



# Neogene Caribbean elasmobranchs: Diversity, paleoecology and paleoenvironmental significance of the Cocinetas Basin assemblage (Guajira Peninsula, Colombia)

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


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**Abstract.** The Cocinetas Basin is located on the eastern flank of La Guajira Peninsula, northern Colombia (South Caribbean). During  Oligocene through Pliocene, much of the basin was submerged. The extensive deposits in this area suggest a transition from a shallow marine to a fluvio–deltaic system, with a rich record of invertebrate and vertebrate fauna. The elasmobranch assemblages of the early Miocene to late Pliocene succession in the Cocinetas Basin (Jimol, Castilletes and Ware Formations, and Patsúa Valley) are described for the first time. The assemblages include at least 30 taxa of sharks (Squaliformes, Pristiophoriformes, Orectolobiformes, Lamniformes and Carcharhiniformes) and batoids (Rhinopristiformes and Myliobatiformes), of which 24 taxa are reported from the Colombian Neogene for the first time. Paleoecological and paleoenvironmental interpretations are based on the feeding ecology, and on estimates of paleosalinity using stable isotope compositions of oxygen in the biapatite of shark teeth.  The isotopic composition of studied specimens corroborates the paleoenvironmental settings  for the studied units suggested on the basis of other proxies.  The Neogene elasmobranch assemblages from the Cocinetas Basin, provide new insights of the shark and ray diversity inhabiting the coastal and estuarine environments of the northwestern margin of South America, both during the existence of the gateway between the Atlantic and Pacific Oceans, and following its closure.

## 1 Introduction

15 During the Neogene, large areas of the northern margin of South America were submerged (see Iturralde–Vincent and MacPhee, 1999) and influenced by the paleoceanographic connection between the Pacific and Atlantic oceans along the Central American Seaway (CAS). The CAS is defined here as a deep oceanic connection between the Pacific and Atlantic oceans along the tectonic boundary of Caribbean and the South American plates (Jaramillo et al., 2017). The CAS existed throughout the Cenozoic, but was reduced in width by the early Miocene (Farris et al., 2011), and the transfer of deep–water ceased by the



late Miocene 12–10 Ma (Montes et al., 2015; Bacon et al., 2015; Jaramillo et al., 2017). Shallow marine connections between Caribbean and Pacific waters existed until about 4.2–3.5 Ma, when a complete closure occurred (Coates and Stallard, 2013). The Cocinetas Basin, located on the eastern flank of La Guajira Peninsula, northern Colombia, records a transition in marine and terrestrial paleoenvironments during this regional change in conditions. This region presents extensive and well exposed sedimentary deposits spanning the last 25 Myr (Moreno et al., 2015). The paleoenvironments are characterized by a transition from shallow marine deposits to a fluvio–deltaic system (Moreno et al., 2015), with a rich fossil record of invertebrates (Hendy et al., 2015) and vertebrates (Aguilera et al., 2013, 2017b; Moreno et al., 2015; Cadena and Jaramillo, 2015; Amson et al., 2016; Carrillo–Briceño et al., 2016b; Moreno–Bernal et al., 2016; Pérez et al., 2016). Ages for many of the fossiliferous units in the sequence have been estimated using Sr isotope stratigraphy (see Hendy et al., 2015).

Neogene marine chondrichthyan faunas from the southern Proto–Caribbean (especially from the northern margin of South America) are well known from Venezuela and some Lesser Antilles (e.g., Leriche, 1938, Casier, 1958, Casier, 1966, Aguilera, 2010, Aguilera and Lundberg, 2010, Carrillo–Briceño et al., 2015b, Carrillo–Briceño et al., 2016a, and references therein). But reports on chondrichthyans from the Neogene of Colombia are scarce. Previous reports from the Cocinetas Basin include fossil elasmobranchs without taxonomic description (Lockwood, 1965), a checklist of 14 families (Moreno et al., 2015), and the description of a small assemblage of 13 taxa from the early Miocene Uitpa Formation (Carrillo–Briceño et al., 2016b).

A taxonomic revision is presented of the elasmobranch fauna collected in the Cocinetas Basin (Figs. 1–2), from the Jimol (Burdigalian), Castilletes (late Burdigalian–Langhian), Ware (Gelasian–Piacenzian) Formations, and two localities of the Patsúa Valley (Burdigalian–Langhian). The assemblage includes 30 taxa, of which 24 are new reports for Colombian Neogene deposits. Additionally, paleoecological and paleoenvironmental interpretations based on the feeding ecology of extant counterpart species, as well as estimates of the paleosalinity using stable isotope compositions of oxygen in the bioapatite of shark teeth are discussed. The Cocinetas Basin represents a valuable window into dynamic changes in paleodiversity experienced by ancient Proto–Caribbean Neogene chondrichthyan faunas.

## 2 Material and Methods

The fossil elasmobranch assemblages (Table 1, Tables S1–S3; File S4) consists of 2529 specimens from 36 localities (Table S1) from the Cocinetas Basin, Guajira Peninsula, northeastern Colombia (Fig. 1). The elasmobranch faunas were collected in the early Miocene Jimol Formation (six localities and 113 specimens), early–middle Miocene Castilletes Formation (20 localities and 1232 specimens), and the late Pliocene Ware Formation (eight localities and 215 specimens) (Tables S1–S2). Localities STRI 290468 and 290472 (968 specimens) in the Patsúa Valley, close to Flor de Guajira, along the southern margin of the Cocinetas Basin (Fig. 1), are from strata that cannot be readily correlated with either the Jimol or Castilletes Formation. Because of these difficulties, and differences in their facies, and invertebrate and vertebrate fauna, we treat them as undifferentiated Jimol/Castilletes Formation, and they are referred to herein as the Patsúa assemblage.

The samples were collected by JDCB, AH and other collaborators during several expeditions between 2010 and 2014. Large specimens were collected directly from the outcrop. The 50 kg bulk sediment subsequent picking of smaller specimens



were collected from the locality 290468 (Patsúa assemblage) and Castilletes Formation (localities 290632 and 390094). The bulk sediments sieved and screen washed (mesh sizes: 0.5 and 2 mm). Overall, Cocinetas Basin elasmobranch specimens (File S4) are housed in the paleontological collections of the Mapuka Museum of Universidad del Norte (MUN), Barranquilla, Colombia. The nomenclature follows Cappetta (2012) and Compagno (2005), with the exception of Rhinopristiformes Last et al., 2016, Aetobatidae Agassiz, 1958 (Table 1) and *Carcharocles* Agassiz, 1838, for which we follow the nomenclature discussed in Last et al. (2016), White and Naylor (2016) and Ward and Bonavia (2001), respectively. Identifications are based on literature review (e.g., Santos and Travassos, 1960, Müller, 1999, Purdy et al., 2001, Cappetta, 1970, Cappetta, 2012, Reinecke et al., 2011, Reinecke et al., 2014, Voigt and Weber, 2011, Bor et al., 2012, Carrillo–Briceño et al., 2014, Carrillo–Briceño et al., 2015a, Carrillo–Briceño et al., 2015b, Carrillo–Briceño et al., 2016a, Aguilera et al., 2017a, among others) and comparative analysis between fossil and extant specimens from several collections including Museu Paraense Emilio Goeldi (MPEG–V), Belém, Brazil; Fossil Vertebrate Section of the Museum für Naturkunde, Berlin, Germany (MB.Ma.); Natural History Museum of Basel (NMB), Switzerland; the paleontological collections of the Alcaldía del Municipio Urumaco (AMU–CURS) and Centro de Investigaciones Antropológicas, Arqueológicas y Paleontológicas of the Universidad Experimental Francisco de Miranda (CIAAP, UNEFM–PF), both in Venezuela; 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), and René Kindlimann private collection, Uster, Switzerland.

Quantitative data includes percentages of specimens by order, families and genera recorded in the overall assemblages of the Cocinetas Basin (Table 1, Tables S1–S2, Fig. S5). Paleoeological interpretations of fossil chondrichthyan assemblages have limitations related to the scarce information offered by the fossil record. Extant sharks and rays as a whole have a wide range of diets; however, each taxon has specific food preferences (see Cortés et al., 2008; Klimley, 2013) that could be used to infer dietary strategies of their fossil relatives (e.g., Carrillo–Briceño et al., 2016a). Information regarding feeding ecology (dietary composition and behavior) of extant/relative species of the taxa recorded in the Cocinetas assemblages (Table S3) was compiled from Cortés et al. (2008), Compagno et al. (2005); Voigt and Weber (2011); Ebert and Stehmann (2013); and the FishBase website (Froese and Pauly, 2017).

Analyses of  $\delta^{18}\text{O}_{\text{PO}_4}$  were made in the Stable Isotope Laboratory at University of Lausanne (UNIL) (Table 2). Powder samples of shark teeth enameloid were obtained by abrasion of the crown surface using a micro-drill. Micro fragment samples were obtained by cutting the tip of teeth, in a few cases when only small or fragmented teeth were available bulk samples were taken (enameloid and dentine). Based on previous studies, data provide valuable information about ecological features of sharks along geochronological sequences (Fischer et al., 2012, 2013a, b; Kocsis et al., 2014; Leuzinger et al., 2015; Aguilera et al., 2017a). All samples were cleaned in ultrapure water in an ultrasonic bath to reduce sedimentary contamination. International reference of NBS–120c phosphorite and in-house laboratory standards were prepared parallel with the batch. Pre-treatment followed the method described by Koch et al. (1997), where powdered teeth were first washed in 1M acetic acid–Ca acetate (pH = 4.5, 2h) to remove any exogenous carbonates. They were thoroughly rinsed several times in ultrapure water. To obtain the  $\delta^{18}\text{O}_{\text{PO}_4}$  values the phosphate group in apatite was separated via precipitation as silver phosphate (O'Neil et al., 1994; Dettman et al., 2001; Kocsis, 2011). The method was adapted from the last review on silver phosphate microprecipitations by



Mine et al. (2017). Triplicates or duplicates of each  $\text{Ag}_3\text{PO}_4$  sample were analyzed on a TC/EA (high-temperature conversion elemental analyzer) (Vennemann et al., 2002) coupled to a Finnigan MAT 253 mass spectrometer, where silver phosphate is converted to CO at 1450 °C via reduction with graphite. Measurements were corrected to in-house  $\text{Ag}_3\text{PO}_4$  phosphate standards (LK-2L: 12.1 ‰ and LK-3L: 17.9 ‰) that had better than  $\pm 0.3$  ‰ ( $1\sigma$ ) standard deviations during measurements. The NBS-120c phosphorite reference material had an average value of  $21.7$  ‰  $\pm 0.1$  ‰ ( $n = 6$ ). The isotope ratios are expressed in the  $\delta$ -notation relative to Vienna Standard Mean Ocean Water (VSMOW).

The  $\delta^{18}\text{O}_{\text{PO}_4}$  values in shark teeth is a well known environmental proxy, especially when enameloid derived samples are employed (Vennemann et al., 2001; Zazzo et al., 2004a, b; Lécuyer, 2004; Kocsis, 2011). Longinelli and Nuti (1973a, b) were the first who recognized that the  $\delta^{18}\text{O}_{\text{PO}_4}$  values of several ectothermic fishes are related to two environmental parameters: the water temperature (T) and the  $\delta^{18}\text{O}$  value of the water ( $\delta^{18}\text{O}_w$ ). Based on these studies, an equation that empirically represents the oxygen isotope fractionation between biogenic phosphate and water was suggested ( $T$  (°C) =  $111.4 - 4.3 (\delta^{18}\text{O}_{\text{PO}_4} - \delta^{18}\text{O}_w)$ ), which was later revised (Kolodny et al., 1983; Pucéat et al., 2010; Lécuyer et al., 2013). This equation is used by paleontologists as a paleothermometer (Barrick et al., 1993; Lécuyer et al., 1993, 1996). Recently the  $\delta^{18}\text{O}_{\text{PO}_4}$  values have also been used to estimate the horizontal migrations of fishes into brackish sub-environments (Kocsis et al., 2007; Klug et al., 2010; Fischer et al., 2012, 2013a, b; Leuzinger et al., 2015).

Paleotemperatures from the  $\delta^{18}\text{O}_{\text{PO}_4}$  values were also calculated using the latest equation of Lécuyer et al. (2013) [ $T$  (°C) =  $117.4 - 4.5 \times (\delta^{18}\text{O}_{\text{PO}_4} - \delta^{18}\text{O}_w)$ ]. For the late Pliocene samples (Ware Formation) a seawater value of 0 ‰ (VSMOW: Vienna Standard Mean Ocean Water) while for the early-middle Miocene samples (Patsúa assemblage, Jimol and Castilletes) a value of  $-0.4$  ‰ was used following estimates of the global seawater isotopic composition (Lear et al., 2000; Billups and Schrag, 2002).

### 3 Geological and Stratigraphic setting

#### 3.1 Jimol Formation (Burdigalian)

This formation is one of the most extensive Cenozoic units in the Cocinetas Basin (Fig. 1b), with a thickness of approximately 203 m, though this composite section was poorly exposed in the middle parts of the Formation (Moreno et al., 2015). The lower and upper contacts of the Jimol Formation are conformable with the Uitpa and Castilletes Formations respectively (Fig. 1b). According to Moreno et al. (2015) and Hendy et al. (2015), the unit is characterized by coarse detritic and calcareous lithologies with fewer bedded muddy levels deposited in a shallow marine paleoenvironment, inner shelf depth (< 50 m). Abundant invertebrates (Hendy et al., 2015) and some vertebrate remains (Moreno et al., 2015; Moreno-Bernal et al., 2016) have been recorded. A late early Miocene (17.9–16.7 Ma) age is assigned to the unit on the basis of macroinvertebrate biostratigraphy and  $^{87}\text{Sr}/^{86}\text{Sr}$  isotope chronostratigraphy (see Hendy et al., 2015).





### 3.2 Castilletes Formation (Burdigalian–Langhian)

This geological unit crops out along the eastern margin of the Cocinetas Basin (Fig. 1b). The lithology of the Castilletes Formation is characterized by successions of mudstones interbedded with thin beds of biosparites and sandstones, with an estimated thickness of 440 m. The lower contact is conformable with the underlying Jimol Formation, and the upper is unconformable (angular contact) with the overlying Ware Formation (Moreno et al., 2015). The unit was deposited in shallow marine to fluvio–deltaic environments, with abundant marine, fluvio–lacustrine and terrestrial fossils (e.g., plants, mollusks, crustaceans, fishes, turtles, crocodylians, and mammals) (Aguilera et al., 2013, 2017b; Cadena and Jaramillo, 2015; Hendy et al., 2015; Moreno et al., 2015; Amson et al., 2016; Moreno–Bernal et al., 2016; Aguirre–Fernández et al., 2017). Isotope chronostratigraphy ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) supports an age of 16.2 Ma (range: 16.33–16.07) for the lower section, and 15.30 Ma (range: 15.14–15.43) for the middle part of the unit (Moreno et al., 2015).

### 3.3 Undifferentiated Jimol and Castilletes Formation (Burdigalian–Langhian)

Sediments of Bahia Cocinetas in the Patsúa Valley have been previously mapped as the Castilletes Formation (Moreno et al., 2015; Moreno–Bernal et al., 2016). They unconformably overly carbonates of the Siamana Formation (late Oligocene–early Miocene), and are in turn overlain with an angular unconformity by the Ware Formation along the shoreline of Bahia Cocinetas. Despite these stratigraphic relationships, this succession cannot be physically correlated with any particular beds in either Jimol or Castilletes Formations in the central and northern parts of Cocinetas Basin. The lithofacies preserved in this succession, which includes fossiliferous conglomerate and coarse sands and distinct fossil assemblages (Teredo, wood, an oceanic fauna of mollusks and echinoderms, and diverse elasmobranch and bony fish faunas), are also anomalous. For the purposes of analyzing the biodiversity and paleoecology of elasmobranch faunas in Cocinetas Basin it is best to refer to these beds as the undifferentiated Jimol/Castilletes Formation. The underlying Siamana Formation may be as young as Aquitanian–early Burdigalian (Silva–Tamayo et al., 2017) thereby constraining the maximum age of these beds as Burdigalian.

### 3.4 Ware Formation (late Pliocene)

The type section of the Ware Formation is located immediately east of the village of Castilletes, and correlated deposits are distributed along the eastern margin of Cocinetas Basin (Fig. 1b), cropping out as conspicuous isolated hills with near horizontal strata (Hendy et al., 2015; Moreno et al., 2015). The lithology of the Ware Formation is composed of light gray mudstones, grayish–yellow fine sandstones, and muddy sandstones, reddish–gray pebbly conglomerates, yellowish–gray packstone biosparites, and sandy to conglomeratic biosparites, with an estimated thickness of approximately 52 m. The lower contact is unconformable with the underlying Castilletes Formation, and the upper contact is a fossiliferous packstone in the stratotype that marks the youngest preserved Neogene sedimentation in the Cocinetas Basin (Moreno et al., 2015; Pérez–Consuegra et al., 2018). The basal section of the unit was deposited in a fluvio–deltaic environment, and abundant plant and vertebrate remains (including sharks herein referred, fishes, turtles, crocodylians, and mammals) have been found in the conglomeratic layers (Moreno et al., 2015; Amson et al., 2016; Moreno–Bernal et al., 2016; Pérez et al., 2016). Only marine invertebrates



have been found in the top beds of the Ware Formation (e.g., Hendy et al., 2015), suggesting an exposed open–ocean shoreface and nearshore settings near coral reefs (Moreno et al., 2015). A late Pliocene (Piacenzian) range of 3.40 Ma to 2.78 Ma age is assigned to the Ware Formation on the base of macroinvertebrate biostratigraphy and  $^{87}\text{Sr}/^{86}\text{Sr}$  isotope chronostratigraphy (Moreno et al., 2015).

## 5 4 Results

### 4.1 Elasmobranch paleodiversity

The taxonomical composition of the 36 fossiliferous localities (Table S1) includes at least 30 taxa of squalomorphs, galeomorphs and batoids (Table 1, Figs. 3–8). Squalomorphs are represented by two species, two genera and two families of Squaliformes and Pristiophoriformes. Galeomorphs are represented by at least 20 species, 13 genera and seven families of Orectolobiformes, Lamniformes and Carcharhiniformes (Table 1). Batoids include seven species, seven genera and seven families of Rhinopristiformes and Myliobatiformes (Table 1).

• **Squaliformes Goodrich, 1909.** This group (Table 1) is represented by two specimens referable to *Dalatias* cf. *D. licha* (Bonnaterre, 1788) (Fig. 3a–d, Table S2) from the Jimol Formation (Table S1). This taxon was previously recorded from Cocinetas Basin (Uitpa Formation) by Carrillo–Briceño et al. (2016b).

• **Pristiophoriformes Berg, 1958.** Five isolated crowns of rostral teeth of indet. *Pristiophorus* Müller and Henle, 1837 (Fig. 3e–g, Table 1, Table S2), were collected in the Patsúa Valley from the locality 290468 (Table S1). Similar specimens were recorded from the Uitpa Formation by Carrillo–Briceño et al. (2016b).

• **Orectolobiformes Applegate, 1972.** Eight specimens referable to an indet. species of *Nebrius* Appell, 1837 (Fig. 3h–o, Table 1, Table S2), were collected exclusively from Burdigalian localities of the Castilletes Formation (Table S1). The specimens are morphologically similar to those of *Nebrius* sp. reported from the Cantaure Formation (Burdigalian) in the Falcon Basin, Venezuela and Pirabas Formation (Aquitanian–Burdigalian), Brazil (Aguilera et al., 2017a). For summarized information about taxonomy and stratigraphic range of *Nebrius* in the Americas see Carrillo–Briceño et al. (2016a, p. 6).

• **Lamniformes Berg, 1937.** These sharks represent the second most diverse group from the Cocinetas elasmobranch assemblages (Fig. 9a), with records for the Jimol and Castilletes Formations and Patsúa assemblage (locality 290468) (Fig. 9b, Tables S1–S2). *Isurus* cf. *I. oxyrinchus* Rafinesque, 1810 (Fig. 3p–t), †*Paratodus edenii* (Le Hon, 1871) (Fig. 3u–v), †*Carcharocles chubutensis* (Ameghino, 1901) (Figs. 3w–z, 4a–d), *Alopias* cf. †*A. exigua* Probst, 1879 (Fig. 4n–q), and †*Anotodus retroflexus* (Agassiz, 1843) (Fig. 4r–s), are recorded exclusively for the locality 290468 (Table S1), whereas *Carcharocles* sp. (Fig. 4m) occurs in the Jimol Formation, and †*Carcharocles megalodon* (Agassiz, 1843) (Fig. 4e–l) from only three localities of the late Burdigalian strata of the Castilletes Formation (Table S1). †*Carcharocles chubutensis* and †*C. megalodon* are the most abundant lamniforms from all studied localities of the Cocinetas Basin (Table S1). Due to the relatively small size of the †*C. chubutensis* teeth from the localities 290468 and 290472, (Table S1), these likely belong to juvenile individuals (Figs. 3w–z, 4a–d).



• **Carcharhiniformes Berg, 1937.** With 14 taxa this is the most diverse and the second most abundant elasmobranch group from the Cocinetas assemblages (Fig. 9a). The Carcharhinidae Jordan and Evermann, 1896 with five genera and 11 species [*†Galeocerdo mayumbensis* Dartevelle and Casier, 1943 (Fig. 4x–z); *†Carcharhinus ackermannii* Santos and Travassos, 1960 (Fig. 5a–d); *Carcharhinus* cf. *C. brachyurus* (Günther, 1870) (Fig. 5e–h); *†Carcharhinus gibbesii* (Woodward, 1889) (Fig. 5k–o); *Carcharhinus leucas* (Müller and Henle, 1839) (Fig. 5p–s); *Carcharhinus* cf. *C. limbatus* (Müller and Henle, 1839) (Fig. 5t–u); *Carcharhinus* cf. *C. perezi* (Poey, 1876) (Fig. 5v–w); *Carcharhinus* cf. *†C. priscus* (Agassiz, 1843) (Figs. 5x–z’, 6a–d); *†Isogomphodon acuarius* (Probst, 1879) (Fig. 6h–i); *†Negaprion eurybathrodon* (Blake, 1862) (Fig. 6j–n); *†Physogaleus contortus* (Gibbes, 1849) (Fig. 6o–r)] is the most diverse family represented in the Cocinetas assemblages (Fig. S5). Other less diverse group of carcharhiniforms are represented by Sphyrnidae Gill, 1872 [*†Sphyrna arambourgi* Cappetta, 1970 (Fig. 6s–v); *†Sphyrna laevis* (Cope, 1867) (Fig. 6w–z’)] and Hemipristidae Hasse, 1879 [*†Hemipristis serra* (Agassiz, 1835) (Fig. 4t–w)], the latter being the most abundant taxon of this group of sharks (Tables S1–S2). From the above referred taxa from the Cocinetas Basin, only *†N. eurybathrodon* shows a record from the early Miocene to the late Pliocene. Although taxonomic discussions are out the scope of this contribution, teeth of *†N. eurybathrodon* are indistinguishable from extant species *Negaprion brevirostris* (Poey, 1868), which also have been noted in the fossil record of the Americas (see Carrillo–Briceño et al., 2015a, table 2; 2016b, table 2). As there is no detailed revision supporting or rejecting the above assumption, just as Carrillo–Briceño et al. (2016a), we use *†N. eurybathrodon* (for fossil specimens) sustained by the principle of priority of the International Code of Zoological Nomenclature. In reference to the *Carcharhinus* spp. teeth (Fig. 6e–g), we have referred all specimens that are broken, eroded and without any diagnostic features for specific identification.

• **Rhinopristiformes Last, Séret and Naylor, 2016.** Two taxa of this group of batoids are represented in the Cocinetas assemblages (Fig. 9, Table 1, Fig. S5). One of them is represented by few isolated and indet. teeth of *Rhynchobatus* Müller and Henle, 1837 (Fig. 7a–i), which are recorded only for the Castilletes Formation (Table S1). Our *Rhynchobatus* sp. specimens resemble those from the Neogene of Venezuela and other locations of Tropical America (Carrillo–Briceño et al., 2016a; Aguilera et al., 2017a), however, we refrain at taxonomic identification at the species level of our specimens, because the range of dental variation in extant species is unknown, and little is known about fossil species from the Americas (Carrillo–Briceño et al., 2016a). The other taxon is represented by a fragment of rostrum and a few rostral denticles of indet. *Pristis* Linck, 1790 (Fig. 7j–m) from the Castilletes and Ware Formations (Table S1). As noted by Carrillo–Briceño et al. (2015b), rostral fragments and denticles are not diagnostic for accurate specific taxonomic determinations.

• **Myliobatiformes Compagno, 1973.** Represented by five taxa [*†Plinthicus stenodon* Cope, 1869 (Fig. 8u–x) and indet. teeth of *Dasyatis* Rafinesque, 1810 (Fig. 7n–u); *Aetobatus* Blainville, 1816 (Fig. 7v–x); *Aetomylaeus* Garman, 1913 (Fig. 8a–j); and *Rhinoptera* Cuvier, 1829 (Fig. 8k–t)], this group of batoids (Table 1) is the most abundant and the third most diverse elasmobranch representatives of the Cocinetas assemblages (Fig. 9, Tables S1–S2, Fig. S5). Teeth assigned to *Aetobatus* sp., *†P. stenodon* and *Dasyatis* sp. are scarce and only found in the Castilletes Formation and Patsúa assemblage (locality 290468) (Table S1). *Aetomylaeus* sp. is reported only in Jimol and Castilletes Formations, the locality 290468; whereas, *Rhinoptera* sp. has a record in the Cocinetas assemblages from the early Miocene to the late Pliocene, being the most abundant taxon (Tables S1–S2). More than 419 hardly identified and broken teeth without any diagnostic features for generic determination have



been assigned to Myliobatoidea indet. (Table S1), however, we do not rule out that these teeth could belong to *Aetomylaeus* or *Rhinoptera*.

## 4.2 Dietary preferences

Although extant representatives of the fossil elasmobranchs present in the Cocinetas assemblages exhibit a wide range of diets, four feeding preferences of benthic–pelagic predators and filter feeders can be noted (Table S3). For the Jimol Formation, the most diverse feeder group is that of the piscivorous (Fig. 10), dominated by carcharhiniforms, lamniforms, and a minority of squaliforms representatives (Table S3). The second most diverse durophagous/cancritrophic group (mollusk, crustacean, coral feeders), which is the most abundant in the Jimol assemblages (Fig. 10) and dominated mainly by myliobatiforms (Table S3). †*Carcharocles* sp. is the only possible eurytrophic/sarcophagous (diverse prey source: fishes, reptiles, birds, mammals, etc.) representatives in this unit. Like the Jimol Formation, the assemblage of the Castilletes Formation shows a diversity dominated by piscivorous representatives (Fig. 10), with an abundance dominated by the durophagous/cancritrophic group (represented in the Castilletes assemblage mainly by myliobatiforms) (Table S3). In the Castilletes assemblage, †*Carcharocles megalodon* and †*Galeocerdo mayumbensis* are the only representatives of the eurytrophic/sarcophagous and the filter feeders (diet based mainly on planktonic microorganisms) is represented only by the mobulid †*Plinthiscus stenodon*, being the less abundant and diverse groups of the Castilletes assemblages (Fig. 10, Table S3). In contrast with the assemblages of the Jimol and Castilletes Formations, the Patsúa assemblage (localities 290468 and 290472) is characterized by a higher diversity and abundance of piscivorous followed by durophagous/cancritrophic diets (Fig. 10, Table S3). Eurytrophic/sarcophagous and filter feeders also are represented in the localities 290468 and 290472 (Fig. 10, Table S3). In contrast with elasmobranch diversity of the Jimol, Castilletes and Patsúa assemblages, the assemblage from the Ware Formation shows a low diversity and abundance (Fig. 10, Tables S1–S3).

## 4.3 Stable isotope analysis of shark teeth

The  $\delta^{18}\text{O}_{\text{PO}_4}$  values of the 73 shark teeth ranged from 15.7 ‰ to 21.7 ‰ (VSMOW, Table 2). Samples were grouped in accordance with their geochronological position in the stratigraphic column (Fig. 11). Layers containing few teeth and/or very close to adjacent levels were averaged for better representation and reliability of the  $\delta^{18}\text{O}_{\text{PO}_4}$  values within the same beds is up to 4 ‰ (e.g., the highest is in the Patsúa assemblage, locality 290468), however, a large variation is not exclusively found in levels where many samples were analyzed (e.g., Castilletes, locality 390093).

Several teeth were available from the Patsúa assemblage ( $n = 26$ ) and these were carefully interpreted since the age of the assemblage is unknown. Still, the ecological data from the seven shark species present on both localities (290468, 290472) can be discussed. The average isotope data from the two stratigraphically uncertain Patsúa levels are very similar ( $t$  test:  $t(24) = 0.275$ ;  $p > 0.78$ ), hence can be considered as one whole dataset.

Regarding the Castilletes Formation, the mean  $\delta^{18}\text{O}_{\text{PO}_4}$  values do differ along the sedimentary profile (Fig. 11a). Isotopic values increase towards the middle Miocene (localities 130024, 430202:  $20.4 \pm 1.0$  ‰,  $n = 5$ ), but then decrease in the following intervals (locality 390093:  $18.7 \pm 1.3$  ‰,  $n = 4$ ). However, importantly when pairwise Student's  $t$  tests are performed following



stratigraphic orders then no significant differences are observed between the sample batches that are following each other.

Still, the top youngest data of the Castilletes Formation gives the lowest average  $\delta^{18}\text{O}_{\text{PO4}}$  value for this lithostratigraphic unit.

When Tukey's pairwise comparison is applied to the data of the Castilletes layers, the top bed is significantly different from the two middle beds of 290438 and 430202–130024.

- 5 In the youngest unit of the Ware Formation low  $^{18}\text{O}/^{16}\text{O}$  were measured for the bull shark *C. leucas* specimens (CL.1–CL.12:  $17.6 \pm 1.1 \text{‰}$ ,  $n = 12$ , Fig. 11a). Interestingly, when the average data of the Ware beds is compared to the youngest bed of the Castilletes Formation they do not show significant differences ( $t$  test:  $t(16) = 0.748$ ,  $p > 0.46$ ).

From the Jimol Formation only two teeth were analyzed, but their average is undistinguishable from that of the overall average value of both the Castilletes and Patsúa assemblages. Three larger assemblages of Patsúa, Castilletes and Ware

- 10 can be compared on a boxplot (Fig. 11b). The averages of the first two are undistinguishable; however, both are significantly different from that of Ware dataset. There is one outlier from each of the Patsúa and Castilletes fauna which are teeth of *†Carcharocles chubutensis* (290468) and *†Megapriion eurybathrodon* (390093) respectively.

## 5 Discussion

### 5.1 Diversity and biostratigraphy significance

- 15 Of the elasmobranch assemblages described here from the Cocinetas Basin ( $\sim 30$  taxa) at least half of the fauna is characterized by extinct taxa (Table 1). With the exception of *Alopias* cf. *†A. exigua* (Fig. 4n–q, Tables S1–S2), representing the first record of this taxon from Tropical America, the remaining taxa from the Cocinetas assemblages have been found in other Neogene deposits of the Americas (e.g., Kruckow and Thies, 1990, Purdy et al., 2001, Aguilera and Lundberg, 2010, Cappetta, 2012, Carrillo–Briceño et al., 2014, 2015b, 2016a, Landini et al., 2017; and references therein). From the Cocinetas assemblages, 17
- 20 shark taxa (*Nebrius* sp., *†P. benedenii*, *†C. chubutensis*, *†C. megalodon*, *Alopias* cf. *†A. exigua*, *†A. retroflexus*, *†G. mayumbensis*, *†C. ackermannii*, *Carcharhinus* cf. *C. brachyurus*, *C. leucas*, *Carcharhinus* cf. *C. limbatus*, *Carcharhinus* cf. *C. perezi*, *Carcharhinus* cf. *†C. priscus*, *†I. acuarius*, *†N. eurybathrodon*, *†P. contortus*, and *†S. arambourgi*) and seven batoids (*Rhynchobatus* sp., *Pristis* sp., *Dasyatis* sp., *Aetobatus* sp., *Aetomylaeus* sp., *Rhinoptera* sp., and *†P. stenodon*) are reported for the first time from Colombian Neogene deposits. The elasmobranch assemblages of the Jimol and Castilletes Formations and the
- 25 Patsúa assemblage, share certain faunal similarity with the fauna previously described from the underlying Uitpa Formation (e.g., Carrillo–Briceño et al., 2016b).

- The elasmobranch fauna of the Cocinetas assemblages show a clear differentiation in paleodiversity between the geological units (see Fig. S5). The Castilletes Formation and Patsúa assemblage are the most diverse units of the overall assemblages from the Cocinetas Basin (Tables S1–S2, Fig. S5). In contrast, the Jimol and Ware Formations are the least diverse units (Tables S1–S2, Fig. S5). These paleodiversity differences between the geological units of the Cocinetas Basin, in fact, could be attributable to 1) less intensive sampling, also especially to the less systematic sieving of all studied localities (see Material and Methods section) and/or 2) different lithologic, taphonomic and preservational conditions, without leaving aside the direct response to the paleoenvironmental and paleoecological conditions (see the below Paleoenvironments of the Cocinetas Basin





subsection). The Castilletes Formation and Patsúa assemblage preserve one of the most diverse elasmobranch faunas known from the early–middle Miocene of the Americas (Fig. S6).

Of biostratigraphic significance to the elasmobranch fauna of the Cocinetas assemblages is the record of †*C. megalodon*, †*G. mayumbensis*, †*C. gibbesii* and †*C. ackermannii*. The presence of †*C. megalodon* in late Burdigalian sediments of the Castilletes Formation (localities 130024, 290824 and 430202, Fig. 2b), confirms the presence of this species during late early Miocene, an assertion that has been discussed previously for other American localities by Carrillo–Briceño et al. (2016a, p. 21, and references therein). The age of the above referred localities of the Castilletes Formation have been estimated by  $^{87}\text{Sr}/^{86}\text{Sr}$  isotope stratigraphy (Hendy et al., 2015, fig. 16, tab. 6). In the case of †*C. chubutensis*, this species is restricted to the Patsúa assemblage, which suggests that the previous specimens of †*Carcharocles* sp. referred to the Uitpa Formation by Carrillo–Briceño et al. (2016b, fig. 4.12–13), could belong to the former species. †*Carcharhinus gibbesii* in Jimol Formation, as well as the Patsúa assemblage is also present in the Burdigalian sediments of the Cantaure Formation in Venezuela (Carrillo–Briceño et al., 2016a). These records from the late part of early Miocene are notable as the last appearance of †*C. gibbesii* has been regarded as Aquitanian (Carrillo–Briceño et al., 2016b). †*Carcharhinus ackermannii* is reported here from the Burdigalian sediments of the Castilletes Formation and Patsúa assemblage (Tables S1–S2). However, previously it has been exclusively reported from the early Miocene Cantaure (Venezuela) and Pirabas (Brazil) Formations (Santos and Travassos, 1960; Carrillo–Briceño et al., 2016a; Aguilera et al., 2017a). Due to the scarce fossil record of this extinct species, it is difficult to propose a determined biostratigraphic and geographical range. The absence of this species in other geological units, younger than early Miocene in the Americas or other regions, could suggest that this species is restricted to the early Miocene.

In reference to †*Galeocerdo mayumbensis*, still little is known about its distribution and chronostratigraphy, which has been figured in the scientific literature only from a few early Miocene localities of Africa (Darteville and Casier, 1943; Andri-anavalona et al., 2015; Argyriou et al., 2015) and South America (Carrillo–Briceño et al., 2016a; Aguilera et al., 2017a). Some taxonomical misidentifications also include †*G. mayumbensis* from the early Miocene of Africa (Cook et al., 2010, fig. 3c), Asia (Patnaik et al., 2014, plate. 2.12), Central America (Pimiento et al., 2013, fig. 4b), and South America (Santos and Travassos, 1960, fig. 3; Reis, 2005, fig. 6; Costa et al., 2009, fig. 1e). There is not a consensus about unpublished †*G. mayumbensis* teeth (labelled/collections) and their localities in the eastern coast of the US, which questionably have been assigned to a middle to late Miocene and Pliocene age. The absence of †*G. mayumbensis* in locations younger than early Miocene (with the exception of the above record from ), and the tendency of the overall stratigraphical distribution of †*G. mayumbensis*, including the new referred record of the Castilletes Formation and the Patsúa assemblage (Table S1), could suggest that this extinct tiger shark was probably restricted to the early Miocene a widespread distribution in tropical environments.

## 5.2 Paleoenvironments of the Cocinetas Basin

### 5.2.1 Faunal assemblage evaluation

The Neogene sedimentary sequence of the Cocinetas Basin has been characterized by a transition from a shallow marine to a fluvio–deltaic paleoenvironment (e.g., Moreno et al., 2015; Pérez–Consuegra et al., 2018). The geological and paleontological





evidence (mainly based on mollusks; Hendy et al., 2015) of Jimol Formation indicate depositional conditions characterized by a shallow marine environment (inner shelf depth < 50 m). The elasmobranch fauna from the Jimol Formation is characterized by a higher diversity of carchariniforms, lamniforms, and piscivorous species (Figs. 9–10). However, in this assemblage, the durophagous/cancritrophic representatives are the most abundant, which could support habitat and feeding preferences of this later group, related mainly with the abundance of potential prey in marginal marine and brackish environments (see Hendy et al., 2015). The elasmobranch fauna from the Castilletes Formation is mainly characterized by carchariniforms and myliobatiforms, where more than the 80% of the abundance correspond to species of durophagous/cancritrophic feeding preferences (Figs. 9–10). Extant representatives, as well as fossils of the elasmobranch species of the Castilletes Formation, suggest that these taxa are closely related to marginal marine and brackish environments (see Carrillo–Briceño et al., 2015a, 2015b, 2016a and references therein). Abundant marine and terrestrial fossils such as plants, mollusks, crustaceans, fishes, turtles, crocodylians, and mammals in the Castilletes Formation (Aguilera et al., 2013; Cadena and Jaramillo, 2015; Hendy et al., 2015; Moreno et al., 2015; Amson et al., 2016; Moreno–Bernal et al., 2016; Aguirre–Fernández et al., 2017), suggest a depositional environment associated to a shallow marine to fluvio–deltaic environment, similar to those habitats that characterize the Neogene Urumaco sequence in Western Venezuela (Carrillo–Briceño et al., 2015b). Similar also to the elasmobranch fauna from the Urumaco sequence (Carrillo–Briceño et al., 2015b), durophagous/cancritrophic taxa with capacity to triturate hard shells (*Aetomylaeus*, *Rhinoptera* and *Myliobatoidea* indet.) are the most abundant elasmobranch remains in the Castilletes Formation. This could be related to the abundance of their potential benthic prey of mollusks and crustaceans, as well as the presence of †*Carcharocles megalodon* in the brackish paleoenvironments of the Urumaco sequence (Aguilera and de Aguilera, 2004; Carrillo–Briceño et al., 2015b), its presence in marine/fluvio–deltaic environment of the Castilletes Formation, support possible physiological capabilities that allowed it to withstand the variations in salinity in estuarine and possibly river mouth habitats (see Carrillo–Briceño et al., 2015b, p. 24). The Patsúa assemblage, especially the locality 290468, is characterized by a high diversity and abundance of carchariniforms, lamniforms, and piscivorous species (Figs. 9–10). The presence of the lamniform *Isurus* cf. *Loxyrinchus*, the otodontid †*Paratodus edenii*, the alopids *Urolophus* cf. †*A. eximia* and †*Anotodus retroflexus*, and the pristigasteriform *Pristiophorus* sp., could suggest a shallow marine environment. It is supported by associated bony fishes (Acanthuridae, Labridae, Scaridae, Sparidae, Sphyrnidae, Balistidae and Diodontidae, (see Fig. S7), corals, bryozoans, echinoderms and mollusks, suggesting a subtidal marine environment with limited influence from major freshwater input (see Hendy et al., 2015). The mollusks and echinoderms, in part, are distinctive from those of the Jimol and Castilletes Formations that have been extensively sampled in central and eastern parts of the Cocinetas Basin. The Patsúa assemblage preserves a diversity of species that covers fully marine sandy bottom and reef habitats (e.g., *Spondylus*), while freshwater and brackish water species are absent. Other notable fossils include abundant fragments of wood that contain *Teredolites* (traces of *Teredo* or shipworm), *Aturia* (nautiloid), which presumably were washed up onto a more exposed coastal setting, an isolated and incomplete Odontoceti tooth also was recorded in the locality 290472 (specimen MUN–STRI–44517).

In contrast with the diverse early–middle Miocene elasmobranch assemblages of the Jimol and Castilletes Formations, the Patsúa assemblage, the fauna of the late Pliocene Ware Formation is low in diversity and abundance (Fig. 9, Tables S1–S3, Fig. S5). In the same conglomeratic–fossiliferous layer where the elasmobranchs come from, abundant vertebrates, turtles,



crocodilians, and mammals, also have been found (Moreno et al., 2015; Amson et al., 2016; Moreno-Bernal et al., 2016; Pérez et al., 2016). A fluvio-deltaic depositional environment has been described for this basal section of the Ware Formation (Moreno et al., 2015; Pérez-Consuegra et al., 2018). The sharks *Carcharhinus leucas* and †*Negaprion eurybathrodon*, as well as the batoids *Pristis* sp. and *Rhinoptera* sp., are the only representative species of this unit (Table S1). These species are able to inhabit both marine and brackish environments (see Carrillo-Briceño et al., 2015b, for details). *Carcharhinus leucas* and *Pristis* also have the capacity to enter into rivers and live permanently in freshwater lakes (Voigt and Weber, 2011; Faria et al., 2013).

### 5.3 The shark bioapatite and paleosalinity

Samples with  $\delta^{18}\text{O}_{\text{PO}_4}$  values less than 18.4 ‰ are likely to have been formed in waters other than exclusively marine ( $\delta^{18}\text{O}_w = 0$  ‰), since the paleotemperatures calculated from much lower  $\delta^{18}\text{O}_{\text{PO}_4}$  are too high to represent typical shark habitats. However, fishes which form their bioapatite in a freshwater influenced settings with less than 0 ‰  $\delta^{18}\text{O}_w$  values (e. g., rivers, lakes) also have lower  $\delta^{18}\text{O}_{\text{PO}_4}$  values at the same temperature of formation (Longinelli and Nuti, 1973a; Kolodny et al., 1983; Kocsis et al., 2007; Fischer et al., 2013a; Leuzinger et al., 2015). Therefore, samples with a low  $\delta^{18}\text{O}_{\text{PO}_4}$  values may indicate the presence of brackish-like environments, due to the mixing of seawater with, for example, river water. The shark tooth  $\delta^{18}\text{O}_{\text{PO}_4}$  values can hence be used to estimate paleoenvironmental and relative salinity conditions for the Patsúa assemblage and two of the three studied formations: Castilletes and Ware (Fig. 11).

• **Patsúa assemblage.** The samples from the Patsúa assemblage have not been separately dated but the teeth from this locality were in situ and their isotopic composition should represent the sediment deposited somewhere within the Burdigalian and Langhian periods. These shark teeth had predominantly "marine" isotopic compositions with one low  $\delta^{18}\text{O}_{\text{PO}_4}$  value measured from a †*Carcharocles chubutensis* specimen (CC.4:  $17.4 \pm 0.3$  ‰, Table 2, Fig. 11b). This composition is typical for brackish waters, was measured for an extinct species, which occupies an analogous habitat to the recent great white shark (*Carcharodon carcharias*). Of the isotopic data of extant and fossil species of this group are characteristic of cold waters, because of its long oceanic migrations and formation of bioapatite in such cold settings (Vennemann et al., 2001; Amiot et al., 2008; Ebert et al., 2013; Aguilera et al., 2017a). Statistical comparisons against the available datasets demonstrate this assemblage as distinguishable from Castilletes Formation (Fig. 11b). Possibly these paleoenvironments were similar and based on the  $\delta^{18}\text{O}_{\text{PO}_4}$  values, the Patsúa assemblage was deposited mainly under marine conditions. Nevertheless, additional sampling and a precise chronological dating of this assemblage are necessary to improve the paleo-interpretation of its isotopic data.

• **Castilletes Fm.** The sedimentary sequence of the Cocinetas Basin is described as a transition from a shallow marine to a fluvio-deltaic paleoenvironment. Like the results from the Patsúa assemblage the  $\delta^{18}\text{O}_{\text{PO}_4}$  values are predominantly marine, besides a single tooth of †*Negaprion eurybathrodon* (NG.14:  $16.7 \pm 0.2$  ‰, Fig. 11a, b), a species from the same genus of the modern lemon shark (*Negaprion brevirostris*). Extant individuals of this group inhabit marine inshore areas and commonly migrate through enclosed bays or river mouths, supporting a freshwater influence on the isotopic composition measured. In fact, we expected more samples covering the 'brackish' range, since the fossil assemblage of Castilletes Formation suggests a deltaic influence at this interval (Moreno et al., 2015). Paleobathymetric estimations using mollusk invertebrates have shown that in the Castilletes Formation, the paleoenvironments were alternating quickly along the stratigraphic succession, changing between a



marine setting to a freshwater influenced environment and vice-versa (Hendy et al., 2015). The  $\delta^{18}\text{O}_{\text{PO}_4}$  mean values show a minor increase from the base towards the middle section of Castilletes ( $20.4 \pm 1.0 \text{‰}$ ,  $n = 5$ , Fig. 11a), decreasing thereafter to the lowest mean value in this formation ( $18.7 \pm 1.3 \text{‰}$ ,  $n = 4$ ). Possibly this indicates regional changes in the paleoenvironment of shark habitat, e.g., marine to estuarine, but since the overall deviation is overlapping between the localities, more samples would be required to refine such topic fluctuation. Nevertheless, the overall shark isotope data represent those parts of Castilletes Formation when fully marine conditions existed in the region. The few outlier specimens (Fig. 11a, b) clearly indicate the near presence of rather brackish conditions which some sharks ventured. This interpretation is in agreement with the higher resolution mollusks from the region (Hendy et al., 2015).

• **Ware Fm.** The isotope data are significantly different from the results from Patsúa and Castilletes (except via locality 390092, Fig. 11a, b). The  $\delta^{18}\text{O}_{\text{PO}_4}$  values are generally lower in this formation, especially for the bull sharks (*Carcharhinus leucas*, CL.12:  $17.6 \pm 1.1 \text{‰}$ ,  $n = 12$ ). This euryhaline species, like the lemon shark, also inhabits in marine inshore zones and occasionally migrates into brackish environments. However, bull sharks are currently well recognized for their ability to persist through coastal sub-environments with brackish conditions, as individuals can also swim hundreds of meters upstream even in freshwater (Ebert et al., 2013). The isotopic range from Ware sharks are in a agreement with the fluvio-deltaic paleoenvironment of deposition described for this formation (Moreno et al., 2015; Pérez-Consuegra et al., 2018). The two samples of lemon shark related have  $\delta^{18}\text{O}_{\text{PO}_4}$  values which probably have been formed under distinct marine conditions rather than under fluvial influence (NG.15:  $20.7 \pm 0.1 \text{‰}$ ; NG.16:  $20.5 \pm 0 \text{‰}$ ). The worn appearances of the teeth from the conglomerate beds of the Ware Formation indicate longer transport and hence also probably a mixed time-averaged fauna originated from different layers of a wider fluvio-deltaic system. Therefore, while the bull sharks reflect clear fluvial conditions, the lemon shark remain may have derived from layers originally deposited in the delta or nearby shallow coastal marine beds.

The bull shark teeth are also smaller compared to other specimens (and species) employed in this study. Modern representatives of adult bull sharks normally have anterior teeth around 2 cm in height, a size considerably bigger than our sampled teeth ( $< 1 \text{ cm}$ , Fig. S8). When taking into consideration more curved and possibly posterior teeth of adult specimens, we estimate that most of our bull shark  $\delta^{18}\text{O}_{\text{PO}_4}$  data were obtained from juvenile and subadult individuals. In previous stable isotope investigations, only samples from young specimens from Lake Nicaragua provided  $\delta^{18}\text{O}_{\text{PO}_4}$  values characteristic of a brackish condition (Kocsis et al., 2015; Aguilera et al., 2017a). Nevertheless, our results highlight the ecological importance of the paleoenvironments from Cocinetas Basin for the bull sharks, even suggesting the usage of this coastal zone as a paleonursery habitat. Today, young specimens of this group are known for using brackish lagoons as a nursery ground (e.g., Maracaibo Lake, Rodríguez, 2001, Tavares and Sánchez, 2012). Moreover, the predominant brackish-like  $\delta^{18}\text{O}_{\text{PO}_4}$  values in this species may imply that at least since the late Pliocene they were already adapted to live in waters with reduced salinity and face the constant environmental changes (global and regional) of their paleohabitats.



## 6 Conclusions

- A diverse elasmobranch fauna containing 30 taxa of sharks and rays was identified, with the most diverse groups being respectively Charhiformes and Lamniformes. This assemblage seems to represent the paleoenvironments described for the fossiliferous formations of Cocinetas Basin (Jimol, Castilletes and Ware).
- A distinctive assemblage is reported from undifferentiated facies of the Jimol and Castilletes Formation, which represents a subtidal marine environment with limited freshwater influence.
  - The biogenic phosphate  $\delta^{18}\text{O}_{\text{PO}_4}$  values of 73 shark teeth were evaluated for the sedimentary sequence of Cocinetas Basin. The isotopic data was used to estimate the paleosalinity (e.g., marine vs brackish vs freshwater) and corroborated the paleoenvironments described for Castilletes and Ware formations.
- A predominant brackish-like  $\delta^{18}\text{O}_{\text{PO}_4}$  value was measured for bull sharks, which are probably anadromous, suggesting that at least since the late Pliocene this species was already well adapted to migrate through conditions with reduced salinity.
  - More samples and additional proxies are recommended to refine our interpretations. Nevertheless, this multidisciplinary study certainly complements further the knowledge about the paleoenvironmental context and evolution of Tropical America.

*Competing interests.* The authors have declared that no competing interests exist

- 15 *Acknowledgements.* This work was supported by Swiss National Science Foundation SNF 31003A-149605 to MRSV and by the Smithsonian Tropical Research Institute (National Geographic Society, Anders Foundation, Gregory D. and Jennifer Walston Johnson, 1923 Fund, Universidad del Norte, and National Science Foundation EAR 0957679 to Carlos Jaramillo). The authors wish to especially thank to Henri Cappetta, Sylvain Adnet, Loic Costeur, Rene Kindlimann, Gustavo Ballen and the Wayuu communities of the Alta Guajira for their generous and important counseling, permission for collection revision and collaboration. Participants of fieldwork in Alta Guajira (2009–2014) are
- 20 thanked for their assistance in collection of samples. Special thanks to the Center for Microscopy and Image Analysis of the University of Zurich for their assistance and support performing the scanning electron microscopy analysis. Z. Luz would like to thanks Thiago Nascimento for all technical assistance to build the manuscript file. Last but not least, we are thankful to the Alcaldía Bolivariana de Urumaco, the Universidad Experimental Francisco de Miranda; Mapuka Museum of Universidad del Norte (Barranquilla, Colombia), Natural History Museum of Basel (Switzerland), Paleontological collection of the Institut des Sciences de l' Evolution, University of Montpellier (France)
- 25 and Palaeontological Institute and Museum at the University of Zurich for their valuable assistance and for access to comparative material.



## References

- Agassiz, L.: Recherches sur les poissons fossiles, Neuchâtel: Petitpierre, 1835–45.
- Agassiz, L.: Remarks on a new species of skate from the Sandwich islands, *Proceedings of the Boston Society of Natural History*, 6, 385, 1958.
- 5 Aguilera, O.: Peces fósiles del Caribe de Venezuela, Gorham Printing, Washington, 2010.
- Aguilera, O. and de Aguilera, D. R.: Giant-toothed white sharks and wide-toothed mako (Lamnidae) from the Venezuela Neogene: Their role in the Caribbean, shallow-water fish assemblage, *Caribbean Journal of Science*, 40, 368–382, 2004.
- Aguilera, O. and Lundberg, J. G.: Venezuelan Caribbean and Orinocoan Neogene fish, in: *Urumaco and Venezuelan Paleontology*, edited by Sánchez-Villagra, M. R., Aguilera, O., and Carlini, F., p. 129–152, Indiana Press University, Bloomington, 2010.
- 10 Aguilera, O., Moraes-Santos, H., Costa, S., Ohe, F., Jaramillo, C., and Nogueira, A.: Ariid sea catfishes from the coeval Pirabas (Northeastern Brazil), Cantaure, Castillo (Northwestern Venezuela), and Castilletes (North Colombia) formations (Early Miocene), with description of three new species, *Swiss Journal of Palaeontology*, 132, 45–68, 2013.
- Aguilera, O., Luz, Z., Carrillo-Briceño, J. D., Kocsis, L., Vennemann, T., de Toledo, P. M., Nogueira, A., Amorim, K. B., Moraes-Santos, H., Polck, M. R., Ruivo, M. L., Linhares, A. P., and Monteiro-Neto, C.: Neogene sharks and rays from the Brazilian ‘Blue Amazon’, *PLoS One*, 12, e0182740, <https://doi.org/10.1371/journal.pone.0182740>, 2017a.
- 15 Aguilera, O., Silva, G. O. A., Lopes, R. T., Machado, A. S., and dos Santos, T. M.: Neogene Proto-Caribbean porcupinefishes (Diodontidae), *PLoS One*, 12, e0181670, <https://doi.org/10.1371/journal.pone.0181670>, 2017b.
- Aguirre-Fernández, G., Carrillo-Briceño, J. D., Sánchez, R., Amson, E., and Sánchez-Villagra, M. R.: Fossil Cetaceans (Mammalia, Cetacea) from the Neogene of Colombia and Venezuela, *Journal of Mammalian Evolution*, 24, 71–90, 2017.
- 20 Ameghino, F.: L’âge des formations sédimentaires de Patagonie, *Anales de la Sociedad Científica Argentina*, 51, 65–91, 1901.
- Amiot, R., Göhlich, U. B., Lécuyer, C., de Muizon, C., Cappetta, H., Hérán, M.-A., and Martineau, F.: Oxygen isotope compositions of phosphate from middle Miocene–early Pliocene marine vertebrates of Peru, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 264, 85–92, <https://doi.org/10.1016/j.palaeo.2008.04.001>, 2008.
- Amson, E., Carrillo, J. D., and Jaramillo, C.: Neogene sloth assemblages (Mammalia, Pilosa) of the Cocinetas basin (la Guajira, Colombia): implications for the Great American Biotic Interchange, *Palaeontology*, 59, 563–582, 2016.
- 25 Andrianavalona, T. H., Ramihangihajason, T. N., Rasoamiaramanana, A., Ward, D. J., Ali, J. R., and Samonds, K. E.: Miocene shark and batoid fauna from Nosy Makamby (Mahajanga Basin, Northwestern Madagascar), *PLoS One*, 10, e0129444, 2015.
- Applegate, S. P.: A revision of the higher taxa of Orectoloboids, *Journal of the Marine Biological Association of India*, 14, 743–751, 1972.
- Argyriou, T., Cook, T. D., Muftah, A. M., Pavlakis, P., Boaz, N. T., and Murray, A. M.: A fish assemblage from an early Miocene horizon from Jabal Zaltan, Libya, *Journal of African Earth Sciences*, 102, 86–101, 2015.
- 30 Bacon, C. D., Silvestro, D., Jaramillo, C., Smith, B. T., Chakrabarty, P., and Antonelli, A.: Biological evidence supports an early and complex emergence of the Isthmus of Panama, *Proceedings of the National Academy of Sciences*, 112, 6110–6115, 2015.
- Barrick, R. E., Fischer, A. G., and Bohaska, D. J.: Paleotemperatures versus sea level: oxygen isotope signal from fish bone phosphate of the Miocene Calvert Cliffs, Maryland, *Paleoceanography*, 8, 845–858, <https://doi.org/10.1029/93PA01412>, 1993.
- 35 Berg, L. S.: A classification of fish-like vertebrates, *Bulletin of the Academy of Sciences of the USSR, Division of Chemical Science*, 4, 1277–1280, 1937.
- Berg, L. S.: *System der Rezenten und Fossilen Fischartigen und Fische*, Deutscher Verlag Wissensch., Berlin, 1958.



- Billups, K. and Schrag, D. P.: Paleotemperatures and ice volume of the past 27 myr revisited with paired Mg/Ca and  $^{18}\text{O}/^{16}\text{O}$  measurements on benthic foraminifera, *Paleoceanography*, 17, 3–11, <https://doi.org/10.1029/2000PA000567>, 2002.
- Blainville, H. M. D.: Prodrome d'une nouvelle distribution systematique du regne animal, *Bulletin de la Société Philomathique de Paris*, 8, 113–124, 1816.
- 5 Blake, C. C.: Shark's teeth at Panama, *Geologist*, 5, 316, 1862.
- Bonnaterre, J. P.: Tableau encyclopédique et méthodique des trois règnes de la nature. Ichthyologie, Panckoucke, Paris, 1788.
- Bor, T. J., Reinecke, T., and Verschuere, S.: Miocene Chondrichthyes from Winterswijk – Miste, the Netherlands, *Palaeontos*, 21, 1–136, 2012.
- Cadena, E. and Jaramillo, C.: Early to middle Miocene turtles from the northernmost tip of South America: Giant Testudinids, Chelids, and  
10 Podocnemidids from the Castilletes Formation, Colombia, *Ameghiniana*, 52, 188–203, 2015.
- Cappetta, H.: Les Sélaciens du Miocène de la région de Montpellier, *Palaeovertebrata, Mémoire Extraordinaire*, p. 1–139, 1970.
- Cappetta, H.: Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth, vol. 3E, Verlag Dr. Friedrich Pfeil, Munich, 2012.
- Carrillo–Briceño, J. D., Aguilera, O., and Rodríguez, F.: Fossil Chondrichthyes from the central eastern Pacific Ocean and their paleoceanographic significance, *Journal of South American Earth Sciences*, 51, 76–90, 2014.
- 15 Carrillo–Briceño, J. D., de Gracia, C., Pimiento, C., Aguilera, O., Kindlimann, R., Santamarina, P., and Jaramillo, C.: A new late Miocene chondrichthyan assemblage from the Chagres Formation, Panama, *Journal of South American Earth Sciences*, 60, 56–70, 2015a.
- Carrillo–Briceño, J. D., Maxwell, E., Aguilera, O., Sánchez, R., and Sánchez–Villagra, M. R.: Sawfishes and other elasmobranch assemblages from the Mio–Pliocene of the South Caribbean (Uruguay Sequence, Northwestern Venezuela), *PLoS One*, 10, e0139230, 2015b.
- Carrillo–Briceño, J. D., Aguilera, O., de Gracia, C., Aguirre–Fernández, G., Kindlimann, R., and Sánchez–Villagra, M. R.: An early Neogene  
20 elasmobranch fauna from the southern Caribbean (Western Venezuela), *Palaeontologia Electronica*, 19.2.27A, 1–32, 2016a.
- Carrillo–Briceño, J. D., Argyriou, T., Zapata, V., Kindlimann, R., and Jaramillo, C.: A new early Miocene (Aquitania) Elasmobranchii assemblage from the Guajira Peninsula, Colombia, *Ameghiniana*, 53, 77–99, 2016b.
- Casier, E.: Contribution à l'étude des poissons fossiles des Antilles, *Mémoire Suisse de Paléontologie*, 74, 1–95, 1958.
- Casier, E.: Sur la faune ichthyologique de la Formation de Bissex Hill et de la Série océanique, de l'île de la Barbade, et sur l'âge de ces  
25 formations, *Eclogae Geologicae Helveticae*, 59, 493–516, 1966.
- Coates, A. G. and Stallard, R. F.: How old is the Isthmus of Panama?, *Bulletin of Marine Sciences*, 89, 801–813, 2013.
- Compagno, L. J. V.: Interrelationships of living elasmobranchs, in: *Interrelationships of fishes*, edited by Greenwood, P. H., Miles, R. S., and Patterson, C., p. 15–61, Academic Press, London, 1973.
- Compagno, L. J. V.: Appendix 1: Global Checklist of living Chondrichthyan Fishes, in: *Sharks, rays and chimaeras: The status of the  
30 chondrichthyan fishes*, edited by Fowler, S. L., Cavanagh, R. D., Camhi, M., Burgess, G. H., Cailliet, G. M., Fordham, S. V., Simpfendorfer, C. A., and Musick, J. A., p. 401–423, IUCN – The World Conservation Union, Oxford, UK, 2005.
- Compagno, L. J. V., Dando, M., and Fowler, S. L.: *Sharks of the World*, Princeton University Press, Princeton, 2005.
- Cook, T. D., Murray, A. M., Simons, E. L., Attia, Y. S., and Chatrath, P.: A Miocene selachian fauna from Moghra, Egypt, *Historical Biology*, 22, 78–87, 2010.
- 35 Cope, E. D.: An addition to the vertebrate fauna of the Miocene period, with a synopsis of the extinct Cetacea of the United States, *Proceedings of the Academy of Natural Sciences of Philadelphia*, 19, 138–156, 1867.
- Cope, E. D.: Descriptions of some extinct fishes previously unknown, *Proceedings of the Boston Society of Natural History*, 12, 310–319, 1869.





- Cortés, E., Papastamatiou, Y. P., Carlson, J. K., Ferry–Graham, L., and Wetherbee, B. M.: An overview of the feeding ecology and physiology of elasmobranch fishes, in: *Feeding and digestive functions in fishes*, edited by Cyrino, J. E. P., Bureau, D. P., and Kapoor, B. G., p. 393–443, Science Publishers, Florida, 2008.
- Costa, S. A. F., Richter, M., de Toledo, P. M., and Moraes–Santos, H.: Shark teeth from Pirabas Formation (lower Miocene), northeastern Amazonia, Brazil, *Boletim do Museu Paraense Emílio Goeldi*, 4, 221–230, 2009.
- 5 Cuvier, G. L. C. F. D.: *Le règne animal, distribué d’après son organisation, pour servir de base à l’histoire naturelle des animaux et d’introduction à l’anatomie comparée*, l’Imprimerie de A. Belin, Paris, Déterville, 2 edn., 1829.
- Dartevelle, E. and Casier, E.: Les poissons fossiles du Bas–Congo et des régions voisines, *Annales du Musée du Congo Belge, Série A (Minéralogie Géologie, Paléontologie)*, 2, 1–200, 1943.
- 10 Dettman, D. L., Kohn, M. J., Quade, J., Ryerson, F. J., Ojha, T. P., and Hamidullah, S.: Seasonal stable isotope evidence for a strong Asian monsoon throughout the past 10.7 m.y, *Geology*, 29, 31–34, 2001.
- Ebert, D. A. and Stehmann, M. F. W.: *Sharks, batoids, and chimaeras of the North Atlantic*, Food and Agriculture Organization of the United Nations, Roma, 2013.
- Ebert, D. A., Fowler, S. L., Compagno, L. J. V., and Dando, M.: *Sharks of the world*, Wild Nature Press, Plymouth, 2013.
- 15 Faria, V. V., Mcdavitt, M. T., Charvet, P., Wiley, T. R., Simpfendorfer, C. A., and Naylor, G. J. P.: Species delineation and global population structure of Critically Endangered sawfishes (Pristidae), *Zoological Journal of the Linnean Society*, 167, 136–164, 2013.
- Farris, D. W., Jaramillo, C., Bayona, G., Restrepo–Moreno, S. A., Montes, C., Cardona, A., Mora, A., Speakman, R. J., Glascock, M. D., and Valencia, V.: Fracturing of the Panamanian Isthmus during initial collision with South America, *Geology*, 39, 1007–1010, 2011.
- Fischer, J., Voigt, S., Franz, M., Schneider, J. W., Joachimski, M., Tichomirowa, M., Götze, J., and Furrer, H.: Palaeoenvironments of the late Triassic Rhaetian Sea: implications from oxygen and strontium isotopes of hybodont shark teeth, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 353–355, 60–72, 2012.
- 20 Fischer, J., Schneider, J. W., Hodnett, J.-P. M., Elliott, D. K., Johnson, G. D., Voigt, S., Joachimski, M., Tichomirowa, M., and Götze, J.: Stable and radiogenic isotope analysis on shark teeth from the early to the middle Permian (Sakmarian – Roadian) of the southwestern USA, *Historical Biology*, 26, 710–727, 2013a.
- 25 Fischer, J., Schneider, J. W., Voigt, S., Joachimski, M., Tichomirowa, M., Tütken, T., Götze, J., and Berner, U.: Oxygen and strontium isotopes from fossil shark teeth: environmental and ecological implications for late Palaeozoic European basins, *Chemical Geology*, 342, 44–62, 2013b.
- Froese, R. and Pauly, D.: FishBase, <http://www.fishbase.org/>, 2017.
- Garman, S.: *The Plagiostomia (Sharks, Skates and Rays)*, *Memoirs of the Museum of Comparative Zoology at Harvard College*, 36, 1–528, 1913.
- 30 Gibbes, R. W.: *Monograph of the fossil Squalidae of the United States*, *Journal of the Academy of Natural Sciences of Philadelphia*, 1, 191–206, 1849.
- Gill, T.: *Arrangement of the families of fishes or Classes Pisces, Marsipobranchii, and Leptocardii prepared for the Smithsonian Institution* by Theodore Gill, *Smithsonian Institution Miscellaneous Collection*, 1872.
- 35 Goodrich, E. S.: *Vertebrata Craniata (First fascicle: Cyclostomes and Fishes)*, in: *A treatise on Zoology*, edited by Lankester, R., p. 1–518, Adam and Charles Black, London, 1909.
- Günther, A.: *Catalogue of the fishes in the British Museum*, British Museum (Natural History), London, 1870.



- Hasse, K. E.: Das natürliche System der Elasmobranchier auf Grundlage des Baues und der Entwicklung ihrer Wirbelsäule: eine morphologische und paläontologische Studie, Gustav Fischer Verlag, Jena, 1879.
- Hendy, A. J. W., Jones, D. S., Moreno, F., Zapata, V., and Jaramillo, C.: Neogene molluscs, shallow marine paleoenvironments, and chronostratigraphy of the Guajira Peninsula, Colombia, *Swiss Journal of Palaeontology*, 134, 45–75, 2015.
- 5 Iturralde-Vinent, M. A. and MacPhee, R. D. E.: Paleogeography of the Caribbean region: implications for Cenozoic biogeography, *Bulletin of the American Museum of Natural History*, 238, 1–95, 1999.
- Jaramillo, C., Montes, C., Cardona, A., Silvestro, D., Antonelli, A., and Bacon, C. D.: Comment (1) on Formation of the “Isthmus of Panama” by O’Dea et al., *Science Advances*, 3, e1602321, 2017.
- Jordan, D. S. and Evermann, B. W.: The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part I, *Bulletin of the United States National Museum*, 47, 1–1240, 1896.
- Klimley, P. A.: *The biology of sharks and rays*, The University of Chicago Press, Chicago, 2013.
- Klug, S., Tütken, T., Wings, O., Pfretzschner, H.-U., and Martin, T.: A late Jurassic freshwater shark assemblage (Chondrichthyes, Hybodontiformes) from the southern Junggar Basin, Xinjiang, Northwest China, *Palaeobiodiversity and Palaeoenvironments*, 90, 241–257, <https://doi.org/10.1007/s12549-010-0032-2>, 2010.
- 15 Koch, P. L., Tuross, N., and Fogel, M. L.: The effects of sample treatment and diagenesis on the isotopic integrity of carbonate in biogenic hydroxylapatite, *Journal of Archaeological Science*, 24, 417–429, 1997.
- Kocsis, L.: Geochemical compositions of marine fossils as proxies for reconstructing ancient environmental conditions, *Chimia*, 65, 787–791, 2011.
- 20 Kocsis, L., Vennemann, T., and Fontignie, D.: Migration of sharks into freshwater systems during the Miocene and implications for Alpine paleoelevation, *Geology*, 35, 451–454, 2007.
- Kocsis, L., Gheerbrant, E., Mouflih, M., Cappetta, H., Yans, J., and Amaghaz, M.: Comprehensive stable isotope investigation of marine biogenic apatite from the late Cretaceous–early Eocene phosphate series of Morocco, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 394, 74–88, 2014.
- 25 Kocsis, L., Vennemann, T., Ulianov, A., and Brunnschweiler, J. M.: Characterizing the bull shark *Carcharhinus leucas* habitat in Fiji by the chemical and isotopic compositions of their teeth, *Environmental Biology of Fishes*, 98, 1609–1622, <https://doi.org/10.1007/s10641-015-0386-4>, 2015.
- Kolodny, Y., Luz, B., and Navon, O.: Oxygen isotope variations in phosphate of biogenic apatites, I. Fish bone apatite—rechecking the rules of the game, *Earth and Planetary Science Letters*, 64, 398–404, [https://doi.org/10.1016/0012-821X\(83\)90100-0](https://doi.org/10.1016/0012-821X(83)90100-0), 1983.
- 30 Kruckow, T. and Thies, D.: Die Neoselachier der Paleokaribik (Pisces: Elasmobranchii), *Courier Forschungsinstitut Sencken*, 119, 1–102, 1990.
- Landini, W., Altamirano-Sierra, A., Collareta, A., di Celma, C., Urbina, M., and Bianucci, G.: The late Miocene elasmobranch assemblage from Cerro Colorado (Pisco Formation, Peru), *Journal of South American Earth Sciences*, 73, 168–190, 2017.
- Last, P. R., Séret, B., and Naylor, G. J.: A new species of guitarfish, *Rhinobatos borneensis* sp. nov. with a redefinition of the family-level classification in the order Rhinopristiformes (Chondrichthyes: Batoidea), *Zootaxa*, 4117, 451–475, 2016.
- Le Hon, H.: *Préliminaires d’un mémoire sur les poissons tertiaires de Belgique*, H. Merzbach, Brussels, 1871.
- Lear, C. H., Elderfield, H., and Wilson, P. A.: Cenozoic deep-sea temperatures and global ice volumes from Mg/Ca in benthic foraminiferal calcite, *Science*, 287, 269–272, <https://doi.org/10.1126/science.287.5451.269>, 2000.



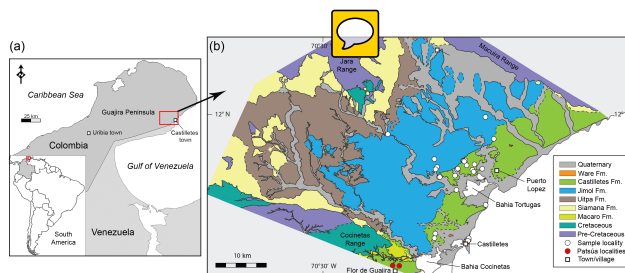
- Lécuyer, C.: Oxygen isotope analysis of phosphate, in: Handbook of Stable Isotope Analytical Techniques, edited by de Groot, P. A., vol. 1, p. 482–499, Elsevier, 2004.
- Lécuyer, C., Grandjean, P., O’Neil, J. R., Cappetta, H., and Martineau, F.: Thermal excursions in the ocean at the Cretaceous–Tertiary boundary (northern Morocco):  $\delta^{18}\text{O}$  record of phosphatic fish debris, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 105, 235–243, [https://doi.org/10.1016/0031-0182\(93\)90085-W](https://doi.org/10.1016/0031-0182(93)90085-W), 1993.
- Lécuyer, C., Grandjean, P., Paris, F., Robardet, M., and Robineau, D.: Deciphering “temperature” and “salinity” from biogenic phosphates: the  $\delta^{18}\text{O}$  of coexisting fishes and mammals of the middle Miocene sea of western France, *Palaeogeography, Palaeoclimatology, Palaeoecology*, 126, 61–74, [https://doi.org/10.1016/S0031-0182\(96\)00070-3](https://doi.org/10.1016/S0031-0182(96)00070-3), 1996.
- Lécuyer, C., Amiot, R., Touzeau, A., and Trotter, J.: Calibration of the phosphate  $\delta^{18}\text{O}$  thermometer with carbonate–water oxygen isotope fractionation equations, *Chemical Geology*, 347, 217–226, <https://doi.org/10.1016/j.chemgeo.2013.03.008>, 2013.
- Leriche, M.: Contribution à L’étude des poissons fossils des pays riverains de la Méditerranée américaine, Venezuela, Trinité, Antilles, Mexique, *Mémoires de la Société Paléontologique du Suisse*, 61, 1–52, 1938.
- Leuzinger, L., Kocsis, L., Billon–Bryat, J. P., Spezzaferri, S., and Vennemann, T.: Stable isotope study of a new chondrichthyan fauna (Kimmeridgian, Porrentruy, Swiss Jura): an unusual freshwater–influenced isotopic composition for the hybodont shark *Asteracanthus*, *Biogeosciences*, 12, 6945–6954, 2015.
- Linck, H. F.: Versuch einer Eintheilung der Fische nach den Zähnen, *Magazin für das Neueste aus der Physik und Naturgeschichte*, 6, 28–38, 1790.
- Lockwood, J. P.: Geology of the Serranía de Jarara Area. Guajira Peninsula, Colombia, Ph.D. thesis, Princeton University, Princeton, New Jersey, 1965.
- Longinelli, A. and Nuti, S.: Revised phosphate–water isotopic temperature scale, *Earth and Planetary Science Letters*, 19, 373–376, [https://doi.org/10.1016/0012-821X\(73\)90088-5](https://doi.org/10.1016/0012-821X(73)90088-5), 1973a.
- Longinelli, A. and Nuti, S.: Oxygen isotope measurements of phosphate from fish teeth and bones, *Earth and Planetary Science Letters*, 20, 337–340, [https://doi.org/10.1016/0012-821X\(73\)90007-1](https://doi.org/10.1016/0012-821X(73)90007-1), 1973b.
- Mine, A. H., Waldeck, A., Olack, G., Hoerner, M. E., Alex, S., and Colman, A. S.: Microprecipitation and  $\delta^{18}\text{O}$  analysis of phosphate for paleoclimate and biogeochemistry research, *Chemical Geology*, 460, 1–14, <https://doi.org/10.1016/j.chemgeo.2017.03.032>, 2017.
- Montes, C., Cardona, A., Jaramillo, C., Pardo, A., Silva, J. C., Valencia, V., Ayala, C., Pérez–Angel, L. C., Rodríguez–Parra, L. A., Ramirez, V., and Niño, H.: Middle Miocene closure of the Central American Seaway, *Science*, 348, 226–229, 2015.
- Moreno, F., Hendy, A. J. W., Quiroz, L., Hoyos, N., Jones, D. S., Zapata, V., Zapata, S., Ballen, G. A., Cadena, E., Cárdenas, A. L., Carrillo–Briceño, J. D., Carrillo, J. D., Delgado–Sierra, D., Escobar, J., Martínez, J. I., Martínez, C., Montes, C., Moreno, J., Pérez, N., Sánchez, R., Suárez, C., Vallejo–Pareja, M. C., and Jaramillo, C.: Revised stratigraphy of Neogene strata in the Cocinetas Basin, La Guajira, Colombia, *Swiss Journal of Palaeontology*, 134, 5–43, 2015.
- Moreno–Bernal, J. W., Head, J., and Jaramillo, C.: Fossil Crocodylians from the High Guajira Peninsula of Colombia: Neogene faunal change in northernmost South America, *Journal of Vertebrate Paleontology*, 36, e1110 586, 2016.
- Müller, A.: Ichthyofaunen aus dem atlantischen Tertiär der USA, *Leipziger Geowissenschaften*, 9–10, 1–360, 1999.
- Müller, J. and Henle, J.: Gattungen der Haifische und Rochen nach einer von ihm mit Hr. Henle unternommenen gemeinschaftlichen Arbeit über die Naturgeschichte der Knorpelfische, *Akademie der Wissenschaften zu Berlin*, 1837, 111–118, 1837.
- Müller, J. and Henle, J.: Systematische Beschreibung der Plagiostomen, Veit, Berlin, 1838–41.



- O'Neil, J. R., Roe, L. J., Reinhard, E., and Blake, R. E.: A rapid and precise method of oxygen isotope analysis of biogenic phosphate, *Israel Journal of Earth Sciences*, 43, 203–212, 1994.
- Patnaik, R., Milankumar–Sharma, K., Mohan, L., Williams, B. A., Kay, R. F., and Chatrath, P.: Additional vertebrate remains from the early Miocene of Kutch, Gujarat, *Special Publication of the Paleontological Society of India*, 5, 335–351, 2014.
- 5 Pérez, M. E., Vallejo–Pareja, M. C., Carrillo, J. D., and Jaramillo, C.: A new Pliocene Capybara (Rodentia, Caviidae) from northern South America (Guajira, Colombia), and its implications for the Great American Biotic Interchange, *Journal of Mammalian Evolution*, 24, 111–125, 2016.
- Pérez–Consuegra, N., Parra, M., Jaramillo, C., Silvestro, D., Echeverri, S., Montes, C., Jaramillo, J. M., and Escobar, J.: Provenance analysis of the Pliocene Ware Formation in the Guajira Peninsula, northern Colombia: Paleodrainage implications, *Journal of South American Earth Sciences*, 81, 66–77, <https://doi.org/10.1016/j.jsames.2017.11.002>, 2018.
- 10 Pimiento, C., Gonzalez–Barba, G., Hendy, A. J. W., Jaramillo, C., MacFadden, B. J., Montes, C., Suarez, S. C., and Shippritt, M.: Early Miocene chondrichthyans from the Culebra Formation, Panama: a window into marine vertebrate faunas before closure the Central American Seaway, *Journal of South American Earth Sciences*, 42, 159–170, 2013.
- Poey, F.: Synopsis piscium cubensium. Catalogo razonado de los peces de la isla de Cuba, *Repertorio Fisico–Natural de la Isla de Cuba*, 2, 15 279–484, 1868.
- Poey, F.: Enumeratio piscium cubensium (Parte III), *Anales de la Sociedad Española de Historia Natural*, 5, 373–404, 1876.
- Probst, J.: Beiträge zur Kenntniss der fossilen Fische aus der Molasse von Baltringen. Hayfische, *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, 35, 127–191, 1879.
- Pucéat, E., Joachimski, M., Bouilloux, A., Monna, F., Bonin, A., Montreuil, S., Morinière, P., Hénard, S., Mourin, J., Dera, G., and Quesne, 20 D.: Revised phosphate–water fractionation equation reassessing paleotemperatures derived from biogenic apatite, *Earth and Planetary Science Letters*, 298, 135–142, <https://doi.org/10.1016/j.epsl.2010.07.034>, 2010.
- Purdy, R., Clellan, J. H. M., Schneider, V. P., Applegate, S. P., Meyer, R., and Slaughter, R.: The Neogene sharks, rays and bony fishes from Lee Creek Mine, Aurora, North Carolina, in: *Geology and paleontology of the Lee Creek Mine, North Carolina, III*, edited by Ray, C. E. and Bohaska, D. J., *Smithsonian Contributions to Paleobiology*, 90, p. 71–202, Smithsonian Institution Press, Washington D.C., 2001.
- 25 Rafinesque, C. S.: Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia con varie osservazioni sopra i medesimi, *Per le stampe di Sanfilippo, Palermo*, 1810.
- Reinecke, T., Louwye, S., Havekost, U., and Moths, H.: The elasmobranch fauna of the late Burdigalian, Miocene, at Werder–Uesen, Lower Saxony, Germany, and its relationships with early Miocene faunas in the North Atlantic, Central Paratethys and Mediterranean, *Palaeontos*, 20, 1–170, 2011.
- 30 Reinecke, T., Balsberger, M., Beaury, B., and Pollerspöck, J.: The elasmobranch fauna of the Thalberg Beds, early Egerian (Chattian, Oligocene), in the Subalpine Molasse Basin near Siegsdorf, Bavaria, Germany, *Palaeontos*, 26, 1–127, 2014.
- Reis, M. A. F.: Chondrichthyan fauna from the Pirabas Formation, Miocene of northern Brazil, with comments on paleobiogeography, *Anuário do Instituto de Geociências*, 28, 31–58, 2005.
- Rodríguez, G.: The Maracaibo System, Venezuela, in: *Coastal Marine Ecosystems of Latin America*, edited by Seeliger, U. and Kjerfve, B., 35 *Ecological Studies*, 144, p. 47–60, Springer Berlin Heidelberg, 2001.
- Rüppell, W. P. E. S. E.: *Fische des Rothen Meeres*, Frankfurt am Main, Frankfurt, 1837.
- Santos, R. S. and Travassos, H.: Contribuição à Paleontologia do estado do Pará. Peixes fósseis da Formação Pirabas, *Serviço gráfico do Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro*, 1960.

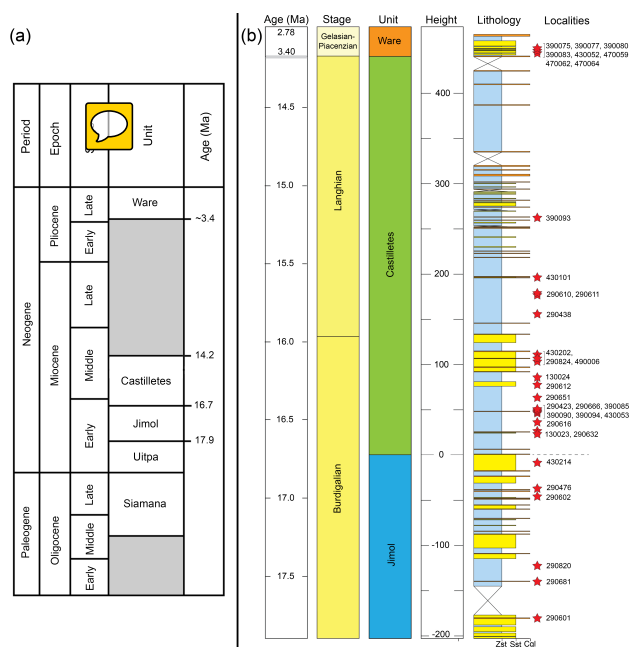


- Silva-Tamayo, J. C., Lara, M. E., Yobo, L. N., Erdal, Y. D., Sanchez, J., and Zapata-Ramirez, P. A.: Tectonic and environmental factors controlling on the evolution of Oligo–Miocene shallow marine carbonate factories along a tropical SE Circum–Caribbean, *Journal of South American Earth Sciences*, 78, 213–237, 2017.
- Tavares, R. and Sánchez, L.: Áreas de cría de tiburones en el Golfo de Venezuela, *Ciencia*, 20, 116–124, 2012.
- 5 Vennemann, T., Hegner, E., Cliff, G., and Benz, G. W.: Isotopic composition of recent shark teeth as a proxy for environmental conditions, *Geochimica et Cosmochimica Acta*, 65, 1583–1599, [https://doi.org/10.1016/S0016-7037\(00\)00629-3](https://doi.org/10.1016/S0016-7037(00)00629-3), 2001.
- Vennemann, T., Fricke, H. C., Blake, R. E., O’Neil, J. R., and Colman, A.: Oxygen isotope analysis of phosphates: a comparison of techniques for analysis of  $\text{Ag}_3\text{PO}_4$ , *Chemical Geology*, 185, 321–336, [https://doi.org/10.1016/S0009-2541\(01\)00413-2](https://doi.org/10.1016/S0009-2541(01)00413-2), 2002.
- Voigt, M. and Weber, D.: Field guide for sharks of the genus *Carcharhinus*, Verlag Dr. Friedrich Pfeil, München, 2011.
- 10 Ward, D. and Bonavia, C.: Additions to, and a review of, the Miocene shark and ray fauna of Malta, *The Central Mediterranean Naturalist*, 3, 131–146, 2001.
- White, W. T. and Naylor, G. J.: Resurrection of the family Aetobatidae (Myliobatiformes) for the pelagic eagle rays, genus *Aetobatus*, *Zootaxa*, 4139, 435–438, 2016.
- Woodward, A. S.: Catalogue of the fossil fishes in the British Museum. Part I, British Museum (Natural History), London, 1889.
- 15 Zazzo, A., Lécuyer, C., and Mariotti, A.: Experimentally–controlled carbon and oxygen isotope exchange between bioapatites and water under inorganic and microbially–mediated conditions, *Geochimica et Cosmochimica Acta*, 68, 1–12, [https://doi.org/10.1016/S0016-7037\(03\)00278-3](https://doi.org/10.1016/S0016-7037(03)00278-3), 2004a.
- Zazzo, A., Lécuyer, C., Sheppard, S. M. F., Grandjean, P., and Mariotti, A.: Diagenesis and the reconstruction of paleoenvironments: a method to restore original  $\delta^{18}\text{O}$  values of carbonate and phosphate from fossil tooth enamel, *Geochimica et Cosmochimica Acta*, 68, 2245–2258, <https://doi.org/10.1016/j.gca.2003.11.009>, 2004b.
- 20

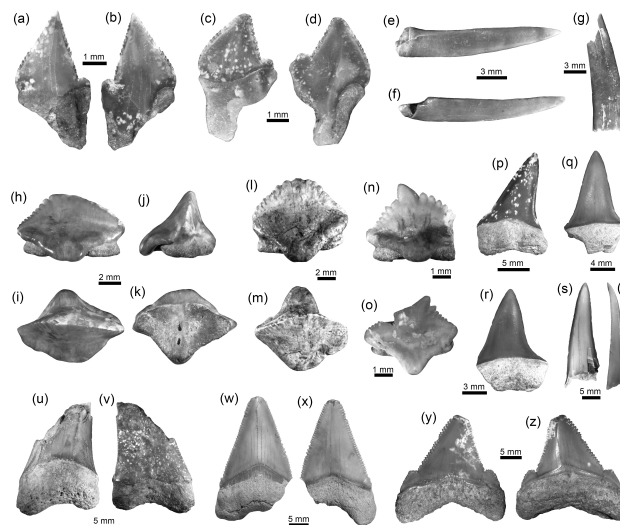


**Figure 1.** Location (a) and geological map of the southeastern Cocinetas Basin (b). Abbreviation: Fm. (Formation).

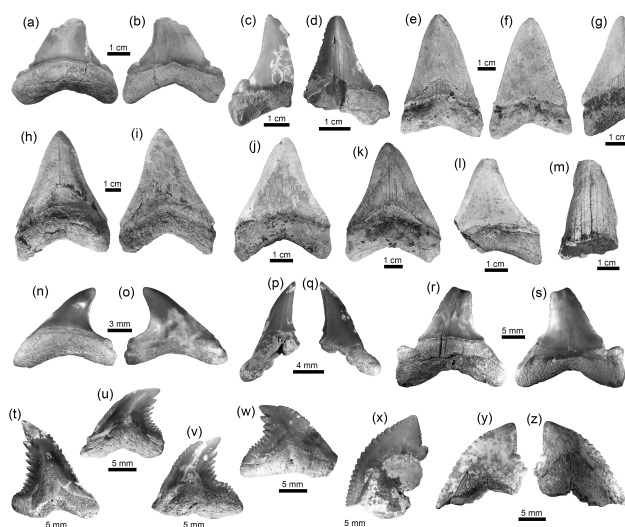




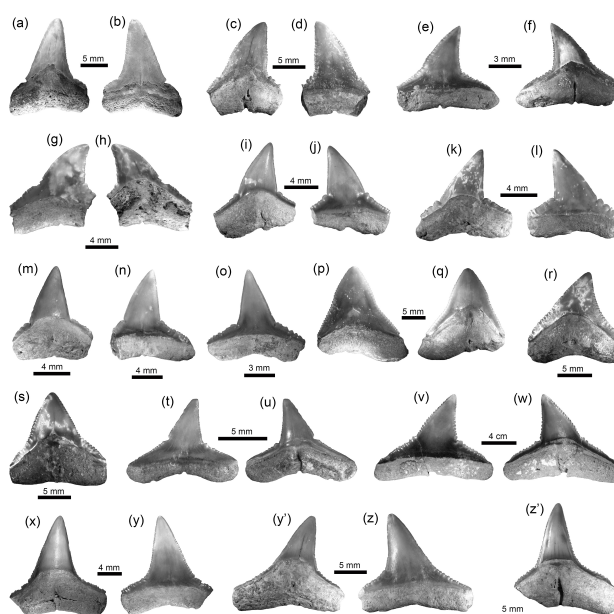
**Figure 2.** Stratigraphy of the Cocinetas Basin. **(a)** Generalized stratigraphy (after Moreno et al., 2015). **(b)** Stratigraphic section and studied localities. Localities of the Patsúa Valley (290468 and 290472) (details in Table S1) are not represented, **because** these belong to another section of the basin **without stratigraphic context**.



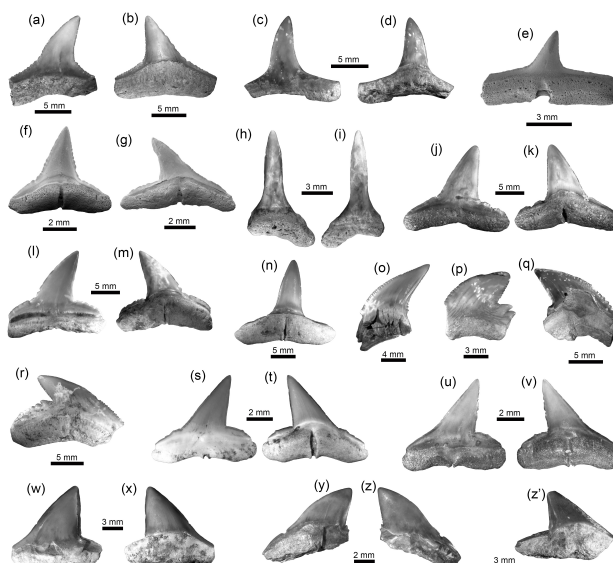
**Figure 3.** Squaliformes, Pristiophoriformes, Orectolobiformes and Lamniformes of the Cocinetas Basin. **(a–d)** *Dalatias* cf. *D. licha* (MUN–STRI–41205). **(e–g)** *Pristiophorus* sp. (MUN–STRI–34788). **(h–o)** *Nebrius* sp. (h–k, n, o: MUN–STRI–41136; l–m: MUN–STRI–41180). **(p–t)** *Isurus* cf. *I. oxyrinchus* (MUN–STRI–37671). **(u–v)** †*Paratodus benedenii* (MUN–STRI–43742). **(w–z)** †*Carcharocles chubutensis* (MUN–STRI–40375). Jaw position: upper (y–z?), lower (a–d, w–x) and indet. (h–v), rostral (e–g). View: labial (b, d, h, l, n–o, v, x–y), lingual (a, c, p–s, u, w, z), profile (j, t), occlusal (i, m) dorsal (e–g), and basal (k). Geological unit: Jimol Fm. (a–d), Castilletes Fm. (h–o), Patsúa assemblage–locality 290468 (e–g, p–z).



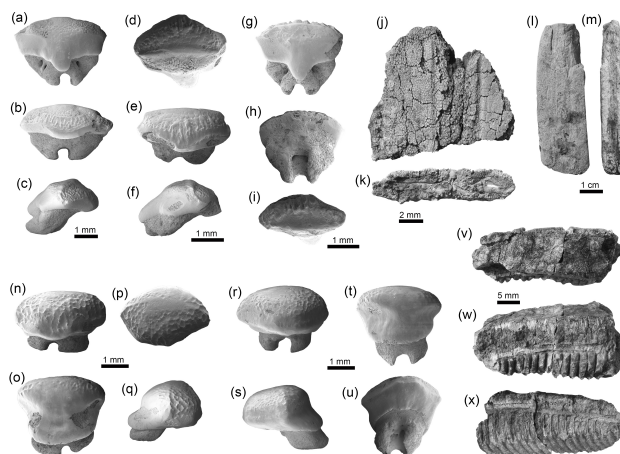
**Figure 4.** Lamniformes and Carcharhiniformes of the Cocinetas Basin. **(a–d)** †*Carcharocles chubutensis* (MUN–STRI–40375). **(e–l)** †*Carcharocles megalodon* (e–g: MUN–STRI–37812; h–i: MUN–STRI–38067; j–l: MUN–STRI–41145). **(m)** †*Carcharocles* sp. (MUN–STRI–41138). **(n–q)** *Alopias* cf. *exigua* (MUN–STRI–43745). **(r–s)** †*Anotodus retroflexus* (MUN–STRI–43740). **(t–w)** †*Hemipristis serra* (MUN–STRI–34790). **(x–z)** †*Galeocerdo mayumbensis* (x: MUN–STRI–41135; y–z: MUN–STRI–40377). Jaw position: upper (j–l, n, u–w), lower (a–b?, c–f, h–i?, p–q?, t) and indet. (g, m, r–s, x–z). View: labial (b–c, f, i–j, l, o, q, s, y), lingual (a, d–e, g–h, k, m–n, p, r, t–x, z). Geological unit: Jimol Fm. (m), Castilletes Fm. (e–l, x), Patsúa assemblage–locality 290468 (a–d, n–w, y–z).



**Figure 5.** Carcharhiniformes of the Cocinetas Basin. **(a–d)** †*Carcharhinus ackermannii* (a–b: MUN–STRI–41128; c–d: MUN–STRI–43743). **(e–h)** *Carcharhinus* cf. *C. brachyurus* (MUN–STRI–41207). **(i–o)** †*Carcharhinus gibbesii* (MUN–STRI–43808). **(p–s)** *Carcharhinus leucas* (p–q: MUN–STRI–37646; r: MUN–STRI–21937; s: MUN–STRI–16287). **(t–u)** *Carcharhinus* cf. *C. limbatus* (MUN–STRI–41153). **(v–w)** *Carcharhinus* cf. *C. perezii* (MUN–STRI–41129). **(x–z')** *Carcharhinus* cf. †*C. priscus* (MUN–STRI–43804). Jaw position: upper (a–z'). View: labial (b, d–e, g, j, l, n–p, t, v, y, z), lingual (a, c, f, h–i, k, m, q–s, u, w–x, y', z'). Geological unit: Jimol Fm. (a–b, e–h, t–w), Castilletes Fm. (t–u). Ware (P–S), Patsúa assemblage–locality 290468 (c–d, i–o, x–z').

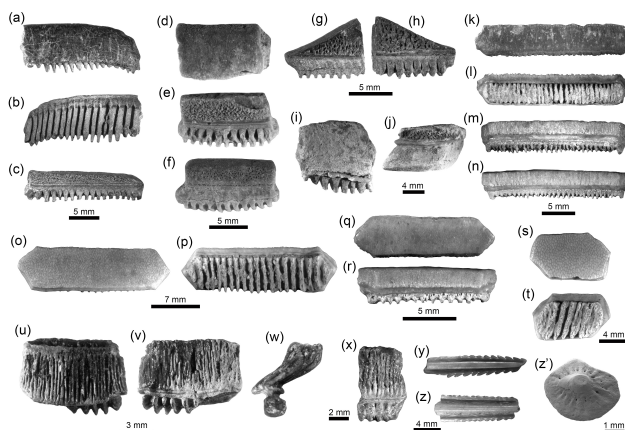


**Figure 6.** Carcharhiniformes of the Cocinetas Basin. **(a–d)** *Carcharhinus* cf. †*C. priscus* (MUN–STRI–43804). **(e–g)** *Carcharhinus* spp. (e: MUN–STRI–42136; f–g: MUN–STRI–42128). **(h–i)** †*Isogomphodon acuarius* (MUN–STRI–41184). **(j–n)** †*Negaprion eurybathrodon* (MUN–STRI–41133). **(o–r)** †*Physogaleus contortus* (o–q: MUN–STRI–40378; r: MUN–STRI–41132). **(s–v)** †*Sphyrna arambourgi* (MUN–STRI–41143). **(w–z')** †*Sphyrna laevisissima* (MUN–STRI–43741). Jaw position: upper (a–b, f–g, j–m, s–z, z'?), lower (c–e, h–i, n) and indet. (o–r). View: labial (a, c, e, i–j, l, p, s, u, w, z), lingual (b, d, f–h, k, m–o, q–r, t, v, x–y, z'). Geological unit: Castilletes Fm. (e–n, r–v), Patsúa assemblage–locality 290468 (a–d, o–q, w–z').

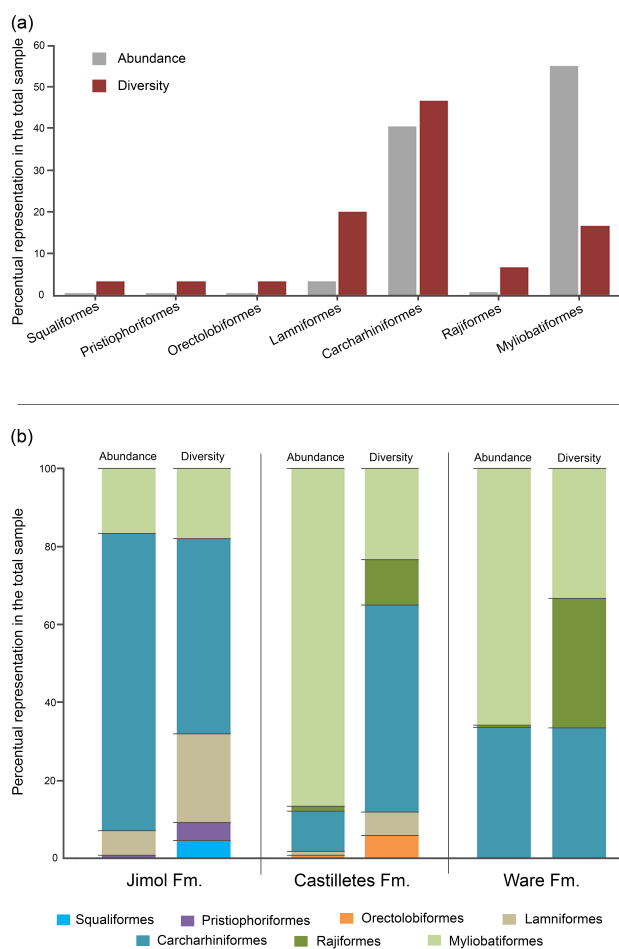


**Figure 7.** Rhinopristiformes and Myliobatiformes of the Cocinetas Basin. **(a–i)** *Rhynchobatus* sp. (MUN–STRI– 42132). **(j–m)** *Pristis* sp. (fragment of rostrum j–k: MUN–STRI–37397; rostral denticle l–m: MUN–STRI–34762). **(n–u)** *Dasyatis* sp. (MUN–STRI–42135). **(v–x)** *Aetobatus* sp. (MUN–STRI–34465). Jaw position: indet. (a–i, n–x). View: labial (b, e, n, r, x), lingual (a, g, o, t, w), profile (c, f, q, s), occlusal (d, i, p, v), dorsal (j, l), posterior (k), basal (h, u). Geological unit: Castilletes Fm. (a–x).

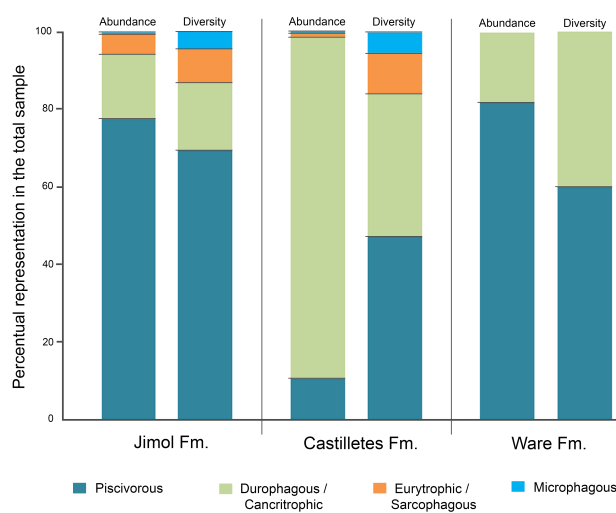




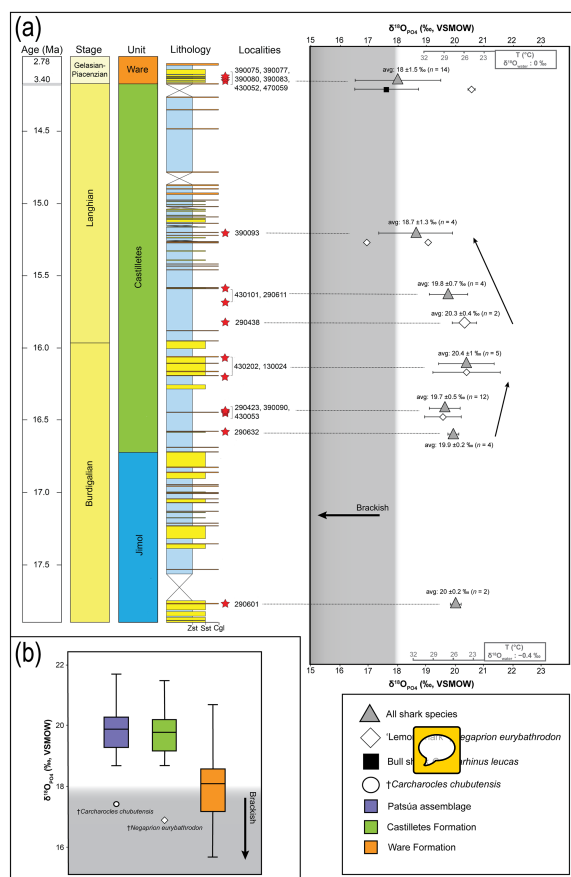
**Figure 8.** Myliobatiformes of the Cocinetas Basin. (a–j) *Aetomylaeus* sp. (a–c: MUN–STRI–41134; d–f: MUN–STRI–43746; g–j: MUN–STRI–41134). (k–t) *Rhinoptera* sp. (MUN–STRI–41138). (u–x) †*Plinthicus stenodon* (MUN–STRI–41203). (y–z') Myliobatiformes indet. (caudal spines y–z: MUN–STRI–34785; denticle z': MUN–STRI–42134). Jaw position: indet. (a–x). View: labial (f, g, n, r, u), lingual (c, e, h, m, v, x), profile (j, w), occlusal (a, d, i, k, o, q, s), ventral (y–z), basal (b, l, p, t). Geological unit: Castilletes Fm. (a–c, g–x, z'), Ware Fm. (y–z), Patsúa assemblage–locality 290468 (d–f).



**Figure 9.** Elasmobranch paleodiversity (orders) of the Cocinetas Basin. **(a)** Overall assemblages. **(b)** Assemblages by geological units.



**Figure 10.** Dietary preference of the overall Cocinetas Basin assemblages by geological units.



**Figure 11.** Stratigraphic distribution of the  $\delta^{18}\text{O}_{\text{PO}_4}$  from sharks of the Cocinetas Basin. The gray-shaded area marks the isotopic range representative of brackish environments. Big symbols give the average of all shark data within the same layer and its standard deviation, while smaller icons are for specific species data. Triangles group all shark species sampled in that layer; while diamonds show the results from †*Negaprion eurybathrodon*, a lemon shark, well represented along the sedimentary sequence (the icon is large for locality 290438 because only *Negaprion* specimens were sampled); and the squares are values from bull sharks of Ware Formation. Temperature bars were estimated from the equation of Lécuyer et al. (2013) are shown at the top (Ware) and at the bottom (Jimol and Castilletes) at  $\delta^{18}\text{O}_w$  of 0 ‰ and  $-0.4$  ‰, respectively (Lear et al., 2000; Billups and Schrag, 2002). **(a)** The mean  $\delta^{18}\text{O}_{\text{PO}_4}$  values show a minor increase along the middle Miocene, with maximum mean value for localities of the late Burdigalian. In the following intervals, the mean values decrease during the early Langhian. Ware Formation samples yielded  $\delta^{18}\text{O}_{\text{PO}_4}$  values predominantly characteristic of brackish environments. **(b)** Boxplot of the  $\delta^{18}\text{O}_{\text{PO}_4}$  values from samples of the Patsúa assemblage, Castilletes and Ware Formations. Each outlier from the Patsúa assemblage and Castilletes are teeth with  $\delta^{18}\text{O}_{\text{PO}_4}$  values considered to form under ‘brackish’ conditions.

**Table 1.** Elasmobranchii paleodiversity of the Cocinetas Basin.

Superorder	Order	Family	Genus	Taxon	
Squalomorphii	Squaliformes	Dalatiidae	<i>Dalatias</i>	<i>Dalatias</i> cf. <i>D. licha</i> (Bonnaterre, 1788)	
	Pristiophoriformes	Pristiophoridae	<i>Pristiophorus</i>	<i>Pristiophorus</i> sp.	
Galeomorphii	Orectolobiformes	Ginglymostomatidae	<i>Nebrius</i>	<i>Nebrius</i> sp.	
		Lamniformes	Lamnidae	<i>Isurus</i>	<i>Isurus</i> cf. <i>I. oxyrinchus</i> Rafinesque, 1810
		†Otodontidae	† <i>Paratodus</i>	† <i>Paratodus</i> <i>enedenii</i> (Le Hon, 1871)	
			† <i>Carcharocles</i>	† <i>Carcharocles chubutensis</i> (Ameghino, 1901) † <i>Carcharocles megalodon</i> (Agassiz, 1843) † <i>Carcharocles</i> sp.	
		Alopiidae	<i>Alopias</i>	<i>Alopias</i> cf. <i>A. exigua</i> (Probst, 1879)	
			† <i>Anotodus</i>	† <i>Anotodus retroflexus</i> (Agassiz, 1843)	
	Carcharhiniformes	Hemigaleidae		<i>Hemipristis</i>	† <i>Hemipristis serra</i> (Agassiz, 1835)
			Carcharhinidae	<i>Galeocerdo</i>	† <i>Galeocerdo mayumbensis</i> Dartevelle and Casier, 1943
				<i>Carcharhinus</i>	† <i>Carcharhinus ackermannii</i> Santos and Travassos, 1960 <i>Carcharhinus</i> cf. <i>C. brachyurus</i> (Günther, 1870) † <i>Carcharhinus gibbesii</i> (Woodward, 1889) <i>Carcharhinus leucas</i> (Müller and Henle, 1839) <i>Carcharhinus</i> cf. <i>C. limbatus</i> (Müller and Henle, 1839) <i>Carcharhinus</i> cf. <i>C. perezii</i> (Poey, 1868) <i>Carcharhinus</i> cf. † <i>C. priscus</i> (Agassiz, 1843) <i>Carcharhinus</i> spp.
				† <i>Isogomphodon</i>	† <i>Isogomphodon acuarius</i> (Probst, 1879)
			<i>Negaprion</i>	† <i>Negaprion eurybathrodon</i> (Blake, 1862)	
			† <i>Physogaleus</i>	† <i>Physogaleus contortus</i> (Gibbes, 1849)	
		Sphyrnidae	<i>Sphyrna</i>	† <i>Sphyrna arambourgi</i> Cappetta, 1970 † <i>Sphyrna laevissima</i> (Cope, 1867)	
Batomorphii		Rhinopristiformes	Rhynchobatidae	<i>Rhynchobatus</i>	<i>Rhynchobatus</i> sp.
	Pristidae		<i>Pristis</i>	<i>Pristis</i> sp.	
	Myliobatiformes	Dasyatidae	<i>Dasyatis</i>	<i>Dasyatis</i> sp.	
		Aetobatidae	<i>Aetobatus</i>	<i>Aetobatus</i> sp.	
		Myliobatidae	<i>Aetomylaeus</i>	<i>Aetomylaeus</i> sp.	
		Rhinopteraidae	<i>Rhinoptera</i>	<i>Rhinoptera</i> sp. Myliobatoidea indet.	
		Mobulidae	<i>Plinthicus</i>	† <i>Plinthicus stenodon</i> Cope, 1869 Myliobatiformes indet.	

**Table 2.** Shark teeth specimens used in geochemical investigation.

Sample ID	Taxon	Formation	Locality	$\delta^{18}\text{O}_{\text{PO}_4}$ (‰, VSMOW)	$\delta^{18}\text{O}_{\text{PO}_4}$ std dev.
HS.1	† <i>Hemipristis serra</i>	Jimol	290601	19.9	0.1
HS.2				20.2	0.2
HS.3		Patsúa assemblage	290472	20.1	0.1
HS.4				20	0.1
HS.5				20.6	0.1
CC.1	† <i>Carcharocles chubutensis</i>			19.9	0.1
CC.2				19.1	0.2
CC.3				19.4	0.1
HS.6	† <i>Hemipristis serra</i>		290468	19.3	0.1
HS.7				20.2	0.3
HS.8				19.9	0.1
NG.1	† <i>Negaprion eurybathrodon</i>			18.9	0.2
NG.2				19.9	0.2
GM.1	† <i>Galeocerdo mayumbensis</i>			20.5	0.1
GM.2				20.3	0.1
GM.3				19.3	0.2
SL.1	† <i>Sphyrna laevis</i>			19.9	0.0
SL.2				19.1	0.1
SL.3				18.7	0.3
CC.4	† <i>Carcharocles chubutensis</i>			17.4	0.3
CC.5				19.2	0.2
CC.6				20.7	0.0
IO.1	<i>Isurus cf. I. oxyrinchus</i>			21.7	0.3
IO.2				20.8	0.0
IO.3				19.3	0.3
PC.1	† <i>Physogaleus contortus</i>			19.8	0.0
PC.2				20.5	0.0
PC.3				19.4	0.1
HS.9	† <i>Hemipristis serra</i>	Castilletes	290632	19.8	0.3
HS.10				19.8	0.1
CS.1	<i>Carcharhinus</i> sp.			20.1	0.2
CS.2				20.1	0.1
HS.11	† <i>Hemipristis serra</i>		290423	19.1	0.2
NG.3	† <i>Negaprion eurybathrodon</i>			19.5	0.3
HS.12	† <i>Hemipristis serra</i>		390090	19.6	0.0

**Table 2.** Continued. Shark teeth specimens used in geochemical investigation.

Sample ID	Taxon	Formation	Locality	$\delta^{18}\text{O}_{\text{PO}_4}$ (‰, VSMOW)	$\delta^{18}\text{O}_{\text{PO}_4}$ std dev.
HS.13	† <i>Hemipristis serra</i>	Castilletes	390090	19.5	0.0
NG.4	† <i>Negaprion eurybathrodon</i>			20.1	0.2
NG.5				18.8	0.2
SA.1	† <i>Sphyrna arambourgi</i>			20.1	0.3
SA.2				19.2	0.1
HS.14	† <i>Hemipristis serra</i>		430053	20.1	0.2
HS.15				20.4	0.0
NG.6	† <i>Negaprion eurybathrodon</i>			20.4	0.1
NG.7				19.2	0.1
NG.8			130024	19.2	0.2
HS.16	† <i>Hemipristis serra</i>		430202	21.1	0.0
HS.17				19.7	0.1
NG.9	† <i>Negaprion eurybathrodon</i>			21.5	0.2
NG.10				20.5	0.2
NG.11			290438	20.1	0.3
NG.12				20.6	0.1
CS.3	<i>Carcharhinus</i> sp.		290611	18.9	0.2
CS.4				20.3	0.2
CS.5				20.2	0.1
HS.18	† <i>Hemipristis serra</i>		430101	19.8	0.1
NG.13	† <i>Negaprion eurybathrodon</i>		390093	19.1	0.1
NG.14				16.9	0.2
CS.6	<i>Carcharhinus</i> sp.			18.7	0.0
CS.7				19.9	0.1
CL.1	<i>Carcharhinus leucas</i>	Ware	430059	18.1	0.1
CL.2				18	0.1
CL.3			430052	18	0.1
CL.4				18.4	0.0
CL.5			390083	18	0.1
CL.6				18.9	0.0
CL.7			390080	18.6	0.1
CL.8				15.7	0.2
CL.9			390077	15.7	0.2
CL.10				18.3	0.0
CL.11			390075	16.4	0.3





**Table 2.** Continued. Shark teeth specimens used in geochemical investigation.

Sample ID	Taxon	Formation	Locality	$\delta^{18}\text{O}_{PO4}$ (‰, VSMOW)	$\delta^{18}\text{O}_{PO4}$ std dev.
CL.12	<i>Carcharhinus leucas</i>	Ware	390075	17.2	0.2
NG.15	† <i>Negaprion eurybathrodon</i>			20.7	0.1
NG.16				20.5	0.0