Title: Early Miocene chondrichthyans from the Culebra Formation, Panama: a window into marine vertebrate faunas before closure the Central American Seaway

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Abstract: The newly described chondrichthyan fauna of the early Miocene Culebra Formation of Panama provides insight into the marine vertebrates occupying shallow seas adjacent to the Central American Seaway, prior to the rise of the Isthmus of Panama. This study takes advantage of a time-limited and unique opportunity to recover fossil from renewed excavations of the Panama Canal. The chondrichthyan fauna of the Culebra Formation is composed of teeth and vertebral centra representing 12 taxa. The species found possessed a cosmopolitan tropical and warm-temperate distribution during the early Neogene and are similar to other assemblages of the tropical eastern Pacific and southern Caribbean. The taxa described suggest a neritic environment, and is in contrast with other interpretations that proposed bathyal water depths for the upper member of the Culebra Formation. The wide depth range of the most common species, Carcharocles chubutensis, and the habitat preference of Pristis sp., suggests varied marine environments, from deep, to shallow waters, close to emerged areas of the evolving isthmus.

Highlights:

- Chondrichthyans from the early Miocene Culebra Formation are reported for the first time.
- The 12 taxa of chondrichthyans support the interpretation of a neritic environment.
- Biogeographic relationships consistent with its position in the vicinty of the Central American Seaway.

Early Miocene chondrichthyans from the Culebra Formation, Panama: a window into marine vertebrate faunas before closure the Central American Seaway

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ABSTRACT: The newly described chondrichthyan fauna of the early Miocene Culebra Formation of Panama provides insight into the marine vertebrates occupying shallow seas adjacent to the Central American Seaway, prior to the rise of the Isthmus of Panama. This study takes advantage of a time-limited and unique opportunity to recover fossil from renewed excavations of the Panama Canal. The chondrichthyan fauna of the Culebra Formation is composed of teeth and vertebral centra representing 12 taxa. The species found possessed a

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cosmopolitan tropical and warm-temperate distribution during the early Neogene and are similar to other assemblages of the tropical eastern Pacific and southern Caribbean. The taxa described suggest a neritic environment, and is in contrast with other interpretations that proposed bathyal water depths for the upper member of the Culebra Formation. The wide depth range of the most common species, *Carcharocles chubutensis,* and the habitat preference of *Pristis* sp., suggests varied marine environments, from deep, to shallow waters, close to emerged areas of the evolving isthmus.

1. Introduction

Marine faunas of tropical America have undergone dramatic evolutionary and ecological changes through the late Cenozoic as a result of major environmental and paleogeographic changes in the region. The Panama region has been pivotal to this story, not only because it is central to tectonic changes associated with closure of the Central American Seaway, but also because it preserves a fossil record that captures key moments in the history of the regional marine biota. It has become the setting for numerous researchers studying changes in local marine ecosystems through the late Neogene (e.g., Woodring, 1966, 1974; Jackson et al., 1993). Of particular interest to these workers is the emergence of the Isthmus of Panama, culminating in the isolation of the Caribbean Sea and Pacific Ocean, and connection of North and South America. It is generally accepted that the final closure of the Central American Seaway took place about 3 million years ago (Duque-Caro, 1990; Coates et al., 1992, 2003, 2004; Coates and Obando, 1996; Bartoli et al., 2005). However, a number of recent studies suggest that the shoaling of the Isthmus began during the middle-late Eocene and likely resulted in the closure of the Central American Seaway during the middle Miocene (Farris et al., 2011; Montes et al., 2012a, 2012b).

The Culebra Formation, which crops out along the Panama Canal in central Panama, records a history of marine environments in this region through an interval of approximately 4 million years during the early Miocene (Kirby et al., 2008). Given its strategic geographic and temporal position, understanding the early Miocene marine vertebrate fauna of Panama is particularly important. The Culebra Formation offers the opportunity to survey chondrichthyans from a range of shallow marine habitats and understand the biogeographic relationships of this fauna during a time when two oceans were joined.

While previous studies have reported the invertebrate marine fauna (Woodring, 1957-1982; Johnson and Kirby, 2006) and some sirenian bones (Uhen et al., 2010) of the Culebra Formation, no chondrichthyans have yet been reported. Previous research on the chondrichthyans of Panama has been limited to the late Miocene Gatun Formation (Blake, 1862; Gillette, 1984; Kruckow and Thies, 1990; Pimiento, 2010; Pimiento et al., 2010). The renewed excavations associated with expansion of the Panama Canal provide a unique opportunity to recover fossils from the early Miocene deposits of the Culebra Formation. These excavations have both re-exposed once overgrown historic localities, as well as uncovered new sediments. This favorable circumstance is however time-limited, because the expansion of the canal is projected be finished by 2014. Consequently, it is urgent to rescue the chondrichthyans from new exposures of the Culebra Formation before excavations are completed; given that once the expansion has finished, most outcrops will be covered and no longer be available for paleontological reconnaissance or field discoveries. The purpose of this study is to describe the new chondrichthyan material that has been recovered from the Culebra Formation, exploiting this critical window into marine vertebrate faunas before the formation of the Isthmus of Panama.

1.1. Abbreviations

CTPA, Center of Tropical Archaeology and Paleobiology, Smithsonian Institution, Panama city, Panama; UF, Vertebrate Paleontology Collection of the Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA; CH, tooth crown height; CW, tooth crown width.

2. Geological, Paleontological and Paleoecological Context

The fossil shark teeth described in this paper were collected from the marine sediments of the Culebra Formation. The formation crops out most extensively along the Panama Canal, where recent excavations associated with expansion of the canal have both re-exposed previously known localities, as well as uncovered new outcrops. Excavations have left most of these localities exposed as terraced surfaces on which rapid erosion has uncovered numerous vertebrate elements. The best of these exposures crop out along the Gaillard Cut, between the Miraflores Locks and the southern limit of the Gatun Lake; these localities are referred to herein as Las Cascadas, Lirio Norte, Lirio Este, Hodges and Cartagena (Fig. 1). This formation is located in the Panama Canal Basin, which is a Cenozoic structural and depositional basin that lies along the tectonic boundary between the Chorotega and Choco blocks of the Panama microplate (Coates and Obando, 1996; Coates, 1999). The Culebra Formation is at least 250 m thick (Kirby et al., 2008) decreasing in thickness northward. It overlies the terrestrial Las Cascadas Formation and underlies the mostly-terrestrial Cucaracha Formation. Pervasive faulting along the Canal exposures mask some of the stratigraphic relationships of the Culebra Formation, in particular its basal contact, which is commonly faulted against strata of Las Cascadas Formation.   {Insert Fig. 1 near here}

The Culebra Formation consists of three members including a lower unnamed member, the Emperador Limestone, and an upper unnamed member, which combined represent a transgressive-regressive cycle. The lower member of the Culebra Formation consists mostly of carbonaceous mudstone with thin tabular interbeds of fossiliferous lithic wacke (Kirby et al., 2008). The Emperador Limestone is composed of five facies, including branching-coral boundstone, white rhodolithic limestone, another branching-coral boundstone, platy-coral

boundstone and rudstone (Johnson and Kirby, 2006). The base of the upper member is defined by alternating beds of sandstone and siltstone that conformably overlie the Emperador Limestone. The sandstone beds become thinner and finer up-section, whereas the interbedded siltstone beds become thicker. The lowermost sandstone bed contains transported corals and abundant molluscs. The siltstone beds contain abundant foraminifera, molluscs, echinoids, shark teeth and burrows.

The lignitic mudstone of the lower member contains benthic foraminifera (Blacut and Kleinpell, 1969), molluscs, trace fossils (*Thalassinoides*) and carbonized compressions of sea grass and wood (Johnson and Kirby, 2006), suggesting a marginal marine near-shore setting such as a lagoon. The Emperador Limestone represents a fringing reef paleoenvironment (Johnson and Kirby, 2006). In regards to the environment of the upper member, previous workers have suggested that its lower part accumulated in upper bathyal depths (Blacut and Kleinpell, 1969; Collins et al., 1996, Johnson and Kirby, 2006; Kirby et al., 2008). Evidence for this interpretation includes the presence of abundant globigerinid foraminifera, the thinning, fining of grain size, and decrease in carbonate content of sandstone beds, and a concomitant increase in the thickness of mudstone beds. Conversely, the abundant molluscan fauna of this succession together with ostracods (Bold, 1972) suggests an offshore paleoenvironment, no deeper than mid-outer shelf. During deposition of the middle portion of the upper member, water depth began to shallow, with sandstone beds increasing in frequency, thickening and coarsening up, and mudstone beds becoming thinner and increasing in carbonaceous plant content (Kirby et al., 2008). Benthic foraminifera (Blacut and Kleinpell, 1969) and molluscs from higher parts of the Culebra Formation, referred to as the transition zone, suggest a return to a sheltered, shallow water paleoevironment. Assemblages of molluscs from the transition zone are consistent with brackish

water conditions, including the presence of mangrove and oyster biostrome habitats. These observations led Kirby et al. (2008) to suggest the progradation of a small river-dominated delta and an overall regressive pattern through the upper Culebra Formation, in which water depth shallowed again to intertidal depths.

This unit has been shown to be early Miocene in age based on a range of biostratigraphic indicators (Woodring, 1957-1982; Blacut and Kleinpell, 1969; Bold, 1972; Johnson and Kirby, 2006; Montes et al., 2012a). Kirby et al. (2008) used strontium isotope analyses of molluscs to show that the basal Culebra Formation accumulated during a 2.5 million year interval between 23.07 -20.62 ± 0.5 Ma, while the uppermost Culebra Formation was deposited between 19.83-19.12 ± 0.4 Ma. A welded lapilli tuff near the base of the upper member of the Culebra Formation yielded a weighted average age of 19.29 ± 0.4 Ma (Montes et al., 2012a).

3. Material and methods

Forty-five isolated teeth and 10 vertebral centra were collected by Panama Canal Project and STRI field participants from five different localities from the early Miocene Culebra Formation, Panama (Fig. 1). An average of 2 people collected during 20 days (40 person days) between August 2006 and September 2011. Most of the material was obtained through surface prospecting of weathered outcrops. These specimens were supplemented by screenwashed bulk samples collected from selected tooth-bearing horizons. Bulk samples comprise approximately 100 kg of sediment from Las Cascadas and Lirio Norte localities (Fig. 1) and were processed using standard screen-washing methods. We used sets of screens of 4 wooded nesting boxes with screen openings of 6, 1.5, 1 and 0.5 mm. Screen-washed matrix was picked for chondrichthyans

using a magnifier glass for the coarser matrix, and a binocular microscope for the finer matrix. Picking yielded few specimens, with only five recognizable teeth belonging to two taxa.

The specimens studied in this report are housed at CTPA and UF, and are available in the online database [www.flmnh.ufl.edu/databases/VP/]. The material collected was measured and described. Terminology follows Cappetta (2012), Kozuch and Fitzgerald (1989), Herman et al. (1997) and Shimada (2002). Literature review of chondrichthyan temporal and spatial distribution was aided by use of the Paleobiology Database [www.paleodb.org] and the Shark Bibliography Database [shark-references.com]; all original sources of data are cited herein.

3. Systematic Paleontology

Class CHONDRICHTHYES Huxley, 1880

Subclass ELASMOBRANCHII Bonaparte, 1838

Order LAMNIFORMES Berg, 1958

Family OTODONTIDAE Glikman, 1964

Genus †*Carcharocles* Jordan and Hannibal, 1923

†*Carcharocles chubutensis* Ameghino, 1906 (Fig. 2)

Synonym: *Carcharodon subauriculatus* Agassiz, 1839:251, pl. 30a: figs. 11-13.

Referred Specimens— Twenty one isolated teeth. Upper anteriors: UF 246005 (Fig. 2A), UF 262171 (Fig. 2B), UF 262170 (Fig. 2C), UF 262165 (Fig. 2D), UF 262182 (Fig. 2E) and UF 262193 (Fig. 2F). Upper laterals: UF 238028 (Fig. 2G), UF 238030 (Fig. 2H), UF 247255 (Fig. 2I), UF 247306 (Fig. 2J), UF 262169 (Fig. 2K), UF 262177 (Fig. 2L) and UF 262183 (Fig. 2M). Lower anteriors: UF 238029 (Fig. 2N), UF 262184 (Fig. 2O), UF 262189 (Fig. 2P) and UF

262176 (Fig. 2Q). Lower laterals: UF 237900 (Fig. 2R) and UF 262168 (Fig. 2S). Indeterminate position: UF 262198 (Fig. 2T) and UF 246004 (Fig. 2U).

Specific Localities—Lirio Norte, UF locality YPA016; Lirio Este, UF locality YPA014; Cartagena, UF locality YPA031; and Las Cascadas, UF locality YPA040.

Stratigraphic and geographic range—*C. chubutensis* ranges from the early to the middle Miocene. This study represents the first report for this species in Panama. In the early Miocene it is recorded in Chile, Peru, Mexico, Brazil, Venezuela, Trinidad, Cuba, USA (North and South Carolina, New Jersey and Florida), Slovakia and India (Leriche, 1938, 1942; Mehrotra et al., 1973; Case, 1980; Applegate, 1986; Holec et al., 1995; Purdy, 1998; Sanchez-Villagra et al., 2000; Aguilera and De Aguilera, 2001; Purdy et al., 2001; Suarez et al., 2006; Costa et al., 2009; Tavora et al., 2010; Visaggi and Godfrey, 2010; Brand et al., 2011).

Remarks—*Carcharocles chubutensis* teeth from the Culebra Formation have a triangular shape, broad serrated crown, pointed apex, distinct serrated cusplets not separated from the crown by a deep notch, medium to broad neck, and thick root with dispersed foramina. They are relatively small, ranging in size from CH = 12.00 to 65.69 mm and CW = 13.8 to 37.50 mm. Most complete teeth (Figs. 2F, 2G, 2H, 2J, 2L, 2S) clearly present lateral cusplets; the rest are incomplete. UF 238029 does not preserve serrations (Fig. 2N). *C. chubutensis* dentitions present dignathic heterodonty (Purdy et al., 2001): upper teeth are broader than the lowers, anterior teeth are large and symmetrical and latero-posterior teeth are asymmetrical with slanted crowns. Antero-posteriorly through the jaw, there is a slight initial increase in size, followed by a progressive decrease that continues to the last tooth. Morphologically, *C. chubutensis* differs from *Carcharocles megalodon* by the presence of lateral cusplets not separated from the crown

on the teeth of subadults and adults; stratigraphically, *C. chubutensis* ranges from the early to the

middle Miocene, whereas *C. megalodon* from the middle Miocene to the Pleistocene (e.g.

Pimiento et al., 2010). Tooth morphology of *C. megalodon* changes with the age. During the

juvenile stage, teeth may or may not present lateral cusplets (Ward and Bonavia, 2001; Pimiento

et al., 2010). When these cusplets are present, they are eventually replaced by cusplets-lacking

teeth as the shark ages. This is a heterochronic process where the ontogenetic changes mimic the

changes in the *Carcharocles* clade through geologic time, separating species in a series of

chrono-species (Applegate and Espinosa-Arrubarrena, 1996; Ward and Bonavia, 2001). Thus, an

adult shark in the Oligocene possesses similar teeth to a young shark in the late Miocene (Ward

and Bonavia, 2001). Consequently and relevant to this study, a *C. chubutensis* from the early

Miocene exhibits/retains lateral cusplets; however, during the late Miocene, the cusplets are lost

in the adult stage of *C. megalodon*, setting apart, the two species. Accordingly, a non ontogenetic

way to separate *C. chubutensis* form *C. megalodon* is based on the age, where an early Miocene

specimen would be *C. chubutensis,* and a late Miocene specimen would be *C. megalodon.* The 1)

dignathic heterodonty, 2) presence of lateral cusplets in most complete teeth and 3) early

Miocene age, justifies the assignment of *C. chubutensis* in the Culebra Formation. Herein, even

when *Cacharocles* specimens from the early Miocene Culebra Formation are morphologically

similar to the single cusplets-retaining *Cacharocles* juvenile tooth from the late Miocene Gatun

Formation of Panama (Pimiento et al., 2010), the sum of the 3 criteria mentioned above assert

our identification. With regards to the ecology, giant-toothed sharks of the genus *Carcharocles*

were common in to warm–temperate coastal habitats (Purdy, 1996).   {Insert Fig. 2 near here}

LAMNIFORMES, incertae sedis (Figs. 3A)

Referred Specimens—One isolated vertebral centrum. UF 262197 (Figs. 3A$_1$-A$_2$).

Specific Locality—Lirio Norte, UF locality YPA016.

Stratigraphic and geographic range—This order ranges from the Cretaceous to Recent. Extant Lamniformes have circumglobal distribution in temperate and tropical seas of the Atlantic, Pacific and Indian Oceans (Compagno et al., 2005).

Remarks—UF 262197 has an oblong appearance, with a diameter larger dorso-ventrally than laterally. It is composed by two calcified cones joined by radiating calcified lamellae, laterally compressed with a concave articular face showing couplets of bands that are interpreted to represent annular growth (Cailliet et al., 1985). A sunken circular depression is distinguishable (Fig. 3A$_1$), indicating the position of the notocordal constriction (Gottfried and Fordyce, 2001). Lateral side is septated. Foramina for the neural and haemal cartilages in the dorsal and ventral faces is present, but poorly preserved (Fig. 3A$_2$). The dorso-ventral diameter is 25.83 mm of and the length is 11.90 mm. Lamniformes centra differ from Carcharhiniformes centra in having partitions all around the lateral edge (Kozuch and Fitzgerald, 1989). Sharks or the order Lamniformes occur mostly in warm waters, however, some prefer cold. They inhabit a variety of marine ecosystems, from the intertidal, to at least 1600 m depth in open ocean. None occur in freshwater (Compagno et al., 2005).   {Insert Fig. 3 near here}

Order CARCHARHINIFORMES Compagno, 1977

Family HEMIGALEIDAE Compagno, 1984

Genus Hemipristis Agassiz, 1843

†*Hemipristis serra* Agassiz, 1835 (Fig. 4A)

Referred Specimens—Nine isolated teeth. Uppers: UF 237899 (Fig. 4A$_1$), UF 238026 (Fig. 4A$_2$), UF 262185 (Fig. 4A$_3$), UF 242872 (Fig. 4A$_4$),, UF 262188 (Fig. 4A$_5$), UF 262191 (Fig. 4A$_6$) and UF 262196 (Fig. 4A$_7$). Lowers: UF 262173 (Fig. 4A$_8$) and UF 262192 (Fig. 4A$_9$).

Specific Localities— Lirio Norte, UF locality YPA016; Lirio Este, UF locality YPA014; Hodges, UF locality YPA042; and Las Cascadas, UF locality YPA040.

Stratigraphic and geographic range—Miocene to Pliocene. In the early Miocene occurs in Costa Rica, Brazil, Venezuela, Barbados, Cuba, USA (Florida, South and North Carolina, Maryland and Virginia), Hungary, Slovakia and India (Leriche, 1938; 1942; Casier, 1958; Mehrotra et al., 1973; Kruckow and Thies, 1990; Holec et al., 1995; Aguilera and De Aguilera, 2001; Purdy et al., 2001; MacPhee et al., 2003; Dos Reis, 2005; Kocsis, 2007; Visaggi and Godfrey, 2010).

Remarks—The upper teeth of *Hemipristis serra* from the Culebra Formation have crowns curved distally and with oblique coarse serrations. UF 237899 (Fig. 4A$_1$) and UF 262191 (Fig. 4A$_6$) are the most complete specimens and display serrations not continuous to the apex, a mesial cutting edge rectilinear at its base, distal cutting edge concave, and with fewer serrations. UF 237899 CH = 21.9 mm, CW = 16.5 mm (Fig. 4A$_1$). UF 262191 CH = 19.96 mm, CW = 19.13 mm (Fig. 4A$_6$). UF 238026 (Fig. 4A$_2$) and UF 262188 (Fig. 4A$_5$) have a broken tip and part of the root is missing. UF 248272 (Fig. 4A$_4$) and UF 262196 (Fig. 4A$_7$) are only represented by the apex. The lower teeth from the Culebra Formation present a long, pointed, and lingually slanted crown with no serrations in the cusp. The labial face is convex. The root is bilobated with a lingual protuberance, and with small serrations near the base. All of the teeth have broken cusplets; however, their bases are visible (Fig. 4A$_{8-9}$). UF 262173 CH = 13.15 mm, CW = 3.94

mm (Fig. $4A_8$). UF 262192 CH = 16.33 mm, CW = 10.00 mm (Fig. $4A_9$). *H. serra* is particularly abundant in neritic deposits containing warm-water faunas and scarce in deposits with cold-adapted species (Cappetta, 1987). The extant *H. elongatus* is a tropical coastal shark that inhabits in–shore and off–shore waters from up to 30 m depth (Compagno, 1984).

{Insert Fig. 4 near here}

Family CARCHARHINIDAE Jordan and Evermann, 1896

Genus *Galeocerdo* Müller and Henle, 1837

Galeocerdo cuvier Peron and Lesueur, 1822 (Fig. 4B)

Referred Specimens—Two isolated teeth. Upper: UF 247292 (Fig. $4B_1$). Lower: UF 238031 (Fig. $4B_2$).

Specific Localities—Lirio Este, UF locality YPA014 and Lirio Norte, UF locality YPA016.

Stratigraphic and geographic range—Miocene to Recent. In the early Miocene is reported in Brazil and India (Mehrotra et al., 1973; Dos Reis, 2005). Extant *G. cuvier* has a cosmopolitan distribution (Compagno, 1984).

Remarks—*Galeocerdo cuvier* teeth from the Culebra Formation are large and robust. Crowns are slightly slanted, basally and apically straight forming an obtuse angle and with serrations at the base. Mesial edges are rounded and distal edges have a pronounced notch. Serrations are coarser on the heel and base. Root shows a V shape. UF 247292 CH = 15.0 mm, CW = 21.9 mm (Fig. $4B_1$). UF 238031 CH = 7.4 mm, CW = 15.0 mm (Fig. $4B_2$). A transverse

groove is present in both teeth. *G. cuvier* is a coastal-pelagic tropical and warm-temperature

shark (Compagno, 1988), with tolerance for a wide range of marine habitats, in depths up to 140

m (Compagno, 1984).

Genus *Physogaleus* Cappetta, 1980

Physogaleus contortus Gibbes, 1849 (Fig. 4C)

Synonym: *Galeocerdo contortus* Gibbes, 1848-1849:193, pl. XXV, figs. 71-74.

Referred Specimens—One isolated tooth. Lower: UF 262186 (Fig. 4C).

Specific Localities—Las Cascadas, UF locality YPA040.

Stratigraphic and geographic range—Early to middle Miocene. In the early Miocene

this species occurs in Cuba, USA (North and South Carolina, Florida and New Jersey) and

Hungary (Leriche, 1942; Case, 1980; Iturralde-Vincent et al., 1996; Purdy, 1998; MacPhee et al.,

2003; Kocsis, 2007; Visaggi and Godfrey, 2010).

Remarks—Teeth of *Physogaleus contortus* from the Culebra Formation have crowns

finely serrated, long, thick and warped; small serrations on heel of distal side; undulating margin

and fine serrations on mesial edge. Root is V shaped, with a very large lingual protuberance on

lingual face and transverse groove (Fig. 4C). They differ from the genus *Galeocerdo* in having

very prominent and bulging root with the deep notch, and a much more erect crown in lateral

view (Leder, 2005); and from *P. aduncus* in having a narrower, more apically erect, slightly

twisted cusp, and finer distal serrations. UF 262186 CH = 12.30 mm, CW = 15.03 mm (Fig. 4C).

P. contortus typically occurs with *Galeocerdo cuvier* in Neogene localities along the east coast

of the United States (Purdy et al., 2001). The closely related species, *P. aduncus*, is the most referred species for the Oligocene Miocene sequence (Rupelian to Burdigalian). *P. contortus* presents a very cosmopolitan distribution, particularly in the middle Miocene (Cappetta, 1987; Reinecke et al., 2008).

Genus *Carcharhinus* Blainville, 1816

Carcharhinus sp. (Fig. 4D)

Referred Specimens—Two isolated teeth. Upper anterior: UF 247259 (Fig. $4D_1$). Upper lateral: UF 262194 (Fig. $4D_2$).

Specific Localities—El Lirio Este, UF locality YPA014 and Las Cascadas, UF locality YPA040.

Stratigraphic and geographic range—The range of this genus extends from the Eocene to Recent. In the early Miocene, *Carcharhinus* sp. it is recorded in Portuguese Guinea, Mexico, Myanmar, Jamaica, Indonesia and USA (Noetling, 1901; Hertlein and Jordan, 1927; Beal, 1948; Leriche, 1954; Reinhart, 1959; Antunes, 1972; Mitchell and Tedford, 1973; Domning, 1978; Kemp, 1991; Yabumoto and Uyeno, 1994; Underwood and Mitchell, 2004). Recent *Carcharhinus* species are present in all tropical and temperate seas (Compagno et al., 2005).

Remarks—*Carcharhinus* sp. teeth from the Culebra Formation are triangular in shape, with a flat labial face and a slightly convex lingual face. Cutting edges are serrated. Roots present a transverse groove (Figs. $4D_{1-2}$). *Carcharhinus* teeth differ from *Negaprion* in having serrated cutting edges; from *Sphyrna* having a thinner root and lack of an expanded lingual heel; and from *Galeocerdo* in the absence of a strongly contorted crown, lack of a large difference

between mesial and distal cutting edge thickness and lengths, coarse serration in heels, and a thinner and non-bulged root. Teeth of *Carcharhinus* sp. from the Culebra Formation are incomplete and do not preserve their tips. UF 247259 CH = 15.1 mm, CW = 13.6 mm, it lost the serration on the edges during the fossilization process (Fig. 4D$_1$). UF 262194 CH = 6.30 mm, CW = 13.11 mm (Fig. 4D$_2$). Sharks of the genus *Carcharhinus* are wide-ranging in tropical waters, with some ranging in warm temperate waters. Most are coastal and a few are oceanic in habitat preference. Some species are very common in coral reefs (Compagno, 1988).

Genus *Negaprion* Whitley, 1940

Negaprion brevirostris Poey, 1868 (Fig. 4E)

Referred Specimens—Two isolated teeth. Upper: UF 238027 (Fig. 4E$_1$). Lower: UF 262187 (Fig. 4E$_2$).

Specific Localities—Lirio Este, UF locality YPA014 and Hodges, UF locality YPA042.

Stratigraphic and geographic range—Eocene to recent. In the early Miocene occurs in Venezuela, Cuba, USA (North Carolina) and India (Iturralde-Vincent et al., 1996; Aguilera and De Aguilera, 2001; Purdy et al., 2001; MacPhee et al., 2003). Extant *N. brevirostris* is distributed in the Atlantic, including the Gulf of Mexico and the Caribbean, and Eastern Pacific (Compagno, 1984).

Remarks—Teeth of *N. brevirostris* from the Culebra Formation have a T shape, and narrow and unserrated crowns perpendicular to the root. Lingual faces are flat, whereas labial faces are slightly convex. Root lobes are elongated. UF 238027 CH = 15.1 mm, CW = 13.6 mm

(Fig. 4E$_1$). UF 262187 CH = 3.40 mm, CW = 14.96 mm (Fig. 4E$_2$). These teeth are different from lower teeth of the genus *Carcharhinus* in having unserrated cutting edges and thicker root. *N. brevirostris* inhabits inshore tropical and temperate estuarine and marine waters (Compagno, 1984; Kent, 1994).

CARCHARHINIFORMES incertae sedis (Fig. 3B)

Referred Specimens—Eight vertebral centra. UF 262167 (Figs. 3B$_{1-2}$), UF 262179 (Figs. 3B$_{3-4}$), UF 262178 (Figs. 3B$_{5-6}$), UF 262190 (Figs. 3B$_{7-8}$), UF 262166 (Figs. 3B$_{9-10}$), UF 262174 (Figs. 3B$_{11-12}$), UF 262180 (Figs. 3B$_{13-14}$) and UF 262172 (Figs. 3B$_{15-16}$).

Specific Locality—Las Cascadas, UF locality YPA040.

Stratigraphic and geographic range—Jurassic to Recent. Extant species have a broad worldwide geographic range in tropical to cold-temperate and arctic waters (Compagno, 1984).

Remarks—Carcharhiniform centra from the Culebra Formation are laterally compressed. They have a concave articular face showing concentric annuli and a distinguishable sunken circular depression (Figs. 3B$_1$, B$_3$, B$_5$, B$_7$, B$_9$, B$_{11}$, B$_{15}$). Specimens are aseptate in lateral view (Figs. 3B$_2$, B$_4$, B$_6$, B$_8$, B$_{10}$, B$_{12}$, B$_{14}$, B$_{16}$). Their dorsal and ventral foramina are either oval or circular. Scattered pores are present around the foramina in some specimens. Carcharhiniform centra differ from the order Lamniformes in having aseptated lateral walls (Kozuch and Fitzgerald, 1989). Most of the centra are complete, ranging from 41.14 mm to 19.00 mm in dorso-ventral diameter and from 15.43 to 8.55 mm in length. UF 262179 (Figs. 3B$_{3-4}$), UF 262180 (Figs. 3B$_{13-14}$) and UF 262172 (Figs. 3B$_{15-16}$), are incomplete; however, they display

asepetate wide walls, diagnostic for this order. All centra show marked incremental couplet

bands that are interpreted to represent annular growth (Cailliet et al., 1985). Sharks of the order

Carcharhiniformes inhabit a variety of habitats from cold, to tropical seas and from intertidal to

deep ocean (Compagno et al., 2005).

Subdivision BATOIDEA Compagno, 1973

Superorder BATOMORPHII Cappetta, 1980

Order PRISTIFORMES Buen, 1926

Family PRISTIDAE Bonaparte, 1838

Genus *Pristis* Linck, 1790

Pristis sp. (Fig. 5A)

Referred Specimens—One oral tooth. Lateral: UF 262199 (Figs. $5A_1$-A_3).

Specific Locality—Las Cascadas, UF locality YPA040.

Stratigraphic and geographic range—Jurassic to Recent. In the early Miocene, *Pristis*

sp. has been reported in Venezuela (Aguilera and De Aguilera, 2001). This study represents the

first report of fossil teeth of this genus in Panama.

Remarks— UF 262181 is a very small oral tooth (1.0 mm wide and 0.5 mm height),

broader than long. The crown is high, rounded and globular, with a marked and sharp transverse

crest, and well-developed central and lateral uvula. The root is labial-lingually compressed, but

developed on the lingual view, with a broad groove (Figs. $5A_1$-A_3). The morphology of the teeth,

particularly the presence of a well-developed uvula (Fig. A3) justifies the assignment of this

specimen to the genus *Pristis*, following the description of recent (Cappetta, 1987; Herman et al., 1997) and fossil (Cappetta, 1970; Sahni and Mehrotra, 1981) specimens. Extant species of the genus *Pristis* are benthic fishes with a worldwide distribution in tropical and subtropical coastal waters, including freshwater environments such as estuaries and river mouths (Compagno and Cook, 1995).   {Insert Fig. 5 near here}

Order MYLIOBATIFORMES Compagno, 1973

Family UROTRYGONIDAE McEachran et al., 1996

Genus *Urobatis* Garman, 1913

Urobatis sp. (Fig. 5B)

Referred Specimens—Four isolated male teeth. Indeterminate position: UF 262200 (Figs. 5B$_1$-B$_2$), UF 262292 – 262293, UF 262175.

Specific Locality—Las Cascadas, UF locality YPA040.

Stratigraphic and geographic range—Eocene to Recent. This study represents the first report of fossil teeth of this genus in the early Miocene. Otherwise known from the Eocene of Belgium (Hovestadt and Hovestadt-Euler, 2010).

Remarks—Species of this genus are very small (up to 2 mm wide, Cappetta, 1987) and show sexual dimorphism (e.g. Bigelow and Schroeder, 1953; Nordell, 1994; Kobelkowsky, 2010). Crowns are trapezoid and low in females and immature males teeth; and triangular and high in mature males. *Urobatis* teeth from the Culebra Formation are male specimens. They are small, with a range of 1.5 to 1.8 mm wide. The crowns are higher than broad. Labial faces are

long and triangular curving backward to the inner side of the mouth. Lingual faces are reduced in relation with the labial faces. They show a hexagonal contour at the base of the crown. Roots have two robust lobes inclined to the lingual face, with a well-developed medial groove. All the specimens from the Culebra Formation have lost their apex during fossilization (e.g. Figs. 5B_1, B_2). Rays of the family Urotrygonidae inhabit estuaries, lagoons and neritic waters (usually in less than 15 m) of tropical and warm temperate seas (Allen and Robertson, 1994; Ebert, 2003). Tooth morphology of the Culebra specimens is very similar to the extant ray *Urobatis halleri*. Fossil specimens of this species are described in Cappetta (1987). *U. halleri* is commonly found in sand rubble or rock bottoms close to reefs where it is a demersal species occurring in depths of no more than 91 m (Michael, 1993; Allen and Robertson, 1994).

Family MYLIOBATIDAE Bonaparte, 1838

Genus *†Plinthicus* Cope, 1869

†Plinthicus sp. (Figs. 5C)

Referred Specimens—One tooth. Indeterminate position: UF 262195 (Figs. 5C_1-C_2).

Specific Localities—Las Cascadas, UF locality YPA040.

Stratigraphic and geographic range—Oligocene to Miocene. In the early Miocene *Plinthicus* sp. has been reported in USA (New Jersey, North Carolina and Maryland), Venezuela and France (Cope, 1869; Leriche, 1942; Case, 1980; Cappetta, 1987; Aguilera and De Aguilera, 2001; Purdy et al., 2001). This study represents the first report of this genus in Panama.

Remarks—The specimen has a high crown with a hexagonal contour inclined ~45°. The labial face is concave (Fig. 5C$_1$) whereas the lingual face is convex (Fig. 5C$_2$). It has a well-developed enameloid laminae, vertical, parallel and regularly folded. Antero-posterior face is compressed and mesio-distally expanded. The occlusal face is hollowed in the lingual side. The root is low with well-differentiated lobes. UF 262195 is broken in two pieces; the most complete fragment is 9.69 mm high, 16.34 mm wide and 4.43 mm long (Fig. 5C). *Plinthicus* sp. from the Culebra Formation differs from *P. kruibekensis* in having lateral sides more developed and robust. Specimens from the Culebra Formation differ with the other known species of the genus mostly because of the discontinuous enameloid laminae on the inner and outer face of the crown. In general, the Culebra specimen shows more affinities with *P. stenodon*. *Plinthicus* occur in neritic sediments from the Oligocene to the Miocene (Cappetta, 1987; Bor, 1990; Gonzalez-Barba, 2008).

BATOIDEA incertae sedis (Fig. 5D)

Referred Specimens—One isolated vertebra. UF 262181 (Figs. 5D$_1$-D$_2$).

Specific Localities— Las Cascadas, UF locality YPA040.

Stratigraphic and geographic range—Batoid vertebral centra are not well known in the fossil record. In the early Miocene, isolated vertebral centra from the genus *Pristis* are recorded from western Africa (Dartevelle and Casier, 1943).

Remarks—This centrum is composed by two calcified cones with a typical batoid compression on the dorsal and ventral sides. It possesses a distinguishable sunken circular

depression and clear concentric annuli on articular face (Fig. 5D$_1$). Laminae are continuous and numerous, similar to some lamniforms. Anterior-posterior face is concave with a thick rim on side view. The centrum is aseptate in the lateral side (Fig. 5D$_2$). It has 12.50 mm of dorso-ventral diameter and 6.52 mm of length. Batoids are primarily marine, but many species can tolerate fluctuating salinities and some live only in fresh water. They are widely distributed in all oceans, occurring close inshore on reefs, off beaches, bays, lagoons, rivers and lakes. They are diverse in shallow continental waters of tropical and warm-temperate seas, but are less frequent at great depths (below 1 500 to 2 000 m), off oceanic islands, and in the open ocean (Carpenter and Niem, 1999).

4. Discussion

The Culebra Formation chondrichthyan fauna is important because it provides insight into the marine vertebrates occupying shallow seas adjacent to the Central American Seaway prior to the rise of the Isthmus of Panama. This study represents the first description of the elements of an early Miocene chondrichthyan fauna in southern Central America, taking advantage of the unique opportunity that renewed excavation of the Panama Canal is providing.

Sediments of the Culebra Formation do not have high density of fossils and they are sparsely distributed across the formation. This could be a consequence of high turbidity and reduced salinity of the environment that the Culebra Formation accumulated. However, the depauperate diversity reported here is likely a result of collection biases, and therefore must be interpreted with caution. Most notable among these biases is collecting effort, which varies substantially between easily accessible and often well-preserved assemblages of the Atlantic

coastal plain and Caribbean or northern South America, including Panama. An additional bias might be size and prize filtering (see Visaggi and Godfrey, 2010 for discussion). Small teeth are often difficult to observe without time-consuming screen-washing procedures, and are overlooked relative to large, rare or unusual teeth such as those of *Carcharocles*. In the absence of an extensive screen-washing program, which was not feasible in this study due to the overall scarcity of teeth, taxa represented by smaller elements are likely to be under-recorded. Consequently, the largest species reported (*Carcharocles chubutensis*), is also the most abundant in the Culebra Formation.

Based on the elements collected, the chondrichthyan assemblage from the Culebra Formation is represented by 12 taxa (Table 1), comprising six families: Carcharhinidae, Hemigaleidae, Lamnidae, Otodontidae, Urotrygonidae, Myliobatidae and Pristidae. The majority of the vertebral centra were identified to the order level and most of these (8 specimens) belong to Carcharhiniformes. One batoid vertebral centrum was indeterminated. Some of the teeth are incomplete and broken, with the roots and tips only partially preserved or completely missing. Based on the appearance of the majority of teeth (with the serrations still sharp), the sediments and other macrofossils, we believe that there is no evidence of post-mortem transportation and therefore, the presence of incomplete teeth may be due to factors associated with post-depositional weathering (e.g. diagenetic processes).

It is appropriate to compare the new record of biodiversity in the early Miocene Culebra Formation to that of the late Miocene Gatun Formation of Panama, which has been far more intensively explored for its chondrichthyan fauna (Blake, 1862; Gillette, 1984; Kruckow and Thies, 1990; Pimiento, 2010; Pimiento et al., 2010). Not surprisingly the Gatun Formation contains a very diverse shark and ray fauna (Gillette, 1984; Pimiento, 2010), with an estimated of

26 taxa. Both the Culebra and Gatun accumulated in neritic environments, although much of the Gatun Formation accumulated in a more open-marine setting than the Culebra Formation (Johnson and Kirby, 2006; Kirby et al., 2008). Six of the taxa found in the Culebra were also found in the Gatun Formation. Vertebral centra of Carcharhiniformes, Laminformes and Batoidea, as well as the teeth of *Pristis* sp*.,* and *Plinthicus* sp. were found only in the Culebra Formation.

All species reported from the Culebra Formation possessed a cosmopolitan tropical and warm-temperate distribution during the early Neogene. Building on earlier biogeographic assessments of the Gatun Formation (Gilette, 1984), we view that the Culebra assemblage belonged to a province that encompassed the tropical eastern Pacific, the southern Caribbean and Atlantic coastal plain in the western Atlantic. The Culebra Formation accumulated through a major transgression and regression, during which sediments accumulated in lagoonal, fringing reef, and shallow-water deltaic depositional environments (Johnson and Kirby, 2006; Kirby et al., 2008). Most of the specimens described here, were collected from alternating deltaic sandstones and mudstones in the basal portion of the upper member in the Culebra Formation (Table 1). Based on paleoecology of ostracods (Bold, 1972), and foraminifera (Blacut and Kleinpell, 1969), depositional environments of the upper member range in depth from shallow subtidal (<5 m) to perhaps as deep as the mid-outer shelf (50-100 m). Depth preferences of the chondrichthyans occurring in the upper member of the Culebra Formation (Fig. 6) are in agreement with this paleobathymetry, which is in contrast with alternative interpretations that proposed bathyal water depths (Blacut and Kleinpell, 1969; Collins et al., 1996; Johnson and Kirby, 2006; Kirby et al., 2008).

The most dominant species recorded from the Culebra Formation was *C. chubutensis* (Table 1). The wide depth range of this abundant predator (Fig. 6), suggests a varied marine environment, with a mixture of shallow and deeper waters. Finally, given the habitat preference of the batoid *Pristis* sp. (see Systematic Paleontology), its occurrence in the lower member of the formation, would suggest a nearby freshwater input. This agrees with the interpretation of a near-shore (lagoonal) environment for the lower member, and implies proximity to emerged areas of the evolving isthmus.

{Insert Table 1 and Figure 6 near here}

5. Conclusions

Chondrichthyans are reported from the early Miocene Culebra Formation of central Panama for the first time. Our field collecting efforts involved extensive surface prospecting (~40 person days) and screen-washing of bulk sediment samples, and yielded 55 specimens and 12 taxa, including both teeth and vertebral centra. The taxonomic composition described here indicates similarity, and hence biogeographic relationships, with other early Neogene assemblages of the tropical eastern Pacific and southern Caribbean, consistent with its position in the vicinity of the Central American Seaway. The paleoecology of the chondrichthyan fauna indicates that the Culebra Formation accumulated in a neritic environment. Despite its low diversity, this fauna fills an important gap in our understanding of marine vertebrate faunas during the early Miocene.

Acknowledgments

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Figure captions

Fig. 1. Geological map of the study area and location of sampling sites. (1) Las Cascadas, UF locality YPA040: 9° 4' 52.1394"N, -79° 40' 42.5994"W; (2) Lirio Norte, UF locality YPA016: 9° 3' 22,327"N, -79° 39' 35,8"W; (3) Lirio Este, UF locality YPA014: 9° 3' 4.6434"N, -79° 38' 58.1784"W; (4) Hodges, UF locality YPA042: 9° 2' 51.7014"N, -79° 39' 13.7298"W; and (5) Cartagena, UF locality YPA031: 9° 1' 14.412"N, -79° 37' 12.61"W. Map modified from Kirby et al. (2008).

Fig. 2. *Carcharocles chubutensis* teeth from the Culebra Formation. **A-F.** Upper anteriors. **G-M.** Upper laterals. **N-Q.** Lower anteriors. **R-S.** Lower laterals. **T-U.** Indeterminate position

Fig. 3. Shark vertebral centra from the Culebra Formation. **A.** Lamniform centrum; (A_1) UF 262197 anterior view; (A_2) UF 262197 dorsal view. **B.** Carcharhiniform centra; (B_1) UF 262167 anterior view; (B_2) UF 262167 ventral view; (B_3) UF 262179 indeterminate dorso-ventral face; (B_4) UF 262179 indeterminate anterior-posterior face; (B_5) UF 262178 anterior view; (B_6) UF 262178 ventral view; (B_7) UF 262190 anterior view; (B_8) UF 262190 ventral view; (B_9) UF 262166 anterior view; (B_{10}) UF 262166 dorsal view; (B_{11}) UF 262174 anterior view; (B_{12}) UF 262174 dorsal view; (B_{13}) UF 262180 indeterminate dorso-ventral face; (B_{14}) UF 262180 indeterminate anterior-posterior face; (B_{15}) UF 262172 Indeterminate dorso-ventral face, (B_{16}) UF 262172 indeterminate anterior-posterior face.

Fig. 4. Carcharhiniform teeth from the Culebra Formation. **A**. *Hemipristis serra*. **B**. *Galeocerdo cuvier*. **C**, *Physogaleus contortus*. **D**. *Carcharhinus* sp. **E**. *Negraprion brevirostris*.

Fig. 5. Batoids from the Culebra Formation. **A**. *Pristis* sp.; (A_1) oral tooth occlusal view; (A_2) oral tooth basal view; (A_3) oral tooth lingual view; **B**. *Urobatis* sp; (B_1) occlusal view; (B_2) basal

view. **C.** *Plinthicus* sp. tooth; **(C$_1$)** lingual view; **(C$_2$)** labial view. **D.** Batoid centrum; **(D$_1$)** centrum, anterior view; **(D$_2$)** centrum ventral view.

Fig. 6. Stratigraphic variations in the abundance of elements, diversity, taxonomic composition and paleobathymetry of the chondrichthyans in the Culebra Formation. Depth preferences of the chondrichthyans based on Aguilera and De Aguilera (2001), 89% frequency of depth distribution.

Figure 1
Click here to download high resolution image

9°5'0"N

N

PANAMA

CANAL

-79°40'0"W

9°2'3"N

-79°37'3"W

Costa Rica
Caribbean
Panama
Pacific
Colombia

Pedro Miguel Formation
Cucaracha Formation
Culebra Formation
Las Cascadas Formation

1 Km
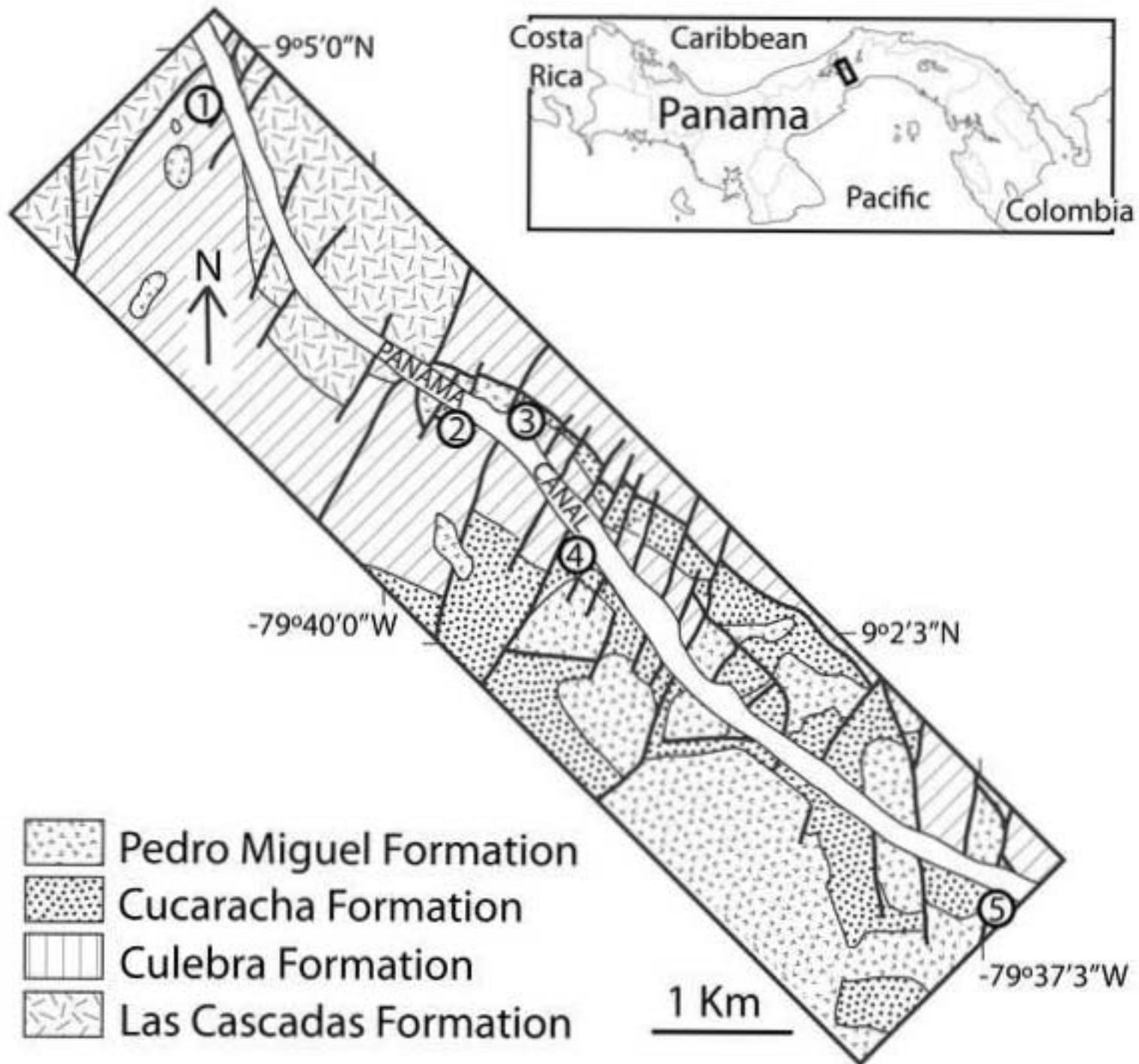
Figure 2
Click here to download high resolution image

A UF 246005
B UF 262171
C UF 262170
D UF 262165
E UF 262182
F UF 262193
G UF 238028
H UF 238030
I UF 247255
J UF 247306
K UF 262169
L UF 262177
M UF 262183
N UF 238029
O UF 262184
P UF 262189
Q UF 262176
R UF 237900
S UF 262168
T UF 262198
U UF 246004

5mm
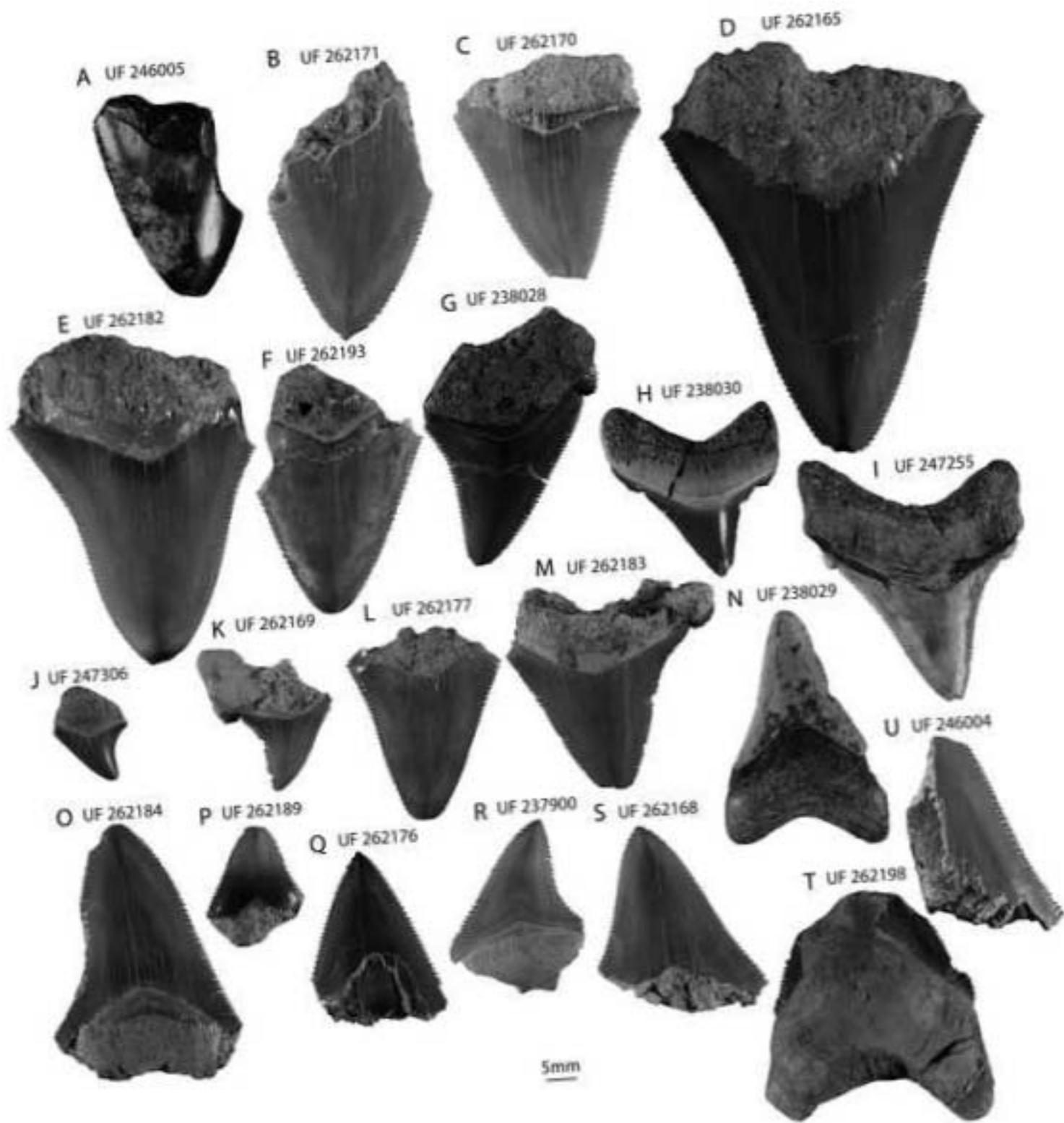
Figure 3
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UF 262197
A₁
A₂

UF 262167
B₁
B₂

UF 262179
B₃
B₄

UF 262178
B₅
B₆

UF 262190
B₇
B₈

UF 262166
B₉
B₁₀

UF 262174
B₁₁
B₁₂

UF 262180
B₁₃
B₁₄

UF 262172
B₁₅
B₁₆

5mm
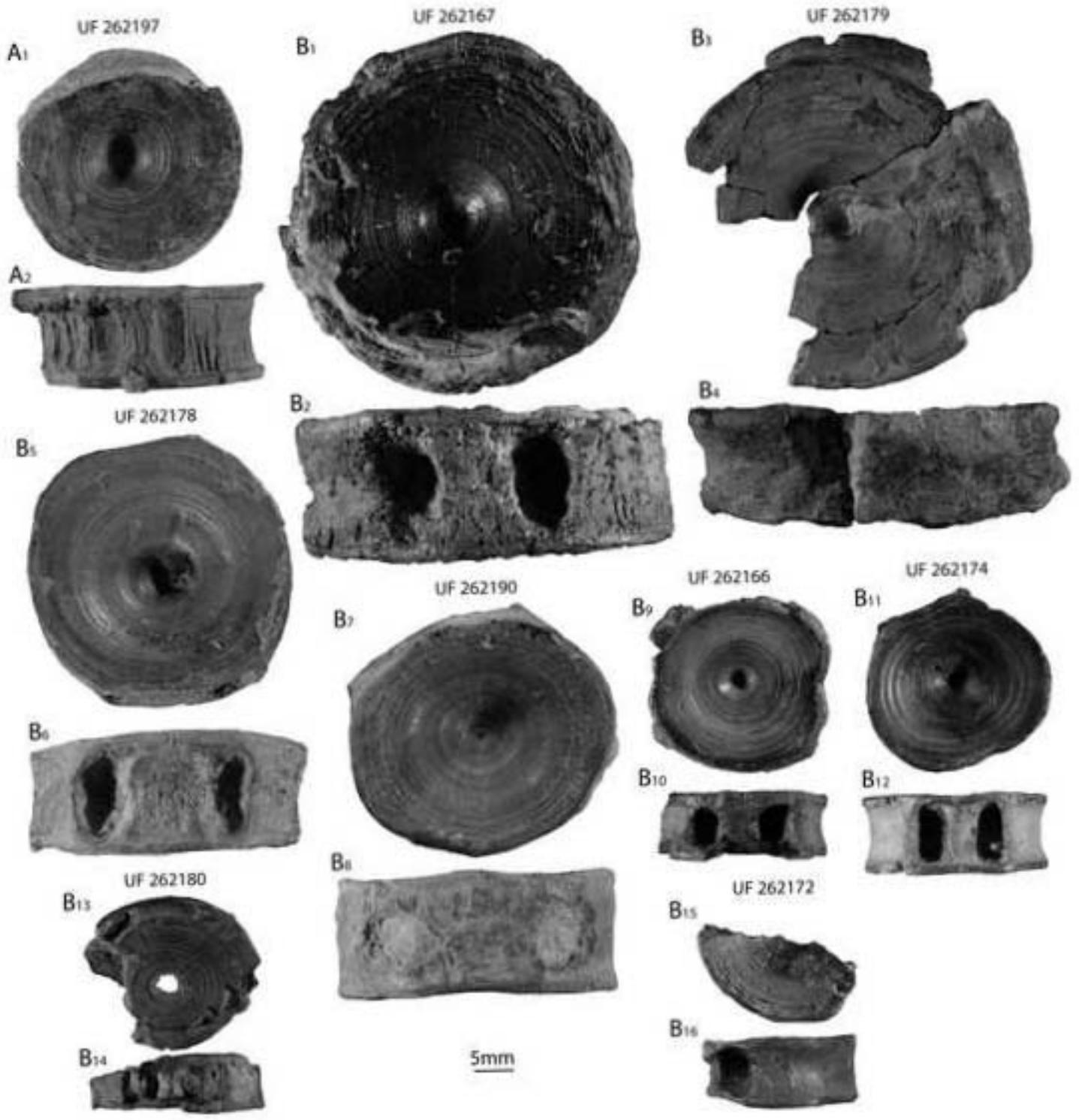
Figure 4
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A₁ UF 237899 A₂ UF 238026 A₃ UF 262185 A₄ UF 242872 A₅ UF 262188

A₇ UF 262196 A₈ UF 262173 B₁ UF 247292

A₉ UF 262192

A₆ UF 262191

B₂ UF 238031 C UF 262186 D₁ UF 247259 D₂ UF 262194

E₁ UF 238027 E₂ UF 262187

5mm
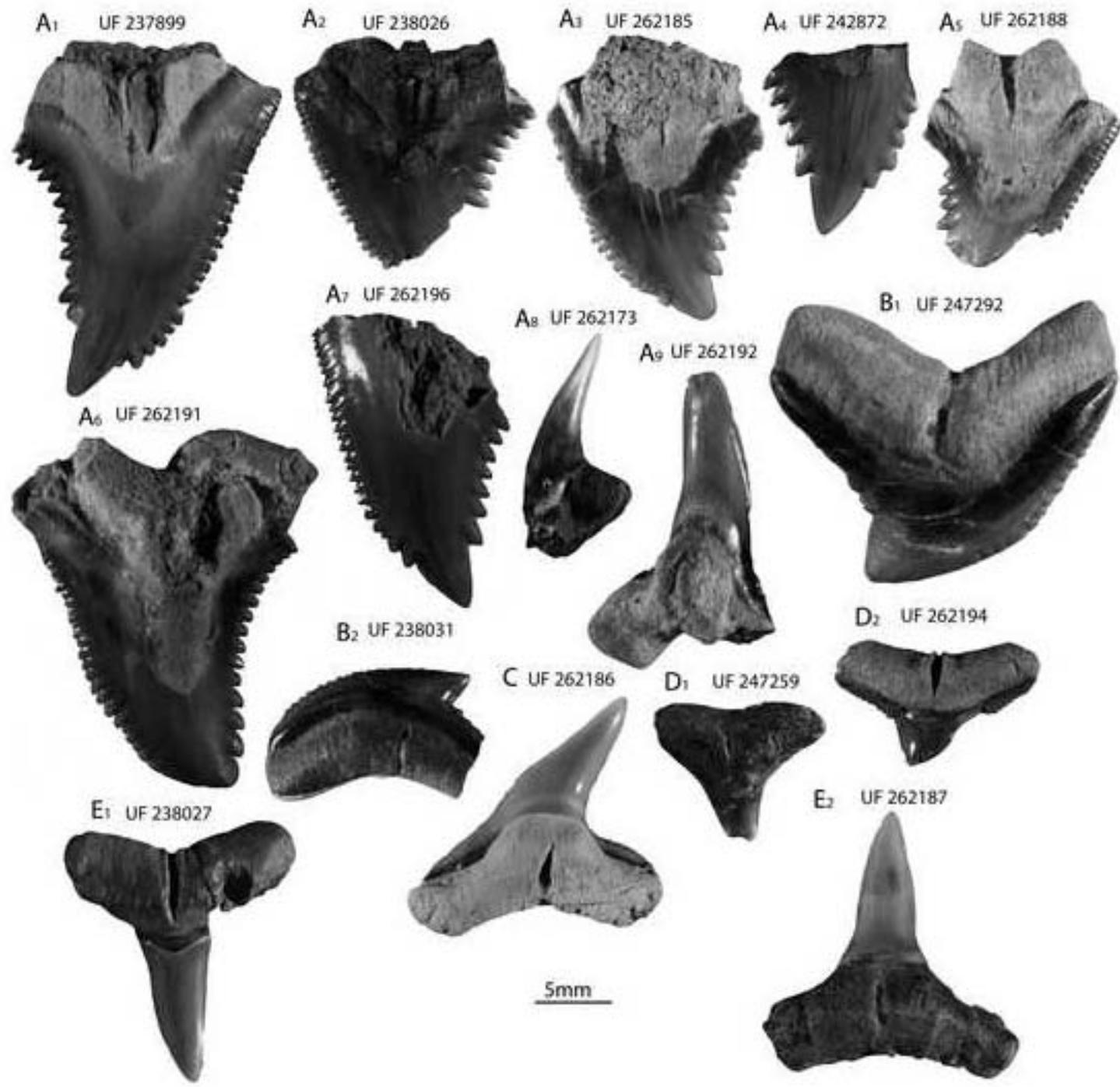
Figure 5
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UF 262199
UF 262200
A₁
B₁
A₂
A₃
B₂
100μm

UF 262182
UF 262181
C₁
D₁
C₂
D₂
5mm
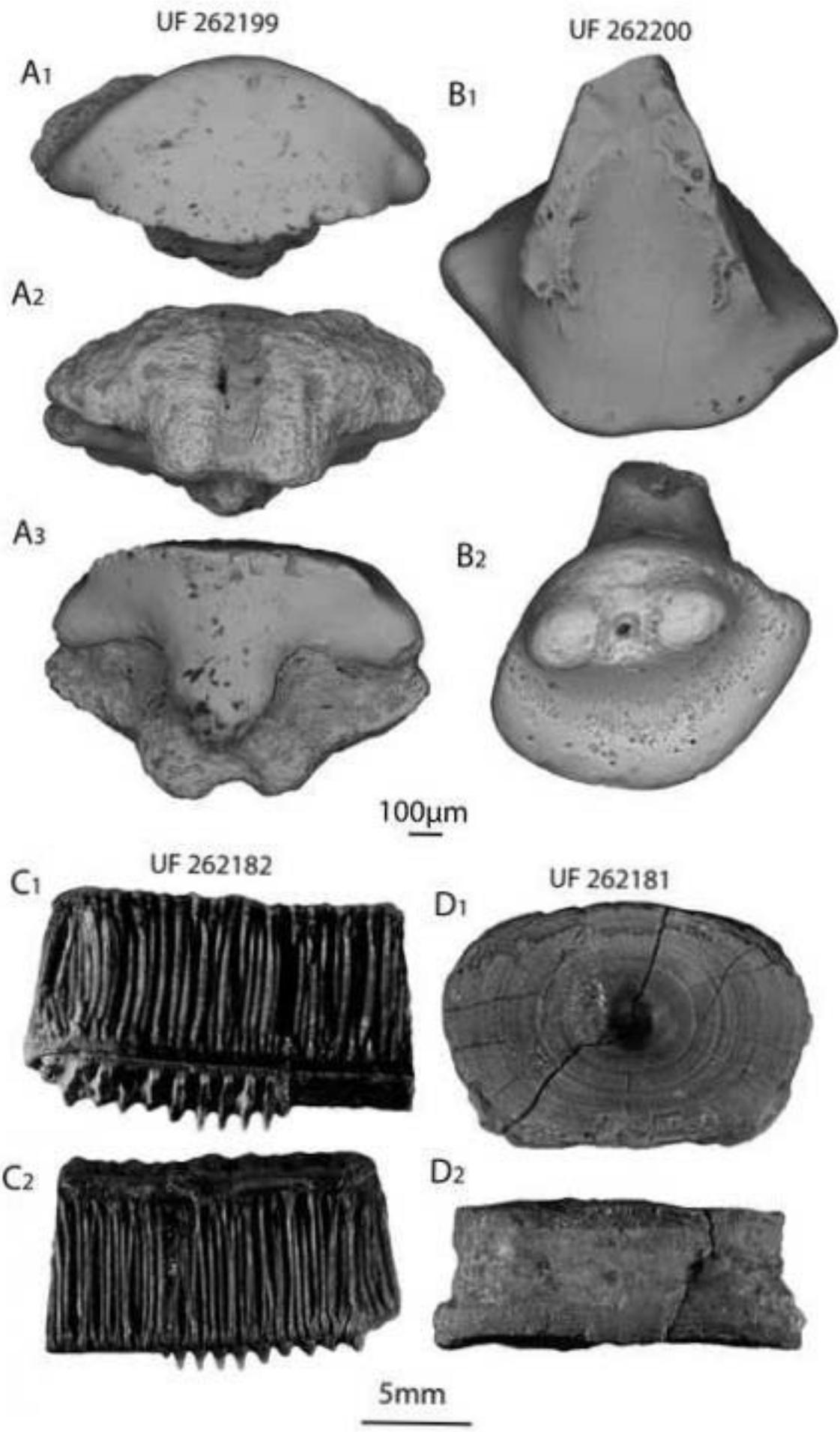
Figure 6
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Figure 6
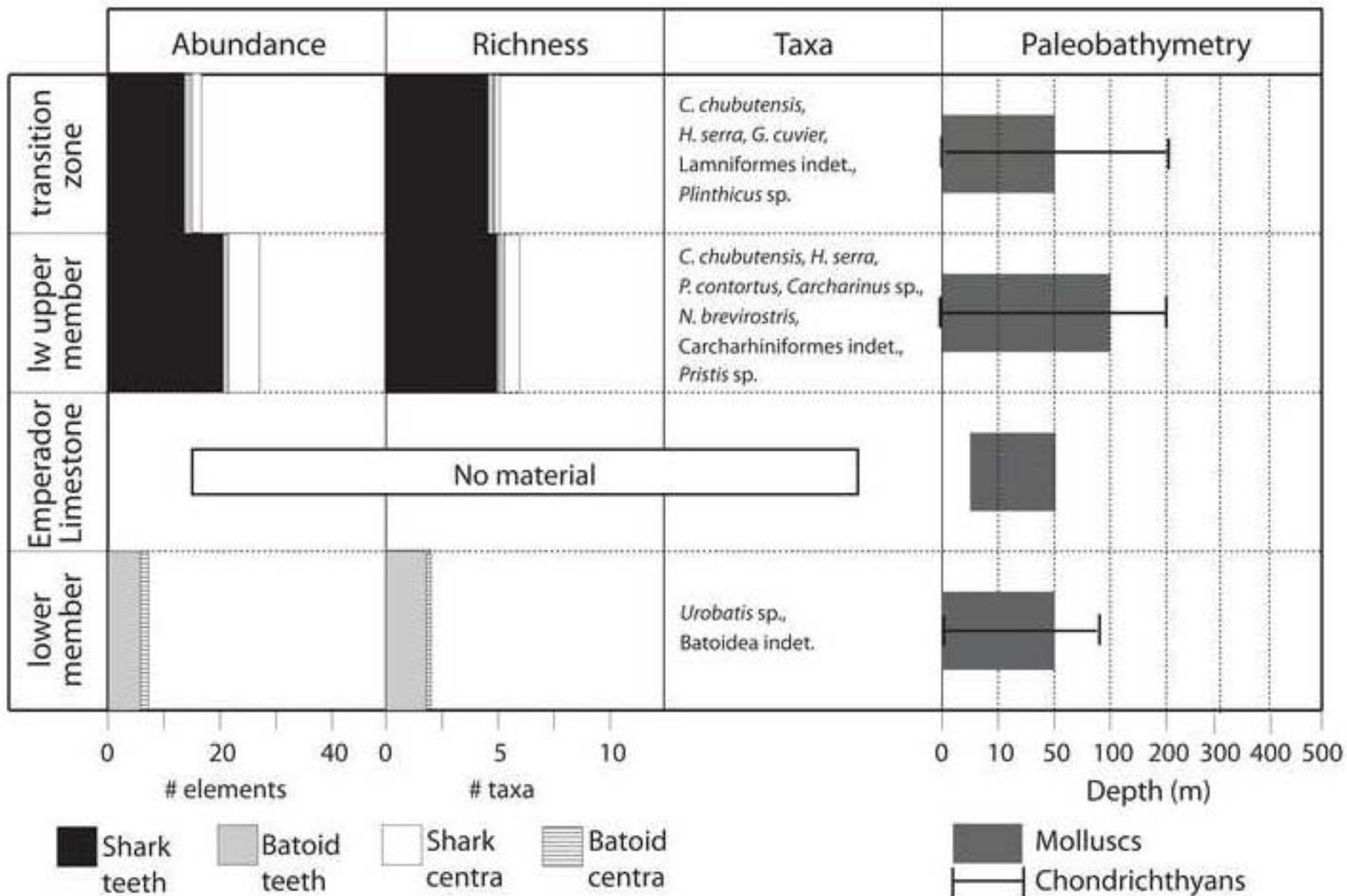
Table 1

Table 1. Stratigraphic distribution and abundance of chondrichthyan elements in the Culebra Formation. Numbers represent individual teeth; numbers in parentheses represent individual vertebra centra. Abbreviations: undiff: undifferentiated unit; basal: basal upper member; trans: transition zone in the upper member; lower: lower member.

	YPA031 (undiff)	YPA042 (basal)	YPA016 (trans)	YPA014 (undiff)	YPA040 (lower)	YPA040 (basal)	YPA040 (trans)
†*Carcharocles chubutensis*	1	-	7	1	-	9	3
Lamniformes indet.	-	-	(1)	-	-	-	-
†*Hemipristis serra*	-	2	1	2	-	4	-
Galeocerdo cuvier	-	-	1	1	-	-	-
†*Physogaleus contortus*	-	-	-	-	-	1	-
Carcharinus sp.	-	-	-	1	-	1	-
Negaprion breviostris	-	1	-	1	-	-	-
Carcharhiniformes indet.	-	-	-	-	-	(8)	-
Pristis sp.	-	-	-	-	-	1	-
Urobatis sp.	-	-	-	-	4	-	-
†*Plinthicus sp.*	-	-	-	-	-	-	1
Batoidea indet.	-	-	-	-	(1)	-	-