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AN OVERVIEW OF THE ILIUM OF ANURANS (LISSAMPHIBIA, SALIENTIA), WITH A CRITICAL APPRAISAL OF THE TERMINOLOGY AND PRIMARY HOMOLOGY OF MAIN ILIAL FEATURES

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ABSTRACT—The ilium has been considered a ‘key’ element in anuran paleontology, but its terminology is inconsistent across the literature. Therefore, we here review the terminology used so far to describe anuran ilia and provide an annotated glossary of main ilial features. We also survey ilial morphology and comment on variation exhibited by each ilial feature among major anuran lineages. We do so with special consideration for myological correlates, provide muscle maps for a few species, and aim to clarify hypotheses of primary homology. We consider previous work that compartmentalizes part of the described variation into cladistic characters, with the intention of providing a starting point for using ilial features in future research on osteology-based phylogenetics of anurans. Finally, we remark on some aspects regarding the dorsal prominence-protuberance complex.

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INTRODUCTION

The ilium of anurans has long been considered to be a valuable element upon which to base the identification of taxa in fossil assemblages of isolated bones (e.g., Holman, 1965; Sanchiz, 1998). This bone has been selected as such a ‘key’ element owing to its high preservation potential amongst disarticulated skeletal material, but also because the ilium is relatively rich in anatomical features that have been shown to vary considerably and consistently between different groups of anurans (e.g., Tyler, 1976; Sanchiz, 1998). For these reasons, numerous authors have considered the ilium as the holotype (or paratype) in the erection of new fossil species or in the recognition of frog families, genera, and species (e.g., Holman, 1959, 1965, 2003; Chantell, 1964; Felix and Montori, 1986; Evans et al., 1990; Parmley et al., 2010; Szentesi and Venczel, 2010, 2012; Báez et al., 2012; Folie et al., 2013; Gómez et al., 2013; Bastir et al., 2014; but see Bever, 2005, for a critique on the taxonomic usefulness of some ilial features at the species level).

Despite the important role of the ilium in anuran paleontology, there is considerable confusion surrounding some features of this element. This might be partially because “terminology of ilial features is inconsistent in the literature, and there is no single article [...] that gives all the terminology,” as Parmley et al. (2010:1879) recently acknowledged. Therefore, we here review the terminology used so far to describe anuran ilia and provide an annotated glossary of main ilial features. Even though ilial morphology has been used extensively for taxonomic purposes in paleontology, variation in ilial features has not been widely used for cladistic analyses of anurans, although a few exceptions exist (e.g.,

Pramuk, 2006; Báez et al., 2012). Taking this into account, we also survey ilial morphology and comment on variation exhibited by each ilial feature among major anuran lineages. With the aim of clarifying hypotheses of primary homology, we document sites of muscle attachment on the ilium based on the literature and personal examination of dissected material and also provide muscle maps for a few species. We consider previous cladistic analyses that exploit part of the described variation; this is intended to provide a foundation for using this bone in future research on anuran phylogenetics. Finally, we discuss the terminology used for the dorsal prominence-protuberance complex.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, U.S.A.; **FCEN**, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina; **FCEN-LPEV**, Colección Anexa del Laboratorio de Paleontología Evolutiva de Vertebrados, 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**, Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; **MACN-HE**, Colección de Herpetología del Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia,’ Buenos Aires, Argentina; **MCN**, Museo de Ciencias Naturales, Universidad Nacional de Salta, Salta, Argentina; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **MLP**, Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, U.S.A.; **MPEF-PV**, Colección de Paleontología de Vertebrados del Museo Paleontológico ‘Egidio Feruglio,’ Trelew, Argentina.

Anatomical Abbreviations—**acf**, acetabular fossa; **acr**, acetabular rim; **adl**, adductor longus; **adm**, adductor magnus; **cil**,

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coccygeiliacus; **cr**, calamita ridge; **cru**, cruralis; **dae**, dorsal acetabular expansion; **dc**, dorsal crest; **dpm**, dorsal prominence; **dpt**, dorsal protuberance; **ge**, gemellus; **glm**, gluteus magnus; **gma**, gracilis major; **gmi**, gracilis minor; **ifb**, iliofibularis; **ife**, iliofemoralis; **ifk**, knob for the iliofibularis-iliofemoralis; **iis**, interiliac scar; **ij**, ilioischiatric juncture; **ilex**, iliacus externus; **ilin**, iliacus internus; **illu**, iliolumbaris; **ip**, ischiatic process; **isc**, ischium; **ish**, ilial shaft; **isy**, interiliac symphysis; **it**, interiliac tubercle; **lor**, lateral oblique ridge; **m**, musculus; **mog**, medial oblique groove; **obex**, obturator externus; **obin**, obturator internus; **pec**, pectineus; **pz**, preacetabular zone; **pu**, pubis; **qf**, quadratus femoris; **saf**, supraacetabular fossa; **sar**, sartorius; **sbr**, semimembranosus; **sg**, spiral groove; **std**, semitendinosus; **tfl**, tensor fasciae latae; **trab**, transversus abdominis; **tuf**, tubercular fossa; **vae**, ventral acetabular expansion; **VSA**, angle between the ventral acetabular expansion anterior margin and the ilial shaft.

MATERIALS AND METHODS

We performed a comparative anatomical survey of the ilium in a wide sample of extant and extinct anurans (see Appendix 1). Dissections, observations, and drawings were done under a Zeiss Stemi SV11 stereoscope with an attached camera lucida, and photographs were taken with a Nikon D90 equipped with a macro lens. Regarding iliac anatomical nomenclature, we took as a starting point those of anglophone authors such as Holman (1959, 1965, 2003), Chantell (1964), Estes and Tihen (1964), Lynch (1971), and Tyler (1976), but we also used many supplementary terms from different sources (Fig. 1; see following section). After each common English term, when available, we provide its equivalent Latin term (in parentheses) as used by many European authors (e.g., Bolkay, 1919; Böhme, 1977; Sanchez, 1998). These and other equivalences between different nomenclatorial schemes are summarized in Table 1. For myological descriptions, we mainly followed the terminology of Gaupp

(1896) and use the works of Dunlap (1960) and Prikryl et al. (2009) as a baseline for comparisons. We also dissected a few specimens representing different anuran lineages (Appendix 1) to aid in the interpretation of some particular osteological structures and to diagram muscular maps of pelvic and thigh muscles on the ilium (Fig. 2).

We follow Gardner et al. (2010) in the operational terms applied to the ilial shaft, using the term ‘proximal’ to indicate ‘toward the acetabulum’ and the term ‘distal’ to indicate ‘toward the tip of the shaft that articulates with the sacrum.’ Our taxonomic and systematic nomenclature mainly follows Frost (2014), but we also use standard names for major groups of ‘archeobatrachians’ (e.g., discoglossoids, pipoids, and pelobatoids).

ILIAL TERMINOLOGY AND MORPHOLOGY

The ilia are the largest and most complex elements of the anuran pelvis. The ilial morphology of anurans deviates considerably from the general pattern present in other tetrapods, being unique in that the acetabulum is located well posteriorly with respect to the sacrum (Ročková and Roček, 2005). The anuran ilium consists of two main portions: (1) an elongated anterior shaft that extends anteriorly almost parallel to the postsacral vertebral column and articulates with the sacrum and (2) a posterior body that forms the anterior half of the acetabulum (Fig. 1). This bone is rich in anatomical features, and a profusion of terms have been proposed to describe its morphological features (Table 1). For each iliac feature in the following account, we provide definitions and comment on major variation present among anurans, indicate sites of muscle attachment, and give references to previous cladistic use followed by the original character number (i.e., author, year:char. number). The list of features is organized after a few main criteria: (1) we first describe the two terms referring to the main portions of the ilium; (2) then we deal with those of the body and after that with those of the shaft;

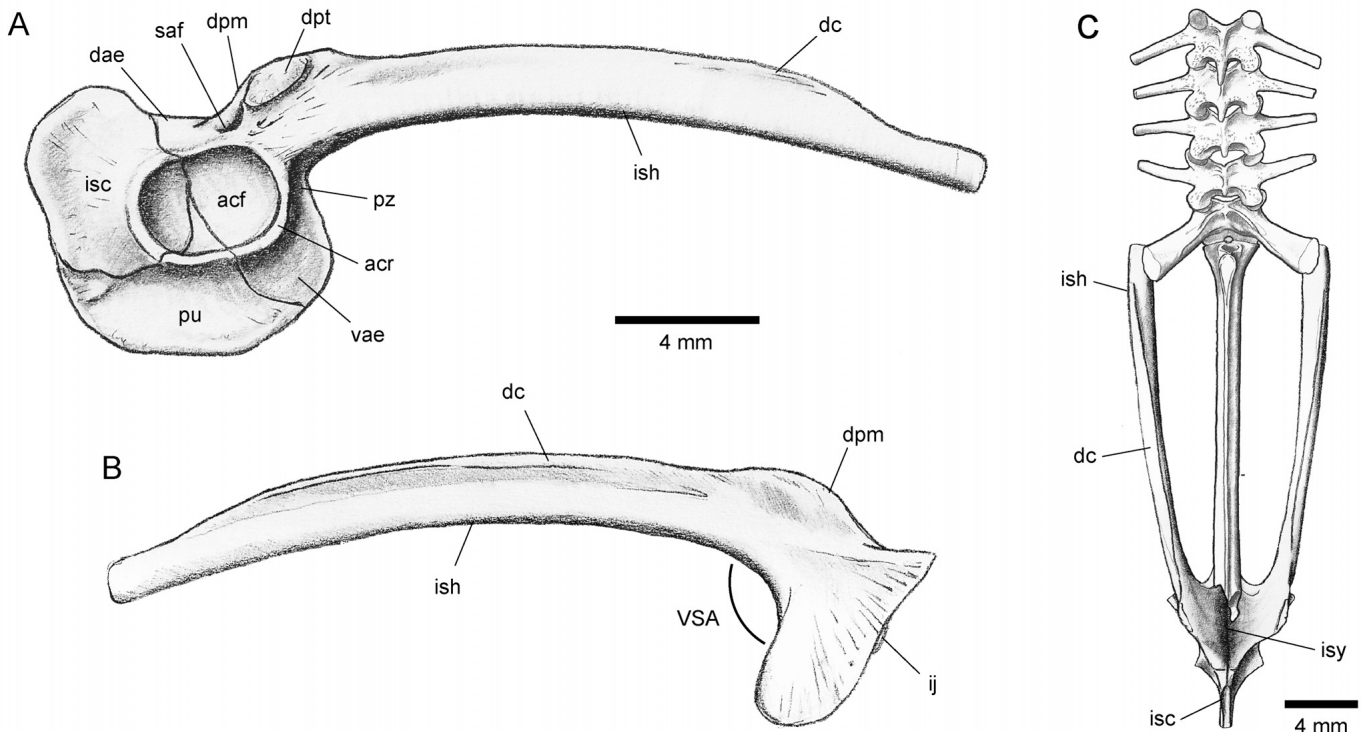


FIGURE 1. Terminology used in this paper as exemplified by the pelvis of *Leptodactylus latrans*. **A**, Right pelvis in lateral (acetabular) view; **B**, right ilium in medial view; **C**, pelvis in dorsal view showing the relation between ilia and sacrum. See text for abbreviations.

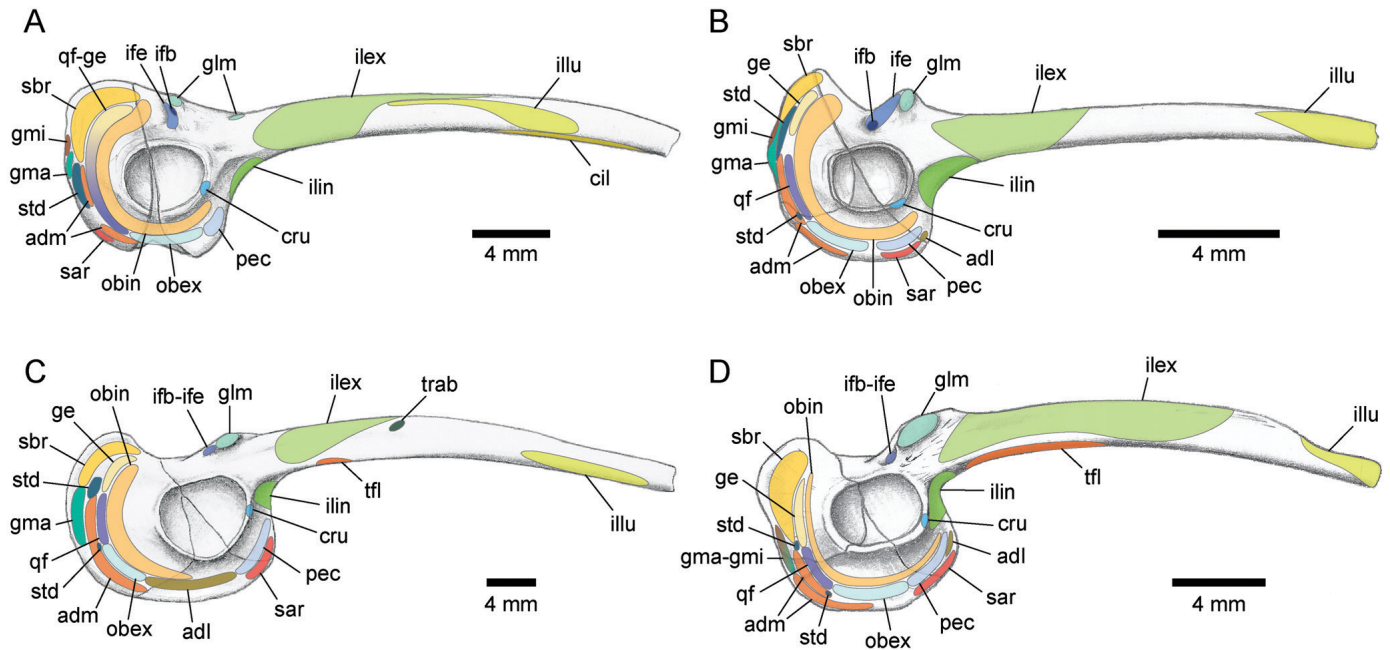


FIGURE 2. Muscle maps of the pelvis in right lateral (acetabular) view. **A**, *Scaphiopus huerterii*; **B**, *Odontophrynus occidentalis*; **C**, *Rhinella arena- rum*; **D**, *Leptodactylus latrans*. See text for abbreviations.

(3) within each part of the list, we first describe those features that are both conspicuous and/or ubiquitous among frogs and then those more subtle and/or with a narrower taxonomic occurrence; and (4) we also consider the topography and connectivity of the features.

Main Portions of the Ilium

Iliac Body (Corpus Ossis Ilii)—Expanded proximal portion of the ilium that includes part of the acetabulum and articulates with the other elements of the pelvis, namely, the pubis and the ischium (Fig. 1A). This part of the ilium is also frequently referred as the acetabular region. Variation in this region of the ilium is discussed separately for each part of it.

Iliac Shaft (Ala Ossis Ilii)—Distal part of the ilium consisting of an elongate, tubular structure, of nearly uniform diameter throughout its length, only slightly tapering distally in acetabular view, and usually circular to oval in cross-section (Fig. 1). Distally, the shaft articulates with the sacrum via a ligamentous connection and its distal terminus is always cartilaginous. Among anurans, the shaft may vary in relative length, curvature, and shape of its cross-section. Additionally, it may bear a variety of ridges, crests, or grooves, which are defined below. In most anurans, iliac shaft length is approximately four times that of iliac body length, but some taxa diverge from this typical condition. For instance, the iliac shafts of extinct basal salientians such as *Triadobatrachus* (Rage and Roček, 1989:fig. 3) and *Prosalirus* (Fig. 3A) or extant *Ascaphus* (Přikryl et al., 2009:fig. 3-2) are relatively shorter (less than three times the length of the iliac body), whereas in pipids, bombinatorids, and some hylids, the iliac shafts are relatively long (more than five times the length of the iliac body). Generally, the iliac shaft is more or less arched dorsally in acetabular view (Figs. 3, 4), but it is almost straight in a few unrelated taxa (e.g., the pipoid *Rhinophrynus dorsalis* and species of the the hyloid genus *Odontophrynus*; Figs. 3C, 4C).

At most, two muscles insert on the distal part of iliac shaft: the m. coccygeiliacus, which usually inserts on the medial side, and

the m. iliolumbaris, which variably inserts near the tip of the shaft in some taxa (Přikryl et al., 2009). In most species, the iliac shaft also provides site of origin for the m. iliacus externus, which broadly attaches dorsally or dorsolaterally, and for the m. tensor fasciae latae, which variably attaches on a small area of the medial or ventral surface of the shaft (Fig. 2). Some anurans, particularly pelobatoids and *Odontophrynus* among the taxa examined, deviate to some extent from the latter scheme in that the m. iliacus externus also originates broadly on the medial surface of the shaft (Fig. 2A, B). Additionally, in several anurans (e.g., *Odontophrynus*, *Rana*, and *Rhinella*), abdominal muscles (mm. transversus abdominis and obliquus externus) originate on the distal part of the iliac shaft, frequently only through weak fibers.

The configuration and relative length of the iliac shaft has been used as a cladistic character by Báez and Basso (1996:chars. 48, 49) in their phylogenetic analysis of basal salientians and subsequently by other authors (e.g., Gao and Wang, 2001:char. 56; Gómez, 2011:chars. 172, 174). Also, the shapes of the proximal and distal cross-sections of the shaft have been codified in separate characters by Báez et al. (2012:chars. 58, 59) in their analysis of pipoid interrelationships.

Features of the Iliac Body

Acetabular Fossa—Also termed the acetabular depression or surface, this is the iliac portion of the acetabulum. The latter is the articular cavity for the head of the femur, mainly formed by the ilium and ischium, but with a minor contribution from the pubis in most taxa (Fig. 1A). Morphological variation comprises the outline shape, depth, relative size, and relative position of the acetabular fossa. In most anurans, the acetabular fossa is semicircular or semioval with convex, proximally divergent margins, corresponding to an acetabulum that is circular or oval, respectively, in outline (Gardner et al., 2010).

Acetabular Rim (Margo Acetabularis)—Laterally projected margin of the acetabular fossa (Fig. 1A). This feature may vary

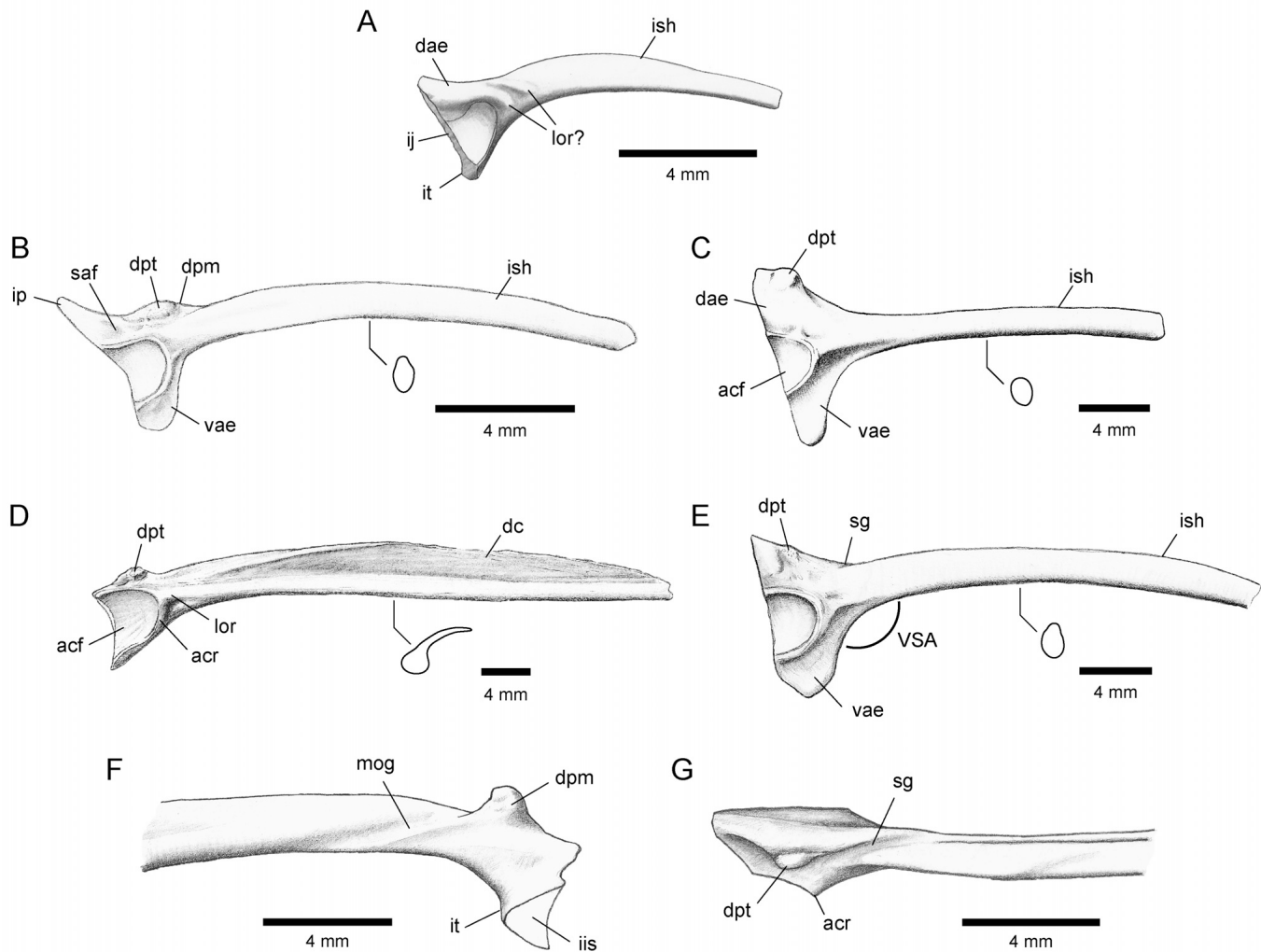


FIGURE 3. Ilium in right lateral (acetabular) view and cross-section of ilial shaft of selected non-neobatrachian salientians. **A**, *Prosalirus bitis* (restoration based on MNA V-8725 and MCZ 9324A); **B**, *Alytes obstetricans* FCEN-LPEV 24; **C**, *Rhinophrynus dorsalis* MACN-HE 42617; **D**, *Pipa pipa* FCEN 1434; **E**, *Scaphiopus couchii* FCEN-LPEV 25; **F**, close-up of proximal part of right ilium in dorsomedial view of *Pipa carvalhoi* MACN-HE 42608; **G**, close-up of proximal part of right ilium in dorsal view of *Scaphiopus couchii* FCEN-LPEV 25. See text for abbreviations.

in extent and degree of protrusion from the corpus among species. In aquatic frogs, such as pipids or species of *Pseudis* (Figs. 3D, 4F), the anteroventral portion of this rim protrudes more laterally from the ilial body than in most anurans.

In most anurans, the outer surface of the anterior or ventral part of this rim serves as site of origin of the m. cruralis; it may also accommodate the origin of the m. obturator internus in pelobatoids (Přikryl et al., 2009; pers. observ.) and species of *Odontophrynus* (Fig. 2A, B). We did not find any reference to cladistic use of acetabular traits in anurans.

Ventral Acetabular Expansion (Pars Descendens)—Part of the ilial body anteroventral to the acetabulum that contacts with the pubis (Fig. 1A). As in the previous feature, variation involves orientation and extent of this structure. The ventral acetabular expansion is developed to varying degrees in anurans and is typically well exposed in acetabular view due to a more or less distinct ventral vector (sensu Lynch, 1971). However, in some anurans such as pipids or bombinatorids, the ventral acetabular expansion has almost no ventral vector, being instead oriented medially; therefore, its exposure in acetabular view is minimal (Figs. 3D). Part of the variation

in this region is measured as the preacetabular angle (i.e., VSA, the angle formed by the anterior margin of the ventral acetabular expansion and the ventral margin of the ilial shaft in acetabular view; e.g., Holman, 1965; Lynch, 1971). This angle is usually larger than 90° in most anurans (Figs. 3B–E, 4C–E), but it is clearly acute in some neobatrachians that have well-developed ventral acetabular expansions, including species of ranids, terraranans, hylodids, cycloramphids, *Pseudis*, and *Leptodactylus* (Lynch, 1971:figs. 38–40; Gómez et al., 2013:fig. 4; Figs. 1B, 4F, H).

In many anurans, the mm. adductor longus and pectineus at least partially originate on the lateral surface of the ventral acetabular expansion (Dunlap, 1960; Přikryl et al., 2009; Fig. 2). In many neobatrachians, a large m. sartorius may also originate on this same surface (Fig. 2C, D), whereas in most ‘archeobatrachians,’ the origin of this muscle (or of the sartorial head of the sartorius-semi-tendinosus complex) is typically located on the pubis, the ventral part of the ischium, and/or the fascia of other muscles (Dunlap, 1960; Holman, 1965; Přikryl et al., 2009).

To date, a few phylogenetic analyses have included characters concerning the preacetabular angle (Pramuk, 2006:55; Ponsa,

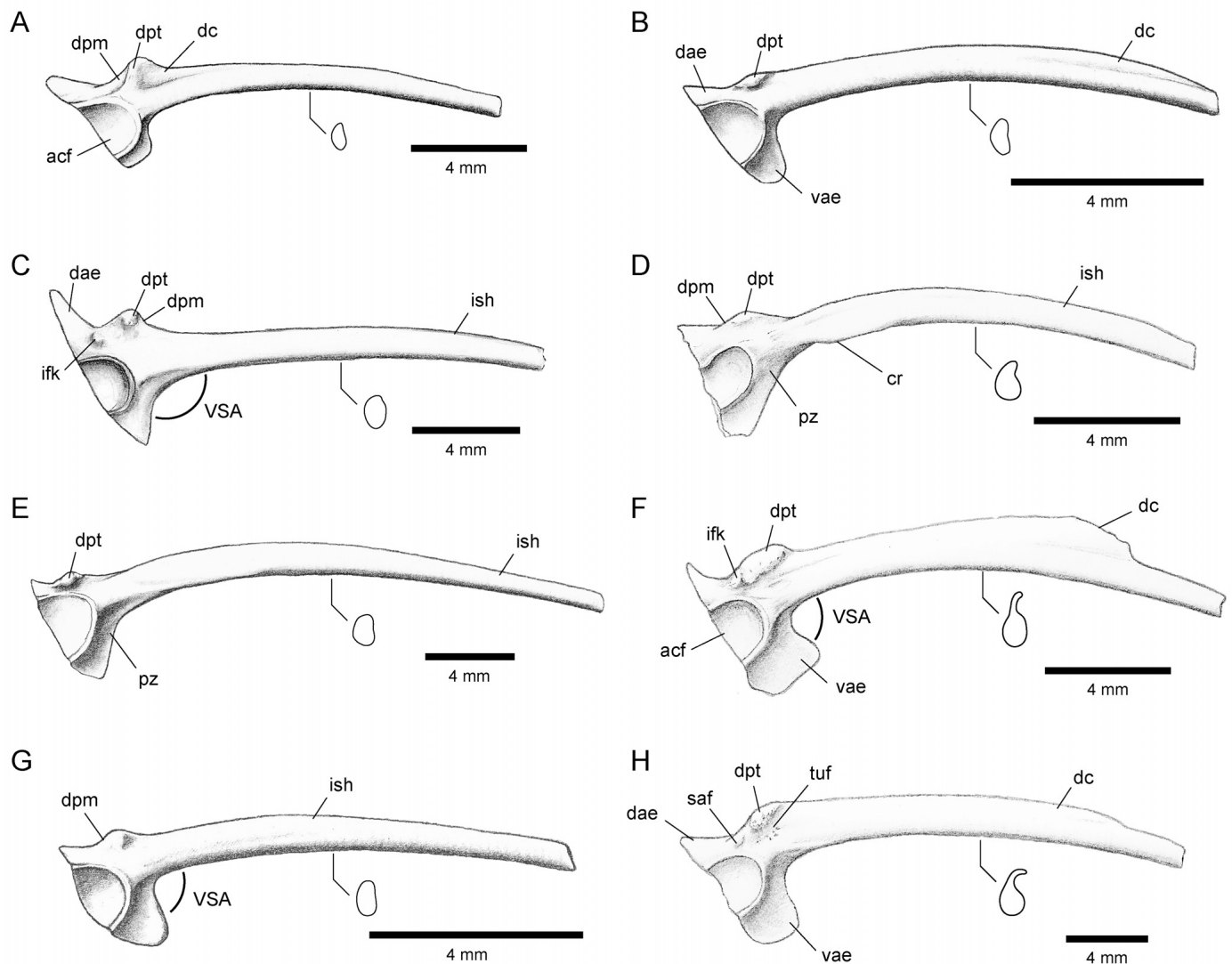


FIGURE 4. Ilium in right lateral (acetabular) view and cross-section of ilial shaft of selected neobatrachian anurans. **A**, *Limnodynastes fletcheri* FCEN 626; **B**, *Oreobates discoidalis* FCEN 1764; **C**, *Odontophrynus occidentalis* FCEN 1218; **D**, *Nannophryne variegata* FCEN 1636; **E**, *Phyllomedusa sauvagii* FCEN 305; **F**, *Pseudis minuta* FCEN 1955; **G**, *Hamptophryne boliviana* KU 205799; **H**, *Rana temporaria* FCEN 1547. See text for abbreviations.

2008:char. 87; Gómez, 2011:char. 176; Báez et al., 2012:char. 71; Báez, 2013:char. 67) or the exposure of the ventral acetabular expansion in acetabular view (Báez and Pugener, 2003:char. 45; Gómez, 2011:char. 175).

Praacetabular Zone—Defined by Lynch (1971:61) as that “area of the ventral acetabular expansion lying anterior to the anterior lip of the acetabulum and dorsal to the ventral lip of the acetabulum,” just below the ilial shaft (Fig. 1A). The condition of this feature should be assessed in acetabular view. An expanded praacetabular zone has been considered an ‘advanced’ feature (e.g., Trueb, 1973), although to date no phylogenetic analysis has properly tested the distribution of this trait. The praacetabular zone is maximally developed in many hylids (Fig. 4E), but is also broad in some myobatrachids (e.g., *Neobatrachus*; Lynch, 1971:fig. 37e).

In most anurans, the m. iliatus internus wraps anteriorly around the praacetabular zone (Fig. 2). However, in some taxa, the origin of this muscle is restricted to the medial surface of the ilium (e.g., *Discoglossus*; Prikryl et al., 2009).

Dorsal Acetabular Expansion (Pars Ascendens)—Part of the ilial body dorsal to the acetabulum that articulates with the ischium (Fig. 1A). Variation involves orientation and extent of this structure (Figs. 3, 4). In most anurans, it develops more or less posterodorsally to the acetabular fossa as a triangular area in acetabular view. However, in some anurans (e.g., pipids), this expansion is medially directed; hence, it is almost indistinguishable in acetabular view (Fig. 3D), but it is well exposed in dorsal view (e.g., Báez et al., 2012).

Different muscles, including the mm. obturator internus, semi-membranosus, and gemellus, originate in part on the most posterior portion of the lateral surface of the dorsal acetabular expansion of some species (e.g., pelobatoids, *Rana*, and *Odontophrynus*; Prikryl et al., 2009; pers. observ.; Fig. 2A, B), although the origin of these muscles is usually restricted to the ischium (Fig. 2C, D). Whatever the case may be, the dorsal acetabular expansion typically has a smooth surface, lacking roughened areas or knobs that indicate the attachment of muscles to it. Among the species examined, only scaphiopodid and pelodytid

pelobatoids show a knob or a rough area, which is a site of origin of the m. gluteus magnus, near the dorsal margin of the dorsal acetabular expansion (Fig. 3E). In these species, posteroventral to the latter, the mm. iliofibularis and iliofemoralis also originate posteroventral to the latter (Fig. 2A).

The degree of exposure of the dorsal acetabular expansion in acetabular view has been used, although codified in different ways, in some cladistic analyses of pipoids (e.g., Báez and Pugenner, 2003:char. 44; Báez et al., 2012:char. 72) and anurans in general (Gómez, 2011:char. 177).

Ischiatic Process—Part of the dorsal acetabular expansion that projects posterodorsally into an acute point (Fig. 3B). A long ischiatic process is characteristic of many extant and extinct alytids or alytid-like discoglossoids, including *Alytes*, *Discoglossus*, *Latonia*, and *Paradiscoglossus* (e.g., Estes and Sanchiz, 1982:fig. 2; Roček, 1994:fig. 18; Fig. 3B). This trait has been considered as a cladistic character by Clarke (1988) in a phylogenetic analysis of discoglossoids and subsequently by other authors (Báez and Basso, 1996:char. 50; Gao and Wang, 2001:char. 57; Gómez, 2011:char. 178).

Ilioischiatic Junction (Junctura Ilioischiadica)—Posterior face of the ilium that articulates with the ischium and pubis (Fig. 5). Variation in this rough surface primarily involves its shape and transverse width, being thick in most pipimorphs (i.e., non-rhynchophrynid pipoids; Fig. 5C) but relatively narrow in most other anurans (Fig. 5A). It is noteworthy that in some taxa (e.g., hymenochirine and some xenopodine pipids and ceratophryids), the ilia completely fuse to the ischia and ossified pubes, making an accurate description of the shape of the juncture impossible, although it is still possible to state whether it is transversely narrow or wide.

The shape of the ilioischiatic juncture has been widely used in taxonomic identifications and characterizations of many extant and extinct anuran species from Europe (e.g., Felix and Montori, 1986; Venczel and Csiki, 2003). However, this type of information has not been published for most species in other regions of the world, and has not been included in cladistic analyses of any group of anurans.

Interiliac Tubercle (Tuber Interiliacus)—Projection from the medial wall of the ilial body that articulates with the contralateral ilium to form an interiliac symphysis (Figs. 3F, 5). The articular surface of this tubercle has been called the interiliac scar by some authors (Gardner et al., 2010; Báez et al., 2012). This structure varies in its relative size, shape, and position among different species (Fig. 5B, C). In several ‘archeobatrachian’ taxa, including *Ascaphus*, many extant discoglossoids, *Gobiatas*, and Miocene pelobatoids of the genera *Eopelobates* and *Pelobates*, this structure is a relatively small to moderately large, distinct tubercle on the ventral and/or the middle region of the ilial body (Rage and Hossini, 2000;

Roček, 2008:fig. 2e1; Gardner et al., 2010:fig. 4c–e, g–i). An interiliac tubercle is maximally developed in the highly aquatic pipids (Figs. 3F, 5C) and palaeobatrachids, in which the broad articular surface of the interiliac tubercle covers most of the medial face of the ilial body (Estes and Sanchiz, 1982; Báez et al., 2012:fig. 4c). Among neobatrachians, a more or less developed interiliac tubercle has only been observed in the aquatic hylids of the genus *Pseudis* (Fig. 5B) and in the Cretaceous frog *Hungarobatrachus* (Szentesi and Venczel, 2010:fig. 2c). In the latter taxon, the interiliac tubercle is extremely broad and occupies almost all the medial surface of the ilial body. If the putative systematic affinities of *Hungarobatrachus* are confirmed, it would be the only known neobatrachian with a pipid-like interiliac tubercle. Although the observed variation appears to be phylogenetically informative, we could find only a few instances where the interiliac tubercle was used in cladistic analyses (Gómez, 2011:char. 182; Báez et al., 2012:char. 70; Báez, 2013:char. 66).

Dorsal Prominence—Outgrowth of smooth, finished bone from the dorsal surface of the ilium, typically positioned between the dorsal acetabular expansion and the ilial shaft (Fig. 1A, B). Where present, variation in this feature among anurans involves its shape, relative height (e.g., with respect to the acetabular fossa), relative position (e.g., position with respect to the anterior rim of the acetabulum), and orientation. Where a dorsal crest is also present and is well developed proximally, the dorsal prominence often merges with the latter, becoming barely discernible (Lynch, 1971; Tyler, 1976; Figs. 1A, 4F, H). A distinct dorsal prominence is absent in the ilia of several basal taxa such as *Ascaphus* (Gardner et al., 2010:fig. 4b), *Leiopelma* (Worthy et al., 2013:fig. 1a, d, e, h), pelobatoids (Fig. 3E), and the basal salientians *Prosalirus* (Shubin and Jenkins, 1995; Fig. 3A), *Notobatrachus* (Báez and Basso, 1996:fig. 15), and *Mesophryne* (Gao and Wang, 2001:fig. 3). Notwithstanding, a conspicuous dorsal prominence is present in the most basal and ancient salientians *Triadobatrachus* and *Czatkobatrachus* (Ročková and Roček, 2005:fig. 8b, d).

On the lateral surface of the posterior part of the dorsal prominence the mm. iliofibularis and iliofemoralis originate, often by a common tendon (Přikryl et al., 2009), which often leaves no scar on the bone (Fig. 2B–D). However, some extant and extinct taxa, including *Ascaphus* (Gardner et al., 2010:fig. 4b), some palaeobatrachids (Estes and Sanchiz, 1982:fig. 4), the hylid *Pseudis* (Fig. 4F), and some species of *Odontophrynus* (Figs. 2B, 4C), among others, show a rough area or even a small knob where these muscles (or at least the m. iliofibularis) originate, or might originate in the case of fossils, as has been interpreted by Estes and Sanchiz (1982).

The absence or presence of a distinct dorsal prominence and/or its general shape have been incorporated as characters in a few phylogenetic analyses (Cannatella, 1985:chars. 109, 110; Gao and Wang, 2001:char. 58; Gómez, 2011:char. 179), whereas variations in its relative height, shape, orientation, and relative position have recently been codified as separate characters in a cladistic analysis of pipoids (Báez et al., 2012:chars. 60–63).

Dorsal Protuberance—Knob-like or shallow projection of rough, unfinished bone adjoined to the lateral surface of the dorsal prominence, where the latter is present, or to the dorsolateral surface of the ilium, usually on the dorsal acetabular expansion or on the most proximal part of the ilial shaft (Figs. 1A, 3C, E). In those taxa in which a distinct dorsal prominence is absent, a shallow dorsal protuberance is often present (e.g., *Ascaphus* and *Leiopelma*; Gardner et al., 2010:fig. 4b; Worthy et al., 2013:fig. 1a, d, e, h). A distinct dorsal protuberance is evident in many anurans, but it is indistinguishable from the dorsal prominence in, for instance, ceratophryids (Lynch, 1971). Among different species, the dorsal protuberance may vary in shape, relative size, position within the dorsal prominence or within the ilium in

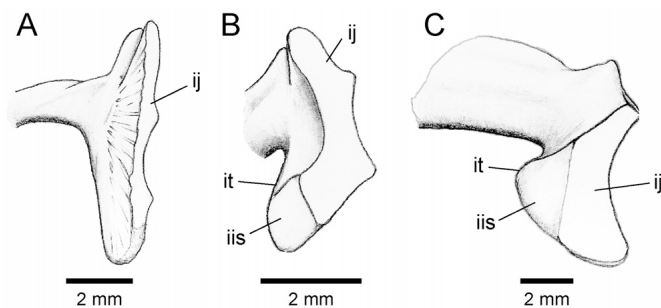


FIGURE 5. Ilium in posteromedial view showing the ilioischiatic juncture and the condition of the interiliac tubercle. **A**, *Odontophrynus lavil-lai* FCEN 1096; **B**, *Pseudis minuta* FCEN 1955; **C**, *Pipa pipa* FCEN 1434. See text for abbreviations.

general, and orientation (Fig. 3). It may be round, oval, elongate, or irregular in outline, and its surface may be lobed as in many bufonids (e.g., Sanchiz, 1977). It has to be noted that the dorsal protuberance ossifies relatively late in anuran ontogeny and apparently from an independent center of ossification (pers. observ.); thus, it might not be preserved well in fossils representing juvenile stages, so caution must be used if there are suspicions that the fossil does not represent an adult individual. This is also evidenced when preparing dry skeletons of juveniles or small adults of some species, in which the already ossified dorsal protuberance frequently detaches from the dorsal prominence.

The dorsal protuberance always serves as the site of origin for the *m. gluteus magnus* (Dunlap, 1960; Holman, 1965; Lynch, 1971; Prikryl et al., 2009; Fig. 2), a fact that is reflected in some of the names applied to this feature, namely, ‘vastus prominence’ of Holman (1965) or ‘gluteal tubercle’ of Estes (1964). Even in taxa with or without a distinct dorsal prominence and in which a dorsal protuberance is barely distinguishable, the *m. gluteus magnus* originates in the same region, near the base of the ilial shaft (see the next section for further discussion). Neither the *m. iliofemoralis* nor the *m. iliofibularis* has its origin on the dorsal protuberance in any anuran species examined.

Variation in the morphology of the dorsal protuberance has been used as a character in phylogenetic analyses of ranoids (Scott, 2005:char. 12), bufonids (Pramuk, 2006:char. 54), pipoids (Báez et al., 2012:chars. 64, 65), and anurans in general (Gómez, 2011:char. 180).

Dorsal Tubercle (Tuber Superius, Tuber Superior)—Collectively includes the dorsal prominence and the dorsal protuberance. This term is often used when no formal distinction is made between the latter two features (e.g., Evans et al., 1990), although some inconsistencies exist regarding the use of this term in the literature (further discussed in the next section).

Supraacetabular Fossa (Fossula Tuberis Superioris)—Depression on the lateral surface of the ilial body, located dorsal to the acetabular fossa and posterior or posteroventral to the dorsal prominence (Fig. 1A). Where present, the supraacetabular fossa is usually delimited by a ridge that merges with the base of the dorsal prominence. It has been described as a poorly delimited, relatively wide, and usually shallow fossa located posterior to the dorsal prominence (Fig. 3B) in extant and extinct non-bombinatorid discoglossoids (e.g., *Alytes*, *Discoglossus*, *Paralatonina*, *Paradiscoglossus*, *Enneabatrachus*, and *Bakonybatrachus*; Estes and Sanchiz, 1982:fig. 2; Evans and Milner, 1993:fig. 1; Venczel and Csiki, 2003:fig. 3; Szentesi and Venczel, 2012:fig. 1; Fig. 3B). Conversely, the supraacetabular fossa is a well-delimited, small, and deep fossa located posteroventral to the dorsal prominence in species of *Leptodactylus* and many ranids (e.g., *Lithobates* and *Rana*), among the species examined (Figs. 1A, 4H). A distinct supraacetabular fossa is absent in several taxa, including *Ascapheus*, pelobatoids, hylids, ceratophryids, *Odontophrynus*, and the basal salientians *Prosalirus* and *Notobatrachus*, among others (Báez and Basso, 1996:fig. 15; Gardner et al., 2010:fig. 4b; Figs. 3A, E, 4C, E, F).

In their survey of extant alytid ilia, Estes and Sanchiz (1982) stated that this fossa is not a site of muscle attachment, but simply an architectural by-product; a statement that might hold true for discoglossoids in general (Prikryl et al., 2009). However, in other anurans we examined (e.g., ranids and leptodactylids), it is clear that in this fossa is the attachment for the tendon of the *m. iliofibularis* or the common tendon of the *mm. iliofemoralis* and *iliofibularis* (Holman, 1965; Fig. 2D), which is consistent with the different morphology of the fossa in different groups (Figs. 1A, 3B, 4H). It becomes evident that the supraacetabular fossa of discoglossoids shares neither the same topological relations with other parts of the ilium (criterion of topological equivalence) nor the same anatomical details regarding, for instance, myological correlates (criterion of special quality of structures), with that of

ranids and leptodactylids; thus, these fossae are not valid primary homologues (sensu de Pinna, 1991). We do not here provide a new term for these fossae, although we encourage referring to the former as the ‘discoglossoid supraacetabular fossa’ in order to avoid confusion. The absence or presence of a supraacetabular fossa might be of systematic value, but to our knowledge, no cladistic analysis has incorporated it as a character. It is noteworthy that, besides the above-mentioned variation, the term supraacetabular fossa is used incorrectly by some authors (e.g., Evans et al., 1990; Blain, 2009) to designate another fossa of the ilium, namely, the tubercular fossa (see next section).

Tubercular Fossa (Fossula Tuberis Superioris)—A shallow depressed area ventral to the dorsal protuberance and dorsal to the ilial shaft (Fig. 3H). This fossa was first named and described as the fossula tuberis superii by Fejérváry (1916), a name that was also used by Bolkay (1919) and subsequently by other authors, with minor differences in the spelling (e.g., Roček, 1994). Other seldom used names also exist in the literature (e.g., dorsal protuberance’s fossette; Venczel and Csiki, 2003). A tubercular fossa has been described for some extant and extinct alytid discoglossoids (e.g., Roček, 1994:fig. 18; Blain, 2009) and a few ranids (*Rana* and *Lithobates*; Fejérváry, 1916; Bolkay, 1919:fig. 63; Fig. 4H), although it is somewhat shallower in the latter. These taxa also share the presence of a conspicuous dorsal protuberance and a well-developed dorsal crest. Our observations confirm the presence of a distinct tubercular fossa in these taxa and also indicate its presence in other ranoids (e.g., *Conraua* and *Hylarana*), but not in the examined hylids having a similarly developed dorsal protuberance and dorsal crest (e.g., *Calyptocephalella*, *Mixophyes*, *Leptodactylus*, and *Pseudis*).

This fossa is not related to muscle attachment in discoglossoids or ranoids; it might be a structural by-product of the morphology and relation of the dorsal protuberance and dorsal crest in these taxa. In not having an obvious functional correlate, this trait potentially could be informative for assessing phylogenetic relatedness. In spite of this, the absence/presence of a tubercular fossa has not yet been included in cladistic analyses.

Praecetabular Fossa (Fossa Praecetabularis)—Depression on the praecetabular zone, distal to the acetabular fossa and just ventral to the ilial shaft. It may be present or not, and where present, variation involves depth and extent of the fossa. The presence and depth of the praecetabular fossa may vary among closely related genera (e.g., European bufonids; Sanchiz, 1977), within a genus (e.g., *Rana* and *Odontophrynus*; Gleed-Owen, 2000; pers. observ.), or even within a single species (e.g., *Barbarophryne brongersmai*; Delfino et al., 2009), limiting its taxonomic usefulness in diagnosing those species in which the trait is polymorphic.

The praecetabular fossa is part of the lateral site of origin of the *m. iliacus internus* that protracts and abducts the femur (Estes and Sanchiz, 1982; Prikryl et al., 2009; Fig. 2). Therefore, variation in its depth and extent might partially correlate with differences in the volume of the *m. iliacus internus* at its origin. This variation has not been considered in phylogenetic analyses thus far, probably due to the polymorphism exhibited by some species. We think it is worth testing this feature in a cladistic framework, but caution that intraspecific variation needs to be carefully considered.

Features of the Iliac Shaft

Dorsal Crest (Crista Dorsalis)—Laminar structure that usually arises from the dorsolateral surface of the ilial shaft (Fig. 1). Where present, it may vary among taxa in height, proximodistal extension, and orientation (Figs. 3, 4). Where poorly developed, the dorsal crest is frequently described as a ridge (e.g., Lynch, 1971; Holman, 2003), and where it is maximally developed, it is

sometimes described as a blade (e.g., Lynch, 1965). On topographical grounds, all these conditions are a priori considered homologous (primary homology) in every cladistic analysis (see below). Its phylogenetic distribution suggests that a dorsal crest appeared independently more than once in anuran history (Báez et al., 2009; Gómez, 2011). A well-developed dorsal crest, although differing in shape across different taxa, is present in the extant alytid *Discoglossus* (Přikryl et al., 2009:fig. 2-2) and some fossil relatives (e.g., *Latonia*; Roček, 1994:fig. 18) and in most pipids (Báez et al., 2012:fig. 4; Fig. 3D) among ‘archeobatrachians’ as well as in several lineages of neobatrachians. Among the latter, it is present in most non-microhylid ranoids (Fig. 4H) and in several hylids, including some australobatrachians (e.g., *Calyptocephalella*, *Mixophyes*, *Lechriodus*, and some species of *Limnodynastes*; Lynch, 1971:fig. 40d; Tyler, 1976:fig. 3; Fig. 4A), some terraranans (Lynch, 1971:fig. 39; Fig. 4B), and species of *Hemiphractus* (Trueb, 1973:fig. 2-11c), *Hylodes* (Lynch, 1971:fig. 38a), *Pseudis*, and *Leptodactylus* (Gómez et al., 2013; Figs. 1A, 4F). Additionally, some fossil frogs of uncertain affinities exhibit a more or less developed dorsal crest, such as *Wealdenbatrachus* (Roček, 2000:fig. 10) and *Hungarobatrachus* (Szentesi and Venczel, 2010: fig. 2) from the Cretaceous of Europe.

Where present, the dorsal crest provides a site for the insertion of the m. coccygeoilicus on its medial surface, and in some taxa, the origin of the lateral head of the m. iliacus externus mainly on its lateral side (Přikryl et al., 2009; Fig. 2D).

The degree of development of the dorsal crest, frequently expressed simply as a presence/absence condition, has been widely used as a character in phylogenetic analyses (Clarke, 1981:char. 21; Cannatella, 1985:char. 104; Cannatella and Trueb, 1988:char. 68; Ford, 1990:char. 102; Scott, 2005:char. 13; Pugener et al., 2003:char. 70; Fabrezi, 2006:char. 52; Pramuk, 2006:char. 56; Báez et al., 2009, 2012:char. 66; Gómez, 2011:char. 173; Báez, 2013:char. 65; Henrici et al., 2013:char. 61). Additionally, variation in the orientation (Cannatella, 1985:char. 105; Trueb and Cannatella, 1986:char. 19; Báez et al., 2012:char. 68) and in the relative proximodistal extent along the shaft (Báez et al., 2012:char. 67; Henrici et al., 2013:char. 62) of the dorsal crest have also been incorporated in phylogenetic characters.

Calamita Ridge (Lamina Calamita)—Lamina calamita is a term coined by Sanchiz (1977) to describe a ridge on the ventrolateral surface of the proximal third of the ilial shaft in the bufonid *Epidalea calamita* (see Holman, 1989:fig. 1, top). The point of maximum development of this ridge lies at a distance of approximately one ilial body length from the anterior margin of the acetabular fossa. This ridge also has been mentioned in the Eurasian bufonids *Strauchbufo raddei* (Hodrová, 1986) and *Bufo bufo* (Gardner et al., 2010), though as a polymorphic feature in the latter. Notwithstanding, among the examined species, a distinct calamita ridge also is present in the bufonid *Nannophryne variegata* (Fig. 4D) and, as a pointed, small ridge, in the basal bufonid *Melanophryniscus* (pers. observ.). Additionally, although not as developed as in the abovementioned taxa, a presumed homologous blunt ridge or edge is distinct in many other bufonids from different continents (e.g., species of *Anaxyrus* and *Schismaderma carens*; pers. observ.). In several distantly related bufonids (e.g., *Melanophryniscus*, *Rhaebo guttatus*, *Bufo* and *Rhinella*; pers. observ.), the m. tensor fasciae latae is a short muscle that originates, at least in part, on the ventrolateral surface of the proximal third of the ilial shaft (Tihen, 1960; McDiarmid, 1971; Přikryl et al., 2009:fig. 7-2; Fig. 2C), where the calamita ridge or a homologous edge is maximally developed. Interestingly, in those bufonids in which the m. tensor fasciae latae is long and originates on the distal part of the ilial shaft (e.g., several species of *Atelopus* and *Ansonia*, among others; Tihen, 1960; McDiarmid, 1971), a ridge

or edge that could be homologized with the calamita ridge is lacking (pers. observ.).

In most other anurans, the m. tensor fasciae latae originates on the medial (some discoglossoids and *Odontophrynus*; Fig. 2B) or ventral (*Ascaphus*, *Pelobates*, and *Rana*) surface of the ilial shaft, usually near its mid-length (Dunlap, 1960; Přikryl et al., 2009: figs. 2-2, 3-2, 6-2, 8-2), but none has a distinct calamita ridge. The observed taxonomic distribution of a more or less developed ventrolateral ridge on the proximal third of the ilial shaft related to the origin of the m. tensor fasciae latae suggests that it might constitute a synapomorphy of bufonids. However, to date, this variation has not been tested in a cladistic framework.

Spiral Groove (Canalicula Transversalis)—Groove on the dorsal surface of the ilial body, near the base of the ilial shaft, wrapping around the ilium from dorsolateral to ventromedial (Fig. 3G). This groove often grades into a medial oblique groove on the internal surface of the shaft (Roček et al., 2013:fig. 12.4; see next section). It was first described as the ‘canalicula transversalis’ in *Pelobates* by Bolkay (1919:338), but most authors follow Evans and Milner (1993) in using the term ‘spiral groove’ to describe this groove. Still others designate this feature as the ‘oblique groove’ (e.g., Gardner et al., 2010; Roček et al., 2010, 2013), although we prefer spiral groove in order to avoid confusion with the medial oblique groove (see below), which might be present in ilia lacking a spiral groove (Roček et al., 2010, 2013; Fig. 3F). It is typical of pelobatoids and has been reported in *Gobiates* (Roček, 2008) and ilia of indeterminate affinities from the Cretaceous of Utah (Roček et al., 2013), but is absent in most anurans.

At least in pelobatoids, the spiral groove together with the medial oblique groove demarcates the origin of the inner part of the m. iliacus externus (Přikryl et al., 2009; Fig. 2A). Despite the presence of a spiral groove having been widely recognized as diagnostic for pelobatoids among extant anurans (e.g., Evans and Milner, 1993; Roček et al., 2013), this feature has rarely been used in phylogenetic analyses including pelobatoids (Gómez, 2011:char. 181; Báez, 2013:char. 64; Henrici et al., 2013: char. 60).

Medial Oblique Groove and Ridge—Shallow groove on the medial surface of the proximal part of the ilial shaft, running dorso proximally to ventrodistally from near the dorsal edge of the bone and almost reaching the ventral margin of the shaft (Fig. 3F). This groove is often delimited ventrally along its length by a rounded oblique ridge (oblique crista of some authors; e.g., Roček et al., 2013:fig. 12.1a), although a distinct oblique ridge might be present in ilia lacking an oblique groove (Báez et al., 2012:fig. 3c; Roček et al., 2013:fig. 12.5). A medial oblique groove (with or without an oblique ridge) is present, to our knowledge, in extant and extinct bombinatorids and pelobatoids, *Gobiates*, some pipids, some *Odontophrynus*, and in several ilia from the Cretaceous of Utah (Roček, 2008:fig. 2F; Folie et al., 2013:fig. 2; Roček et al., 2013:fig. 12.4; pers. observ.; Fig. 3F). At least in some anurans (e.g., *Pelobates* and some pipids), this groove demarcates posteroventrally the area of origin of the pars interna of the m. iliacus externus (Přikryl et al., 2009:figs. 6-2c, 10-2c).

Lateral Oblique Ridge—Short ridge distal to the acetabulum, in the proximal part of the lateral surface of the ilial shaft, extending obliquely from about the midpoint of the acetabular rim to the ventral surface of the ilial shaft (Fig. 3D). An oblique ridge has been noted in *Pipa* and some fossil pipimorphs (e.g., Báez et al., 2012:figs. 3b, 4a; Fig. 3D) and in several ilia from the Upper Cretaceous of Utah, representing different species of indeterminate affinities (Roček et al., 2010, 2013:figs. 12.8–12.11). The early frog *Prosalirus* bears two, instead of only one, short ridges in the same region (Gardner et al., 2010:fig. 4j; Fig. 3A); one of these ridges might be homologous to the oblique ridge. To date, no obvious functional correlate of this structure

TABLE 1. Comparison between selected nomenclatorial schemes for features of anuran ilia.

This paper	Bolkay (1919)	Chantell (1964)	Estes and Tihen (1964)	Sanchiz (1998)	Holman (2003)	Gardner et al. (2010)
Iliac body	Portio acetabularis	—	—	—	Body	Acetabular region
Iliac shaft	Ala ossis ilei/pars cylindriformis ilei	Iliac shaft	Iliac shaft	Pars cylindriformis	Iliac shaft	Iliac shaft
Acetabular fossa	—	Acetabular fossa	Acetabular fossa	—	Acetabular fossa	Acetabular surface
Acetabular rim	Margo acetabularis	—	Acetabular ridge	Acetabular margin	Acetabular rim	Acetabular margin
Ventral acetabular expansion	Pars ascendens ilei	Ventral acetabular expansion	Subacetabular expansion	Pars descendens	Ventral acetabular expansion	Pars descendens
Praecetabular zone	—	—	—	Praecetabular zone	—	—
Dorsal acetabular expansion	Pars ascendens ilei	Dorsal acetabular expansion	Supraacetabular expansion	Pars ascendens	Dorsal acetabular expansion	Pars ascendens
Ischiatic process	—	—	—	—	Ischiatic process	—
Ilioischiatic juncture	Synchondrosis ileo-ischiadica	—	—	—	—	Proximal surface
Interiliac tubercle	—	—	—	—	Interiliac tubercle	Interiliac scar
Dorsal prominence	—	Dorsal prominence	Dorsal prominence	Dorsal prominence	Dorsal prominence	Dorsal prominence
Dorsal protuberance	—	Dorsal protuberance	Dorsal protuberance	Tuber superior	Dorsal protuberance/dorsal tubercle	Dorsal tubercle
Dorsal tubercle	Tuber superius	—	—	Tuber superior	—	—
Supraacetabular fossa	—	—	Supraacetabular depression	Supraacetabular fossa	Supraacetabular fossa	—
Tubercular fossa	Fossula tuberis superii	—	—	—	—	—
Praecetabular fossa	Impressio semilunaris	—	—	—	Praecetabular fossa	—
Dorsal crest	Crista ossis ilei	Dorsal crest	Dorsal crest	Crista dorsalis	Dorsal crest	Dorsal crest
Calamita ridge	—	—	—	Lamina calamita	—	—
Spiral groove	Canalicula transversalis	—	—	—	—	Oblique groove
Lateral oblique ridge	—	—	—	—	—	Oblique ridge

has been proposed. This feature has only recently been considered in a cladistic context by Báez et al. (2012:char. 69).

Medial Crest—Dorsomedially directed crest along the proximal half of the iliac shaft. This crest has only been observed in species of the pipid genus *Hymenochirus* (Cannatella, 1985; Báez et al., 2012:fig. 4g). It is uncertain if this crest has any underlying functional significance (providing site of attachment for pelvic and/or thigh musculature) or if it is just an osteological peculiarity of *Hymenochirus*. This feature has only been considered in an unpublished cladistic analysis (Cannatella, 1985:char. 106).

THE DORSAL PROMINENCE-PROTUBERANCE COMPLEX

We notice that a few terms have recently been used in different ways in studies dealing with iliac morphology of anurans and that there is some misunderstanding regarding the terms ‘dorsal prominence’ and ‘dorsal protuberance.’ This has previously been recognized by other authors, who stated that “description of the dorsal prominence [...] in the literature is confusing” (Gao and Wang, 2001:475) or that the available terminology is “inconsistent” (Parmley et al., 2010:1879). To illustrate this state of confusion, suffice to say that different authors have equated ‘dorsal prominence’ either with ‘tuber superior’ (Blain and Villa, 2006; Worthy et al., 2013) or ‘dorsal protuberance’ (Gao and Wang, 2001), and still others have used ‘dorsal protuberance’ to describe the base of the dorsal prominence (Bever, 2005; Parmley et al., 2010). The latter is probably a misinterpretation of the

definition given in Sanchiz (1998:19) that states “tuber superior (= includes both the dorsal prominence and its base, called sometimes dorsal protuberance),” meaning that the tuber superior sometimes is called the dorsal protuberance.

As described above, the dorsal protuberance is the specific site of origin of the m. gluteus magnus in anurans (Dunlap, 1960; Holman, 1965; Lynch, 1971; Prikryl et al., 2009; Fig. 2), whereas the dorsal prominence is the bony outgrowth of the ilium that bears the dorsal protuberance (Holman, 1959; Chantell, 1964; Lynch, 1971; Figs. 1A, 3, 4). It is noteworthy that where a dorsal prominence is present, a distinct dorsal protuberance might be either present or absent (Lynch, 1971:figs. 36–38), and, similarly, a dorsal protuberance might be present even if a distinct dorsal prominence is lacking (e.g., in *Leiopelma*; Worthy et al., 2013:fig. 1a, d, e, h). Therefore, it is clear that both structures are independent features, and it is recommended to distinguish between them by using the two different terms used here; this is common practice among many authors (e.g., Holman, 1959, 2003; Lynch, 1971; Tyler, 1976; Prasad and Rage, 1995; Báez et al., 2012; Gómez et al., 2013).

Dorsal tubercle (=tuber superior=tuber superius=processus superior; Table 1) is another term associated with the dorsal prominence-protuberance complex. As far as we can interpret from the seminal works of Gaupp (1896), Bolkay (1919), and Böhme (1977), the term ‘dorsal tubercle,’ or any of its synonyms, has been intended to collectively describe what is here called the dorsal prominence and, if present, the dorsal protuberance. None of these authors have discriminated the latter features using different names, indicating that our interpretation is probably correct. In accordance with this view, most current European authors use the term ‘dorsal tubercle,’ ‘tuber superius,’ or ‘tuber

superior' to refer to the dorsal prominence-protuberance complex when no formal distinction is made between the constituent parts (e.g., Sanchiz, 1977, 1998; Evans et al., 1990; Roček et al., 2010, 2013; Folie et al., 2013; Bastir et al., 2014). However, some authors recently employed at the same time the terms 'dorsal prominence' and 'dorsal tubercle'; the former has been employed in the same way as it is used here, but the latter has been used to describe the 'dorsal protuberance' (Gardner et al., 2010). The latter two terms were previously equated by Estes and Tihen (1964), who used the terms 'dorsal prominence' and 'dorsal protuberance' in their descriptions, but this synonymy was not followed by most other authors. Considering the long-standing use of the term 'dorsal tubercle' (or any of its synonyms) to describe the dorsal prominence-protuberance complex by most European authors, we contend that it is inappropriate to use it as a synonym of the 'dorsal protuberance.'

CONCLUDING REMARKS

The ilium has been considered a 'key' element in anuran paleontology (Sanchiz, 1998), but its terminology is inconsistent across the literature (e.g., Parmley et al., 2010). Our expectation is that the definitions of ilial features given here will aid in clarifying terminological inconsistencies, particularly with reference to the dorsal prominence-protuberance complex and the supraacetabular fossa. Besides the terminological problems summarized here, although anuran ilia exhibit considerable morphological variation and there is a long history of using such variation in taxonomic studies of fossil anurans, little of that variation has been exploited in cladistic analyses. In this regard, descriptions of ilial morphology with special consideration given to myological correlates, as is exemplified by our survey of the supraacetabular fossa, could lead to well-grounded primary homology statements (i.e., character statements) in future osteology-based phylogenetic analyses of anurans. Finally, we note that despite there being a considerable body of descriptive work on anuran ilia from Europe, North America, and Australia, comparatively little work has been done on anurans from what are today tropical and subtropical regions of the world, including South America, sub-Saharan Africa, and Southeast Asia. Here we provide some information on tropical and subtropical anuran species, with special emphasis on South American hylids, but it is clear that much more work is needed to have a more comprehensive knowledge of ilial variation in anurans.

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LITERATURE CITED

- Báez, A. M. 2013. Anurans from the Early Cretaceous Lagerstätte of Las Hoyas, Spain: new evidence on the Mesozoic diversification of crown-clade Anura. *Cretaceous Research* 41:90–106.
- Báez, A. M., and N. G. Basso. 1996. The earliest known frogs of the Jurassic of South America: review and cladistic appraisal of their relationships. *Müncher Geowissenschaftliche Abhandlungen, A* 30:131–158.
- Báez, A. M., and L. A. Pugener. 2003. Ontogeny of a new Paleogene pipid frog from southern South America and xenopodinomorph evolution. *Zoological Journal of the Linnean Society* 139:439–476.
- Báez, A. M., R. O. Gómez, and M. L. Taglioretti. 2012. The archaic ilial morphology of an enigmatic pipid frog from the upper Pleistocene of the South American pampas. *Journal of Vertebrate Paleontology* 32:304–314.
- Báez, A. M., G. J. B. Moura, and R. O. Gómez. 2009. Anurans from the Lower Cretaceous Crato Formation of northeastern Brazil: implications for the early divergence of neobatrachians. *Cretaceous Research* 30:829–846.
- Bastir, M., M. Böhme, and B. Sanchiz. 2014. Middle Miocene remains of *Alytes* (Anura, Alytidae) as an example of the unrecognized value of fossil fragments for evolutionary morphology studies. *Journal of Vertebrate Paleontology* 34:69–79.
- Bever, G. S. 2005. Variation in the ilium of North American *Bufo* (Lissamphibia; Anura) and its implications for species-level identification of fragmentary anuran fossils. *Journal of Vertebrate Paleontology* 25:548–560.
- Blain, H.-A. 2009. Contribution de la paléohéropétofaune (Amphibia & Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne. *Treballs del Museo de Geologia de Barcelona* 16:39–170.
- Blain, H.-A., and P. Villa. 2006. Amphibians and squamate reptiles from the early Upper Pleistocene of Bois Roche Cave (Charente, southwestern France). *Acta Zoologica Cracoviensia* 49A:1–32.
- Böhme, G. 1977. Osteologischer Bestimmungsschlüssel für Anuren aus dem Quartär Mitteleuropas. *Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin, mathematisch-naturwissenschaftliche Reihe* 26:283–300.
- Bolkay, S. J. 1919. Osnove uporedne osteologije anurskih batrahija sa dodatkom o porijeklu Anura i sa skicom naravnoga sistema istih. *Glansika Zemaljskog Muzeja u Bosni i Hercegovini, Sarajevo* 31:277–357.
- Cannatella, D. C. 1985. A phylogeny of primitive frogs (archaeobatrachians). Ph.D. dissertation, University of Kansas, Lawrence, Kansas, 404 pp.
- Cannatella, D. C., and L. Trueb. 1988. Evolution of pipoid frogs: intergeneric relationships of the aquatic frog family Pipidae (Anura). *Zoological Journal of the Linnean Society* 94:1–38.
- Chantell, C. J. 1964. Some Mio-Pliocene hylids from the Valentine Formation of Nebraska. *The American Midland Naturalist* 72:211–224.
- Clarke, B. T. 1981. Comparative osteology and evolutionary relationships in the African Raninae (Anura Ranidae). *Monitore Zoologico Italiano (Suppl. XV)*:285–331.
- Clarke, B. T. 1988. Evolutionary relationships of the discoglossoid frogs—osteological evidence. Ph.D. dissertation, City of London Polytechnic and British Museum (Natural History), London, U.K., 431 pp.
- Delfino, M., S. Doglio, Z. Roček, D. Seglie, and L. Kabiri. 2009. Osteological peculiarities of *Bufo brongersmai* (Anura: Bufonidae) and their possible relation to life in an arid environment. *Zoological Studies* 48:108–119.
- Dunlap, D. G. 1960. The comparative myology of the pelvic appendage in the Salienta. *Journal of Morphology* 106:1–76.
- Estes, R. 1964. Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. University of California Publications in Geological Sciences 49:1–180.
- Estes, R., and B. Sanchiz. 1982. New discoglossid and palaeobatrachid frogs from the Late Cretaceous of Wyoming and Montana, and a review of other frogs from the Lance and Hell Creek formations. *Journal of Vertebrate Paleontology* 2:9–20.
- Estes, R., and J. A. Tihen. 1964. Lower vertebrates from the Valentine Formation of Nebraska: American Midland Naturalist 72:453–472.
- Evans, S. E., and A. R. Milner. 1993. Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America. *Journal of Vertebrate Paleontology* 13:24–30.
- Evans, S. E., A. R. Milner, and F. Musset. 1990. A discoglossid frog from the Middle Jurassic of England. *Palaeontology* 33:299–311.
- Fabrezi, M. 2006. Morphological evolution of the Ceratophryinae (Anura, Neobatrachia). *Journal of Zoological Systematics and Evolutionary Research* 44:153–166.

- Fejérváry, G. J. v. 1916. Beiträge zur Kenntnis von *Rana mehelyi* Bolkay. Mitteilungen Jahrbuch der Königlichen Ungarischen Geologischen Reichsanstalt 23:133–155.
- Felix, J., and A. Montori. 1986. Determinación de las especies de anfibios anuros del nordeste ibérico mediante el hueso ilion. *Miscelanea Zoológica* 10:239–246.
- Folie, A., R. S. Rana, K. D. Rose, A. Sahni, K. Kumar, L. Singh, and T. Smith. 2013. Early Eocene frogs from Vastan Lignite Mine, Gujarat, India. *Acta Palaeontologica Polonica* 58:511–524.
- Ford, L. S. 1990. The phylogenetic position of poison-dart frogs (Dendrobatidae): reassessment of the neobatrachian phylogeny with comments on complex character systems. Ph.D. dissertation, University of Kansas, Lawrence, Kansas, 307 pp.
- Frost, D. R. 2014. Amphibian Species of the World: An Online Reference, version 6.0. American Museum of Natural History, New York. Available at <http://research.amnh.org/herpetology/amphibia/>. Accessed July 15, 2014.
- Gao, K.-Q., and Y. Wang. 2001. Mesozoic anurans from Liaoning Province, China, and phylogenetic relationships of archaeobatrachian anuran clades. *Journal of Vertebrate Paleontology* 21:460–473.
- Gardner, J. D., Z. Roček, T. Prikryl, J. G. Eaton, R. W. Blob, and J. T. Sankey. 2010. Comparative morphology of the ilium of anurans and urodeles (Lissamphibia) and a re-assessment of the anuran affinities of *Nezpercius dodsoni* Blob et al., 2001. *Journal of Vertebrate Paleontology* 30:1684–1696.
- Gaupp, E. 1896. Anatomie des Frosches. Erste Abtheilung. Lehre vom Skelet und vom Muskelsystem. Druck und Verlag vom Friedrich Vieweg und Sohn, Braunschweig, Germany, 227 pp.
- Gleed-Owen, C. P. 2000. Subfossil records of *Rana cf. lessonae*, *Rana arvalis* and *Rana cf. dalmatina* from Middle Saxon (ca. 600–950 AD) deposits in eastern England: evidence for native status. *Amphibia-Reptilia* 21:57–65.
- Gómez, R. O. 2011. Los neobatracos (Amphibia: Anura) del Paleoceno de la Formación Santa Lucía, Bolivia: aportes a la historia evolutiva y paleobiogeográfica de los anuros sudamericanos. Ph.D. dissertation, Universidad de Buenos Aires, Buenos Aires, Argentina, 502 pp.
- Gómez, R. O., C. M. Pérez Ben, and M. I. Stefanini. 2013. Oldest record of *Leptodactylus* Fitzinger, 1826 (Anura, Leptodactylidae), from the early Pliocene of the South American Pampas. *Journal of Vertebrate Paleontology* 33:1321–1327.
- Henrici, A. C., A. M. Báez, and L. Grande. 2013. *Aerugoammis paulus*, new genus and new species (Anura: Anomocoela): first reported anuran from the early Eocene (Wasatchian) Fossil Butte Member of the Green River Formation, Wyoming. *Annals of Carnegie Museum* 81:295–309.
- Hodrová, M. 1986. Find of *Bufo raddei* in the upper Pliocene Bural-Obo locality (Mongolia). *Acta Universitatis Carolinae (Geologica) Spinar* 2:171–186.
- Holman, J. A. 1959. Amphibians and reptiles from the Pleistocene (Illinoian) of Williston, Florida. *Copeia* 1959:96–102.
- Holman, J. A. 1965. Early Miocene anurans from Florida. *Quarterly Journal of the Florida Academy of Sciences* 28:68–82.
- Holman, J. A. 1989. Identification of *Bufo calamita* and *Bufo bufo* on the basis of skeletal elements. *British Herpetological Society Bulletin* 29:54–55.
- Holman, J. A. 2003. Fossil Frogs and Toads of North America. Indiana University Press, Bloomington, Indiana, 246 pp.
- Lynch, J. D. 1965. Sacral fusions in some Neotropical *Rana*. *Transactions of the Illinois State Academy of Science* 58:195–199.
- Lynch, J. D. 1971. Evolutionary relationships, osteology, and zoogeography of leptodactylid frogs. University of Kansas Museum of Natural History Miscellaneous Publications 53:1–238.
- McDiarmid, R. W. 1971. Comparative morphology and evolution of frogs of the Neotropical genera *Atelopus*, *Dendrophryniscus*, *Melanophryniscus*, and *Oreophrynella*. *Science Bulletin of the Los Angeles County Museum of Natural History* 12:1–66.
- Parmley, D., K. B. Hunter, and J. A. Holman. 2010. Fossil frogs from the Clarendonian (late Miocene) of Oklahoma, U.S.A. *Journal of Vertebrate Paleontology* 30:1879–1883.
- de Pinna, M. C. C. 1991. Concepts and tests of homology in the cladistic paradigm. *Cladistics* 7:367–394.
- Ponssa, M. L. 2008. Cladistic analysis and osteological descriptions of the species of the *L. fuscus* species group of the genus *Leptodactylus* (Anura, Leptodactylidae). *Journal of Zoological Systematic and Evolutionary Research* 46:249–266.
- Pramuk, J. B. 2006. Phylogeny of South American *Bufo* (Anura: Bufonidae) inferred from combined evidence. *Zoological Journal of the Linnean Society* 146:407–452.
- Prasad, G. V. R., and J.-C. Rage. 1995. Amphibians and squamates from the Maastrichtian of Naskal, India. *Cretaceous Research* 16:95–107.
- Přikryl, T., P. Alerts, P. Havelková, A. Herrel, and Z. Roček. 2009. Pelvic and thigh musculature in frogs (Anura) and origin of anuran jumping locomotion. *Journal of Anatomy* 214:100–139.
- Pugener, L. A., A. M. Maglia, and L. Trueb. 2003. Revisiting the contribution of larval characters to an analysis of phylogenetic relationships of basal anurans. *Zoological Journal of the Linnean Society* 139:129–155.
- Rage, J.-C., and S. Hossini. 2000. Les amphibiens du Miocène moyen de Sansan: pp. 177–217 in L. Ginsburg (ed.), *La Faune Miocène de Sansan et son Environnement*. Mémoires du Muséum national d'Histoire naturelle Paris 183.
- Rage, J.-C., and Z. Roček. 1989. Redescription of *Triadobatrachus massinoti* (Piveteau, 1936) an anuran amphibian from the Early Triassic. *Palaeontographica Abteilung A* 206:1–16.
- Roček, Z. 1994. Taxonomy and distribution of Tertiary discoglossids (Anura) of the genus *Latonia* v. Meyer, 1843. *Geobios* 27: 717–751.
- Roček, Z. 2000. Mesozoic anurans; pp. 1295–1331 in H. Heatwole and R. L. Carroll (eds.), *Amphibian Biology*, Volume 4, *Paleontology: The Evolutionary History of Amphibians*. Surrey Beatty & Sons, Chipping Norton, New South Wales, Australia.
- Roček, Z. 2008. The Late Cretaceous frog *Gobiatos* from Central Asia: its evolutionary status and possible phylogenetic relationships. *Cretaceous Research* 29:577–591.
- Roček, Z., J. G. Eaton, J. D. Gardner, and T. Prikryl. 2010. Evolution of anuran assemblages in the Late Cretaceous of Utah, USA. *Palaeobiodiversity and Palaeoenvironments* 90:341–393.
- Roček, Z., J. D. Gardner, J. G. Eaton, and T. Prikryl. 2013. Anuran ilia from the Upper Cretaceous of Utah—diversity and stratigraphic patterns; pp. 273–294 in A. L. Titus and M. A. Lowen (eds.), *At the Top of the Grand Staircase: The Late Cretaceous of Southern Utah*. Indiana University Press, Bloomington, Indiana.
- Ročková, H., and Z. Roček. 2005. Development of the pelvis and posterior part of the vertebral column in the Anura. *Journal of Anatomy* 206:17–35.
- Sanchiz, B. 1977. La familia Bufonidae (Amphibia, Anura) en el Terciario europeo. *Trabajos Neógeno/Cuaternario* 8:75–111.
- Sanchiz, B. 1998. Saliencia; in P. Wellnhofer (ed.), *Encyclopedia of Paleoherpétology*, Part 4. Verlag Dr. Friedrich Pfeil, Munich, 275 pp.
- Scott, E. 2005. A phylogeny of ranid frogs (Anura: Ranoidea: Ranidae), based on a simultaneous analysis of morphological and molecular data. *Cladistics* 21:507–574.
- Shubin, N. H., and F. A. Jenkins, Jr. 1995. An Early Jurassic jumping frog. *Nature* 377:49–52.
- Szentesi, Z., and M. Venczel. 2010. An advanced anuran from the Late Cretaceous (Santonian) of Hungary. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 256:291–302.
- Szentesi, Z., and M. Venczel. 2012. A new discoglossid frog from the Upper Cretaceous (Santonian) of Hungary. *Cretaceous Research* 34:327–333.
- Tihen, J. A. 1960. Two new genera of African bufonids, with remarks on the phylogeny of related genera. *Copeia* 1960:225–233.
- Trueb, L. 1973. Bones, frogs, and evolution; pp. 65–132 in J. L. Vial (ed.), *Evolutionary Biology of the Anurans: Contemporary Research on Major Problems*. University of Missouri Press, Columbia, Missouri.
- Trueb, L., and D. C. Cannatella. 1986. Systematics, morphology, and phylogeny of the genus *Pipa* (Anura: Pipidae). *Herpetologica* 42:412–449.
- Tyler, M. J. 1976. Comparative osteology of the pelvic girdle of Australian frogs and description of a new fossil genus. *Transactions of the Royal Society of South Australia* 100:3–14.
- Venczel, M., and Z. Csiki. 2003. New discoglossid frogs from the latest Cretaceous of Hațeg Basin (Romania). *Acta Palaeontologica Polonica* 48:599–606.
- Worthy, T. H., A. J. D. Tennyson, R. P. Scofield, and S. J. Hand. 2013. Early Miocene fossil frogs (Anura: Leiopelmatidae) from New Zealand. *Journal of the Royal Society of New Zealand* 43:211–230.

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APPENDIX 1. Specimens examined. **Abbreviations:** **CS**, cleared and stained; **DS**, dry skeleton; **FD**, fixed material used for dissections; **LM**, latex molds; **PD**, photographs and/or drawings; **UN**, unnumbered.

- Alsodidae: *Alsodes nodosus* FCEN 722, DS. *Eupsophus vertebralis* MACN-HE 43704, DS.
- Alytidae: *Alytes cisternasii* FCEN-LPEV UN, DS. *Alytes obstetricans* FCEN-LPEV 24, DS. *Discoglossus pictus* FCEN-LPEV UN, DS; FML 03945, CS.
- Arthroleptidae: *Arthroleptis adolphifriederici* MCN 822, CS. *Leptopelis christyi* MCN 829, CS.
- Ascaphidae: *Ascaphus truei* AMNH A-57970 (DS), PD.
- Batrachylidae: *Hylorina sylvatica* FCEN 304, DS.
- Bombinatoridae: *Bombina variegata* MCN 810, CS; FCEN 401, DS.
- Bufoinidae: *Anaxyrus woodhousii* FCEN 487, DS. *Anaxyrus cognatus* MACN-HE 45417, DS. *Ansonia penangensis* FCEN 1049, DS. *Bufo bufo* FCEN 1535–1544, DS. *Epidalea calamita* MACN-HE 45415, DS. *Melanophryniscus rubriventris* MACN-HE 45412, DS. *Nannophryne variegata* MCN 012, CS; FCEN 1636, DS. *Rhinella arenarum* FCEN 636, DS; FCEN 1637, FD; MACN-HE 45378, DS. *Rhinella fernandezae* MACN-HE 45378, DS. *Strauchbufo raddei* FCEN 1601, DS. *Schismaderma carens* MACN-HE 45419, DS.
- Calyptocephalellidae: *Calyptocephalella gayi* FCEN 1433, DS. *Telmatobufo venustus* KU 161439 (DS), PD.
- Ceratophryidae: *Ceratophrys cranwelli* FCEN 665, 1015, DS. *Ceratophrys ornata* FCEN 1580, DS. *Chacophrys pierotti* FCEN UN, DS. *Lepidobatrachus laevis* FCEN 319, 665, DS.
- Conrauidae: *Conraua crassipes* MCN 834, CS. *Conraua goliath* AMNH A-177110 (DS), PD.
- Craugastoridae: *Oreobates discoidalis* MCN 462, CS; FCEN 1764, DS. *Pristimantis w-nigrum* KU 190094 (DS), PD.
- Cycloramphidae: *Cycloramphus dubius* FCEN 758, DS. *Eupsophus vertebralis* MACN-HE 43704, DS. *Thoropa miliaris* FCEN 595, DS.
- Eleutherodactylidae: *Eleutherodactylus inoptatus* FCEN 1616, DS. *E. martinicensis* FCEN 978, DS.
- Heleophryinae: *Hadromophryne natalensis* KU 195926 (CS), PD.
- Hemiphraactidae: *Gastrotheca gracilis* FML 2965, CS. *Hemiphraactus johnsoni* AMNH A-1343 (DS), PD.
- Hylidae: *Dendropsophus nanus* FCEN-LPEV UN, DS. *Hypsiobas pulchellus* FCEN-LPEV UN, DS. *Litoria australis* FCEN 1272, DS. *Phyllomedusa sauvagii* MCN 795, CS; FCEN 305, DS. *Pseudis minuta* FCEN 1955 (B-96), FD, DS. *Pseudis platensis* FCEN 727, DS. *Scinax granulatus* FCEN-LPEV UN, DS. *Pseudis platensis* MCN 812, CS; FCEN 727, DS. *Scinax granulatus* FCEN UN, DS.
- Hylodidae: *Hylodes asper* FCEN 762, DS.
- Hyperoliidae: *Hyperolius kivuensis* MCN 804, CS. *Phlyctimantis verrucosus* MCN 832, CS.
- Leiopelmatidae: *Leiopelma hochstetteri* AMNH A-17066 (DS), PD.
- Leiuperidae: *Physalaemus biligonigerus* MCN 802, CS. *Pleurodema cinereum* FCEN 93, DS.
- Leptodactylidae: *Leptodactylus labyrinthicus* FCEN 825, DS. *Leptodactylus latrans* FCEN-LPEV UN, DS; FCEN 283, 1931, DS; FCEN 720, FD; FML 00571, DS. *Leptodactylus mystaceus* FCEN 1752, DS.
- Limnodynastidae: *Heleioporus* sp. FCEN 817, DS. *Limnodynastes fletcheri* FCEN 626, DS. *Neobatrachus* sp. FCEN UN, DS. *Platyplectrum ornatum* MACN-HE 42620, DS.
- Megophryidae: *Megophrys nasuta* AMNH A-177048 (DS), PD.
- Microhylidae: *Dermatonotus muelleri* MCN 997, CS. *Hamptophryne boliviana* KU 205799, DS. *Phrynomantis bifasciatus* MCN 830, CS.
- Myobatrachidae: *Crinia signifera* FML 03778, CS. *Mixophyes schevillii* FCEN UN, DS. *Myobatrachus gouldii* KU 110333 (DS), PD.
- Odontophrynidae: *Odontophrynus americanus* FCEN 1096, 1285, DS. *Odontophrynus lavillai* FCEN 1096, DS. *Odontophrynus occidentalis* FCEN 1218, DS; MLP A-5738, FD. *Proceratophrys boiei* FCEN 699, DS.
- Pelobatidae: *Pelobates cultripes* MACN-HE 42618, 42619, CS.
- Pelodytidae: *Pelodytes punctatus* FML 03940, CS.
- Phrynobatrachidae: *Phrynobatrachus acutirostris* MCN 951, CS.
- Pipidae: *Hymenochirus boettgeri* MACN-HE 42621, CS. *Pipa carvalhoi* MACN-HE 42606–42608, DS. *Pipa pipa* FCEN 1434, DS; MACN-HE 42612, 42613, DS. †*Saltenia ibanezi* MLP 62-XII-66, LM. †*Shelania pascuali* MPEF-PV 1150, 1562, LM. *Silurana tropicalis* MACN-HE 42633, DS. *Xenopus laevis* FCEN 1435, DS. *Xenopus muelleri* MACN-HE 42631, DS.
- Ptychadenidae: *Ptychadena mascareniensis* MCN 820, CS.
- Ranidae: *Hylarana albolabris* MCN 805, CS. *Lithobates catesbeianus* FCEN UN, DS. *Lithobates palmipes* FCEN B-54, DS. *Rana temporaria* FCEN 1545–1549, DS.
- Rhacophoridae: *Chiromantis rufescens* MCN 831, CS.
- Rhinophrynidae: *Rhinophrynus dorsalis* FCEN-LPEV UN, DS; MACN-HE 42617, DS.
- Scaphiopodidae: *Scaphiopus couchii* MCN 808, CS; FCEN-LPEV 25, DS. *Scaphiopus hurterii* FCEN 1675, FD.
- Stem-group Anura: †*Notobatrachus degiustoi* MACN 17722, LM; MLP 54-XI-18-1, LM; MPEF-PV 1253, LM. †*Prosalirus bitis* MNA V-8725, PD; MCZ 9324A, PD.
- Telmatobiidae: *Telmatobius hauthali* FML 3315, DS. *Telmatobius macrostomus* FCEN 1208, DS. *Telmatobius scrocchii* FML 1515, DS.