

Hop on the game: identification keys to medium- to large-sized anurans of Argentina using just one bone

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Recibido: 18 de abril de 2026 - **Aceptado:** 22 de julio de 2026 - **Publicado:** 1 de octubre de 2026

Para citar este artículo: Giuliano Sergio Crudo, Guillermo Fidel Turazzini, & Raúl Orencio Gómez (2026). Hop on the game: identification keys to medium- to large-sized anurans of Argentina using just one bone. *Publicación Electrónica de la Asociación Paleontológica Argentina* 26(2): 45–64.

Link a este artículo: <http://dx.doi.org/10.5710/PEAPA.22.07.2026.572>

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ISSN 2469-0228

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HOP ON THE GAME: IDENTIFICATION KEYS TO MEDIUM- TO LARGE-SIZED ANURANS OF ARGENTINA USING JUST ONE BONE

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Abstract. Anurans (frogs, toads, escuerzos) have been an important part of terrestrial ecosystems since the Mesozoic era. Their bones, although relatively fragile, are frequently found as fossils, as well as in pellets, and carry useful taxonomic and ecological data, which in turn have the potential to inform about environmental and climatic conditions. However, these remains are often unidentified as such or, at best, identified as indeterminate anurans, thereby downplaying the value of isolated anuran bones. This situation has been fueled by the scarcity of specialists, but also by the lack of appropriate osteological collections and specialized literature that could provide tools for their study. With the aim of alleviating these shortcomings and hoping to spark interest in the study of amphibian osteology, we provide eight dichotomous keys (both in English and Spanish) for identifying isolated bones of medium- to large-sized anurans from Argentina, which make up most of its amphibian fossil record. In all cases, dichotomous keys allow for the successful identification of families and, in most cases, genera. A case study highlights the effectiveness of these keys in identifying a fossil *Rhinella* toad originally cataloged as *Ceratophrys*. We expect our dichotomous keys to be a useful tool for anyone dealing with the postcranial skeletal morphology of Neotropical anurans, including paleontologists, archaeologists, herpetologists, ornithologists, museum staff, and the general public.

Key words. Amphibia. Anura. Dichotomous key. Fossils. Osteology. Paleontology. Zooarcheology.

Resumen. UNITE AL JUEGO: CLAVES PARA IDENTIFICAR ANUROS DE MEDIANO Y GRAN TAMAÑO DE ARGENTINA CON APENAS UN HUESO. Los anuros (ranas, sapos, escuerzos) son parte importante de los ecosistemas terrestres desde el Mesozoico. Sus huesos, aunque relativamente frágiles, se encuentran con frecuencia como fósiles, así como parte de egagrópidas, y contienen información taxonómica y ecológica, que a su vez tienen el potencial de informar sobre las condiciones ambientales y climáticas. Sin embargo, a menudo sus restos no son identificados como tales o, en el mejor escenario, son identificados como anuros indeterminados, así subestimando el valor de los restos aislados de anuros. Esta situación se ha visto agravada por la escasez de especialistas, pero también por la carencia de colecciones osteológicas apropiadas y de literatura especializada que provea herramientas para su estudio. Con el objetivo de paliar estas carencias y buscando contagiar el interés por el estudio de la osteología de anuros, presentamos ocho claves dicotómicas (en inglés y español) para la identificación de restos aislados de anuros de mediano y gran tamaño de Argentina, que componen la mayor parte del registro fósil de anfibios del país. En todos los casos, las claves permiten identificar correctamente familias y, en la mayoría de ellos, géneros. Un caso de estudio resalta la eficacia de estas claves para identificar un *Rhinella* fósil originalmente catalogado como *Ceratophrys*. Anticipamos que nuestras claves resultarán útiles para cualquiera que estudie la morfología del esqueleto postcraneano de anuros neotropicales, incluyendo paleontólogos, arqueólogos, herpetólogos, ornitólogos, personal de museos y el público en general.

Palabras clave. Anfibios. Anura. Clave dicotómica. Fósiles. Ranas. Osteología. Paleontología. Zooarqueología.

INTRODUCTION

Anurans (frogs, toads, escuerzos) have been an important part of terrestrial ecosystems worldwide since the Mesozoic Era (Gardner et al., 2016; Gómez & Lires, 2019; Lemierre & Blackburn, 2022). Their body plan has remained unchanged for at least the last 200 million years (Pérez-Ben et al., 2024), making them unique and unmis-

takable among vertebrates (Handrigan & Wassersug, 2007). As Inger (1967, p. 369) framed it—paraphrasing the renowned poet Gertrude Stein—“*A frog is a frog, is a frog.*” The conserved body plan of anurans encompasses a distinctive array of traits in their postcranial skeleton: a very short vertebral column with a bicotyler atlas (first presacral), a sacrum (lacking ribs), and a urostyle (fusion of coccyx and

ossified hypochord), an elongated ilia, limbs with fused zeugopodial bones into radio-ulna and tibiofibula, and extremely elongated proximal tarsals (tibiale-fibulare) forming an additional segment of the hindlimbs (Handrigan & Wassersug, 2007; Pugener & Maglia, 2009; Lires et al., 2016). Their conservative skeletal morphology makes identifying individual bones as belonging to anurans relatively easy, while it has also led to rampant homoplasy within the group (Paluh et al., 2020; Pérez-Ben et al., 2024), complicating morphology-based systematics (Báez & Gómez, 2018).

Anuran bones, although relatively fragile, could be major components of fossil assemblages (Roček et al., 2010; Blain et al., 2014; Bisbal-Chinesta et al., 2020; Jansen et al., 2023), as well as of recent pellets from owls and other birds of prey (Roulin & Dubey, 2013; Gómez & Lires, 2015; Alcaráz & Kaufmann, 2022; Formoso et al., 2024). Despite the high levels of homoplasy in anurans, when thoroughly studied, isolated bones can be used to identify families, genera, and, in some cases, species, either based on unique, evolutionary derived features (apomorphies) or diagnostic combinations of osteological traits (Báez et al., 2012; Bastir et al., 2014; Pérez-Ben et al., 2014; Turazzini et al., 2016; Blackburn et al., 2020; Delfino, 2020; Gómez & Turazzini, 2021; Vallejo-Pareja et al., 2024; Lemierre et al., 2025). However, anuran bones are frequently unidentified below the level of Anura (Romano et al., 2002; Quintana, 2016; Escobar et al., 2025; Fernández et al., 2025), and in some cases, despite their uniqueness, they are misidentified and confused with other vertebrate groups (Rodríguez-Villamil et al., 2022). All of this downplays the value of isolated anuran bones.

As water-dependent ectotherms, anurans and other amphibians are closely tied to climate and water availability (Walls et al., 2013) and, thus, are considered good indicators of environmental conditions (Price et al., 2007; Zhelev et al., 2022; de Albuquerque et al., 2024; Glebsattel & Dehling, 2026). Roughly half of all anuran diversity (~4000 species, likely a vast underestimation; Vacher et al., 2020) is concentrated in the Neotropical Realm, 40% of which is thought to be globally threatened (Bolaños et al., 2008; Harfoot et al., 2021; Luedtke et al., 2023). Since most Neotropical anurans have narrow climatic niches and occupy specific microhabitats (Gómez-Rodríguez et al., 2015; Moen

& Wiens, 2017), this makes them particularly sensitive to climate change and habitat loss (Bolaños et al., 2008; Ceron et al., 2023). Just as the presence of extant amphibians can indicate environmental health and lower habitat disturbance, their presence in the fossil record can also reveal significant information about past conditions (Blain et al., 2009; Cruz et al., 2024). Paleoecological approaches based on reliable identification of fossil amphibians from Europe have proven fruitful in inferring past climates and environments (Blain et al., 2009, 2014, 2022; Martínez-Monzón et al., 2023; Villa et al., 2024). However, despite their great potential in informing environmental conditions, very little research has been conducted on fossil anurans from the Neotropics, including Argentina (Pérez-Ben et al., 2019a; Cruz et al., 2024; Gómez et al., 2025).

Around 170 anuran species in 42 genera and 15 families inhabit Argentina today (AmphibiaWeb, 2026), but only a few of them have been recorded as fossils or prey items, mostly including medium- to large-sized bufonids (true toads), ceratophryids (escuerzos), leptodactylids (nest-building frogs), and odontophrynids (lesser escuerzos) (Cione & Báez, 2007; Pérez-Ben et al., 2019a; Turazzini, 2020; Turazzini & Gómez, 2022; Formoso et al., 2024). In addition, pipids and calyptocephalellids, which are not part of the extant batrachofauna from Argentina, have a relatively rich fossil record in the country dating back to the Late Cretaceous (Muzzopappa, 2019; Suazo Lara & Gómez, 2022; Barcelos & dos Santos, 2023). Although major advances in documenting anuran isolated remains from Argentina have been done during the last decades (Cione & Báez, 2007; Báez et al., 2012; Gómez et al., 2013, 2025; Pérez-Ben et al., 2014, 2019a, 2019b; Turazzini et al., 2014, 2016; Gómez, 2016; Gómez & Turazzini, 2016, 2021; Turazzini, 2020; Suazo Lara & Gómez, 2022; Peralta & Ferrero, 2024; Brandoni et al., 2025), several records remain understudied or simply unidentified below the level of Anura (e.g., Quintana, 2016; Escobar et al., 2025; Fernández et al., 2025).

This situation might have been fueled by the scarcity of specialists, but also by the lack of appropriate osteological collections and specialized literature that could provide tools for their study. One such tool that has proven useful in other parts of the world for identifying isolated remains of

understudied vertebrate groups, including anurans (e.g., Bailon, 1999; Pili et al., 2022), is the dichotomous key. Its simplicity and easy-to-use appeal are major strengths of this tool, but despite its potential value in helping with the identification of isolated bones of anurans, dichotomous key for Neotropical taxa has not yet been developed. With the aim of alleviating the abovementioned shortcomings and with the hope of sparking interest in the study of amphibian osteology, we provide eight dichotomous keys (both in English and Spanish) for identifying isolated bones of medium-to-large-sized anurans from Argentina, since they make up most of its amphibian paleontological and archeological record (Cione & Báez, 2007; Barcelos & dos Santos, 2023) and are often reported as prey items in avian pellets (Gómez & Lires, 2015; Formoso et al., 2024). We make the dichotomous keys as accessible as possible to non-specialists, so they could be equally applied to fossils, dry skeletons, avian pellets (extant or fossil), and roadkills, within the realm of different fields such as paleontology, zooarcheology, herpetology, ornithology, and comparative anatomy (Fig. 1).

MATERIALS AND METHODS

Taxon sampling

We surveyed the osteology of anuran species to assemble dichotomous keys that would allow the identification based on isolated bones of medium-to-large-sized anurans from Argentina. These species represent less than 20% of the extant anura diversity in the country (AmphibiaWeb, 2026), yet account for most of the known fossil record (Cione & Báez, 2007; Barcelos & dos Santos, 2023). Included taxa are typically common and widespread in the region and have a relatively high preservation potential (e.g., *Rhinella* toads), whereas many small anurans often have more limited geographical ranges, being lacking from the fossil record (e.g., *Melanophryniscus*). We therefore limited our sample to medium-to-large-sized species to keep the keys as simple as possible while maximizing their applicability to extant and extinct anuran groups from Argentina. Our sample consisted of adults of extant species with snout-vent lengths greater than 50 mm, belonging to ten different groups (genera and species groups within a single genus) with a fossil record in Argentina. Pipids, with

an extensive fossil record in Argentina (Báez et al., 2012; Suazo Lara & Gómez, 2022), were represented by extant members of the two most diverse genera (*Pipa*, from South America, and *Xenopus*, from Africa) to encompass morphological disparity within the group, although neither genus has been reliably identified in the fossil record of the country (Barcelos & dos Santos, 2023). Similarly, *Calyptocephalella*, with an extensive record in Patagonia (Muzzopappa, 2019; Suazo Lara & Gómez, 2022), was represented by its sole extant species currently restricted to forests of central Chile. Other genera, each with two to several extant species in Argentina, were sampled seeking to broadly represent their taxonomical and morphological diversity. We sampled all the species of *Ceratophrys* and *Lepidobatrachus*, and most of *Odontophrynus* inhabiting Argentina. Following previous studies and our own preliminary observations (Pérez-Ben et al., 2019a; Turazzini, 2020; Pereyra et al., 2021), the extremely diverse genus *Rhinella*, including widespread medium-to-large-sized toads, was further subdivided into species groups (i.e., Gr. *R. marina*, *R. granulosa*, *R. spinulosa*). The speciose but relatively morphologically conserved genus *Leptodactylus* (Lynch, 1971; Magalhães et al., 2020), represented by several species in our sample, could not be consistently subdivided into species groups, despite some osteological differences have been reported (Gómez et al., 2013).

Specimens

In total we examined firsthand 103 dry skeletons and 21 mesh models based on micro-CT data from MorphoSource (www.morphosource.org; Blackburn et al., 2024), representing eight genera with extant or extinct medium-to-large-sized representatives from Argentina and 38 species (Supplementary Material, Table S1). Mesh models were generated using Fiji (ImageJ v.1.53c; Schindelin et al., 2012) and 3D Slicer v.4.11.2 (Fedorov et al., 2012; Kikinis et al., 2014), following the workflow of Buser et al. (2020). Images of mesh models were generated in Meshlab v.2020.06 (Cignoni et al., 2008). Photographs of dry specimens were taken with a Nikon D3200 digital camera equipped with a macro lens.

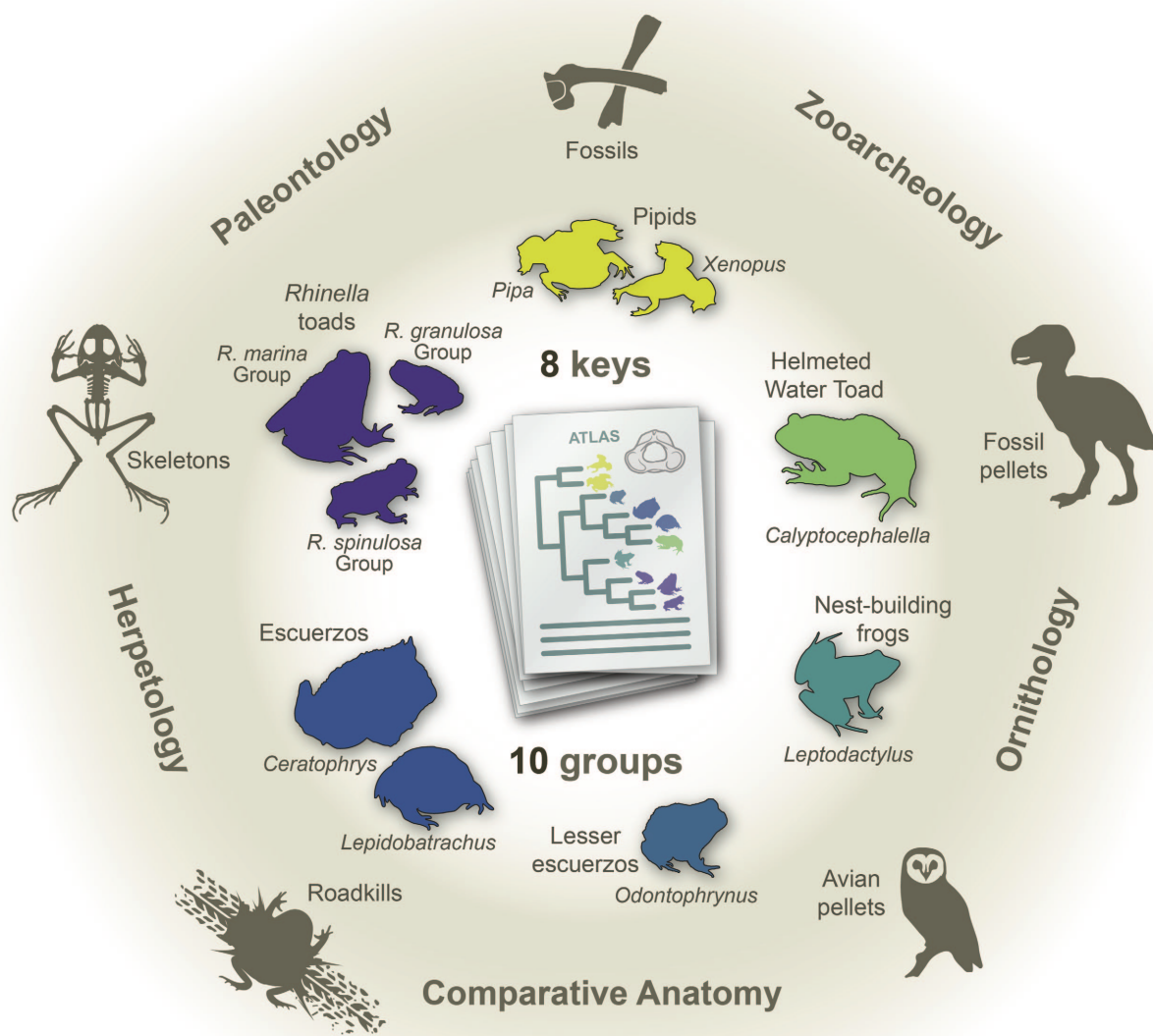


Figure 1. Schematic synopsis of the present work, eight dichotomous keys based on isolated bones (atlas, sacrum, urostyle, humerus, radio-ulna, tibiofibula, tibiale-fibulare, ilium) for ten groups of anurans (*i.e.*, two pipid genera, *Calyptocephalella*, *Leptodactylus*, *Odontophrynus*, two ceratophryid escuerzos, and three species groups of *Rhinella* toads), and its potential application to different kinds of specimens (fossils; skeletons; extant and fossil avian pellets; roadkills), within different fields (paleontology; zooarcheology; herpetology; ornithology; comparative anatomy).

Dichotomous keys

We assembled eight separate dichotomous keys, one for each of eight postcranial bones of the anuran skeleton that are relatively easy to recognize as belonging to frogs and are frequently found as fossils or in avian pellets (Gómez & Turazzini, 2016; Turazzini, 2020; Mignino, 2021; Fernández et al., 2025). The selected bones were the atlas (first

presacral vertebra), sacrum, and urostyle from the vertebral column; humerus, radio-ulna, tibiofibula, and tibiale-fibulare from the limbs; and the ilium, which has long been considered the best single element for identifying anurans (Gómez & Turazzini, 2016). For the dichotomous keys, we used several osteological features that were previously considered in systematic studies (Gómez, 2016; Gómez &

Turazzini, 2021; Supplementary Material, Table S2) to maximize their diagnostic nature in a phylogenetic framework, but were re-stated to make them as accessible as possible to non-specialists. We also incorporated several new characters that were not explicitly included in previous data matrices, but were considered in paleontological studies of diverse anuran taxa from southern South America (Turazzini et al., 2016; Pérez-Ben et al., 2019a; Turazzini, 2020; Suazo Lara & Gómez, 2022; Gómez et al., 2024, 2025). Additionally, we considered several bone proportions based on linear measurements (Fig. 2; Supplementary Material, Table S3), which were taken using a digital caliper (0.01 mm). It is important to note that, when key steps include multiple characters, it is not necessary to evaluate all of them. This is particularly important when identifying fragmentary elements, which is common when dealing with fossils. In this case, it is sufficient to evaluate at least one of the listed characters to progress to the next step of the dichotomous key. Anatomical terminology is depicted in Figure 2 and followed Gómez and Turazzini (2016) for the ilium, Lynch (1971) for the types of atlas, and Turazzini and Gómez (2023) for all other bones. The orientation of limb bones followed Gaupp (1896). The taxonomy and geographic distribution of anuran genera followed AmphibiaWeb (2026). The effectiveness of dichotomous keys was expressed as the proportion of families and genera/species groups that could be positively identified in each case (*i.e.*, x/6 families; x/10 genera/species groups). The usefulness of dichotomous keys was further assessed with a case study involving an already cataloged fossil (MACN-Pv 14321) from the Monte Hermoso Formation (Lower Pliocene), which was originally misidentified as an escuerzo (*Ceratophrys*).

Institutional acronyms. **FCEN**, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Autónoma de Buenos Aires, Argentina; **MACN-He**, Colección de Herpetología, Museo de Ciencias Naturales “Bernardino Rivadavia”, Ciudad Autónoma de Buenos Aires, Argentina; **MACN-Pv**, Colección de Paleontología de Vertebrados, Museo de Ciencias Naturales “Bernardino Rivadavia”, Ciudad Autónoma de Buenos Aires, Argentina; **MCZ:H**, Herpetological Collection, Museum of Comparative Zoology, Harvard University, Harvard, USA; **MLP-A**, Colección de Anfibios,

Museo de La Plata, Universidad Nacional de La Plata, La Plata, Argentina; **MVZ:H**, Herpetological Collection, Museum of Vertebrate Zoology, University of California, Berkeley, USA; **UF:H**, Herpetological Collection, University of Florida, Florida Museum of Natural History, Gainesville, USA.

RESULTS

Dichotomous keys

Below we provide eight dichotomous keys for eight different postcranial bones of the anuran skeleton to identify families and/or genera/species groups of medium-to-large-sized anurans that have extant or extinct representatives in Argentina. In Table 1 (Supplementary Material, Table S4 in Spanish) are compiled those based on bones from the vertebral column (atlas, sacrum, urostyle), which are figured for ten different groups in Figure 3. Table 2 (Supplementary Material, Table S5 in Spanish) includes keys based on long bones from limbs (humerus, radio-ulna, tibiofibula, tibiale-fibulare), which are figured for ten different groups in Figure 4. Table 3 (Supplementary Material, Table S6 in Spanish) is the dichotomous key based on the ilium, which is figured for ten different groups in Figure 5. Family level can be successfully reached in all eight keys (6/6), allowing identification of: Pipidae, Calyptocephalellidae, Ceratophryidae, Leptodactylidae, Odontophrynidae, and Bufonidae. In all cases, isolated bones of the bizarre-looking Pipidae can be distinguished from neobatrachian frogs in the first step of each dichotomous key. In all eight keys, six out of eight genera can also be identified: *Pipa*, *Xenopus*, *Calyptocephalella*, *Leptodactylus*, *Odontophrynus*, and *Rhinella*, whereas the escuerzos' genera *Ceratophrys* and *Lepidobatrachus* (family Ceratophryidae) can be identified in only half of the keys (atlas, urostyle, humerus, radio-ulna). Additionally, most keys allow some discrimination between different species groups of *Rhinella* toads (atlas, sacrum, urostyle, radio-ulna, tibiofibula, ilium). This way, all ten genera/species groups considered can be identified based on atlas (10/10), urostyle (10/10), and radio-ulna (10/10), whereas all but some *Rhinella* toads and/or escuerzos' genera can be identified based on the remaining dichotomous keys, as follows: sacrum (6/10), humerus (8/10), tibiofibula (6/10), tibiale-fibulare (6/10), ilium (6/10).

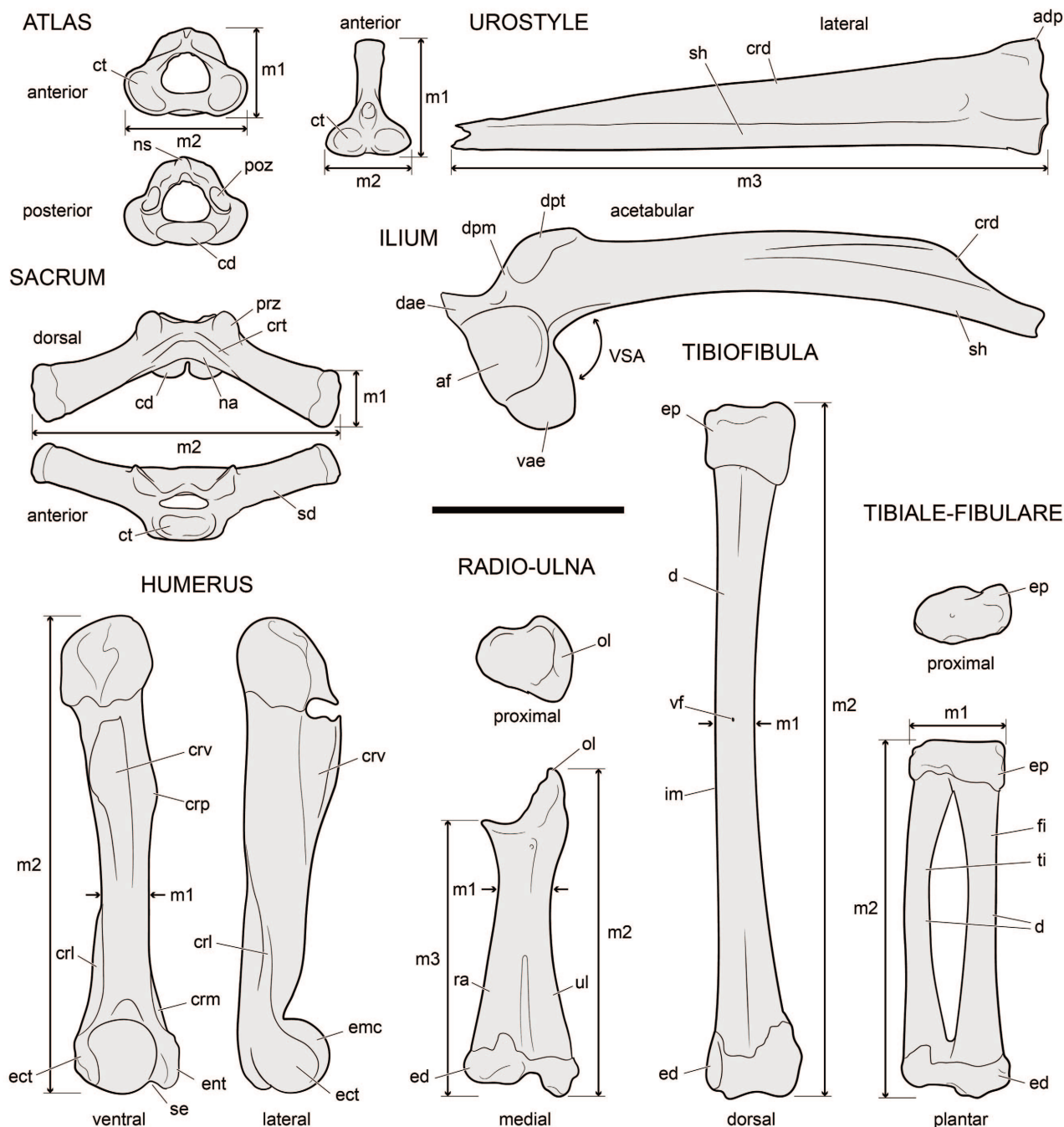


Figure 2. Bones used in the dichotomous keys. Atlas, sacrum, urostyle, humerus, radio-ulna, tibiofibula, tibiale-fibulare, and ilium of *Leptodactylus latrans* (MVZ:H:176272). Measurements are explained in Table S3. Abbreviations: adp, anterodorsal process; af, acetabular fossa; cd, condyle; crd, dorsal crest; crl, lateral crest; crm, medial crest; crp, parietal crest; crt, transverse crest; crv, ventral crest; ct, cotyle; d, diaphysis; dae, dorsal acetabular expansion; dpm, dorsal prominence; dpt, dorsal protuberance; ect, ectepicondyle; ed, distal epiphysis; emc, eminentia capitata (humeral ball); ent, entepicondyle; ep, proximal epiphysis; fi, fibulare; im, internal margin; na, neural arch; ns, neural spine; ol, olecranon; poz, postzygapophysis; prz, prezygapophysis; ra, radius; sd, sacral diapophysis; se, entepicondylar groove (sulcus); sh, shaft; ti, tibiale; ul, ulna; vae, ventral acetabular expansion; vf, ventral foramen; VSA, angle between ventral acetabular expansion and ilial shaft. All bones are at the same scale. Scale = 1 cm.

TABLE 1. Dichotomous keys to medium-to-large-sized anurans from Argentina using isolated bones from the vertebral column. When a key step involves multiple characters, it is sufficient to evaluate one of them to progress to the next step.

Atlas

Figures 2, 3

1.	Centrum concave posteriorly, forming a cotyle (opisthocoelous). Pipidae	2
-	Centrum convex posteriorly, forming a condyle (procoelous). Neobatrachia	3
2.	Anterior cotyles nearly round; atlas completely fused to next vertebra	<i>Pipa</i>
-	Anterior cotyles kidney-shaped; atlas typically discrete, unfused	<i>Xenopus</i>
3.	Neural spine tall or moderately tall	4
-	Neural spine low	7
4.	Anterior cotyles separated (Type II); postzygapophyseal facets small, round, facing lateroventrally	<i>Odontophrynus</i>
-	Anterior cotyles adjacent or confluent (Type III); postzygapophyseal facets large	5
5.	Atlas very tall ($m1/m2 > 0.95$); condyle nearly round; postzygapophyseal facets long, facing posteriorly	<i>Ceratophrys</i>
-	Atlas moderately tall ($m1/m2: 0.75-0.95$); condyle oval; postzygapophyseal facets facing posterolaterally	6
6.	Postzygapophyseal facets moderately long, undivided	<i>Lepidobatrachus</i>
-	Postzygapophyseal facets relatively short, divided in dorsal (larger) and ventral (smaller) parts	<i>Calyptocephalella</i>
7.	Anterior cotyles large and nearly round; condyle depressed, curved laterally (smile-shape)	<i>Leptodactylus</i>
-	Anterior cotyles elongated; condyle oval or depressed (not smile-shape). <i>Rhinella</i>	8
8.	Atlas low ($m1/m2 < 0.75$); cotyles well separated; condyle depressed, less so laterally (lemniscate-shape)	<i>Rhinella: R. granulosa</i> Gr.
-	Anterior cotyles barely separated; condyle oval; neural arch relatively tall	9
9.	Anterior cotyles kidney-shaped with completely round margins; postzygapophyseal facets simple, facing lateroventrally	<i>Rhinella: R. spinulosa</i> Gr.
-	Anterior cotyles with more angled lateral and ventral margins; postzygapophyseal facets divided in dorsal (larger) and ventral (smaller) parts; neural arch rectangular-shape	<i>Rhinella: R. marina</i> Gr.

Sacrum

Figures 2, 3

1.	Sacrum fused to urostyle (sacrourostyle); anterior condyle; diapophyses expanded ($m1/m2 > 0.6$). Pipidae	2
-	Sacrum bicondylar posteriorly; anterior cotyle (procoelous); diapophyses less dilated ($m1/m2 < 0.55$). Neobatrachia	3
2.	Prezygapophyseal facets simple, lacking crests; neural arch longer than wide	<i>Pipa</i>
-	Prezygapophyseal facets with crests; neural arch wider than long or squared	<i>Xenopus</i>
3.	Diapophyses flattened distally. <i>Rhinella</i>	4
-	Diapophyses round distally	5
4.	Prezygapophyseal facets oval, transversely oriented; diapophyses slightly dilated ($m1/m2: 0.27-0.35$)	<i>Rhinella: R. marina</i> Gr.
-	Prezygapophyseal facets round, oblique in dorsal view; diapophyses more dilated ($m1/m2: 0.40-0.55$)	<i>Rhinella: R. granulosa</i> Gr., <i>R. spinulosa</i> Gr.
5.	Neural spine high; diapophyses somewhat dilated ($m1/m2: 0.27-0.35$); transverse crest poorly developed	<i>Calyptocephalella</i>
-	Transverse crest present, extended onto diapophyses	6
6.	Diapophyses relatively narrow ($m1/m2 < 0.27$), oriented posterolaterally; prezygapophyseal facets oval, poorly projected from neural arch	<i>Leptodactylus</i>
-	Diapophyses clearly oriented laterodorsally in posterior view (V-shape); prezygapophyseal facets large, round	7
7.	Transverse crest with sharp edges, ending abruptly distally; prezygapophyses narrowly separated (less than one prezygapophyseal width)	<i>Odontophrynus</i>
-	Transverse crest with round edges, merging into diapophyses distally; prezygapophyses more separated (about one prezygapophyseal width)	Ceratophryidae

TABLE 1. Continuation.

Urostyle

Figures 2, 3

1.	Urostyle fused to sacrum (sacrourostyle); urostyle very slender ($m2/m3 < 0.1$). Pipidae	2
-	Urostyle discrete; two anterior cotyles (bicondylar joint); variably robust, but not particularly slender ($m2/m3$: 0.1–0.3). Neobatrachia	3
2.	Dorsal crest distinct, sharp anteriorly; ventral surface round	<i>Pipa</i>
-	Dorsal crest broad, blunt anteriorly; ventral surface keeled	<i>Xenopus</i>
3.	Urostyle robust ($m2/m3$: 0.2–0.3)	4
-	Urostyle relatively slender ($m2/m3 < 0.2$)	6
4.	Urostyle clearly higher than wide anteriorly ($m1/m2 > 1.25$)	<i>Ceratophrys</i>
-	Urostyle as high as wide anteriorly ($m1/m2 \approx 1$)	5
5.	Anterodorsal process small	<i>Lepidobatrachus</i>
-	Anterodorsal process large	<i>Odontophrynus</i>
6.	Urostyle clearly higher than wide anteriorly ($m1/m2 > 1.25$)	7
-	Urostyle nearly as high as it is wide anteriorly or lower ($m1/m2 < 1.2$)	8
7.	Dorsal crest short, occupying 2/3 of the urostyle length; shaft nearly round	<i>Calyptocephalella</i>
-	Dorsal crest long, occupying all of the urostyle length; shaft flattened	<i>Leptodactylus</i>
8.	Anterodorsal process indistinct; dorsal crest relatively short	<i>Rhinella</i> : <i>R. granulosa</i> Gr.
-	Anterodorsal process distinct	9
9.	Urostyle slightly wider than high anteriorly ($m1/m2 < 1$)	<i>Rhinella</i> : <i>R. spinulosa</i> Gr.
-	Urostyle slightly higher than wide anteriorly ($m1/m2$: 1–1.2)	<i>Rhinella</i> : <i>R. marina</i> Gr.

Case study

We test the dichotomous keys on a fossil anuran from the Monte Hermoso Formation (Lower Pliocene) originally cataloged as *Ceratophrys* sp. (MACN-Pv 14321). We selected this fossil because it was originally misidentified as a *Ceratophrys* escuerzo and preserves three bones considered in our dichotomous keys, allowing us to test the accuracy and consistency of the identifications. The fossil consists of a badly preserved skull fragment and an almost complete, partially articulated vertebral column, including atlas and other seven presacral vertebrae, an almost complete sacrum, and the anterior half of the urostyle (Fig. 6). In principle, atlas, sacrum, and urostyle could be evaluated using the respective dichotomous keys (Tab. 1; Supplementary Material, Table S4). The atlas of MACN-Pv 14321 is articulated to the second presacral, concealing the morphology of

the posterior condyle and postzygapophyseal facets, which are relevant features of the key to identify neobatrachian taxa. However, a posterior condyle (procoelous condition) can be inferred based on the contact with presacral II, as defined in ventral view, easily allowing the exclusion of pipids (step 1: go to 3). The neural spine is relatively broad and low, allowing the exclusion of ceratophryids, *Odontophrynus*, and *Calyptocephalella* (step 3: go to 7). The elongate shape of anterior cotyles allows excluding *Leptodactylus* and identifies *Rhinella* (step 7: go to 8). The shape of the barely separated cotyles, with angled margins, together with the general proportions of the atlas, including its relatively tall neural arch, further allows excluding the *R. granulosa* species group (step 8: go to 9) and the *R. spinulosa* species group, thereby identifying the atlas as belonging to the *R. marina* species group (final step 9).

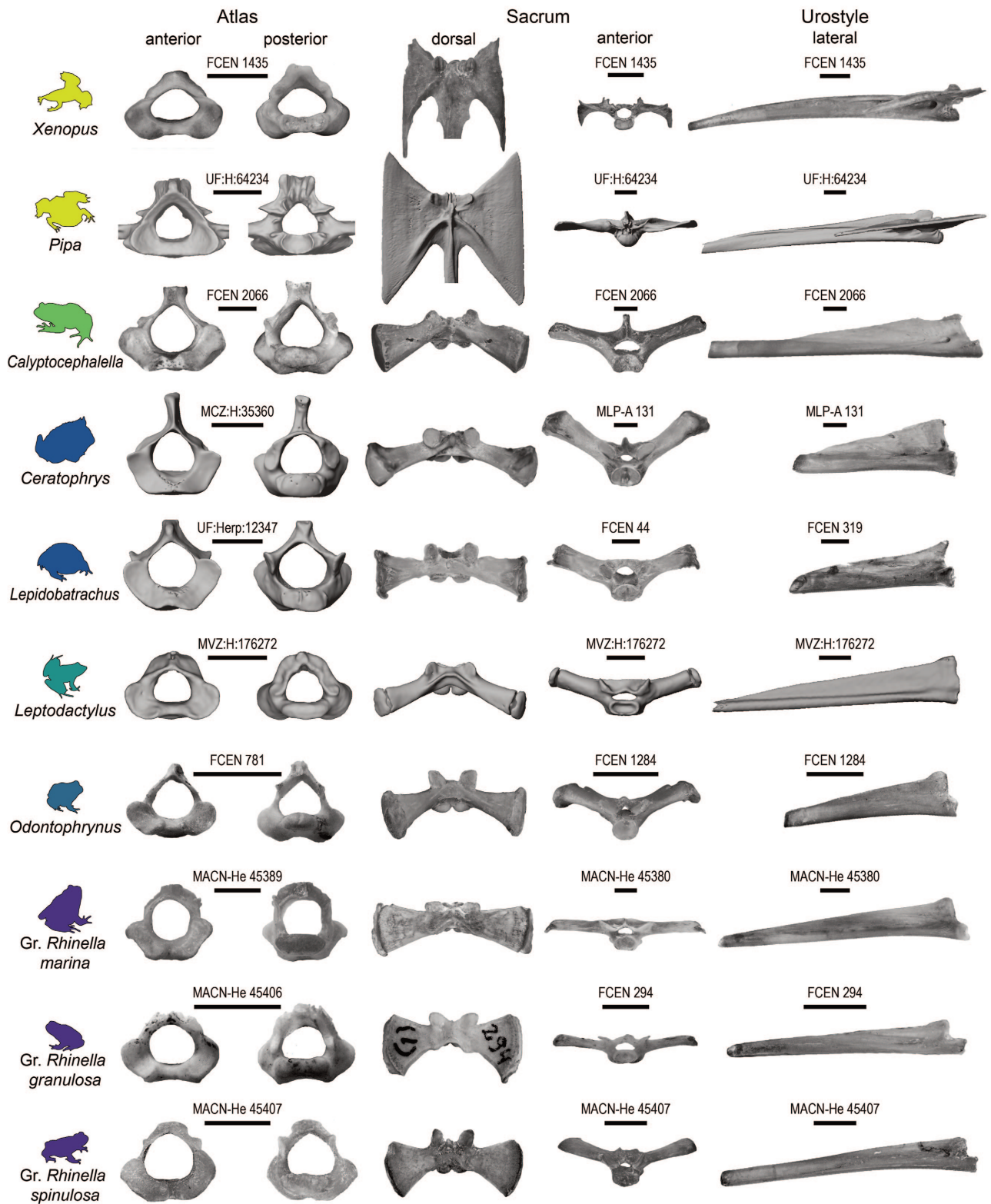


Figure 3. Comparative anatomy of vertebral column bones used in the dichotomous keys. Atlas (anterior and posterior views). Sacrum (dorsal and anterior views). Urostyle (right lateral view). Scale = 4 mm.

TABLE 2. Dichotomous keys to medium-to-large-sized anurans from Argentina using isolated bones of the limbs. When a key step involves multiple characters, it is sufficient to evaluate one of them to progress to the next step.

Humerus

Figures 2, 4

1.	Humerus very slender ($m1/m2 < 0.075$), nearly straight; humeral ball (eminencia capitata) small; ventral (deltoid) crest small; epicondyles small, almost symmetrical. Pipidae	2
-	Humerus more robust ($m1/m2 > 0.075$); humeral ball large; ventral crest larger; entepicondyle more projected distally than ectepicondyle. Neobatrachia	3
2.	Parietal crest poorly developed; entepicondyle blunt, poorly projected; entepicondylar groove narrow	<i>Pipa</i>
-	Parietal crest well-developed, triangular; entepicondyle pointed; entepicondylar groove broad	<i>Xenopus</i>
3.	Humerus slightly arched laterally; ectepicondyle compressed laterally; medial and lateral crests distinct, large in males (sexual dimorphism)	4
-	Humerus strongly arched laterally; ectepicondyle projected laterally; medial and lateral crests indistinct	5
4.	Ventral crest broad proximally, decreasing abruptly distally, with a thickened margin that, together with a distinct parietal crest, delimits a medial groove; medial and lateral crests greatly enlarged in males	<i>Leptodactylus</i>
-	Ventral crest broadest at its mid-length, decreasing gradually distally; parietal crest poorly developed; medial and lateral crests moderately enlarged in males	<i>Rhinella</i>
5.	Ectepicondyle broad, similar to entepicondyle; parietal crest developed, long; humeral ball robust	<i>Calyptocephalella</i>
-	Ectepicondyle clearly smaller than entepicondyle; parietal crest less distinct, shorter	6
6.	Ventral crest long, decreasing gradually	<i>Odontophrynus</i>
-	Ventral crest shorter, decreasing abruptly	7
7.	Humerus very robust ($m1/m2$ around 0.1)	<i>Ceratophrys</i>
-	Humerus less robust ($m1/m2$: 0.8–0.9)	<i>Lepidobatrachus</i>

Radio-ulna

Figures 2, 4

1.	Radial diaphysis flattened; ulnar edge nearly straight; articular surface of radial distal epiphysis poorly developed medially. Pipidae	2
-	Radial diaphysis cylindrical; ulnar edge curved inward; articular surface of radial distal epiphysis well developed medially. Neobatrachia	3
2.	Radio-ulna very slender ($m1/m2 < 0.1$); olecranon with its articular margin straight in medial view; crests absent	<i>Xenopus</i>
-	Radio-ulna more robust ($m1/m2 > 0.13$); olecranon with its articular margin curved in medial view; radial and ulnar crests present	<i>Pipa</i>
3.	Radial diaphysis cylindrical, ulnar diaphysis flattened	4
-	Both radial and ulnar diaphyses cylindrical	7
4.	Ulnar distal epiphysis little projected; olecranon relatively small; anterior tubercle on radial epiphysis indistinct	<i>Odontophrynus</i>
-	Ulnar distal epiphysis well projected; olecranon larger; anterior tubercle on radial epiphysis distinct	5
5.	Radial diaphysis clearly narrower than ulnar one distally; crests absent	<i>Calyptocephalella</i>
-	Radial and ulnar diaphyses almost the same width distally; radial and ulnar ridges typically present	6
6.	Radio-ulna robust ($m1/m2 > 0.17$)	<i>Ceratophrys</i>
-	Radio-ulna more slender ($m1/m2$: 0.14–0.16)	<i>Lepidobatrachus</i>
7.	Ulnar epiphysis well projected distally beyond the level of the radial epiphysis; anterior tubercle on radial epiphysis indistinct	<i>Leptodactylus</i>
-	Ulnar epiphysis barely projected distally; anterior tubercle on radial epiphysis distinct, oblique	8
8.	Radio-ulna relatively slender ($m1/m2$: 0.12–0.14); crestas absent	<i>Rhinella</i> : <i>R. spinulosa</i> Gr.
-	Radio-ulna more robust ($m1/m2$: 0.14–0.16); radial and ulnar ridges present	9
9.	Olecranon well developed medially; radial proximal articular edge short in medial view	<i>Rhinella</i> : <i>R. marina</i> Gr.
-	Olecranon less developed medially; proximal radial articular edge broad in medial view	<i>Rhinella</i> : <i>R. granulosa</i> Gr.

TABLE 2. Continuation.

Tibiofibula

Figures 2, 4

1.	Tibiofibula sigmoidal in lateral view; proximal epiphysis clearly larger than distal one; ventral/dorsal foramen located on the proximal/distal half of the diaphysis. Pipidae	2
-	Tibiofibula nearly straight in lateral view; proximal and distal epiphysis about the same size; ventral/dorsal foramen located near the center of the diaphysis. Neobatrachia	3
2.	Tibiofibula robust ($m1/m2 > 0.08$); diaphysis with crests, angled margins	<i>Pipa</i>
-	Tibiofibula more slender ($m1/m2 < 0.08$); crests absent	<i>Xenopus</i>
3.	Tibiofibula very robust ($m1/m2 \geq 0.1$); diaphysis flattened	4
-	Tibiofibula more slender ($m1/m2 \leq 0.09$); diaphysis cylindrical or prismatic	5
4.	Diaphysis internal margin clearly concave	<i>Odontophrynus</i>
-	Diaphysis internal margin nearly straight	Ceratophryidae
5.	Tibiofibula moderately robust ($m1/m2: 0.08-0.09$); diaphysis prismatic, clearly asymmetrical	<i>Calyptocephalella</i>
-	Tibiofibula robustness variable ($m1/m2 \leq 0.09$); diaphysis more cylindrical and symmetrical	6
6.	Tibiofibula slender ($m1/m2 \leq 0.07$), slightly arched dorsally; diaphysis symmetrical; cnemial crest low and long, extending over diaphysis	<i>Leptodactylus</i>
-	Tibiofibula variably robust ($m1/m2: 0.065-0.09$), straight in lateral view; diaphysis less symmetrical; cnemial crest low and short, limited to the epiphysis	7
7.	Tibiofibula moderately robust ($m1/m2: 0.075-0.09$); medial crest well developed	<i>Rhinella: R. marina</i> Gr.
-	Tibiofibula more slender ($m1/m2: 0.065-0.075$); medial crest absent or inconspicuous; diaphysis medial margin clearly concave	<i>Rhinella: R. granulosa</i> Gr., <i>R. spinulosa</i> Gr.

Tibiale-fibulare

Figures 2, 4

1.	Tibiale and fibulare on the same plane; diaphyses not overlapping at their ends, reaching the same level distally. Pipidae	2
-	Tibiale and fibulare on distinct planes; diaphyses overlapping at their ends, reaching different levels distally. Neobatrachia	3
2.	Diaphyses triangular in cross-section, each with two sharp crests; bony articulation between diaphyses broad distally	<i>Pipa</i>
-	Diaphyses nearly cylindrical, with blunt ridges; bony articulation between diaphyses narrow distally	<i>Xenopus</i>
3.	Epiphyses poorly ossified (even in large adults); tibiale and fibulare broadly overlapping proximally	<i>Calyptocephalella</i>
-	Epiphyses more ossified; tibiale and fibulare less overlapping proximally	4
4.	Tibiale-fibulare robust ($m1/m2 > 0.45$) / Tibial-fibular robusto ($m1/m2 > 0.45$)	5
-	Tibiale-fibulare more slender ($m1/m2 < 0.45$)	6
5.	Tibiale distal epiphysis slightly more projected than fibulare one	<i>Odontophrynus</i>
-	Fibulare distal epiphysis clearly more projected than tibiale one	Ceratophryidae
6.	Fibulare proximal epiphysis poorly projected, nearly at the same level as tibiale one; tibial distal epiphysis lacking medial process	<i>Leptodactylus</i>
-	Fibulare proximal epiphysis more projected than tibiale one; tibial distal epiphysis with medial process	<i>Rhinella</i>



Figure 4. Comparative anatomy of limb bones used in the dichotomous keys. Right humerus (ventral view). Right radio-ulna (medial view). Right tibiofibula (dorsal view). Right tibiale-fibulare (plantar view). Scale = 4 mm.

TABLE 3. Dichotomous key to medium-to-large-sized anurans from Argentina using the ilium. When a key step involves multiple characters, it is sufficient to evaluate one of them to progress to the next step.

Ilium		
Figures 2, 5		
1.	Bony interiliac joint very broad; dorsal and ventral acetabular expansions oriented medially, acetabular fossa occupying most of the ilial body in acetabular view. Pipidae	2
-	Bony interiliac joint reduced or absent; dorsal and ventral acetabular expansions well exposed in acetabular. Neobatrachia	3
2.	Dorsal prominence low, almost symmetrical in acetabular view; dorsal crest broadest at mid-length, oriented laterally	<i>Pipa</i>
-	Dorsal prominence high, asymmetrical; dorsal crest low, limited to anterior half of ilial shaft, oriented more dorsally	<i>Xenopus</i>
3.	Dorsal prominence spike-like; dorsal acetabular expansion high; ilial shaft slightly curved; dorsal crest absent or as a low ridge	4
-	Dorsal prominence low or merging a dorsal crest; ilial shaft well curved; dorsal crest variable	5
4.	Dorsal acetabular expansion pointed, higher than acetabular fossa	<i>Odontophrynus</i>
-	Dorsal acetabular expansion triangular, as high as the acetabular fossa, at most	Ceratophryidae
5.	VSA angle broad ($> 90^\circ$); dorsal acetabular expansion strong posterodorsally; dorsal protuberance ridge-like; dorsal crest high, arched margin	<i>Calyptocephalella</i>
-	VSA straight or acute ($\leq 90^\circ$); dorsal acetabular expansion smaller, oriented more medially; dorsal protuberance and crest variable, but different from above	6
6.	Dorsal crest high with straight or inwardly curved margin; ventral acetabular expansion broad; acute VSA ($< 90^\circ$); dorsal protuberance large, smooth	<i>Leptodactylus</i>
-	Dorsal crest indistinct; ventral acetabular expansion moderately broad, delimiting a straight VSA (around 90°); dorsal protuberance small, rough	7
7.	Dorsal prominence posterior to the level of the anterior acetabular rim; lamina calamita absent	<i>Rhinella</i> : <i>R. granulosa</i> Gr.
-	Dorsal prominence more anterior; lamina calamita present	<i>Rhinella</i> : <i>R. marina</i> Gr., <i>R. spinulosa</i> Gr.

The sacrum is almost completely preserved in MACN-Pv 14321 and, although it is articulated with the last presacral and the urostyle, its procoelous and posteriorly bicondylar conditions are evident, allowing the exclusion of pipids (step 1: go to 3). The distally flattened diapophyses of the fossil allow us to identify it as *Rhinella* among the taxa being compared (step 3: go to 4). The slight dilation of the sacral diapophyses and the oval, transversely oriented prezygapophyses further indicate affinities within the *R. marina* species group (final step 9).

The urostyle of MACN-Pv 14321, which is not fused to the sacrum and has a bicondylar articulation with it, also allows us to exclude pipids (step 1: go to 3). The incomplete

condition of this element in the fossil specimen does not allow an accurate estimation of the total length to calculate its robustness, but the preserved portion indicates that it was relatively slender, disagreeing with the condition of escuerzos and *Odontophrynus* (step 3: go to 6). The urostyle is only slightly higher than wide anteriorly, allowing the exclusion of *Calyptocephalella* and *Leptodactylus*, and pointing to *Rhinella* (step 6: go to 8). Within this latter genus, a distinct anterodorsal process (step 8: go to 9) and its proportions (final step 9) allow us to identify the fossil as part of the *R. marina* species group, in agreement with the identifications derived from the atlas and sacrum.

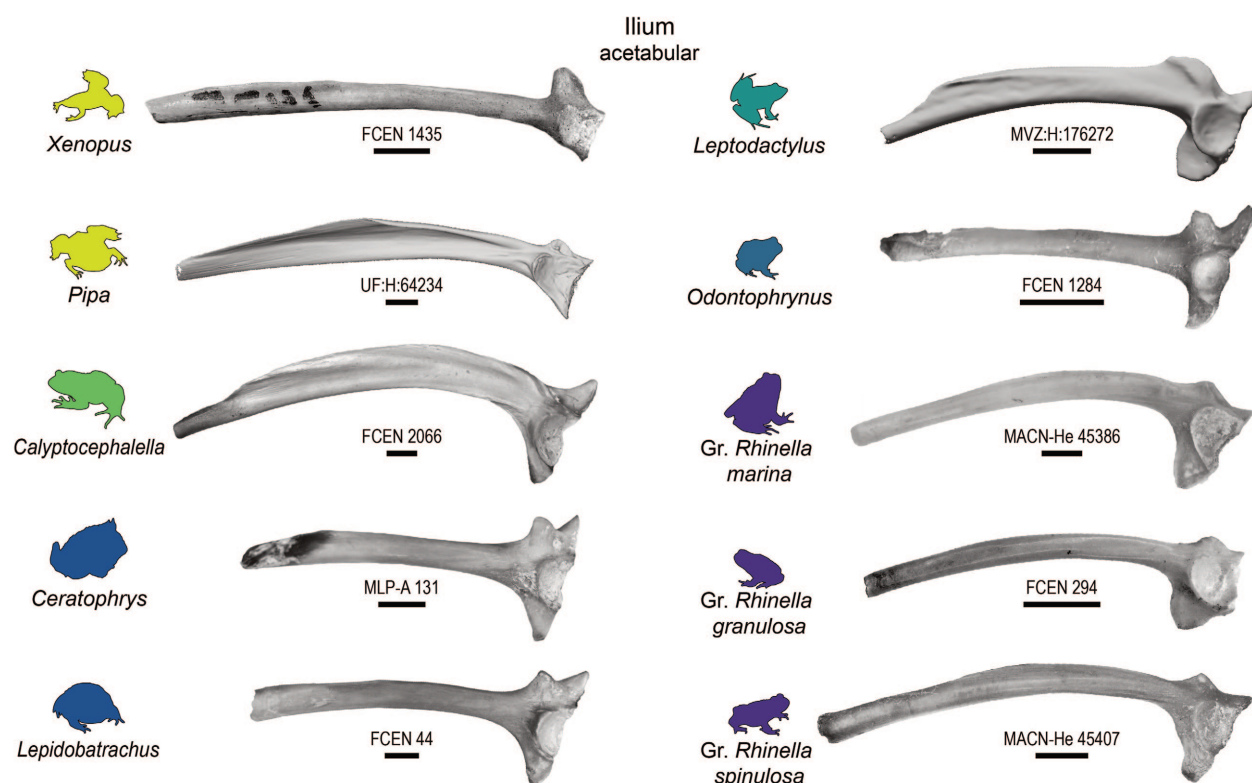


Figure 5. Comparative anatomy of ilium (acetabular view). Scale = 4 mm.

DISCUSSION

Anurans are major components of extant and past tetrapod assemblages in the Neotropics (Bolaños et al., 2008; Vacher et al., 2020; Gómez & Turazzini, 2021; Jansen et al., 2023), but their bones, often found as fossils or as part of avian pellets, are frequently unidentified below the level of Anura (Romano et al., 2002; Quintana, 2016; Escobar et al., 2025; Fernández et al., 2025), thereby downplaying the biological and ecological information that they carry. The dichotomous keys that we present here show that several postcranial bones of the anuran skeleton can be used to effectively identify families and most genera/species groups of medium-to-large-sized anurans from Argentina, either extant or extinct.

Identification of families and even genera only needs a single or very few steps in some cases, as is the case of Pipidae, which can be identified with a single step in every key. This is important because pipids, with a rich, well-known Cretaceous–Paleogene record from South America (Cione & Báez, 2007; Suazo Lara & Gómez, 2022; Barcelos

& dos Santos, 2023) are increasingly being registered in the Quaternary of Argentina (Báez et al., 2012; Pérez-Ben et al., 2019a; Turazzini, 2020). In addition, although pipids are nowadays absent from the native batrachofauna of Argentina, the invasive African clawed frog *Xenopus laevis* has already colonized part of central Chile (Mora et al., 2019) and environmental suitability models predict a high potential for its ongoing expansion over extensive areas of Argentina (Lobos et al., 2013; Rödder et al., 2017). Since this invasive pipid species is considered a major threat to aquatic environments worldwide (Measey et al., 2012; Ihlow et al., 2016), its easy detection in avian pellets or roadkills could be determinant to an early management intervention that could prevent its further spread.

Neobatrachian anuran groups can also be identified using the dichotomous keys based on isolated bones with little effort, including the escuerzos in *Ceratophrys*, with an extensive paleontological and archaeological record in Argentina (Gómez & Turazzini, 2021), and in *Lepidobatrachus*, which have only recently been recognized in the fossil record

of Argentina and worldwide (Tomassini et al., 2011; Gómez & Turazzini, 2021; Turazzini & Gómez, 2022). Similarly, keys allow easy recognition of the distantly related lesser escuerzos in the genus *Odontophrynus*, which have also been recovered as fossils only recently (Turazzini et al., 2016; Turazzini, 2020). As their common names suggest, escuerzos and lesser escuerzos, although now considered to be distantly related (Portik et al., 2023), share vaguely similar postcranial skeletal morphologies (Lynch, 1971), which could be related to broadly similar locomotor modes and burrowing behaviors (Keeffe & Blackburn, 2020, 2022; Pérez-Ben et al., 2024). However, our dichotomous keys agree with recent paleontological work (Turazzini et al., 2016; Turazzini, 2020), demonstrating that *Odontophrynus* can be distinguished from escuerzos based on isolated postcranial bones. Notably, the fossil record of *Lepidobatrachus* is restricted to stem taxa known from two incomplete skulls from Buenos Aires province (Gómez & Turazzini, 2021) and one incomplete articulated skeleton including part of the skull from Mendoza province (Turazzini & Gómez, 2022), all of Pliocene age. Therefore, it is expected that our dichotomous keys will facilitate the recognition of isolated postcranial bones of this genus currently inhabiting the Chaco ecoregion.

Other neobatrachian groups studied herein that have previously been understood to fall within the same overall morphotypes regarding postcranial bones are *Calyptocephalella* and *Leptodactylus* (Lynch, 1971), despite being distantly related (Lynch, 1971; Portik et al., 2023). *Calyptocephalella gayi* (the only extant species in the genus) and close extinct relatives stand out among anurans by their peculiar hyperossified skulls, having ornamented cranial bones that are relatively common in the Late Cretaceous–Miocene fossil record of Argentina and Chile (Muzzopappa & Báez, 2009; Gómez et al., 2011; Muzzopappa, 2019; Suazo Lara & Gómez, 2022; Barcelos & dos Santos, 2023). However, their postcranial bones, although being also relatively common as fossils (Muzzopappa & Báez, 2009; Otero et al., 2014; Suazo Lara & Gómez, 2022), have received considerably less attention. Despite some vague similarities, dichotomous keys allow easy identification of postcranial bones of *Calyptocephalella* from those of *Leptodactylus* and other neobatrachians. Despite

Leptodactylus currently comprising more than 80 species across the Neotropics and being well represented in Argentina (AmphibiaWeb, 2026), the genus has only a few certain fossil records dating back to the Late Miocene (Gómez et al., 2013; Turazzini, 2020; Barcelos & dos Santos, 2023; Brandoni et al., 2025). The dichotomous keys, which show that the genus can be unequivocally identified using all eight postcranial bones, certainly would help in expanding its still meager documented fossil record.

Rhinella toads are nowadays conspicuous elements of the Neotropical batrachofauna, represented in Argentina by more than a dozen species of medium- to large-sized toads, which are divided into three species groups (Pereyra et al., 2021; AmphibiaWeb, 2026). Their documented fossil record in Argentina, almost invariably including skull remains, dates back to the Pliocene (Barcelos & dos Santos, 2023). Most of these records belong to the *R. marina* group (Pérez-Ben et al., 2014, 2019b; Deschamps & Tomassini, 2016; Cruz et al., 2018; Turazzini, 2020; Barcelos & dos Santos, 2023) and only a few to the *R. spinulosa* group (Cruz et al., 2018; Ponssa et al., 2022). In addition, the *R. granulosa* group has been recognized in the Quaternary of Buenos Aires province (Turazzini, 2020; Turazzini et al., 2025), but awaits its formal publication. Species groups of *Rhinella* have relatively diverse hyperossified skulls (Ventura & Gómez, 2025), facilitating identification of cranial remains based on previously defined cranial apomorphies, ornamentation patterns, or the shape of some bones (Pérez-Ben et al., 2014; Pereyra et al., 2021). The dichotomous keys provided here demonstrate that *Rhinella* species groups can often be distinguished based on isolated postcranial bones.

Notably, among postcranial bones used here that allow complete discrimination among genera/species groups are some that are often omitted or poorly described in osteological studies (*i.e.*, atlas; urostyle; radio-ulna), for being considered, without justification, poorly variable and uninformative for assessing systematic relationships (*e.g.*, Holman, 2003; but see Bastir et al., 2014; Gómez et al., 2025). In this regard, most bones included in our dichotomous keys have seldom been considered in phylogenetic analyses of anurans. To illustrate this, highly used data matrices comprising 49–74 osteological

characters do not include a single character from the humerus, radio-ulna, tibiofibula, or tibiale-fibulare (Báez & Pugener, 2003; Fabrezi, 2006; Pramuk, 2006; Evans et al., 2008; Báez et al., 2009). More recent, larger datasets comprising 142–256 osteological characters, while including some characters of the humerus, tibiofibula, and tibiale-fibulare, still do not include a single feature of the radio-ulna (Gómez, 2016; Báez & Gómez, 2018; Gómez & Turazzini, 2021; Supplementary Material, Table S2). Thereby, given their diagnostic efficacy, the characters considered in the dichotomous keys would be helpful additions to existing datasets to infer phylogenetic relationships of fossil anurans, particularly when only a few postcranial bones are available. This can be illustrated by the case study presented here, in which the affinities of a fossil specimen, mainly represented by a vertebral column and originally identified as *Ceratophrys* sp. (Fig. 6), can be properly tested and reassessed (to *Rhinella marina* species group) based on only three postcranial bones.

We expect our dichotomous keys to be a useful tool for anyone dealing with the postcranial skeletal morphology of Neotropical anuran taxa, whether extant or extinct, including paleontologists, archaeologists, herpetologists, ornithologists, museum staff, and the general public. We intend to make these keys as accessible as possible by publishing them in an open-access online journal, to encourage widespread and unlimited use. This way, we hope to spark interest in the study of anuran osteology in

order to uncover their evolutionary history in the Neotropics and unlock their potential to enrich environmental and paleoenvironmental interpretations.

ACKNOWLEDGMENTS

We are grateful to David Blackburn and his team (University of Florida), M. Ezcurra and J. Faivovich (Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia'), Sergio Bogan (Fundación de Historia Natural Félix de Azara), José Rosado (Museum of Comparative Zoology), Carol Spencer (Museum of Vertebrate Zoology), and Jorge Williams (Museo de La Plata), for providing access to specimens under their care and for their kind assistance. We really appreciate the help of Andrés Lires in the preparation of dry specimens. Thanks are extended to Celeste Pérez-Ben and an anonymous reviewer for their suggestions, which certainly improved this work. We would also like to thank the University of Buenos Aires for continuous support during this challenging period for Science and University Education in Argentina. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

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Figure 6. Case study. Fossil *Rhinella* from the Monte Hermoso Formation originally cataloged as *Ceratophrys* sp. (MACN-Pv 14321).

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doi: 10.5710/PEAPA.22.07.2026.572

Recibido: 18 de abril de 2026

Aceptado: 22 de julio de 2026

Publicado: 1 de octubre de 2026

