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Review of Cretaceous dipnoans from Argentina (Sarcopterygii: Dipnoi) with descriptions of new species

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Abstract: In this paper we review the fossil ceratodontiform record from the Cretaceous of Argentina. We report the oldest dipnoan record from Argentina, coming from the Cenomanian of Northwestern Patagonia, Río Negro province. The species *«†Ceratodus» iheringi* is reassigned. Additionally, four new species are described. Ceratodontiforms were considered extinct in Laurasia after the mid-Cretaceous, with a brief «reappearance» during the Maastrichtian before their definitive extinction from South America and most of the world by K/P boundary. Based on our phylogenetic analysis, using characters derived primarily from tooth plates, we propose that the genus *†Metaceratodus* is more closely related to *Neoceratodus* than either is to *†Ceratodus* or *†Ptychoceratodus*, supporting prior hypotheses. In two most parsimonious trees, the two new genera here described are basal, being one of them sister taxa to Ceratodontoidea nov. and the other unresolved with respect to *Protopterus*.

Key words: Paleontology, Cretaceous, dipnoans, Patagonia, Argentina.

Dipnoi (lungfishes) are a monophyletic group of sarcopterygians, restricted today to the Southern Hemisphere (Kemp, 1997). They are represented by two living orders: Lepidosireniformes (Africa and South America) and Ceratodontiformes (Australia). During the Paleozoic and Mesozoic, however, dipnoans had a global distribution. In South America, the record of ceratodontiforms spans the Late Cenomanian (Apesteguía *et al*., 2001) through the Paleocene (Schultze, 1991). In Argentina, ceratodontiforms are perhaps the most abundant fossils found in formations representing the 'Lacustrine Senonian', the first stages of the Campanian-Maastrichtian sea transgression (e.g. Los Alamitos, La Colonia, Paso del Sapo Formations; Pascual & Bondesio, 1976).

Since Ameghino (1899) described the tooth plate of *´†Ceratodus´ iheringi*, from the Mata Amarilla Formation (see F. Ameghino, 1906 and C. Ameghino, 1916), their systematic position remained uncertain (Martin, 1981, 1982). Despite the fact that in Argentina, localities yield an abundance of fossil dipnoan tooth plates (Fig. 1a), the diversity and stratigraphic distribution of these specimens has not been reported throughly. This is also true for the remaining countries of South America, where the Cretaceous record of dipnoans is sparse and strongly biased (Souza Cunha & Ferreira, 1980; Gayet & Brito, 1989; Schultze, 1991).

Few phylogenetic reviews have been conducted on fossil dipnoans from Argentina due to the lack of morphological data beyond tooth plates. Martin (1982: p. 56) reviewed the ceratodontiform record of Argentina as part of an analysis of postpaleozoic lungfishes, and from the Campanian-Maastrichtian of the Los Alamitos Formation. Cione (1987) described *'†Ceratodus' iheringi*. Both Martin (1982) and Cione (1987) related *'†Ceratodus' iheringi* with *†Ptychoceratodus madagascarensis*. Kemp (1997) reassigned *'†Ceratodus' iheringi* to *†Metaceratodus,* whereas Schultze (1991) (see also Kirkland, 1987) proposed that they were related to those coming from the Upper Jurassic of North America and the Upper Cretaceous of Madagascar.

In this paper we conduct a new study of Argentinian ceratodontiform systematics, prompted by the discovery of well-preserved ceratodontiform tooth plates from several Cretaceous beds of Patagonia. We also address the value of tooth plates in systematic analyses and review the temporal distribution of South American Ceratodontiformes.

METHODS

Our character matrix includes characters adapted from Martin (1982), Martin *et al*. (1999), Kirkland (1988), and Kemp (1998), as well as new characters discovered and scored for this study

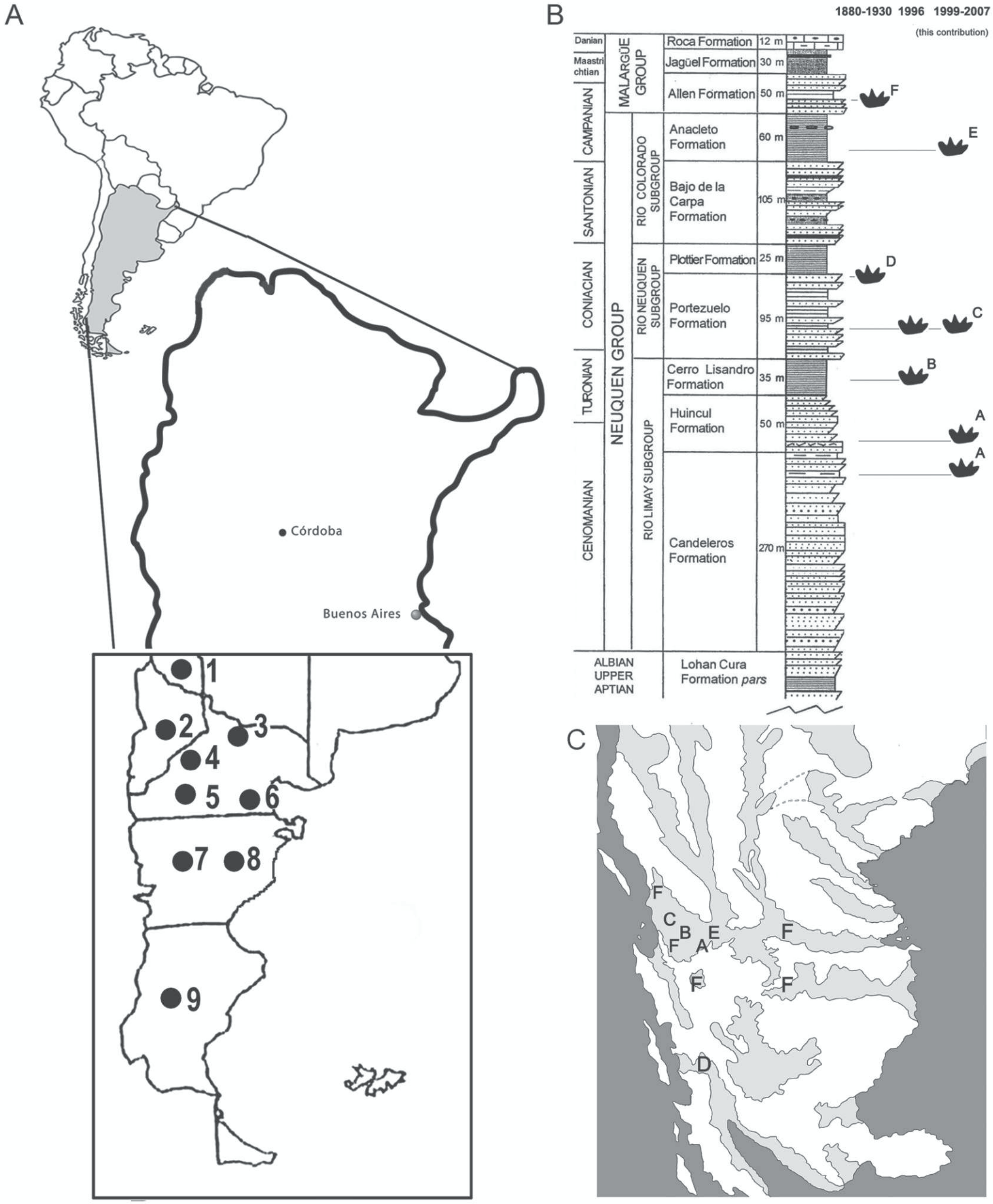

Fig. 1. **A.** Map of South America showing fossiliferous localities. Patagonian region into the box shows the localities that provided dipnoan remains, identified with the following numbers: **1**, Ranquil Có; **2**, Sierra del Portezuelo; **3**, Paso Córdova; **4**, La Buitrera; **5**, Ingeniero Jacobacci; **6**, Los Alamitos; **7**, Paso del Sapo; **8**, La Colonia; **9**, Mata Amarilla. **B**, Stratigraphic column showing the aproximate levels of ceratodontiform findings and the bearing units in the studied region. Shaded tooth plates do not represent any special taxon. D and F include also findings outside the Neuquén Group areal distribution. The inclusion in the stratigraphic column is only for reference. C, Paleogeographic reconstruction of the southernmost tip of South America during Santonian to Early Campanian times, before the Kawas Sea ingression (modified from Apesteguía, 2002). Lettering represent the dipnoan findings related to the bearing stratigraphic level; aulacogens are corrected; valley shapes and coastal details are not rigorous.

(see Appendix 1). Parsimony analysis was performed on the matrix of 9 taxa and 28 characters (see Appendix 2). Ceratodontiform tooth plates examined are primarily Jurassic and post-Jurassic, with one exception, the Triassic †ceratodontid *†Ptychoceratodus* (Jaeckel 1926) due to its relevance to Gondwanan taxa. The matrix was analyzed with NONA (Goloboff, 1993). The analysis resulted in two most parsimonious trees, the strict consensus of which resulted in a single tree (Fig. 6). (Tree description using NONA: 70 length, CI 67, and RI 55.

Abbreviations and terminology. MACN, Museo Argentino de Ciencias Naturales «Bernardino Rivadavia», Buenos Aires; MLP, Museo de Ciencias Naturales de La Plata, La Plata; MEF, Museo Paleontológico «Egidio Feruglio», Trelew; PVPH, Museo Provincial «Carmen Funes», Plaza Huincul; MPCA, Museo Provincial «Carlos Ameghino», Cipolletti; MPCN, Museo Patagónico de Ciencias Naturales, General Roca, Río Negro; ROM, Royal Ontario Museum, Collection of Vertebrate Fossils, Toronto, Canada. Kemp (1998) is followed for cranial bone terminology.

SYSTEMATIC PALAEONTOLOGY

Dipnoi Müller, 1845
Ceratodontiformes Berg, 1940

†Chaoceratodus gen. nov.

Type species. †Chaoceratodus portezuelensis.

Diagnosis. Small sized (see Table I). Upper tooth plates with four ridge crests, being the second the smallest. A non-sculptured tubercle is present on the labial side of each ridge crest and midway up the first.

Etymology. Chao: from mapuche ´father´.

†Chaoceratodus portezuelensis, nov. sp.
(Fig. 2A)

Diagnosis. As for the genus.

Etymology. From Sierra del Portezuelo, the place of discovery.

Holotype. MCF-PVPH-373, left upper tooth plate.

Horizon and locality. This specimen was found in Portezuelo Formation, Sierra del Portezuelo, Neuquén Province (Turonian; see Novas, 1997).

Description. The tooth plate is subtriangular, with four robust and short ridge crests. Clefts between the ridges are wide and shallow. The labial profile of the crests is not steep and ends in a single last crest. The first crest is long and broad, without a marked slope. The crests are relatively straight and radiating. The fourth crest is very large when compared with the second and the third. Occlusal pits are nearly absent on the occlusal surface. There are large tubercles in the labial edge of the crests except in the first where the tubercle is located toward the central region.

†Chaoceratodus represents a basal genus when considering it in reference to Ceratodontiformes. It retains several plesiomorphic traits, such as a straight lingual margin of the tooth plate. The occlusal surface is uniformly and completely punctuated and shows a very short first ridge crest.

Also from the Portezuelo Formation at Sierra del Portezuelo, a partial lower tooth plate (PVPH 373; Fig. 2B) of a large indeterminate dipnoan was recovered. This plate represents a pathological specimen because it shows two abnormal bumps on its crushing surface.

Unnamed Node 1

Definition. Ceratodontiform dipnoans more closely related to *†Ameghinoceratodus* and Ceratodontoidea nov. than to *†Chaoceratodus*.

Diagnosis. ABC angle less than 110º; upper tooth plates with five ridge crests.

Comments. This node includes all post-Jurassic ceratodontiform taxa except the genus *†Chaoceratodus*.

†Ameghinoceratodus gen. nov.

Type species. †Ameghinoceratodus iheringi (Ameghino, 1899).

Diagnosis. Small sized (see Table I). All the ridge crests of tooth plates are acute and gracile. Upper tooth plates have five ridge crests and the lower have four. The first upper ridge crest is curved and the others are nearly straight. The last two upper ridge crests are rather similar in size and oriented strongly backwards.

Etymology. Ameghino, for Florentino, Carlos and Juan, the formidable team of brothers that strenghtened the Paleontological bases in Argentina.

†Ameghinoceratodus iheringi **(Ameghino, 1899)** ***nov. comb.***(Fig. 2 C – E)

Diagnosis. As for the genus.*Holotype*. MLP 21-967, left upper tooth plate (Fig. 2C).

Referred material. Materials recently collected in the Mata Amarilla Formation (Goin *et al*., 2002, and pers. obs., Fig. 2E); MPCA 401, left lower tooth plate, Huincul Formation (see Apesteguía *et al*. 2001; Fig. 2D); MACN PV RN157C, right lower tooth plate, Los Alamitos Formation (see Bonaparte *et al*. 1984), and

Table 1. Measurements (in mm) of fossil tooth plates.

Taxon Studied	Specimen	Total Length	Height	
			1º ridge crest	2º ridge crest
†Chaoceratodus portezuelensis	MCF-PVPH-373	12.8	8.3	4.5
†Ptychoceratodus cionei	MACN-RN 157B	—	—	18.8
†Ptychoceratodus wichmanni	MACN-RN 157A	—	—	14.1
†Ameghinoceratodus iheringi	MPCA 401	13.5	—	8.5
†Ceratodus argentinus	MPCA 402	—	—	21
†Ceratodus kaopen	MPCN-PV 1-1	31	21.6	16

Portezuelo Formation at Cerros Colorados (south) (MCF-PVPH-572, Fig. 5g).

Horizon and locality. The type specimen comes from the Mata Amarilla Formation (Coniacian), Santa Cruz Province.

Description. Upper tooth plates with five ridge crests, whereas the lower have only four. Each crest is narrow and slender. Clefts corresponding to ridges are narrow and deep. The labial profile of the crests is steep and ends in a single vertical ridge. The first crest is relatively long and thin, with a marked angle on the labial side. All crests can be curved, though the degree of curvature may vary. The fourth crest is usually long (when compared with other ceratodontiform genera, e.g. *†Ceratodus*). The lingual profile could be straight or slightly concave. Occlusal pits are nearly absent.

Comments. *†Ameghinoceratodus iheringi*, consigned by Ameghino as *Ceratodus iheringi*, has an exceptionally wide biochron that extends from Cenomanian to Maastrichtian times. We did not include *†Ameghinoceratodus iheringi* nov. within the genera *†Metaceratodus* or *†Ptychoceratodus* (*contra* Kemp, 1997; Martin, 1982) because it lacks several derived characters shared by the aforementioned genera, such as: medial edge of lower tooth plates not bent and lingual margin of tooth plates straight or concave (instead of convex). The material MCF-PVPH-572 from the Portezuelo Formation (Fig. 5g) can be assigned to this genus because of the strongly backwards oriented last two upper ridge crests, that are also similar in size each other.

Ceratodontoidea *nov.*

Type species. *†Ceratodus latissimus* Agassiz, 1838 (Fig. 2j)

Definition. The node that includes Neoceratodontidae, †Ceratodontidae (†Ptychoceratodontinae + †Ceratodontinae), their common ancestor and all of its descendants.

Diagnosis. The medial edge of the lower tooth plate is bent; the lingual margin of the upper and lower tooth plates is convex; anteroposterior length of tooth plates more than 2,5 cm; upper plates with six ridge crests.

†Ceratodontidae Gill, 1872

Type species. *†Ceratodus latissimus* Agassiz, 1838.

Modified definition. Ceratodontiform dipnoans more closely related to *†Ceratodus sturii* and *†Ptychoceratodus serratus* than to *Neoceratodus forsterii*.

Diagnosis. JLM descendant process absent; posterior calvarium formed by YZ, JLM, I, ABC; short ridge crests on tooth plates; upper symphysis oblong, lower symphysis linear; Four to five ridge crests on lower tooth plates.

Remarks. †Ceratodontidae (*sensu* Gill, 1872) refers to the type species *†Ceratodus latissimus* (Agassiz, 1838), and for diagnosis of the subfamily †Ceratodontinae. Taking into account the almost identical morphology of *†Ceratodus sturii* respect to *C. latissimus* (Fig. 2j) and the presence of highly diagnostic cranial materials, we have used *†Ceratodus sturii* (Teller, 1891) as the representative of the genus in our phylogenetic analysis (Fig. 6).

†Ceratodontinae (Gill, 1872) *nov. comb.*

Type species. *†Ceratodus latissimus* Agassiz, 1838.

Modified definition. Ceratodontiform dipnoans more closely related to *†Ceratodus sturii* than to *†Ptychoceratodus serratus*. The taxon was evaluated only for species of *Ceratodus* but further phylogenetic analyses could show other genera as included here.

Diagnosis. Tooth plates with low and wide ridge crests.

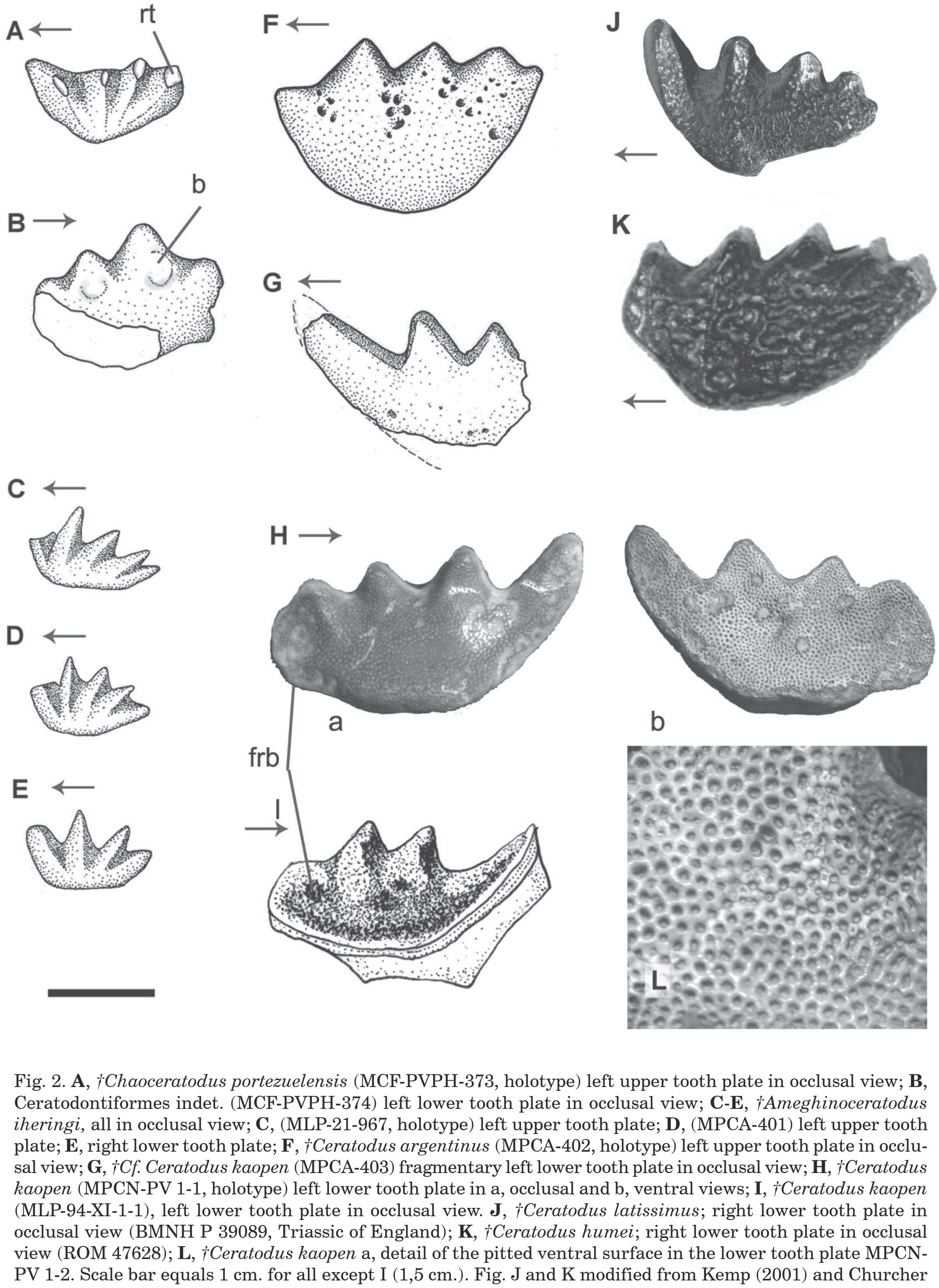

Fig. 2. **A**, *†Chaoceratodus portezuelensis* (MCF-PVPH-373, holotype) left upper tooth plate in occlusal view; **B**, Ceratodontiformes indet. (MCF-PVPH-374) left lower tooth plate in occlusal view; **C-E**, *†Ameghinoceratodus iheringi,* all in occlusal view; **C**, (MLP-21-967, holotype) left upper tooth plate; **D**, (MPCA-401) left upper tooth plate; **E**, right lower tooth plate; **F**, *†Ceratodus argentinus* (MPCA-402, holotype) left upper tooth plate in occlusal view; **G**, *†Cf. Ceratodus kaopen* (MPCA-403) fragmentary left lower tooth plate in occlusal view; **H**, *†Ceratodus kaopen* (MPCN-PV 1-1, holotype) left lower tooth plate in a, occlusal and b, ventral views; **I**, *†Ceratodus kaopen* (MLP-94-XI-1-1), left lower tooth plate in occlusal view. **J**, *†Ceratodus latissimus*; right lower tooth plate in occlusal view (BMNH P 39089, Triassic of England); **K**, *†Ceratodus humei*; right lower tooth plate in occlusal view (ROM 47628); **L**, *†Ceratodus kaopen* a, detail of the pitted ventral surface in the lower tooth plate MPCN-PV 1-2. Scale bar equals 1 cm. for all except I (1,5 cm.). Fig. J and K modified from Kemp (2001) and Churcher & de Iuliis (2001) respectively. Arrows indicate rostral direction. Abbreviatures: b, bump; frb, fourth ridge basin; rt, ridge tubercle.

***†Ceratodus argentinus* sp. nov.**(Fig. 2 F)

Diagnosis. Mid-sized (see Table I). Upper tooth plates with five ridge crests. The third crest is larger than the fourth. The plate becomes thinner at the back.

Etymology. From Argentina, the country in which the new species was found.

Holotype. MPCA 402, left upper tooth plate that lacks most of its first crest.

Horizon and locality. Candeleros Formation (Cenomanian). La Buitrera (Río Negro Prov.).

Description. The tooth plate is low, subtriangular, with four robust, short crests. A fifth crest is present though reduced in size. Clefts between the ridges are wide and shallow. The labial profile of the crests is not steep and ends in a heel. The crests are subequal in size and morphology, nearly straight and radiating. Occlusal pits are sparse and are distributed mainly between the crests.

†Ceratodus argentinus is similar to*† C. concinnus* (sensu Martin, 1982) in having a reduced fifth ridge crest and a tall third crest ridge. It is similar to *†C. fossanovum* (Kirkland, 1988) of the Upper Jurassic Morrison Formation (United States) in having a lingually expanded margin forming a flat crushing surface.

***†Ceratodus kaopen* sp. nov.**
(Fig. 2 H)

Diagnosis. Mid-sized (see Table I). Upper tooth plates with four crests. The anterolingual region forms a tall ridge. The second and third crests are tall and bent lingually. The fourth crest is very low and squared.

Etymology. From *kaopen*, meaning «reddish» in the northern Tehuelchean (Patagonian natives) language, because of its finding in sediments of the Río Colorado («Red River») Subgroup.

Holotype. MPCN-PV 1-1, complete left lower tooth plate.

Referred material. MLP 94-XI-1-1, complete left lower tooth plate, MPCN-PV 1-2, anterior fragment with two ridges of a right lower tooth plate, MPCN-PV 1-3, anterior fragment with two ridges of a right upper tooth plate with cranial bone attached.

Horizon and locality. Bajo de la Carpa Formation (Santonian). Paso Córdova (Río Negro Province).

Description. The tooth plate is subtriangular, with four robust and short crests. Clefts between the ridges are wide and shallow. The labial profile of the crests is not steep and ends in a single last crest. The crests are nearly straight. The first crest is long and broad, more pronounced than the adjacent two crests, without a marked slope and only slightly bent, preserving a rostral instead of a lateral direction. The ABC angle is pronounced as in *Ameghino-ceratodus* rather than gentle as in *Ptycho-ceratodus*. The fourth crest is very wide, square and its occlusal surface is nearly flat. Caudally and lingually from the fourth crest, there is a marked depression for an upper crest. Occlusal pits are nearly absent in the occlusal surface. The second and third crests are dorsally convex.

†Ceratodus kaopen is similar to *†C. frazieri*, (Ostrom, 1970) from the Jurassic Morrison Formation (United States) in having a large first ridge crest, and in showing an anteroposteriorly expanded fourth ridge crest forming a flat crushing surface (Kirkland, 1987).

Other ceratodontids

By 1995 to 1999, Rodolfo Coria's parties to the Bayo Mesa, Cerros Colorados and Portezuelo Hills collected abundant material of ceratodontiform dipnoans. They were briefly mentioned in an abstract (Coria *et al*., 1996) and kindly offered to be studied here. These specimens are important as they are stratigraphically far from any marine transgression and they clearly support the abundance and big size of dipnoans in fluvial and lacustrine fully freshwater environments.

Recorded ceratodontids include the material MCF-PVPH-426,432,500 (Figs. 4a, c, e), belonging to the genus *Ceratodus* itself, considering their rounded crests, with a low occlusal surface. This material comes from the Cerro Lisandro Formation at the Cerro Bayo Mesa (426,432) and the Cerros Colorados localities.

†Ptychoceratodontinae (Martin, 1982)
nov. comb.

†Ptychoceratodus Jaeckel, 1926

Type species. †Ptychoceratodus serratus (Agassiz 1838).

Modified definition. Ceratodontiform dipnoans more closely related to †Ptychoceratodus serratus than to †Ceratodus sturii. The taxon was evaluated only for species of Ptychoceratodus but further phylogenetic analyses could show other genera as included here.

Modified diagnosis. Calvarian bones distribution: three bones in medial and mediolateral series; posterior calvarium formed by I, AB; calvarium emarginated only on its posterior edge; occlusal perforations distributed mainly among the ridge crests; four acute ridge crests in the lower tooth plates; fourth ridge crest on lower tooth plate present and well developed.

†Ptychoceratodus cionei sp. nov.
(Fig. 3 A, B)

Diagnosis. Mid-sized (see Table I). Upper tooth plate with four crests that widens towards the labial edge. The 2nd ridge crest is the largest.

Etymology. After Prof. Dr. Alberto Cione, Argentinian paleoichthiologist.

Holotype. MACN PV RN157B, left lower tooth plate.

Referred material. MACN PV RN157 *pars*; Wichmann (1924; Plate VII, fig. 5).

Horizon and locality. Los Alamitos Ranch (Río Negro Province). Los Alamitos Formation (Campanian-Maastrichtian; see Bonaparte *et al*. 1984).

Description. The tooth plate is subtriangular, with four robust and acute crests. Clefts between the ridges are wide and deep. The labial profile of the crests is steep and ends in a single last crest. The first crest shows a marked slope. The crests are nearly straight and radiating. Occlusal pits are present and are well developed over the crests. The crests are dorsoventrally expanded in its labial side.

†Ptychoceratodus cionei is similar to *†P. madagascariensis* (=*Ferganaceratodus* of Martin *et al*., 1999) in having an obtuse lingual angle and smooth ridge crests not directed anteriorly (Martin, 1982). It shares with *†P. wichmanni* (see description) only four ridge crests (instead of five) on upper tooth plates. Additionally, *P. cionei* differs from *P. wichmanni* in being more robust and in having the cleft between the ridge crests shallower.

†Ptychoceratodus wichmanni sp. nov. (Fig. 3 C - D)

Diagnosis. Mid-sized (see Table I). Upper and lower tooth plates with four ridge crests. Lower tooth plates have sharp long and thin ridge crests. The first is very elongate, and the fourth is posteriorly directed.

Etymology. After Dr. Ricardo Wichmann, the early twentieth century geologist who made important contributions to the study of the referred area.

Holotype. MACN PV RN157A, left upper tooth plate (Fig. 3C).

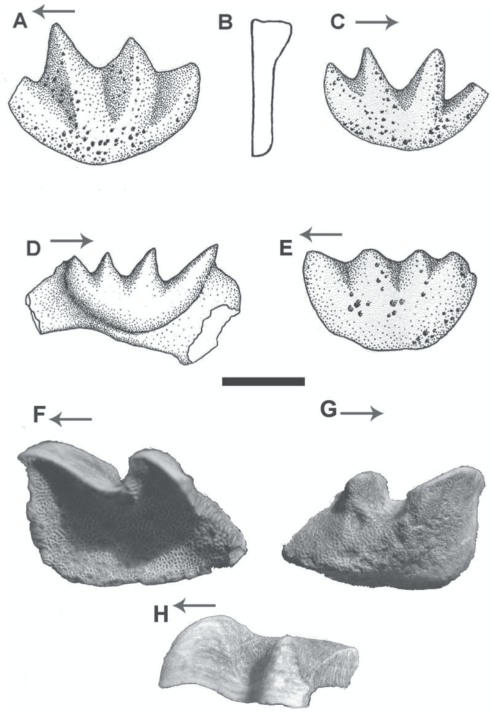

Fig. 3. **A-B** *†Ptychoceratodus cionei* (MACN-RN-157b, holotype) right upper tooth plate in (A) occlusal view, (B) cross section; **C-D**, *†Ptychoceratodus wichmanni* in occlusal view; **C**, (MACN-RN 157a, holotype) left upper tooth plate; **D**, right upper tooth plate (referred specimen, modified from Cione, 1987); **E**, *†Metaceratodus wollastoni*, left upper tooth plate in occlusal view (referred specimen, modified from Pascual and Bondesio, 1976); **F-H**, ?Lepidosirenidae (MPCN-PV 1-6), fragmentary plate in ventral (F), occlusal (G), and labial (H) views, preserving only two ridges. Scale bar equals 1 cm. Arrows indicate rostral direction.

Referred material. Wichmann (1924: Plate VII, fig. 6; 1927: fig. 1, 3; 12) Cione, (1987: fig. 1.N.) and González Riga (1999, fig. E.).

Horizon and locality. The holotype and the referred material come from the Los Alamitos Formation (Campanian-Maastrichtian). Estancia Los Alamitos (Río Negro Province).

Additional material. Several isolated tooth plates referred to the same species as that from the Los Alamitos Formation come from equivalent units at Arroyo Yaminué, Trapal-có and several localities where the Allen Formation is exposed (Río Negro Province; Wichmann, 1927). Additional material comes from southern Mendoza localities (e.g. Ranquil-Co; González Riga, 1999) of the Loncoche Formation (also equivalent to the Los Alamitos Formation).

Description. Tooth plates with narrow and acute crests. Clefts between the ridges are narrow and deep. The labial profile of the crests is not steep.

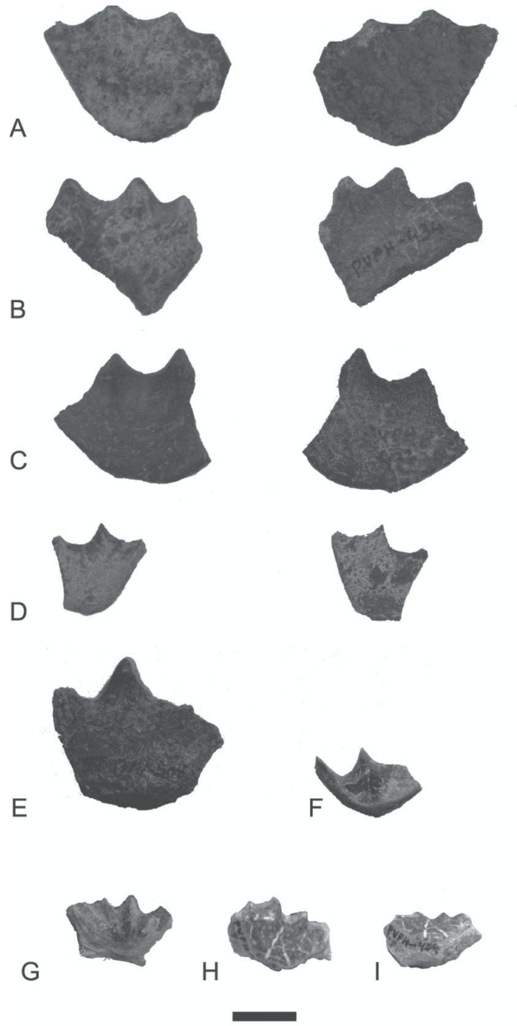

Fig. 4. **A** (MCF-PVPH-426), **C** (MCF-PVPH-432), **E** (MCF-PVPH-500), Ceratodontidae indet., lower tooth plates; **F** (MCF-PVPH-506, upper), **H** (MCF-PVPH-424, lower), **I** (PVPH-424, lower, different angle), Ptychoceratodontidae indet., tooth plates; **G** (MCF-PVPH-572, lower), *Ameghinoceratodus* sp.; **B** and **D**, unnumbered material from the Cerro Lisandro Formation at Cerro Bayo Mesa.

The first crest is relatively long and thin, with a marked slope. The crests are nearly straight and radiating, and the fourth crest is the shortest. Occlusal pits are well developed and are mainly distributed over the crests. Occlusal surface is flat.

As was indicated earlier, *†P. wichmanni* is similar to *†P. cionei*, from which it differs, among other characters (see specific diagnoses) in having more gracile tooth plates and deeper and narrower clefts between ridge crests. *†P. wichmanni* also shares feathers with *†P. madagascariensis* as was implied by Martin (1982) and Cione (1987; see above).

The plates of *†P. wichmanni* were originally referred by Martin (1982) and Cione (1987) to the species *«†Ceratodus» iheringi* (*†Ameghino ceratodus iheringi* herein). *†P. wichmanni*, however, is larger than *†A. iheringi* (see Table 1) and has deep and abundant occlusal pits and broad, low and acute ridge crests absent in *†Ameghinoceratodus*. Additionally *†P. wichmanni* shows a strongly convex lingual margin of the tooth plates. We would also like to point out that *†P. wichmanni* is the most common dipnoan species present in Campanian – Maastrichtian beds from Argentina.

Other ptychoceratodontids

Recorded ptychoceratodontids include the material MCF-PVPH-424, 506 (Figs. 4d, f, h, i), considering the acute crests and well developed crunching surface. This material comes from the Cerro Lisandro Formation at the Cerros Colorados south (506) and the Portezuelo Formation at the homonimous locality (424).

The material on Fig. 5 share very fragile and acute crests, probably a same *Ptychoceratodus* species, which is very comparable to *†Ptychoceratodus madagascariensis* (=*Ferganaceratodus* of Martin *et al*., 1999).

Neoceratodontidae Miles, 1977

Type species. Neoceratodus forsteri (Krefft, 1870).

Modified definition. Ceratodontiform dipnoans more closely related to *Neoceratodus forsteri* than to *†Ceratodus sturii* (Fig. 6).

Modified diagnosis. Double prearticular sulcus; seven upper tooth ridge crests; more than six lower tooth ridge crests (reversed in M. wollastoni, but present in other †Metaceratodus species, such as M. bonei).

†Metaceratodus wollastoni (Chapman, 1914) (Fig. 3 E)

Type species. *†Metaceratodus wollastoni* (Chapman, 1914).

Referred material. Pascual & Bondesio (1976; Plate I, fig. 9); Wichmann (1924; Plate VII, fig. 4).

Horizon and locality. Ingeriero Jacobacci (Río Negro province). Coli Toro Formation (Campanian-Maastrichtian; see Pascual & Bondesio, 1976).

Comments. The genus *†Metaceratodus* is considered here to be the sister group of *†Mioceratodus* + *Neoceratodus* (Neoceratodontidae), not of †Ceratodontidae (Schultze, 1992; contra Kemp,

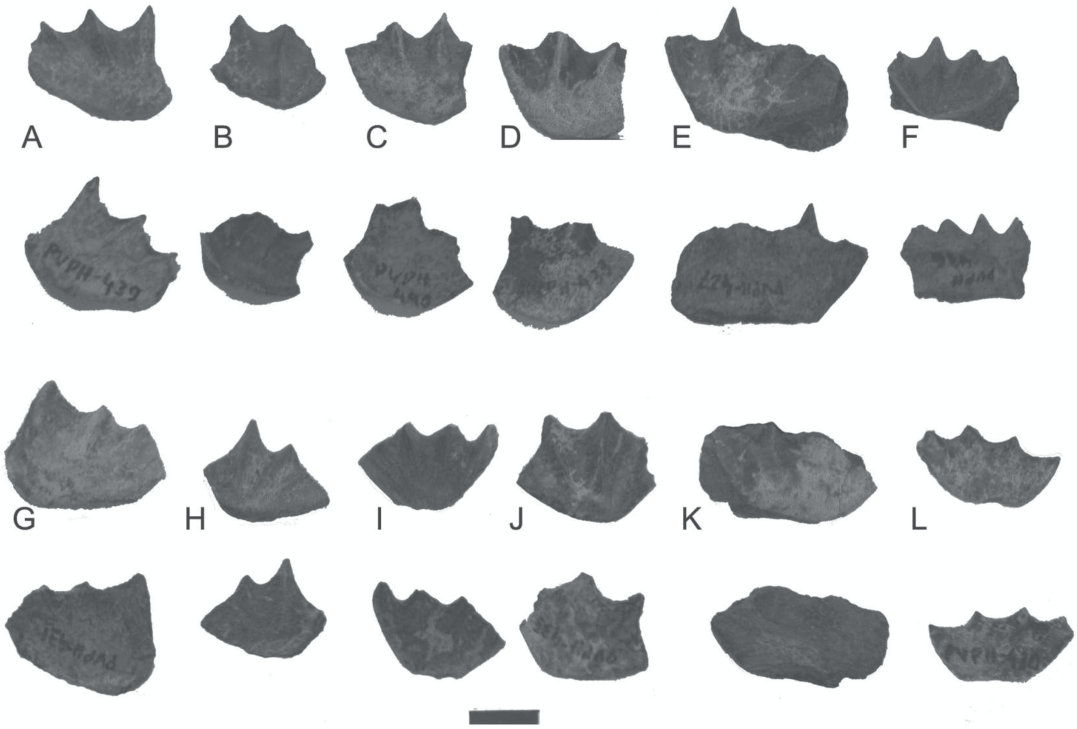

Fig. 5. Ptychoceratodontidae indet., **A** (MCF-PVPH-439), **B**, **C** (MCF-PVPH-440), **D** (MCF-PVPH-453), **E** (MCF-PVPH-427, upper), **F** (MCF-PVPH-436, upper), **G** (MCF-PVPH-431), **H**, **I**, **J** (MCF-PVPH-435, upper), **K**, **L** (MCF-PVPH-430, lower).

1997). †*Metaceratodus* tooth plates differ mainly because in †*Metaceratodus* the first ridge crest on lower tooth plates is subequal to the lingual margin, whereas in remaining Neoceratodontidae it is much shorter.

†*Metaceratodus* is present from the Lower Cretaceous to the Pliocene of Australia (see Kemp, 1997). Here we refer the Argentinian material to †*Metaceratodus* (as previously proposed by Kemp, 1997) on the basis of the following combination of characters: robust ridge crests that originate medially, more than four ridge crests on lower tooth plates, first crest of lower tooth plates acute, occlusal pits wide and deep. Additionaly, ridge crests are more acute in †*Metaceratodus* than in †*Ceratodus*. Whereas in *Ceratodus* the angles between crests are close to straight (90°), in *Metaceratodus* they are acute (60-70°). The Argentinian material could be referred to the Cretaceous species *M. wollastoni* because the tooth plates are broader, stouter and have wider ridge crests than other species of the genus (i.e. *M. elliotti*; *M. palmeri*; *M. bonei*), and lacks the typical lingual keel. Additionaly, it shows the occlusal pits distributed in furrows and around the tooth plate (Kemp, 1997).

?Lepidosirenidae (MPCN-PV 1-6) (Fig. 3 F-H). A fragmentary dipnoan tooth plate was collected from the Anacleto Formation at Río Negro Province. It preserves only the anterior two ridges. The anteroposteriorly flattened ridges end in vertical transverse crests that follow a perpendicular plane respect to the skull. This material belongs to a different kind of dipnoan, probably a lepidosirenid.

DISCUSSION

On the systematic value of tooth plates

From 1899 to 1996, a single tooth plate represented the ceratodontiform record in Argentina from the Coniacian (Ameghino, 1899) and other fragments from the Campanian-Maastrichtian (Wichmann, 1924; 1927; Cione, 1987). In years to follow, our understanding of the stratigraphic record has greatly increased and today we have information on a substantial portion of the Late Cretaceous (Fig. 1b). The record of lungfishes is still restricted to findings from the Cenomanian of the Candeleros (Apesteguía *et al*. 2001) and the Cerro Lisandro Formations (Apesteguía *et al*., 2001; Coria *et al*., 1996 consigned there as Huincul Formation), Late Turonian of the Portezuelo Formation (herein), Coniacian of the Mata Amarilla Formation (Ameghino, 1899; Goin *et al.*, 2002), Early Campanian of the Anacleto Formation (herein), and several units of the Late Campanian to Maastrichtian equivalent to the Allen Formation (Wichmann, 1924, 1927; Cione, 1987; Apesteguía & Cambiaso, 1999; González Riga, 1999).

Distinguishing supraspecific taxa of lungfishes based on isolated tooth plates is difficult (Kemp & Molnar, 1981). In fact, Kirkland (1988) states that dipnoan taxa cannot be defined by means of tooth plates and that the skull roof is essential for generic classification (Kirkland, 1988; Schultze, 1991). Intraspecific variation in tooth plate morphology (i.e. number of ridges, and the related presence or absence of a posterior heel) noted by Kemp and Molnar (1981) has been attributed to growth. Additionally, Churcher (1995) maintains that the formation of deep grooves with acute angles between the ridge crests and chewing movements in relation to a hard diet could induce the occlusal surface marks. However, as Campbell & Barwick (1990) pointed out, tooth plates are directly correlated to skull and mandible morphology, and they together can be useful for indicating position within lineages.

Much of the available fossil material for ceratodontiforms consists of isolated tooth plates. Therefore, in order to optimize the knowledge on ceratodontiform phylogeny, our work supports the inclusion of characters present in tooth plates. Tooth plates from Los Alamitos and La Colonia Formations are available in abundance, allowing several tooth plates to be analyzed from a single locality in order to recognize the most consistent features. Ideally, more characters (i.e. cranial and post-cranial) would contribute more understanding to an analysis, but we and other researchers (Martin, 1982; Martin *et al*. 1999) consider tooth plates to offer an abundant source of information that should not be ignored.

Biogeography

In addition to obvious differences in size, mobility and routes of dispersion, ceratodontiform dipnoans have a similar regional and stratigraphical distribution to that of †titanosauriform sauropods, which have a vast Jurassic and early Cretaceous record in North America through the Cenomanian (Bonaparte 1986). Ceratodontiforms and †titanosauriforms were considered extinct at the early late Cretaceous of North America. However, they reappeared during the Maastrichtian before their final extinction within Laurasia at the end of the Mesozoic. The North American Maastrichtian dipnoans (Parris *et al*., 2001) and titanosaurs (Gilmore, 1922), seem to prove a South American origin based on their continuous record from the Cenomanian through the Maastrichtian in Southern Continents.

With the exception of those found in the early Paleocene of Bolivia (Schultze, 1991), there is no record of ceratodontiforms in the South American Tertiary. Pascual & Bondesio (1976) proposed that the †ceratodontid extinction in Patagonia likely resulted from an inability to migrate north to warmer regions when the climate changed. The authors also discuss a connection between Patagonia and Australia through Antarctica based on similarities between the Australian lungfish *Neoceratodus forsteri* and the Patagonian species *†Ameghinoceratodus iheringi*. Pascual & Bondesio (1976) also noted the presence of *†Metaceratodus wollastoni* and several species of *†Ptychoceratodus* in both landmasses. Therefore, we do not reject the hypothesis of a connection between Patagonia and Australia even though we consider *†Ameghinoceratodus* and *Neoceratodus* to be distantly related taxa.

Members of †Ptychoceratodontinae, may have had a wide pre-Cretaceous distribution throughout greater Gondwana (Apesteguía, 2002) including India, Madagascar, Australia and possibly Antarctica, where they currently have not been recovered (Martin *et al*. 1999). The occurrence of ptychoceratodontines in South America begins by the Campanian-Maastrichtian transgression or perhaps earlier (Fig. 5d,f,h,I; Fig. 6). Thus, it is probable that the different species of *†Ptychoceratodus* from the Campanian-Maastrichtian of Patagonia represent a later invasion from India, Madagascar, or Australia (through Antarctica).

Most pre-Campanian Cretaceous dipnoans from Argentina represent both endemic South American lineages (e.g., *†Chaoceratodus*; *†Ameghinoceratodus*) as well as relicts of widely distributed Jurassic ceratodontiforms (e.g., *†Ceratodus* sp.). We also see that Cretaceous post-Campanian dipnoans are dominated by possibly immigrant forms (e.g. ptychoceratodontines, *†Metaceratodus*) and poorly represented endemic lineages (e.g. *†Ameghinoce-ratodus*). A similar faunal pattern has also been reported for other vertebrate groups (Bonaparte, 1986).

Brief comments on phylogenetic relationships

Cione (1987), based on Martin (1982), considers *†Ptychoceratodus wichmanni* to be the sister taxon to *P. madagascarensis* (=*Fergana-*

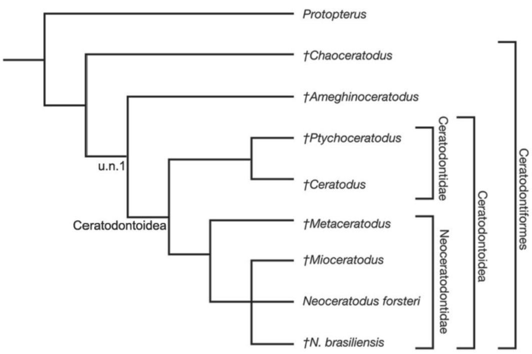

Fig. 6. Phylogenetic relationships of post-Triassic ceratodontiform dipnoans. Synapomophic characters detailed in the text. Clades Ceratodontinae and Ptychoceratodontinae are represented by genera *Ceratodus* and *Ptychoceratodus* respectively.

ceratodus; Martin *et al.*, 1999) based on the presence of only four ridge crests in the tooth plates and the ontogenetic formation of a chewing surface. Although is not possible to follow developmental patterns of these extinct dipnoans, adult morphology is in agreement with this interpretation and thus we consider *P. wichmanni* and *P. cionei* as closely related to the *P. madagascariensis* species group (*sensu* Martin, 1982).

In this paper two new genera endemic to South America, *†Chaoceratodus* and *†Ameghinoceratodus*, are considered basal to the «modern» clade of dipnoans, termed here as Ceratodontoidea, which includes the families †Ceratodontidae (†Ceratodontinae + †Ptychoceratodontinae) and Neoceratodontidae. The latter family is composed by *†Metaceratodus* and *†Mioceratodus* + *Neoceratodus*, which are characterized by a double prearticular sulcus and an increasing number of ridge crests per tooth plate.*†Metaceratodus* was considered by other authors as belonging either to the family †Ceratodontidae (Kemp & Molnar, 1981; Kemp, 1997) or Ptychoceratodontidae (Martin, 1982). However, these authors based their hypothesis mainly on plesiomorphic traits (e.g. medial origin of ridge crests, upper tooth plates close or contiguous, upper symphysis oblong) that are widely distributed among dipnoans (e.g. *Lepidosiren, Sagenodus*; Fernández *et al*. 1973; Kemp, 1996).

Some authors (Kemp, 1998; Martin *et al*. 1999) proposed that both †Ceratodontidae and Ptychoceratodontidae were closely related clades. In this paper we agree with previous interpretations and we include both groups as subfamilies within the single family †Cerato-dontidae.

Paleobiological considerations

The rock units relevant to the «Lacustrine Senonian» are considered to be the first stages in the progressive flooding that formed the epeiric Kawas sea (Casamiquela, 1978). The marine nature of these outcrops was mainly based on the presence of batoid fishes and plesiosaurs (e.g. Gasparini & De la Fuente, 2000). Furthermore, the freshwater and terrestrial taxa also recovered in the same beds were considered as allochtonous additions although they lack any sign of transport.

The batoids present in several units of the «Lacustrine Senonian» (e.g. Los Alamitos and Loncoche Formations) actually pertain to the freshwater family Rhinobatidae (A. Forasiepi, *pers. comm*.; Gayet, 1992). Furthermore, the plesiosaur record does not necessarily imply marine sediments, as they have occasionally been found in freshwater sediments (R. Molnar, *pers. comm.*). Additionally, several other faunal remains indicating a freshwater environment (e.g. Chelidae turtles, freshwater gatropods; Gasparini & De la Fuente, 2000; A. Forasiepi, *pers. comm.*) have been recovered.

The ceratodontiforms from the «Lacustrine Senonian» appear to be common in the sediments prior to the marine transgression and Casamiquela (1978) proposed that they were tolerant to brackish waters, in contrast with the strict freshwater living forms. Schultze (1991) proposed that extinct ceratodontiforms could be good swimmers and that they could undertake extensive sea voyages, which may explain their wide distribution in the Late Cretaceous. However, dipnoans disappeared abruptly during the first stage of the marine Turonian transgression of the Western sea in North America (Eaton & Kirkland, 1999). Just as in Patagonia, dipnoans disappeared from the record when the Kawas sea flooded the continent, as evidenced by the faunal content of the clearly marine Upper section of the Los Alamitos Formation (and equivalents; Andreis, 1987). The freshwater environments inhabited by extant dipnoans, plus the fluvial pre-Campanian sediments of the Cretaceous South American ceratodontiforms, supports the conclusion that the «Lacustrine Senonian» forms inhabited freshwater environments.

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Appendix 1. Description of characters used in phylogenetic analysis.

1. Calvarium bones distribution (Kemp 1998): Two bones in each of the medial and mediolateral series (0); Two unpaired in medial and one in mediolateral series (1); Three bones in medial and mediolateral series (2).
2. Posterior calvarium formed by (Kemp 1998): YZ, JLM, I, ABC (1); AB, IJ, YZ (2); I, AB (3).
3. Calvarium is emarginated (Kemp 1998): no (0); yes (1); only in the posterior edge (2).
4. JLM descending process (Kemp 1998): complex curved articular socket for twisted ascending pterygopaltine process what is covered laterally (0); simple peg-like fitting into the broad grooved pterygopalatine and exposed laterally (1); has a straight grooved process to articulate with a straight pterigopalatine process that is exposed laterally (2); absent (3).
5. KLM descending process (Kemp 1998): absent (0); present (1).
6. XK (Kemp 1998): absent (0); present (1).
7. Ornamented calvarium bones (Kemp 1998): absent (0); present (1).
8. Symphysis shape (Kemp 1998): superior oval, inferior linear (0); both oval (1); superior elliptic, inferior linear (2); superior oblong, inferior linear (3).
9. Upper tooth plate ridge crests No. 3 (0); 4 (1); 5(2); 6(3); 7(4).
10. Lower tooth plate ridge crests No. 3 (0); 4-5(1); >6(2).
11. Punctation distribution: over most of surface (0); between ridge crests (1); absent (2).
12. Mesolingual keel: present (0); absent (1).
13. Upper tooth plate medial edge: straight (0); bent (1).
14. Lower tooth plate medial edge: straight (0); bent (1).
15. Ridge crests: long and sharp (0); short and sharp (1); short and rounded (2).
16. Dentine mantle (Kemp 1997, 1998): limited (0); broad (1).
17. Ridge crests origin (Kemp 1997, 1998): medial (0); anterior (1).
18. Upper tooth plates position (Kemp 1997, 1998): close or adjacent (0); separated (1), adjacent (2).
19. Occlusal perforations (Kemp 1997): absent (0); present (1).
20. Punctation distribution: with patern (0); without pattern (1).
21. ABC angle (Kirkland 1988): >110º(0); <110º(1).
22. Tooth plates size: 1-2,5 cm(0); >2,5 cm(1).
23. 4º ridge crest: absent (0); present and well developed (1); present and poorly developed (2).
24. Labial margin: stepped (0); non-stepped (1).
25. First ridge crest: similar to the second (0); 20% bigger (1); 20% smaller (2).
26. First ridge crest: shorter than lingual margin (0); longer than lingual margin (1); approximately equal to lingual margin (2).
27. Lingual margin: straight or slightly concave (0); convex (1).
28. Prearticular sulcus: single (0); double (1).

Appendix 2. Character codes used for the phylogenetic analysis.

Taxon	Characters																											
					5					10					15					20					25			28
Protopterus anectens	1	1	1	1	0	0	1	1	0	0	2	1	1	0	2	0	0	2	0	0	0	0	0	1	2	2	0	0
†*Chaoceratodus portezuelensis*	?	?	?	?	?	?	?	?	1	?	0	0	?	0	1	?	0	?	?	1	0	0	2	1	1	0	0	?
†*Ceratodus sturii*	1	2	0	3	0	1	1	3	?	1	0	1	1	1	1	0	0	0	1	1	1	1	2	1	1	2	1	0
†*Ameghinoceratodus iheringi*	?	?	?	?	?	?	?	?	2	?	0	?	0	0	0	0	0	0	1	1	1	0	2	0	1	1	0	?
†*Ptychoceratodus serratus*	2	3	2	3	1	1	0	3	3	1	1	1	0	1	1	0	1	2	1	1	1	1	1	1	0	2	1	0
†*Metaceratodus wollastoni*	?	?	?	?	?	?	?	?	4	2	0	1	1	1	1	1	1	1	1	1	1	2	1	1	2	1	1
Neoceratodus forsteri	0	0	0	0	0	1	0	0	4	2	0	1	1	1	0	1	1	1	0	1	1	1	2	1	1	0	0	1
†*Neoceratodus brasiliensis*	?	?	?	?	?	?	?	?	4	2	0	1	1	1	0	1	1	?	1	1	1	1	2	1	0	0	1	1
†*Mioceratodus anemosyrus*	0	?	?	2	0	1	0	2	4	2	0	1	1	0	1	1	1	0	0	1	0	1	2	0	1	0	1	1