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Original article

Oldest record of the Great White Shark (Lamnidae, *Carcharodon*; Miocene) in the Southern Atlantic

Alberto Luis Cione [a,*], Daniel Alfredo Cabrera [a], María Julia Barla [b]

[a] *CONICET, División Paleontología de Vertebrados, Museo de La Plata, FCNyM, Universidad Nacional de La Plata, Paseo del Bosque s/n, B1900FWA, La Plata, Argentina*
[b] *Facultad de Ciencias Naturales y Museo, 1900, La Plata, Argentina*

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ABSTRACT

Lamnid teeth close to but more plesiomorph than *Carcharodon carcharias* were collected in the late Miocene beds of the Paraná Formation in the central eastern Argentina. We propose, as other authors, that some species formerly assigned to *Isurus* or to *Cosmopolitodus* should be included in *Carcharodon*. Some workers suggested that *C. carcharias* originated by phyletic evolution in the Pacific basin. The teeth from Paraná could pertain to a new species of *Carcharodon* already known from Perú. In contrast with the Pacific basin, *Carcharodon* sp. was sympatric with the wide toothed species *Carcharodon plicatilis* in central Argentina. This is the oldest record of *Carcharodon* in the southern Atlantic.

1. Introduction

The great white shark (*Carcharodon carcharias*) is very rare along the Argentinean coast nowadays (Siccardi et al., 1981). Until now, it was known in southwestern South America during the Pleistocene and the Holocene when it was much more abundant than today (Cione and Bonomo, 2003; Cione and Barla, 2008).

During field work in the Provincia de Entre Ríos, central eastern Argentina, two shark teeth very close to *C. carcharias* were collected in late Miocene outcrops of the Paraná Formation by Carlos Steger (Figs. 1 and 2). Most Miocene records of *C. carcharias* have been questioned (see below). In this contribution, we comment the fossil record of *C. carcharias* in southern South America, describe the new teeth, and discuss their relationships. Additionally we briefly discuss Miocene to Holocene records of the great white shark in southern South America.

2. Fossil and archaeological records of *Carcharodon carcharias* in southern South America

Frenguelli (1920, 1922) identified a broken tooth as *Carcharodon rondeleti* (a junior synonym of *Carcharodon carcharias*); the material came from the "Entrerriense". This unit is presently included in the Paraná Formation (Aceñolaza, 2001; see discussion about the age below). Andres (2006) mentions that Thenius (1959) attributed the "Entrerriense" to the Pliocene. However, this information is outdated. The material of Frenguelli was not found in any museum collections. According to the description and illustration, the tooth presents a chevron-shaped neck area in lingual view and very fine and even serrations (Frenguelli, 1920: pl. I, figs. 1 and 2; see Fig. 3). These characters separate this tooth from *C. carcharias* and are similar to a juvenile *Carcharocles megalodon* (Cione, 1988).

Teeth of *C. carcharias* are fairly abundant in the Pliocene of Chile and in the Pliocene and Pleistocene of Peru (Muizon and DeVries, 1985; Long, 1993; Suárez and Brito, 2000; Ehret et al., 2009a). However, teeth putatively assigned to *C. carcharias* were reported without description or figuration from Miocene beds at Bahía Inglesa, Chile, which underlie an ash stratum dated 7.6 ± 1.3 Ma (Walsh and Suárez, 2005).

In the Estado do Rio Grande do Sul (Brazil), several teeth coming from indeterminate Quaternary beds were reported from two localities (Richter, 1987; Sekiguchi, 1994). Teeth of *C. carcharias* are frequently found in early-middle Holocene archaeological sites along the coasts of Rio de Janeiro, São Paulo, Santa Catarina, and Rio Grande do Sul in Brazil (Barbosa and Franco, 1991; Gadig and Rosa, 1996).

In Argentina, Ameghino (1898: 243) described and named (but did not figure) a new species, *Carcharias pampeanus*, from the "Belgranense, Pampeano medio of La Plata". The short description ("Carcharias pampeanus *Ameghino con dientes en forma de triángulo isósceles perfecto, de 3 centímetros de alto por 2 de ancho, de cara interna muy convexa, la externa plana y los bordes dentellados en toda su extensión, con dientecillos muy gruesos*...") agrees in size and

* Corresponding author.
E-mail address: acione@museo.fcnym.unlp.edu.ar (A.L. Cione).

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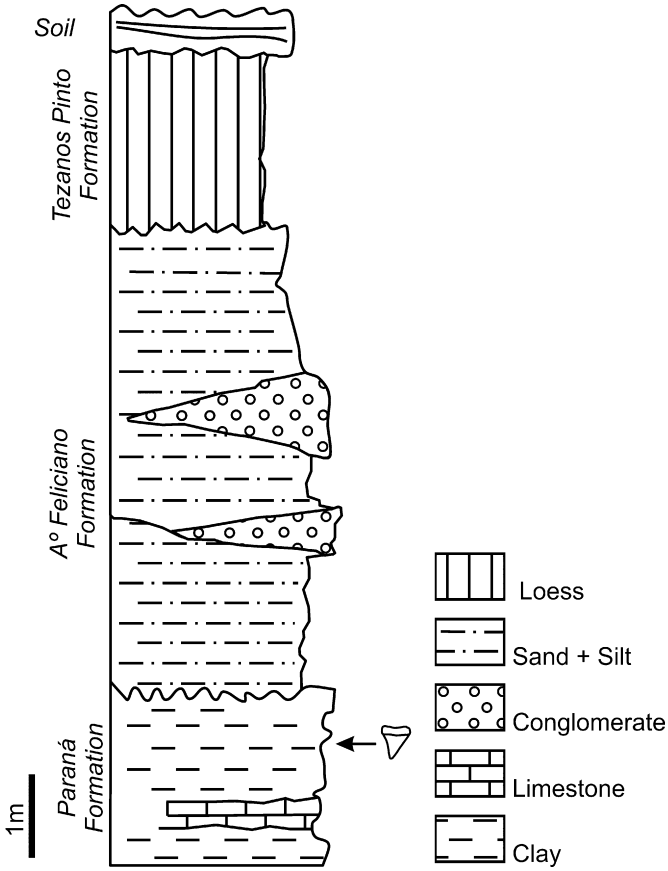

Fig. 1. Stratigraphic section exposed at the Ensenada stream cliffs.
Modified after Noriega et al. (2007).

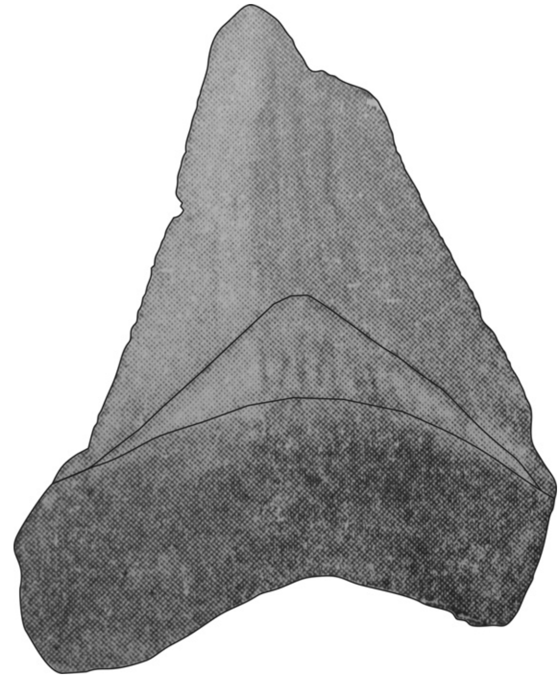

Fig. 3. Tooth of a juvenile specimen of *Carcharocles megalodon* identified by Frenguelli (1920) as *Carcharodon rondeleti*.
Modified from Frenguelli (1920).

morphology (i.e. coarse serrations) with the teeth of *C. carcharias* (Cione, 1983). However, the original material was not found in the museum collections where Ameghino deposited the fossils. Furthermore, the beds assigned to the "Belgranense" near La Plata are presently correlated with the last interglacial (Illinois-Wisconsin, Oxygen Isotope Stage 5, *ca*. 120 ka; Pardiñas et al., 1996). Other Quaternary teeth of *C. carcharias* have been reported from paleontological and archaeological sites at Pehuencó and Centinela del Mar in eastern Provincia de Buenos Aires (Cione, 1983; Arratia and Cione, 1996; Cione and Bonomo, 2003). Recently, Cione and Barla (2008) suggested that the present dearth of *C. carcharias* in the Argentinean coasts in comparison with the more abundant fossil and archeological record could be related with the extermination of pinnipeds around the central Argentina area.

3. Stratigraphy

The teeth were found *in situ* in light green clays with sandy levels, partially cemented by whitish carbonates of late Miocene age within the upper part of the Paraná Formation (Fig. 1). The collection site is in the base of the Arroyo Ensenada valley (32° 05′ 00″ S, 60° 29′ 30″ W), between the cities of Diamante and

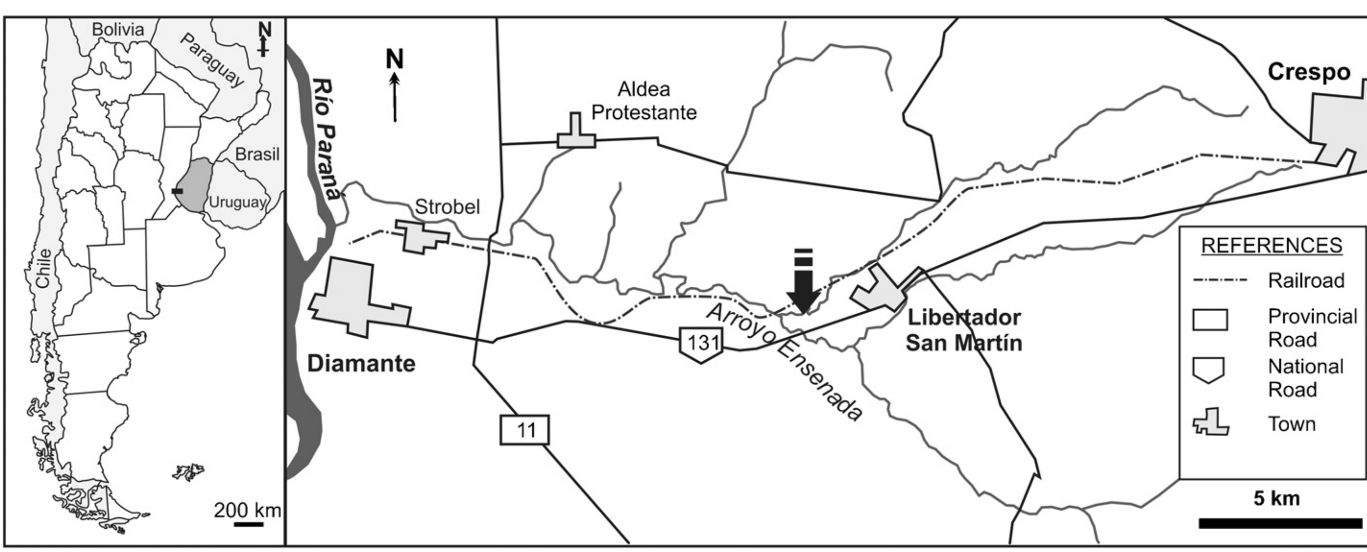

Fig. 2. Locality map of Libertador San Martín, Entre Ríos. The fossil locality is marked with an arrow.

Libertador General San Martín, Departamento Diamante, Provincia de Entre Ríos, Argentina (Fig. 2).

Two Miocene units are recognizable in the area: the mostly marine Paraná Formation which is overlain by a thick fluvial sequence (Ituzaingó Formation). The Paraná Formation was deposited during the large marine transgression that covered the Chacopampean region during the middle Miocene and part of the late Miocene (“Mid Transgressive Onlap Sequence”; Uliana and Biddle, 1988; Cione et al., 2000, 2005; Uba et al., 2009). Marine mammals occurring in the top of the Paraná Formation indicate a late Miocene age (Cione et al., 2000). Likewise, Sr isotope ages obtained from the correlative Puerto Madryn Formation from Patagonia indicate a Tortonian age (Scasso et al., 2001) as well as a date from the top of the Yecua Formation of Bolivia (U-Pb date of 7.17 ± 0.34 Ma; Uba et al., 2009). Mammals occurring at the base of the overlying Ituzaingó Formation are Huayquerian in age in the South American chronology (Cione et al., 2000; Cione and Tonni, 2005). The Huayquerian ranges from about 8 Ma to about 6 Ma, with radiometric and magnetostratigraphic calibration in western Argentina (Tortonian-Messinian, late Miocene; Flynn and Swisher, 1995; Cione et al., 2000; Cione and Tonni, 2005). A continental Pliocene-Pleistocene (Marplatan to Platan in the South American chronology) sequence overlies both units (Cione et al., 2000; Candela et al., 2007). Moreover, the Ituzaingó Formation does not outcrop at the collection site. No Pliocene, Pleistocene or Holocene marine beds are known in the region. In the southwestern Atlantic, a few small Patagonian outcrops of marine beds located about 2000 km to the south are considered Pliocene in age (Feruglio, 1949). Consequently, the uppermost levels of the Paraná Formation appear to be older than 6 Ma.

Several fish taxa occur in the same beds as the teeth described in this study, including: *Carcharodon plicatilis*, *Carcharocles megalodon*, *Carcharias taurus*, *Megascyliorhinus trelewensis*, *Galeocerdo aduncus* (we consider that this species relates to genus *Galeocerdo* and not to *Physogaleus*), *Hemipristis serra*, *Sphyrna* sp., *Carcharhinus* spp., *Heterodontus* sp., *Squatina* sp., *Dasyatis* sp., Rajidae indet., Holocephali indet., Sciaenidae indet., Ariidae indet., Sparidae indet. (Cione et al., 2000, 2005). *M. trelewensis* is known only in the Miocene and *G. aduncus* is an Oligocene to Miocene species with a putative Pliocene report. From the same beds and area, a skeleton of an indeterminate balaenopterid whale with predation marks (attributed to a *C. plicatilis* attack) has been described (Noriega et al., 2007).

4. Systematic paleontology

Subclass ELASMOBRANCHII Bonaparte, 1838
Order LAMNIFORMES Berg, 1958
Family LAMNIDAE Müller and Henle, 1838
Genus ***Carcharodon*** Smith in Müller and Henle, 1838
Carcharodon sp.
Fig. 4

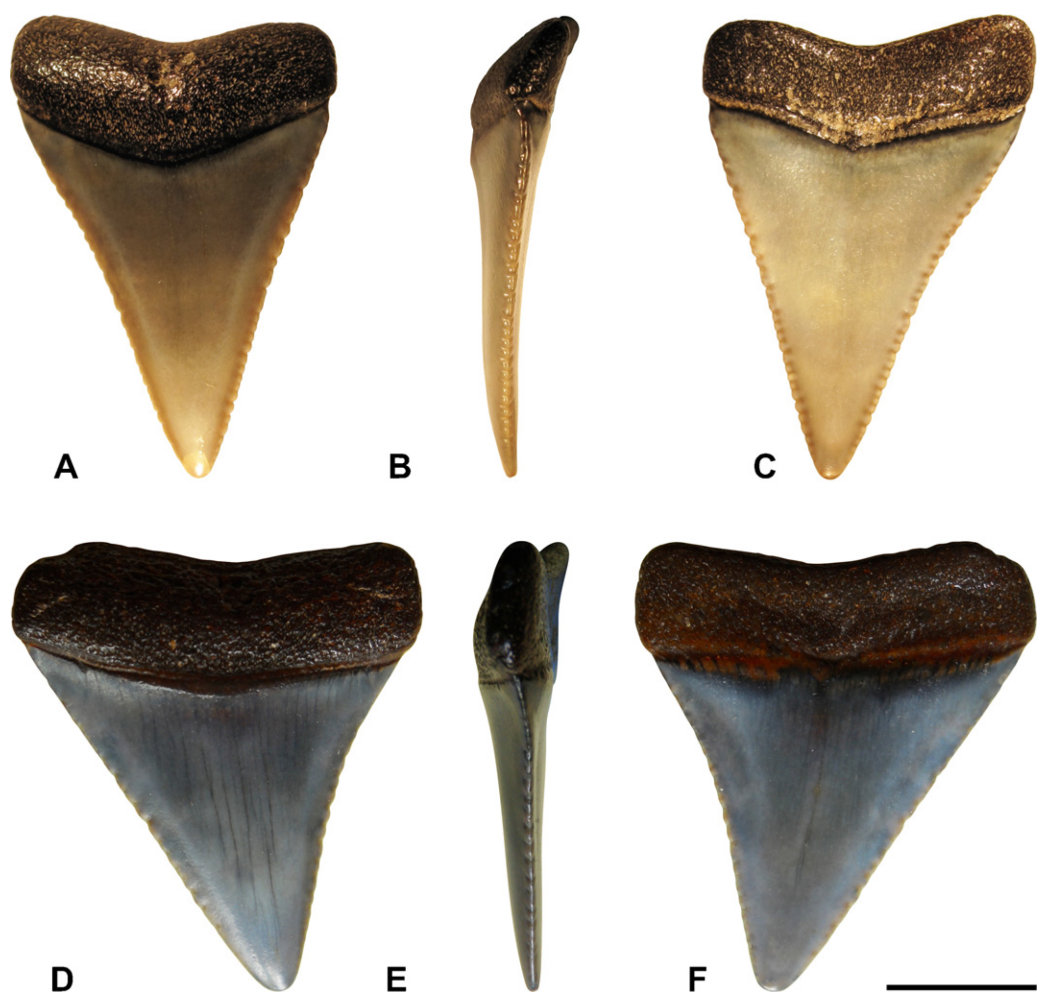

Fig. 4. *Carcharodon* sp. from Paraná Formation. Top row shows UAP 1303 tooth; **A**: lingual view; **B**: distal view; **C**: labial view; Bottom row shows UAP 1301 tooth; **D**: lingual view; **E**: distal view; **F**: labial view. Scale bar: 10 mm.

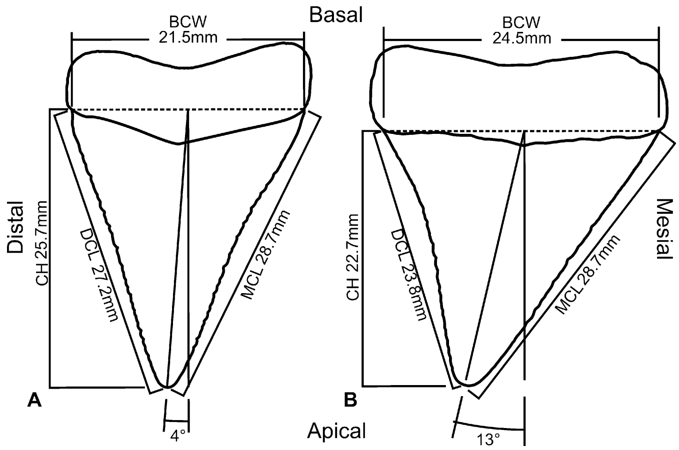

Fig. 5. Tooth measurements in labial view. **A**: UAP 1303; **B**: UAP 1301. BCW: basal crown width; CH: crown height; DCL: distal crown edge length; MCL: mesial crown edge length.
According to Shimada (2002b).

Material: UAP 1303, upper second anterior right tooth; UAP 1301, upper lateral right tooth, 1st or 2nd lateral.

Repository: Museo de la Universidad Adventista del Plata, 25 de Mayo 29, 3103 Libertador General San Martín, Argentina.

Description: Teeth correspond to medium-sized specimens. Cutting edge serrations are worn. UAP 1301 tip is worn. Enameloid surfaces are relatively well preserved although teeth show some post-mortem basoapical cracks. Root surfaces are moderately worn. Crowns are triangular, broad near the base. There are no lateral cusplets or large basal serrations. Mesial cutting edges are straight and commissural cutting edges are concave. Cutting edge serrations are relatively strong and even. There are 12 serrations per cm in UAP 1303 and 11 serrations per cm in UAP 1301. The points of basal serrations are oriented 90° to the cutting edge and distally. Labial face is relatively flat in UAP 1301 and basoapically concave in UAP 1303. Lingual faces are transversally convex. Roots are low, gently concave labially, and gently convex lingually. Labial contact root/crown is slightly concave in UAP 1301 but angled in UAP 1303. Lingual contact root/crown is angled in both.

Tooth measurements can be seen in Fig. 5. Total body length (TBL) was calculated for both teeth by using crown height according to Shimada (2002a). UAP 1301 estimated TBL = 310 cm ($y = 4.911 + 13.433\ x$) and UAP 1303 estimated TBL = 307 cm ($y = -2.160 + 12.103\ x$).

5. Discussion

There are two alternative taxonomic hypotheses, based on tooth characters, for explaining the relationships of the great white shark *Carcharodon carcharias*. One relates it to the clade of large Cenozoic sharks that became extinct with *Carcharocles megalodon* (a very large species with finely serrated cutting edges; Ehret et al., 2009a) during the Pliocene. Another theory, widely accepted today, postulates that *C. carcharias* is the most derived species of a clade of relatively "wide-toothed" lamnid sharks with smooth cutting edges, and traditionally assigned to the genus *Isurus* Rafinesque, 1810 (aka *Oxyrhina* Agassiz, 1838; see Casier, 1960 and Fig. 6). These species include *I. flandricus*, *I. hastalis*, *I. xiphodon*, among others. The clade ranges at least from the Oligocene to the Pliocene. Another species with slightly crenulated cutting edges ("*I*". *escheri*) was considered not directly related to *C. carcharias* (Lutz, 2002). The full discussion of lamnid phylogeny is beyond the scope of this paper. However, we briefly comment the relationships and nomenclature of some of the species related to *C. carcharias*.

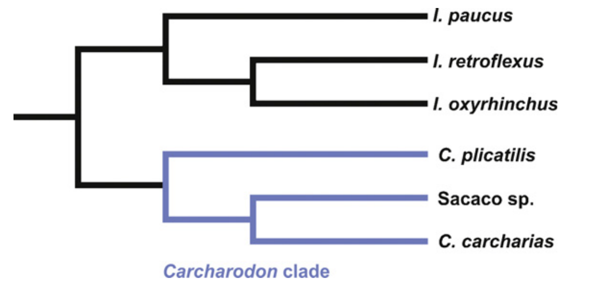

Fig. 6. Schematic representation of possible *Carcharodon carcharias* relationships. Modified after Cione, 1988; Compagno, 1990; Nyberg et al., 2006.

The generic name *Isurus* applies to the recent species *I. oxyrinchus* and *I. paucus*, and possibly to some fossil species (Cappetta, 1987). Molecular evidence suggests that the clade to which the recent species pertain separated at least 40 million years ago from that of *Carcharodon* (Martin, 1996; Martin et al., 2002). Ward and Bonavia (2001) referred *I. hastalis* to the genus *Cosmopolitodus* Glikman, 1964. However, if we consider that several species of "wide-toothed" lamnid sharks were assigned to *Cosmopolitodus* (e.g., *I. planus*, *I. hastalis*, *I. xiphodon*; Bourdon, 2002; Cappetta, 2006), and that one of these (*I. xiphodon*; Whitenack and Gottfried, 2010) was considered to be the putative sister species of *Carcharodon*, *Cosmopolitodus* might be paraphyletic (Siverson in Bourdon, 2002). Some authors suggest that *I. hastalis* and *I. xiphodon* are difficult to differentiate and consequently recognize only one species (Ward and Bonavia, 2001). Moreover, Ward and Bonavia (2001) proposed that *I. xiphodon* is a *nomen dubium* (see also Cappetta, 1987, 2006). However, notwithstanding the problem with the name and type, there is a recognizable species that appears to be the putative sister group of *C. carcharias* and that is different from *I. hastalis* (Cione, 1988; Purdy et al., 2001; Bourdon, 2002; Nyberg et al., 2006; Whitenack and Gottfried, 2010). We suggest that an available and valid name for this species is "*Isurus*" *plicatilis* Agassiz, 1843 (Cione, 1988). Besides, taking into account the relationships of the species assigned to *Isurus*, this genus might be paraphyletic from a cladistic point of view. For this, the species *plicatilis* should be referred to *Carcharodon*.

Muizon and DeVries (1985) proposed that the transformation of *Carcharodon plicatilis* (*Isurus hastalis* for them) into *C. carcharias* is gradually evident in successive beds of the Pisco Formation in southwestern Peru. They found that:

- teeth of *C. plicatilis* without cutting edge serrations occur in lower beds of late Miocene age;
- weakly serrated teeth occur in overlying beds of latest Miocene age;
- teeth with the typical strong serrations of *C. carcharias* occur in beds of Pliocene age.

A similar pattern was recognized in the Capistrano Formation of California (Stewart and Rashke, 1999). Remarkably, Nyberg et al. (2006) demonstrated that there was no significant difference in tooth shape between *C. carcharias* and the "wide-toothed" species *C. plicatilis* (*I. xiphodon* for them) from the upper Miocene, differing only in the serrated cutting edges of the former species. The serrations of *C. carcharias* change their relative size throughout ontogeny, becoming less coarse (Hubbell, 1996). At the same time, tooth crown becomes wider. For this, although there is some intraspecific variation, it is important to compare teeth of specimens of similar size.

Recently, an exceptionally well-preserved articulated "transitional" new species of *Carcharodon* was reported from beds of the Pisco Formation presently dated at 6-6.5 Ma (i.e. latest Miocene; Ehret et al., 2009a, 2009b; D. Ehret, personal communication). *Carcharodon* nov. sp. has larger serrations than those of "*I.*" *escheri* but smaller and less well-defined than those of *C. carcharias*, amongst other differences. This material could not be the oldest *Carcharodon*, because there are some few references of older putative *Carcharodon* specimens in the literature (e.g., Gottfried and Fordyce, 2001).

Several characters present in the Arroyo Ensenada teeth (size, thickness, root and crown shape, absence of a chevron-shaped neck area and lateral cusplets, and well-developed serrations) agree with those of the sharks *Carcharodon* nov. sp. from Sacaco and *C. carcharias*. The serrations of the Arroyo Ensenada specimens are also much larger than those of "*I.*" *escheri* (Leriche, 1926) and of teeth with slight serrations of the upper Miocene of Peru (Muizon and DeVries, 1985) but are smaller than those of the typical recent and Pliocene *C. carcharias* of similar size. Serrations appear to be larger than those of the Sacaco specimen. However, the Sacaco specimen corresponds to a much larger fish than the teeth of the Arroyo Ensenada. Also, the serrations are oriented diagonally to the cutting edge and distally directed in "transitional" teeth mentioned by Andres (2006) and Ehret et al. (2009a). In UAP 1303 serrations are oriented at 90° from the cutting edge. The "transitional" Arroyo Ensenada teeth appear to differ from those of *Carcharodon* nov. sp. from Sacaco in having lower roots and wider crowns and lacking larger basal serrations. However, there are only two relatively worn teeth (of a small specimen) and we cannot discard that they would pertain to the Sacaco species.

In sum, according to present evidence, at least two lamnid sharks might have developed serrations in different areas during the Neogene. Small serrations appeared in the extinct species "*Isurus*" *escheri* which was endemic of the northern Atlantic and more important serrations evolved in populations of the Pacific Ocean. The Pacific populations became the present great white shark *Carcharodon carcharias*. Some of the sharks with intermediate serrations migrated into the Atlantic Ocean, occurring along with typical *C. plicatilis* in the Arroyo Ensenada. Afterwards, during the Pliocene, the typical species *C. carcharias* distributed around the world in tropical to temperate waters.

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