

Article

Dental Morphology, Palaeoecology and Palaeobiogeographic Significance of a New Species of Requiem Shark (Genus *Carcharhinus*) from the Lower Miocene of Peru (East Pisco Basin, Chilcatay Formation)

Alberto Collareta ^{1,2,*} , René Kindlimann ³, Alessio Baglioni ¹, Walter Landini ⁴, Giovanni Sarti ¹ , Alí Altamirano ⁵, Mario Urbina ⁵  and Giovanni Bianucci ^{1,2} 

¹ Dipartimento di Scienze della Terra, Università di Pisa, 56126 Pisa, Italy
² Museo di Storia Naturale, Università di Pisa, 56011 Calci, Italy
³ Haimuseum und Sammlung R. Kindlimann, Aathal, 8607 Zurich, Switzerland
⁴ Accademia Lunigianese di Scienze “Giovanni Capellini”, 19121 La Spezia, Italy
⁵ Departamento de Paleontología de Vertebrados, Museo de Historia Natural-UNMSM, Jesús María, Lima 15072, Peru
* Correspondence: alberto.collareta@unipi.it



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Abstract: Nowadays, the requiem sharks comprise one of the most diverse and widespread families of selachians, i.e., Carcharhinidae. Among the carcharhinids, the genus *Carcharhinus* has the largest number of living species, namely, at least 35. Known from fossils as old as the Cretaceous, the requiem sharks did not significantly radiate before the Eocene (when *Carcharhinus* also appeared), and their diversification mainly occurred in Neogene times. Here, we describe a new species of requiem shark, *Carcharhinus dicelmai* sp. nov., based on fossil teeth from Lower Miocene (18.4–18.1 Ma) strata of the Chilcatay Formation of the East Pisco Basin (southern Peru). Upper teeth of *C. dicelmai* sp. nov. are typically provided with a slender, smooth-edged cusp; a marked coronal twist; and a distal heel that bears 1–5 coarse, angularly lobate serrae that become more prominent toward the base of the cusp. The dentition of *C. dicelmai* sp. nov. appears less akin to that of most other carcharhines to the cutting-clutching type, and seemingly testifies to the development of more predominantly clutching adaptations. A carcharhinid tooth from the Burdigalian to lower Langhian Cantaure Formation of Venezuela is reassigned to *C. dicelmai* sp. nov., suggesting a trans-Panamanian distribution for this extinct shark species.

Keywords: Burdigalian; Carcharhinidae; Carcharhiniformes; *Carcharhinus dicelmai* sp. nov.; Central American Seaway; clutching-type dentition; Elasmobranchii; systematics; taxonomy; vertebrate palaeontology

1. Introduction

Carcharhinidae, also known as requiem sharks, comprise one of the most diverse and widespread families of modern selachians. Among the carcharhinids, the genus *Carcharhinus* has the largest number of living species, at least 35 [1]. Typical field marks of *Carcharhinus* include small, widely spaced nostrils; no spiracles; labial furrows confined to mouth corners; usually serrated or crenulated upper teeth; no cusplets on lower teeth; no keels on caudal peduncle; transverse, crescentic precaudal pits; first dorsal mid-base closer to pectoral bases than to pelvics or, at most, about equidistant between them; second dorsal fin less than half the height of first; second dorsal origin usually about opposite anal origin; and anal fin with preanal ridges short to absent, as well as with a deeply notched posterior margin [2]. Ranging in total body length between less than one and more than three metres, *Carcharhinus* spp. inhabit a broad spectrum of frankly marine, mostly warm-water environments, from shelfal to open-ocean settings, although some species (e.g.,

Carcharhinus leucas and *Carcharhinus melanopterus*) can also enter brackish or even fresh waters [2–7].

The evolutionary history of requiem sharks is relatively shallow if compared to that of other carcharhiniform families such as Scyliorhinidae and Triakidae [8]; indeed, the geologically oldest remains of Carcharhinidae date back to the upper part of the Upper Cretaceous [9], but carcharhinids did not significantly diversify before the Cretaceous/Palaeogene extinction event. A first, reef-associated requiem shark radiation began ca. 45 million years ago and resumed during the Oligocene [10]; however, most of the carcharhinid diversification occurred in Neogene times [9]. As regards the genus *Carcharhinus*, it appears to have emerged in the framework of the first carcharhinid radiation, during the Lutetian (early middle Eocene) [11]. Lately, our knowledge of the past diversity of the genus *Carcharhinus* has been growing steadily, as evidenced by the ten extinct carcharhine species that have been described during the last fifteen years based on fossil remains [12–19].

The fossil record of Carcharhinidae consists mostly of isolated teeth that were predominantly recovered from deposits of the Northern Hemisphere (Marramà et al. [20], and references therein), and the same could be said for the genus *Carcharhinus*. One significant exception is represented by the Middle Eocene to Pliocene sedimentary infill of the East Pisco Basin of Peru—one of the most significant marine vertebrate Fossil-Lagerstätten worldwide [21–66]. Indeed, starting in the last few years, investigations focused on exceptionally preserved specimens [42,67], rare and elusive taxa [68] and a handful of outstandingly productive tooth-bearing localities [69,70] have disclosed a rich elasmobranch fossil record that includes abundant and taxonomically diverse remains of Carcharhinidae, and even ancient nurseries of *Carcharhinus* [70,71].

Our main aim here is to describe a new species of *Carcharhinus* based on teeth from the Lower Miocene (18.4–18.1 million years ago) strata of the Chilcatay Formation of the East Pisco Basin. In doing so, the palaeoecological affinities and palaeobiogeographic bearing of the new species will also be discussed. Interestingly, the fossils dealt with in the present paper also testify to the aftermath of a supposed extinction event in sharks, dated at about 19 million years ago (Sibert and Rubin [72], but see also Feichtinger et al. [73] and Naylor et al. [74] for a rebuttal of Sibert and Rubin's hypothesis).

2. Materials and Methods

2.1. Abbreviations

Ma = million years (ago); MUSM = Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Jesús María, Lima, Peru; RK = Haimuseum und Sammlung R. Kindlimann (private collection with public access), Aathal, Zurich, Switzerland.

Open nomenclature abbreviations are used herein according to Bengtson [75]; when reported from previous studies, they follow the same format as found in the original papers.

2.2. Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature (ICZN), and hence the new name contained herein is available under that code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID for this publication is: urn:lsid:zoobank.org:pub:478AE192-7F74-4C6C-9CAA-28864F511ED0.

2.3. (Allo)Stratigraphic Context

The Chilcatay Formation was deposited between the latest Oligocene and the early Miocene in the southern Peruvian East Pisco Basin (Figure 1a), which at that time was shaped as a semi-enclosed, shallow-marine embayment bordered seaward by a chain of basement islands (Figure 1b) [50,76–80].

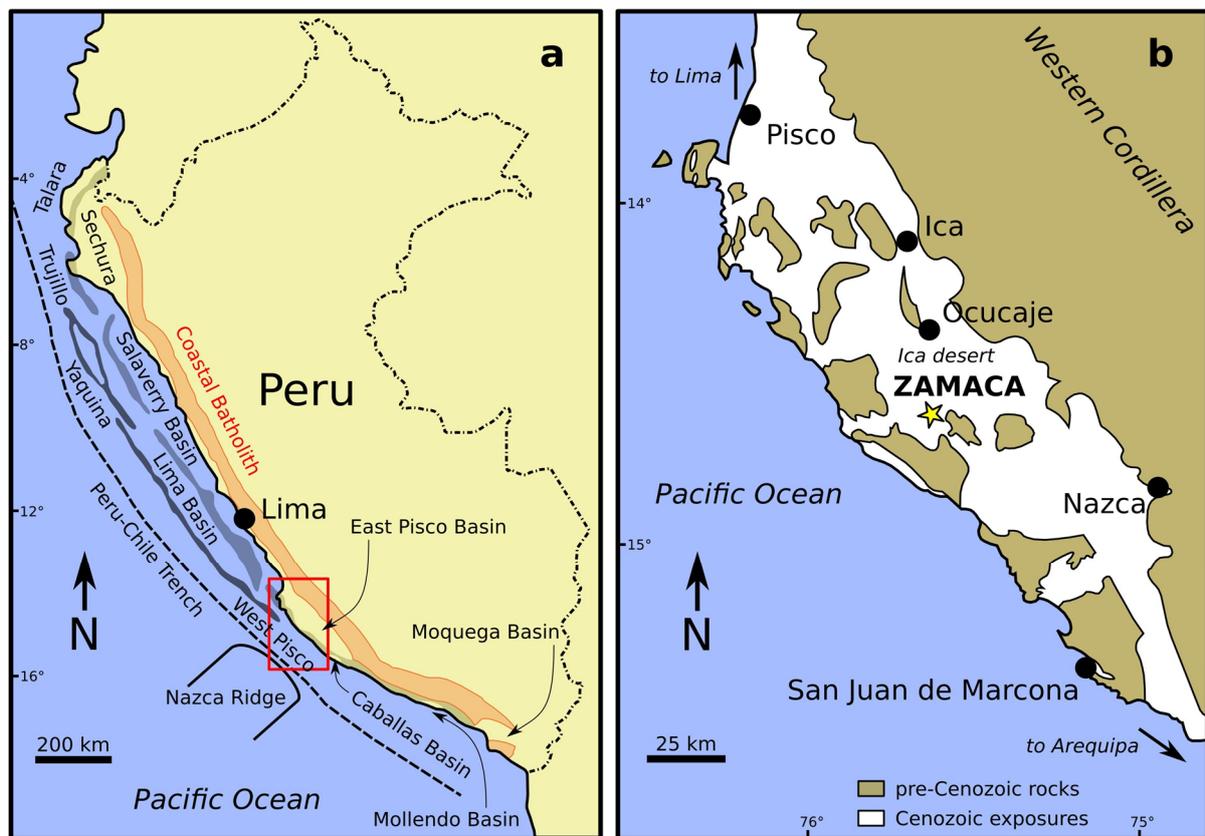


Figure 1. Geographic and geological setting. (a) Map of the major Cenozoic sedimentary basins along the coast of Peru. Major structural highs are the Coastal Batholith, the Outer Shelf High and the Upper Slope Ridge. Redrawn and modified from Travis et al. [81] and Thornburg and Kulm [82]. (b) Schematic palaeogeographic map of the East Pisco Basin, showing the areas of the Cenozoic outcrop. Redrawn and modified from DeVries and Schrader [83]; the star indicates the type locality of *Carcharhinus dicelmai* sp. nov. at Zamaca.

Along the right bank of the Ica River, including our study area of Zamaca (Figure 1b), the Chilcatay Formation is Lower Miocene in age and consists of two distinct allomembers or depositional sequences (Ct1 and Ct2, from older to younger) that are separated from each other by an intraformational unconformity (CE0.2) [56–58,84,85] (Figure 2a). In addition, an older Chilcatay sequence (Ct0) has recently been recognised at the remote localities of Laberinto and Media Luna, in the southern and western parts of the Ica Desert, respectively [79,80]. Both the base of Ct1 and that of Ct2 are locally marked by a lag with boulders, pebbles with *Gastrochaenolites* borings, phosphatic nodules, shark teeth, fragmentary bones and large-sized *Gyrolithes* burrows.

Three facies associations comprise the Ct1 allomember. In ascending stratigraphic order, these facies associations are known as Ct1c (made of massive sandstones interbedded with boulder-sized clasts and conglomeratic levels), Ct1a (made of sandstones and siltstones intercalated with beds of coarse-grained sandstones and conglomerates) and Ct1b (made of coarse-grained, mixed siliciclastic-carbonate, clinostratified deposits). Ct1c, Ct1a and Ct1b reflect shoreface, offshore and submarine delta deposition, respectively. Two facies associations comprise the Ct2 allomember, namely, Ct2a (made of highly fossiliferous, massive, intensely bioturbated sandstones) and the overlying Ct2b (made of silty mudstones intercalated with minor, laterally persistent, very fine-grained sandstone interbeds as well as submarine slump-related deformed strata), reflecting shoreface and offshore deposition, respectively.

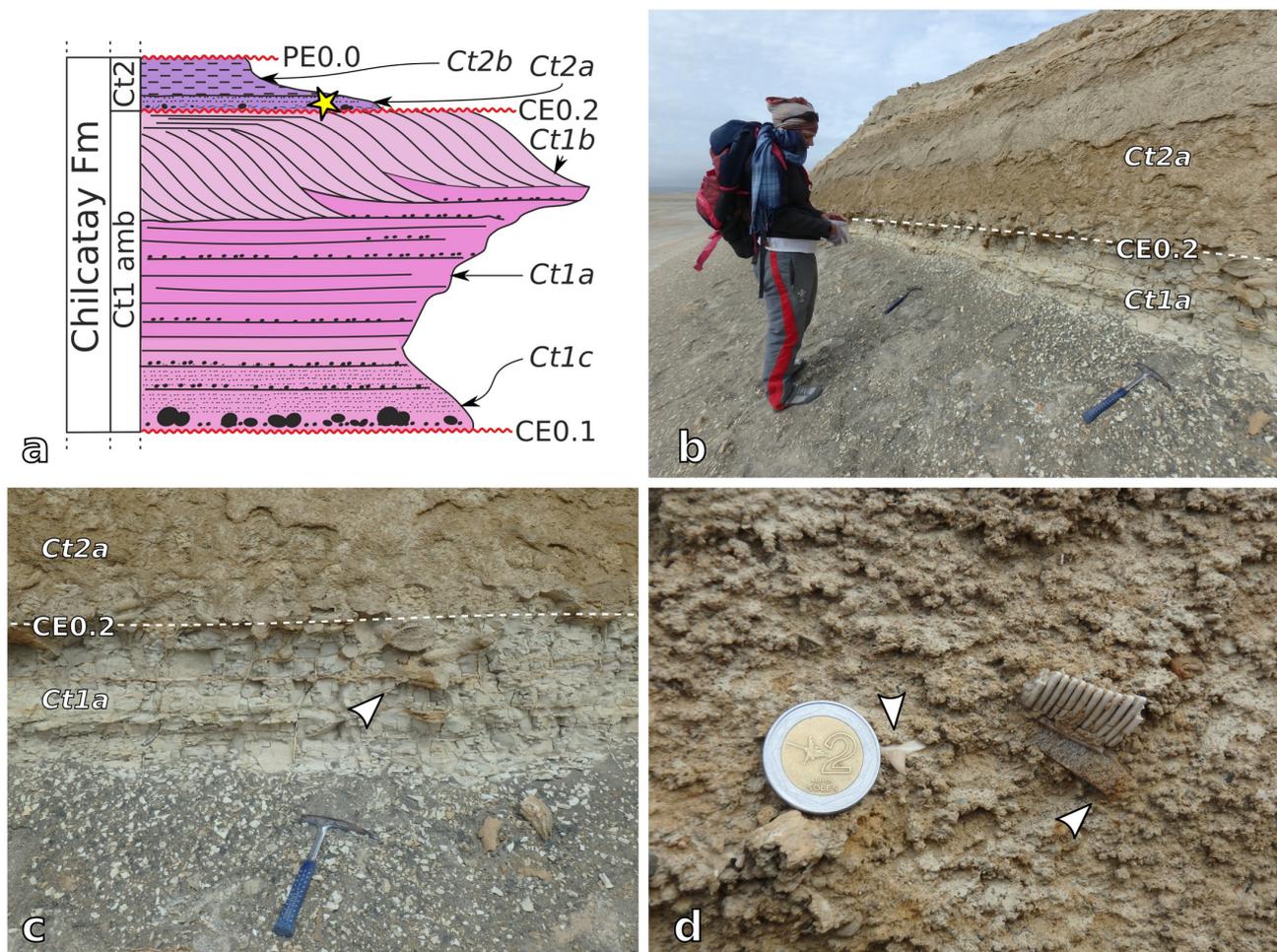


Figure 2. Stratigraphy, sedimentology and palaeontology of the type locality and horizon of *Carcharhinus dicelmai* sp. nov. at Zamaca. (a) Schematic stratigraphic column of the Lower Miocene succession exposed in the East Pisco Basin, and its internal subdivision into sequences/allomembers and facies associations. Redrawn and modified from Di Celma et al. [57]; notice that the Ct0 sequence/allomember is not figured herein, as it has not been recognised anywhere in the Zamaca area. The star indicates the type horizon of *Carcharhinus dicelmai* sp. nov., occurring at the base of the Ct2a facies association and coinciding with the ShB-4 level of Landini et al. [70]. Abbreviations: amb, allomember; Fm, formation. (b) General view of the outcrop; notice that the Ct1b facies association is locally missing. (c) Close-up of the CE0.2 intraformational unconformity that separates the Ct2a facies association from the underlying Ct1a facies association; notice the damaged *Gyrolithes* burrow, indicated by an arrowhead, that penetrates the top of Ct1a. (d) Carcharhinid and myliobatoid teeth (indicated by arrowheads) cropping out from the Ct2a sandstones that comprise the ShB-4 tooth-bearing interval.

At the study site (approximate geographic coordinates: 14°37'00.9" S, 75°38'48.5" W), the Ct1b facies association is locally missing, and Ct2a contacts the underlying Ct1a through the CE0.2 intraformational unconformity (Figure 2b,c). Like several other elasmobranch fossils (Figure 2d), all the specimens described herein originate from within the Ct2a strata.

2.4. Palaeontological Background

Fossil vertebrates from the Chilcatay Formation consist of cetaceans (both toothed and baleen-bearing whales), seabirds, sea turtles, bony fishes and elasmobranchs (both sharks and rays). Most cetaceans belong to Odontoceti, and specifically to Inticetidae (*Inticetus vertizi*), the so-called “Chilcetus-clade” of early toothed whales (*Chilcetus cavirhinus*), Platanistoidea (the squalodelphinids *Furcetus flexirostrum*; *Huaridelphis raimondii*,

Macrosqualodelphis ukupachai and *Notocetus vanbenedeni*; the platanistid aff. *Araodelphis* sp.; the basal platanistoid *Ensidelphis riveroi* and other indeterminate forms), Eurhinodelphinidae (represented by indeterminate forms only), Physeteroidea (cf. *Diaphorocetus* sp. and *Rhaphicetus valenciae*) and Kentriodontidae (*Kentriodon*) [29,31,34,37,49,50,52,57,58,66,86,87]. Mysticetes are also present with rare, indeterminate specimens [58]. Seabirds consist of Spheniscidae (*Palaeospheniscus*) [88]. Sea turtles are represented by a member of Dermochelyidae (possibly *Natemys peruvianus*) [50,58,89]. Bony fishes comprise indeterminate Scombridae as well as Istiophoridae (aff. *Makaira* sp.) and scales that resemble the extant genus *Sardinops* [50,57,58].

The Chilcatay strata feature an abundant and taxonomically rich content of fossil elasmobranch remains (mostly teeth and spines) that concentrate in a few discrete horizons of Ct0, Ct1 and Ct2 [50,57,58,70,80]. Though specific data on the Chilcatay fossil sharks and rays were provided by Alván De la Cruz [90], Renz [91] and Shimada et al. [68], a comprehensive overview of the shark and ray assemblage from the Chilcatay strata was not available until the recent works by Bianucci et al. [50] and Landini et al. [70]. Focussing on the Zamaca area, the latter study recognised the presence of four tooth-bearing intervals, taking their place within *Ct1a* (i.e., ShB-1 and ShB-2), *Ct1b* (i.e., ShB-3) and *Ct2a* (i.e., ShB-4, the richest such interval from which all the fossil specimens studied herein originate) [70]. As regards ShB-4, so far it has yielded more than 2300 teeth and dermal elements belonging to Squatiniformes (*Squatina* sp.), Lamniformes (*Alopias superciliosus*, *Alopias* cf. *vulpinus*, *Anotodus agassizi*, *Cosmopolitodus hastalis* (also known as *Carcharodon hastalis*), *Cosmopolitodus plicatilis* (also known as *Carcharodon plicatilis*), *Isurus oxyrinchus*, *Megachasma* cf. *applegatei*, *Carcharias* sp., *Carcharocles chubutensis* (also known as *Otodus chubutensis*), *Megalolamna paradoxodon* and *Parotodus benedeni*), Carcharhiniformes (*Carcharhinus brachyurus*, *Galeocerdo aduncus*, *Negaprion brevirostris*, *Physogaleus contortus*, *Hemipristis serra* and *Sphyrna zygaena*), Myliobatiformes (*Dasyatidae* gen. et sp. indet. and *Myliobatoidea* gen. et sp. indet.) and Rhinopristiformes (cf. *Anoxypristis* sp.) [70]. New sampling efforts conducted in 2019 led to the discovery of some hundred new specimens, including the teeth of the new carcharhinid taxon described herein as well as finds of *Rhinoptera* sp. (representing the first fossil record of the myliobatiform family Rhinopteridae in the East Pisco Basin; A.C. and A.B., pers. obs.).

The shark and ray assemblage from ShB-4 can be briefly described as follows: its taxonomic composition is dominated by two shark lineages, Lamniformes and Carcharhiniformes, the former being dominant in terms of alpha-diversity; two taxa, *C. brachyurus* (the commonest shark species) and *C. hastalis*, account together for more than three fifths of the total number of specimens; and the entire assemblage exhibits a distinctly juvenile imprint. On the whole, the ShB-4 elasmobranch assemblage recalls those from the Middle and lower Upper Miocene strata of the East Pisco Basin [44,69,71], thus suggesting the persistence of a similar ecological structure through most of the Miocene at least [72].

In addition to the aforementioned vertebrate taxa, the Chilcatay Formation also features an abundant and rather diverse macroinvertebrate fossil fauna that includes bivalves, gastropods, barnacles, crabs, bryozoans, cirratulids, echinids and brachiopods [57,78,92–98].

2.5. Geochronological Framework

At the localities of Ullujaya and Roca Negra, the Chilcatay beds have recently been assigned to the Burdigalian (upper Lower Miocene) by means of biostratigraphy and isotope geochronology. Micropalaeontological data concerning silicoflagellates, diatoms and nannoplankton constrain the deposition of the Ct1 and Ct2 allomembers between ca. 19–18 Ma; this age range is further supported by $^{40}\text{Ar}/^{39}\text{Ar}$ ages obtained from two volcanic ash layers from Ct1, dated at 19.25 ± 0.05 Ma (at Roca Negra) and 19.00 ± 0.28 Ma (at Ullujaya), as well as from one volcanic ash layer occurring near the top of Ct2, dated at 18.02 ± 0.07 Ma (at Los Dos Cerritos) [34,57,99,100]. At Ullujaya and Roca Negra, $^{87}\text{Sr}/^{86}\text{Sr}$ dates from well-preserved biogenic carbonates (oysters, pectinids and barnacles) from the Ct1 sequence and gives concordant ages of 18.9–18.3 Ma [80,99]. At the study area of Zamaca, strontium isotope stratigraphy on shark tooth enameloid assigns a preferred

age of 18.25 Ma and an age range of 18.4–18.1 Ma to the tooth-bearing ShB-4 horizon, in excellent agreement with other dates from both Ct1 and Ct2 [80].

3. Results

Systematics

Order Carcharhiniformes Compagno [101]

Family Carcharhinidae Jordan and Evermann [102]

Genus *Carcharhinus* de Blainville [103]

Type species: *Carcharias melanopterus* Quoy and Gaimard [104]

Carcharhinus dicelmai sp. nov.

2016—*Carcharhinus* cf. *C. macloti*; Carrillo-Briceño et al. [105], Figure 6, panels 9 and 10 Figures 3 and 4

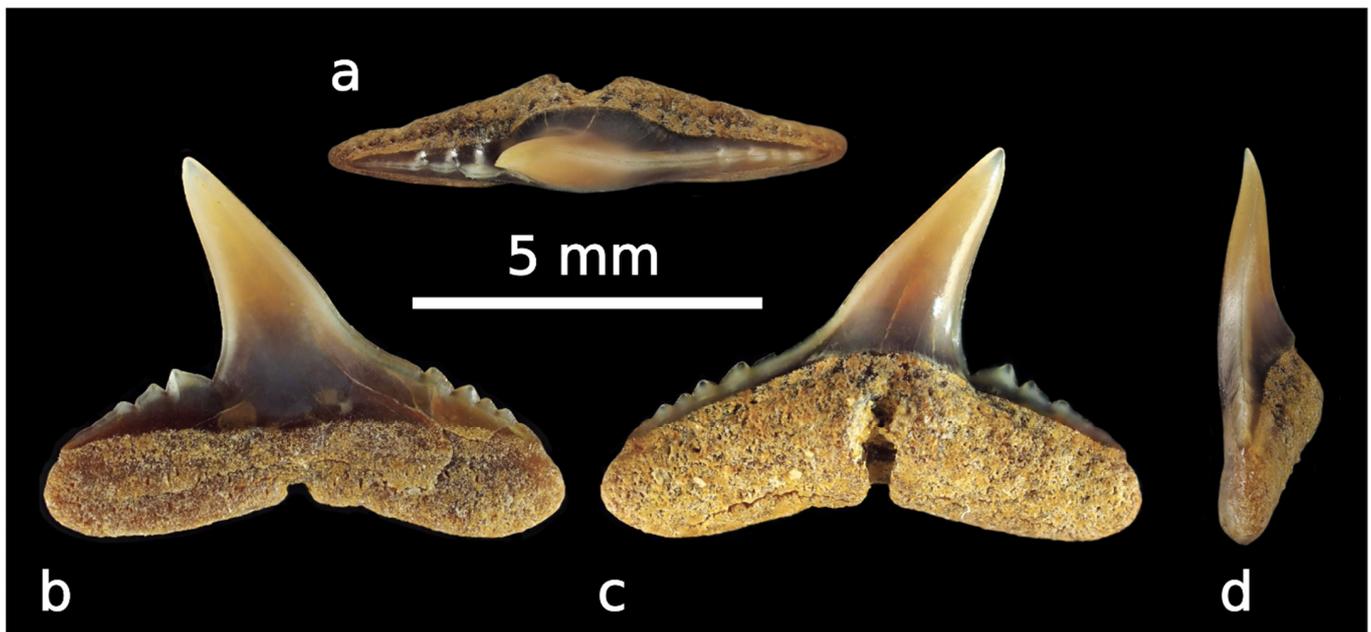


Figure 3. *Carcharhinus dicelmai* sp. nov., MUSM 4697 (holotype), left upper lateral tooth from the Lower Miocene (Burdigalian) of Zamaca (East Pisco Basin, Peru) in (a) apical; (b) labial; (c) lingual; and (d) profile views.

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Etymology: Named after Claudio Di Celma, renowned stratigrapher and scholar of the sedimentary successions of the East Pisco Basin.

Holotype: MUSM 4697, a left upper lateral tooth.

Type locality and collector: The holotype was collected by one of the authors (A.C.) at Zamaca, East Pisco Basin, Peru. Approximate geographic coordinates of the type locality: 14°37'00.9'' S, 75°38'48.5'' W.

Type horizon: Chilcatay Formation, Ct2 allomember, base of the Ct2a facies association (=ShB-4 tooth-bearing interval); Lower Miocene (Burdigalian), 18.4–18.1 Ma.

Referred material: MUSM 4698 to MUSM 4709, twelve upper teeth from the same locality and horizon as the holotype.

Diagnosis: *Carcharhinus dicelmai* sp. nov. differs from all other extant and extinct species of *Carcharhinus* as its upper teeth display the following unique combination of characters: crown provided with a triangular, narrow-based, slender, smooth-edged cusp; cusp labiolingually thick at base, semicylindrical, sigmoidal, exhibiting a marked coronal twist that causes the labial face to be partially visible in apical view; cusp apex bending towards the commissure in lateral teeth; mesial and distal heels much thinner labiolingually than the cusp, the latter being separated from the distal heel by a clear notch; distal heel

featuring one to five, coarse, angularly lobate serrae that become more prominent toward the base of the cusp; similar serrae often present on the mesial heel too.

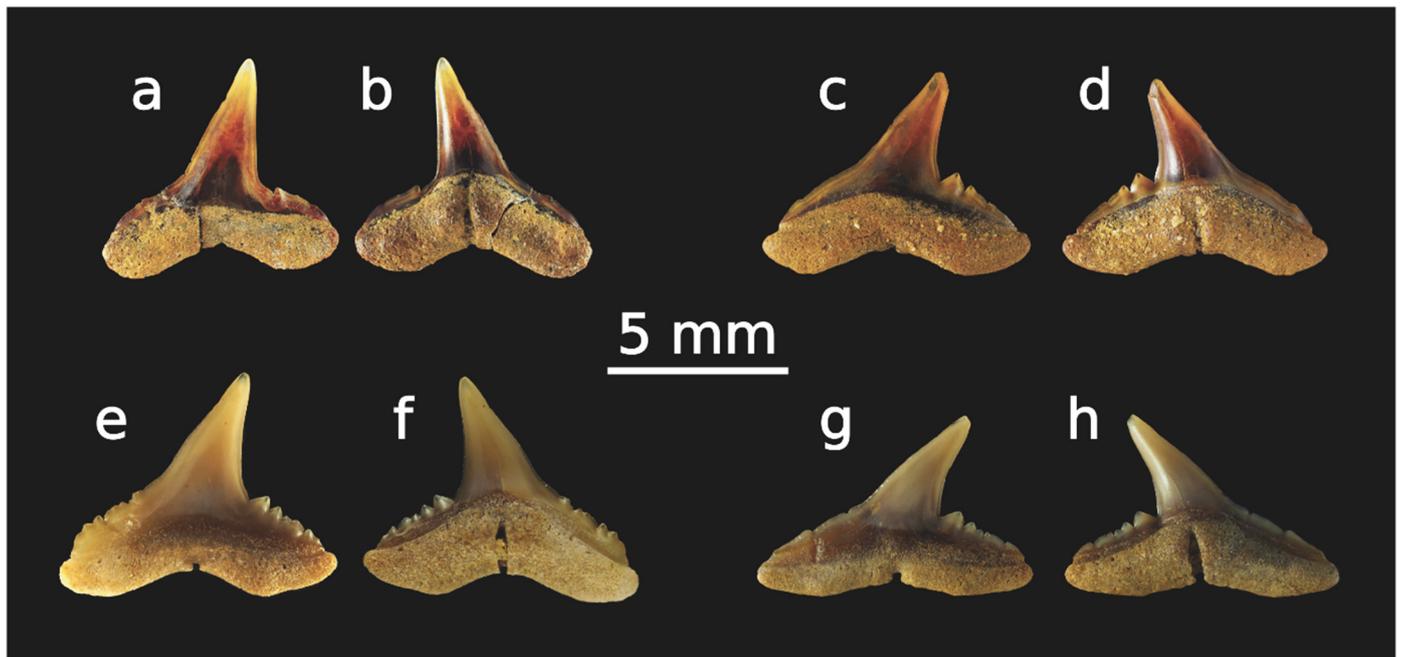


Figure 4. *Carcharhinus dicelmai* sp. nov., referred specimens from the Lower Miocene (Burdigalian) of Zamaca (East Pisco Basin, Peru). (a,b) MUSM 4698, right upper anterior tooth in (a) labial and (b) lingual views. (c,d) MUSM 4699, right upper lateral tooth in (c) labial and (d) lingual views. (e,f) MUSM 4700, right upper lateral tooth in (e) labial and (f) lingual views. (g,h) MUSM 4701, right upper lateral tooth in (g) labial and (h) lingual views. All specimens from the type locality and horizon.

Description: Teeth of *Carcharhinus dicelmai* sp. nov. range between 5 and 9 mm in transverse width, and from slightly less than 5 mm to slightly more than 6.5 mm in apicobasal height.

The holotype MUSM 4697 (Figure 3) is a left upper tooth. As it is wider than high and features a distally deflected cusp (Figure 3b,c); MUSM 4697 is here regarded as representative of a lateral position. The cusp is elongated, acutely pointed and completely smooth-edged (Figure 3b,c). It appears as distinctly sigmoid in profile view (Figure 3d); furthermore, it is provided with a marked coronal twist (i.e., coronal torque; see Richter and Ward [106], Mannering and Hiller [107] and Carrillo-Briceño et al. [108]), so that the labial cusp face can be partly seen in apical view (Figure 3a). The mesial and distal heels are clearly demarked from the cusp (Figure 3b,c), the latter being labiolingually thicker (especially at its base) and semicylindrical (Figure 3a). Both the heels bear coarse, angularly lobate serrae that increase in prominence toward the base of the cusp (Figure 3b,c). The root is bilobate. The root lobes are subequal in size, have rounded terminations and form an obtuse, almost flat angle with each other (Figure 3b,c). A moderately prominent lingual bulge is present (Figure 3c,d). The nutrient groove is vertically oriented and well developed (Figure 3c), forming a notch at the root base (Figure 3b,c).

Other upper lateral teeth (Figure 4c–e) mainly differ from the holotype as regards the number, shape and extent of the serrae occurring on the mesial heel, which in some specimens (e.g., MUSM 4699) appear as substantially absent (Figure 4c,d), as well as with respect to the inclination of the cusp. Variations in the latter are likely related to some degree of gradient monognathic heterodonty, as observed in other extinct and extant carcharhines; that said, ontogenetic shifts in dental morphology may also have occurred. Differences also

exist, among the upper laterals, regarding the extent of notching of the mesial cutting edge (Figure 4c–f).

The upper anterior teeth are roughly as wide as high. Specimen MUSM 4698 (Figure 4a,b), a right anterior tooth, displays a suberect cusp, a thoroughly smooth mesial cutting edge and a single, elongated serra on the distal heel. The root lobes are relatively short, forming an angle that is slightly more acute than typically observed in the upper laterals.

Comparisons and remarks: Among the many extant species of *Carcharhinus*, the upper teeth of *C. dicelmai* sp. nov. are especially similar to those of the hardnose shark, *Carcharhinus macloiti*, and the Pondicherry shark, *Carcharhinus hemiodon*. These three species share the essentially smooth-edged condition of the cusp as well as the occurrence of coarse, angularly lobate serrae along the distal heel at least. Direct comparisons were thus performed between the holotype and referred specimens of *C. dicelmai* sp. nov. and two dried jaws of *C. macloiti* stored in the RK collection (Figure 5). Based on our observations, the upper teeth of *C. dicelmai* sp. nov. are unambiguously distinguishable from those of *C. macloiti* by virtue of the following characters:

- (1) The cusp is transversely narrower and, especially, more narrowly based.
- (2) The cusp exhibits a sigmoid profile (which is only incipient in *C. macloiti*) and a distinct coronal twist.
- (3) The labial crown face is weakly convex transversely (rather than almost flat as in *C. macloiti*).
- (4) In labial/lingual view, the cusp of the lateral teeth is characteristically “hook-shaped”, with the crown apex bending distinctly toward the commissure. This is due to the mesial and distal cutting edges of the cusp becoming progressively more convex and concave, respectively.
- (5) The cusp is labiolingually thick at the base and semicylindrical, whereas the distal and mesial heels are remarkably thinner. In apical view, the cusp is clearly divided from the distal heel by means of an abrupt variation of the labiolingual thickness of the crown. In *C. macloiti*, the cusp is proportionally thinner at the base and not semicylindrical, and the thickness of the crown decreases regularly towards its distobasal end.

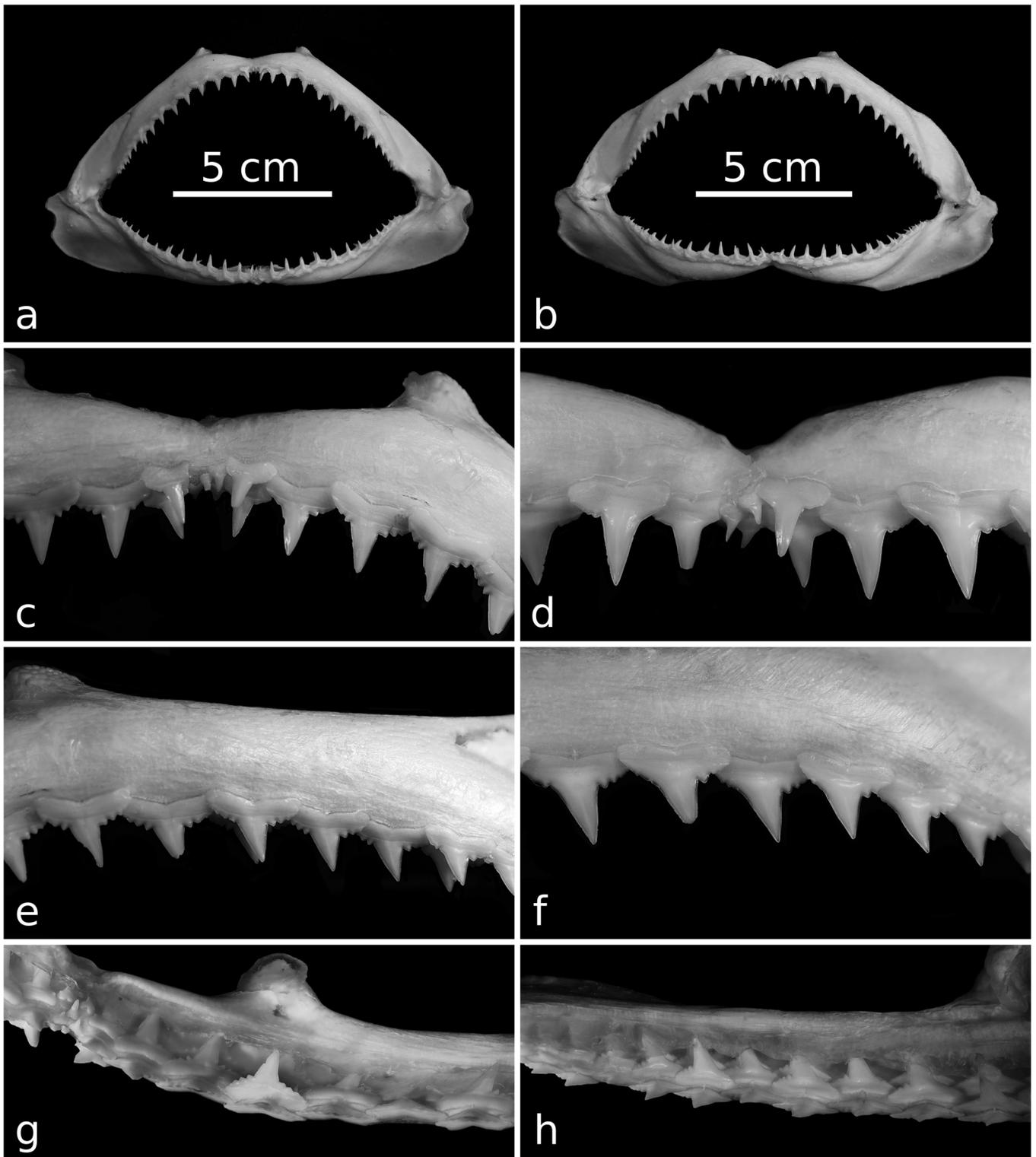


Figure 5. Dried jaws of two specimens (**a,c,e,g** and **b,d,f,h** tentatively identified as a male and a female, respectively) of the extant hardnose shark, *Carcharhinus macloti*, stored in the RK collection (both specimens from the Philippines). (**a,b**) General appearance of the jaws in labial view. (**c,d**) Close-up of the upper anterior teeth in labial view. (**e,f**) Close-up of the upper lateral teeth in labial view. (**g,h**) Close-up of the upper anterior and lateral teeth comprising the functional tooth row. For the dimensions of the details depicted in panels (**c**) to (**h**), please refer to the scale bar present in panels (**a,b**).

The Pondicherry shark, which strongly recalls *C. macloti* in terms of dental morphology, further differs from *C. dicelmai* sp. nov. by displaying upper lateral teeth with essentially straight mesial margins that form no distinct mesial heels and are often finely serrated (or crenulated) basally [4,5].

Among the extinct carcharhines, *Carcharhinus caquetius* (known from the Middle–Upper Miocene of Venezuela and the Upper Miocene of Ecuador; Carrillo-Briceño et al. [15]) resembles *C. dicelmai* sp. nov. more than any other formally named species by displaying an elongated, sigmoidal cusp as well as a distal heel that is clearly separated from the cusp by a deep notch. However, the upper teeth of *C. dicelmai* sp. nov. differ from those assigned to *C. caquetius* by the following combination of characters:

- (1) The mesial and distal cutting edges of the cusp are completely smooth (rather than being finely serrated to approximately their mid-points);
- (2) The distal heel bears one to five, coarse, angularly lobate serrae that become more prominent toward the cusp (rather than finer, more abundant serrations).

Although the teeth of *C. dicelmai* sp. nov. clearly differ on morphological grounds from those of all other extant and extinct species of *Carcharhinus*, their unambiguous identification may sometimes prove difficult, especially when dealing with worn-out and/or substantially incomplete teeth. The hopeful discovery of new specimens of *C. dicelmai* sp. nov. may prove precious for further defining the dental morphology of this extinct requiem shark species, possibly also by means of morphometric surveys [109].

4. Discussion

4.1. Palaeoecology

Four shark tooth-bearing intervals were recognised in the Zamaca area by Landini et al. [70]. All the specimens of *Carcharhinus dicelmai* sp. nov. that are known to date come from the uppermost of these intervals, namely, the ShB-4 shark tooth-bearing bed of Landini et al. [70], which in turn corresponds to the basal 1–2 m of the Ct2a facies association of Di Celma et al. [56–58,85]. The exquisite preservation state of the holotype and referred specimens of *C. dicelmai* sp. nov. indicates that these teeth are not reworked from older deposits (e.g., those comprising the underlying Ct1 sequence).

The Ct2a strata have been interpreted as reflecting deposition in a littoral, very shallow, shoreface palaeoenvironment [57]. Although the apparent absence of teeth of *C. dicelmai* sp. nov. from the other shark tooth-bearing beds of the Zamaca area could be partly explained by evoking taphonomic or collection biases, it may suggest that *C. dicelmai* sp. nov. was a very littoral shark. Furthermore, considering that various members of the elasmobranch assemblages from the Chilcatay strata (including *Anoxypristis* sp., *Carcharhinus* cf. *leucas* and *Hemipristis serra*) are regarded as suggestive of warm waters [50,70], *C. dicelmai* sp. nov. may also have been an essentially thermophilic shark.

The dentition of most carcharhines has been identified as representative of the “cutting–clutching” type; it features monocuspid lower teeth that enable the predator to hold the prey, while the flattened upper teeth cut like a trimmer thanks to their finely serrated cutting edges [8,110,111]. That said, the smooth-edged, semicylindrical, distinctly sigmoid cusp of the upper teeth of *C. dicelmai* sp. nov. does not seem particularly fit for cutting. In turn, a significant degree of coronal twist and the occurrence of few well-individualised serrae (rather than finer serrations or crenulations) at one or both sides of the cusp evoke some functional analogies with the more strictly clutching teeth of, e.g., frilled sharks. In light of these considerations, the dentition of *C. dicelmai* sp. nov. appears less akin to that of most other carcharhines to the cutting–clutching type, and seemingly testifies to the development of more predominantly clutching adaptations. Similar considerations may apply to other extinct requiem sharks such as *Abdounia belselensis* [112] and *Kruckowlamna costarricana*. Although most extant carcharhinids display a cutting–clutching dentition, some species in the family (e.g., *Rhizoprionodon* spp.) feature clutching-type teeth on both the upper and lower jaws [113,114].

Given the dimensions of its teeth, and similar to *C. macloti*, *C. dicelmai* sp. nov. was likely a diminutive carcharhine. All things considered, *C. dicelmai* sp. nov. may have relied on small-sized prey items (including, e.g., small bony fishes and invertebrates) that were captured and ingested one-by-one through feeding actions that involved clutching.

4.2. Palaeobiogeography

The discovery of teeth belonging to a new species of *Carcharhinus* in the Lower Miocene of Peru encouraged us to search the palaeoichthyological literature for illustrations and descriptions of conspecific specimens. In doing so, we mainly focused on teeth that had been assigned to the extant species *Carcharhinus macloti*, whose dental characters are particularly reminiscent of those of *C. dicelmai* sp. nov. One interesting record from the Burdigalian to lower Langhian Cantaure Formation of Falcón State (Venezuela) was provided by Carrillo-Briceño et al. [105] and depicted in their Figure 6, panels 9 and 10. It consists of an upper left tooth identified as belonging to *Carcharhinus* cf. *C. macloti*. Though incomplete, lacking the tip of the cusp and the termination of the mesial root lobe, this tooth compares favourably, in terms of both size and morphology, to the holotype and referred specimens of *C. dicelmai* sp. nov. In particular, it conforms to *C. dicelmai* sp. nov. by featuring a slender, semicylindrical cusp that displays a distinct degree of coronal twist. The occurrence of *C. dicelmai* sp. nov. in the Burdigalian or lower Langhian of the Caribbean palaeo-area is consistent with the palaeogeography of the Central American region. Indeed, throughout the Miocene, the Central American Seaway allowed for unrestricted communications and faunal interchanges between the low-latitude Eastern Pacific and Western Atlantic water masses [51,115–121]. As a consequence of this, some species of *Carcharhinus* (e.g., the copper shark *C. brachyurus*) had a trans-Panamanian distribution that was subsequently lost with the eventual establishment of the Isthmus of Panama in Pliocene times (Landini et al. [122]; but see also Collareta et al. [123]). In addition to the aforementioned Venezuelan record, teeth that conform to *C. dicelmai* sp. nov. may be searched for in the Lower Miocene collections of *Carcharhinus macloti* from the eastern USA, including the Pungo River and Calvert formations [124,125]. That said, the dispersal capabilities of *C. dicelmai* sp. nov. were likely low, as no occurrences—either confirmed or presumed on the basis of records of similar species such as *C. macloti*—exist for this form outside the Americas. This may be explained by a preference for nearshore habitats, as hypothesised in the previous paragraph.

We take advantage of this section to rectify the taxonomic identification and palaeobiogeographic affinities of another record of *Carcharhinus* aff. *C. macloti* from Central America. This consists of teeth from the Upper Miocene (Tortonian) Chucunaque Formation of Lago Bayano (Panama) that were described by Perez et al. [113] and depicted in their Figure 6, panels 8–13. These specimens are slightly wider than high; they feature a slender, smooth-edged cusp (which in at least one specimen displays a distinct degree of coronal twist); a labial crown face that is rather convex at its base; well-developed mesial and distal heels bearing up to three prominent, erect cusplets; a straight labial limit of the enameloid; and a labiolingually thick root. In terms of both size and shape, the Lago Bayano specimens appear as indistinguishable from those assigned by Laurito Mora [126] to *Kruckowlamna costarricana*, an extinct *Abdounia*-like carcharhinid known so far only from the Messinian–Zanclean of Costa Rica (see also Cappetta [8] and Maisey [127]). Thus, the teeth assigned by Perez et al. [113] to *Carcharhinus* aff. *C. macloti* represent the geologically oldest occurrence of *K. costarricana*, its first description from outside Costa Rica, and the first published record of this taxon after its erection by Laurito Mora [126].

5. Conclusions

A new requiem shark species, *Carcharhinus dicelmai* sp. nov., has been described on the basis of Lower Miocene (18.4–18.1 Ma) fossils from the Chilcatay Formation of Peru. This new taxon is represented by upper teeth that resemble those of *Carcharhinus caquetius*, *Carcharhinus hemiodon* and *Carcharhinus macloti*, but with unique features. In particular, *C.*

dicelmai sp. nov. characteristically displays the following dental traits: a slender, smooth-edged cusp; a distinct coronal twist; and a distal heel that bears a few coarse, angularly lobate serrae that increase in prominence toward the cusp. The dental morphology of *C. dicelmai* sp. nov. appears as more akin to the so-called clutching-type than that of most other carcharhines. A roughly coeval requiem shark tooth from Venezuela has been re-assigned to *C. dicelmai* sp. nov., thus evoking a trans-Panamanian distribution for this extinct elasmobranch species.

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