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A new species of chimaeriform (Chondrichthyes, Holocephali) from the uppermost Cretaceous of the López de Bertodano Formation, Isla Marambio (Seymour Island), Antarctica

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Abstract: We describe a new chimaeriform fish, *Callorhinchus torresi* sp. nov., from the uppermost Cretaceous (late Maastrichtian) of the López de Bertodano Formation, Isla Marambio (Seymour Island), Antarctica. The material shows it is distinct from currently known fossil and extant species of the genus, whereas the outline of the tritors (abrasive surfaces of each dental plate) shows an intermediate morphology between earlier records from the Cenomanian of New Zealand and those from the Eocene of Isla Marambio. This suggests an evolutionary trend in tritor morphology in the lineage leading to modern callorhynchids, during the Late Cretaceous-Palaeogene interval.

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Introduction

Chondrichthyans from the Late Cretaceous of Isla Marambio have been known since the early 20th century. Woodward (1906) indicated the presence of large vertebral centra, doubtfully assigned to *Ptychodus* Agassiz, 1835, but Welton & Zinsmeister (1980) expressed doubt that they belonged to this taxon. Other reports of cartilaginous fishes from the Late Cretaceous of Isla Marambio indicate the presence of the genus *Isurus* Rafinesque, 1810 (Grande & Eastman 1986), later reassigned to *Sphenodus* Agassiz, 1843 by Richter & Ward (1991), and *Notidanodon dentatus* Woodward, 1886 (Cione & Medina 1987, Grande & Chatterjee 1987). In addition, sand-tiger sharks of the genus *Odontaspis* Agassiz, 1838 and cf. *Odontaspis* sp. were reported from the Maastricthtian of Isla Marambio (Martin & Crame 2006). Further records in Campanian beds of the James Ross Island indicate the presence of the genera *Scapanorhynchus* Woodward, 1889 and *Paraorthacodus* Glückman, 1957, as well as a chronostratigraphic extension for *Chlamydoselachus thompsoni* Richter & Ward, 1991. Also, endemic synechodontiform sharks referred to *Paraorthacodus antarcticus* Klug *et al*., 2008 have been identified from the same locality (Klug *et al*. 2008).

Callorhynchid fishes (Holocephali, Chimaeriformes) are an early branch of the chimaeriforms (Didier 2004), and are characterized by having crushing tooth plates with well developed, robust tritorial pads (Stahl 1999, Stahl & Chatterjee 1999) which are hypermineralized in some taxa and therefore considered as a diagnostic feature. In this group, the mandibular apparatus is comprised of six dental pieces, which are paired mandibular, palatine and vomerine plates, and together with dorsal spines, they are the most frequently found body parts of the group. The first reference to fossil holocephalans in Isla Marambio is from Grande & Eastman (1986), who described a palatine and mandibular plates tentatively referred to the genus *Ischyodus* Egerton, 1843, from levels of La Meseta Formation, assigned by these authors to the late Eocene–early Oligocene. These same specimens were later identified as *Ischyodus dolloi* Leriche, 1905, and constrained to the late Eocene of the La Meseta Formation (Ward & Grande 1991). Additionally, the latter authors described a new species, *Chimaera seymourensis* Ward & Grande, 1991, from the same unit. The first Late

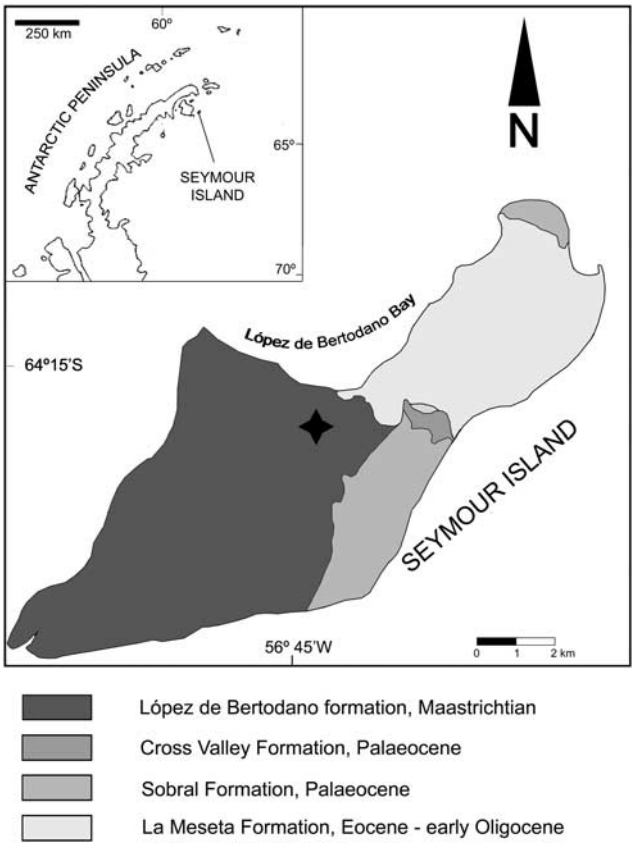

Fig. 1. Schematic map of Isla Marambio (Seymour Island), showing the main geologic units. The asterisk indicates the type locality where the studied material was recovered.

Cretaceous callorhynchid recovered from Isla Marambio belong to a new species, *Chimaera zangerli* Stahl & Chatterjee, 1999, from the Maastricthian López de Bertodano Formation, after extended to the Campanian of the James Ross Island (Kriwet *et al*. 2006). Later, Stahl & Chatterjee (2002) also recognized the presence of *I. dolloi* in the López de Bertodano Formation. The first occurrence of the genus *Callorhinchus* Laćepède, 1798 in Antarctica is known by a new species, *Callorhinchus stahli* Kriwet & Gaździcki, 2003, from the late Ypresian (Telm 2 stratigraphic unit *sensu* Sadler 1988) of the La Meseta Formation. Finally, Martin & Crame (2006) reported the first occurrence of the genus *Callorhinchus* in Maastrichtian beds of Isla Marambio.

The present paper describes a new callorhynchid fish from the uppermost Cretaceous of Isla Marambio. The material was collected in January of 2011 during fieldwork of the Chilean expedition supported by the Antarctic Ring Project (Anillo de Ciencia Antártica ACT-105, 2010–11, Conicyt - Chile). The particular configuration of the preserved tritors allows identification of a new species among callorhynchids, adding to the known diversity of holocephalans in higher latitudes of the Weddellian Biogeographic Province (*sensu* Zinsmeister 1979) during the end of the Cretaceous.

Locality and geological setting

The samples were collected from Isla Marambio (Fig. 1), in the north-eastern part of the Antarctic Peninsula. This island, together with Vega, James Ross and Snow islands contains the most representative outcrops of sedimentary rocks of the James Ross Basin, deposited during the Late Cretaceous–Palaeogene. All collected material from Isla Marambio was found in upper levels of the López de Bertodano Formation. Based on Macellari (1988), the studied locality (64°16'11.4"S, 56°44'30.6"W) is included in the middle part of the Klb9 unit. The recovered specimens were found associated and had been slightly transported over the recent soil by snow and mud slides, and were found with additional scattered samples. Fossil-bearing levels comprise fine-to-medium sandstones intercalated with sandy siltstones. Erosion has exposed abundant concretionary nodules containing vertebrate and invertebrate remains. The hosting cross section reaches *c.* 30 m and is formed by a succession of sandy marls with thin intercalations of fine-to-medium carbonate cemented sandstone, and a thin glauconitic marl bed near to the base of the section (namely, 11LB1 section, following our field notation, Fig. 2). Our stratigraphic section is equivalent to the middle part of the Klb9 unit of Macellari (1988). The succession includes frequent, associated remains of elasmosaurid plesiosaurs and mosasaurs, together with scarce and fragmentary neoselachian teeth and osteichthyan vertebrae. Fossil invertebrates are mostly represented by lytoceratids, kossmaticeratids and pachydiscid ammonoids (e.g. *Anagaudryceras seymourense* Macellari, 1986, *Maorites densicostatus* Killian & Reboul, 1909, *Pachydiscus riccardi* Macellari, 1986), gastropods, serpulids, and bryozoans. In addition, two rock samples in the stratigraphic section contain some palinomorphs. The biostratigraphic framework is done by the mentioned ammonoids especially *P. riccardi* which constrain the age of *Callorhinchus torresi* sp. nov. to the *P. riccardi* Zone of Macellari (1988), at the late Maastrichtian. Additional scattered dental plates of the studied taxon were collected in the same area, but their respective stratigraphic provenance could not be rigorously determined due to transport by erosion.

Materials and methods

The nomenclature used follows Kriwet & Gaździcki (2003). The material was collected in a small valley filled by recent mud at the bottom, with fresh outcrops of sedimentary rocks exposed on the flanks. Two plates (left mandibular and incomplete right palatine) were found directly on top of the sandstone outcrop and near the uppermost part of this valley, indicating minimal transport from the original fossil-bearing level. A third plate

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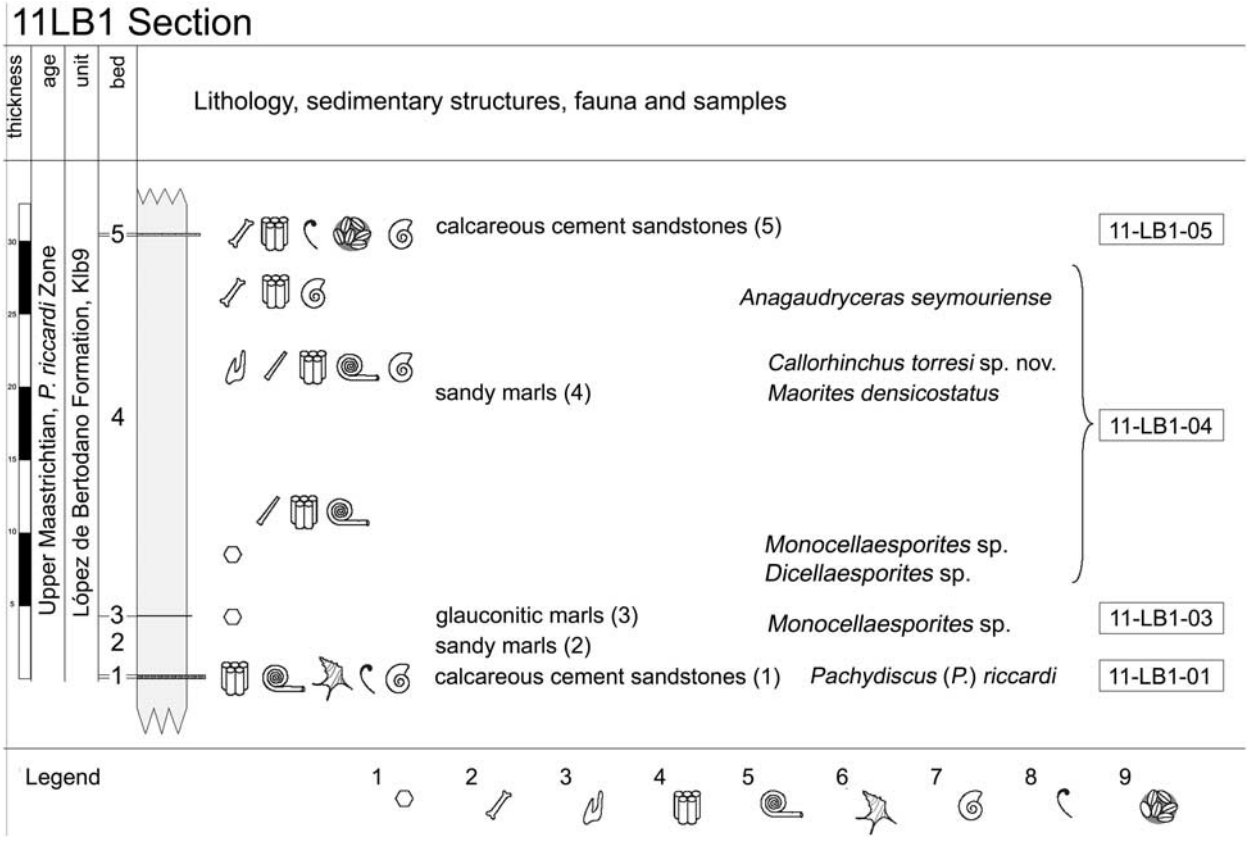

Fig. 2. Stratigraphic section of the upper López de Bertodano Formation (Klb9, *sensu* Macellari 1988) on Isla Marambio (Seymour Island). Legend: 1) palynomorphs, 2) vertebrates remains, 3) *Callorhinchus torresi* sp. nov., 4) bryozoans, 5) annelids, 6) gastropods, 7) ammonites, 8) bivalves, and 9) little bivalve agglomerate.

(right mandibular) was recovered about 1 m downwards. Additionally, this plate is anatomically complementary and similar in size to the other two plates. Despite this, it cannot be confidently determined that all the material belongs to the same individual because of slight differences in the wearing patterns, and the position of the tritors. Additional scattered plates were collected in the same area. For taxonomic determination, three main criteria were considered:

1) Synapomorphies. Following Didier (1995), important synapomorphies can be recognized in dental plates of holocephalans related to the shape and size of plates, and particularly, the morphology of tritors, their relative position, and their number. These criteria are useful for determining genera and species in well-preserved samples and are valid for extant and fossil specimens.
2) Ontogenetic stage. The continuous growth of dental plates in chimaeriforms can cause differences in tritor shape and position. In mandibular plates, the growth of the basal surface can cause a thickening of the portion between the symphysis and the anterior inner tritor, while the median and outer tritors become progressively separated. Concerning the collected samples, these are very similar in size, but have very conservative shapes and distribution of the tritors, especially on mandibular plates. In the recovered palatines, these are slightly different in size, but also similar in shape to the median tritor, markedly bifid in the anterior portion. The similar sizes and shapes of all recovered plates suggest that these belonged to individuals of similar ontogenetic stages.
3) Wear pattern. The apical surface is most worn, followed by the occlusal surfaces. Because of this, the anterior margin of mandibulars and palatines could appear to be variable in shape. The occlusal surfaces can display slight variations in the shape of each tritor as a consequence of the abrasive contact between mandibular, palatine and vomerine plates. Despite these considerations, apical surfaces and median tritors of all recovered mandibular plates are very similar in shape. The same seems to apply to the palatines, but since they are incomplete, these cannot be fully compared.

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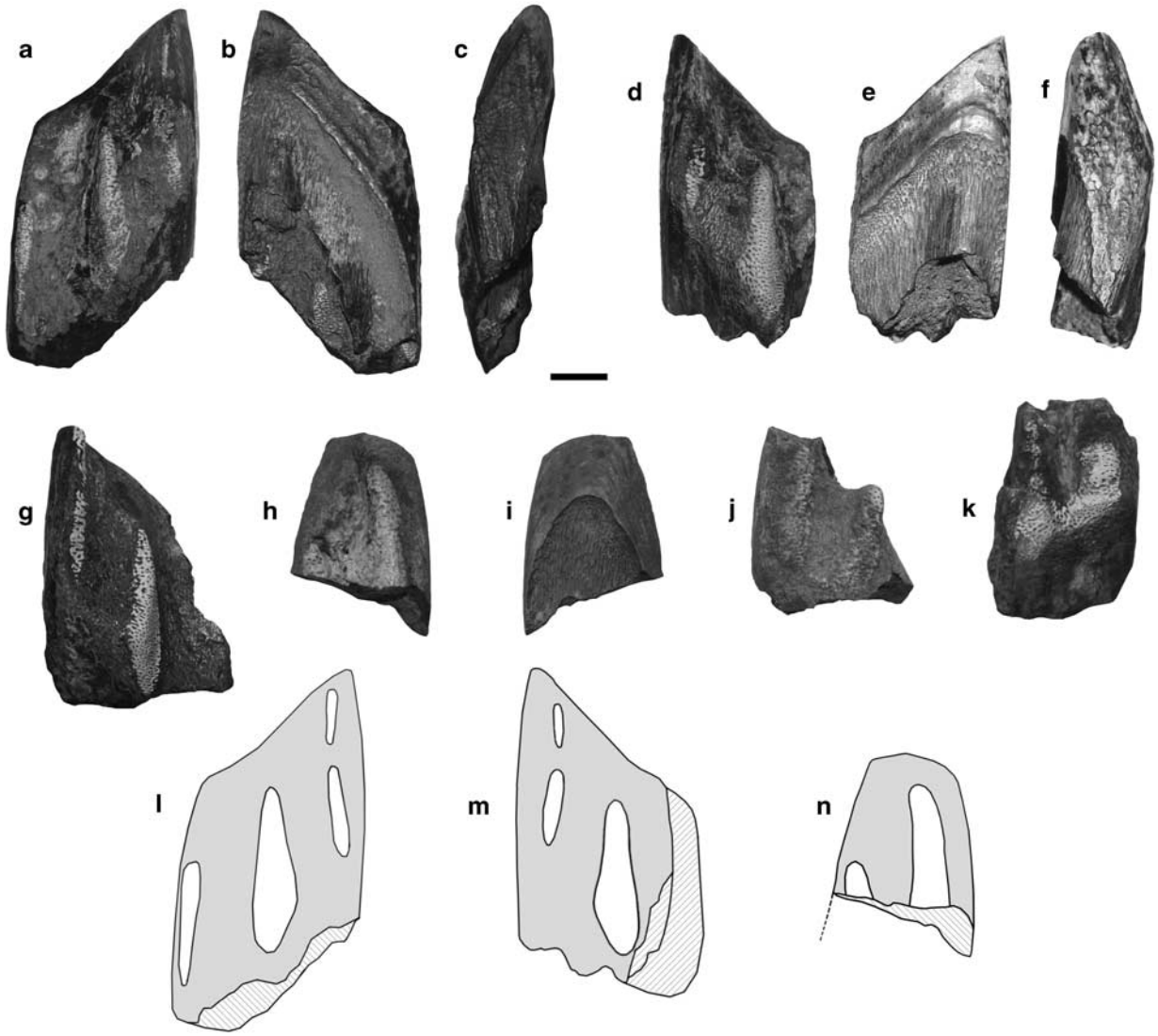

Fig. 3. SGO.PV.22011. *Callorhinchus torresi* sp. nov. Holotype: **a.** left mandibular in occlusal view, **b.** ventral view, and **c.** symphysial view. SGO.PV.22012. Paratypes. SGO.PV.22012a: **d.** right mandibular in occlusal view, **e.** ventral view, and **f.** symphysial view. SGO.PV.22012b: **g.** right mandibular in occlusal view. SGO.PV.22012c: **h.** right palatine plate in occlusal view, and **i.** dorsal view. SGO.PV.22012d: **j.** isolated, incomplete left palatine, and **k.** isolated, incomplete right palatine. Schematic occlusal outlines of the most informative plates. **l.** SGO.PV.22011, the holotype. **m.** SGO.PV.22012a, right mandibular. **n.** SGO.PV.22012c, right palatine. Scale bar equals 10 mm.

Institutional abbreviations

SGO.PV = Museo Nacional de Historia Natural, Santiago, Chile; DJ = Collection of Palaeontology, British Antarctic Survey, Cambridge.

Systematic palaeontology

CHONDRICHTHYES Huxley, 1880
HOLOCEPHALI Bonaparte, 1832
CHIMAERIFORMES Obruchev, 1953
Family CALLORHYNCHIDAE Garman, 1901
Subfamily CALLORHYNCHINAE Stahl, 1999
Genus *CALLORHINCHUS* Laćepède, 1798

Type species. Callorhinchus callorhynchus (L. 1758), extant taxon from the Southern Hemisphere.

Diagnosis: As for the genus (Kriwet & Gaździcki 2003), considering only dental plates; mandibular tooth plate with a single central hypermineralized pad restricted to the distal part of the coronal surface, flanked by narrow tritors on the symphyseal and/or labial edges. Middle tritor of palatine tooth is bifid towards the labial margin, with the symphysial branch being the longest. Vomerine tooth plate quadrilateral with single middle tritorial pad.

Distribution: Albian and Cenomanian of Russia (Nessov & Averianov 1996); Cenomanian of New Zealand (Newton 1876); Santonian of Russia (Averianov 1997); Maastrichtian

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Table I. Measurements of the preserved tritors in each studied plate, over the occlusal surface, taken with Vernier caliper (± 0.5 mm). Partial measurements available for incomplete tritors are indicated by *, non applicable by #, and missing data is indicated by —. All results are expressed in mm.

Collection number (MNHN)	Material	Anatomical element	Anterior inner tritor		Posterior inner tritor		Median tritor		External tritor	
			length	width	length	width	length	width	length	width
SGO.PV.22011	holotype	left mandibular	12.4	2.9	16.8	3.9	29.3	8.3	22.6	4.3
SGO.PV.22012a	paratype	right mandibular	12.3	3.0	12.7	3.7	26.8	8.8	—	—
SGO.PV.22012b	paratype	right mandibular	11.6	3.2	15.1	3.6	28.5	7.8	—	—
SGO.PV.22012c	paratype	right palatine	21.2*	18.5	#	#	#	#	#	#
SGO.PV.22012d	paratype	left palatine	24.1*	18.9	#	#	#	#	#	#
SGO.PV.22012e	paratype	right palatine	22.5*	18.6	#	#	#	#	#	#

of central Chile (Suárez *et al*. 2003); Maastrichtian and Eocene of Isla Marambio (Kriwet & Gaździcki 2003, Martin & Crame 2006); Thanetian and Ypresian of England (Gurr 1962, Ward 1973); Miocene of Argentine Patagonia (Woodward & White 1930); Miocene-Pliocene of central and northern Chile (Suárez *et al*. 2004, 2006), New Zealand (McKee in Stahl 1999), and Peru (Muizon & DeVries 1985); Recent, widespread on Southern Hemisphere (Stahl 1999).

Callorhinchus torresi sp. nov.
(Fig. 3a–n)

Holotype: SGO.PV.22011 (Fig. 3a, b, c & l), an almost complete left mandibular.

Paratypes: SGO.PV.22012a, b (Fig. 3b–k, m & n), two incomplete right mandibular plates; SGO.PV.22012c, one anterior portion of a right palatine; SGO.PV.22012d, one incomplete left palatine; SGO.PV.22012e, and one concretionary nodule containing one partial right palatine.

Referred material: DJ.1020.2-F. *Callorhinchus* sp. left palatine. López de Bertodano Formation (Klb9), latest Maastrichtian (Martin & Crame 2006).

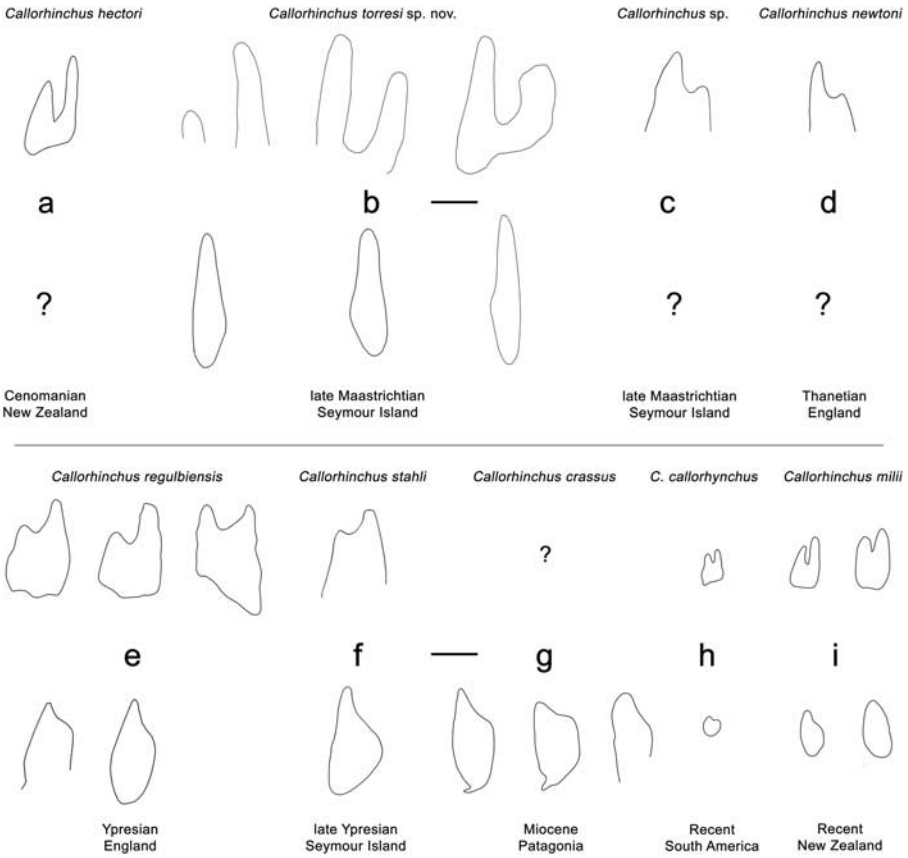

Fig. 4. Schematic outlines of palatine and mandibular tritors of known species of the genus *Callorhinchus*. Upper row displays general tritor shape in palatine plates, while the lower row displays the shape of median tritors for each taxon indicated. **a. d. e. f. g. h.** and **i.** Taken and modified from Kriwet & Gaździcki (2003, figs 7 & 8). **b.** This study. **c.** Modified from Martin & Crame (2006, fig. 3). **h.** Modified from Kriwet & Gaździcki (2003, fig. 8) and Suárez *et al*. (2004, fig. 2). Scale bar equals 10 mm.

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Type locality: Small valley about 1500 m south of the López de Bertodano Bay, Isla Marambio, Antarctica.
Type horizon: López de Bertodano Formation, *P. riccardi* Zone, Klb9 *sensu* Macellari (1988), late Maastrichtian.
Type strata: Bed 11LB1-4, 11LB1 Section (Fig. 2), López de Bertodano Formation.
Derivation of name: The specific name honours Dr Teresa Torres (Universidad de Chile), director of the present research project, for more than twenty years of contribution to Antarctic palaeobotany, and her continuous support to new generations of Chilean palaeontologists, including some of the authors.
Diagnosis: *Callorhinchus torresi* can be distinguished among other species of the genus by the following unique characters: estimated adult size with large plates, having mandibulars with rhomboidal outline; slender median tritors extended in axial direction, slightly thickened in their posterior inner margin; anterior inner tritor reduced and located in apical position; slender posterior inner tritor, covering about one third of the symphysial margin and anteriorly extended immediately posterior to the vomerine facet; slender external tritor, broader in its anterior portion and covering about half of the post-occlusal margin; no accessory tritors present; palatine plates with prominent, bifid anterior tritor, with a clearly larger symphysial branch and deep embayment between the two branches.

Discussion

In summary, there are five known taxa of callorhynchids from Isla Marambio: a) *Chimaera zangerli*, Maastricthtian of López de Bertodano Formation (Stahl & Chatterjee 1999); b) *Callorhinchus stahli*, early Eocene (late Ypresian) of the La Meseta Formation (Kriwet & Gaździcki 2003); c) *Ischyodus dolloi*, Maastrichtian of the López de Bertodano and late Eocene of the La Meseta formations (Ward & Grande 1991); d) *Chimaera seymourensis*, from the late Eocene of La Meseta Formation (Ward & Grande 1991); and e) *Callorhinchus* sp. from the Maastricthtian of the López de Bertodano Formation (Martin & Crame 2006).

Considering the similar size and shape of all the plates studied here (Table I), these probably are from adult or sub-adult individuals. The external tritor can be observed only in the holotype, being the only mandibular collected preserving the outer margin, where this structure occurs. The posterior margin of all the recovered palatines is poorly preserved and is best observed in the right palatine SGO.PV.22012d, having a posterior margin that is relatively straight and diagonally disposed. Despite the lack of better-preserved plates, the observed outlines of median tritors in mandibular plates and those of anterior inner tritors in palatines are different from all known callorhynchids.

When comparing the specimens of *C. torresi* sp. nov. with known fossil and extant species of the genus (Fig. 4), in known Cretaceous species the palatines tend to show a deep embayment between both branches of the anterior inner tritor, that progressively became shallower and smaller from Cenomanian to Maastrichtian representatives, as observed in recent species. Apart from *C. torresi*, there are no records of mandibular plates of any Cretaceous species of the genus. Thus, *C. torresi* provides the only Cretaceous reference to discuss the evolution of this anatomical element. Palaeogene records include two species from the Eocene with preserved mandibulars, *C. regulbiensis* Gurr, 1962, and *C. stahli*. Both have a posterior portion of the medial tritor that is broader than in *C. torresi*, while the apical projection of the anterior portion is reduced compared to *C. torresi*. The same situation is observed in the Miocene species *C. crassus* Woodward & White, 1930, and it is particularly evident in the extant species *C. milii* Bory de Saint-Vincent, 1823 and *C. callorhynchus* both with very reduced tritors and relatively small dental plates.

Records in other localities of the Weddellian Biogeographic Province

Late Cretaceous holocephalans have been reported in south-western South America since the 19th century. Philippi (1887, plate 55, fig. 5) described a dental plate from the Late Cretaceous of the Quiriquina Island, central Chile, tentatively referred by this author to the genus *Chimaera* L. 1758. The material is a mandibular plate figured with its anterior portion downwards. Nevertheless, it is possible to see a descending lamina in the symphysial margin and the absence of hypermineralized tritors, suggesting a closer affinity with the genus *Edaphodon* Buckland, 1838. Several other taxa were later mentioned from Late Cretaceous units of central Chile. Suárez *et al*. (2003) figured a vomerine plate referred to the genus *Edaphodon*, from early Maastrichtian beds exposed in Algarrobo (120 km west of Santiago), and mentioned the presence of the genus *Chimaera* in the same levels. Additionally, these authors indicated the presence of the genus *Callorhinchus* in late Maastrichtian beds of the Quiriquina Island. The genus *Ischyodus* was reported from late Eocene–early Oligocene beds of southernmost Chile (Le Roux *et al*. 2010), and is still unreported in older units along the south-western margin of South America. The genus *Callorhinchus* was also reported from three different Chilean units with an Eocene–early Pliocene range (Suárez *et al*. 2004, 2006, Le Roux *et al*. 2010) and also in the Miocene of the Argentinian Patagonia (Woodward & White 1930, Kriwet & Gaździcki 2003). This genus is extant in waters of southern South America.

The genus *Edaphodon* was reported from Campanian–Danian levels of Chatham Islands, New Zealand with the endemic species *Edaphodon kawai* Consoli, 2006. All these reports indicate that chimaeriform fishes were widespread and abundant in the Weddellian Biogeographic Province during the Late Cretaceous–Palaeogene.

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Chimaeriform fishes have proven to be a persistent group subsequent to the Cretaceous–Paleogene event, having common genera with widespread distribution in the Weddellian Biogeographic Province and several endemic species from Antarctica and New Zealand. Like other marine vertebrates, chimaeriforms were later affected by major tectonic and oceanographic changes such as the opening of the South Tasman Rise and the deepening of the Drake Passage, with the subsequent establishment of deep seaways (Lawver & Gahagan 2003), along with important climatic changes leading to gradual Antarctic cooling, which reduced the diversity of chondrichthyans in higher latitudes of the Southern Hemisphere at the Eocene-Oligocene boundary (Cione *et al*. 2007). Callorhynchids were constrained to lower latitudes during the Neogene being especially abundant in the Miocene–Pliocene of northern Chile (Suárez *et al*. 2004). Since the Miocene, the establishment of the Humboldt Current influenced the distribution of callorhynchids, which today is exclusively restricted to shallow waters of the Southern Hemisphere (Stahl & Chatterjee 2002).

Conclusions

Callorhinchus torresi sp. nov. is the third fossil record of this genus from Isla Marambio, the second occurrence from Late Cretaceous levels of this locality, and the first species of chimaeriform fish identified in the late Maastrichtian of the López de Bertodano Formation. The studied material allows us to discount morphological variation due to different ontogenetic states, while the unique outlines of mandibular median tritors, and palatine anterior inner tritors, allows us to distinguish it from all known fossil and extant species of the genus. The studied material adds to the record of *Callorhinchus* during the Cretaceous, suggesting an evolutionary trend in the lineage leading to modern representatives, from slender median tritors extended anteriorly in mandibular plates to a broader posterior portion of the medial tritor with a reduced anterior apical projection in more recent species. *Callorhinchus torresi* also shows that, as in other Cretaceous species, there is a deep embayment between branches of the anterior inner tritors in the palatines, confirming the notion that the smaller and shallower embayment of more recent species has evolved from this condition.

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