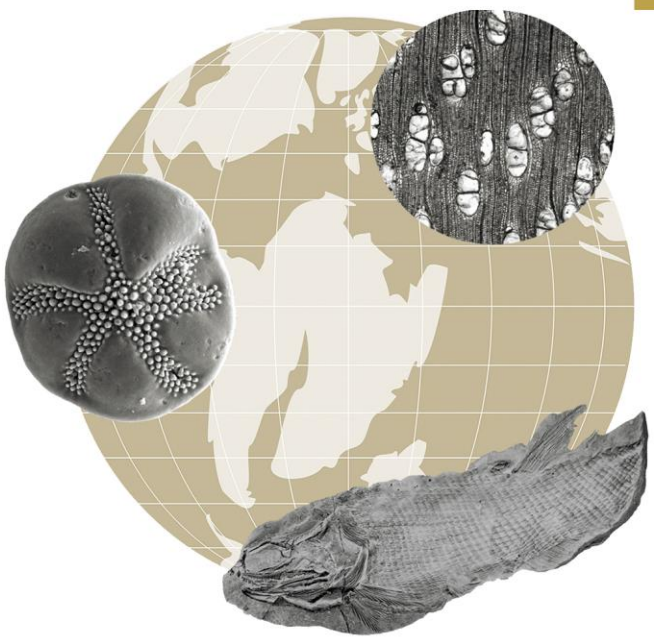
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Submitted: 29 May 2026 - **Accepted**: 12 October 2026 - **Posted online**: 13 November 2026

To link and cite this article:

doi: 10.5710/AMGH.12.10.2026.3701

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Lost and found: Taxonomic assessment of early Pliocene toads (Anura, Bufonidae) from the Monte Hermoso Formation, Argentina

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32 pages (text+references); 4 figures; 2 tables

Running Header: Turazzini and Gómez: *Rhinella* cf. *diptycha* from Monte Hermoso Formation

Short Description: Description of disarticulated fossil remains of a large toad from the early Pliocene of Monte Hermoso identified as *Rhinella* cf. *diptycha*.

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Abstract. The Late Miocene–early Pliocene transition marks a pivotal interval during which several modern anuran genera from the Neotropics first appear in the fossil record. The Monte Hermoso Formation (early Pliocene, Montehermosan SALMA) at Farola Monte Hermoso, southern Buenos Aires Province, yields the most diverse anuran assemblage from the Pliocene of Argentina. This assemblage putatively includes two bufonid taxa previously reported as *Rhinella* cf. *diptycha* and *R.* cf. *pisanoi*, neither of which had been formally described. Here, we assess the taxonomic affinities of the fossil toads from Farola Monte Hermoso through comparative and quantitative analyses. Our results do not support the presence of *R. arenarum* (= *R.* cf. *pisanoi*) at this locality, and we recommend against including this taxon in faunal lists of the Monte Hermoso Formation until diagnostic material has been formally described. Conversely, we corroborate the presence of the *R. diptycha* lineage, though morphometric analyses suggest the fossils may represent an as-yet-undescribed extinct species. These specimens constitute either the oldest Pampean record of *R. diptycha* or an extinct close relative, extending the known range of this lineage approximately 800 km south of its current distribution and providing new insights into the biogeography and paleoenvironmental history of the southern Pampas during the early Pliocene.

Keywords. Anura. Bufonidae. Early Pliocene. Montehermosan. Farola Monte Hermoso.

Resumen. Perdidos y encontrados: evaluación taxonómica de los sapos (Anura, Bufonidae) del Plioceno temprano de la Formación Monte Hermoso, Argentina. La transición del Mioceno Tardío al Plioceno Temprano marca un intervalo fundamental durante el cual varios géneros modernos de anuros del Neotrópico aparecen por primera vez en el registro fósil. La Formación Monte Hermoso (Plioceno Temprano, SALMA Montehermosense) en Farola Monte Hermoso, sur de la provincia de Buenos Aires, presenta la asociación de anuros más diversa del Plioceno de Argentina. Esta asociación

incluye presuntamente dos taxones de bufónidos reportados previamente como *Rhinella* cf. *diptycha* y *R.* cf. *pisanoi*, ninguno de los cuales fue descripto formalmente. Aquí evaluamos las afinidades taxonómicas de los sapos fósiles de Farola Monte Hermoso mediante análisis comparativos y cuantitativos. Nuestros resultados no respaldan la presencia de *R. arenarum* (= *R.* cf. *pisanoi*) en esta localidad, y recomendamos no incluir este taxón en listados de la Formación Monte Hermoso hasta que se describa formalmente material diagnóstico. Por el contrario, corroboramos la presencia del linaje de *R. diptycha*, aunque los análisis morfométricos sugieren que los fósiles podrían representar una especie extinta aún no descripta. Estos especímenes constituyen ya sea el registro pampeano más antiguo de *R. diptycha* o un pariente extinto cercano, extendiendo el rango conocido de este linaje aproximadamente 800 km al sur de su distribución actual y aportando nuevos elementos sobre la biogeografía y la historia paleoambiental de la Pampa austral durante el Plioceno Temprano.

Palabras clave. Anura. Bufonidae. Plioceno temprano. Montehermosense. Farola Monte Hermoso.

Introduction

Anurans (frogs and toads) represent a highly speciose group of extant land vertebrates, with almost 8000 extant species described (Frost, 2026). Although they are extremely diverse and inhabit the most disparate environments in six of the seven continents, their fossil record is comparatively one of the scarcest and most poorly known. A recent review of the lissamphibian fossil record of South America revealed that it is predominantly composed of anurans (97,6%), the majority of which occur in Argentina (52%) (Barcelos & dos Santos, 2023). The South American anuran record is dominated by Pipimorpha, Calyptocephalellidae, Ceratophryidae, and Bufonidae (Barcelos & dos Santos, 2023), whereas most other groups have been recorded only recently (Turazzini et al., 2016; Gómez et al., 2024, 2025) or are still lacking from the fossil record (Barcelos & dos Santos, 2023). However, the temporal and geographical distributions of these fossil records are not homogeneous. The early Cenozoic anuran fossil record in Argentina is clearly dominated by aquatic calyptocephalellids and pipids (Gómez et al., 2011; Suazo Lara & Gómez, 2022), distributed predominantly in Patagonia and the Andean range. From the Late Miocene onward, these two groups almost disappear, and the record shifts mainly to East Central Argentina (Pampean region), being dominated by ceratophryids and bufonids, large terrestrial hyperossified taxa, and leptodactylids, odontophryinids, and hylids, with a "modern" batrachofauna recognizable since the Middle-Late Pleistocene (Gómez et al., 2013; Turazzini et al., 2016; Turazzini, 2020; Gómez & Turazzini, 2021; Barcelos & dos Santos, 2023; and references therein).

The latest Late Miocene/Early Pliocene therefore marks a pivotal period in the history of anuran associations of Argentina, during which some modern genera are documented (e.g. *Ceratophrys*, *Lepidobatrachus*, *Rhinella*, *Leptodactylus*), although predominantly represented by extinct or indeterminate species (e.g. *C. ameghinorum*, *L.*

australis, *L. dibumartinez*, *R. loba*, *Leptodactylus* sp.) (Fernicola, 2001; Gómez et al., 2013; Nicoli, 2015; Pérez-Ben et al., 2019a; Turazzini & Gómez, 2022; Brandoni et al., 2025). The most relevant fossil locality of this time range is undoubtedly Farola Monte Hermoso (FMH from now on; southern Buenos Aires province, Argentina), where the Monte Hermoso Formation (Early Pliocene, Montehermosan SALMA) yields the most diverse Neogene anuran association, with five reported anuran taxa: *Rhinella* cf. *diptycha* (as *Bufo* cf. *paracnemis* or *R.* cf. *schneideri*), *R.* cf. *pisanoi*, *Ceratophrys ameghinorum*, *Lepidobatrachus australis*, and *Leptodactylus* sp. (Gasparini & Báez, 1975; Fernicola, 2001; Gómez et al., 2013; Tomassini et al., 2013; Deschamps & Tomassini, 2016). The presence of the two bufonid taxa is problematic since no description or illustration of these fossil toads from FMH has been provided, nor have any collection numbers been given. In the particular case of *R.* cf. *diptycha*, the reference is based on the mention of fossils that resemble this taxon, without proper justification (see Gasparini & Báez, 1975; Báez, 1986). If confirmed, these fossils would represent the earliest evidence of the *R. diptycha* lineage, which is otherwise only documented from a few South American Quaternary sites (see below; Fig. 1). Therefore, their formal description is warranted. In this work, we thoroughly assess the previously proposed taxonomic affinities of the toads from FMH using comparative anatomy and quantitative approaches.

Rhinella **and its fossil record**

Rhinella Fitzinger (1826) is the second most speciose genus of bufonids, comprising 97 extant species of South American true toads (Frost, 2026), formerly under the genus *Bufo* (Chaparro et al., 2007). Phylogenetic relationships within *Rhinella* have been addressed using multiple sources of evidence. Early hypotheses were based primarily on osteological and external morphological characters and led to the recognition of

traditional species groups within the genus (Tihen, 1962; Cei, 1972; Martin, 1972a, 1972b; Duellman & Schulte, 1992). Later, explicit phylogenetic analyses integrating morphological data were conducted by Pramuk (2006), while most subsequent large-scale analyses of Bufonidae and Anura relied mainly on molecular datasets (Van Bocxlaer et al., 2010; Pyron & Wiens, 2011; Portik et al., 2023). More recently, a comprehensive total-evidence phylogeny combining molecular and phenotypic characters from several anatomical systems has provided the most complete hypothesis of relationships within the genus (Pereyra et al., 2021).

From an osteological perspective, *Rhinella* is distinguished by a combination of cranial features within Bufonidae, including well-developed cranial crests, extensive dermal ornamentation of the roofing bones — comprising pits, striations, and rugosities particularly evident on the nasals and frontoparietals — and the robust development of elements such as the squamosals and frontoparietals (Pramuk, 2006; Pereyra et al., 2021). Phylogenetic analyses integrating morphological and molecular evidence have progressively refined the internal classification of the genus, leading to the recognition of eight Groups organized into two major Clades (Pereyra et al., 2021). The *R. marina* Clade comprises the *R. arunco*, *R. crucifer*, *R. granulosa*, *R. marina*, and *R. spinulosa* Groups. Of these, the *R. granulosa* and *R. marina* Groups have been consistently recovered as monophyletic across analyses varying considerably in taxon and character sampling (Pramuk, 2006; Maciel et al., 2010; Van Bocxlaer et al., 2010; Pyron & Wiens, 2011; Pereyra et al., 2015, 2021). Members of the *R. marina* Group share a particularly robust cranial architecture, including strongly developed preorbital, supraorbital, and pretympanic crests, broad and heavily ornamented frontoparietals, and expanded dermal bones forming a reinforced cranial roof (Pramuk, 2006; Pereyra et al., 2021), which are features relevant to the taxonomic identification of fossil cranial remains.

The fossil record of *Rhinella* in South America spans from the Miocene to the Holocene (Fig. 1), and it is largely concentrated within the *R. marina* Group. The oldest putative records are from the Lower Eocene of Itaboraí (Brazil), consisting of still undescribed, isolated bones (Estes, 1970). From the upper Oligocene of Salla (Bolivia), several fragmentary postcranial remains have been referred to *Bufo* (now *Rhinella*; Hoffstetter, 1968). Later on, these were referred to the *Rhinella marina* Group, and a single partial ilium was identified as aff. *R. arenarum* (Báez & Nicoli, 2004), although these identifications should be taken with caution due to the fragmentary nature of the specimens and the limited sample of extant taxa used in the comparisons (Gómez et al., 2025). Two records identified as cf. *Rhinella*, based on single isolated postcranial remains, are known from the Middle Miocene of central Chile (Guevara et al., 2022) and the Late Miocene of the Brazilian Amazonia (Muniz et al, 2022). The oldest unambiguous record of *Rhinella* consists of a partially articulated specimen from the Middle Miocene of La Venta, Colombia, assigned to the extant *R. marina* (Estes & Wassersug, 1963).

In Argentina, the earliest records come from the Early Pliocene Monte Hermoso Formation, where the presence of *R.* cf. *diptycha* has been mentioned (as *R.* cf. *paracnemis*; Gasparini & Báez, 1975; Báez, 1986), although this material has never been formally described or figured. From the Upper Pliocene Chapadmalal Formation of coastal Buenos Aires Province, *Rhinella arenarum* (former *R. "pisanoi"*; Casamiquela, 1967; Pérez-Ben et al., 2014) has been documented based on cranial remains (Pérez-Ben et al., 2014), and *Rhinella loba* Pérez-Ben et al., 2019a — the only formally described extinct species of the *R. marina* Group to date — was erected on the basis of a partial skull differing from all extant members of the *R. marina* Group (Pérez-Ben et al., 2019a). Other late Pliocene records from Argentina, which come from Córdoba and Jujuy provinces, represent the *R. spinulosa* Group (Cruz et al., 2018; Ponssa et al., 2022). All

other bufonid fossils from Argentina and other parts of South America are limited to the Quaternary (Fig. 1). Published Quaternary records mainly come from Argentina, but also from Brazil, Chile, Bolivia, and Peru, and document members of the *R. marina* or *R. spinulosa* Groups, or indeterminate species of *Rhinella* (Vergnaud-Grazzini, 1968; Frailey & Campbell, 1980; Araújo-Júnior & Moura, 2014; Araújo-Junior et al., 2016; Pérez-Ben et al., 2019b; Barcelos & Verdade, 2020; Labarca et al., 2020; Brizuela & Tassara, 2023; da Costa et al., 2026; Table 1). However, several other bufonid records remain undescribed (Turazzini, 2020; Barcelos & dos Santos, 2023; Table 1; Fig. 1).

The lineage represented today by *R. diptycha* has been documented in the Quaternary of Ñuapua, Bolivia (as *R.* cf. *paracnemis*; Vergnaud-Grazzini, 1968), and of northeastern Brazil (as *R. jimi* and *R. schneideri*; Araújo-Júnior & Moura, 2014). In Argentina, the single documented fossil record of *R. diptycha* consists of pelvic girdle and hindlimb bones coming from the Late Holocene site of Laguna Tres Reyes, but has not yet been described (Salemme & Madrid, 2007).

The fossils tentatively identified as *R.* cf. *diptycha* from the Monte Hermoso Formation were first mentioned by Gasparini and Báez (1975, pp. 403–404), who described them as "cranial remains and vertebrae" exhibiting morphology and size comparable to those of *R. diptycha* (as *Bufo paracnemis* in that study). At the time, these remains were under study (by A.M. Báez), thereby the determination was considered to be preliminary (Gasparini & Báez, 1975; Báez, 1986). With no description, illustration or collection number, the whereabouts of these fossils remained a mystery until recently, when they were found and identified by G.F.T. during his PhD thesis (and confirmed by his thesis supervisor, A.M. Báez) as those mentioned as *R.* cf. *diptycha* in the literature (Gasparini & Báez, 1975; Báez, 1986).

Institutional abbreviations. AMNH, American Museum of Natural History, New York, USA; CFA, Fundación de Historia Natural Félix de Azara, Buenos Aires, Argentina; CICYTTP, Centro de Investigacion Científica y de Transferencia Tecnológica a la Producción, Diamante, Argentina; 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; MCZ, Museum of Comparative Zoology, Harvard University, Harvard, USA; MD, Museo Municipal de Ciencias Naturales "Carlos Darwin", Punta Alta, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MMH, Museo Municipal de Ciencias Naturales "Vicente Di Martino", Monte Hermoso, Argentina; MMP, Museo Municipal de Ciencias Naturales Lorenzo Scaglia, Mar del Plata, Argentina; PVL, Paleontología de Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina; RBINS: Royal Belgian Institute of Natural Sciences, Brussels, Belgium; UF: University of Florida, Florida Museum of Natural History, Gainesville, USA; USNM: National Museum of Natural History, Washington, USA; UTA, University of Texas, Arlington, USA.

Geological setting

The fossil locality of FMH, situated in the southwest Atlantic coast of Buenos Aires province, Argentina (Fig. 1), has a long and rich history of paleontological studies that started with Darwin (1846) and comprises almost two centuries of continuously growing paleontological literature on palynology, sedimentology, invertebrate and vertebrate paleontology, taphonomy, and magnetostratigraphy (see Tomassini, et al 2013; Deschamps & Tomassini, 2016; and references therein). The stratigraphic provenance data of the fossil specimen indicate that it comes from the 'litostratigraphic unit II', which comprises the upper half of the Monte Hermoso Formation sequence (Fidalgo & Tonni,

1982). Several authors recognized two units at this locality, differentiated in color and separated by an erosive discontinuity: the 'Hermosense típico' (lower half, litostratigraphic unit I) and the 'Piso Chapadmalense' (upper half, litostratigraphic unit II) (see references in Tomassini et al., 2013). A detailed biostratigraphic and biochronologic study of the Monte Hermoso Formation at its type locality (FMH) concluded that the whole sequence, despite its minor sedimentological differences, biostratigraphically belongs to a single unit, the *Eumysops laeviplicatus* Range Zone (Tomassini et al., 2013). In this new interpretation, the 'litostratigraphic unit II' where the studied fossil specimens were found correspond to lateral accretion deposits (Tomassini et al., 2013, fig. 2).

There are no absolute dates from the Monte Hermoso Formation to allow exact dating of its fauna, but recently, its age has been rigorously estimated using Maximum Likelihood-Appearance Event Ordination in combination with other multivariate methods, resulting in a Monte Hermoso fauna age calculated to be 4.3 Myrs BP, with a median maximum and minimum ages of 4.71 and 3.728 Myrs BP, respectively, which means that the Monte Hermoso fauna is exclusively early Pliocene (Zanclean) in age (Prevosti et al., 2021).

Material and methods

The fossil specimens consist of isolated, well-preserved cranial and postcranial bones, some of them broken (Fig. 2), housed at the vertebrate paleontology collection of the Museo de La Plata (MLP). In view of preliminary observations, comparisons were made to a broad sample of *Rhinella* species, with emphasis on those of the *R. marina* Group. Whenever possible, we relied on first-hand examination of dry skeletons and three-dimensional models from micro-CT data listed in the Appendix. Photographs of

dry specimens were taken with a Nikon D3200 digital camera equipped with a macro lens. We took measurements of the maxilla (Table 2; Fig. 3A), including the minimum preorbital height (H1), the antorbital height (H2), and the total length (L). These were taken with an electronic digital caliper (0.01 mm resolution) and used to assess the taxonomic affinities of the fossil maxilla from FMH, exploring maxillary proportions and their variation in samples of extant *R. diptycha* and *R. arenarum*, also including PVL 2197 of "*Bufo pisanoi*" that has been synonymized with *R. arenarum* (Pérez-Ben et al., 2014). Comparisons were made with available specimens of the *R. marina* group (see Appendix), emphasizing comparisons with the two species previously mentioned for FMH (*i.e. R. dypticha* and *R. arenarum*). These are also the only extant species of the *R. marina* group with an austral distribution that reaches Argentina, with *R. arenarum* the only species currently inhabiting the Pampas and with a Pliocene record in this region (Fig. 1). The proportion H1/H2 in these taxa and the fossils was depicted in box plots, and significant differences between the species were tested through a Kruskal-Wallis test (since variances were considered equal according to an *F* test). A biplot of H1 against L was used to explore general maxillary proportions while also depicting size, whereas a non-metric Multi-Dimensional Scaling (nm-MDS) including the three measurements (H1, H2, L) allowed exploration of the distribution of taxa in the maxillary morphospace. All analyses and plots were performed in the statistical package PAST v.4.13 (Hammer et al., 2001). Anatomical terminology follows Gaupp (1896) and Turazzini and Gómez (2023). Taxonomy of species follows Frost (2026) and AmphibiaWeb (2026), whereas their geographic distribution follows IUCN (2026). The phylogenetic arrangement and terminology of *Rhinella* follow Pereyra et al. (2021), capitalizing along the manuscript well-supported Clades and Groups. Due to the

fragmentary nature of fossils and the lack of tested apomorphies, we opted for the use of open taxonomic nomenclature (Sigovini et al., 2016).

Systematic Paleontology

Bufonidae Gray, 1825

Rhinella Fitzinger, 1826

Type species. *Rhinella margaritifera* (Laurenti, 1768)

Rhinella cf. *diptycha*

Figures 2 A–O, 3 A–B.

Referred specimens. MLP 87-II-25-5 (1–3), three right maxillae. Figure 2 A–D, 3 A–B.

Description. MLP 87-II-25-5 (1–3) includes a complete edentulous right maxilla of a large individual, and two fragments of edentulous right maxillae of slightly smaller size. The labial surface of the pars facialis is predominantly covered by tubercular ornamentation, exhibiting the most substantial density in the posterior two-thirds of the element. The anterior margin is lobed, with a smaller, pointed anterodorsal lobe clearly surpassing the larger, rounded anteroventral lobe anteriorly. The ventral margin is straight and forms a continuous ridge. The dorsal margin, anterior to the short nasal process, exhibits a slight concavity and it is devoid of ornamentation. Posterior to the nasal process, the dorsal margin exhibits a slight increase in height relative to the anterior portion, having an irregularly straight contour due to abundant ornamentation in this region. The latter is interrupted by a deep groove (which likely accommodated blood vessels), which runs at a steep angle and bifurcates into anterior and posterior branches. Posterior to this groove, the dorsal margin decreases its height forming a ~27° angle with the ventral margin. In lingual view, the pars dentalis is approximately equivalent in height

to the pars facialis. The pars palatina is robust, has a rounded margin, and its dorsal surface aligns anteriorly with the notch that separates the anterior lobes. The comparatively smaller fragments (still considered large for a toad) show a similar profuse pattern of ornamentation, a deeply incised bifurcating groove (Fig. 2C), and taller pars facialis posterior to the nasal process (Fig. 2D), suggesting they all correspond to the same taxon.

Comparisons. The clear absence, in all specimens, of a broad articulation surface with the maxillary process of the nasal along the dorsal margin of the pars facialis precludes identifying MLP 87-II-25-5 as part of the *R. margaritifera* Clade and *R. granulosa* Group (see ch.7; Pramuk, 2006). Of the remaining *Rhinella* Groups, the heavy ornamentation is only congruent with that observed in species of the *R. marina* Group, being much less profuse in other groups like *R. spinulosa* (Pereyra et al., 2021) and *R. crucifer* (Fig. 4). The *R. marina* group comprises a South-Central clade and a North-Central clade, containing *R. arenarum* and *R. diptycha*, respectively (Maciel et al., 2010; Pereyra et al., 2021). Preliminary comparisons of the maxillary morphology resulted in clear differences between these taxa in the height of the pars facialis. The pars facialis of *R. diptycha* is relatively taller posterior to the nasal process than anterior to it (Fig. 3 C), whereas the opposite occurs in *R. arenarum* (Turazzini, 2020; Fig. 3 D, E). Morphometric analyses of maxillary proportions confirm that *R. diptycha* and *R. arenarum* are significantly different regarding this feature (Kruskal-Wallis test, $H = 16.5$, $P < 0.0001$; Fig. 3 F). MLP 87-II-25-5(1) closely resembles *R. diptycha*, whereas PVL 2197 (formerly "*Bufo pisanoi*") resembles extant *R. arenarum*, both falling within the intraspecific variation of the respective extant species (Fig. 3 F). Although MLP 87-II-25-5(1) and most specimens of *R. diptycha* are larger than PVL 2197 and most of extant *R. arenarum*, these differences are not linked to size, as shown by the biplot of H1/H2 against L (Fig. 3 G). The nm-MDS

morphospace shows that MLP 87-II-25-5(1) lies far from the sampled *R. arenarum*, slightly outside the morphospace defined by the extant sample of *R. diptycha* (Fig. 3 H).

Referred specimens. MLP 87-II-25-(7–9), three fragments of different right frontoparietals. Figure 2 E–G.

Description. In all three specimens, only the anterolateral portion of the frontoparietal is preserved. Despite differences in size, they all share the same characteristics and represent medium to large individuals. The orbital margin shows a well-developed supraorbital crest with a rounded margin. Striated ornamentation is present covering only the supraorbital crest. The preserved anterior margins show clear articulation with the nasal.

Comparisons. As mentioned, the presence of well-defined and heavily ornamented supraorbital crests is characteristic of the frontoparietals of toads of the *R. marina* Group (Pramuk, 2006; Pereyra et al., 2021). Striated ornamentation, usually best developed over the crests, seems to be the common pattern of the group, to the exclusion of *R. arenarum* and *R. loba*, which show a characteristic tubercular type of ornamentation (Fig. 4F; Pérez-Ben et al., 2014, 2019a). The fossil specimens show finely striated ornamentation over thick supraorbital crests, allowing their allocation within the *R. marina* Group and distinguishing them from *R. arenarum* and *R. loba*.

Referred specimens. MLP 87-II-25-13, complete atlas. Figure 2 H–J.

Description. The atlas (presacral vertebra I) corresponds to the type 1 morphology of Lynch (1971). It is not fused to the presacral II, is procoelous, and has a bicotylar anterior articulation. The cotyles are large, kidney-shaped, and are separated ventromedially by a deep narrow notch. The long axis of the cotyles forms an angle of approximately 95°. The neural canal is characterized by its substantial width and height, which constitute nearly half of the total vertebral height. The neural arch is tall and long, with a short longitudinal crest, and a broad blunt neural spine (the exposed cancellous tissue denotes a non-ossified

spine apex). The dorsal surface of the neural arch presents minute striations evidencing large areas of muscle insertions (m. intercruralis). The posterior surface of the neural spine has a large flat rectangular surface that indicates a wide articulation with the anterior surface of the presacral II neural spine. This articulation scar separates medially two deep posteriorly facing muscle insertion areas (m. intercruralis). The postzygapophysis are large, elliptical and oriented at an angle slightly greater than 45° relative to the axial plane. The centrum is broad and dorsoventrally compressed, with a posterior condyle that is twice as wide as it is tall, and as wide as the neural arch.

Comparisons. The few characters for presacral vertebrae included in phylogenetic analysis (Pereyra et al., 2021) are uninformative for *Rhinella*. The fossil atlas can be distinguished from *R. dorbignyi* (*R. granulosa* Group) that has a wide intercotylar notch (associated with the widely separated occipital condyles proposed as one of the five possible osteological synapomorphies of the *R. granulosa* Group; Pereyra et al., 2015), ¨L¨ shaped postzygapophyses, and a slender centrum that is 3 times as wide as it is tall (Turazzini, 2020). Among the species of the *R. marina* Group that we have detailed anatomical information on the atlas, it is distinguishable from that of *R. arenarum*, which has the postzygapophyses oriented in a steeper (more vertical) angle (Crudo et al., 2006). The described fossil atlas is indistinguishable from the atlases of *R. diptycha* available for comparison.

Referred specimens. MLP 87-II-25-17, posterior presacral vertebra. Figure 2 K–L.

Description. The large procoelous presacral vertebra has a large cylindrical centrum slightly constricted in the middle. The cotyle and condyle have a marginal rim slightly wider than the centrum body. Their articular surfaces are deeply concave/convex, almost conical. The neural arch dorsal surface has broad finely striated muscle insertion surfaces (m. intercruralis), separated in the middle by a thin longitudinal neural crest. The well-

defined oblique crest extends from the middle of the neural crest into the dorsal surface, reaching the posterolateral margin of the postzygapophyses. The preserved transverse process is short, with its anterior margin perpendicular to the axial plane of the centrum, and the posterior margin slightly anteriorly oriented.

Referred specimens. MLP 87-II-25-19, complete sacral vertebra. Figure 2 M–N.

Description. The procoelous sacral vertebra has a bicondylar posterior articulation for the urostyle. The posterior condyles are elliptical and separated medially by a narrow and shallow groove. Each condyle is symmetrical, with its height being two-thirds of its width. The neural canal is very small and elliptical. The neural arch is short and robust, with broad elliptical prezygapophyses oriented with their longest axis almost perpendicular to the axial plane. The arch has no discernible neural spine, but presents a low longitudinal crest and a low posterior oblique crest that briefly extends over the base of the sacral diapophysis. The latter are slightly posteriorly and dorsally oriented at an angle of approximately 10°. The diapophyses are dorsoventrally compressed and slightly expanded distally. A conspicuous muscle insertion scar (m. coccygeosacralis?) forms a depression on the dorsoposterior surfaces of the diapophyses.

Comparisons. In toads of the *R. granulosa* Group the sacral diapophyses are broadly dilated and flat (width equal to, or greater than, their length) (Pramuk, 2006; Pereyra et al., 2015, 2021). Although there are no apomorphic characters to support an unequivocal identification, the presence of slightly expanded and posteriorly oriented sacral diapophyses is congruent with its tentative allocation into the *R. marina* Group (Crudo et al., 2026). We were able to do a direct comparison with a representative sample only of *R. arenarum* and *R. diptycha*. Within these, there is some variation in the expansion of the diapophyses, being commonly more expanded in *R. arenarum* than in *R. diptycha* (Turazzini, 2020). The size, general morphology of the sacral diapophyses, and minute

neural canal are all characteristics observed in specimens of *R. diptycha*, from which the fossil could not be distinguished.

Discussion

True toads (Bufonidae) rank among the best-represented anurans in the South American fossil record, particularly from the Late Miocene onward (Pérez-Ben et al., 2014, 2019a, 2019b; Turazzini, 2020; Guevara et al., 2022; Ponssa et al., 2022; Barcelos & dos Santos, 2023). However, our survey reveals that approximately half of the published references to fossil toads (See Fig. 1; Tab. 1, and references therein)lack adequate specimen descriptions, figures, or collection numbers. This deficiency has direct consequences for the evaluation of specific records, a situation that we intend to amend for the early Pliocene fossils from FMH presented here.

The latest Late Miocene/early Pliocene constitutes a key period for understanding the rise of modern anuran faunas in southern South America, including the first appearances of the modern genera *Ceratophrys*, *Lepidobatrachus*, *Leptodactylus*, and *Rhinella* (Gómez & Turazzini, 2021; Turazzini & Gómez, 2022; Barcelos & dos Santos, 2023; Brandoni et al., 2025). These modern genera have a relatively conspicuous Late Cenozoic record, all being present at FMH (Fernicola, 2001; Gómez et al., 2013; Nicoli, 2015; Gómez & Turazzini, 2021; this paper). Notably, at this locality, *Leptodactylus* is represented by an indeterminate species (Gómez et al., 2013), whereas the escuerzos *Ceratophrys* and *Lepidobatrachus* are represented by extinct taxa, whose phylogenetic position is either uncertain or lies outside their respective genus crown group (Gómez & Turazzini, 2021; Turazzini & Gómez, 2022). In addition, at FMH, two different taxa representing —or closely related to— extant species of the toad genus *Rhinella* (i.e., *R. diptycha* and *R. arenarum*) were recurrently mentioned in the literature (see Gasparini &

Báez, 1975; Báez, 1986; Tomassini & Montalvo, 2013; Tomassini et al., 2013; Deschamps & Tomassini, 2016; Pérez-Ben et al., 2019a; Barcelos & Verdade, 2020; Ponssa et al., 2022; Barcelos & dos Santos, 2023). These might constitute the oldest Pampean records of extant anuran species, but despite their potential significance, they have not previously been supported by a formal description.

Our study of the toad fossils from FMH does not corroborate the presence of *Rhinella arenarum* at this locality, which appears in recent faunal lists cited as *R.* cf. *pisanoi* (Tomassini & Montalvo, 2013; Tomassini et al., 2013; Deschamps & Tomassini, 2016). The latter taxon has been described from two different localities of the southern Pampas, the Quequén Salado River Valley and coastal cliffs south of Mar del Plata (Casamiquela, 1967; Pérez-Ben et al., 2014), from levels of Pliocene age that could be partially coeval with those of the Monte Hermoso Formation (Pardiñas et al., 2017). To note, "*Bufo pisanoi*" was originally described as a large toad close to *R. diptycha* and *R. arenarum* (Casamiquela, 1967), but was later synonymized with *R. diptycha* by Sanchiz (1998) without further justification, a synonym that persists in most herpetological portals (AmphibiaWeb, 2026; Frost, 2026). However, Pérez-Ben et al. (2014) presented compelling qualitative and quantitative evidence that led them to place "*Bufo pisanoi*" in synonymy with *R. arenarum*, mainly based on features of the frontoparietal. Our analyses of the maxillae, including part of the holotype of "*Bufo pisanoi*" (PVL 2197), confirm this latter view. None of the fossils examined by us from the Monte Hermoso Formation, housed at different paleontological collections (i.e., MACN, MD, MMH, MLP; see Institutional abbreviations), could be identified as belonging to *R. arenarum*.

Conversely, our study corroborates that the lineage represented today by *Rhinella diptycha* is present in the anuran fauna of FMH. Our assignments of the fossils described herein to *R.* cf. *diptycha* agree with the original mention of this taxon as being part of the

assemblage of the Monte Hermoso Formation (Gasparini & Báez, 1975). It should be noted that we do not directly refer the fossils to extant *R. diptycha* because, although they clearly resemble the respective elements of this species, they provide only limited diagnostic features at the species level. Moreover, the morphometric analyses of the maxillae demonstrate that, while the proportions of MLP 87-II-25-5(1) from FMH fall within the range of variation of extant *R. diptycha*, this specimen lies outside the morphospace defined by the extant sample in the nm-MDS plot (Fig. 3H). Given the age of the Monte Hermoso Formation (no younger than 3.7 Ma; Tomassini et al., 2013; Prevosti et al., 2021) and that other anurans from this unit, based on more complete material, represent extinct species (i.e., *Ceratophrys ameghinorum*, *Lepidobatrachus australis*), this large toad likely belongs to an as-yet-undescribed species morphologically similar to the extant *R. diptycha*. Nevertheless, in the absence of apomorphic traits that unambiguously diagnose the fossils from FMH, the designation *Rhinella cf. diptycha* remains appropriate, pending the recovery of more complete material.

In this context, the fossils of *Rhinella* from FMH are of particular significance because they either constitute the oldest Pampean record of an extant species, *Rhinella diptycha*, or represent an extinct member of the same lineage. Interestingly, FMH is located about 800 km south of the most austral limit of the current distribution of *Rhinella diptycha* (AmphibiaWeb, 2026; Caseiro-Silva et al., 2026; IUCN, 2026; Fig. 1). Such an early extralimital occurrence, in turn, would provide substantial additions to the evolutionary history and biogeography of the *R. marina* Group (Maciel et al., 2010; Vallinoto et al., 2010; Pereyra et al., 2021; Rivera et al., 2022; Menéndez-Guerrero et al., 2024), but also to unveil the paleoenvironmental conditions of the southern Pampas during the early Pliocene (Tomassini & Montalvo, 2013; Sanz-Pérez et al., 2024).

461 **Acknowledgments**

462 We want to thank Natalia E. Sánchez and Maximiliano Rueda, directors of the MMH and
463 MD, respectively, for facilitating access to the paleontological collections under their
464 charge. We also appreciate the patience and help of Susana Bargo, Yanina Herrera, and
465 the rest of the team in charge of the vertebrate paleontological collection of the MLP. We
466 thank Sergio Bogan and the Azara Foundation for providing open access to their
467 herpetological collection, and Matias Peralta for providing photographs of two *R.*
468 *diptycha* collected by him. We thank the editorial team and the reviewers for the time
469 they spent to improve the manuscript. This research was partially funded by the APA -
470 Bunge & Born grant for young researchers 2025 to GFT. We want to make a special
471 recognition to the Universidad de Buenos Aires, where both authors have their workspace
472 and teaching positions. Despite the considerable budgetary constraints imposed by the
473 current government administration, the University of Buenos Aires (and the public
474 university system in general) has demonstrated a steadfast commitment to promoting
475 research and providing high-quality, public, and free education.

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738
739 **Appendix**
740 Specimens of extant and extinct Bufonidae used for comparisons. See Institutional
741 abbreviations.
742 *Atelopus zeteki*: MCZ:H 136548 (ark:/87602/m4/M42791); *Melanophryniscus moreirae*:
743 USNM:AR 207760 (ark:/87602/m4/M98144); *M. rubriventris*: MACN-He 45412; *M.*
744 *stelzneri*: UF:H 63183 (doi:10.17602/M2/M12431); *Nannophryne variegata*: FCEN
745 1636, RBINS:A 12826 (ark:/87602/m4/M98210), USNM:H 15124
746 (ark:/87602/m4/M42228); *Rhaebo blombergi*: UF:H 104602 (ark:/87602/m4/M165504);
747 *Rhaebo haematiticus*: UTA-A 57579 (ark:/87602/m4/658064); *Rhinella arenarum*: CFA-
748 AN 277, 298, 304, 318, 37, FCEN 636, 1109, MACN-He 45378, 45382, 45384, 45385,
749 45386, 45388, 45389, 45390, 45392, 45393, 43395, 45398, 45400, 45404, 45405, 45411,
750 USNM:H 70620 (ark:/87602/m4/M43880), 70622 (ark:/87602/m4/M43881), PVL 2197
751 (holotype of "*Bufo pisanoi*"); *R. cataneotica*: USNM:H 518809
752 (ark:/87602/m4/M43883); *R. crucifer*: MACN-He 45420; USNM:H 70613
753 (ark:/87602/m4/M43884), 70614 (ark:/87602/m4/M43885); *R. dapsilis*: USNM:H

754 201814 (ark:/87602/m4/M45484); *R. diptycha*: CFA-AN 36, 39, 126, CICYTTP-ZV-An-
755 021, FCEN 352(3), 664(1), 795(1), B-14, B-32, B-33, B-61, USNM:H 281765
756 (ark:/87602/m4/M45492); *R. dorbignyi*: CFA-AN 035, 109, 269, 271, 303, 307, 311,
757 FCEN 1929/1, 1929/2, MACN-He 45406, MCN:FZB 10500; *R. festae*: AMNH:H 94026
758 (ark:/87602/m4/602683); *R. icterica*: FCEN 20, USNM:H 100954
759 (ark:/87602/m4/M45487), 100957 (ark:/87602/m4/M45488); *R. loba*: MMP 1003; C; *R.*
760 *marina*: FCEN 524, UF:H 172560 (ark:/87602/m4/M163250); *R. merianae*: USNM:H
761 566017 (ark:/87602/m4/M45485), 566018 (ark:/87602/m4/M45486); *R. poeppigii*:
762 USNM:H 346829 (ark:/87602/m4/M45490), 346830 (ark:/87602/m4/M45491); *R.*
763 *spinulosa*: CFA-AN-285, MACN-He 45407, 45408, 45409, 45413. *Rhinella* indet.:
764 MACN-PV 14321, MD-FM-09-12, MD-FM-09-25, MD-FM-09-39, MD-FM-09-42,
765 MD-FM-09-43, MD-FM-08-88.
766
767 **Figure captions**
768 **Figure 1.** Fossil bufonids from South America. Map showing localities from which fossil
769 true toads were found, highlighting with an asterisk (*) those that have been described or
770 illustrated, and the current distribution of *Rhinella diptycha* and *R. arenarum*. Localities
771 marked with a white icon represent sites with fossils representing the lineage of *R.*
772 *diptycha*. See Table 1 for further details.
773 **Figure 2.** *Rhinella* cf. *diptycha* from the Monte Hermoso Formation. **A,** right complete
774 maxilla, MLP 87-II-25-5 (1), in labial, and **B,** lingual views; **C, D,** fragments of right
775 maxillae, MLP 87-II-25-5 (2–3), in labial view; **E–G,** fragments of right frontoparietals,
776 MLP 85-II-25-(7–9), in dorsal view; Atlas, MLP 87-II-25-13, in **A,** dorsal, **I,** posterior,
777 and **J,** anterior views; Posterior presacral vertebra, MLP 87-II-25-17, in **K,** dorsal, and **L,**

778 ventral views. Sacral vertebra, MLP 87-II-25-19, in **M,** dorsal, and **N,** posterior views..
779 Scale bar equals 1 cm.

780 **Figure 3.** Comparative morphology of maxillae of *Rhinella diptycha* and *R. arenarum*.
781 Right maxillae in labial view of: A–B, fossil *R.* cf. *diptycha* from the Monte Hermoso
782 Formation, MLP 87-II-25-5(1), A, drawing depicting measurements (H1, H2, L) used in
783 the analyses, B, photograph of the specimen; C, extant *R. diptycha*; D, extant *R.*
784 *arenarum*; E, fossil *R. arenarum* (formerly "*Bufo pisanoi*"). F, Boxplots comparing
785 maxillary proportion H1/H2 between species; asterisk (*) denotes significant differences
786 (Kruskal-Wallis test, $H = 16.5$, $P < 0.0001$). G, Biplot of H1/H2 against L; note the large
787 size of MLP 87-II-25-5(1). H, non-metric-Multi-Dimensional Scaling of the three
788 maxillary measurements. Scale bar equals 1 cm. See Materials and Methods and Results
789 for further details.

790 **Figure 4.** Skull 3D models, based on microCT, of selected bufonid taxa in anterolateral
791 view. **A,** *Nannophryne variegata*, **B,** *Rhinella festae* (*R. margaritifera* Clade) **C,** *R.*
792 *dorbignyi* (*R. granulosa* Group), **D,** *R. crucifer* (*R. crucifer* Group), **E,** *R. diptycha* (*R.*
793 *marina* Group), **F,** *R. arenarum* (*R. marina* Group). Scale bars equal 5 mm.

Tables

Table 1. Fossil record of Bufonidae from South America. See Figure 1.

Fossil sites	**Taxa**	**Age**	**References**
1. Farola Monte Hermoso, Buenos Aires Province, Argentina	*Rhinella* cf. *diptycha* (mentioned as *Bufo* cf. *paracnemis* and *R.* cf. *schneideri*); ?*Rhinella* cf. *arenarum*; *R.marina* Group; Bufonidae indet.	Early Pliocene	Gasparini & Báez, 1975; Báez, 1986; Tomassini & Montalvo, 2013; Tomassini et al., 2013; Barcelos & Verdade, 2020; Crudo et al., 2026; This paper
2. Sitio Don Aldo 1, Río Negro Province, Argentina	"*Bufo*" sp.	late Holocene	Prates et al., 2006
3. Chacra Santo Domingo, Arroyo Nepostá Grande, Argentina	Bufonidae indet.	Late Pleistocene–early Holocene	Deschamps & Tomassini, 2016
4. Laguna Tres Reyes 1, Buenos Aires Province, Argentina	*Rhinella* cf. *diptycha* (as *Bufo* cf. *paracnemis*)	Holocene	Salemme & Madrid, 2007
5. Quequén Salado, Buenos Aires Province, Argentina	*Rhinella arenarum* (as "*Bufo pisanoi*", in part)	Late Pliocene	Casamiquela, 1967; Pérez-Ben et al., 2014

6. Centinela del Mar, Buenos Aires Province, Argentina	*Rhinella* cf. *arenarum; R. granulosa* Group	Late Pleistocene	Turazzini, 2020; Turazzini et al., 2026
7. Chapadmalal (various sites), Buenos Aires Province, Argentina	*Rhinella loba* (*R.marina* Group); *R. arenarum* (as "*Bufo pisanoi*", in part)	Late Pliocene	Casamiquela, 1967; Pérez-Ben et al., 2014, 2019a
8. Yacimiento Constitución, Buenos Aires Province, Argentina	Bufonidae indet.	Late Pleistocene	Turazzini et al., 2014
9. Mar Chiquita, Buenos Aires Province, Argentina	cf. *Rhinella*	Middle Plaeistocene	Brizuela & Tassara, 2023
10. Daireaux, Buenos Aires Province, Argentina	*Rhinella arenarum*	Late Pleistocene	Pérez-Ben et al., 2019b
11. Río Reconquista (Merlo), Buenos Aires Province, Argentina	*Rhinella* sp.	Late Pleistocene	Turazzini et al., 2015
12. Río Luján (Luján), Buenos Aires Province, Argentina	*Rhinella* cf. *arenarum* (as *Bufo* cf. *arenarum*)	Holocene	Lezcano et al., 1993
13. Molino Doll, Entre Ríos Province, Argentina	cf. *Rhinella*	Holocene	Peralta & Ferrero, 2024

14. Paso del Río Arriba, Córdoba Province, Argentina	?*Rhinella cf. arenarum*; ?*R.* cf. *spinulosa*	Late Pliocene	Cruz et al., 2018; Barcelos & Verdade, 2020
15. San Roque (Humahuaca), Jujuy Province, Argentina	*Rhinella xerophylla* (*R. spinulosa* Group)	Late Pliocene	Ponssa et al., 2022
16. Cerro Rucañanco, Araucanía, Chile	cf. *Rhinella*	Middle Miocene	Guevara et al., 2022
17. Laguna de Tagua Tagua, Los Lagos, Chile	*Rhinella* sp.	Late Pleistocene–early Holocene	Labarca et al., 2020
18. Quereo, Coquimbo, Chile	*Rhinella spinulosa* (as *Bufo spinulosus*, lost; Bufonidae indet.	Late Pleistocene–early Holocene	Núñez et al., 1987; Jiménez-Huidobro & Sallabaerry, 2015
19. Tarija, Tarija, Bolivia	*Rhinella marina* Group (as *Bufo marinus*)	Late Pleistocene	Vergnaud-Grazzini, 1968; Barcelos & Verdade, 2020
20. Ñuapua, Chuquisaca, Bolivia	*Rhinella* cf. *diptycha* (as *Bufo paracnemis*)	Late Pleistocene–early Holocene	Vergnaud-Grazzini, 1968
21. Salla (various sites), Salla-Luribay Basin, Bolivia	?*Rhinella marina* Group (as *Bufo* sp. and *B.* aff. *arenarum*)	Late Oligocene	Hoffstetter, 1968; Báez & Nicoli, 2004; Gómez et al., 2025
22. Quebrada de Cachimayu, Cuzco, Peru	*Rhinella spinulosa*	Late Pleistocene	Frailey & Campbell, 1980
23. Talara, Piura, Peru	Bufonidae indet.	Late Pleistocene	Seymour, 2015

24. La Venta, Valle del Río Magdalena, Colombia	*Rhinella marina*	Middle Miocene	Estes & Wassersug, 1963
25. Curití, Santander, Colombia	Bufonidae indet.	Late Pleistocene	Porta, 1969
26. Gêmeo Abyss, Iporanga, Brazil	"*Bufo*" sp.	Late Pleistocene–early Holocene	Pinto, 2010
27. São José de Itaboraí, Brazil	Bufonidae indet.	Early Eocene	Estes, 1970
28. Lagoa Santa, Minas Gerais, Brazil	*Rhinella* sp.	Late Pleistocene–early Holocene	Hubbe et al., 2009
29. Gruta do Ioiô, Bahia, Brazil	*Rhinella diptycha* (as *R. jimi*)	Late Pleistocene	Muniz et al, 2020
30. Riacho Verde, Ouro Branco, Brazil	*Rhinella diptycha* (as *R. jimi*)	Late Pleistocene–early Holocene	Araújo-Júnior et al., 2016
31. Apodi, Rio Grande do Norte, Brazil	cf. *Rhinella*	Late Quaternary	da Costa et al., 2026
32. João Cativo, Itapipoca, Brazil	*Rhinella* cf. *diptycha* (as *R. jimi* and *R. schneideri*)	Late Pleistocene–early Holocene	Araújo-Júnior & Moura, 2014; Barcelos & Verdade, 2020
33. Talismã, Amazonia, Brazil	cf. *Rhinella*	Late Miocene	Muniz et al, 2022

Table 2. Measurements of the maxilla (in mm) used in the analyses. See Figure 3.

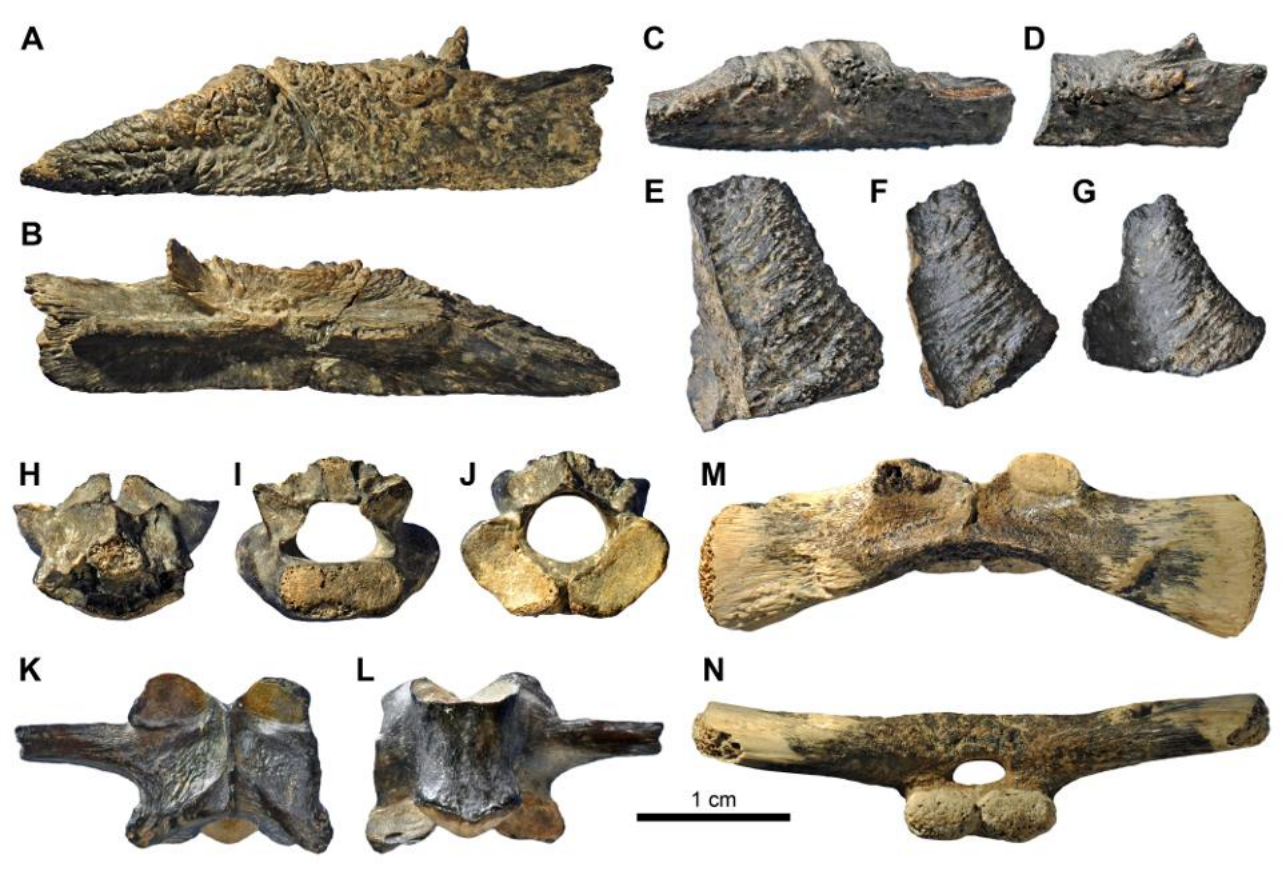
Taxon	Specimen	L	H1	H2	H1/H2
Rhinella diptycha	FCEN 352 (3)	22.25	3.49	3.52	0.99
Rhinella diptycha	FCEN 795 (1)	24.36	4.43	4.57	0.97
Rhinella diptycha	FCEN B-32	33.71	5.43	5.62	0.97
Rhinella diptycha	FCEN B-33	34.60	5.41	5.91	0.92
Rhinella diptycha	FCEN 664 (1)	39.03	6.99	7.47	0.94
Rhinella diptycha	FCEN B-61	34.19	5.72	5.75	0.99
Rhinella diptycha	CFA-AN-39	36.13	5.57	6.80	0.82
Rhinella diptycha	CFA-AN-36	35.70	6.93	6.94	1.00
Rhinella diptycha	CFA-AN-126	31.88	5.42	5.81	0.93
Rhinella diptycha	FCEN B-14	34.57	6.17	6.33	0.97
Rhinella diptycha	CICYTTP-ZV-An-021	33.10	5.95	6.70	0.89
Rhinella arenarum	FCEN 1109	34.19	5.58	5.10	1.09
Rhinella arenarum	MACN-HE 45389	26.04	4.71	4.06	1.16
Rhinella arenarum	MACN-HE 45386	23.74	3.97	3.47	1.14
Rhinella arenarum	MACN-HE 45404	20.60	3.35	3.05	1.10
Rhinella arenarum	MACN-HE 45405	20.53	3.61	3.13	1.15
Rhinella arenarum	MACN-HE 45400	25.04	4.04	3.68	1.10

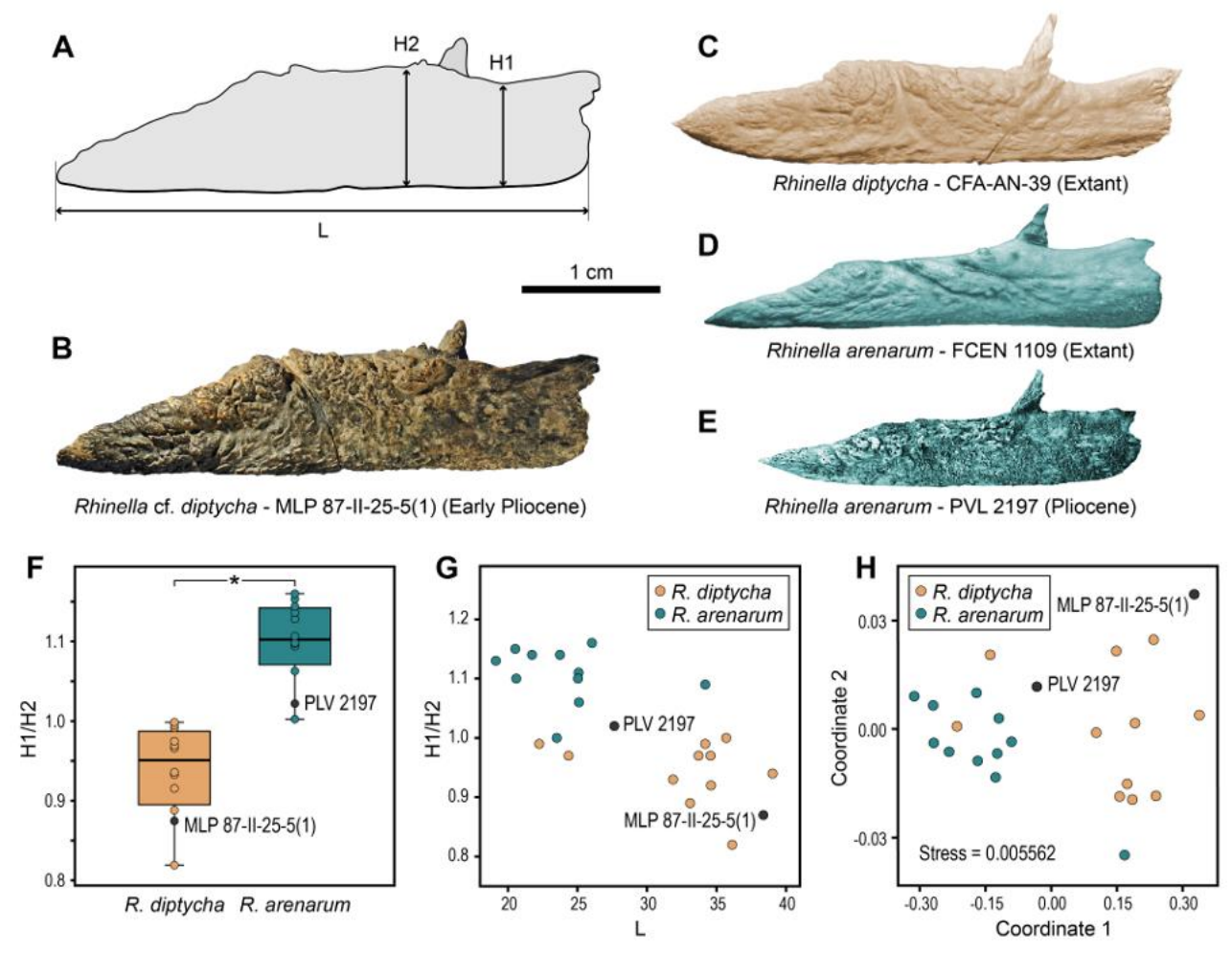
Rhinella arenarum	MACN-HE 45385	23.51	4.06	4.05	1.00
Rhinella arenarum	MACN-HE 45390	21.73	3.58	3.15	1.14
Rhinella arenarum	FCEN 636	25.08	4.26	3.85	1.11
Rhinella arenarum	MACN-HE 45411	19.13	3.43	3.04	1.13
Rhinella arenarum	MACN-HE 45392	25.11	4.39	4.13	1.06
Rhinella cf. *diptycha*	MLP 87-II-25-5 (1)	38.37	7.32	8.37	0.87
"*Bufo pisanoi*"	PVL 2197	27.65	5.11	5.00	1.02

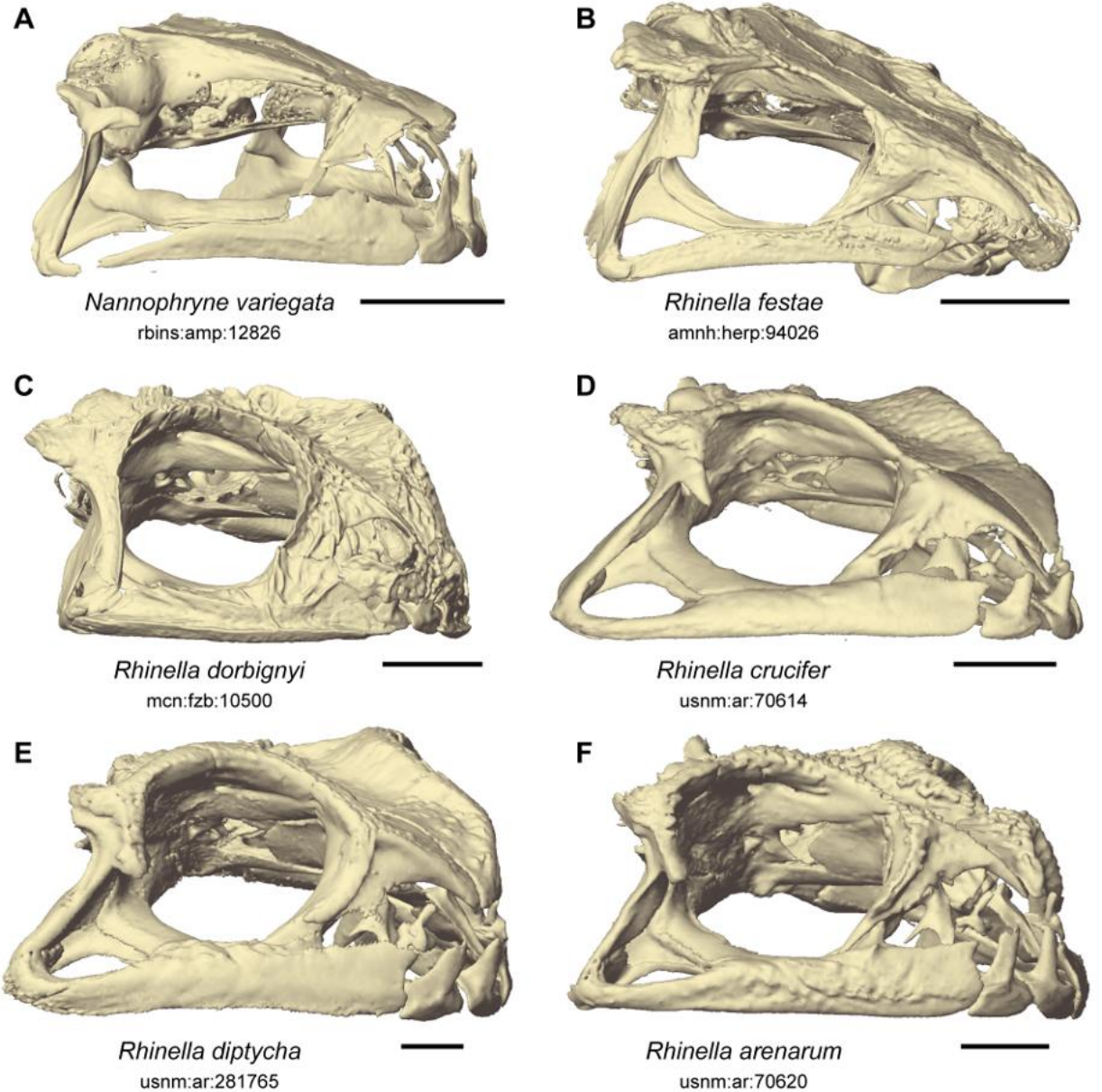
799



Fossil sites with toads described in this paper (‡) and in the literature (*). All other listed records remain unpublished or undescribed.


A
B
C
D
E
F
G
H
I
J
M
K
L
N
1 cm


A
H2
H1
L
1 cm
B
Rhinella cf. diptycha - MLP 87-II-25-5(1) (Early Pliocene)
C
Rhinella diptycha - CFA-AN-39 (Extant)
D
Rhinella arenarum - FCEN 1109 (Extant)
E
Rhinella arenarum - PVL 2197 (Pliocene)
F
H1/H2
PLV 2197
MLP 87-II-25-5(1)
R. diptycha R. arenarum
G
R. diptycha
R. arenarum
PLV 2197
MLP 87-II-25-5(1)
H1/H2
L
H
R. diptycha
R. arenarum
MLP 87-II-25-5(1)
PLV 2197
Stress = 0.005562
Coordinate 2
Coordinate 1


A
Nannophryne variegata
rbins:amp:12826
B
Rhinella festae
amnh:herp:94026
C
Rhinella dorbignyi
mcn:fzb:10500
D
Rhinella crucifer
usnm:ar:70614
E
Rhinella diptycha
usnm:ar:281765
F
Rhinella arenarum
usnm:ar:70620