

Review

# The Elasmobranch Fossil Record of the Indo-Australian Archipelago since the Miocene: A Literature Review and New Discoveries from Northern Borneo

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**Abstract:** The Indo-Australian Archipelago (IAA) today exhibits the highest marine biodiversity, which has been evolving since the early Miocene. The existence of this high palaeobiodiversity is attested to by the presence of many fossil invertebrates; however, the region's fossil fish record is sparse and understudied, which is also the case for cartilaginous fishes. Elasmobranch fossils are dominantly represented by shark and ray teeth in the geological record and can give a quick overview of the composition of the fauna. The first IAA elasmobranch fossils, shark teeth were described from Java (Indonesia) at the end of the 19th century, and until today, most of the publications are known from this island. In the early and middle of the 20th century, remarkable fossils were also reported from the islands of Madura (NE Java) and Sulawesi, some with detailed taxonomical descriptions. In addition, only sporadic reports on fossil occurrences exist elsewhere from the IAA, but these lack any detailed taxonomic accounts. In 2019 our research group reported a late Miocene elasmobranch fauna from Brunei (Borneo), which is now the most diverse known shallow water fossil assemblage from the entire IAA. This fauna was described from a single fossiliferous outcrop, called Ambug Hill. However, several new localities have been discovered and studied over the years, as a result the number of fossils increased, and their age range extended. Here we provide an overview of these new sites and their elasmobranch fossils, and describe remains from ten taxa among, of which eight are new to the IAA fossil record (*Chiloscyllium* sp., cf. *Hemitriakis* sp., *Paragaleus* sp., *Carcharhinus borneensis*, *C. limbatus*, *Lamiopsis* sp., *Scoliodon* sp., *Rhinobatos* sp.). The overall north Bornean elasmobranch assemblage is then compared with other IAA occurrences. An extended fauna list is given based on literature review and preliminary investigation of the Naturalis Biodiversity Centre collection in Leiden (The Netherlands) where most of the fossil fishes of the early explorations are stored. These assemblages are also briefly summarized, and attention is drawn to some of the unique and thus far unreported taxa (e.g., *Dalatias licha*).

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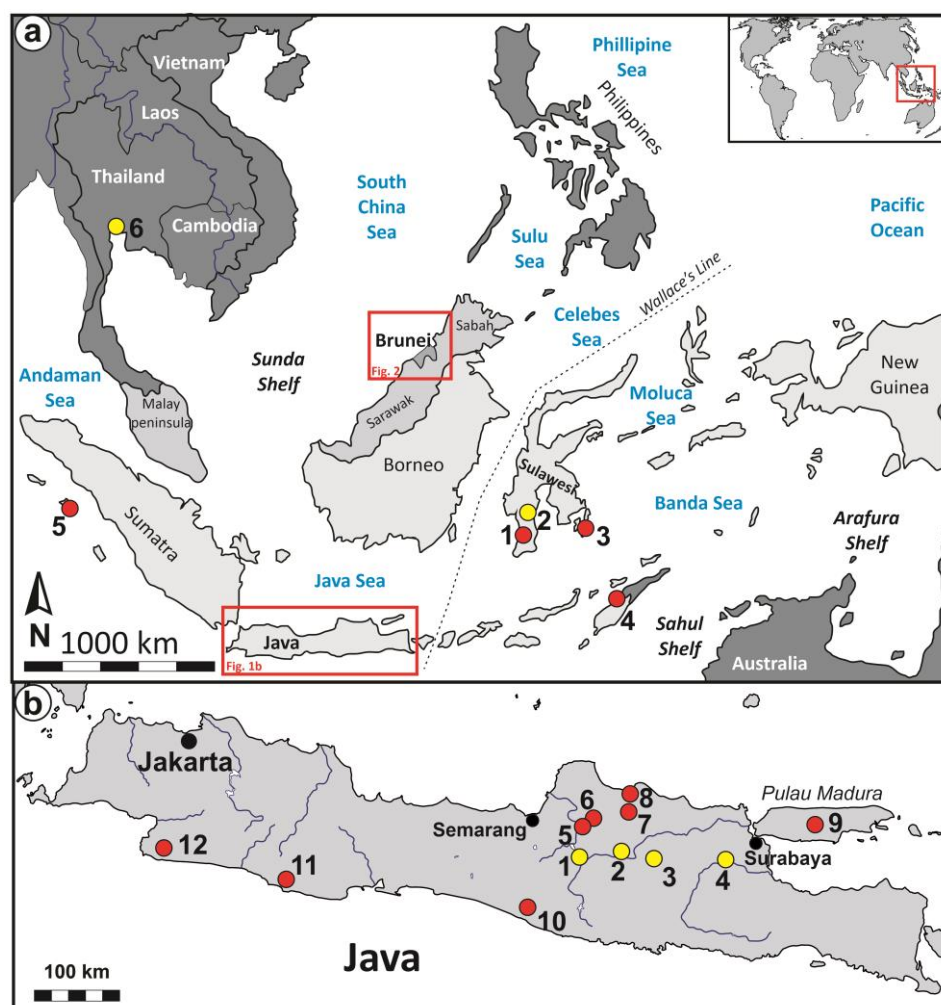
**Keywords:** Southeast Asia; shark; ray; fossil; palaeobiodiversity

## 1. Introduction

In Southeast Asia, the Indo-Australian Archipelago (IAA), also often called the Malay or Indonesian archipelago, currently have the greatest marine biodiversity on Earth, among these the highest species richness of marine fishes [1,2]. However, the fossil record of these organisms in the region is understudied, and our knowledge on large scale palaeobiodiversity and its evolution through time is therefore very sparse. In this study we focus on the elasmobranch fossil record of the IAA from the Neogene and Quaternary periods (the last 23 million years). Elasmobranchs have quick tooth replacement, and depending on the species, an individual can shed several hundreds of teeth during their lifetime. Together with the high preservation potential of their teeth, which are composed of bioapatite, it is not surprising that shark and ray teeth are among the most common

vertebrate remains in marine Cenozoic beds. Body fossils of these fishes are much rarer in the fossil record due to their cartilaginous skeleton, which degrades more readily after the death of the fishes and during diagenesis in the sedimentary environment. Therefore, such remains can be preserved and found only in special depositional settings.

Elasmobranch fossils have been known from the IAA since the 19th century, and the first publication came from Central Java's Miocene beds in Indonesia [3] (Figure 1). Since then, most of the studies report elasmobranch remains from Miocene to Quaternary beds from Java, e.g., [4–7], Sulawesi [8,9], and some nearby islands such as Madura in the northeast of Java [10] and Buton in the southeast of Sulawesi [11,12]. It is likely that marine deposits in other islands of the IAA also contain elasmobranch fossils, and therefore a targeted study of these remains would reveal more about their distribution in space and time. Our knowledge of these fossils is currently limited to key regions such as the island of Sumatra in Indonesia or the archipelago with hundreds of islands in the Philippines. Borneo has also long been a blind spot; however, our relatively recent, long-term research has revealed an elasmobranch fauna from one single outcrop (Ambug Hill) [13], which showed higher elasmobranch diversity than the rest of the known occurrences in the IAA [14]. This highlights the fact that regular field surveys combined with screen-washing methods can uncover the hidden values of fish palaeobiodiversity. Here, we provide a detailed literature review of the IAA's fossil–elasmobranch record, and an updated fauna and occurrence lists from northern Borneo with the description of newly found taxa. In addition, the IAA collection of the Naturalis Biodiversity Centre in Leiden (RGM) was examined, where many of the specimens published in the older literatures are stored. A combined IAA fauna list is put forward with this preliminary investigation.



**Figure 1.** Fossil elasmobranch localities from the Indo-Australian Archipelago (IAA) known from the literature or from museum specimens. **(a)** 1. Patoenoeang [8,15]; 2. Beru-Sompoh [9], 3. Waisioe, Buton Island (RGM); 4. Timor (RGM), 5. Nias (RGM), 6. Bangkok Clay Thailand [16]. **(b)** Java: 1. Sangiran [17], 2. Trinil [6], 3. Kedung Brubus (RGM), 4. Jetis-Perning (RGM); 5. Ngembak [3], 6. Grobogan [6], 7. Blora-Nanas (RGM), 8. Rembang (RGM), 9. Durin, Madura (RGM, [10]), 10. Kleripan (RGM, [11]), 11. Cimindi and 12. Surade [18,19]. Yellow and red symbols indicate Holocene–Pleistocene and Pliocene–Miocene sites, respectively.

## 2. IAA's Fossil Elasmobranch Record—A Literature Review

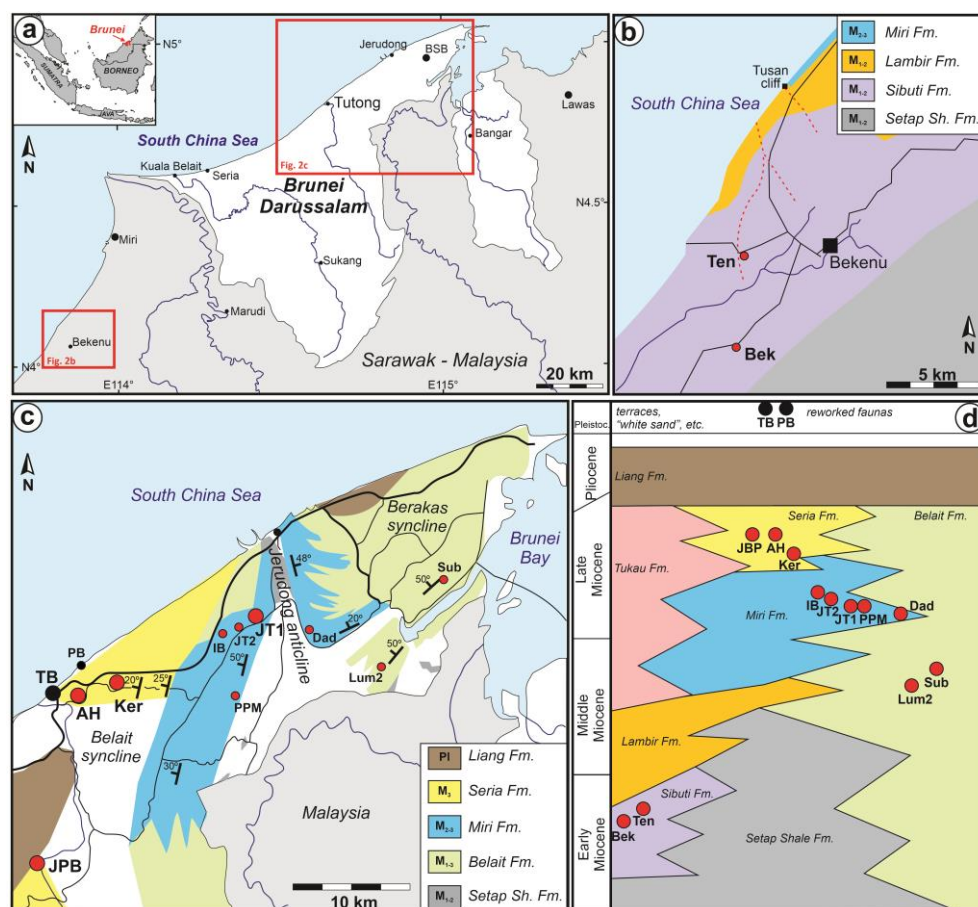
The first published report on elasmobranch fossils with illustration and description is from the Island of Java in Indonesia and is found in the work of Martin in 1883 [3]. The material comes from an oil-bearing limestone near Ngembak, possibly from the middle–late Miocene [20]. Martin described nine shark taxa based on teeth, among them three new species: *Galeocerdo javanus*, *Carcharias (Prionodon) javanus*, and *Carcharias (Prionodon) dijki*. Today these species names have only a historical significance and are no longer valid [14]. Martin also reported IAA's first *Otodus megalodon* tooth from Ngembak with the mention of other known specimens from Selatajau (West Java) and Madura Island (NE of Java) [3]: (pp. 23–24) (Figure 12). During the early part of the 20th century, several expeditions were undertaken in order to investigate the Pleistocene beds of Central and East Java for studying early human fossils (e.g., Trinil). Some of the excavations and collection trips also discovered sporicidal fish remains, among them some shark teeth, shark vertebra, and rostral tooth of a saw fish [4,21]. These fish fossils were included in the fauna list of Martin's palaeontology and geology book about Java [20]. Later, full body fossils of fishes were discovered in southeast Sulawesi in micritic laminated limestones of the late–early Miocene age [22], while the only known IAA elasmobranch body fossil, a sting ray, was also reported from these beds [8]. This exceptional fossil was recently restudied and renamed as *Protohimantura vorstmani* [15]. Then, early Miocene shark teeth were described from the base of the Kleripan Mn ore mine from Java's Yogyakarta region [11]. Seven taxa are mentioned, including *O. megalodon*. Interestingly, Beaufort has also briefly commented on the presence of this species from Buton Island (SW Sulawesi), where the teeth were found in asphalt-bearing limestone (Kabungka) [11]. In fact, these teeth were used for assessing a younger age of late Miocene–Pliocene for these deposits than the previously thought Oligocene age [12].

In 1931, Beaufort provided a summarized fossil fish fauna list for the IAA, among them Cretaceous fishes from Timor [23]; meanwhile, the Neogene fauna list contains the following genera based on modern nomenclature and preliminary revision: *Isurus*, *Otodus*, *Hemipristis*, *Carcharhinus*, *Galeocerdo*, *Pristis*, and *Protohimantura* [5]. Later, the Dubois collection from Java was reinvestigated by Kouman (1949) [6]. However, beside the Pleistocene remains of Trinil, he reported *O. megalodon* and *Isurus* teeth from localities near the Rembang Zone (Grobogan, Nanas-Blora) that are possibly of the middle–late Miocene age. Among the Trinil fossils, the teeth of the so-called river shark (*Glyphis*) are the most common. In 1954, selachian remains appeared in the publication of Leriche (1954) [10] from Madura Island (NE of Java), including only two taxa: *O. megalodon* that is represented by small-sized teeth, and *Hemipristis serra*. These probably originated from mid–late Miocene beds, with a similar age as that of the shark remains of the Rembang Zone in northeast Java. In the same year, a Pleistocene elasmobranch fauna was described from the Sopeng District of southwest Sulawesi [9], with the following updated genus list: *Carcharias*, *Isurus*, *Hemipristis*, *Carcharhinus*, *Glyphis*, *Galeocerdo*. In addition, a fragmentary Myliobatiformes spine was reported. Apparently, these remains were not found in situ, which, given the fact that most of the fossils are worn and broken, means that the material could have been reworked from older, late Neogene marine sediments. In 1978, four selachian and two batoid taxa were reported from the Pleistocene Sangiran Formation, with only two of these figured and described: sawfish rostral teeth and river shark teeth [17]. However, based on the illustration, the shark teeth more likely belong to the genus

*Carcharhinus*, and most possibly to the species *C. amboinensis* [14]. Most of the mentioned fossils described in the last centuries are deposited in the fossil collection of the Naturalis Biodiversity Centre in Leiden, The Netherlands. However, several collections exist in Indonesia, especially in Java (Bandung, Sangiran, Yogyakarta), which were recently investigated by Yuda et al. (2018) [7]. They studied over 150 Plio–Pleistocene shark teeth and sorted them into seven families (Odontaspidae, Lamnidae, Otodontidae, Alopiidae, Hemigaleidae, Carcharhinidae, Sphyrnidae). However, based on the few illustrations provided, some of the identification need thorough revision and the presence of some of the listed families need firmer proof. Still, studying the fish fossils at local institutes closer to the fossil bearing sites is encouraged and should be continued. Even more recently, late Miocene–Pliocene fossil shark discoveries have been reported from West Java in local journals [18,19], where the authors focused on the enigmatic *Otodus megalodon*. Other than the Indonesian fossil elasmobranch literature, and a recently published mid-Holocene fauna from the Bangkok Clay in Thailand [16], our works from northern Borneo conclude the known published elasmobranch record of the IAA (see below).

#### *Brunei and Eastern Sarawak (Malaysia)*

In 2019, our research group published a report on the most diverse shallow water fossil elasmobranch assemblage from the entire IAA from one single late Miocene locality in Brunei called Ambug Hill [14]. Twenty-four elasmobranch taxa were reported from four selachian (Otodontidae, Hemigaleidae, Carcharhinidae, Sphyrnidae) and six batoid families (Pristidae, Rhinidae, Dasyatidae, Aetobatidae, Myliobatidae, Rhinopteridae). Besides two extinct shark species (*Otodus megalodon*, *Hemipristis serra*), the fauna contains elements that are closely related to modern taxa. Previously, only sporadic reports and occasional photos of shark teeth occurred in geological books from Brunei and from Sarawak, the nearby state of Malaysia in Borneo [24]: (p. 91, xvi); [25]: (pp. 93–94); [26]: (p. 229). We have also reported a detailed description of small *O. megalodon* teeth known from Brunei [27], and a reworked fauna represented by six shark and one ray taxa discovered on the Penanjong beach in Brunei [28]. Besides Ambug Hill and the Penanjong beach, several other Neogene localities yielded elasmobranch remains from Brunei. Here, we provide a new list of outcrops with brief geological background (Figure 2) and an updated fauna list for the region's Neogene elasmobranch assemblages. The discovered new taxa are illustrated and described more thoroughly here.



**Figure 2.** Fossil elasmobranch localities from Brunei and Sarawak. (a) Overview map of the area. (b) Geological map of the Sarawak sites. (c) Geological map of the Bruneian sites. Note that the size of the symbols reflects the amount of elasmobranch fossils found at the sites (big symbol > 15 specimens). (d) Temporal distribution of the studied sites and their lithostratigraphic units. Red dots are outcrops, black dots are sites where the fossils found reworked.

### 3. Geological Background

Brunei is a small country on the northern coast of Borneo Island in Southeast Asia. Its geology was extensively studied during mapping and in the search for natural resources, e.g., [24,29,30], and its geological heritage of large oil and gas reservoirs are still an important part of its economy [25]. The sedimentary rocks have a siliciclastic origin and are dominantly deposited in shallow marine coastal settings and tide- and wave-influenced deltas from the early Miocene onwards [31,32]. Besides the economic importance, some of the sedimentary layers are very rich in marine and terrestrial fossils, and intensive palaeontological research has started only recently. These investigations have revealed diverse marine fauna, often with taxa new to science or to the region [14,33–35] and noteworthy floral remains [36–38]. These fossils come from four lithostratigraphic units (Figure 2): Belait, Miri, Seria, and Liang formations [25]. The Belait Formation is of the early-to-late Miocene age and mostly contains thick-bedded sandstone and claystone. Its total thickness is more than 6 km. The sediments represent shallow water facies with a strong deltaic influence. Occasionally, fossil-rich beds occur along the succession, but other than trace fossils, the rocks are very often barren, and if any calcareous remains occur those are often badly preserved. The upper part of the unit is intercalated with the late Miocene Miri and Seria formations in Brunei. It should be noted that some authors consider these formations locally as part of the Belait Formation and its more distal developments, e.g., [39,40]. The Seria Formation is younger and conformably overlies the Miri Formation. Both units represent shallow marine facies. Generally, their sedimentary successions are

built up of several parasequences that start with claystone beds at the bottom and grade into coarser sediments of siltstone and sandstone with erosional surface towards the top before a new cycle starts. The thickness of the individual sequences varies. The basal claystone layers are often rich in marine fossils. Both in abundance and diversity the fauna of the Seria Formation is richer compared with the Miri Formation and probably represent more open marine conditions, e.g., [34,41]. All of these lithostratigraphic units are covered by the Pliocene Liang Formation, which contains sediments of lagoonal and fluvial origin, often intercalated with thick conglomerate beds, and claystone–siltstone rich in plant remains [38].

The fossiliferous marine beds of key outcrops were further dated using Sr-isotope stratigraphy (SIS), and an age range of 13.5 to 6.5 My (Serravallian, Messinian) was determined [42]. Several marine fossils, dominantly vertebrates, were found to be re-deposited along the shoreline near Tutong town at the Tutong and Penanjong beaches [28,42]. Selected fish remains yielded SIS ages associated with the late Miocene, indirectly suggesting an origin from the Seria Formation [42].

Elasmobranch fossils are known from the marine beds of the mentioned lithostratigraphic units (Belait, Miri, and Seria), and as reworked remains from the beaches near Tutong. A summary of these localities and their fossil elasmobranch content is provided in this paper (Table 1). Some shark teeth were also reported from Sarawak (Malaysia) near the border of Brunei from the older part of the Miri Formation and from the early Miocene beds of the fossiliferous Sibuti Formation [26]. Fossiliferous layers outcropping near Bekenu, were also dated using SIS, which provided ages from 17.7 to 16.7 Mys (Burdigalian) (Figure 2) [42], and hence could be considered, so far, as the oldest known Neogene elasmobranch sites in northern Borneo.

## 4. Materials and Methods

### 4.1. Brunei and Sarawak

From 2014 till 2022, we conducted several geological field surveys and collecting trips to the fossiliferous beds of the Belait, Miri, and Seria formations in Brunei. Among our studied sites, many yielded only a small number of sporadic elasmobranch fossils, while others are rich in shark and ray teeth [14,41]. The oldest studied sites are from the Belait Formation near Subok (Sub) and Lumapas (Lum2) and are from the middle Miocene age. The Miri Formation is represented by five sites: Dadap (Dad) from the eastern flank of the Jerudong anticline, and Pengkalan Panchor Murai (PPM), Tanjong Nangka (JT-1), Jalan Tutong 2 (JT-2), and Ikas Bandung (IB) from the western flank. The localities of the Seria Formation are further west and southwest, with the following outcrops: Keriam (Ker), Ambug Hill (AH), and Jalan Pak Bidang (JPB). In addition, fossil vertebrates were collected on the Tutong (TB) and Penanjong (PB) beaches near Tutong town.

The bigger fossils were hand-picked on the surface of the sites, especially after big rains, while many clay-rich fossiliferous layers were screen-washed for micropalaeontological studies [35,41]. The latter approach also yielded micro-elasmobranch remains and resulted in many taxa, especially batoids, that have not been previously known from the IAA's fossil record [14]. Two fossiliferous sites in Sarawak were also occasionally visited (Bek on Bekenu Road and Ten in the Tengah outcrops), and some elasmobranch teeth were recovered (Table 1, Figure 2).

### 4.2. Leiden Collection (RGM)

The Southeast Asian Neogene elasmobranch collection of the Naturalis Biodiversity Centre in Leiden (RGM) was studied in 2023. The material consists of over 400 specimens from Indonesia, and contain mainly shark teeth, some ray teeth and caudal spines, and one exceptional body fossil of the stingray *Protohimantura vorstmani* [8,15] (Appendix Tables A1 and A2). Most of the fossils were collected in the beginning and middle of the last century and are dominantly from the islands of Java (59.4%) and Sulawesi (39.3%). The

remainder consists of some teeth from Nias Island, west of Sumatra ( $n = 1$ ); Madura Island, northeast of Java (2); and Timor (1), and Buton Island, southeast of Sulawesi (2). Many of the specimens appear in old literature [3,6,9], but there are exceptions that have never been published (e.g., the Jetis collection by J. Cosijn; the Sangiran collection by G.H.R. von Koenigswald—note that specimens from his 1978 publication were not found in Leiden). There are also publications from the same regions and similar stratigraphic units, but the specimens are not in the Naturalis collection (Trinil: [21]; Madura: [10]). Key elements of the fauna are illustrated in Appendix C Figures A1–A4.





Myliobatiformes	Dasyatidae	<i>Himantura</i> sp.	+		+	+	+			
		<i>Pastinachus</i> sp.	+		+	+		+	+	
		<i>Taeniurops</i> sp.				+				+
	Aetobatidae	<i>Aetobatus</i> sp.	+	+		+		+	+	
	Myliobatidae	<i>Aetomylaeus</i> sp.	+			+				
		<i>Myliobatis</i> sp.-1	+		+	+	+	+		
		<i>Myliobatis</i> sp.-2	+			+				
	Rhinopteridae	<i>Rhinoptera</i> sp.	+		?	+				
cadual spines			+			+				

## 5. Results

### 5.1. Brunei and Sarawak

Several Miocene localities containing marine deposits in Brunei and Sarawak yielded elasmobranch teeth, but most of these produced only a small number of sporadically found specimens. We report here 12 localities from Brunei and 2 from Sarawak (Figure 2 and Table 1). From the oldest beds (Sibuti in Sarawak and Belait in Brunei) only some teeth are known so far, meanwhile, from the claystone beds of the Miri Formation along the Jalan Tutong (e.g., JT-1) somewhat more remains were recovered (>10). Contrary to this, the Seria Formation localities are much richer in shark and ray teeth (AH > 400, JPB > 50; Ker > 20). From many of these latter sites, lots of small bones and teeth were found in the screen-washed residue (>0.5 mm), among them elasmobranch teeth. However, the material is fragmented and often only the tooth crowns are preserved. Still, several new taxa have been found based on the few, exceptionally preserved remains from Ker, JPB, and JT-2. Here, these newly discovered taxa are described and illustrated (see systematic chapter and Figures 3–8). These fossils are inventoried in the Geological Collection of the Natural History Museum Universiti Brunei Darussalam (GUBD).

Contrary to the in situ localities, most elasmobranch remains were found on the Tutong beach (TB\*), with over 500 teeth. These fossils were washed out from the beds of the nearby Seria Formation. Many of the remains are worn and fragmented, and usually the bigger teeth are those that have survived the winnowing processes and wave actions along the coastline. The recovered fauna is very similar to those of Ambug Hill [14], though proportionally more specimens were found from the taxa of *Glyphis*, *Pristis*, and *O. megalodon*.

The Bruneian fossil teeth are black, grey, and sometimes brownish. However, due to longer exposure to weathering and sunlight, many teeth have changed their colour to white, and the longer the exposure, the more worn and fragmentary the teeth become. This change in colour is well-documented for example in some of the *Glyphis* teeth (Figure 7A,D) and in a *Lamiopsis* tooth (Figure 7I) the latter of which has a black labial side and a white lingual side. Sometimes the weathering is so advanced that the white enameloid of teeth falls off and is easily separable from the underlying dentine.

### Systematic Part

Class: Chondrichthyes Huxley 1880  
 Subclass: Elasmobranchii Bonaparte 1838  
 Superorder: Galeomorphii Compagno 1973  
 Order: Orectolobiformes Applegate 1972  
 Family: Hemiscylliidae Gill T.N. 1862  
 Genus: *Chiloscyllium* Müller and Henle 1937  
*Chiloscyllium* sp.

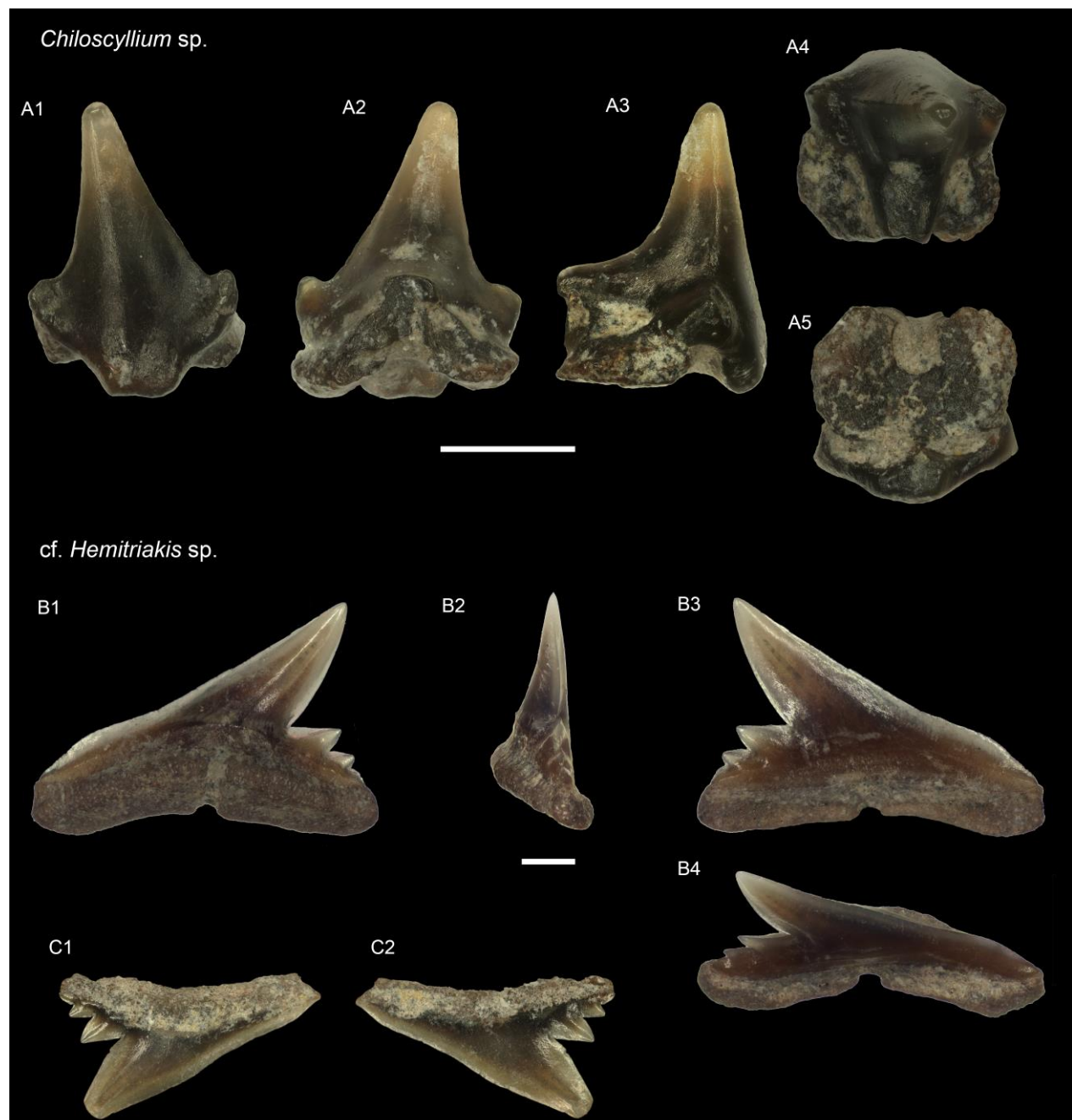
Figure 3A

Material: 1 tooth (Ker: GUBD V0250)

Description: A small tooth (W: 0.8 mm, H: 1.1 mm) with a slightly laterally inclined main cusp and two short, less developed lateral cusplets. The enamel forms a wide apron on the labial side that overhangs the base of the tooth. Its basal margin is slightly concave. The enameloid is smooth and lacks any ornamentations. Lingually a prominent uvula is present at the base of the crown. The very end of it, together with the lingual side of the root, is broken off. In lingual view the root shows two lobes, producing a generally concave base, which bears a large, rather lingually positioned basal opening. Though it is filled with sediment, this opening contains a central foramen.

Remarks: The tooth reported here is very similar to the teeth of *C. plagiosum*, especially the lower anterolateral teeth [43]: (Plates 9–11: Figure 1a). The only difference is that the Bruneian tooth is somewhat higher and less wide. There are eight modern bamboo

shark species, among which five lives in the IAA region, including *C. plagiosum* [44]. The other species are *C. griseum*, *C. hasseltii*, *C. indicum*, and *C. punctatum*. The latter has teeth that lack the lateral cusplets [45]: (Figure 142), while the others have rather similar tooth morphology [45]: (Figure 142–*C. indicum*); [46,47]: (*C. griseum*). The other genus within the family, *Hemiscyllium* (epaulette sharks), has somewhat similar teeth but instead of lateral cusplets, the tooth bears rather enamel heels, while its main cusp is shorter [43,45]. The fossil tooth described here clearly belongs to the genus *Chiloscyllium*, though species identification is not possible based on only one specimen and without knowledge on dental variation among the modern species. Nevertheless, the Bruneian tooth is not only the first fossil bamboo shark record from the IAA, but also the very first fossil representative of the order Orectolobiformes in the region.



**Figure 3.** (A) Hemiscylliidae, *Chiloscyllium* sp. (Ker: GUBD V0250). (A1) Labial, (A2) lingual, (A3) lateral, (A4) apical, and (A5) basal views. (B,C) Triakidae. cf. *Hemitriakis* sp. (B) Lower tooth (JPB:

GUBD V0251). (B1) Lingual, (B2) lateral (distal), (B3) labial, and (B4) apicolabial views. (C) Upper lateral (Ker: GUBD V0252). (C1) Lingual, and (C2) labial views. Scale bars 0.5 mm.

Order: Carcharhiniformes Compagno 1973

Family: Triakidae Gray 1851

Genus: *Hemitriakis* Herre 1923

cf. *Hemitriakis* sp.

Figure 3B–C

Material: Two teeth, one lower (JPB: GUBD V0251) and one upper (Ker: GUBD V0252).

Description: Both teeth have a distally inclined main cusp with smooth cutting edge and mesial enamel heel, while on the distal heel two cusplets appear decreasing in size followed by a small enamel heel. Both the lingual and the labial sides of the crowns are smooth, though the bigger and better-preserved tooth (W: 3.1 mm, H: 2.2 mm) looks like having some small striae at the base of lingual side of the crown. This feature is very faint and might be the result of strain on the enamel. The bigger tooth has a mesial cutting edge that is straight and somewhat concave, while the small one (W: 2.4 mm, H: 1.3 mm) has a convex, slightly bulging cutting edge. The small tooth lacks most of its root, but the other one show bilobed feature with deep nutritive groove.

Remarks: Based on the mesial cutting edge, the bigger tooth was in a rather lower position, while the small tooth in upper one as seen for many triakids [48]. The teeth of the genera *Hypogaleus* and *Hemitriakis* are very similar to our teeth. The crown of the *Hypogaleus* teeth looks proportionally a bit higher, especially at the mesial heel, which makes the main cusp not as slender as the Bruneian tooth [48]: (Plate 14); [49]: (Plate 2). In case of many *Hemitriakis* the crown looks like slightly overhanging the root at the labial side [48]: (Plate 7); [50]: (Figure 3), which is not observable on our teeth. Nevertheless, the crown shape and the mesial cutting edge resemble more to that of the *Hemitriakis* teeth. Therefore, the fossils specimens here are described with open nomenclature as cf. *Hemitriakis* till new finds allow more exact classifications.

There are six known *Hemitriakis* species in the wider IAA region among which *H. japonica* is the most widespread and occurs from Korea till Australia. It has demersal habitat and lives from 20 to 345 m depth [44]. *Hypogaleus* is monospecific, and *H. hyugaensis* lives in similar depth range [51] but distributed in a wider range such as from East Africa till Japan and Australia [44].

Family: Hemigaleidae Hasse 1879

Genus: *Paragaleus* Budker 1935

*Paragaleus* sp.

Figure 4A–C

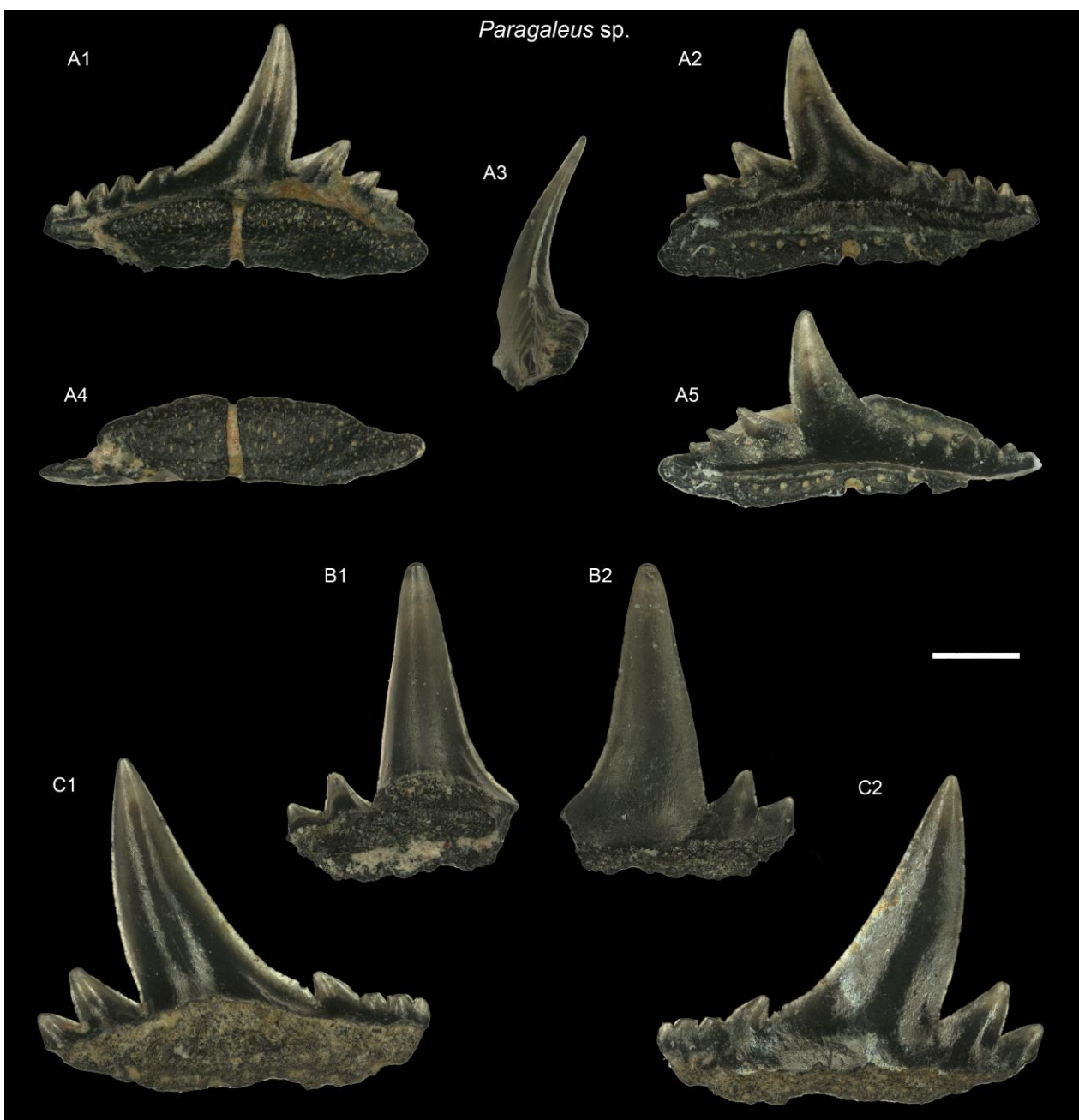
Material: 3 teeth (JPB: GUBD V0253).

Description: The best-preserved tooth is the smallest (W: 2.2 mm, H: 1.4 mm), that lacks only a small bit of its mesial root lobe. The crown's main cusp is distally positioned, slightly curved lingually, its mesial cutting edge is strongly concave, while the distal one is convex. The mesial heel bears five, the distal heel four small cusplets that are decreasing in size towards the margins. The cutting edges and the cusplets bear no serration, the crown surfaces are smooth. The root is low, it is divided into two lobes by a deep nutritive groove on the lingual side, which extends basally and forms a deep furrow. The labial side of the root have a series of bigger foramen. The biggest tooth lacks most of the root (W > 2.2, H > 1.9), but the preserved crown parts show features similar to the small tooth. The third is tooth even more fragmentary, nearly no root present, and the entire mesial part is missing. The crown is more erect and less inclined distally. This tooth could be in more anterior position.

Remarks: The general build-up of the teeth resemble that of the upper teeth of the genus *Paragaleus* [52]: (Plates 17–18); [53]: (Figures 3 and 6). However, these teeth have

main cusps with rather convex mesial cutting edge, and they do not bear mesial cusplets at all. Exceptions are some anteriors that may show concave cutting edge and occasional tiny, single cusplet on the mesial side, but these teeth are higher than wider that contrast of the here described specimens.

The teeth mostly resemble the lower teeth of the fossil species *Paragaleus pluchellus* [45]: (Figure 279); [54]: (Plate 62) that is mentioned from the European Miocene. This similarity is mainly due to the strong concave mesial cutting edge of the main cusp which is followed by several small lateral cusplets on the distal heel. However, none of the *P. pluchellus* bears multiple cusplets in the mesial heel. Therefore, this feature seems unique for the Bruneian teeth and may point to the presence of a new fossil species from IAA. However, due to the low number of teeth, describing a new taxon is not attempted here. Four modern *Paragaleus* species exist today, among which *P. tengi* lives the closest to Borneo in the northern part of the South China Sea [51].



**Figure 4.** (A–C) *Paragaleus* sp. teeth (JPB: GUBD V0253). (A) Lateral tooth, (A1) lingual, (A2) labial, (A3) lateral (mesial), (A4) basal, and (A5) apicolabial views. (B) Anterior tooth, (B1) lingual and (B2) labial views. (C) Lateral tooth, (C1) lingual, and (C2) labial views. Scale bar 0.5 mm.

Family: Carcharhinidae Jordan and Evermann 1896

Genus: *Carcharhinus* Blainville 1816

*Carcharhinus borneensis* (Bleeker 1858)

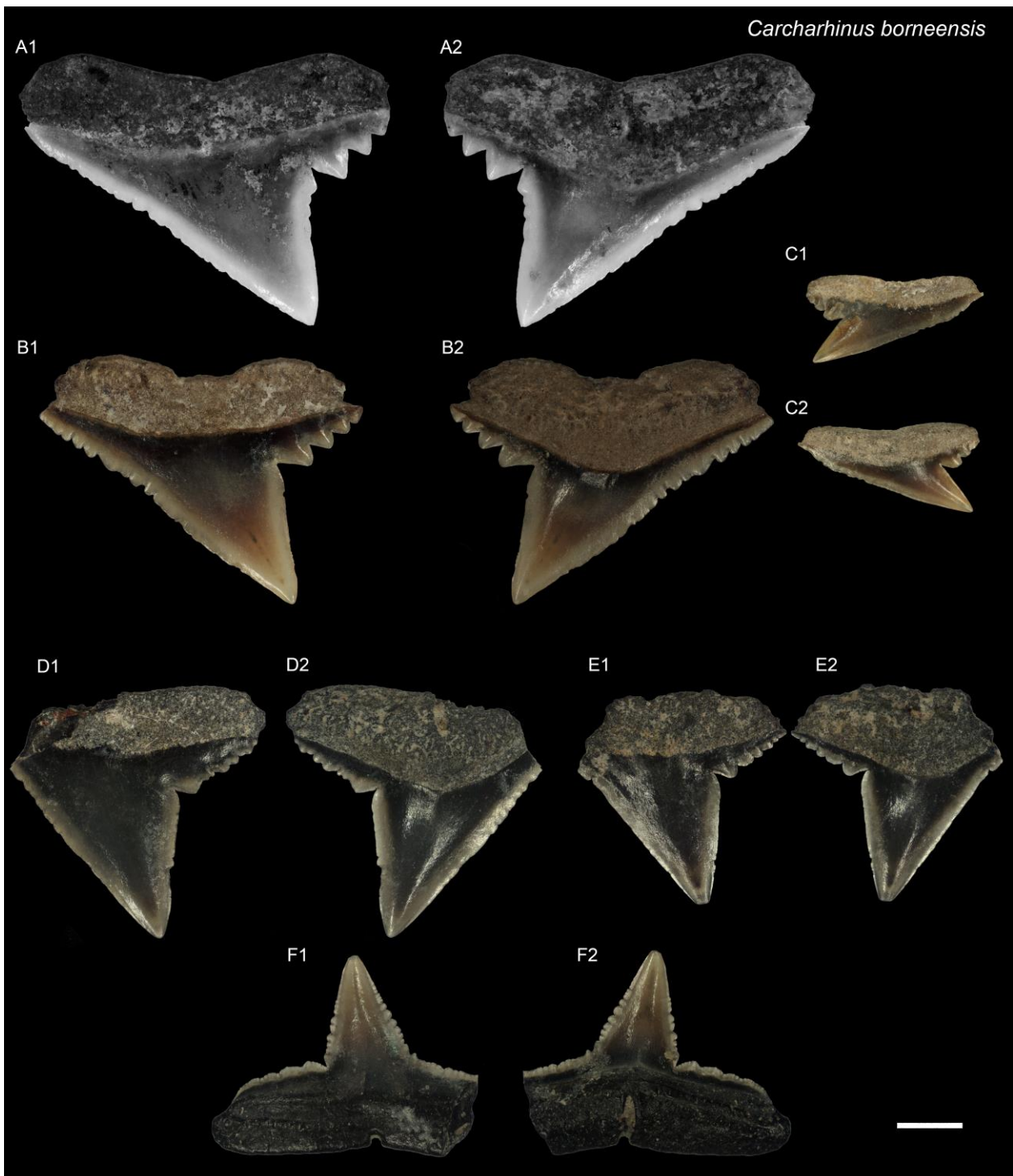
Figure 5A–F

Material: 5 upper teeth (Ker: 3, JBP: 2) and 1 lower tooth (JPB). (Ker: GUBD V0254, JPB: GUBD V0255).

Description: Small teeth with varying sizes and most missing some parts (uppers W: 2.7–5.4 mm H: 1.3–4.0 mm; lower: W > 4.4, H: 2.9 mm). The upper teeth have a distally inclined main cusp wide at their base. The mesial heel is straight to slightly convex, it bears small cusplets or coarse serrations that gets finer apically and diminishes completely at the apex. The distal cutting edge is smooth, and it is separated by a distinct notch from the distal heel. This latter has 3 to 5 cusplets reducing in size distally. However, on the teeth from JPB the cusplets less developed and the heel rather bears coarse serration (Figure 5(4)). The root is bilobed, runs parallel with the base of the crown. On the better-preserved teeth from JPB, a nutritive groove is visible.

The lower tooth has a triangular, slightly distally inclined main cusp, with both mesial and distal cutting edge strongly serrated, except the very tip of the crown. The serration continues on the mesial heel. The distal heel is separated by a notch and have small cusplets that are coarsely serrated. The root is horizontal, it bears a large nutritive groove, which extends basally.

Remarks: The teeth are mostly identical to modern *C. borneensis* teeth of female specimens [55]: (Figure 83), [56]: (Figure 3), and [57]: (Figure 9). The upper teeth with coarse serration on the mesial heel instead of distinct cusplets are considered a variation within the species. *C. obsolerus* also has similar teeth [57]: (Figures 4 and 5), however the mesial cutting edge is more concave than the straight or slightly convex specimens of *C. borneensis*. Additionally, the teeth of *C. sorrah* somewhat resemble the Bruneian fossil teeth; however, for this species the mesial cutting edge of the crown is more curved, while its distal cutting edge is always serrated [55]: (Figure 76), [57]: (Figure 9), [58]: (Plate 13). *C. borneensis* is a rare small carcharhinid species (TL up to 70 cm), endemic to the IAA, found inshore in coastal areas [51].



**Figure 5.** (A–F) *Carcharhinus borneensis* (Ker: GUBD V0254, JPB: GUBD V0255). (A,B) Upper lateral teeth (Ker). (C) Upper posterior tooth (Ker). (D,E) Upper laterals (JPB) and lower tooth (JPB). (1) Labial and (2) lingual views. Scale bar 1 mm.

*Carcharhinus sealei* (Pietschmann 1913)

Figure 6A

Material: One tooth (JT-2: GUBD V0256)

Description: A small upper anterior tooth (W: 4.6 mm, H: 4.9 mm). The tooth bears a distally inclined main cusp with smooth cutting edges. The mesial is straight to very slightly concave, while the distal is straight but turns convex apically. The mesial heel is narrow and smooth, whereas the distal heel has four, gradually decreasing cusplets. The

root is high on the lingual side, its base is nearly horizontal and has a basal furrow in the centre.

Remarks: From our previous study at Ambug Hill, seven upper lateral/anterolateral teeth and one lower tooth have been attributed to the species *C. sealei* [14] (Figure 5I–M). The newly found tooth displayed here was clearly in more of an anterior position in the upper jaw. Though the *C. sealei* upper teeth have fine to coarse serration on the mesial cutting edge, this feature might be worn from the fossil tooth. In fact, the presence of very faint former serrae might be seen in a closeup view on the labial side. The *C. sealei*–*dussumieri* complex includes at least four shark species that all have similar dentations [59]. The upper teeth of *C. dussumieri* and *C. tujoti* have a main cusp with serrated distal cutting edge and the lateral cusplets often bear secondary serrations, whereas *C. coatesi* has a more slender and narrower main cusp [59].

*C. sealei*, the blackspot shark, has been reported across the entire IAA. It has been observed in Malaysia, Indonesia, and the Philippines in southeast Asia. It is a small shark (~100 cm) inhabiting mainly the continental shelf area from the intertidal region to deeper water [51].

*Carcharhinus limbatus* (Müller and Henle 1839).

Figure 6A

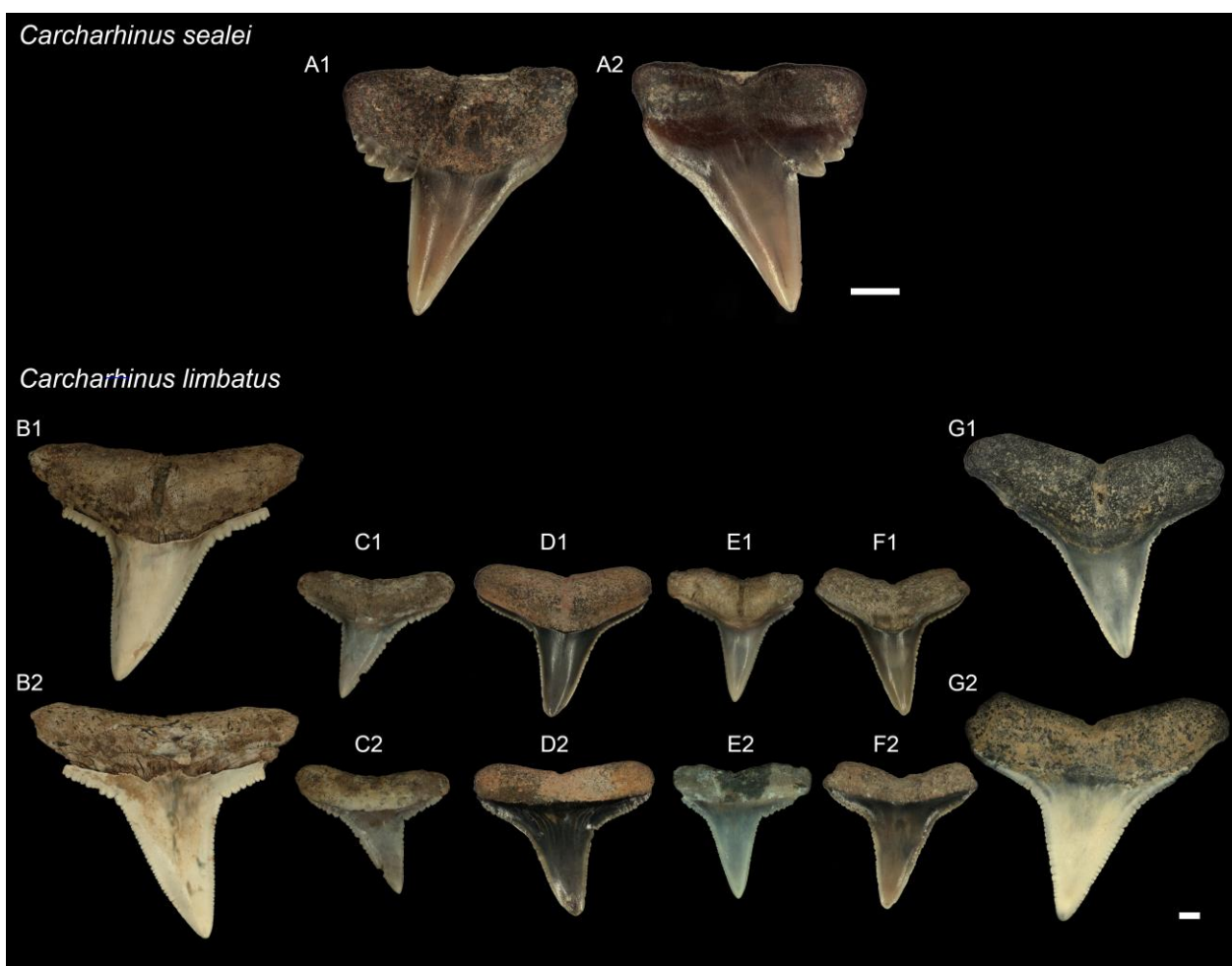
Synonym: *Carcharhinus* cf. *brachyurus* in [14]: Figure 5A–F.

Material: Six upper teeth (Ker: 2–GUBD V0257; JPB: 4–GUBD V0258).

Description: The teeth have a straight to distally inclined main cusp. Their cutting edges are straight or slightly convex, they are strongly serrated, but the serrae gradually disappears or gets finer towards the apex. The serration continues towards the mesial and distal heels, with an occasional small notch before the latter. The serrae on the heels become even coarser on some teeth. The root is bilobed, runs almost horizontally, and bears a deep nutritive groove.

Remarks: Similar teeth have been described from Ambug Hill under the name *Carcharhinus* cf. *brachyurus* [14]; however, after more careful examination and in the view of new specimens, it has been concluded that these teeth belong instead to *C. limbatus*. The upper teeth of *C. brachyurus* have a different mesial cutting edge, with stronger convex curvature, that sometimes seems to bulge out prominently [55]: (Figure 80), [58]: (Plate 11). However, the mesial cutting edge of the *C. limbatus* is rather straight or slightly convex as it inclines distally [55]: (Figure 18), [58]: (Plate 5). *C. limbatus* (blacktip shark) is a common shark in shallow marine and reef-associated environments in the tropical and subtropical regions [44].





**Figure 6.** (A) *Carcharhinus sealei* upper anterior (JT-2: GUBD V0256). (A1) Lingual and (A2) labial views. (B–G) *Carcharhinus limbatus* upper anterior and anterolateral teeth, (B,C,E,G) from JPB and (D,F) from Ker (Ker: GUBD V0257; JPB: GUBD V0258). (1) Lingual and (2) labial views. Scale bar 1 mm.

Genus: *Glyphis* Agassiz 1843

*Glyphis* spp.

Figure 7A–H

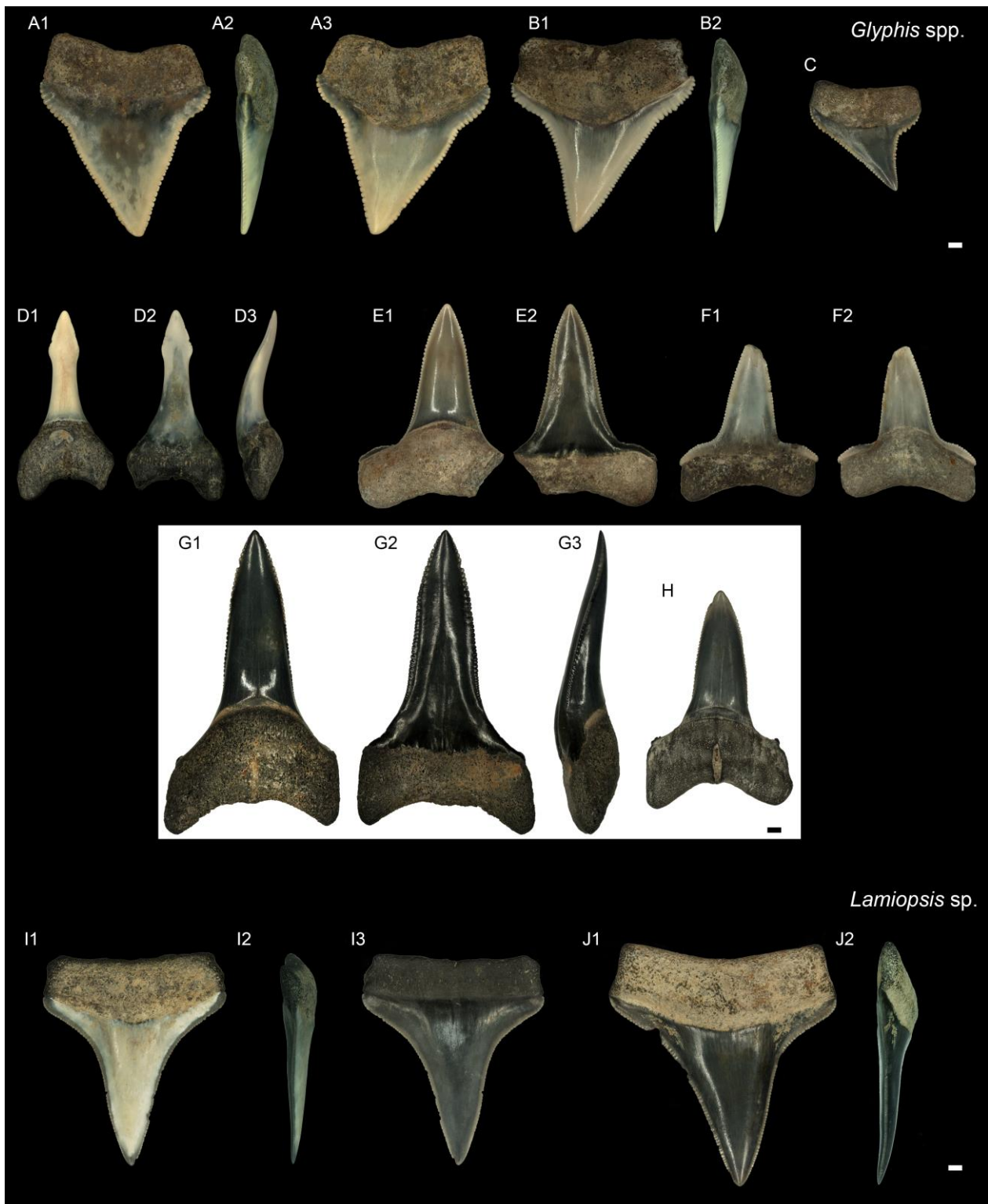
Material: Three upper teeth (Figure 7A–C) and four lower teeth (Figure 7D–H). (Ker: GUBD V0259–261, JBP: GUBD V0262–263).

Description: The teeth come in different sizes and shapes, depending on their position in the jaw and the age of the sharks. The upper teeth are labio-lingually flattened, their cusp is broad at their base and inclines distally on the anterolateral and lateral teeth. The cutting edges and the heels are strongly serrated. The roots have straight, nearly vertical mesial and distal margins, while at their base they are nearly horizontal. Two types of lower anterior teeth have been distinguished, one that possess a spearhead shaped apex (Figure 7D) and another that is only pointed (Figure 7G). Both are bent lingually and have a sinusoid shape in lateral view. The cutting edges of the pointed type are strongly serrated as far as the apex and may bear very small lateral cusplets. On the lateral teeth the cusplets are wide and serrated, and form rather mesial and distal heels. The root of the anteriors is strongly bilobed and the lobes form a U-shape. The lateral lower teeth have more horizontally extended root lobes.

Remarks: Several teeth from Ker, JPB, and TB\* have been discovered, here only the already inventoried are described and displayed. Both lower tooth morphology of spearhead vs. pointed apexed crowns appear in our record. The genus *Glyphis* are commonly

referred to as river sharks because they often occur and are observed in or nearby the large tropical river systems in the Indo-West Pacific [60]. There are five species according to FishBase [44] that are related to certain regions in south-southeast Asia and northern Australia and can be separated into two groups based on the tooth morphologies: (1) *G. fowlerae* (Borneo river shark), *G. gangeticus* (Ganges shark), and *G. siamensis* (Irrawaddy river shark) bear pointed apexed, “gangeticus” type of lower teeth. Based on DNA studies, these species are very closely related, and the data suggest recent gene flow between widely spread regional populations (Pakistan, India, Myanmar, and Borneo), and, in fact, these taxa are probably conspecific and could be regarded as *G. gangeticus* [61]. (2) The other two species, *G. garricki* (northern river shark) and *G. glyphis* (Speartooth shark) occur in the waters of northern Australia, Papua New Guinea and both bear spearhead shaped lower anterior teeth [62]. Even if they are overlapping in their habitat, genetically they differ enough to represent separated species [61].

The lateral cusplets and heels on the lower teeth are often regarded as specific for the *G. gangeticus* species [45]; however, such a feature can also be observed on the anterolateral teeth of some *G. glyphis* specimens [62]. Moreover, the upper teeth of these species can also be very similar. Therefore, it currently appears that the only undoubtful character is the apex shape of the lower anterior teeth. However, the question of how any of these characters vary during ontogeny and/or among populations, or whether there is any clear gender related variation in the dentation need to be further addressed in future research. Previously, few fossil *Glyphis* teeth had been reported from Ambug Hill [14] and, based on one spearhead shaped lower tooth, these were considered as *G. cf. glyphis*. Now, the Bruneian fossil record has both lower tooth types and these probably represent at least two species that coexisted during the Miocene in the coastal waters of northern Borneo. Nevertheless, these teeth are described here only as *Glyphis* spp.



**Figure 7.** (A–H). *Glyphis* spp. (A) Upper anterior (Ker: GUBD V0259a). (A1) Labial, (A2) lateral, and (a31C) lingual views. (B) Upper anterolateral. (B1) Lingual and (B2) lateral views (Ker: GUBD V0259b). (C) Upper lateral in lingual view (Ker: GUBD V0260). (D) Lower anterior. (D1) Lingual, (D2) labial, and (D3) lateral views (JPB: GUBD V0263). (E) Lower anterolateral. (E1) Lingual and (E2) labial views (Ker: GUBD V0261a). (F) Lower anterolateral. (F1) Lingual and (F2) labial views (Ker: GUBD V0261b). (G) Lower anterior. (G1) Lingual, (G2) labial, and (G3) lateral views (JPB: GUBD V0262a). (H) Lower anterior in lingual view (JPB: GUBD V0262b). (I,J) *Lamiopsis* sp. (JPB: GUBD V0264). (I) Upper anterolateral. (I1) Labial, (I2) lateral, and (I3) lingual views (JPB). (J) Upper anterolateral. (J1) Lingual and (J2) lateral views (JPB). Scale bars 1 mm.

Genus: *Lamiopsis* Gill 1862.

*Lamiopsis* sp.

Figure 7I–J

Material: Two upper teeth (JPB: GUBD V0264).

Description: Relatively large-sized teeth (W: 14–17 mm, H: 15–18 mm). They are labio-lingually flattened. Their cusp is relatively narrow, straight, and symmetrical, or slightly asymmetrical (Figure 7J). Their cutting edge and the mesial and distal heels are finely serrated. The root is horizontal or slightly bent basally, while their mesial and distal margins are vertical/subvertical.

Remarks: The fossil teeth most resemble the teeth of the modern species *Lamiopsis temminickii* (Broadfin shark) in their main cusp that is narrow at their base and their finely serrated cutting edges [63,64]. The other species, *L. tephrodes* (Borneo broadfin shark), has more similarity to the upper teeth of *Glyphis*, but their cusp is relatively higher and more erect [63]. It is worth mentioning that *Glyphis* and *Lamiopsis* are genetically closely related [61]. *Lamiopsis* is a coastal, shallow water shark in the tropical region of the Indian Ocean and the IAA and also tolerates brackish conditions [51].

Genus: *Scoliodon* Müller and Henle 1838.

*Scoliodon* sp.

Figure 8A

Material: One tooth (Ker: GUBD V0265).

Description: A worn tooth that lacks most of its root (W: ~2.6 mm, H: >2.1 mm). It has a slender main cusp that strongly inclines laterally. Its cutting edges are smooth. The long mesial edge has a strong sinusoid curvature. Under the main cusp appears a small wide-based cusplet.

Remarks: The tooth is very similar to the anterior tooth of the modern species *Scoliodon laticaudus* (spadenose shark) that is widespread in the Indo-West Pacific [52]: (Plate 27–28), [65]: (Figure 3). However, another species, the *S. macrorhynchus* (pacific spadenose shark), exists in the region [66] and its dentition is less known. As a result, the Bruneian fossil tooth is described only at the genus level. Several labio-lingually flattened crowns with elongated mesial cutting edge have been found (Figure 8B) that can fit the dentation of *Scoliodon*; however, other genera such as *Loxodon* or *Rhizoprionodon* may also be considered [52,65]. *Scoliodon* is a small shark with a maximum length of 80 to 100 cm. They live in tropical shallow seas and often migrate in brackish milieu.

Superorder: Batomorphii Cappetta 1980.

Order: Rhinopristiformes Naylor et al. 2012.

Family: Rhinobatidae Müller and Henle 1837.

Genus: *Rhinobatos* Linck 1790.

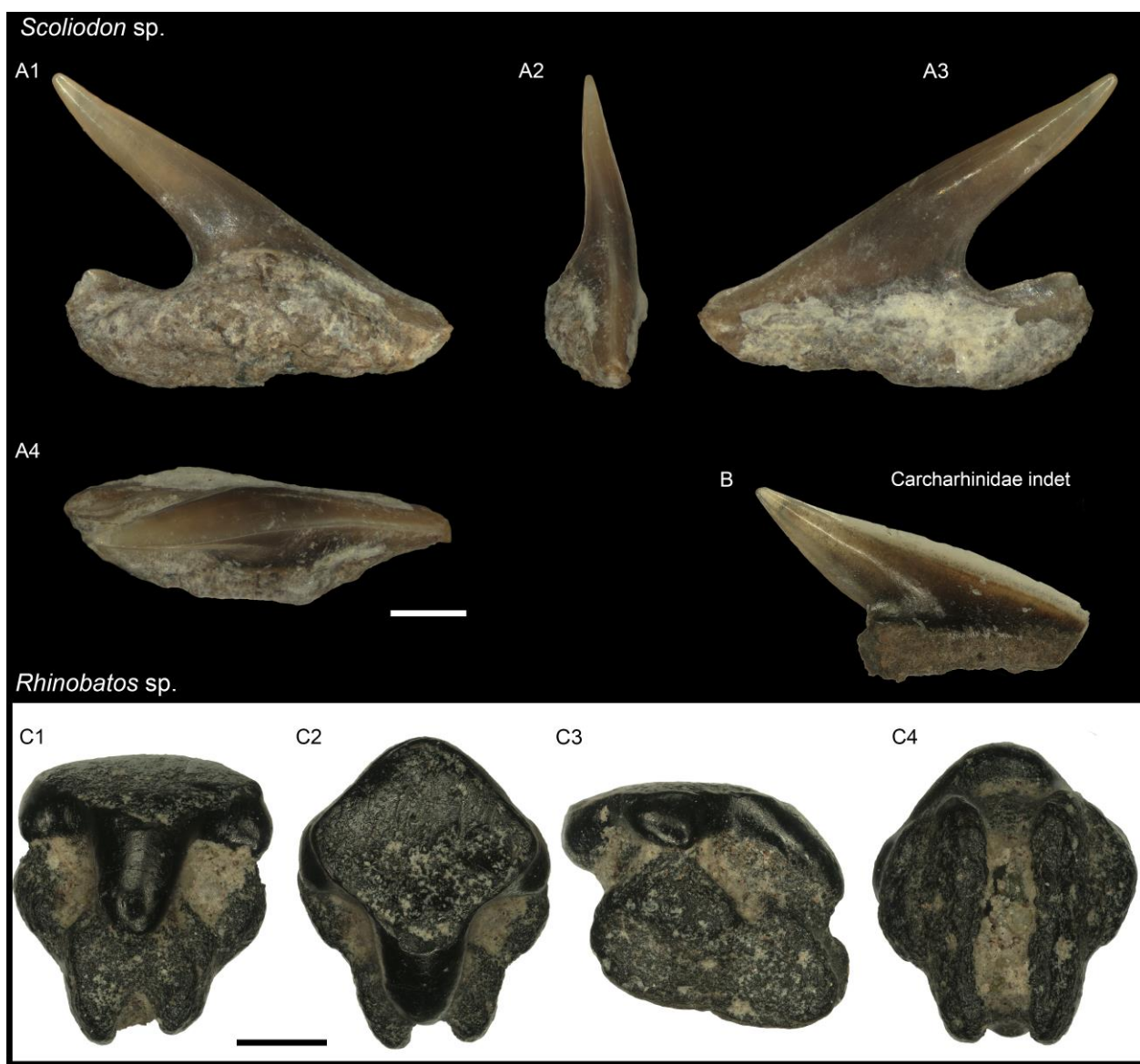
*Rhinobatos* sp.

Figure 8C

Material: Three teeth (JPB: GUBD V0266).

Description: The teeth are very small, but only one is fully preserved, which is displayed here (W: 1.4 mm, H: 1.6 mm). Its crown has a worn, flatten occlusal surface, probably due to dietary wear, otherwise the enameloid is smooth. The crown slightly overhangs the root labially. At the lingual side it has a prominent and long central uvula, while on both lateral sides a much less developed uvulae appears. The root is thicker than the crown and extends lingually. Basally between the two lobes a deep furrow occurs.

Remarks: The characteristic of these teeth concur with those of described from the genus *Rhinobatos* [45]: (Figure 332), [67]: (Plates 26–28). The morphology of these teeth shows minor variation among the species, hence the fossil teeth from Brunei are described only at the genus level. There are twenty *Rhinobatos* species, among which nine live in the wider IAA region [44]. Guitarfishes have a demersal habitat, and most of the IAA species have a total length of less than 100 cm.



**Figure 8.** (A) *Scoliodon* sp. (Ker: GUBD V0265). (A1) Lingual, (A2) lateral (mesial), (A3) labial, and (A4) apical views. (B) *Carcharhinidae* indet, lingual view, note that such a crown shape can be related to *Scoliodon*, *Loxodon*, or *Rhizoprionodon* genera. (C) *Rhinobatidae*, *Rhinobatos* sp. (JPB: GUBD V0266). (C1) Lingual, (C2) occlusal/apical, (C3) lateral, and (C4) basal views (JPB). Scale bars 0.5 mm.

### 5.2. Leiden Collection

In the collection of the Naturalis Biodiversity collection (RGM) 453 elasmobranch remains were investigated from several sites (Tables 2 and A1). Some specimens were found without indicating the exact locality (RGM.1332577–95, RGM.1332575, RGM.1332576); however, based on appearance, preservation, and their place in the RGM collection, they are assumed to belong to Cosijn's collection from the region of Jetis in East Java [68,69]. The updated fauna list and the collection number of the specimens are registered in Appendix Table A2. Many specimens have been revised and the proposed updated taxonomical names often differ from the ones appearing in the old literature.

Miocene remains cover only 10.4% of the entire IAA elasmobranch collection. Most of the specimens were collected a long time ago, e.g., [5,20] and the bulk of remains are from Java. Exceptions are the body fossils of the early Miocene *Protohimantura vorstmani* (Appendix Figure A1) [8,15] from Sulawesi, two *O. megalodon* teeth from each island, Buton and Madura, and a *Hemitpistis serra* tooth from Timor (Appendix Table A2). The most

interesting and unique element of the Miocene fauna, that has not been described so far, is the only known Squaliformes fossil of the IAA, a tooth of the deep-water shark *Dalatias licha* (kitefin shark) (RGM.42356, see Appendix Figure A2a). The specimen was found in Ngembak, probably during the expedition of Martin (1883) [3]. Other interesting parts of the fauna are the presence of more open water and large pelagic taxa such as the extinct species of *Cosmopolitodus hastalis*, already mentioned in Kouman (1949) [6]: (Plate II: Fig5—RGM.DUB.11643.a 1/4), and *Parotodus benedeni* (RGM.DUB.11643.a 1/4) (Appendix Figures A2b–c). The genus *Parotodus* has so far been mentioned only in the work of Yuda et al. 2018 [7]: (Figure 11) from Java; however, their *Alopias supersilius* specimen [7]: (Figure 9Y) most probably also belongs to the *P. benedeni* species.



Over 89% of the IAA elasmobranch teeth in the RGM collection were reported from Pleistocene beds, mainly from Java, e.g., [6] and from Sulawesi [9]. Moreover, two localities dominate the assemblages: the Sangiran site in Java (early Pleistocene) [70], which counts for 37.5%, while the Tjabenge region (Sopeng District) of Sulawesi covers 39.3% of all of the RGM remains. However, most of the teeth from the Sulawesi sites are badly preserved and clearly show the influence of transport. As they were not found in situ [9], they could have been reworked from older beds. At both sites, the most common taxa are the *Glyphis* and *Carcharhinus*. The most abundant species in the latter is the *C. leucas* (bull shark); however, sometimes their teeth can be confused with that of *C. amboinensis* [14]. Therefore, some specimens of these teeth are listed as *C. leucas/amboinensis* (Appendix Table A2, Figure A3a). Myliobatid and Rhinopterid teeth (e.g., *Aetobatus*, *Rhinoptera*) are also an important part of the Sangiran fauna (~20%), and in fact this is the only site in the RGM collection from which such teeth were found (Appendix Figure A3b–d). In addition, both sites contain the teeth of the fossil taxon *Hemipristis serra* that was common during the Neogene. The Sulawesi sites in fact represent the youngest report of this species [45], and here these teeth count for 10% of the assemblage. However, considering the possible reworked origin of this fauna, this “youngest” occurrence may not be adequate.

In addition, some teeth of more open water sharks, such as *Carcharias*, *Isurus*, and *Sphyrna*, were also collected in some of the Pleistocene localities. Other large-bodied taxa were also found and reported; however, these are considered to have become extinct by the time of the Pleistocene (e.g., Jetis—*Otodus megalodon*: RGM.1332571, Appendix Figure A4c or *Parotodus benedeni* [7]). Therefore, the stratigraphic origin of these teeth should be taken with caution (e.g., collection bias, stratigraphy and redeposition) and further investigations are needed to clarify their exact age.

Other intriguing parts of the collection are twenty-seven teeth of *Isurus paucus* (RGM.1332577–95) that clearly come from the same individual. The position of the teeth in the jaw is marked in the boxes, but unfortunately, not their origin. However, a rock specimen that contains two teeth, the imprint of a third, and also probably part of the jaw, was collected in Jetis by Cosijn (RGM.1320054). These teeth also belong to *I. paucus*, but they have a similar look, size, and preservation state as the teeth of unknown origin. Therefore, it can be proposed that they all belong to the very same specimen (Appendix Figure A4a–b). However, in future, the age of the Jetis marine fossils and their taphonomy should be further verified and assessed.

## 6. Discussion

The discoveries of new elasmobranch fossils from Brunei’s Miocene deposits are very exciting and our previous fauna list [14] could be extended by many new taxa (Table 1). The tiny bamboo shark tooth (*Chiloscyllium*) is the very first fossil representative of the entire order Orectolobiformes in the IAA. Nevertheless, the shark fauna is dominated by the Carcharhiniformes and, within it, by the Carcharhinidae family (Table 1, Figure 9). New requiem shark genera such as *Lamiopsis* and *Scoliodon* are also reported for the first time from the IAA’s fossil record. In addition, it can be assumed that at least two species of the river shark (*Glyphis*) co-existed in northern Borneo in the late Miocene. Within the genus *Carcharhinus*, the fossil teeth of the endemic IAA species, *C. borneensis*, were found for the first time, while the previously described *C. brachyurus* [14] was revised here and instead the presence of *C. limbatus* is confirmed. Other completely new elements of the fossil assemblage are the presence of Triakidae teeth (cf. *Hemitriakis*). Others are the tiny teeth of the genus *Paragaleus* within the family Hemigaleidae. Remarkably, these teeth are somewhat different from those of the modern and other known fossil taxa, and they may represent a new species. However, to clarify this, more specimens are needed, together with more detailed modern comparative investigations. Regarding the batoids, the first fossil IAA record of common guitar fishes (*Rhinobatus*, Rhinobatidae) is also described here. To sum up, the overall late Miocene elasmobranch assemblage list in northern Borneo has



been extended by eight new taxa. At this stage three shark and two batoid orders are known, and the recovered taxa are sorted into fourteen families (seven sharks and seven batoids) (Table 1, Figure 9). Remains of Carcharhiniformes and Myliobatiformes are the most common and abundant. Most of the described taxa are linked to modern species, but often only generic identification could be achieved, due to the similarities in dentation of closely related extant forms that undermine confident species description. Only two extinct species have been discovered, *Otodus megalodon*, the only representative of the Lamniformes order in Brunei, and the Hemigaleidae *Hemipristis serra*, a close relative of the modern snaggle tooth shark (*H. elongata*).

The fauna mainly contains shallow water, coastal taxa, among which some are known to visit brackish milieu as well (e.g., *Glyphis*, *Lamiopsis*, *Scoliodon*, *Pristis*, *Himantura*, and *Pastinachus*). The dominance of the shallow marine forms fit well with the sedimentary environment from which the fossils were derived and with the overall palaeoenvironmental reconstruction, with nearby river deltas or estuaries [31,32]. However, there are more open water taxa, like the mega-toothed shark (*Otodus*), tiger shark (*Galeocerdo*) or hammer head (*Sphyrna*). Interestingly, the mega-toothed shark is only known from small teeth [14,27], and, since its first description, all of the newly discovered specimens are small, and clearly come from juveniles. This would further concur with the coastal marine settings and may indicate that the small-sized megalodons either looked for easy prey or hid from larger predators in the shallow marine environment [27].

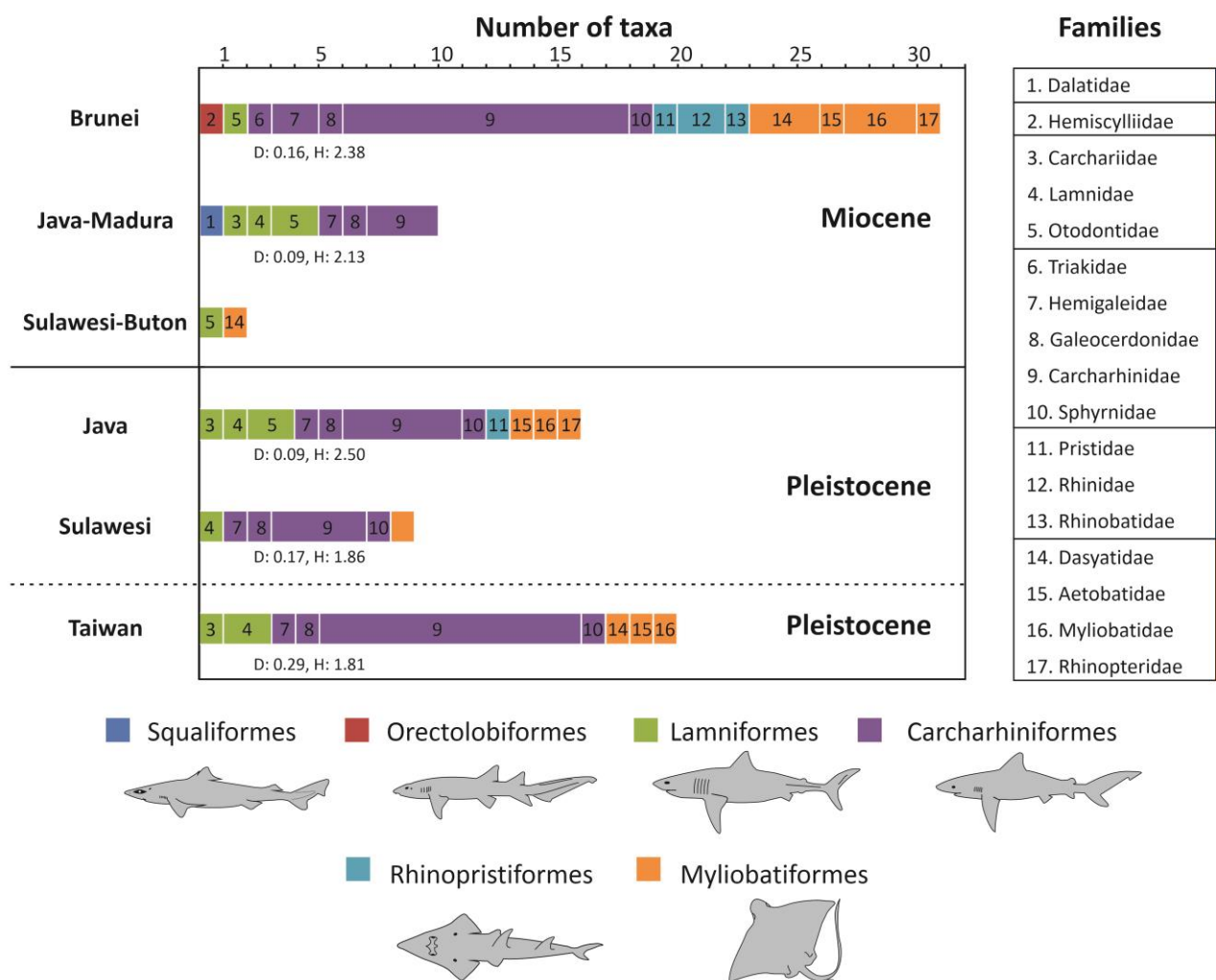


Figure 9. Comparative chart of the presence of different elasmobranch taxa in the Indo-Australian Archipelago during the Miocene and the Pleistocene (see also Tables 1 and 2). Data from recently

published revised Pleistocene elasmobranch fauna from Taiwan, situated just north of South China Sea and the IAA, are also included [71]. Note that sporadic occurrences are not illustrated here (Sumatra, Timor, see Table 2). Diversity indices based on number of taxa within the families are shown below the bars: D–Dominance and H–Shannon index.

When the north Bornean fauna is compared with other Miocene IAA sites, mainly Java (Table 2), several striking differences can be recognized. First, there is hardly any record of batoids from this period except for the body fossil of *Protohimantura vorstmani* from Sulawesi [8,15] (Figure 9). This clearly indicates a sampling bias, and that, probably during field surveys, the batoid remains were overlooked, unrecognized, or unreported. Most of the batoid fossils are known from younger layers, such as the Pleistocene beds in Java (Table 2, Appendix Figure A3b–d), and those mainly belong to taxa with larger tooth plates (e.g., *Aetobatus*, *Rhinoptera*) or big rostral teeth (*Pristis*) [17]. These are common between the assemblages, but in Brunei, a screen-washing technique was applied to check the micro-remains of many fossiliferous layers. This approach yielded several smaller teeth, and batoid taxa like *Rhina*, *Rhynchobatus*, *Rhinobatos*, *Himantura*, *Pastinachus*, and *Taeniurops*, which were all revealed by this method. However, many newly discovered shark taxa can also be attributed to this technique (*Chiloscyllium*, cf. *Hemitriakis*, *Paragaleus*, *C. borneensis*, *Scoliodon*). Therefore, the seemingly higher diversity at northern Borneo, and between the Miocene and Pleistocene sites in Indonesia, are best explained by sampling bias. Clearly, conducting more regular fieldwork while checking micro-remains could further enhance our knowledge about the elasmobranch diversity of these regions of the IAA.

The second contrast between the regional fauna is the presence of more open-water taxa, especially within the Lamniformes. The pelagic taxa are the *Isurus*, or the extinct forms like *Cosmopolitodus hastalis*, *Parotodus benedeni*, and *O. megalodon*, the latter of which is represented by many large teeth in the RGB collection; however, the genus *Carcharias* could also be listed here at the more open water taxa. Moreover, a rather deep-water taxon, the tooth of the kitefin shark (*Dalatias licha*) was also discovered in the Leiden collection and is in fact the sole and only known member of the order Squaliformes in the IAA's fossil record so far. All of these taxa point to different environmental conditions than that of the shallow marine sites in Brunei, and to connections to more pelagic and deeper waters. It must be emphasized that the Indonesian data are gathered from several locations based on the RGM collection and literature, and many of the sites contain only few remains, most without detailed knowledge of the stratigraphy and depositional environment. Moreover, there are specimens in which the indicated stratigraphic origin can be questioned and needs to be further clarified (e.g., Jetis in Java and Sompoh in Sulawesi). Therefore, in future, key fossil-rich outcrops and lithostratigraphy units should be investigated with detailed recording of the depositional environment together with more precise assessment of their depositional ages. This approach was applied to Pleistocene elasmobranch fauna from the subtropical region of Taiwan, an island north of the IAA, at the northern rim of the South China Sea. Museum collections were adequately revised, and new field data were obtained, which revealed remarkable palaeobiodiversity with better evaluated palaeoecological conditions [71] (Figure 9).

## 7. Conclusions

The presented review of the elasmobranch fossil record of the IAA and new data from Brunei revealed several taxa, among them the first record of Squaliformes, Orectolobiformes, Triakidae, and Rhinobatidae. The IAA fossil fauna now contains over 40 taxa, which are sorted in 4 orders and 17 families. The northern Bornean late Miocene sites represent a diverse shallow-marine, coastal fauna, while the Indonesian records contain more pelagic and even fewer deep-water elements. However, it is evident that the compositions of these latter fauna are patchy, and that sampling bias plays a critical role. Further investigations could be addressed using the museum collections in Indonesia and in the Philippines, and a more revised spatial and temporal view could be obtained.

It is expected that active field surveys involving enhanced and regular collection and screen-washing of a large quantity of sediments could disclose more about the palaeobiodiversity of the IAA elasmobranch assemblages. We hope that our approach in Brunei can be extended to other parts of the IAA and more data will be forthcoming in the near future. Local research groups, museums, and universities should be encouraged and supported to carry out such fundamental research in these directions, together with public outreach and a focus on preserving the recovered fossils as part of a national heritage.

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## Appendix A

**Table A1.** Fossil elasmobranch localities based on specimens in the Naturalis Biodiversity Centre collection in Leiden (The Netherlands). Question marks indicate unknown or uncertain lithostratigraphic units and/or ages.

Island	Locality	Lithostratigraphy/Deposits	Age	Collector—Literature	No. Material
Sumatra	Nias island	?	?Pliocene	Collected by Schröder	1
Java	Kedoeng Broeboes–Kedung Brubus	Kabuh Formation (=Bapang Fm.)	Mid-Pleistocene	Dubois collection, Koumans 1949 [6]	1
	Trinil	Kabuh Formation (=Bapang Fm.)	Mid-Pleistocene	Dubois collection, Koumans 1949 [6]	20
	Djetis–Jetis–Perning	Pucangan Formation	Early Pleistocene	Cosijn’s collection (Cosijn 1931, 1932) [68-69]	10 + 27
	Soemberingin–Sumberingin				
	Sangiran	Sangiran Formation (=Pucangan Formation)	Early Pleistocene	von Koenigswald’s collection— (not his 1978 [17] specimens)	170
	Ngembak	oil-bearing limestone	?Middle-Late Miocene	Martin 1883 [3], 1919 [20]; Beaufort 1928, 1931 [5,11]	14
	Rembang	?	?Middle-Late Miocene	Kampmeindert, J.M. collection—1920	1
	Nanas (Blora)	?	?Middle-Late Miocene	Dubois collection	10
Grobogan	?	?Middle-Late Miocene	Koumans 1949 [6]	1	
Kleripan–Kulun Progo	Mn-ore seams	?Lower Miocene	Beaufort 1928, 1931 [5,11]	9	
	unknown or no precise locality	?		6	
Madura (NE of Java)	Durin	?	Miocene	not Leriche 1954 [10] specimens	2
Sulawesi	Patoenoeang, Maros District	Tonasa Formation—laminated limestone	Lower Miocene	Beaufort 1926 [8]; Marrama et al 2018 [15]	1
	Sompoh & Beru (Tjabengè)	river deposits, worn teeth, age might be questionable	Lower Pleistocene→?	Hoojier 1954 [9]; Heeker 1958 [72]	177
Buton (SE of Sulawesi)	Waisioe–Waisiu	asphaltic marls— ?Sampalokosa Fm./Tondo Fm.	Upper Miocene–Pliocene	Beets 1952 [12]; Beaufort 1928 [11]	2
Timor	Lelowai I, Lalian		Miocene	Coll. Vianney 1966	1

## Appendix B

**Table A2.** List and sum of the IAA elasmobranch fossils from the Naturalis Biodiversity Centre collection (RGM) in Leiden (The Netherlands). Note that few specimens are written in green. For these items, there was no clear origin indicated on the collection labels; however, due to their similarities to nearby specimens in the drawers they were putatively sorted under the indicated localities. Question marks indicate further unknown or uncertain locality and/or origin.

Order	Family/Superfamily	Species/Genus	No.	Collection No.	Locality
<b>PLEISTOCENE</b>					
<b>Java</b>					
Lamniformes	Carchariidae	<i>Carcharias</i> sp.	2	RGM.DUB.11644 (2)	Trinil
				RGM.1320054 (2)	Jetis
	Lamnidae	<i>Isurus paucus</i>	30	RGM.1332577-95 (27)	?Jetis—29 teeth
				RGM.631093	Sangiran
	Otodontidae	<i>Otodus (Megaselachus) megalodon</i>	2	RGM.1332571, RGM.1332575 (1/2),	Jetis, ?Jetis
	Lamniformes indet		1	RGM.1332574	Jetis
Carcharhiniformes	Hemigaleidae	<i>Hemipristis serra</i>	2	RGM.631092 (2)	Sangiran
	Galeocerdonidae	<i>Galeocerdo cuvier</i>	1	RGM 1322596	Jetis
		<i>Galeocerdo</i> sp.	1	RGM.631094 (1/108)	Sangiran
	Carcharhinidae	<i>Carcharhinus</i> cf. <i>amblyrhynchos</i>	1	RGM.631094 (1/108)	Sangiran
		<i>Carcharhinus</i> cf. <i>leucas/amboinensis</i>	10	RGM.DUB.11642 (10/16)	Trinil
		<i>Carcharhinus</i> cf. <i>leucas</i>	90	RGM.1332573, RGM.1320072,	Jetis,
				RGM.631094 (88/108)	Sangiran
		<i>Carcharhinus</i> sp.	4	RGM.631094 (4/108)	Sangiran
				RGM.DUB.11642 (6/16)	Trinil
		<i>Glyphis</i> sp.	19	RGM.1320058, RGM.1332572,	Jetis, ?Jetis
				RGM.1332575 (1/2), RGM.1332576 (2)	Sangiran
				RGM.631094 (8/108)	
	Carcharhinidae indet.		5	RGM.631094 (5/108)	Sangiran
	Sphyrnidae	<i>Sphyrna</i> sp.	1	RGM.631094 (1/108)	Sangiran
	Selachimorpha indet				
Myliobatiformes	Aetobatidae	<i>Aetobatus</i> sp.	4	RGM.631095 (4/46)	Sangiran
	Rhinopterae	<i>Rhinoptera</i> sp.	10	RGM.631095 (10/46)	Sangiran
	Myliobatoidea	cf. <i>Myliobatis/Rhinoptera</i>	32	RGM.631095 (32/46)	Sangiran
				RGM.DUB.11639c	Trinil
	Myliobatiformes indet	cadual spines	14	RGM 1332570	Jetis,
				RGM.631097 (12)	Sangiran
Neoselachii indet		vertebras	3	RGM.DUB.11646a, RGM.DUB.11646 (1/10),	Kedung Brubus, Trinil
				RGM 631099	Sangiran

232

PLEISTOCENE

Sulawesi

Lamniformes	Lamnidae	<i>Isurus</i> sp.	1	RGM.630744,	Beru
Carcharhiniformes	Hemigaleidae	<i>Hemipristis serra</i>	18	RGM.630746-51 (6), RGM.630711-21 (9), RGM.630752, RGM.630713-14 (2)	Sompoh, Beru
	Galeocerdonidae	<i>Galeocerdo cuvier</i>	2	RGM.630709, RGM.630710	Sompoh
	Carcharhinidae	<i>Carcharhinus</i> cf. <i>amboinensis</i>	2	RGM.630726-27 (2),	Sompoh
		<i>Carcharhinus</i> cf. <i>leucas</i>	8	RGM.630734-35 (2), RGM.630740-42 (3), RGM.630755 (3/20),	Sompoh
		cf. <i>C. leucas/amboinensis</i>	3	RGM.630738, RGM.630743, RGM.630755 (1/20),	Sompoh
		<i>Carcharhinus</i> sp.	17	RGM.630757 (5/21), RGM.630736, RGM.630756 (5/25), RGM.630758 (6/65),	Sompoh
		<i>Glyphis</i> sp.	51	RGM.630722-25 (4), RGM.630728-33 (6), RGM.630757 (4/21), RGM.630739, RGM.630756 (20/25), RGM.630755 (15/20), RGM.630759,	Sompoh, Beru
		cf. <i>Glyphis</i> sp.	43	RGM.630755 (1/20), RGM.630758 (42/65),	Sompoh
	Carcharhinidae indet.		19	RGM.630757 (12/21), RGM.630758 (7/65),	Sompoh
	Sphyrnidae	<i>Sphyrna</i> cf. <i>mokarran</i>	1	RGM.630736,	Sompoh
	Selachimorpha indet		10	RGM.630758 (10/65),	Sompoh
Myliobatiformes	Myliobatiformes indet	caudal spines	2	RGM.630753, RGM.630754	Sompoh

177

<b>PLIOCENE</b>					
<b>Sumatra-Nias</b>					
Lamniformes	Lamnidae	<i>Isurus</i> sp.	1	RGM 175443	Idano Mola, Nias
<b>MIOCENE</b>					
<b>Java-Madura</b>					
Squaliformes	Dalatidae	<i>Dalatias licha</i>	1	RGM.42356	Ngembak
Lamniformes	Carchariidae	<i>Carcharias</i> sp.	2	RGM.631767 (2)	Kleripan
	Lamnidae	<i>Cosmopolitodus hastalis</i>	1	RGM.DUB.11643.a (1/4)	Nanas
	Otodontidae	<i>Otodus (Megaselachus) megalodon</i>	11	RGM.11776, RGM.DUB.1468 (6), RGM.DUB.11645, RGM.1320057, RGM.1320056 (2)	Ngembak, Nanas, Grobogan, Rembang, Madura
		<i>Parotodus benedeni</i>	1	RGM.DUB.11643.a (1/4)	Nanas
	Lamniformes indet		3	RGM.DUB.11643.a (2/4), RGM.11775 (1/2)	Nanas
Carcharhiniformes	Hemigaleidae	<i>Hemipristis serra</i>	4	RGM.11766, RGM.42358, RGM.631771 (2)	Ngembak, Kleripan,
	Galeocerdonidae	<i>Galeocerdo cuvier</i>	2	RGM.11767, RGM.631769,	Ngembak, Kleripan
	Carcharhinidae	<i>Carcharhinus</i> cf. <i>falciformis</i>	1	RGM.11768	Ngembak
		<i>Carcharhinus</i> sp.	6	RGM.11772, RGM.42348, RGM.631765, RGM.631768 (3)	Ngembak, Kleripan
		cf. <i>Negaprion</i> sp.	1	RGM.42357 (1/2)	Ngembak
	Carcharhinidae indet		1	RGM.11769 (1/2)	Ngembak
Selachimorpha indet			3	RGM.42357 (1/2), RGM.11775 (1/2), RGM.11769 (1/2)	Ngembak, Kleripan

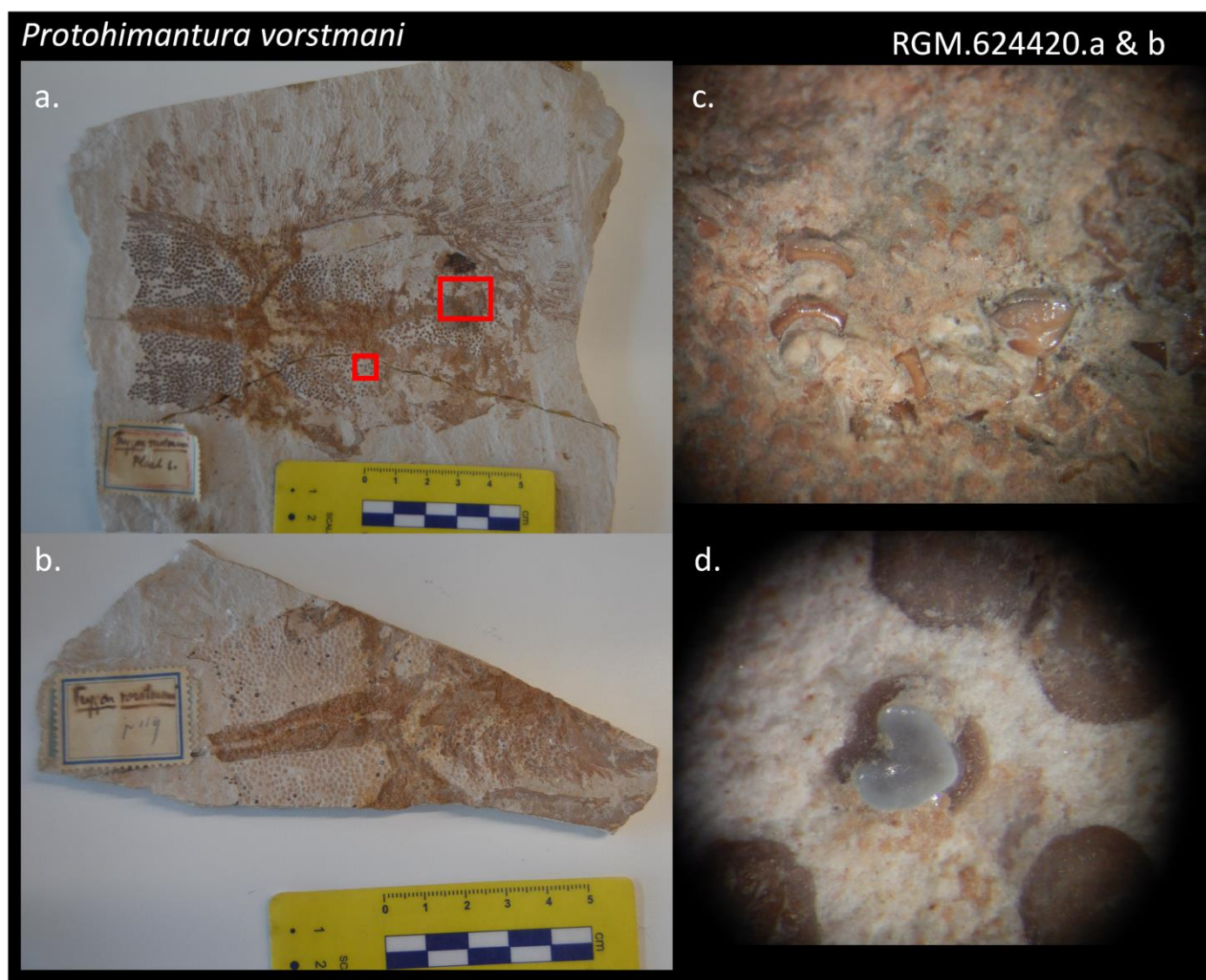
37

**MIOCENE**  
**Sulawesi-Buton**

Lamniformes	Otodontidae	<i>Otodus (Megaselachus) megalodon</i>	2	RGM 43425, RGM 1320059	Waisioe–Waisiu, Buton
Myliobatiformes	Dasyatidae	<i>Protohimantura vorstmani</i>	1	RGM.624420.a & b	Patoenoeang, Sulawesi
<b>MIOCENE – Timor</b>					
Carcharhiniformes	Hemigaleidae	<i>Hemipristis serra</i>	1	RGM 175442	Lelowai I, Lalian
<b>?Java</b>					
Carcharhiniformes	Hemigaleidae	<i>Hemipristis serra</i>	1	RGM.DUB.101 (cf.)	?
	Carcharhinidae	<i>Carcharhinus</i> sp.	1	RGM 42395	?Houtvesting Mangga
TOTAL SUM:			<b>453</b>		

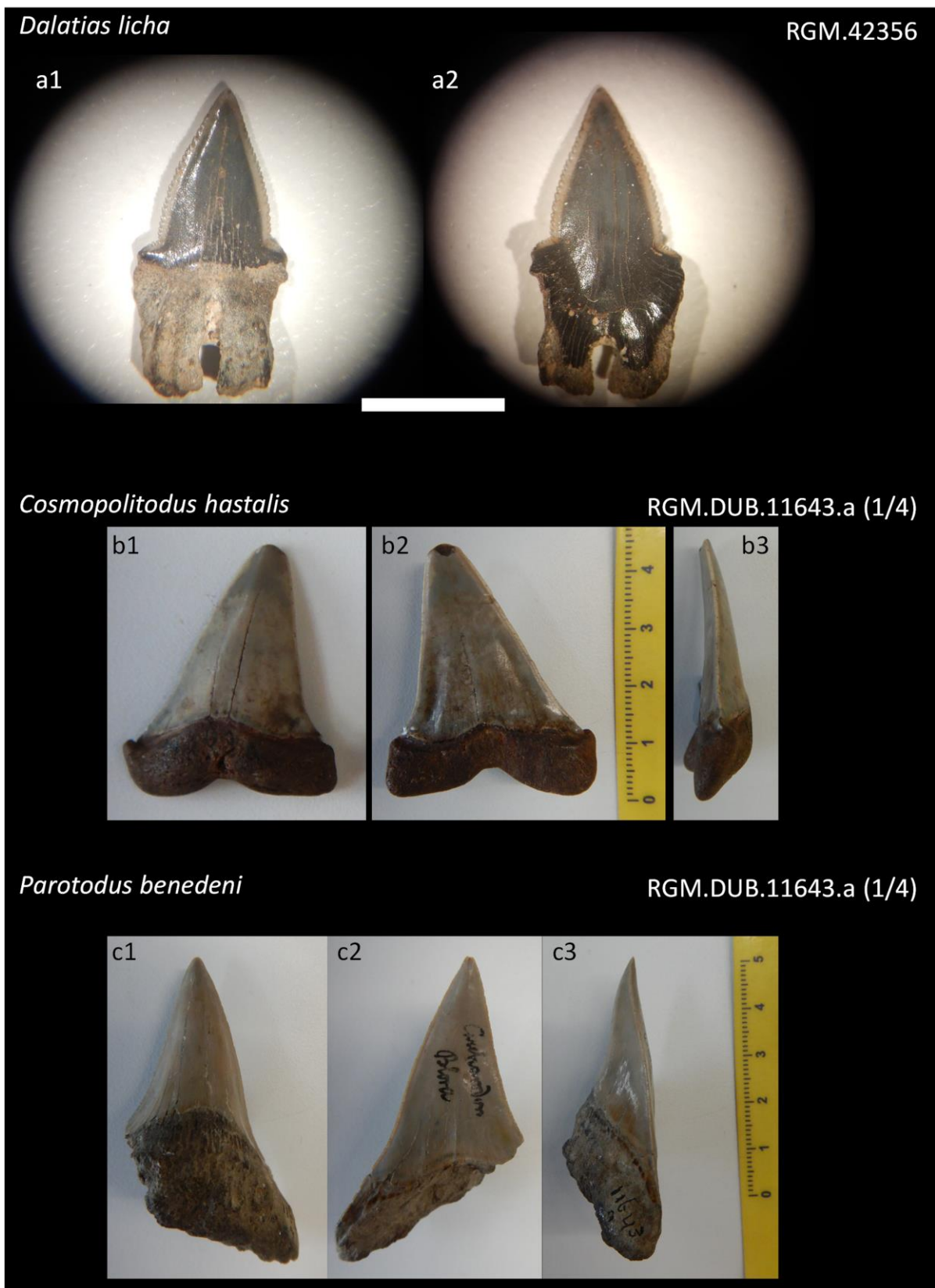
### Appendix C

Selected elasmobranch specimens from the Naturalis Biodiversity Centre collection in Leiden (The Netherlands) are displayed in the four subsequent figures. Note that these images are not edited as these were used for preliminary investigations.

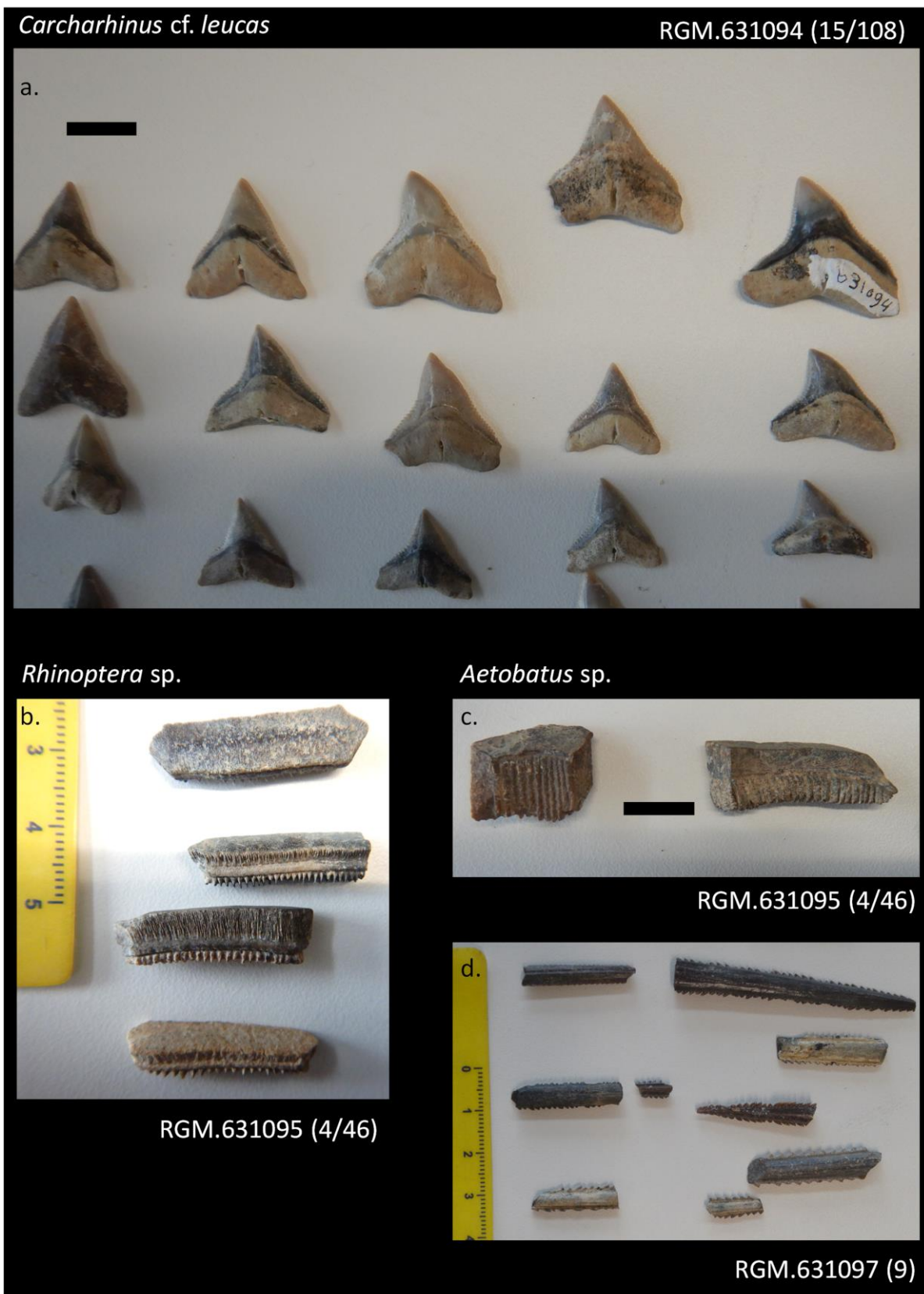


**Figure A1.** Body fossil of *Protohimantura vorstmani* (RGM 624420 a–b, [8,15]), early Miocene, Patoenoeang, Sulawesi, Indonesia. (a,b) The holotype and its counter slab. (c) Closeup of some of the teeth (bigger red box in a). (d) Closeup of a dermal denticle (smaller red box in a).

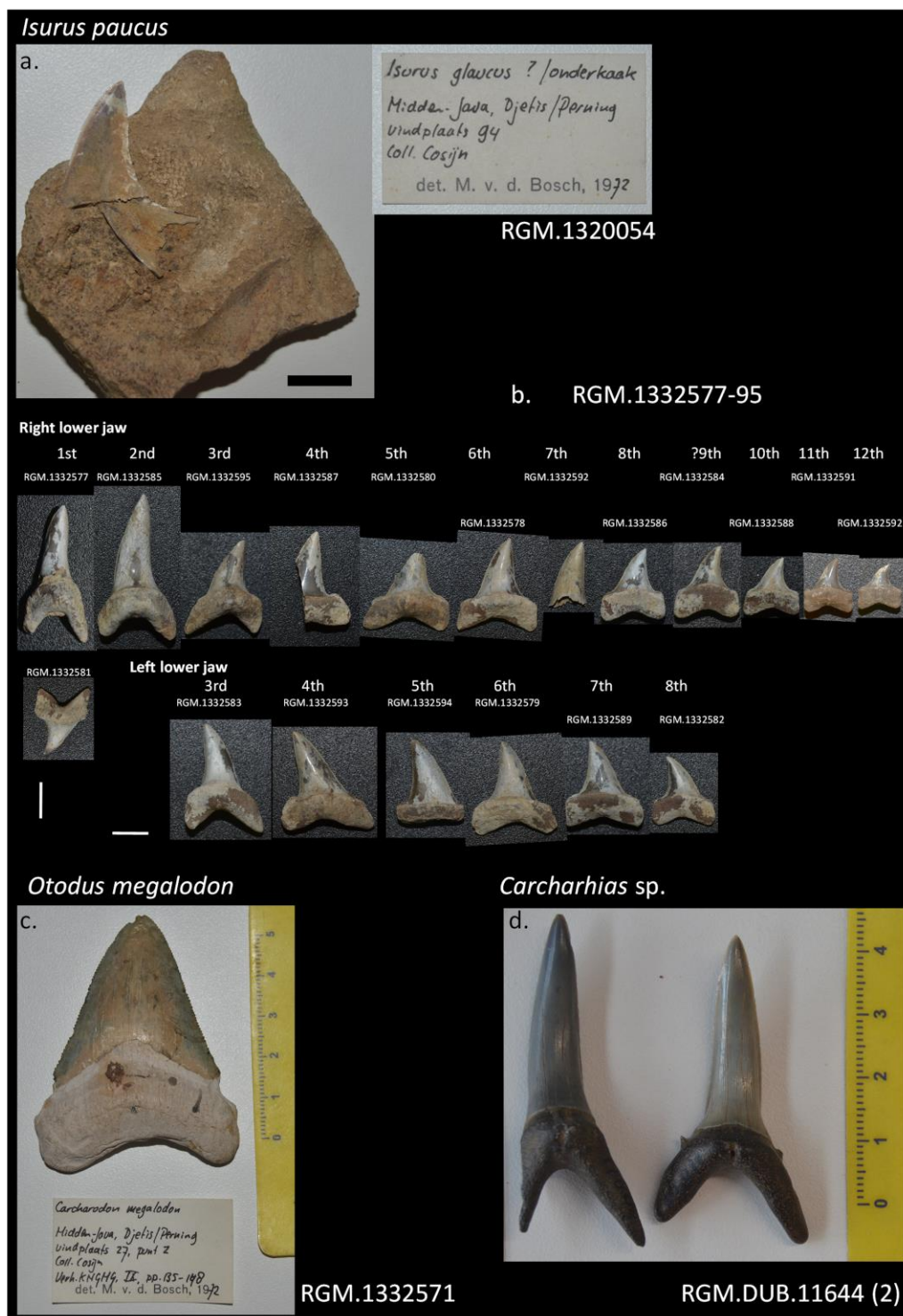




**Figure A2.** (a) *Dalatias licha* (RGM.42356), lower tooth, ?middle–late Miocene, Ngembak, Java. (a1) Lingual and (a2) labial views. Scale bar 0.5 cm. (b) *Cosmopolitodus hastalis* (RGM.DUB.11643.a, 1 of 4) ?middle–late Miocene, Nanas, Java. (b1) Lingual, (b2) labial, and (b3) lateral views. (c) *Parotodus benedeni* (RGM.DUB.11643.a, 1 of 4) ?middle–late Miocene, Nanas, Java. (c1) Lingual, (c2) labial, and (c3) lateral views.



**Figure A3.** (a) Fifteen *Carcharhinus cf. leucas* upper teeth (RGM.631094, 15 of 108), early Pleistocene, Sangiran, Java, all are in lingual views. (b) Four *Rhinoptera* sp. teeth (RGM.631095 4 of 46) early Pleistocene, Sangiran, Java. (c) Two *Aetobatus* sp. tooth fragments (RGM.631095 2 of 46) early Pleistocene, Sangiran, Java. (d) Nine Myliobatiformes cadual spines (RGM.631097) early Pleistocene, Sangiran, Java. Scale bars: 1 cm.



**Figure A4.** (a) *Isurus paucus* (RGM.1320054), early Pleistocene, Jetis, Java. Scale bar 1 cm. (b) Tooth series of *Isurus paucus* (RGM.1332577–95). There are 27 teeth (26 lower and 1 upper) that belong to the same individual. All of the teeth are in lingual views. There was no indication of locality in the RGM collection, but they were together with Cosijn’s specimens from Jetis. The teeth have similar size, preservation, and partly coloration as the teeth in the block from Jetis above (C4.1). Therefore, they may derive from the same fossil shark specimen. Scale bar 1 cm. (c) *Otodus megalodon* (RGM.1332571) early Pleistocene, Jetis, Java. Note that the taxon is considered to have become extinct by the Pleistocene. Therefore, either this specimen represents the youngest occurrence of this species or the age of the locality and/or origin of the tooth need to be further investigated. (d) *Carcharias* sp. (RGM.DUB.11644) middle Pleistocene, Trinil, Java. Note that these teeth have been described as *Odontaspis cuspidata*, which corresponds to *Araloselachus cuspidatus* based on modern

nomenclature [45]. However, this latter taxon has teeth with smooth enameloid on the lingual face of the crown, but the crown of the Trinil teeth bear fine striation.

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