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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

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ABSTRACT

A new species of the genus *Atlantoceratodus* is diagnosed and described on the basis of isolated tooth plates from several localities of the Allen Formation (Campanian-Maastrichtian), Río Negro province, northern Patagonia, Argentina. The new species belongs to the genus *Atlantoceratodus* Cione et al., 2007 (senior synonym of *Ameghinoceratodus* Apesteguía; Agnolin; Claeson, 2007) together with *A. iheringi* and *A. elliotti* nov. comb. A new phylogenetic analysis including tooth plates and calvarian morphology has been conducted in order to evaluate the relationships among post-Paleozoic dipnoans of the clade Ceratodontoidei. The first ceratodontoid dichotomy includes, on one hand the Neodipnoi nov. (Lepidosirenidae + Neoceratodontidae) and on the other side the “High Crowned Dipnoans” clade (Ceratodontidae + (Asiatoceratodontidae + Ptychoceratodontidae)). Based on this analysis, all South American ptychoceratodontid remains are included within the genus *Ferganoceratodus*. The ceratodontid genus *Metaceratodus* is restricted to include the single species *M. wollastoni*, which is recorded from several Upper Cretaceous localities of

Australia and Patagonia. The Late Cretaceous Argentinean record of the genus *Ceratodus* is represented by Jurassic relics of ulterior Pangean distribution. The Neoceratodontidae is here regarded as a family endemic to Gondwana. In the Cretaceous of South America, three different stages in the composition of dipnoan faunas may be recognized: 1) the pre-Campanian record includes endemic Gondwanan taxa, Jurassic relics, and South American endemicities; 2) record the Campanian-Maastrichtian (probably also Lower Paleocene) includes immigrant taxa from Australia and Malgasy; and finally 3) the Late Paleocene-Recent record, includes only Lepidosirenidae of the genus *Lepidosiren*.

PALAVRAS CHAVE:
América do Sul
Cretáceo
Paleógeno
Dipnóico
Atlantoceratodus

RESUMO – NOVAS ESPÉCIES DO GÊNERO *ATLANTOCERATODUS* TEM SUA DIAGNOSE E DESCRIÇÃO BASEADA EM PLACAS DENTARICAS PROVENIENTES DE VÁRIAS LOCALIDADES DA FORMAÇÃO ALLEN (CAMPANIANO-MAASTRICHTIANO), PROVÍNCIA DE NEUQUÉN, NORTE DA PATAGÔNIA, ARGENTINA. As novas espécies pertencem ao gênero *Atlantoceratodus* Cione et al., 2007 (sinônimo júnior de *Ameghinoceratodus* Apesteguía; Agnolin; Claeson, 2007) junto com *A. iheringi* e *A. elliotti* nov. comb. Uma nova análise filogenética incluindo placas dentárias e morfologia calvariana tem sido conduzida para avaliar as relações destes dipnóicos pós paleozóicos do clado Ceratodontoidei. A primeira dicotomia de ceratodontoide inclui, por outro lado os Neodipnoi nov. (Lepidosirenidae + Neoceratodontidae) são os clados de "Dipnóicos mais derivados" (Ceratodontidae + (Asiatoceratodontidae + Ptychoceratodontidae). Baseado nesta análise, de todos ptychoceratodontideos Sul-Americanos são incluídos dentro do gênero *Ferganoceratodus*. O gênero de ceratodontídeo *Metaceratodus* esta restrito a única espécie *M. wollastoni*, a qual é registrada em vários localidades do Cretáceo Superior da Austrália e Patagônia. O registro do gênero *Ceratodus* do Neocretáceo argentino é representado por registros, assim como de forma Jurássica de relicto de distribuição pangeica. Neoceratodontidae é aqui considerado como uma família endêmica para o Gondwana. No Cretáceo da América do Sul, três diferentes estágios na composição da fauna de dipnóicos podem ser consideradas: 1) a de registro pré-Campaniana que inclui taxa endêmicos gondwânicos, remanescentes do Jurássico, e endemicidades Sul-Americanas; 2) registros do Campaniano-Maastrichtiano (possivelmente também do Paleoceno Inferior) que inclui taxa imigrantes da Austrália e Madagascar; e por último 3) o Neopaleoceno registros recentes, incluí somente de Lepidosirenidae do gênero *Lepidosiren*.

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1. Introduction

Up to now, the fossil record of dipnoans in South America is patchy and biased. Fossil South American dipnoans are represented by isolated plates, sometimes attached to mandibles and maxillary bones (SOTO; PEREA, 2010). Currently, the fossil record of Mesozoic and Cenozoic dipnoans around the world is taxonomically distributed within five families (i.e. Asiatoceratodontidae, Neoceratodontidae, Ceratodontidae, Ptychoceratodontidae, and Lepidosirenidae; MARTIN, 1982; KEMP, 1998) based mainly on the structure and morphology of tooth plates (see MARTIN, 1982; MARTIN; BARBIERI; CUNY, 1999). All post-Paleozoic dipnoans very probably form a monophyletic group, a proposal based on cranial and tooth plate features (MARTIN, 1982; KEMP, 1997a).

In spite of relative abundance among Cretaceous strata, Mesozoic dipnoans remain nearly unknown in South America (see SOTO; PEREA, 2010). The first author who mentioned and described remains of South American dipnoans, was the Argentinean paleontologist Florentino Ameghino, who in 1899 coined the name *Ceratodus iheringi* to include an isolated dipnoan tooth plate from the Mata Amarilla Formation (Coniacian, Upper Cretaceous; GOIN et al. 2002), south of the Sehuén River, Santa Cruz province, Patagonia, Argentina. Later, Patagonian dipnoans were briefly mentioned or figured without any comment about their status or phylogenetic relationships (e.g. AMEGHINO, 1916; WICHMANN, 1924; 1927). More recently, Pascual and Bondesio (1976) and Fernández; Pascual; Bondesio (1973) described and discussed some remains of "ceratodontids" and *Lepidosiren* from several Cretaceous and Paleogene localities of Argentina. Cione (1987) and Schultze (1992b) described several additional specimens putatively referable to *Ceratodus iheringi* from the uppermost Cretaceous of Patagonia, and the Paleogene of Bolivia, respectively. These referred specimens were considered by Martin (1982; MARTIN; BARBIERI; CUNY, 1999) as closely related to *Ferganoceratodus madagascariensis* from the Maastrichtian of Madagascar, and by Cione et al. (2007) as belonging to the Australian genus *Metaceratodus* (KEMP, 1997a). In the same way, Kemp (1997a) indicate that some specimens illustrated by Pascual and Bondesio (1976) and the *Ceratodus iheringi* holotype may belong also to *Metaceratodus*.

Souza Cunha and Ferreira (1980) described the species *Ceratodus brasiliensis*, from the Lower Cretaceous of Brazil, which was included within *Neoceratodus* by Martin (1984a) who also suggested that this species may be a junior synonym of *N. africanus* from the Cretaceous of Africa. Additionally, Dutra and Malabarba (2001; see also CASTRO et al., 2004) reported isolated tooth plates as probably belonging to the African-Asiatic species *Asiatoceratodus tiguidensis* Tabaste, 1963 from the same Brasilian localities (see MARTIN, 1982). Silva and Azevedo (1992; 1996) and Brito et al. (1994) reported isolated specimens as belonging to *Neoceratodus* from several localities of the Lower Cretaceous Brejo Santo Formation. The lungfish fossil record from Brazil was analyzed briefly by Toledo and Bertini (2005).

Schultze (1992b) reported some remains of ceratodontid and lepidosirenid dipnoans, including specimens comparable to *Ceratodus iheringi* and *Lepidosiren paradoxa*, as well an innominated new genus and species of ceratodontid lungfish. All this material was collected in the Upper Cretaceous and lower Paleocene El Molino and Santa Lucía Formations (SCHULTZE, 1992b).

Apesteguía; Agnolin; Claeson (2007) reviewed the fossil record of dipnoans from the Cretaceous of Argentina, and erected new taxa belonging to the genera *Ptychoceratodus* and *Ceratodus* and coined the new genus and species *Chaoceratodus portezuelensis*. Moreover, they proposed that *Ceratodus iheringi* does not belongs to *Ceratodus* but to a new genus that they named *Ameghinoceratodus*. Apesteguía; Agnolin; Claeson (2007) also pointed out the presence of the Australian species *Metaceratodus wollastoni* (CHAPMAN, 1914) in several localities of the uppermost Cretaceous of Patagonia.

In the same year Cione et al. (2007) established a new genus for the species *Ceratodus iheringi* on the basis of the holotype and of about 200 referred isolated tooth plates. The new genus was named *Atlantoceratodus* and included both "*Ceratodus*" *iheringi* and the Late Cretaceous Malagasy species *Ferganoceratodus madagascariensis* Priem, 1924 (see MARTIN; BARBIERI; CUNY, 1999).

The goal of the present paper is to describe a new dipnoan species closely related to "*Ceratodus*" *iheringi* Ameghino, 1899, and to give a brief overview of the South American Cretaceous and Paleogene lungfish record, on the light of new additional material of several species and on the increasing knowledge of fossil Cretaceous dipnoans of Gondwana (CHURCHER; DE IULIIS; KLEIDIENST, 2006;: CAVIN et al. 2007; CIONE et al. 2007).

2. Methods

Here I follow the morphological nomenclature of tooth plates employed by Kirkland (1987), and the hard tissue nomenclature proposed by Kemp (2001). The cranial terminology follows Cavin et al. (2007).

We have conducted a cladistic analysis of post-Paleozoic dipnoans (i.e. Ceratodontoidei) using as outgroup the well known genus *Gnathorhiza* (BERMAN, 1976; CAVIN et al. 2007). We focused our phylogenetic analysis on calvarian morphology and tooth plates. Thus, we included in the phylogenetic analysis those species known by calvarian and tooth plate morphology together, with the single exception of the species *Metaceratodus wollastoni* known only from tooth plates. The genera *Arganodus* and *Asiatoceratodus* are here considered as synonymous, following the well-founded proposal of Kemp (1998; but see CAVIN et al. 2007). We excluded from the analysis the Triassic genera *Gosfordia*, *Paraceratodus, Beltanodus,* and *Microceratodus* because their tooth plates are not properly known (KEMP, 1994), and the Cretaceous genera *Chaoceratodus, Atlantoceratodus* and *Retodus*, which are known only by isolated tooth plates. With respect to tooth plate morphology, several features previously considered as phylogenetically informative are clearly age-related or the consequence of individual variation, thus, they were not included in the phylogenetic analysis. For example, the ornamentation and the presence of tubercles on the occlusal surface, the morphology of the clefts between crests, presence or absence of labial cusps, presence or absence of posterior heel at the end of the tooth plate, and the biometric parameters based on angles between crests (KEMP; MOLNAR, 1981; KEMP, 1997b).

The presence of occlusal pits is here considered as related to the presence of islands of circumdenteonal dentine within the interdenteonal mass, because the former is softer and abrades faster, thus forming occlusal pits (KEMP, 2001).

The phylogenetic analysis was made using NONA 3.0 (GOLOBOFF, 1993), and all character states have been considered with free polarity. The analysis used traditional parameters (heuristic search, multiple TBR+ TBR mult* max*) and yielded a single most parsimonious tree of 48 steps, and RI, 77, CI 70 (Figure 1). The data matrix includes 29 characters coded for 9 taxa.

The genus *Ceratodus* was coded on the basis of the calvarian material of *C. sturii* and tooth plate morphology of *C. latissimus* (KEMP, 1998; 2001). *Ptychoceratodus* was coded using cranial information of *P. serratus* (KEMP, 1998, CAVIN et al. 2007) and combined tooth plate morphology of several species (see Martin; Barbieri; Cuny, 1999). *Asiatoceratodus* was based on *A. atlantis* (KEMP, 1998), whereas *Neoceratodus* was coded using the living species *N. forsteri*. *Mioceratodus* includes the combination of features present in the species *M. anemosyrus* and *M. gregoryi* (KEMP, 1998). Lepidosirenid codifications include the living genera *Lepidosiren* and *Protopterus*, which show highly homogeneous calvarian and tooth plate conformation (CAVIN et al. 2007). Data from *Metaceratodus* include those published by Kemp (1997a). Finally, the codification of *Ferganoceratodus* was based on the combination of the species *F. jurassicus* and *F. martini* (CAVIN et al. 2007).

Abreviations. MACN PV, Collection of Vertebrate Paleontology, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Buenos Aires, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MML**, Museo Municipal Héctor Cabazza, Lamarque, Argentina; **MPCA**, Museo Provincial “Carlos Ameghino”, Cipolletti, Argentina.

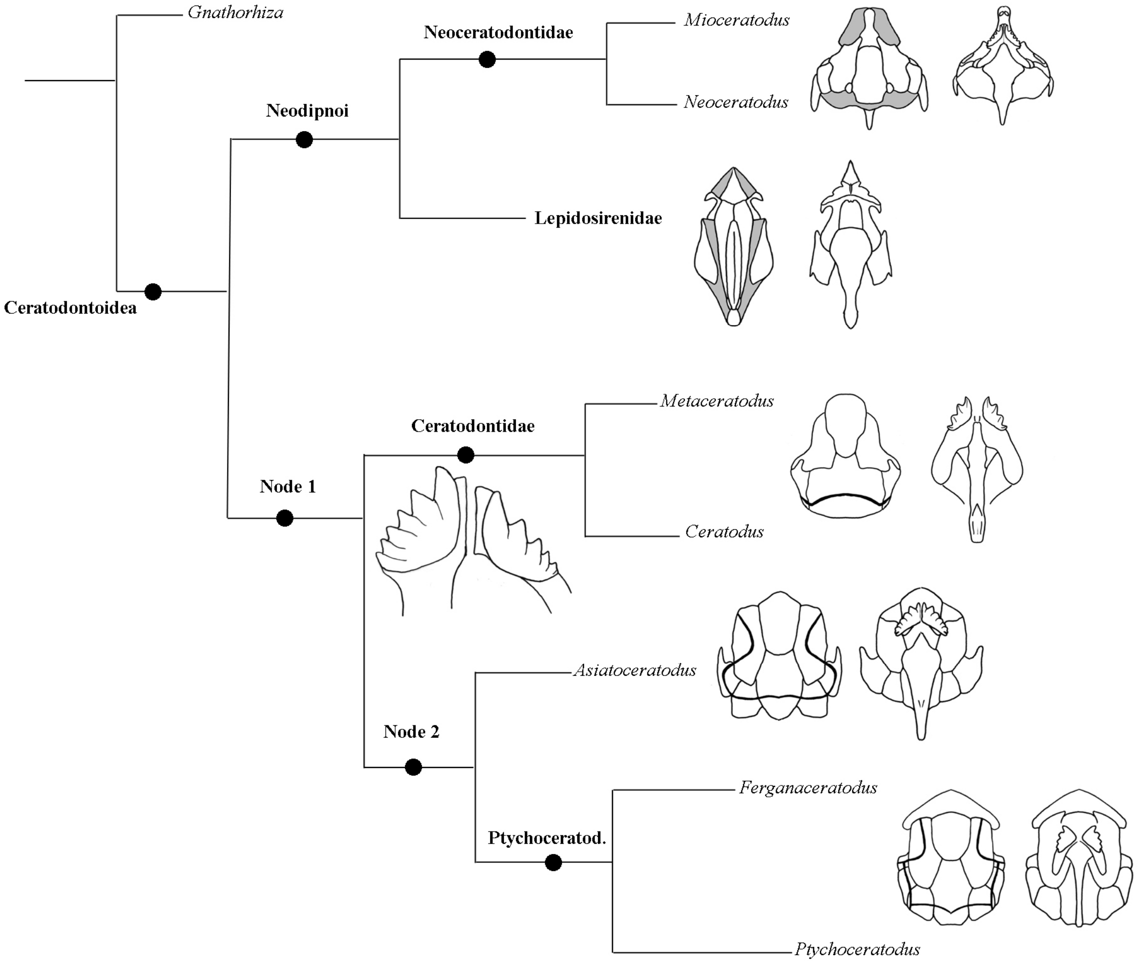

Figure 1. Cladogram showing phylogenetic relationships among post-Paleozoic dipnoans. Ceratodontoidei: **9**(1); **21**(1-2); **22**(1); Neodipnoi: **17**(1), **19**(1), **20**(1), **21**(2), **28**(1); Neoceratodontidae: **4**(1), **8**(1), **13**(1), <u>**16**(1)</u>; Node 1 (high crowned dipnoans): **7**(1), <u>**12**(1)</u>, **23**(1), **25**(1); Ceratodontidae: **10**(2); Node 2 (Ptychoceratodontidae+Asiatoceratodontidae): <u>**11**(2)</u>, **18**(1), **27**(1), **29**(1); Ptychoceratodontidae: <u>**10**(1)</u>, **24**(1), **26**(1). Numbers in bold indicate character number, and numbers between brackets represent character states. Underlined traits are homoplasies. On the right side of the figure the calvaria of representative taxa are shown in dorsal (left) and ventral (right) views. From top to bottom: *Neoceratodus forsteri, Protopterus annectens, Ceratodus sturii, Asiatoceratodus atlantis,* and *Ferganoceratodus martini*. At the node Ceratodontidae the upper (left) and lower (right) tooth plates and tooth bearing bones of *Metaceratodus wollastoni* are illustrated. Ptychoceratod. means Ptychoceratodontidae.

Systematic paleontology

Order Dipnoiformes Múlller, 1845

Ceratodontoidei Nikolski, 1954

Synonym: Ceratodontoidea Apesteguía; Agnolin; Claeson, 2007

Genus *Atlantoceratodus* Cione; Gouiric; Goin; Poiré, 2007

Synonymy. *Ameghinoceratodus* Apesteguía; Agnolin; Claeson, 2007; *Metaceratodus in part* Kemp,1997a, *non* Chapman, 1914.

Emmended diagnosis (from CIONE et al., 2007; APESTEGUÍA; AGNOLIN; CLAESON, 2007): Small sized dipnoan diagnosable on the basis of the following apomorphic traits: 1) tooth plates with acute and slender crests separated by deep and narrow furrows, exhibiting a large angle formed by the first and last crests (120-130°), and 2) two last crests being subequal in shape and orientation; both are oriented backwards being the last nearly subparallel to the main lingual margin of the tooth plate (see additional features below; Figures 3-5).

Included species: *Atlantoceratodus iheringi* (Ameghino, 1899); *A. elliotti* (Kemp, 1997) nov. comb.; *A. patagonicus* nov. sp.

Atlantoceratodus patagonicus nov. sp.

Holotype. MML 196, right upper tooth plate (Figure 3 A-B, Figure 4 A).

Locality and Horizon. Trapal Có, Bajo de Los Menucos, Río Negro province, Patagonia, Argentina (Figure 2). Allen Formation (Campanian-Maastrichtian; Upper Cretaceous; MARTINELLI; FORASIEPI, 2004).

Measurements of holotype specimen (MML 196). Total length: 22 mm., depth of second crest: 17 mm.

Paratypes. MML, 197, incomplete right lower tooth plate (Figure 3 C-D); MACN PV RN 1080, left and right upper tooth plates (Figure 4); MACN PV RN157C, very incomplete right lower tooth plate; Wichmann (1927; plate III, fig. 12; right upper tooth plate).

Locality and Horizon. MACN PV RN 1080, Bajo de Santa Rosa, Río Negro province, Patagonia, Argentina. Allen Formation (Campanian-Maastrichtian; Upper Cretaceous). MACN PV RN157C, Estancia Los Alamitos, Río Negro province, Patagonia, Argentina. Los Alamitos Formation (Campanian-Maastrichtian; BONAPARTE, 1987). The plate figured by Wichmann (1927) comes from Trapal-co, Bajo de los Menucos, Río Negro province, Patagonia, Argentina. Allen Formation (Campanian-Maastrichtian; MARTINELLI; FORASIEPI, 2004).

Diagnosis. Species of the genus *Atlantoceratodus* diagnosable on the basis of the following combination of features (exclusively present in upper tooth plates): 1) short first crest, being shorter than remaining crests (in *A. iheringi* and *A. elliotti* the first crest is the largest of the tooth plate); 2) inner angle distally positioned (inner angle approaches 120°; in *A. iheringi* and *A. elliotti* this angle is medially positioned and usually approaches 130°); 3) well defined inner angle (nearly absent in *A. iheringi*); 4) crests and clefts between crests broad and short (crests acute and long, being larger than the breadth of occlusal surface; and inter crest clefts narrow and deep in *A. iheringi* and *A. elliotti*);

Description**.** The holotype is well preserved only lacks its first crest. Bone attached to the tooth plate is not preserved. The plate is relatively stout, subtriangular in contour, with a broad occlusal surface; it is relatively low crowned when compared with *Ceratodus, Ptychoceratodus,* and *Ferganoceratodus*, being taller than *A. iheringi* (see discussion). The inner angle is medially positioned, and is of about 120°. There is no mediolingual keel. The lingual margin is straight.

There are five crests, which are short and broad, being shorter than the breadth of occlusal surface of the tooth plate. The first crest is stout and broad, showing a convex mesial margin. This ridge is shorter than remaining crests, including the last one. Second and last crests meet in a point anteriorly. The fourth crest is strongly directed backwards, and the last (fifth) crest is nearly parallel to the lingual face of the tooth plate. Crests originate anteromedially and are radiating. Occlusal pits are absent; punctuations simple, without pattern. Petrodentine absent. Pulp cavity wide. Enamel and dentine mantle restricted to margins.

Lower tooth plates are poorly known. Known specimens are large and robust. Crest relatively long and slender. Third and fourth crest directed backwards. Occlusal pits absent. Petrodentine absent. Enamel and dentine mantle restricted to margins.

Comments**.** *A. patagonicus* nov. sp. shows all the synapomorphic features cited in the diagnosis of the genus (see discussion) together with a unique combination of traits (not exclusively derived) also present in remaining *Atlantoceratodus* species (see below). The new taxon is clearly distinct from remaining species (i.e. *A. iheringi* and *A. elliotti*), showing larger and broader tooth plates. Its position within the genus is uncertain, because it does not clearly approaches in morphology any of the other known *Atlantoceratodus* species.

Apesteguia *et al.* (2007) described as belonging to *A. iheringi* a lower tooth plate (MACN PV RN157C) from the Los Alamitos Formation. This badly preserved tooth plate is here referred to *A. patagonicus* based mainly on its large size and robustness, being clearly different from holotype specimen of *A. iheringi.*

Martinelli and Forasiepi (2004) described a specimen of *Atlantoceratodus patagonicus* as Ceratodontidae gen. et sp. indet., indicating similarities to *Atlantoceratodus iheringi* and the specimen figured by Wichmann (1927). In agreement with such proposal, we consider all these specimens as belonging to the single species *A. patagonicus* in the present paper (see below).

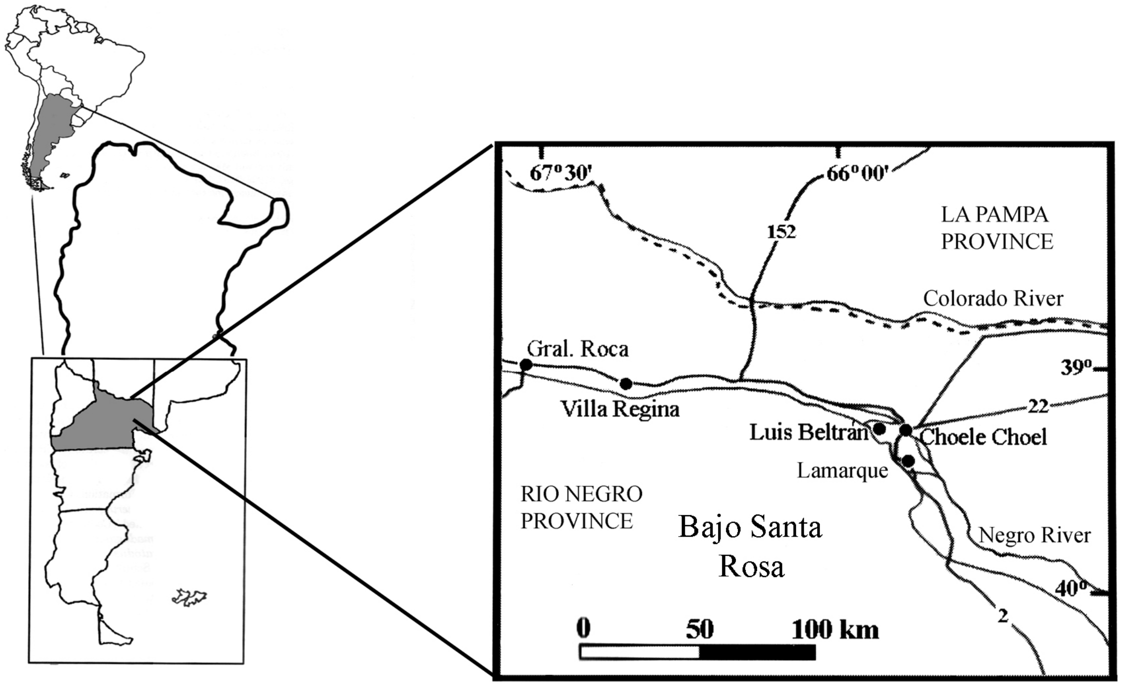

Figure 2. Map showing fossiliferous localities mentioned in the text. Scale bar 5 kilometers.

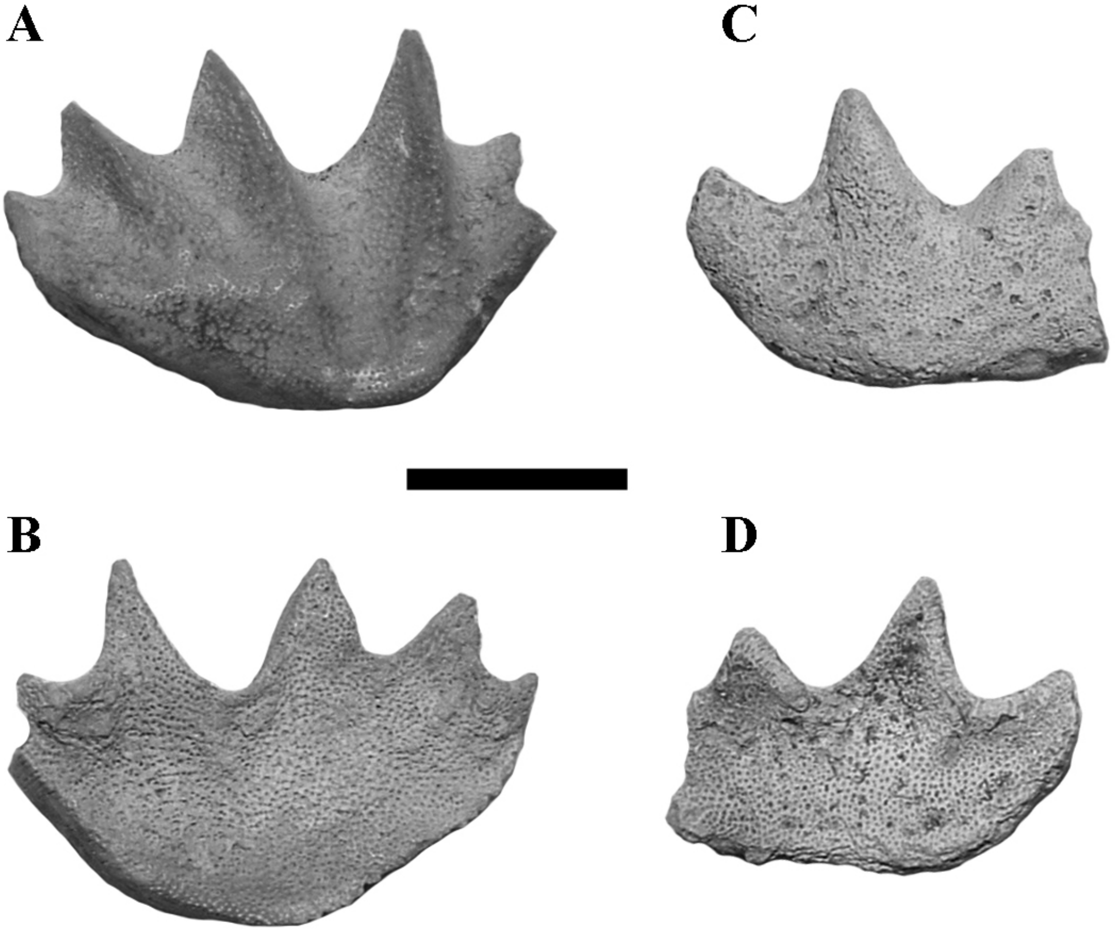

Figure 3. *Atlantoceratodus patagonicus* nov. sp. **A-B**, MML 196 (holotype), right upper tooth plate in (**A**) occlusal and (**B**) ventral views; **C-D**, MML 197, incomplete right lower tooth plate in (**A**) occlusal and (**B**) ventral views. Scale bar: 1 cm.

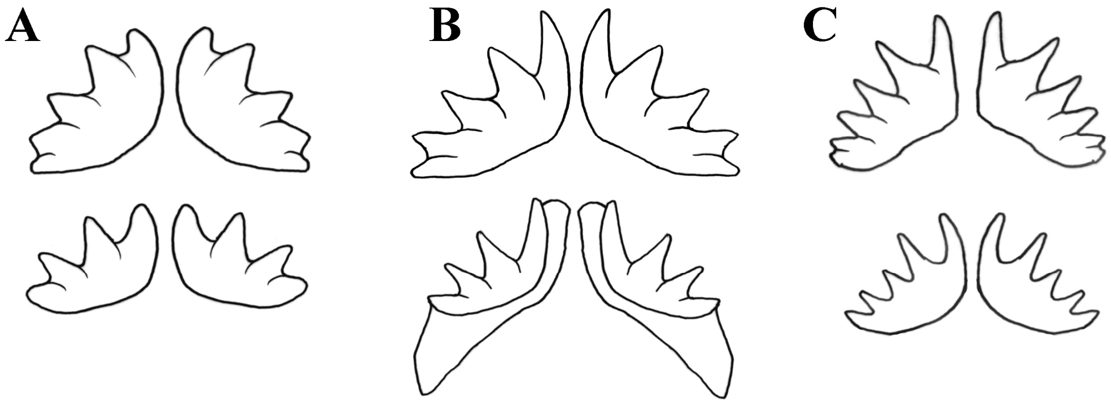

Figure 4. Drawings of occlusal profiles of tooth plates of *Atlantoceratodus* species including drawn mirror image. At top, upper tooth plates, at bottom, lower ones. **A,** *Atlantoceratodus patagonicus* nov. sp., **B,** *A. iheringi*, and **C,** *A. elliotti*. Not to scale. (B, modified from Cione et al. 2007; C, modified from Kemp 1997a).

3. Discussion and conclusions

In this section we discuss the affinities and morphology of several Cretaceous and Paleogene dipnoans from South America.

The clade Ceratodontoidei Nikolski, 1954

The clade Ceratodontoidea was coined by Apesteguía; Agnolin; Claeson (2007) to include the families Neoceratodontidae, Ceratodontidae and Ptychoceratodontidae. However, these authors have not noticed that a similar agrupation of taxa was previously employed by Nikolski in 1954 (H. SCHULTZE pers. com.), and thus, Ceratodontoidea becomes a junior synonym of Ceratodontoidei. The Ceratodontoidei was diagnosed by Apesteguía; Agnolin; Claeson (2007; Ceratodontoidea therein) on the basis of the following derived features: 1) the medial edge of the lower tooth plate is bent; 2) the upper and lower tooth plates lingual margin is convex; 3) anteroposterior length of tooth plates more than 2,5 cm; 4) upper plates with six crests. However, these traits deserve the following comments: the feature number 1 is not present in several ptychoceratodontids, such as *Ferganoceratodus* and the "South American" ptychoceratodontid species group, *Metaceratodus wollastoni*, and *Ceratodus diutinus*, among others (KEMP, 1993). The feature 2 is present in most ptychoceratodontid, neoceratodontid, and asiatoceratodontid species. However, the lingual edge in some derived ceratodontoid species is not convex, including as for example *Archaeoceratodus theganus* Kemp, 1997b, *Mioceratodus diaphorus* Kemp, 1997b, *Ptychoceratodus serratus*, *P. hislopianus* (MARTIN; BARBIERI; CUNY, 1999), and *Ferganoceratodus szechuanensis* (MARTIN et al. 1997). This suggests that the presence of a strongly convex lingual margin of tooth plates is an ambiguous feature of equivocal distribution among ceratodontoids. With respect to the feature 3, although most ceratodontoid species are large to medium sized, the size is not diagnostic at any taxonomic level within dipnoan tooth plates (see above). The trait 4 is variable among species of the same genus (e.g. *Neoceratodus, Ceratodus*; KEMP; MOLNAR, 1981), and correspondingly it may not be considered as a derived trait of Ceratodontoidei.

Apesteguía; Agnolin; Claeson (2007) defined Ceratodontoidea (= Ceratodontoidei herein) as the node that includes Neoceratodontidae, Ceratodontidae (Ptychoceratodontinae + Ceratodontinae), their common ancestor and all of its descendants. This name may be used to include also other dipnoan subgroups, including Asiatoceratodontidae and Lepidosirenidae (see MARTIN, 1982; 1984a; SCHULTZE, 2004; CAVIN et al. 2007).

A main basal dichotomy may be recognized within Ceratodontoidei. Ceratodontoidei includes on one hand the sister families Neoceratodontidae and Lepidosirenidae, and on the other hand remaining dipnoans (i.e. Ptychoceratodontidae, Asiatoceratodontidae, and Ceratodontidae). The clade Neoceratodontidae + Lepidosirenidae is diagnosed on the basis of several derived features, including the pterygopalatine process of upper tooth plates above the level of the third crest (MARTIN, 1982), tapered snout composed by capillary loops and associated structures (CAVIN et al. 2007), made up by elongation of anteriormost bone of the median series (but see CAVIN et al. 2007), sensory canals superficial, not marking bones (KEMP, 1998), and a single mediolateral ossification (KEMP, 1998). This clade is here named as Neodipnoi nov. The other dipnoan clade that includes Ceratodontidae, Ptychoceratodontidae, and Asiatoceratodontidae (*sensu* KEMP, 1998) is diagnosed on the basis of a large and broad anterior medial bone, straight anterior margin of skull roof, (CAVIN et al. 2007), craniocaudally extended anterior mediolateral bone, and broad and short crests on lower tooth plates (APESTEGUÍA; AGNOLIN; CLAESON, 2007) (Figure 5). The relationships among Ceratodontidae, Ptychoceratodontidae and Asiatoceratodontidae are pointed out below.

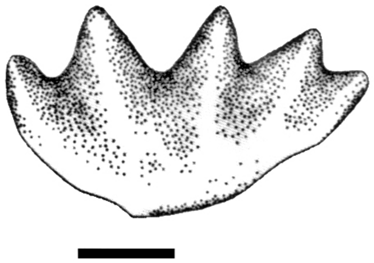

Figure 5. *A. patagonicus* nov. sp. MACN PV RN 1080, left upper tooth plate in occlusal view (referred specimen). Scale bar: 1 cm. (taken from Martinelli and Forasiepi, 2004).

Basal ceratodontoid genera *Chaoceratodus* and *Atlantoceratodus*.

The genus *Chaoceratodus* Apesteguía, Agnolin, and Claeson, 2007 was based on an isolated lower tooth plate (considered upper by APESTEGUÍA; AGNOLIN; CLAESON, 2007) from the Turonian Portezuelo Formation (Upper Cretaceous) of Sierra del Portezuelo, Neuquén province, Argentina. The genus *Chaoceratodus* is very poorly known, and is only represented by a single species: *C. portezuelensis*. This species was found associated with indeterminate remains of *Ceratodus* species (APESTEGUÍA; AGNOLIN; CLAESON, 2007). The holotype of *Chaoceratodus* was considered as an upper tooth plate in its original description. However, the holotype is actually a lower tooth plate, as can be shown by the absence of a twinned last crest, very large and anteriorly directed first crest with convex mesial margin, and obtuse angle between first crest and occlusal surface of the tooth plate (MARTIN, 1982; KIRKLAND, 1987; MILNER; KIRKLAND, 2006).

Chaoceratodus was diagnosed on the basis of the presence of peculiar tubercles on the labial edge of crests, very low second ridge crest, with its labial margin very rounded, and absence of oclusal pits (APESTEGUÍA; AGNOLIN; CLAESON, 2007), among other features. However, the presence of tubercles on the labial margin of tooth plates was indicated by Kemp (1996) in living and fossil dipnoan species, as indicative of tooth plate anomaly, and thus devoid of systematic value. The absence of occlusal pits and tubercles is a feature shared by *Chaoceratodus, Atlantoceratodus,* Neoceratodontidae, and Lepidosirenidae, being both present and well developed in most Ceratodontidae and Ptychoceratodontidae (MARTIN, 1982; CIONE et al. 2007). Additionally, *Chaoceratodus* resembles *Atlantoceratodus* in the crests originating near the mediolingual face, as occurs in Neoceratodontidae (e.g.

Neoceratodus, Archaeoceratodus, Mioceratodus; KEMP, 1997b), whereas these crests originate medially in Ceratodontidae (e.g. *Metaceratodus, Ceratodus, Ferganoceratodus*; KEMP, 1997a; MARTIN; BARBIERI; CUNY, 1999).

Apesteguía; Agnolin; Claeson (2007) considered Lepidosirenidae and *Chaoceratodus* as the successive sister group of *Atlantoceratodus,* Ceratodontidae, Ptychoceratodontidae and several Neoceratodontidae because of the inner angle larger than 110º, and upper tooth plates with less than five crests. However, as was noted above, the inner angle is larger than 120° in *Atlantoceratodus* and several Neoceratodontidae (KEMP, 1997b), and the presence of less than five crests on upper tooth plates is also present in the "South American" ptychoceratodontid group (see below).

Based on the ambiguous features noted above, *Chaoceratodus* is here considered as Ceratodontoidei *incertae sedis*, and based on its unique combination of features, rather different from other dipnoans, the genus may represent a peculiar South American endemicity.

The species *Ceratodus iheringi* was described by Ameghino (1899) under the following words: "*Ceratodus iheringi* n. sp. very small sized. The lower tooth is not triangular, but elongate shaped, with five ramifications or horns on the external side, separated by deep clefts and which thickness diminishes, as its length, from anterior to posterior; this tooth has 22 millimeters in length and 12 millimeters in transverse diameter at the second ramification; on its general contour, is similar to the tooth of *Ceratodus runcinatus* Priem; figured by Zittel…". Later, the genus *Ameghinoceratodus* was created by Apesteguía; Agnolin; Claeson (2007) to include the holotype of *"Ceratodus" iheringi* Ameghino, 1899 from the Mata Amarilla Formation (Coniacian) of southern Santa Cruz province, Argentina. These authors also referred to this species some additional tooth plates of the holotype locality and horizon (GOIN et al. 2002), and from the Turonian Huincul Formation (APESTEGUÍA; AGNOLIN; CLAESON, 2007), and from the Cenomanian Candeleros Formation (lower-upper Cretaceous) of Río Negro province, Argentina. Additionally, Apesteguía; Agnolin; Claeson (2007) reported fragmentary remains referred to this species from the Campanian-Maastrichtian Los Alamitos Formation (BONAPARTE, 1987) also from Río

Negro province. These specimens are here regarded as belonging to the new species *Atlantoceratodus patagonicus* (see above). Independently, Cione et al. (2007) coined the name *Atlantoceratodus* also to include the holotype and referred specimens of "*Ceratodus*" *iheringi* and those of *Ferganoceratodus madagascariensis* (MARTIN; BARBIERI; CUNY, 1999) from the Campanian of Malagasy. Thus, the names *Ameghinoceratodus* and *Atlantoceratodus* are based on the same specimen, and are objective synonyms. The available generic name for *Ceratodus iheringi* should be *Atlantoceratodus* Cione, Gouiric, Goin, and Poiré, 2007 since it was published on the first week of June 2007, whereas the name *Ameghinoceratodus* Apesteguía, Agnolin, and Claeson, 2007 was published at the end of June 2007, being in consequence a junior synonym of *Atlantoceratodus*. The genus *Atlantoceratodus* is diagnosed on the basis of several traits, including the slender and acute crests separated by deep and narrow furrows, the large angle formed by the first and last crests (about 130°), and two later crests caudally oriented, being the last nearly subparallel to the main lingual axis of the tooth plate (APESTEGUÍA; AGNOLIN; CLAESON, 2007; CIONE *et al.* 2007) (Figure 4). Additionally, as was pointed above, *Atlantoceratodus* lacks occlusal pits, shows limited dentine mantle, punctuations without distributional pattern, rounded occlusal surface on crests, inner apex rounded, crests originated anteriorly, and restricted pulp cavity (CIONE et al. 2007). We conclude that lower tooth plates were probably not in contact to each other in this genus because of the absence of wear facet on the mesial angle of lower tooth plates in *Atlantoceratodus* (CIONE et al. 2007). APESTEGUIA; AGNOLIN; CLAESON (2007) also included as an *Atlantoceratodus* diagnostic feature the presence in upper tooth plates of a curved first ridge crest, whereas the others are nearly straight. However, as was indicated by Martin; Barbieri; Cuny (1999) the direction of each crest is highly variable within populations, and thus, it can not be considered as a generic nor specific diagnostic trait (see also KEMP; MOLNAR, 1981).

All the above mentioned diagnostic traits of *Atlantoceratodus* are also present in the Patagonian species *A. patagonicus* nov. sp., and in *"Metaceratodus" elliotti* Kemp, 1997a from the Upper Cretaceous of Australia (Figure 4). Accordingly, Kemp (1997a) indicated great morphological resemblance between the Australian species and the Patagonian *A. iheringi*, suggesting that both species are congeneric. Concordantly, "*M.*" *elliotti* is consequently included within that genus. However, *Atlantoceratodus elliotti* differs from *Atlantoceratodus iheringi* in the wider pulp cavity, suggesting that it may represent the basal most species within the genus, because this plesiomorphic trait is present in most ceratodontiform genera, such as *Ceratodus, Metaceratodus, Ptychoceratodus,* and Neoceratodontidae (KEMP, 1997a,b; 2001). In contrast, the pulp cavity of *Atlantoceratodus iheringi* is apomorphically restricted (*sensu* CIONE et al. 2007; the condition is unknown in *A. patagonicus* nov. sp.).

On the other hand, Cione et al. (2007) closely allied *A. iheringi* with *Ferganoceratodus madagascariensis* (= *Ptychoceratodus madagascariensis*; MARTIN, 1982) on the basis of the following combination of features: 1) tooth plates of medium size; 2) high crowned, and with sharp, slender and acute crests; 3) crests originating anteriorly; 4) five crests on upper plates and four in lower; 5) inner apex not so well defined and rounded; 6) relatively large angle between first and last crests; 6) occlusal tubercles present; 7) limited mantle of dentine visible on occlusal surface; 8) punctuations simple (petrodentine absent); and 9) punctuations not arranged with a particular pattern (MARTIN, 1984a; CIONE et al. 2007). However, feature 1) is not diagnostic at the generic level (see above), features 2, 6, 7, 8 are traits also present in most dipnoan taxa including the ptychoceratodontid genera *Ferganoceratodus* and *Ptychoceratodus* (MARTIN; BARBIERI; CUNY, 1999), and thus are not uniquely shared by *F. madagascariensis* and *Atlantoceratodus*. With respect to the feature number 2) *Atlantoceratodus* differs from *Ferganoceratodus* (including the species *F. madagascariensis*) and *Ptychoceratodus* in having crests with low and rounded occlusal surface (as also present in *Ceratodus* and several *Metaceratodus* species; KEMP, 1997a), rather than cutting crests as diagnostic of ptychoceratodontid genera (MARTIN, 1982). Crests clearly originate anteriorly in *A. iheringi* (CIONE et al. 2007), whereas they radiate medially in *Ferganoceratodus madagascariensis* (see MARTIN; BARBIERI; CUNY, 1999: Plate II, figs. 1-12). In *Atlantoceratodus* exists five crests on upper plates and four on lower ones (feature 4), as they are present in *Ferganoceratodus madagascariensis*

(CIONE et al. 2007). However, this ridge number is also common to other ptychoceratodontid species, such as *Ptychoceratodus acutus, P. hislopianus* and *Ferganoceratodus* (MARTIN; BARBIERI; CUNY, 1999).

The trait number 5 is true only for lower tooth plates, because upper tooth plates of *Ferganoceratodus madagascariensis* shows a well defined and acute inner angle (resembling a keel), being very different from the rounded contour present in *Atlantoceratodus* (see discussion above). Finally, the relatively large angle between first and last crests (trait 6) is not true for *Ferganoceratodus madagascariensis*. Whereas in *Atlantoceratodus iheringi* the inner angle of lower tooth plates is about 130°, in *Ferganoceratodus madagascariensis* it is lower than 105°, being similar in this aspect to other *Ferganoceratodus* species and *Ptychoceratodus* (see MARTIN; BARBIERI; CUNY, 1999; CIONE et al. 2007). Moreover, Cione et al. (2007) distinguished *Atlantoceratodus* (including *Ferganoceratodus madagascariensis*) from Ptychoceratodontidae on the basis of the following features: 1) tooth plates with inner apex poorly defined; 2) first and last crests forming a large angle; 3) high crown; 4) limited mantle of dentine visible on occlusal surface; 5) slender, short, and acute crests; 6) crests originate anteriorly; and 7) punctuations simple, not arranged in a particular pattern. As was pointed out above features 3 and 5 are not true for the genotypical species *A. iheringi* or remaining *Atlantoceratodus* species. Features 1, 2, 7 were discussed above and were considered as not uniquely shared by *Atlantoceratodus* species and *Ferganaceratods madagascariensis*; the latter two traits are also present in *Ptychoceratodus*. Finally, feature 6 is not true for *Ferganoceratodus madagascariensis*, in which furrows of occlusal pits exist between crests, being a common trait among ptychoceratodontids (see KEMP, 1998).

Additionally, clear differences exist between *Atlantoceratodus* and *Ferganoceratodus madagascariensis*. The latter resembles of Ptychoceratodontidae, rather than *Atlantoceratodus* in the following additional traits: 1) wide pulp cavity (a plesiomorphy also present, as for example, in *Ceratodus, Asiatoceratodus,* and *Metaceratodus*; KEMP, 1993; 1997a; 1998); 2) short and acute cutting crests (not acute in *Atlantoceratodus*); 3) occlusal pits present and located between furrows (also present in *Asiatoceratodus* and *Metaceratodus*; Kemp, 1998).

Pascual and Bondesio (1976) and Cione (1987) (see also MARTIN, 1982; MARTIN; BARBIERI; CUNY, 1999) referred several Campanian-Maastrichtian lungfish specimens from Patagonia to *Ceratodus iheringi*. These authors indicated these specimens are closely related to *Ferganoceratodus madagascariensis*. Posteriorly Cione et al. (2007) suggested that these specimens may belong to *Metaceratodus*. Apesteguía; Agnolin; Claeson (2007) established two new ptychoceratodontid species to include the specimens previously referred by those authors and considered them only as distantly related to "*Ceratodus*" *iheringi* (actually *Atlantoceratodus*).

Apesteguía; Agnolin; Claeson (2007) referred an isolated lower tooth plate coming from the Portezuelo Formation (Coniacian) at Cerros Colorados locality (Neuquén province, Argentina) to *Atlantoceratodus*. However, this specimen differs from *Atlantoceratodus* in having shallow clefts between crests, an inner angle approaching 110°, very low crests (specially from third to fifth), the second crest is the largest and longest of all crests, the presence of a twinned last crest, abrupt and well defined inner angle indicating a large and wide contact between opposite lower tooth plates. The Neuquén specimen resembles the Early Cretaceous ?lepidosirenid species *Lavocatodus protopteroides* (MARTIN, 1984b) in all these features, and thus, it is referred to the genus *Lavocatodus* being the first record for this taxon in South America.

Concluding, the species *Ceratodus iheringi* is the type species of the genus *Atlantoceratodus*, in which *A. patagonicus* nov sp. and the Australian *A. elliotti* (KEMP, 1997a) could be also included. Additionally, the species *Ferganoceratodus madagascariensis* and the specimens referred to "*C*". *iheringi* by Pascual and Bondesio (1976), Martin (1982), Cione (1987) and Martin; Barbieri; Cuny (1999) are here included within the family Ptychoceratodontidae being only distantly related to the true "*Ceratodus*" *iheringi*.

With respect to its different phylogenetic relationships, *Atlantoceratodus* approaches the morphology of Lepidosirenidae, Neoceratodontidae, and *Chaoceratodus* because of its low crowned plates without occlusal pits and a concave lingual margin. However, *Atlantoceratodus*, as *Chaoceratodus* are so poorly known that their phylogenetic relationships are obscure, and both are here regarded as Ceratodontoidei *incertae sedis*.

The clade Neodipnoi nov.

As was indicated in previous paragraphs, a lepidosirenid-neoceratodontid clade has been recognized by most authors (e.g. MARTIN, 1982; 1984a; BEMIS, 1984; MARSHALL, 1987; THOMSON, 1990; SCHULTZE; MARSHALL, 1993; SCHULTZE; CHORN, 1997; SCHULTZE, 2004). This clade is diagnosed on the basis of five unambiguous synapomorphic features absent in remaining fossil dipnoans. Thus, the name Neodipnoi nov. may be applied to crown group dipnoans.

Neodipnoi nov.

Diagnosis. Dipnoans with the following synapomorphies: 1) pterygopalatine process of upper tooth plates above the level of the third ridge crest, 2) tapered snout composed by capillary loops and associated structures, 3) made up by elongation of anteriormost bone of the median series, 4) sensory canals superficial, and 5) one or two mediolateral ossifications (Figure 6 A-C).

Definition**.** Neodipnoi is defined here as the clade that includes Lepidosirenidae + Neoceratodontidae plus all of its descendants (Figure 1).

Etymology. Neo: recent; dipnoi: lungfish.

Comments. Neodipnoi constitutes the crown-group dipnoans, which includes among some extinct forms (i.e. *Mioceratodus, Archaeoceratodus*), and the extant *Neoceratodus* and Lepidosirenidae (including *Lepidosiren* and *Protopterus*). Both living and extinct neodipnoans are restricted to Gondwanan landmasses (i.e. South America, Africa, Australia).

Family Lepidosirenidae Bonaparte, 1841

This family of living lungfishes is composed of the recent genera *Lepidosiren* Fitzinger, 1837, *Protopterus* Owen, 1839, and probably the extinct *Lavocatodus* (with the Lower Cretaceous African species *L. protopteroides* (Tabaste,1963)(MARTIN, 1982, 1997; see the current concept of this species in CHURCHER; DE IULIIS, 2001) (KEMP, 1998; MARTIN, 1997). Lepidosirenidae show an Amphiatlantic distribution (*sensu*

RINGUELET, 1974), they are present in both Africa and South America (ARRATIA, 1997). In South America, the genus *Lepidosiren* is represented by the living *L. paradoxa* Fitzinger, 1837 and the extinct *L. megalos* from the Miocene of Brazil (SILVA SANTOS, 1987). On the other side the genus *Protopterus* is represented by four living and several extinct species from Cretaceous and Tertiary deposits from Africa (CHURCHER; DE IULIIS, 2001; MARTIN, 1997).

Although Apesteguía; Agnolin; Claeson (2007) considered that Lepidosirenidae as the sister group of remaining post-Paleozoic dipnoans (*sensu* MARTIN, 1983), current knowledge of the group indicates that Lepidosirenidae is a derived branch within Neozoic dipnoans, as was pointed out previously by several authors (e.g. MARTIN, 1982; 1984a; KEMP, 1998). Lepidosirenidae were considered by Martin (1982) as closely related to Neoceratodontidae on the basis of the position of the pterygopalatine process above the level of the third ridge crest. Additionally, several authors have indicated numerous features linking both Neoceratodontidae and Lepidosirenidae (see discussion in KEMP, 1997b). Tooth plates of Lepidosirenidae are diagnosed on the basis of the following derived features: tetra or tri.radiate tooth plates (loss of fifth ridge), third crest large and falcate, second and first crests reduced in size, and tooth plates with restricted dentine mantle (MARTIN, 1982; 1984a; KEMP, 1998; 2001).

Fossil *Lepidosiren* from South America were referred to *L. paradoxa* (FERNANDEZ; PASCUAL; BONDESIO, 1973), *Lepidosiren sp.* (SCHULTZE, 1992b; TOLEDO; BERTINI, 2005), or as *L. megalos* (SILVA SANTOS, 1987). Several large sized tooth plates cited by several authors from the Miocene Solimoes Formation (Acre basin) of Brazil (TOLEDO; BERTINI, 2005) and the Miocene of Colombia (Honda Group; BONDESIO; PASCUAL, 1977; LUNDBERG, 1997) could be assigned to the latter species. Remains indistinguishable from that of the living species *L. paradoxa* were found in the Eocene La Lumbrera Formation (Salta province, Argentina; FERNÁNDEZ; PASCUAL; BONDESIO, 1973), the Late Cretaceous and Lower Paleocene El Molino and Santa Lucía Formations, respectively (South-central Bolivia; SCHULTZE, 1992b), and the upper Cretaceous of Perú (SCHULTZE, 1992b).

As was commented above, the questionable presence of the probable lepidosirenid *Lavocatodus* (MARTIN, 1984b) is present in the upper Cretaceous of Neuquén province, based on a single isolated tooth plate.

Apesteguía; Agnolin; Claeson (2007) reported the presence of a ?Lepidosirenidae at the Anacleto Formation (Campanian) of Río Negro province. This specimen consist of a highly abraded and incomplete ?upper tooth plate. Although poorly preserved, this specimen differs from Lepidosirenidae in having a wider pulp cavity, more acute crests, a small third ridge crest, occlusal pits and in lacking columnar petrodentine (see above). Moreover, its cutting crests are similar to ptychoceratodontids. Concluding, this putative lepidosirenid may belong, in fact, to Ptychoceratodontidae.

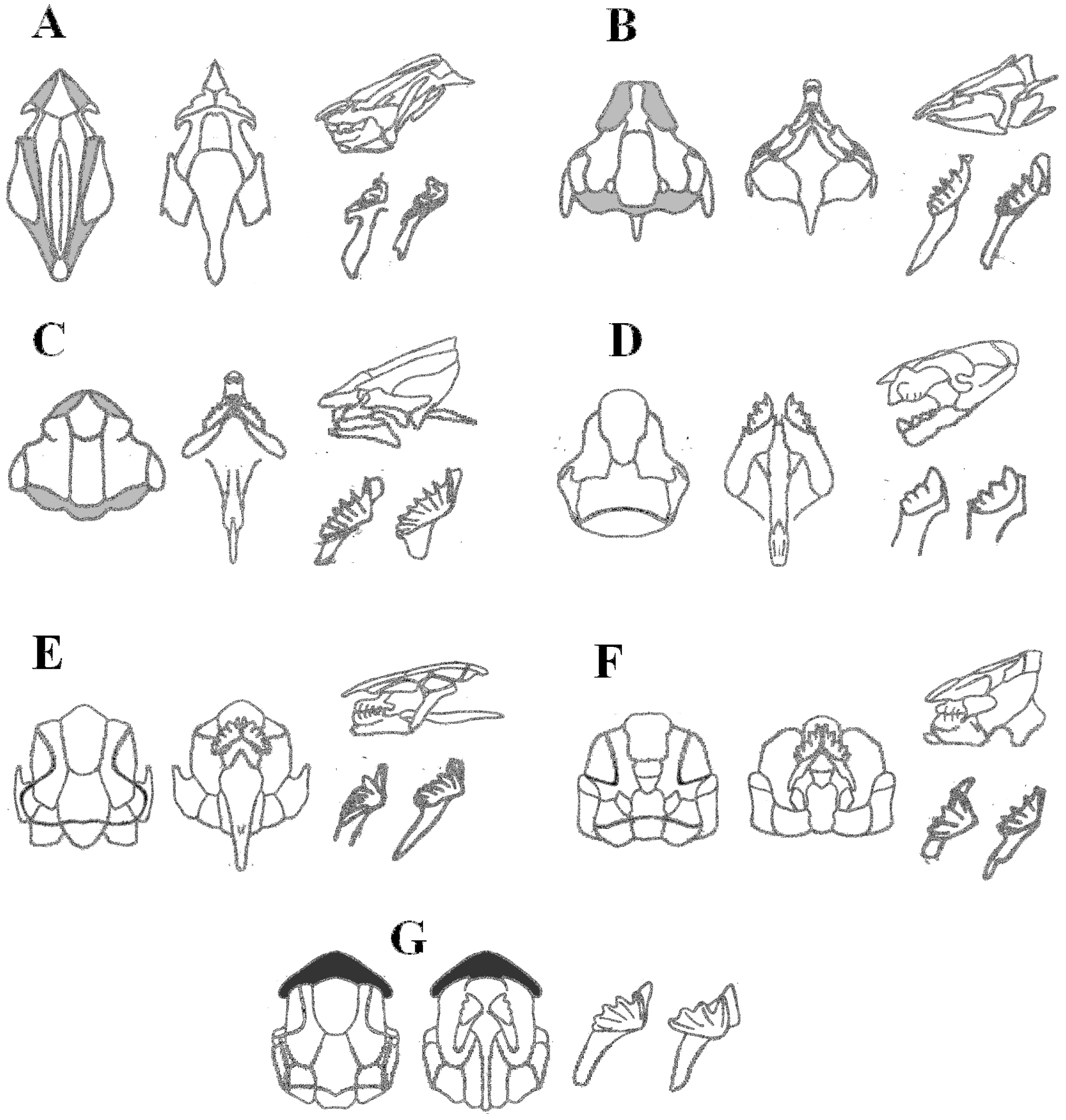

Figure 6. Schematic drawings of the calvaria of representative dipnoan lungfishes mentioned in the text. **A,** *Protopterus annectens,* **B**, *Neoceratodus forsteri*, **C**, *Mioceratodus* spp., **D**, *Ceratodus sturii*, **E**, *Asiatoceratodus atlantis*, **F**, *Ptychoceratodus serratus*, **G**, *Ferganoceratodus* spp. In each figure are indicated: calvarium in dorsal view (left), calvarium in ventral view (centre), cranium in left lateral view (top right), lower tooth plates and tooth bearing bones (right centre), upper tooth plates and tooth bearing bones (right bottom). Sensory canals are drawn in black. Cartilage is shaded in grey. Not to scale. All figures modified from Kemp (1991, 1997a,b, 1998), Calvin et al. (2007) and personal interpretations.

Family Neoceratodontidae Miles, 1977

This family, together with the Lepidosirenidae represents the few living lungfishes, with the species *Neoceratodus forsteri* (de Castelnau, 1876) from freshwater environments of Australia. The Neoceratodontidae are represented by living and fossil species of the genus *Neoceratodus* de Castelnau, 1876 and numerous species of the extinct genera *Mioceratodus* Kemp, 1997b and

Archaeoceratodus Kemp, 1997. Moreover, several species previously referred to the ceratodontid genus *Metaceratodus* may belong to Neoceratodontidae (i.e. *M. bonei* and *M. palmeri*; see MARTIN; BARBIERI; CUNY, 1999; APESTEGUÍA; AGNOLIN; CLAESON, 2007; this paper). The tooth plates of the family Neoceratodontidae could be diagnosed on the basis of several derived traits, such as the presence of more than six well developed crests (seven on upper tooth crests, and more than six on lower tooth crests; convergently present in Asiatoceratodontidae), mantle of dentine extensive, and loss of the radiating pattern on adult tooth plates (MARTIN, 1982; 1984a; APESTEGUÍA; AGNOLIN; CLAESON, 2007).

The genus *Neoceratodus* includes the living species *N. forsteri* known from Tertiary deposits from Australia (the Early Cretaceous record of this species reported by KEMP; MOLNAR, 1981 was rejected by MARTIN, 1984a) and several extinct species recently summarized by Kemp (1997b; see also MARTIN, 1982). This genus differs from remaining Neoceratodontidae on the basis of absence of petrodentine (KEMP, 1997b), and has been reported from several fossiliferous localities from Australia, Africa and isolated records from South America (KEMP; MOLNAR, 1981; KEMP, 1997b; TOLEDO; BERTINI, 2005; BERTINI et al., 1993). The remaining genera *Archaeoceratodus* and *Mioceratodus* are united by the presence of a limited dentine mantle (KEMP, 1996). Both genera are restricted to isolated remains from Australian Cretaceous and Eocene-Pleistocene beds, respectively.

The species *Metaceratodus palmeri* (Kreft, 1874) and *M. bonei* Kemp, 1997b are included within the Neoceratodontidae on the basis of the traits listed above. The first species differs from *Neoceratodus* and resembles *Archaeoceratodus* and *Mioceratodus* in having a limited dentine mantle and petrodentine (KEMP, 2001; both traits are not preserved in the specimens referred to *M. bonei*). "*Metaceratodus*" *palmeri* may be included within *Archaeoceratodus* because of the presence of elongated tooth plates (specially the lower), robust short crests, and no inner angle (KEMP, 1997b). *"M." palmeri* differs from remaining *Archaeoceratodus* in having broader and thicker tooth plates. Thus, the Australian species may be referred to *Archaeoceratodus palmeri* (Kreft, 1874). On the other hand, the species "*M.*" *bonei* Kemp, 1997 resembles *Neoceratodus* in having broad, subtriangular tooth plates with a well defined inner angle (different from the delicated plates of *Mioceratodus* and the elongate tooth plates of *Archaeoceratodus*) (KEMP, 1997b). "*M.*" *bonei* differs from other species of the genus (e.g. *N. forsteri, N. eyrensis, N. nargum, N. africanus*; MARTIN, 1982; 1984a; KEMP, 1997b) in having broader and more flattened tooth plates, with shorter and broader crests. Thus, the genus *Metaceratodus* is composed only by its type species *M. wollastoni* Chapman, 1914, excluding with the species *M. elliotti* (see above), *M. palmeri,* and *M. bonei.*

The Early Cretaceous African species *C. pectinatus* Tabaste, 1963 is also referable to Neoceratodontidae, following MARTIN (1981; 1982; 1984a). Morphological features support this view are, the presence of more than six crests on tooth plates, extensive mantle of dentine, loss of the radiating pattern of crests, and crests strongly directed backwards. The generic placement of "*C.*" *pectinatus* within neoceratodontids, is uncertain, but the presence of very deep and narrow clefts between crests, and the relatively robust, short, and straight crests resemble *Archaeoceratodus* (KEMP, 1997b). The presence of inner angle distinguishes "*C*". *pectinatus* from *Archaeoceratodus* and approaches in this aspect the genera *Mioceratodus* and *Neoceratodus* (KEMP, 1997b). "*C*". *pectinatus* differs from remaining neoceratodontids in having more than eight crests on tooth plates, and the pterygopalatine process located between fourth and fifth crests (CHURCHER; DE IULIIS; KLEIDIENST, 2006). So, although the generic assignment of "*C*". *pectinatus* is still uncertain, several traits suggesta placement within *Archaeoceratodus*.

The South American record of the family Neoceratodontidae is rather poor, being represented only by some isolated plates referred to *Neoceratodus brasiliensis* (SOUZA CUNHA; FERREIRA, 1980), *N. sulamericanus* Silva; Azevedo (1996) and *Neoceratodus* sp. (see GAYET; BRITO, 1989; TOLEDO; BERTINI, 2005) from the Lower Cretaceous of Brazil. Additional, *Neoceratodus* specimens were mentioned from the Upper Cretaceous of Patagonia (KEMP; MOLNAR, 1981; KEMP, 1997b). As was pointed out by other authors, most Brazilian neoceratodontid remains belong to the species *N. africanus*, of which *N. brasiliensis* and *N. sulamericanus* are junior synonyms (MARTIN, 1984a; TOLEDO; BERTINI, 2005). *N. africanus* and all

Neoceratodus specimens from Brasil are distinguished from remaining species of the genus because by a short first crest (specially on lower tooth plates; probably apomorphic for the species), not anteriorly directed first crest (in contrast to *N. forsteri*), and very thin and acute second to last crests (broader in *N. forsteri*). Thus, as was pointed out by Martin (1984a) the Early Cretaceous *N. africanus* may be one of the most recent vertebrate species shared by both continental landmasses (see also discussion within Lepidosirenidae, Ptychoceratodontidae and Asiatoceratodontidae). Kemp (1997b) questioned the referral of *N. africanus* to the genus *Neoceratodus* and even to the Neoceratodontidae. However, Kemp (1997b) did not cite any trait to reinforce her doubts. On the other hand, all the features cited below as diagnostic of neoceratodontid and *Neoceratodus* tooth plates (see also KEMP, 1997a,b) are present in *N. africanus* and thus, it is still retained within *Neoceratodus* in the present paper.

In regards to the putative Patagonian record of *Neoceratodus*, Kemp and Molnar (1981), and Kemp (1993; 1997b) indicate that Pascual and Bondesio (1976) reported the presence of specimens assignable to *Neoceratodus*. However, this may be considered as a misinterpretation, because Pascual and Bondesio (1976) did not mention any specimen that may be referable or assignable to the Neoceratodontidae (SOTO; PEREA, 2010). On the contrary, Pascual and Bondesio (1976) related most Patagonian taxa to *Ceratodus*. As was pointed out by Apesteguía; Agnolin; Claeson (2007), all the individuals reported by Pascual and Bondesio (1976) are referable to the genera *Metaceratodus, Atlantoceratodus* and *Ptychoceratodus*, but there are no neoceratodontid-like specimens (SOTO; PEREA, 2010). It is worthy to note, that neoceratodontids are the most abundant and diversified post-Triassic dipnoans of Australia unlike any other Continent, they form a large radiation including at least three genera and more than a dozen species (see KEMP, 1991). The record of Neoceratodontidae is restricted to Africa, South America, and Australia, suggesting that this dipnoan clade was widespread, and probably endemic to Gondwana (they were not found in the patchy and biased upper Cretaceous deposits of India, Madagascar, and Antarctica up to now).

The peculiar genus *Retodus*

The genus *Retodus* was established by Churcher; De Iuliis; Kleindesteinst (2006) to include the species "*Ceratodus*" *tuberculatus* Tabaste, 1963 from Albian-Campanian time span from Northern Africa. This species was originally referred by Tabaste in 1963 to the genus *Ceratodus*. *"C"*. *tuberculatus* was later transfered to the Neoceratodontidae as *Neoceratodus tuberculatus* (TABASTE, 1963) by Martin (1982; 1984a). *Retodus* Churcher; De Iuliis; Kleindesteinst, 2006 resembles neoceratodontids in the loss of the radiating pattern on adult tooth plates and in having crests strongly directed backwards (MARTIN, 1982; 1984a). *Retodus* is also similar to ceratodontoids in having less than six broad crests (a plesiomorphic trait also exhibited by *Chaoceratodus, Atlantoceratodus*, Ptychoceratodontidae, and Lepidosirenidae). Thus, the phylogenetic position of the genus *Retodus* is problematic and may be located at the base of Neoceratodontidae or as a link between this family and Ceratodontoidei.

Schultze (1992b) described isolated plates as belonging to a new genus and species of Ceratodontidae from the Paleocene of Tiupampa, southcentral Bolivia. These specimens show the peculiar and unique combination of features present in *Retodus* as well as the presence of synapomorphous transverse crests at the base of the crests (see above and CHURCHER et al., 2006). However, Bolivian specimens differs from *R. tuberculatus* in lacking the peculiar row of tubercles at the base of each crest and in having transverse crests with respect to the main axis of the plate (CHURCHER; DE IULIIS; KLEIDIENST, 2006). Thus the South American material is here considered as *Retodus* nov. sp.

The clade of broad-toothed ceratodontoids

Apesteguía; Agnolin; Claeson (2007) recognized a clade of broad toothed dipnoans that included current ptychoceratodontids and ceratodontids (Figure 1: Node 2). They considered this clade as Ceratodontidae, including the subfamilies Ptychoceratodontinae and Ceratodontinae. However, they excluded from their phylogenetic analysis the clade Asiatoceratodontidae Vorobyeva, 1967.

Apesteguía; Agnolin; Claeson (2007) based this clade on the following apomorphies: 1) JLM descendant process absent; 2) posterior calvarium formed by YZ, JLM, I, INNER; 3) short crests on tooth plates; 4) four to five crests on lower tooth plates; and 5) upper symphysis oblong, lower symphysis linear. Features 1 and 2 are variable within ceratodontid, ptychoceratodontid and *Asiatoceratodus*, and thus they are not diagnostic of this dipnoan clade (see KEMP, 1998). The trait number 3 appears to be a valid derived trait, since it is present in all broad toothed dipnoans. On the other hand, although feature 4 is present in most ptychoceratodontid and ceratodontid species, it is absent in *Asiatoceratodus*, in which more than six crests on tooth plates are invariably present (MARTIN, 1981;1982; 1984a).

Within broad crowned dipnoans, Asiatoceratodontidae and Ptychoceratodontidae appear to be more closely related to each other rather than to Ceratodontidae in having the following derived traits: 1) single XYZ bone (KEMP`s, 1998 terminology), 2) “U” shaped lateral sensory canal on anterior mediolateral bone (unknown in *Ferganoceratodus*; CAVIN et al. 2007), 3) broad ascending process of pterygopalatine bone forms a strong articulation with skull roof, 4) high crowned tooth plates with long and slender acute crests (MARTIN, 1982; KEMP, 1998; SOTO; PEREA, 2010), and 5) tooth plates with occlusal pits present, but restricted to inter-ridge furrows (KEMP, 1998) (Figure 6). Additionally, a transversely compressed interorbital region may be considered as a derived trait shared by Asiatoceratodontidae and Ptychoceratodontidae, however it is not included in the present analysis because it is a feature rather difficult to observe in the currently available cranial remains of fossil dipnoans (MARTIN, 1982).

Family Asiatoceratodontidae Vorobyeva 1967

This family was established by Vorobyeva 1967 to include several species of post-Triassic Mesozoic dipnoans previously referred to as *Arganodus* (MARTIN, 1982; KEMP, 1996, 1998). This family was considered the sister group of Ptychoceratodontidae on the basis of several cranial features and high crowned tooth plates with acute crests (see below). *Asiatoceratodus* is the only Cretaceous asiatoceratodontid genus, and is clearly distinct from other Late Mesozoic dipnoans in having tooth plates with very short and, acute crests originated anteriorly (VOROBYEVA, 1967). The record of Asiatoceratodontidae in South American Cretaceous beds is rather poor, and is restricted to some records from the Lower Cretaceous Alcântara Formation of Brasil (CASTRO et al. 2004; SOTO; PEREA, 2004; 2010). All specimens were referred to the Early Cretaceous African species *A. tiguidiensis*, from which they are nearly indistinguishable.

Family Ptychoceratodontidae Martin, 1982

The family contains the genera *Ptychoceratodus* Jackel, 1926 [type species *P. serratus*; (Agassiz 1838)], and *Ferganoceratodus* Kaznyshkin and Nessov, 1985 (type species *F. jurassicus* Kaznyshkin and Nessov, 1985), each of which include a large amount of species distributed in post-Mesozoic beds around the world (MARTIN, 1982; MARTIN et al. 1997; MARTIN; BARBIERI; CUNY, 1999; CAVIN et al. 2007). Both genera may be united by 1) the reduced contact suture between bones of the median series (even lost in *Ptychoceratodus*), 2) two large paired bones on the mediolateral series, and 3) dental tooth plates with occlusal surface of cutting type (MARTIN, 1982; CAVIN et al. 2007).

Formerly, Martin (1982) recognized four *Ptychoceratodus* species-group based on the tooth plate morphology: 1) the first group shows upper tooth plates with six crests. This group may be called the *Ptychoceratodus sensu stricto* because the genotype species *P. serratus* Agassiz, 1838 from the Triassic of Europe is included together with other Triassic species. 2) This second group includes species with obtuse inner angle of tooth plates. This group includes Triassic species from different Gondwanan landmasses (i.e. Africa, Australia, India; MARTIN; BARBIERI; CUNY, 1999), including *P. virapa* and *P.hislopianus*, among others. 3) The third group includes species that show crests more robust and less acute, and embraces most species now regarded as *Ferganoceratodus* (MARTIN et al. 1997). 4) Finally, the fourth group unites species without any sign of inner angle, including *Ferganoceratodus madagascariensis* (Priem, 1924) and *Ferganoceratodus wichmanni* (cited as *Ceratodus iheringi* by MARTIN, 1982). Although the formation of the inner angle was considered as variable within the ontogeny by Martin; Barbieri; Cuny (1999), the large ontogenetic series of specimens of different dipnoans analysed by Kemp (1997b) and Cione et al. (2007) indicate that this feature is not variable within a single species.

Thus, current knowledge of ptychoceratodontids indicates the presence of two different genera i.e. *Ferganoceratodus* and *Ptychoceratodus* (MARTIN; BARBIERI; CUNY, 1999). Both *Ptychoceratodus* and *Ferganoceratodus* are clearly distinguishable on the basis of calvarian morphology (CAVIN et al. 2007) (Figure 6 F-G). On the other hand, tooth plates are similar in both genera; however the inner angle lacks a clear tip in *Ferganoceratodus* (MARTIN et al. 1997), and upper tooth plates show less than five crests (more than five in *Ptychoceratodus*), whereas lower tooth plates show only four crests (MARTIN, 1982). *Ferganoceratodus* further differs from *Ptychoceratodus* in having a broad prearticular bone and tooth plates clearly separated from each other (CAVIN et al. 2007; KEMP, 1998).

Most Jurassic and Cretaceous tooth plates previously considered as *Ceratodus* or *Ptychoceratodus* from North America (KIRKLAND, 1987; 1988; MILNER; KIRKLAND, 2006; MARTIN; BARBIERI; CUNY, 1999), the Trias-Jurassic Eurasian species *P. virapa* (Oldham, 1859), *P. acutus* (Priem, 1924), several Asiatic species [e.g. *F. szechuanensis* (Young, 1942), *F. sharategensis* (Krupina, 1994); see MARTIN; BARBIERI; CUNY, 1999; CAVIN et al. 2007], and the Late Cretaceous *P. madagascariensis* (Priem, 1924) (MARTIN et al. 1997; MARTIN; BARBIERI; CUNY, 1999) may be included within *Ferganoceratodus*. The tooth plates and mandibular bones of these species are clearly distinct from *Ptychoceratodus* and are highly similar to *Ferganoceratodus* in the traits indicated below. However, the Late Jurassic North American species *"Ceratodus" fossanovum* Kirkland, 1998, included tentatively as a *Ferganoceratodus*-like form by Martin (1982) and Martin; Barbieri; Cuny (1999) differs from *Ferganoceratodus* in having contact between upper tooth plates, a derived feature present in other lungfishes, including *Ptychoceratodus* (CAVIN et al. 2007). Thus, *C. fossanovum* is here considered as belonging to the genus *Ptychoceratodus sensu stricto*.

In the same way, the previously described South American Cretaceous species "*Ptychoceratodus*" *cionei* Apesteguía, Agnolin, and Claeson, 2007, and "*P*". *wichmanni* Apesteguía, Agnolin, and Claeson, 2007 are here referred to *Ferganoceratodus*, on the basis of its low number of crests, their rounded medial angle, and of the broad prearticular and separated lower tooth plates at least in the case of "*P*". *wichmanni* (MML 198, 199, 200, 201, 202; Figure 6). Moreover, South American species are closely related to *F. madagascariensis* in lacking any sign of inner angle as was indicated by Martin (1982). The "South American" group of ptychoceratodontid dipnoans are further distinguished from other ptychoceratodontid species (including *F. madagascariensis*) in showing only four well developed crests on upper tooth plates (APESTEGUÍA; AGNOLIN; CLAESON, 2007).

Ferganoceratodus cionei (APESTEGUÍA; AGNOLIN; CLAESON, 2007) and *F. wichmanni* (APESTEGUÍA; AGNOLIN; CLAESON, 2007) are the most common dipnoan species in uppermost Cretaceous deposits from South America. Both species were established on the basis of material from the Estancia Los Alamitos (Río Negro province, Argentina), Los Alamitos Formation (Campanian-Maastrichtian; see BONAPARTE *et al.* 1984). The species *F. cionei* was named by Apesteguía; Agnolin; Claeson (2007) to include a robust morphotype distinguishable from the closely related *F. wichmanni* in having crests that widen towards the labial edge, and in having a large 2nd ridge crest. To this uncommon species, they referred a specimen illustrated by Wichmann (1924; Plate VII, fig. 5) from the Allen Formation (Campanian-Maastrichtian), at General Roca (also Río Negro province, Argentina) together with other topotype specimens. A single and badly eroded left lower tooth plate from the Allen Formation at Trapal Có locality may be referred also to this species (Figure 8 A). The left lower tooth plate illustrated by Wichmann (1927; Plate I, fig. 5) is here also referred to this robust species. However, among the features cited by Apesteguía; Agnolin; Claeson (2007) as diagnostic of this species, the widening of the labial edge of the tooth plates, together with the large size of the second crest are traits highly variable within a single population, and are probably modified by wear (CHURCHER, 1995; CHURCHER; DE IULIIS, 2001). Thus, *F. cionei* may be distinguished from *F. wichmanni* on the basis of its more robust proportions and in having mesiodistally extended crests separated by very shallow clefts (APESTEGUÍA; AGNOLIN; CLAESON, 2007).

F. wichmanni (Apesteguía; Agnolin; Claeson, 2007) represents the most common dipnoan species from the Campanian-Maastrichtian of Patagonia, including findings in different outcrops from Mendoza, Río Negro, and Santa Cruz provinces (WICHMANN, 1924: Plate VII, fig. 6; 1927: fig. 1, 3, 12; PASCUAL; BONDESIO, 1976, Plate I, fig. 5; CIONE, 1987: fig. 1.N.;

GONZÁLEZ RIGA, 1999, fig. E.; Martinelli and Forasiepi, 2004: Pl. 2 fig. I). Additional unpublished specimens come from the Allen Formation (Campanian-Maastrichtian) at Cerro Puyén, General Roca, Paso del Sapo, and Abra Pampa (APESTEGUÍA; CAMBIASO, 1999; MACN, MPEF, and MPCA *pers. obs.*), and a large amount of plates from the same Formation at Cerro Dos Hermanas and Trapal Có localities, Río Negro province (Figure 7). *F. wichmanni* differs from *F. cionei* in having more gracile tooth plates and deeper and narrower clefts between crests.

The plates belonging to *F. wichmanni* were incorrectly referred to the species "*Ceratodus*" *iheringi* by Martin (1982; MARTIN; BARBIERI; CUNY, 1999) and Cione (1987). Posteriorly, Apesteguía; Agnolin; Claeson (2007; see also here) referred these specimens to *Ptychoceratodus* (*Ferganoceratodus* herein) under the new name of *P. wichmanni*. On the other hand, Cione et al. (2007) indicated that these specimens could be referred to the genus *Metaceratodus* Chapman, 1914. However, Patagonian tooth plates differ from those of the genotype *M. wollastoni* in having cutting crests, a narrow first crest of lower tooth plates, and occlusal pits placed between crests, a set of features shared by all ptychoceratodontids (see above).

Apesteguía; Agnolin; Claeson (2007) indicated the presence of pre-Campanian ptychoceratodontids. These authors reported indeterminate Ptychoceratodontidae from the Cerro Lisandro Formation (Turonian) at Bayo Mesa and Cerros Colorados localities (Neuquén province, Argentina). However, these specimens lack the typical cutting crests and the furrows of occlusal pits that characterize most ptychoceratodontids (see below). Their short and broad tooth plates with wide crushing crest occlusal surfaces indicate inclusion of these materials within Ceratodontidae. These specimens may be assigned to *Ceratodus* rather than *Metaceratodus* in the morphology of first crest and the distribution of occlusal pits (see above). Thus, these tooth plates are here considered as *Ceratodus* sp. and are assigned to the single innominated species reported by Apesteguía; Agnolin; Claeson (2007) from the same fossiliferous localities.

Martin; Barbieri; Cuny (1999; see also RAGE, 1996) indicated that Malagasy *Ferganoceratodus* may have originated in Asia, and could have reached Madagascar landmasses by dispersal from Laurasia to India (in

Triassic times). Later, Apesteguía and Agnolin (2001), and Apesteguía; Agnolin; Claeson (2007) suggested a late (Late Cretaceous) dispersal from Malagasy (or probably Australia) via Antarctica to Patagonia, where their last record is reported. Ptychoceratodontids disappear from the South American (and world) record in Tertiary times.

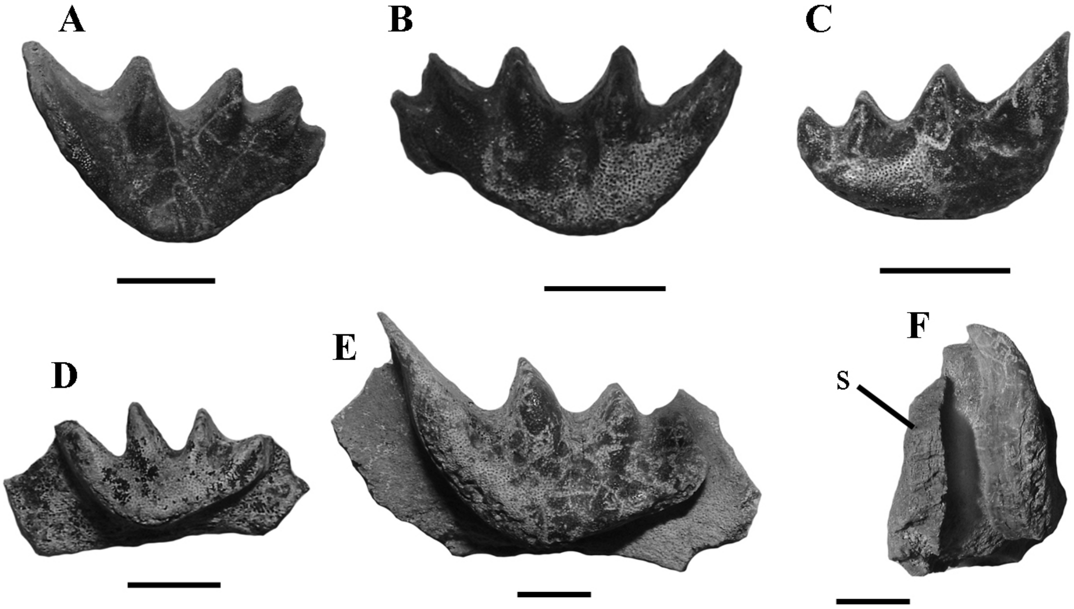

Figure 7. *Ptychoceratodus wichmanni*, **A**, left upper tooth plate in occlusal view (MML 198), **B**, right upper tooth plate in occlusal view (MML 199), **C**, left lower tooth plate in occlusal view (MML 200), **D**, right lower tooth plate in occlusal view and tooth bearing bone (MML 201), **E-F** right lower tooth plate and tooth bearing bone (MML 202) in: **E**, occlusal view, and **F** symphyseal view. Scale bar: 1 cm. Abreviation: **S**, symphysis.

The family Ceratodontidae Gill, 1872

This family is composed of a large array of different species widely distributed in the Cretaceous, but also found as a relict as late as in Oligocene times (MARTIN, 1982; KEMP, 1993). Ceratodontids show several calvarian diagnostic features, for example the presence of a fused median posterior bone, together with the pair of mediolateral bones (MARTIN, 1982) and heavily ornamented skull (KEMP, 1998). Ceratodontid tooth plates are unique in having broad, robust and rounded crests, with crushing occlusal surface (MARTIN, 1982; CAVIN et al. 2007). Only two post-Triassic genera have been recognized among ceratodontids: the genus *Ceratodus* including a large number of species (see MARTIN, 1982; KIRKLAND, 1987, 1988) distributed worldwide (KEMP, 1993), and the genus *Metaceratodus*, with the single species *M. wollastoni* Chapman, 1914 from the Lower-Upper Cretaceous of Australia and the uppermost Cretaceous of South America (KEMP, 1993; APESTEGUÍA; AGNOLIN; CLAESON, 2007). The latter may be tentatively distinguished from typical *Ceratodus* in having more elongate and acute crests, a large and anteriorly protruding first crest (specially on lower tooth plates), occlusal pits distributed within furrows and surrounding the tooth plate, and double prearticular sulcus (KEMP, 1997a). This combination of features allows considering *Metaceratodus* provisionally as a valid genus.

Metaceratodus wollastoni (CHAPMAN, 1914), was reported from several Campanian-Maastrichtian beds at Ingeniero Jacobacci, Coli Toro, General Roca, and El Abra localities, Río Negro province, Patagonia, Argentina (PASCUAL; BONDESIO, 1976, Plate I, figs. 3, 9; WICHMANN, 1924, Plate VII, fig. 4; MACN *pers. obs.*), by Kemp (1997a), Apesteguía and Agnolin (2001), and Apesteguía; Agnolin; Claeson (2007).

Metaceratodus was included by Apesteguía; Agnolin; Claeson (2007) within neoceratodontids (see also SCHULTZE, 1992a). These authors distinguished it from remaining members of the family in having a larger and protrudent first ridge crest. Apesteguía; Agnolin; Claeson (2007) based their assignment on features of the tooth plate morphology of some species of *Metaceratodus* (here included within different genera of Neoceratodontidae), but not on the type species *M. wollastoni*. Thus the phylogenetic position of *Metaceratodus* sustained by those authors is unwarranted. On the other hand, *Metaceratodus* was considered by Martin (1982; see also MARTIN; BARBIERI; CUNY, 1999) as belonging to Ptychoceratodontidae. He based its assignment on the long first ridge crest, invisible apex of inner angle and a gentle curvature formed by the mesial and lingual edge in large specimens, radiating pattern of sharp crests (when unworn), and less than 7 crests. As was indicated above, all these features are present in *Ceratodus*, and the curved inner angle is also present in Neoceratodontidae and other taxa, being diagnostic of Ceratodontoidei (see below). Finally, the presence of less than seven crest is a plesiomorphic trait exhibited by most ceratodontoids, including *Chaoceratodus* and *Atlantoceratodus*. Thus, neoceratodontid or ptychoceratodontid affinities for *Metaceratodus* are here rejected.

The *Ceratodus* record in the Cretaceous of South America is scanty and biased. It is represented by three formally described species represented by a handfull of specimens. The African species *C. humei* was also recovered from the mid-Cretaceous of Brazil on the basis of some isolated plates (TOLEDO et al., 2005; SOTO; PEREA, 2010). The mid-sized species *C. argentinus* Apesteguía, Agnolin, Claeson, 2007, was collected in the Candeleros Formation (Cenomanian, Lower-upper Cretaceous) and was based on a highly worn upper tooth plates from the La Buitrera locality, Río Negro province. Recent findings of additional topotype material referable to this species corroborate the assignation to the genus *Ceratodus* (MPCA *pers. obs.*). *C. argentinus* was diagnosed by Apesteguía; Agnolin; Claeson (2007) on the basis of five crests on upper tooth plates, the third being larger than the fourth, and the tooth plate becoming thinner at the back. However, the new specimens indicate that the latter feature is wear dependent. Apesteguía; Agnolin; Claeson (2007) considered that *C. argentinus* is similar to *C. fossanovum* (KIRKLAND, 1988) from the Upper Jurassic Morrison Formation (United States) in having a lingually expanded margin forming a flat crushing surface, and in the features cited by Apesteguía; Agnolin; Claeson (2007) in the specific diagnosis of *C. argentinus*. However *C. argentinus* does not show the acute and sharp crests present in *C. fossanovum* (considered as belonging to *Ptychoceratodus* herein), and also lacks the inter-furrow distribution of occlusal pits. On the other hand, *C. argentinus* shows general proportions and similar occlusal profiles to that of the Triassic European species *C. kaupi* Agassiz, 1844 (KEMP, 1993). *C. argentinus*, could be clearly distinguished from the latter because it shows more slender and gracile built tooth plates.

Another *Ceratodus* species described by Apesteguía; Agnolin; Claeson (2007) is *C. kaopen*, from the Bajo de la Carpa Formation (Santonian), Paso Córdova locality, Río Negro Province, Argentina. Apesteguía; Agnolin; Claeson (2007) based this species on several isolated lower tooth plates. This medium sized lungfish was diagnosed by those authors on the basis of the following traits (presumably derived): 1) the anterolingual region forms a tall ridge; 2) the second and third crests are tall and bent lingually; and 3) the fourth crest is very low and squared. However, features 1 and 2 are clearly related to wear, and thus, are not diagnostic at any taxonomic level. On the other hand, the large and squared last crest, forming a large crushing occlusal surface, may be a useful diagnostic feature of *C. kaopen*. A similar condition is also found in the North American Early Cretaceous species *C. frazieri* Ostrom, 1970, which also shows (although in much lesser degree) a posterior crushing platform (KIRKLAND, 1987).

Apesteguía; Agnolin; Claeson (2007) briefly analyzed and discussed several plates referred to an innominated species of *Ceratodus* (see discussion of Ptychoceratodontidae). This species was reported from several Coniacian-Turonian fossiliferous localities (i.e. Cerro Lisandro Formation at Cerros Colorados and Cerro Bayo Mesa; Portezuelo Formation at Cerros Colorados locality). All the available specimens show labially acute crests, and very elongated lower tooth plates, a morphology shared with the Late Cretaceous African species *Ceratodus humei* Priem, 1914 (CHURCHER; DE IULIIS, 2001). In spite of its superficial resemblances with *C. humei*, the innominated Patagonian species show no clear morphological relatives within the genus *Ceratodus*.

In contrast with its high diversity and abundance in Lower and Lower-upper Cretaceous deposits, the latest Cretaceous record of *Ceratodus* is rather poor. Only one relatively large and robust species is found in Campanian-Maastrichtian beds of Patagonia. This still undescribed species was illustrated by Wichmann (1924; Plate VII, fig. 3; 1927; Plate II, figs. 8-11) as coming from General Roca, Bajo de Santa Rosa, Trapal Có (Bajo de Los Menucos), Río Negro province, and from Palau Có, Mendoza province, Argentina. Moreover, a large number of tooth plates referable to this new species have been collected from the Allen Formation (Campanian-Maastrichtian) at El Abra and Cerro Dos Hermanas localities, Río Negro province, Agentina (MML 204, 205; MACN *pers. obs.*; Figure 8 B-C). This undescribed species appears to be closely related to the Australian *Ceratodus diutinus* Kemp, 1993 (from several Cretaceous-Oligocene localities; KEMP, 1991) in having broad and transversely expanded tooth plates, with strongly convex lingual margin, and acute and narrow first upper ridge crest. The Patagonian species differs in lacking a mesial keel and in having lower tooth plates with its lingual margin concave.

The three species of the genus *Ceratodus* recorded from Argentina are clearly distinct, and do not show any clear similarities to each other. The Early-late Cretaceous species *C. argentinus*, *C. kaopen* and *Ceratodus* sp. indet. probably belong to non-related lineages of suggested Pangean distribution that remained as relics in the Cretaceous of South America (see discussion). Moreover, the undescribed Late Cretaceous *Ceratodus* species from Patagonia is related to the Australian *C. diutinus* suggesting a Late invasion from Australia, as is the case of ptychoceratodontids or, less probably, the species may belong to an unknown endemic Gondwanan lineage.

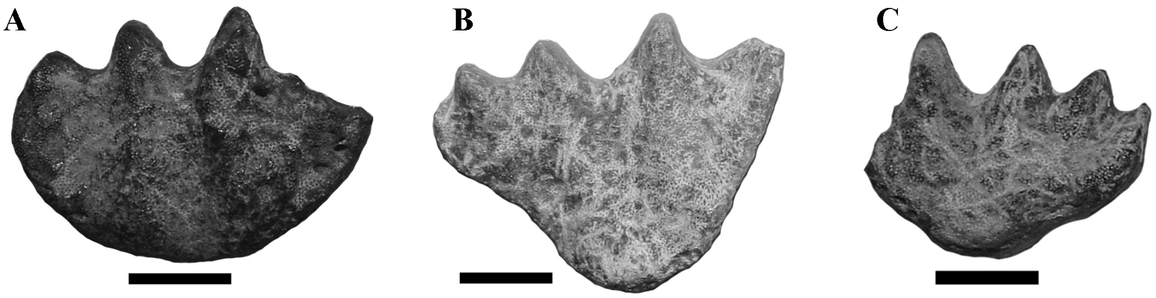

Figure 8. A, *Ferganoceratodus cionei*, left lower plate in occlusal view (MML 203), **B-C**, *Ceratodus* sp., **B**, right upper tooth plate in occlusal view (MML 204), **C**, left lower tooth plate in occlusal view (MML 205). Scale bar: 1 cm.

Some putative dipnoan records from South America

Wichmann (1927) illustrated several specimens of teleostean fishes as belonging to dipnoans. Among them, he illustrated isolated scales from the Allen Formation, Bajo Santa Rosa, Río Negro province, Argentina (WICHMANN, 1927; Pll VI, figs. 36-37). However, these scales are clearly not dipnoan, and the peculiar pattern of grooves well known for lepisosteid holosteans is highly reminiscent to the genus and species *Paraikichthys ornatissimus* Ameghino, 1899 (*pers. obs.*). He also illustrated several well ossified vertebral centra, that based on the high degree of ossification do not belong to dipnoans (centra are lacking in extant and post-Triassic lungfishes, BEMIS, 1984; ARRATIA; SCHULTZE; CASCIOTTA, 2001), but to Teleostei

(Wichmann, 1927; Pl. IV, fig. 23; Pl. V, figs 29-35; Pl. VI, figs. 38-39), as was previously indicated by Cione (1987). Moreover, a single vertebra, coming from the Allen Formation at Bajo Santa Rosa also shows a well ossified centrum, indicating that it belongs to Teleostei. Therefore, this specimen shows an open notochordal foramen, fused neural arch forming a tube with a small articular structure on its dorsal portion, which together indicate possible affiliation with Aspidorhynchidae (*pers. obs.*).

Phylogenetic relationships among higher dipnoan clades

The phylogenetic hypothesis proposed in the present paper allows us to discuss and compare it with previous phylogenetic hypothesis. As was pointed out by most previous authors, a large consensus exists on the monophyletic condition of all post-Paleozoic dipnoans (see CAVIN et al. 2007). This taxonomic group was first recognized by Martin (1982) on the basis of tooth plate features, and is here termed as Ceratodontoide Nikokolski, 1954. Regrettably, only a couple of phylogenetic analyses include several ceratodontoid genera. Among them, the analyses made by Schultze (2004) and Cavin et al. (2007) are the most comprehensive. When we compare these analysis with the one performed in the present paper (Figure 1) we note several similarities and differences. Schultze (2004) indicated a basal dichotomy including *Arganodus* (here considered as the junior synonym of *Asiatoceratodus*) and *Ferganoceratodus* as the sister group of remaining ceratodontoids, whereas in the present analysis these taxa are nested within derived high crowned dipnoans. In resemblance with the present work, Schultze (2004) recognized two large ceratodontoid clades: the first of them includes the Neoceratodontidae plus Lepidosirenidae (Neodipnoi herein) and the other the genera *Ceratodus, Metaceratodus* and *Ptychoceratodus* (= high crowned dipnoans herein). However, in contrast with the present phylogeny, Schultze (2004) considered *Asiatoceratodus* (here regarded as the senior synonym of the high crowned dipnoan *Arganodus*, following the careful analysis performed by KEMP, 1998) as closely related to Neodipnoi, whereas in the present analysis it was found as the sister group of ptychoceratodontid dipnoans (see below). Thus, excluding some incongruences, both the present phylogeny and that proposed by Schultze (2004) are relatively similar.

With respect to the phylogeny ran by Cavin et al. (2007) there are major incongruences in most of the clades proposed by those authors and the present analysis, except in the recognition of a monophyletic Ceratodontoidei. Most differences have been criticized and pointed out in several sections of the present work. Curiously, paleobiogeographical inferences proposed by those authors are very similar to that arrived in the present analysis.

Another phylogenetic proposal was made up in recent times is that of Apesteguía; Agnolin; Claeson (2007) who proposed several dipnoan clades clearly different from the present phylogenetic proposal. They do not include the genera *Asiatoceratodus* nor *Ferganoceratodus* in their analysis. They proposed Lepidosirenidae as the sister group of remaining post-Paleozoic dipnoans, and indicated *Chaoceratodus* and *Atlantoceratodus* as basal taxa with respect to their Ceratodontoidei (Neoceratodontidae + (Ptychoceratodontinae + Ceratodontinae)). *Chaoceratodus* and *Atlantoceratodus* were not included in the present phylogeny because they are based only on isolated tooth plates. However, as was indicated above, both may probably be related to Neodipnoi, but the material representing each genus ir rather poor to be conclusive about their phylogenetic relationships, and are here considered as Ceratodontoidei *incertae sedis*. Moreover Apesteguía; Agnolin; Claeson (2007) recognized within Ceratodontoidei two main clades. One includes the Ptychoceratodontidae and Ceratodontidae (represented there only by *Ptychoceratodus* and *Ceratodus*), as sister groups of Neoceratodontidae and *Metaceratodus*. Both clades are also recovered in the present paper. However, within Neodipnoi, Neoceratodontidae is considered the sister group of Lepidosirenidae, and both as sister groups of the clade Ceratodontidae + Ptychoceratodontidae + Asiatoceratodontidae). In this analysis the species of the genus *Metaceratodus* have been reassigned to Neoceratodontidae, and *Atlantoceratodus*, and finally the genotype species *M. wollastoni* is retained within *Metaceratodus* and in the family Ceratodontidae (as proposed by KEMP, 1997a). In conclusion, the present phylogeny is clearly concordant with the traditional proposals made up by Martin (1982; 1984a) and Kemp (1998), as was discussed above.

Paleobiogeography and temporal distribution

Apesteguía; Agnolin; Claeson (2007) considered two main stages in the composition of dipnoan faunas in South America. The first includes pre-Campanian forms represented both South American endemic (i.e. *Chaoceratodus*), and relic forms (i.e. *Ceratodus*), together with ancient Gondwanan taxa (i.e. *Ameghinoceratodus*, *Lavocatodus, Neoceratodus africanus, Asiatoceratodus tiguidensis*). They also remarked the absence of ptychoceratodontid specimens. The second stage of dipnoan faunas embraces the Late Cretaceous (post-Campanian-?Paleocene), in which plesiomorphic forms and ancient Gondwanan forms are present only as relegate groups, being dominated by probable immigrant taxa (e.g. *Ferganoceratodus*, *Metaceratodus, Ceratodus* aff. *C. diutinus*) (APESTEGUÍA; AGNOLIN; CLAESON, 2007; this paper). These forms are present in Greater Gondwana´s (i.e. Madagascar, India, and Australia; APESTEGUÍA, 2002) upper Cretaceous (to Tertiary) outcrops. A concordant faunal pattern has also been reported for other vertebrate groups, such as dinosaurs and mammals (BONAPARTE, 1986; 1996; BONAPARTE, 1987). Finally, a third faunal layer may be recognized, since Paleocene to Recent times the dipnoan faunas of South America have been dominated by the Lepidosirenidae of the genus *Lepidosiren* together with rare Mesozoic relics that survived until Paleocene times (i.e. *Atlantoceratodus*, *Retodus,* possible ceratodontids; SCHULTZE, 1992b; GOUIRIC et al. 2010).

Within South America a distributional pattern may be observed with respect to dipnoan clades. In northern South America, the families Ceratodontidae, Neoceratodontidae and Asiatoceratodontidae are represented by species also found in Africa, whereas in the Southern cone, species with Australian (and Malagasy) affinities are found (e.g. *Atlantoceratodus, Metaceratodus*). This suggests a paleobiogeographic differentiation between both northern and southern South America, a pattern also reported in other vertebrates, such as dinosaurs and turtles (APESTEGUÍA, 2002). Moreover, this distributional pattern is also seen in living fish faunas, in which a clear differentiation between northern South America (Brazilian Region) and southern South America (Austral Region) is evident (RINGUELET, 1974).

Arratia (1997), on the basis of living fish faunal assemblages indicated that the Brazilian Region is closely related to the African one, and that the Austral Region is clearly influenced by some Australian elements. This composition is clearly observable in the fossil lungfish faunas from the Cretaceous of South America.

As was pointed out before (APESTEGUÍA; AGNOLIN; CLAESON, 2007) the Patagonian dipnoan record indicates that ceratodontoid dipnoans (excluding lepidosirenids) disappeared from Patagonia (or nearly so) when the Kawas sea penetrated from the Atlantic (CASAMIQUELA, 1978; PASCUAL; BONDESIO, 1976). This is concordant with the hypothesis that proposes that dipnoans from the Cretaceous were intolerant to brackish or marine waters (KEMP, 1993; GAYET; MEUNIER, 1998; CHURCHER; DE IULIIS, 2001; APESTEGUÍA; AGNOLIN; CLAESON, 2007*;* CAVIN et al. 2007).

4. Conclusions

In the present paper we arrive to the following conclusions:

1- A new species of the genus *Atlantoceratodus* is here named as *A. patagonicus*, and is clearly distinguishable from the remaining species of the genus in having shorter and stouter tooth plates. This species comes from Campanian-Maastrichtian beds from several Patagonian localities of Argentina. Within *Atlantoceratodus* the species *A. iheringi* (Ameghino, 1899), *A. elliotti* (Kemp, 1997a) nov comb. (previously included within *Metaceratodus*), and *A. patagonicus* nov. sp. are recognized. The genus is only present in Cretaceous (and Paleogene) deposits of Australia and South America.

2- The phylogenetic analysis yielded the following systematic arrangement of post-Paleozoic dipnoans (i.e. Ceratodontoidei): ((Lepidosirenidae+Neoceratodontidae) + ((Ptychoceratodontidae+Asiatoceratodontidae)+Ceratodontidae). The first clade is here termed Neodipnoi, and includes the extant ceratodontoid dipnoans. The second clade is here informally termed as High Crowned

Dipnoans. Within the Ptychoceratodontidae, we include the genera *Ptychoceratodus* and *Ferganoceratodus*. On the other hand, *Ceratodus* and *Metaceratodus* (restricted to *M. wollastoni*) are included into Ceratodontidae. The genera *Atlantoceratodus* and *Chaoceratodus* are considered as Ceratodontoidei *incertae sedis* being probably related to Neodipnoi.

3- All ptychoceratodontid South American species are temporally restricted to Campanian-Maastrichtian times; and are included within the genus *Ferganoceratodus*, being closely related to the Malagasy species *F. madagascariensis*. *Ferganoceratodus* may have originated in Asia, and could have reached the Malagasy landmasses by dispersal from Laurasia (to India). Posteriorly dispersed from Madagascar (or probably Australia) via Antarctica to Patagonia. Ptychoceratodontids disappeared from South American (and the world) in Tertiary times.

4- The three species of the genus *Ceratodus* recorded from South America are clearly distinct, and do not show clear morphological resemblances to each other. The "Mid"-Cretaceous species *C. argentinus* and *C. kaopen* are related to different Jurassic North American lineages that probably remained as relics in the Cretaceous of South America. On the other hand, an undescribed latest Cretaceous *Ceratodus* species from Patagonia appears to be related to the Australian *C. diutinus*, that suggests a late invasion from Australia, as proposed for ptychoceratodontid species.

5- The genus *Metaceratodus* is considered as represented by the single species *M. wollastoni* recorded in Cretaceous deposits of Australia and South America. Other putative congeneric species are included within Neoceratodontidae (i.e. *M. bonei*, *M. palmeri*) and *Atlantoceratodus* (i.e. *M. elliotti*).

6- The family Neoceratodontidae appears to be an endemic taxon of Gondwana, being present in northern South America, Africa, and finally Australia, where the clade shows a large radiation and abundance. The record of *Neoceratodus*-like dipnoans is definitively excluded from Argentina.

7- Three different stages in the composition of dipnoan faunas may be recognized in South America: 1) the pre-Campanian record includes abundant endemic Gondwanan taxa (i.e. *Atlantoceratodus*, *Neoceratodus, Asiatoceratodus, Lavocatodus*), Jurassic relics (i.e. *Ceratodus*), and South American endemic (i.e. *Chaoceratodus*); 2) the Campanian-Maastrichtian record (and probably also Early Paleocene) includes abundant new taxa probably coming from Australia (i.e. *Ceratodus, Metaceratodus*) and/or Malagasy (i.e. *Ferganoceratodus*), with underrepresented ancient Gondwanan lineages (i.e. *Atlantoceratodus*); and finally the 3) post Paleocene-Recent record, is restricted to the lepidosirenid genus *Lepidosiren*.

8- In South America a palaeobiogeographic pattern may be detected with respect to dipnoan clades, during the Cretaceous. In northern South America, Cretaceous fossil record includes the families Neoceratodontidae and Asiatoceratodontidae with species also found in Africa, whereas South American species with Australian (and Malgasy) affinities are found (e.g. *Atlantoceratodus, Metaceratodus*) in the Southern cone. This suggests a palaeobiogeographic differentiation between both northern and southern South America, a distributional pattern observed in other vertebrates. Moreover, clear differences in faunal composition are also seen in living fish faunas, in which the northern South American fishes are clearly related to African ones, and Austral ichthyofaunas are influenced by Australian elements. Additionally, there is no single Cretaceous record of fossil Lepidosirenidae in Chile, Argentina or Uruguay, except isolated tooth plates in northernmost Argentina, and broad-toothed Dipnoans (e.g. *Ceratodus*, *Ferganoceratodus*) appear to be absent in Brazil and other northern South American countries (see also TOLEDO; BERTINI, 2005).

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Appendix 1. List of characters

Tooth plates

1) Tooth plates: 0, low crowned; 1, high crowned (Kemp, 1998).
2) Crests originate: 0, medially; 1, anteromedially (Martin, 1982).
3) Lingual margin of upper tooth plates: 0, straight or concave; 1, strongly convex.
4) Radiating pattern of crests on tooth plates: 0, present; 1, absent (Martin, 1984a).
5) Inner angle on upper tooth plates (angle between first crest and last ridge crest): 0, more than 110°; 1, less than 110° (modified from Martin, 1982).
6) Upper tooth plates ridge crest, number: 0, three; 1, four-five; 2, more than six (Martin, 1982; Apesteguía; Agnolin; Claeson, 2007).
7) Morphology of the crests of the tooth plates: 0, long and narrow; 1, broad and short (Apesteguía; Agnolin; Claeson, 2007).
8) Crests orientation: 0, medially oriented; 1, curved backwards (Martin, 1984a).
9) First crest of upper tooth plate: 0, longer, or as long as the lingual margin; 1, shorter (Martin, 1982).
10) Morphology of the occlusal surface of the crests: 0, long and rounded oclusal surface; 1, long and acute occlusal surface of cutting type; 2, short and rounded occlusal surface of crushing type (Martin, 1982; Cavin et al. 2007).
11) Occlusal pits: 0, absent or non-apparent; 1, present but without defined pattern; 2, present but disposed on inter-ridge furrows (Martin, 1982; Kemp, 1996).
12) Petrodentine: 0, present; 1, absent (Kemp, 1993).
13) Mantle of dentine: 0, limited; 1, extensive (Kemp, 2001).
14) Upper tooth plates, contact each other: 0, absent; 1, present (Cavin et al. 2007).
15) Lower tooth plates, contact each other: 0, absent; 1, present (Cavin et al. 2007).
16) Prearticular sulcus on lower tooth plates: 0, single; 1, double (Kemp, 1997a).
17) Position of pterygopalatine process of upper tooth plates: 0, below the level of the third ridge crest; 1, above the level of the third crest (Martin, 1982).

Calvarium

18) Ascending process of pterygopalatine bone: 0, forms a weak articulation; or 1, forms a strong articulation with skull roof (Kemp, 1998).
19) Snout: 0, tapered, composed by an ossified anterior extension of the anteriormost median bone; 1, straight; 2, tapered, composed by an elongation of the anterior portion of the mid-median bone (Cavin et al. 2007).
20) Snout composed by capillary loops and associated structures: 0, absent; 1, present (Cavin et al. 2007).
21) Ossifications of median and mediolateral series: 0, more than three; 1, two; 2, two median ossifications, but only one mediolateral ossification (Cavin et al. 2007).
22) Mid median bone: 0, double; 1, single (Cavin et al. 2007).
23) Mid-median bone: 0, elongate; 1, robust, large, and broad.
24) Suture between bones of the median series (mid and posterior ossifications): 0, large contact suture; 1, reduced or absent contact suture.
25) Anterior mediolateral bone: 0, craniocaudally short; 1, craniocaudally extended.
26) Two large paired bones on the mediolateral series: 0, absent; 1, present.
27) XYZ bone: 0, double; 1, single (Kemp, 1998).
28) Sensory canals: 0, marking bones; 1, superficial, not marking bones. (Schultze and Chorn, 1997).
29) “U” shaped lateral sensory canal on anterior mediolateral bone: 0, absent; 1, present (Cavin et al. 2007).

Appendix 2. Data matrix

Gnathorhiza
00000 10000 00000 00000 00000 0000
Neoceratodus
01110 20110 01100 11021 21000 001-
Mioceratodus
01110 20110 00110 1102? 21000 001-
Lepidosirenidae
11001 00010 00011 01021 21000 001-
Ceratodus
10101 11012 11010 00010 11101 0000
Ptychoceratodus
1[01][01]01 11011 21011 00110 11111 1101
Ferganoceratodus
11101 11011 21000 00110 11111 1101
Asiatoceratodus
11101 21011 01011 00110 11101 0101
Metaceratodus
10101 11012 21010 10??0 ????? ????