New Paleogene records of cartilaginous fishes (Chondrichthyes) from central Chile, including the oldest lamnid diversity from the southeastern Pacific (#116570)

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New Paleogene records of cartilaginous fishes (Chondrichthyes) from central Chile, including the oldest lamnid diversity from the southeastern Pacific

Rodrigo A. Otero Corresp. 1, 2, 3

Corresponding Author: Rodrigo A. Otero Email address: otero2112@gmail.com

Background. The Paleogene chondrichthyan diversity of the southern hemisphere is mostly known in Antarctica, southernmost South America and New Zealand, but records from the southeastern Pacific remain sparse to date. Among these, lamnid sharks (the lineage of the great white shark) are one of the scarcer groups in the southern hemisphere prior to the Eocene; moreover, their occurrences prior to the Neogene remained unreported in the southeastern Pacific. This contribution presents new Paleogene chondrichthyans recovered from two different horizons at Loanco, in central Chile, including the first local records of lamnids, with the description of a new species.

Methods. Sections of two geologic units were studied. These provided new dental pieces of chondrichthyans, as well as a single associated tooth set plus fragments of jaw cartilague and vertebrae. The material was taxonomically identified and compared with other local occurrences and other coeval assemblages from the southern hemisphere.

Results. This research recognizes a lower Paleocene-lower Eocene assemblage including material referable to *Palaeohypotodus* sp., *Megasqualus* sp. and Hexanchidae indet., the latter being the oldest known record in the southwestern Pacific. In addition, material from upper Eocene-lower Oligocene levels include dental pieces referable to the lamnids *Macrorhizodus praecursor* Leriche, and to a new species, *Lethenia carranzaensis* sp. nov., the latter represented by an exceptional specimen preserving a dental set, mandibular cartilage and vertebrae. Although discrete, this fauna shows the presence of Paleocene-lower Eocene elements commonly present in Antarctica and the Austral Basin, suggesting a typical Weddellian distribution during that timespan. On the contrary, the presence of the genus *Lethenia* reinforces the evidence of direct a vertebrate interchange with the north Atlantic during the late Eocene early Oligocene, previously suspected by the shared presence of blochiid billfishes. Evidence of such bioceanic interchange is also present during the late Paleocene, based on the previous reports of *Palaeogaleus*, *Physogaleus*, and *Premontreia*, genera with similar known geographic occurrences. The new records of *Macrorhizodus* and *Lethenia* also represent the oldest known record of Lamnidae in the southwestern Pacific, proving its early presence previous to its widespread and abundant occurrence during the Neogene.

¹ Museo de Historia Natural y Cultural del Desierto de Atacama, Calama, Región de Antofagasta, Chile

² Millennium Nucleus Early Evolutionary Transitions of Mammals, ANID-Milenio, Chile., Santiago, RM, Chile

³ Red Paleontológica U-Chile. Laboratorio de Ontogenia y Filogenia, Departamento de Biología, Facultad de Ciencias, Universidad de Chile, Santiago, RM, Chile



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- 2 (Chondrichthyes) from central Chile, including the
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6 Rodrigo A. Otero¹

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- 8 ¹ Red Paleontológica U-Chile. Laboratorio de Ontogenia y Filogenia, Departamento de Biología,
- 9 Facultad de Ciencias, Universidad de Chile. Las Palmeras 3425, Ñuñoa, Santiago, Chile.
- 10 ² Millennium Nucleus Early Evolutionary Transitions of Mammals, ANID-Milenio, Chile.
- 11 ³ Museo de Historia Natural y Cultural del Desierto de Atacama. Interior Parque El Loa s/n,
- 12 Calama, Chile.

13

- 14 Corresponding Author:
- 15 Rodrigo A. Otero¹
- 16 Las Palmeras 3425, Ñuñoa, 7750000, Santiago, Chile.
- 17 Email address: rodrigo.otero@paleoconsultores.cl

18

- 19 Abstract
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- 21 known in Antarctica, southernmost South America and New Zealand, but records from the
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- 23 great white shark) are one of the scarcer groups in the southern hemisphere prior to the
- 24 Eocene; moreover, their occurrences prior to the Neogene remained unreported in the
- 25 southeastern Pacific. This contribution presents new Paleogene chondrichthyans recovered
- 26 from two different horizons at Loanco, in-central Chile, including the first local records of
- 27 lamnids, with the description of a new species.

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- 29 **Methods.** Sections of two geologic units were studied. These provided new dental pieces of
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Results. This research recognizes a lower Paleocene-lower Eocene assemblage including material referable to Palaeohypotodus sp., Megasqualus sp. and Hexanchidae indet., the latter being the oldest known record in the southwestern Pacific. In addition, material from upper Eocene-lower Oligocene levels include dental pieces referable to the lamnids *Macrorhizodus* praecursor Leriche, and to a new species, Lethenia carranzaensis sp. nov., the latter represented by an exceptional specimen preserving a dental set, mandibular cartilage and vertebrae. Although discrete, this fauna shows the presence of Paleocene-lower Eocene elements commonly present in Antarctica and the Austral Basin, suggesting a typical Weddellian distribution during that timespan. On the contrary, the presence of the genus Lethenia reinforces the evidence of direct a vertebrate interchange with the north Atlantic during the late Eocene - early Oligocene, previously suspected by the shared presence of blochiid billfishes. Evidence of such bioceanic interchange is also present during the late Paleocene, based on the previous reports of Palaeogaleus, Physogaleus, and Premontreia, genera with similar known geographic occurrences. The new records of *Macrorhizodus* and *Lethenia* also represent the oldest known record of Lamnidae in the southwestern Pacific, proving its early presence previous to its widespread and abundant occurrence during the Neogene.

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Introduction

Paleogene marine vertebrates from the southern Pacific are well-known in Antarctica, New Zealand and the Austral (=Magallanes) Basin, representing a valuable source of paleoenvironmental, paleogeographic and paleobiologic information. The faunal affinities present in different austral localities since the Late Cretaceous until the Eocene, worked as major support for the Weddellian Biogeographic Province (Zinsmeister, 1979; WBP hereafter), a concept initially based on the common distribution of marine invertebrates, later proved to apply also for marine vertebrates (Reguero et al. 2012; 2022; and references therein).

In this scenario, the Paleogene marine vertebrate diversity from the southwestern Pacific (particularly from central Chile) is relevant by providing mid-latitude records, although, these have been historically disattended. Fortunately, in recent years new research allowed fresh insights, but detailed comparisons to known assemblages from other parts of the WBP remain unpracticed.

This contribution presents new discoveries from central Chile, including both late Paleocene-early Eocene, and late Eocene-early Oligocene chondrichthyan material. The new elements adds to previous records allowing a first paleogeographic approach, suggesting a



faunal continuity of the typical WBP diversity during the late Paleocene, but coupled to the interchange of few chondricthtyan taxa typical of the north Atlantic. These conditions seem to persist during the late Eocene-early Oligocene, pointing to a stronger influence of the north Atlantic fauna during that time span, therefore, suggesting a latitudinal range and chronostratigraphic lapse for the declination of the WBP.

Locality and Geologic Setting

Locality—Loanco is a small cove in the Región del Maule (Maule Region, administrative division of Chile) placed ca. 350 km south from Santiago (Fig. 1A).

Geologic Setting—In its coast line crops out different sedimentary units deposited during a transgressive-regressive cycle that spanned between the late Campanian to the Eocene/Oligocene boundary. The basement rocks are conformed by Paleozoic metamorphic rocks. From base to roof, the older sedimentary rocks belong to the Quiriquina Formation (Biró-Bagóczky, 1982), followed by a small section referable to the Lebu Group (Cecioni, 1968), and by a larger section of the Millongue Formation (Tavera, 1942). Covering most of these outcrops, there are Neogene marine terraces likely correlated to the Navidad Formation (Darwin, 1846). The detailed description of the fossil-bearing units studied is provided as following:

Lebu Group (Cecioni, 1968; Le Roux et al., 2008)—A small section of soft, yellowish sandstones of variable thickness below 5 m (Fig. 1B), it overlies through an angular unconformity to a large anticline (ca. 900 m) of the Quiriquina Formation. These levels yielded material referable to the chondrichthyan genus Palaeohypotodus (this study), thus, suggesting a Paleocene age. This unit is segregated from the Quiriquina Formation based on the unconformable contact and different lithology. It is here correlated to the basal levels of the Lebu Group, particularly with the marine Pilpilco Formation (Muñoz-Cristi, 1968), which represents a first moment of the transgressive cycle. The Pilpilco Formation was regarded as ca. 150 m of fine-grained, greenish sandstones with clay intercalations (Muñoz-Cristi, 1968). The studied section is consistent with this lithology but much narrower in thickness, suggesting a likely relict of the Pilpilco Formation or else, a different Paleocene marine transgression.

Millongue Formation (Tavera 1942; Muñoz Cristi 1946, 1973; García, 1968; Pineda, 1983)— 2.5 km south from Loanco crops out another fossiliferous sedimentary unit characterized by brownish, clayly sandstones of variable grain size (Fig. 1A, B). The contact between these levels and those of the Quiriquina Formation is covered by recent sands. Fossil content includes bivalvians (Pinna sp., Pectinidae), serpulids (aff. Rotularia isp.), terebratulid brachiopods, nautiloids (Aturia sp.), decapods (Minohellenus araucanus), and endemic blochiid



fishes (Otero, 2019). The lithology and age of the studied outcrops allow correlating them to the middle-to-upper Eocene Millongue Formation (Tavera 1942; Muñoz Cristi 1946).

Stratigraphic Sections—Otero (2024) provided several Upper Cretaceous stratigraphic sections exposed in different points along the coast close to Loanco, numbered as point 1 to point 5. Two of the stratigraphic sections studied here are equivalent to the points 1 (point A of this study) and the upper levels at point 2 (point B of this study) of Otero (2024). Two additional sampling point are here added, consistently labeled as point C and point D. All these are described as following:

Point A (35° 33′ 14.1" S; 72° 36′ 45.8" W)—Former point 1 of Otero (2024). The base of this section is covered by recent sands. From base to roof: 4,4 m of a massive clayly sandstone, regularly soft, grey to reddish, with fine to coarse grain and small fossiliferous concretions. The level dips ca. 30° west, being partially overlain by landslides. Fossils include typical vertebrates and invertebrates representative of the Quiriquina Formation (see Otero, 2024). In the northern visible flank of the anticline, teeth referable to Megasqualus sp. and to Hexanchidae indet. (this study) were recovered. The roof of this level shows frequent traces (Thalassinoides isp.) and decapod remains (Protocallianasa saetosa). It overlays to levels of the Quiriquina Formation (which conforms the anticline); 6,7 m of sub-horizontal, grey, compact, hard sandstone with concretions, overlying in angular unconformity. It shows probable bioturbation near its roof; 5,7 m of grey-to-yellowish, fine sandstone, laminated in its base and having abundant reddish, hard, ferruginous nodules; 3,5 m of fine compact sandstone, with abundant traces (Skolithos isp.).

Point B (35° 33' 37.8" S; 72° 37' 04.8"W)—Former point 2 of Otero (2024). The base of this section belongs to the Quiriquina Formation and is located close to the anticline axis. From base to roof: 6 m of green to grey, hard sandstone with abundant fossiliferous concretions of variable size; 4 m of poorly consolidated, clayly sandstones, lying in angular unconformity over the anticline. Near its base there are reworked fossils (actinopterygian scales and fragments Pacitrigonia hanetiana). A single in situ tooth was recovered from this level (referred to Palaeohypotodus sp. en this study); 8,5 m grey, unconsolidated, fine sandstones without fossils.

Point C (35° 33' 46.8" S; 72° 37' 53.8"W)—The base of this section is covered by recent sands. 3 m of greenish sandstones with serpulid banks; 0.5 m with no outcrop; 2 m of reddish sandstones; 2 m with no outcrop; 1.8 m of brown mid-grained sandstone with micaceous fragments, and having a fine conglomerate near its base. Fossils in this level include teeth of Macrorhizodus praecursor (this study), a phragmocone of the nautiloid Aturia sp. (SGO.PI.6776), and an articulated individual of Minohellenus ('Imaizula') araucanus; 14.3 m of mid-grained, yellow-to-green sandstone with lenses including banks of Terebratulidae indet.;



pectinids and carbonized wood fragments occur near the roof of the level; 6 m of mid-grained, reddish to brown sandstones, with several *in situ* individuals of *Pinna* sp. in life position. This level also includes an isolated lamniform vertebra (*in situ*), serpulid traces, carbonized wood fragments, and *Teredolites* isp.

Point D (35°36'12.39"S; 72°38'13.26"W)—Following Valdés (2019), this section comprises ca. 30 m of quartz sandstones, intercalated by brownish and green sandstones with few glauconitic levels. The section is very fossiliferous, diminishing in abundance from base to roof. Grain size increases from base to roof. The upper part of the exposed section becomes orange near the roof. The brownish levels are comparatively prominent with respect to the green sandstones, showing better resistance to the tidal erosion. Most of the brownish levels lack bivalvians, but contains frequent traces of calcareous worms (Rotularia sp.) and occasional terebratulid brachiopods. On the contrary, green levels include bivalvians, terebratulids, and marine vertebrates (associated chondrichthyan teeth, SGO.PV.6635).

Age of the Outcrops Studied Here—The presence of Palaeohypotodus (with well-preserved crown and cusplets) on the younger unit (here correlated to the Pililco Formation at points A and B), suggests a Paleocene age based on the known biochron of this genus (Cappetta, 2012), although austral occurrences of Palaeohypotodus are also known in the lower Eocene (Long, 1992; Kriwet, 2005; Reguero et al., 2013; Otero and Soto-Acuña, 2015; Kriwet et al., 2016), thus, supporting a local Paleocene-early Eocene age.

The younger unit (Millongue Formation, points C and D) crops out in the southern part of the studied locality. Its eventual contact with the Quiriquina Formation is obscured by recent coastal deposits. The presence of *Aturia* sp. and *Minohellenus araucanus* constrain the unit to an Eocene age, suggesting an eventual extension into the Oligocene (Nielsen et al., 2006; Schweitzer and Feldmann, 2002; Schweitzer et al., 2010). In addition, the local presence of blochiid fishes (Otero, 2019) suggest a middle-to-late Eocene age based on the known biochron of blochiids (Fierstine and Monsch, 2002), while the presence of the genus *Lethenia* (see further text) suggests a late Eocene or even lower Oligocene age, considering the age of the unique previously known record of the genus (Baut and Génault, 1999). The relative age of these outcrops, their distinctive lithology and its-marine environment, support a correlation with the Millongue Formation (Tavera 1942) which is present in southern and northern localities of the Arauco Basin (Tavera, 1942; Muñoz-Cristi, 1958; Tavera, 1980). The age of the Millongue Formation was independently constrained to the middle-to-late Eocene based on fossil invertebrates in other localities of central Chile (Tavera, 1942; 1980). The faunal assemblage



168	locally recognized in Loanco (points C and D) indicates a late Eocene or even a early Oligocene
169	age for these outcrops.
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172	Materials & Methods
173	Institutional Abbreviations—SGO.PV., Área Paleontología, Museo Nacional de Historia
174	Natural, Santiago, Chile.
175	The studied material was collected in several fieldworks. The specimen SGO.PV.6635 was
176	collected by the author on 2008, and subsequently prepared by hand tools. Natural crackings of
177	the original sandstone block affected several teeth. These were separated from the matrix and
178	later re-joined with cyanocrilate, although the contact surfaces were damaged in few cases. Few
179	teeth are preserved in hardened nodules. Then, its preparation was risky considering the
180	presence of very delicate lateral cusplets.
181	The remaining teeth were recovered as isolated elements during successive field works
182	between 2010-2015, being later separated from its hosting matrix by hand tools.
183	
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185	Results: Systematic Paleontology
186	
187	Chondrichthyes Huxley, 1880
188	Elasmobranchii Bonaparte, 1838
189	Neoselachii Compagno, 1977
190	Squaliformes Compagno, 1973
191	Squalidae de Blainville, 1816
192	Genus <i>Megasqualus</i> Herman, 1982
193	
194	Megasqualus sp.
195	(Fig. 2A-B)
196	
197	Centrophoroides sp.: Suárez and Otero, 2008
198	Centrophoroides sp.: Otero, 2015.
199	Type Species—'Notidanus orpiensis' Winkler, 1874, upper Paleocene of Belgium.
200	Material—SGO.PV.6625, a single lateral tooth.





201 Locality and Horizon—Loanco, Point A, basal marine unit of the Lebu Group (Pilpilco 202 Formation), Paleocene-lower Eocene. 203 Description—Squalid large tooth (6 mm wide) with a crown strongly recurved backwards. 204 having a nearly straight cutting edge with few irregular slight serrations over its mesial margin. 205 The crown has slightly protruding uvula. The labial apron is broken, but its contour is preserved. 206 This shows a basal projection that does not reach the root base. The root base is concave and it 207 has a rhomboidal outline. There are no mesial or distal hollows, indicating that the dental 208 overlap is weak in this taxon. 209 Remarks—SGO.PV.6625 was initially referred to as Centrophoroides sp. by Suárez and 210 Otero (2008). After additional preparation, the basal projection of the labial apron was revealed. 211 This is basally projected but not extended beyond the root base, differing from the typical local 212 teeth of the Arauco Basin referred to Centrophoroides, which have a large apron that basally 213 surpasses the entire root (Otero, 2024). The crown cutting edge of SGO.PV.6625 is almost 214 straight, also differing from the local records referable to Centrophoroides, which have 215 comparatively higher crowns with irregularly serrated cutting edges, and in some cases, a 216 differentiated mesial cutting edge with fine serrations and a distal cutting edge with a higher 217 angle and more marked irregular serrations, resembling a separation between the lateral cusp 218 and the crown (Otero, 2024). 219 The Upper Cretaceous austral record of Squaliformes includes similar ecomorphotypes. 220 Particularly, *Protosqualus argentinensis* Bogan et al. (2016) was described from upper 221 Maastrichtian beds of Argentinean Patagonia. This taxon has unusually irregular serrations, a 222 high triangular crown posteriorly recurved, and a triangular, lingually projected uvula. These 223 traits are not present in SGO.PV.6625. Moreover, the low crown highly recurved backwards, the 224 shallowly projected apron and the slight serrations are characters described for the genus 225 Megasqualus (see Cappetta, 1987: p. 55). SGO.PV.6625 is slightly larger than the typical 226 Centrophoroides teeth found in the Arauco Basin, which rarely exceeds 5 mm in length (Otero, 227 2024). The genus Megasqualus has been reported in the upper Paleocene-lower Eocene of 228 Belgium and England (Gurr, 1962; Herman, 1982; Cappetta, 1987; 2012), and the lower-middle 229 Paleocene of New Zealand (Mannering and Hiller, 2008). 230 231 Hexanchiformes de Buen, 1926 232 Hexanchidae Gray, 1851 233 234 Hexanchidae indet.



235	(Fig. 2C)
236	
237	cf. <i>Echinorhinus</i> sp.: Suárez and Otero, 2008; Otero, 2015.
238	Material—SGO.PV.6626, an isolated crown fragment.
239	Locality and Horizon— Loanco, Point A, basal marine unit of the Lebu Group (Pilpilco
240	Formation), Paleocene-lower Eocene.
241	Description—Triangular cusp strongly recurved backwards, with complete cutting edges.
242	Its labial face is flat and the lingual face convex. The preserved cusp bears basal wrinkles and
243	few longitudinal striations over the enameloid. Over the cutting edges, small radial striations are
244	visible. A small fragment of the root is attached to the cusp base, which allows delimiting the
245	complete cusp height.
246	Remarks—This cusp was previously considered to be related to the genus Echinorhinus
247	(Suárez and Otero, 2008). However, the presence of a convex lingual face differs from the very
248	flat crown present in homodont teeth of <i>Echinorhinus</i> (Cappetta, 1987 <u>;</u> 2012). Even more, the
249	longitudinal striations over the lingual face of the cusp and the radial striations associated to the
250	cutting edges are features seen in hexanchids such as Notidanodon (see Bogan et al., 2016:
251	fig. 2B). The isolated cusp SGO.PV.6626 is not enough for a generic identification, reason why
252	it is kept as an indeterminate hexanchid.
253	The eventual presence of hexanchids in pre-Neogene units of central Chile was first
254	regarded by Philippi (1887) who referred to Notidanus few teeth from the lower Maastrichtian of
255	Algarrobo, central Chile. Auspiciously, the material was figured by Philippi (1887: Plate 55, figs.
256	11a, b), revealing that these indeed belong to teeth of squaliforms (likely Centrophoroides),
257	thus, discarding its adscription to hexanchids.
258	Previous to this research and considering the updated information, hexanchids were
259	known in central Chile from the Miocene and onwards. Thus, SGO.PV.6626 is the first and to
260	date the unique evidence of this clade in the Paleocene-lewer Eocene of the southeastern
261	Pacific. On the contrary, WBP hexanchids have been frequently reported in the upper
262	Campanian-lower Maastrichtian of James Ross Island, Antarctica (Richter and Ward, 1990), the
263	upper Maastrichtian of Seymour Island, Antarctica (Grande and Chatterjee, 1987) and the upper
264	Maastrichtian of the Austral Basin (Bogan et al., 2016). During the Paleogene, hexanchids have
265	been reported in all the main localities within the WBP (Cione and Reguero, 1994; Kriwet, 2005;
266	Mannering and Hiller, 2008; Reguero et al., 2012; 2022; Otero et al., 2012; 2013; Kriwet et al.,
267	2016), except the southeastern Pacific.

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269	Lamniformes Berg, 1958
270	Odontaspididae Müller and Henle, 1838
271	Genus <i>Palaeohypotodus</i> Glickman, 1964
272	
273	Type species—'Odontaspis' (=Palaeohypotodus) rutoti Winkler, 1874. Late Paleocene of
274	Belgium.
275	
276	Palaeohypotodus sp.
277	(Fig. 2D, E)
278	
279	Triakidae indet.: Otero, 2015.
280	Material—SGO.PV.6780, a single posterior tooth.
281	Locality and Horizon—Loanco, point B, basal marine unit of the Lebu Group (Pilpilco
282	Formation), Paleocene-lower Eocene.
283	Description—Posterior tooth with a low triangular crown. Its labial face has strong folds
284	that fade into the tip, while the lingual face has a smooth enameloid. Labially, the crown
285	overhangs to the root by a bulge. The distal side has two triangular and robust cusplets, and the
286	mesial side lacks any cusplet. The root has two separated and thick lobes with a shallow medial
287	nutritious groove.
288	Remarks—This tooth was first referred by Otero (2015) as an indeterminate triakid,
289	without providing its repository neither figuring it. Additional preparation revealed the presence
290	of a triangular crown, two distal cusplets and absence of mesial cusplets. Such features
291	resemble teeth of several Carcharhiniformes (e.g., the genus <i>Galeorhinus</i>). However, the root
292	has two prominent, divergent lobes and a shallow medial nutritious groove, differing from all
293	Carcharhiniformes (i.e., Scyliorhinidae, Proscyllidae, Pseudotriakidae, Triakidae and
294	Carcharhinidae), which possess deep medial grooves, and a medial part of the root thicker than
295	the root lobes, the latter being rarely divergent (Cappetta, 2012).
296	SGO.PV.6780 current reassessment allows recognizing informative features. First, the
297	separated lobes and shallow groove are coincident with those of posterior teeth of
298	odontaspidids. The lack of mesial cusplets can be explained due to a very posterior tooth
299	position. In addition, the two distal cusplets are both triangular and they are medially recurved.
300	The separated root lobes, the labial bulge separating the crown and the root, and the strong
301	labial enameloid folds are features present in the odontaspidid genus Paleohypotodus
302	(Cappetta, 1987 <u>;</u> 2012).





303	
304	Lamnidae (Müller and Henle, 1838)
305	Genus macrorhizodus Glikman, 1964
306	Macrorhizodus praecursor (Leriche, 1905)
307	(Fig. 2F-I)
308	
309	Macrorhizodus praecursor: Otero, 2015
310	Type Species—Isurus praecursor (Leriche, 1905). Middle Eocene, Belgium.
311	Locality and Horizon—Loanco, Point C. Millongue Formation, upper Eocene-lower
312	Oligocene.
313	Referred Material—SGO.PV.6633. Two complete lateral teeth.
314	Description—The larger tooth has a high triangular crown with complete, non-serrated
315	cutting edges. The labial face is flat, while the lingual face is convex. The root has two slightly
316	divergent lobes with a squared contour. Its general shape suggests a lower anterior position.
317	The smallest tooth has similar features. Its crown is comparatively short and mesiodistally
318	larger, with the tip recurved backwards, evidencing its lateral position. The mesial side of the
319	tooth is broken. The root, the cutting edges and the enameloid show signs of erosion, indicating
320	transportation prior its burial.
321	Remarks—Eocene teeth of this lamnid morphotype found in Antarctica have been first
322	adscribed to the genus Isurus (Cione and Reguero, 1994; Reguero et al., 2012; Kriwet et al.,
323	2016). However, the genus Isurus has extant species (Isurus oxyrhincus and Isurus paucus)
324	with teeth much different possessing slender and sigmoidal crowns, and roots with divergent
325	lobes (Compagno, 2001). In addition, the cutting edge is complete in teeth of Macrorhizodus
326	whereas in teeth of Isurus it generally does not reach the base (Cappetta, 2012; Carlsen and
327	Cuny, 2017. Similar lamnid teeth have been found in two middle-to-late Eocene localities of
328	southernmost Chile, being referred to Macrorhizodus praecursor based on the differences listed
329	above (Otero et al., 2012; 2013), but also considering their similarity to Neogene taxa such as
330	'Carcharodon' hastalis and Carcharodon carcharias (Ehret et al., 2012), characterized by large,
331	triangular upper anterior teeth. Following these criteria, the new specimens from central Chile
332	are also referred to Macrorhizodus praecursor.
333	
334	Genus Lethenia Baut and Génault, 1999
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336	Type Species—'Odontaspis Van der Broecki' (Winkler, 1880; p. 77-78), lower Oligocene
337	of Limburg, Belgium.
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339	Lethenia carranzaensis sp. nov.
340	lsid:zoobank.org:act:012B0463-22D3-4A40-916A-F005532BD09B
341	(Fig. 3A-Q)
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343	Isurolamna sp.: Suárez and Otero, 2010
344	Isurolamna sp.: Otero, 2015
345	Isurolamna sp.: Otero, 2019
346	Holotype—SGO.PV.6635. Associated remains of a single specimen including five
347	anterior or near anterior teeth, four lateral teeth, one posterior tooth, two vertebrae and
348	manibular cartilage fragments.
349	Locality and Horizon—Loanco, Point D. Millongue Formation, upper Eocene-lower
350	Oligocene.
351	Diagnosis—Species within Lethenia having two blunt triangular lateral cusplets in
352	anterior, lateral and posterior teeth.
353	Etymology—After the toponymy of Carranza lighthouse, north Loanco, Región del
354	Maule, central Chile.
355	Description—Anterior teeth with straight cusp in lateral and profile views, with complete
356	cutting edges. The main cusp has a D-shaped section, without ornamentation. There are two
357	lateral cusplets with triangular outline on each side of the main cusp. The larger cusplet is blunt
358	and it has complete cutting edges. The base of the larger cusplet is detached from the main
359	cusp. The smallest cusplets are mesially and distally placed. These are triangular but having
360	rounded tips. The root is mesiodistally larger than the main cusp height. Roots have a slightly
361	squared contour without divergent lobes. Labiolingually, the roots are thin, without any bulk or
362	projection.
363	Remarks—The originally monotypic genus Lethenia Baut and Génault (1999) included
364	only the species Lethenia vanderbroecki (Winkler, 1880). This taxon was diagnosed by the
365	presence of low lateral cusplets without any ornamentation and well-separated from the crown,
366	with sub-circular cross-section, plus very compressed root branches without divergent
367	branches. SGO.PV.6635 shares with Lethenia vanderbroecki the unornamented cusplets
368	separated from the crown, as well as the distinctive compressed shape of the root branches. On
369	the contrary, it differs from the latter species by possessing two lateral cusplets on each side,



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and by having cusplets comparatively blunter, with a triangular outline, contrary to the sharp and thin cusplets of *Lethenia vanderbroecki* (Winkler, 1880: p. 77; Baut and Génault, 1999: fig. 11; Nolf, 1988: pl. 47). While *Lethenia vanderbroecki* was originally described based on twenty complete but isolated teeth, the Chilean specimen represents a partial dental set of a single individual, plus few other associated skeletal remains. This set allows assessing the morphology of the anterior, lateral and posterior teeth. All the teeth similarly possess two cusplets on each side of the crown (this can be assessed in the incomplete teeth based on the basal section of the missing cusplets) On posterior-most teeth, the crown and the cusplets appear as immediately adjacent elements without an evident separation, differing from the separated crown and cusplets considered as a diagnostic trait of *Lethenia* (Baut and Génault, 1999: p. 23). However, the specimens figured by Nolf (1988: pl. 467, figs. 2 and 3) show its crown and cusplets with a complete contact between them. Thus, the variable separation between the crown and cusplets could be related to the individual tooth growth, being presumably contacted in recently replaced teeth, but acquiring a marked separation in old, mature teeth. If this is the case, this trait should be abandoned as part of the diagnosis of the genus.

Previous to this research, SGO.PV.6635 was considered to be related to the genus Isurolamna Cappetta (1976), mostly based in the non-divergent root branches observed in the first teeth recovered from the matrix during its preparation (Suárez and Otero, 2010; Otero, 2015; Otero, 2019). However, SGO.PV.6635 dental set shows that the crown of all teeth is straight, contrary to the sigmoidal profile regarded in the diagnosis of *Isurolamna* (Cappetta, 1976; 1987). SGO.PV.6635 also lacks a marked heterodonty (as described for *Isurolamna* by Cappetta, 1976), instead having a low heterodonty, mostly relying on the posterior curvature of the crown of lateral and posterior teeth. Based on the available set, there is also no evidence of a dignathic heterodonty on SGO.PV.6635. Moreover, the crowns of the known species within Isurolamna (i.e., Isurolamna barajunasi Glikman and Zhelezko, 1985; Isurolamna inflata Leriche, 1905 and Isurolamna gracilis Le Hon, 1871) are high and sigmoidal, comparatively blunter in the case of I. gracilis and I. barajunasi, and the roots show divergent branches in the three species. On the contrary, all the material historically referred to the genus *Lethenia*, shows straight crowns and non-divergent root branches. While the species Lethenia vanderbroecki has been included within Isurolamna by some authors (e.g., Dutheil, 1991), the traits discussed by Baut and Génault (1999) for supporting Lethenia as a taxon different from Isurolamna, are verified here on the basis of the first available associated dental set including anterior, lateral and posterior elements of a single individual. Considering these facts, this research proposes a second species within *Lethenia*, being its first occurrence in the southern hemisphere. On



contrary, the dental features of *Isurolamna* are still based on artificial sets (Le Hon, 1871;
Cappetta, 1976; Zhelezko and Koslov, 1955) and likely, the genus may represent a wastebasket taxon.

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Discussion

110	Previous Records of Paleogene Chondrichthyans in central Chile—Earliest reports
111	include the mention of Odontaspis elegans from Eocene beds of central Chile (Oliver-
112	Schneider, 1936), although, the material was never figured and its repository is currently
113	unknown. Suárez and Marquardt (2003) referred to 'Myliobatis sp.' several plates from the
114	Eocene of Algarrobo, but their repository was not provided and the specimens were not figured,
115	making impossible its reassessment. Later, Muñoz-Ramirez et al. (2007) described a rich
116	chondrichthyan diversity from Talcahuano (ca. 135 km south from the localities studied here)
117	considering them as part of the Late Cretaceous Quiriquina Formation (Biró-Bagóczky, 1982),
118	and including the taxa Squalus sp₁ Squatina sp., Cretorectolobus sp., Carcharias sp.,
119	Palaeohypotodus sp., Scapanorhynchus sp., Palaeogaleus sp., Galeorhinus sp.,
120	Paraorthacodus sp., Dasyatis sp., Rhinoptera sp., ?Dasyatidae indet. Suárez and Otero (2010)
121	described the presence of <i>Isurolamna</i> sp. on Loanco, Región del Maule, which is the material
122	here described as a new species of Lethenia. After, Groz and Palma-Heldt (2013) reviewed the
123	assemblage described by Muñoz-Ramirez et al. (2007), recognizing that several known
124	biochrons were indeed restricted to the Paleocene. Suárez (2015) reviewed (among others) the
125	Paleogene record from central Chile, listing all these previous records. Otero (2015) mentioned
126	the presence of Macrorhizodus praecursor in the middle-to-upper Eocene of Loanco. The
127	specimens were not figured nor repository was indicated then. These are described here for the
128	first time. Later, Fernández-Jiménez et al. (2016) reported additional chondrichthyans referred
129	to Carcharias "hopei", Carcharias sp., Striatolamia macrota, and Myliobatis sp., reinforcing the
130	presence of Paleocene-Eocene levels at Talcahuano.
131	More recently, Rodriguez et al. (2023) reported additional late Paleocene
132	chondrichthyans from Talcahuano in central Chile, with material referred to the taxa
133	Paraorthacodus clarkii, Squalus minor, Squalus orpiensis, Centrophorus sp., Squatina prima,
134	Anomotodon novus, Striatolamia striata, Carcharias spp., Sylvestrilamia teretidens, Odontaspis
135	winkleri, Palaeohypotodus speyeri, Palaeohypotodus rutoti, Isurolamna inflata, Premontreia

gilberti, Physogaleus secundus, Palaeogaleus vincenti and Hypolophodon sylvestris. It must be





observed that this diversity needs a critical review. The identification of three squalid taxa (i.e., Squalus minor, Squalus orpiensis and Centrophorus sp.) was based on a single tooth, respectively. Squalidae are characterized by poor monognathic and dignathic heterodonty, meaning that teeth from the upper and lower jaw are similar and the teeth of each jaw are also similar in different dental positions (Cappetta, 2012: fig. 12C). moreover, teeth of different squalid genera can reach similar general shape during individual tooth growth. Because of this, usage of isolated squalid teeth is problematic for granting specific determinations. A similar problem occurs among Odontaspididae and Mitsukurinidae. These groups have marked dignathic dentition and they also have a marked dental variation along each jaw; however, different genera can show remarkably similar teeth depending on their dental position or jaw (Cunningham, 2000; Cappetta and Nolf, 2005). For preventing these issues, a large sampling is recommended and has proved to work on other local fossil odontaspidids and squalids (e.g., the Late Cretaceous record of Carcharias gracilis was based on 196 teeth from the same locality and level; see Otero, 2024). On the other hand, part of the specimens of Rodriguez et al. (2023) are reported to be abraded (i.e., Centrophorus sp., Squatina sp.), leaving the possibility of reworked material from older strata. Both squalid and squatinid sharks are known in local older underlying units such as the Quiriquina and Cosmito formations (Suárez et al., 2003; Muñoz-Ramirez et al., 2007; Groz and Palma-Heldt, 2013).

With these considerations, this contribution recommends that the specific identifications of squatinids, mitsukurinids and odontaspidids based in a single sample as provided by Rodriguez et al. (2023), should kept under open nomenclature awaiting larger samplings that could support their specific adscription, with the exception of *Striatolamia striata* and *Hypolophodon sylvestris* which are supported by a fair number of dental pieces. On the other hand, the records of *Sylvestrilamia teretidens* (n=1; Rodriguez et al., 2023: fig. 7N, O) and *Isurolamna inflata* (based on n=1; Rodriguez et al., 2023: fig. 8C,D) likely represent posterior teeth of other odontaspidids and are difficult to assure even to genus level on the grounds of a single available tooth.

A summary of the Paleogene chondrichthyan records from central Chile with remarks on their status (after the comments above), are provided in Table 1.

Paleobiographic Relevance of the Studied Material—The new material of Palaeohypotodus sp. adds to previous undifferentiated Paleocene (Muñoz-Ramirez et al., 2007; Groz and Palma, 2013) and late Paleocene records of the genus (Rodriguez et al., 2023) in central Chile. Additional records of Palaeohypotodus in the WBP are known in lower Eocene



units of the Austral Basin (Otero and Soto-Acuña, 2015) and Antarctica (Long, 1992; Kriwet, 2005; Reguero et al., 2013; Kriwet et al., 2016), although, the genus remains unreported in coeval units of New Zealand. Otherwise, in the northern hemisphere, *Palaeohypotodus* was restricted to the Danian-Thanetian of Europe, North America, central Asia and northern Africa (Cappetta, 2012). Thus, their current southeastern Pacific records (=central Chile) are coeval with those records from the northern hemisphere, but comparatively older than known high-latitude austral occurrences of *Palaeohypotodus*. These age differences likely represent an extension of the former Danian-Thanetian biochron of *Palaeohypotodus* (Cappetta, 2012) into the lower Eocene (in Antarctica and the Austral Basin), suggesting that the taxon was a relict in high latitudes of the southern hemisphere prior to its extinction.

Occurrences of the genus *Megasqualus* in the WBP have been reported in the Danian-Selandian of New Zealand (Mannering and Hiller, 2008), while northern records are known in the middle Paleocene-lower Eocene of Europe (Cappetta, 2012 and references therein). The current material from central Chile represents the second known occurrence of *Megasqualus* in the WBP.

On the other hand, the new occurrence of *Macrorhizodus praecursor* in middle-to-late Eocene levels of Loanco represents the northernmost occurrence of the taxon in the WBP. Their previous austral records were restricted to the Eocene of Antarctica (Cione and Reguero, 1994; Reguero et al., 2012) and the Eocene of the Austral Basin in southern South America (Otero et al., 2012; 2013). A closely related lamnid taxon likely occurs in the Paleocene of New Zealand but the material was incomplete for an accurate taxonomical referral (Mannering and Hiller, 2008: fig. 15). Otherwise, the genus *Macrorhizodus* had a widespread distribution along Europe, Atlantic Africa and Asia during the lower Eocene - lower Oligocene (Cappetta, 2012 and references therein).

In addition, the description of *Lethenia carranzaensis* sp. nov. represents the first occurrence of the genus in the southern hemisphere. Previous reports are known in the lower Oligocene of Belgium (Baut and Génault, 1999), France and Kazakhstan (Cappetta, 2012), and the upper Oligocene of Europe (Cappetta, 2012).

Finally, the presence of and indeterminate hexanchid represents its current oldest record along the southeastern Pacific. Austral record of hexanchids can be tracked back to the Late Jurassic of New Zealand (Cappetta and Grant-Mackie, 2018). There is a major gap during the austral Cretaceous. The group was frequently reported in the James Ross Basin since the Late Cretaceous until the Eocene (Grande and Chatterjee, 1987; Richter and Ward, 1990; Long, 1992; Cione and Reguero, 1994; Kriwet et al., 2006; Reguero et al., 2012; Engelbrecht et al.,



2017). Hexanchids are also known in the Paleocene of New Zealand (Mannering and Hiller, 2008). On South America, the oldest hexanchid records in the Austral (=Magallanes) Basin are known in the Maastrichtian of Calafate Lake (Bogan et al., 2016). Younger records are relatively frequent and broadly distributed along the entire basin during the Eocene (Otero et al., 2012; 2013). On the contrary, records of hexanchids along the southeastern Pacific are known since the Miocene and onwards (Long, 1993; Carrillo-Briceño et al., 2013; Suárez, 2015; Chávez-Hoffsmeister and Villafaña, 2023), but its local presence before the Miocene remained unreported until now.

Palaeogeography — The Paleocene chondrichthyan diversity previously described from central Chile (Muñoz-Ramirez et al., 2007; Groz and Palma-Heldt, 2013; Rodriguez et al., 2023) includes several genera with widespread representation along the WBP or even being cosmopolitan (i.e., genera Squatina, Carcharias, Palaeohypotodus, Scapanorhynchus, Galeorhinus, Paraorthacodus, Dasyatis, Rhinoptera, Centrophorus, Anomotodon, Striatolamia, Odontaspis and Hypolophodon). Exceptions are the single record of a worn tooth of Cretorectolobus sp. (Muñoz-Ramirez et al., 2007) that might belong to reworked material from older units, considering its known bichron restricted to the Hauterivian-Maastrichtian (Cappetta, 2012).

The new Paleocene-lower Eocene records of *Palaeohypotodus* sp., *Megasqualus* sp. and Hexanchidae indet. extend their known distribution in the WBP. The same applies for the new record of *Macrorhizodus praecursor*, also present in austral Eocene WBP localities.

On the contrary, the reported presence of *Palaeogaleus*, *Physogaleus*, and *Premontreia* in the upper Paleocene of central Chile (Rodriguez et al., 2023) support an early connection with the North Atlantic. While these taxa remain unreported in high latitudes of the WBP, the three genera are known in Europe, North America, north and west Africa, and the Near East (Cappetta, 2012). In addition, the new record of the genus *Lethenia* (represented by *Lethenia carranzaensis* sp. nov.), complements a similar scenario during the late Eocene-early Oligocene. Previous to this research, the genus *Lethenia* was exclusively reported in the Oligocene of Europe and central Asia (Baut and Génault, 1999; Cappetta, 2012), remaining unreported in any coeval locality of the southern hemisphere.

This pattern of an Atlantic influence into the WBP, likely beginning in the late Paleocene and extending into the early Oligocene, is reinforced by the similar distribution of the billfish clade Blochiidae, a group firstly described in the Eocene of Italy (Fierstine and Monsch, 2002), but later shown to be present in the middle-to-late Eocene of central Chile (particularly in



Loanco, the locality here studied), represented by an endemic genus and species (Otero, 2019). This suggests an emerging picture for a temporal and latitudinal declination of the WBP. While endemic taxa indeed occur (i.e., *Lethenia carranzaensis*, *Loancorhynchus catrillancai*: Otero, 2019; this study), their closest relatives are known in the North Atlantic.

These faunal interchanges and its chronostratigraphic occurrences were expectable, considering the composition of the Neogene chondrichthyan fauna known in central and northern Chile (Carrillo-Briceño et al., 2013; Suárez, 2015; Chávez-Hoffsmeister and Villafaña, 2023), which contrasts in diversity to the Eocene assemblages of southernmost Chile and Antarctica (Long, 1992; Kriwet, 2005; Kriwet et al., 2016; Reguero et al., 2012; 2022; Otero et al., 2012; 2013). Previous to this research, there was no evidence of a latitudinal segment in the southeastern Pacific, neither a time span for the beginning of such faunal turnover.

These faunal interchanges occurred in a moment of major global geographic and climatic dynamics which especially affected the southern hemisphere by the opening of the Tasmanian Gateway, the deepening of the Drake Passage (Lawver and Gahagan, 2003; Case, 2007), the extension of the Antarctic ice sheet, plus variations in the Antarctic ocean circulation patterns (Goldner et al., 2014) and sea temperature (Kennedy et al., 2015). Although sparse, the new material described in this contribution sheds the first insights on the marine vertebrate faunal changes coupled to these global dynamics along the southern Pacific coast of South America.

Conclusions

New Paleogene chondrichthyan remains from central Chile are here studied. The oldest studied sections correlates with the Paleocene-lower Eocene Pilpilco Formation, which includes the northernmost occurrences along the Pacific of the taxa Palaeohypotodus sp., Megasqualus sp. and Hexanchidae indet. The new record of Megasqualus is the second known in the WBP, while the material referred to Hexanchidae indet. represents the earliest known evidence of the group in the southeastern Pacific.

Two additional sections of a second younger unit (Millongue Formation) have yielded material referable to lamnid sharks, represented by *Macrorhizodus praecursor* (Leriche), and by *Lethenia carranzaensis* sp. nov., here described. The new record of *Macrorhizodus* represents its northernmost occurrence in the WBP, although this was a cosmopolitan taxon during the Eocene. On the contrary, the new record of *Lethenia* represents its first occurrence in the southern hemisphere. Its distribution has a similar pattern previously recognized in coeval



573	billfishes of the clade Blochiidae. Moreover, both taxa share a similar distribution with the
574	chondrichthyan genera Palaeogaleus, Physogaleus, and Premontreia, previously reported in the
575	upper Paleocene of central Chile. All these taxa remain unreported in higher latitudes of the
576	WBP but they are known in the Atlantic realm during the same time span, suggesting that a
577	southeastern Pacific-north Atlantic faunal interchange occurred at least since the upper
578	Paleocene until the lower Oligocene. Such interchange could represent the starting point of the
579	WBP declination as a recognizable bioprovince, prior to the establishment of typical Neogene
580	marine vertebrate faunas along the southeastern margin of the Pacific Ocean.
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587	
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Table 1(on next page)

Summary of the Paleogene chondrichthyan record from central Chile.

Available publications, identified taxa and provenance, ordered from older to younger chronostratigraphic occurrences, and comments on their updated status.



- 1 Table 1: Summary of the available publications, identified taxa and provenance of the Paleogene
- 2 chondrichthyan record from central Chile, ordered from older to younger chronostratigraphic
- 3 occurrences, and comments on their updated status.

original reference	identified taxa	Age	horizon	locality	Repository	updated status
Muñoz- Ramirez et al., 2007	Squalus sp. Squatina sp., Cretorectolobus sp., Carcharias sp., Palaeohypotodus sp., Scapanorhynchus sp., Palaeogaleus sp., Galeorhinus sp., Paraorthacodus sp., Dasyatis sp., Rhinoptera sp., ?Dasyatidae indet.	Paleocene	Cosmito Formation	Talcahuano , Región del Biobio	Museo Lajos Biró (Q.)	_
Groz and Palma- Heldt, 2013	Squalus sp., Squatina sp., Carcharias sp., Palaeohypotodus sp., Scapanorhynchus sp., Paraorthacodus sp., Rhinoptera sp., Cretorectolobus sp., Palaeogaleus sp., Galeorhinus sp., Dasyatis sp.	Paleocene	Cosmito Formation	Talcahuano , Región del Biobio	not indicated. Likely, Museo Lajos Biró (Q.)	review and stratigraphic assessment of samples described by Miñoz-Ramirez et al. (2007)
Rodriguez et al., 2023	Paraorthacodus clarkii, Squalus minor, Squalus orpiensis, Centrophorus sp., Squatina prima, Anomotodon novus, Striatolamia striata, Carcharias spp., Sylvestrilamia teretidens, Odontaspis winkleri, Palaeohypotodus speyeri, Palaeohypotodus rutoti, Isurolamna inflata, Premontreia gilberti, Physogaleus secundus, Palaeogaleus vincenti, Hypolophodon sylvestris.	late Paleocene	Pilpilco Formation	Puente Perales and Cerro San Martín, Región del Biobio	Museo Lajos Biró (Q.)	Review needed. This study suggest keeping under open nomenclature the following taxa due to dubious adscription based on a single sample: Paraorthacodus sp., Squalus sp., Centrophorus sp., Squatina sp., Anomotodon sp. Carcharias spp., Sylvestrilamia teretidens, Odontaspis winkleri, Palaeohypotodus speyeri, Palaeohypotodus rutoti and Isurolamna inflata. On the other hand, Premontreia gilberti, Physogaleus secundus, Palaeogaleus vincenti are easily distinguishable based on a single tooth; finally Striatolamia striata and Hypolophodon sylvestris are based in several samples.
Fernández et al., 2016	Carcharias "hopei", Carcharias sp., Striatolamia macrota, Myliobatis sp.	Eocene (undifferentiated)	Cosmito Formation	Coliumo, Región del Biobio	Museo Lajos Biró (Q.)	_
Oliver- Schneider, 1936a, b	Odontaspis elegans	Eocene (undifferentiated)	Lebu Group, without further resolution	Lota and Lebu river, Región del Biobio	unknown	Inverifiable
Oliver- Schneider, 1936b	Odontaspis contortidens	Eocene (undifferentiated)	Lebu Group, without further resolution	Lebu	unknown	Inverifiable





Suárez and Marquardt, 2003	Myliobatis sp.	Eocene (undifferentiated)	Estratos de Algarrobo	Algarrobo, Región de Valparaíso	unknown	unknown repository; at least two genera of Myliobatoidea occur in Algarrobo (Otero, 2024)
Suárez and Otero, 2010	'Isurolamna' sp.	middle-upper Eocene	Millongue Formation	Loanco, Región del Maule	MNHN (SGO.PV.6 635)	Lethenia carranzaensis sp. nov.; this study
Otero, 2015	'Isurolamna' sp., Macrorhizodus praecursor	middle-upper Eocene	Millongue Formation	Loanco, Región del Maule	not indicated then (MNHN; SGO.PV.6	not changed. Described by first time in this study



Figure 1

Locality and stratigraphic sections.

(A) map indicating the locality of Loanco, in central Chile. Geologic scheme of the outcrops exposed along the coast and cliffs in Loanco. Modified from Otero (2024). (B) Studied stratigraphic sections. Each point is marked on the geologic scheme in (A). Point A and B columns, modified from Otero (2024).

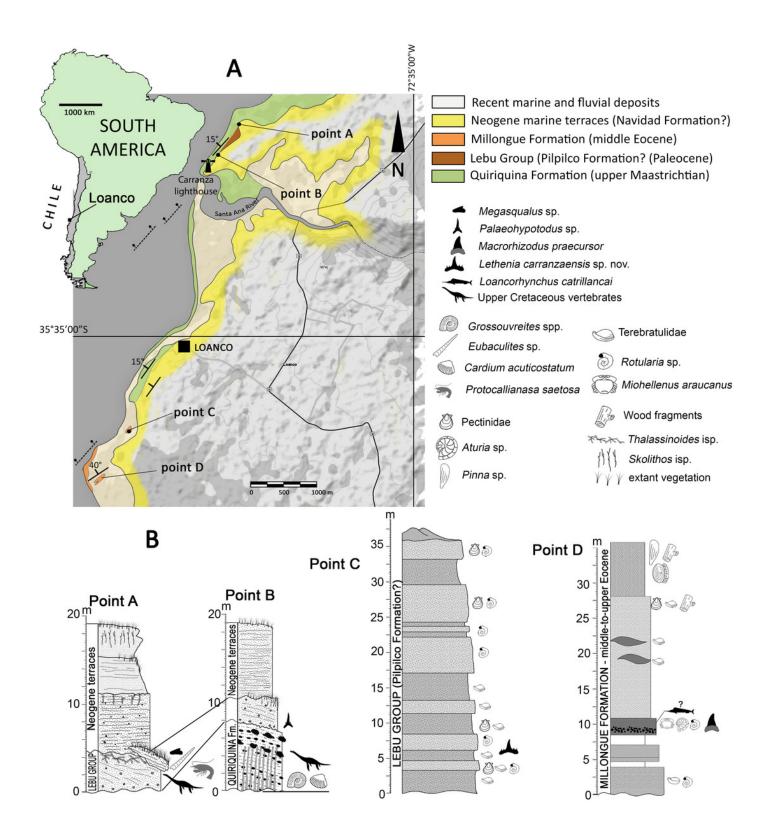


Figure 2

Chondrichthyans from Loanco, central Chile.

(A) *Megasqualus* sp. (SGO.PV.6625), isolated lateral tooth in labial view. (B) same in lingual view. (C) Hexanchidae indet. (SGO.PV.6626) isolated main crown in lingual view. (D) *Palaeohypotodus* sp. (SGO.PV.6780), single posterior tooth. Pilpilco Formation, upper Paleocene-lower Eocene. (F) *Macrorhizodus praecursor* (Leriche, 1905) (SGO.PV.6633a, referred) upper inferior tooth in labial view. (G) same in lingual view. (H) *Macrorhizodus praecursor* (Leriche, 1905) (SGO.PV.6633b, referred), incomplete tooth in labial view. (I) same in lingual view. Millongue Formation, upper Eocene-lower Oligocene. Scale bar equals 10 mm in both cases.

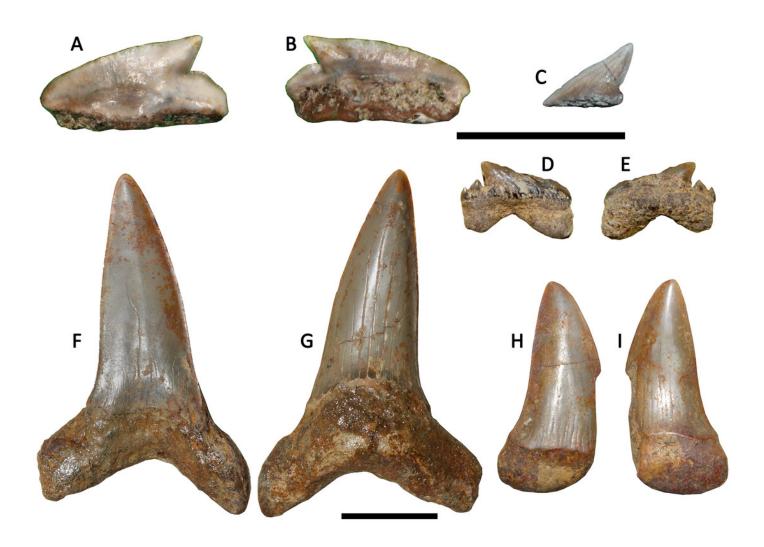




Figure 3

Lethenia carranzaensis sp. nov. (SGO.PV.6635, holotype).

lateral view. Scale bars equals 10 mm, except N-Q, 50 mm.

Preserved teeth. (A) anterior tooth in labial view. (B) same in lingual view. (C) profile view. (D) incomplete anterior tooth. (E) anterolateral tooth in labial view. (F) same in lingual view. (G) anterior tooth in labial view. (H) anterolateral tooth in labial view. (I) posterolateral tooth in labial view. (J) anterior tooth in labial view. (K, L, M) Different posterolateral teeth. (N, O) Cartilaginous fragments of the jaw. (P) associated vertebra in articular view. (Q) same in

