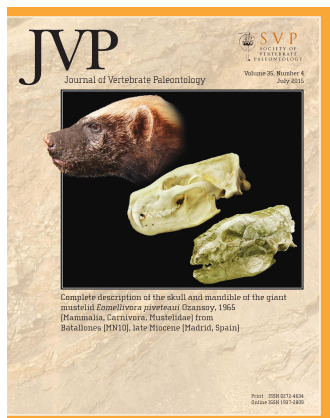


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### New fossil species of the extant genus *Lepidobatrachus* (Anura, Ceratophryidae) from the Late Miocene-Early Pliocene of central Argentina

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## NEW FOSSIL SPECIES OF THE EXTANT GENUS *LEPIDOBATRACHUS* (ANURA, CERATOPHRYIDAE) FROM THE LATE MIOCENE-EARLY PLIOCENE OF CENTRAL ARGENTINA

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**ABSTRACT**—I describe a new fossil species of the extant anuran genus *Lepidobatrachus* from late Miocene-early Pliocene sediments of central Argentina. This species was erroneously attributed to the living species *L. laevis* in prior studies. However, reanalysis of the fossil material demonstrated that some anatomical structures, as well as their taxonomic significance, were misinterpreted. The description and comparative analysis presented here demonstrate that this specimen represents a new fossil species of *Lepidobatrachus*. Although it possesses most of the possible synapomorphies of *Lepidobatrachus*, some features of the architecture of the skull of the specimen, specifically the relationships of the palatal surface of the maxilla with the surrounding bones, resemble the skull of other ceratophryid genera. Additionally, the new species differs from all ceratophryids in the absence of a supraorbital shelf. The paleoenvironmental significance of this discovery is also discussed.

### INTRODUCTION

*Lepidobatrachus* is an extant anuran genus included in the well-supported clade of South American horned frogs, Ceratophryidae (Haas, 2003; Darst and Cannatella, 2004; Correa et al., 2006; Fabrezi, 2006; Frost et al., 2006; Grant et al., 2006; Evans et al., 2008; Fabrezi and Quinzio, 2008; Báez et al., 2009; Pyron and Wiens, 2011; Laloy et al., 2013; Evans et al., 2014). The genus includes three living species—*L. asper*, *L. laevis*, and *L. llanensis*. These moderate- to large-sized frogs have stout bodies, short legs, and a huge mouth; they are restricted to the South American Gran Chaco (Faivovich, 1994; De la Riva et al., 2000; Brusquetti and Lavilla, 2006; Moreira Sugai et al., 2013). This extensive semiarid region is located in central South America (Fig. 1) and has a marked climatic seasonality (Prado, 1993; Cabrera, 1994). In cold and dry winters, *Lepidobatrachus* remains underground cloaked in a protective cocoon (McClanahan et al., 1976; Cei, 1980). Breeding and feeding occur during the rainy season in temporary ponds where these aggressive, voracious frogs usually are found seated or floating in shallow water with only their eyes and nostrils emergent (Reig and Cei, 1963; Hulse, 1978). Tadpoles of these frogs also are carnivorous and undergo rapid development (Ruibal and Thomas, 1988; Wassersug and Heyer, 1988; Fabrezi and Quinzio, 2008).

Little is known about the evolutionary history of *Lepidobatrachus*. Although the monophyly of Ceratophryidae [*Lepidobatrachus* + *Chacophrys* + *Ceratophrys*] is well supported (Haas, 2003; Darst and Cannatella, 2004; Correa et al., 2006; Fabrezi, 2006; Frost et al., 2006; Grant et al., 2006; Evans et al., 2008; Fabrezi and Quinzio, 2008; Báez et al., 2009; Pyron and Wiens, 2011; Laloy et al., 2013; Evans et al., 2014), the relationships among ceratophryids or among Ceratophryidae and other anuran families still are controversial (Frost et al., 2006; Grant et al., 2006; Pyron and Wiens, 2011). Several fossil remains have been considered to represent ceratophryids (Rovereto, 1914; Rusconi, 1932; Casamiquela, 1963; Marshall and Patterson, 1981; Ameghino, 1989; Báez and Perí, 1989, 1990; Perí, 1993a; Contreras and Acosta, 1998; Rinderknecht, 1998; Fernicola, 2001; Agnolín, 2005; Evans et al.,

2008); however, none has been attributed to *Lepidobatrachus*. Recently, however, a fossil skull from late Neogene units of central Argentina was associated with the living species *L. laevis* (Tomassini et al., 2011). However, my studies on the anatomy of *Lepidobatrachus* indicate that these fossil remains are not those of *L. laevis*, but pertain to a novel species that is described in this paper.

### GEOLOGIC AND PALEONTOLOGIC CONTEXT

The specimen examined (MMH 85-12-2a) was collected in sediments of the Monte Hermoso Formation exposed in the Farola Monte Hermoso Locality, on the Atlantic Coast of the Buenos Aires Province in central Argentina (Fig. 1). Although neither absolute ages nor magnetostratigraphic studies exist for this formation, faunal correlations in bounding strata of known ages allow the Monte Hermoso Formation to be constrained to the late Miocene-early Pliocene (Cione et al., 2007 and papers cited therein). A recent attribution to this unit of a more defined age range (early Pliocene by Tomassini et al., 2013) is fundamentally based in the comparison of the “evolutionary stage” of the faunal content of each stratum, a reasoning that has been questioned specifically for the late Cenozoic units of Buenos Aires province (Cione and Toni, 1995). The analysis of geological facies and architectural elements suggests that the sediments of this formation were deposited in a high-sinuosity, muddy, fine-grained fluvial-system environment (Zavala, 1993; Zavala and Navarro, 1993). The specimen MMH 85-12-2a was found in the upper part of the Monte Hermoso Formation, in a bed composed of conglomerate sandstones and breccias that was interpreted as a lag-channel deposit (Tomassini et al., 2013).

Farola Monte Hermoso (FMH) has been known since the 19th century because of the abundance and diversity of fossil vertebrates found there; these include fishes, anurans, turtles, lizards, snakes, birds, and numerous mammals (Tonni, 1974; Albino, 1992; Arratia and Cione, 1996; Goin and Pardiñas, 1996; de la Fuente, 1997; Tonni and Noriega, 1998; Fernicola, 2001; McDonald et al., 2008; Albino and Brizuela, 2009; Albino et al., 2009;



FIGURE 1. Map showing the fossiliferous locality, (indicated by star), the present distribution of the different species of *Lepidobatrachus* (localities mentioned in Faivovich, 1994; Brusquetti and Lavilla, 2006; Moreira Sugai et al., 2013), and the extent of the South America Gran Chaco region.

Echarri et al., 2009; Agnolin and Tomassini, 2012; Deschamps et al., 2012; Gómez et al., 2013; Tomassini et al., 2013, and references cited therein). The other fossil anurans that have been reported from this locality are an undetermined species of *Leptodactylus* (Gómez et al., 2013), *Ceratophrys ameghinorum* (Fernicola, 2001), and a species related to *Rhinella schneideri* (as *Bufo paracnemis*; Báez, 1986).

#### MATERIALS AND METHODS

Specimen MMH 85-12-2a is a roughly preserved three-dimensional skull, with no evidence of deformation. Several parts of the specimen were covered with a protective layer of shellac in which there were sediment remains that obscured some anatomical details of the fossil. Because the layer did not adhere to the bones, it was mechanically removed.

Fossil and extant skeletal material was examined with a Nikon SMZ 800 stereoscope. Overall views of the skull were photographed with a Sony DSC-XZ200 digital camera, whereas cranial details were imaged with a Micrometrics digital camera attached to the stereoscope fitted with a 0.5 reducing lens. Sets of photographs at progressive focal depths of each specimen or detail were combined to generate the final image depicted in Figures 2–4.

The taxon sampling of ceratophryids in all of the phylogenetic analyses is limited, and, as was mentioned, the topological relationships among them and with other anurans are incongruent (Haas, 2003; Darst and Cannatella, 2004; Correa et al., 2006;

Fabrezi, 2006; Frost et al., 2006; Grant et al., 2006; Evans et al., 2008; Fabrezi and Quinzio, 2008; Báez et al., 2009; Pyron and Wiens, 2011; Laloy et al., 2013; Evans et al., 2014). Some of the analyses that included ceratophryids have incorporated skeletal information (Fabrezi, 2006; Fabrezi and Quinzio, 2008; Báez et al., 2009; Laloy et al., 2013), and a few osteological synapomorphies have been proposed for Ceratophryidae and some of its genera. However, the osteological characters included in those analyses are limited; there are additional features that characterize ceratophryid genera and Ceratophryidae as a whole relative to other anurans. As part of a more inclusive phylogenetic analysis, the skeletal anatomy of ceratophryids was analyzed and compared with that of putative closely related taxa (Frost et al., 2006; Grant et al., 2006; Pyron and Wiens, 2011) to identify possible osteological synapomorphies of Ceratophryidae and its genera. This information was based on comparative material (Appendix 1) and a literature survey (e.g., Grandison, 1961; Reig and Limeses, 1963; Lynch, 1971, 1972, 1978, 1982; Reig, 1972; Pires Gayer, 1984; Laurent and Lavilla, 1986; Lavilla and Lobo, 1992; Wild, 1997, 1999; Lavilla and Ergueta Sandoval, 1999; Izecksohn et al., 2005; Da Silva Vieira et al., 2006; Fabrezi, 2006; Rosset et al., 2007; Prado and Pombal, 2008; Rosset, 2008; Lavilla et al., 2010). Osteological terminology mainly follows Trueb (1973), with additional terms from Roček (2003) and Jurgens (1971); otherwise, it is clarified in the text. Institutional acronyms follow those of Leviton et al. (1985), with the addition of MMH: Museo de Ciencias Naturales ‘Vicente Di Martino,’ Monte Hermoso, Argentina.

#### SYSTEMATIC PALEONTOLOGY

ANURA Fischer von Waldheim, 1813  
 CERATOPHRYIDAE Tschudi, 1838  
*LEPIDOBATRACHUS* Budgett, 1899

**Type Species**—*Lepidobatrachus laevis* Budgett, 1899.

*LEPIDOBATRACHUS AUSTRALIS*, sp. nov.  
 (Figs. 2A, D; 3A; 4A)

*Lepidobatrachus laevis* (non Budgett, 1899): Tomassini et al., 2011:1006, fig. 2. Specimen misidentification.

**Holotype**—MMH 85-12-2a, incomplete skull.

**Locality and Horizon**—Farola Monte Hermoso, Buenos Aires, Argentina. Monte Hermoso Formation, late Miocene–lower Pliocene (Cione et al., 2007).

**Etymology**—The species name ‘australis’ is Latin, meaning ‘southern’ in reference to the distribution of this fossil species, which was found about 700 km south of the most austral record of extant *Lepidobatrachus*.

**Diagnosis**—A species of *Lepidobatrachus* that differs from all its congeners in lacking a supraorbital shelf on the frontoparietal, having a subtriangular pterygoid process of the maxilla, and lacking a pars palatina on the maxilla anterior to the pterygoid process.

#### DESCRIPTION

The specimen is a well-ossified, solidly articulated, and extremely flat skull (Fig. 2A, D). Because the skull is roughly and incompletely preserved, general proportions cannot be estimated. Proportionally small, nearly round orbits are located at the mid-length of the skull and have complete bony margins (Fig. 2A, D). Most bones are fused with adjacent elements and few sutures are evident among them, although the smooth areas between sculptured areas indicate zones of articulation and synostosis. The dermal bones of the skull roof have extensive dermal

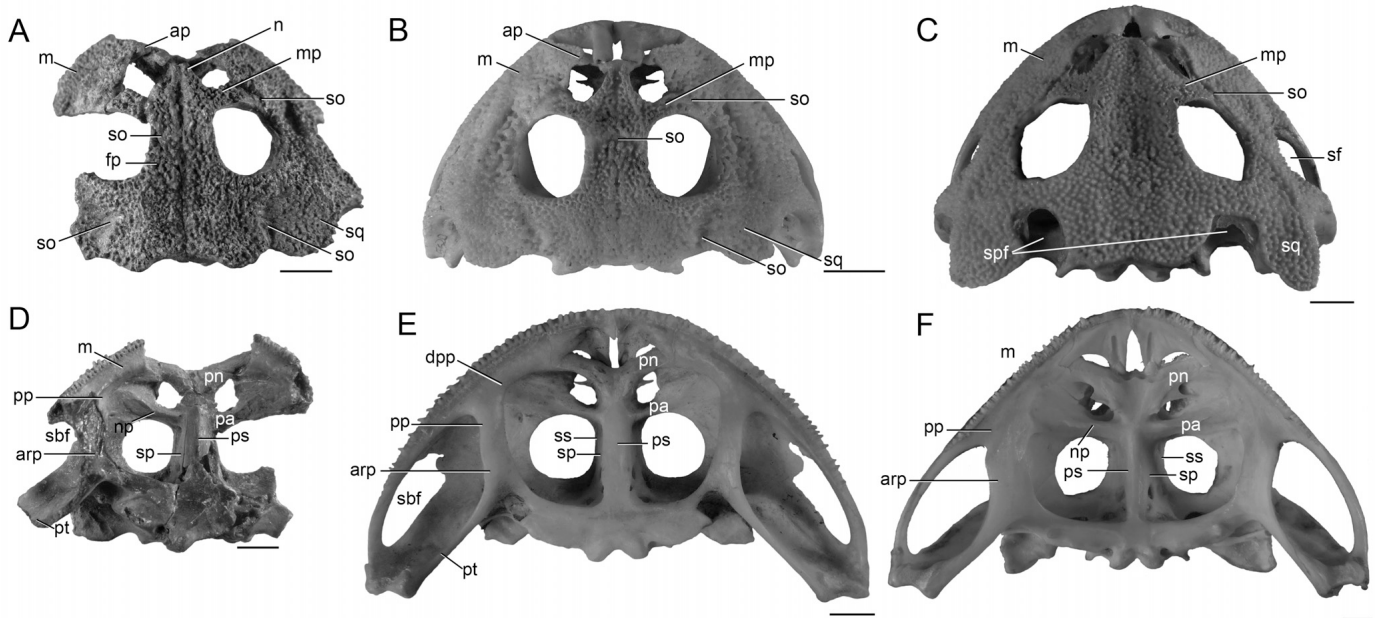


FIGURE 2. Skulls of selected Ceratophryidae. **A–C**, dorsal view; **D–E**, ventral view. **A, D**, *Lepidobatrachus australis* (MMH 85-12-2a); **B, E**, *Lepidobatrachus llanensis* (FML 5220); **C, F**, *Ceratophrys cranwelli* (FML 5477). **Abbreviations:** ap, anterior process; ar, anterior ramus of pterygoid; dpp, pars palatina of maxilla; fp, frontoparietal; m, maxilla; mp, maxillary process of nasal; n, nasal; np, neopalatine; pa, planum antorbitale; pn, pares naris ossification; pp, maxillary pterygoid process; ps, parasphenoid; pt, pterygoid; sbf, subtemporal fenestra; spf, supratemporal fenestra; so, region of smoothed or interrupted dermal ornamentation; sp, sphenethmoid; sq, squamosal; ss, supraorbital shelf. All scale bars equal 5 mm.

sculpturing in a tuberculate pattern (Fig. 2A). The ornamentation is interrupted abruptly in some regions, such as the articulation between the maxillary process of the nasal and the pars facialis of the maxilla (Fig. 2A). In other regions (e.g., between nasals and between the squamosal and frontoparietal), the ornamentation decreases gradually and is indistinguishable in the region of the fused articulations (Fig. 2A). Several cracks are visible in the surface of the specimen. Given the degree of ossification and the conspicuous ornamentation of the only known specimen of *L. australis*, it is here considered an adult.

The nasals are broad and synostosed with one another, the maxillae, and the frontoparietals. The anterior portion of the skull is not preserved, and the anterior tips of the nasals may be broken. It is evident, however, that nasals cover at least the posterior half of the olfactory region of the braincase, and their anterior margins are deeply concave (Fig. 2A). The maxillary processes are anterolaterally directed, robust, and hourglass-shaped. A smooth transverse band is evident in the skull roof between the orbits, presumably this represents the zone of contact of nasals and frontoparietals, but it may also represent the exposed dorsolateral margin of the sphenethmoid (Fig. 2A).

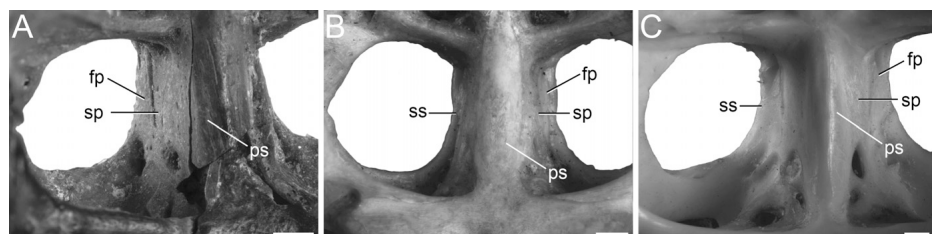
The frontoparietals are indistinguishably fused to each other, the nasals, and the squamosals. In the interorbital region, the margins of the frontoparietal are flush with that of the braincase formed by the sphenethmoid and prootic; thus, a supraorbital

shelf or flange is absent (Figs. 2D, 3A). The otic capsules are completely covered by the skull roof, and it is not possible to observe the extension or shape of the epiotic eminences (contra Tomassini et al., 2012).

As with other bones of the skull table, the synostosis of the squamosal obscures the exact margins of the element. Nevertheless, it is evident that an extensive part of the squamosal participates in the skull roof. The otic and zygomatic rami cannot be differentiated from one another. A well-developed otic plate is evident in the posterolateral portion of the skull. The occipital margin of the skull roof is broadly scalloped, but possesses a shallow indentation in the region of the frontoparietal-squamosal contact (Fig. 2A). This posterior margin is anterior to the level of the occipital condyles.

Premaxillae are not preserved, and the maxillae are incompletely preserved. The maxillary pars facialis is high. The dorsal portion of its anterior margin projects medially in a long process, the anterior process, which reaches the anterior wall of the nasal capsules (Fig. 2A). The labial surface of the pars dentalis also projects anteriorly in a process that would have overlapped the pars dentalis of the premaxilla. The margins of the oval subtemporal fenestra are well defined (Fig. 2A, D); no dermal ossification projects over the fenestra. In ventral view, the anterior margin of the maxilla has a notch at the level of the second maxillary tooth to accommodate the maxillary process of the

FIGURE 3. Detail of the contact of frontoparietal and sphenethmoid in selected Ceratophryidae (ventral view). **A**, *Lepidobatrachus australis* (MMH 85-12-2a); **B**, *L. llanensis* (FML 1016); **C**, *Ceratophrys cranwelli* (FML 5477). **Abbreviations:** fp, frontoparietal; ps, parasphenoid; sp, sphenethmoid; ss, supraorbital shelf. All scale bars equal 2 mm.



premaxilla (Fig. 4A). No discrete pars palatina can be discerned anterior to the subtriangular pterygoid process (Figs. 2D, 4A). A few broken teeth are preserved; their non-pedicellate condition cannot be established (contra Tomassini et al., 2012).

The ossification of the neurocranium extends far forward and includes the nasal capsules: anterior nasal wall, solum, tectum and septum nasi, pares naris, and planum antorbitale (postnasal wall + planum triangulare sensu Jurgens, 1971; Fig. 2D). Several pieces of dermal bone that might represent parts of a vomer seem to be present on the ventral surface of the right ossified pares naris. The robust planum antorbitale is oriented anterolaterally from the braincase and has a rounded ventral surface. The vestiges of the neopalatines bear a conspicuous odontoid ridge and are fused to the ossified planum antorbitale (Fig. 2D). The neopalatines terminate medially on the plana and do not reach the lateral walls of neurocranium. The ventral surface of the neurocranium in the orbital region is nearly flat (Fig. 2D). The sphenethmoid, prootic, exoccipital, and parasphenoid are synsotically united. The size and shape of the parasphenoid can only be inferred from some differences in texture and coloration from adjacent bones (contra Tomassini et al., 2012). The anterior terminus of the cultriform process of the parasphenoid seems to lie beyond the planum antorbitale. The cultriform process in the region of the optic fenestra is badly damaged; however, the presence of a pair of symmetrical constrictions at its base suggests that the lateral margins of the bone are entirely preserved (Fig. 2D). The flat ventral surface of the parasphenoid in this region is broad.

The left pterygoid is incompletely preserved; the bony cortex of an important part of the anterior ramus and all the posterolateral margin of the bone are missing. Thus, the shape of the anterior ramus and the presence of a ventral process cannot be evaluated (contra Tomassini et al., 2011). The absence of a discernable pars palatina on the maxilla anterior to the pterygoid process suggests that the anterior ramus of pterygoid extended anteriorly and fused with the pars palatina as it does in *Ceratophrys* (Figs. 2D, E; 4A, C). The medial ramus is long and in contact with the parasphenoid ala.

On the occipital aspect of the skull, the bony extension of squamosal and pterygoid completely occludes the suprapterygoid fenestra sensu Tihen (1962). Only the left condyle is preserved but seems to reach the midline, suggesting that condyles were narrowly separated from one another.

## DISCUSSION

### Taxonomic Attribution of *Lepidobatrachus australis*

A series of non-exclusive osteological synapomorphies have been proposed for Ceratophryidae (Fabrezi, 2006; Fabrezi and Quinzio, 2008). Those corresponding to the known skeletal regions of the examined fossil specimen are also present in *Lepidobatrachus australis*: skull exostosis, presence of a parietosquamosal arch, zygomatic ramus of squamosal in contact with the maxilla, and otic ramus of squamosal expanded and overlapping the prootic (Fig. 2A–C). Ceratophryidae also lacks a discrete pars palatina on the premaxilla and the

anterior portion of the maxilla; although the pars palatina is present in early developmental stages, it projects dorsally during ontogeny and fuses with the ventral surface of the corresponding pars facialis or other surrounding bones (Figs. 2E, F; 4B, C; 5). In published phylogenetic analyses, this exclusive feature of Ceratophryidae has been only evaluated in the premaxilla (Baez et al., 2009, char. 16) together with the presence or absence of a discrete palatine process (Fabrezi, 2006, char. 14; Fabrezi and Quinzio, 2008, char. 70). Although the premaxillae of *L. australis* are not preserved, the maxillae lack a discrete pars palatina (Figs. 2D; 4A).

The few synapomorphies proposed for the different ceratophryid genera (Fabrezi, 2006; Fabrezi and Quinzio, 2008) are not in the skull regions preserved in *L. australis*. *Lepidobatrachus australis*, however, agrees with the extant species of *Lepidobatrachus* in a series of characters that could be synapomorphies of the genus. These include the presence of (1) small, round orbits located at the mid-length of the skull (vs. small, round orbits located posterior to the mid-length of the skull in *Ceratophrys*; in *Chacophrys* and other close relatives, orbits are neither round nor small); (2) robust, hourglass-shaped maxillary processes of the nasals (vs. a robust bar of uniform width in *Ceratophrys* and a slender, sharp process in *Chacophrys* and the other close relatives when this process is present); (3) nasal-frontoparietal articulation perpendicular to midline (vs. oblique in *Ceratophrys*, *Chacophrys*, and the other close relatives when this contact is present); (4) squamosal and frontoparietal in broad contact without forming a postorbital fenestra (present in *Ceratophrys*; in *Chacophrys* and other relatives, squamosal and frontoparietal lacking broad contact); and (5) anterior terminus of parasphenoid anterior to the level of the planum antorbitale (vs. at the level of the planum antorbitale in *Ceratophrys* and *Chacophrys* and posterior to it in close relatives).

There is enough evidence to consider *L. australis* a representative of the extant genus *Lepidobatrachus*. However, it differs from *Lepidobatrachus* and agrees with *Ceratophrys* and *Chacophrys* in the absence of a discrete maxillary pars palatina (Figs. 2D–F; 4). In all ceratophryids, the dorsally directed pars palatina of the maxilla articulates anteriorly with the pars palatina of the premaxilla and is fused with the pars facialis and the ossified pares naris (Figs. 2E, F; 4B, C). Although the pars palatina is also fused with the surrounding bones in the posterior region of the maxilla in *Ceratophrys* and *Chacophrys* (and *L. australis*), this is not the case in extant species of *Lepidobatrachus* (Figs. 2D–F; 4). The posterior end of the pars palatina is modified into a bar-shaped pterygoid process that projects posteromedially in the extant species of *Lepidobatrachus* (Figs. 2E; 4B; 5A). The anterior ramus of the pterygoid articulates (and fuses) with the pars palatina via this process (Figs. 4B; 5A). A discrete, dorsally directed pars palatina forms a groove with the pars facialis of the maxilla between the pterygoid process and the planum antorbitale (Figs. 2E; 4B). In contrast, the pterygoid processes of *Ceratophrys* and *Chacophrys* are subtriangular (Fig. 5B). The anterior ramus of the pterygoid extends

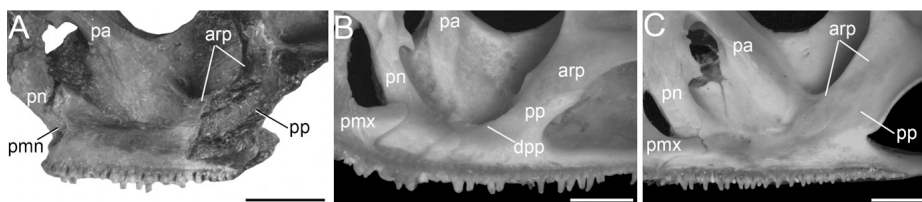


FIGURE 4. Detail of the maxillae of selected Ceratophryidae (lingual view). **A**, *Lepidobatrachus australis* (MMH 85-12-2a); **B**, *L. llanensis* (FML 5221); **C**, *Ceratophrys cranwelli* (FML 5477). **Abbreviations:** arp, anterior ramus of pterygoid; dpp, discrete maxillary pars palatina; pa, planum antorbitale; pmn, notch that would receive the maxillary process of the premaxilla; pmx, premaxilla; pn, pares naris ossification; pp, maxillary pterygoid process. All scale bars equal 5 mm.

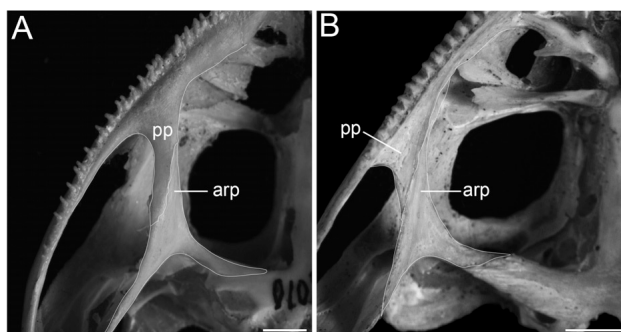


FIGURE 5. Detail of the contact of the maxillary pterygoid process and the anterior ramus of the pterygoid in juvenile Ceratophryidae (ventral view). Given the hyperossified skull of adult Ceratophryidae, it is useful to analyze the bone relationships in juvenile specimens. The margins of the detailed structures are highlighted. **A**, *Lepidobatrachus llanensis* (FML 1089); **B**, *Ceratophrys ornata* (FML 1193). **Abbreviations:** arp, anterior ramus of pterygoid; pp, maxillary pterygoid process. Both scale bars equal 3 mm.

anteriorly to fuse with the pars palatina of the maxilla up to the level of the anterior margin of the neopalatines (Figs. 2F; 4C; 5B). Thus, a discrete pars palatina is absent also between the pterygoid process and the planum antorbitale (Figs. 2F; 4C). Although parts of the anterior ramus of the pterygoid and the distal portion of the pterygoid process of *L. australis* are damaged, the well-preserved region evidences a subtriangular pterygoid process and the absence of a discrete pars palatina between the pterygoid process and the planum antorbitale (presumably because of the fusion of pars palatina and the anterior ramus of pterygoid as it occurs in *Ceratophrys*; Figs. 2E; 4A).

In addition, *Lepidobatrachus australis* lacks a supraorbital flange; the frontoparietals do not extend laterally beyond the neurocranial walls (Figs. 2D; 3A) as they do in all other ceratophryids (Figs. 2E, F; 3B, C). In other ceratophryids, the lamina perpendicularis of the frontoparietal, which is flush with the neurocranial wall, is separated from the orbital margin of the bone, forming a shelf between the neurocranial wall and the orbit (Fig. 3B, C). This condition is observed even in juvenile and poorly ossified ceratophryids (e.g., *C. ornata* FML 1193; *C. pierotti* FML 1019; *L. asper* FML 2569; *L. llanensis* FML 1089). This supraorbital flange is absent in most close relatives of ceratophryids except some Odontophryinidae (e.g., *Proceratophrys*, *Macrogenioglottus*); thus, presence of a supraorbital flange could be a ceratophryid synapomorphy that was reversed in *L. australis*.

Among *Lepidobatrachus*, *L. australis* differs from *L. laevis* in the presence of a shallow indentation in the occipital margin of the skull roof (vs. straight occipital margin of skull roof in *L. laevis*). In the same way, the ventral surface of the robust planum antorbitale in *L. asper*, *L. australis*, and *L. llanensis* is slightly rounded, whereas in *L. laevis*, the planum is slender and angular.

In conclusion, *Lepidobatrachus australis* has a unique combination of characters indicative of a new species. It is attributed to *Lepidobatrachus* owing to its possession of nearly all the morphological synapomorphies of the genus except two. *Lepidobatrachus australis* lacks a bar-shaped pterygoid process of the maxilla and a discrete dorsally directed pars palatina along the maxilla between the pterygoid process and the level of the planum antorbitale; these features are shared with members of *Ceratophrys* and *Chacophrys*. At the same time, *L. australis* differs from all other ceratophryids in the absence of a supraorbital shelf.

### On the Attribution of the *Lepidobatrachus* from FMH to *L. laevis*

Tomassini and collaborators (2011) attributed *Lepidobatrachus australis* to *L. laevis* because it possesses (1) a wide, robust anterior ramus of the pterygoid (Peri, 1993b); (2) a posterior subtemporal notch that is poorly ornamented; and (3) a large and elongate posterolateral fenestra; in addition, (4) it lacks a well-developed pterygoid process of the medial surface of the maxilla (Peri, 1993b).

It is difficult to evaluate the condition of the anterior ramus of the pterygoid from drawings and photos. Based on examination of comparative material, I observed that the anterior pterygoid ramus is wide and robust in all ceratophryids, but it is wider in *Lepidobatrachus laevis* and the species of *Ceratophrys* than in *Chacophrys*, *L. asper*, and *L. llanensis*. The preservation of the anterior pterygoid ramus of *L. australis* (described above) prevents evaluation of its shape; however, the preserved portion is neither wider nor more robust than that of *L. asper* and *L. llanensis*.

In the comparative description of the fossil from FMH provided by Tomassini et al. (2011), the ‘posterior subtemporal notch’ refers to the supratemporal fenestra (sensu Lynch, 1971) present in *Ceratophrys*. Like all *Lepidobatrachus*, *L. australis* lacks a supratemporal fenestra; instead, it has a smooth area in the postorbital region, presumably representing the synostosis of the squamosal and frontoparietal—a condition also observed in several specimens of the extant species of *Lepidobatrachus* (e.g., *L. laevis* FML 13703; *L. llanensis* FML 5220, 1010; *L. asper* FML 5469)—and seemingly a normal variation in the development of the dermal ornamentation.

The condition of the posterolateral fenestra was attributed to Reig and Cei (1963; following Vellard, 1948) who considered *L. asper* and *L. laevis* a single species (*L. asper*). Consequently, the ‘large and elongate posterolateral fenestra’ described the condition of both species; this was confirmed in the available material for comparisons (Appendix 1).

The condition of the pterygoid process must have been misinterpreted, because all ceratophryids possess a well-developed pterygoid process on the maxilla (as was also described by Peri, 1993b).

### Environmental Interpretations of FMH and Significance of the Presence of *Lepidobatrachus*

During the middle Miocene, an Atlantic marine transgression, informally named the Paranean Sea, flooded the South American Chaco-Pampean region. After the regression of that sea in the late Miocene–early Pliocene, the development of widespread continental plains characterized a period recognized as ‘the Age of the Southern Plains’ (Pascual and Bondesio, 1982; Pascual et al., 1996). During this time, the Patagonian and principal South American cordilleras were successively uplifted, an ice cap was developed in eastern Antarctica, and ocean temperatures fell approximately 4°C (Pascual et al., 1996; Ortiz-Jaureguizar and Cladera, 2006). Consequently, the climate of austral South America began to cool down and seasonality became more marked than in the middle Miocene, with more environmental diversity (Pascual et al., 1996; Ortiz-Jaureguizar and Cladera, 2006).

Unfortunately, no paleobotanical evidence of this period is available from the region. Paleoenvironmental conditions used to be inferred from the analysis of the putative habits of the faunal content. In this way, the Neogene environment of FMH and the surrounding region were thought to resemble that of the extant South American Chacoan region (Chani, 1976; Pascual, 1984; Scillato-Yané, 1986; Pascual et al., 1996; Ortiz-Jaureguizar and Cladera, 2006; Tomassini et al., 2011). However, whereas

some of these paleoecological inferences seem to be justified, others are questionable.

The extant South American Gran Chaco has a markedly seasonal regime with relatively low average rainfall, with vegetation principally consisting of semiarid forests and woodlands (Ab' Saber, 1977; Prado, 1993; Cabrera, 1994). Cariamid birds collected in FMH and attributed to an extinct species of *Chunga* seem to indicate a seasonal, dry, open environment given the distribution of its extant species (Tonni, 1974; Gonzaga, 1996). Similarly, lizard remains from FMH were considered representative of a fossil species of the extant genus *Callopistes* (Chani, 1976). This genus is currently restricted to arid and semiarid environments from southern Ecuador to central Chile, west of the Andes (Chani, 1976; Krause, 1985; Albino and Brizuela, 2009); however, *Callopistes* does not have a northern Argentine distribution as reported by Tomassini et al. (2011).

In contrast, the paleoecological significance of a series of other species from FMH, also considered to be indicators of chacoan environment (Chani, 1976; Pascual, 1984; Scillato-Yané, 1986; Pascual et al., 1996; Ortiz-Jaureguizar and Cladera, 2006; Tomassini et al., 2011), is more problematic. These include a bufonid toad considered to be closely related to *Rhinella schneideri* (= *Bufo paracnemis* of Báez, 1986), a snake with doubts assigned to the Boinae genus *Boa* (Albino, 1992), anteaters attributed to an extinct species of the extant genus *Myrmecophaga* (Scillato-Yané, 1986; McDonald et al., 2008), and some fossil hystricognathi of the Echimyidae (*Eumysops* and *Paramyocastor*) and Dinomyidae (*Telicomys*) clades (Verzi et al., 2002; Deschamps et al., 2012; Olivares et al., 2012; Tomassini et al., 2013).

*Rhinella schneideri* has a wide distribution in South America that largely exceeds chacoan limits, including wetlands, Cerrado, and Atlantic Forest (Ceí, 1980; Frost, 2014). Similarly, the extant genus *Boa* has an extremely wide American distribution, occurring in a great variety of environmental conditions, demonstrating an ample tolerance of a wide range of altitudes, rainfall, and temperatures (Albino, 1992; Henderson et al., 1995). Living *Myrmecophaga* are broadly distributed in Central and South America; in addition to the Gran Chaco, members of this genus are found in tropical moist forest, dry forest, savanna habitats, and open grasslands (Miranda and Medri, 2010).

Among hystricognathi Echimyidae, the sister taxon of *Eumysops*, the living ground-dwelling *Thrichomys* is found in bushlands of the cerrado and the pantanal (Fabre et al., 2012; Verzi et al., 2014). *Paramyocastor* is closely related to the extant coypu *Myocastor* (Verzi et al., 2002), a large, herbivorous, semi-aquatic rodent with a broad native distribution in South America south of 23° S latitude (Carter and Leonard, 2002). The single living species of Dinomyidae, *Dinomys branickii*, is a poorly known, herbivorous, medium-sized rodent that inhabits humid forested areas of the eastern Andes in northwestern South America (Saavedra-Rodríguez et al., 2012). Dinomyidae, however, has an enormous extinct diversity, the paleoecological significance of which is unknown (Rinderknecht et al., 2011).

An exhaustive analysis of the paleoecological significance of the extensive fossil fauna of the FMH far exceeds the goals of this paper. It seems evident, however, that its significance and the reconstruction of the paleoenvironment of FMH during the late Neogene should be revisited. Moreover, the presence of a high biomass of varied grazing herbivores has been considered evidence of a wetter grassland environment in that area than in the modern Chaco (Pascual, 1984; Pascual et al., 1996). Additionally, the giant fossil turtle *Chelonoidis australis* present in FMH is thought to have required permanent water, forested areas with shadow, and a temperate climate for thermoregulation, given its supposed inability to hibernate (Gasparini et al., 1986).

Despite the fact that *Lepidobatrachus* is currently restricted to the South American Chacoan region (sensu Cabrera, 1994; Faivovich, 1994; Brusquetti and Lavilla, 2006; Moreira Sugai

et al., 2013), it is important to remember that the Chaco is quite extensive (Fig. 1) and characterized by a variety of environmental conditions (Prado, 1993). Although the whole region has a markedly stationary regimen, with cold and dry winters and hot and rainy summers, there are strong intraregional differences in the lengths of the wet-dry seasons, the temperature ranges, and the rainfall (Ab' Saber, 1977; Prado, 1993; Cabrera, 1994). Thus, the Chaco is primarily characterized by xeric forests, but also contains savannahs, palm groves, scrublands, and halophytic steppes (Prado, 1993; Cabrera, 1994). Consequently, *Lepidobatrachus* ranges from the arid xeric forests in La Rioja Province in the west (*L. llanensis*; Faivovich, 1994; fig. 1), with annual rainfall of about 350 mm, to the humid river margin forest in Santa Fe Province in the east (*L. laevis* and *L. asper*; Faivovich, 1994; fig. 1), with about 1000 mm annual rainfall. This ecological amplitude should be kept in mind when interpreting the presence of *Lepidobatrachus* at Farola Monte Hermoso during the Pleistocene as evidence of the paleoenvironmental conditions of this locality.

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APPENDIX 1. Specimens examined for comparisons. Most specimens are cleared-and-stained; dry skeletons are noted with an asterisk. Fossils denoted with a †.

*Alsodes gargola* MACN 37845, 37930, 37951, 38942.

*Atelognathus patagonicus* CENAI 1070–1; *A. reverberii* MACN 33973; *A. salai* MACN 41327.

*Batrachyla antantardica* BB2143; *B. leptopus* MACN 38006, 41291; *B. taeniata* CENAI 6865–6, 6921.

*Calyptocephalella gayi* MACN 45741–3\*.

*Ceratophrys ameghinorum*† MACN 14317–9, 14324–5, 19731, MLP 52-IX-27-11, 88-VII-20-1–2; MMH 84-1-15, 85-2-11; *C. calcarata* AMNH 177036\*; *C. cranwelli* MLP 273\*; FML 5472\*, 5474–7\*; *C. ornata* MLP 137\*, 247\*, FML 1193\*.

*Chacophrys pierotti* FML 1019, 9012.

*Crossodactylus schmidti* MACN 35122.

*Eupsophus calcaratus* MLP 4011; *E. roseus* MACN 37976, 37979, 37981; *E. vertebralis* MACN 43704\*.

*Hymenochirus boettgeri* MACN 42621.

*Insuetophrynus acarpicus* CENAI 6896.

*Lepidobatrachus asper* FML 5469\*-70\*; *L. laevis* FML 13703\*-4\*, 13709\*, 1089\*; *L. llanensis* CENAI 8519, FML 420\*, 1016\*, 5220–1\*, 1089\*.

*Limnomedusa macroglossa* MACN 4644, MLP 1410.

*Macrogenioglottus alipioi* CFBH 4261\*.

*Odontophrynus achalensis* CENAI 2972, 2975, 2977; *O. americanus* CENAI 3938–9, 3939, 3942, MACN 25236, 25237; *O. carvalhoi* MNRJ 15358; *O. cordobae* CENAI 4522, MACN 26199; *O. cultripes* CENAI 9839, 9841; *O. occidentalis* MACN 24953, 26228, 26229; MLP 4385, 3916; *O. lavillai* CENAI 5811, 6461, 5794, 6465; *O. maisuma* MLP 4828, ZVCB 1517; *O. salvatori* MNRJ 27756.

*Proceratophrys appendiculata* CENAI 9064; *P. avelinoi* MACN 36854, MLP 938; *P. boiei* MLP 76. *P. cristiceps* MNRJ 15358.

*Rhinella major* MACN 45955.

*Rhinoderma darwini* CENAI 5491. *Telmatobius bolivianus* CBF 2063, 5379; *T. oxycephallus* FML 2867, 3836; *T. marmoratus* CBF 2167, 3621, KU 164079–80\*; *T. rubigo* FML 20829; *T. verrucosus* CBF 2765, 5372.