

**Shark teeth from Pirabas Formation
(Lower Miocene), northeastern Amazonia, Brazil**
Dentes de tubarões da Formação Pirabas
(Mioceno Inferior), Amazônia Oriental, Brasil

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Abstract: The shark fauna (Chondrichthyes: Elasmobranchii) of Pirabas Formation is one of the most representative and diversified of the Neogene of South America. This fauna is associated with the early Miocene transgression resulting from the global sea level rise. In this paper, the composition of the Pirabas shark fauna is re-evaluated based on new fossil findings. The occurrence of the following taxa is confirmed: *Carcharhinus* sp.1, *Carcharhinus* sp.2, *Carcharhinus* cf. *macloti*, *Carcharhinus* *priscus*, *Galeocерdo* sp., *Sphyrna* cf. *media*, *Hemipristis* *serra*, *Carcharodon* *subauriculatus*, *Isurus* sp., *Ginglymostoma* sp., *Nebrius* *obliquus*.

Keywords: Pirabas Formation. Chondrichthyes. Neogene. Amazonia.

Resumo: A fauna de tubarões (Chondrichthyes: Elasmobranchii) da Formação Pirabas é uma das mais representativas e diversificadas do Neógeno da América do Sul. Ela está associada à transgressão ocorrida no início do Mioceno, em consequência do aumento global do nível do mar. Neste trabalho, a composição da fauna de tubarões previamente identificada para a Formação Pirabas é reavaliada com base em novos achados fósseis. É confirmada a ocorrência dos seguintes táxons: *Carcharhinus* sp.1, *Carcharhinus* sp.2, *Carcharhinus* cf. *macloti*, *Carcharhinus* *priscus*, *Galeocерdo* sp., *Sphyrna* cf. *media*, *Hemipristis* *serra*, *Carcharodon* *subauriculatus*, *Isurus* sp., *Ginglymostoma* sp., *Nebrius* *obliquus*.

Palavras-chave: Formação Pirabas. Chondrichthyes. Neógeno. Amazônia.

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INTRODUCTION

The lower Miocene Pirabas Formation occurs within coastal sedimentary basins between the states of Piauí and Pará, Northern Brazil. The best outcrops are found in the northwestern coast of the State of Pará, especially in the Salgado Zone region. Deposits of this formation include mostly carbonates intercalated with black and greenish shales and, secondarily, yellow sandstones (Rossetti & Góes, 2004). These rocks were formed under a variety of palaeoenvironmental conditions, including outer and inner shelf as well as tidal channel, lagoon, tidal and mangrove associated with barrier island systems. These depositional settings allowed the establishment of a diverse and abundant palaeofauna (Góes *et al.*, 1990).

The fossiliferous assemblage of the Pirabas Formation has been described since the end of the 19th century and most of the studies have focused on invertebrates (e.g. Maury, 1925; Ferreira & Cunha, 1957; Távora, 1998), including microfossils (Távora, 1998; Ramos *et al.*, 2004). Due to the fact that they are less commonly found, the vertebrates have received less attention. They are represented by sirenians (Toledo & Domning, 1989), fishes (Santos & Travassos, 1960; Costa *et al.*, 2004) and, less frequently, crocodylians, chelonians and birds (Ackermann, 1964).

Among the vertebrates, fishes, which comprise osteichthyans and chondrichthyans, represent the most abundant and diverse group, showing the largest temporal and palaeogeographic distribution (Costa *et al.*, 2004). This raises their potential as palaeoenvironmental and biostratigraphic proxies. The Pirabas fish fauna was firstly studied by Santos & Travassos (1960), who described nine shark species: *Carcharhinus ackermanni*, *C. egertoni*, *Hemipristis serra*, *Scoliodon taxandriae*, *Galeocercdo paulinoii*, *Sphyrna magna*, *S. prisca*, *Ginglymostoma serra* and *G. obliquum*. Later, large lamnid forms as *Carcharodon megalodon* and *Isurus nova*, and the genus *Hipoprion* were included (Santos &

Salgado, 1971). More recently, Reis (2005) recognized a total of 13 taxa for the Pirabas Formation, ten of them representing extant taxa.

The chondrichthyan record from the Pirabas Formation is commonly restricted to isolated teeth and scales. In particular, the identification of elasmobranch fauna has been based on relatively small number of teeth (Santos & Travassos, 1960; Santos & Salgado, 1971; Reis, 2005). Based on knowledge about intraspecific variation of extant sharks, it becomes evident that a significant number of teeth is necessary for a precise taxonomic determination. The study of the dental morphological patterns in modern species has revealed a high degree of heterodonty in both jaws. Consequently, determinations based on isolated teeth can lead to misidentifications (Purdy *et al.*, 2001).

In the last few years, systematic fieldwork in the Pirabas Formation led by researchers at the Museu Paraense Emílio Goeldi (MPEG) resulted in the addition of 289 new shark teeth to the MPEG paleontological collection. This represents a significant increase in the number of specimens when compared to materials described by Santos & Travassos (1960), Santos & Salgado (1971) and Reis (2005). This work aims to re-evaluate the shark taxa present in the Pirabas Formation, using shark teeth fossils deposited in the MPEG and from the collection of the Departamento Nacional de Produção Mineral (DNPM), in the state of Rio de Janeiro.

RESULTS AND DISCUSSION

Class Chondrichthyes
 Subclass Elasmobranchii
 Superorder Galea
 Order Carcharhiniformes
 Family Carcharhinidae
 Subfamily Carcharhininae
Carcharhinus Blainville, 1816
Carcharhinus sp.1 (Santos & Travassos, 1960)
 (Figure 1A, Figure 2A)



Carcharhinus ackermannii Santos & Travassos, 1960, p. 4, pl. 1, fig. 8-10.

Material: MPEG - 94-V, 109-V, 113-114-V, 124-V, 130-131-V, 155-157-V, 160-V, 178-V, 180-V, 183-V, 189-V, 190-V, 192-194-V, 274-277-V, 726-V, 729-730-V, 773-V, 786-V, 788-792-V, 797-V, 815-826-V, 828-829-V, 859-860-V, 907-V, 920-921-V, 937-V, 951-952-V, 954-V, 977-980-V, 988-V, 1032-V, 1033-V, 1095-V, 1097-V, 1106-1109-V, 1131-1133-V e DGM 651-P (holotype).

Dental diagnose: Crown triangular, unicuspidated, completely serrated with strong basal serration and an either deep or shallow basal notch. The teeth are straight in labial view and slightly convex in lingual view. Anterior teeth show straight and larger crowns, compared to posterior teeth. The holoaulacorhize root is flat with a central foramen.

Discussion: Diagnostic characters of *Carcharhinus* are only found on anterior upper teeth (Naylor & Marcus, 1994). The diagnosis provided for *C. ackermannii* (Santos & Travassos, 1960), contains characters currently only utilized to define the genus, except for the presence of small notches on the crown margin. The examination of 73 teeth has shown that such notches can not be considered diagnostic features. They are not uniform and vary in depth (Figure 1A, Figure 2A), thus they do not sustain the assignment to a species.

Carcharhinus sp.2
(Figure 1B, Figure 2B)

Material: MPEG - 100-V, 184-V, 198-V, 772-V, 785-V, 827-V, 830-835-V, 906-V, 919-V, 1064-V, 1154-1156-V.

Dental diagnose: Crown triangular, unicuspidated, completely serrated, with strong serration at the base, and lack of any notches. In the anterior tooth rows, the crowns are straighter than those in posterior rows. The teeth are straight in labial view and slightly convex lingual. The root is flat, holoaulacorhize and with a central foramen.

Discussion: *C. egertoni* is one of the *Carcharhinus* species most frequently cited in the literature. However, its distribution in the fossil record is highly contentious due to the difficulty of identifying isolated teeth (Cappetta, 1987).

Reassessment of material from the Neogene of North Carolina, USA, demonstrated that the material previously referred to *C. egertoni* in fact comprises three species, namely *C. brachyurus*, *C. falciformis* e *C. leucas* (Purdy *et al.*, 2001).

Previous identification of *C. egertoni* in the Pirabas Formation was based on two isolated teeth and their description by Santos & Travassos (1960) included only generic characters. Considering that the re-examined teeth occupied a lateral position on the jaw as indicated by their posteriorly inclined crowns, they cannot be ascribed to a particular species. As noted by Naylor & Marcus (1994), only anterior teeth bear characters diagnostic of *Carcharhinus* species.

Carcharhinus cf. *macloti* (Müller & Henle, 1839)
(Figure 1C)

Material: MPEG - 923-V, 984-V, 1031-V and DGM 969-P.

Dental diagnose: Small tooth (3-7 mm in height), crown triangular, unicuspidated, with the central portion of the cusp smooth and strong basal serrations. The teeth are straight in labial view and slightly convex lingually. Holoaulacorhize root with a central foramen.

Discussion: This specimen resembles the *C. macloti* documented in the Miocene (Pungo River Formation) and lower Pliocene (Yorktown Formation) deposits of USA (Purdy *et al.*, 2001). Regardless of the scarcity of material (i.e., only two teeth), the characteristic strong serrations at the base of the crown and the smoothness of the central, higher portion of the crown suggest the presence of this species in the Pirabas Formation.

Carcharhinus *priscus* (Agassiz, 1843)
(Figure 1D, Figure 2C)

Material: MPEG - 93-V, 101-V, 102-V, 104-V, 110-V, 112-V, 117-V, 119-V, 127-V, 132-V, 159-V, 162-163-V, 164-165-V, 167-168-V, 170-V, 173-V, 186-V, 771-V, 773-774-V, 795-796-V, 848-851-V, 914-V, 933-936-V, 950-V, 975-V, 1013-V, 1034-1036-V, 1081-1082-V, 1140-1142-V, 1153-V and DGM 656-P.

Dental diagnose: Crown triangular and fine, unicuspidated, with uniform serrations along the entire border. The crowns in the anterior rows are straight and larger than those on posterior



rows. Teeth straight in labial view and slightly convex lingually. Holoaulacorhize root with a central foramen.

Discussion: *Carcharhinus priscus*, together with *C. egertoni*, are some of the most cited species in the shark tooth literature. *Carcharhinus priscus* can easily be mistaken as representatives of the genus *Sphyrna* (Cappetta, 1987), as seems to have happen initially with materials from Pirabas Formation described by Santos & Travassos (1960). Although only two teeth were utilized in their descriptions, those authors had already pointed out differences between the teeth from the Pirabas Formation and those figured by Leriche (1927). Studying Miocene sharks from Ecuador, Longbottom (1979) referred the material from Pirabas Formation to *Carcharhinus priscus*.

Galeocerdo Müller & Henle, 1837

Galeocerdo sp.

(Figure 1E, Figure 2D)

Galeocerdo paulinonii Santos & Travassos, 1960, p. 8, pl. 1, fig. 13-14.

Material: MPEG - 95-96-V, 121-V, 146-V, 149-150-V, 176-177-V, 199-V, 784-V, 857-V, 861-V, 929-V, 930-V, 931-V, 943-V, 1101-1103-V and DGM 106-P (holotype), DGM 653-P.

Dental diagnose: Crown triangular, unicuspidated, curved posteriorly. Mesial border convex, elongated and slightly sigmoidal. Crown strongly serrated with secondary serrations only in the median and basal parts of the crown. Holoaulacorhize root with a central foramen.

Discussion: Based on four complete and some fragmentary teeth, Santos & Travassos (1960) erected an endemic species for the Pirabas Formation. Nevertheless, the diagnosis presented by those authors contains only generic characters and even with the new collected material, it was not possible to confirm the presence of *G. paulinonii* in this formation.

On the other hand, features as tooth morphology, size of the principal cusp and type of compose serrations (Cigala-Fulgosi & Mori, 1979) show that the tooth from the Pirabas Formation could be ascribed to *G. cuvier*. However, these characters can also be found in the Miocene species *G. aduncus* (Purdy *et al.*, 2001). As distinction between

these two species can not be safely determined, this material is only identified at generic level herein.

Sphyrna Rafinesque, 1810

Sphyrna cf. *media* Springer, 1940

(Figure 1F)

Material: MPEG - 111-V, 118-V, 120-V, 122-123-V, 125-126-V, 169-V, 171-V, 174-175-V, 181-V, 187-V, 278-V, 775-778-V, 821-V, 837-844-V, 846-847-V, 914-915-V, 925-V, 927-928-V, 976-V, 987-V, 1008-1009-V, 1059-V, 1063-V, 1066-V, 1068-V, 1069-V, 1077-V, 1104-1105-V, 1143-1147-V, 1149-1152-V.

Dental diagnose: Crown triangular, unicuspidated, slightly curved towards the labial side and without serrations. Teeth on anterior rows with straight crowns and larger than posterior ones. Flat, holoaulacorhize root with a central foramen.

Discussion: The diagnostic criteria of the genus *Sphyrna* can, in some cases, be misleadingly attributed to either *S. media* or other members of the subfamily Carcharhininae, mostly *Rhizoprionodon*. However, among extant representatives of these two genera, the crown is small, less than 4 mm high in *Rhizoprionodon*, while in *Sphyrna* the same measure is 1 to 2 cm (Cappetta, 1987). The crown height is, thus one of the criteria for the identification of the material from Pirabas Formation. In addition, the crown with either totally smooth borders or soft crenulations on the basal expansions are features typical of *Sphyrna* (Purdy *et al.*, 2001). These characteristics led to relate the studied material in the Pirabas Formation to *S. cf. media*.

Carcharhininae indet.

Material: MPEG - 182-V, 188-V, 197-V, 787-V, 811-V, 836-V, 845-V, 858-V, 908-909-V, 924-V, 926-V, 955-V, 1014-V, 1037-V, 1062-V, 1078-V, 1157-V and DGM 654-655-P.

Dental diagnose: Crown triangular, unicuspidated, smooth and straight, showing only soft serrations at the base. Teeth in anterior rows show straight crowns that are larger than teeth on posterior rows. Root holoaulacorhize with a central foramen.

Discussion: Teeth belonging to this subfamily were ascribed to *Scoliodon* (Santos & Travassos, 1960). A review



of the genus led to assign the *Scoliodon* species to three genera, including *Rhizoprionodon*, *Loxodon* and *Scoliodon* (Springer, 1964). This author was pessimistic about the possibility to distinguish between these genera based only on isolated fossil teeth. The close similarity between the teeth of *Rhizoprionodon* and *Scoliodon* and the lack of knowledge about the dental variations of living representatives of these genera hinder the determination of palaeontological material.

Compagno (1984) adopted the same diagnoses for *Scoliodon* and *Rhizoprionodon*, stressing the absence of serrations. However, a detailed study of complete dentitions of extant *Rhizoprionodon* shows that they bear either completely smooth teeth or teeth whose crown bases show various degrees of serrations (according to U. L. Gomes, in his Master Dissertation, entitled "A dentição como um subsídio taxonômico dos Pleurotremata (Pisces, Chondrichthyes, Elasmobranchii)", defended in 1988). This finding precludes the secure identification at species level of isolated teeth.

Subfamily Hemigaleinae

Hemipristis Agassiz, 1843

Hemipristis serra Agassiz, 1843

(Figure 1G, H; Figure 2E)

Material: MPEG - 106-108-V, 145-V, 147-148-V, 153-V, 179-V, 273-V, 279-280-V, 724-725-V, 738-V, 779-783-V, 785-V, 793-794-V, 852-856-V, 905-V, 916-918-V, 922-V, 938-941-V, 1012-V, 1028-1030-V, 1055-V, 1099-V, 1100-V, 1134-1139-V.

Dental diagnose: Upper teeth with labio-lingually compressed, triangular crowns, strongly serrated. Lower teeth with hook-like, sharp crowns with narrow roots.

Discussion: *Hemipristis serra* is one of the commonest shark species in Miocene deposits and its strong dignatic heterodonty has led to erroneous identification of fossil materials (Cappetta, 1987). The dentition of the extant *Hemipristis* is well known, which facilitates precise identification of isolated teeth (Longbottom, 1979; Cappetta, 1987; Iturralde-Vinent *et al.*, 1996; Purdy *et al.*, 2001). Although the teeth of *H. serra* are similar to those of the extant species *H. elongatus*, studies have

shown that the extinct species has smaller teeth and that sharks of this genus progressively increased the size of their teeth through geological time (Chandler *et al.*, 2006). This information was taken into consideration for the identification of the material from Pirabas Formation. Additionally, based on recent and fossil material (S. A. F. Costa, personal observation), *Hemipristis* teeth from this unit are too large to represent juvenile specimens and too small to match the size of teeth of extant adult sharks of this genus. These characteristics further support the attribution of this material to *H. serra*.

Family Alopiidae

Subfamily Lamninae

Carcharodon Smith in Müller & Henle, 1838

Carcharodon subauriculatus Agassiz, 1839

(Figure 1I)

Material: MPEG - 97-99-V, 154-V, 224-V, 723-V, 907-V, 1004-V and DGM 967-P.

Dental diagnose: Large teeth up to 840 mm in height, crown triangular, cusplets separated from the principal cusp by a slight notch. Holoaulacorhize root with rounded lateral lobes.

Discussion: The teeth from the Pirabas Formation belonging to this species were initially misidentified as *C. megalodon* (Santos & Salgado, 1971, p. 2). This was probably due to the fact that teeth of juvenile *C. megalodon* are reduced in size and also present lateral cusplets as *C. subauriculatus*. However, only *C. subauriculatus* possesses the distinctive notch separating the principal cusp from the lateral ones (Purdy *et al.*, 2001). Additionally, *C. megalodon* remains are not known from rocks older than the middle Miocene (Applegate & Espinosa-Arrubarrena, 1996) and the Pirabas deposits belong to the early Miocene.

Isurus Cuvier, 1816

Isurus sp.

Material: MPEG - 932-V, 910-V e DGM 968-P.

Dental diagnose: Teeth with narrow crowns, higher than longer and without serrations or lateral cusplets. Teeth



sigmoidal in lateral view. Bulky holoaulacorhize root with prominent lingual side.

Discussion: Identification of this genus in the Pirabas Formation was based on the presence of symphyial teeth (Santos & Salgado, 1971). However, these authors concluded that it was not possible to ascribe the teeth to a particular species within this genus. The new material is also fragmentary and insufficient to determine the *Isurus* species they belong to.

Family Rhincodontidae

Ginglymostoma Müller & Henle, 1837

Ginglymostoma sp.

(Figure 1J)

Material: MPEG - 813-V, 1073-V e DGM 657-P.

Dental diagnose: Teeth longer than higher, symmetrical with the lower part of the crown overhanging the root and forming a short protuberance. There is one principal central cusp with both sides presenting up to seven lateral cusplets. The root is hemiaulacorhize and flat.

Discussion: Teeth of *Ginglymostoma*, resemble those of *Nebrius*, which belongs to the same family. These are differentiated because in the latter the shorter cusps are linked together at their bases, forming a high platform. Additionally, *Ginglymostoma* bears seven lateral cusplets either side of the principal cusp, whilst in *Nebrius* there are eight cusplets either side (Cappetta, 1987).

The species *G. serra* was described in the Pirabas Formation on the basis of one single tooth (Santos & Travassos, 1960, p. 12) that does not show any characters that would allow a specific identification. The additional available specimens also do not present diagnostic features other than generic ones.

Nebrius Rüppell, 1837

Nebrius obliquus (Leriche, 1942)

(Figure 1K)

Material: MPEG - 814-V.

Dental diagnose: Teeth longer than higher, symmetrical with the base of the crown overhanging the root and forming a short protuberance. Median cusp not

distinct from the lateral cusplets, which sum eight on either side. The root is hemiaulacorhize and flat.

Discussion: This species was identified as *Ginglymostoma obliquum* (Leidy, 1877) on the basis of two lateral teeth displaying middle cusp bending towards one of the crown margins (Santos & Travassos, 1960, p.13). However, this is also one of the marked characters of *Nebrius* (Bourdon & Heim, 2004). The only specimen of *Nebrius* in the paleontological collection of the MPEG is a fragmentary tooth, but it still shows diagnostic features as symmetrical crown and eight cusplets in either side of the middle cusp (see Purdy *et al.*, 2001).

CONCLUSIONS

The following taxa were confirmed in the Pirabas Formation after a revision of previously described materials, as well as 289 new shark teeth recovered during recent fieldwork in the State of Pará, Northern Brazil:

Order Carcharhiniformes

Family Carcharhinidae

Subfamily Carcharhininae

Carcharhinus sp.1

Carcharhinus sp.2

Carcharhinus cf. *macloti*

Carcharhinus *priscus*

Galeocerdo sp.

Sphyrna cf. *media*

Carcharhininae indet.

Subfamily Hemigaleinae

Hemipristis serra

Order Lamniformes

Family Alopiidae

Subfamily Lamninae

Carcharodon subauriculatus

Isurus sp.

Order Orectolobiformes

Family Rhincodontidae

Ginglymostoma sp.

Nebrius obliquus



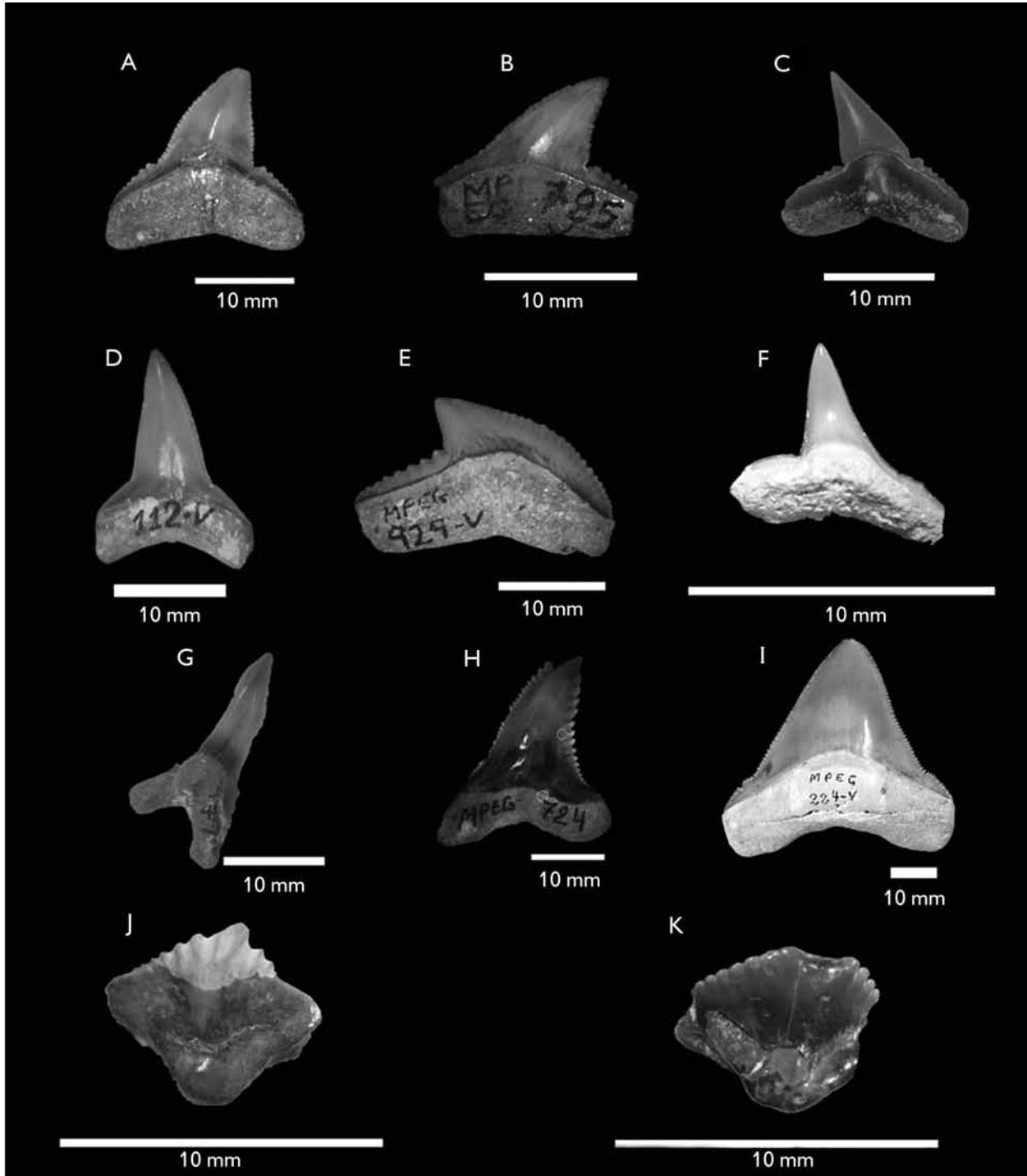


Figure 1. Isolated shark teeth from the Pirabas Formation in the Paleontological Collection at the Museu Paraense Emílio Goeldi (MPEG) in Belém, Brazil: A – *Carcharhinus* sp.1 MPEG 954-V; B – *Carcharhinus* sp.2 MPEG 785-V; C – *Carcharhinus* sp.3 MPEG 1031-V; D – *Carcharhinus priscus* MPEG 112-V; E – *Galeocerdo* sp. MPEG 929-V; F – *Sphyrna* cf. *media* MPEG 1077-V; G-H – *Hemipristis serra* MPEG 281-V e MPEG 724-V; I – *Carcharodon subauriculatus* MPEG 227-V; J – *Ginglymostoma* sp. MPEG 813-V; K – *Nebrius obliquus* MPEG 814-V. Scale = 10 mm.

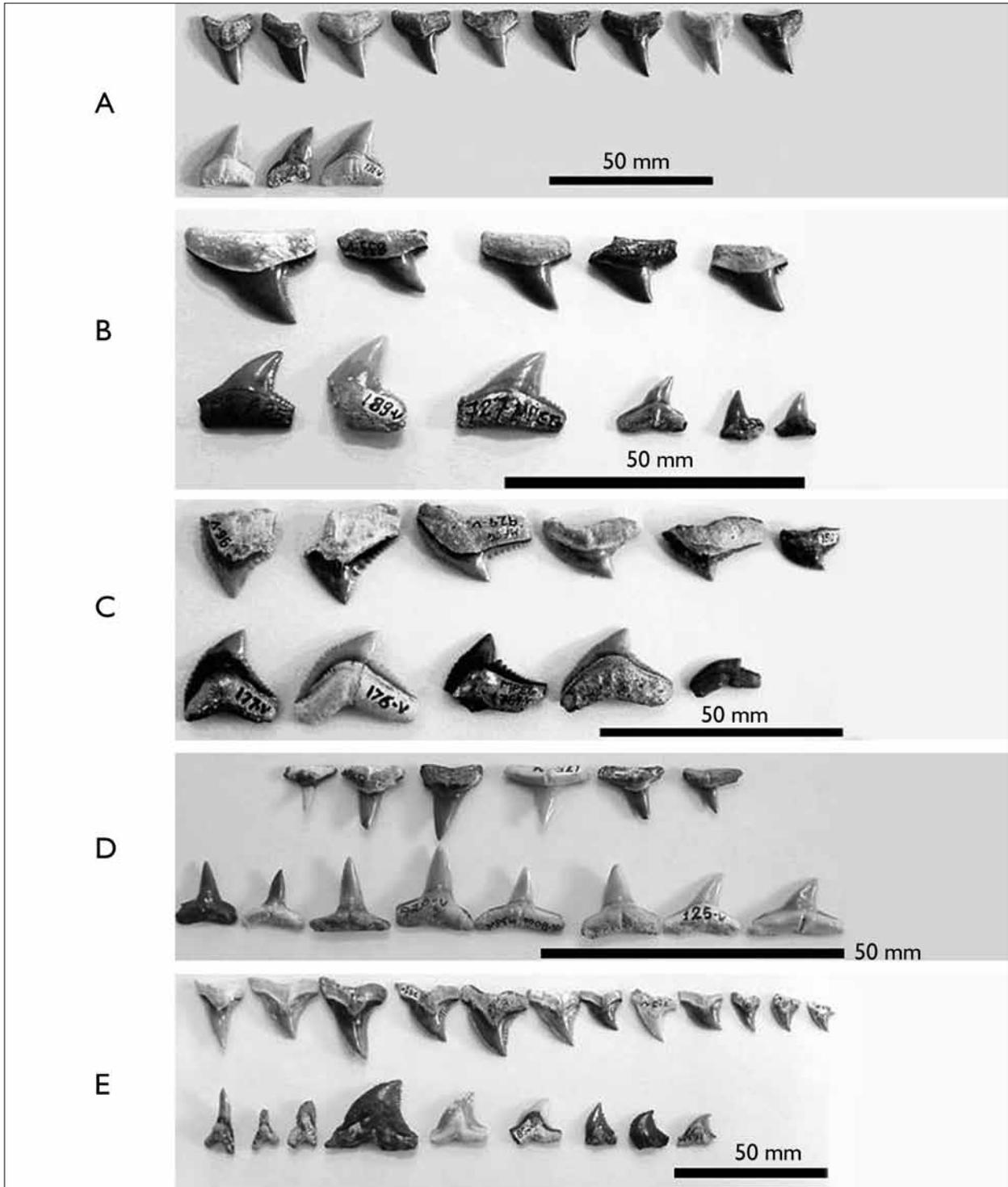


Figure 2. Shark teeth from the Pirabas Formation in the Paleontological Collection at the Museu Paraense Emílio Goeldi (MPEG) in Belém, Brazil: A – *Carcharhinus* sp.1; B – *Carcharhinus* sp.2; C – *Galeocerdo* sp.; D – *Sphyrna* cf. *media*; E – *Hemipristis serra*. Scale = 50 mm.

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