, indistinctly carinate long midline, posterior margin broadly, obtusely triangular and slightly upturned anterior to scutellum. Scutellum small, round.

Elytra 1/2 wider than pronotum, widest at humeri, humeri moderately prominent, intervals equal to or slightly broader than striae, striae coarsely punctate.

Mesosternum concave, deeply emarginate at posterior margin to receive apex of rostrum with slightly elevated, narrowly rounded lateral margins, anterior margin of metasternum strongly declivous. In lateral view abdominal ventrite 1 weakly convex, 1.50 mm long along midline, ventrite 20.55 mm long along midline, strongly declivous at posterior margin, ventrites 3–5 narrow, subequal in length, ventrite 5 slightly longer. From front, procoxae broadly oval with large tooth on inner margin. Metafemora with distinct tooth at distal 2/3, mesofemora with weaker tooth beyond middle, profemora with tiny distinct tooth at distal 2/3.

Specimen examined: Holotype: Ecuador: Pinchincha Prov., 15 km E Sto. Domingo Tinalandia, 700 m, 26.02.1981, H, F. Howden (CMNC).

Derivation of name: This species is named in honor of its collector, the late coleopterist Henry Howden.

Discussion: *Philenis howdeni* is unusual among the species treated here in the genus in being unpatterned and uniformly brownish-red dorsally and black ventrally.

Philenis kuscheli **Hespenheide new species**

Figure 10e,r

http://zoobank.org/urn:lsid:zoobank.org:act:3ECE76CB-A889-4883-A846-625F045104A4

Description: Holotype female: body size 4.60 mm long, 2.40 mm wide. Moderately robust, elliptical, narrower anteriorly; head, ventral surface and femora black, rostrum, pronotum, elytra, and tibiae dark reddish brown; sparsely to somewhat densely and uniformly covered with complex pattern of scales: scales dark reddish-brown on disc of pronotum on lighter most of elytra; dorsally scales white along lateral margins of pronotum, in narrow bands at bases and apices of elytra, on elytral intervals 1–2 along apical 2/3 of elytral suture and in oblique fascia from apical 2/3 of elytra; scales white on frons and rostrum above antennal insertions and ventrally, denser on procoxae and on pronotum just above procoxae, on and mesepimeron and metepisternum; sides of pronotum and rostrum beyond antennal insertions glabrous. (Figure 10e)

Head 1.05 mm wide, 0.45 mm long, convex in dorsal view, eyes separated by 2 rows of small scales; rostrum weakly curved, polished below antennal insertions, somewhat flattened dorsoventrally, widening slightly at apex, 1.30 mm long, antennae inserted at basal 1/5.

Pronotum 1.50 mm long, 1.65 mm wide at base, lateral margins slightly convex from base to distinct anterior collar, in lateral view gibbous at basal 1/3 and declivous anteriorly. weakly carinate along medial 1/3 of midline, posterior margin extended posteriorly and rounded anterior to scutellum. Scutellum very small.

Elytra 0.5 wider than pronotum, humeri slightly prominent, intervals 1.5–2× broader than striae, rounded, striae coarsely punctate.

Mesosternum declivous, concave and deeply emarginate to receive apex of rostrum, lateral angles acute and weakly carinate, anterior margin of metasternum declivous. In lateral view abdominal ventrite 1 weakly convex, 1.50 mm long along midline, ventrite 2 0.45 mm long along midline, declivous at posterior margin, ventrites 3–5 narrow, subequal in length, ascending. From front, procoxae oval with large tooth on inner margin. Meso- and metafemora with distinct tooth at distal 2/3.

Allotype male. As holotype, except body size 3.80 mm long, 1.90 mm wide. Anterior and posterior elytral fasciae indistinct, possibly abraded. Genitalia as in Figure 10f.

Specimens examined: Holotype: Ecuador: Rio Palenque, 47 km S St. Domingo, 700′, 22-27.02.1976, H, & A. Howden (CMNC). Allotype: Ecuador: Rio Palenque R.S., 200 m, 4.02.1983, Masner & Sharkey (CMNC). Paratype: Colombia: Narino, Barbacoas, 2–6.05.1976, M. Cooper (BMNH).

Derivation of name: This species is named in honor of Guillermo ("Willi") Kuschel and his extensive study of the Curculionidae, including the Conoderinae, and his residence in South America.

Discussion: The sharp, nearly linear contrast between the dark disc of the pronotum and the white scales of the sides is distinctive. The pattern of scales on the elytra is similar to that of several Central American species, but the uniformly black ventral coloration is not. This is the smallest South American species treated here; specimens vary in length from 3.80–4.60 mm, (x = 4.11, N = 3).

3.1.2. Key to Species of *Philenis*

1	Pronotum broad with transverse fascia of yellow setae, species more robust in shape; associated with plants in Araceae	2
1A	Pronotum with longitudinal stripes of setae, often noticeably narrower than elytra; species more elongate and slender, plant associations unknown	3
2	Apices of elytra black posterior to posterior transverse fascia; Costa Rica and Panamá	*P. flavipes*
2A	Elytra uniformly reddish brown with apical triangular areas of yellowish scales; Costa Rica and Panamá	*P. anzaldoi*
3	Pronotum in dorsal view and elytra uniformly reddish brown without complex pattern of scales; black ventrally; Ecuador	*P. howdeni*
3A	Pronotum and elytra with more or less complex variation in ground coloration and pattern of scales dorsally and ventrally	4
4	Pronotum dorsally with lateral stripes of pale scales on posterior 1/2 and covered with red scales on anterior 1/2, elytra simply marked with pale scales along suture and anterior and posterior margins Panamá	*P. muscamimetica*
4A	Pronotum dorsally with lateral stripes of pale scales for entire length, some species with medial stripe, elytra marked with transverse and/or oblique bands of scales	5
5	Species essentially all black dorsally and ventrally except pale brown tibiae, scales white dorsally, strong medial stripe on pronotum; Costa Rica	*P. auritibiae*
5A	Species largely brown dorsally, at least on most of elytra	6
6	Species completely or largely lighter or darker brown dorsally	7
6A	Pronotum all or mostly black, elytra completely brown or marked with black	10
7	Species completely lighter or darker brown dorsally, including elytra; Central America	8
7A	Species with black areas on elytra; South America	9
8	Species lighter brown dorsally and mostly brown ventrally except area black around mesocoxae and abdominal ventrites 3–4, pronotum matte, covered with small scales; Costa Rica and Panamá	*P. brunnea*
8A	Species darker brown dorsally and black ventrally, pronotum medially mostly glabrous medially, shining, Chiriqui highlands, Panama	*P. chiriquiensis*
9	Elytral humeri black, patches of black ventrally on mesocoxal area, metepimera and abdominal ventrite 1; Ecuador	*P. ferruginea*
9A	Elytra with apical triangular areas black, ventrally brown; Guyane	*P. guyanensis*
10	Elytra uniformly dark brown	11
10A	Elytra red brown, usually black posterior to posterior oblique fascia	12
11	Ornamented dorsally and ventrally with bright yellow scales, pronotum with medial stripe of scales, 4.9–6.5 mm long, Costa Rica	*P. laselvaensis*
11A	Ornamented dorsally and ventrally with pale tan or white scales, pronotum without medial stripe of scales 3.80–4.60 mm long, Colombia, Ecuador	*P. kuscheli*
12	Pronotum moderately gibbous, not conspicuously narrower than elytra at base, metafemoral tooth strong, in lateral view line from eyes to rostrum nearly straight, size 5.00–5.70 mm long; Costa Rica	*P. costaricensis*
12A	Pronotum declivous in lateral view, usually conspicuously narrower than elytra at base, metafemoral tooth minute or absent, in lateral view line from eyes to rostrum angulate, size 3.75–4.80 mm long, Costa Rica and Panamá	*P. fuscofemorata*

3.2. Ecology

Hosts: Although nothing is known about the plant hosts of most of the species reported here, *Philenis anzaldoi* has been cut from a gall on a liana in the Araceae in Panamá, probably in the genus *Philodendron* Schott, and an adult *P. flavipes* has been associated with a species of Araceae in Costa Rica. Aroids have a relatively high plant diversity in Neotropical regions. with 778 species in 26 genera known from Central America [9]. At least one other genus of conoderine weevils, *Hoplocopturus* Heller, is associated with species of *Xanthosoma* Schott in the Araceae (Hespenheide, unpublished), one of which makes galls on an undetermined terrestrial species (Kenji Nishida, unpublished). Several undescribed species are associated with aerial roots of species in the genus *Monstera* Adanson [10].

Sampling: The Arthropods of La Selva (ALAS) project used a variety of standardized sampling techniques—Malaise, light and pitfall trapping, and canopy fogging—to sample the fauna at La Selva over 11 years [3] and then for several weeks of sampling during one of four years at sites along an altitudinal transect on the slopes of Volcan Barva to the south and west of La Selva. Samples were taken year-round at La Selva and only for several weeks during the dry season at 250–350 m, 450–550 m, 1050–1150 m, and 1450–1550 m along the altitudinal transect. A total of 123 specimens of *Philenis* were collected by standardized sampling, plus 8 additional specimens collected non-systematically by hand. Of the specimens collected by passive trapping, most (118) were collected by Malaise traps, 4 by light traps, one by one of the few flight intercept trap samples, and none by canopy fogging or pitfall trapping. From the ALAS sampling program alone, clearly Malaise trapping is by far the best way to collect specimens of *Philenis*. This pattern is similar to that of the genus *Microzygops* Champion [2]—species that are rarely collected by hand can be rather common in Malaise traps. Conoderine weevils are usually day-active, so the specimens taken in light traps are few but significant, three of *P. fuscofemorata* and one of *P. laselvaensis*.

Of the 56 specimens collected by others than the ALAS project, 46 are from Central America and 10 from South America. Of the South American specimens, 3 were taken in Malaise traps, 4 in window traps and 3 by hand. Of the Central American specimens, 9 are labeled from flight intercept traps, and 7 from Malaise traps. Of the remaining 30 specimens, most were collected by parataxonomists collecting for the former Instituto Nacional de Biodiversidad. I suspect many of these were collected by Malaise traps but not labelled as such.

The 43 specimens collected by year-round standardized sampling at La Selva give interesting ecological information about habitat and seasonal phenology. Only one specimen was collected in an early successional area; the rest were collected in secondary forest (11), primary forest (16), at tree falls (7), or in other situations (9). Phenological data is best for *P. laselvaensis* which accounted for 32 of the 47 specimens, including the hand collected ones. Most (24 of 32, or 75%) were collected during the dry season, January-April and 5 in September. Specimens of other species were not so concentrated, but no *Philenis* were collected May or July; and only one in each of June, November, and December. All transect samples were made in February to April during the dry season and cannot give information on year-round phenology.

In terms of the altitudinal distribution of *Philenis* species along the Barva transect, 47 were collected at La Selva (50–150 m in elevation), which was also the most intensively sampled site over 10 years. The other sites were each visited in only a single one of four years for similar amounts of time. At these, 39 *Philenis* were collected at the 250–350 m site, 40 at the 450–550 m site, 5 at the 1050–1150 m site, and 3 at the 1450–1550 m site, all of one species, *P. auritibiae*. *Philenis* thus appears to be a genus most characteristic of lower middle elevations.

Mimicry: Probably because they are often medium to large day-active species, mimicry is common among conoderine weevils [5,10]. Perhaps the most frequent putative models are flies [5,7,11], and *Philenis muscamimetica* is an example of that type of mimicry. On the other hand, mimicry of social Hymenoptera other than ants [12] is very infrequent among conoderines, and the putative examples of *Philenis flavipes* and *P. anzaldoi* with their coloration of variegated yellow, brown and black are the only ones known to me. The bold coloration of *Philenis fuscofemorata* and *P. costaricensis* (Figures 3 and 5) may indicate that they are also involved in mimicry, but the models are less obvious.

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Conflicts of Interest: The author declares no conflict of interest.

References

1. Champion, G.C. Curculionidae, Curculioninae, Zygopina. In *Biologia Centrali-Americana, Insecta, Coleoptera, Volume IV, 5*; Godman, F.D., Salvin, O., Eds.; R. H. Porter: London, UK, 1906; pp. 1–130.
2. Hespenheide, H.A. A review of *Microzygops* Champion, 1906, with description of a new species (Coleoptera: Curculionidae: Conoderinae). *Coleopt. Bull.* **2018**, *72*, 113–117. [CrossRef]

3. Longino, J.T.; Colwell, R.K. Biodiversity assessment using structured inventory: Capturing the ant fauna of a tropical rainforest. *Ecol. Appl.* **1997**, *7*, 1263–1277. [CrossRef]
4. Anzaldo, S.S. Review of the genera of Conoderinae (Coleoptera, Curculionidae) from North America, Central America, and the Caribbean. *ZooKeys* **2017**, *683*, 58–138. [CrossRef] [PubMed]
5. Hespenheide, H.A. Mimicry in the Zygopinae (Coleoptera: Curculionidae). *Mem. Entomol. Soc. Wash.* **1995**, *14*, 145–154.
6. Philaenis. Available online: https://en.wikipedia.org/wiki/Philaenis (accessed on 29 June 2018).
7. Hespenheide, H.A. A novel mimicry complex: Beetles and flies. *J. Entomol. Ser. A-Gener.* **1973**, *48*, 49–56. [CrossRef]
8. Lyal, C.H.C.; Douglas, D.A.; Hine, S.J. Morphology and systematic significance of sclerolepidia in the weevils (Coleoptera: Curculionoidea). *Syst. Biodivers.* **2006**, *4*, 203–241. [CrossRef]
9. Ortiz, O.O.; Croat, T.B.; Baldini, R.M. Current status of aroid species diversity in Panama, including new records for the country. *Webbia* **2018**, 1–13. [CrossRef]
10. Hespenheide, H.A. The role of plants in structuring communities of mimetic insects. In *Neotropical Biodiversity and Conservation*; Gibson, A., Ed.; Mildred Mathias Botanical Garden: Los Angeles, CA, USA, 1996; pp. 109–126.
11. Hespenheide, H.A. Weevils of the genera *Archocopturus* Heller and *Zygopsella* Champion, sibling species, and mimetic homoplasy (Coleoptera: Curculionidae: Conoderinae). *Proc. Entomol. Soc. Wash.* **2005**, *107*, 671–685.
12. Hespenheide, H.A. Mimicry of ants of the genus *Zacryptocerus* (Hymenoptera: Formicidae). *J. N. Y. Entomol. Soc.* **1986**, *94*, 394–408.

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Article

Review of Cape Verde *Aphanommata* Wollaston, 1873 (Coleoptera: Curculionidae: Cossoninae) with Description of New Species, Larva and Notes on Biology and Distributional Patterns

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Abstract: The genus *Aphanommata* in the Old World is reviewed. *Aphanommata kuscheli* sp. nov. from São Nicolau and *A. strakai* sp. nov. from Fogo (both Cape Verde islands) are described. *Aphanommata euphorbiarum* (Wollaston, 1867) from Santo Antão in the Cape Verde islands is redescribed and its lectotype is designated. All three *Aphanommata* species from the Cape Verde islands as well as *A. filum* (Mulsant and Rey, 1859) from Old World are diagnosed, illustrated, and keyed. Mature larva of *A. kuscheli* sp. nov. is described, larval morphology is discussed and the current state of knowledge about immature stages of Cossoninae is summarized. Vertical and inter-insular distributional pattern of Cape Verde *Aphanommata* and *Pselactus* is reviewed and discussed.

Keywords: Curculionidae; Cossoninae; Rhyncolini; Rhyncolina; taxonomy; new species; mature larva; morphology; host plant; Cape Verde; biogeography; microclimate; species competition

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1. Introduction

Islands and archipelagos are particularly important for biodiversity not only because they host many threatened species but also because they are biodiversity hotspots due to their high levels of endemism [1,2]. The Cape Verde Archipelago consists of ten main islands and several islets located between 550 and 800 km west of the Senegal coast, all the islands are volcanic in origin. The geographical isolation of this archipelago exhibited a specific area with many endemic plants, and animals including beetles.

Research on Cape Verde Coleoptera started 150 years ago with a remarkable monograph by Thomas V. Wollaston [3]. However, since that time, only limited data were accumulated about biology, larvae, evolution, distribution and the phylogenetical relationship of beetle taxa endemic to the archipelago [4–9]. Weevils are not an exception and recent field research produced a significant amount of undescribed endemic species which can shed light on the history of this group within the archipelago [8,9]. Historically, the genera *Dinas* Wollaston, 1867 and *Pselactus* Broun, 1886 were the only weevil genera with more than one species within the archipelago. Biological notes based on original observations are limited to the collecting notes for several genera made by Wollaston [3] and for the endemic genus *Dinas* made by Skuhrovec and Batelka [8]. With six genera now recorded the diversity of the Cossoninae endemic to the Cape Verde archipelago is considerably higher than previously realised.

The aim of this paper is to review the Cape Verde members of the genus *Aphanommata*. The genus was described by Wollaston for a single species *A. euphorbiarum* (Wollaston, 1873) from the island Santo Antão (Cape Verde) and all other species currently assigned to *Aphanommata* were described in different genera. *Aphanommata* Wollaston, 1873 is a small genus currently placed in the tribe Rhyncolini, subtribe Rhyncolina [10]. This genus includes five described species [7], but only two species are currently known from the Old World. *Aphanommata filum* (Mulsant & Rey, 1858) is a west Palaearctic species so far known from Albania, Bulgaria, Croatia, France (including Corsica), Italy, Spain and Algeria; and *A. euphorbiarum* is known only from Cape Verde (Santo Antão). The inclusion of three New World species, *A. corrosa* (Champion, 1909) from Panama, *A. perlonga* (Champion, 1909) from Belize and Guatemala and *A. tenuis* (Casey, 1892) from the USA to the genus *Aphanommata* is only due to the inclusion of three American genera, *Rhamphocolus* Casey, 1892, *Macrancyloides* Champion, 1909 and *Oocorynus* Champion, 1909 in *Aphanommata* by Kuschel in Wibmer and O'Brien [11] and should be verified in the future.

In this paper, we describe two new *Aphanommata* species from São Nicolau and Fogo and provide a description of the larva of new species from São Nicolau and some details on biology and biogeography of the genus. It seems that with three species, the Cape Verde archipelago is a center of the diversity of the genus.

2. Materials and Methods

2.1. Field Survey

Larvae and adults of both *Aphanommata* species were obtained from dead woody parts of various native and introduced plants (see Collection circumstances for particular species). The collectors identified the plants. The larvae of *Aphanommata* were preserved in fixation liquid directly at the locality.

2.2. Morphological Descriptions of Adults

The adult specimens were examined with a Leica S8APO stereomicroscope with diffuse lighting at magnifications up to ×128. Dry mounted specimens were relaxed in the warm water and dissected; male and female terminalia were macerated in KOH solution, embedded in Euparal and illustrated; all dissected parts were mounted on plastic labels and pinned together with the respective specimen. Illustrated structures were studied using a ZEISS stereoscopic microscope and figured using the camera lucida. Photos of adults were taken with Canon EOS 700D cameras with an MP-E 65 mm macro lens and combined using Zerene Stacker and GIMP2 software. Details of adults were taken and corrected with HIROX (RH-2000, digital microscope).

The terminology of the rostrum and the genitalia follows Oberprieler et al. [12]. The head length was measured from the anterior margin of pronotum (base of head) to the anterior margin of the frontal rostrum; head width was measured across the eyes; the elytral length was measured along the suture; the width refers to the maximum width of pronotum. The body length is a combined length of the head, pronotum and elytra, measured separately.

Label data are cited verbatim. All labels of the studied material are printed; '/' separates different labels; (p) denotes printed labels, (h) denotes handwritten labels. All type specimens were provided with the following red printed label: HOLOTYPE, PARATYPE, LECTOTYPE or PARALECTOTYPE generic and specific name of the taxon, J. Skuhrovec, P. Hlaváč and J. Batelka det., 2018.

2.3. Deposition of Material

The material is deposited in the following collections:

BMNH—Natural History Museum, London, United Kingdom (formerly British Museum of Natural History) (Michael Geiser);

CJB—private collection of Jan Batelka, Prague, Czech Republic;

CJS—private collection of Jiří Skuhrovec, Prague, Czech Republic;
CPH—private collection of Peter Hlaváč, Prague, Czech Republic;
NMPC—National Museum, Prague, Czech Republic (Jiří Hájek);
OUMNH—Hope Entomological Collections, Oxford University Museum of Natural History, United Kingdom (Amoret Spooner);
SMNS—Staatliches Museum für Naturkunde, Stuttgart, Germany (Wolfgang Schawaller).

2.4. Morphological Descriptions of Larvae

A few larvae were fixed individually in Pampel fixation liquid (see [13]). These specimens are now deposited in CJS. To prepare the slides, we followed May [14]: a larva was decapitated, and the head was cleaned with a 10% potassium hydroxide (KOH) solution and then rinsed with distilled water. After cleaning, the mouthparts were separated from the head capsule, and the head capsule and all mouthparts were mounted on permanent microscope slides in Euparal. All other body parts were mounted on temporary microscope slides in 10% glycerine.

The observations and measurements were conducted using a light microscope with calibrated oculars (BX 40, Olympus, Tokyo, Japan and Eclipse 80i, Nikon, Tokyo, Japan). The following characteristics were measured for each larva: head width, length of the body laterally (larvae fixed in a C-shape were measured in segments), and width of the body in the widest place (i.e., metathorax or abdominal segments I–IV). The thorax and abdomen were not sclerotized, and it is unlikely that the fixation process altered the proportions of the weevils; measurements of these parts are provided for comparison purposes only.

Drawings were created with a drawing tablet (Intuos Pro S, Wacom, Saitama Prefecture, Japan) and the digital images subsequently processed with Adobe Photoshop, Corel Photo-Paint 11 and/or GIMP 2. The numbers of setae on bilateral structures were given for one side only.

We used the terms and abbreviations for the setae of the mature larvae found in Scherf [15], May [14,16], Marvaldi [17,18], Trnka et al. [19] and Skuhrovec et al. [20].

3. Results

Aphanommata **Wollaston, 1873**

Aphanommata Wollaston, 1873: 463. Type species *Rhyncolus euphorbiarum* Wollaston, 1868.
Brachytemnoides Folwaczny, 1973: 155. Type species: *Rhyncolus filum* Mulsant and Rey, 1859, synonymy in Alonso-Zarazaga, 1989: 325.
Macrancyloides Champion, 1909: 75. Type species: *Macrancyloides perlongus* Champion, 1909, synonymy by Kuschel in Wibmer and O'Brien, 1986: 5.
Oocorynus Champion, 1909: 76. Type species: *Oocorynus corrosus* Champion, 1909, synonymy by Kuschel in Wibmer and O'Brien, 1986: 5.
Rhamphocolus Casey, 1892: 702. Type species: *Rhamphocolus tenuis* Casey, 1892, synonymy by Kuschel in Wibmer and O'Brien, 1986: 5.
Aphanommata Wollaston: Alonso-Zarazaga, 1989: 325 (review).

The genus *Aphanommata* is readily distinguishable from other genera of the tribe Rhyncolini by the combination of following character states: (1) body in cross section circular; (2) head narrow, conical, tapered anteriad, rostrum longer than wide; (3) eyes not prominent; (4) antennae short and stout, funicule with seven antennomeres; (5) basal margin of pronotum straight; (6) humeri well-defined, elytra parallel-sided; (7) scutellum visible and (8) apical tarsomere expanded to apex.

Aphanommata euphorbiarum **(Wollaston, 1867)**

(Figure 1a,b, Figures 4e,f, 6c and 8a)

Rhyncolus euphorbiarum Wollaston, 1867: 119. Type locality: interior of Santo Antão, 4 syntypes in the Ribeira Fria and 1 syntypus in Ribeira da Babosa.

Aphanommata euphorbiarum: Alonso-Zarazaga, 1989: 327 (redescription, illustration of habitus, lateral view of head and aedeagus).

Type material studied: Lectotype, sex not determined, here designated: (h) *euphorbia*/round label with red margin (p) Type/(p) T. V. Wollaston Coll., B. M. 1867-82, CAPE VERDE IS./original white label with a green corner. BMNH. Paralectotype, ♂, hardly damaged specimen, aedeagus and some other parts mounted in Euparal: (p) T. V. Wollaston Coll., B. M. 1867-82, CAPE VERDE IS. BMNH.

Remark I. *Green corner on the original label is a mark of Wollaston and means that the specimen was collected on the island Santo Antão.*

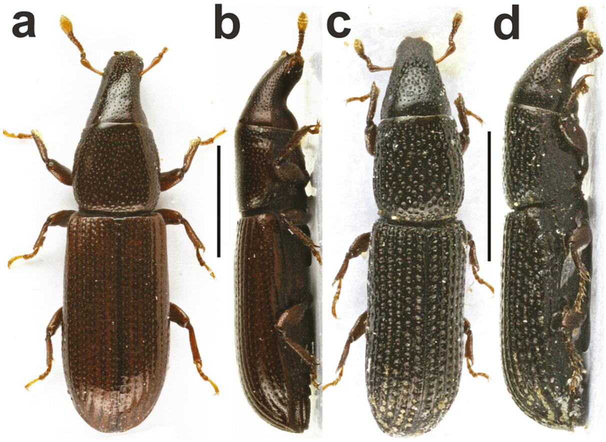

Figure 1. *Aphanommata euphorbiarum*, habitus, (**a**) Dorsal view; (**b**) Lateral view; *A. filum*, habitus; (**c**) Dorsal view; (**d**) Lateral view. Scale bars: 1 mm.

Diagnosis: Smaller species with body length under 3.5 mm, maximum width of elytra 0.96 mm, colour reddish-brown. Antennal scape slightly pedunculate at apex, short, shorter than funicule, funicule with 7 antennomeres; funicular antennomere I slightly longer than wide, about 1.5 times as long as II; antennal club about 1.4 times as long as wide; head and pronotum shiny, finely shagreened, evenly punctate with fine punctures; anterior margin of pronotum slightly narrower than base; eyes oval, flat, about 1.7 times higher than wide, temples short, width of eye equal to distance from margin of eye to pronotal margin (Figure 4f); pronotum widest in posterior third; elytra with 15 rows of punctures of different size, in sutural region cross-cracked, elytral intervals flat.

Differential diagnosis. *Aphanommata euphorbiarum* is distinguishable from its Old World congeners by the combination of the following character states: (1) body large, more than 3 mm but less than 3.5 mm long (Figure 1a); (2) pronotum with fine punctures, distance between punctures always superior to diameter of punctures (Figure 6c); (3) sides of pronotum evenly rounded (Figure 6c); (4) pronotum smooth (Figure 6c); (5) apex of elytra with very small erect setae (Figure 8a); (6) funicular antennomere I parallel-sided (Figure 1a) and (7) different shape of apex of aedeagus (Alonso-Zarazaga, 1989: 328, Figures 3 and 4). *Aphanommata euphorbiarum* is readily separated from *A. kuscheli* sp. nov. and *A. strakai* sp. nov. by different size, the absence of setae on the apex of elytra and the shape of aedeagus.

Remark II. *The species A. euphorbiarum has been redescribed by Alonso-Zarazaga [7] according to one male from the syntype series and distinguished in the key from A. filum (Mulsant and Rey, 1858) which were in the same work transferred in this genus due to the synonymy of the genus Brachytemnoides Folwaczny, 1973 to Aphanommata. One of the main diagnostic characters cited for A. euphorbiarum was the rostrum with the shallow median sulcus. We have examined 2 syntypes deposited in BMNH and did not find such a sulcus on the* *rostrum. The rostrum of both specimens examined by us is simple, lacking any trace of the sulcus, with only the sparse puncturation (Figure 4e,f). As the aedeagus illustrated by Alonso-Zarazaga [7] well corresponds with the aedeagus studied by us, we believe that the sulcus on the rostrum could be more an artefact than the case of interspecific variability, but more material will be needed to definitely solve this question.*

Remark III. *A. euphorbiarum has been described according to five specimens sifted by V. Wollaston on two localities in the interior of the island Santo Antão [3:120]. We were searching all syntypes, but it seems that the specimen studied by Alonso-Zarazaga [7] as well as other two syntypes were lost, they are neither in BMNH (Max Barclay, per. comm.) nor in OUMNH (Amoret Spooner, per. comm.) where Wollaston's collection is deposited.*

Biology: Syntype series were collected from the decayed stem of the *Euphorbia tuckeyana*.
Distribution: Cape Verde (Santo Antão).

Aphanommata kuscheli **sp. nov.**

(Figure 2a–c, Figure 3a–f, Figure 4a,b, Figure 5a, Figure 6a, Figures 7a, 9a–f and 10a–d)

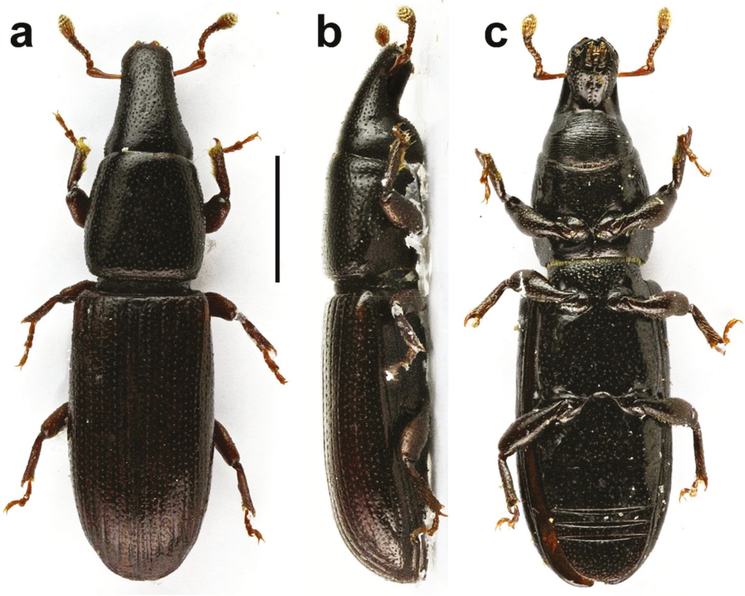

Figure 2. *Aphanommata kuscheli* **sp. nov.**, habitus, male, holotype: (**a**) Dorsal view; (**b**) Lateral view; (**c**) Ventral view.Scale bar: 1 mm.

Adult material studied

Type material. HOLOTYPE, ♂: CAPE VERDE Isl., 10.X.2013, SAO NICOLAU, W, Mt. Gordo summit, 16.625089, -24.350854, J. Straka and J. Batelka lgt. (p)/windward slopes in rotten wood of *Euphorbia tuckeyana* (p) (SMNS). **PARATYPES:** 47 ex.: the same data as holotype. SMNS (18), BMNH (3), OUMNH (2), NMPC (2), CJS (10), CPH (10), CJB (2). **Non-type material**. 3♀: SAO NICOLAU, W.-S of Cachaco, 13.XI.2011, 16°37′ N, 24°21′ W, J. Straka and J. Batelka lgt., in rotten wood of *Agave sisalana*. CJS, CPH, CJB.

Remark IV. *Specimens from São Nicolau, W-S of Cachaco are not included in the type series due to the lack of a male.*

Diagnosis. Antennal scape slightly pedunculate at apex, short, shorter than funicule, funicule with 7 antennomeres; funicular antennomere I slightly longer than wide, about 1.75 times as long as II; antennal club about 1.7 times as long as wide; head and pronotum shiny, finely shagreened, evenly puncturate with fine punctures; anterior margin of pronotum slightly narrower than base; pronotum widest in posterior fourth; elytra with 14–16 rows of punctures of different size, in anterior half cross-cracked, elytral intervals flat.

Description (Figure 2a–c). Body convex, shiny, pitch-black, sometimes elytra brownish, tarsi and antennae brownish (Figure 2a). Length 3.60–4.45 mm, maximum width of elytra 1.08–1.30 mm.

Head 1.15–1.25 times as long as wide, with sparse, fine punctures. Rostrum slightly convex, more than three times as long as head behind eyes (Figure 4a,b). Antennal scrobe lateral, not visible in dorsal view, short, deep, curved downward before eye, the point of antennal insertion located on anterior third of head (Figure 4a,b). Antennae (Figure 5a) stout, with long, sparse setae, antennal club with dense, golden pubescence on apical margin of first and second antennomeres of club; antennal scape short, pedunculate at apex, about 4.20–4.60 times as long as funicular antennomere I and shorter than funicule; funicule with seven antennomeres, funicular antennomere I expanded to apex, 1.40 times as long as wide, slightly longer and wider than II, later about 1.60 times as long as III, III–VII transverse, V–VII subequal, slightly longer than III and IV, antennal club with three antennomeres, first clearly longest, club apically pointed, 1.50–1.60 times as long as wide. Eyes oval, flat, about 1.50 times higher than wide, temples long, width of eye inferior, about 1.5 times, to distance from margin of eye to pronotal margin (Figure 4b).

Pronotum (Figure 6a) with dense, fine, even punctures, pronotal punctures equal in size to punctures on head but puncturation denser, distance between punctures considerably superior to diameter of punctures. Pronotum 1.00–1.05 times as long as wide, 1.15–1.30 times as long as head, widest in posterior fourth, basal margin straight. Scutellum well-defined, oval, wider than long.

Elytra (Figure 7a) 1.80–1.95 times as long as wide, 2.10–2.30 times as long as pronotum, convex, fused, surface smooth and shiny, with about 14–16 striae formed by rows of punctures of different size, distance between punctures varies but always superior to diameter of puncture, in anterior half cross-cracked, elytral intervals flat, humeri prominent, humeral calli well-defined. Hind wings absent.

Prosternum at the same level as meso and metaventrite, finely shagreened, with very few uneven punctures, long, disc depressed in anterior part, depression with transverse furrow, anterior margin finely dentate; procoxae separated by narrow isthmus, hypomerae fused with median part of prosternum; mesoventrite short, about 2.50 times shorter than metaventrite, both finely shagreened, shiny, mesoventrite roughly punctured mainly in anterior part, anterior margin with golden setae, mesoventral process long, wide, truncate, shagreened and punctured, metaventrite evenly punctured, mesocoxae separated, isthmus about as wide as half of coxa, metacoxae strongly separated by large process of first ventrite, puncturation on metaventrite denser than on ventrite I and II, ventrite I about 1.35 times as long as ventrite II, all ventrites shagreened and punctured, posterior part of ventrite I and anterior part of ventrite II medially depressed, ventrites III and IV subequal in length, ventrite V semicircular in shape, more than three times as long as ventrite IV.

Legs (Figure 2a–c) brownish, finely shagreened, tibiae with strongly arcuate uncus and well-defined mucro, fore tibiae with dense, golden setation on inner part of apical half of tibia, apex of mid and hind tibiae decent setae, tarsi with four tarsomeres, tarsomere I long, about as long as II–III combined, III bilobed in apical half, onychium long, about as long as I–III combined, with two free, divaricate, tarsal claws equal.

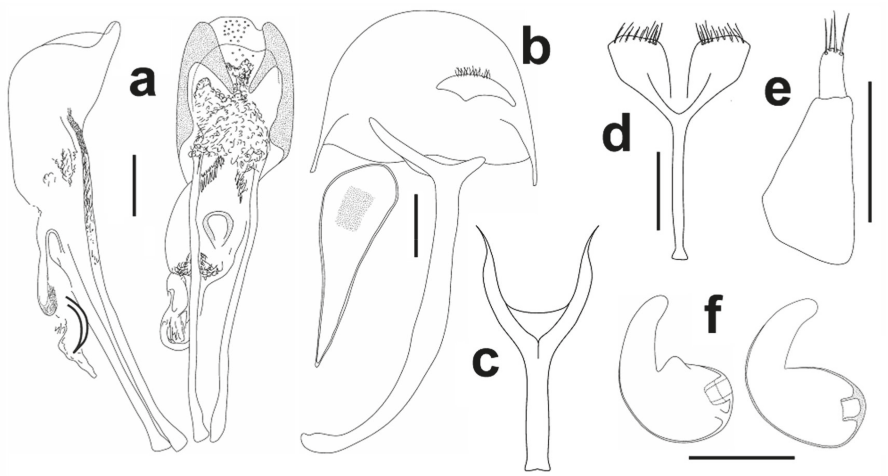

Figure 3. *Aphanommata kuscheli* **sp. nov.**, male genitalia: (**a**) Aedeagus, lateral and dorsal view; (**b**) Male sternite 9 (spiculum gastrale), hemisternite, and rectal loop; (**c**) Tegmen; and female genitals: (**d**) Female sternite 8 (spiculum ventrale); (**e**) Gonocoxite; (**f**) Spermatheca, dorsal and ventral view. Scale bars: 0.2 mm.

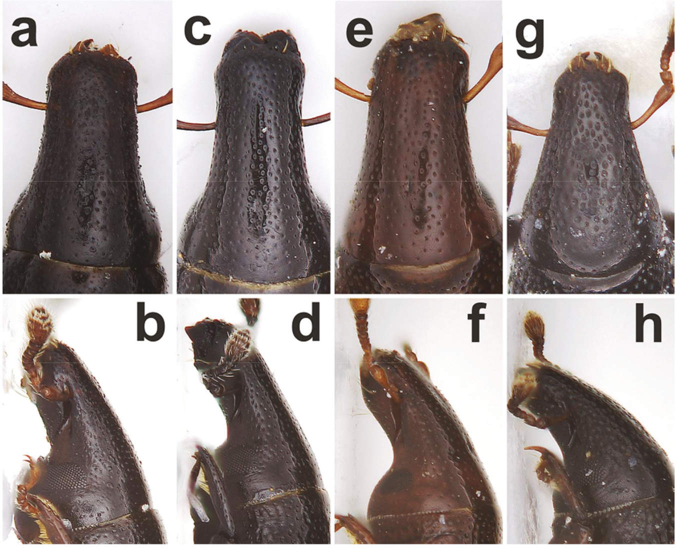

Figure 4. *Aphanommata kuscheli* **sp. nov.**, rostrum, male, holotype: (**a**) Dorsal view; (**b**) Lateral view. *A. strakai* **sp. nov.**, rostrum, male, holotype: (**c**) Dorsal view; (**d**) Lateral view. *A. euphorbiae*, rostrum, male: (**e**) Dorsal view; (**f**) Lateral view. *A. filum*, rostrum, male: (**g**) Dorsal view; (**h**) Lateral view.

Male genitalia. Aedeagus (Figure 3a), male sternite 9 (spiculum gastrale), hemisternite and rectal loop (Figure 3b).

Female genitalia. Spermatheca (Figure 3f), female sternite 8 (spiculum ventral) (Figure 3d), gonocoxite (Figure 3e).

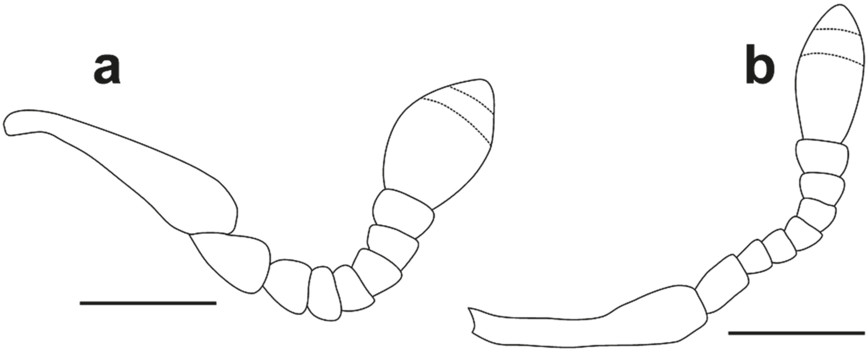

Figure 5. Antenna of *Aphanommata* species: (**a**) *A. kuscheli* **sp. nov.**, holotype; (**b**) *A. strakai* **sp. nov.**, holotype. Scale bars: 0.2 mm.

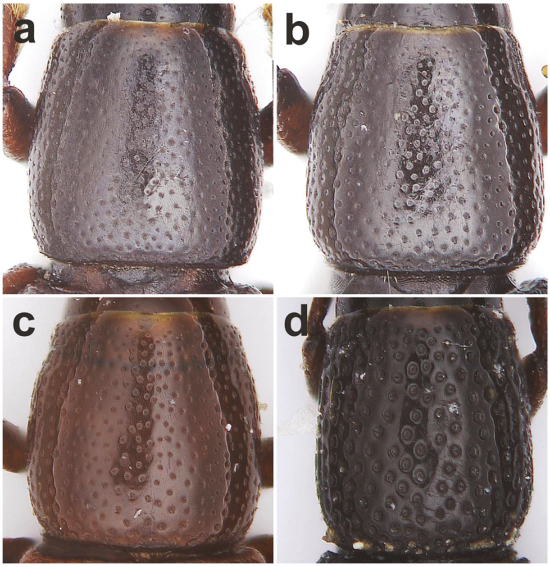

Figure 6. Pronota of *Aphanommata* species, males: (**a**) *A. kuscheli* **sp. nov.**, holotype; (**b**) *A. strakai* **sp. nov.**, holotype; (**c**) *A. euphorbiae*; (**d**) *A. filum*.

Sexual dimorphism. Ventrites I and II in females simple, lacking median depression.

Differential diagnosis. *Aphanommata kuscheli* sp. nov. is distinguishable from its Old World congeners by the combination of the following character states: (1) body large, more than 4 mm long; (2) pronotum with fine punctures, distance between punctures always superior to diameter of punctures (Figure 6a); (3) sides of pronotum evenly rounded (Figure 6a); (4) pronotum shagreened (Figure 6a); (5) apex of elytra with any erect setae (Figure 7a); (6) funicular antennomere I expanded to apex (Figure 5a); (7) different shape of apex of aedeagus (Figure 3a); and (8) apex of cornu on spermatheca slightly bent (Figure 3f). *Aphanommata kuscheli* sp. nov. is readily separated from *A. strakai* sp. nov. by the different surface of pronotum, the shape of antenna, aedeagus and spermatheca; and from *A. euphorbiarum* by different size, the absence of setae on the apex of elytra and the shape of aedeagus.

Etymology. Patronymic, named after Guillermo Kuschel, an eminent Curculionidae worker who has also contributed significantly to knowledge of the subfamily Cossoninae.

Figure 7. Elytra of *Aphanommata* species, males: (**a**) *A. kuscheli* **sp. nov.**, holotype; (**b**) *A. strakai* **sp. nov.**, holotype.

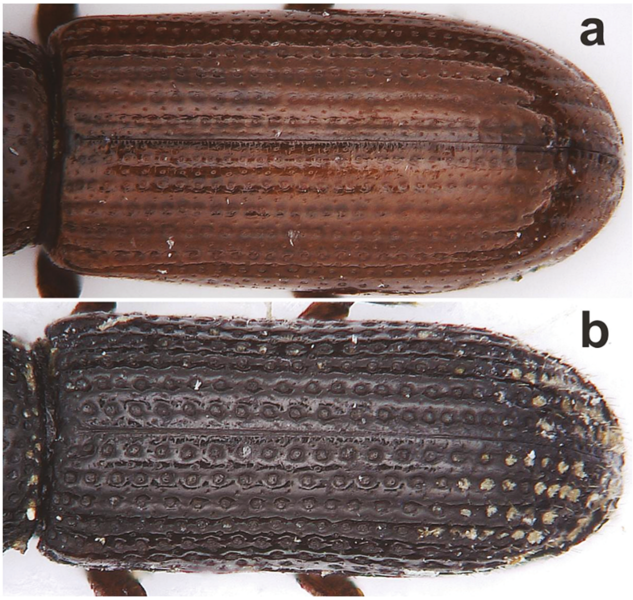

Figure 8. Elytra of *Aphanommata* species, males: (**a**) *A. euphorbiae*; (**b**) *A. filum*.

Description of mature larva

Material examined. 2 mature larvae: Cape Verde Isl., São Nicolau W—Mt. Gordo Summit, 10.x.2013, 16.625089 N, 24.35084 W, J. Straka and J. Batelka lgt., windward slopes, in rotten wood of *Euphorbia tuckeyana* Steud. (Euphorbiaceae).

Measurements (in mm). Body length: 5.48–6.15. The widest body part (abdominal segments II–VI) 1.47. Head width: 0.87–0.96.

General. Body elongate, slightly curved, rounded in cross section (Figure 10a).

Colouration. Dark yellow to pale brown head around suture white (Figure 10a). All thoracic and abdominal segments white and dorsum with fine speckling (Figure 10a).

Vestiture. Setae on body very long to very short, orange and clearly visible.

Head capsule (Figure 9a). Head suboval and distinctly rounded laterally, endocarinal line absent. Frontal sutures on head very broad and well visible, extended to antennae. One stemmata (st) feebly visible, in the form of a minute pigmented spot with convex cornea, located on each side anterolaterally, behind antenna. Setae on head piliform, varying in length, from very long to short. Des_1 and des_2 located behind the middle part of the central part of epicranium, very long des_1 near to the middle part of epicranium, and medium des_2 near to side of epicranium, very long des_3 located anteriorly on epicranium in or very close to frontal suture, medium des_4 close to des_3, very long des_5 located anterolaterally (Figure 9a); des_2 and des_4 as long as third of length of remaining three *des*. Dorsal part of epicranium with 2 sensilla; one between des_1 and des_2, and next one close to des_4. Fs_1 of medium length located posteriomedially, and almost in the frontal suture, fs_2 located medially, fs_3 and fs_4 located anterolaterally; and fs_5 close to antennae; fs_1, fs_2 and fs_4 as long as des_4, and fs_3 and fs_5 very long as long as des_5 (Figure 9a). Les_1 and les_2 as long as des_1; both *ves* short, as long as third length of *les*. Epicranial area with 3–4 *pes*.

Antennae located at the end of the frontal suture on each side, membranous and conical basal article bearing one conical triangular sensorium located centrally; basal membranous article with 2(3) very short basiconic sensillae (Figure 9d).

Clypeus (Figure 9e) slightly trapezium-shaped, anterior margin of clypeus slightly concave; approximately 2 times as wide as long; cls_1 very long, placed posteromedially, cls_2 of medium length to long, localized posterolaterally; 1 sensillum *clss* placed between cls_1 and cls_2.

Mouth parts. Labrum (Figure 9e) also slightly trapezium-shaped, approximately twice as wide as long, with 3 piliform *lms*, of different lengths; lms_1 very long, lms_2 and lms_3 as long as two third of length of lms_1; all *lms* protrudes well over the anterior margin of labrum; lms_1 placed medially in the central part of labrum, lms_2 located anteromedially and lms_3 located anterolaterally; anterior margin bi-sinuate. Epipharynx (Figure 9f) with 3 finger-like *als*, als_1 more than twice as long as als_2 and als_3, all in line to labral rods; with 3 *ams* piliform, ams_1 as long as als_1, ams_2 as long as half or one third length of ams_1, and ams_3 very short as als_2 and als_3; and with 2 very short to minute, finger-like *mes*; labral rods (lr) narrow, elongate, parallel. Mandibles (Figure 9c) slightly curved, distinctly broad, with divided apex; bifid, teeth of unequal length; slightly truncate; mds_1 very long, and mds_2 long, piliform, located in distinct holes. Maxilla (Figure 9b) stipes with 1 *stps*, 2 *pfs* and 1 *mbs* with one sensillum close to *mbs*, *stps* and $pfs_{1–2}$ very long, *mbs* minute to very short; mala with 7 finger-like *dms*; 4 *vms*, different in length, one very short seta, one short and two as long as *dms*; 2 *vms* distinctly shorter than *dms*. Maxillary palpi with two palpomeres; basal palpomere with 1 relatively long *mxps* and two sensilla; length ratio of basal and distal palpomeres: 1:1; distal palpomere with one sensillum and a group of conical, cuticular apical processes. Prelabium (Figure 9b) oval-shaped and feebly elongate, with 1 long *prms*; ligula with sinuate margin, 2 relatively long to short *ligs*, and one sensillum; premental sclerite feebly visible. Labial palpi with two palpomeres; length ratio of basal and distal palpomeres, basal palpomere much wider than distal: 1:1.3; distal palpomere elongate, with one sensillum and short, cuticular apical processes; basal palpomere with 1 dorsal sensillum.

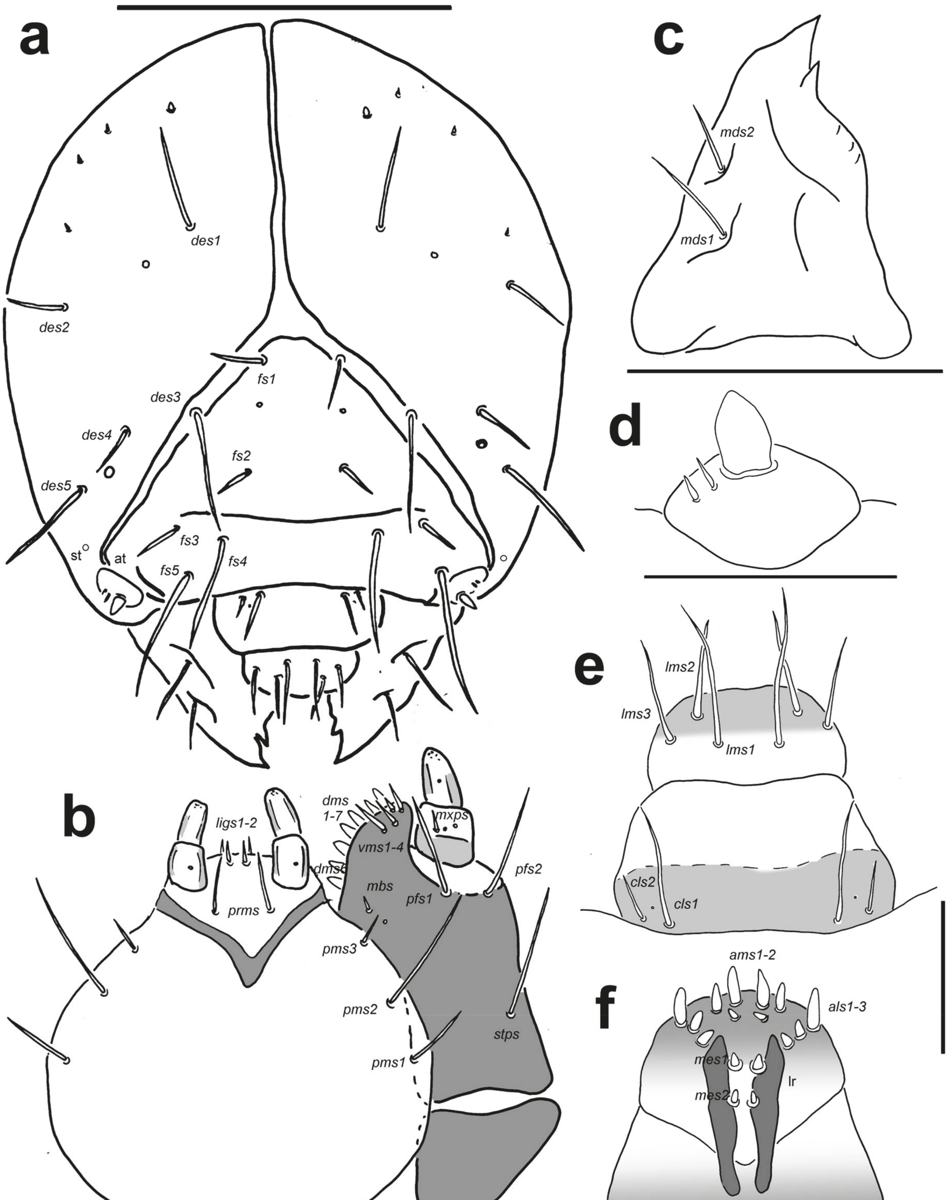

Figure 9. *Aphanommata kuscheli* **sp. nov.**, mature larva: (**a**) Head, frontal view (*des*—dorsal epicranial seta; *fs*—frontal epicranial s.; *les*—lateral epicranial s.; at—antenna); (**b**) Maxillolabial complex consisting of left maxilla (*dms*—dorsal malar s.; *vms*—ventral malar s.; *mpxs*—maxillary palps s.; *mbs*—basioventral s.; *pfs*—palpiferal s.; *stps*—stipital s.), prementum and postmentum, ventral view (*prms*—premental s.; *pms*—postmental s.; *ligs*—ligular s.); (**c**) Right mandible (*mds*—mandible dorsal s.), ventral view; (**d**) Antenna; (**e**) Labrum and clypeus (*lms*—labral s., *cls*—clypeal s.), dorsal view; (**f**) Epipharynx (*ams*—anteromedial s.; *als*—anteriolateral s.; *mes*—median s.; lr—labral rods), ventral view. Scale bars: (**a**) 0.5 mm; (**b**,**c**) 0.25 mm; (**d**) 0.05 mm; (**e**,**f**) 0.1 mm.

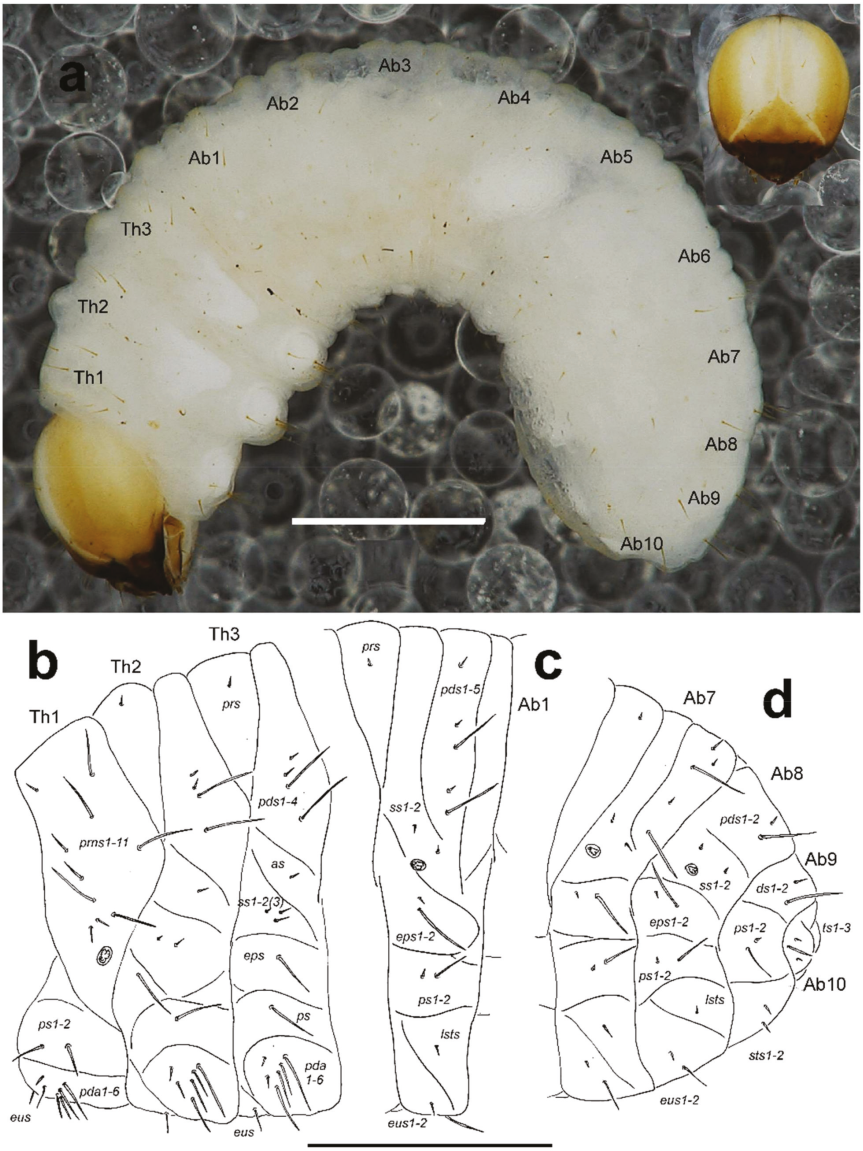

Figure 10. *Aphanommata kuscheli* **sp. nov.**, mature larva: (**a**) Habitus, left lateral view; (**b**) Left lateral view of thoracic segments; (**c**) Left lateral view of abdominal segment I; (**d**) Left lateral view of abdominal segments VII-X (*prns*—pronotal s.; *prs*—prodorsal s.; *pds*—postdorsal s.; *as*—alar s.; *ss*—spiracular s.; *eps*—epipleural s.; *ps*—pleural s.; *pda*—pedal s.; *lsts*—laterosternal s.; *eus*—eusternal s.; *ds*—dorsal s.; *sts*—sternal s.; Th1-3—number of thoracic segments; Ab1-10—number of abdominal seg.). Scale bars: 1 mm.

Postlabium (Figure 9b) with 3 *pms*, all *pms* located laterally; pms_1 and pms_2 very long, but pms_1 as long as two third of pms_2, pms_3 long, more than 2 times shorter than pms_1.

Thorax. Prothorax smaller than meso- and metathorax. Spiracle bicameral, placed between the pro- and mesothorax (see Skuhrovec et al. [9]). Prothorax (Figure 10b) with 10 short to very long *prns* (3 placed apically (one short and 2 very long); 1 or 2 very long and 2 relatively long medially; 4 form a group close to spiracle, 2 very long, and 2 short); 2 very long to long *ps*; and 1 relatively long *eus*. Mesothorax (Figure 10b) with 1 short to very short *prs*, 4 *pds* different in length (order: very short, very short, very long, very long); 1 short to very short *as*; 1 very short and 1–2 short to relatively long *ss*; 1 very long *eps*; 1 very long *ps*; and 1 long to very long *eus*. Chaetotaxy of metathorax (Figure 10b) almost identical to that of mesothorax. Each pedal area of thoracic segments well separated, with 4 very long and 2 relatively long to short *pda*.

Abdomen. Abdominal segments I–VI of almost equal length, remaining abdominal segments decreasing in width gradually posterad. Abdominal segment X reduced to four anal lobes of unequal size, the dorsal being distinctly the largest, the lateral pair equal in size, and the ventral lobe very small. Anus located terminally; ambulatory ampullae bilobate to circular. Spiracles bicameral, the eight abdominal spiracles located medially, close to the anterior margin of abdominal segments I–VIII. Abdominal segments I–VII (Figure 10c) with 1 very short to short *prs*; 5 *pds* different in length (order: short, very short, very long, very short, very long); 2 short *ss*; 1 very short and 1 very long *eps*; 1 very short and 1 very long *ps*; 1 relatively long *lsts*; and 1 relatively long and 1 very long *eus*. Abdominal segment VIII (Figure 10d) with 2 *pds* different in length (order: short, very long); 2 short *ss*; 1 very short and 1 very long *eps*; 1 very short and 1 very long *ps*; 1 relatively long *lsts*; and 1 relatively long and 1 very long *eus*. Abdominal segment IX (Figure 10d) with 1 short to relatively long and 1 very long *ds*, located close to posterior margin of segment; 1 very long and 1 very short *ps*; and 2 relatively long to short *sts*. Abdominal segment X (Figure 10d) with 3 *ts*, 1 long and 2 very short to minute.

Collection circumstances. Imagines and larva collected in 2011 south-west of Cachaco were extracted from the outer layer of the rotten stem of *Agave sisalana*, growing by the mountain trail circa 1050 m a.s.l. More specimens of the species were obtained in 2013 from the rotten stem of *Euphorbia tuckeyana* on the northern slope of Monte Gordo, not far from the summit, some 1200 m a.s.l. The stem of *Euphorbia* was much eaten by larvae of the species, imagines were in the larval galleries and pupal chambers.

Distribution: Cape Verde (São Nicolau)

Aphanommata strakai sp. nov.

(Figures 4c,d, 5b, 6b, 7b, 11a–c and 12a–f)

Type material studied. HOLOTYPE, ♂: CAPE VERDE Isl., FOGO—Chã des Caldeiras 8.–9.X.2009, J. Straka and J. Batelka lgt. (p) (SMNS). **PARATYPES:** 9 ex.: the same data as holotype. SMNS (1), BMNH (1), OUMNH (1), NMPC (1), CJS (2), CPH (2), CJB (1).

Diagnosis. Antennal scape slightly pedunculate at apex, short, shorter than funicule, funicule with seven antennomeres; funicular antennomere I about 1.60 times as long as wide, almost parallel-sided, about 1.75 times as long as II; antennal club about twice as long as wide; head and pronotum shiny, head finely shagreened, pronotom not shagreened, evenly puncturate with fine punctures, punctures on pronotum bigger; elytra with 14–15 rows of punctures of different size, finely cross-cracked in anterior half only close to sutura, elytral intervals flat; anterior margin of pronotum slightly narrower than base; pronotum widest in posterior fourth.

Description (Figure 11a–c)**.** Body convex, shiny, reddish-brown to dark reddish-brown, tarsi and antennae of the same colour (Figure 11a–c). Length 4.00–4.25 mm, maximal width of elytra 1.10–1.20 mm.

Head 1.15–1.20 times as long as wide, with sparse, fine punctures. Rostrum slightly convex, more than three times as long as head behind eyes (Figure 4c,d). Antennal scrobe lateral, not visible in dorsal view, short, deep, curved downward before eye, the point of antennal insertion located on anterior third of head (Figure 4c,d). Antennae (Figure 5b) stout, with long, sparse setae, antennal club with dense, golden pubescence on apical margin of first and second antennomeres of club; antennal scape short, pedunculate at apex, about 4.65–4.75 times as long as funicular antennomere I and shorter than funicule; funicule with seven antennomeres, funicular antennomere I parallel-sided, 1.60 times as long as wide and 1.75 times as long as II, later about 1.30 times as long as III, III–VII transverse, V–VI subequal, VII about 1.2 times as wide as VI, antennal club with three antennomeres, first clearly longest, club apically pointed, 1.40–1.50 times as long as wide. Eyes oval, flat, about 1.2–1.3 times higher than wide, temples long, width of eye inferior, about 1.33 times, to distance from margin of eye to pronotal margin (Figure 4d).

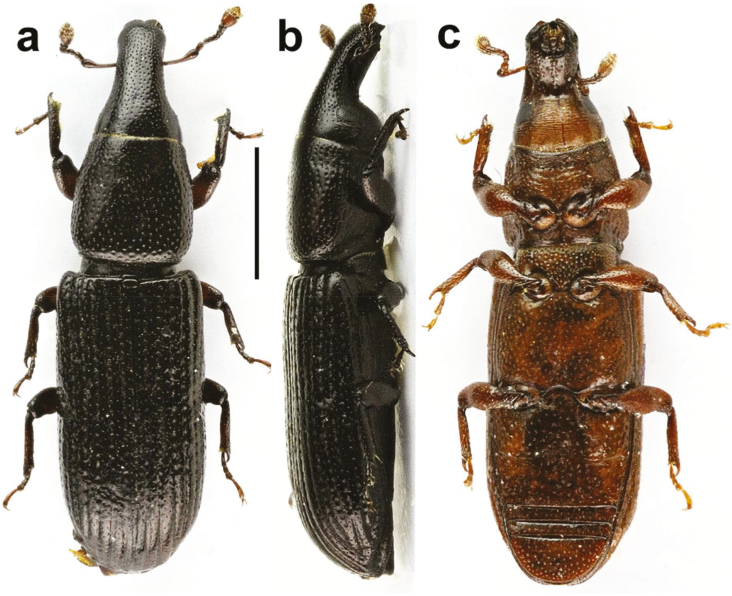

Figure 11. *Aphanommata strakai*, **sp. nov.**, habitus, male, holotype: (**a**) Dorsal view; (**b**) Lateral view; paratype: (**c**) Ventral view.

Pronotum (Figure 6b) with dense, fine, even punctures, pronotal punctures larger and denser than punctures on head, distance between punctures varies considerably, from inferior, equal to clearly superior to diameter of punctures, pronotum 1.00–1.05 times as long as wide, 1.10–1.25 times as long as head, widest in posterior fourth, basal margin straight. Scutellum well-defined, oval, wider than long.

Elytra (Figure 7b) 1.95–2.05 times as long as wide, 2.30–2.45 times as long as pronotum, convex, fused, surface smooth and shiny, with about 14–16 striae formed by punctures of different size, distance between punctures varies but always superior to diameter of puncture, in anterior half cross-cracked only close to suture, elytral intervals flat, humeri prominent, humeral calli well-defined. Hind wings absent.

Prosternum at the same level as meso and metaventrite, finely shagreened, with uneven punctures, long, disc depressed in anterior part, depression with transverse furrow, anterior margin finely dentate; procoxae separated by narrow isthmus, hypomerae fused with median part of prosternum; mesoventrite long, about 1.75 times shorter than metaventrite, both finely shagreened, shiny, mesoventrite roughly punctured mainly in anterior part, anterior margin with golden setae, mesoventral process long, wide, truncate, shagreened and punctured, metaventrite sparsely unevenly punctured, mesocoxae separated, isthmus about as wide as half of coxa, metacoxae strongly separated by large process of first ventrite, puncturation on metaventrite about as dense as on ventrite I and II, ventrite I about 1.30 times as long as ventrite II, all ventrites shagreened and punctured, posterior part of ventrite I and anterior part of ventrite II medially depressed, ventrites III and IV subequal in length, ventrite V semicircular in shape, more than three times as long as ventrite IV.

Legs (Figure 11a–c) brownish, finely shagreened, tibiae with strongly arcuate uncus and well-defined mucro, fore tibiae with dense, golden setation on inner part of apical half of tibia, apex of mid and hind tibiae decent setae, tarsi with four tarsomeres, tarsomere I long, about as long as II–III combined, III bilobed in apical half, onychium long, about as long as I–III combined, with two free, divaricate, tarsal claws equal.

Male genitalia. Aedeagus (Figure 12a), male sternite 9 (spiculum gastrale) (Figure 12b).

Female genitalia. Spermatheca (Figure 12f), female sternite 8 (spiculum ventral) (Figure 12d), gonocoxite (Figure 12e).

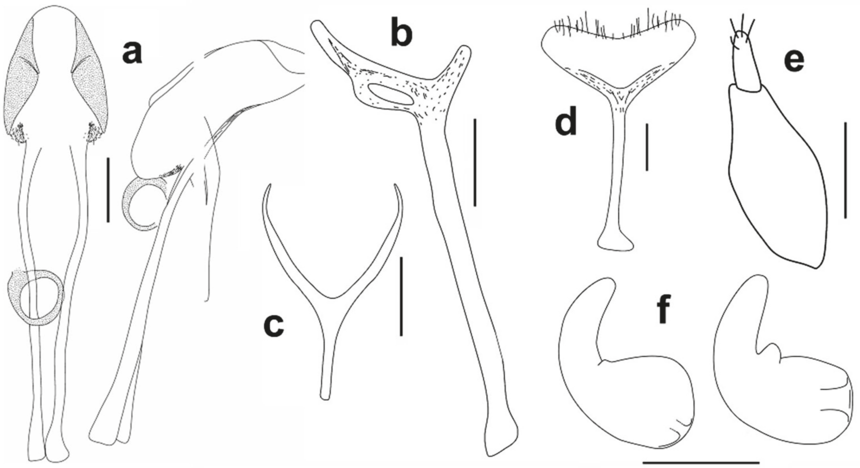

Figure 12. *Aphanommata strakai* **sp. nov.**, male genitalia: (**a**) Aedeagus, dorsal and lateral view; (**b**) Male sternite 9 (spiculum gastrale); (**c**) Tegmen; and female genitals: (**d**) Female sternite 8 (spiculum ventrale); (**e**) Gonocoxite; (**f**) Spermatheca, dorsal and ventral view. Scale bars: 0.2 mm.

Sexual dimorphism. Ventrites I and II in females simple, lacking median depression.

Differential diagnosis. *Aphanommata strakai* sp. nov. is distinguishable from its Old World congeners by the combination of the following character states: (1) body large, more than 4 mm long; (2) pronotum with fine punctures, distance between punctures always superior to diameter of punctures (Figure 6b); (3) sides of pronotum evenly rounded (Figure 6b); (4) pronotum smooth (Figure 6b); (5) apex of elytra with any erect setae (Figure 7b); (6) funicular antennomere I parallel-side (Figure 5b); (7) different shape of apex of aedeagus (Figure 12a); and (8) apex of cornu on spermatheca straight (Figure 12f). *Aphanommata strakai* sp. nov. is readily separated from *A. kuscheli* sp. nov. by the different surface of pronotum, the shape of antenna, aedeagus and spermatheca; and from *A. euphorbiarum* by the different size, the absence of setae on the apex of elytra and the shape of aedeagus.

Etymology. The species name is dedicated to the Czech entomologist Jakub Straka (Praha, Charles University) in appreciation of his friendship and his energetic field research on the Cape Verde Curculionidae.

Collection circumstances. All adults were collected under the bark of dead *Euphorbia tuckeyana* on the floor of the caldera of the Fogo volcano, about 2 km SW of Portela village, circa 1710 m a.s.l.

Distribution. Cape Verde (Fogo).

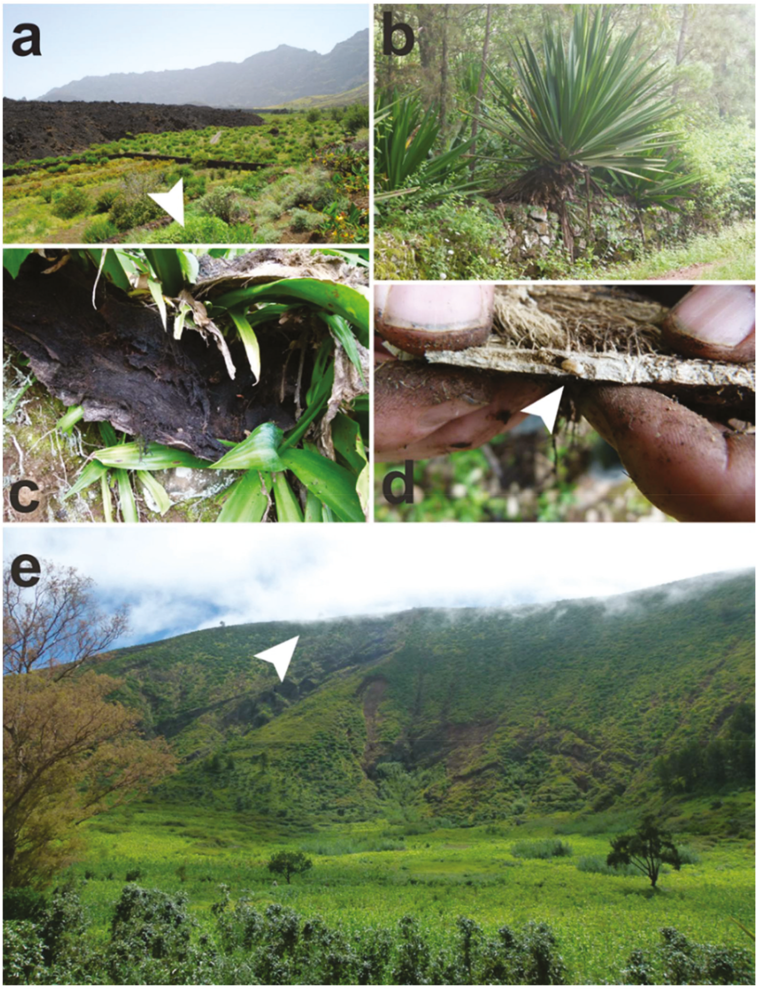

Figure 13. Images of habitat of *Aphanommata* species: (**a**) The type locality of *Aphanommata strakai* sp. nov. (indicated by arrowhead): FOGO, Chã des Caldeiras, ca. 1710 m, the (Photo 8.–9.X.2009 J. Batelka); (**b**–**e**) localities and habitats of *Aphanommata kuscheli* sp. nov.; (**b**–**d**) rotten wood of *Agave sisalana* (Agavaceae) with larva of the new species: SAO NICOLAU, W, S of Cachaco, 16°37′ N, 24°21′ W (Photos 13.XI.2011 J. Straka); (**e**) windward (north) slope with *Euphorbia tuckeyana* (Euphorbiaceae), the locality is indicated by arrowhead: SAO NICOLAU, W, Mt. Gordo, (Photo 10.X.2013 J. Straka).

Key to *Aphanommata* species of Old World

1 Small species, body length 2.30–2.80 mm (Figure 1c,d). Pronotum with rough, dense punctures, the distance between punctures inferior to the diameter of punctures (Figure 6d). Sides of pronotum parallel (Figure 6d). Distribution: known from southern Europe, and Algeria. . . . . *A. filum* **(Mulsant and Rey)**

\- Larger species, body length more than 3 mm (Figure 1a,b; Figure 2a–c; Figure 11a–c). Pronotum with fine punctures, distance between punctures always superior to the diameter of punctures

(Figure 6a–c). Sides of pronotum evenly rounded (Figure 6a–c). Distribution: only on the Cape Verde islands. **2**

2 Smaller species, body length less than 3.5 mm (Figure 1a,b). The apex of elytra with small erect setae (Figure 8a). . . . . **A. euphorbiarum (Wollaston)**

\- Larger species, body length more than 4.0 mm (Figure 2a–c; Figure 11a–c). The apex of elytra lacking erect setae (Figure 7a,b). **3**

3 Pronotum shagreened (Figure 6a). Funicular antennomere I expanded to apex, 1.40 times as long as wide, slightly longer and wider than II, later about 1.60 times as long as III (Figure 5a). The apex of cornu on spermatheca slightly bent (Figure 3f). **A. *kuscheli* sp. nov.**

\- Pronotum smooth, not shagreened (Figure 6b). Funicular antennomere I parallel-sided, 1.60 times as long as wide and 1.75 times as long as II, later about 1.30 times as long as III (Figure 5b). The apex of cornu on spermatheca straight (Figure 12f). . . . . **A. *strakai* sp. nov.**

4. Discussion

4.1. Comparison with Larvae of Other Cossoninae Species

The larvae of 54 Cossoninae taxa in 31 genera have been previously described [9,15,16,21–23]. The larva we report on here was compared with the majority of the species described or drawn by Anderson [21] and May [14,23]. Their illustrations are all of high or sufficient quality and are, therefore, useful; however, the described characteristics are useful only for differential diagnoses.

The precise general description of larvae of the subfamily Cossoninae, which is summarized by 10 character sets, was first published by May [23]: (1) labral lateral setae as long as anterior setae; (2) epipharyngeal lining with 2 groups of sensilla (3) tormae strong, separate (with a few exceptions); (4) spiracle on abdominal segment VIII lateral; (5) mandibular setae (two) aligned longitudinally; (6) spiracles bicameral; (7) rectal bracon forms a pigmented loop; (8) head with 4 *fs* (*fs*$_1$ absent); (9) abdominal segments II–VI with 4 dorsal folds (except Cotasterini Voss, 1953 (in [21]; recently synonym of Dryotribini LeConte, 1876)); and finally (10) each abdominal segment with 2 dorsal setae. May [23] commented in detail the state of these characters for each of specific Cossoninae groups. All these characters with one main exception (character 8) fit well with *Aphanommata* larva described here. Larva of *Aphanommata* species have five frontal setae (Figure 9a), but normally Cossoninae larvae have only four setae. This character state is also shared with some other genera, such as *Pselactus* Broun, 1886; *Hexarthrum* Wollaston, 1860; *Stenoscelis* Wollaston, 1861; *Nyssonotus* Casey, 1892; *Catolethrus* Boheman, 1838; *Pseudopentaarthrum* Wollaston, 1873 (in [21] as *Pentarthrinus* Casey, 1892) and also tribes Acamptini LeConte, 1876 and Anchonini Imhoff, 1856 (in [21]; both recently assigned to Molytinae). This situation is not exceptional for Cossoninae. For example, *Eiratus suavis* T. Broun, 1885 from the tribe Cotasterini has only one mandibular seta, not two as it is typical for this subfamily [23].

Anderson [21] published the most comprehensive review of the morphology of larvae of Cossoninae including data on 25 genera. In his tribal key, the genus *Aphanommata* was assigned to the tribe Cossonini Schoenherr, 1825 based on the following characters; (1) labial palpi two-segmented (Figure 9b); (2) pedal area of thoracial segments with six or more setae (Figure 10a,b); (3) spiracles on abdominal segment VIII lateral in position, and not larger than on previous segments (Figure 10a,d); (4) epipharynx with 2 *mes* (Figure 9f); and finally (5) epipharynx without discernible asperities (Figure 9f).

In the key of the tribe Cossonini [21], the genus *Aphanommata* is located close to the genera *Catolethrus* and *Nyssonotus* or genera *Rhyncolus* Germar, 1817 and *Phloeophagus* Schoenherr, 1837, where *Catolethrus* is placed in the tribe Dryotribini LeConte, 1876 and *Nyssonotus*, *Rhyncolus* and *Phloeophagus* are probably closed genera together with *Aphanommata* actually placed in the tribe Rhyncolini Gistel, 1856 [10]. These seven morphological larval characters are common for these three genera; (1) epipharynx with three *als* (Figure 9f); (2) meso- and metathorax with 4 or 5 *pds* (Figure 10b); (3) sternum of thoracic segments with one seta (Figure 10b); (4) spiracles on abdominal segments bicameral (Figure 10c,d); (5) anterolateral setae on epipharynx not in a straight, longitudinal row (Figure 9f); (6) anteromedian setae on epipharynx arranged transversely (Figure 9f), and finally (7) typical abdominal segments with four or five dorsal folds (Figure 10a). Larval morphology of *Aphanommata* species suggests a close relationship with *Nyssonotus*, *Rhyncolus* and *Phloeophagus*, but the classification of these four genera within the tribe Rhyncolini needs further verification (as discussed above).

Larvae of *Aphanommata* are easily separated from those of *Rhyncolus* and *Phloeophagus* by the former having (1) five frontal setae (vs. four frontal setae) (Figure 9a); from *Nyssonotus* by having (1) mala with seven dorsal setae (vs. mala with six dorsal setae) (Figure 9b); and (2) eusternum on typical abdominal segments with the more lateral seta short, the more ventral seta long (vs. eusternum on typical abdominal segments with the setae short to moderately long, subequal) (Figure 10c,d), and finally from *Catolethrus* by having (1) clypeal setae 1 very long and cls_2 long (Figure 9e) (vs. clypeal seta very short, and cls_2 short), and (2) five postdorsal setae of which 3 and 5 are very long, 1, 2 and 4 short to very short (Figure 10c) (vs. five postdorsal setae of which 1, 3 and 5 are long, 2 and 4 short to very short).

4.2. Biology and Distribution

The humid environment caused by mist is the most influential factor contributing to the vertical distribution of Cape Verde endemic plants [24]. This phenomenon plays the most important role also in distribution of endemic animals, notably insects depending on these plants as herbivores (e.g., Curculionidae), or predaceous insects feeding on these endemic insect groups. The scarce water source, in otherwise arid to semiarid archipelago with infrequent rain, is limited to the highest slopes of each island, although the absolute height margin between dry and wet conditions varies significantly among islands and mountain ranges [24].

This pattern of vertical distribution is notably apparent in some endemic genera of beetles with more species, e.g., *Melanocoma* (Tenebrionidae) [25] and *Dinas* (Curculionidae: Entiminae) [8], or in endemic radiations of the genus *Cymindis* (Carabidae) [26] and genera *Aphanommata* and *Pselactus* (Curculioniae: Cossoninae) ([9], and this study), which all are restricted to wet slopes and summits all over the archipelago. The genera *Dinas*, *Aphanommata* and *Pselactus* are also of interest as a model organisms for studying speciation and evolutionary history in the Cape Verde islands, because they are at present the only weevil genera with more than one species within the archipelago and because all species of these three genera so far known are flightless single island endemics occurring several hundred meters above sea level. All three genera, however, differ significantly in their horizontal inter- and intra-insular distribution. *Dinas*, with 14 taxa and two subgenera is widespread all over the archipelago (except Sal and small islets) with distributional pattern influenced likely by geological history of the archipelago and each particular island and by the wind currents [8]. Intra-generic habitat-shift with morphological adaptations exists between nominotypical subgenus and subgenus *Microspina* Skuhrovec & Batelka 2014, which both are sharing the same localities in São Vicente and São Nicolau, but differ in niches inhabited by adults [8].

Available records of *Aphanommata* and *Pselactus* provide however a different picture of their distribution within the archipelago. Larvae of both genera primarily develop in dead wood stems of the endemic shrub *Euphorbia tuckeyana*, but both are also capable of developing in rotten above-ground parts of some introduced plants, i.e., *Aphanommata* in *Agave* (Agavaceae) (this study) (Figure 13b–d) and *Pselactus* in *Jatropha* (Euphorbiaceae) [9]. So far, larvae of both genera have not been observed in underground parts of any plant. Interestingly, they also have not yet been collected in the same locality. From Fogo only *Aphanommata strakai* sp. nov. is known (Figure 13a), from Santo Antão only *A. euphorbiarum* (Wollaston, 1867), and from São Vicente only *Pselactus obesulus* (Wollaston, 1867). São Nicolau is the only island where both genera are known (*Aphanommata kuscheli* sp. nov., and *Pselactus strakai* Skuhrovec, Hlaváč and Batelka, 2017) (Figure 13b–e). Available data indicate the possibility that both lastly mentioned species do not overlap in their distribution on the island with the respect to the vertical gradient of the locality. *Pselactus strakai* was collected at localities 580 and 800 m high [9], while *Aphanommata kuscheli* sp. nov. is so far known from 1050 and 1200 m.

Field results suggest that an altitude between 800 and 1000 limits the vertical distribution of both genera across the archipelago. The species *Aphanommata euphorbiarum* is reported from Ribeira Fria and Ribeira Baboso situated in the western part of Santo Antão without altitude details, but both valleys comprise localities between 600 and 1000 m, and the highest summits of respective mountain ranges reach slightly above 1800 m. *Aphanommata* species have not been so far collected in São Vicente (with its highest point Monte Verde, 750 m) and the eastern part of São Nicolau (i.e., *Former Eastern Island* sensu Skuhrovec and Batelka [8], with its highest point Alto das Cabaças, 687 m), maybe because localities with suitable microclimate are absent, and this factor may impede members of the genus to colonize or to survive on these islands or, on proto-islands, because of competition with *Pselactus*.

Available data for both cossonine genera may be currently interpreted as a habitat shift because of competition for the same larval niche (exposed rotten wood) and subsequent adaptation for slightly different microclimatic conditions. More research, however, has to be done to test this hypothesis, e.g., whether *Aphanommata* is capable of developing at lower altitudes in islands where *Pselactus* is absent or where microclimatic conditions of altitudes below 1000 m are similar to those characteristic for this genus (e.g., climatic inversion in the valley) (Figure 13a,e).

Author Contributions: Jiří Skuhrovec drafted the manuscript and described the immature stages. Peter Hlaváč described the new species and wrote all the taxonomic part, and Jan Batelka carried out field research and described the biological and biogeographic part of the manuscript. All authors read and approved the final manuscript.

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References

1. Myers, N.; Mittermeier, R.A.; Mittermeier, C.G.; da Fonseca, G.A.B.; Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **2000**, *403*, 853–858. [CrossRef] [PubMed]
2. Kier, G.; Kreft, H.; Lee, T.M.; Jetz, W.; Ibisch, P.L.; Nowicki, C.; Mutke, J.; Barthlott, W. A global assessment of endemism and species richness across island and mainland regions. *Proc. Natl. Acad. Sci. USA* **2009**, *106*, 9322–9327. [CrossRef] [PubMed]
3. Wollaston, T.V. *Coleoptera Hesperidum Being an Enumeration of the Coleopterous Insects of the Cape Verde Archipelago*; John van Vorst: London, UK, 1867.
4. Roudier, A. Coléoptères curculionides nouveaux rappor tés des îles du Cap Vert par le Dr. Håkan Lindberg en 1953-54. *Commun. Biol.* **1957**, *16*, 1–20.
5. Geisthardt, M. Die Gattung *Dinas* von den Kapverden und Beschreibung einer neuen Art (Coleoptera: Curculionidae: Brachyderinae). *Mitt. Int. Entomol. Ver.* **1995**, *20*, 23–29.
6. Osella, G. *Proëces hesperidum* n. sp. di Capo Verde (Coleoptera: Curculionidae: Cossoninae). *Boll. Mus. Civ. Stor. Nat. Verona* **1986**, *12*, 493–499.
7. Alonso-Zarazaga, M.A. The genus *Aphanommata* Wollaston, 1873 in the Old World (Coleoptera: Curculionidae: Cossoninae). *Entomol. Scand.* **1989**, *19*, 325–331. [CrossRef]
8. Skuhrovec, J.; Batelka, J. Taxonomy of the Cape Verde endemic weevil genus *Dinas* (Coleoptera: Curculionidae: Entiminae). Part I: Description of a new subgenus, and two new species from São Nicolau island. *Acta Entomol. Mus. Natl. Pragae* **2014**, *54*, 315–336.
9. Skuhrovec, J.; Hlaváč, P.; Batelka, J. Review of Cape Verde *Pselactus* Broun, 1886 (Coleoptera: Curculionidae: Cossoninae) with description of a new species, larvae and notes on biology. *Zootaxa* **2017**, *4317*, 225–246. [CrossRef]
10. Alonso-Zarazaga, M.A.; Lyal, C.H.C. *A World Catalogue of Families and Genera of Curculionoidea (Excepting Scolytidae and Platypodidae)*; Entomopraxis: Barcelona, Spain, 1999; pp. 1–315. ISBN 84-605-9994-9.

11. Wibmer, G.J.; O'Brien, C.W. *Annotated Checklist of the Weevils (Curculionidae Sensu Lato) of South America (Coleoptera: Curculionoidea)*; American Entomological Institute: Gainesville, FL, USA, 1986; Volume 39, 563p.
12. Oberprieler, R.G.; Anderson, R.S.; Marvaldi, A.E. 3. Curculionoidea Latreille, 1802: Introduction, Phylogeny. In *Handbook of Zoology, Arthropoda: Insecta; Coleoptera, Beetles*; Morphology and Systematics (Phytophaga); Leschen, R.A.B., Beutel, R.G., Eds.; De Gruyter: Berlin, Germany; Boston, MA, USA, 1994; Volume 3, pp. 285–300.
13. Stejskal, R.; Trnka, F.; Skuhrovec, J. Biology and morphology of immature stages of *Coniocleonus nigrosuturatus* (Coleoptera: Curculionidae: Lixinae). *Acta Entomol. Mus. Natl. Pragae* **2014**, *54*, 337–354.
14. May, B.M. An introduction to the immature stages of Australian Curculionoidea. In *Australian weevils (Coleoptera: Curculionidae)*; Brentidae, Eurhynchidae, Apionidae and a Chapter on Immature Stages; Zimmerman, E.C., Ed.; CSIRO: Canberra, Australia, 1994; Volume 2, pp. 365–755. ISBN 9780643051461.
15. Scherf, H. *Die Entwicklungsstadien der Mitteleuropäischen Curculioniden (Morphologie, Bionomie, Ökologie)*; Senckenbergische Naturforschende Ges: Frankfurt am Main, Germany, 1964; Volume 506, 335p.
16. May, B.M. Immature stages of Curculionidae: Larvae of soil dwelling weevils of New Zealand. *J. R. Soc. N. Z.* **1977**, *72*, 189–228. [CrossRef]
17. Marvaldi, A.E. Larvae of South American Rhytirrhininae (Coleoptera: Curculionidae). *Coleopt. Bull.* **1998**, *52*, 71–89.
18. Marvaldi, A.E. Morfología larval en Curculionidae (Insecta: Coleoptera). *Acta Zool. Lillo.* **1999**, *45*, 7–24.
19. Trnka, F.; Stejskal, R.; Skuhrovec, J. Biology and morphology of immature stages of *Adosomus roridus* (Coleoptera: Curculionidae: Lixinae). *Zootaxa* **2015**, *4021*, 433–446. [CrossRef] [PubMed]
20. Skuhrovec, J.; Gosik, R.; Caldara, R.; Košťál, M. Immatures of Palaearctic species of the weevil genus *Sibinia* (Coleoptera, Curculionidae): New descriptions and new bionomic data with suggestions on their potential value in a phylogenetic reconstruction of the genus. *Zootaxa* **2015**, *3955*, 151–187. [CrossRef] [PubMed]
21. Anderson, W.H. Larvae of some genera of Cossoninae (Coleoptera: Curculionidae). *Ann. Entomol. Soc. Am.* **1952**, *45*, 281–309. [CrossRef]
22. Anderson, D.M. Curculionidae (broad sense) (Curculionoidea). In *Immature Insects*; Stehr, F.W., Ed.; Kendall Hunt Publishing Company: Dubuque, IA, USA, 1991; Volume 2, pp. 594–612. ISBN 978-0757556111.
23. May, B.M. *Fauna of New Zealand, 28. Larvae of Curculionoidea (Insecta: Coleoptera): A Systematic Overview*; Manaaki Whenua Press: Lincoln, New Zealand, 1993; pp. 1–225. ISBN 0-478-04505-0.
24. Brochmann, C.; Rustan, Ø.H. Distributional and ecological patterns of the endemic vascular flora of the Cape Verde Islands. *Cour. Forsch. Inst. Senckenberg* **1987**, *95*, 155–173.
25. Geisthardt, M. Tenebrionidae as an indicator for climatic changes on the Cape Verde Islands (Insecta, Coleoptera). *Spec. Bull. Jpn. Soc. Coleopterol.* **2003**, *6*, 331–337.
26. Mateu, A. Coleópteros Carábidos de las Islas de Cabo Verde. *Soc. Sci. Fenn.* **1964**, *27*, 1–47.

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Communication

Validation of the Names of Two Weevil Species Described by Skuhrovec et al., Review of Cape Verde *Aphanommata* Wollaston, 1873 (Coleoptera: Curculionidae: Cossoninae) with Description of New Species, Larva and Notes on Biology and Distributional Patterns; *Diversity* 2018, *10*, 28

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Abstract: Two new species of the cossonine genus *Aphanommata* Wollaston, 1873 from Cape Verde are described, *Aphanommata kuscheli* sp. n. and *Aphanommata strakai* sp. n, with bibliographic reference to fuller descriptions and illustrations in the recent paper by Skuhrovec et al. (2018) published in the journal *Diversity* 10 (2), 28, in which the names were not made available under the rules of the International Code of Zoological Nomenclature dealing with electronic publication. A lectotype is also here designated for *Rhyncolus euphorbiarum* Wollaston, 1867, currently assigned to the genus *Aphanommata*.

Keywords: Cossoninae; Rhyncolini; Rhyncolina; taxonomy; new species

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1. Introduction

The recent paper by Skuhrovec et al. published in *Diversity* 10 (2) [1] was not in full compliance with the International Code of Zoological Nomenclature [2] regarding publication of online taxonomic papers. Article 8.5. states that, to be considered published [within the meaning of the Code], "a work issued and distributed electronically must be registered in the Official Register of Zoological Nomenclature (ZooBank) (see Article 78.2.4) and contain evidence in the work itself that such registration has occurred" (Article 8.5.3.). Because the paper by Skuhrovec et al. (2018) was not registered in ZooBank prior to publication and therefore evidence of registration was not included in it, the new taxonomic names proposed in the paper are not available under the Code [3]. The purpose of this paper is to make those names available.

To fulfill the requirements of Article 8.5. of the Code, this paper has been registered in ZooBank, with the LSID above, and the names of the species described below have also been registered, following recommendation 10B of the Code. Nomenclatural acts other than new taxon names cannot presently be registered in ZooBank, but we also here validate the lectotype designation of *Rhyncolus euphorbiarum* that was proposed by Skuhrovec et al. [1].

To meet the requirements of Article 13.1.2. of the Code, the names listed below are accompanied by a bibliographic reference to their full descriptions and are thereby made available from the publication of this paper. The wording of Article 13.1.2. is somewhat ambiguous as to the status of descriptions based on bibliographic reference, so to avoid any further problems we have added below a brief description differentiating each taxon and a holotype designation with the repository identified; these are repeated from the original paper [1].

2. New Nomenclatural Acts

Aphanommata euphorbiarum (Wollaston, 1867)

Lectotype designation. Lectotype (here designated): Type/(p) T. V. Wollaston Coll., B. M. 1867–82, CAPE VERDE IS. [original white label with a green corner] (Repository: The Natural History Museum, London, United Kingdom). For further details of the specimen and of the paralectotype, see Skuhrovec, Hlaváč & Batelka, 2018: 4 [1].

Aphanommata kuscheli Skuhrovec, Hlaváč & Batelka, **sp. n.**

> *Aphanommata kuscheli* Skuhrovec, Hlaváč & Batelka, 2018: 5 [1] (not available)
>
> http://zoobank.org/urn:lsid:zoobank.org:act:2C1F2BA6-683D-45D8-8584-BD3D976488C7

Description. Antennal scape slightly pedunculate at apex, short, shorter than funicule, funicule with 7 antennomeres; funicular antennomere I slightly longer than wide, about 1.75 times as long as II; antennal club about 1.7 times as long as wide; head and pronotum shiny, finely shagreened, evenly finely punctate; anterior margin of pronotum slightly narrower than base; pronotum widest in posterior fourth; elytra with 14–16 rows of punctures of different size, in anterior half cross-cracked, elytral intervals flat. See Skuhrovec, Hlaváč & Batelka, 2018: 5–7, Figures 2, 3, 4a, 4b, 5a, 6a, 7a, 9, 10 [1] for full description.

Holotype, ♂: "CAPE VERDE Isl., 10.X.2013, SAO NICOLAU, W, Mt. Gordo summit, 16.625089, −24.350854, J. Straka and J. Batelka lgt. (p)/windward slopes in rotten wood of *Euphorbia tuckeyana* (p)" (Repository: Staatliches Museum für Naturkunde, Stuttgart, Germany). Paratypes listed in [1].

Distribution. Cape Verde Islands: São Nicolau.

Aphanommata strakai Skuhrovec, Hlaváč & Batelka, **sp. n.**

> *Aphanommata strakai* Skuhrovec, Hlaváč & Batelka, 2018: 13 [1] (not available)
>
> http://zoobank.org/urn:lsid:zoobank.org:act:22933B26-34C1-4F8D-924F-3F006B3A3374

Description. Antennal scape slightly pedunculate at apex, shorter than funicule, funicule with 7 antennomeres; funicular antennomere I about 1.60 times as long as wide, almost parallel-sided, about 1.75 times as long as II; antennal club about twice as long as wide; head and pronotum shiny, head finely shagreened, pronotom not shagreened, evenly finely punctate, punctures on pronotum bigger; elytra with 14–15 rows of punctures of different size, finely cross-cracked in anterior half only close to sutura, elytral intervals flat; anterior margin of pronotum slightly narrower than base; pronotum widest in posterior fourth. See Skuhrovec, Hlaváč & Batelka, 2018: 13–15, Figures 4c, 4d, 5b, 6b, 7b, 11, 12 [1] for full description.

Holotype, ♂: "CAPE VERDE Isl., FOGO—Chã des Caldeiras 8.–9.X.2009, J. Straka and J. Batelka lgt. (p)" (Repository: Staatliches Museum für Naturkunde, Stuttgart, Germany). Paratypes listed in [1].

Distribution. Cape Verde Islands: Fogo.

Author Contributions: The authors contributed to this paper the same way. All authors read and approved the final manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

References

1. Skuhrovec, J.; Hlaváč, P.; Batelka, J. Review of Cape Verde *Aphanommata* Wollaston, 1873 (Coleoptera: Curculionidae: Cossoninae) with Description of New Species, Larva and Notes on Biology and Distributional Patterns. *Diversity* **2018**, *10*, 28. [CrossRef]
2. International Commission on Zoological Nomenclature. 2012. INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE Fourth Edition [Incorporating Declaration 44, Amendments of Article 74.7.3, with Effect from 31 December 1999 and the Amendment on E-Publication, Amendments to Articles 8, 9, 10, 21 and 78, with Effect from 1 January 2012]. Available online: http://www.iczn.org/iczn/index.jsp (accessed on 26 July 2018).
3. International Commission on Zoological Nomenclature. Amendment of Articles 8, 9, 10, 21 and 78 of the International Code of Zoological Nomenclature to expand and refine methods of publication. *Zookeys* **2012**, *219*, 1–10. [CrossRef]

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Article

Invasive Bark Beetles (Coleoptera, Curculionidae, Scolytinae) in Chile and Argentina, Including Two Species New for South America, and the Correct Identity of the *Orthotomicus* Species in Chile and Argentina

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Abstract: The rate of establishment of non-native bark beetle species is accelerating in many parts of the world and is considered a serious threat to forests and forest crops. Distributional data for exotic bark beetles are urgently needed, but they must be based on sound taxonomy. Using primary literature and original records, I review for the first time the invasive bark beetle (Scolytinae) species in Chile and Argentina, and I give a short risk assessment for each. I also provide the best sources for identifying these species. The invasive pine bark beetle commonly referred to in Chilean research as *Orthotomicus erosus* (Wollaston) is not that species: evidence suggests that the only *Orthotomicus* that is or has been in Chile is *O. laricis* (Fabricius), which is also the *Orthotomicus* species reported in the most recent research from Argentina. I add new information on the distributions of two other abundant pine-breeding invasive species, *Hylurgus ligniperda* (F.) and *Hylastes ater* (Paykull), and I report that populations of *Hylastes linearis* Erichson have been found in Chile. This is the first known occurrence of the species in South America. *Phloeotribus willei* Schedl, a tiny bark beetle collected from domestic fig trees in Chile and Peru, has been considered native heretofore. I argue that it must be an introduced Neotropical species, and I present new localities for Chile. I present the first Chilean records of the Myrtaceae specialist ambrosia beetle *Amasa truncata* (Erichson), an Australian species recently found in southern Brazil and northeastern Uruguay, and new Argentinian records that seem to be the earliest finds of *Xylosandrus crassiusculus* (Motschulsky) in South America. The Canary Island palm seed specialist *Dactylotrypes longicollis* (Wollaston) is reported for the first time from South America, from Chile. The presence in Chile of another spermatophage, *Coccotrypes dactyliperda* (F.), is confirmed. New Chilean regions and new host records are given for *Pagiocerus frontalis* (F.), a species that breeds in Lauraceae seeds but also in stored maize. Other exotic species treated briefly include *Hylastinus obscurus* (Marsham), *Hylesinus taranio* (Danthione), *Scolytus multistriatus* (Marsham), *S. rugulosus* (Müller), *Coccotrypes cyperi* (Beeson), and *Xyleborinus saxeseni* (Ratzeburg). Finally, reports of several species from Chile or Argentina are considered unsupported by evidence: *Scolytus kirschii* Skalitzky, *Pityokteines curvidens* (Germar), *Coccotrypes robustus* Eichhoff, and *Hypothenemus hampei* (Ferrari).

La velocidad de establecimiento de especies de coleópteros descortezadores no nativos se está acelerando en muchas partes del mundo y se considera una amenaza seria a bosques y cultivos forestales. Se requiere datos distribucionales urgentemente, pero estos tienen que basarse en taxonomía sólida. Utilizando literatura primaria y registros originales, reviso por primera vez la fauna invasora de especies de descortezadores (Scolytinae) en Chile y Argentina, y ofrezco una evaluación breve del riesgo de cada una. También proporciono los mejores referencias para identificar estas especies. La especie descortezador invasora de pinos comunmente citado en investigaciones chilenas como *Orthotomicus erosus* (Wollaston) no es esa: la evidencia sugiere que la única especie de *Orthotomicus* actualmente o históricamente presente en Chile es *O. laricis* (Fabricius), la cual es la especie de *Orthotomicus* reportado en las investigaciones mas recientes de Argentina. Agrego información nueva sobre las distribuciones de otros dos especies abundantes invasoras que se reproducen en pinos, *Hylurgus ligniperda* (F.) y *Hylastes ater* (Paykull) y comunico que poblaciones de *Hylastes linearis* Erichson se han encontrado en Chile, siendo esta el primer hallazgo de la especie en Sudamérica. *Phloeotribus* willei Schedl, una especie minúscula colectado de higueras cultivadas en Chile y Peru, se ha considerado nativa hasta ahora: presento argumentos que debe de ser una especie neotropical introducida y presento nuevas localidades para Chile. Presento los primeros registros chilenos de *Amasa truncata* (Erichson) coleóptero ambrosial, especialista en Myrtaceae, especie australiana recientemente encontrada en el sur de Brasil y nordeste de Uruguay, y nuevos registros argentinos que parecen ser los primeros hallazgos de *Xylosandrus crassiusculus* (Motschulsky) en Sudamérica. Se registra la especialista en semillas de palma, *Dactylotrypes longicollis* (Wollaston), originario de las Islas Canárias pro primera vez de Sudamérica; se confirma la presencia en Chile de otra espermatófago, *Coccotrypes dactyliperda* (F.). Se presentan nuevos registros regionales de Chile y de hospederas por *Pagiocerus frontalis* (F.), especie que se reproduce en semillas de Lauraceae pero también en maíz almacenado. Otras especies exóticas tratadas brevemente incluyen *Hylastinus obscurus* (Marsham), *Hylesinus taranio* (Danthione), *Scolytus multistriatus* (Marsham), *S. rugulosus* (Müller), *Coccotrypes cyperi* (Beeson), y *Xyleborinus saxeseni* (Ratzeburg). Finalmente, registros de varias especies de Chile o de Argentina se consideran sin apoyo de evidencia: *Scolytus kirschii* Skalitzky, *Pityokteines curvidens* (Germar), *Coccotrypes robustus* Eichhoff, y *Hypothenemus hampei* (Ferrari).

Keywords: Alien; invasive; exotic; biodiversity; Patagonia; *Pinus radiata*; *Eucalyptus*

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1. Introduction

Half a century ago, Stephen L. Wood [1] published the first paper discussing in detail the intra- and intercontinental spread of Scolytinae. Since then, awareness has grown that introduced bark beetles pose serious threats to forests, forest products, and certain crops [2–12]. The effects of invasive scolytines on their hosts are often due to or magnified by symbiotic microorganisms borne by the beetles. The consequences of these parasite–symbiont–host plant interactions are further complicated by climate change [4,13–16].

Awareness of the potential threats posed by exotic bark beetles has, in turn, led many countries to develop or strengthen quarantine restrictions and to initiate monitoring of forests or of sites (such as ports) where imports arrive. Quarantines can severely impact the economies of countries exporting timber or wood products, so correct identification of potential pest species is critical. Monitoring has greatly increased our knowledge of the diversity and numbers of bark beetles coming into a region, e.g., [2,3,17], and of the native fauna as well e.g., [18]. As a result, we now know much about the invasive species *sensu* [7] (p. 229) in North America and Europe but much less where monitoring is relatively new and where the native fauna is not well known, such as the southern regions of South America. Established non-native Scolytinae in Chile and Argentina can potentially impact both quarantine issues and native and urban forests as well as trees in plantations.

During visits to Chilean insect collections and via correspondence with foresters in both Chile and Argentina, I have found specimens of several exotic species new to Chile or Argentina. I have also recorded collection data for many non-native species previously only known from country records, some of which significantly extends their known ranges.

This paper is a contribution to the memorial issue in honor of the late Guillermo "Willy" Kuschel. Willy Kuschel was well aware of the importance of detecting and identifying alien species, though "foreign" species was a focus in only one of his papers [19]. Similarly, though his interests were broad with respect to weevils [20], bark beetles are the prodigal child of weevilology, and few of his papers dealt extensively with Scolytinae; he did treat bark beetles thoroughly in his papers on the weevil fauna of *Araucaria* [21] and the suburban beetles of New Zealand [22]. He was nonetheless instrumental in investigating the bark beetle fauna of Chile (native or otherwise) by engaging the lasting interest of the Austrian world expert Karl E. Schedl via two significant loans of material in the 1950s [23,24].

2. Methods

2.1. Sources of Data

The data reported here come primarily from museum loans of Scolytinae, correspondence with collectors in Chile and Argentina, and short visits to the main SAG entomological collections outside of Santiago, the Chilean Natural History Museum in Santiago, the University of Concepción, and the coleopterist Juan Enrique Barriga. During these visits, I recorded identifications and borrowed small numbers of specimens. A visit to my lab by Paula ("Vicky") Klasmer supplied me with important specimens from Bariloche in Argentina. I also examined older faunistic papers for records missed by Wood in his monograph of the bark beetles of South America [25], particularly papers by Karl E. Schedl for both countries and Manuel J. Viana for Argentina. The recent review of the weevil fauna of Chile [26] summarizes Scolytinae species in Chile based on the MNNC collections as well as on Schedl's older review [27].

2.2. Abbreviations Used for Collections

SAGC	*Servicio Agrícola y Ganadero* (Agricultural and Livestock Service), Lo Aguirre, Chile
LRKC	Lawrence R. Kirkendall collection, Univ. Bergen, Norway
MNNC	*Museo Nacional de Historia Natural*, Santiago, Chile
NHMW	*Naturhistorisches Museum Wien*, Vienna, Austria
UCCC	*Universidad de Concepción*, *Museo de Zoología*, Concepción, Chile
USNM	United States National Museum, Washington, D.C., USA

Frequently used common names (e.g., "the Granulate Ambrosia Beetle") are capitalized, to distinguish them from descriptive text.

Chilean provinces in collection data are often referred to by number given as a Roman numeral, as in "Región V," plus greater Santiago, which is known as Región Metropolitana (RM). The region numbers basically run from north to south, but the recently added region XV is now the northernmost region. Publications, on the other hand, use the formal names of the provinces (Valparaíso instead of Región V). For maximum clarity, I have generally followed both systems by adding names where region numbers are used and vice versa. Province names for Chile and Argentina are given in Figure 1.

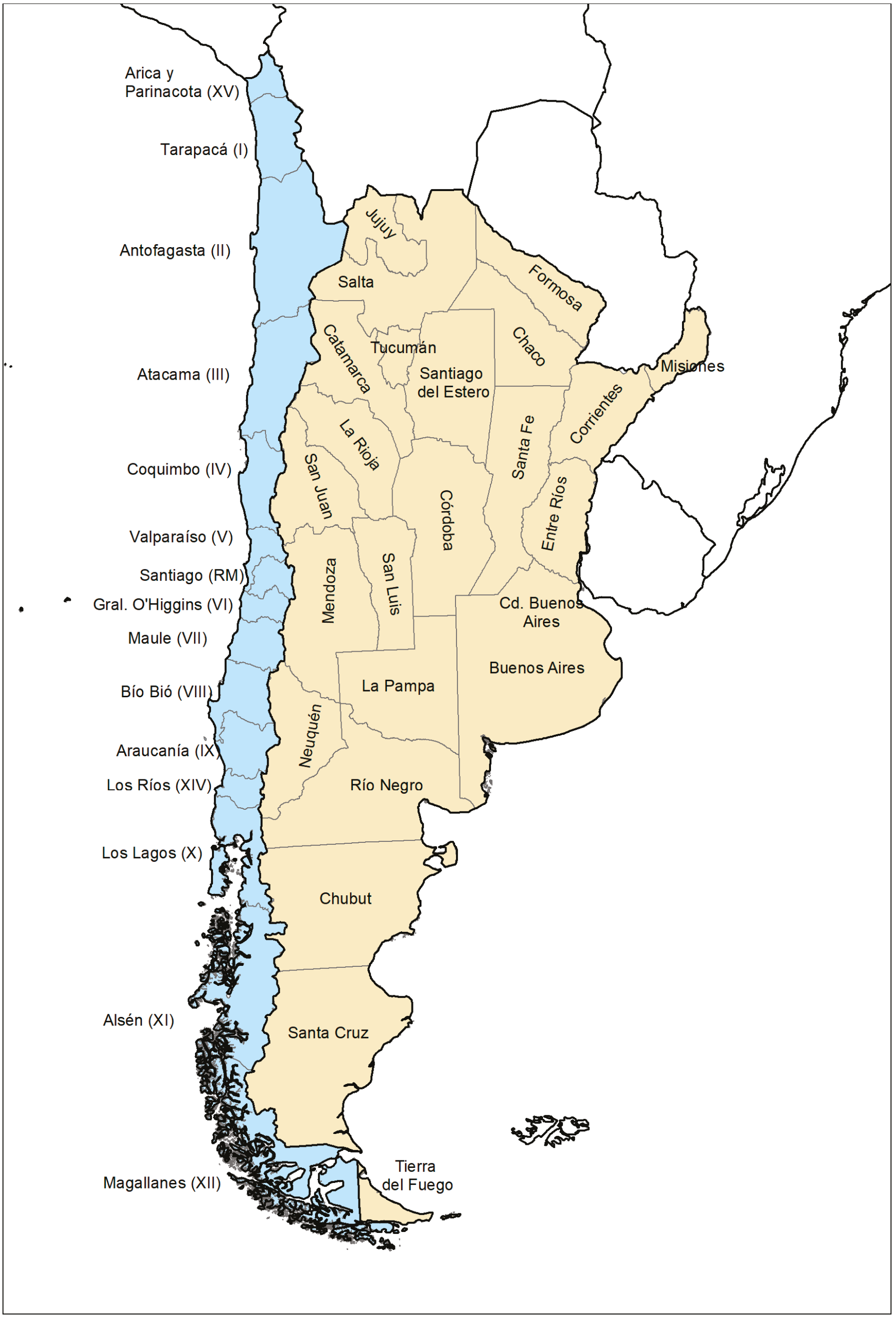

Figure 1. Map of Chile and Argentina, with province names and numbers for Chile, prepared by T. H. Atkinson.

2.3. Resources for Identification by Non-Specialists

There are general resources available for aid in identifying the species in this paper. The monographs of the bark beetle fauna of North and Central America [28] and that of South America [25] include non-native species which have been established for at least several decades. (Sadly, no such monographs exist for other continents.) Non-native species are included in the keys in these works. For identifying more recently established species, I give alternative sources. The primary sources for good photos of Scolytinae are T. H. Atkinson's website http://www.barkbeetles.info, Forestry Images https://www.forestryimages.org, and PaDIL http://www.padil.gov.au. The European bark beetles mentioned in this paper are also illustrated in [29,30].

Detailed collection data are given only for specimens I have personally examined. Generally, my identifications were based on comparisons with type material or with specimens in NHMW which were identified by K. E. Schedl or, for European species, specimens in my reference collection that were identified by Miloš Knížek (Forestry and Game Management Research Institute, Prague, Czech Republic).

Species are organized by ecology and feeding behaviors, which generally also clusters species similar in appearance. "Bark beetles" in the context of feeding behavior refers to species that breed in the inner bark of woody plants. In other contexts, "bark beetles" is used taxonomically to refer to Scolytinae. The "ambrosia beetles" treated here breed in wood, but larvae and adults feed on symbiotic fungi cultivated by parent beetles in the tunnel systems. As the name suggests, "seed beetles" reproduce in seeds that are large enough to support a bark beetle brood. Within each ecological category, species are ordered primarily by significance of the new record(s) and secondarily by alphabet.

3. Results

Fourteen exotic Scolytinae species are apparently established in continental southern South America: two are highly polyphagous ambrosia beetles, four are bark beetles breeding in plantations of exotic pines, one is an ambrosia beetle that breeds in exotic *Eucalyptus* plantations, five are bark beetles, and three are seed beetles that are associated with agricultural crops or urban trees. A 15th species (an extreme host generalist bark beetle) is found on Easter Island (Chile). Four species previously attributed to Chile or Argentina could not be verified and should not be considered established in the region.

3.1. Bark Beetles

3.1.1. *Orthotomicus Laricis* (Fabricius) Is the *Orthotomicus* in Southern South America

New records: **CHILE**, [Maule] Talca, Constitución, August 1984, L. Cerda (1, SAGC); [Los Ríos] [Biobío] Talcahuano, in *Pinus*, 16 May 1986, R. Muñóz (2, SAGC); [Araucanía] Gorbea, in pine, 16 May 1986, J. Luna (1, SAGC); Valdivia, Santo Domingo, 13 August 1989, E. Krahmer (3, SAGC). **ARGENTINA**, Neuquén, −40.1561, −71.5589, 4 November 2010, ex *Pinus ponderosa*, P. Klasmer (4, 1 in LRKC). Note that this species was collected frequently from both Chubut and Neuquén in 2009–2011 for the bluestain fungus study of de Errasti et al. ([31] and de Errasti pers. comm. 21 February 2018).

Comments. Orthotomicus laricis (F.) is one of the three pine-breeding Scolytinae discovered 30 years ago by William Ciesla to be common in Chile's extensive monocultures of Monterrey pine (*Pinus radiata*) [32]. However, the *Orthotomicus* species was reported as *O. erosus* (Wollaston) by Ciesla and most subsequent authors. The Chilean records given here are the earliest collections in the SAGC. Elgueta and Marvaldi [26] give the distribution as Maule Province (VII) to Bio-Bio (VIII); the 1987 specimens are from Valparaíso (V), and Lanfranco et al. [33] trapped specimens in small numbers in regions Bio-Bio and Los Lagos (X). Ruiz and Lanfranco [34], the most recent source, give the range as Valparaíso to Los Lagos (V–X), throughout the range of *Pinus radiata* in Chile.

The report of *O. erosus* from Chile was by forest entomologist William Ciesla, who was carrying out an FAO survey of pine bark beetles there [32]. Ciesla's 1987 Chilean specimens of *Orthotomicus* are from Valparaíso, Vina del Mar, 1987 in *P. radiata*, and are in the S. L. Wood Collection housed in the USNM: these are all *O. laricis*, identified by Sarah Smith, a bark beetle expert (R. Rabaglia, pers. comm., 14 February 2018, Sarah Smith, pers. comm., 14 February 2018). Photographs taken at the time by William Ciesla show the unique gallery structure of *O. laricis*, the only *Orthotomicus* known to me that lays eggs in clusters in a large chamber rather than in niches along narrow tunnels e.g., ([29]; see forestimages.org or http://baza.biomap.pl/en/taxon/genus-orthotomicus-onthotomicus/photos_rc/tr/y). The European bark beetle expert Miloš Knížek (pers. comm.) concluded that beetles sent to him taken from Parral, Chile (SAG specimens) were *O. laricis*, and I can confirm that all specimens I have examined in the SAGC (March 2017) were correctly identified by curator Sergio Rothmann or by SAG entomologist Margarita Peralta as *O. laricis*. Earlier bark beetle lists for Chile or for Argentina do not include any records of *Orthotomicus* [27,35–37], so its presence in southern South America is recent.

The *Orthotomicus* in Chile has been referred to as *O. erosus* in a wide variety of publications since Ciesla's report [25,33,34,38–45]. This species is correctly cited as *O. laricis* by de Errasti et al. [31], for both Argentina and for Chile, in a paper on the ophiostomoid fungi associated with pine bark beetles in Patagonian Argentina. Haack (Table 9 in [2]) and Brockerhoff (Table 1 in [5]) list both *Orthotomicus* species as being found in Chile. However, both Haack and Brockerhoff have confirmed that their published records of *O. erosus* were based on the literature, not on new identifications (both, pers. comm. 14 February 2018).

Orthotomicus specimens were sent to S. L. Wood for identification (Ciesla, pers. comm. January 2018), so the original error stems from Wood. It is unknown what led to this mistake. Since Wood had little direct experience with European bark beetles, it could be that his identification as *O. erosus* was based on specimens misidentified by someone else; he may have been unaware of the general similarity of *O. erosus* to *O. laricis* and the small details (such as the sutures of the antennal club) separating the two species, though they are well illustrated in at least one work he must have possessed [29]. *Orthotomicus erosus*, known as the Mediterranean pine beetle, is originally from southern Europe, northern Africa, and Asia minor but is now distributed around the world [38,39]. The well-known wide distribution of this *O. laricis* look-alike may then have led Wood and subsequent researchers to assume that the species in Chile was also *O. erosus*.

The first published record of *Orthotomicus* in Argentina seems to be [46] in 2010, where the species was identified as *O. laricis* by bark beetle expert Anthony Cognato (Michigan State Univ., USA). Tiranti reported two collections from *Pinus ponderosae* in Neuquén, the earliest being from 2007. Massimo Faccoli, a forest entomologist well familiar with these species, has only seen *O. laricis* in specimens sent to him from a trapping study currently underway in pine plantations close to Bariloche (Faccoli, pers. comm. 6 October 2017 and 31 January 2018). Similarly, the one Argentinian specimen I have examined (also from near Bariloche) is *O. laricis*.

In conclusion, while it is possible that both *Orthotomicus* have been in Chile at some point, no specimens of *O. erosus* from Chile or from Argentina have been seen by SAG personnel, Miloš Knížek, Massimo Faccoli, or myself. Interestingly, the species which has recently colonized many Uruguayan pine plantations actually is *O. erosus* [47]. Uruguay, then, is the only South American country currently hosting *O. erosus*.

Identification. The subtle differences between *O. laricis* and *O. erosus* are described (but not illustrated) in [1,47]. Good illustrations of the differences in the sutures of the antennal club, the most easily used character, are in [29,30].

Risks. Orthotomicus laricis has not proven to be an important pine pest in Chile, where it is said to now be difficult to find [25,38]. *Orthotomicus erosus* is one of the most frequently intercepted exotic species in the USA and New Zealand and has succeeded in colonizing pine plantations around the world, and consequently has attracted a great deal of attention from foresters and researchers [2,5,38,39]. *Orthotomicus laricis*, by contrast, is much less frequently intercepted [2,5], and I know of no other established exotic populations. The species is native to Eurasia and North Africa, and the populations in Chile and Argentina seem to be the only successful establishments of the species outside its native range.

3.1.2. Further Argentina Locality Records for *Hylurgus Ligniperda* (Fabricius), and the Earliest Date for Chile

Collections. **CHILE**, Valparaíso, July 1981, P. Ojeda, ex *Pinus* (3, MNNC). Valparaíso, "*trampas*" [traps], March 1988, J. Godoy (5, MNNC). **ARGENTINA**, Chubut, −41.9992, −71.5442, ex *Pinus contorta*, 23 February 2010, P. Klasmer (4, 1 in LRKC); Neuquén, −40.1561, −71.5589, ex *Pinus ponderosa*, 11 December 2009, P. Klasmer (1, LRKC). Note that this species was collected frequently from both Chubut and Neuquén (in 2009–2011), for the bluestain fungus study of de Errasti et al. ([31] and de Errasti pers. comm. 21 February 2018).

Comments. This is said to be the most abundant of the three pine bark beetles in Chile [33,34]. Elgueta and Marvaldi [26] give the range as Maule to Araucania (VII–IX), Wood [25] has records ranging from Valparaíso (V) to Bio-Bio (VIII), and Lanfranco et al. [33] trapped many in both Bio-Bio and Los Lagos (X). Ruiz and Lanfranco [34], the most recent source, give the range as Valparaíso to Los Lagos (V–X), throughout the range of *Pinus radiata* in Chile. A 1985 SAG collection from Bio-Bio (VIII) from 1985 seems to be the earliest published record [25].

I can find no papers that specify where this species occurs (or does not) in Argentina, and the CABI datasheet on this species lists Chile, Brazil, and Uruguay but not Argentina as South American countries with *H. ligniperda* (https://www.cabi.org/isc/datasheet/27364m, visited 15 February 2018). Andres de Errasti (CIEFAP, Argentina: pers. comm. 23 February 2018) informed me that the *H. ligniperda* in their study [31] were collected from both Chubut and Neuquén. Tiranti [46] reports the species from both Chubut and Neuquén from 2007 and 2008. Records in neighboring Uruguay go back at least to 1956 [35].

Known as the Red-Haired Bark Beetle, this Eurasian species is established in pine plantations around the world [48]. It was first discovered in Chile in the 1980s [32]. Of the three species discovered at the same time in Chile [28], *H. ligniperda* has been the most successful and now occupies the entire distribution of Monterrey pine in the country [49]. The Valparaíso specimens from 1981 seem to be the earlier record of any of the pine-breeding species in Chile.

For Argentina, *Hylurgus ligniperda* is not included as a significant pest in the recent FAO report on forest pests of that country [50]. *Hylurgus ligniperda* attacks logging residues, including stumps, roots, and logs, and can breed on roots of seedlings and saplings; they also feed on the root collars of one- and two-year-old seedlings, both in natural regeneration and plantations.

Identification: *Hylurgus* is larger, less elongate, and more densely "hairy" than the *Hylastes* species in southern South American pines. Excellent photos of *H. ligniperda* are widely available on the internet.

Risks. It is suspected *H. ligniperda* can vector *Leptographium* root diseases [51]; otherwise, breeding in logs leads to discoloration due to the associated blue-stain fungi, which can lower their eventual value for lumber.

3.1.3. *Hylastes Linearis* Erichson New to South America

New records. **CHILE**: [Región V] Valparaíso, El Turco, 16 May 2013, funnel trap, M988, FP 40507, H. Rodriguez (1, LRKC).

Comments. According to Sergio Rothmann of SAG (pers. comm., 5 February 2018), *H. linearis* was first detected over a decade ago in September of 2006. It is most frequent in Región VI (O'Higgins region), where SAG has collected it from Las Cabras, Santa Cruz, Litueche, Marchigüe, and Peralillo. In addition, the species has been detected in Región V (Valparaíso Region), the Región Metropolitana (Paine), and Región VIII (Bio-Bio Region, Bulnes and Ranquil).

These established Chilean populations and those in South Africa are the only long-distance establishments of *H. linearis* and are anthropogenic. The populations on Madeira and the Canary

Islands could represent either anthropogenic or natural dispersal to islands close to natural source populations. The Chilean populations could stem from either Mediterranean Europe, the source of US interceptions [2,9], or South Africa.

Identification. Recent descriptions can be found in [52,53]. Photos are available in [53] and at Forestry Images, PaDIL, http://coleoptera-neotropical.org/paginas/3ac_familias/CURCULIONOIDEA/2sp/Scolytinae/Hylastini/Hylastes-linearis.html.

Risks. Hylastes linearis breeds in the dead roots and stumps of various pine species [53]. It is not considered a significant pest species, so there is little research into its biology, which seems to be similar to that of *Hylastes ater* [54]. Even its distribution in Europe seems to be poorly known [52,53], and it is considered to be a rare species [53,55,56]. It is not considered an economically important species where it is native, other than some feeding damage to the root collar of seedlings, nor do invasive populations in Israel cause concern [54]. In South Africa, where it is introduced and established (the only long-distance introduction of the species), individuals carry *Verticicladiella alacris*, a root fungus, but it has not been demonstrated that they actually vector the disease-causing organism; the fungus apparently only attacks wounded or severely stressed pines [57]. It could become a pest of planted seedlings in Chile [58,59]. Lee et al. [41] consider *H. linearis* to be an intercepted species that, though not currently in the United States, could potentially establish populations and become a pest species if introduced.

3.1.4. *Hylastes ater* (Paykull), Second Province for Argentina

New records. **CHILE**: Valparaíso, March 1988, traps, J. Godoy (5, MNNC); Valparaíso, July 1981, *Pinus*, P. Ojeda (3, MNNC). **ARGENTINA**, Chubut, −42,0361, −71,5456, *P. ponderosa*, 14 February 2011 (1, LRKC); Neuquén, −40,1561, −71,5589, *P. ponderosa*, 25 November 2011 (1, LRKC). This species was collected from Neuquén and Chubut (in 2009–2011) in the bluestain fungus study [31] (de Errasti, pers. comm. 23 February 2018).

Comments. *Hylastes ater*, the Black Pine Bark Beetle, is a Eurasian species that is now established in pine plantations in most of the world, though not yet in North America (https://www.plantwise.org/KnowledgeBank/Datasheet.aspx?dsid=28047). It is common and abundant in pine plantations in Chile. The most recent source [34] give the range as Valparaíso to Los Lagos (V–X) throughout the range of *Pinus radiata* in Chile.

Though the occurrence of the Black Pine Bark Beetle is apparently known to foresters in Argentina, I can find only one published province (Neuquén) for the country [46,60]. The most recent CABI invasive species data sheet lists Chile but not Argentina [61].

Identification. *Hylastes* species are most similar to *Hylurgus* species. *Hylastes ater* is very similar to *H. linearis*, which is also present in Chile, but is larger (nearly 5 mm, vs 3 mm for *H. linearis*). Identifying the genera and species can be accomplished by careful use of keys and photos.

Risk: *Hylastes ater* breeds primarily in the roots of weakened, sick, or recently killed Pinaceae, but can also breed in dead trunks and large branches. Its economic damage is to seedlings, which can be girdled by the feeding activities of recently emerged adults; though often not lethal in themselves, open wounds on seedlings are frequently invaded by fungi [58]. Dense populations of this species can result in significantly reduced regeneration in pine plantations and nurseries [59,62,63] (but see [64] for a contrary view). However, the draft report [49] concludes that *H. ater* has been outcompeted by *H. ligniperda* and no longer an abundant species in Chile.

3.1.5. New Records for an Olive Tree Bark Beetle, *Hylesinus taranio* (Danthione)

New records. **CHILE**: Reg. VII, Rauco, Nov. 1996, olive tree, leg. L. Peralta (1, SAGC); Reg. Metropolitaniana, El Monte, 1 March 1990, olive tree, leg. M. Beeche (1, SAGC); Reg. V, Panquehue, December 1999, olive tree, E. Pastor (1, SAGC); Reg. VI, Rancagua, October 1999, olive tree, leg. E. Prado (2, SAGC).

Comments. The species is common around the Mediterranean, where it breeds in *Fraxinus* (ash), *Fagus*, and *Syringia* as well as olive [29,45]. The earliest dated collection is from Chile, for the holotype of *H. antipodus* Schedl (a junior synonym) collected from Rengo in 1947 [27] (synonymy verified by me). Wood [25] adds Colchagua, 1977 from *Olea* (olive) (Región VI). Elgueta and Marvaldi [26] give the range as Arica to Bio-Bio (XV–VIII) but without giving specific collection data.

Argentina is listed as only a country record [25]. For Argentina, Bosq [65] remarks on two collections of *H. oleiperda* (the most common junior synonymy) from the province of Buenos Aires but gives no dates. Schedl [35,66] reports collections from Buenos Aires in 1941 and 1953, the latter from olive branches, while Holgado [67] cites a 1939 interception in the port of Buenos Aires, in olives imported from Italy, as the possible starting point for the colonization of Argentina. Miriam Holgado's ecological investigation [67], based on research carried out in the early 1990s, was carried out in Mendoza, where the species was first recorded around 1982. From these data, it would appear that *H. taranio* has been in Chile and Argentina equally long.

Identification. Excellent photos are available on the internet (e.g., https://www.forestryimages.org/browse/subthumb.cfm?sub=10223), and Grüne has keys and drawings. There are also keys and some illustrations in other European works, though most are in languages other than English.

Risks. Attacks on young branches and twigs can lead to reduced olive production [67]. The olive oil industry is growing fast in Chile, so this species should be carefully monitored.

3.1.6. The Smaller European Elm Bark Beetle, *Scolytus multistriatus* (Marsham), in Chile and Argentina

New records. **CHILE**, [Región Metropolitana] Pudahuel, October 1993, M. Beéche (1, MNNC); [Región Metropolitana] Aerop. A. M. B., *Ulmus*, M. Beéche (1, LRKC). These specimens are apparently vouchers for [68].

Comments. The Smaller European Elm Bark Beetle, *Scolytus multistriatus*, is native to Europe, Asia and northern Africa, and is invasive to North America (including Mexico). The only South American records in [25] are country records for Argentina and, as a questionable record, Chile, and Wood had not seen specimens himself from these countries. The first confirmed South American find is that of Beéche and Muñoz [68], who surveyed elms in Región Metropolitana (Santiago and environs) and Región V (Valparaíso) immediately north in 1992–1993. They found *S. multistriatus* in four different metropolitan localities but none in Región V.

Smith and Cognato [69] confirmed the presence of *S. multistriatus* in Brazil (Mato Grosso) and Argentina (Buenos Aires and Mendoza). These recent finds suggest that the species is now established in temperate South America, but it should be emphasized that only single specimens are known from each collection.

Identification. Note that *Scolytus schevyrewi* Semenov (not yet reported from S. America) is extremely similar in morphology and ecology [70,71] (their Figure 1). The best sources for photos, keys, and descriptions for these invasive elm bark beetles are [69,71]. There is a description of *S. multistriatus* in Spanish and an illustration in [68].

Risks: The Smaller European elm bark beetle is the principle vector of Dutch Elm Disease in North America, where it has decimated both wild and planted elm trees across the continent. It is also an important vector of the disease pathogens in its native range. It must be considered a potential threat to urban elms in Chile and Argentina, though to my knowledge no such problems have yet been detected. Similarly, both *S. multistriatus* and *S. schevyrewi* are present in Mexico, but there has so far been no sign of the disease there (Thomas H. Atkinson, Univ. Texas Insect Collection, pers. comm. 27 January 2018).

Comments. In the Museo Nacional de Historia Natural (Santiago, Chile), there are 11 specimens of which only 3 are labeled: the labels read "ex pruni/Laudbeck I 1882"—meaning, probably, from *Prunus*, Région I (Tarapacá), collector Laudbeck. This is the only record cited in [27], in Schedl's summary of the bark beetles of Chile. This record is first given in [23]. Klein Koch and Waterhouse [44] list it from regions IX and X (Araucanía and Los Lagos) without giving any specific dates or places.

In Argentina, the earliest record seems to be a collection from a cherry tree in 1917 in Buenos Aires [72]. Otherwise, Schedl [73] reports collections from Tigre and Martín García in 1938. Schedl [74] lists a collection but no date from Buenos Aires. Schedl [72] records the species from Córdoba, Calamuchita in 1938, and he adds an additional collection from Buenos Aires [75]. Viana [37] lists a variety of locations but without any more collection data. These are probably the specimens Schedl cites in papers based on Viana's collection. Córdoba and Atkinson [76] add La Riója. From these new records and the published data, we must conclude that *S. rugulosus* is fairly widespread in both countries, though the paucity of collections could mean that it is not abundant.

Identification: Photos are readily available on the internet, and the species can be keyed out in Wood [25,28]. The best source for photos and keys is [69].

Risks: This species is listed in [40] as an exotic species in urban trees of Chile but not discussed in the text, suggesting that it is not a noteworthy pest. *Scolytus rugulosus* is generally considered a secondary bark beetle, only breeding in dead or stressed trees and not causing much damage [77]. Klein Koch and Waterhouse [44] list apple (*Malus*) and a variety of fruit and nut trees (*Prunus* spp.). On the other hand, Viana [37] (but no later authors?) describes *S. rugulosus* as a true pest of fruit trees, even healthy ones.

3.1.8. The Bark Beetle Collected from Fig Trees in Chile and Peru, *Phloeotribus willei* Schedl

New records. **CHILE**: Región RM, Metropolitana, El Monte, Septermber 1993, M. Beeche (3, SAGC); Región I, Qda. de Chaca, Em. 15, 12 June 1999, *Ficus carica*, M. Beeche (4, SAGC); Región I, Qda. de Chaca "Em. 15. 12. June 1999", 12 June 1999, *Ficus carica* branch, M. Beeche (2, SAGC); Región I, Quebrada de Chaca, *Ficus*, 2001, M. Beeche (8, LRKC); Región XV, Arica, Azapa, 28 February 2001, *Ficus*, SAGC (2, SAGC); Región V, Valparaíso, Arch. Juan Fernandez, Masatierra, Cerro Centinela, 23 April 2004, deforested area, H. Gonzalez (1, SAGC); Región III, Atacama, Copiapó, 4 February 2011, *Ficus*, R. Vieyra (1, SAGC); Región III, Atacama, Vallenar, 10 August 2011, blacklight, V. Zlater (1, SAGC); Región RM, Santiago, Rinconada de Maipu, 11 October 2011, J. Mondaca (1, SAGC). PERU, Lima, Lima, 18 February 1999 (1, SAGC).

Comments. The holotype of *Phloeotribus willei* Schedl is from Lima, Peru, while the holotype of the junior synonym *Ph. chiliensis* Eggers was collected from Valparaíso, Chile [27]. Specimens examined by Wood [25] are from Lima, Peru, and from regions I (Tarapacá) and V (Valparaíso) in Chile. The only host specified is *Ficus* (1 record). Schedl [24] reports two interesting early collections from *Ficus carica* twigs by Willy Kuschel, one from Masatierra, the Juan Fernández Islands [23], the other from Región XV (Arica and Parinacota) in the far north in 1948. The earliest record is a country record, "Chile, C. E. Porter, 1912" [27].

This species has been considered a native species in Chile. There are few collections and the known localities seem to be disjunct (Lima, northern Chile, central Chile, Juan Fernandez Islands). On the other hand, bark beetles in western Peru and coastal Chile are undercollected. Notably, the only host recorded is an introduced species, the cultivated edible fig *Ficus carica*; the beetle has been collected multiple times from this tree, in both countries, and from no other hosts. There are no native *Ficus* in coastal Chile. The fact that the species has only been found in disjunct localities and only in an introduced host species argues that it is an exotic species in Chile and possibly in western Peru as well. If so, the most likely origin is the Neotropics; there are several Neotropical species which are similar in appearance [25]. If it is non-native, then since it is clearly well adapted to arid and semiarid climates, it should be looked for in woody Moraceae (*Brosimum*, *Ficus*, etc.) in drier forest ecosystems in the Americas.

Identification. The key and description in Wood [25] are useful. This is the only *Phloeotribus* species known from Chile. Curiously, no *Phloeotribus* are known from drier regions of Argentina.

Risks. None known, but the biology of *Ph. willei* has not been investigated.

3.1.9. The Clover Root Borer, *Hylastinus obscurus* (Marsham)

New records. **CHILE**: S. Barbara, 29 April 1986, trifolium rosada [*Trifolium pratense*], leg. R. Arce (1, UCCC); Región X, Rio Bueno, 15 April 1991, Trifolium rosada, leg. SAGC X (SAGC 5, LRKC 3); Reg. Bio-Bio [VIII], Nacimiento, CMPC STA.FE, 10 October 2008, M. Beeche.

Comments. *Hylastinus obscurus* is native to Europe and North Africa but is a widespread invasive species in North America. Elgueta and Marvaldi [26] give the range as Talca to Llanquihue (Región VII–Región X). Wood [25] gives records for Araucanía (IX) that are probably from MNNC.

Identification. Can be keyed out in standard works; excellent photos can be found on a variety of websites.

Risks. As an invasive species to North America and Chile, it is a serious pest of the important forage crop red clover *Trifolium pratense* [78–81]. In Chile, it is considered the main cause of *T. pratense* decline, and pesticides have not been able to control it [81]. In its native range, it breeds primarily in woody legumes [29].

3.2. Ambrosia Beetles

3.2.1. First Chilean Record of *Amasa truncata* (Erichson) in Chile, an Ambrosia Beetle Breeding in Eucalyptus and Relatives

New records: **CHILE**: Valparaíso, Villa Alemana, Fundo Lo Moscoso, funnel trap, 25 February 2016, O. Ibaceta, 24143/11 (1, SAGC); Same locality, collected from *Eucalyptus* and funnel trap, 21 March 2017 (details from Margarita Peralta of SAG, pers. comm.). Valparaíso, Limache, funnel traps, 2016 and 2017 (information from owner, via Sergio Rothmann of SAG, pers. comm.). Valparaíso, Los Andes, funnel traps, 2018 (Rothmann, pers. comm.).

Comments: These traps were in *Eucalyptus* plantations. The traps at Fundo Lo Moscoso and Limache are ca 12 km apart. Los Andes is a town near the Andes mountain range, elevation ca 800 m, about 90 km west of Limache. This is the easternmost and highest locality for *A. truncata* in Chile.

The biology of *A. truncata* is reviewed in [82,83]. Known as the Keyhole Ambrosia Beetle because of the shape of the egg tunnel, this distinctive Australian species is only the second non-native ambrosia beetle to be collected from Chile. The species has recently invaded Brazil, the first land to be colonized other than New Zealand [82]. It was collected in late 2015 in northeast Uruguay [84] in mixed *Eucalyptus* plantations that had been monitored since 2012. Funnel trap collections made over two years from two localities 12 km apart in Valparaíso province indicate the presence of at least one established population in Chile. In Brazil, the species is clearly established but has thus far only been collected from traps in *Eucalyptus* plantations, as in Uruguay. It does not seem to have spread significantly from the sites from which it was first reported (Flechtmann pers. comm., October 2017; [84]). In Australia, *A. truncata* normally breeds in *Eucalyptus* and a few other Myrtaceae, but the species has been collected breeding in *Acacia* and *Albizia* (Fabaceae) in New Zealand, a country in which the species has been present since at least the 1930s [83].

Identification: In southern South America, photos are sufficient to identify this *Amasa*; the best photo is in [84]. There are no similar ambrosia beetle species in these temperate regions of South America (or indeed in the Neotropics).

Risks: *Amasa* could become a pest of *Eucalyptus* plantations in Chile and Argentina, and Gómez et al. [84] worry that it could move onto native Myrtaceae. However, though the species attacks stressed and even healthy live trees, it is not considered a pest of *Eucalyptus* in Australia or New Zealand [82,83], and no significant damage has been reported from the recently established populations in Brazil or Uruguay (C. Flechtmann, pers. comm., October 2017; [84]).

3.2.2. The Earliest Collections of *Xylosandrus crassiusculus* (Motschulsky) in South America, and a Second Province in Argentina.

New records: **ARGENTINA**, Misiones, Corpus, February 2001, leg. D. Carpintero (14 specimens); Misiones, Corpus, February 2001 (1); Misiones, Corpus, November 2003 (1).

Comments: The Granulate Ambrosia Beetle, *Xylosandrus crassiusculus*, has spread in recent times from Asia to warmer regions of Africa, Europe, Oceania, and the Americas [85,86]. This highly polyphagous ambrosia beetle was first reported from eastern North America in 1974, and the first Neotropical collections were from 1996 for Costa Rica and 2003 for Panama [85]. Flechtmann and Atkinson [86] subsequently found a specimen collected from Guatemala in 2008 and report collections from French Guiana (2009) and coastal Brazil (2008–2014).

The three collections from Misiones are the third report of the Granulate Ambrosia Beetle in Argentina. The first report comprises two collections in 2013 from Campana, Buenos Aires [87]. Most recently, Córdoba and Atkinson [76] add Famaillá, Tucumán, in 2016. The Misiones collections predate by a decade the earliest trap records from coastal Brazil. The first collection in Uruguay is from 2010 [87]. Given the long-term trapping programs in Brazilian and Uruguayan forest plantations, the species was likely absent from Brazil at the time the Argentinian specimens were collected. This suggests that either there may have been an initial introduction of *X. crassiusculus* to Argentina, and the species then moved up the coast into Uruguay and Brazil, or that one or more subsequent introductions produced the current distribution.

Identification: This ambrosia beetle can be identified from descriptions and careful comparison with photos [87,88]. It can also be identified by DNA barcoding [87].

Risks: *Xylosandrus crassiusculus* is on the EPPO Alert List [89] and considered a high risk quarantine pest by CABI [90]. It can be a pest of nurseries or stressed young trees in natural forests, and colonization of stacked lumber can produce economic loss [88,90]. Occasional attacks on apparently healthy small trees have been reported [88,90].

3.2.3. Range Expansions for *Xyleborinus saxeseni* (Ratzeburg) in Chile and Argentina.

New Records. **CHILE:** [Región VI] San Fernando, Nov. 1978, trunk of apple, R. Charlin (3, UCCC) [Región VI] San Fernando, 4–10 December 1978, trunk of apple, R. Charlin (1, UCCC); Región X, Santo Domingo, Valdivia, 5 October 1980, E. Krahmer (11, UCCC); Región X, Valdivia, 21 October 1984 (3, UCCC); Región VII, Curicó, 20 km E Portrero Grande, *Nothofagus dombeyi*, 153963, 25 February 2004, J. E. Barriga (5, LRKC). **ARGENTINA**: Chubut, −42.0361, −71.5456, 29 December 2010, ex *P. contorta*.

Comments. This widespread invasive ambrosia beetle has been recorded from Paraguay, Brazil, Argentina, and Chile in South America. There are no Chilean localities given by Wood [25] and only two in Schedl's review [27] (under *Xyleborus paraguayensis* Schedl): for a specimen from Bio-Bio in 1950, the earliest date for the species, and for a specimen from Valdivia in 1962 (as *Xyleborus saxeseni*). In [26], the range is given as from Atacama (III) Los Rios (XIV), and [33] extends the southern limits of the range to Los Lagos (X).

Previous Argentina records (Buenos Aires, Entre Rios) are from subtropical provinces in the north, including new finds in Tucumán and Salta [76]. The earliest record seems to be a collection by Bosq from Entre Rios in 1920 [91]. The Chubut collection reported here is the much further south, and in a cold temperate climate.

Identification. The species can be identified by keys and photos in the standard works.

Risks. This ambrosia beetle is native to Eurasia and North Africa but is cosmopolitan in distribution [92]. It is highly polyphagous, breeding in many families of both gymnosperms and angiosperms. CABI [88] rates it a "high-risk quarantine pest," but, where it is an established exotic species, it is not currently thought to cause significant problems for native or crop forests.

3.3. Seed Beetles

3.3.1. First Record of the Palm Seed Specialist *Dactylotrypes longicollis* (Wollaston) in South America

New records. **CHILE**: R. M. Colina, Fdo. San Miguel, ex *Phoenix canar*., 09 December 2016, leg. R. Cabrera, 65952/16 (5 on one pin, LRKC); R. M. Colina, Reg. Artilleria Antiaerea, funnel trap 10 May 2016 R. Cabrera (22, 5 each on three pins and 7 in a gelatin capsule, SAGC).

Comments. The monotypic *Dactylotrypes longicollis* (tribe Dryocoetini) coevolved with the Canary Island date palm (*Phoenix canariensis*), both of which are endemic to the Canary Islands. In recent decades, *D. longicollis* has rapidly expanded its range to include Madeira, the Mediterranean, and northern Africa [7]. It was found very recently in California in western North America [93]. It is often found in the same localities as one or the other of two other seed predators, *Coccotrypes carpophagus* (Hornung) and *C. dactyliperda* (F.), which species are now circumtropical in their distribution. In Chile, the two collections of *D. longicollis* are from the town of Colina, ca 30 km N of Santiago. *Dactylotrypes longicollis* seems to be common in this one town, but it is likely more widespread since fallen date seeds are often overlooked by general collectors. The colonization is probably recent: Schedl was familiar with this species but does not list it in his Chile papers, there are no specimens in the Museo Nacional de Historia Natural, and those at SAG are from 2016. No other records have been published for South America for *D. longicollis*. Given the secretive habits of the species, this could be due to undercollecting.

Identification. The description, key and photos in [89] will help separate *D. longicollis* from species of *Coccotrypes* or of superficially similar scolytines.

Risks. This species primarily breeds in seeds of palm trees (Arecaceae) and thrives in urban areas with planted palms. It is a potential predator of seeds of the narrowly distributed endemic Chilean wine palm (*Jubaea chilensis*) and hence could hamper local attempts at reforestation.

3.3.2. Range Expansion for *Coccotrypes dactyliperda* (Fabricius)

New records. **CHILE**: Región Metropolitana, Santiago, SAGC funnel trap, March 2002, J. Mondaca (1 female, SAGC); 12078/04, Santiago, Zool. Metrop. 15–IV–2004, leg. J. Mondaca (1 female, LRKC); Región Metropolitana, Santiago, Museo Nacional de Historia Natural, seed *Phoenix canariensis*, 25 March 2008, L. R. Kirkendall (1, LRKC).

Comments. This date seed specialist is known from tropical and subtropical regions around the world. Wood [25] cites unspecified country records for Chile and Argentina, unaware that more specific data existed at the time. For Chile, Schedl [27] summarizes his previously published records: "Chile" (no more exact locality information), ex *Chamaerops gracilis* in 1915, and Antofagasta [Región II] in 1942. Elgueta and Marvaldi [26] summarize the range as Antofagasta to Valparaíso; the new records here for the metropolitan region extend the known range further south.

Bosq [65] lists Buenos Aires (Isla Martín García) for the species, without more data, and states that the species is established. Schedl [35] reports collections in 1950 of *C. dactyliperda* from both Buenos Aires and Entre Rios in Argentina.

Though rare in collections, it would appear that the species is widely (if perhaps discontinuously) distributed in southern South America and has been in this part of the continent for over a century.

Identification: Most species of *Coccotrypes* cannot be identified by nonspecialists, other than by DNA barcoding.

Risks. See *Dactylotrypes longicollis*.

3.3.3. New Regions and New Hosts for the Lauraceae Seed Specialist *Pagiocerus frontalis* (Fabricius) in Chile

New records. **CHILE**: Región III, Copiapó, Aug. 1998, ex *Persea americana* (avocado), H. Carrillo (1, LRKC). Región Metropolitana, Santiago, Providencia, Plaza La Alcadesa, ex. "belloto del norte" [*Beilschmiedia meirsii*, Lauraceae], 5 June 2008, H. Carrillo (4, SAGC).

Comments. Gómez and Aguilera [94] report that the species was only found in Región I and had only been found in maize. Wood [25] has one Chile record: [Región I] Valle [de] Lluta, Arica, Prov. Tarapacá, XI–1996, J. Jimenez. Elgueta and Marvaldi [26] report only Arica. Only a country record is reported for Argentina in Wood [25], but Córdoba and Atkinson [76] have a record from Tucumán in the north, which is probably part of the natural range of the species.

Pagiocerus frontalis is the only widespread species in its genus. The other four species are known only from southern Brazil [25]. In nature, this species has been found most often in large seeds of tropical and subtropical Lauraceae (*Persea*, *Nectandra*, *Ocotea*) [45]. *Pagiocerus frontalis* is known to breed in seeds of commercial avocados [95,96] and is considered the main pest of stored maize in the Andes [97–99]. It has spread (or been spread) widely, obscuring traces of its original distribution. The specimens from Chile are probably not native. There are no collections from Lauraceae in native forests of Chile or from bordering Argentinian Patagonia. The one collection from a native host was from a planted tree in the capital city of Santiago. The closest collection to these is from subtropical forests of northern Argentina (Tucumán), where natural hosts occur. For these reasons, I treat it as an exotic species for Chile. The three Chilean localities are well separated (the Arica site is near the border with Peru), suggesting that the species is well established in the country. The only Argentinian locality known is from a recent collection from Tucumán [76], which is presumably part of its native range. Bosq [65] remarks on collections made from maize imported from Peru, but states that the species is not established in nature, a conclusion cited without further comment by Viana [37].

Identification. The species can be identified using keys and photos in the standard works.

Risks. Importantly, the Chilean specimens from Providencia are from "belloto del norte," *Beilschmiedia miersii*, a native lauraceous tree from central Chile, indicating that *P. frontalis* could potentially become a seed predator in native forests.

3.3.4. *Coccotrypes cyperi* (Beeson) Recorded from Easter Island

New record. Valparaíso, Easter Island, October 2009, trampa tablero (1 female, SAGC)

Comments. This polyphagous *Coccotrypes* is widely distributed in tropical and subtropical environments around the world, and breeds in everything from seeds and twigs to under bark of branches. It has not yet been identified from all suitable New World regions [100], but this is most likely due to undercollecting. It is to be expected to eventually colonize at least northern Argentina and perhaps northern or central Chile. The only record for these countries thus far is Easter Island.

Identification: Most species of *Coccotrypes* cannot be identified by nonspecialists, other than by DNA barcoding.

Risks. None known.

3.4. Species Not Included

3.4.1. *Scolytus kirschii* Skalitzky

This small Eurasian elm bark beetle is known from southern Brazil [25]. The record for Argentina is said to be an "oral report, not confirmed" [25]. A single specimen was collected by Vicky Klasmer from Rio Negro province, near El Bolsón, in 2008, but the collection record states it was collected from *Pinus radiata*. The identification as *S. kirschii* was by Lee Humble in 2010 (Vicky Klasmer, pers. comm.). Given that the differences among similar *Scolytus* species are very slight, this identification should be confirmed by an expert. However, the specimen could not be located. Further, it was recorded as being collected from a non-host and in a region with no elm trees (Vicky Klasmer, pers. comm.). Regardless, being only a single specimen, if it is not one of the currently established *Scolytus* species, it is possible that it represents a failed invasion. The species can vector the fungus responsible for Dutch Elm Disease and is considered a threat to elms both in parts of its native range and where it is invasive [101].

3.4.2. *Pityokteines curvidens* (Germar)

Though listed in Wood and Bright [45] and earlier works as occurring in Argentina, there are no modern records that confirm the presence of this tiny spruce bark beetle in South America, and it is not included in Wood's monograph of the bark beetles of South America [25]. There are no native spruces in Argentina.

3.4.3. *Coccotrypes robustus* (Eichhoff)

In NHMW, there is an old specimen of this species labeled Chile (identification confirmed by me), with no further data.

3.4.4. *Hypothenemus hampei* (Ferrari)

There is a single record of the coffee berry borer from Isla Martín García, Buenos Aires, Argentina [72] (as *Stephanoderes glabellus* Schedl). However, Argentina is not a coffee-producing country (https://www.indexmundi.com/agriculture/?country=ar&commodity=green-coffee&graph=production), and there have been no further reports of *H. hampei* from Argentina. It is likely this was either a misidentification or an interception.

4. Discussion

The native bark beetle fauna of South America is indisputably undercollected [25,76,102,103], and the finds reported here suggest that the exotic bark beetle fauna, too, is poorly known. It is probable that the rate of establishment of non-native scolytines is increasing for this part of the continent, just as it is for North America [9] and Europe [7,8]. We can also conclude (if cautiously) that the ranges of many of the introductions are increasing or have reached the distributional limits of their hosts. Many or most of the species listed here seem most likely to have come directly from Europe, though some may have come from other South American populations (e.g., *Amasa truncatus*) or from almost anywhere with an appropriate climate (*Coccotrypes dactyliperda*).

Three guilds of bark beetles are represented in the exotic faunas of Chile and Argentina, bark beetles, ambrosia beetles, and seed feeders. These have probably followed three well-known pathways for invasive insects: wood (dunnage, crating, timber); infested imported plants or plant parts; and commodities, such as dried maize for *P. frontalis* [104]. Species breeding in hosts such as pines, *Eucalyptus*, stone fruit trees, or avocado find large monocultures of their host plants in Chile and Argentina, many of which are close to ports or nurseries. Species breeding in hosts that are widely planted in temperate cities (such as figs, ornamental olives, ornamental fruit trees, ashes, elms, or palms) also find many potential hosts near ports of entry. On the other hand, those requiring dead plant tissues (such as dead branches or tree trunks) will find little host material in well-tended cities and towns.

The historical misidentification of *Orthotomicus laricis* as *O. erosus* has repercussions for the risk assessment of Chilean timber exports. Although the general biology of the two species may be similar, we simply do not know in what ways the species do differ. There might (or might not) be significant differences in the effects of fungi and other microbes associated with *O. laricis* vs *O. erosus*, for example. Since *O. laricis* has not been considered an aggressive species in Europe and only recently has been recognized as an alien species, there is little detailed knowledge of its ecology and behavior.

The detection of alien species is directly correlated with the intensity of monitoring [11,104]. There is currently little research being done on bark beetles in most parts of South America, but where systematic investigation (especially trapping) has been initiated, new invasive species have been quickly detected [47,86,87,105]. Documenting the future spread of potentially destructive non-native scolytines will require effective monitoring strategies and the collaboration of taxonomic specialists.

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References

1. Wood, S.L. Introduced and exported American Scolytidae (Coleoptera). *Great Basin Nat.* **1977**, *37*, 67–74.
2. Haack, R.A. Intercepted Scolytidae (Coleoptera) at U.S. ports of entry: 1985–2000. *Integr. Pest Manag. Rev.* **2001**, *6*, 253–282. [CrossRef]
3. Haack, R.A. Exotic bark- and wood-boring Coleoptera in the United States: Recent establishments and interceptions. *Can. J. For. Res.* **2006**, *36*, 269–288. [CrossRef]
4. Kühnholz, S.; Borden, J.H.; Uzunovic, A. Secondary ambrosia beetles in apparently healthy trees: Adaptations, potential causes and suggested research. *Integr. Pest Manag. Rev.* **2001**, *6*, 209–219. [CrossRef]
5. Brockerhoff, E.G.; Bain, J.; Kimberley, M.; Knizek, M. Interception frequency of exotic bark and ambrosia beetles (Coleoptera: Scolytinae) and relationship with establishment in New Zealand and worldwide. *Can. J. For. Res.* **2006**, *36*, 289–298. [CrossRef]
6. Lee, C.E.; Remfert, J.L.; Chang, Y.-M. Response to selection and evolvability of invasive populations. *Genetica* **2007**, *129*, 179–192. [CrossRef] [PubMed]
7. Kirkendall, L.R.; Faccoli, M. Bark beetles and pinhole borers (Curculionidae, Scolytinae, Platypodinae) alien to Europe. *Zookeys* **2010**, *56*, 227–251. [CrossRef] [PubMed]
8. Sauvard, D.; Branco, M.; Faccoli, M.; Lakatos, F.; Kirkendall, L.R. Weevils and bark beetles (Coleoptera: Curculionoidea). Chapter 8.2. *BioRisk* **2010**, *4*, 219–266. [CrossRef]
9. Haack, R.; Rabaglia, R. Exotic bark and ambrosia beetles in the USA: Potential and current invaders. In *Potential Invasive Pests of Agricultural Crops*; Peña, J.E., Ed.; CAB International: Wallingford, UK, 2013; pp. 48–74.
10. Vega, F.E.; Hofstetter, R.W. *Bark Beetles, Biology and Ecology of Native and Invasive Species*; Elsevier: San Diego, CA, USA, 2015; Volume XIX, 620p.
11. Rassati, D.; Faccoli, M.; Haack, R.A.; Rabaglia, R.J.; Toffolo, E.P.; Battisti, A.; Marini, L. Bark and ambrosia beetles show different invasion patterns in the USA. *PLoS ONE* **2016**, *11*. [CrossRef] [PubMed]
12. Lantschner, M.V.; Atkinson, T.H.; Corley, J.C.; Liebhold, A.M. Predicting North American Scolytinae invasions in the Southern Hemisphere. *Ecol. Appl.* **2017**, *27*, 66–77. [CrossRef] [PubMed]
13. Dukes, J.S.; Mooney, H.A. Does global change increase the success of biological invaders? *Trends Ecol. Evol.* **1999**, *14*, 135–139. [CrossRef]
14. Huang, D.; Haack, R.A.; Zhang, R. Does global warming increase establishment rates of invasive alien species? A centurial time series analysis. *PLoS ONE* **2011**, *6*. [CrossRef] [PubMed]
15. Hulcr, J.; Dunn, R.R. The sudden emergence of pathogenicity in insect-fungus symbioses threatens naive forest ecosystems. *Proc. R. Soc. Lond. B Biol. Sci.* **2011**, *278*, 2866–2873. [CrossRef] [PubMed]
16. Ploetz, R.C.; Hulcr, J.; Wingfield, M.J.; de Beer, Z.W. Destructive tree diseases associated with ambrosia and bark beetles: Black swan events in tree pathology? *Plant Dis.* **2013**, *97*, 856–872. [CrossRef]
17. Brockerhoff, E.G.; Jones, D.C.; Kimberley, M.O.; Suckling, D.M.; Donaldson, T. Nationwide survey for invasive wood-boring and bark beetles (Coleoptera) using traps baited with pheromones and kairomones. *For. Ecol. Manag.* **2006**, *228*, 234–240. [CrossRef]

18. Cognato, A.I.; Barc, N.; Philip, M.; Mech, R.; Smith, A.D.; Galbraith, E.; Storer, A.J.; Kirkendall, L.R. The native and introduced bark and ambrosia beetles of Michigan (Coleoptera: Curculionidae, Scolytinae). *Great Lakes Entomol.* **2009**, *42*, 101–120.
19. Kuschel, G. Foreign Curculionoidea established in New Zealand (Insecta: Coleoptera). *N. Z. J. Sci.* **1972**, *15*, 273–289.
20. Brown, S.; Oberprieler, R.G.; Leschen, R.A.B.; Crosby, T.K. Guillermo (Willy) Kuschel (13 July 1918–1 August 2017). *N. Z. Entomol.* **2017**, *40*, 92–97. [CrossRef]
21. Kuschel, G. La fauna curculiónica (Coleoptera: Curculionoidea) de la *Araucaria araucana*. *Rev. Chil. Entomol.* **2000**, *27*, 41–50.
22. Kuschel, G. *Beetles in a Suburban Environment: A New Zealand Case Study. The Identity and Status of Coleoptera in the Natural and Modified Habitats of Lynfield, Auckland (1974–1989)*; DSIR Plant Protection Report; CABI: Wallingford, UK, 1990; Volume 3, 118p.
23. Schedl, K.E. Chilenische Borkenkäfer I. (Coleoptera Scolytoidea) 114. Beitrag zur Morphologie und Systematik der Scolytoidea. *Rev. Chil. Entomol.* **1951**, *1*, 15–22.
24. Schedl, K.E. Chilenische Borkenkäfer II (Coleoptera Scolytidae) 140. Beitrag zur Morphologie und Systematik der Scolytoidea. *Rev. Chil. Entomol.* **1955**, *4*, 255–259.
25. Wood, S.L. *The Bark and Ambrosia Beetles of South America (Coleoptera, Scolytidae)*; Monte, L., Ed.; Bean Life Science Museum, Brigham Young University: Provo, Utah, 2007; 230 plates; 900p.
26. Elgueta, M.; Marvaldi, A.E. Lista sistemática de las especies de Curculionoidea (Insecta: Coleoptera) presentes en Chile, con su sinonimia. *Bol. Mus. Natl. Hist. Nat. Chile* **2006**, *55*, 113–153.
27. Schedl, K.E. Die borkenkäfer von Chile. 264 Beitrag. *Mitt. Münchener Entomol. Ges.* **1972**, *62*, 129–153.
28. Wood, S.L. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Nat. Mem.* **1982**, *6*, 1–1359.
29. Balachowsky, A. *Coléoptères Scolytidae. Faune de France 50*; Libraire de la Faculte des Sciences: Paris, France, 1949; 320p. Available online: https://faunedefrance.org/bibliotheque/docs/A.BALACHOWSKY(FdeFr50)Col.Scolytides.pdf (accessed on 24 May 2018).
30. Grüne, S. *Brief Illustrated Key to European Bark Beetles*; M. & H. Schaper: Hannover, Germany, 1979; 182p.
31. de Errasti, A.; Pildain, M.B.; Rajchenberg, M. Ophiostomatoid fungi isolated from three different pine species in Argentinian Patagonia. *For. Pathol.* **2017**. [CrossRef]
32. Ciesla, W.M. Pine bark beetles: A new pest management challenge for Chilean foresters. *J. For.* **1988**, *86*, 27–31.
33. Lanfranco, D.; Ide, S.; Ruiz, C.; Peredo, H.; Vives, I. Escarabajos de la corteza presentes en plantaciones de *Pinus radiata* en Chile. *Bosque* **2002**, *23*, 101–109. [CrossRef]
34. Ruiz, C.; Lanfranco, D. Los escarabajos de corteza en Chile: Una revisión de la situación actual e implicancias en el comercio internacional. Bark beetles in Chile: A review of the current situation and its effects in the international trade [in Spanish with English abstract]. *Bosque* **2008**, *29*, 109–114. [CrossRef]
35. Schedl, K.E. Neotropische Scolytoidea VIII. 238. Betrag zur Morphologie und Systematik der Scolytoidea. *Entomologische Arbeiten aus dem Museum G. Frey Tutzing Bei Muenchen* **1966**, *17*, 74–128.
36. Schedl, K.E. Zur Borkenkaferfauna von Chile. 344. Beitrag zur Morphologie und Systematik der Scolytoidea. *Entomologische Blaetter fuer Biologie und Systematik der Kaefer* **1980**, *75*, 159–162.
37. Viana, M.J. Datos ecologicos de Scolytidae Argentinos (Coleoptera). *Rev. Soc. Entomol. Argent.* **1965**, *27*, 119–130.
38. *Orthotomicus erosus* (Mediterranean Pine Beetle). Available online: https://www.cabi.org/isc/datasheet/37954 (accessed on 10 Feburary 2018).
39. Seybold, S.J.; Penrose, R.L.; Graves, A.D. Invasive bark and ambrosia beetles in California Mediterranean forest ecosystems. In *Insects and Diseases in Mediterranean Forest Systems*; Paine, T.D., Lieutier, F., Eds.; Springer: Cham, Switzerland, 2016; pp. 583–662.
40. Estay, S.A. Invasive insects in the Mediterranean forests of Chile. In *Insects and Diseases of Mediterranean Forest Systems*; Paine, T.D., Lieutier, F., Eds.; Springer: Cham, Switzerland, 2016; pp. 379–396.
41. Lee, J.C.; Haack, R.A.; Negron, J.F.; Witcosky, J.J.; Seybold, S.J. *Invasive Bark Beetles*; Forest Insect and Disease Leaflet, No. 176; US Department of Agriculture, US Forest Service: Washington, DC, USA, 2007.
42. Food and Agriculture Organization (FAO). *Global Review of Forest Pests and Diseases*; FAO: Roma, Italy, 2005; Volume 156, pp. vii–222.

43. Lanfranco, D.; Ide, S.; Peredo, H. An analysis of health risk reduction in Chilean primary forest products for export. *Forestry* **2004**, *77*, 193–203. [CrossRef]
44. Koch, C.K.; Waterhouse, D.F. *The Distribution and Importance of Arthropods Associated with Agriculture and Forestry in Chile (Distribución e Importancia de los Artrópodos Asociados a la Agricultura y Silvicultura en Chile)*; Australian Centre for International Agricultural Research: Canberra, Australia, 2000; 234p.
45. Wood, S.L.; Bright, D.E. A Catalog of Scolytidae and Platypodidae (Coleoptera), Part 2: Taxonomic Index. *Great Basin Nat. Mem.* **1992**, *13*, 1–1553.
46. Tiranti, S.I. Observaciones sobre los escolítidos de los pinos en la Patagonia andina, con el primer registro del género *Orthotomicus* para Argentina [Observations on scolytids from pines in Andean Patagonia, with the first record of the genus *Orthotomicus* for Argentina]. *Boletin de Sanidad Vegetal Plagas* **2010**, *36*, 87–90.
47. Gómez, D.; Martínez, G. Bark beetles in pine tree plantations in Uruguay: First record of *Orthotomicus erosus* Wollaston (Coleoptera: Curculionidae: Scolytinae). *Coleopt. Bull.* **2013**, *67*, 470–472. [CrossRef]
48. Mausel, D.L.; Gara, R.I.; Lanfranco, D.; Ruiz, C.; Ide, S.; Azat, R. The introduced bark beetles *Hylurgus ligniperda* and *Hylastes ater* (Coleoptera: Scolytidae) in Chile: Seasonal flight and effect of *Pinus radiata* log placement on colonization. *Can. J. For. Res.* **2007**, *37*, 156–169. [CrossRef]
49. Pasek, J.E.; Burdsall, H.H.; Cavey, J.F.; Eglitis, A. Draft Report: Pest Risk Assessment for Importation of Solid Wood Packing Materials into the United States. 2000, Volume xv, 275p. Available online: https://works.bepress.com/judith_pasek/23/ (accessed on 24 May 2018).
50. Food and Agriculture Organization (FAO). Overview of forest pests of Argentina. In *Forest Health and Biosecurity Working Papers*; FBS/9E; FAO: Roma, Italy, 2007; pp. iii–20.
51. Davydenko, K.; Vasaitis, R.; Meshkova, V.; Menkis, A. Fungi associated with the red-haired bark beetle, *Hylurgus ligniperda* (Coleoptera: Curculionidae) in the forest-steppe zone in eastern Ukraine. *Eur. J. Entomol.* **2014**, *111*, 561–565. [CrossRef]
52. Doychev, D.D. *Hylastes linearis* Erichson (Coleoptera: Curculionidae: Scolytinae)—First report in Bulgaria. *Silva Balc.* **2012**, *13*, 70–76.
53. Olenici, N.; Knížek, M.; Olenici, V.; Duduman, M.-L.; Biriş, I.-A. First report of three scolytid species (Coleoptera: Curculionidae, Scolytinae) in Romania. *Ann. For. Res.* **2014**, *57*, 87–95. [CrossRef]
54. Mendel, Z.; Madar, Z.; Golan, Y. Comparison of the seasonal occurrence and behavior of seven pine bark beetles (Coleoptera: Scolytidae) in Israel. *Phytoparasitica* **1985**, *13*, 21–32. [CrossRef]
55. Eichhoff, W.J. *Die Europäischen Borkenkäfer. Für Forstleute, Baumzüchter und Entomologen*; Julius Springer: Berlin, Germany, 1881; Volume viii, 315p.
56. Wichmann, H.E. Ipidae. In *Biologie der Tiere Deutschlands*; Schulze, P., Ed.; Gebrüder Bornträger: Berlin, Germany, 1927; pp. 347–381.
57. Wingfield, M.J.; Knox-Davies, P.S. Root disease, associated with *Verticicladiella alacris*, of pines in South Africa. *Plant Dis.* **1980**, *64*, 569–571. [CrossRef]
58. Reay, S.D.; Walsh, P.J.; Ram, A.; Farrell, R.L. The invasion of *Pinus radiata* seedlings by sapstain fungi, following attack by the Black Pine Bark Beetle, *Hylastes ater* (Coleoptera: Scolytidae). *For. Ecol. Manag.* **2002**, *165*, 47–56. [CrossRef]
59. Reay, S.D.; Thwaites, J.M.; Farrell, R.L.; Walsh, P.J. The role of the bark beetle, *Hylastes ater* (Coleoptera: Scolytidae), as a sapstain fungi vector to *Pinus radiata* seedlings: A crisis for the New Zealand forestry industry? *Lntegr. Pest Manag. Rev.* **2001**, *6*, 283–291. [CrossRef]
60. Gómez, C.A. *Principales Especies de Insectos Forestales en Plantaciones de Pino de la Patagonia*; Serie Técnica: Manejo Integrado de Plagas Forestales; Cuadernillo: Buenos Aires, Argentina, 2008; 12p.
61. *Hylastes ater* (Black Pine Bark Beetle). Available online: https://www.cabi.org/isc/datasheet/28047 (accessed on 3 January 2018).
62. Bevan, D. *Forest Insects: A Guide to Insects Feeding on Trees in Britain*; Forestry Commission Handbook UK; Her Majesty's Stationary Office: London, UK, 1987; 153p.
63. Neumann, F.G. Insect pest management in Australian radiata pine plantations. *Aust. For.* **1979**, *42*, 30–38. [CrossRef]
64. Milligan, R.H. *Hylastes ater (Paykull) (Coleoptera: Scolytidae) Black Pine Bark Beetle*; Forest and Timber Insects in New Zealand; Forest Research Institute, New Zealand Forest Service: Rotorua, NewZealand, 1978; pp. 1–6.
65. Bosq, J.M. Segunda lista de Coleópteros de la República Argentina, dañinos a la Agricultura. *Ing. Agron.* **1943**, *4*, 5–79.

66. Schedl, K.E. Fauna Argentinensis. VII. 136. Beitrag zur Morphologie und Systematik der Scolytoidea (Coleoptera). *Acta Zool. Liloana* **1958**, *16*, 33–46.
67. Holgado, M.G. Bioecología de *Hylesinus oleiperda* F. "taladrillo del olivo" (Coleoptera—Scolytidae) en Mendoza (Argentina). [Bioecology of *Hylesinus oleiperda* F. "olive borer" (Coleoptera—Scolytidae) in Mendoza (Argentina).] [In Spanish, with English abstract]. *Revista de la Facultad de Ciencias Agrarias UNCuyo* **2007**, *39*, 51–54.
68. Beéche, M.; Muñoz, R.S. Primer registro del escolitido del olmo, *Scolytus multistriatus* (Marsham) (Coleoptera: Scolytidae), en Chile [First record of the elm bark beetle *Scolytus multistriatus* (Marsham) (Coeloptera: Scolytidae), in Chile] (in Spanish with English abstract). *Rev. Chil. Entomol.* **1994**, *21*, 181–183.
69. Smith, S.M.; Cognato, A.I. A taxonomic monograph of Nearctic *Scolytus* Geoffroy (Coleoptera, Curculionidae, Scolytinae). *Zookeys* **2014**, *450*, 1. [CrossRef] [PubMed]
70. Johnson, P.L.; Hayes, J.L.; Rinehart, J.; Sheppard, W.S.; Smith, S.E. Characterization of two non-native invasive bark beetles, *Scolytus schevyrewi* and *Scolytus multistriatus* (Coleoptera: Curculionidae: Scolytinae). *Can. Entomol.* **2012**, *140*, 527–538. [CrossRef]
71. LaBonte, J.R. The Banded Elm Bark Beetle, *Scolytus schevyrewi* Semenov (Coleoptera, Curculionidae, Scolytinae) in North America: A taxonomic review and modifications to the Wood (1982) key to the species of *Scolytus* Geoffroy in North and Central America. *ZooKeys* **2010**, *56*, 207–218. [CrossRef] [PubMed]
72. Schedl, K.E. Fauna Argentinensis V 96. Contribution to the morphology and taxonomy of the Scolytoidea. *Acta Zool. Liloana* **1951**, *12*, 443–463.
73. Schedl, K.E. Fauna Argentinensis. III. 70a comunicación a la morfologia y sistematica de Scolytoidea (Col.). *Inst. Museo Univ. Nac. Plata Notas Museo Plata* **1939**, *4*, 407–413.
74. Schedl, K.E. Scolytidae y Platypodidae. 64a comunicación. *Inst. Museo Univ. Nac. Plata Notas Museo Plata* **1939**, *4*, 169–174.
75. Schedl, K.E. Fauna Argentinensis IX. 331. Contribution to the morphology and taxonomy of the Scolytoidea. *Acta Zool. Liloana* **1979**, *33*, 57–61.
76. Córdoba, S.; Atkinson, T.H. New Records of Scolytinae (Coleoptera: Curculionidae) from Argentina. *Coleopt. Bull.* **2018**, in press.
77. Chittenden, F.H. *The Fruit-Tree Bark-Beetle*; Second Series Circular 29; U.S. Department of Agriculture (USDA): Washington, DC, USA, 1898; pp. 1–8.
78. Webster, F.M. *The Clover Root-Borer (Hylastinus obscurus Marsham)*; U.S. Department of Agriculture (USDA): Washington, DC, USA, 1910; pp. 1–5.
79. Ortega, F.; Parra, L.; Quiroz, A. Breeding red clover for improved persistence in Chile: A review. *Crop Pasture Sci.* **2014**, *65*, 1138–1146. [CrossRef]
80. Koehler, C.S.; Gyrisco, G.G.; Newsom, L.D.; Schwardt, H.H. *Biology and Control of the Clover Root Borer, Hylastinus obscurus (Marsham)*; Cornell University Agricultural Experiment Station, New York State College of Agriculture: Ithaca, NY, USA, 1961; Volume 376, pp. 1–36.
81. Quiroz, A.; Ortega, F.; Ramirez, C.C.; Wadhams, L.J.; Pinilla, K. Response of the beetle *Hylastinus obscurus* Marsham (Coleoptera: Scolytidae) to red clover (*Trifolium pratense* L.) volatiles in a laboratory olfactometer. *Environ. Entomol.* **2005**, *34*, 690–695. [CrossRef]
82. Flechtmann, C.A.H.; Cognato, A.I. First report of *Amasa truncata* (Erichson) (Coleoptera: Curculionidae: Scolytinae) in Brazil. *Coleopt. Bull.* **2011**, *65*, 417–421. [CrossRef]
83. Zondag, R. *Xyleborus truncatus Erichson (Coeloptera: Scolytidae)*; Forest and Timber Insects in New Zealand; Forest Research Institute, New Zealand Forest Service: Rotorua, NewZealand, 1977; pp. 1–3.
84. Gómez, D.; Suárez, M.; Martínez, G. *Amasa truncata* (Erichson) (Coleoptera: Curculionidae: Scolytidae): A new exotic ambrosia beetle in Uruguay. *Coleopt. Bull.* **2017**, *71*, 825–826. [CrossRef]
85. Kirkendall, L.; Odegaard, F. Ongoing invasions of old-growth tropical forests: Establishment of three incestuous beetle species in southern Central America (Curculionidae: Scolytinae). *Zootaxa* **2007**, *1588*, 53–62.
86. Flechtmann, C.A.H.; Atkinson, T.H. First records of *Xylosandrus crassiusculus* (Motschulsky) (Coleoptera: Curculionidae: Scolytinae) from South America, with notes on its distribution and spread in the New World. *Coleopt. Bull.* **2016**, *70*, 79–83. [CrossRef]

87. Landi, L.; Gómez, D.; Braccini, C.L.; Pereyra, V.A.; Smith, S.M.; Marvaldi, A.E. Morphological and molecular identification of the invasive *Xylosandrus crassiusculus* (Coleoptera: Curculionidae: Scolytinae) and its South American range extending Into Argentina and Uruguay. *Ann. Entomol. Soc. Am.* **2017**, *110*, 344–349. [CrossRef]
88. Atkinson, T.H.; Foltz, J.L.; Wilkinson, R.C.; Mizell, R.F. *Granulate Ambrosia Beetle Xylosandrus crassiusculus (Motschulsky) (Insecta: Coleoptera: Curculionidae: Scolytinae)*; IFAS Extension, University of Florida EENY: Gainesville, FL, USA, 2010; Volume 131, pp. 1–4.
89. European and Mediterranean Plant Protection Organization (EPPO). *Xylosandrus crassiusculus (Coleoptera: Scolytidae)*; EPPO Alert List: Paris, France, 2009; pp. 1–4.
90. *Xylosandrus crassiusculus* (Asian Ambrosia Beetle). Available online: https://www.cabi.org/isc/datasheet/57235 (accessed on 5 April 2018).
91. Schedl, K.E. Scolytidae und Platypodidae 53. Beitrag. Diagnosen neuer und Fundorte bereits bekannter Argentinischer Arten. *Rev. Soc. Entomol. Argent.* **1938**, *10*, 21–28.
92. *Xyleborinus saxesenii* (Fruit-Tree Pinhole Borer). Available online: https://www.cabi.org/isc/datasheet/57038 (accessed on 10 Feburary 2018).
93. LaBonte, J.R.; Takahashi, C.Y. *Dactylotrypes longicollis* (Wollaston) (Coleoptera: Curculionidae: Scolytinae): An exotic bark beetle new to California and North America. *Pan-Pac. Entomol.* **2012**, *88*, 222–230. [CrossRef]
94. Gómez, D.L.; Aguilera, P.A. Biología de *Pagiocerus frontalis* (Fab.) (Coleoptera: Scolytidae) en la I Región de Chile. [Biology of *Pagiocerus frontalis* (Fab.) Coleoptera: Scolytidae) in region I of Chile.]. *Idesia (Chile)* **1982**, *6*, 79–92.
95. Yust, H.R. Biology and habits of *Pagiocerus fiorii* in Ecuador. *J. Econ. Entomol.* **1957**, *50*, 92–96. [CrossRef]
96. Costilla, M.A.; Coronel, N.B. El taladrillo de la semilla del palto *Pagiocerus fiorii* Eggers, 1940 (*Bostrichus frontalis* Fabricius, 1801) (Coleoptera–Scolytidae). [The borer of avocado seeds *Pagiocerus fiorii* . . .]. *Rev. Ind. Agric. Tucumán* **1994**, *71*, 63–68.
97. Yust, H.R.; Cevallos, M.A. Insecticide protection against *Pagiocerus fiorii* in Ecuador. *J. Econ. Entomol.* **1958**, *51*, 468–469. [CrossRef]
98. Gianoli, E.; Ramos, I.; Alfaro-Tapia, A.; Valdéz, Y.; Echegaray, E.R.; Yábar, E. Benefits of a maize-bean-weeds mixed cropping system in Urubamba Valley, Peruvian Andes. *Int. J. Pest Manag.* **2006**, *4*, 283–289. [CrossRef]
99. Okello, S.; Reichmuth, C.; Schulz, F.A. Observations on the biology and host specificity of *Pagiocerus frontalis* (Fabricius) (Coleoptera: Scolytidae) at 20 degrees C and 25 degrees C and 75% rh. *Z. Pflanzenkrankh. Pflanzenschutz J. Plant Dis. Prot.* **1996**, *103*, 377–382.
100. Bark and Ambrosia Beetles. Available online: http://www.barkbeetles.info/ (accessed on 6 April 2018).
101. Six, D.L.; de Beer, Z.W.; Beaver, R.A.; Wingfield, M.J. Exotic invasive elm bark beetle, *Scolytus kirschii*, detected in South Africa. *S. Afr. J. Sci.* **2005**, *101*, 229–232.
102. Smith, S.M.; Petrov, A.V.; Cognato, A.I. Beetles (Coleoptera) of Peru: A survey of the families (Curculionidae: Scolytinae). *Coleopt. Bull.* **2017**, *71*, 77–94. [CrossRef]
103. Jordal, B.H. New species and records of *Scolytodes* (Coleoptera, Curculionidae: Scolytinae) from South America. *Zootaxa* **2013**, *3721*, 529–551. [CrossRef] [PubMed]
104. Work, T.; McCullough, D.; Cavey, J.; Komsa, R. Arrival rate of nonindigenous insect species into the United States through foreign trade. *Biol. Invasions* **2005**, *7*, 323–332. [CrossRef]
105. Gomez, D.; Martinez, G.; Beaver, R.A. First record of *Cyrtogenius luteus* (Bandford) (Coleoptera: Curculionidae: Scolytinae) in the Americas and its distribution in Uruguay. *Coleopt. Bull.* **2012**, *66*, 362–364. [CrossRef]

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Article

On the Phylogenetic Position of the Weevil Tribe Acentrusini Alonso-Zarazaga, 2005 (Coleoptera: Curculionidae: Curculioninae)

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Abstract: Based on intrinsic morphological and extrinsic bionomic characters, the systematic position of the weevil tribe Acentrusini Alonso-Zarazaga, 2005 (Coleoptera: Curculionidae: Curculioninae) was determined. Maximum parsimony and Bayesian inference as well as nonmetric multi-dimensional scaling were used to analyze 34 morphological characters of adults, complemented by four host plant characters associated with particular weevil tribes. Sixteen species belonging to two subfamilies (Brachycerinae, Curculionidae) and seven tribes (Acentrusini, Anthonomini, Ellescini, Erirhinini, Smicronychini, Storeini, Styphlini) of the family Curculionidae and one outgroup species (Attelabidae) were studied. Phylogenetic and multi-dimensional analyses revealed the tribe Smicronychini as most closely related to Acentrusini. Of the tribes of Curculioninae studied, Styphlini, Anthonomini and Ellescini showed a certain degree of phylogenetic relation to Acentrusini, whereas Storeini were found to be least related.

Keywords: Coleoptera; Curculionidae; Curculioninae; Acentrusini; phylogeny

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1. Introduction

The tribe Acentrusini was described quite recently by Alonso-Zarazaga [1]. Until the description of two additional taxa [2], the tribe was monotypical and contained only *Cryptorhynchus histrio* Boheman, 1837, the type species of the genus *Acentrus*. *Acentrus histrio* (Boheman, 1837), *A. boroveci* (Košťál, 2014) and *A. zarathustra* (Košťál, 2014) are morphologically highly similar, apparently forming a monophyletic group [2]. Hence, the tribe is morphologically uniform, showing no subgeneric divergence and was characterized by Alonso-Zarazaga [1] by a body covered with densely arranged light scales; normal, horizontally movable mandibles with teeth on the inner side; antennae with seven funicular segments; eyes more close to each other on the ventral than on the dorsal part of the head; a lower rostrum margin in the lateral view directed to the middle of eye; postocular lobes on the anterior margin of the pronotum; prosternum with emargination; a precoxal distance twice as long as the metacoxal distance; ventrite 2 longer than ventrites 3–4 combined; the distance between metacoxae larger than the metacoxal width; free claws; and other, presumably apomorphic characters. The phylogenetic relation of Acentrusini has not yet been studied. Only Alsonso-Zarazaga [1] suggested a tentative hypothesis of their possible close relationship to Styphlini, without identifying any shared tribal characters. Later, some characters typical of Acentrusini, but also of other tribes, like ventrally contiguous eyes, were reported as descriptive characters without drawing phylogenetic affinities to Acentrusini [3]. The distribution of Acentrusini extends from the Iberian Peninsula and North Africa through the Mediterranean to southern Ukraine, Caucasus, the Middle East, Iran and

Turkmenistan. All known host plants belong to the family Papaveraceae. Alonso-Zarazaga [1] suspected that Acentrusini is most closely related to Styphlini, however noting the necessity of more detailed analysis of the phylogenetic relationships to this tribe.

2. Materials and Methods

2.1. Taxonomic and Morphological Methods

Sixteen weevil species from the family Curculionidae s. l., belonging to seven tribes, and one outgroup species from the family Attelabidae, tribe Rhynchitini (*Rhynchites bacchus* (Linnaeus, 1758)), were studied. Tribes of the subfamily Curculioninae from the Palaearctic region included in this study were selected based on published (Styphlini) [1] and unpublished assumed phylogenetic relationships to Acentrusini with respect to the morphological similarity to Acentrusini. Characters reported in the detailed redescription of Acentrusini as presumable apomorphies [1] were used as the tribe selection guideline. These characters include scales on the body (head and rostrum), dentation of the mandibles, the number of antennal funicle segments, the dorsal vs. ventral distance of eyes, the direction of the lower rostrum margin in relation to the eye, the presence or absence of postocular lobes and prosternal impression, the ratio of the precoxal and postcoxal distance and the medial length of ventrite 2 and ventrites 3–4 combined, and claw connation at the base [1]. As an additional important character, we consider here the venation of the hind wings. Of the 21 currently reported Palaearctic tribes of Curculioninae [4], only six meet to some extent a substantial part of the characters listed above. Those tribes that are generally not consistent with Acentrusini in most characters of higher taxonomic weight were not included. To support the validity of the phylogenetic tree, we also included three species of the subfamily Brachycerinae, tribe Erirhinini, which might remotely resemble Acentrusini in several plesiomorphies.

The taxonomy follows the latest higher taxonomical classification of Curculionoidea by Zarazaga et al. [4]. We included two subfamilies of Curculionidae, Brachycerinae Billberg, 1820 and Curculioninae Latreille, 1802, into the phylogenetic and multi-dimensional phenetic analyses. Brachycerinae were represented by the tribe Erirhinini Schoenherr, 1825, with the following species listed in alphabetical order: *Notaris scirpi* (Fabricius, 1772), *Thryogenes fiorii* Zumpt, 1928, and *T. scirrhosus* (Gyllenhal, 1835). Curculioninae were represented by the following tribes and species reported in brackets, both listed in alphabetical order: Acentrusini Alonso–Zarazaga, 2005 (*Acentrus histrio* (Boheman, 1837), *A. zarathustra* Košťál, 2014), Anthonomini C.G. Thomson, 1859 (*Anthonomus behnei* Košťál, 2014, *Bradybatus seriesetosus* Petri, 1912), Ellescini C.G. Thomson, 1859 (*Dorytomus taeniatus* (Fabricius, 1781), *Ellescus bipunctatus* (Linnaeus, 1758)), Smicronychini Seidlitz, 1891 (*Smicronyx jungermanniae* (Reich, 1797), *S. reichii* (Gyllenhal, 1835), *Sharpia* sp.), Storeini Lacordaire, 1863 (*Pachytychius hordei hordei* (Brullé, 1832), *P. sparsutus* (Olivier, 1807)), Styphlini Jekel, 1861 (*Pseudostyphlus pillumus* (Gyllenhal, 1835), *Trachystyphlus beigerae* (Smreczyński, 1975)).

We studied both sexes of well-preserved, mature adult specimens. External characters were always examined in male specimens. All measurements were made under a stereomicroscope (Intraco Micro NSZ-810) using an ocular micrometer. Dissection of genitalia was carried out in both sexes after at least 24 h incubation in a wet chamber. Male genital structures were dissected and treated for five days in 10% KOH, which was then transferred to water and observed in glycerol. Female genitalia were studied, embedded in Solakryl BMX on a transparent plastic board. The hind wings of *A. histrio* were photographed embedded in Solakryl BMX, using a high-resolution camera (Canon EOS 50D) under the stereomicroscope in transmitted light. The spiculum ventrale (female eighth sternite) was mounted on a transparent board in Solakryl BMX and photographed under a laboratory microscope (Intraco Micro LMI T PC). Multilayer pictures were processed using the software Combine ZP.

The morphologic nomenclature was used according to the latest interpretation [5], following updates of the online glossary of weevil characters proposed in the International Weevils Community Website (18 February 2018) (http:/weevil.info/glossary-weevil-characters) (accessed 14 March 2018).

The following abbreviations are used: Char. = character, n = not applicable.

2.2. Characters Used for Phylogenetic and Multi-Dimensional Phenetic Analyses

2.2.1. Morphological Characters

Morphological characters were selected *de novo* according to the aforementioned criteria and they were complemented by hind wing venation characters. The habitus of *Acentrus histrio* is shown in Figure 1.

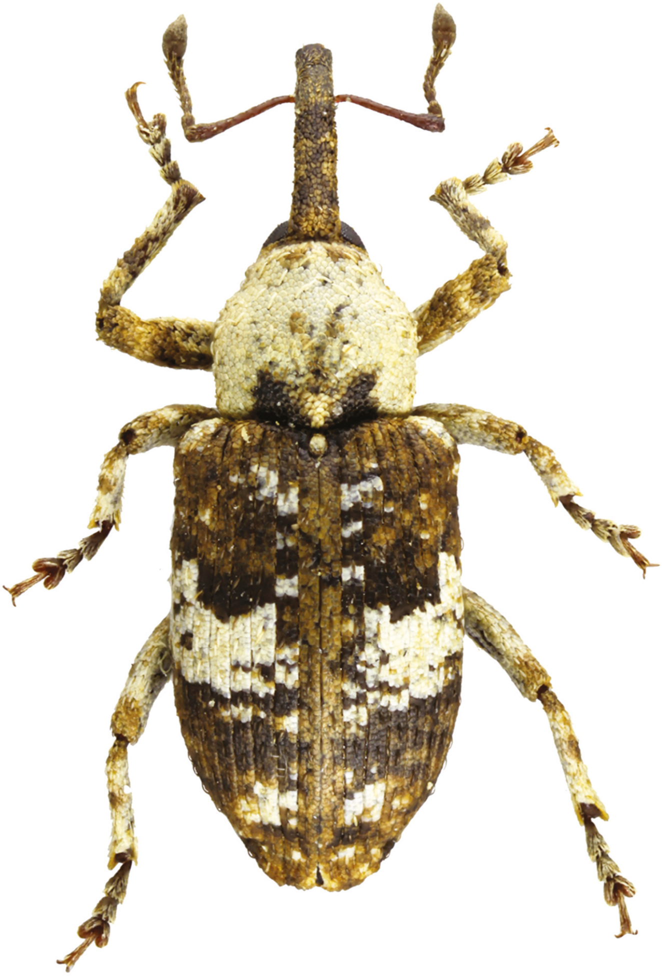

Figure 1. *Acentrus histrio*. Male. According to [2]. (Not to scale). Copyright confirmed by M. Jäch (Koleopterologische Rundschau), 30 April 2018.

Char. 1: (0) eyes small to medium large, situated exclusively on lateral part of head; (1) eyes large, situated either only on lateral part of head or also partially on dorsal part of head, or medium large situated partially on dorsal part of head.

Char. 2: (0) head between eyes broad, of more than half of rostrum width at base; (1) head between eyes narrow, of at most half of rostrum width at base.

Char. 3: (0) distance between eyes larger or equal on ventral side of head than on forehead; (1) distance between eyes smaller on ventral side of head than on forehead.

Char. 4: (0) lower rostrum margin directed to inferior part of eye or below eye; (1) lower rostrum margin directed to middle of eye.

Char. 5: (0) antennal funicle with six or less segments or not differentiated from scape; (1) antennal funicle with seven segments.

Char. 6: (0) head and rostrum base dorsally bare or sparsely to semidensely, not confluently covered with hairs or scales, integument at least partially visible; (1) head and rostrum base covered with confluently densely arranged scales fully covering integument.

Char. 7: (0) antennal segment 1 bare or sparsely covered with hairs or seta-like scales; (1) antennal segment 1, at least in distal part densely covered with shortly elongated scales.

Char. 8: (0) lateral margin of mandibles with one or more large teeth; (1) lateral margin of mandibles without or with one small tooth or tubercle.

Char. 9: (0) lateral anterior margin of pronotum without postocular lobes; (1) lateral anterior margin of pronotum with postocular lobes.

Char. 10: (0) anterior margin of prosternum with no or shallow emargination, of less than 1/3 of the medial prosternal length; (1) anterior margin of prosternum with deep emargination, of at least 1/3 of the medial prosternal length.

Char. 11: (0) prosternum in medial part without impression along its whole medial length; (1) prosternum in medial part with impression along its whole medial length.

Char. 12: (0) mesoventral process markedly longer than wide at base; (1) mesoventral process at most as long as wide at base or slightly longer.

Char. 13: (0) distance between metacoxal apices less than twice as long as distance between precoxal apices; (1) distance between metacoxal apices twice as long or more as distance between precoxal apices.

Char. 14: (0) medial length of ventrite 1 shorter or equal to medial length of ventrite 2; (1) medial length of ventrite 1 longer than medial length of ventrite 2.

Char. 15: (0) medial length of ventrite 2 shorter or of the same length as medial length of ventrites 3–4 combined; (1) medial length of ventrite 2 longer than medial length of ventrites 3–4 combined.

Char. 16: (0) claws free; (1) claws at least at base connate.

Char. 17: (0) parameres absent, rudimentary in form of tubercles, "brush-like", transformed to plates or connate in their whole length; (1) parameres present, separated or connate only in basal part.

Char. 18: (0) tegmen oval to markedly elongated, always closed; (1) tegmen round, subround or moderately elongated, closed or open [6].

Char. 19: (0) manubrium tegmeni short to medium length, at most as long as longitudinal diameter of tegmen; (1) manubrium tegmeni long, longer than longitudinal diameter of tegmen [6].

Char. 20: (0) temones longer than median lobe; (1) temones shorter or equally as long as median lobe or rudimentary [6].

Char. 21: (0) intertemonal sclerites absent; (1) intertemonal sclerites present.

Char. 22: (0) saccus internus in median lobe without sclerites or sclerotized ductus; (1) saccus internus in median lobe with sclerites or sclerotized ductus.

Char. 23: (0) spiculum ventrale without arch-like arms; (1) spiculum ventrale with two arch-like arms and developed apodeme (Figure 2).

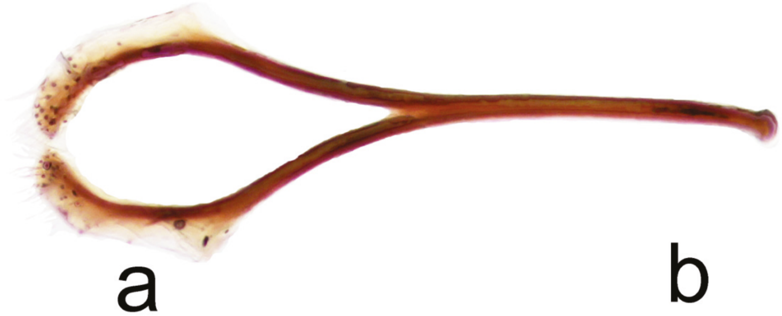

Figure 2. Spiculum ventrale (female eighth sternite) of *Acentrus histrio*. "Arch"-like arms (**a**), apodeme (**b**). (Not to scale).

Char. 24: (0) spermatheca simple, strongly sclerotized, not transparent, U-shaped, with almost undistinguishable corpus and cornu; (1) spermatheca more or less differentiated, moderately to slightly sclerotized, semi-transparent, with distinguishable corpus and cornu.

Char. 25: (0) ramus of spermatheca absent; (1) ramus of spermatheca present.

Char. 26: (0) nodulus of spermatheca present; (1) nodulus of spermatheca absent.

Char. 27: (0) cornu of spermatheca long, of more than maximal diameter of corpus; (1) cornu of spermatheca short, not longer than maximal diameter of corpus.

Char. 28: (0) hind wings absent or brachypterous; (1) hind wings fully developed.

Char. 29: (0) radial tending zone of hind wings long, of at least 0.45 wing length; (1) radial tending zone of hind wings short, of less than 0.45 wing length (Figure 3).

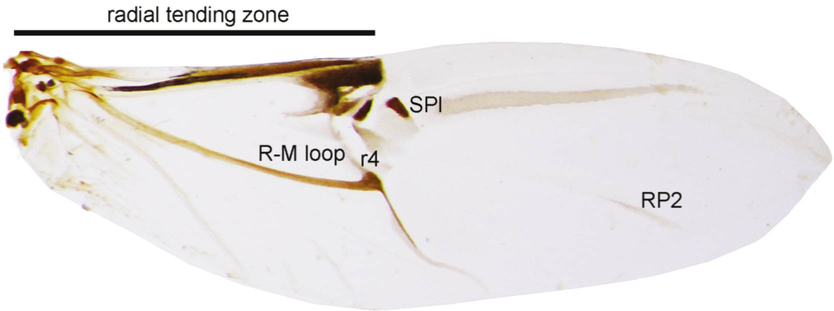

Figure 3. Hind wing of *Acentrus histrio*. Lateral sclerotized plate (SPl), radio-medial loop (R–M loop), radius posterior 2 (RP2), r4 vein (r4). (Not to scale).

Char. 30: (0) hind wings with well-developed RP2 (radius posterior); (1) hind wings with no or indistinct RP2 (Figure 3).

Char. 31: (0) radial cell (RC) of hind wings developed; (1) radial cell (RC) of hind wings absent (Figure 3).

Char. 32: (0) central field of hind wings with no or indistinct lateral sclerotized plate (SPl); (1) central field of hind wings with well-developed SPl (Figure 3).

Char. 33: (0) R–M loop of hind wings feebly visible or missing, r4 indistinct or missing; (1) R–M loop of hind wings well developed, r4 clearly visible (Figure 3).

Char. 34: (0) apical blood sinus ("pterostigma") clearly visible; (1) apical blood sinus ("pterostigma") absent or indistinct (Figure 3).

2.2.2. Host Plant Characters

Char. 35: (0) host plants not Eudicots [7]; (1) host plants Eudicots.
Char. 36: (0) host plants not Ranunculares [7]; (1) host plants Ranunculares.
Char. 37: (0) host plants Superrosids [7]; (1) host plants not Superrosids.
Char. 38: (0) host plants Superasterids [7]; (1) host plants not Superasterids.

2.3. Phylogenetic and Multi-Dimensional Phenetic Methods

Phylogenetic analyses were conducted on the data set (Table 1) comprising 34 morphological characters (characters 1–34) and four extrinsic characters concerning the host plants and their phylogenetic relationships [7]. All character states were unordered and unweighted except for characters 7, 14–16, 30, 32, 33, which were double-weighted, characters 2, 8, 11, 13, 18, 21, 23, 29, 36, which were triple-weighted and characters 1, 3, 4, 12, 17, 24, 31, which had a weight of 5. The weighting of the characters reflected their assumed taxonomic importance.

Phylogenetic trees were computed in maximum parsimony and Bayesian frameworks. The most parsimonious tree was found in PAUP* ver. 4.0b8 [8] using a heuristic search and 10 random addition species replicates. The accelerated transformation (ACCTRAN) optimization algorithm as well as the three bisection–reconnection (TBR) branch-swapping algorithm were applied. The reliability of its branching pattern was assessed using the bootstrap method with 100 replicates. Phylogenetic relationships were reconstructed also using Bayesian inference in the computer program MrBayes ver. 3.2.1 [9]. Bayesian analyses were conducted with the standard discrete evolutionary model and symmetric Dirichlet distribution for state rate variation among characters. The standard discrete model is analogous to the Jukes–Cantor evolutionary model in that any particular change from one state to another is equally probable, but has a variable number of states as it is in the one-parameter Markov k-state model. Two parallel runs with four chains were performed as part of the Markov chain Monte Carlo simulations. Posterior probabilities of the branching pattern were estimated from one million generations and trees sampled every 100 generations. The first 25% of sampled trees were discarded before constructing the 50% majority-rule consensus tree and calculating its posterior probabilities. Stationarity in the Bayesian analyses was confirmed in that the average standard deviation of the split frequencies was well below 0.01, the potential scale reduction factor approached 1, and no obvious trends were in the plots of generation vs. log probability.

The evolutionary history of all characters was reconstructed using the most parsimonious tree inferred from the matrix in Table 1 and the parsimony ancestral character state reconstruction method implemented in Mesquite ver. 3.40 [10].

The similarity of the analyzed taxa was assessed by nonmetric multi-dimensional scaling, as implemented in the scikit-learn ver. 0.19.1 package in Python [11]. When a character was not applicable to at least one taxon, it was excluded from the analysis. The SMACOF algorithm was run with 1000 initializations, each run had 20,000 iterations, and ε was set to 1×10^{-8} to declare convergence.

Table 1. Character matrix of tribes of the family Curculionidae ordered alphabetically and one outgroup species of the family Attelabidae.

Family	Subfamily	Tribe	Species	Character No.																																					
													1										2										3								
				1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Attalabidae	Rhynchitinae	Rhynchitini	*Rhynchites bacchus*	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1	1	1	0	0	1
Curculionidae	Brachycerinae	Erirhinini	*Notaris scirpi*	1	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1
Curculionidae	Brachycerinae	Erirhinini	*Thryogenes fiorii*	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	1	0	n	n	n	n	n	n	0	0	1	1
Curculionidae	Brachycerinae	Erirhinini	*Thryogenes scirrhosus*	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	1	1	1	1	0	1	1	1	1	1	0	0	1	1
Curculionidae	Curculioninae	Acentrusini	*Acentrus histrio*	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Curculionidae	Curculioninae	Acentrusini	*Acentrus zarathustra*	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Curculionidae	Curculioninae	Anthonomini	*Anthonomus behnei*	1	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	1	1	1	0	0	0	1	0	1	0	1	0	0	1	1	0	0	1	0	0	1
Curculionidae	Curculioninae	Anthonomini	*Bradybatus seriesetosus*	1	0	0	0	0	0	0	1	0	1	0	1	0	1	0	1	0	1	1	1	0	0	0	1	0	1	0	1	0	0	1	1	0	0	1	0	0	1
Curculionidae	Curculioninae	Ellescini	*Dorytomus taeniatus*	1	1	0	0	1	0	0	1	0	0	0	1	0	1	0	0	1	1	1	0	0	1	0	1	1	1	1	1	1	0	1	1	0	0	1	0	0	1
Curculionidae	Curculioninae	Ellescini	*Ellescus bipunctatus*	1	1	0	0	1	0	0	1	0	1	1	1	0	1	0	0	1	1	1	1	0	1	0	1	1	0	0	1	1	0	1	1	0	1	1	0	0	1
Curculionidae	Curculioninae	Smicronychini	*Sharpia* sp.	1	0	1	1	1	1	0	1	0	1	0	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	0	1	1	1	1	1	1	0	1	0	0	1
Curculionidae	Curculioninae	Smicronychini	*Smicronyx jungermanniae*	1	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1	1	1	1	0	1	1	1	1	1	0	1	0
Curculionidae	Curculioninae	Smicronychini	*Smicronyx reichii*	1	0	1	1	1	0	0	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	0	1	0	1	1	0	1	1	1	1	1	0	1	0
Curculionidae	Curculioninae	Storeini	*Pachytychius sparsutus*	1	0	0	0	1	0	0	1	0	1	0	0	0	1	1	0	1	1	0	1	0	0	0	1	1	1	0	1	0	1	1	1	1	0	1	0	0	1
Curculionidae	Curculioninae	Storeini	*Pachytychius hordei*	1	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0	1	1	1	1	0	0	0	1	1	0	0	0	n	n	n	n	n	n	0	0	1	1
Curculionidae	Curculioninae	Styphlini	*Trachystyphlus beigerae*	1	0	1	0	1	0	0	1	1	1	0	0	1	1	0	0	0	1	1	1	1	0	0	1	1	1	0	0	n	n	n	n	n	n	1	0	1	0
Curculionidae	Curculioninae	Styphlini	*Pseudostyphlus pillumus*	1	0	1	0	1	1	0	1	0	1	0	0	0	1	0	0	0	1	1	0	1	0	0	1	1	1	0	1	1	1	1	1	1	1	1	0	1	0

3. Results and Discussion

The weighted maximum parsimony analysis revealed only a single most parsimonious tree with a length of 161 steps, a consistency index of 0.56 and a retention index of 0.77. The 50% majority-rule consensus tree inferred by Bayesian inference had a branching pattern identical to the most parsimonious tree and therefore posterior probabilities were mapped onto it along with maximum parsimony bootstrap values (Figure 4). Morphological character changes were also mapped on the most parsimonious tree (Figure 5). Interestingly, although multi-dimensional scaling is a phenetic method based only on similarity, the results were fully consistent with clades inferred by phylogenetic techniques (Figure 6). Taking into account the results of both phylogenetic and phenetic analyses, we assumed that the similarity of the weevil tribes in terms of the studied characters also reflected their phylogenetic relatedness.

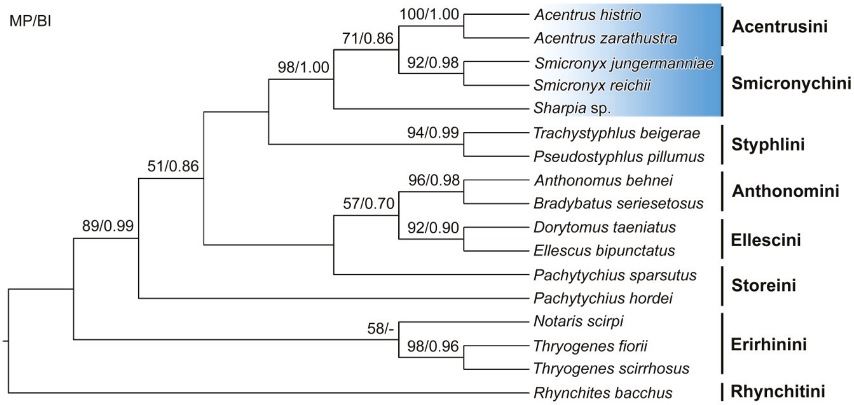

Figure 4. Weighted most parsimonious tree inferred from 38 characters of 16 species belonging to seven tribes of the family Curculionidae and one outgroup species (*Rhynchites bacchus*). The tree was constructed with the maximum parsimony method using PAUP*. Nodal supports are indicated as maximum parsimony (MP) bootstrap values in % and posterior probabilities for the Bayesian inference (BI). A dash indicates support below 0.50. Nodes without statistical support were not recognized in Bayesian and MP bootstrap analyses.

Smicronychini were recognized as the most closely phylogenetically-related tribe to Acentrusini. The monophyletic origin of the Smicronychini–Acentrusini group was supported by 98% maximum parsimony bootstrap and a posterior probability of 1.00 in the Bayesian tree (Figure 4). Likewise, Acentrusini and Smicronychini formed the most distinct cluster in the ordination diagram of nonmetric multi-dimensional scaling (Figure 6). Smicronychini, represented in this study by two species of *Smicronyx* and one species of *Sharpia*, were however depicted as a paraphyletic tribe encompassing Acentrusini in the phylogenetic trees. Specifically, *Smicronyx* was classified as a sister taxon of *Acentrus* with medium (71% bootstrap) to poor (posterior probability 0.86) statistical support (Figure 4). On the other hand, after nonmetric, multi-dimensional scaling, Smicronychini and Acentrusini each formed a homogenous group, corroborating the validity and distinctness of both tribes (Figure 6).

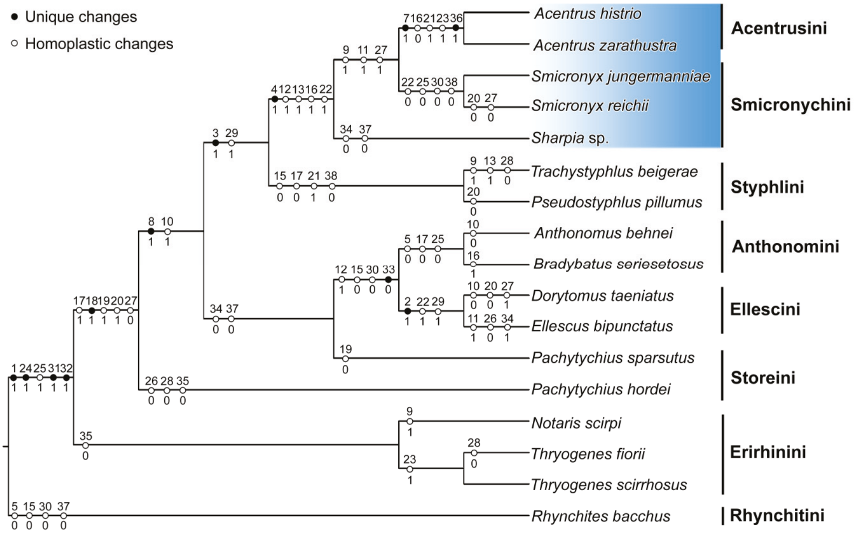

Figure 5. Evolution of character states in seven tribes of the family Curculionidae and one outgroup species (*Rhynchites bacchus*). Changes in character states were mapped on the most parsimonious tree shown in Figure 4, using the parsimony reconstruction method implemented in Mesquite. Black dots indicate unique character changes, while white dots indicate homoplastic changes.

In accordance with the current taxonomic concept, all other tribes of Curculioninae, except for Storeini, were revealed to be monophyletic, usually with strong statistical support. Thus, only the node separating members of Storeini was very poorly statistically supported (51% MP bootstrap and 0.86 posterior probability). Hence, the monophyly of *Pachytychius* species could also not be excluded. The monophyletic origin of the subfamily Curculioninae was well corroborated, while the subfamily Brachycerinae, represented here by the tribe Erirhinini, was only weakly statistically supported (58% MP bootstrap and posterior probability below 0.50) (Figure 4). The clusters recognizable in the ordination diagram were also basically consistent with and supported the current taxonomic concept (Figure 6).

The close phylogenetic relationship of Acentrusini and Styphlini proposed by Alonso-Zarazaga [1] was only partially confirmed by the present phylogenetic and multi-dimensional phenetic analyses. Similarly, the other supposedly related tribe Storeini is even less related to Acentrusini than Styphlini. Moreover, Storeini are presently regarded as a disputable tribe. Two Palaearctic genera, *Pachytychius*, included in this study, and *Aubeonymus* Jaquelin du Val, 1855, are considered genera *incertae sedis* [3]. According to the newest higher taxonomy concept, the tribe is treated as "*sensu lato*" [4]. The paraphyly of this tribe, revealed in this study (Figure 4), also reflects these doubts about the common origin of Storeini. On the other hand, the grouping of Acentrusini and Smicronychini was consistently recognized in all our analyses. Their most important apomorphy is the lower rostrum margin directed to the middle of the eye (char. 4). Styphlini is part of the clade that unites Acentrusini and Smicronychini, with a smaller ventral interocular distance (char. 3). However, the difference between the dorsal and the ventral interocular distance is not so strikingly expressed in Styphlini as it is in Acentrusini and Smicronychini. Despite the relatively small number of apomorphies in the cladogram (Figure 5), at least one apomorphy was found for almost each clade. For instance, the feebly visible R-M loop and r4 (char. 33) is synapomorphic for the tribes Anthonomini and Ellescini. The latter tribe is, in addition, characterized by an unequivocal apomorphy, with a narrow head between eyes (char. 2).

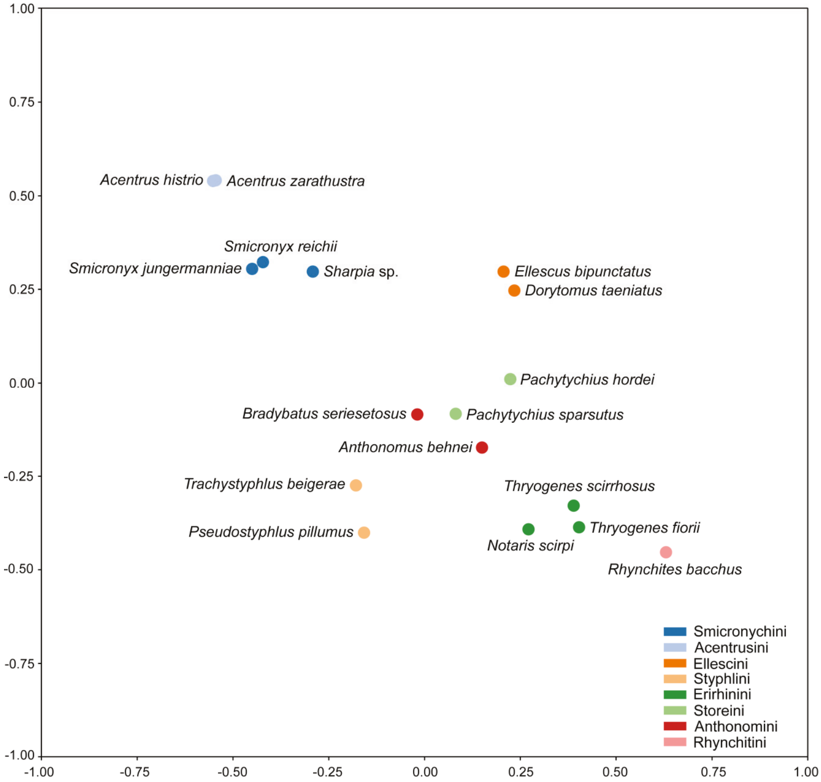

Figure 6. Nonmetric multi-dimensional scaling of 16 species belonging to seven tribes of the family Curculionidae and one outgroup species (*Rhynchites bacchus*). The ordination diagram was constructed from 32 characters, using the scikit-learn package in Python.

4. Conclusions

The weighted cladistic and multi-dimensional phenetic analyses showed that Smicronychini is the most closely related tribe to Acentrusini. On the other hand, Styphlini and Storeini were shown to be relatively unrelated to Acentrusini.

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References

1. Alonso-Zarazaga, M.A. Diagnosis preliminares de nuevos táxones de Curculionidae (Coleoptera). *Bol. SEA* **2005**, *37*, 89–93.
2. Košťál, M. Revision of the genus *Acentrus* Desmarest, 1839 (Coleoptera: Curculionidae). *Koleopt. Rdsch.* **2014**, *84*, 329–336.

3. Caldara, R.; Franz, N.M.; Oberprieler, R.G. Curculioninae Latreille, 1802: Introduction, Phylogeny. In *Handbook of Zoology Volume 3*; Leschen, R.A.B., Beutel, R.G., Eds.; Walter de Gruyter GmbH: Berlin, Germany; Boston, MA, USA, 2014; Volume 3, pp. 589–628.
4. Alonso–Zarazaga, M.A.; Barrios, H.; Borovec, R.; Bouchard, P.; Caldara, R.; Colonnelli, E.; Gültekin, L.; Hlaváč, P.; Korotyaev, B.; Lyal, C.H.C.; et al. *Cooperative Catalogue of Palaearctic Coleoptera Curculionoidea*; Monografias Electrónicas SEA 8. Sociedad Entomológica Aragonesa, S.E.A.: Zaragosa, Spain, 2017; p. 729.
5. Oberprieler, R.G.; Anderson, R.S.; Marvaldi, A.E. Curculionoidea Latreille, 1802: Introduction, Phylogeny. In *Handbook of Zoology Volume 3*; Leschen, R.A.B., Beutel, R.G., Eds.; Walter de Gruyter GmbH: Berlin, Germany; Boston, MA, USA, 2014; Volume 3, pp. 285–300.
6. Košťál, M.; Košťálová, Z. Description of the male of *Acentrus boroveci* Košťál, 2014 (Coleoptera: Curculionidae: Acentrusini). *Zootaxa* **2016**, *4121*, 77–80. [CrossRef] [PubMed]
7. Byng, J.W.; Chase, M.W.; Christenhusz, M.J.M.; Fay, M.F.; Judd, W.S.; Mabberley, D.J.; Sennikov, A.N.; Soltis, D.E.; Soltis, P.S.; Stevens, P.F.; et al. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *Bot. J. Linn. Soc.* **2016**, *181*, 1–20.
8. Swofford, D.L. PAUP*. In *Phylogenetic Analysis Using Parsimony (*and Other Methods)*, version 4; Sinauer Associates: Sunderland, MA, USA, 2002; p. 144.
9. Ronquist, F.; Teslenko, M.; van der Mark, P.; Ayres, D.L.; Darling, A.; Höhna, S.; Larget, B.; Liu, L.; Suchard, M.A.; Huelsenbeck, J.P. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* **2012**, *61*, 539–542. [CrossRef] [PubMed]
10. Maddison, W.P.; Maddison, D.R. Mesquite: A Modular System for Evolutionary Analysis. Version 3.40. Available online: http://mesquiteproject.org (accessed on 30 April 2018).
11. Pedregosa, F.; Varoquaux, G.; Gramfort, A.; Michel, V.; Thirion, B.; Grisel, O.; Blondel, M.; Prettenhofer, P.; Weiss, R.; Dubourg, V.; et al. Scikit-learn: Machine learning in Python. *J. Mach. Learn. Res.* **2011**, *12*, 2825–2830.

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A Review of the Tribe Cryptoplini (Coleoptera: Curculioninae), with Revision of the Genus *Menechirus* Hartmann, 1901 and Description of a New Genus Associated with *Macadamia*

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Abstract: This paper presents the results of a study that was largely initiated to describe a genus and species of weevil damaging macadamia fruits in plantations in New South Wales and Queensland, Australia. This taxon is described as *Kuschelorhynchus macadamiae* gen. et sp. n., the genus named in honour of the late Guillermo (Willy) Kuschel (1918–2017). The related genus *Menechirus* Hartmann is also revised, resulting in the description of three new species, *M. howdenae* sp. n., *M. parryi* sp. n. and *M. mundus* sp. n. The other genera of the small Australian weevil tribe Cryptoplini, *Cryptoplus* Erichson, *Haplonyx* Schoenherr, *Sigastus* Pascoe and *Zeopus* Pascoe, are diagnosed and their host associations summarised, and a revised diagnosis of the tribe Cryptoplini is presented, together with a key to its six genera. The extraordinary aedeagus of Cryptoplini, featuring a tectal plate as is characteristic of more primitive weevils, is discussed and illustrated.

Keywords: Cryptoplini; taxonomy; weevils; tectal aedeagus; *Kuschelorhynchus*; *Macadamia*; *Syzygium*; Australia; New Guinea

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1. Introduction

The weevil tribe Cryptoplini as currently known is confined to Australia except for one species, *Menechirus oculatus* Hartmann, which occurs in New Guinea [1]. The taxon was first established as a group Cryptoplides in Lacordaire's tribe Erirhinides, which included as other groups the true Erirhinides, Eugnomides, Hydronomides and Storeides [2]. Originally, the Cryptoplides included besides *Cryptoplus* Erichson, 1842 seven other genera, all of which have since been removed from this tribe. The single species placed in *Cryptoplus* by its author, *C. perdix* Erichson, 1842 [3], remained unknown to authors such as Lacordaire, Pascoe and Blackburn, and Lea only managed to examine its type in 1931, discovering that it is congeneric with *Aolles* Pascoe, 1870 [4], which had been described later in the tribe Haplonychini Lacordaire, 1865 [5]. Lea consequently transferred *Cryptoplus* to Haplonychini (as Haplonycides) but failed to realise that the name of this tribe then became a junior synonym of the older name Cryptoplini Lacordaire, 1863. This error was perpetuated in the literature until the end of the 20th century, being rectified only in 1999 [6].

The early work on the taxonomy of the Cryptoplini (as Haplonychinae) was undertaken by Pascoe [5], who added the genera *Aolles* and *Sigastus* Pascoe, 1865 as well as *Metatyges* Pascoe, 1865 and *Physarchus* Pascoe, 1865 to this previously monotypic tribe. However, the last two of these genera are now classified in a different tribe, Metatygini, with the name *Metatyges* as a synonym of *Omophorus* Schoenherr, 1835. Lea also made significant contributions to the knowledge of the Cryptoplini, being the first to develop a basic key to its genera [7], undertake a review of the large genus *Haplonyx*

Schoenherr, 1836 [8], describe many new species [7–11] and eventually discover that *Cryptoplus* is congeneric with *Aolles* [4]. Since Pascoe and Lea, the Cryptoplini have only received little and sporadic taxonomic attention. Zimmerman [12] added the genera *Cranopoeus* Marshall, 1931, *Cratoscelocis* Lea, 1927, *Fergusoniella* Alonso-Zarazaga & Lyal, 1999 and *Spanochelus* Marshall, 1931 to the tribe, but these were subsequently placed in a separate tribe, Cranopoeini [13]. Zimmerman also discovered that *Sigastus tropicus* Lea, 1928 had previously been described as *Menechirus fuscodorsalis* Heller, 1922 [12], but neither he nor Lea were familiar with the genus *Menechirus* Hartmann, 1901 and neither assigned it to Cryptoplini, nor did Schenkling & Marshall [14] in their catalogue of the tribe nor Alonso-Zarazaga & Lyal [6], who listed it in the tribe Trigonocolini. Pullen et al. [15] recently started to clarify the blurred concept of *Sigastus* by transferring *S. casuarinae* Lea, 1909 to *Haplonyx* and, having examined the type species of *Menechirus*, the New Guinean *M. oculatus* Hartmann, 1901, synonymised *Menechirus* with *Sigastus*. Caldara et al. [1] provided a summary of the composition, distribution, characters and biology of the tribe. Currently it includes only four genera, *Cryptoplus*, *Haplonyx*, *Sigastus* and *Zeopus* Pascoe, 1872, all however in need of further study and delimitation. In this paper, we reinstate *Menechirus* as a valid genus, clarify its concept and characters and describe three new species in it, and we describe an additional, related new genus and species from Australia.

Cryptoplini are largely associated with the plant family Myrtaceae, some taxa apparently being quite host-specific. *Cryptoplus*, *Haplonyx*, *Sigastus* and *Zeopus* are predominantly associated with *Eucalyptus*, the larvae developing in flower and fruit buds but also in galls, often those incited by other insects, such as brachyscelid coccids [16], wasps and fergusoninid flies [17]. The females typically lay a single egg into a bud and then cut off the entire cluster of buds [18], which can result in large-scale budfall in some regions and years. In large woody galls, several larvae may develop together. Some *Haplonyx* species have also been recorded as developing in the flower buds of *Melaleuca* and in galls on *Leptospermum*, whereas *H. casuarinae* has been reared from fruits and coccid galls of *Casuarina* (Casuarinaceae). *Menechirus* develops in the fleshy fruits of *Syzygium* (often recorded as *Eugenia* on host labels, also as *Acmena* and *Waterhousea*) and perhaps also in those of *Rhodomyrtus*. In contrast to these associations with Myrtaceae, the new genus and species described here, *Kuschelorhynchus macadamiae*, lives on *Macadamia* (Proteaceae), being regarded as an emerging pest of macadamia nuts in north-eastern New South Wales and north-eastern Queensland [19–22]. The naming and description of this taxon, as well as of an undescribed *Menechirus* species associated with the endangered Magenta Lilly Pilly (*Syzygium paniculatum*) in New South Wales, is a further aim of this paper.

2. Materials and Methods

2.1. Specimens

The study is based on 233 specimens of *Menechirus* and *Kuschelorhynchus*. In addition, numerous specimens of the other genera were examined for a comparison of characters. The genitalia of 47 relevant specimens were dissected in the usual manner, by extracting the ventrites and terminalia of softened specimens under the microscope, macerating them in a hot solution of 10% KOH, rinsing them in ethanol and then clearing and storing them in glycerol, initially on cavity slides and later in microvials attached to the pins of the specimens. All specimens are deposited in the Australian National Insect Collection (ANIC), CSIRO, Canberra, except where otherwise indicated, as follows:

CMNC	Canadian Museum of Nature, Ottawa, Canada
QDPI	Queensland Department of Primary Industries Insect Collection, Brisbane, Australia
QMBA	Queensland Museum, Brisbane, Australia

2.2. Descriptions and Label Data

Body length was measured from the anterior tip of the pronotum to the apex of the elyta in lateral view, and width was measured across the widest expanse of the structure. The terms of the structures are those commonly used in weevils [23], whereby tarsite is preferred over tarsomere for the tarsal segments (following Kuschel, Zimmerman and Oberprieler, akin to sternite, ventrite and similar terms and also consistent with the common term cryptotarsite used for the hidden, fourth segment in Phytophaga), and onychium is used for the terminal, claw-bearing tarsite (also following Kuschel and others). In the spermatheca, the term collum refers to the part in which the duct is inserted, when this is differentiated. In the antennae, the term segment is used purely in a descriptive sense, as part of a larger structure, thus the club comprising four segments when they are discernible as such. Label data are given verbatim, a slash (/) denoting different lines on a label and a double slash (//) denoting different labels on the same specimen pin.

2.3. Illustrations

Photographs of weevils and their genitalia were taken using a Leica DFC500 camera mounted on a Leica M205C microscope. Photographs taken at different focus levels were combined into single images using the software program Leica Application Suite (LAS) V4.9, and these images were enhanced as necessary using the Photoshop CS6 software. Scanning electron microscope (SEM) images were taken using a Hitachi TM3030Plus Tabletop Microscope and enhanced as necessary using the Photoshop CS6 software.

3. Systematics

3.1. Diagnosis of the Tribe Cryptoplini

Tribe Cryptoplini Lacordaire, 1863
Cryptoplides Lacordaire, 1863: 486 [2]
Haplonycides Lacordaire, 1865: 16 [24]

Diagnosis (modified after Lea [11] and Caldara et al. [1]). Elytra uniformly convex from base to apex; pronotum and elytra densely squamose; rostrum usually stout and relatively straight (except for *Zeopus*); maxillary and labial palps 3-segmented; funicles 6- or 7-segmented, with segment 7 sometimes closely appressed or fused to club, resulting in a 4- or 5-segmented club, clubs elongate; procoxae narrowly separate to contiguous (*Zeopus*); femora dentate with one or more unequal teeth; tibiae with large uncus and smaller premucro inside a tuft of setae; tarsi with onychium narrow or reduced to absent; claws simple and either connate, single or absent; proventriculus undifferentiated, lacking plates and paired brushes; penis with tectal plate fused with pedon at base; gonocoxites without styli, spermathecal gland with sclerotised funnel-shaped base.

Remarks. This small tribe is well characterised by the unusual tectal plate of the penis, the sclerotised, funnel-shaped base of the spermathecal gland and the undifferentiated proventriculus, characters that indicate it to constitute a monophyletic group. The delimitation of its six genera, however, is in need of further study, as their traditional distinguishing characters, the segmentation of the funicles and the condition of the tarsal claws [7], are variable and not easy to segregate into distinct conditions. The six-segmented funicles of *Cryptoplus* and *Zeopus* are due to the seventh (last) segment being more or less closely appressed to the club, a condition that may, as in other weevils, have originated several times, and the fine claws vary from being separate but parallel in *Menechirus*, *Sigastus* and *Kuschelorhynchus* to largely fused (separate at the apex) in a few *Haplonyx* species to a single claw in most *Haplonyx* and some *Cryptoplus* species to being entirely absent in most species of *Cryptoplus* and in *Zeopus*. To this end, the distinction between *Cryptoplus* and *Haplonyx* has been questioned before [4,9,10], and the distinction between *Cryptoplus* and *Zeopus* is equally tenuous based on these features. More comprehensive study of all species of these three genera is required to place their distinction on a more secure footing.

3.2. Key to the Genera of Cryptoplini

1. Funicles 6-segmented, last segment appressed to club, this appearing 5-segmented; tarsi with onychium minute, hidden in apical cleft of third tarsite, usually clawless 2
- Funicles 7-segmented, clubs 4-segmented; tarsi with distinct, exposed onychium bearing one or two claws 3

2. Rostrum short, straight to slightly curved; penis with flat, symmetrical endophallic sclerite; spermathecal gland bulbous .... *Cryptoplus*
- Rostrum long and thin, distinctly curved; penis with bent, twisted, double endophallic sclerite; spermathecal gland mushroom-shaped .... *Zeopus*

3. Onychia with single claw (rarely apically bifid) .... *Haplonyx*
- Onychia with two separate claws, divergent or parallel 4

4. Rostrum apically broadened in dorsal view only, narrowed or straight in lateral view; pronotum with two pairs of small, low admedian tubercles; elytra with three to four pairs of small, low tubercles .... *Menechirus*
- Rostrum apically broadened in dorsal and lateral view; pronotum with two pairs of large, fasciculate admedian tubercles and one to two pairs of smaller lateral ones; elytra with seven or eight pairs of larger, sometimes fasciculate tubercles 5

5. Funicle segments 7 closely appressed to club (funicles appearing 6-segmented); body sparsely covered with black hair-scales; elytra with eight pairs of large fasciculate tubercles on interstriae 3 and 5, apically rounded; claws closely associated and parallel .... *Sigastus*
- Funicle segments 7 separate from club (funicles distinctly 7-segmented); body densely covered with greenish-grey scales (reddish-brown on pronotal tubercles); elytra with one pair of huge, compressed, squamose tubercles on interstriae 3 and with four smaller tubercles anterolaterally of these, apically truncate; claws separate and slightly divergent .... *Kuschelorhynchus*

3.3. Diagnoses of the Genera of Cryptoplini

Genus ***Cryptoplus*** Erichson, 1842 (Figure 1)

Cryptoplus Erichson, 1842:198 [3] (type species, by monotypy: *Cryptoplus perdix* Erichson, 1842)

Aolles Pascoe, 1870:450 [5] (type species, by subsequent designation [15]: *Aolles rubiginosus* Pascoe, 1870); Lea, 1931:50 [4] (synonymy)

Diagnosis. Body small, oval in dorsal view (Figure 1a), uniformly convex in lateral view; rostrum moderately long, straight to slightly curved (Figure 1b); antennae inserted in apical third of rostrum, with funicle 6-segmented and club 5-segmented (Figure 1c); pronotum trapezoidal, punctate; procoxae narrowly to very narrowly separate; elytra punctate, squamose with varying patterns; scutellar shield oval to roundly triangular; tarsi with onychium small, hidden in apical cleft of tarsite 3, usually clawless (Figure 1d), rarely with a small single claw; penis with apical margin of pedon narrowed, temones long; endophallus spinulose, with weak pair of elongate internal sclerites (Figure 1e) (*C. fasciatus* (Lea), *C. maculipennis* (Lea)); gonocoxites elongate, apically narrowed, bursa copulatrix elongate (Figure 1f), spermatheca thickly crescentic, gland oval with sclerotised funnel-shaped base (Figure 1g).

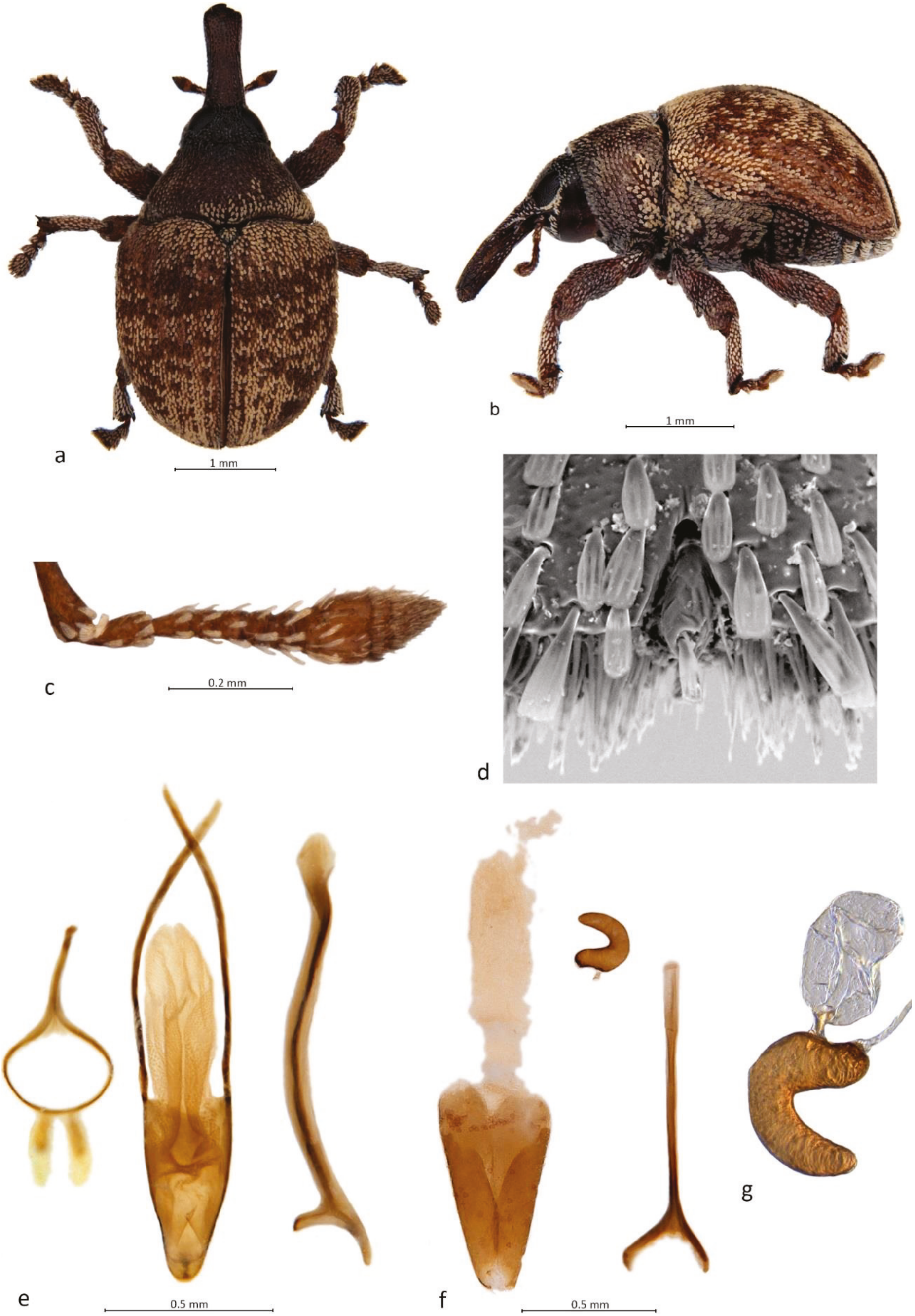

Figure 1. Habitus and diagnostic characters of *Cryptoplus* Erichson (*C. maculipennis* (Lea)): (**a**) habitus of male, dorsal view; (**b**) habitus of male, left lateral view; (**c**) right antenna, male, dorsal view; (**d**) tarsite 3 with onychium, apical view; (**e**) genitalia, male, dorsal view; (**f**) genitalia, female, dorsal view; (**g**) spermatheca with gland.

Remarks. This genus currently comprises 33 species [15] and is largely associated with *Eucalyptus* [1,25], the females laying their eggs into flower buds and severing the bud clusters afterwards [26]. Erichson's original description is incorrect in that the funicles are described as being seven-segmented, but Lea (1931) [4], on examination of the type of *C. perdix*, noted this error and confirmed that they are six-segmented. On this character *Cryptoplus* and *Zeopus* can be readily distinguished from *Haplonyx*, *Kuschelorhynchus*, *Menechirus* and *Sigastus*, all of which have seven-segmented funicles. However, *Cryptoplus* is difficult to distinguish from *Zeopus*, the latter sharing its tarsal condition and only differing in having a much longer, curved rostrum and some dissimilar genital structures. *Cryptoplus* typically has extremely reduced onychia, concealed in a small short cleft at the apex of the third tarsite and bearing no claw but one or two short stiff setae (Figure 1d), although a few species, such as *C. ornatipennis* (Blackburn), *C. tibialis* (Lea), C. *trifasciatus* (Lea) and *C. variegatus* (Lea), possess longer onychia protruding from the apex of the third tarsites and bearing a single small claw (as well as setae). Lea's (1927) [7] assertion that *C. tibialis* has two claws is incorrect; all specimens in the ANIC so identified have a distinct single claw.

Genus ***Haplonyx*** Schoenherr, 1836 (Figures 2 and 3)

Haplonyx Schoenherr, 1836: 606 [27] (type species, by original designation: *Haplonyx spencei* Gyllenhal, 1836)

Diagnosis. Body short, oval in dorsal view (Figures 2a and 3a), distinctly convex in lateral view (Figures 2b and 3b); rostrum robust, moderate in length, straight to slightly curved (Figures 2b and 3b); antennae with funicle clearly 7-segmented and club 4-segmented (Figures 2c and 3c); procoxae separate; elytra punctate, squamose with varying patterns; scutellar shield oval to roundly triangular; tarsi with onychium narrow but distinct, with a single claw (Figure 2d) or an apically shortly bifid one (*H. casuarinae*, Figure 3d); penis parallel-sided with rounded apex (Figure 2e) to navicular with pointed apex (Figure 3e); endophallus spinulose, with internal sclerites variable (Figures 2e and 3e); gonocoxites apically narrowed with apical setae (Figure 2f) to truncate and setose (Figure 3f), spermatheca crescentic with elongate, oval gland (Figures 2g and 3g).

Remarks. *Haplonyx* is a large and variable genus, currently comprising approximately 61 species, but numerous synonymies are indicated [15] and many undescribed species are in collections. The genus is in need of thorough revision. Its most distinguishing feature are the single tarsal claws (Figure 2d), but in *H. casuarinae* the claws are apically shortly bifid (indicating fusion of an original pair) (Figure 3d), and in some *Haplonyx* specimens there is a much reduced but free claw present on the inside of the large one. Most *Haplonyx* species appear to develop in flower and fruit buds like those of *Cryptoplus* do, but several develop in woody galls incited by brachyscelid coccids, Hymenoptera or by the weevil larvae themselves [1,8,16,25]. The oviposition behaviour of *H. vicinus* Chevrolat on *Eucalyptus* flower buds has been studied in detail [26], and that of other species is likely to be similar.

Genus ***Sigastus*** Pascoe, 1865 (Figure 4)

Sigastus Pascoe, 1865: 423 [28] (type species, by monotypy: *Sigastus fascicularis* Pascoe, 1865)

Diagnosis. Body large, oval (Figure 4a), distinctly convex in lateral view (Figure 4b); rostrum robust and moderately short, dorsoventrally flattened and thickened towards apex in dorsal and lateral view (Figure 4a,b); antennae with funicle 7-segmented but segment 7 densely squamose and very closely appressed (but not fused) to club, club 4-segmented (Figure 4c); procoxae separate; scutellar shield oval; tarsi with onychium distinct, with 2 separate but closely parallel claws (Figure 4d); penis elongate, parallel-sided, apically broadly truncate, tectal plate narrow, temones short; endophallus with internal sclerites reduced (Figure 4e); gonocoxites moderate in length, with apical setae (Figure 4f); spermatheca crook-shaped, narrowed at base, gland elongate, oval (Figure 4g).

Figure 2. Habitus and diagnostic characters of *Haplonyx* Schoenherr (*H. spencei* Gyllenhal): (**a**) habitus of male, dorsal view; (**b**) habitus of male, left lateral view; (**c**) right antenna, male, dorsal view; (**d**) tarsite 3 with onychium, apical view; (**e**) genitalia, male, dorsal view; (**f**) genitalia, female, dorsal view; (**g**) spermatheca with gland.

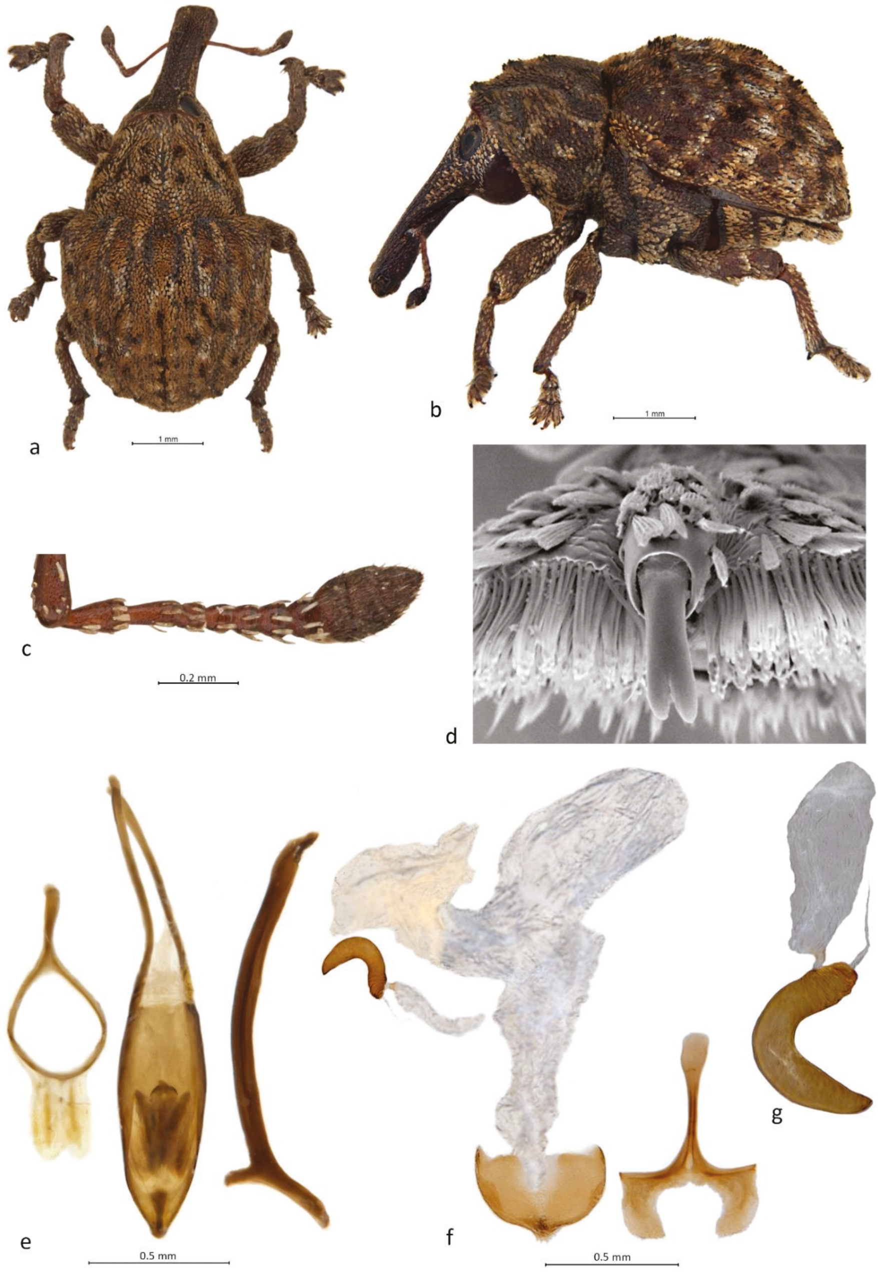

Figure 3. Habitus and diagnostic characters of *Haplonyx* Schoenherr (*H. casuarinae* (Lea)): (**a**) habitus of male, dorsal view; (**b**) habitus of male, left lateral view; (**c**) right antenna, male, dorsal view; (**d**) tarsite 3 with onychium, apical view; (**e**) genitalia, male, dorsal view; (**f**) genitalia, female, dorsal view; (**g**) spermatheca with gland.

Figure 4. Habitus and diagnostic characters of *Sigastus* Pascoe (*S. fascicularis* Pascoe): (**a**) habitus of male, dorsal view; (**b**) habitus of male, left lateral view; (**c**) right antenna, male, dorsal view; (**d**) tarsite 3 with onychium, apical view; (**e**) genitalia, male, dorsal view; (**f**) genitalia, female, dorsal view; (**g**) spermatheca with gland.

Remarks. As here constituted, *Sigastus* is a monotypic genus, including only the type species, *S. fascicularis*. *Sigastus casuarinae* was recently transferred to *Haplonyx* on account of its similarity in vestiture, sculpture and male genitalia to *H. fasciculatus* Boheman [15], despite its tarsal claws being bifid at the apex, not single, and *S. fuscodorsalis* (Heller) and *S. ocularis* (Hartmann) are here again classified in their original genus, *Menechirus*. In the original description of *S. fascicularis*, the claws are described as being connate at the base [28], but Lea noted that they are indeed free along their entire length [11], as they are in *Menechirus*. From this genus *Sigastus* differs readily in habitus (size, shape, sculpture), in the antennae (funicle segments 7 appressed to the clubs) and in the male genitalia (the penis parallel-sided and apically truncate, the endophallic sclerites different) and the spermatheca (the collum distinctly elongate). From *Kuschelorhynchus* it can easily be distinguished on colour, shape, vestiture and male genitalia. Its larvae develop in woody galls on *Eucalyptus* [29,30].

Genus ***Zeopus*** Pascoe, 1872 (Figure 5)

Zeopus Pascoe, 1872: 460 [31] (type species, by monotypy: *Zeopus storeoides* Pascoe, 1872)

Diagnosis. Body small, oval (Figure 5a), distinctly convex in lateral view (Figure 5b); rostrum long, slender and distinctly curved (Figure 5b); antennae with funicle 6-segmented, segment 7 forming part of club, club thus 5-segmented (Figure 5c); pronotum trapezoidal, at base twice as broad as at apex; procoxae very narrowly separate; elytra 1.2× longer than wide together, punctate, covered in pale brown to black scales; scutellar shield rounded; tarsi with onychium strongly reduced and concealed in apical cleft of third tarsite, without claws (Figure 5d); penis parallel-sided, apically subtruncate; endophallus spinulose, with double-bowed, asymmetrical internal sclerite (Figure 5e); gonocoxites elongate, with apical setae (Figure 5f), bursa copulatrix spinulose, spermatheca crescentic with truncate base, gland mushroom-shaped with distinct funnel-shaped sclerotised base (Figure 5g).

Remarks. The genus is also monotypic, including only the type species, *Zeopus storeoides*. It was originally described as having no onychia, but there is a very small, short segment hidden in a narrow short cleft of the third tarsites, as is the condition in *Cryptoplus*. The distinction between *Zeopus* and *Cryptoplus* is weak, resting primarily on the greater length and curvature of the rostrum in the former [7]. However, the endophallic sclerites of the penis and the peculiarly shaped spermathecal gland of *Zeopus* are different from those of all of the *Cryptoplus* species we examined, and we therefore retain *Zeopus* as a valid genus. It is widely distributed in the southern parts of Australia, from Western Australia across South Australia (the type locality of *Z. storeoides*) and Victoria into New South Wales. In spite of this large range, there are no appreciable differences between the specimens and only one species is indicated to exist. It is generally collected on *Eucalyptus* [7], but its life history appears unknown; the long, strong, curved rostrum of the female suggests that the eggs may be laid into deep plant tissues, probably flower or fruits buds as well.

Genus ***Menechirus*** Hartmann, 1901 (Figures 6–10)

Menechirus Hartmann, 1901: 278 [32] (type species, by original designation: *Menechirus oculatus* Hartmann, 1901); Klima, 1935: 1 [33] (in Trigonocolinae); Alonso-Zarazaga & Lyal, 1999: 208 [6] (in Trigonocolini); Caldara et al., 2014: 605–606 [1]

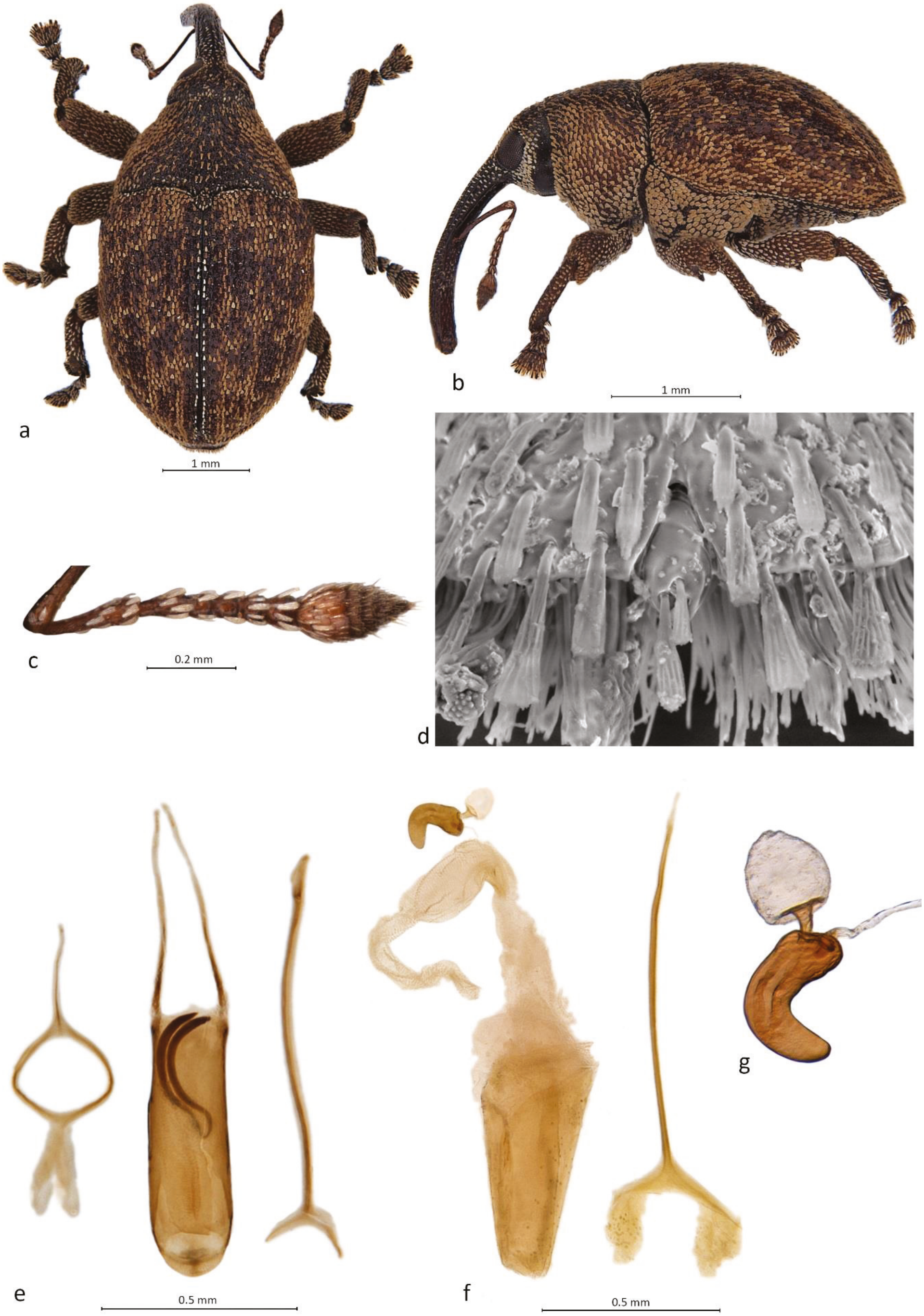

Figure 5. Habitus and diagnostic characters of *Zeopus* Pascoe (*Z. storeoides* Pascoe): (**a**) habitus of male, dorsal view; (**b**) habitus of male, left lateral view; (**c**) right antenna, male, dorsal view; (**d**) tarsite 3 with onychium, apical view; (**e**) genitalia, male, dorsal view; (**f**) genitalia, female, dorsal view; (**g**) spermatheca with gland.

Diagnosis. Body short and wide, vestiture with scattered brown and white scales forming more or less distinct patterns on pronotum and elytra; rostrum robust, relatively short and straight, dorsoventrally flattened, widening apicad in dorsal view but narrowing apicad or substraight in lateral view, with distinct dorsolateral and sometimes dorsomedian carinae, scrobes deep, narrow, running onto venter of rostrum but not meeting; antennae with funicle 7-segmented, segment 7 usually clearly distinct from club, club 4-segmented; pronotum strongly convex to tumescent, with small anterior and larger central pair of low tubercles, strongly patterned with dark and pale scales, the latter usually forming one or two transverse arcs; procoxae narrowly separate; elytra short and broad, disc with a number of paired tubercles forming a broad V, laterally with a large, dark subtriangular patch; scutellar shield ogival to oval; tarsi with onychium as long as tarsite 3 but protruding from it, narrow, with fine, subparallel or slightly divergent claws; abdominal ventrites 1 and 2 equal in length, almost 2× longer than 3 and 4, ventrite 5 with a pair of one or two long setae near caudal margin; penis narrowly navicular with acutely pointed apex, temones about as long as penis body, simple; endophallus with a pair of narrow long internal sclerites, sometimes fused at apex or absent; gonocoxites narrowly triangular to faintly sinuate, apex broadly subtruncate with several stiff setae, styli absent, bursa copulatrix and oviduct membranous, spermatheca shortly crescentic, thick, undifferentiated, gland shortly to moderately elongate, arising from short, lightly sclerotised, funnel-shaped duct, sternite VIII short and broad, bladal part with large desclerotised median area, margin fringed with several stiff setae, apodeme about as long as bladal part.

Remarks. As here constituted, *Menechirus* contains two previously described species, *M. oculatus* and *M. fuscodorsalis*, and we add another three new ones below. The claws of *Menechirus* were not mentioned in its original description [32] nor in the later description of *M. fuscodorsalis* [34], but in a footnote accompanying the latter Heller wrote that "*Menechirus* represents a *Haplonyx* with two unguiculi" and suggested placing it in the same group (as "Haplonicidae"). *Menechirus* was recently merged into *Sigastus* [15], mainly on the basis of their similar claw structure, although the differences in vestiture, length of rostrum and antennae and structure of the penis between their type species were noted. From our more detailed study of all available species and material of these taxa, including of the genitalia, we conclude that there are sufficient differences between *Menechirus* and *Sigastus* (including the hostplants) to regard them as different genera, and we consequently here reinstate *Menechirus* as a valid genus. It differs from *Sigastus* in its shorter, squatter body, larger rostrum, patterned pronotum and elytra, the free funicle segments 7 (not appressed to the club), the pointed penis with a pair of long, narrow endophallic sclerites, the shorter ovipositor and a short to absent collum of the spermatheca. In its tubercle arrangement on the elytra and its vestiture it is most similar to *Kuschelorhynchus*, from which it differs in its smaller size, much weaker dorsal sculpture and flatter, more wedge-shaped rostrum in lateral view as well as in its male and female genitalia. It develops in the fleshy flower and fruit buds of *Syzygium* and possibly *Rhodomyrtus* (Myrtaceae).

3.4. Key to the Species of Menechirus

1. Elytra with sutural interstriae jointly raised to about middle of elytral length; pronotum with central pair of tubercles small, low, not jointly elevated; dorsolateral carinae of rostrum as high as area between dorsomedian carinae; funicles with segment 7 closely appressed to club; clubs short, thick (2× longer than wide); dorsal colour pattern variable (Australia, Northern Territory) .... *M. fuscodorsalis* Heller

\- Elytra with sutural interstriae not or only faintly and shortly elevated behind scutellar shield; pronotum with central pair of tubercles large, elevated on a joint hump; dorsolateral carinae of rostrum lower than area between dorsomedian carinae; funicles with segment 7 distinctly separate from club; clubs mostly longer than wide 2

2. Body length > 5 mm; pronotum with large pair of central tubercles and pale setae distributed widely on disc and sides; sutural interstriae in male with pale, flat scales behind scutellar shield 3

- Body length < 5 mm; pronotum with small pair of central tubercles and pale setae forming one to two narrow bands arching from bases across central tubercles; sutural interstriae in male with short, V-shaped patch of pitch-black, erect scales behind scutellar shield 5

3. Rostrum with distinct dorsomedian carinae; pronotum with broad band of black setae across base but without pairs of small, glabrous dots (Australia, northern Queensland) .... *M. howdenae* sp. n.

- Rostrum without dorsomedian carinae defined; pronotum without black setae across base but with two pairs of small, glabrous (non-squamose) dots, one opposite striae 3 and the other opposite humeri (New Guinea) 4

4. Pronotum with black scales limited to a pair of subtriangular patches laterally of median tubercles; tubercles low, small; clubs short, less than 2× longer than wide; elytra with creamy and brown scales admixed, black scales forming fragmented band across middle (Papua New Guinea) .... *M. oculatus* Hartmann

- Pronotum with black scales forming larger irregular macula laterally of median tubercles; tubercles high, large; clubs elongate, more than 2× longer than wide; elytra with creamy, brown and black scales largely segregated into patches forming a variegated pattern (Indonesia, West Papua) .... *Menechirus* sp.

5. Pronotum with two pairs of small black tubercles, one in middle and one on anterior border, and one pale band curving from behind median tubercles to basal corners; elytra with four pairs of tubercles on anterior slope well developed; pale patch on elytral declivity well demarcated, narrow .... *M. parryi* sp. n.

- Pronotum with one pair of small black tubercles in middle and two pale bands curving from before and behind median tubercles to basal corners; elytra with four pairs of tubercles on anterior slope poorly developed, except for posterior one on interstriae two; pale patch on elytral declivity poorly demarcated, broader .... *M. mundus* sp. n.

3.5. Revision of the Species of Menechirus

Menechirus oculatus Hartmann, 1901 (Figure 6)

Menechirus oculatus Hartmann, 1901: 279 [32]; Klima, 1935: 1 [33]; Pullen et al., 2014: 458 [15].

Diagnosis. Body short, oval, 5.5–5.8 mm long, 3.5–4.0 mm wide; moderately densely covered with pale brown and black scales interspersed with few white ones, forming distinct pattern on head, pronotum and elytra (Figure 6a); rostrum slightly longer than pronotum, robust, apically broadened in dorsal view, in lateral view straight, flattened (Figure 6b), dorsomedian carinae indistinct, slightly diverging anteriad, higher than dorsolateral ones; antennae slender, with club robust, ca. 2.5× broader than funicle (Figure 6c); pronotum in centre of disc with pair of large, low, blunt tubercles covered with dark erect scales along base, with 2 pairs of small denuded spots; scutellar shield inversely ogival, flat, sparsely squamose; elytra as broad across humeri as long, with irregular broad dark transverse band behind humeri; tibiae with premucro much smaller than uncus, tarsi with claws slightly divergent (Figure 6d); penis with sides subparallel, apex broadly triangular, temones longer than penis body, endophallus with internal sclerite large, thick, V-shaped (Figure 6e); gonocoxites narrowly triangular (Figure 6f), spermathecal gland large, drop-shaped (Figure 6g).

Material examined (1 ♂, 3 ♀). 1 ♀: "Mt Lamington / N. E. Papua / 1300 to 1500 feet / C. T. McNamara // ANIC / Image // ♀// *Menechirus* / *oculatus* Hartmn / (ex description) / det. R. G. Oberprieler 2014"; 1 ♀: same label and data except for identification label; 1 ♂: same data but on handwritten label and without identification label.

Distribution. Eastern Papua New Guinea (Madang and Oro provinces) as known; probably more widespread.

Hostplants. None recorded but probably *Syzygium* (Myrtaceae), the host genus of all other *Menechirus* species.

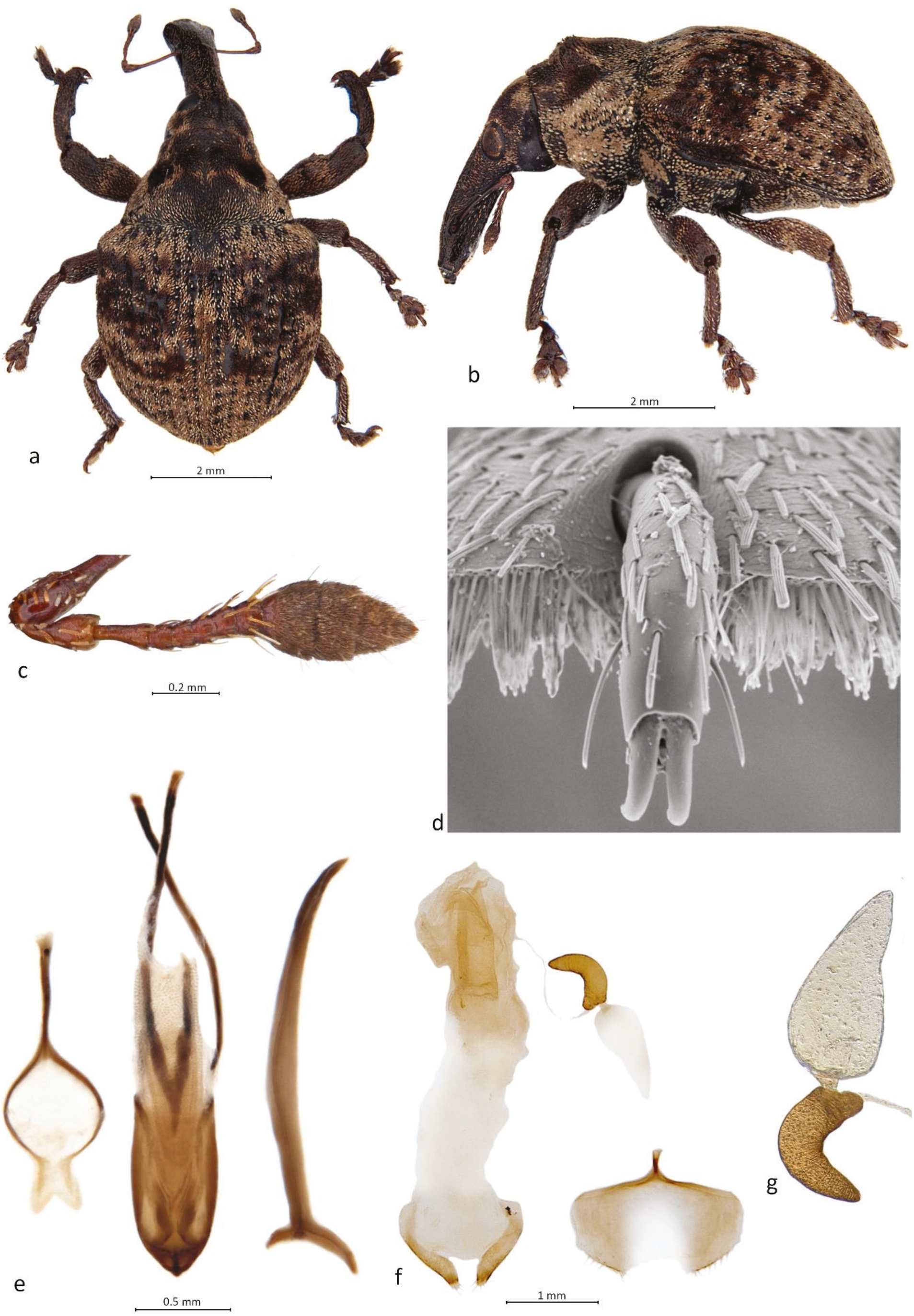

Figure 6. Habitus and diagnostic characters of *Menechirus oculatus* Hartmann: (**a**) habitus of male, dorsal view; (**b**) habitus of male, left lateral view; (**c**) right antenna, male, dorsal view; (**d**) tarsite 3 with onychium, apical view; (**e**) genitalia, male, dorsal view; (**f**) genitalia, female, dorsal view; (**g**) spermatheca with gland.

Remarks. This species was described from Bongu in the Madang province [32] and appears to be the only species of *Menechirus* recorded from New Guinea so far. However, another species is represented in the ANIC by a single female (missing some legs), collected in September 1944 by Cari Mohr at Sansapore in West Papua. It differs from *M. oculatus inter alia* in having larger pronotal protuberances, a larger and more irregular dark macula next to them (not small, round, 'eye'-like as in *M. oculatus*), more elongate antennal clubs, a more strongly sculptured rostrum and a more variegated pattern of elytral scales. *Menechirus oculatus* can be distinguished from all other known species by its pair of subtriangular dark pronotal maculae, which appear eye-like and for which it was named. Among the Australian species, *M. oculatus* is most similar to *M. howdenae*, differing as in the key above and also in its long, V-shaped endophallic sclerite (Figure 6e). As *Syzygium* is a very diverse genus in New Guinea, it is likely that more species of *Menechirus* occur in New Guinea.

Menechirus fuscodorsalis Heller, 1922 (Figure 7)

Menechirus fuscodorsalis Heller, 1922: 556 [34]; Klima, 1935: 1 [33]
Sigastus fuscodorsalis (Heller): Zimmerman, 1994: 677 [12]; Juniper & Britton, 2010: 300 [30]; Caldara et al., 2014: 606 [1]; Pullen et al., 2014: 191 [15]
Sigastus tropicus Lea, 1928: 103 [11]; Zimmerman, 1994: 677 [12] (syn.); Pullen et al., 2014: 191 [15]

Diagnosis. Body short, oval in dorsal view (Figure 7a), strongly convex in lateral view (Figure 7b), 5.2–8.0 mm long, 2.5–5.5 mm wide; densely covered with pale brown, black and white scales, brown and black ones forming pattern, white ones interspersed, pronotum often with pale triangular median macula laterally bordered by broad or divided dark band and elytra usually with opposite pale parabolic basal median macula on interstriae 1–3, similarly bordered by broad dark band, but colour pattern very variable; rostrum robust, as long as pronotum, flattened in apical half, broadest at apex, in posterior half with dorsolateral carinae distinct, dorsomedian ones obscured by scales (Figure 7a,b); antennae reddish in colour, funicle 7-segmented, club 4-segmented (Figure 7c); pronotum in centre of disc with pair of small, short tubercles covered with black, erect scales (Figure 7a); scutellar shield small, ogival, squamose; femora with very small ventral teeth or angulations, tibiae with large, subequal uncus and premucro (both smaller on mesotibiae), tarsi with claws subparallel (Figure 7d); penis narrowly navicular, apically narrowed, temones as long as penis body, endophallus spinulose with paired, tube-like internal sclerites (Figure 7e); gonocoxites short, apically setae, bursa copulatrix spinulose (Figure 7f), spermatheca weakly crescentic with rounded base, gland elongate, apically narrowed (Figure 7g).

Material examined (43 ♂, 44 ♀). 1 ♂: "Darwin / G.F. Hill // *Sigastus* / *tropicus* / Lea / Det '75 by E.C. Zimmerman // ♂"; 1 ♀: "Darwin / G.F. Hill // in fruit of / Eugenia / suborbicul / -aris. // Menechirus / fuscodorsalis / Heller / Det. '75 E.C. Zimmerman // ♀"; 1 ♀: "Darwin / G.F. Hill // ♀"; 2 ♂, 1 ♀: "Darwin, N.T. / 17/12/50 // K.G. Brown. // Col. 20/11 / EM. 17/12 / Host / Wild Apple / Eugenia // F.H. UTHER BAKER / BEQUEST / 1992 // *Sigastus tropicus* / Lea / cv. SAM / det. F.H. Uther Baker"; 1♀: "Humpty Doo, N.T. / 30.12.53 / I.D. Crawford // G1 // Ento. Section / N.T.A. Darwin // ♀"; 1 ♀: "Humpty Doo, N.T. / 30.12.53 / ~~I.D. Crawford~~ // Found on rice // Genus ? near / Sigastus / CURCULIONIDAE / Haplonycinae / Det. T.G. Campbell // ♀"; 1 ♂: same data except for label "Found on rice"; 1 ♂, 1 ♀: "Br. Ck [Brock's Creek] / 11/12/31 / T.G.C[ampbell]."; 1 ♂: "Tortilla Flats, N.T. / 2nd Nov. 1967 / EMG. 11-12. Nov.1967 / Coll. C.S. Li // Found on / Eugenia / suborbicularis // Haplonyx ? / HAPLONYCHINAE // Ento. Section / N.T.A. Darwin // ♂"; 1 ♀: "N. Territory / Dec. 1950 / W.F. Nixon-Smith // On Wild Apple / (Eugenia sp.) // COM. INST. ENT. /COLL. No. 12205 // Genus ? near / Sigastus–not in BM / Det. G.A.K. Marshall // ANIC / Image // ♀"; 3 ♂, 3 ♀: "Site AH 020 / 8-xi-1977 / bred from / Syzygium / suborbiculare / J. Waldeck"; 1 ♂: "12.25S 132.58E / 1 km N of Cahills Crossing / (East Alligator River), N.T. / 31.x.72, at light, E. Britton // ♂"; 1 ♀: "12.23S 132.56E / 7 km NW by N of / Cahills Crossing, / (East Alligator River) / 4.xi.72, at light, E. Britton // ♀"; 1 ♀: "12.23S 132.56E / 7 km NW, by N, of Cahills Crossing, / (East Alligator River) N.T. / 12.ix.72, M.S. Upton // ♀"; 1 ♂, 2 ♀: "Australia NT / Border Store / Kakadu

NP / 2 Dec 2003 G. Bellis // Emerged from / fruit/seed of / *Syzygium* / *suborbiculare* // ANIC / Image // Sigastus / fuscodorsalis / det. R.G. Oberprieler 2017 // ♀”; 1 ♂: “Pickertaramoor / Melville Island / 19.ii.1981 N.T. / A. Allwood. // Ex fruit of / Eugenia / armstrongii // *Sigastus* / *tropicus* / Lea / Det. ’82 E.C. Zimmerman // ♂”; 1 ♂, 1 ♀: “Pickertaramoor / Melville Island, N.T. / 20.xii.1976 / A. Allwood. // bred from Szigium [*sic*] / suborbicularis [*sic*] //*Sigastus* / *tropicus* / Lea / Det. ’77 by E.C. Zimmerman // ♂”; 1 ♂: “11.01 S 136.45 E / Rimbija Is. / Wessels Islands / NT / 3-14 Feb. 1977 / T.A. Weir // Compared with / HOLOTYPE E.C.Z. / Menechirus / fuscodorsalis / Heller [on pink card] // ♂”; 1 ♂: same data except pink identification label, instead “Specimen / figured / ECZ // Sigastus / fuscodorsalis / (Heller) / Det. E.C. Zimmerman // ♂”; 5 ♂, 4 ♀: same data but no identification labels; 18 ♂, 19 ♀: “12°19′48′′S 136°56′01′′E / NT: Macassans Beach / 19 August 2007 / R. Oberprieler RO 705 // *Sigastus fuscodorsalis* / det. R. Oberprieler 2007 / on *Syzygium*”; 5 ♂, 2 ♀: “12°16′43′′S 136°53′46′′E / NT: Gove, Shady Creek / 25 Aug 2007 / R. Oberprieler RO 719 // *Menechirus fuscodorsalis* / det. R. Oberprieler 2017 / on *Syzygium* / *suborbiculare*”; 1 ♂, 4 ♀: “12°09′40′′S 136°46′48′′E / NT: Gove, Cape Wirrawoi / 26 Aug 2007 / R. Oberprieler RO 719”.

Distribution. Common and seemingly widespread in coastal areas and along rivers in the Northern Territory, where its hostplant occurs, but not recorded from northern Queensland and northern Western Australia, where this host also grows; not evidently established in the Philippines, from where it was described.

Hostplants. Mainly *Syzygium suborbiculare* (Myrtaceae), the larvae developing in the fleshy flower buds and fruits; apparently also in fruits of *Syzygium armstrongii* but frequency and extent of this host association to be determined.

Remarks. This is the largest species of *Menechirus* known. It was originally described from Luzon, Philippines, based on seemingly a single specimen reared from the fruit (”seeds”) of *Syzygium suborbiculare* imported from Darwin, Australia [12,34]. Lea [11] was vague about the type series of the synonym *Sigastus tropicus*, citing the localities as “Darwin (G.F. Hill)” and “Cairns district (A.M. Lea)” and referring to the type, “a second specimen, from Darwin” and as a specimen from Cairns. He thus evidently had two additional specimens from Darwin collected by G.F. Hill (see Material examined). The specimen from Cairns represents a different species, described as *M. howdenae* below. The pronotum and elytra of *M. fuscodorsalis* usually have a distinct pattern of opposite subtriangular maculae of pale scales bordered by a broad band of darker ones, but specimens with different or no patterns occur among ones so patterned.

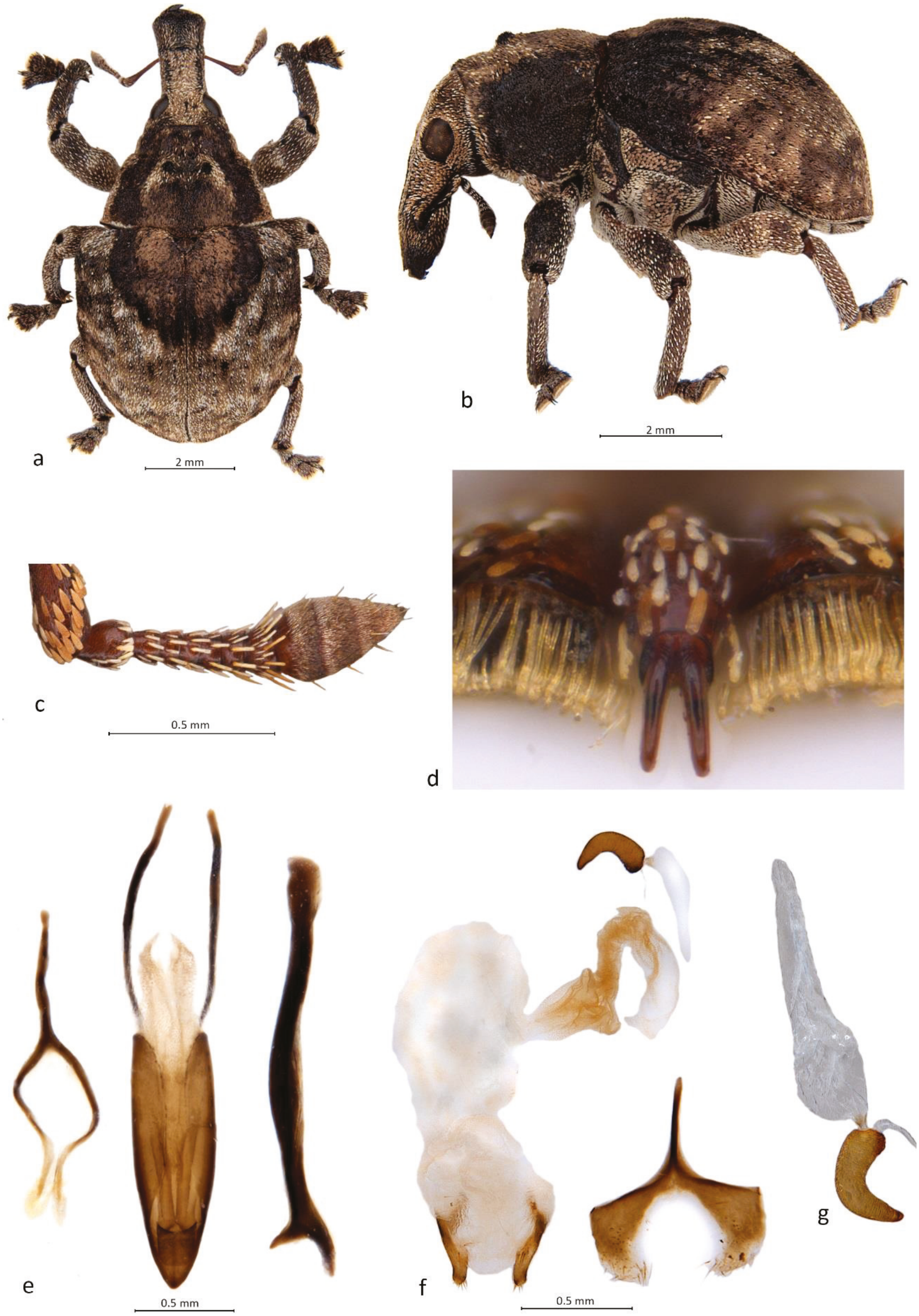

Figure 7. Habitus and diagnostic characters of *Menechirus fuscodorsalis* Heller: (**a**) habitus of male, dorsal view; (**b**) habitus of male, left lateral view; (**c**) right antenna, male, dorsal view; (**d**) tarsite 3 with onychium, apical view; (**e**) genitalia, male, dorsal view; (**f**) genitalia, female, dorsal view; (**g**) spermatheca with gland.

Menechirus howdenae Jennings & Oberprieler, **sp. n.** (Figure 8)

Description: Shape. Body very short, ovoid, length 5.0–6.4 mm in both sexes (holotype 6.4 mm), width ca. 0.8× length (Figure 8a), distinctly convex in lateral view (Figure 8b). **Colour and vestiture.** Body densely covered with pale brown to black scales (with few white ones scattered in between); head with pale scales interrupted by a dark broad median stripe and a pair of similar stripes behind dorsal half of eyes; pronotum in male largely with black scales except for narrow curved band of pale scales laterally, in female more uniformly pale; elytra largely with pale scales except for irregular broad dark band curving from interstria 4 in about middle of disc towards humerus (Figure 8a); rostrum mostly with dark scales; legs and underside with pale ones (Figure 8a). **Rostrum.** Short (about 1.15× longer than pronotum in male, 1.25× in female), robust, straight, dorsoventrally flattened, apically broadened in dorsal view, distal half dorsally coarsely punctate, proximal half with pairs of distinct, thick dorsomedian and dorsolateral carinae, the latter lower than the former (Figure 8a,b). **Eyes.** Subcircular in outline, slightly convex but not protruding (Figure 8b). **Antennae.** Inserted in apical third of rostrum; scapes reaching to below anterior margin of eye in repose; funicles with segments 1 and 2 subequal, each 2× longer than each of segments 3 to 7; clubs elongate, 2.5× longer than broad, finely pubescent (Figure 8c). **Pronotum.** Trapezoidal in shape, 1.8× wider at base than at apex; disc tumescent, culminating in a pair of blunt, elongate, broadly separated central tubercles carrying a tuft of black erect scales, in male with band of pale scales curving laterad from tubercles towards anterior margin (Figure 8a), in female completely covered with pale scales laterally; surface shallowly punctorugulose. **Scutellar shield**. Roundly triangular to cordiform, margins bluntly rounded, sparsely covered with elongate narrow scales. **Elytra.** 1.8× longer than pronotum, joint width 1.3× length, slightly wider than base of pronotum; humeri broadly rounded, slightly protruding (Figure 8a,b). **Legs**. Femora with 2 unequal ventral teeth, anterior one very small; tibiae with premucro smaller than uncus; tarsi with claws slightly divergent (Figure 8d). **Genitalia**. Penis narrowly elongate (6× longer than broad), sides subparallel, apically narrowed, pointed, temones slightly shorter than penis body, endophallus with long, hairpin-shaped internal sclerite (Figure 8e); gonocoxites narrow, apically bluntly rounded, setose (Figure 8f), bursa copulatrix spinulose, spermatheca thick, right-angled, gland moderately long, elongate oval, narrowing apicad (Figure 8g).

Material examined (9 ♂, 7 ♀). Holotype, ♂: "QLD: Garradunga, Polly / Creek / 11 Nov 2003 / J. Hasenpusch // ANIC / image // ♂ // HOLOTYPE / *Menechirus howdenae* / Jennings & Oberprieler, 2018" (ANIC). Paratypes (all labelled "PARATYPE / *Menechirus howdenae* / Jennings & Oberprieler, 2018"): 1 ♂, 2 ♀: same data as holotype; 6 ♂, 5 ♀: "Julatten, QLD / em 27 Jan. 1987 / A.T. Howden // Ex mature / fruit of / Syzygium sp. // ♂/♀"; 1 ♂: "Ex Rhodomyrtus / macrocarpus / Mission Beach / 24.9.54 WAS // D.P.I. QLD // 701 / ♂".

Distribution (Figure 13). North-eastern Queensland.

Hostplants. *Syzygium* species, seemingly also *Rhodomyrtus macrocarpus* (Myrtaceae).

Derivation of name. The species is named for the late Anne Howden (1927–2016) of Ottawa, Canada, who collected the majority of the type specimens of this species and also made important other contributions to the knowledge of the Australian weevil fauna, in particular to the biology of the iconic tribe Amycterini, and to oviposition behaviour in weevils in general.

Remarks. This is one of two species thus far known to occur in Queensland. It is most similar to the New Guinean *M. oculatus*, of a similar size and with similar markings on the prothorax and elytra but with a shorter and rounder body shape. It further differs from *M. oculatus* in having distinct dorsomedian carinae in the basal half of the rostrum, a broad band of black setae across the base of the pronotum, the central pronotal tubercles larger and the endophallic sclerite of the penis narrowly hairpin-shaped, not broadly V-shaped as in *M. oculatus.* In the female terminalia, *M. howdenae* has broader gonocoxites, a longer sternite VIII and a more rectangular spermatheca. From the smaller *M. parryi* and *M. mundus*, *M. howdenae* also differs conspicuously in the lack of black scales behind the scutellar shield in the male, the less ornate pronotal and elytral colour patterns, the divergent claws and the shape of the endophallic sclerite of the penis.

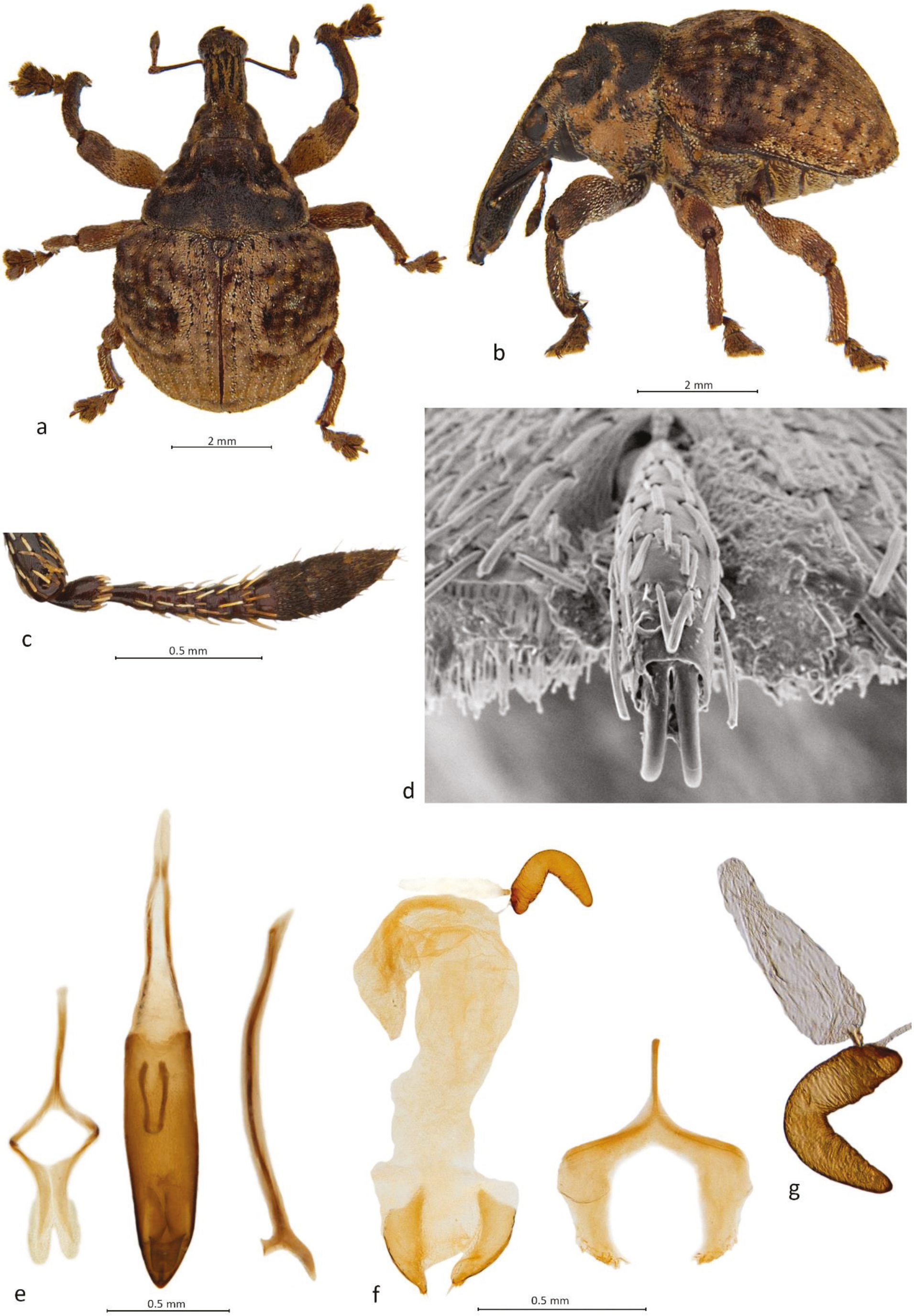

Figure 8. Habitus and diagnostic characters of *Menechirus howdenae* sp. n.: (**a**) habitus of male, dorsal view; (**b**) habitus of male, left lateral view; (**c**) right antenna, male, dorsal view; (**d**) tarsite 3 with onychium, apical view; (**e**) genitalia, male, dorsal view; (**f**) genitalia, female, dorsal view; (**g**) **spermatheca** with gland.

Menechirus parryi Jennings & Oberprieler, **sp. n.** (Figure 9)

Sigastus new species 1: Juniper & Britton, 2010: 300 [30]

Description: Shape and size. Body short, ovoid in dorsal outline, length 3.4–4.6 mm in both sexes (holotype 4.1 mm), width ca. 0.7× length (Figure 9a), strongly convex in lateral view (Figure 9b). **Colour and vestiture.** Body densely covered with pale brown to black scales (with few white scales scattered in between); head with pale scales except two pairs of large indistinct brown patches dorsolaterally and laterally behind eyes; pronotum with brown scales except for 2 narrow, transverse bands of pale scales arching from sides of base across anterior half of disc; elytra typically with 3 similar but opposite arches from bases of interstriae 2, 4 and 6 across elytral disc, in male also with a median patch of black scales behind scutellar shield; sides with black scales, ventrites and parts of legs with pale ones (Figure 9a). **Rostrum.** Short (about 1.2× longer than pronotum in male, 1.3× in female), robust, straight, dorsoventrally flattened, apically broadened in dorsal view, distal third dorsally coarsely shallowly punctate, proximal two-thirds indistinctly rugose with faint median carina and indistinct dorsolateral carinae, no dorsomedian ones (Figure 9a,b). **Eyes.** Broadly ovoid in outline, slightly convex but not protruding (Figure 9b). **Antennae.** Inserted in apical third of rostrum; scapes not reaching to below anterior margin of eye in repose; funicles with segments 1 and 2 subequal, each almost 2× longer than each of the segments 3 to 7; clubs shortly elongate, 2× longer than broad, finely pubescent (Figure 9c). **Pronotum.** Trapezoidal in shape, 2× wider at base than at apex; disc tumescent, culminating in a pair of low, blunt, broadly separated central tubercles with a tuft of black scales, a similar but smaller pair of tubercles on anterior margin and another pair of indistinct ones laterally, the posterior curved band of pale scales passing just behind central tubercles and the anterior, medially interrupted band just behind lateral tubercles (Figure 9a). **Scutellar shield**. Roundly subtriangular, sparsely covered with long, suberect scales. **Elytra.** 2× longer than pronotum, joint width only slightly less than length, wider than base of pronotum; interstriae 1 slightly elevated at base, interstriae 2 with single large tubercle with tuft of erect brown scales in middle of length, interstriae 3 with 2 more anteriorly placed, similarly tufted tubercles, interstriae 5 with similar pair of smaller tubercles; single tubercle of interstriae 2, posterior tubercle of interstriae 3 and tubercle 1 of interstriae 5 connected by a pale band forming a conspicuous V (Figure 9a). **Legs**. Femora with 2 unequal ventral teeth, anterior one minute; tibia with premucro much smaller than uncus; tarsi with claws parallel, very close together (Figure 9d). **Genitalia**. Penis elongate (4.5× longer than broad), sides subparallel, apically narrowed, pointed, temones as long as penis body, endophallus spinulose, without distinct internal sclerites (Figure 9e); bursa copulatrix with two long bands of dense, elongate spicules (Figure 9f), spermatheca crescentic, about evenly thick, gland large, oval, broadly rounded apically (Figure 9g).

Figure 9. Habitus and diagnostic characters of *Menechirus parryi* sp. n.: (**a**) habitus of male, dorsal view; (**b**) habitus of male, left lateral view; (**c**) right antenna, male, dorsal view; (**d**) tarsite 3 with onychium, apical view; (**e**) genitalia, male, dorsal view; (**f**) genitalia, female, dorsal view; (**g**) spermatheca with gland.

Material examined (12 ♂, 7 ♀). Holotype, ♂: "NSW: Canton Beach Rd, Toukley. / 33°15′56″S, 151°32′26″E. / 08 May 2007. Cate Inwood. / Ex Syzygium paniculatum fruit. / 6 m street tree. Emerged: 22/06/2007 // ♂// ANIC / Image // HOLOTYPE / *Menechirus parryi* / Jennings & Oberprieler, 2018" (ANIC). Paratypes (all labelled "PARATYPE / *Menechirus parryi* / Jennings & Oberprieler, 2018" in ANIC). 1 ♀: same data as holotype except "Emerged: 12/07/2007"; 1 ♂: "33°16′17″S 151°33′03″E / NSW: Noraville, Canton / Parade / 7 Mar 2008 P. Juniper / on *Syzygium paniculatum* // ♂// ANIC / Image"; 2 ♂: "33°16′17″S 151°33′03″E / NSW: Noraville, Canton / Parade / 7 Mar 2008 P. Juniper / on *Syzygium paniculatum* // ♂"; 1 ♂: "NSW: Wingham / 14 Nov. 1990 ex / riparian r′for / G. Williams // on T.1. / Waterhousea / floribunda / blossom // ♂"; 1 ♂: "NSW: Wingham / 22 Nov. 1990 ex / riparian r′for / G. Williams T.I. // on Waterhousia [*sic*] / floribunda / blossoms // ♂// ANIC / Image"; 1 ♂: "2.3 km N Harrington / NSW 9 Oct. 1983 / G. Williams ex lit. / rainfor. Margin // ♂"; 1 ♀: "@3 km NE Harrington / NSW 13 Dec. 1985 / G. Williams ex / littoral rainforest // ♀"; 1 ♂: "Cessnock, NSW / W. Duboulay // ♂"; 1 ♀: "3 km N Lansdowne / via Taree NSW / 26 Sept. 1983 / G. Williams coll. / wet sclero. for. // ♀"; 1 ♀: "3 km, N. Lansdowne, / N.S.W. 29 Nov. 1991 / G. Williams. / ex Waterhousea / floribunda / blossoms // ♀"; 1 ♀: "Toowomba / 14 Dec 74 Q. // ♀// ANIC / Image"; 1 ♀: "Peachester / 16 Dec. 68 / R.A. Yule / Dept. QLD // ex / Euc. / flower // 13 // ♀"; 1 ♂, 1 ♀: "H. Hacker / N Pine R. / 12-10-25 // ♂"; 1 ♂: "Pine Creek S of / Bundaberg QLD / 23.xi.75 H. Frauca // ♂"; 1 ♀: "Pine Creek S of / Bundaberg QLD / 2.xii.75 H. Frauca // ♀"; 1 ♂: "Windsor Tableland, via / Mt. Carbine, N. Qld / 7 Jan. 1978 / R.I. Storey // ♂".

Distribution (Figure 13). Central coast of New South Wales to north-eastern Queensland (Cairns area).

Hostplants. Mainly *Syzygium paniculatum*, also *S. australe* and *S. floribundum* (Myrtaceae).

Derivation of name. This species is cordially named after David Parry, our local Leica representative, for his ongoing support and expert advice concerning our microscopes and the LAS imaging systems as well as for his unfailing humour, with which he brightens up our mundane taxonomic work.

Remarks. *Menechirus parryi* is most similar to *M. mundus*, differing externally in its more pronounced colour pattern of the elytra and internally in the shape of the penis, gonocoxites and spermatheca and, most distinctly, in the bursa possessing a pair of bands of spicules. It also appears to be separated from *M. mundus* geographically as it is not known to occur in the Northern Territory. From the other species occurring in Queensland, *M. howdenae*, *M. parryi* is easily distinguishable by its smaller size, different dorsal colour pattern and differences in the male and female genitalia. As in *M. mundus*, the males are distinguishable from the females by the patch of black scales behind the scutellar shield.

The larvae of this species can cause significant fruit loss on *Syzygium paniculatum*, an endangered tree species in New South Wales [30]. Juniper & Britton [30] recorded the species from 51% of fruits sampled at five locations in central New South Wales, mostly based on adults emerging from pupal shelters among damaged fruits in rearing containers.

Menechirus mundus Jennings & Oberprieler, **sp. n.** (Figure 10)

Description: Shape. Body short, ovoid, length 4.1–4.8 mm in both sexes (holotype 4.6 mm), width ca. 0.7× length (Figure 10a), distinctly convex in lateral view (Figure 10b). **Colour and vestiture.** Body densely covered with pale brown to black scales (with few white scales scattered in between); head with pale scales on forehead and vertex, dark brown ones behind eyes; pronotum with brown scales except for 2 narrow, transverse bands of pale scales arching from sides of base across anterior half of disc and for more poorly defined areas of pale scales along base; elytra with pale scales except for a pair of large, dark lateral patches in middle, restricting pale scales into a narrow hour-glass shape, in male also with a median patch of black scales behind scutellar shield; venter and legs with mostly pale scales (Figure 10a). **Rostrum.** Short (as long as pronotum in male, 1.3× longer in female), robust, straight, dorsoventrally slightly flattened, apically broadened in dorsal view, distal third coarsely punctate, proximal two-thirds indistinctly rugose with distinct median carina and indistinct dorsolateral carinae, no dorsomedian ones (Figure 10a,b). **Eyes.** Subcircular in outline, very slightly convex but not protruding (Figure 10b). **Antennae.** Inserted in apical third of rostrum; scapes not reaching to below anterior margin of eye in repose; funicles with segments 1 and 2 subequal, each almost 3× longer than each of segments 3 to 7; clubs shortly elongate, 2× longer than broad, finely pubescent (Figure 10c). **Pronotum.** Trapezoidal in shape, 2× wider at base than at apex; disc strongly convex, in centre with a pair of very slight, broadly separated elevations (not forming tubercles) with only a few or no black scales, a similar pair of elevations on anterior margin and another pair laterally, the posterior curved band of pale scales passing just behind central elevations and the anterior band just behind anterior and lateral elevations (Figure 10a,b). **Scutellar shield**. Broadly ovoid to roundly subtriangular, covered with broad pale scales. **Elytra.** 2.2× longer than pronotum, joint width subequal to length, wider than base of pronotum; humeri broadly rounded, hardly protruding; interstriae 1 in male slightly elevated at base, interstriae 2 with single elongate tubercle with a tuft of erect brown scales in middle of length, interstriae 3 with 2 more anteriorly placed, similarly tufted tubercles but anterior one very faint, interstriae 5 with similarly faint anterior tubercle only; single tubercle of interstriae 2, posterior tubercle of interstriae 3 and single tubercle of interstriae 5 demarcating posterior edge of anterior triangle of the pale hour-glass-shaped macula (Figure 10a). **Legs**. Femora with 2 unequal ventral teeth, anterior one minute; tibiae with premucro much smaller than uncus, especially on metatibiae; tarsi with claws parallel, very close together (Figure 10d). **Genitalia**. Penis elongate, very narrow (7× longer than broad), sides subparallel, apically narrowly pointed, temones shorter than penis body, endophallus spinulose, without distinct internal sclerites (Figure 10e); bursa copulatrix without bands of spicules (Figure 10f), spermatheca weakly crescentic, thicker in basal than in apical half, gland large, narrowly rounded apically (Figure 10g).

Material examined (7 ♂, 7 ♀). Holotype, ♂: "Darwin, N.T. / 27.xi.1994 / A. Allwood // Ex fruit of / Eugenia sp. // ♂ // ANIC / image // HOLOTYPE / *Menechirus mundus* / Jennings & Oberprieler, 2018" (ANIC). Paratypes (all labelled "PARATYPE / *Menechirus mundus* / Jennings & Oberprieler, 2018" in ANIC). 6 ♂, 6 ♀: same data as holotype except "ANIC / image"; 1 ♀: "Pickertaramoor / Melville Is. N.T. / 18.ii.1976 / T. Angeles // Bred from / Acmena / hemilampra // ♀".

Distribution (Figure 13). North-western Northern Territory.

Hostplants. *Syzygium hemilamprum* (Myrtaceae) and possibly other species of *Syzygium*. The host recorded as *Eugenia* on labels is probably *Syzygium hemilamprum* too, which occurs in the Tiwi Islands and at least in the botanical garden in Darwin. It also occurs along the Queensland coast, but no specimens of *M. mundus* have been recorded from there.

Derivation of name. The name of the species is a Latin adjective meaning neat or elegant, in reference to its smoother pronotum and elytra compared with those of all other *Menechirus* species.

Remarks. *Menechirus mundus* is most similar to *M. parryi*, differing externally in its less pronounced colour pattern of the pronotum and elytra and internally in its genitalia, the penis being much narrower, the gonocoxites broader, the spermatheca of uneven thickness and, most distinctly, the bursa not possessing a pair of bands of spicules. However, all available specimens of *M. mundus* are teneral (reared from fruits), and the genitalia of mature specimens should be examined to verify these differences. *Menechirus mundus* also appears to be geographically separated from *M. parryi*, being only known from the north-western parts of the Northern Territory.

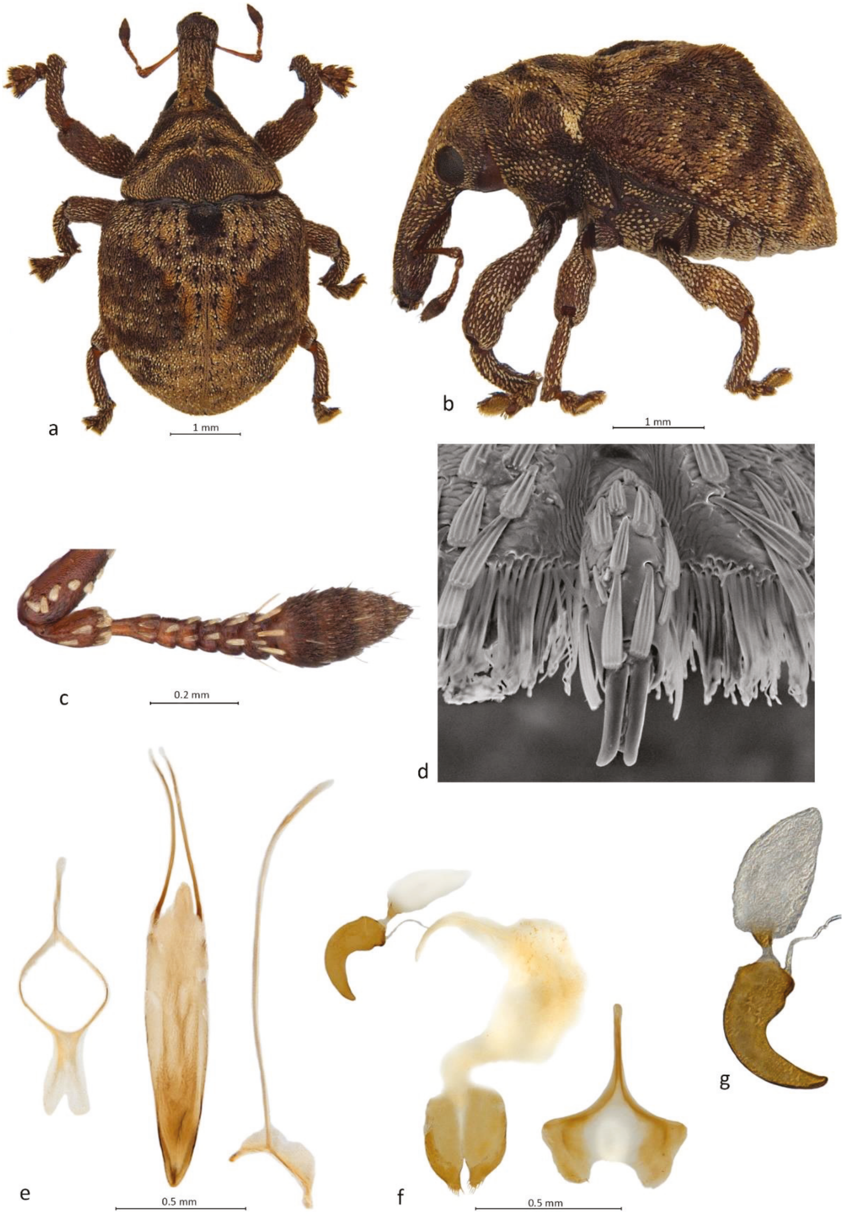

Figure 10. Habitus and diagnostic characters of *Menechirus mundus* sp. n.: (**a**) habitus of male, dorsal view; (**b**) habitus of male, left lateral view; (**c**) right antenna, male, dorsal view; (**d**) tarsite 3 with onychium, apical view; (**e**) genitalia, male, dorsal view; (**f**) genitalia, female, dorsal view; (**g**) spermatheca with gland.

3.6. Description of Kuschelorhynchus macadamiae *gen. et sp. n.*

Genus ***Kuschelorhynchus*** Jennings & Oberprieler, **gen. n.** (Figures 11 and 12)

Type species: *Kuschelorhynchus macadamiae* Jennings & Oberprieler, **sp. n.**

Description: Shape. Body medium-sized, short and broad, robust, strongly sculptured. **Colour and vestiture**. Body densely covered with whitish, yellowish, reddish brown and dark brown, striate, imbricate scales, forming distinct colour pattern especially on pronotum and elytra. **Rostrum.** Short, robust, almost straight, subcylindrical at base but flattening and broadening apicad, dorsally strongly sculptured; laterally with deep, straight scrobes running onto venter of head, not quite meeting in middle but sharply bent into shallower grooves running parallel to each other anteriad almost to labium, receiving funicles and clubs when antennae retracted. **Head.** Spherical, densely squamose, dorsally impressed and tuberculate. **Eyes.** Subcircular in outline, slightly convex but not protruding. **Antennae.** Scapes almost straight, subcylindrical, gradually inflated distad, slightly longer than funicles, funicles 7-segmented, with segment 1 about 2× longer than others, 7 appressed to club but distinct; clubs 3-segmented with small apical cone, shortly elongate, slightly compressed, finely pubescent. **Thorax.** Pronotum shortly trapezoidal, slightly constricted anteriorly, with pair of large, double-pointed central tubercles and smaller ones anteriorly and laterally; lateral margin not drawn into ocular lobes; procoxal cavities in about middle of prosternal length, separated by about one-third of their width. Scutellar shield elongate-ovoid, convex, densely squamose. Pterothoracic sclerites distinct; meso- and metacoxal cavities separated by nearly their width; mesoventrite very short, steeply sloping; metaventrite also short, transversely convex; metanepisternal sutures distinct, complete, without sclerolepidia. **Elytra.** As broad across humeri as long, with pair of large, flattened central tubercles and some smaller lateral ones in line towards humeri; at apex conjointly truncate, no pygidium exposed. **Legs**. Procoxae large, spherical; femora robust, subcylindrical, slightly sinuate, with large ventral tooth in middle of length and much smaller tooth immediately distally of it; tibiae straight, well compressed, at apex with strong uncus and smaller premucro in a tuft of long, testaceous setae; tarsi short, broad, compact, with onychium narrow, short, about as long as tarsite 1, claws small, slightly divergent. **Abdomen**. Ventrites 1 and 2 equal in length, almost 2× longer than 3 and 4, 5 slightly longer than 4, apically broadly rounded. **Genitalia**. Penis elongate, with distinct tectal plate, temones shorter than penis body, endophallus with large, symmetrical, looped internal sclerite. Gonocoxites short, narrow, not well differentiated into proximal and distal parts, apically narrowed, bluntly rounded, with numerous long setae but no styli; bursa copulatrix bulbous, unsclerotised, ventrally at junction with vagina with a short, tubular extension braced by a stack of several semicircular, sclerotised bows, leading broadly into oviduct; spermatheca crescentic, not differentiated, cornu acute, gland bulbous with funnel-shaped, sclerotised stalk, spermathecal duct inserted dorsally on oviduct just anteriorly of sclerotised bows; sternite VIII short and broad, bladal part with large desclerotised median area, margin fringed with several stiff setae, apodeme shorter than bladal part, narrow.

Derivation of name. The genus is respectfully named for the late Guillermo (Willy) Kuschel (1918–2017), who contributed so much to the knowledge of the global and the Australian weevil faunas, including the Cryptoplini [13], and who has been a close friend and mentor of the second author for three decades. The genus name is masculine in gender; the second part of the name is latinised from the Greek noun *rhynchos* (snout), a common component of genus and species names in Curculionoidea.

Remarks. The genus is described for a single, striking Australian species of Cryptoplini that is associated with *Macadamia* (Proteaceae). *Kuschelorhynchus* is similar to *Menechirus* and *Sigastus* in having two small, separate tarsal claws, but it differs from these two genera in its pronotal and elytral sculpture and in its male and female genitalia, specifically in the endophallic sclerite of the male and the peculiar sclerotisation of the bursa/oviduct of the female, which are unique among Cryptoplini. It also differs from all other Cryptoplini in its host, the larvae developing in the fruits of *Macadamia* (Proteaceae) rather than in those of Myrtaceae.

Kuschelorhynchus macadamiae Jennings & Oberprieler, sp. n. (Figures 11 and 12)
Sigastus weevil: Fay et al. 2001: 137–140 [19]; Bright, 2017: 1–4 [21], 2017: 1–5 [22]
Sigastus new species 2: Juniper & Britton, 2010: 300 [30]

Description: Shape. Body short, subhexagonal in outline, length 7.1–9.5 mm in both sexes (holotype 8.4 mm), width ca. 0.75× length (Figure 11a), convex in lateral view with large tubercles on pronotum and elytra (Figure 11b). **Colour and vestiture.** Body densely covered with a mixture of silvery white, pale and dark brown scales, giving it a greenish-grey colour; head with complex pattern of dark brown and pale brown/whitish scales; pronotum greenish-grey except for centre and dorsal anterior margin around tubercles reddish-brown and reddish-brown elongate lateral patches (Figure 11c); elytra with pale greenish-grey scales on dorsum, darker greenish-grey ones laterally of tubercles up to interstriae 6, interstriae 7, 8 and 9 with dark reddish-brown scales laterally; legs banded with pale and dark brown scales interspersed with scattered white ones; venter largely with pale brown scales (Figure 11a). **Rostrum.** Short (about 0.8× as long as pronotum in both sexes), very robust, straight, dorsoventrally slightly flattened, apically broadened in dorsal view (Figure 11d,e), with sharp median carina throughout length and irregular dorsolateral ones, these interrupted and bridged above antennal insertions and ending in short, squamose tubercle between eyes (Figure 11d,e). **Eyes.** Subcircular in outline, slightly convex, not protruding (Figure 11d,e). **Antennae.** Inserted in apical third of rostrum; scapes reaching to below anterior margin of eye in repose (Figure 11e); funicles with segment 1 ca. 2× longer than 2, 3 to 7 progressively shorter towards club; clubs shortly elongate, 2.5× longer than broad in dorsal view (the narrow side), finely pubescent (Figure 11f). **Pronotum.** Trapezoidal in shape, 1.8× wider at base than at apex; disc strongly tumescent, culminating in a pair of tall, double-peaked central tubercles carrying a tuft of long, erect, reddish-brown setae, at anterior margin a similarly tufted inner pair of tubercles and a smaller outer pair, laterally of central pair another pair of smaller, squamose tubercles (Figure 11a–c). **Scutellar shield.** Elongate, strongly convex, densely covered with dark brown scales. **Elytra.** 2× longer than pronotum, joint width 0.95× length, 0.75× as broad as pronotum; humeri broadly rounded, slightly protruding; interstriae 1 slightly elevated behind scutellar shield and with black scales flanking it in both sexes, interstriae 2 without tubercles, interstriae 3 with small, squamose tubercle just behind scutellar shield and a huge elongate tubercle behind it, flattened on outer side and with yellowish scales on mesal and dark brown to black ones on outer side, interstriae 4 without tubercles but almost vertical on outside of large tubercle of interstriae 3, interstriae 5 with large, pointed anterior tubercle just anteriorly of tubercle of interstriae 3 and with smaller, flatter one on declivity involving also interstriae 4 and 6 next to and behind it, interstriae 6 with small anterior tubercle next to tubercle of interstriae 5, all tubercles demarcating anterior and posterior sides of the large, brown, subtriangular lateral elytral macula (Figure 11a,b). **Legs**. Femora with two unequal ventral teeth, anterior one smaller (very small on metafemora); tibiae with premucro prominent but smaller than uncus (very small on metatibiae); tarsi with claws slightly divergent (Figure 11g). **Genitalia**. Penis shortly elongate (5× longer than broad), sides parallel, apically rounded except for small apical point, temones 0.62× as long as penis body, endophallus with long, strongly sclerotised, looped internal sclerite, ventral part narrow, flat, dorsal part broad, apically cleft (Figure 12a,b); oviduct beneath bursa copulatrix with ca. 20 semicircular sclerotised bows stacked together (Figure 12c,d), spermatheca roundly crescentic, cornu acute, gland large, oval (Figure 12e).

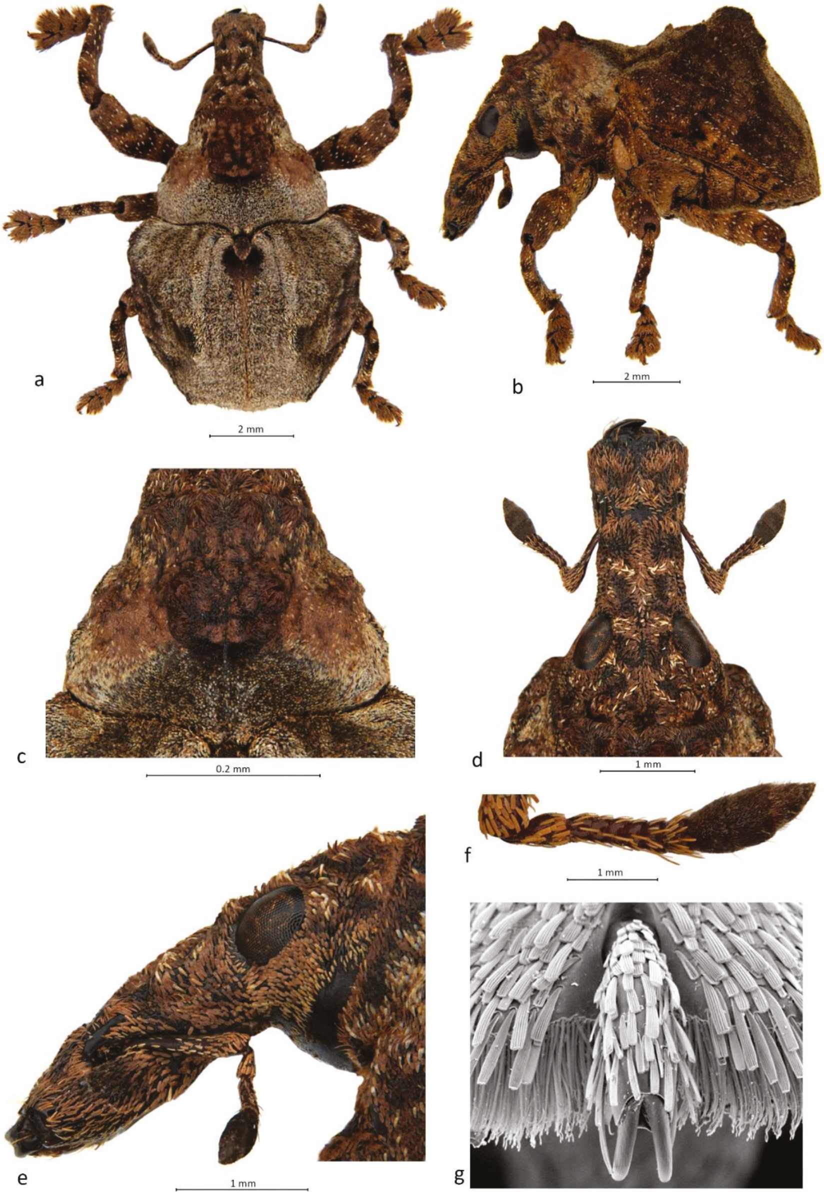

Figure 11. Habitus and diagnostic characters of *Kuschelorhynchus macadamiae* gen. & sp. n.: (**a**) habitus of male, dorsal view; (**b**) habitus of male, left lateral view; (**c**) pronotum, dorsal view; (**d**) head and rostrum, dorsal; (**e**) head and rostrum, lateral; (**f**) right antenna, male, dorsal view; (**g**) tarsite 3 with onychium, apical view.

Figure 12. Genitalia of *Kuschelorhynchus macadamiae* gen. & sp. n.: (**a**) genitalia, male, dorsal view; (**b**) genitalia, male, lateral view; (**c**) genitalia, female, dorsal view; (**d**) genitalia, female, lateral view; (**e**) spermatheca, female.

Material examined (29 ♂, 38 ♀). Holotype, ♂: "Chewko Rd. Walkamin, Nth. Qld / Watkins Orchard / Ex-Macadamia / 28th. Nov 2001 / R. Blanche & R. Bauer // ANIC / Image // ♂// HOLOTYPE / *Kuschelorhynchus macadamiae* / Jennings & Oberprieler, 2018" (ANIC). Paratypes (all labelled "PARATYPE / *Kuschelorhynchus macadamiae* / Jennings & Oberprieler, 2018"): 1 ♂, 3 ♀: same data as holotype (ANIC); 4 ♂, 1 ♀: "Walkamin, Nth. Qld / DPI Research Station / Ex-Macadamia / 7th. Nov 2001 / R. Blanche and R. Bauer" (ANIC, QMBA); 1 ♀; "Atherton, Nth. Qld / Felderhofs Orchard / Ex-Macadamia / 27th. Nov 2001 / R. Blanche and R. Bauer // ♀" (ANIC); 1 ♂, 4 ♀: "Wongabel Rd. Atherton, Nth. Qld / Robbins Orchard / Ex-Macadamia / 27th. Nov 2001 / R. Blanche and R. Bauer" (ANIC); 5 ♀: "Higgins Rd. Kairi, Nth. Qld / Rees Orchard / Ex-Macadamia / 27th. Nov 2001 / R. Blanche and R. Bauer // ♀" (ANIC, QMBA); 1 ♂, 2 ♀: "Tinaroo Rd. Kairi, Nth. Qld / Cummings Orchard / Ex-Macadamia / 27th. Nov 2001 / R. Blanche and R. Bauer" (ANIC); 1 ♂: "Emerald Ck. / Mareeba, Qld / 5.XI.1994 / J. Allen // bred ex / Macadamia / fruit // ♂"; 6 ♂, 11 ♀: "AUSTRALIA: n. Qld / Kay Rd, Emerald Ck / via Mareeba. 27.X.1994 / J. Allen and K. Lewis // Larvae feeding on / Macadamia fruit // ♂" (ANIC, QDPI, QMBA); 2 ♂, 2 ♀: "Kay Rd. Mareeba, Nth. Qld / Reppels Orchard / Ex-Macadamia / 28th. Nov 2001 / R. Blanche and R. Bauer" (ANIC); 2 ♂: "Beantree Rd. Tolga, Nth. Qld / Staines Orchard / Ex-Macadamia / 26th Nov 2001/ R. Blanche and R. Bauer // ♂" (ANIC); 1♀: "Beantree Rd. Tolga, Nth. Qld / Inderbitzens Orchard / Ex-Macadamia / 28th.Nov 2001 / R. Blanche and R. Bauer // ♀" (ANIC); 3 ♂: "Kennedy Hway. Tolga, Nth. Qld / O'Neils Orchard / Ex-Macadamia / 28th. Nov 2001 / R. Blanche and R. Bauer // ♂" (ANIC); 7 ♂, 8 ♀.: "AUSTRALIA: n. Qld / Tolga 11-18.X.1994 / J. Watson // Larvae feeding on / Macadamia fruit // ♂" (ANIC, CMNC, QDPI, QMBA); 1 ♂: "Tolga, Qld / 1.XI.1994 / J. Watson // live on Macadamia ♂"(ANIC); 1 ♂, 1 ♀: "Tolga, Qld / 27.IX.1994 / J. Watson // bred ex / seed / Macadamia" (QDPI).

Distribution (Figure 13). Recorded from north-eastern Queensland and north-eastern New South Wales but natural distribution outside of these areas of commercial macadamia plantations unknown, probably largely congruent with that of *Macadamia* along the east coast of Australia.

Host plants. *Macadamia* (Proteaceae). The commonly recorded host is likely to be the commercial hybrid cultivar *M. tetraphylla* / *M. integrifolia*. Whether *K. macadamiae* occurs on both these species also in the wild, and/or on the other two species in the genus *Macadamia*, *M. jansenii*, and *M. ternifolia*, and on closely related genera, is unknown.

Derivation of name. The species is named after its host genus, *Macadamia*, its name being a noun in the genitive case.

Remarks. The species has usually been referred to as the "Sigastus weevil" in publications dealing with macadamia pests [19–22], following its initial but tentative assignment to the genus *Sigastus* by Fay [19], although Blanche et al. [20] indicated that it was likely to belong to a different (undescribed) genus. This is confirmed by the present study and the description of both the species and the genus, and therefore its alternative common name, Macadamia Seed Weevil [22], is much more appropriate.

Kuschelorhynchus macadamiae emerged as a 'pest' of macadamia trees in plantations on the Atherton Tableland in 1994 [19] and continues to cause serious infestations of this crop there and in the region of the northern rivers in New South Wales [21,22], where it appeared more recently. Its life history and behaviour have been studied in some detail [19,21,22]. The female weevil scarifies the husk of green macadamia fruits ('nuts') with her mandibles and then lays a single egg into the husk. She then severs the stalk of the fruit so that it drops to the ground. The larva feeds on the kernel and pupates in the fruit, from which the next-generation adult emerges about two months later. Infestation rates (crop loss) in plantations average about 30% but can be as high as 73%. Control is achieved by a combination of insecticide application (to kill the adults) and orchard sanitation (removing the dropped fruits with developing larvae). Exposure of the infested fruits to sunlight was also found to cause 100% mortality of the larvae [19]. Being a native insect with presumably natural hosts in areas surrounding macadamia plantations, *Kuschelorhynchus macadamiae* stands to re-infest plantations every season.

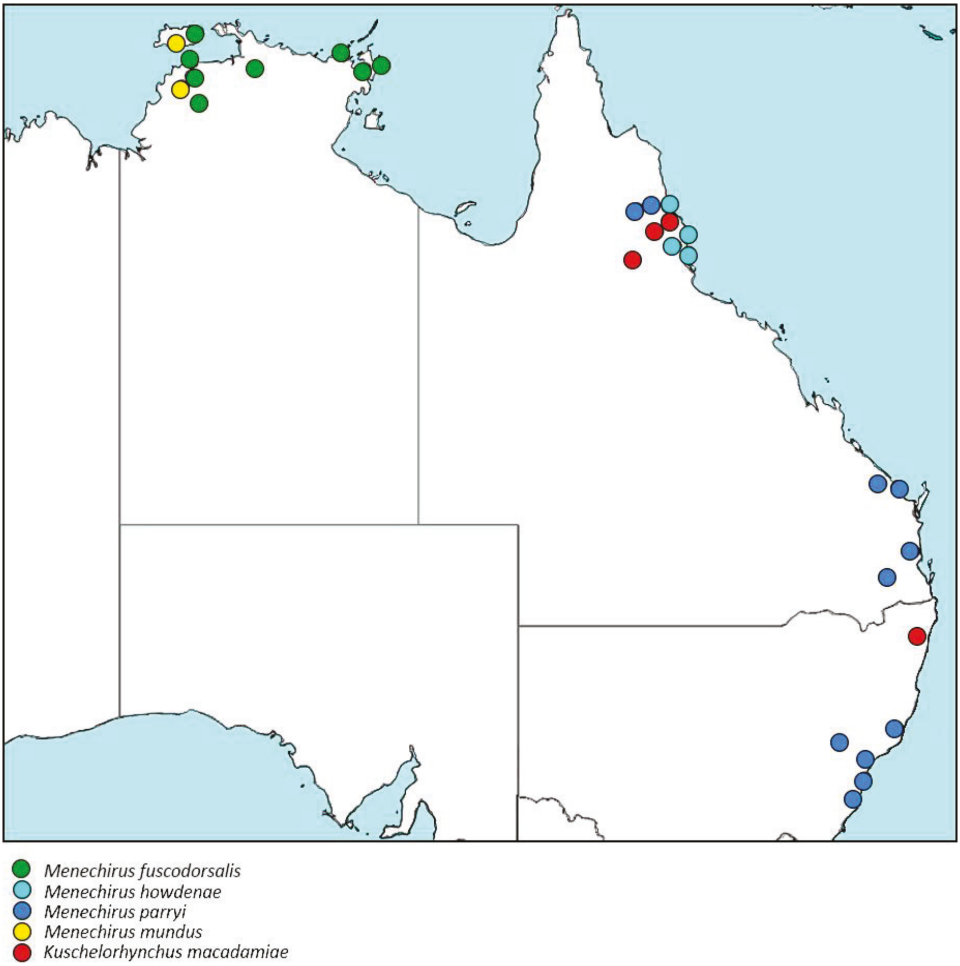

Figure 13. Distribution of the species of *Menechirus* Hartmann and *Kuschelorhynchus* gen. n. in Australia.

4. Discussion

The most intriguing feature of the Cryptoplini is the apparent pedotectal structure of their penis. This type of penis, consisting of distinct ventral and dorsal parts, respectively the pedon and tectum, is characteristic of the more basal families of weevils (Nemonychidae to Brentidae) as well as of the basal lineages of Curculionidae (Brachycerinae-Erirhininae), whereas the 'higher' Curculionidae (the CEGH and CCCMS clades [35]) have a pedal type of penis, without a tectum. There are other differences between these two types of male genitalia in weevils too, concerning the structure of the temones and the tegmen as well as of the sternites VIII and IX associated with the aedeagus. In the typical pedotectal aedeagus, the temones have two basal arms (a dorsal one connecting to the tectum and a ventral one to the pedon), the tegmen has a large dorsal plate with short parameral lobes and is laterally articulated, sternite VIII is complete and typically carries a small spiculum relictum [36], and sternite IX has a large basal plate, whereas in the pedal aedeagus the temones only have a ventral arm (connected to the pedon), the tegmen has a dorsal pair of narrow parameres and is laterally not hinged, sternite VIII is divided into two crescentic hemisternites, and in sternite IX the basal plate forms a narrow fork [37].

As the pedotectal type occurs in the phylogenetically more basal weevil families as well as in those of the sister-group of Curculionoidea, the Chrysomeloidea, it is regarded as the plesiomorphic type, with the pedal type indicated to be more derived and a possible apomorphy of the 'higher' curculionids. The transition between these two types is not entirely clear as few cases of obvious intermediary forms appear known, although it is evident that the tectum may become reduced from the sides, becoming thread-like (as in *Perieges* Schoenherr of Cryptolaryngini [36]), or become shorter and desclerotised (as in many species of *Echinocnemus* Schoenherr of Erirhinini), before vanishing completely. An apparent further step in this reduction of the tectum is represented by the genus *Cranoides* Kuschel (Cranopoeini), in which the remnants of the dorsal temonal arms remain, but unconnected to a tectum [13]. A similar condition also occurs in several species of *Echinocnemus*. In the pedal penis, the dorsal side of the pedon is usually membranous (the penis dorsally 'open'), but the lateral walls may extend dorsad and meet along the midline for a shorter or longer distance, sometimes transforming the pedon into a closed tube.

In Cryptoplini a different type of reduction of the pedotectal penis may have taken place. In all of the species examined, the penis has a distinct, long dorsal plate that is fused to the pedon at the base but free and tongue-like at the apex (Figure 14). It is slightly narrower and shorter than the pedon and laterally membranously connected to it along the basal two-thirds of its length, but in the apical third it is laterally free and flexible up and down, allowing the internal sclerite of the endophallus to evert through the ostium (beneath the tip of the dorsal plate) during copulation. Apart from the basal fusion, this plate is very similar to the tectum of the pedotectal penis. In the other genital structures, the aedeagus of the Cryptoplini is not of the pedotectal type, in that the temones have no dorsal (tectal) arm, the ring of the tegmen is laterally fused, its dorsal part consists of long parameres (though medially fused along most of their length), the basal plate of sternite IX is narrowly forked and sternite VIII is divided into two hemisternites. Two interpretations of this tectal plate in Cryptoplini appear plausible: either it is the remnant of the tectum of more primitive weevils, resulting not from a sideways reduction of the tectum but from a basal fusion of tectum and pedon (i.e., it is homologous with the tectum), or it is a secondary, sclerotised, tectum-like elongation and extension the dorsal membrane of the pedon formed after the complete reduction of the tectum (i.e., it is analogous with the tectum). A more detailed examination of this unique plate is required to understand its origin, but either way it is a seemingly unique feature of the tribe Cryptoplini.

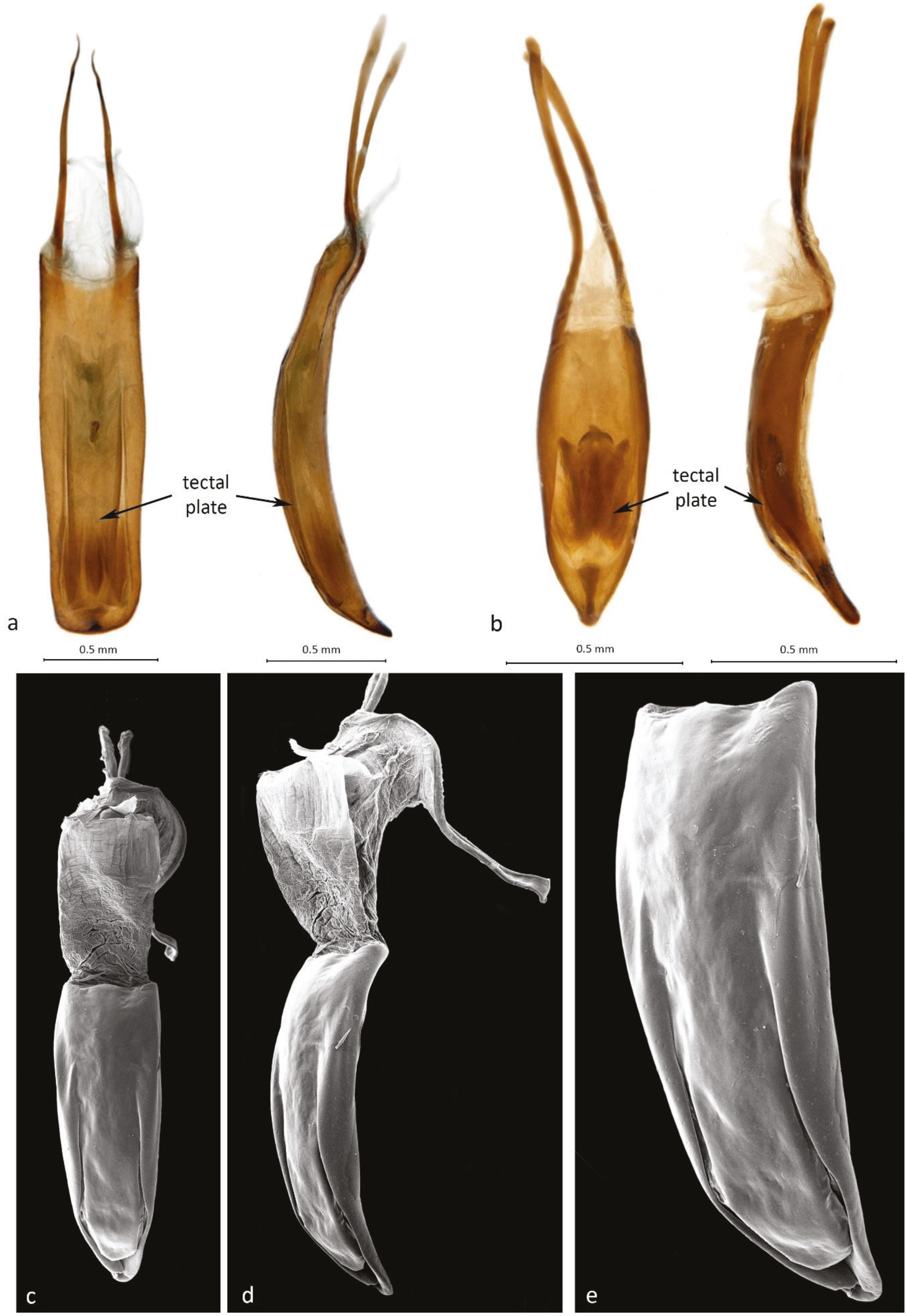

Figure 14. Tectal plates of Cryptoplini: (**a**) penis of *Sigastus fascicularis* Pascoe, dorsal and lateral view; (**b**) penis of *Haplonyx casuarinae* (Lea), dorsal and lateral view; (**c**) aedagus of *Haplonyx maximus* Lea, dorsal view (tegmen pulled forward over temones); (**d**) aedagus of *Haplonyx maximus* Lea, dorsolateral view (tegmen pulled forward over temones); (**e**) apical part of penis of *Haplonyx maximus* Lea, dorsolateral view.

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References

1. Caldara, R.; Franz, N.M.; Oberprieler, R.G. 3.7.10 Curculioninae Latreille, 1802. In *Handbook of Zoology. Coleoptera, Beetles (Phytophaga: Chrysomeloidea, Curculionoidea): Morphology and Systematics*; Leschen, R.A.B., Beutel, R.G., Eds.; Walter de Gruyter GmbH: Berlin, Germany; Boston, MA, USA, 2014; Volume 3, pp. 589–628, ISBN 978-3-11-027370-0.
2. Lacordaire, T. Histoire Naturelle des Insectes. In *Genera des Coléoptères ou Exposé Méthodique et Critique de tous les Genres Proposés Jusqu'ici dans cet Ordre d'Insectes*; Tome Sixième; Librairie encyclopédique de Roret: Paris, France, 1863; 637p. [CrossRef]
3. Erichson, W.F. Beitrag zur Insecten-Fauna von Vandiemensland, mit besonderer Berücksichtigung der geographischen Verbreitung der Insecten. *Arch. Naturgesch.* **1842**, *8*, 83–287. [CrossRef]
4. Lea, A.M. Notes on some miscellaneous Coleoptera, with descriptions of new species. Part VIII. *Trans. R. Soc. S. Aust.* **1931**, *55*, 39–64.
5. Pascoe, F.P. Contributions towards a knowledge of the Curculionidae [part]. *J. Linn. Soc. Lond. Zool.* **1870**, *10*, 434–458. [CrossRef]
6. Alonso-Zarazaga, M.A.; Lyal, C.H.C. *A World Catalogue of Families and Genera of Curculionoidea (Insecta: Coleoptera) (excepting Scolytidae and Platypodidae)*; Entomopraxis: Barcelona, Spain, 1999; 315p, ISBN 84-605-9994-9.
7. Lea, A.M. The clawless and apparently clawless Curculionidae of Australia. *Trans. R. Soc. S. Aust.* **1927**, *51*, 144–168.
8. Lea, A.M. Descriptions of new species of Australian Coleoptera. Part IV. *Proc. Linn. Soc. N. S. W.* **1897**, *22*, 584–638. [CrossRef]
9. Lea, A.M. Descriptions of Australian Curculionidae, with notes on previously described species. Part VIII. *Trans. R. Soc. S. Aust.* **1910**, *34*, 13–58.
10. Lea, A.M. Notes on Australian Curculionidae in the collection of the German Entomological National Museum of Berlin (Col.). *Deutsch. Entomol. Z.* **1910**, *153–172*, 505–526.
11. Lea, A.M. Australian Curculionidae of the subfamilies Haplonycides and Cryptorhynchides. *Trans. R. Soc. S. Aust.* **1928**, *52*, 95–164.
12. Zimmerman, E.C. *Australian Weevils (Coleoptera: Curculionoidea). Volume I. Orthoceri. Anthribidae to Attelabidae. The Primitive Weevils*; CSIRO: Melbourne, Australia, 1994; p. xxxii + 741, ISBN 0643105603, 9780643105607.
13. Kuschel, G. New tribe, new genus and species for an Australasian weevil group with notes and keys [Coleoptera, Curculionidae]. *Revue Française d'Entomologie (Nouvelle Series)* **2009**, *30*, 41–66.
14. Schenkling, S.; Marshall, G.A.K. Haplonychinae. In *Curculionidae: Prionomerinae, Aterpinae, Amalactinae, Haplonychinae, Omophorinae*; Coleopterorum Catalogus Auspiciis et Auxilio W. Junk; Pars 150; Schenkling, S., Ed.; W. Junk: 's-Gravenhage, The Hague, The Netherlands, 1936; pp. 1–8.
15. Pullen, K.R.; Jennings, D.; Oberprieler, R.G. Annotated catalogue of Australian weevils (Coleoptera: Curculionoidea). *Zootaxa Monogr.* **2014**, *3896*, 1–481. [CrossRef] [PubMed]
16. Froggatt, W.W. *Australian Insects*; W. Brooks & Co.: Sydney, Australia, 1907; 449p, ISBN 4444006657824.
17. Morgan, W.L. Flies and nematodes associated in flower bud galls of spotted gum. *Agric. Gaz. N. S. W.* **1933**, *44*, 125–127.
18. Newman, L.J.; Clark, J. The tuart bud weevil (*Haplonyx tibialis*). *J. Dep. Agric. West Aust.* **1924**, *1*, 351–360.
19. Fay, H.A.C.; De Faveri, S.G.; Storey, R.I.; Watson, J. *Sigastus* weevil—An emerging pest of macadamias in north Queensland. In Proceedings of the Sixth Workshop for Tropical Agricultural Entomologists, Darwin, Australia, 10–15 May 1998; Young, G., Ed.; Technical Bulletin. Department of Primary Industry and Fisheries: Darwin, Australia, 2001; Volume 288, pp. 137–140.

20. Blanche, R.; Bauer, R.; Cunningham, S.; Floyd, R. *Services and Dis-Services of Rainforest Insects to Crops in North Queensland*; Cooperative Research Centre for Tropical Rainforest Ecology and Management: Cairns, Australia, 2002; pp. 1–20.
21. Bright, J. *Sigastus Weevil Update*; Australian Macadamia Society: Lismore, Australia, 2017; pp. 1–4.
22. Bright, J. *Sigastus* weevil, life-cycle and monitoring. *Primefact* **2017**, *1586*, 1–5.
23. Oberprieler, R.G.; Anderson, R.S.; Marvaldi, A.E. 3 Curculionoidea Latreille, 1820: Introduction, Phylogeny. In *Handbook of Zoology. Arthropoda: Insecta. Coleoptera, Beetles. Volume 3: Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Eds.; Walter de Gruyter: Berlin, Germany; Boston, MA, USA, 2014; pp. 285–300.
24. Lacordaire, T. *Histoire Naturelle des Insectes. Genera des Coléoptères ou Exposé Méthodique et Critique de tous les Genres Proposés Jusqu'ici dans cet Ordre D'insectes. Tome Septième*; Librairie Encyclopédique de Roret: Paris, France, 1865; 620p.
25. May, B.M. An introduction to the immature stages of Australian Curculionoidea. In *Australian Weevils (Coleoptera: Curculionoidea). Volume II. Brentidae, Eurhynchidae, Apionidae and a Chapter on Immature Stages by Brenda May*; Zimmerman, E.C., Ed.; CSIRO: Melbourne, Australia, 1994; pp. 365–721, ISBN 9780643051461.
26. Howden, A.T. Structures related to oviposition in Curculionoidea. *Mem. Entomol. Soc. Wash.* **1995**, *14*, 53–100.
27. Schoenherr, C.J. Genera et Species Curculionidum, cum Synonymia Hujus Familiae. Species Novae aut Hactenus Minus Cognitae, Descriptionibus a Dom. In *Boheman et Entomologis Aliis, Illustratae; Tomus Tertius, Pars Secunda*; Leonardo Gyllenhal, C.H., Ed.; Roret: Paris, France; Fred. Fleischer: Leipzig, Germany, 1836; 356p.
28. Pascoe, F.P. On some new genera of Curculionidae. Part 1. *J. Entomol.* **1865**, *2*, 413–432.
29. Fuller, C. Notes and descriptions of some species of Western Australian Coccidae. *Trans. Entomol. Soc. Lond.* **1899**, 435–473. [CrossRef]
30. Juniper, P.A.; Britton, D.R. Insects associated with the fruit of *Syzygium paniculatum* (Magenta Lillypilly) and *Syzygium australe* (Brush Cherry). *Aust. J. Entomol.* **2010**, *49*, 296–303. [CrossRef]
31. Pascoe, F.P. Contributions towards a knowledge of the Curculionidae. Part III. *J. Linn. Soc. Lond. Zool.* **1872**, *11*, 440–492. [CrossRef]
32. Hartmann, F. Neue Rüsselkäfer aus Kaiser-Wilhelms-Land. *Deutsche Entomol. Z.* **1901**, *2*, 273–295. [CrossRef]
33. Klima, A. Subfam. Trigonocolinae. In *Curculionidae: Alophinae, Diabathrariinae, Rhynchaeninae, Ceratopinae, Trigonocolinae, Xiphaspidinae, Nerthopinae, Euderinae, Camarotinae, Acicnemidinae*; Coleopterorum Catalogus Auspiciis et Auxilio W. Junk; Pars 145; Schenkling, S., Ed.; W. Junk: 's-Gravenhage, The Hague, The Netherlands, 1935; 76p, (In 10 Separately Paginated Parts).
34. Heller, K.M. New Philippine Coleoptera. *Philipp. J. Sci.* **1922**, *19*, 523–627. [CrossRef]
35. Gunter, N.L.; Oberprieler, R.G.; Cameron, S.L. Molecular phylogenetics of Australian weevils (*Coleoptera*: *Curculionoidea*): Exploring relationships in a hyperdiverse lineage through comparison of independent analyses. *Aust. Entomol.* **2016**, *55*, 217–233. [CrossRef]
36. Thompson, R.L. Observations on the morphology and classification of weevils (Coleoptera, Curculionoidea) with a key to major groups. *J. Nat. Hist.* **1992**, *26*, 835–891. [CrossRef]
37. Oberprieler, R.G. 3.7.1 Brachycerinae Billberg, 1820. In *Handbook of Zoology. Arthropoda: Insecta. Coleoptera, Beetles. Volume 3: Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Eds.; Walter de Gruyter: Berlin, Germany; Boston, MA, USA, 2014; pp. 424–451.

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Article

Kuschelysius, a New Alpine Genus of Eugnomine Weevil (Coleoptera: Curculionidae: Curculioninae) from New Zealand

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Abstract: *Kuschelysius* **new genus** is described for four species, *K. hollowayae* **new species**, *K. durus* **new species**, *K. verbalis* **new species** and *K. nitens* **new species**, which are found in alpine regions along the length of the South Island of New Zealand. The genus most closely resembles members of the genus *Eugnomus* but is distinguished from them by the presence of a small pair of post-ocular tubercles and by having appressed scales on the dorsal surfaces. Some members of *Kuschelysius* appear to be flight-capable with well-developed hindwings, while others have reduced hindwings and are presumably flightless. Many specimens have been collected from the flowers of *Dracophyllum traversii*, *Celmisia* and other alpine plants, and the guts of examined specimens contained pollen. We hypothesise that the species of *Kuschelysius* are pollinators of the New Zealand alpine flora.

Keywords: taxonomy; identification; diagnostics; pollination; flightlessness

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1. Introduction

The Eugnomini Lacordaire, 1863 are a tribe of curculionine weevils with a primarily Southern Hemisphere distribution. The tribe is present in Australia, New Zealand, New Caledonia, South America extending northward to Central America, with undescribed members also known from Indochina [1]. The Eugnomini reach their greatest diversity in New Zealand, with approximately 100 species in 19 endemic genera, one genus (*Rhopalomerus* Blanchard) shared with Australia and South America and another (*Pactola* Pascoe) shared with New Caledonia and Fiji [2]. They form a distinctive element of the New Zealand weevil fauna, where their diurnal activity, often bizarre morphologies masquerading as faeces while feigning death, and flower-frequenting behaviour [3,4] attract the attention of natural historians.

The exact composition of the Eugnomini remains unclear. A suite of characters has been used to characterise the tribe. These characters include an elongate head with the eyes separated from the head constriction by a distance greater than their own length, scrobes that run below the lower surface of the rostrum, front coxae conical, and a large, obvious tooth on the hind tibia [3]: some of these characters are not universally shared and there have not yet been any phylogenetic studies to identify synapomorphies that unequivocally indicate the monophyletic nature of the tribe [1]. Substantial advances have been made in recent years on the eugnomine weevil fauna of New Caledonia and the Pacific [2,5–9], but the remainder of the Eugnomini of the world remain understudied.

Despite the lack of regional or global revisions of the tribe, the lowland eugnomine weevils of New Zealand are reasonably well known and have been named and inventoried through Broun's pioneering taxonomic research [10–14], illustrated accounts of several species by Hudson [15,16] and a key to genera by Marshall [17]. However, it is becoming apparent that the diversity of weevils in alpine areas has yet to be fully appreciated, with many species belonging to several genera being found exclusively above the treeline [18].

This contribution describes a new genus of eugnomine weevil containing four distinctive, large, alpine species, which we dedicate to our late friend, mentor and colleague Guillermo (Willy) Kuschel. We also name the type species after our friend and colleague Beverly Holloway, Willy's wife, a leading coleopterist in her own right. Although Willy's published contributions on the Eugnomini were only ever part of broader works [19–22], he was fascinated by the group and worked on the fauna of New Zealand during his first lengthy visit to the country and soon after his permanent settlement in New Zealand. Regrettably, the results from this research were not published in his lifetime.

2. Materials and Methods

Morphological features are described using standard terminology [23–25], with the following additions. Body length was measured in lateral view, from the anterior margin of the eyes to the elytral declivity. Body height was measured in lateral view as a straight line from the hind coxae to the dorsal surface of the elytra. Rostrum width was measured across the antennal insertions. The curve formed by the connection of the head and rostrum, as observed in lateral view, is termed the "ventral curvature of the head". The degree of curvature can be described as "gently curved" (i.e., having a large circle of curvature) or "tightly curved" (i.e., having a small circle of curvature). Wing venation terminology follows Kukalová-Peck and Lawrence [26], as applied to Curculionoidea by Oberprieler et al. [23]. This relates to the terminology of Zherikhin and Gratshev [27] in the following way: C = C; Sc = Sc; RA = R; RC = w; rf = rf; RP = Rr; RP_1 = pst; RP_2 = h & mst; rs = rs; MP_{1+2} = Cu; msc = msc; ms = af; MP_3 = $1A_1$; MP_4 = $1A_2$; CuA = 2A; CuA_1 = a_1–a_2 AA = 3A; ac = ac; AP = 4A; J = J.

Descriptions of colour follow the terminology provided by the National Bureau of Standards [28], which gives 267 centroid colours with natural-language descriptions. Digital representations of these colours have been provided by Jaffer [29].

Genitalia were photographed in KY Jelly (Johnson & Johnson Pacific, Broadway, NSW, Australia) before being stored in glycerol in a vial pinned below the specimen. Illustrations were prepared from photographs, using Inkscape (v. 0.91, [30]). Habitus photographs were taken using Nikon DS-Ri1 (Melville, NY, USA) fitted with a digital camera and a mechanical z-stepper. Nikon NIS Elements v. 4.10 was used to prepare the image stack and to produced the final montaged image.

Specimens were examined and deposited in the following collections:

FRNZ: The National Forest Insect Collection, Scion, Rotorua, New Zealand
LUNZ: Lincoln University Entomology Research Museum, Lincoln, Canterbury, New Zealand
NHM: Natural History Museum, London, United Kingdom
NZAC: New Zealand Arthropod Collection, Manaaki Whenua Landcare Research, Tamaki, Auckland, New Zealand

Label data from holotypes are transcribed using the following conventions. Data from individual labels are enclosed using quotes ('...'), lines are indicated with a solidus (/) and metadata are given in square brackets ([...]). Two-letter regional codes (NN, BR, FD, etc., Figure 1) follow those proposed by Crosby et al. [31].

3. Results

3.1. *Kuschelysius* Brown and Leschen New Genus

Type species: *Kuschelysius hollowayae* Brown and Leschen new species, by present designation.

3.1.1. Diagnosis

Large-bodied (body length > 5.0 mm, height > 1.7 mm, width > 2.2 mm); dorsal surfaces covered with appressed scales; antennal club with segment 3 shorter than segments 1 and 2 combined; length of the rostrum longer than the head; head not constricted behind eyes, tubercles present behind eyes; distinct spines absent from pronotum and elytra; elytra with a humeral callus; all femora with a single ventral tooth; all tibiae sinuous; tarsal claws simple, lacking a tooth.

The presence of a pair of small tubercles present behind the eyes will distinguish *Kuschelysius* from most other genera of New Zealand eugnomine weevils. *Kuschelysius* is most similar to species of *Eugnomus* Schönherr: the presence of appressed scales which conceal the integument, and sinuous pro- and mesotibiae distinguish them from *Eugnomus*, which have dorsal vestiture of fine hairs that reveal the integument, head evenly convex behind the eyes and straight pro- and mesotibiae. *Tysius* Pascoe also has tubercles behind the eyes; however, this genus can be distinguished from *Kuschelysius* by its much smaller size (body length < 3 mm), eyes placed further onto the rostrum, round scutellar shield and by the elytra having facia on interstria 3 and a low tubercle on interstria 5 on the elytral declivity.

3.1.2. Description

Rostrum. Mandibles stout, not exodont. Maxillae with long and flexible palps. Antennae inserted laterally, at distal 1/4 of rostrum. Scrobes oblique, running along ventral surface for 2/3 length, terminating just short of eyes. **Head**. Eyes hemispherical, prominent, positioned anterior of point of maximum ventral head curvature. Head not constricted behind eyes. Tubercles present behind eyes. In lateral view, angle formed by ventral margin of rostrum and head capsule c. 130°. **Antennae**. Scape reaching posterior margin of eyes when in repose, resting position running along ventral margin of rostrum. Funicle with 7 segments. Segments stout, clothed with dense thick setae; segments 1 and 2 lengths subequal, each about as long as 3 and 4 combined. **Pronotum**. Widest posteriorly, about 3/5 as wide as combined width of elytra; width at anterior margin much narrower than width at posterior margin. Lateral margins constricted in anterior 1/4 before abruptly widening, subparallel in posterior 2/3. Scales on disc larger than those on the elytra. **Elytra**. Stria 10 complete. Humeral callus developed. Disc without tubercles or spines. **Wings**. Reduced to fully developed. Costal margin straight, apex widely rounded. RA strongly sclerotised, and widest around middle. Radial cell (RC) completely sclerotised. RP_2 clearly evident. MP_{1+2} wide and strongly sclerotised. CuA wide at base, divided in middle to form a long and narrow pseudocell. AP short, not reaching wing margin. **Thoracic ventrites**. Prosternum projecting ventrally, resulting in it having an anterior face. Mesoventral process swollen. **Legs**. All femora armed with a single ventral tooth; metafemoral tooth large, not excised at base of distal edge. All tibiae sinuous. Tarsal segment 1 stout, shorter than combined length of remaining segments; segment 5 about 1.5 times as long as segment 3. **Male genitalia**. Pedon tubular, relatively short, broad and high; membranous ventrally; base of pedon with a narrow, strongly sclerotised ventral brace. Temones approximately as long as pedon. Parameroid lobes elongate, fused along proximal 1/2. Manubrium stout, shorter than temones. Spiculum gastrale with furcal arms very broad, maximum width approximately 0.5 times length of apodeme. **Female genitalia**. Styli slender, inserted on ventral margin of gonocoxites. Gonocoxites short and broad. Bursa copulatrix long, apparently with two chambers. Sternite 8 entire, apex broadly rounded. Spermatheca C-shaped, slender.

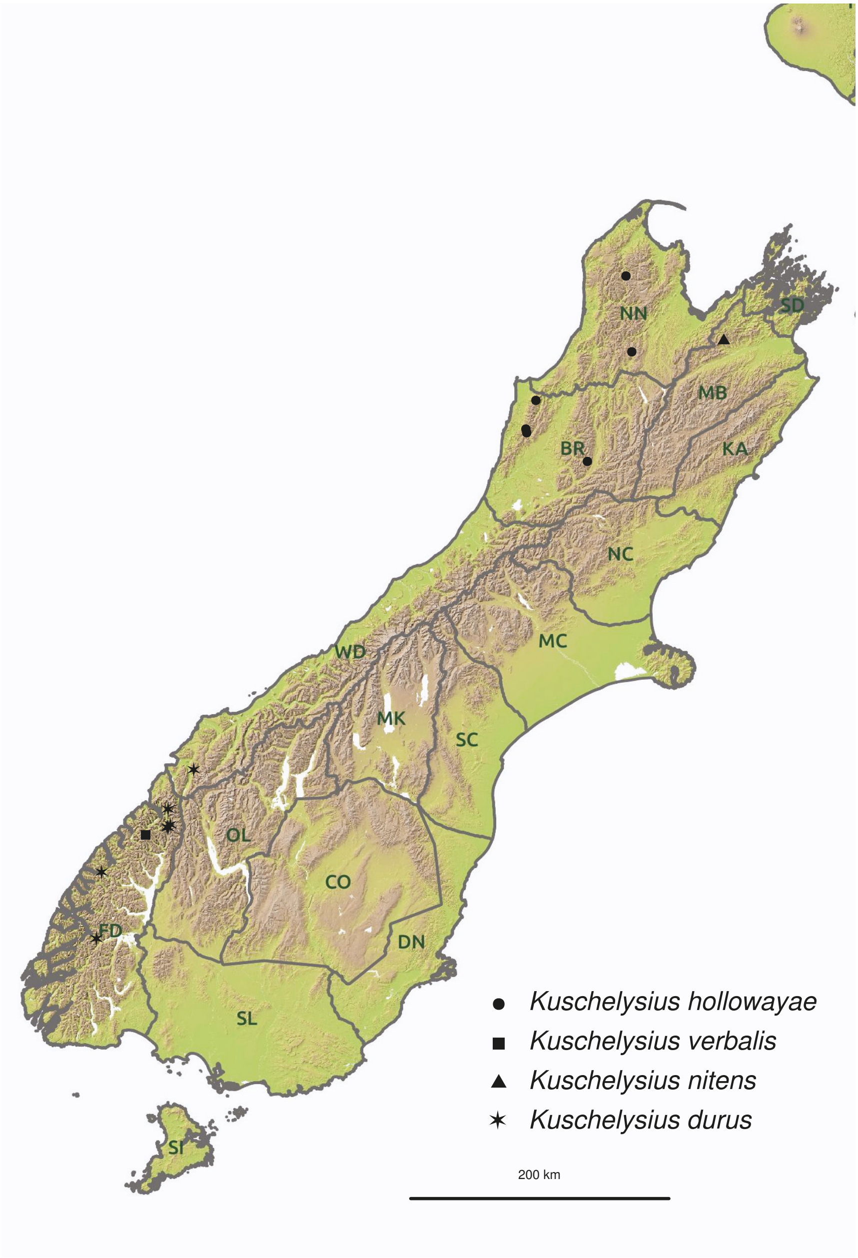

Figure 1. Distribution of *Kuschelysius hollowayae* (circles), *K. verbalis* (square), *K. nitens* (triangle) and *K. durus* (stars) in the South Island of New Zealand. Two-letter codes indicate the regions defined by Crosby et al. [31].

3.1.3. Etymology

Named after Dr Guillermo Kuschel Gerdes (1918–2017) whose research into the weevils of the Southern Hemisphere gave substantial insight into weevil classification. The ending 'elysius' refers to Elysium, the 'Land of Joy' of Antiquity, which was located by Plato at the antipodes [32].

3.2. ***Kuschelysius hollowayae*** **Brown and Leschen New Species**

Figures 2a,b; 3a; 4a; 5a–c; 6a–j.

3.2.1. Diagnosis

Uniformly light greyish brown, vestiture largely decumbent. Elytra long, 1.75 times longer than wide and 3.6 times longer than pronotum; declivity gently sloping; elytral apices square. Profemoral tooth small.

3.2.2. Description

Body length 7.22 mm to 8.05 mm ($\bar{X}$ = 7.80 mm, s = 0.39, n = 4), height 2.46 mm to 2.65 mm ($\bar{X}$ = 2.57 mm, s = 0.08, n = 4). Integument reddish black. Pronotum and elytra covered with adpressed light greyish brown scales and sparse, erect, trichiform setae. Scales present on head, rostrum, procoxae, mesoventrite and distal 1/3 of tibiae, paler than scales on dorsum. **Rostrum**. Length 1.78 mm to 1.98 mm ($\bar{X}$ = 1.88 mm, s = 0.09, n = 4), width 0.49 mm to 0.59 mm ($\bar{X}$ = 0.54 mm, s = 0.04, n = 4), length/width ratio 3.12 to 3.67 ($\bar{X}$ = 3.48, s = 0.25, n = 4). Straight in lateral view. Dorsal surface with elongate, matte scales. **Antennae**. Figure 4a. Scape clothed with scales and setae. Funicle segments 3–6 subequal, approximately as long as wide, segment 7 transverse. **Head**. Postocular tubercles evident. Ventral curvature of head tightly curved. **Pronotum**. Length 1.56 mm to 1.70 mm ($\bar{X}$ = 1.63 mm, s = 0.06, n = 4), width 1.60 mm to 1.77 mm ($\bar{X}$ = 1.71 mm, s = 0.07, n = 4), length/width ratio 0.93 to 0.98 ($\bar{X}$ = 0.96, s = 0.02, n = 4). Lateral margins moderately constricted in dorsal view in anterior 1/4. Scales on disc matte, sparser than elytral scales. Scutellar shield square. **Elytra**. Length 5.61 mm to 5.99 mm ($\bar{X}$ = 5.81 mm, s = 0.18, n = 4), width 3.04 mm to 3.54 mm ($\bar{X}$ = 3.33 mm, s = 0.23, n = 4), length/width ratio 1.63 to 1.85 ($\bar{X}$ = 1.75, s = 0.10, n = 4). Lateral margins subparallel in anterior 2/3 in dorsal view, tapering toward apex in posterior 1/3. Scales smaller, more elongate, denser than on pronotum. All interstriae evenly convex. Elytral declivity gently curved in lateral view. Apices of each elytron square. **Wings**. Figure 3a. Fully developed, 9.34 mm long from apex to jugal margin, 3.01 mm wide at midpoint (n = 1). MP_3 long, touching wing margin; MP_4 much shorter, c. 1/3 length of MP_3, not touching wing margin. AA parallel to CuA along most of length, becomes weak and inconspicuous before joining CuA proximally to the branching of CuA_1. **Thoracic ventrites**. Mesoventrite densely clothed with pale scales, contrasting with sparser vestiture on mesanepisternum. Mesoventral projection narrowly rounded at apex. **Abdomen**. Tergite 7 wider than long in males; longer than wide, with rounded apex in females. Tergite 8 subquadrate, exposed in males (Figure 6a); strongly arched, bifurcate with acute apices, concealed under tergite 7 in females (Figure 6f,g). Ventrite 5 depressed medioapically in males; raised medioapically in females. **Legs**. Profemoral tooth small (Figure 5a). Mesofemoral tooth moderate (Figure 5b). Metafemoral tooth large (Figure 5c). **Male genitalia**. Figure 6a–e. Pedon with lateral lobes separated dorsally. Internal sac armed with small teeth, localised into elongate regions dorsally and ventrally. **Female genitalia**. Figure 6h–j. Apices of styli with a long flexible seta. Gonocoxites in lateral view high in the basal 7/8, rapidly narrowing to styli.

3.2.3. Holotype

Male (NZAC). Specimen mounted on card triangle; left metanepisternite partially dissociated; abdomen removed for dissection, stored in glass vial pinned below specimen. Labelled: 'Mt. Owen 5000′/Nelson, 21.10.62/J.I. Townsend' [first two lines handwritten, last line printed, rectangular off white paper], 'Celmisia/armstrongii' [printed, rectangular off white paper], [narrow strip of green paper], 'HOLOTYPE/*Kuschelysius*/*hollowayae*/Brown & Leschen 2018' [printed, red card].

3.2.4. Paratypes

A total of 42 specimens (31 males, 10 females, 1 of undetermined sex) designated as paratypes, bearing blue paratype label. Paratype specimens deposited in NZAC, LUNZ, NHM, FRNZ.

NN. Mt. Owen 5000′, 21 Oct 1962, JI Townsend, *Celmisia armstrongii* (NZAC: 8); Mt. Owen 5000′, 30 Dec 1962, JI Townsend (NZAC: 2); Mt. Owen, 12 Jan 1962, JS Dugdale (NZAC: 2); Mt. Owen, 7 Nov 1961, D Kershaw (FRNZ: 1); Mt. Aorere, 5 Dec 1962, W.A.H. (FRNZ: 1). **BR**. Paparoa Range, Mt. Dewar 1100 m, Dec 1969, JI Townsend, *Dracophyllum traversii* flower heads (NZAC: 13, NHM: 4); Paparoa Range, Mt. Dewar 1060 m, Dec 1969, JG McBurney (NZAC: 1); Paparoa Range, Lochnagar Ridge 3500–3800′, 2–10 Dec 1969, JS Dugdale (NZAC: 1); Paparoa Range, Lochnagar Ridge 1067 m, Dec 1969, JS Dugdale and JI Townsend, *Dracophyllum traversii* (NZAC: 6); Paparoa Range, Lochnagar Ridge, camp area 1060 m, Dec 1969, JI Townsend (NZAC: 1); Paparoa Range, Buckland Peaks, Townson Tarn 1200 m, 15 Nov 1987, BP Stephenson, under rocks (LUNZ: 1); Victoria Range, south end, head of Rahu Creek trib., 16 Jan 1967, JS Dugdale (NZAC: 1).

3.2.5. Distribution

South Island, NN, BR: Domett Range, Mount Owen, Paparoa Range, Victoria Range (Figure 1).

3.2.6. Biology

This species has frequently been collected on the flowerheads of *Dracophyllum traversii* Hook. f., and less commonly on *Celmisia armstrongii* Petrie. Further research is required to ascertain whether these records are an accurate indication of the larval host plant, or if the adults were only incidentally feeding on these plants. Adults have been collected at elevations between 1060 and 1520 m above sea level. Larvae are currently unknown.

3.2.7. Etymology

Named after Dr Beverley Holloway, Willy Kuschel's wife of over 50 years. She has made significant contributions to the taxonomy of the Anthribidae and the Lucanidae and is a fellow of the Entomological Society of New Zealand.

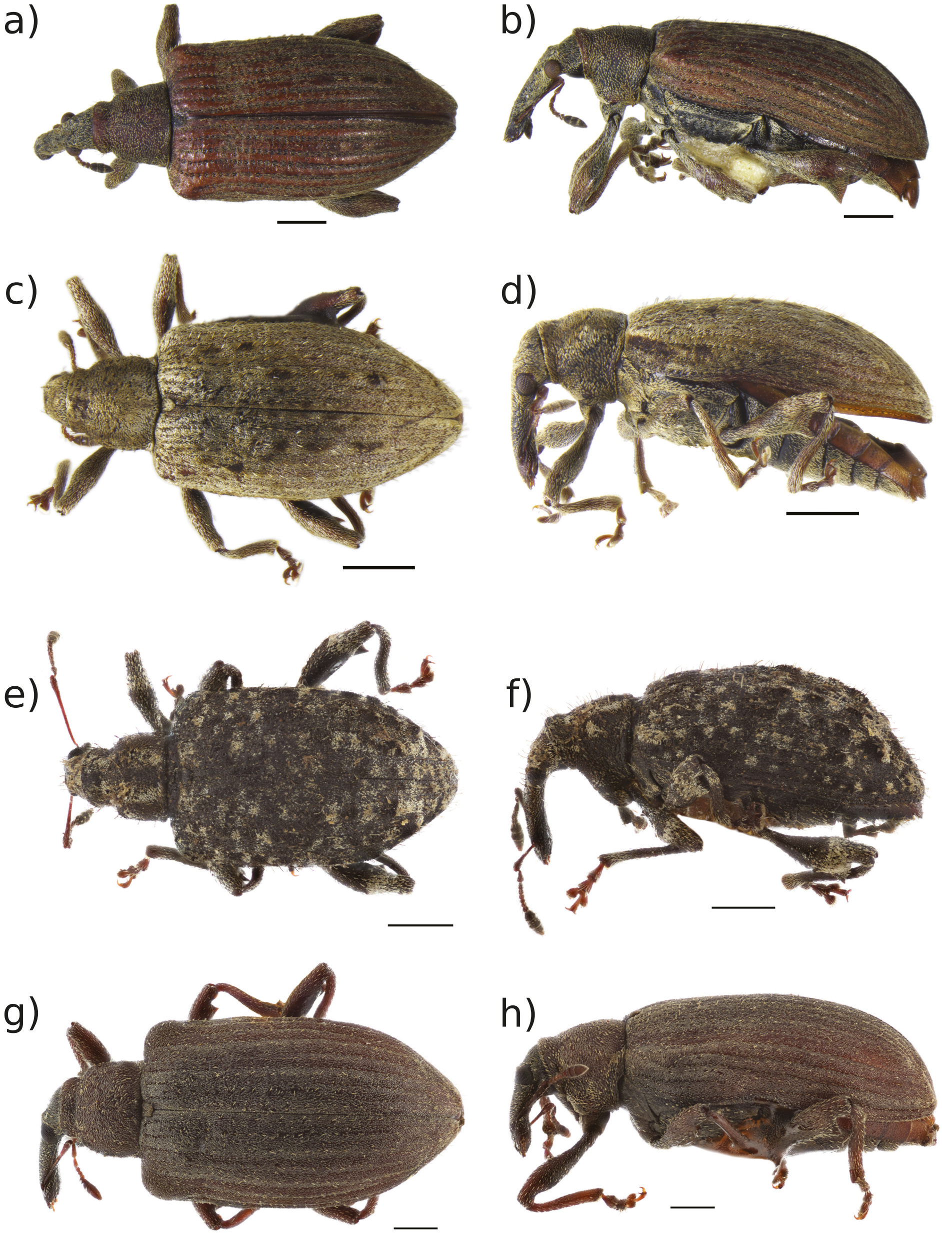

Figure 2. Habitus figures of *Kuschelysius* species. (**a**) *K. hollowayae*, dorsal view; (**b**) *K. hollowayae*, lateral view; (**c**) *K. durus*, dorsal view; (**d**) *K. durus*, lateral view; (**e**) *K. verbalis* holotype, dorsal view; (**f**) *K. verbalis* holotype, lateral view; (**g**) *K. nitens* holotype, dorsal view; (**h**) *K. nitens* holotype, lateral view. Scale bars = 1 mm.

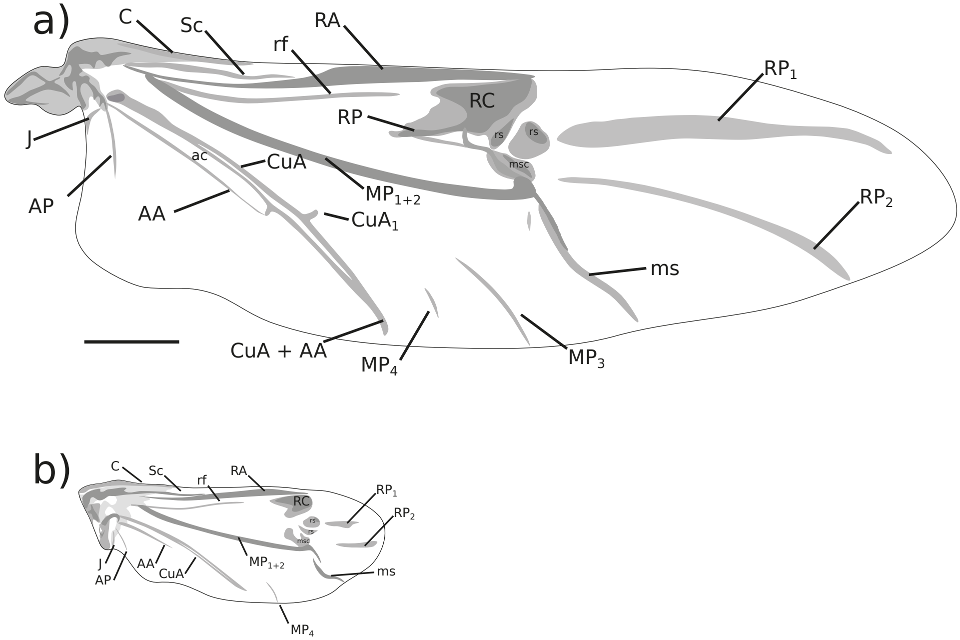

Figure 3. Hind wing of *Kuschelysius* species. (**a**) *K. hollowayae*; (**b**) *K. durus*. AA: anal anterior vein; ac: anal cell; AP: anal posterior vein; C: costal vein; CuA: cubitus anterior vein; J: jugal vein; MP: media posterior veins; ms: medial spur; msc: medial sclerotisation; RA: radius anterior vein; RC: radial cell; rf: radial fold; RP: radius posterior veins; rs: radial sclerites; Sc: Subcostal vein. Wings drawn to the same scale; scale bar = 1 mm.

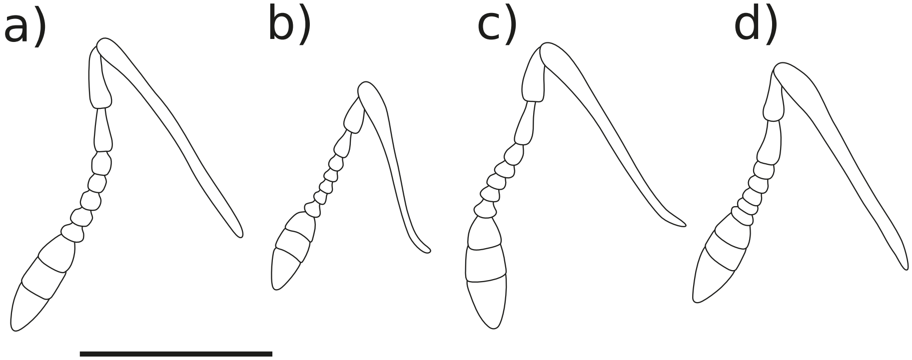

Figure 4. Right antennae, anterior view, of *Kuschelysius* species. (**a**) *K. hollowayae*; (**b**) *K. durus*; (**c**) *K. verbalis*; (**d**) *K. nitens*; scale bar = 1 mm.

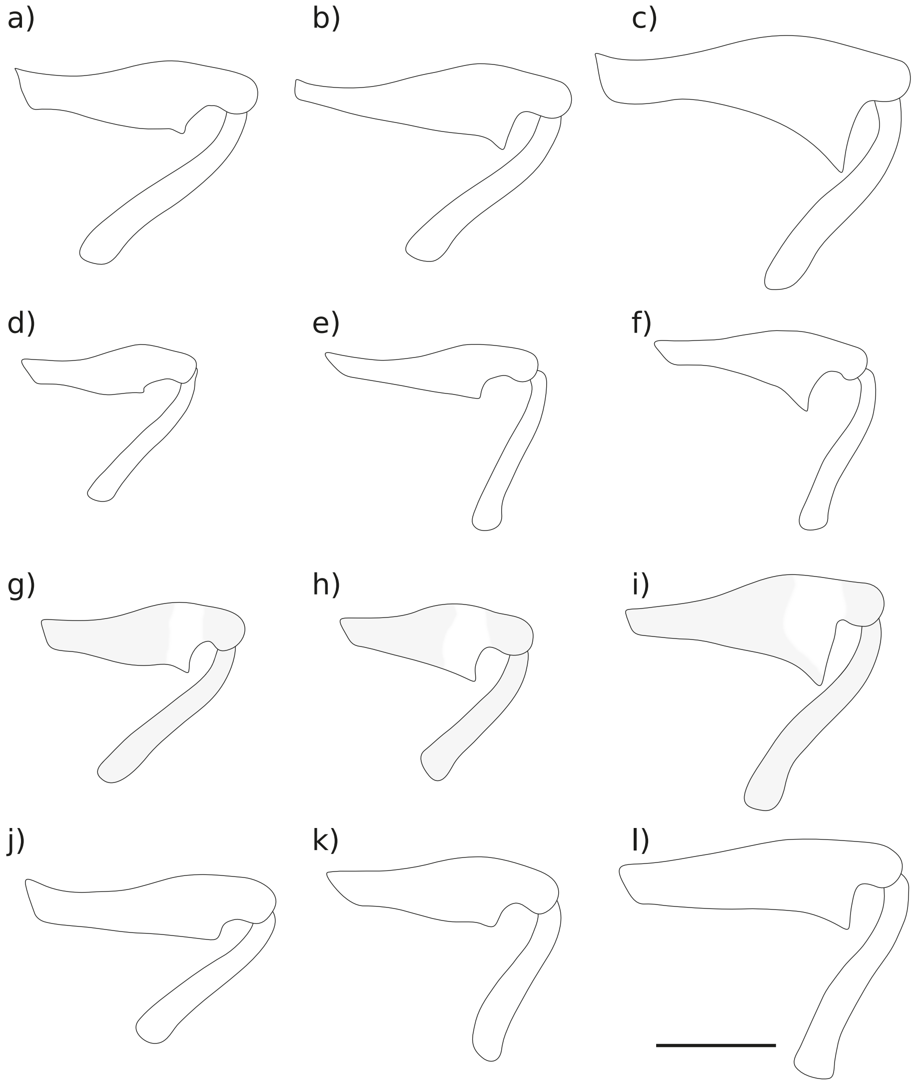

Figure 5. Left femora and tibae, anterior view, of *Kuschelysius* species. *Kuschelysius hollowayae*: (**a**) profemur and tibia; (**b**) mesofemur and tibia; (**c**) metafemur and tibia; *Kuschelysius durus*: (**d**) profemur and tibia; (**e**) mesofemur and tibia; (**f**) metafemur and tibia; *Kuschelysius verbalis*: (**g**) profemur and tibia; (**h**) mesofemur and tibia; (**i**) metafemur and tibia; *Kuschelysius nitens*: (**j**) profemur and tibia; (**k**) mesofemur and tibia; (**l**) metafemur and tibia; scale bar = 1 mm.

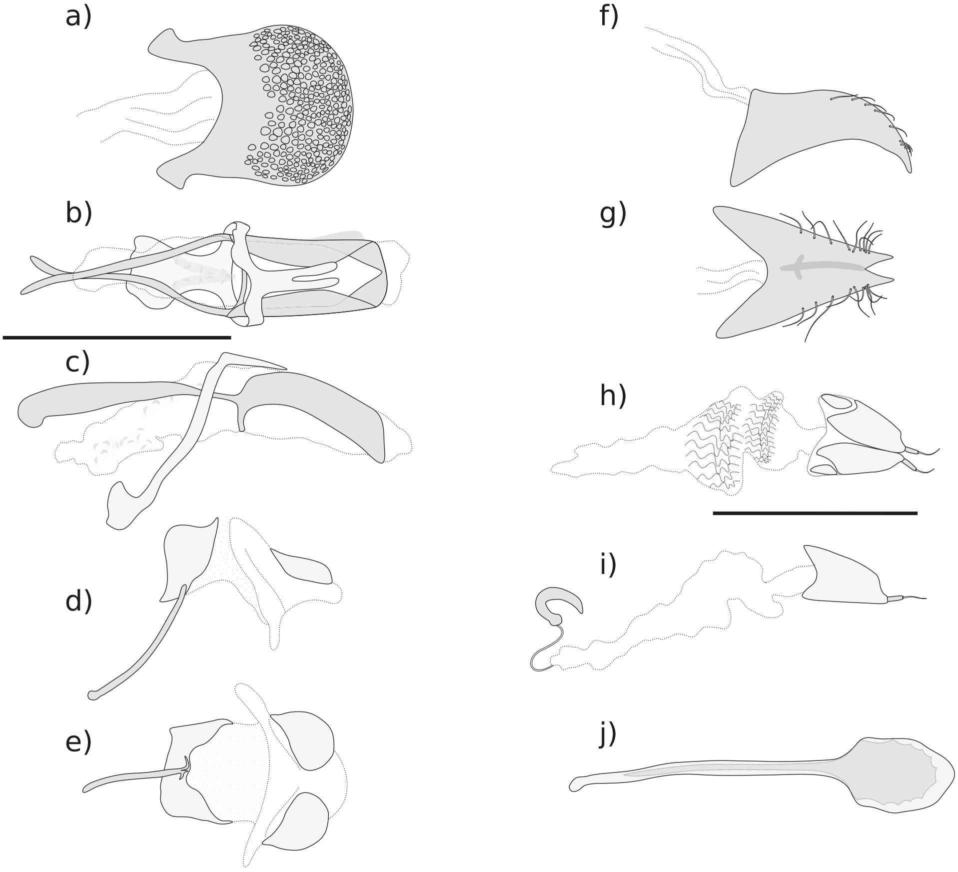

Figure 6. Male and female genitalia of *Kuschelysius hollowayae*. (**a**) male tergite 8, dorsal view; (**b**) aedeagus, dorsal view; (**c**) aedeagus, lateral view; (**d**) male sternite 8, lateral view; (**e**) male sternite 8, ventral view; (**f**) female tergite 8, lateral view; (**g**) female tergite 8, dorsal view; (**h**) gonocoxites and bursa copulatrix, dorsal view; (**i**) gonocoxites, bursa copulatrix and spermatheca, lateral view; (**j**) female sternite 8, ventral view. Scale bars = 1 mm, **a–e** at same scale, **f–j** at same scale.

3.3. ***Kuschelysius durus*** **Brown and Leschen New Species**

Figures 2c,d; 3b; 4b; 5d–f; 7a–j.

3.3.1. Diagnosis

Evenly yellowish grey; small dark greyish brown maculae on elytra. Elytra long, 1.7 times longer than wide and 3.2 times longer than pronotum. Profemoral tooth small.

3.3.2. Description

Body length 5.39 mm to 5.86 mm ($\bar{X}$ = 5.64 mm, s = 0.21, n = 4), height 1.74 mm to 2.24 mm ($\bar{X}$ = 1.98 mm, s = 0.21, n = 4). Integument reddish to black. Pronotum and elytra covered with appressed yellowish grey scales and sparse, erect trichiform setae; small dark greyish brown maculae present on the elytra, position variable but often with two maculae present on interstria 3 on disc and at top of elytral declivity. Thoracic ventrites clothed with yellowish grey scales; abdominal ventrites with short hairs. **Rostrum**. Length 1.12 mm to 1.21 mm ($\bar{X}$ = 1.16 mm, s = 0.04, n = 4), width 0.40 mm to 0.42 mm ($\bar{X}$ = 0.41 mm, s = 0.01, n = 4), length/width ratio 2.73 to 2.88 ($\bar{X}$ = 2.82, s = 0.07, n = 4). Straight in lateral view. Dorsal surface with oval, matte scales. **Antennae**. Figure 4b. Scape clothed with setae only. Funicle segments 3–6 subequal, approximately as long as wide, segment 7 transverse. **Head**. Postocular tubercles reduced. Ventral curvature of head tightly curved. **Pronotum**. Length 1.14 mm to 1.38 mm ($\bar{X}$ = 1.27 mm, s = 0.10, n = 4), width 1.19 mm to 1.36 mm ($\bar{X}$ = 1.28 mm, s = 0.08, n = 4), length/width ratio 0.96 to 1.02 ($\bar{X}$ = 1.00, s = 0.03, n = 4). Lateral margins moderately constricted in dorsal view in anterior 1/4. Scales on disc overlapping, matte, larger but about as dense as scales on elytra. Scutellar shield pentagonal. **Elytra**. Length 3.85 mm to 4.26 mm ($\bar{X}$ = 4.04 mm, s = 0.20, n = 4), width 2.22 mm to 2.59 mm ($\bar{X}$ = 2.42 mm, s = 0.16, n = 4), length/width ratio 1.63 to 1.75 ($\bar{X}$ = 1.67, s = 0.06, n = 4). All interstriae evenly convex. Scales on disc overlapping, matte, about as dense as scales on pronotum. Elytral declivity gently curved in lateral view. Apices square. **Wings**. Figure 3b. Reduced, particularly with respect to the apical sector, 3.05 mm to 3.08 mm long from apex to jugal margin, 1.03 mm to 1.21 mm wide at midpoint (n = 2). RP_1 and RP_2 present, but much reduced in length. MP_3 absent; MP_4 touching wing margin. AA parallel to CuA, no evidence of it joining CuA. CuA_1 absent. **Thoracic ventrites**. Mesoventrite, mesanepisternum, metanepisternum and lateral 1/4 of the first two abdominal ventrites densely clothed with pale yellow scales, contrasting with brilliant yellow hairs on disc of metaventrite. Mesoventral projection truncate at apex. **Abdomen**. Tergite 7 wider than long in males; elongate with rounded apex in females. Tergite 8 subquadrate, exposed in males (Figure 7a); weakly arched, bifurcate with blunt apices, concealed under tergite 7 in females (Figure 7f). Ventrite 5 depressed medioapically in males; raised medioapically in females. **Legs**. Profemoral tooth small (Figure 5d). Mesofemoral tooth small (Figure 5e). Metafemoral tooth large, acute (Figure 5f). **Male genitalia**. Figure 7a–e. Pedon with lateral lobes dorsally fused in basal 1/4, with a lobe projecting apicad. Internal sac armed with two large, toothed sclerites. **Female genitalia**. Figure 7f–j. Apices of styli with multiple long setae. Gonocoxites in lateral view of roughly even height along length, gradually narrowing to styli.

3.3.3. Holotype

Female (NZAC). Specimen glued onto card mount; entire. Labelled: 'Gertrude Saddle'/Homer 5.2.63/R.M.Bull' [handwritten, rectangular off white paper], 'R.M. Bull/Collection' [printed, rectangular white card], 'HOLOTYPE/*Kuschelysius*/*durus*/Brown & Leschen 2018' [printed, red card].

3.3.4. Paratypes

A total of 17 specimens (6 males, 11 females) designated as paratypes, bearing blue paratype label. Paratype specimens deposited in NZAC, NHM.

WD. Annetta Mountain, Barrier Valley, 2 Feb 1975, JS Dugdale, in turf (NZAC: 1). **FD**. Mt. Titiroa, Borland side W, 6 Feb 2009, R Hoare, On cushion plant gravel field 45.04° S 167.31° E (NZAC: 1); Gertrude Saddle, Homer, 4500′, 5 Feb 1963, JI Townsend, *Astelia nivicola* (NZAC: 6, NHM: 2); Gertrude Saddle, Homer, 4500′, 5 Feb 1963, JI Townsend, *Celmisia* (NZAC: 1); Homer Tunnel, 3000′, 5 Feb 1963, RM Bull (NZAC: 2); South Basin, Tutoko Bench, Darran Mt.s, 1219–1372 m, 15 Jan 1977, JS Dugdale (NZAC: 1); Homer Saddle, 4200′, 29 Jan 1946, R Forster, in leafmould (NZAC: 1); Mt. Barber, 1350 m, Jan 1970, J Dugdale, *Celmisia walkeri* (NZAC: 2).

3.3.5. Distribution

South Island, WD: Annetta Mountain. FD: Darran Mountains, Homer Tunnel, Mount Titiroa, Mount Barber (Figure 1).

3.3.6. Biology

This species has been collected in leaf litter, in turf, on unidentified cushion plants and on *Celmisia walkeri* Kirk. A large series of specimens have been collected from *Astelia nivicola* Ckn. ex Cheesm.

The gut contents of the two dissected specimens collected from *A. nivicola* were filled almost exclusively with a single form of pollen. The specimen from Mt. Titiroa was collected in an unusual granite sand plain ecosystem [33,34]. Adults have been collected at elevations between 900 and 1380 m above sea level. Larvae are currently unknown.

3.3.7. Etymology

Based on the Latin *durus*, 'strong, tough', in reference to the hardiness of this species which survives in the harsh environment of the Fiordland mountains. It is also a trait demonstrated by Willy, whose endurance while undertaking collecting expeditions in the Juan Fernandez Islands, New Zealand and elsewhere in the South Pacific is awe-inspiring.

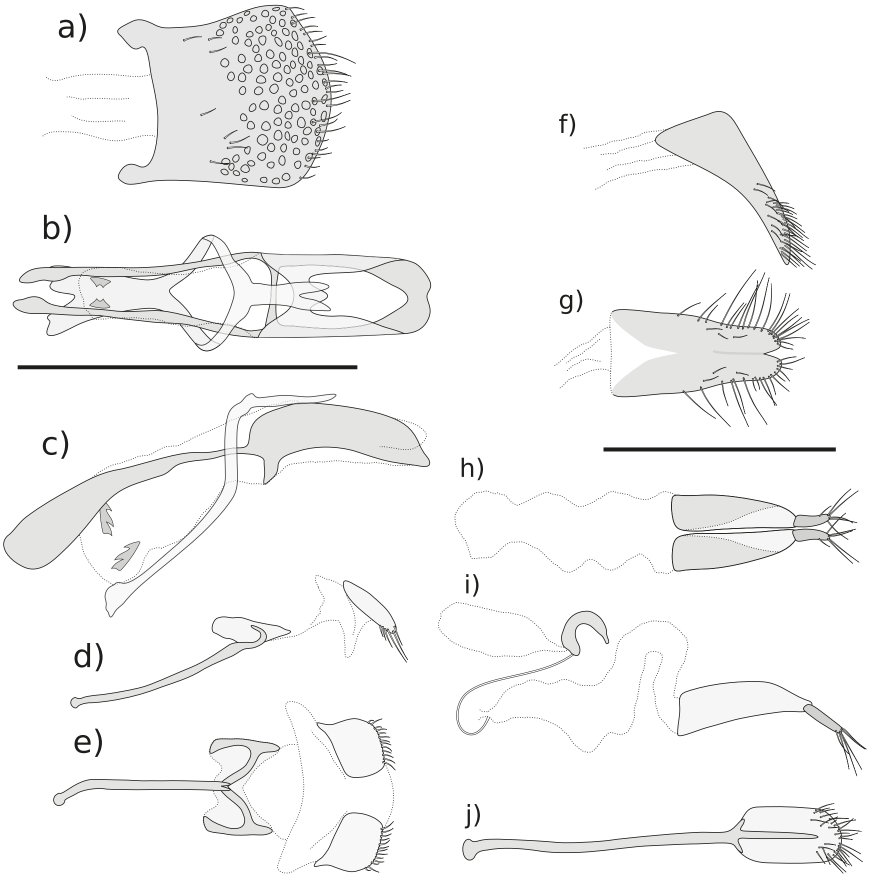

Figure 7. Male and female genitalia of *Kuschelysius durus*. (**a**) male tergite 8, dorsal view; (**b**) aedeagus, dorsal view; (**c**) aedeagus, lateral view; (**d**) male sternite 8, lateral view; (**e**) male sternite 8, ventral view; (**f**) female tergite 8, lateral view; (**g**) female tergite 8, dorsal view; (**h**) gonocoxites and bursa copulatrix, dorsal view; (**i**) gonocoxites, bursa copulatrix and spermatheca, lateral view; (**j**) female sternite 8, ventral view. Scale bars = 1 mm, (**a**–**e**) at same scale, (**f**–**j**) at same scale.

3.4. ***Kuschelysius verbalis*** **Brown and Leschen New Species**

Figures 2e,f; 4c; 5g–i.

3.4.1. Diagnosis

Mottled dark olive brown and greyish yellow. Mottling on elytra not forming any particular pattern, but forming paired dorsal vittae on the pronotum and broad bands on the distal 1/4 of the femora. Elytra relatively short, 1.5 times longer than wide and 3.2 times longer than pronotum. Profemoral tooth large (Figure 5g).

3.4.2. Description

Body length 6.20 mm (n = 1), height 2.38 mm (n = 1). Integument black; all surfaces covered with oval scales, mainly coloured dark olive brown but greyish yellow scales forming a ventral stripe below and posterior maculae above the eyes, paired dorsal vittae on the pronotum, a mottled pattern on the elytra, a patch on the anterior surface of the prosternum and broad bands on the distal 1/4 of the femora. Sparse, erect trichiform setae present on the rostrum, pronotum and elytra. **Rostrum**. Length 1.76 mm (n = 1), width 0.48 mm (n = 1), length/width ratio 3.67 (n = 1). Evenly curved in lateral view. Dorsal surface with oval, matte scales. **Antennae**. Figure 4c. Scape clothed with setae only. Funicle segment 3 longer than wide; segments 4–6 subequal, approximately as long as wide, segment 7 transverse. **Head**. Postocular tubercles reduced. Ventral curvature of head gently curved. **Pronotum**. Length 1.37 mm (n = 1), width 1.41 mm (n = 1), length/width ratio 0.97 (n = 1). Lateral margins strongly constricted in dorsal view in anterior 1/4. Scales on disc overlapping, matte, about as dense as scales on elytra. Scutellar shield square. **Elytra**. Length 4.37 mm (n = 1), width 2.92 mm (n = 1), length/width ratio 1.50 (n = 1). Interstriae 3 and 5 raised around the elytral declivity. Scales on disc overlapping, matte, about as dense as scales on pronotum. Elytral declivity evenly sloped in lateral view. Apices square. **Thoracic ventrites**. Densely clothed with scales of similar colour to dorsum, but longer, thinner and with different texture. Mesoventral projection truncate at apex. **Abdomen**. Ventrite 5 of females swollen medially. **Legs**. Profemoral tooth moderate (Figure 5g). Mesofemoral tooth moderate (Figure 5g). Metafemoral tooth large (Figure 5i). **Male genitalia**. Unknown. **Female genitalia**. Not examined.

3.4.3. Holotype

Female (NZAC). Specimen mounted on card triangle; entire. Labelled: 'MacKinnan[sic] Pass 3500′/1.1.63 B.M.May/On Celmisia sp.' (handwritten, rectangular off white paper, 'Celmisia' underlined), 'HOLOTYPE/*Kuschelysius*/*verbalis*/Brown & Leschen 2018' [printed, red card].

3.4.4. Distribution

South Island, FD: Mackinnon Pass (Figure 1).

3.4.5. Etymology

Based on the Latin *verbalis*, 'of words,' an allusion to Willy's enjoyment of language.

3.5. Kuschelysius nitens **Brown and Leschen New Species**

Figures 2g,h; 4d; 5j–l.

3.5.1. Diagnosis

Uniformly medium grey; pronotum, elytra and legs with fine pale yellow-green setae that project over ground vestiture. Elytra long, 1.68 times longer than wide and 3.9 times longer than pronotum; declivity rounded in lateral view; elytral apices individually rounded. Profemoral tooth small.

3.5.2. Description

Body length 7.79 mm (n = 1), height 2.96 mm (n = 1). Integument black; rostrum, pronotum, elytra, legs and venter covered with fine, glossy adpressed medium grey scales and sparse, decumbent, pale yellow-green trichiform setae. **Rostrum**. Length 1.82 mm (n = 1), width 0.55 mm (n = 1), length/width ratio 3.31 (n = 1). Straight in lateral view. Dorsal surface with oval, glossy scales. **Antennae**. Figure 4d. Scape clothed with scales and setae. Funicle segments 3–5 subequal, approximately as long as wide, segments 6 and 7 transverse. **Head**. Postocular tubercles reduced. Ventral curvature of head tightly curved. **Pronotum**. Length 1.51 mm (n = 1), width 1.81 mm (n = 1), length/width ratio 0.83 (n = 1). Lateral margins moderately constricted in dorsal view in anterior 1/4. Scales on disc oval, glossy, about as dense as scales on elytra. Scutellar shield square. **Elytra**. Length 5.95 mm (n = 1), width 3.55 mm (n = 1), length/width ratio 1.68 (n = 1). All interstriae evenly convex. Scales on disc oval, glossy, about as dense as scales on pronotum but smaller. Elytral declivity strongly curved in lateral view. Apices of each elytron individually rounded. **Thoracic ventrites**. Mesoventral projection rounded at apex. **Legs**. Profemoral tooth small, broadly rounded (Figure 5j). Mesofemoral tooth small (Figure 5k). Metafemoral tooth moderate (Figure 5l). **Male genitalia**. Not examined. **Female genitalia**. Unknown.

3.5.3. Holotype

Male (NZAC). Specimen mounted on card triangle; entire, head bent to the left. Labelled: 'Mt. Richmond/5000 23.4.63/G. Ramsay' [handwritten, rectangular off white paper], 'HOLOTYPE/*Kuschelysius*/*nitens*/Brown & Leschen 2018' [printed, red card].

3.5.4. Distribution

South Island, MB: Mt. Richmond (Figure 1).

3.5.5. Etymology

Based on the Latin *nitens* 'shining,' in reference to the glossy scales that distinguish this species from others in the genus.

3.5.6. Remarks

Four New Zealand peaks are named Mt. Richmond. The one identified as the type locality is Mt. Richmond in the Richmond Range (MB; 41.4744° S 173.3957° E). This peak is readily accessible from Nelson, where G.W. Ramsay was living at the time of the collection of this specimen. Its maximum elevation is 1760 m (=5800 feet), which is consistent with the elevation inferred from the label (5000 feet = 1524 m).

The alternatives include Mt. Richmond, in the Southern Alps north of Lake Tekapo (MK; 43.5294° S 170.4314° E, 2509 m), which is flanked by glaciers and with very steep gradients around the elevation of interest; Mt. Richmond in the Livingstone Mountains, west of North Mavora Lake (OL; 45.2331° S 168.1110° E, 1673 m) which is of appropriate elevation but is poorly accessible; or Ōtāhuhu/Mount Richmond on the Auckland isthmus (AK; 36.9339° S 174.8385° E, 48 m) which is too low to be the type locality.

4. Key to Species of *Kuschelysius*

1. Dorsum mottled darker and lighter brown, without any clear pattern. Rostrum greater than 3.5 times longer than wide. Elytra around 1.5 times longer than wide. Profemoral tooth large, acute . . . . *K. verbalis*

– Dorsum uniformly coloured, brown or grey, or yellowish grey with small dark brown spots on interstriae 3 and 5. Rostrum less than 3.5 times longer than wide. Elytra greater than 1.6 times longer than wide. Profemoral tooth small, broadly rounded . . . . 2.

2 (1). Body length less than 6 mm. Scape clothed with setae only . . . . *K. durus*

– Body length greater than 7 mm. Scape clothed with appressed scales as well as setae . . . . 3.

3 (2). Scales on pronotum and elytra matte. Elytral declivity gently sloping in lateral view, apex pointed. Setae on pronotum and elytra erect, dark . . . . *K. hollowayae*

– Scales on pronotum and elytra glossy. Elytral declivity rounded in lateral view, apex rounded. Setae on pronotum and elytra decumbent, pale yellow-green . . . . *K. nitens*

5. Discussion

Although there have been several surveys of alpine insects in New Zealand [34,35], investigations into the evolutionary history of these taxa and the high level of endemism in these environments are still in their infancy [36]. The alpine beetle fauna is quite rich, and almost every mountain range in the Southern Alps is home to endemic species [18,37]. The New Zealand Eugnominae are common in alpine environments, with four other genera (*Eugnomus* Schönherr, 1847, *Oreocalus* May 1993, *Pactolotypus* Broun, 1909, *Stephanorhynchus* White, 1846) found in these areas [18]. The description of this exclusively alpine weevil genus increases our understanding of the diversity of Coleoptera found in these habitats.

High-altitude eugnomine weevil richness and abundance may correlate with the high diversity of alpine plants. There are approximately 600 species of plants in the Southern Alps [38]. The New Zealand alpine flora has an extraordinarily high proportion of white flowers, with the proportion of white flowered species in New Zealand being double that compared of other alpine regions in the world [39]. It is thought that the pollinator fauna is rather depauperate and unspecialised [40], but the presence of eugnomine weevils and other beetles found exclusively on alpine flowers indicates that there is some level of host plant specialisation [41,42]. Although beetles have been frequently acknowledged as being frequent flower visitors [39,40,43,44], they have not yet received specific attention to evaluate their role or effectiveness as pollinators in New Zealand ecosystems. Research in other countries has revealed a number of systems in which beetles, and weevils specifically, are primarily pollinators [45–49]. It is possible that *Kuschelysius* and other alpine weevils may play an important role in pollination of alpine plants, including the pollination of high-altitude populations of the forest-inhabiting *Dracophyllum traversii*.

The difference in wing size between *K. hollowayae* and *K. durus* suggests that the importance of flight is very different for these two taxa. The shrubland and alpine forest habitat where *K. hollowayae* is found, is likely to require greater flight abilities than the tussock grassland and herbfields inhabited by *K. durus*, consistent with hypotheses that more homogenous environments promote flightlessness [50]. Of these two, the larger species, *K. hollowayae*, was fully winged, the opposite of the general trend in New Zealand alpine stoneflies [51]. Wing reduction or loss occurs as part of a syndrome of characters that repeatedly evolve in alpine insect taxa [52,53], like having a dark pigmented cuticle [37], or presence of quiescence instead of diapause [36]. Flightlessness caused by wing reduction is likely to be one reason driving the species diversification in New Zealand alpine environments. In the Lucanidae, for example, wing reduction seems to have promoted speciation through the isolation of localised allopatric populations [54].

A full appreciation of the evolution of New Zealand's eugnomine weevil fauna, its relationships to host plants and the origin of the alpine fauna will require phylogenetic and faunistic studies coupled with more natural history observations. Furthermore, we expect to find additional species of *Kuschelysius*, especially in alpine areas with limited access. This paper is the first installment of what we hope will be a series of papers describing the New Zealand fauna and forming the basis for a full systematic treatment of the Eugnomini, which will underpin ecological and evolutionary studies.

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References

1. Caldara, R.; Franz, N.M.; Oberprieler, R.G. 3.7.10 Curculioninae Latreille, 1802. In *Handbook of Zoology, Arthropoda: Insecta. Coleoptera, Beetles Volume 3: Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Eds.; Walter De Gruyter: Berlin, Germany, 2014; pp. 589–628, doi:10.1515/9783110274462.
2. Mazur, M.A. *Koghicola karolinae*, new genus and species of the Eugnomini from New Caledonia (Coleoptera: Curculionidae). *Ann. Zool.* **2014**, *64*, 9–14. [CrossRef]
3. Cawthra, E.M. A redefinition of the subfamily Eugnominae to include the Meriphinae. *Trans. R. Soc. N. Z. Zool.* **1966**, *7*, 171–178.
4. May, B.M. Larvae of Curculionoidea (Insecta: Coleoptera): A systematic overview. *Fauna N. Z.* **1993**, *28*, 1–223.
5. Mazur, M.A. First record of the tribe Eugnomini Lacordaire, 1863 (Coleoptera: Curculionidae) from Fiji with description of *Pactola fiji* sp. n. *Zootaxa* **2012**, *3517*, 63–70.
6. Mazur, M.A. Review of the New Caledonian species of the genus *Pactola* Pascoe, 1876 (Coleoptera: Curculionidae: Eugnomini), with description of two new species. *Zootaxa* **2014**, *3814*, 202–220. [CrossRef] [PubMed]
7. Mazur, M.A. A new genus and nine new species of Eugnomini (Coleoptera, Curculionidae) from New Caledonia. *ZooKeys* **2016**, *554*, 87–118. [CrossRef] [PubMed]
8. Mazur, M.A.; Tron, F.; Mille, C. *Pactola kuscheli* sp. nov. (Coleoptera: Curculionidae), a potential cause for the decline of the threatened New Caledonian conifer, *Agathis montana* de Laubenfels, 1969 (Araucariaceae). *Austral Entomol.* **2017**, *56*, 268–276. [CrossRef]
9. Mazur, M.A.; Jezuita, A. A new species of *Pactola* Pascoe, 1876 (Coleoptera: Curculionidae: Eugnomini) from New Caledonia. *Zootaxa* **2015**, *3931*, 279–285. [CrossRef] [PubMed]
10. Broun, T. *Manual of the New Zealand Coleoptera*; Government Printer: Wellington, New Zealand, 1880; Volume 1.
11. Broun, T. *Manual of the New Zealand Coleoptera*; Government Printer: Wellington, New Zealand, 1893; Volumes 5–7.
12. Broun, T. *Manual of the New Zealand Coleoptera*; Government Printer: Wellington, New Zealand, 1886; Volumes 3 and 4.
13. Broun, T. Descriptions of new genera and species of Coleoptera. *Bull. N. Z. Inst.* **1914**, *1*, 143–266. [CrossRef]
14. Broun, T. Descriptions of new genera and species of Coleoptera. *Trans. Proc. N. Z. Inst.* **1913**, *45*, 97–163.
15. Hudson, G.V. *Fragments of New Zealand Entomology*; Ferguson & Osborn Ltd.: Wellington, New Zealand, 1950.
16. Hudson, G.V. *New Zealand Beetles and Their Larvae: An Elementary Introduction to the Study of Our Native Coleoptera*; Ferguson & Osborn Ltd.: Wellington, New Zealand, 1934.
17. Marshall, G.A.K. New Curculionidae (Col.) from New Zealand. *Trans. R. Soc. N. Z.* **1937**, *67*, 316–340.
18. Brown, S.D.J. *Austromonticola*, a new genus of broad-nosed weevil (Coleoptera: Curculionidae: Entiminae) from montane areas of New Zealand. *ZooKeys* **2017**, *707*, 73–130. [CrossRef] [PubMed]
19. Kuschel, G. New Zealand Curculionoidea from Captain Cook's voyages (Coleoptera). *N. Z. J. Sci.* **1970**, *13*, 191–205.
20. Kuschel, G. Insects of Campbell Island. Coleoptera: Curculionidae of the subantarctic islands of New Zealand. *Pac. Isl. Monogr.* **1964**, *7*, 415–493.
21. Kuschel, G. Apionidae and Curculionidae (Coleoptera) from the Poor Knights Islands, New Zealand. *J. R. Soc. N. Z.* **1982**, *12*, 273–282. [CrossRef]
22. Kuschel, G. *Beetles in a Suburban Environment: A New Zealand Case Study*; DSIR Plant Protection Report Volume 3; Department of Scientific and Industrial Research: Auckland, New Zealand, 1990.

23. Oberprieler, R.G.; Anderson, R.S.; Marvaldi, A.E. 3 Curculionoidea Latreille, 1802: Introduction, Phylogeny. In *Handbook of Zoology, Arthropoda: Insecta. Coleoptera, Beetles Volume 3: Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Eds.; Walter De Gruyter: Berlin, Germany, 2014; pp. 285–300. [CrossRef]
24. Lawrence, J.F.; Beutel, R.G.; Leschen, R.A.B.; Ślipiński, A. 2. Glossary of Morphological Terms. In *Handbuch der Zoologie/Handbook of Zoology. Band/Volume IV Arthropoda: Insecta Teilband/Part 38. Coleoptera, Beetles. Vol. 2. Morphology and Systematics (Polyphaga Partim)*; Leschen, R.A.B., Beutel, R.G., Lawrence, J.F., Eds.; W. DeGruyter: Berlin, Germany, 2010; pp. 9–20. [CrossRef]
25. Wanat, M. Alignment and homology of male terminalia in Curculionoidea and other Coleoptera. *Invertebr. Syst.* **2007**, *21*, 147–171. [CrossRef]
26. Kukalová-Peck, J.; Lawrence, J.F. Evolution of the hind wing in Coleoptera. *Can. Entomol.* **1993**, *125*, 181–258. [CrossRef]
27. Zherikhin, V.V.; Gratshev, V.G. A comparative study of the hind wing venation of the superfamily Curculionoidea, with phylogenetic implications. In *Biology, Phylogeny and Classification of Coleoptera. Papers Celebrating the 80th Birthday of Roy A Crowson*; Pakaluk, J., Slipinski, S.A., Eds.; Muzeum i Instytut Zoologii PAN: Warszawa, Poland, 1995; pp. 633–777.
28. Kelly, K.L.; Judd, D.B. *Color: Universal Language and Dictionary of Names*; U.S. Department of Commerce, National Bureau of Standards: Washington, DC, USA, 1976.
29. Jaffer, A. Color-Name Dictionaries: NBS/ISCC centroids. Available online: http://people.csail.mit.edu/jaffer/Color/Dictionaries#nbs-iscc (accessed on 22 July 2018).
30. Inkscape Team. Inkscape: A Vector Drawing Tool. Available online: http://www.inkscape.org (accessed on 22 July 2018).
31. Crosby, T.K.; Dugdale, J.S.; Watt, J.C. Area codes for recording specimen localities in the New Zealand subregion. *N. Z. J. Zool.* **1998**, *25*, 175–183. [CrossRef]
32. Brockhampton Press. *Dictionary of Classical Mythology*; Brockhampton Press: London, UK, 1995.
33. Hoare, R.J.B. A new species of *Hierodoris* Meyrick (Lepidoptera: Oecophoridae) with a telescopic ovipositor, from granite sand plains in Fiordland. *N. Z. Entomol.* **2012**, *35*, 51–57. [CrossRef]
34. Hoare, R.J.B.; Millar, I.; Richardson, S.J. The insect fauna of granite sand plains: A naturally rare ecosystem in New Zealand. *N. Z. Entomol.* **2016**, *39*, 1–14. [CrossRef]
35. Barratt, B.I.P.; Patrick, B.H. Insects of snow tussock grassland on the East Otago Plateau. *N. Z. Entomol.* **1987**, *10*, 69–98. [CrossRef]
36. Buckley, T.R.; Krosch, M.; Leschen, R.A.B. Evolution of New Zealand insects: Summary and prospectus for future research. *Austral Entomol.* **2015**, *54*, 1–27. [CrossRef]
37. Leschen, R.A.B.; Buckley, T.R. Revision and phylogeny of *Syrphetodes* (Coleoptera: Ulodidae): implications for biogeography, alpinization and conservation. *Syst. Entomol.* **2015**, *40*, 143–168. [CrossRef]
38. Heenan, P.B.; McGlone, M.S. Evolution of New Zealand alpine and open-habitat plant species during the late Cenozoic. *N. Z. J. Ecol.* **2013**, *37*, 105–113.
39. Wardle, P. Origin of the New Zealand mountain flora, with special reference to trans-Tasman relationships. *N. Z. J. Bot.* **1978**, *16*, 535–550. [CrossRef]
40. Primack, R.B. Insect pollination in the New Zealand mountain flora. *N. Z. J. Bot.* **1983**, *21*, 317–333. [CrossRef]
41. Webb, C.J.; Kelly, D. The reproductive biology of the New Zealand flora. *Trends Ecol. Evol.* **1993**, *8*, 442–447. [CrossRef]
42. Minoshima, Y.N.; Seidel, M.; Wood, J.R.; Leschen, R.A.B.; Gunter, N.L.; Fikáček, M. Morphology and biology of the flower-visiting water scavenger beetle genus *Rygmodus* (Coleoptera: Hydrophilidae). *Entomol. Sci.* **2018**. [CrossRef]
43. Godley, E.J. Flower biology in New Zealand. *N. Z. J. Bot.* **1979**, *17*, 441–466. [CrossRef]
44. Newstrom, L.; Robertson, A.W. Progress in understanding pollination systems in New Zealand. *N. Z. J. Bot.* **2005**, *43*, 1–59. [CrossRef]
45. Armstrong, J.E.; Irvine, A.K. Floral biology of *Myristica insipida* (Myristicaceae), a distinctive beetle pollination syndrome. *Am. J. Bot.* **1989**, *76*, 86–94. [CrossRef]
46. Pellmyr, O.; Thien, L.B.; Bergström, G.; Groth, I. Pollination of New Caledonian Winteraceae: Opportunistic shifts or parallel radiation with their pollinators? *Plant Syst. Evol.* **1990**, *173*, 143–157. [CrossRef]

47. Hall, J.A.; Walter, G.H.; Bergstrom, D.M.; Machin, P.J. Pollination ecology of the Australian cycad *Lepidozamia peroffzkyana* (Zamiaceae). *Aust. J. Bot.* **2004**, *52*, 333–343. [CrossRef]
48. Ratnayake, R.M.C.S.; Gunatilleke, I.A.U.N.; Wijesundara, D.S.A.; Saunders, R.M.K. Pollination ecology and breeding system of *Xylopia championii* (Annonaceae): Curculionid beetle pollination, promoted by floral scents and elevated floral temperatures. *Int. J. Plant Sci.* **2007**, *168*, 1255–1268. [CrossRef]
49. Franz, N.M. Pollination of *Anthurium* (Araceae) by derelomine flower weevils (Coleoptera: Curculionidae). *Int. J. Trop. Biol.* **2007**, *55*, 269–277. [CrossRef]
50. Roff, D.A. The evolution of flightlessness in insects. *Ecol. Monogr.* **1990**, *60*, 389–421. [CrossRef]
51. McCulloch, G.A.; Waters, J.M. Does wing reduction influence the relationship between altitude and insect body size? A case study using New Zealand's diverse stonefly fauna. *Ecol. Evol.* **2018**, *8*, 953–960. [CrossRef] [PubMed]
52. Darlington, P.J. Carabidae of mountains and islands: Data on the evolution of isolated faunas, and on atrophy of wings. *Ecol. Monogr.* **1943**, *13*, 37–61. [CrossRef]
53. Mani, M.S. *Ecology and Biogeography of High Altitude Insects*; Dr W. Junk Publishers: The Hague, The Netherlands, 1968. [CrossRef]
54. Holloway, B.A. Wing development and evolution of New Zealand Lucanidae (Insecta: Coleoptera). *Trans. R. Soc. N. Z.* **1963**, *3*, 99–116.

diversity

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Diversity of Curculionoidea in Humid Rain Forest Canopies of Borneo: A Taxonomic Blank Spot

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Abstract: From 1992 to 2009, 334 trees were sampled by insecticidal knockdown on Borneo, Malaysia. Here, we describe the taxonomic composition of the 9671 specimens and 1589 species Curculionoidea collected (with additional notes on Cerambycidae). We found a largely unknown fauna with an assumed proportion of over 80% of species new to science, including all 33 Apionidae and 26 Ceutorhynchinae species. Specialists could usually identify only a few specimens leaving the remaining beetles for further investigation. The samples contain numerous genera, two tribes (Egriini, Viticiini), one subfamily (Mesoptiliinae) and one family (Belidae) new to Borneo and several genera not recorded west of the Wallace line before. These data show how little is known about canopy diversity. The lack of taxonomic knowledge implies a respective lack of autecological knowledge and is alarming. Some taxa differed conspicuously between primary and disturbed forests. In contrast to common literature, our results let us conclude that current efforts to narrow down the extent of tropical diversity and its ecological importance must consider the enormous species diversity of the canopy.

Keywords: Borneo; tropical forest canopies; fogging; diversity; forest disturbance; weevil fauna; longhorned beetle (Cerambycidae); new species

1. Introduction

Despite all efforts, the global extent of biodiversity is still insufficiently known and controversial [1,2]. This lack is mostly due to poor knowledge of tropical rain forests where large areas and habitats like the canopy remain insufficiently researched. Although scientists have known for decades that arthropod richness is very high in the canopy of tropical trees [3,4], no comprehensive data or long-term studies have yet been published from the canopy of any near-equator rain forest worldwide. Considering the importance of biodiversity for ecosystem function and services [5] research in tropical rain forests—and from our perspective in the canopy—should be prioritized. Primary forests are ruthlessly exploited worldwide and pushed back to a few wildlife sanctuaries [6]. Evidence is growing that disturbed forests differ fundamentally from primary forests not only in respect to species diversity but also to system services on which humans depend [7]. Understanding the fundamental processes requires working in pristine forests where most species are usually new to science [8–10], which makes research even more difficult. Besides preliminary work on morphospecies sorting only the exact identification of this largely unknown diversity ensures advanced future ecological analyses. Moreover, the lack of taxonomic knowledge causes an almost general ignorance about the autecological requirements of species and makes predictions concerning the future of disturbed forests rather imprecise.

There is an urgent need for well processed data documenting the distribution of biodiversity within and between forest types. Our work narrows this lack of knowledge by analyzing the faunistic and taxonomic composition of arboreal beetles which have been collected from 334 trees in primary and disturbed forests of southeast Asia from 1992 to 2009. Here, we present data on the Curculionoidea, one of the most diverse and abundant group of beetles [11]. We provide insight into the faunistic-taxonomic composition of the arboreal weevil fauna and report some striking differences in taxa abundance between primary and disturbed forests.

2. Materials and Methods

2.1. Study Area

All fogging sites are located in Sabah, the northeastern part of East Malaysia, Borneo. Research was carried out in different primary and disturbed forests. Most data were gathered in primary "Mixed Dipterocarpaceae lowland forests" between 300 m and 900 m a.s.l. mainly in different substations of the Kinabalu National Park, Malaysia (06°02′54.18″ N, 116°41′56.34″ E) but also on Gaya Island (6°0′51.36″ N, 116°1′13.74″ E) and in the National Parks Crocker Range (5°24′43.68″ N, 116°5′24.84″ E) and Tawau (4°24′1.26″ N, 117°53′24.66″ E) as the most southern area. There were in total 171 trees. In addition, 43 trees were sampled at different altitudes ranging from 1000 m to 2500 m a.s.l. at Mt. Kinabalu and in the Crocker Range. Different types of disturbed forest were also sampled: 10- to 15-year-old pioneer vegetation on the two small islands Bakkungan Kecil (6°10′0.66″ N, 118°6′32.88″ E) and Selingaan (6°10′31.38″ N, 118°3′41.10″ E)—10 trees together. Three secondary forests of 5, 15 and 40 years after natural regrowth which were growing close to the Kinabalu Park (6°19′0.84″ N, 116°44′2.1997″ E) and another three isolated secondary forests of 10, 20 and 50 years after natural regrowth in a distance of at least 10 km to the Crocker Range primary forest (5°26′0.68″ N, 116°7′58.78″ E). Altogether, these were 80 trees. We also sampled 15 oil palms that were growing in direct neighborhood to the primary forest of Tawau and 15 fruit trees of different species in garden areas (6°17′36.84″ N, 116°43′5.76″ E) in the Kinabalu region. All disturbed forests were found in areas originally covered with lowland forest (between 5 m and 400 m a.s.l.). More details including a map have been published in [9].

2.2. Collecting and Sorting of Canopy Beetles, Genus and Species Identification

During 1992 and 2009, arthropods were collected by means of insecticidal knock-down ('fogging'). Natural pyrethrum diluted in a highly purified white oil was used as insecticide because it degrades within hours in sunlight leaving no poisonous substances in the trees. Fogging was carried out in the early morning or late in the afternoon when there was little wind. All arthropods that dropped into the collecting sheets installed beneath a tree crown after two hours following fogging were transferred into vials filled with ethanol. More technical information has been published elsewhere [12]. Here, we focus on weevils following preferably the classification proposed by Alonso-Zarazaga and Lyal [13], with slight modifications; see Oberprieler [14]. We are aware that there are also several changes at the subfamily level in between, but did not follow these proposals for practical reasons. Beetles were sorted to morphotypes (morphospecies) and specimens were distinguished by optical means. Morphotypes were treated as real species when sorted by taxa specialists. A dissection of the genitalia was usually not carried out and left to specialists.

Besides specialist knowledge, current taxonomic papers and revisions were used for species determination. Furthermore, the SDEI museum collections in Eberswalde (now Müncheberg) and Dresden were helpful, especially for Conoderinae, Dryophthoridae and Entiminae.

2.3. Sampled Trees

Tree diversity is very high with more than 1000 species found in the Kinabalu area and more than 3000 species reported from Borneo [15]. The sampled tree species represent 23 plant families in the primary forests. These were Annonaceae, Burseraceae, Clusiaceae, Cornaceae, Dipterocarpaceae, Elaeocarpaceae, Euphorbiaceae, Fagaceae, Lamiaceae, Lauraceae, Lecythidaceae, Malvaceae, Meliaceae, Moraceae, Myrtaceae, Olacaceae, Phyllanthaceae, Podocarpaceae, Polygalaceae, Putranjivaceae, Rhizophoraceae, Sapotaceae, and Urticaceae. Twenty-one families were sampled in the disturbed forests, namely Anacardiaceae, Annonaceae, Aquifoliaceae, Arecaceae, Clethraceae, Combretaceae, Ericaceae, Escalloniaceae, Euphorbiaceae, Fabaceae, Lamiaceae, Lauraceae, Malvaceae, Meliaceae, Myrtaceae, Phyllanthaceae, Podocarpaceae, Sapindaceae, Sapotaceae, Symplocaceae, and Theaceae, with nine families represented in both types. Most foggings were carried out on *Aporosa lagenocarpa* A. Shaw and *A. subcaudata* Merr. (Phyllanthaceae) which were frequently found in the understory of the studied primary forests. Common trees in the secondary forests were *Melanolepis* sp. (Euphorbiaceae-Acalyphoideae), *Melochia umbellata* (Hoult.) Stapf (Malvaceae-Byttnerioideae) and *Vitex pinnata* L. (Lamiaceae-Verbenioideae). These trees were not found in the primary forests.

3. Results and Discussion

3.1. Suitability of Fogging for Collecting Canopy Weevils

From all 334 trees, we collected 9671 individual Curculionoidea in 1589 species. Due to the high number of species from the groups Curculionini, Ochyromerini and Rhynchitidae, as well as smaller groups like Ceutorhynchinae, Nanophyidae or Rhamphini, the data show that canopy fogging is well-suited to collect arboreal species that inhabit leaves, flowers and fruits of trees. This seems to hold also for several groups that are usually regarded as saproxylic, like Anthribidae, Conoderinae, Cossoninae, Cryptorhynchinae, Molytinae and Scolytinae which were also represented by more than 100 species each. Lower numbers than expected were found in Attelabidae with one species apart from genus *Euops* and Dryophthoridae (15 species in each family).

3.2. Faunistic-Taxonomic Classification of Canopy Beetles

The fogging results are presented in Table 1. It contains all relevant taxonomic weevil groups found in the samples, the number of species and specimens, the experts included in the analyses and the number of identified genera and species before 2013.

Table 1. Canopy weevils from the superfamily Curculionoidea in the samples from Malaysia (Borneo).

Taxa	Number of Morpho-Species	Number of Specimens	Identified (Genus/Species Level)	Identified by *
CURCULIONOIDEA				
Anthribidae	217	710	-	
Belidae	1	1	1/0	
Rhynchitidae	110	358	-	
Attelabidae	15	60	14/0	Riedel
Brentidae	32	65	22/9	Bartolozzi, Mantilleri
Apionidae	33	279	3/0	Wanat
Nanophyidae	44	162	-	
Dryophthoridae	15	29	10/0	
CURCULIONIDAE				
Baridinae	36	141	16/1	Prena
Ceutorhynchinae	26	203	13/0	Yoshitake, Colonnelli
Conoderinae	171	418	-	
Cossoninae	107	494	-	
Cryptorhynchinae	106	258	-	
Curculioninae-Acalyptini	32	521	8/0	Sprick
Curculioninae-Anoplini	6	12	6/0	
Curculioninae-Anthonomini	5	93	4/1	Sprick
Curculioninae-Curculionini	122	649	-	
Curculioninae-Demimaeini	3	3	3/0	
Curculioninae-Derelomini	1	50	1/1	
Curculioninae-Ochyromerini	133	1090	93/3	Sprick
Curculioninae-Rhamphini	52	178	42/3	Sprick
Curculioninae-Storeini	2	7	2/0	

Table 1. *Cont.*

Taxa	Number of Morpho-Species	Number of Specimens	Identified (Genus/Species Level)	Identified by *
		CURCULIONIDAE		
Entiminae	38	658	-	
Hyperinae	1	1	1/1	
Mesoptiliinae	1	3	0/0	
Molytinae	139	455	-	
Scolytinae	111	2665	109/50	Beaver
Platypodinae	17 **	99	11/14	Beaver
doubtful assignments	ca 20–30			
		CHRYSOMELOIDEA		
Cerambycidae	219	621	199/37	Holzschuh, Weigel

*: if no specialist is mentioned there is only morphospecies sorting carried out by the authors without complete determination of the group; **: seventeen further morphotypes had been found in later samples.

3.3. Special Part

Belidae-Oxycoryninae

There is one specimen of the genus *Metrioxena* in the sense of Alonso-Zarazaga and Lyal [13]. According to Legalov [16], it is now placed in *Vladimirixena* (Figure 1). *Metrioxena* is distributed in Malaysia and Indonesia, and *Vladimirexena* in Indonesia. *Metrioxena* sensu lato was also detected in Baltic Amber indicating a minimum age of 35 million years. It is the first record on Borneo, also of the entire family, even though its occurrence was to be expected there.

Attelabidae

In our data, we found one *Allolabus* species and 14 of the genus *Euops*, mainly subgenus *Suniops* (Figure 1). Five morphospecies were identified to species level but all are in need of confirmation by the study of type specimens. Thus, at least 10 species are undescribed.

Apionidae

Our samples contain 33 species of which 21 are in the tribe Piezotrachelini, 11 in the tribe Ixapiini and 1 in the Rhadinocybini. None of the specimens could be identified to species and thus all of them may be new to science (Wanat, pers. comm.). Only three genera could be identified: *Microconapion*, *Ommatocybus* and *Piezaplemonus* with one species each (Figure 1). The last genus, described by Wanat [17], was hitherto known only from Thailand and the genus *Microconapion* from Japan, Taiwan and Vietnam. *Ommatocybus* was erected by Wanat [18] during his study on Australo-Pacific Apionidae. This means that all the genera were not previously recorded from Borneo and Malaysia, and this is also true for the tribe Rhadinocybini (see Alonso-Zarazaga and Lyal [13]). According to Wanat, the remaining 30 species represent four as yet undescribed genera. At least these data show that the Bornean Apionidae canopy fauna is completely unexplored.

Brentidae

There are 32 species and, apart from the circumtropical *Cylas formicarius* (Fabricius, 1798), eight of them were identified to the species level. A further species was described as new, *Microtrachelizus floreni* Mantilleri, 2012 [19], and 11 species were identified to a genus level of which three will be described later (*Cordus* sp., *Homophylus* sp., *Hypomiolispa* sp.) (Figure 2). The samples contained 10 species, mainly of the subfamily Cyphagoginae, which remained unidentified (without genus diagnosis). The genus *Cordus* was up to now only known from Australasia (Australia, New Guinea, Solomon Islands) and the species *Calodromus insignis* (Senna, 1895) only from Sumatra (Figure 3).

The checklist of Brentidae includes 204 species from Borneo including three mentioned species known only from "Indonesia" without further location [20]. From all species fogged, only nine (28%) could be determined to the species level, representing 4.4% of the known Bornean fauna of Brentidae. If the difficult genus *Cyphagogus* is excluded, the values change to 32% and 4.9%, respectively. The data demonstrate that, within a group for which all available data are summarized at the present time (see the world catalogue of Sforzi and Bartolozzi [20]), the tree crowns apparently harbor a rather little known Brentidae fauna on Borneo.

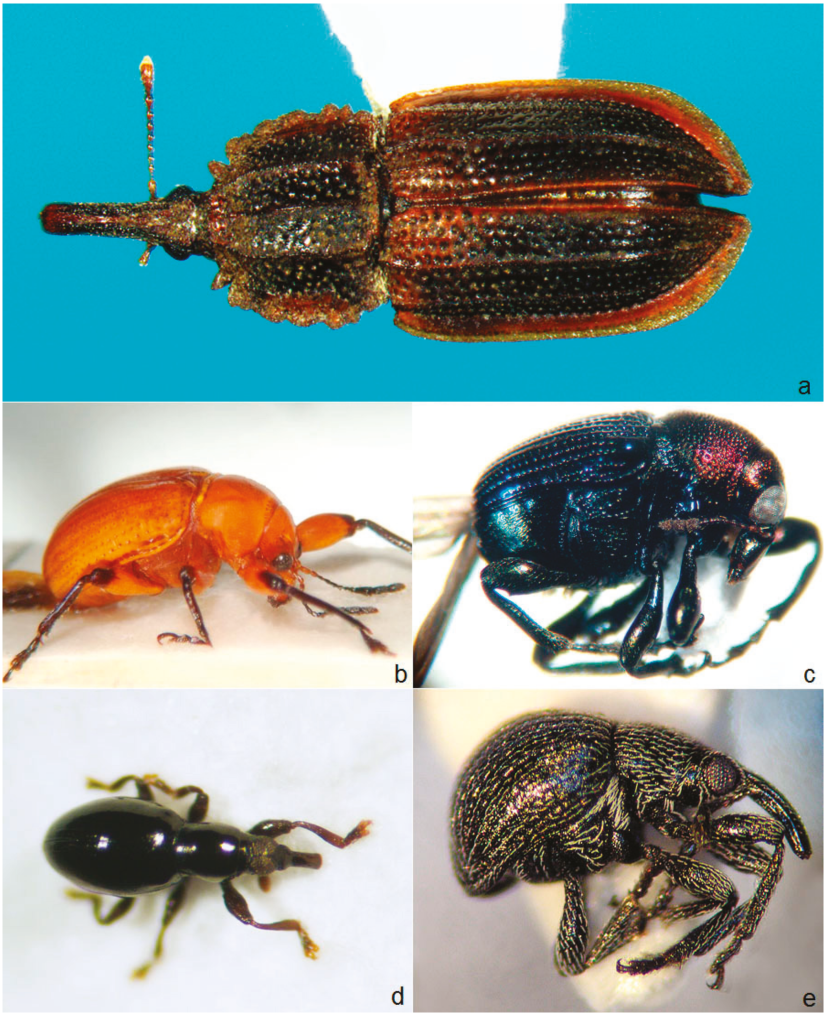

Figure 1. *Metrioxena* s.l., now. to *Vladimirixena* sp. (Belidae) (**a**); *Allolabus* sp. (**b**); *Euops* sp. (both Attelabidae) (**c**); *Ommatocybus* sp. (**d**); and a new species of the tribe Ixapiini (both Apionidae) (**e**).

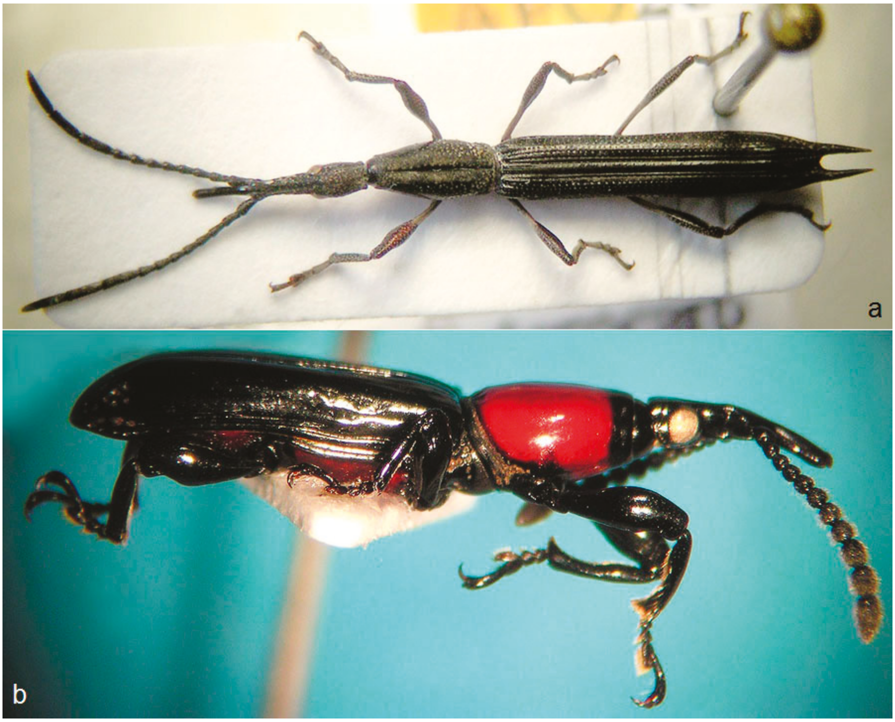

Figure 2. *Achrionota* sp. (**a**) and *Homophylus* sp. (both Brentidae) (**b**).

Curculionidae-Baridinae

Only one species could be identified without doubt to species level: *Anoplobaris sabahna*, described by Morimoto and Yoshihara [21], based on one specimen from Mt. Kinabalu. It has now been collected again in the same area, represented by four individuals. Two further species were identified provisionally. The following genera were determined: *Acythopeus* (1–2 species), *Anoplobaris*, *Athesapeuta*, *Centrinertus*, *Hollisiella* (1–2 species), *Lophobaris*, *Mononychobaris* (1–3 species) and *Nespilobaris* (3–4 species) and two further genera with doubt: *Aponychius* and *Omobaris*.

The genera *Centrinertus*, *Hollisiella*, *Lophobaris* and *Nespilobaris* are new to Malaysia and Borneo (Figure 3). The first was formerly known only from the Philippines, the second from China, the third from Taiwan to Java and the Philippines, so that its occurrence on Borneo could be expected. This is also true for *Nespilobaris*, which was known from Eastern Siberia, Japan, China, Australia and Africa [13,22]. The considerable number of Baridinae genera that had not been recorded from Borneo demonstrates the poor knowledge on the distribution of this group of weevils in Southeast Asia.

Curculionidae-Ceutorhynchinae

The morphospecies sorting revealed 24 species, but Enzo Colonnelli and Hiraku Yoshitake, who checked it in part, both separated one more species each, resulting in a total number of 26 Ceutorhynchinae species. The tribe Mecysmoderini is the main group, represented by 17 species, followed by Ceutorhynchini with five species, Hypohypurini with three and Egriini with one, a *Megahypurus* species (det. E. Colonnelli by photo). None of them could be identified to species level suggesting that all of them are new to science. Besides *Coelioderes* (one species) and *Watanabesaruzo* (two species), two genera just recently described by Yoshitake and Yamauchi [23] and Yoshitake and

Ito [24], there are two *Coeliosomus* and one *Cysmemoderes* species (aff. *C. gibbicollis* (Hustache, 1925), det. Yoshitake) and several species from further undescribed Mecysmoderini genera in the samples. The Ceutorhynchini are represented by *Hainokisaruzo* and the Hypohypurini by the single genus *Hypohypurus*. Unfortunately, Yoshitake, who was interested in receiving all Ceutorhynchinae weevils, has not described any to date.

Figure 3. Adult (**a**) and conspicuous hind tibiae (**b**) of *Calodromus insignis* (Brentidae), *Centrinertus* spec. (**c**); *Nespilobaris* sp. (both Baridinae) (**d**); *Watanabesazuro* sp. (Mecysmoderini) (**e**); and *Megahypurus* sp. from the tribe Egriini (both Ceutorhynchinae) (**f**).

The insufficient knowledge about this group in Malaysia and Indonesia is shown by the fact that *Watanabesaruzo* was found until now only in Bali (Indonesia), Yunnan (China) and Perak (Malaysia) [23,25], *Coelioderes* in Eastern Siberia, Japan, Korea and China [24,26]) and *Hainokisaruzo* by several species in China, Taiwan, India and Japan [27,28]. The tribe Hypohypurini, erected by Colonnelli in 2004 [26], was recorded from China and Vietnam, North Australia, Madagascar and Central Africa, and the tribe Egriini was also not reported from Malaysia or Borneo before 2012 [29]. *Megahypurus* Korotyaev, 1989 was described from Vietnam (Figure 3). As previous collecting in Indonesia revealed a rather small number of Ceutorhynchinae (see, for example: [26]), fogging was very successful in collecting arboreal Ceutorhynchinae. In a current fogging study on Java, there were also a few Ceutorhynchinae of the genus *Watanabesaruzo* and other Mecysmoderini genera (A. Floren, own data).

Curculionidae-Curculioninae (Figures 4–7)

This group of weevils is represented by a great number of morphospecies in the samples. Due to the extensive work of mainly Japanese authors (see citations below), there is current information about the occurrence of some tribes in southeast Asia (especially Acalyptini, Anthonomini, Ochyromerini and Rhamphini). Here, we mainly present results for Acalyptini, Ochyromerini, Rhamphini and some species-poor tribes.

The following tribes could be identified (number of morphospecies in brackets): Acalyptini (31), Anoplini (6), Anthonomini (5), Curculionini (122), Demimaeini (3), Derelomini (1), Storeini (2), Rhamphini (52; see below), and Ochyromerini (previously Tychiini, subtribe Ochyromerina) (133). Morphotype differentiation in Acalyptini and in Ochyromerini is still a matter of some uncertainty because there is a rather large proportion of small yellowish weevils of great similarity (in Acalyptini, about two thirds of the total; Figures 4, 5 and 7). Hence, an analysis of the morphospecies numbers, including the dissection of the genitalia, could change the numbers. Usually, dissections were not made to avoid incidental destructions, as most species were present in only small numbers.

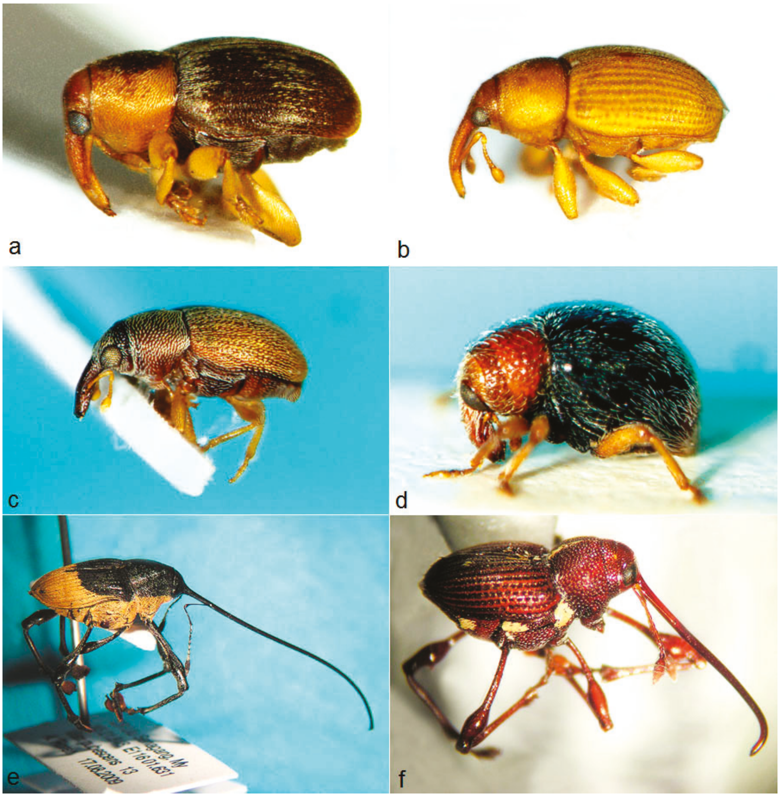

Figure 4. Curculioninae I. *Parimera* spec. (**a**) and two unknown small genera of Acalyptini (**b**,**c**); the latter cf. *Niseida* (**c**); a scymnine-like, red-and-black coloured *Demimaea* species with trifid hairs ventrally and at the base of the elytra (**d**) and two long-nosed Curculionini species (**e**,**f**); one of them (**f**) a *Pseudoculio* species.

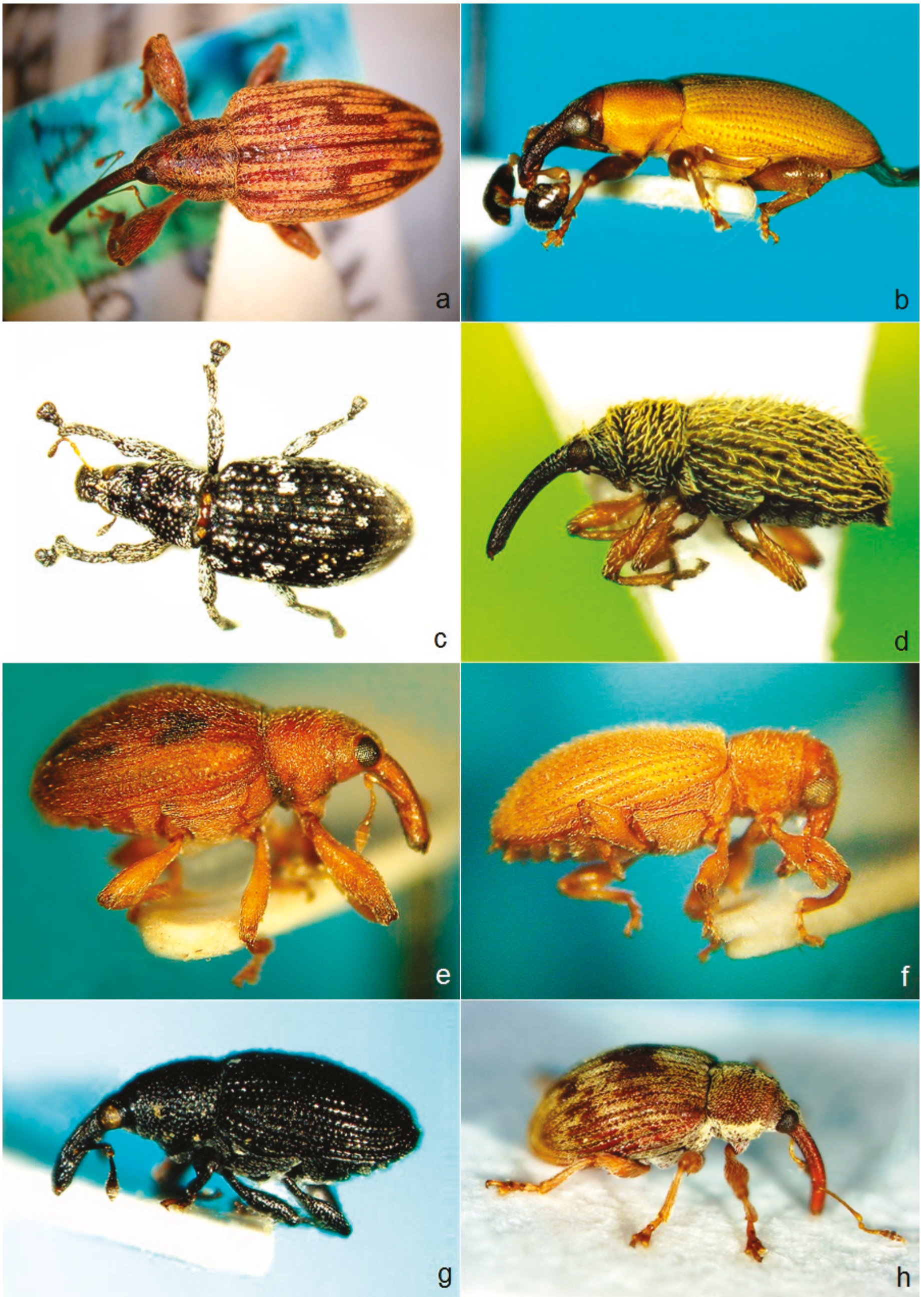

Figure 5. Curculioninae II. Ochyromerini: *Opseoscapha* cf. *alternans* Faust, 1888 (**a**); *Katsurazo* sp. (**b**); *Viticis* spec. (**c**); *Lepidimerodes* sp. (**d**); *Endaeus* sp. (**e**); a small yellowish *Ochyromera* species (**f**); resembling *Endaeus* species, but with seven funicular segments, and one unidentified and possibly new genus with seven funicular segments (**g**). The last photo (**h**) shows a member of Anthonomini (*Usingerius parvidens*) resembling Ochyromerini.

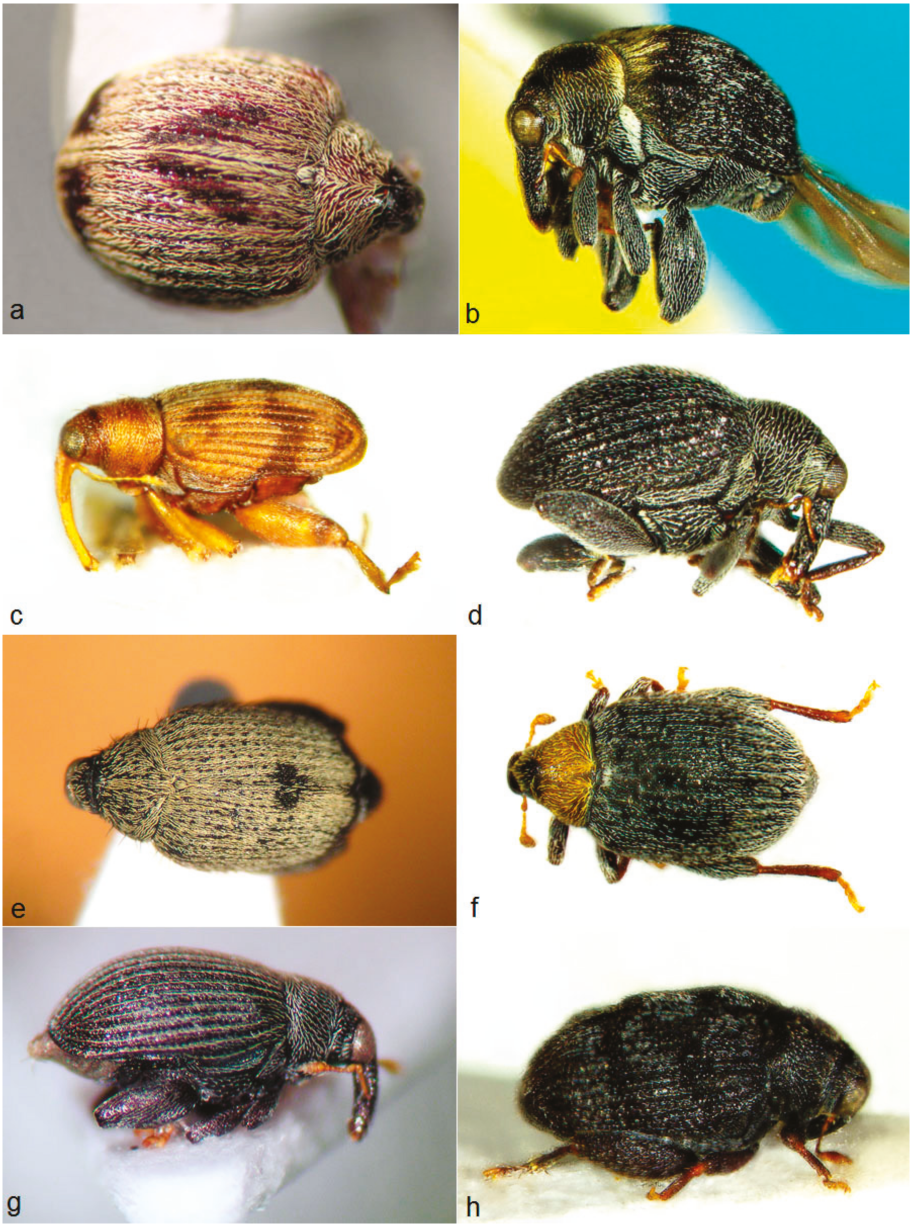

Figure 6. Curculioninae III. Rhamphini. *Sphaerorchestes* sp. (**a**); *Imachra siamensis* (**b**); *Indodinorrhopalus* sp. (**c**); *Morimotonomizo* sp. (**d**); *Orchestes* (*Orchestes*) sp. (**e**); *Orchestes* (*Nomizo*) sp. (**f**); and two unknown and probably new genera (**g**,**h**).

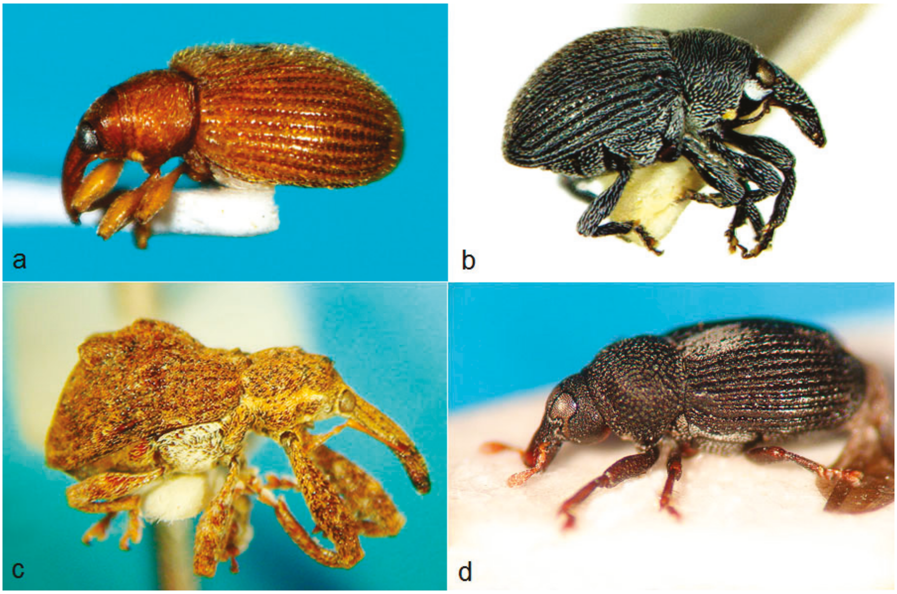

Figure 7. *Endaenidius* sp. (Ochyromerini) (**a**); *Sphinxis* sp. (Anoplini) (**b**); *Anthonomus* (*Tachypterellus*) (Anthonomini) sp. (**c**); the only recorded Laemosaccini species (Mesoptiliinae) with remarkable eye shape (**d**).

The following genera could be identified by the following works: [30–43] and museum collections: *Amorphoidea* (5 species) and *Parimera* (3) in Acalyptini, *Sphinxis* (6) in Anoplini (or Ochyromerini), *Anthonomus* (*Tachypterellus*) (3) and *Usingerius* (1) in Anthonomini, *Curculio* and *Pseudoculio* in Curculioninae, *Demimaea* in Demimaeini (3), *Elaeidobius* in Derelomini (1), *Imathia* in Storeini (2) as well as *Endaenidius* (35), *Endaeus* (17), *Eugryporrhynchus* (2), *Katsurazo* (3), *Lepidimerodes* (3), *Morimotozo* (2), *Ochyromera* (24), *Omphasus* (6) and *Opseoscapha* (1) in Ochyromerini. Two of the three *Katsurazo* species are clearly different from those described by Kojima (1997) from Sabah. *Elaeidobius kamerunicus* (Faust, 1898) from the tribe Derelomini is an introduced species inhabiting oil palms [41,44]. In Curculionini, the genera *Carponinus* and *Labaninus* were identified provisionally. Most species with a tumid base of the rostrum could not be assigned with certainty to *Indocurculio* due to insufficient illustration of the key of Pelsue and O'Brien [42]. The lack of well identified specimens which could be used for comparison is another serious obstacle.

In Acalyptini (Figure 4), there is a large proportion of species unidentified to genus. Most of them are very small, 1–2 mm long, and of a yellowish color. Apart from their small size, they resemble the Derelomini from palm flowers and may inhabit flowering trees. These species are not considered as members from the Acalyptini genus *Derelomorphus* because they have edentate femora. Two further species of a small size may represent the genus *Niseida* or a similar undescribed genus. *Niseida* is up to now restricted to Aru Island [41]. These results are of special interest because there are the only data for two Acalyptini genera (with one species each), *Amorphoidea* and *Eudela*, recorded from Borneo [41]. In the catalogue of Alonso-Zarazaga and Lyal [13], not a single genus of Acalyptini was listed for Borneo. This means that *Parimera* from our samples is another genus new to this island.

Three species of *Anthonomus* (*Tachypterellus*) have been recorded from Borneo [44]. In our samples, there are also three, but, without dissection of the genitalia, we cannot state if they are identical. With the availability of the paper of Kojima and Idris [43], the identification of *Usingerius parvidens* Zimmerman, 1946 was enabled, a genus that we regarded at first erroneously as Ochyromerini. The former Entiminae tribe Viticiini, represented by two small distinct species, with the genus

Viticis well characterized by the lack of tarsal claw segments [14], is now represented by two species. The genus is new to Borneo and at the same time the westernmost occurrence of this mainly Pacific genus (see [45]). These are the first records of the genus *Viticis* west of the Wallace line.

Despite current taxonomic work, the identification of Ochyromerini is difficult. Most of the many species are of small size (usually smaller than 3 or 4 mm, especially in *Endaeus, Endaenidius, Eugryporrhynchus, Lepidimerodes* and *Morimotozo*). Reliably identified species from other collections are lacking. The proportion of undescribed species is high. The identification of only three species is considered trustworthy: *Eugryporrhynchus malayanus* Kojima and Morimoto, 1995, *Morimotozo ovipennis* (Kojima and Morimoto, 1995) and *M. rotundicollis* (Kojima and Morimoto, 1995). However, a few species were also doubtfully assigned to this tribe: on first examination, three species looked like Cryptorhynchinae, but they have the abdominal segment sutures directed abruptly posteriad close to the margin. This is usually a good character to distinguish Ochyromerini from Anthonomini and Acalyptini. The number of weevils that could not be assigned with certainty to a higher taxon did not exceed 20 or 30 species and thus cannot really affect the data given in Table 1. (In some groups, for example, Anthribidae, Cryptorhynchinae, and in part Molytinae, an assignment to certain tribes proved to be impossible without extensive study and has been left to experts.)

Curculionidae-Curculioninae-Rhamphini (Figure 6)

This group was studied in detail by one of the authors (P.S.) based particularly on the papers on East Asian Rhamphini by Kojima [38], Morimoto [46], Kojima and Morimoto [47], and Morimoto and Miyakawa [48]. The morphospecies sorting revealed 52 species. These are far more than the total 35 described and three undescribed Rhamphini species from the entire area of southeast Asia from India to South China (Fujian included), Taiwan and Thailand to Indonesia and the Philippines [47,48].

Forty-two species were determined to genus level: 8 *Imachra*, 2 *Indodinorrhopalus*, 2 *Morimotonomizo*, 23 *Orchestes* (*Orchestes*), 4 *Orchestes* (*Nomizo*), 1 *Rhamphus* (*Trichorhamphus*) and 2 *Sphaerorchestes* species. In the remaining species, the genus could not be determined without doubt. These species should represent new genera or new subgenera of *Orchestes*. In *Orchestes* (s. str.), there were many rather small species that were also assigned here, due to the hollowed metatibiae, the outer margin of hind femora with denticles, and the raised setae on the elytra and pronotum. The genus *Indodinorrhopalus* has not been recorded from Borneo or Malaysia previously, *Morimotonomizo* not from Borneo and *Rhamphus* only by an undescribed species from East Malaysia [49]. All 52 species are rather small; there is not a single one measuring more than 3 mm. The remarkable southeast Asian Rhamphini genera *Dinorhopala* and *Ixalma* with body size usually >3.5 mm were not represented in the samples.

Only three species could be identified to species level: *Imachra bifasciata* Morimoto & Miyakawa, 1996, *I. ruficollis* Pascoe, 1874, and *I. siamensis* Morimoto & Miyakawa, 1996. *I. ruficollis* is widespread in the Oriental region, and its range is extended in one area just in the Palaearctic region (China: Fujian). *I. siamensis* was described from South Thailand, and *I. bifasciata* was re-discovered at the type locality (Kinabalu). Except for the three *Imachra* species and *Morimotonomizo* (with one species that could be identical with *M. sphinxioides* (Morimoto and Miyakawa, 1996) from West Malaysia), all remaining 48 Rhamphini species are very probably undescribed (see [47,48]).

Curculionidae-Mesoptiliinae (Figure 7)

Only one species (three specimens) in this subfamily has been collected. Apparently, it is a member of the tribe Laemosaccini, a tribe only known from Australia and New Zealand with the exception of the American genus *Laemosaccus*. This is the first record of a member of subfamily Mesoptiliinae on Borneo and west of the Wallace line.

Curculionidae-Scolytinae

These species were determined by Roger Beaver, e.g., [49]. He distinguished 111 species that makes this taxon together with Anthribidae, Rhynchitidae, Conoderinae, Cossoninae, Curculionini, Cryptorhynchinae, Molytinae and Ochyromerini (each over 100 species), one of the commonest in the fogging data. From all 111 species, 50 could be identified to species level, the remainder at least to the genus level (two species with some doubt). The state of knowledge in this potentially economically relevant group is therefore much better than in all other weevils (except Platypodinae, see the next section). However, even in Scolytinae, 61 species could not be identified and are very probably new to science.

Curculionidae-Platypodinae

Species in this group were sorted and identified by Roger Beaver. However, he received only 50% of the species. From these, 17 species, 14 genera and 11 species could be identified. Six species are new to science.

Remaining Weevil Groups

There is only very scattered information about all the remaining weevil groups (see Table 1): Anthribidae, Nanophyidae, Rhynchitidae (11 Auletini, 36 Deporaini and 63 Rhynchitini species) and the Curculionidae subfamilies Entiminae, Conoderinae, Cossoninae, Cryptorhynchinae and Molytinae. In Figure 8, some long-legged weevils from the subfamilies Conoderinae and Molytinae, which may be typical for tree crowns, are shown. In Nanophyidae, one species could be identified with the key of Lyal and Curran [50] as *Damnux tenebriosa* Lyal, 2003, but all others remained unidentified.

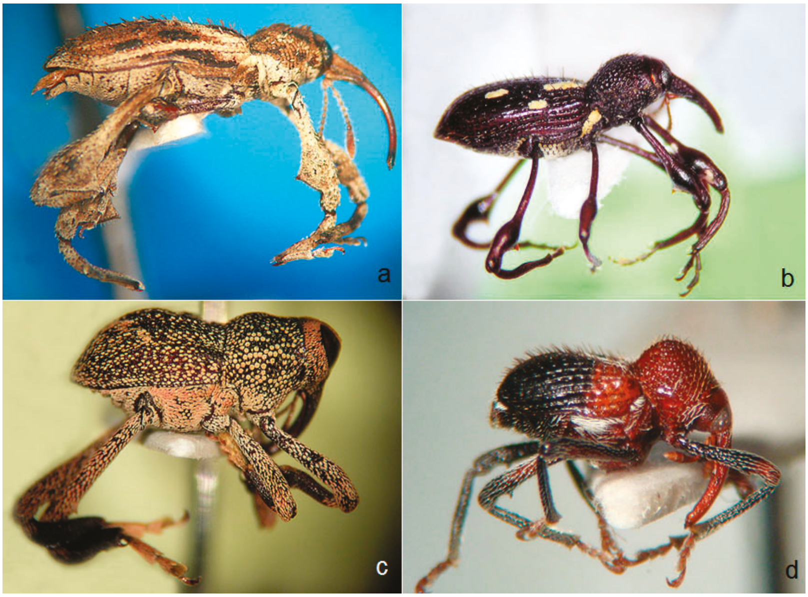

Figure 8. Long-legged weevils. Long legs may be an adaptation to life in the canopy and were mainly found in Curculionini (see Figure 4), Trachodini and Conoderinae, e.g., *Acicnemis* (**a**); *Pseuderodiscus* (**b**); *Odoacis* (**c**); and *Talimanus* (**d**). More than 60 Trachodini morphotypes were recognized.

The Dryophthoridae were represented by only four sizable specimens of the genera *Aplotes*, *Cryptoderma* and *Laogenia*, probably a species of Diocalandrini, and mainly by several Litosomini species of the genera *Sitophilus* (six species) and *Myocalandra* or a closely related genus (four species). In Entiminae, there are single *Dermatodes* (Dermatodini) and *Eugnathus* (Sitonini) species, some Ottistirini and many Cyphicerini, but there is also a rather large number of species of unidentified tribes (perhaps in part Myllocerini). *Apocyrtidius chlorophanus* Heller, 1908, is the only member of

Pachyrhynchini on Borneo, and it is represented by 47 specimens in samples from the Mesilau region of Kinabalu in the montane forest.

In Conoderinae (Figure 8), the bulk of the 171 morphospecies probably belong to Othippiini and a rather significant number to the usually black-and-white-coloured Menemachini, the remaining to Coryssomerini, Mecopini (s.l.), Campyloscelini and unidentified tribes. We are aware that the taxonomy of the higher tribes is rather uncertain especially in this subfamily [51]. A few genera could be identified with little doubt by the keys of Hustache [52], the Intkey CD [53], and museum collections: *Phaenomerus*, *Talimanus*, *Telephae* and *Tomicoproctus*—and with some doubt: *Agametis*, *Metialma*, *Odoacis*, and *Osphilia*, but none of the probably largest tribe Othippiini, which has mainly small species. According to Alonso-Zarazaga and Lyal [13], the well-characterized genus *Tomicoproctus*, represented by one species, was not recorded from Borneo previously, only east of the Wallace line and in Africa.

In Molytinae, there was a great number of Trachodini (63 species), including two *Pseuderodiscus* species, previously placed in Curculioninae-Erodiscini, followed by Ithyporini (37), Hylobiini (16), Mecysolobini (14), Lithinini (about eight species, one of them identified as *Seleuca* by C. Lyal by photo) and Trigonocolini (1), but, among Ithyporini, there may also be other tribes with small species, one of them, for example, looking like *Seticotasteromimus* (tribe Pissodini), a genus recently erected by Germann [54]. In "Ithyporini sensu lato", the differentiation from Cryptorhynchinae was not clear in several cases. Some species from these groups and from Ochyromerini, with more or less doubtful assignments, are depicted in Figures 9 and 10. The genus *Phaeopholus* (Figure 9a) is the only representative of Hyperinae; prior to this study, it has only been recorded from China and Japan and is thus another genus new to Borneo.

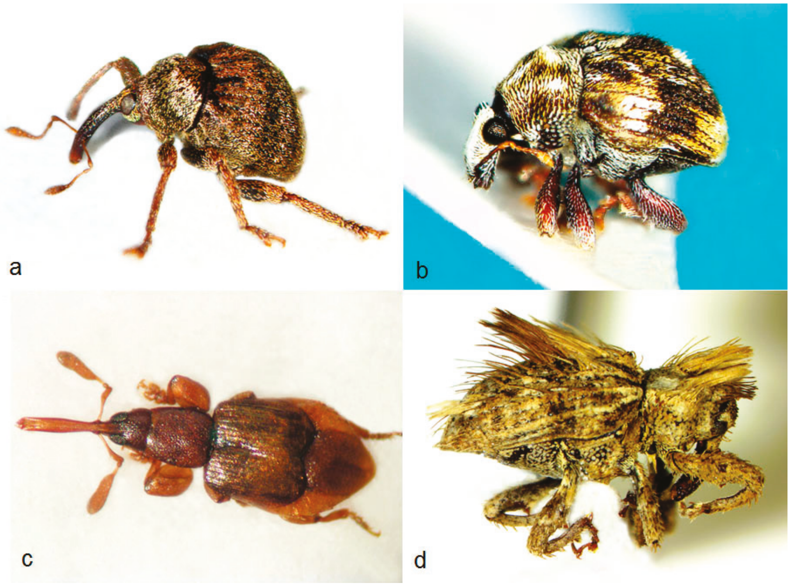

Figure 9. Weevils with doubtful assignments I. The first species (**a**) represents the Hyperini genus *Phaeopholus* (confirmed by Jiři Skuhrovec). The second species (**b**) probably belongs to Microstylini, a tribe of rather uncertain placement (Curculioninae or Molytinae). The third species (**c**) has a very extraordinary habitus: small, flat, shortened elytra, very thick profemora, and a very long antennal club. There is also sexual dimorphism. The long-nosed female is shown. The assignment is unknown, perhaps Acalyptini (M.A. Alonso-Zarazaga, pers. comm.). The next species (**d**) is probably a Sophrorhinini species.

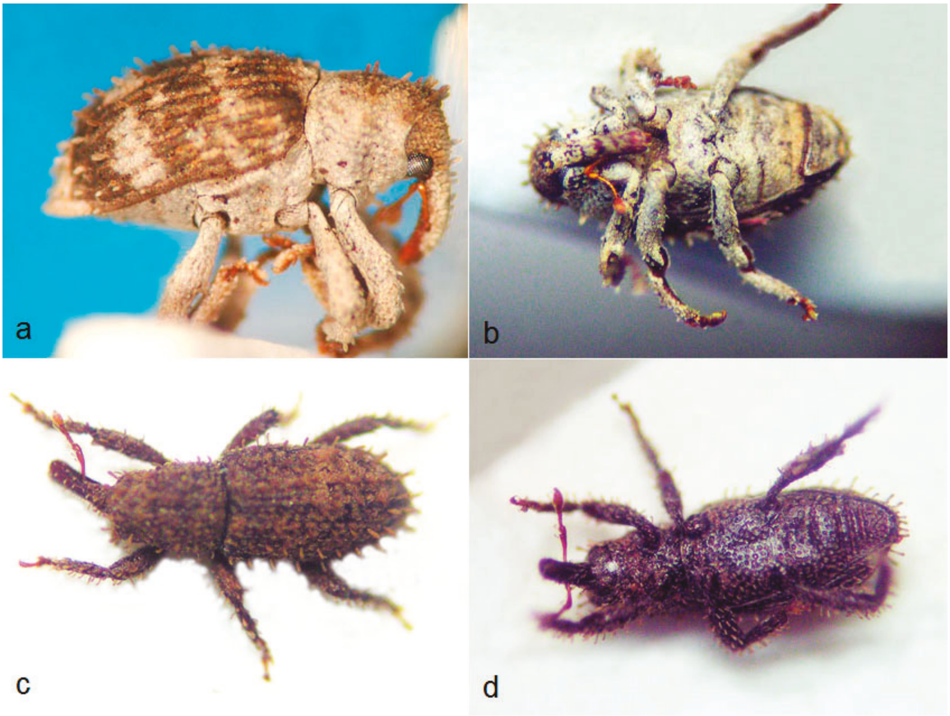

Figure 10. Weevils with doubtful assignments II. The weevil on the first photos (**a**,**b**) is provisionally regarded as Ithyporini. Species with a similar habitus look like inhabitants of the soil, but they were found in rather large numbers in the tree crowns; usually, they have a rostral furrow. In the last small species, such a furrow is absent, and this species is regarded provisionally as *Seticotasteromimus* (Pissodini) or a closely related genus (**c**,**d**).

Cerambycidae

For reasons of comparison, the highly diverse longhorned beetles, many of great economic importance and of special interest for collectors, were also included in this work. Like in the other beetle taxa, there are many undescribed species, underlining how little is still known about the canopy fauna of Bornean primary forests. In addition, 219 species were distinguished by Carolus Holzschuh. Nine species could not be identified to genus level and another 11 with doubt, 37 species were identified to species level and another 19 with doubt. Thirteen species from this dataset were described by Holzschuh as new [55–57]; and work is still in progress. A current checklist of Bornean Cerambycidae contains 1270 species [58], but the total number is estimated to exceed more than 2000 species [55]. The most species-rich tribes in the samples were Apomecynini with 61 and Pteropliini with 31 species, both in subfamily Lamiinae, with genera like *Pterolophia*, *Ropica* and *Sybra*. Only 37 (16.9%) of the 219 recorded species could be identified up to 2012, representing only 2.9% of the Bornean fauna and revealing the conspicuous gaps of knowledge even in a 'collectors' group'.

3.4. Brief Summary

The analysis of the canopy weevils provides a first impression on the distribution of higher weevil taxa in Bornean rain forests. Except Brentidae and a few other groups with long narrow body form, there is a very large number of rather small species not exceeding 4 mm. The data suggest that the proportion of species new to science is very high. Several taxa like Apionidae and Ceutorhynchinae contain what appear to be exclusively new species and others mainly new species, such as Baridinae, Brentidae and Rhamphini (Curculioninae). We also verified the existence of at least 15 genera, one subfamily and one family formerly not known from Borneo. Furthermore, a high proportion of non-identifiable specimens was confirmed even for larger groups of general interest like the bark and ambrosia beetles (Scolytinae) or the longhorned beetles (Cerambycidae). Information on several other taxa confirm a similar poor state of taxonomic knowledge; this refers to Alticinae (Chrysomelidae, processed by the late M. Döberl), Anthicidae (D. Telnov), Pselaphinae (Staphylinidae, V. Brachat), Scirtidae (B. Klausnitzer) and Tenebrionidae (Alleculinae and Lagriinae excluded; R. Grimm, H. J. Bremer), which were sorted and determined by several specialists. Taking all this into consideration, we cautiously estimate that the proportion of Curculionoidea, as one of the most species-rich taxa in beetles that are new to science, considerably exceeds 80%. Comparable results were found by other authors, too: Oberprieler et al. [11] reported similar proportions of undescribed species for litter-inhabiting species in Central America. In a case study on New Guinea, Basset et al. [59] found a ratio of 4.6:1 of undescribed to described species for arboreal weevils in poorly studied groups, such as Rhynchitidae, Entiminae, Molytinae and Curculioninae s.l. Lees et al. [10] found a ratio of 5.7:1 in Gracillariidae moths from the Neotropics demonstrating that similar faunistic and taxonomic limitations are also found in other taxa.

We also observed conspicuous changes in the species frequency distribution between primary and disturbed forests for several groups of arboreal weevils. These are especially noticeable for those groups which had increased in individual and/or species numbers in the disturbed forests despite a much lower number of foggings than in the primary forests (214 versus 120 samples, Table 2). The total number of collected beetles in both primary and disturbed forests was almost identical (4783 versus 4888), but species numbers were much higher in the primary forests (1287 vs. 473 species).

Table 2. Weevil groups showing the most conspicuous differences in individual and species numbers between primary and disturbed forests.

	Number of Species		Number of Individuals	
	Primary	Disturbed	Primary	Disturbed
Acalyptini	24	15	80	441
Ochyromerini	106	39	497	593
Baridinae	26	13	50	91
Scolytinae	53	68	251	2383

Similarity in numbers was largely caused by Scolytinae which were very abundant and—as the only group—collected with more species in the disturbed forests than in the primary forests. Ochyromerini occurred in large numbers especially in the disturbed forests whereas species richness was much higher in the primary forest. Acalyptini and Baridinae were also found in higher numbers, but lower species richness in the trees of the disturbed forests. It is also noteworthy that not a single individual of Ceutorhynchinae (203 specimens in 26 species) or Attelabidae (60 specimens in 15 species) was collected in the disturbed forests. To what extent these differences can be linked to anthropogenic forest disturbance as suggested for canopy spiders [60] is currently being analysed. The mentioned changes in the rank-abundance distribution were often based on a few species that occurred in large numbers. In Scolytinae, for example, one species of ambrosia beetles of the genus *Scolytogenes* was collected in more than 1500 individuals from *Vitex pinnata* (Lamiaceae-Verbenioideae). This might indicate an unknown relationship between this weevil and its host tree. In Acalyptini and Ochyromerini, with the many small light yellowish species, the high abundance in the disturbed forests may be partially attributed to flowering and fruit trees. Several Ochyromerini species and many specimens were collected from *Melochia umbellata* and from *V. pinnata*. The most abundant species of Acalyptini (341 individuals) was mainly collected from *Terminalia catappa* L., *Premna corymbosa* Rottl.

and Willd. and *Mallotus* spec. These few examples are representative for the limited knowledge on the diversity and biological interactions of beetles in the humid tropical forests.

4. Conclusions

In our opinion, the high diversity and the current poor taxonomic state of knowledge of tropical arthropods provide an inadequate basis to assess the extent of this diversity, its distribution or even its functional importance. There are very few studies dealing with the biology of arboreal weevils from southeast Asia and which provide data about their ecology like those of Lyal and Curran [50,61]. Scattered biological information was published in current taxonomic studies about SE-Asian, Japanese, New Zealand, Australian and Pacific weevils, but the overlap with the Bornean fauna is rather low. In light of the quickly disappearing primary forests of Borneo, this hints towards a massive loss of biodiversity and biological information. This also indicates that ecological analyses are still far behind those of Central European countries, e.g., Floren and Schmidl [62]. Given the importance of tropical rain forests and their ongoing destruction, it is incomprehensible why biodiversity and taxonomic research is not much more intensified.

Author Contributions: A.F. performed all field work. Sorting all specimens and type identification was done mostly by P.S. Analysing the data and writing the MS was done equally by both authors.

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References

1. Caley, M.J.; Fisher, R.; Mengersen, K. Global species richness estimates have not converged. *Trends Ecol. Evol.* **2014**, *29*, 187–188. [CrossRef] [PubMed]
2. Stork, N.E. How Many Species of Insects and Other Terrestrial Arthropods Are There on Earth? *Ann. Rev. Ent.* **2018**, *63*, 31–45. [CrossRef] [PubMed]
3. Erwin, T.L. Tropical Forests. Their richness in Coleoptera and other arthropod species. *Coleopts. Bull.* **1982**, *36*, 74–75.
4. Basset, Y.; Cuénoud, P.; Didham, R.K.; Guilhaumon, F.; Missa, O.; Novotny, V.; Ødegaard, F.; Roslin, T.; Schmidl, J.; Tishechkin, A.K.; et al. Arthropod diversity in a tropical forest. *Science* **2012**, *338*, 1481–1484. [CrossRef] [PubMed]
5. Mace, G.M.; Norris, K.; Fitter, A.H. Biodiversity and ecosystem services: A multilayered relationship. *Trends Ecol. Evol.* **2012**, *27*, 19–26. [CrossRef] [PubMed]
6. Bryan, J.E.; Shearman, P.L.; Asner, G.P.; Knapp, D.E.; Aoro, G.; Lokes, B. Extreme Differences in Forest Degradation in Borneo: Comparing Practices in Sarawak, Sabah, and Brunei. *PLoS ONE* **2013**, *8*, 1–7. [CrossRef] [PubMed]
7. Watson, J.E.M. and 27 further authors. The exceptional value of intact forest ecosystems. *Nat. Ecol. Evol.* **2018**, *2*, 599–610. [CrossRef] [PubMed]
8. Borkent, A.; Brown, B.V.; Adler, P.H.; Amorim, D.S.; Barber, K.; Bickel, D.; Boucher, S.; Brooks, S.E.; Burger, J.; Burington, Z.L.; et al. Remarkable fly (Diptera) diversity in a patch of Costa Rican cloud forest: Why inventory is a vital science. *Zootaxa* **2018**, *4422*, 53–90. [CrossRef] [PubMed]
9. Horstmann, K.; Floren, A.; Linsenmair, K.E. Ichneumonidae (Hymenoptera) from the canopy of tropical forests in Sabah, Malaysia: A comparison between primary and secondary forests. *Ecotropica* **2005**, *11*, 41–52.

10. Lees, D.C.; Kawahara, A.Y.; Rougerie, R.; Ohshima, I.; Kawakita, A.; Bouteleux, O.; De Prins, J.; Lopez-Vaamonde, C. DNA barcoding reveals a largely unknown fauna of Gracillariidae leaf-mining moths in the Neotropics. *Mol. Ecol. Res.* **2014**, *14*, 289–296. [CrossRef] [PubMed]
11. Oberprieler, R.G.; Marvaldi, A.E.; Anderson, R.S. Weevils, weevils, weevils everywhere. *Zootaxa* **2007**, *1668*, 491–520.
12. Floren, A. Sampling arthropods from the canopy by insecticidal knockdown. In *Manual on Field Recording Techniques and Protocols for All Taxa Biodiversity. Inventories and Monitoring*; ABC Taxa: Brussels, Belgium, 2010; pp. 158–172.
13. Alonso-Zarazaga, M.A.; Lyal, C.H.C. *A World Catalogue of Families and Genera of Curculionoidea (Insecta: Coleoptera) (Excepting Scolytidae and Platypodidae)*; Entomopraxis S.C.P.: Barcelona, Spain, 1999.
14. Oberprieler, R.G. Curculionidae. In *Handbook of Zoology. Arthropoda: Insecta. Coleoptera, Beetles*; Volume 3: Morphology and Systematics (Phytophaga); Walter de Gruyter GmbH: Berlin, Germany; Boston, MA, USA, , 2014.
15. Ashton, P. *On the Forests of Tropical Asia*; University of Chicago Press: Chicago, IL, USA, 2014.
16. Legalov, A.A. Annotated checklist of fossil and recent species of the family Belidae (Coleoptera) from the world fauna. *Am. Zool. J.* **2009**, *1*, 296–324.
17. Wanat, M. Studies on Oriental Apionidae (Coleoptera). 1. New genera and species from Thailand, Sumatra, Moluccas and New Caledonia. *Annales Zool. (Warsaw)* **1990**, *43*, 347–361.
18. Wanat, M. *Genera of Australo-Pacific Rhadinocybinae and Myrmacicelinae, with Biogeography of the Apionidae (Coleoptera: Curculionoidea) and Phylogeny of the Brentidae (s. lato)*; Wydawnictwo Mantis: Olsztyn, Polen, 2001.
19. Mantilleri, A. Taxonomy, nomenclature and phylogeny of the tribes Hoplopisthiini Senna & Calabresi, 1919 and Microtrachelizini Zimmerman, 1994 (Coleoptera, Brentidae). *Zoosystema* **2012**, *34*, 561–633.
20. Sforzi, A.; Bartolozzi, L. Brentidae of the world (Coleoptera, Curculionoidea). *Monogr. Mus. Reg. Sci. Nat.* **2004**, *39*, 976.
21. Morimoto, K.; Yoshihara, K. On the genera of the Oriental Baridinae (Coleoptera, Curculionidae). *Esakia* **1996**, *36*, 1–59.
22. Prena, J.; Yang, J.; Ren, L.; Wang, Z.; Liu, N.; Zhang, R. Nomenclatural changes, new country records and range extensions of Baridinae (Coleoptera, Curculionidae) from China. *Zootaxa* **2014**, *3841*, 339–363. [CrossRef]
23. Yoshitake, H.; Yamauchi, T. A new genus of the Oriental tribe Mecysmoderini (Coleoptera: Curculionidae: Ceutorhynchinae), with descriptions of two new species from Indonesia and Malaysia. *Spec. Bull. Jpn. Soc. Coleopterol.* **2002**, *5*, 413–423.
24. Yoshitake, H.; Ito, M. A new genus and species of the tribe Mecysmoderini from Japan, with comments on the subgenus *Coelioderes* (Coleoptera: Curculionidae: Ceutorhynchinae). *Ent. Rev. Jpn.* **2007**, *62*, 75–86.
25. Huang, J.; Zhang, R.; Pelsue, F.W., Jr. A new species of the genus *Watanabesaruzo* (Coleoptera: Curculionidae: Ceutorhynchinae) from China. *Zootaxa* **2006**, *1124*, 41–46.
26. Colonnelli, E. *Catalogue of Ceutorhynchinae of the World, with a Key to Genera (Insecta: Coleoptera: Curculionidae)*; Argania editio S.C.P.: Barcelona, Spain, 2004.
27. Huang, J.; Yoshitake, H.; Zhang, R.; Ito, M. Two new species of *Hainokisaruzo* Yoshitake & Colonnelli from China, with a checklist of the species of the genus (Coleoptera: Curculionidae: Ceutorhynchinae). *Zootaxa* **2008**, *1776*, 59–68.
28. Yoshitake, H.; Lu, S.-S.; Lee, C.-F.; Ito, M. A new *Hainokisaruzo* (Coleoptera: Curculionidae) discovered from a Taiwan beech forest in Mt. Taipingshan, Taiwan. *Jpn. J. Syst. Ent.* **2015**, *21*, 235–239.
29. Yoshitake, H.; Colonnelli, E. Taxonomic study of the genus *Ceutorhynchoides* Colonnelli, 1979 from Japan, with establishment of an allied new genus (Coleoptera: Curculionidae: Ceutorhynchinae). *Esakia* **2005**, *45*, 117–153.
30. Morimoto, K.; Kojima, H. Notes on the Curculionidae from Taiwan I *Tachypterellus* (Coleoptera). *Spec. Bul. Essa. Ent. Soc.* **1994**, *2*, 291–297.
31. Kojima, H.; Morimoto, K. Two new genera of the tribe Ochyromerini (Coleoptera, Curculionidae) with five segments in the funicle. *Elytra* **1995**, *23*, 133–141.
32. Kojima, H.; Morimoto, K. Study on the tribe Ochyromerini (Coleoptera, Curculionidae) from East Asia I, descriptions of new species of the genera *Endaeus* and *Endaenidius*. *Esakia* **1995**, *35*, 63–102.
33. Kojima, H.; Morimoto, K. Study on the tribe Ochyromerini (Coleoptera, Curculionidae) from East Asia II, genus *Imerodes* Marshall. *Esakia* **1995**, *35*, 103–112.

34. Kojima, H.; Morimoto, K. Systematics of the weevil genus *Gryporrhynchus* Roelofs (Coleoptera, Curculionidae). *J. Fac. Agr. Kyushu Univ.* **1995**, *40*, 117–134.
35. Kojima, H.; Morimoto, K. The tribe Ochyromerini (Coleoptera, Curculionidae) of Japan I. Genera with six segments in the funicle. *Jpn. J. Ent.* **1995**, *63*, 557–571.
36. Kojima, H.; Morimoto, K. The tribe Ochyromerini (Coleoptera, Curculionidae) of Japan III. Genera with seven segments in the funicle and key to genera. *Jpn. J. Ent.* **1996**, *64*, 733–743.
37. Kojima, H.; Morimoto, K. The tribe Ochyromerini (Coleoptera, Curculionidae) of Japan II. Genus *Ochyromera* Pascoe. *Jpn. J. Ent.* **1996**, *64*, 570–586.
38. Kojima, H. New Oriental weevils of the tribes Rhamphini and Ochyromerini (Coleoptera, Curculionidae). *Esakia* **1997**, *37*, 121–134.
39. Kojima, H.; Morimoto, K. New *Imathia* from Japan and Taiwan (Coleoptera, Curculionidae, Curculioninae, Storeini). *Entomol. Sci.* **1998**, *1*, 249–255.
40. Kojima, H.; Morimoto, K. Systematics of the genus *Sphinxis* Roelofs (Coleoptera: Curculionidae). *Entomol. Sci.* **2000**, *3*, 529–556.
41. Kojima, H.; Morimoto, K. Weevils of the tribe Acalyptini (Coleoptera: Curculionidae: Curculioninae): Redefinition and a taxonomic treatment of the Japanese, Korean and Taiwanese species. *Esakia* **2005**, *45*, 69–115.
42. Pelsue, F.W., Jr.; O'Brien, C.W. A redefinition of the Curculionini of the world, with a key to subtribes and genera, and two new genera: *Pseudoculio* and *Megaoculis* (Coleoptera: Curculionidae: Curculioninae). *Zootaxa* **2011**, *3102*, 27–49.
43. Kojima, H.; Idris, A.B. The Anthonomini from Malaysia, with notes on the Oriental taxa (Coleoptera: Curculionidae). *Serangga* **2004**, *9*, 103–129.
44. Caldara, R.; Franz, N.M.; Oberprieler, R.G. *Handbook of Zoology. Coleoptera, Beetles*; Walter de Gruyter GmbH: Berlin, Germany; Boston, MA, USA, 2014.
45. Zimmerman, E.C. Marquesas Island *Viticis* (Coleoptera: Curculionidae, Brachyderinae). *Pac. Insects* **1963**, *5*, 899–903.
46. Morimoto, K. The family Curculionidae of Japan. IV. Subfamily Rhynchaeninae. *Esakia* **1984**, *22*, 5–76.
47. Kojima, H.; Morimoto, K. Systematics of the flea weevils of the tribe Rhamphini (Coleoptera, Curculionidae) from East Asia. II. Phylogenetic analysis and higher classification. *Esakia* **1996**, *36*, 97–134.
48. Morimoto, K.; Miyakawa, S. Systematics of the flea weevils of the tribe Rhamphini (Coleoptera, Curculionidae) from East Asia. I. Descriptions of new taxa and distribution data of some species. *Esakia* **1996**, *36*, 61–96.
49. Beaver, R.A.; Sittichaya, W.; Liu, L.Y. A synopsis of the Scolytine ambrosia beetles of Thailand (Coleoptera: Curculionidae: Scolytinae). *Zootaxa* **2014**, *3875*, 1–82. [CrossRef] [PubMed]
50. Lyal, C.H.C.; Curran, L.M. More than black and white: A new genus of nanophyine seed predators of Dipterocarpaceae and a review of *Meregallia* Alonso-Zarazaga (Coleoptera: Curculionoidea: Nanophyidae). *J. Nat. Hist.* **2003**, *37*, 57–105. [CrossRef]
51. Kojima, H.; Lyal, C.H.C. New Oriental and Australian Conoderinae, with taxonomic notes on the tribe Othippiini (Coleoptera: Curculionidae). *Esakia* **2002**, *42*, 161–174.
52. Hustache, E. Essai d'un tableau synoptique des zygopides d'Afrique et de Madagascar. In *Livre du Centenaire*; Société Entomologique de France: Monolieu, France, 1932.
53. Lawrence, J.F.; Hastings, A.M.; Dallwitz, M.J.; Paine, T.A.; Zurcher, E.J. *Beetles of the World. A Key and Information System for Families and Subfamilies*; CSIRO Publishing: Clayton, Australia, 2002.
54. Germann, C. *Seticotasteromimus* gen. n. *jarawa* sp. nov. from the Andaman Islands (Coleoptera, Curculionidae). *Revue Suisse Zool.* **2013**, *120*, 125–129.
55. Holzschuh, C. Beschreibung von elf neuen Bockkäfern (Coleoptera: Cerambycidae) aus Sabah, Borneo. *Zeitschr. Arbeitsgem. Österreich. Ent.* **2014**, *66*, 71–84.
56. Holzschuh, C. Beschreibung von sieben neuen Bockkäfern aus Asien (Coleoptera, Cerambycidae). *Les Cahiers Magellanes* **2016**, *24*, 105–113.
57. Holzschuh, C. Neue Lamiinae (Coleoptera: Cerambycidae) aus Asien und zur Synonymie einiger Taxa. *Zeitschr. Arbeitsgem. Österreich. Entomol.* **2017**, *69*, 139–167.
58. Heffern, D.J. Catalog and Bibliography of Longhorned Beetles from Borneo (Coleoptera: Cerambycidae). Available online: http://www.cerambycoidea.com/titles/heffern2005.pdf (accessed on 22 October 2018).

59. Basset, Y.; Springate, N.D.; Samuelson, G.A. Feeding habits and range of body size: A case study in Papua New Guinea using arboreal leaf-beetles and weevils (Coleoptera: Chrysomelidae, Curculionidae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* **1994**, *67*, 347–361.
60. Floren, A.; Müller, T.; Deeleman-Reinhold, C.; Linsenmair, K.E. Effectsof forest fragmentation on canopy spider communities in SE-Asian rain forests. *Ecotropica* **2011**, *17*, 15–26.
61. Lyal, C.H.C.; Curran, L.M. Seed-feeding beetles of the weevil tribe Mecysolobini (Insecta: Coleoptera: Curculionidae) developing in seeds of trees in the Dipterocarpaceae. *J. Nat. Hist.* **2000**, *34*, 1743–1847. [CrossRef]
62. Floren, A.; Schmidl, J. (Eds.) *Canopy Arthropod Research in Central Europe-Basic and Applied Studies from the High Frontier*; Bioform: Nuremberg, Germany, 2008.

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Review of the Hygrophilous Weevils in Israel (Coleoptera: Curculionoidea)

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Abstract: Forty-one species in 20 genera of hygrophilous weevils belonging to Brentidae and Curculionidae, associated with inland aquatic habitats, have been recorded recently from Israel, eight of them for the first time. Thirty-four species are extant, while five species have probably become extinct recently, and two are fossil species, known from Late Cretaceous deposits. Sixteen species are either aquatic or semi-aquatic, while the rest occur only or predominantly on riparian vegetation. Distributional and biological data for most of the species are provided. A key to all hygrophilous weevil taxa and illustrations for most of the species are provided.

Keywords: Curculionoidea; weevil; hygrophilous; aquatic; semi-aquatic; riparian; key; Israel

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1. Introduction

Weevils are the largest monophyletic group of beetles, comprising more than 62,000 described species [1]. Only a minority of these are aquatic or semi-aquatic, and completely aquatic species comprise less than 1% of the weevil world fauna [2]. Most of the aquatic weevils inhabit inland freshwater habitats, although there are some weevil taxa (mainly Cossoninae) that inhabit the supratidal zone (splash zone) and develop on marine algae driven ashore [3] or on timber floating in seawater [4–6]. Many weevil species, albeit not directly associated with water, occur mainly or predominantly in wetlands, near or above the water, primarily because their host plants are hygrophilous. This is especially noticeable in semi-arid countries with a dry climate, like Israel. Completely aquatic and semi-aquatic weevils are confined to standing water or to water with a very slow current, and are therefore mostly found in lakes, swamps, ponds, floodplains, or eddies of slow-moving rivers or in artificial or temporary ponds [7]. Those hygrophilous weevils that are not aquatic are less limited in their distribution and can be found adjacent to any water body of considerable size, with either standing or flowing water, if their host plants are available.

One of the earliest geographical descriptions of the Land of Israel, in the Book of Deuteronomy (8:7), refers to it as "a land with brooks, streams, and deep springs gushing out in the valleys and mountains." The current State of Israel [8] (matching partly the historical Land of Israel) is a country encompassing a Mediterranean-type, as well as semi-arid and arid climatic zones (Figure 17). A rapid rainfall gradient spreads along less than 450 km, from almost 1000 mm in the north to barely 20 mm in the south [9]. The northern part of the country (Galilee, Golan Heights, Upper Jordan Valley, Yizre'el (=Jezreel) Valley, Carmel Ridge), and the coastal plain and western slopes of the Samarian and Judean Hills possess typical Mediterranean vegetation (phrygana and batha), while the southern part (Negev Desert), eastern slopes of the Samarian and Judean Hills (Samarian and Judean Deserts) and the southern part of the Jordan Valley, Dead Sea Area and Arava Valley are semi-deserts or deserts with either steppe type (at higher altitudes) or eremic type vegetation. The coastal plain is fringed by a strip of sand dunes, wider in the southern part and tapering northwards, which in the past played an important role in the formation of the coastal swamps.

In spite of the arid nature of its climate, Israel possesses numerous and varied aquatic biotopes. Its inland water system is affected by the complex geological history of the area. Most of the country lies on the western slope of the northernmost tip of the Rift Valley. The water systems are therefore divided longitudinally by the Galilee mountains and Samarian and Judean Hills into the coastal system in the west, including approximately 15 streams flowing into the Mediterranean Sea, and the Rift Valley itself in the east, subdivided into the Jordan Valley (Jordan River, its tributaries, the Hula Lake, and Lake Kinneret) and the Dead Sea with its tributaries. The coastal and the Jordan Valley systems were partially connected until the second half of the 20th century by the low Yizre'el Valley (swampy in the past) [10,11]. In the Mediterranean zone the banks are covered by thickets of *Rubus* edged by *Arundo*, *Phragmites*, *Lythrum*, *Melilotus* (Figures 1c and 2c), and Mentha (Figure 2a) along the water edge and *Persicaria* inside the water (Figure 3e). The northern Hula Valley and the Upper Galilee also feature relicts of the historical riparian forests, comprising *Salix*, *Tamarix*, *Platanus*, *Fraxinus*, and *Populus*. Toward the south the vegetation becomes more hallophylic, mainly comprising thickets of *Tamarix*, *Pluchea*, *Arundo*, *Phragmites*, *Atriplex*, and *Juncus*, characteristic also for the shores of the Dead Sea (Figure 1a,b). The aquatic flora of Israel is rich and variable, although many water plants have a very restricted distribution [12–14].

The inland water bodies in Israel can be classified as following: rivers, streams, lakes, springs, swamps, and vernal pools.

The largest river in Israel is the River Jordan (=Nehar haYarden), flowing from Mount Hermon through the bottom of the Rift Valley into the Dead Sea (Figure 1f). There are other smaller rivers, streams or brooks ("Nahal" in Hebrew), which flow either into the Mediterranean Sea or the Jordan Valley, most of them seasonal, containing water between once every few years to 1–2 months in winter, while the rest contain water throughout the year or at least for most of the year. Numerous springs occur throughout Israel, some of them used for agriculture or as tourist sites (Figure 3f). These natural springs are surrounded by thick vegetation.

A chain of three lakes formed at the bottom of a tectonic depression stretches along the Jordan Valley: the freshwater Hula Lake, the Sea of Galilee (=Yam Kinneret), and the extremely saline Dead Sea (=Yam haMelah). The shallow Hula Lake (14 km^2) surrounded by the Hula swamp (30–60 km^2, depending on the precipitation in any particular year) was once exceptionally rich in flora and fauna, until it was drained in the 1950s in order to eradicate malaria and to release land for agriculture. The drainage dessicated the lake and its surroundings, resulting in the loss of most of its biota, with some of the animal and plant species completely disappearing and populations of the remaining species strongly reduced [10,15–17]. Currently, 3.2 km^2 comprise the Hula Nature Reserve (Figure 3a–d) with its remnants of the natural vegetation, while 8–10 km^2 belong to the artificially flooded Agmon haHula, where attempts are being made to reintroduce the natural biota [18–20]. The Sea of Galilee (170 km^2) is the largest freshwater body in Israel. Its shores suffer strongly from human activities (urbanization, agriculture, tourism) and from a lowering of the water level as a result of dessication. The natural vegetation has remained relatively untouched in only a few preserved areas along its east-northern edge. Most of its coast is now either cultivated or features monocultural stands of *Arundo*, *Phragmites,* or *Tamarix*. The Dead Sea (605 km^2) features extremely halobiontic conditions. The salinity of its water reaches 35%, and no multicellular organisms can survive in it, although soldier fly larvae (Diptera: Stratiomyidae) have been reported, probably having drifted in with the freshwater flow [21]. Its shores too are strongly saline. In recent years the water level in the Dead Sea has been receeding, and the shores are drying out and crumbling, which strongly affects the coastal flora and fauna.

Figure 1. (**a**) Enot Zuqim Nature Reserve, oasis on the NW coast of the Dead Sea, thicket of *Tamarix* spp.; (**b**) same place, *Arundo donax*, *Juncus* sp., *Phoenix dactylifera*, *Pluchea dioscoridis*, *Populus euphratica*, *Tamarix* spp.; (**c**) Wadi Malha Wetland Nature Reserve, saltmarsh, Jordan Valley, in the foreground *Atriplex halimus* and *Suaeda aegyptiaca*, on the background *Tamarix* sp.; (**d**) Corimaliini in *Tamarix* litter (courtesy Amikam Shoob); (**e**) Nahal Qibbuzim, Bet She'an Valley, the author is sweeping Nanophyini from *Lythrum salicaria* (photograph taken by one of the author's children); (**f**) Park haYarden, bank of the Jordan River.

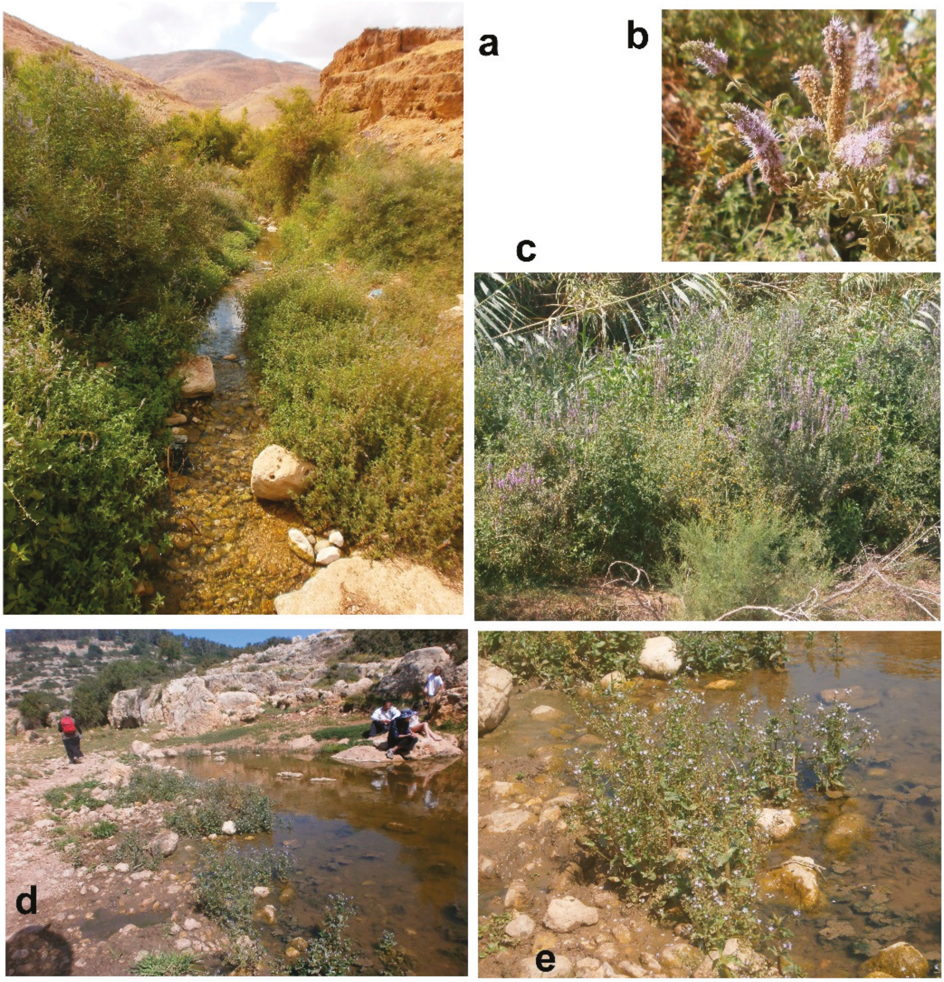

Figure 2. (**a**) ‘En Peza‘el, Nahal Peza‘el, Jordan Valley, *Mentha longifolia*, *Vitex agnus-castus*, *Ziziphus spina-christi*; (**b**) same place, blooming *Mentha longifolia*; (**c**) Arik Bridge, bank of the Jordan River, *Lythrum salicaria*, *Melilotus albus*, *Phragmites australis* and *Tamarix* sp.; (**d**) Nahal Qana, Turtles Pond, Samarian Hills, *Veronica anagallis-aquatica* growing along the water; (**e**) same place, *Veronica anagallis-aquatica*.

Swamps once constituted the most common biotope in the lower areas of Israel, like the coastal plain, Yizre’el Valley and Hula Valley, at least since the Holocene. A nearly continuous chain of swamps once stretched along the Mediterranean coast, dammed in the west by the strip of dunes. These swamps were drained at the end of the 19th and beginning of the 20th century in order to release land for human use and eradicate malaria. Most of them have disappeared completely, while some have become vernal ponds (e.g., ‘En Gonen, Ahu Binyamina, Dora, Netanya Pool, Ga’ash Pool (Figure 4f,g)), Basa of Herzliyya, Levinski Pool, Robert’s Pool (4h) or were strongly reduced (e.g., Berekhat Ya’ar (Figure 4a), ‘En Nimfit (Figure 4c), ‘En Afeq, Hula (Figure 3a–d)) and remained only as nature reserves (the latter two are also under the protection of the RAMSAR convention [22].

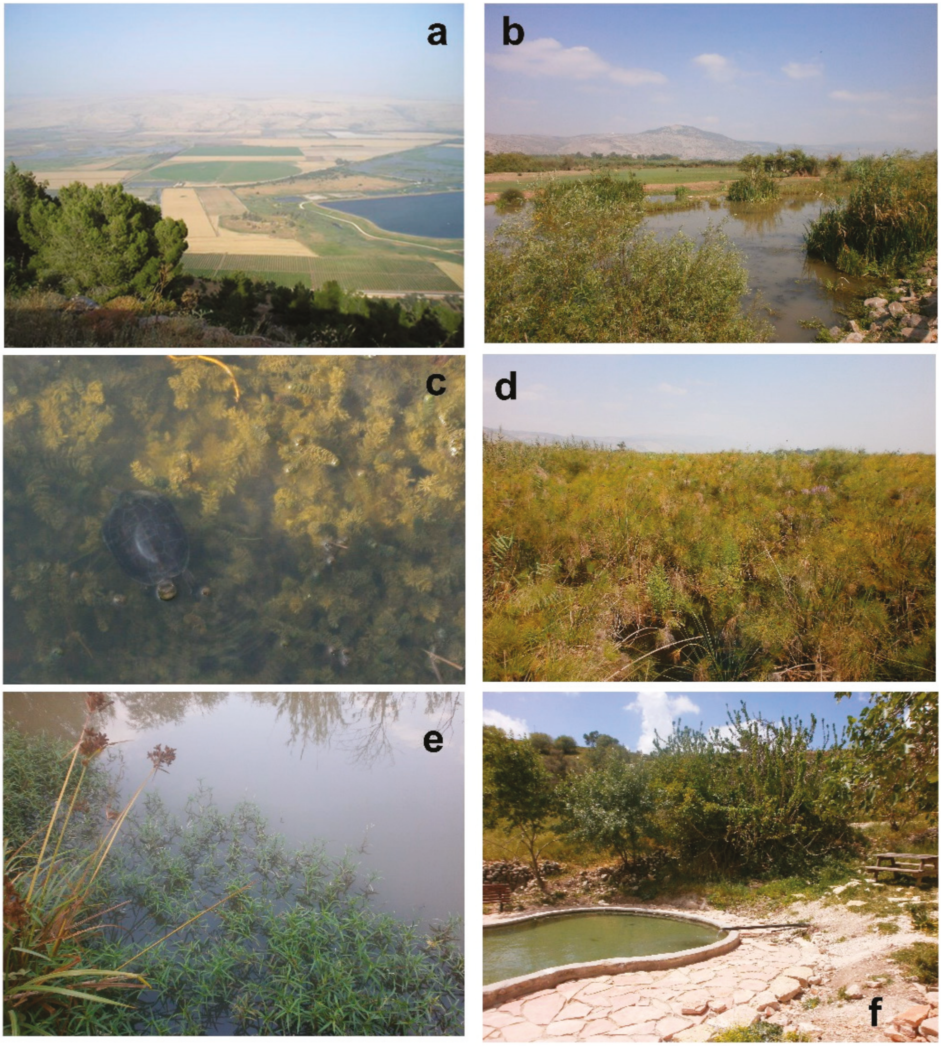

Figure 3. (**a**) Hula Valley, cultivated part, seen from Naftali Hills, E Upper Galilee; (**b**) Hula Nature Reserve; (**c**) Hula NR, *Ceratophyllum demersum*; (**d**) Hula NR, *Cyperus papyrus*, *Lythrum salicaria*; (**e**) Park haYarden, bank of the Jordan River, *Persicaria decipiens*, *Cyperus* sp.; (**f**) 'En 'Amassa spring at the foot of Mt. Gerizim, Samarian Hills, cultivated.

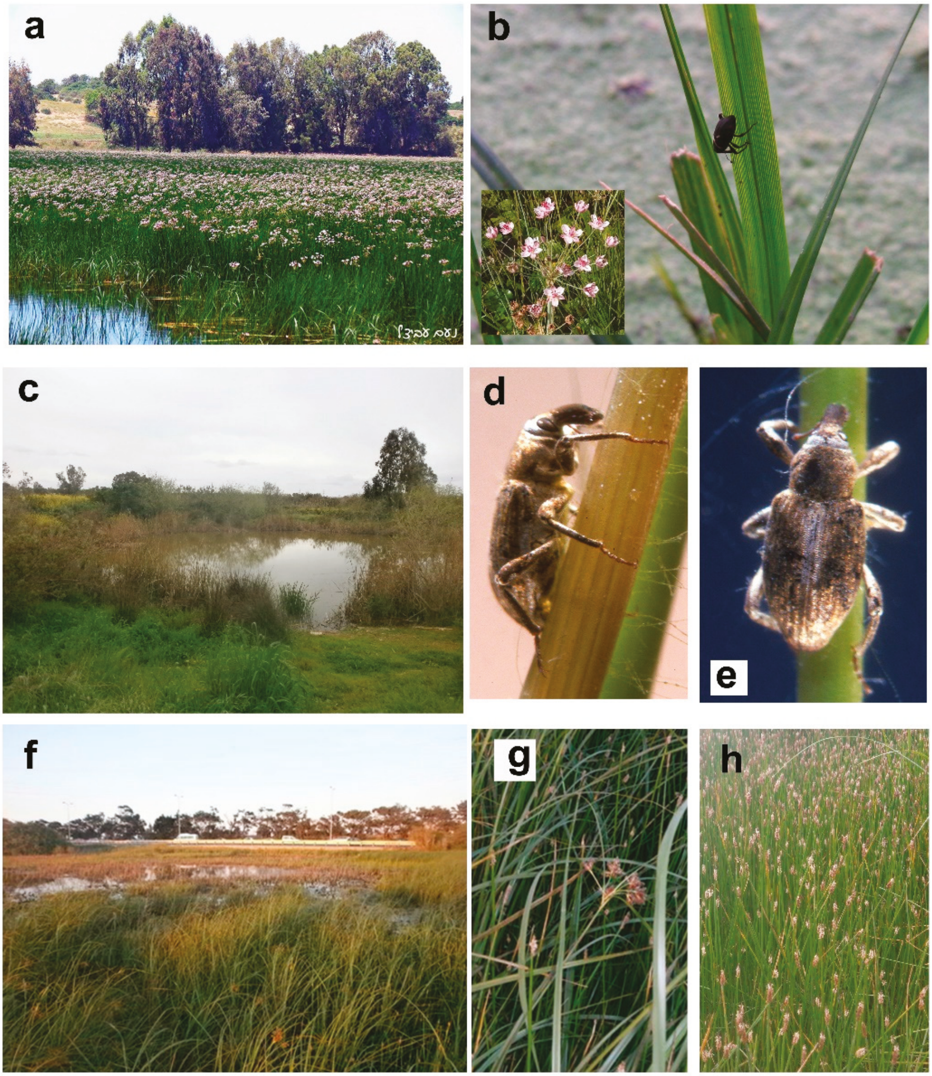

Figure 4. (**a**) Berekhat Ya'ar, Central Coastal Plain, *Butomus umbellatus* blooming (courtesy Noam Avitzel); (**b**) same place, *Bagous validus* feeding on *Butomus umbellatus* (courtesy David Furth), on smaller photograph flowers of *B. umbellatus*; (**c**) 'En Nimfit Nature Reserve, Migdalit haNehalim Pond, vernal pond; (**d**) *Picia syriaca*, lateral view, photographs taken in lab, Tel Aviv University (courtesy Amikam Shoob); (**e**) same, dorsal view (courtesy Amikam Shoob); (**f**) Ga'ash Winter Pool Nature Reserve, vernal pool, *Eleocharis palustris* and *Scirpus maritimus*; (**g**) same place, *Scirpus maritimus*; (**h**) Nizzanim Dunes Nature Reserve Roberts' Pool, vernal pool, *Eleocharis palustris*.

Vernal (seasonal, ephemeral) pools, featuring water only during the winter and early spring, occur in Israel along the coastal plain, on the western slopes of the Samarian and Judean Hills, in the uplands of the Upper and Lower Galilee, and on the Golan Heights. In the coastal area they have mainly replaced the historical swamps. Some of the vernal pools may contain water throughout the winter, while others are full for only 1–3 months a year or can remain dry for several years. The unique ecosystem of vernal pools enables specialized plants to thrive, some of which can survive or produce dormant life-stages during the dry season.

All wetland habitats in Israel are particularly vulnerable and are under constant threat of physical disappearance, destruction or pollution, particularly because of their fragility and small size. Even innocent and natural human activities such as tourism or cattle grazing can cause serious damage to the riparian and aquatic vegetation, leading to the disappearance of the invertebrate fauna. During the 20th century wetlands in Israel were both exploited actively and destroyed accidently, which led to the loss of up to 80% of these habitats [23–25]. The insect aquatic fauna too was naturally denser and more variable 100 years ago (e.g., [16,17,19,26]). Today, we can only study it in its decline.

In Israel, the taxonomic knowledge on aquatic insects as a whole is limited. However, some groups, such as Ephemeroptera, Odonata, Trichoptera, Diptera (e.g., [16,27–31]), and some of the aquatic beetles [26,32–35] have been studied and published. The aquatic weevil fauna in Israel nonetheless has remained completely unknown. The first records of water weevils in Israel were descriptions of *Picia syriaca* (Reitter) and *Echinocnemus sahlbergi* Shilsky. Since then an unidentified species of *Bagous* was recorded from the Hula Valley [18]. Caldara and O'Brien [36] recorded five species of *Bagous* in their revision of the Palaearctic *Bagous*, based on the material deposited in European and American museums. Alonso-Zarazaga and Lyal [37] recorded *Aorus anthracinus* Branczik; and Friedman [4] recorded *Arthrostenus fullo* Boheman and *Icaris sparganii* (Gyllenhal). Comprehensive data on the distribution and biology (where available) of the hygrophilic species of Israel are presented here for the first time.

2. Materials and Methods

The majority of the studied material is deposited in the National Collection of Insects, the Steinhardt Museum of Natural History, National Research Center, Tel Aviv University, Israel (SMNHTAU); therefore, this abbreviation is omitted from the Material Examined section. For the specimens from the other museums the following abbreviations are used:

BMNH—Natural History Museum, London, UK (M. Barclay).
HNHM—Hungarian Natural History Museum, Budapest, Hungary.
USNM—National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (L. Chamorro).
ZSMU—Zoologische Staatssamlung München, Munich, Germany (M. Balke).

Drawings and measurements were made using a drawing tube and a stereomicroscope Leica M125, Leica Microsystems GmbH, Wetzlar, Germany. Drawings were scanned and processed using Adobe Illustrator 9.0, Adobe Systems Incorporated, San Jose, CA, USA. Total body length in dorsal view was measured along a straight line from the base of the rostrum to the tip of the elytra. Images of the weevil habitus were captured with a Leica DfC295 digital camera, Leica Microsystems GmbH, Wetzlar, Germany, mounted on a Leica M205c microscope, Leica Microsystems GmbH, Wetzlar, Germany, stacking images with Leica Application Suite 4.2.0, Leica Microsystems GmbH, Wetzlar, Germany, and Helicon Focus 5.3, Helicon Soft Ltd., Kharkiv, Ukraine, and editing the final images when necessary with Adobe Photoshop CS4 Extended, Adobe Systems Incorporated, San Jose, CA, USA. Genitalia were extracted by soaking dry specimens in hot water, removing the posterior abdominal sternites, and boiling them in a 10% water solution of potassium hydroxide. Extracted genitalia were preserved in glycerin in polyethylene stoppered vials, pinned next to the specimens. Photographs were made by the author, apart from Figures 1d,e and 4a,b,d,e.

Transliterated names of localities in Israel follow the Israel Touring Map and List of Settlements published by the Survey of Israel [8]. Where names of localities have changed, the most recent transliterated Hebrew names are given followed by the old names in brackets: for example—Yeriho [Jericho]. Erroneous spellings are also included in brackets following the correct spelling. Plant names and distribution follow Danin and Fragman-Sapir [38]. Regional subdivision of Israel follows Theodor [39], with changes made by Ionescu and Eyer [40].

The hygrophilous weevil species in Israel can be divided into three eco-groups, not always distinct: aquatic, semi-aquatic, and riparian. Aquatic species are considered here to be only those that live on water-growing plants and possess clear adaptations for aquatic life (streamlined body form, rostrum short or bent under the body, body covered by flat attached scales, abdominal segments covered by short dense pubescence, tibia long and slender, with longitudinal row of denticles or/and setae, etc.), and their swimming abilities have been proven either by my own observations or from records in the literature. Aquatic weevils mainly swim in the water rather than on its surface. Semi-aquatic weevils are those that live on the water plants or on the riparian vegetation and seldom enter the water, possessing weak or unclear adaptations to their aquatic surroundings. If they are able to swim, they swim either in the water or on its surface [41]. Riparian species are those that live on the riparian plants, having no adaptations to aquatic life and entering the water only accidentally.

3. Taxonomy

3.1. List of the Hygrophilous Weevils of Israel

BRENTIDAE
Apioninae
Kalcapiina
Squamapion delagrangei (Desbrochers des Loges, 1895)

Nanophyinae
Corimaliini
Allomalia quadrivirgata (Costa, 1863)
Allomalia setulosa (Tournier, 1868)
Corimalia schatzmayri Giordani-Soika, 1937
Corimalia torretrassoi Giordani-Soika, 1937
Corimalia latifrons (Pic, 1897)
Hypophyes sp.
Nanophyini Gistel, 1848
Dieckmanniellus chevrieri (Boheman, 1845)
Dieckmanniellus nitidulus (Gyllenhal, 1838)
Nanomimus sp.
Nanophyes sp. 1
Nanophyes sp. 2
Nanophyes sp. 3

CURCULIONIDAE
Bagoinae
Bagous (*Bagous*) *bagdatensis* Pic, 1904
**Bagous* (*Macropelmus*) *argillaceus* Gyllenhal, 1836
**Bagous* (*Macropelmus*) *biimpressus* Fåhraeus, 1845
Bagous (*Macropelmus*) *lyali* Caldara & O'Brien, 1998
Bagous (*Macropelmus*) *mingrelicus* Tournier, 1874
Bagous (*Macropelmus*) *septemcostatus* Chevrolat, 1860
Bagous (*Macropelmus*) *subruber* Reitter, 1890
**Bagous* (*Macropelmus*) *tempestivus* (Herbst, 1795)
**Bagous* (*Macropelmus*) *validus* Rosenhauer, 1897
**Bagous* (*Parabagous*) *libanicus* Schilsky, 1911

Brachycerinae

Erirhinini
Echinocnemus reitteri Schilsky, 1907
Echinocnemus sahlbergi Schilsky, 1911
Echinocnemus gerofiticus Grachev, 2008
Echinocnemus qetura Grachev, 2008
Icaris sparganii (Gyllenhal, 1835)
Picia syriaca (Reitter, 1889)
Tanysphyrini
Arthrostenus fullo Boheman, 1836
Stenopelmus rufinasus Gyllenhal, 1835

Curculioninae
Mecinini
Gymnetron niloticum Kirsch, 1881
Gymnetron tibiellum Desbrochers des Loges, 1900

Tychiini
Tychius bicolor C. N. F. Brisout de Barneville, 1863
Tychius meliloti Stephens, 1831

Conoderinae
Ceutorhynchitae
Phytobiini
Rhinoncus pericarpius (Linnaeus, 1758)
Rhinoncus perpendicularis (Reich, 1797)

Entiminae
Sitonini
Sitona lividipes Fåhraeus, 1840
Tanymecini
Tanymecus (*Geomecus*) *musculus* Fåhraeus, 1840

Lixinae
Lixus (*Eulixus*) *iridis* Olivier, 1807

Molytinae:
Aorus anthracinus Brancsik, 1898
* indicates a new record for the Israeli fauna.

3.2. Identification Keys to the Hygrophilous Weevils in Israel

Key to of the weevil taxa in Israel found on, in, or close to water
(species of *Bagous* are keyed separately)

1. Trochanter oblong, at least twice as long as wide, base of femur not touching coxa .... **Brentidae 2**
- Trochanter short, at most as long as wide, base of femur touching coxa.. **Curculionidae 8**
2. Antenna straight, scapus much shorter than funicle, funicle 7-segmented; body oblong, dark; bases of pronotum and elytra not crenulate; pronotum at base usually narrower than elytra (Figures 5a and 6a,b); on *Mentha longifolia* (Figure 2b)........................ **Apioninae: *Squamapion delagrangei***
- Antenna geniculate, scapus longer than or as long as funicle, funicle 4- or 5-segmented; body globular, yellow to light brown; bases of pronotum and elytra crenulate; pronotum at base as wide as elytra (5b-h, 6c-i); on *Lythrum salicaria* or *Tamarix*........................ **Nanophyinae 3**

3. Antennal club compact, comprised of fused segments with sutures distinctly visible, obsolete or invisible (5b–f, 6c–g); male tibia not mucronate; claws free; on *Tamarix* (Figure 1a–d)..**Corimaliini 4**

\- Antennal club loose, comprised of distinctly separated segments; male tibia mucronate; claws fused at least at base; on *Lythrum* (Figures 1e, 2c and 3d)..**Nanophyini 6**

4. Antennal funicle 5-segmented, antennal club with distinct sutures..***Corimalia***

\- Antennal funicle 4-segmented, antennal club with distinct or indistinct sutures..**5**

5. Antennal club with distinct sutures; elytra distinctly crenulate at base; femora with two denticles; if with one denticle only, then denticle distinctly longer than wide; body length 1.5–2.0 mm.. ***Allomalia***

\- Antennal club without distinct sutures; elytra not crenulate at base; femora with one denticle or without denticles; body length 0.8–1.5 mm..***Hypophyes***

6. 8th elytral interstria completely not crenulate; male pygidium apically with round fovea; femora without denticles or (rarely) with minute denticle..***Nanophyes***

\- 8th elytral interstria crenulate at least close to base; male pygidium without fovea; femora dentate..**7**

7. 8th elytral interstria crenulate at basal quarter; femora strongly incrassate, with large proximal and small distal denticles..***Dieckmanniellus***

\- 8th elytral interstria crenulate between base and humeral callus; femora slightly incrassate, with one minute denticle or (rare) without denticle ....***Nanomimus***

8. Claws dentate; mesothoracic epimeron visible in dorsal view; rostrum as long as pronotum, thick, hidden in rostral channel; body stout, 1.5–4.0 mm (Figure 12a–d) ....***Rhinoncus* 9**

\- Claws not dentate; mesothoracic epimeron not visible in dorsal view; rostrum and body of various shapes and size, rostral channel present or absent..**10**

9. Claw denticle short, 0.3X as long as claw, straight, not contiguous to opposite claw denticle at apex; body laterally rounded, black, with slight bluish tinge, body length 2.5–4.0 mm (Figure 12a,c) .... ***Rhinoncus pericarpius***

\- Claw denticle long, 0.5X as long as claw, curved, nearly contigous to oposit claw denticle at apex; body laterally subparallel, testaceous to dark brown, body length 1.5–2.0 mm (Figure 12b,d)..***Rhinoncus perpendicularis***

10. Antennal funicle 5-segmented; on *Veronica anagallis-aquatica* (Figure 2d,e) .... ***Gymnetron* 11**

\- Antennal funicle 7-segmented..**12**

11. Scales on elytral interstriae denser, arranged in three irregular rows (Figure 14e); male rostrum strongly tapering at apex, slightly turned up at apex in lateral view (Figure 14a), female rostrum slightly evenly curved (Figure 14b); body length 1.7–2.0 mm ....***Gymnetron niloticum***

\- Scales on elytral interstriae sparser, arranged in one regular row (Figure 14f); male rostrum slightly tapering at apex, slightly evenly bent, not turned up at apex in lateral view (Figure 14c), female rostrum nearly straight (Figure 14d); body length 1.5–1.8 mm ....***Gymnetron tibiellum***

12. Rostrum as long as wide or shorter, shorter than pronotum..**13**

\- Rostrum at least 1.5X as long as wide, as long as or longer than pronotum **15**

13. Rostrum as long as wide; 3rd tarsomere narrow, as wide as 2nd, with lobes separated in distal half only; abdomen segments covered with round scales; body stout, 1.6–2.0 mm long (Figure 10d,e)..***Stenopelmus rufinasus***

- Rostrum shorter than wide; 3rd tarsomere distinctly wider than 2nd, entirely divided into two rounded lobes; abdomen covered with either piliform scales or combination of round and piliform scales; body oblong, 3.0–7.0 mm long **14**

14. Fore margin of pronotum laterally without postocular tuft of setae; mandibles without mandibular cusp or round scar; body covered by appressed scales only, laterally with wide, pale lateral stripe of white scales (Figure 12g,i)..***Sitona lividipes***

- Fore margin of pronotum laterally with postocular tuft of setae; mandibles without mandibular cusp or round scar; body covered by appressed, erect and semi-erect scales, unicolorous, laterally without pale lateral stripe of scales (Figure 12h,j) ....***Tanymecus musculus***

15. Rostrum anteriorly tapering at least from antennal insertion, apically pointed; on *Melilotus albus* .... ***Tychius* 16**

- Rostrum cylindrical, at most slightly widened apically...**17**

16. Metafemur with anteromedian denticle, male protibia without denticle medially; rostrum in lateral view less curved at base and gradually tapering towards apex; upper part of body covered with yellowish scales, scales truncated apically (Figure 14g,i–k) ....***Tychius bicolor***

- All femora without denticles, male protibia with strong denticle medially; rostrum in lateral view strongly curved at base and strongly tapering from antennal insertion place toward apex; upper part covered with whitish scales, scales pointed apically (Figure 14h,l–n) ....***Tychius meliloti***

17. Elytra apically produced into divergent pointed processes; body oblong, laterally subparallel, 3.8–4.0X as long as wide (Figure 12f,k) ....***Lixus iridis***

- Elytra apically not produced; body of various shapes, at most 3.3X as long as wide **18**

18. Rostral channel absent; postocular lobes of pronotum absent, at most fore margin of pronotum laterally slightly rounded; antennal sulci covered by scales or bare **19**

- Rostral channel present; postocular lobes distinct; antennal sulci bare **25**

19. Body black, slender, oblong, smooth and shiny, completely bare (Figure 10g and Figure 11h,i) .... ***Aorus anthracinus***

- Body of various color, shape and texture, covered densely by scales **20**

20. 3rd tarsomere cordate; rostrum slender, 4X as long as wide (Figures 10b and 11a) ....***Icaris sparagnii***

- 3rd tarsomere narrow, sub-cylindrical, as wide as 2nd at apex; rostrum stout, 2X as long as wide **21**

21. Tarsomeres 1st–3rd slender, oblong, above 2X as long as wide, 3rd not bilobed distally; elytra laterally parallel at basal two thirds, strongly acuminate in apical third (Figures 10c and 11b) ....***Picia syriaca***

- Tarsomeres 1st–3rd robust, short, at most 1.3X as long as wide, 3rd scarcely to distinctly bilobed distally; elytra parallel at basal 4/5, at apical 1/5 weakly acuminate (Figures 10a and 11c) ....***Echinocnemus***

22. Extant..**23**

- Fossil **24**

23. Rostrum moderately and evenly curved; tarsi short, 1st tarsomere as long as wide, 2nd–3rd tarsomeres wider than long, 3rd tarsomere distinctly wider than 2nd, bilobed at apex; body length 3.2 mm (Figures 10a and 11c) .... ***Echinocnemus reitteri***
- Rostrum straight; tarsi oblong, 1st–3rd tarsomeres longer than wide, equal in length and width; body length 4.5–6.5 mm...***Echinocnemus sahlbergi***

24. Elytron narrower, 5.1 mm long, uniformly colored.......................................***Echinocnemus qetura***
- Elytron wider, 4.5 mm long, with wide transverse bands.........................***Echinocnemus gerofiticus***

25. Head constricted posterior to eyes, eyes prominent, antennal sulci ventral; body covered by oblong apically truncated attached scales (Figures 10f and 11d–g) .... ***Arthrostenus fullo***
- Head not constricted posterior to eyes, eyes flat or slightly prominent, antennal sulci lateral; body covered solidly by round scales, usually producing mosaic pattern and sole semierect scales (Figure 7a–Figure 8k)..***Bagous***

Key to species of *Bagous* in Israel

1. Tarsal segments 1–3 transverse or at most as long as wide; 7th segment of flagellum as as wide as 6th, or slightly wider, pubescent in same extent; geophile (collected by sifting or in pitfalls) (Figures 7k–m and 8j,k) ....***libanicus***
- Tarsal segments 1–3 longer than wide; 7th segment of flagellum distinctly wider than 6th, more densely pubescent; either aquatic or geophiles **2**

2. 1st segment of antennal club bare, smooth, shiny (Figure 8c) .... ***biimpressus***
- 1st segment of antennal club pubescent, not shiny **3**

3. Tarsal segments cylindrical or nearly so, as long as wide or slightly longer; 3rd tarsal segment not or slightly wider than 2nd tarsal segment at apex **4**
- Tarsal segments trapezoidal, distinctly longer than wide; 3rd tarsal segment cordate or at least distinctly wider than 2nd tarsal segment at apex **6**

4. Tarsal segments narrowly trapezoidal; body covered with round smooth shiny scales (Figures 7b and 8b) ....*argillaceus*
- Tarsal segments cylindrical; scales not smooth and shiny..**5**

5. Pronotum granulate; elytral disc flat, no elytral intervals convex; body elongate, slender, legs long, slender (Figures 7i and 8h); aquatic..***tempestivus***
- Pronotum punctate; elytral disc moderately convex, odd-numbered elytral intervals convex; body rounded, stout, legs short, stout; geophilous...**6**

6. Pronotum with small punctures, intervals between punctures distinctly convex, granulose, larger than punctures; elytra subquadrate, 1.30X as long as wide; tarsomere 2 and 3 subglobose, nearly as wide as long; antennae dark brown (Figures 7g and 8f)..***subruber***
- Pronotum with large punctures, intervals between punctures more or less convex, narrower than punctures: elytra more rectangular, 1.40–1.55X as long as wide; tarsomere 2 and 3 slightly but distinctly longer than wide; antennae dark reddish (Figures 7h and 8g) .... ***septemcostatus***

7. Pronotum rounded laterally, nearly as wide as elytra; body narrow, 3X as long as wide; body length 3 mm (Figures 7d and 8d) .... ***mingrelicus***
- Pronotum subparallel laterally, distinctly narrower than elytra; body oblong, 2.25–2.50X as long as wide **8**

8. 3rd tarsomere narrow, as long and as wide as 1st and 2nd, or only slightly larger, more or less cordate; body length 2.2–4.5 mm **9**
- 3rd tarsomere wide, at least 1.5 as long and as wide as 1st and 2nd, distinctly cordate, lobes separated at one third of its length, 5.5–7.0 mm (Figures 7j and 8j) ....***validus***

9. 3rd tarsomere cordate, lobes separated at least at one third of its length, tarsomeres bare or covered at ventral part by short scales; body length 2.2–2.7 mm (Figures 7a and 8a) .... ***bagdatensis***

- 3rd tarsomere subcordate, lobes separated at most at one fifth of its length, tarsomeres covered densely by long thin erect scales, partly piliform and partly wider; body length 3.7–4.5 mm (Figures 7e,f and 8e) ....***lyali***

3.3. Treatment of Genera and Species

BRENTIDAE Billberg, 1820 [42]

Apioninae Schoenherr, 1823 [43]

Apioninae are distributed worldwide [44], comprising approximately 700 species in the Palaearctic region [45]. None of the Palaearctic species are known to be aquatic, but some are associated with aquatic or semi-aquatic hostplants and therefore consistently found near the water. Seventy-five species of Apionidae have been recorded so far from Israel, developing on annuals and perennials and inhabiting a wide variety of biotopes, mainly completely terrestrial, all fully-winged and able to fly [46]. Some of them can be found occasionally to frequently in wet habitats, resting on the trees above the water or developing in the annuals along the bank (e.g., *Protapion* spp., *Onychapion poupillieri* (Wencker, 1864) [47]), but *Squamapion delagrangei* is the only species exclusively riparian.

Kalcapiina Alonso-Zarazaga, 1990

Squamapion delagrangei (Desbrochers des Loges, 1895) [48]

(Figure 5a, Figure 6a,b and Figure 13a)

Material examined: 58 exx.

ISRAEL: **Har Hermon:** Nahal Nimrod, 1082 m, 33°15′ N 35°45′ E, 18.x.2009, L. Friedman (2 males); **Golan Heights:** Yehudiyya Forest Nature Reserve [Golan, Qusbiye], 4.v.1979, D. Furth (1 male); **Hula Valley:** Tel Dan, 6.v.1979, D. Furth (1 female); Tel Dan, 168 m, 33°15′ N 35°39′ E, 19.x.2009, L. Friedman (2 females) ; Tel Hay, 2 km N, 24.viii.1972, D. Furth (2 males); 'En Gonen Nature Reserve, channel, 19:30–21:00, 18.viii.2014, L. Friedman, on *Mentha longifolia* (3 males); 'Enot Gonen, 19.viii.2014, L. Friedman, on *Mentha longifolia* (1 male); 'Enot 'Enan, 18.xi.1973, D. Furth (1 male); Hula Nature Reserve, 12.v.2010, L. Friedman, on *Mentha longifolia* (16 males, 2 females); Park haYarden, 32°55′ N 35°38′ E, −200 m, 19.vii.2009, L. Friedman (1 male, 1 female), 24.viii.2014, L. Friedman, on *Mentha longifolia* (4 males, 1 female); **Upper Galilee:** Sifsufa, 18.xi.1973, D. Furth (1 female); **Lower Galilee:** HaSolelim, 3.x.2001, L. Friedman, on *Mentha longifolia* (11 males, 12 females).

Distribution: Greece, Turkey, Israel [45,46]. In Israel, occuring on Golan Heights, in Hula Valley, Upper Galilee, and Lower Galilee, on banks of streams, ponds, and vernal pools, on its host plant, *Mentha longifolia*. The latter is widely distributed throughout Israel along various water sources, including extremely arid areas (Samarian and Judean Deserts, Arava Valley), but this weevil was not found south of the Lower Galilee.

Biology: Riparian. On *Mentha longifolia* L. (Lamiaceae) (Figure 2a,b). Adults active in May–November.

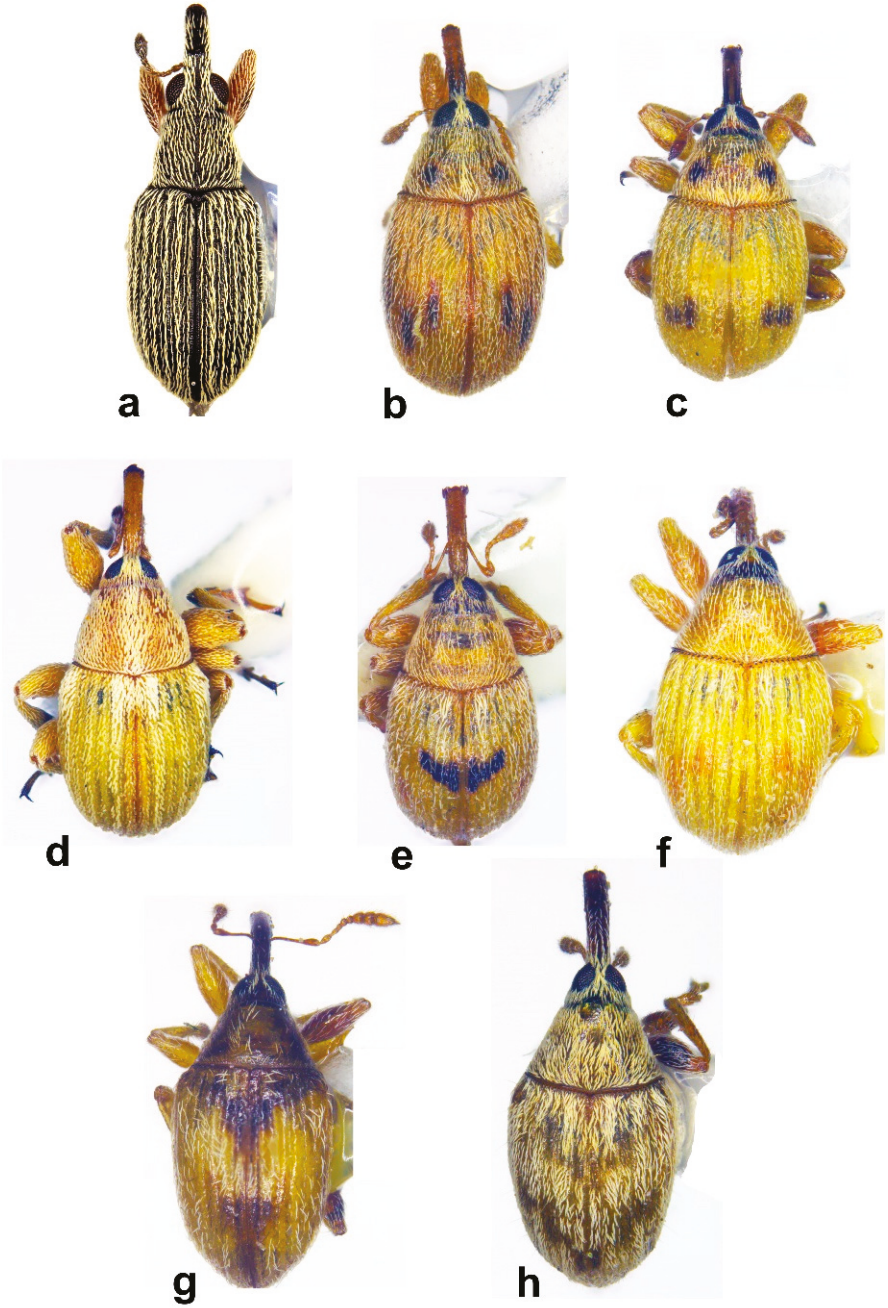

Figure 5. Habitus in dorsal view of (**a**) *Squamapion delagrangei*, male; (**b**) *Allomalia quadrivirgata*, male; (**c**) *Allomalia setulosa*, male; (**d**) *Corimalia latifrons*, male; (**e**) *Corimalia schatzmayri*, female; (**f**) *Corimalia torretrassoi*, male; (**g**) *Nanomimus* sp., male; (**h**) *Nanophyes* sp. 1, male (not on the same scale).

Nanophyinae Gistel, 1848 [49]

Nanophyinae are mainly distributed in the Old World Tropics and Eurasia, scarce in the Nearctic region and Australasia, and absent from Central and South America [50,51]. They comprise 107 species in the Palaearctic region [45]. This subfamily has recently been subdivided into two tribes: Corimaliini (47 spp.), associated exclusively with Tamaricaceae (*Tamarix*, *Reamuria*) and Nanophyini (60 spp.), associated with various plant families, but mostly with Lythraceae, Ericaceae, Crassulaceae, and Cupressaceae [50,51]. There are no aquatic species among Nanophyinae, although there are many riparian ones, living on *Tamarix* spp. and *Lythrum* spp. Nanophyinae have well-developed flight wings and fly very well but are unable to swim.

The full data on the Israeli fauna of Nanophyinae await publication because the survey of this group is still incomplete, with some species remaining unidentified and some probably representing undescribed species.

Corimaliini Alonso-Zarazaga, 1989 [50]

(Figures 1a–d, 5b–f and 6c–g)

Corimaliini comprises nine species in three genera in Israel: two species of *Allomalia* Alonso-Zarazaga, 1989 [50], six species of *Corimalia* Gozis, 1885 [52], and one species of *Hypophyes* Reitter, 1916 [53], all associated with *Tamarix* spp. Six species are riparian. There are approximately 13 species of *Tamarix* in Israel, some extremely difficult to identify. Some of the *Tamarix* species prefer saline soil and brackish water and, therefore, grow along the central and lower Jordan River, on the shores of the Sea of Galilee and the Dead Sea and surrounding streams, near springs, streams, and water reservoirs in the Central Negev, and in the swamps and around the natural ponds and artificial fish ponds along the Coastal Plain and the Jordan Valley. *Allomalia quadrivirgata* (Costa, 1863) [54] (Figures 5b and 6c) and *A. setulosa* (Tournier, 1868) [55] (Figures 5c and 6d) are the most common Corimaliini species throughout the country, both in the Mediterranean zone and in the desert. They usually occur in large numbers, often with both species occuring together on the same plants. Of six species of *Corimalia*, *C. schatzmayri* Giordani-Soika, 1937 [56] (Figures 5e and 6f) and *C. torretrassoi* Giordani-Soika, 1937 [56] (Figures 5f and 6g) occur along both the northern and central parts of the Mediterranean coast and in the oases along the north-west shore of the Dead Sea (e.g., 'Enot Zuqim Nature Reserve (Figure 1a,b)); *C. latifrons* (Pic, 1897) [57] (Figures 5d and 6e) occurs in the swamps along the lower Jordan Valley (e.g., Malha Swamp (Figure 1c)) and along the Dead Sea. *Hypophyes* sp. is rarely found in the Coastal Plain but is common in the Jordan Valley and along the Dead Sea, found frequently both near the water and in completely dry areas.

Biology: Members of Corimaliini in Israel develop in the inflorescence of *Tamarix* spp. (Tamaricaceae) (Figure 1d). Adults can be found all year round, but are mostly active during the blooming season of *Tamarix*, when hundreds of specimens, comprising all or some of the aforementioned species, can be observed. Corimaliini are frequently collected in water, but it is clear to me that they have been either swept from the plant or fell down accidently. After falling into the water these small (1–3 mm long) and very light weevils do not sink; they remain above the water and are able to spread their wings and return to the tree.

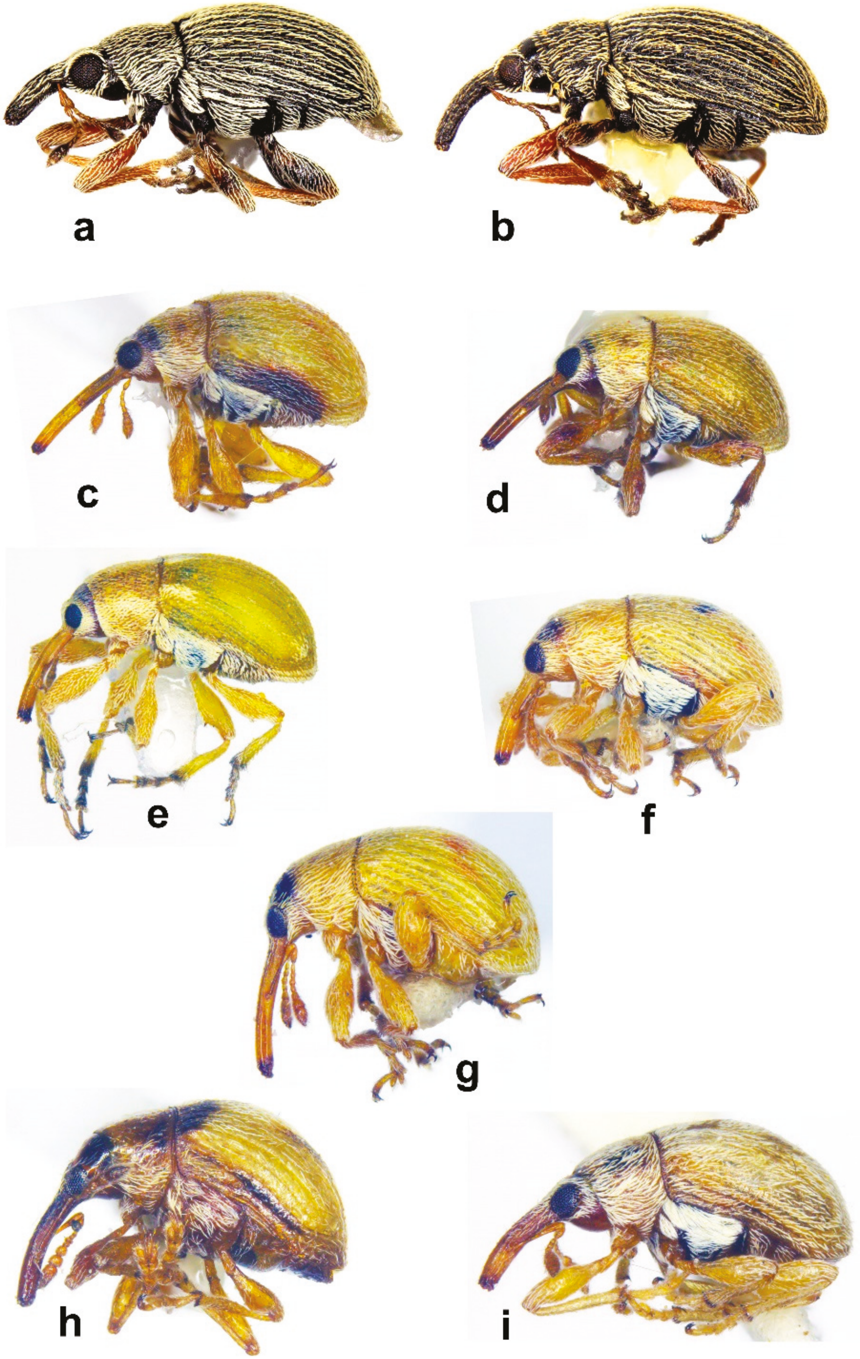

Figure 6. Habitus in lateral view of (**a**) *Squamapion delagrangei*, male; (**b**) *Squamapion delagrangei*, female; (**c**) *Allomalia quadrivirgata*, female; (**d**) *Allomalia setulosa*, female; (**e**) *Corimalia latifrons*, female; (**f**) *Corimalia schatzmayri*, male; (**g**) *Corimalia torretrassoi*, female; (**h**) *Nanomimus* sp., male; (**i**) *Nanophyes* sp. 1, male (not on the same scale).

Nanophyini Gistel, 1848 [49]

(Figures 1e, 2c, 5g,h and 6h,i)

In Israel, there are seven species in four genera. Six species are riparian: *Dieckmanniellus chevrieri* (Boheman, 1845) [58], *D. nitidulus* (Gyllenhal, 1838) [59] (both widely distributed in the Palaearctic region), one species of *Nanomimus*, and three species of *Nanophyes* (still not identified). All are associated with *Lythrum* spp. The distribution of these species corresponds to the distribution of *Lythrum*, on the banks of streams and ponds and at the edges of swamps, although the majority of species are found in the north of the country. They occur mainly in the Hula Valley, around the Sea of Galilee, on the Golan Heights, in the upper part of the Jordan Valley, and in the Northern Coastal Plain (particularly in the ʻAkko Valley), although two species of *Nanophyes* occur in the northern part of the Central Coastal Plain (Berekhat Ya'ar), and *Dieckmanniellus* sp. and *Nanomimus* sp. are found along the Yarqon River and around Tel Aviv. The third species of *Nanophyes* is known from three specimens collected only on the bank of Nahal haQibbuzim in the Bet Sheʻan Valley (central part of the Jordan Valley) (Figure 1e).

Biology: All the aforementioned species live, feed, and develop on *Lythrum* (Lythraceae), predominantly *Lythrum salicaria* L., the most common *Lythrum* species in Israel (Figures 1e and 2c). Some of the species were collected from several localities in the Hula Valley on *Lythrum junceum* Banks and Sol. *Dieckmanniellus* spp. and *Nanophyes* spp. develop in inflorescences. *Nanomimus* sp. develops in the stem, but unlike the European species, no stem galls have been found to date. Adults are found in March-September, but mainly in July–August, when the plants are verdant and blooming.

CURCULIONIDAE Latreille, 1802 [60]

The majority of the Recent weevils belong in this cosmopolitan family; which comprises over 51,000 described species [1]. In Israel, it is represented by approximately 800–900 species in 16 subfamilies [4] and unpublished data, 24 of them aquatic, semi-aquatic, or riparian.

Bagoinae C. G. Thomson, 1859 [61]

Bagoini C. G. Thomson, 1859 [61]

A group of unclear status within Curculionidae, but distinct and clearly monophyletic; it comprises about 300 described species (nearly half of them in the Palaearctic region, with no species known from Central or South America) in four closely-related genera [2,62]. The members of Bagoini are predominantly aquatic or nearly aquatic, mainly monophagous (very rarely oligophagous) on aquatic or riparian Angiospermae (Alismatales and Poales), although some are soil-dwellers; some of the species are flightless and some are able to fly; most species are able to swim, possessing morphological adaptations for swimming and breathing in the water [2,36,62,63]. Although Bodenheimer collected a few *Bagous* specimens, he did not include them in his first list of Israeli weevils [64]; the first time *Bagous* sp. was mentioned in the literature from Israel was by Dimentman et al. [18]. Five species have been recorded from Israel to date [36,45], and five are recorded here for the first time, all 10 species in the genus *Bagous*.

Bagous Germar, 1817 [65]

Comprises three subgenera in Israel: *Macropelmus* Dejean, 1821 [66] with eight species and *Bagous* (s. str.) and *Parabagous* Schilsky, 1907 [67] with a single species each [62]. This genus, known to be nearly completely aquatic, is represented in Israel by a composition of five clearly aquatic species, one species (probably extinct) either aquatic or semi-aquatic, three soil-dwellers, and one with unclear habits.

Bagous (Bagous) bagdatensis Pic, 1904 [68]

(Figure 7a, Figure 8a and Figure 9a)

Material Examined: 6 exx.

ISRAEL: **Hula Valley:** Hula Nature Reserve, 33°04′11″ N 35°36′13″ E, pitfall trap, 8.iv.2010, L. Friedman, C. Drees (2 males, 1 female), 31.vii.2010, L. Friedman, C. Drees (1 female); Hulata, 20.vi.1952, J. Wahrman (1 male); **Sea of Galilee Area:** Migdal, 27.iii.1932, Y. Palmoni (1 male).

Distribution: South-east Europe (Austria, Hungary, Romania, Italy, Montenegro, Albania, Greece) and south-west Asia (Armenia, Turkey, Israel, Iraq, Iran) [36,45]. In Israel, in the Hula Valley and in the past in the Sea of Galilee Area, in swamps and vernal ponds.

Biology: Probably aquatic. Four specimens from the Hula Nature Reserve in 2010 were collected with pitfall traps placed on the bank of the Hula Lake, which suggests that the weevils spend at least part of their life on the ground. The closely-related European *Bagous glabrirostris* Herbst, 1795 was recorded from *Stratiodes aloides* (Hydrocharitaceae) and *Ceratophyllum submersum* (Ceratophyllaceae). While *C. submersum* is extremely rare in Israel, its relative *Ceratophyllum demersum* L. is a common aquatic plant in the Hula Valley (Figure 3c).

Notes: The specimen from Hulata was probably the source of the record in Dimentman et al. [18].

Bagous* (*Macropelmus*) *argillaceus Gyllenhal, 1836 [69]

(Figures 7b, 8b and 9a)

Material Examined: 7 exx.

ISRAEL: **Central Negev:** Ma'agar Yeroham [Negev, Yerokham], 458 m, 30°59.389′ N 34°54.109′ E, 28.ii.2009, Starke (1 male); Ma'agar Yeroham, 24.iv.2014, I. Renan, light trap (4 exx.); **Dead Sea Area:** 'En Boqeq, 29.vi.2014, I. Renan light trap (2 exx.).

Distribution: West Palaearctic (Europe, Russia, North Africa, Caucasus, Middle and Central Asia) [36,45]. First record for Israel. For distribution in Israel see comments below.

Biology: Halobiont [36,70], presumably semi-aquatic. Adults active in February-June. Host plant remains unknown. Dieckmann [70] recorded it on *Alisma plantago-aquatica* L. (Alismatidae), and *Polygonum* spp., *Rumex* spp. (Polygonaceae) in Hungary and Cunev ([71] and pers. comm.) collected a single specimen of *Polygonum* sp. in Slovakia. The records from Polygonaceae seem occasional. *Alisma plantago-aquatica* commonly occurs in Israel in the Hula Valley and rarely on the Golan Heights and is completely absent from *B. argilaceus* habitats.

Note: *Bagous argillaceus* is the only species among the Israeli aquatic weevils that occurs in the desert. This species is distributed widely throughout the Palaearctic region, but is restricted to places with high salinity [26]. In spite of its wide distribution its host plant is unknown. In Israel it was found in two quite different habitats: an artificial freshwater reservoir in the Central Negev (Ma'agar Yeroham = Yeroham Reservoir, at 450 m a.s.l., with still water; and a spring with brackish water, flowing into the Dead Sea ('En Boqeq), at −350 m b.s.l., and resembling it in its high salinity of the banks and aridity of the area. In both places weevils were collected in light traps, in Ma'agar Yeroham one specimen was collected on the vegetation close to the water (Starke, pers. comm.). It can be assumed that *B. argillaceus* is associated with the same host plant in both localities. The vegetation of 'En Boqeq was thoroughly studied, but no strictly aquatic plants were found. The riparian vegetation comprises *Tamarix nilotica* (Tamaricaceae), *Juncus rigidus* (Juncaceae), *Arundo donax*, *Phragmites australis,* and *Imperata cylindrica* (Poaceae), *Doellia bovei* (Asteraceae) and *Adiantum capillus-veneris* (Adiantaceae) [72]; the first five also occur in Ma'agar Yeroham. Michael Blecher (pers. com.) suggested that *B. argillaceus* could have arrived from the nearby Ma'agar Heymar (=Heymar Reservoir, ~5 km to the south of 'En Boqeq), in which the abiotic factors and aquatic vegetation resemble more those of Ma'agar Yeroham than of 'En Boqeq.

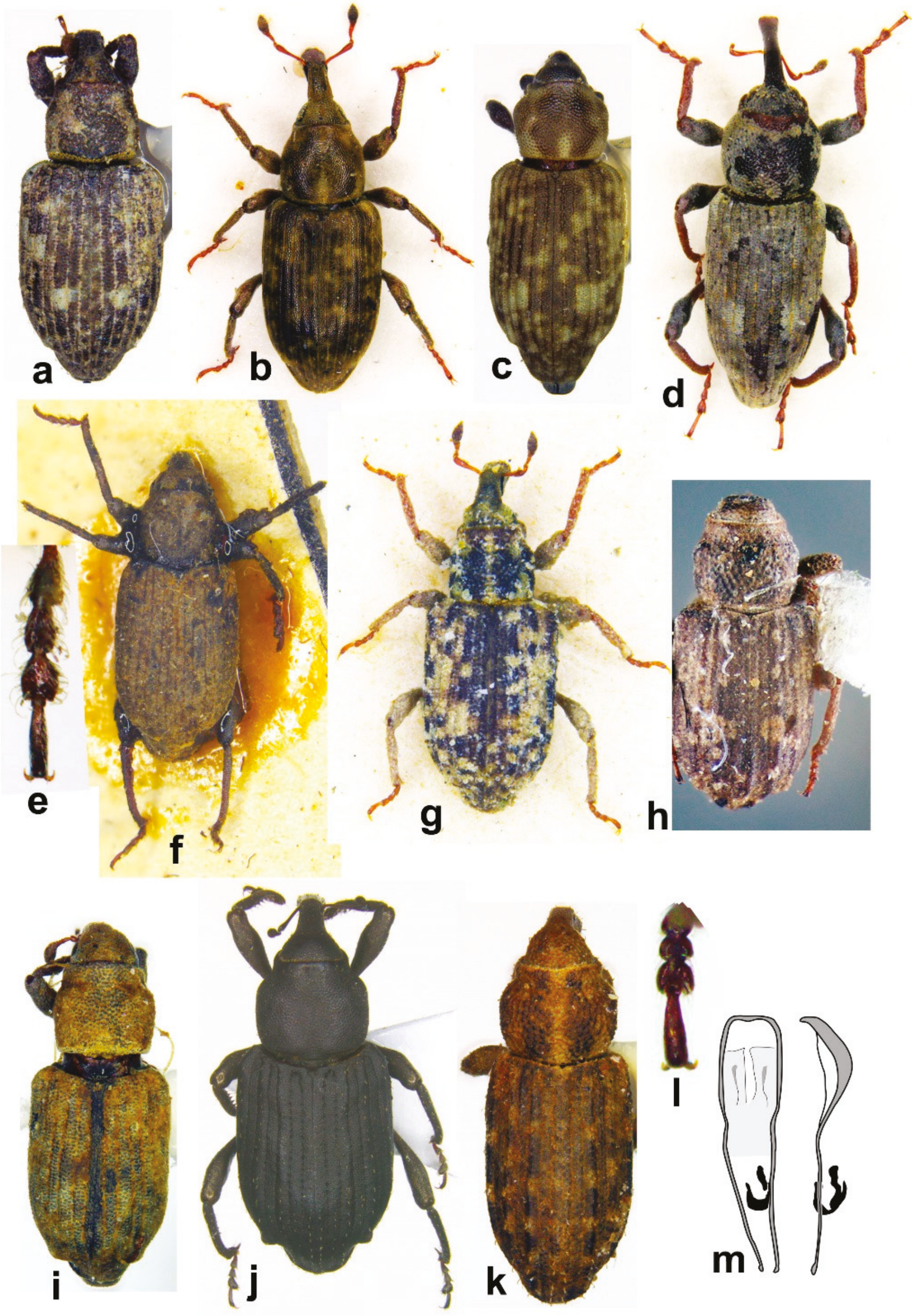

Figure 7. Habitus in dorsal view of (**a**) *Bagous bagdatensis*, male; (**b**) *Bagous argillaceus*, male; (**c**) *Bagous biimpressus*, female; (**d**) *Bagous mingrelicus*, female; (**e**) *Bagous lyali*, tarsus, male; (**f**) *Bagous lyali*, male; (**g**) *Bagous subruber*, male (IRAQ: Basra, 1.iv.1936, Frey, ZSMU); (**h**) *Bagous septemcostatus*, male; (**i**) *Bagous tempestivus*, male; (**j**) *Bagous validus*, male; (**k**) *Bagous libanicus*, female; (**l**) *B. libanicus*, tarsus; (**m**) *B. libanicus*, aedeagus (not on the same scale).

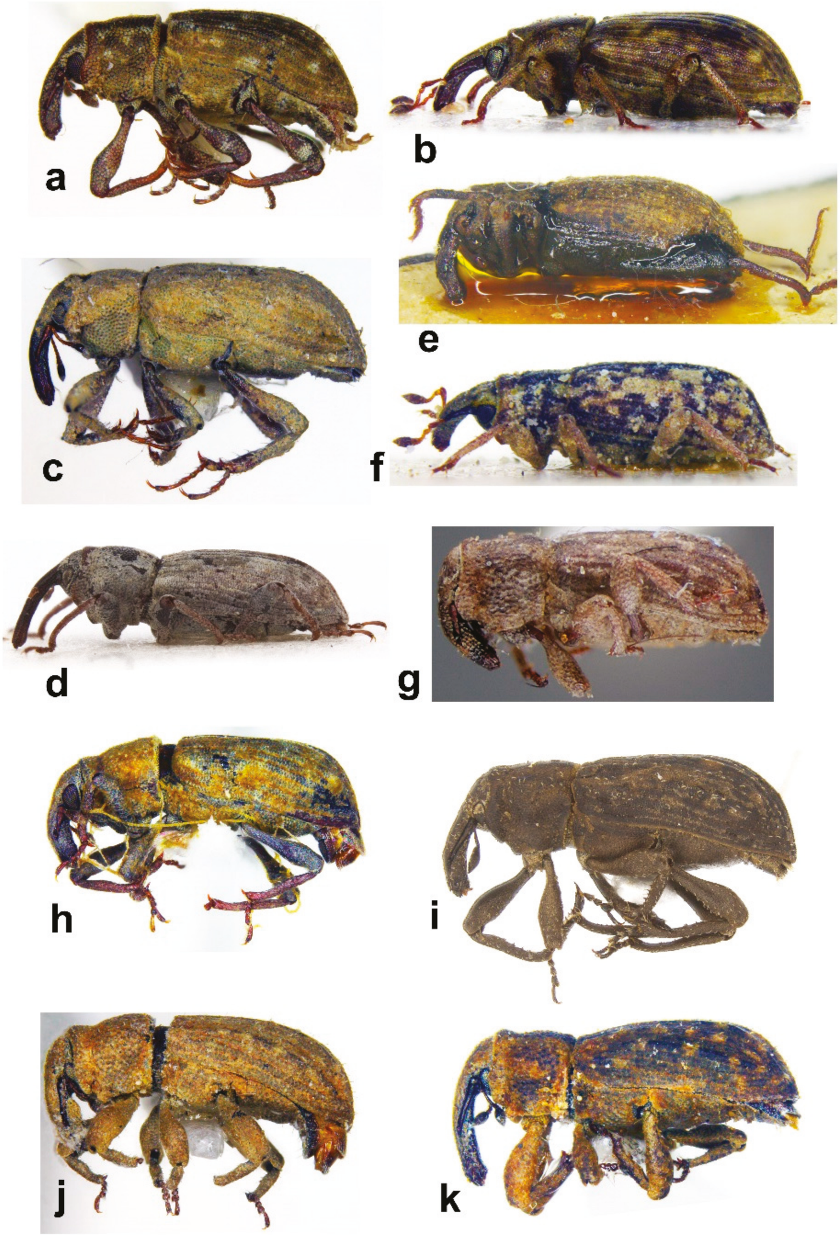

Figure 8. Habitus in lateral view of (**a**) *Bagous bagdatensis*, male; (**b**) *Bagous argillaceus*, male; (**c**) *Bagous biimpressus*, female; (**d**) *Bagous mingrelicus*, female; (**e**) *Bagous lyali*, male; (**f**) *Bagous subruber*, male (IRAQ: Basra, 1.iv.1936, Frey, ZSMU); (**g**) *Bagous septemcostatus*, male; (**h**) *Bagous tempestivus*, male; (**i**) *Bagous validus*, male; (**j**) *Bagous libanicus*, male; (**k**) *B. libanicus*, female (not on the same scale).

Bagous **(*Macropelmus*)** ***biimpressus*** Fåhraeus, 1845 [73]

(Figures 7c, 8c and 9a)

Material Examined: 5 exx.

ISRAEL: **Upper Galilee:** Dovev Pool, 12.iii.2007, S. Pilosof (1 male); Dovev, 16.iii.2007, S. Pilosof (1 female); Hawwat Matityahu, winter pool [Matytyahu, Hafura], 12.iii.2007, S. Pilosof (1 male); Ramat Dalton, 1.v.2007, S. Pilosof (1 female); **Central Coastal Plain:** Berekhat Ya'ar, 28.ii.1984, A. Gasith (1 female).

Distribution: Mediterranean region (France, Greece, Italy, Spain, Algeria, Turkey) and Middle Asia (Turkmenistan) [36,45]. First record for Israel. In Israel it is found in winter pools in the Upper Galilee (more recent records) and in the Central Coastal Plain (a single old record).

Biology: Host unknown. Caldara and O'Brien [36] suggested it is halophilic, although in Israel it has been found in non-saline locations. Adults active in February–May. Collected in water—therefore, probably aquatic.

Bagous (***Macropelmus***) ***lyali*** Caldara & O'Brien, 1998 [36]

(Figures 3d, 7e,f, 8e and 9b)

Material Examined: 10 exx.

ISRAEL: **Hula Valley:** Hula [Hulah], 5.vii.1934, F. S. Bodenheimer, on papyrus (4 males, 6 females)—topotypes.

Distribution: Described from Israel [36]. Probably an endemic of the Hula Valley.

Biology: Presumably semi-aquatic. It is noted on the labels that the specimens were collected on *Cyperus papyrus* L. (Cyperaceae) (Figure 3d). It is unclear whether the weevils are associated with this plant, or were just collected in the thicket of papyrus characterizing the Hula swamp. My numerous attempts to re-collect this species on *C. papyrus* or surrounding vegetation in the Hula failed.

Note: To date the species is known only from the single series, resulting from a single collecting event. Five specimens were sent by F.S. Bodenheimer to the British Museum in London for identification and became types 50 years later, and 10 specimens remained in Bodenheimer's collection, later incorporated in the SMNHTAU collection. *B. lyali* has not been collected since, despite my numerous recent atttempts. I suspect the species has become extinct after the drainage of the Hula Valley; however, I do not give up hope that it will be rediscovered, as happened with the Hula painted frog *Latonia nigriventer* [15,74].

Bagous (***Macropelmus***) ***mingrelicus*** Tournier, 1874 [75]

(Figures 7d, 8d and 9b)

Material Examined: 5 exx.

ISRAEL: **Golan Hights:** Yehudiyya Forest Nature Reserve [Qusbiye], 28.iv.1974, D. Furth (1 female); **Yizre'el Valley:** Nahalal, 27.iii.1932, Y. Palmoni (1 female); **Central Coastal Plain:** Nahal Barqan, 13.iv.1997, R. Hoffman (1 male, 2 females).

Distribution: Greece, south of the European part of Russia, Georgia, Turkey, Israel [36,45]. The collecting records suggest that at least in the past *B. mingrelicus* was widely distributed throughout northern and central Israel, but it has not been collected in the last few decades. Recorded by Caldara and O'Brien [36] from the Southern Coastal Plain (Miqwe Yisrael Agricultural School [Mikve Israel], 1931, F. S. Bodenheimer (2 exx., BMNH)) and Judean Hills (Yerushalayim [Jerusalem], Reitter (1 exx, HNHM)). The record from Yerushalayim by Reitter does not really note the existence of *B. mingrelicus* in the city (750–800 m a.s.l., arid surrounding), but probably refers to one of the numerous springs on the western slopes of the Judean Hills, most of them recently dry or used for agriculture or cultivated and visited by many tourists, and therefore their flora and fauna strongly degraded.

Biology: Aquatic. No data on host plants are available.

Bagous (***Macropelmus***) ***septemcostatus*** Chevrolat, 1860 [76]

(Figures 7h, 8g and 9c)

Material examined: No material is deposited in SMNHTAU. Caldara and O'Brien [36] recorded it from Israel for one specimen, deposited in USNM, labeled: "Israel, 1-7.iii.1968, S. Bleszynski". I was provided with the photographs of this specimen and its label by Lourdes Chamorro, USNM.

Distribution: Mediterranean (Spain, Morocco, Algeria, Tunisia, Libya, Turkey, Israel) [36,45].

Biology: Geophilic. No data on host plants are available.

Notes: The collecting label of a single specimen of *B. septemcostatus* lacks the name of the locality, probably because the collector did not have an opportunity to label it himself. The late lepidopterist Stanislaw Bleszynski (1927–1969), a specialist of Crambidae (Lepidoptera), was killed in a road accident in 1969 [77] and Freidberg (pers. comm.). In 1968 he spent nearly an entire year in Israel, studying the Israeli Crambidae fauna, collecting mainly in light traps. Some of the insects that he collected (mainly moths) are deposited in SMNHTAU, most of them have remained unlabeled and kept separately until recently. It was thus clear that at the beginning of March 1968, he was collecting around the southern part of the Sea of Galilee (Kinneret (settlement), 4.iii.1968, Tel Qazir, 5.iii.1968, Teverya, 7.iii.1968). Caldara and O'Brien [36] noted that the mesothoracical wings are fully developed, and the weevil is probably able to fly. Therefore, it is possible that it was collected in a light trap in the southern part of the Sea of Galilee. This is a low (200 m b.s.l.), humid area, which was swampy in the past, and has recently undergone almost complete change due to human activities (roads, agriculture, industry, etc.). The ongoing drying of the Sea of Galilee and lowering of its water level have exterminated most of the natural habitats, particularly in its southern more human-populated part, so that it is unclear whether *B. septemcostatus* still occurs in this area or where to look for it.

Bagous (***Macropelmus***) ***subruber*** Reitter, 1890 [78]

(Figures 7g, 8f and 9c)

Material examined: No material is deposited in SMNHTAU. Caldara and O'Brien [26] recorded it from Israel from 10 specimens from Wadi Ghuzze, collected by N. Scott (the collecting date is not noted) and deposited in BMNH. The photographs show a male specimen from Iraq (IRAQ: Basra, 1.iv.1936, Frey, ZSMU).

Distribution: Mediterranean (Spain, Greece, Algeria, Libya, Tunisia, Egypt, Israel) and south-west Asia (Iraq, Iran, Saudi Arabia) [36,45]. The name Wadi Ghuzze refers to the lower part of Nahal Besor, one of the largest brooks in the southern part of Israel, stretching for approximately 80 km from the Boqer plateau to the Mediterranean coast. Therefore, the only record from Israel is either from the Southern Coastal Plain or the Northern Negev.

Biology: Geophilic. Collected by sifting in saline soil under *Arthrocnemum* sp. (Chenopodiaceae) (Meregalli and Borovec, pers. comm.) and under *Frankenia pulverulenta* L. (Frankeniaceae) (Sprick, pers. comm.) [36]. These plants are absent or vary rare in the lower Nahal Besor (the only collecting locality of *B. subruber* in Israel), but occur in the swamps and salt marshes around 'Akko in the Northern Coastal Plain.

Bagous (***Macropelmus***) ***tempestivus*** (Herbst 1795) [79]

(Figures 7i, 8h and 9c)

Material examined: 1 ex.

ISRAEL: **Upper Galilee:** Ramat Dalton, 21.ii.2007, S. Pilosof (1 male).

Distribution: Europe, Siberia, Russian Far East, Georgia, Turkey [36,45]. In Israel a single specimen was found in a vernal pond. First record from Israel, apparently the southernmost border of its distribution.

Biology: Aquatic. In Europe reared from the stems of *Ranunculus repens* L. (Ranunculaceae) and collected on *Ranunculus* spp. and *Potamogeton* spp. (*P. lucens* L., *P. natans* L., *P. crispus* L.) (Potamogetonaceae) [36]. Twenty-one species of *Ranunculus* and eight species of *Potamogeton* occur in Israel; the aquatic *Ranunculus constantinopolitanus* (DC.) D'Urv., *R. peltatus* Schrank, *R. scandicinus* (Boiss.) P.H. Davis, *Potamogeton nodosus* Poir. and *P. pectinatus* L. occur in the the Upper Galilee and can be potential hosts.

Bagous* (*Macropelmus*) *validus Rosenhauer 1847 [80]

(Figures 4a,b, 7j, 8i and 9c)

Material Examined: 50 exx.

ISRAEL: **Central Coastal Plain:** Berekhat Ya'ar, 21.iii.2000, A. Gasith (1 female), 14.v.2003, L. Friedman (5 males, 4 females), 23.v.2003, A. Freidberg (8 males, 2 females), L. Friedman (11 males, 6 females), 6.vi.2003, A. Freidberg (1 male), 28.iv.2004, L. Friedman (2 males, 2 females), 23.iii.2009, G. Wizen (1 male, 1 female), 32°24′39′′ N 34°45′02′′ E, pitfall trap, 16.iii.2010, L. Friedman, C. Drees (1 female), 17.iii.2010, L. Friedman, C. Drees (1 male, 3 females), 20.vii.2010, L. Friedman, C. Drees (1 female), 15.iii.2018, L. Friedman (1 male, 1 female).

Distribution: Central and Southern Europe, Turkey, Syria [36,45]. First record for Israel. The closest previous record is from central Syria (Homs) [70], more than 300 km north of the recent locality.

In Israel it is found exclusively in Berekhat Ya'ar (=Forest Pool) (Figure 4a), the seasonal winter pool and swamp south of Hadera, the last remnant of the swamp belt stretching along the coast until the drainage in the 1930s. Most of the specimens were collected by sweeping and beating the water plants, six specimens were collected in pitfall traps placed close to the water, three specimens were observed on 15.iii.2018 in the evening, feeding on leaves of *B. umbellatus* (Figure 4b).

Biology: Aquatic. *Butomus umbellatus* L. (Butomaceae) (4a,b); larvae develop in leaves [70]. *B. umbellatus* is a very common water plant in the seasonal and constant water bodies throughout the Central Coastal Plain and in the Golan Heights, but *B. validus* was found only in Berekhat Ya'ar. Adults active in March–May.

Bagous* (*Parabagous*) *libanicus Schilsky, 1911 [81]

(Figures 7k,l,m, 8j,k and 9b)

Material Examined: 16 exx.

ISRAEL: **Upper Galilee:** 'En Ya'aqov, 14.i.2007, I. Shtirberg (1 male); Hurfeish, batha, 675 m, 33°01′ N 35°21′ E, pitfall, 27.xii.2005, A. Timm, Th. Assmann (1 female), 10.i.2006, A. Timm, Th. Assmann (1 male), 6.ii.2006, A. Timm, Th. Assmann (1 male); Ziv'on, batha, 712 m, 33°01′ N 35°25′ E, pitfall, 5.iii.2006, A. Timm, Th. Assmann (1 male, 1 female); Har Meron, 5.ii.2007, T. Levanony (1 male); Biriyya, batha, plot 21(1), sifting, 18.iii.2008, T. Levanony (1 female); **Lower Galilee:** ?Segev, 1985–1986, M. Warburg (1 male); **Yizre'el Valle:** Merhaviyya, 2.ii.2001, L. Peled (1 female), 9.ii.2004, L. Peled (1 female); **Judean Hills:** 'Adullam, 3.iv.2003, E. Columbus, T. Levanony (1 female), 15.i.2004, E. Columbus, T. Levanony (3 males, 1 female).

Distribution: Described from Lebanon [36]. First record for Israel. In Israel it appears to be widespread throughout the Mediterranean zone from the Lebanese border in the north to at least the south-west slopes of the Judean Hills.

Biology: Geophilic, lives in soil under leaf litter in the Mediterranean oakwoodland and shrubland (batha). Most of the specimens were collected with pitfall traps or by soil sifting. Hosts unknown. Adults active in January–April.

Notes: This enigmatic species was described from a single female from Lebanon (precise locality unknown), supposedly deposited in the Schilsky Collection in the Museum der Naturkunde für Humboldt Universität zu Berlin, Germany, but was not found there by Caldara and O'Brien [36], who published a translation of its original description from German into English. Its photographs and the schematic drawing of its aedeagus are published here for the first time.

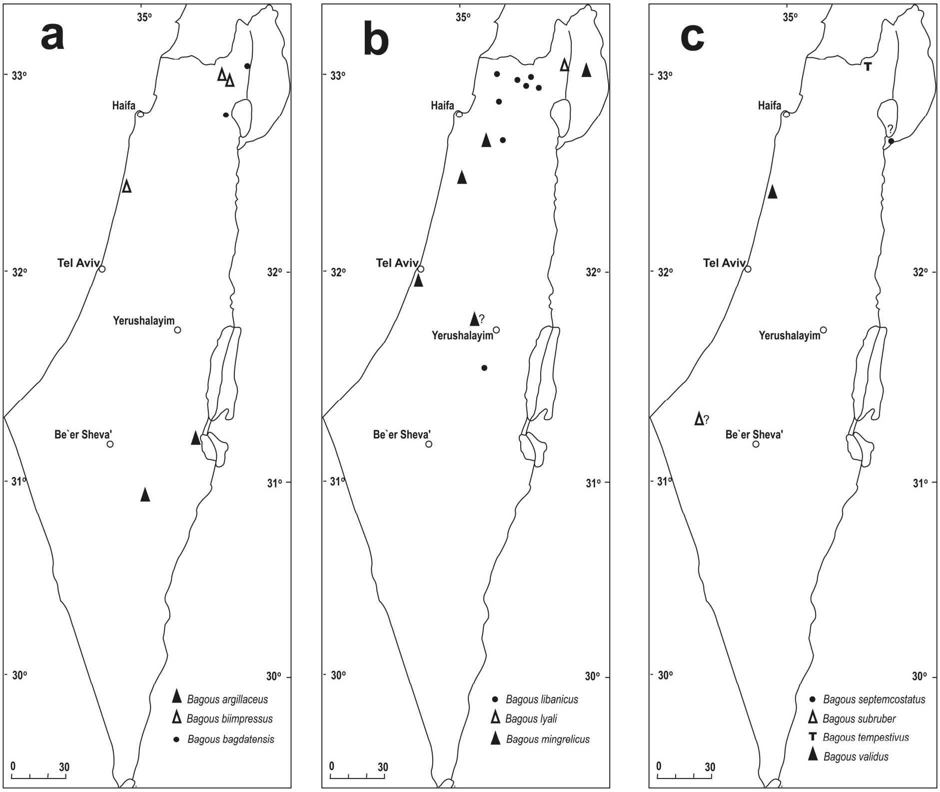

Figure 9. Distributional maps of *Bagous* (**a**) *B. argillaceus*, *B. bagdatensis*, *B. biimpressus*; (**b**) *B. libanicus*, *B. lyali*, *B. mingrelicus*; (**c**) *B. septemcostatus*, *B. subruber*, *B. tempestivus*, *B. validus*.

Brachycerinae Billberg, 1820 [42]

Tribe Erirhinini Schoenherr, 1825 [82]

Echinocnemus Schoenherr, 1843 [83]

An aquatic genus with twelve species in the Palaearctic region [45], and above 100 species in Afrotropical, Oriental, and Australasian regions [37,84]. Two extant and two fossil species were recorded from Israel. The fossil species are from the Late Cretaceous (Turonian, 89.8–93.9 Ma) deposits in the southern Arava Valley (in Qetura and Gerofit, respectively): *Echinocnemus qetura* Grachev, 2008, and *E. gerofiticus* Grachev, 2008 [85] (Figure 13b), both known only from a single right elytron. In the

Turonian this area mainly comprised mangroves and coastal marshes on the shore of the ancient Tethys Sea [86,87]. The southern part of the Arava Valley is currently an extreme desert with sparce and irregular precipitation and very limited water sources, comprising springs and fast-drying vernal winter pools, making the finding of any aquatic or semi-aquatic species there very unlikely.

The extant species, *Echinocnemus reitteri* and *E. sahlbergi*, were only collected in 1904 and have not been collected since. Two additional *Echinocnemus* species occur in Egypt: *E. aegyptiacus* Desbrochers des Loges and *E. tibialis* Tournier [45,88], the latter species recorded from the Mediterranean zone—Kirdasa (near Cairo, lower Nile Valley) [88], an environment quite similar to the Mediterranean coast of Israel, where it coexists together with *E. reitteri*. I assume that they could occur in Israel, at least in the past.

Based on the data on the recent taxa, one can assume that the biology of the extinct species was quite similar to that of the extant *Echinocnemus*, feeding and developing on the semi-aquatic Poaceae (e.g., *Oryza*) in the Palaearctic, Afrotropical, and Oriental regions and on the aquatic fern *Marsilea* (Marsileaceae) in Australia [7,89–92].

Echinocnemus reitteri Schilsky, 1907 [67]

(Figures 10a, 11c and 13b)

Material examined: 1 ex. No material is deposited in SMNHTAU. ISRAEL: Tel Aviv, Sharona [Sarona], U. Sahlberg (1 female, SZMU, ex collection of K. Daniel).

Distribution: Egypt [45,88]. First record for Israel.

Biology: Aquatic. Host plant unknown. According to Sahlberg [93] was collected at February.

Notes: John Sahlberg and his son Unio collected 19 (!) specimens of what they considered *E. sahlbergi* on the clay bottom of agricultural water bodies (irrigation canals of rice fields?) close to Wadi el Miserara (=Nahal Ayalon) near Sarona, the German Templer agricultural colony [93]. This area is now in the center of Tel Aviv megapolis, Nahal Ayalon is diverted to a new bottom and enclosed in the artificial channel up to its entrance into the Yarqon River, and its old bottom is occupied by the Ayalon Highway, the major intracity transpostation artery of the Gush Dan (Tel Aviv megapolis), including multi-lane highway and a multi-track railway. The only specimen that I studied clearly belongs to *Echinocnemus reitteri* according to the original description. I assume that the collected series of *Echinocnemus* included specimens of two species.

No additional specimens of *E. reitteri* were collected since. The species is either extinct or extremely rare. Its extinction is clearly as a result of the habitat loss.

Echinocnemus sahlbergi Schilsky, 1911 [81]

(Figure 13b)

Material examined: No material is deposited in SMNHTAU. According to the original description [81], the type series comprised four specimens, two granted to Schilsky by Sahlberg, and two remained with Sahlberg.

Distribution: Described from Israel, probably endemic [93,94]. So far known from a single locality, Tel Aviv, Sharona, Nahal Ayalon (see comments to *E. reitteri*).

Biology: Aquatic. Host plant unknown. According to Sahlberg [93] was collected in February.

Notes: This species was overlooked since its description and was not mentioned in any catalog or publication, apart to Sahlberg [93] for more than 100 years. The validity of this species should be proven either by finding the type specimens or by collecting new material. *E. sahlbergi* was never re-collected since its description, its habitat (assumabely swamps or vernal ponds in the Central Coastal Plain) is largerly disappeared, therefore I assume that this species is either extinct or extremely rare.

Icaris Tournier, 1874 [75]

A monospecific genus, that is distributed in the Palaearctic and Afrotropical regions [37,90].

Icaris sparganii (Gyllenhal, 1835) [95]

(Figures 4f,g, 10b, 11a and 13a)

Material Examined: 28 exx.

ISRAEL: **Central Coastal Plain:** Ga'ash, 24.iv.1974, D. Furth (1 male), 10.iii.1975, A. Freidberg (1 male, 1 female), 9.iii.1978, D. Furth (1 male, 1 female), 3.iv.1978, D. Furth (1 male, 2 females), 21.ii.1980, in water (1 male, 1 female), 11.ii.2001, L. Friedman, on *Scirpus maritimus* (13 males, 4 females), 7.v.2015, L. Friedman, on *Scirpus maritimus* (1 male).

Distribution: *Icaris sparganii* is widely distributed throughout the Palaearctic region, forming three subspecies: *I. s. cinereus* Miller, 1861 [96] (Turkey, Syria), *I. s. pertinax* Gyllenhal, 1835 [95] (European Russia, Western Siberia, Middle Asia, NE China) and *I. s. sparganii* Gyllenhal, 1835 [95] (Central, Southern and East Europe, SE Russia, Ukraine, Iran, Mongolia, Russian Far East, and SW China) [45,97,98]. Recorded from Israel by Friedman [4]. According to this distributional map, the Israeli population should belong in *I. s. cinereus*. The subdivision into subspecies is based on Faust [99], who provides a key to the subspecies (which he considers good species). According to this key the Israeli *Icaris* falls into the nominative subspecies *I. s. sparganii*. However, the intraspecific variation, even within the 28 Israeli specimens, and the controversy over the key and the distributional ranges of the subspecies leads me to the conclusion that either the subdivision into subspecies is erroneous or *I. sparganii* comprise a single widely distributed species with some local variation. Consequently, a revision of the Palaearctic *Icaris* is urgently needed.

In Israel the distribution of *Icaris sparganii* is restricted to the Ga'ash winter pool (38.5 m^2), a vernal pond north of Tel Aviv, wedged between Kibbutz Ga'ash and the coastal highway (Rt. 2), one of the most overcrowded roads in Israel (Figure 4f). However, the host plant is common along the Northern and Central Coastal Plain, in the Yizre'el and Jordan Valleys and on the Golan Heights.

Biology: Aquatic. In Israel is associated with *Scyrpus maritimus* L. (Cyperaceae) (Figure 4f,g). Recorded from Europe on *Eleocharis* spp. (Cyperaceae) [100], *Juncus* spp. (Juncaceae), *Sparganium* spp. (Sparganiaceae) [101]. Adults active in February–May.

Picia Tournier, 1895 [102]

A completely aquatic genus. Comprises three species in the Palaearctic region, distributed mainly in its eremic part (East Mediterranean, Middle East, Middle Asia) [45,84]. *Picia sinuatocollis* Faust feeds and develops on rice *Oryza sativa* L. (Poaceae), adults feed on the underwater parts of plants and remain for prolonged periods under water, larvae live inside roots and breathe the air from the aeriferous plant structures. After water drainage they feed on the roots externally. Pupation occurs in the soil pupal chamber [88,89,103]. *P. sinuatocollis* causes serious damage to rice and is considered a severe pest of rice in Middle Asia. In Israel, *Picia* is represented by a single species, originally described from the northern part of Israel.

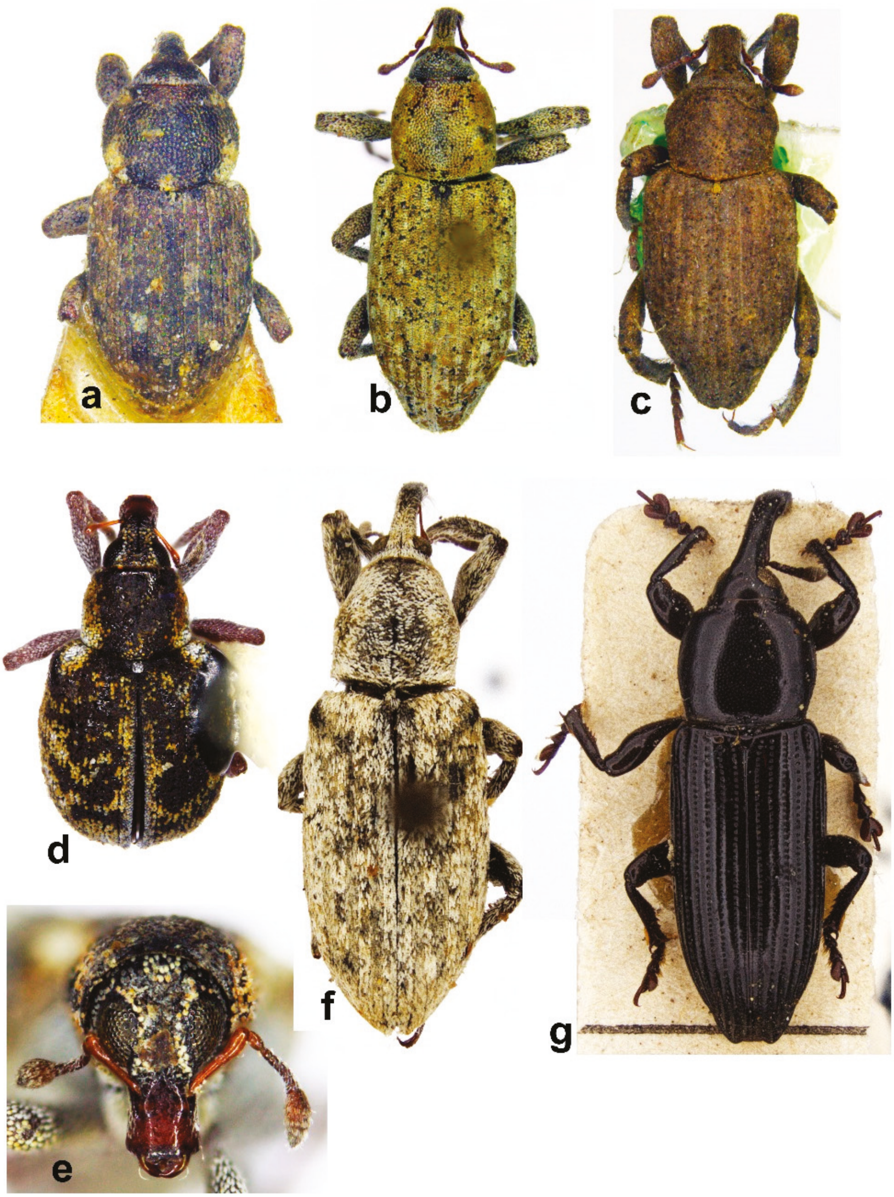

Figure 10. Habitus in dorsal view of (**a**) *Echinocnemus reitteri*, female; (**b**) *Icaris sparganii*, male; (**c**) *Picia syriaca*, male; (**d**) *Stenopelmus rufinasus*, female; (**e**) *S. rufinasus*, head, female; (**f**) *Arthrostenus fullo*, male; (**g**) *Aorus anthracinus*, male (not on the same scale).

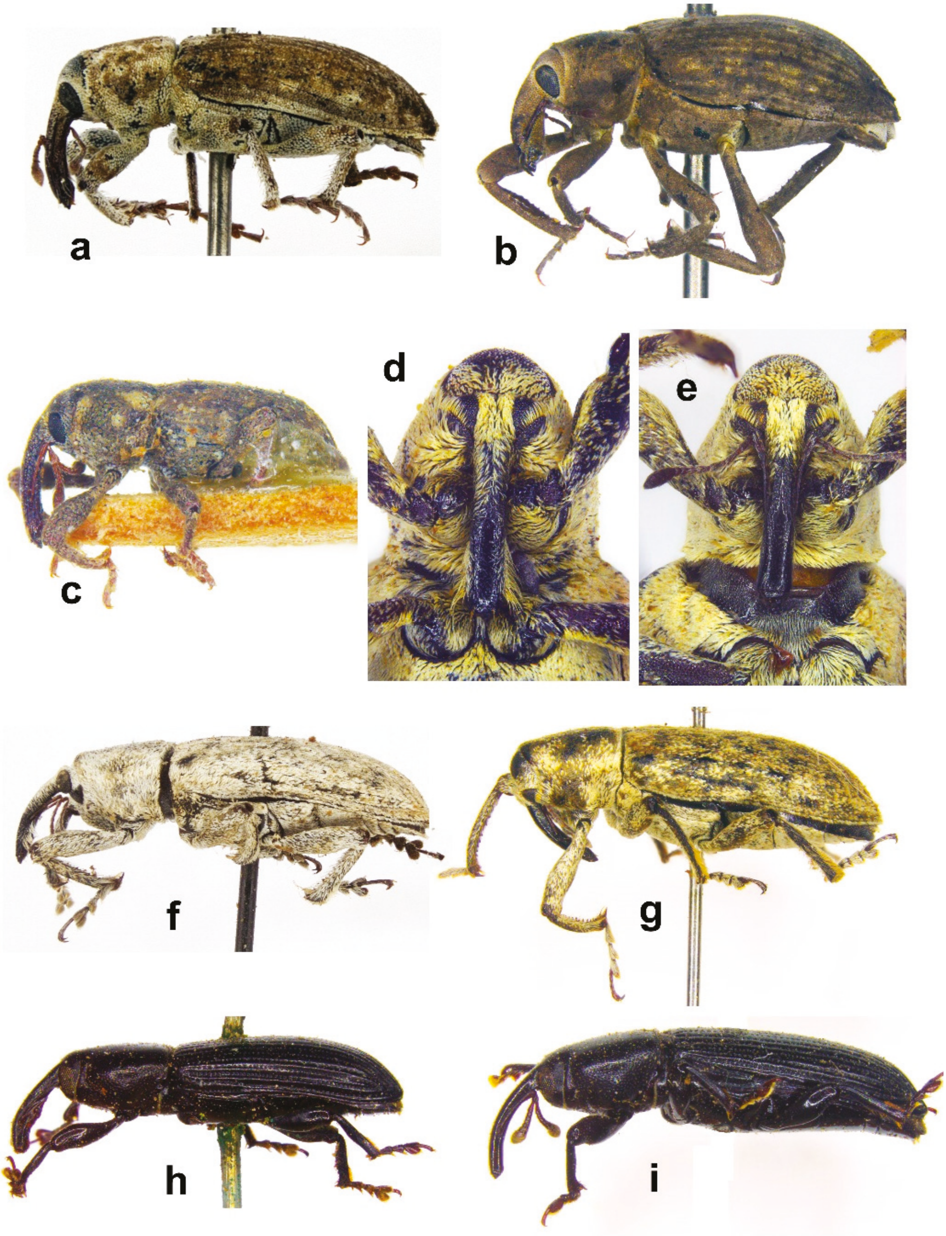

Figure 11. Habitus (**a**) *Icaris sparganii*, male, lateral view; (**b**) *Picia syriaca*, male, lateral view; (**c**) *Echinocnemus reitteri*, female, lateral view; (**d**) *Arthrostenus fullo*, head and pronotum, male, ventral view; (**e**) *A. fullo*, head and pronotum, female, ventral view; (**f**) *A. fullo*, male, lateral view; (**g**) *A. fullo*, female, lateral view; (**h**) *Aorus anthracinus*, male, lateral view; (**i**) *A. anthracinus*, female, lateral view (not on the same scale).

Picia syriaca (Reitter, 1889) [104]

(Figures 4d,e, 10c, 11b and 13a)

Material Examined: 8 exx.

ISRAEL: **Central Coastal Plain:** Berekhat Ya'ar, 14.v.2003, L. Friedman (1 female), 23.v.2003, A. Freidberg (1 male, 1 female); Netanya, pool, 4.iii.2005, A. Gasith (1 female); Ga'ash, 14.iv.1973, D. Furth (1 male, 3 females); Tel Aviv, Sharona [Sarona], ii.1904, J. Sahlberg (1 male, 1 female, ZSMU, ex collection of K. Daniel).

Distribution: East-Mediterranean (Greece, Cyprus, Turkey, Syria, Israel) [45,84]. Described from Israel. In Israel found in the winter vernal pools along the Central Coastal Plain.

Biology: Aquatic. Host plant unknown. The specimens from Berekhat Ya'ar (Figure 4a) in May 2003 were collected together with *Icaris sparganii*. The larvae of *Picia sinuatocollis* Faust, 1885 (recorded under its junior synonym *alfierii* Pic) in Egypt feed on rice roots in rice swamps [87], which might suggest the same or similar habits in *P. syriaca*. Adults active in February–May.

Notes: *Picia syriaca* was recorded by Sahlberg [93] as *Hydronomus sinuaticollis* Faust; he collected 19 specimens in the Sarona German Templer agricultural colony, which is today one of the neighborhoods in the center of the Tel Aviv megapolis. I studied two specimens deposited in ZSMU.

The first specimen of *P. syriaca* I had ever seen was brought to me alive from Berekhat Ya'ar by Prof. Avital Gasith in April 2002. I was fascinated by its swimming abilities—it swam easily and elegantly in a glass jar, where it was photographed by Amikam Shoob, the then photographer of the Department of Zoology, Tel Aviv University (Figure 4d,e). Planning to photograph it swimming the next day, I covered the jar with a lid with a metal mesh window. Next morning, I found that somebody had removed the lid and the weevil had disappeared, proving—alas—that it was able to fly.

Arthrostenus Schoenherr, 1826 [105]

Comprises nine semi-aquatic species in warm and arid parts of the Palaearctic region (East Mediterranean, Caucasus, Middle Asia) [45,91]. Associated with Poaceae, Sparganiaceae, and Typhaceae [91,106].

Arthrostenus fullo Boheman, 1836 [107]

(Figures 10f, 11d–g and 13c)

Material Examined: 22 exx.

ISRAEL: "69" (2 females); **Hula Valley:** Tel Dan, 27.v.1959 (1 female); Dan, 12.vi.1958 (1 male); Sede Nehemya, 23.v.1957, Y. Palmoni (1 male); Sede Nehemya [Hulioth], 18.v.1956 (1 female), 14.vi.1958 (2 males); Lahavot haBashan [L'havoth Habashan], 7.vi.1958, L. Fishelsohn (1 female), 28.v.1975, Z. Shoham (1 male); Hula, 13.vi.1954, L. Fishelsohn (1 male, 1 female), Y. Palmoni (1 female), 30.v.1956 (2 males, 2 females); 'Enot 'Enan [Malaha], 13.vi.1954, on *Phragmites* (2 females); Hulata, 10.v.19??, H. Bytinsky-Salz, on *Typha* (1 male, 1 female), 11.ii.1956 (1 female); **Northern Coastal Plain:** Shave Ziyyon, 24.viii.1971, Z. Shoham (1 male); **Central Coastal Plain:** ?Kefar Vitkin, ?summer 1945, H. Nemlokh (1 male).

Distribution: Recorded from South-East Europe (Greece, South of the European part of Russia, Ukraine), Caucasus (Armenia), Middle East (Syria) and Middle Asia (Turkmenistan) [45].

Recorded from Israel by Friedman [4]. In Israel was common in the Hula Valley (until the drainage of the Hula Lake in the 1950s) and in the swamps along the Mediterranean coast, but has not been re-collected since the 1970s. This either suggests a strong decrease in the population size or even an extinction of this species in Israel, mainly due to loss of the appropriate biotope.

Biology: Semi-aquatic. Develops on *Phragmites australis* (Cav.) Trin. ex Steud. (Poaceae) [104]. In Israel was collected on *Phragmites australis* (Figure 2c) and *Typha* sp. (probably the most common *T. domingensis* (Pers.) Steud.) (Typhaceaceae) (the last record is somewhat doubtful, probably based on an uncertain identification of the plant). Adults were collected all year round, but predominantly in June–August.

Notes: The male of *A. fullo* possesses a peculiar moustache comprising long woolly setae on its prorostrum, while the female lacks this character (Figure 11d,e).

The specimens collected by Ze'ev Shoham, an amateur moth researcher, were collected in light traps, and these are also the most recent collected specimens. Light trapping in the Hula Valley and the wetlands of the Northern Coastal Plain (e.g., 'En Afeq Nature Reserve, 'En Nimfit Nature Reserve (Figure 4c), 'Akko swamp) might therefore reveal the existence of the remaining population of *A. fullo*.

Tanysphyrini Gistel, 1848 [49]

Stenopelmus Schoenherr, 1835 [108]

A Nearctic genus comprising three aquatic species distributed in USA, Central and South America, one of them introduced occasionally into Europe and Japan and deliberately into South Africa, associated with the water ferns *Azolla* (Salviniaceae) [45,91]. In Israel, it is represented by a single species, probably introduced occasionally with an ornamental *Azolla*.

Stenopelmus rufinasus Gyllenhal, 1835 [95]

(Figures 10d,e and 13c)

Material Examined: 2 exx.

Israel: **Central Coastal Plain:** Berekhat Ya'ar Nature Reserve, 20.vii.2010, 32°24′39″ N 34°45′02″ E, L. Friedman, C. Drees, pitfall trap (1 female); **Central Negev:** Nahal Qarqash, opposite to the entrance to Midreshet Sede Boqer, 30°51′15″ N 34°46′08″ E, 13.iv.2010, L. Friedman, C. Drees, pitfall trap (1 female).

Distribution: Nearctic. It was occasionally introduced with ornamental *Azolla* in Western Europe, Japan and Israel [109,110] and deliberately introduced into southern Africa for biocontrol of *Azolla* [91,111]. In Israel collected with pitfall traps only in 2010. The escape of *Azolla* from an aquatic plants farm into Berekhat Ya'ar in 2010 was recorded by Dufour-Dror [112], and could be the source of a specimen collected there. The reason for the appearance of *S. rufinasus* in the Central Negev desert, at the bottom of the upper Nahal Qarqash, opposite the entrance to Midreshet Sede Boqer, an extremely dry place lacking any natural or artificial water body, is completely unclear. However, there is a nursery in Midreshet Sede Boqer, coincidentally named Mishtelet Qarqash (Karkash Nursery, https://www.karkash.com/), which could be a sourse of *Azolla*. It is unclear whether the weevil has become established in Israel or has disappeared.

Biology: Aquatic. Monophagous on *Azolla* spp. (e.g., *Azolla filiculoides*, *A. caroliniana*) (Salviniaceae) [70,91].

Molytinae Schoenherr, 1823 [43]

Amalactini Lacordaire, 1863 [113]

Aorus Schoenherr, 1835 [108]

An Afro-Oriental genus comprising eight species [30,37,114]. The larvae of *Aorus* were recorded burrowing in the stems of *Cyperus* and *Scirpus* (Cyperaceae) and *Pennisetum* (Poaceae), and adults feeding on grasses [30]. Marshall [114] reported the mass appearance of adults of *A. ferrugineus* Boheman on ears of rice in Vietnam. In Israel, *Aorus* is represented by an African species, and is the northernmost point of its distribution.

Aorus anthracinus Brancsik, 1898 [115]

(Figures 10g, 11h,i and 13c)

Material Examined: 19 exx.

ISRAEL: **Hula Valley:** Hula [Hulah], 5.vii.1934, F. S. Bodenheimer, in Papyrus (1 female), [Huleh], 12.iii.1946, H. Bytinski-Salz (1 male, 2 females), 10.v.19??, H. Bytinski-Salz, in *Papyrus* (4 males, 5 females), viii.19??, H. Bytinski-Salz, in *Papyrus* (4 males, 5 females); ?**Central Coastal Plain**: Kabara swamp? (1 ex., Berkovitch Collection, Ma'agan Mikha'el).

Distribution: Afrotropical (Senegal, Uganda, Mozambique, Zambia) [114]. In the Palaearctic region recorded only from Israel [37], although not collected since the 1950s, and therefore considered extinct [4]. All specimens in the SMNHTAU come from the warm and humid swamps of the Hula Valley, the northernmost tip of the Rift Valley. I found an unlabeled specimen of *A. anthracinus* in the private collection of the late Dov Berkovitch in Kibbutz Ma'agan Mikha'el. I was able to talk to Mr Berkovitch a couple of years before he passed, but he was not able to recall collecting this specimen while nevertheless insisting that his collection was mainly from the surroundings of Ma'agan Mikha'el, including the Kabara swamp, recently drained. Therefore, I assume that this specimen might have been collected in the Kabara swamp, indicating its occurrence also in the coastal swamps.

Biology: Most of the specimens were collected on *Cyperus papyrus* L. (Cyperaceae) (Figure 3d), which is most likely its host. This corresponds well with the knowledge on the other species of *Aorus* [114]. The 3rd tarsal segment of *A. anthracinus* has wide round lobes, pilose beneath, suggesting it climbs on plants better than it swims, the body is completely glabrous, devoid of any scales or therefore I assume it is semi-aquatic.

Conoderinae Schoenherr, 1833 [116]

This subfamily is distributed worldwide except the polar regions, comprising 7571 species in 940 genera [117].

Ceutorhynchitae Gistel, 1848 [49]

This supertribe is distributed worldwide except for southern part of South America and Antarctica, comprising 1371 species in 175 genera [117]. The study of the Israeli Ceutorhynchitae is still incomplete, but I estimate that there are approximately 100 species. Israeli Ceutorhynchitae are mainly monophagous or narrow-oligophagous, predominantly on species of the plant families Amaranthaceae, Anacardiaceae, Boraginaceae, Brassicaceae, Caryophyllaceae, Chenopodiaceae, Ephedraceae, Fabaceae, Fagaceae, Lamiaceae, Liliaceae, Papaveraceae, Polygonaceae (listed in alphabetical order). Ceutorhynchitae comprise numerous aquatic and semi-aquatic species and genera [117–120]; however, in Israel, only two species of *Rhinoncus* are found in aquatic habitats.

Phytobiini Gistel, 1848 [49]

This is the largest tribe among Ceutorhynchitae and the most widely distributed, lacking in tropical America [117]. Most of its representatives are aquatic or semi-aquatic [7,121].

Rhinoncus Schoenherr, 1825 [82]

Comprises 36 species in Palaearctic, Nearctic, Afrotropical, Oriental and Australasian regions. Those whose biology is known are associated with Polygonaceae (*Persicaria*, *Polygonum*, *Rheum*, and *Rumex*) [118].

Rhinoncus pericarpius (Linnaeus, 1758) [122] (Figures 12a,c and 13d)

Material Examined: 11 exx.

ISRAEL: **Golan Heights:** Panyas, Upper [Baniass Up.], 5.iv.1978, D. Furth (1 female); Yehudiyya Nature Reserve [Qusbiye], 21.ii.1974, D. Furth (1 female); **Carmel Ridge:** 'En haShofet, 23.iii.1973, D. Furth (1 female); **Central Coastal Plain:** Berekhat Ya'ar, 14.v.2003, L. Friedman (1 female); Berekhat Ya'ar, South, 23.v.2003, L. Friedman (1 female); Berekhat Ya'ar, 32°24′39′′ N 34°45′02′′ E 16.iii.2010, L. Friedman, C. Drees, pitfall (3 males, 3 females).

Distribution: Holarctic (excluding North Africa) [45,118]. First record for Israel and for the Middle East. In Israel collected rarely and locally on the banks of mountain streams (Panyas, Yehudiyya, 'En haShofet) and Berekhat Ya'ar vernal pond. The localities have little in common, making it unclear which is its preferred microhabitat.

Biology: Presumably semi-aquatic. On *Rumex* spp., *Polygonum* spp., *Rheum rhabarbarum* L. (Polygonaceae) [118]. Host in Israel unknown. Adults active in February–April.

Note: *R. pericarpius* occurs in Israel at the southernmost border of its distribution. Only five specimens were collected by sweeping during the last 45 years, while six specimens were collected in pitfall traps during one collecting event. I assume that *R. pericarpius* is not as rare as it might appear to be, but is either nocturnal (avoiding high temperatures during the daytime) or lives on low, creeping plants along the water edge, which are difficult to sweep (or both).

Rhinoncus perpendicularis (Reich, 1797) [123] (Figures 12b,d,e and 13d)

Material Examined: 93 exx.

ISRAEL: **Hula Valley:** Dan, Bet Ussishkin, 33°14′ N 35°39′ E, 183 m, 1.v.2016 (14 males, 6 females), 7.v.2017 (2 males); Gonen, 18.vi.1973, D. Furth (3 males); 'Enot 'Enan, 33°5′ N 35°35′ E, 4.x.2001, L. Friedman (1 female); 'Enot 'Enan, 1.v.2006, L. Friedman (1 male, 3 females), 13.vii.2011, L. Friedman (2 males); Hula Nature Reserve, 13.vii.2011, D. Furth (1 male); Park haYarden, 17.v.2009, L. Friedman (3 males, 2 females); Park haYarden, 32°55′ N 35°38′ E, -200m, 19.vii.2009, L. Friedman (8 males, 1 female); Park haYarden, 32°54.5′ N 35°37.5′ E, −210 m, 19.vii.2011, L. Friedman (1 female); Park haYarden, −200 m, 18:00–21:00, 17.viii.2014, L. Friedman, on *Persicaria decipiens* (=*salicifolia*) (22 males, 8 females), 24.viii.2016, L. Friedman, on *Persicaria decipiens* (6 males, 4 females); **Sea of Galilee Area:** Gesher Arik, N. Kinneret, 19.vi.2012, L. Friedman (1 male); Bet Zayda Nature Reserve, Nahal Yehudiyya spill, 13.ix.2011, Z. Yanai (1 female); Ma'agan Island, South Kinneret, 23.xi.2009 (1 female); **Central Coastal Plain:** Meqorot haYarqon, Nufarim Pool, 1.xii.2005, T. Eshkoli (1 male); **Southern Coastal Plain:** Ashdod Port, 5620, 3.xi.2016, PPIS, on wood from Ukraine, under bark (1 male).

Distribution: Palaearctic, introduced into North America [4,31]. First record for Israel. In Israel it is very common in the Hula Valley, occurs locally also around the Sea of Galilee and along the Coastal Plain, on the banks of any constant water source (streams and ponds), but not in vernal ponds.

Biology: Semi-aquatic. On *Persicaria* spp., *Polygonum* spp., occasionally on *Rumex* spp. [118,120]. In Israel on *Persicaria decipiens* (R.Br.) K.L. Wilson (Figure 3e), larvae develop in rootstalk knots. The host plant is found in the shallow waters along the shore. Adults active all year round, but mainly in May-September, more active in the evening and early night, when the temperature drops, and then can be easily collected on the host plant. Semi-aquatic. Adults are able to swim. The abdominal sternites, particularly the last abdominal segment, bear longer thin erect hairs (Figure 12e), characteristic of different aquatic weevils, which probably take part in air-breathing of the weevil in the water. Adults probably active all year round.

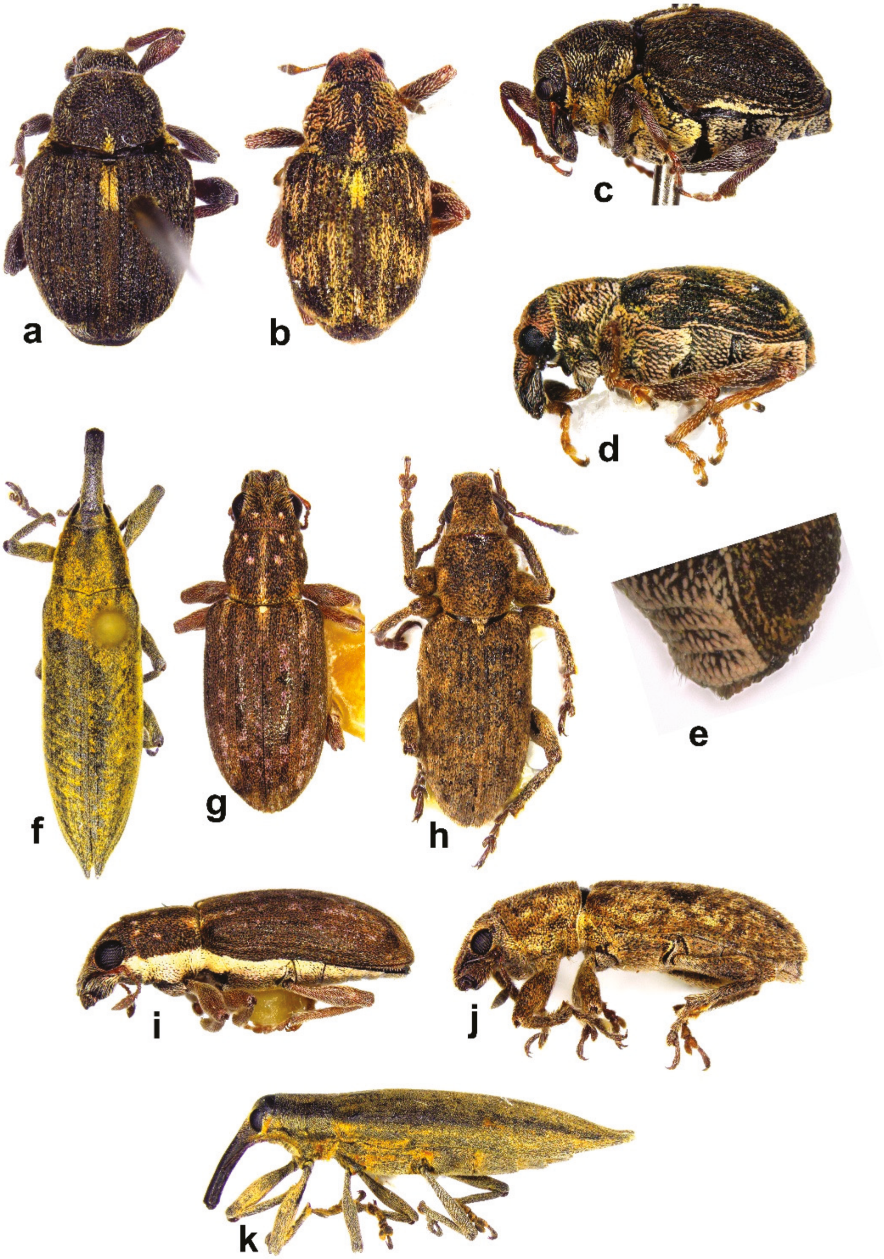

Figure 12. Habitus (**a**) Rhinoncus pericarpius, male, dorsal view; (**b**) R. perpendicularis, male, dorsal view; (**c**) *R. pericarpius*, male, lateral view; (**d**) *R. perpendicularis*, male, lateral view; (**e**) *R. perpendicularis*, male, abdominal sternites, lateral view; (**f**) *Lixus iridis*, male, dorsal view; (**g**) *Sitona lividipes*, male, dorsal view; (**h**) *Tanymecus musculus*, male, dorsal view); (**i**) *S. lividipes*, male, lateral view; (**j**) *T. musculus*, male, lateral view); (**k**) *L. iridis*, female, lateral view.

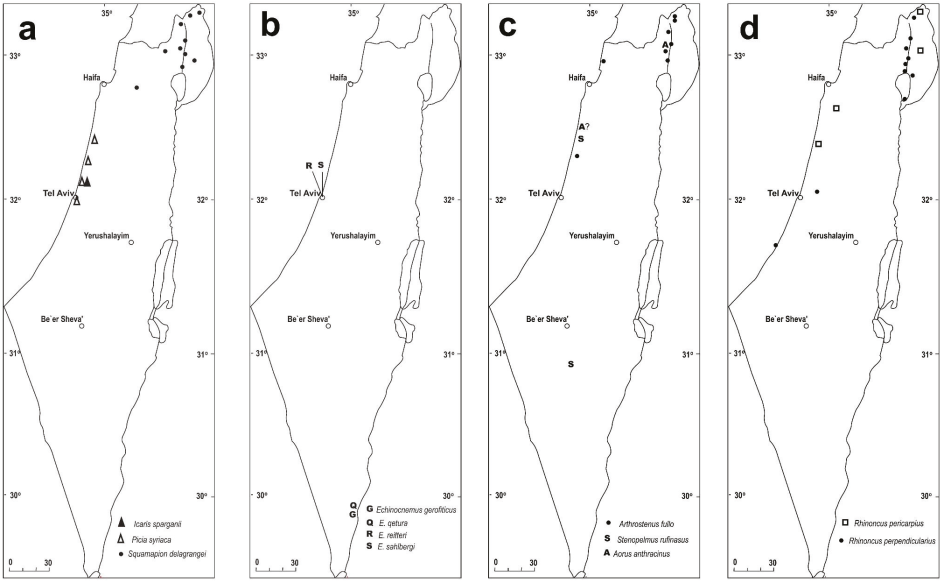

Figure 13. Distributional maps of (**a**) *Icaris sparganii*, *Picia syriaca*, *Squamapion delagrangei*; (**b**) *Echinocnemus reitteri*, *E. sahlbergi*, *E. gerofiticus*, *E. qetura*; (**c**) *Arthrostenus fullo*; *Stenopelmus rufinasus*, *Aorus anthracinus*; (**d**) *Rhinoncus pericarpius*, *R. perpendicularis*.

Curculioninae Latreille, 1802 [60]

Mecinini Gistel, 1848 [49]

Comprises six genera with ca. 250 species in the Old World, mainly associated with Scrophulariaceae, Plantaginaceae, and Campanulaceae [62]. All six genera are represented in Israel [45].

Gymnetron, Schoenherr, 1825 [82]

This genus comprises ca. 100 species in the world and 33 in the Palaearctic region with four species recorded for Israel [45,62]. In Israel associated with *Scrophularia*, *Verbascum* and *Veronica* (Scrophulariaceae).

Gymnetron niloticum Kirsch, 1881 [124] (Figure 2d,e, Figure 14a,b,e and Figure 15b)

Material Examined: 39 exx.

ISRAEL: **Golan Heights:** Ma'agar Bental, 33°09″ N 35°47″ E, 955 m, 22.v.2014, L. Friedman, on *Veronica anagallis-aquatica* (1 female); **Hula Valley:** Park haYarden, 32°55′ N 35°38′ E, 2.iii.2010, A. Freidberg (1 female); **Carmel Ridge:** 'En haShofet, 23.iii.1973, D. Furth (1 female); **Samaria:** Barqay [Barkai], 9.v.1978, D. Furth (2 males); Nahal Qana Nature Reserve, 26.ii.2014, L. Friedman, on *Veronica anagallis-aquatica* (6 males, 4 females); Nahal Qana Nature Reserve, 'En Tanur, Turtles' Pond, iv.2018, L. Friedman, on *Veronica anagallis-aquatica* (12 males, 6 females); **Central Coastal Plain:** Zikhron Ya'aqov, 1.iv.1997, R. Hoffman (1 female); Sedot Yam, 4.v.1998, M. Fine (1 male); Lehavot Haviva, 14.vi.1977, J. Halperin, on *Prunus passardi* (1 male, 3 females).

Distribution: South-East Europe, North Africa, Caucasus, Middle East, Middle Asia [45,125]. In Israel single specimens were occasionally collected on the Golan Heights, in the Hula Valley, on and at the foot of the Carmel Ridge and in the Central Coastal Plain. I recently found a large dense population of

G. niloticum in Nahal Qana (Qana Stream) in the Samarian Hills, on its host plant along the water edge (Figure 2d,e).

Biology: Riparian. On *Veronica* spp. (Scrophulariaceae) [125]. In Israel monophagous on *Veronica anagallis-aquatica* L. (Figure 2e). Adults active in February–June.

Gymnetron tibiellum Desbrochers des Loges, 1900 [126]

(Figures 14c,d,f and 15b)

Material Examined: 164 exx.

ISRAEL: **Golan Heights:** Panyas, 33°14′55′′ N 35°41′40′′ E, 20.vii.2009, L. Friedman (5 males, 7 females); Ma'agar Bental, 12.v.2014, L. Friedman (1 male, 2 females); **Upper Galilee:** Ga'ton, 6.ii.2000, L. Friedman (1 male); **Hula Valley:** Dan, 22.v.2002, L. Friedman, on *Veronica anagallis-aquatica* (30 exx.), 27.v.2003, L. Friedman, on *Veronica anagallis-aquatica* (14 males, 21 females), 25.v.2005, L. Friedman (11 males, 19 females), 2.vi.2008, L. Friedman (1 male, 2 females + unsexed 24 exx.); Park haYarden, 32°55′ N 35°38′ E, −200 m, 8.v.1997, L. Friedman (8 males, 8 females), A. Freidberg (1 male), V. Chikatunov (1 male, 2 females), 17.v.2009, L. Friedman (2 females), 19.vii.2009, L. Friedman (1 female); **Samaria:** Har Berakha, 'Amassa Springs, 4.iv.2013, L. Friedman (1 female); **Carmel Ridge:** Nahal Tut, Hagit Forest [Tut Hagit], Y. Hershkovitz (1 male); **Foothills of Judea:** Park Canada, 29.v.1987, Y. Zvik (1 male).

Distribution: South-east Europe, Caucasus, south-west Asia [45,125]. In Israel very common in the low humid Hula Valley and relatively humid and high northern part of the Golan Heights, occasionally occurs in the highlands of the Upper Galilee, Carmel Ridge, Samarian and Judean Hills. Occurs on banks of streams and ponds.

Biology: Riparian. Monophagous on *Veronica anagallis-aquatica* L. (Scrophulariaceae) (Figure 2e), first record of the host plant. Adults active in April-July, but mainly in May.

Tychiini C. G. Thomson, 1859 [61]

This tribe is distributed worldwide except Australasia, associated with Aizoaceae, Caryophyllaceae, Fabaceae, Moraceae, Oleaceae, Plumbaginaceae [62].

Tychius Germar, 1817 [65]

Comprises 227 species in the Palaearctic region, with 24 species recorded for Israel, all associated with Fabaceae [45,62].

Tychius bicolor C. N. F. Brisout de Barneville, 1863 [127]

(Figures 14g,i–k and 15c)

Material Examined: 46 exx.

ISRAEL: **Hula Valley:** Almagor, Park haYarden, 32°55′ N 35°36′ E, vii.2010, W. Kuslitzky (1 male); Park haYarden, 8.v.1997, L. Friedman (7 males, 5 females), A. Freidberg (1 female), V. Chikatunov (1 female); Park haYarden, 32°54.5′ N 35°38′ E, −210 m, 14.iv.2011, E. Morgulis (2 males); Park haYarden, −200 m, 18:00–21:00, 17.viii.2014, L. Friedman, on *Melilotus albus* (13 males, 11 females), 24.viii.2016, L. Friedman, on *Melilotus albus* (1 male); **Sea of Galilee Area:** Hof Rotem-Shezaf, 3kmS 'En Gev, −200 m, 32°46′ N 35°38.3′ E, A. Freidberg (1 male, 1 female); **Northern Coastal Plain:** 'En Nimfit Nature Reserve, Migdalit haNehalim Pond, 15.iii.2018, L. Friedman, on *Melilotus* (1 female); **Southern Coastal Plain:** Palmahim, vi.1961, Katznelson (1 male, 1 female).

Distribution: Mediterranean [45,128]. In Israel occurs mainly in the Hula Valley, but also around the Sea of Galilee and along the Coastal Plain, at least in the past reaching its southern part. On the banks of Nehar haYarden (=Jordan River) and its tributaries (Figures 1f and 2c) and in the coastal swamps (Figure 4c). *T. bicolor* occurs in Israel within its normal range of distribution.

Biology: Riparian. On *Melilotus officinalis* (L.) Pall., *M. segetalis* (Brot.) Ser. (=*leiosperma* Pomel.), Astragalus *monspessulanus* L. (Fabaceae) [128]. In Israel on *Melilotus albus* Medik. ex Desr. Adults active in March–August.

Tychius meliloti Stephens, 1831 [129]

(Figures 14h,l–n and 15c)

Material Examined: 107 exx.

ISRAEL: **Hula Valley:** Nahal Senir Nature Reserve, 21.viii.2012, L. Friedman (1 male); Park haYarden, 8.v.1997, L. Friedman (13 males, 1 female), A. Freidberg (1 male); Park haYarden, −200 m, 18:00–21:00, 17.viii.2014, L. Friedman, on *Melilotus albus* (34 males, 43 females); 24.viii.2016, L. Friedman, on *Melilotus albus* (6 males, 1 female); **Sea of Galilee Area:** Gesher Arik, HaYarden, 17.viii.2014, L. Friedman (3 males, 3 females); 'En Gev, 10 kmN, 8.v.1997, L. Friedman (1 female).

Distribution: Palaearctic, introduced in Afrotropical and Nearctic regions [45]. Was recorded from Israel by Caldara [97,128], but omitted by Alonso-Zarazaga et al. [45]. Here it is returned to the weevil list of Israel. In Israel occurs only in the Hula Valley (common) and around the Sea of Galilee (rare), being at its southernmost border of distribution. Occurs on its host plant on the banks of Nahar haYarden (= Jordan River) and its tributaries (Figures 1f and 2c).

Biology: Riparian. *Melilotus altissimus* Thuil., *M. officinalis* (L.) Pall., *M. albus* Medik. (Fabaceae) [128]. In Israel on *Melilotus albus* Medik. ex Desr. Adults active in May-August.

Entiminae Schoenherr, 1823 [43]

Entiminae comprises about 1370 genera with above 12,000 species, distributed worldwide, including sub-Antarctic regions [130]. Larvae usually develop in soil, on the plant roots, adults feed on green parts of plants. Entiminae are mostly polyphagous or wide-oligophagous, associated with dicotyledons, monocotyledons, gymnosperms and even ferns, but an enormous number of species are associated with Fabaceae [130].

Sitonini Gistel, 1848 [49]

This tribe is distributed in Holarctic realm, South Africa, Madagascar and south-east Asia, associated with Fabaceae and Mimosaceae [37,131]. Twenty-three species in four genera are recorded for Israel [132].

Sitona Germar, 1817 [65]

Sixteen species are recorded from Israel in this genus, all associated with wild or cultivated Fabaceae [132].

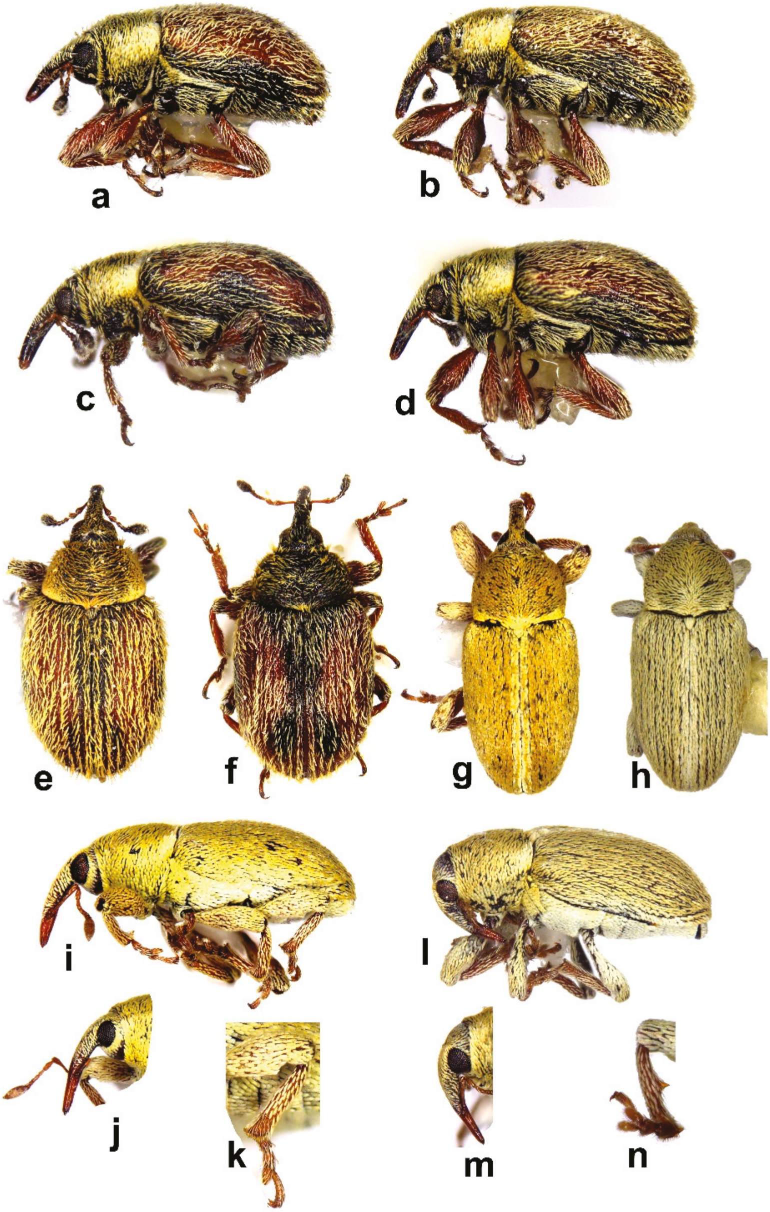

Figure 14. Habitus (**a**) *Gymnetron niloticum*, male, lateral view; (**b**) *G. niloticum*, female, lateral view; (**c**) *Gymnetron tibiellum*, male, lateral view; (**d**) *G. tibiellum*, female, lateral view; (**e**) *G. niloticum*, male, dorsal view; (**f**) *G. tibiellum*, male, dorsal view; (**g**) *Tychius bicolor*, male, dorsal view; (**h**) *T. meliloti*, male, dorsal view; (**i**) *T. bicolor*, male, lateral view; (**j**) *T. bicolor*, female, lateral view; (**k**) *T. bicolor*, hind leg, male; (**l**) *T. meliloti*, male, lateral view; (**m**) *T. meliloti*, female, lateral view; (**n**) *T. meliloti*, fore tibia, male (not on the same scale).

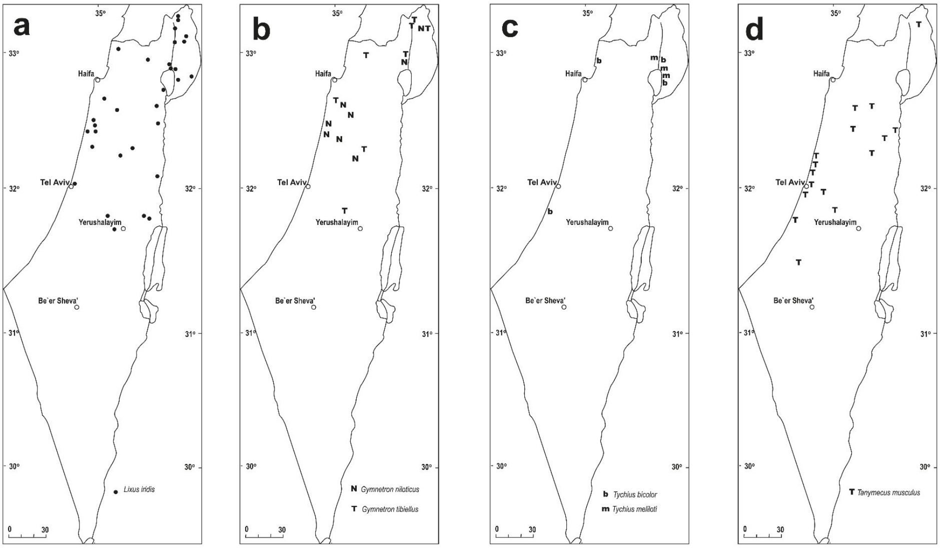

Figure 15. Distributional maps of (**a**) *Lixus iridis*; (**b**) *Gymnetron niloticum*, *G. tibiellum*; (**c**) *Tychius bicolor*, *T. meliloti*; (**d**) *Tanymecus musculus*.

Sitona lividipes Fåhraeus, 1840 [133]

(Figure 12g,i)

Material Examined: 108 exx.

ISRAEL: **Hermon:** Har Hermon, 1600 m, 20.v.1997, L. Friedman (1 female), 12.vi.2003, A. Freidberg (1 male); Nabi Hazuri, 33°15′′ N 35°44′′ E, 18.x.2009, L. Friedman (1 male); **Golan Heights:** Panyas [Baniass Up.], 8.iv.1978, D. Furth (1 female); Panyas [Banias], 25.v.1982, J. Halperin, on *Salix* (3 exx.); Panyas, 16.v.2003, V. Kravchenko, light trap (1 female); Panyas Hydrometric Station, 4.iii.2001, L. Friedman (2 males; 1 male); Berekhat Ram [Birket Ram], 27.iv.1978, D. Furth (1 female); El-Rom, 15.vi.2002, V. Kravchenko, light trap (1 female); Merom Golan, Bental Reservoir, 33°08′′ N 35°47′′ E, 30.iv.2006, L. Friedman (1 male), 7.v.2006, L. Friedman (1 female); Ma'agar Bental, 33°08′′ N 35°47′′ E, 7.v.2007, L. Friedman (1 male), 1.vi.2008, L. Friedman (1 female); Qazrin, 4.v.1999, L. Friedman (2 males), 21.v.2002, L. Friedman (1 female); Yehudiya Forest Nature Reserve [Qusbiye], 17.xi.1973, D. Furth (1 female), 28.iv.1974, D. Furth (1 male), 4.v.1979, D. Furth (1 male); **Hula Valley:** Tel Dan, 20.vii.1983, Y. Zvik (1 male); Nahal Senir, 24.v.1999, L. Friedman (1 male; 2 females); Sede Nehemya [Huliot], 20.v.1968 (3 males, 3 females); Amir, 5.iv.1978, D. Furth (1 male); Shamir, 5.vi.1984, J. Halperin, on *Fraxinus syriacus* (2 females); Hula, 5.vi.1974, D. Furth (1 male, 2 females); Gadot, 25 km N Tiberias, 8.vi.1971, S. Bet-Aharon (1 male); Mahanayim, 17.xi.1974, D. Furth (1 male); **Upper Galilee:** Nahal Keziv, 1.i.1999, M. Finkel (1 female); 'En Ya'aqov, 12.vi.2006, I. Shtirberg (1 female); Har Meron, 1100, 32°59′′ N 35°25′′ E, 22.xi.2006, L. Friedman (1 male; 2 females), A. Freidberg (1 female); Har Meron [Mt. Meron], 12.vii.2002, V. Kravchenko, light trap (1 male); Har Meron, 2006, H. Tsegai (1 male); Nahal 'Ammud [N. Amud], 30.iv.1978, D. Furth (2 males); **Lower Galilee:** Nazeret [Nazareth], 30.ix.1982, Q. Argaman (1 male); **Carmel Ridge:** Nahal Oren, 17.xi.1997, V. Chikatunov, T. Pavliček (1 male), 15.xii.1997, V. Chikatunov, T. Pavliček (1 male); Nahal Tut [N. Tut], 4.v.1978, D. Furth (1 female); **Jordan Valley:** Biq'at Bet Zayda [Btecha], 18.x.1971, A. Goldstein (1 female); Park haYarden, 17.v.2009, L. Friedman (2 males, 1 female); Kursi, 15.xii.1972, D. Furth (3 males); Ashdot Ya'aqov [Ashdot Yaacov], 27.vii.1972, A. Goldstein (1 male); **Yizre'el Valley:** 'En Harod [Ein Charod], 9.x.1948, H. Bytinski-Salz

(1 male, 1 female); Tel Yosef, 9.xii.1939, on *Trifolium* (1 male); **Central Coastal Plain:** Ma'agan Mikha'el, 4.v.1998, A. Freidberg (1 male, 2 females); Binyamina, 25.i.1997, R. Hoffman (1 male); Hadera, 16.xi.1973, D. Furth (2 males), 28.iv.1979, D. Furth (1 male); Berekhat Ya'ar, 14.v.2003, L. Friedman (2 males, 2 females), 28.iv.2004, L. Friedman (1 female), A. Freidberg (1 male); Ramat haSharon, 32°08″ N 34°50″ E, 5.v.2007, D. Gerling, Malaise trap (1 male); Rosh ha'Ayin, 24.iii.1973, D. Furth (1 female); **Southern Coastal Plain:** Bet Dagan [Bet Dagon], 2.ii.1957, on *Trifolium* (1 male; 1 female), 21.xi.1957, on *Trifolium* (1 female); Bet Dagan, 26.xii.1956, on *Trifolium* (1 female; 1 male), 8.ii.1957, on *Trifolium* (1 female), 21.ii.1957, on *Vicia* (1 female); Yavne, 27.iv.1986, Q. Argaman (1 male, 1 female); Gan Shelomo [Kvuzat Shiler], 2.v.1958, E. Rivnay, on *Medicago* (2 female); Giv'at Brenner, xii.1959, Perez, Div. Plant. Prot. Dept. Agr. Israel, on *Trifolium* (12 exx.), 7.i.1951, H. Bytinski-Salz, on alfalfa (4 exx.); Gedera, 26.xi.1973, D. Furth (1 male, 1 female); Re'em Junction [Masmia], 16.i.1957, on *Trifolium* (2 male), 18.v.1957, on *Trifolium* (1 male; 1 female).

Distribution: Mediterranean [45]. In Israel occurs throughout the Mediterranean part of the country, very common.

Biology: This weevil also occurs in areas far from water sources, both temporary and permanent, although it is mostly common in humid ravines, on the banks of brooks, streams, and ponds, and comprises a considerable component in any riparian biotope. On *Medicago* spp. and *Trifolium* spp. (Fabaceae) [132]. Adults found all year round.

Tanymecini Lacordaire, 1863 [113]

Tanymecini are distributed worldwide, particularly in Neotropical region [37]. In Israel represented by three species (Friedman, unpublished data).

Tanymecus Germar, 1817 [65]

The genus is distributed in Holarctic, Neotropical, and Afrotropical regions [37], in Palaearctic region comprises 34 species [45]. Polyphagous, larvae live in soil on roots of different plants [120].

Tanymecus* (*Geomecus*) *musculus Fåhraeus, 1840 [133]

(Figures 12h,j and 15d)

Material examined: 166 exx.

ISRAEL: **Golan Heights:** Merom Golan, Ma'agar Bental = Bental Reservoir, 33°08″ N 35°47″ E, 12.vi.2000, V. Chikatunov (6 exx.), 1.vi.2004, I. Zonstein (4 exx.), 25.v.2005, L. Friedman (35 exx.), 30.iv.2006, L. Friedman (2 exx.), 9.v.2006, L. Friedman (4 exx.), M. Meir (1 ex.), 7.v.2007, M. Orlova (1 ex.), K. Levi & T. Huges Games (1 ex.), L. Younger & E. Kauffmann (1 ex.), A Hahn & O. Yelinek (1 ex.), 1.vi.2008, C. Bilu (1 ex.), S. Cohen (1 ex.), V. Liberman (1 ex.), W. Mansour (1 ex.), O. Pearlstein (1 ex.), 11.v.2010, L. Friedman (5 exx.), 11.v.2011, G. Dekel & I. Gran (1 exx.), 14.v.2012, L. Friedman (11 ex.), on *Eleocharis palustris* (2 exx.), 7.v.2013, L. Friedman (12 exx.), A. Bespalko (1 ex.), R. Folkman (1 ex.), D. Tarhov (1 ex.), 12.v.2014, L. Friedman (8 exx.), 22.v.2014, L. Friedman (1 ex.), 11.v.2015, L. Friedman, on *Eleocharis palustris* (12 exx.); **Jordan Valley:** Ma'oz Hayyim, 4.vi.1971, Z. Shoham (1 ex.); **Yizre'el Valley:** 'Afula [Afoolah], 28.iii.1942, Bylinski-Salz (1 ex.); Newé Ya'ar, spring, on fields of legums, Y. Palmoni (3 exx.); **Samaria:** Ma'ale Gilboa', 8.vii.1982, Q. Argaman (1 ex.); Me 'Ammi, 2.iv.1985, on cotton, I. Susman (1 ex.); Nahal Tirza [W. Faria], 21.iii.1978, D. Furth (1 ex.); **Central Coastal Plain:** Netanya, 9.iii.1978, D. Furth (1 ex.); Ga'ash, 24.iv.1974, D. Furth, (1 ex.), 10.iii.1976, F. Kaplan (1 ex.), 3.iv.2011, D. Kestin (1 ex.); Ga'ash Pool Nature Reserve, 7.v.2015, L. Friedman, on *Eleocharis palustris* (12 exx.); Herzliyya, swamp, 32°10.3″ N 34°49.4″ E, 27.vi.2008, A. Freidberg (3 exx.); Tel Aviv, 10.v.2013, A. Shlagman (1 ex.); **Southern Coastal Plain:** Miqwe Yisrael, 20.iii.1945, Bylinski-Salz (1 ex.); Holot Nizzanim Nature Reserve, Roberts' Pool, 10.iv.2018, L. Friedman & N. Dorchin, on *Eleocharis palustris* (30 exx.); **Judean Foothills:** Shoham, 31.iii.2006, W. Kuslitzky (1 ex.); Park Canada [Deir-Ayoub], 20.iii.1939, wheat plot, J. H. Brair (2 exx.); **Northern Negev:** Bitronot Ruhama, Nahal Hazav, 31°32′′ N 34°42′′ E, 5.iv.2005, L. Friedman (1 ex.).

Distribution: Syria, Israel, Iraq, Saudi Arabia, Egypt [45,64]. In Israel occurs throughout the country, except the desert areas, in swamps and on the banks of springs and vernal ponds, corresponding to the distribution of the host plant (Figure 4f,h).

Biology: Semi-aquatic or riparian. Feeds exceptionally on *Eleocharis palustris* (L.) Roem. & Schult. (Cyperaceae) (Figure 4h). There is a clear correspondence between the occurence of the plant and the adult weevils, although it is unclear whether the larvae also prefer *E. palustris*. First host record. Adults active in March-July, but they are commonly found on the host plant only in March-April, later they occur under stones or in soil, at least during the daytime, when numerous pairs are in copula.

Lixinae Schoenherr, 1823 [43]

This subfamily comprises approximately 1500 species in 90 genera, cosmopolitan, with major diversity in the Palaearctic and Afrotropical regions [134]. Around 100 species in Israel, mostly with no special hygrohillous affinities.

Lixini Schoenherr, 1823 [43]

Comprises 13 genera with 236 species in the Palaearctic region [45].

Lixus Fabricius, 1801 [135]

The genus comprises 175 species in the Palaearctic region [45]. Thirteen species are recorded for Israel [45], although there are at least ten additional species (Friedman, unpublished data). Mostly associated with Asteraceae, Amaranthaceae, Apiaceae, Brassicaceae, and Chenopodiaceae. Most of these occur in Mediterranean, steppe or desert habitats and are not associated with water.

Lixus* (*Eulixus*) *iridis Olivier, 1807 [136]

(Figures 12f,k and 15a)

Material Examined: 64 exx.

Golan Heights: Zomet Shiryon, 5 kmW, Rt. 91, 33°02.9′ N 35°42.3′ E, 530 m, 22.v.2011, A. Freidberg (1 male); Nahal Qazrin, 4.v.1999, Y. Zamri (1 female), 25.v.2005, M. Cohen, O. Cohen, P. Yaniv (1 male); Susita, 15.iv.1982, Y. Nussbaum (1 male); Khispin, 28.x.1983, Y. Nussbaum (1 female); **Hula Valley:** Tel Dan [Tel el Kadi], 18.v.19??, H. Bytinski-Salz (1 female); Nahal Dan, 21.vii.1983, Y. Zvik (1 male); Nahal Hazbani, 23.v.1988, Y. Zvik (2 females); ‘Amir, 8.iii.1946, H. Bytinski-Salz (1 male, 1 female); Hula, 23.vi.1952, J. Wahrman (1 female); Hula [Huleh], 1.v.1953, Kornhaus (1 female); Park haYarden, 32°54.5′ N 35°37.5′ E, −210 m, 14.iv.2011, E. Morgulis (1 female), 24.viii.2014, 18:00–21:00, L. Friedman (2 males, 4 females); **Sea of Galilee Area:** Gesher Arik, HaYarden, 17.viii.2014, L. Friedman (1 male); Nahal Samakh, 1.vii.1979 (1 female); Deganya A, 25.iii.1940, Y. Palmoni (1 female); **Upper Galilee:** Nahal Keziv, 12.v.1997, R. Hoffman (1 male, 1 female); Nahal ‘Ammud, 3.iii.1984, E. Shney-Dor (1 female); Mahanayyim, 6.x.1974, F. Kaplan (1 female); **Lower Galilee:** Nahal Keini, Megido, 30.iv.1993, Y. Zvik (2 males, 2 females); Nahal Tavor, 26.iii.2001, L. Friedman (1 male, 1 female); **Carmel Ridge:** ‘En haShofet, 25.vi.2003, Y. Hershkovitz (1 male), A. Mozer (1 male); ‘En haShofet, Irish Bridge, 16.vi.2004, A. Gasith, Y. Hershkovitz (1 male, 2 females), 16.vi.2004, A. Gasith (1 female); **Central Coastal Plain:** Binyamina [Benjamina], 16.iii.19??, H. Bytinski-Salz (1 male); Binyamina [Benjaminah], 6.iii.1924, on *Asphodelus* (1 male); Ahu Binyamina, 3.viii.1996, R. Hoffman (1 male); Nahal Barqan, 1.iii.1997, R. Hoffman (1 female); Hadera, 10.v.1939, Y. Palmoni (1 male); Berekhat Ramadan [Birquat Ramadan], 13.iii.1940, H. Bytinski-Salz (2 females); Tel Aviv, 12.viii.2003, N. Perlmutter (1 male); **Samaria:** Upper Nahal Tirza [Up. W. Faria], 28.iv.1976, M. Kaplan (1 female); Nahal Tirza [W. Faria], ii-iii.1973, D. Furth (1 male, 3 females), 2.iii.1973, D. Furth (1 male); Nahal Qana, ‘Ein-el-Juze, 23.x.2016, L. Friedman, on *Mentha longifolia* (2 females); **Judean Hills:** ‘En Hemed [Aqua Bella], 29.iii.1954, J. Wahrman (1 male), 24.iv.1961, J. Wahrman (1 female), 26.v.1961, Ritte (1 male); Yerushalayim [Jerusalem], 20.iv.1957, Ginsburg (1 male); **Jordan Valley:** Sede Eliyyahu, 6.iv.1961, D. Gerling, on plants (1 male); 'Enot Peza'el, −70 m, 23.v.2016, L. Friedman (1 male); **Dead Sea Area:** 'Ein Duyuq, 28.v.1971 (1 ex.), 7.v.1972 (1 ex.), 8.vi.1976 (1 female); Yeriho [Jericho], 18.iv.1982, Q. Argaman (1 female).

Distribution: West Palaearctic (Europe, North Africa, Caucasus, Middle East, Middle Asia) [45]. First record for Israel. In Israel found in humid biotopes: on the banks of streams, swamps, and ponds, in deep shady ravines. All specimens that I collected personally, or those whose collectors I was able to interview or to trace their collecting sites, which comprise the majority of the examined specimens, were collected on water plants above the water or as close as possible to the water.

Biology: Riparian. On *Anthriscus silvestris* L., *Peucedanum palustre* (L.) Moench, *Angelica*, *Berula*, *Chaerophyllum*, *Cicuta*, *Conium*, *Heracleum*, *Levisticum*, *Oenanthe*, *Selinum*, *Sium*, *Pastinaca* (Apiaceae) [137]. Larvae develop in stem [138,139]. In Israel the host remains unknown despite the relative commonness of the species. Adults are active in April–August.

4. Discussion

Israel is, on the one hand, a small country situated on the southern arid margin of the Palaearctic region; while on the other hand constituting a crossroads between Europe, Asia, and Africa [140]. This unique geographical position strongly affects its faunistic composition. Forty-one hygrophilous species are recorded here from Israel, including two fossil species. Among the extant 39 species, ten are aquatic, five are semi-aquatic, and 20 species are riparian. While three species, *Bagous libanicus*, *B. septemcostatus* and *B. ruber*, are geophilous, not necessarily associated either with water or wet habitats, they are also listed here as being part of the predominantly aquatic genus *Bagous* and as being active in wet soil in the winter only.

The extant hygrophilous weevil fauna of Israel (excluding the fossil species) is distinctly Palaearctic, comprising 36 Palaearctic, one Holarctic, one Afrotropical, and one introduced Nearctic species. Half of the Palaearctic species (16) have a fairly wide distribution throughout the Palaearctic region (three wide Palaearctic, six west Palaearctic and seven circum-Mediterranean), and half are restricted to the arid warm areas of the Mediterranean, Near East, and Middle Asia. Most of these species occur at the southernmost point of their distribution. The only Afrotropical species, *Aorus anthracinus*, is, in contrast, at its northernmost distributional point, and is probably a relic from the distant epoch when the Jordan Valley was still connected directly to the rest of the Rift Valley (its African part) by a chain of freshwater or brackish water bodies, presenting a vector of introduction of tropical species from sub-Saharan Africa, similar to the introduction of numerous plant and animal species into Israel [10,14,16,140,141]. The Nearctic *Stenopelmus rufinasus* appeared in 2010 in two completely different places in Israel. It is unclear whether this was a single invasional event or the species was established in Israel – no additional specimens have been collected since. Two species are probably endemic: *Bagous lyali* is an endemic of the Hula swamp and *Echinocnemus sahlbergi* is an endemic of the Central Coastal Plain. Both these endemic species are either extinct or very rare and have not been re-collected for many years. *Bagous libanicus*, described from a single specimen from Lebanon, is widely distributed throughout the less arid and more temperate parts of Israel, being to date an endemic of the Levant. I assume that it is widely distributed also in Syria and maybe also reaches Turkey, but this can only be proven following additional collecting efforts (sifting and collecting in pitfall traps).

Most Israeli hygrophilous weevils have a restricted distribution within the country, which is, of course, prescribed by their association with water sources. Many occur only in the humid upper Jordan Valley (Hula Valley (Figure 3a–d) and the Sea of Galilee Area) and/or in the Northern and Central Coastal Plain, where small areas of the primeval wetlands still exist. However, there are some species restricted to a single locality, such as *Bagous bagdatensis*, *B. lyali*, and *Aorus anthracinus*, known only from the Hula swamp; *Bagous validus*, restricted to the Berekhat Ya'ar winter pool (Figure 4a); and *Icaris sparganii*, which occurs only in the small (38.5 m^2) Ga'ash winter pool (Figure 4f).

The riparian weevil species in Israel can be roughly divided into those associated only with their riparian host plants (Nanophyiinae, *Gymnetron* spp., *Tanymecus musculus*); and those restricted to the riparian belt by the abiotic factors (humidity, temperature, etc.), while their host plants have a wider distribution (*Squamapion delagrangei*, *Tychius* spp., *Lixus iridis*, *Sitona lividipes*).

Most of the riparian species are common and appear in large numbers on their host plants, at least in some localities, whereas the aquatic and semi-aquatic weevils are comparatively rarely collected, usually as singletons or in short series. This does not necessarily mean, however, that they are rare. Many of these species are probably nocturnal, with diurnal collecting revealing individual specimens only. This is probably the case, for example, with *Bagous bagdatensis* and *Rhinoncus pericarpius*, collected several times in pitfalls, probably at night. *B. validus* and *I. sparganii* were predominantly collected in the evening. However, most of the localities in which aquatic weevils occur are nature reserves (e.g., Hula, Berekhat Ya'ar, Ga'ash, 'En Afeq), in which all activities are forbidden at night and I was therefore unable to validate my speculation. The collecting at night on the banks of the Jordan River near where it flows into the Sea of Galilee (Park haYarden) resulted in mass collecting of *Rhinoncus perpendicularius*, *Squamapion delagrangei*, *Tychius bicolor*, and *T. meliloti*, but no other hygrophilous weevils were found.

Compared to the Palaearctic fauna, the Israeli fauna is poor in aquatic species, which can be explained by the aridity of the climate. Many of the aquatic and semi-aquatic taxa widely distributed and common in the Palaearctic are lacking in Israel, e.g., erirhinin genera *Grypus* Germar, *Notaris* Germar, *Tanysphyrus* Germar, *Thryogenes* Bedel, *Tournotaris* Alonso-Zarazaga & Lyal [7,45]. The conoderin tribe Phytobiini, richest in the hygrophilous taxa, commonly represented in the West Palaearctic by the genera *Eubrychius* C. G. Thomson, *Neophytobius* Wagner, *Pelenomus* C. G. Thomson, *Phytobius* Schoenherr, *Rhinoncus* Schoenherr, and *Tapinotus* Schoenherr [7,45], is represented in Israel solely by *Rhinoncus*, with two species, both quite restricted in their distribution. The predominantly aquatic species-rich genus *Bagous* with ca. 300 described species [2], is represented in Israel by ten species. This number is probably higher than might be expected in an arid country like Israel, but it is remarkable that, of these ten species, three are geophilous, not associated with wetlands, and two are semi-aquatic.

The degradation and loss of the wetland biotopes as a consequence of human activity distinctly threaten the hygrophilous weevils. Five of them have already reached the red line of endangerment: *Aorus anthracinus*, *Arthrostenus fullo*, and *Echinocnemus reitteri;* and the endemic *Bagous lyali* and *Echinocnemus sahlbergi* have become either extinct or extremely rare as a result of drainage of the Hula swamp and extermination of the wetland habitats throughout the Coastal Plain. Additional efforts are required to confirm their status. Because the Hula Nature Reserve, which includes the remnants of the Hula swamp, is overly protected, this makes insect collecting there very difficult. I nonetheless do not give up hope of re-discovering these species in the Hula, being inspired by the rediscovery of the Hula painted frog *Latonia nigriventer* (Mendelssohn and Steinitz) (Amphibia: Alytidae) endemic to the Hula Valley, which had not been collected since 1955, was declared as extinct in 1996, but was since occasionally re-discovered in 2011 [15,74].

Additional hygrophilous weevil species might also occur in Israel. The genus *Echinocnemus* has two additional representatives in Egypt [45,88], inhabiting biotopes resembling those of the Coastal Plain of Israel. *Grypus equiseti* Fabricius is a widely-distributed Palaearctic species, associated with *Equisetum* spp. (Pteridophyta: Equisetaceae). Two species of *Equisetum* occur in Israel: *E. telmateia* Ehrh. in the northern Hula Valley, on the banks of Nahal Senir, Nahal Dan, and Nahal Qoren (Figure 16a–c); and *E. ramosissimum* Desf. in the Hula Valley, Upper Galilee, Coastal Plain, and Samarian Hills (where it is severely grazed by goats and sheep), on the banks of the streams (Figure 16d,e). Numerous unidentified aquatic weevils were observed in Saluqiyya Springs ('Eden Springs) near Qazrin, Golan Heights, in May 2017 (Liron Goren, pers. comm.); unfortunately, I have been unable to date to check this interesting record.

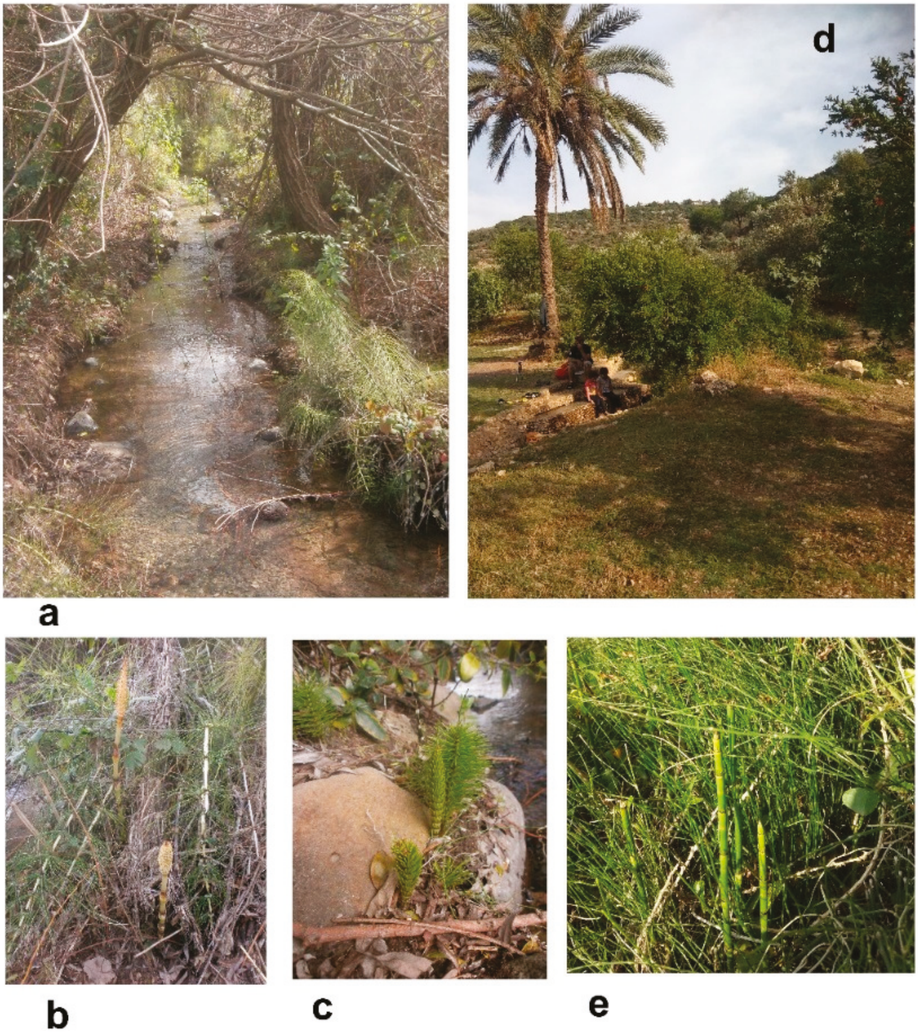

Figure 16. (**a**) Nahal Senir Nature Reserve, Equisetum telmateia on banks of Nahal Senir; (**b**,**c**) same place, *Equisetum telmateia*; (**d**) Nahal Qana, 'Ein-el-Basa, *Equisetum ramosissimum* growing in a thicket of *Ephedra sp.*, *Rubus sanctus* and Smilax aspera; (**e**) same place, *Equisetum ramosissimum*.

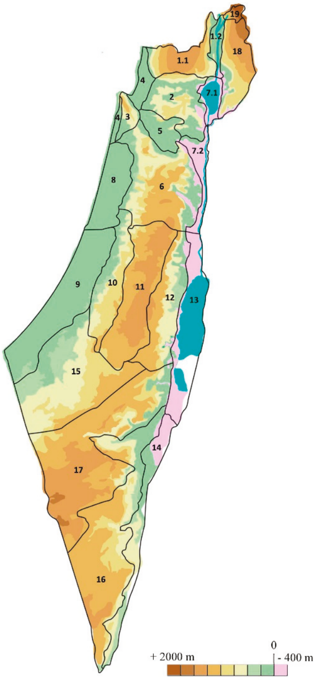

Figure 17. Zoogeographical map of Israel.

Names of the geographic regions of Israel (Figure 17).

1. Upper Galilee
1.1. Upper Galilee Hills
1.2. Hula Valley
2. Lower Galilee
3. Karmel (Carmel) Ridge
4. Northern Coastal Plain
5. Yizre’el (Jezreel) Valley
6. Shomeron (Samaria)
7. Jordan Valley & Southern Golan
7.1. Sea of Galilee Area
7.2. Jordan Valley
8. Central Coastal Plain
9. Southern Coastal Plain
10. Judean Foothills
11. Judean Hills
12. Judean Desert
13. Dead Sea area
14. ‘Arava Valley
15. Northern Negev
16. Southern Negev
17. Central Negev
18. Golan Heights
19. Mount Hermon

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References

1. Oberprieler, R.G.; Marvaldi, A.E.; Anderson, R.S. Weevils, weevils, weevils everywhere. *Zootaxa* **2007**, *1668*, 491–520.
2. Caldara, R.; O'Brien, C.W.; Meregalli, M. A phylogenetic analysis of the aquatic weevil tribe Bagoini (*Coleoptera*: *Curculionidae*) based on morphological characters of adults. *Zootaxa* **2017**, *4287*, 1–63. [CrossRef]
3. Egorov, A.B.; Korotyaev, B.A. Review of the weevil tribe Emphyastini (*Coleoptera*, *Curculionidae*), habitants on supralittoral of the Sea of Japan, Ochotian and Behring seas. *Proc. Zool. Inst. Acad. Sci. USSR* **1976**, *77*, 43–55. (In Russian)
4. Friedman, A.L.L. Review of the biodiversity and zoogeographical patterns of the weevils (*Coleoptera*, *Curculionoidea*) in Israel. *ZooKeys* **2009**, *31*, 133–148. [CrossRef]
5. Kuschel, G. The foreign *Curculionoidea* established in New Zealand (*Insecta*: *Coleoptera*). *N. Z. J. Sci.* **1972**, *15*, 273–289.
6. Oevering, P.; Pitman, A.J. Characteristics of attack of coastal timbers by *Pselactus spadix* (Herbst) (Col.: Curc.: *Cossoninae*) and an investigation of its life history. *Holzforschung* **2002**, *56*, 335–359. [CrossRef]
7. Caldara, R.; O'Brien, C.W. *Curculionidae*: Aquatic weevils of China (*Coleoptera*). In *Water Beetles of China*; Jäch, M.A., Ji, L., Eds.; Zoologisch-Botanische Gesellschaft in Österreich and Wiener Coleopterologenverein: Wien, Austria, 1995; pp. 389–408.
8. Survey of Israel. *Israel Touring Map (1:250,000) and List of Settlements (English Version)*; State of Israel, Ministry of Labor, 2 Sheets; Survey of Israel: Tel Aviv, Israel, 2009.
9. Israel Meterological Services, Ministry of Transport (IMS). 2018. Available online: http://www.ims.gov.il/IMS/CLIMATE/LongTermRain/ (accessed on 16 May 2018).
10. Goren, M.; Ortal, R. Biogeography, diversity and conservation of the inland water fish communities in Israel. *Biol. Conserv.* **1999**, *89*, 1–9. [CrossRef]
11. Por, D. An outline of the Zoogeography of the Levant. *Zool. Scr.* **1975**, *4*, 5–11. [CrossRef]
12. Shmida, A.; Aronson, J.A. Sudanian elements in the flora of Israel. *Ann. Mo. Bot. Gard.* **1986**, *73*, 1–28. [CrossRef]
13. Waisel, Y.; Liphschitz, N. *Water Plants in Israel*; Nature Conservation Authority: Tel Aviv, Israel, 1973; p. 82. (In Hebrew)
14. Waisel, Y.; Cohen, Y.; Pollak, G. *Ecology of the Vegetation of Israel*; Tel Aviv University. Sifriat Poalim: Tel Aviv, Israel, 1982; p. 462. (In Hebrew)
15. Biton, R.; Geffen, E.; Vences, M.; Cohen, O.; Bailon, S.; Rabinovich, R.; Malka, Y.; Oron, T.; Boistel, R.; Brumfeld, V.; et al. The rediscovered Hula painted frog is a living fossil. *Nat. Commun.* **2013**, *4*. [CrossRef] [PubMed]

16. Dumont, H.J. *Odonata of the Levant. Fauna Palaestina: Insecta V*; The Israel Academy of Sciences and Humanities: Jerusalem, Israel, 1991; p. 300.
17. Furth, D.G. The Huleh and its lost aquatic leaf beetle. *Atala* **1976**, *4*, 4–9.
18. Dimentman, C.; Bromley, H.J.; Por, F.D. *Lake Hula. Reconstruction of the Fauna and Hydrobiology of a Lost Lake*; The Israel Academy of Sciences and Humanities: Jerusalem, Israel; Keter Press Enterprises: Jerusalem, Israel, 1992; p. 196.
19. Hambright, K.D.; Zohary, T. Lakes Hula and Agmon: Destruction and creation of wetland ecosystems in northern Israel. *Wetl. Ecol. Manag.* **1998**, *6*, 83–89. [CrossRef]
20. Karmon, Y.; Livne, M. The Hula Valley and its vicinity. *Ariel* **1990**, *75–76*, 1–192.
21. Freidberg, A. Life in the Dead Sea. *Isr. J. Ent.* **1981**, *15*, 101–102.
22. Ortal, R.; Gabai, S.; Frankenberg, E. National Report on the Implementation of the RAMSAR Convention on Wetlands. Israel. National Reports to Be Submitted to the 10th Meeting of the Conference of the Contracting Parties, Republic of Korea, 28 October–4 November 2008; p. 37. Available online: http://www.sviva.gov.il/InfoServices/ReservoirInfo/DocLib2/Publications/P0401-P0500/P0473.pdf (accessed on 20 May 2018).
23. Gasith, A. Conservation and management of the coastal streams of Israel: An assessment of stream status and prospect for rehabilitation. In *River Conservation and Management*; Boon, P.J., Calow, P., Petts, G.E., Eds.; John Wiley & Sons Ltd.: New York, NY, USA, 1992; pp. 51–63.
24. Levin, N.; Lahav, H.; Ramon, U.; Heller, A.; Nizry, G.; Tsoar, A. Landscape continuity analysis: A new approach to conservation planning in Israel. *Landsc. Urban Plan.* **2007**, *79*, 53–64. [CrossRef]
25. Levin, N.; Elron, E.; Gasith, A. Decline of wetland ecosystems in the coastal plain of Israel during the 20th century: Implications for wetland conservation and management. *Landsc. Urban Plan.* **2009**, *92*, 220–232. [CrossRef]
26. Furth, D.G. Aquatic entomofauna of a Dead Sea oasis. *Hydrobiologia* **1983**, *102*, 3–25. [CrossRef]
27. Botosaneanu, L.; Gasith, A. Contributions taxonomiques et ecologiques a la connaissance des trichopteres (*Insecta*) d'Israel. *Isr. J. Zool.* **1971**, *20*, 89–129.
28. Bromley, H.J. A note on the Plecoptera of Israel. *Isr. J. Ent.* **1988**, *22*, 1–12.
29. Demoulin, G. Contribution à l'étude des Ephéméroptères d'Israel. Introduction et I. Heptageniidae. *Bull. Inst. R. Sci. Nat. Belg.* **1973**, *49*, 1–19.
30. Lyal, C.H.C. 3.7.7. Molytinae Schoenherr, 1823. pp. 529–570. In *Handbook of Zoology. Arthropoda: Insecta; Coleoptera, Beetles. Vol. 3. Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Kristensen, N.P., Beutel, R.G., Eds.; Walter de Gruyter: Berlin, Germany; Boston, MA, USA, 2014; Volume 3, p. 675.
31. Sartori, M. Mayflies from Israel (Insecta; Ephemeroptera) I. Heptageniidae, Ephemerellidae, Leptophlebiidae & Palingeniidae. *Rev. Suisse Zool.* **1992**, *99*, 835–858.
32. Hebauer, F. The Hydrophiloidea of Israel and the Sinai (*Coleoptera*, *Hydrophiloidea*). *Zool. Middle East* **1994**, *10*, 73–137. [CrossRef]
33. Jäch, M.A.; Ortal, R. The large water beetles of Israel—On the verge of extinction. *Soc. Prot. Nat. (Israel)* **1988**, *6*, 37–49.
34. Wewalka, G. Die Arten der Gattung Scarodytes aus Griechenland und eine neue Art dieser Gattung aus Israel (*Dytiscidae*, Col.). *Kol. Rundsch.* **1977**, *53*, 137–144.
35. Wewalka, G. Systematic and faunistic notes on Noteridae and *Dytiscidae* of the Near East (*Coleoptera*). *Kol. Rundsch.* **1989**, *59*, 143–152.
36. Caldara, R.; O'Brien, C.W. Systematics and evolution of Weevils of the genus Bagous. VI. Taxonomic treatment of the species of the Western Palearctic Region (Col. *Curculionidae). Mem. Soc. Ent. It.* **1998**, *76*, 131–347.
37. Alonso-Zarazaga, M.A.; Lyal, C.H.C. *A World Catalogue of Families and Genera of Curculionoidea (Insecta: Coleoptera) (Excepting Scolytidae and Platypodidae)*; Entomopraxis, S.C.P.: Barcelona, Spain, 1999; p. 315.
38. Danin, A.; Fragman-Sapir, O. Flora of Israel Online. 2017. Available online: http://flora.org.il/en/plants (accessed on 12 June 2018).
39. Theodor, O. *Diptera Pupipara. Fauna Palaestina. Insecta I*; The Israel Academy of Sciences and Humanities: Jerusalem, Israel, 1975; p. 170.

40. Ionescu, A.; Eyer, P.-A. Notes on Cataglyphis Foerster, 1850 of the bicolor species-group in Israel, with description of a new species (*Hymenoptera*: *Formicidae*). *Isr. J. Ent.* **2016**, *46*, 109–131.
41. Caldara, R. *Curculionidae*: Bagoinae, pp. 172–176. In *Catalogue of Palaearctic Coleoptera*; Löbl, I., Smetana, A., Eds.; Brill: Leiden, The Netherlands, 2013; Volume 8, p. 700.
42. Billberg, G.J. *Enumeratio Insectorum in Museo Gust. Joh. Billberg*; Typis Gadelianis: Stockholm, Sweden, 1820; p. 138.
43. Schoenherr, C.J. Curculionides. [Tabula synoptica familiae Curculionidum]. *Isis Oken* **1823**, *13*, 1132–1146.
44. Alonso-Zarazaga, M.A.; Wanat, M. 3.6.3. Apioninae Schoenherr, 1823. pp. 395–415. In *Handbook of Zoology. Arthropoda: Insecta; Coleoptera, Beetles. Vol. 3. Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Kristensen, N.P., Beutel, R.G., Eds.; Walter de Gruyter: Berlin, Germany; Boston, MA, USA, 2014; p. 675.
45. Alonso-Zarazaga, M.A.; Barrios, H.; Borovec, R.; Bouchard, P.; Caldara, R.; Colonnelli, E.; Gültekin, L.; Hlaváč, P.; Korotyaev, B.; Lyal, C.H.C.; et al. Cooperative catalogue of Palaearctic *Coleoptera Curculionoidea*. *Monogr. Electrón. Soc. Entomol. Aragon.* **2017**, *8*, 1–729.
46. Friedman, A.L.L.; Freidberg, A. The Apionidae of Israel and the Sinai Peninsula (*Coleoptera*: *Curculionoidea*). *Isr. J. Ent.* **2007**, *37*, 55–180.
47. Wencker, J.A. Apionides, tribu des curculionides. *L'Abeille* **1864**, *1*, 109–270.
48. Desbrochers des Loges, J. Espèces inédites de curculionides de l'Ancien-Monde IV. [Cont.]. *Le Frelon* **1895**, *4*, 81–96.
49. Gistel, J.N.F.X. *Naturgeschichte des Thierreichs. Für Höhere Schulen Bearbeitet Durch Johannes Gistel. Mit Einem Atlas von 32 Tafeln (Darstellend 617 illuminirte Figuren) und Mehreren dem Texte Eingedruckten Xylographien*; Hoffmann'sche Verlags-Buchhandlung: Stuttgart, Germany, 1848; p. 216.
50. Alonso-Zarazaga, M.A. Revision of the supraspecific taxa in the Palaearctic Apionidae Schoenherr, 1823 (1. Introduction and subfamily Nanophyinae. *Fragm. Ent. Roma* **1989**, *21*, 205–262.
51. Alonso-Zarazaga, M.A. 3.6.4. Nanophyinae Gistel, 1848. pp. 416–423. In *Handbook of Zoology. Arthropoda: Insecta; Coleoptera, Beetles. Vol. 3. Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Kristensen, N.P., Beutel, R.G., Eds.; Walter de Gruyter: Berlin, Germany; Boston, MA, USA, 2014; p. 675.
52. Des Gozis, M. Notes et remarques pour le futur catalogue de la faune gallo-rhénane (2e série). *Rev. Ent.* **1885**, *4*, 116–132.
53. Reitter, E. Fauna Germanica. In *Die Käfer des Deutsches Reiches. Nach der Analytische Methode Bearbeitet*; V. Band; K. G. Lutz: Stuttgart, Germany, 1916; p. 343.
54. Costa, A. Nuovi studii sulla entomologia della Calabria Ulteriore. *Atti Della Accad. Sci. Fis. Nat. Napoli* **1863**, *1*, 1–80.
55. Tournier, H. De quelques nouveaux coléoptères d'Europe et d'Algérie. *Ann. Soc. Ent. Fr.* **1868**, *7*, 561–570.
56. Giordani-Soika, A. Risultati scientifici delle spedizioni entomologiche di S.A.S. il Principe Alessandro della Torre e Tasso nel Bacino del Mediterraneo. I. Le specie mediterranee del genere Corimalia (Col. Curc.). *Publ. Mus. Ent. Pietro Rossi* **1937**, *2*, 1–29.
57. Pic, M. Coléoptères nouveaux. *Misc. Ent.* **1897**, *5*, 26–29.
58. Boheman, C.H. *[new taxa]. In Genera et Species Curculionidum, cum Synonymia Hujus Familiae. Species Novae aut Hactenus Minus Cognitae, Descriptionibus a Dom. L. Gyllenhal, C. H. Boheman, O. J. Fahraeus et Entomologis Aliis Illustratae*; Tomus octavus.—Pars secunda. Supplementum Continens; Parisiis: Roret; Schoenherr, C.J., Ed.; Flescher: Lipsiae, Germany, 1845; pp. 1–504.
59. Gyllenhal, L. *[new taxa]. In Genera et Species Curculionidum, cum Synonymia Hujus Familiae. Species Novae aut Hactenus Minus Cognitae, Descriptionibus a Dom. Leonardo Gyllenhal, C. H. Boheman, et Entomologis Aliis Illustratae*; Tomus quartus.—Pars secunda; Parisiis: Roret; Schoenherr, C.J., Ed.; Flescher: Lipsiae, Germany, 1838; pp. 601–1124.
60. Latreille, P.A. *Histoire Naturelle, Générale et Particulière, des Crustacés et des Insectes. Ouvrage Faisant Suite aux Oeuvres de Leclerc de Buffon, et Partie du Cours Complet D'histoire Naturelle Rédigé Par C. S. Sonnini, Membre de Plusieurs Sociétés Savantes*; Tome troisième; F. Dufart: Paris, France, 1802; p. 467.
61. Thomson, C.G. *Skandinaviens Coleoptera, Synoptiskt Bearbetade*; Berlingska Bocktryckeriet: Lund, Sweden, 1859; p. 290.

62. Caldara, R.; Franz, N.M.; Oberprieler, R.G. 3.7.10. Curculioninae Laterille, 1802. pp. 589–628. In *Handbook of Zoology. Arthropoda: Insecta; Coleoptera, Beetles. Vol. 3. Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Kristensen, N.P., Beutel, R.G., Eds.; Walter de Gruyter: Berlin, Germany; Boston, MA, USA, 2014; p. 675.
63. Sprick, P. Suitability of an insect group for the Habitats Directive of the EU: The weevil subfamily Bagoinae (Col., *Curculionidae*). Contributions to the Ecology of Phytophagous Beetles VII. *Snudebiller* **2001**, *2*, 7–40.
64. Bodenheimer, F.S. Prodromus Faunae Palestinae. Essai sur les élements zoogéographiques et historiques du sud-ouest du sous-régne paléarctique. *Mém. Inst. Egypte* **1937**, *33*, 1–286.
65. Germar, E.F. Miscellen und Correspondenz-Nachrichten. *Mag. Ent.* **1817**, *2*, 339–341.
66. Dejean, P.F.M.A. *Catalogue de la Collection de Coléoptères de M. le Baron Dejean*; Crevot: Paris, France, 1821.
67. Schilsky, J. *Die Käfer Europa's. Nach der Natur beschrieben von Dr. H.C. Kuster und Dr. G. Kraatz. Heft 44*; Bauer und Raspe (E. Küster): Nürnberg, Germany, 1907; p. 100.
68. Pic, M. Descriptions d'un Bryaxis et de plusieurs malacodermes ou rhyncophores. *L'Échange Rev. Linn.* **1904**, *20*, 49–51.
69. Gyllenhal, L. *[new taxa]. In Genera et Species Curculionidum, Cum Synonymia Hujus Familiae. Species Novae Aut Hactenus Minus Cognitae, Descriptionibus a Dom. Leonardo Gyllenhal, C. H. Boheman, et Entomologis Aliis Illustratae*; Tomus tertius.—Pars secunda; Parisiis: Roret; Schönherr, C.J., Ed.; Flescher: Lipsiae, Germany, 1836; pp. 506–858.
70. Dieckmann, L. Beiträge zur Insektenfauna der DDR: Coleoptera—Curculionidae (Tanymecinae, Leptopiinae, Cleoninae, Tanyrhynchinae, Cosonina, Raymondionyminae, Bagoinae, Tanysphyrinae). *Beitr. Entomol.* **1983**, *33*, 257–381.
71. Cunev, J. Nové a zaujívané nálezy chrobákov (*Coleoptera*) nadčel'ade *Curculionoidea* na území Slovenska. *Entomofauna Carpathica* **2013**, *25*, 1–14.
72. Blecher, M.; Blecher, I. Changes in vegetation in Nahal Boqeq: Is it due to the aqua pollution? *Ecol. Vesviva* **2011**, *4*, 255–256. (In Hebrew)
73. Fåhraeus, O.I. *[new taxa]. In Genera et Species Curculionidum, Cum Synonymia Hujus Familiae. Species Novae Aut Hactenus Minus Cognitae, Descriptionibus a Dom. Leonardo Gyllenhal, C. H. Boheman, O. J. Fåhraeus, et Entomologis Aliis Illustratae; Tomus octavus.—Pars secunda. Supplementum Continens; Parisiis: Roret*; Schoenherr, C.J., Ed.; Flescher: Lipsiae, Germany, 1845; p. 504.
74. Bina Perl, R.G.; Gafny, S.; Malka, Y.; Renan, S.; Woodhams, D.C.; Rollins-Smith, L.; Pask, J.D.; Bletz, M.C.; Geffen, E.; Vences, M. Natural history and conservation of the rediscovered Hula painted frog, Latonia nigriventer. *Cont. Zool.* **2017**, *86*, 11–37.
75. Tournier, H. Matériaux pour servir à la monographie de la tribe des Erirrhinides de la familie des Curculionides (Coléoptères). *Ann. Soc. Ent. Belg.* **1874**, *17*, 63–116.
76. Chevrolat, L.A.A. Description de coléoptères nouveaux d'Algérie. *Rev. Mag. Zool. Pure Appl.* **1860**, *12*, 509–511.
77. Roesler, U. In Memoriam Dozent Dr. Stanislaw Blezsynski. *Ent. Nachr.* **1971**, *18*, 33–36.
78. Reitter, E. Neue Coleopteren aus Europa, den angrenzenden Ländern und Sibirien, mit Bemerkungen über bekannte Arten. Neunter Teil. *Deutsch. Ent. Zeit.* **1890**, *10*, 145–164.
79. Herbst, J.F.W. *Natursystem Aller Bekannten in- und Ausländischen Insekten, Als Eine Fortsetzung der von Büffonschen Naturgeschichte*; Der Käfer Sechster Theil; Joachim Pauli: Berlin, Germany, 1795; p. 520.
80. Rosenhauer, W.G. *Beiträge zur Insekten-Fauna Europas, Erstes Bändchen; Enthält die Beschreibung von Sechzig Neuen Käfern aus Bayern, Tyrol, Ungarn, etc., Sowie die Käfer Tyrols, Nach Dem Ergebnisse von Vier Reisen Zusammengestellt*; Theodor Blaesing: Erlangen, Germany, 1847; p. 159.
81. Schilsky, J. *Die Käfer Europa's. Nach der Natur Beschrieben von Dr. H.C. Küster und Dr. G. Kraatz. Heft 47*; Bauer und Raspe (E. Küster): Nürnberg, Germany, 1911; p. 100.
82. Schoenherr, C.J. Continuatio tabulae synopticae familiae curculionidum. *Isis Oken* **1825**, *5*, 581–588.
83. Schoenherr, C.J. *Genera et Species Curculionidum, Cum Synonymia Hujus Familiae. Species Novae aut Hactenus Minus Cognitae, Descriptionibus a Dom. L. Gyllenhal, C. H. Boheman, O. J. Fåhraeus et Entomologis Aliis Illustratae*; Tomus septimus. Pars secunda. Supplementum Continens; Parisiis: Roret; Flescher: Lipsiae, Germany, 1843; p. 461.
84. Caldara, R. A taxonomic revision of the weevil genus *Picia* Tournier, 1895 (*Coleoptera*: *Curculionoidea*: Erirhinidae). *Zootaxa* **2008**, *1959*, 39–57.

85. Grachev, V.G. Family Curculionidae Latreille, 1802. pp. 196–198. In *Plant-Arthropod Interactions in the Early Angiosperm History: Evidence from the Cretaceous of Israel; Part II. Fossil Insects in the Cretaceous Mangrove Facies of Southern Negev, Israel*; pp. 189–224; Anisyutkin, L.N., Grachev, V.G., Ponomarenko, A.G., Rasnitsyn, A.P., Vršanský, P., Krassilov, V., Rasnitsyn, A., Eds.; Pensoft Publishers: Sofia, Bulgaria; Brill: Leiden, The Netherlands, 2008; p. 229.
86. Krassilov, V.; Silantieva, N.; Lewy, Z. Part I. Traumas on Fossil Leaves from the Cretaceous of Israel, pp. 1–187. In *Plant-Arthropod Interactions in the Early Angiosperm History: Evidence from the Cretaceous of Israel*; Krassilov, V., Rasnitsyn, A., Eds.; Pensoft Publishers: Sofia, Bulgaria; Brill: Leiden, The Netherlands, 2008.
87. Rabinovich, R.; Hanan, H.; Schudack, M.; Schudack, U.; Ashckenazi-Polivoda, S.; Rogolsky, G. A late Cretaceous elasmosaurid of the Tethys Sea margins (southern Negev, Israel), and its palaeogeographic reconstruction. *Neth. J. Geosci.* **2015**, *94*, 73–86.
88. Alfieri, A. The *Coleoptera* of Egypt. *Mém. Soc. Ent. Egypte* **1976**, *5*, 1–362.
89. Korotyaev, B.A. Family *Curculionidae*. pp. 145–149. In *Key to Harmful and Useful Insects and Mites on Grain Plants in the USSR*; Kopaneva, L.M., Ed.; Kolos: Leningrad, Russia, 1980. (In Russian)
90. Marshall, G.A.K. On the West African species of *Echinocnemus* Schoen. (Col., *Curculionidae*). *Ann. Mag. Nat. Hist.* **1950**, *3*, 765–774. [CrossRef]
91. Oberprieler, R. 3.7.1. Brachycerinae Billberg, 1820. pp. 424–451. In *Handbook of Zoology. Arthropoda: Insecta; Coleoptera, Beetles. Vol. 3. Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Kristensen, N.P., Beutel, R.G., Eds.; Walter de Gruyter: Berlin, Germany; Boston, MA, USA, 2014.
92. Singh, J.; Dhaliwal, G.S. Rice root weevil problem in India—An overview. *Ind. J. Ent.* **1990**, *52*, 217–222.
93. Sahlberg, J.R. *Coleoptera* mediterranea orientalia, quae in Aegypto, Palaestina, Syria, Caramania atque in Anatolia occidentali anno 1904 collegerunt John Sahlberg et Unio Saalas. *Öfversigt Fin. Vetensk-Soc. Förhandlingar (A)* **1913**, *55*, 1–281.
94. Schilsky, J. *Die Käfer Europa's. Nach der Natur Beschrieben von Dr. H.C. Kuster und Dr. G. Kraatz. Heft 44*; Bauer und Raspe (E. Küster): Nürnberg, Germany, 1907; p. 100.
95. Gyllenhal, L. *[new taxa]. In Genera et Species Curculionidum, Cum Synonymia Hujus Familiae. Species Novae Aut Hactenus Minus Cognitae, Descriptionibus a Dom. Leonardo Gyllenhal, C. H. Boheman, et Entomologis Aliis Illustratae*; Tomus tertius—Pars prima. [1836]; Parisiis: Roret; Schoenherr, C.J., Ed.; Flescher: Lipsiae, Germany, 1835; p. 505.
96. Miller, L. Neue Käfer aus Kindermann's Vorräthen. *Wien. Ent. Monatsch.* **1861**, *5*, 201–209.
97. Caldara, R. *Curculionidae*: Curculioninae, pp. 117–172. In *Catalogue of Palaearctic Coleoptera*; Löbl, I., Smetana, A., Eds.; Brill: Leiden, The Netherlands, 2013; Volume 8, p. 700.
98. Zumpt, F. Revision der Genera *Notaris* Germ., *Lepidonotaris* m., *Thryogenes* Bed., *Grypus* Germ., *Icaris* Tourn. und *Picianus* m. (Col. Curc.). *Col. Cent.* **1929**, *3*, 213–239.
99. Faust, J. Die europäischen und asiatischen Arten der Gattungen *Erirhinus*, *Notaris*, *Icaris*, *Dorytomus*. *Bull. Soc. Impériale Nat. Moscou* **1882**, *57*, 113–188.
100. Benedikt, S.; Borovec, R.; Fremuth, J.; Kratky, J.; Schoen, K.; Skuhrovec, J.; Tryzna, M. Annotated checklist of weevils (*Coleoptera*: *Curculionoidea* excepting Scolytinae and Platypodinae) of the Czech Republic and Slovakia. *Klapalekiana* **2010**, *46*, 1–363.
101. Dieckmann, L. Beiträge zur Insektenfauna der DDR: *Coleoptera—Curculionidae* (Erirhinae). *Beitr. Entomol.* **1986**, *36*, 119–181.
102. Tournier, H. [Rectification]. *Bull. Soc. Ent. Fr.* **1895**, *63*.
103. David'yan, G.E. Interactive Agricultural Ecological Atlas of Russia and Neighboring Countries. Economic Plants and their Diseases, Pests and Weeds. *Hydronomus sinuaticollis* Faust—Rice Water Weevil. 2009. Available online: http://www.agroatlas.ru/en/content/pests/Hydronomus_sinuaticollis/index.html (accessed on 11 June 2018).
104. Reitter, E. Coleopterologische Ergebnisse der im Jahre 1886 und 1887 in Transcaspien von Dr. G. Radde, Dr. A. Walter und A. Konchin ausgeführten Expedition. *Verh. Naturforschenden Vereines Brünn* **1889**, *27*, 95–133.
105. Schoenherr, C.J. *Curculionidum Dispositio Methodica Cum Generum Characteribus, Descriptionibus Atque Observationibus Variis, Seu Prodromus ad Synonymiae Insectorum, Partem IV*; Fridericum Fleischer: Lipsiae, Germany, 1826; p. 338.
106. Isaev, A.Y. *Opredelitel Zhukov Srednego Povolzhia. Part 3. Polyphaga—Phytophaga*; Vector-S: Ulyanovsk, Russia, 2007; p. 256. (In Russian)

107. Boheman, C.H. *[new taxa]. In Genera et Species Curculionidum, Cum Synonymia Hujus Familiae. Species Novae Aut Hactenus Minus Cognitae, Descriptionibus a Dom. Leonardo Gyllenhal, C. H. Boheman, et Entomologis Aliis Illustratae; Tomus tertius.—Pars secunda; Parisiis: Roret*; Schoenherr, C.J., Ed.; Flescher: Lipsiae, Germany, 1836; Volume 4, 505p.
108. Schoenherr, C.J. *Genera et Species Curculionidum, Cum Synonymia Hujus Familiae. Species Novae Aut Hactenus Minus Cognitae, Descriptionibus a Dom. Leonardo Gyllenhal, C. H. Boheman et Entomologis Aliis Illustratae; Tomus tertius. Pars prima [1836]*; Parisiis: Roret; Flescher: Lipsiae, Germany, 1835; p. 505.
109. Caldara, R. Erirhinidae. In *Catalogue of Palaearctic Coleoptera*; Löbl, I., Smetana, A., Eds.; Apollo Books: Stenstrup, Denmark, 2011; Volume 7, pp. 192–198.
110. Friedman, A.L.L. The first record of the Azolla frond weevil *Stenopelmus rufinasus* (*Curculionidae*: Brachycerinae: Tanysphyrini) in Israel. *Isr. J. Ent.* **2017**, *47*, 103–106.
111. Hill, M.P.; McConnachie, A.J. Azolla filiculoides Lamarck (Azollaceae). In *Biological Control of Tropical Weeds Using Arthropods*; Muniappan, R., Reddy, G.V.P., Raman, A., Eds.; Cambridge University Press: Cambridge, UK, 2009; pp. 74–87.
112. Dufour-Dror, J.-M. Invasive Aquatic Plants. *Kalanit*. 2014. Available online: http://www.kalanit.org.il/?p=279 (accessed on 15 October 2017). (In Hebrew)
113. Lacordaire, J.T. *Histoire Naturelle des Insectes. Genera des Coléoptères ou Exposé Méthodique et Critique de tous les Genres Proposés Jusqu'ici Dans cet Ordre D'insectes*; Tome Sixième; Roret: Paris, France, 1863; p. 637.
114. Marshall, G.A.K. On the genus *Aorus*, Schh. (*Coleoptera*, *Curculionidæ*). *Ann. Mag. Nat. Hist.* **1919**, *4*, 338–343. [CrossRef]
115. Brancsik, K. Coleoptera africana nova. Trencsén Természettud. *Egylet Évkönyve* **1989**, *19–20*, 108–131.
116. Schoenherr, C.J. *Genera et Species Curculionidum, Cum Synonymia Hujus Familiae. Species Novae Aut Hactenus Minus Cognitae, Descriptionibus a Dom. Leonardo Gyllenhal, C. H. Boheman et Entomologis Aliis Illustratae; Tomus primus.—Pars prima*; Parisiis: Roret, Kenya, 1833; p. 381.
117. Prena, J.; Colonnelli, E.; Hespenheid, H.A. 3.7.9. Conoderinae Schoenherr, 1823. pp. 577–589. In *Handbook of Zoology. Arthropoda: Insecta; Coleoptera, Beetles. Vol. 3. Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Kristensen, N.P., Beutel, R.G., Eds.; Walter de Gruyter: Berlin, Germany; Boston, MA, USA, 2014; p. 675.
118. Colonnelli, E. *Catalogue of Ceutorhynchinae of the World, with a Key to Genera (Insecta: Coleoptera: Curculionidae)*; Argania Edito: Barcelona, Spain, 2004; p. 124.
119. Korotyaev, B.A. A review of the weevil genus *Rhinoncomimus* Wagner (*Coleoptera*: *Curculionidae*: Ceutorhynchinae). *Ent. Abh.* **2006**, *63*, 99–122.
120. Rheinheimer, J.; Hassler, M. *Die Rüsselkäfer Baden-Württembergs*; Verlag Regionalkultur: Ubstadt-Weiher, Germany, 2010; p. 944.
121. Colonnelli, E. Checklist of Phytobiini of the world, with a key to the genera and description of a new species from South Africa (*Coleoptera*, *Curculionidae*, Ceutorhynchinae). *Fragm. Ent.* **1986**, *19*, 155–168.
122. Linnaeus, C. *Systema Naturae per Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, Cum Caracteribus, Differentiis, Synonymis*; Laurentii Salvii: Holmiae, Sweden, 1758; p. 824.
123. Reich, G.C. *Mantissae Insectorum Iconibus Illustratae Species Novas Aut Nondum Depictas Exhibentis*; Felsecker: Norimbergae, Germany, 1797; p. 16.
124. Kirsch, T.F.W. Neue oder seltene Rüsselkäfer-Arten aus dem Gebiete des Mittelmeerbeckens. *Ent. Monatsbl.* **1881**, *2*, 3–16. [CrossRef]
125. Caldara, R. Revisione delle specie paleartiche del genere *Gymnetron* (*Insecta*, *Coleoptera*: *Curculionidae*). *Aldrovandia* **2008**, *4*, 27–104.
126. Desbrochers des Loges, J. Espèces inédites de curculionides de l'Ancien Monde. VI. *Le Frelon* **1900**, *8*, 1–16.
127. Brisout de Barneville, C.N.F. Méthode dichotomique appliquée aux Tychius de France et description de quelques espèces nouvelles des genres Tychius et Miccotrogus. *Ann. Soc. Ent. Fr.* **1863**, *2*, 756–780.
128. Caldara, R. Revisione tassonomica delle specie paleartiche del genere *Tychius* Germar (*Coleoptera Curculionidae*). *Mem. Soc. Ital. Sci. Nat. Mus. Civ. Stor. Nat. Milano* **1990**, *25*, 51–218.
129. Stephens, J.F. *Illustrations of British Entomology; or, a Synopsis of Indigenous Insects: Containing Their Generic and Specific Distinctions; with an Account of Their Metamorphoses, Times of Appearance, Localities, Food, and Economy, as Far as Practicable. Mandibulata*; Baldwin, Cradock: London, UK, 1831; p. 413.

130. Marvaldi, A.E.; Lanteri, A.A.; Guadalupe del Rio, M.; Oberprieler, R.G. 3.7.5. Entiminae Schoenherr, 1823. pp. 529–570. In *Handbook of Zoology. Arthropoda: Insecta; Coleoptera, Beetles. Vol. 3. Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Kristensen, N.P., Beutel, R.G., Eds.; Walter de Gruyter: Berlin, Germany; Boston, MA, USA, 2014.
131. Velázquez de Castro, A.J.; Alonso Zarazaga, M.A.; Outerelo, R. Systematics of Sitonini (Col.: *Curculionidae*: *Entiminae*) with a hypothesis on evolution of feeding habits. *Syst. Ent.* **2007**, *32*, 212–331. [CrossRef]
132. Velázquez de Castro, A.J.; Friedman, A.L.L.; Borovec, R. Sitonini (*Curculionidae*: *Entiminae*) of Israel. *Isr. J. Ent.* **2010**, *40*, 71–108.
133. Fåhraeus, O.I. *[new taxa]. In Genera et Species Curculionidum, Cum Synonymia Hujus Familiae; Species Novae Aut Hactenus Minus Cognitae, Descriptionibus a Dom. L. Gyllenhal, C. H. Boheman, O. J. Fåhraeus et Entomologis Aliis Illustratae*; Tomus sextus. Pars prima; Parisiis: Roret; Schoenherr, C.J., Ed.; Flescher: Lipsiae, Germany, 1840; p. 474.
134. Meregalli, M. 3.7.6. Lixinae Schoenherr, 1823. pp. 523–529. In *Handbook of Zoology. Arthropoda: Insecta; Coleoptera, Beetles. Vol. 3. Morphology and Systematics (Phytophaga)*; Leschen, R.A.B., Beutel, R.G., Kristensen, N.P., Beutel, R.G., Eds.; Walter de Gruyter: Berlin, Germany; Boston, MA, USA, 2014.
135. Fabricius, J.C. *Systema Eleutheratorum Secundum Ordines, Genera, Species: Adiectis Synonimis, Locis, Observationibus, Descriptionibus*; Impensis Bibliopolii Academici Novi: Kiel, Germany, 1801; p. 687.
136. Olivier, A.G. *Entomologie, ou Histoire Naturelle des Insectes, Avec Leurs Caractères Génériques et Spécifiques, Leur Description, Leur Synonymie, et Leur Figure Enluminée. Coléoptères*; Tome cinquième; Desray: Paris, France, 1807; p. 612.
137. Scherf, H. Die Entwicklungsstadien der mitteleuropäischen Curculioniden (Morphologie, Bionomie, Ökologie) [Morphology, bionomy and ecology of developmental stages of Central European Curculionids]. *Abh. Senckenberg. Nat. Ges.* **1964**, *506*, 1–335.
138. Volovnik, S.V. On the oviposition of weevils of the genus *Lixus* (*Coleoptera*, *Curculionidae*). *Zool. Zhurnal* **1994**, *73*, 49–54, (In Russian, Translated in *Ent. Rev.* **1995**, *74*, 115–120).
139. Volovnik, S.V. On Distribution and Ecology of Some Species of Cleonines (*Coleoptera*, *Curculionidae*): IV. Genus *Lixus* F., Subgenus *Eulixus* Reitt. *Entomol. Obozr.* **2007**, *86*, 521–529, (In Russian, Translated in *Ent. Rev.* **2008**, *87*, 840–847). [CrossRef]
140. Furth, D.G. Israel, a great biogeographic crossroads. *Discovery* **1975**, *11*, 2–13.
141. Bytinski-Salz, H. The Ethiopian element in the insect fauna of Israel. In Proceedings of the XI International Congress of Entomology, Vienna, Austria, 17–25 August 1960.

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