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Alcheringa: An Australasian Journal of Palaeontology
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/talc20

Metaceratodus kaopen comb. nov. and M. wichmanni comb. nov., two Late Cretaceous South American species of an austral lungfish genus (Dipnoi)

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Available online: 31 May 2012

To cite this article: Alberto L. Cione & Soledad Gouiric-Cavalli (2012): Metaceratodus kaopen comb. nov. and M. wichmanni comb. nov., two Late Cretaceous South American species of an austral lungfish genus (Dipnoi), Alcheringa: An Australasian Journal of Palaeontology, 36:2, 203-216

To link to this article: http://dx.doi.org/10.1080/03115518.2012.621804

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Erratum

- ✓ Page 209, second column, first paragraph where it says "MPCN PV 003 (Figs 3E, 8F, G)" should say: **MPCN PV 003 (Figs 8G, G)**.

- ✓ Page 211 Figure caption 8: missing **F-G: MPCN PV 003 holotye of *Metaceratodus kaopen* (Apesteguía, Agnolin & Claeson, 2007).**

- ✓ Page 212, second column, second paragraph where it says "*Ptychoceratodus cionei, P. wichmanni* and *C. kaopen* are consistent with the circumscription of *Metaceratodus* in having a double prearticular sulcus (Fig. 3B, E), similar occlusal profiles (Fig. 3A, D), and less extensively developed occlusal pits.", should say ***Ptychoceratodus cionei, P. wichmanni* and *C. kaopen* are consistent with the circumscription of *Metaceratodus* in having a double prearticular sulcus (Fig. 4B, E), similar occlusal profiles (Fig. 5A, D), and less extensively developed occlusal pits.**

- ✓ Page 213, Figure caption 10 where it says "Fig. 10. Reconstructions of *Metaceratodus* Kemp, 1997, tooth plates showing the occlusal patterns, upper jaw on the left, lower jaw on the right. Scale bar=2 cm. A, B, *M. wollastoni* Chapman, 1914; C, D, *M. palmeri* (Krefft, 1874); E, F, *M. ellioti* Kemp 1997a; G, M. bonei Kemp, 1997a; H, *M. wichmanni* (Apesteguıía, Agnolin & Claeson, 2007) based on MLP 06-VII-1-1-3 and MACN-RN- 1080b; I, based on MLP 06-VII-1-1-2. Most modified from Kemp (1997a)." should say: **Fig. 10. Reconstructions of *Metaceratodus* Kemp 1997 tooth plates showing the occlusal patterns, upper jaw on the left, lower jaw on the right. Scale bar = 2cm. A-F , *M. wollastoni* Chapman, 1914; B-G, *M. palmeri* (Krefft, 1874); C-H, *M ellioti* Kemp, 1997a; D, *M. bonei* Kemp 1997a; E-I, *M. wichmanni* (Apesteguía, Agnolin & Claeson, 2007) E based on MLP 06-VII 1-1-3 and MACN 1080b, I based on MLP 06-VII-1-1-2 and MLP 06-VII-1-1-4 . Most modified from Kemp (1997a).**

Metaceratodus kaopen comb. nov. and *M. wichmanni* comb. nov., two Late Cretaceous South American species of an austral lungfish genus (Dipnoi)

ALBERTO L. CIONE AND SOLEDAD GOUIRIC-CAVALLI

CIONE, A.L. & GOUIRIC-CAVALLI, S., June 2012. *Metaceratodus kaopen* comb. nov. and *M. wichmanni* comb. nov., two Late Cretaceous South American species of an austral lungfish genus (Dipnoi). *Alcheringa 36*, 203–216. ISSN 0311-5518.

Metaceratodus wollastoni, an Australian species, was reported from Upper Cretaceous beds of Patagonia in 1997. Later, three new species (*Ceratodus wichmanni*, *Ptychoceratodus kaopen* and *Ptychoceratodus cionei*), based on scarce material, were described from the same region. Two of these species were later referred to *Ferganoceratodus*. After examining much more abundant and better-preserved material, we conclude that neither the occurrence of *Metaceratodus wollastoni* nor those of *Ptychoceratodus* and *Ferganoceratodus* in the Cretaceous of South America are supported. We consider that *C. wichmanni* and *P. cionei* are synonyms and we reassign the three putative species to *Metaceratodus* under two new combinations: *M. kaopen* comb. nov. and *M. wichmanni* comb. nov. Both differ from the other species of the genus in having pits over most of the occlusal surface and a different occlusal profile of the tooth plate, and most have four ridges in the lower and upper tooth plates. *Metaceratodus wichmanni* differs from *M. kaopen* in oclussal profile, inner angle, and symphysis development among other features. *Metaceratodus kaopen* is known from the upper Santonian–lower Campanian Anacleto Formation of Río Negro province and *M. wichmanni* from upper Campanian–lower Maastrichtian units of Chubut, Río Negro, Neuquén and Mendoza provinces, Argentina. The occurrence of *Metaceratodus* in southern South America corroborates a close biogeographical relationship with Australia in the latest Cretaceous.

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Key words: Lungfish, Dipnoi, Cretaceous, Argentina, South America, Australia.

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LUNGFISHES are known almost worldwide during the Mesozoic mostly by their strong tooth plates (Martin 1982, Arratia & Cione 1996, Kemp 1997a, Schultze 2004). In South America, dipnoan tooth plates have been documented from Triassic to Miocene rocks, but they are particularly abundant in Upper Cretaceous beds (Schultze 2004, Apesteguía *et al*. 2007, Cione *et al*. 2007, Richter & Toledo 2008, Cione *et al*. 2010, Soto & Perea 2010).

Pardo *et al*. (2010) stressed that the systematic utility of tooth plates is relatively poor (see also Cavin *et al*. 2007). However, in large numbers, with specimens representing different ontogenetic stages, and combined with attached jaw bones, tooth plates can provide useful information for testing taxonomic hypotheses.

Several fossil lungfish species have been described from southern South America (Ameghino 1898, Wichmann 1927, Pascual & Bondesio 1976, Cione 1987, González-Riga 1999, Martinelli & Forasiepi 2004, Apesteguía *et al*. 2007, Cione *et al*. 2007, Agnolin 2010). Moreover, the first lungfish reported from South America was *Atlantoceratodus iheringi* (Ameghino 1898) from the Mata Amarilla Formation (Cenomanian–Coniacian) of Patagonia (see Cione *et al*. 2007). This species is the southernmost lungfish known since the Triassic (currently 49°35′S; palaeolatitude about 55°S according to Scotese 1987). The last lungfish record from southern South America is late Paleocene–early Eocene in age (Cione *et al*. 2010). Presently, no lungfishes inhabit the area (Arratia & Cione 1996).

Kemp (1997a) identified some tooth plates from the Upper Cretaceous of Patagonia figured by Pascual & Bondesio (1976) as possible representatives of the Australian species *Metaceratodus wollastoni*. This identification was accepted by Apesteguía *et al*. (2007). However, Apesteguía *et al*. (2007) also identified other new lungfish taxa from different Upper Cretaceous beds of Patagonia based on tooth plate characters: *Chaoceratodus portezuelensis*, *Ceratodus argentinus*, *C. kaopen*, *Ptychoceratodus cionei*,

ISSN 0311-5518 (print)/ISSN 1752-0754 (online)
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http://dx.doi.org/10.1080/03115518.2012.621804

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P. wichmanni and ?Lepidosirenidae. Based on material from the Allen Formation of Río Negro province, Agnolin (2010) transferred the species previously assigned to *Ptychoceratodus* Jaekel, 1926 by Apesteguía *et al.* (2007) to *Ferganoceratodus* Kaznyshkin & Nessov, 1985. Furthermore, Agnolin (2010) created the new species *Atlantoceratodus patagonicus* on the basis of scarce and poorly preserved material from the Allen Formation at Trapal Có, Río Negro province.

Here, following the collection of better material, we discuss several of the previously recognized taxa and the stratigraphic provenance of one species, and propose two new combinations and a synonymy. Morphological terminology employed herein is according to Kemp (1997a, 1997b, 2001).

Institutional abbreviations. MLP (Museo de Ciencias Naturales de La Plata), Buenos Aires, MACN (Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires), MPCN (Museo Patagónico de Ciencias Naturales, General Roca, Río Negro), MPCA (Museo Provincial 'Carlos Ameghino,' Cipolletti, Río Negro), MML (Museo Municipal Héctor Cabazza, Lamarque, Río Negro).

Geological setting

The material described herein derives from the Upper Cretaceous of northern Patagonia (Chubut and Río Negro) and Cuyo (Mendoza), Argentina (Fig. 1A). The fossiliferous units occur near the top of the Neuquén Group and the Malargüe Group. Both the Neuquén and Malargüe groups range in age from Cenomanian to Danian (Calvo *et al.* 2007).

According to Apesteguía *et al.* (2007), the type material of *Metaceratodus kaopen* comes from the Santonian of the Bajo de la Carpa Formation at Paso Córdova, Río Negro province. However, the material was actually found in the Anacleto Formation at Paso Córdova, Río Negro province (Figs 1B, 2; Pablo Chafrat, curator of the MPCN, pers. comm. cited by de la Fuente *et al.* 2010). The Anacleto Formation is the uppermost unit of the Neuquén Group, and it is considered older than early Campanian (Dingus *et al.* 2000) or late Santonian–early Campanian (de la Fuente *et al.* 2010).

The holotype of *Metaceratodus wichmanni* comes from the Los Alamitos Formation, Río Negro province. *Metaceratodus wichmanni* is also found in the correlative Allen and Coli-Toro formations (Río Negro province), Loncoche Formation (Mendoza province), and La Colonia Formation (Chubut province; Fig. 1A; Pascual & Bondesio 1976, Cione 1987, Bonaparte 1990, 2002, Bonaparte *et al.* 1984, 1987, González-Riga 1999, Pascual *et al.* 2000, Martinelli & Forasiepi 2004). All these units are considered middle Campanian–early Maastrichtian in age based on ostracod (Ballent 1980) and palynomorph evidence (Salgado *et al.* 2007), and stratigraphic position.

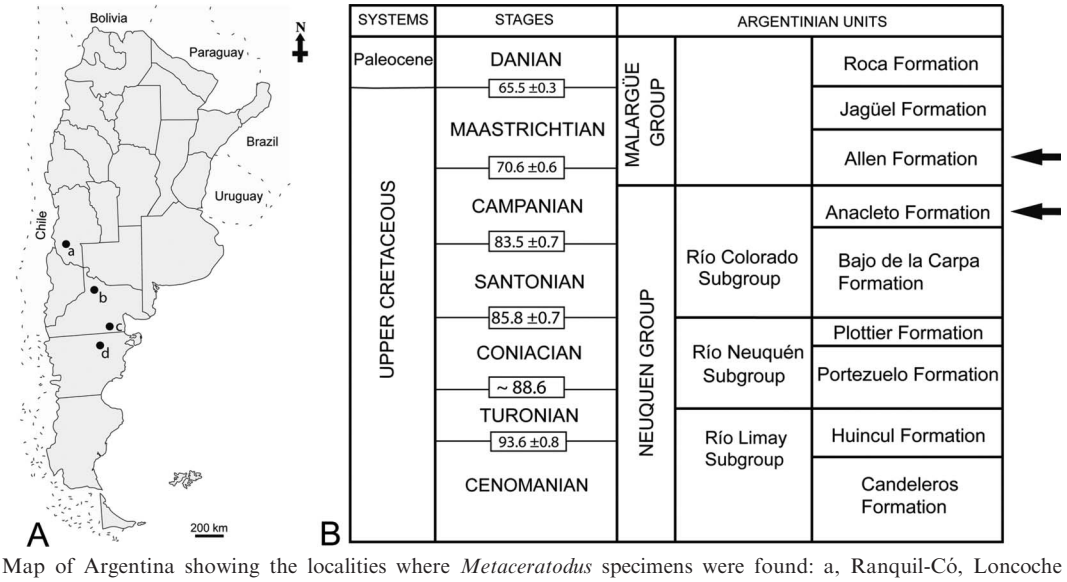

Fig. 1. **A**, Map of Argentina showing the localities where *Metaceratodus* specimens were found: a, Ranquil-Có, Loncoche Formation, Mendoza province; b, Paso Córdova, Anacleto Formation, Río Negro province; c, Estancia Los Alamitos, Los Alamitos Formation, Río Negro province; d, Arroyo el Mirasol, La Colonia Formation, Chubut province. **B**, stratigraphic units. The arrows indicate the fossiliferous units.

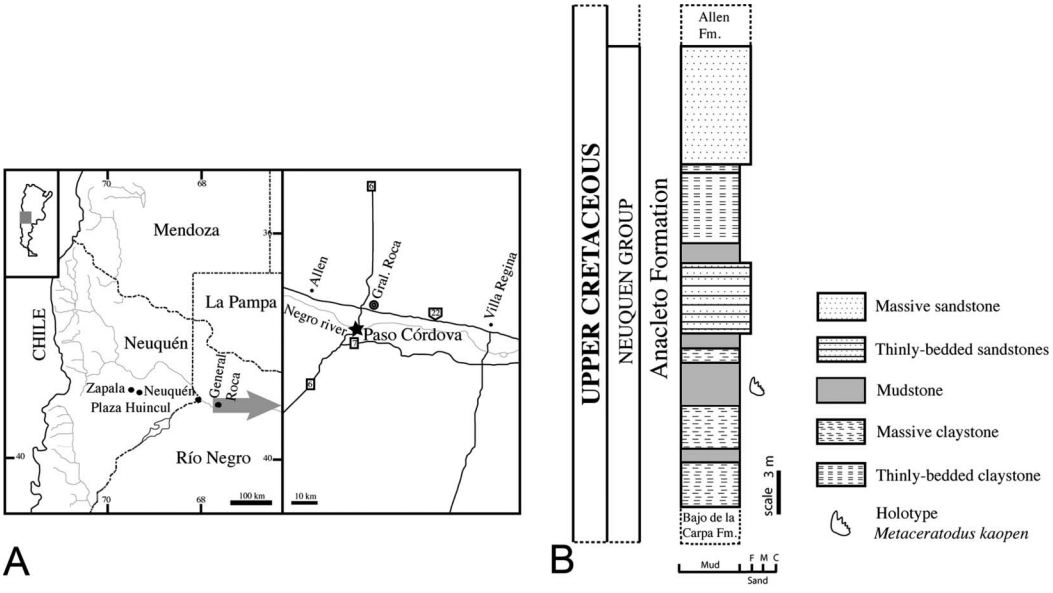

Fig. 2. **A**, Location map (modified from de la Fuente *et al.* 2010). Star indicates the type locality of *Metaceratodus kaopen*. **B**, Stratigraphic column of the type locality of *M. kaopen*.

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Systematic palaeontology

DIPNOI Müller, 1845

CERATODONTIDAE Gill, 1872

Metaceratodus Chapman, 1914

1914 *Ceratodus* (*Metaceratodus*) Chapman, pp. 25–27, pl. V, figs 1–3.
1837 *Ceratodus* Agassiz, pp. 174–176.
1927 *Ceratodus* Wichmann partim, p. 401, pl. I, figs 1, 3, 5.
1976 *Ceratodus* Pascual & Bondesio, p. 570, pl. 1, figs 4, 5.
1987 *Ceratodus* Kirkland, pp. 5, 7.
2007 *Ceratodus* Apesteguía, Agnolin & Claeson, p. 32.
1987 *'Ceratodus'* Cione, p. 116.
1992 *Metaceratodus* (Chapman, 1914); Schultze, p. 315.
1997 *Metaceratodus* (Chapman, 1914); Kemp, p. 26. [1997a]
1926 *Ptychoceratodus* Jaekel partim, fig. 42.
2007 *Ptychoceratodus* Apesteguía, Agnolin & Claeson, p. 33.
1996 *'Ptychoceratodus'* Arratia & Cione, p. 72.
2010 *Ferganoceratodus* Agnolin, p. 30.

Type species. *Metaceratodus wollastoni* Kemp, 1997a.

Diagnosis (based only on tooth plates and jaw bones). Pulp cavity wide; mantle dentine limited; ridges originate medially; all ridges robust; ridge 1 obtuse or acute in upper tooth plate, acute in lower; posterior ridges acute; upper tooth plates close or contiguous; lower widely separated; upper symphysis oblong or elliptic, lower oblong; pterygopalatine process present; prearticular sulcus double; punctations simple; occlusal pits present; rounded crests (slightly modified from Kemp 1997a).

Occurrence. *Metaceratodus* has been found in several Cretaceous, Oligocene, Miocene, Pliocene and Pleistocene assemblages of Australia (Kemp 1997a) and Cretaceous assemblages of southern South America.

Metaceratodus wichmanni (Apesteguía, Agnolin & Claeson, 2007) comb. nov. (Figs 3A–B, 4, 5, 6A)

1898 *Ceratodus iheringi* Ameghino partim, p. 134.
1927 *Ceratodus* sp. Wichmann partim pl. 1, figs 1, 3, 5.
1976 *Ceratodus iheringi* Pascual & Bondesio, pl. I, fig. 5.
1987 '*Ceratodus' iheringi* Cione, p. 115, fig. 1N.
1996 '*Ptychoceratodus' iheringi* Arratia & Cione, p. 72.
1999 *Ceratodus* sp. González-Riga, p. 403, fig. 3E.
2007 *Ptychoceratodus wichmanni* Apesteguía, Agnolin & Claeson, p. 33, fig. 3c, d.
2007 *Ptychoceratodus cionei* Apesteguía, Agnolin & Claeson, p. 33, fig. 3a, b.
2010 *Ferganoceratodus wichmanni* Agnolin, p. 30, fig. 7.

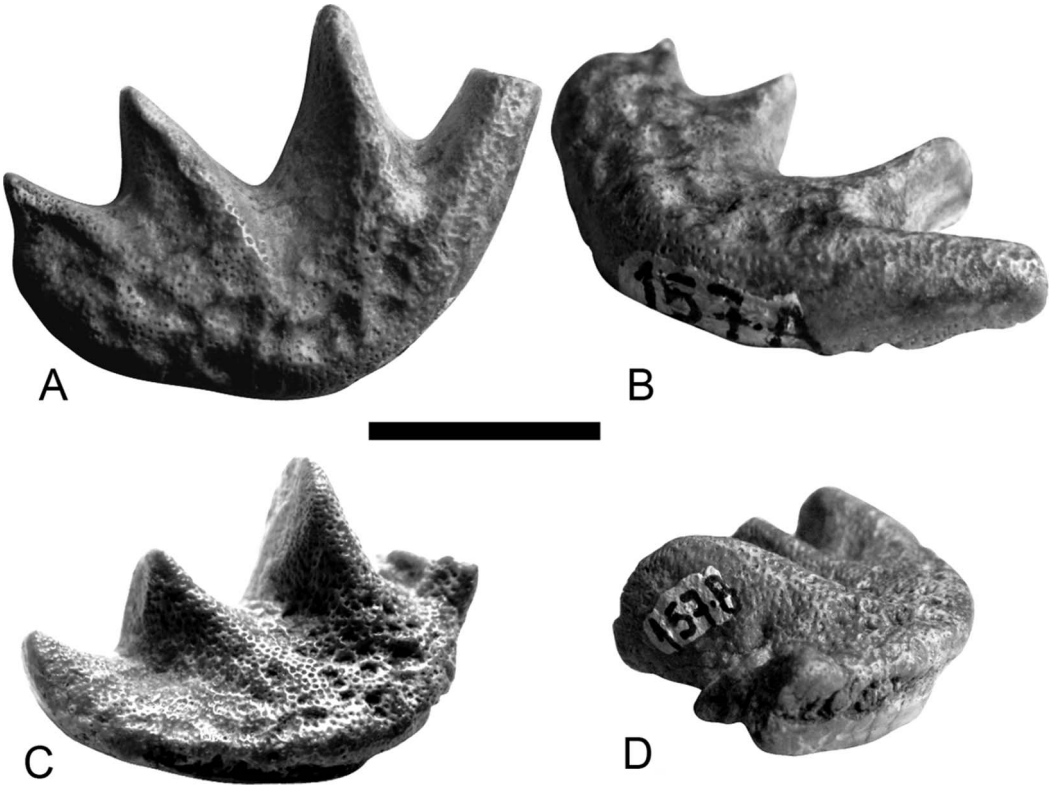

Fig. 3. Holotypes. Scale bar=1 cm. **A–B**, MACN PV RN 157A, *Metaceratodus wichmanni* (Apesteguía, Agnolin & Claeson, 2007); **C–D**, MACN PV RN 157B, *M. cionei* (Apesteguía, Agnolin & Claeson, 2007), reversed image.

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Type. MACN PV RN 157A, right lower tooth plate [holotype of *P. wichmanni* (Fig. 3A–B)].

Diagnosis (based only on tooth plates and jaw bones). Thick tooth plates reaching large size (the lower up to 41 mm long); most with four robust ridges (some with five) that originate medially in upper and lower tooth plates (they are relatively acute in unworn specimens); clefts between the ridges are relatively shallow and rounded; punctations without pattern or arranged in lines; occlusal pits common around the crown and between the ridges, but occurring over the whole surface of the crown; medial edge slightly curved in upper tooth plates and strongly curved in lower; upper tooth plates subtriangular, lower elongated; ridge 1 in lower tooth plates curving outward anteriorly from symphysis; enamel to bone junction rising slightly between each ridge labially; enamel covering only the base of the lateral face of tooth plates; lower tooth plates widely separated; upper tooth plates contiguous.

Occurrence. The holotype comes from the Los Alamitos Formation (late Campanian–early Maastrichtian) of Río Negro province, northern Patagonia (de la Fuente *et al*. 2010).

Referred material. Coli-Toro Formation at Ingeniero Jacobacci, Río Negro: MJHG 185/12 upper right tooth plate (Pascual & Bondesio 1976, pl. I, fig. 5). Coli-Toro Formation at Arroyo Yaminhué, Río Negro: lower left tooth plate (Wichmann 1927, pl. 1, fig. 3); lower right tooth plate (Wichmann 1927, pl. 1, fig. 1); upper left tooth plate (Wichmann 1927, pl. 1, fig. 5). Material from the Allen Formation at Bajo Santa Rosa, Río Negro: MACN-RN-1080b, right upper tooth plate with attached jawbone (Fig. 5D–F); MACN-RN-1079, fragmentary tooth plate the first and second crest are partially preserved. Material from the Allen Formation at Cerro Dos Hermanas, Trapal Có and Bajo Trapalcó, Río Negro: MML-198, left upper tooth plate (Agnolin 2010, fig. 7A); MML 199, lower left tooth plate (Agnolin 2010, fig. 7B; Agnolin 2010 identified this as an upper tooth plate); MML 200, left lower tooth plate (Agnolin 2010, fig. 7C); MML 201, right lower tooth plate with attached jaw bone (Agnolin 2010, fig. 7D); MML 202, right lower tooth plate with attached jaw bone (Agnolin 2010, fig. 7E–F); MLP-08-XII-1-1-1, right lower tooth plate with attached jaw bone (Fig. 7G); MLP-08-XII-1-1-2, right lower tooth plate with attached jaw bone. Loncoche Formation at Ranquil-Co, Mendoza: Wichmann

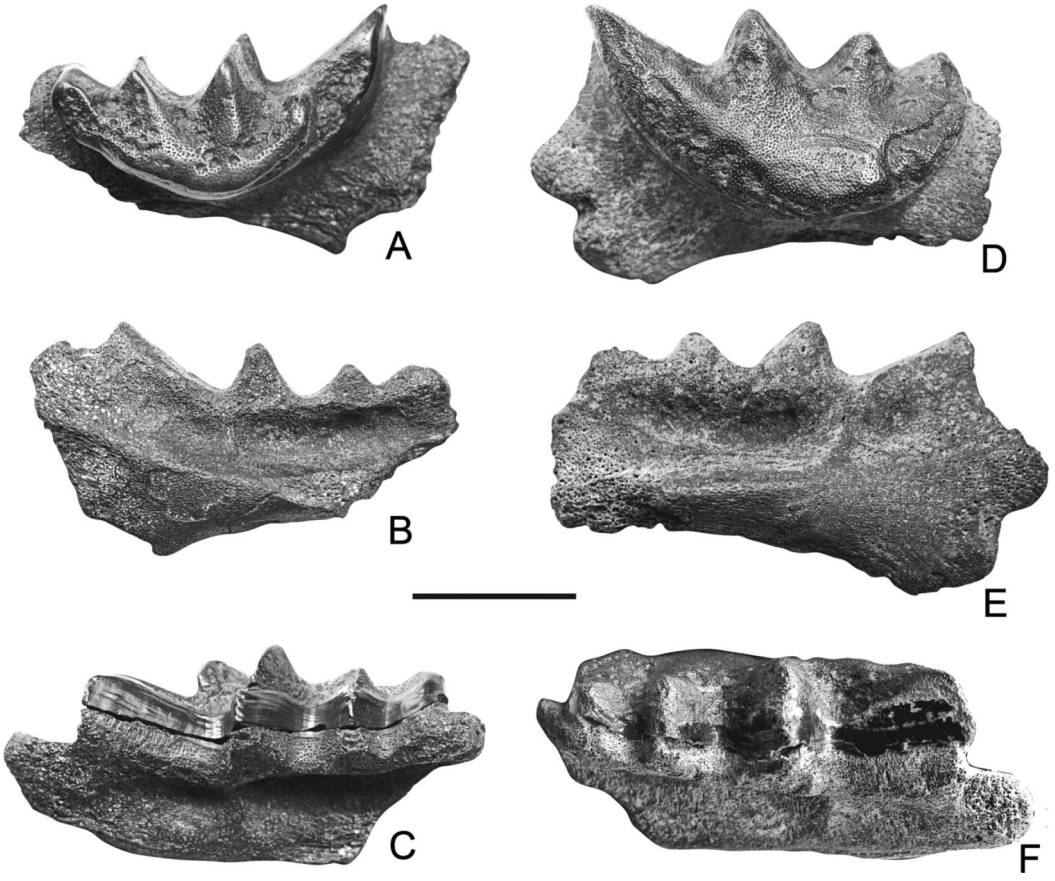

Fig. 4. Metaceratodus wichmanni (Apesteguía, Agnolin & Claeson, 2007), lower tooth plates with attached jaw bone. Scale bar=2 cm. **A–C**, MLP 06-VII-1-1-1: **A**, occlusal view; **B**, ventral view; **C**, labial view; **D–F**, MLP 06-VII-1-1-2: **D**, occlusal view; **E**, ventral view; **F**, labial view.

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(1924, pl. VII, fig. 6); CORD-PZ 17315, tooth plate with broken first ridge (González-Riga 1999, fig. E). Los Alamitos Formation at Estancia Los Alamitos, Chubut: MACN PV RN 157B (Fig. 3C–D), right upper tooth plate, holotype of *P. cionei* (Apesteguía *et al*. 2007 identified this latter as an upper tooth plate). La Colonia Formation at Arroyo Mirasol Chico Creek, Bajada Moreno area, Chubut: MLP 06-VII-1-1-3, left upper tooth plate with attached jaw bone (Fig. 5A–C); MLP 06-VII-1-1-1, right lower tooth plate with attached bone (Fig. 4A–C); MLP 06-VII-1-1-2, left lower tooth plate with attached bone (Fig. 4D–F); MLP 06-VII-1-1-4, left lower tooth plate without jaw bone attached; MLP 06-VII-1-1-5, right lower jaw bone; MLP 06-VII-1-1-6, left upper tooth plate without attached jaw bone; MLP 06-VII-1-1-7, incomplete right upper tooth plate without attached jaw bone; MLP 06-VII-1-1-8, incomplete right lower tooth plate without attached jaw bone.

Description. Tooth plates corresponding to different ontogenetic stages are available, the smallest being *ca* 15 mm long and the largest 41 mm long (Fig. 7). The upper tooth plates are subtriangular, with a clear inner angle. The lower are longer with a barely evident inner angle (Fig. 4). The general morphology of the tooth plates is preserved during ontogeny, although they became stouter (Fig. 7). The upper and lower tooth plates have mostly four (some five) robust ridges, the last in some cases only represented by a heel (possibly a fusion of fourth and fifth ridges). The enamel is preserved only at the base of the lateral face of the tooth plate (Fig. 4). The enamel to bone junction rises slightly between each ridge labially in the upper tooth plates but rises highly in lower tooth plates. Loss of enamel and dentine on the mediolingual face, a destructive pre-mortem process related to environmental factors, appears to have been slight or absent (Kemp 1997a). The labial profile of the ridges is steep. In a few specimens occlusal cusps are present (Figs 4C, 5D). Ridges originate medially in upper and lower tooth plates. Posteriorly, in adult specimens, the ridges tend to disappear from the surface of the tooth plate due to pre-mortem erosion (Figs 4D, 5A). The first ridge of the upper tooth plate is shorter than the lower; it is narrow and curves out slightly from the symphysis (Fig. 5). The first ridge of the lower

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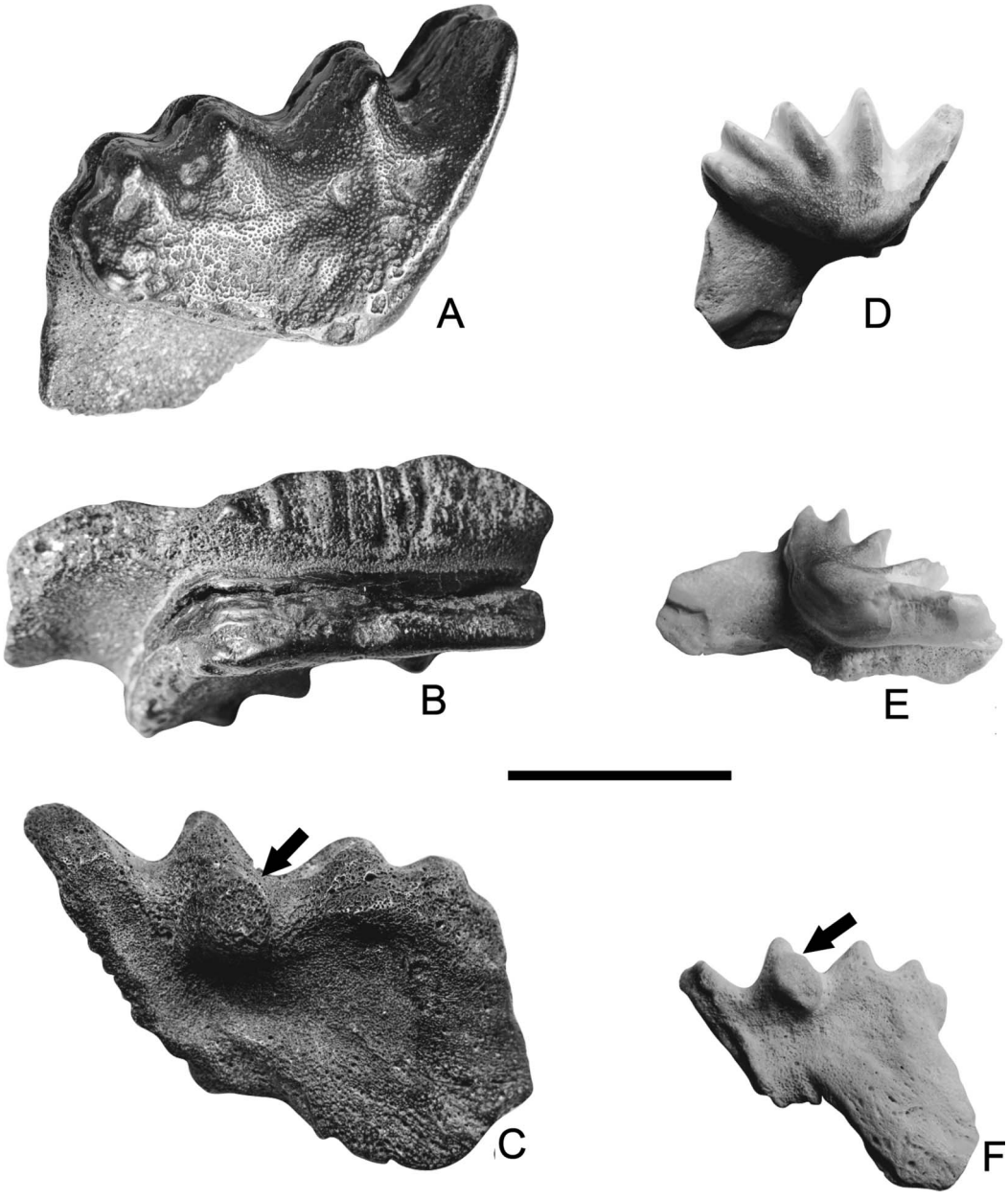

Fig. 5. Metaceratodus wichmanni (Apesteguía, Agnolin & Claeson 2007), upper tooth plates with attached jaw bone. Scale bar=2 cm; **A–C**, MLP 06-VII-1-1-3: **A**, occlusal view [reversed image]; **B**, symphysial view; **C**, labial view; **D–F**, MACN-RN-1080b, **D**, occlusal view; **E**, symphysial view; **F**, labial view.

tooth plate curves out strongly from the symphysis (Fig. 4). The other ridges are straight and radiating. In upper and lower tooth plates, clefts between the ridges are wide, rounded and shallow and form an angle of 90° or less. Punctations are either random or arranged in lines. Occlusal pits are distributed mainly around the tooth plate but also occur between and on the ridges. The prearticular sulcus is double, the anterior portion is shallow and the bridge that divides the sulcus is located at the height of the bottom of the first cleft. The upper symphysis is oblong (Fig. 5B, E) and the lower is linear. There are upright grooves in the suture between both prearticular plates, the grooves of the upper symphysis are numerous, straight, deep and marked. In the lower symphysis, the grooves are less distinct. The lower tooth plates are widely separated (Fig. 4). The upper plates are contiguous. The base of the robust pterygopalatine process is circular and positioned above ridge 2 (Fig. 5C, F).

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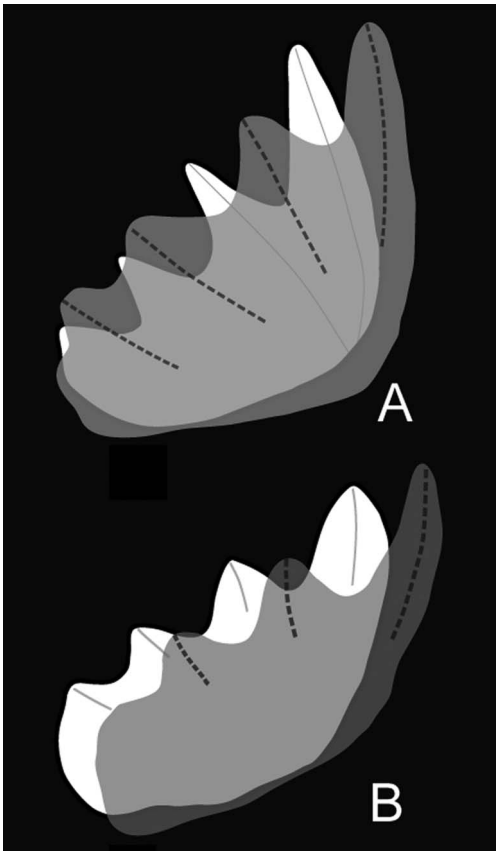

Fig. 6. Reconstruction of the occlusal position of upper and lower tooth plates of *M. wichmanni* (**A**) and *M. kaopen* (**B**). The outlines are derived from real specimens but they are not to scale. **A**, upper plate, MLP 06-VII-1-1-3; lower plate, MACN-PV-157 *partim*. **B**, upper plate, MLP 94-XI-1-1; lower plate, MPCN PV 003).

Metaceratodus kaopen (Apesteguía, Agnolin & Claeson, 2007) comb. nov. (Figs 6B, 8, 9A, B).

2007 *Ceratodus kaopen* Apesteguía, Agnolin & Claeson, p. 32, fig. 2h, i.
2010 *Ceratodus kaopen* Agnolin, p. 196.

Diagnosis (based only on tooth plates and jaw bones). Thick tooth plates reaching moderate size (smaller than *M. wichmanni*, up to 27 mm long); with three robust ridges plus a wide posterior area. Ridges originate medially (they are relatively acute in unworn specimens); clefts between the ridges are relatively shallow and rounded; punctations without pattern or arranged in lines; occlusal pits on all the surface of the crown; medial edge rather strongly curved in upper tooth plates. Upper tooth plates elongated and narrow; enamel to bone junction rising slightly between each ridge labially; enamel covers the lateral face of tooth plates (Fig. 8C, G). Upper tooth plates moderately separated in the symphysis; lower tooth plates widely separated in the symphysis.

Type. MPCN PV 003 (Figs 3E, 8F, G), isolated left lower tooth plate [= holotype of *C. kaopen* (Apesteguía *et al*. 2007, fig. 2H, erroneously assigned the collection number MPCN PV 1-1 to this holotype; Pablo Chafrat, pers. comm.)].

Occurrence. The holotype and the only other known material come from the Anacleto Formation (upper Santonian–lower Campanian) of Río Negro province, northern Patagonia (de la Fuente *et al*. 2010).

Referred material. Anacleto Formation at Paso Córdova, Río Negro: MPCN-PV 005, left broken prearticular bone without attached tooth plate (Fig. 8D, E). Apesteguía *et al*. (2007, p. 32) identified this specimen as a right upper tooth plate: 'anterior fragment with two ridges of a right upper tooth plate with cranial bone attached'. Moreover, Apesteguía *et al*. (2007) assigned an erroneous collection number to it (MPCN-PV 1–3; Pablo Chafrat, pers. comm.); MPCN-PV-06, fragmentary tooth plate (Apesteguía *et al*. 2007 erroneously assigned the collection number MPCN-PV 1-2 to it; Pablo Chafrat, pers. comm.); MLP 94-XI-1-1, left upper tooth plate with attached jaw bone (Fig. 8A–C).

Description. The tooth plates are subtriangular, and the inner angle is not very well defined (Fig. 8). The general morphology of tooth plates is preserved during ontogeny. The upper and lower tooth plates have four ridges; the last one develops a wide and rounded posterior area (Fig. 8F). The enamel is preserved only around the tooth plate in our material. Enamel to bone junction rises considerably between each ridge labially in both, upper and lower tooth plates. Loss of enamel and dentine on the mediolingual face appears to have been slight or absent. The labial profile of the ridges is steep. Ridges originate medially in upper and lower tooth plates. In adult specimens, the ridges tend to disappear from the surface of the tooth plate due to pre-mortem erosion (Fig. 8F). The ridges are straight and radiating. Clefts between the ridges are wide, rounded and shallow, and form an angle of 90°. Punctations lack any pattern or are arranged in lines. Occlusal pits are distributed mainly around the tooth plate but also occur between the ridges. The upper plates are moderately separated (Fig. 8A, B). The upper symphysis is oblong; the grooves are numerous, straight and shallow. The base of the pterygopalatine process is oval or even lachrymiform and is

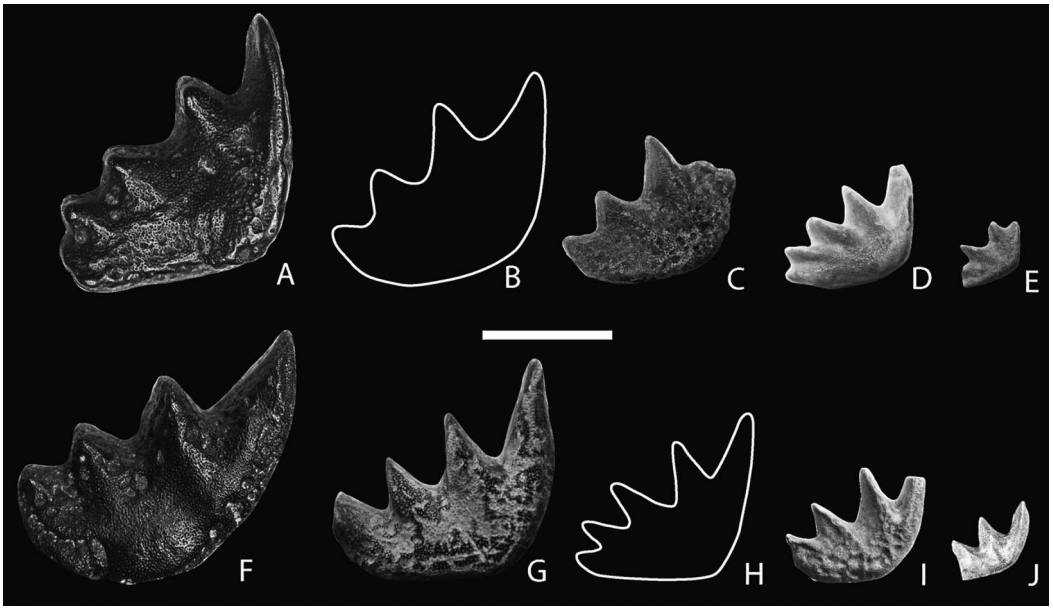

Fig. 7. Metaceratodus wichamnni, ontogenetic series. **A–E**, Upper tooth plates (**A**, MLP 06-VII-1-1-3 [reversed image]; **B**, hypothetical intermediate; **C**, MACN PV RN 157B [reversed image]; **D**, MACN-RN-1080b; **E**, MACN-RN-157 *partim*); **F–J**, lower tooth plates (**F**, MLP 06-VII-1-1-1 [reversed image]; **G**, MLP 06-VII-1-1-6 [reversed image]; **H**, hypothetical intermediate; **I**, MACN PV RN 157A; **J**, MLP 06-VII-1-1-4). Scale bar=2 cm.

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positioned at the level or even slightly below that of ridge 2 (Fig. 8B). The lower tooth plates are widely separated.

Discussion

Apesteguía *et al.* (2007) described several new species from Upper Cretaceous beds of Patagonia and assigned to new and previously established genera (see above). Three of these species are analyzed here: *Ceratodus kaopen*, *Ptychoceratodus cionei* and *P. wichmanni*.

Five lungfish families were recognized in the Mesozoic and Cenozoic by Schultze (2004): Ceratodontidae, Neoceratodontidae, Lepidosirenidae, Arganodontidae and Asiatoceratodontidae. However, there is considerable debate about the relationships of post-Palaeozoic dipnoans and the genera included in the different families (see Martin 1982, Kemp 1997a, 1997b, Schultze 2004, Cavin *et al.* 2007, Pardo *et al.* 2010).

Ptychoceratodus cionei, *P. wichmanni* and *C. kaopen* tooth plates differ markedly from those of *Neoceratodus, Mioceratodus, Archaeoceratodus, Lepidosiren, Protopterus, Lavocatodus, Lupaceratodus*, *Arganodus*, *Asiatoceratodus*, *Paraceratodus*, *Potamoceratodus*, *Retodus*, *Atlantoceratodus* and *Chaoceratodus* (see Schultze 1981, 2004, Kemp 1997b, 1998, Apesteguía *et al.* 2007, Cavin *et al.* 2007, Cione *et al.* 2007, Gottfried *et al.* 2009, Soto & Perea 2010). Both *P. cionei* and *P. wichmanni* were referred to *Ptychoceratodus* Jaekel, 1926 by Apesteguía *et al.* (2007) and to *Ferganoceratodus* Kaznyshkin & Nessov, 1985 by Agnolin (2010). However, *P. cionei* and *P. wichmanni* clearly differ from the Triassic genotype *Ptychoceratodus serratus* (Agassiz, 1838) (see Schultze 1981, Kemp 1998), and the Jurassic genotype *Ferganoceratodus jurassicus* Kaznyshkin & Nessov, 1985 because they have tooth plates with a much large inner angle, different occlusal profile and more robust ridges (Fig. 9). *Ptychoceratodus cionei* and *P. wichmanni* also differ from *P. serratus* and the Triassic '*P.*' *phillipsi* in the presence of widely distributed occlusal pits, lower tooth plates separated in the mid-line, and in lacking a mediolingual keel (see Kemp 1998), and from the Jurassic *Ferganoceratodus szechuanensis* and *F. martini* in the different occlusal profile (see Cavin *et al.* 2007). Furthermore, neither *Ptychoceratodus* nor *Ferganaceratodus* species are known with confidence from the Cretaceous (Schultze 2004; contra Martin 1982 and Agnolin 2010). Agnolin (2010) assigned *P. cionei* and *P. wichmanni* to *Ferganoceratodus* because he incorrectly considered that the small number of crests, rounded medial angle, and broad prearticular bone separating the lower tooth plates were characters of this genus. A small number of crests are present in many genera, and the second and third traits do not occur in the genotype.

We refer, *P. cionei*, *P. wichmanni* and *C. kaopen* to Ceratodontidae *sensu* Kemp (1997a; i.e., including

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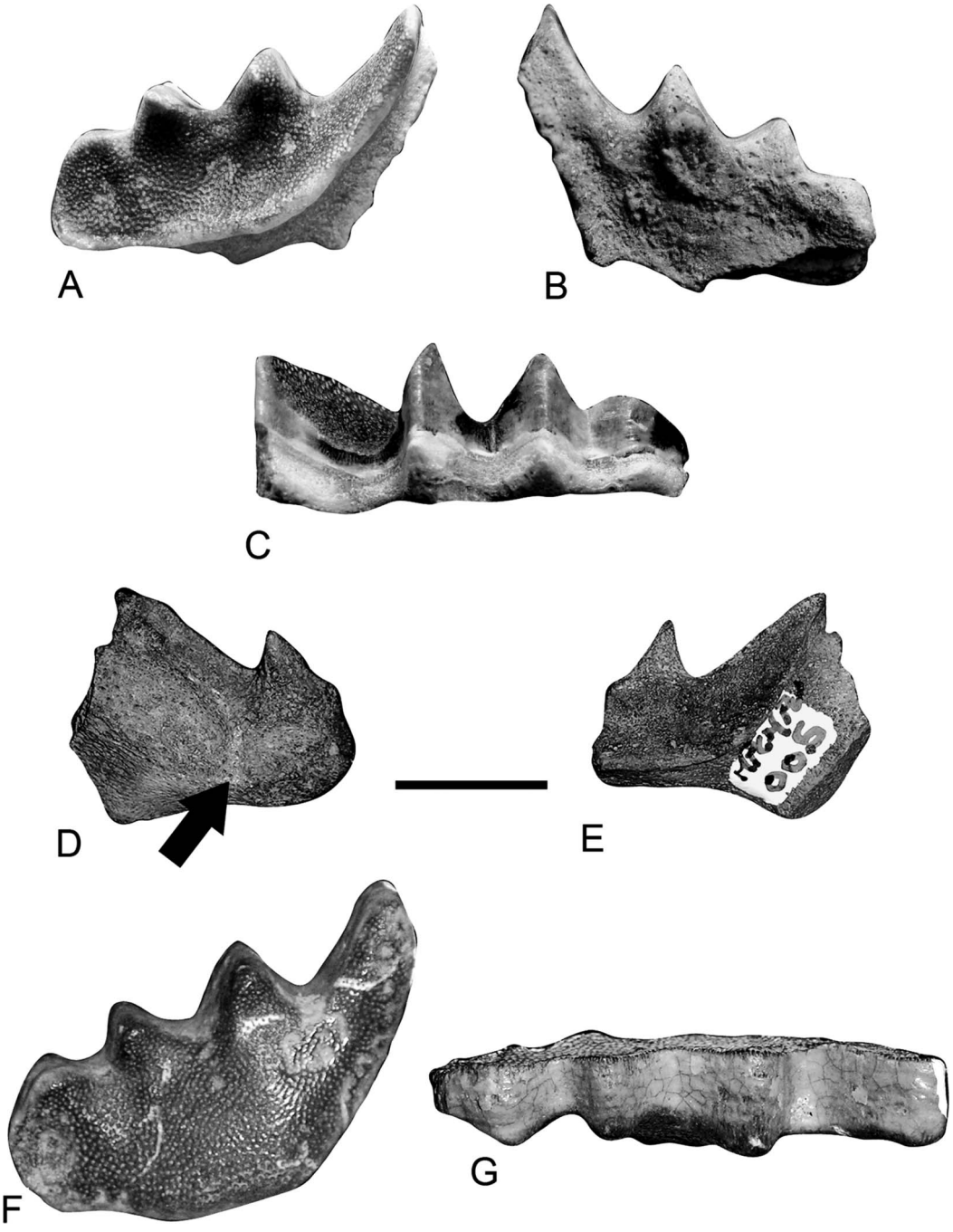

Fig. 8. Metaceratodus kaopen (Apesteguía, Agnolin & Claeson, 2007). **A–C**, MLP 94-XI-1-1 upper tooth plates; **D–E,** MPCN-PV-005 isolated prearticular bone, arrow indicates the double prearticular sulcus. Scale bar=1 cm.

the closely allied genera *Ceratodus* and *Metaceratodus*). *Ceratodus* and *Metaceratodus* are considered sister groups by most authors (Schultze 2004, Cavin *et al*. 2007). We follow the characterization of *Metaceratodus* by Kemp (1997a) *non* Agnolin (2010). *Metaceratodus* dentition and jaw bones are similar to those of *Ceratodus* (see Kemp 1997a, 2001, Schultze 2004). Kemp (1997a, p. 26), in a list of characters (independent of growth, wear and inherent variation), mentioned 'there is only one difference between *Ceratodus* and *Metaceratodus*, an unfortunate circumstance dictated by the poor preservation of specimens'. This difference is the prearticular sulcus being double instead of simple. This feature is evident only in lower tooth plates with bone attached. However, Kemp (1997a) also observed that occlusal pits were less extensive in *Metaceratodus* than in *Ceratodus* and occlusal profiles differed.

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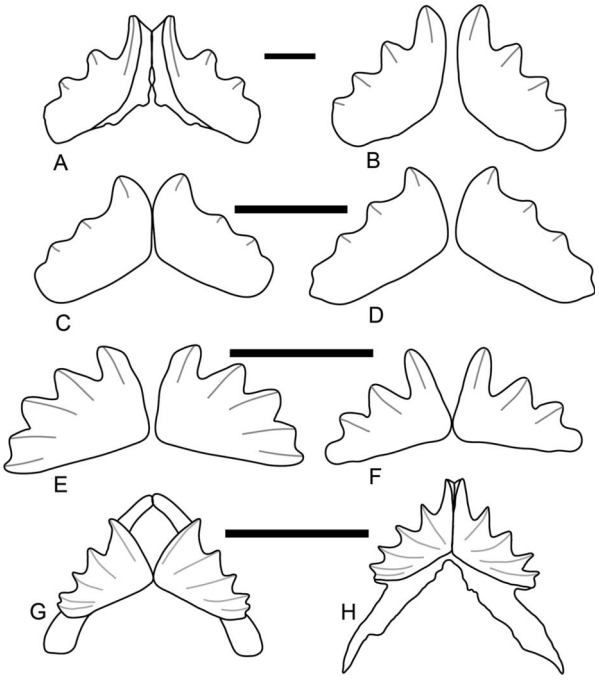

Fig. 9. Comparative reconstructions of tooth plates showing the occlusal patterns, upper jaw on left, lower jaw on right: **A–B**, *Metaceratodus kaopen* (scale bar=1 cm); **C–D**, *Ceratodus latissimus* (Agassiz, 1838) (modified from Kemp 1993). Scale bar=5 cm; **E–F**, *Ferganaceratodus jurassicus* Kaznyshkin & Nessov, 1985 (modified from Kaznyshkin & Nessov 1985). Scale bar=10 cm; **G–H**, *Ptychoceratodus serratus* (Agassiz 1838) (modified from Kemp 1998). Scale bar=10 cm.

Actually, the occlusal pits are very marked in the genotype, *C. latissimus* Agassiz, 1838 but they are restricted in some species such as *C. kaupi* (see Kemp 1993). Additionally, Kemp (1997a) suggested that *Ceratodus* has mainly a boreal distribution (with some exceptions: e.g., *C. diutinus* Kemp 1993 in the Cretaceous and Cenozoic of Australia). Many species assigned to *Ceratodus* have been referred to other genera and others require re-evaluation (see Soto & Perea 2010). Moreover, it has become progressively clear that this assemblage is not monophyletic and may represent either a phyletic grade, an ecomorph or both (Pardo *et al.* 2010).

Kemp (1997a) noted that some tooth plates described and figured by Pascual & Bondesio (1976) from the Cretaceous of northern Patagonia might belong to the Australian species *Metaceratodus wollastoni*. The material was originally identified as *C. iheringi* or *Ceratodus* sp. (Pascual & Bondesio 1976). Later, Apesteguía *et al.* (2007) suggested that a tooth plate figured by Pascual & Bondesio (1976, pl. I, fig. 9) represented a specimen of *M. wollastoni*. Certainly, in comparison with the Australian species (*M. wollastoni*, *M. ellioti*, *M. palmeri* and *M. bonei*), the tooth plates described by Pascual & Bondesio (1976) and many southern South American Late Cretaceous tooth plates resemble those of *M. wollastoni*. However, after studying new and more complete material we found that they differ from those of *M. wollastoni* because most have four ridges in the lower and upper tooth plates (vs five or six), the lower tooth plates are widely separated (rather than contiguous), and occlusal pits are present over the whole occlusal surface (vs no or few occlusal pits on ridges).

Ptychoceratodus cionei, *P. wichmanni* and *C. kaopen* are consistent with the circumscription of *Metaceratodus* in having a double prearticular sulcus (Fig. 3B, E), similar occlusal profiles (Fig. 3A, D), and less extensively developed occlusal pits. Moreover, we propose that the first two of these species are synonyms. The holotype of *M. cionei* (Fig. 3C, D) represents a fragmentary upper tooth plate, and the holotype of *M. wichmanni* (Fig. 3A, B) is a fragmentary lower one. We adopt *M. wichmanni* as the senior synonym.

Apesteguía *et al.* (2007, p. 33) mentioned that the 'crests are dorsoventrally expanded in its labial side' as a character of *M. cionei*. Later Agnolin (2010, p. 31) stressed that this character is 'variable within a single population'. Examination of the holotype shows that this expansion is what remains of the medial pre-mortem erosion of the tooth plate (Fig. 3C, D); see also Churcher & de Iuliis (2001) for similar erosion in *C. humei*. Apesteguía *et al.* (2007, p. 33) mentioned that in *P. cionei* 'the second ridge crest is the largest'. However, the first crest is missing in the holotype, and the character is not seen in the other examples (Apesteguía *et al.* 2007, their fig. 3A, B). This was also noticed by Agnolin (2010), although that author stated that *M. cionei* is distinguished by its more robust proportions, and for having mesiodistally extended crests separated by very shallow clefts (Agnolin 2010 p. 31). These are not valid characters in this case. We found that they are actually upper tooth plates that became eroded during ontogeny. Agnolin (2010; his fig. 8A) referred a specimen from Bajo Trapal Có (Río Negro province) to *M. cionei*, but the tooth plate is markedly different. As for the holotype, this tooth plate lacks the first crest.

All three species discussed here were considered 'mid-sized' and with four ridges (Apesteguía *et al.*, 2007). With more and better-preserved material, we find that at least *M. wichmanni* (including *M. cionei*) actually reach a large size and some plates bear five ridges. However, they are smaller than the largest *Metaceratodus* species (*M. bonei*), which has

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lower tooth plates reaching almost 70 mm long (Kemp 1997a).

Metaceratodus wichmanni and *M. kaopen* differ from the Australian species *M. wollastoni, M. ellioti, M. bonei* and *M. palmeri* (Fig. 10) because most upper and lower tooth plates bear four ridges (vs 5–6 or more); from *M. wollastoni, M. ellioti* and *M. palmeri* because occlusal pits are commonly present on the whole occlusal surface and, in the particularly case of *M. palmeri*, the occlusal pits are coarse and arranged in chevrons. They differ from *M. wollastoni* because the lower tooth plates are widely separated and both upper and lower tooth plates are smaller; and from *M. palmeri* in having a very different occlusal profile, absence of a mediolingual keel, straight (vs curved) lingual edge. They are distinguished from *M. ellioti* in bearing broader and shorter ridges; marked, straight, numerous and more or less deep grooves in the upper symphysis; a pterygopalatine process at the base of the second ridge (against at the base of the third ridge or in the space between the second and third ridges); and the enamel to bone junction rising slightly between each ridge labially.

Metaceratodus wichmanni differs from *M. kaopen* in reaching a larger size, in having more triangular and much shorter upper tooth plates with a smaller inner angle (about 90°), and in being in contact in the symphysis (separated in *M. kaopen*) (Figs 4, 5, 8). Finally, both the upper and lower tooth plates of *M. kaopen* have a wide posterior area (marked heel) instead of a fourth ridge (Fig. 8).

Finally, Apesteguía *et al.* (2007, fig. 3F–H) referred a fragmentary tooth plate from the Anacleto Formation of Río Negro Province to Lepidosirenidae?. The correct collection number of this specimen is MPCN-PV-05-1 according to Pablo Chafrat (pers. comm.). The tooth plate does not appear to belong to a lepidosirenid: the occlusal profile is markedly different, and the occlusal surface is covered with pits. The tooth plate probably belongs to *M. kaopen*.

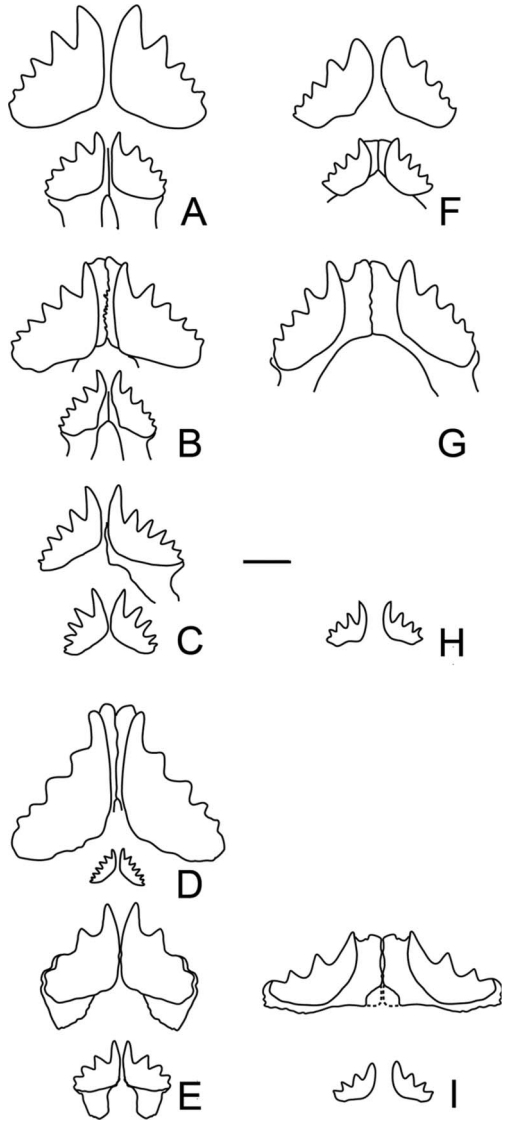

Fig. 10. Reconstructions of *Metaceratodus* Kemp, 1997, tooth plates showing the occlusal patterns, upper jaw on the left, lower jaw on the right. Scale bar=2 cm. **A, B**, *M. wollastoni* Chapman, 1914; **C, D**, *M. palmeri* (Krefft, 1874); **E, F**, *M. ellioti* Kemp 1997a; **G**, *M. bonei* Kemp, 1997a; **H**, *M. wichmanni* (Apesteguía, Agnolin & Claeson, 2007) based on MLP 06-VII-1-1-3 and MACN-RN-1080b; **I**, based on MLP 06-VII-1-1-2. Most modified from Kemp (1997a).

Biogeographic implications

Dipnoans were cosmopolitan during the early and middle Mesozoic. The diversity of preserved lungfishes increased in the Late Triassic with the expanded distribution of fluvial sediments (Schultze 2004). In the Jurassic, with an increase in marine sedimentation, they declined in abundance (Schultze 2004). During the Cretaceous, they were restricted to southern continents except for a few examples from North America (e.g., Kirkland 1987, Kemp 1997a, 1997b, Schultze 2004, Pardo *et al.* 2010). After the Triassic they are unknown from Antarctica. In Cenozoic rocks, dipnoans were reported from several units of Oligocene, Miocene and Pliocene age in Australia (Kemp 1997a, 1997b) and Eocene, Paleocene and Oligocene age in Africa (Longbottom 1984, Murray 2000).

The youngest record of non–lepidosirenid lungfish in Africa is from the Eocene (Longbottom 1984) and in South America from the late Paleocene–earliest Eocene (Cione *et al.* 2010).

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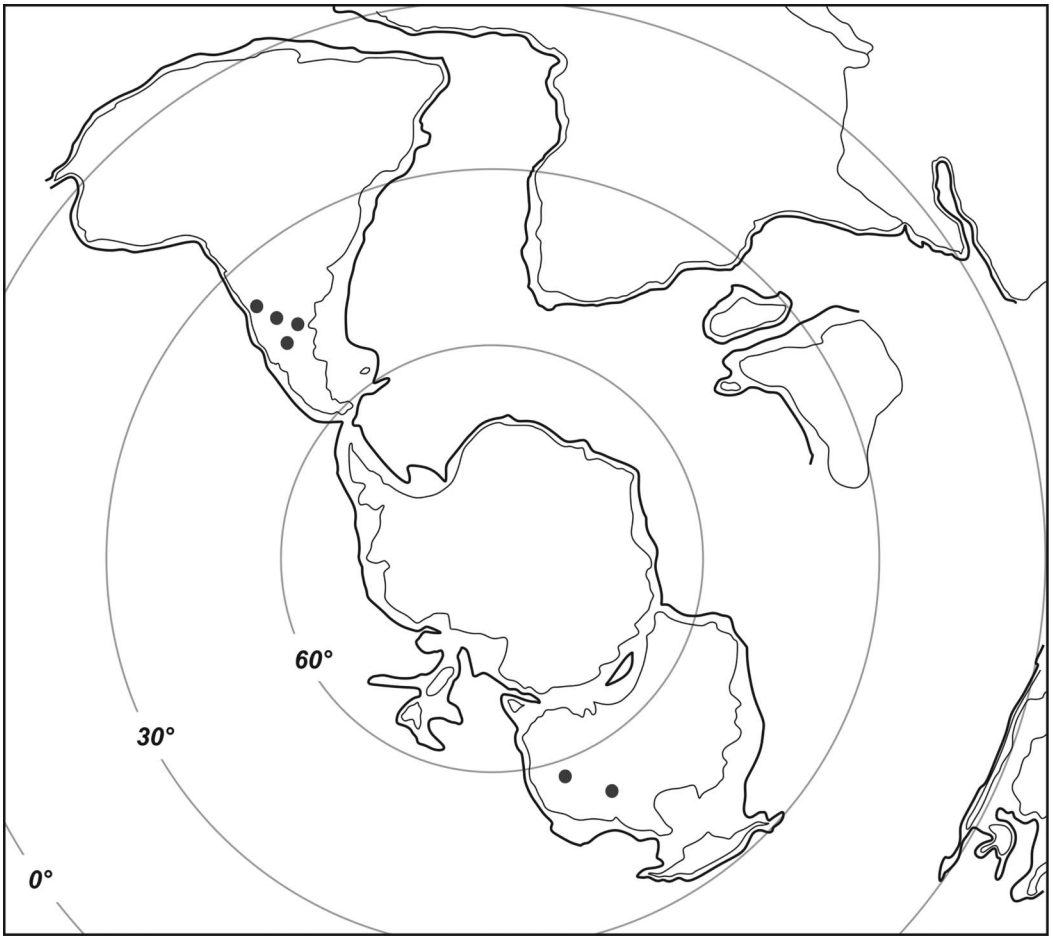

Fig. 11. Late Cretaceous (*ca* 75 Ma) palaeogeographic reconstruction (modified from Vizcaíno *et al.* 1998). Dots show the distribution of *Metaceratodus* in South America and Australia.

The Mesozoic dipnoans are considered primarily freshwater inhabitants, but Schultze (2004) suggested that they could tolerate saltwater. Furthermore, they are also known from fluvial, paralic and marine deposits in the Mesozoic of the United States and Africa (Tabaste 1963, Schultze 1981, Murray 2000). However, the presence of several species in the Late Cretaceous of Australia and South America might be explained by the connection of these landmasses with Antarctica during the Cretaceous (Fig. 11). Moreover, the distributions of various other fossil and recent taxa such as the southern beeches (*Nothofagus* spp.), teleosts such as the osmeriforms Galaxiidae and Aplochitonidae and the perciform Percichthyidae, hadrosaur and ankylosaur dinosaurs, lizards, snakes and marsupial mammals reflect a common pattern (Crisci *et al.* 1991, Pascual *et al.* 2000, Swenson *et al.* 2001, McCarthy 2005, Barrett *et al.* 2010). However, there is an increasing number of Southern Hemisphere taxa for which divergence time estimates do not readily fit the temporal framework of continental fragmentation (Sampson *et al.* 1998). This lack of concordance has led some to conclude that the distribution of these organisms resulted from long-distance (trans-oceanic) dispersal events rather than from a vicariant history. Although trans-oceanic dispersal may have played an important role in several taxa, the possibility that terrestrial connections have existed longer than assumed under traditional geological models has received limited attention in the dispersal–vicariance debate (Van Bocxlaer *et al.* 2006). However, no matter whether theories of prolonged connections, intervening landmasses or a completely enclosed Pacific Basin in the Late Cretaceous prove to be correct, several of the younger phylogenies might still be explained by Gondwanan vicariance (McCarthy 2005; see also Ali & Krause 2011).

Acknowledgements

For partial financial support: ANPCyT (PICT 913), CONICET (PIP 5608) and Universidad Nacional de La Plata. For valuable information: A. Kemp,

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J.R. Casciotta, N. Krupina, A. Murray and M. Manceñido. For permision to examine dipnoan material: Museo Padre Molina, Río Gallegos, Argentina (A. Tauber); Museo de La Plata, La Plata, Argentina (M. Reguero); Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina (A. Kramarz); Museo 'Carmen Funes', Plaza Huincul, Argentina (R. Coria); Museo Patagónico de Ciencias Naturales, General Roca, Río Negro, Argentina (P. Chafrat); Museo Prof. Dr Juan Olsacher (A. Garrido); Natural History Museum, London, England (A. Longbottom). For photographic material: P. Chafrat. For assistance with the figures and English: Lic. L.L. Rasia and Lic. D.A. Cabrera. For review of the manuscript and valuable comments: L. Cavin and an anonymous reviewer.

References

Agassiz, L., 1833–1844. Recherches sur les poissons fossiles. Neuchâtel et Soleure (Petitpierre) Tome II (1833–1843), pt. 1, xii + 306 pp., pt. 2 (1843), 336 pp; Tome III (1833–1843), viii + 390 pp.

Agnolin, F., 2010. A new species of the genus *Atlantoceratodus* (Dipnoiformes: Ceratodontoidei) from the uppermost Cretaceous of Patagonia and a brief overview of fossil dipnoans from the Cretaceous and Paleogene of South America. *Brazilian Geographical Journal: Geosciences and Humanities Research Medium 1*, 162–210.

Ali, J.R. & Krause, D., 2011. Late Cretaceous bioconnections between Indo-Madagascar and Antarctica: refutation of the Gunnerus Ridge causeway hypothesis. *Journal of Biogeography*. doi:10.1111/j.1365-2699.2011.02546.x.

Ameghino, F., 1898. Sinopsis geológico-paleontológica. *Segundo Censo de la República Argentina 1. Territorio, Tercera Parte 1*, 111–255, figs 1–104.

Apesteguía, S., Agnolin, F. & Claeson, K., 2007. Review of Cretaceous dipnoans from Argentina (Sarcopterygii: Dipnoi) with descriptions of new species. *Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' 9*, 27–40.

Arratia, G. & Cione, A.L., 1996. The fish fossil record of southern South America. *Münchener Geowissenschaft Abhanlungen 30A*, 9–72.

Ballent, S.C., 1980. Ostrácodos de ambiente salobre de la Formación Allen (Cretácico Superior) en la Provincia de Río Negro (República Argentina). *Ameghiniana 17*, 67–82.

Barrett, P.M., Rich, T.H., Vickers-Rich, P., Tumanova, T.A., Inglis, M., Pickering, D., Kool, L. & Kear, B.P., 2010. Ankylosaurian dinosaur remains from the Lower Cretaceous of southeastern Australia. *Alcheringa 34*, 205–217.

Bonaparte, J.F., 1990. New Late Cretaceous mammals from the Los Alamitos Formation, northern Patagonia. *National Geographic Research 6*, 63–93.

Bonaparte, J.F., 2002. New Dryolestida (Theria) from the Late Cretaceous of Los Alamitos, Argentina, and paleogeographical comments. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 224*, 339–371.

Bonaparte, J.F., Franchi, M.R., Powell, J.E. & Sepulveda, E.C., 1984. La Formación Los Alamitos (Campaniano–Maastrichtiano) del sudeste de Río Negro, con descripción de *Kritosaurus australis* nov. sp. (Hadrosauridae). Significado paleogeográfico de los vertebrados. *Revista de la Asociación Geológica Argentina 39*, 284–299.

Bonaparte, J.F., Báez, A.M., Cione, A.L., Andreis, R., Broin, F., Powell, J.E. & Albino, A., 1987. Résumé. In *The Late Cretaceous Fauna from Los Alamitos*. Bonaparte, J.F., ed., *Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Paleontología 3*, 171–178.

Calvo, J.O., Porfiri, J.D., González-Riga, B.J. & Kellner, A.W.A., 2007. A new Cretaceous terrestrial ecosystem from Gondwana with the description of a new sauropod dinosaur. *Anais da Academia Brasileira de Ciências 79*, 529–541.

Cavin, L., Suteethorn, V., Buffetaut, E., Tong, H., 2007. A new Thai Mesozoic lungfish (Sarcopterygii, Dipnoi) with an insight into post-Palaeozoic dipnoan evolution. *Zoological Journal of the Linnean Society 149*, 141–177.

Chapman, F., 1914. On a new species of *Ceratodus* from the Cretaceous of New South Wales. *Proceedings of the Royal Sociey of Victoria 27*, 25–27.

Churcher, C. & De Iuliis G., 2001. A new species of *Protopterus* and a revision of *Ceratodus humei* (Dipnoi: Ceratodontiformes) from the Late Cretaceous Mut Formation of eastern Dakhleh Oasis, Western Desert of Egypt. *Palaeontology 44*, 305–323.

Cione, A.L., 1987. The Late Cretaceous fauna of Los Alamitos, Patagonia, Argentina. The fishes. *Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Paleontología 3*, 111–120.

Cione, A.L., Gouiric–Cavalli, S., Goin, F.J. & Poiré, D., 2007. *Atlantoceratodus*, a new genus of lungfish from the Upper Cretaceous of South America and Africa. *Revista del Museo de La Plata 10*, 1–12.

Cione, A.L., Gouiric–Cavalli, S., Goin, F.J. & Gelfo, J.N., 2010. The youngest non-lepidosirenid lungfish of South America (Dipnoi, latest Paleocene–earliest Eocene, Argentina). *Alcheringa 35*, 193–198.

Crisci, J.V., Cigliano, M.M., Morrone, J.J. & Roig, S., 1991. Historical biogeography of southern South America. *Systematic Zoology 40*, 152–171.

De La Fuente, M., Barbieri, R. & Chafrat, P., 2010. Una tortuga Chelidae (Testudines: Pleurodira) de cuello largo en el Grupo Neuquén, Río Negro, Argentina. Significado cronológico y paleobiogeográfico. *Andean Geology 37*, 399–413.

Dingus, L., Clarke, J., Scott, G.R., Swisher, C., Chiappe, L.M. & Coria, R.A., 2000. Stratigraphy and magnetostratigraphic/faunal constraints for the age of sauropod embryo-bearing rocks in the Neuquén Group (Late Cretaceous, Neuquén Province, Argentina). *American Museum Novitates 3290*, 1–11.

Gill, T., 1872. Arrangement of the families of fishes, or classes Pisces, Marsipobranchii and Leptocardii. *Smithsonian Miscellaneous Collections 247*, 1–49.

González-Riga, B.J., 1999. Hallazgo de vertebrados fósiles en la Formación Loncoche, Cretácico Superior de la Provincia de Mendoza, Argentina. Edad y procedencia estratigráfica. *Ameghiniana 36*, 401–409.

Gottfried, M.D., Stevens, N.J., Roberts, E.M., O'Connor, P.M. & Chami, R., 2009. A new Cretaceous lungfish (Dipnoi: Ceratodontidae) from Rukwa rift Basin, Tanzania. *African Natural History 5*, 31–36.

Jaekel, O., 1926. Zur Morphogenie der Gebisse und Zähne. *Vierteljahrsschrift Zahnheilkunde 1926*, 217–242.

Kaznyshkin, M.N. & Nessov, L.A., 1985. A lungfish and turtle from Upper Jurassic of Northern Fergana, Lhirghiz SSR. *Vestnik Zoologii 1*, 33–39.

Kemp, A., 1993. *Ceratodus diutinus*, a new ceratodont from Cretaceous and Late Oligocene–medial Miocene deposits in Australia. *Journal of Paleontology 67*, 883–888.

Kemp, A., 1997a. Four species of *Metaceratodus* (Osteichthyes: Dipnoi, Family Ceratodontidae) from Australian Mesozoic and Cenozoic deposits. *Journal of Vertebrate Paleontology 17*, 26–33.

Kemp, A., 1997b. A revision of Australian Mesozoic and Cenozoic lungfish of the Family Neoceratodontidae (Osteichthyes: Dipnoi), with a description of four new species. *Journal of Paleontology 71*, 713–733.

Kemp, A., 1998. Skulls of post–Paleozoic lungfish. *Journal of Vertebrate Paleontology 18*, 43–63.

Kemp, A., 2001. Petrodentine in derived dipnoan tooth plates. *Journal of Vertebrate Paleontology 21*, 422–437.

Kirkland, J.I., 1987. Upper Jurassic and Cretaceous lungfish tooth plates from the western interior, the last dipnoan faunas of North America. *Hunteria 2*, 1–16.

Krefft, G., 1874. Fossil tooth of *Ceratodus palmeri*. *Nature 9*, 293.

Longbottom, A.E., 1984. New Tertiary pycnodonts from the Tilemsi valley, Republic of Mali. *Bulletin of the British Museum Natural History 38*, 1–26.

Martin, M., 1982. Nouvelles donnés sur la phylogénie et la systématique des dipneustes postpaléozoiques. Conséquences stratigraphiques et paléogéographiques. *Geobios, Mémoire Spéciale 6*, 53–64.

Martinelli, A.G. & Forasiepi, A.M., 2004. Late Cretaceous vertebrates from Bajo Santa Rosa (Allen Formation), Río Negro Province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). *Revista del Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia' 6*, 257–305.

McCarthy, D., 2005. Biogeographical and geological evidence for a smaller, completely-enclosed Pacific Basin in the Late Cretaceous. *Journal of Biogeography 32*, 2161–2177.

Müller, J., 1845. Über den bau un die Grezen der ganoiden und über das natürliche System der Fische. *Abhandlungen der akademie der Wissenschaften zu Berlin 1844*, 117–216.

Murray, A.L., 2000. The Palaeozoic, Mesozoic and early Cenozoic fishes of Africa. *Fish and Fisheries 1*, 111–145.

Pardo, J.D., Huttenlocker, A.K., Small, B.J. & Gorman II, M.A., 2010. The cranial morphology of a new genus of lungfish (Osteichthyes: Dipnoi) from the Upper Jurassic Morrison Formation of North America. *Journal of Vertebrate Paleontology 30*, 1352–1359.

Pascual, R. & Bondesio, P., 1976. Notas sobre vertebrados de la frontera Cretácico-Terciaria. III: Ceratodontidae (Pisces, Osteichthyes, Dipnoi) de la Formación Coli-Toro y de otras unidades del Cretácico tardío de Patagonia y sur de Mendoza. Sus implicancias paleobiogeográficas. *Actas del Congreso Geológico Argentino 1*, 565–578.

Pascual, R., Goin, F.J., González, P., Ardolino, A. & Puerta, P., 2000. A highly derived docodont from the Patagonian Late Cretaceous: evolutionary implications for Gondwanan mammals. *Geodiversitas 22*, 395–414.

Richter, M. & Toledo, C.E., 2008. The first Triassic lungfish from South America (Santa Maria Formation, Parana Basin) and its bearing on geological correlations within Pangea. In *Fishes and the Break-up of Pangaea*. Cavin, L., Longbottom, A. & Richter, M., eds, Geological Society, London, Special Publication 295, 43–54.

Salgado, L., Coria, R.A., Magalhaes Ribeiro, C.M., Garrido, A., Rogers, R., Simón, M.E., Arcucci, A.B., Rogers, K.C., Carabajal, A.P., Apesteguía, S., Fernández, M., García, R.A. & Talvei, M., 2007. Upper Cretaceous dinosaur nesting sites of Río Negro (Salitral Ojo de Agua and Salinas de Trapalcó-Salitral de Santa Rosa), northern Patagonia, Argentina. *Cretaceous Research 28*, 392–404.

Sampson, S.D, Witmer, L.M., Forster, C.A., Krause, D.W., O'Connor, P.M., Dodson, P. & Ravoavy, F., 1998. Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana. *Science 280*, 1048–1051.

Schultze, H-P., 1981. A dipnoan tooth plate from the Lower Cretaceous of Kansas, USA. *Transactions of the Kansas Academy of Sciences 84*, 187–195.

Schultze, H-P., 1992. Dipnoi. In *Fossilium Catalogus I: Animalia 131*, F. Westphal, ed. 1–464.

Schultze H-P., 2004. Mesozoic sarcopterygians. In *Mesozoic Fishes 3—Systematics, Paleoenvironment and Biodiversity*. Arratia, G. & Tintori A., eds, Verlag Dr Friedrich Pfeil, München, 463–492.

Scotese, C.R., 1987. *Atlas of Mesozic and Cenozoic plate tectonic reconstructions*. Technical Report N°90, Paleoceanographic Mapping Project, Institute for Geophysics, University of Texas.

Soto, M. & Perea, D., 2010. Late Jurassic lungfishes (Dipnoi) from Uruguay, with comments on the systematics of Gondwanan ceratodontiforms. *Journal of Vertebrate Paleontology 30*, 1049–1058.

Swenson, U., Hill, R. & McLoughlin, S., 2001. Biogeography of *Nothofagus* supports the sequence of Gondwana break-up. *Taxon 50,* 1025–1041.

Tabaste, N., 1963. Étude des restes des poissons du Crétacé Saharien. *Mémoires de l'Institute Français d'Afrique Noire, Mélange Ichthyologique 68*, 437–485.

Van Bocxlaer, I., Roelants, K., Biju, S.D., Nagaraju, J. & Bossuyt, F., 2006. Late Cretaceous vicariance in Gondwanan amphibians. *PLoS ONE 1,* e74 doi:10.1371/journal.-pone.0000074.

Vizcaíno, S.F., Pascual, R., Reguero, M.A. & Goín, F.J., 1998. Antarctica as background for Mammalian evolution. *Asociación Paleontológica Argentina, Publicación Especial 05*, 199–209.

Wichmann, R., 1924. Nuevas observaciones geológicas en la parte oriental del neuquén y en el territorio del Río Negro. *Dirección General de Minas, Geología e Hidrogeología (Sección: Geología) 2*, 1–32.

Wichmann, R., 1927. Sobre las facies lacustre Senoniana de los estratos con dinosaurios y su fauna. *Boletin de la Academia Nacional de Ciencias de Córdoba 30*, 383–405.

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