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## NEW SELACHIAN RECORDS FROM THE UPPER CRETACEOUS OF SOUTHERN PATAGONIA: PALEOBIOGEOGRAPHICAL IMPLICATIONS AND THE DESCRIPTION OF A NEW TAXON

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**ABSTRACT**—We describe isolated shark teeth collected in levels of the Calafate Formation (Maastrichtian, Late Cretaceous) on the southeast coast of Argentino Lake, Calafate City, Santa Cruz Province, Argentina. The teeth belong to the hexanchiform *Notidanodon dentatus*, a new species of the squaliform *Protosqualus*, and an indeterminate species of the echinorhiniform genus *Echinorhinus*. The record of *Notidanodon* constitutes the first in South America. The report of *Notidanodon* associated with plesiosaur remains is in accordance with previous records from around the world. *Protosqualus argentinensis*, nov. sp., which is the first record of the genus in South America, is characterized by having teeth with a apicobasally tall root and serrated cutting edges, among other features. *Echinorhinus* sp. constitutes one of the oldest records of this genus on the continent and one of the few Mesozoic records worldwide. This shark association is clearly distinct from coeval selachian faunas from northern Patagonia, which exhibit clear Tethyan influences. Instead, it shows some similarities to other high-latitude selachian faunas, including Australia, New Zealand, and Antarctica. It is possible that the Cretaceous selachian assemblages of Patagonia may be separated into two different associations: northern Patagonian faunas are related to more temperate associations of lower paleolatitudes, whereas those of southern Patagonia are closer to other southern localities.

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### INTRODUCTION

Most of the Cretaceous fossil shark record in South America is restricted to pioneering finds made by the Argentinian paleontologist Florentino Ameghino (1893, 1901, 1906). The specimens reported by Ameghino come from the Upper Cretaceous (Coniacian) of Patagonia and belong to indeterminate odontaspids and hexanchids, *Cretolamna* sp., and some selachians of uncertain validity (Arratia and Cione, 1996).

In addition to Ameghino's early work, the selachian record of the late Maastrichtian of northern Argentine Patagonia has recently increased with the discovery of new localities that yield abundant and well-preserved teeth of lamniform sharks and batoids (Bogan and Agnolin, 2010; González Riga et al., 2010). A large array of taxa from fossiliferous levels of the Jagüel Formation at Trapal-Co, Río Negro Province, Argentina, have been described. These include the batoid *Hypolophodon patagoniensis* (Bogan and Gallina, 2011; Cione et al., 2013), the sharks *Serratolamna serrata*, *Squalicorax pristodontus*, *Cretolamna* sp., *Carcharias* sp., and *Odontaspis* sp., as well as teleosteans of the genus *Enchodus* (Bogan and Agnolin, 2010). In addition, González Riga et al. (2010; see also Prámparo et al., 2014) described teeth of *Serratolamna serrata* and *Squalicorax pristodontus* from the Jagüel Formation, but from Mendoza Province, western Argentina (González Riga et al., 2010; Prámparo et al., 2014). Both ichthyofaunal

assemblages indicate that the selachians of the latest Cretaceous-Paleogene interval of northern Patagonia and western Argentina belong to cosmopolitan taxa of Tethyan affinities (Bogan and Gallina, 2011). In the last decade, the fossil record of sharks from the Cretaceous of Chile has greatly improved, with the discovery of new localities that have yielded abundant batoid and selachian fishes (Otero and Suárez, 2008; Suárez and Otero, 2008; Otero et al., 2013). Among other findings, Otero et al. (2013) reported the presence of *S. serrata* in Maastrichtian beds of the Dorotea Formation at latitudes below 60°, representing the southernmost distribution for this warm-water-associated taxon.

In the present paper, new selachian specimens from the upper levels of the Calafate Formation (Late Maastrichtian) of Santa Cruz Province, southern Patagonia, are described. The specimens were found in close association with a partial skeleton of a large elasmosaurid plesiosaur (Novas et al., 2011). They include a new taxon, described here, as well as extend the geographic distribution and temporal range of some other species.

### MATERIALS AND METHODS

**Locality and Horizon**—The fossiliferous locality is in the southern margin of Argentino Lake, approximately 500 m north of the International Airport of El Calafate City (S50°16'09", W72°02'39") (Fig. 1).

The specimens were found at the same stratigraphic level from the upper levels of the Calafate Formation, which is dominated

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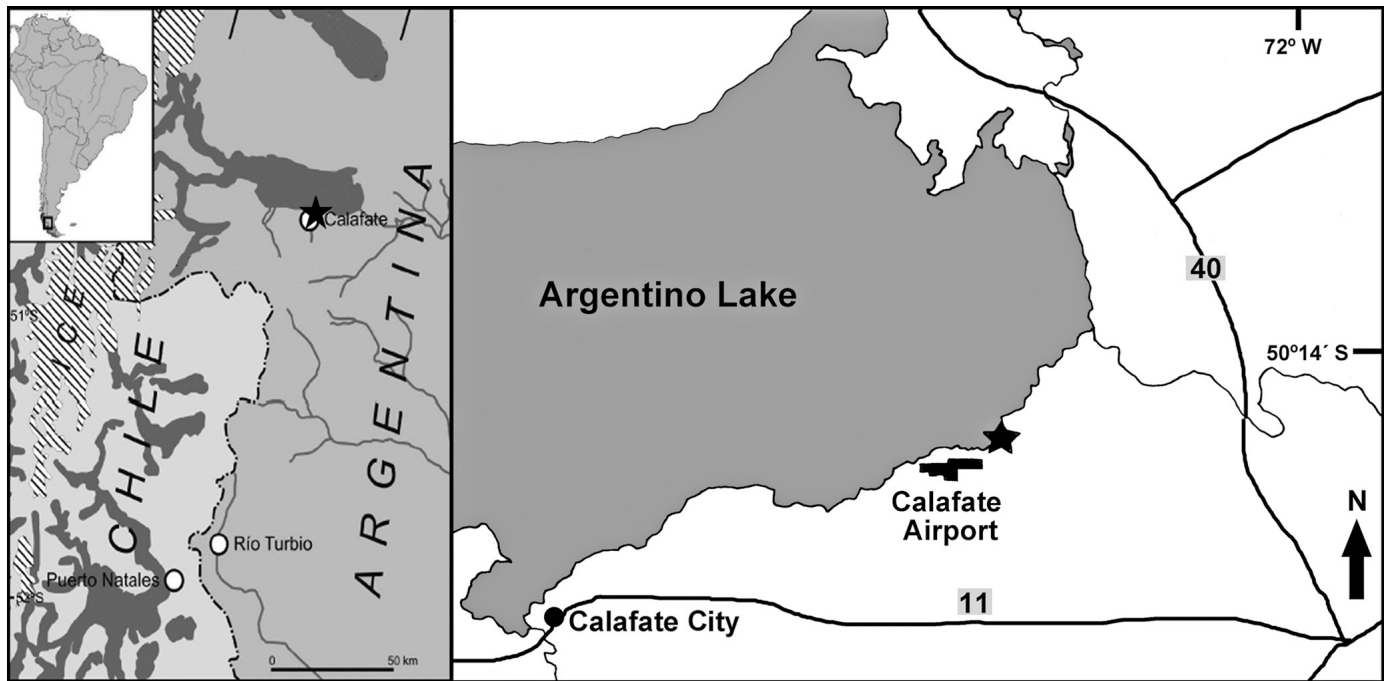


FIGURE 1. Map showing fossiliferous locality. The star indicates the fossil site.

by sandstones with occasional beds of conglomerates and very few glauconitic mudstones, showing a typically greenish coloration (Marensi et al., 2004). The Calafate Formation is considered to mainly represent inter- to subtidal deposits under an estuarine regime (Arbe and Hechem, 1984).

All the specimens described here were found in the laboratory during the preparation of a very large elasmosaurid plesiosaur. The specimens were found with the naked eye and picked by the technicians who mechanically prepared the fossil reptile. Because the rock is strongly consolidated and forms a very hard sedimentary unit, and the plesiosaur was found under the water level of the lake, more precise collecting techniques or sedimentary sieving were not possible.

**Anatomical Terminology and Taxonomical Nomenclature**—The present paper follows the dental terminology employed by Cappetta (2012). The general taxonomic nomenclature follows Cappetta (1975), Thies (1987), and Cione (1996) for *Notidanodon*, Adnet and Cappetta (2001) and Adnet et al. (2008) for *Protosqualus*, and Pfeil (1983) for *Echinorhinus*.

**Institutional Abbreviation**—MPM, Museo Padre Molina, Río Gallegos City, Santa Cruz Province, Argentina.

#### SYSTEMATIC PALEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880  
 Subclass ELASMOBRANCHII Bonaparte, 1838  
 Order HEXANCHIFORMES Buen, 1926  
 Family HEXANCHIDAE Gray, 1851  
 Genus *NOTIDANODON* Cappetta, 1975  
*NOTIDANODON DENTATUS* Woodward, 1886

**Referred Material**—MPM 10021, anterior upper tooth (Fig. 2A); MPM 10020, lower anterolateral tooth (Fig. 2B); MPM 10022, lateral tooth (Fig. 2C).

**Description**—The upper anterior tooth (MPM 10021) preserves four cusps. The main cusp is large and straight, and its distal and mesial cutting edges are nearly straight. Mesial and distal cusplets are well developed and subequal in size. Their

respective mesial and distal cutting edges are nearly straight. Distal cusplets are distally inclined, whereas the only preserved mesial cusp is apicomésially oriented. The root is apicobasally deep.

The lower anterolateral tooth (MPM 10020) is 33 mm long, representing a relatively large specimen of the genus. The main cusp is long and apically oriented. It is very well differentiated from the remaining cusps, indicating that it is a lower anterolateral tooth (Hovestadt et al., 1983). Mesial and distal cusplets are large and elongate and subequal in size and morphology. They exhibit slightly convex mesial cutting edges, whereas in the main cusp and the second cusp, the respective mesial cutting edges are slightly concave towards their bases. The distal cutting edge of the main and second cusps is slightly concave, whereas this margin in mesial and distal cusplets is gently convex. There are four preserved mesial cusplets that are slightly apicodistally oriented, whereas in *N. loozi* these cusplets are apicomésially oriented (Hovestadt et al., 1983; Cione, 1996). There is a low number of distal cusplets (only six are preserved). The root is apicobasally deep.

The lower posterolateral (MPM 10022) tooth is 36 mm long. The crown is apicobasally low, and the main cusp is relatively low, being poorly differentiated from the remaining cusplets. Both the main cusp and distal cusplets are strongly inclined distally. This indicates that this tooth is a posterolateral one (Hovestadt et al., 1983). Mesial and distal cusplets are relatively low and stout, being subequal in morphology, decreasing in size towards the distal end of the tooth. Both mesial and distal cusplets exhibit a strongly convex mesial cutting edge, whereas the distal edge is highly concave. Seven distal cusplets are preserved. The root appears to be low but shows a well-developed medial tilting that projects the root towards the lingual side.

**Remarks**—The specimens here described are referred to *Notidanodon* on the basis of the well-developed, acute, and numerous mesial cusplets on anterolateral lower teeth (Cappetta, 1975; Thies, 1987; Cione, 1996). These specimens are clearly distinguished from the Paleogene species *N. loozi* and *N. brotzeni*

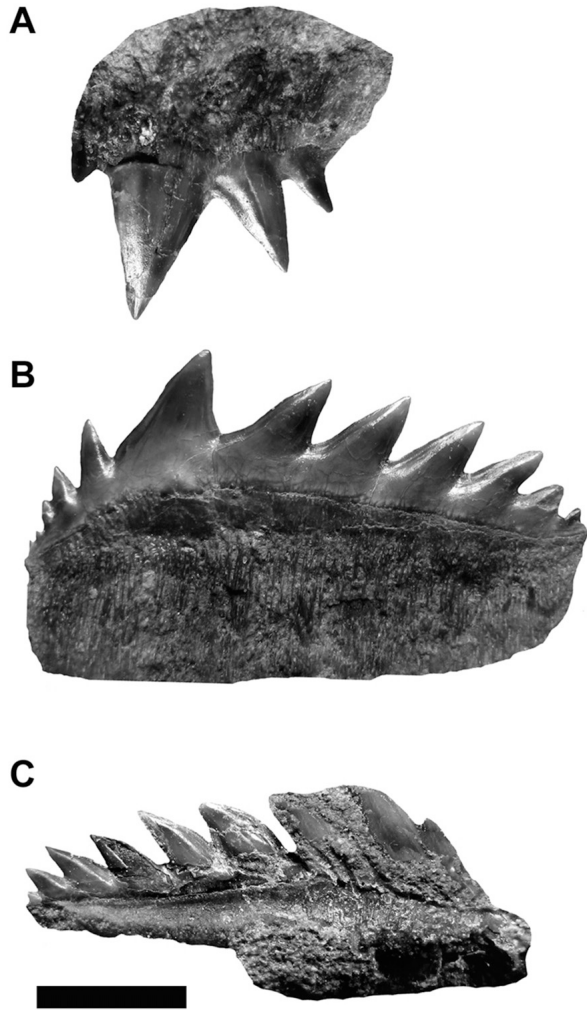


FIGURE 2. *Notidanodon dentatus*. **A**, anterior upper tooth (MPM 10021) in labial view; **B**, lower anterolateral tooth (MPM 10020) in labial view; **C**, lateral tooth (MPM 10022) in labial view. Scale bar equals 1 cm.

(Hovestadt et al., 1983; Siverson, 1995). In *N. loozi*, the distal cutting edge of the principal and distal cusplets is strongly convex, and the mesial cusplets are apicomesially oriented (Cione, 1996), both traits being absent in the specimens here reported. Besides, *N. brotzeni* has a larger number of mesial cusplets (more than six), larger and more elongate main cusp and cusplets, and a basal borderline of the crown that is convex (Long et al., 1993; Siverson, 1995).

Regarding Cretaceous species of *Notidanodon*, in the most recent revision of the genus Cione (1996) indicated that lateral teeth of *N. dentatus* differ from those of *N. lanceolatus* in larger size and deeper roots, a larger number of distal cusplets, convex mesial cutting edge in mesial and distal cusplets, and well-developed mesial accessory cones nearly as high as the acrocone (Ward, 1979; Cione and Medina, 1987; Ward and Thies, 1987; Cione, 1996; Antunes and Cappetta, 2002).

The present specimens of *Notidanodon* were found in close association with an elasmosaurid plesiosaur (Novas et al., 2011), a pattern also reported for several fossiliferous localities around the world (Welles, 1943; Applegate, 1965; Cione and Medina,

1987; Ward and Thies, 1987; Long et al., 1993). The association of *Notidanodon* teeth with these marine reptiles supports the idea that this shark was an opportunistic scavenger (Cione and Medina, 1987; Long et al., 1993).

Order SQUALIFORMES Compagno, 1973

Family SQUALIDAE Blainville, 1816

Genus *PROTOSQUALUS* Cappetta, 1977

*PROTOSQUALUS ARGENTINENSIS*, nov. sp.

**Diagnosis**—Very large *Protosqualus* that is distinguished from remaining species of the genus on the basis of the following combination of characters (autapomorphies marked by an asterisk\*): (1) mesial heel with an irregularly denticulated cutting edge\* (Fig. 4), (2) mesiodistally wide uvula with its distal end acute and subvertically oriented\*, (3) linguallly extended uvula, and (4) apicobasally deep tooth root.

**Etymology**—*Argentinensis* in reference to Argentino Lake, the locality that yielded the specimens here described.

**Holotype**—MPM 10023, anterolateral tooth (Fig. 3A, D).

**Paratypes**—MPM 10024, lateral tooth (Fig. 3C, F); MPM 10025, lateral tooth (Fig. 3H); MPM 10026, commissural tooth (Fig. 3J, K); MPM 10027, lateral tooth (Fig. 3L); MPM 10028, lateral tooth (Fig. 3B, E); MPM 10029, lateral tooth (Fig. 3I); MPM 10030, lateral tooth (Fig. 3G); MPM 10031, lateral tooth; MPM 10032, lateral tooth; MPM 10033, lateral tooth; MPM 10037, lateral tooth; MPM 10038, lateral tooth; MPM 10039, lateral tooth; MPM 10040, lateral tooth; MPM 10041, lateral tooth; MPM 10042, lateral tooth; MPM 10043, lateral tooth; MPM 10044, lateral tooth.

**Description**—Available lateral teeth are of very large size for the genus (7–9 mm in total length). The main cusp is relatively elongate and acute and very distally oriented. Its mesial cutting edge is strongly denticulated by irregular denticles along all its length (Fig. 4). The distal cutting edge is nearly smooth, lacking any sign of denticulation. The distal heel is mesiodistally extended, with a dorsally convex margin, and its cutting edge is irregularly denticulated. The apron is well developed, subtriangular in contour, and is not well raised from the rest of the crown. The apron shows a rounded and mesiodistally wide base. The lingual face exhibits a very large uvula that is distally pointed. Its main axis is subvertical, nearly perpendicular to the main mesiodistal axis of the teeth root. In lingual view, the crown-root boundary shows a row of small foramina and notches. The ventral margin of the crown distal to the apron is undulating. The root is apicobasally tall and labiolingually thick. It is simple, basally flat, and lacks a deep ventral concavity or notch. The root exhibits several small-sized distolabial foramina. The axial foramina amalgamate on an infundibulum, forming a subvertical groove, a condition present in species of *Protosqualus*, *Squalus*, and *Megasqualus* (Adnet et al., 2008; Cappetta, 2012). Several additional foramina may be present in the area between the mediocentral foramen and the apron. The mesial notch is absent, which suggests that the dental overlap was moderate. The labial root edge bears a thin and elongate mesial expansion and a broader distal one.

The available anterolateral tooth (MPM 10023) is similar to the other lateral teeth. It differs from them in being mesiodistally shorter, and in having an apicobasally taller crown and more deeply crenulated cutting edge of the mesial heel.

The commissural tooth (MPM 10026) differs from the remaining teeth in being mesiodistally extended and apicobasally low. The cutting edge of the mesial heel is slightly crenulated. The distal heel is apicobasally low, slightly convex in outline, and anteroposteriorly extended. Its length is nearly half of the total mesiodistal tooth length. The apron is relatively small but well defined.

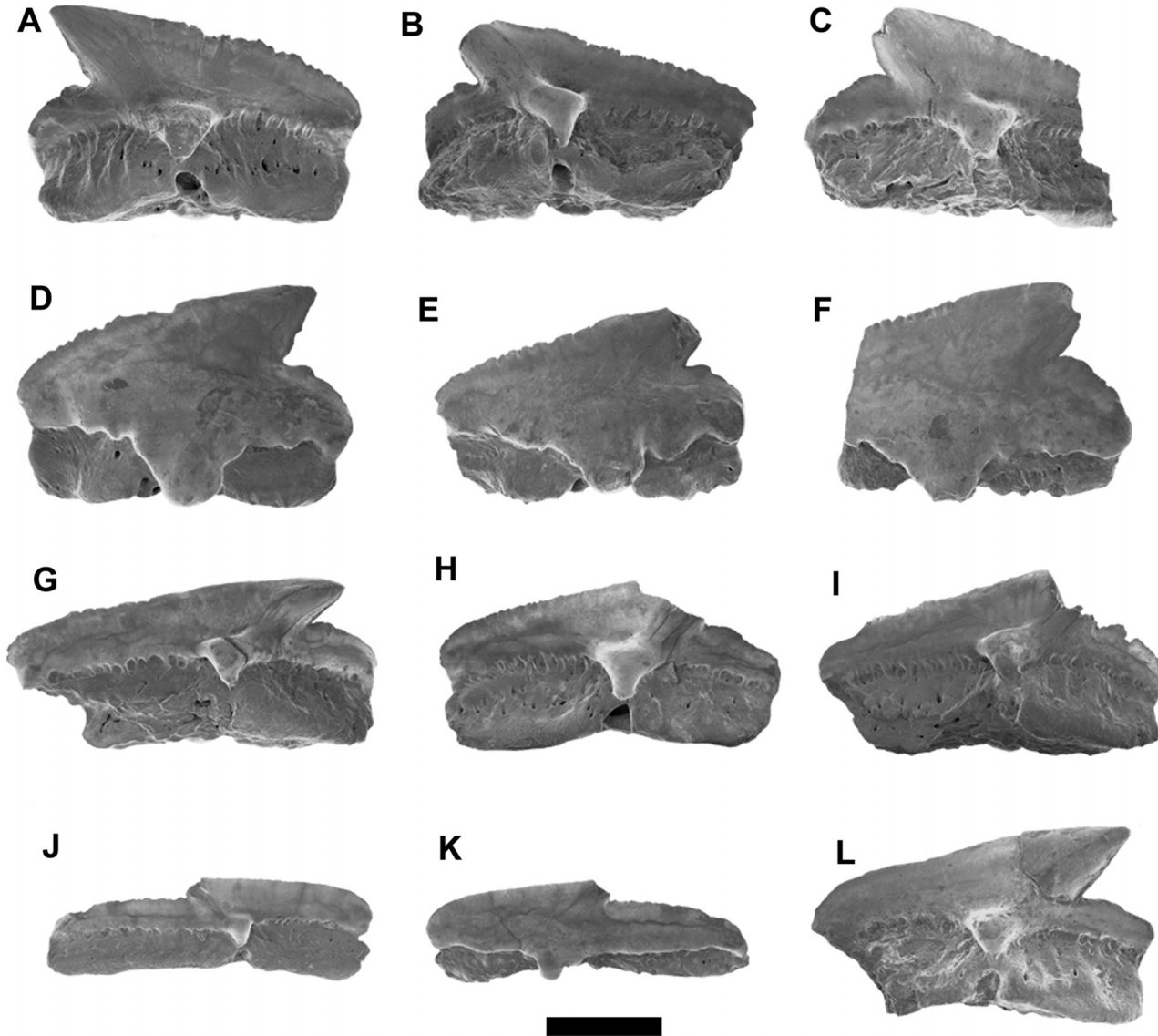


FIGURE 3. *Protosqualus argentinensis*, nov. sp. Selected teeth. **A, D**, anterolateral tooth (holotype, MPM 10023) in **A**, lingual and **D**, labial views; **B, E**, lateral tooth (MPM 10028) in **B**, lingual and **E**, labial views; **C, F**, lateral tooth (MPM 10024) in **C**, lingual and **F**, labial views; **G**, lateral tooth (MPM 10030) in lingual view; **H**, lateral tooth (MPM 10025) in lingual view; **I**, lateral tooth (MPM 10029) in lingual view; **J, K**, commissural tooth (MPM 10026) in **J**, lingual and **K**, labial views; **L**, lateral tooth (MPM 10027) in lingual view. Scale bar equals 0.2 cm.

**Remarks**—Adnet and Cappetta (2001) performed a detailed analysis of squaliform phylogeny and evolution. Within the Squaliformes, they recognized five main dentary groups. The material here described can be assigned to the ‘second dentary group’ of Adnet and Cappetta (2001), which includes the genera *Megasqualus*, *Cirrhigaleus*, *Squalus*, and *Protosqualus*. All these genera are united in having a relatively large and well-differentiated apron when compared with genera such as *Somniosus* and *Squaliolus* (Adnet and Cappetta, 2001), labiolingually wide crowns, and a basal face of the root near perpendicular to the labial face of the crown (Adnet and Cappetta, 2001). Within this dental group, the specimens here described resemble *Protosqualus* and differ from most genera, including *Centrophoroides* (Family Centrophoridae) and *Squalus* (Family Squalidae), in lacking a deep mesial root notch (indicative of a reduced dental overlap) and having a very short apron (Adnet and Cappetta,

2001; Adnet et al., 2008). The new species here described also resembles the genus *Megasqualus* in several traits, including relatively large size of teeth, tooth crown with serrated cutting edges, and broad and robust apron (the latter feature also shared with *Protosqualus*; Herman, 1982; Cappetta, 2012). In spite of these similarities, *Megasqualus* differs from the new taxon here described, as well as other members of the genus *Protosqualus*, in having a particularly flattened root base, an extremely large number of deep and wide labial root foramina, and a deep mesial notch in the root, indicative of important dental overlap (Herman, 1982).

Teeth of *Squalus* and *Protosqualus* are rather similar in general shape and characters (Cappetta, 1987, 2012; Siverson, 1993), and the two are usually regarded as closely related (Adnet and Cappetta, 2001). The teeth here described differ from *Squalus* and resemble *Protosqualus* in having poorly labiolingually

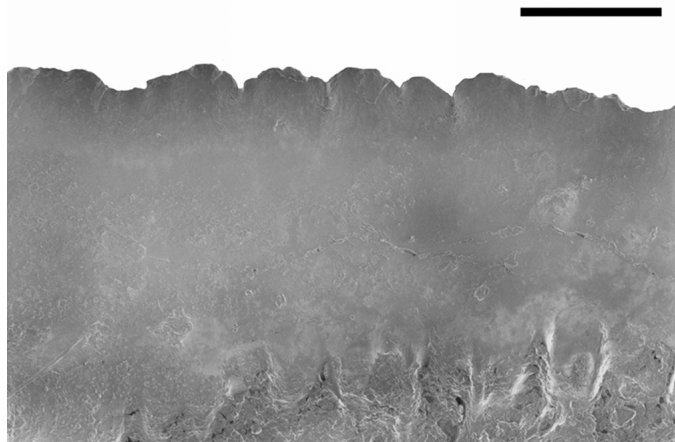


FIGURE 4. *Protosqualus argentinensis*, nov. sp., detail of serrated cutting edge of the main cusp of an anterolateral tooth (holotype, MPM 10023). Scale bar equals 2 cm.

compressed crowns, a poorly differentiated, rounded and triangular apron that is not distinctly separated from the labial limit of the enamel band, and the absence of a mesial notch in the root (Siverson, 1993; Underwood, 2004; Adnet et al., 2008; Ward, 2010). In *Squalus* species, the apron is very well raised from the rest of the crown, shows its mesial and distal margins subvertically oriented (Siverson, 1993), and usually exhibits a deeply notched tooth root (Adnet et al., 2008). The present specimens also resemble *Protosqualus* species in having teeth with some notches in the distal cutting edge of the distal heel (Cappetta, 1987; Adnet et al., 2008), and an undulated ventral margin of the crown distal to the apron (Adnet et al., 2008). The above-mentioned combination of characters allows us to refer the teeth here described to the genus *Protosqualus*. Within the genus *Protosqualus*, five valid species are currently recognized: *P. sigesi* Cappetta, 1977, *P. albertsi* Thies, 1981, *P. pachyrhiza* Underwood and Mitchell, 1999, *P. glickmani* Averianov, 1997, and *P. barringtonensis* Guinot et al., 2013 (Cappetta, 1987; Underwood and Mitchell, 1999; Adnet et al., 2008; Ward, 2010; Underwood et al., 2011; Guinot et al., 2013). The new species *P. argentinensis* is clearly distinguishable from most previously described species on the basis of the autapomorphies indicated in the specific diagnosis (see above).

Underwood et al. (2011) reported from the Cenomanian of south India an isolated *Protosqualus* tooth that they referred to an indeterminate, probably new, species. Although poorly preserved, the specimen reported by Underwood et al. (2011) is reminiscent of *P. argentinensis* due to the presence of an irregularly denticulated cutting edge of the mesial heel, a feature that is absent in remaining taxa of the genus, as recognized by Underwood et al. (2011). In addition, Kemp (1991) reported from the Coniacian-Santonian of Australia several *Protosqualus* and ‘*Centrophoroides*’ teeth belonging to indeterminate species. These specimens resemble *P. argentinensis* in having very deep roots and denticulated cutting edges of the mesial heel. However, until a first-hand revision of the specimens becomes available, the specific identification of these teeth is still uncertain. The same may be said of isolated ‘*Centrophoroides*’ teeth coming from several Maastrichtian beds from Chile (Suárez and Otero, 2008; Otero et al., 2013). Although a more complete description of the specimens is wanting, they resemble *P. argentinensis* in having a relatively tall root, serrated mesial margin of the cutting edge, and relative large size, as well as in general proportions

and gross morphology. On the basis of the figures by Suárez and Otero (2008) and Otero et al. (2013), the notch at the base of the root appears to be poorly developed, and the apron is not strongly ventrally extended, features that suggest the exclusion of these specimens from *Centrophoroides*.

It is worth mentioning that the new Maastrichtian species described here represents one of the geologically youngest occurrences of this genus.

Order ECHINORHINIFORMES Buen, 1926  
Family ECHINORHINIDAE Gill, 1862  
Genus *ECHINORHINUS* Blainville, 1816  
*ECHINORHINUS* sp.

**Referred Material**—MPM 10036, lateral tooth lacking the apex of the main cusp (Fig. 5A); MPM 10034, incomplete lateral tooth (Fig. 5B); MPM 10035, incomplete lateral tooth.

**Description**—The specimens represent a large-sized *Echinorhinus* species (mesiodistal length of the most complete tooth = 1.4 cm). The crown has a single main cusp that is highly compressed labiolingually and is strongly distally inclined. There are no additional cusplets. The crown (including the main cusp) has a crenulated mesial cutting edge. The distal cutting edge is smooth, lacking any sign of crenulation or denticles. The distal heel shows a nearly straight to slightly convex cutting edge, which exhibits a crenulated margin. The root is apicobasally tall and highly labiolingually compressed. The root is simple and of the anaulacorhize type (Cappetta, 1987), with vertically oriented grooves on the labial side.

**Remarks**—The specimens here described are referred to *Echinorhinus* for their labiolingually compressed crown and root, anaulacorhize root, and strong distal orientation of the main cusp (Pfeil, 1983; Cappetta, 1987). Within *Echinorhinus*, the large size of the available teeth and the presence of a single cusp in the crown resemble the morphology seen in several Cretaceous basal species of the genus and is different from most multicuspied Paleogene and Neogene taxa (Purdy et al., 2001). Regrettably, the incomplete nature of available specimens precludes identification beyond the generic level.

Recently, Otero and Suárez (2008) reported the existence of an indeterminate *Echinorhinus* species from the upper Maastrichtian of Chile, which was the first Mesozoic record for the genus in South America. These specimens are similar to the specimens here reported in being relatively large, and in having a single cusp with crenulate mesial margin and smooth distal margin. This combination of characters suggests that the Chilean and Argentinian specimens belong to the same species of *Echinorhinus*.

Additionally, Suárez and Otero (2008) reported the presence of another fragmentary echinorhinid tooth from the Campanian-Maastrichtian of Loanco, Chile. The incomplete nature of the latter specimen, however, precludes its identification below the family level.

## DISCUSSION

**The New Shark Assemblage and Its Implications for Selachian Mesozoic Faunas**—As indicated above, the fossil selachian faunas from the Mesozoic of South America are very poorly known (Arratia and Cione, 1996; Otero et al., 2013). The selachians here described include taxa that improve our knowledge of the still patchy Mesozoic chondrichthyan record and shed light on the early distribution of several shark taxa on the southern continents.

Late Cretaceous records of the genus *Notidanodon* comprise isolated findings in southwestern U.S.A. (Applegate, 1965; Ward in Underwood et al., 2011) and several specimens collected in Gondwanan localities (Woodward, 1886; Chapman, 1918; Cione

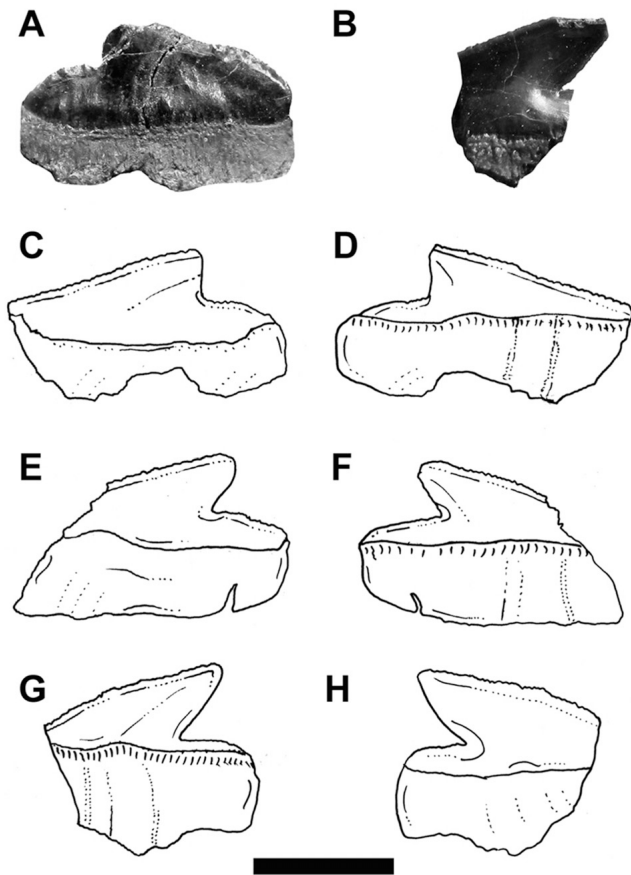


FIGURE 5. *Echinorhinus* sp., selected teeth. **A**, lateral tooth (MPM 10036) in labial view; **B**, incomplete lateral tooth (MPM 10034) in labial view; **C–H**, referred lateral teeth in **C, E, G**, labial and **D, F, H**, lingual views. **C–H**, modified from Otero and Suárez (2008). Scale bar equals 1 cm.

and Medina, 1987; Cappetta, 1987, 2012; Richter and Ward, 1990; Cione, 1996; Antunes and Cappetta, 2002; Kriwet et al., 2006; Underwood et al., 2011; this paper). The present record is the first for the genus in southern South America.

The genus *Protosqualus* is represented by several species coming from the early to late Cretaceous of Europe and Russia (Cappetta, 1977; Müller and Diedrich, 1991; Averianov, 1997; Underwood and Mitchell, 1999; Adnet et al., 2008), Australia (Kemp, 1991; Siverson in Underwood et al., 2011), and India (Underwood et al., 2011). These records were interpreted by Underwood et al. (2011) as indicative of an antitropical distribution for this genus. The record of *Protosqualus* in South America (present paper) is in agreement with the bipolar distributional pattern proposed by those authors. The new species described here exhibits interesting derived dental features, including the presence of a crenulated cutting edge of the mesial heel, that are shared with other *Protosqualus* taxa coming from Australian and Indian localities (Kemp, 1996; Underwood et al., 2011), thus suggestive of phylogenetic ties. In addition, the new Patagonian taxon constitutes one of the most recent records for the genus.

The Cretaceous record of *Echinorhinus* species is rather scarce and biased. The oldest report of *Echinorhinus* is teeth coming from the Valanginian and late Hauterivian of France (Adnet et al., 2011; Guinot et al., 2014). In addition, late Early Cretaceous records belong to the Gondwanan species *E. australis* from the Aptian-Albian of Australia (Chapman, 1908; Herman, 1975; Cappetta, 1987; Kemp, 1991; Pledge, 1992; Siverson, 1997), and

possibly echnorhinids from the Early Cretaceous (Albian-Cenomanian) of England (Underwood and Mitchell, 1999). In addition, the species *E. eyrensis* (Pledge, 1992) and *E. lapaoui* (Antunes and Cappetta, 2002) were described from the Late Cretaceous of Angola and Australia, respectively. Finally, Kitamura (2013) described the species *E. wadanohanaensis* from the Upper Cretaceous of Japan. To this meagre list we add the presence of a large echnorhinid in southern Patagonia, representing one of the oldest records for the order Echnorhiniformes in South America.

### Selachian Assemblages and Mesozoic Paleobiogeography of Southern Continents

The set of selachian records here described is in agreement with previous paleobiogeographical proposals based on other lines of evidence. Southern Patagonian faunas (Austral Basin) include cold-water taxa forming part of the ‘Weddellian Bioprovince,’ which also includes the seas covering Australia, New Caledonia, New Zealand, and Antarctica (Fleming, 1963; Kauffman, 1973; Zinsmeister, 1979; Camacho, 1992; Griffin and Hünicken, 1994; Casadío, 1998; del Río, 2002; Aguirre-Urreta et al., 2008). This is also supported by geological data suggesting that southern Patagonia showed an oceanic circulation pattern totally different from that seen in northern Patagonia and other localities (Ciesielski et al., 1977).

Regarding the selachian record, Kriwet et al. (2006) studied a large amount of selachian material from the Late Cretaceous of Antarctica and identified a possible high-latitude association of fish species that may be characteristic of the Late Cretaceous Weddellian Bioprovince. This association includes the sharks *Notidanodon dentatus*, *Synechodus*, *Paraorthacodus*, and possibly also *Squatina*. Cretaceous selachians from southern Patagonia (Austral Basin) reported by Ameghino include *Paraorthacodus* and synechodontiforms (Ameghino, 1893, 1901, 1906; Kriwet et al., 2006), and the present report adds *Notidanodon* to this selachian list.

On the other side, in northern Patagonia, chondrichthyans are mainly represented by lamniform and batoid teeth (Bogan and Agnolin, 2010; González Riga et al., 2010; Bogan and Gallina, 2011; Cione et al., 2013; Pámpraro et al., 2014), which are underrepresented in southern localities. These associations are dominated by taxa typical of temperate and tropical Maastrichtian waters of Brazil, Caribbean, North Africa, and Madagascar (Woodward, 1907; Oliveira and Silva Santos, 1950; Arambourg, 1954; Rebouças and Silva Santos, 1956; Cappetta, 1987; Gottfried et al., 2001; Silva, 2007; Carrillo et al., 2008). In this way, northern Patagonian selachian faunas were dominated by Tethyan taxa characteristic of warm temperatures, and there is no clear evidence of the presence of Weddellian fishes in these northern fossiliferous localities. This pattern fits well with known invertebrate distribution (Náñez and Malumíán, 2008) and selachian remains described by Otero et al. (2013) from the Maastrichtian of southern Chile. The latter authors hypothesize that southern fossil records evidence constraining conditions for taxa of warm temperate waters to inhabit high latitudes, a conclusion that is in agreement with the specimens here reported.

In spite of the discussion above, some differences noted between northern and southern selachian associations in Patagonia may represent bathymetric or ecological variation. This hypothesis should be tested with more detailed geological data and more complete faunistic assemblages.

### CONCLUSION

The present record of *Notidanodon* and *Protosqualus* constitutes the first for each genus in South America. The *Echinorhinus* specimens represent the oldest record for the continent, and one of the few Mesozoic records for the genus worldwide.



In agreement with invertebrate, micropaleontological, geological, and vertebrate data, we conclude that the selachian faunas from Patagonia in the Late Cretaceous were related to two different faunistic realms. The first occurs in southern Patagonia (Austral Basin) and appears to be influenced by cold-water taxa related to the Weddellian Bioprovince (e.g., synchodontiforms, squaliforms, hexanchiforms). The other associations belong to northern and central Patagonia (Colorado, Neuquén, and San Jorge Gulf basins), and show an influence of warm-water taxa of Tethyan affinities (e.g., batoids, lamniforms).

The differences between northern and southern Patagonian selachian associations indicate the concurrent existence of two different faunas in the latest Cretaceous of Patagonia, as advocated by previous authors for invertebrate taxa.

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