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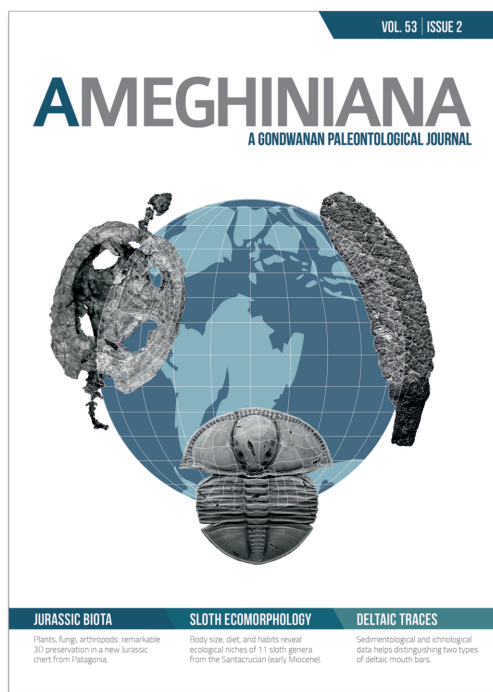
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A NEW EARLY MIOCENE (AQUITANIAN) ELASMOBRANCHII ASSEMBLAGE FROM THE LA GUAJIRA PENINSULA, COLOMBIA

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Abstract. Recent field expeditions have led to the discovery of a selachian assemblage from the earliest Miocene (Aquitanian) deposits of the Uitpa Formation in the La Guajira Peninsula, Colombia. This elasmobranch assemblage provides a unique glimpse into the Caribbean biodiversity at the onset of the Neogene. The assemblage consists of 13 taxa, of which some are reported from Miocene deposits for the very first time. There are also new records of taxa the in southern Caribbean region. The taxonomic composition of the selachian assemblage was used to conduct a paleoenvironmental and paleobathymetric analysis of the lower Uitpa Formation. The maximum likelihood estimation of paleobathymetry suggests that the lower part of the Uitpa Formation was probably accumulated at a water depth of 100 to 200 m. This indicates a rapid increase in relative sea level or basin deepening, providing new insights into the possible causes of marine biota changes in the Cocinetas Basin during the Oligocene/Miocene transition.

Key words. Neogene. Tropical America. Caribbean. Sharks. Rays. Paleobathymetry. Paleoenvironments.

Resumen. UN NUEVO ENSAMBLE DE ELASMOBRANCHII DEL MIOCENO TEMPRANO (AQUITANIANO) DE LA PENÍNSULA DE LA GUAJIRA, COLOMBIA. Recientes trabajos de campo han llevado al descubrimiento de un conjunto de seláceos procedente del Mioceno temprano (Aquitaniense) en los depósitos más antiguos de la Formación Uitpa en la Península de La Guajira, Colombia. Este conjunto de elasmobranquios provee una visión única de la paleobiodiversidad del Caribe a inicios del Período Neógeno. El conjunto aquí descrito se compone de 13 taxones, algunos de los cuales son reportados por vez primera para el Mioceno. Esta fauna también incluye nuevos registros para la región sur del Caribe. La composición taxonómica del nuevo ensamble permitió realizar un análisis paleoambiental y paleobatimétrico en la sección más inferior de la Formación Uitpa. La estimación de paleobatimetría usando *maximum likelihood* sugiere que la parte inferior de la Formación Uitpa fue probablemente depositada a profundidades entre los 100 y 200 m. Esto indica un rápido incremento en el nivel relativo del mar o en la profundización de la cuenca, proveyendo nueva información sobre las posibles causas que dieron origen a los cambios en la biota marina de la Cuenca de Cocinetas durante la transición del Oligoceno/Mioceno.

Palabras clave. Neógeno. América Tropical. Caribe. Tiburones. Rayas. Paleobatimetría. Paleoambientes.

THE beginning of the Neogene was a time when world climate was warmer and sea level was higher than at present (Zachos *et al.*, 2001). Large scale geological processes, including the closure of the Central American Seaway and the rise of the Panamanian Isthmus, had not yet been completed (Woodburne, 2010; Montes *et al.*, 2012a,b; Coates and Stallard, 2013; Montes *et al.*, 2015). Large areas of the northern margin of South America were submerged during the early Miocene (see Iturralde-Vinent and MacPhee, 1999 and references therein). This was also the case in the southern Caribbean Cocinetas Basin, where there are widespread early Miocene marine sedimentary deposits that have

yielded a rich record of invertebrate (Becker and Dusenbury, 1958; Lockwood, 1965; Rollins, 1965; Thomas, 1972; Hendy *et al.*, 2015) and vertebrate fossils of which most are chondrichthyans (Lockwood, 1965; Moreno *et al.*, 2015).

Early Miocene marine chondrichthyan faunas from Tropical America are still poorly known with only a few relevant reports from Barbados (Casier, 1958), Brazil (Santos and Travassos, 1960; Santos and Salgado, 1971; Reis, 2005; Costa *et al.*, 2009), Cuba (Iturralde-Vinent *et al.*, 1996), Mexico (Gonzales-Barba and Thies, 2000), Panama (Pimiento *et al.*, 2013a), Trinidad (Leriche, 1938), the Grenadines (Portell *et al.*, 2008) and Venezuela (Leriche, 1938; Sánchez-Villagra *et*

al., 2000; Aguilera and Rodrigues de Aguilera, 2004; Aguilera, 2010; Aguilera and Lundberg, 2010) available. These studies depict the composition of marine vertebrate Caribbean faunas before the complete closure of the Central American Seaway (Woodburne, 2010; Montes *et al.*, 2012a,b; Coates and Stallard, 2013; Montes *et al.*, 2015). Reports on marine chondrichthyans from the Miocene of Colombia are scarce in the literature and previous works on the Cocinetas Basin (La Guajira Peninsula) only include a brief mention of elasmobranch fossils with no accompanying taxonomic description by Lockwood (1965) and a list of 14 families presented in Moreno *et al.* (2015).

The Cocinetas Basin is located in the eastern flank of La Guajira Peninsula, northern Colombia (Fig. 1), and provides an extensive and well-exposed sedimentary and paleontological record of the last 30 million years (Ma) (Jaramillo *et al.*, 2015; Moreno *et al.* 2015). Recent expeditions to the La Guajira Peninsula (Cocinetas Basin) brought about the extensive surface collection of vertebrate fossils, including the chondrichthyan assemblage from the early Miocene (Aquitania) Uitpa Formation reported here. We studied the taxonomic composition of this assemblage and its paleobioge-

graphical and chronostratigraphic significance. Additionally, we conducted a paleoenvironmental and paleobathymetric analysis of the data to explore possible causes related to the marine biota changes that occurred in the Cocinetas Basin during the Oligocene/Miocene transition (OMT). Furthermore, we compared the Uitpa Formation chondrichthyans to other coetaneous faunas from Tropical America such as the Venezuela and Trinidad collection described by Leriche (1938). The new assemblage reported herein, which includes taxa previously unreported from the Caribbean region, is one of the oldest shark-ray associations known from the Neogene of Tropical America.

GEOLOGICAL AND STRATIGRAPHICAL SETTING

The Uitpa Formation and its type section were described by Renz (1960, p. 340) and named after the water spring of the Uitpa village, located to the SE of the Serranía de Jarara. The formation was re-described by Rollins (1965). The Uitpa Formation is one of the most extensive Cenozoic units in the La Guajira Peninsula and boasts a thickness of approximately 230 m. It conformably overlies the Siamana Formation while conformably underlying the Jimol Formation (Fig. 2). While an Oligocene to early Miocene age was proposed by Becker and Dusenbury (1958) based on benthic foraminifera, Lockwood (1965) and Rollins (1965) suggested an early Miocene age (Aquitania) based on foraminifera and ostracods. More recently, an early Miocene to earliest middle Miocene age was proposed by Hendy *et al.* (2015) based on mollusks and stratigraphic relations. The outcrop studied herein is located close to the Uitpa village (Fig. 1) and the chondrichthyan-bearing strata (Fig. 2) lie at 0.5 to 10 m from the base of the Uitpa Formation. The lower part of the Uitpa Formation comprises well-differentiated layers of soft light brown shales and calcareous bioturbated silty-sandstones presenting thin selenite layers. We have also observed abundant mollusks, echinoids, crustaceans and bony fish fragmentary remains.

MATERIALS AND METHODS

The fossils studied herein (Figs. 3–5) were collected from the base of the Uitpa Formation in the course of three field trips conducted between 2008 and 2014. Fossil specimens came from stratigraphic meters 0.5 to 10 (Fig. 2) in the Arroyo Uitpa locality, ID locality: 360181, 12° 1' 32.73"

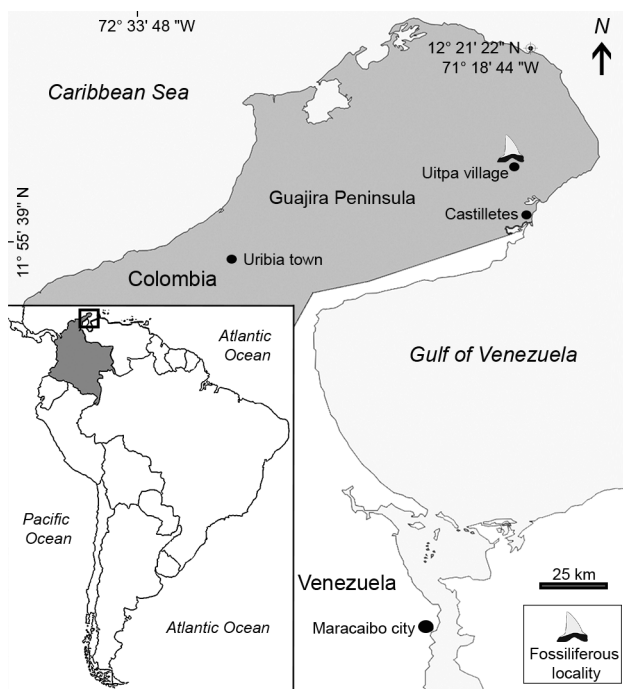


Figure 1. Location map of the fossiliferous locality.

N, 71° 25' 4.94" W, ~0.9 km SW of the Uitpa village. Photographs of the fossils were taken with a Leica MZ16F and multifocal stereomicroscope. As for the imaging of small teeth, a Scanning Electronic Microscope was used. We identified all fossil chondrichthyan teeth and narrowed their classification down to the lowest possible taxonomic level. This material is deposited at the Mapuka Museum of Universidad del Norte (**MUN-STRI**), Barranquilla, Colombia. While the dental terminology utilized herein is the one coined by Cappetta (2012), the systematics applied for fossil and recent taxa are consistent with Compagno (2005) and Cappetta (2012). The sole exception to this approach is the extinct genus *Carcharocles* Jordan and Hannibal, 1923, whose assignment in this study has prolonged the discussion presented by Pimiento *et al.* (2010). Measurements taken refer to the entire tooth, including the root, and consist of height, width and length. For incomplete teeth we used only crown measurements. In addition to MUN-STRI

materials, specimens housed at the Natural History Museum of Basel (**NMB**), Basel, Switzerland, were also included here. Taxonomic identification involved an extensive bibliographical review and comparative studies concerning fossil and extant specimens from other collections such as the Fossil Vertebrate Section of the Museum für Naturkunde, Berlin, Germany; the Museu Paraense Emilio Goeldi, Belem, Brazil; the Paleontological collections of the Alcaldía Bolivariana de Urumaco, Urumaco, Venezuela; the Palaeontological Institute and Museum at the University of Zurich, Zurich, Switzerland; the René Kindlimann private collection, Uster, Switzerland; and the Universidad Nacional Experimental Francisco de Miranda, Coro, Venezuela.

In this work, the term "Tropical America" (Neotropics) refers to the geographical area of the western hemisphere located between the Tropic of Cancer (23° 27' N) and the Tropic of Capricorn (23° 27' S). "Southern South America" is a region composed of the southernmost areas of South

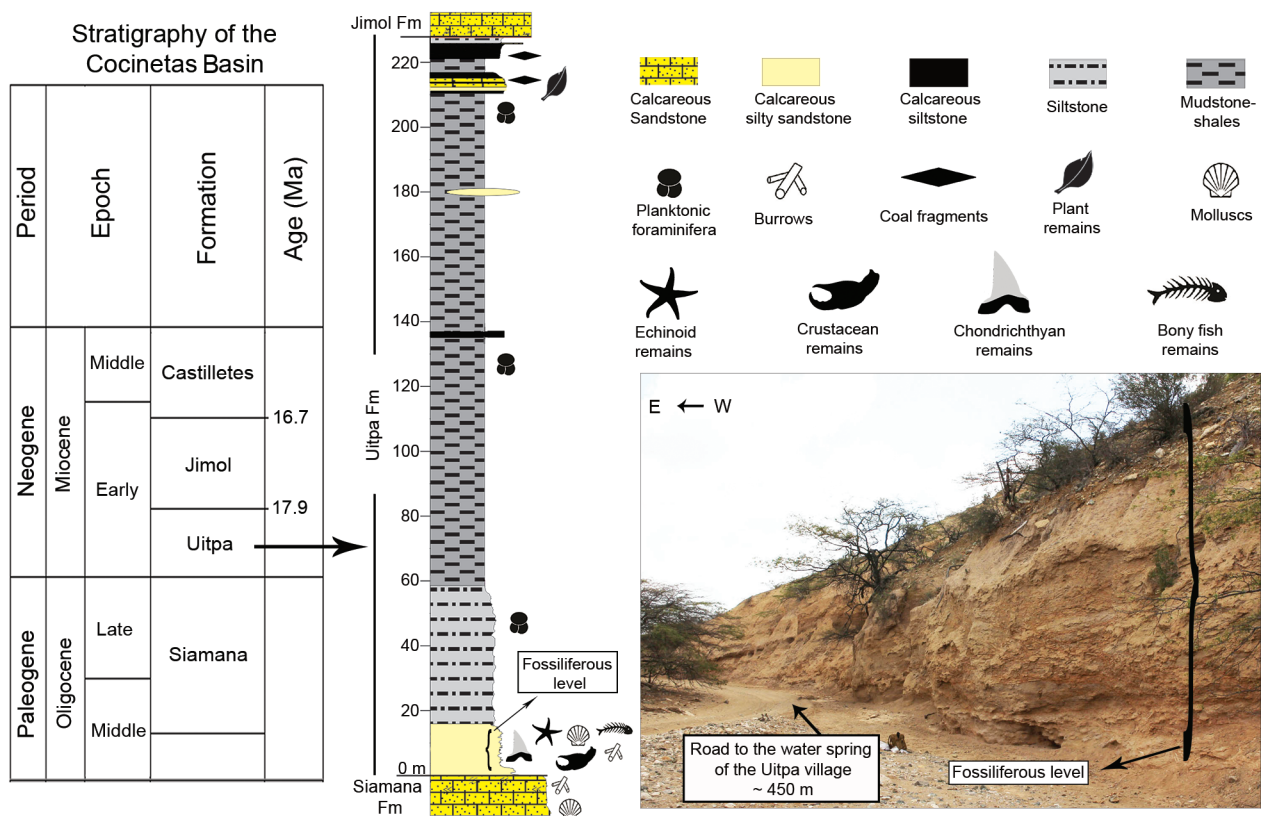


Figure 2. Generalized stratigraphy of the Cocinetas Basin (after Moreno *et al.*, 2015), including a complete stratigraphic section of the Uitpa Formation and an illustration of the studied outcrop, that corresponds to the lowest 10 stratigraphic meters of the formation.

America; namely, Argentina, Chile, Paraguay and Uruguay (south of the Tropic of Capricorn). We refer to Canada, the USA and the northern part of Mexico as “North America” (north of the Tropic of Cancer).

We compiled information on the paleodistribution of all chondrichthyan taxa known from the Neogene of the Americas (Appendix 1) [e.g., Tropical America (Leriche, 1938; Casier, 1958, 1966; Santos and Travassos, 1960; Gillette, 1984; De Muizon and Devries, 1985; Kindlimann, 1990; Kruckow and Thies, 1990; Iturralde-Vinent *et al.*, 1996; Laurito, 1999; Donovan and Gunter, 2001; Reis, 2005; Portell *et al.*, 2008; Aguilera and Lundberg, 2010; Pimiento *et al.*, 2010, 2013a, b; Aguilera *et al.*, 2011; Carrillo-Briceño *et al.*, 2014, 2015), Southern South America (Long, 1993a; Arratia and Cione, 1996; Suárez and Marquardt, 2003; Suárez *et al.*, 2006; Cione *et al.*, 2011; Carrillo-Briceño *et al.*, 2013) and North America (Case, 1980; Kruckow and Thies, 1990; Long, 1993b; Müller, 1999; Gonzales-Barba and Thies, 2000; Purdy *et al.*, 2001; Boessenecker, 2011)]. For conducting the paleoenvironmental interpretation, we used Compagno (1984a,b), Compagno and Last (1999), Compagno *et al.* (2005), Musick *et al.* (2004), Kiraly *et al.* (2003), Cao *et al.* (2011), Voigt and Weber (2011) and the FishBase website (Froese and Pauly, 2015) for collecting bathymetric and habitat information for both the taxa present in the Uitpa Formation and their extant relatives. In addition, we performed a maximum likelihood estimation of paleobathymetry following the method developed and extensively described in Punyasena *et al.* (2011), with which the probability that a fossil assemblage is derived from a given depth can be calculated. Drawing on information that was compiled from the literature (Fig. 6), all species with extant relatives were individually modeled with normal probability densities to replicate each species abundance distribution along a depth gradient. Probability density reflects the likelihood of finding a given species at a given point along a depth gradient. For the analysis put forth herein, we use the function *rtruncnorm* in the package *truncnorm* in R (R-Development-Core-Team, 2012) to simulate the probability density. Likelihood values for the depth estimates are the sum of the log likelihoods of the species found within a fossil sample (identical to the joint product of the probability densities of these families). The likelihood estimation was performed using the software package developed by

Punyasena *et al.* (2011) that can be downloaded at <https://www.life.illinois.edu/punyasena-download/>. The R-code used to run the analysis can be found in Appendix 2.

RESULTS

Elasmobranch taxonomical composition

The elasmobranch assemblage described herein comprises 13 taxa attributed to 12 genera, 11 families and six orders (Appendix 1).

SYSTEMATIC PALEONTOLOGY

CHONDRICHTHYES Huxley, 1880

NEOSELACHII Compagno, 1977

SQUALOMORPHII Compagno, 1973

HEXANCHIFORMES Buen, 1926

HEPTRANCHIDAE Barnard, 1925

Heptranchias Rafinesque, 1810

Type species. *Squalus cinereus* Gmelin, 1789.

† *Heptranchias* cf. *howellii* (Reed, 1946)

Figure 3.1–7

1938 *Notidanion tenuidens* Leriche, p. 3–4, fig. 2, pl. 1, figs. 1–4.

1946 *Notidanion howellii* Reed, p. 1–2, figs. 1–3, p. 3, fig. 4.

1971 *Heptranchias* Waldman, p. 166, pl. 1, figs. 1–2.

1968 *Heptranchias ezoensis* Applegate and Uyeno, p. 197–198, pl. 1A.

1974 *Heptranchias howellii* (Reed), Welton, p. 3, fig. 1 A–B, p. 7, pl. 2.

1981 *Heptranchias howellii* (Reed), Cappetta, p. 568, pl. 1, fig. 1–1'.

2015 *Heptranchias howellii* (Reed), Adolfssen and Ward, p. 319–320, fig. 2K–L.

Referred material. Five lower teeth (MUN-STRI-34777, MUN-STRI-34784a and MUN-STRI-39926) and one upper tooth (MUN-STRI-34784b).

Geographic and stratigraphic occurrence. See Remarks.

Description. The five lower teeth, of which two correspond to the mesial part of the tooth (Fig. 3.1–3.2) while the remaining three to the distal part (Fig. 3.3–3.4), are incomplete. All specimens are strongly compressed labiolingually. The mesial specimens present a developed acrocone, which is larger than the distal cusplets, with two small but well differentiated mesial cusps preserving the first two distal cusplets (accessory conules). The other specimens that correspond to the distal part of the teeth only preserve between three and four distal cusplets. In these

specimens, the acrocone and distal cusplets are smooth and inclined distally while their root is poorly preserved. The upper antero-lateral tooth (Fig. 3.5) preserves only the crown, which is tall and narrow with sigmoidal contour.

Remarks. *Heptranchias howellii* ranges from the early Paleocene to the late Oligocene with records from Africa (Morocco), Asia (Japan), Australia, Europe, North America and South America (Venezuela) (Leriche, 1938; Reed, 1946; Applegate and Uyeno, 1968; Welton, 1974; Kemp, 1978; Cappetta, 1981, 2012; Bieñkowska-Wasiluk and Radwański, 2009; Adolfssen and Ward, 2015). The teeth of *Heptranchias howellii* are very similar to those of the extant *Heptranchias perlo* Bonnaterre, 1788. However, the teeth of *H. howellii* tend to be larger, reaching up to 25 mm in length, and exhibit a broader and less attenuated acrocone than that of *H. perlo* (Kemp, 1978). According to Cappetta (1981), the acrocone of the *H. howellii* teeth is much less developed in comparison with their distal cusplets. The specimens of *Heptranchias (Notidanion) tenuidens* (Fig. 3.6–3.7) described from the locality of Mene de Acosta in Venezuela (Menecito Member of the San Lorenzo Formation: early to middle Miocene) by Leriche (1938, pl. 1, figs. 1–3), exhibit clear morphological similarities to the teeth of *Heptranchias* cf. *howellii* from both the Uitpa Formation described herein and those referred to the latter species found in African, European and North American deposits (Welton, 1974; Cappetta, 1981, 2012; Bieñkowska-Wasiluk and Radwański, 2009; Adolfssen and Ward, 2015). This resemblance suggests that *Heptranchias (Notidanion) tenuidens* could be a synonym of *H. howellii*. The merging of the two species was previously suggested by Cappetta (1981, 2012); nevertheless, the aforementioned author did not provide a direct comparison between the *H. tenuidens* specimens of the Leriche collection and *H. howellii*. It should also be noted that one of the specimens referred to as *H. tenuidens* by Leriche (1938, pl. 1, fig. 4) most likely corresponds to an upper anterior tooth of cf. *Centrophorus* (Fig. 3.16–3.17).

SQUALIFORMES Goodrich, 1909

CENTROPHORIDAE Bleeker, 1859

Centrophorus Müller and Henle, 1837

Type species. *Squalus acanthias* Linnaeus, 1758.

Centrophorus sp.

Figure 3.8–15

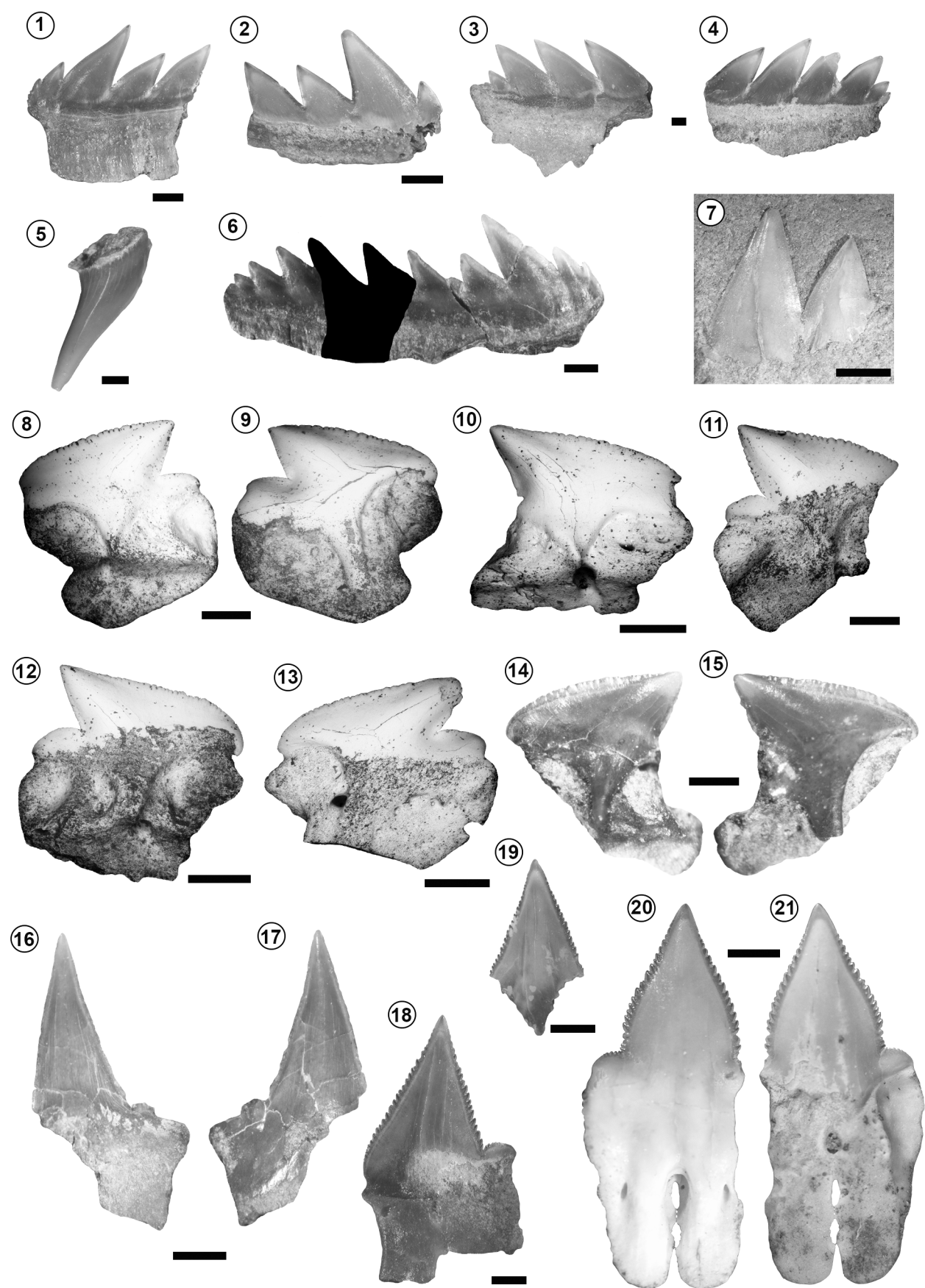
Referred material. Five poorly preserved lower teeth (MUN-STRI-39927).

Geographic and stratigraphic occurrence. See Remarks.

Description. These specimens exhibit ranges in height of about 3 to 4 mm and, in width, between 3.5 to 5 mm. The teeth are labio-lingually compressed and taller than broad, with a distally inclined triangular cusp. The mesial cutting edge of the main cusp is convex and markedly serrated. Such disposition contrasts with the distal cutting edge, which is straight to convex and presents finer serrations. The distal heel is high, convex and very weakly serrated. The apron is prominent and long but ends before reaching the base of the root. The uvula is less prominent and short. The labial face of the root is short and presents a well-defined external depression. On the lingual face, a large infundibulum opens below the tip of the uvula.

Remarks. *Centrophorus* ranges from the Late Cretaceous to the present (Adnet *et al.*, 2008; Kriwet and Klug, 2009). Extant *Centrophorus* comprises at least 12 species characterized by complex interspecific morphological variations. Additionally, their dentition also displays ontogenetic changes and sexual dimorphism (White *et al.*, 2008). The teeth described herein are not adequately preserved and consequently, although they do resemble the *Centrophorus* sp. teeth referred by Carrillo-Briceño *et al.* (2014) from the middle to late Miocene of Ecuador, they cannot be assigned to any known species. The specimen illustrated as *Acanthias stehlini* by Leriche (1938, pl. 1, fig. 5) from the locality of Mene de Acosta in Venezuela (San Lorenzo Formation: early–middle Miocene) is, instead, a lower tooth of *Centrophorus* (Fig. 3.14–3.15), as previously suggested by Cappetta (2012, p. 116). The poorly preserved single isolated and fragmented tooth used by Leriche (1938) to erect *Acanthias stehlini* (*Centrophorus stehlini*) does not exhibit any diagnostic features that may distinguish it from the specimens from the Uitpa Formation or any other known fossil or recent species. We consider Leriche's species a *nomen dubium* of questionable taxonomical validity.

DALATIIDAE Gray, 1851



***Dalatias* Rafinesque, 1810**

Type species. *Dalatias sparophagus* Rafinesque, 1810.

***Dalatias* cf. *lich*a (Bonnaterre, 1788)**

Figure 3.18–21

1788 *Squalus lich*a Bonnaterre, p. 2.

1948 *Dalatias lich*a (Bonnaterre), Bigelow and Schroeder, p. 502, figs. 96, 97.

1970 *Scymnorhinus lich*a (Bonnaterre), Ledoux, p. 353, figs. 20, 21.

1975 *Dalatias lich*a (Bonnaterre), Uyeno and Matsushima, p. 46, pl. 2, fig. 2a–b.

Referred material. Three lower teeth, one symphyseal (MUN-STRI-39928) and two laterals (MUN-STRI-39929).

Geographic and stratigraphic occurrence. See Remarks.

Description. The symphyseal tooth is complete and displays a height of 9.5 mm and a width of 4.1 mm. The tooth is labio-lingually compressed and bears an upright and triangular crown with strongly serrated cutting edges. The serrations are directed apically. Two short, narrow, weakly convex and finely serrated heels flank the main cusp. In labial view, the apron is flat and markedly deep, reaching the base of the tooth. A transverse slit divides the basal half of the apron in two. The root is high and presents convex distal and mesial edges. There is a well-developed medio-lingual foramen and a broad elliptical button hole with a broad channel-shaped depression. The lateral teeth are incomplete, lacking parts of their roots. Their main cusps are similar to those of the symphyseal tooth yet slightly inclined distally. Only one distal heel is observed in the lateral teeth but it is similar to that of the symphyseal. The root is high and resembles that of the symphyseal tooth though presenting a convex distal and a concave medial edge.

Remarks. *Dalatias* ranges from the early Paleocene to the Recent (see Kriwet and Klug, 2009; Cappetta, 2012), with the oldest record of *Dalatias lich*a known from the middle Eocene of New Zealand (Keyes, 1984; Kriwet and Klug,

2009). The tooth morphology of the Neogene species is identical to that of the recent *D. lich*a (Cappetta, 2012). Its fossil record includes occurrences in the Caribbean, Europe, Japan and New Zealand (Kriwet and Klug, 2009; Cappetta, 2012). A specimen previously referred to *Hemipristis serra* Agassiz, 1843, by Casier (1958, pl. 2, fig. 1; 1966, pl. 1, fig. 9), from the early Miocene of Barbados, is hereby identified as a crown of a *Dalatias*. The fossil record of *Dalatias* from the Americas is shown in Appendix 1.

PRISTIPHORIFORMES Berg, 1958

PRISTIPHORIDAE Bleeker, 1859

***Pristiophorus* Müller and Henle, 1837**

Type species. *Pristis cirratus* Latham, 1794.

***Pristiophorus* sp.**

Figure 4.1–3

Referred material. Thirteen rostral teeth (MUN-STRI-39930; MUN-STRI-39931).

Geographic and stratigraphic occurrence. See Remarks.

Description. The root is missing in all specimens. The crowns, which measure between 4 and 17 mm in length, are long and slender while dorso-ventrally compressed and bearing smooth edges. The fairly flat enameled cusp is slightly inclined distally.

Remarks. *Pristiophorus* ranges from the Late Cretaceous to the Recent and its rostral teeth are readily distinguishable from those of *Pliotrema* Regan, 1906 since the latter present a barbed posterior cutting edge (Cappetta, 2012). The *Pristiophorus* specimens from the Uitpa Formation described herein constitute the oldest known record of the genus from Tropical America. Other records from the Americas are shown in Appendix 1.

Figure 3. 1–7, *Heptranchias* cf. *howellii*; 1–4, lower teeth (1: MUN-STRI-34777, 2–4: MUN-STRI-34784a); 5, upper tooth (MUN-STRI-34784b); 6–7, lower *Heptranchias* teeth referred by Leriche (1938) as *Notidanion tenuidens* (6: NMB S.a.1314, 7: NMB S.a.1315). 8–15, *Centrophorus* sp.; 8–13, lower teeth (MUN-STRI-39927); 14–15, lower *Centrophorus* sp. tooth referred by Leriche (1938) as *Acanthias stehlini* (NMB S.a.1314). 16–17, upper tooth of cf. *Centrophorus* referred by Leriche (1938) as *Notidanion tenuidens* (NMB S.a.1316). 18–21, *Dalatias* cf. *lich*a lower teeth (18–19: MUN-STRI-39929, 20–21: MUN-STRI-39928). Views: labial (1, 2, 9, 12, 15, 17, 18, 20), lingual (3, 4, 6, 8, 10, 11, 12, 13, 14, 16, 19, 21), lateral (5), indet. (7). Scale bar= 1 mm.

GALEOMORPHII Compagno, 1973

LAMNIFORMES Berg, 1937

LAMNIDAE Müller and Henle, 1838

Isurus Rafinesque, 1810

Type species. *Isurus oxyrinchus* Rafinesque, 1810.

Isurus cf. *oxyrinchus* Rafinesque, 1810

Figure 4.4–11

1810 *Isurus oxyrinchus* Rafinesque, p. 12, pl. 13, fig. 1.

2001 *Isurus oxyrinchus* Rafinesque, Purdy *et al.* p. 114–116, figs. 25, 26.

Referred material. Seven teeth. Two upper teeth (MUN-STRI-39932), five lateral teeth of indeterminate position (MUN-STRI-39933).

Geographic and stratigraphic occurrence. See Remarks.

Description. All teeth are incomplete and present damaged roots. The crown height measures between 9 and 45 mm. The upper anterior tooth exhibits a wide, asymmetrical and distally inclined crown. Both the lingual and the labial sur-

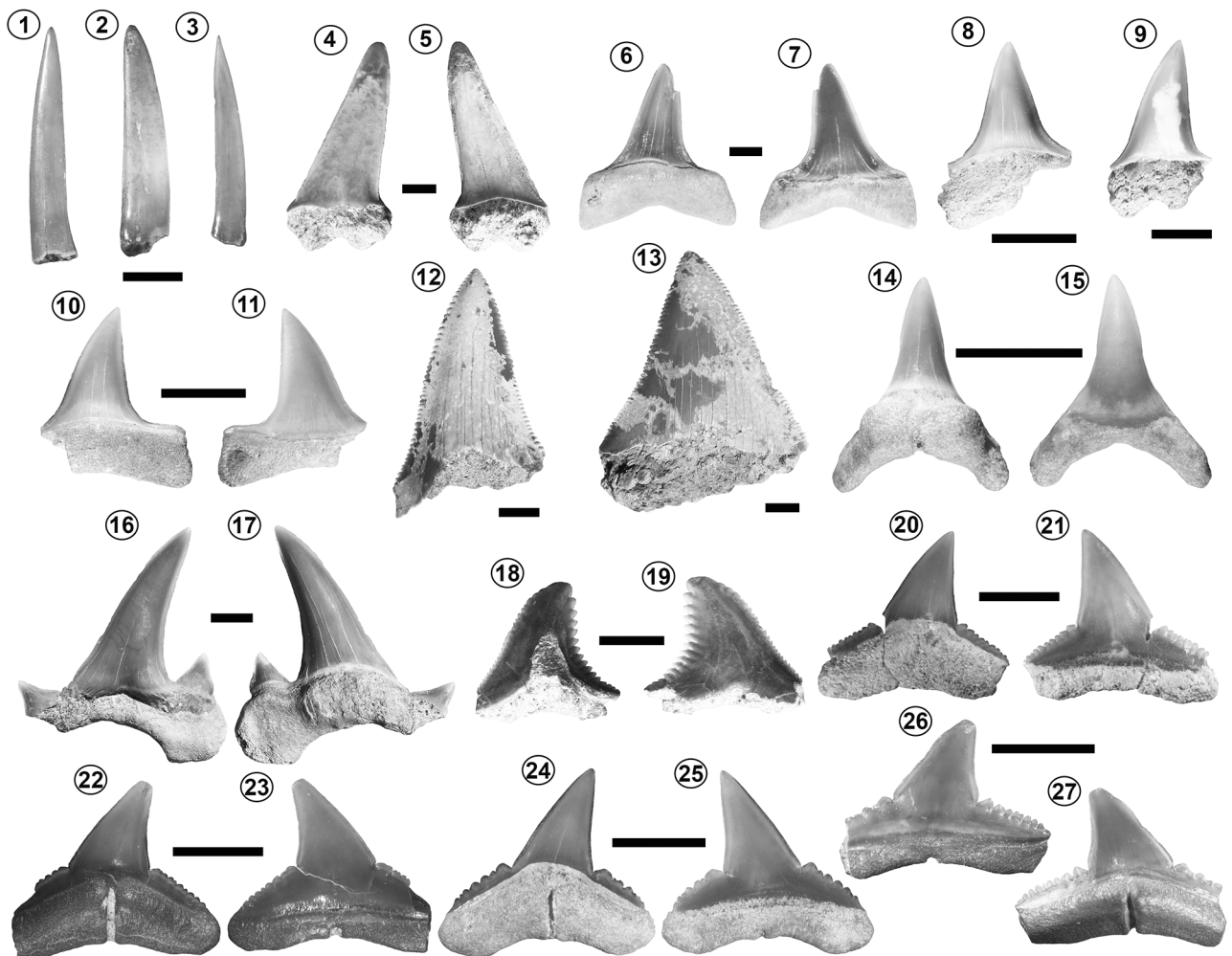


Figure 4. 1–3, *Pristiophorus* sp.; 1–3 rostral teeth (MUN-STRI-39930). 4–11, *Isurus* cf. *oxyrinchus*; 4–5, upper tooth (MUN-STRI-39932); 6–11, indet. position (6–7: MUN-STRI-39932, 8–11: MUN-STRI-39933). 12–13, *Carcharocles* sp.; 12, lower tooth (MUN-STRI-39934); 13, upper tooth (MUN-STRI-39934). 14–15, *Alopias* cf. *supercilius* lower tooth (MUN-STRI-39936). 16–17, Lamniformes gen. et sp. indet. upper tooth (MUN-STRI-39937). 18–19, *Hemipristis serra* upper tooth (MUN-STRI-39938). 20–27, *Carcharhinus gibbesii*; 20–25, upper teeth (MUN-STRI-39945); 26–27, upper tooth referred by Leriche (1938) as *Hypoprion* sp. (NMB S.a.1389). Views: labial (4, 7, 11, 15, 16, 19, 21, 23, 25, 26), lingual (5, 6, 8, 9, 10, 12, 13, 14, 17, 18, 20, 22, 24, 27), dorsal (1, 2, 3). Scale bar= 5 mm.

faces are smooth. The upper lateral tooth displays a slightly inclined triangular crown marked by smooth cutting edges. Its root is rather low with an obtuse V-shaped basal surface. Similarly, the teeth of indeterminate jaw position, of which some even preserve fragments of the eroded root, also exhibit a triangular crown with smooth cutting edges. In all seven teeth, the crown presents a flat labial face and a moderately convex lingual one.

Remarks. *Isurus oxyrinchus* ranges from the late Oligocene (middle Chattian) to the present (see Reinecke *et al.*, 2011 for an excellent summary of the fossil record of the genus). Although the specimens from the Uitpa Formation are mostly incomplete, the fact that their teeth do exhibit a close resemblance to teeth of the extant *Isurus oxyrinchus* allows us to associate them with this taxon. We adopt the taxonomic proposal suggested by Purdy *et al.* (2001) and ratified by Reinecke *et al.* (2011) by which narrow-cusped *Isurus* teeth from Miocene–Pliocene deposits referred by other authors (see Purdy *et al.*, 2001) to *Isurus desori* Agassiz, 1843, should be assigned to *Isurus oxyrinchus*. The tooth referred to *Oxyrhina* cf. *desori* by Leriche (1938, pl. 1, fig. 15) from the northeast of the Mene de Acosta locality in Venezuela (San Lorenzo Formation *sensu* Leriche, 1938) is hereby reattributed to a lower lateral-posterior tooth of *Isurus oxyrinchus*. The fossil record of *Isurus oxyrinchus* in the Americas is shown in Appendix 1.

†OTODONTIDAE Glikman, 1964

†*Carcharocles* Jordan and Hannibal, 1923

Type species. *Carcharodon megalodon* Agassiz, 1835.

†*Carcharocles* sp.

Figure 4.12–13

Referred material. Three incomplete teeth. Two upper teeth (MUN-STRI-39934; MUN-STRI-39935) and one lower tooth (MUN-STRI-39934).

Geographic and stratigraphic occurrence. See Remarks.

Description. The teeth are incomplete and only preserve the crown, which is triangular in shape and strongly serrated while presenting a pointed apex. Lateral cusplets are not preserved and the crowns of the upper teeth are broader than those of the lower ones. The crown height measures

between ~31 and 45 mm.

Remarks. In the Neogene deposits, *Carcharocles* are mainly represented by *Carcharocles chubutensis* Ameghino, 1901 and *Carcharocles megalodon* Agassiz, 1843 (e.g., Pimiento *et al.*, 2010, 2013a,b; Pimiento and Clements, 2014; Pimiento and Balk, 2015). While *Carcharocles chubutensis* ranges from the early to the middle Miocene, *Carcharocles megalodon* ranges from the middle Miocene to the late Pliocene (Pimiento and Balk, 2015). However, other authors have suggested that *C. megalodon* also occurs in the early Miocene (Burdigalian) of Europe and North America (e.g., Leriche, 1938; Purdy *et al.*, 2001; Visaggi and Godfrey, 2010; Reinecke *et al.*, 2011). The generic assignment of *C. chubutensis*, *C. megalodon* and the other species of the lineage has been debated over the years and hitherto there is no consensus among paleoichthyologists concerning the different taxonomical approaches that are still in use (e.g., Cappetta, 2012; Pimiento *et al.*, 2010, 2013b; Reinecke *et al.*, 2011; Bor *et al.*, 2012). According to Pimiento *et al.* (2013a), the teeth of sub-adult and adult specimens of *C. chubutensis* differ morphologically from those of *C. megalodon* by possessing a pair of lateral cusplets that are not separated from the main cusp. Although the teeth of *Carcharocles chubutensis* from the early Miocene exhibit/retain lateral cusplets, these were lost in the adult stage of *C. megalodon* during the late Miocene. This phenomenon is a heterochronic process by which the ontogenetic changes mimic the changes in the *Carcharocles* clade throughout geologic time (Applegate and Espinosa-Arrubarrena, 1996; Ward and Bonavia, 2001; Pimiento *et al.*, 2010, 2013a,b; Pimiento and Balk, 2015). According to Pimiento *et al.* (2013a) *Carcharocles chubutensis* can be distinguished from *C. megalodon* based on the age of the fossils, e.g., an early Miocene specimen would be *C. chubutensis* while a late Miocene specimen would be *C. megalodon*. However, *C. megalodon* is present in Burdigalian deposits (Leriche, 1938; Purdy *et al.*, 2001; Visaggi and Godfrey, 2010; Reinecke *et al.*, 2011). The specimens from the Uitpa Formation correspond to an early Miocene (Aquitania) age, which could justify an assignment to *Carcharocles chubutensis*, but their poor preservation does not allow us to identify any species-diagnostic elements. Thus, we prefer to keep those specimens in open nomenclature. The fossil record of *Carcharocles* in the Americas is shown in Appendix 1.

ALOPIIDAE Bonaparte, 1838

Alopias Rafinesque, 1810

Type species. *Alopias macrourus* Rafinesque, 1810.

Alopias cf. *superciliosus* (Lowe, 1841)

Figure 4.14–15

1958 *Alopias acutidens* Casier, p. 39, pl. 1, fig. 20.

1970 *Alopias* cf. *superciliosus* (Lowe), Antunes and Jonet, p. 150, pl. 7, 8, fig. 4.

1988 *Alopias superciliosus* (Lowe), Cigala-Fulgosi, p. 95, pl. 1, figs. 1–2.

2001 *Alopias* aff. *superciliosus* (Lowe), Aguilera and Rodrigues de Aguilera, p. 740, fig. 6.22–6.23.

Referred material. One lower anterior tooth (MUN-STRI-39936).

Geographic and stratigraphic occurrence. See Remarks.

Description. The tooth is complete and is 8 mm high and 6.5 mm wide. The crown, which exhibits smooth cutting edges, is upright, elongated and inclined lingually. The root is low and the basal surface is U-shaped. The lingual protuberance is prominent and bears a shallow nutrient groove.

Remarks. *Alopias superciliosus* ranges from the early Miocene to the present and occurs in deposits in Asia, Europe and North-South America (Antunes and Jonet, 1970; Case, 1980; Laurito, 1999; Aguilera and Rodriguez de Aguilera, 2001; Purdy *et al.*, 2001; Antunes and Balbino, 2003; Cigala-Fulgosi *et al.*, 2009; Nazarkin and Malyshkina, 2012). *Alopias superciliosus* is characterized by sexual dimorphism as the teeth of the males are considerably higher and thinner with more slanted crowns than those of the females (Gruber and Compagno, 1981). The tooth from the Uitpa Formation is similar to the lower anterior teeth of a male *A. superciliosus* illustrated by Herman *et al.* (2004). The fossil record of *Alopias superciliosus* in the Americas is shown in Appendix 1. Additionally, a tooth from the early Miocene of Barbados erroneously referred to *Alopias acutidens* by Casier (1958), is also tentatively included in the living species.

LAMNIFORMES Berg, 1937

LAMNIFORMES gen. et sp. indet.

Figure 4.16–17

Referred material. One upper tooth (MUN-STRI-39937).

Geographic and stratigraphic occurrence. See Remarks.

Description. The tooth measures 28 mm in height and 27 mm in width and, bearing a main cusp flanked by a cusplet on each side, is of typical lamniform morphology. The lateral cusplets are sharp, broad and present tiny accessory cusps. The crown is slim, biconvex and bent distally while its cutting edges are smooth and reach the base of the crown. The latter clearly overhangs the root, labially. The root is short with rounded and flattened lobes while the lingual collaret is narrow and the median bulge is prominent. There is a small lingual nutritive foramen.

Remarks. This very rare, medium sized lamniform shark is only represented by a few isolated teeth from several regions of the world. It is found in the Paratethyan deposits in Austria, Switzerland and Germany (all in private collections, pers. obs. RK) while similar finds are also known from Sardinia (Tethyan/ Mediterranean deposits) (private collection RK). Records outside Europe include Peru and the east coast of North America (Atlantic), particularly the Miocene deposits of the Calvert Cliffs in Maryland (pers. obs. RK). Its distribution was cosmopolitan and it likely inhabited cold to subtropical waters. It is only abundant in the ichthyofauna of the Miocene Calvert Formation of Maryland. This taxon might be closely related to the otodontids and most likely represents an unknown member of this group that coexisted with the other known large otodontid shark *Carcharocles*. Alternatively, this tooth belongs to a yet unnamed lamnid shark. Both a study of the relevant material in private collections and a comparison with other taxa are required before naming and properly assigning this new shark to a family. This, however, remains beyond the scope of the present work and will be presented separately in the future.

CARCHARHINIFORMES Compagno, 1973

HEMIGALEIDAE Hasse, 1879

Hemipristis Agassiz, 1835

Type species. *Hemipristis serra* Agassiz, 1835.

†*Hemipristis serra* Agassiz, 1835

Figure 4.18–19

1835 *Hemipristis serra* Agassiz, p. 237, pl. 27, figs. 18–30.

1970 *Hemipristis serra* Agassiz, Antunes and Jonet, p. 167, pl. 11, figs. 63–64, pl. 12, figs. 65–67.

2012 *Hemipristis serra* Agassiz, Cappetta, p. 296, fig. 279g–i.

Referred material. One upper, lateral tooth (MUN-STRI-39938).

Geographic and stratigraphic occurrence. See Remarks.

Description. The single specimen recovered exhibits a crown 40 mm high and 30 mm wide. The tooth is labio-lingually compressed with a triangular crown curved distally. The mesial cutting edge is strongly concave and bears fine serrations that end shortly before reaching the apex. The distal edge is concave and coarsely serrated with the serrated part also terminating before reaching the apex. Even though the lingual face of the crown is damaged and the root is mostly missing, there is evidence for the presence of a strong lingual protuberance near the crown-root margin.

Remarks. *Hemipristis serra* is one of the most common fossil elasmobranch species around the world. It is particularly abundant in Neogene tropical to subtropical neritic deposits. Most of the records of this taxon come from Miocene and Pliocene deposits (see Cappetta, 2012). This taxon has also been found in the middle-late Oligocene of Baja California, Mexico (González-Barba and Thies, 2000), and the Oligocene-early Miocene deposits in the Atlantic Coastal Plain, USA (Müller, 1999; Chandler *et al.*, 2006; Cicimurri and Knight, 2009). The fossil record of *Hemipristis serra* in the Americas is shown in Appendix 1.

CARCHARHINIDAE Jordan and Evermann, 1896

Carcharhinus Blainville, 1816

Type species. *Carcharhinus melanopterus* Quoy and Gaimard, 1824.

† *Carcharhinus gibbesii* Woodward, 1889

Figure 4.20–27

1889 *Carcharias* (*Aprionodon*) *gibbesii* Woodward, p. 437.

1938 *Hypoprion* sp. Leriche, p. 29, pl. 4, fig. 27.

1956 *Negaprion gibbesii* (Woodward), White, p. 139, figs. 77–86, pl. 2, fig. 9.

1980 *Negaprion gibbesii* (Woodward), Case, p. 88, pl. 5, figs. 9a–9b, 10a–10b.

1999 *Carcharhinus gibbesii* Woodward, Müller, p. 49.

2009 *Carcharhinus gibbesii* Woodward, Cicimurri and Knight, p. 632, fig. 5A–D.

Referred material. Seven teeth. Six upper ones and a lower one (MUN-STRI-39945; MUN-STRI-39946).

Geographic and stratigraphic occurrence. See Remarks.

Description. The teeth range between 7 and 9.5 mm in

height and between 9 and 11 mm in width. The upper teeth present low triangular crowns that are slightly inclined distally. While their mesial cutting edges are slightly convex, their distal ones are slightly concave. Both cutting edges are smooth and well differentiated from the heels by a notch. The mesial and distal heels are rather straight and strongly serrated. These serrations increase in size towards the base of the main cusp. The root is low, the lobes are slightly rounded and flattened, the lingual surface of the root is slightly inflated and the transverse medial lingual groove is narrow and reaches the base of the root forming a basal notch. The lower tooth presents a triangular crown marked by smooth cutting edges. There is no notch between the main cusp and the lateral heels, which bear completely smooth cutting edges. The root is low and its lobes rounded with a narrow medial lingual groove.

Remarks. *Carcharhinus gibbesii* is well known from the Oligocene of the Gulf and Atlantic Coastal Plains, USA (Case, 1980; Kruckow and Thies, 1990; Müller, 1999; Manning, 2006; Cicimurri and Knight, 2009), and the late Oligocene of Germany (Reinecke *et al.*, 2014). According to White (1956) and Cicimurri and Knight (2009), the upper teeth of *C. gibbesii* present a smooth cusp flanked by serrated mesial and distal heels while the lower teeth exhibit a cusp flanked by low and smooth-edged heels. The upper teeth of *C. gibbesii* are similar to those of *Carcharhinus elongatus* Leriche, 1910, but the latter species can be distinguished by possessing more weakly serrated or smoother lateral heels (*e.g.*, Génault 1993; Baut and Génault, 1999; Reinecke *et al.*, 2001, 2005; Haye *et al.*, 2008). In contrast, the upper teeth of *Carcharhinus gibbesii* from the Uitpa Formation display strongly serrated mesial and distal heels, which allows us to differentiate them from those of *C. elongatus* reported from the Oligocene of Europe (*e.g.*, Baut and Génault, 1999; Reinecke *et al.*, 2001, 2005; Haye *et al.*, 2008) and North America (Müller, 1999). Additionally, the tooth referred to *Hypoprion* sp. by Leriche (1938, pl. 4, fig. 27) from the Miocene of Trinidad belongs to an upper lateral tooth of *C. gibbesii* (Fig. 4.26–27).

Carcharhinus sp.

Figure 5.1–3

Referred material. Seven incomplete teeth (MUN-STRI-39947).

Description. The specimens are markedly damaged and the crowns heavily eroded. Due to fragmentary conditions and bad preservation in most cases, the remaining specimens are not distinguishable to the species level. However, given that the isolated main cusps (upper and lower) bear clearly serrated cutting edges, we suggest that these specimens differ from those referred to *Carcharhinus gibbesi*, also found in this assemblage.

SPHYRNIDAE Gill, 1872

Sphyrna Rafinesque, 1810

Type species. *Squalus zygaena* Linnaeus, 1758.

†*Sphyrna laevis-sima* (Cope, 1867)

Figure 5.4–5.5

1867 *Galeocерdo laevis-sima* Cope, p. 141–142, pl. 79–80.

1942 *Sphyrna laevis-sima* (Cope), Leriche, p. 84, pl. 7, figs. 23–27.

1980 *Sphyrna zygaena* (Linnaeus, 1758), Case, p. 98, pl. 8, fig. 2a–2b.

1999 *Sphyrna laevis-sima* (Cope), Müller, p. 54, pl. 8, figs. 5–8.

2011 *Sphyrna laevis-sima* (Cope), Reinecke, Louwye, Havekost, and Moths, p. 81–86, fig. 30, pl. 79, figs. 1a–7c, pl. 80, figs. 1a–5d.

Referred material. One upper lateral tooth (MUN-STRI-39948).

Geographic and stratigraphic occurrence. See Remarks.

Description. The tooth is complete and measures 8 mm high and 6.5 mm wide. The triangular crown, which is high and wide as well as distally inclined, exhibits a strongly convex lingual face and a flat labial face. Whereas the mesial edge is convex, the distal one is straight. Both cutting edges are completely smooth. The mesial cutting edge continues on the mesial heel without being interrupted by a notch. In contrast, a shallow notch separates the distal heel from the main cusp. The root is low and marked by rounded lobes and a slightly concave basal surface. The lingual protuberance is well-developed and bears a deep groove that extends to the base of the root and forms a very shallow notch.

Remarks. Some authors (e.g., Purdy *et al.*, 2001; Cicimurri and Knight, 2009) noted the close morphological similarities shared by the living *Sphyrna zygaena* Linnaeus, 1758, and the extinct *Sphyrna laevis-sima*. They described the latter from the early Miocene of Pungo River Formation, USA, and suggested that *S. laevis-sima* is a synonym of *S. zygaena* (e.g., Purdy *et al.*, 2001). Despite this, authors like Reinecke *et al.* (2011) and Bor *et al.* (2012) have pointed out significant

morphological differences between *S. zygaena* and *S. laevis-sima* and considered the latter as a valid species. Teeth of *S. laevis-sima* differ from those of *S. zygaena* in presenting a broader and more upright cusp in their upper teeth as well as a shorter and more triangular-shaped cusp in their lower anterior and anterior-lateral teeth (Reinecke *et al.*, 2011). The morphological features observed in the specimen from the Uitpa Formation are comparable to those described by Reinecke *et al.* (2011) thus allowing us to assign this tooth to *S. laevis-sima*. According to Reinecke *et al.* (2011), *S. laevis-sima* probably first appeared in the upper Oligocene of USA (see Müller, 1999; Cicimurri and Knight, 2009), has a fossil record reaching the middle Miocene and most likely gave rise to *S. zygaena* (see Reinecke *et al.*, 2011, p. 86 for more information about the fossil record of *S. laevis-sima*).

BATOMORPHII Cappetta, 1980

MYLIOBATIFORMES Compagno, 1973

MOBULIDAE Gill, 1893

Mobula Rafinesque, 1810

Type species. *Mobula auriculata* Rafinesque, 1810.

Mobula sp.

Figure 5.6–5.8

Referred material. One tooth of indeterminate position (MUN-STRI-39949).

Geographic and stratigraphic occurrence. See Remarks.

Description. The tooth, 1.4 mm long and 3 mm wide, is broader than long. The crown is higher than the root and its apical part is wider than the collar between the base of the crown and the root. The occlusal section shows a rectangular shape with a coarse ornamentation. The labial visor of the crown displays some traces of reticular ornamentation. The root is low, polyaulacorhizous and presents five irregularly spaced grooves along its width.

Remarks. *Mobula* has a fossil record ranging from the Oligocene to the present (Cicimurri and Knight, 2009; Cappetta, 2012) and its dental morphology is both variable and characterized by marked sexual dimorphism (Adnet *et al.*, 2012). Our knowledge of the dental patterns in extant and fossil Mobulidae is scarce (Adnet *et al.*, 2012; Cappetta, 2012) and therefore any specific taxonomic assignment of fossil speci-

mens becomes difficult. The teeth of the specimen from the Uitpa Formation resemble those of *Mobula tarapacana* Philippi, 1892, illustrated by Adnet *et al.* (2012). However, the scarcity of this taxon in the Uitpa assemblage and the poor preservation of the single specimen recovered preclude further taxonomic identification below the genus level. The fossil record of *Mobula* in the Americas is shown in Appendix 1.

ACTINOPTERYGII Cope, 1887

TELEOSTEI Müller, 1846

TELEOSTEI gen. et spp. indet.

Figure 5.9–5.10

Referred material. Four fragmented teeth (MUN-STRI-39952).

Description. Two distinct morphologies of teleost teeth are present in our sample. The first morphology (Fig. 5.9–5.10) is represented by three specimens in which elongated and curved teeth with an elliptical basal outline can be observed. The presumed anterior face bears a cutting edge stretching from the base towards the missing apex of the teeth. Numerous striations, extending from base to apex, are present on the lateral surfaces of the teeth. The second morphology (Fig. 5.11) is represented by one low and triangular tooth with an elliptical basal outline and continuous cutting edges along its anterior and posterior surfaces. The lateral surfaces of the tooth are not ornamented.

Remarks. The small sample size and the incomplete state of preservation of the teeth preclude a more precise identification. The two morphologies correspond to two different teleost genera of marine affinities.

Elasmobranch habitat preferences and paleobathymetric analysis

The Uitpa Formation contains chondrichthyans whose extant relatives are characterized by diverse environmental and bathymetric affinities. Most taxa recognized in the assemblage, including *Carcharhinus*, *Hemipristis*, *Sphyrna* and *Mobula*, have extant representatives that are usual inhabitants of coastal environments, but can also occur in adjacent deep waters (Fig. 6). Species such as *Carcharhinus*, *Sphyrna* and *Mobula* are pelagic and are able to move along

significant distances over oceanic basins (e.g., Compagno, 1984b; Compagno and Last, 1999; Compagno *et al.*, 2005; Voigt and Weber, 2011; Thorrold *et al.*, 2014). The only *Carcharhinus* from the Uitpa assemblage identified to the species level is *C. gibbesii*, which has been previously reported to be associated with relatively shallow and neritic

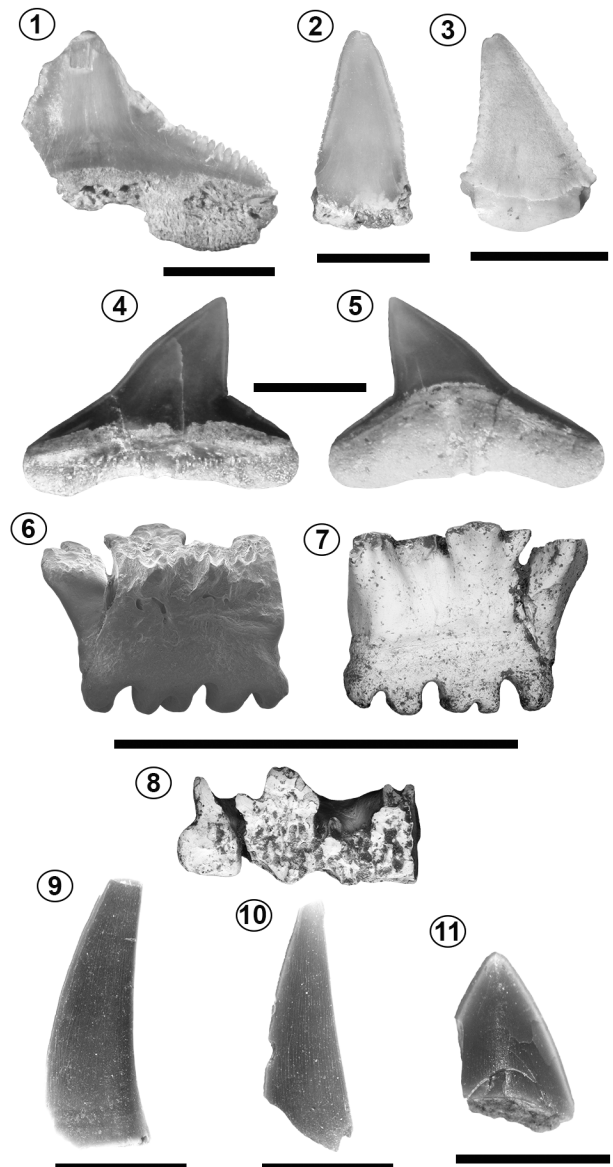


Figure 5. 1–3, *Carcharhinus* sp. (MUN-STRI-39947). 4–5, *Sphyrna laevisissima* upper tooth (MUN-STRI-39948). 6–8, *Mobula* sp. (MUN-STRI-39949). 9–10, teleost teeth of first morphology (MUN-STRI-39952). 11, teleost tooth of the second morphology (MUN-STRI-39952). Views: labial (1, 2, 3, 4, 6), lingual (5, 7), occlusal (8), indet. view (9–11). Scale bar = 5 mm.

environments (e.g., Cicimurri and Knight, 2009). As evidenced by *C. gibbesii* fossils in European deposits (Reinecke *et al.*, 2014), the species was able to move across oceanic basins. In parallel to modern hammerheads, the extinct *S. laevis* has been found in inner to outer shelf deposits (e.g., Purdy *et al.*, 2001; Cicimurri and Knight, 2009; Reinecke *et al.*, 2011). Additionally, the extinct *Carcharocles* and the carcharhiniform *Hemipristis serra* are commonly found in coastal assemblages (e.g., Pimiento *et al.*, 2010, 2013b; Cappetta, 2012) but must have also been present in open oceanic depositional environments (Carrillo-Briceño *et al.*, 2015). Their fossil record and cosmopolitan distribution (Cappetta, 2012) suggest that these large species were able to move along significant distances over oceanic basins.

Almost one third of the taxa from the Uitpa assemblage which can relate to living counterparts corresponds to benthopelagic Squalomorphii species (*Heptanchias* cf. *howellii*, *Centrophorus* sp., *Dalatias* cf. *licha* and *Pristiophorus* sp.) that prefer deep waters near the continental slope (Fig. 6). These taxa are abundant in our sample (~50%). The extant *Heptanchias perlo* Bonnatere, 1788, together with *Dalatias licha* and many species of *Centrophorus* and *Pristiophorus*, can be found in both shallow and deep-water environments but prefer depths greater than 100 m. Also, they are frequently found on the outermost margin of the continental shelves and upper slopes (Fig. 6) (Compagno, 1984a; Castro *et al.*, 1999; Hennemann, 2001; Kiraly *et al.*, 2003; Compagno *et al.*, 2005). The only *Pristiophorus* species living in the Western Central Atlantic (Bahamas) is *Pristiophorus schroederi* Springer and Bullis, 1960, which prefers continental and insular slopes at depths of between 400 and 1000 m (Kiraly *et al.*, 2003). A small component of this assemblage corresponds to *Isurus* cf. *oxyrinchus* and *Alopias* cf. *superciliosus*. Their extant representatives inhabit open waters (Fig. 6) (Compagno *et al.*, 2005).

The maximum likelihood estimates concerning the paleobathymetric analysis (Fig. 7, Appendix 2) indicate that the most probable depth for the Uitpa assemblage is the 100 to 150 m interval (probability of 0.243) followed by the 150 to 200 m interval (probability of 0.240). Depths deeper than 200 m have probabilities <0.14 while depths shallower than 100 m have probabilities <0.17 (Fig. 7, Appendix 2 and Supplementary Online Information).

DISCUSSION

Taxonomical composition

The chondrichthyan assemblage described herein consists of 13 taxa assigned to 12 genera, 11 families and six orders (Appendix 1). While all taxa are reported for the first time from Colombian deposits, the fauna constitutes one of the earliest Miocene assemblages reported from the Caribbean and Tropical America. Other Aquitanian assemblages include the Bissex Hill, Barbados (Casier, 1958, 1966). Additional early Miocene Tropical American faunas have been reported in Barbados, Brazil, Cuba, Mexico, Panama and Venezuela (e.g., Casier, 1958, 1966; Santos and Travassos, 1960; Santos and Salgado, 1971; Iturralde-Vinent *et al.*, 1996; Gonzales-Barba and Thies, 2000; Sánchez-Villagra *et al.*, 2000; Reis, 2005; Portell *et al.*, 2008; Costa *et al.*, 2009; Aguilera, 2010; Aguilera and Lundberg, 2010; Pimiento *et al.*, 2013a).

The taxa *Heptanchias* cf. *howellii*, *Carcharocles* sp., *Hemipristis serra*, *Carcharhinus gibbesii*, *Sphyrna laevis* and the specimen referred to Lamniformes gen. et sp. indet., are extinct. Most of the remaining taxa correspond to genera or species (Appendix 1) that boast living representatives with a cosmopolitan distribution that includes Tropical America (see Compagno, 1984a,b; Compagno *et al.*, 2005; Voigt and Weber, 2011). Genera such as *Heptanchias*, *Centrophorus*, *Dalatias*, *Pristiophorus*, *Isurus*, *Carcharocles*, *Hemipristis*, *Carcharhinus*, *Sphyrna* and *Mobula* have been previously recognized in the Cenozoic fossil record of the Americas (see Appendix 1). *Heptanchias howellii* and *Carcharhinus gibbesii* had been previously reported only in North America (Welton, 1974; Case, 1980; Kruckow and Thies, 1990; Müller, 1999; Manning, 2006; Cicimurri and Knight, 2009) and herein we expand their distribution to include Tropical America. Both the specimens of *Heptanchias* cf. *howellii* from the Uitpa Formation (Aquitanian) and those reported by Leriche (1938) from the Mene de Acosta in Venezuela (Menecito Member of the San Lorenzo Formation; early–middle Miocene) represent the youngest record of the taxon. The assemblage from western Venezuela described by Leriche (1938) was originally proposed as of late Oligocene age. Yet, recent studies suggest an early to middle Miocene age (Díaz de Gamero, 1985).

Specimens of *Carcharhinus gibbesii* from the Uitpa Formation and the conspecific tooth, which had erroneously

been assigned to *Hypoprion* sp. from the Miocene of Trinidad by Leriche (1938), represent the youngest fossil record for this taxon. The previous youngest record of *C. gibbesii* is from the Chattian of the Thalberg Beds in Bavaria, Germany (Reinecke *et al.*, 2014).

Paleoenvironment and paleobathymetry

Previous studies have suggested that the Uitpa Formation was deposited in an open water environment (Becker and Dusenbury, 1958; Rollins, 1965; Thomas, 1972; Hendy *et al.*, 2015). Becker and Dusenbury (1958) proposed, based on benthic foraminifera, a depositional depth of between 100 and 300 fathoms (182 m to 549 m) for the base of the unit. Based on an invertebrate fauna that prefers outer shelf to upper bathyal waters (100–250 m), a recent and more detailed report for the Uitpa Formation by Hendy *et al.* (2015) confirms the previous paleoenvironmental interpretations for the base of the Uitpa Formation. Hendy *et al.*

(2015) also note a shallowing trend towards the top of the Uitpa Formation.

Our maximum likelihood paleobathymetrical analysis indicates that the lower 10 m of the Uitpa Formation (Fig. 2) were most likely deposited in depths ranging between 100 and 200 m (Figs. 6, 7) in a middle-outer shelf environment. The Uitpa assemblage shows a predominance of benthopelagic Squalomorphii sharks (*Heptanchias* cf. *howellii*, *Centrophorus* sp., *Dalatias* cf. *licha* and *Pristiophorus* sp.). The extant species corresponding to such sharks prefer environments with deep-water near the continental slope (Fig. 6).

Oligocene/Miocene Transition in the Cocinetas Basin

The Oligocene/Miocene Transition in the Caribbean region was accompanied by a significant change in the regional biota marked by a widespread extinction of the Oligocene Tethyan reef biota and the origin of many extant

BATHYMETRIC PREFERENCES OF THE UITPA CHONDRICHTHYANS

FOSSIL TAXA	EXTANT SPECIES	n SPECIMENS	LIFESTYLE	PREFERRED HABITAT	BATHYMETRIC RANGE (m)			Inner shelf	mid-outer shelf			continental slope						
					MIN	MAX	COMMON	50m	100m	150m	200m	250m	300m	350m	400m	450m	500m	
<i>Heptranchias</i> cf. <i>howellii</i>	<i>Heptranchias perlo</i>	6	BP	MP/BP	0	1000	180-450											
<i>Centrophorus</i> sp.	<i>Centrophorus</i> spp.	5	BP	MP/BP	50	1440	180-600											
<i>Dalatias</i> cf. <i>licha</i>	<i>Dalatias licha</i>	6	BP	MP/BP	37	1800	200-1800											
<i>Pristiophorus</i> sp.	<i>Pristiophorus</i> spp.	13	BP	N/E- MP/BP	0	1000	100-300											
<i>Isurus</i> cf. <i>oxyrinchus</i>	<i>Isurus oxyrinchus</i>	7	P	N/E- MP/BP	0	500	100-150											
<i>Carcharocles</i> sp.		3	?	?	?	?	?											
<i>Alopias</i> cf. <i>superciliosus</i>	<i>Alopias superciliosus</i>	1	P	N/E- MP/BP	0	730	10-400											
Lamniformes indet.		1	?	?	?	?	?											
<i>Hemipristis serra</i>	<i>Hemipristis elongatus</i>	1	BP	N/E	0	130	inshore											
<i>Carcharhinus gibbesii</i>	<i>Carcharhinus</i> spp.	7	P-BP	N/E- MP/BP	0	1000	inshore											
<i>Carcharhinus</i> sp.	<i>Carcharhinus</i> spp.	7	P-BP	N/E- MP/BP	0	1000	inshore											
<i>Sphyrna laevis</i>	<i>Sphyrna</i> spp.	1	P-BP	N/E- MP/BP	0	1000	inshore											
<i>Mobula</i> sp.	<i>Mobula</i> spp.	1	BP	N/E	0	>1000	less than 150											

Figure 6. Lifestyle, habitat and bathymetric preferences of the Uitpa Formation chondrichthyan taxa, based on the biology of their extant relatives (references in text). The dark gray shaded area indicates the most probable depositional depth. The horizontal bars represent the water depth inhabited by each taxon with the preferred water depths indicated by thicker bars. Only taxa with recent relatives were considered for this analysis. Abbreviations are as follows: N, Neritic; E, Epipelagic; P, Pelagic; BP, Benthopelagic; MP, Mesopelagic.

lineages of reef corals that are characteristic of the western Atlantic at present (Johnson *et al.*, 2009). This major biotic rearrangement has been attributed to changes in the quality of the regional water (*e.g.*, Edinger and Risk, 1994; Johnson *et al.*, 2008, 2009). For example, the collapse of the San Luis coral-reef ecosystems in the northwestern Falcón Basin (Venezuela) is attributed to a decline in water quality resulting from increased sedimentary influx from the complex drainage system of the region during the OMT (Johnson *et al.*, 2009). In the nearby Cocinetas Basin, the Siamana-Uitpa sequence contains thick late Oligocene reef strata (Renz, 1960; Lockwood, 1965; Rollins, 1965; Thomas, 1972) overlain, in an abrupt transition, by the shales of the Uitpa Formation studied herein. Lockwood (1965) indicated that this fast transition could correspond to a strong environmental change from near-shore to offshore facies.

Reefs are relatively resilient to rises in sea level because corals are almost entirely subtidal and are able to accrete vertically. However, such resilience will deeply depend on the rate of rise (Hamylton *et al.*, 2014). A rapid sea-level increase will produce a collapse of the reef system (Blanchon *et al.*, 2009; Done, 2011; Hamylton *et al.*, 2014).

Our chondrichthyan data indicate that, while the lowermost Uitpa Formation was most likely deposited in the mid-outer shelf (100 to 200 m) (Fig. 6), the Siamana reef deposits probably accumulated close to sea level (*e.g.*, Rollins, 1965). These paleobathymetric changes suggest a rapid increase (100 to 200 m) in relative sea level at the Uitpa-Siamana contact during the early Aquitanian. Therefore, the collapse of coral reefs of the Guajira Siamana For-

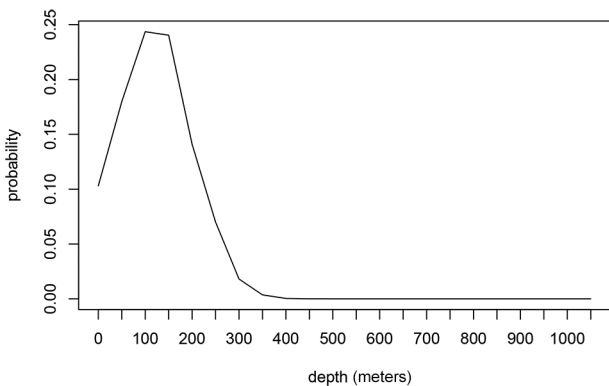


Figure 7. Maximum likelihood estimates for bathymetry of the Uitpa fossil assemblage.

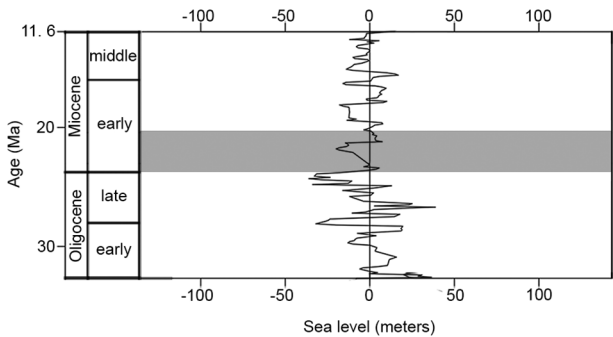


Figure 8. Cenozoic Eustatic Sea Level curve after Miller *et al.* (2005). The lower Uitpa Formation accumulated during the lower part of the early Miocene that has a ~35 m eustatic sea level rise.

mation is more likely related to a rapid increase in relative sea level than to an increase in sediment supply as proposed for the San Luis coral-reef ecosystems in the northwestern Falcón Basin (Venezuela) (Johnson *et al.*, 2009).

A rapid increase in relative sea level could be explained by an increase in eustatic sea level and/ or an increase in tectonic subsidence. The Aquitanian begins with a brisk increase in eustatic sea level (~40 m, Miller *et al.*, 2005) (Fig. 8) that would nevertheless not be enough to account for the 100–200 m rise in relative sea level at the Uitpa-Siamana transition. An increase in regional tectonic subsidence as a result of the collision of the Panama Microplate and South America during the late Oligocene/early Miocene (Weber *et al.*, 2010; Escalona and Mann, 2011; Farris *et al.*, 2011) could also be responsible for this deepening. During the Oligocene–early Miocene, tectonic subsidence increases in western Venezuela (Falcón area) thus extending the Falcón Basin to the south and E-W (Escalona and Mann, 2011). According to Rollins (1965) and Lockwood (1965), a continuous subsidence and opening of the basins may be responsible for the marine transgression and deepening of the Cocinetas Basin in the beginning of the Miocene.

CONCLUSION

We provide descriptions of 13 selachian taxa that constitute the first fossil chondrichthyan assemblage from Colombia to be studied in detail and, also, one of the earliest Neogene occurrences of elasmobranchs in Tropical America. Our paleobathymetric and paleoenvironmental analyses suggest that the lower Uitpa Formation accumulated in waters ranging between 100 and 200 m.

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APPENDIX 1. Chondrichthyan assemblage of Ujipa Formation and its fossil record in the Cenozoic of the Americas

Taxon	Tropical America and the Caribbean															NA		SSA											
	Barbados	Bonaire	Brazil	Costa Rica	Cuba	Dominican Republic	Ecuador	Haiti	Jamaica	Martinique	Panama	Peru	Puerto Rico	Trinidad	The Grenadines	Venezuela	Southern Mexico	Northern Mexico	U.S.A	Argentina	Chile	Uruguay							
<i>[†]Heptanchias cf. howellii</i>	LMI-P ●															LMI ●		EMI, LMI-P ●		MMI-● MMI-●		LO							
<i>Centrophorus sp.</i>																MMI-LMI		LMI		LMI-P		LMI							
<i>Dalatis cf. licha</i>	EMI ●															LMI		LMI-P											
<i>Pristiophorus sp.</i>																MMI-EP		LMI		MI		LO, EMI-P		EMI, LMI-P					
<i>[†]Lamniformes gen. et sp. indet.</i>																		MI				MI							
<i>Isurus cf. oxyrinchus</i>	EMI ?															MMI		LMI-P		EMI-MMI		EMI		MO-P		EMI-P		EMI-P	
<i>[†]Carcharodes sp.</i>	LMI	LMI	EMI	LMI-EP	EMI-LMI	P	LMI-EP	P	MI-P	EMI	EMI	MMI-P	LM	EMI-EP	EMI-MMI	EMI-EP	EMI	LO-P	LO-P	EMI-LMI	LMI-P	LMI							
<i>Alopias cf. superciliosus</i>	EMI		LMI-P													LMI		LMI-P		EMI-P									
<i>[†]Hemipristis serra</i>	EMI		EMI-MMI		MMI-EP		EMI-LMI		LMI-EP		MI		EMI-LMI		LMI-P		EMI, EP		MMI		EMI-P		EMI, LMI						
<i>[†]Carcharhinus gibbesii</i>																		MI						LO					
<i>Carcharhinus sp.</i>																													
<i>[†]Sphyrna laevisima</i>	EMI		EMI																				LO-MMI						
<i>Mobula sp.</i>	LMI-P			LMI			LMI			LMI			EMI			MMI-LMI			LO-LMI										

E: early, M: middle, L: late, O: Oligocene, Mi: Miocene, P: Pliocene ● indicates presence of the genus, NA: North America, SSA: Southern South America.

APPENDIX 2.**Code in R used to run the Maximum Likelihood Analysis**

```

library(truncnorm)
perlo=rtruncnorm(n=1000, a=0, b=1000, mean=315, sd=135)
centrophorus=rtruncnorm(n=1000, a=50, b=1440,
mean=(180+(600-180)/2), sd=600-(180+(600-180)/2))
dalatia=rtruncnorm(n=1000, a=37, b=1800, mean=(200+(1800-
200)/2), sd=1800-(200+(1800-200)/2))
pristiophorus=rtruncnorm(n=1000, a=0, b=1000,
mean=(100+(300-100)/2), sd=300-(100+(300-100)/2))
isurus=rtruncnorm(n=1000, a=0, b=500, mean=(100+(150-
100)/2), sd=150-(100+(150-100)/2))
alopias=rtruncnorm(n=1000, a=0, b=730, mean=(10+(400-
10)/2), sd=400-(10+(400-10)/2))
hemipristis=rtruncnorm(n=1000, a=0, b=130, mean=(5+(128-
5)/2), sd=128-(5+(128-5)/2))
carcharhinus=rtruncnorm(n=1000, a=0, b=1000, mean=(5+(200-
5)/2), sd=200-(5+(200-5)/2))
sphyma=rtruncnorm(n=1000, a=0, b=1000, mean=(5+(200-5)/2),
sd=200-(5+(200-5)/2))
mobula=rtruncnorm(n=1000, a=0, b=1000, mean=(5+(150-5)/2),
sd=150-(5+(150-5)/2))

perlo.hist=hist(perlo,breaks = seq(0, 1800, by = 50))
centrophorus.hist=hist(centrophorus,breaks = seq(0, 1800, by = 50))
dalatia.hist=hist(dalatia,breaks = seq(0, 1800, by = 50))

pristiophorus.hist=hist(pristiophorus,breaks = seq(0, 1800, by = 50))
isurus.hist=hist(isurus,breaks = seq(0, 1800, by = 50))
alopias.hist=hist(alopias,breaks = seq(0, 1800, by = 50))
hemipristis.hist=hist(hemipristis,breaks = seq(0, 1800, by = 50))
carcharhinus.hist=hist(carcharhinus,breaks = seq(0, 1800, by = 50))
sphyma.hist=hist(sphyma,breaks = seq(0, 1800, by = 50))
mobula.hist=hist(mobula,breaks = seq(0, 1800, by = 50))

bathymet=rbind(seq(0,1750,by = 50),perlo.hist$counts,centro-
phorus.hist$counts,dalatia.hist$counts,pristiophorus.hist$count,
isurus.hist$counts,alopias.hist$counts,hemipristis.hist$counts,car-
charhinus.hist$counts,sphyma.hist$counts,mobula.hist$counts)

rownames(bathymet)=c("depth", "perlo", "centrophorus", "dalatia",
"pristiophorus", "isurus", "alopias", "hemipristis", "carcharhinus", "sp-
hyma", "mobula")

write.table(bathymet, file="bathym.csv", quote=FALSE,
sep=";", row.names = TRUE, col.names=FALSE)

uitpa.ml=read.table("uitpaML",sep="\t", header=TRUE) #ML results

plot(uitpa.ml$depth,uitpa.ml$Probability, xlab="depth (m.)",
ylab="probability", type="l", lab=c(20,5,7))#figure

abline(v=100, col="red")
abline(v=150, col="red")

```