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SHORT COMMUNICATION

A NEW LUNGFISH (DIPNOI) FROM THE LATE TRIASSIC OF SOUTH AMERICA

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Lungfishes belong to the sarcopterygian clade Dipnoi. Living forms are represented by three genera distributed among South America, Africa, and Australia. The oldest fossil record of lungfishes is Devonian (see Long, 2010), but they become notably abundant in post-Paleozoic deposits (Martin, 1982; Schultze, 2004). The oldest South American records of fossil lungfishes come from Permian beds in Brazil (Cox and Hutchinson, 1991; Toledo and Bertini, 2005; Toledo, 2006). These specimens consist of isolated tooth plates assigned to Ceratodontidae and Gnathorizidae. Triassic finds are restricted to a single and incomplete tooth plate from the Santa María Formation (Carnian) of Brazil (Richter and Toledo, 2008). The specimen was referred to *Ptychoceratodus*, being probably related to the European form *P. phillipsi*. Because of the paucity of the record, Triassic South American lungfishes almost completely lack mention in most paleobiogeographical analyses of early Mesozoic dipnoan distribution and radiation. In Jurassic beds, the record is restricted to isolated plates belonging to *Ceratodus* and '*Arganodus*' from isolated localities in Brazil and Uruguay (Soto and Perea, 2010). In contrast, the Cretaceous and Paleogene lungfish record is especially abundant and diverse (Fernández et al., 1973; Pascual and Bondesio, 1976; Toledo and Bertini, 2005; Apesteguía et al., 2007; Cione et al., 2007, 2010; Agnolin, 2010; Cione and Gouiric, 2012; Alves et al., 2013).

Here, we expand the record of South American dipnoans, describing a tooth plate and associated jaw bone from the Late Triassic (Carnian) Potrerillos Formation at the Agua de las Avispas fossiliferous locality, Mendoza Province, Argentina (Fig. 1). This is a well-known fossiliferous spot that has yielded a large number of plant and arthropod specimens, as well as fragmentary actinopterygian material (Zavattieri and Prámparo, 2006; Morel et al., 2010; Gallego et al., 2011; Lara et al., 2012). The specimen here described is assigned to a new species of the widespread genus *Ptychoceratodus* and is the most complete Triassic dipnoan from South America.

MATERIALS AND METHODS

Terminology—We follow the terminology of Churcher et al. (2006; see also Churcher and De Iuliis, 2001) for the tooth plates, and that of Martin (1981) for jaw bone

structures. The angle between the medial and lingual margins of the tooth plate is termed inner angle following Vorobyeva and Minikh (1968). Histological terminology follows Kemp (2001). Measurements were taken as in Apesteguía et al. (2007).

Institutional Abbreviation—IANIGLA-PV, Vertebrate Paleontology Collection, Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales, Mendoza, Mendoza Province, Argentina.

SYSTEMATIC PALEONTOLOGY

DIPNOI Müller, 1844
PTYCHOCERATODONTIDAE Martin, 1982
Ptychoceratodus Jaekel, 1926
Ptychoceratodus cuyanus, sp. nov.

Holotype—IANIGLA-PV 415, right incomplete pterygopalatine bone bearing a complete tooth plate (Fig. 2). It is identified as an upper element because of the well-developed pterygopalatine process (Martin, 1980). Furthermore, the tooth plate lacks wear on the medial surface of first ridge (Martin, 1981).

Etymology—'Cuyanus,' meaning 'coming from Cuyo.' Cuyo is the geographical region where the outcrops that yielded the new dipnoan here described are located.

Type Locality and Horizon—The Agua de las Avispas fossiliferous locality (33°04′52″S, 69°08′56″W) is placed at the southern flank of Cacheuta Hill (cerro Cacheuta), at the Lujan de Cuyo Department, Mendoza Province, Argentina (Fig. 1). The stratigraphic column was studied in detail by Morel (1994; see also Zavattieri and Prámparo, 2006; Morel et al., 2010). The upper part of the sequence is composed of cross-bedded sandstones, mudstones, bituminous shales, and tuffs of braided fluvial systems developed in a muddy floodplain that represents the Potrerillos Formation (Carnian). The specimen was found in the uppermost levels of the Potrerillos Formation embedded in thin sandstones.

Diagnosis—Medium-sized lungfish diagnosable on the following combination of characters (asterisk indicates possible autapomorphies): occlusal pits absent; upper tooth plates in wide contact along the mesiobuccal margin; upper tooth plates having five ridges; first ridge of upper tooth plates nearly straight (feebly curved); robust, and notably elongate, being slightly longer than
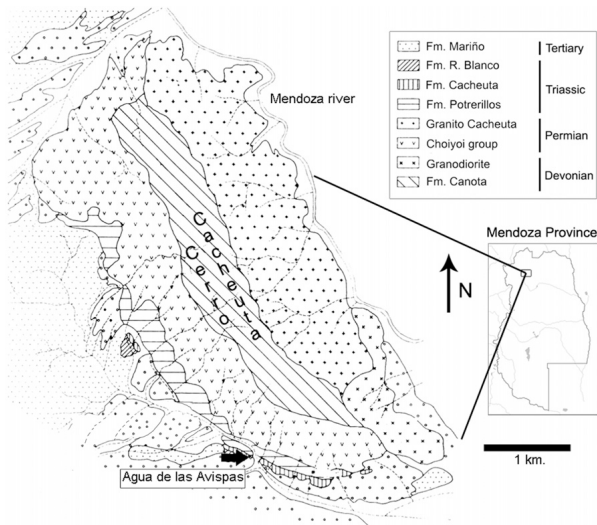
*Corresponding author.

FIGURE 1. Map showing the Cacheuta Hill area, Mendoza, Argentina. Arrow indicates where the holotype of *Ptychoceratodus cuyanus* was found. Modified from Morel (1994).

the lingual margin*; and mesiointernal angle located at level of the third ridge*.

DESCRIPTION

The holotype and only known specimen of *P. cuyanus* has its surface eroded by wear near the mesiointernal angle, whereas the crests of the ridges are acute towards the buccal margin. This pattern fits with the second stage of wear defined by Martin (1980), which suggests that the plate did not belong to a juvenile or a senile individual.

The tooth plate is roughly subtriangular and relatively high-crowned. The inner angle is about 115°. The occlusal surface of the plate is narrow and slightly concave, smooth, and lacking occlusal pits, the last feature being shared with *Neoceratodus* (Kemp, 1997). The whole plate surface is covered by randomly arranged punctuations corresponding to pulp canals of the dentine (Bemis and Northcutt, 1992). There is no trace of hypermineralized dentine free of denteons or petrodentine (Kemp, 2001).

The plate has five acute ridges, showing low crests along at the buccal half of each ridge. The ridges do not converge at the mesiointernal angle of the plate, and do not originate anteriorly as in several neoceratodontids (sensu Kemp, 1997). The fifth ridge is narrow and is not twinned. The ridges are relatively straight, and the first ridge is only slightly posteriorly curved and has a gently convex mesiobuccal margin. Ridge size is as follows: 1 > 3 > 2 > 5 > 4.

The mesiointernal angle is not pronounced, being represented by a poorly developed bump. The mesial and lingual margins thus form a nearly continuous and gently convex margin. In contrast with other known *Ptychoceratodus*, the mesiointernal angle is located at the level of the third ridge, rather than being located at the level of the first or second ridge (Martin et al., 1999; Skrzycki, 2015). Denticulations are not observed in the buccal margin of the crests. Inter-ridge sulci are relatively deep and wide, with a rounded lingual end. The first sulcus is deeper and wider than other sulci.

The mesiobuccal margin of the plate is flat, representing the contact for the opposite tooth plate. This is in agreement with presence of a narrow to nonexistent space between the margin of the plate and the symphysis of the prearticular bone.

The pterygopalatine bone is narrow, thin, and fragile, being slightly curved and relatively long and narrow on its posterior part. The tooth plate is fully attached to the pterygopalatine bone (Martin, 1981).

Due to the very short symphyseal process of the pterygopalatine bone, the tooth plates are contiguous to each other. The articular surface of the symphysis is decorated by upright minute grooves and ridges. The symphysis is notably dorsoventrally low and buccolingually extended, forming a linear symphysis as defined by Kemp (1998). There is a poorly defined groove below the pterygopalatine. It is shallow and is subdivided by a subvertical, poorly developed, and smooth ridge. The pterygopalatine process is represented only by its base. It is relatively robust and oval in section and is located at the level of the second ridge, being slightly posteriorly curved.

Measurements—Total length: 40.1 mm; total length of first ridge: 22.3 mm; total length of second ridge: 4.9 mm; total length of third ridge: 7.5 mm; total length of fourth ridge: 4.1 mm; total length of fifth ridge: 3.7 mm; length of lingual margin: 19.8 mm.

DISCUSSION

Post-Paleozoic dipnoans bear prominent masticatory structures made up of several kinds of enamel and dentine known as tooth plates. Due to their high fossilization potential, tooth plates are usually the only known elements of Mesozoic and Tertiary fossil dipnoans (Martin, 1982; Cavin et al., 2007; Skrzycki, 2015). Since the 19th century, these isolated teeth have been referred to the genus *Ceratodus*. However, it is now known that these plates belong to a large number of genera, as first demonstrated by Martin (1980, 1981, 1982, 1984). In this way, the taxonomy of fossil lungfishes is complicated by the fact that many important changes in the structure of the tooth plates are due to abnormal growth, or to the diet of the individual (Kemp, 1990). In spite of these drawbacks, in most cases isolated tooth plates show enough features to allow determination at the species level, and possibly to even help to infer phylogenetic relationships (see also Cione and Gouiric-Cavalli, 2012; Skrzycki, 2015; Fanti et al., 2016). Further, recent authors have argued that tooth plates have stronger functional constraints and are probably less variable than skull bones, and tooth plate characters allow discrimination between known genera (Skrzycki, 2015).

Comparisons

Having relatively robust and thick crushing upper tooth plates, with five or less ridges lacking tubercles and a convex lingual margin, and pterygopalatine process located at the level of the second ridge in the pterygopalatine bone, distinguishes *P. cuyanus* from all known pre-Triassic dipnoans (Martin, 1982, 1984; Apesteguía et al., 2007). Among ceratodontiforms, presence of five or less ridges on upper tooth plates is a feature exclusively shared by species of Ceratodontidae or Ptychoceratodontidae (the latter composed only of *Ptychoceratodus*; Martin, 1984; Cavin et al., 2007). Presence of five crests, together with acute ridges (versus rounded, broad, and crushing; Martin, 1984; Schultze, 1991; Kemp, 1993; Cavin et al., 2007), indicates that *P. cuyanus* belongs to the genus *Ptychoceratodus* (sensu Martin, 1982; see also Skrzycki, 2015).

Ptychoceratodontid-like tooth plates are also present in the genus *Ferganoceratodus* (Martin, 1982; Martin et al., 1999; Cavin et al., 2007; Fig. 3). In several species of *Ptychoceratodus*, the upper tooth plates are contiguous at midline (in the case of *P. cuyanus*, forming an extensive faceted contact; see Kemp, 1998; Agnolín, 2010), whereas in *Ferganoceratodus* the upper tooth plates are not in contact with each other (a plesiomorphic condition based on Cavin et al., 2007). In addition, *Ferganoceratodus* has plates having the three anterior-most ridges sharp, whereas the two posterior ones are blunt (Cavin et al., 2007) a condition
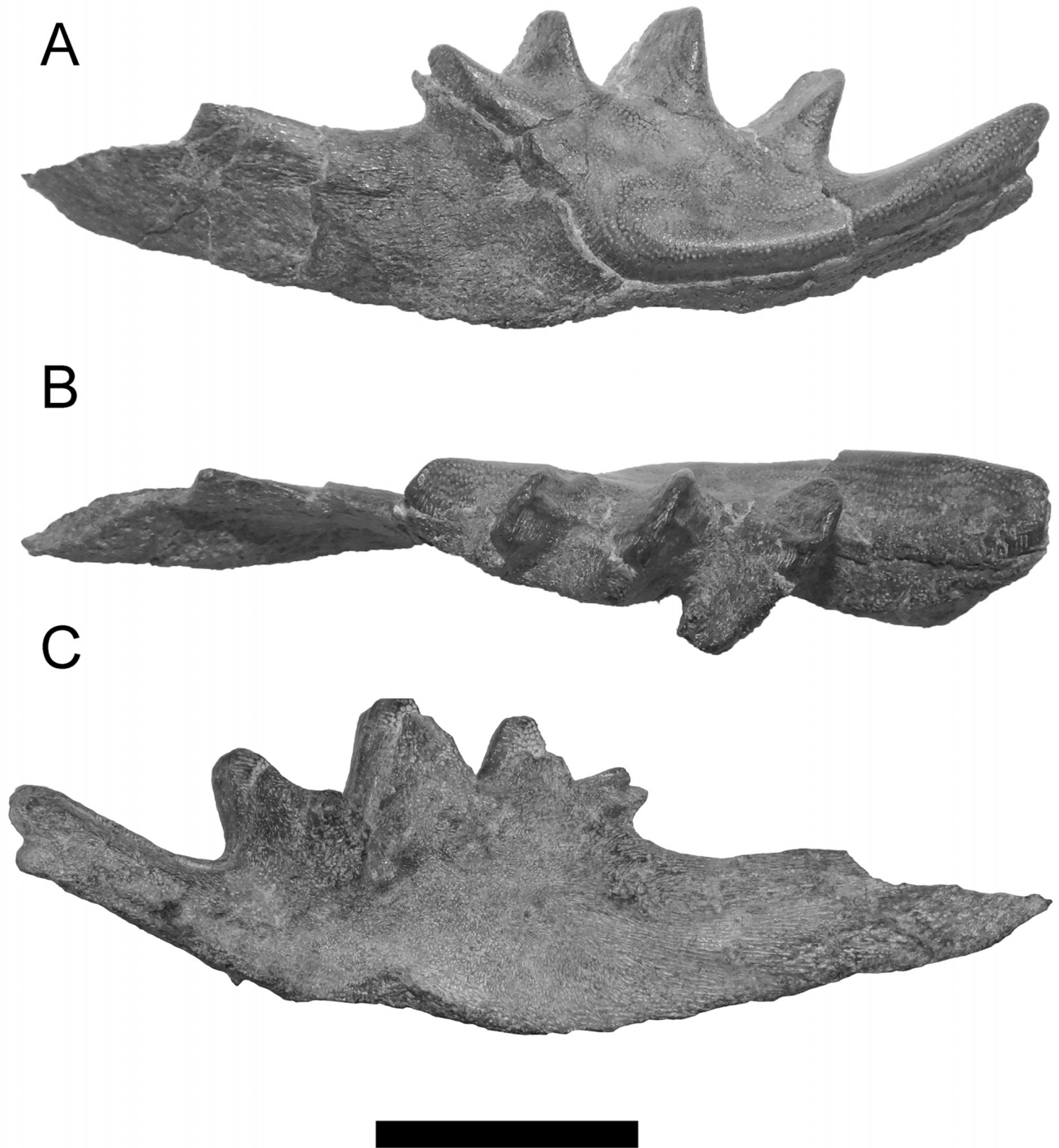
FIGURE 2. Lower left tooth plate of *Ptychoceratodus cuyanus* (IANIGLA-PV 415, holotype) in **A**, occlusal; **B**, buccal; and **C**, ventral views. Scale bar equals 10 mm.

that contrasts with *P. cuyanus*. Furthermore, in *Ferganoceratodus*, the tooth plates show a conspicuous mesiointernal keel and a mesiolingual angle of about 90° (Soto and Perea, 2010). In sum, *P. cuyanus* may be assigned to *Ptychoceratodus*.

Among *Ptychoceratodus, P. cuyanus* belongs to the 'First Group' of species defined by Martin (1982; see also Martin et al., 1999), which are distinguished by having only five ridges on

upper tooth plates, a reduced mesiointernal angle and keel, a nearly straight lingual margin, an obtuse inner angle, and a notably long first ridge that is at least as long as the lingual margin, a combination of characters absent in most other *Ptychoceratodus* species (e.g., *P. phillipsi, P. rectangularis, P. serratus, P. roemeri*; Martin, 1980, 1982; Martin et al., 1999; Skrzycki, 2015; Fig. 3). In *P. concinnus* and *P. silesiacus*, the first ridge is subequal to the
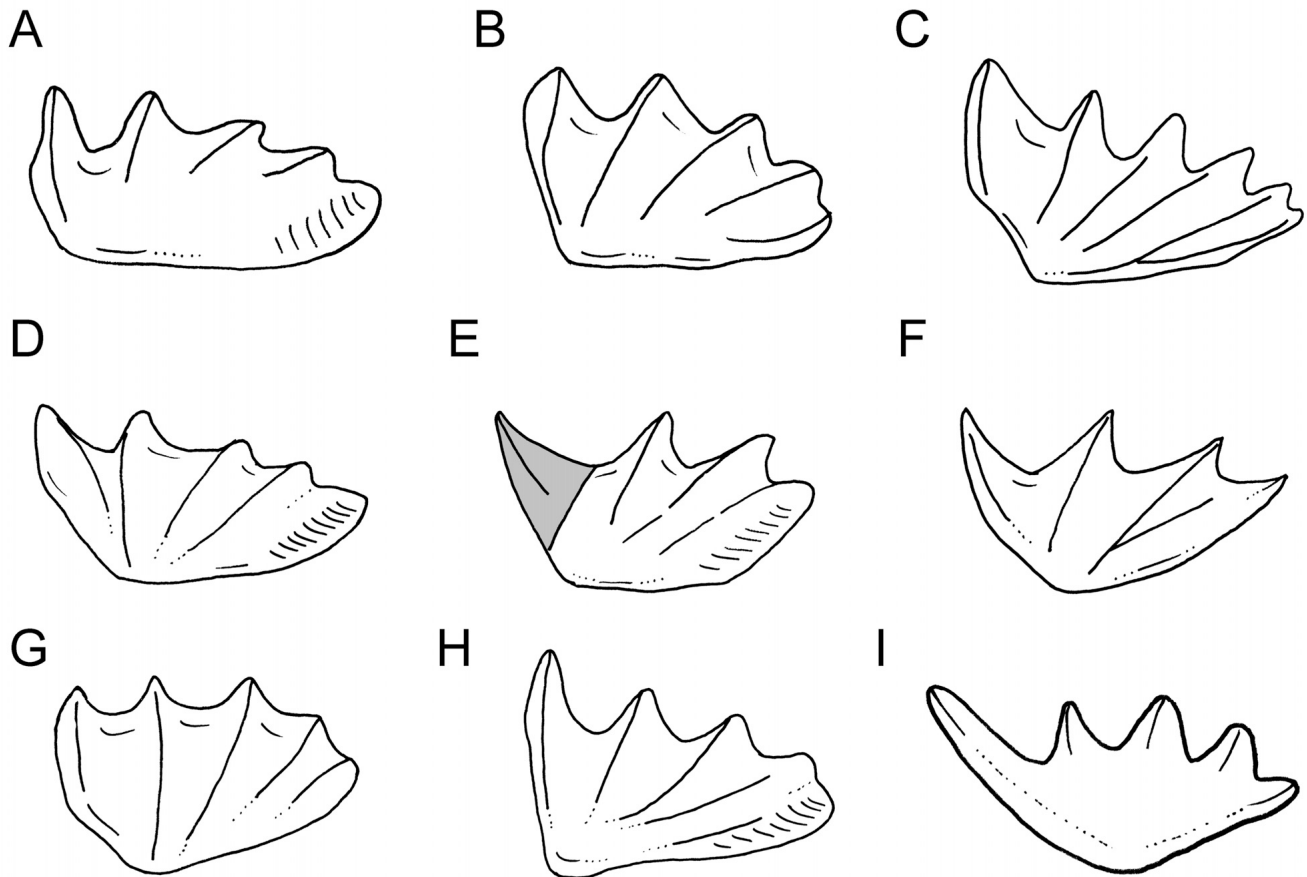
FIGURE 3. Left upper tooth plates of selected dipnoans in occlusal view. **A**, *Ptychoceratodus rectangulus*; **B**, *Ptychoceratodus roemeri*; **C**, *Ptychoceratodus serratus*; **D**, *Ptychoceratodus hislopianus*; **E**, *Ptychoceratodus acutus*; **F**, *Ptychoceratodus virapa*; **G**, *Ptychoceratodus phillipsi*; **H**, *Ferganoceratodus szechuanensis*; **I**, *Ptychoceratodus cuyanus*, sp. nov. (reversed). **A**, **B**, **C**, redrawn from Skrzycki (2015); **D**, **E**, **F**, redrawn from Martin et al. (1999); **G**, redrawn from Martin (1980); **H**, redrawn from Cavin et al. (2007). Not to scale.

lingual margin (Skrzycki, 2015). However, *P. cuyanus* clearly differs from the latter taxa in having much narrower tooth plates, notably wider and deeper inter-ridge sulci, and different position of the mesointernal keel, among other features.

Among the 'First Group' of species (Martin, 1982), *P. cuyanus* differs from *P. virapa* and *P. acutus* in having a well-developed and distinct fifth ridge (Martin, 1982). In addition, *P. acutus* differs from the tooth plate here described in having very large and robust plates with sharp and straight ridges (Martin et al., 1999). In *P. virapa*, the tooth plate has a more convex lingual margin (Martin et al., 1999), whereas in *P. cuyanus* this margin is slightly concave. In contrast to *P. hislopianus*, in *P. cuyanus* the last ridge does not form a flattened crushing surface (Martin et al., 1999).

Other features may be also helpful to diagnose *P. cuyanus*. In this taxon, as in *P. phillipsi*, the last ridge is almost parallel to the lingual face (Kemp, 1996; Richter and Toledo, 2008). It clearly differs from *P. phillipsi* and *P.* cf. *phillipsi* (Richter and Toledo, 2008) in lacking a mesiolingual keel, in that the ridges do not converge in the mesiolingual angle, and in the presence of a well-developed fifth ridge (Richter and Toledo, 2008).

In addition, among ptychoceratodontids, the total absence of occlusal pits on the tooth plate is a feature unique to *P. cuyanus*, whereas in most other *Ptychoceratodus* species the pits are present and distributed in furrows between the ridges (Apesteguía et al., 2007; Skrzycki, 2015). The absence of occlusal pits is shared with *P. silesiacus* and *P. phillipsi* (Skrzycki, 2015).

Palaeoecological Implications

Ptychoceratodus cuyanus was found in deposits of the Potrerillos Formation, which are exclusively fluvial in origin (Morel, 1994) and lack any sign of marine influence. In this regard, Cavin et al. (2007; see also Fernández et al., 1973; Kirkland, 1988) proposed that most, if not all, post-Paleozoic dipnoans were adapted to freshwater habitats (contra Schultze, 1991), a fact supported by the depositional origins of most known fossils, including the specimen here described.

Based on the classification of Kemp (2005), it is possible that *Ptychoceratodus cuyanus* was a durophagous fish. Grinding abrasion was probably the dominant mode of mastication, with reduced crushing movements. This is related to some features, such as rounded and shallow inter-ridge sulci, intermediately acute crests, and a flat inner occlusal surface.

Paleobiogeographical Implications

At the end of the Triassic, ichthyofaunas retained a large number of sarcopterygians, including dipnoans (López-Arbarello,
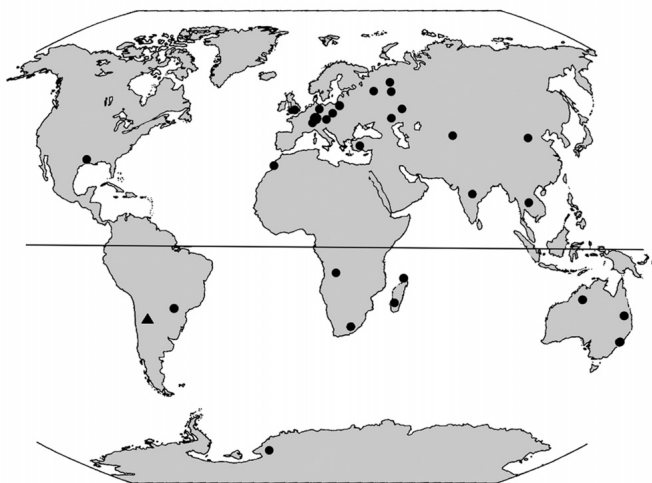
FIGURE 4. Map showing the fossil record of dipnoans coming from Triassic outcrops. The triangle indicates the find reported here. Modified from Schultze (2004).

2004). In South America, Triassic ichthyofaunas are almost unknown, and until recently, dipnoans were absent from the Argentinian record (Fig. 4; Arratia and Cione, 1996; López Arbarello, 2004). Thus, the find of a lungfish in the Triassic of central Argentina constitutes an important addition to the fish faunas, corroborating the existence of these fishes in the Southern Cone.

It is worth mentioning that *P. cuyanus* belongs to a *Ptychoceratodus* species group that contains taxa reported in other Gondwanan landmasses (i.e., Madagascar, India; Martin et al., 1999). Further, the Triassic tooth plate from Brazil (*P.* cf. *P. phillipsi*; Ritcher and Toledo, 2008) is morphologically similar to tooth plates recovered in the Triassic of Africa and Australia (Kemp, 1996). Gondwanan lungfishes of the genus *Ptychoceratodus* are in agreement with the paleobiogeographical pattern proposed for Late Triassic tetrapods (Ezcurra, 2010). This model consists of the definition of several paleo-latitudinal belts that reflect that tetrapod lineages of Gondwanan territories were more closely related to each other than to Laurasian ones (Ezcurra, 2010).

The lack of published Triassic dipnoan records in South America before the year 2008 resulted in this continent not forming part of the palaeobiogeographical analyses of early modern dipnoans of the Triassic (e.g., Pascual and Bondesio, 1976; Martin, 1982; Kemp, 1991, 1996; López Arbarello, 2004). Apesteguía et al. (2007) proposed that *Ptychoceratodus* was of late appearance in South America, as an immigrant from other 'greater Gondwanan' landmasses, where it was present since the Triassic (India, Madagascar, Australia, Africa; Martin et al., 1999). The presence of a Triassic *Ptychoceratodus* in central Argentina indicates that the genus was probably present in the continent throughout the Mesozoic. This also reinforces the idea that the genus *Ptychoceratodus* was widely distributed in the Northern and Southern hemispheres prior to the splitting up of Pangea.

In South America, the oldest recorded Mesozoic dipnoans are *Ptychoceratodus* cf. *phillipsi* from the Late Triassic Santa María Formation of Brazil (Richter and Toledo, 2008) and the present report from the Late Triassic of Argentina. Previous to these discoveries, the oldest Mesozoic dipnoans from the continent were those described from the Middle Jurassic of Uruguay (Soto and Perea, 2010). The present find fills a geographic gap, indicating that dipnoans were present in the

Triassic of South America. Furthermore, because the present specimen is morphologically different from the Triassic material coming from Brazil, it suggests that the diversity of Triassic dipnoans in South America is far from being well known and understood.

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