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A new Late Miocene chondrichthyan assemblage from the Chagres Formation, Panama

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ABSTRACT

The lLate Miocene Chagres Formation from northern Panama contains the youngest outcrops of the Panama Canal Basin. Here we report two chondrichthyan assemblages that include 30 taxa from both the Rio Indio and Chagres Sandstone Members of the Chagres Formation. We report 18 new fossil records for Panama and four for tropical America, constituting the most diverse chondrichthyan association for the Cenozoic of Panama. We performed a paleobathymetry analysis based on the modern water depth preference of extant chondrichthyan taxa. The assemblage from the Rio Indio Member is characterized by taxa with neritic affinities, suggesting depths <100 m, whereas the assemblage from the Chagres Sandstone Member is dominated by taxa with oceanic affinities, suggesting 200–300 m water depths. The Chagres Sandstone Member could have accumulated at the edge of a platform–upper slope, bordered by a deep oceanic margin.

1. Introduction

Panamanian sedimentary basins preserve an extensive Neogene fossil record of marine biota useful for understanding the evolution of the Isthmus of Panama. The isthmus was formed by complex tectonic processes that isolated the Atlantic from the Pacific Ocean and connected North and South America, precipitating major biogeographic, oceanographic, and environmental changes (Coates and Obando, 1996; Woodburne, 2010; Coates and Stallard, 2013; Leigh et al., 2013). The formation of the Isthmus of Panama was completed during the Pliocene, between 4.2 and 3.5 Ma (Duque-Caro, 1990; Coates et al., 1992, 2003, 2004; Coates and Obando, 1996; Haug and Tiedemann, 1998; Bartoli et al., 2005; Woodburne, 2010; Haug et al., 2001; Coates and Stallard, 2013). Additional geological evidence suggests that the rise of the isthmus was considerably older and more complex, with an initial collision between South America and the Panama Block between 25 and 23 Ma (Farris et al., 2011; Montes et al., 2012a, 2012b). By 20 Ma, Panama would have been a peninsula connected to North America (MacFadden et al., 2010; Montes et al., 2012a; Rincon et al., 2012), with an oceanic pathway between Panama and South America, the Central American Seaway (CAS, defined here as the deep oceanic seaway along the tectonic boundary of the South American plate and the Panama microplate), connecting the Pacific and Atlantic Oceans (Montes et al., 2012a, 2012b). By 10 Ma, a full closure of CAS had occurred, ending the exchange of deep and intermediate waters between the Caribbean and the Pacific (Coates et al., 2004; Montes et al., 2012a; Sepulchre et al., 2014). However, shallow-water exchange continued between the two oceans along pathways other than CAS, allowing the migration of chondrichthyans between basins (Pimiento et al., 2013b), until the complete rise of the Isthmus at 3.5 Ma (Duque-Caro, 1990; Haug and Tiedemann, 1998; Haug et al., 2001; Coates et al., 1992, 2003, 2004; Coates and Stallard, 2013). Ultimately, the formation of the Isthmus of

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Panama affected tropical American marine communities and increased the biogeographic complexity of the region (e.g., Woodring, 1957, 1966, 1974; Coates and Obando, 1996; Schneider and Schmittner, 2006; O'Dea et al., 2007; Aguilera et al., 2011; Leigh et al., 2013).

Previous studies of the Neogene chondrichthyans from Panama include Blake (1862), Gillette (1984), Aguilera et al. (2011) and Pimiento et al. (2010, 2013a, 2013b). Gillette (1984) described 14 chondrichthyan taxa from the middle-Late Miocene Gatun Formation (Gillette, 1984). Most recently, Pimiento et al. (2010, 2013b) updated the fossil record of the chondrichthyan fauna from the same formation; evaluated its diversity, paleobiogeography, paleoenvironment, and paleoecology; and proposed that this area served as a nursery habitat for *Carcharocles megalodon*. The list of Neogene tropical American fish taxa provided by Aguilera et al. (2011) included 19 chondrichthyan taxa from the Neogene of Panama. Pimiento et al. (2013a) described the chondrichthyan fauna from the early Miocene Culebra Formation and studied their paleoenvironmental setting and paleobiogeography. These studies are important because they provide insight into the marine vertebrates, prior to and during the rise of the Isthmus of Panama. However, they have been restricted to the Early and Middle-Late Miocene of Panama and as a result, very little is known about the younger chondrichthyan assemblages of the isthmus.

Based on the collection of 513 specimens, here we report two new chondrichthyan assemblages from the youngest deposits of the Panama Canal Basin, the Late Miocene Chagres Formation. We studied the taxonomic composition of these assemblages and analyzed their bathymetric affinities. We found that, in contrast to previously described faunas from Panama, which are mostly neritic (e.g., Pimiento et al., 2010, 2013a, 2013b), the Chagres chondrichthyan assemblages are characterized by a mixture of faunas from a heterogeneous environmental setting and mixed taxonomic similarities, relative to other associations from Tropical America. Herein we present a comprehensive interpretation of the paleoenvironments of the Late Miocene chondrichthyan assemblages of the Chagres Formation and provide a more complete view of the ancient biodiversity of Panama.

2. Methods

The fossil materials presented here were collected from the Rio Indio and Chagres Sandstone members (Figs. 1–3). The specimens were collected by the Smithsonian Tropical Research Institute of Panama (STRI), during 21 field trips from March 2009 to September 2013. Collection methods included surface prospecting and screen-washing of bulk samples. The screen-washed material was obtained by washing 69.3 kg of sediments, using standard sieves of 2.0 mm and 0.5 mm mesh. Chondrichthyan teeth and bony fish

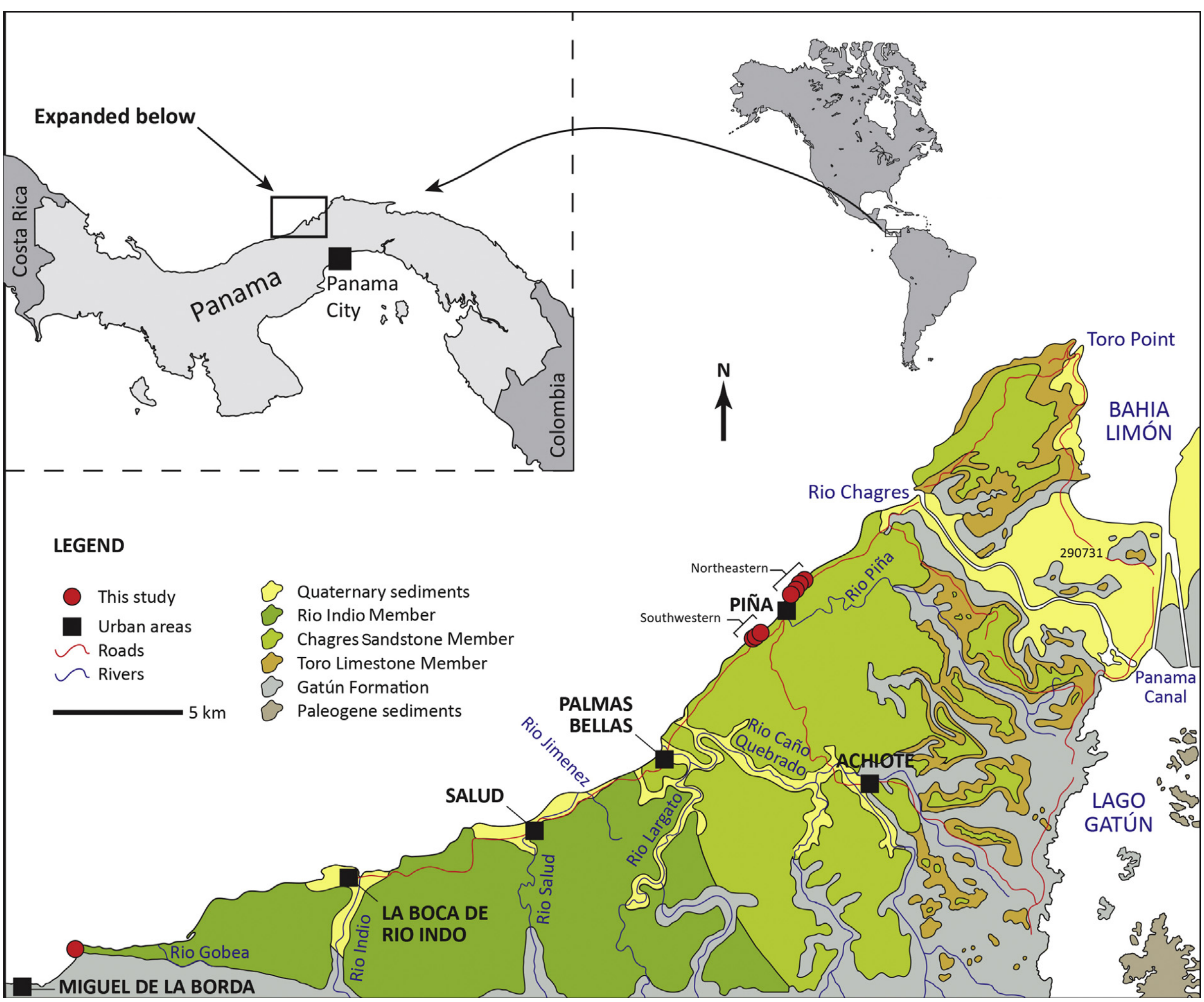

Fig. 1. Location, stratigraphic and geological setting of Rio Indio and Chagres Sandstone localities in Costa Abajo Colon, Panama (Modified from Collins et al. (1996)).

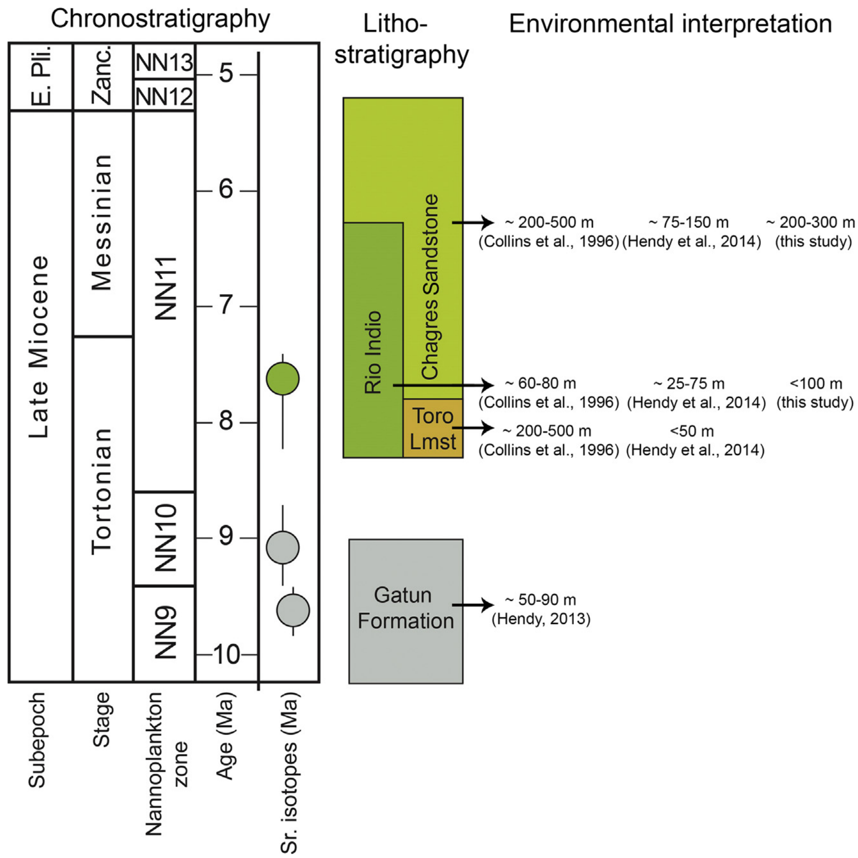

Fig. 2. Lithostratigraphy, age, and paleobathymetry of the Chagres Formation (Modified from Collins et al. (1996) and Hendy et al. (in press).

otoliths were picked from the sample by using a magnifier glass for the 2.0 mm matrix, and a stereoscope for the 0.5 mm matrix. Photographs were made with a Leica MZ16F multifocal stereomicroscope and Scanning Electronic Microscope (SEM) for small teeth. The stratigraphic column for the Chagres sandstone was modified from Coates (1999). A new stratigraphic column for the Rio Indio locality in Punta Mansueto was made from the beach level to the top of the cliff (Fig. 3). During the latter process, sediment and invertebrate samples (mainly mollusks) were collected.

We identified all fossil chondrichthyan teeth to the lowest taxonomic level possible. This material is deposited at the Palaeontological Institute and Museum at the University of Zurich, Switzerland (PIMUZ A/I catalogue). The classifications follow Compagno (1973, 1977) and the terminology is based on Cappetta (2012). Taxonomic identification included an extensive bibliographic review (Antunes and Jonet, 1970; Cappetta, 1970, 2012; Ledoux, 1970; Case, 1980; Gillette, 1984; Herman et al., 1988, 1989, 1991, 2004, 2005; Kent, 1999; Laurito, 1996, 1999; Purdy et al., 2001; Aguilera and Rodriguez de Aguilera, 2001, 2010; Marsili, 2007; Pimiento et al., 2010, 2013a, 2013b; Reinecke et al., 2011; Voigt and Weber, 2011; Bor et al., 2012; Cione et al., 2012; Carrillo-Briceño et al., 2014) and comparative studies with fossil and extant specimens from the following collections: Departamento Nacional de Pesquisas Minerais (DNPM), Brazil; Museo Nacional de Historia Natural de Santiago (SGO-PV), Chile; Museu Paraense Emilio Goeldi (MPEG-V), Brazil; Natural History Museum of Basel (NMB), Switzerland; Paleontological collections of the Alcaldía de Urumaco (AMU-CURS), Venezuela; Palaeontological Institute and Museum at the University of Zurich (PIMUZ), Switzerland; René Kindlimann (private collection, Switzerland); Sección de Geología, Departamento de Historia Natural, Museo Nacional de Costa Rica (CFM), Costa Rica; Smithsonian Tropical Research Institute (STRI-PPP-T), Panama; Universidad Nacional Experimental Francisco de Miranda (UNEFM-PF), Venezuela; Vertebrate Paleontology collection of the Florida Museum of Natural History (FLNMH), USA; Department of Paleobiology, Smithsonian National Museum of Natural History (USNM), USA.

We collated the bathymetric range and habitat of all taxa with living representatives (Table 1) using Compagno (1984a, b), Compagno et al. (2005), Musick et al. (2004), Kiraly et al. (2003), Voigt and Weber (2011), and the FishBase website (http://www.fishbase.org). In addition, we gathered information on the biogeographic distribution of chondrichthyans during the Late Miocene–Early Pliocene of Tropical America (Table 2) (e.g., Leriche, 1938; Casier, 1958; Longbottom, 1979; Gillette, 1984; De Muizon and DeVries, 1985; Kindlimann, 1990; Kruckow and Thies, 1990; Long, 1993a; Iturralde-Vinent et al., 1996; Laurito, 1999, 2004; Donovan and Gunter, 2001; Apolín et al., 2004; Underwood and Simon, 2004; Alván, 2007; Laurito and Valerio, 2008; Portell et al., 2008; Aguilera and Lundberg, 2010; Aguilera et al., 2011; Pimiento et al., 2010, 2013a, 2013b; Carrillo-Briceño et al., 2014), Southern South America (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) and North America (Case, 1980; Kruckow and Thies, 1990; Müller, 1999; Long, 1993b; Gonzales and Thies, 2000; Purdy et al., 2001; Boessenecker, 2011; Hulbert, 2001).

We carried out an analysis of abundance using percentages of specimens by order and species. In addition, we performed a paleobathymetric analysis following the methodology of Nolf and Brzobohaty (1996). For this analysis we included only species/genera with living counterparts, using the number of taxa per

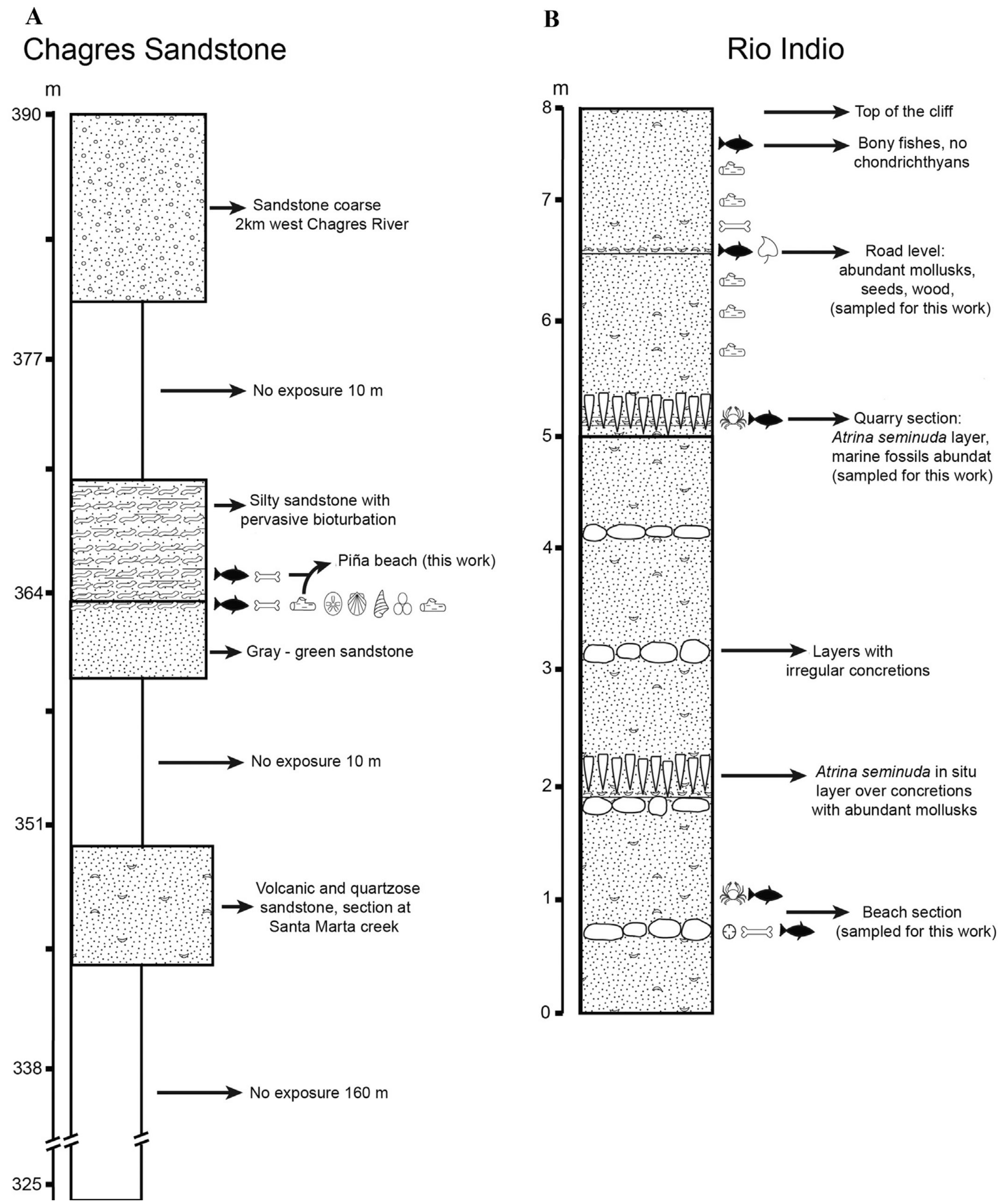

Fig. 3. Stratigraphic column of two studied localities from Chagres Formation. **A** Chagres Sandstone Member, Piña beach (modified of Coates (1999)). **B** Rio Indio Member, Punta Mansueto locality.

depth interval. The bathymetric range for fossil shark taxa was inferred from the results of this analysis. We also applied a "leaf one out" jackknife analysis using R (R Development Core Team, 2012). This is resampling technique useful to estimate variance and bias of our bathymetric estimations. The analysis resamples the dataset systematically leaving out each observation at a time, then it calculates the parameter (e.g. bathymetry) for each resampling. The jacknife then finds the average of these calculations (Miller, 1974).

In this work we use the term "Tropical America" (Neotropics) to refer to 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, including Argentina, Chile, Paraguay and Uruguay, and "North America" includes Canada, the USA, and the northern part of Mexico (north of the Tropic of Cancer).

3. Geological setting

The Chagres Formation (Macdonald, 1915) crops out in the northern region of Panama (Fig. 1). It is ~250 m thick and disconformably overlaps the Gatun Formation (Coates, 1999). It is Late Miocene in age, extending from ~8.3 to 5.3 Ma (Figs. 1–2) (Collins et al., 1996; Coates, 1999; Hendy, 2013; Hendy et al., in press), and consists of three members: Toro, Rio, Indio and Chagres Sandstone.

The Toro Member (base of the Chagres Formation) is exposed between Toro Point and Naranjitos Point (Fig. 1). It presents a well-

Table 1
Chondrichthyans found in this study. Localities: Chagres Sandstone Member (1); Rio Indio Member (2). Abbreviations: Mn (minimum); Mx (maximum). Bathymetrical ranges: Neritic/Epipelagic (0–200 m); Bathyal/Meso-Bathypelagic (200–2000 m).* Indicates that maximal depth range is that of the family.

Taxonomy					Number of specimens			Habitat of living representatives								Iconography
Superorder	Order	Family	Taxon	Taxon number	Piña locality	Punta Mansueto loc.	Total number	Benthic	Bentopelagic	Pelagic	Neritic/ Epipelagic	Bathyal/ Meso-bathypelagic	Bathymetry depth (in meters)		Comments	
													Mn	Mx		
Squalomorphii	Hexanchiformes	Heptranchidae	*Heptranchias perlo* (Bonnaterre, 1788)	1	4	0	4		X			X	0	1000	Usually 180–450 m	3 A, B
	Squaliformes	Squalidae	*Squalus* sp.	2	44	0	44		X	X	X	X	0	1500	Usually less than 80 m	3 C, D
		Centrophoridae	*Centrophorus* aff. *granulosus* (Bloch and Scheinder, 1801)	3	11	0	11		X			X	50	1440	Usually 200–600 m	3 E, F
		Etmopteridae	*Trigonognathus* sp.	4	1	0	1		X			X	270	360	Usually less than 300 m	3 G, H,I
		Dalatiidae	*Dalatias licha* (Bonnaterre, 1788)	5	15	0	15		X			X	37	1800	Usually 200–1800 m	3 J, K
			Isistius sp.	6	272	0	272			X	X	X	0	3700	Usually 0–1000 m	3 L, M
	Pristiophoriformes	Pristiophoridae	*Pristiophorus* sp.	7	38	0	38		X		X	X	0	1000	Usually less than 30 m	3 N
	Squatiniformes	Squatinidae	*Squatina* sp.	8	13	0	13	X			X	X	10	1400		3 O
Galeomorphii	Heterodontiformes	Heterodontidae	*Heterodontus* sp.	9	1	0	1	X			X		0	280		3 P, Q
	Lamniformes	Odontaspididae	*Carcharias* sp.	10	0	1	1		X	X	X		0	191		3 R, S
		Pseudocarchariidae	*Pseudocarcharias* cf. *kamoharai* (Matsubara, 1936)	11	3	0	3			X	X	X	0	590	Usually 0–200 m	4 A, B
		Lamnidae	†*Carcharodon plicatilis* (Agassiz, 1843)	12	1	1	2		?	X	X	?	0*	1300*		4 C
		Otodontidae	†*Carcharocles megalodon* (Agassiz, 1843)	13	2	1	3		?	X	X	?	0	200?		4 D
		Alopiidae	*Alopias superciliosus* (Lowe, 1841)	14	4	0	4			X	X	X	0	730	Usually 0–100 m	4 E, F
	Carcharhiniformes	Scyliorhinidae	†*Premontreia* sp.	15	1	0	1	X	?		?	?	0*	>2000*		4 G,H
		Triakidae	*Galeorhinus* cf. *galeus* (Linnaeus, 1758)	16	5	0	5		X		X	X	0	1100	Usually 2–400 m	4 I,J
			Mustelus sp.	17	2	0	2		X		X	X	0	900		4 K, L
		Hemigaleidae	†*Hemipristis serra* (Agassiz, 1835)	18	8	7	15		X	?	X		0	130	Data from the living species	4 M, N
		Carcharhinidae	*Galeocerdo cuvier* (Péron and Lesueur, 1822)	19	1	2	3		X		X		0	371	Usually less than 150 m	4 O, P
			Rhizoprionodon sp.	20	1	0	1		X		X		1	500	Usually less than 100 m	4 Q, R
			Carcharhinus brachyurus (Günther, 1870)	21	7	0	7		X		X		0	360	Usually less tan 100 m	4 S, T
			†*Carcharhinus* cf. *cionei* (Laurito, 1999)	22	5	0	5		?	X	X		0	?		5 A, B, C, D

			Carcharhinus leucas (Valenciennes, 1839)	23	0	3	3		X		X		0	152	Usually 0–30 m	5 E, F
			Carcharhinus obscurus (LeSueur, 1818)	24	3	4	7		X		X	X	0	400	usually 25–200 m	5 G, H
			Carcharhinus plumbeus (Nardo, 1827)	25	13	0	13		X		X		0	280	usually 20–65 m	5 I, J
			Carcharhinus signatus (Poey, 1868)	26	3	0	3		X		X	X	0	600	Usually 50–100 m	5 K, L
			Carcharhinus spp.	27	24	0	24		?	?	?		0	?		5 M, N
			Negaprion brevirostris (Poey, 1868)	28	0	2	2		X		X		0	92		5 O, P
		Sphyrnidae	*Sphyrna* cf. *lewini* (Griffith and Smith, 1834)	29	1	0	1		X		X		0	512	Usually 0–25 m	5 Q, R, S
Batomorphii	Myliobatiformes	Myliobatidae	*Myliobatis* sp.	30	6	0	6	X	X		X	X	0	>300		5 S, T, U
Batomorphii indet.				31	1	1	2	X	X		?	?	0	?		5 V

developed echinoid-mollusk-barnacle coquina (~60 m thick) and an association of bathyal benthic foraminifera. Consequently, this unit has been interpreted as a high-energy deposit with a strong Pacific affinity and an upper bathyal depth range (~200–500 m, Collins et al., 1996). However, the presence of some mollusks of the genus *Anadara* and abundant barnacles fragments could indicate a shallow-water depositional environment (Woodring, 1973).

The Rio Indio Member (Fig. 1), which laterally replaces the Toro Member to the west, has an age of ~7.64 Ma (Hendy et al. in press). This member consists of fine silty-sandstone deposited in waters of ~50–80 m depth (Collins et al., 1996). New outcrops of this member, exposed in 2008 during Miguel de la Borda road construction, were studied here. They are located on the coast of Punta Mansueto, Donoso District, Colon Province (9° 9′ 23.4″ N, 80° 17′ 36.6″ W, Fig. 1).

The Chagres Sandstone is the youngest member (~7.9–5.3 Ma). It overlaps the Toro Member and it is exposed from the mouth of the Chagres River to the mouth of Rio Caño Quebrado (Figs. 1–2). The outcrop studied here is located on the coast near the town of Piña, Colon Province (9° 16′ 53.4″ N, 80° 2′ 40.9″ W, Fig. 1). It consists of gray volcanic quartzose grains and silty-sandstones, with scattered remains of mollusk, urchins, fishes, and cetaceans (Fierstine, 1978; Coates, 1999; Schwarzhans and Aguilera, 2013; Velez-Juarbe et al. in press) (Fig. 3).

4. Results

4.1. Taxonomic composition

The chondrichthyan assemblages from the Chagres Formation include at least 30 taxa attributed to 24 genera, 19 families and 8 orders (Table 1, Figs. 4–6). Of these taxa, five are extinct (†*Carcharodon plicatilis* (syn. *C. xiphodon*), †*Carcharocles megalodon*, †*Premontreia* sp., †*Hemipristis serra*, and †*Carcharhinus* cf. *cionei*), 18 were found to be new fossil records for Panama (*Heptranchias perlo*, *Squalus* sp., *Centrophorus* aff. *granulosus*, *Trigonognathus* sp., *Dalatias licha*, *Isistius* sp., *Pristiophorus* sp., *Squatina* sp., *Carcharias* sp., *Pseudocarcharias* cf. *kamoharai*, *C. plicatilis*, *Alopias superciliosus*, *Premontreia* sp., *Galeorhinus* cf. *galeus*, *Mustelus* sp., *Carcharhinus brachyurus*, *C.* cf. *cionei* and *Carcharhinus signatus*), and four are new records for Tropical America (*Centrophorus* aff. *granulosus*, *D. licha*, *Premontreia* sp., and *C. signatus*). Most of the chondrichthyan taxa from the Chagres Formation were also found in other Neogene marine deposits of the Americas (Table 2). Exceptions include *Carcharhinus* cf. *cionei*, which was thought to be restricted to Costa Rica (Laurito, 1999), and *Trigonognathus* sp. from the Late Miocene–Early Pliocene of Venezuela (Aguilera and Rodriguez de Aguilera, 2001), the latter closely related to the extant *Trigonognathus kabeyai*, restricted to the northwest Pacific and the Hawaiian Islands (Mochizuki and Ohe, 1990; Mundy, 2005). The rest of the fossil fauna from the Chagres Formation includes taxa with a cosmopolitan distribution (*C. plicatilis*, *C. megalodon*, *Premontreia* sp., and *Hemipristis serra*) (Cappetta, 2012) or a regional distribution throughout the Western Atlantic and Eastern Pacific during the Late Miocene (Table 2).

4.1.1. Rio Indio

Chondrichthyans from the Rio Indio Member are scarce (Table 1) and represent only the 4.3% (22 specimens) of the total Chagres Formation collection. They are dominated by the order Carcharhiniformes (81.84%) with a few representatives of Lamniformes (13.62%) and Myliobatiformes (4.54%) (Fig. 7). The carcharhiniforms are represented by the families Carcharhinidae (*Galeocerdo cuvier*, Fig. 5O–P; *Carcharhinus leucas*, Fig. 6E–F; *Carcharhinus obscurus* and *Negaprion brevirostris*, Fig. 6O–P) and Hemigaleidae (*Hemipristis*

Table 2
Late Miocene–Early Pliocene fossil record across the Americas of the Chondrichthyan taxa found in the Chagres Formation.*indicates presence of the genus; (?) doubtful record; ● first fossil record for Panama.

	Tropical America and the Caribbean															NA			SSA	
Taxon (Chagres Formation)	Barbados	Bonaire	Costa Rica	Cuba	Dominican Republic	Ecuador	Haiti	Jamaica	Martinique	Panama	Peru	Puerto Rico	Trinidad	The Grenadines	Venezuela	Southern Mexico	Northern Mexico	U.S.A	Argentina	Chile	Uruguay
● *Heptranchias perlo*			x*												x						
● *Squalus* sp.			x												x		x	x	x		x
● *Centrophorus* aff. *granulosus*						x*									x*		x*				
● *Trigonognathus* sp.															x*						
● *Dalatias licha*															x*						
● *Isistius* sp.			x			x									x		x	x			
● *Pristiophorus* sp.						x					x				x			x		x	
● *Squatina* sp.			x			x					x				x		x	x	x	x	
Heterodontus sp.			x							x	x				x		x	x	x	x	
● *Carcharias* sp.											x				x		x	x	x	x	x
● *Pseudocarcharias* cf. *kamoharai*															x						
● †*Carcharodon plicatilis*											x				x		x	x	x	x	x
†*Carcharocles megalodon*	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
● *Alopias superciliosus*			x												x			x			
● †*Premontreia* sp.																					
● *Galeorhinus* cf. *galeus*			x*												x*		x*	x		x	
● *Mustelus sp.*			x*												x		x	x			
†*Hemipristis serra*			x	x		x		x		x	x		x		x		x	x	x		
Galeocerdo cuvier										x					x		x	x			
Rhizoprionodon sp.			x			x*				x*							x	x*			
● *Carcharhinus brachyurus*						x					x				x			x		x	
● †*Carcharhinus* cf. *cionei*			x																		
Carcharhinus leucas										x	x						x	x			
Carcharhinus obscurus			x			x				x					x		x	x			
Carcharhinus plumbeus										x					x			x			
● *Carcharhinus signatus*																		?			
Carcharhinus spp.						x	x			x	x		x		x		x	x	x	x	x
Negaprion brevirostris			x*			x				x	x				x*		x	x			
Sphyrna cf. *lewini*										x	x	x					x	x			
Myliobatis sp.			x			x				x	x				x	x	x	x	x	x	x
Batomorphii indet.																					

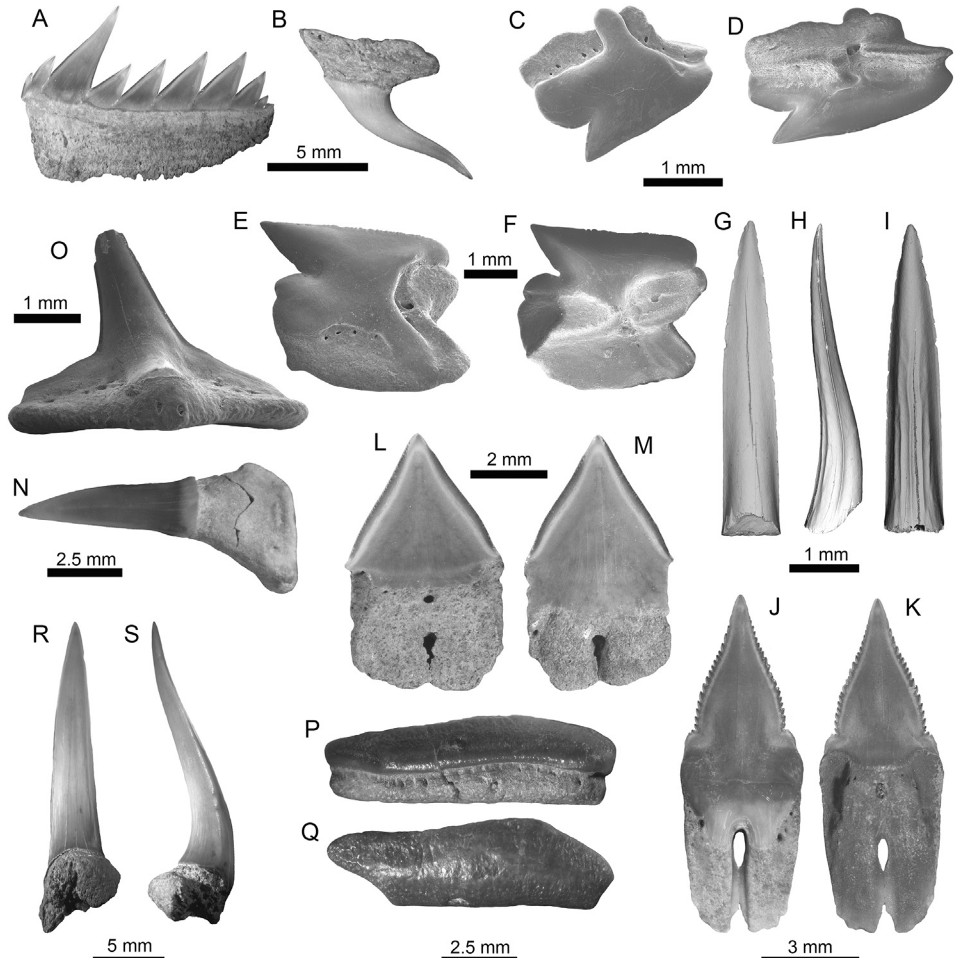

Fig. 4. **A**, **B** *Heptranchias perlo* (A: PIMUZ-A/I-4177, B: PIMUZ-A/I-4178). **C**, **D** *Squalus* sp. (C: PIMUZ-A/I-4187, D: PIMUZ-A/I-4192). **E**, **F** *Centrophorus* aff. *granulosus* (E: PIMUZ-A/I-4267, F: PIMUZ-A/I-4268). **G**, **H**, **I** *Trigonognathus* sp. (PIMUZ-A/I-4179). **J**, **K** *Dalatias licha* (PIMUZ-A/I-4263). **L**, **M** *Isistius* sp. (PIMUZ-A/I-4202). **N** *Pristiophorus* sp. (PIMUZ-A/I-4198). **O** *Squatina* sp. (PIMUZ-A/I-4185). **P**, **Q** *Heterodontus* sp. (PIMUZ-A/I-4198). **R**, **S** *Carcharias* sp. (PIMUZ-A/I-4186). View: labial (C, E, G, K, L, P), lingual (A, D, F, I, J, M, O, R), lateral (B, H, S), occlusal (Q), dorsal (N).

serra, Fig. 5M–N). The lamniforms are represented by the families Odontaspididae (*Carcharias* sp., Fig. 4R–S), Lamnidae (*C. plicatilis*), and Otodontidae (*C. megalodon*). Batoids are represented only by one isolated caudal spine (Batomorphii indet. Fig. 6V).

4.1.2. Chagres Sandstone

Chondrichthyans from Chagres Sandstone represent 95.7% (491 specimens) of the specimens from the Chagres Formation (Table 1), and are dominated by taxa from the Squaliformes order (69.9%, Fig. 7). This order is represented by several families including Squalidae (*Squalus* sp., Fig. 4C–D), Centrophoridae (*Centrophorus* aff. *granulosus*, Fig. 4E–F), Etmopteridae (*Trigonognathus* sp., Fig. 4G–I), and Dalatiidae (*Isistius* sp., Fig. 4L–M; *D. licha*, Fig. 4J–K). The order Pristiophoriformes (7.73%, Fig. 7) is represented by the family Pristiophoridae (*Pristiophorus* sp., Fig. 4N). The orders Hexanchiformes (Hexanchidae: *H. perlo*, Fig. 4A–B), Squatiniformes (Squatinidae: *Squatina* sp., Fig. 4O), Heterodontiformes (Heterodontidae: *Heterodontus* sp., Fig. 4P–Q), and Lamniformes (Alopiidae: *A. superciliosus*, Fig. 5E–F; Lamnidae: *C. plicatilis* Fig. 5C; Otodontidae: *C. megalodon*, Fig. 5D; Pseudocarchariidae: *Pseudocarcharias* cf. *kamoharai*, Figs. 5A–B) are scarce and constitute less than 6% of specimens in the Chagres Sandstone assemblage (Fig. 7).

The order Carcharhiniformes (15.19%) is represented by the families Carcharhinidae (*G. cuvier*; *Rhizoprionodon* sp., Fig. 5Q–R; *C. brachyurus*, Fig. 5S–T; *Carcharhinus* cf. *cionei*, Fig. 6A–D; *C. obscurus*, Fig. 6G–H; *Carcharhinus plumbeus*, Fig. 6I–J; *C. signatus*, Fig. 6K–L, and *Carcharhinus* spp., Fig. 6MN), Hemigaleidae (*Hemipristis serra*), Scyliorhinidae (*Premontreia* sp. Fig. 5G–H), and Triakidae (*Galeorhinus* cf. *galeus* Fig. 5I–J; *Mustelus* sp. Fig. 5K–L) (Fig. 7).

Batoid specimens constitute 1.42% (Fig. 7) of the Chagres Sandstone assemblage, with only 6 isolated *Myliobatis* teeth (Figs. 6S–U) and one isolated caudal spine. The low proportion of batoids does not seem to be related to the collecting method, as we used a standard screen-washing methodology (see Methods) by which we found abundant micro-otoliths and shark teeth as small as those of *Squalus*, *Trigonognathus*, *Premontreia*, and *Mustelus*.

4.2. Paleobathymetric analysis

4.2.1. Rio Indio

The chondrichthyan assemblage from Rio Indio is dominated by carcharhiniforms. *G. cuvier* has a preference for waters up to 140 m deep (Compagno et al., 2005). *C. obscurus* is common in coastal and oceanic waters up to 400 m in depth, whereas *C. leucas* is most frequently found in waters less than 30 m deep (Compagno, 1984b; Compagno et al., 2005), and *N. brevirostris* occurs mainly in depths of less than 90 m. Finally, even though *Hemipristis serra* is an extinct

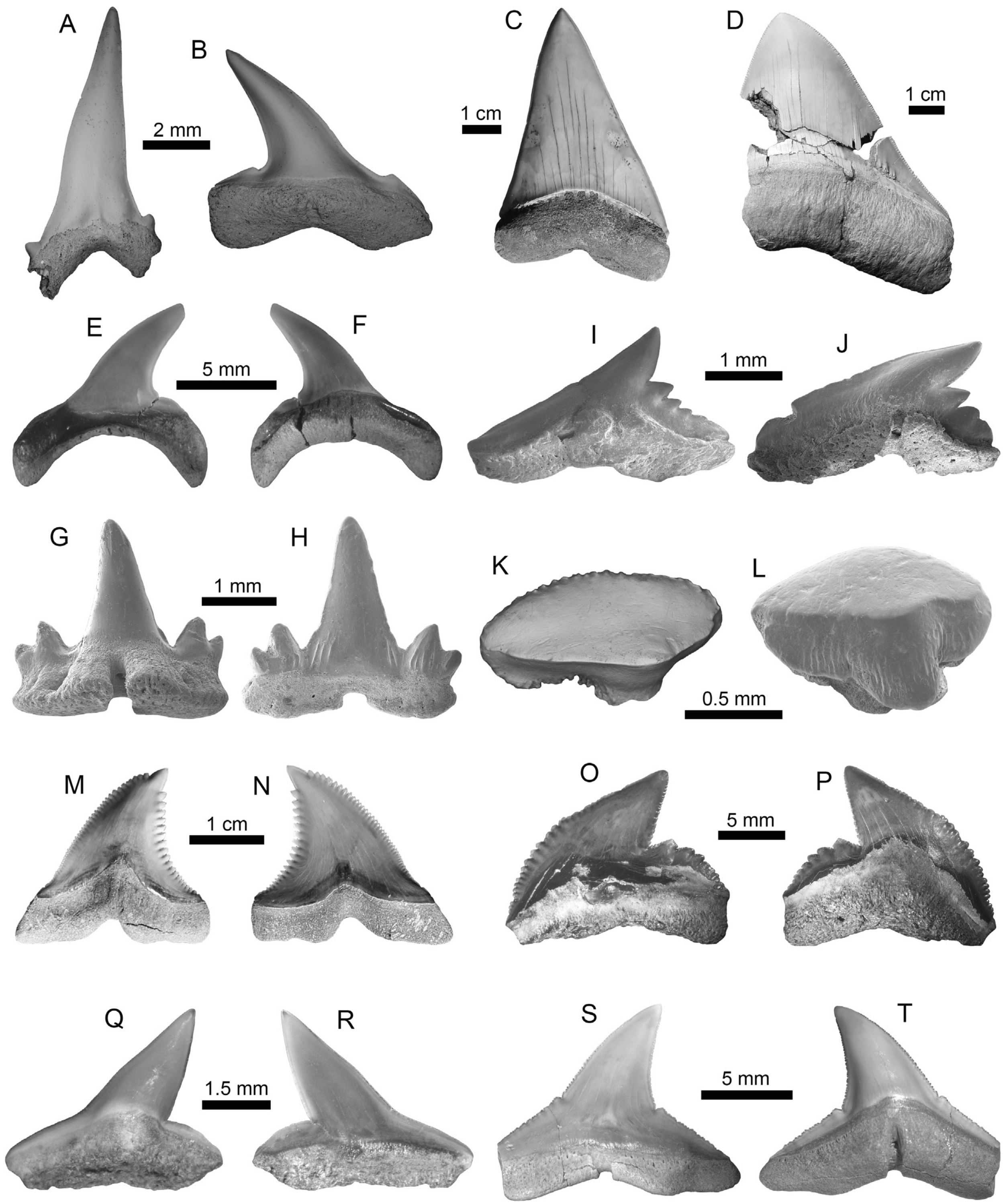

Fig. 5. **A**, **B***Pseudocarcharias* cf. *kamoharai* (A, B: PIMUZ-A/I-4271). **C***Carcharodon plicatilis* (PIMUZ-A/I-4226, Chagres Sandstone). **D***Carcharocles megalodon* (PIMUZ-A/I-4228, Chagres Sandstone). **E**, **F***Alopias superciliosus* (PIMUZ-A/I-4230). **G**, **H***Premontreia* sp. (PIMUZ-A/I-4272). **I**, **J***Galeorhinus* cf. *galeus* (I: PIMUZ-A/I-4274, J: PIMUZ-A/I-4275). **K**, **L***Mustelus* sp. (K: PIMUZ-A/I-4232, L: PIMUZ-A/I-4231). **M**, **N***Hemipristis serra* (PIMUZ-A/I-4238, Rio Indo). **O**, **P***Galeocerdo cuvier* (PIMUZ-A/I-4277, Rio Indo). **Q**, **R***Rhizoprionodon* sp. (PIMUZ-A/I-4244b). **S**, **T***Carcharhinus brachyurus* (PIMUZ-A/I-4296). View: labial (A, E, H, N, O, R, S), lingual (B, C, D, F, G, I, J, M, P, Q, T), occlusal (K, L).

species, it is abundant in neritic deposits (Cappetta, 2012; Pimiento et al., 2013a, 2013b) with an extant representative (*Hemipristis elongatus*) inhabiting waters of up to 30 m depth (Compagno, 1984b). Regarding the lamniforms, *C. megalodon* has been inferred to inhabit coastal habitats (e.g., Purdy, 1996; Pimiento et al., 2010, 2013b), and *C. plicatilis* has been reported from Neogene sediments along with other neritic taxa (Purdy et al., 2001; Aguilera, 2010; Avila et al., 2012; Ehret et al., 2012). Because the only specimen of *Carcharias* sp. recovered was so poorly preserved, we could not identify it to species level; however, we infer a neritic depth preference given that its only living representative, *Carcharias taurus*, inhabits coastal environments of less than 25 m depth

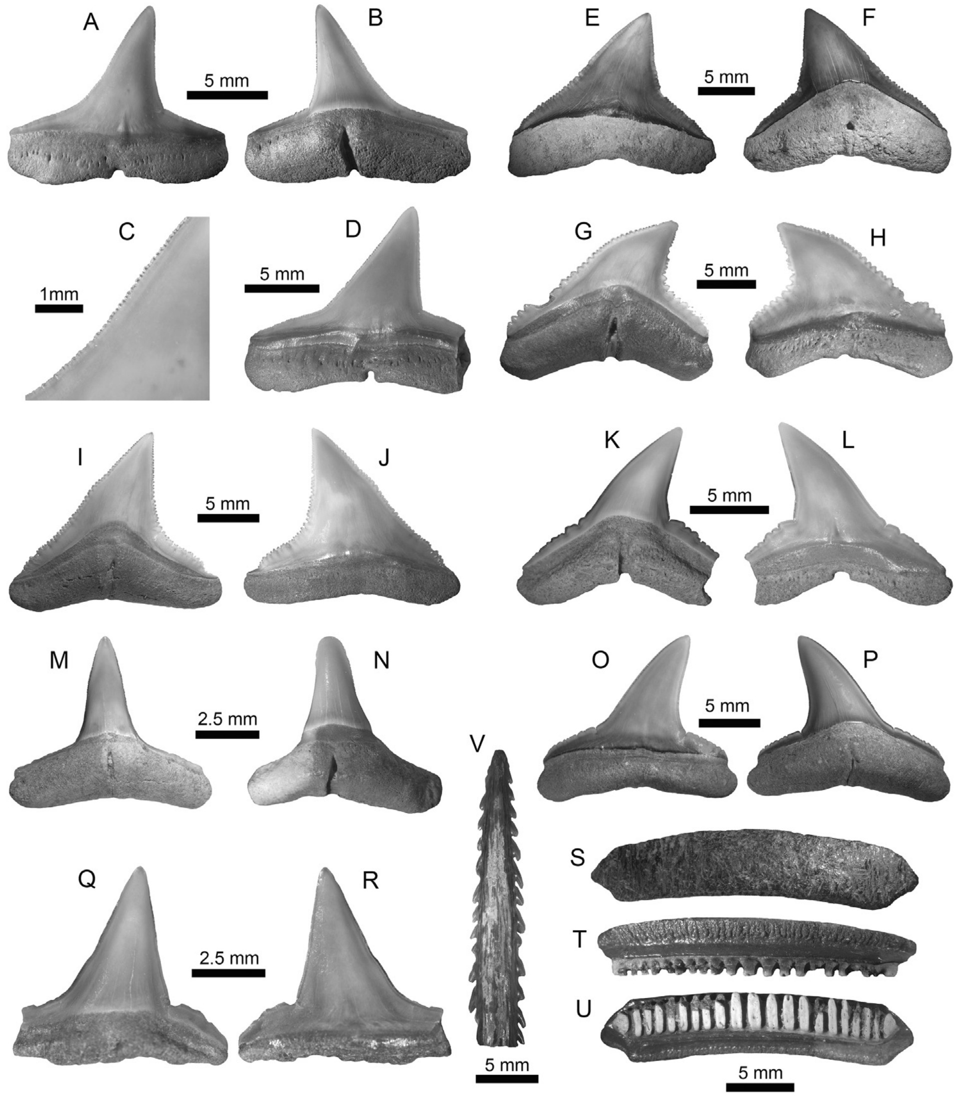

Fig. 6. **A**, **B**, **C**, **D***Carcharhinus cionei* (PIMUZ-A/I-4279). **E**, **F***Carcharhinus leucas* (PIMUZ-A/I-4241). **G**, **H***Carcharhinus obscurus* (PIMUZ-A/I-4282, Chagres Sandstone). **I**, **J***Carcharhinus plumbeus* (PIMUZ-A/I-4284). **K**, **L***Carcharhinus signatus* (PIMUZ-A/I-4285). **M**, **N***Carcharhinus* spp. (K: PIMUZ-A/I-4298, L: PIMUZ-A/I-4297). **O**, **P***Negaprion brevirostris* (PIMUZ-A/I-4286). **Q**, **R***Sphyrna* cf. *lewini* (PIMUZ-A/I-4287). **S**, **T**, **U***Myliobatis* sp. (PIMUZ-A/I-4242). **V** Batomorphii indet. (PIMUZ-A/I-4244, Rio Indio). View: labial (A, D, E, H, J, L, O, R), lingual (B, F, G, I, K, M, N, P, Q, T), basal (U), occlusal (S), dorsal (V).

(Compagno et al., 2005). Although taxa such as *G. cuvier* and *C. obscurus* are also common in oceanic waters (Compagno, 1984b; Compagno et al., 2005; Pepperell, 2010; Voigt and Weber, 2011), our paleobathymetric analysis shows that 100% of the taxa from Rio Indio populate neritic environments (Fig. 8).

4.2.2. *Chagres Sandstone*

The most abundant orders of the Chagres Sandstone member are the Squaliformes and Pristiophoriformes. They consist of benthopelagic and pelagic taxa such as *Isistius* sp., *Squalus* sp., *D. licha*, *Centrophorus* aff. *granulosus*, *Trigonognathus* sp. and *Pristiophorus* sp. (see Table 1, Fig. 8). *Isistius* sp. is the most abundant taxon of the assemblage (Fig. 7). Today it inhabits the epipelagic-bathypelagic zone of open oceanic waters, and is found mostly between the surface and depths up to 3700 m. Often, *Isistius* occur in shallower depths at night, and then is caught in surface trawls. This pattern suggests that these sharks perform nocturnal vertical migrations from deep to shallow waters (Jahn and Haedrich, 1987; Nakano and Tabuchi, 1990; Kiraly et al., 2003; Compagno et al., 2005). *Squalus* sp. and *Pristiophorus* sp. are respectively the second and third most abundant taxa of the Chagres Sandstone (Fig. 7). Living species of these genera inhabit both shallow and deep water (Kiraly et al., 2003; Compagno et al., 2005), and because we were unable to identify either of the taxa to the species level, no certain bathymetric range can be assessed for them. However, in the case of *Pristiophorus* sp., the only living representative in the Americas (*Pristiophorus schroederi*) occurs over continental and insular slopes between 400 and 1000 m (Kiraly et al., 2003). Extant representatives of the taxa *H. perlo*, *D. licha*, and *Centrophorus* aff. *granulosus* inhabitant both shallow and deep waters (Table 1), but they have preference for deep-water environments, usually along the outermost continental shelves and upper slopes (Castro et al., 1999; Hennemann, 2001; Kiraly et al., 2003; Compagno, 1984a; Compagno et al., 2005). The benthopelagic *Trigonognathus* sp. has a living representative, *T. kabeyai*, which is a typical deep-water shark that inhabits the upper continental slope at depths ranging between 330 and 360 m, and the uppermost slope of seamounts, at 270 m depth (Mochizuki and Ohe, 1990; Compagno et al., 2005). The scarcity of *Trigonognathus* sp. in the Chagres Sandstone assemblage and the poor preservation of the single specimen

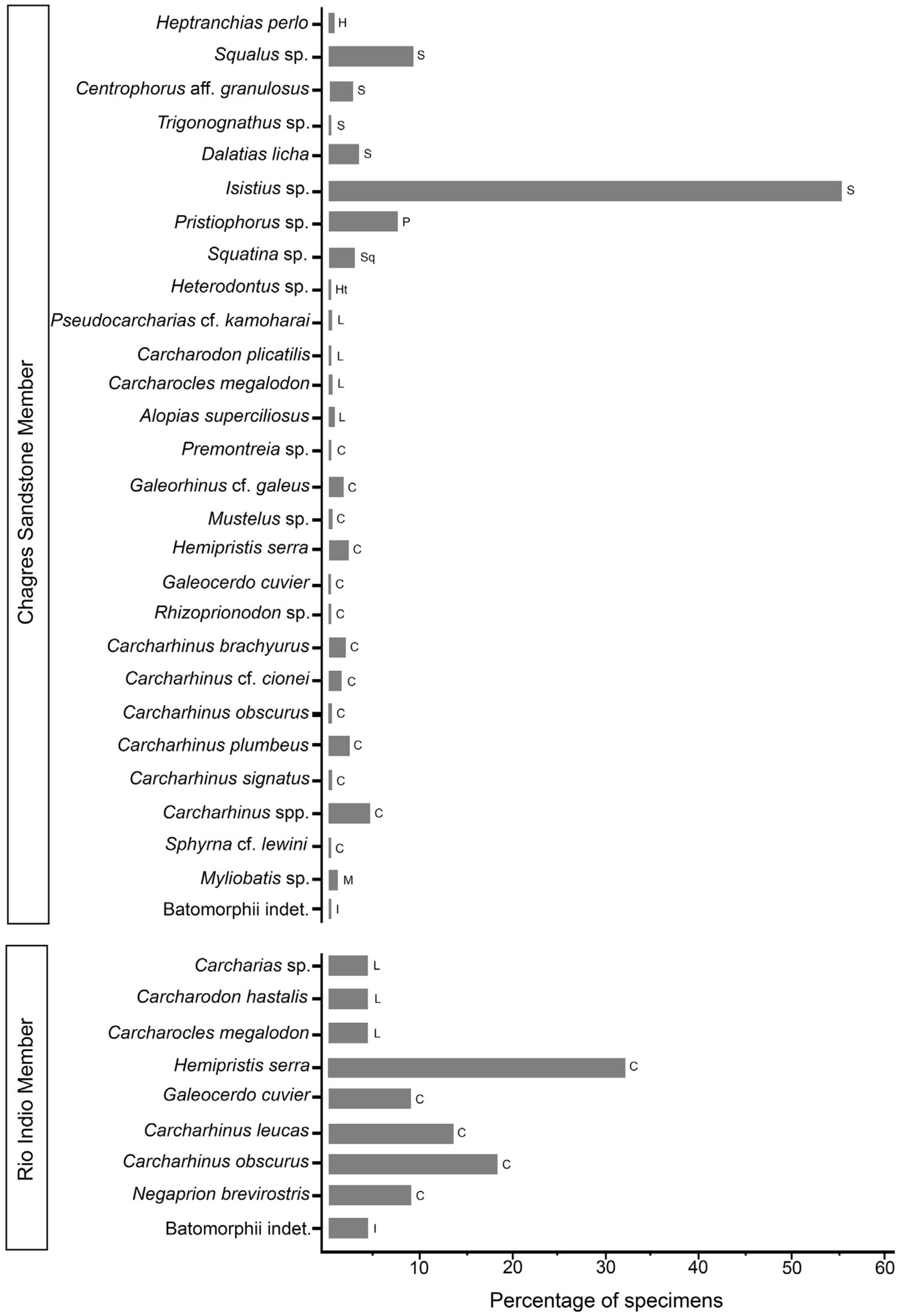

Fig. 7. Relative abundance of chondrichthyans in the Chagres Formation: Chagres Sandstone Member (100% = 491 specimens), Rio Indio Member (100% = 22 specimens). H: Hexanchiformes; S: Squaliformes; P: Pristiophoriformes; Sq: Squatiniformes; Ht: Heterodontiformes; L: Lamniformes; C: Carcharhiniformes; M: Myliobatiformes; I: Batomorphii indeterminate.

recovered preclude any further taxonomic identification, below the genus level. Specimens of the benthic Squatiniform *Squatina* sp. and heterodontiform *Heterodontus* sp. represent 2.84% of the assemblage, and living representatives of these genera have wide bathymetric ranges that include neritic and bathyal habitats (Compagno et al., 2005; Musick et al., 2004) (Table 1, Fig. 8).

The presence of neritic taxa of the orders Lamniformes and Carcharhiniformes in the Chagres Sandstone assemblage could suggest shallower waters. However, specimens of these taxa constitute less than 18% of the complete assemblage, and some taxa in these orders (e.g., *Pseudocarcharias* cf. *kamoharai*, *A. superciliosus*, *Galeorhinus* cf. *galeus*, *Mustelus*, *G. cuvier*, *Rhizoprionodon* sp., *C. brachyurus*, *C. obscurus*, *C. plumbeus*, and *Sphyrna lewini*) can also occur in adjacent deep waters (e.g., Compagno, 1984b; Musick et al., 2004; Compagno et al., 2005; Pepperell, 2010; Voigt and Weber, 2011).

The batoids of the Chagres Sandstone are characterized by a low abundance of *Myliobatis* sp. (6 specimens) and a complete absence of other groups that are present in other Neogene localities of the Caribbean (e.g., Laurito, 1999, 2004; Laurito and Valerio, 2008;

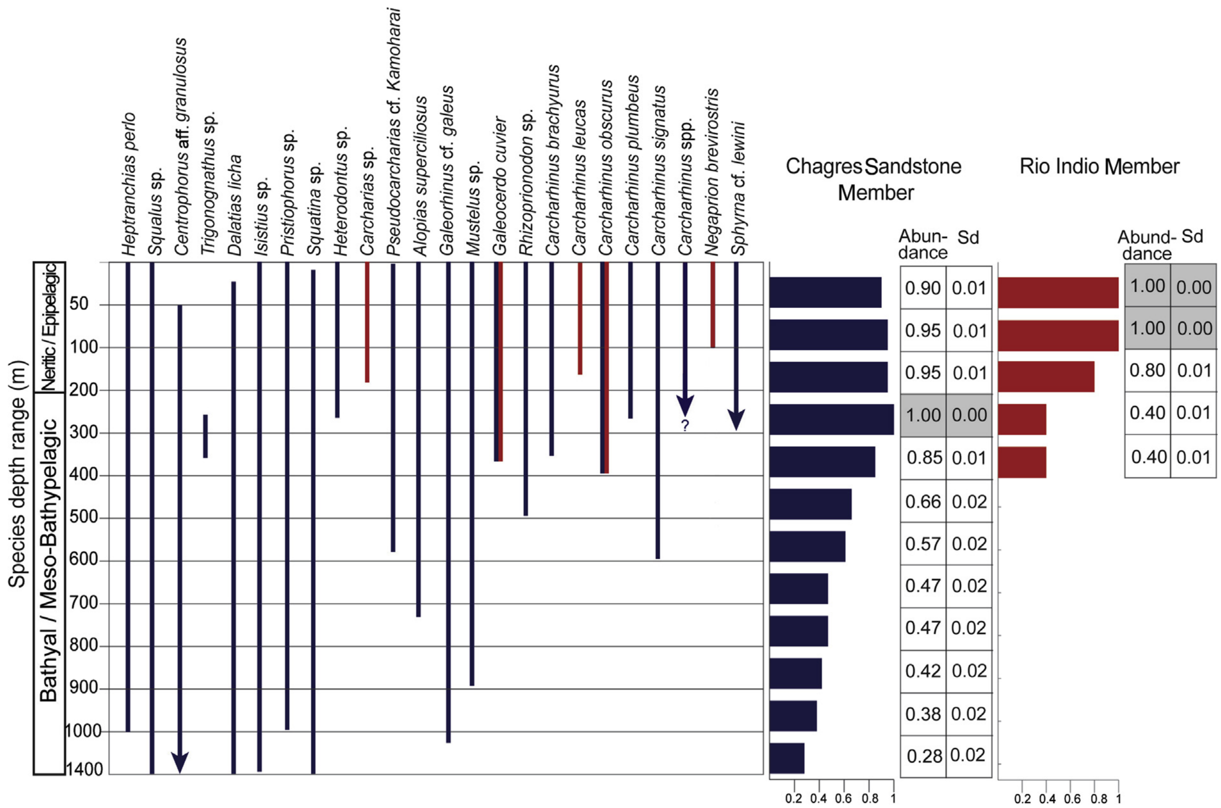

Fig. 8. Present-day bathymetrical ranges of taxa that were found in the Rio Indio Member (blue line) and Chagres Sandstone Member (red line) of the Chagres Formation. The numbers of the taxa and depth ranges from Table 1. Arrows indicate that the taxa range is greater (see Table 1). Abundance = frequency of species in each depth interval, Sd = Standard deviation. Total taxa analyzed in Piña = 5 and Chagres Sandstone = 21. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Aguilera et al., 2011; Pimiento et al., 2013b; Carrillo-Briceño et al., 2014). This could be related to the depositional environment of the Chagres Sandstone, and probably to some ecological limitations influenced by depth and food recourses to batoids, as indicated by the scarce evidence of shellfish in this facies. Otoliths are extremely abundant in this facies (e.g. Schwarzhans and Aguilera, 2013), which it is very unusual. Otoliths are mostly from Myctophidae, the largest mesopelagic fish family, and it is possible that their high abundance together with the high abundance of sharks, indicates that Myctophidae were the main prey to the sharks.

Our paleobathymetric analysis indicates that the most probable depth of deposition of the Chagres Sandstone Member ranged from 200 to 300 m (Fig. 8). One hundred percent of taxa in analyzed sample have bathymetric ranges that overlap this depth range (Fig. 8). The second most probable depth range for the Chagres Sandstone Member is between 50 and 200 m, which coincides with the 95% of the taxa in the analyzed sample (Fig. 8).

5. Discussion

It has been proposed that the both Toro and Chagres Sandstone Members were deposited at water depths of 200–500 m (e.g., Fierstine, 1978; Collins and Coates, 1993; Collins et al., 1996, 1999; Collins, 1999). This paleobathymetry was refuted by Hendy (2013) and Hendy et al. (in press) (where the Chagres Sandstone Member is referred as the "Rio Indio facies"). These authors propose a depth of <50 m for the Toro Member and 75–150 m for the Chagres Sandstone, based on their molluscan assemblages. Our bathymetric analysis shows that the Chagres Sandstone has a predominance of benthopelagic and benthonic sharks, which prefer oceanic environments with depths ranging between 200 and 300 m (Fig. 8), although the second most probable depth is in the range of 50–200 m. Our interpretation is further supported by (1) benthic foraminifera (Collins et al., 1996); (2) the oceanic signature found in bones of fossil fish from the Chagres Sandstone Member based on rare-earth element analyses (Symister et al., 2012); (3) the presence and abundance of otoliths of Myctophidae, the dominant mesopelagic fish group (Schwarzhans and Aguilera, 2013); (4) the occurrence of pelagic billfishes (Fierstine, 1978; De Gracia, 2012), which are common in oceanic waters (Nakamura, 1983, 1985; Pepperell, 2010); and (5) the abundance of the whales, billfishes, and the ectoparasitic shark *Isistius* (Widder, 1998) (Velez-Juarbe et al., in press).

The Chagres Sandstone Member includes not only chondrichthyans taxa from oceanic waters, but also shallower waters (Fig 8). Similar mixtures are sometimes found in some marine deposits of the middle Miocene of France (Vialle et al., 2013). This mixture could be explained by two scenarios: (a) deep-water faunal elements migrating into shallow waters as a result of coastal upwelling or (b) shallow-water elements being washed into deeper water by turbidity currents or slumping. Our results strongly support the first scenario, as we did not find any sedimentological evidence indicating either turbidites or slumping. Chagres Sandstone probably accumulated at the edge of an outer platform-upper slope bordered by a deep oceanic margin. The Chagres Sandstone Member seems also to be associated with a highly productive upwelling environment as indicated by the elevated densities of fish remains (Kotlarczyk and Uchman, 2012; Schwarzhans and Aguilera, 2013).

We did not found enough chondrichthyans in the Toro Member to produce a paleobathymetric estimation; therefore, the discrepancy between benthic foraminifera (200–500 m water depth,

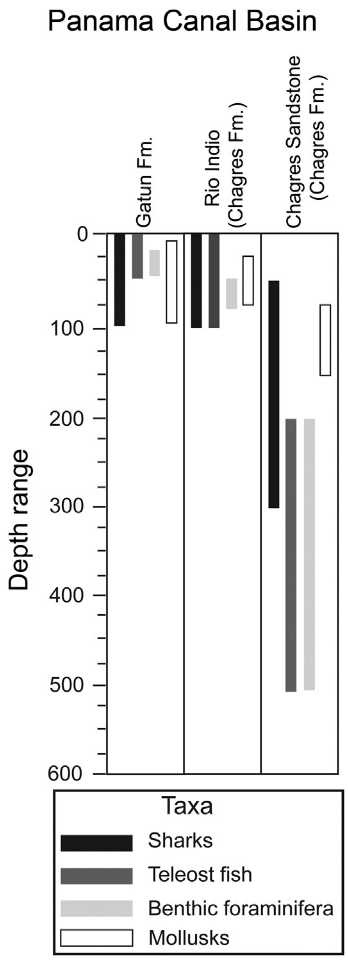

Fig. 9. Paleobathymetric interpretations of Chagres and Gatun Formations using several proxies including chondrichthyans (this study, Pimiento et al., 2013), benthic foraminifera (Collins et al., 1996, 1999) and mollusks (Hendy et al., 2015).

Collin et al., 1996) and mollusks (<50 m, Hendy et al., in press) still needs to be resolved. Previous studies suggest that the Rio Indio Member accumulated at depths of <80 m (50–80 m, according to both benthic foraminifera [Collins et al., 1996] and teleostean fauna [Aguilera and Rodriguez de Aguilera, 1999], and 25–75 m, according to molluscan fauna [Hendy et al. in press]). Our bathymetric estimations derived from the chondrichthyan fauna indicate depths <100 m (Figs. 8–9), in agreement with those previous studies.

6. Conclusion

We report 30 chondrichthyan taxa; 18 of them are new fossil records for Panama and four are new records for Tropical America, constituting the most diverse associations known from the Neogene of Panama. The bathymetric analysis of the Rio Indio Member suggests a shallow depositional environment with depths <100 m, in agreement with previous studies. The Chagres Sandstone Member accumulated at depths between 200 and 300 m at the edge of an external platform to upper slope, close to a deep oceanic margin.

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