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Chondrichthyan Fauna from the Pirabas Formation, Miocene of Northern Brazil, with Comments on Paleobiogeography

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Resumo

A fauna de Chondrichthyes da Formação Pirabas é redescrita no presente trabalho. Apenas treze taxa nominais são considerados como válidos. Desses taxa, dez foram considerados como ainda viventes (*Carcharhinus sorrah, Carcharhinus perezii, Galeocerdo cuvier, Rhizoprionodon lalandii, Sphyrna sp., Hemipristis elongatus, Carcharodon carcharias, Isurus oxyrinchus, Nebrius ferrugineus*, Myliobatidae), confirmando a idade Neogênica desta formação. Essa elasmofauna é comparada com as faunas do Terciário do Caribe e da África.
Palavras-chave: Chondrichthyes, Mioceno, Formação Pirabas, Norte do Brasil.

Abstract

The chondrichthyan fauna from the Pirabas Formation is redescribed. Only thirteen nominal taxa are considered valid. From these taxa, ten were reassigned to extant taxa (*Carcharhinus sorrah, Carcharhinus perezii, Galeocerdo cuvier, Rhizoprionodon lalandii, Sphyrna sp., Hemipristis elongatus, Carcharodon carcharias, Isurus oxyrinchus, Nebrius ferrugineus*, and indeterminate Myliobatidae), confirming the Neogene age of this formation. This elasmofauna is compared with other Caribbean and African Tertiary faunas.
Keywords: Chondrichthyans, Miocene, Pirabas Formation, Northern Brazil.

1 Introduction

The Pirabas Formation crops out in the Bragantina Region, State of Pará, Northern Brazil (White, 1887; Maury, 1924; Ferreira, 1967; Brito, 1993) (Figure 1), and is bounded by the Marajó Basin, the Maranhão coastal Zone and the low Parnaíba, in the Piauí State (Brito, 1979).

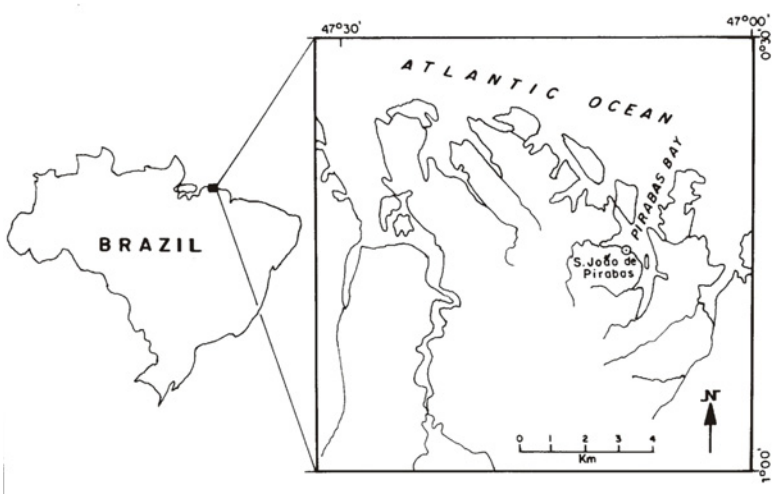

Figure 1 Location map of the Pirabas Bay (modified from Távora & Fernandes, 1994).

The Pirabas Formation was originally defined by White (1887) who considered to be of Cretaceous age. Later studies of its fauna suggested a Miocene age for this unit, and a tropical environment (Ferreira, 1966).

This lithostratigraphic unit display three distinct facies: Castelo, Capanema and Baunilha Grande. The Castelo facies represents a neritic, open sea and shallow water environment, rich in foraminiferans and coral reefs. The Capanema facies, suggest reduced salinity and shallower waters, with a rich molluscan fauna. In some places this facies yields a coastal thanatocenosis, with terrestrial plants, malacostracans crustaceans and cirripedes, which are a typical hard-ground fauna. The Baunilha Grande facies suggests a swamp environment which is demonstrated by the abundance of fossil crabs (Brito, 1979; Fernandes, 1979).

The aim of this paper is to redescribe the elasmobranch fauna of the Pirabas Formation, comparing it with other Caribbean and African Neogene faunas, as

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well as with extant taxa, and commenting on a number of paleobiogeographic problems.

Fossil material is housed in the following institutions: Universidade Federal do Rio de Janeiro – Departamento de Geologia (UFRJ-DG); Departamento Nacional de Produção Mineral (DNPM) and Museu Nacional-UFRJ (MN). The extant material belongs to the Universidade do Estado do Rio de Janeiro (UERJ), Rio de Janeiro, Brazil.

The dental terminology used partially follows Compagno (1988). Comparisons with Neogene Caribbean fauna are based on Gillette (1984) and Neogene African fauna are based on White (1926) and Antunes (1964, 1978).

2 Description

Class Chondrichthyes Huxley, 1880

Order Carcharhiniformes Compagno, 1973
Family Carcharhinidae Jordan & Evermann, 1896
Genus *Carcharhinus* Blainville, 1816
Carcharhinus sorrah (Valenciennes in Muller & Henle, 1841)
(Figure 2A, B)

1960 *Carcharhinus ackermannii* Santos & Travassos, 4-5

Material: MN 2634-V (one tooth); DGM 650-P (one tooth); DGM 651-P (two teeth); UFRJ-DG 176 Pd (two teeth).

Description: All the specimens are upper teeth, with a single cusp and serrated crown edges. In labial view, the foot is wide, turning abruptly toward the apex of the tooth. The shoulders have serrations coarser than those in the remainder of the cutting edges. The root is almost flat, with a transverse groove.

Discussion: Based on the aspect of the crown, that is wide, oblique, with a lateral groove and lateral serrations, these teeth originally described as *Carcharhinus ackermannii* by Santos & Travassos (1960) are assigned to the extant species *Carcharhinus sorrah*, found today in the Indian Ocean, the Red Sea, Indo-Australian area and west Pacific (Garrick, 1982).

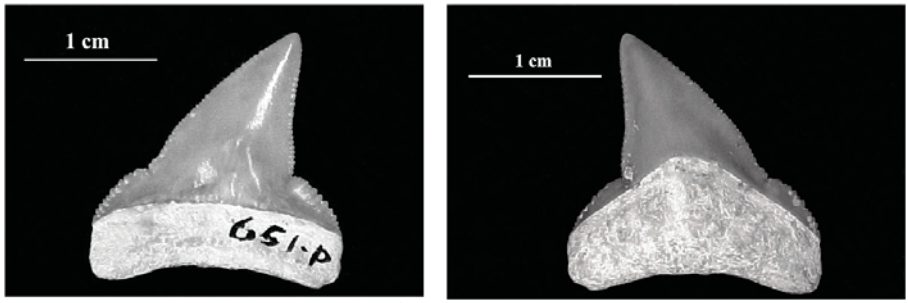

Figure 2 Elasmobranchii tooth from the Pirabas Formation. *Carcharhinus sorrah* (DGM 651-P) in labial view (A) and lingual view (B).

Carcharhinus perezii (Poey, 1876)
(Figure 3A, B)

1843 *Carcharhinus egertoni* Agassiz, 228

Material: MN 2635-V (two teeth).

Description: Upper teeth, with shoulders almost continuous with the crown blades. In labial view, the foot is wide, turning slightly toward the apex of the cusp. The crown is serrated, but the serrations are more conspicuous on the shoulders. The root presents a transverse groove and a central foramen.

Discussion: Santos & Travassos (1960) have identified this material as *Carcharhinus egertoni*. Nevertheless, isolated teeth of this genus are difficult to assign to a particular species (see Antunes & Jonet, 1970). Comparing these fossils with recent teeth from *Carcharhinus perezii*, these specimens display the same characteristics, as the crown morphology descripted above, and are here considered synonymous.

Carcharhinus perezii occurs in the Tertiary of the Caribbean Province (*sensu* Gillette, 1984), including the Ecuadorian Miocene fauna (Longbottom, 1979), and is found today close to Caribbean, including Cuba, Bahamas, Jamaica, Virgin Islands, Barbadas, Los Hermanos Island and Venezuela (Garrick, 1982) (see Figure 18, 19).

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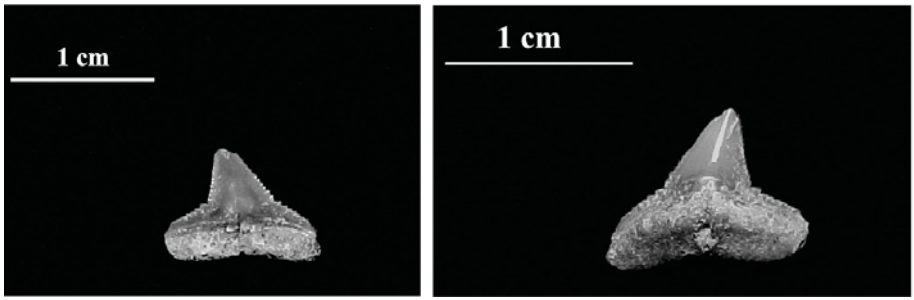

Figure 3 Elasmobranchii tooth from the Pirabas Formation. *Carcharhinus perezii* (MN 2635-V) in labial view (A) and lingual view (B).

Carcharhinus priscus (Agassiz, 1843)
(Figure 4A, B)

1843 *Sphyrna prisca* Agassiz, 234

Material: DGM 656 - P (two teeth, upper and lower)

Description: Upper tooth – The crown has only one cusp, with serrated cusps and shoulders, except in the apex. The symphysial shoulder is almost continuous with the crown foot, but the commissural shoulders have a small notch. The root is almost straight with a transverse groove.

Lower tooth - Straight cusp with slightly serrated cutting edges, small shoulders and narrow foot. The lower teeth of the genus *Carcharhinus* do not permit a specific diagnosis (Garrick, 1982; Naylor & Marcus, 1994), and the tooth is identified here as *Carcharhinus* sp.

Discussion: This tooth identified as *Sphyrna prisca* (Santos & Travassos, 1960), was considered as *Carcharhinus priscus* by Cappetta *et al*. (1967, fig. 4). This species is found in the Miocene of Pacific Ecuador and may occur in some other localities from the Tertiary Caribbean Faunal Province (Longbottom, 1979; Gillette, 1984) as well as in the Pliocene of Angola (Antunes, 1978) (see Figure 19).

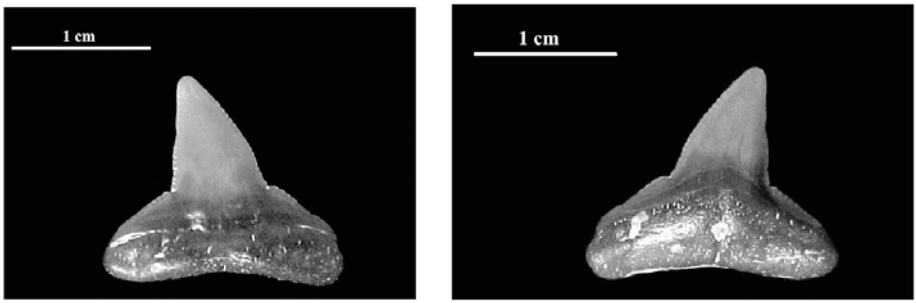

Figure 4 Elasmobranchii tooth from the Pirabas Formation. *Carcharhinus priscus* (DGM 656-P) in labial view (A) and lingual view (B).

Carcharhinus sp.
(Figure 5)

1971 *Hypoprion* sp. Santos & Salgado, 6-7

Material: DGM 969-P (one tooth).

Description: DGM 969-P - A tooth with serrated shoulders, almost continuous with the cutting edges.

Discussion: Santos & Salgado (1971) described this tooth as *Hypoprion* sp. This tooth is here considered as *Carcharhinus* sp. by the crown morphology, mainly the cusp and the shoulders.

Teeth from *Carcharhinus* sp. occur in the Tertiary Caribbean Faunal Province (Longbottom, 1979; Gillette, 1984) and in the Pliocene of Angola (Antunes, 1978) (see Figure 19).

Genus *Galeocerdo* Müller & Henle, 1838

Galeocerdo cuvier (Peron & LeSueur, 1822 in LeSueur, 1822)
(Figure 6A, B)

1960 *Galeocerdo paulinoi* Santos & Travassos, 8-10

Material: DGM 653-P; DGM 106-P; DGM 107-P; UFRJ-DG 175 Pd (Seven teeth)

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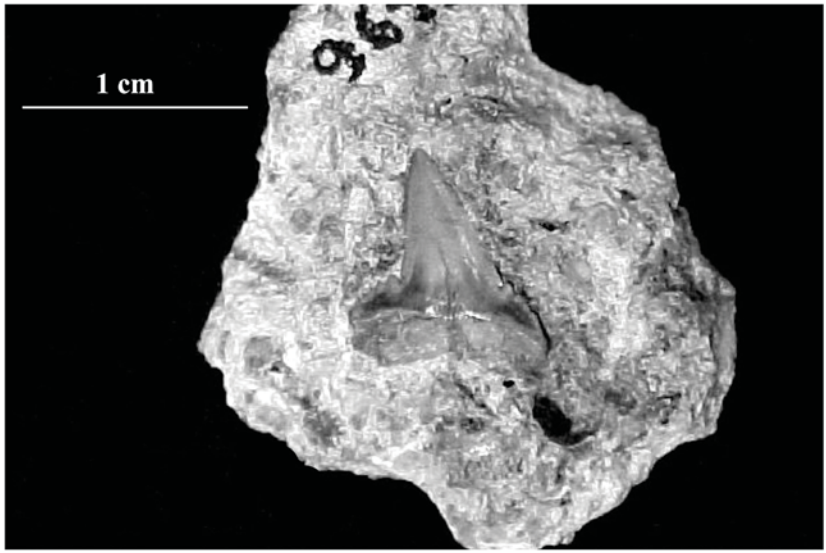


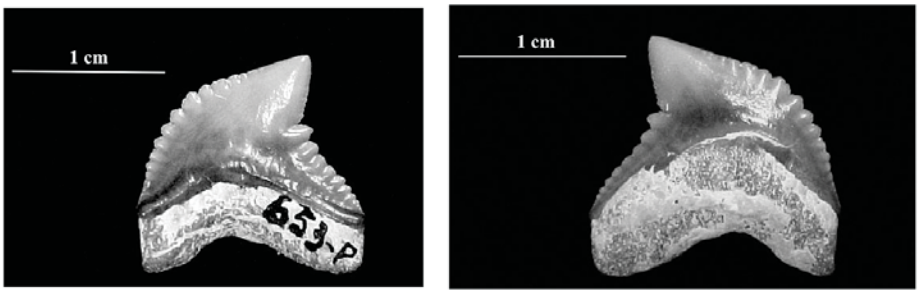
Figure 5 Elasmobranchii tooth from the Pirabas Formation. *Carcharhinus* sp. (DGM 969-P) in labial view.

Description: Teeth with serrated cutting edges and a robust foot. The cusp bears a notch on the distal blade. The root has a V -shaped, and a transverse groove.

Discussion: *Galeocerdo paulinoi* was identified based on the aspect of the lower lobe of the distal edge of the crown and the length and curvature of the mesial edge of the posterior lateral teeth (Santos & Travassos, 1960). However, these differences have been interpretated as a monognathic heterodonty, usually seen in the jaws of *Galeocerdo cuvier.*

Galeocerdo cuvier occurs in all tropical oceans today, and in the Atlantic from the area of the Bermudas to the north of Argentina (Compagno, 1984).

This species is also found in the Angola Pliocene (Antunes, 1978) (see Figure 19).



A B

Figure 6 Elasmobranchii tooth from the Pirabas Formation. *Galeocerdo cuvier* (DGM 653-P) in labial view (A) and lingual view (B).

Genus *Rhizoprionodon* Whitley, 1929

Rhizoprionodon lalandii (Valenciennes, 1839 in Muller & Henle, 1839)
(Figure 7A, B)

1926 *Scoliodon taxandriae* Leriche, 431

Material: MN 2643-V (one tooth); DGM 652 - P (one tooth).

Description: Teeth with a single cusp, with sharp cutting edges and wide foot, turning abruptly towards the apex. In labial view, the mesial face of the crown has a small elevation and the apex is slightly curved towards the symphysis. The distal face of the crown is slightly convex. There is a notch on the distal shoulders, but the symphysial shoulders are continuous with the cusp. The root is straight.

Discussion: Santos & Travassos (1960) have identified this material as *Scoliodon taxandriae* based on similarities with the teeth described by Leriche (1926) from the Belgium Neogene. However, comparing these teeth with recent material, they are identical to those of *Rhizoprionodon lalandii*, (e.g. the presence of a curved crown for the distal face of the crown and on the lack of serrations on the cutting edges). Dental sexual dimorphism has been reported in *Rhizoprionodon lalandii* (Springer, 1964; Gomes & Reis, 1987; Compagno,

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1988), as well as in the genus *Scoliodon* (Springer, 1964; Herman *et al.*, 1991). The presence of a cylindrical crown, suggests that these teeth belong to a male. By contrast, the teeth of females have flattened crowns in lingual and labial view (Gomes & Reis, 1987).

Rhizoprionodon lalandii is found in the Gatun Formation and in the Pacific Ecuador Miocene in the Tertiary Caribbean Faunal Province (Longbottom, 1979; Gillette, 1984) (Figure 19). The recent geographical distribution of this species is along the north and east coast of South America from Panama to Florianópolis (Compagno, 1984; 1988).

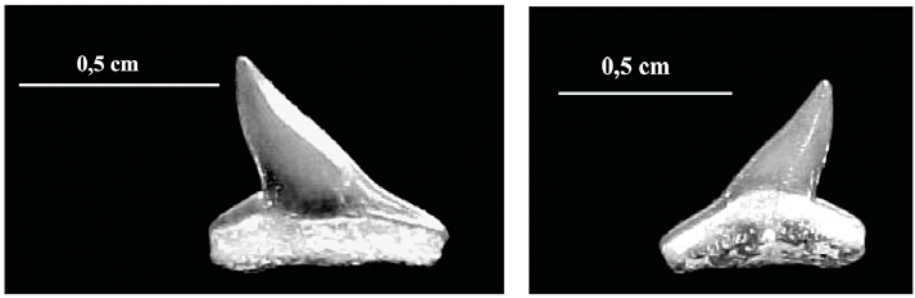

Figure 7 Elasmobranchii tooth from the Pirabas Formation. *Rhizoprionodon lalandii* (DGM 652-P) in labial view (A) and lingual view (B).

Sphyrna sp.

(Figure 8A, B)

1960 *Sphyrna magna* Santos & Travassos, 10-11

Material: DGM 654-P; DGM 655-P; UFRJ-DG 174 Pd. (Seven teeth).

Description: Teeth with only one cusp, sharp cutting edges and serrations on the shoulders. Wide foot, in labial view, narrowing abruptly towards the apex. The upper teeth distal shoulder (DGM 654-P and UFRJ-DG 174-Pd) is separated from the crown blade by a notch. The root is straight with a transverse groove and a central foramen.

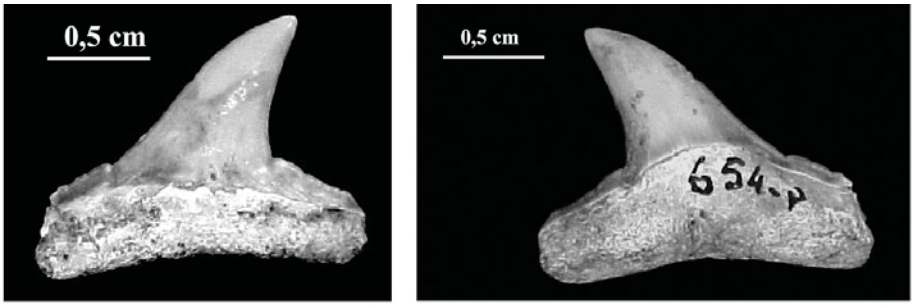

Figure 8 Elasmobranchii tooth from the Pirabas Formation. *Sphyrna* sp. (DGM 654-P) in labial view (A) and lingual view (B).

Genus *Hemipristis* Agassiz, 1843

Hemipristis elongatus (Klunzinger, 1871)

(Figure 9A, B)

1843 *Hemipristis serra* Agassiz, 237

Material: MN 2633-V (two teeth); DGM 649-P; DGM 105-P; UFRJ-DG 177 Pd (Seven teeth).

Description: The crown has serrated edges, except at the apex, and there are no shoulders. The root is U-shaped, presenting a lingual protuberance, a transverse groove and a central foramen.

Discussion: The fossil teeth of *Hemipristis* are found from the Eocene until the Pliocene, with a world-wide distribution (Romer, 1966; Glikman, 1967; Fowler, 1968; Antunes & Jonet, 1970), including almost all the Tertiary Caribbean Faunal Province (Longbottom, 1979; Gillette, 1984) and the Pliocene of Angola (Antunes, 1978) (Figure 19). *Hemipristis serra* was described from Pirabas Formation by Santos & Travassos (1960), based on isolated teeth. This species

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occurs today in Cuba, Venezuela, the Atlantic coast of the United States, Portugal, Spain, south and southwest of France and Switzerland, Germany, Austria, Holland, Italy and northern Africa. In this study is considered a synonym of the recent species *Hemipristis elongatus*; however this species is only found in the Indian Ocean and west Pacific (Compagno, 1984; 1988).

Compagno (1973; 1979) suggested that osteodont histological type of the recent species *Hemipristis elongatus* was derived from the orthodont type found at least in some of the fossil *Hemipristis* (cf. *H. serra*) through histological reversal. However, this change in the histological type does not affect in the external morphology of the tooth.

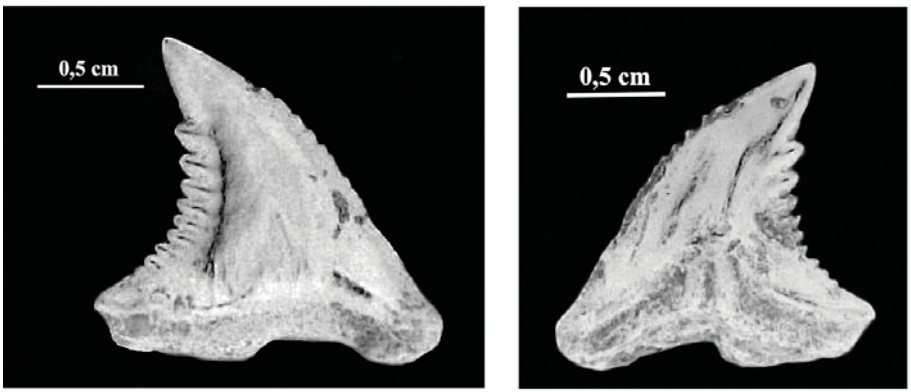


Figure 9 Elasmobranchii tooth from the Pirabas Formation. *Hemipristis elongatus* (MN 2633-V) in labial view (A) and lingual view (B).

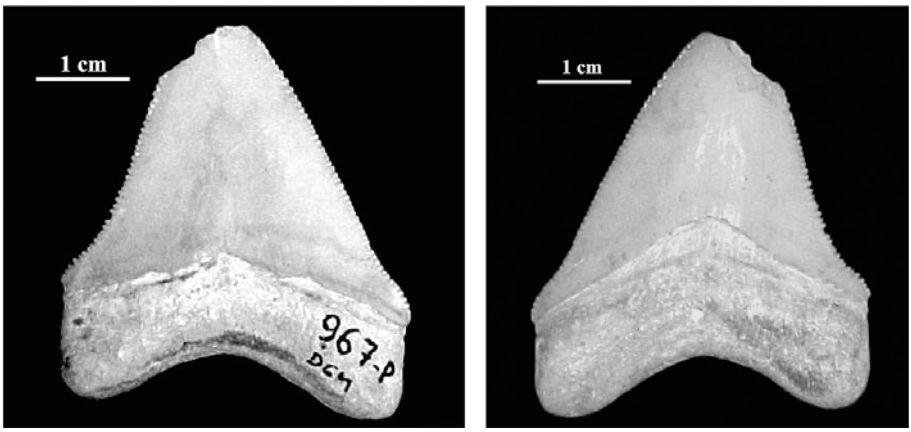
Order Lamniformes Berg, 1958
Family Alopiidae Bonaparte, 1838
Genus *Procarcharodon Casier*, 1960
Procarcharodon megalodon (Casier, 1960)
(Figure 10A, B)

1843 *Carcharodon megalodon* Agassiz, 247

Material: MN 3865-V; DGM 967-P (Five teeth).

Description: Teeth with a triangular, very sharp crown, which is rather broad at the foot. The cutting edges have strong serrations. The root is U-shaped.

Discussion: *Carcharodon megalodon* was previously considered as belonging to the genus *Procarcharodon* (Casier, 1960). It is found through Eocene to Pliocene deposits of coast and pelagic zones of tropical and subtropical seas (Serralheiro, 1954; Antunes & Jonet, 1970), including all Tertiary Caribbean Faunal Province (Longbottom, 1979; Gillette, 1984) and the Pliocene of Angola (Antunes, 1978) (see Figure 19).



A B

Figure 10 Elasmobranchii tooth from the Pirabas Formation. *Procarcharodon megalodon* (DGM 967-P) in labial view (A) and lingual view (B).

Genus *Carcharodon* Müller & Henle 1838

Carcharodon carcharias (Linnaeus, 1758)

(Figure 11A, B)

Material: UFRJ-DG 178 Pd (Five teeth).

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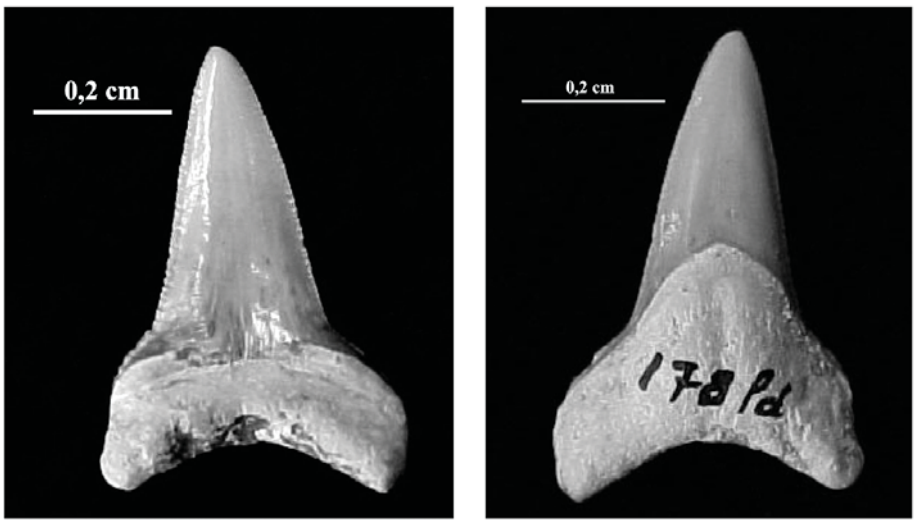
Description: Teeth with only one high cusp, with serrations in the crown blade. The shoulders are concave. The root is a U-shaped, bearing a transverse groove and a lingual protuberance.

Discussion: Based on the serrations on the crowns, all five teeth are interpreted as lower teeth of *Carcharodon carcharias*. This taxon occurs over most of the Tertiary Caribbean Faunal Province (Gillette, 1984) and in the Pliocene of Angola (Antunes, 1978) (see Figure 19).

Today this species can be found in the western and eastern Atlantic, western Indian and western and central Pacific oceans.



A B

Figure 11 Elasmobranchii tooth from the Pirabas Formation. *Carcharodon carcharias* (UFRJ-DG 178 Pd) in labial view (A) and lingual view (B).

Genus *Isurus* Rafinesque, 1810

Isurus oxyrinchus (Rafinesque, 1810)

(Figure 12A, B)

1874 *Isurus nova* Winkler, 7

Material: DGM 968-P (One tooth).

Description: Tooth with only one high cusp with sharp cutting edges, and without shoulders. The tip is strongly reflexed, that is a diagnostic character of this species. The root is a U-shaped, with a transverse groove, a central foramen and a lingual protuberance.

Discussion: Santos & Salgado (1971) identified this material as *Isurus nova*, but this material is here considered as *Isurus oxyrinchus* by the crown tip strongly reflexed. Besides this species occur in the Pliocene of Angola (Antunes, 1978) and is not found in deposits younger than middle Eocene (Antunes & Jonet, 1970) (see Figure 19).

Isurus oxyrinchus has a wide recent geographical distribution. It can be found in the tropical and temperate seas, mainly from the Caribbean to Argentina (Compagno, 1984).

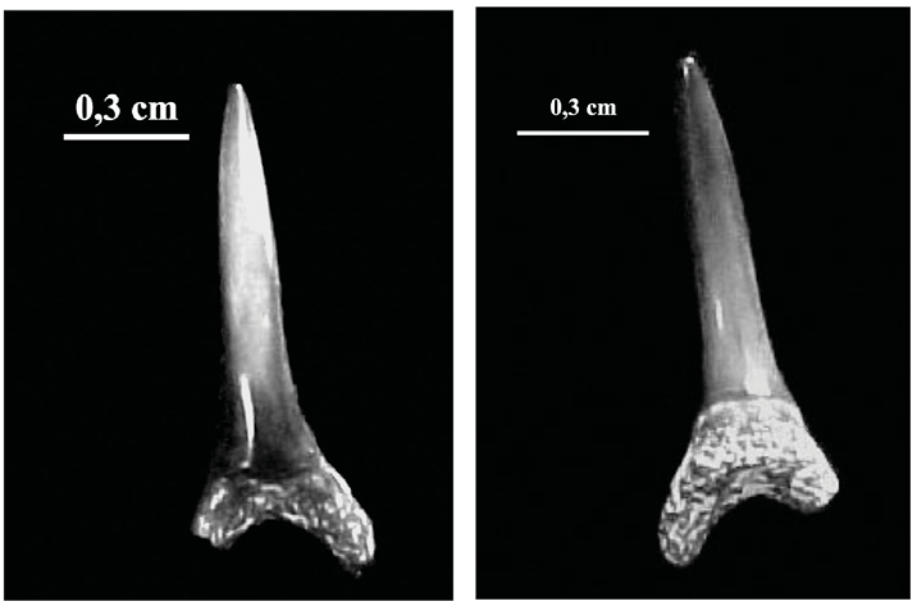


Figure 12 Elasmobranchii tooth from the Pirabas Formation. *Isurus oxyrinchus* (DGM 968-P) in labial view (A) and lingual view (B).

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Order Orectolobiformes Applegate, 1972

Family Gynglymostomatidae Gill, 1862

Genus *Ginglymostoma* Müller & Henle, 1837

Nebrius ferrugineus (Lesson, 1830)
(Figure 13A, B)

1877 *Ginglymostoma obliquum* Leidy, 250

Material: MN 2644-V (Two teeth).

Description*:* The crown has one principal cusp and seven lateral denticles on one side and six on the other, covering almost the whole of the cutting edge of the crown.

Discussion: This specimen was identified as *Ginglymostoma obliquum* by Santos & Travassos (1960). Based on the characters above, this species is here considered synonymous with *Nebrius ferrugineus*. Nevertheless, this recent species is only found in the west of Indian Ocean and in the central Pacific (Compagno 1984). There is a prominent labial apron below the foot; a character also found in Orectolobiformes, Pristiophoriformes and Squatiniformes (Herman *et al*., 1992; Figs. 1-45). The root has a central foramen.

Ginglymostoma serra (Leidy, 1877)
(Figure 14A, B)

Material: DGM 657-P (one tooth).

Description: Tooth with one cusp and five lateral denticles on each side, with sharp cutting edges. The root has a central foramen.

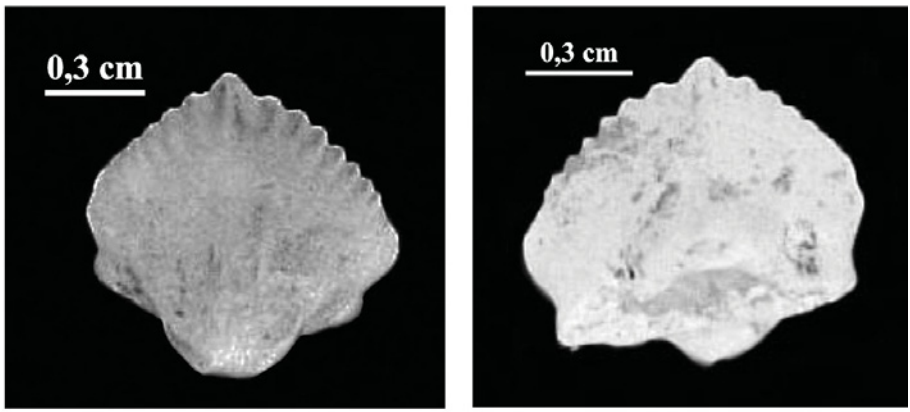

Figure 13 Elasmobranchii tooth from the Pirabas Formation. *Nebrius ferrugineus* (MN 2644-V) in labial view (A) and lingual view (B).

Discussion: Leidy (1877) had described *Ginglymostoma serra* and *Ginglymostoma obliquum* from South Carolina Miocene, under the genus *Acrodobatis*.

Ginglymostoma serra is also found in the Eocene of Nigeria (White, 1926) (see Figure 19).

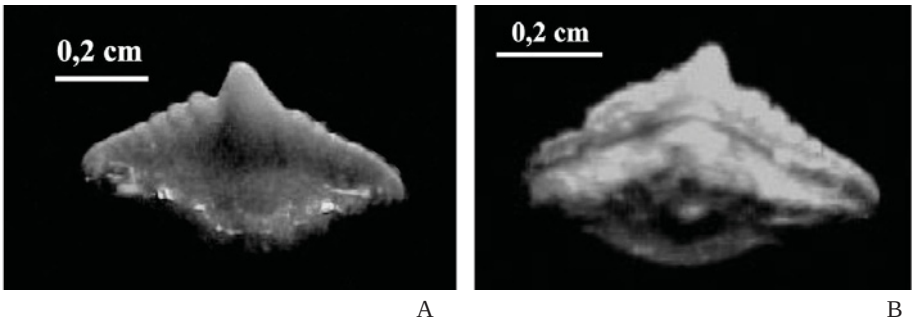

Figure 14 Elasmobranchii tooth from the Pirabas Formation. *Ginglymostoma serra* (DGM 657-P) in labial view (A) and lingual view (B).

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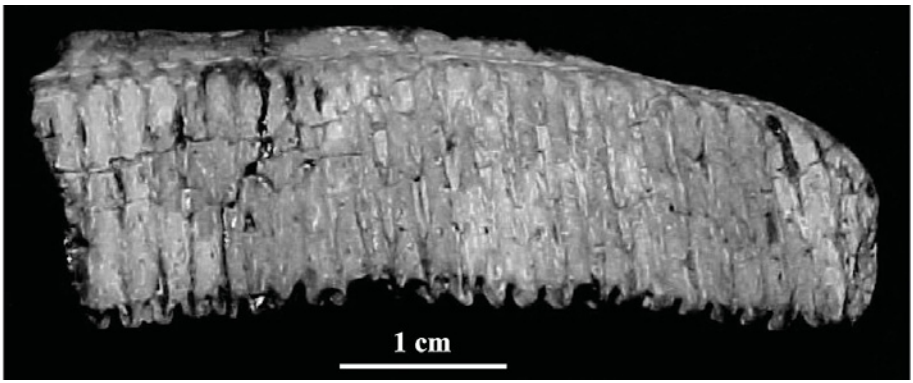
Superorder Batomorphii Cappetta, 1980

Order Myliobatiformes Compagno, 1973

Family Myliobatidae Bonaparte, 1838
(Figure 15A, B; 16A, B; 17)

1960, Rhizochlatridae Santos & Travassos: 16



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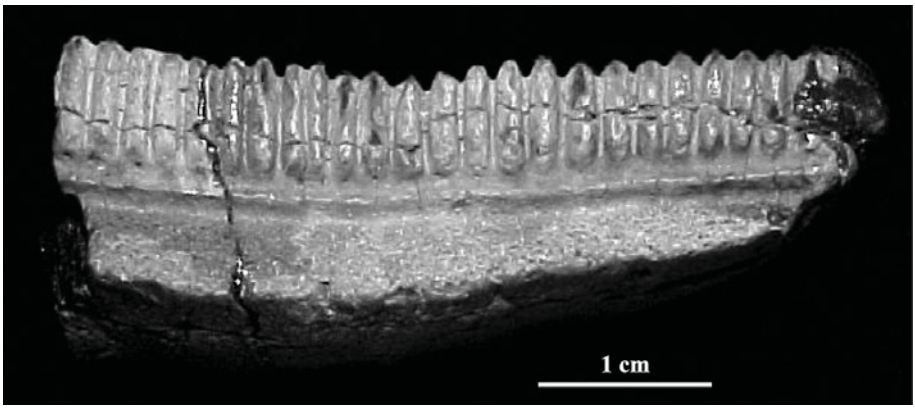

B

Figure 15 Elasmobranchii tooth from the Pirabas Formation. Myliobatidae (MN 2645-V) in occlusal view (A) and lingual view (B).

Material: Described as *Rhinoptera studieri* by Santos & Travassos (1960) - MN 2639-V (one fragment of tooth); DGM 658-P (one tooth); DGM 659-P (three fragments of teeth); DGM 660-P (two fragments of teeth);

Described as *Myliobatis* sp. By Santos & Travassos (1960) - MN 2645-V (five fragments of teeth); DGM 103-P (two fragments of teeth); MN 2640-V (a fragment of a caudal sting spine);

Described as *Rhizochlatrus vidalis* by Santos & Travassos (1960) - MN 2646-V (one fragment of tooth); DGM 661-P (one tooth); DGM 662-P (two fragments of teeth); DGM 668-P (one fragment of tooth);

Described as *Paleomyliobatis pirabensis* by Santos & Travassos (1960) - DGM 663-P (two fragments of teeth); DGM 666-P (one fragment of tooth).

Description: Crushing teeth. The high crown with several transverse groove, lacks cusps. The root is highly eroded (Figure 15A, B).

Discussion: The specimens DGM 658-P, DGM 659-P, DGM 660-P, and MN 2646-V, described as *Rhinoptera studeri* (Santos & Travassos, 1960) is very similar to *Myliobatis* teeth, by the crown and root characteristics, but are narrower (Figure 16A, B). The distinction between the dental morphology of *Myliobatis* and Rhinoptera is only possible by comparing the teeth in their respective places in the jaws, therefore this material is here only identified to a high taxonomic level.

Santos & Travassos (1960) described punctuations in the occlusal surface of the tooth (specimen DGM 658-P), as small pores from groves through the tooth thickness. The teeth are probably eroded.

The Rhizochlatridae, with the genus *Rhizochlatrus* and *Palaeomyliobatis*, was erected by Santos & Travassos (1960) on the basis of the polyaulacorhize type (*sensu* Casier, 1947) of root. However, only some scratches were observed in the root, probably also caused by diagenetic processes. The polyaulacorhize type of root is found in the central and medium-lateral teeth of some Myliobatiformes (e.g. *Apocopodon*, *Rhinoptera*, *Myliobatis* and *Aetobatus*). Only the lateral teeth of these *taxa* are of the holaulacorhize type (*sensu* Casier, 1947) (Silva, 1999). The family Rhizochlatridae was considered as synonymous with Myliobatidae (Cappetta, 1987), based on the lack of a synapomorphy for this clade.

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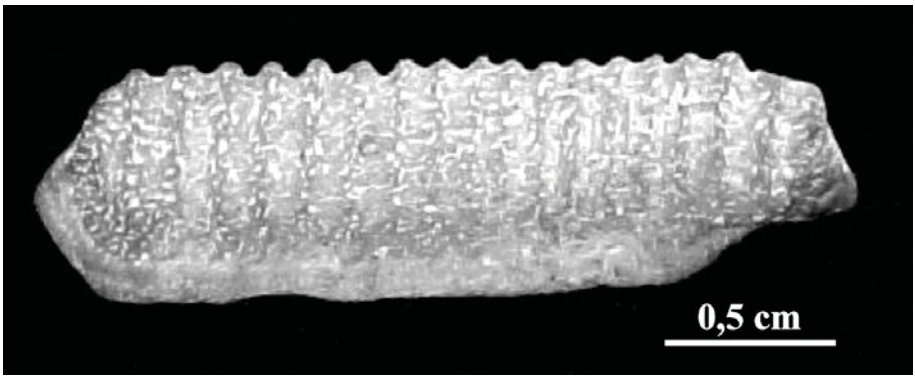
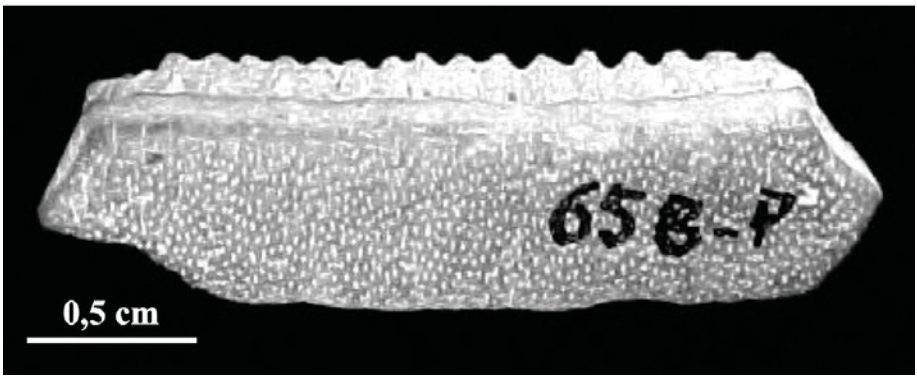


A



B

Figure 16 Elasmobranchii tooth from the Pirabas Formation. Myliobatidae (DGM 658-P) in occlusal view (A) and labial view (B).

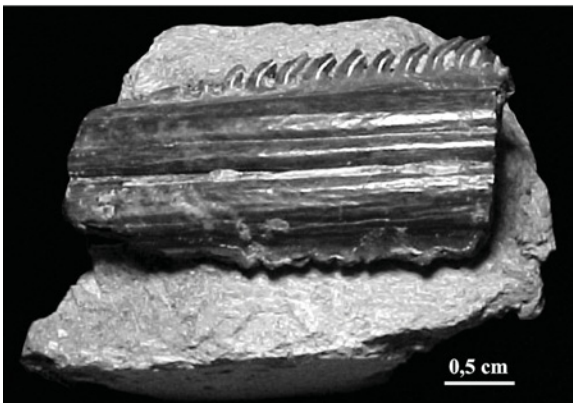


Figure 17 Elasmobranchii caudal sting spine from the Pirabas Formation. Myliobatidae (MN 2640-V) in anterior view.

The specimen MN 2640-V is probably a caudal sting spine of a Myliobatidae, having pointed denticles on each side, and longitudinal grooves in anterior view (Figure 17).

Myliobatidae teeth are found in the Pliocene of Angola (Antunes, 1978) and in three units from the Tertiary Caribbean Faunal Province: Gatun Formation, Pungo River Formation and Pacific Ecuador Miocene (Longbottom, 1979; Gillette, 1984) (see Figure 19).

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3 Discussion

In the present work, teeth of *Carcharhinus ackermannii*, *Hemipristis serra* and *Ginglymostoma obliquum,* from the Pirabas Formation are revised and considered as a junior synonyms of the respective recent species: *Carcharhinus sorrah*, *Hemipristis elongatus* and *Nebrius ferrugineum* that have a distinct recent geographical distribution, living in the Indian Ocean and in the western and central areas of the Pacific. However, the Panamanian isthmus emerged only during the Plio/Pleistocene and the circulation pattern was different from that of today. During the Late Oligocene to Middle Miocene, there was a communication between the Pacific and the Equatorial Atlantic (Iturralde-Vinent & MacPhee, 1999) (Figure 18), and equatorial Atlantic water would have been carried into the Pacific by the Circumtropical current (Mullins *et al*., 1987; Droxler *et al*., 1998). In the Late Miocene, water circulation may have diverged to the Northwest due to the reduction in the width of the Panamanian seaway. During the Pliocene to Holocene, the Panamanian waterway was completely closed, followed by the termination of the Circumtropical current and establishing the modern pattern of water circulation with a Caribbean current, transporting equatorial Atlantic water to Caribbean Sea (Iturralde-Vinent & MacPhee, 1999). Gillette (1984) noted similarities between the Miocene shark faunas of the Caribbean and Ecuador on the Pacific side. During the Miocene there was an interchange between the marine fauna from Pirabas and the Pacific fauna. Separation of the East Pacific and the Caribbean Sea, by the development of Panamanian Isthmus, was a typical vicariant event. Accepting the synonymy between these three Pirabas species and the extant Pacific *taxa* implies that, after the appearance of the vicariant barrier, these *taxa* have became extinct only in the oriental part of the Panamanian seaway.

A recurrent problem found with the fossil material is that descriptions based on isolated teeth can lead to mistakes in systematic identification, because

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sexual dimorphism and ontogenetic differences may occur within a species, and even individuals (heterodonty or teeth anomalies).

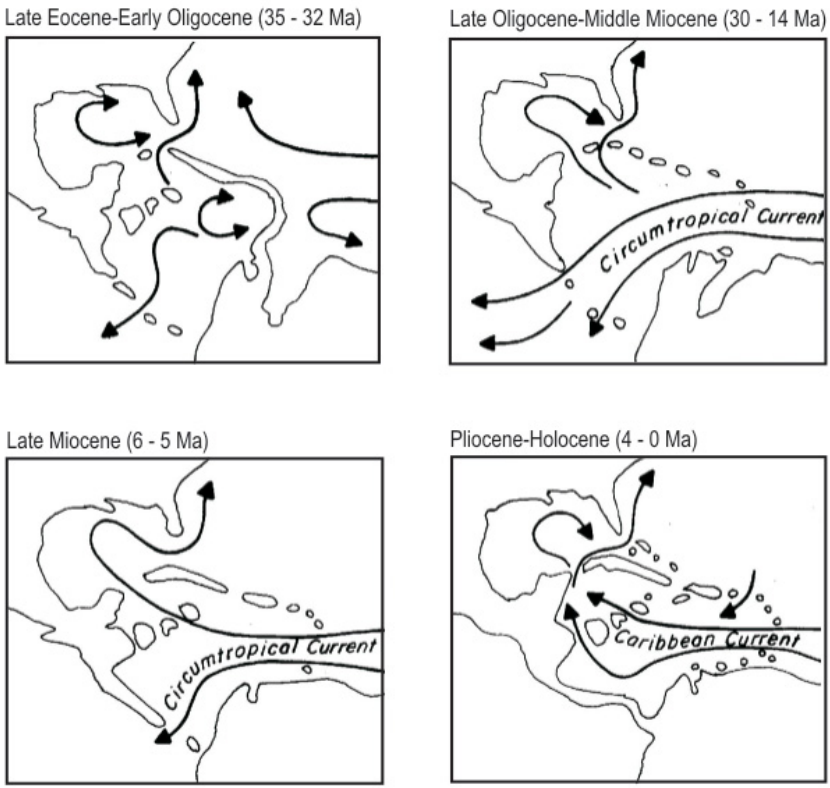

Figure 18 Water circulation and the communication between the Pacific and the Equatorial Atlantic, since the Late Eocene (modified from Iturralde-Vinet & MacPhee, 1999).

In the case of the Pirabas' elasmobranch fauna, some mistakes had been previously made concerning identification and descriptions. The major problem is that, as no synapomorphies could be pointed, these taxa should have been considered as metataxa (for discussion of this systematic problem see Smith, 1994).

Pirabas Fm.	Pungo River Fm. (North Carolina, U.S.A)	Yorktow Fm. (North Carolina, U.S.A)	Caribbean Miocene	Gatún Fm. (Panamá)	Pacific Ecuador Miocene	Nigéria (Eocene)	Angola (Pliocene)
Carcharhinus sorrah							
Carcharhinus perezzi	?	?	X	?	X		
Carcharhinus priscus	?	?		?	X		
Carcharhinus sp.	X	X		X	X		X
Galeocerdo cuvier							X
Rhizoprionodon lalandii				X	X		
Sphyrna sp.							
Hemipristis	X	X	X	X			X
Procarcharodon megalodon	X	X	X	X	X		X
Carcharodon carcharias	X	X		X	X		X
Isurus oxyrinchus							X
Nebrius ferrugineus							
Ginglimostoma serra						X	
Myliobatidae	X			X	X		X

Figure 19 Table showing the comparison of the Elasmofauna from the Pirabas Formation with the other principal Tertiary faunas in the Caribbe and Africa.

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One solution for a better identification of the studied material was comparing the fossil teeth with those of extant species and with Neogene Caribbean and African fauna. The results show that the ichthyofauna from Pirabas is typically Neogene with many of the species still living today (Figure 19).

4 Conclusions

The elasmofauna from the Pirabas Formation is composed by the following taxa:Carcharhinidae (*Carcharhinus* sp.; *Carcharhinus sorrah*; *Carcharhinus perezii*; *Carcharhinus priscus*; *Galeocerdo cuvier, Rhizoprionodon lalandii, Sphyrna* sp. and *Hemipristis elongatus*); Alopiidae (*Isurus oxyrinchus*; *Carcharodon carcharias* and *Procarcharodon megalodon*); Gynglymostomatidae (*Nebrius ferrugineus*; *Ginglymostoma serra*); Myliobatidae *Incertae sedis*. There are thirteen taxa, ten of which are synonymous with extant taxa. Thus, the majority of the elasmobranchs from the Pirabas Formation have a wide geochronological range, appearing in the Early Miocene. A similar pattern occurs with the mollusc (Ferreira & Cunha, 1957a; 1957b) and the crustacean faunas (Brito, 1993).

Carcharhinus egertoni, Carcharhinus ackermani, Galeocerdo paulinoi, Hemipristis serra, Scoliodon taxandriae, Isurus nova and Ginglymostoma obliquum, previously recorded from the Pirabas Formation, are considered here as junior synonyms of the following recent species, respectively: *Carcharhinus perezi, Carcharhinus sorrah, Galeocerdo cuvier, Hemipristis elongatus, Rhizoprionodon lalandii, Isurus oxyrinchus and Nebrius ferrugineum.*

Following the acceptance of the synonymy between *Carcharhinus ackermannii, Hemipristis serra* and *Ginglymostoma obliquum* with the extant taxa *Carcharhinus sorrah, Hemipristis elongatus* and *Nebrius ferrugineus*, and taking into account their recent distribution, the following biogeographical hypothesis is suggested. The separation of the East Pacific and Caribbean Sea, by the complete development of Panamanian isthmus occurred only during the Pliocene. In the Miocene the Equatorial Atlantic and Pacific oceans were still linked.

The nominal species *Rhinoptera studeri, Palaeomyliobatis pirabensis* and *Rhizochlatrus vidalis* is considered here as Myliobatidae indeterminate, as no diagnostic character could be found.

Comparing the Pirabas elasmofauna with the Neogene Caribbean Faunal Province and African fauna we can conclude that the species *Carcharhinus perezii, Carcharhinus priscus, Rhizoprionodon lalandii, Hemipristis elongatus, Procarcharodon carcharias, Carcharodon carcharias* and the Myliobatidae occur in some of the localities from Neogene Caribbean Faunal Province. These correspond to almost 55% of the Pirabas elasmofauna. *Carcharhinus* sp., *Galeocerdo cuvier, Hemipristis elongatus, Procarcharodon carcharias, Carcharodon carcharias, Isurus oxyrinchus* and the Myliobatidae are found in the Pliocene of Angola and only *Ginglymostoma serra* occurs in the Eocene of Nigeria. Almost 55% of the Pirabas elasmofauna is also found in Africa.

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