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Late Miocene chondrichthyans from Lago Bayano, Panama: Functional diversity, environment and biogeography

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Abstract.—This newly described chondrichthyan fauna from the late Miocene Chucunaque Formation of Lago Bayano reveals a prolific and highly diverse assemblage from Panama, and one of the richest shark faunas from the Neotropics. Strontium geochronology indicates an age of 10–9.5 Ma for the chonrichthyan-bearing strata. Field efforts resulted in 1429 identifiable specimens comprising at least 31 taxa, of which at least eight are new to the documented fossil record of Panama. With this information an analysis of functional diversity was conducted, indicating ecosystems dominated by generalist species feeding upon a wide range of organisms, from plankton to marine mammals. A probabilistic approach of paleobathymetric estimation suggests a neritic environment. Previous studies based on foraminifera have suggested that the Chucunaque Formation had a greater Pacific Ocean affinity, making this the first Miocene chondrichthyan fauna described from the Pacific shelf of Panama. However, our geographic comparisons show that this fauna has mixed Caribbean and Pacific biogeographic affinities, which likely supports the previously purported connection between chondrichthyan faunas during the late Miocene.

Introduction

Lago Bayano in Panama Province, Panama is an artificial lake that contains an extraordinarily rich assemblage of chondrichthyans. Hundreds of shark and ray teeth erode from host sediments and concentrate on the shorelines of emerged lake islands as a result of annual water-level fluctuations. Prior to the damming of the Rio Bayano drainage that created Lago Bayano, Stewart (1966) made a geological reconnaissance of this region and mapped what is now Lago Bayano as the Chucunaque Formation (Shelton, 1952). Chondrichthyan remains were noted to be common in the marine mudstones and sandstones of the deeply incised river valleys, although no collections were retained. More recently, Coates et al. (2004) mapped the Chucunaque Formation throughout the Darien Province of Panama. Even though marine vertebrates were not reported, this study confirmed a late Miocene age for the unit, and noted a foraminiferal assemblage indicating a Pacific Ocean affinity. In the present study, new biostratigraphic and Sr-isotope analyses derived from marine invertebrate fauna yield ages of 10–9.5 Ma for chondrichthyan-bearing strata in Lago Bayano.

The closure of a Central American Seaway (CAS) and consequent formation of the Isthmus of Panama during the Neogene extremely affected tropical American (=Neotropical) marine communities and increased the biogeographic complexity of the region (e.g., Coates and Obando, 1996). Miocene chondrichthyan faunas are fundamental to understand these processes because they were: (1) abundant and widely distributed during this time, and (2) have been proven to be good paleobathymetry indicators of the deposits adjacent to the CAS (e.g., Pimiento et al., 2013a; Carillo-Briceño et al., 2015a). However, previous studies on Miocene chondrichthyans of Panama have been limited to Caribbean faunas (e.g., the Gatun Formation, Gillette, 1984; Pimiento et al., 2010; Pimiento et al., 2013a; the Culebra Formation, Pimiento et al., 2013b; and the Chagres Fromation, Carrillo-Briceño et al., 2015a). Hence, the chondrichthyan fauna of Lago Bayano is the first Miocene fauna from the Pacific shelf of Panama to be described. The only other chondrichthyan fauna described from the Pacific of Panama was the Eocene Tonosi Formation from the Azuero Peninsula (Vasquez and Pimiento, 2014). Other late Miocene shark assemblages from the region include Ecuador (Longbottom, 1979; Carrillo-Briceño et al., 2014), Venezuela (Sánchez-Villagra et al., 2000; Aguilera and Rodrigues de Aguilera, 2001; Carrillo-Briceño et al., 2015b), Jamaica (Donovan and Gunter, 2001), Costa Rica (Laurito and Valerio, 2008), and Grenada (Portell et al., 2008). All of these studies have provided a better understanding on the composition of marine communities during a time of rapid change.

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It has been argued that while most works on ancient chondrichthyan faunas provide valuable information about taxonomic diversity, they are somehow limited in their ecological interpretations because they ignore species functions in ecosystems (Moore, 2001; Hooper et al., 2002). To address this issue, functional diversity is often measured as a means to quantify the impact of species on ecosystems (Petchey and Gaston, 2006). The correlation that exists between tooth morphology and diet can be used to apply a functional diviersity approach to the study fossil chondrichthyan faunas (e.g., Bertolini, 1933; Moss, 1977; Cappetta, 1986, 1987, 2012; Frazzetta, 1988; Kent, 1994). Specifically, a classification scheme has been outlined by Kent (1994) in which chondrichthyan dentitions are subdivided into nine types: five homodont forms (cutting, grasping, clutching, crushing, and vestigial) and four heterodont forms (cutting-grasping, grasping-cutting, grasping-crushing, and clutching-crushing). A more complex scheme was developed by Compagno (1990) that grouped sharks, rays, and chimaeroids into ecomorphotypes based on varying life histories, which incorporates the morphology, habitat, and behavior of each taxon. These ecomorphotypes have been utilized in numerous studies of extant sharks, especially those pertaining to conservation (Martin, 2005; Zhou and Griffiths, 2008; Lucifora et al., 2011; Grogan et al., 2012; Ritter, 2014), but have not been employed in many paleontological studies. Here, we integrate dentition types and ecomorphotypes as a measure of functional diversity. This approach provides novel information regarding the function of chondrichthyan species in the ecosystems adjacent to the CAS during the late Miocene.

This paper describes the taxonomy and systematics of the chondrichthyan fauna from Lago Bayano and interprets the diversity, paleoenvironment, and paleobiogeographic significance of this new and prolific marine vertebrate fauna. These interpretations will be based in functional diversity analyses and a unique approach toward analyzing paleobathymetry. We will show that this new discovery sheds a light on the dynamics of ancient marine faunas in the New World tropics during the late Miocene.

Geologic setting

The thick sequence of Cretaceous through Neogene sediments that occupy the central lowlands paralleling the San Blas and Darien highlands of Darien Province in eastern Panama forms the Bayano, Chucunaque-Tuira, and Atrato basins (Stewart, 1966; Duque-Caro, 1990; Coates et al., 2004). The Chucunaque-Tuira and Atrato basins were subject to a detailed review by Coates et al. (2004) who established the lithostratigraphy used herein, provided biostratigraphic and paleobathymetric context, and interpreted their geological history. The Bayano Basin was not investigated, however, and our present understanding of the geology is built around the geological reconnaissance of Stewart (1966), extrapolation of Coates et al. (2004), and more recent mapping as a part of a broader study into the tectonic history of the Panama Isthmus (Montes et al., 2012a, 2012b). Attempts to map this region, locate contacts, and measure stratal thickness have been challenged by lack of exposure, discontinuous outcrops (often submerged or forested), and obscure folding and faults. In a general sense, the succession in the Lago Bayano area consists of Cretaceous volcanic intrusives (Darien Formation), Oligocene–early Miocene agglomerates (Porcona Formation), early–middle Miocene limestone (Clarita Formation), turbiditic sandstone and claystone (Membrillo Formation), overlain by late Miocene fossiliferous and conglomeratic sandstone and siltstone (Chucunaque Formation) (Terry, 1956; Stewart, 1966; Coates et al., 2004). These units can be observed along the shoreline of southern Lago Bayano, Rio Maje, Rio Tigre, Carratera Panamericana, and minor roads (Fig. 1; Table 1).

Stewart's (1966) original description of the geology in this region was done prior to the damming of the Rio Bayano and the formation of the artificial lake that is now Lago Bayano. In this initial description he noted the presence of chondrichthyan remains in Miocene-aged sandstones of the Chucunaque Formation in the deeply incised Rio Bayano and its tributaries. Other marine fossils (e.g., molluscs and foraminifera) were recognized in other Miocene-aged units, but chondrichthyan remains were restricted to the sandstone facies of the Chucunaque Formation. The construction of the Bayano Dam in 1976 flooded 350 km^2 of rainforest to form Lago Bayano, making it difficult to reconstruct original sediment composition and sedimentary structures of the Chucunaque Formation at many of the chondrichthyan-bearing localities. The chondrichthyan remains utilized in this study are left as a residue among reworked gravel, sand, and mud grains along island shorelines. In the southeastern-most portion of the lake, exposed uneroded blocks comprise strongly weathered and sparsely fossiliferous orange mudstone. The islands in the northern portion of southern Lago Bayano contain a more varied range of facies, including fossiliferous, gritty orange sandstone and a fine-grained tuffaceous white sandstone.

In much of the Darien Province, the Chucunaque Formation of Shelton (1952) is Messinian in age (7.1–5.6 Ma), although Coates et al. (2004) suggested that it could be older than 9.4 Ma in the western part of their study area on the basis of calcareous nannofossil biostratigraphy. This age is consistent with $^{87}Sr/^{86}Sr$ dates of 10–9.5 Ma derived from calcerous *Lindapectin* shells that were deposited in association with the chondrichthyan remains on the shoreline of STRI 290138 (N 9.1552, W 78.7824) and STRI 300032 (N 9.1411, W 78.7545; Tables 1, 2). In July 2015, a research group returned to Lago Bayano and observed unusually low lake levels, which resulted in some minor exposures of the *in situ* fossiliferous layer along STRI 290116 and STRI 300032. Calcareous microfossils picked from this *in situ* layer were dated using $^{87}Sr/^{86}Sr$ isotopic ratios from STRI 300032, and found to be consistent with the ages of the *Lindapectin* (personal communication, A. Waite, 2016). This fauna is therefore Tortonian in age and correlative with the other important chondrichthyan-bearing units in Central and South America, including the Gatun Formation and Alajuela Formation of central Panama (Gillette, 1984; Pimiento et al., 2013a; MacFadden et al., 2017), Angostura Formation of Ecuador (Carrillo-Briceño et al., 2014), and upper Urumacro Formation of Venezuela (Carrillo-Briceño et al., 2015b).

Materials and methods

In 2010 we began to collect fossils from Miocene sediments exposed along the islands of Lago Bayano (Fig. 1). The sharks and ray teeth are most easily collected when lake levels are low and fossiliferous sedimentary zones are exposed.

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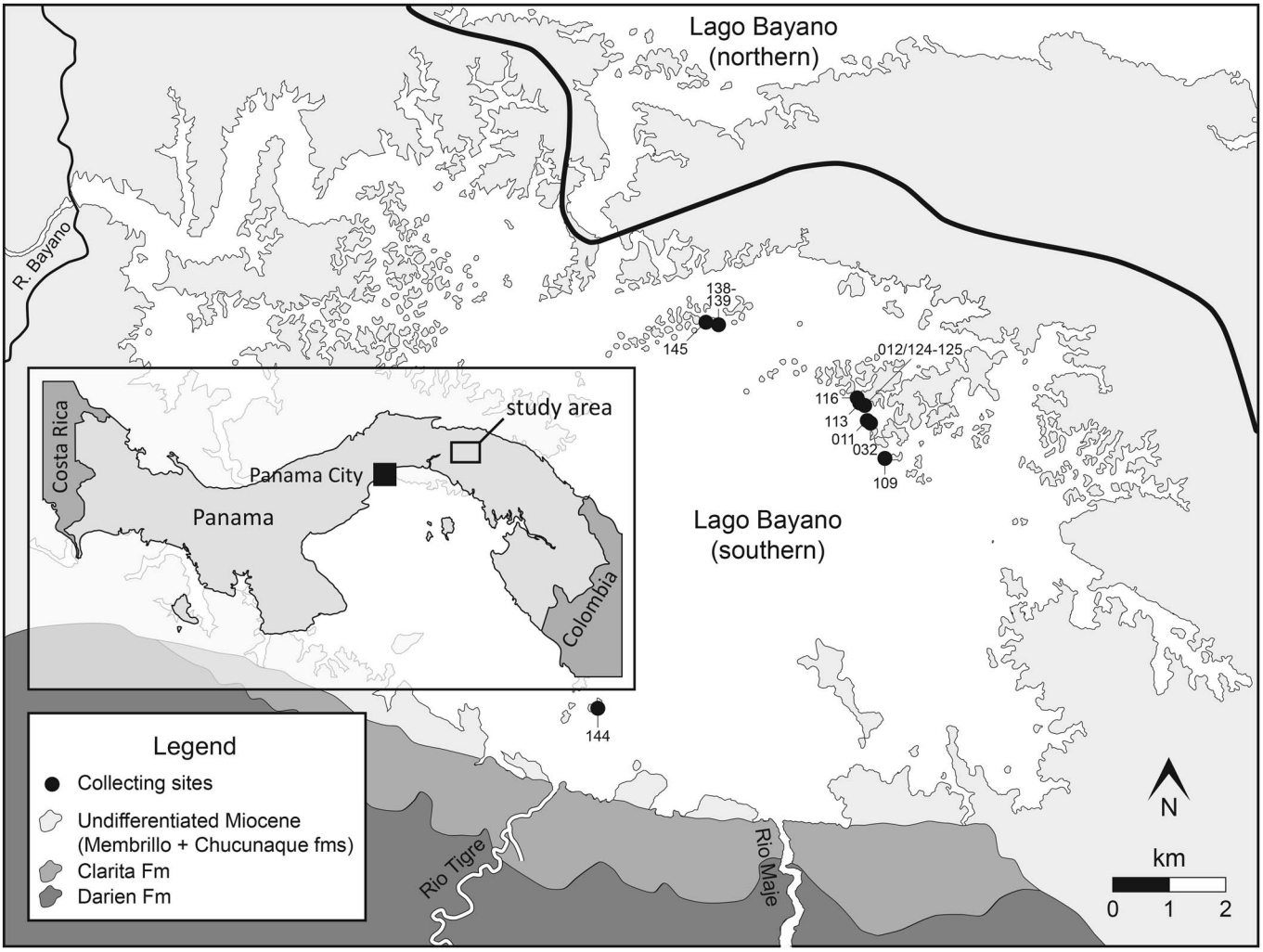

Figure 1. Map of Lago Bayano, Panama with collecting sites denoted by black circles. Numbers labelling each collecting site refer to the last three digits of the Smithsonian Tropical Research Institute (STRI) field number (Table 1).

Table 1. List of localities bearing chondrichthyan remains within Lago Bayano. GPS coordinates of STRI 300029 (Bayano 8) were improperly recorded and are not reported here; most likely this locality is within the cluster of islands that did bear chondrichthyan remains in southeastern Lago Bayano (Fig. 1). Specimens from Bayano 12 are all from a single locality, however sample labels and GPS coordinates were lost during transport and reported by FLMNH Site Key in the text. All GPS coordinates were taken using WGS84 datum. STRI locality (STRI Loc.) numbers can be searched in the STRI Geological Sample Database (http://biogeodb.stri.si.edu/jaramillo/fossildb). FLMNH = Florida Museum of Natural History and STRI = Smithsonian Tropical Research Institute.

STRI Loc.	FLMNH Site Name	FLMNH Site Key	Fig 1 ID	Latitude	Longitude
290109	Bayano 1	YPA066	109	9.1346	−78.7509
290113	Bayano 2	YPA095	113	9.1436	−78.756
290116	Bayano 3	YPA096	116	9.1454	−78.7582
290125	Bayano 4	YPA097	124–125	9.1432	−78.7549
290139	Bayano 5	YPA098	138–139	9.1545	−78.7836
290144	Bayano 6	YPA099	144	9.0942	−78.7981
290145	Bayano 7	YPA100	145	9.154	−78.7853
300029	Bayano 8	YPA101	NA	-	-
300032	Bayano 9	YPA102	032	9.1411	−78.7545
430011	Bayano 10	YPA103	011	9.1413	−78.7546
430012	Bayano 11	YPA104	012	9.1432	−78.7549
unknown	Bayano 12	YPA105	NA	-	-

Chondrichthyan remains were collected from 12 localities within Lago Bayano, resulting in 1422 teeth and seven non-dental elements. Surface collecting was done at all 12 localities and produced 768 chondrichthyan teeth and two vertebral centra. Matrix was collected from five of the 12 localities and washed through a set of screens with 6, 1.5, 1.0, and 0.5 mm mesh, which produced 654 chondrichthyan teeth, two vertebral centra, two stingray caudal spines, and one stingray dermal denticle. To illustrate that we have accurately sampled both surface and screenwashed material, randomized species accumulation curves were created

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Table 2. Strontium isotope data and age estimates from the Chucunaque Formation of Lago Bayano.

Locality (STRI)	Height (m)	Analytical sample	Taxon	$^{87}Sr/^{86}Sr$	Age (Ma)	Age range (Ma)
300032	n/a	LB-32A	*Lindapecten* sp.	0.708901	9.57	9.35–9.77
300032	n/a	LB-32B	*Lindapecten* sp.	0.70889	9.90	9.70–10.07
300032	n/a	LB-32C	*Lindapecten* sp.	0.7088864	10.00	9.82–10.20
290138	n/a	LB-38A	*Lindapecten* sp.	0.7089003	9.60	9.40–9.80
290138	n/a	LB-38B	*Lindapecten* sp.	0.7089039	9.50	9.25–9.67
290138	n/a	LB-38C	*Lindapecten* sp.	0.708899	9.65	9.42–9.82

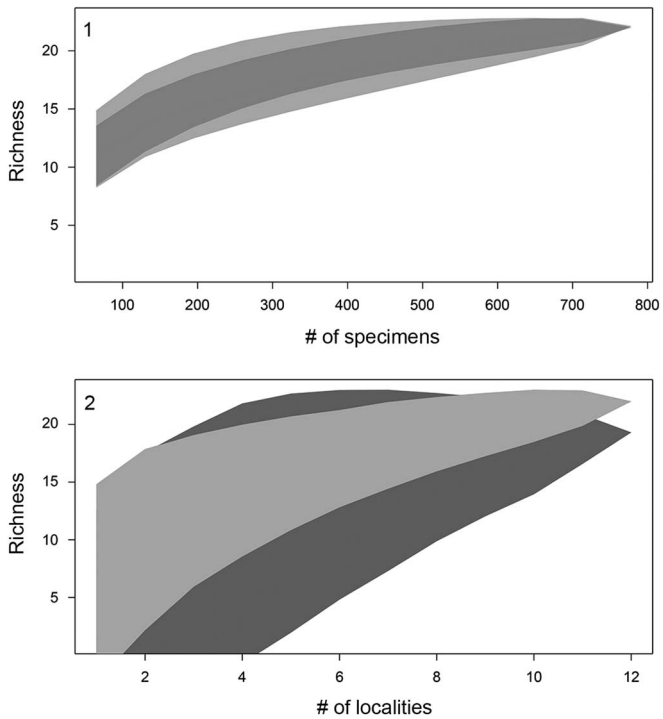

Figure 2. Sampling effort for surface-collected and screenwashed material via two randomized species accumulation curves. (**1**) Accumulation curves reported as number of specimens versus number of species (i.e., richness) for surface-collected (light gray) and screenwashed material (dark gray), respectively; shaded polygons represent confidence intervals. (**2**) Accumulation curve reported as number of localities (i.e., collecting sites versus richness) for surface-collected (light gray) and screenwashed material (dark gray), respectively; shaded polygons indicates the confidence interval.

(Fig. 2) using the vegan package (Oksanen et al., 2010) in the program R (R Development Core Team, 2012).

Age estimates derived from $^{87}Sr/^{86}Sr$ isotopic ratios of marine calcareous shells and marine calcareous sediment may be compared to global ratios of $^{87}Sr/^{86}Sr$ through geologic time to estimate a geological age (Burke et al., 1982; Koepnik et al., 1985; Hodell and Woodruff, 1994; McArthur, 1994). Samples were obtained from the Lago Bayano assemblage itself, and from presumably coeval strata outcropping nearby (Table 2). Age estimates were determined using the Miocene and Pliocene portions of Look-Up Table Version 4:08/03 (Howarth and McArthur, 1997; McArthur et al., 2001) associated with the strontium isotopic age. Strontium isotope analyses of Lago Bayano samples used well-preserved calcitic shells and followed the sampling and analytical protocols of Kirby et al. (2007, 2008). These were performed on a Micromass Sector 54 Thermal Ionization Mass Spectrometer (TIMS) in the Department of Geological Sciences at UF. Strontium was loaded onto oxidized tungsten single filaments and run in triple collector dynamic mode. Data were acquired at a beam intensity of ~1.5 V for ^{88}Sr, with corrections for instrumental discrimination made assuming $^{86}Sr/^{88}Sr$ ratio of 0.1194. Errors in measured $^{87}Sr/^{86}Sr$ are better than ± 0.00002 (2 σ), based on long-term reproducibility of NBS 987 ($^{87}Sr/^{86}Sr = 0.71024$). Due to the poor preservation of shell material in the Lago Bayano succession, $^{87}Sr/^{86}Sr$ isotope analyses were only conducted on samples from two localities (STRI 290138 and 300032) where calcitic shells of *Lindapecten* were present; at many localities even calcitic taxa are represented as external molds.

Information regarding biology, anatomy, distribution, habitat preferences, and feeding mechanisms were gathered from the literature cited below. Much of this information can be found in a coherent format in The IUCN Red list of Threatened Species (www.iucnredlist.org) or Fishbase (www.fishbase.org). Measurements of macro teeth were taken using calipers, whereas measurements of micro teeth were taken directly from SEM images. Crown height (CH = the distance between the crown tip and crown-root margin) and crown width (CW = maximum distance between the mesial and distal edge at the crown-root margin) were measured for labio-lingually flatten teeth (i.e., most taxa belonging to the subdivision Selachii). Crown length (CL = tooth thickness, defined herein as the maximum distance between the labial and lingual edge in occlusal view) was additionally measured in teeth with a broad occlusal surface (i.e., those belonging to the superorder Batomorphii and the genus *Mustelus*). In order to measure CH, a line was drawn from the crown apex perpendicular to the crown-root contact (e.g., Pimiento et al., 2010, fig. S2). It is important to note that many other authors will report the tooth height, which is generally a measurement of the entire tooth (crown and root) and is not directly comparable to the CH measurements reported herein.

Taxonomic composition is reported as a histogram depicting the relative abundance of chondrichthyan genera. Functional diversity is interpreted via two proxies (dentition types and ecomorphotypes). Dentition types, as defined by Kent (1994), were assigned to each taxon based on tooth morphology of fossil and modern representatives. For example, in the case of *Carcharhinus plumbeus*, fossil occurrences were limited to upper teeth that have a cutting-type morphology; however, based on the dentition of the living representatives, we can infer a cutting-grasping type dentition. Ecomorphotypes, as defined by Compagno (1990), were assigned to each taxon based on morphology, habitat, and behavior of modern analogs. Both proxies were then plotted as pie charts that illustrate the relative abundance of dentition types and ecomorphotypes, respectively. A weighted analysis of paleodepth frequency was performed using R. This analysis incorporated the abundance (in the fossil assemblage) and depth preference (as reported in the literature) from taxa with modern analogs. Taxa that

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Table 3. Complete taxonomic list of the chondrichthyes of Lago Bayano, including a summary of all relevant data for the subsequent analyses. References for common depth ranges and biogeographic affinity (i.e., Atlantic vs. Pacific) can be found in the Systematic Paleontology section, ecomorphotypes are based on Compagno (1990), and descriptions of dentition types can be found in Kent (1994). * indicates a new taxon for the fossil record of Panama. † indicates an extinct species.

Taxon	# of Specimens	Common Depth (m)	Avg. Depth (m)	Ecomorphotype	Dentition Type	Atlantic/Pacific
Centrophorus sp.	1	200–600	400	Microceanic	Cutting	
†*Carcharocles megalodon*	60			Littoral: Archipelagic	Cutting	
**Isurus oxyrinchus*	7	0–500	250	Macroceanic: Tachypelagic	Grasping-Cutting	Both
Alopias superciliousus	3	100–500	300	Macroceanic	Cutting	Both
**Alopias* cf. *A. vulpinus*	5	1–366	184	Macroceanic	Cutting	Both
*cf. *Iago* sp.	36			Littoral: Cancritrophic	Clutching	
Mustelus sp.	16			Littoral: Cancritrophic	Crushing	
†*Hemipristis serra*	61			Littoral: Eurytrophic	Cutting-Grasping	
†*Galeocerdo aduncus*	2			Littoral: Eurytrophic	Cutting	
Galeocerdo cuvier	15	0–140	70	Littoral: Eurytrophic	Cutting	Both
†*Physogaleus contortus*	19			Littoral: Eurytrophic	Cutting-Grasping	
*†*Physogaleus* sp.	14			Littoral: Teuthitrophic	Cutting-Grasping	
Carcharhinus falciformis	4	200–500	350	Macroceanic	Cutting-Grasping	Both
**Carcharhinus brevipinna*	147	0–100	50	Littoral	Cutting-Grasping	Both
**Carcharinus* aff. *C. macloti*	10	0–170	85	Littoral	Cutting-Grasping	Pacific
Carcharhinus obscurus	184	0–400	200	Littoral: Eurytrophic	Cutting-Grasping	Both
Carcharhinus plumbeus	8	20–55	38	Littoral	Cutting-Grasping	Both
Carcharhinus spp.	405			Littoral	Cutting-Grasping	
Negaprion brevirostris	3	0–92	46	Littoral	Cutting-Grasping	Both
Rhizoprionodon spp.	66			Littoral: Teuthitrophic	Clutching	
Sphyrna lewini	13	0–275	138	Semilittoral: Sphyrnid	Cutting-Grasping	Both
Sphyrna mokarran	4	1–80	40	Littoral: Sphyrnid	Cutting	Both
Sphyrna zygaena	96	0–200	100	Littoral: Sphyrnid	Cutting-Grasping	Both
Rhynchobatus sp.	1			Rhyncobenthic	Crushing	
Urobatis sp.	2			Rajobenthic	Crushing	
**Dasyatis* sp.	19			Rajobenthic	Crushing	
Aetobatus sp.	6			Aquilopelagic	Crushing	
Rhinoptera sp.	38			Aquilopelagic	Crushing	
Mobula thurstoni	16	0–100	50	Aquilopelagic	Vestigial	Both
**Mobula* cf. *M. tarapacana*	10	0–30	15	Aquilopelagic	Vestigial	Both
Mobula spp.	140			Aquilopelagic	Vestigial	
	1422					

Table 4. Results of the weighted paleobathymetric analysis. Min and max values represent 95% confidence intervals. Previous estimates are based on Pimiento et al. (2013a) for the Gatun and Carrillo-Briceño et al. (2015a) for the Piña Sandstone facies of the Chagres Formation.

	Average depth (m)			Maximum depth (m)			
Formation	Min	Max	Mean	Min	Max	Mean	Previous Estimates (m)
Chucunaque	105	119	112	208	236	222	
Gatun	50	61	55	98	118	108	<100
Chagres (Piña Sandstone)	293	458	372	509	804	654	200–300

were unable to be assigned to the species level and those that are extinct were not included in this analysis in order to reduce potential bias. The data were then resampled 10,000 times and plotted as a histogram that provides a 95% confidence interval and a mean depth. This method was applied to the chondrichthyan fauna from the Chucunaque Formation, the Gatun Formation, and the Piña Sandstone facies of the Chagres Formation. The average and maximum depth estimates are reported in Figure 14 and Table 4. The average depth is the average of the usual depth range and the maximum depth is the upper limit of the usual depth range of each taxon. All data utilized for these analyses are available in Table 3.

Institutional abbreviations and repositories.—The specimens described here are conserved in the Vertebrate Paleontology Collection of the Florida Museum of Natural History (FLMNH), University of Florida (UF). Specimen information can be found in the FLMNH Vertebrate Paleontology Database (http://www.flmnh.ufl.edu/vertpaleo-search/) or in the Smithsonian Tropical Research Institute (STRI) Geological Sample Database (http://biogeodb.stri.si.edu/jaramillo/fossildb).

Systematic paleontology

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Order Squaliformes Goodrich, 1909
Family Centrophoridae Bleeker, 1859
Genus *Centrophorus* Müller and Henle, 1837

Type.—*Centrophorus granulosus* Müller and Henle, 1837 (Cappetta, 2012).

Centrophorus sp.
Figure 3.1, 3.2

Occurrence.—STRI 290109.

Description.—Small, asymmetric tooth with a broad crown and an apron indicative of the order Squaliformes. However, it is worth noting that the apron is not characteristic of all families within the order Squaliformes, as it is absent in the upper teeth of Dalatiidae, Oxynotidae, and Etmopteridae. The mesial edge is convex basally and straight apically, has coarse serrations near the base that become smaller apically and disappear prior to the apex; the distal edge is slightly convex with a complete cutting edge. There is a prominent notch on the distal edge; however, the distal heel is not entirely preserved. The labial face is

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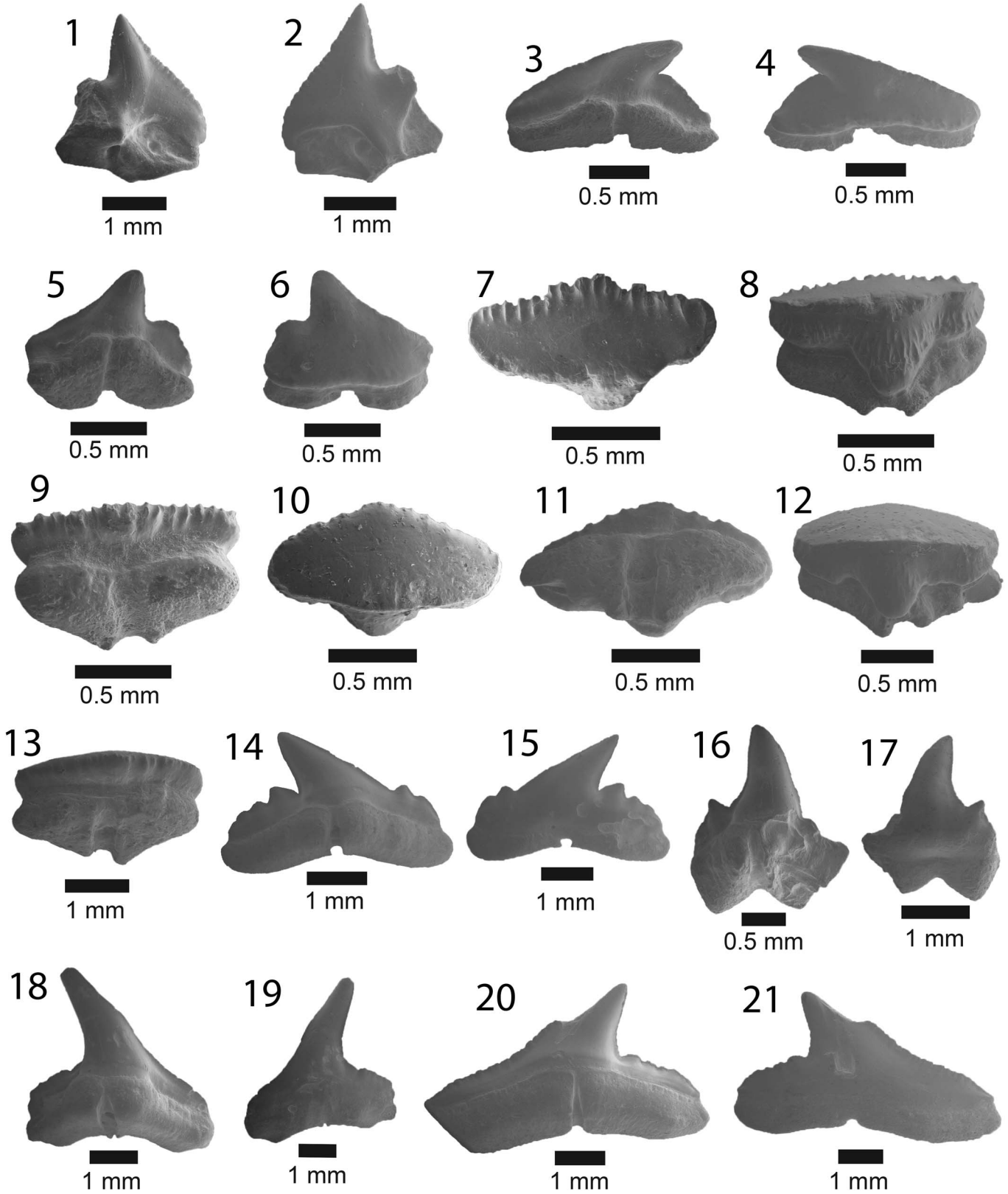

Figure 3. SEM images of specimens belonging to the subdivision Selachii. (**1, 2**) *Centrophorus* sp., UF 281349, lower anterolateral tooth in lingual and labial view, respectively; (**3–6**) cf. *Iago* sp.: (**3, 4**) UF 281382, lateral tooth in lingual and labial view, respectively; (**5, 6**) UF 281383, anterolateral tooth in lingual and labial view, respectively; (**7–9**) *Mustelus* sp., UF 281384, indeterminate position in occlusal, lingual, and baso-labial view, respectively; (**10–13**) *Mustelus* sp., UF 281386, indeterminate position in occlusal, basal, lingual, and labial view, respectively; (**14–19**) *Physogaleus* sp.: (**14, 15**) UF 281354, upper lateral tooth in lingual and labial view, respectively; (**16, 17**) UF 281353, anterior tooth in lingual and labial view, respectively; (**18, 19**) UF 281351, indeterminate position in lingual and labial view, respectively; (**20, 21**) *Carcharhinus* sp., UF 281338, pathologic upper tooth in lingual and labial view, respectively.

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flat with an elongate apron that extends well onto the root. The lingual face is convex with a short uvula that comes to a point. In labial view on the mesial side, the root is narrow, has a slightly concave basal margin, and a large foramen adjacent to the apron. On the distal side, the root is mostly broken off, but appears to have been larger than the mesial side. On the lingual face, there is a slight lingual bulge at the extremity of the uvula, a large infundibulum beneath the uvula, and a depression on the mesial side of the root. *Centrophorus* sp. from the Chucunaque Formation has a CH = 2.06 mm and CW = 2.28 mm.

Material.—One isolated tooth; anterolateral: UF 281349.

Remarks.—No teeth from the order Squaliformes were identified from the Gatun Formation (Pimiento et al., 2013a); however, they dominate the Piña Sandstone facies of the Chagres Formation (Carrillo-Briceño et al., 2015a). In contrast, only a single tooth from the Chucunaque Formation was identified as belonging to this order. Cappetta (1987, 2012) mentioned that the apron does not extend past the root in *Centrophorus*; however, that character cannot be addressed with this specimen (Fig. 3.2). Cappetta (1987, p. 53) described *Centrophorus* as being "not rare in bathyal deposits" in the Miocene of France. Carrillo-Briceño et al. (2015a) identified 11 teeth as *Centrophorus* aff. *C. granulosus*. Extant *Centrophorus granulosus* are widespread with occurrences in the Eastern Atlantic, Western Central Atlantic, the Indian Ocean, and the Western Pacific (Compagno, 1984; Last and Stevens, 1994; and Compagno and Niem, 1998); however, it is not known from the Eastern Pacific (White et al., 2013). Extant representatives of the family Centrophoridae most commonly occur at depths of 1000–1500 m, however they have been reported at depths as shallow as 50 m (Compagno et al., 2005).

Order Lamniformes Berg, 1958
Family Otodontidae Glikman, 1964
Genus Carcharocles Jordan and Hannibal, 1923

Type.—*Carcharodon auriculates* Blainville, 1818 (Cappetta, 2012).

Carcharocles megalodon (Agassiz, 1835)
Figure 4.1–4.5

Holotype.—An upper anterior tooth attributed to *Carcharodon megalodon* (TE-PLI 18) preserved in the Staatliches Museum für Naturkunde in Karlsruhe, Germany (Purdy et al., 2001). Originally described in Agassiz (1835, pl. 29, figs. 2, 3).

Occurrence.—STRI 290116, STRI 290125, STRI 290139, STRI 290144, STRI 290145, STRI 300029, STRI 300032, STRI 430011, and STRI 430012.

Description.—Large, triangular teeth; broad crown, uniform (or nearly uniform) serrations, convex lingual face with a distinct neck (i.e., bourlette), flat or convex labial face. Robust, thick, and U-shaped root with dispersed foramina; foramina tend to be concentrated at the crown-root contact on the labial face (Fig. 4.1, 4.2). *Carcharocles megalodon* exhibits monognathic and dignathic heterodonty. Upper teeth are broader, especially at the crown apex, with more convex cutting edges. Lower teeth are narrower with sigmoidal, straight, or concave cutting edges. There is an increasing asymmetry antero-laterally throughout the jaw. Posterior teeth are much smaller than anterior teeth with a more obtuse to nearly straight basal root margin. One specimen, UF 275108, has a reduced lateral cusplet (i.e., a vestigial cusplet; Fig. 4.3–4.5). *Carcharocles megalodon* from the Chucunaque Formation range from CH = 24.6–88.2 mm and CW = 28.6–88.0 mm.

Materials.—Sixty isolated teeth; upper anterior: UF 275085, UF 275097, UF 275110, UF 275111, UF 275118, and UF 275132; lower anterior: UF 275129 and UF 275136; upper lateral: UF 275084, UF 275092, UF 275109, UF 275114, UF 275128, and UF 275139; lower lateral: UF 275086, UF 275131, and UF 275134; posterior: UF 275053; indeterminate position: UF 275051–52, UF 275096, UF 275098–99, UF 275107–08, UF 275112–13, UF 275117, UF 275126–27, UF 275130, UF 275133, UF 275135, UF 275137, UF 275138, UF 275148, UF 275151, and UF 275156.

Remarks.—The generic assignment of this species has been highly contested over the last century, with *Carcharocles*, *Megaselachus*, *Carcharodon*, *Procarcharodon*, and *Otodus* all being suggested as the most appropriate. A morphometrics study by Nyberg et al. (2006) determined that *C. megalodon* is not ancestral to *Carcharodon carcharias*, suggesting it belongs in a separate lineage with *Otodus obliquus* as the ancestor. Consequently, the oldest alternative generic assignment takes precedence, which is *Carcharocles* (Jordan and Hannibal, 1923). For a more detailed discussion on this topic see Pimiento et al. (2010). In the Chucunaque Formation, *C. megalodon* is intermediate in size between that of the Gatun Formation and the Yorktown Formation (Purdy et al., 2001; Pimiento et al., 2013a; Pimiento and Balk, 2015), but more closely aligns with the size range observed in the Gatun Formation, which has been proposed to be a paleonursery for *C. megalodon* (Pimiento et al., 2010). The lack of lateral cusplets and a broader crown are said to delineate *C. megalodon* from *Carcharocles chubutensis*, although neither of those characteristics is absolutely definitive (Kent, 1994). Lateral cusplets may still occur in juvenile individuals of *C. megalodon* (Pimiento et al., 2010), or as vestigial characters in adults (Fig. 4.3–4.5). *Carcharocles megalodon* had a cosmopolitan distribution, occurring in tropical to temperate coastal habitats (Gottfried et al., 1996; Purdy, 1996; Pimiento et al., 2016). Recent studies have calculated the most likely time of extinction of this species to be 2.6 Ma (Pimiento and Clements, 2015). In the region, *C. megalodon* occurs in both the Caribbean and the Pacific (Longbottom, 1979; De Muizon and DeVries, 1985; Long, 1993; Iturralde-Vinent et al., 1996; Laurito, 1999; Aguilera and Rodrigues de Aguilera, 2001; Donovan and Gunter, 2001; Nieves-Rivera et al., 2003; Portell et al., 2008; Carrillo-Briceño et al., 2015a).

Family Lamnidae Müller and Henle, 1838
Genus *Isurus* Agassiz, 1843

Type.—*Isurus oxyrinchus* (Rafinesque, 1810) (Cappetta, 2012).

Isurus oxyrinchus (Rafinesque, 1810)
Figure 4.6–4.16

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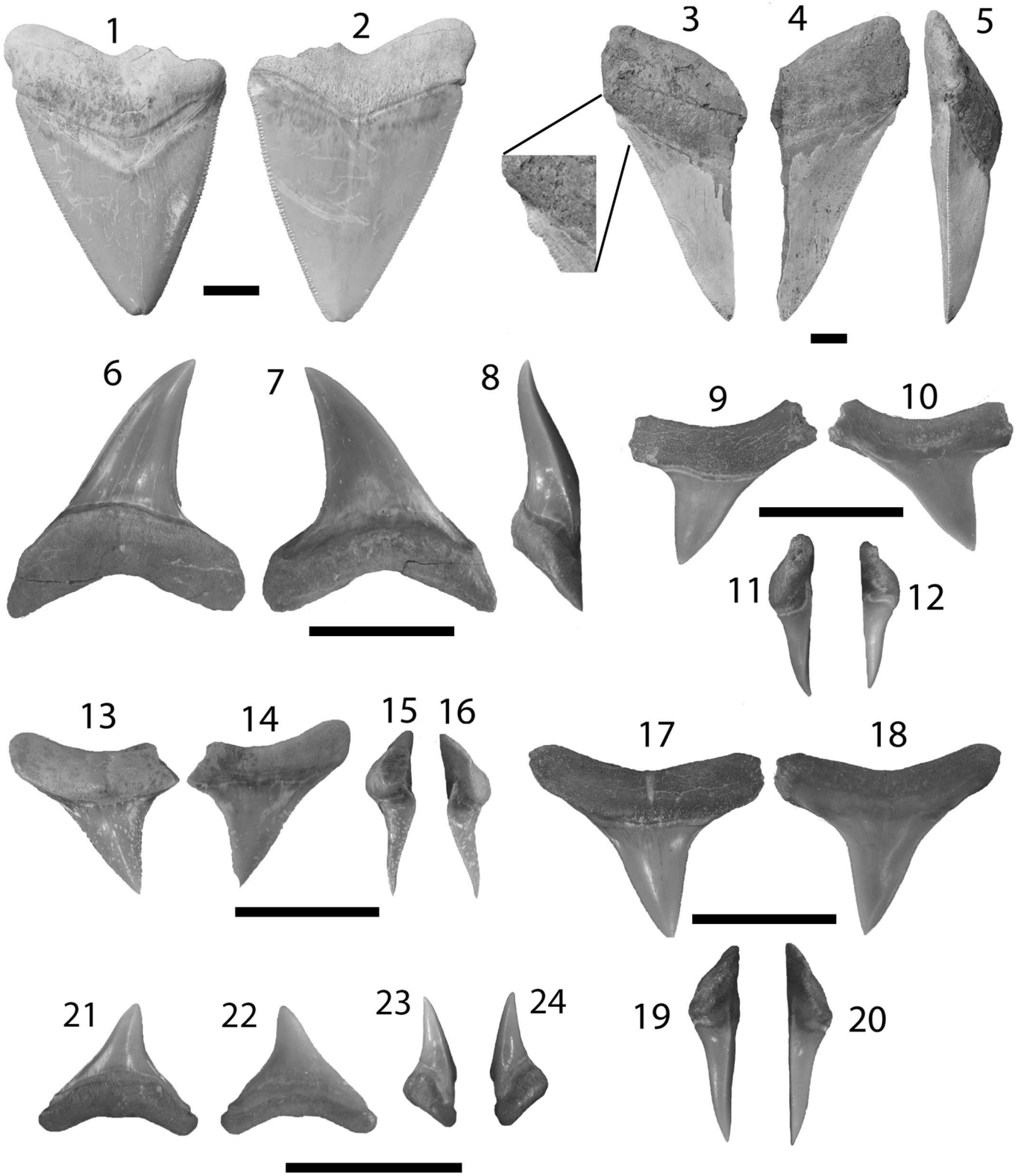

Figure 4. Lamniformes: *Carcharocles*, *Isurus*, and *Alopias* from the Chucunaque Formation. (**1–5**) *Carcharocles megalodon* (Agassiz, 1843): **(1, 2)** UF 275110, upper right anterior (most complete tooth) in lingual and labial view, respectively (scale bar = 5 cm); (**3–5**) UF 275108, upper tooth bearing a vestigial lateral cusplet in lingual, labial, and lateral view, respectively (scale bar = 5 cm); (**6–16**) *Isurus oxyrinchus* (Rafinesque, 1810): (**6–8**) UF 275124, lower right lateral in lingual, labial, and distal lateral view, respectively (scale bar = 1 cm); (**9–12**) UF 281169, upper left lateral in lingual, labial, mesial lateral, and distal lateral view, respectively (scale bar = 1 cm); (**13–16**) UF 281181, upper lateral tooth in lingual, labial, distal lateral, and mesial lateral view, respectively (scale bar = 1 cm); (**17–20**) *Alopias superciliosus* (Lowe, 1840), UF 275057, lower position in lingual, labial, distal lateral view, and mesial lateral, respectively (scale bar = 1 cm); (**21–24**) *Alopias* cf. *A. vulpinus* (Bonnaterre, 1788), UF 281321, upper position in lingual, labial, mesial lateral, and distal lateral view, respectively (scale bar = 1 cm). Photo credit: S. Moran and R. Leder.

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Holotype.—Originally described as *Oxyrhina desori* by Agassiz (1843, pl. 37, figs. 8–10) from the Miocene of Switzerland. Purdy et al. (2001) recognized one tooth among the syntypes (ETHGI P145) described by Agassiz (1843) as the second upper anterior of *Isurus*, and named it the lectotype of *Isurus oxyrinchus*.

Occurrence.—STRI 290145, STRI 300029, STRI 300032, and STRI 430011.

Description.—Moderately large, triangular teeth lacking serrations; with a convex lingual face and flattened labial face. The crown apex is reflexed toward the labial face, and has a sigmoidal or straight profile. The root is robust, lacks a nutrient groove, and has an angled or U-shaped basal margin with pointed or rounded root lobes. Anterolaterally, the crown becomes shorter, increasingly asymmetric, and less noticeably recurved labially; and the root lobes become shorter and more compressed (Kent, 1994; Purdy et al., 2001). Upper teeth differ from lower teeth in having a broader basal root angle and a much weaker sigmoidal profile (Kent, 1994). *Isurus oxyrinchus* from the Chucunaque Formation ranges from CH = 8.6–15.0 mm and CW = 13.3–14.1 mm.

Materials.—Seven isolated teeth; upper laterals: UF 281169, UF 281173, and UF 281181; lower laterals: UF 275068, UF 275102, UF 275124, and UF 281172.

Remarks.—Labial recurvature of the apex is considered to be a diagnostic feature (Purdy et al., 2001; Reis, 2005); however, Purdy et al. (2001) noted that this feature is most apparent in upper anterior teeth and may not be present in lateral teeth. Portell et al. (2008) identified six *I. oxyrinchus* teeth from the Miocene of Carriacou, Grenada, with the largest tooth being a lateral tooth with CH = 13.5 mm and CW = 6.6 mm. Teeth from the Chucunaque Formation are slightly larger than those from Carriacou. Anterior teeth from the Pungo River Formation range from CH = 27.0–50.0 mm and CW = 17.0–29.0 mm, whereas anterior teeth from the Yorktown Formation range from CH = 28.0–58.0 mm and CW = 11.0–32.0 mm (Purdy et al., 2001). Measurements from Purdy et al. (2001) are not directly comparable to those in this study or that of Portell et al. (2008) because they were taken from anterior teeth. Even so, the teeth described by Purdy et al. (2001) represent much larger sharks that those observed in the Chucunaque Formation. *Isurus oxyrinchus* has also been observed from the Miocene of Brazil (Reis, 2005) and the Pliocene of Angola (Antunes, 1978). *Isurus oxyrinchus* is not recorded from the Gatun Formation of Panama (Pimiento et al., 2013a). Extant individuals are coastal and oceanic with a cosmopolitan distribution in temperate and tropical seas (Compagno et al., 2005), occurring most frequently from the Caribbean to Argentina (Compagno, 1984). *Isurus oxyrinchus* is predominantly epipelagic, but has been reported close inshore (Last and Stephens, 1994; Yamada et al., 1995; Mundy, 2005). Direct telemetry data in the North Pacific (Holts and Bedford, 1993), as well as temperature and occurrence data inferred from longline records in the Atlantic (Hoey, 1983), suggest that *Isurus oxyrinchus* has a preferred temperature range of 14–22°C (Heist et al., 1996). This temperature range corresponds with the common depth range of 100–150 m observed by Bianchi et al. (1999), however Compagno et al. (2005) reported a depth range of 0–500 m.

Family Alopiidae Bonaparte, 1838
Genus *Alopias* Rafinesque, 1810

Type.—*Alopias macrourus* Rafinesque, 1810 (Cappetta, 2012).

Alopias superciliosus (Lowe, 1841)
Figure 4.17–4.20

Holotype.—Originally described as *Alopecias superciliosus* by Lowe (1841, p. 39) based on a single young specimen with no mention of its provenance. According to Eschmeyer (1998), the holotype is unknown; however, the type locality is Madeira, eastern Atlantic (Compagno, 2001, p. 83).

Occurrence.—STRI 300032 and STRI 430011.

Description.—Small to moderate-sized, triangular crown that is broad, erect, and lacks serrations. The mesial edge is straight to slightly convex, while the distal edge is straight to slightly concave. The lingual face is convex and the labial face is flat with enameloid extending well onto the root. Flattened root with rounded root lobes, distinct nutrient groove, and obtusely angled basal margin. The moderately broad crown and distally oriented asymmetry indicate a lateral position (Kent, 1994; Purdy et al., 2001). *Alopias superciliosus* from the Chucunaque Formation has a CH = 4.2–10.3 mm and a CW = 6.3–15.4 mm.

Materials.—Three isolated teeth; lower lateral: UF 275057, UF 281318, and UF 281319.

Remarks.—*Alopias* differs from *Isurus* in having a shorter, broader crown with a concave basal root margin. *Alopias superciliosus* differs from *Alopias* cf. *A. vulpinus* in having a more slender crown, a distinct nutrient groove, and less robust root lobes (Kent, 1994). *Alopias superciliosus* is an uncommon species, with only three teeth identified from the Chucunaque Formation. Purdy et al. (2001) only described a single anterior tooth from the Pungo River Formation, and Kent (1994) stated that *A. superciliosus* is uncommonly found in the Calvert Formation of the Chesapeake Bay region. The anterior tooth of *Alopias* cf. *A. superciliosus* reported by Purdy et al. (2001) has a height of 13 mm and a width of 9 mm. Extant individuals in the genus *Alopias* reach a maximum TL = 6 m (Springer and Gold, 1989), although half of the body length is represented by its elongated caudal fin (Kent, 1994). *Alopias superciliosus* has been reported from the lower Miocene of North Carolina (Case, 1980); the middle Miocene of Parma, Italy (Cigala-Fulgosi, 1983) and Lisbon, Portugal (Antunes, 1970); the late Miocene of Panama (Carrillo-Briceño et al., 2015a); and the Pliocene of Tuscany, Italy (Cigala-Fulgosi, 1988). The extant species has a circumglobal distribution in tropical and temperate seas; occurring in coastal waters over continental shelves, sometimes close inshore in shallow waters, and far from land in open ocean (Compagno, 1984). *Alopias superciliosus* is a highly migratory species found in oceanic, pelagic, and near

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bottom waters at depths of 0–730 m (McMillan et al., 2011), but most frequently occurs between 100 and 500 m (Compagno, 1984, 2001; Compagno et al., 2005; Mundy, 2005). *Alopias superciliosus* is more tolerant of cold water, as low as 6°C, than most other sharks identified from Lago Bayano and has been observed occupying colder, deep water (200–550 m and 6–11°C) during the day and shifting to warmer, mixed layers at night (50–130 m and 15–26 °C; Smith et al., 2008).

Alopias cf. *A. vulpinus* (Bonnaterre, 1788)
Figure 4.21–4.24

Holotype.—Originally described as *Squalus vulpinus* by Bonnaterre (1788, p. 9, pl. 85, fig. 349). According to Eschmeyer (1998), the holotype is unknown; however, the type locality is the Mediterranean Sea (Compagno, 2001, p. 86).

Occurrence.—STRI 290109 and YPA105.

Description.—Short, triangular teeth with a broad base and acutely pointed apex. The cutting edges are complete, but lack serrations. The mesial edge is straight and the distal edge is convex or vertical. The enameloid extends well onto the root on the labial face. Robust root usually lacking a nutrient groove, root lobes are rounded and elongate, basal margin is smoothly concave. *Alopias* cf. *A. vulpinus* from the Chucunaque Formation range from CH = 1.2–7.1 mm and CW = 4.5–8.3 mm.

Materials.—Five isolated teeth; upper: UF 281321; indeterminate position: UF 275049 and UF 281320.

Remarks.—Kent (1994) identified two species of *Alopias* in the Chesapeake Bay region: *Alopias superciliosus* and *Alopias latidens*. However, Purdy et al. (2001) questioned the validity of *Alopias latidens* and, consequently, identified *Alopias superciliosus* and *Alopias vulpinus* as the only two thresher sharks that occur in the Lee Creek Mine. Descriptions of both *A. latidens* (Kent, 1994) and *A. vulpinus* (Purdy et al., 2001) align well with what is observed for *Alopias* cf. *A. vulpinus* from the Chucunaque Formation. Anterolateral teeth of *A. vulpinus* from the Pungo River Formation range from CH = 8.0–15.0 mm and were estimated to have correlated to a TL = 4.5–6 m (Purdy et al., 2001), which indicates that individuals from the Chucunaque Formation were smaller in size. Extant individuals of *A. vulpinus* have a cosmopolitan distribution in temperate and tropical seas, occurring in coastal and oceanic waters at depths from 0–550 m (Compagno, 1984; Cox and Francis, 1997); but most frequently are found near land at depths of 1–366 m (Compagno et al., 2005; Mundy, 2005). Young individuals are often found close inshore and in shallow bays (Compagno et al., 1989; Compagno et al., 2005). *Alopias vulpinus* is frequently encountered in temperate waters and more common in coastal environments than any of the other thresher sharks (Smith et al., 2008).

Order Carcharhiniformes Campagno, 1973
Family Triakidae Gray, 1851
Genus *Iago* Compagno and Springer, 1971

Type.—*Eugaleus omanensis* Norman, 1939 (Cappetta, 2012).

cf. *Iago* sp.
Figure 3.3–3.6

Occurrence.—STRI 290109 and YPA105.

Description.—Extremely small teeth with a short crown and root. The crown is distally arched with complete cutting edges. The mesial edge is slightly sigmoid, with a concave base and straight or concave apex; while the distal edge is convex or straight. There is a prominent rounded distal heel that forms a distinct notch. Lingual face is convex and the labial face is flat with weak folds at the crown base. The crown-root contact on the lingual face shows two distinct depressions on the mesial and distal edges where the crown thins out. On the labial face this contact is sharp, forming a distinct ridge. The root is high up on the lingual face with an observable lingual protuberance and distinct transverse furrow that penetrates the labial face. From the Chucunaque Formation cf. *Iago* sp. range from CH = 0.61–0.86 mm and CW = 1.01–1.67 mm.

Materials.—Thirty-six isolated teeth; lateroposterior: UF 281374, UF 281376, UF 281379; indeterminate position: UF 281373; UF 281375, UF 281377, UF 281378, and UF 281380–83.

Remarks.—These are among the smallest shark teeth found in Lago Bayano and are only found through screenwashing efforts. Teeth of cf. *Iago* sp. are about half the size of those attributed to *Physogaleus* sp. There are distinct similarities to *Iago oamanensis* imaged in Herman et al. (1988), particularly the complete cutting edges with a rounded distal heel that forms an acute notch with the principle cusp. Lateral teeth of some species of *Triakis*, such as *T. semifasciata* and *T. acutipinna*, have a similar morphology (Herman et al., 1988); however, anterior teeth bear lateral cusplets that were not observed in any of the recovered specimens. Neither *Iago* nor *Triakis* have previously been reported from the fossil record of Panama. There are two extant species of *Iago*, *I. garricki* and *I. omanensis*, both of which have a bathydemersal habit. *Iago garricki* is a tropical species occurring in the Pacific Ocean on upper continental and insular slopes between 250 and 475 m. *Iago omanensis* occurs in the Indian Ocean and prefers warm, poorly oxygenated water at depths of less than 110 to over 1000 m (Compagno et al., 2005).

Genus *Mustelus* Linck, 1790

Type.—*Squalus mustelus* Linnaeus, 1758 (Cappetta, 2012).

Mustelus sp.
Figure 3.7–3.13

Occurrence.—STRI 290109, STRI 290113, and YPA105.

Description.—The occlusal surface is smooth and has an elongate, roughly elliptical outline in apical view. The labial edge forms a prominent ridge at the crown-root margin and has a convex edge with folds that may be weak or strongly pronounced. The lingual face has a large central uvula with

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vertical, flexuous enameloid ripples and a somewhat sinuous outline. Root is thick with a medial groove that forms two short, asymmetric root lobes; there is a foramen nested within the medial groove that is oriented toward the labial side; the basal margin is flat, but slopes toward the labial face. The folds on the labial edge and the enameloid ripples on the lingual uvula are a diagnostic feature for the genus *Mustelus* (Herman, 1982; Cappetta, 1987; Leder, 2013). Two specimens of *Mustelus* sp. were imaged: UF 281384 in Figure 3.7–3.9 has a CH = 0.23 mm, CW = 1.17 mm, and CL = 0.64 mm; and UF 281386 in Figure 3.10–3.13 has a CH = 0.27 mm, CW = 1.37 mm, and a CL = 0.64 mm.

Materials.—Sixteen isolated teeth; indeterminate position: UF 281384–88.

Remarks.—*Mustelus* sp. from the Chucunaque Formation bears similarities to those described by Carrillo-Briceño et al. (2015a), with weak folding on the lingual uvula; however the images provided by Carrillo-Briceño et al. (2015a) do not show the labial face or the root. *Mustelus* sp. from the Pungo River Formation of the Lee Creek Mine have a CW = 1–1.3 mm and a CL roughly half the length of the CW (Purdy et al., 2001). Among the 28 extant species of *Mustelus*, all have a demersal habit, with most preferring subtropical to tropical conditions; however, *Mustelus antarcticus*, *M. asterias*, and *M. mustelus* prefer temperate waters (Compagno et al., 2005). Some species occur in up to 800 m depth (Kiraly et al., 2003), but most species generally occur at depths <200 m (Compagno, 1984).

Family Hemigaleidae Campagno, 1984
Genus *Hemipristis* Agassiz, 1843

Type.—*Hemipristis serra* Agassiz, 1843 (Cappetta, 2012).

Hemipristis serra Agassiz, 1843
Figure 5.1–5.16

Holotype.—Originally described by Agassiz (1843, pl. 27, figs. 18–30) from the Miocene of southern Germany. Cappetta (2012, fig. 279G–I) illustrated two syntypes: an upper lateral, UM LEE 4, and a lower anterior, UM LEE 5.

Occurrence.—STRI 290109, STRI 290116, STRI 290125, STRI 290139, STRI 290145, STRI 300029, STRI 300032, and STRI 430011.

Description.—Upper teeth are broad and distally inclined with serrated cutting edges that terminate prior to the apex. The mesial edge is convex with relatively uniform, moderate-sized serrations. The distal edge is concave with serrations that increase in size apically. The root is compressed, bearing a strong lingual protuberence with a deep nutrient groove that forms a Z-shaped basal margin. There is obvious monognathic and dignathic heterodonty, with increasing asymmetry antero-laterally. Lower teeth are narrow, elongate, and unserrated with incomplete cutting edges and small lateral cusplets. The lingual face is convex, whereas the labial face is convex basally and flattens apically. The root is bilobate with a high lingual protuberance and deep nutrient groove. *Hemipristis serra* ranges from CH = 10.4–32 mm and CW = 4.4–32 mm in the Chucunaque Formation.

Materials.—Sixty-one isolated teeth; upper anterior: UF 281404; upper symphyseal: UF 281396; upper: UF 275032, UF 275047, UF 275054, UF 275065, UF 275078, UF 275093, UF 275115, UF 275122, UF 275144, UF 275152, UF 281174; lower: UF 275100, UF 281389–95, and UF 281405.

Remarks.—*Hemipristis serra* has a cutting-grasping type dentition (Kent, 1994) and the largest teeth among the carcharhiniform sharks from the Chucunaque Formation. Upper teeth of *H. serra* differ from the genus *Carcharhinus* in having a smooth apex and coarser serrations on the distal edge; lower teeth differ from the genus *Carcharias* in having incomplete cutting edges that only comprise roughly the upper third of the crown (Kent, 1994). Purdy et al. (2001) observed *H. serra* teeth from the lower Miocene Pungo River Formation and from the early Pliocene Yorktown Formation and postulated that *H. serra* increased in size throughout its evolutionary history. Teeth from the Chucunaque Formation are larger than that of the younger Pungo River Formation (CH = 14.1–29.1 mm and CW = 12.3–35.5 mm) and smaller than the older Yorktown Formation (CH = 16.4–41.0 mm and CW = 14.0–43.5 mm) and, as such, follow the trend proposed by Purdy et al. (2001). Pimiento et al. (2013a) observed size ranges of CH = 5.4–21.6 mm and CW = 5.2–29.0 mm from the Gatun Formation, which contradicts the trend observed by Purdy et al. (2001). However, the Gatun Formation was described as a shark paleonursery (Pimiento et al., 2010; Pimiento et al., 2013a), in which smaller teeth might be anticipated. Compagno (1988) noted an increase in distal serrations on upper lateral teeth of the extant *Hemipristis elongatus* during ontogeny; so observation of serration abundance on upper lateral teeth of *H. serra* from the Gatun Formation may be used to distinguish between juvenile and adult individuals. *Hemipristis serra* occurs in Atlantic and Pacific deposits from the middle Eocene to at least the Pleistocene; and was particularly abundant in neritic, warm-water environments during the Miocene and Pliocene (Cappetta, 1987). Carrillo-Briceño et al. (2015a) observed *H. serra* in neritic Rio Indio facies and bathyal Piña Sandstone facies of the Chagres Formation. The much smaller, extant species, *Hemipristis elongatus*, is a coastal species that occurs inshore and offshore on continental and insular shelves, generally at depths of 1–132 m (Compagno, 1984; Last and Stephens, 1994; Compagno et al., 2005).

Family Carcharhinidae Jordan and Evermann, 1896
Genus *Galeocerdo* Müller and Henle, 1837

Type.—*Squalus cuvier* Peron and Lesueur, 1822 (Cappetta, 2012).

Galeocerdo aduncus (Agassiz, 1835)
Figure 5.17–5.20

Holotype.—Originally described as *Galeocerdo aduncus* by Agassiz (1835, pl. 26, figs. 24–28) from the Schwabia region of southwestern Germany, according to Purdy et al. (2001). These specimens were deposited in Staatliches Museum für

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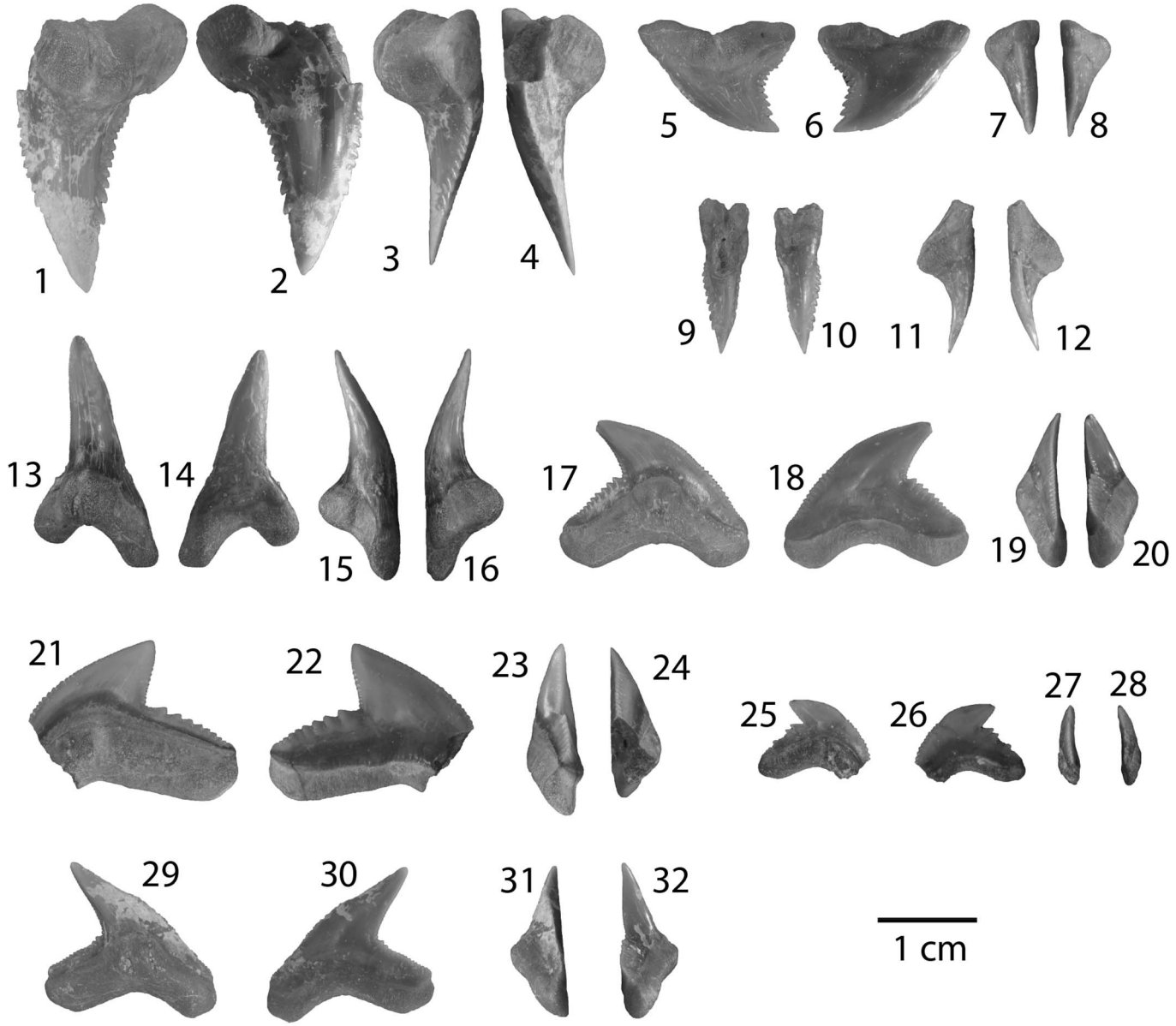

Figure 5. Carcharhiniformes I: *Hemipristis*, *Galeocerdo*, and *Physogaleus* from the Chucunaque Formation. (**1–16**) *Hemipristis serra* Agassiz, 1843: (**1–4**) UF 281404, upper anterior tooth in lingual, labial, distal lateral, and mesial lateral view, respectively; (**5–8**) UF 281174, upper lateral tooth in lingual, labial, distal lateral, and mesial lateral view, respectively; (**9–12**) UF 281396, upper symphyseal tooth in lingual, labial, distal lateral, and mesial lateral view, respectively; (**13–16**) UF 281405, lower lateral tooth in lingual, labial, mesial lateral, and distal lateral view, respectively; (**17–20**) *Galeocerdo aduncus* (Agassiz, 1835), UF 275083, indeterminate position in lingual, labial, mesial lateral, and distal lateral view, respectively; (**21–28**) *Galeocerdo cuvier* (Peron and Lesueur, 1822): (**21–24**) UF 281397, indeterminate position in lingual, labial, distal lateral, and mesial lateral view, respectively; (**25–28**) UF 275145, indeterminate position in lingual, labial, distal lateral, and mesial lateral view, respectively; (**29–32**) *Physogaleus contortus* (Gibbes, 1849), UF 281170, indeterminate position in lingual, labial, mesial lateral, and distal lateral view, respectively. Photo credit: R. Leder.

Naturkunde, Karlsruhe, but have since been lost (Purdy et al., 2001).

Occurrence.—STRI 290116 and STRI 430011.

Description.—Moderately large teeth with a thick, distally arched crown; deeply notched on the distal edge. The mesial edge is convex with moderately sized serrations basally and fine serrations apically; the distal side has a coarsely serrated distal heel lacking secondary serrations and a concave cutting edge with fine serrations. The root is thick with a prominent lingual protuberance and concave basal margin; there are numerous nutrient pores and a transverse nutrient groove may be poorly developed (e.g., UF 275083) or distinct (e.g., UF 281398); the distal root lobes are lingually recurved at the extremities, indicating overlapping teeth within the dentition (Purdy et al., 2001). *Galeocerdo aduncus* from the Chucunaque Formation has a CH = 10.2–11.7 mm and CW = 18.7–18.9 mm.

Materials.—Two isolated teeth; indeterminate position: UF 275083, UF 281398.

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Remarks.—There is much debate regarding the validity of *Galeocerdo aduncus* as a distinct species (Gottfried, 1993; Kent, 1994; Purdy et al., 2001; Ward and Bonavia, 2001). It has been suggested that *G. aduncus* and *Physogaleus contortus* represent teeth from a single species, with *G. aduncus* representing upper teeth and *P. contortus* representing lower teeth (Gottfried, 1993; Kent, 1994). However, the living tiger shark, *Galeocerdo cuvier*, lacks this marked dignathic heterodonty. *Galeocerdo aduncus* has a broader crown than *Physogaleus contortus*, but is narrower than *Galeocerdo cuvier*. *Galeocerdo aduncus* lacks the secondary serrations on the distal heel that are diagnostic of *G. cuvier* and the warped profile that is diagnostic of *P. contortus*. *Galeocerdo aduncus* was identified from the Gatun Formation by Gillette (1984), however the original specimens were missing and additional *Galeocerdo* specimens recovered by Pimiento et al. (2013a) were assigned to *Galeocerdo cuvier*. Our presumption would be that under greater scrutiny, with a particular focus on the distal cutting edge and the serrations on the distal heel, both *G. aduncus* and *G. cuvier* would be present in the Gatun Formation. Because the original holotype of *G. aduncus* described by Agassiz has since been lost, Purdy et al. (2001) referred to *G. aduncus* as a nomen dubium and, subsequently, classified the equivalent morphospecies as *Galeocerdo* sp. Herein, *G. aduncus* is recognized as a distinct species given the few unique characters discussed above, however, the tooth form of *G. aduncus* is quite similar to *G. cuvier*, implying a similar ecological niche. The teeth of *G. cuvier* are more robust and have a more advanced adaptation toward cutting, which may have given *G. cuvier* an advantage over *G. aduncus*.

Galeocerdo cuvier (Peron and Lesueur, 1822)
Figure 5.21–5.28

Holotype.—Originally described as *Squalus cuvier* from the northwest coast of New Holland by Peron and Lesueur (1822).

Occurrence.—STRI 290109, STRI 290116, STRI 290145, STRI 300029, STRI 300032, and STRI 430011.

Description.—Moderately large, robust teeth with a distally angled crown. Weakly convex distal edge with coarse serrations on the heel that are secondarily serrated and fine serrations apical of a deep distal notch; strongly convex mesial edge with serrations that decrease in size around the same height as the distal notch. Root has a concave basal margin, central foramen absent or weakly present. *Galeocerdo cuvier* from the Chucunaque Formation has a CH = 3.5–14.8 mm and CW = 10.4–25.1 mm.

Materials.—Fifteen isolated teeth; indeterminate position: UF 275045, UF 275060, UF 275062, UF 275082, UF 275095, UF 275105, UF 275120, UF 275145, and UF 281397.

Remarks.—*Galeocerdo cuvier* differs from *Galeocerdo aduncus* and *Physogaleus contortus* in having a broader crown with a more convex mesial edge and a convex distal edge. In profile view, the mesial edge of *Galeocerdo cuvier* is straight to nearly straight, whereas *P. contortus* appears to have a twist in the crown near the apex giving it a weakly sigmoidal appearance (Kent, 1994). *Galeocerdo cuvier* is an aggressive shark equipped with a cutting-type dentition bearing robust teeth adapted for both slicing and ripping (Frazzetta, 1988), which explains its wide variety of prey options (Kent, 1994). Teeth from the Gatun Formation, CH = 7.4–17.8 mm and CW = 14.4–24.5 mm (Pimiento et al., 2013a), and from the Yorktown Formation, CH = 13.5–29.1 mm and CW = 24.4–33.0 mm (Purdy et al., 2001), are larger than those found in the Chucunaque Formation. According to Kent (1994), extant *G. cuvier* reach lengths up to 7.4 m, but fossil evidence suggests that earlier individuals were likely less than half this length. *Galeocerdo cuvier* is a highly migratory species with circumglobal distribution in tropical and temperate seas occurring in: Western Atlantic: Massachusetts, USA to Uruguay, including the Gulf of Mexico and the Caribbean; Eastern Atlantic: Iceland to Angola; Indo-Pacific: Red Sea and East Africa to Hawaii and Tahiti, north to southern Japan, south to New Zealand; and Eastern Pacific: southern California, USA to Peru (Garcia, 1994). It has been recognized in a wide variety of habitats, but occurs most frequently at depths less than 140 m (Compagno, 1984, 1988; Smith, 1997; Compagno et al., 2005).

Genus *Physogaleus* Cappetta, 1980

Type.—*Trigonodus secundus* Winkler, 1876 (Cappetta, 2012).

Physogaleus contortus (Gibbes, 1849)
Figure 5.29–5.32

Holotype.—Originally described as *Galeocerdo contortus* from the Eocene of South Carolina and the Miocene of Virginia by Gibbes (1849, pl. 25, figs. 71–74).

Occurrence.—STRI 290109, STRI 290116, STRI 290145, STRI 300029, STRI 300032, and STRI 430011.

Description.—Moderately large teeth with a slender, distally angled crown. The mesial edge is finely serrated with a warped profile, while the distal edge is notched with fine serrations on the heel and even finer serrations apical of the notch. The root is robust with a U-shaped basal margin and a large lingual protuberance bearing a nutrient groove. *Physogaleus contortus* from the Chucunaque Formation range from CH = 6.1–14.9 mm and CW = 9.2–17.1 mm.

Materials.—Eighteen isolated teeth; indeterminate position: UF 275037, UF 275059, UF 275064, UF 275069, UF 275125, UF 275146, UF 281170, and UF 281171.

Remarks.—Distinguishing features between *Physogaleus* and *Galeocerdo* are mentioned above, however it is worthwhile to also mention that *Physogaleus* has finer serrations on the distal heel with a less drastic distal notch and a more pronounced lingual protuberance on the root. The distribution of *Physogaleus contortus* is difficult to surmise given the confusion that exists regarding its distinction from the genus *Galeocerdo* (Cappetta, 1980, 1987, 2012; Gillette, 1984; Kent, 1994; Purdy et al., 2001; Ward and Bonavia, 2001) and recent re-assignment to the genus

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Physodon (Leder, 2013). Springer (1964) stated that the type specimen of *Physodon muelleri* described by Müller and Henle (1841) actually belonged to a male *Scoliodon laticaudus*, and chose to synonymize the two genera (Cappetta, 1987, 2012). Leder (2013) described *Physodon* (= *Physogaleus*) *contortus* from the Eocene of Crimea; in which he noted similarities with both *Galeocerdo* and *Physogaleus*, but overall determined it was unique and, consequently, chose to resurrect the genus *Physodon* described by Müller and Henle (1841). Cappetta (1980, 1987, 2012) described *P. contortus* as being a characteristic component of the Miocene deposits of the Gulf Atlantic Coastal Plain that does not occur in Europe; however, Purdy et al. (2001) recognized misidentifications by Storm (1894), Leriche (1927), and Caretto (1972) that actually represent *P. contortus* from Europe. *Physogaleus contortus* from the Gatun Formation range from CH = 10.0–11.1 and CW = 12–15.5 mm (Pimiento et al., 2013a) and from the Pungo River Formation range from CH = 12.0–19.4 mm and CW = 12.0–19.5 mm (Purdy et al., 2001). Purdy et al. (2001) noted that *P. contortus* is twice as common as *Galeocerdo* in the Lee Creek Mine, whereas only two specimens of *P. contortus* were identified from the Gatun Formation (Pimiento et al., 2013a). In the Chucunaque Formation, *P. contortus* (N = 19) and *Galeocerdo* (N = 17) have nearly the same abundance. The slender, more delicate crown of *P. contortus* indicates a greater reliance on grasping than cutting during feeding, suggesting a different ecological niche than that of *Galeocerdo*.

Physogaleus sp.
Figure 3.14–3.19

Occurrence.—STRI 290109 and YPA105.

Description.—Small teeth, with a triangular shape and a distally arched, labio-lingually compressed crown. The mesial edge is convex or straight; the distal edge is slightly concave to nearly straight. There is a strong distal notch with well-defined lateral cusplets on the distal heel; the mesial heel may or may not bear lateral cusplets. Anterior teeth are more erect and symmetrical than lateral teeth; anterior teeth have a CH:CW ratio close to 1:1, whereas lateral teeth have a CH:CW ratio closer to 1:2. Leder (2013) reported similar height:width ratios for *Physogaleus tertius* teeth of 1:1 to 5:6 for anteriors and 1:2 for the posterolateral positions. The root has a lingual bulge with nutrient pores at the crown-root margin and a prominent axial nutrient groove that penetrates the labial face; the labial face is narrow with a smooth, nearly horizontal crown-root margin. *Physogaleus* sp. from the Chucunaque Formation has a range of CH = 1.61–3.21 mm and CW = 1.81–3.83 mm.

Materials.—Fifteen isolated teeth; anterior: UF 281353; upper: UF 281354, UF 281357; lower anterior: UF 281351, UF 281359; indeterminate position: UF 281352, UF 281356, UF 281358, and UF 281360.

Remarks.—Interpretation of *Physogaleus* and related genera, such as *Galeorhinus* and *Physodon*, among others, is highly debated. Cappetta (1987, 2012) suggested that fossils identified as *Galeorhinus* and *Physodon* may be male and female teeth belonging to the extinct genus *Physogaleus*. The genus *Physogaleus* has not yet been reported from Panama, with the exception of *Physogaleus contortus*, which has since been reassigned to the genus *Physodon* based on the work of Leder (2013). *Galeorhinus* cf. *G. galeus* identified from the Chagres Formation (Carrillo-Briceño et al., 2015a) shares many similarities with *Physogaleus* sp. reported herein; however, they are distinct. *Galeorhinus* often has a concave mesial apex and convex distal edge, lacks lateral cusplets on the mesial edge, and has robust serrations on the distal heel that rise high up the crown. These teeth are also similar to cf. *Iago* sp., but differ, especially, in terms of size and the presence of lateral cusplets. *Physogaleus* sp. is about twice the size of cf. *Iago* sp. and has well-defined lateral cusplets, although the presence of cusplets may vary depending on the position within the jaw. *Physogaleus* has been reported from the Eocene of Morocco, West Africa, Egypt, Belgium, Crimea, and Georgia, United States; the Oligocene of Belgium, France, and Hungary; and the Miocene of France (Cappetta, 1987; Leder, 2013).

Genus *Carcharhinus* Blainville, 1816

Type.—*Carcharias melanopterus* Quoy and Gaimard, 1824 (Cappetta, 2012)

Carcharhinus falciformis (Bibron, 1841 in Müller and Henle, 1839–1841)
Figure 6.1–6.4

Holotype.—Originally described as *Carcharias* (*Prionodon*) *falciformis* by Bibron (1841 in Müller and Henle, 1839–1841, p. 47). The holotype, MNHN 1134, a 528 mm female fetus from

Figure 6. Carcharhiniformes II: *Carcharhinus* from the Chucunaque Formation. (**1–4**) *Carcharhinus falciformis* (Bibron, 1841 in Muller and Henle, 1839–1841), UF 281162, upper tooth in lingual, labial, distal lateral, and mesial lateral view, respectively (scale bar = 1 cm); (**5–7**) *Carcharhinus brevipinna* (Blainville, 1816), UF 281159, upper tooth in lingual, labial, and distal lateral view, respectively (scale bar = 1 cm); (**8–13**) *Carcharinus* aff. *C. macloti* (Müller and Henle, 1839): (**8, 9**) UF 281323, upper anterior tooth in lingual and labial view, respectively (scale bar = 0.5 cm); (**10**) UF 281325, upper lateral in lingual view (scale bar = 0.5 cm); (**11–13**) UF 275061, upper lateral tooth in lingual, labial, and mesial lateral view, respectively (scale bar = 1 cm); (**14–20**) *Carcharhinus obscurus* (Lesueur, 1818): (**14–16**) UF 281147, upper tooth in lingual, labial, and distal lateral view, respectively (scale bar = 1 cm); (**17–20**) UF 281152, lower tooth in lingual, labial, mesial lateral, and distal lateral view, respectively (scale bar = 1 cm); (**21–24**) *Carcharhinus plumbeus* (Nardo, 1827), UF 281143, upper tooth in lingual, labial, mesial lateral, and distal lateral view, respectively (scale bar = 1 cm); (**25–49**) *Carcharhinus* sp.: (**25–28**) UF 281165, upper anterior tooth in lingual, labial, distal lateral, and mesial lateral view, respectively (scale bar = 1 cm); (**29–32**) UF 281348, upper anterior tooth in lingual, labial, distal lateral, and mesial lateral view, respectively (scale bar = 1 cm); (**33–36**) UF 275141, lower anterior tooth in lingual, labial, distal lateral, and mesial lateral view, respectively (scale bar = 1 cm); (**37–39**) UF 275141, lower lateral tooth in lingual, labial, distal lateral, and mesial lateral view, respectively (scale bar = 1 cm); (**40–42**) UF 281164, lower posterior tooth in lingual, labial, distal lateral view, respectively (scale bar = 1 cm); (**43–46**) UF 281182, lower posterior tooth in lingual, labial, mesial lateral, and distal lateral view, respectively (scale bar = 1 cm); (**47**) UF 281402, upper pathologic tooth in lingual view; (**48**) UF 281167, upper pathologic tooth in lingual view (scale bar = 1 cm); (**49**) UF 281168, upper pathologic tooth in apical view (scale bar = 1 cm). Photo credit: R. Leder.

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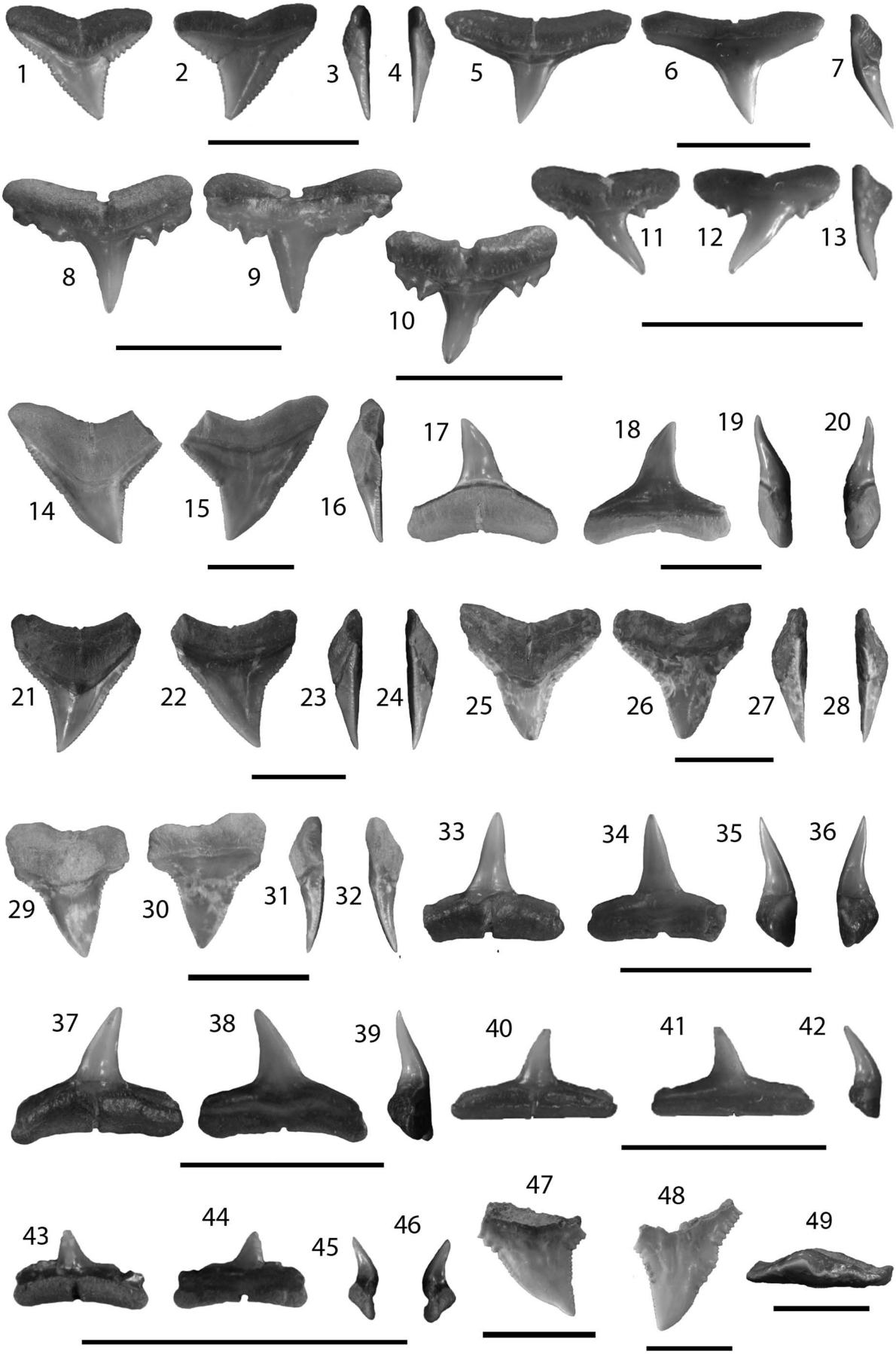

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Cuba, resides in the Museum National d'Histoire Naturelle, Paris, France (Garrick et al., 1964; Compagno, 1984).

Occurrence.—STRI 290109 and STRI 300032.

Description.—Small, triangular teeth; relatively narrow crown, straight mesial edge, concave or angular distal edge, notch on mesial and distal edges marks a transition from coarser basal serrations to finer apical serrations. Thin root with a nutrient groove and a flat or obtusely concave basal margin. Features distinguishing *C. falciformis* from other *Carcharhinus* species are its small size, narrow crown with a notch on both cutting edges, and a relatively flat basal root margin. *Carcharhinus falciformis* from the Chucunaque Formation range from CH = 5.5–6.1 mm and CW = 6.5–11.7 mm.

Materials.—Four isolated teeth; upper lateral: UF 281160, UF 281161, and UF 281162.

Remarks.—*Carcharhinus falciformis* is a solitary species (Claro, 1994) and yet, is commonly caught by fisheries (Bonfil et al., 2009). However, this species has a relatively sparse fossil record; Pimiento et al. (2013a) reported three isolated upper teeth from the Gatun Formation and Purdy et al. (2001) referred to five teeth in the USNM collection from the Pungo River Formation. Pimiento et al. (2013a) recorded a range from CH = 5.1–7.2 mm and CW = 4.9–6.4 mm; whereas Purdy et al. (2001) only measured a single tooth with CH = 14.2 mm and CW = 15.0 mm that was estimated to have originated from an ~3 m shark. The teeth from the Chucunaque Formation are more closely aligned with the size range observed from the Gatun Formation. In past descriptions of this species, a gap in the serrations on the mesial edge around the midpoint of the crown has been used as a definitive feature (Purdy et al., 2001; Pimiento et al., 2013a). However, this feature is not observed in extant individuals of *Carcharhinus falciformis* (Purdy et al., 2001) and, as such, should not be considered definitive. This interpretation of a gap in serrations can likely be attributed to the transition from coarse to fine serrations at the mesial notch. Extant *C. falciformis* has a circumtropical distribution and are commonly found at depths ranging from 18 to 500 m near the edge of continental and insular shelves, but also occur in open sea and occasionally inshore (Compagno, 1984; Compagno et al., 2005; Bonfil et al., 2009).

Carcharhinus brevipinna (Müller and Henle, 1839)
Figure 6.5–6.7

Holotype.—Originally described as *Carcharias* (*Aprion*) *brevipinna* by Müller and Henle (1839, p. 31–32, pl. 9). The holotype is a 785 mm mounted skin, RMNH D2525, from Java, Indonesia that resides in Naturalis - National Natuurhistorisch Museum, Leiden, Netherlands (Compagno, 1984).

Occurrence.—STRI 290109, STRI 290113, STRI 290116, STRI 300029, STRI 300032, STRI 430011, STRI 430012, and YPA105.

Description.—Small, triangular teeth; slender, finely serrated crown that is often inclined lingually, with straight mesial and distal cutting edges. The lingual face is convex and the labial face is flat apically and convex basally, forming a ridge along the crown-root margin. The root is short with a nutrient groove and horizontal basal margin. Differentiating between upper and lower teeth is difficult, however in extant individuals upper teeth are often slightly broader (personal observation, V.J. Perez, 2015). *Carcharhinus brevipinna* from the Chucunaque Formation range from CH = 2.7–8.6 mm and CW = 5.4–13.2 mm.

Materials.—One hundred forty-seven isolated teeth; lower: UF 281159; indeterminate position: UF 275041, UF 275070, UF 281153–58, and UF 281322.

Remarks.—*Carcharhinus brevipinna* is a relatively common species; however, its range and abundance are difficult to surmise given the constant confusion with the closely related species, *Carcharhinus limbatus* (Burgess, 2009). The two differ in that *C. brevipinna* has a shorter, slightly more asymmetric crown than *C. limbatus*. Also, upper teeth of *C. limbatus* typically have coarser serrations on the shoulders, particularly on the distal heel. Naylor (1990) conducted a principal component analysis to determine if upper teeth of these two species could be distinguished when monognathic variation was removed (i.e., could isolated upper teeth of these two species be distinguished from one another). The statistical analysis found that the two do in fact form distinct clusters, suggesting that isolated upper teeth can be identified to the species level. However, teeth belonging to *C. brevipinna* formed two sub-clusters that separated juveniles from adults, implying that ontogenetic variability could still pose a problem in identifying *C. brevipinna*. Neither *C. brevipinna* nor *C. limbatus* have been identified from the fossil record of Panama. Aguilera et al. (2011) did not recognize *C. brevipinna* from any Neogene locality from the Caribbean Neotropics, and only recognized *C. limbatus* from Venezuela. Carillo-Briceño et al. (2015b) identified two upper lateral teeth of *C. limbatus* from the middle-late Miocene Urumaco Formation in Venezuela. *Carcharhinus brevipinna* typically occurs on continental and insular shelves at depths of 0–100 m in warm temperate to tropical waters in the Atlantic, Mediterranean, and Indo-West Pacific (Compagno, 1984; Reiner, 1996; Burgess, 2009).

Carcharhinus aff. *C. macloti* (Müller and Henle, 1839)
Figure 6.8–6.13

Holotype.—Originally described as *Carcharias* (*Hypoprion*) *macloti* by Müller and Henle (1839, p. 34, pl. 10). The holotype is an adult male from New Guinea deposited in Rijksmuseum van Natuurlijke Historie, Leiden (Compagno, 1984).

Occurrence.—STRI 290109, STRI 290113, STRI 290145, STRI 300032, and YPA105.

Description.—The crown is small with complete cutting edges that lack serrations; however the heels are equipped with distinct lateral cusplets. On the labial face, the enamel extends well onto the root. The robust root is bilaterally symmetrical with a nutrient groove that penetrates the horizontal basal margin.

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Images of *Carcharhinus macloti* from Purdy et al. (2001) indicate that the crown becomes increasingly more distally arched posteriorly and the root lobes diminish toward the posterior, forming a more horizontal basal margin. This heterodonty was also observed in the Chucunaque Formation (anterior tooth position, Fig. 6.8, 6.9; lateral tooth positions, Fig. 6.10–6.13). Purdy et al. (2001) noted that lower teeth of *C. macloti* do not bear lateral cusplets. *Carcharhinus* aff. *C. macloti* from the Chucunaque Formation range from C = 4.2–6.3 mm and CW = 4.2–6.1 mm.

Materials.—Ten isolated teeth; upper: UF 275061, UF 281166, UF 281185, and UF 281323–281325.

Remarks.—*Carcharhinus macloti* is extremely abundant from the Pungo River Formation. Purdy et al. (2001) referred to over 400 teeth in their description, with upper teeth ranging from CH = 5.0–7.3 mm and CW = 5.0–9.1 mm. *Carcharhinus* aff. *C. macloti* is relatively uncommon in the Chucunaque Formation and has not been identified in the Gatun Formation, although this may be an artifact caused by a collection bias given the extremely small size of the teeth. According to Purdy et al. (2001), lower teeth are smaller than upper teeth, symmetrical, and lack the distinctive lateral cusplets. This description aligns well with that of *Carcharhinus isodon*, and may explain why *C. isodon* was not recognized from Lee Creek by Purdy et al. (2001) despite the fact that it is recognized as being present in Lee Creek (www.elasmo.com). *Carcharhinus macloti* has been reported from the Miocene of Peru (Lambert et al., 2010) and, tentatively, from the middle Eocene of Georgia (Hulbert et al., 1998). Mondal et al. (2009) also reported *C. macloti* from the Miocene of India, however the specimen imaged in their publication does not seem definitive for *C. macloti*. Garrick (1985) reported that abundance of lateral cusplets in upper teeth of extant *C. macloti* vary, but could not ascertain if the variation was attributed to sexual dimorphism or geographic variation. There is little known about extant individuals beyond that they occur in the Indo-West Pacific and Arafura Sea in inshore and offshore waters of continental and insular shelves (Compagno, 1984). *Carcharhinus macloti* has a demersal habit and typically occurs at depths of 0–170 m (Last and Stephens, 1994; Compagno et al., 2005).

Carcharhinus obscurus (Lesueur, 1818)
Figure 6.14–6.20

Holotype.—Originally described as *Squalus obscurus* by Lesueur (1818, p. 223, pl. 9). There is no holotype; however, the type locality is North America (Compagno, 1984).

Occurrence.—STRI 290109, STRI 290113, STRI 290116, STRI 290125, STRI 290145, STRI 300029, STRI 300032, STRI 430011, and STRI 430012.

Description.—Upper teeth are broad and triangular. The mesial edge is apically convex and either straight or concave basally forming a weak notch. The distal edge is significantly notched and is nearly vertical apical of the notch. Serrations are coarser basally and finer apically on both edges, and there is a distal deflection at the crown apex. The root is thick with a transverse groove and an obtusely angled basal margin. Lower teeth are narrow, have incomplete cutting edges with fine serrations that only comprise the upper third of the crown, a sigmoidal profile, and a distal deflection at the apex. Root is robust, thick, with a transverse groove and an obtusely angled basal margin. Upper teeth can be distinguished from other species of *Carcharhinus* by the apically convex mesial edge, the distal deflection of the apex, and the vertical distal cutting edge (Purdy et al., 2001). *Carcharhinus obscurus* from the Chucunaque Formation ranges from: upper CH = 4.7–13.4 mm and CW = 8.3–18.0 mm; lower CH = 5.6–10.8 mm and CW = 6.9–15.2 mm.

Materials.—One hundred eighty-four isolated teeth; upper: UF 275040, UF 275123, UF 275155, UF 281144–45, UF 281147; lower: UF 275039, UF 275072, UF 275087, UF 275090, UF 275094, UF 275121, UF 281147–52; indeterminate position: UF 281146.

Remarks.—Lower teeth can be distinguished from other species of *Carcharhinus* and the genus *Negaprion* by their wider apex with a distal deflection and incomplete cutting edges with fine serrations limited to the upper third of the crown. The description of lower teeth from *Carcharhinus egertoni* by Kent (1994) is analogous to the description of lower *Carcharhinus obscurus* teeth herein. Observation of modern *C. obscurus* dentitions indicates that the lower *C. egertoni* teeth describe by Kent (1994) are synonymous with lower teeth of *C. obscurus* (personal communication, G. Hubbell, 2015). *Carcharhinus obscurus* is the most abundant species identified from the Chucunaque Formation, but is relatively uncommon in the Gatun Formation (Pimiento et al., 2013a). In the middle Miocene Grand Bay Formation of Carriacou, *C. obscurus* outnumbers other species by more than three to one (Portell et al., 2008). Carrillo-Briceño et al. (2015a) observed *C. obscurus* as the second most abundant species in the neritic Rio Indio facies and as a relatively uncommon species in the bathyal Piña Sandstone facies of the late Miocene Chagres Formation. Teeth from the Chucunaque Formation are larger than those from the Gatun Formation (CH = 7.7–10.1 mm and CW = 11.2–16.28 mm; Pimiento et al., 2013a), but much smaller than the *C. obscurus* teeth described from the Yorktown Formation (CH = 17.0–22.0 mm and CW = 18.0–25.0 mm; Purdy et al., 2001). Extant individuals with tooth sizes corresponding to those reported from the Yorktown Formation are about 3 m TL (Purdy et al., 2001), which suggests that *C. obscurus* from the younger Chucunaque Formation were smaller. *Carcharhinus obscurus* has a cosmopolitan distribution in the modern tropical and warm temperate seas, commonly occurring on continental and insular shelves, inshore and in oceanic waters (Compagno, 1984; Compagno et al., 2005). Adults most commonly occur at depths of 200–400 m, while younger individuals can be found in shallower nursery areas (Compagno, 1984; Bass et al., 1986; Compagno et al., 2005).

Carcharhinus plumbeus (Nardo, 1827)
Figure 6.21–6.24

Holotype.—Originally described as *Squalus plumbeus* by Nardo (1827, p. 477). There is no holotype; however, the type locality is the Adriatic Sea (Compagno, 1984).

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Occurrence.—STRI 300032 and STRI 430011.

Description.—Upper teeth have a moderately broad crown; the mesial edge is straight with relatively uniform, moderately sized serrations and the distal edge is concave with finer serrations apically. There is no notch on either cutting edge, the lingual face is convex, and the labial face is flat. The root is thick with a transverse groove and obtusely angled basal margin. *Carcharhinus plumbeus* from the Chucunaque Formation ranges from CH = 5.8–11.9 mm and CW = 8.1–14.5 mm.

Materials.—Eight isolated teeth; upper: UF 281141–43.

Remarks.—*Carcharhinus plumbeus* can be distinguished from other species of *Carcharhinus* by its straight mesial edge with fairly uniform serrations and moderate width; *C. obscurus* is broader and *C. perezi* is narrower (Purdy et al., 2001). *Carcharhinus plumbeus* is relatively uncommon in the Chucunaque Formation (N = 8), the Gatun Formation (N = 5; Pimiento et al., 2013a), and the Pungo River Formation (N = 6; Purdy et al., 2001). *Carcharhinus plumbeus* is intermediary in size between specimens from the Gatun Formation (CH = 6.8–10.6 mm and CW = 10.3–16.1 mm; Pimiento et al., 2013a) and the Pungo River Formation (CH = 14.0–19.0 mm; Purdy et al., 2001), but more closely aligned with the individuals from the Gatun Formation. The teeth from the Pungo River Formation correspond to TL = 2 m (Purdy et al., 2001), indicating smaller individuals in both the Chucunaque and Gatun Formations. In the bathyal Piña Sandstone facies *C. plumbeus* represents ~3% of the chondrichthyan fauna, but is not observed in the neritic Rio Indio facies of the Chagres Formation (Carrillo-Briceño et al., 2015a). *Carcharhinus plumbeus* have also been recognized in the Miocene deposits of Venezuela and Cuba (Iturralde-Vinent et al., 1996; Aguilera and Rodrigues de Aguilera, 2001; MacPhee et al., 2003). Extant individuals are benthopelagic, commonly found inshore and offshore on continental and insular shelves and adjacent deep water (Compagno, 1984). *Carcharhinus plumbeus* occurs at depths less than 280 m, but are most commonly found in the range of 20–55 m (Compagno, 1984; Compagno et al., 2005).

Carcharhinus spp.
Figures 3.20, 3.21, 6.25–6.49

Occurrence.—STRI 290109, STRI 290113, STRI 290116, STRI 290145, STRI 300029, STRI 300032, STRI 430011, STRI 430012, and YPA105.

Description.—Teeth range from small to moderate size. Upper teeth are broad and triangular with serrated edges, have a flat labial face and convex lingual face. Teeth become increasingly asymmetric in lateroposterior positions. The root has a transverse nutrient groove or a nutrient pore, convex crown-root margin on the lingual face, and an arciform basal margin. Lower teeth are symmetrical with a tall, narrow crown and complete cutting edges. The root is thick with two prominent lobes and a transverse groove; the basal margin may be near horizontal or arcuate.

Materials.—Four hundred twenty-seven isolated teeth; upper anterior: UF 281165, UF 281328, UF 281331–32, UF 281335, UF 281344, UF 281346, UF 281348; upper: UF 275038, UF 275140, UF 281167, UF 281327, UF 281334, UF 281339, UF 281343, UF 281345; upper pathologic: UF 281168, UF 281338, UF 281347, UF 281402; lower: UF 275035, UF 275042, UF 275063, UF 275074, UF 275076, UF 275081, UF 275089, UF 275141, UF 275143, UF 275154, UF 281163, UF 281164, UF 281326, UF 281330, UF 281333, UF 281337, UF 281340, UF 281342, UF 281403; posterior: UF 281182–83, UF 281361–63, UF 281269; indeterminate position: UF 275034, UF 275036, UF 275067, UF 275077, UF 275079, UF 275088, UF 275101, UF 275119, UF 275149, UF 281329, UF 281336, and UF 281341.

Remarks.—The genus *Carcharhinus* is the most abundant among the chondrichthyans from the Chucunaque Formation. There is much debate regarding the assignment of teeth from this genus to the species level (Naylor and Marcus, 1994; Purdy et al., 2001; Pimiento et al., 2013a), especially in the case of lower teeth (Kent, 1994). Lower teeth are very similar to *Negaprion brevirostris*, but can be distinguished by having a shorter crown. This confusion can be attributed to the convergent dignathic heterodonty expressed by this genus, in which the lower jaw has a grasping function and the upper jaw has a cutting function. Naylor and Marcus (1994) determined that upper lateral teeth are the most diagnostic teeth within the dentition and can accurately be identified to the species level. Pimiento et al. (2013a) reported tooth sizes ranging from CH = 1.9–12.9 mm and CW = 4.1–17.6 mm, which is much smaller than the maximum CH of 20 mm observed by Cappetta (1987). Four upper teeth from the Chucunaque Formation exhibit distinct pathologies (Figs. 3.20, 3.21, 6.47–6.49), represented by two morphotypes. The first pathologic morphotype is a lack of serrations on one cutting edge near the crown apex (Figs. 3.20, 3.21, 6.48) and the second morphotype is a disruption of the cutting edge indicated by a wrinkled pattern (Fig. 6.47, 6.49). The cause of these pathologies is unclear, however, most tooth deformities are often attributed to feeding damage related to bones or tail spines getting lodged into the jaw (Gudger, 1937). *Carcharhinus* spp. are the most abundant sharks in shallow, nearshore environments, with at least 30 known living species (Kent, 1994; Naylor and Marcus, 1994). This genus has a widespread distribution, occurring in all temperate and tropical seas (Cappetta, 1987), and can most commonly be found in coastal waters (Compagno, 1984).

Genus *Negaprion* Whitley, 1940

Type.—*Aprionodon acutidens* subsp. *queenslandicus* Whitley, 1939 (Cappetta, 2012).

Negaprion brevirostris (Poey, 1868)
Figure 7.1–7.4

Holotype.—Originally described as *Hypoprion brevirostris* by Poey (1868, p. 451, pl. 4, figs. 5, 6, 20). The holotype is unknown; however, the type locality is Cuba (Compagno, 1984).

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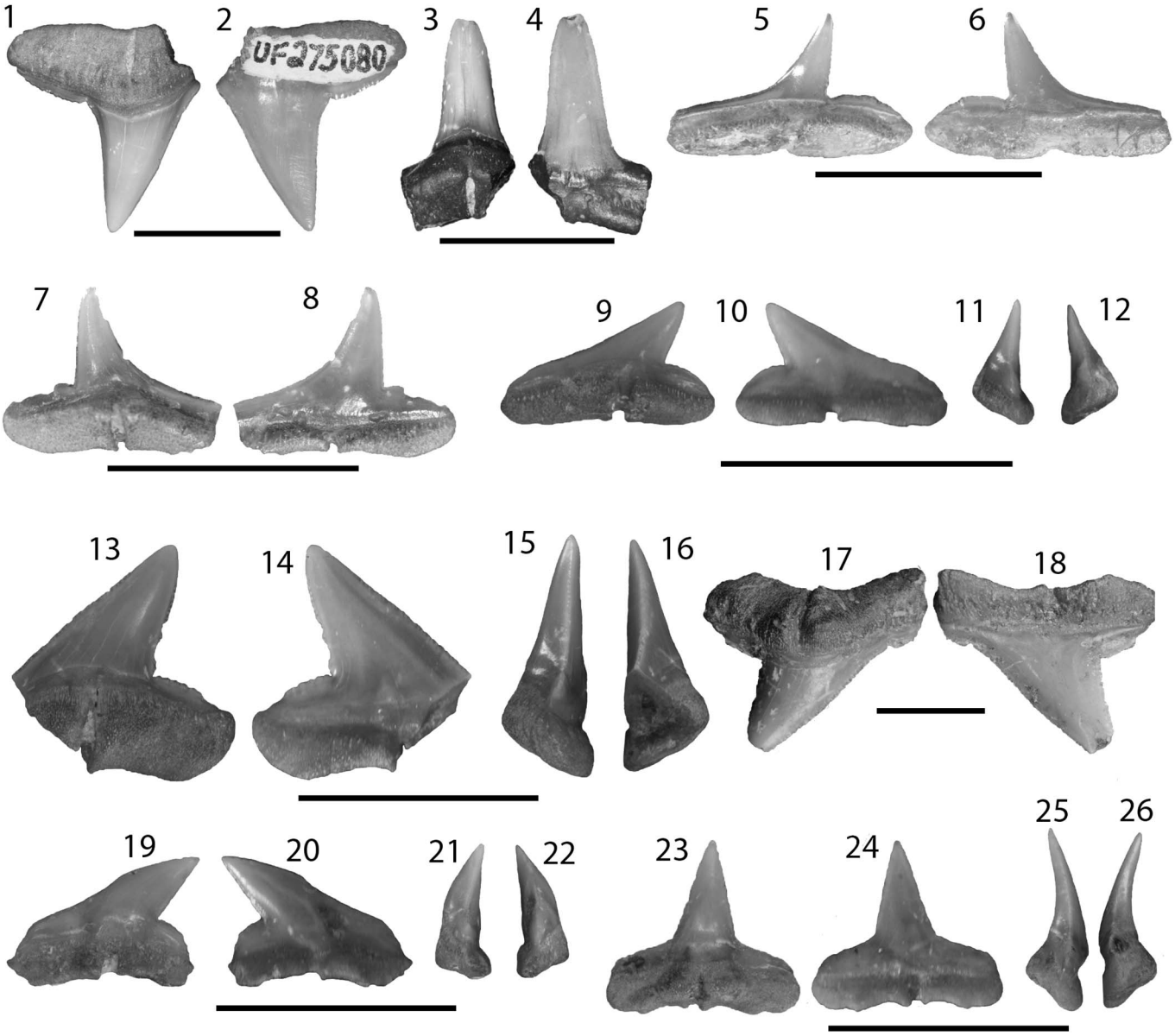

Figure 7. Carcharhiniformes III: *Negaprion*, *Rhizoprionodon*, and *Sphyrna* from the Chucunaque Formation. (**1–4**) *Negaprion brevirostris* (Poey, 1868), scale bar = 1 cm: (**1, 2**) UF 275080, upper left lateral tooth in lingual and labial view, respectively; (**3, 4**) UF 275080, lower tooth in lingual and labial view, respectively; (**5–8**) *Rhizoprionodon* sp., scale bar = 0.5 cm: (**5, 6**) UF 322848, indeterminate position in lingual and labial view, respectively; (**7, 8**) UF 322849, indeterminate position in lingual and labial view, respectively; (**9–12**) *Sphyrna lewini* (Griffith and Smith, 1834), UF 281176, upper position in lingual, labial, mesial lateral, and distal lateral view, respectively (scale bar = 1 cm); (**13–18**) *Sphyrna mokarran* (Ruppell, 1837): (**13–16**) UF 275043, upper position in lingual, labial, mesial lateral, and distal lateral view, respectively, (scale bar = 1 cm); (**17, 18**) UF 275066, upper lateral tooth in lingual and labial view, respectively (scale Bar = 0.5 cm); (**19–26**) *Sphyrna zygaena,* scale bar = 1 cm: (**19–22**) UF 275073, upper lateral tooth in lingual, labial, mesial lateral, and distal lateral view, respectively; (**23–26**) UF 275073, lower anterior tooth in lingual, labial, distal lateral, and mesial lateral view, respectively. Photo credit: R. Leder.

Occurrence.—STRI 290116 and STRI 430012.

Description.—Tall, narrow crown, with a convex lingual face and flat labial face that extends onto the root. The cutting edges are complete and extend onto the heels, and may or may not bear serrations. Root is moderately thick with a weak transverse groove. Lateral teeth tend to bear a distal inclination and subsequently exhibit increasing asymmetry. A distinct dignathic heterodonty exists, with upper teeth having a broader crown than lower teeth. *Negaprion brevirostris* from Lago Bayano range from CH = 7.7–11.6 mm and CW = 4.8–16.1 mm.

Materials.—Three isolated teeth; upper: UF 275080; lower: UF 275150.

Remarks.—In the Miocene, this species has been identified as an extinct species, *Negaprion eurybathrodon* (Cappetta, 1987; Kent, 1994; Purdy et al., 2001); however Pimiento et al. (2013a) recognized that the Miocene morphotype is analogous to the extant species, *Negaprion brevirostris*, and aptly reassigned it to *N. brevirostris*. Purdy et al. (2001) reported anterolateral teeth of *N. eurybathrodon* (= *N. brevirostris*) from Lee Creek ranging from CH = 14.0–21.0 mm, corresponding to a mature adult

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body size range of TL = 2.1–3 m (Compagno, 1984). Teeth from the Chucunaque Formation and the Gatun Formation (CH = 3.7–13.7 mm; Pimiento et al., 2013a) are smaller than those of Lee Creek. *Negaprion brevirostris* has been identified in the Miocene of Venezuela, Cuba, and Ecuador (Longbottom, 1979; Iturralde-Vinent et al., 1996; Aguilera and Rodrigues de Aguilera, 2001; MacPhee et al., 2003). Carrillo-Briceño et al. (2015a) reported two teeth attributed to *N. brevirostris* from the neritic Rio Indio facies, but no occurrences in the bathyal Piña Sandstone facies of the Chagres Formation. Extant individuals occur in tropical and temperate, estuarine and marine waters generally at depths of 0–92 m (Compagno, 1984; Kent, 1994). *Negaprion brevirostris* frequents mangrove fringes and coral reefs, but occasionally can be found in open ocean near surface waters for migration purposes (Compagno, 1984; Compagno et al., 2005).

Genus *Rhizoprionodon* Whitley, 1929

Type.—*Carcharias* (*Scoliodon*) *crenidens* Klunzinger, 1880 (Cappetta, 2012).

Rhizoprionodon sp.
Figure 7.5–7.8

Occurrence.—STRI 290109, STRI 290116, and YPA105.

Description.—Small teeth with a short, slender crown; complete cutting edges; and a recurved mesial edge and straight to convex distal edge forming a distinct notch with a rounded distal heel. The root is thin with a deep transverse groove that penetrates a horizontal basal margin. *Rhizoprionodon* sp. from the Chucunaque Formation range from CH = 1.9–2.4 mm and CW = 4.1–5.1 mm.

Materials.—Fifty-five isolated teeth; indeterminate position: UF 275091, UF 281364–281268, and UF 281370.

Remarks.—Much confusion remains regarding the identification of *Rhizoprionodon* teeth, due to the closely aligned teeth of *Sphyrna* and, possibly synonymous, teeth of *Scoliodon* and *Loxodon* that were established by Springer (1964). *Rhizoprionodon* sp. differs from *Sphyrna lewini* in having a shorter crown, recurved mesial edge, and less pronounced root. *Rhizoprionodon* sp. differs in proportional size relative to *Sphyrna*, with *Sphyrna* having a greater crown height to width ratio (Purdy et al., 2001). Cappetta (1987) mentioned a marked sexual dimorphism in *Rhizoprionodon*, but it is possible that fossil specimens described may actually represent the morphologically similar *Scoliodon* and/or *Loxodon*. Consequently, identification of teeth from this genus should be treated with some degree of skepticism. Cappetta (1987) states that *Rhizoprionodon* teeth do not exceed CH = 4 mm; however, Purdy et al. (2001) reported a range from CH = 3.2–5.2 mm and CW = 4.3–5.7 mm. Teeth of the Gatun Formation (CH = 2.5–3.3 mm and CW = 3.9–5.6 mm; Pimiento et al., 2013a) are more closely aligned with those of the Chucunaque Formation. *Rhizoprionodon* previously has been reported from the middle and late Miocene of France, Belgium, and Portugal (Cappetta, 1987). Carrillo-Briceño et al. (2015a) noted *Rhizoprionodon* as a small component (~4%; N = 20) of the bathyal Piña Sandstone facies, but no occurrences in the neritic Rio Indio facies of the Chagres Formation. Extant individuals can be found worldwide in shallow, nearshore tropical and temperate waters (Compagno, 1984; Kent, 1994). *Rhizoprionodon terraenovae* occurs at depths ranging from the intertidal zone to 280 m, but usually occur at depths less than 10 m (Compagno, 1984; Compagno et al., 2005).

Family Sphyrnidae Gill, 1872
Genus *Sphyrna* Rafinesque, 1810

Type.—*Squalus zygaena* Linnaeus, 1758 (Cappetta, 2012).

Sphyrna lewini (Griffith and Smith, 1834)
Figure 7.9–7.12

Holotype.—Originally described as *Zygaena lewini* by Griffith and Smith (1834 in Cuvier, Griffith, and Smith, 1834, p. 640, pl. 50). Holotype information is unknown, however the type locality is the south coast of New Holland (Australia) (Compagno, 1984).

Occurrence.—STRI 290109, STRI 290113, STRI 290125, and STRI 290145.

Description.—Small teeth with a stout to slender, distally inclined crown and prominent distal heel. Cutting edges are complete and lack serrations; the mesial edge is straight to slightly concave and the distal edge is straight and inclined forming a deep notch. The distal heel is rounded and has an unserrated cutting edge. The root is thick with a deep nutrient groove that penetrates a horizontal basal margin. *Sphyrna lewini* from the Chucunaque Formation ranges from CH = 2.0–4.6 mm and CW = 4.9–7.5 mm.

Materials.—Thirteen isolated teeth; upper: UF 281176; indeterminate position: UF 275048, UF 275050, UF 275075, UF 275106, and UF 275153.

Remarks.—*Sphyrna lewini* differs from *Rhizoprionodon* in having a straighter mesial edge, taller crown, and thicker root. *Sphyrna lewini* specimens from the Chucunaque Formation are smaller than those recorded from the Gatun Formation (CH = 2.7–5.4 mm and CW = 5.2–11.0 mm; Pimiento et al., 2013a) and the Yorktown Formation (CH = 7.3–7.8 mm and CW = 6.5–9.6 mm; Purdy et al., 2001). However, it is possible that some of the larger teeth identified as *Sphyrna zygaena* actually represent *S. lewini*, which would result in a more comparable size range. *Sphyrna lewini* has also been reported from the late Miocene Chagres Formation of Panama (Carrillo-Briceño et al., 2015a) and the Miocene of Cuba (Iturralde-Vinent et al., 1996; MacPhee et al., 2003). Extant *Sphyrna lewini* have a circumglobal distribution in warm temperate and tropical seas, occurring over continental and insular shelves and adjacent deep water less than ~275 m depth (Compagno, 1984; Compagno et al., 2005). Large schools of small individuals have been observed migrating poleward in the summer, however permanent resident populations also exist (Compagno, 1984).

Sphyrna mokarran (Ruppell, 1837)
Figure 7.13–7.18

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Holotype.—Originally described as *Zygaena mokarran* by Ruppell (1837, p. 64, pl. 18, fig. 1). According to Klausewitz (1960), a 2515 mm stuffed male from Massaua, Red Sea, SMB 3590, serves as a lectotype in Naturmuseums Senckenberg (Compagno, 1984).

Occurrence.—STRI 290109 and STRI 300032.

Description.—Moderately large teeth with a broad, serrated crown; straight or convex mesial edge and straight distal edge with a distal inclination that forms a deep notch; and a prominent distal heel that is rounded and serrated. The root is robust with a deep nutrient groove that penetrates a horizontal basal margin. *Sphyrna mokarran* from the Chucunaque Formation ranges from CH = 6.6–9.8 mm and CW = 9.3–14.7 mm.

Materials.—Four isolated teeth; upper: UF 275043, UF 275066, and UF 281184.

Remarks.—*Sphyrna mokarran* is easily distinguished from other species of *Sphyrna* by its larger size and regular serrations. Pimiento et al. (2013a) noted the paucity of documented occurrences of *Sphyrna mokarran* in the fossil record, mentioning that in the Neotropics it has only been reported from the Miocene of Cuba without any description of the specimens (MacPhee et al., 2003). Teeth from the Chucunaque Formation are comparable in size to those found in the Gatun Formation (CH = 7.6–9.4 mm and CW = 9.6–16.4 mm; Pimiento et al., 2013a). Extant individuals reach a maximum TL = 6.1 m and have a circumtropical distribution, occurring close inshore and well offshore (Compagno, 1984). *Sphyrna mokarran* most commonly populates bottom and reef associated waters in a depth range of 1–80 m (Compagno, 1984; Compagno et al., 2005).

Sphyrna zygaena (Linnaeus, 1758)
Figure 7.19–7.26

Holotype.—Originally described as *Squalus zygaena* by Linnaeus (1758, p. 234); however, Compagno (1984) does not acknowledge a holotype.

Syntype.—Naturhistoriska Riksmuseet, Department of Vertebrate Zoology, Ichthyology Section, Stockholm, Sweden, NRM 88, 215 mm specimen.

Occurrence.—STRI 290109, STRI 300032, STRI 430011, STRI 430012, and YPA105.

Description.—Moderately broad, labio-lingually flattened crown; convex to sigmoidal mesial edge and straight to concave distal edge. There is a distal inclination forming an acute notch with a rounded distal heel. The cutting edges and heel may or may not bear weak serrations. The root is thick with a transverse groove that penetrates a horizontal basal margin. Anterior teeth are more erect and lack the acute distal notch. *Sphyrna zygaena* from the Chucunaque Formation range from CH = 2.6–8.1 mm and CW = 4.8–9.6 mm.

Materials.—Ninety-six isolated teeth; indeterminate position: UF 275044, UF 275058, UF 275073, UF 275142, UF 281175, and UF 281371–73.

Remarks.—*Sphyrna zygaena* tend to have thicker, broader crowns and a more sigmoid mesial edge than *Sphyrna lewini*; however, the differences between the two species are sparse, especially in smaller individuals of *S. zygaena*. Compagno (1988) noted that there is weak ontogenetic heterodonty in the genus *Sphyrna*. In juveniles and young adults of the extant *S. zygaena*, teeth have smooth cutting edges, but larger individuals become weakly serrate (Gilbert, 1967). Gillette (1984) originally identified *S. zygaena* from the Gatun Formation, however Pimiento et al. (2013a) reassigned these teeth to *S. lewini* (CH = 2.7–5.4 mm and CW = 5.2–11.0 mm) and *Sphyrna* sp. (CH = 3.1–8.9 mm and CW = 7.4–10.6 mm). Purdy et al. (2001) reported teeth from the Pungo River Formation occurring in a size range of CH = 8.0–11.0 mm, which corresponds with the larger teeth identified as *S. zygaena* from the Chucunaque Formation. Teeth from all three formations are much smaller than the upper limit of 20 mm reported by Cappetta (1987). Extant *Sphyrna zygaena* inhabit all temperate and tropical seas, and most commonly occur in coastal waters over continental shelves from depths of 0–200 m (Compagno et al., 1989); however, it has been proposed that the distribution of *S. zygaena* in tropical environments is incompletely known due to probable confusion with *S. lewini* (Casper et al., 2005).

Order Carcharhiniformes incertae sedis
Figure 8.1–8.11

Occurrence.—STRI 290139, STRI 290145, and YPA105.

Description.—Scyliorhiniod-type (Tessman, 1966) vertebral centra with smooth dorsoventral edges and two sets of paired foramina; the caudal and cranial faces are concave with a circular to oval-shaped outline and distinct annuli, except in the smallest specimen (UF 281399). In lateral view, the centra have a cylindrical, disk-like to hourglass shape. Posterior vertebrae are more compressed than anterior positions (Kent, 1994). The shape of the dorsal and ventral foramina, the presence or absence of septa, and the distribution of vertebral pores are diagnostic characteristics for identifying different genera (Kent, 1994; Purdy et al., 2001). These centra can confidently be assigned to the order Carcharhiniformes because they lack the septate dorsoventral walls diagnostic for Lamniformes; however, they lack features that would allot for more specific identification. These centra range from a dorsoventral diameter of 1.27–33.56 mm and a wall length of 0.87–14.38 mm.

Materials.—Four isolated vertebrae; indeterminate position: UF 281195–96 and UF 281399–400.

Remarks.—Post-cranial elements are rare for chondrichthyan taxa. Typically the only non-dental remains recovered are vertebral centra because they are more densely calcified than the rest of the cartilaginous skeleton (Kent, 1994). However, the morphologic variability in vertebral centra is more conservative than that of teeth, making it difficult to identify isolated

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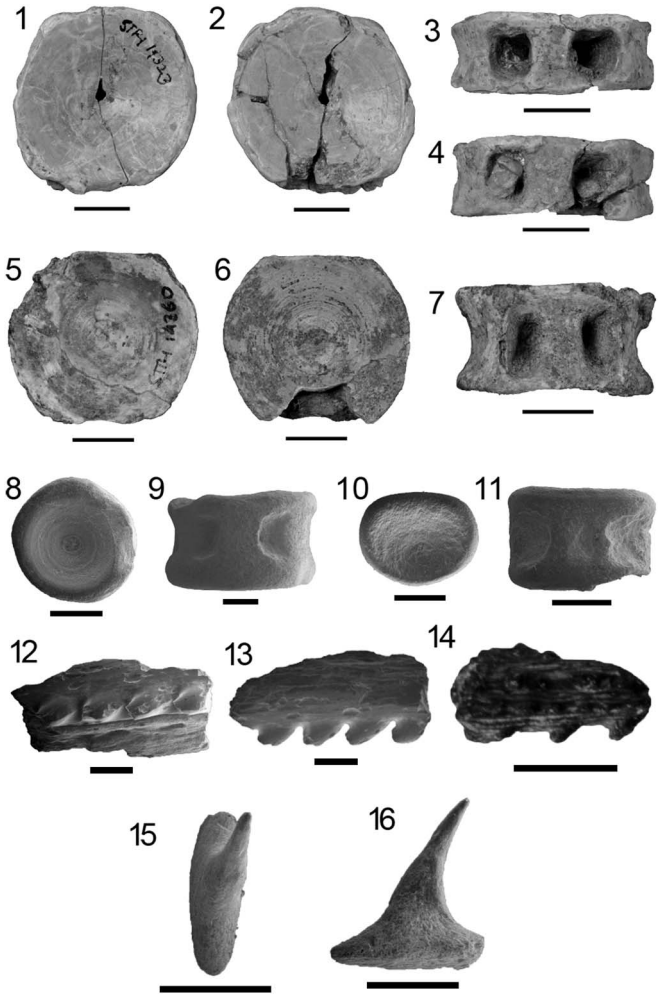

Figure 8. Non-dental elements from the Chucunaque Formation. (**1–11**) Carcharhiniform centra: (**1–4**) UF 281195, posterior, anterior, ventral, and dorsal view, respectively (scale bar = 1 cm); (**5–7**) UF 281196, anterior, posterior, and dorsal view, respectively (scale bar = 1 cm); (**8, 9**) UF 281400: (**8**) indeterminate anterior-posterior face (scale bar = 200 µm); (**9**) indeterminate dorsal-ventral face (scale bar = 100 µm); (**10, 11**) UF 281399, indeterminate anterior-posterior face and indeterminate dorsal-ventral face, respectively (scale bar = 100 µm). (**12–14**) Myliobatiformes incertae sedis: (**12, 13**) UF 281317, caudal spine in lateral and dorsal view, respectively (scale bar = 1 mm); (**14**) UF 281499, caudal spine in dorsal view (scale bar = 1 mm); (**15, 16**) Batomorphii incertae sedis, UF 281401, dermal denticle in apical and lateral view, respectively (scale bar = 1 mm). Photo credit: S. Moran.

specimens to genus or species. Purdy et al. (2001) identified vertebrae of *Hemipristis serra*, *Galeocerdo* cf. *G. cuvier*, and *Carcharhinus* spp. based on dispersal of nutrient pores and the shape of dorsal and ventral foramen. Vertebrae from the Chucunaque Formation lack characteristics to warrant identification beyond Carcharhiniformes, in part because of their preservation, but mostly due to their inherent non-descript nature. Chondrichthyan vertebral centra have been recovered from the Eocene Tonosi Formation (Vasquez and Pimiento, 2014) and the early Miocene Culebra Formation (Pimiento et al., 2013b) of Panama. The four centra described here are the first chondrichthyan vertebral elements described from the late Miocene of Panama. Despite their lack of taxonomic information, vertebral centra can provide a lot of information about the individual from which they originated and the environment in which they resided. Vertebral centra have coupled growth bands, in which light bands represent growth during cold seasons and dark bands represent growth during warm seasons (Calliet et al., 1985, 1986, 2006; Calliet and Goldman, 2004).

Subdivision Batoidea Compagno, 1973
Order Rajiformes Berg, 1940
Family Rhynchobatidae Garman, 1913
Genus *Rhynchobatus* Müller and Henle, 1837

Type.—*Rhinobatus laevis* Bloch and Schneider, 1801 (Cappetta, 2012).

Rhynchobatus sp.
Figure 9.1–9.3

Occurrence.—STRI 290116.

Description.—In apical view, the crown is convex with a transverse crest dividing the lingual and labial faces. On the labial face, the crown is downward sloping with a well-defined uvula and secondary keel; there are foramina on the mesial and distal edges of the root. The lingual face is smooth with a high root that forms a distinct ridge at the crown-root contact; there is a prominent medial groove, with a foramen, that divides the root and lateral lobes on both the mesial and distal edges, giving the root a trilobate form (Pimiento et al., 2013a). The dimensions of this specimen are a CW = 4.17 mm, a CL = 2.48 mm, and a CH = 3.64 mm.

Materials.—One isolated tooth; indeterminate position: UF 281314.

Remarks.—The dimensions of this tooth are much larger than those reported from the Gatun Formation (length = 0.9 mm, width = 0.9 mm; Pimiento et al., 2013a); however Compagno (1987) reported a CW of up to 5 mm for *Rhynchobatus*. Aguilera and Rodrigues de Aguilera (2001) documented this genus from the Miocene of Venezuela. There are six extant species of *Rhynchobatus* that occur in the tropical and subtropical Indo-Pacific and a single species in the eastern Atlantic, *R. luebberti* (Compagno and Marshall, 2006). *Rhynchobatus luebberti* is a benthic species often occurring in the intertidal zone, from 0–70 m depth, but most commonly found in less than 35 m depth (Compagno and Marshall, 2006). *Rhynchobatus djiddensis* is a reef-associated species that occurs inshore and in shallow estuaries, generally between 2 and 50 m depth (Sommer et al., 1996).

Order Myliobatiformes Compagno, 1973
Family Urotrygonidae McEachran et al., 1996
Genus *Urobatis* Garman, 1913

Type.—*Raja (Leiobatus) sloani* Garman, 1913 (Cappetta, 2012).

Urobatis sp.
Figure 9.4–9.6

Occurrence.—YPA105.

Description.—In apical view, the crown has an elliptical to nearly hexagonal outline with a reticulate ornamentation, a transverse depression, and a significant lingual protuberance.

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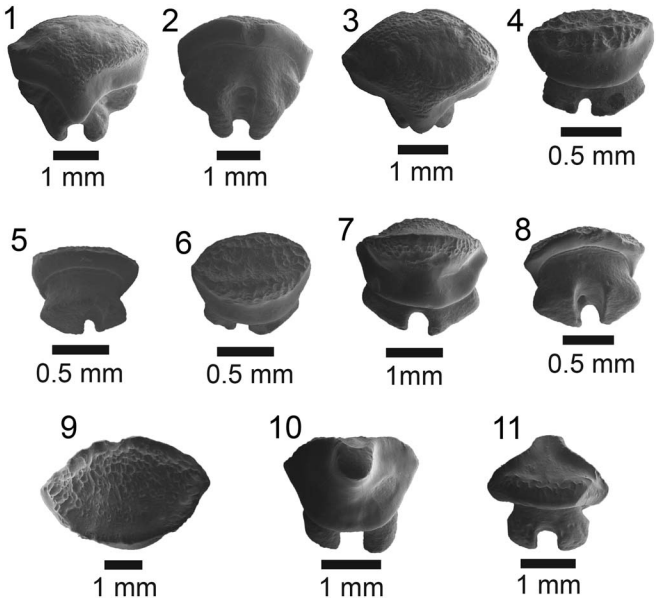

Figure 9. Batoid I: *Rhynchobatus*, *Urobatis*, and *Dasyatis* SEM images from the Chucunaque Formation. (**1–3**) *Rhynchobatus* sp., UF 281314, indeterminate position in apico-lingual, baso-labial, and occlusal view, respectively; (**4–6**) *Urobatis* sp., UF 281316, indeterminate female tooth in lingual, baso-labial, and occlusal view, respectively; (**7–11**) *Dasyatis sp.*: (**7–9**) UF 281233, indeterminate female tooth in apico-lingual, baso-labial, and occlusal view, respectively; (**10, 11**) UF 281237, indeterminate male tooth in apico-lingual and labial view, respectively.

The lingual face is smooth and overhangs the root. There is a shallow depression at the crown-root contact that forms a distinct ridge. The root is divided by a medial groove that forms two prominent root lobes with flat bases; in lingual view the right lobe is significantly larger, indicating a lateral position. The flat, lozenge-shaped crown is a diagnostic feature of a female (Cappetta, 2012; Pimiento et al., 2013a). The imaged specimen (Fig. 9.4–9.6) has a CL = 0.63 mm and a CW = 1.05 mm.

Materials.—Two isolated teeth; female lateral position: UF 281315–16.

Remarks.—*Urobatis* sp. recognized in the Gatun Formation (Pimiento et al., 2013a) is similar to that of the Chucunaque Formation described above, however the specimen from the Gatun Formation has a smooth transverse depression on the lingual half of the crown. It is possible that they reflect two different species, or that they represent positional differences. Specimens from the Gatun Formation and the Chucunaque Formation share similarities with the extant *Urobatis halleri* (previously referred to as *Urolophus halleri*; Cappetta, 1987, 2012), which today is found in the eastern Pacific from northern California to Panama (McEachran, 1995). *Urobatis halleri* is a demersal species known to occur in depths of 0–91 m (Michael, 1993), but most frequently occurs at depths of 0–21 m (Love et al., 2005).

Family Dasyatidae Jordan, 1888
Genus *Dasyatis* Rafinesque, 1810

Type.—*Dasyatis ujo* Rafinesque, 1810 (Cappetta, 2012).

Dasyatis sp.
Figure 9.7–9.11

Occurrence.—STRI 290109, STRI 290113, STRI 290116, and YPA105.

Description.—In apical view, female teeth have an elliptical outline with a reticulate surface and a transverse keel; the surface becomes smooth toward the lingual face and forms a completely smooth lingual uvula; the labial face overhangs well over the root forming a prominent ridge. Thick root divided into two lobes by a deep, transverse groove; there is a large foramen nested within the transverse groove; the base of the root lobes is flat with a semicircular to triangular outline. The male teeth have a higher crown with a triangular outline and a prominent cusp that is smooth and lingually oriented; the occlusal surface is fluted, forming distal and mesial crests; there is also a weak medial, labio-lingual ridge and irregular folds on the convex labial edge. The root is bipartite with rounded lobes that are divided by a deep nutrient groove. Female and male teeth differ in that the female teeth have reticulate surface with a transverse crest, no prominent cusp, and broader root lobes. Also, the occlusal surface of female teeth is somewhat rounded and convex, whereas the male teeth have a more triangular appearance (Purdy et al., 2001). The female tooth (Fig. 9.7–9.9) has a CH = 1.30 mm, CW = 2.34 mm, and CL = 1.56 mm. The male specimen imaged (Fig. 9.10, 9.11) has a CH = 1.38 mm, CW = 2.33 mm, and CL = 1.63 mm.

Materials.—Nineteen isolated teeth; three male: UF 281228, UF 281237; 14 female: UF 281229, UF 281231–36, UF 281238; two indeterminate: UF 281230.

Remarks.—*Dasyatis* sp. has not been identified in Panama, from either the Gatun Formation or the overlying Chagres Formation. The closest related species known from the Gatun Formation is *Taeniura* aff. *T. grabata* (Pimiento et al., 2013a), which is in the family Dasyatidae (now recognized as *Taeniurops* aff. *T. grabata* by Cappetta, 2012). Purdy et al. (2001) recognized three species of *Dasyatis* from the Lee Creek Mine: *D. say*, *D. centroura*, and *D.* cf. *americana*, however *D. centroura* is only known from dermal denticles and *D.* cf. *americana* is only known from a single tooth. *Dasyatis say* specimens from the Pungo River Formation and the Yorktown Formation range from CH = 2.6–3.8 mm and CW = 2.8–3.9 mm, which is larger than the specimens identified herein. Cappetta (1987) reported that teeth of this genus can be up to 6 mm wide, nearly three times as large as the teeth from the Chucunaque Formation and twice as large as the teeth described from Lee Creek. Extant species of this genus have a demersal habit and are common in subtropical to tropical waters (Compagno, 1984).

Family Myliobatidae Bonaparte, 1838
Genus *Aetobatus* Blainville, 1816

Type.—*Raja narinari* Euphrasen, 1790 (Cappetta, 2012).

Aetobatus sp.
Figure 10.1–10.3

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Occurrence.—STRI 290145 and STRI 300032.

Description.—Flat, wide teeth with a low crown, a smooth occlusal surface, and often trapezoidal outline. Labial edge is straight or convex; lingual edge straight or concave; extremities of tooth plates are oriented distally. Root is short and polyaulacorhizid with oblique, parallel root lobes. In occlusal view, the root extends beyond the crown on the labial edge.

Materials.—Six isolated tooth fragments; indeterminate position: UF 281225–26.

Remarks.—Teeth of *Aetobatus* sp. can be distinguished from *Rhinoptera* by their lower crown, rounded and distally oriented extremities, and oblique root lobes that extend beyond the crown (Laurito and Valerio, 2008). *Aetobatus* cf. *A. narinari* was reported from the Gatun Formation and was fairly common (N = 22); however, only one specimen was a complete tooth with the following dimensions: CW = 66.0 mm, CL = 8.0 mm, and CH = 4.5mm (Pimiento et al., 2013a). In contrast, *Aetobatus* sp. from the Chucunaque Formation is fairly uncommon (N = 6) and no complete specimens were recovered for an accurate size comparison. *Aetobatus* and *Rhinoptera*, as well as *Myliobatis* and *Aetomylaeus*, have dental plates that are formed by numerous interlocking teeth that comprise a large crushing surface primarily used to feed on mollusks and decapods (Compagno, 1997). Extant *Aetobatus narinari* has a cosmopolitan distribution in subtropical and tropical seas, commonly occurring in shallow waters between 1 and 60 m depth (Mundy, 2005).

Family Rhinopteridae Jordan and Evermann, 1896
Genus *Rhinoptera* Kuhl in Cuvier, 1829

Type.—*Myliobatis marginata* Geoffroy Saint-Hilaire, 1809 (Cappetta, 2012).

Rhinoptera sp.
Figure 10.4–10.15

Occurrence.—STRI 290109, STRI 290116, STRI 300029, STRI 300032, and STRI 430011.

Description.—Thick, elongate teeth with a smooth occlusal surface and hexagonal outline; fragmented tooth plates often have a rectangular outline. In cross-section, the enamel is comprised of vertical prisms that radiate outward from the pulp cavity, indicating extensional growth. Labial face bears a transverse platform, which interlocks with the lingual visor of the proceeding tooth (Pimiento et al., 2013a). Symphyseal teeth interlock with smaller lateral teeth via their angular extremities (Cappetta, 1987). In lateral teeth, the crown is thicker towards the mesial edge than the distal edge. Root is polyaulacorhizid with numerous lobes, fewer lobes in the smaller lateral teeth; the root is short relative to the crown. *Rhinoptera* sp. from the Chucunaque Formation has a CH = 1.9–4.3 mm, CW = 3.1–5.7 mm, and CL = 6.4–16.4 mm.

Materials.—Thirty-eight isolated teeth; 10 complete and 18 fragments; symphyseal: 281307; lateral: UF 281227, UF 281304, UF 281308, UF 281311, UF 281313; indeterminate position: UF 281302-281303, UF 281305–06, and UF 281309-281311.

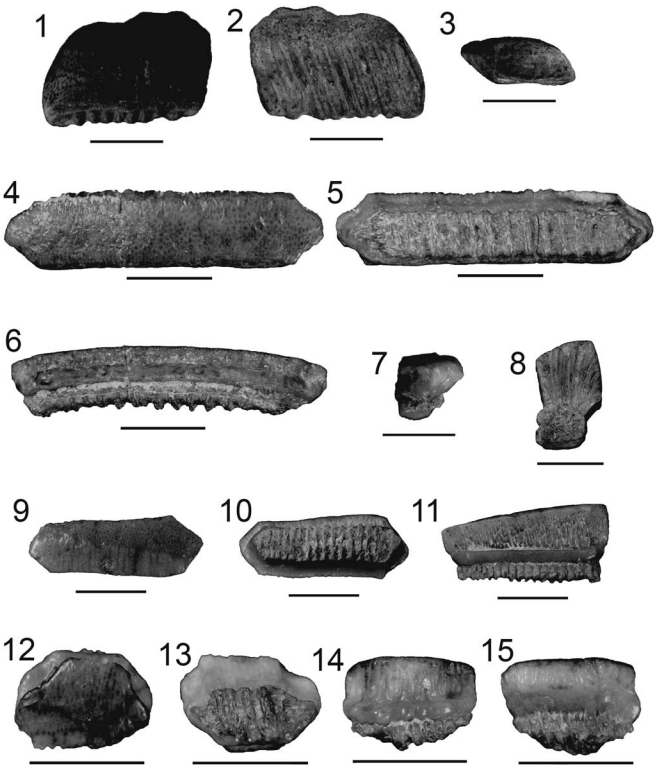

Figure 10. Batoid II: *Aetobatus* and *Rhinoptera* images from the Chucunaque Formation. (**1–3**) *Aetobatus* sp., UF 281226, distal tooth fragment in occlusal, basal, and lateral view, respectively; (**4–15**) *Rhinoptera* sp.: (**4–7**) UF 281307, symphyseal (i.e., medial) tooth in occlusal, basal, lingual, and lateral view, respectively; (**8**) UF 281309, cross-section in lateral view; (**9–11**) UF 281308, lateral (i.e., intermediate) tooth in occlusal, basal, and lingual view, respectively; (**12–15**) UF 281304, lateral (i.e., distal) tooth in occlusal, basal, lingual, and labial view, respectively (scale bars = 5 mm). Photo credit: S. Moran.

Remarks.—*Rhinoptera* can be distinguished from *Aetobatus* by its high crown and hexagonal outline with angular extremities. *Rhinoptera* is also often confused with *Myliobatis*; however, *Rhinoptera* differs in having a higher crown, a more angular occlusal surface, and a thicker lingual cingulum (Laurito and Valerio, 2008). *Myliobatis* was not observed in the Chucunaque Formation, but has been reported from the Gatun Formation, along with *Rhinoptera* cf. *R. steindachneri* (Pimiento et al., 2013a). The small, yet significant, relative abundance of *Rhinoptera* in the Gatun Formation (~4%) is comparable to that seen in the Chucunaque Formation (2.7%; Fig. 12). The size range of *Rhinoptera* teeth from the Gatun Formation (CH = 3.0–5.0 mm, CW = 3.0–26.0 mm, and CL = 4.0–5.0 mm) is fairly close to that observed in Bayano. The significantly larger range in CW can likely be explained by the occurrence of a large symphyseal tooth in the Gatun Formation. *Rhinoptera steindachneri* occurs in tropical waters in the eastern Pacific, usually between 0 and 30 m depth (Humann and Deloach, 1993).

Family Mobulidae Gill, 1893
Genus *Mobula* Rafinesque, 1810

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Type.—*Mobula auriculata* Rafinesque, 1810 (Cappetta, 2012).

Mobula thurstoni (Lloyd, 1908)
Figure 11.1–11.15

Holotype.—Originally described as *Dicerobatis thurstoni* by Lloyd (1908).

Occurrence.—STRI 290109 and YPA105.

Description.—In occlusal view, teeth have a roughly elliptical outline with a "blistered" ornamentation. The lingual edge is irregular and cuspidate, whereas the labial edge is convex or sinuous. The number of cusps on the lingual edge increases in more elongate specimens (Adnet et al., 2012) and the enamel extends well onto the root on the lingual face. The labial visor is rounded and may be incised with furrows. The root may have two or more lobes, depending on the position of the tooth and the age of the individual (Adnet et al., 2012); the root is narrow relative to the crown. The crown slopes inward basally, creating an angular contact with the divergent root lobes. In UF 281256 (Fig. 11.11–11.13), the root is divided into two lobes by a shallow medial groove (e.g., holaulacorhize stage); in labial view, the right lobe is larger, indicating a left lateral position. Teeth range from CH = 0.47–0.63 mm, CW = 0.98–1.40 mm, and CL = 1.37–2.04 mm.

Materials.—Sixteen isolated teeth; lateral: UF 281256, UF 281291–93, UF 281295, UF 281481; indeterminate position: UF 281283–85, UF 281288, UF 281294, and UF 281482.

Remarks.—Adnet et al. (2012) noted reduced sexual dimorphism in *Mobula thurstoni*, with the only major difference being that males are more deeply scored by furrows on the labial face. Pimiento et al. (2013a) identified two female teeth as *Mobula thurstoni* from the Gatun Formation. The specimen of *M. thurstoni* imaged in Pimiento et al. (2013a) has four cusps on the lingual edge, irregular folding on the labial edge, and a relatively smooth occlusal surface (CW = 0.6 mm and CL = 1.1 mm), which bears a strong resemblance to the female teeth of *Mobula tarapacana* described by Adnet et al. (2012). The additional cusps on the Gatun specimen can be explained by the fact that the number of cusps increases as teeth become more elongate (Notarbartolo Di Sciara, 1987; Adnet et al., 2012). Adnet et al. (2012) provisionally placed *M. thurstoni* into a group of Mobulids characterized by having comb-like teeth, along with *M. munkiana* and *M. hypostoma*, but distinguished *M. thurstoni* from the latter two by having an ornamented crown and shorter cusps. However, this distinction is tenuous (Adnet et al., 2012) and may not hold true in the fossil record. This species likely has a circumtropical distribution, but is known from scattered reports throughout the Pacific and Atlantic (Notarbartolo Di Sciara, 1987; Compagno, 1997). Extant individuals occur in oceanic and coastal waters, but most frequently are encountered in coastal environments from 0–100 m (Notarbartolo Di Sciara, 1988; McEachran and Notarbartolo Di Sciara, 1995; Clark et al., 2006a).

Mobula cf. *M. tarapacana* (Philippi, 1892)
Figure 11.16–11.25

Holotype.—Originally described as *Cephaloptera*? *tarapacana* from Chile by Philippi (1893, p. 8, pl. 3, fig. 2).

Occurrence.—STRI 290109 and UF YPA105.

Description.—Sexual dimorphism is a marked character in *Mobula tarapacana* (Adnet et al., 2012). Male teeth are elongate in occlusal view with deeply scored furrows and a subhexagonal outline. The labial edge is convex and slightly irregular. The lingual edge is sharp and cuspidate. The crown apex is much broader than the base of the crown. The root is polaulocorhizid with numerous labiolingually compressed lobes (Fig. 11.16–11.20). Female teeth have a relatively smooth occlusal surface with a subhexagonal outline. The crown is high relative to the root, with a slender profile. Adnet et al. (2012) observed crown heights two to three times greater than the root height in extant individuals. The labial edge is deeply grooved and the lingual edge is irreglularly cuspidate. The root is polaulocorhizid, root lobes are rounded and irregularly divided.

Materials.—Ten isolated teeth; male: UF 281270–71, UF 281276, UF 281485, UF 281497; female: UF 281289, UF 281483–84; indeterminate: UF 281487.

Remarks.—*Mobula tarapacana* has not previously been reported from the fossil record of Panama. *Mobula* cf. *M. tarapacana* specimens from the Chucunaque Formation have a significant dental sexual dimorphism, primarily reflected by the stronger ornamentation of male teeth. Adnet et al. (2012) also observed this feature in extant individuals, however the deep labiolingual furrows exhibited in the fossil specimens seem more irregular. It is possible that this morphotype represents an extinct species. Cappetta (1970) noted similarities with the extant species, *Mobula tarapacana*, in his original description of *Mobula loupianensis* and *Mobula pectinata*. Adnet et al. (2012) placed *M. tarapacana* in a distinct group within the mobulids characterized by having a cobblestone tooth plate. Extant individuals have a circumglobal distribution in temperate and tropical environments (Notarbartolo Di Sciara, 1987; Clark et al., 2006b). *Mobula tarapacana* is predominantly oceanic, but also occurs in coastal waters, inhabiting depths of 0–30 m (Feitoza et al., 2003).

Mobula spp.
Figure 11.26–11.50

Occurrence.—STRI 290109, STRI 290113, STRI 290116, and YPA105.

Description.—Numerous tooth forms with varying degrees of ornamentation were observed; however, they can be broadly placed into three morphotypes. Type I teeth lack ornamentation altogether (Fig. 11.26–11.31), and may be irregularly cuspidate (Fig. 11.26), bicuspidate (Fig. 11.31), or have a single cusp (Fig. 28). The crowns of Type I teeth are broad apically and slender basally, with enamel that extends well onto the root on the lingual face and forms a distinct ridge at the crown-root contact on the labial face. The root may be holaulochorizid or polyaulochorizid with slender, divergent root lobes. Many of these characters are similar to extant female *Mobula tarapacana*

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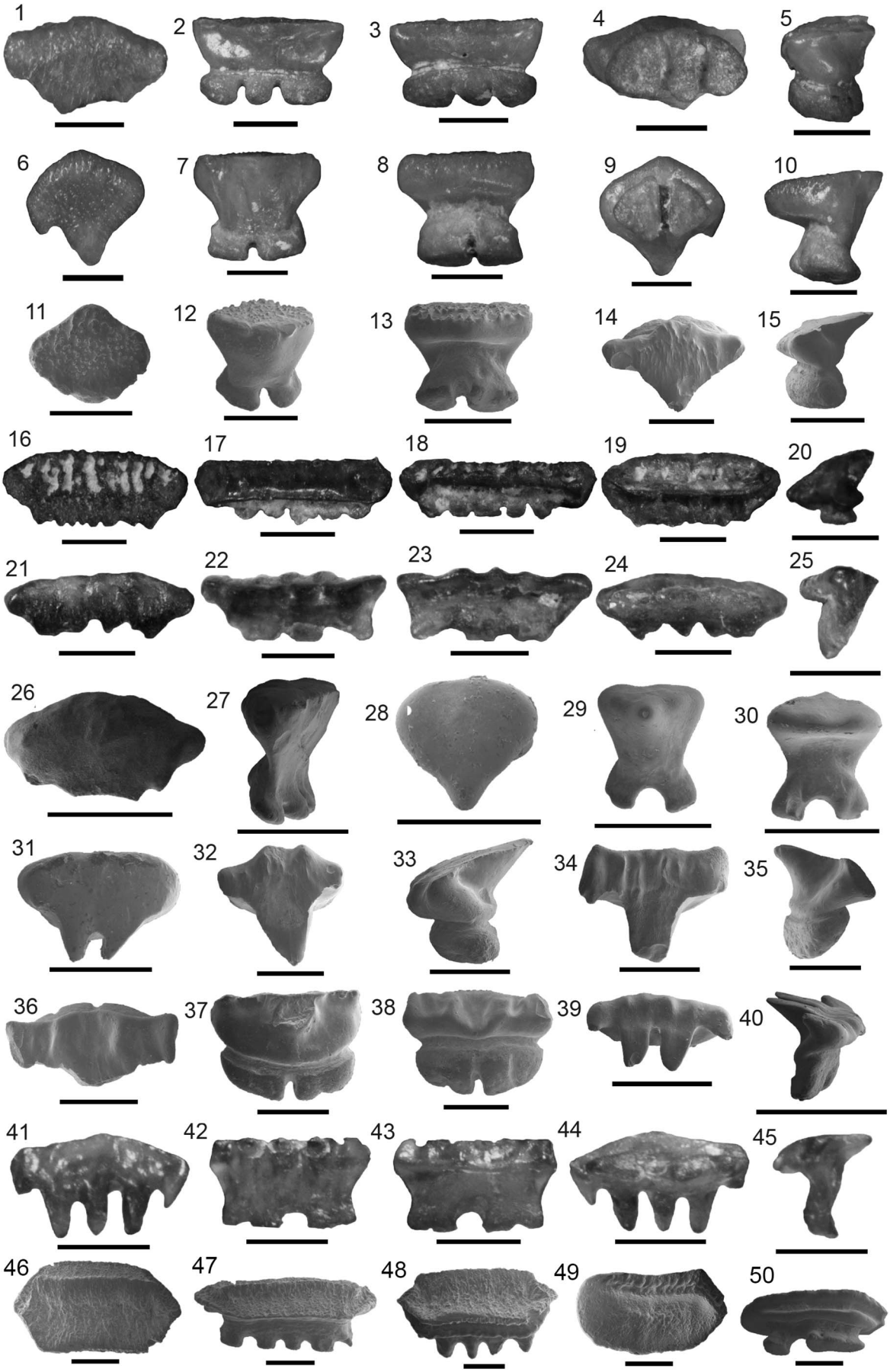

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as well as the extinct species *Mobula loupianensis*, which is not unexpected given that Cappetta (1970) noted similarities between the two in his original description of *M. loupianensis.* UF 281287 has a CH = 0.91 mm, CW = 1.06 mm, and CL = 1.59 mm (Fig. 11.31).

Type II teeth have a prominent central cusp and may have two or more minor lateral cusplets on the distal and mesial edges (Fig. 11.32–11.45). In apical view, the occlusal surface is smooth, but bears deep troughs and complimentary ridges that extend onto the labial edge. The root is low and narrow relative to the crown and is divided into two or three lobes; in UF 281251 and UF 281490 (Fig. 11.36, 11.43) the two lobes are weakly incised, beginning to form two additional lobes. This multicuspidate form strongly resembles extant males of the species *Mobula hypostoma*, but also bears similarities with extant males of *Mobula rochebrunei* and the extinct species *Mobula loupianensis*. UF 281251 has a CH = 0.71 mm, CW = 0.92 mm, and a CL = 2.09 mm (Fig. 11.36–11.38).

Type III teeth are elongate with a nearly hexagonal outline; the crown is shallow and inclined with a concave occlusal surface bearing a granular ornament (Fig. 11.46–11.50). There is a transverse crest that follows the contour of the labial edge; the labial edge is slightly convex; and the lingual edge is straight to slightly concave. The mesial and distal edges may be angular or subrounded, likely due to positional variability within the dental plate (Adnet et al., 2012). The root is high relative to the crown, and may be holaulocorhizid or polyaulacorhizid. In UF 281299, the crown is short and subhexagonal, bearing a transverse crest that follows the contour of the labial edge. The labial side of the crest is coarsely ornamented; the lingual side has a fine ornamentation that fades out distally (Fig. 11.49, 11.50; CH = 0.17 mm, CW = 1.51 mm, and CL = 0.82 mm). The largest specimen, UF 281255 (Fig. 11.46–11.48), has a CW = 3.48 mm and CL = 1.86 mm.

Materials.—One hundred forty; Type I (N = 8): UF 281268, UF 281278–81, UF 281287–88, UF 281496; Type II (N = 60): UF 281239, UF 281241, UF 281243, UF 281246, UF 281248–49, UF 281251, UF 281253–54, UF 281257–58, UF 281261–63, UF 281265–67, UF 281273, UF 281282, UF 281286, UF 281290, UF 281296, UF 281298–99, UF 281490–91; Type III (N = 70): UF 281240, UF 281244–45, UF 281247, UF 281250, UF 281252, UF 281255, UF 281259–60, UF 281264, UF 281269, UF 281274–75, UF 281277, UF 281297, UF 281486, UF 281489, UF 281492–95, UF 281498; indeterminate fragments (N = 2): UF 281300–01.

Remarks.—Notarbartolo Di Sciara (1987) noted that heterodonty is one of the most salient mobulid characteristics and suggested that tooth morphology as a systematic tool may be problematic. Adnet et al. (2012) provided a comprehensive overview of the evolutionary history of mobulid rays with a particular focus on dental characters and the evolution of planktivory. The distinction between different species, and especially between different genders, is largely based on crown ornamentation. However, additional work must still be done to better understand the robustness of crown ornamentation as a phylogenetic tool, especially in consideration of other Miocene-aged extinct species such *Mobula loupianensis*, *Mobula pectinata*, *Mobula fragilis*, and *Plinthicus*. Cappetta (2012) attributed the reduction in tooth size and crown ornamentation in the genus *Burnhamia* to a change in diet, which may indicate a greater relationship between ornamentation and environment than with evolutionary history. The tooth morphology of Type III teeth definitely resembles that of *Burnhamia*, which is considered a stem mobulid by Cappetta (1987, 2012). *Burnhamia* is an extinct genus that has been reported from the late Paleocene through the Eocene, and was placed in the family Mobulidae due to its reduced tooth size relative to rhinopterids (Cappetta, 2012).

Given that sexual dimorphism is an extremely marked character in the genus *Mobula* (Notarbartolo Di Sciara, 1987; Adnet et al., 2012; Cappetta, 2012), it seems likely that Type III teeth are female counterparts to the male Type II morphotype. The more cuspidate crowns of males compared to females likely reflect different feeding mechanisms and possibly different prey items, which would aid in reducing competition between genders. Adnet et al. (2012) places *Mobula hypostoma* in a group of mobulids characterized by having comb-like teeth, which are similar to the Type II morphotype described herein. Male teeth are imbricated with their cusps oriented lingually (Radcliffe, 1916; Notarbartolo Di Sciara, 1987), which may aid in grasping small prey and directing it inward. *Mobula hypostoma* feed primarily on zooplankton, but will also eat small pelagic crustaceans and ray-finned fishes (McEachran and Carvalho, 2002). *Mobula hypostoma* has been identified from the Gatun Formation of Panama (Pimiento et al., 2013a) and the late Miocene–Pliocene of Costa Rica (Laurito, 1999); however, Laurito (1999) only identified male *M. hypostoma* teeth. Extant individuals occur in tropical to subtropical waters in the Western Atlantic, and often have a coastal preference, but may occur in oceanic waters as well (Notarbartolo Di Sciara, 1987; McEachran and Carvalho, 2002; Bizzarro et al., 2009). Mobulid rays are placed in the aquilopelagic ecomorphotype described

Figure 11. Batoid III: Images of *Mobula* teeth from the Chucunaque Formation. (**1–15**) *Mobula thurstoni* (Lloyd, 1908): (**1–5**) UF 281291, lateral tooth in occlusal, lingual, labial, basal, and profile view, respectively; (**6–10**) UF 281292, anterolateral tooth in occlusal, lingual, labial, basal, and lateral view, respectively; (**11–13**) UF 281256, SEM image of a left lateral tooth in occlusal, lingual, and labial view, respectively; (**14, 15**) UF 281283, SEM image of a lateral tooth in occlusal and lateral view, respectively; (**16–25**) *Mobula* cf. *M. tarapacana* (Phillippi, 1893): (**16–20**) UF 281270, lateral male tooth in occlusal, lingual, labial, basal, and lateral view, respectively; (**21–25**) UF 281289, lateral female tooth in occlusal, lingual, labial, basal, and lateral view, respectively; (**26–50**) *Mobula* sp.: (**26–31**) Type I: (**26, 27**) UF 281279, SEM image of a lateral tooth in occlusal and lateral view, respectively; (**28–30**) UF 281280, SEM image of an anterior tooth in occlusal, lingual, and labial view, respectively; (**31**) UF 281287, SEM image of a indeterminate tooth position in occlusal view; (**32–45**) Type II: (**32, 33**) UF 281243, SEM image of an anterior tooth in occlusal and lateral view, respectively; (**34, 35**) UF 281241, SEM image of an anterior tooth in occlusal and lateral view, respectively; (**36–38**) UF 281251, SEM image of an aneterior male tooth in occlusal, lingual, and lateral view, respectively; (**39, 40**) UF 281253, SEM image of a lateral male tooth in occlusal and lateral view, respectively; (**41–45**) UF 281490, lateral tooth in occlusal, lingual, labial, basal, and lateral view, respectively; (**46–50**) Type III: (**46–48**) UF 281255, SEM image of a female? lateral tooth in occlusal, lingual, and apico-labial view, respectively (**49, 50**) UF 281299, SEM image of a female? tooth in occlusal and lingual view, respectively (scale bars = 1 mm).

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by Compagno (1990) because of their birdlike locomotive behavior and coastal to oceanic habitat.

Order Myliobatiformes incertae sedis
Figure 8.12–8.14

Occurrence.—YPA105.

Description.—Fragmentary dorsoventrally compressed caudal spines. UF 281317 has four barbs that are directed toward the base of the spine. The barbs and dorsal surface are covered in an enameloid sheath. There is a nutrient pore beneath each of the barbs. The caudal spine fragment has a length of 4.50 mm and a width of 2.09 mm (Fig. 8.12, 8.13).

Materials.—Two isolated caudal spine fragments: UF 281317 and UF 281499.

Remarks.—It is difficult to identify complete caudal spines to the genus or species level, let alone a fragment of one. Pimiento et al. (2013a) described a single caudal spine from the Gatun Formation and attributed it to the genus *Urobatis*. Carrillo-Briceño et al. (2015a) reported a single caudal spine in both the neritic Rio Indio facies and the bathyal Piña Sandstone facies of the Chagres Formation, but was unable to identify either beyond Batomorphii. Schwartz (2007) analyzed 34 extant species of rays in search of diagnostic characters for stingray caudal spines. Characteristics taken into account were total spine length, pre-base length, number of serrations, presence of serrations on the spine base, and presence and size of a dorsal groove. Schwartz (2007) found that no single character was sufficient for identifying a spine, however an aggregate of all of these characters could elucidate the identity. The fragment described herein lacks sufficient characters to identify it beyond the order Myliobatiformes.

Superorder Batomorphii incertae sedis
Figure 8.15, 8.16

Occurrence.—YPA105.

Description.—A simple, slender dermal denticle with a reticulate dentine interior coated by an enameloid sheath. The basal plate is elongate and oval-shaped, forming a platform for a conical, posteriorly oriented apex. The dermal denticle has a basal length of 1.40 mm, basal width of 0.47 mm, and a height of 1.51 mm.

Materials.—One isolated dermal denticle: UF 281401.

Remarks.—Dermal denticles, or placoid scales, have a composition analogous to teeth with a pulp cavity, dentine interior, and enameloid exterior (Kent, 1994); and it has been stated that teeth were evolutionarily derived from dermal denticles (Peyer, 1968). In sharks, dermal denticles tend to cover the entire body—aiding in hydrodynamics, acting as a predation deterrent, and reducing skin abrasion (Applegate, 1967; Reif, 1988; Kent, 1994). In stingrays, and some sharks, dermal denticles are often modified as a defensive measure (Kent, 1994). The dermal denticle described herein is likely of this sort; in which it has been modified as a defensive thorn, lacking the flattened, fluted morphology typical of dermal denticles that primarily function for enhanced hydrodynamics. A number of batoids possess caudal thorns that are specialized for a defensive purpose, including *Dasyatis*. Typically, caudal thorns of *Dasyatis* have a stellate basal plate (Nair and Soundararajan, 1976; Silas and Selvaraj, 1985); however the morphology of dermal denticles can vary based on position in the body, throughout ontogeny, between sexes, between individuals, and between different species (Roberts and Karnasuta, 1987). No other dermal denticles have been described from the fossil record of Panama, however this is likely due to a collection bias given their extremely small size and relatively delicate form.

Discussion

Taxonomic composition.—In total, 1422 dental remains revealed at least 31 different chondrichthyan taxa (Table 3), 23 of which belong to the subdivision Selachii (modern sharks) and 8 of which belong to the subdivision Batomorphii (skates, rays, and sawfish). There are five orders consisting of 12 families and 19 genera (Fig. 12). Seven non-dental remains were also described, including four vertebral centra, one dermal denticle, and two fragmentary caudal spines. At least 15 of the 31 taxa identified represent extant species (Table 3), confirming that the late Miocene chondrichthyans are long-lived species. Also, among the 31 taxa recognized, at least eight are new records for the fossil record of Panama (Table 3).

There is undoubtedly some degree of bias in the sample, whether it is due to collection, preservation, or identification. The best way to reduce the potential bias is with a large sample size, and the sample described herein (N = 1422) is the largest reported from Panama to date. Furthermore, our sampling efforts, as exhibited in randomized species accumulation curves

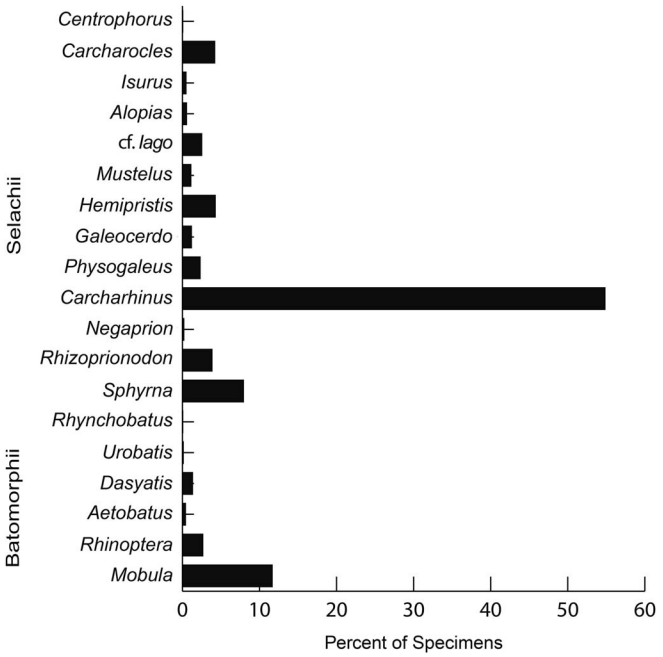

Figure 12. Relative abundance of chondrichthyan genera from the Chucunaque Formation.

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(Fig. 2) indicate that it is unlikely that more collecting (either surface prospecting or screewhasing) will result in many additional taxa. Hence, the sample utilized in this study comprises an accurate representation of the chondrichthyan biodiversity present in the Chucunaque Formation. There are three additional marine Miocene formations from Panama that have documented chondrichthyan remains: the early Miocene Culebra Formation with 12 taxa represented by 45 dental remains and 10 vertebral centra (Pimiento et al., 2013b); the middle–late Miocene Gatun Formation with 26 taxa represented by 800 dental remains (Pimiento et al., 2013a); and the late Miocene Chagres Formation with 30 taxa represented by 513 dental remains (Carrillo-Briceño et al., 2015a). The 1422 teeth collected and 31 taxa described herein from Lago Bayano comprise the most prolific and diverse chondrichthyan fauna known from Panama. Despite significant collection effort, all of these samples are subject to some degree of collection bias, and likely taphonomic bias. As such, proportions are reported to aid in the juxtaposition of these faunas, but should still be interpreted with caution.

Carcharhinus is by far the most abundant genus present in the Chucunaque Formation, representing over 50% of specimens identified (Fig. 12). Species of the genus *Carcharhinus* are the most abundant and diverse sharks in modern nearshore environments, with over 30 different species attributed to this genus (Compagno, 1984; Kent, 1994; Naylor and Marcus, 1994). *Carcharhinus* is also the most abundant genus represented in the Gatun Formation (~40%; Pimiento et al., 2013) and tied with *Hemipristis* as the most abundant genus in the Rio Indio Member of the Chagres Formation (~32%; Carrillo-Briceño et al., 2015a). In contrast, the deeper water Piña Sandstone facies of the Chagres Formation is dominated by species within the order Squaliformes, with only ~11% of the chondrichthyan fauna being represented by the genus *Carcharhinus* (Carrillo-Briceño et al., 2015a).

The second most abundant genus in the Chucunaque Formation is *Mobula* (~12%; Fig. 12). Mobulids (*Mobula* and *Manta* rays) are the largest stingrays alive today, and typically have a pelagic, coastal habit in tropical and sub-tropical waters (Notarbartolo Di Sciara, 1987; Adnet et al., 2012). *Mobula* has been recognized from the Gatun Formation of Panama, but is much less abundant (~1%; Pimiento et al., 2013a). The paucity of *Mobula* in the paleontology literature can likely be attributed to preservation and collection bias. *Mobula* teeth are extremely small and have a very thin enameloid, and yet they are very common in the Chucunaque Formation. Increased screenwashing efforts in other tropical and sub-tropical Neogene localities may reveal more *Mobula* occurrences.

Functional diversity.—Six of the nine dentition types described by Kent (1994) were observed: cutting, crushing, clutching, vestigial, cutting-grasping, and grasping-cutting (Table 3; Fig. 13.1). The generalist, cutting-grasping type dentition was the most prevalent, being represented by ~69% of the total sample. This dentition type is the most common today, and it allows for a wide variety of prey options, but it is most commonly found among sarcophagous (i.e., those eating fleshy prey such as bony fishes and marine mammals) and ichthyophagous (those eating fish) sharks (Kent, 1994). The second most common dentition type is the vestigial form (~12%), which is essentially a specialized tooth form for filter

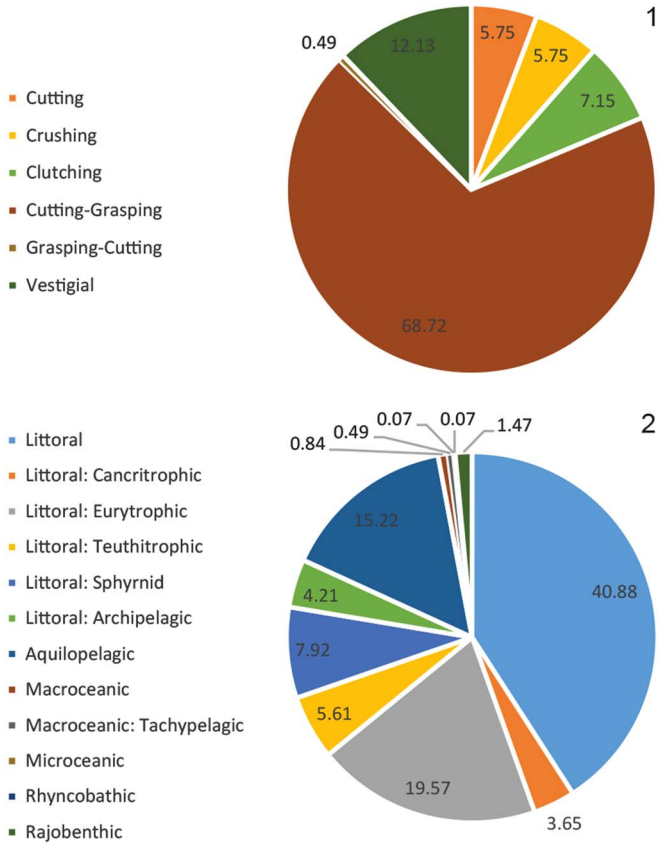

Figure 13. Two proxies for functional diversity. (**1**) Relative abundance of different dentition types as described by Kent (1994); (**2**) Relative abundance of different ecomorphotypes as described by Compagno (1990).

feeding, reflecting a planktivorous diet (Kent, 1994). This dentition type is represented by species within the genus *Mobula*. However, teeth of *Mobula* are not solely for filter feeding, but also possess some characteristics indicative of clutching and/or grinding. It has even been suggested that *Mobula* teeth may play a role during reproduction (Michael, 1993). Third is the clutching type (~7%), which is more typical of small to moderately sized sharks that primarily feed on small fishes and hard-bodied, benthic taxa (i.e., crustaceans, molluscs, and echinoids) by grabbing and gripping their prey with powerful shortened jaws (Kent, 1994). The fourth and fifth most common dentition types are the cutting type and the crushing type, both comprising 5.75% of the specimens identified. The cutting type is adapted for sarcophagous taxa (Kent, 1994). The crushing type is a specialized form for feeding on armored benthic invertebrates (i.e., durophagous), such as molluscs and crustaceans, and is most typically found in bottom-dwelling taxa (Kent, 1994). Lastly, a very small portion, 0.5%, had a grasping-cutting type dentition, which is represented by taxa in the genus *Isurus*. This dentition type relies more on capturing rather than dismembering the prey, which may be a more effective feeding strategy when operating in open water and feeding on more active prey items. Kent (1994) attributed this dentition type to ichthyophagous and teuthyophagous (i.e., those feeding on squid) sharks. It is also worth noting the absence of any taxa that have solely a grasping type dentition, such as *Carcharias*, which is a relatively common genus in Miocene deposits and in modern nearshore environments. In fact, among the

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four chondrichthyan-bearing Miocene deposits in Panama, only one tooth identified as *Carcharias* has been reported from the Chagres Formation (Carillo-Briceño et al., 2015a).

Furthermore, there were 12 ecomorphotypes represented by the chondricthyan fauna of Lago Bayano, most of which represent littoral taxa (Table 3; Fig. 13.2). The littoral ecomorphotype refers to relatively non-specialized taxa that inhabit continental shelves and feed on moderately sized prey comprised of bony fishes, crustaceans, and cephalopods, among other organisms (Compagno, 1990). Within the littoral habitus there are more specialized ecomorphotypes, including the cancritrophic (demersal sharks primarily feeding on bottom dwelling crustaceans), teuthitrophic (diet primarily consisting of cephalopods), sphyrnid (littoral to semilittoral with a specialized cephalofoil bowplane), eurytrophic (omnivores trending toward apex predator), and archipelagic (apex predators), that were also observed (Table 3; Fig. 13.2). Compagno (1990) grouped the eagle rays and cownose rays (Myliobatidae) with the devilrays (Mobulidae) into the aquilopelagic habitus because of their pectoral-driven locomotion, despite their very different feeding adaptations (Adnet et al., 2012). The aquilopelagic habitus represents ~15% of the chondrichthyan fauna from the Chucunaque Formation. The oceanic habitus (~1.5%) is represented by three ecomorphotypes: macroceanic, tachypelagic, and microceanic. The remaining taxa are batoids placed in the rajobenthic (~1.5%) and rhynchobathic (<0.1%) ecomorphotypes. Based on our functional diversity analyses, the ecosystems of Lago Bayano were dominated by generalist taxa that lived in nutrient-rich waters with abundant zooplankton.

Paleobathymetry.—The weighted paleobathymetry method was applied to the chondrichthyan fauna of the Chucunaque Formation, as well as the Gatun Formation and the Piña Sandstone facies of the Chagres Formation. For the Chucunaque Formation, 15 species of the 31 total taxa were included, which were represented by 525 specimens (37% of the total number of material collected). For the Gatun Formation, 17 of the 26 taxa identified by Pimiento et al. (2013a) were included, which represented ~32% (N = 257) of the specimens identified. For the Piña Sandstone facies of the Chagres Formation, 12 of the 28 taxa identified by Carrillo-Briceño et al. (2015a) were included, which represented ~14% (N = 70) of the specimens identified. This paleobathymetry method was not tested on the Rio Indio facies of the Chagres Formation because the chondrichthyan fauna therein is comprised of only four taxa identified to the species level that have modern analogs (Carrillo-Briceño et al., 2015a).

Our results (Table 4; Fig. 14) show that the Chucunaque Formation was most likely deposited in a neritic environment (mean depth of 110 m). Previous studies (see Coates et al., 2004) proposed that this formation was deposited in the inner-neritic to upper-bathyal zone at different localities, based on benthic foraminiferal asssemblages. Variability in paleobathymetry throughout the Neogene succession and within individual sections was thought to correspond to spatial and temporal differences in sediment deposition and basin tectonics. Nevertheless, the river outcrops surveyed by Coates et al. (2004) were deposited in adjacent sedimentary basins (Chucunaque-Tuira and Sambu), whereas Lago Bayano resides on the western margin of the Bayano Basin, which likely experienced reduced subsidence and less accommodation space. Therefore there is little issue with the chondrichthyan fauna indicating a neritic environment for the Chucunaque Formation of Lago Bayano.

Similar to the Chucunaque Formation, the Gatun was deposited in a neritic environment (mean depth of 55 m), whereas the Piña Sandstone facies was deposited within the upper bathyal zone (mean depth of 370 m). The Chucunaque Formation and the Gatun Formation are both dominated by the order Carcharhiniformes (~78% and ~83%, respectively), which is the most diverse and abundant group alive today in nearshore environments (Compagno, 1990; Kent, 1994). In contrast, the deeper water Piña Sandstone facies of the Chagres Formation is dominated by the order Squaliformes (~70%). The most abundant taxon identified from the Chagres Formation, *Isistius* sp. (N = 272), was not included in the paleobathymetric analysis because it was only identified to the generic level, and hence the depth range can only be inferred from the different living species within this genus or via other fossil occurrences. Carrillo-Briceño et al. (2015a) reported that *Isistius* (~70% of the Piña Sandstone facies) occurs at depths of 0–3700 m, usually between 0 and 1000 m, based on the extant species

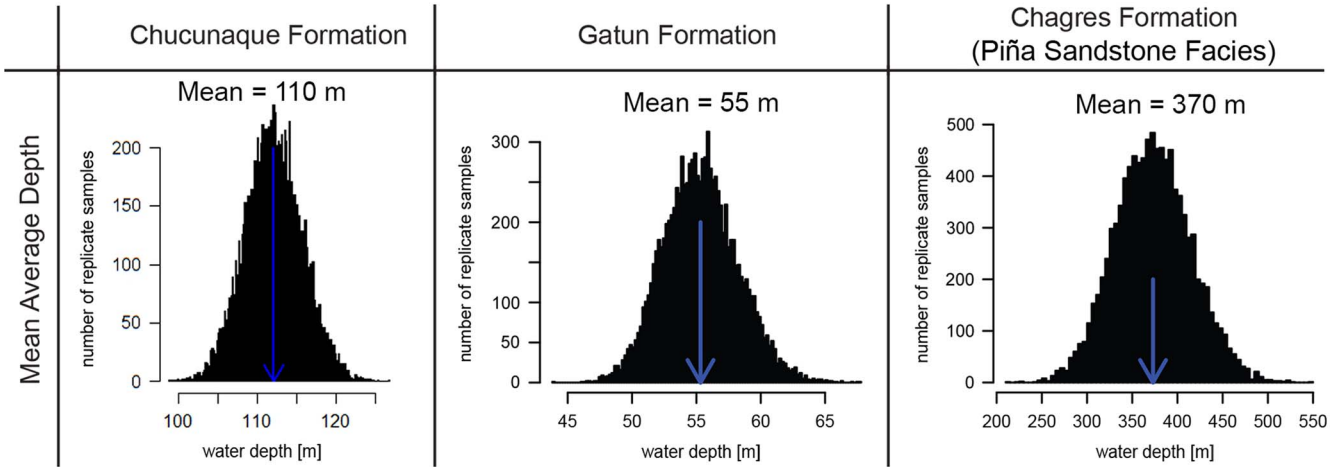

Figure 14. Paleobathymetric estimates for the Chucunaque Formation, Gatun Formation, and the Piña Sandstone facies of the Chagres Formation, showing the mean average depth. Depth ranges used in this analysis can be found in the Systematic Paleontology section as well as in Table 3.

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Isistius brasiliensis; however, they also noted that other living species of *Isistius* prefer shallow water and even make daily vertical migrations through the water column. If the preferred depth of *I. brasiliensis* were used as a proxy, its inclusion would have increased the mean average to ~470 m, but the estimate would still remain in the bathyal zone. The estimate for the Piña Sandstone facies is deeper than what was determined by Carrillo-Briceño et al. (2015a) based on chondrichthyan evidence alone. However, Collins et al. (1996) reported that the Chagres Formation was deposited in 200–500 m depth based on foraminiferal assemblages. Therefore, the depth inferred herein for the Piña Sandstone facies of the Chagres Formation would still fall within the range predicted by Collins et al. (1996) and is permissible given the presence of other deep-water taxa such as whales and billfishes (Uhen et al., 2010; Carrillo-Briceño et al., 2015a; Velez-Juarbe et al., 2015).

Despite the fact that both the Chucunaque Formation and the Gatun Formation are interpreted as having been deposited in the neritic zone, the paleobathymetric prediction for the Chuncunaque Formation is nearly twice as deep as the Gatun Formation. This can be explained by the presence of pelagic taxa such as *Isurus* and *Alopias* in the Chucunaque Formation, which are absent in the Gatun Formation (Pimiento et al., 2013a). Furthermore, there are at least six taxa from the Chucunaque Formation (*Isurus oxyrinchus*, *Alopias superciliosus*, *Alopias* cf. *A. vulpinus*, *Carcharhinus falciformis*, *Carcharhinus obscurus*, and *Sphyrna lewini*), comprising 15% of the chondrichthyan fauna, that have depth ranges beyond the neritic zone (Table 3). The presence of these taxa may indicate the influence of deeper oceanic waters in the Bayano Basin (e.g., via upwelling systems) or may be explained by the migratory habits of these sharks. Many oceanic species migrate to shallow, coastal waters to give birth (Compagno, 1984, 1998; Bass et al., 1986; Mundy, 2005), which aids in reducing competition between juveniles and adults, and may help to prevent cannibalism (Compagno, 1990). Likewise, Carrillo-Briceño et al. (2014) recognized a chondrichthyan fauna, from the middle Miocene to early Pliocene of Ecuador, indicating a shallow- to deep-water assemblage and suggested that it may reflect a short platform environment bordered by deep water. The late Miocene Curré Formation (Laurito and Valerio, 2008) from Costa Rica bears a sparse chondrichthyan assemblage (N = 89), relative to the Chucunaque Formation; however the two faunas are similar given that both are dominated by the order Carcharhiniformes, but also contain the genus *Isurus*. Laurito and Valerio (2008) inferred a neritic depth based on the chondrichthyan fauna and suggested that the depth is likely less than 35 m based on the occurrence of Pholididae traces. The presence of deep-water taxa along the Pacific Shelf of Costa Rica, Panama, and Ecuador during the late Miocene supports the idea of a proximal open ocean environment influencing the neritic Chucunaque Formation.

Our estimates presented here are a reflection of the taxonomic composition of the three localities studied and are in agreement with previous studies. However, there are obvious limitations to this method; namely, ignoring a large number of specimens either due to an inability to identify to the species level or because the species is extinct and lacks a modern analog to constrain its depth prefence. Further, there is undoubtedly some degree of preservational and/or collection bias, either due to uneven sampling efforts between screenwashed and surface collected material, or as an unavoidable result of thanatocoenosis (i.e., accumulation and deposition after death), as was suggested by Cappetta and Nolf (1991) in their paleobathymetric analysis. Even so, using the subsample of taxa that do have modern analogs and taking into account their relative abundance offers a quantitative, probabilistic approach that in theory will provide a more accurate paleodepth estimate. Likewise, Carrillo-Briceño et al. (2015c) employed a similar probabilistic approach using maximum likelihood estimation to predict the paleobathymetry of the Miocene Uitpa Formation in Colombia based on chondrichthyan occurrences.

Paleobiogeography.—The chondrichthyan fauna from the Gatun Formation has mixed biogeographic affinities, with evidence of taxa currently restricted to the Atlantic including *Carcharhinus perezi*, *Rhynchobatus luebberti*, *Mobula hypostoma*, and *Taeniurops* aff. *T. grabata* and Pacific-restricted taxa including *Myliobatis* cf. *M. californica*, *Rhinoptera* cf. *R. steindachneri*, and *Mobula munkiana* (Pimiento et al., 2013a). Of the 15 extant taxa observed from the Chucunaque Formation, all occur in both the Atlantic and the Pacific oceans today, with the possible exception of *C.* aff. *macloti*, given that extant *C. macloti* is restricted to the Pacific. Also, it is possible that the Type II *Mobula* teeth observed in the Chucunaque Formation actually belong to *Mobula hypostoma*, which would mean that there is an Atlantic-restricted species on the Pacific side of the evolving Panamanian isthmus. If even one of these species were accurately identified as representing a species that is currently restricted to the opposing side of the isthmus, it would support the hypothesis that there was a continued marine connection between 9 Mya and 10 Mya.

The Chucunaque Formation of Lago Bayano is roughly contemporaneous with the upper part of the Gatun Formation (Hendy, 2013; Pimiento et al., 2013a). The Gatun Formation of the Panama Canal Basin is considered to have had a Caribbean affinity based on benthic foraminiferal assemblages (Collins et al., 1996), whereas the Chucunaque Formation of the Bayano Basin has been interpreted as having a Pacific affinity (Coates et al., 2004). The two distinct foram assemblages have been utilized to interpret restriction of deep-water circulation by ~8 million years ago; however, this deep-water connection is thought to have returned ~6 million years ago based on Pacific foraminifera in the bathyal Chagres Formation (Collins et al., 1996). Despite the fact that there was, likely, ongoing shoaling of the Isthmus of Panama and restriction of deep-water circulation (Montes et al., 2012a, 2012b; Sepulchre et al., 2014), there must have still remained a marine connection between the Caribbean Sea and Pacific Ocean ~10 million years ago to allow for exchange of marine vertebrates (Pimiento et al., 2013a). Sepulchre et al. (2014) incorporated neodymium isotopic data into a model in order to resolve the history of water masses connecting the Pacific to the Caribbean, and found that a seaway 50–200 m deep would likely have been present ~10 million years ago, which is consistent with the depth estimates for the Gatun and Chucunaque Formations, derived from the weighted paleobathymetric analysis (Table 4; Fig. 14).

The Lago Bayano fauna is therefore highly significant because it represents the first described Miocene chondrichthyan fauna from the Pacific shelf of Panama. The only other Miocene

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chondrichthyan faunas that have been described from the Pacific shelf of the evolving Central American isthmus are from the middle Miocene Punta Judas Formation (Laurito, 2004) and the late Miocene Curré Formation (Laurito and Valerio, 2008) from Costa Rica. The Curré Formation was tentatively assigned as being late Miocene because of the occurrence of chondrichthyan taxa typical of the Miocene and terrestrial mammal remains (Laurito and Valerio, 2005, 2008; Valerio and Laurito, 2008). The co-occurrence of terrestrial taxa as well as marine fauna in the Curré Formation is very similar to that of the late Miocene Alajuela Formation (MacFadden et al., 2015, 2017), providing evidence that at least some emergent land was present within the Central American isthmus. Coates and Obando (1996) reconstructed the CAS during the late Miocene as an archipelagic strait on the basis of tectonic evidence and nannofossil assemblages. Alternatively, it has been proposed that a continuous peninsula connected Panama to North America as early as 19 million years ago, based on comparable body sizes between contemporaneous land mammals found in North America and Panama (Kirby and MacFadden, 2005; Kirby et al., 2008). However, neither reconstruction excludes the notion of a marine connection between the Pacific Ocean to the Caribbean Sea throughout the Miocene.

After uplift of the Isthmus of Panama and complete closure of the CAS many taxa had populations in both the Pacific and Atlantic, with a few species becoming restricted to either side. With the information available we cannot yet ascertain if the reason these taxa became restricted is due to the closure of the CAS, but it is highly probable that the uplift of the Isthmus of Panama was a contributing factor. Given that chondrichthyan taxa are highly mobile, and that many are capable of trans-oceanic migrations, it is possible that they could continue to exchange between the Pacific and Atlantic via a meridional route after complete closure of the CAS. However, temperature restrictions would make this unlikely. A more reasonable explanation for the co-occurrence of Atlantic-restricted and Pacific-restricted taxa between 9 and 10 million years ago is that there was in fact a marine connection between the Caribbean Sea and the Pacific Ocean.

Conclusion

This overview of the chondrichthyan fauna from the late Miocene Chucunaque Formation reveals the most prolific and diverse assemblage from Panama, with at least 31 taxa, eight of which are new to the fossil record of Panama. Furthermore, the Lago Bayano fauna is the first described Miocene chondrichthyan assemblage from the Pacific shelf of the Panamanian isthmus, and $^{87}Sr/^{86}Sr$ isotopic ratios reported provide the first geochronology for the region. At least 15 of the taxa identified have affinities with extant species, which offers the opportunity to utilize the habitat preferences of the corresponding living species to make inferences regarding functional diversity, paleoenvironment, and paleobiogeography. The Bayano ecosystems are dominated by generalist sharks (with cutting-grasping type dentitions) and filter-feeding rays. A weighted paleobathymetric analysis provides evidence for a paleoenvironment in the neritic zone, with a mean average estimate of 110 m. Finally, the geographic ranges of the fauna indicate mixed geographic affinity, which offers insight into a marine connection between the Caribbean Sea and the Pacific Ocean during a time of active shoaling in Central America.

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