



Fossil Chondrichthyes from the central eastern Pacific Ocean and their paleoceanographic significance



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ABSTRACT

The study of the chondrichthyan fauna from the Angostura, Onzole, Canoa and Jama formations, in the Neogene of Bordón and Manabí basins, Ecuador, reveals the presence of 30 taxa, including the deep water shark †*Chlamydoselachus landinii* sp. nov. The assemblages are dominated by tropical shallow and deep water chondrichthyans, suggesting paleoenvironments associated with a short platform shelf bordering a deep margin. These assemblages are the most diverse shark and ray association known from the Tropical Central Eastern Pacific Ocean in the South American coastal basin, and provide new information on the paleoecology and paleodiversity of Neogene chondrichthyans.

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1. Introduction

Fossil chondrichthyan assemblages from the eastern Pacific Ocean are still poorly known in spite of several publications on the subject, including: Longbottom (1979) and Aguilera et al. (2011) on Ecuador; De Muizon and Devries (1985), Kindlimann (1990), Apolín et al. (2004) and Avalán et al. (2007) on Perú; Long (1993a), Suárez and Marquardt (2003), Suárez et al. (2006) and Carrillo-Briceño et al. (2013) on Chile; Laurito (2004), and Laurito and Valerio (2008) on Central America, and Long (1993b), González-Barba and Thies (2000), and Boessenecker (2011) on North America. These previous contributions are not uniform in terms of sampling and geochronological control, preventing comparative quantitative analyses among faunas. However, the faunal assemblages along the tropical eastern Pacific coast have been the subject of studies about faunal distribution in Tropical America and the proto-Caribbean area (Iturralde-Vinent and MacPhee, 1999; Landini et al., 2002a, 2002b; Aguilera et al., 2011; Carnevale et al., 2011).

In terms of regional relevance, the central eastern Pacific Ocean represents a geographic and oceanographic complex influenced by geologic and tectonic events along the Panamanian Atlantic–Pacific

seaway (Hoernle et al., 2002; Pindell et al., 2005), related to the uplift of the Isthmus of Panama (Coates and Obando, 1996; O’Dea et al., 2007; Coates and Stallard, 2013), the Andean uplift (Garzzone et al., 2008; Martinoid et al., 2010), the Ecuadorian subduction, the submarine trench system (Lonsdale, 1978; Ratzov et al., 2010) and the oceanographic dynamic (Fiedler and Talley, 2006) derived in successions of neritic to depth sea paleoenvironment changes. Longbottom (1979) described the early chondrichthyan fauna assemblage from the Miocene of the Onzole Formation and Aguilera et al. (2011) reported the presence of additional Miocene-Pleistocene taxa from the Angostura, Onzole and Jama formations from Ecuador. Teleostean records from the Neogene basin in Ecuador are known from otoliths reported from the Onzole and Canoa formations (Landini et al., 2002a, 2002b; Aguilera et al., 2011; Carnevale et al., 2011).

In this work we provide a taxonomic revision of the chondrichthyan fauna from Ecuador, resulting in an increased fossil record for the region and a better understanding of the Neogene shark and ray associations in Tropical America, especially along the eastern Pacific coast of South America.

2. Methods

The chondrichthyan assemblages (Table 1) were collected from nine localities (Fig. 1) of four Neogene geological units in Ecuador, including: Cayapas River [Telembí (0° 58′ 57″ N, 78°51′ 42″ W)],

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Table 1
Chondrichthyan assemblages from the Neogene of Ecuador.

Superorder	Order	Family	Species	Geological formations				
				Angostura (MM-LM)	Onzole (LM-EP)	Canoa (LP-PI)	Jama (EPI)	Onzole Longbottom (1979)
Squalomorphii	Hexanchiformes	Chlamydoselachidae	† <i>Chlamydoselachus landinii</i> sp. nov.	X				
	Squaliformes	Centrophoridae	<i>Centrophorus</i> sp.	X	X			
		Dalatiidae	† <i>Isistius</i> cf. <i>triangulus</i>		X			X
	Pristiophoriformes	Pristiophoridae	<i>Pristiophorus</i> sp.		X			
	Squatiniiformes	Squatinaidae	<i>Squatina</i> sp.		X			
Galeomorphi	Orectolobiformes	Ginglymostomatidae	<i>Ginglymostoma</i> sp.	X				
	Lamniformes	Odontaspidae	† <i>Carcharias acutissima</i>					X
		†Odontidae	† <i>Megaselachus megalodon</i>					X
	Carcharhiniformes	Hemigaleidae	† <i>Hemipristis serra</i>	X				X
			<i>Paragaleus</i> sp.				X	
		Carcharhinidae	† <i>Galeocerdo aduncus</i>					X
			<i>Rhizoprionodon longurio</i>	X		X		
			<i>Rhizoprionodon taxandriae</i>	X		X		X
			<i>Rhizoprionodon</i> sp.	X	X	X	X	
			<i>Carcharhinus albimarginatus</i>		X			
			<i>Carcharhinus brachyurus</i>	X		X		
			† <i>Carcharhinus egertoni</i>					X
			<i>Carcharhinus obscurus</i>	X			X	
			† <i>Carcharhinus priscus</i>					X
			<i>Carcharhinus</i> cf. <i>porosus</i>	X				
			<i>Carcharhinus</i> sp.	X	X		X	X
			<i>Negaprion brevirostris</i>	X				
			† <i>Negaprion eurybathrodon</i>					X
			<i>Sphyrna media</i>		X	X		
Batomorphii	Myliobatiformes	Sphyrnidae						
		Dasyatidae	<i>Dasyatidae</i> indet.	X				
		Myliobatidae	<i>Aetobatus</i> sp.					X
			<i>Myliobatis</i> sp.				X	
		Rhinopteridae	<i>Rhinoptera</i> sp.				X	
		Mobulidae	<i>Mobula</i> sp.	X				
			cf. <i>Mobula</i>	X	X			
				X				

Abbreviations: Middle Miocene (MM), Late Miocene (LM), Early Pliocene (EP), Late Pliocene (LP), Pleistocene (PL), Early Pleistocene (EPL).

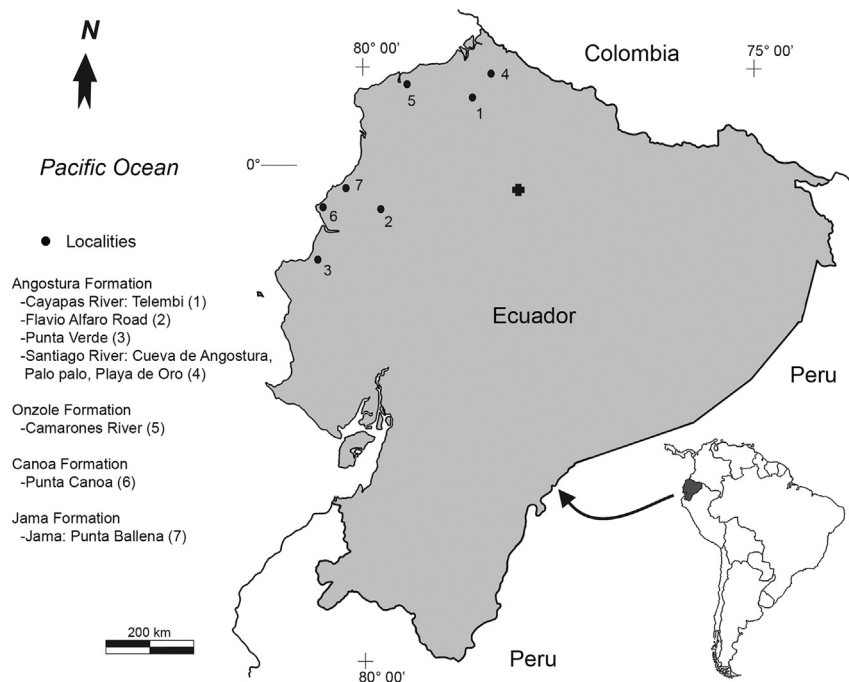


Fig. 1. Location map and localities.

Flavio Alfaro road (0° 44' 19" N, 79° 56' 39" W), Punta Verde (0° 35' 55" N, 80° 25' 47" W) and Santiago River [Cueva de Angostura, Palo palo, Playa de Oro (0° 53' N, 78° 50' W)] in the Angostura Formation (Middle-Late Miocene); Camarones River (0° 58' 04" N, 79° 36' 47" W) in the Onzole Formation (Late Miocene-Early Pliocene); Punta Canoa (0° 26' 43" N, 80° 28' 08" W) in the Canoa Formation (Late Pliocene-Pleistocene); and Jama [Punta Ballena (0° 10' 21" N, 80° 19' 31" W)] in the Jama Formation (Early Pleistocene). The assemblages are represented by a total of 91 specimens and 23 taxa. The specimens were collected during a field trip between June 11–23 in 1999, to the Bordón and Manabí basins in Ecuador (Figs. 1 and 2) by one of the authors (O.A.A.) as part of the Panama Paleontology Project at the Smithsonian Tropical Research Institute, Panama (STRI). These were collected directly on the outcrop and screen washed in bulk samples (10 Kg each) using a 2 mm diameter mesh. All specimens described here are deposited at STRI (STRI-PPP-T catalogue). The classifications follow Compagno (1973, 1977) and Cappetta (2012), and the terminology is based on Pfeil (1983) and Cappetta (2012). Photographs of shark and ray teeth were made with a Leica M205A multifocal stereomicroscope. Images from small teeth were made with a Scanning Electronic Microscope (SEM).

The identification was based on the comparative analysis with fossil and extant specimens in the following collections: Departamento Nacional de Pesquisas Minerais, Brazil (DNPM); Museo Nacional de Historia Natural de Santiago, Chile (SGO-PV); Natural History Museum of Basel (NMB), Paleontological collections of the Alcaldía Bolivariana de Urumaco, Falcon, Venezuela (AMU-CURS); Palaeontological Institute and Museum at the University of Zurich, Switzerland (PIMUZ); Museu Paraense Emilio Goeldi, Belén, Brazil (MPEG-V); Smithsonian Tropical Research Institute, Naos Marine laboratory Panama (STRI-PP-T); and Universidad Nacional

Experimental Francisco de Miranda, Coro, Venezuela (UNEFM-PF). Taxonomic abbreviations are: h (height), w (width) l (length), and these are used for the entire tooth including the root.

In this work we use the term “Tropical America” (Neotropics) to refer the geographic area of the western hemisphere located between the Tropic of Cancer (23° 27' N) and the Tropic of Capricorn (23° 27' S). “Southern South America” is a region composed of the southernmost areas of South America, south of the Tropic of Capricorn and this includes Argentina, Chile, Paraguay and Uruguay, and “North America” includes Canada, the USA and the northern part of Mexico (north of the Tropic of Cancer). Only the countries with fossil records of Neogene chondrichthyan have been included in the tables.

3. Geological setting

The Angostura Formation is located in the western Borbón Basin, on the northwestern coast of Ecuador, and this has been assigned to the Middle-Late Miocene (Cantalamesa et al., 2007). The Angostura Formation overlies the Lower-Middle Miocene Viche Formation, and its lithology consists principally of muddy, fine-grained sandstones with abundant mollusk shells (Baldock, 1982; Cantalamesa et al., 2007). An integrated analysis of facies and paleontological content of this geological unit suggests shore-face and inner-shelf paleoenvironments (Cantalamesa et al., 2007).

The Onzole Formation is assigned to the Late Miocene-Early Pliocene (Schulman et al., 1965; Whittaker, 1988; Carnevale et al., 2011). Whittaker (1988) subdivided the Onzole Formation into two main units (informally named lower Onzole Formation and upper Onzole Formation) separated by a regionally extensive angular unconformity of Late Miocene-Early Pliocene age. The fossil specimens referred to here come from the lower Onzole Formation, the same section from which the shark teeth referred by Longbottom (1979) come from. These outcrops are situated near Punta Gorda and Esmeraldas, and are composed mainly of fine-grained muddy turbidites, having regular vertical sequences of sedimentary structures associated with fining upward sequences, and bioturbation restricted mostly to the tops of the beds. The remainder of the beds measured consists of volcanic ash, mud pelagite, and glauconitic silt-sand turbidites. Vertical sequential analyses of stratigraphic sections for the most part show no pronounced trends in bed thickness or grain size. Facies relations, paleontological data, and regional geologic settings suggest sediment accumulation on an inner trench slope in a basin situated ocean-ward of the Pliocene trench-slope break (Aalto and Miller, 1999).

The Canoa Formation has extensive outcrops along the sea cliff south of Manta in the Manabí Province (Landini et al., 2002a, b), and its age has been attributed to the Late Pliocene-Pleistocene (Tsuchi et al., 1988; Whittaker, 1988; Bianucci et al., 1997; Landini et al., 2002a, b; Di Celma et al., 2005). The lithology of the Canoa Formation consists mainly of sandstone and sandy mudstone, divided into two sections (Pilsbry and Olsson, 1941). The lower Canoa Formation, exposed on the sea cliff south of Punta Canoa, is a 36-m thick, cyclothemic succession of bluish, chiefly fine-grained strata that rest unconformably on Miocene rocks of the Tosagua Formation. The upper Canoa Formation consists of 38-m thick shore face and inner-shelf deposits, and all of them represent shallow water deposits (Di Celma et al., 2005).

The Jama Formation has been assigned to the Early Pleistocene (Pilsbry and Olsson, 1941), and has an 180-m thick clastic succession deposited in an array of terrestrial and shallow-marine settings along the eastern margin of the Esmeraldas-Caraquez Basin (Rosania, 1989). It is located along the Bahía Jama in the Manabí Province, and is subdivided into three main informal units

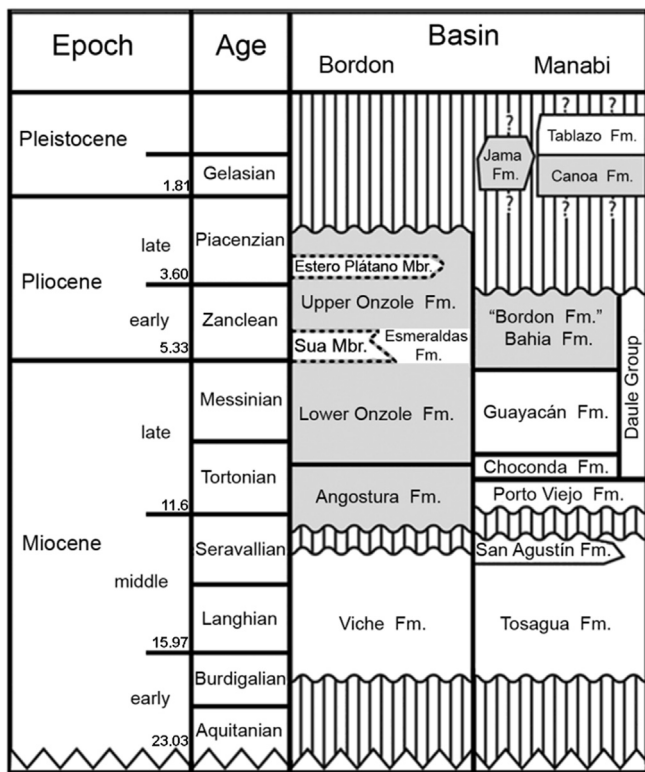


Fig. 2. Neogene stratigraphy of major outcrops in northwestern Ecuador (modified from Landau et al., 2012). Light grey color represents the formations treated in this study.

(Cantalamesa et al., 2005). The lower Punta Pasa Borracho Member (~20-m thick) is exposed between Punta Pasa Borracho and Punta Cabuya; and the Punta Ballena Member (~100-m thick) is exposed from Punta Cabuya to Punta Alcatraz; the El Matal Member (~60 m-thick) is exposed between Punta Alcatraz and the village of El Matal. The age of the Punta Ballena and El Matal members yielded a weighted mean radioisotopic age of 1.16 ± 0.06 Ma (Cantalamesa et al., 2005).

4. Systematic paleontology

Chondrichthyes Huxley, 1880

Neoselachii Compagno, 1977

Squalomorphii Compagno, 1973

Hexanchiformes Buen, 1926

Chlamydoselachidae Garman, 1884

Chlamydoselachus Garman, 1884

† *Chlamydoselachus landinii* sp. nov.

(Fig. 3A–D)

Derivation of name – The species is named in honor of Walter Landini, University of Pisa, Italy, for his valuable contributions to the knowledge of fossil fish from Ecuador.

Holotype – A single specimen (PPP-3455-T-1), indeterminate position from Playa de Oro, Santiago River, Angostura Formation (Middle-Late Miocene).

Type locality – Santiago River, Playa de Oro, Angostura Formation ($0^{\circ} 53' N$, $78^{\circ} 50' W$).

Diagnosis – Tooth with three well-developed and acute cusps slightly bent in lingual direction. These have a marked coronal twist (coronal torque), with the labial and lingual surfaces being completely smooth. Intermediary cusps are absent. The root is wide, labio-lingually short and the lobes poorly differentiated.

Description – The tooth measurements are h 5.1 mm, w 3.6 mm and l 3.2 mm. Three cusps form the crown; the distal cusp is broken. The medial and mesial cusps are robust and acute, the basal region is wide and there is a prominent coronal twist. The angle formed between both cusps is 32° . The basal section of the mesial cusp is slightly wider than the medial one. Both cusps are slightly inclined in the lingual direction. The medial cusp is 5.2 mm long from the root to the apex. The angle between the cusp and the tangential root is 55° . The cutting edge in the distal and mesial side is narrow. Both labial and lingual cusp surfaces are completely smooth. No intermediary cusps are present. The root is wide and labio-lingually short. The root base is slightly concave, and the mesial and distal lobules undifferentiated. In the lingual section of the root a large transverse groove bordered by a prominent crest is present in the occlusal surface. It has a large central foramen, and additional small foramina are distributed on the root surface.

Remarks – The recent *Chlamydoselachus* species *Chlamydoselachus anguineus* Garman, 1884 and *Chlamydoselachus africana* Ebert and Compagno, 2009, are inhabitants of deep water with soft bottoms between 120 and 1.450 m depths (Shiobara et al., 1987). *Chlamydoselachus* includes 10 fossil species (Cappetta, 2012; Mannering and Hiller, 2008), with the earliest record represented by †*C. thomsoni* Richter and Ward, 1990, from the Early Campanian (Upper Cretaceous) of James Ross Island, Antarctica. Others fossil species include: †*C. goliath* Antunes and Cappetta, 2002 (Late Campanian, Angola), †*C. gracilis* Antunes and Cappetta, 2002 (Late Campanian through Early Maastrichtian, Angola), †*C. tatere* Consoli, 2008 (Early Paleocene, New Zealand), †*C. keyesi* Mannering and Hiller, 2008 (Paleocene, New Zealand), †*C. fiedleri* Pfeil, 1983 (Middle Eocene, Austria), †*C. tobleri* Leriche, 1928 (Oligocene-Miocene?, Trinidad), †*C. bracheri* Pfeil, 1983 (Early Miocene, Austria), †*C. garmani* Welton in Pfeil (1983) (Early Miocene,

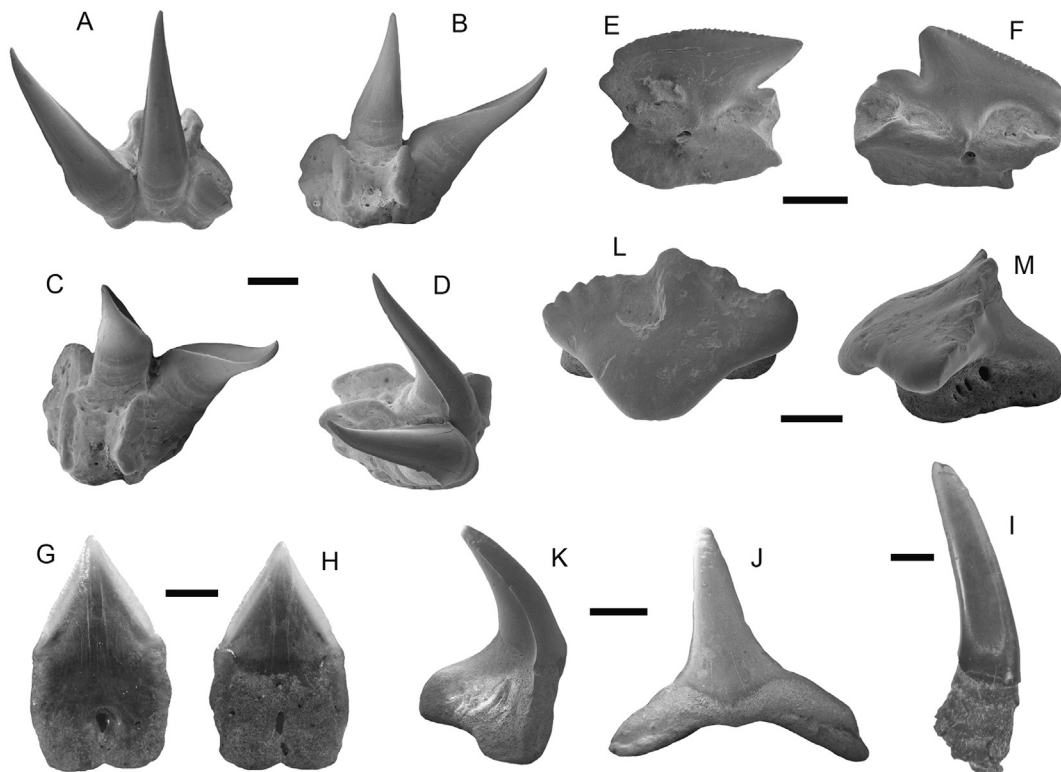


Fig. 3. A–D *Chlamydoselachus landinii* sp. nov. (PPP-3455-T-1); E, F *Centrophorus* sp. (PPP-3476-T-1 and PPP-3455-T-2); G, H *Isistius* cf. *triangulus* (PPP-3492-T-1); I, *Pristiophorus* sp. (PPP-3484-T-1); J, K *Squalatina* sp. (PPP-3486-T-1); L, M *Ginglymostoma* sp. (PPP-3465-T-1). A, G, J, L labial view; B, C, E, F, H lingual view; D mesial view; K, K distal view; I dorsal view. Scale bar 1 mm.

California), and †*C. lawleyi* Davis, 1887 (Early Pliocene, Italy). The extant species *C. anguineus* was recorded from the Pliocene of Italy (Marsili, 2007). Additional *Chlamydoselachus* spp., have been recorded from the Cretaceous and the Neogene of North America, Asia and Europe (Cappetta, 2012). †*C. tobleri* is known only from one specimen (Leriche, 1928), with had been missing for more than 70 years until it was found by one of the authors (J.D.C.B.) in September 2013 in the paleontological collection of the Natural History Museum of Basel (NMB), Switzerland.

†*Chlamydoselachus landinii* sp. nov. differs from the Cretaceous species †*C. thomsoni*, †*C. goliath* and †*C. gracilis* by the very different combination of root and cusp morphology (see Richter and Ward, 1990; Antunes and Cappetta, 2002). †*C. landinii* sp. nov. can be distinguished from the Paleogene, Neogene and recent congeners by morphological characters present in the following taxa: from †*C. tateri* because this has the main cusps without the coronal twist and with vertical striations in the shoulder on labial and lingual faces; from †*C. keyesi* because this has large teeth (>1 mm) without a coronal twist, with short and vertical striations in the labial face of the cusps; from †*C. fiedleri* because the teeth of this taxon have intermediary cusps and strong striations on the labial face of the main cusps; from †*C. tobleri* because its holotype has a crown with graceful (elongated) main and intermediary cusps; from †*C. bracheri* because the crown in this taxon has intermediary cusps and graceful main cusps with a coronal twist and vertical striations on the labial and lingual face; from †*C. lawleyi*, *C. anguineus* and *C. africana* because these taxa have graceful main cusps, and intermediary cusps. Except for †*C. garmani*, the teeth of the extant *C. anguineus* and *C. africana* and the remaining Neogene *Chlamydoselachus* have intermediary cusps. The dental morphology closest to †*C. landinii* sp. nov. that we have identified are the teeth of †*C. garmani* from the Miocene of North America (see Welton, 1979; Pfeil, 1983). As in †*C. landinii* sp. nov., the crown of †*C. garmani* lacks intermediate cusps, however †*C. garmani* has a robust, conical main cusp with strong vertical striations on the labial face, characters that are not present in †*C. landinii* sp. nov. The roots of †*C. garmani* resemble those of †*C. landinii* sp. nov., however, in the latter the lingual lobes are less developed and the transverse groove is flanked by a pair of prominent parallel ridges, characters not evident in †*C. garmani*. The distinctive character that can clearly differentiate both taxa is the absence of a coronal twist (coronal torque) and presence of strong vertical ribs on the labial face of the main cusp of †*C. garmani*. Bearing in mind that †*C. landinii* sp. nov., there is a marked coronal twist, with the labial and lingual faces of the cusps completely smooth. No previous record of *Chlamydoselachus* is known from South America, and †*C. landinii* sp. nov. is the first fossil of the genus described from the Pacific coast of South America.

Squaliformes Goodrich, 1909

Centrophoridae Bleeker, 1859

Centrophoridae Müller and Henle, 1837

Centrophorus sp.

(Fig. 3E, F)

Materials – Four lower lateral teeth. Two teeth from Playa de Oro (PPP-3455-T-2) and Punta Verde (PPP-3476-T-1), Santiago River, Angostura Formation (Middle–Late Miocene); 2 teeth from Camarones River (PPP-3493-T-3), Onzole Formation (Late Miocene–Early Pliocene).

Description – The dental measurements are h 2.6–3.5 mm and w 3.5–4.7 mm. The teeth are very compressed labio-lingually, and taller than broad, with the cusp inclined distally. The distal heel is high and convex. The apron is long, and broader at its base than at its extremity, which flattens without reaching the root's lower edge. The mesial cutting edge of the cusp is slightly serrated. The uvula is not very prominent and slightly short. The mesial part of

the root is high and narrow, and the concave contour has a well-marked external depression, with a large marginal-labial foramen and smaller foramina. The distal part of the root is larger, not as tall and has several small foramina. On the lingual surface, a large infundibulum opens beneath the uvula.

Remarks – Centrophoridae comprises the genera *Deania* Jordan and Snyder, 1902, and *Centrophorus* (Compagno, 2005), both having a similar tooth morphology. However, both taxa can be distinguished by the foramina located behind the uvula on the lingual face (De Schutter and Wijnker, 2012). *Deania* has two well-differentiated foramina and *Centrophorus* has a large foramen called the infundibulum (Ledoux, 1970). Early *Centrophorus* fossils were described from the Cenomanian (see Adnet et al., 2008). Extant *Centrophorus* comprise at least 12 species (Compagno, 2005), which are characterized by complex interspecific morphological variation, teeth and dermal denticles display ontogenetic changes and sexual dimorphism (White et al., 2008). The record of *Centrophorus* sp. from the Cubagua Formation (Late Miocene–Early Pliocene) in Venezuela (Aguilera and Rodríguez de Aguilera, 2001; Aguilera, 2010), and the specimens described here from the Angostura and Onzole formations represent the only records known from the Neogene of the Caribbean, Tropical America and Southern South America.

Dalatiidae Gray, 1851

Isistius Gill, 1864

Isistius cf. *triangulus* (Probst, 1879)

(Fig. 3G, H)

Materials – Twelve lower teeth [PPP-3484-T-3 (4 teeth), PPP-3492-T-1, PPP-3493-T-2 (7 teeth)], from Camarones River, Onzole Formation (Late Miocene–Early Pliocene).

Description – Lower teeth with ranges in size of h 3.9–4.9 mm, w 2.3–3.3 mm. The lower teeth are very compressed labio-lingually and have a high equilateral triangular crown, with very weakly serrated cutting edges. The apron is very flat with a poorly marked lower boundary that descends to the level of the elliptical opening. The root very flat, high, and square. It has a medial-lingual foramen, and a medial-labial opening in the upper part of the buttonhole. In line with the foramina on both faces, there are slight depressions reaching the basal edge of the root. The overlap depression of the tooth is high and well marked, especially on the lingual face where they are deep.

Remarks – The genus comprises two extant species (*Isistius brasiliensis* Quoy and Gaimard, 1824; *Isistius plutodus* Garrick and Springer, 1964) and two extinct species (†*Isistius triturator* Probst, 1879; †*Isistius triangulus*). The stratigraphic range is from the Early Paleocene to the Recent (Cappetta, 2012). *Isistius triturator* is known from the Early Paleocene to the Eocene and *I. triangulus* from the Miocene to the Pliocene (Cappetta, 2012). Longbottom (1979) mentioned and illustrated *I. triangulus* from the Miocene of Ecuador (Onzole Formation). Previous records of *I. triangulus* in America have been reported from the Miocene–Pliocene of the Caribbean and North America (Table 2).

Pristiophoriformes Berg, 1958

Pristiophoridae Bleeker, 1859

Pristiophorus Müller and Henle, 1837

Pristiophorus sp.

(Fig. 3I)

Material – One single rostral tooth (PPP-3484-T-1), from Camarones River, Onzole Formation (Late Miocene–Early Pliocene).

Description – The tooth measurement is l 9 mm. The rostral tooth is long and slender, and is compressed dorso-ventrally. It consists of a basal peduncle elongated antero-posteriorly with a basal face that is strongly concave and oval. The fairly flat enameloid cusp is slightly inclined distally. The sharp cutting edges are dulled above the well-marked basal bulge. The root is broken.

Table 2
Chondrichthyan assemblages from Ecuador and their fossil record in the Neogene of the Americas.

Chondrichthyan taxa from Ecuador	Tropical America and the Caribbean															NA		SSA			
	Barbados	Bonaire	Brazil	Costa Rica	Cuba	Dominican Republic	Haiti	Jamaica	Martinique	Panama	Peru	Trinidad	The Grenadines	Venezuela	Southern Mexico	Northern Mexico	U.S.A	Argentina	Chile	Uruguay	
† <i>Chlamydoselachus landinii</i> sp. nov.																	X				
<i>Centrophorus</i> sp.														X			X				
† <i>Isistius</i> cf. <i>triangulus</i>				X										X		X					
<i>Pristiophorus</i> sp.										X				X		X	X		X		
<i>Squatina</i> sp.				X						X				X		X	X		X		
<i>Ginglymostoma</i> sp.			X	X						X						X					
† <i>Carcharias acutissima</i>																X	X			X	
† <i>Megaselachus megalodon</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	
† <i>Hemipristis serra</i>	X		X	X	X		X	X		X	X	X	X	X	X	X	X				
<i>Paragaleus</i> sp.														X		X					
† <i>Galeocerdo aduncus</i>				X	X						X			X		X	X	X			
<i>Rhizoprionodon longurio</i>															X		X				
† <i>Rhizoprionodon taxandriae</i>			X	X										X		X					
<i>Rhizoprionodon</i> sp.				X						X				X		X					
<i>Carcharhinus albimarginatus</i>				X											X		X		X		
<i>Carcharhinus brachyurus</i>										X					X		X		X		
† <i>Carcharhinus egertoni</i>	X			X						X	X	X		X		X	X				
<i>Carcharhinus obscurus</i>				X	X					X			X	X		X	X				
† <i>Carcharhinus priscus</i>			X	X						X	X			X		X					
<i>Carcharhinus cf. porosus</i>																X					
<i>Carcharhinus</i> sp.			X				X			X	X			X		X	X	X	X	X	
<i>Negaprion brevirostris</i>					X					X	X			X		X	X				
† <i>Negaprion eurybathrodon</i>				X	X					X				X		X	X				
<i>Sphyrna media</i>			X													X	X				
<i>Dasyatidae</i> indet.																X	X				
<i>Aetobatus</i> sp.			X	X	X					X	X			X		X	X		X		
<i>Myliobatis</i> sp.			X	X	X					X	X			X	X	X	X		X	X	
<i>Rhinoptera</i> sp.				X						X				X		X	X	X	X		
<i>Mobula</i> sp.														X		X	X				
cf. <i>Mobula</i>														X		X	X				
Batomorphii Indet.														X							

Tropical America and Caribbean: Leriche, 1938; Casier, 1958; Santos and Travassos, 1960; Gillette, 1984; De Muizon and Devries, 1985; Kruckow and Thies, 1990; Iturralde-Vinent et al., 1996; Laurito, 1999, 2004; Laurito and Valerio, 2008; Monsch, 1998; Iturralde-Vinent et al., 1998; Kindlimann, 1990; Monsch, 1998; Donovan and Gunter, 2001; Apolín et al., 2004; Underwood and Simon, 2004; Reis, 2005; Avalán et al., 2007; Laurito and Valerio, 2008; Portell et al., 2008; Aguilera and Lundberg, 2010; Aguilera et al., 2011; Pimiento et al., 2010, 2013a, b.

Southern South America (SSA): Long, 1993a; Arratia and Cione, 1996; Suárez and Marquardt, 2003; Suárez et al., 2006; Cione et al., 2011; Cabrera et al., 2012; Carrillo-Briceño et al., 2013.

North America (NA): Case, 1980; Kruckow and Thies, 1990; Müller, 1999; Long, 1993b; González-Barba and Thies, 2000; Purdy et al., 2001; Boessenecker, 2011; Hulbert, 2001.

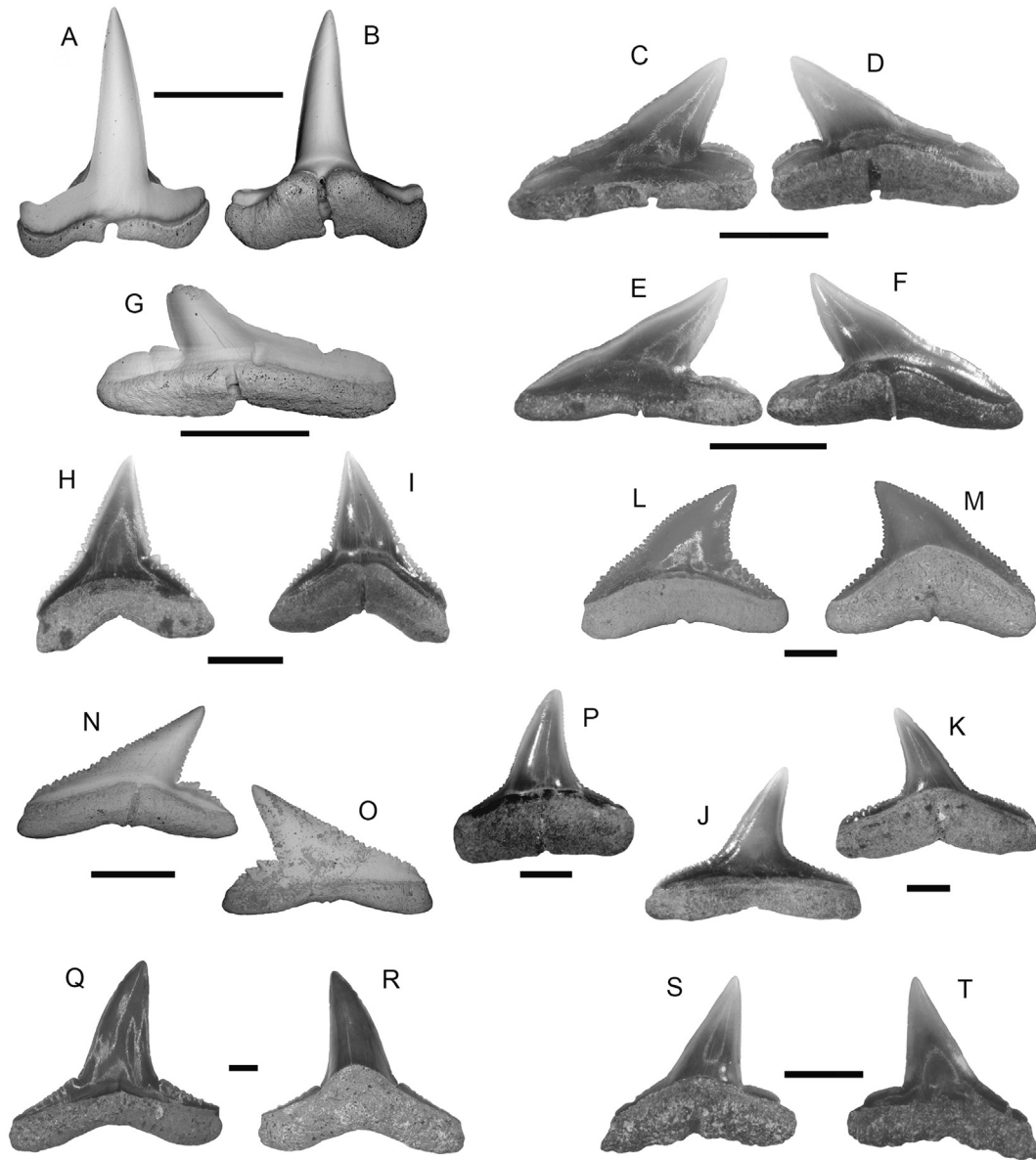


Fig. 4. **A, B** *Paragaleus* sp. (PPP-3562-T-2); **C, D** *Rhizoprionodon longuirio* (PPP-3465-T-7); **E, F** †*Rhizoprionodon taxandriae* (PPP-3514-T-1); **G** *Rhizoprionodon* sp. (PPP-3563-T-5); **H, I** *Carcharhinus albimarginatus* (PPP-3484-T-5); **J, K** *Carcharhinus brachyurus* (PPP-3457-T-2); **L, M** *Carcharhinus obscurus* (PPP-3587-T-2); **N, O** *Carcharhinus* cf. *porosus* (PPP-3432-T-2); **P** *Carcharhinus* sp. (PPP-3406-T-3); **Q, R**, *Negaprion brevirostris* (PPP-3587-T-1); **S, T** *Sphyrna media* (PPP-3516-T-1). A, C, E, H, J, L, O, Q, T, labial view; B, D, F, G, I, K, M, N, P, R, S, lingual view. Scale bar 2.5 mm.

Remarks – *Pristiophorus* is known from the Upper Cretaceous to the Recent and its rostral teeth are distinguished from those of *Pliotrema* Regan, 1906, by having a barbed posterior cutting edge (Cappetta, 2012). The specimen PPP-3484-T-1 is the first fossil record from Ecuador and other records of *Pristiophorus* include North America, Tropical America and Southern South America (Table 2).

Squatiniformes Buen, 1926

Squatiniidae Bonaparte, 1838

Squatina Dumeril, 1806

Squatina sp.

(Fig. 3J, K)

Material – One anterior tooth (PPP-3486-T-1) from Camarones River, Onzole Formation (Late Miocene–Early Pliocene).

Description – The dental measurements are h 3.7 mm, w 4.26 mm. The tooth exhibits a short and slender crown. The crown is curved lingually. Both cutting edges are concave, completely smooth and reach the base of the crown. The labial bulge of the

crown overhangs the root and develops a prominent bulb. The root is low and wider, and the basal edge has a triangular shape.

Remarks – *Squatina* is known from a complete and articulated skeleton from Jurassic deposits in Germany and isolated teeth up through to the Recent. Isolated teeth are difficult to identify because similar characters are persistent in geological time, especially from the Neogene (Cappetta, 2012). This taxon has a wide fossil record in the Neogene of the Americas (Table 1).

Galeomorphii Compagno, 1973

Orectobififormes Applegate 1972

Ginglymostomatidae Gill 1862

Ginglymostoma Müller and Henle 1837

Ginglymostoma sp.

(Fig. 3L, M)

Material – One tooth of indeterminate position (PPP-3465-T-1) from Playa de Oro, Santiago River, Angostura Formation (Middle–Late Miocene).

Description – The tooth measurements are h 2.3 mm, w 4.0 mm. The crown is slightly asymmetric and the enameloid is smooth. The cutting edge is not well preserved in the distal section. However, the mesial edge has five secondary cusps that are complete and well defined. The apron does not reach the basal plane of the root. The medial-lingual protuberance is high and well developed. The root is thin with a flat, irregular basal face and a central foramen.

Remarks – *Ginglymostoma* has a stratigraphic range from the Upper Cretaceous to the Recent, and its teeth are distinguished from the teeth of *Nebrius* Rüppel (1837), by having a symmetric crown and short apron (Cappetta, 2012). This new report from Ecuador and those referred by Espinoza-Arrubarena and Applegate and Espinoza-Arrubarena (1981) from the Pleistocene of Baja California (*Ginglymostoma* sp.) and Apolín et al. (2004) from the Late Miocene of Peru (*Ginglymostoma* sp. aff. *G. cirratum*) are the unique records known of this genus from the Neogene of the Eastern Pacific; other fossil records in the Americas are listed in Table 2.

Carcharhiniformes Compagno, 1973

Hemigaleidae Hasse, 1879

Paragaleus Budker, 1935

Paragaleus sp.

(Fig. 4A, B)

Material – One lower anterior tooth (PPP-3562-T-2) from Punta Ballena, Jama, Jama Formation (Early Pleistocene).

Description – The tooth measurements are h 5 mm, w 4 mm. The cusp is prominent and straight, with smooth cutting edges. The cusp and the root resemble an inverted “T”. The distal heels are large, prominent and smooth, without cusps and slightly recurved to the lingual face. The root is low and the basal surface is flat. The lingual protuberance is slightly prominent and has a well-defined lingual crown.

Remarks – *Paragaleus* is characterized by having strong heterodonty between upper and lower teeth (Compagno, 1984b). Lower anterior teeth have a high and erect cusp that gives the tooth a characteristic inverted “T”. These may lack accessory cusps in their distal heels (Compagno, 1984b). The anterior lower teeth are easily distinguishable from the rest of the teeth of both jaws, and are characterized by a more triangular crown that is inclined distally and has accessory cusps on its distal heel. From the Americas the fossil record of *Paragaleus* sp. includes the Middle Miocene of North America (Purdy et al., 2001), and the Early Miocene of Venezuela (Aguilera and Rodríguez de Aguilera, 2001).

Carcharhinidae Jordan and Evermann, 1896

Rhizoprionodon Whitley, 1929

Rhizoprionodon longurio (Jordan and Gilbert, 1882)

(Fig. 4C, D)

Material – Six teeth from Playa de Oro, Santiago River [PPP-3465-T-6 (3 teeth)], Punta Verde (PPP-3465-T-7), Angostura Formation (Middle-Late Miocene); Punta Canoa [PPP-3514-T-1 (2 teeth)], Canoa Formation (Late Pliocene-Pleistocene).

Description – Tooth measurements are h 3.2–4 mm and w 5–6 mm. The upper teeth have a high cusp inclined distally. The mesial cutting edge is slightly concave, and the distal cutting edge is straight or slightly sigmoid; both cutting edges are smooth. The distal heel is high with small serrations and clearly separated from the cusp by a notch. The root is low with a slightly concave basal face; the labial face is slightly convex, and the lingual face has a slight lingual protuberance with a deep medial groove. In lower teeth the mesial edge is concave, the distal heel is serrated with small serrations, and the root is low with a flat basal face.

Remarks – The stratigraphic range of *Rhizoprionodon* extends from the Early Eocene to the Recent (Cappetta, 2012). Neogene species comprise †*Rhizoprionodon acutaus* Rüppel, 1837, †*Rhizoprionodon fischeuri* Joleaud, 1912, †*Rhizoprionodon taxandriae*

Leriche, 1926, *R. longurio* and *Rhizoprionodon terraenovae* Richardson, 1836. Extant *Rhizoprionodon* includes seven species with a distribution in tropical and temperate waters (Compagno, 1984b; Compagno et al., 2005). The species *R. longurio* is an inhabitant exclusively in the Eastern Pacific from California up to Peru (Compagno et al., 2005). Previous fossil records of *R. longurio* had been described from the Pliocene of Baja California (González-Barba and Thies, 2000), and in the Late Pleistocene of California (Long, 1993b), along the Pacific coast of North America.

† *Rhizoprionodon taxandriae* (Leriche, 1926)

(Fig. 4E, F)

Material – Three upper teeth. One tooth (PPP-3386-T-1) from Punta Verde, Angostura Formation (Middle-Late Miocene); two teeth (PPP-3514-T-1) from Punta Canoa, Canoa Formation (Late Pliocene-Pleistocene).

Description – The dental measurements are h 2.4–3.4 mm, w 4.5–5.9 mm. The crown is triangular and asymmetric, with a high cusp inclined distally. The cutting edges of the crown are completely smooth. The mesial cutting edge is straight toward the apex, and the distal cutting edge is straight or slightly sigmoid. The root is broad, and the basal face is rather broad and flat, with a deep medial sulcus and slightly prominent lingual protuberance. The labial root surfaces have numerous and small foramina.

Remarks – †*R. taxandriae* (=†*Scoliodon taxandriae*) was originally described from the Miocene of Europe by Leriche (1926), and its records also include the Neogene of North America and Tropical America (Table 2).

Rhizoprionodon sp.

(Fig. 4G)

Material – Thirteen teeth of indeterminate position. Two teeth from Cueva de Angostura (PPP-3438-T-1, PPP-3443-T-1), Palo palo (PPP-3457-T-1), and Playa de Oro (PPP-3469-T-1, PPP-3467-T-1) Santiago River, Angostura Formation (Middle-Late Miocene); one tooth (PPP-3484-T-8) from Camarones River, Onzole Formation (Late Miocene-Early Pliocene); two teeth from Punta Canoa (PPP-3514-T-2, PPP-3537-T-1), Canoa Formation (Late Pliocene-Pleistocene); four teeth [PPP-3562-T-1 (three teeth), PPP-3563-T-5] from Punta Ballena, Jama, Jama Formation (Early Pleistocene).

Remarks – Considering the morphological variability of the teeth of *Rhizoprionodon* and the state of conservation of most teeth referred to here, which are mostly broken and eroded, they present no diagnostic morphological characters for a specific taxonomic classification.

Carcharhinus Blainville, 1816

Carcharhinus albimarginatus (Rüppel, 1837)

(Fig. 4H, I)

Material – Two antero-lateral teeth (PPP-3484-T-4, PPP-3484-T-5) from Camarones River, Onzole Formation (Late Miocene-Early Pliocene).

Description – The dental measurements are h 8.4–8.9 mm, w 10.2–10.8 mm. The crowns are triangular, and slightly inclined distally. The mesial and distal cutting edges are straight. Both edges are well differentiated from the heels by a notch, which is more evident in the distal edge. The serrations are strong on the heels and become fine along the cutting edge toward the apex. The root is low, the lobes slightly rounded, the lingual surface of the root is slightly inflated, and the medial lingual groove is narrow.

Remarks – Upper teeth with the mesial and distal cutting edges serrations well separated from the heels are also characteristic in *C. falciformis* Bibron, 1839, *C. perezii* Poey, 1876, *C. plumbeus* Nardo, 1827, and *C. amblyrhynchos* Rüppel, 1837 (Laurito et al., 2008). However, *C. albimarginatus* can be distinguished from *C. falciformis* by having a shorter crown, shallow notch between the heel and the cusp, and discontinuous serrations along the mesial edge (Purdy et al., 2001). The specimens PPP-3484-T-4 and PPP-3484-T-5

represent the first records from Ecuador, while other reports are from the Caribbean, North America and Southern South America (Table 2).

Carcharhinus cf. brachyurus (Günther, 1870)

(Fig. 4J, K)

Material – Two lower lateral teeth. One tooth (PPP-3457-T-2) from Palo Palo, Santiago River, Angostura Formation (Middle-Late Miocene); one tooth (PPP-3516-T-2) from Punta Canoa, Canoa Formation (Late Pliocene-Pleistocene).

Description – The dental measurements are h 7–7.2 mm, w 11–12 mm. The crown is tall and triangular, and slightly inclined distally. The lingual face of the cusp is slightly inflated, and the labial face is flat. The mesial cutting edge is slightly concave, and the distal edge is convex. The serrations are strongly developed on the mesial edge compared with the distal edge. However, on both edges, the serrations become fine toward the apex. Both heels have coarse serrations and are well differentiated from the cutting edges. The root is wider than the crown and slightly concave; the labial face is flat and the lingual protuberance is slightly developed and bears a shallow nutrient groove.

Remarks – *Carcharhinus brachyurus* has a stratigraphic range from Miocene to Recent, with abundant records in the Americas (Table 2), Asia and Europe (Marsili, 2007). The presence of *Carcharhinus cf. brachyurus* in the Angostura and Canoa formations represents the first fossil records of this taxon from the Neogene of Ecuador.

Carcharhinus obscurus (Lesueur, 1818)

(Fig. 5L, M)

Material – Two upper teeth. One tooth (PPP-3563-T-7) from Carretera Flavio Alfaro, Angostura Formation (Middle-Late Miocene); one tooth (PPP-3587-T-2) from Punta Ballena, Jama, Jama Formation (Early Pleistocene).

Description – The dental measurements are h 9.6–13.3 mm, w 13.2–13.8 mm. The upper teeth have a triangular, high, wide crown, slightly inclined distally. The labial face of the crown is flat, and the lingual face is strongly convex. The mesial cutting edge is slightly arched and incised by small serrations. The distal cutting edge is concave and incised by numerous small serrations. The serrations on both edges are fine towards the apex. The root is high with rounded lobes; the lingual protuberance is slightly developed and bears a shallow groove with a clear nutritive foramen. The basal edge of the root is slightly concave.

Remarks – Teeth of *Carcharhinus obscurus* are reported in the fossil record from the Early Miocene to Recent (Scudder et al., 1995; Purdy et al., 2001; Marsili, 2007). Its teeth can be separated from other *Carcharhinus* species based on the characteristic mesial cutting edge, which is convex with the apex distally recurved (Purdy et al., 2001). This species has been reported from the Neogene of the Caribbean and North America (Table 2).

Carcharhinus aff. porosus (Ranzani, 1839)

(Fig. 4N, O)

Material – One upper lateral tooth (PPP-3432-T-2) from Telembí, Cayapas River, Angostura Formation (Middle-Late Miocene).

Description – The dental measurements are h 3.9 mm, w 6.5 mm. The crown is high and triangular; the cusp is oblique and slightly inclined distally. The lingual face of the cusp is slightly inflated, and the labial face is flat. Both mesial and distal edge serrations are fine or absent toward the apex. The mesial heel is undifferentiated from the cutting edge, and has coarse serrations; the distal heel is characterized by stronger serrations. The root is low with rounded lobes and has a basal face that is slightly concave. The lingual protuberance is slightly developed and bears a shallow nutrient groove.

Remarks – The upper teeth of *C. porosus* are characterized by a triangular and semi-erect crown, and serrations are strongly

developed along the cusp and the mesial heel; the distal heel is characterized by well-developed serrations (Compagno, 1984b). This morphology is similar to the Recent species *C. borneensis* Bleeker, 1859, *C. sorrah* Valenciennes, 1839, *C. fitzroyensis* Whitley, 1943 and *C. signatus* Poey, 1868. However, these species can be distinguished from *C. porosus* based on the dental characters discussed by Compagno (1984b) and figured by Garrick (1982), and Voigt and Weber (2011). Previously known fossil *C. porosus* specimens were recorded by González-Barba and Thies (2000) from the Pliocene of Baja California, Mexico.

Carcharhinus spp.

(Fig. 4P)

Material – Twenty-three teeth, from Telembí, Cayapas River (PPP-3406-T-3, PPP-3432-T-1), Playa de Oro, Santiago River [PPP-3465-T-4, PPP-3465-T-5, PPP-3469-T-2 (two teeth), Punta Verde (PPP-3476-T-2)], Angostura Formation (Middle-Late Miocene); Camarones River [PPP-3484-T-7 (five teeth), PPP-3493-T-5 (five teeth), PPP-3502-T-1], Onzole Formation (Late Miocene-Early Pliocene); Punta La Gorda (PPP-3582-T-2), Bahía, Bahía Formation (Early Pliocene); Punta Ballena (PPP-3563-T-2, PPP-3563-T-3, PPP-3563-T-4), Jama, Jama Formation (Early Pleistocene).

Description – Most specimens are broken crowns from lower teeth, and a few are fragments of upper teeth. PPP-3406-T-3 is the only complete lower tooth; its crown is slender and slightly recurved in a lingual direction with cutting edges finely serrated.

Remarks – Ontogenetic and sexual dimorphism is observed in *Carcharhinus* species and makes diagnosis not possible (Kent, 1994). Generally, the lower teeth do not have diagnostic characters to distinguish them at the species level. Due to the fragmentary conditions and bad preservation in most cases, the remaining specimens are not distinguishable to the species level.

Negaprion Whitley, 1940

Negaprion brevirostris (Poey, 1868)

(Fig. 4Q, R)

Material – One upper lateral tooth (PPP-3587-T-1) from Flavio Alfaro road, Angostura Formation (Middle-Late Miocene).

Description – The dental measurements are h 18 mm, w 20 mm. This upper tooth shows a rather high, triangular cusp that is slightly inclined distally. The cutting edge of the crown is completely smooth, except the low and weakly serrated lateral heels. The root lobes are extended, and the basal face is rather broad and flat, with a clear medial lingual nutrient groove.

Remarks – Early records of *Negaprion* are known from the Early Miocene (Cappetta, 2012). †*Negaprion eurybathrodon* Blake, 1862, is the widely distributed Neogene species, and the fossil record of the species includes North America (Kruckow and Thies, 1990; Purdy et al., 2001), Tropical America and the Caribbean (Longbottom, 1979; Kruckow and Thies, 1990; Laurito, 2004; Aguilera, 2010; Aguilera et al., 2011; Pimiento et al., 2013b). The fossil record of the extant *N. brevirostris* includes Tropical America, the Caribbean and North America (Table 2).

Sphyrnidae Gill, 1872

Sphyrna Rafinesque, 1810

Sphyrna media (Springer, 1940)

(Fig. 4S, T)

Material – One upper lateral tooth (PPP-3484-T-6) from Camarones River, Onzole Formation (Late Miocene-Early Pliocene). One lower antero-lateral tooth (PPP-3516-T-1), Punta Canoa, Canoa Formation (Late Pliocene-Pleistocene).

Description – The dental measurements are h 6.1–8.0 mm, w 7.1–6.8 mm. The upper tooth crown is high and triangular, with an asymmetrical crown that is not distally inclined. The cutting edges are straight and completely smooth. The distal heel is well separated from the main cusp by an acute notch. The lower tooth crown is not distally inclined, and the mesial and distal cutting edges are

straight. In both teeth the root is low; the basal surface is flat in the lower teeth and concave in the upper teeth. The medial lingual protuberance is well developed, bearing a deep nutrient groove.

Remarks – *Sphyrna* is known from the Lower Oligocene to Recent, and its teeth have a morphologic shape close to those of *Rhizoprionodon* (Cappetta, 2012). However, *Sphyrna* teeth can be distinguished because these are larger than *Rhizoprionodon* (up to 2 cm height), with a lingual protuberance that is well-developed with a mesial cutting edge that is slightly concave (Purdy et al., 2001). *S. media* has been identified from the early Miocene of Brazil (Costa et al., 2009) and North America (Purdy et al., 2001; González-Barba and Thies, 2000).

Batomorphii Cappetta, 1980

Myliobatiformes Compagno, 1973

Dasyatidae Jordan, 1888

Dasyatidae Indet.

(Fig. 5A–I)

Material – Three teeth of indeterminate position from Cueva de Angostura (PPP-3434-T-1), and Playa de Oro (PPP-3465-T-2; PPP-3465-T-3), Santiago River, Angostura Formation (Middle-Late Miocene).

Description – The dental measurements are from h 2.1–2.4 mm. The teeth are meso-distally elongated, convex and oblique labially; the occlusal surface is divided by a transverse keel ornamented with small alveoli; the labial occlusal surface is ornamented with irregular and reticular crests; and the lingual occlusal surface is

smooth, trapezoidal and has a shallow medial depression. The transverse keel in PPP-3465-T-2 is irregular and exhibits two deep channels continuous to the lingual surface. PPP-3465-T-3 is the tooth of a male, characterized by a high crown with a conspicuous cusp distally inclined; the lingual surface has a deep concavity below the umbo. All specimens have a wide, bilobed root with a basal surface that is slightly flat.

Remarks – The Dasyatidae has a fossil record spanning the Lower Cretaceous to Recent. Extant taxa are distributed in more than 10 genera and subgenera. Since the studies about their limited tooth teeth are *Myliobatis* sp., it is difficult to identify the numerous fossil species (Cappetta, 2012). Isolated teeth with a “dasyatid-design” have simply been referred to the genus *Dasyatis*, but with better knowledge of the Recent, it will alter the generic status of most taxa (Cappetta, 2012). Due the close dental morphology between genera, the poor knowledge about dental patterns in both extant and fossil species, and by the few fossil specimens that have been identified, for the time we prefer to maintain these specimens in open nomenclature.

Myliobatidae Bonaparte, 1838

Myliobatis Cuvier, 1816

(Fig. 5J, K)

Material – One fragment of a central tooth (PPP-3563-T-6) from Punta Ballena, Jama, Jama Formation (Early Pleistocene).

Description – Tooth measurements are l 14.0 mm, w 5.0 mm. The tooth is broader than long, rectilinear, has a hexagonal contour and

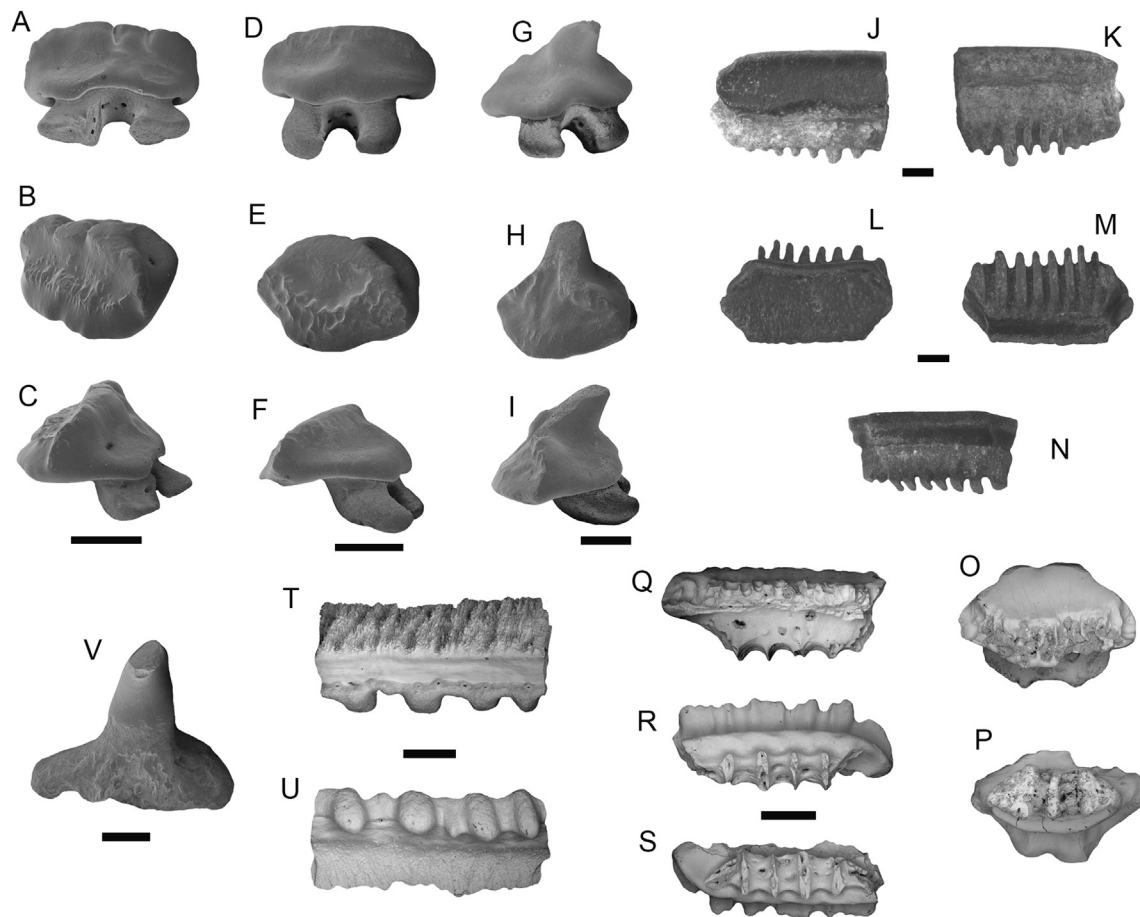


Fig. 5. A–I Dasyatidae Indet. [PPP-3465-T-2 (A–C), PPP-3434-T-1 (D–F) and PPP-3465-T-3 (G–I)]; J, K *Myliobatis* sp. (PPP-3563-T-6), L–N *Rhinoptera* sp. (PPP-3563-T-1). O, P *Mobula* sp. (PPP-3455-T-5); Q–U cf. *Mobula*. (PPP-3455-T-6, PPP-3455-T-4); V Batomorphii indet. (PPP-3493-T-1). A, D, G, J, Q lingual view; B, E, H, K, N, R labial view; C, F, I lateral; L, O, T, occlusal view; P, S, U, M basal view. Scale bar 1 mm.

recurved distally. The crown is rather high and smooth; the labial and lingual faces are slightly ornamented. The occlusal surface is smooth and slightly convex. The root exhibits numerous and alternatively parallel laminae with small foramina.

Remarks – *Myliobatis* has a fossil record spanning the Paleocene to the Recent (Cappetta, 2012). The dentition of *Myliobatis* is very close to the dentition of *Pteromylaeus*, but there are some differences in the latter, especially in the lower teeth and the labial and lingual faces of the crown, which are strongly ornamented in *Pteromylaeus* (see Cappetta, 2012). The identification of fossil species in *Myliobatis* with isolated teeth is extremely difficult due to the wide dental variation within the group (Welton and Zinsmeister, 1980; Nishida, 1990); for this reason a specific assignment is not possible, and we refer the specimen to *Myliobatis* sp. *Myliobatis* has a large fossil record in the Neogene of the Americas (Table 2).

Rhinopteridae Jordan and Evermann, 1896

Rhinoptera Cuvier, 1829

Rhinoptera sp.

(Fig. 5L–N)

Material – Two central teeth and one lateral tooth (PPP-3563-T-1) from Punta Ballena, Jama, Jama Formation (Early Pleistocene).

Description – Tooth measurements range: l 11.2–14.4 mm, w 4.6–4.8 mm. The crown is high, hexagonal in shape, and straight to slightly convex labially. The occlusal surface is flat, and the lingual face shows a thick fold in the crown base. The root exhibits numerous and alternatively parallel laminae with small foramina.

Remarks – As in *Myliobatis*, the taxonomic identification in isolated teeth of *Rhinoptera* is extremely difficult due to the wide dental variation present within the group (Nishida, 1990). The fossil record of *Rhinoptera* extends from Paleocene to Recent (Cappetta, 2012), and its records in the Neogene of the Americas include a wide distribution (Table 2).

Mobulidae Gill, 1893

Mobula Rafinesque, 1810

Mobula sp.

(Fig. 5O, P)

Material – One tooth (PPP-3455-T-5) from Playa de Oro, Santiago River, Angostura Formation (Middle-Late Miocene).

Description – The specimen is 2 mm wide, the crown is trapezoidal with the occlusal surface smooth; the labial edge ornamentation is characterized by a rough, irregular edge making it look worn and bifid with their projections. The root looks to be of the polyaulacorhize triangular type with only three lobes.

Remarks – *Mobula* has a fossil record spanning the Oligocene to Recent (Cicimurri and Knight, 2009; Cappetta, 2012), and its dental morphology is varied, with marked sexual dimorphism (Adnet et al., 2012). The specimen PPP-3455-T-5 has a morphology similar to a female lower tooth of *Mobula munkiana* Notarbartolo Di Sciara, 1987, as illustrated by Adnet et al. (2012). This species inhabits the Eastern Pacific, from California down to Ecuador (Michael, 1993). However, the scarce number of fossil specimens and the limited reference material for comparison make it difficult to arrive at specific taxonomic determinations, so we refer this specimen at the generic level only. The fossil record of *Mobula* from the Neogene of Tropical America and the Caribbean includes: *M. munkiana*, *M. thurstoni* Lloyd, 1908, and *M. hypostoma* Bancroft, 1831, from the Late Miocene of Panama (Pimiento et al., 2013b), *Mobula* cf. *hypostoma* and *M. lorenzolanoi* Laurito, 1999, from the Late Miocene-Early Pliocene of Costa Rica (Laurito, 1999), and *Mobula* sp. from the Caribbean and North America (Table 2).

cf. *Mobula*.

(Fig. 5Q–U)

Material – Four teeth of indeterminate position from Playa de Oro (PPP-3455-T-3, PPP-3455-T-4, PP-3455-T-6), Santiago River,

Angostura Formation (Middle-Late Miocene), and Camarones River (PPP-3493-T-7), Onzole Formation (Late Miocene).

Description – With a width of less than 4 mm, specimens PPP-3455-T-3 and T-3455-T-4 are similar, however, they are partially broken, with PPP-3455-T-4 being the most complete. PPP-3455-T-4 has a high crown, and is slightly rectangular with a smooth and concave occlusal section; the labial edge is concave with a marked ornamentation characterized by small cavities; and the lingual edge is convex with successive undulations that give it an irregular appearance. The root is not preserved but apparently was polyaulacorhize with at least five lamellae or lobes. PPP-3455-T-6 and PPP-3493-T-7 are similar, with a width that does not exceed 4 mm in PPP-3455-T-6 and 6.5 mm in PPP-3493-T-7, however, both teeth are broken at their ends. The crowns have a certain inclination with respect to the tangent of the root, giving this a rectangular appearance with a smooth labial edge and an irregular lingual edge. The roots of specimens PPP-3455-T-6 and PPP-3493-T-7 are polyaulacorhize, consisting of several elongated lobes, and the lingual section displays a marked heterogeneity in size; there are no foramina in the basal face of the root, but they are in the lingual canal that connects the lobes with the basal part of the crown.

Remarks – The knowledge of fossil Mobulidae is based solely on isolated teeth. Given that these are rare in marine deposits due to their delicate and fragile condition and reduced enameloid layer they are seldom preserved (Adnet et al., 2012). The knowledge about dental patterns in extant and fossil Mobulidae is scarce (Cappetta, 2012; Adnet et al., 2012), which makes taxonomic assignment of fossil specimens difficult. In the specimens referred here we did not find morphological patterns related to the extant and fossil species referred by Cappetta (2012), and Adnet et al. (2012); but this could be a result of the poor knowledge and studies about dental patterns of extant and fossil Mobulidae. With a limited number of specimens that are in a fragmentary state, we have decided to identify these as cf. *Mobula*.

Batomorphii Indet.

(Fig. 5V)

Material – One spine (PPP-3406-T-2) from Telembí, Cayapas River, Angostura Formation (Late Miocene).

Description – Dermal spine is 2 mm tall; the basal section is circular and flattened; there is a projection ending in an acute tip.

Remarks – An isolated dermal spine cannot be used for accurate identification.

5. Discussion

5.1. Taxonomic composition and paleobiogeography

Neogene sharks from Ecuador have been restricted to dozens of shark teeth identified by Longbottom (1979) from the Late Miocene of the lower Onzole Formation. In addition, Aguilera et al. (2011) provided a preliminary list which is revised here. Longbottom (1979) illustrated 11 taxa that are currently taxonomically valid, except for †*Procarcharodon megalodon* Agassiz, 1843 [=†*Otodus* (*Megaselachus*)], †*Scoliodon taxandriae* (=†*R. taxandriae*), and †*Odontaspis acutissima* Agassiz, 1843 (=†*Carcharias acutissima*) (see Cappetta, 2012). Of the taxa referred by Longbottom (1979), †*R. taxandriae*, †*I. cf. triangulus* and *Myliobatis* sp., have been identified by the authors in this work, while †*C. landinii* sp. nov., *Centrophorus* sp., *Pristiophorus* sp., *Squatina* sp., *Ginglymostoma* sp., *Paragaleus* sp., *R. longurio*, *Carcharhinus* cf. *brachyurus*, *C. albimarginatus*, *C. obscurus*, *C. aff. porosus*, *N. brevisrostris*, *S. media*, *Rhinoptera* sp., *Dasyatidae*, *Mobula* sp., and cf. *Mobula* correspond to new records from the Neogene of Ecuador. Longbottom (1979) referred 51 (mostly broken) teeth to *Carcharhinus egyptoni*. These specimens represent at least two different dental morphological patterns,

most likely representing *C. leucas* and *C. obscurus*. However, it is difficult to make an accurate determination based on the original images. It would be important to review these teeth, because *C. egertoni* has been referred to as a waste basket-taxon, with several similar species of *Carcharhinus* being lumped together (Marsili, 2007).

The chondrichthyan assemblages from Ecuador (Table 1) are characterized by a paleodiversity of 30 taxa; the Angostura Formation (15 taxa) and the Onzole Formation (18 taxa) being the most diverse. The fauna of the Onzole Formation includes the species referred by Longbottom (1979). The chondrichthyan diversity known from the other formations, including Canoa and Jama, is less, possibly as a result of the sampling methods and the few systematic works undertaken in these geological units. Within the chondrichthyan assemblages referred to here (Table 1), 10 species are now extinct, and the remaining taxa are representative of extant species with wide biogeographic distributions (see Compagno, 1984a, b; 2005; Compagno et al., 2005; Voigt and Weber, 2011; Cappetta, 2012). With the exception of the extinct species, and the extant taxa such as *Centrophorus*, *Pristiophorus*, *Paragaleus* and *C. obscurus*, the remainder of the fossil taxa are still common inhabitants of the Eastern Pacific, especially in the tropical zone (Compagno, 1984a, b; 2005; Compagno et al., 2005; Voigt and Weber, 2011). *Centrophorus*, *Pristiophorus* and *Paragaleus* are not inhabitants of the Eastern Pacific (See Compagno, 2005); but records of *Paragaleus* from Ecuador, *Centrophorus* from Ecuador and Mexico (González-Barba and Thies, 2000), and *Pristiophorus* from Ecuador, Chile and Peru (De Muizon and Devries, 1985; Arratia and Cione, 1996; Kindlimann, 1990; Suárez and Marquardt, 2003; Carrillo-Briceño et al., 2013), are a clear indication that these taxa were inhabitants of the Eastern Pacific before becoming regionally extirpated. The presence of *Pristiophorus* (Bahamas-Western Central Atlantic) and *Centrophorus* in the Western Atlantic (Compagno, 1984a; Compagno et al., 2005) and their disappearance from the Pacific coast of the Americas is possibly a consequence of environmental changes during the final stages of the closure of the Panamanian isthmus (Schneider and Schmittner, 2006; O'Dea et al., 2007; Aguilera et al., 2011). This changed the patterns of circulation of the ocean currents, affected physical and chemical water mass conditions and resulted in the formation of the Caribbean Sea. It also had a direct influence over the Neogene American marine communities, with faunal changes that were characterized by local extinction during the Miocene/Pliocene (see Coates and Obando, 1996; Schneider and Schmittner, 2006; O'Dea et al., 2007; Aguilera et al., 2011).

5.2. Paleoenvironmental inferences

The chondrichthyan fauna of the Angostura Formation was collected at five localities (Fig. 1). The presence of *C. obscurus* and *N. brevirostris* at the Flavio Alfaro road locality is an indication of a neritic paleoenvironment, because these taxa are common inhabitants of this environment today (Compagno, 1984a, b; Compagno et al., 2005; Voigt and Weber, 2011). *Carcharhinus* aff. *porosus* from the Telembí locality (Cayapas River), suggests a shallow water paleoenvironment, because extant individuals can be found down to a maximum of 40 m of depth (Voigt and Weber, 2011). The extant species of *Centrophorus* has a depth range from 20 m up to more than 400 m. However, the presence of *R. longurio* could indicate shallow water paleoenvironments, because extant individuals are typically coastal, inhabiting waters with depths not exceeding 27 m (Compagno, 1984b; Compagno et al., 2005).

†*Chlamydoselachus landinii* sp. nov., together with *Ginglymostoma* sp., *Centrophorus* sp., *R. longurio*, *C. brachyurus*, *Carcharhinus* sp., and *Mobula* sp., were found at the Santiago River localities

(Fig. 1). The presence of †*C. landinii* sp. nov. suggests deep waters, because extant species are only known from this region, over soft bottoms between 120 and 1.450 m deep (Shiobara et al., 1987; Ebert and Compagno, 2009). However, †*C. landinii* sp. nov., has been found at the same locality, Playa de Oro (Santiago River), as *R. longurio* and *Ginglymostoma* sp., which are typical inhabitants of shallow waters, not exceeding 100 m deep (see Compagno et al., 2005). In zones such as the Suruga Bay (Japan) where the sea bottom profile is steep and bathyal depths are found within short distances from the coast, the presence of deep water chondrichthyans is common (Kubota et al., 1991). In this bay, abundant specimens of the extant *C. anguineus* were captured during the night, at depths between 51 and 60 m, thus demonstrating the great vertical wandering of this bathy-benthic to mesopelagic species (Kubota et al., 1991). Cantalamessa et al. (2007) suggested that the Angostura Formation represents a shore-face and inner-shelf environment, based on *Glossifungites* and *Skolithos* ichnofacies and invertebrates. The presence of †*C. landinii* sp. nov., and *Centrophorus* sp., may indicate an upper bathyal paleoenvironment (upper slope to outer continental shelf) within a short distance of the coast.

The chondrichthyan assemblage from the Onzole Formation (Table 1) was collected in the lower portion of this formation, which is the same section from which the shark teeth collected by Longbottom (1979) were recovered. The Late Miocene fauna and sedimentary evidence found in the lower Onzole Formation suggest a shallow water paleoenvironment (Carnevale et al., 2011). Extinct taxa such as †*Megaselachus megalodon*, †*Hemipristis serra*, †*Negaprion eurybathrodon* (= *N. brevirostris*) and †*Carcharias acutissima* identified by Longbottom (1979) have been referred to Neogene sediments associated with the neritic zone (Cappetta, 2012; Pimiento et al., 2013b). The extant *C. albimarginatus* is a coastal-pelagic shark reported from inshore and offshore waters (Voigt and Weber, 2011), and *S. media* is a typical inhabitant of inshore waters (Compagno, 1984b). The presence of †*Isistius* cf. *triangulus*, *Centrophorus* sp., and *Pristiophorus* sp. may indicate an upper bathyal paleoenvironment with a short distance from the coast, which allows for the vertical wandering of these bathy-benthic species to shallower waters.

The presence of *R. longurio*, *Carcharhinus* cf. *brachyurus* and *S. media* in the Canoa Formation (Punta Canoa) may suggest a shallow paleoenvironment (see Compagno, 1984b; Compagno et al., 2005; Voigt and Weber, 2011). Previous studies suggest that the Canoa Formation was deposited in shore-face to mid-shelf depositional environments (Landini et al., 2002a; Di Celma et al., 2005). The abundance of fish otoliths in this geologic unit, representing 105 taxa (see Landini et al., 2002a, b), contrasting with the scarce records of chondrichthyans, could be the result of sampling biases. The chondrichthyan assemblage from the Jama Formation could suggest neritic waters paleoenvironments, considering taxa such as *C. obscurus*, *Paragaleus*, *Myliobatis* and *Rhinoptera* are common inhabitants of this zone (Compagno, 1984b, 2005; Cappetta, 2012; Pimiento et al., 2013b).

Conclusion

The Angostura and Onzole formations are characterized by shallow-deep water chondrichthyan assemblages, which may suggest a paleoenvironment of a short platform shelf bordered by a deep margin, at least between the Middle Miocene-Early Pliocene. Chondrichthyan taxa from the Canoa and Jama formations are scarce. However, some of the taxa could suggest paleoenvironments related with neritic waters, because extant taxa that are represented in the fossil sample are common inhabitants of these environments. These chondrichthyan assemblages

reported here, with a total of 30 taxa, are some of the most diverse shark and ray associations known from Tropical America and the Western Pacific. Their taxonomic composition shows a great deal of commonality with other marine assemblages from the Eastern Pacific and proto-Caribbean regions during the late Miocene, possibly as a result of the fauna interchange allowed by the Central America Seaway before the definitive closure of the Panamanian isthmus.

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