The youngest non-lepidosirenid lungfish of South America (Dipnoi, latest Paleocene–earliest Eocene, Argentina) 

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The first lungfish tooth plate from the Las Flores Formation, Chubut, southern Argentina, is described. This is the youngest ceratodontid known from the continent. In Africa, ceratodonts disappeared in the Eocene. Afterwards, they are only known from Australia until their extinction during the Pleistocene. The Las Flores tooth plate also represents the southernmost lungfish known since the Coniacian (early Late Cretaceous).

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DURING the Mesozoic, lungfish were diverse and almost cosmopolitan (Schultze 2004). However, most genera became extinct before the Cenozoic. Since the beginning of the Cenozoic, lungfish have been almost exclusively represented by the Neoceratodontidae and Lepidosirenidae, and have become restricted to southern continents (South America, Africa and Australia; Nelson 2006).

The only previously known Cenozoic lungfish other than Lepidosirenidae and Neoceratodontidae are the ceratodontid Ceratodus humei Priem, 1914 from the Paleocene and Eocene of Saharan Africa (Longbottom 1984, Churcher & de Iuliis 2001), C. diutinus Kemp, 1993 from the Oligocene–Miocene of Australia, Metaceratodus bonei Kemp, 1997[a] from the upper Oligocene to middle Miocene of Australia, M. palmeri Krefft, 1874 from the Pliocene and Pleistocene of Australia (Kemp 1993, 1997a) and indeterminate ceratodonts and Ceratodus sp. from the Danian Santa Lucía Formation of Bolivia (Schultze 1991).

A fragmentary tooth plate found in latest Paleocene–earliest Eocene beds in Patagonia by two of us (JNG and FJG) shows that non–lepidosirenid lungfish survived until this time in southern South America. Terminology is according to Kemp (1993, 1997a,b, 2001).

Geographic and stratigraphic provenance

The main exposures of the continental Las Flores Formation (Raigemborn et al. 2009) are at the eastern tip of Gran Barranca, south of Lago Colhue Huapi (south-central Sarmiento department, Chubut province, Argentina; Fig. 1). Together with the underlying Las Violetas and Peñas Coloradas formations, and the overlying Koluel Kaike Formation, it is currently included
within the Rio Chico Group, an essentially continental sedimentary succession of late Paleocene to middle Eocene age in the San Jorge Gulf Basin (Fig. 2). Stratigraphic charts and profiles of these formations were provided by Raigemborn et al. (2009).

At Gran Barranca, the Las Flores Formation reaches 44 m thick. It consists mostly of greyish mudstones and minor epiclastic and volcanioclastic sandstones deposited in floodplain–shallow lacustrine environments (Raigemborn et al. 2009). The fossiliferous bed is a <2 m thick sandstone near the base of this formation (45°43’26”S, 68°37’14”W). There is no evidence of reworked material at this level and locality. Apart from the ceratodontid lungfish described here, around 1500 mammal remains (mostly, isolated teeth) have been exhumed and are currently under study. This rich mammalian fossil assemblage indicates an Itaboraian age of the South American Chronological Scale (Paleocene–earliest Eocene; Bond et al. 1995, Gelfo et al. 2009).

All evidence (sedimentary, mineralological, palaeobotanical) analyzed by Raigemborn et al. (2009) is consistent with the Las Flores Formation being deposited in ‘tropical’ or ‘subtropical’ climates, with warm temperatures and abundant precipitation. Its mammal content, including the impressive marsupial fauna dominated by frugivorous forms, conforms to this interpretation.

Systematic palaeontology
DIPNOI Müller, 1845
CERATODONTIDAE Gill, 1872

Ceratodontidae indet. (Fig. 3A–E)

Material. MLP 90-II-5-990, a fragmentary upper tooth plate preserving the greater part of the first ridge and the whole second ridge. The biological wear was normal, and the material does not show any evidence of significant post-mortem abrasion.

Repository. División Paleontología Vertebrados, Museo de La Plata (W1900FWA) La Plata, Argentina.

Description. The tooth plate is small. The very deep second cleft would indicate that there were few ridges, perhaps five (Fig. 3E). The medial edge of the plate is convex, and the mesiolingual edge appears to have been relatively concave. The mediolingual junction is angled (ca 118°). The loss of enamel and dentine on the mediolingual face is slight. The two preserved ridges are sharp, slender, high, straight and acute (the second), and originate anteriorly. The first ridge tip is broken. The labial profile of the second ridge is steep and there are no cusps. The angle between the preserved ridges is 28°. The first cleft is relatively shallow and rounded. The pulp cavity is large. The enamel strongly ascends in the cleft labially. Punctations are simple (petrodentine sensu Kemp 2001 absent) and cover the occlusal
surface. Some punctuations appear to be arranged in radiating series. Most are irregular. No occlusal pits are evident. Tooth plates appear to have not been in close contact. The small size of the tooth plate and the large size of the punctations suggest a juvenile. A pterygopalatine process is present, just behind the first and second ridge (Fig. 3B–C).

**Comparisons.** The combination of sharp, slender, high, straight, acute crests that originate anteriorly, deep and rounded clefts, irregular punctations arranged in lines, absence of occlusal pits, absence of cusps, large pulp cavity, lack of petrodentine, obtuse crest angle and relatively well marked inner angle and the occlusal profile (as preserved) separates the tooth plate from those of Mesozoic and Cenozoic Lepidosirenidae, Asiatoceratodontidae, Arganodontidae, Ptychoceratodontidae, *Ferganoceratodus* Kaznyshkin & Nessov, 1985, *Atlantoceratodus* Cione et al., 2007 and some genera of Neoceratodontidae and Ceratodontidae.

The tooth plate, although fragmentary, clearly differs from the South American Lepidosirenidae and neoceratodontid genera *Mioceratodus* Kemp, 1998 and *Archaeoceratodus* Kemp, 1997[b] in the occlusal...
profile and the absence of petrodentine. It also does not resemble Neoceratodus Castelnau, 1876.

The material is similar to tooth plates of some Ceratodontidae such as Ceratodus Agassiz, 1838 and Metaceratodus in occlusal profile. However, it differs from the type species of Ceratodus, C. latissimus Agassiz, 1838, from C. humei from the Paleocene and Eocene of Africa and from other Ceratodus by its deep clefts; sharp, slender, high, straight crests; and apparent absence of occlusal pits (see Kemp 1993, Churcher et al. 2006). It differs from C. diutinus from the Miocene of Australia in occlusal profile, from the putative new genus of Ceratodontidae from the Danian of Bolivia (Schultze 1991) in the occlusal surface pattern and from ‘Ceratodus sp.’ from the Upper Cretaceous of Pajcha Pata of Bolivia (Gayet et al. 2001) in the occlusal profile, the different inner angle and orientation of crests, and the mesiolingual concave profile.

MLP 90-II-5-990 is similar to some tooth plates of the Cretaceous to Pleistocene ceratodontid genus Metaceratodus. Crest shape and a concave lingual edge resemble those of the Australian Cretaceous species M. elliottii Kemp, 1997[a]. However, we have not observed the typical occlusal pits of that genus.

Discussion

Dipnoans were cosmopolitan during the early Mesozoic, but gradually became restricted to their current distribution in the Southern Hemisphere during the Cretaceous (Fig. 4). There is no explanation for their demise in the Northern Hemisphere. The youngest record of non–lepidosirenid lungfish in Africa is from the Eocene and in South America from the late Paleocene–earliest Eocene (Longbottom 1984; this paper). Presently, lepidosirenids inhabit Africa and South America (Nelson 2006).
In Australia, lungfish remained diverse during the Cenozoic, with two families (Ceratodontidae and Neoceratodontidae) incorporating several genera and species. Ceratodontidae, a cosmopolitan family during much of the Mesozoic, became extinct in Australia (*Ceratodus* in the Miocene and *Metaceratodus* in the Pleistocene; Kemp 1993, 1997a, 2001). Neoceratodontidae, known with certainty only in Australia, included three genera: *Archaeoceratodus*, *Mioceratodus* and *Neoceratodus* (Kemp 1997b). Presently, *N. forsteri* Krefft, 1870 is the only dipnoan living in Australia (Nelson 2006).

The extinction of non-lepidosirenid lungfish in Africa and South America may be related to environmental changes. Their extinction closely matched a peak in global temperatures, the early Eocene Climatic Optimun (EECO) (Fig. 2), and with the diversification of many teleost orders.

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