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ARTICLE

FIRST FOSSIL RECORD OF THE SOUTH AMERICAN FROG GENUS *ODONTOPHRYNUS* REINHARDT AND LÜTKEN, 1862 (ANURA, NEOBATRACHIA)

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ABSTRACT—The frog genus *Odontophrynus* comprises 10 species arranged in three species groups that inhabit southeastern South America. In Argentina, it is represented by the *O. americanus* and *O. occidentalis* species groups and, despite being a fairly common taxon of the extant herpetofauna, it has no known fossil record. Here we report on the first fossil record of the genus, based on an almost complete right ilium from the lower levels of the Buenos Aires Formation (OIS 11, Bonaerian age, middle Pleistocene) in the Bonaerian Pampas of Argentina. The taxonomic allocation is derived from a thorough survey of anuran ilia and is grounded in a set of distinct ilial characters that, in combination, do not occur in any other anuran. These include: ilium not fused to ischium; well-developed dorsal acetabular expansion; broad preacetabular zone with a shallow preacetabular fossa; straight ilial shaft lacking dorsal ridge; and spike-like dorsal prominence bearing a distinct dorsal protuberance. Additionally, after comparing with a large sample of specimens representing most species of *Odontophrynus*, we propose two main characters (high spike-like dorsal prominence, absence of a lateral knob on the dorsal prominence) that allow referral to *Odontophrynus* aff. *O. americanus* or *O. cordobae*.

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

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INTRODUCTION

The genus *Odontophrynus* Reinhardt and Lütken, 1862, comprises 10 species of small ceratophryid-like frogs from southeast South America (Frost, 2015). These species are arranged into three nominal species groups (*americanus, cultripes, occidentalis*), on the basis of external morphology and behavioral ecology (Savage and Cei, 1965; Cei, 1987; Caramaschi, 1996; Martino and Sinsch, 2002; Rosset et al., 2006, 2007; Rosset, 2008). The *americanus* (*O. americanus, O. cordobae, O. lavillai*, and *O. maisuma*) and *occidentalis* (*O. achalensis, O. barrioi*, and *O. occidentalis*) species groups are those with the southernmost occurrence in the continent, with species (except *O. maisuma*) widely distributed in central-northeastern and central-western Argentina, respectively (Rosset et al., 2006, 2007) (Fig. 1). Of the six species of *Odontophrynus* distributed in Argentina, only *O. americanus* and *O. occidentalis* currently inhabit the Bonaerian Pampas (Peiretti et al., 2002; Rosset et al., 2006).

Even though there are several recent studies of anuran phylogeny (Frost et al., 2006; Roelants et al., 2007; Heinicke et al., 2009), and others describing interpopulation variability and new cryptic species within the genus (Martino and Sinsch, 2002; Rosset et al., 2006, 2007; Rosset, 2008; Salas and Martino, 2009; Caramaschi and Napoli, 2012; Grenat et al., 2012), none of these addressed the phylogenetic relationships among *Odontophrynus* species. Furthermore, the osteology of *Odontophrynus* has not been studied in detail, nor have osteological synapomorphies been proposed for the genus or any of the species (Rosset, 2008).

Despite *Odontophrynus* being a fairly common taxon of the extant herpetofauna of South America, the genus has no known fossil record heretofore. We document the first fossil of *Odontophrynus* from the Pampas of Argentina, an almost complete ilium. We provide new comparative data for ilial morphology across hyloid anurans with ceratophryid-like ilia, and further discuss the systematic affinities of the fossil within *Odontophrynus*, providing a set of ilial features that vary among species groups of the genus and to further differentiate a few species within the *americanus* species group.

Institutional Abbreviations—FCEN, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina; **FML**, Instituto de Herpetología de la Fundación Miguel Lillo, Tucumán, Argentina; **KU**, Natural History Museum, The University of Kansas, Lawrence, Kansas, U.S.A.; **MACN-HE**, Colección de Herpetología, Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia,' Buenos Aires, Argentina; **MCN**, Museo de Ciencias Naturales, Universidad Nacional de Salta, Salta, Argentina; **MLP**, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina; **MMP**, Museo Municipal de Ciencias Naturales 'Lorenzo Scaglia,' Mar del Plata, Argentina; **MUFAL**, Museu de História Natural, Universidade Federal de Alagoas, Maceió, Brazil.

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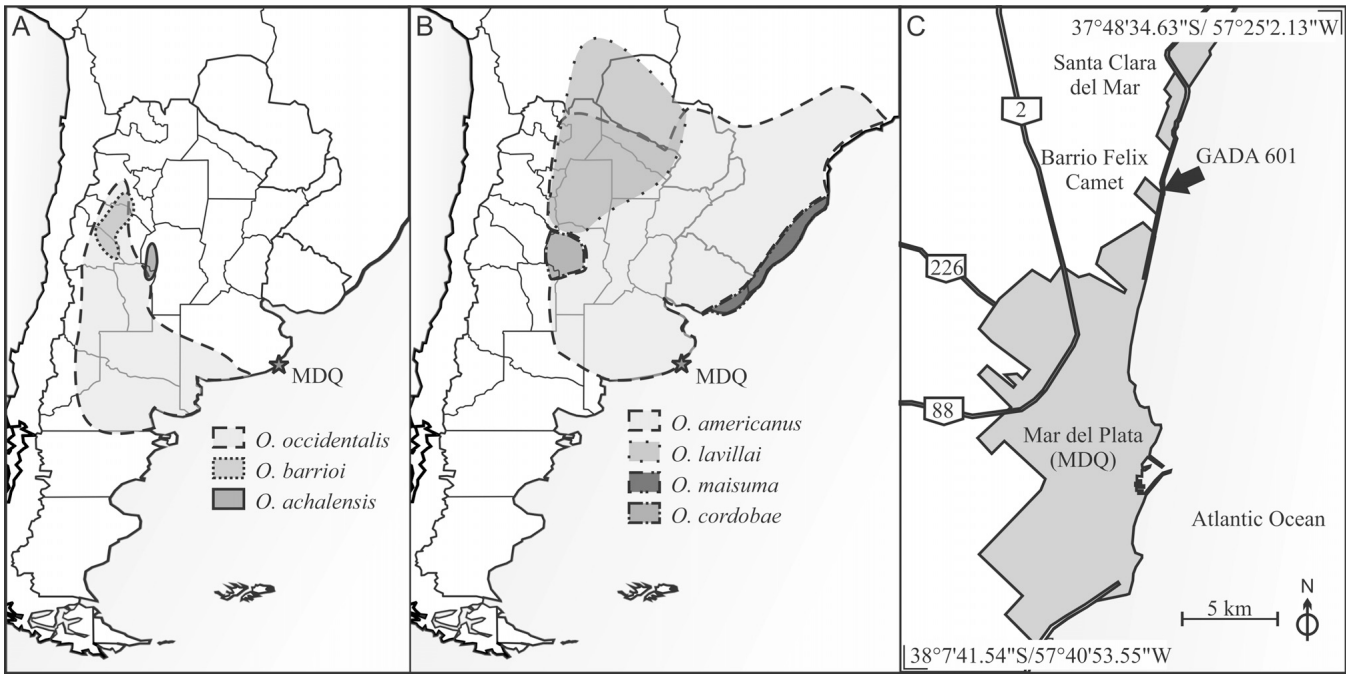

FIGURE 1. Distribution maps of species of the **A**, *O. occidentalis* and **B**, *O. americanus* species groups. **C**, location map of the GADA 601 locality.

GEOLOGICAL BACKGROUND

The specimen, MMP 5355, was recovered at the GADA 601 locality (37°53′52.44″S, 57°31′19.96″W), Mar del Plata, Buenos Aires Province, Argentina (Fig. 1C). The outcrop represents the interval Pleistocene–Holocene and comprises the *Mesotherium cristatum, Megatherium americanum*, and *Equus* (*Amerhippus*) *neogenus* biozones (Cione et al., 2007). A magnetic reversal has been recorded at the base of the profile and interpreted as the Brunhes–Matuyama boundary (0.78 Ma) (Bidegain et al., 2005). The stratigraphic sequence comprises four units (Fig. 2) and consists mainly of channel and floodplain facies of loessic sediments. Cumulic hydromorphic paleosols, associated with a high-sinuosity fluvial system, are best preserved. The succession of facies represents the filling sequence of a channel system placed in a mature floodplain that prevents extensive lateral migration. The fossil comes from conglomeratic facies with trough cross-bedding stratification (Ctc) of unit 2 (Fig. 2), assigned to the lower Buenos Aires Formation (Ameghino, 1908). Unit 2 represents a low meandering channel fill with a typical fining upward sequence. The presence of quartz sands in unit 2 indicates that this ancient drainage system follows the same pattern present in current drainage waterways, produced by the denudation of the Cambrian–Ordovician sandstones located southwest of the studied area (Tandilia ranges). Unit 2 (and therefore MMP 5355) is dated to lower Bonaerian local age (middle Pleistocene) based on the fossil content of paleosol 1, where remains of *Ctenomys kraglievichi* (MMP 5639) were recovered. This species is the marker of the *C. kraglievichi* sub-biozone (possibly OIS 11; Verzi et al., 2004) of the *Megatherium americanum* biozone (Cione et al., 2007).

MATERIALS AND METHODS

Specimen MMP 5355 consists of an almost complete right ilium, only lacking the distal tip of the ilial shaft, and is housed at the Museo Municipal de Ciencias Naturales 'Lorenzo Scaglia' of Mar del Plata, Argentina (MMP). This bone preserves sufficient anatomical detail to allow meticulous comparisons with ilia of extant frogs.

An apomorphy-based approach to the identification of the fossil (Bell et al., 2010) is currently impossible due to the lack of well-resolved phylogenies that include ilial characters. We examined and described characters considered diagnostic at a generic and, to some degree, a specific level. A detailed, comprehensive trait analysis resulting in a complete phylogenetic assessment is not within the scope of this paper.

To assess the systematic affinities of the fossil, we compared it with a taxonomically diverse sample of extant anurans (Supplemental Data, Appendix S1), as well as with published work (e.g., Lynch, 1971; Prado and Pombal, 2008; Přikryl et al., 2009; Roček et al., 2012; Dos Santos Dias et al., 2013; Gómez and Turazzini, 2015). Given our observations, we further focused comparisons on species of *Odontophrynus*, including 32 specimens (dry skeletons) (Appendix S1) as well as figures from the literature (Lynch, 1971; Rosset, 2008) and photographs representing most species of the genus and all the species groups. Following recommendations by Bever (2005) and Bell et al. (2010), we did not restrict comparisons to species of *Odontophrynus* currently found in the area surrounding the fossil deposit (Buenos Aires Province), but instead we selected a good representation of the taxonomic diversity within *Odontophrynus* to avoid geographic biases. A few species of the *cultripes* group (i.e., *O. monachus, O. carvalhoi*), restricted to northeastern Brazil, could not be included due to lack of available dry or cleared specimens in collections or absence of accurate osteological descriptions in the literature. We also dissected several specimens of *Odontophrynus* (Appendix S1) in order to account for the myological correlates of some particular osteological features. Detailed comparisons were also made with other odontophrynid taxa, including *Macrogenioglottus alipioi* and species of *Proceratophrys*.

Observations and drawings were done under a Nikon SMZ 1000 stereoscope with an attached camera lucida, and

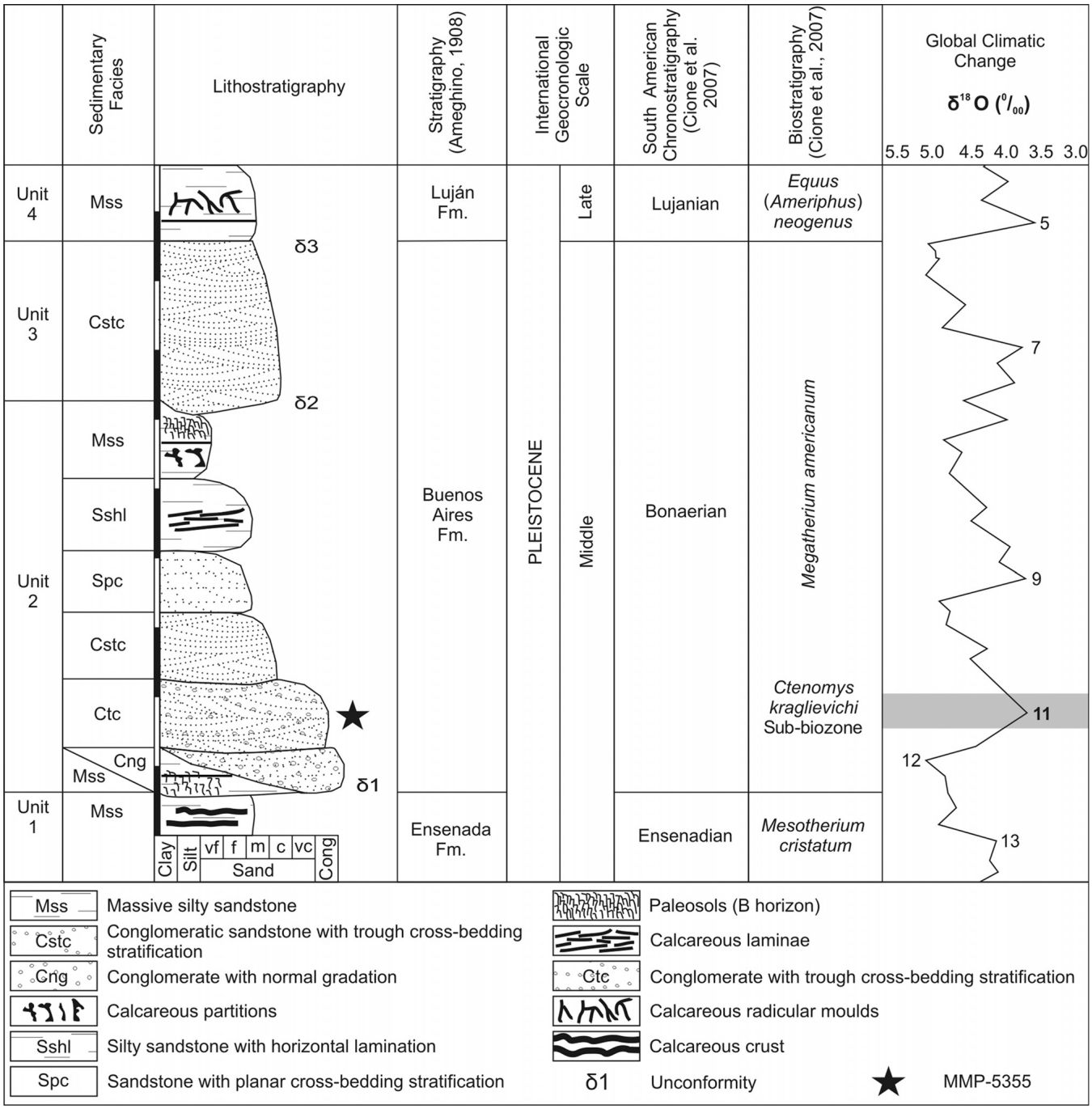

FIGURE 2. Stratigraphic profile of locality GADA 601, showing the stratigraphic provenance of the fossil MMP 5355.

photographs were taken with a Nikon D90 equipped with a macro lens. Terminology follows Gómez and Turazzini (2015) and references therein. Measurements were taken to the nearest 0.01 mm with digital calipers under a stereoscope. Measured dimensions of the ilium are similar to those of Bever (2005) and Báez et al. (2012). We use taxonomic nomenclature mainly derived from Frost et al. (2006) and Frost (2015). The software Infostat (Di Rienso et al., 2014) was used to perform a simple linear regression to calculate the estimated SVL of the fossil specimen, based on 21 *Odontophrynus* specimens (measures in Appendix S2), using the combined height of the acetabular fossa and dorsal acetabular expansion as the dependent variable.

SYSTEMATIC PALEONTOLOGY

ANURA Fischer von Waldheim, 1813
ODONTOPHRYNIDAE Pyron and Wiens, 2011
ODONTOPHRYNUS Reinhardt and Lütken, 1862
ODONTOPHRYNUS aff. *O. AMERICANUS* Duméril and Bibron, 1841, or *O. CORDOBAE* Martino and Sinsch, 2002
(Fig. 3)

Referred Specimen—MMP 5355, right ilium.

Locality and Age—GADA 601 paleontological site, northern coastal cliffs of Mar del Plata, Barrio Félix Camet, southeastern Buenos Aires Province. Buenos Aires Formation (sensu

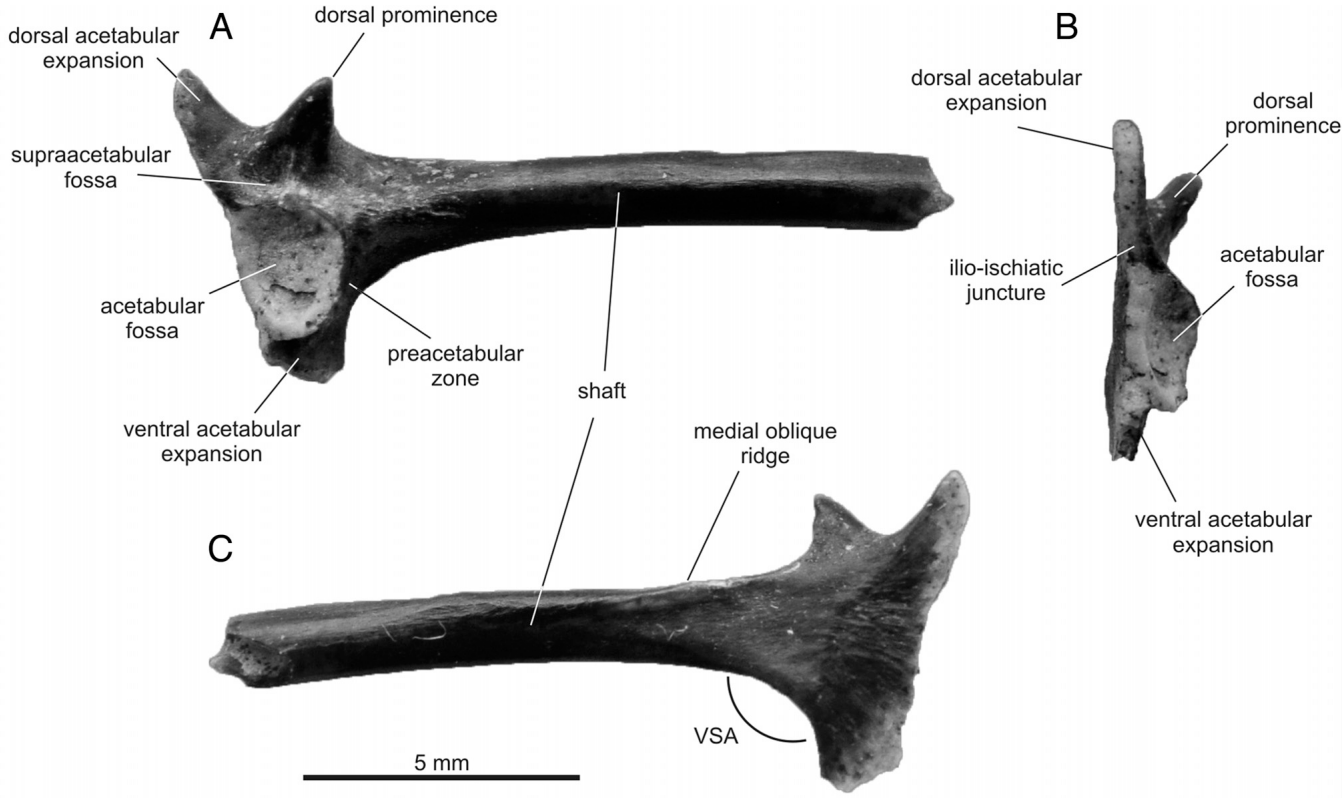

FIGURE 3. Right ilium of *Odontophrynus* cf. *O. americanus* (MMP 5355) in **A**, acetabular, **B**, posterior, and **C**, medial views. **Abbreviation**: **VSA**, angle between the ventral acetabular expansion anterior margin and the ilial shaft.

Ameghino, 1908), lower Bonaerian stage (sensu Cione and Tonni, 2005), middle Pleistocene.

Description—MMP 5355 is an almost complete right ilium lacking the distal tip of the ilial shaft. This ilium is well ossified and presumably belonged to an adult frog with an estimated snout-vent length (SVL) of ca. 48 mm (see below); despite its high degree of ossification, it is clear that this element was not fused with the ischium or the pubis. The ilial shaft is nearly straight in both acetabular and dorsal views. The shaft has an oval cross-section distally, being only slightly mediolaterally compressed, but proximally it is medially flat and laterally convex. The dorsal crest is limited to a moderately sharp edge on the dorsolateral surface of the shaft. A distinct medial oblique ridge is present on the medial surface of the proximal half of the ilial shaft, running posterodorsally-anteroventrally from the anterior limit of the dorsal prominence to nearly the mid-height of the shaft. A spike-like dorsal prominence as high as the dorsal acetabular expansion is present on the dorsal margin of the ilial body. Its main axis is dorsolaterally oriented about 25° with respect to the plane defined by the ilial body. The dorsal prominence is a little slanted anteriorly, with a steeper anterior than posterior slope. It is relatively posteriorly located, with its anterior margin posterior to the anterior margin of the acetabular fossa. The dorsal prominence bears a poorly defined dorsal protuberance (origin of the muscle glutaeus magnus in extant frogs) near the anterior edge of its anterolateral, slightly concave surface. A relatively wide but poorly delimited, shallow supraacetabular fossa extends from this latter position to just dorsal to the acetabular fossa. The dorsal acetabular expansion is large and has a distinct dorsal vector, with its ischiatic margin slightly higher than the acetabular fossa. The acetabular fossa is relatively small and is subcircular to subquadrangular, with its dorsal margin aligned with the axis of the ilial shaft. The acetabular rim is strongly projected laterally, particularly in the anterior margin. Anterior to the acetabular fossa, there is a moderately developed preacetabular zone that gently merges into the ilial shaft. In this region, a small preacetabular fossa pierced by a small foramen is present. The ventral acetabular expansion is much smaller than the dorsal acetabular expansion, and its anterior margin forms an angle of approximately 100° with respect to the ilial shaft. The pubic margin of the ventral acetabular expansion is irregular, as is typical of forms with a cartilaginous pubis. In posterior view, the ilio-ischiatic juncture is remarkably thin and there is no trace of an interiliac tubercle.

DISCUSSION AND CONCLUSIONS

The ilium has long been considered to be the single best element upon which to base the identification of disarticulated fossil frogs at the familial, generic, and/or specific levels (e.g., Tihen, 1962; Chantell, 1964; Holman, 1965; Sanchiz, 1998), because this element is relatively rich in anatomical traits that show considerable and consistent variation amongst different groups of anurans (Lynch, 1971; Tyler, 1976).

In this regard, the joint occurrence in MMP 5355 of a nearly straight ilial shaft without an evident dorsal crest, large dorsal acetabular expansion with a distinct dorsal vector, relatively small ventral acetabular expansion forming a wide angle with the ilial shaft, and a spike-like dorsal prominence bearing a somewhat poorly defined dorsal protuberance is characteristic of a ceratophryid-like ilium (Lynch, 1971). Among anurans, ilia with these features are present only in a few groups of neobatrachians, including some limnodynastids, ceratophryids and odontophrynids among hyloids (Lynch, 1971; Fig. 4), and brevicipitids and *Tomopterna* among ranoids (Matthews et al., 2015). However, the ceratophryid-like ilia of limnodynastids and the

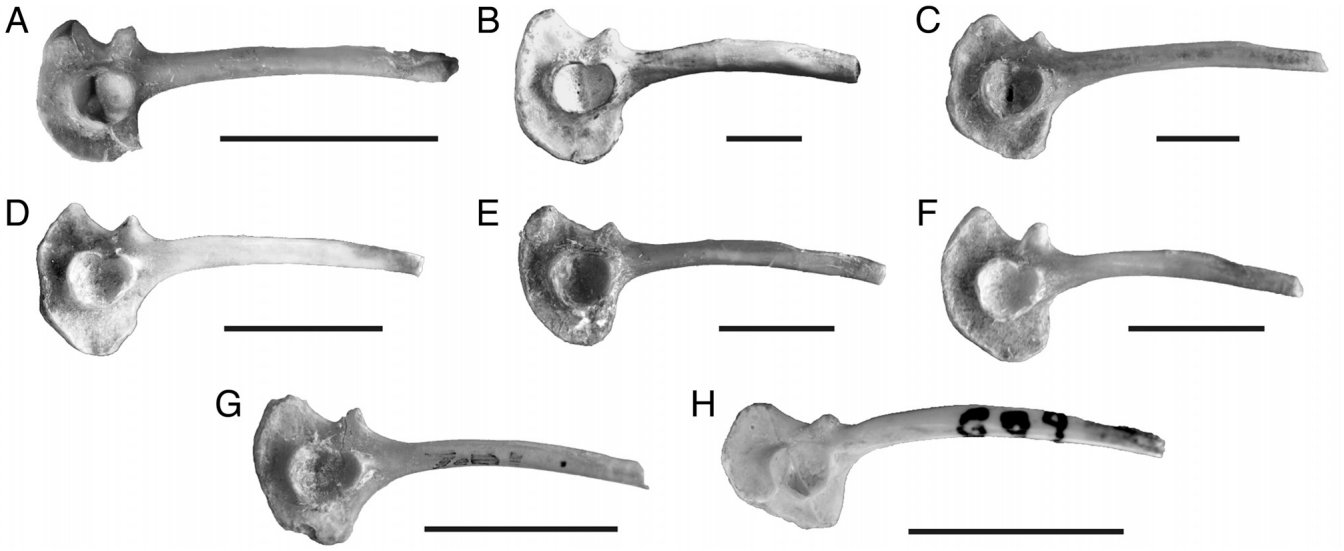

FIGURE 4. Ceratophryid-like pelvic girdles in right acetabular view of extant anurans. **A**, *Odontophrynus americanus*; **B**, *Proceratophrys boiei*; **C**, *Ceratophrys ornata*; **D**, *C. cranwelli*; **E**, *C. cornuta*; **F**, *Lepidobatrachus laevis*; **G**, *L. llanensis*; **H**, *L. asper*. Scale bars equal 10 mm.

above-mentioned ranoids clearly differ from the fossil ilium in several features, including shape of the dorsal acetabular expansion, acetabular fossa, and dorsal prominence, as well as ilial shaft curvature.

Moreover, despite overall similarity with ceratophryids, MMP 5355 shows a combination of characters that set it apart. Ilia of ceratophryids differ from MMP 5355 in having an ilial dorsal ridge (in most species), a shaft with a distinctive curvature, a dorsal prominence that is significantly lower than the dorsal acetabular expansion, and lacking a distinct dorsal protuberance (Fig. 4B–G).

Among frogs, features of MMP 5355 are only consistent with those of some odontophrynids (Fig. 5). Both *Proceratophrys* (Figs. 4H, 5A) and the monospecific *Macrogenioglottus*

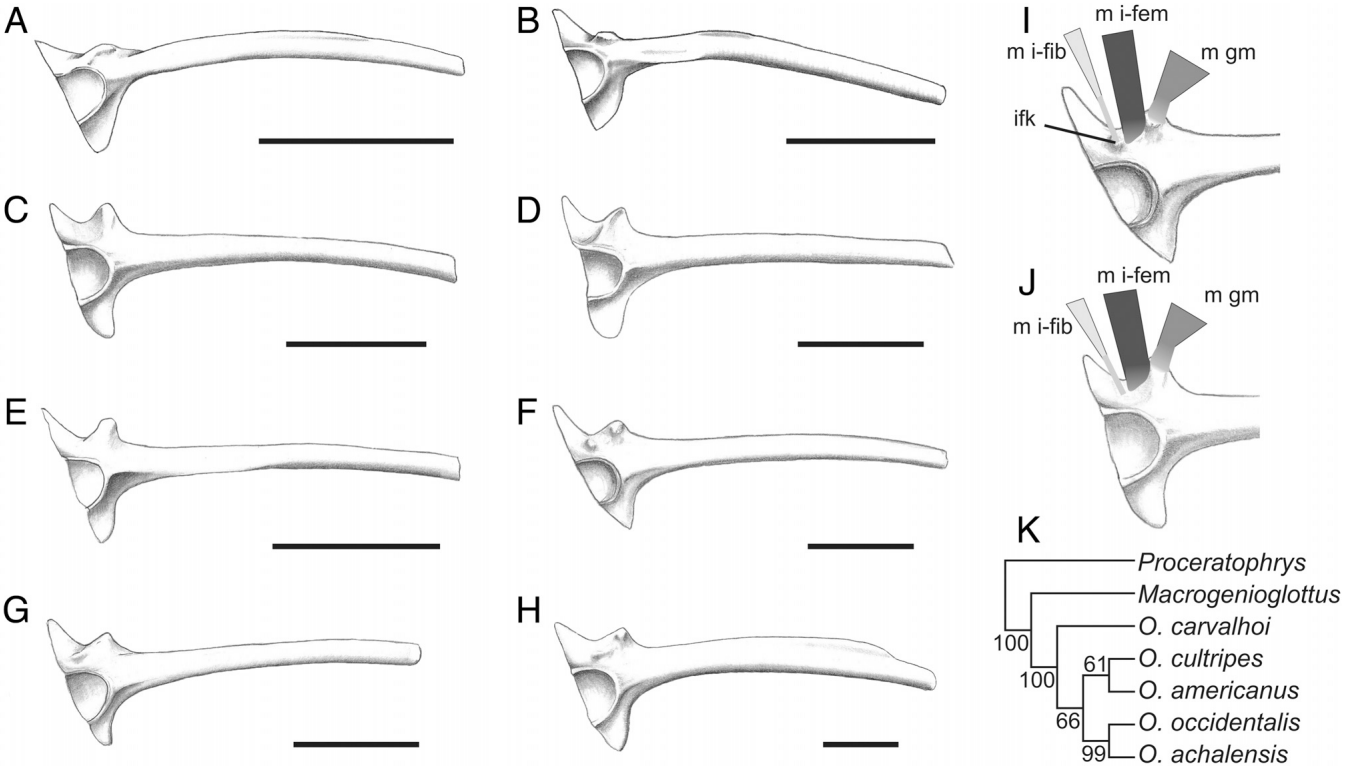

FIGURE 5. Ilia in right acetabular view of extant species of Odontophrynidae. **A**, *Macrogenioglottus alipioi*; **B**, *Proceratophrys avelinoi*; **C**, *O. americanus*; **D**, *O. cordobae*; **E**, *O. lavillai*; **F**, *O. occidentalis*; **G**, *O. achalensis*; **H**, *O. cultripes*. **I**, **J**, detail of muscle attachment on the dorsal prominence in *O. occidentalis* and *O. americanus*. **K**, phylogenetic relationships within Odontophrynidae with bootstrap node support values (modified from Pyron and Wiens, 2011). **Abbreviations**: **gm**, gluteus maximus; **i-fem**, iliofemoralis; **i-fib**, iliofibularis; **ifk**, knob for the iliofibularis/iliofemoralis muscle; **m**, muscle. Scale bars equal 10 mm.

(Fig. 5B) differ from MMP 5355 and species of *Odontophrynus* in the joint occurrence of a more or less curved ilial shaft with a low dorsal ridge, a low dorsal prominence, and a variably developed calamita ridge. *Macrogenioglottus* further differs from MMP 5355 and all other odontophrynids in having a broader ventral acetabular expansion and a blunt dorsal prominence.

These comparisons indicate that MMP 5355 represents a species of *Odontophrynus*. To date, only a few authors have provided an osteological characterization of species of *Odontophrynus* and most of these are focused on cranial anatomy (e.g., Caramaschi, 1996; Rosset et al., 2007). Therefore, a thorough sampling of *Odontophrynus* ilia was undertaken. Our observations show that ilial morphology in *Odontophrynus* is relatively uniform within each of the species groups, consistent with previous reports regarding cranial anatomy and glandular patterns in the genus (Rosset et al., 2007; Rosset, 2008; Caramaschi and Napoli, 2012; Do Nascimento et al., 2013). It also agrees with the relatively low levels of intraspecific osteological variation reported for other anurans (Trueb, 1977; Pérez Ben et al., 2010), in contrast to the findings of Bever (2005), who reports high levels of intraspecific variation in North American bufonids, a result that might be due to the analysis of nonstandard linear measures of samples of adult and subadult toads.

Within *Odontophrynus*, MMP 5355 differs most from *O. cultripes*, in which a slightly curved shaft bears a distinct dorsal ridge and an accessory knob is present on the lateral surface of the dorsal prominence (Fig. 5H). The fossil shares with the *americanus* and *occidentalis* groups a straight ilial shaft lacking a dorsal ridge, but differs from the latter (Fig. 5F–G) in having a higher spike-like dorsal prominence with steeper anterior and posterior slopes and in lacking a lateral accessory knob. When present, this knob marks the origin of the iliofibularis muscle (Fig. 5I), which otherwise attaches directly to the posterior lateral surface of the dorsal prominence on a shallow fossa or leaving no distinctive scar, as in the *americanus* group (Fig. 5J). In this context, MMP 5355 compares well with ilia of species of the *americanus* group in having a high spike-like dorsal prominence and lacking any obvious knob related to the origin of the iliofibularis muscle. The phylogenetic hypothesis of Pyron and Wiens (2011) implies that the absence of an ilial dorsal ridge, straight ilial shaft, and tall spike-like dorsal prominence of the *americanus* and *occidentalis* species groups might represent states derived from the plesiomorphic condition exhibited by *Macrogenioglottus* and *Proceratophrys*.

Among species of the *americanus* group, MMP 5355 shares with *O. americanus* and *O. cordobae* a shallow preacetabular zone that gently merges into the ilial shaft. This condition differs from that in *O. lavillai*, in which the ventral margin of the ilial shaft is well demarcated from the preacetabular zone by a blunt edge arising from the acetabular rim. A similar configuration has also been observed in *O. barrioi* and some specimens of *O. occidentalis*. We agree with Rosset (2008) that *O. lavillai* appears to be morphologically distinct within the *americanus* group.

The fossil ilium belonged to a frog of an estimated SVL of roughly 48 mm (estimated SVL = 47.7 mm; $r^2 = 0.56$; $P < 0.0001$), a size that falls within the adult range of many extant species of *Odontophrynus* (Rosset et al., 2007; Rosset, 2008; Caramaschi and Napoli, 2012; Table 1). Therefore, the estimated SVL is consistent with the similarities between the fossil ilium and ilia of *O. americanus* and *O. cordobae*.

From the preceding comparisons, and given the phylogenetic hypothesis of Pyron and Wiens (2011), it follows that MMP 5355 represents a species related to the *americanus* species group. Within the latter group, the fossil can be distinguished from *O. lavillai* by its anatomy and size and from *O. maisuma* only by its size (we could not directly compare it with a dry skeleton of this species), but it is indistinguishable in its morphology and size from ilia of *O. americanus* and *O. cordobae*. The latter species are regarded as morphologically cryptic, being almost identical in osteology as well as external morphology (Rosset, 2008; Grenat et al., 2012; G.F.T., pers. observ.); therefore, we refer MMP 5355 to *Odontophrynus* aff. *O. americanus* or *O. cordobae*. Currently, *O. cordobae* is restricted to Córdoba Province in central Argentina, so it would be more parsimonious that the fossil represents *O. americanus*, which has a broad distribution across central and northeastern Argentina (including the paleontological site), Uruguay, Paraguay, and southern Brazil (Fig. 1). Today, odontophrynids are common components of the extant herpetofauna of South America, but they hitherto have not been documented in the fossil record. Thus, the ilium described here, from the lower Bonaerian (middle Pleistocene, OIS 11, ~400 ka; Lisiecki and Raymo, 2005) of northern Mar del Plata, constitutes the first fossil record of *Odontophrynus*, adding new data on the evolution of this group of anurans.

TABLE 1. SVL ranges of different species of *Odontophrynus*.

Species	SVL range (mm)		References
	Males	Females	
O. achalensis	39.9–49.4		Rosset et al. (2007)
O. americanus	34.5–53.2	37.6–54.3	Rosset (2008)
O. barrioi	46.5–67.5		Rosset et al. (2007)
O. carvalhoi	51.6–69.4	53.3–76.5	Caramaschi and Napoli (2012)
O. cordobae	39.2–51.6	48.1–58.1	Rosset (2008)
O. cultripes	50–60	45–70	Caramaschi and Napoli (2012)
O. lavillai	49.4–64.5	52.6–65.7	Rosset (2008)
O. maisuma	34.4–40.9	37.9–43.6	Rosset (2008)
O. monachus	40.6–54.1	55.5	Caramaschi and Napoli (2012)
O. occidentalis	40.35–63		Rosset et al. (2007)

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