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Atlantoceratodus, a new genus of lungfish from the upper Cretaceous of South America and Africa

Alberto Luis Cione[1], Soledad Gouiric[1], Francisco Goin[1] and Daniel Poiré[2]

[1]Departamento Paleontología Vertebrados, Museo de La Plata,
Paseo del Bosque s/n, 1900 La Plata, Argentina. E-mail:acione@museo.fcnym.unlp.edu.ar.
[2]Centro de Investigaciones Geológicas, Calle 1 y 45, 1900 La Plata, Argentina.

ABSTRACT. The only previously known material of *"Ceratodus" iheringi* Ameghino, 1898 (the holotype, a tooth plate) was collected by Carlos Ameghino along with other marine and freshwater fossils in the "Piso Shehuenense" in Pari Aike, Río Shehuen, southern Patagonia. The material was figured but not described. Fortunately, the holotype was preserved in the Museo de La Plata. The bearing beds are presently included in the Mata Amarilla Formation which is considered Cenomanian-Coniasian in age. Additional lungfish material from the southern part of Mendoza and Río Negro provinces was erroneously reported by several authors to this species.In the present contribution, based on about 200 complete and fragmentary tooth plates from the type locality, we describe and diagnose the species *"Ceratodus" iheringi* and a new genus, *Atlantoceratodus*. The species appears to be only known in the type area. *Atlantoceratodus iheringi* most closely resembles *"Ceratodus" madagascariensis* Priem, 1924 from the upper Cretaceous (Campanian) of Madagascar and we suggest that both species pertain to the same genus.

Key words: *Dipnoi, Cretaceous, Argentina, South America, Madagascar*

RESUMEN. El único material previamente conocido de "*Ceratodus*" *iheringi* Ameghino, 1898 (el holotipo, una placa dentaria), fue colectado por Carlos Ameghino con otros fósiles marinos y de agua dulce en el "Piso Shehuenense" en Pari Aike, Río Shehuen, Patagonia austral. El material fue figurado pero no fue descripto. Afortunadamente, el holotipo se conservó en el Museo de La Plata. Actualmente, se considera que las capas portadoras integran la Formación Mata Amarilla, de edad Cenomaniana-Coniasiana. Posteriormente, otras placas de dipnoos colectadas en el sur de Mendoza y en Río Negro fueron erróneamente referidas a esta especie por varios autores. En la presente contribución, basados en cerca de 200 placas dentarias completas y fragmentarias, nosotros describimos y diagnosticamos a la especie "*Ceratodus*" *iheringi* y un nuevo género, *Atlantoceratodus*. La especie es sólo conocida en el área tipo. *Atlantoceratodus iheringi* se asemeja más cercanamente a "*Ceratodus*" *madagascariensis* Priem,

1924 del Cretácico superior (Campaniano) de Madagascar y sugerimos que pertenecen al mismo género.

Palabras clave: *Dipnoi, Cretácico, Argentina, América del Sur, Madagascar.*

Introduction

Studies on fossil freshwater fishes from southern South America began at the end of the XIX century with the discovering of the lungfish "*Ceratodus" iheringi* along with *Lepidotes*-like teeth (Ameghino, 1898). The species "*C.*" *iheringi* was based on a single tooth plate collected by Carlos Ameghino in his "Piso Shehuenense" at Pari Aike, Río Shehuen, southern Patagonia. Lungfishes are mainly known by tooth plates after the Devonian; unfortunately, bone remains are very rare, especially after the Triassic (Cavin *et al.* 2007). In the present contribution, based on about 200 additional complete and fragmentary tooth plates from the type area, we describe and diagnose the species "*Ceratodus" iheringi* Ameghino, 1898 and discuss its generic allocation.

Results

Geographic and stratigraphic provenance. The original locality of Ameghino (1898) was vaguely described. It should correspond to one of the two nearby localities that yielded "*C.*" *iheringi* teeth during 2001 by Francisco Goin and Daniel Poiré. Both are located to the south of Río Shehuen, southwestern Provincia de Santa Cruz, Argentina (Figures 1, 2). The "Piso Shehuenense" is presently considered to correspond to the Mata Amarilla Formation (Riccardi & Rolleri, 1980; Goin *et al.* 2002; see also discussion in Arratia & Cione, 1996).

Piedra Clavada and the immediately overlying Mata Amarilla formations constitute a clear example of deltaic systems, developed during the Cretaceous in southern Patagonia. In recent years, a number of sedimentological, ichnological and paleontological studies have been carried out on both formations in the Tres Lagos area which have provided sedimentological and palaeoecological characteristics of these units within a extra-Andean region of the Austral Basin in great detail (Goin *et al.* 2002 and papers cited therein).

The Mata Amarilla Formation is mainly composed by a distinct alternance of whitish sandstones and grey and black mudstones, sandstones and bioclastic sandstones bearing marine and continental fossils in between. This unit shows abundant vertebrates, invertebrates and plants throughout. However, in the lower portion there is a more prominent participation of marine invertebrates compared to the upper one. All this evidence clearly indicates that, even though continental fauna and flora prevail, the lower part sporadically includes marine elements, this representing a typical palaeoecological association of subaereal delta transitional to fluvial systems (Figs. 1, 2)

The analysis of sedimentary facies, bioturbations, and fossils allows the determination of five associations of characteristic facies. Fossil dipnoan come from the associations IV and V. Association IV is made up of fine massive sandstones which eventually develops in interdigitated lobes with massive mudstones rich in carbonous material, with abundant vertebrates and vegetal strands corresponding to crevasses in flooding plains. One of the most conspicuous facies associations (V) occur in the medial and upper part of the Mata Amarilla Formation and is formed by black mudstones with

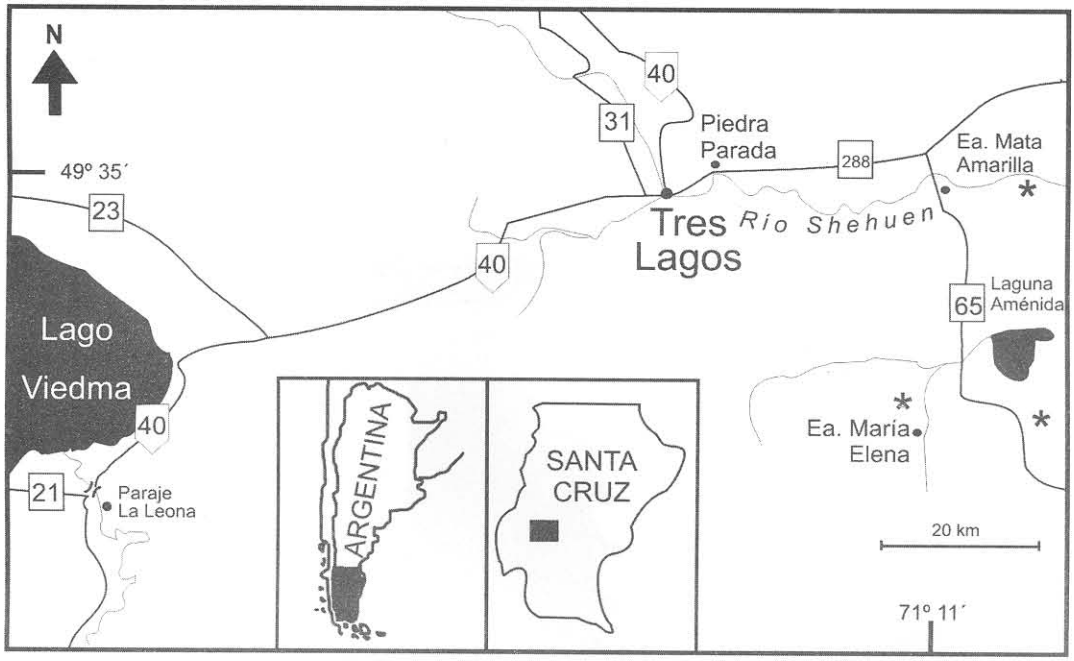

Figura 1. Map of location

abundant organic matter, vegetal strands and well preserved cuticles and continental vertebrates, sparse shark remains, which suggest litoral lagoons with mainly marshy facies, eventually connecting to the sea (Goin *et al.* 2002). The analysis of invertebrates recorded at the marine transgressions of the Mata Amarilla Formation suggests a Coniacian age (Riccardi & Rolleri, 1980).

The localities that yielded dipnoan material are (Fig.1): Tres Lagos 1 (3LAG1): (49° 45' 49.5" S, 71° 05' 13.1" W). South of Río Shehuen, in the Estancia Bajada de los Orientales. Vertebrates were found 30 below the top of the Mata Amarilla Formation. They include most of the lungfish tooth plates and actinopterygian scales, turtle plates, and crocodile skull bones. Tres Lagos 2 (3LAG2): 49° 37' 07.4" S, 71° 07' 46.1" W. The site is located in the base of the first terrace south of Río Shehuen, in the Estancia La Soriana. This should be the type section of the original locality of *"C." iheringi.* One lungfish tooth plate, actinopterygian bones, turtle postcranial bones and some shark teeth were collected there.

Dipnoi
Family indeterminate
Genus ***Atlantoceratodus nov. gen.***
Figures 3,4

Diagnosis (based only on tooth plates). Tooth plates of medium size, high crowned and with sharp, slender and acute ridges that originate anteriorly; five ridges in the upper plates and four ridges in the lower plates; restricted pulp cavity; occlusal tubercles absent; limited mantle dentine visible on occlusal surface; punctations simple (petrodentine sensu Kemp, 2001 absent) and not arranged with a particular pattern. Tooth plates most resemble those of *Ptychoceratodus* and *Ferganaceratodus* but differ from them in that the inner apex it is not so well defined, it is rounded, a larger angle is usually formed by first and last ridges, and the ridges are more slender and acute.

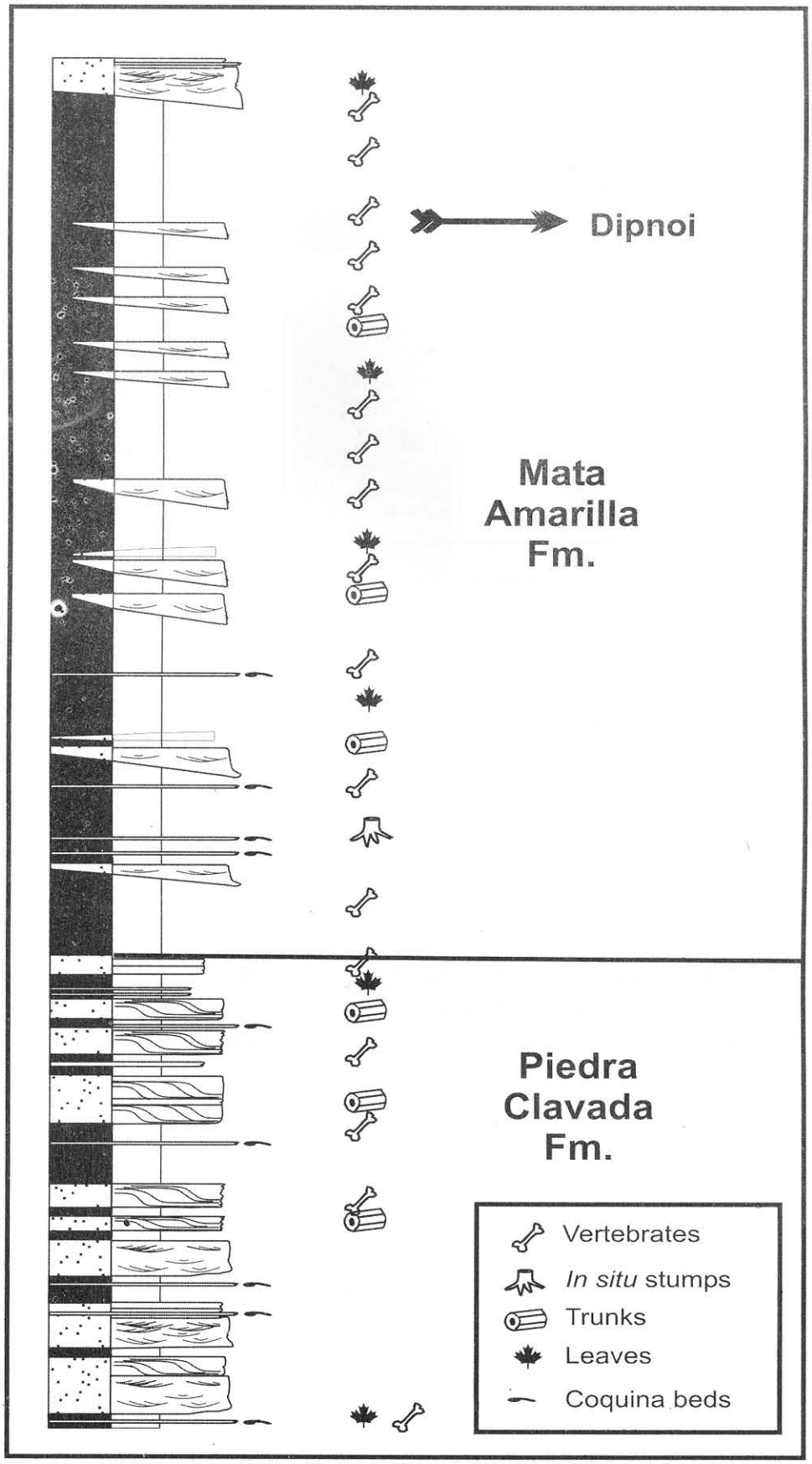

Figura 2. Stratigraphic section

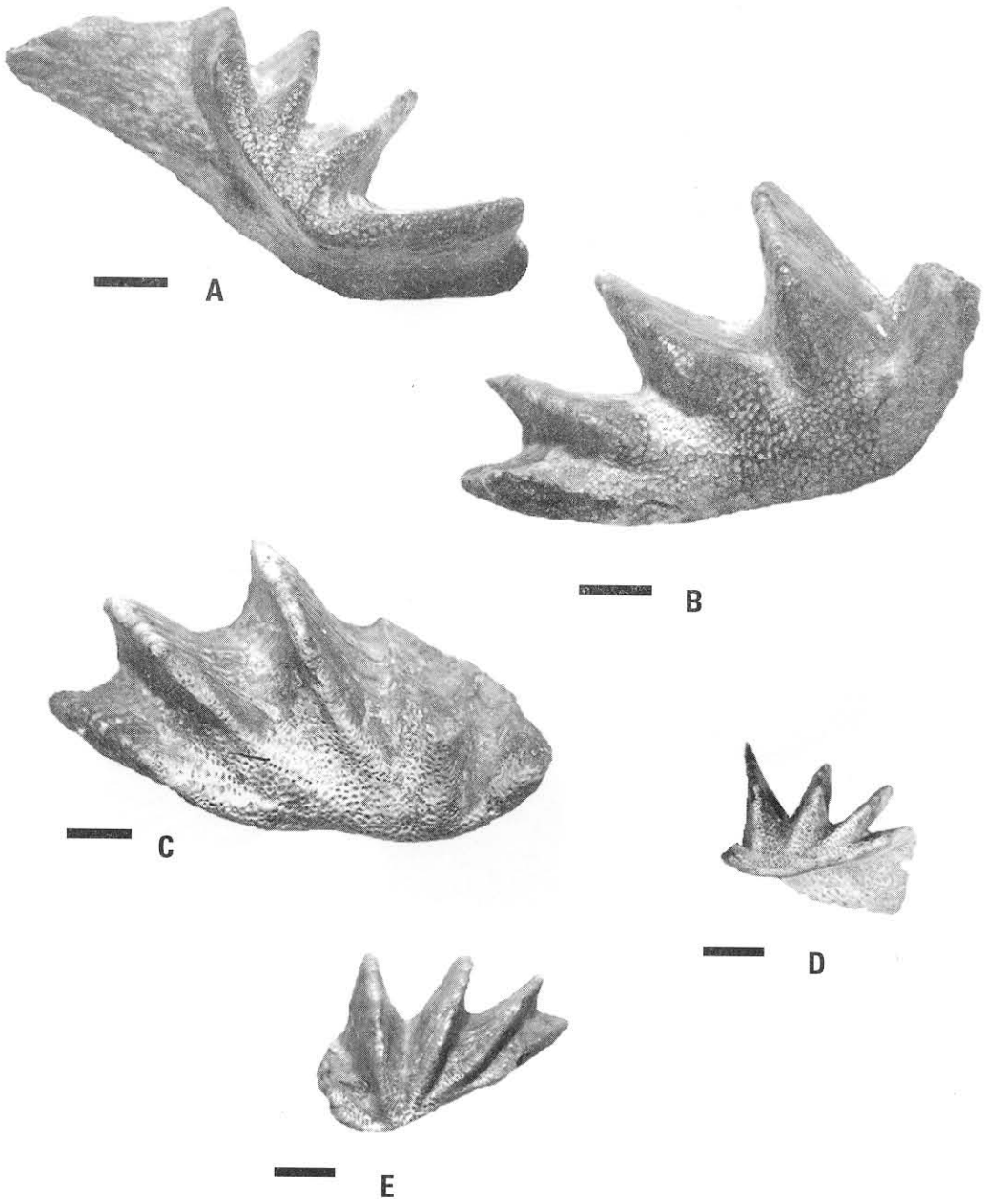

Figura 3. *Atlantoceratodus iheringi.* A, MPM-PV-1160.1, lower tooth plate with attached bone. B, C, D, E upper tooth plates. B, MPM-PV-1160.2. C, MPM-PV-1163.1, D, MPM-PV-1164,1. E, MPM-PV-1160.2. Line: 2mm.

Synonyms

Ceratodus Agassiz, 1838 partim

Derivatio nominis

Atlantic Ocean and *Ceratodus*.

Species: The type species *A. iheringi* (Ameghino, 1898), from the Coniasian Mata Amarilla Formation of southern Patagonia (Goin *et al.* 2002) (Figs. 3, 4) and *A. madagascariensis* (Priem, 1924), from the Campanian Marovoay sandstones and Ankazomihaboka clays and sandstones of the Mahajanga basin in Madagascar (Martin *et al.* 1999) (Fig. 5).

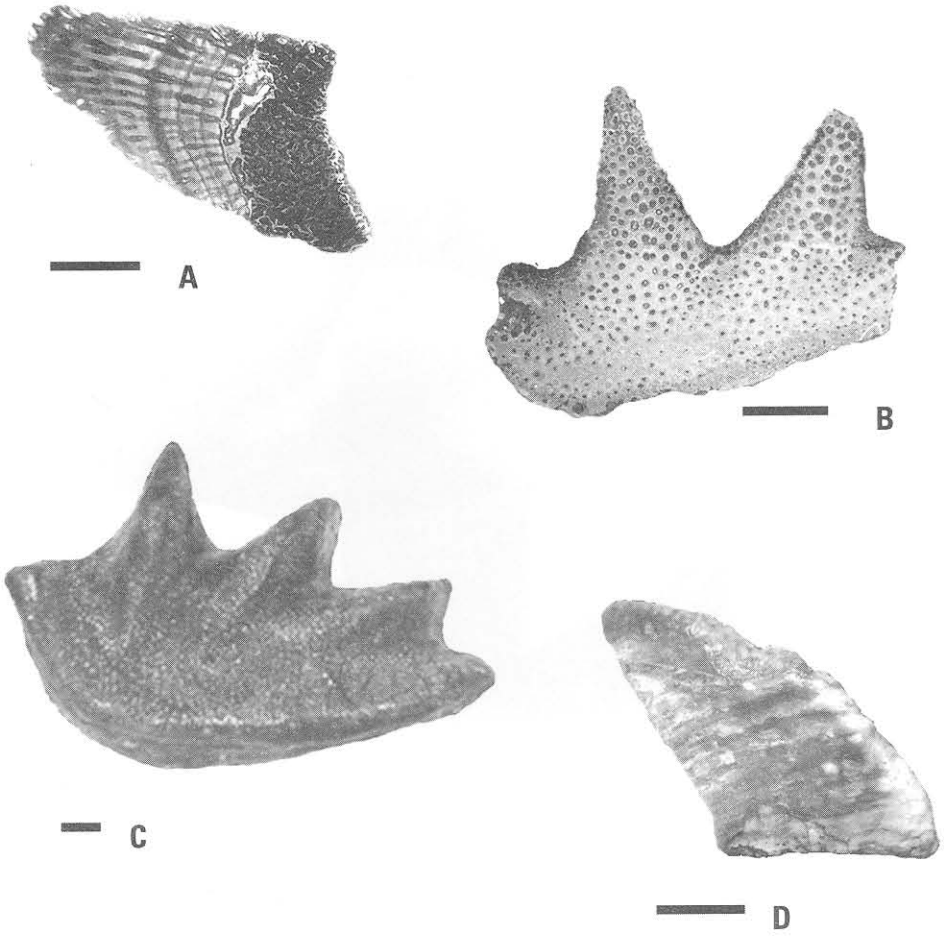

Figura 4. *Atlantoceratodus iheringi.* A, MPM-PV-1194.1; thin horizontal section; Denteons with circumdenteonal dentine and surrounded by interdenteonal dentine can be observed; marginal dentine and enamel are also shown. B, MPM-PV-1194.2; thin basoapical section. C, MLP 21-967, holotype. D, MPM-PV-1164.1, detail of crests. Line: 2mm.

Discussion

Several authors recognize five lungfish families in the Mesozoic and Cenozoic: Ceratodontidae, Neoceratodontidae, Lepidosirenidae, Asiatoceratodontidae, and Ptychoceratodontidae (Martin, 1982, 1984; Kemp, 1998). However, recent cladistic analyses consider genera individually and found that several of these families would be paraphyletic (eg. Schultze, 2004; Cavin *et al.* 2007).

Atlantoceratodus tooth plates differ from those of *Ceratodus* because they present ridges acute and originating near mediolingual face (not medially), mediolingual face angled, and no occlusal pits. The material of *C. iheringi* does not resemble that of the generic type species *Ceratodus latissimus*. Cione (1987) and Schultze (1992) had referred the Patagonian material to *Ceratodus*. However, these authors did not studied material from the type locality but from younger beds from northern Patagonia that correspond to a species of *Metaceratodus*.

Atlantoceratodus tooth plates do not belong to Neoceratodontidae because they present fewer ridges (4 and 5), mediolingual face angled and not widely convex, mantle

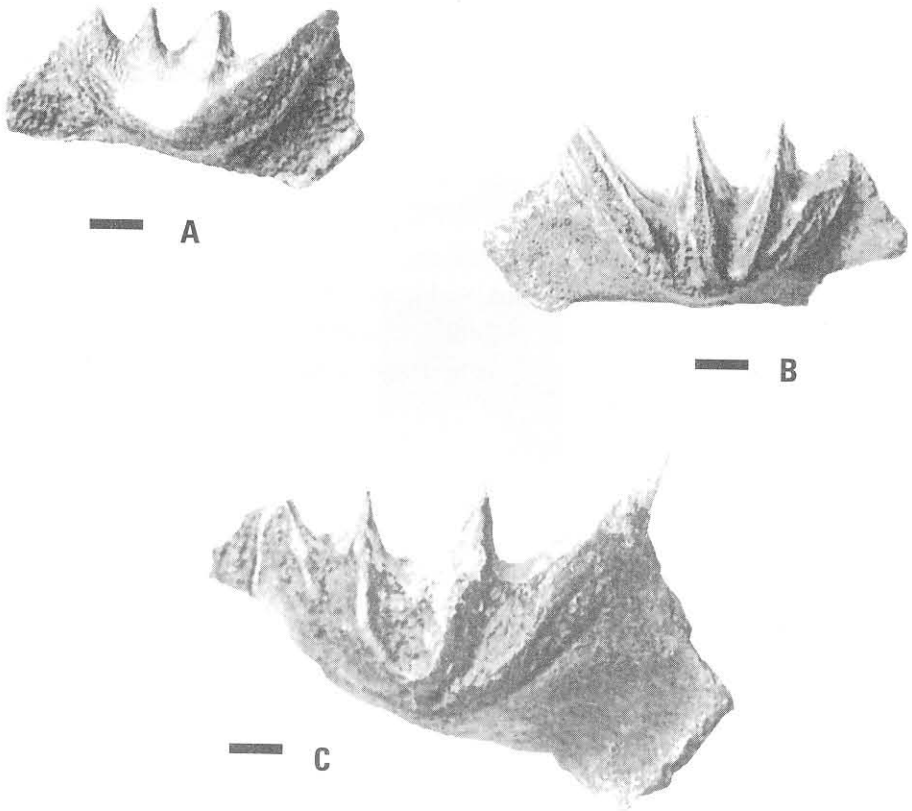

Figura 5. *Atlantoceratodus madagascariensis.* A, lower left tooth plate. B, lower rigth tooth plate. C., lower left tooth plate. Taken from Priem (1924). Line: 4mm.

dentine limited, and no petrodentine sensu Kemp (2001; tissue that it is present in the neoceratodontids *Mioceratodus* and *Archaeoceratodus*).

Atlantoceratodus tooth plates do not belong to Lepidosirenidae because they present more than 3 ridges, longer 1 and 2 ridges, mediolingual face more widely angled, and no petrodentine, and tooth plates are not in close contact.

Atlantoceratodus differs from other Mesozoic lungfishes such as *Arganodus* and *Asiatoceratodus* because the smaller ridge number and from *Gnathorhiza* and *Paraceratodus* in the general shape of plates.

Mata Amarilla Formation tooth plates most closely resemble *Ptychoceratodus* (see Jaekel, 1926; Kemp, 1996) and *Ferganaceratodus* (see Nessov & Kaznyshkin, 1985; Martin *et al.* 1997), which were included in Ptychoceratodontidae by Martin *et al.* (1997). However, *Atlantoceratodus* differs from these genera because its pterygopalatine and prearticular tooth plates present: an inner apex not so well defined, first and last ridges usually forming a large angle (about 130°; not about 90° as in *Ptychoceratodus* and *Ferganaceratodus*), high crown; restricted pulp cavity; occlusal tubercles absent; limited mantle of dentine visible on occlusal surface; slender, short and acute ridges that originate anteriorly; punctations simple (petrodentine sensu Kemp, 2001 absent) and not arranged with a particular pattern.

Martin *et al.* (1999: 12-13) suggested that "many species wordly recorded exhibit features which are visible in cf. *F. madagascariensis* 1) long first ridge, 2) invisible apex

of the inner angle and 3) a gentle curve formed by the mesial and lingual edge in large specimens, 4) radiating pattern of sharp ridges (when unworn), 5) less than 7 ridges. These characters are consistent with the referral to the ptychoceratodontids but are also indicative of close relationships (the curve in large specimens could be an apomorphic character)". They include in this "group" [which supposedly should correspond to genus *Ferganaceratodus*] the following species: *Ceratodus concinnus, C. iheringi, C. guentheri, C. frazieri, C. felchi, C. gustasoni, Metaceratodus wollastoni, Ceratodus pattinsonae, Ceratodus temporatus,* and *C. porrectus.* "Most of the large tooth plates of these different species exhibit the curve formed by the lingual and mesial edge and when the same formation of the same locality have yielded both small and large specimens the small ones possess an evident inner angle whereas the curve is present on the large ones. Kirkland (1987) has erected two new species *C. felchi* and *C. gustasoni* which could be junior synonyms of *C. guentheri*, *Ceratodus porrectus* could be a junior synonym of *C. temporatus* which is a large completely worn tooth plate" (Martin *et al.* 1997:13).

However, we suggest that the "invisible apex of the inner angle" and the "gentle curve" are characters that are not necessarily linked to ontogeny. Small specimens of *Metaceratodus* from the La Colonia Formation of the Upper Cretaceous of northern Patagonia are similar in this feature with respect to the largest specimens. Besides, Kemp (1997b) figured sketches of larger and smaller specimens of *Metaceratodus wollastoni*, *M. ellioti*, *M. palmeri* and *M. bonei* with also do not present significant variation in the feature (see also Kemp, 2003). Character 1 would not be typical of *Ferganaceratodus* and is present in ceratodontids such as *Metaceratodus* (Pascual & Bondesio, 1976; Kemp, 1997b) and neoceratodontids such as *Mioceratodus* (see Kemp, 1997a). Characters 4 "radiating pattern of sharp ridges (when unworn)" and 5 "less than 7 ridges" are present in all *Ptychoceratodus* and *Ferganaceratodus*. Actually, we find difficult to differentiate isolated teeth of *Ferganaceratodus* and *Ptychoceratodus* notwithstanding that they appear to differ in skull bones morphology (see Nesov & Kaznyshkin, 1985; Kaznyshkin, 1993; Kemp, 1996).

Atlantoceratodus is present in late Cretaceous beds of Madagascar and Patagonia, *Ptychoceratodus* in Triassic and Jurassic beds of Eurasia and Africa and *Ferganaceratodus* in Jurassic beds of Asia. *Ceratodus felchi* Kirkland, 1987 of the Jurassic of North America would be attributed to *Ptychoceratodus* or *Ferganaceratodus.*

Martin (1981) had proposed a close relationship between "*Ceratodus" iheringi* and "*Ceratodus" madagascariensis* based on the presence of only four ridges and the supposed acquisition of a crushing surface early in ontogeny. We agree in that both species pertain to the same genus but based on the combination of characters: tooth plates of medium size, high crowned and with sharp, slender and acute ridges that originate anteriorly; five ridges in the upper plates and four ridges in the lower plates; inner apex not so well defined and rounded, relatively large angle formed by first and last ridges; occlusal tubercles absent; limited mantle dentine visible on occlusal surface; punctations simple (petrodentine sensu Kemp, 2001 absent) and not arranged with a particular pattern.

Atlantoceratodus iheringi (Ameghino, 1898) nov. comb.
Figs. 3,4

Ceratodus iheringi Ameghino, 1898, p. 134.
Ceratodus iheringi Ameghino, 1898. Ameghino, 1899, p. 12.
Ceratodus iheringi Ameghino, 1898. Ameghino, 1900-1903, p.144.
Ceratodus iheringi Ameghino, 1898. Ameghino, 1906, p. 502.

Ceratodus iheringi Ameghino, 1898. Ameghino, 1916, p. 169.
Ceratodus iheringi Ameghino, 1898. Pascual & Bondesio 1976, p. 578.

Diagnosis (based only on tooth plates). *Atlantoceratodus iheringi* differs from the other species, *A. madagascariensis* in the smaller size (less than 25mm); the mediolingual keel absent; the lingual edge straight; deeper clefts that originate more medially and appear to be higher; the inner angle larger (usually 130°).

Type material. MLP 21-967, one upper plate without the first ridge, figured by Ameghino (1900). The material is deposited in the División Paleontología de Vertebrados of the Museo de La Plata, La Plata, Argentina.

Additional material. The repository is the Museo Padre Molina, Río Gallegos, Provincia de Santa Cruz, Argentina. About 200 complete and fragmentary teeth: MPM-PV-1160, MPM-PV-1162, MPM-PV-1163, MPM-PV-1164, MPM-PV-1166, MPM-PV-1167, MPM-PV-1169, MPM-PV-1171, MPM-PV-1172, MPM-PV-1173, MPM-PV-1176, MPM-PV-1194.

Stratigraphic and geographic provenance. Coniasian, Mata Amarilla Formation, southern Patagonia (see above).

Description of the holotype. The tooth plate is well preserved. The first ridge is fragmented. There is no bone attached to the tooth plate. There is some wear proximally. The holotype is one of the largest tooth plates known of the species (about 25mm). The holotype is relatively slender, subtriangular in outline, with narrow occlusal surface, and high crowned. There are 5 ridges which are longer than the breadth of the occlusal surface and very acute. There cusps on the labial face of ridge 5 (Fig. 4c). The inner angle at the mediolingual junction is about 120°. There is no mediolingual keel. The lingual edge is straight. The last ridge is almost parallel to the lingual face, and clefts between the ridges are wide and deep. Ridge crests are radiating. The first and the last ridges are curved to the middle of the plate. The second to the last ridges meet in a point anteriorly but the first base is medially displaced. Labial profiles of the ridges are steep (Fig. 4c).

There is no buttress along lingual face but there is an expansion in the angle. Enamel and mantle dentine are restricted to margins (Fig. 4c). Enamel to bone junction on the labial face appears to be straight.

New material. Many plates are relatively well preserved. The first ridge is fragmented in most plates. Plates are of medium size, the smallest of about 12 mm and the largest does not exceed 25 mm. They are relatively slender, subtriangular in outline, with narrow occlusal surface, and high crowned. Most of the plates do not show post mortem abrassion. Most have the first ridge broken. There are 5 ridges in the upper plates and 4 ridges in the lower plates. Ridges are longer than the breadth of the occlusal surface and acute. Cusps are numerous and distinct on the labial face of ridges. Notwithstanding that there are some very small tooth plates (Fig. 3a) there are no cusps on the occlusal face of the ridge. Both upper and lower plates are subtriangular, with an inner angle greatly exceeding 90° at the mediolingual junction, usually of about 130°. There is no mediolingual keel as in the species *Ptychoceratodus serratus*, *P. philippsi*, *Ferganaceratodus szechuanensis*, and *F. jurassicus* (see Liu & Yeh, 1960; Schultze, 1981; Kemp, 1996; Martin *et al.* 1997). The lingual edge is straight.

The last ridge is almost parallel to the lingual face, and clefts between the ridges are wide, deep and curved. Ridge crests are radiating, usually faceted. The first and the last ridges appear to be curved to the middle of the plate in both the upper and lower tooth plates (Fig. 3); in *Ptychoceratodus philippsi*, the first ridge is curved in the upper tooth plate. The second to the last ridges meet in a point anteriorly but the first base is medially displaced (Fig. 3) as in *A. madagascariensis*. Labial profiles of the ridges are very steep (Fig. 4). Occlusal inter-ridge furrows are wide and deep (Figs. 3,4). Some of the plates show wear.

There are no pits on the occlusal surface as in the species of *Metaceratodus* from Los Alamitos Formation of northern Patagonia or *Ceratodus* from other not even in inter-ridge furrows such as in *Ptychoceratodus serratus* (Schultze, 1981 amended by Kemp, 1998: 59).

Enamel to bone junction on the labial face of both jaws is straight. In *Metaceratodus* from Los Alamitos Formation it raises a little between crests. There are no cusps in the occlusal surface even in small specimens. Enamel and mantle dentine are restricted to margins (Fig. 4). No petrodentine (sensu Kemp, 2001) was detected.

The sulcus on the ventral side of the prearticular bone is badly preserved and it was not possible determine if it is double or simple.

There is no wear facet on the medial face of lower tooth plates as in *P. phillipsi*. This facet is present in *P. serratus* (Priem, 1924; Deschaseaux, 1949; Martin *et al.* 1999). For this, it is possible to assume that the lower tooth plates were in contact in the midline.

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References

Ameghino, F. 1898. Sinopsis geológico-paleontológica de la Argentina. In Segundo Censo Nacional de la República Argentina; *Territorio* 1: 115-228.

Ameghino, F. 1899. Sinopsis geológica-paleontológica. *Suplemento y Correcciones*: 1-13.

Ameghino, F. 1900-1903. L'âge des formations sédimentaires de Patagonie. *Anales de la Sociedad Científica Argentina* 50: 109-130, 145-165, 209-229; 51: 20-39, 65-91; 52: 189-197, 244-250; 54: 161-180, 220-249, 283-342.

Ameghino, F. 1906. Les formations sédimentaires du Crétacé superieur et du Tertiaire de Patagonia, avec an paralèlle entre leurs faunes mammalogiques et celles de l'ancien continent. *Anales del Museo Nacional de Buenos Aires* 15: 1-568.

Ameghino, C. 1916. Sobre *Ceratodus Iheringi* de la Formación Guaranítica de la Patagonia. *Physis*, Buenos Aires 2: 169.

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

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

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

Goin, F.J., D. Poiré, M. de la Fuente, A. Cione, O. Ferrer, N. Canessa, A. Carlini, J. Ferigolo, A. Ribeiro, M. Sales Viana, R. Pascual, M. Reguero, M.G. Vucetich, & S. Marenssi. 2002. Paleontología y Geología de los sedimentos del Cretácico Superior aflorantes al sur del río Shehuen (Mata Amarilla, provincia de Santa Cruz, Argentina). *Actas del XV Congreso Geológico Argentino*, Calafate 2002. CD.

Iglesias, A., A.B. Zamuner, D.G. Poiré & Larriestra, F. 2007. Diversity, taphonomy and palaeoecology of an Angiosperm flora from the Cretaceous (Cenomanian–Coniacian) in Southern Patagonia, Argentina. *Palaeontology* 50 (2): 445-466.

Jaekel, O. 1926. Zur Morphologie der Gebisse und Zähne. Vjschr. Zahnheilkde 1926: 217-242.

Kaznyshkin, M.N. 1993. On the phylogeny and systematics of dipnoan fishes Ceratodontoidei. In T. N. Bogdanova & L.I. Khosatzky (eds.) *Phylogenetical aspects of paleontology*. Proceedings of the XXXV Session of the All-Union Paleontological Society: 170-180. Nauka, Saint Petersburg. In Russian.

Kemp, A. 1996. Triassic lungfish from Gondwana, p. 409-416. In G. Arratia & G. Viohl (eds.), *Mesozoic Fishes - Systematics and Paleoecology*, Verlag Dr. Friedrich Pfeil, München, Germany.

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

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

Kemp, A. 1998. Skull structure in post-paleozoic lungfish. *Journal of Vertebrate Paleontology* 18: 43-63.

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

Kemp, A. 2003. Developmental anomalies in the tooth plates and jaw bones of lungfish. *Journal of Vertebrate Paleontology* 23: 517-531.

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

Liu, T. H. & H.K. Yeh. 1960. New *Ceratodus* from Shenmu, N. Shensi. *Vertebrata Palasiatica* 4: 14-17.

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

Martin, M. 1984. Révision des Arganodontidés et des Néocératodontidés (Dipnoi, Ceratodontiformes) du Crétacé africain. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 169: 225-260.

Martin, M., E. Buffetaut, T. Haiyan & V. Suteethorn. 1997. New Jurassic dipnoans from Thailand. *Geological Society of Denmark*, on line Series 1. http://www.2dgf/online/newjur.htm

Martin, M., L. Barbieri & G. Cuny. 1999. The Madagascan Mesozoic ptychoceratodontids (Dipnoi). Systematic relationships and paleobiogeographical significance. *Oryctos* 2: 3-16.

Nessov, L.A. & M.N. Kaznyshkin. 1985. A lungfish and turtle from Upper Jurassic of Northen Fergana, Khirghiz SSR. *Vestnik zoologii*. 1: 33-39. In Russian.

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

Priem, F. 1924. Paléontologie de Madagascar. *Annales de Paleontologie* 13: 107-132.

Riccardi, A. & E. Rolleri. 1980. Cordillera patagónica austral. In *Actas del Simposio Geológico Regional Argentino* 2: 1173-1306.

Schultze, H.P. 1981. Das Schädeldach eines ceratodontiden Lungenfisches aus der Trias Süddeutschlands (Dipnoi, Pisces). *Stuttgarter Beiträge zur Naturkunde, Ser.* B, *Geologie und Paläontologie* 70: 1-31.

Schultze, H.P. 2004. Mesozoic sarcopterygians. Pp. 463-492. In G. Arratia & A. Tintori (eds.). *Mesozoic fishes 3 – systematics, paleoenvironment, and biodiversity*. Verlag Dr Friedrich Pfeil, München.