Maastrichtian plesiosaurs from northern Patagonia

Zulma Gasparini[a]*, Leonardo Salgado[b], Silvio Casadío[c]

[a] *Dpto. Paleontología de Vertebrados, Museo de La Plata, Universidad Nacional de La Plata, Paseo del Bosque s/n, 1900 La Plata, Buenos Aires, Argentina*
[b] *Museo de Geología y Paleontología, Universidad Nacional del Comahue, Buenos Aires 1400, 8300 Neuquén, Argentina*
[c] *Universidad Nacional de La Pampa, Uruguay 151, 6300 Santa Rosa, La Pampa, Argentina*

Abstract

Three relatively complete elasmosaurid plesiosaurs were recently recovered from the north of Patagonia, Argentina. They were found in the uppermost levels of the Jagüel Formation (upper Maastrichtian). One of the specimens was found only 0.3 m below the Cretaceous/Paleogene boundary, this being the youngest record of a Mesozoic reptile in Patagonia. Two specimens are referred to cf. *Mauisaurus* sp. and the other to *Tuarangisaurus*? *cabazai* sp. nov. This study has revealed that some character states, previously regarded as mere ontogenetic variations, could be taxonomically valid. Comparison of the Upper Cretaceous elasmosaurids of Patagonia with those from the Upper Cretaceous of central Chile, the northeastern islands of the Antarctic Peninsula, and New Zealand reinforce the hypothesis of a south Gondwanan distribution for some pelagic reptiles.
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1. Introduction

The first remains of Cretaceous plesiosaurs from South America were found in Chile, in the lower Maastrichtian of the Quiriquina Formation (Stinnesbeck, 1986). Gay (1848) referred them to his species *Plesiosaurus chilensis*. Almost one century later, Cabrera (1941) described *Aristonectes parvidens* (upper Maastrichtian of Chubut Province, Argentina), the first plesiosaur from the Argentinian Patagonia, and tentatively related it to the Elasmosauridae. Bardet et al. (1991) and Gasparini et al. (in press) confirmed this familial assignment. Both this record and studies of Cretaceous plesiosaurs from Patagonia were scorce up to the end of the twentieth century. Casamiquela (1969, 1980) reported plesiosaurs from southern Río Negro Province. Gasparini & Goñi (1985) described remains of

a plesiosaur from the area around Lago Pellegrini (northwestern Río Negro Province), which they referred to *Trinacomerum lafqueniaum*. This specimen, and others found later in Campanian–Maastrichtian levels of the Allen Formation, Río Negro Province, were studied again by Gasparini & Salgado (2000) and reinterpreted to belong to an indeterminate species of Elasmosauridae, probably close to *Elasmosaurus platyurus* Cope, 1868. A polycotilid, *Sulcusuchus erraini* Gasparini & Spalletti, 1990, from the upper Campanian–lower Maastrichtian and the lower–middle Maastrichtian of Chubut Province (Gasparini & de la Fuente, 2000; Gasparini et al., 2001), and isolated remains of elasmosaurids from the provinces of Mendoza, Río Negro and Chubut, complete the record of Patagonian plesiosaurs from the end of the Mesozoic (González Riga, 1999; Gasparini et al., 2001). This synthesis shows that, except for *Aristonectes parvidens*, most Patagonian plesiosaurs have been recovered from the Campanian–middle Maastrichtian interval.

Between 1998 and 2001 Mr Héctor Cabaza and collaborators from the Museum and the Municipality of Lamarque, discovered the remains of three mosasaur

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* Corresponding author: Dr Z. Gasparini, Dpto. Paleontología Vertebrados, Paseo del Bosque s/n, La Plata 1900, Argentina. Tel.; +54-2214234921; fax: +54-2214257527
E-mail addresses: zgaspari@museo.fcnym.unlp.edu.ar (Z. Gasparini), lsalgado@uncoma.edu.ar (L. Salgado), sacasadio@hotmail.com (S. Casadío).
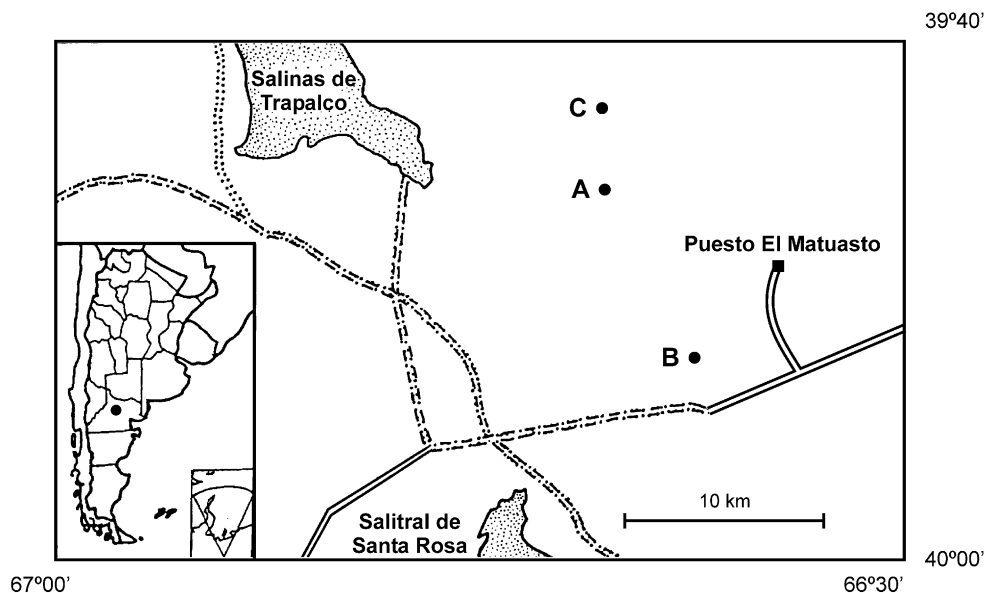
Fig. 1. Map of the study area, centre of Río Negro Province, Argentina. A–C, paleontological localities.

lizards and three long-necked plesiosaurs. These reptiles were found in the central area of Río Negro Province (Fig. 1), in the uppermost levels of the Jagüel Formation (upper Maastrichtian) (Fig. 2). One of the plesiosaurs (MML-PV4) was found 0.3 m below the Cretaceous/Paleogene boundary (Gasparini et al., 2002), this being the youngest record of a Mesozoic reptile in Patagonia.

The systematics of Upper Cretaceous plesiosaurs is not yet clear because, although they are one of the first known tetrapod clades (Williston, 1903; Bakker, 1993), studies based on complete specimens are comparatively few (Welles, 1943). Several studies based on skulls have recently been undertaken, resulting in a greater consensus concerning systematic hypotheses (Carpenter, 1996, 1997, 1999; Storrs, 1999; Druckenmiller, 2002; Gasparini et al. (in press)). However, when only the postcranium is available, as in the specimens described here, identification is not simple, since the postcranial anatomy is relatively conservative and some differences have been interpreted as ontogenetic variation (Adams, 1997; Storrs, 1999).

The three new specimens of elasmosaurid plesiosaurs from northern Patagonia permitted an analysis of characters previously considered to be exclusively ontogenetic variation, conditioning taxonomic determinations. The comparison of the new specimens with those, generally more incomplete, from the Upper Cretaceous of Patagonia, central–western Chile, the northeastern islands of the Antarctic Peninsula, and New Zealand, reinforces the hypothesis of a clear south Gondwanan distribution of some pelagic reptiles (Novas et al., 2002). Likewise, an analysis of the fossil-bearing rocks and the biota related to the carcasses of the new elasmosaurids from Río Negro, throw light upon the environmental conditions of northern Patagonia, just before the end of the Cretaceous Period.

Abbreviations. NZGS, CD, New Zealand Geological Survey, Fossil Chordata Collection; MCS, Museo de Cinco Saltos, Río Negro, Argentina; MLP, Museo de La Plata, Argentina; MML, Museo Municipal de Lamarque, Río Negro, Argentina; MUCPv, Museo de la Universidad Nacional del Comahue, Neuquén, Argentina, collection of paleovertebrates; TTU-P, Museum of Texas Tech University, Lubbock, Texas.

2. Geological setting

One of the most significant geodynamic events that took place in southern South America between the Campanian and the Danian was the relative sea-level change related to the subsidence of the Atlantic margin, accounting for important flooding. This subsidence was caused by lithospheric cooling and sediment loading (Uliana & Biddle, 1988) which, in northern Patagonia, was coeval with the development of a foreland basin in the east of the Andes (Tunik, 2001). During the Cretaceous/Paleogene transition, the southern tip of South America was reduced to an archipelago in which the central part of the Somuncurá and Deseado massifs remained emergent (Yrigoyen, 1969; Riccardi, 1988; Uliana & Biddle, 1988; Urien et al., 1995; Malumián, 1999). Malumián & Caramés (1995) calculated the minimum area of the presently emerged Patagonia that was covered by the sea during the early Danian to be 507,000 km^2. This wide, flooded surface was important from a palaeogeographic standpoint, and it certainly played a primary role in the climatic and
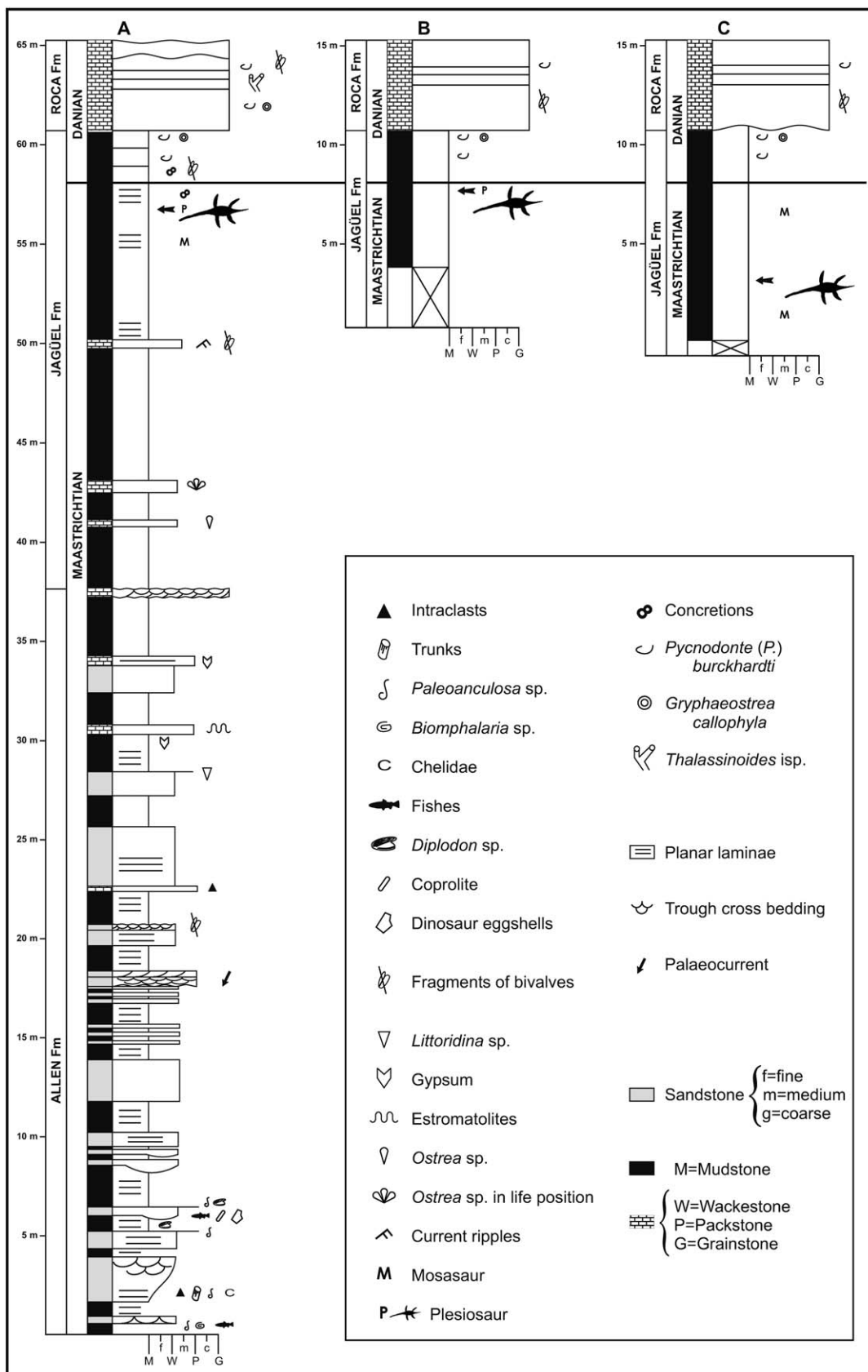
Fig. 2. Correlation of measured stratigraphic sections.

evolutionary events recorded in Patagonia and the Antarctic Peninsula.

The transgression is recorded in the sedimentary rocks of the Malargüe Group in the Neuquén Basin, northwestern Patagonia; it is widely exposed in southern Mendoza, northeastern Neuquén, western La Pampa and the northern Río Negro provinces. These rocks have been studied by several authors since the nineteenth century (see Camacho, 1992). In recent years, interest in them has increased because they include the Cretaceous/Paleogene boundary in both marine and continental facies (Parras & Casadío, 1999). These rocks record excellent examples of Upper Cretaceous ecosystems in middle latitudes of the Southern Hemisphere.

North of the Neuquén Basin, the Malargüe Group crops out widely along the foothills of the Andes (Dessanti, 1973, 1975; González Díaz, 1975; Holmberg, 1975; Ramos, 1981), and is more than 400 m thick. It is composed, from base to top, of the Loncoche, Jagüel, Roca, and Pircala formations. In the southeastern area, this Group is less than 200 m thick, and comprises the Allen, Jagüel, Roca, and Carrizo formations.

Uliana & Dellape (1981) inferred a littoral to restricted marine environment for the Allen Formation. Barrio (1991) pointed out that, while in the eastern sector of the basin the facies association represents intertidal environments, in the western sector its features are those of a tide-dominated estuary. This difference was attributed to different tidal rates, directly related to the geometry of the basin. The equivalent unit in the Andean area is the Loncoche Formation. The Allen Formation and its equivalents are covered by marine rocks of the Jagüel Formation, mainly shales, as well as by its correlatives, the Coli Toro, Aguada Cecilio, and Malargüe formations, all Maastrichtian in age (Casadío, 1994).

The Jagüel Formation is transitionally overlain by mainly carbonate and regressive levels of the Roca Formation, assigned to the Maastrichtian–Danian on the basis of its fossil content (Casadío et al., 1998). The evaporitic deposits of the Carrizo Formation overlie the Roca Formation in the area. In the Andean region, the Roca Formation continues transitionally into the continental sandstones of the Pircala Formation (Parras et al., 1998).

Differences in depositional environments between the Andean and eastern areas lie mainly in the predominance of continental and deltaic facies, as well as in the abundant pyroclastic material of the Andean area. This suggests the vicinity of an emergent and volcanically active zone (Digregorio, 1978; Parras et al., 1998; Parras & Casadío, 1999). In addition, the eastern area comprises mostly marine deposits, mainly shales, limestones, and evaporites, suggesting a distal position with respect to the supply area, and a proximal oceanic relationship.

The elasmosaurids reported in this paper were found at three localities in the depressions of Trapalcó and Santa Rosa, central Río Negro Province, on the southern margin of the Neuquén Basin (Fig. 1). The plesiosaur MML-PV3 was found at locality A (39°46′20″S, 66°40′42″W), and MML-PV4 at locality B (39°51′37″S, 66°37′22″W); both are referred to cf. *Mauisaurus* sp. Specimen MML-PV5, referred to *Tuarangisaurus?* *cabazai* sp. nov., was found at locality C (39°50′45″S, 66°40′40″W).

The fossils were exhumed from mudstones assigned to the Jagüel Formation, which in the localities studied transitionally overlies the lacustrine deposits of the Allen Formation, and transitionally underlies the limestones of the Roca Formation (Concheyro et al., 2002; Gasparini et al., 2002). In the area of Trapalcó and Santa Rosa, the Jagüel Formation is composed of olive green mudstones, laminated in some sections (Fig. 2). It contains scarce Maastrichtian marine bivalves, such as *Ambigostrea clarae* (Ihering von, 1907) and '*Pecten*' *mahuidaensis* (Weaver, 1931). This unit also bears a very rich association of calcareous nannofossils from Zone CC26, late Maastrichtian, the most conspicuous of which are *Arkhangelskiella cymbiformis, Biscutum melaniae, Cribrosphaerella daniae, Lithraphidites quadratus, Nephrolithus frequens* and *Prediscosphaera stoveri* (Concheyro et al., 2002).

The top of the Jagüel Formation lies at the base of the first level of coquina formed by *Pycnodonte* (*Phygraea*) *burckhardti* (Böhm, 1903) and *Gryphaeostrea callophyla* (Ihering von, 1903). In this area, the Cretaceous/Paleogene boundary is in the Jagüel Formation (Fig. 2).

Concheyro et al. (2002) pointed out that in the lower section of the Jagüel Formation at locality A, an inner-platform foraminiferal association underlies another association, probably of middle-platform origin, suggesting a transgressive pulse during the late Maastrichtian. This has also been observed at other localities in northern Patagonia (Casadío, 1994; Parras et al., 1998; Parras & Casadío, 1999).

The plesiosaur MML-PV3 was found 1.5 m below the Cretaceous/Paleogene boundary, MML-PV4, 0.3 m and MML PV5, 5 m below this boundary. The level in which MML-PV5 was found is enclosed within 'intervalo A' of Concheyro et al. (2002). These authors proposed a shallow inner-platform environment for this interval because of the occurrence of a high percentage of agglutinated foraminifers and the absence of planktonic foraminifers. A continuous bed 0.2 m thick composed of medium-grained bioclastic limestone with hummocky cross stratification is recognized at this level of the section over the entire area. This bed lies 3 m below the level with specimen MML-PV5.

MML-PV3, collected at locality A, was preserved at the base of the 'Intervalo B' of Concheyro et al. (2002). These authors recognized an increase in diversity of

planktonic foraminifers as well as an increase in the planktonic/benthic ratio that, together with the size of the planktonic foraminifers, suggest a deepening with respect to the previous level to a middle platform level. These conditions are similar to those at the level from which specimen MML-PV4 was collected at locality B. In all of these cases, the absence of invertebrates is puzzling. Only a few specimens of bivalves assigned to 'Pecten' mahuidaensis and Ambigostrea clarae were collected. Very few levels show lamination, which may be owning to a low gradient of water temperature rather than to the activity of benthic organisms.

The three plesiosaurs are relatively complete. MML-PV3 includes a mandibular fragment and a large number of associated gastroliths, suggesting that the animal was still complete when it reached the bottom. MML-PV4 is a trunk fragment with an articulated paddle. The skull and neck of MML-PV5 were not preserved, but the rest of the body was articulated.

3. Systematic Paleontology

3.1. Taxon 1

Plesiosauria de Blainville, 1835
Plesiosauroidea (Gray, 1925) Welles 1943
Elasmosauridae Cope, 1869
Mauisaurus Hector, 1874

cf. Mauisarus sp.
Figs. 3 and 4

Material. Remains of two incomplete specimens. MML-PV3 (Fig. 3A–C, Fig. 4B): right mandibular fragment, prefrontal, four incomplete cervical vertebrae (one anterior, one medial and two posterior), two incomplete dorsal, one sacral and four caudal vertebrae; right femur, ten phalanges of a single (?) paddle, one indeterminate tarsal, rib fragments, several gastroliths. MML-PV4 (Fig. 3D–G, Fig. 4A, G): one incomplete cervical vertebra, 13 incomplete dorsals, three sacrals, 24 caudals, two ilia and the left anterior paddle (humerus, radius, ulna, proximal and distal carpals and phalanges).

Locality and horizon. MML-PV 3, Locality A (39°46′20″, 66°40′42″); MML-PV 4, Locality B (39°51′37″, 66°37′22″) (Fig. 1). Upper part of the Jagüel Formation (upper Maastrichtian) (Fig. 2).

Description
As MML-PV3 and MML-PV4 are considered to be a single taxon, the following description encompasses both specimens.
Mandible (Fig. 3C). Right mandibular fragment, 60 mm long, with three incomplete alveoli for functional teeth and two complete alveoli for replacement teeth. As in all plesiosaurs, the alveoli for replacement teeth are located posteromedial to the alveoli for functional teeth (Edmund, 1960). The external alveoli for functional
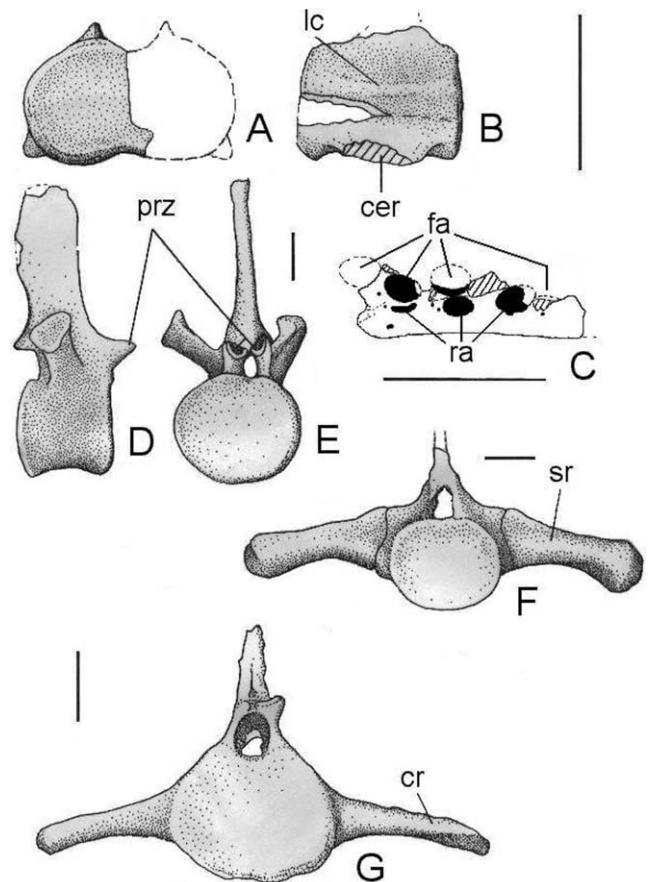

Fig. 3. cf. *Mauisaurus* sp. A–C, MML-PV3 and D–G, MML-PV4. Anterior cervical vertebra in anterior (A) and right lateral (B) views. C, right mandibular fragment in dorsal view. Posterior dorsal vertebra in right lateral (C) and anterior (D) views. E, sacral vertebra in anterior view. F, caudal vertebra in anterior view. cer, base the cervical rib; cr, caudal rib; fa, alveoli for functional teeth; lc, lateral crest; prz, prezygapophysis; ra, alveoli for replacement teeth; sr, sacral rib. Scale bars represent 50 mm.

teeth are very close to each other and the antero-posterior diameter is approximately 10 mm. No teeth have been found *in situ* or isolated.
Cervical vertebrae (Fig. 3A, B). The body of the anterior cervical of MML-PV3 is wider (56 mm) than long (47 mm), and longer than high (33 mm). There are two foramina in ventral view on both sides of the longitudinal keel. The measurements of the most complete posterior cervical vertebra of MML-PV3 are similar to those the anterior cervical (width, 112 mm; length, 87 mm; height, 68 mm). It is kidney-shaped in anterior view, with the ventral notch characteristic of elasmosaurids. The lateral horizontal crest that characterizes the elasmosaurids is observed (Fig. 3B), but it is only slightly developed, as in usual is the posterior cervicals (Bardet & Godefroit, 1995). MML-PV4 has half a centrum, which is very deteriorated, and probably a middle to posterior cervical. The centrum is longer than high, and a slight horizontal crest crosses the lateral side.
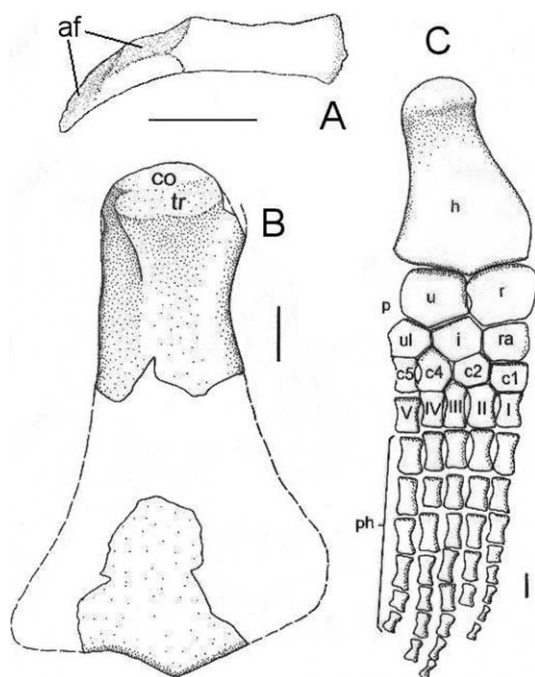
Fig. 4. cf. *Mauisaurus* sp. A, C, B, MML-PV4 and MML-PV3. A, ilium, and B, right femur in dorsal view; C, left anterior paddle in ventral view. c1–c5, distal carpals; af, articular facets; co, condyle; h, humerus; I, intermedium; p, pisciform; ph, phalanges; r, radius; ra, radiale; tr, trochanter; u, ulna; ul, ulnare; I–V, metacarpals. Scale bars represent: 50 mm.

Dorsal vertebrae (Fig. 3D, E). These are best preserved in MML-PV4, which has 13 dorsal vertebrae. The centra are wider than high and than long, the transverse processes are compressed, directed upward and expanded at their distal ends. The prezygapophyses are long, and deeply concave (Fig. 3D, E). The neural spines, complete from the sixth to the ninth, are very high and compressed, and the neural arch (spine included) is twice the height of the vertebral centrum. The dorsals of MML-PV3 and MML-PV4 are identical to those of some undetermined elasmosaurids from the Upper Cretaceous of New Zealand (Wiffen & Moisley, 1986, figs. 51–52).

Sacral vertebrae (Fig. 3F). MML-PV3 has the complete body of a sacral vertebra, without the ribs attached. The body is wider (100 mm) than high (74 mm) and higher than long (65 mm). The facet for the articulation of the rib is oval, occupying almost all of the lateral side of the vertebral body. The ventral side is flat, with two nutrition foramina. MML-PV4 has three sacrals whose centra are similar in morphology and dimensions to those of MML-PV3. The sacral ribs are compressed with a conspicuous posterior depression. Distally there are two faces; the ilium probably articulated with one of them.

Caudal vertebrae (Fig. 3G). MML-PV3 has four centra of caudal vertebrae. These are wider than high

and relatively short. The anterior and posterior facets for the articulation with hemapophyses are well defined. The ventral side of the centrum is flat. MML-PV4 has 18 caudal vertebrae in different degrees of preservation. The caudal ribs are long and compressed. The bases of the ribs are not well developed dorso-ventrally, unlike the sacral ribs. The neural spines are narrower antero-posteriorly than in the dorsals, and they are more backwardly directed.

Paddles (Fig. 4). The left fore paddle of MML-PV4 is almost complete (Fig. 4C). The humerus is short and robust, without a conspicuous neck; the capitulum and tuberosity are scarcely distinguishable because of the poor preservation of this area. The distal part is wide with two articulating surfaces relatively well marked. The humerus lacks the knee or posterior expansion of its distal end, as in most elasmosaurs, except for *Hydralmosaurus* (Carpenter, 1999). The morphology of the humerus is similar to that of *Mauisaurus haasti* Hector 1874 (Welles & Gregg, 1971, fig. 7) from the uppermost Cretaceous of New Zealand.

The radius is approximately rectangular and slightly larger than the ulna; both form the epipodial foramen. The ulna is irregularly hexagonal. The radiale and the ulnare are of similar size. Between them, the intermedium is an irregular hexagon, the longest sides of which articulate proximally with the ulna, and distally with carpals 2 and 4. The contact between the intermedium and the radius is less than with the ulna.

The longest finger of MML-PV4, the fifth, develops on the concave margin of the paddle, being clearly posterior and linked to the ulna. Carpal 1 articulates with metacarpal I and has a facet for metacarpal II. Carpal 2 articulates distally with metacarpal II, and with metacarpal III through a posterodistal facet. Likewise, carpal 4 (third carpal element; see Welles & Bump, 1949, p. 528) articulates proximally with the intermedium and ulnare through a facet, each approximately equal in size.

Phalanges of MML-PV3 and 34 phalanges of MML-PV4 have been preserved. They are flat, spool-shaped, with very expanded ends and relatively flat articular surfaces (Fig. 3C). The expansion of the ends is approximately one and a half times the transverse diameter of the phalange on its middle part. Phalanges of MML-PV3 probably belong to the hind limb, while those of MML-PV4, to the left forelimb. In both cases, the distal phalanges are shorter and more cylindrical than the proximal ones.

MML-PV3 preserves the proximal and distal ends of the right femur (Fig. 3B). A convex condyle and a flat trochanter are located on different planes of the proximal end. An isthmus of periosteal tissue that normally separates both articular surfaces is not yet developed. The areas for the insertion of the retraction muscles of the femur are only just visible on the

posteroventral side of the femur. Unlike the humerus (preserved in MML-PV4), the neck of the femur is well defined, as in *Mauisaurus haasti* (Hector, 1874, pl. 29, fig. a). The articular surfaces for the tibia and fibula are concave and relatively well defined.

As for the metapodials, MML-PV3 preserves the intermedium of the hind limb. It is pentagonal, similar in shape to that of the holotype of *Mauisaurus haasti* (Hector, 1874, pl. 29, fig.a), but different from that of the anterior paddle (preserved in MML-PV 4), which is hexagonal. This difference in the number of sides of the anterior and posterior intermedium has been seen in other elasmosaurids (Welles, 1952, 1962, fig. 15).

Ilium (Fig. 4A). MML-PV4 has both ilia. Each ilium is compressed, and its proximal end contacts the sacrum. It is thin and sharp, with three well-defined sides, while the opposite end, which dorsally closes the acetabulum, is slightly expanded. The morphology and proportions are similar to those of the Patagonian elasmosaur illustrated by Gasparini & Goñi (1985), pl. II, 1.

Discussion

Following Welles (1952), MML-PV3 may be interpreted as an immature individual (Brown, 1981) because of the presence of an isthmus of periosteal bone at the proximal end of the femur. However, this interpretation cannot be accepted because the different elements of the vertebrae are fused. MML-PV3 and MML-PV4 probably represent adult specimens whose estimated body length is between 9 and 11 m. Cervical vertebrae with a horizontal crest on the lateral side of the body suggest their referral to the Elasmosauridae (Brown, 1981).

Humerus proportions, the shape of radius and ulna, and the pentagonal hind limb intermedium match those of *Mauisaurus haasti* (Welles & Gregg, 1971) from the upper Maastrichtian of New Zealand. In *Styxosaurus snowi* (Carpenter, 1999) the posterior intermedium is also pentagonal, but the anterior, though hexagonal as in MML-PV4, has parallel sides, while the hexagon of the Patagonian specimen is irregular (Fig. 4C), as shown in the description above.

Welles & Gregg (1971) referred several New Zealand specimens to *Mauisaurus* on the basis of very incomplete material. Wiffen & Moisley (1986) described and referred materials to *Mauisaurus haasti* based on some diagnostic characters of this species, among them, a central pit on the articular face of the dorsal vertebrae centrum. A similar structure may be observed in specimens from Seymour Island, Antarctic Peninsula, related to *Mauisaurus* (Fostowicz-Frelik & Gazdzicki, 2001). This pit is not found in the Patagonian specimens.

In MML-PV4, the contact between the intermedium and the radius is less than with the ulna, unlike other elasmosaurids such as the Jurassic species *Muraenosaurus beloclis* (Brown, 1981, p. 293), and Cretaceous

forms such as *Styxosaurus snowi* (=*Alzadasaurus pembertoni* Welles, 1962, fig. 15; Welles & Bump, 1949, fig. 5a), *Alzadasaurus colombiensis* (Welles, 1962, fig. 6), *A. riggsi* (Welles, 1962, fig. 10), *Morenosaurus stocki* (Welles, 1962, fig. 22) and *Aristonectes parvidens* (Cabrera, 1941, fig. 6). In this sense the metapodials of MML-PV4 are most similar to those of cf. '*Cimoliosaurus*' *andium* (Broili, 1930, fig. 1). The ulnare has a wide articulation surface for the pisciform, similar in extension to that of cf. '*Cimoliosaurus*' *andium* (Broili, 1930, fig. 1) and *Styxosaurus snowi* (=*Alzadasaurus pembertoni* Welles, 1962, fig. 15). This facet is less well developed in other elasmosaurs (*Aphrosaurus furlongi*, Welles, 1962, fig. 18; *Alzadasaurus riggsi*, Welles, 1962, fig. 10; *Morenosaurus stocki* Welles, 1962, fig. 22) or almost absent (*Aristonectes parvidens*, Cabrera, 1941, fig. 6). Another difference from the Patagonian species is that in *Aristonectes parvidens* the distal facets of the ulnare for carpals 4 and 5 are equal, whereas in MML-PV4 the facet for the carpal 4 is somewhat larger than that for carpal 5.

So far there is no definitive definition of this taxon; consequently MML-PV3 and MML-PV4 are referred to cf. *Mauisaurs* sp. Broili (1930), referred a paddle found in the Quiriquina Formation, (upper Maastrichtian; Stinnesbeck, 1986) of central-southern Chile to cf. '*Cimoliosaurus*' *andium*. From the new evidence reported in this paper the anterior paddle illustrated by Broili (1930), fig. 1) appears to be very similar to that of MML-PV4 and the Central 4 (C3 of Broili) is wrongly orientated. When the location of this element is corrected, both paddles are similar, and consequently the elasmosaurid from Quiriquina is also referred to cf. *Mauisaurus* sp.

Chatterjee & Small (1989) briefly described several remains of the Elasmosauridae from the uppermost section of the López de Bertodano Formation, close to the Cretaceous/Paleogene boundary, on northern Seymour Island (northeastern Antarctic Peninsula). The specimen TTU-P 9217 was identified as a posterior paddle. However, the hexagonal-shaped intermedium suggests that it is an anterior paddle. Likewise, the humerus of this specimen seems longer and more slender because it is reconstructed from two pieces. When these fragments are put together, the humerus is identical in shape and proportions to that of MML-PV4. In addition, MML-PV4 and TTU-P 9217 are similar in other ways, namely in the shape of ulna and radius, the hexagonal intermedium with irregular margins, and the general architecture of the paddle. Because of this, TTU-P 9217 is also referred to cf. *Mauisaurus* sp. Coincidentally, when referring to the dorsal vertebrae of another specimen (TTU-P 9221), Chatterjee & Small (1989) pointed out that they show similar features to those of *Mauisaurus* (Wiffen & Moisley, 1986).
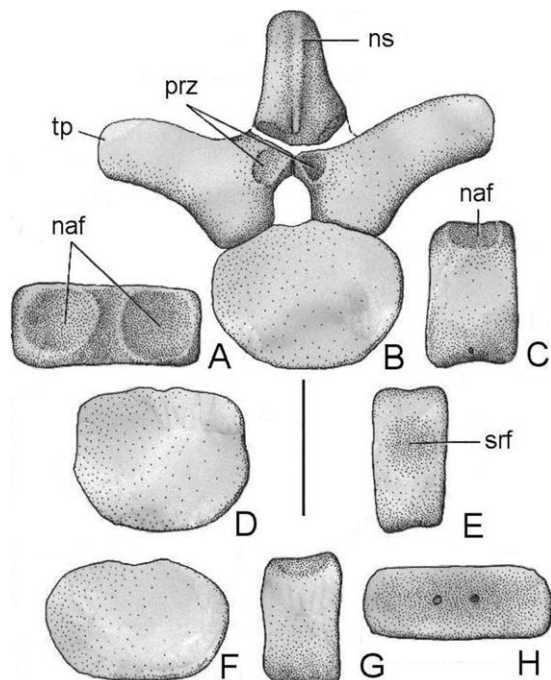
Fig. 5. *Tuarangisaurus*? *cabazai* sp. nov. MML-PV5, holotype, axial skeleton. Dorsal centrum in dorsal (A), anterior, with the articulated neural arch (B) and lateral (C) views; sacral centrum in anterior (D) and lateral (E) views; caudal centrum in anterior (F), lateral (G) and ventral (H) views. naf, facets for the neural arch; ns, neural spine; prz, prezygapophyses; srf, facet for the sacral rib; tp, transverse process. Scale bars represent 50 mm.

Fig. 6. *Tuarangisaurus*? *cabazai* sp. nov. MML-PV5, holotype, appendicular skeleton. Scapula fragment in lateral (A) and proximal (B) views; left coracoid in dorsal (C) and medial (D) views; E, left ilium in dorsal view; F, left pubis in dorsal view; G, left ischium in dorsal view. ac, acetabulum; icv, intercoracoid vacuity; pif, pubo-ischiatic fenestra; scm, area for the subcoracoid muscle. Scale bar represents 50 mm.

3.2. Taxon 2

Tuarangisaurus? Wiffen & Moisley 1986

Tuarangisaurus? cabazai sp. nov.
Figs. 5–7

Derivation of name. The species is dedicated to Mr Héctor Cabaza, who has discovered numerous Cretaceous animals and plants in Rio Negro Province and promoted the foundation of the Museo Municipal de Lamarque.

Holotype. MML-PV5. An incomplete specimen without skull and neck, with 17 dorsal vertebrae, 30 caudals, ribs and gastralia, incomplete anterior and posterior limbs, left coracoid and fragments of the right scapula, complete ischium and pubis.

Locality and horizon. Locality C (39°50′45″S, 66°40′40″W). Upper part of the Jagüel Formation (upper Maastrichtian) (Figs. 1 and 2).

Diagnosis. Elasmosaur with thick postcranial elements and rounded external. Relatively high and short vertebral centra, with low and thick neural spines, and short prezygapophyses. Coracoid with robust posterior process. Ischium short and narrow.
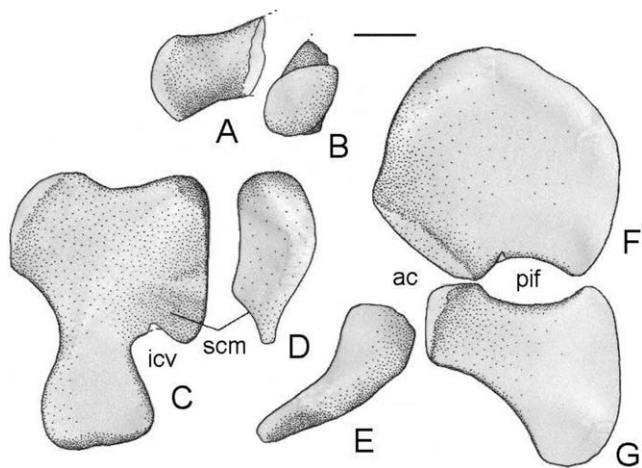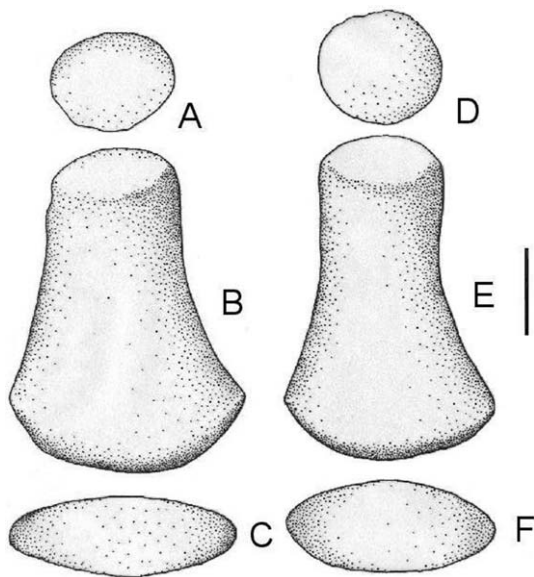

Fig. 7. *Tuarangisaurus*? *cabazai* sp. nov. MML-PV5, holotype, appendicular skeleton. Propodials. Humerus in proximal (A), lateral (B) and distal (C) views; femur in proximal (D), lateral (E) and distal (F) views. Scale bar represents 50 mm.

Description

Dorsal vertebrae (Fig. 5A–C). MML-PV3 has 17 dorsal centra. They are short and wide (length approximately 60% of the height). Measurements of one of the vertebrae (Fig. 5A–C) are: length 31 mm; height 51 mm; width 69 mm. Most vertebrae show a central depression on the anterior and posterior sides of the body. In every dorsal vertebra the neural arch is not fused, suggesting that the specimen may be a subadult (Brown, 1981). The

articulation surface of the neural arch has a central subquadrangular scar that occupies the entire body length. Coincidentally, the articular faces of the neural arch are subquadrate. The neural spines are thick, very low, with the distal end markedly convex (Fig. 5B). The prezygapophyses are extremely short. The transverse processes are very short, subcylindrical, without an expanded distal end.

Sacral vertebrae (Fig. 5D, E). Only one centrum of sacral vertebra has been recovered. It is short, and quadrangular in anterior view. The lateral side of the centrum shows depressions for ribs, which do not occupy the whole length of the body and are higher than long.

Caudal vertebrae (Fig. 5F–H). The 30 caudal vertebrae recovered are also short. There are two foramina on the flat ventral side, and only one on the floor of the neural canal. The facets for the hemapophyses are slightly marked and in some they are not evident.

Pectoral girdle (Fig. 6). The left coracoid is complete, and notably robust (Fig. 6 C, D). The medial lamina, through out the right coracoid contacts, is very thick anteriorly, while it narrows distally or posteriorly. No antero-medial process suggests the existence of a pectoral bar in the coracoid.

The postero-medial margin of the coracoid is little expanded and suggests that the intercoracoid vacuity was wide posteriorly. On the visceral side of the coracoid of MML-PV5 there is a slight prominence dividing two slightly concave surfaces. The smaller posterior one is interpreted as the area for the insertion of the sub-coracoid muscle (Fig. 6C, D). The area of the glenoid cavity of the scapula has been preserved (Fig. 6A, B).

Pelvic girdle (Fig. 6E–G). As for the coracoid, the elements of the pelvic girdle are notably thick. In this sense, they are very different from other Patagonian elasmosaurids (Gasparini & Salgado, 2000). The ischium is short and the pubis is subcircular, with the anterior margin strongly convex. The acetabular articulation is very robust and, unlike in MCS-4, there is no pelvic bar. The pubo-ischiatic fenestra is transversely elongate. The different pelvic bones do not seem to be fused. The pubes are closely comparable to those of NZGS, CD429 (aff. *Tuarangisaurus keyesi*) (Wiffen & Moisley, 1986, fig. 30).

The ilia are short, with very thick acetabular portions, even thicker than in MML-PV4 (Fig. 6E), and MCS-4 and MLP 71-II-13-1 (Gasparini & Goñi, 1985, pl. II, 1). The dorsal end of the ilium is slightly compressed, and the three planes observed in MML-PV4 (referred to cf. *Mauisaurus* sp.), are not evident (Fig. 6E).

Paddles (Fig. 7). The humeri and femora are short and very robust. The humerus is slightly longer (193 mm) than the femur (186 mm). The condyle and the tuberosity are not clearly distinguishable at the proximal end of the humerus. Likewise, the condyle cannot be differentiated from the trochanter in the femur. In both the humerus and the femur the distal sector is very thick and lacks defined articulation faces to contact with the epipodials.

The mesopodials include subcircular and oval elements of the fore and hind paddles (Fig. 7G). These series are incomplete, and the lack of articular faces render it impossible to determine their homology and topological location.

The phalanges are very short, spool like and subcircular in section, and the central area is little compressed, which makes them different from MML-PV3 and MML- PV4 referred to cf. *Mauisaurus* sp. The phalanges of these latter forms are elongate, compressed, and with strangled central and expanded distal areas.

The ribs and gastralia are represented by numerous fragments. They are robust and circular to subcircular in section.

Discussion

Some authors (e.g., Brown, 1981) have stated that certain characters depend on whether or not the specimen is juvenile. Among these are short and flat vertebral bodies, unfused neural arches, short neural spines, absence of a pectoral bar, rounded anterior margin of the pubis, absence or little development of a pelvic bar, tuberosity/trochanter not separated by a condylar isthmus, and poor definition of the articular facets of the propodials and mesopodials. MML-PV5 shows some of these characters, consequently one could presume that several of the characters interpreted as diagnostic of *Tuarangisaurus? cabazai* may be owing to its juvenile condition. However, to determine the juvenile condition of a particular specimen, an ontogenetic series of the species must be known, and in the case of plesiosaurs, immature specimens of known taxa are very scarce (Carpenter, 1999).

Comparison of different developmental stages among taxa may lead to mistakes as these characters do not vary in the same way during the ontogeny of different species. For example, the pectoral bar is absent (or incompletely formed) in juvenile specimens of some plesiosaurs that display it in adult stages (Carpenter, 1999), but most plesiosaurs definitely lack bars. Likewise, juveniles of different taxa vary significantly from each other. For instance, juvenile specimens of *Aphrosaurus furlongi* Welles, which are of similar size to juvenile specimens of *Fresnosaurus drescheri* Welles, 1943, display very different propodials. The first taxon has well-defined articular faces and coracoid with an anterior projection, and a posterior process that is somewhat expanded (Welles, 1952, fig. 23).

In MML-PV5, low neural spines or short vertebral centra are not necessarily a consequence of its juvenile condition. The robustness of the whole postcranium, and the flange on the visceral side of the coracoid for the

insertion of strong subcoracoid muscles suggest that MML-PV5 had passed the juvenile stage and was subadult or a young adult.

It is unlikely that such marked differences as those observed between MML-PV5 and MML-PV3 and MML-PV4, will have decreased during ontogeny. In the same way, the Elasmosauridae found on Seymour Island (Chatterjee & Small, 1989), undoubtedly a juvenile, shows strong differences from MML-PV5, being closer to adult forms of other elasmosaurids. These arguments undoubtedly suggest that MML-PV5 is not a juvenile of cf. *Mauisaurus* sp. Coincidentally, Wiffen & Moisley (1986), p. 221) did not find similarities between the same elements of the juvenile they referred to aff. *Tuarangisaurus keyesi* (NZGS, CD429), and juvenile forms of *Mauisaurus haasti*. Finally, MUCPv-131 from northwestern Río Negro Province (Gasparini et al., 2001), here considered as *Tuarangisaurus* sp., has vertebrae, mesopodials and phalanges that are identical to those of MML-PV5, but larger. This supports the hypothesis that some characters, supposedly indicative of immaturity, do not vary significantly during ontogeny and are, therefore, taxonomically useful.

When MML-PV5 is compared with polycotilids, they differ because the coracoids do not form an intercoracoid vacuity and ischia are strongly elongate backwards (Carpenter, 1996). Although the ischia of very juvenile polycotilids are short as in elasmosaurids, the coracoids of MML-PV5 are clearly different, since in both *Dolichorhynchops* Williston, 1903 and *Trinacromerum* Cragin, 1888, even in juveniles, a wide contact between coracoids does not leave a vacuity between them (Carpenter, 1996, fig. 3). They also differ because the propodials of MML-PV5 are thick, with as unexpanded distal margin, while those of polycotilids are thin and distally expanded.

Despite the fact that MML-PV5 lacks a skull and cervical vertebrae, it is provisionally referred to the Elasmosauridae because of the short ischium and the morphology of the coracoid. The general anatomy of MML-PV5 coincides with that of the specimens referred by Wiffen & Moisley (1986) to cf. *T. keyesi* (NZGS, CD427), aff. *T. keyesi* (NZGS, CD428), aff. *Tuarangisaurus keyesi* (NZGS, CD429), and *Plesiosaurus australis* (Owen 1862) (Hector, 1874, pl. 27, fig. A), from the upper Maastrichtian of New Zealand. Welles & Gregg (1971) considered the last of those to be a juvenile *Mauisaurus haasti*. Although we agree with Welles & Gregg (1971) that it is not *Plesiosaurus*, a genus from the Lower Jurassic (Storrs, 1997), it is unlikely to be a juvenile specimen of *Mauisaurus* because the characters of this latter genus are also observed in adults of MUCPv-131. *Tuarangisaurus* is defined on the skull and cervical vertebrae; consequently Wiffen & Moisley (1986) tentatively refered other incomplete specimens to this genus. We follow this criterion here, differentiating

the new species *Tuarangisaurus*? *cabazai* on the basis of the shorter neural spines and the somewhat elongate ischia compared to the specimens referred to the type species.

4. Elasmosaurids from southern Gondwana

Until a few years ago, the record of marine reptiles from the Upper Cretaceous of Patagonia was scarce, and generally not determinable below family rank (Gasparini et al., 2001). Currently, it is known that the marine herpetofauna was diverse and, although dominated by elasmosaurids (*Aristonectes*, cf. *Mauisaurus* sp., *Tuarangisaurus*? *cabazai,* and other indeterminate taxa), there were also polycotilids, including the longirostran *Sulcusuchus* (Gasparini & de la Fuente, 2000), and mosasaurine mosasaurs (Gasparini et al., 2001).

Plesiosauroids, and particularly elasmosaurids, were slow swimmers (compared with pliosaurs) (Massare, 1997). This is compatible with a recent study of their ecomorphology in which it is stated that the long-necked taxa were generally specialized for efficiency and cruising (O'Keefe, 2001), and also with the hypothesis that some taxa may have had a very wide geographic distribution. It is noteworthy that fragmentary and isolated remains (teeth or postcrania) of marine reptiles from the Upper Cretaceous of southern Gondwana are frequently assigned to taxa from the Northern Hemisphere. However, more complete skeletons demonstrate that, although they are referable to families recorded in Laurasian seas, there were differences at generic or specific level. This is the case for the polycotilid *Sulcusuchus erraini* of Patagonia, the elasmosaurid *Aristonectes* (=*Morturneria*) of Patagonia, Chile, and the Antarctic Peninsula (Gasparini et al., in press), and a new tylosaurine mosasaur (Novas et al., 2002) of Ross Island, northeastern Antarctic Peninsula.

The distribution of Patagonian plesiosaurs, now including cf. *Mauisaurus* sp., *Tuarangisaurus*? sp., and *Tuarangisaurus*? *cabazai*, supports the hypothesis of Novas et al. (2002) in suggesting a more marked taxonomic differentiation between marine reptiles of the Northern and Southern Hemispheres by the end of the Cretaceous Period. The Gondwanan distribution of some taxa is more evident when considered in relation to Southern Gondwana (Fig. 8). The elasmosaurid *Morturneria seymouriensis* Chatterjee & Small (1989) from the Campanian–Maastrichtian of Seymour Island is a juvenile of *Aristonectes parvidens* Cabrera (Gasparini et al., in press); *Mauisaurus* of the upper Maastrichtian of New Zealand shows affinities with cf. *Mauisaurus* from the upper Maastrichtian of Ross Island and probably the lower Maastrichtian from Seymour Island (Fostowicz-Frelik & Gazdzicki, 2001), in addition to cf. *Mauisaurus* sp. from the lower Maastrichtian of Quiriquina (Chile) and cf. *Mauisaurus*
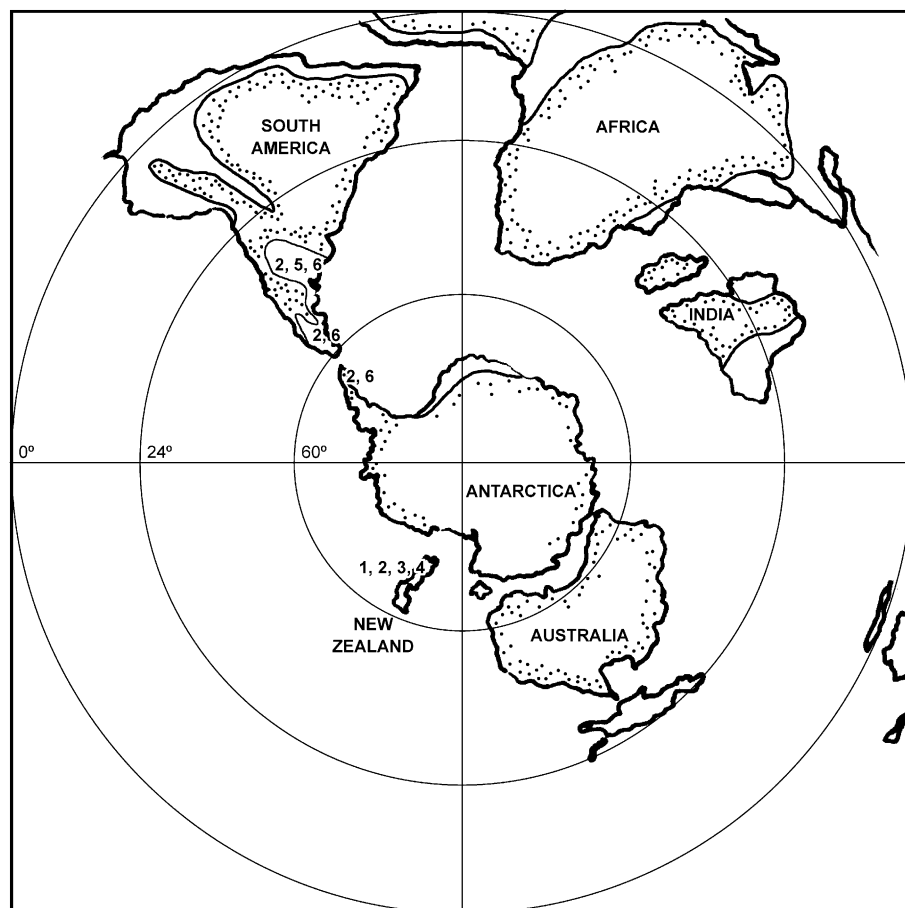
Fig. 8. Upper Cretaceous elasmosaurid plesiosaurs in the South Gondwana. 1, *Mauisaurus haasti*; 2, cf. *Mauisaurus* sp.; 3, *Tuarangisaurus keyesi*; 4, cf. *Tuarangisaurus keyesi*; 5, *Tuarangisaurus*? *cabazai* sp. nov.; 6, *Aristonectes* (see Wiffen & Moisley, 1986; Chatterjee & Small, 1989; Gasparini et al. (in press); Base map modified from Smith et al., 1981 and Scotese et al., 1988).

sp. from northern Patagonia (MML-PV3 and MML-PV4) (this paper). Moreover, there are remarkable similarities between several specimens assigned to aff. *Tuarangisaurus keyesi* and cf. *T. keyesi* from the upper Maastrichtian of New Zeland with *Tuarangisaurus*? sp. from the Campanian?–Maastrichtian from northwestern Patagonia (MUCPv-131), and *Tuarangisaurus*? *cabazai* (MML-PV5), from the uppermost Maastrichtian of north-central Patagonia.

The distribution of other elements of the biota from Patagonia and the Antarctic Peninsula, such as molluscs and crustaceans, changed both in time (Campanian–late Maastrichtian) and latitudinally (northern Patagonia–Antarctic Peninsula). Molluscs from the Maastrichtian–Danian in northern Patagonia show a significant degree of endemism at species level, but generically they show (according to Camacho, 1992) Weddellian and Tethyian associations, with northern Patagonia being a transitional biogeographic area. This agrees with the distribution of foraminifers, for which Austral, Transitional and Tethyian provinces have been recognized previously (Sliter, 1977; Huber, 1990, 1991). The Malvinas

(Falklands) Plateau may have been the boundary between the Austral and Transitional provinces during the Maastrichtian (Ciesielski et al., 1977; Sliter, 1977; Huber, 1990; Malumián & Náñez, 1996).

According to Casadío et al. (1998) and Feldmann et al. (1997), the southward displacement of Tethyian organisms between the Maastrichtian and Danian may have resulted from a counter-clockwise oceanic circulation pattern in the South Atlantic.

5. Conclusions

One of the most significant of the geodynamic phenomena that occurred in southern South America between the Campanian and Danian was the relative sea-level change related to subsidence of the Atlantic margin, which led to major flooding. During the period of the Cretaceous/Paleogene transition, the southern tip of South America was an archipelago in which the central part of the Somuncurá and Desado massifs remained emerged (Malumián, 1999). The marine transgression is recorded in sediments of the Malargüe

Group, which are widely exposed in northern Patagonia. In the centre of the Río Negro Province, at the top of the Jagüel Formation, three long-necked plesiosaurs (Elasmosauridae) were found, one of them (MML-PV4) only at 0.3 m below to the Cretaceous/Paleogene boundary. This latter specimen, referred to cf. *Mauisaurus* sp., is the youngest record of a Mesozoic reptile in Patagonia.

The new specimens are referred to cf. *Mauisaurus* sp. (MML-PV3 and MML-PV4) and to the new species *Tuarangisaurus*? *cabazai* (MML-PV5). Some of the characters observed in the postcranium of MML-PV5, such as the short neural spines, propodials and mesopodials with poorly defined articular facets, and the absence of pelvic and pectoral bars, were previously thought to be related to a juvenile condition. However, after an examination of all of the evidence, these are here considered to be taxonomically valid.

The Upper Cretaceous elasmosaurids in Patagonia are closely related to those of the Maastrichtian of central Chile, the northeastern island of the Antarctic Peninsula and New Zealand, which reinforces the hypothesis of a southern Gondwanan distribution for some pelagic reptiles (Novas et al., 2002).

Acknowledgements

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