New Eocene Antarctic chimeroid fish
(Holocephali, Chimaeriformes)

Jürgen KRIWET[1] and Andrzej GAŹDZICKI[2]

[1] *Department of Earth Sciences, University of Bristol, Queen's Road, Bristol, BS8 1RJ, UK*
<juergen.kriwet@bristol.ac.uk>

[2] *Instytut Paleobiologii PAN, ul. Twarda 51/55, 00-818 Warszawa, Poland*
<gazdzick@twarda.pan.pl>

ABSTRACT: Until now Eocene chimeroid holocephalians of Antarctica have been known from only a few specimens attributed to two species from the Eocene of Seymour Island. New material collected by Polish and English field parties includes numerous tooth plates and fin spine fragments from the Eocene La Meseta Formation. We describe a new species, *Callorhinchus stahli*, based on two mandibular and a single fragmentary palatine tooth plate. In addition, the stratigraphic distribution and diversity of Eocene Antarctic chimeroids is discussed. The chimeroid *Ischyodus* shows the greatest stratigraphic distribution with its greatest abundance in the middle parts of the La Meseta Formation while *Chimaera* and *Callorhinchus* are restricted to the lower ones. Changes in the environment and habitat availability most probably triggered the distributional pattern and the disappearance of chimeroids.

K e y   w o r d s: Antarctica, La Meseta Formation (Eocene), palaeontology (chimeroid fish), new species, ecology.

Introduction

Extant holocephalians are mostly deep-water cartilaginous fishes with continuously growing tooth plates in the upper and lower jaws. They have long been regarded as an obscure lineage (Didier 1995) and their relationships are considered controversial. Zangerl (1981) divided the chondrichthyans into the subclasses Elasmobranchii and Subterbranchialia (that is chondrichthyans with branchial arches located beneath the posterior part of the neurocranium). Maisey (1986), Lund (1986), Didier (1995), Lund and Grogan (1997), and Stahl (1999) proposed classification hypotheses based on cladograms for holocephalians. According to these, Chimaeriformes is the crown-group subterbranchialians.

Chimaeriformes comprises four suborders: Echinochimeroidei, Squalora-joidei, Myriacanthoidei, and Chimeroidei with chimeroids being the most derived chimaeriforms containing all extant taxa – *Callorhinchus*, *Chimaera*, *Hydrolagus*, *Rhinochimera*, *Hariotta*, *Neohariotta* (Stahl 1999). These taxa are arranged in three families, the Callorhynchidae (*Callorhinchus*), Rhinochimaeridae (*Rhino-chimaera*, *Neoharriotta*, *Hariotta*), and Chimaeridae (*Chimaera*, *Hydrolagus*). Didier (1995) identified the family Callorhynchidae as the most plesiomorphic chimeroids. Plesiomorphic characters are, *inter alia*, a descending lamina and crushing tooth plates with robust tritorial pads (Patterson 1992, Stahl 1999). Consequently, Stahl (1999) placed all fossil and extant forms with tritorial tissue arranged in pads in the Callorhynchidae, which was subdivided into two subfamilies Callorhynchinae and Edaphodontinae.

Fossils of chimeroids are mainly represented by isolated tooth plates, fin spines, and egg cases. The oldest known chimeroid remains come from Early Jurassic deposits of Europe (Ward and Duffin 1989, Stahl 1999). Twenty one fossil genera are currently placed within Chimeroidei. To date the fossil record of chimeroids in Antarctica comprises isolated tooth plates and fin spines of three chimeroid taxa, *Chimaera zangerli* Stahl and Chatterjee 1999 from the Maastrichtian López de Bertodano Formation, and *Ischyodus dolloi* Leriche 1902 and *Chimaera seymourensis* Ward and Grande 1991 from the Eocene La Meseta Formation of Seymour Island.

We report here on chimeroid remains collected by the Polish Antarctic field party that include a new taxon unknown for Antarctica so far. The investigated specimens are kept in the Institute of Paleobiology of the Polish Academy of Sciences, Warszawa under catalogue number ZPAL P.9. In addition, the distribution and palaeoecology of Eocene Antarctic chimeroids is discussed based on material in the British Museum of Natural History, London (M. Richter and J.J. Hooker collections).

Geological and stratigraphical setting

The La Meseta Formation (Elliot and Trautman 1982) is the Eocene sequence of richly fossiliferous shallow marine-estuarine deposits exposed in the northern portion of Seymour (Marambio) Island, Antarctic Peninsula (Fig. 1). It represents some 800 m thick succession of poorly consolidated sandstones and siltstones with an exceptional record of Eocene biota (*e.g.* Feldmann and Woodburne 1988, Stilwell and Zinsmeister 1992, Gaździcki 1996, 2001a, b; Porębski 1995, 2000; Marenssi *et al.* 1998, Aronson and Blake 2001, Reguero *et al.* 2002).

The new species of chimeroid fish occurs in the lower unit Telm2 of the La Meseta Formation *sensu* Sadler (1988) at locality ZPAL 8 (north flank of the Cross Valley, South Section) – see Figs 1–2, 4). An incomplete dorsal fin spine was col-
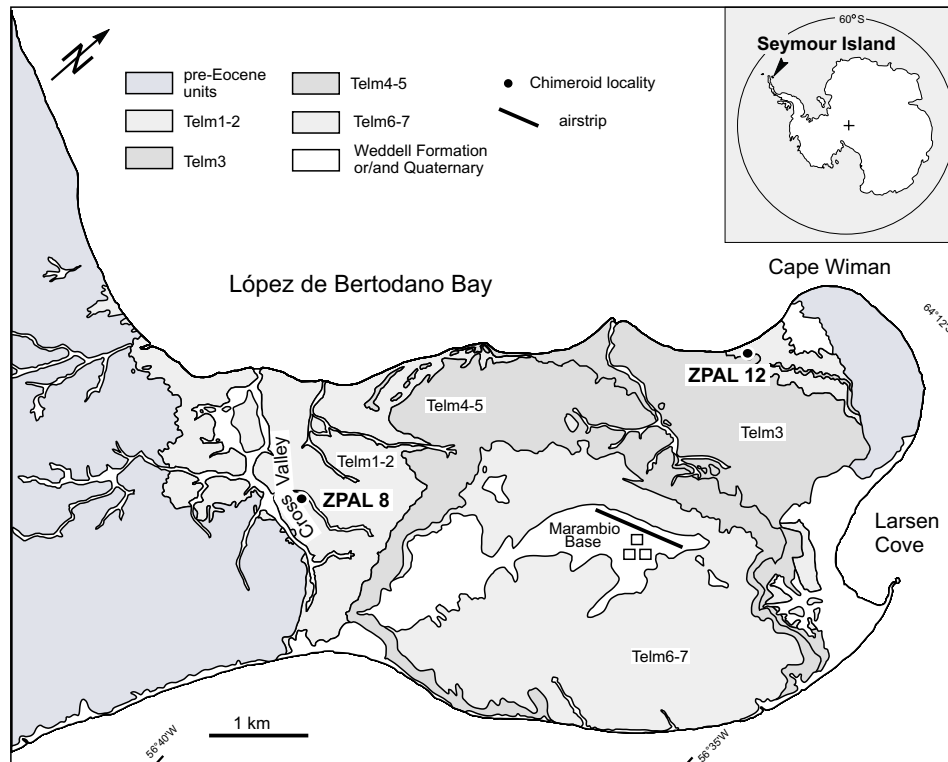
Fig. 1. Map of the northern part of Seymour Island showing the localities (ZPAL 8, ZPAL 12) where remains of studied chimeroid fishes were collected.

lected from Telm1unit at locality ZPAL 12 (*Sadler Stacks*) situated on the left side of Silent Valley near Cape Wiman (North Section) (Figs 1, 3; see also Gaździcki and Tatur 1994, pl. 1, fig. 2, pl. 2, fig. 1).

The age of the lower part of the La Meseta Formation (Telm1–2 units) is Upper Lower Eocene (Upper Ypresian) based of dinoflagellate cysts (Coccoza and Clark 1992). The uppermost part of the formation (top of Telm7) is Upper Eocene (34.2 Ma, Priabonian) in age (Dingle and Lavelle 1998, see also Dutton *et al.* 2002).

Material and terminology

The material described in this study was discovered by the junior author in 1994 and is from the lower parts of the Eocene La Meseta Formation (Telm1–2) of Seymour Island (Fig. 4). Two mandibular and a fragmentary palatine tooth plate were found at locality ZPAL 8, whereas the imperfect fin spine at locality ZPAL 12 (Figs 1–3).

Fig. 2. View of the locality ZPAL 8. Telm2. *Photograph by A. Gaździcki, February 1994.*

Fig. 3. View of the locality ZPAL 12. Telm1. *Photograph by A. Gaździcki, February 1994.*

The terminology used in this study follows that adopted by Patterson (1992) and Stahl (1999) and is shown in Fig. 5. The mandibular tooth plate is sub-triangular and thus has mesial, distal, labial, and lingual edges. Ward and Grande
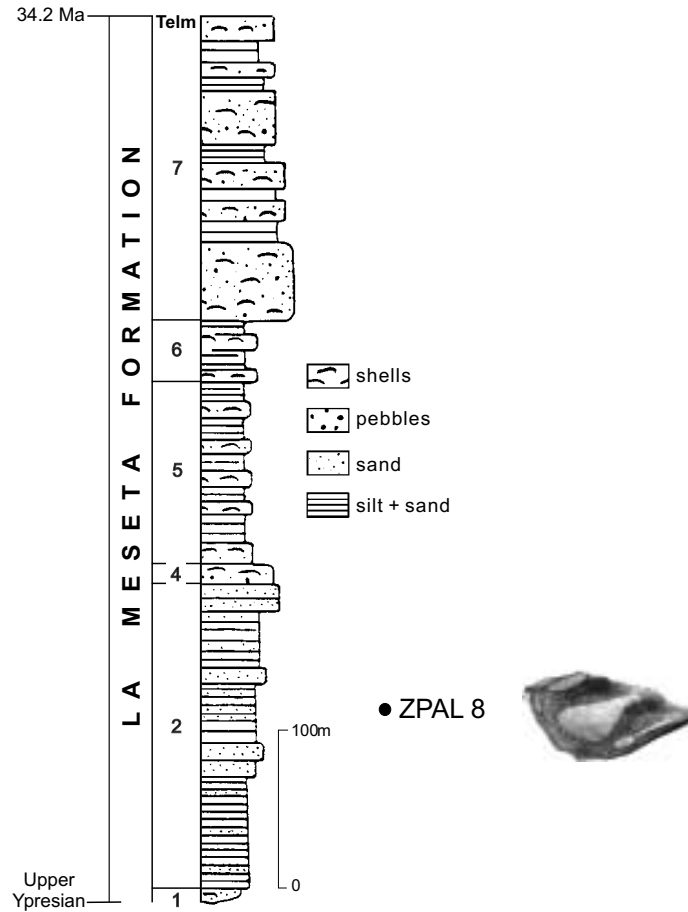
Fig. 4. Stratigraphic log of the La Meseta Formation (South Section) with horizon from which the tooth plates of *Callorhinchus stahli* sp. n. were collected. Log adapted from Sadler (1988).
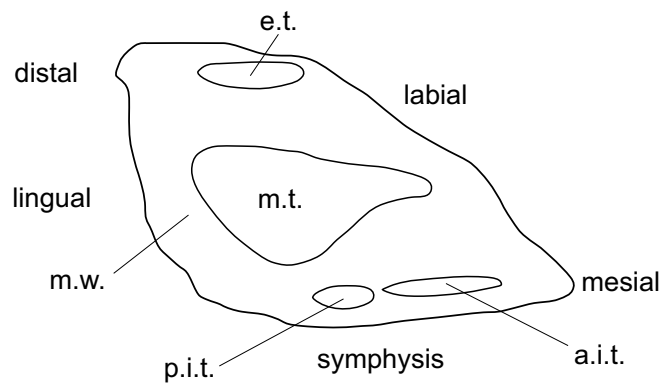

Fig. 5. Terminology for the mandibular tooth plate of *Callorhinchus stahli* sp. n. Tooth plate displayed in occlusal view.

(1991) called the labial edge occlusal. Anterior inner tritor (a.i.t.), posterior inner tritor (p.i.t.), middle tritor (m.t.), anterior external tritor (a.e.t.), and external tritor (e.t.) are distinguished in the mandibular tooth plate. The margin of wear (m.w.) separates the worn and unworn parts of the oral surface of the tooth plate. The middle tritor is the only tritorial pad present on the palatine tooth plate. The term descending lamina was introduced by Patterson (1992) for basal projections from the labial and symphysial margins of the tooth plate.

Systematic palaeontology

The taxonomy follows that of Stahl (1999).

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Class **Chondrichthyes** Huxley, 1880
Subclass **Subterbranchialia** Zangerl, 1979
Superorder **Holocephali** Bonaparte, 1832
Order **Chimaeriformes** Obruchev, 1953
Suborder **Chimeroidei** Patterson, 1965
Family **Callorhynchidae** Garman, 1901
Subfamily **Callorhynchinae** Stahl, 1999
Genus *Callorhinchus* Laćepede, 1798 (*ex*. Gronovius, 1763)

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Type species: *Callorhinchus callorhynchus* (Linnaeus, 1758), a recent marine fish of the Southern Hemisphere.

Revised diagnosis. — Chimeroids characterized by the following combination of characters: Elongated snout with a fleshy plough-shaped flap. Lateral lines closed. Eyes small. Caudal fin heterocercal and anal fin present. Males with simple scroll-like pelvic claspers without denticles, broad. Flat frontal clasper with denticles. Additional patch of denticles opposite those of the clasper directly attached to the integument. Complex prepelvic tentacles in pelvic pockets present. Tooth plates large, mandibular lozenge-shaped to sub-triangular, palatine plate elongated and quadrilateral. Mandibular tooth plate with a single central hypermineralised pad restricted to the distal part of the coronal surface, flanked by narrow tritors on the symphysial and/or labial edges. Middle tritor of palatine tooth bifid towards the labial margin with the symphysial branch being the longer. Vomerine tooth plate quadrilateral and lozenge-shaped with single middle tritorial pad. Fin spine with sharp and serrated anterior ridge and smooth convex lateral faces. Posterior face concave in cross section. Lateral margins with two rows of small, basally pointed denticles. Egg cases with wide, ribbed lateral web.

Remarks. — The frontal clasper and the patch of denticles is called the tentacular complex by Herman *et al.* (2001). These authors also present a rather detailed description and illustrations of vomerine, palatine, and mandibular tooth plates of extant chimeroids. The spelling *Callorhynchus* Gronovius, 1763 was rejected by

the International Commission on Zoological Nomenclature (Opinion 261, 1954) legitimising *Callorhinchus* Lacépede, 1798 (Stahl 1999).

Stratigraphical and geographical range. — Albian (Lower Cretaceous) of Russia; Cenomanian (Upper Cretaceous) of New Zealand; Santonian (Upper Cretaceous) of Russia; Thanetian and Ypresian (Palaeogene) of England; Miocene (Neogene) of Patagonia; Recent Australia, New Zealand, South America, Tasmania, and South Africa.

Callorhinchus stahli sp. n.
(Fig. 6)

Holotype: ZPAL P.9/1, complete left mandibular tooth plate.

Paratypes: ZPAL P.9/2, incomplete right palatine tooth plate; ZPAL P.9/3, incomplete mandibular tooth plate.

Type horizon: Telm2, La Meseta Formation, Early Eocene (Late Ypresian).

Type locality: Cross Valley, Seymour Island, Antarctic Peninsula.

Etymology: The species name honours Barbara J. Stahl (Manchester/New Hampshire, U.S.A.) for her contributions to holocephalian fish systematics.

Diagnosis. — Species of *Callorhinchus* characterized by large mandibular tooth plates with short, broad, and triangular mesial edge. Middle tritor elongated, cleaver-like in outline. Lingual border oblique to symphysial following the form of the wear margin. Symphysial margin of middle tritor sigmoidal. Inner tritors arranged in line and well separated from the middle tritor.

Description. — The material of *Callorhinchus stahli* sp. n. comprises a well-preserved left mandibular and an incomplete right mandibular as well as a very fragmentary right palatine tooth plate. The complete left mandibular tooth plate (ZPAL P.9/1) measures 51 mm mesio-distally and 31 mm labio-symphysially and is subtriangular in occlusal view (Fig. 6a). The mesial corner is rather broad, short, and projects anteriorly at the symphysis. The symphysial edge is straight and slightly curves posteriorly to meet the lingual margin. The edge between symphysial and lingual borders is broken. The lingual border is slightly curved. The distal angle forms a blunt and rectangular structure that projects lingually. The labial border is subdivided into an oral and a postoral portion. The oral margin is oblique and gently undulates medially in occlusal view with a clear convexity between middle and anterior inner tritors. The postoral margin is more or less parallel to the symphysial border and slightly curved forming a rectangular angle with the lingual margin distally. The postoral margin of the labial border is thickened forming a triangular platform like area.

The occlusal surface is undulating in labial view, because of depressions between the external, middle, and inner tritors and the pillow-like shape of the tritors. The wear surface occupies almost the entire occlusal plane. The lingual, unworn
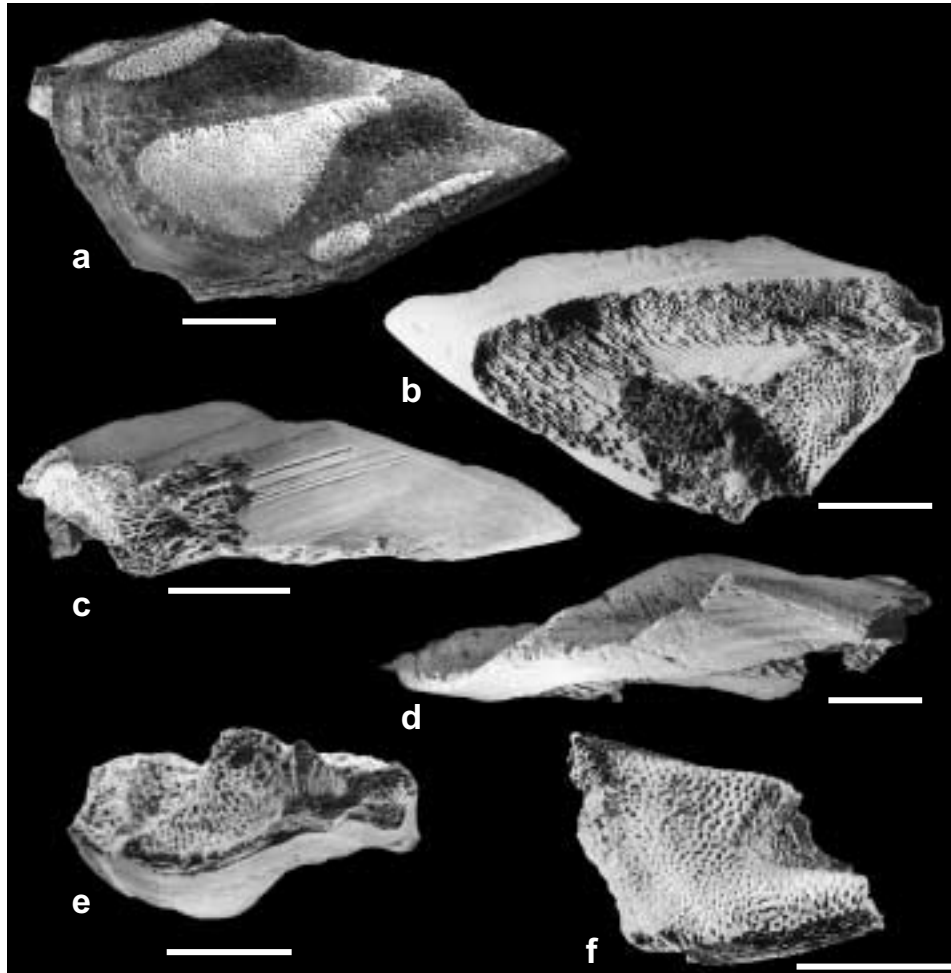
Fig. 6. Tooth plates of *Callorhinchus stahli* sp. n. a–e, left mandibular tooth plate, specimen ZPAL P.9/1; f, incomplete right palatine tooth plate, specimen ZPAL P.9/3: **a**. occlusal view; **b**. basal view; **c**. symphysial view; **d**. labial view; **e**. lingual view; **f**. occlusal view. Scale bars 1 cm. Specimens b–e coated with ammonium chloride.

portion towards the open growth margin is very narrow and displays closely arranged growth lines following the lingual border.

The hypermineralised tissue is in form of large tritorial pads. No laminated tritors are present. There is a single middle hypermineralised tritorial pad (m.t.), which is flanked by an external tritor located at the margin of the labial postoral border and two inner tritors arranged in line along the symphysial border. The middle tritor is elongated, cleaver-liked in outline with a narrow, rather short and narrow anterior and a bulbous rounded posterior portion. The lingual border of the middle tritor is oblique to the symphysial plane and follows the form of the wear margin (m.w.). The symphysial border of the middle tritor is almost sigmoidal curved.

The inner tritors are arranged in line and well separated from the middle tritor. The posterior one (p.i.t.) is placed below the posterior symphysial border of the middle tritor. It is rather short and rounded in outline.

The anterior inner tritor (a.i.t.) is narrower but more elongated. It does not reach the mesial edge. Both, the a.i.t. and p.i.t., are almost fused because of the progressive abrasion of the occlusal surface of the tooth plate.

The external tritor is heavily abraded. The remaining portion is oval in outline and narrow. It reaches the oblique oral margin of the lingual border anteriorly and is parallel to the postoral portion.

Closely arranged vascular canals that enter the hard tissue obliquely in the central part and more vertically towards the labial and symphysial surfaces perforate the basal surface of the tooth plate (Fig. 6b). The posterior open growth surface of the basal surface is very narrow and smooth without vascular canal openings but with some faint growth lines. The descending lamina is smooth with weak growth lines. The labial and symphysial descending laminae meet mesially separating the basal surface from the broad symphysial and the narrow labial surfaces (Figs 6c, d). The descending laminae are rather deep where they meet at the mesial edge and decrease in height lingually towards the open growth surface.

The lingual open growing margin of the Antarctic specimen reveals the typical mesh-like appearance of trabecular hard tissue surrounded by a thin edge of dense tissue that covers the occlusal, labial, and symphysial surfaces of the tooth plate of extant *Callorhinchus* spp. (Patterson 1992) (see Fig. 6e).

The second mandibular tooth plate is very fragmentary but exhibits the characteristic middle tritor. The specimen correlates well with the one described above in size but does not provide any further morphological informations.

Only a fragmentary right palatine tooth plate was recovered (Fig. 6f). The fragment measures 20.5 mm mesio-distally and 17.5 mm labio-symphysially. The hypermineralised tritorial pad exhibits the typical bifid morphology. The symphysial prong is rather long with the anterior tip lacking, whereas the labial one is very short and triangular in occlusal view. The notch between both branches is V-shaped with an angle of about 45°. The basal surface is divided into basal, symphysial, and labial surfaces by the descending lamina. Obliquely arranged vascular canals perforate the basal surface. Both labial and symphysial surfaces are rather broad and smooth except for faint growth lines. Lingually, along the fracture zone, the characteristic mesh-like trabecular hard tissue is exposed.

Discussion. — The hypermineralised tooth plates are one of the most important synapomorphies of holocephalians (Didier 1995). The shape and size of tooth plates and relative positions, numbers, and morphology of the tritors are the criteria that determine generic and specific identifications especially in fossil forms. However, the continuously growth from the posterior margin, ontogenetic stage, and wear of tritors as well as variations in size and tritorial form can cause problems in specific determinations, which must be considered.
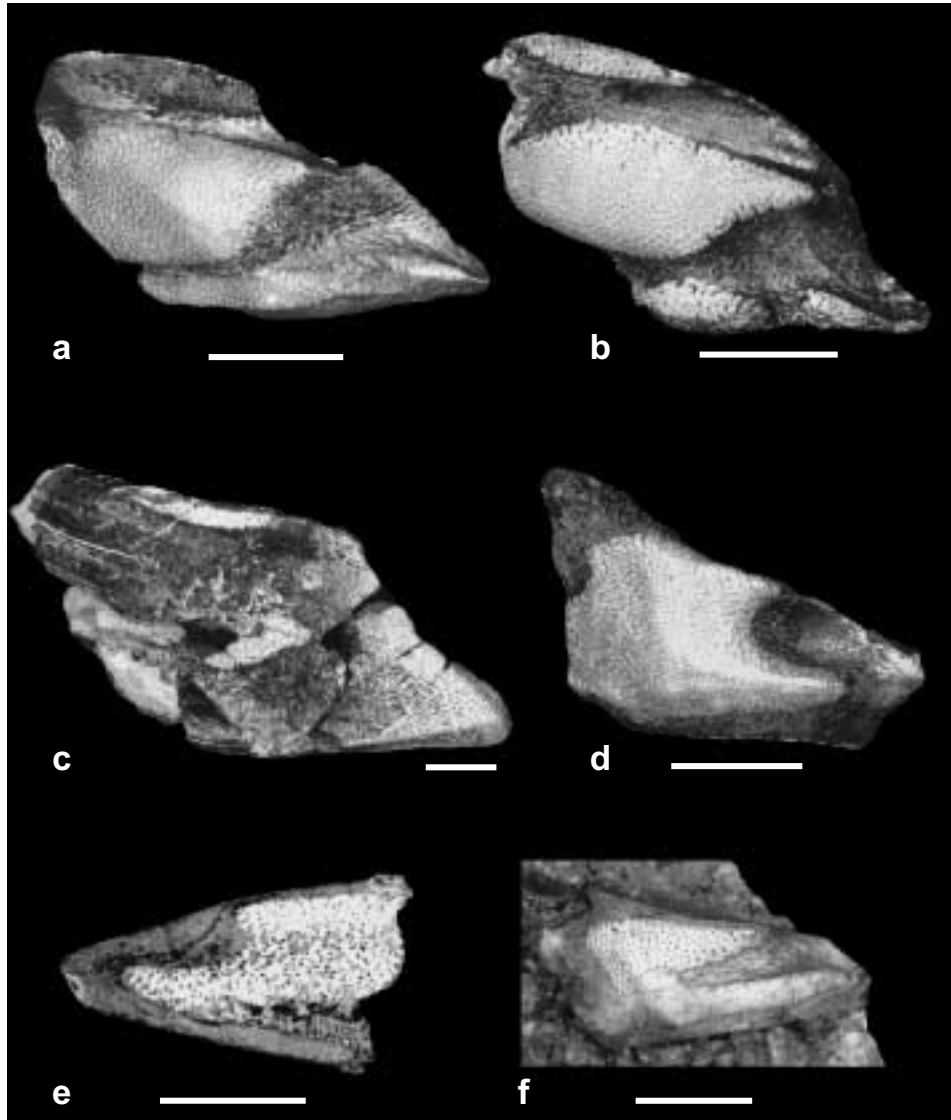
Fig. 7. Mandibular and palatine tooth plates of *Callorhinchus* spp. **a**. *C. regulbiensis* Gurr, 1963, left mandibular, BMNH P.55316. **b**. *C. regulbiensis* Gurr, 1963, left mandibular, BMNH P.55310. **c**. *C. crassus* Woodward and White, 1930, left mandibular, holotype BMNH P.2301. **d**. *C. regulbiensis* Gurr, 1963, right palatine, holotype, BMNH P.44039. **e**. *C. newtoni* Ward, 1973, left palatine, holotype, BMNH P.55313. **f**. *C. hectori* Newton, 1876, right palatine, holotype, BMNH P.2301. Scale bars 1 cm.

The presence of a single middle hypermineralised tritor is one of the synapomorphies of *Callorhinchus*. Ontogenetic differences are found in the morphology of the palatine tritor in extant *Callorhinchus* spp. (Didier *et al.* 1994). In juveniles, the tritor is separated into two elongated symphysial and middle tritors. The two tritors

fuse during growth until the characteristic pattern is established. Nessov and Averianov (1996) indicated variation in the number of palatine tritors in the Albian species *C. borealis*. Two specimens exhibit two separate hypermineralised pads (symphysial and middle) (text-figs 1, 3a) whereas the two pads are fused in other specimens. In stratigraphically younger species, the tritors are always united forming an exposed hump with two anteriorly directed branches. Nessov and Averianov (1996) suggested that the palatine tritors remained occasionally separated in adult specimens of *C. borealis*. However, the observed pattern is more likely related to ontogenetic variation.

Fossil species were mainly established for isolated palatine tooth plates. Mandibular tooth plates are rare. Although the new species is mainly based on the mandibular tooth plate the palatine tritor pattern may also display differences to contemporaneous taxa. Material examined for comparison includes the following specimens (Figs 7–8): an incomplete left mandibular plate (BMNH P.9093, holotype), a right mandibular tooth plate (BMNH P.9828), and two incomplete palatine plates (BMNH P.9094 and 9094a) of *Callorhinchus crassus* Woodward and White, 1930 from the Miocene of Patagonia; a right palatine plate (BMNH P.2301, holotype) of *Callorhinchus hectori* Newton, 1876) from the Cenomanian of New Zealand; a left palatine plate (BMNH P.55313, holotype) of *Callorhinchus newtoni* Ward, 1973 from the Thanetian of England; a right palatine tooth plate (BMNH P44039 the holotype) and a left mandibular plate (BMNH P.55310) of *Callorhinchus regulbiensis* Gurr, 1963 (for 1962) (the mandibular tooth plate was ascribed to *Chimaera eophantasma* by Ward (1973) but allocated to *Callorhinchus regulbiensis* by Ward and Grande (1991).

Additional material of *Chimaera seymourensis* and *Ischyodus dolloi* as well as some fin spine fragments in the BMNH collections was examined to reconstruct the stratigraphic distribution and diversity of Eocene Antarctic chimeroids.

The palatine tritor of *C. regulbiensis* exhibits a very similar pattern (Figs 8a–c), especially specimen BMNH P.44037 (Fig. 8b). The angle between the symphysial and labial prongs ranges from 50° to 60° and is related to the grade of abrasion but also intraspecific variation. Specimen BMNH P.55315 (Fig. 8c) differs from the holo- and paratype in the almost equal length of the prongs. Characterisitcs of *C. stahli* sp. n. include a more triangular labial prong with a straight labial margin. These differences are, however, minor and may not represent real distinguishable characters. Nevertheless, *C. stahli* sp. n. differs significantly in the morphology of the mandibular tooth plate and especially in the form of the middle tritor from *C. regulbiensis* (Figs 8d–e). The posterior symphysial and lingual margin of the middle tritor is straight in *C. regulbiensis* while the posterior symphysial margin is strongly convex and the lingual one obliquely straight in *C. stahli* sp. n. The anterior prong of the m.t. is very narrow and the labial margin of the m.t. is sigmoidal resulting in a cleaver-shape appearance of the middle tritor. Graphic simulation of abrasion patterns of mandibular plates of both species resulted in significanty different shapes and differences in the relative position of m.t. and p.i.t. Thus, the form of the middle
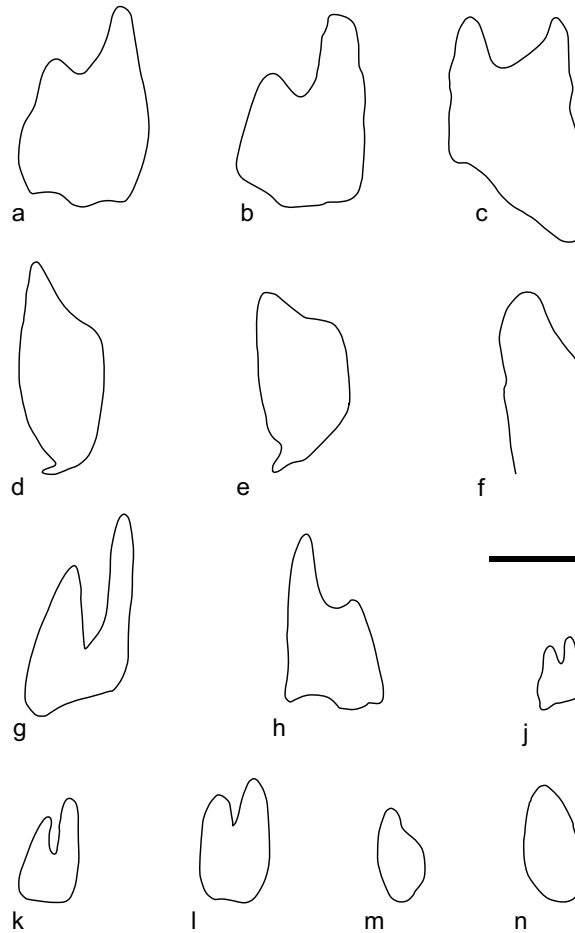
Fig. 8. Schematic outline drawing of middle tooth plate tritors of *Callorhinchus* spp. **a–c:** palatine tritors of *C. regulbiensis* Gurr, 1963. **a**. holotype, BMNH P.44039; **b**. paratype BMNH P.44037; **c**. specimen BMNH P.55315. **d–e**: mandibular tritors of *C. regulbiensis* Gurr, 1963. **d**. specimen BMNH P.55310; **e**. specimen BMNH P.55316; **f**. mandibular tritor of *C. crassus* Woodward and White, 1930 (holotype BMNH P.2301); **g**. palatine tritor of *C. hectori* Newton, 1876 (holotype BMNH P.2301); **h**. palatine tritor of *C. newtoni* Ward, 1973 (holotype BMNH P.55313); **j**. palatine tritor of *C. callorhynchus* (Linnaeus, 1758), redrawn from di Giácomo and Perier (1996); k. palatine tritor of *C. milii* Bory de St. Vicent, 1823 (BMNH uncat., fig. 4A of Patterson 1992); **l**. palatine tritor of *C. milii* Bory de St. Vicent, 1823 (BMNH uncat., fig. 3A of Patterson 1992); **m**. mandibular tritor of *C. milii* Bory de St. Vicent, 1823 (BMNH uncat., fig. 4C of Patterson 1992); **n**. mandibular tritor of *C. milii* Bory de St. Vicent, 1823 (BMNH uncat., fig. 3C of Patterson 1992). Scale bar 0.5 cm.

tritor and its relationship to the symphysial tritors is regarded here as as an important character. In *C. regulbiensis*, the inner tritors are close to the m.t. The form of the middle mandibular tritor of *C. crassus*, as far as it is discernible, possesses a rather broad and stout anterior prong that is almost as wide as the posterior portion (Fig. 8f). *C. hectori* differs in the comparable more elongated labial prong in the palatine

tooth plate (Fig. 8g). The angle between both palatine tooth plate tritor prongs of *C. newtoni* is shallow and broadly convex whereas it is more deep and V-shaped in *C. stahli* sp. n. (Fig. 8h). The palatine tritors of the extant species *C. callorhynchus* and *C. milii* also differ in the form of the notch between both prongs and in the morphology of the labial prong (Figs 8j–l). The middle mandibular tritor of *C. milii* shows some variability (Figs 8m–n) but can be distinguished in the general form especially the lingual and symphysial margins. The angles between both palatine tritor prongs are: *C. newtoni* (BMNH P.55313): 52°; *C. hectori* (BMNH P.2301): 11°; *C. regulbiensis* (BMNH P.44039): 65°; *C. regulbiensis* (BMNH P.44037): 50°; *C. regulbiensis* (BMNH P.55315): 48°; *C. milii* (BMNH uncat.): 8° and 25°, *C. callorhynchus* (BMNH uncat.): 26°; *C. stahli* sp. n.: 50°. Although this represents no definite distinguishing character it may help forming a statistic basis for further studies. It is possible to subdivide *Callorhinchus* spp. into two distinct groups according to these data. The first group is characterized by angles less than 30° and includes the extant forms investigated for this study and *C. hectori*. The second group has rather large angles (>40°) and only contains fossil taxa.

Occurrence. — Seymour Island, La Meseta Formation (Eocene), ZPAL 8, Telm2.

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Genus and species indet.
(Fig. 9)

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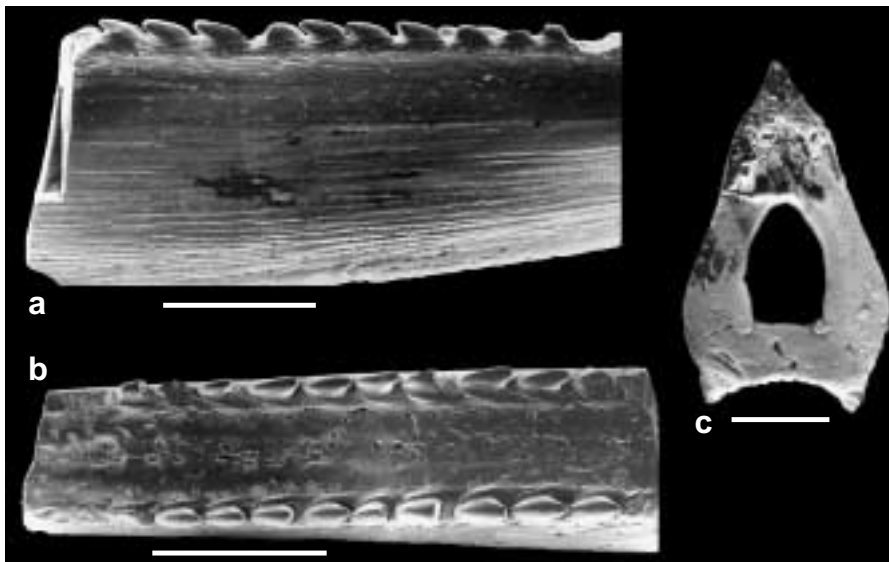**Material**. — An incomplete dorsal fin spine: ZPAL P.9/4.

Fig. 9. Fin spine fragment of Callorhynchidae indet., specimen ZPAL P.9/4. **a**. lateral view; **b**. posterior (distal) view; **c**. cross section. Scale bars 0.5 cm.

Remarks. — The fin spine fragment is characterised by a distinctive anterior ridge and convex lateral faces (Figs 9a–b). The posterior face is slightly concave and bears two rows of basally directed and pointed tubercles (Fig. 9c). This specimen differs from fin spines of *Chimaera* by the presence of a single anterior ridge and a sub-triangular cross-section. Fin spines of *Ischyodus* are sub-oval with more or less straight lateral faces in cross-section. For description and figures of fin spines of *Chimaera* and *Ischyodus* compare also Patterson (1965). The fin spine from Seymour Island resembles most closely fin spines of extant *Callorhinchus* sp. The dorsal fin spine from Telm5 figured by Grande and Eastman (1986) was attributed to *Ischyodus dolloi* by Ward and Grande (1991).

Occurrence. — Seymour Island, La Meseta Formation (Eocene), ZPAL 12, Telm1.

Palaeogeographic and palaeoecological implications

The evolutionary history of *Callorhinchus*, based on dentitional remains, encompasses a period of about 113 million years. Egg cases ascribed to *Callorhinchus* have been reported from the Middle Jurassic of southern Germany (Jaekel 1901) and the Late Cretaceous of North America and Russia (Stahl 1999). Averianov (1997) indicated remains of *Callorhinchus* in the Jurassic of England and Russia based on papers by Averianov (1992), Ward and McNamara (1977), and Woodward (1892). Nevertheless, the latter two authors did not indicate any Jurassic finds of this genus. The oldest indubitable tooth plate remains are from the Albian (Early Cretaceous) of Russia (Nessov and Averianov 1996). Late Cretaceous remains are more abundant and occur on both Southern and Northern Hemisphere. *C. hectori* was initially described based on a single specimen from the Cenomanian of Amuri Bluff, New Zealand by Newton (1876). McKee (in Stahl 1999) indicates additional finds of this species. Nessov and Averianov (1996) referred to *Callorhinchus* tooth plates in the Cenomanian of Russia and Averianov (1997) reported on a small vomerine tooth plate attributable to *Callorhinchus* from the upper Santonian of Russia. Cenozoic species are also known in both Northern and Southern Hemispheres. *C. newtoni* Ward, 1973 occurs in the Thanetian (Palaeocene) and *C. regulbiensis* Gurr, 1963 (for 1962) in the Ypresian (Eocene) of SE England. Woodward and White (1930) identified rather large mandibular and palatine tooth plates from the Miocene of southern Patagonia as *C. crassus*. Dentitional remains of *Callorhinchus* also occur in the Pliocene (early Piacenzian) of New Zealand (McKee in Stahl 1999) and as *C.* cf. *callorhynchus* in the Pliocene Piso Formation of Peru, Sacao area (Cappetta in de Muizon 1981, de Muizon and de Vries 1985).

The three extant elephant fish species are restricted to the Southern Hemisphere. *C. callorhynchus* (Linnaeus, 1758) displays a rather wide distribution along the western and eastern South American coastlines (di Giácomo and Perier
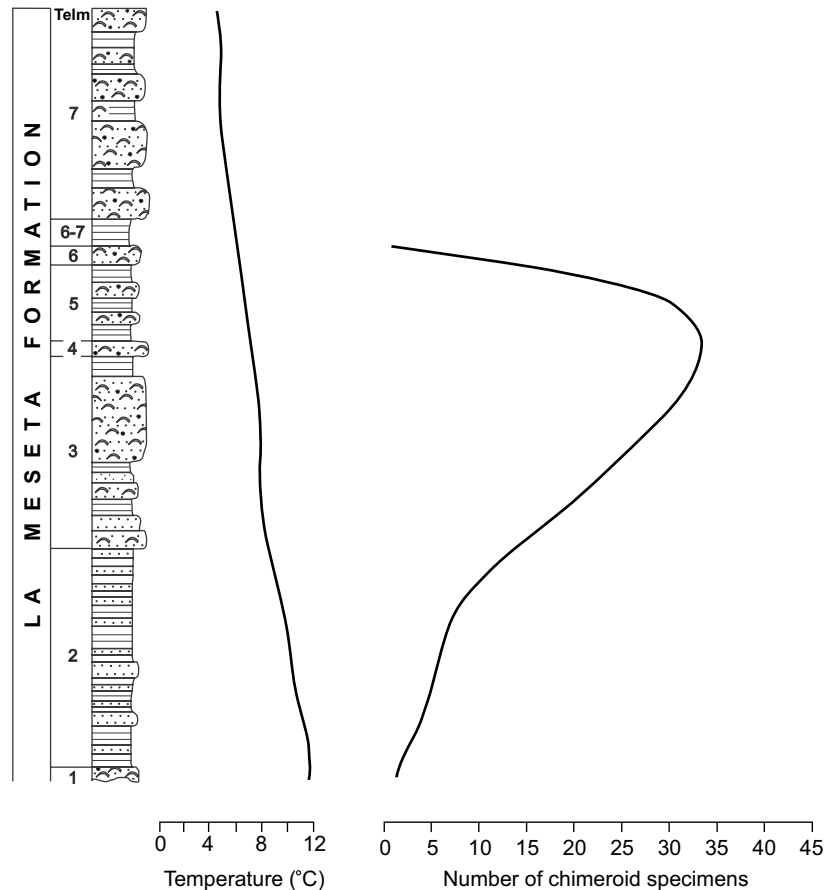
Fig. 10. Correlation between water temperature and chimeroid abundance for the interval during which the La Meseta Formation was deposited. Temperature curve for the interval based on Zachos *et al*. (2001, fig. 2). Data points of the temperature curve of Zachos *et al.* (2001) are omitted for clarity purposes. The occurrences of chimeroid remains are presented as interpolated and smoothed curve, because it is not always possible to correlate findings to exact horizons.

1996, López *et al.* 2000). *C. capensis* Duméril, 1865 occurs in shallow waters on the upper slopes off South Africa and *C. milii* Bory de Saint Vincent, 1823 is found along the coastlines of New Zealand (di Giácomo and Perier 1996).

The new record of *Callorhinchus* from the Eocene La Meseta Formation of Antarctica fills the gap between the Late Cretaceous and Neogene occurrences in the Southern Hemisphere. *Callorhinchus* displays a bipolar distribution in the Late Cretaceous up to the early Eocene (Fig. 11). The distributional pattern changes dramatically in the upper Palaeogene or lower Neogene when *Callorhinchus* becomes extinct in the Northern Hemisphere.

Other chimeroids from the La Meseta Formation of Seymour Island are *Ischyodus dolloi* Leriche, 1902, that also occurs in the Late Cretaceous López de
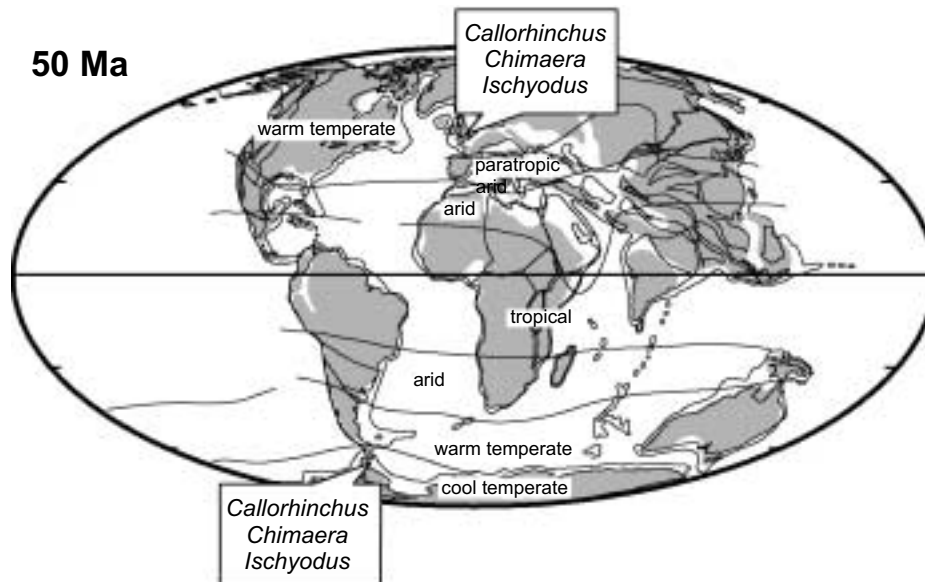
Fig. 11. Distribution of *Chimaera–Callorhinchus–Ischyodus* associations during the Eocene displaying the bipolar occurrences in warm and cool temperate latitudes. Base map modified from Scotese (2001).

Bertodano Formation (Stahl and Chatterjee 2002), and *Chimaera seymourensis* Ward and Grande, 1991. Both occur together with *Callorhinchus* in the lowermost part of the La Meseta Formation, which is Late Ypresian in age (Cocozza and Clarke 1992). This con-generic pattern is also found in the Ypresian but not in the Thanetian of SE England (Ward 1973, Stahl 1999). Ward and Grande (1991) assign seven dentitional and a possible fin spine to *Ischyodus dolloi* and a single tooth plate to *Chimaera seymourensis* from the Eocene of Antarctica. Additional material of chimeroids in the BMNH, London (M. Richter and J.J. Hooker collections) reveals interesting distributional patterns of the chimeroids within the La Meseta Formation. In the lower parts (Telms1–2), all three taxa occur together. However, they appear to be rare faunal elements during this depositional cycle. *Chimaera seymourensis* and *C. stahli* sp. n. vanish at the end of Telm 2 with *Ischyodus dolloi* being the only remaining chimeroid. This taxon becomes very abundant in Telm3 to 5 with its greatest diversity in Telm4. The abrupt increase in diversity of *Ischyodus* and the instantaneous disappearance of *Chimaera* and *Callorhinchus* as well as the absence of chimeroid remains in Telm7 is remarkable. The reasons for this may be climatic changes, habitat transformations, and the specific life-styles (see Myrcha *et al*. 2002).

Southern Hemisphere specimens of *Ischyodus* are *I. thurmanni* Pictet and Campiche, 1885 and *I. brevirostris* Egerton, 1843 from the Albian of New Zealand (Stahl 1999), unspecified taxa from the Maastrichtian of New Zealand (Stahl 1999), *I.* cf. *dolloi* Leriche, 1902 from the Miocene of Victoria (Kemp 1991), and

I. mortoni from the Miocene of Tasmania (Kemp 1991). *Chimaera* species known outside Antarctica are *C.* sp. from the Maastrichtian of Chile (Suarez 2001) and *C. anomala* Woodward and White, 1930 from the Miocene of Victoria.

Extant elephant fishes (*Callorhinchus* spp.) are typical benthic foragers and show the shallowest marine/estuarine to littoral distribution of all holocephalians (López *et al.* 2000). They are often caught in very shallow water areas that represent nursery grounds and even enter rivers in large numbers (Bigelow and Schroeder 1953). The vertical distribution is generally from less than 20 m to about 130 m (di Giácomo and Perier 1996, López *et al.* 2000). *Callorhinchus* is thus a typical representative of the inner shelf mixed fish faunas of cool-temperate and subpolar latitudes in the Southern Hemisphere today preferring temperatures ranging from 5 to 10° C at depth of 22 to 115 m (López *et al.* 2000). Although elephant fishes display a rather wide habitat distribution, nursering areas are located within calm and protected areas.

The La Meseta Formation is generally interpreted as a coastal, shallow marine-estuarine environment (*e.g.* Sadler 1988, Stilwell and Zinsmeister 1992; Porębski 1995, 2000; Baumiller and Gaździcki 1996, Bitner 1996a, Hara 2001). Deposition took place between Upper Ypresian and 34.2 Ma (Priabonian) based on Sr isotopic data (Dingle and Lavelle 1998, see also Dutton *et al.* 2002). The lowermost part, Telm1, is interpreted as a local transgressive event (Sadler 1988, Stilwell and Zinsmeister 1992). Deposition of Telm2 occurred in low-energy and/or protected environments while Telm3 and 4 represent high-energy settings with dominance of venerid bivalves in Telm3 (Sadler 1988). Telm5 to 7 again correspond to shallow-marine, coastal environments (Stilwell and Zinsmeister 1992, Myrcha *et al.* 2001).

The selachian fauna of the La Meseta Fm. is dominated by odontaspidids (e.g., *Carcharias*, *Palaeohypotodus*, *Striatolamia*). Extant odontaspidids occur from inshore, continental and insular waters, to deep-water habitats down to about 1600 m (Compagno 1984). Based on odontaspidid and squalid occurrences, Long (1992) suggested a structured habitat consisting of local deep-water basins. Squalids are typical deep-water sharks nowadays. But there are indications that squalids also lived in shallow marine areas in the past. The overwhelming dominance of squalids in Cenomanian shallow water basins of northern Germany and Albian of NE England supports this interpretation (JK *personal commun.*, C. Underwood *personal commun.*). The mixed assemblages of shallow- and deep-water brachiopods of the La Meseta Formation can also be explained by the structured environment (Bitner 1996b).

The composition of the marine invertebrate fauna of the La Meseta Formation implies palaeotemperatures from about 9 to 20° C (*e.g.* Woodburne and Zinsmeister 1984, Stilwell and Zinsmeister 1992, Bitner 1996a, Dutton *et al.* 2002). The climate during deposition of Telm1 to 2 is regarded as very warm, wet, and non-seasonal, and it is through to have persisted until the middle Eocene (Dingle

et al. 1998, Myrcha *et al.* 2002). The climate changed to strongly seasonal and temperate during Telm3 to 5. A considerable, gradual cooling towards the top of the La Meseta Formation is supported by the structure of the benthic fauna, sedimentological data, and oxygen isotope data (*e.g.* Gaździcki *et al.* 1992, Stilwell and Zinsmeister 1992, Dingle *et al.* 1998, Aronson and Blake 2001, Myrcha *et al.* 2002, Dutton *et al.* 2002). This local cooling correlates with the Eocene/Oligocene boundary-cooling event in the Southern Ocean (Zachos *et al.* 2001).

The presence of a partially relict cool-water Palaeocene selachian fauna, including *Palaeohypotodus rutoti*, in the upper parts of the La Meseta Fm. is in good agreement with the assumed temperature decline (D. J. Ward *personal commun.* 2002).

Results from oxygen isotopic studies of bottom-dwelling, deep-sea foraminifers reflecting past deep-sea and high-latitude sea-surface temperatures, as well as continental ice volume presented by Zachos *et al.* (2001), correspond well with the La Meseta setting. The temperature curve of Zachos *et al.* (2001) shows a continuous decrease in temperature for the Eocene until a steep temperature decline at the Eocene–Oligocene boundary (Fig. 10). The La Meseta deposits indeed herald the final stage of the Gondwana break-up and the onset of the late Eocene glaciation with ice-shield formation on the Antarctic Peninsula 4 million years later (Dingle and Lavelle 2000, Dzik and Gaździcki 2001). The glaciation event certainly reduced the shallow, near coastal habitats dramatically.

The plotting of chimeroid specimen occurrences against the temperature curve reveals an apparent correlation between temperature decrease and a continuous increase of chimeroid diversity at least for Telm1 to 5 (Fig. 10). Although this abundance curve represents only a qualitative interpretation based on rather limited data sets and sample horizons, some of which are not even precisely identifiable, this graph might give some insight into Antarctic chimeroid diversity in the Antarctic.

The decrease of chimeroids in Telm6 and their complete absence in Telm7 is probably related to habitat structure and availability for selachians. The end of the Eocene is marked by a significant sea-level fall at the Priabonian–Rupelian boundary. The only fish remains recovered in Telm7 so far belong to teleosts (Jerzmańska 1988, Jerzmańska and Świdnicki 1992). Additionally, whale and penguine remains are locally abundant, while selachian remains are lacking (Myrcha *et al.* 2002).

The diversity of chimeroids in the low-energy and/or protected environments during warm, wet, and seasonal climatic conditions (Telm2) is well balanced with three specimens of *Chimaera seymourensis*, three specimens of *Callorhinchus stahli* sp. n. and two of *Ischyodus dolloi*. The end of Telm2 witnesses a local extinction (as defined by Dulvy and Reynolds 2002) of *Chimaera* and *Callorhinchus*. The possible disappearance of food competitors and changes in physical parameters of the depositional area probably permitted *Ischyodus dolloi* to migrate in larger numbers into the depositional area. *Ischyodus dolloi* became abundant during the establishment of high-energy environments and strongly seasonal and temperate climatic conditions. The dominance of venerid bivalves and other

molluscs could have been a major factor supporting the rapid spread of *Ischyodus*. Neither *Chimaera* nor *Callorhinchus* seem to subsequently have re-entered the depositional area of the La Meseta Formation. A similar chimeroid assemblage as that of the La Meseta Formation, consisting of *Callorhinchus*, *Chimaera*, and *Ischyodus* occurs in warm temperate latitudes in the Ypresian of southern England (Fig. 11).

Conclusions

Additional findings of *Callorhinchus stahli* sp. n. from the Eocene of Antarctica are required to provide supplementary informations on the variation of mandibular tooth plate morphology and to establish a detailed account of palatine tooth plates. Nevertheless, the specimens display sufficiently different characters to distinguish them from all known species of *Callorhinchus* and to found a new species.

The discovery of *Callorhinchus* and other chimeroid remains has significantly increased the knowledge of Southern Hemisphere chimeroid distribution and allows the discussion of their palaeobiogeographic and palaeoclimatological patterns. In sum, it appears that the observed differences in distribution and diversity of Eocene Antarctic chimeroids are related to palaeoenvironmental conditions. Habitat structure and availability and environmental factors influenced the diversity and vanishing of Cenozoic chimeroids in subpolar areas. Species size and diet emerge as less important. An important factor was the onset of the Antarctic glaciation in the Late Eocene (*e.g.* Barrett 1996) and sea-level fall at the Eocene–Oligocene boundary. Remarkably, the selachian fauna shows its greatest diversity in Telm5 (JK *unpubl. data*). In Telm6 a steep decline in diversity is apparent and no chondrichthyan remains have been recorded from Telm7 so far.

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