



First marine ichthyofauna from the late Eocene of Santa Cruz province, Patagonia, Argentina[☆]

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ABSTRACT

The fossil record of chondrichthyans in Argentina is still poorly known. The aim of the present contribution is to describe teeth representing a chondrichthyan assemblage from Man Aike Formation (late Eocene) exposed in the Lago Argentino area, at Santa Cruz province, Argentina. This report includes *Striatolamia macrota*, *Macrorhizodus praecursor*, *Carcharias* sp., a possible member of the family Pristiophoridae, for the Argentine territory. Previous Eocene reports of *Striatolamia macrota* from Argentina are based on incorrect determination of specimens. The shark association, especially the abundance of lamniforms, may be indicative of littoral and shallow (less than 30 m depth) temperate to cold waters, as suggested by micropaleontological content.

1. Introduction

The Austral Basin is located at southern South America along the southern portion of Patagonia and its marine platform, including Tierra del Fuego (Nullo et al., 1999; Malumián, 1999; Pérez Panera, 2013). Because this basin is surrounded by active tectonic limits (Sickmann et al., 2019) it is constantly influenced by the compressive action of Pacific and South American plates (Ramos, 1989; Yrigoyen, 1989; Coutand et al., 1999; Diraison et al., 2000; Somoza and Ghidella, 2005; Ghiglione and Cristallini, 2007).

This basin extended during the rupture of Gondwana by the Triassic-Jurassic time span (Uliana et al., 1989). It exhibits a complex sedimentary succession made by siliciclastic rocks and its geological history is related to three main tectonic stages (Biddle et al., 1986; Robbiano et al., 1996; Ramos, 2002; Kraemer et al., 2002; Peroni et al., 2002; Rodríguez and Miller, 2005).

The record of fossil fishes from the Cenozoic in the Austral Basin begins with the Mesozoic findings from the "estratos de Mata Amarilla", "Pari Aiken" o "Shehuen" (Cenomanian-Santonian), in the area encompassed by the Viedma Lake and Argentino Lake, at Santa Cruz Province, Argentina. These localities yielded continental and marine fishes

published by Florentino Ameghino and Arthur Smith Woodward. These authors described several taxa, including the lungfish *Atlantoceratodus iheringi* (Ameghino, 1898; Cione et al., 2007), and exclusively marine fishes, as *Protosphyraena*, and the lamnid shark *Cretalamna appendiculata* and the paleospinacid *Paraorthacodus patagonicus* (Ameghino 1935; Duffin and Ward, 1993). From the younger Cerro Fortaleza Formation (Campanian-Maastrichtian) in La Leona Valley from Santa Cruz province, isolated teeth belonging to indeterminate Lamniformes were reported (Schroeter et al., 2014). More recently, from the Calafate Formation (Maastrichtian) at the Argentino Lake, abundant shark remains were discovered. The specimens, mostly isolated teeth, include the lamnid *Cretalamna appendiculata*, the squalid *Protosqualus argentinensis*, the echinorhinid *Echinorhinus maremagnum* and the first record for the continent of the hexanchid *Notidanodon dentatus* (Bogan et al. 2016, 2017).

On the other side of the Andes, at southern Chile, Mesozoic fishes from Maastrichtian beds at the Sierra Baguales locality, at northern Magallanes Region are relatively well-known. This locality yielded the sharks *Centrophorooides* sp., *Serratolamna* aff. *S. serrata* (Agassiz), *Carcharias* sp., and the rays *Ischyryhiza chilensis* (Philippi), and Dasyatidae indet. (Otero and Suárez 2009; Otero et al., 2013).

[☆] RH. First Eocene Ichthyofauna from Santa Cruz Province, Argentina.

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After the K/Pg extinction event, the marine associations of fossil sharks from Patagonia and southern Chile are dominated by lamniforms (Oliver Schneider 1936; Arratia and Cione, 1996). From Paleogene beds, Suárez and Marquardt (2003) described the first shark remains from the Eocene Loreto Formation (Hoffstetter et al., 1957), at the Magallanes Region, being the species *Striatolamia macrota* the most abundant taxon in the entire assemblage. From the late Eocene (Priabonian; Otero et al., 2012) from Río Baguales Formation (=Man Aike Formation in Argentina) at Sierra Baguales, Magallanes Region, Otero et al. (2013) reported *Otodus obliquus*, *Megascylorhinus* sp., *Carcharias* aff. "hopei", *Odontaspis winkleri*, *Carcharoides catticus*, *Striatolamia macrota*, *Carcharocles auriculatus*, *Striatolamia* sp., *Anomotodon* sp., *Macrorhizodus praecursor*, *Galeorhinus* sp., *Abdounia* sp., *Hexanchus agassizi*, *Notorhynchus* sp., *Squatina* sp., cf. *Rhizoprionodon* sp., *Pristiophorus* sp., *Myliobatis* sp., Myliobatoidea indet., *Ischyodus dolloi*, and the endemic species *Jaekelotodus bagualensis* (Otero et al., 2013; Suárez et al., 2015).

Further, from Río de Las Minas, near Punta Arenas city, from the upper portion of the Loreto Formation, Otero et al. (2012) reported the first findings of *Megascylorhinus cooperi*, *Pristiophorus* sp., *Callorhinchus* sp. and *Rhinoptera* sp. In addition, from the Cerro Dorotea, located at northwest Puerto Natales city, Otero et al. (2012) described from the Eocene Río Turbio Formation (Bartonian-Priabonian) an assemblage composed by *Striatolamia macrota*, *Carcharias* sp. 'hopei', *Palaeohypotodus rutoti*, *Paraorthacodus* sp., *Rhinoptera* sp., indeterminate myliobatoids and callorhynchids (Sallaberry et al., 2010; Suárez et al., 2015).

The aim of the present contribution is to describe for the first time teeth representing a chondrichthyan assemblage from Eocene beds exposed in the Lago Argentino area, at Santa Cruz Province, Argentina.

1.1. Locality and geological setting

The study area belongs to the 25 de Mayo Farm, located at the south of El Calafate city, southwestern Santa Cruz Province, Argentina (Fig. 1).

The sedimentary infilling of the Austral basin is a succession integrated by Lower Cretaceous sandstones and black shales and thick Albian–Cenomanian deposits (Riccardi, 1988). The formers were associated with uplift processes in the western and southern areas of the basin. From the Campanian until the end of the Paleogene in northwestern areas there was a progradation of fluvial and shallow marine facies (Macellari et al., 1989; Ghiglione et al., 2009; Pearson et al., 2012; Varela et al., 2012). According to Macellari et al. (1989) the Late Cretaceous–Paleogene succession was deposited in a foreland basin and is almost entirely composed of sediments derived from an andesitic magmatic arc. In the Lago Argentino area Macellari et al. (1989) recorded three Upper Cretaceous depositional sequences. The youngest included the Calafate Formation that progressively overlies older rocks in a northward direction.

The beginning of the Paleogene in Patagonia is marked by the Maastrichtian-Danian transgression, an important paleogeographic feature that surely played a key role in climatic and evolutionary events taking place at that time in this part of the continent. The onset of carbonatic sedimentation in the Neuquén Basin during the late Maastrichtian-early Danian suggests a temperature increase in northern Patagonia. Such a change spanned through the Danian (Woelders et al., 2017) and reached the southern tip of South America, where it is recorded in beds included in the Cerro Dorotea Formation (Malumíán et al., 1998). The influence of warm waters along the Atlantic seaboard reached down to at least 45°S, as evidenced by paleontological record in the Salamanca and Lefipán formations (Malumíán and Caramés, 1995; Feldmann et al., 1997; Barreda et al., 2012; Jud et al., 2017; Vellekoop et al., 2017). Manceñido and Griffin (1988) suggested that such influence may have reached even further South to latitudes approaching the Antarctic Peninsula. However, this influence is only fully noticeable south of 50°S during the middle Eocene (Douglas et al., 2014).

According to Marenni et al. (2004) and Guler et al. (2005) the Calafate Formation is Maastrichtian in age and is covered by the Eocene Man Aike Formation (Marenni et al., 2002). During the Eocene, older foreland deposits were uplifted, eroded and deposited into the Cenozoic basin (Fosdick et al., 2014). The front of the fold-and-thrust belt move eastward during the middle Eocene to place the depositional systems included in the Man Aike Formation in a wedge-top setting (Sickmann et al., 2019). This is supported by regional geologic mapping (Malumíán et al., 2000) and balanced structural cross sections (Fosdick et al., 2011). A wedge-top structural setting was suggested upon on the apparent angularity between the Man Aike Formation and underlying Cretaceous strata (e.g., Malumíán et al., 2000; Fosdick et al., 2011).

Along the study area and near the Cerro Calafate, there are wide outcrops belonging to the Man Aike Formation (Furque, 1973). Based on sedimentological and micropaleontological data, the age of Man Aike Formation was regarded as middle Eocene (Malumíán, 1990; Carrizo et al., 1990; Concheyro, 1991; Malumíán y Caramés, 1997; Camacho et al., 1998). Malumíán (1999) suggested that Man Aike Formation included the P11 to P14 planktonic zones, this is the most recent part of the middle Eocene (42–37 My; Casadio et al., 2009; Malumíán and Námez, 2011).

The Man Aike Formation at 25 de Mayo Farm represents the evolution of an incised valley since its beginning with sediments representing freshwater environments towards fully marine outcrops at its top (Casadio et al., 2009). The specimens here reported belong to the uppermost section of the stratigraphic column, belonging to the FA5 defined by Casadio et al. (2009; Fig. 2). The sediments are sandy deposits characterized by predominance of greenish beds with high proportion of glauconite (Bogan et al., 2011) interpreted as deposited in an open marine (lower to middle shoreface). Dinoflagellate cysts from the upper part of the FA5 described by Guerstein et al. (2014) indicate the

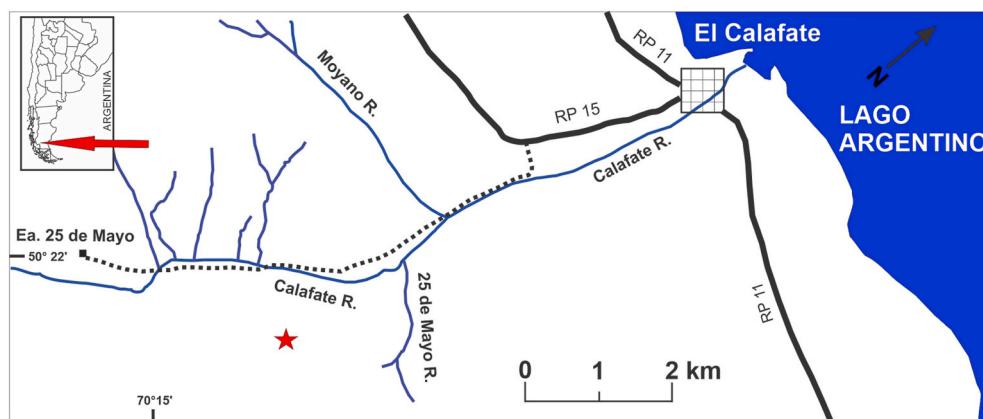


Fig. 1. Map showing the fossil site that yielded the fossil specimens here described. The star indicates the exact site of findings.

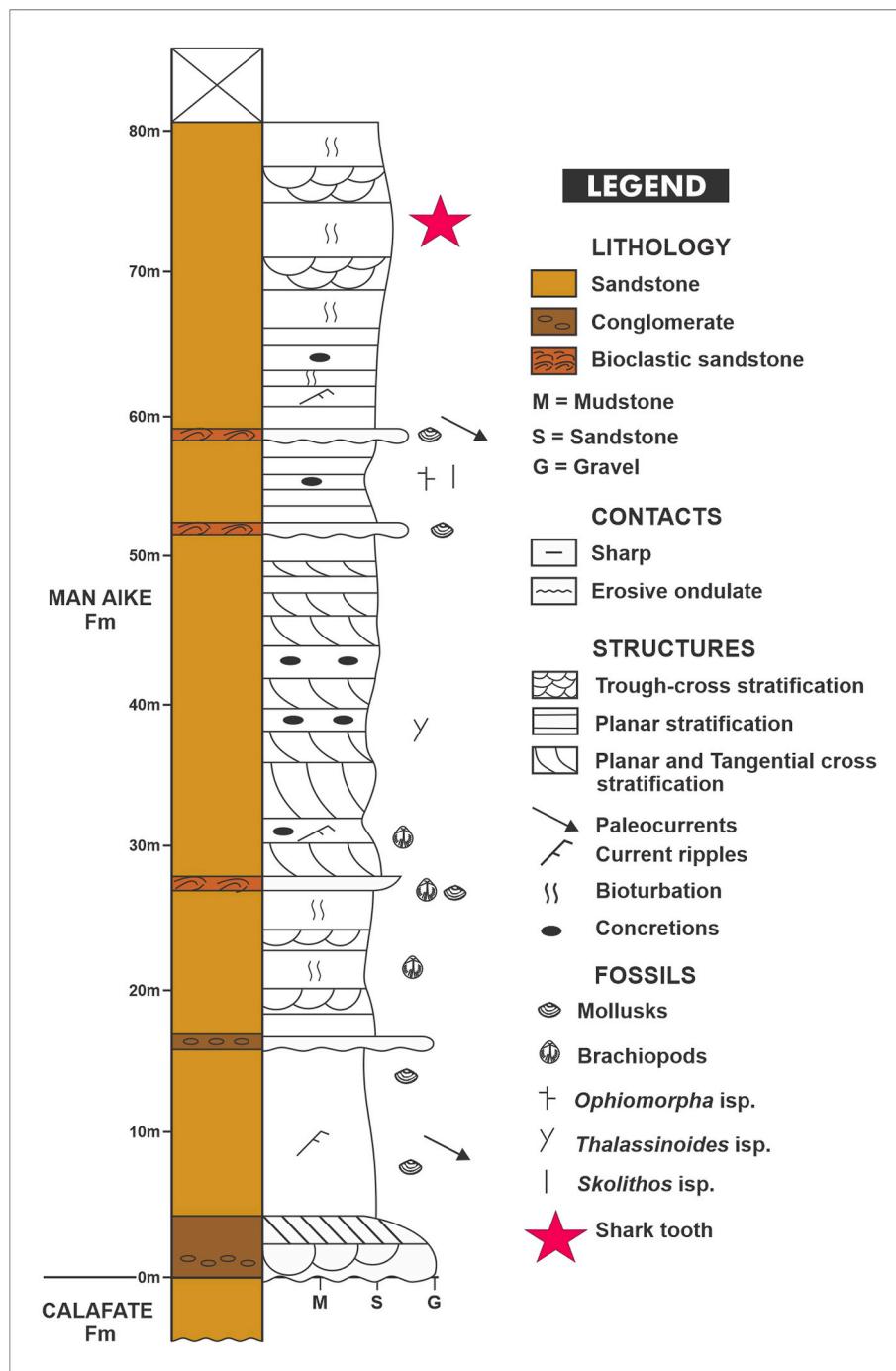


Fig. 2. Stratigraphic column indicating the geological units that yielded the fossil specimens here described. The star shows the fossiliferous levels with selachians.

influence of relatively warm, marine open waters in an inner shelf environment.

The specimens here described were collected during paleontological prospection by visual inspection of the soil surface. No screen-washing techniques were applied, and thus, small taxa are not present in the assemblage.

1.2. Systematic paleontology

Class Chondrichthyes Huxley, 1880

Order Lamniformes Berg, 1958.

Family Mitsukurinidae Jordan, 1898.

Genus *Striatolamia* Glikman, 1964.

Striatolamia macrota (Agassiz, 1843).

Referred material: MPM-PV 21700 anterior teeth (Fig. 3A–C); MPM-PV 21701 lateral teeth (Fig. 3D–I).

Description: This taxon is represented by relatively large-sized teeth (estimated maximum apicobasal height of about 40 mm; Fig. 3). Anterior teeth show an elongate and acute crown that shows a gently sigmoidal curvature. There are mesial and distal smooth cutting edges that extend towards the base of the crown. One of the most salient features of the elements is the presence of thick striations at the base of the crown when viewed lingually. Lateral cusplets are reduced and absent in some cases. The root has two main lobes and a prominent lingual torus.

The lateral teeth show relatively lower and notably mesiodistally

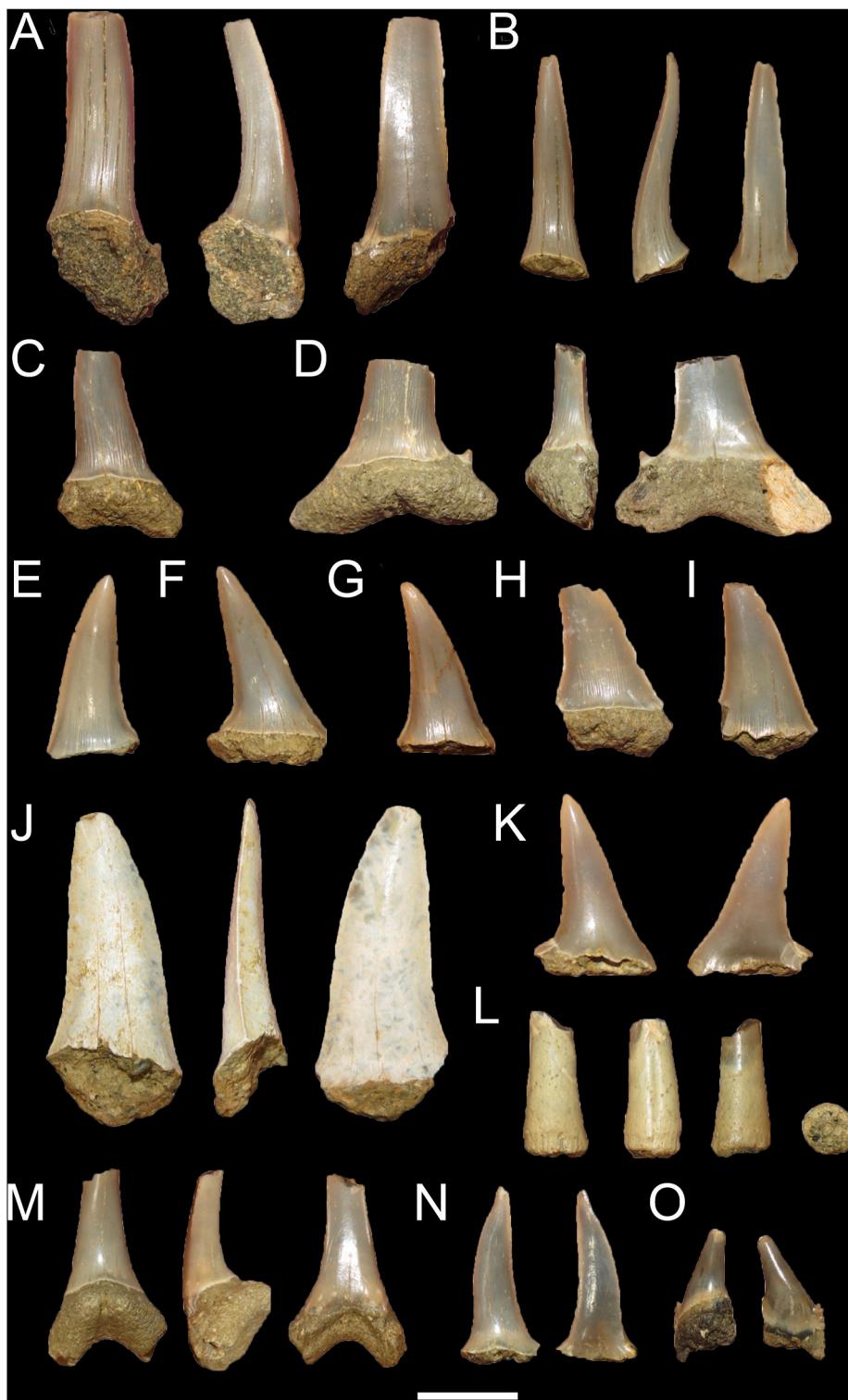


Fig. 3. A-I, *Striatolamia macrota*; J-K, *Macrorhizodus praecursor*; L, cf. *Pristiophoridae* indet.; M-O, *Carcharias* sp. All figures from left to right: A, lingual, lateral, and labial views; B, lingual, lateral, and labial views; C, lingual; D, lingual, lateral, and labial views; E-I, lingual view; J, lingual, lateral, and labial views; K, lingual and labial views; L, lingual, lateral, labial, and basal views; M, lingual, lateral, and labial views; N, lingual and labial views; O, lingual, and labial views. Scale bar: 10 mm.

wide (roughly subtriangular in contour) crowns, with less defined lingual striations. The crown is reclined towards the commissural margin. Some specimens show reduced lateral cusplets, that in some cases are represented just by a heel.

Remarks. *Striatolamia macrota* is the most abundant shark in the site, with collected teeth belonging to different parts of the jaws. Cappetta (1987, 2012) indicates that species of the genus *Striatolamia* tend

to have larger teeth in more modern forms, as well as to the mesiodistal widening of the lateral teeth, a condition that is notably evident in posterior teeth of *S. macrota*. Cappetta (1987, 2012) also indicates that in this taxon the lateral cusplets are reduced and form a roughly pectinated aspect, being relatively thickened and rounded. Further, lingual striations become less evident and in some cases are totally absent. This combination of characters is present in the material here reported, and

thus, is referred to the species *S. macrota*.

S. macrota was mentioned for the Eocene Loreto and Río Baguales (=Man Aike) Formations by Suárez and Marquardt (2003) in Chile, and both authors consider it as a species that is characteristic from southern Eocene seas (see Otero et al., 2012; 2013a; Otero and Soto Acuña, 2015). This species was also found in middle Eocene beds (Bartonian-Priabonian) from Antarctica (Reguero et al., 2013), and is mentioned for Santa Cruz Province by Cione (1988) and Arratia and Cione (1996).

Cione (1979), on the basis of Ameghino (1906, 1935) and D'Erasmo (1934) recognized the Paleogene presence of lamniforms with striated tooth crowns that may be adscribed to the genus *Odontaspis*. Later, Cione (1988) analyzed the specimens in more detail and recognized with some doubts the presence of four different species: *Eugomphodus striatus*, *E. substriatus*, *E. whitei* y *E. macrota*. The same specimens were listed by Arratia and Cione (1996) under the genus *Carcharias*. The first three species come from the Paleocene of Chubut province, particularly, Punta Peligro site (Frenguelli, 1922; D'Erasmo, 1934). The specimens listed as *C. macrota* are not from this species and come from more recent beds.

Cione (1988) described as belonging to *S. macrota* (cited there as *Eugomphodus macrotus*) more than 20 teeth coming from the San Julián Formation, Gran Bajo Member from the Gran Bajo de San Julián. These specimens (housed under the collection number MACN Pv 14631; Fig. 4) were collected by the geologist Carmelo De Ferraris (1912–1998) in 1937 whom indicated in the collection card that the material comes from the “Patagoniense Inferior (Julienense)”, this is Oligocene-Miocene. A review of the available specimens indicates that 21 of the available teeth belong to a form closely related to *Isurus desori* and a single large fragmentary tooth belongs to *Carcharocles* sp. (Fig. 4). These identifications are in agreement with De Ferraris indication that specimens do not came from Eocene or Paleocene beds.

Family Lamnidae (Müller y Henle, 1838).

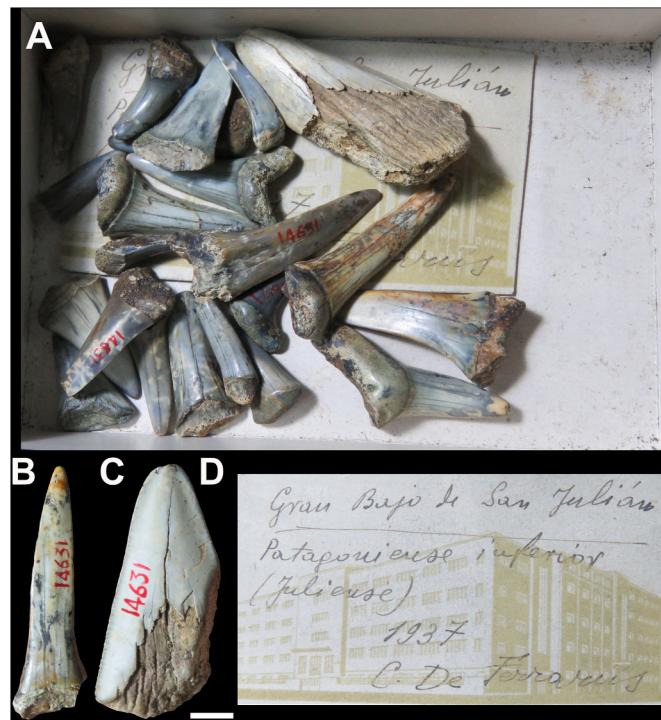


Fig. 4. A, MACN-PV-14631, lot including the teeth previously referred to *Eugomphodus macrotus* (Agassiz, 1843) by Cione (1988). B, lower teeth of *Isurus desori* in labial view; C, incomplete teeth belonging to *Carcharocles* sp.; D, original label with the collector handwriting C. De Ferraris (1937) indicating that the specimens come from the “Patagoniense inferior (Julienense)” (late Oligocene-early Miocene) “Gran Bajo de San Julián”, Chubut province, Argentina. Scale bar: 5 mm.

Genus *Macrorhizodus* Glikman, 1964.

Macrorhizodus praecursor (Leriche, 1905).

Referred material: MPM-PV 21702 anterior tooth (Fig. 3J); MPM-PV 21703 lateral tooth (Fig. 3K).

Description. The teeth show an apicobasally tall and elongate crown (preserved apicobasal height of MPM-PV 25178 about 35 mm; Fig. 3) that is subtriangular in contour and becomes mesiodistally wider towards its base. The labial face is flat, with nearly smooth enamel, showing scarce foldings near the contact with the root. The lingual face is convex. The available elements lack the root, and the enamel in the lingual surface shows some typical post-burial enamel longitudinal cracking.

Remarks. Despite of being poorly preserved, the material here described can be confidently referred to *Macrorhizodus praecursor* on the basis of the following unique combination of characters: large teeth having absent or greatly reduced lateral denticles, smooth enamel and cutting edges, anterior teeth relatively elongated, lateral teeth broadly triangular, and reduced crown height and relatively stout crowns (Glikman, 1964; Cione and Reguero, 1994). Regrettably, no autapomorphy is known from this species, all dental features being plesiomorphic for lamniforms (see Cione and Reguero, 1994). *M. praecursor* is widely known from Eocene deposits around the world (Cappetta, 1980), including Seymour Island, in Antarctica (Cione and Reguero, 1994) and the Eocene of southern Austral Basin in Chile (Loreto and Man Aike Formations; see Otero et al., 2012; 2013a,b).

Family Odontaspidae Müller and Henle, 1838.

Genus *Carcharias* Rafinesque, 1810.

Carcharias sp.

Referred material: MPM-PV 21704 three anterior teeth (Figure 3M, N); MPM-PV 21705 one symphyseal tooth (Figure 3O).

Description. Anterior teeth show a relatively tall and narrow crown. It is subcircular in cross-section and relatively robust, showing a gently sigmoidal curvature in labiolingual view (Fig. 3). One of the specimens show a sigmoidal mesiodistally curved crown. The teeth show the lingual surface slightly convex and the apex is labially oriented. The enamel is totally smooth. The torus is prominent and shows a nutrional foramen and groove. The root is bilobate, with divergent root lobes.

The symphyseal tooth shows a relatively low and robust crown. It is subtriangular in labial or lingual views and is strongly reclined. At its base it shows at least two secondary cusps that are recurved and each one having two additional cuspules. In lingual view, the base of the crown shows poorly developed enamel foldings. The crown is relatively tall and robust.

Remarks. The available teeth are here referred to *Carcharias* on the basis of heterodont dentition, with relatively robust crown with thickened apex, and short but curved secondary cusps (Cappetta, 1987; Purdy et al., 2001; Cunningham, 2000). Regrettably, because of the few number of available elements here described and the confuse taxonomy of fossil *Carcharias* species (see Cappetta, 2012) we refrain to determine the material to the specific level.

Order Pristiophoriformes Berg, 1958

Pristiophoridae Berg, 1859

Genus and species indeterminate

Referred material: MPM-PV 21706 basal fragment of enlarged rostral denticle (Figure 3L).

Description. The preserved portion of the rostral denticle is subcylindrical in shape. It becomes gradually narrow from the base to the tip (Figure 3L). It shows a base that is subcircular in cross-section and shows a narrow band having longitudinal ridges and subtle folding. This forms a neck that is separated from the rest of the denticle. The base is closed and lacks a deep central excavation. The enamel cap is continuous with the rest of the spine and is not separated by a neck or thickening. One of the sides of the tooth shows a longitudinal groove.

Remarks. The rostral denticle here reported differs from the simpler teeth of sawshark genera of the Pristidae clade by lacking continuously growing rostral teeth, that are dorsoventrally compressed, and show an

acute anterior surface and a concave posterior one (Cappetta, 1987; Wueringer et al., 2009). On the other side, it is similar to those of sclerorhynchids in having an enameloid cap and a peduncle with a closed basal face (Cappetta, 1974). However, the austral record of sclerorhynchids is mostly Late Cretaceous (Cappetta, 2012). In addition, most sclerorhynchids have marked cutting edges in their crowns, giving them a lenticular cross-section and a marked crown/peduncle neck, features that are absent from the material here described. On the other side, the morphology of the preserved portion of the rostral spine here reported is not very different from that of the Pristiophoridae clade (Cappetta, 1987). Further, Pristiophoridae is a group vastly recorded in the austral Paleogene and Neogene, with several records in roughly coeval beds from Chile and Antarctica (Otero and Soto Acuña, 2015). Thus, in spite that MPM-PV 21706 shows a unique morphology that is not matched by any known taxon, its incomplete nature precludes a more precise determination.

2. Discussion

Eocene invertebrate faunas from marine rocks in Santa Cruz are well-known since the 20th century (ver Griffin, 1991; Malumíán, 1993; Camacho et al., 2000; 2001). In contrast to these records, vertebrate reports are notably scarce, being *Striatolamia macrota* (cited by Cione, 1988 as *Eugomphodus macrotus* and by Arratia and Cione, 1996, as *Carcharias macrota*) the only previous local mention for a coeval age, coming from the upper Eocene (currently Oligocene) San Julián Formation (Cione, 1988). However, as noted above, the age of the specimens appears to be dubious at least. Further, they do not belong to *S. macrota* but to a species of the genus *Isurus* (Fig. 4).

The Man-Aike Formation is well-known by its abundant fossil record (Casadio et al., 2009; Guerstein et al., 2014). However, the only vertebrates mentioned from Argentina are indeterminate lamniforms (Casadio et al., 2009; Bogan et al., 2011). The present contribution includes the first description and detailed taxonomical referral of chondrichthyans in this stratigraphic unit. In the same way, in the present work constitutes the first certain record of *S. macrota* in Eocene beds from Argentina. It is worthy to mention that *S. macrota* is far the most abundant species of the assemblage here described, in agreement with its frequent occurrence at roughly coeval assemblages from Chile (Otero et al., 2012).

In addition, we report for the first time in Argentina *Macrorhizodus praecursor* and *Carcharias* sp. These taxa conform a fauna assemblage highly reminiscent to those described from penecontemporaneous beds in Chile (Otero et al., 2012; Otero and Soto-Acuña, 2015; Suárez et al., 2015).

The similarities noted above, with several taxa shared between Argentina, Chile and Antarctica may be indicative of Weddellian affinities. The Weddellian BioProvince as defined by Zinsmeister (1979) is a wide biogeographical area including Antarctica, New Zealand, Australia, and southern South America. This bioprovince was mainly based on invertebrate composition, but also including fossil fishes, and lasted between the latest Cretaceous towards the late Eocene (Cione and Medina, 1987; Grande and Eastman, 1986; Richter and Ward, 1990; Ward and Grande, 1991; Kriwet and Gadzicki, 2003; Kriwet, 2005; Kriwet et al., 2006; Suárez and Otero, 2008; Otero et al., 2012, 2013; Bogan et al., 2016). However, the chondrichthyan species here described and shared between Chile, Antarctica and Argentina are not exclusively Weddellian and are frequent in fish faunas from the North Atlantic seas (Otero et al., 2013).

3. Conclusions

The Austral Basin shows a relatively rich fossil fish record from Late Cretaceous to Neogene times. In spite that the Eocene outcrops of this basin in Argentina are well-known; however, the fossil record of Eocene fishes is nearly unknown and is mainly restricted to sedimentary

deposits from Chile.

Here are described from the first time the record of some chondrichthyans from Eocene beds at southern Patagonia, Argentina. These include *Striatolamia macrota*, *Macrorhizodus praecursor*, *Carcharias* sp., and a possible member of the family Pristiophoridae. All these taxa are of widespread geographical distribution. All these taxa were previously known from roughly coextensive beds from Chile and Antarctica.

The few specimens here described constitute a starting point for assembly the inventory of Paleogene fossil fishes from Argentina.

Authors statement

Dear Editor, Authors state that Federico Agnolin, Sergio Bogan and Silvio Casadio contributed equally for each part of the manuscript, including Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Resources; Software; Supervision; Validation; Visualization; Roles/Writing - original draft; Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could be perceived as influencing the work reported in this paper.

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