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Abstract: Lamnid teeth close to but slightly more primitive than *Carcharodon carcharias* were collected in late Miocene beds of the Paraná Formation in the central eastern Argentina. Some authors suggested that this species originated by phyletic evolution in the Pacific. The geographic and stratigraphic evidence shows that the putative sister species of *C. carcharias*, "*Isurus*" *xiphodon*, occurred in the Miocene but not in the Pliocene beds of the Pacific coast of South and North America and *C. carcharias* (or the transitional forms) occurred in the late Miocene-Pliocene of the same area. "*Isurus*" *xiphodon* was present in the Miocene and Pliocene beds of the Atlantic ingressions of North America, South America, and Europe but *C. carcharias* was only present in Pliocene beds of the same area. According to present knowledge, it appears that *C. carcharias* originated in the Pacific and dispersed from there to the rest of the world during the latest Miocene-Pliocene. "*I.*" *xiphodon* should have become extinct in the Pacific at the end of the Miocene. In Entre Ríos, the *Carcharodon* cf. *carcharias* was sympatric with "*I.*" *xiphodon*.

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# **A Miocene record of the Great White Shark (Lamnidae, *Carcharodon* aff. *C. carcharias*) in South eastern South America**

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## **Abstract**

Lamnid teeth close to but slightly more primitive than *Carcharodon carcharias* were collected in late Miocene beds of the Paraná Formation in the central eastern Argentina. Some authors suggested that this species originated by phyletic evolution in the Pacific. The geographic and stratigraphic evidence shows that the putative sister species of *C. carcharias*, “*Isurus*” *xiphodon*, occurred in the Miocene but not in the Pliocene beds of the Pacific coast of South and North America and *C. carcharias* (or the transitional forms) occurred in the late Miocene-Pliocene of the same area. “*Isurus*” *xiphodon* was present in the Miocene and Pliocene beds of the Atlantic ingressions of North America, South America, and Europe but *C. carcharias* was only present in Pliocene beds of the same area. According to present knowledge, it appears that *C. carcharias* originated in the Pacific and dispersed from there to the rest of the world during the latest Miocene-Pliocene. “*I.*” *xiphodon* should have become extinct in the Pacific at the end of the Miocene. In Entre Ríos, the *Carcharodon* cf. *carcharias* was sympatric with “*I.*” *xiphodon*.

**Key words.** Elasmobranchii, Lamniformes, Entre Ríos, Neogene.

## 1. Introduction

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

Presently, there are two main hypotheses concerning the origin of *Carcharodon carcharias*: 1) "*Isurus*" *xiphodon* is the sister group of *C. carcharias* (or even its direct ancestor by phyletic evolution); and 2) *C. carcharias* is closely related (and co-generic) to the huge megatoothed sharks that became extinct with *Carcharocles megalodon* in the Pliocene (for discussions supporting both hypotheses and bibliography see Cione, 1988; Cione et al., 2000; Purdy et al., 2001; Cione et al., 2005; Andres, 2006; Nyberg et al., 2006; Moss and Agnew, 2008; Ehret et al., 2009a). Most workers, including us, subscribe to the first hypothesis today.

During field work near Libertador San Martín, Provincia de Entre Ríos, central eastern Argentina, two shark teeth very close to but slightly more primitive than *C. carcharias* were collected in late Miocene outcrops of the Paraná Formation by Carlos Steger (Figures 1, 2). Most Miocene records of *C. carcharias* have been questioned (see Andres, 2006 but see Walsh and Suárez, 2005 and Ehret et al. 2009b). In this contribution, we discuss the fossil record of *C. carcharias* in southern South America, describe the new teeth, comment their characters, and discuss their relationships.

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

Frenguelli (1920a, 1922) identified a broken tooth as *Carcharodon rondeleti* (a junior synonym of *Carcharodon carcharias*). The material came from the "arenas arcillosas del segundo horizonte (patagónico de Doering) al cual seguramente corresponde: por presentar un estado de fosilización menos avanzado y muy distinto del de los odontolitos que se encuentran en los conglomerados subyacentes, por el color gris verdoso de su raíz y por no presentar rastros de haber sido rodado" (Frenguelli, 1920a:16). According to Frenguelli (1920 b:102), this horizon corresponds to the "Entrerriense." This "unit" is presently included in the Paraná Formation (Aceñolaza, 2001; see discussion about the age below). Andres (2006) mention that Thenius (1959) attributed the "Entrerriense" to the Pliocene. However, this information is outdated (see below). The material

of Frenguelli was not found in collections of any museum. According to the description and illustration, the tooth presents a chevron-shaped neck area in lingual view and very fine and even serrations (Frenguelli, 1920a; his Plate I, Figures 1, 2; our Figure 3). These characters separate this tooth from *C. carcharias* or "*Isurus xiphodon*" and relate it to a juvenile *Carcharocles megalodon* (see Cione, 1988).

Teeth of *C. carcharias* are fairly abundant in the Pliocene of Chile and Peru (Muizon and DeVries, 1985; Long, 1993; Suárez and Brito, 2000; Ehret et al., 2009a). However, teeth assignable to *C. carcharias* occur in Miocene phosphatic beds at Bahía Inglesa, Chile (Walsh and Suárez, 2005). The bearing beds underlay an ash stratum dated  $7.6 \pm 1.3$  Ma.

In the Estado do Rio Grande do Sul (Brazil), several teeth coming from undetermined Quaternary beds were reported from two localities (Richter, 1987; Sekiguchi, 1994).

In Argentina, Ameghino (1898:243) described and named (but not figured) 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 denticillos muy gruesos...") agrees in the size and the coarse serrations with that of teeth of *C. carcharias* (see Cione, 1983). However, the original material was not found in the museums where Ameghino donated fossils. The beds assigned to the "Belgranense" near La Plata are presently correlated with the last interglacial (Illinois-Wisconsin, 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).

Teeth of *C. carcharias* are frequently found in early-middle Holocene archaeological sites in 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).

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 in central Argentina area.

### 3. Stratigraphy

The tooth was found in situ in light green clays with sandy levels, partially cemented by whitish carbonates of late Miocene age of the upper part of the Paraná Formation (Figure 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 Libertador General San Martín, Departamento Diamante, Provincia de Entre Ríos, Argentina (Figure 2).

The continental and marine beds outcropping in southwestern Provincia de Entre Ríos, Argentina have been scientifically known since 1827 when Alcide D'Orbigny visited the area (D'Orbigny, 1842). 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 encroachment that covered the Chacopampean region during the middle Miocene and part of the late Miocene ("Mid Transgressive Onlap Sequence;" see Uliana and Biddle, 1988; Aceñolaza, 2001; 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 (an U-Pb date of  $7.17 \pm 0.34$  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; see Flynn and Swisher, 1995; Cione et al., 2000, 2005; Cione and Tonni, 2005). A continental Pliocene-Pleistocene (Marplatian to Platanian in the South American chronology) sequence covers both units (Cione et al., 2000; Candela et al., 2007). No Pliocene, Pleistocene or Holocene marine beds are known in the region. Actually, in southwestern Atlantic, only some small Patagonian outcrops of marine beds are considered Pliocene in age (Feruglio, 1949). They are located about 2000 km to the South. Consequently, the uppermost levels of the Paraná Formation appear to be older than 6 Ma.

Several fish taxa occur in the same beds than the teeth here described: "*Isurus*" *xiphodon*, *Carcharocles megalodon*, *Carcharias taurus*, *Megascyliorhinus trelewensis*, *Galeocerdo aduncus*, *Hemipristis serra*, *Sphyrna* sp., *Carcharhinus* spp., *Heterodontus* sp., *Squatina* sp., *Dasyatis* sp., Rajidae indet., Holocephali indet., Sciaenidae indet., Ariidae indet., Sparidae indet. *Megascyliorhinus trelewensis* is

known only in the Miocene and *Galeocерdo aduncus* is an Oligocene to Miocene species with a putative Pliocene report.

From the same beds and area, a skeleton of an indeterminate baleopterid whale with predation marks (attributed to an “*I.*” *xiphodon* attack) was described recently (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* aff. *C. carcharias* (Linnaeus, 1758)

Figure 4.

**Material:** UAP 1303, upper second anterior left tooth. UAP 1301, upper lateral left tooth, 5 th to 6th rows (1th to 2<sup>nd</sup> laterals).

**Comparative material:** Two jaws in the Sección Ictiología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," Buenos Aires, Argentina. One jaw in the handicraft market at La Paloma, Uruguay. Several jaws in the American Museum of Natural History, New York, United States.

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

**Description:** Teeth correspond to a medium-sized specimen. Crown cutting edge serrations are worn. UAP 1301 tip is worn. Enameloid surface relatively well preserved although teeth show some post-mortem basopical cracks. Root surface is moderately worn. Crown is triangular, broad near the base. There are no lateral cusplets or even large basal serrations. Mesial cutting edges are straight and comisural cutting edge 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. Serrations are not restricted to cutting edges. Labial face is relatively flat in UAP 1301 and

basoapically concave in UAP 1303. Lingual faces are transversally convex. Root 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.

Teeth measurements are seen in Figure 5.

Total body length (TBL): It was calculated for both teeth by using crown height according to Shimada (2002a). UAP 1301 estimated TBL= 310 cm ( $y=4.911+13.433x$ ) and UAP 1303 estimated TBL=307 cm ( $y=-2.160+12.103x$ ).

## 5. Discussion.

The family Lamnidae comprises three recent genera (*Isurus*, *Lamna*, and *Carcharodon*) and several fossil ones (Cappetta, 1987, 2006). *Isurus* shows smooth cutting edges and no lateral denticles, *Lamna* shows smooth cutting edges and lateral denticles, and *Carcharodon* shows strong serrated cutting edges and no lateral denticles in adult specimens. The allocation of several fossil species, only known by isolated teeth with smooth cutting edges and lacking lateral denticles, to the lamnid genus *Isurus* has recently been questioned: e.g. *I. praecursor*, *I. planus*, *I. hastalis*, *I. xiphodon*. Some authors have assigned them to the fossil lamnid genus *Cosmopolitodus* and *Macrorhizodus* (see Suárez et al., 2006; Cappetta, 2006). However, *Cosmopolitodus* is paraphyletic (e.g. the species *Cosmopolitodus xiphodon* is considered by several authors as the sister group of *Carcharodon*; consequently, the species of *Cosmopolitodus* might be referred to the putative junior synonym *Carcharodon*). We find no unique characters to sustain genus *Macrorhizodus*. Actually, the relationships of the different lamnid genera and species are not well known. Molecular studies suggest that the divergence between typical recent *Isurus* species and *Carcharodon carcharias* date from middle Paleogene (Martin et al., 1996). That means that *Isurus* is certainly represented only by the recent *I. oxyrinchus* and *I. paucus*; for this we prefer to use quotation marks for the other species.

Purdy et al. (2001), based on several characters, considered that the “wide-toothed” species “*I.*” *xiphodon* is a different species than the “narrow-toothed” “*I.*” *hastalis* (we share this view; see Cione, 1988; Cione et al., 2000). In southern South America, “*I.*” *hastalis* occurs in the lower Miocene and “*I.*” *xiphodon* in the middle and upper Miocene (Cione et al., 2000, 2005; Suárez et al., 2006).

Casier (1960) suggested that *C. carcharias* originated from the species "*I. hastalis*" (considering "*I. xiphodon*" as a junior synonym of "*I. hastalis*"). Muizon and De Vries (1985) proposed that this transformation is gradually evident in successive beds of the Pisco Formation in southwestern Peru. They found that 1) teeth without cutting edge serrations, identified as "*I. hastalis*" by Muizon and De Vries (1985) but actually "*I. xiphodon*" occur in lower beds of late Miocene age, 2) weakly serrated teeth occur in overlying beds of latest Miocene age (the serration of these teeth appear different to the Pliocene "*I. escheri*" from Belgium, see below), and 3) teeth with the typical strong serrations of *C. carcharias* occur in beds of Pliocene age. Muizon and De Vries (1985) did not find "*I. xiphodon*" in the Pliocene beds. A similar pattern was recognized in California (Stewart and Rashke, 1999). Remarkably, Nyberg et al. (2006) demonstrated that there was no significant difference in tooth shape between *C. carcharias* and "*I. xiphodon*", differing only in the serrated cutting edges of the latter. The serrations of *C. carcharias* change their relative size through ontogeny, becoming relatively smaller. At the same time, teeth become wider. For this, it is important to compare teeth of specimens of similar size. Andres (2006) proposed that the evolutionary change from "*I. xiphodon*" to *C. carcharias* with intermediate "transitional" forms took place in the Pacific and from there *C. carcharias* dispersed to the rest of the world. He only recognized the species *C. carcharias* from the early Pliocene to the Recent. Andres (2006) argued that serrations would be more appropriate for feeding on marine mammals than smooth cutting edges and that *C. carcharias* provoked the extinction of "*I. xiphodon*" in the Pacific.

A gradual phyletic transformation was proposed for other shark taxa (Cione, 1988; Ward and Bourdon, 2005). Cione (1988) recalled that many large sharks such as the extant *Rhiniodon typus*, *Cetorhinus maximus*, and the extinct *Carcharocles* spp. could present a relatively small total number of individuals notwithstanding that they are widely distributed around the world. Lamniform and orrectolobiform genera with individuals of large size are frequently monospecific. The remarkable mobility of these large fishes would permit genetic flux with distant areas what does not favor allopatric speciation. The morphological modifications shown in the fossil record would indicate that some of them have changed gradually their allelic frequencies along the Cenozoic what permit to sustain chronospecies but not real species. Tagging and tracking studies and DNA analyses of *C. carcharias* have demonstrated that this species undertakes long distance trans-oceanic movements. Consequently, its distribution should not be considered disjunct, albeit that



interchange between some distant populations may be limited (Fergusson et al., 2005). However, in conjunction with other shared life-history features, including low fecundity, long lifespan and late age at maturity, Pardini et al. (2001) suggested that the population biology of *C. carcharias* may be more similar to that of marine mammals than to that of other fish. The contrast between the sequence differentiation revealed for the maternally inherited genetic marker and the lack of nuclear-gene differentiation indicates that female sharks are probably philopatric and that males may undertake transoceanic excursions (Pardini et al., 2001). Jorgensen et al. (2009) stressed that the gene flux could be not as important as previously believed. Perhaps the relative isolation of some populations could explain the variability of the recent *C. carcharias* dentition (see Hubbell, 1996). As mentioned above for *Carcharodon*, family Lamnidae includes large sharks which putatively are capable of long-range swimming. *Carcharodon* is represented by a single species widely distributed in temperate to tropical seas today. However, this is not the case of other large sharks (e.g. other lamnid genera present two species that are allopatric or sympatric). *Lamna ditropis* is distributed in the northern Pacific and *Lamna nasus* both in northern Atlantic and around temperate waters in the southern hemisphere (Compagno, 2001). Conversely, *Isurus oxyrinchus* and *I. paucus* are sympatric around the temperate and tropical belts all over the world. The disjunct distribution of the species of *Lamna* could support the Andres (2006) hypothesis of a Pacific origin for the presently ecumenic *C. carcharias*.

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* n. sp. has larger serrations than those of “*I.*” *escheri* of the same size and smaller than *C. carcharias*.

Several characters present in the Arroyo Ensenada teeth (size, thickness, root and crown shape, and absence of a chevron-shaped neck area and of lateral denticles) agree with those of the sharks “*I.*” *xiphodon*, “*I.*” *escheri*, *Carcharodon* n.sp. (from Sacaco), and *C. carcharias* (Figure 6). The presence of well developed serrations is characteristic of the two latter. The Arroyo Ensenada teeth show smaller serrations than those of typical recent and many Pliocene *C. carcharias* of similar size but larger serrations than in the Sacaco specimen (Figures 4, 6). The points of 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. Serrations are much larger than those of “*I.*” *escheri* (Leriche, 1926)

and those of “*I.*” *xiphodon* with slight serrations in the base of the cutting edge of the upper Miocene of Peru (Muizon and De Vries, 1985). Besides, the Arroyo Ensenada teeth differ from those of *Carcharodon* n.sp. from Sacaco in having a lower root and wider crown, and lacking larger basal serrations or lateral cusplets. For this, the Arroyo Ensenada teeth resemble more to teeth of the same size of *C. carcharias* than to the “transitional” white shark of Sacaco. This latter (and putatively the more plesiomorphic species) also differs from the recent white shark in an important character, the distal inclination of the intermediate tooth. The mesial inclination of intermediate teeth is not a common feature in sharks. Actually, the Peruvian *Carcharias* n.sp. does not fit in the known intraspecific variation of *C. carcharias* and deserves to be recognized as a different species (Ehret, personal communication; see Hubbell, 1996; Bourdon, 2002).

Andres (2006) analyzed the Miocene records of *C. carcharias* and concluded that they are not well supported. However, Walsh and Suárez (2005) reported *C. carcharias* from Miocene beds older than 7.6 Ma in Chile, Bourdon (2002) accept a record of *C. carcharias* from the upper Miocene of Japan, *Carcharodon* n.sp. from Sacaco is 6-6.5 Ma in age, and the Arroyo Ensenada teeth are older than 6 Ma. Those records would indicate that the transition from “*I.*” *xiphodon* to *C. carcharias* might have been older than previously supposed.

In the Pacific, it appears that “*I.*” *xiphodon* became extinct before the Pliocene (Andres, 2006). This was not the case for the Atlantic where both “*I.*” *xiphodon* and *C. carcharias* are found in early Pliocene beds (Belgium, Leriche, 1926; eastern USA, Purdy et al., 2001; Spain, García et al., 2009 as “*I.*” *hastalis*). Additionally, the species “*I.*” *escheri* was identified in the lower Pliocene of Belgium (Leriche, 1926) and Spain (García et al., 2009). Consequently, the fossil record indicates that the “mother” species “*I.*” *xiphodon* (and “*I.*” *escheri*) coexisted with the “daughter” species *C. carcharias* in the Atlantic until this latter became extinct about the end of early Pliocene times. The coexistence of plesiomorphic and apomorphic tooth characters is seen in the size of lateral cusps in sympatric and coeval Oligocene and Miocene specimens of genus *Carcharocles* (*C. angustidens*, Otekaike Limestone Formation, middle late Oligocene, Gottfried and Fordyce, 2001; *C. chubutensis*, Gaiman Formation of Argentina, early Miocene, Cione, 1988). As an hypothesis for explaining the evolution of serrations, Nyberg et al. (2006) suggested that the Pisco Formation *Carcharias* n.sp., along with “*I.*” *escheri*, showed the potential of members of the “*I.*” *hastalis* (including “*Isurus*” *xiphodon*) lineage to develop serrations that are similar in size and density to the serrations of *C.*

*carcharias*, and it would have not been improbable that serrations evolved independently in parallel in *C. carcharias*, “*I.*” *escheri*, and the Pisco Formation *Carcharias* n.sp. Certainly, serrations have developed independently several times in very distant or closely related elasmobranch clades (e.g. in the family Lamnidae, genera *Carcharoides* and *Carcharodon* or in the genus *Squalicorax* of the family Anacoracidae; see Cappetta, 1987). However, in the case of the large lamnid species analyzed and according to the present evidence, it appears likely that a phyletic transition from “*I.*” *xiphodon* to *C. carcharias* took place in the Pacific. In the Atlantic, feeble serrations could have been developed independently in the species “*I.*” *escheri*. The Paraná Formation specimens could be immigrants from the Pacific via the Drake area (which had higher temperatures during the Miocene than today) or the Panama area (before the establishment of the isthmus about 3 Ma; Cione and Tonni, 1995).

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## Explanations of figures

Figure 1. Stratigraphic section exposed at the Ensenada stream cliffs (modified from Noriega et al., 2007).

Figure 2. Location map. The arrow points to the locality.

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

Figure 4. *Carcharodon* aff. *C. Carcharias* 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.

Figure 5. Teeth 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).

Figure 6. Silhouettes of A2 teeth for comparison of cutting edges. **A**, “*Isurus*” *xiphodon*; **B**, *Carcharodon* sp. from Sacaco; **C**, *Carcharodon carcharias*. Scale bar 10 mm.

Figure 1  
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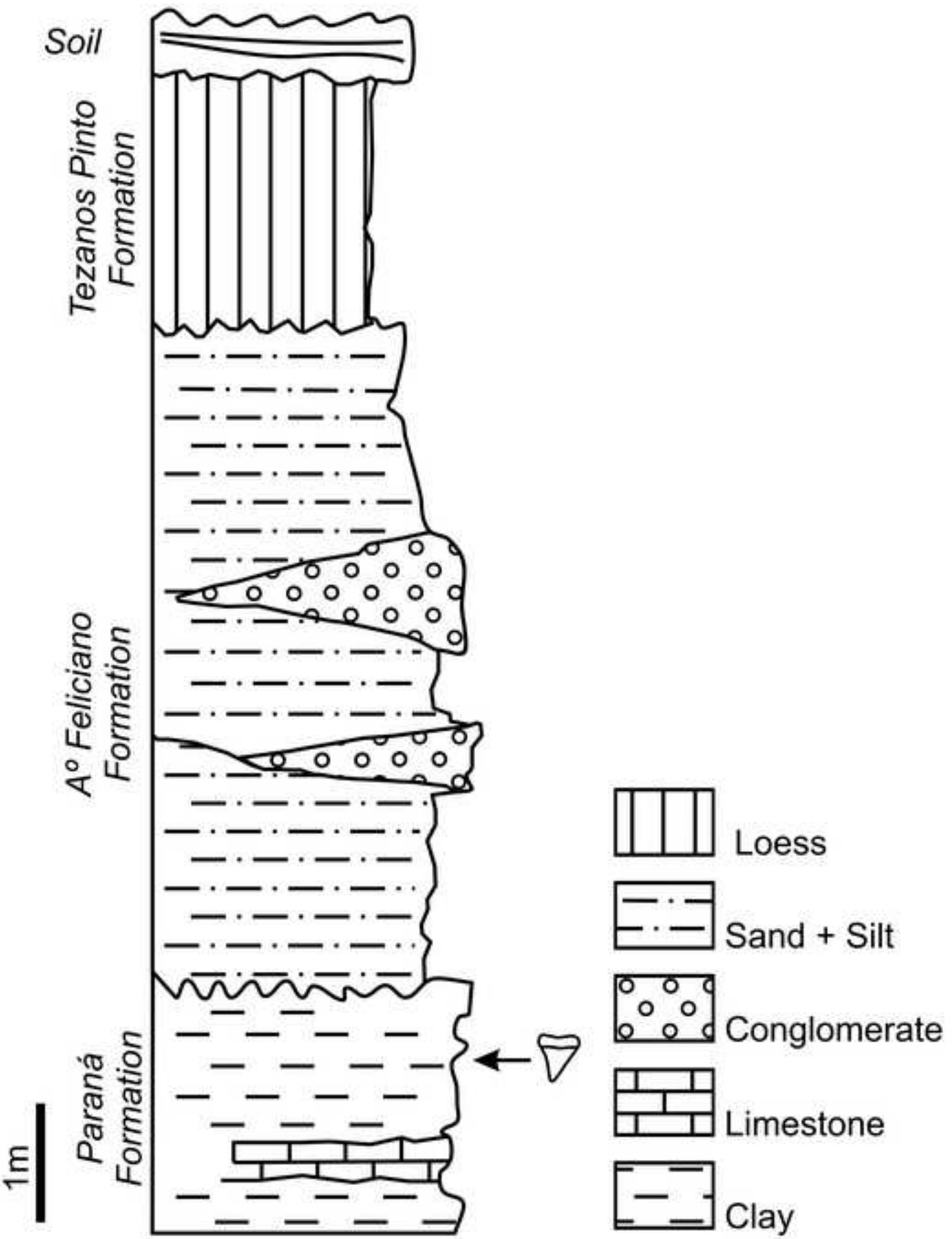


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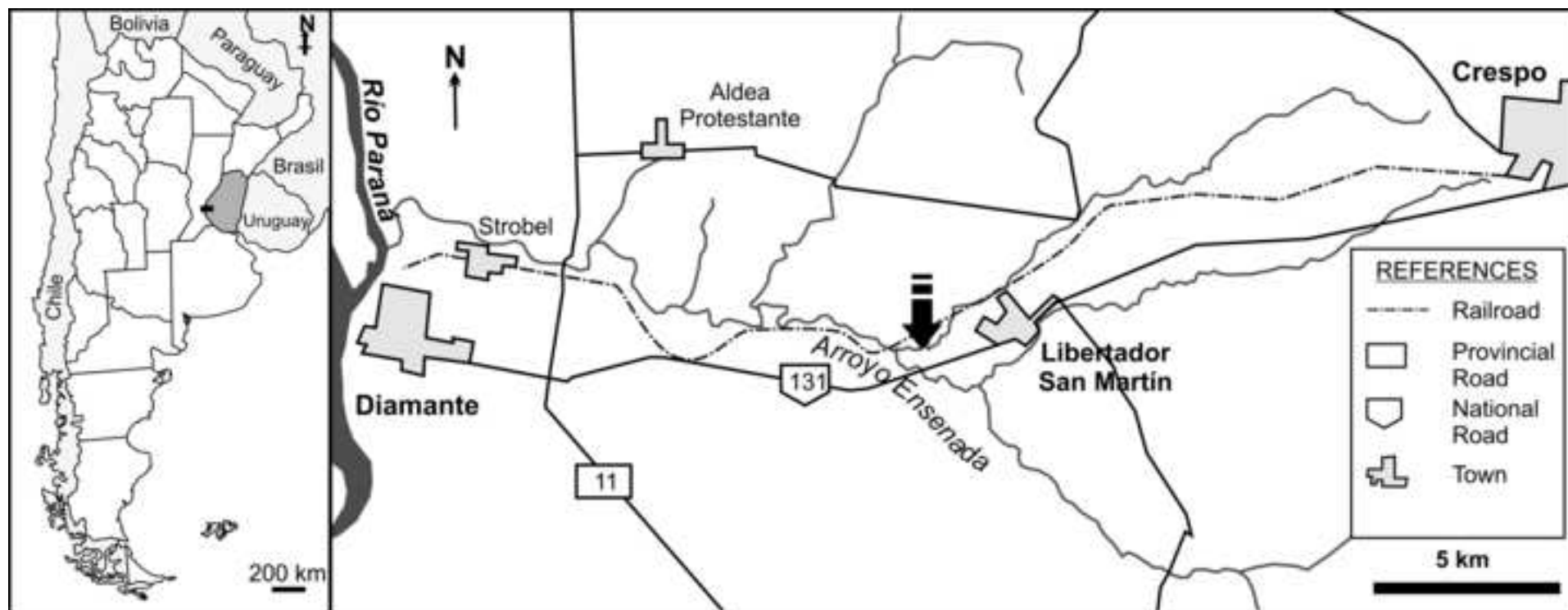


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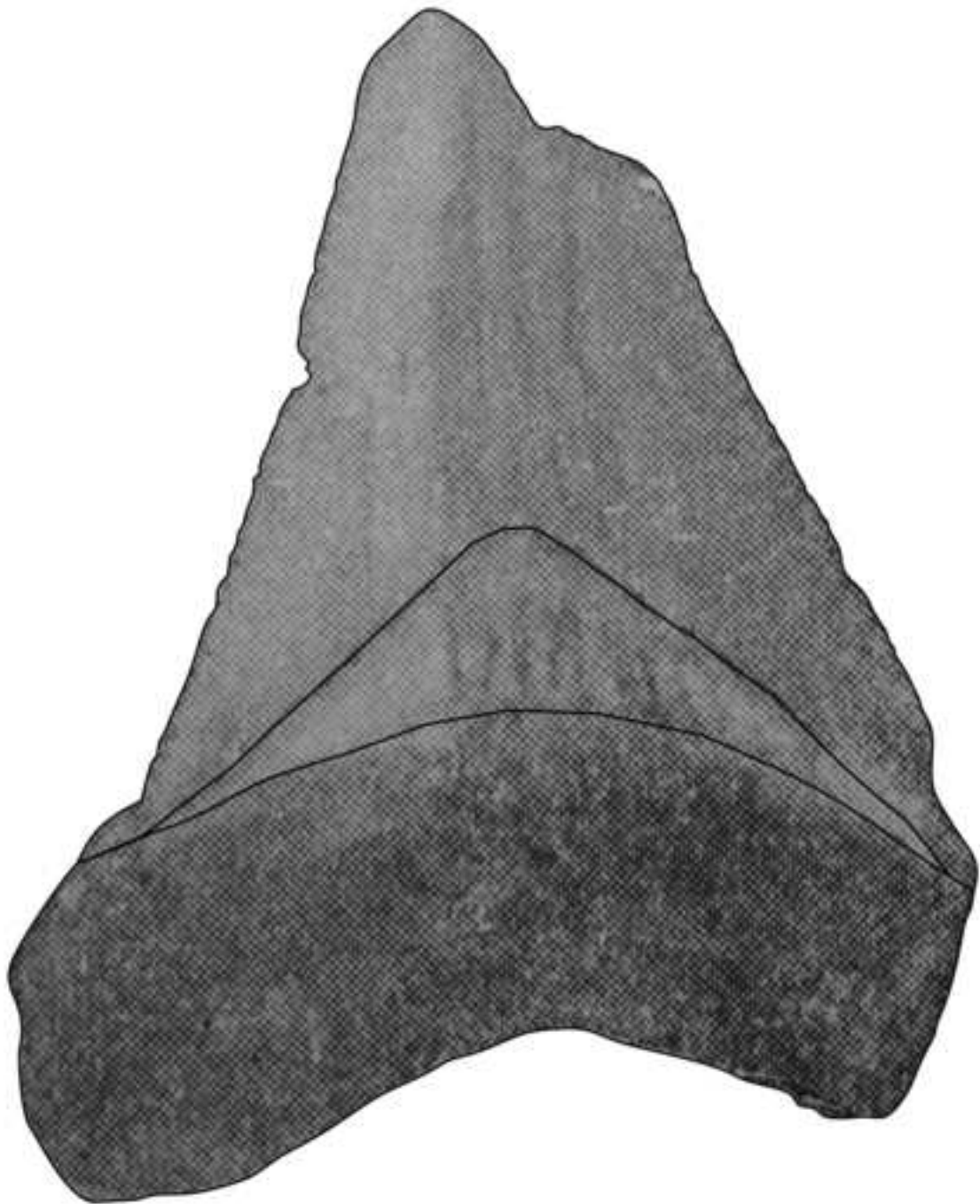


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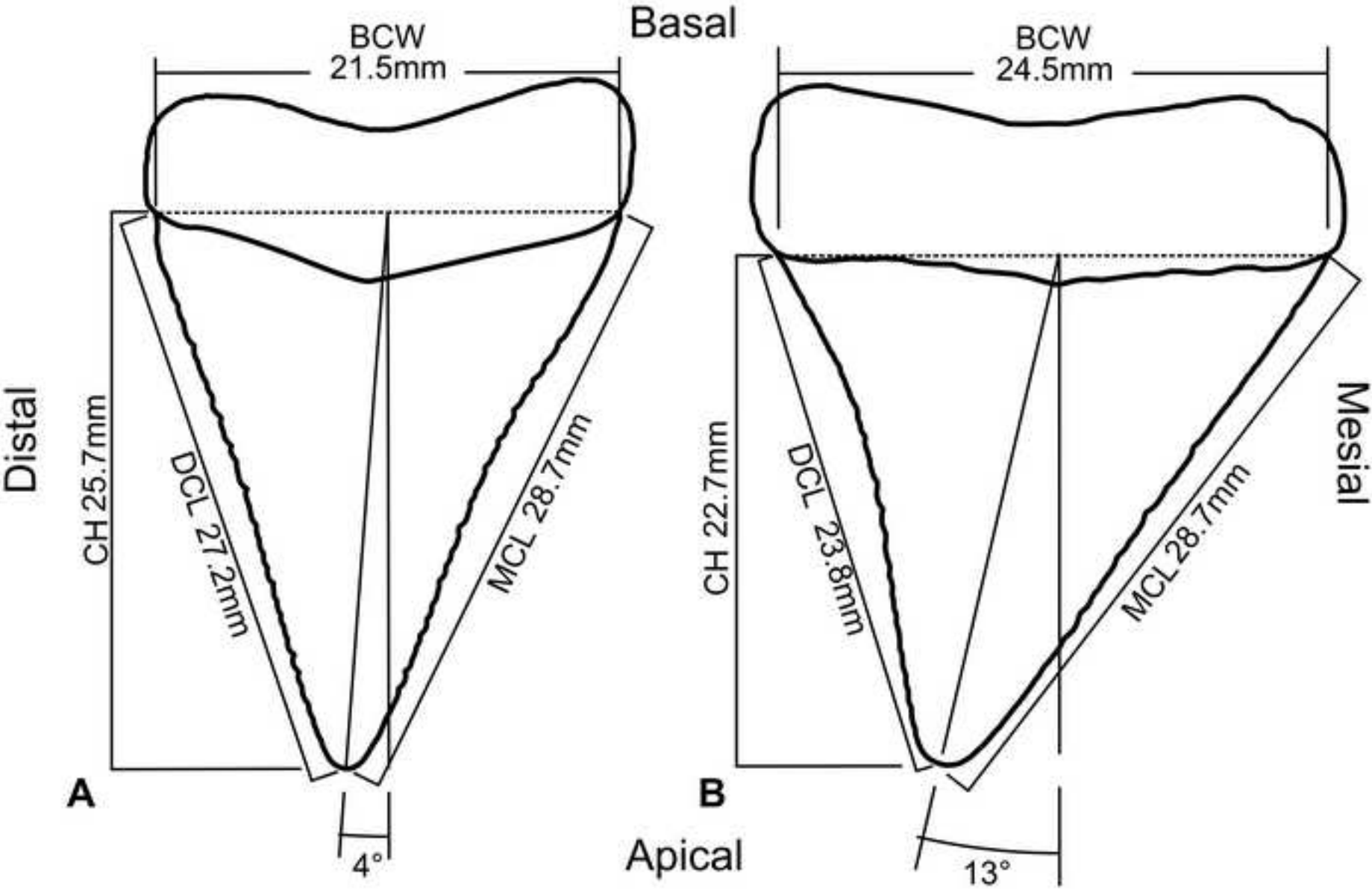


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