INTRASPECIFIC MORPHOLOGICAL VARIATION AND ITS IMPLICATIONS IN THE TAXONOMIC STATUS OF ‘BUF0 PISANOI,’ A PLEISTOCENE ANURAN FROM EASTERN ARGENTINA

CELESTE M. PÉREZ BEN,1,* RAÚL O. GÓMEZ,1 and ANA M. BÁEZ1,2

1CONICET, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Buenos Aires 1428, Argentina; cperezben@gl.fcen.uba.ar; raulgomez@gl.fcen.uba.ar; baez@gl.fcen.uba.ar;

2CONICET, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Avenida Ángel Gallardo 470, Buenos Aires 1405, Argentina

ABSTRACT—The true toad family Bufonidae is one of the most speciose and widespread clades of neobatrachian anurans. Despite being well represented in South America at present, bufonids have a poor fossil record on this continent. ‘Bufo pisanoi’ from Pliocene outcrops of coastal Buenos Aires Province, Argentina, is the only extinct South American bufonid taxon recognized to date. In this study, we investigated the validity of the putative diagnostic characters of this extinct species to confirm its taxonomic status based on revision of the holotype and referred material. Comparisons with several extant bufonid species led us to include the taxon represented by this fossil material within the Rhinella marina clade, close to R. arenarum. Further comparisons and a geometric morphometric analysis based on a relatively large sample of the latter species demonstrated that the morphology of ‘B. pisanoi’ falls within the variation range of R. arenarum. Therefore, we consider that the names ‘B. pisanoi’ and R. arenarum represent the same taxon, with the latter having priority. This work emphasizes the importance of considering intraspecific variation whenever possible, because this leads to a more rigorous approach to the identification of fossil specimens and tests the taxonomic value of different osteological characters.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

The true toad family Bufonidae is one of the most speciose clades of neobatrachian anurans, with 558 extant species described to date (Frost, 2013). This large group has a nearly cosmopolitan distribution, being native to all areas except the Australopapuan Realm (excluding Sulawesi), Madagascar, Antarctica, and the Arctic. The diversification and intrarelationships of Bufonidae have been addressed recently based mostly on molecular data, as part of either broad-scaled (Frost et al., 2006; Pyron and Wiens, 2011) or more restricted (Pramuk, 2006; Pramuk et al., 2008; Maciel et al., 2010; Van Bocxlaer et al., 2010) studies. As a result of these investigations, several names of taxa within Bufonidae have been changed in accordance with the retrieved phylogenetic relationships. In this regard, the widely used generic name Bufo is now applied only to a small clade of Eurasian toads, whereas most of the South American species that had been referred to Bufo form a clade named Rhinella (Chaparro, 2007). Rhinella is recovered as the most derived clade among South American bufonids in recent phylogenetic analyses (e.g., Van Bocxlaer et al., 2010; Pyron and Wiens, 2011), although its relationships to the non-South American groups are still contentious. Despite being well represented in South America at present, bufonids have a poor fossil record in this continent consisting mostly of fragmentary, isolated bones that are generally difficult to identify at the species level. Bufo (now Rhinella) pisanoi from Pliocene outcrops of coastal Buenos Aires Province, Argentina (Fig. 1) (Casamiquela, 1967), is the only extinct South American bufonid taxon that has been recognized to date, although Sanchiz (1998) placed this binomen into synonymy with the extant Rhinella (formerly Bufo) schneideri (Werner, 1894).

In this study, the holotype and the referred material of ‘Bufo pisanoi’ originally described by Casamiquela (1967) were examined with the aim to investigate whether the morphology of ‘B. pisanoi’ is actually different from other extant species and to test the validity of the putative diagnostic characters of this fossil species to confirm its taxonomic status. Preliminary observations revealed the similarity of ‘B. pisanoi’ to the extant Rhinella (formerly Bufo) arenarum (Hensel, 1867), a species that inhabits the region where the fossil sites that yielded this material are located. Therefore, our study focused on the skeletal morphology and intraspecific variability of this taxon, although we also expanded our comparative sample to avoid the problem of assumption of geographic or temporal stability as discussed by Bell et al. (2010).

Institutional Abbreviations—FCEN, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina; MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina; MMP, Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Argentina; PVL, Paleontología de Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina; ZMB, Zoologisches Museum, Berlin, Germany.

MATERIALS AND METHODS

We examined all of the materials that have been assigned to ‘Bufo pisanoi,’ including the holotype, which was erected, described, and figured by Casamiquela (1967). These fossil
FIGURE 1. Map showing the provenance of the fossil materials of ‘Bufo (=Rhinella) pisanoi’ in Buenos Aires Province (stars), Argentina, and the current distribution of Rhinella arenarum (highlighted in dark gray).

specimens, listed below, are three-dimensionally preserved and most belong to a single individual. Comparisons between this material and numerous bufonid species from South America were based on direct observation of skeletons whenever possible (Supplementary Data), as well as on published data. Given our preliminary observations, we focused on species of the Rhinella marina species group and, particularly, on the living R. arenarum. In this regard, the close resemblance of the fossil elements to the corresponding bones of this species led us to analyze the intraspecific variation of some discrete characters of cranial and postcranial elements in 34 specimens of R. arenarum and to perform a geometric morphometric analysis of the frontoparietals of the latter species and ‘Bufo pisanoi.’ All of the examined skeletons of the living species belong to adult individuals, the snout-vent lengths of which range between 96.72 mm (male) and 147 mm (male). The majority of these specimens (27) were collected in a small area of northeastern Buenos Aires Province (Fig. 1) and presumably belong to the same population, although a few specimens of the same species (7) from other regions of its present distributional range were studied as well (Supplementary Data). Our total sample of R. arenarum included 22 males, five females, and seven specimens of undetermined sex.

The frontoparietal was selected for the morphometric analysis because it has frequently been used as a diagnostic element of bufonids in neontological studies (e.g., Martin, 1972) and also because it is well preserved enough to confidently place landmarks in one of the fossil specimens. The articulated condition of most of the skeletons in our sample of the living species prevented the use of the maxilla and nasal. The dorsal shape of the left frontoparietal in dorsal view was captured through five two-dimensional (2D) landmarks (Fig. 2). The image files (TPS) were created using tpsUTIL 1.40 (Rohlf, 2008) and landmark digitization was carried out using tpsDIG 2.10 (Rohlf, 2006). Using TpsRelW 1.45 (Rohlf, 2007), landmarks were aligned by means of a generalized Procrustes analysis (Rohlf and Slice, 1990; Bookstein, 1991). Subsequently, the Euclidean distances between Procrustes coordinates were calculated and an unweighted pair group average (UPGMA) cluster analysis (Fig. 2) was carried out with Past 2.17 (Hammer et al., 2001) in order to summarize the phenetic relationships among the individuals of R. arenarum and ‘Bufo pisanoi.’

Osteological terminology mainly follows that of Trueb (1973), although we also have used terms exclusively applied to bufonids (Martin, 1972).

SYSTEMATIC PALEONTOLOGY

ANURA Fischer von Waldheim, 1813
NEOBATRACHIA Reig, 1958
BUFONIDAE Gray, 1825
RHINELLA Fitzinger, 1826
RHINELLA ARENARUM (Hensel, 1867) (Figs. 3, 4A)

Bufo pisanoi Casamiquela, 1967:162–163.

Holotype—Not designated. Seven syntypes noted, although location of depository not designated. Kwet et al. (2006) located three of the seven syntypes in the Zoologisches Museum of Berlin and designated ZMB 6779 as lectotype (Frost, 2013).

Type Locality—Rio Grande, Rio Grande do Sul, Brazil.

Emended Diagnosis—A large toad of the R. marina group that differs from other species of the group in having enlarged paratoid glands, which are posteriorly followed by prominent round or granular warts, and tubercular cranial ornamentation.

Referred Material of ‘B. pisanoi’—(1) PVL 2197, an individual represented by three-dimensionally preserved cranial and postcranial elements, which consist of a left, almost complete frontoparietal fused to the very incomplete otoccipital, complete right maxilla, presacral vertebrae VII and VIII with poorly preserved transverse processes, sacrum with incomplete left diapophysis, urostyle lacking its posterior part, and fragmentary diaphysis of right femur (Fig. 3). This material was designated as the holotype of ‘B. pisanoi’ by Casamiquela (1967). (2) MMP 779, three-dimensionally preserved right nasal and anterior portion of left maxilla (Fig. 3). The nasal is proportionally larger than the maxilla; therefore, these elements represent two different individuals. These bones were referred to ‘B. pisanoi’ by Casamiquela (1967), who listed the nasal as a left element.

Localities and Horizons of ‘B. pisanoi’—(1) Outcrops of the Irene ‘formation’ sensu Reig (1955), about 2 km south of the bridge of National Route 3, right margin of the
Quequén Salado River valley, Buenos Aires Province, Argentina. The Irene ‘formation’ has been traditionally considered to be correlated with the Chapadmalalan Age/Stage (3.9–3.2 Ma), at least in part (Goin et al., 1994; Tambussi, 1998). However, recently it has been proposed that this informal stratigraphic unit spans the Huayquerian-Montermosan-lower Chapadmalalan ages (late Miocene–late Pliocene) based on study of the caviomorph rodent remains from pertinent sequences of Buenos Aires Province (Deschamps et al., 2012). The lack of precise stratigraphic data on the PVL 2197–bearing levels prevents ascription to a more specific age. (2) Punta Lobéria, Buenos Aires Province, Argentina. Chapadmalal Formation, ‘upper Chapadmalalan’ Stage, Pliocene (Deschamps et al., 2012).

Comments—The dermal cranial elements formerly assigned to ‘Bufo pisanoi’ bear heavy ornamentation consisting of clusters of tubercles (Fig. 3A–D). The tubercles are present on the entire dorsal surface of both the frontoparietal (PVL 2197) and the nasal (MMP 779), but clusters are particularly well developed on the crests (Fig. 3A, C). The ornamentation of the maxillae is best developed on the most dorsal part of the pars facialis and posterior to the preorbital process (Fig. 3B).

The anterior margin of the frontoparietal (PVL 2197) is perpendicular to the skull midline (Fig. 3A), indicating the presence of a transverse suture between this element and the nasal, whereas the referred nasal (MMP 779) presents an oblique posterior margin (Fig. 3C).

RESULTS AND DISCUSSION

The holotype of ‘Bufo pisanoi’ (PVL 2197) clearly belongs to the Rhinella (formerly Bufo) marina species group, as concluded by Casamiquela (1967). The R. marina group is one of the phenetic groups of extant bufonids recognized by different authors (e.g., Martin, 1972) based mainly on skeletal, mostly cranial, features. In recent molecular phylogenetic analyses (e.g., Van Boeckel et al., 2010), this bufonid group was recovered as monophyletic. With the exception of Rhinella marina, the range of which reaches as far north as Texas, species of the R. marina group are endemic to South America (Vallinoto et al., 2010). It is noteworthy that members of this clade of well-ossified, relatively large toads are characterized by a similar osteology (Tihen, 1962a), making it problematic to identify fossil material at the species level. Only one of the skeletal synapomorphies proposed for this group (the anterior edge of the sacral diapophyses are angled posteriorly with respect to the longitudinal axis of the vertebrae; Maciel et al., 2010) can be assessed in the available material of ‘B. pisanoi’ due to its incompleteness. However, this material has a combination of features that only occurs in members of the R. marina group amongst South American bufonids. This combination consists of ‘broad’ skull (sensu Martin, 1972), heavy cranial ornamentation, defined supraorbital crests, nearly transverse anterior margins of frontoparietals, and the absence of parietal crests.

With regard to the 10 species that currently compose the R. marina group (Maciel et al., 2010), a survey of their cranial ornamentation patterns shows that the tubercular type of ornamentation of ‘B. pisanoi’ is only present in R. arenarum. In contrast, a striated or wrinkled pattern characterizes the remaining living species of the clade (Fig. 4), including R. rubescens, R. achavali, and R. icterica, which form the sister clade of R. arenarum (Maciel et al., 2010; Vallinoto et al., 2010), and R. schneideri, the taxon to which Sanchiz (1998) synonymized ‘B. pisanoi.’ Further detailed osteological comparisons among members of the ‘south-central clade’ (R. arenarum, R. rubescens, R. achavali, and R. icterica sensu Maciel et al., 2010) were limited by the limited sample available to us.

The tubercular pattern of cranial ornamentation is invariably present in the studied sample of R. arenarum. Despite this similarity, the supraorbital crests show a range of development, varying from low to relatively high (Fig. 5), although the crests are less developed than in other species of the R. marina group (e.g., R. schneideri) (Fig. 4). The extent and degree of ornamentation of the frontoparietals are also variable in R. arenarum. In some individuals, the ornamentation is limited to the supraorbital crests, whereas the medial surface of the frontoparietals is rather smooth (Fig. 4D, G); conversely, other specimens have the ornamentation more evenly distributed (Fig. 4F). Likewise, the tubercles may be sparse or densely distributed. This variation is not linked to sexual dimorphism and occurs in specimens from the same
FIGURE 3. ‘Bufo (= Rhinella) pisanoi.’ PVL 2197: A, left frontoparietal, dorsal view; B, right maxilla, lateral view; E, urostyle, left lateral view; F, presacral vertebra, dorsal view; G, last presacral and sacral vertebrae, dorsal view; H, right femur, medial view. MMP 779: C, right nasal, dorsal view; D, left maxilla, lateral view.

area. This demonstrates that the frontoparietal of ‘B. pisanoi’ falls within the variation range of that of R. arenarum. It is evident that Casamiquela (1967), in his discussion of ‘B. pisanoi,’ was not aware of this variation when he stated that ‘B. pisanoi’ can be distinguished from R. arenarum by a unique combination of poorly developed cranial crests, a character that he misinterpreted as a juvenile feature, together with a heavy cranial ornamentation, an adult feature. The observed variation also contrasts with the characterization of R. arenarum as having very high cranial crests and a relatively smooth cranial surface between the crests of previous studies (Estes and Wassersug, 1963).

In addition to the features commented on above, the cluster analysis based on the morphometric data of the frontoparietal resulted in the element of ‘B. pisanoi’ being recovered nested among the R. arenarum specimens (Fig. 2). This indicates that the overall shape of the frontoparietal of ‘B. pisanoi’ agrees with that of the extant species.

The nasal (MMP 779) ascribed to ‘B. pisanoi’ by Casamiquela (1967) has distinctive canthal and preorbital crests (sensu Martin, 1972), and contacted the maxilla only by means of the maxillary process, as in members of the R. marina group among South American bufonids. It also bears the tubercular ornamentation characteristic of R. arenarum, as stated previously. It is also worth noting that although the posterior margins of the nasals when in articulation with the frontoparietals frequently seem perpendicular to the midline in R. arenarum, disarticulated nasals actually have oblique posterior margins, as in MMP 779.

As with the frontoparietal, other features that Casamiquela (1967) considered unique for ‘B. pisanoi’ (e.g., obtuse angle formed between the anterior margin of the crest of the urostyle and the horizontal plane of the element) also occur in some individuals of our sample of R. arenarum. Although the fossil specimens represent individuals larger (130–140 mm in snout-vent length; Casamiquela, 1967) than most R. arenarum (88–112 mm; Cei, 1980), the inferred body size is similar to those of aged toads of the extant species that we examined.

In summary, after examining a relatively large sample of R. arenarum, we were unable to find features differentiating the holotype and referred specimens of ‘B. pisanoi’ from this extant species. Furthermore, the putative distinguishing morphological traits and shape of the frontoparietal of the fossil species occur within the range of intraspecific variation of the living species. Therefore, we consider that the names ‘B. pisanoi’ and R. arenarum represent the same taxon, with the latter having priority.

Anuran remains from the Oligocene of Bolivia (Báez and Nicoli, 2004) and Mio-Pliocene of Argentina (Tihen, 1962b; Tauber, 1989) have been considered to be close to the extant R. arenarum, but their fragmentary condition casts doubt on their species-level assignment. Thus, the fossil remains studied herein represent the oldest confident fossil record of R. arenarum. The presence of this species in upper Miocene–Pliocene strata at the Quequén Salado and Punta Lobería fossil localities of Buenos Aires Province is in accordance with its present geographic distribution (Fig. 1). Our results are also consistent with the late
Miocene and early Pliocene divergence of the lineage represented by this species proposed by Maciel et al. (2010) based on a calibrated phylogenetic analysis of molecular data.

The interspecific and intraspecific comparisons performed in this study show that the tubercular cranial ornamentation is a consistent and distinctive feature of *R. arenarum* among members of the *R. marina* group; thus, we included this trait in the diagnosis of this species.

### Species Recognition and Intraspecific Variation in Paleontology

Species are the fundamental units of evolution; thus, the nature of these entities, as well as how they are recognized, has long been the object of thoughtful discussions (e.g., Mayr, 1982; Templeton, 1989). Species delimitation is essential to carry out biogeographic and ecological studies, as well as to deduce macroevolutionary patterns and processes (Smith, 1994). Although different and apparently incompatible species concepts have been erected (see Mayden, 1997, for an account), it has been proposed that a conceptual unity about what species are underlies all of these definitions, and what differentiates them is how these entities can be delimited (e.g., De Queiroz, 2007). According to De Queiroz (2007), the differences between species delimitation criteria rely on which properties acquired by lineages during the course of divergence are taken into account. In this regard, systematists typically delimit species based on the presence of ‘fixed’ (i.e., intraspecifically invariant) morphological characters, or combination of characters, that don’t overlap those of other species (Wiens and Servedio,
Although it is not always made explicit, the notion that non-overlapping, fixed characters (if genetically based) provide evidence that gene flow with other similar entities has been interrupted underlies these studies. However, the decoupling of morphological and taxic changes during the evolutionary process suggests that there can be no absolute criteria for recognizing species based on morphology (Tattersall, 1986). Even so, fossil species are distinguished as separate entities only if they are morphologically distinct.

When fixed morphological characters are used as species delimitation criteria, two main problems may occur (Wiens andervedio, 2000): (1) the number of species present in a sample of individuals could be underestimated if the characters taken into account are insufficient to differentiate the real units; and (2) the number of species could be overestimated by considering characters as fixed when they are actually intraspecific variants. Studies of fossil vertebrates are particularly prone to these problems because in general, the only available information is based on the hard parts, and, in addition, these remain are seldom preserved well enough to retain the full suite of skeletal characters observable in living specimens. Moreover, the acceptance of certain characters as fixed is a sensitive issue when dealing with single fossil individuals from different localities/horizons, where the properties of their respective populations are inferred by extrapolating the morphology of these unique specimens.

Not surprisingly, the identification at the species level of the fossil material studied herein raised these theoretical and methodological issues concerning the delimitation and recognition of species in paleontology. It is true that the range of morphological variation between closely related species may partially, or even substantially, overlap, but in his discussion on ‘Bufo pisanoi,’ Casamiquela (1967) considered some skeletal characters of Rhinella arenarum as fixed, probably as an artifact of sample size, when actually they are not, as revealed by our sample of this extant species. The putative diagnostic (fixed) characters of ‘B. pisanoi’ overlap the range of variation of those of R. arenarum and, thus, fail to discriminate the two species with the available evidence. We were unable to find any other discrete character or suite of characters that might support the distinction of these two entities. However, aware of the above-stated problem number 1, we cannot discard that the discovery of new and more complete remains might provide new data suggesting the presence of an extinct species of Rhinella in the Neogene of Buenos Aires Province.

Although from an instrumentalist point of view species can be recognized as the smallest cluster of individuals that might be distinguished from other clusters by unique traits or combination of traits, substantial variation may occur within a cluster (e.g., Bever, 2005). In this regard, it has been demonstrated that polymorph (excluding ontogenetic and between-gender variation) morphological characters may contain significant phylogenetic information (Campbell and Frost, 1993; Wiens, 1995; Wiens and serve-dio, 1997); therefore, this variation should be evaluated carefully whenever possible, as recommended by Trueb (1977) in one of the few studies dealing with intrapopulational variation in anurans. This information, however, is not usually discussed explicitly (Bell et al., 2010), and, frequently, features that vary in the terminal taxa are excluded from phylogenetic analyses.

**ACKNOWLEDGMENTS**

The authors acknowledge the contribution of A. Dondas (Museo Municipal de Ciencias Naturales “Lorenzo Scaglia”, Mar del Plata) and J. Powell (Instituto Miguel Lillo, Tucumán) for the loan of specimens under their care. They also thank L. Trueb (University of Kansas), R. Maneyro (Universidad de la República, Uruguay), and L. Ambrosio (Universidade de Brasília, Brasil) for providing information or photographs of specimens housed in their respective institutions. Thanks are extended to D. Blackburn, Z. Röcek, and the Handling Editor, J. Anderson, for their suggestions that improve the manuscript. This work was funded through a grant (PICT 1895/11) from the Agencia Nacional de Promoción Científica y Tecnológica a M. Báez.

**LITERATURE CITED**

Báez, A. M., and L. Nicoli. 2004. Bufonid toads from the late Oligocene beds of Salla, Bolivia. Journal of Vertebrate Paleontology 24:73–79.

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 (Lisamphibia, Anura) and its implications for species-level identification of fragmentary anuran fossils. Journal of Vertebrate Paleontology 25:548–560.

Bookstein, F. L. 1991. Morphometric Tools for Landmark Data: Geometry and Biology. Cambridge University Press, Cambridge, U.K., 455 pp.

Campbell, J. A., and D. R. Frost. 1993. Anguid lizards of the genus Abro- nius: reivisionary notes, descriptions of four new species, a phyloge-netic analysis, and key. Bulletin of the American Museum of Natural History 216:1–121.

Casamiquela, R. M. 1967. Sobre un nuevo Bufo fósil de la provincia de Buenos Aires (Argentina). Ameghiniana 5:161–169.

Cei, J. M. (ed.). 1980. Amphibians of Argentina. Monitore Zoologico Italiano, N. S., Monografia 2, Florence, 609 pp.

Chaparro, J. C., J. B. Pramuk, and A. G. Gluesenkamp. 2007. A new species of arboreal Rhinella (Anura: Bufonidae) from cloud forest of southeastern Peru. Herpetologia 63:203–212.

De Queiroz, K. 2007. Species concepts and species delimitation. Systematic Biology 56:879–886.

Deschamps, C. M., M. G. Vacichet, D. H. Verzi, and A. I. Olivares. 2012. Biostatigraphy and correlation of the Monte Hermoso Formation (early Pliocene, Argentina): the evidence from caviomorph rodents. Journal of South American Earth Sciences 35:1–9.

Estes, R., and R. Wassersug. 1963. A Miocene toad from Colombia, South America. Breviora 193:1–13.

Fischer von Waldheim, G. 1813. Zoögnosia Tabulis Synoptics Illustrata, in Usnum Praelectionum Academiae Imperialis Medico-Chirurgicae Mosquensis edita, third edition. Nicolai Sergeißis Vsevolozsky, Moscow, 464 pp.

Fitzinger, L. F. F. 1826. Neue Classification der Reptilien nach ihren natürlichen Verwandtschaften nebst einer Verwandtschafts-Tafel und einem Verzeichnisse der Reptilien-Sammlung des K. K. Zool-o-gisches Museums zu Wien. J. G. Heubner, Vienna, 66 pp.

Frost, D. R. 2013. Amphibian species of the world: an online reference. American Museum of Natural History, New York. Available at [http://research.amnh.org/vz/herpetology/amphibia](http://research.amnh.org/vz/herpetology/amphibia). Accessed January 17, 2013.

Frost, D. R., T. Grant, J. Faivovich, R. Bain, A. Haas, F. B. Haddad, R. O. De Sá, A. Channing, M. Wilkinson, N. Donnellan, C. J. Raxworthy, J. Campbell, B. L. Blotto, P. Moler, R. Drewes, R. Nussbaum, J. D. Lynch, D. M. Green, and W. C. Wheeler. 2006. The amphibian tree of life. Bulletin of the American Museum of Natural History 297:1–291.

Goicoechea, J. U., F. J. Pardinas, and M. Lezcano. 1994. Un nuevo resto del conocefalosteo Plitejestes Reig, 1955 (Mammalia, Marsupialia) del Plie- ceno de la provincia de Buenos Aires. Ameghiniana 31:15–21.

Gray, J. E. 1825. A synopsis of the genera of reptiles and Amphibia, with a description of some new species. Annals of Philosophy 10:193–217.

Hämer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: Palaeontological Statistics Software Package for Education and Data Analysis. Palaeontology Electonica 4: PE1.4.A. Available at [http://palaeoelectonica.org/2001_1/past/issue1_01.htm](http://palaeoelectonica.org/2001_1/past/issue1_01.htm). Accessed January 17, 2013.

Hensel, R. 1867. Beitrage zur kenntniss der Wirbeltiere S ¨udbrasiliens Ba-
key for the identification of the species in the Chaunus marinus group. Icheringia. Serie Zoologia 96:479–485.

Maciel, N. M., R. Garcia Collevatti, G. Rinaldi Colli, and E. Ferroli Schwartz. 2010. Late Miocene diversification and phylogenetic relationships of the huge toads in the Rhinella marina (Linnaeus, 1758) species group (Anura: Bufonidae). Molecular Phylogenetics and Evolution 57:787–797.

Martin, R. F. 1972. Evidence from ontology; pp. 37–70 in W. F. Blair (ed.), Evolution in the Genus Bufo. University of Texas Press, Austin, Texas.

Mayden, R. L. 1997. A hierarchy of species concepts: the denouement in the saga of the species problem; pp. 381–424 in M. F. Claridge, H. A. Dawah, and M. R. Wilson (eds.), Species: The Units of Biodiversity. Chapman and Hall, London.

Mayr, E. (ed.). 1982. The Growth of Biological Thought: Diversity, Evolution, and Inheritance. Belknap Press of Harvard University Press, Cambridge, Massachusetts, 974 pp.

Pramuk, J. B. 2006. Phylogeny of South American Bufo (Anura: Bufonidae) inferred from combined evidence. Zoological Journal of the Linnean Society 146:407–452.

Pramuk, J. B., T. Robertson, J. Sites, and B. Noonan. 2008. Around the world in 10 million years: biogeography of the nearly cosmopolitan true toads (Anura: Bufonidae). Global Ecology and Biogeography 17:72–83.

Pyron, R. A., and J. J. Wiens. 2011. A large-scale phylogeny of Amphibia including over 2,800 species, and a revised classification of extant frogs, salamanders, and caecilians. Molecular Phylogenetics and Evolution 61:543–583.

Reig, O. A. 1955. Un nuevo gênero y especie de cenolestinos del Plioceno de la Provincia de Buenos Aires (República Argentina). Revista Asociación Geológica Argentina 10:60–71.

Reig, O. A. 1958. Proposiciones para una nueva macrosistemática de los anuros. Physis 21:109–118.

Rohlf, F. J. 2006. TpsDig 2.1, Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, New York.

Rohlf, F. J. 2007. TpsRelw 1.45. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, New York.

Rohlf, F. J. 2008. TpsUtil 1.40. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook, New York.

Rohlf, F. J., and D. E. Slice. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. Systematic Zoology 39:40–59.

Sánchez, B. 1998. Salientia. Handbuch der Paläoherpetologie, Part 4. Verlag Dr. Friedrich Pfeil, Munich, 275 pp.