

Short communication

First record of elasmobranchs from the Lower Cretaceous of Argentina (Neuquén Basin)



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ABSTRACT

The material reported herein comes from the Lower Cretaceous Agrio Formation (Neuquén Basin, west-central Argentina). These fishes dwelled in a Pacific Ocean embayment in southwestern Gondwana before the establishment of the Andean Cordillera. The material consists of an incomplete dorsal fin spine of the widespread Hybodontoida clade (from upper Valanginian beds) and a partial tooth of one of the earliest known lamniforms (from upper Hauterivian beds).

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1. Introduction

In southwestern Gondwana (South America and Antarctica) chondrichthyans are frequently reported from Upper Cretaceous and Cenozoic beds but Jurassic and Lower Cretaceous records are extremely rare (Arratia and Cione, 1996; see Table 1). Moreover, elasmobranchs from pre-Aptian (early Cretaceous) times are scarcely known worldwide (Guinot and Cavin, 2015).

In this paper, we present a fragmentary hybodont fin spine and a lamniform shark tooth collected at two different stratigraphic levels of the Agrio Formation in the Neuquén Basin and assess the relevance of these new records.

2. Material and methods

The studied specimens here were by-catch recovered while performing a stratigraphic log and sampling of invertebrates of the Agrio Formation at Pichaihue section (Fig. 1). After twenty-five

years of exploration and exploitation of the section, these are the first chondrichthyan remains found in this formation.

2.1. Institutional abbreviations

MOZ, Museo Provincial Prof. Dr. Juan A. Olsacher, Zapala, Neuquén, Argentina; **MLP**, Museo de La Plata, La Plata, Buenos Aires, Argentina.

2.2. Material preparation techniques

The specimens were mechanically prepared using pneumatic tools, needles, and widia tool tips. The study was done under a binocular microscope with different magnifications. Photographs were taken with digital cameras. Measurements were taken with digital Vernier caliper directly on the material as well as with the Fiji free software using high-resolution photographs.

2.3. Descriptive terminology

Anatomical description terminology follows Patterson (1966), Maisey (1978), and Cappetta (2012); the one for the histology follows Maisey (1978).

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Table 1
Southwestern Gondwana (South America and Antarctica) Late Jurassic–Early Cretaceous elasmobranch records.

Taxa	Unit/Locality	Age	References
Batomorphii			
'Rhinobatidae' indet.	Vaca Muerta Formation, Argentina	Late Jurassic	Cione (1999); Cione et al. (2002).
Batomorphii			
<i>Stahlraja sertanensis</i>	Santana Formation, Brazil	Early Cretaceous	Brito et al. (2013)
Heterodontiformes	Apleg Formation, Chile	Early Cretaceous	Bell and Suárez (1997); Suárez (2015)
Hexanchiformes			
Hexanchidae indet.	Kotick Point Formation, Antarctica	Early Cretaceous	Cione and Medina (2009)
Hyodontiformes			
<i>Priohyodus arambourgi</i>	Tacuarembó Formation, Uruguay	Late Jurassic Kimmeridgian–?earliest Cretaceous	Perea et al. (2001); Soto et al. (2012)
Hyodontiformes			
<i>Lissodus nitidus</i>	Ilhas Formation, Brazil	Early Cretaceous	Brito and Richter (2015)
Hyodontiformes	Missão Velha Formation, Brazil	earliest Cretaceous/pre-Aptian	Cupello et al. (2012)
Hyodontiformes			
<i>Tribodus limae</i>	Santana Formation, Brazil	Early Cretaceous	Brito and Ferreira (1989)
Hyodontiformes			
<i>Acrodus nitidus</i>	Marfim Formation, Brazil	Early Cretaceous	Woodward (1888); Lindoso et al. (2016)
Hyodontiformes			
<i>Planohyodus marki</i>	Malhada Vermelha Formation, Brazil	Early Cretaceous	Pinheiro et al. (2011)
Hyodontiformes			
gen. et sp. indet.	Rosablanca Formation, Colombia	earliest Cretaceous	Carrillo-Briceño et al. (2016)
Synechodontiformes			
Palaeospinascidae indet.	Lo Valdés Formation, Chile	Late Jurassic	Suárez and Otero (2011); Suárez (2015)
Palaeospinascidae indet.	Spartan Glacier Formation, Antarctica	Early Cretaceous	Kriwet (2003)

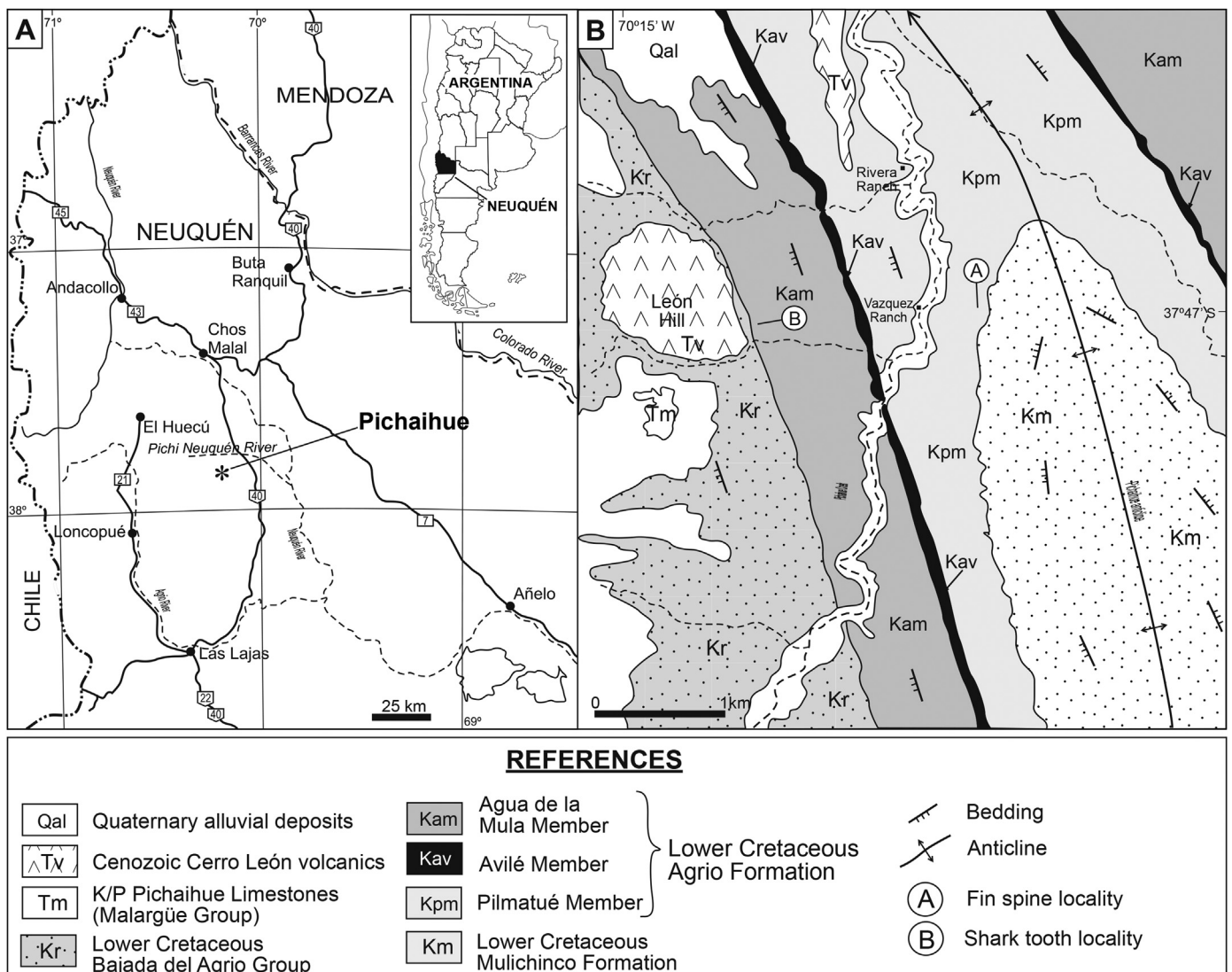


Fig. 1. A, Location map of Pichaihue, Neuquén Basin, west-central Argentina. B, Detailed geological map of Pichaihue showing fossil localities A and B. Geology according to Aguirre-Urreta et al. (2011).

2.4. Biostratigraphy and ages

The fin spine bearing-bed belongs to the upper Valanginian while the shark tooth bearing-bed is younger and belongs to the upper Hauterivian (see Fig. 2). Ages are based on associated ammonoids and follow the refined ammonoid zonation of the Agrio Formation proposed by Aguirre-Urreta et al. (2007, 2008a, 2015), and Aguirre-Urreta and Rawson (2012) that in turn has been correlated with the European Standard Zonation (see Aguirre-Urreta et al., 2007 and Reboulet et al., 2014).

3. Geological setting

3.1. The Neuquén Basin and Agrio Formation

The Neuquén Basin was a back-arc depocentre developed during Early Jurassic–Early Cretaceous times, located in west-central Argentina along the foothills of the Andes, between 32° and 40° South Latitude. Alternating marine and continental deposits accumulated in the basin due to periodic transgressions from the Pacific Ocean. A broadly triangular epeiric sea embayment was formed during times of high sea level (Howell et al., 2005). In particular, the Mendoza Group was deposited from Kimmeridgian to Barremian

times and encompasses, from base to top, the Tordillo, Vaca Muerta, Mulichinco, and Agrio formations (Leanza et al., 2006).

The Agrio Formation was defined by Weaver (1931) in the Río Agrio section within the Neuquén Embayment. In the type area, the section reaches more than 1000 m in which the three members of the unit are well-developed (Fig. 2). The lower or Pilmatué Member is mainly composed of massive clay shales interbedded with thin layers of sandstones and shell beds, and has been interpreted as a shallow marine ramp (shoreface to offshore) with storm influence. The middle or Avilé Member, a thin continental unit, is represented by yellowish-brown cross-bedded coarse sandstones of aeolian and fluvial origin, representing a second-order sea-level fall. The Avilé facies are the result of a short regressive episode at the end of the early Hauterivian (the Intra-Hauterivian Unconformity; Legarreta and Gulisano, 1989), and are covered by a transgressive surface that depicts the return to open marine conditions (Veiga et al., 2002). The upper or Agua de la Mula Member is composed largely of massive shales in the lower part and gray calcareous shales interbedded with sandy limestones and sandstones in the upper part. It represents a new marine transgression into the basin (see Leanza et al., 2006; Spalletti et al., 2011).

Undoubtedly, the Agrio Formation corresponds to one of the most complete Lower Jurassic–Lower Cretaceous marine faunal

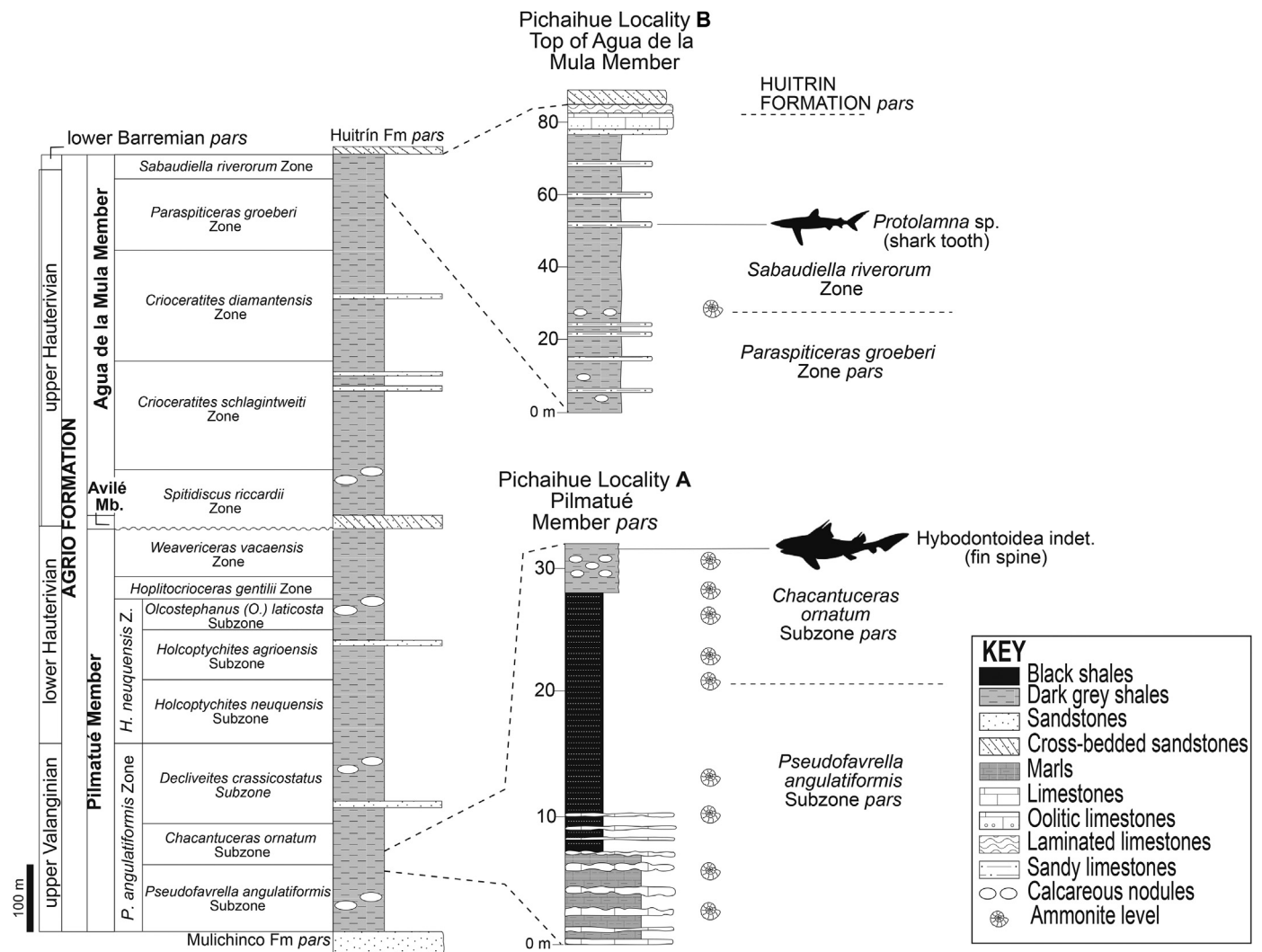


Fig. 2. Stratigraphic log of the Agrio Formation at Pichaihue locality and detailed logs of fossil localities A and B.

successions of the Southern Hemisphere. The rich and abundant fossil record, first described in detail by Weaver (1931), is composed mainly of invertebrates (bivalves, gastropods, nautiloids, ammonites, corals, crustaceans, echinoderms, bryozoans, and serpulids), diverse trace-fossil assemblages, and scarce vertebrate remains including, up to date, ichthyosaurs (Cichowolski and Lazo, 2000), elasmosaurid plesiosaurs (Lazo and Cichowolski, 2003; O'Gorman et al., 2015), and pycnodontiform fishes (Bocchino, 1977; Cione and Pereira, 1990; Lazo et al., 2005). The fauna as a whole has mainly Tethyan affinities, but some taxa have Andean affinities and even endemic taxa are present (Aguirre-Urreta et al., 2008b). The invertebrates indicate shallow warm-temperate waters (Lazo et al., 2005).

The unit was assigned a late early Valanginian to earliest Barremian age based on integrated biostratigraphy calibrated with U–Pb zircon ages (see Aguirre-Urreta et al., 2008a, 2015). Integrated studies on ammonoids, nannoplankton and palynomorphs from the Agrio Formation have provided an excellent biostratigraphic framework for the unit and allows good correlation with the European Standard Zonation (see Reboulet et al., 2014) and the Chilean Chañarcillo Basin zonation (see Aguirre-Urreta et al., 2007; Lazo et al., 2009; Aguirre-Urreta and Rawson, 2012).

3.2. Fossil localities and ages

The fin spine and tooth reported here were collected in the Pichaihue section (37°46'59"S, 70°13'03"W) in two different stratigraphic levels of the Agrio Formation (see localities A and B in Figs. 1B, 2). The Pichaihue section is located along the Pichaihue Creek valley, west of the Chorriaca anticline. Access to the section is through a track running due east off state road 4, 12 km east of Colipilli settlement (Fig. 1A). The Agrio Formation is well-exposed on both banks of the stream (Fig. 1B). This section is located towards the western of the Neuquén Basin and thus more distally placed on the marine ramp of the Agrio Formation closer to the open waters of the Pacific Ocean. The unit at Pichaihue shows a clear predominance of fine-grained facies, including thick beds of black and dark gray shales, representing a predominance of low-energy fall-out deposits. In fact, the fin spine and shark tooth were recovered from dark gray shales and gray sandy limestones, respectively, that represent an offshore low-energy setting below the storm wave base.

The fin spine was collected from locality A, in the lower third of the Pilmatué Member. A 35 m-thick section was measured bed-by-bed just in front of the Vázquez Ranch, encompassing the top of the *Pseudofavrella angulatiformis* Subzone and the base of the *Chacantuceras ornatum* Subzone, including the fin spine-bearing bed (Fig. 2).

The shark tooth was collected at locality B from beds of the upper third of the Agua de la Mula Member, about 30 m below the top of the unit. An 80 m-thick section was measured bed-by-bed encompassing the top of the *Paraspiticeras groeberi* Zone and the *Sabaudiella riverorum* Zone including the shark tooth-bearing bed near to the eastern flank of León Hill (Fig. 2).

4. Systematic paleontology

Subclass Elasmobranchii Bonaparte, 1838

Order Hybodontiformes Maisey, 1975

Superfamily Hybodontoidea Owen, 1846 *sensu* Zangerl, 1981

Hybodontoidea fam., gen., and sp. indet.

Fig. 3

Material. MOZ-Pv 6988, incomplete dorsal fin spine.

Description. Although only two medial portions of the spine are preserved, the general shape indicates that it was elongated. The

fin spine was laterally compressed and oval in cross-section. It widens posteriorly and towards the basal opening, of which only a small portion is preserved. The spine had a keel along the anterior margin formed by an enamel ridge. In cross-section, its walls appear festooned (Fig. 3D, F). The surface of the spine is ornamented with strong and apico-basally directed parallel enameloid ridges (= costated *sensu* Maisey, 1978) that cover the entire free (= exposed) anterior and lateral faces. They are not interrupted and there are not tubercles. Ridges are parallel and equidistant (ca. 1 mm). While the anteriormost ridges are compressed, high, and sharp, the posterior most ones are wider and blunt. The fin spine has 27 ridges in the proximal piece and 21 ridges in the distal piece (Fig. 3A). Only fifteen teardrop-shaped denticle bases are preserved, they are arranged in two rows over the posterior fin spine face (Fig. 3B–C). The denticle disposition may vary over the fin spine length being opposite and/or interspersed. Denticles are approximately 4 mm long and 3 mm wide. The distance between each denticle row and the first wall ridge ranges from 5 mm (distal) to 3.5 mm (proximal). The internal structure comprises a well-developed central pulp cavity which is oval and narrow. It is surrounded by a layer of lamellar tissue (of about 1–2 mm thick) which forms almost half the thickness of the fin spine wall, a well-developed trabecular tissue (=osteodentine) layer that covers the lamellar one, and a thin enameloid layer (Fig. 3F). Trabecular tissue develops over the entire fin spine, being more developed in its anterior and posterior region (reaching 5 mm thick) and less developed laterally (reaching 1 mm wide). The lamellar tissue decreases basally and is absent in the proximal portion. The pulp cavity opens posteriorly in the most basal part of the preserved fin spine (ca. 10 mm posterior to the last denticles). The total fin spine length may had been c. 300 mm. Based on the reconstruction and proportions of the first fin spine of *Hybodus* sp. by Maisey (1982), the shark could have measured about 2000 mm in total length.

Comparisons and discussion. Several chondrichthyans have fin spines preceding their dorsal fins. MOZ-Pv 6988 resembles those of hybodontiforms and differs from the other – xenacanthids, ctenacanthids, squaliforms, heterodontids, holocephalians, and batomorphs – because it has an oval cross-section, the trabecular tissue is more developed anteriorly and posteriorly (being thinner laterally), ridges are parallel and equidistant covering the entire fin spine surface, and because the denticles are arranged in two rows always on the middle part of the posterior face of the spine (not along its borders). Hybodontiform fin spines are difficult or impossible to assign to a certain genus or species (Maisey, 1978; Rees, 1998). Fin spines are known only in Distobatidae (*Tribodus* Brito and Ferreira, 1989), Hybodontidae (*Hybodus* Agassiz, 1837, *Pryohyodus* Erasmo, 1960), Acrodontidae (*Acrodus* Agassiz, 1838, *Asteracanthus* Agassiz, 1837), Polyacrodontidae (*Palaeobates* Meyer, 1849, *Polyacrodus* Jaekel, 1889), and Lonchidiidae (*Lissodus* Brought, 1935, *Lonchidion* Estes, 1964) (Maisey, 1978; Brito in Maisey, 1991; Duffin, 2001; Cappetta, 2012). MOZ-Pv 6988 differs from *Asteracanthus* and some Late Cretaceous *Hybodus*, because in those genera the ridges of the fin spines are replaced by tubercles arranged in longitudinal series (Cappetta, 2012). Spines of Lonchidiidae (*Lissodus*, *Lonchidion*) present only one series of posterior denticles (Cappetta, 2012). MOZ-Pv 6988 appears difficult to distinguish from fin spines of the distobatid *Tribodus*, hybodontids, the acrodontid *Acrodus*, and polyacrodontids. However, *Tribodus* spines are smaller (up to 125 mm in length). The material studied here shows some differences but also similarities to members of Hybodontidae: for instance, MOZ-Pv 6988 has a double series of denticles, a character shared with *Hybodus*.

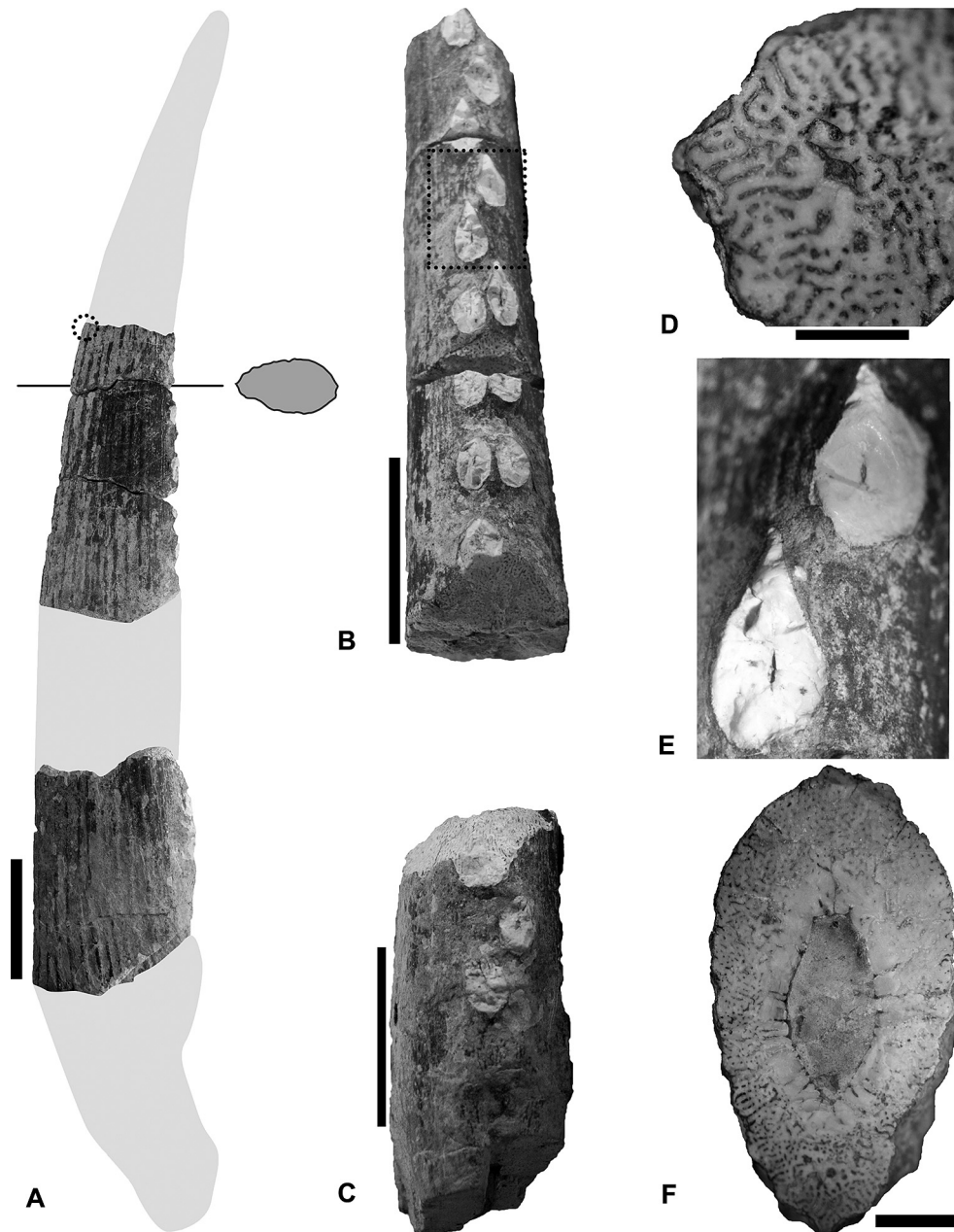


Fig. 3. MOZ-Pv 6988, Hybodontiformes fin spine. A, Silhouette of the fin spine in which preserved parts are shown. B–C, Posterior fin spine margin to show the denticle bases. D, Cross section of the fin spine in their anterior margin at level illustrated in A with a circle. E, Close-up of B to show denticle bases. F, Cross section of the fin spine at level shown in A. Scale bars = 20 mm in A–C; 2 mm in D; 3 mm in E–F.

Order Lamniformes [Berg, 1958](#)

Family Eoptolamnidae [Kriwet, Klug, Canudo, and Cuenca-Bescós, 2008](#)

Genus *Protolamna* [Cappetta, 1980a](#)

Protolamna sp.

[Fig. 4](#)

Material. MOZ-Pv 6989, an incomplete tooth.

Description. MOZ-Pv 6989 is a small tooth (4 mm high). The tip of the cusp is missing. The cusp is narrow, slightly convex labially and strongly cambered lingually. It is not lingually bent and the labial face base is depressed. The mesial and distal edges of the main cusp change their direction abruptly. A complete, large, well separated, and lingually pointing distal lateral cusplet is

preserved; its lingual face is strongly convex and the labial face is flat. The cutting edges are complete. The mesial lateral cusplet is missing. There are very strong lingual, mainly parallel folds in the whole preserved portion of the main cusp and lateral cusplet and strong basal labial parallel folds in the main cusp and lateral cusplet (possibly 1/5 of the crown height). The base of the labial crown is convex, not triangular. The labial crown-root boundary is concave, forming a turned “U.” The root branches are long and dissimilar, with expanded bases. The lingual protuberance is not preserved.

Comparison and discussion. The material is morphologically similar to teeth of the Cretaceous carcharhiniforms genus *Pteroscylidium* [Cappetta, 1980b](#) and lamniform family Eoptolamnidae (see [Kriwet et al., 2008](#); [Cappetta, 2012](#)). However, after a radiograph the

specimen MOZ-Pv 6989, does not show a pulp cavity (A. Cione pers. obs. 2017). Moreover, MOZ-Pv 6989 differs from *Pteroscyllium* in that the lateral cusplet does not show increased lingual orientation relative to the main cusp, the labial ornamentation is less strong, and the main cusp and lateral cusplet have very large basoapical ridges on the lingual face (Kriwet et al., 2009; Schmitz et al., 2010). Besides, the present material is much older than the oldest record of that genus (Aptian; Cappetta, 2012). MOZ-Pv 6989 differs from the eoptolamnid *Eoptolamna* Kriwet et al., 2008 in the general shape, the absence of a distinct median crest extending from the base to almost the apex of the crown, the lateral cusplets separated from the main cusp and in the same line than main cusp, and the less convex lingual face of main cusp (see Kriwet et al., 2008; Guinot et al., 2013). MOZ-Pv 6989 differs from the eoptolamnid *Leptostyrax* Willinston, 1900 in the wider, basally unconstricted cusp, lateral cusplets not needle-like and separated from main cusp, cutting edges continuous between main cusp and lateral cusplets, and root lobes uncompressed not forming a V-shaped labial crown/root boundary (see Kriwet et al., 2009; Schmitz et al., 2010). MOZ-Pv 6989 resembles teeth of the eoptolamnid genus *Protolamna* in the following traits: slender lateral cusplets widely separated from main cusp; lateral cusplets in plane of labial side of main cusp; labial crown-root boundary distinctly concave, forming a turned “U” in anterior and lateral teeth; bulky and high root (see Rees, 2005; Schmitz et al., 2010; Guinot et al., 2013). MOZ-Pv 6989 is similar, in labial view, to the paratype 1 of *Protolamna sarstedtensis* Schmitz et al., 2010 (figs. 3.9–10) from the early Barremian of NW Germany. However, it differs in the strong lingual ornamentation and distally expanded root branches. The genus *Protolamna* was named for teeth from the Aptian of France by Cappetta (1980a). The genus was recognized from the Valanginian to the Maastrichtian (Cappetta, 2012; Guinot et al., 2013). Seven species have been assigned to the genus so far (Kriwet et al., 2008, 2009; Cappetta, 2012). However, the morphological diversity that the teeth assigned to *Protolamna* show suggests that they could represent more than one genus (Kriwet, 1999). This is the first record of *Protolamna* in South America.

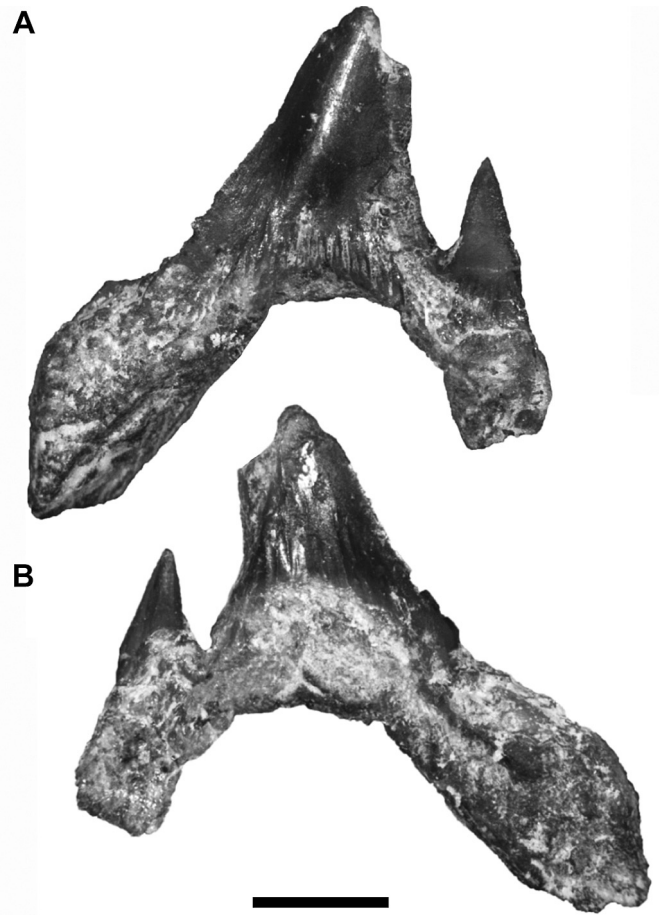


Fig. 4. MOZ-Pv 6989, *Protolamna* sp. A, Labial view. B, Lingual view. Scale bar = 2 mm.

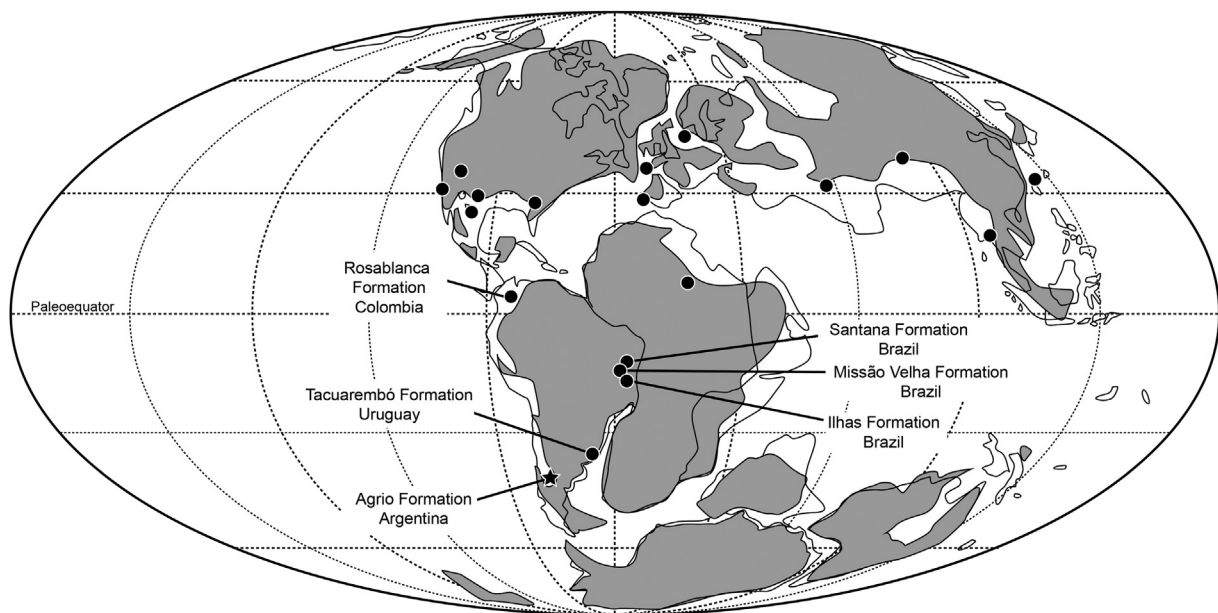


Fig. 5. Hybodontiform paleobiogeography during the Berriasian–Hauterivian time interval. Records compiled from Cappetta (2012); Soto et al. (2012), Brito and Richter (2015), Cupello et al. (2012), Lindoso et al. (2016), and Carrillo-Briceño et al. (2016). Only South American formations are mentioned. Paleobiogeographic reconstruction modified from Lazo (2007) and Smith et al. (1994).

5. Final remarks

Chondrichthyans are very poorly known from Jurassic and Lower Cretaceous times of southwestern Gondwana (Fig. 5). Actually, the fin spine and tooth described here are the first chondrichthyans of the Valanginian–Hauterivian time interval. The fin spine, along with the Late Jurassic spine from the Vaca Muerta Formation (Cione et al., 2002), represent the southernmost hybodontiform marine records in the world. Despite hybodontiforms have a worldwide distribution being commonly found and highly diverse during the Mesozoic in Europe, North America, Asia, and Africa, they are scarce in South America. A bias due to collection may not be discarded. Neoselachians are relatively well known in Jurassic rocks. One of the most important crown groups, Lamniformes, is known since the Valanginian. Both hybodontids and *Protolamna* became extinct during the K–Pg mass extinction. Pre-Aptian Cretaceous elasmobranch faunas are at the crossroads between Jurassic faunas (acrodontids, stem hexanchiforms, synchondontiforms, small-sized orectolobiforms, and carcharhiniforms) and mid-Cretaceous faunas characterized by diverse lamniforms (cretoxyrhinids, archaeolamnids, anacoracids, and paraisurids), numerous ptychodontids and batoids (sclerorhynchiforms, rajids, and cyclobatids), and some squaliforms (squalids and centrophorids) (Guinot and Cavin, 2015). According to Guinot and Cavin (2015), Lamniformes probably appeared in the Middle Jurassic although they remained relatively inconspicuous (mainly *Eoptolamna* and *Protolamna*) until the Aptian–Albian. Therefore, any information about Lamniformes from pre-Aptian times is relevant.

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