A Family Affair: Diagnosing and Delimiting Prostygnidae (Opiliones: Gonyleptoidea) †

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Abstract: The former subfamily Prostygninae was recently elevated to family rank, and its phylogenetic relationships were investigated based on molecular data. In this study, we provide a revised morphological diagnosis for the family, focusing on characters from the exomorphology and male genital morphology. Morphological data supporting their inclusion in the MECO clade are provided. Additionally, a key to the genera is presented, and Prostygnus stellatus sp. nov., a new Ecuadorian species, is described. The geographic distribution of prostygnid species is mapped. An overview of the inclusion and exclusion of genera formerly within Prostygninae, but currently in Gonyleptoidea incertae sedis, is presented, and the following new familial assignments are proposed: Binamballeus Roewer, 1952 and Puna metatarsalis (Kury, 1994) comb. nov. (transferred to Cranaidae), Sclerostygnellus Roewer, 1943 (transferred to Manaosbiidae) and Globitarus Roewer, 1913, Lisarea Roewer, 1943, Meridanaus Roewer, 1943, Micropachylus Roewer, 1913, Prostygnidius Roewer, 1915, and Troya Roewer, 1914 (all transferred to Nomoclastidae). Three subjective synonyms of Troya are proposed: Peladus Roewer, 1914 syn. nov., Prostygnellus Roewer, 1914 syn. nov., and Minyssus Roewer, 1943 syn. nov., combining their species with Troya and, finally, Prostygnellus riveti Roewer, 1914 is considered as a junior secondary homonym of Troya riveti Roewer, 1914 syn. nov.

Keywords: Ecuador; Cranaidae; new species; Peru; Prostygninae; taxonomy

1. Introduction

Prostygnidae is a micro-diverse family of Grassatores with six species [1] distributed in southern Ecuador and northern Peru. The systematic placement of Prostygninae/Prostygnidae within Gonyleptoidea has undergone a series of changes. It transitioned from being nested within Gonyleptoidea, to Cranaidae, and ultimately emerged as an autonomous family within the unranked clades Carunculata Kury, 2020 (=MECO + Askawachidae Kury & Carvalho, 2020) and MECO Kury & Villareal, 2015 (formerly Me/Co =Cosmetidae Koch, 1839 + Metasarcidae Kury, 1994 + Prostygnidae Roewer, 1913). The internal composition of this subfamily/family also changed significantly over time.

In the current project, we provide an account of the evolution of the Prostygnidae concept, elucidating its taxonomic framework, evolutionary history, and geographical distribution, and we offer a comprehensive genus-level key to facilitate the classification of related taxa. Additionally, we introduce a new species from Ecuador and provide a description thereof. Finally, we propose several family reassignments of species previously affiliated with Prostygninae.
1.1. Taxonomic Historical Background of Prostygnidae

Roewer [2] proposed a reorganization of the family Gonyleptidae, dividing it into numerous subfamilies. One such subfamily was Prostygninae, which was based on the absence of features of the other subfamilies (plesiomorphic states of characters). In Roewer’s original classification of Prostygninae, he included six genera, which are now distributed across various families, apart from the type genus, one in Manaosbiidae (*Camelianus* Roewer, 1912), one in Agoristenidae (*Sabanilla* Roewer, 1913), two in Nomoclastidae (*Globitarsus* Roewer, 1913, *Micropachylus* Roewer, 1913), and one peculiar gonyleptoid that remains unplaced as of yet (*Ostracidium* Perty, 1833). This practice of grouping unrelated genera in Prostygninae reached its pinnacle in the work of Soares, Soares, and Jim [3], who listed several genera, mostly monotypic, that currently correspond to various families within Gonyleptoidea.

Over the years, the family Gonyleptidae was splintered, leading to the extraction of several taxa to establish their own distinct families, such as Cryptogeobiidae, Metasarciidae, Stygnidae (Sørensen in [4–6]). Kury [7] introduced the concept of a separate family Cranidae, including Prostygninae. However, it became increasingly evident that Prostygninae was not in the immediate phylogenetic vicinity of the Cranidae.

Kury [8] pointed out that the male genitalia of *Prostygnus* Roewer, 1913 bore a stronger resemblance to those of Cosmetidae rather than those of Cranidae. Villarreal and García [9] presented illustrative comparisons between the stylus of *Prostygnus* and of a cosmetid species. They highlighted the presence of a wattle in both *Prostygnus* and the cosmetid, while noting that both lacked a stylar cap, a possible synapomorphy for cranaid species.

Morphologically-based phylogenetic analysis of the Cranidae [10] revealed that Prostygninae stood near the unranked MECO clade, which, at that time, encompassed Cosmetidae and Metasarcidae. These findings were subsequently supported by the similarities in the ventral plate microsetae pattern between Prostygninae and the MECO clade, rather than the Cranidae family [11].

Meanwhile, Kury and Carvalho [12] introduced the new Askawachidae family and established the new unranked taxon Carunculata that encompassed Cosmetidae, Metasarcidae, Prostygnidae, and Askawachidae. They alluded to the impending cranaid paper while taking this step. Medrano et al. [13] concurred with the placement of Prostygnidae in MECO as the possible sister-group of Cosmetidae.

Derkarabetian et al. [14], employing UCEs (Ultra-Conserved Elements), provided further validation for the placement of Prostygnidae within the MECO clade, as the sister-group of Metasarcidae + Cosmetidae. This corroboration was substantiated by evidence from an entirely distinct dataset, adding an extra layer of molecular confirmation to the earlier morphological findings.

Therefore, all the recent literature places Prostygnidae outside Cranidae and nested within MECO. We concur with this placement and, as such, do not need to repeat any testing here, although a few comments on the morphology are given in the “Discussion” section.

1.2. Composition of Prostygninae/Prostygnidae

Due to the diagnosis of Prostygninae, as originally conceived by Roewer, to be based on sympleisiomorphies, it was likely to gather unrelated genera. It took a significant amount of time for this motley crew to be purged. In Table 1, we present an overview of the inclusion and exclusion of genera within Prostygninae.
Table 1. Entries and dismissals of genera in Prostygninae. Destinations marked with the superscript index C mean the genus is being transferred to Cranaidae and index N is being transferred to Nomoclastidae in this paper (see below). Genera marked with the superscript index S signify that the genus is currently under synonymy or being brought under synonymy herein.

<table>
<thead>
<tr>
<th>Genus, Author, Year</th>
<th>Entered Prostygninae in</th>
<th>Last Assignment before Prostygninae</th>
<th>Removed from Prostygninae in</th>
<th>Ultimate Destination (Current)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prostygnus Roewer, 1913</td>
<td>[2]</td>
<td>none—then new</td>
<td>type-genus to which Prostygninae is anchored</td>
<td>Prostygnidae</td>
</tr>
<tr>
<td>Napostygnus Roewer, 1929</td>
<td>[21]</td>
<td>none—then new</td>
<td>[23]</td>
<td>Nomoclastidae</td>
</tr>
<tr>
<td>Iquitoza Roewer, 1943</td>
<td>[26]</td>
<td>none—then new</td>
<td>[27]</td>
<td>Cranidae</td>
</tr>
<tr>
<td>Lisarea Roewer, 1943</td>
<td>[26]</td>
<td>none—then new</td>
<td>[16]</td>
<td>Gonyleptoidea incertae sedis</td>
</tr>
<tr>
<td>Meridanatus Roewer, 1943</td>
<td>[26]</td>
<td>none—then new</td>
<td>[16]</td>
<td>Gonyleptoidea incertae sedis N</td>
</tr>
<tr>
<td>Poassa Roewer, 1943 S</td>
<td>[26]</td>
<td>none—then new</td>
<td>[23]</td>
<td>Nomoclastidae</td>
</tr>
<tr>
<td>Sclerostygnellus Roewer, 1943</td>
<td>[26]</td>
<td>none—then new</td>
<td>[16]</td>
<td>Gonyleptoidea incertae sedis</td>
</tr>
<tr>
<td>Tschaudicancha Roewer, 1957</td>
<td>[29]</td>
<td>none—then new</td>
<td>[22]</td>
<td>Metasarcinae/Metasarcidae</td>
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<tr>
<td>Cutervolus Roewer, 1957</td>
<td>[7]</td>
<td>Phalangodidae Tricommatinae</td>
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<td>Prostygnidae</td>
</tr>
<tr>
<td>Yania Roewer, 1914</td>
<td>[7]</td>
<td>Phalangodidae Tricommatinae</td>
<td>n/a</td>
<td>Prostygnidae</td>
</tr>
<tr>
<td>Llaguenia Kury &amp; Pérez-González, 2015</td>
<td>[31]</td>
<td>none—then new</td>
<td>n/a</td>
<td>Prostygnidae</td>
</tr>
</tbody>
</table>
2. Materials and Methods

The specimens examined for this study are deposited in the Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP-curator: R. Pinto-da-Rocha). The patterns of description follow Villarreal et al. [32,33] with slight modifications. The descriptions of colors use the standard names of the 267 Color Centroids of the NBS/IBCC Color System (online at http://people.csail.mit.edu/jaffer/Color/Dictionaries#nbs-iscc) (accessed on 10 October 2023) as described in Kury an Orrico [34]. The terminology for the integumentary ornamentation follows DaSilva and Gnaspini [35], the chaetotaxy of penis ventral plates follows Kury and Villarreal [36], the dorsal scutal outline types follow Kury and Medrano [37], and the penial microsetae follows Kury [11]. The color description refers to specimens preserved in ethyl alcohol. All measurements are in mm unless otherwise noted. Pictures were made using a Sony Cybershot DSC-V1 camera (Rio de Janeiro, Brazil) attached to a stereomicroscope. The multiple images of each species at different focal planes were combined with CombineZP to increase the depth of field and were posteriorly edited in Adobe Photoshop CC 2014 software. Drawings were made using the Inkscape 1.3 and Adobe Illustrator CC 2017 software. Scanning Electron Microscopy (SEM) was carried out with a JEOL JSM-6390LV microscope (Rio de Janeiro, Brazil) at the Center for SEM of the Museu Nacional/UFRJ with an accelerating voltage of 10 kV after sputter-coating with gold-palladium. When listing the examined material, countries are written in bold letters and the first order administrative divisions are written in small caps. The distribution map was made using ESRI ArcGIS 10.4. The colored shapes refer to WWF Terrestrial Ecoregions of the World [38]. The type material of *Prostygnus stellatus* sp. nov. was unfortunately destroyed during the fire at the MNRJ in September 2018 [39], limiting certain aspects of the description of this species. Nonetheless, the information presented is considered sufficient for the accurate diagnosis and future unequivocal identification of the species.

The abbreviation transl. nov. (=translatio nova; new transfer/assignment) is used here for new familial assignments. We avoid the term “attribution” for possible confusion with “Creative Commons Attribution License”.

Morphological abbreviations: DS, dorsal scutum; MS, macrosetae; VP, ventral plate (ventrodistal setigerous region of penis); macrosetae A1–A3, basal macrosetae of VP; B, ventro-basal macrosetae of VP; C1–C3, distal macrosetae of VP; D1, dorso-lateral subdistal small setae of VP; VP = ventral plate (penis).

3. Results

3.1. Taxonomic Key to Prostygnidae Genera (Males)

1.a.- Mesotergal area III unarmed
1.b.- Mesotergal area III armed with a pair of paramedian spines
2.a.- Without preocular mound; ocularium high, more than five times higher than the ocular diameter; DS with yellow or white spots; MS-C clearly larger than the MS-A
2.b.- Preocular mound present; ocularium low, twice the ocular diameter; DS without yellow or white spots; MS-A clearly larger than the MS-C
3.a.- Spines of the scutal area III separated from each other; MS-C located distal on the VP; larger than MS-A
3.b.- Spines of the scutal area III arising from a common base, partially fused to each other; MS-C positioned subdistal on the VP, same size of MS-A

Yania
Llaguenia
Prostygnus
Cutervolus

3.2. Taxonomy

Order Opiliones Sundevall, 1833
Suborder Laniatores Thorell, 1876
Superfamily Gonyleptoidea Sundevall, 1833

Family Prostygnidae Roewer, 1913

- Prostygninae (subfamily of Gonyleptidae) Roewer 1913c: 140 (incl. *Camelianus*, *Globiarsus*, *Micropachylus*, *Ostracidium*, *Prostygnus*, *Sabanilla*). Type genus: *Prostygnus* Roewer, 1913 (stem: *Prostygn-*)


“Prostigninae” (subfamily of Gonyleptidae): Mello-Leitão 1926: 346 (incorrect subsequent spelling (with ligature)).


“Prostigninas” (subfamily of Gonyleptidae): Mello-Leitão 1932: 103. (incorrect subsequent spelling (rendered to Portuguese vernacular)).

Prostigninae (subfamily of Cranaidae)—Kury 1994b: 140 (diagn., compos.) (first use as a subfamily of Cranaidae).


Prostignidae: Kury & Carvalho 2020: 55 (incl. in MECO) (first use as a family).

Prostignidae—Medrano et al. 2021: 590 (phylog. position); Derkarabetian, Lord, Angier, Frigyk & Giribet 2023: 10 (molec. anal.).

Diagnosis. Medium size (dorsal shield length approximately 4 mm). Outline of DS type kappa (Prostygynus) (Figures 1A and 2A) or alpha (Llaguenia, Yania) (Figure 3A). Dorsal scutum with four well-defined mesotergal areas (Figures 1A,B and 2A,B), area III may have a pair of paramedian spiniform tubercles with a fused (Cutervolus), normally separate (Prostygynus) (Figures 1A and 2A) or entirely unarmed (Llaguenia, Yania) (Figure 3A,B). Chelicerae hyperelic in males (Figures 1A,B,D, 2A,B and 3A,B). Pedipalp femur with ventral ornamentation represented by a row of tubercles of equal size and regularly distributed (Figures 1D, 2D, and 3B) (absent in Llaguenia). Pedipalp femur without ectal row of tubercles, and without dorso-distal tubercle. Pedipalp tibia, dorsally tuberculated. Legs short. Tibia IV without conspicuous ornamentation like rows of thorns, or any tubercles conspicuously larger than the rest (Figures 1B and 3B). Male genitalia sui generis (Figures 3C,D and 4A,B), with the formation of a ventral plate covered ventrally by type-4 microsetae, distributed in two large lateral areas separated by a central unarmed region (Figure 4C,D). These microsetae can extend and are also present in the lateral areas and slightly up to the most dorsal region at the base of the ventral plate, surrounding the MS-A (Figure 4B,D). Stylus with ventral wattle and thumb-like process (Figures 3E,F and 4A,B,E). Ventral plate without laterobasal projections in the form of spiny saccs (Figure 3C,E) and the distal edge straight or slightly concave without distal cleft (Figures 3D and 4A–C). Large and curved MS-C, larger than MS-A (Figures 3C–F and 4A–D), except Llaguenia, where they are clearly smaller; two pairs of MS-A, located basally on the ventral plate, ungrouped from the MS-C; MS-B absent (Figures 3E,F and 4C); MS-D1 present; and MS-D2 absent (Figure 4A,B).


Distribution and natural history. Our understanding of family diversity remains limited, with known species mainly stemming from type material. This hampers ecological and biogeographical predictions. Yet, it is notable that all species inhabit high-altitude Andean regions in Ecuador and Peru (Figure 5), primarily between 2260 and 3000 m, except for Yania flavolimbata, which reaches up to 4536 m. This species exhibits the highest records (ranging between 3000 and 4536 m). Cutervolus albopunctatus has been recorded as cave-dwelling, as well as inhabiting nearby cloud forest environments [24].
Genus Prostygnus Roewer, 1913

Prostygnus Roewer 1913c: 141. Type-species by monotypy: Prostygnus vestitus Roewer, 1913.


Etymology. From Greek πρό (before, forth) + pre-existing genus Stygnus. Gender masculine.

Diagnosis. DS outline type kappa. Four scutal areas, area III with a pair of large spines separated from each other. Ocularium domed, high, and tuberculated. DS with yellowish spots on lateral and scutal areas. VP of penis sub-rectangular, with distal border sub-straight or subtle concave, MS-C larger than MS-A.

Included species. “Prostygnus” calcar Roewer, 1943; Prostygnus stellatus sp. nov.; Prostygnus vestitus Roewer, 1913.

Remarks. Prostygnus calcar does not exhibit the diagnostic characters of the genus or even the family; rather, it seems to be a member of Nomoclastidae, with its generic assignment appearing to be impossible given the current state of knowledge regarding this species. Consequently, we have chosen to tentatively retain its placement within Prostygnus, despite recognizing its lack of affiliation with this group, until specimens of this species can be thoroughly examined.

Figure 1. Prostygnus stellatus sp. nov. (MZUSP 57274), male holotype: (A) habitus, dorsal view; (B) habitus, lateral view; (C) coxae III-IV, stigmatic area and free sternites, ventral view; (D) left chelicera and pedipalp, ectal view. Scale bars: 1 mm.

Prostygnus stellatus sp. nov.

urn:lsid:zoobank.org:act:DE8A563F-133C-45E8-8E49-8BB2A23338AF
(Figures 1, 2, 4 and 5)
Prostygnus sp. Villarreal & García 2016: 35.

Type material examined. Holotype. Male, ECUADOR, Zamora, S. Francisco, alt. 2.000 m; 2009, barkspray leg. (MZUSP 57274).

Diagnosis. Differs from P. vestitus Roewer, 1913 by: (1) the color pattern of the dorsal shield, consisting of a succession of yellow spots in the lateral areas of the dorsal shield (Figures 1A,B and 2A,B) instead of diffuse spots in the lateral zones of the mesotergal areas; (2) size of the paired tubercles of the ocularium, short and not spiniform (Figures 1A,B and 2A,B); and (3) presence of round yellow tubercles on the prolateral side of the coxae IV (Figures 1A–C and 2A,B).
Description. Measurements: dorsal scutum length = 4.5; dorsal scutum width = 4.1; interocular distance = 1.5; pedipalp: coxa = 0.6, trochanter = 0.9, femur = 1.9, patella = 1.0, tibia = 1.4; tarsus = 1.5, tarsal claw = 1.1; total = 8.4; leg IV: femur = 3.2, patella = 1.2, tibia = 1.9, metatarsus = 3.2. Dorsum (Figure 1A,B). Dorsal scutum outline kappa. Anterior margin of prosoma with 3-4 anterolateral yellow tubercles; cheliceral sockets shallow, between two short processes, medial process short. Eyes on a common ocularium, oval and domed, high, three times the ocular diameter; densely covered by tubercles and with a dorsal paramedian pair of large tubercles. Lateral margin with a row of yellow rounded granules. Mesotergum divided into four areas: I divided medially into two triangular halves, with one pair of yellow granules on each side; II unarmed and entire, with a row of yellow tubercles, invading medially area I, but not reaching the carapace; III with a paramedian pair of strong, large, and straight spines and some tubercles on each side. Posterior margin almost straight, with a row of small yellow tubercles. Free tergites I–III with a row of small yellow tubercles, and III with a paramedian pair of acuminated large spines. Venter (Figure 1C). Coxae I–IV with rows of scattered granules. Stigmatic area with a transversal row of granules and stigmata oval and sub-parallel. Chelicerae (Figures 1D and 2B,C). Segment I with the bulla globose and smooth; II swollen and smooth, fixed finger with one medial large tooth and four distal small teeth (iiii); mobile finger with a large basal tooth and with a distal dentate lamella. Pedipalps (Figures 1D and 2D). Coxae dorsally with a proximal low hump. Trochanter with one dorsal, one large ventral, and two ecto-ventral tubercles. Femur ventrally straight and dorsally curved in lateral view, dorsally smooth and ventrally with a row of nine tubercles (IIiiIIiii). Patella slightly swollen sub-distally, with tiny dorsal granules, ventrally smooth. Tibia dorsally with abundant tubercles, ventrally smooth; tibia ectal IIiIIi. Tarsus dorsally with tiny granules and ventrally smooth; tarsus ectal IIIiIIIi. Legs (Figures 1B and 2E). Coxa IV with four prolateral conspicuous and rounded yellow tubercles, some small uncolored tubercles, and one dorso-distal large spine. Trochanter I–II smooth; III globose, dorsally with scattered tubercles and one conspicuous retrolateral distal tubercle; IV sub-square, with three prodorsal and one proventral tubercle, one retroventral, and one dorsodistal large tubercle. Femur I–II with longitudinal rows of granules; III–IV slightly swollen, with longitudinal row of wide tubercles and presence of dorso-distal large tubercles, III with some large proximal tubercles, and IV with large proventral tubercles. Patella III–IV with longitudinal rows of tubercles, III with retroventral large tubercles, and IV with pro and retroventral large tubercles, and prolateral large distal tubercle. Tibia III–IV with longitudinal row of conspicuous sub-equal tubercles. Tarsal segmentation: 6(3)/?/7(3)/7(3). Penis (Figure 4). VP sub-rectangular elongate, slightly constricted in the subapical portion, with the apical corners rounded and almost straight distal margin. With three pairs of large and curved MS-C on the latero-distal corners; one pair of subapical MS-D located sub-dorsally. Two pairs of MS-A basally in ventral plate, straight, conical, and shorter than MS-C, located almost dorsally. Two pairs of short MS-E in the apical portion of the VP, close to MS-C; without MS-B. Ventral and lateral surfaces of the VP covered by numerous microsetae of type 4, (except the ventromedial portion). Glans columnar elongate inserted in no podium in apical part of the truncus, with ventral wattle and stylus cylindrical and dorsally curved, with apex compressed, flat crest around the ventral half of the opening, with a few ventro-distal projections. Coloration in alcohol (Figure 1). Dorsal scutum brownish orange with mesoteral areas and postero-lateral of dark brown carapace; ocularium, dark orange, yellow. Free tergites, proximally dark brown and distally brownish orange; paramedian spines, brilliant greenish yellow. Medial zone of area I–II with irregular spots, brilliant greenish yellow; lateral tubercles on the DS, vivid greenish yellow. Chelicerae, brownish orange with reticulate dark brown. Pedipalps, brownish orange with dark brown bands. Legs I–II, brilliant greenish yellow with dark brown irregular spots; metatarsus and tarsus, dark brown. Coxae and trochanter III–IV, deep orange yellow. Femora, patellae, and tibia III–IV, deep brown. Metatarsus III–IV, proximally brilliant greenish yellow and distally dark brown. Female. Unknown.

Etymology. From Latin stellatus (with stars), in reference to the high quantity of yellow tubercles that this species has in different parts of the body, which resemble stellar constellations.
Distribution. Only known from the type locality.

![Figure 2](image-url) Prostygnus stellatus sp. nov. (MZUSP 57274), male holotype: (A) habitus, dorsal view; (B) habitus, lateral view; (C) right chelicera, frontal view; (D) left pedipalp, ectal view; (E) left tarsomeres I, retrolateral view. Scale bars: 1 mm.

Genus *Yania* Roewer, 1914


Etymology. From the toponym Yana Urcu. Gender feminine.

Diagnosis. DS outline type Alpha, with coda almost as wide as the medial bulges. Four scutal areas unarmed. Ocularium domed, high, and tuberculated. DS with yellowish spots on lateral borders. VP of penis amphora-shaped, with distal border straight, MS-C larger than MS-A.

Included species. *Yania flavolimbata* Roewer, 1914

![Figure 3](image-url) *Yania flavolimbata*, male (MZSP 57276). (A) Habitus, dorsal view. (B) Ditto, lateral view. (C) Penis, dorsal view. (D) Ditto, apical portion. (E) Penis, lateral view. (F) Ditto, apical portion. Not scaled figures.
Yania flavolimbata Roewer, 1914
(Figures 3 and 5)
- Yania flavolimbata Roewer 1914c: 130, pl. 13, figure 6.

Material examined. Male, ECUADOR, Loja, Cajanuma, páramo, alt. 3000 m; 29 September 2008; J. Schmid leg. (MZUSP 57276).

Figure 4. Prostygnus stellatus sp. nov. (MZUSP 57274), penis, distal portion: (A) dorsal view; (B) lateral view; (C) ventral view; (D) laterodistal corner, detail in ventral view; (E) stylus, apical view. Scale bars: A, B, C = 50 µm; D = 20 µm; E = 10 µm.

Figure 5. Geographical distribution of the family Prostygnidae.
3.3. New Familial Assignments

Superfamily Gonyleptoidea

Family Manaosbiidae Roewer, 1943

Genus Sclerostygnellus Roewer, 1943 transl. nov.

- Sclerostygnellus Roewer 1943: 35. Type-species by monotypy: Sclerostygnellus rotundus Roewer, 1943.

  Taxonomy. Sclerostygnellus rotundus is documented based on a female specimen (which was incorrectly identified as male by Roewer). There is no positive evidence to establish a connection between Sclerostygnellus rotundus and Cranaidae. Conversely, the scutum outline, area armature, and pedipalp shape all exhibit strong congruence with the characteristics observed in Manaosbiidae.

Family Cranaidae Roewer, 1913

Binamballeus Roewer, 1952 transl. nov.


  Taxonomy. DS outline type possibly gamma, pedipalpal morphology and dorsal ornamentation, scutal areas, and legs ornamentation are all consistent with Cranaidae.

Puna Roewer, 1925

- Puna festae Roewer 1925: 29, figure 22a-b. Type-species by original designation: Puna festae Roewer 1925.
- Puna festae—Roewer 1932: 319, Figure 34; Soares & Soares 1948b: 615; Kury 2003: 97.

“Puna” metatarsalis (Kury, 1994) comb. nov.


  Taxonomy. The observed pedipalpal morphology, characterized by a dorsal keel on femora, patellae, and tibiae dorsally tuberculated; the scutal area pattern; and the leg IV ornamentation with a subdistal spine are suggestive of belonging to the Cranaidae family. Particularly, the alpha outline of the DS, the relatively short legs, high and domed ocularium, and dorsal keel on the pedipalp align it with a subgroup of Cranainae genera, including Puna. Despite the ongoing ambiguity surrounding Cranaidae’s taxonomy and generic boundaries, we tentatively place this species within Puna.

Family Nomoclastidae Roewer, 1943

Genus Globitarsus Roewer, 1913 transl. nov.

- Globitarsus Roewer 1913a: 145. Type-species by monotypy: Globitarsus angustus Roewer, 1913.

  Taxonomy. DS outline type zeta, the number of scutal areas, morphology of pedipalps without dorsal ornamentation and ocularium, scutal areas, and legs ornamentation are all consistent with Nomoclastinae (Nomoclaster-like) and not with Cranaidae or Prostygnidae.

Genus Lisarea Roewer, 1943 transl. nov.


  Taxonomy. DS outline type zeta, the number and ornamentation of scutal areas, and morphology of pedipalps and ocularium, and legs length and ornamentation are all consistent with Nomoclastinae (Nomoclaster-like) and not with Cranaidae or Prostygnidae.

Genus Meridanatus Roewer, 1943 transl. nov.

- Meridanatus Roewer 1943: 34. Type-species by monotypy: Meridanatus berlandi Roewer, 1943.

  Taxonomy. DS outline type beta, the number of mesotergal areas, morphology of pedipalps, ocularium, and legs ornamentation are all consistent with Nomoclastinae (Quindina-like) and not with Cranaidae or Prostygnidae.
Genus *Micropachylus* Roewer, 1913 transl. nov.

Taxonomy. DS outline type zeta, the number of mesotergal areas, morphology of pedipalps and ocularium, and legs length and ornamentation are all consistent with Nomoclastidae (*Nomoclastes*-like) and not with Cranidae or Prostygnidae.

Genus *Prostygnidius* Roewer, 1915 transl. nov.

Taxonomy. DS outline type zeta, the number of mesotergal areas, morphology of pedipalps without dorsal ornamentation, and shape of the femora, ocularium, and legs length and ornamentation are all consistent with Nomoclastidae (*Nomoclastes*-like) and not with Cranidae or Prostygnidae.

Genus *Troya* Roewer, 1914 transl. nov.

Taxonomy. DS outline type zeta, the number of mesotergal areas, morphology of pedipalps and ocularium, and legs length and ornamentation are all consistent with Nomoclastidae (*Nomoclastes*-like) and not with Cranidae or Prostygnidae.

*Troya isabellina* (Roewer, 1943) comb. nov.

*Troya pustulata* (Roewer, 1915) comb. nov.
- *Prostygnidius pustulatus* Roewer 1915: 103, figure 56.

*Troya riveti* Roewer, 1914
- *Troya riveti* Roewer 1914: 133, pl. 13, figures 8–8a.

4. Discussion

Even though the composition of Prostygnidae has undergone drastic changes over time and its definition has been mostly incomplete, for the past few years, this family has been unequivocally placed in the immediate vicinity of Cosmetidae. Furthermore, it is no longer considered to be closely related to or nested within Cranidae, as was initially believed since the conception of the family [7].

A recent molecular study using UCEs confirms its position inside the clade that includes Metasarcidae and Cosmetidae (MECO) [14] (figure 2), as was initially suggested by Villarreal and García [9] and supported in the topology of the phylogenetic trees obtained by Kury [6] (figure 6), Villarreal [10] (figure 1), Medrano et al. [13] (figure 7).

The shape of the VP; the structure of the macrosetae and microsetae; and, especially, the presence of a wattle ventrally on the stylus firmly place *Prostygnus* and allies in MECO. However, the internal relationships within MECO are still uncertain. The more recent morphological analysis by Medrano et al. [13] proposed Prostygnidae as the sister group.
of Cosmetidae, with Metasarcedidae outside, whereas the molecular analysis proposed by Derkarabetian et al. [14] inverted this relation, with Prostygnidae being the sister-group of Cosmetidae + Metasarcedidae.

The presence of lateral spiny sacs on VP is a synapomorphy for the species of Metasarcedidae [27] and are, therefore, absent in Prostygnidae, and the pedipalpal shape, with a compressed femur and foliar patella and tibia, is also a synapomorphy for the species of Cosmetidae. The pedipalps of Prostygnidae are usually strong, with dorsal ornamentation on the patella and tibia (tuberculated), which initially led to the hypothesis of their relationship with Cranidae. The type and distribution of microsetae on the VP in Prostygnus are reminiscent of those of Cosmetidae and not the typical pattern of Cranidae, as shown in Kury [11]. The strongly dimorphic chelicerae and carapace, and the DS outline shape of Prostygnidae with a relatively long coda and well-marked lateral constrictions, resemble the conditions found in some early derivative Cosmetidae, such as Metergininae. Given the comparative morphology of several cosmetid styli, as presented in Medrano and Kury [40], the proystgnyd wattle resembles that of Flirtea picta (Perty, 1833) more closely, by starting midway along the stylus and without stylar bars.

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