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

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Abstract. The Cocinetas Basin is located on the eastern flank of La Guajira Peninsula, northern Colombia (South Caribbean). During the late 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 f~~F~~ormations, 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 interpretations are based on the feeding ecology, and on estimates of the paleohydrology (relative salinity, temperature)~~paleosalinity~~ using stable isotope compositions of oxygen in the bioapatite of shark teeth. The isotopic composition of the studied specimens corroborates ~~the~~ paleoenvironmental settings for the studied units ~~suggested on the basis of other proxies~~ that were previously estimated based on the sedimentology and biology of the taxa. These 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

During the Neogene, large areas of the northern margin of South America were submerged (see Iturralde–Vinent 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 the 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 the~~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) f~~F~~ormations, 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 measurements of the ratio~~estimates of the paleosalinity using~~ of stable oxygen isotopes~~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 with distinct paleofauna and facies from those of~~that cannot be readily correlated with either~~ Jimol and~~or~~ Castilletes formations~~Formation~~. ~~Because of these difficulties, and differences in their facies, and invertebrate and vertebrate fauna,~~ They are considered~~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 surface collected and~~collected directly from the outcrop, while~~ 50 kg bulk sediment was collected, sieved and screen washed (mesh sizes: 0.5 and 2 mm) for subsequent picking of smaller specimens ~~were collected~~ from the localities~~y~~ 290468 (Patsúa assemblage), 290632 and 390094 (Castilletes Formation).~~and Castilletes Formation (localities 290632 and 390094). The bulk sediments were sieved and screen washed (mesh sizes: 0.5 and 2 mm).~~

T~~t~~he ~~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~~ N~~n~~omenclature 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, family~~families~~ and genus~~genera~~ recorded in the overall assemblages of the Cocinetas Basin (Table 1, Tables S1–S2, Fig. S5). ~~Paleoecological 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 $\delta^{18}O_{PO4}$ were made in the Stable Isotope Laboratory at the University of Lausanne (UNIL) (Table 2). Powder samples of 1–1.5 mg from shark tooth~~teeth~~ enameloid were obtained by abrasion of the crown surface using a micro–drill~~,~~ and small~~micro~~ fragment samples were obtained by cutting off the tooth tips~~the tip of teeth~~. In a few cases when only small or fragmented teeth were available bulk samples were taken (1–1.5 mg of enameloid and dentine). Based on previous studies, isotopic data ~~still~~ provide valuable information about the paleoecology of sharks along stratigraphic~~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 deionized~~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 each sequence of samples~~the batch~~. Pretreatment 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 and~~,~~ then were thoroughly rinsed several times in deionized~~ultrapure~~ water. To obtain the $\delta^{18}O_{PO4}$ 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 Ag_3PO_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 Ag_3PO_4 phosphate standards (LK–2L: 12.1 ‰ and LK–3L: 17.9 ‰) that had better than ±0.3 ‰ (1σ) standard deviations during measurements. The NBS–120c phosphorite reference material had an average value of 21.7 ‰ ±0.1 ‰ (n = 6). The isotope ratios are expressed in the δ–notation relative to Vienna Standard Mean Ocean Water (VSMOW).

The $\delta^{18}O_{PO4}$ value~~s~~ 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 $\delta^{18}O_{PO4}$ values of several ectothermic fishes are related to two environmental parameters: ~~the~~ water temperature (T) and the $\delta^{18}O$ value of the water ($\delta^{18}O_w$). Based on these studies, an equation that empirically represents the oxygen isotope fractionation between biogenic phosphate and water was calculated~~suggested~~ ([T (°C) = 111.4 – 4.3 ($\delta^{18}O_{PO4}$ – $\delta^{18}O_w$)]), 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 $\delta^{18}O_{PO4}$ 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 $\delta^{18}O_{PO4}$ values were also calculated using the latest equation of Lécuyer et al. (2013) [T (°C) = 117.4 – 4.5 × ($\delta^{18}O_{PO4}$ – $\delta^{18}O_w$)]. For the late Pliocene samples (Ware Formation) a seawater value of 0 ‰ was used (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.~~,~~ However, the formation is represented by a composite section with some poorly preserved beds in the middle portion (Moreno et al. 2015)~~although this composiste 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 f~~F~~ormations 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 few~~er~~ interbedded muddy levels deposited in a shallow marine paleoenvironment, likely an~~in~~ inner shelf ~~depth~~environment (< 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 E~~e~~arly Miocene (17.9–16.7 Ma) age is assigned to the unit on the basis of macroinvertebrate biostratigraphy and $^{87}Sr/^{86}Sr$ isotope chronostratigraphy (see Hendy et al., 2015).

3.2 Castilletes Formation (Burdigalian–Langhian)

This lithostratigraphic~~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.~~, being~~ T~~t~~he 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, crocodilians, 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 ($^{87}Sr/^{86}Sr$) 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 were~~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 the Jimol or Castilletes f~~F~~ormations 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*~~Teredo~~–bored wood, an oceanic fauna of mollusks and echinoderms, and diverse elasmobranch and bony fish faunas)~~,~~ which 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, crocodilians, 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 basis~~e~~ of macroinvertebrate biostratigraphy and ^{87}Sr/^{86}Sr isotope chronostratigraphy (Moreno et al., 2015).

4 Results

4.1 Elasmobranch paleodiversity

The taxonomic~~al~~ 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 identified in~~recorded from~~ the 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*~~Nebrius~~ Rüppell, 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 f~~F~~ormations and Patsúa assemblage (locality 290468) (Fig. 9b, Tables S1–S2). *Isurus* cf. *I. oxyrinchus* Rafinesque, 1810 (Fig. 3p–t), †*Paro~~a~~todus benedenii* (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 at~~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 the Sphyrnidae Gill, 1872 [†*Sphyrna arambourgi* Cappetta, 1970 (Fig. 6s–v); †*Sphyrna laevissima* (Cope, 1867) (Fig. 6w–z')] and the Hemigaleidae Hasse, 1879 [†*Hemipristis serra* (Agassiz, 1835) (Fig. 4t–w)], the latter being the most abundant taxon among the studied carcharhiniforms~~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 of 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, T~~t~~able 2; 2016b, T~~t~~able 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). *Rhynchobatus* Müller and Henle, 1837 was recovered from the Castilletes Formation~~Fm.~~ and are represented by a few isolated teeth (Fig. 7a–i, Table S1)~~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 in~~of~~ Tropical America (Carrillo–Briceño et al., 2016a; Aguilera et al., 2017a). W~~, however, w~~e refrain ~~any~~ 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). *Pristis* Linck, 1790 is present in both the Castilletes and Ware formations and represented by rostral denticles and a fragment of rostrum (Fig. 7j–m, Table S1)~~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 fFormations (Table S1)~~. N~~As n~~oted by Carrillo–Briceño et al. (2015b), rostral fragments and denticles are not diagnostic for accurate specific taxonomic determinations.

- **Myliobatiformes Compagno, 1973.** This order is r~~R~~epresented 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)]. T, this group of batoids (Table 1) is the most abundant and the third most diverse group of chondrichthyans inelasmobranch 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 fFormations, and the locality 290468; whereas, *Rhinoptera* sp. has a record in the Cocinetas assemblages from the early Miocene to the late Pliocene and is, being the most abundant taxon (Tables S1–S2). More than 419 highlyhardly eroded and broken teeth without any diagnostic features for generic determination have been assigned to Myliobatoidea indet. (Table S1), however, theywe 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 recognizednoted (Table S3). For the Jimol Formation, the most diverse feeding group is piscivorous, which isfeeder group is that of the piscivorous (Fig. 10), dominated by carcharhiniforms, lamniforms, and a fewminority of squaliforms representatives(Fig. 10, Table S3). The second most diverse group is durophagous/cancritrophic group(mollusk, crustacean, coral feeders), which is the most abundant in the Jimol assemblages (Fig. 10) and dominated mainly by myliobatiforms taxa (Table S3). †*Carcharocles* sp. is the only possible eurytrophic/sarcophagous (diverse prey sources: fishes, reptiles, birds, mammals, etc.) representatives of this unit. Like the Jimol Formation, the Castilletes Formation fauna also shows a diversity dominated by piscivorous taxa (Fig. 10), and abundance dominated by the durophagous/cancritrophic group (represented in the Castilletes assemblages mainly by myliobatiforms) (Table S3). In the Castilletes assemblage, †*Carcharocles megalodon* and †*Galeocerdo mayumbensis* are the only representatives of the eurytrophic/sarcophagous niche, and the filter feeding nichefeeders (diet based mainly on planktonic microorganisms) is represented only by the mobulid †*Plinthicus 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 fFormations, the Patsúa assemblage (localities 290468 and 290472) is characterized by a higher diversity and abundance of piscivorespiscivorous, 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 Jimol, Castilletes and Patsúa assemblages, the elasmobranch assemblage from the Ware Formation shows low diversity and abundance of taxa (Fig. 10, Tables S1–S3).

4.3 Stable isotope analysis of shark teeth

The $\delta^{18}O_{PO4}$ values of the 73 shark teeth analyzed have a 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). Adjacent lLayers containing few teeth and/or very close to adjacent levels were averaged to be representative for a wider periodfor better representation. The rangeVariability of the $\delta^{18}O_{PO4}$ values within the same beds varyis up to 4 ‰, and the highest is in the Patsúa assemblage (locality 290468), where many teeth from different species were available (seven species, n = 26)however, a large variation was not exclusively found in levels where many samples were analyzed (e. g., Castilletes, locality 390093).

Results from sharks of the Patsúa assemblage are mainly discussed in terms of paleoecology, since the age of the assemblage is unknownSeveral 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 compositionsdata from the two stratigraphically uncertain Patsúa layerslevels are very similar (localities 290468 and 290472, *t* test: $t(24) = 0.275$; $p > 0.78$), hence can be considered as one whole dataset.

InRegarding the Castilletes Formation, the mean $\delta^{18}O_{PO4}$ values do differ along the stratigraphic columnsedimentary profile (Fig. 11a). Statistical tests performed in the following stratigraphic orders have not shown significant differences between the sample batches that are following each other, except for the uppermost locality 390093Isotopic values increase towards the middle Miocene (localities 130024, 430202: 20.4 ±1.0 ‰, n = 5), but then decrease in the following intervals (locality 390093: 18.7 ±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 $\delta^{18}O_{PO4}$ value for this lithostratigraphic unit. WhenTukey's pairwise comparison distinguishedis applied to the data of the Castilletes layers, then the top bed asis significantly different from the two lowermiddle levels of 290438 and 430202–130024. Samples from this layer had the lowest average $\delta^{18}O_{PO4}$ value for this lithostratigraphic unit (18.7 ±1.3 ‰, *n* = 4).

In the youngest unit of the Ware Formation low $^{18}O/^{16}O$ were measured for the bull shark *C. leucas* specimens (CL.1–CL.12: 17.6 ±1.1 ‰, *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 older Jimol Formation only two teeth were analyzed, but their average is inundistinguishable from that of the overall average value of both the Castilletes and Patsúa assemblages. When the Patsúa, Castilletes and Ware assemblages are compared on a boxplot, the averages of the first two are indistinguishable (Fig. 11b)The three larger assemblages of Patsúa, Castilletes and Ware can be compared on a boxplot (Fig. 11b). The averages of the first two are undistinguishable; h. However, both are significantly different from thethat of Ware samplesdataset. Outliers toward lower isotopic values were found inThere is one outlier from each of the Patsúa and Castilletes faunas, which are teeth of a †*Carcharocles chubutensis* (290468) and a †*Negaprion eurybathrodon* (390093) specimens, respectively.

5 Discussion

5.1 Diversity and biostratigraphy significance

Of the elasmobranch assemblages described here from the Cocinetas Basin (∼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 shark taxa (*Nebrius* sp., †*P. benedenii*, †*C. chubutensis*, †*C. megalodon*, *Alopias* cf. †*A. exigua*, †*A. retroflexus*, †*G. mayum-*

bensis, †*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 f~~F~~ormations and the Patsúa assemblage, share certain similarities~~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 all the ~~overall~~ assemblages from the Cocinetas Basin (Tables S1–S2, Fig. S5). In contrast, the Jimol and Ware f~~F~~ormations 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 attribut ed~~able~~ to: 1) less intensive sampling, ~~and~~ 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 dismissing~~leaving aside~~ a 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 ~~too~~ has been previously discussed for ~~an~~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}Sr/^{86}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. Due to the relatively small size of the †*C. chubutensis* teeth from the localities 290468 and 290472 (Table S1), these likely belong to juvenile and sub-adults individuals (Figs. 3w–z, 4a–d). The specimens assigned here to †*C. chubutensis* are characterized by the presence of pair of lateral cusplets that are not separated from the main cusp and a narrower cusp in lower teeth, while those assigned to †*C. megalodon* have a wider crown in lower teeth and lack lateral cusplets.

†*Carcharhinus gibbesii* in Jimol Formation, besides being present~~as well~~ in the Patsúa assemblage it 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 the 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 previously from the early Miocene Cantaure (Venezuela) and Pirabas (Brazil) f~~F~~ormations (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.

With~~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 (Dartevelle and Casier, 1943; Andrianavalona et al., 2015; Argyriou et al., 2015) and South America (Carrillo–Briceño et al., 2016a; Aguilera et al., 2017a). According to the morphology of some illustrated teeth (resembling the morphology of those of †*G. mayumbensis*), taxonomical misidentifications could also include specimens 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, 2c), for which a more detailed review of these specimens would be necessary. Abundant unpublished teeth of †*G. mayumbensis* (labelled in public and private collections) from the east coast of the US, questionably have been assigned to a middle to late Miocene and Pliocene age without a detailed stratigraphic information. However, many specimens are certainly present at least in the earlier portion of the middle Miocene section of the Bone Valley Formation in Florida (DJE Ehret, personal communication, August 2, 2018). The absence of †*G. mayumbensis* in locations younger than early Miocene (with the exception of the above record Bone Valley Formation), and the tendency of the overall stratigraphical distribution of †*G. mayumbensis*, including the new referenced 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 and beginning of middle Miocene, with a widespread distribution.~~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, 2c). There is not a consensus about unpublished †*G. mayumbensis* teeth (labelled/collections) and their localities from 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 US), 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 with 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, see 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 piscivorous carchariniform~~s~~ and lamniform~~s piscivorous~~ species (Figs. 9–10). However, in this assemblage, durophagous/cancritrophic representatives are the most abundant group (i. e., rays), which are potential prey in marginal marine and brackish environments for piscivirous sharks (see Hendy et al., 2015). This could support habitat and feeding preferences of carchariniform and lamniform species in the Jimol Formation.~~, 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 carcharhiniforms and myliobatiforms, where more than the 80% of the taxa~~abundance~~ correspond~~s~~ to ~~species of~~ durophagous/cancritrophic feeding preferences (Figs. 9–10) and commonly these fishes are~~. 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, crocodilians, 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 depositional environment, similar to those habitats that characterize the Neogene Urumaco sequence in Western Venezuela (Aguilera et al., 2013; Carrillo–Briceño et al., 2015b; 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).~~(Carrillo–Briceño et al., 2015b).~~ The elasmobranch fauna of the Castilletes Formation is similar to the Urumaco sequence because it is dominated by durophagous/cancritrophic taxa (such as *Aetomylaeus*, *Rhinoptera*, and Myliobatoidea indet.) (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 similarity 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 piscivorous carchariniform~~s~~ and lamniform~~s piscivorous~~ species (Figs. 9–10). The presence of the lamniform *Isurus* cf. *I. oxyrinchus*, the otodontid †*Par*o~~a~~*todus benedenii*, the alopiids *Alopias* cf. †*A. exigua* and †*Anotodus retroflexus*, and the prist~~h~~iophoriform *Pristiophorus* sp., could suggest a fully marine environment. ~~It is supported by t~~The associated bony fishes (Acanthuridae, Labridae, Scaridae, Sparidae, Sphyraenidae, Balistidae and Diodontidae, (see Fig. S7), corals, bryozoans, echinoderms and mollusks~~,~~ suggest~~ing~~ a subtidal marine environment with limited influence from major freshwater input (see Hendy et al., 2015). The mollusks and echinoderms~~, in particular,~~ are distinctive from those of the Jimol and Castilletes f~~F~~ormations 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*~~Teredo~~ or shipworm)~~,~~ and *Aturia* (nautiloid), which presumably were washed up onto a more exposed coastal setting. An isolated and incomplete Odontoceti tooth also was recorded from~~in the~~ locality 290472 (specimen MUN–STRI–44517).

In contrast with the diverse early–middle Miocene elasmobranch assemblages of the Jimol and Castilletes fFormations, and 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 vertebrate fishes, turtles, crocodilians, and mammals, also have also 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 thethis basal portionsection of the Ware Formation (Moreno et al., 2015; Pérez–Consuegra et al., 2018). The sharks *Carcharhinus leucas*, and †*Negaprion eurybathrodon*, as well the batoids *Pristis* sp. and *Rhinoptera* sp., are the only representative chondrichthyan species for this unit (Table S1). TAll these species are able to inhabit both marine and brackish environments (Feldheim et al., 2002; Matich and Heithaus, 2013; Ebert and Stehmann, 2013; Ebert et al., 2013; Carlson et al., 2013; Carrillo–Briceño et al., 2015b) (see Carrillo–Briceño et al., 2015b, fig. 10). *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 Paleoenvironmental reconstruction based on the $\delta^{18}O_{PO4}$ dataThe shark bioapatite and paleosalinity

Samples with $\delta^{18}O_{PO4}$ values less than 18.4 ‰ are likely to have been formed in waters that are not other than exclusively marine ($\delta^{18}O_w$ = 0 ‰), since the paleotemperatures calculated from much lower $\delta^{18}O_{PO4}$ values are too high to represent typical shark habitats. However, fishes which form their bioapatite in a freshwater influenced settings with less than 0 ‰ $\delta^{18}O_w$ values (e. g., rivers, lakes) also have lower $\delta^{18}O_{PO4}$ values at the same ambient temperature of formation (Longinelli and Nuti, 1973a; Kolodny et al., 1983; Kocsis et al., 2007; Fischer et al., 2013a; Leuzinger et al., 2015). STherefore, samples with a such low $\delta^{18}O_{PO4}$ values may thus indicate the presence of brackish–like environments., due to the mixing of seawater with, for example, river water.

Therefore, The shark tooth $\delta^{18}O_{PO4}$ 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 formations (Fig. 11).

- **Patsúa assemblage.** The age of this fauna is not as well established as it is for the other sites, therefore the obtained isotopic values represent paleoenvironmental conditions somewhere within the Burdigalian and Langhian periods.The samples from the Patsúa assemblage have not been separately dated but the teeth from this locality were in situ and their isotopic composition represent the sediment deposited somewhere within the Burdigalian and Langhian periods. These shark teeth had predominantly "marine" isotopic compositions with one low $\delta^{18}O_{PO4}$ value measured from a †*Carcharocles chubutensis* specimen (CC.4: 17.4 ±0.3 ‰, Table 2, Fig. 11b). This isotopic composition is typical for brackish waters although †*Carcharocles chubutensis* utilized a habitat similar to the recent great white shark (*Carcharodon carcharias*).was measured for an extinct species, which has analogous habitat, and Mmost of the isotopic data forin the extant and fossil species of lamniform sharks are characteristic of cold waters, because of its long oceanic migrations and formation of bioapatite in such cold settings (Barrick et al., 1993; Vennemann et al., 2001; Amiot et al., 2008; Ebert et al., 2013; Aguilera et al., 2017a). Therefore, the low $\delta^{18}O_{PO4}$ value from this species is quite surprising and may indicate some hidden habitat trait for this ancient shark. Statistical comparisons usingagainst the available datasets demonstrate this assemblage isas inundistinguishable from Castilletes Formation (Fig. 11b). Possibly these paleoenvironments were similar and based on the $\delta^{18}O_{PO4}$ 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 Formation~~Fm~~.** The sedimentary sequence of the Cocinetas Basin is described as a transition from a shallow marine to a fluvio–deltaic paleoenvironment (i. e., a regression). Similar to~~Like~~ the results from the Patsúa assemblage, the $\delta^{18}O_{PO4}$ values are predominantly marine, except for~~besides~~ a single tooth of †*Negaprion eurybathrodon* (NG.14: 16.7 ±0.2 ‰, Fig. 11a, b)~~, a species from the same genus of the modern lemon shark (*Negaprion brevirostris*)~~. Extant individuals of this genus~~group~~ inhabit marine inshore areas and commonly migrate through enclosed bays or river mouths, supporting an isotopic freshwater–influenced habitat (Castro, 1993; Feldheim et al., 2002)~~a freshwater influence on the isotopic composition measured~~. In fact, more samples covering the 'brackish' range were expected~~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 estimat~~eion~~s using mollusks~~ 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~~ like a transgressive–regressive cycle (Hendy et al., 2015). The $\delta^{18}O_{PO4}$ mean values show a minor increase from the base towards the middle section of Castilletes (20.4 ±1.0 ‰, *n* = 5, Fig. 11a), decreasing thereafter to the lowest mean value in this formation (18.7 ±1.3 ‰, *n* = 4). This possibly~~Possibly this~~ indicates regional changes in the paleoenvironment of~~ the~~ shark habitats (e. g., marine to estuarine). However, because~~, but since~~ the overall deviation is overlapping between the localities, more samples would be required to refine such an isotopic fluctuation. While the overall shark isotope data represent marine conditions during the deposition of the Castilletes Formation,~~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~~ nearby~~ presence of~~ rather~~ brackish conditions nearby into which some sharks ventured. This interpretation is in agreement with the higher resolution mollusk~~s~~ data from the region (Hendy et al., 2015).

- **Ware Formation~~Fm~~.** ~~Here~~ T~~t~~he isotope data are significantly different for the Ware Formation from the~~ result from~~ Patsúa assemblage and Castilletes Formation (except for~~vs~~ locality 390093, Fig. 11a, b). The $\delta^{18}O_{PO4}$ values are generally lower in this formation, especially for~~ the bull sharks (~~ *Carcharhinus leucas* (~~,~~ CL.1–CL.12: 17.6 ±1.1 ‰, *n* = 12). This euryhaline species, like *Negaprion brevirostris*~~the lemon shark~~, also inhabits~~ in~~ marine inshore zones and occasionally migrates into brackish environments. However, *Carcharhinus leucas* is today well-known~~ bull sharks are currently well recognized~~ for their ability to persist in~~through~~ coastal ~~sub–~~environments with brackish conditions, as individuals can also swim hundreds of meters upstream into~~even in~~ freshwater (Matich and Heithaus, 2013; Ebert et al., 2013). The isotopic range for the Ware Formation~~from Ware~~ sharks are in a agreement with the fluvio–deltaic paleoenvironment of deposition described for this F~~f~~ormation (Moreno et al., 2015; Pérez–Consuegra et al., 2018) and also with the euryhaline predominant fauna presented here (*Pristis* sp., *C. leucas*, *Rhinoptera* sp., †*Negaprion eurybathrodon*). The two samples of †*Negaprion eurybathrodon*~~lemon shark relatives~~ have $\delta^{18}O_{PO4}$ values which probably~~ have been~~ formed under distinct marine conditions rather than under fluvial influence (NG.15: 20.7 ±0.1 ‰; NG.16: 20.5 ±0 ‰). 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 originating~~ated~~ from different layers within~~of~~ a wider fluvio–deltaic system. Therefore, while the *Carcharhinus leucas* specimens~~bull shark teeth~~

reflect clear fluvial conditions, the †*Negaprion eurybathrodon* teethlemon shark remains may have been derived from layers originally deposited in athe prodelta or nearby shallow coastal marine beds. Eventually, these *Negaprion* teeth grown under marine conditions could have been lost in the fluvio–deltaic paleoenvironment exploited by sharks.

Carcharhinus leucas teeth are also smaller compared to other specimens (and species) utilized employed in this study. Modern representatives of adult *Carcharhinus leucas* normally have anterior teeth around 2 cm in height (Ebert et al., 2013, personal observation), a size considerably largerbigger than our sampled teeth (< 1 cm, Fig. S8). Even when taking into consideration more curved and possibly posterior teeth of adult specimens, we estimate that most of our *Carcharhinus leucas* $\delta^{18}O_{PO4}$ data were obtained from juvenile and subadult individuals. In previous stable isotope investigations, only samples from young specimens from Lake Nicaragua provided $\delta^{18}O_{PO4}$ values characteristic of a brackish condition (Kocsis et al., 2015; Aguilera et al., 2017a). Since our *Carcharhinus leucas* teeth yielded predominantly $\delta^{18}O_{PO4}$ values typical of brackish waters, possibly they were using the coastal zone of Cocinetas Basin as a paleonursery habitat. 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 of adjacent areas as a nursery ground (e.g., Maracaibo Lake, Rodríguez, 2001, Tavares and Sánchez, 2012). Moreover, the predominant brackish–like $\delta^{18}O_{PO4}$ 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 Carcharhiniformes and Lamniformes respectively. The fossil assemblage seems to agree with paleoenvironmental descriptions from previous studiesto represent the paleoenvironments described for the fossiliferous formations of Cocinetas Basin (Jimol, Castilletes and Ware).

• An distinctive assemblage is reported from undifferentiated facies of the Jimol and Castilletes Formation, and represents a subtidal marine environment with limited freshwater influence.

• The biogenic phosphate $\delta^{18}O_{PO4}$ values of 73 shark teeth were evaluated withinfor the sedimentary sequence of the Cocinetas Basin. The isotopic data werewas used tofor estimate paleoenvironmental settingsthe paleosalinity (e.g., marine vs brackish vs freshwater), corroborating with previous descriptionsand corroborated the paleoenvironments described for Castilletes and Ware formations.

• A predominant brackish–like $\delta^{18}O_{PO4}$ value was measured for *Carcharhinus leucas*bull sharks, which are likelyprobably juveniles, suggesting that at least since the late Pliocene this species was already well adapted to migrate into habitatsthrough 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

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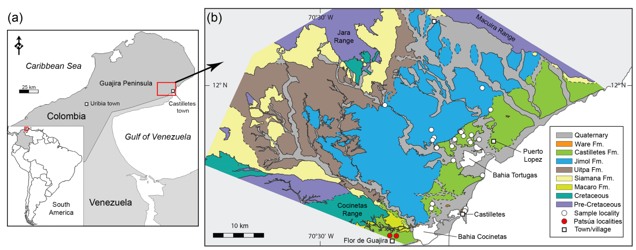

Figure 1. Location **(a)** and geological map of the southeastern Cocinetas Basin **(b)**. Abbreviation: Fm. (Formation).

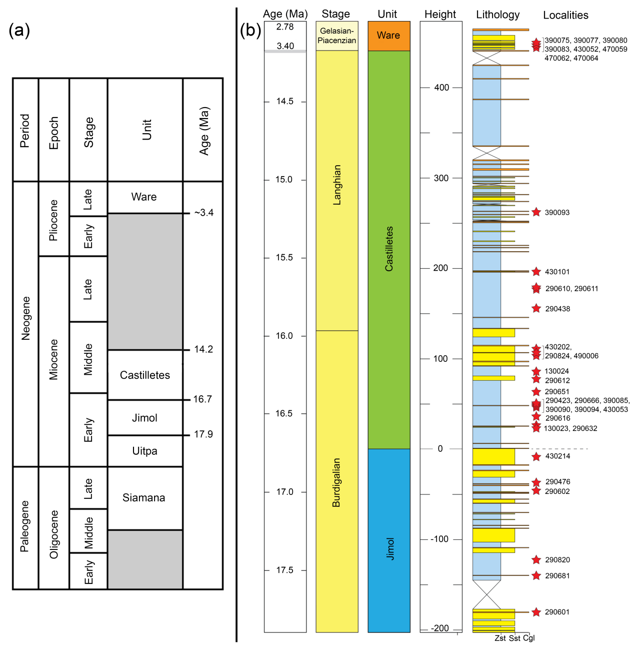

Figure 2. Stratigraphy of the Cocinetas Basin. **(a)** Generalized stratigraphy (after Moreno et al., 2015). **(b)** Stratigraphic section and studied localities. Localities of the Patsúa Valley (290468 and 290472) (details in Table S1) are not represented, because these localities~~due these~~ belong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

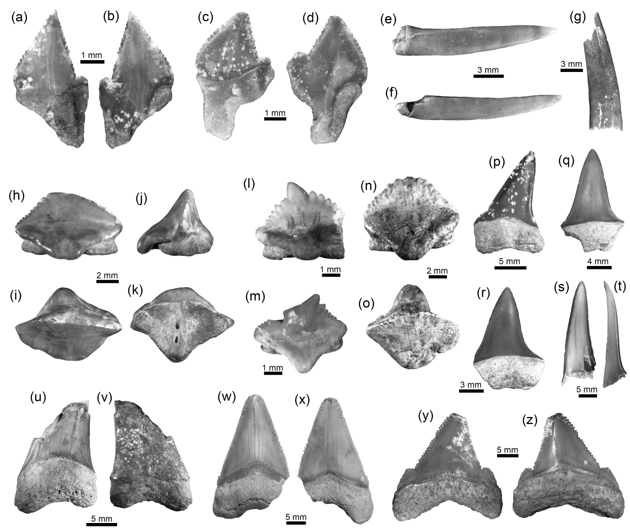

Figure 3. Squaliformes, Pristiophoriformes, Orectolobiformes and Lamniformes of the Cocinetas Basin. **(a–d)** *Dalatias* cf. *D. licha* (MUN–STRI–41205). **(e–g)** *Pristiophorus* sp. (MUN–STRI–34788). **(h–o)** *Nebrius* sp. (h–m~~k, n–o~~: MUN–STRI–41136; n–o~~l–m~~: MUN–STRI–41180). **(p–t)** *Isurus* cf. *I. oxyrinchus* (MUN–STRI–37671). **(u–v)** †*Paro~~a~~todus 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).

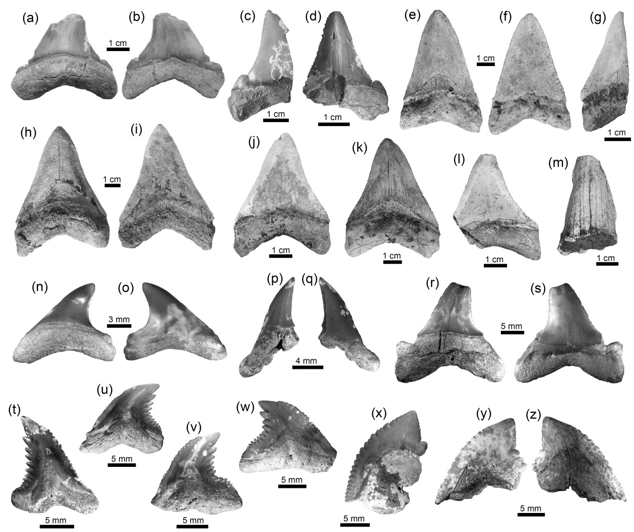

Figure 4. Lamniformes and Carcharhiniformes of the Cocinetas Basin. **(a–d)** †*Carcharocles chubutensis* (MUN–STRI–40375). **(e–l)** †*Carcharocles megalodon* (e–g: MUN–STRI–37812; h–i: MUN–STRI–38067; j–l: MUN–STRI–41145). **(m)** †*Carcharocles* sp. (MUN–STRI– 41138). **(n–q)** *Alopias* cf. *A. exigua* (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).

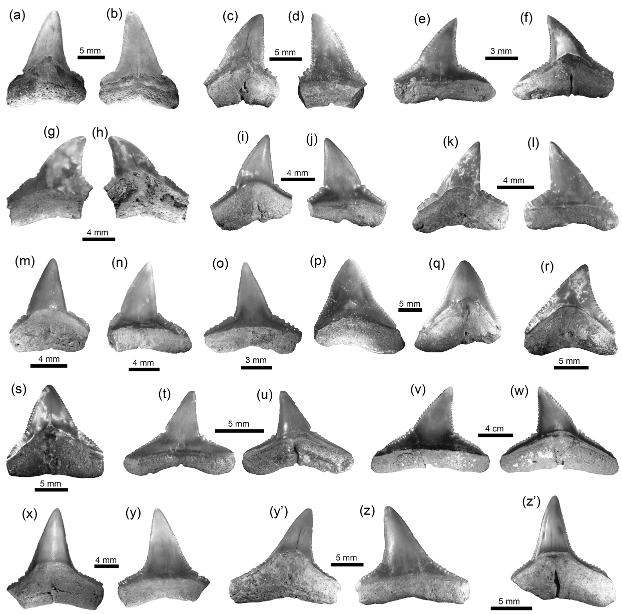

Figure 5. Carcharhiniformes of the Cocinetas Basin. **(a–d)** †*Carcharhinus ackermannii* (a–b: MUN–STRI–41128; c–d: MUN–STRI–43743). **(e–h)** *Carcharhinus* cf. *C. brachyurus* (MUN–STRI–41207). **(i–o)** †*Carcharhinus gibbesii* (MUN–STRI–43808). **(p–s)** *Carcharhinus leucas* (p–q: MUN–STRI–37646; r: MUN–STRI–21937; s: MUN–STRI–16287). **(t–u)** *Carcharhinus* cf. *C. limbatus* (MUN–STRI–41153). **(v–w)** *Carcharhinus* cf. *C. perezi* (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').

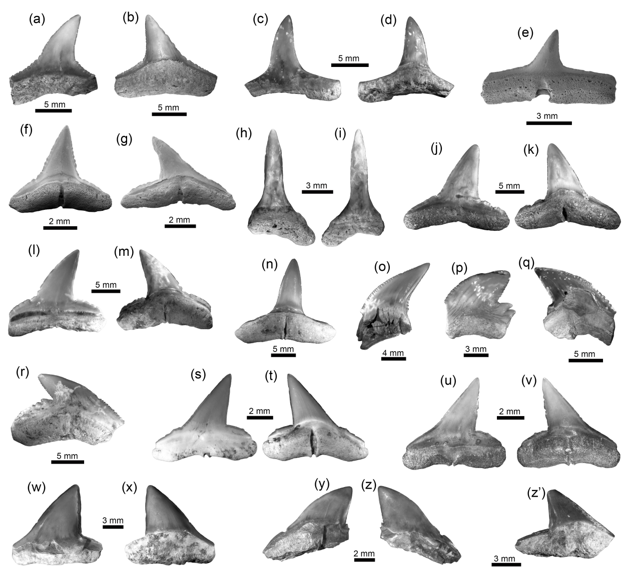

Figure 6. Carcharhiniformes of the Cocinetas Basin. **(a–d)** *Carcharhinus* cf. †*C. priscus* (MUN–STRI–43804). **(e–g)** *Carcharhinus* spp. (e: MUN–STRI–42136; f–g: MUN–STRI–42128). **(h–i)** †*Isogomphodon acuarius* (MUN–STRI–41184). **(j–n)** †*Negaprion eurybathrodon* (MUN–STRI–41133). **(o–r)** †*Physogaleus contortus* (o–q: MUN–STRI–40378; r: MUN–STRI–41132). **(s–v)** †*Sphyrna arambourgi* (MUN–STRI–41143). **(w–z')** †*Sphyrna laevissima* (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').

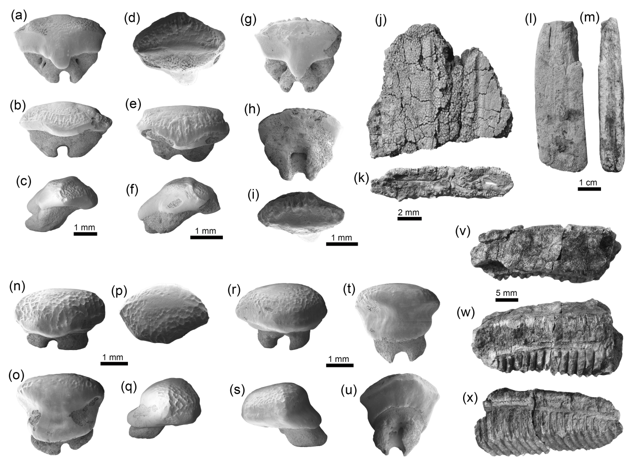

Figure 7. Rhinopristiformes and Myliobatiformes of the Cocinetas Basin. **(a–i)** *Rhynchobatus* sp. (MUN–STRI– 42132). **(j–m)** *Pristis* sp. (fragment of rostrum j–k: MUN–STRI–37397; rostral denticle l–m: MUN–STRI–34762). **(n–u)** *Dasyatis* sp. (MUN–STRI–42135). **(v–x)** *Aetobatus* sp. (MUN–STRI–34465). 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).

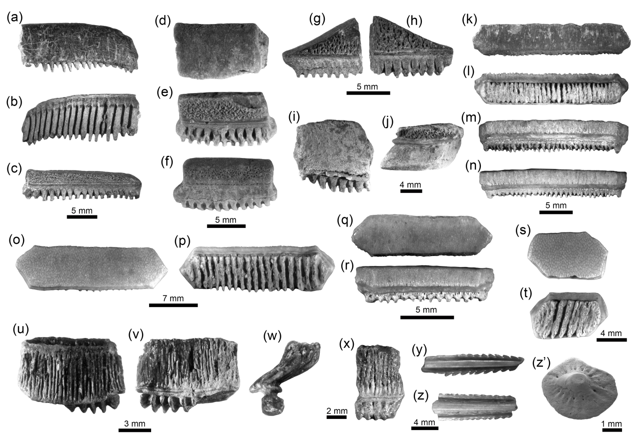

Figure 8. Myliobatiformes of the Cocinetas Basin. **(a–j)** *Aetomylaeus* sp. (a–c: MUN–STRI–41134; d–f: MUN–STRI–43746; g–j: MUN–STRI–41134). **(k–t)** *Rhinoptera* sp. (MUN–STRI–41138). **(u–x)** †*Plinthicus stenodon* (MUN–STRI–41203). **(y–z')** Myliobatiformes indet. (caudal spines y–z: MUN–STRI–34785; 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).

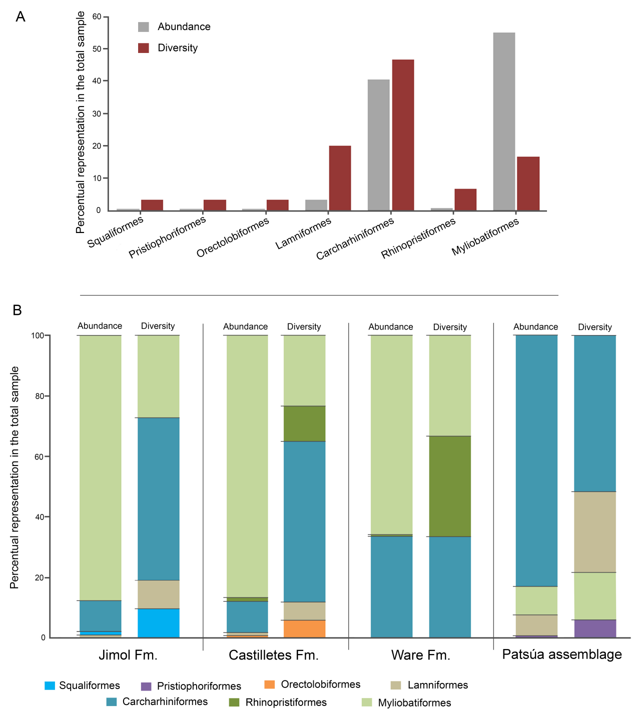

Figure 9. Elasmobranch paleodiversity (orders) of the Cocinetas Basin. **(a)** Overall assemblages. **(b)** Assemblages by geological units.

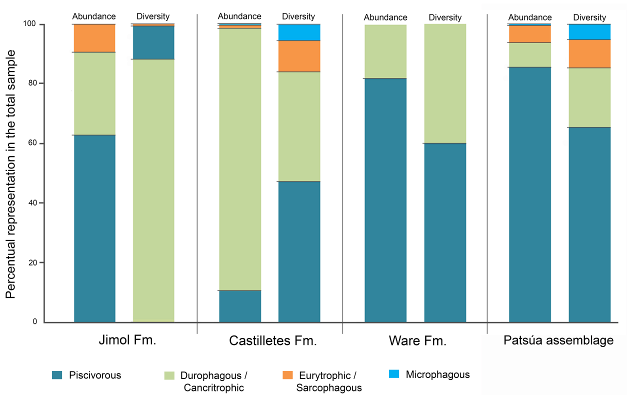

Figure 10. Dietary preferences of the elasmobranch paleofauna fromoverall Cocinetas Basin assemblages by geological units.

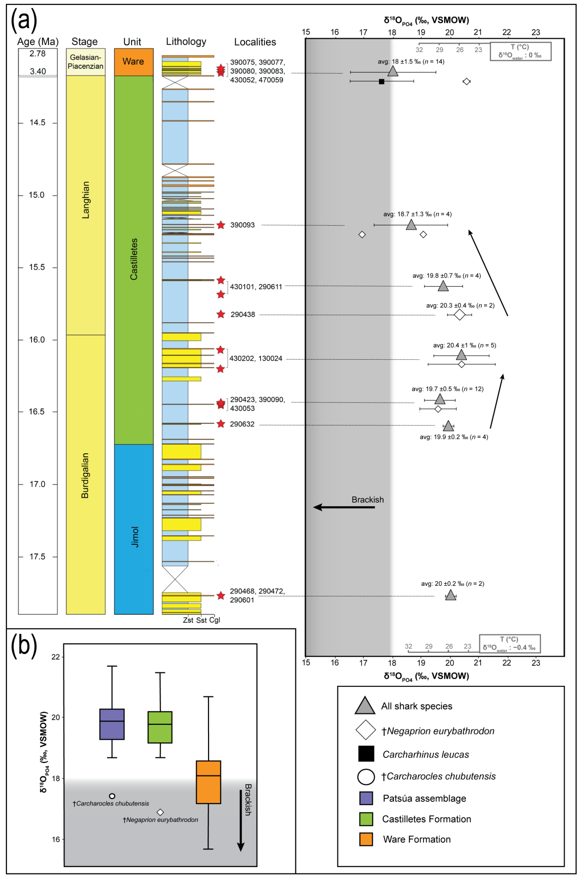

Figure 11. Stratigraphic distribution of the $\delta^{18}O_{PO4}$ from sharks of the Cocinetas Basin. The gray–shaded area marks the isotopic range representative of brackish environments. Big symbols give the average of all shark data within the same layer and its standard deviation, while smaller icons 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 *Carcharhinus leucas*~~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 $\delta^{18}O_w$ of 0 ‰ and –0.4 ‰, respectively (Lear et al., 2000; Billups and Schrag, 2002). **(a)** The mean $\delta^{18}O_{PO4}$ 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 have~~yielded~~ $\delta^{18}O_{PO4}$ values predominantly characteristic of brackish environments. **(b)** Boxplot of the $\delta^{18}O_{PO4}$ values from samples of the Patsúa assemblage, Castilletes and Ware f~~F~~ormations. Each outlier from the Patsúa assemblage and Castilletes are teeth with $\delta^{18}O_{PO4}$ values considered to form under 'brackish' conditions.

Table 1. Elasmobranchii paleodiversity of the Cocinetas Basin.

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

Table 2. Shark teeth specimens used in geochemical investigation.

Sample ID	Taxon	Formation	Locality	$\delta^{18}O_{PO4}$ (‰, VSMOW)	$\delta^{18}O_{PO4}$ std dev.
HS.1	†*Hemipristis serra*	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	†*Carcharocles chubutensis*			19.9	0.1
CC.2				19.1	0.2
CC.3				19.4	0.1
HS.6	†*Hemipristis serra*		290468	19.3	0.1
HS.7				20.2	0.3
HS.8				19.9	0.1
NG.1	†*Negaprion eurybathrodon*			18.9	0.2
NG.2				19.9	0.2
GM.1	†*Galeocerdo mayumbensis*			20.5	0.1
GM.2				20.3	0.1
GM.3				19.3	0.2
SL.1	†*Sphyrna laevissima*			19.9	0.0
SL.2				19.1	0.1
SL.3				18.7	0.3
CC.4	†*Carcharocles chubutensis*			17.4	0.3
CC.5				19.2	0.2
CC.6				20.7	0.0
IO.1	*Isurus* cf. *I. oxyrinchus*			21.7	0.3
IO.2				20.8	0.0
IO.3				19.3	0.3
PC.1	†*Physogaleus contortus*			19.8	0.0
PC.2				20.5	0.0
PC.3				19.4	0.1
HS.9	†*Hemipristis serra*	Castilletes	290632	19.8	0.3
HS.10				19.8	0.1
CS.1	*Carcharhinus* sp.			20.1	0.2
CS.2				20.1	0.1
HS.11	†*Hemipristis serra*		290423	19.1	0.2
NG.3	†*Negaprion eurybathrodon*			19.5	0.3
HS.12	†*Hemipristis serra*		390090	19.6	0.0

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

Sample ID	Taxon	Formation	Locality	δ^{18}O$_{PO4}$ (‰, VSMOW)	δ^{18}O$_{PO4}$ std dev.
HS.13	†*Hemipristis serra*	Castilletes	390090	19.5	0.0
NG.4	†*Negaprion eurybathrodon*			20.1	0.2
NG.5				18.8	0.2
SA.1	†*Sphyrna arambourgi*			20.1	0.3
SA.2				19.2	0.1
HS.14	†*Hemipristis serra*		430053	20.1	0.2
HS.15				20.4	0.0
NG.6	†*Negaprion eurybathrodon*			20.4	0.1
NG.7				19.2	0.1
NG.8			130024	19.2	0.2
HS.16	†*Hemipristis serra*		430202	21.1	0.0
HS.17				19.7	0.1
NG.9	†*Negaprion eurybathrodon*			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	*Carcharhinus* sp.		290611	18.9	0.2
CS.4				20.3	0.2
CS.5				20.2	0.1
HS.18	†*Hemipristis serra*		430101	19.8	0.1
NG.13	†*Negaprion eurybathrodon*		390093	19.1	0.1
NG.14				16.9	0.2
CS.6	*Carcharhinus* sp.			18.7	0.0
CS.7				19.9	0.1
CL.1	*Carcharhinus leucas*	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	$\delta^{18}O_{PO4}$ (‰, VSMOW)	$\delta^{18}O_{PO4}$ std dev.
CL.12	*Carcharhinus leucas*	Ware	390075	17.2	0.2
NG.15	†*Negaprion eurybathrodon*			20.7	0.1
NG.16				20.5	0.0

RC 1 (Anonymous Referee)

Dear Anonymous Referee,

Thank you very much for your considerations about our submitted manuscript. We revised our writing and many sentences were rewritten. We hope that now the manuscript is adequate for publication in the Biogeosciences journal.

Considerations and points raised are answered below:

Interactive comment responses

Comment: "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 authors address this taxonomic revision in <10 lines per family within the results (p. 6–7) with many families containing more than one taxon. If there are revisions to the taxonomy (or even establishment of taxa or taxon), a more careful description of the specimens, previous taxonomic classification, justification for the changes, and discussion of the systematics are needed at the individual taxa level, either genus or species depending on the classification.

Answer: We are grateful with this important suggestion from the referee. First we want to apologize, because it has been a mistake from us, when we were not clearer in the introduction or methods sections. It generated misunderstandings for the readers. The focus of this manuscript was not a detailed taxonomic revision of the fossil assemblage. For 30 taxa we should dedicate a long description section which could resulted in a long monograph, far for the plan and objectives expected for this manuscript. Any specimens referred in our contribution do not represent a new species or taxon, for which a description is not required. We have linked all the references for the original descriptions of each taxon, other descriptions and their record in Tropical America for supporting our assignations. Usually paleontological and neontological manuscripts with only taxonomic list do not require a detailed description. In our case, we have presented general information for each taxon, detailed and high quality pictures with the best representative specimens for each taxon. Additionally, supplementary information (e. g., Table S2) with information about total number, tooth measurements, jaw position and provenance of all the fossil specimens are provided.

Comment: "The assemblage includes 30 taxa, of which 24 are new reports for Colombian Neogene deposits." Again, an assemblage description needs to be more careful and detailed with information on tooth morphology including but not limited to tooth shape, size, position, wear, etc.

Answer: Continuing the idea of the above answer, the assemblage from Colombia is not represented by new taxa for the scientific community. It represents new records from the country of taxa that were previously described and referred from other regions of the Caribbean, Tropical America and the Americas in general (see references section). We presented a paleodiversity compilation of the fossil assemblages. Fossil assemblages have different ways to be described, for example: a) with detailed taxonomic description (which is out the focus of our manuscript), b) just as simple taxonomic lists with or without illustrative support, and c) taxonomic lists, with general information about taxonomic comments and information supported by a detailed supplementary and illustrative information. The last one is our case.

Comment: There are no paleosalinity estimates given in this manuscript. There are oxygen isotope values that indicate lower salinity environments, but the authors do not give actual paleosalinity and only refer to broad and qualitative interpretations of environmental conditions. It is possible for the authors to use a paleosalinity model as established in the literature if they use estimates of temperature and freshwater oxygen isotope composition from the literature.

Answer: Indeed, no net paleosalinity values are given. Since we lack additional proxies for estimating the freshwater oxygen isotope composition (e. g., marine mammal bones), we have chosen to replace the term ‘paleosalinity’.

Changes: Replaced in P. 1 L. 8; P. 2 L. 21; P. 13, L. 12; P. 15 L. 26.

Comment: Next, the authors present the generalized diet for modern analogues to discern feeding ecology. However, the authors do not give specific species for modern analogues; many modern families referred to for the fossil specimens have a wide variety of diet and habitat preferences that cannot be easily summarized and condensed as they are in the current manuscript (P. 8 L 4-20). The modern analogues are not identified and furthermore, little to no justification for how and why the fossil taxa should follow these modern ecological classifications. Further, if the modern analogues were named, I am almost certain that a careful and deeper search of the modern shark ecology research would yield more specifics on dietary preference, migration patterns, and other important aspects of ecology.

Answer: About “However, the authors do not give specific species for modern analogues”, one of the most complex topics and challenges in paleoecology is the inferences about paleo diets. How it is referred in the text “Extant sharks and rays exhibit 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”. A dietary composition and behavior of extant/relative species of the taxa recorded in the Cocinetas assemblages is compiled in the Table S3. Every fossil taxon with living representative is referred with their analogous living species. Fossil taxa without extant representative at species level are compiled according to the preferences of all extant species present in the genus. For extinct species without extant representatives (e. g., families and genera), their paleoecology and potential feeding preferences have been inferred according their fossil record (based on references), tooth morphology and adaptative dental types, diagnostic characters to infer feeding preferences in shark and rays (see Cappetta, 2012, pp. 17-23).

Comment: The authors have a substantial variation in the δ^{18}O values from shark teeth. Given the range of Formations, lithology, and likely depositional environments, the results need to be better organized to reflect these differences. In addition, the paleoenvironmental reconstruction based on these oxygen isotope compositions must consider the habitat reference of the shark that is the basis of geochemical analysis. A shark’s tooth mineralizes at a fairly fast rate below the epithelium but there is a delay until this tooth reaches the first series within the jaw where it is used and lost (and hence deposited into the fossil record). Therefore, for migratory sharks the δ^{18}O value of a tooth may not represent the depositional environment.

Answer: We have tried to summarize the information about the δ^{18}O of shark’s bioapatite formation and incorporation of low δ^{18}O values in the beginning of the discussion about isotopes (P. 13 L. 13–22). A new sentence about the subject was also added in the P. 15 L. 2–3, when referring about *Negaprion* results from Ware Fm.

Changes: Sentence added in P. 15 L. 2–3.

Comment: Parsing out details for modern analogues and their lifestyle can help the authors classify and interpret the variation in δ^{18}O values.

Answer: We have revised some sentences which we mention modern analogues in our stable isotope discussion section. Since *Carcharhinus leucas* is an extant species, only †*Negaprion eurybathrodon* and †*C. chubutensis* needed relevant examples of a modern analogues. For †*C. chubutensis*, *Carcharodon carcharias* is mentioned (P. 13 L. 27–31) and for †*Negaprion eurybathrodon*, *Negaprion brevirostris* is referred (P. 14 L. 6–8).

We hope to have answered all considerations and to have attended the requirements to publish in the Biogeosciences Journal.

Best regards,

Zoneibe Luz.

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