An Early Neogene Elasmobranch fauna from the southern Caribbean (Western Venezuela)

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Abstract: The Cantaure Formation (Burdigalian to ?early Langhian) is located in the Falcón Basin, North Western Venezuela, and includes one of the most diverse Neogene teleostean and benthonic invertebrate faunas in Tropical America. The paleoenvironmental preferences of the members of this fauna, as well as published paleogeographic reconstructions, suggest that the Cantaure Formation was deposited in a highly-productive shallow water environment, associated with coastal upwelling. We documented a paleodiversity of 39 shark and ray species, including 15 previously unreported taxa for Venezuela and six for Tropical America. We performed a bathymetric analysis of the fossil assemblage based on the distribution of closely-related extant chondrichthyan relatives of fossil taxa and discuss the ecological role and stratigraphic significance of the latter. Our results support the hypothesis that the Cantaure Formation was deposited in an insular inner-middle shelf environment. The elasmobranch fauna is characterized by a predominance of benthopelagic sharks with piscivorous feeding preferences (e.g., †Paratodus, Galeorhinus, Hemipristis, Rhizoprionodon, Carcharhinus, Isogomphodon, Negaprion, †Physogaleus and Sphyra) followed by durophagous/cancritrophic feeders (e.g., Heterodontus, Nebrius, Mustelus, Rhynchobatus, Pristis, Dasyatis, cf. Pteroplatytrygon, cf. Taeniourus, Aetobatus, Aetomylaeus and Rhinoptera). Filter (e.g., Mobula and †Plinthicus), eurytrophic/sarcophagous (e.g., †Carcharocles and Galeocerdo) and teuthitrophic (e.g., Alopias) feeder species were also found. Teeth of Carcharocles megalodon found in Burdigalian sediments of the Cantaure Formation support the presence of this species already in the early Miocene. Some taxa (Nebrius, Carcharhinus cf. C. macloti and Rhynchobatus) are absent from the extant Caribbean and Western Atlantic fauna, but were present in the region before the closure of the Central American Seaway.
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ABSTRACT

The Cantaure Formation (Burdigalian to ?early Langhian) is located in the Falcón Basin, North Western Venezuela, and includes one of the most diverse Neogene teleostean and benthonic invertebrate faunas in Tropical America. The paleoenvironmental preferences of the members of this fauna, as well as published paleogeographic reconstructions, suggest that the Cantaure Formation was deposited in a highly-productive shallow water environment, associated with coastal upwelling. We documented a paleodiversity of 39 shark and ray species, including 15 previously unreported taxa for Venezuela and six for Tropical America. We performed a bathymetric analysis of the fossil assemblage based on the distribution of closely-related extant chondrichthyan relatives of fossil taxa and discuss the ecological role and stratigraphic significance of the latter. Our results support the hypothesis that the Cantaure Formation was deposited in an insular inner-middle shelf environment. The elasmobranch fauna is characterized by a predominance of benthopelagic sharks with piscivorous feeding preferences (e.g., †Paratodus, Galeorhinus, Hemipristis, Rhizoprionodon, Carcharhinus, Isogomphodon, Negaprion, †Physogaleus and Sphyrna) followed by durophagous/cancritrophic feeders (e.g., Heterodontus, Nebrius, Mustelus, Rhynchobatus, Pristis, Dasyatis, cf. Pteroplatytrygon, cf. Taeniura, Aetobatus, Aetomylaeus and Rhinoptera). Filter (e.g., Mobula and †Plinthicus), eurytrophic/sarcophagous (e.g., †Carcharocles and Galeocerdo) and teuthitrophic (e.g., Alopia) feeder species were also found. Teeth of Carcharocles megalodon found in Burdigalian sediments of the Cantaure Formation support the presence of this species already in the early Miocene. Some taxa (Nebrius, Carcharhinus cf. C. macloti and Rhynchobatus) are absent from the extant Caribbean and Western Atlantic fauna, but were present in the region before the closure of the Central American Seaway.
INTRODUCTION

Sharks and rays are essential and diverse elements of tropical marine ecosystems (Cortés et al., 2008; Klimley, 2013), and their fossils are ubiquitous in many localities (e.g., Cappetta, 2012). In “Tropical America” – the geographic area of the Western Hemisphere located between the Tropic of Cancer and the Tropic of Capricorn, Neogene chondrichthyan assemblages are known from Barbados (Casier, 1958, 1966), Brazil (Santos and Travassos, 1960; Santos and Salgado, 1971; Reis, 2005; Costa et al., 2009), Cuba (Iturralde-Vinent et al., 1996; MacPhee et al., 2003), Southern Mexico (González-Rodríguez et al., 2013), Panama (Pimiento et al., 2013a), Peru (Alván et al., 2006), Trinidad (Leriche, 1938), The Grenadines (Portell et al., 2008) and Venezuela (Leriche, 1938; Sánchez-Villagra et al., 2000; Aguilera, 2010; Aguilera and Rodríguez de Aguilera, 2004; Aguilera and Lundberg, 2010). Despite all previous efforts, the chondrichthyan fossil record from the Caribbean is still fragmentary and poorly known, making it difficult to reconstruct paleoфаunas that could help our understanding of the major ecological and biogeographical changes that happened in the area during the Neogene. Among those changes are those associated with the uplift of the Central American land bridge (Coates and Stallard, 2013; Montes et al., 2015), which interrupted the interoceanic corridor known as the Central American Seaway (CAS), and influenced the water circulation patterns of Pacific and the Caribbean (O’Dea et al., 2007, Leigh et al., 2014). The geographic position of Venezuelan deposits renders them as relevant for investigating the effects of those major paleogeographic rearrangements.

More than 20 years of paleontological expeditions in the Paraguaná Peninsula, North Western Venezuela, produced a collection of 1836 fossil elasmobranch specimens from the Cantaure Formation. This geological unit is thought to have been deposited under fully marine conditions (Díaz de Gamero, 1974; Rey, 1996), exhibiting a well-known high diversity of invertebrates (Ingram, 1947; Jung, 1965; Gibson-Smith, 1974; Gibson-Smith and Gibson-Smith, 1974; Aguilera et al., 2010; Landau et al., in press) and teleostean fishes (Nolf and Aguilera, 1998; Aguilera, 2010; Aguilera and Lundberg, 2010). We hereby present a new taxonomic study of the elasmobranch fauna from the Cantaure Formation and a discussion of the paleoenvironmental and feeding preferences of these elasmobranchs, based on comparisons with extant species.

GEOLOGICAL AND STRATIGRAPHIC SETTING

The Cantaure Formation (Jung, 1965) has been dated as early Miocene, based on biozones of planktonic foraminifera (N7-8) and calcareous nannofossils (NN4-5) (Díaz de Gamero, 1974; Rey, 1996). According to Gradstein et al. (2012), biozones N7 and N8 correspond to the Lower to Middle Miocene transition (upper Burdigalian to lower Langhian). Griffiths et al. (2013) assigned a Burdigalian age (16.5±0.4 Ma.) to a horizon of the Cantaure Formation using Sr isotopes from corals (Figure 1.2). Landau et al. (in press) suggested that the gastropod assemblage from The Cantaure Formation is typical for early-middle Miocene deposits. The stratotype of the Cantaure Formation is located approximately 10 km west of Pueblo Nuevo on the Paraguaná Peninsula, Falcón State, Venezuela. Outcrops are found south of Casa Cantaure (Figure 1.1) and are composed of fossiliferous silty shales interbedded with thin algal limestones and shell beds (Hunter and Bartok, 1974). Jung (1965) estimated a thickness of 75 m for the composit section of the Cantaure Formation. Hunter and Bartok (1974) divided the Cantaure Formation into three sections: 1) fossiliferous basal breccia unconformably overlaying the granite basement, 2) lower section comprised mainly of
shales and some sandy horizons [including the mollusk rich horizons illustrated by Jung (1965)], and 3) upper section represented by silty shales interbedded with thin algal limestones and shell beds. However, Hunter and Bartok (1974) did not provide a stratigraphic column, while they mentioned that the landscape of the area prevents a detailed measurement of the complete section. In contrast, Rey (1996) constructed a stratigraphic column of the suggested basal and middle sections, and also assumed that the mollusks described by Jung (1965), Gibson-Smith (1974) and Gibson-Smith and Gibson-Smith (1974), were derived from the upper section.

The top of the Cantaure Formation is conformably overlain by limestone layers that have been interpreted by Jung (1965) and Hunter and Bartok (1974) as post-Cantaure and pre-Pliocene sedimentation. Rey (1996) suggested that the upper contact of the Cantaure Formation represents an unconformity with the Amuay Member (early Pliocene) of the Paraguaná Formation. Our field observations (OAA, JDCB, pers. obs.) indicate possible lateral variations in a short distance, with fossiliferous outcrops (e.g., thick layers of barnacles) that are not exposed in the previously known and described fossiliferous localities (e.g., Jung, 1965; Hunter and Bartok, 1974; Rey, 1996, among others). All the above clearly indicates that the Cantaure Formation is a more complex sequence than previously thought, in need of a new, detailed stratigraphic redescription.

**MATERIAL AND METHODS**

The fossil elasmobranch fauna described here (Table 1; Appendix 1) consists of 1836 specimens from four localities in the Cantaure Formation (Figure 1.1), which have been collected by the authors and other collaborators during several expeditions since 1992. Locality 1 (11° 56’ 20'' N, 70° 1’ 2'' W) corresponds to an artesian well ~44 m deep (Figure 1.2) and locality 2 (a’: 11° 56’ 23'' N,
70° 1' 3'' W and b': 11° 56' 2'' N, 70° 0' 55'' W) is an outcrop (overlying the section of locality 1) with a ~300 m long collecting surface (Figures 1.1-1.2). The corals used by Griffiths et al. (2013) for Sr isotope analysis were collected at locality 2 (Figure 1.1-1.2). This suggests that localities 1 and at least the lower section of locality 2 are of Burdigalian age (Figure 1.2). Localities 3 (11° 55' 59'' N, 70° 1' 1'' W) and 4 (11° 55' 48'' N, 70° 00' 40'' W) correspond to surface collecting areas along the south of Barbasco Creek, on the north escarpment of the Cerro San Carlos (Figure 1.1). Without a detailed stratigraphical knowledge of the outcrops south of Barbasco Creek, it is not possible to establish if localities 3 and 4 are different vertical strata (facies) along the Cantaure section or horizontal variations of localities 1 and 2. Field observations (OAA, JDCB and GAF pers. obs.) suggest that localities 3 and 4 are stratigraphically older than the limestones layers attributed to post-Cantaure sedimentation (Jung, 1965; Hunter and Bartok, 1974).

Large specimens were surface-collected directly from the outcrop, while microsamples were collected after screen-washing approximately 1000 and 380 kg of sediments (mesh sizes: 0.5 and 2 mm) from locality 1 and 2, respectively. Approximately 50 kg of sediment was processed from locality 3, but it did not contain otoliths or elasmobranch micro-teeth. Specimens from locality 4 were only surface collected. The Cantaure specimens (Appendix 2) are housed in the paleontological collections of the Alcaldía Bolivariana de Urumaco (AMU-CURS), Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas of the Universidad Experimental Francisco de Miranda (CIAAP, UNEFM-PF), and the Museo de Ciencias de Caracas (MCNC), all in Venezuela.
The taxonomy follows Cappetta (2012) and Compagno (2005), with the exception of the extinct genus *Carcharocles* Jordan and Hannibal, 1923, for which we follow the nomenclature of Pimiento et al. (2010). Taxonomic identification was based on an extensive literature review, and also comparative analyses between fossil and recent specimens from the following collections: Mapuka Museum of Universidad del Norte (MUN-STRI), Barranquilla, Colombia; Museu Paraense Emílio Goeldi (MPEG-V), Belem, Brazil; Natural History Museum of Basel (NMB), Switzerland; Paleontological collection of the Institut des Sciences de l’Evolution, University of Montpellier (UM), France; Palaeontological Institute and Museum at the University of Zurich (PIMUZ), Switzerland and René Kindlimann private collection, Uster, Switzerland.

We analyzed the abundance using percentages of specimens by order, families and species using the 39 securely recognized taxa that are represented by 1711 specimens (out of the 1836 collected in total) (Appendix 1). For conducting the paleoecological interpretation, we compiled information on habitat preference (benthic, benthopelagic, pelagic, neritic and bathyal) and feeding ecology (dietary composition and behavior) of extant taxa recorded in the Cantaure Formation (Appendix 3), following Compagno (1984a, 1984b); Cortés (1999); Compagno et al. (2005); Musick et al. (2004); Kiraly et al. (2003); Voigt and Weber (2011); Cortés et al. (2008); Ebert and Stehmann (2013); and the FishBase website (Froese and Pauly, 2015). The paleobathymetric analysis was performed following the methodology of Nolf and Brzobohaty (1994), adapted to fossil sharks (Carrillo-Briceño et al., 2015a, 2016). For this analysis we included only species/genera with closely related extant taxa. Extinct species and taxa with-
out clear identification to genus were removed from the analysis. A total of 34 (out of 39) taxa, for which ecological information is available, were analyzed.

Taking into consideration the limitations associated with paleoecological interpretations of fossil assemblages, we tried to approach the ecological role that members of the Cantaure elasmobranch fauna played in this ancient marine environment. We use the categorization of elasmobranch feeding preferences suggested by Cortés (1999) and Cortés et al. (2008). Living sharks and rays as a whole exhibit a wide range of diets, but each species has specific preferences. The latter are used to infer the diet of taxa we documented from the Cantaure assemblage (Appendix 3).

RESULTS

Taxonomical Composition

The taxonomical composition of the four study localities includes at least 39 species of galeomorphs and batoids (Table 1; Appendix 1, 4). Galeomorphs are represented by 26 species, 15 genera, and eight families of Heterodontiformes, Orectolobiformes, Lamniformes, and Carcharhiniformes (Table 1; Figure 2). Batoids include 13 species attributed to 10 genera and six families of Rajiformes and Myliobatiformes (Table 1; Figure 2). Pictures of the chondrichthyan teeth, vertebrae, and caudal and rostral denticles in Figures 3-12, were illustrated following the taxonomic classification shown in Table 1.

Heterodontiformes Berg, 1937. The record of this group (Heterodontidae Gray, 1851) consists of a single undetermined specimen of Heterodontus Blainville, 1816. The tooth was collected from locality 2 (Appendix 1, 4), and was previously reported by Aguilera and Lundberg (2010) and Aguilera (2010). The specimen is missing from the UNEFM collection and it is not illustrated here.

Orectolobiformes Applegate, 1972. The orectolobiform specimens are characterized by a long apron and a short main cusp flanked by more than seven pairs of lateral cusplets (Figure 3.1-3.9). This condition is diagnostic for Nebrius Rüppell, 1837, a genus recorded from North America going back to the Eocene (e.g., Kent, 1994; Müller, 1999). The specimens from the Cantaure assemblage (Figure 3.1-3.9; Appendix 1, 4) were previously assigned to Ginglymostoma del fortreti (Daimeries, 1889) (Aguilera and Rodrigues de Aguilera, 2004; Aguilera, 2010; Aguilera and Lundberg, 2010). Fossils of Nebrius in the Americas have not been thoroughly studied, and there is no clear consensus about their taxonomy at the species level or stratigraphic range (e.g., Kent, 1994; Cicimurri and Knight, 2009). Therefore we refrain from assigning species to our specimens. Cicimurri and Knight (2009) suggested that some fossil teeth of Nebrius (from North America) have been misidentified as Ginglymostoma Müller and Henle, 1837. The specimens referred to G. del fortreti from Panama (Pimiento et al., 2013b) and Ginglymostoma sp. from Brazil (Costa et al., 2009) resemble our Nebrius teeth from the Cantaure Formation.

Lamniformes Berg, 1937. These sharks are represented by one species of Alopiidae Bonaparte, 1838 and two genera and two species of †Otodontidae Glikman 1964 (Figure 2). Alopias cf. A. vulpi nus (Bonnaterre, 1788) is represented by three specimens (Figure 3.22-3.26; Appendix 1, 3) while the otodontid †Paratodus benedenii (Le Hon, 1871) is the least abundant lamniform (Figure 3.10-3.11; Appendix 1, 4). The most abundant lamniform is the otodontid †Carcharocles megalodon (Agassiz, 1843), with more than 100 specimens (Figure 3.12-3.21) from all studied localities (Appendix 1, 4). Many C. megalodon teeth are broken; however, most of them, especially large specimens, preserve the wide triangular shape (crown without lateral cusplets), a v-shaped 'neck', a fine serrations, and the large size that characterize this species (Purdy et al., 2001; Cappetta, 2012; Pimiento et al., 2010, 2013b). Small teeth having a pair of short lateral cusplets may belong to juvenile and/or subadult individuals of C. megalodon (Figure 3.12-3.16), a feature not present in adult teeth (Figure 3.17-3.21). Morphologically, the younger species Carcharocles chubutensis (Ameghino, 1901), differs from C. megalodon by the presence of lateral cusplets not separated from the crown on the teeth of juveniles, subadults and adults (Cappetta, 2012; Pimiento et al., 2013a). In more derived populations as C. megalodon, lateral cusplets disappear, except sometimes on very lateral files or in juvenile individuals (Cappetta, 2012). This absence of lateral cusplets in C. megalodon adult teeth has been interpreted as the result of heterochronic processes in the Carcharocles clade through geologic time (Pimiento et al., 2010, 2013a, 2013b; Pimiento and Balk, 2015). The absence of lateral cusplets in all well-preserved teeth interpreted as adults (including also some teeth that may belong to juvenile/subadults specimens) allows us to assign our specimens to C. megalodon. In addition, adult teeth of C. megalodon referred here, are very similar to those of the
same species, found in the late Burdigalian section (~16.2 Ma.) of the Castilletes Formation at North East Colombia (under study by JDCB).

**Carcharhiniformes Compagno, 1973.** This order is represented by four families, 10 genera and 21 species, thus being the most abundant and diverse one of the Cantaure assemblage (Figures 2, 4-8; Table 1; Appendix 1, 4). Triakidae Gray, 1851 [two genera and two species: *Galeorhinus* cf. *G. galeus* (Linnaeus, 1758) (Figure 4.1-4.2), and *Mustelus* Linck, 1790 (*Mustelus* sp.) (Figure 4.3-4.7)], Hemigaleidae Hasse, 1879 [†*Hemipristis serra* (Agassiz, 1835) (Figure 7.21-7.25), and *Sphyrna* cf. †*S. laevissimas* (Cope, 1867) (Figure 8.1-8.5)], are the less diverse families of this order in the Cantaure assemblage (Figure 2; Appendix 1, 4). Nevertheless, *Hemipristis serra* with 425 specimens (Appendix 1, 4), is the second most abundant species of the assemblage, representing 23% of the total specimens collected. The specimen referred by Aguilera and Rodrigues de Aguilera (2004) to *Paragaleus* sp. corresponds to a juvenile posterior lower tooth of *H. serra* (Figure 4.8).

**FIGURE 2.** Elasmobranch paleodiversity of the Cantaure Formation. 1. Orders and 2. Families and genera.
The Carcharhinidae Jordan and Evermann, 1896, with six genera and 16 species, is the most diverse and abundant family of the assemblage (Figure 2; Table 1; Appendix 1, 4). The genera Rhizoprionodon Whitley, 1929 [Rhizoprionodon sp. (Figure 5.1-5.5)], Isogomphodon Gill, 1862 [†Isogomphodon acuarius (Probst, 1879) (Figure 7.1-7.5)], Negaprion Whitley, 1940 [†Negaprion eurybathrodon (Blake, 1862) (Figure 7.6-7.10)], and †Physogaleus Cappetta, 1980 [†Physogaleus contortus (Gibbes, 1849) (Figure 7.11-7.15)], are represented by one species each. Galeocerdo Müller and Henle, 1837 is represented by two species †Galeocerdo aduncus Agassiz, 1843 (Figure 4.14-4.18), and †Galeocerdo mayumbensis Dartevelle and Casier, 1943 (Figure 4.19-4.23). Negaprion eurybathrodon with 586 specimens (Appendix 1, 4) is the most abundant species of the assemblage.
representing 32% of the total specimens collected. Specimens referred to *Mustelus* sp. (Triakidae) and *Rhizoprionodon* sp. (Carcharhinidae), are few and fragmentary, lacking diagnostic characters for accurate species assignment.

The genus *Carcharhinus* Blainville, 1816, with nine species, represents the most diverse genus from the Cantaure assemblage (Figures 2, 5.6-5.25, 6.1-6.24; Table 1; Appendix 1, 4). With the exception of the extinct †*Carcharhinus ackermanni* Santos and Travassos, 1960 (Figure 5.6-5.10) and †*Carcharhinus gibbesii* (Woodward, 1889) (Figure 6.1-6.4), the species *Carcharhinus brachyurus* Günther, 1870 (Figure 5.11-5.15),

Carcharhinus falciformis (Müller and Henle, 1839) (Figure 5.16-5.20), Carcharhinus cf. C. galapagensis (Snodgrass and Heller, 1905) (Figure 5.21-5.25), Carcharhinus cf. C. limbatus (Müller and Henle, 1839) (Figure 6.5-6.8) and Carcharhinus perezi (Poey, 1876) (Figure 6.13-6.17), have living counterparts and most of them inhabit the Atlantic and Pacific coast of America (Compagno et al., 2005). Carcharhinus macloti (Müller and Henle, 1839) (Figure 6.9-6.12) is today an exclusive inhabitant of the Indo-west Pacific Ocean (Compagno et al., 2005). The specimens referred to Carcharhinus sp.1 (Figure 6.18-6.22), have a dental morphology different, especially in the form of the crown, which differentiate these teeth from the rest of the Carcharhinus species found in the Cantaure assemblage. Due to the scarcity of specimens (Appendix 1) and the lack of preserved diagnostic characters in Carcharhinus teeth we have used for comparison (fossil and recent speci-
(12) specimens), we prefer to keep these specimens to a
generic level. We have referred all specimens that
are broken and eroded, without any diagnostic fea-
tures for specific identification (Figure 6.23-6.24),
to Carcharhinus spp. Some of the specimens clas-
sified as Carcharhinidae indet. (Figure 7.16-7.20;
Table 1; Appendix 1, 4), exhibit a very prominent
lingual protuberance with a sigmoid cusp, which
could be the basis of a more detailed taxonomical
identification in future studies.

FIGURE 7. Carcharhiniformes of the Cantaure Formation. 1-5. †Isogomphodon acuarius (1-2: AMU-CURS-950 and 3-
and lingual (1, 3-5, 7-8, 10, 12, 14-16, 19-21, 23).
Rajiformes Berg, 1937. This group of batoids is represented by two families, two genera and two species (Figure 2). Concerning Rhynchobatidae Garman, 1913, we report indeterminate teeth of *Rhynchobatus* Müller and Henle 1837 (Figure 8.6-8.11; Appendix 1, 4), resembling previously figured isolated teeth of *Rhynchobatus* from the late Miocene of Costa Rica, Panama and Venezuela (Laurito, 1999; Pimiento et al., 2013b; Carrillo-Briceño et al., 2015b). We refrain from taxonomic identification at the species level of the Cantaure *Rhynchobatus*, because the range of dental variation in extant species is unknown, and little is known about fossil species from the Americas. The Pristidae Bonaparte, 1838 is represented by a few specimens of oral teeth and rostral denticles of *Pristis* Linck, 1790 (Figure 8.12-8.20, Appendix 1, 4). As noted by Carrillo-Briceño et al. (2015b), *Pristis* rostral denticles are not diagnostic at species level, while isolated oral teeth are somewhat difficult to identify, because those of extant species are poorly known and are morphologically diverse.

Myliobatiformes Compagno, 1973. This group is represented by four families, eight genera and 11 species, being thus the second most abundant and diverse order from the Cantaure assemblage (Figure 2; Table 1; Appendix 1, 4). The Dasyatidae Jordan, 1888, is represented by three genera and four
species, and the Myliobatidae Bonaparte, 1838 and Rhinopteridae Jordan and Evermann, 1896 by one genus and one species each (Figure 2; Table 1). Due to the small number of specimens and the lack of diagnostic characters, teeth referred to *Dasyatis* Rafinesque, 1810 (Figure 9.1-9.10), *cf. Pteroplatytrygon* Fowler, 1910 (Figure 9.11-9.17), *cf. Taeniurops* Garman, 1913 (Figure 9.18-9.21), and *Dasyatidae indet.* (Figure 9.22-9.27), cannot be assigned to species. As noted by Carrillo-Briceño et al. (2015b), there is very little known available about the morphological diversity of dental patterns in extant and fossil *Dasyatidae* from the Americas.

Teeth referred to *Aetobatus* Blainville, 1816 (Figure 10.1-10.3), and *Aetomylaeus* Garman, 1913 (Figure 10.4-10.14), are fragmented and incomplete; but preserve diagnostic characters that made their generic identification possible. Teeth of *Rhinoptera* Cuvier, 1829 (Figure 10.15-10.29) are common in all localities (especially at locality 2), being the third most abundant species of the assemblage (Appendix 1, 4). Previous work on the Cantaure Formation has reported the presence of *Myliobatis* Cuvier, 1816 teeth (Aguilera and Rodrigues de Aguilera, 2004; Aguilera and Lundberg, 2010; Aguilera, 2010). However, our revision of fossils led to the identification of isolated medial and lateral teeth, which exhibit the typical imbrication pattern and morphology of *Rhinoptera*. *Mobulidae* Gill, 1893 is represented by two genera and four species (Figure 2; Table 1; Appendix 1, 4). The mobulids †*Mobula fragilis* Cappetta, 1970 (Figure 11.1-11.11), *Mobula cf. †M. loupianensis* Cappetta, 1970 (Figure 11.12-11.18) and *Mobula sp.* (Figure 11.19-11.23) are scarce (Appendix 1, 4), and their teeth have been recovered from localities 1 and 2 only. One tooth of †*Plinthicus stenodon* Cope, 1869 was found at locality 3.

All eroded, broken and non-diagnostic caudal spines (Figure 12.1-12.6) are referred to *Myliobatiformes indet.* In addition, specimens referred to *Chondrichthyes indet.* correspond to fragmented and non-diagnostic vertebrae (Figure 12.7-12.8).

**Elasmobranch Paleobathymetric Analysis**

The Cantaure elasmobranch fauna is characterized by a predominance of benthopelagic sharks and rays, the extant relatives of which inhabit diverse environments and have diverse bathymetric preferences, especially in neritic/epipelagic environments (Appendix 3). Our paleobathymetric analysis indicates that the most probable deposition depth for the Cantaure assemblage is the 0 to 50 m interval, followed by the 50 to 100 m interval as the second most probable (Figure 13). This sug-
suggests that the Cantaure Formation was deposited in an inner-middle shelf environment. The presence of *Nebrius* sp., *Carcharhinus* cf. *C. limbatus*, *C. perezi*, *Isogomphodon acuarius*, *Negaprion eurybathrodon*, *Rhynchobatus* sp. and *Rhinoptera* sp. support this hypothesis, due to the fact that their extant representatives inhabit waters shallower than those of middle shelf environments (Appendix 3). Other taxa recognized in the first and second most probable depth intervals (Figure 13) include *Alopiidae*, *Carcharhinidae*, *Sphyrnidae*, *Rinchobatidae*, *Pristidae*, *Dasyatidae*, *Myliobatidae* and *Mobulidae*, whose extant representatives are associated with coastal environments. However, it is important to keep in mind that some of those species also have a wide vertical distributional range (Appendix 3), or are even able to move along significant distances over oceanic basins (Compagno, 1984b; Compagno et al., 2005; Voigt and Weber, 2011; Froese and Pauly, 2015).

**Dietary Preferences of the Cantaure Elasmobranchs**

The dietary composition of the elasmobranch assemblage from the Cantaure Formation can be represented by five food categories, from filter feeders to benthic-pelagic predators (Figure 14; Appendix 3). In this assemblage the most abundant feeder group is that of the piscivorous, representing 49% of the total species count (Figure 14; Appendix 3). We have included in this group the pelagic lamnid *Paratodus benedenii* (Cappetta, 1987, Kent and Powell, 1999) and the carcharhinid *Physogaleus confortus*, extinct species with a cut-
ting-clutching dental type that could suggest a fish-based diet. The durophagous/cancritrophic (mollusk, crustacean, coral feeders) group is the second most abundant, corresponding to 30% of the species in the Cantaure assemblage, with a predominance of Myliobatiformes and Rajiformes (Figure 14; Appendix 3). In this group the most abundant taxon is *Rhinoptera* sp., living species of which are opportunistic/generalists consuming mainly mollusks. The filter feeder group (Figure 14) is represented in the Cantaure assemblage only by mobulids (Table 1; Appendix 1, 4), whose living counterparts are characterized by a diet based mainly on planktonic microorganisms (Klimley, 2013). One of its representatives is the extinct mobulid *Plinthicus stenodon*, whose fragile teeth also suggest a possible filter diet of soft prey (Cappetta, 2012). In the eurytrophic/sarcophagous group (diverse food source: fishes, reptiles, birds, mammals, etc.) (Figure 14), we have included large sharks with a broad habitat preference. Those species include *Carcharocles megalodon*, *Galeocerdo aduncus* and *G. mayumbensis*, which could have had the role of apex predators. In reference to the teuthitrophic group, it is represented only by *Alopias* cf. *A. vulpinus*, whose living counterpart has a higher preference for cephalopods (Cortés, 1999; Appendix 3).

FIGURE 13. Bathymetric ranges estimated for Cantaure Formation taxa and their relative abundance. Arrows indicate that the bathymetric range is greater; question mark symbol indicates uncertainty about the extent of the range. A dashed red line indicates that there is no information for the taxa. The gray shadow indicates the more probably depth range for this assemblage. In the relative abundance graphic the y-axis is shortened between 2 and 3 to improve the values visualization; note the greater abundance of shallow water taxa. The extinct species including *P. benedenii*, *C. megalodon*, *P. contortus*, and *P. stenodon*, and taxa without clear identification, including *Carcharhinus* spp., *Carcharhinidae* indet., *Myliobatis* indet. and *Chondrichthyes* indet., were removed from the analysis.
DISCUSSION

Paleodiversity Significance

Forty-four percent of the Cantaure elasmobranch assemblage consists of genera or species with living representatives in Tropical America (Compagno, 1984a, 1984b; Compagno et al., 2005; Voigt and Weber, 2011). Five genera and 15 species present are extinct (Table 1). Nebrius sp., Carcharhinus cf. C. macloti, and Rhynchohatus sp., are present in our fossil sample and are currently extinct in the Caribbean, but have living counterparts in the eastern Atlantic and Indo-West Pacific (Compagno et al., 2005; Froese and Pauly, 2015). Their fossil record confirms that these taxa became extinct in the Caribbean, Western Atlantic and Eastern Pacific (Compagno et al., 2005; Froese and Pauly, 2015). Their fossil record confirms that these taxa became extinct in the Caribbean, Western Atlantic and Eastern Pacific, possibly as a consequence of ecological competition with other species or environmental changes during the final stage of the CAS (e.g., Coates and Stallard, 2013).


Early Neogene marine elasmobranch assemblages known from the Americas are summarized in Figure 15 and include North America (Purdy et al., 2001; Visaggi and Godfrey, 2010), Southern South America (Suárez et al., 2006; Cione et al., 2011) and Tropical America (Leriche, 1938; Casier, 1966; MacPhee et al., 2003; Alván et al., 2006; Portell et al., 2008; Costa et al., 2009; Aguilera and Lundberg, 2010; Pimiento et al., 2013b, Laurito et al., 2014; Carrillo-Briceño et al., 2016). From these assemblages the Uitpa Formation (Colombia) has been referred to the Aquitanian (Carrillo-Briceño et al., 2016), while the Calvert and Pungo River formations in North America (Purdy et al., 2001; Visaggi and Godfrey, 2010) and the Cantaure (in this work) and Castillo (Rincón et al., 2014) formations in Venezuela, have been referred to the Burdig-
The remaining formations (Figure 15) have been assigned to an unresolved early Miocene age. The Pungo River (~38 spp.) and Cantaure (39 spp.) assemblages preserve the most diverse elasmobranch faunas known from early Miocene of the Americas.

The late Burdigalian age (16.5±0.4 Ma.) of the Cantaure Formation based on Sr isotopes from corals from locality 2 of Griffiths et al. (2013) (Figure 1.2), suggests that all specimens found in localities 1 and 2 could be coetaneous or older than 16.5±0.4 Ma. The poorly known stratigraphic position of localities 1 and 2 (different vertical strata along the Cantaure section or horizontal variation of localities 1 and 2), does not permit an accurate age estimation for them, but their stratigraphic position (underlying the limestones interpreted as post-Cantaure sedimentation; Jung, 1965; Hunter and Bartok, 1974), suggests that these localities (3 and 4) are close to the top section of the Cantaure Formation. A Burdigalian age (Griffiths et al., 2013), or even that of a Burdigalian-Langhian boundary for the upper section of the Cantaure Formation (assuming that the biozones N7-8 and NN4-5 represent the lower to middle Miocene transition), would extend the stratigraphic range of two galeomorphs and of a batoid found in this assemblage. Fossils of *Carcharhinus cf. C. galapagensis*, from the Cantaure Formation, represent the oldest record for this species. It was previously known from the late Miocene of Mexico (González-Rodríguez et al., 2013). The same applies to *Carcharhinus gibbesii*, the youngest record was reported by Carrillo-Briceño et al. (2016) as the Aquitanian of Colombia. In reference to the batoid *Pteropleatrygon* sp., its record from the Cantaure Formation could be the oldest known to this stingray species.

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**FIGURE 15.** Early Neogene chondrichthyans diversity in the Americas. Tropical America: Barbados (Ba), Brazil (Br), Colombia (Co), Costa Rica (Cs), Cuba (Cu), The Grenadines (Gr), Panamá (Pa), Perú (Pu), Trinidad (Tr) and Venezuela (Ve). North America: United States of America (US). Southern South America: Argentina (Ar) and Chile (Ch). Aquitanian (Anq), Burdigalian (Brd), Langhian (Lngh); early Miocene without differentiation (EM), early-Middle Miocene (E-MM). Formation (Fm.), early (E). Note: to references see “Paleodiversity significance” (see Discussion).
The presence of *Carcharocles megalodon* in Burdigalian sediments of the Cantaure Formation (in at least localities 1 and 2) confirms the presence of this species during late early Miocene. It has been generally accepted that the record of *Carcharocles chubutensis* spans from the early to the middle Miocene, whereas *Carcharocles megalodon* spans from the middle Miocene to the late Pliocene (Pimiento and Clements, 2014; Pimiento and Balk, 2015). However, other authors have suggested that *C. megalodon* also occurs in the Burdigalian of Europe and North America (Leriche, 1938; Purdy et al., 2001; Visaggi and Godfrey, 2010; Reinecke et al., 2011). According to Leriche (1938), the two *C. megalodon* specimens he collected (Leriche, 1938, Planche III, Figures 5-6) in southern Mexico (Tabasco and Isthmus of Tehuantepec) came from early Miocene strata and are similar to teeth he previously collected in the Burdigalian of Europe. Another early Miocene unpublished occurrence of *C. megalodon* from Tropical America is from the late Burdigalian section (~16.2 Ma.) of the Castilletes Formation at North East Colombia (under study by JDCB). The specimens of *C. megalodon* from the Cantaure sequence have been found in all four localities studied here (Figure 1, Appendix 1), but with a greater abundance in localities 2 and 3 (Appendix 1). The presence of *C. megalodon* tooth (UNEFM-PF-322) at least 6-10 m deep in the artisan well (Figure 1.2) could suggest an older age than the 16.5±0.4 Ma for the species. More detailed information about the American and worldwide Neogene stratigraphic range of the remaining elasmobranch taxa recovered from the Cantaure Formation (Table 1) can be found in Kruckow and Thies (1990), Cicimurri and Knight (2009), Reinecke et al. (2011), Bor et al. (2012), Adnet et al. (2012), Cappetta, (2012), Pimiento et al. (2013b), and Carrillo-Briceño et al. (2014, 2015a, 2016).

Furthermore, it is important to note that the elasmobranch fauna from the Cantaure Formation shows a clear differentiation in paleodiversity amongst the four localities studied here (Appendix 1, 4). As is shown in Appendix 4.2, localities 1 and 2 (Figure 1) have a higher diversity than those of localities 3 and 4, a fact that could be attributable to: 1) less intensive sieving and sampling of the localities 3 and 4 (see Material and Methods section) or 2) different lithologic, taphonomic and preservation conditions. Future, more accurate dating of the deposits could offer new insights into the age of the Cantaure deposits, and especially of the sections located south of Barbasco Creek.

**Paleoenvironment and Paleoecology**

On the basis of planktonic foraminifera, calcareous nannofossils and mollusks, it has been proposed that the Cantaure Formation was deposited in a shallow, coastal tropical marine environment, with clear waters and normal salinity (Jung, 1965; Diaz de Gamero, 1974; Rey, 1996; Landau et al., in press). A conspicuous absence of typical herbivore gastropods suggests that sea-grass habitats were probably not represented in this environment (Landau et al., in press). The teleostean assemblage reported by Nolf and Aguilara (1998) reflects a shallow environment with a water depth of less than 50 m. The crustacean assemblage (Aguilera et al., 2010) is also suggestive of inner-shelf environments. The barnacle epifauna attached to a shark tooth AMU-CURS-720 (Figure 12.9-12.10) further indicates that the Cantaure Formation was deposited in a shallow marine environment, as barnacles live either in intertidal (26%) or sublittoral areas of ≤100 m (73%) (Doyle et al., 1996). Our bathymetric analysis of the Cantaure Formation, suggesting most likely an estimated deep interval depth between 0 to 50 m (Figure 13), supports the assumption of an inner-middle shelf environment (Figure 16). Additional support to this estimation is derived from the presence of the benthopelagic sharks *Nebrius* sp., *Carcharhinus* cf. *C. limbatus*, *C. perezi* and *Isogomphodon acuarius*, whose extant representatives usually prefer waters shallower than 40 m deep (Appendix 3). As shown in Figure 13, many of the benthopelagic and pelagic elasmobranch taxa of the Cantaure fauna have extant representatives associated with coastal environments, but can also occur in adjacent deep waters (Appendix 3), and even move significant distances over oceanic basins, suggesting a wide environmental range (Compagno et al., 2005; Voigt and Weber, 2011).

The Cantaure sequence rests on metamorphic and igneous rocks that were above water level during early Miocene (Gonzalez de Juana et al., 1980; Macellari, 1995). During the Cantaure sedimentation, these positive reliefs played the role of islands or archipelagos, as illustrated in the paleogeographic reconstruction of the Falcon Basin by Gonzalez de Juana et al. (1980) and Macellari (1995). According to Landau et al. (in press), 47.8% of the gastropod species (188 spp.) in the Cantaure Formation are exclusive, representing a very high level of endemism. This species endemism could support the hypothesis of an isolated, insular mollusk-community in the northern part of the Falcon Basin during early Miocene. However,
expanded knowledge of their localities will certainly lower that estimate. The Cantaure gastropod assemblage also has a small freshwater component, corresponding to typical species of late Oligocene early Middle Miocene NW South-American inland freshwater faunas (Landau et al. in press). This is likely suggestive of insular areas allowing the existence of terrestrial faunas. In addition, the diverse teleostean fauna from the Cantaure Formation, with more than 65 species (Nolf and Aguilera, 1998; Aguilera, 2010; Aguilera and Lundberg, 2010), suggests a high-productivity environment associated with a coastal upwelling (Aguilera and Rodrigues de Aguilera, 2001).

A few large sharks from the Cantaure assemblage such as *Carcharocles megalodon*, *Galeocerdo aduncus* and *G. mayumbensis*, could have alternatively occupied different environments and fed on various resources, such as teleosteans, chondrichthyans, reptiles, birds and mammals. In extant marine communities many sharks are perceived as apex predators, occupying the same trophic level with marine mammals (Klimley, 2013). In the Cantaure fauna such large sharks (*C. megalodon*, *G. aduncus* and *G. mayumbensis*), together with a medium-sized odontocete (?Squalodelphinidae) (Cozzuol and Aguilera, 2008; likely occupied the apex predator role. Moreover, cetacean (squalodontids) and sirenid (dugongids) skeletal remains found in the Cantaure Formation exhibit shark bite marks, suggesting that these mammals also were prey (Cozzuol and Aguilera, 2008). A cetacean lumbar vertebra with an embedded tooth of *Carcharocles megalodon* was reported from the early Pliocene Paraguana Formation, in the “El Yacural” locality (Aguilera et al., 2008). Recent field work in the “El Yacural” produced new specimens that include cetacean remains (vertebra and a skull fragment; AMU-CURS-709 and 710, respectively) and a crocodilian vertebra (AMU-CURS-708).

Those specimens lack any evidence for predation. The geographic coordinates of locality 4...
served in the Cantaure Formation. Crocodile and turtle remains are also present in the eastern Atlantic and western Pacific. This suggests that the vertebral column, with an embedded Carcharocles megalodon tooth, could belong to the Cantaure Formation and not to the early Pliocene Paraguaná Formation (Aguilera et al., 2008). As previously mentioned, the Cantaure Formation is a complex sequence that needs a new detailed stratigraphic redescription, which could offer new geological information. The sections located at the south of the Barbasco Creek are of particular relevance for future research. In addition, the crocodilian vertebra (AMU-CURS-708) and the small eroded turtle-shell fragments, although not offering useful information for taxonomical classification, verify the presence of at least two reptiles in this ancient high-productive marine environment of the Cantaure Formation.

CONCLUSIONS

The elasmobranch fauna from the Cantaure Formation, containing 39 species, is characterized by a predominance of benthopelagic sharks with piscivorous feeding preferences, followed by durophagous/cancritrophic feeders. The elasmobranch habitat preferences and paleobathymetric analyses support the hypothesis that the Cantaure Formation was deposited in a high-productivity, inner-middle shelf environment, around positive reliefs (island/archipelago), in the northern part of Falcon Basin during early-middle Miocene. This shark and ray fauna, is one of most diverse assemblages from early Neogene of the Americas, and contains many forms now extinct in the Caribbean, but present in the eastern Atlantic and western Pacific. Crocodile and turtle remains are also preserved in the Cantaure Formation.

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APPENDIX 1.

Elasmobranchi of the Cantaure Formation and their record per localities, jaw position and tooth measurements. Abbreviations: number of specimens (N°), total number of specimens (N° T) and indeterminate (indet.).

<table>
<thead>
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<th>Taxon</th>
<th>Localities</th>
<th>Jaw position</th>
<th>Teeth measurements (mm)</th>
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<td>3</td>
<td>4</td>
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<td>Lower</td>
<td>indet.</td>
<td>Height</td>
<td>Width</td>
<td>Length</td>
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<td>1</td>
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<td>&lt;4</td>
<td>&lt;4</td>
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<tr>
<td>Pristi sp.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>19</td>
<td></td>
<td></td>
<td>&lt;3</td>
<td>&lt;3</td>
<td>&lt;3</td>
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</tr>
<tr>
<td>Dasyatis sp.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>33</td>
<td></td>
<td></td>
<td>&lt;3</td>
<td>&lt;3</td>
<td>&lt;3</td>
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<tr>
<td>cf. Pteroplatytrygon sp.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>5</td>
<td></td>
<td></td>
<td>&lt;5</td>
<td>&lt;3</td>
<td>&lt;3</td>
<td></td>
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<tr>
<td>cf. Taeniura sp.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>1</td>
<td></td>
<td></td>
<td>&lt;3</td>
<td>&lt;3</td>
<td>&lt;3</td>
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<tr>
<td>Dasyatidae indet.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>2</td>
<td></td>
<td></td>
<td>&lt;3</td>
<td>&lt;3</td>
<td>&lt;3</td>
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<td></td>
</tr>
<tr>
<td>Aetobatus sp.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>19</td>
<td></td>
<td></td>
<td>4.1 to 6</td>
<td>&lt;4.5 to 10</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aetotheres sp.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>3</td>
<td></td>
<td></td>
<td>&lt;3</td>
<td>&lt;3</td>
<td>&lt;3</td>
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<tr>
<td>Rhincodon sp.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>145</td>
<td>2</td>
<td>6</td>
<td>5 to 29</td>
<td>3 to 8</td>
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<td></td>
</tr>
<tr>
<td>Mobula fragilis</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>4</td>
<td></td>
<td></td>
<td>2.5 to 3</td>
<td>3.5 to &gt;6</td>
<td>1 to 1.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mobula cf. M. longipinennis</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>3</td>
<td></td>
<td>&lt;3</td>
<td>&lt;2</td>
<td>&lt;2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mobula sp.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>3</td>
<td></td>
<td></td>
<td>&lt;3</td>
<td>&lt;2</td>
<td>&lt;2</td>
<td></td>
<td></td>
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<tr>
<td>Phocoena stenodon</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>1</td>
<td></td>
<td></td>
<td>8</td>
<td>15.5</td>
<td>4</td>
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<tr>
<td>Myliobatoidea sp.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>11</td>
<td></td>
<td></td>
<td>&lt;3</td>
<td>&lt;3</td>
<td>&lt;3</td>
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<td></td>
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<tr>
<td>Chondrichthyes sp.</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>6</td>
<td></td>
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<td>&lt;3</td>
<td>&lt;3</td>
<td>&lt;3</td>
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</table>

Total: 170 786 764 116 1836
APPENDIX 2.

Referred fossil specimens and collection numbers.

Referred fossil specimens

- *Nebrinus* sp. [1 tooth (AMU-CURS-982), 1 tooth (AMU-CURS-986)].

- *†Paratodus benedenii* [1 tooth (AMU-CURS-645)].

- *†Carcharocles megalodon* [4 teeth (AMU-CURS-512), 3 teeth (AMU-CURS-513), 2 teeth (AMU-CURS-514), 2 teeth (AMU-CURS-515), 3 teeth (AMU-CURS-516), 4 teeth (AMU-CURS-517), 3 teeth (AMU-CURS-518), 1 tooth (AMU-CURS-519), 4 teeth (AMU-CURS-650), 1 tooth (AMU-CURS-996), 1 tooth (AMU-CURS-997), 1 tooth (AMU-CURS-998), 7 teeth (AMU-CURS-1034), 1 tooth (UNEFM-PF-321), 1 tooth (UNEFM-PF-322), 13 teeth (UNEFM-PF-s/n), 17 teeth (UNEFM-PF-s/n), 21 teeth (UNEFM-PF-s/n), 17 teeth (MCNC-s/n)].

- *Alopias* cf. *A. vulpinus* [1 tooth (AMU-CURS-983), 1 tooth (AMU-CURS-984), 1 tooth (AMU-CURS-985)].

- *Galeorhinus* cf. *G. galeus* [1 tooth (AMU-CURS-974)].

- *Mustelus* sp. [3 teeth (AMU-CURS-975)].

- *†Hemipristis serra* [66 teeth (AMU-CURS-502), 1 tooth (AMU-CURS-506), 6 teeth (AMU-CURS-520), 24 teeth (AMU-CURS-644), 3 teeth (AMU-CURS-712), 1 tooth (AMU-CURS-731), 1 tooth (AMU-CURS-973), 1 tooth (AMU-CURS-993), 1 tooth (AMU-CURS-994), 1 tooth (AMU-CURS-1014), 46 teeth (AMU-CURS-1031), 156 teeth (UNEFM-PF-s/n), 118 teeth (UNEFM-PF-s/n)].

- *†Galeocerdo aduncus* [13 teeth (AMU-CURS-647), 1 tooth (AMU-CURS-730)].

- *†Galeocerdo mayumbensis* [8 teeth (AMU-CURS-646), 1 tooth (AMU-CURS-995)].

- *Rhizoprionodon* sp. [14 teeth (AMU-CURS-959), 3 teeth (AMU-CURS-960)].

- *†Carcharhinus ackermanni* [3 teeth (AMU-CURS-713), 2 teeth (AMU-CURS-714)].

- *Carcharhinus brachyrurus* [28 teeth (AMU-CURS-668), 4 teeth (AMU-CURS-990)].

- *Carcharhinus falciformis* [72 teeth (AMU-CURS-669), 6 teeth (AMU-CURS-991), 11 teeth (AMU-CURS-953), 17 teeth (AMU-CURS-1035)].

- *Carcharhinus cf. C. galapagensis* [17 teeth (AMU-CURS-973)].

- *†Carcharhinus gibbesii* [2 teeth (AMU-CURS-958)].

- *Carcharhinus cf. C. limbatis* [2 teeth (AMU-CURS-944)].

- *Carcharhinus cf. C. macloii* [2 teeth (AMU-CURS-957)].

- *Carcharhinus perezi* [1 tooth (AMU-CURS-954), 3 teeth (AMU-CURS-955), 11 teeth (AMU-CURS-956)].

- *Carcharhinus* sp. [1 [8 teeth (AMU-CURS-943)].

- *Carcharhinus* spp. [22 teeth (AMU-CURS-651), 26 teeth (AMU-CURS-652), 14 teeth (AMU-CURS-940), 7 teeth (AMU-CURS-941), 10 teeth (AMU-CURS-942), 7 teeth (AMU-CURS-972), 1 tooth (AMU-CURS-1015), 1 tooth (AMU-CURS-1017), 10 teeth (AMU-CURS-1085)].

- *†Isogomphodon acuarius* [8 teeth (AMU-CURS-950), 25 teeth (AMU-CURS-951), 1 tooth (AMU-CURS-952)].

- *†Negaprion eurybathodon* [165 teeth (AMU-CURS-503), 65 teeth (AMU-CURS-504), 56 teeth (AMU-CURS-505), 1 tooth (AMU-CURS-509), 47 teeth (AMU-CURS-649), 13 teeth (AMU-CURS-987), 1 tooth (AMU-CURS-998), 52 teeth (AMU-CURS-989), 1 tooth (AMU-CURS-1013), 35 teeth (AMU-CURS-1032), 150 teeth (UNEFM-PF-s/n)].

- *Physogaleus contortus* [29 teeth (AMU-CURS-648), 2 teeth (AMU-CURS-992), 1 tooth (AMU-CURS-1033), 1 tooth (AMU-CURS-719), 1 tooth (AMU-CURS-720)].
APPENDIX 2 (CONTINUED).

- Carcharhinidae indet. [2 teeth (AMU-CURS-938), 8 teeth (AMU-CURS-939)].
- †Sphyra arambourgi [14 teeth (AMU-CURS-961), 13 teeth (AMU-CURS-962)].
- Sphyra cf. †S. laevisstina [1 tooth (AMU-CURS-963), 5 teeth (AMU-CURS-964), 1 tooth (AMU-CURS-965)].
- Rhynchobatus sp. [4 teeth (AMU-CURS-653), 2 teeth (AMU-CURS-654), 3 teeth (AMU-CURS-968), 4 teeth (AMU-CURS-969), 1 tooth (AMU-CURS-970), 1 tooth (AMU-CURS-971)].
- Pristis sp. [7 rostral denticles and 1 rostrum fragment (AMU-CURS-242), 1 rostral denticle (AMU-CURS-717), 3 teeth (AMU-CURS-655), 1 tooth (AMU-CURS-1019), 1 tooth (AMU-CURS-966), 5 teeth (AMU-CURS-717)].
- Dasyatis sp. [1 tooth (AMU-CURS-657), 1 tooth (AMU-CURS-658), 12 teeth (AMU-CURS-929), 5 teeth (AMU-CURS-930), 10 teeth (AMU-CURS-931), 1 tooth (AMU-CURS-932), 1 tooth (AMU-CURS-933), 1 tooth (AMU-CURS-934), 1 tooth (AMU-CURS-935)].
- cf. Pteroplatytrygon sp. [5 teeth (AMU-CURS-926)].
- cf. Taeniura sp. [1 tooth (AMU-CURS-925)].
- Dasyatidae indet. [1 tooth (AMU-CURS-936), 1 tooth (AMU-CURS-937)].
- Aetobatus sp. [1 tooth (AMU-CURS-508), 1 tooth (AMU-CURS-659), 4 teeth (AMU-CURS-663), 4 teeth (AMU-CURS-665), 6 teeth (AMU-CURS-716), 2 teeth (AMU-CURS-718), 1 tooth (AMU-CURS-729)].
- Actomylaeus sp. [1 tooth (AMU-CURS-750), 2 teeth (AMU-CURS-766)].
- Rhinoptera sp. [80 teeth (AMU-CURS-660), 1 tooth (AMU-CURS-664), 4 teeth (AMU-CURS-977), 6 teeth (AMU-CURS-978), 28 teeth (AMU-CURS-979), 11 teeth (AMU-CURS-980), 15 teeth (AMU-CURS-981)].
- †Mobula fragilis [2 teeth (AMU-CURS-947), 1 tooth (AMU-CURS-948), 1 tooth (AMU-CURS-949)].
- Mobula cf. †M. loupiensis [3 teeth (AMU-CURS-946)].
- Mobula sp. [3 teeth (AMU-CURS-945)].
- †Plinthiscus stenodon [1 tooth (AMU-CURS-715)].
- Myliobatiformes indet. [10 caudal spines (AMU-CURS-507), 1 tooth (AMU-CURS-510), 1 tooth (AMU-CURS-1018)].
- Chondrichthyes indet. [4 vertebrae (AMU-CURS-511), 2 denticles (AMU-CURS-656)].
### APPENDIX 3.

Bathymetric and feeding preferences of the Cantaure Formation elasmobranch taxa, based on the biology of their extant relatives. The gray shadow indicates the feeding preferences. Abbreviations: minimum (Mn), maximum (Mx) and meters (m).

<table>
<thead>
<tr>
<th>Cantaure Formation taxa</th>
<th>Extant species</th>
<th>Bathymetric depth (m)</th>
<th>Comments</th>
<th>Feeding ecology</th>
<th>Time feeding</th>
<th>Social feeding</th>
<th>Diet</th>
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<td></td>
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<td></td>
</tr>
<tr>
<td>Heterodontus sp.</td>
<td>Heterodontus sp.</td>
<td>X X X 0 280</td>
<td></td>
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<tr>
<td>Nebrius sp.</td>
<td>Nebrius ferrugineus</td>
<td>X X 1 30 usually less than 30 m</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Parasuchus helenensis</em></td>
<td></td>
<td>X X ? ? ?</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Carcharocles megalodon</em></td>
<td></td>
<td>? X X ? ?</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Alstros cf. A. vulpinus</em></td>
<td><em>Alstros vulpinus</em></td>
<td>X X X 0 550 usually less than 200 m</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Galeocerdoe cf. G. galaeus</td>
<td>G. galaeus</td>
<td>X X X 0 1100 usually 2-400 m</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mestacanthus sp.</td>
<td>Mestacanthus sp.</td>
<td>X X X 0 900</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
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<tr>
<td><em>Hemipristis serra</em></td>
<td><em>Hemipristis elongata</em></td>
<td>X X 0 130</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
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<tr>
<td><em>Galeocerdoe aduncus</em></td>
<td>G. aduncus</td>
<td>X X ? 0 370 usually less than 150 m</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td>X X</td>
</tr>
<tr>
<td><em>Galeocerdoe myxobatis</em></td>
<td>G. myxobatis</td>
<td>X X ? 0 370 usually less than 150 m</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td>X X</td>
</tr>
<tr>
<td><em>Batisnomaon sp.</em></td>
<td><em>Batisnomaon sp.</em></td>
<td>X X 0 500 usually less than 100 m</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td>X X</td>
</tr>
<tr>
<td><em>Carcharhinus ackermanni</em></td>
<td><em>Carcharhinus sp.</em></td>
<td>X X ? 0 &gt;1000</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Carcharhinus breachiurus</em></td>
<td><em>Carcharhinus breachiurus</em></td>
<td>X X X 0 600 usually less than 100 m</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carcarhinus falciformis</td>
<td><em>Carcarhinus falciformis</em></td>
<td>X X X 0 4000 most in waters &gt; 200 m</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Carcarhinus cf. C. galapagensis</em></td>
<td><em>C. galapagensis</em></td>
<td>X X 0 180</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Carcarhinus gibbone</em></td>
<td><em>Carcharhinus sp.</em></td>
<td>X X ? 0 &gt;1000</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Carcarhinus cf. C. limbata</em></td>
<td><em>Carcharhinus limbata</em></td>
<td>X X 0 100 usually less than 30 m</td>
<td></td>
<td></td>
<td>X X</td>
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<tr>
<td><em>Carcarhinus cf. C. maclochi</em></td>
<td><em>Carcharhinus maclochi</em></td>
<td>X X 0 170</td>
<td></td>
<td></td>
<td>X X</td>
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<tr>
<td><em>Carcarhinus perigrinatus</em></td>
<td><em>Carcharhinus perigrinatus</em></td>
<td>X X 0 65 usually less than 50 m</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
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<tr>
<td><em>Carcarhinus sp.</em></td>
<td><em>Carcarhinus sp.</em></td>
<td>? ? X ? 0 &gt;1000</td>
<td></td>
<td></td>
<td>X ?</td>
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<td><em>Hybodus xenosaurus</em></td>
<td><em>Hybodus xenosaurus</em></td>
<td>X X 0 46</td>
<td></td>
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<td>X X</td>
<td></td>
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<tr>
<td><em>Nagadorus eurynrhynchus</em></td>
<td><em>N. brevirostris</em></td>
<td>X X 0 92</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
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<tr>
<td><em>Pterobatis notorius</em></td>
<td><em>Pterobatis notorius</em></td>
<td>? ? X ? 0 &gt;1000</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sphyraena arnostrongi</em></td>
<td><em>Sphyraena sp.</em></td>
<td>X X ? 0 &gt;1000</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sphyraena cf. S. leucochea</em></td>
<td><em>S. leucochea</em></td>
<td>X X 0 &gt;1000 usually less than 20 m</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
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<tr>
<td><em>Rhyacochilus sp.</em></td>
<td><em>Rhyacochilus sp.</em></td>
<td>X X 0 60</td>
<td></td>
<td></td>
<td>X X</td>
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<tr>
<td><em>Protaurus sp.</em></td>
<td><em>Protaurus sp.</em></td>
<td>X X 0 120 most in waters &lt; 20 m</td>
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<td></td>
<td>X X</td>
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<tr>
<td><em>Dasyatis sp.</em></td>
<td><em>Dasyatis sp.</em></td>
<td>X X 0 470 usually in waters &lt; 50 m</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
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<tr>
<td>cf. Paralipotyphunct sp.</td>
<td><em>P. lipotyphunct sp.</em></td>
<td>X X X 0 381 usually 1-100 m</td>
<td></td>
<td></td>
<td>X X X</td>
<td></td>
<td></td>
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<tr>
<td>cf. Taeniurus sp.</td>
<td><em>T. cf. sp.</em></td>
<td>X X X 0 10 500 usually 20-60 m</td>
<td></td>
<td></td>
<td>X X X</td>
<td></td>
<td></td>
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<tr>
<td><em>Dasyatis indebat</em></td>
<td><em>Dasyatis indebat</em></td>
<td>X X X 0 470</td>
<td></td>
<td></td>
<td>X X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Aetobatus sp.</em></td>
<td><em>A. squalus</em></td>
<td>X X 0 &gt;100 usually less than 40 m</td>
<td></td>
<td></td>
<td>X X X</td>
<td></td>
<td></td>
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<tr>
<td><em>Aetomyxus sp.</em></td>
<td><em>A. ferrugineus</em></td>
<td>X X 0 110</td>
<td></td>
<td></td>
<td>X X X</td>
<td></td>
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<tr>
<td><em>Rhiodacrus sp.</em></td>
<td><em>R. spinifer</em></td>
<td>X X 0 &lt; 60 usually less than 30 m</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Mobula cf. S. longipinnis</em></td>
<td><em>M. longipinnis</em></td>
<td>X X ? 0 &gt;200 usually less than 100 m</td>
<td></td>
<td></td>
<td>X X</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Mobula sp.</em></td>
<td><em>M. cf. sp.</em></td>
<td>X X ? 0 &gt;200 usually less than 100 m</td>
<td></td>
<td></td>
<td>X X</td>
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</tr>
</tbody>
</table>
APPENDIX 4.

Relative abundance of elasmobranchs in the Cantaure Formation. 1. Abundance percentage per locality per taxon. 2. Total abundance per locality. Ht: Heterodontiformes; Or: Orectolobiformes; La: Lamniformes; Ca: Carcharhiniformes; Ra: Rajiformes; My: Myliobatiformes; In: Indeterminate; Loc.: locality; †: extinct taxon. *: Percentage does not include *Carcharhinus* spp., Myliobatiformes indet. and Chondrichthyes indet.