Journal of Vertebrate Paleontology 31(5):1005–1009, September 2011

ARTICLE

FIRST FOSSIL RECORD OF THE GENUS *LEPIDOBATRACHUS* BUDGETT, 1899 (ANURA, CERATOPHRYIDAE), FROM THE EARLY PLIOCENE OF ARGENTINA

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ABSTRACT—The first fossil occurrence of the genus *Lepidobatrachus* is reported. The specimen comes from the Farola Monte Hermoso locality (Buenos Aires Province, Argentina), more specifically from the early Pliocene levels of the Monte Hermoso Formation. The specimen belongs to the living species *L. laevis*, a frog that currently inhabits the Chacoan region of northern Argentina, Paraguay, and Bolivia. The presence of this anuran represents the southernmost record for the genus *Lepidobatrachus*, and is in agreement with previous hypothesis suggesting that during the Pliocene the climatic environmental conditions of the southern Pampas were likely those of the modern Chacoan region. The disjunct distribution of extant *L. laevis* suggests that the retraction of Chacoan areas to the north modified the former distribution of this taxon, and that its current geonemy may represent relics of a formerly more extensive geographic distribution.

INTRODUCTION

The Ceratophryidae is a peculiar group of living Neotropical anurans composed of medium- to large-sized frogs with short and stout proportions, small limbs, and a disproportionately large, dentate mouth (Cei, 1980). They are frequent inhabitants of desert or semi-desert areas, and are capable of burrowing into the ground during the dry season and forming skin cocoons in order to reduce water loss (Wells, 2007). Their enormous heads, wide mouths, and large buccal cavities for ingesting large prey allow ceratophryids to feed mainly on meat, specially invertebrates, birds, and small mammals. They frequently eat other frogs and toads, and occasional cannibalistic behavior has also been reported (Cei, 1968; Scott and Aquino, 2005).

The Ceratophryidae is represented by three living genera: the monotypic genus *Chacophrys*, *Ceratophrys*, represented by eight species, and *Lepidobatrachus*, the most derived member of the group. This latter genus is composed of the species *L. laevis*, *L. asper*, and *L. llanensis*, which are distributed in the Chacoan region of Argentina, Bolivia, and Paraguay (Reig and Cei, 1963; Peri, 1993; Frost et al., 2006; Wells, 2007).

The fossil record of Ceratophryidae is relatively meager and patchy, being represented by the Late Cretaceous Malagasy extinct genus *Beelzebufo ampinga* (Evans et al., 2008) and *Baurubatrachus pachecoi* Báez and Perí, 1989, from the Late Cretaceous of Brazil. The Tertiary record of this family is also biased, being represented in the Paleogene by an indeterminate ceratophryid from the Oligocene of Patagonia (Agnolin, 2005) and a probable ceratophryid, *Thaumastosaurus*, from the Eocene of France and England (Rage and Rocek, 2007). From the Miocene of Patagonia, the extinct *Wawelia gerrholdi* (Casamiquela, 1963; Báez and Perí, 1990) and other ceratophryid remains have been reported (Fernicola and Vizcaíno, 2006). From the late Miocene to Pleistocene, the fossil ceratophryid record is better (Contreras and Acosta, 1998; Fernicola, 2001; Agnolin, 2005). However, most specimens are referable to the living genus *Ceratophrys*; we are still lacking reports of the other ceratophryid genera.

In the lower–middle Pliocene Monte Hermoso Formation (Zavala, 1993), the anuran record is very patchy, being represented by the bufonid *Rhinella* cf. *R. schneideri* (Gasparini and Báez, 1974) and the extinct ceratophryid species *Ceratophrys ameghinorum* (Fernicola, 2001). In the present contribution we report for the first time a fossil specimen referable to the living genus *Lepidobatrachus* (MMH-FMH 85-12-2a), from the type locality of the Monte Hermoso Formation, Farola Monte Hermoso. This record constitutes a considerable expansion of the biochron for the genus, extending it to the beginning of the Pliocene.

Institutional Abbreviation—MMH-FMH, Museo Municipal de Ciencias Naturales de Monte Hermoso (Monte Hermoso, Buenos Aires Province, Argentina), Farola Monte Hermoso collection.

GEOGRAPHIC AND STRATIGRAPHIC CONTEXT

Farola Monte Hermoso (39°00′30″S; 61°30′10″W) is located on the Atlantic coast, approximately 53 km from Bahía Blanca city and 12 km southwest of Pehuen Có Beach (Buenos Aires Province, Argentina: Fig. 1). This locality was studied by numerous authors (e.g., Darwin, 1846; Ameghino, 1887; Bonaparte, 1960), who described the diversity and abundance of vertebrate fossil remains present. In addition, Farola Monte Hermoso constitutes the type locality of the Monte Hermoso Formation (lower–middle Pliocene: Zavala, 1993) and of the Montehermosan and Lower Chapadmalalan Stage/Age, corresponding to the late Miocene–early Pliocene and early Pliocene, respectively (Cione and Tonni, 2005).

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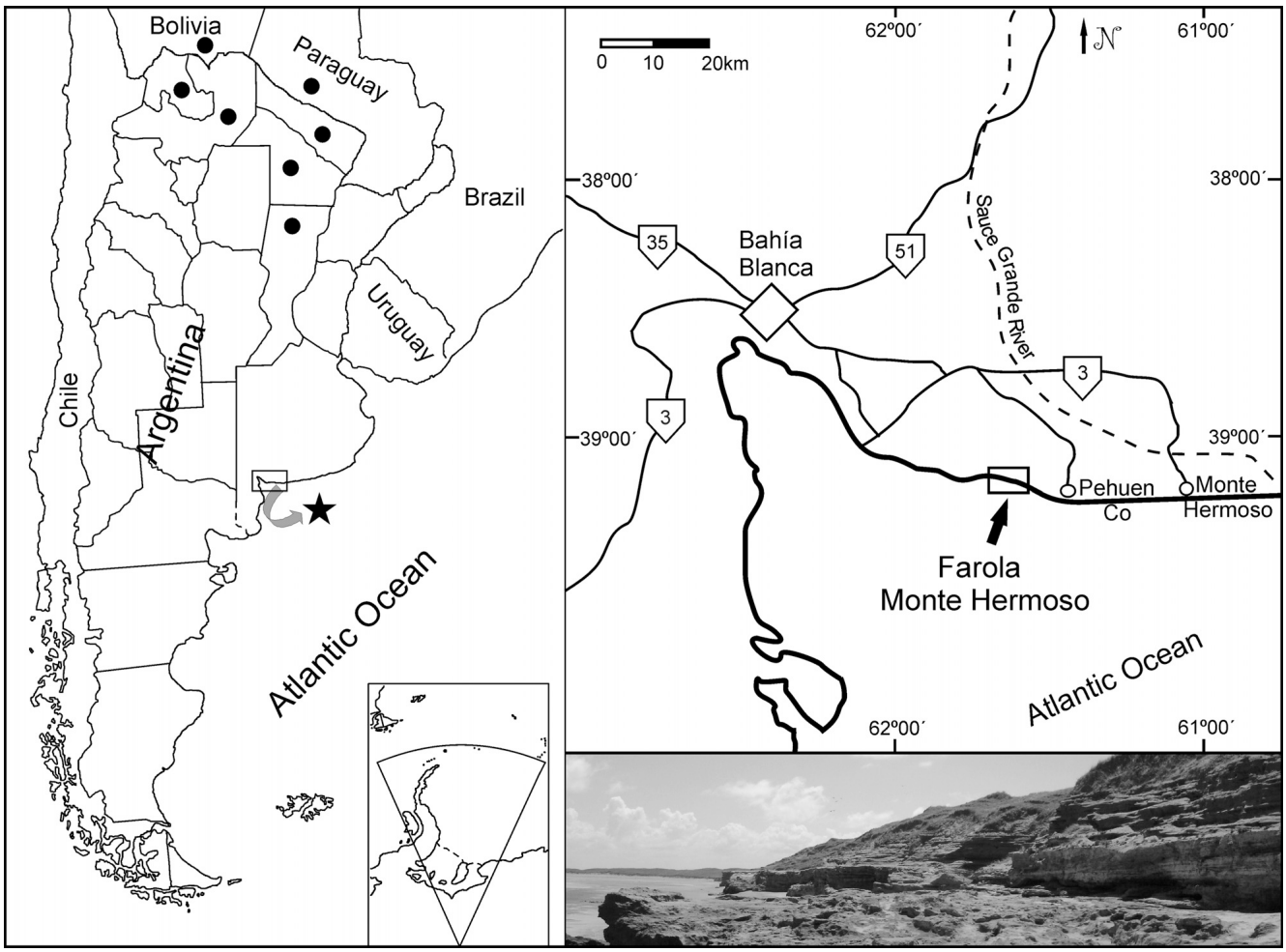

FIGURE 1. Location map of Farola Monte Hermoso locality. The circles represent the current distribution of *Lepidobatrachus laevis* and the star represents the fossiliferous locality.

The Monte Hermoso Formation is composed of deposits that represent floodplain and fluvial channel sub-environments (Zavala and Navarro, 1993). The specimen studied (MMH-FMH 85-12-2a) comes from a bed constituted of conglomerate sandstones and breccias, which correspond to lag-channel deposits. This bed is included in the *Neocavia depressidens* Biozone, which constitutes the biostratigraphic basis of the Stage/Age Lower Chapadmalalan (early Pliocene: Cione and Tonni, 2005).

SYSTEMATIC PALEONTOLOGY

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

Type Species—*Lepidobatrachus laevis* Budgett, 1899.

LEPIDOBATRACHUS LAEVIS Budgett, 1899

Referred Specimen—MMH-FMH 85-12-2a, nearly complete cranium, lacking the left posterior half, premaxillae, quadrates, and posterior halves of both maxillae.

Description—Anteroposteriorly short and transversely wide akinetic skull, with extensive fusion of cranial bones. Frontoparietal, maxilla, squamosal, and nasal showing extensive tuberculate exostotic ornamentation, as diagnostic of most ceratophryids (Lynch, 1971). Both nasal and frontoparietal bones have attenuated external ornamentation along the midline. The frontoparietals are sub-rectangular in contour, and firmly fused to each other and with nasals. The nasals are sub-triangular in shape, showing a gently concave lateral margin.

The maxillae show strong nasal ascending processes (Fig. 2A, C), and although they are not well preserved, what is present indicates that they are rather similar to those of *Lepidobatrachus laevis*. As in all known ceratophryids, the maxillae carry a large number of acute and non-pedicelate teeth (Reig and Limeses, 1963; Fabrezi, 2001). The alveolar margin of the maxilla is devoid of external exostotic ornamentation (Fig. 2C). The medial palatal process of the maxillae is reduced, as occurs in all Ceratophryidae (Lynch, 1971). The maxilla is separated from the orbit by the nasals and squamosal. The otic plate of the squamosal is medially expanded and sub-quadrangular in shape, showing a rounded and weakly projecting external corner (Fig. 2A, E), as also occurs in *Lepidobatrachus* species (Reig and Cei, 1963); this contrasts with *Ceratophrys* (*Stombus*) species, in which the otic plate forms an acute and pointed process (Agnolin, 2005), and from *Chacophrys*, in which such a plate is absent (Peri, 1993). The posttemporal notch is mostly covered by exostotic bone and only remains as a poorly tuberculated zone (Fig. 2A), a condition that clearly distinguishes *Lepidobatrachus* from *Chacophrys* and *Ceratophrys*, in which the notch

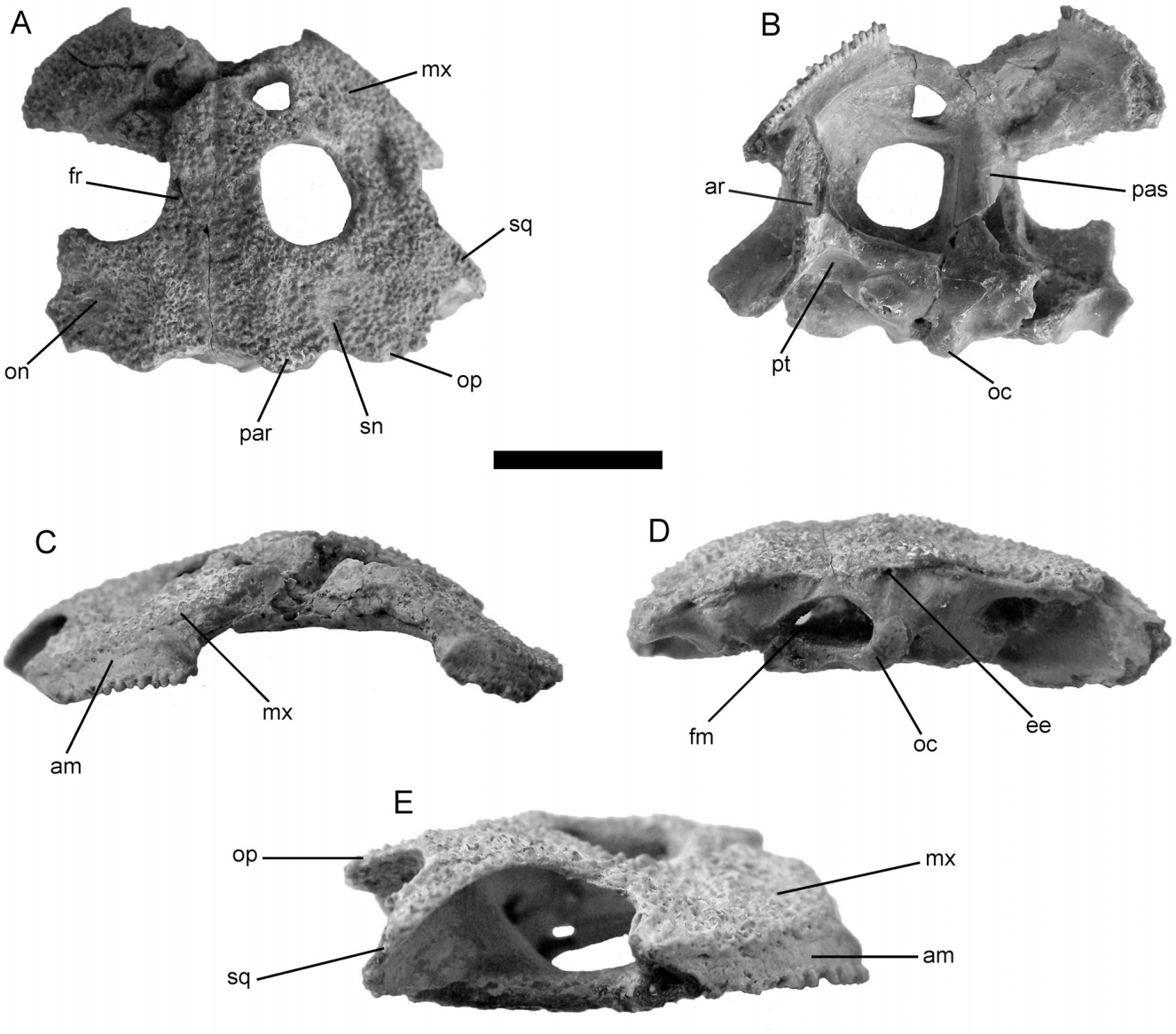

FIGURE 2. Skull of *Lepidobatrachus laevis* (MMH-FMH 85-12-2a). **A**, dorsal view; **B**, ventral view; **C**, anterior view; **D**, posterior view; **E**, lateral view. **Abbreviations**: **am**, alveolar margin of maxilla; **ar**, anterior ramus of the pterygoid bone; **ee**, epiotic eminence; **fm**, foramen magnum; **fr**, frontal; **mx**, maxilla; **oc**, occipital condyle; **on**, otic notch; **op**, otic plate; **par**, parietal; **pas**, parasphenoid; **pt**, pterygoid; **sn**, subtemporal notch; **sq**, squamosal. Scale bar equals 1 cm.

is evident and free of exostotic ornamentation (Lynch, 1971; Fernicola, 2001). The posterior ramus of the squamosal is incomplete, but appears not to be strongly directed backwards (Fig. 2A, E). The lateroposterior fenestra is very large and anteroposteriorly elongate.

In ventral view (Fig. 2B), the skull is similar to that of extant *Lepidobatrachus* species. It shows a robust parasphenoid rostrum, with a very wide base that is very different from the thin and delicate structure seen in other ceratophryid species, such as *Ceratophrys ameghinorum* (Fernicola, 2001). The pterygoid shows a wide and strong anterior ramus, a condition resembling *Ceratophrys* and *L. laevis*, but very different from the delicate and rod-like structure seen in other *Lepidobatrachus* and *Chacophrys* species (Peri, 1993).

In posterior view (Fig. 2D), the skull shows a subdivided occipital condyle. The foramen magnum is large and ovoid in contour. The jugular foramen is relatively well developed and lies ventrolateral to the occipital condyle. The foramen for the carotid artery is smaller and is located above the occipital condyles, just below the posterior margin of the frontoparietals. The epiotic eminences are minute, much smaller than in *Ceratophrys* and *Chacophrys* species (Lynch, 1982; Peri, 1993).

DISCUSSION

MMH-FMH 85-12-2a is here referred to the Ceratophryidae on the basis of the following synapomorphies: (1) robust skull, which is sub-triangular in outline when viewed dorsally; (2) non-pedicelate, ankylosed, and strongly calcified teeth; (3) extreme exostosis in the bones of the skull, which are strongly ornamented by tubercles; (4) reduced palatal shelf on maxillae; (5) maxillae excluded from the orbital margin; and (6) nasals

widely contacting each other (Lynch, 1971, 1982; Peri, 1993; Rage and Rocek, 2008). Moreover, within ceratophryids, MMH-FMH 85-12-2a may be referred to *Lepidobatrachus* by the presence of the following apomorphies: (1) parasphenoid rostrum robust and anteriorly extended; (2) dorsal surface of squamosal and frontoparietal bones transversely expanded; (3) otic plate of the squamosal sub-rectangular in shape, well extended medially; (4) reduced epiotic eminences; and (5) reduced posttemporal notch (Reig, 1960; Reig and Cei, 1963; Lynch, 1971, 1982; Peri, 1993).

From the same locality and stratigraphic unit where MMH-FMH 85-12-2a was found, the extinct ceratophryid *Ceratophrys ameghinorum* is recorded as a rather common species (Fernicola, 2001). However, MMH-FMH 85-12-2a is clearly distinguishable from this species on the basis of many features (see above), and also on the different shape of the otic plate, which in *C. ameghinorum* is transversally narrower, and has an external corner that is acute, sub-triangular in contour, and dorsally oriented. In contrast, in MMH-FMH 85-12-2a, as in remaining *Lepidobatrachus* species, this plate is transversely wide, medially extended, and shows a weakly projecting and rounded external corner (see Peri, 1993; Fernicola, 2001).

Within *Lepidobatrachus*, MMH-FMH 85-12-2a is referred to the extant species *L. laevis* because of the very wide and robust anterior ramus of the pterygoid, an autapomorphy of this species, convergently acquired with the genus *Ceratophrys* (Peri, 1993). In addition, the fossil specimen resembles *L. laevis* in the retention of a posterior subtemporal notch as a poorly ornamented area, and of a very large and elongate posterolateral fenestra (Reig and Cei, 1963). In contrast, *L. llanensis* shows a very ornamented skull with a reduced fenestra and subtemporal notch (Reig and Cei, 1963; Peri, 1993). *L. laevis* further differs from *L. asper* Budgett, 1899 and *L. llanensis* Reig and Cei, 1963, in lacking a well-developed pterygoid process of the medial surface of the maxilla (Peri, 1993).

Lepidobatrachus laevis is a poorly known ceratophryid species, currently distributed as disjunct populations in poorly vegetated areas, swamps, and lagoons, alongside Chacoan rivers from north-central to northeastern Argentina, Bolivia, and Paraguay (Cei, 1980; Peri, 1993; De La Riva et al., 2000; Fig. 1). This taxon is restricted in its geographic distribution, in selected zones within the Chacoan Phytogeographic and Zoogeographic District, being a species characteristic of the Septentrional Chaco (Reig and Cei, 1963). This district is included within the Dry Subtropical Climatic Region, which has a highly continental climate with a low percentage of atmospheric humidity, and intense solar radiation. The mean annual temperature oscillates between 20°C and 23°C and the rainfall, mainly in the summer season, varies between 500 mm in the west to 1200 mm in the east (Barrio, 1968; Prohaska, 1976).

Because *Lepidobatrachus laevis* is clearly a Chacoan endemic (Reig and Cei, 1963), its presence in southern Buenos Aires Province is unexpected, being more than 1000 km south of its current geographical distribution (Fig. 1). The locality of Farola Monte Hermoso is actually located at the Pampean Phytogeographic and Zoogeographic District (Cabrera and Willink, 1980). This district was considered by Ringuelet (1961) as a large ecotone that shared considerable similarities with northern Chacoan realms, currently representing a depauperate Chacoan District. This author suggested that in Pliocene times, the Argentine Pampas environment may have been very similar to Chaco woodlands, and since the Pliocene, the Chacoan faunistic influence diminished. Probably, the late ingression of more southern lineages coming from Patagonia, when the climate becomes more rigorous in Pleistocene times, displaced the strong Chacoan faunistic influence from the Pampas (Ringuelet, 1961).

In fact, there are several fossil specimens collected in the Monte Hermoso Formation that support Ringuelet's (1961) hypothesis of more widely expanded Chacoan faunas in the Pliocene. These include the presence of the typically Chacoan mammalian anteaters (Vizcaíno et al., 2006), tropical and subtropical rodents of the families Echimyidae and Dinomyidae (Pascual et al., 1996), and cariamid birds (Tonni, 1974), which are currently restricted to wooded areas from the Chaco and central Argentina (Olrog, 1963). On the basis of these faunas, several authors (e.g., Pascual, 1984; Pascual et al., 1996; Tonni, 1974) suggested that the Farola Monte Hermoso locality, during the Pliocene, exhibited a warmer climate, being covered by wooded xeric areas, as occurs today in the Chacoan region, but probably with greater humidity. The same applies to the presence of a boid snake, closely related to the genus *Boa* (Albino, 1992), and a fossil lizard related to a northern Argentina species (*Callopistes bicuspidatus*; Chani, 1976).

Ringuelet's hypothesis is also supported by the anuran fossil record, with the presence of typical subtropical taxa, such as *Rhinella* cf. *R. schneideri* in Pliocene sediments from the same locality (Gasparini and Báez, 1974). In the same way, the abundance of *Ceratophrys ameghinorum*, a species closely related to living taxa currently distributed in northern South America and the Amazon region, also points to more humid and warmer environments (Peri, 1993; Agnolín, 2005). To this meager list of taxa, we now add the species *Lepidobatrachus laevis*, a taxon endemic to and characteristic of the Chacoan region (Reig and Cei, 1963). In this way, the presence of *L. laevis* supports the existence of xeric wooded areas with temporary swamps in the early Pliocene of the southern Pampas.

As indicated above, since its original description, most studies regarding the distribution of *L. laevis*, as well as other *Lepidobatrachus* species, considered the disjunct distribution of this taxon to be the result of a formerly widely distributed species that restricted its geonemy due to habitat change and constraint (Cei, 1958, 1960; Reig and Cei, 1963). The presence of a fossil *L. laevis* in the southern Pampas agrees with such an interpretation. In fact, the species probably had a very wide geographic range in the Pliocene, but in post-Pliocene times, probably due to the climatic changes mentioned above, the species became restricted in its geographic distribution to more northern regions. With the consequent retraction of Chacoan areas to the north, the currently disjunct populations of *L. laevis* probably remain as relics of a formerly more extensive geographic distribution.

ACKNOWLEDGMENTS

The authors thank to the late V. Di Martino, ex-Director of the Museo Municipal de Ciencias Naturales de Monte Hermoso, for access to the material and comments on Farola de Monte Hermoso stratigraphy. We also thank Sergio Bogan for his comments on the fossil specimen, and for the loan of comparative material. Finally, we thank J. C. Rage and S. E. Evans for their enlightening comments on the manuscript.

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Submitted March 23, 2011; revisions received May 26, 2011; accepted June 8, 2011.

Handling editor: Jason Anderson.