

This article was downloaded by: [Universidad de Buenos Aires], [Celeste Pérez Ben]

On: 12 November 2013, At: 07:32

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Journal of Vertebrate Paleontology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/ujvp20>

Oldest record of *Leptodactylus* Fitzinger, 1826 (Anura, Leptodactylidae), from the early Pliocene of the South American Pampas

Raúl O. Gómez^{a b}, Celeste M. Pérez Ben^{a b} & M. Ignacio Stefanini^b

^a CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina

^b Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Buenos Aires, 1428, Argentina

Published online: 12 Nov 2013.

To cite this article: Raúl O. Gómez, Celeste M. Pérez Ben & M. Ignacio Stefanini (2013) Oldest record of *Leptodactylus* Fitzinger, 1826 (Anura, Leptodactylidae), from the early Pliocene of the South American Pampas, *Journal of Vertebrate Paleontology*, 33:6, 1321-1327

To link to this article: <http://dx.doi.org/10.1080/02724634.2013.771779>

PLEASE SCROLL DOWN FOR ARTICLE

Taylor & Francis makes every effort to ensure the accuracy of all the information (the "Content") contained in the publications on our platform. However, Taylor & Francis, our agents, and our licensors make no representations or warranties whatsoever as to the accuracy, completeness, or suitability for any purpose of the Content. Any opinions and views expressed in this publication are the opinions and views of the authors, and are not the views of or endorsed by Taylor & Francis. The accuracy of the Content should not be relied upon and should be independently verified with primary sources of information. Taylor and Francis shall not be liable for any losses, actions, claims, proceedings, demands, costs, expenses, damages, and other liabilities whatsoever or howsoever caused arising directly or indirectly in connection with, in relation to or arising out of the use of the Content.

This article may be used for research, teaching, and private study purposes. Any substantial or systematic reproduction, redistribution, reselling, loan, sub-licensing, systematic supply, or distribution in any form to anyone is expressly forbidden. Terms & Conditions of access and use can be found at <http://www.tandfonline.com/page/terms-and-conditions>

OLDEST RECORD OF *LEPTODACTYLUS* FITZINGER, 1826 (ANURA, LEPTODACTYLIDAE), FROM THE EARLY PLIOCENE OF THE SOUTH AMERICAN PAMPAS

RAÚL O. GÓMEZ,^{*,1,2} CELESTE M. PÉREZ BEN,^{1,2} and M. IGNACIO STEFANINI²

¹CONICET, Consejo Nacional de Investigaciones Científicas y Técnicas, Argentina;

²Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Buenos Aires 1428, Argentina, raulgomez@gl.fcen.uba.ar; cperezben@gl.fcen.uba.ar; nachostefanini@gmail.com

ABSTRACT—The Neotropical frog genus *Leptodactylus* is one of the most taxonomically diverse of all neobatrachian anurans. Despite the genus being highly diversified and widely distributed today, the fossil record is scanty and restricted to the Quaternary of the Neotropics. Here, we report and describe a new record of total group *Leptodactylus* from the Chapadmalalan (early Pliocene) of the South American Pampas. We evaluate both qualitative and quantitative characters and discuss the taxonomic value of body size in the context of living *Leptodactylus*. A number of features of the fossil elements suggests an affinity with the living species of the *L. latrans* species group and, particularly, with *L. latrans*. However, the lack of resolution of *Leptodactylus* interrelationships and, thus, the lack of osteological synapomorphies of the species groups and species within the genus conspire to force allocation of the fossils to crown *Leptodactylus* until they are studied in a rigorous phylogenetic context. In any case, the new material constitutes the oldest record of total group *Leptodactylus* and extends their stratigraphic range back to the early Pliocene.

INTRODUCTION

The frog genus *Leptodactylus* Fitzinger, 1826, composed of 81 extant species (AmphibiaWeb, 2012), is one of the most taxonomically diverse of all neobatrachian anurans. The genus is divided into four nominal species groups (*L. fuscus*, *L. melanonotus*, *L. latrans*, and *L. pentadactylus* groups) on morphological and behavioral grounds (Heyer, 1969; Maxson and Heyer, 1988). A fifth species group, the *L. marmoratus* group, is regarded by several authors as a separate genus, namely *Adenomera* (Heyer, 1974; Ponsa and Heyer, 2007; Kwet et al., 2009). Although there is still no consensus on interrelationships within *Leptodactylus*, recent phylogenetic studies agree in recovering these phenotypic species groups as essentially monophyletic (Ponsa, 2008; Heyer and de Sá, 2011; Pyron and Wiens, 2011).

Species of *Leptodactylus* are widely distributed in the Neotropics, occupying a variety of environments, from Texas to southern South America and the West Indies (CeI, 1980; AmphibiaWeb, 2012). In Argentina, 12 species representing all major groups of *Leptodactylus* are present in northern and central regions of the country, although only members of the *L. fuscus* (*L. mystacinus*, *L. gracilis*, and *L. latinasus*) and *L. latrans* (*L. latrans*) species groups are found in the Pampas (CeI, 1980; Lavilla et al., 2000).

Despite the genus *Leptodactylus* being highly diversified and widely distributed today, their fossil record is scanty and restricted to the Quaternary (Sanchiz, 1998). The aim of this paper is to report and describe the oldest known record of *Leptodactylus* from the South American Pampas, to discuss its systematic relationships, and to ponder its significance in the context of the known fossil record of the genus.

Institutional Abbreviations—**FCEN**, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina; **FML**, Instituto de Herpetología de la Fundación

Miguel Lillo, Tucumán, Argentina; **MACN**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; **MCN**, Museo de Ciencias Naturales, Universidad Nacional de Salta, Salta, Argentina; **MLP**, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina.

GEOLOGIC AND PALEONTOLOGIC CONTEXT

The new frog fossil remains come from stratigraphic levels of the Monte Hermoso Formation outcropping at Farola de Monte Hermoso, a well-known paleontological locality situated about 53 km east of Bahía Blanca and 12 km southwest of Pehuén-Có, on the coast of southern Buenos Aires Province, Argentina (Fig. 1). The materials studied herein come from Lithostratigraphic Unit II of Cione and Tonni (2005). This unit comprises the upper levels of the Monte Hermoso Formation, which have yielded a rich vertebrate fauna that was recognized as the *Neocavia depressidens* Biozone, the biostratigraphic basis of the lower Chapadmalalan Stage, early Pliocene (Zavala, 1993; Cione and Tonni, 2005; Deschamps et al., 2012). These deposits have been interpreted as the result of a fluvial channel migrating over its associated floodplain (Zavala and Navarro, 1993).

Previous paleontological work at this locality has provided a scanty record of fossil anurans and is restricted to hyperossified frogs, including the bufonid *Rhinella* cf. *schneideri* (Gasparini and Báez, 1974) and the ceratophryid species *Ceratophrys ameghinorum* (Fericola, 2001) and *Lepidobatrachus laevis* (Tomassini et al., 2011). Smaller and less ossified frogs that inhabit the Pampas today, such as hylids and leptodactylines, have not been recorded in this locality so far.

MATERIALS AND METHODS

The fossil specimens described herein are housed at the MLP and include a proximal part of a right ilium (MLP 87-II-25-5)

*Corresponding author.

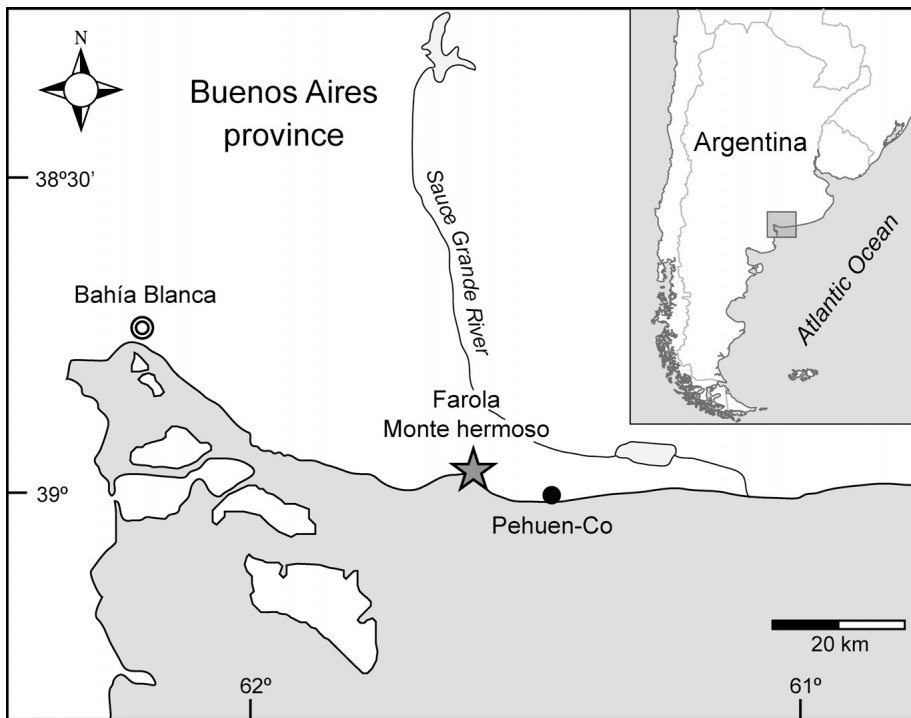


FIGURE 1. Map showing the provenance of the fossil material in the south of Buenos Aires Province.

and a nearly complete sacrum with the left diapophysis broken off (MLP 87-II-25-6). These bones are three-dimensionally preserved and, despite their incompleteness, show good anatomical detail to allow meaningful comparisons with extant taxa.

The taxonomic assessment of the new material was based on unique combinations of characters, which were identified by the examination of the ilium and sacrum of a wide sample of extant anurans (Appendix 1). Given our preliminary observations, we focused subsequent comparisons within the extant genus *Leptodactylus* and collected data from dried skeletons of 11 species (Appendix 1) representing previously recognized phenotypic groups (Maxson and Heyer, 1988). This way, comparisons were made reflecting taxonomic diversity within the genus rather than geographic location or temporal age in order to avoid biases in the identification process (Bever, 2005; Bell et al., 2010).

Observations and drawings were done under a Nikon SMZ 1000 stereoscope with an attached camera lucida and photographs were taken with a Nikon Coolpix 990 digital camera. Osteological and operational terminology follows that of Maglia et al. (2007), Báez et al. (2012), and references therein. Linear measurements (Fig. 2A; Appendix 2) were taken to the nearest 0.01 mm with a digital caliper, under a stereoscope. Measured dimensions of the ilium are similar to those considered by Bever (2005).

The linear measurements (for the ilium and sacrum separately) were size-scaled using the geometric mean (Mosimann, 1970) to adjust for isometric scaling. Jitter plots (Fig. 2B) and bivariate scatter plots (Fig. 2C, D) of adjusted as well as uncorrected measurements were used to highlight quantitative differences and similarities among the fossils and species of *Leptodactylus*. The linear measurements were regressed on snout-vent length (SVL) in order to estimate the SVL of the individuals represented by the fossils using reduced major axis (RMA) regressions passing through the origin in the statistical package PAST (Hammer et al., 2001; Appendix 2).

SYSTEMATIC PALEONTOLOGY

ANURA Fischer von Waldheim, 1813
 NEOBATRACHIA Reig, 1958
 LEPTODACTYLIDAE Werner, 1896
LEPTODACTYLUS Fitzinger, 1826
LEPTODACTYLUS, sp. indet.

(Fig. 3)

Referred Specimens—MLP 87-II-25-5, right ilium; MLP 87-II-25-6, sacrum.

Locality and Age—Farola Monte Hermoso, about 12 km west of Pehuen-Có, southern Buenos Aires Province. Monte Hermoso Formation, Lithostratigraphic Unit II (Cione and Tonni, 2005), *Neocavia depressidens* Biozone, lower Chapadmalalan Stage, early Pliocene (Deschamps et al., 2012).

Description—MLP 87-II-25-5 is a right ilium lacking a small part of the ventral acetabular expansion and most of the shaft (Fig. 3A–C). The proximal portion of the shaft has an oval cross-section, being mediolaterally compressed. A well-developed dorsal crest is present on the preserved portion of the shaft; it is slightly curved medially and gently slopes distally from a large dorsal prominence. The dorsal prominence merges with the dorsal crest anteriorly and obliquely slopes posteriorly. It is located in a relatively anterior position, since about two-thirds of its length lies anterior to the anterior limit of the acetabular fossa. The dorsal prominence bears on most of its medial surface a bulky dorsal protuberance, which has an almost quadrangular contour with protruding margins (Fig. 3A). A conspicuous supraacetabular fossa is present dorsal to the acetabular fossa and slightly anterior to the posterior slope of the dorsal prominence. The moderately developed dorsal acetabular expansion projects slightly posterodorsally. The ventral acetabular expansion is broad and well exposed in acetabular view, forming an acute angle with the iliac shaft (Fig. 3A). Although the anteroventral margin of the

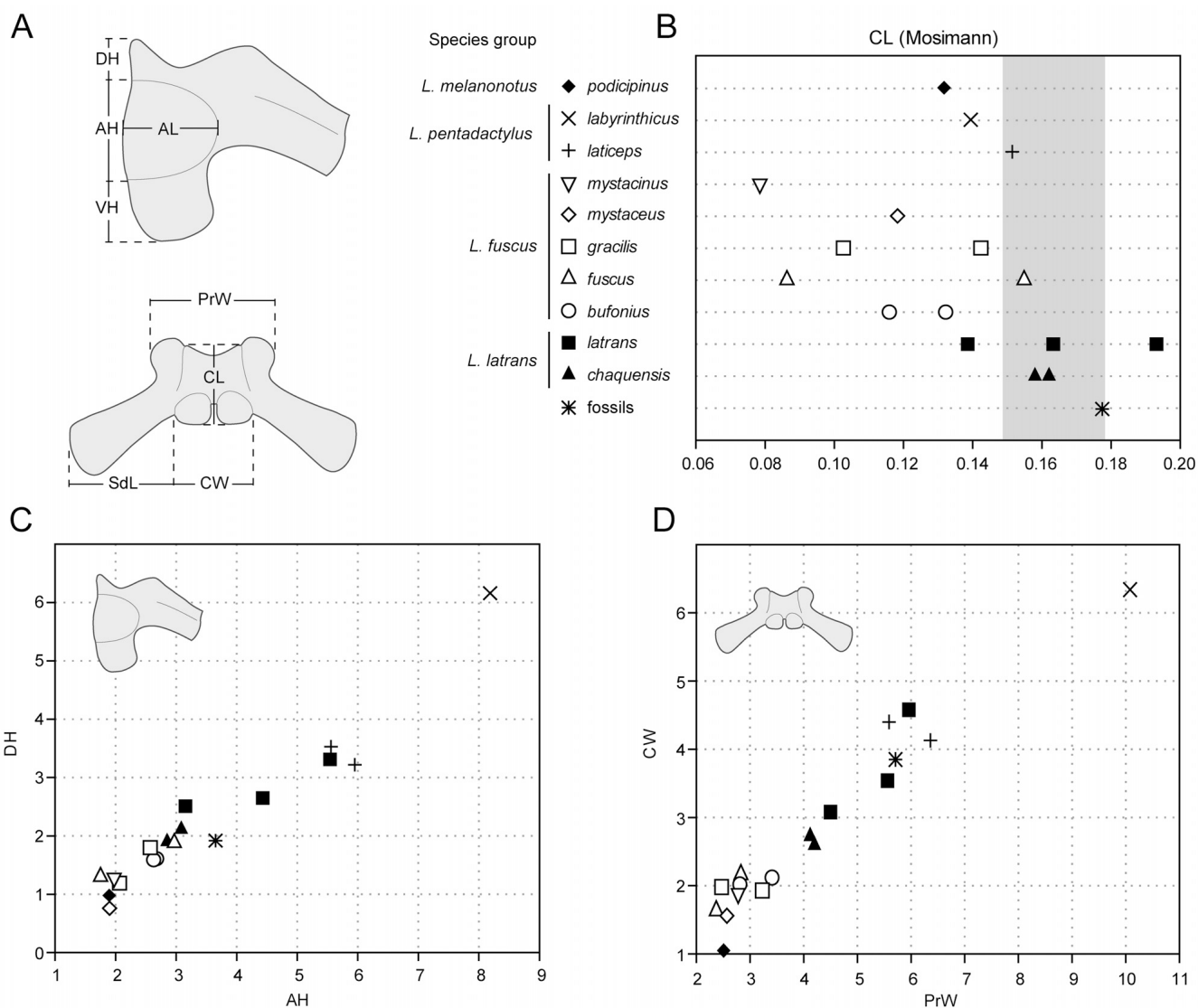


FIGURE 2. Morphometrics of the ilium and sacrum of fossil specimens and species of *Leptodactylus*. **A**, linear measurements of ilium (top) and sacrum (bottom). **B**, jitter plot of size-scaled CL (Mosimann variable); the gray rectangle depicts the second quartile (25–75%, calculated by interpolation) for the *L. latrans* species group. Comparative bivariate scatter plots of selected linear measurements of ilium (**C**) and sacrum (**D**). **Abbreviations**: **AH**, acetabular fossa height; **AL**, acetabular fossa length; **CL**, centrum length; **CW**, condyle width; **DH**, dorsal acetabular expansion height; **PrW**, prezygapophyseal width; **SdL**, sacral diapophyseal proximodistal length; **VH**, ventral acetabular expansion height.

ventral acetabular expansion is incompletely preserved, it is almost certain that the structure did not extend much more anteriorly than the conspicuous preacetabular zone. The rounded acetabular fossa is broad and moderately deep, being well delimited by a distinct acetabular rim with equally extruded ventral and dorsal margins. Medially (Fig. 3C), a narrow but distinct interiliac tubercle is present. The ilio-ischiadic junction, visible in posterior view (Fig. 3B), is relatively thin. The available evidence indicates that the ilium was not fused to the ischium and that the pubis presumably was cartilaginous.

MLP 87-II-25-6 is an almost complete sacrum, only lacking most of the left diapophysis (Fig. 3D–F). The centrum is procoelous and slightly depressed dorsoventrally (Fig. 3E). It bears posteriorly two slightly ventrally projected condyles that articulated with the urostyle and are clearly separated from one another by a deep notch (Fig. 3D, F). The neural canal is dorsoventrally depressed

and kidney-shaped in anterior view. The relatively wide and short neural arch bears rounded and obliquely dorsally inclined prezygapophyses that project well beyond the anterior margin of the neural arch roof. The neural arch bears a low neural ridge dorsally, and a high transverse crest extending onto the proximal part of the diapophyses (Fig. 3D). The sacral diapophyses are narrow, only slightly expanded distally, and almost rounded in lateral view. They are proximodistally short, posterolaterally oriented, and mildly inclined dorsally. Faint, short ridges are visible on the anterior and dorsal surfaces of the right diapophysis (Fig. 3D, E).

DISCUSSION AND CONCLUSIONS

Despite the paucity and the fragmentary condition of the fossil material, the anatomical detail of the specimens and the co-occurrence of some particular osteological features permit an

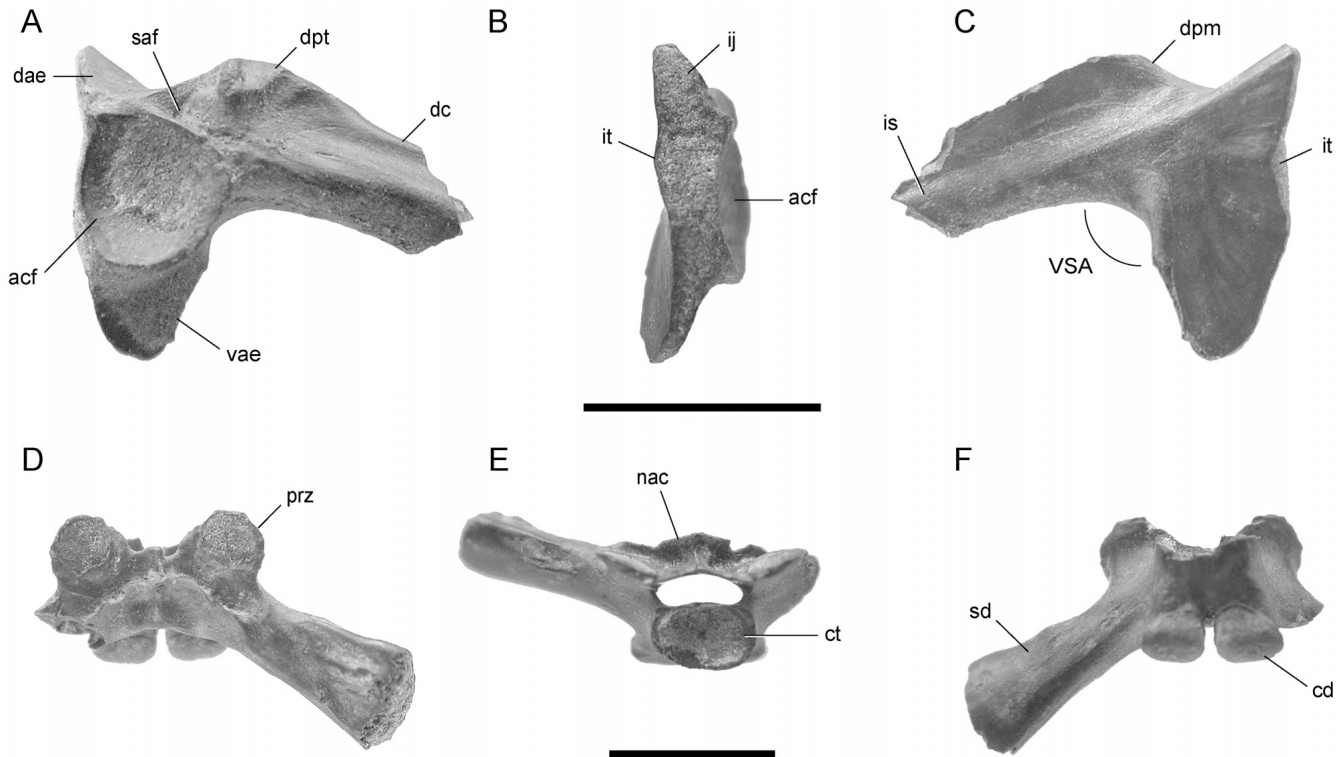


FIGURE 3. Fossil material of *Leptodactylus* from Farola de Monte Hermoso. Right ilium (MLP 87-II-25-5) in **A**, acetabular; **B**, posterior; and **C**, medial views. Sacrum (MLP 87-II-25-6) in **D**, dorsal; **E**, anterior; and **F**, ventral views. **Abbreviations:** **acf**, acetabular fossa; **cd**, condyle; **ct**, cotyle; **dae**, dorsal acetabular expansion; **dc**, dorsal crest; **dpm**, dorsal prominence; **dpt**, dorsal protuberance; **ij**, ischiadic junction; **is**, iliac shaft; **it**, interiliac tubercle; **nac**, neural arch transverse crest; **prz**, prezygapophysis; **sd**, sacral diapophysis; **vae**, ventral acetabular expansion; **VSA**, angle between the ventral acetabular expansion margin and the iliac shaft. Scale bars equal 5 mm.

accurate taxonomic assessment. An ilium with a well-developed dorsal crest, broad ventral acetabular expansion forming an acute angle with the ilial shaft, and only moderately developed dorsal acetabular expansion, on one hand, and a procoelous sacrum with narrow rounded diapophyses, and bicondylar condition posteriorly, on the other, are known to occur jointly only in nobleobatrachian hyloids. Furthermore, only a few groups among nobleobatrachians show this combination of features, including species of *Terrarana* (sensu Hedges et al., 2008), some hylodids, and *Leptodactylus*. However, besides the overall morphology, certain anatomical peculiarities of the ilium (e.g., morphology of the dorsal protuberance, deep supracetabular fossa) and the sacrum (e.g., high, sharp transverse crest on the neural arch) from the Monte Hermoso Formation only agree with that of living species of *Leptodactylus*.

The genus *Leptodactylus* has been regarded as osteologically homogeneous (Lynch, 1971). However, although the overall morphology of the ilium and sacrum is quite uniform among different taxa, the fossils show a combination of qualitative and quantitative characters that are not widespread within the genus. In this regard, the combined presence of (1) a dorsal prominence that is relatively low with a truncated dorsal edge, (2) a proportionally small acetabular fossa, and (3) a dorsal acetabular expansion that is as high as it is long in the fossil ilium (MLP 87-II-25-5) distinguishes it from most species of *Leptodactylus* (Figs. 2, 3). This combination of features is only shared with members of the *L. latrans* species group (Fig. 3A) among the species that were available for comparisons (Appendix 1). In members of other species

groups, the dorsal prominence is higher and distally rounded and the dorsal acetabular expansion is longer than it is high (e.g. *L. mystacinus*, *L. labyrinthicus*; Fig. 4B, C). Also, the ventral acetabular expansion of MLP 87-II-25-5 is clearly shorter with respect to the acetabular fossa than in *L. chaquensis*, resembling the condition in *L. latrans* (Fig. 4A).

The fossil sacrum (MLP 87-II-25-6) also conforms to that seen in the *L. latrans* species group (Fig. 3D) and contrasts with those of other examined species of *Leptodactylus* because of the joint occurrence of (1) nearly rounded prezygapophyses; (2) a sharp, high transverse crest on the neural arch; (3) relatively proximodistally short diapophyses; and (4) a proportionally longer centrum. Other taxa have transversely elongated prezygapophyses (e.g., *L. labyrinthicus*; Fig. 4E), a lower transverse crest (e.g., *L. fuscus*, *L. bufonius*), longer diapophyses (e.g., *L. podicipinus*, *L. labyrinthicus*; Fig. 4E), and/or comparatively shorter centra (e.g., *L. gracilis*, *L. mystacinus*; Fig. 2B) than MLP 87-II-25-6.

In contrast with the relatively uniform overall morphology of the skeletal elements, there is considerable and consistent variation in absolute size among *Leptodactylus* species groups. In this regard, adults of the *L. latrans* group are characteristically larger than those of the *L. fuscus* and *L. melanonotus* groups and of similar size or smaller than those of the *L. pentadactylus* group (Fig. 2C, D). It has been noted that clear differences in body size between populations might constitute sound evidence of the occurrence of multiple species within otherwise phenotypically uniform groups (e.g., Sota et al., 2000; Siström et al., 2012). In the case of *Leptodactylus* species groups, the apparent divergence in body

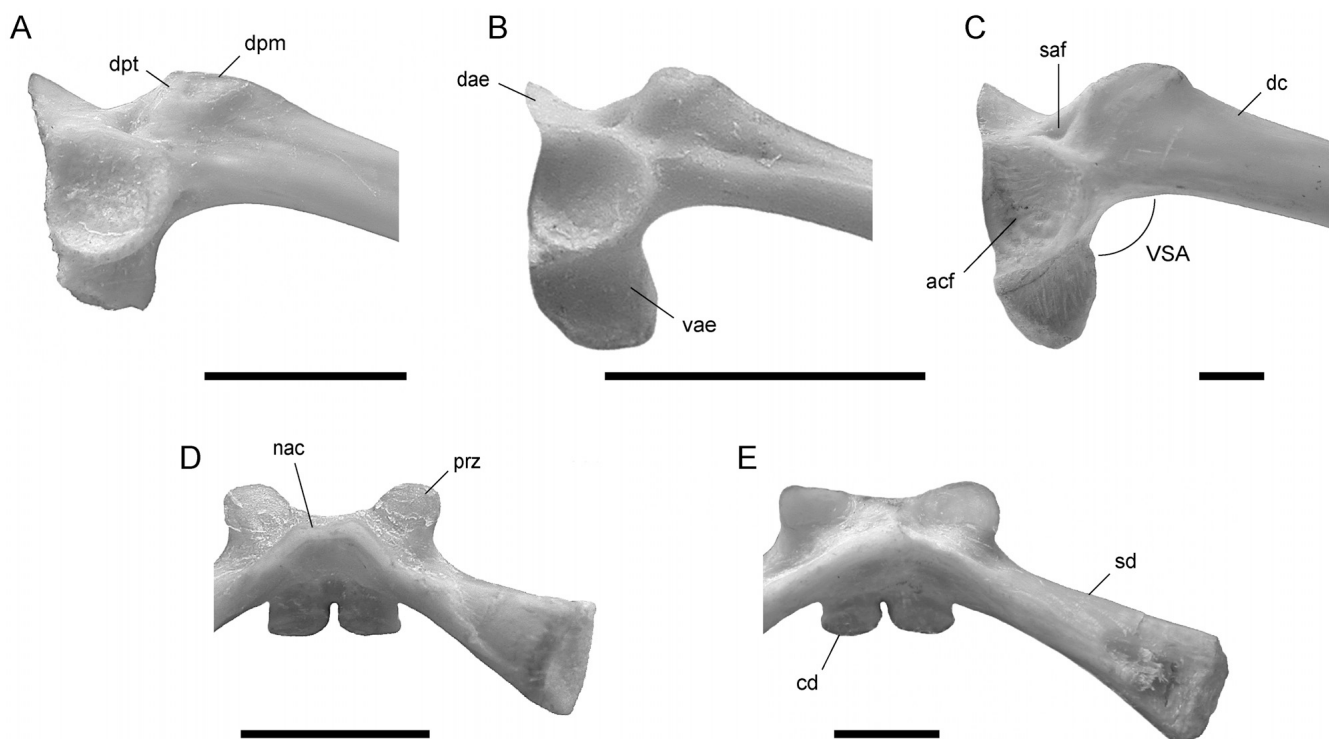


FIGURE 4. Iliac and sacral morphology of extant *Leptodactylus*. Right ilia in acetabular view of **A**, *L. latrans* (FCEN 283); **B**, *L. mystacinus* (FCEN 113); and **C**, *L. labyrinthicus* (FCEN 825). Sacra in dorsal view of **D**, *L. latrans* (FCEN 283) and **E**, *L. labyrinthicus* (FCEN 825). **Abbreviations:** **acf**, acetabular fossa; **cd**, condyle; **dae**, dorsal acetabular expansion; **dc**, dorsal crest; **dpm**, dorsal prominence; **dpt**, dorsal protuberance; **nac**, neural arch transverse crest; **prz**, prezygapophysis; **sd**, sacral diapophysis; **vae**, ventral acetabular expansion; **VSA**, angle between the ventral acetabular expansion margin and the iliac shaft. Scale bars equal 5 mm.

size might have played an important role in the differentiation and evolution of these lineages.

The fossil ilium and sacrum are consistent with adults of roughly 66 and 87 mm SVL, respectively (Appendix 2), being within the size range of adults of the *L. latrans* species group and particularly within that of *L. latrans*.

From the foregoing comparisons, it is clear that the fossil ilium and sacrum from the Monte Hermoso Formation represent a species of total group *Leptodactylus*. The morphology of the fossil elements most closely resembles that of *L. latrans* and suggests an affinity with the *L. latrans* species group. However, the lack of resolution of *Leptodactylus* interrelationships and, thus, the lack of osteological synapomorphies of the species groups and species do not allow establishing whether the morphology of *L. latrans* is primitive or derived within *Leptodactylus*. In other words, the fossils could represent either a species of stem *Leptodactylus* or a member of the *L. latrans* species group. Therefore, until new information shed light on the phylogenetic relationships within the clade, the available data only support an identification of the fossils to total group *Leptodactylus*.

So far, the known fossil record of *Leptodactylus* is scanty and is restricted to the Quaternary of the Neotropics, being reported from a few localities in Mexico, the West Indies, Bolivia, Brazil, Uruguay, and Argentina (Vergnaud-Grazzini, 1968; Lynch, 1971; Mones, 1975; Pregill, 1981; Van Devender et al., 1985; Lezcano et al., 1993; Sanchiz, 1998). These records have been ascribed either to extant forms or have been regarded as indeterminate species. The putative record of *Leptodactylus* from the Miocene of Florida, '*Leptodactylus*' *abavus* (Holman, 1965), was subsequently

removed from the genus and ascribed to *Rana* (Lynch, 1971). Therefore, the specimens described herein constitute the oldest record of the total group *Leptodactylus*, and potentially of the crown group, and extend their stratigraphic range back to the early Pliocene. To date, the use of the Plio-Pleistocene fossil record as calibration points in estimating divergence times in Neotropical frogs is far from having been thoroughly explored. New discoveries and reliable identifications, as with the one presented herein, will improve our still limited knowledge on the South American batrachofauna during the last few million years and will surely enhance the potential use of the anuran fossil record in dating phylogenies.

ACKNOWLEDGMENTS

We thank M. Reguero and L. Pomi (MLP) for the loan of the fossil material. We also thank M. Fabrezi (MCN) and J. Faivovich (MACN) for access to materials under their care. Thanks to R. Heyer, an anonymous reviewer, and the Editor, J. Anderson, for their suggestions that improved the manuscript. This work was funded through a grant (PICT 1895/11) from the Agencia Nacional de Promoción Científica y Tecnológica to A. M. Báez.

LITERATURE CITED

AmphibiaWeb. 2012. Information on amphibian biology and conservation. Berkeley, California. Available at www.amphibiaweb.org. Accessed July 20, 2012.

- Báez, A. M., R. O. Gómez, and M. L. Taglioretti. 2012. The archaic ilial morphology of an enigmatic pipid frog from the upper Pleistocene of the South American pampas. *Journal of Vertebrate Paleontology* 32:304–314.
- Bell, C. J., J. A. Gauthier, and G. S. Bever. 2010. Covert biases, circularity, and apomorphies: a critical look at the North American Quaternary herpetofaunal stability hypothesis. *Quaternary International* 217:30–36.
- Bever, G. S. 2005. Variation in the ilium of North American *Bufo* (Lissamphibia; Anura) and its implications for species-level identification of fragmentary anuran fossils. *Journal of Vertebrate Paleontology* 25:548–560.
- Cei, J. M. 1980. Amphibians of Argentina. *Monitoreo Zoologico Italiano* 2:1–609.
- Cione, A. L., and E. P. Tonni. 2005. Bioestratigrafía basada en mamíferos del Cenozoico superior de la provincia de Buenos Aires, Argentina; pp. 183–200 in R. E. de Barrio, R. O. Etcheverry, M. F. Caballé, and E. Llambías (eds.), *Geología y Recursos Minerales de la Provincia de Buenos Aires*. XVI Congreso Geológico Argentino, La Plata, September 21–30, 2005. Relatorio 11, Universitaria de La Plata, La Plata, Argentina.
- Deschamps, C. M., M. G. Vucetich, D. H. Verzi, and A. I. Olivares. 2012. Biostratigraphy and correlation of the Monte Hermoso Formation (early Pliocene, Argentina): the evidence from caviomorph rodents. *Journal of South American Earth Sciences* 35:1–9.
- Fernicola, J. C. 2001. Una nueva especie de *Ceratophrys* (Anura, Leptodactylidae) en el Neógeno de la provincia de Buenos Aires, Argentina. *Ameghiniana* 38:385–391.
- Fischer von Waldheim, G. 1813. *Zoognosia Tabulis Synopticis Illustrata*, in *Usum Praelectionorum Academiae Imperialis Medico-Chirurgicae Mosquensis Edita*, third edition. Nicolai Sergeidis Vsevolozsky, Moscow.
- Fitzinger, L. J. F. J. 1826. Neue Classification der Reptilien nach ihren Natürlichen Verwandtschaften nebst einer Verwandtschafts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des K. K. Zoologisch-Museums zu Wien. J. G. Heubner, Vienna.
- Gasparini, Z., and A. M. Báez. 1974. Aportes al conocimiento de la herpetofauna terciaria de la Argentina; pp. 377–415 in *Actas, I Congreso Argentino de Paleontología y Bioestratigrafía*, Tucumán, Argentina, August 12–16, 1974, Volume 2.
- Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontologia Electronica* 4:1–9.
- Hedges, S. B., W. E. Duellman, and M. P. Heinicke. 2008. New World direct-developing frogs (Anura: Terrarana): molecular phylogeny, classification, biogeography, and conservation. *Zootaxa* 1737:1–182.
- Heyer, W. R. 1969. Studies on the genus *Leptodactylus* (Amphibia, Leptodactylidae) III. A redefinition of the genus *Leptodactylus* and a description of a new genus of leptodactylid frogs. *Natural History Museum of Los Angeles County, Contributions in Science* 155:1–14.
- Heyer, W. R. 1974. Relationships of the *Marmoratus* species group (Amphibia, Leptodactylidae) within the subfamily Leptodactylinae. *Natural History Museum of Los Angeles County, Contributions in Science* 253:1–46.
- Heyer, W. R., and R. O. de Sá. 2011. Variation, systematics, and relationships of the *Leptodactylus bolivianus* complex (Amphibia: Anura: Leptodactylidae). *Smithsonian Contributions to Zoology* 635:1–58.
- Holman, J. A. 1965. Early Miocene anurans from Florida. *Quarterly Journal of the Florida Academy of Sciences* 28:68–82.
- Kwet, A., J. Steiner, and A. Zillikens. 2009. A new species of *Adenomera* (Amphibia, Anura, Leptodactylidae) from the Atlantic rain forest in Santa Catarina, southern Brazil. *Studies on Neotropical Fauna and Environment* 44:93–107.
- Lavilla, E. O., M. L. Ponssa, D. Baldo, N. Basso, A. Bosso, J. Céspedes, J. C. Chébez, J. Faivovich, L. Ferrari, R. Lajmanovich, J. A. Langone, P. Peltzer, C. Úbeda, M. Vaira, and F. Vera Candioti. 2000. Categorización de los Anfibios de Argentina; pp. 11–34 in E. O. Lavilla, E. Richard, and G. J. Scrocchi (eds.), *Categorización de los Anfibios y Reptiles de la República Argentina*. Asociación Herpetológica Argentina, Tucumán, Argentina.
- Lezcano, M. J., U. F. Pardiñas, and E. P. Tonni. 1993. Restos de vertebrados en el Holoceno del Nordeste de la provincia de Buenos Aires, Argentina. *Sistemática y paleoambientes*. *Ameghiniana* 30:332.
- Lynch, J. D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactylid frogs. University of Kansas Museum of Natural History Miscellaneous Publications 53:1–238.
- Maglia, A. M., L. A. Pugener, and J. M. Mueller. 2007. Skeletal morphology and postmetamorphic ontogeny of *Acris crepitans* (Anura: Hylidae): a case of miniaturization in frogs. *Journal of Morphology* 268:194–223.
- Maxson, L. R., and W. R. Heyer. 1988. Molecular systematics of the frog genus *Leptodactylus* (Amphibia: Leptodactylidae). *Fieldiana Zoology* 41:1–13.
- Mones, A. 1975. Notas paleontológicas uruguayas, III. Vertebrados fósiles nuevos o poco conocidos (Chondrichthyes, Osteichthyes, Amphibia, Mammalia). *Ameghiniana* 12:343–349.
- Mosimann, J. E. 1970. Size allometry: size and shape variables with characterizations of the lognormal and generalized gamma distributions. *Journal of the American Statistical Association* 65:930–945.
- Ponssa, M. L. 2008. Cladistic analysis and osteological descriptions of the species of the *L. fuscus* species group of the genus *Leptodactylus* (Anura, Leptodactylidae). *Journal of Zoological Systematic and Evolutionary Research* 46:249–266.
- Ponssa, M. L., and W. R. Heyer. 2007. Osteological characterization of two species of *Adenomera* (Anura, Leptodactylidae). *Zootaxa* 1403:37–54.
- Pregill, G. 1981. Late Pleistocene herpetofaunas from Puerto Rico. University of Kansas Museum of Natural History Miscellaneous Publications 71:1–72.
- Pyron, R. A., and J. J. Wiens. 2011. A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders, and caecilians. *Molecular Phylogenetics and Evolution* 61:543–583.
- Reig, O. A. 1958. Proposiciones para una nueva macrosistemática de los anuros. *Physis* 21:109–118.
- Sanchiz, B. 1998. Salientia; in P. Wellnhofer (ed.), *Encyclopedia of Palaeoherpetology*, Part 4. Verlag Dr. Friedrich Pfeil, Munich, 275 pp.
- Sistrom, M., D. L. Edwards, S. Donnellan, and M. Hutchinson. 2012. Morphological differentiation correlates with ecological but not with genetic divergence in a *Gehyra* gecko. *Journal of Evolutionary Biology* 25:647–660.
- Sota, T., Y. Takami, K. Kubota, M. Ujiie, and R. Ishikawa. 2000. Interspecific body size differentiation in species assemblages of the carabid subgenus *Ohomopterus* in Japan. *Population Ecology* 42:279–291.
- Tomassini, R. L., F. Agnolin, and C. Oliva. 2011. First fossil record of the genus *Lepidobatrachus* Budgett, 1899 (Anura, Ceratophryidae), from the early Pliocene of Argentina. *Journal of Vertebrate Paleontology* 31:1005–1009.
- Van Devender, T. R., A. M. Rea, and M. L. Smith. 1985. The Sangamon interglacial vertebrate fauna from Rancho la Brisca, Sonora, Mexico. *Transactions of the San Diego Society of Natural History* 21:23–55.
- Vergnaud-Grazzini, C. 1968. Amphibiens Pléistocènes de Bolivie. *Bulletin de la Société Géologique de France* 7:688–695.
- Werner, F. 1896. Beiträge zur Kenntniss der Reptilien und Batrachier von Centralamerika und Chile, sowie einiger seltenerer Schlangennarten. *Verhandlungen des Zoologisch-Botanischen Vereins in Wien* 46:344–365.
- Zavala, C. 1993. Estratigrafía de la localidad de Farola Monte Hermoso (Plioceno–Reciente), provincia de Buenos Aires; pp. 228–235 in *Actas, XII Congreso Geológico Argentino y II Congreso de Exploración de Hidrocarburos*, Mendoza, Argentina, October 10–15, 1993, Volume 2.
- Zavala, C., and E. Navarro. 1993. Depósitos fluviales en la Formación Monte Hermoso (Plioceno inferior–medio), provincia de Buenos Aires; pp. 236–244 in *Actas, XII Congreso Geológico Argentino y II Congreso de Exploración de Hidrocarburos*, Mendoza, Argentina, October 10–15, 1993, Volume 2.

Submitted August 27, 2012; revisions received January 16, 2012; accepted January 27, 2012.

Handling editor: Jason Anderson.

APPENDIX 1. Specimens examined. **Abbreviations:** **CS**, cleared and stained; **DL**, data taken from the literature; **DS**, dry skeleton; **UN**, uncataloged.

Alytidae: *Discoglossus pictus* FCEN UN, DS.

Bufonidae: *Melanophryniscus stelzneri* MCN UN, CS; FCEN UN, DS. *Rhinella arenarum* FCEN 724, 1014, UN, DS. *Rhinella fernandezae* FCEN 294, UN, DS.

Calyptocephalellidae: *Calyptocephalella gayi* FCEN 1433, UN, DS.

Ceratophryidae: *Ceratophrys ornata* FCEN 1015, 1580, DS. *Lepidobatrachus laevis* FCEN 319, 665, DS. *Telmatobius scrocchii* FML 1515, DS.

Cycloramphidae: *Cycloramphus dubius* FCEN 758, DS. *Eupsophus vertebralis* MACN 43704, DS. *Odontophrynus americanus* FCEN 1096, 1285, DS. *Odontophrynus occidentalis* FCEN 1218, DS.

Eleutherodactylidae: *Eleutherodactylus inoptatus* FCEN 1616, DS. *E. martinicensis* FCEN 978, DS.

Hemiphractidae: *Hemiphractus fasciatus* DL (Trueb, 1974).

Hylidae: *Hypsiboas pulchellus* FCEN UN, DS. *Phyllomedusa sauvagii* MCN 795, CS; FCEN 305, DS. *Pseudis platensis* MCN 812, CS; FCEN 727, DS. *Scinax granulatus* FCEN UN, DS.

Hylodidae: *Hylodes asper* FCEN 762, ES.

Leiuperidae: *Physalaemus biligonigerus* MCN 802, CS. *Pleurodema cinereum* FCEN 93, DS.

Leptodactylidae: *Leptodactylus bufonius* MCN 074, CS; FCEN 412-1, 416, DS. *L. chaquensis* MCN 039, CS; FCEN 57-1, 350, DS. *L. fuscus* FCEN 1704, 2062, DS. *L. gracilis* FCEN 1525, UN, DS. *L. labyrinthicus* FCEN 825, DS. *L. laticeps* FCEN 2067, FML 00611, DS. *L. latinasus* FCEN UN, DS. *L. latrans* FCEN 283, 1931, UN, FML 00571, DS. *L. mystaceus* FCEN 1752, DS. *L. mystacinus* FCEN 113, DS. *L. podicipinus* FCEN 730, DS.

Limnodynastidae: *Platyplectrum ornatum* MACN 42620, DS.

Microhylidae: *Dermatonotus muelleri* MCN 997, CS.

Myobatrachidae: *Mixophyes schevilli* FCEN UN, DS.

Ranidae: *Lithobates catesbeianus* FCEN UN, DS. *Rana temporaria* FCEN 1545–1549, DS.

Strabomantidae: *Oreobates discoidalis* MCN 462, CS; FCEN 1764, DS.

APPENDIX 2. Length measurements (in mm) of selected ilial (AH, AL, DH, VH) and sacral (PrW, CW, SdL, CL) dimensions of the fossils and species of *Leptodactylus*. **Abbreviations:** **AH**, acetabular height; **AL**, acetabular fossa length; **CL**, centrum length; **CW**, condyle width; **DH**, dorsal acetabular expansion height; **PrW**, prezygapophyseal width; **SdL**, sacral diapophyseal proximodistal length; **SVL**, snout-vent length; **VH**, ventral acetabular expansion height.

Specimen	AH	AL	DH	VH	PrW	CW	SdL	CL	SVL
MLP 87-II-25-5 (ilium)	3.65	3.31	1.92	1.81	—	—	—		66
MLP 87-II-25-6 (sacrum)	—	—	—	—	5.71	3.85	6.67	3.32	87
<i>L. bufonius</i> FCEN 412	2.68	4.49	1.61	2.88	2.81	2.02	3.57	1.89	47
<i>L. bufonius</i> FCEN 416	2.63	4.21	1.59	2.74	3.41	2.12	3.76	1.74	51
<i>L. chaquensis</i> FCEN 350	2.85	3.32	1.94	2.25	4.2	2.63	4.65	2.36	65
<i>L. chaquensis</i> FCEN 57-1	3.08	3.37	2.15	2.33	4.12	2.76	5.78	2.57	67
<i>L. fuscus</i> FCEN 1704	2.97	1.67	1.92	1.20	2.83	2.2	4.79	1.87	50
<i>L. fuscus</i> FCEN 2062	1.75	1.86	1.34	0.77	2.37	1.67	2.67	1.26	40
<i>L. gracilis</i> FCEN 1525	2.06	2.17	1.19	1.87	2.47	1.98	3.03	1.43	43
<i>L. gracilis</i> FCEN UN	2.57	1.53	1.80	1.31	3.23	1.93	4.31	1.72	42
<i>L. labyrinthicus</i> FCEN 825	8.19	5.36	6.16	4.14	10.08	6.34	14.83	5.69	145
<i>L. laticeps</i> FCEN 2067	5.56	5.08	3.53	2.92	5.59	4.4	7.43	3.52	90
<i>L. laticeps</i> FML 00611	5.95	5.17	3.22	3.61	6.36	4.13	7.93	3.89	93
<i>L. latrans</i> FCEN 283	4.43	2.52	2.65	0.88	5.56	3.54	6.16	3.12	80
<i>L. latrans</i> FCEN UN	3.15	3.64	2.51	2.67	4.5	3.08	5.35	2.75	69
<i>L. latrans</i> FML 00571	5.54	4.71	3.31	4.80	5.96	4.58	8.47	3.48	95
<i>L. mystaceus</i> FCEN 1752	1.90	2.93	0.76	1.54	2.57	1.56	3.29	1.52	38
<i>L. mystacinus</i> FCEN 113	1.97	3.49	1.24	2.78	2.78	1.85	3.34	1.35	45
<i>L. podicipinus</i> FCEN 730	1.89	1.50	0.98	0.92	2.51	1.05	2.78	1.44	38

SVL values of the fossil ilium and sacrum (in bold) were estimated by reduced major axis regressions passing through the origin of AH and PrW, respectively, on SVL.