



First report on a diverse Neogene cartilaginous fish fauna from Borneo (Ambug Hill, Brunei Darussalam)

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The highest biodiversity of marine fishes occurs in South-east Asia in the Indo-Australian Archipelago (IAA). However, the fossil record of fishes is very sparse and extremely incomplete in the IAA. Here we present a diverse fossil cartilaginous fish fauna from Borneo, found in late Miocene sediments in Brunei Darussalam. This fauna provides the first insight into the types of fishes that existed in the IAA region about 6.5–8 million years ago. The chondrichthyan remains belong to 24 selachian and batoid taxa. The shark fauna is dominated by Carcharhiniformes, comprising three families with at least 12 taxa, most related to modern species: Hemigaleidae (one species), Carcharhinidae (nine) and Sphyrnidae (two). In addition, the teeth of one Lamniformes shark, the extinct giant macro-predator *Otodus* (*Megaselachus*) *megalodon*, are present in the fauna. The batoids are dominated by Myliobatiformes from the following families: Dasyatidae (three species), Aetobatidae (one), Myliobatidae (three), Rhinopteridae (one), while three taxa of the order Rhinopristiformes were also recovered: Pristidae (one species), and Rhinidae (two). Such diversity of fossil cartilaginous fish has never before been reported from the tropical region of South-east Asia. The dominance of the carcharhinid sharks and small rays suggests a shallow marine, coastal palaeoenvironment. The presence of the freshwater shark genus *Glyphis* indicates a nearby fluvial influence. Some species of the ray genera, such as *Himantura* or *Pastinachus*, have also been reported from estuaries and fresh water. The lack of some generally common Neogene taxa, such as Odontaspidae, Lamnidae and Alopidae, may be linked to such local factors and the coastal shallow-water environment.

Keywords: Late Miocene; fossil sharks; fossil batoids; Indo-Australian Archipelago; palaeobiodiversity; palaeoecology

Introduction

The late Miocene deposit of Ambug Hill in the Tutong District yields one of the most fossiliferous marine assemblages in Brunei Darussalam. Abundant macro- and microfossil remains have been discovered here, including foraminifera, molluscs, crustaceans and fish, among which are shark and ray teeth. This paper focuses on the fish fauna, which is unique because cartilaginous fish remains have not been studied previously in Brunei and only in little detail in the rest of South-east Asia. The marine life around Borneo and in the whole Indo-Australian Archipelago (IAA) is considered to be the most diverse in the world (i.e. the ‘coral triangle’; Hoeksema 2007), and this includes fishes as well (Cowman 2014; Weigmann 2016). However, our knowledge of fish diversity in the past in the IAA is quite limited. This is due to the lack of detailed studies, and of available fossil-rich deposits. The Ambug Hill outcrop is a site with the potential to give us the first

detailed insight into ancient cartilaginous fish diversity in the region.

Neogene shark teeth are occasionally reported in works from Indonesia and Malaysia (e.g. Martin 1887; Hennig 1911; Beaufort 1931; Kouman 1949; Hooijer 1954; Leriche 1954, Wannier *et al.* 2011). However, thorough modern taxonomical studies have never been done on these remains. From Brunei and the nearby Malaysian state of Sarawak only a few localities are mentioned where shark teeth have been found. Based on the few figured specimens the following genera can be identified: *Carcharhinus*, *Hemipristis* and the giant shark *Otodus* (*Megaselachus*) *megalodon* (James 1984, pp. 91, xvi; Sandal 1996, pp. 93–94; Wannier *et al.* 2011, pp. 229, 244). Apart from these reports, there is no literature that figures shark or ray teeth from Borneo.

Generally, shark teeth are common fossils in many Cenozoic marine beds. This is due to the fact that sharks are continuously growing and shedding their teeth, and one individual can produce some thousands of teeth

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during its lifetime (Cappetta 2012). The other factor is that the teeth have good preservation potential due to their mineralogical composition, as they consist of fluorineapatite (e.g. Moller *et al.* 1975).

The tooth morphology of sharks and rays varies among the different groups; hence, they are relatively easily classified in higher taxonomical groups. Some taxa show prominent differences between upper and lower teeth (dignathic heterodonty) or along the same jaw (monognathic heterodonty). Sexual dimorphism and ontogenetic variations also occur in certain species. Additionally, some teeth may exhibit abnormal morphology, i.e. pathologies (Cappetta 2012). For certain shark groups, these possible variations could cause some difficulties when classification is considered at species level (e.g. Carcharhinidae). Therefore, in order to describe species more confidently, reconstruction of fossil tooth series is suggested whenever the fossil material allows it (e.g. Purdy *et al.* 2001). On the other hand, there are some conservative groups for which species-level determination of the fossil material does not make sense due to the lack of or very minor variation in tooth morphologies among the fossils, and this is especially true for some modern taxa as well (e.g. *Squatina* or some batoids).

In this study we focus on detailed taxonomic and ecological descriptions of the cartilaginous fish remains found at Ambug Hill in Brunei Darussalam, together with a general review of the relevant literature from South-east Asia. We use the most modern taxonomical literature (Cappetta 2012; White 2012, 2014; White & Naylor 2016; Last *et al.* 2016a, b, c) and compare the fossil teeth with the associated tooth series of modern species (e.g. Bass *et al.* 1973, 1975; Garrick 1982, 1985).

Geological setting

Ambug Hill is located in Tutong District, near the coast of the South China Sea in Brunei Darussalam (Fig. 1). Based on the geological map, the outcropping sediments of the region belong to the Seria and Liang formations and have an age range from late Miocene to late Pliocene (Wilford 1961; Sandal 1996). At the southern part of Ambug Hill a 72 m-thick siliciclastic sedimentary sequence crops out. The beds gently dip west-north-west at an angle of 12–18°. The sedimentary series contains four sub-units (Kocsis *et al.* 2018), of which the first (0–27 m) is dominated by an *Ophiomorpha-Thalassionides* bioturbated sandstone. The following unit 2 (27–59 m) is the most fossiliferous, especially at the base, where it contains a grey claystone about 9.5 m thick (Fig. 1). These layers are very rich in gastropods, bivalves, crabs and fish remains such as teeth, bones and otoliths. The microfauna is dominated by rotaliid foraminifera and the assemblage indicates a shallow marine environment deposited in eutrophic and

oligophotic conditions (Roslim *et al.* 2016). The layers of unit 2 become siltier up-section and the fossils become rarer. This part of the section contains several red or yellow horizons interpreted as ‘event beds’ resulting from low-energy gravity flows (Atkinson *et al.* 1986). Some of these levels are rich in casts and moulds of molluscs and crabs, and also in shark teeth (Fig. 1C, see R1 and R3–4). Unit 2 is overlain by bioturbated, fine sandstone, which is separated by an erosional surface from unit 3 (Fig. 1). The youngest units (3 and 4) do not contain any calcareous fossils and dating them is rather difficult. On the other hand, combined biostratigraphy and Sr-isotope stratigraphy on samples from the lower part of unit 2 yielded a reliable late Tortonian–early Messinian age (~6.5–8 million years) (Kocsis *et al.* 2018).

Methods and material

Most of the larger shark and ray remains were picked from the surface of the sediments as they easily weather out from the clayey deposits. The majority of the teeth come from the claystone at the base of unit 2 (27–36.5 m), especially the lowest 2–3 m. This 9–10 m fossil-rich interval is referred to as the main bed (MB). A few specimens were also recovered from the very top part of the bioturbated sandstone in unit 1 (26–27 m). Selachian remains also occurred more frequently in some of the red beds of unit 2, namely R1 (~40 m), R3 (~44 m) and R4 (~45 m) (see Fig. 1C).

Additionally, the fossil-rich claystone was sampled along the profile and about 20–30 kg of sediment was screen-washed for micro-remains (see Fig. 1C, S1–9). These bulk clay samples were first dried, then washed with hot tap water, with hydrogen peroxide (H₂O₂) sometimes added. Three different mesh sizes (600 µm, 1 mm and 2 mm) were used to wash through the sediments. The obtained residues were checked through and teeth and bones were picked using a stereomicroscope. This method yielded a large number of small teeth, especially those of batoids.

The recovered specimens were cleaned, then the labial, lingual and in some cases lateral views were photographed. For anatomical descriptions of the teeth see Figure 2, and for more detailed terminology see Cappetta (2012) and Purdy (2006). Where distinguishing between upper and lower teeth was possible the teeth were illustrated pointing either down or up, respectively. For some taxa, tooth series were assembled with the help of modern dentitions (e.g. Bass *et al.* 1973, 1975; Garrick 1982, 1985). For the purpose of better illustration some specimens were mirrored; these are mentioned in the respective figure captions.

The taxonomy mainly follows the work of Cappetta (2012), except for some recent regroupings within the

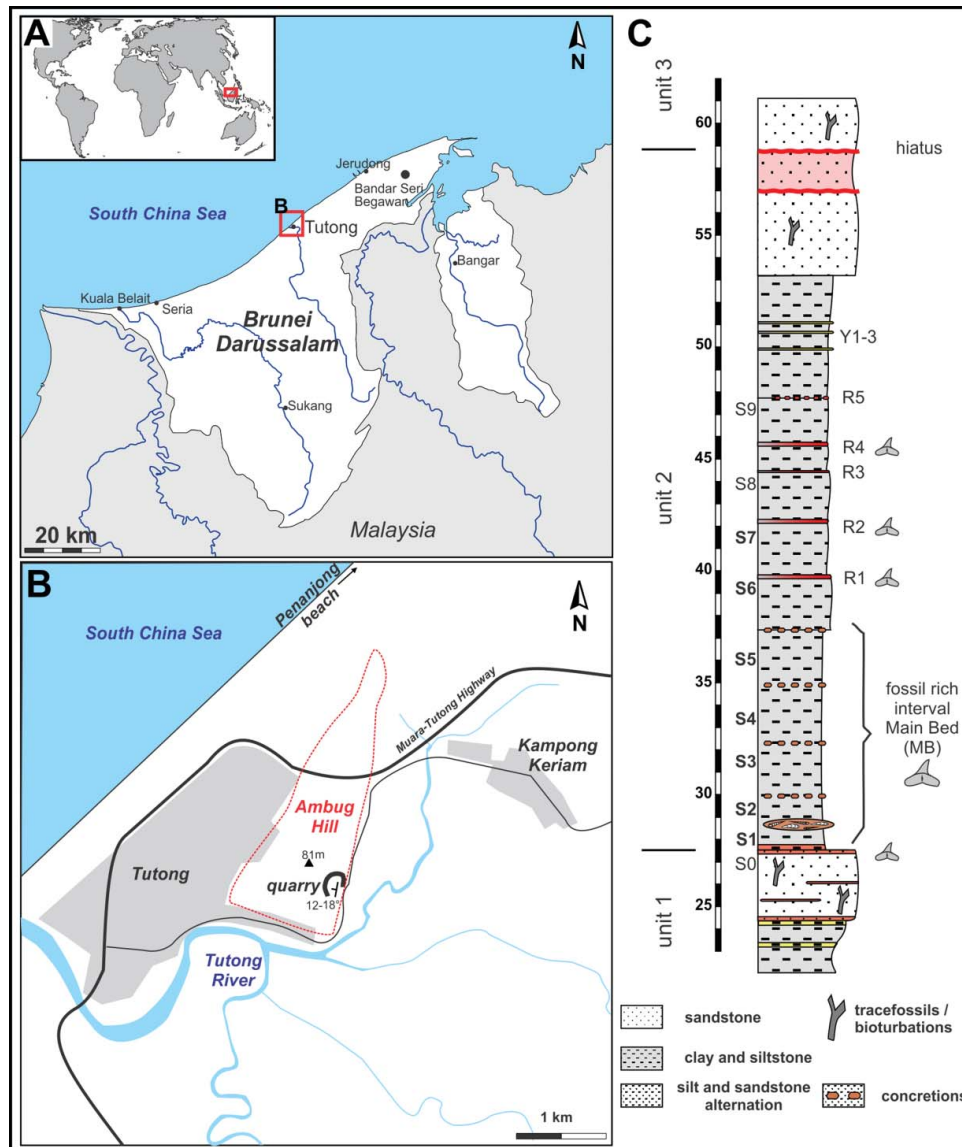


Figure 1. A, B, geographical position of Ambug Hill in Brunei Darussalam. C, sedimentary section of the Ambug Hill outcrop with the layers bearing fish teeth.

batoids (Last *et al.* 2016c). Our synonym lists generally focus on South-east Asian occurrences and reports.

Described material is stored in the Geological Collection of the Natural History Museum, Universiti Brunei Darussalam (GUBD).

Systematic palaeontology

Class **Chondrichthyes** Huxley, 1880
 Subclass **Elasmobranchii** Bonaparte, 1838
 Superorder **Galeomorphii** Compagno, 1973
 Order **Lamniformes** Berg, 1937
 Family: **Otodontidae** Glikman 1964

Genus **Otodus** (*Megaselachus*) Glikman, 1964
Otodus (*Megaselachus*) *megalodon* Agassiz, 1843
 (Fig. 3A)

1887 *Carcharodon megalodon* Agassiz; Martin: pl. 1, fig. 12 [Java, Indonesia].

1949 *Carcharodon* cf. *megalodon* Agassiz; Kouman: pl. 2, fig. 2 [Java, Indonesia].

1954 *Carcharodon megalodon* forma *indica* (Leriche): pl. 1, figs 1–9 [Java, Indonesia].

1984 Shark tooth James: 91, pl. 16, top [Borneo, Brunei].

1996 Shark tooth Sandal: 94, fig. 4.7 [Borneo, Brunei].

Material. One upper lateral tooth GUBD V0001 from MB.

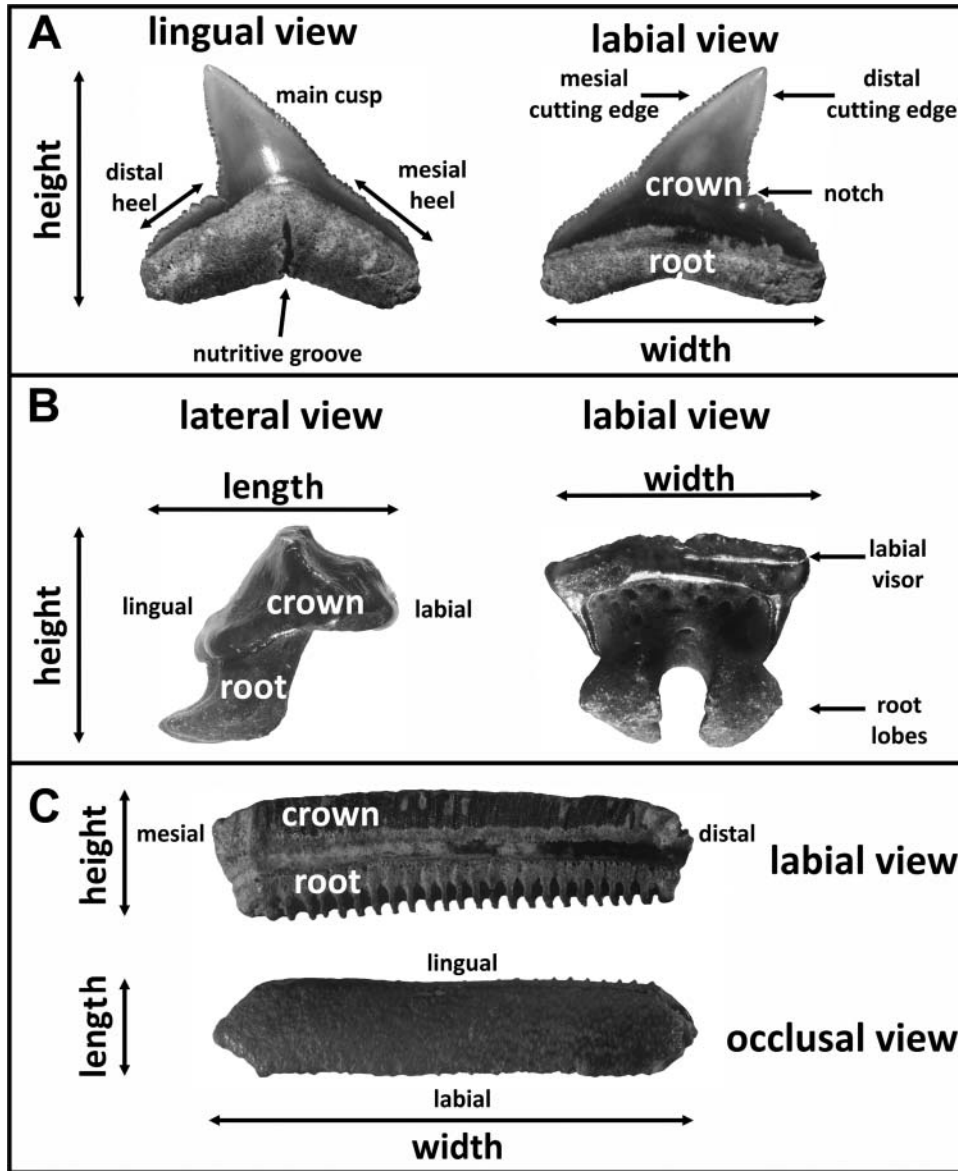


Figure 2. Tooth terminology. **A**, carcharhinid shark tooth (*Carcharhinus amblyrhynchos*). **B**, dasytid ray tooth (*Taeinurops* sp.). **C**, Myliobatoidea ray tooth (*Rhinoptera* sp.). For more detailed terminology see Cappetta (2012) and Purdy (2006).

Description. The tip of the tooth is broken and almost the whole root is missing. The height of the crown is about 4 cm, while its width is 4.5 cm. The labial surface of the crown is flat, while the lingual one is strongly convex. On both surfaces at the base of the crown, a black line clearly marks the crown-neck (also known as the bourlette), which is strongly V-shaped and much thicker on the lingual side. The cutting edges are strongly serrated, the mesial one is straight, while the distal edge has a small notch towards the base. The crown is wide at the base relative to its height, therefore it represents an upper tooth, probably a right 4th or 5th lateral (see Purdy *et al.* 2001, fig. 37; Applegate & Espinosa-Arrubarrena 1996, fig. 12).

Remarks. This species was very common worldwide mainly in subtropical and temperate latitudes during the Miocene and Pliocene and was the apex predator of its time (Cappetta 2012). Within the IAA, the species has been reported from the Miocene of Java (Martin 1887; Kouman 1949) and the nearby island of Pulau Madura (Leriche 1954). Additionally, one shark tooth, figured in James (1984) and Sandal (1996), was found on Penanjong beach in Brunei that also belongs to this species and probably represents an upper anterior tooth. This locality is very close to Ambug Hill (Fig. 1B) and, based on the geometry of the layers as they cross the coastline at

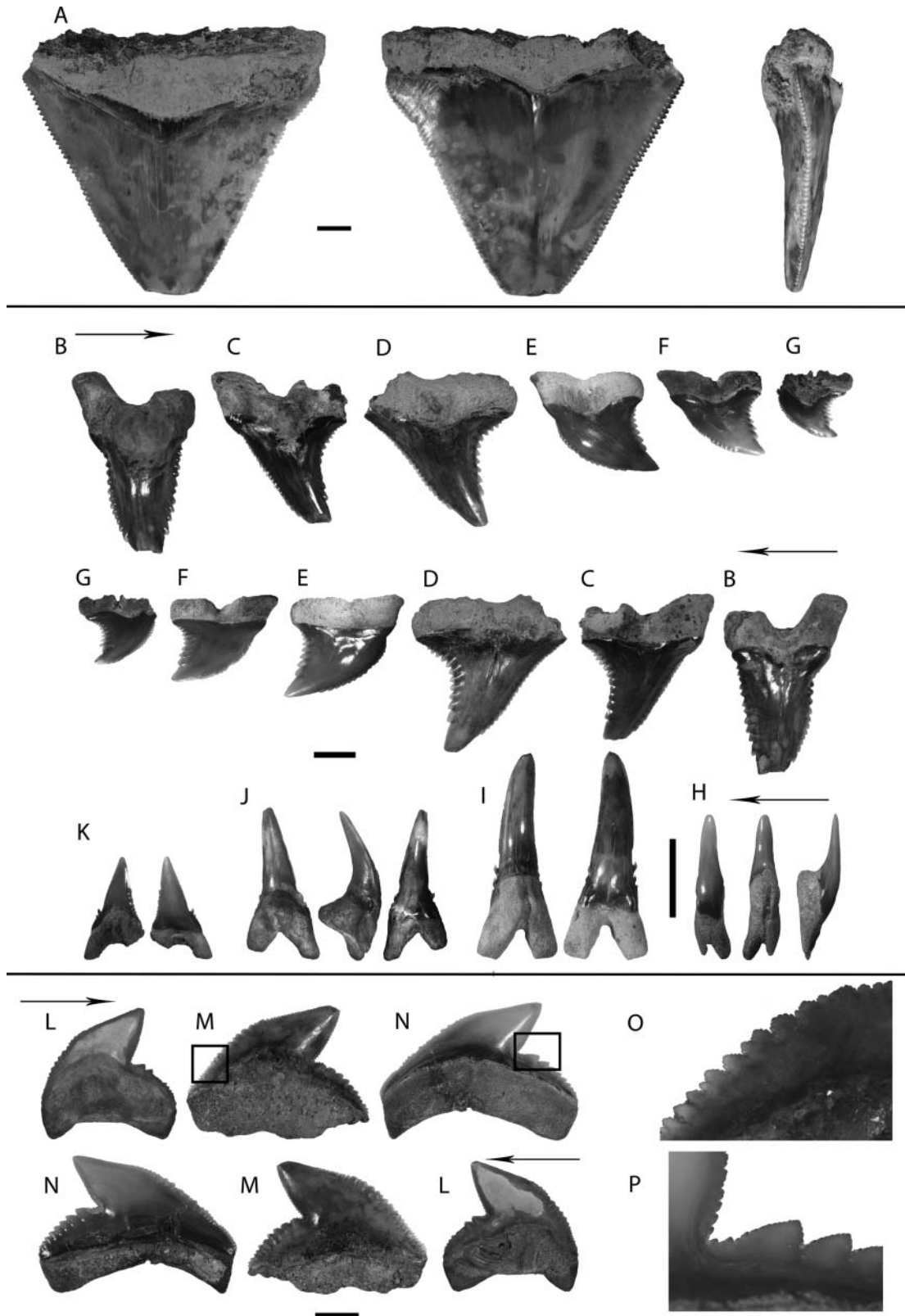


Figure 3. **A**, *Otodus (Megalachus) megalodon*, GUBD V0001, upper lateral tooth in lingual, labial and lateral views. **B–K**, *Hemipristis serra*; **B–G**, upper tooth series in lingual and labial views from a tooth in anterior position towards more lateral files, GUBD V0002; **H–K**, lower teeth from right to left; **H**, symphyseal tooth in labial, lingual and lateral views, GUBD V0006; **I**, anterior tooth in lingual and labial views (GUBD V0004); **J**, anterior tooth in lingual, lateral and labial views, GUBD V0005; **K**, lateral tooth in lingual and labial views, GUBD V0004. **L–P**, *Galeocerdo cuvier*; **L**, lingual and labial views of an anterior tooth, GUBD V0010; **M, N**, lingual and labial views of lateral teeth, GUBD V0008; **O, P**, secondary superimposed serrations on the serrae on the mesial cutting edge (**O**) and the distal shoulder (**P**). Specimens in **B, C, E** and **F** are mirrored images. Scale bars = 5 mm.

Penanjong beach, the tooth could derive from the same formation.

Order **Carcharhiniformes** Compagno, 1973

Family **Hemigaleidae** Hasse, 1879

Genus **Hemipristis** Agassiz, 1835

Hemipristis serra Agassiz, 1843

(Fig. 3B–K)

1887 *Hemipristis serra* Agassiz; Martin: pl. 2, fig. 17 [Java, Indonesia].

1954 *Hemipristis* cf. *serra*; Hooijer: pl. 1, figs 2–4, 7–10, 14 [Sulawesi, Indonesia].

1954 *Hemipristis serra* Agassiz; Leriche: pl. 1, figs 10–13 [Java, Indonesia].

1978 *Hemipristis serra* Agassiz; Uyeno: pl. 1, fig. 2 [Taiwan].

2011 Shark tooth; Wannier, Lesslar, Lee, Raven, Sor-khabi, & Abdullah: 244, pl. 4.7.4b, fig. 12a [Borneo, Sarawak, Malaysia].

Material. Nineteen teeth, GUBD V0002 and V0003 uppers (nine); V0004 and V0005 lowers (three), V0006 symphyseal two) and V0007 fragments (five); from MB and R4.

Description. The upper and lower teeth show very different morphologies. The upper teeth are serrated, generally with a flat labial side. The first upper anteriors are straight; the following teeth become more and more bent distally. The serration of upper files is stronger on the distal cutting edge than the mesial one, and it does not reach the apex of the crown on either side. The mesial cutting edge on the first upper laterals is slightly concave at the base and becomes convex towards the apex; however, on the more lateral teeth the edge is fully convex. The distal cutting edge of the upper teeth is always concave. The lower teeth are rather hook-like in the anterior position. The labial surface is convex, the crown is inclined lingually. The cutting edges do not reach the base of the crown, where two or three pairs of small cusplets appear. The lower lateral teeth are rather triangular in shape, and beside the mesial cusplets they may display raw serration at the base of the distal cutting edge. The root is quite bulky on both uppers and lowers and shows a clear protuberance on the lingual side, which is more expressed on the anterior files. Two symphyseal teeth were also found. The root of these tiny teeth is asymmetrical, and the lobes partly coalesce. The crown is smooth without any serration. Since both upper and lower symphyseal teeth have similar characteristics, the exact position of the Ambug Hill symphyseals cannot be given.

Remarks. *Hemipristis serra* is known worldwide from the Miocene and Pliocene, and generally inhabited shallow tropical and warm temperate seas (Cappetta 2012).

The species has also been mentioned from the fossil record of the IAA and nearby regions such as the Miocene of Java (Martin 1887; Leriche 1954) and Taiwan (Uyeno 1978), and an upper tooth has been figured from Sarawak, Malaysia, that also belongs to this species (Wannier *et al.* 2011). The youngest occurrence comes from this region as well, from the Pleistocene deposits of Sulawesi (Hooijer 1954). *Hemipristis serra* is closely related to the modern species *H. elongata* (snaggletooth shark), which has smaller and somewhat narrower teeth (see Bass *et al.* 1975). The modern species is only known from the Indo-West Pacific (Compagno 1988; Compagno *et al.* 2005).

Family **Carcharhinidae** Jordan & Evermann, 1896

Genus **Galeocerdo** Müller & Henle, 1837a

Galeocerdo cuvier (Lesueur, 1822)

(Fig. 3L–P)

1954 *Galeocerdo cuvier* (Péron & Lesueur, 1822); Hooijer: pl. 1, figs 1, 5, 6 [Sulawesi, Indonesia].

Material. Six teeth, GUBD V0008–V0010; from the top of unit 1, MB of unit 2.

Description. The upper and lower teeth are very similar and difficult to distinguish. On the other hand the teeth change along the jaw and the height/width ratio becomes lower along the lateral files. All the teeth have a broad and compressed, serrated crown, with a main cusp bent distally, which is followed by a prominent notch and a convex, strongly serrated distal heel (also known as the distal shoulder). The labial surfaces of the crowns are flat, while the lingual ones are slightly convex. The mesial cutting edge of the crown is convex, with irregular serration that becomes finer towards the apex. The distal cutting edge is straight to slightly convex and covered by fine serration. The serrae on the distal heel bend and decrease in size distally. Superimposed secondary serration occurs both on the larger serrae of the mesial cutting edge and the distal heel. The root is high on the lingual face and somewhat thicker on the more anterior teeth.

Remarks. The modern tiger shark *Galeocerdo cuvier* is reported from the Pliocene (Cappetta 2012), while the genus is known from the Lower Eocene. There are two Miocene species, the cosmopolitan *G. aduncus* and *G. mayumbensis*, that are mentioned from Africa and North America (Cappetta 2012) and South America (e.g. Aguilera *et al.* 2017). The first of these species is rather smaller than *G. cuvier* and the superimposed secondary serration may appear only on the distal heel (e.g. Cigala-Fulgosi & Mori 1979), while *G. mayumbensis* is clearly different in having a less developed notch and rather straight distal heel (e.g. Andrianavalona *et al.* 2015). The genus appears in the fossil record of the IAA too, as Martin (1887) described a new Miocene species *G.*

javanus from Java. However, Hooijer (1954) considered this species to represent the modern *G. cuvier* when he reported the Pleistocene occurrence of *G. cuvier* from Sulawesi. This author mentioned the double serration of the Sulawesi specimens as an important character, which indeed links these teeth to the modern species. On the other hand, based on the figured broken teeth of Martin's *G. javanus*, these characters are hard to verify. Another nearby report of *Galeocerdo* comes from the Miocene of Taiwan (Uyeno 1978) as *G. aduncus*.

Genus *Carcharhinus* Blainville, 1816

Remarks. *Carcharhinus* is the most abundant shark taxon found at Ambug Hill. The genus includes more than 30 modern species, each having a different tooth morphology (Compagno *et al.* 2005). Carcharhinid sharks have strong dognathic heterodonty, their upper teeth are more characteristic for classification, and based on these several tooth morphology groups can be identified (Garrick 1982, 1985). For many species the lower teeth are simple and very similar, with a straight and/or lingually bent crown that has either finely serrated or smooth cutting edges. Due to this similarity it is often difficult to classify the lower teeth beyond genus level. On the other hand, certain species have more characteristic lower teeth and the match with the upper teeth can be more obvious. A few Neogene and Pleistocene teeth that clearly belong to *Carcharhinus* have been reported or figured from the IAA by Martin (1887), Hennig (1911), Hooijer (1954), Koenigswald (1978), Uyeno (1978), Sandal (1996) and Wannier *et al.* (2011). Even local *Carcharhinus* species have been described from Java under the names *Carcharhias (Prionodon) javanus* and *Carcharhias (Prionodon) dijki* (Martin 1887). While the first is based on two crown fragments (Martin 1887, pl. 2, figs 19, 20), the second is based on three mostly fragmented teeth (Martin 1887, pl. 2, figs 21–23) that probably belong to three different carcharhinid taxa. These species can clearly be considered *nomina dubia*. Many of the other reported fossil teeth from the region are hard to classify at species level based solely on the reported figures. Nevertheless, where similarities with the Ambug fauna occur, they are mentioned below the given taxon.

Carcharhinus amblyrhynchoides (Whitley, 1934) (Fig. 4A–G)

1982 *Carcharhinus amblyrhynchoides*; Garrick: fig. 20 [modern].

Material. Fourteen upper teeth, GUBD V0011-0014, from MB.

Description. Several small upper teeth have been assigned to this species. They are relatively narrow with

nearly horizontal, bi-lobed roots. The crown of the teeth is erect. It bends slightly lingually, quickly narrows towards the tip and has a triangular shape. The cutting edges are rather straight and finely serrated. Enamel shoulders appear on both sides of the crown and they are separated by a minor notch from the main cusp. The notch is always present on the distal side, but it can be absent on the mesial side. The serration on the enamel shoulders is coarser than on the main cusp. The root is broad and flat with weak protuberances on the lingual side.

Remarks. The upper teeth of *C. amblyrhynchoides* are similar to those of *C. limbatus*, which has a more widespread distribution. However, the tooth crown of the latter is narrower with much finer serration (see Garrick 1982, figs 15, 18). The lower teeth of *C. amblyrhynchoides* have a single, straight, erect crown that is very finely serrated (Garrick 1982). Several such lower teeth occur in our collection; however, many other carcharhinids have similar lower teeth.

This is the first report of a fossil of *C. amblyrhynchoides* (graceful shark). The species is known today in the tropical Indo-West Pacific and is common around Borneo (Compagno *et al.* 2005). Its habitat is poorly known, but it is an inshore, coastal pelagic species (Compagno & Niem 1998).

Carcharhinus amblyrhynchos (Bleeker, 1856) (Fig. 4H–L)

1973 *Carcharhinus amblyrhynchos* (Bleeker, 1856); Bass, D'Aubrey, & Kistnasamy: pl. 16 [modern].

1982 *Carcharhinus amblyrhynchos* (Bleeker, 1856); Garrick: fig. 49 [modern].

Material. Ten upper teeth, GUBD V0015-V0020, from MB and R4.

Description. The crown of the upper teeth is broad at the base and gradually becomes lower and more curved distally in the lateral files. The mesial heel and cutting edge form a continuous line covered by fine, regular serration, though a small break may occur on the anterior teeth. The distal cutting edge of the crown is also finely serrated but separated with a deeper notch from the distal shoulder. This latter is much coarsely serrated and the serrae sometimes even appear as small gradually decreasing cusplets of 4–5. The roots are bilobed, wide and thin.

Remarks. *Carcharhinus amblyrhynchos* is considered to be synonymous with *C. wheeleri* (Compagno *et al.* 2005), but the published tooth sets of these taxa show some differences (Garrick 1982; Bass *et al.* 1973). Regarding the original tooth series of *C. wheeleri* (see Garrick 1982, fig. 51), the mesial cutting edge of the upper teeth looks rather straight, while in *C. amblyrhynchos* it is slightly

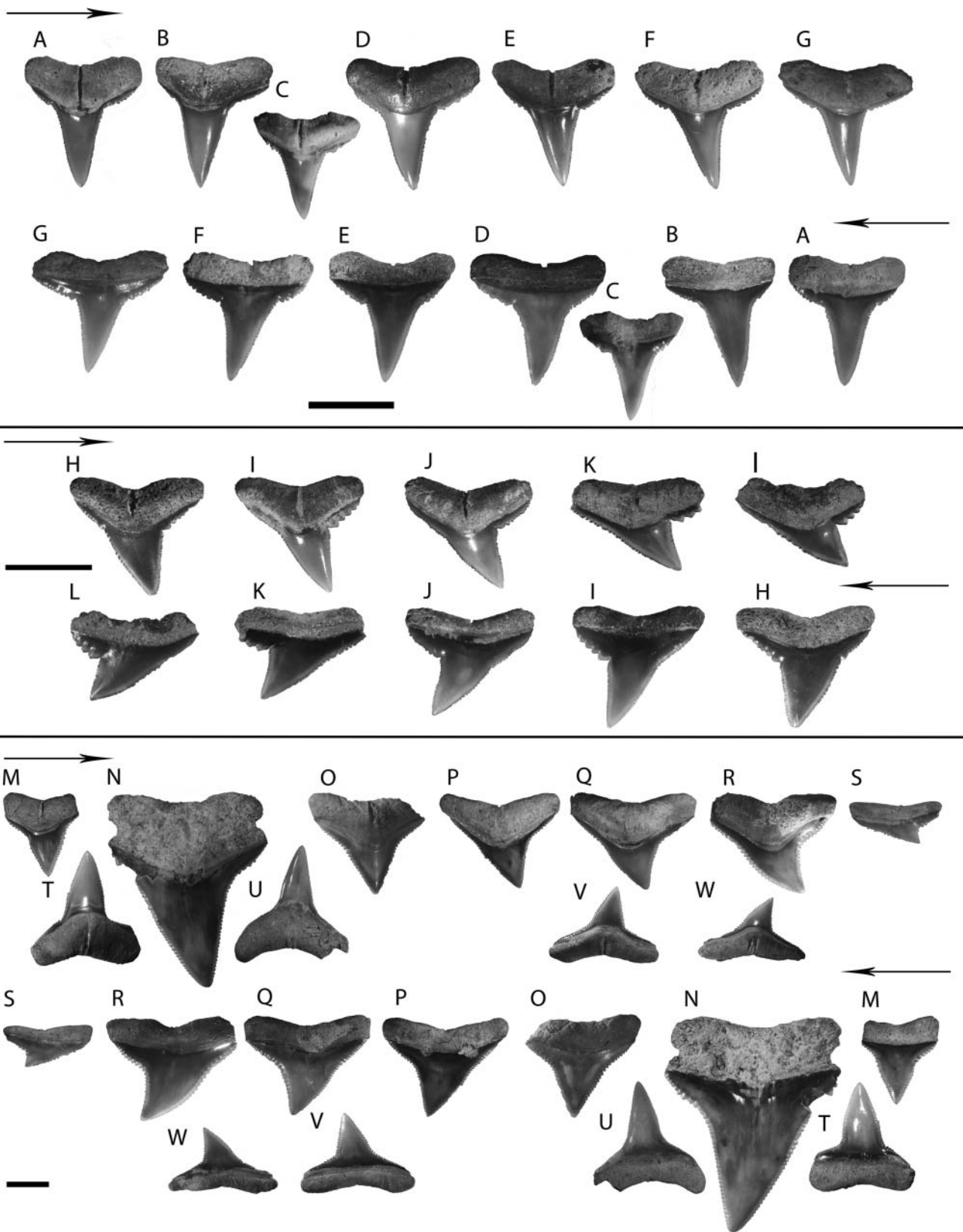


Figure 4. A–G, *Carcharhinus amblyrhynchoides*, upper tooth series in lingual and labial views, GUBD V0011, V0012, V0013; note that there are teeth in similar positions but smaller in size (B vs C), indicating the presence of different ontogenetic stages. H–L, *Carcharhinus amblyrhynchos*, lingual and labial view of an upper tooth series from more anterior to posterior positions, GUBD V0016, V0018. M–W, *Carcharhinus amboinensis*; upper (M–R) (GUBD V0021, V0022, V0024, V0025, V0027, V0029) and lower (S–V) (GUBD V0030, V0031, V0032) tooth series in lingual and labial views; note that the tooth in N is much larger and would be in the anterior-antrolateral position of such as the tooth in M. Specimens in B, E, N, O, R, S, U and V are mirrored images. Scale bars = 5 mm.

convex. Additionally, the teeth of *C. wheeleri* look somewhat wider and the serration on the distal heel is less coarse. Interestingly, the *C. amblyrhynchos* described by Garrick (1982, fig. 49) and Bass *et al.* (1973, pl. 16) are females and clearly juveniles, with total lengths of 85 and 68 cm, respectively. However, Garrick's *C. wheeleri* is bigger, with a size of 132 cm. As the two species are accepted as synonyms, all the observed differences in the dentition could reflect ontogenetic and maybe gender-related variations in the dentition. The teeth from Ambug Hill are small and similar to the teeth reported for *C. amblyrhynchos*; hence, these teeth are most probably from juveniles.

This is the first report of fossils of *Carcharhinus amblyrhynchos* (grey reef shark). The species is widespread in warm waters of the tropical Indo-West to central Pacific and hence is common in the IAA region (Compagno *et al.* 2005). It is an inshore shark, which lives in continental and insular shelves and the adjacent oceanic waters; however, it is most common over coral reefs, often near the bottom (Compagno & Niem 1998). It has been observed in water depths between 0 and 140 m (Compagno *et al.* 2005).

Carcharhinus amboinensis (Müller & Henle, 1839)
(Fig. 4M–W)

1911 *Prionodon* sp.; Hennig: pl. 11, figs 4, 5 [Java, Indonesia].

1954 *Carcharhinus* cf. *brachyurus*; Hooijer: pl. 1, figs 11–13, 15–18 [Sulawesi, Indonesia].

1973 *Carcharhinus amboinensis*; Bass, D'Aubrey, & Kistnasamy: pl. 8 [modern].

1978 *Eulamia gangetica*; Koenigswald: pl. 1, fig. 1 [Java, Indonesia].

1978 *Carcharhinus* sp.; Uyeno: pl. 2, fig. 10 [Taiwan].

Material. Thirty-five teeth, GUBD V0021–V0029 uppers (16), V0030–V0032 lowers (six), V0033–V0035 worn, broken specimens (13); from MB, R1, R3 and R4.

Description.

Upper teeth. The crown is rather broad at the base with flat labial and convex lingual surfaces. They are oblique except for the more anterior files. Both the mesial and distal cutting edges bear strong serration that is coarser at the base. The mesial cutting edge is straight or convex, while the distal one is straight to concave and it joins the distal heel with a continuous serration (i.e. no notch). The root is thick, high on the lingual side and the lobes are nearly horizontal.

Lower teeth. Narrower than the uppers, the lower teeth are quite broad at their bases. The cutting edges and the enamel shoulders are fully serrated. The anteriors are erect and slightly bent lingually, while the laterals are

distally inclined. The root base is concave but becomes straight/horizontal basally.

Remarks. The teeth of *Carcharhinus amboinensis* bear a very close resemblance to those of *C. leucas*, and it is often very hard to separate them. Moreover, the two species are sympatric in South-east Asia; hence, finding their remains in the same sediment can be expected, though the modern *C. amboinensis* does not venture into fresh waters, which is a well-known habitat for *C. leucas* (Compagno *et al.* 2005). The upper teeth of *C. leucas* are somewhat narrower, and the crowns are higher and less distally curved when compared to *C. amboinensis* (see Bass *et al.* 1973, pl. 9). The distal heel is more obviously separated on *C. amboinensis* teeth, it is closer to the base of the crown and it links to the distal cutting edge of the crown at an angle rather than with smooth curve as is the case for *C. leucas*. Also the root lobes of *C. leucas* are inclined in an approximate U-shape (see Bass *et al.* 1973, pl. 9); however, this is not always obvious and on smaller specimens the root lobes tend to be rather straight/horizontal (see Garrick *et al.* 1982, fig. 41). Based on these differences, the teeth described here are better classified as *C. amboinensis*. Many similar teeth were reported from the IAA under several different names (see synonym list), that are considered here to belong to this species.

Carcharhinus amboinensis (pigeye or java shark) is a common shark of the Indo-West Pacific and is widely distributed in South-east Asia as well. It lives along the continental coast and beaches at a depth range from 0 to 150 m (Compagno & Niem 1998; Compagno *et al.* 2005).

Carcharhinus* cf. *brachyurus (Günther, 1870)
(Fig. 5A–F)

cf. 1973 *Carcharhinus brachyurus* (Günther, 1870); Bass, D'Aubrey, & Kistnasamy: pl. 11 [modern].

cf. 1982 *Carcharhinus brachyurus* (Günther, 1870); Garrick: fig. 80 [modern].

Material. Twenty-two upper teeth, GUBD V0036–V0039; from MB, R1, R4.

Description. These upper teeth have distally curved crowns with fine, irregular serration that becomes coarser on the enamel shoulders at the base. This transition is continuous on the mesial side, while there is a small notch on the distal side before the heel. The mesial cutting edge of the crown is convex, while the distal one is straight to concave. Ontogenetic size changes for the same tooth position have been recognized (see Fig. 5B–D). Also, one larger tooth with the same general features shows a somewhat thinner and twisted crown, with a sinusoidal mesial cutting edge (Fig. 5F). The root is nearly straight/horizontal and has a slight bulge on the lingual side.

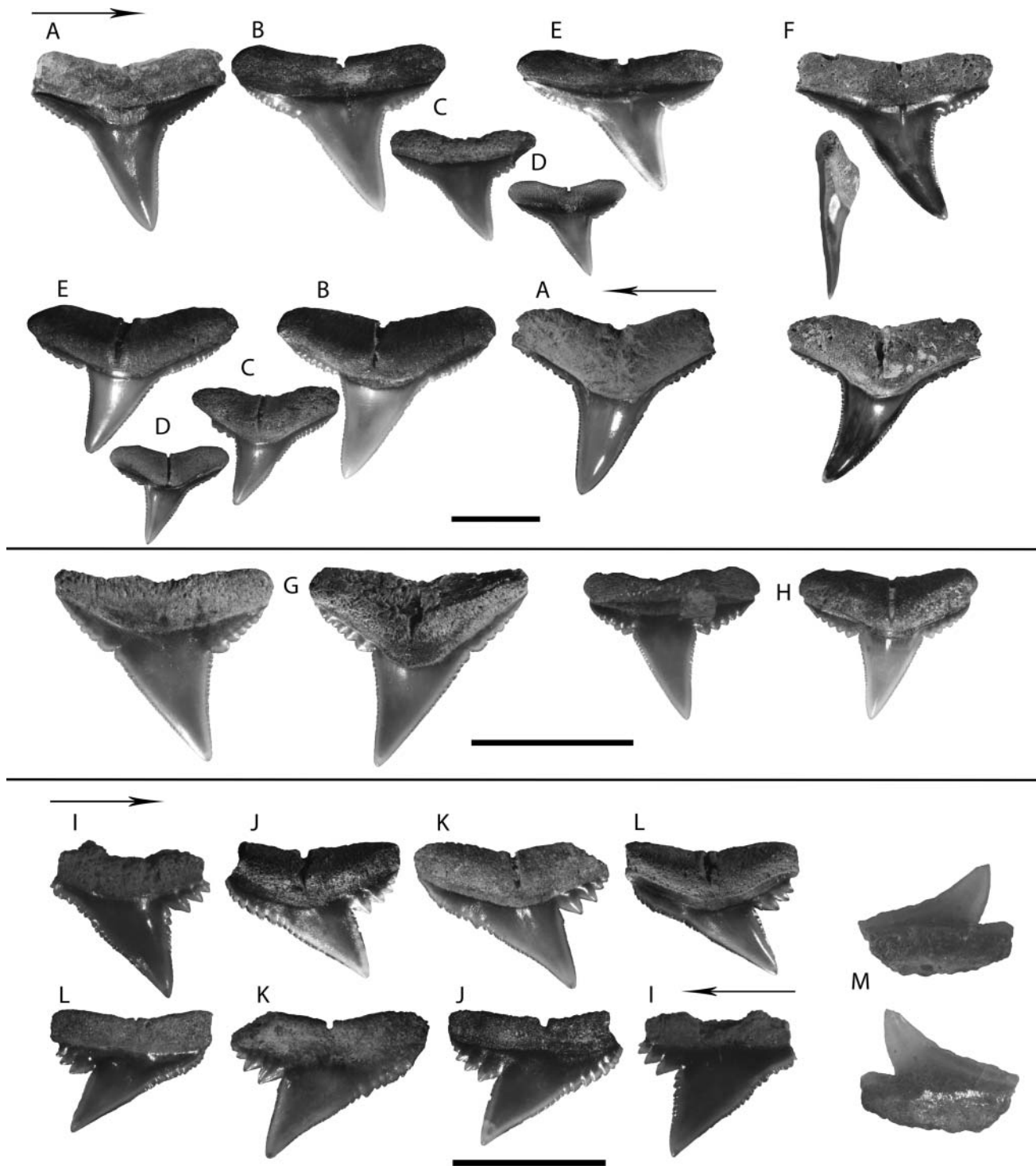


Figure 5. A–F, *Carcharhinus cf. brachyurus*; A–E, upper teeth from a more anterior to a rather lateral position; note the size range for the same position (B–D) in different ontogenetic stages, GUBD V0037; F, tooth with narrower, curving crown, probably from a young male adult, in labial, lateral and lingual views (the other teeth belonged to females), GUBD V0036. G, *Carcharhinus falciformis*, labial and lingual views, GUBD V0040. H, *Carcharhinus aff. melanopterus*, labial and lingual views, GUBD V0041. I–M, *Carcharhinus sealei*; J–M, part of the upper tooth series in lingual and labial views from a more anterior position towards a lateral position, GUBD V0042; N, worn lower tooth in lingual and labial views, GUBD V0045. Specimens in A and D are mirrored images. Scale bars = 5 mm.

Remarks. *Carcharhinus brachyurus* is known for the sexual dimorphism in its dentition, as the teeth of the males have thinner, narrower, somewhat scythe-like and rather pointed crowns compared to those of the females (see Bass *et al.* 1973; Garrick 1982). Most of the Ambug Hill teeth are very similar to modern *C. brachyurus* female teeth, with, however, less pronounced convexity on the mesial cutting edge of the teeth and coarser distal shoulder serration. The bigger tooth with a narrower, twisted crown may have belonged to an immature male shark (see Bass *et al.* 1973, pl. 11). However, mature male *C. brachyurus* individuals have much thinner and more pointed crowns (see Garrick 1982, fig. 81). Because of the differences observed here we describe the teeth mentioned above as *C. cf. brachyurus*.

This species was mentioned from the Miocene of North and South America (e.g. Purdy *et al.* 2001; Carrillo-Briceño *et al.* 2014) and Australia (Kemp 1991). The teeth of the fossil species *C. priscus*, which was widespread during the Miocene in Europe, are also very similar to those of *C. brachyurus*, and it is often considered its ancestor (e.g. Kocsis 2007; Reinecke *et al.* 2011). Hooijer (1954) mentioned this species from the IAA, but the figured teeth belong instead to *C. amboinensis*.

Carcharhinus brachyurus (copper shark or bronze whaler) is usually found worldwide in warm temperate and subtropical waters, but it occasionally occurs in tropical seas (e.g. Bass *et al.* 1973). It is a coastal and offshore shark with an active migratory habitat (Compagno *et al.* 2005).

Carcharhinus falciformis (Müller & Henle, 1839)
(Fig. 5G)

1973 *Carcharhinus falciformis* (Müller & Henle, 1839);
Bass, D'Aubrey, & Kistnasamy: pl. 7 [modern].
1982 *Carcharhinus falciformis* (Müller & Henle, 1839);
Garrick: fig. 74 [modern].

Material. One upper tooth, GUBD V0040, from R4.

Description. One upper tooth with a distally bent, triangular, high crown and finely serrated cutting edges is assigned here. The enamel shoulders bear stronger serrations, which are separated by distinct notches from the crown both mesially and distally. The labial surface is flat and from this view the crown appears elevated. The root is slightly thick and higher on the lingual side. It shows a weak nutritive groove and a rather straight root base.

Remarks. *Carcharhinus falciformis* (silky shark) is well known worldwide in tropical and sub-tropical waters. It inhabits oceanic waters near and beyond the continental slope but is also found in coastal waters. It usually lives near the surface but occurs also in much deeper water (to 500 m) (Compagno & Niem 1998; Compagno *et al.* 2005). Fossil teeth of *C. falciformis* have been reported

from North and South America (e.g. Purdy *et al.* 2001; Aguilera *et al.* 2011).

Carcharhinus aff. melanopterus
(Quoy & Gaimard, 1824)
(Fig. 5H)

aff. 1982 *Carcharhinus melanopterus* (Quoy & Gaimard, 1824); Garrick: fig. 44 [modern].

Material. One upper tooth, GUBD V0041; from MB.

Description. The only specimen is an upper tooth, which has a slightly bent, erect, triangular main cusp and a wide horizontal root base. Both the mesial and distal cutting edges of the crown are equally well serrated. The enamel shoulders are clearly separated from the main crown cusp by notches. They have much coarser serration, with five apparent individual small cusplets.

Remarks. The tooth resembles the fifth upper teeth of *C. melanopterus* figured by Garrick (1982, fig. 44); however, the specimen from Ambug Hill has much more cusplet-like serration on the enamel shoulders rather than just serration. Additionally, the tooth morphology cannot be confidently matched to other documented dentition sets of *C. melanopterus* (e.g. Bass *et al.* 1973, pls 10a, b). This may also indicate a large variety within the dentition of the modern species and more detailed study is necessary to confirm the classification of this tooth. Moreover, there is another species with similar teeth – *C. macloiti* – but the cutting edges on its main cusps are completely smooth and have only three lateral cusplets on each side instead of five (see Garrick 1985, fig. 12). The features of the tooth, such as the serration and deep notches between the cusp and the distal shoulder, make it somewhat similar also to the previously described tooth (*C. falciformis*). However, the distal shoulders are at a lower angle relative to the base of the tooth and due to its height/width ratio it does not fit any of the positions of the *C. falciformis* tooth set (see Garrick 1985, fig. 74). Nevertheless, because of all these uncertainties, this tooth will be classified as *Carcharhinus aff. melanopterus* pending the availability of further material.

Carcharhinus melanopterus (blacktip reef shark) is abundant in very shallow tropical to sub-tropical seas near coral reefs and drop-offs mainly in the Indo-West Pacific region (Compagno *et al.* 2005). It is sympatric with *C. macloiti* (hardnose shark) which, however, ventures into deeper waters down to 170 m. *Carcharhinus melanopterus* has never been mentioned from the fossil record, while *C. macloiti* has been reported from the Miocene of the Americas (e.g. Purdy *et al.* 2001; Aguilera *et al.* 2011).

Carcharhinus sealei (Pietschmann, 1913)
(Fig. 5I–M)

- 1982 *Carcharhinus sealei* (Pietschmann, 1913); Garrick: fig. 25 [modern].
 2012 *Carcharhinus sealei* (Pietschmann, 1913); White: fig. 10 [modern].
 2014 *Galeorhinus* sp.; Milankumar & Patnik: pl. 5, figs 7–10 [India].

Material. Eight teeth, GUBD V0042-V0044 uppers (seven), V0045 lower (one); from MB, levels S1, S2 and S5.

Description. Several small, upper teeth were found, that have a broad crown base with a distally bent main cusp that starts directly at the mesial edge of the tooth, its apex rising well on the distal side. The mesial cutting edge is slightly concave on the more lateral files, while straight or mildly convex on the more anterior ones. It bears coarse serration at the base that becomes finer and eventually smooth apically. The cutting edge on the distal side is either completely smooth or a small serration appears above the base. After a deep notch the main cusp is followed by a distal shoulder that contains four cusplets gradually decreasing in size distally. The root lobes are rather straight/horizontal with weak protuberances and a deep nutritive groove on the lingual side. One lower tooth was also identified, with a lingually curved, distally inclined crown where the apex appears above the distal side of the tooth. Its mesial cutting edge is smooth and strongly concave. A distal notch separates the cusp from a smooth enamel heel.

Remarks. Recently, White (2012) revised the modern *Carcharhinus sealei-dussumieri* group (Garrick 1982) by resurrecting two additional species, *C. coatesi* and *C. tju-tjut*. Based on the physical characters of these small sharks two sub-groups are distinguished, which is also reflected in their dentition. The Ambug Hill teeth are very similar to those of the *C. sealei-coatesi* subgroup. Within this group the upper teeth of *C. coatesi* seem to have a better defined mesial enamel shoulder, which makes the cutting edge slightly convex at the base, and additionally the main cusp is narrower and looks more elongated than that of *C. sealei* (see White 2012, figs 3 and 10). These differences are based on 1-1 anterolateral teeth from these species; therefore, further comparison might be needed. However, the two species are also separated geographically. *Carcharhinus sealei* can be found in South-east Asia around Borneo, Indonesia and the Philippines, while *C. coatesi* lives off the northern coast of Australia and probably off New Guinea (White 2012). *Carcharhinus sealei* (blackspot shark) is a coastal, inshore species and can be found from the intertidal zone down to 60 m depth (Compagno *et al.* 2005). *Carcharhinus sealei* has not been reported in the fossil record so far, but very similar teeth from the Miocene Baripada beds of Eastern India have been described under the name *Galeorhinus* sp.

(Milankumar & Patnik 2014, pl. 5, figs 7–10), which most probably represent *C. sealei*.

Carcharhinus spp.

Material. Fifty-three teeth, GUBD V0046-V0051 uppers (25), GUBD V0052-V0059 lowers (28); from MB, R4.

Description. The lower teeth have a straight or slightly distally curved, narrow crown whose cutting edges are either finely/moderately serrated or, in rare cases, smooth. Some have distinct, thin, horizontal enamel shoulders. The root is elongated horizontally or slightly concave. The upper teeth specimens are partially broken.

Remarks. Although the lower teeth are well preserved, they cannot be confidently grouped under the described species of *Carcharhinus amblyrhynchoides*, *C. amblyrhynchos*, *C. cf. brachyurus*, *C. falciformis* or *C. aff. melanopterus*, and more comparative studies are necessary. A parsimonious interpretation is that the broken upper teeth most possibly represent some of the carcharhinid species described here.

Genus *Glyphis* Agassiz, 1843

Glyphis cf. glyphis (Müller & Henle, 1839)
(Fig. 6A–F)

Materials. Six teeth, GUBD V0060 upper anteriors (two), V0061 upper laterals (three) and V0062 lower (one); from MB.

Description.

Upper teeth. The teeth are quite thin with crowns that are flat on the labial surface and slightly convex on the lingual surface. The anteriors are almost symmetrical, with an elongated triangular crown and a broad base. Minor distal and mesial enamel shoulders are present, which become more pronounced laterally along the anterior teeth positions. Serrations are fine and regular throughout the cutting edges. The root is thick on the lingual face with a weak nutritive groove, present only on a second anterior tooth. The basal root edge for the first anterior teeth is straight and concave for the second. The lateral and posterior teeth are gradually asymmetrical with a straight or slightly concave mesial cutting edge, while the distal cutting edge is strongly concave and continuously reaches the distal end of the root. The cutting edges are covered with fine serration that becomes coarser basally. The roots are relatively thin with a straight basal line, though some specimens are broken.

Lower tooth. The crown is elongated, narrow, erect and slightly curved lingually. It has a spearhead shape at the tip of the crown that bears very weak serration. The root is broad and curved, though the lobes are very short. A deep nutritive groove is also observable.

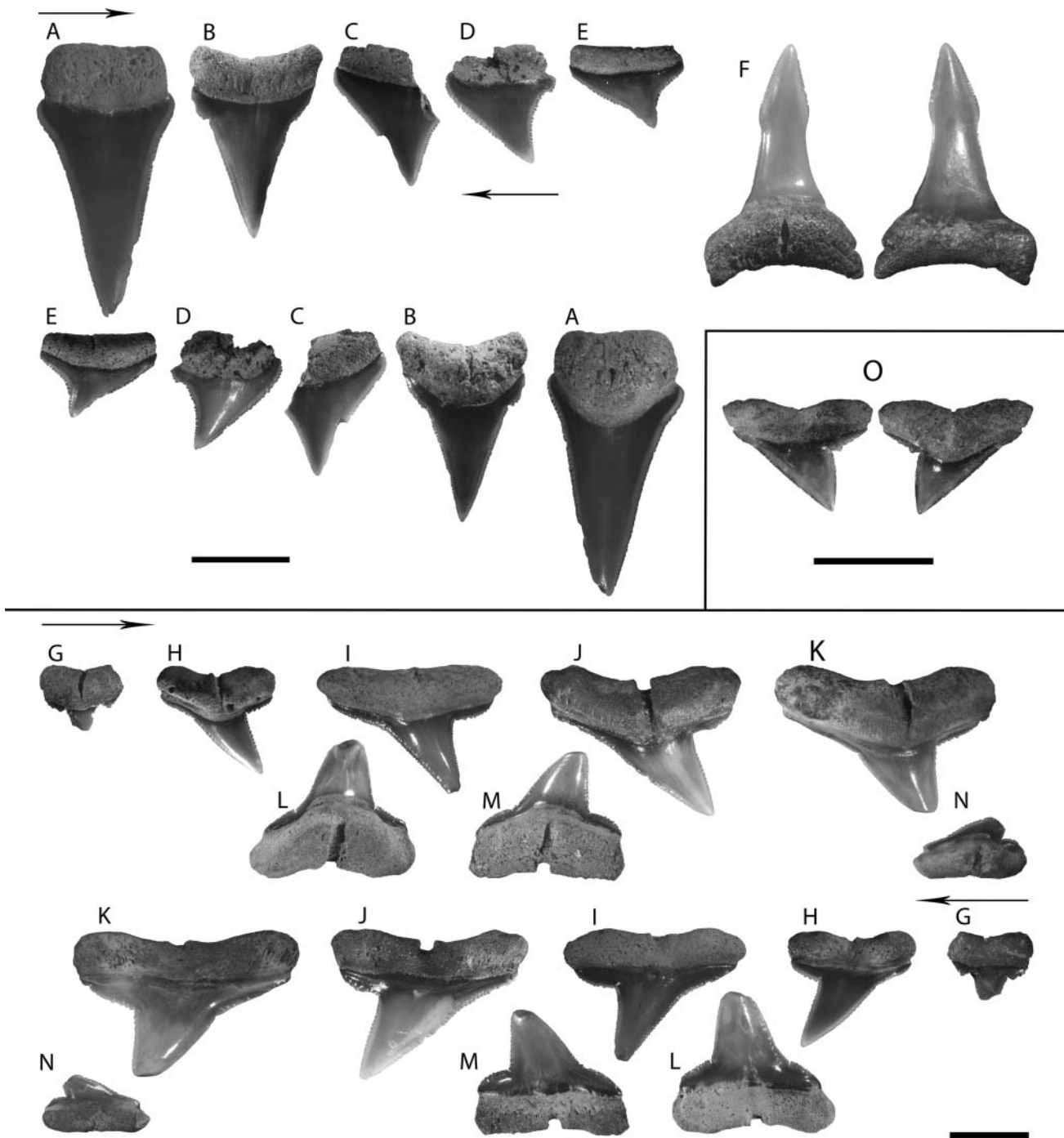


Figure 6. A–F, *Glyphis cf. glyphis*; A–E, part of the upper tooth series with anteriors (A, B) (GUBD V0060) and laterals (C–E) (GUBD V0061) in labial and lingual views; F, typical lower tooth with spear-shaped crown tip in lingual and labial views, GUBD V0062. G–N, *Sphyrna cf. mokarran*; upper (G–K) and lower (L–N) teeth as a part of a tooth series in lingual and labial views, GUBD V0065, V0066, V0068, V0069; G, symphyseal, L, posterior, the rest are different lateral teeth. O, ?*Sphyrna aff. zygaena*, labial and lingual views of an upper lateral tooth, GUBD V0071. Specimens in D, E, G, K and M are mirrored images. Scale bars: A–L = 5 mm; O = 3 mm.

Remarks. *Glyphis* is a special Indo-West Pacific tropical shark genus that inhabits rivers and estuaries, though it sometimes also appears in coastal waters (Compagno *et al.* 2005). Our knowledge of these river

sharks is quite limited, as they are rare and it is difficult to identify them. *Glyphis glyphis* (spartooth shark) has characteristic lower anterior-anterolateral teeth with a spearhead-shaped tip of the crown (see also Cappetta

2012, fig. 288). The upper teeth are quite similar to those of *G. gangeticus* (ganges shark); however, the lower teeth are rather pointed and often have a pair of lateral cusplets beside the main crown (see Cappetta 2012, fig. 287). *Glyphis glyphis* was redescribed together with a new species, *G. garricki*, by Compagno *et al.* (2008). The two species have quite similar dentition and based on the available descriptions and photographs they cannot be confidently separated using isolated teeth (see Compagno *et al.* 2008, figs 3 and 10). Therefore, the Bruneian teeth are described here only as *Glyphis* cf. *glyphis*. The two species are reported from the same area of Northern Australia and New Guinea. From Borneo another species is known, *G. fowleare*; however, it has completely different lower teeth (Compagno *et al.* 2010).

Concerning the fossil record, Shimada *et al.* (2016) revised the extinct species of *G. pagoda* whose remains are found in fresh water and nearshore marine settings of Lower to early Upper Miocene beds in India and Myanmar. They provided a thorough literature review and revision of the *Glyphis*-related literature from Asia and produced a detailed synonymy. They reported several types of lower teeth under this species, among them the spearhead type (Shimada *et al.* 2016, fig 2B, E–J) and the pointed narrow-cusped crown with lateral cusplets (Shimada *et al.* 2016, fig 2S) that are features of *G. glyphis* and *G. gangeticus*, respectively. This may indicate that at least two or even three different species might have co-habited these river systems, or that the morphological variations in the teeth within the river shark species are much larger than previously believed. Nevertheless, due to the age and the geographical differences plus the described morphological mixture, a link between the Ambug teeth and *G. pagoda* is rejected here. Still, it cannot be ruled out that the fossil teeth presented here might also consist of more species, as the classification here relies strongly on the lower tooth only.

Fossil *Glyphis* teeth not discussed by Shimada *et al.* (2016) have been reported from the IAA. Pleistocene deposits of Sulawesi (Hooijer 1954: *Carcharhinus* cf. *gangeticus*) and Java (Kouman 1949: *Eulamia gangetica*) have yielded some undoubted river shark teeth. The teeth described by Hooijer (1954) look quite robust compared to the Ambug teeth and only one lower tooth seems to have a spearhead-shaped tip (Hooijer 1954, pl. 2, fig. 19). As for the Java teeth, no such feature appears, although one upper tooth is quite similar to our upper anteriors (Kouman 1949, pl. 2, fig. 7). Most of these reported remains were related to *G. gangeticus*, but more study is needed for a clearer taxonomy. Still, these reports, together with the Bruneian fossils, obviously indicate a wider presence of river sharks in the ancient IAA as well. It must be mentioned that Koenigswald (1978) described some teeth under the name *Eulamia gangetica* from Java. However,

these teeth clearly do not belong to *Glyphis* but instead are similar to those of *C. amboinensis* reported here.

Unidentified *Carcharhinidae*

Materials. Twenty-two teeth, GUBD V0063–V0064; from MB.

Description. Worn and broken upper and lower tooth crowns from members of the family.

Family **Sphyrinidae** Gill, 1872
Genus ***Sphyrna*** Rafinesque, 1810
Sphyrna* cf. *mokarran (Rüppell, 1837)
(Fig. 6G–N)

cf. 1975 *Sphyrna mokarran* (Rüppell, 1837); Bass, D'Aubrey & Kistnasamy: pl. 11 [modern].

Material. Thirteen teeth, GUBD V0065–V0067 uppers (nine), V0068–V0070 lowers (four); from MB, R3 and R4.

Description. Both upper and lower teeth have characteristic bulky, thick and high roots with a prominent wide nutritive groove that reaches the base of the tooth, and which is also clearly seen in labial view as a gap at the base. The symphyseal and first anterior teeth have straight, erect crowns, while along the lateral files the crown becomes more and more curved distally. The cutting edges and the enamel shoulders bear rather coarse, irregular serration both on the uppers and lowers. The upper teeth have triangular and bent crowns, which are broad at the base. The apex is narrow and rises well distally. The mesial cutting edge of the crown is rather convex or straight, but concave at the base as the crown rises from the mesial heel. The distal cutting edge is straight and has a notch at the base, followed by a coarsely serrated distal heel. The root lobes are straight/horizontal or slightly concave. The mesial lobes look somewhat longer than the distal ones. The lower teeth are narrower and bulkier. The crowns are rather erect and less inclined distally compared to those of the uppers.

Remarks. Among the modern members of Sphyrinidae, *Sphyrna mokarran* (great hammerhead shark) is the only species whose teeth are strongly serrated, though fine serration might appear on the teeth of *S. zygaena* as well (Cappetta 2012). Besides the serration, the narrow, bulky lower teeth and most of the upper teeth are a good fit to the modern dentition set of *S. mokarran* (Bass *et al.* 1975, pl. 11). However, some of the assigned upper teeth (Fig. 6L, K) have less bent crowns and rather straight mesial cutting edges that are somewhat different from the figured modern teeth. Admittedly, Bass *et al.* (1975, p. 44) observed slight sexual dimorphism, with more erect and thinner teeth for adult males. Hence, these teeth

could represent male specimens. Nevertheless, due to the observed variation the teeth are described as *S. cf. mokarran*.

The great hammerhead has a worldwide distribution in tropical seas. It is a coastal-pelagic, semi-oceanic species that is found by coral reefs, from close inshore to far off-shore (Compagno *et al.* 2005).

?*Sphyrna aff. zygaena* (Linnaeus, 1758)
(Fig. 6O)

Material. One tooth, GUBD V0071; from MB.

Description. One tiny upper tooth with a distally bent crown that is wide at the base. A small, short mesial heel is followed by the straight mesial cutting edge of the crown. The distal cutting edge is slightly convex. The crown and the mesial heel are completely smooth. On the distal side, however, at the base of the crown after a notch, a slightly oblique distal enamel shoulder appears with a few distally decreasing serrae. The root protrudes; it is bulky on the lingual side, and its base is slightly concave.

Remarks. The tooth resembles the fossil teeth of *Sphyrna zygaena* (Cappetta 2012, fig. 301); however, the Ambug tooth is narrower and the distal heel is serrated. Examination of the modern tooth series of Bass *et al.* (1975, pl. 12) indicates that, in view of the low width/height ratio and the wide crown base, the tooth would be better fit to the upper anterior series. But these mature teeth have a strongly curved mesial cutting edge and, again, a smooth distal heel. Based on only one tooth and the differences described here, this tooth is more suitably classified as ?*Sphyrna aff. zygaena*.

Sphyrna zygaena (smooth hammerhead) is known from the Miocene (Cappetta 2012). The modern species has a worldwide distribution in tropical and temperate waters.

Unidentified **Carcharhiniformes**

Material. Twelve tooth fragments, GUBD V0072-V0076, from MB, R1 and R4.

Description. Tooth fragments that belong to either Carcharhinidae or Sphyrnidae.

Superorder **Batomorphii** Cappetta, 1980
Order **Rhinopristiformes** Naylor, Caira, Jensen,
Rosana, Straube, & Lakner, 2012
Family **Pristidae** Bonaparte, 1838
Genus ***Pristis*** Linck, 1790
***Pristis* sp.**
(Fig. 7A)

Material. One rostral tooth, GUBD V0077; from MB.

Description. One elongated, rather straight dextral rostral tooth was found. It is pointed at the distal end where it

is posteriorly curved. The proximal end where it joined to the rostrum is broken. The anterior edge is slightly curved and convex, while the posterior side is distinctly concave and asymmetrical with a more pronounced rim on the upper surface. The upper side curves slightly down, while the lower is rather flat.

Remarks. *Pristis* is a genus of sawfish, which is known from the early Eocene (Cappetta 2012). A few fossil remains have been reported from the IAA of Java by Hennig (1911, pl. 11, fig. 7, as *Pristis* sp.) and Koenigswald (1978, fig. 2, as *Pristiopsis cf. microdon*).

It must be mentioned that, based on strong molecular evidence from modern taxa, the family Pristidae has been placed with Rhinidae (also including Rhynchobatidae) under the same order, Rhinopristiformes (Naylor *et al.* 2012). Today, four modern species are considered to be valid, of which three can be found around Borneo (Last *et al.* 2016c). They are common in tropical and subtropical coastal environments but are also known for entering estuaries and venturing upstream of rivers (Last *et al.* 2016c).

Family **Rhinidae** Müller & Henle, 1841
Genus ***Rhina*** Bloch & Schneider, 1801
Rhina ancylostoma Bloch & Schneider, 1801
(Fig. 7B, C)

1978 *Dasyatis* sp. Uyeno: pl. 4, fig. 26 [Taiwan].

Material. Three teeth, GUBD V0078, from MB.

Description. The teeth are rhombic in shape in occlusal view, with a convex globular occlusal surface. Though the teeth are worn, seven to eight transverse ridges can be observed that are slightly arched lingually. These ridges are connected with lower, irregular enameloid folds. The lingual face of the crown is also covered by longitudinal enameloid folds on the largest tooth (Fig. 7B), while on the smaller ones this is rather smooth. In the centre of the lingual side a prominent rounded median uvula appears also with enameloid folds. The lateral edge of the crown is undulose on both side of the uvula, giving the impression of weakly developed marginal uvulae. On the labial side the crown overhangs the root, forming a small angular visor. The root is much narrower than the crown and beside a deep, basal nutritive groove, two marginal foramina can be observed below the lingual edge of the crown.

Remarks. These fossil teeth are very similar to the teeth of the only modern species, *Rhina ancylostoma* (bow-mouth guitarfish); hence, they are described under this taxon. The teeth are the first clear evidence for the presence of *Rhina* in the fossil record. So far only one ray tooth has been reported, from Taiwan (Uyeno 1978 as *Dasyatis* sp.), which most probably also belongs to this

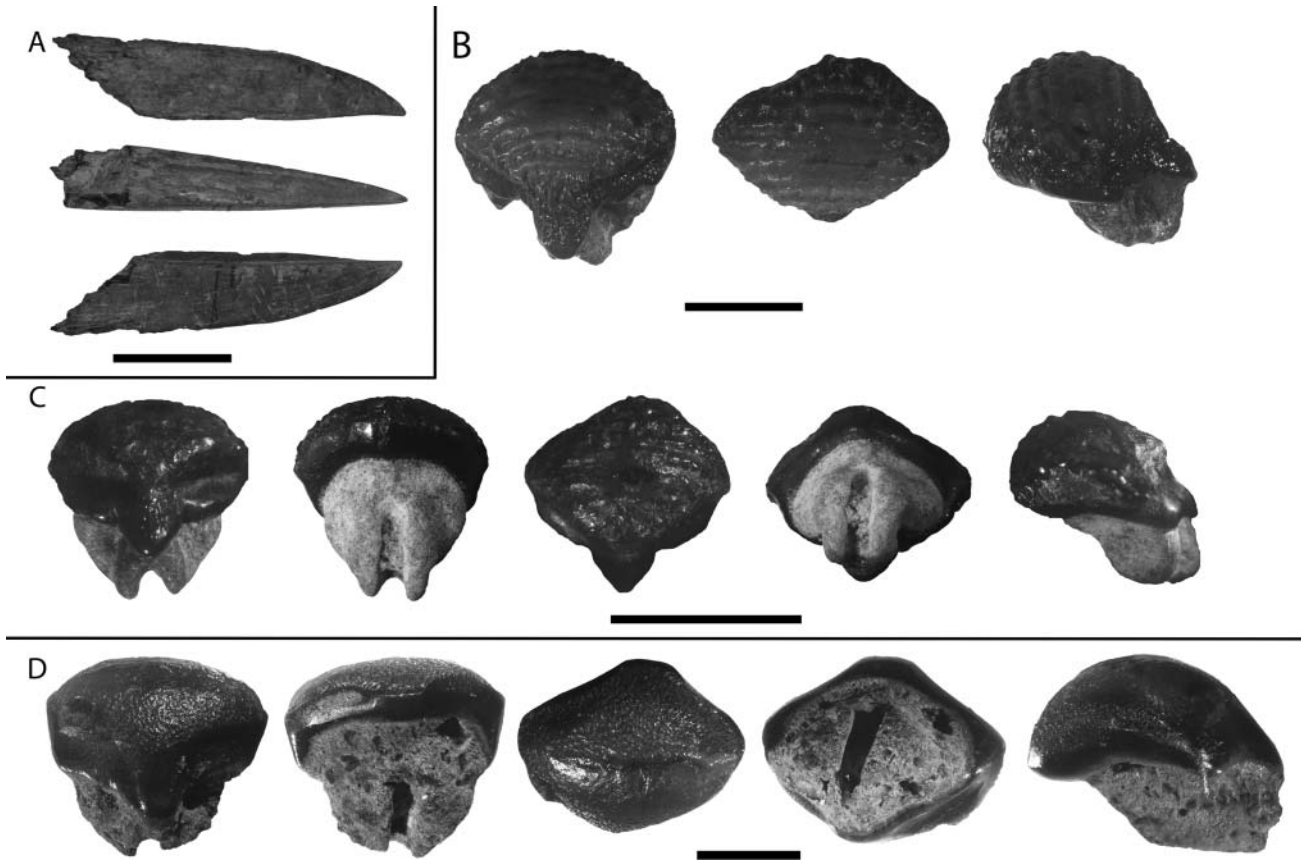


Figure 7. **A**, *Pristis* sp., rostral tooth in dorsal, posterior and ventral views, GUBD V0077. **B, C**, *Rhina ancylostoma*, GUBD V0078; **B**, lingual, occlusal and lateral views; **C**, lingual, labial, occlusal, basal and lateral views. **D**, *Rhynchobatus* sp., lingual, labial, occlusal, basal and lateral views, GUBD V0079. Scale bars: A = 10 mm; B–D = 3 mm.

species (Cappetta 2012). *Rhina ancylostoma* is common in the Indo-West Pacific tropics. It is a bottom-dweller and inhabits coastal areas and the surrounds of coral reefs at depths of at least 70 m (Last *et al.* 2016c).

Genus *Rhynchobatus* Müller & Henle 1837a

Rhynchobatus sp.

(Fig. 7D)

Material. One tooth, GUBD V0079; from MB.

Description. The crown is wider than it is long, rhombic in shape in occlusal view and convex in lateral view. Although the surface of the crown is somewhat worn, an ornamentation of enameloid granules and a clear transverse crest separating the labial and the lingual zones are still observable. On the other hand, the lingual face of the crown is rather smooth and bears a massive medial uvula. The lingual lateral edges of the crown are straight. On the labial side the crown overhangs the root, forming a small angular visor. The root is narrower than the crown and a deep, basal nutritive groove and two marginal foramina can be observed below the lingual edge of the crown.

Remarks. The characters described here fit the general tooth design of the genus (see Cappetta 2012, fig. 326). The genus *Rhynchobatus* (wedgfishes) previously had its own family Rhynchobatidae; however, recent molecular studies show a close relationship to the genus *Rhina*; hence, the two genera are now grouped into the family Rhinidae (Last *et al.* 2016b). Eight modern species are known, of which two are widespread in South-east Asia in the IAA, *R. australiae* and *R. springeri* (Last *et al.* 2016c). They are bottom-dwellers and mostly live in coastal shallow open waters, though *R. springeri* also frequents brackish estuarine environments (Last *et al.* 2016c). Regarding the fossil record, *Rhynchobatus* is known from the Lower Eocene. It has not been reported from the IAA, but the closest Neogene remains from Asia are known from Japan (Cappetta 2012) and India (Milan-kumar & Patnik 2013, fig. 5F).

Order **Myliobatiformes** Compagno, 1973

Superfamily **Dasyatoidea** Whitley, 1940

Family **Dasyatidae** Jordan, 1888

Remarks. Recently, the family Dasyatidae has been revised and many new genera have been introduced or resurrected based on molecular and morphological studies of several recent specimens (Last *et al.* 2016a). At least 89 modern species exist (Last *et al.* 2016c). Regarding the fossil record, which is mainly based on isolated teeth, *Dasyatis* dominates the family with at least 32 fossil species, of which some might belong to *Himantura* (Cappetta 1987, 2012). Originally *Dasyatis* contained 36 modern species, but these have now been reduced to five and the rest are grouped into seven other genera. Similarly, the genus *Himantura* now includes only four species but previously contained about 20, which are now distributed between five other genera. In view of this new taxonomy, it is clear that even the genus-level classification of fossil teeth will remain problematic until detailed studies of the tooth morphology of specimens in the modern taxa are performed. Nevertheless, Cappetta (2012) gave detailed dental descriptions of some modern and fossil species, and based on the reported morphological features the Ambug Hill fossils are grouped in the genera below.

Genus *Himantura* Müller & Henle, 1837b

Himantura sp.

(Fig. 8A–D)

Material. Eighteen teeth, GUBD V0080–V0083; from MB levels S2, S3 and S5.

Description. The teeth are rather rhombic in occlusal view, with a rounded labial contour and a somewhat pointed lingual one. The crown is rather high; its labial face displays a shallow transverse depression a bit closer to the lingual zone of the crown. On unworn teeth the whole labial surface is covered by strong, irregular enameloid folds and granules. On the smaller teeth this ornament is much more enhanced, with relatively higher enameloid ridges and a deeper lingual zone depression. A sharp transverse crest separates the labial and lingual faces of the crown. This crest on one of the small teeth is rather pointed and salient (Fig. 8C). The upper part of the lingual face is always covered by enameloid folds that run rather vertically. The lower part is smooth and has a salient median lingual ridge. The root, when preserved, is narrower than the crown, and often labio-lingually elongated; the basal surface is flat and the lobes are separated by a large furrow.

Remarks. Cappetta (2012) described the teeth of the modern species *Himantura uarnak* and mentioned minor sexual dimorphism. The ornamentation and the general shape of the teeth are very similar to those of the Ambug teeth, except that most of the teeth are much larger and narrower when compared to the figured modern specimens (Cappetta 2012, fig. 411). Most of the teeth belonged to females, while the only small one with a

rather pointed transverse crest represents a male tooth. Though the recent revision of Dasyatidae reduced the number of *Himantura* species (Last *et al.* 2016a, c) and we have no knowledge of the dentition of the new or resurrected taxa, based on the similarities to the still-valid *H. uarnak*, the teeth described here are classified under this genus. The Ambug Hill *Himantura* teeth come from two size classes with slight qualitative differences (e.g. ornamentation). This indicates either that there are two different species in our fauna, or that the small teeth in our record represent juveniles. At this stage the latter scenario is preferred.

Regarding the fossil record of *Himantura*, the oldest possible remains were reported from the late Eocene Fayum deposits in Egypt (Underwood *et al.* 2011); however, the specimens are not figured. On the other hand, the reported *Taeniura* sp. (Underwood *et al.* 2011, fig. 7M–O) seem instead to belong to *Himantura*, based on the short folds on the upper part of the lingual face of the crown. Other remains have been reported from the Early Oligocene of Pakistan (Adnet *et al.* 2007) and the Miocene of Madagascar (Andrianavalona *et al.* 2015, fig. 5B–G). Additionally, teeth resembling those of this genus have also been found and reported from the Miocene of Peninsular India (Sahni & Mehrotra 1981, pl. 3, fig. 9, and probably pl. 4, fig. 3 [*Raja* sp.]; Milankumar & Patnik 2013, fig. 6E [*Dasyatis menoni*] and fig. 6F–H [*Dasyatis* sp. 1 and sp. 2]). Today the four modern species of this whipray live in the Indo-Pacific region. They inhabit inshore waters but some have also been reported from lagoons, brackish estuaries and mangrove swamps; they are bottom-dwellers with a preference for soft substrates (Last *et al.* 2016c).

Genus *Pastinachus* Rüppell, 1829

Pastinachus sp.

(Fig. 8E–G)

Material. Nine teeth, GUBD V0084; from MB.

Description. The teeth are wider than they are long and are hexagonal in shape in occlusal view, except one whose width/length ratio is close to 1 (Fig. 8E). The top surface is flat and smooth. The labial and lingual faces of the crown are rather vertical. The labial face is slightly convex and has a small overhanging visor, while the lingual face is concave with a small transverse bulge at the base. In labial/lingual view the crown is either horizontal or oblique. The root is completely under the crown; it has two large vertical lobes separated by a deep and broad furrow. The base of the root is flat and each lobe has a sort of pentagonal outline in basal view.

Remarks. These teeth clearly belong to *Pastinachus* (see Cappetta 2012, fig. 413), which has a strong dignathic heterodonty and crushing/grinding-type dentition. The

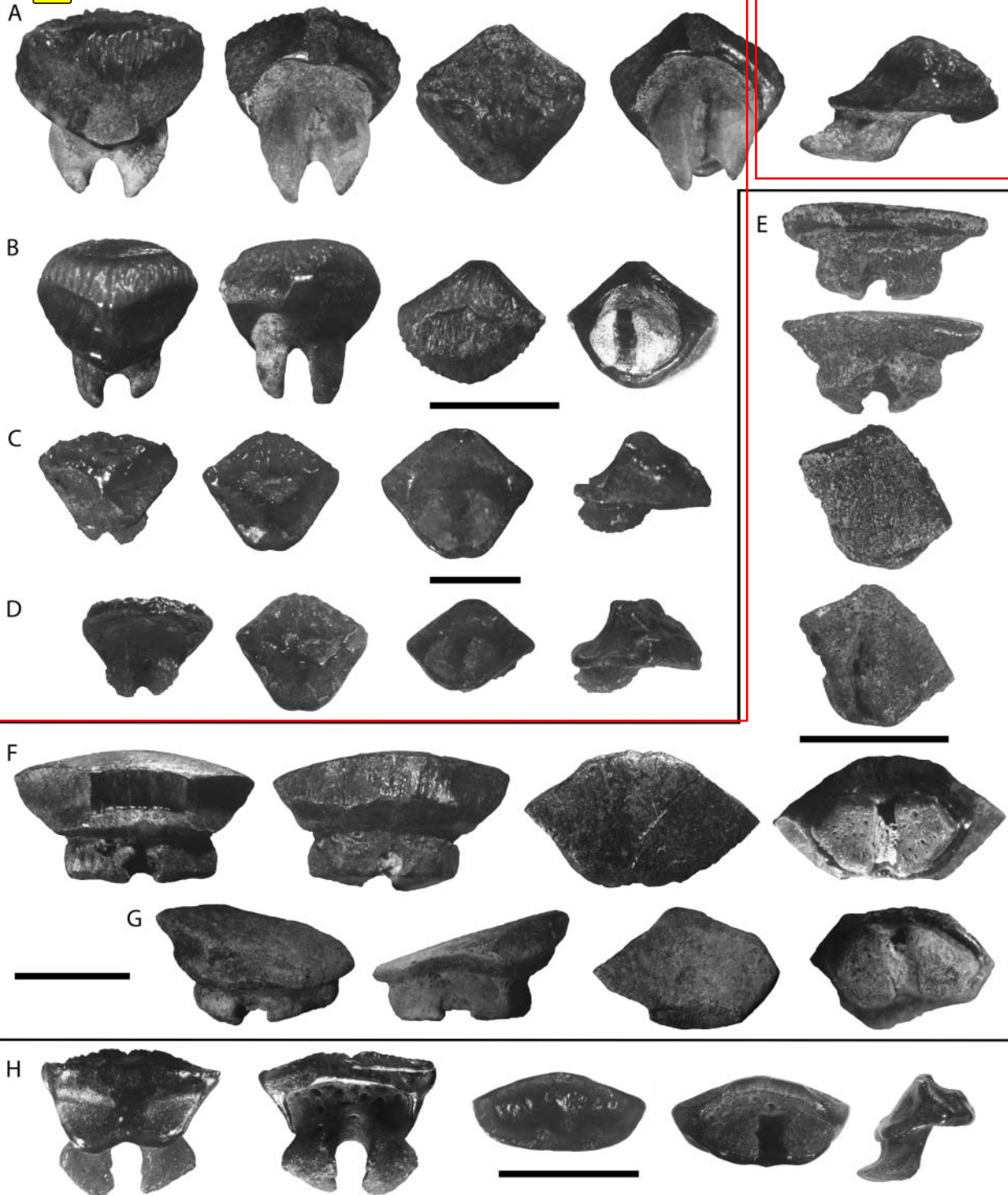


Figure 8. A–D, *Himantura* sp., from left to right (A, B) lingual, labial, occlusal and basal views plus lateral view for (A), GUBD V0080; C, lingual, occlusal, basal and lateral views, GUBD V0082; D, labial, occlusal, basal and lateral views, GUBD V0083. E–G, *Pastinachus* sp., GUBD V0084; E, very lateral tooth, from top to bottom in labial, lingual, occlusal and basal views; F, G, symmetrical and asymmetrical lateral teeth, from left to right in lingual, labial, occlusal and basal views. H, *Taeniurops* sp. (GUBD V0085) From left to right, lingual, labial, occlusal, basal and lateral views. Scale bars: A, B = 5 mm; C, D = 1 mm; E–H = 3 mm.

morphology is also very distinct from that of other dasyatids. Based on a comparison with modern jaws from Borneo, the teeth are either upper laterals, with a more lateral position for the narrow tooth (Fig. 8E), or lower teeth.

The oldest fossil record of *Pastinachus* comes from the late Eocene Fayum deposits of Egypt (Underwood *et al.* 2011, fig. 7L). In the Neogene fossil record *Pastinachus* appears in the Indian Miocene under the names *Hypolophus sylvestris mohuliyi* (Ghosh 1959, pl. 88, figs 2, 9), *Dasyatis sylvestris* (Sahni & Mehrotra 1981, pl. 3, figs 5, 6; Milankumar & Patnik 2013, fig. 6A) and *Dasyatis mahuleinsis* (Milankumar & Patnik 2013, fig. 6B–D). A tooth reported from Taiwan as *Dasyatis* sp. (Uyeno 1978, pl. 4, fig. 25) probably also belongs to *Pastinachus*. The modern *Pastinachus* (cowtail stingray) is widespread in the tropical Indo-Pacific region and was long thought to be monospecific (*P. sephen*). However, in view of new studies and molecular data, five modern species are now distinguished, of which four live in South-east Asia (Last *et al.* 2016b). The most common and best known of these is *P. ater*, which inhabits coastal waters and the surrounds of coral reefs, but occasionally enters fresh water and can be found in estuaries (Last *et al.* 2016c).

Genus *Taeniurops* Garman, 1913

Taeniurops sp.
(Fig. 8H)

Material. One tooth, GUBD V0085; from MB.

Description. The tooth is much wider than it is long and has a high crown. The labial edge of the crown is convex, while the lingual is straight in occlusal view. The occlusal surface has a clear, elongated transverse hollow with a slightly deeper part in the centre. The depression is bordered by sharp crests both lingually and labially, of which the latter are more prominent and also bear enameloid folds. The labial face of the crown is smooth; the basal margin is slightly longer just above the root lobes. At the labial surface of the crown a narrow visor overhangs the root. The root is positioned completely under the crown and the two lobes are separated by a deep furrow.

Remarks. The features described here fit completely the description of the genus provided by Cappetta (2012). However, the illustrated teeth of *Taeniurops* aff. *grabata* (Cappetta 2012, fig. 413) are clearly different from the Ambug tooth as they are much narrower and have enameloid folds on the upper part of the lingual face of the crown. *Taeniurops* has two Recent species, *T. grabata* which lives around the coastal waters of Africa, and *T. meyeri* which is an Indo-Pacific species common in the seas of South-east Asia (Last *et al.* 2016c). So far there is no comparative dentition set available for *T. meyeri* and therefore the tooth described here is classified only at the genus level.

Taeniurops meyeri (blotched stingray) has a benthic habitat around coral reefs and also offshore on soft substrates. It is found from very shallow, coastal waters down to more than 400 m (Last *et al.* 2016c). Fossil *Taeniurops* teeth have been mentioned from Europe (Cappetta 2012) and the genus possibly also occurs in South America (Carrillo-Briceño *et al.* 2016).

Unidentified Dasyatidae

Material. Six teeth, GUBD V0086–V0090; from MB levels S1, S2 and S5.

Remarks. Several quite worn teeth with clear affinity to the Dasyatidae occur. Most probably belong to *Himantura*, and one may belong to *Pastinachus*.

Superfamily **Myliobatoidea** Compagno, 1973

Family **Aetobatidae** White & Naylor, 2016

Genus *Aetobatus* Blainville, 1816

Aetobatus sp.
(Fig. 9B, C)

Material. Twenty-one teeth, GUBD V0091 lower tooth plate fragments (15), V0092 upper tooth plate fragments (six); from MB.

Description. The lower teeth are strongly arched labially; the crown is high and slightly longer in the medial region than in the marginal one. The labial and lingual faces of the crown are close to vertical or slightly oblique lingually. At the base of the lingual side of the crown a narrow rim and a distinct furrow run side by side. On the labial side the complement of these features can be observed. The root extends extremely lingually and is flattened dorso-ventrally. The upper teeth of this genus are rather rectilinear and they curve lingually only at the marginal edges. At the Ambug Hill site only tooth fragments with this marginal, backward-curving edge were found (Fig. 9C).

Remarks. *Aetobatus* (bonnet ray) has a single row of medial teeth forming the dental plate in the upper and lower jaws. Based on the described characters these tooth plates or their fragments can be identified with confidence. Hovestadt & Hovestadt-Euler (2013) studied the dentition of modern *Aetobatus* and reported that the locking mechanism of these teeth possesses ornamentation with horizontally directed furrows. Such features can be observed on the better preserved specimens from Ambug Hill, especially on the lingual side at the base of the crown. The genus is known from the Upper Paleocene, with many fossil species (Cappetta 2012). The closest fossil occurrences to the IAA region are reported from the Miocene of India (Mondal *et al.* 2009; Milankumar & Patnik 2013). Today five species exist, of which two occur in the IAA (White 2014; Last *et al.* 2016c), *A. ocellatus* and *A. flagellum*.

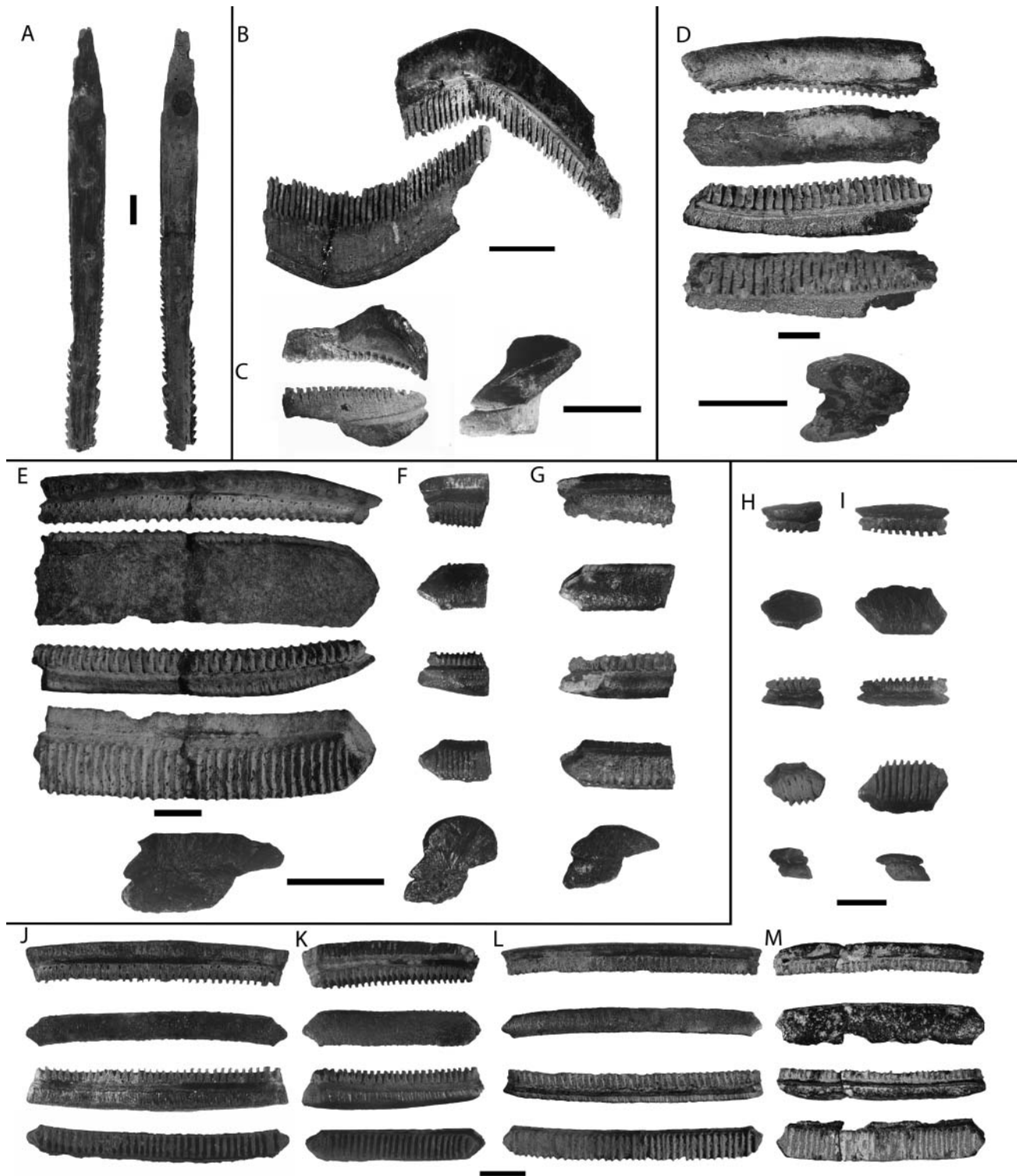


Figure 9. **A**, caudal spine of Myliobatiformes, GUBD V0100. **B**, **C**, *Aetobatus* sp.; **B**, occlusal and basal view of a lower tooth, GUBD V0091; **C**, lateral end of upper tooth, GUBD V0092. **D**, *Aetomylaeus* sp., medial tooth, from top to bottom in labial, occlusal, lingual, basal and lateral views, GUBD V0093. **E–G**, *Myliobatis* spp. medial tooth fragments; **E**, *Myliobatis* sp. 1, GUBD V0094; **F**, **G**, *Myliobatis* sp. 2, GUBD V0095; from top to bottom: labial, occlusal, lingual and basal views, and below cross-sections of each tooth. **H–M**, *Rhinoptera* sp.; **H**, **I**, posterior teeth, GUBD V0098; **J**, **L**, **M**, medial teeth, GUBD V0096; **K**, lateral tooth, GUBD V0097; from top to bottom: labial, occlusal, lingual and basal views, while below the posterior teeth lateral views added. Scale bars = 5 mm (the larger scale bars are for the lateral and cross-section views).

They are benthopelagic and are common inshore, as well as offshore, in rather shallow warm temperate and tropical seas (< 100 m), but some also frequent brackish environments (Last *et al.* 2016c).

Family **Myliobatidae** Bonaparte, 1838

Genus ***Aetomylaeus*** Garman, 1908

***Aetomylaeus* sp.**

(Fig. 9D)

Material. Three teeth, GUBD V0093; from MB.

Description. The teeth are badly preserved and broken. The best specimen is a medial tooth that is slightly arched lingually, and its preserved lateral edge is angular in occlusal view. The crown is thicker medially and its labial face is rather convex. On the lingual side, the crown overhangs the root forming a rim, and a distinct ridge appears at its base. The basal side of the crown rim bears irregular tubercles. The root is directed slightly more lingually than the lingually overhanging crown. The two other teeth also have a distinct basal ridge at the lingual base of the crown and also bear the same type of tubercle-like ornamentation.

Remarks. *Aetomylaeus* and *Pteromylaeus* were synonymized by White (2014), which is accepted here. *Aetomylaeus* has dental plates that consist of one very wide median file and three pairs of small lateral ones. Cappetta (2012) discussed the dentition of *Aetomylaeus* and *Pteromylaeus* separately and pointed out slight differences, such as the fact that the crown of the medial teeth of *Aetomylaeus* is higher in the centre than at the edges, while the root of *Pteromylaeus* thins out towards the lateral edges. On the other hand, Hovestadt & Hovestadt-Euler (2013) reported large intraspecific and intrageneric variations in their tooth morphology and strong ontogenetic changes in case of *Aetomylaeus*. Apparently, juveniles bear seven tooth files; however, with age the lateral teeth gradually disappear. Such a change was not observed for *Pteromylaeus*. The ornamentation of the locking mechanism for *Aetomylaeus/Pteromylaeus* comprises fine vs coarse scattered costules, respectively (Hovestadt & Hovestadt-Euler 2013). These are considered a good character for distinguishing individual teeth from other genera such as *Myliobatis* and *Aetobatus*. Although the teeth from Ambug Hill are quite worn, their morphology differs in having an overhanging crown on the lingual side, plus the basal surface of this rim is covered by characteristic tubercular patterns. Such patterns can be observed only on these teeth and might represent a weathered version of the type of ornamentation at the locking mechanisms described by Hovestadt & Hovestadt-Euler (2013).

Regarding the fossil record, *Aetomylaeus* has been reported only from the Miocene; however, many forms previously described as *Myliobatis* might belong to this

genus (Cappetta 2012). This eagle ray genus has seven species today, of which four occur in the IAA (Last *et al.* 2016c). The two species that are common around Borneo are *A. maculatus* and *A. nichofii*. They are pelagic, mainly over soft bottoms, and inhabit rather shallow water, mostly inshore or over the continental shelf (Last *et al.* 2016c).

Genus ***Myliobatis*** Cuvier, 1816

***Myliobatis* sp. 1**

(Fig. 9E)

Materials. Four teeth, GUBD V0094; from MB.

Description. The teeth are broken, but clearly all are medial files with angular lateral margins that would form hexagonal shapes in occlusal view if they were complete. On the two larger specimens a slight lingual arching is observable in occlusal view, and their occlusal surfaces are rather flat, or slightly convex. The crown is low and overhangs strongly on the labial side, forming a distinct rim. The labial face of the crown is very thin, with a convex edge. The basal surface of the rim bears vertical ornamentation. The upper part of the lingual face is rather vertical and partially covered by vertical ornamentation. On the lower part of the lingual face, the crown has a distinct, oblique shelf, below which the enameloid reaches the top part of the root. The root extends slightly lingually.

***Myliobatis* sp. 2**

(Fig. 9F, G)

Material. Two teeth, GUBD V0095; from MB.

Description. These teeth bear most of the features described for the previous taxon; however, the length of the labial rim is somewhat shorter, the crown is higher and the occlusal surface is strongly to mildly globular. The teeth are fragmentary and therefore it cannot be seen whether or not they are arched lingually.

Remarks. *Myliobatis* has dental plates with one wide medial and generally three pairs of small lateral files in both the upper and the lower jaws. The interlocking design between tooth plates, with the shelf forming on the lingual side of the crown and the somewhat lingually extended root, are typical features of the genus. The locking ornamentation of vertically directed costules is apparently also unique to this genus (Hovestadt & Hovestadt-Euler 2013). The two *Myliobatis* species recognized here are based mainly on the thickness and occlusal shape of the crown, while the other features are very similar between the two. However, the more globular and convex-shaped crown of *Myliobatis* sp. 2 might indicate less worn teeth of the same species, especially in view of the height differences between the two teeth in this group (see cross-sections Fig. 9F, G). Nevertheless, the crown of

Myliobatis sp. 1 also looks longer. Therefore, until new remains turn up, these two tooth designs are classified as different taxa.

Myliobatis is very common in the fossil record and is known to have existed since the Early Paleocene (Cappetta 2012). These eagle rays have not been reported from the Neogene of the IAA, but Miocene deposits of many nearby regions in Asia have yielded their remains (e.g. Tiwari & Ralte 2012; Milankumar & Patnik 2013). Eleven modern *Myliobatis* species exist (White & Naylor 2016), of which only *M. hamlyni* appears in the IAA, while the next closest one is *M. tobijei*, which lives around Japan and East China. These two taxa should be the targets for future comparative studies involving fossil teeth. Whereas *M. hamlyni* is a rather deep-water form (> 200 m), *M. tobijei* has a preference for shallow marine habitats (0–220 m) (Last *et al.* 2016c).

Family **Rhinopteridae** Jordan & Evermann, 1896

Genus **Rhinoptera** Cuvier, 1829

Rhinoptera sp.

(Fig. 9H–M)

Material. Eight teeth, GUBD V0096 medial teeth (three), V0097 laterals (three), V0098 posteriors (two); from MB.

Description.

Medial teeth. Two wide, narrow symmetrical teeth were found that are slightly lingually arched and have hexagonal shapes in occlusal view (Fig. 9J, L). One has a higher crown than the other, but on both the labial and lingual crown faces are vertical. At the base of the lingual face a prominent, protruding ridge runs along the width of the teeth. On the labial side, the crown slightly overhangs the root and has a small rectilinear furrow at its base. The root is short and is positioned completely under the crown. A third, worn, yet symmetrical tooth has similar features, but is slightly longer and its width is somewhat less compared to the other medial teeth (Fig. 9M).

Lateral teeth. The major characters are the same as the medial teeth but these teeth are asymmetrical in labial/lingual view, the crown is higher mesially and they are narrower (Fig. 9K). The root extends a little lingually on the first laterals, a feature which is enhanced in the case of the more posterior positioned, very narrow teeth (Fig. 9H, I).

Remarks. *Rhinoptera* (cownose ray) have dental plates with a median tooth followed by three or four pairs of gradually less wide laterals. The morphology described above clearly fits this genus. Individual teeth might be confused with those of *Myliobatis* but the presence of wide and asymmetrical teeth, the interlocking design (e.g. absence of a lingual shelf) and the often-greater width/length ratio of the teeth are characteristic of *Rhinoptera*.

The genus appeared in the Late Paleocene, and several fossil species exist (Cappetta 2012). This is the first fossil *Rhinoptera* record from the IAA, but there are other Neogene occurrences in tropical-subtropical Asia (e.g. Milankumar & Patnik 2013). Of the eight modern species, three are present in the IAA: *R. javanica*, *R. jayakari* and *R. neglecta* (Last *et al.* 2016c). These are tropical-subtropical, marine benthopelagic forms found in coastal areas, often in reef-associated habitats (Last *et al.* 2016c). In order to see whether the Ambug teeth can be linked to any of these species, a future comparative study will be necessary.

Unidentified **Myliobatoidea**

Material. Seven teeth, GUBD V0099; from MB.

Remarks. Several badly preserved, worn and broken tooth fragments clearly belong to this superfamily. They could represent the genera *Aetomylaeus*, *Myliobatis* or *Rhinoptera*.

Unidentified **Myliobatiformes**

(Fig. 9A)

Materials. Thirteen caudal spines or their fragments, GUBD V0100; from MB.

Remarks. Caudal spines are characteristic features of most of the taxa in this order. However, due to their very similar characters, even among the modern forms (Hovestadt & Hovestadt-Euler 2013), lower level taxonomy of these remains is difficult.

Discussion

The recovered elasmobranch teeth come from four orders, of which two belong to sharks and two to rays (Table 1). Among the sharks, the order Carcharhiniformes dominates, with three families and many species: Hemigaleidae (one species), Carcharhinidae (nine) and Sphyrnidae (two). The other order, Lamniformes, is represented by a single species, the largest predatory shark of the Neogene, *Otodus (Megaselachus) megalodon*. This large species and the Hemigaleidae species *Hemipristis serra* are the only extinct forms in the Ambug Hill fauna. All of the other sharks have modern representatives, but interestingly some are reported here from the fossil record for the very first time (*Carcharhinus amblyrhynchoides*, *C. amblyrhynchos*, *C. amboinensis* and *C. sealei*). Molecular data-based phylogenetic trees concur well with our data (Sorenson *et al.* 2014), as most of the predicted first occurrence ages for the carcharhinid species are before or around the age of the Ambug Hill fauna (6.5–8 Ma). However, for the newly reported species *C. amblyrhynchoides*

Table 1. List of the recovered elasmobranch fossils from Ambug Hill, and their numerical abundance. Extinct species are indicated by daggers.

Order	Family/superfamily	Genus/species	No.	
Lamniformes	Otodontidae	<i>Otodus (Megaselachus) megalodon</i> †	1	
Carcharhiniformes	Hemigaleidae	<i>Hemipristis serra</i> †	19	
		Carcharhinidae	<i>Galeocerdo cuvier</i>	7
			<i>Carcharhinus amblyrhynchoides</i>	14
			<i>Carcharhinus amblyrhynchos</i>	10
			<i>Carcharhinus amboinensis</i>	35
			<i>Carcharhinus</i> cf. <i>brachyurus</i>	22
			<i>Carcharhinus falciformis</i>	1
			<i>Carcharhinus</i> aff. <i>melanopterus</i>	1
			<i>Carcharhinus sealei</i>	8
			<i>Carcharhinus</i> spp.	53
			<i>Glyphis</i> cf. <i>glyphis</i>	6
		indet. Carcharhinidae		22
		Sphyrnidae	<i>Sphyrna</i> cf. <i>mokarran</i>	13
	? <i>Sphyrna</i> aff. <i>zygaena</i>		1	
indet. Carcharhiniformes			12	
Rhinopristifomres	Pristidae	<i>Pristis</i> sp.	1	
	Rhinidae	<i>Rhina ancylostoma</i>	3	
		<i>Rhynchobatus</i> sp.	1	
Myliobatiformes	Dasyatidae	<i>Himantura</i> sp.	18	
		<i>Pastinachus</i> sp.	9	
		<i>Taeniurops</i> sp.	1	
		indet. Dasyatidae		6
	Aetobatidae	<i>Aetobatus</i> sp.	21	
	Myliobatidae	<i>Aetomylaeus</i> sp.	3	
		<i>Myliobatis</i> sp. 1	4	
<i>Myliobatis</i> sp. 2		2		
Rhinopteridae	<i>Rhinoptera</i> sp.	8		
	indet. Myliobatoidea		7	
indet. Myliobatiformes		caudal spines	13	

and *C. sealei* the predicted first occurrences are younger (Sorenson *et al.* 2014), and their presence in our fauna could help to refine phylogenetic trees.

Regarding the batoids, the order Myliobatiformes contributes most of the fauna, with four families and several taxa: Dasyatidae (three species), Aetobatidae (one), Myliobatidae (three) and Rhinopteridae (one). Additionally, a few remains were found from the families Pristidae (one species) and Rhinidae (two) of the order Rhinopristiformes. All the reported batoid genera were known previously from the fossil record. However, for most this is the first report from the IAA (e.g. *Rhina*, *Rhynchobatus*, *Himantura*, *Pastinachus*, *Taeniurops*, *Aetomylaeus*, *Myliobatis* and *Rhinoptera*).

The level of taxonomy followed here is somewhat different between the selachians and the batoids. While the sharks were classified more readily at the species level, the batoids were kept mostly at the genus level without

definite species identification. The latter group has more conservative dentition, and in addition their recently updated classification involving many new genera (especially Dasyatidae) (Last *et al.* 2016c) makes it difficult to classify these fossil teeth confidently at a lower taxonomic level until detailed studies have been carried out on their dentitions. Moreover, while reports on the tooth series of modern sharks are readily available (e.g. Bass *et al.* 1973, 1975; Garrick 1982, 1985), similar studies on rays are rather rare (Cappetta 2012). Nevertheless, a total of 24 cartilaginous fish taxa have been recognized from the Late Miocene sediments of Ambug Hill.

To emphasize the uniqueness of the fauna, it can be compared with the available fossil data from the IAA (Fig. 10; Supplemental Table). Neogene and Pleistocene fossil chondrichthyans have been reported only from Java (e.g. Martin 1887; Hennig 1911; Kouman 1949), Pulau Madura (Leriche 1954) and Sulawesi (Hooijer 1954), and

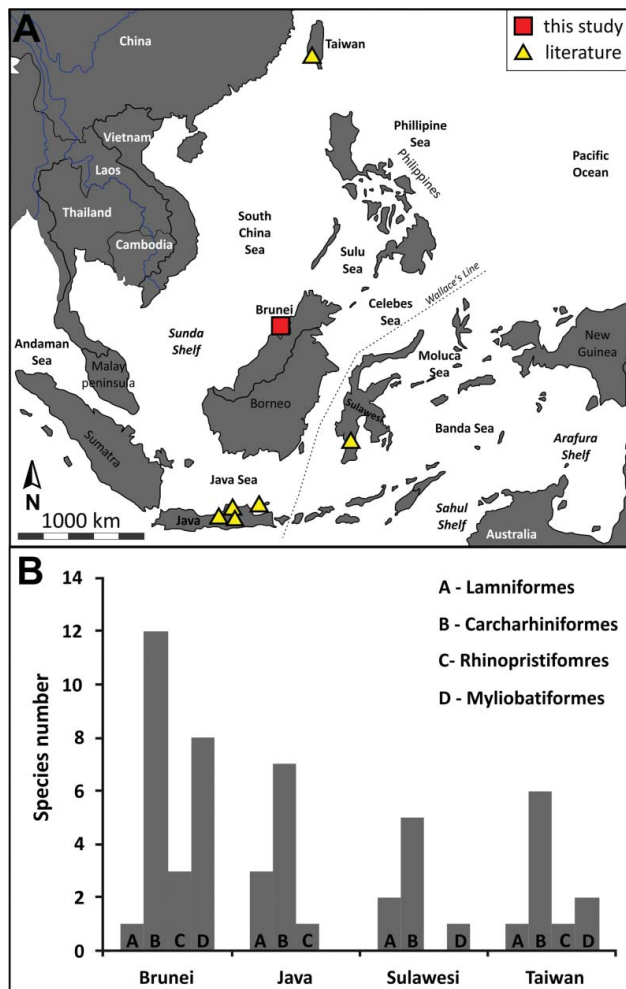


Figure 10. **A**, geographical map of the Indo-Australian Archipelago showing localities from which fossil cartilaginous fish remains have been reported. **B**, comparison of the Neogene and Pleistocene cartilaginous fish fauna between Brunei, Java (Miocene: Martin 1887; Kouman 1949; Leriche 1954; Pleistocene: Hennig 1911; Kouman 1949; Koenigswald 1978), Sulawesi (Pleistocene: Hooijer 1954) and Taiwan (Miocene: Uyeno 1978) at ordinal level showing species diversities (see also Supplemental material).

as a part of a wider northern extension from Taiwan (Uyeno 1978). Generally, most of the reported taxa belong to the same four orders as the Ambug Hill fauna, although revision of some forms in the old literature is needed. Nevertheless, when the species numbers in these regions are compared, a contrast in diversities is apparent. Everywhere the order Carcharhiniformes is the most diverse as well as the richest fauna found in Brunei. Additionally, both batoid orders have a higher species diversity in Brunei compared to the other localities. On the other hand, the order Lamniformes is very underrepresented in Brunei, as it is also in the IAA. The diversity differences among the different regions are best explained by sampling bias and a lack of detailed research in the other

regions of the IAA. The map in Figure 10 also emphasizes that there are numerous blank regions in the IAA (e.g. Sumatra, peninsular Malaysia, Vietnam, Philippines) for which no data exist. Future research should target these regions.

Most of the sharks and rays described here are typical tropical-subtropical forms inhabiting shallow coastal seas, and many are restricted to the Indo-Pacific region. The dominance of Carcharhiniformes, and especially of the family Carcharhinidae, reflects the modern diversity of requiem sharks in tropical shallow marine environments. The most common shark taxa are *Carcharhinus amboinensis*, *C. brachyurus*, *Hemipristis serra* and *C. amblyrhynchoides*, while among the rays the genera *Aetobatus*, *Himantura*, *Pastinachus* and *Rhinoptera* are the most numerous (Fig. 11; Table 1).

There are a few cosmopolitan and more open-water forms, such as the tiger shark (*Galeocerdo cuvier*), the great hammerhead (*Sphyrna mokarran*) and the silky shark (*Carcharhinus falciformis*). The presence of the extinct macro-predatory shark *Otodus (Megaselachus) megalodon* is somewhat surprising, especially in view of the fact that no other Lamniformes have been discovered. No remains of Odontaspidae or Lamnidae sharks have been found, which otherwise are common shark taxa of many Miocene faunas (Cappetta 2012) and have also been reported from Java (Kouman 1949) and Sulawesi (Hooijer 1954). The lack of these taxa is probably linked to the tropical, shallow coastal environment, which was often influenced by continental run-off. The wandering of *O. (Megaselachus) megalodon* into the shallows may indicate the search for special food sources such as marine mammals like dugongs. These animals are well known in the modern IAA, but as far as we know they have not been reported from the fossil record in Borneo.

The river shark (*Glyphis cf. glyphis*) is an interesting element of the fauna. The presence of this species would indicate nearby freshwater or brackish conditions, such as a river mouth or estuaries. Other taxa such as *Pristis*, *Himantura* and *Pastinachus* have also been reported from estuaries and fresh water. In contrast, the invertebrates of the locality indicate fully marine conditions with, however, some peculiarities. Many gastropod species are of unusually small sizes (Harzhauser *et al.* 2018), while the benthic foraminiferan fauna is dominated by two taxa (Roslim *et al.* 2016), both features which might point to suboptimal environmental conditions. In view of the mixed fish fauna, these suboptimal conditions could relate to the proximity of riverine influence (i.e. turbid water and/or fluctuating salinity). Whether the river sharks lived near this shallow coastal environment or their remains were transported to or re-worked at the depositional site is hard to assess, but by performing, for example, trace element and stable isotope analyses of the teeth these questions could be tested in the future. In either case, their

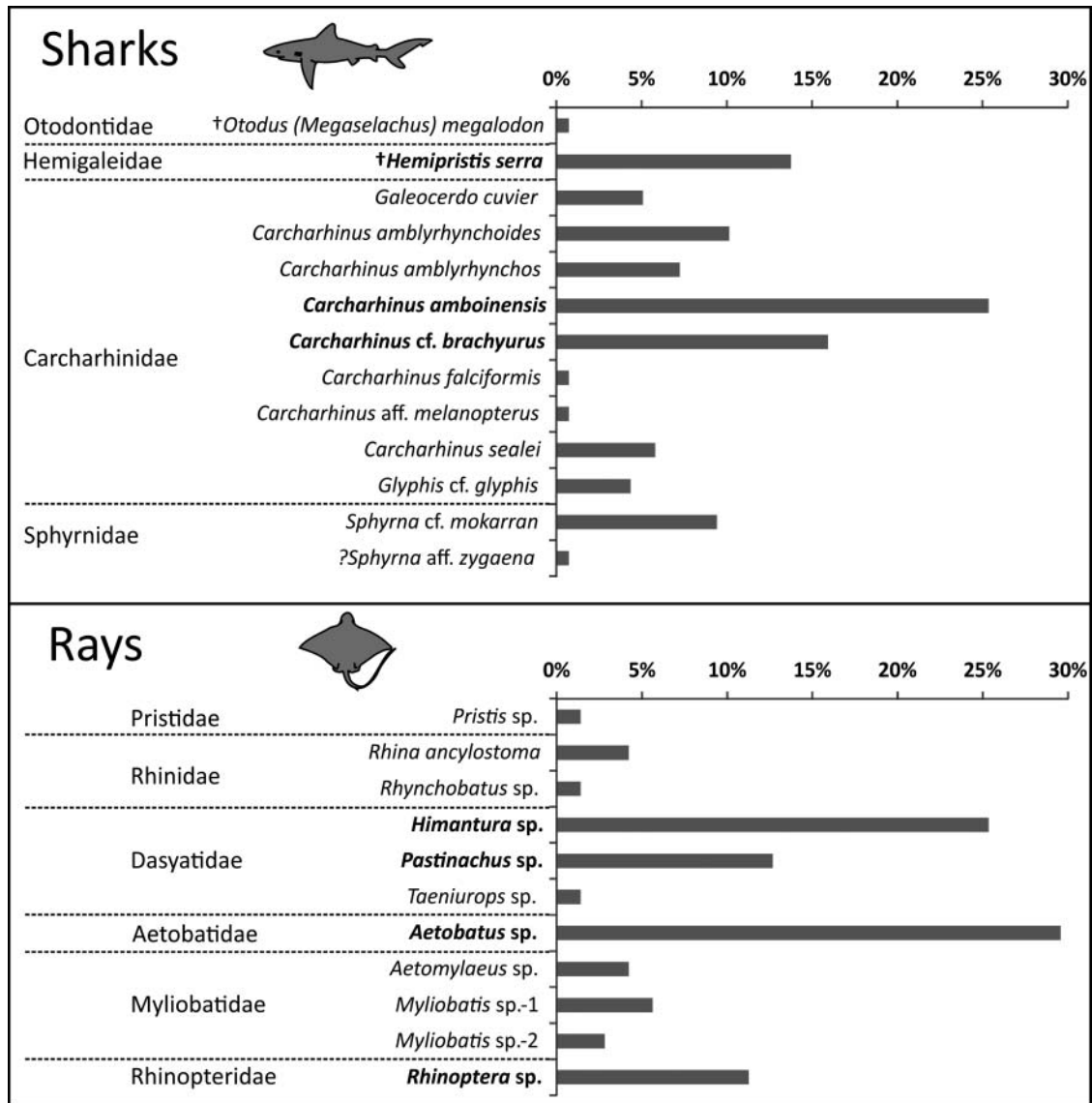


Figure 11. The relative abundance of shark and ray taxa at Ambug Hill. The most common taxa are in bold.

presence in the fauna clearly indicates a nearby fluvial influence. This may be one of the key factors, together with the general coastal ecological environment, accounting for the scarcity and lack of some of the otherwise common, more open-water shark taxa like *Otodus (Megaselachus) megalodon* and other Lamniformes such as *Isurus* and *Alopias*. Other pelagic taxa such as the carcharhinid shark *Carcharhinus longimanus* can be included as well.

On the other hand, mangroves, estuaries and coastal regions are often used as nursery grounds by rays and sharks (e.g. Heupel *et al.* 2007) and some species even venture into river systems during reproductive times (e.g. Heupel & Simpfendorfer 2008). In our fauna some sharks clearly show different ontogenetic stages, with the

presence of smaller teeth coming from juveniles (see *Carcharhinus amblyrhynchoides*: Fig. 4B, C; *C. cf. brachyurus*: Fig. 5B–D). This may be an indication that the region was used as a nursery ground by these species at least, although more studies are needed on this topic.

Regarding dietary preferences, most of the shark taxa are piscivorous. The remains of teleost fishes such as otoliths, and teeth and bone fragments, are very common fossils at Ambug Hill. Together with the rays, these indicate that abundant food sources were available for the sharks. *Otodus (Megaselachus) megalodon* and *Galeocerdo cuvier* could have had more diverse diets, involving the consumption also of marine reptiles, mammals or birds. The presence of turtles in the ancient ecosystem is recognized from fragments of turtle carapaces in the sediments.

The cutting-type dentition of the tiger shark is well adapted to cut through the shells of turtles. Therefore, these marine reptiles are often included in their diet. As mentioned earlier, *O. (Megaselachus) megalodon* might have ventured into coastal regions in search of marine mammal such as dugongs. However, there is so far no indication of these animals in the fossil record of Ambug Hill. Most of the batoids described here have durophagous diets based on their dentition, and they lived mostly on molluscs, whose hard shells they crushed up. Some rays may also have had a cancritrophic diet, involving the consumption of crustaceans. The Ambug Hill sediments are very rich in molluscs (Harzhauser *et al.* 2018) and in many types of decapod crabs, which could have been the major source of nourishment for these fishes.

Conclusions

The remains of 24 taxa of selachians and batoids were recovered from the Late Miocene of Ambug Hill in northern Borneo. The shark fauna is dominated by Carcharhiniformes and specifically by the Carcharhinidae. Several species of *Carcharhinus*, common today in South-east Asia, are identified for the first time in the fossil record (*C. amblyrhynchoides*, *C. amblyrhynchos*, *C. amboinensis* and *C. sealei*). In addition, the teeth of the cosmopolitan tiger shark *Galeocerdo cuvier* and of the river shark *Glyphis* cf. *glyphis* belonging to the same family are reported. Also found were *Hemipristis serra*, an extinct widespread tropical shark of the Miocene belonging to Hemigaleidae, and possibly two species of the hammerhead sharks (Sphyrnidae), *Sphyrna* cf. *mokarran* and ?*S. aff. zygonea*. Only one other shark order, Lamniformes, has a representative in the fauna, which is the giant extinct shark *Otodus (Megaselachus) megalodon*.

Two batoid orders are present in the fauna, Rhinopristiformes and the Myliobatiformes, of which the latter is the more dominant. The most common taxon is Myliobatoidea, with of *Aetobatus* sp., *Aetomylaeus* sp., two species of *Myliobatis*, and *Rhinoptera* sp. This is followed by the almost equally common Dasyatidae, with *Himantura* sp., *Pastinachus* sp. and *Taeniurops* sp. Rhinopristiformes is represented by only a few remains of three taxa: *Pristis* sp., *Rhina ancylostoma* and *Rhinchobatus* sp.

Although the diversity of modern elasmobranchs in the IAA is much higher, such fossil diversity has never before been recorded in South-east Asia. Many of the fossil taxa recorded are typical coastal, shallow water forms in the tropical-subtropical region of the Indo-Pacific today. Except for the two extinct species *Otodus (Megaselachus) megalodon* and *Hemipristis serra*, all the other taxa are extant. The dominance of carcharhinid sharks and small rays suggests a shallow marine, coastal palaeoenvironment. The presence of the freshwater shark *Glyphis* and

the rays *Himantura* and *Pastinachus* indicates nearby fluvial influence.



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Supplemental data

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