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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

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ARTICLE

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

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ABSTRACT—Ilia of anurans (frogs) and urodeles (salamanders) are commonly recovered from microvertebrate fossil localities. Ilia in these clades are distinctive when complete and articulated with the rest of the pelvic girdle, but when preserved as isolated and broken fossils they may appear superficially similar. Reliable identification of urodele ilia is further hampered by limited information about the basic structure and contacts of the bone and its variation within the clade. Here we demonstrate that the ilium is more variable among urodeles than previously realized and provide the first detailed inventory of features that are potentially useful for differentiating ilia of anurans and urodeles. Many of these features relate to differences between the two clades in the orientation of the ilium and its contacts with other bones and with soft tissues. Based on the results of our survey, we re-interpret the holotype and two referred ilia of *Nezpercius dodsoni* (Late Cretaceous; Montana, U.S.A.) as being from an indeterminate urodele, not an anuran as originally described. Additional examples of Late Cretaceous urodele ilia are documented to highlight some of the variation seen in fossil urodele ilia and to aid in the proper identification of such specimens.

INTRODUCTION

The Mesozoic record of anurans (frogs) in North America is heavily biased towards isolated bones (e.g., Estes, 1964; Sahni, 1972; Estes and Sanchíz, 1982; Brinkman, 1990), and it is widely recognized that interpreting the taxonomic identities and associations of such fossils can be challenging (e.g., Roček and Nessov, 1993; Sanchiz, 1998; Holman, 2003; Gardner, 2008). Blob et al. (2001) described three incomplete, but distinctive ilia (Fig. 1) from the Judith River Formation (middle–upper Campanian) of Montana, U.S.A., which they interpreted as belonging to a new anuran that they named *Nezpercius dodsoni*. *Nezpercius* has been accepted without comment as an anuran by at least two workers (Gardner, 2005; Roček, 2008). Holman (2003) criticized Blob et al.'s (2001) interpretation that *Nezpercius* was an anuran and even that the three bones were ilia, but did not offer any alternatives. The three described *Nezpercius* specimens admittedly are difficult to interpret, because they are tiny and preserve only the acetabular region and adjacent portion of the shaft. They also exhibit several features—such as an elongate tuberosity on the lateral surface of the iliac shaft near the acetabulum—that are not known in any unequivocal anurans, but which are seen in at least some urodeles (salamanders). Isolated fossil urodele ilia have rarely been reported in the literature (e.g., Estes, 1981; Nessov, 1981; Evans et al., 1988; Peng et al., 2001) and, to our knowledge, detailed criteria for their identification have never been presented. Here we (1) provide and evaluate a suite of features that are potentially useful for differentiating the ilia of anurans and urodeles, (2) use that information to assess whether the type series of *Nezpercius* ilia are from an anuran or a urodele, and (3) document the occurrence of similar ilia in several other Upper Cretaceous units.

Institutional Abbreviations—**AMNH**, American Museum of Natural History, New York, New York, U.S.A.; **FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; **MNA**, Museum of Northern Arizona, Flagstaff, Arizona, U.S.A.; **NDGS**, North Dakota Geological Survey, Bismark, North Dakota, U.S.A.; **TMP**, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; **UALVP**, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada; **UMMZ**, University of Michigan Museum of Zoology, Ann Arbor, Michigan, U.S.A.; **UMNH**, Utah Museum of Natural History, Salt Lake City, Utah, U.S.A.; and **USNM**, National Museum of Natural History (Smithsonian Institution), Washington, D.C., U.S.A..

ILIA OF ANURANS AND URODELES

Ilia of anurans are relatively easy to characterize. Thanks to the constraints that jumping and swimming impose on the

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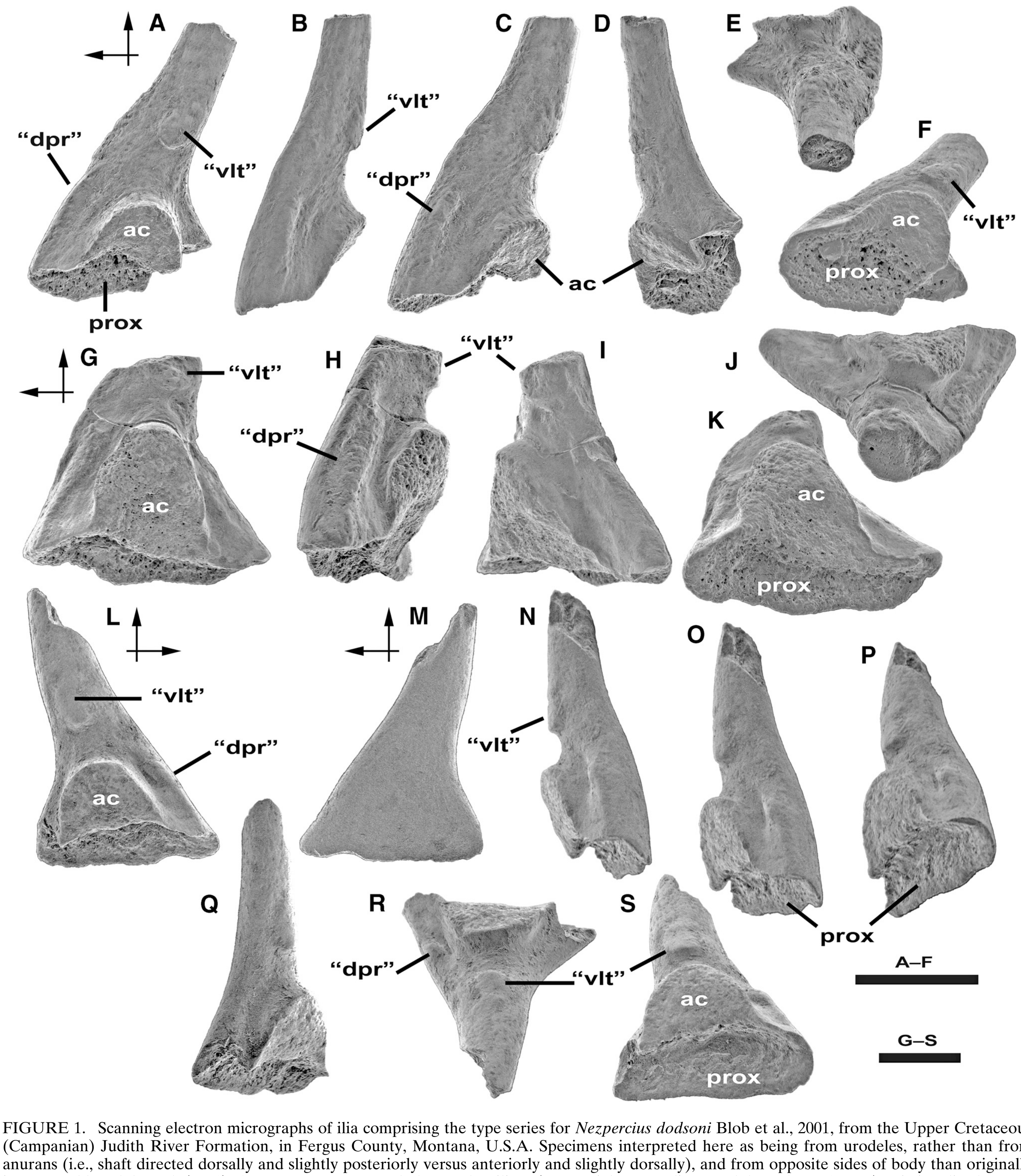


FIGURE 1. Scanning electron micrographs of ilia comprising the type series for *Nezpercius dodsoni* Blob et al., 2001, from the Upper Cretaceous (Campanian) Judith River Formation, in Fergus County, Montana, U.S.A. Specimens interpreted here as being from urodeles, rather than from anurans (i.e., shaft directed dorsally and slightly posteriorly versus anteriorly and slightly dorsally), and from opposite sides of body than originally interpreted by Blob et al. (2001). **A**–**F**, FMNH PR 2078, holotype, left ilium (versus right, according to Blob et al., 2001:fig. 2), missing distal part of shaft and posteroventral corner from proximal end of acetabular region: **A**, lateral view, oriented in approximate life position with shaft projecting posterodorsally; **B**, anterior and slightly dorsal view; **C**, anterolateral and slightly dorsal view; **D**, posterolateral and slightly ventral view; **E**, dorsolateral and slightly anterior view; **F**, ventral (= proximal) and slightly lateroposterior view. **G**–**K**, FMNH PR 2079, referred specimen, left ilium (versus right, according to Blob et al., 2001:fig. 3A), missing all but base of shaft and only small sections of medial and posterior edges from proximal end of acetabular region: **G**, lateral view, oriented in approximate life position with shaft projecting posterodorsally; **H**, anterior and slightly dorsolateral view; **I**, posterolateral view; **J**, dorsal and slightly lateral view; **K**, ventrolateral and slightly anterior view. **L**–**S**, FMNH PR 2080, referred specimen, right ilium (versus left, according to Blob et al., 2001:fig. 3B), missing distal part of shaft and small section of anterior edge from proximal end of acetabular region: **L**, lateral view, oriented in approximate life position with shaft projecting posterodorsally; **M**, medial view, oriented in approximate life position with shaft projecting posterodorsally; **N**, anterodorsal and slightly lateral view; **O**, anterodorsal and more lateral view; **P**, anterolateral and slightly ventral view; **Q**, posterolateral and slightly ventral view; **R**, dorsolateral view; **S**, ventrolateral view. Perpendicular arrows associated with lateral and medial views indicate anterior and dorsal directions. Abbreviations: **ac**, acetabulum; **"dpr"**, "dorsal prominence" of Blob et al. (2001); **prox**, proximal surface; **"vlt"**, "ventrolateral tuberosity" of Blob et al. (2001). Specimens at different scales; both scale bars equal 1 mm.

anuran pelvis (e.g., Palmer, 1960; Whiting, 1961; Emerson, 1979; Emerson and de Jongh, 1980; Jenkins and Shubin, 1998), the basic structure of the ilium is distinct and relatively uniform among anurans. Additionally, there is a wealth of published information on the structure of the anuran ilium and its associated musculature and on variation within the clade (e.g., Lynch, 1971; Trueb, 1973; Tyler, 1976; Sanchiz, 1998; Přikryl et al., 2009). However, there is little published information for anurans on the medial and proximal surfaces of the ilium; that dearth of information is unfortunate, because certain features of those surfaces differ significantly between anurans and urodeles. In contrast to the situation with anurans, urodele ilia have received almost no attention in the literature. To cite two examples, Francis (1934:44) devoted only a few lines to the structure of the ilium and Duellman and Trueb (1986:341) described the ilium simply as "club-shaped." Although the implication appears to be that urodele ilia are rather uniform, our preliminary survey of representative extant urodele taxa reveals considerable variation in this bone. Such variation should not be surprising, considering that the Urodela contain a range of terrestrial and aquatic forms, and several families (e.g., Plethodontidae, Amphiumidae) include species with reduced hind limbs. Appendix 1 summarizes features that are potentially useful for differentiating ilia of anurans and urodeles. Below we consider these features in greater detail, with particular reference to how useful those are for differentiating fossil ilia of the two clades.

Ilia of anurans and urodeles are similar in their overall build and contacts (Figs. 2–5). Both consist of two portions: (1) an expanded portion (= acetabular region) at one end that articulates with other bones of the pelvic girdle and laterally bears the iliac portion of the acetabulum (= acetabular fossa) for articulation with the femur and (2) an elongate shaft that emerges from the expanded portion and articulates at its far end with the sacral rib (in urodeles) or the sacral diapophysis (in anurans) via a ligamentous connection. As indicated in Appendix 1, there are numerous features—some distinct and some subtle—that differ between the ilia of anurans and urodeles. Many of these features relate to differences in the structure of the pelvic girdle and associated musculature in the two clades.

Although similar in construction, a fundamental difference between the ilia of anurans and urodeles is the anatomical orientation of the bone in living animals (Appendix 1: feature 1). When viewed in lateral aspect, the iliac shaft projects anteriorly to slightly dorsoanteriorly in anurans, but dorsally to slightly posterodorsally in urodeles, a difference of approximately 90° between the two clades (e.g., Figs. 2, 3). Unfortunately, that distinction is difficult to recognize in isolated ilia. For that reason, in our descriptions of iliac features that follow we will apply an operational terminology to ilia of both anurans and urodeles, 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.' These terms correspond to 'anterior' and 'posterior' for the life orientations of ilia in anurans and to 'ventral' and 'dorsal' for the life orientations of ilia in urodeles. We recognize that, because in living animals, the acetabulum is closer to the limb than the shaft (which is embedded in the trunk), our definitions differ from standard anatomical usage in which 'proximal' would indicate a position closer to the body and 'distal' a position closer to the periphery. However, because the construction of the ilium in both clades causes a tapering shaft to emerge from a larger component with a center of rotation, we favor the aforementioned operational definition as being more intuitive.

Compared to anurans, urodeles have pelves that more closely resemble the primitive tetrapod condition (e.g., Duellman and Trueb, 1986; Báez and Basso, 1996; Přikryl et al., 2009; for examples of the plesiomorphic condition in representative nonlissamphibian temnospondyls, see Warren and Snell, 1991:fig. 9; Pawley and Warren, 2006:fig. 8; Witzmann and Schoch, 2006:text, fig. 7; Pawley, 2007:fig. 11; Werneburg, 2009:fig. 13). In urodeles (Figs. 2D, 3A–F), the paired ilia are oriented more or less vertically and are broadly separated by the ventral puboischiadic plate. Contact between the ilium and the rest of the pelvic girdle thus is limited to the proximal (ventral in life) edge of the ilium. Because a substantial portion of the puboischiadic plate may be cartilaginous, contact between each half of the puboischiadic plate and the corresponding ilium typically includes a cartilaginous component and the ventral edge of the ilium will be unfinished or excavated to accommodate the cartilage. The iliac shaft projects slightly laterally and dorsally to posterodorsally, varies from relatively short to moderately elongate, and may expand distally. The shaft also is curved laterally (i.e., bows outwards) and, often, slightly anteriorly (i.e., procurved). Urodele ilia lack many of the grooves, processes, and crests that variably occur in anurans and which are associated in the latter clade with enhanced pelvic and hind limb muscles.

Anurans (Figs. 2A–C, 3G–K) deviate from the typical tetrapod pelvic configuration in that their ilia rotate posteriorly about 90° during metamorphosis (Ročková and Roček, 2005) and the iliac shafts are greatly elongated; these changes result in the acetabulum being shifted far behind the sacrum and the long axis of the shaft lying in a more nearly horizontal plane (i.e., directed anteriorly). Additionally, the proximal (posterior in life) portions of the paired ilia are in direct and relatively firm bony contact medially. The proximal edge of the ilium still contacts the rest of the pelvic girdle, specifically with the ossified ischium dorsally and with the usually cartilaginous pubis ventrally, but unlike in urodeles the contact surface with the rest of the girdle along the proximal end of the ilium is consistently flat, solidly ossified, and mediolaterally thicker. In dorsal or ventral aspect, the iliac shaft projects anteriorly and slightly laterally and is typically straight or only shallowly curved laterally. In lateral aspect, the shaft is nearly straight to shallowly curved (i.e., convex) dorsally. Anurans also have a characteristic, bowl-shaped acetabulum that is semi-circular or subtriangular in lateral outline, at least partially sunk or recessed into the bone of the acetabular region, and is surrounded by a laterally projecting, flange-like rim. By contrast, urodeles have a more generalized acetabulum consisting of a saddle-shaped or shallowly concave articular surface, a much less distinct margin, and a more variable outline and the acetabulum is at least partially elevated on a laterally projecting, bony pedestal.

Although the above comparisons and inventory of features in Appendix 1 suggest that anuran and urodele ilia should be easy to differentiate, in practice this task can be challenging when dealing with isolated or incomplete specimens. Neither the direction that the iliac shaft projects (feature 1) nor the direction that the articular surface of the acetabulum faces (feature 11) are informative for isolated ilia, because both features rely on knowing the life orientation of the bone. The direction in which the shaft curves in lateral aspect (feature 3) potentially can be determined from isolated ilia, but only if the side of the body from which the specimen originated is reliably known; that task is relatively easy with anurans, but is more challenging with urodeles.

Although some anuran and urodele species attain relatively large adult body sizes (e.g., snout–vent length of 300 mm in the extant anuran *Conraua goliath* and total body length of 1440 mm in the extant urodele *Andrias davidianus*; Duellman and Trueb, 1986), typically adults in both clades are much smaller and there is a repeated trend towards reduced body size (see review by Clarke, 1996). Except for the giant Maastrichtian species *Beelzebufo ampinga*, for which a maximum snout–vent length of over 400 mm has been estimated (Evans et al., 2008), Mesozoic anurans had snout–vent lengths of about 100 mm or much less (e.g., Báez and Basso, 1996; Henrici, 1998; Roček, 2000; Gao and Wang, 2001; Roček et al., in press). In general, anuran and urodele ilia are small (i.e., long axis typically <30 mm) and only moderately robust, so fossilized examples often are broken. The

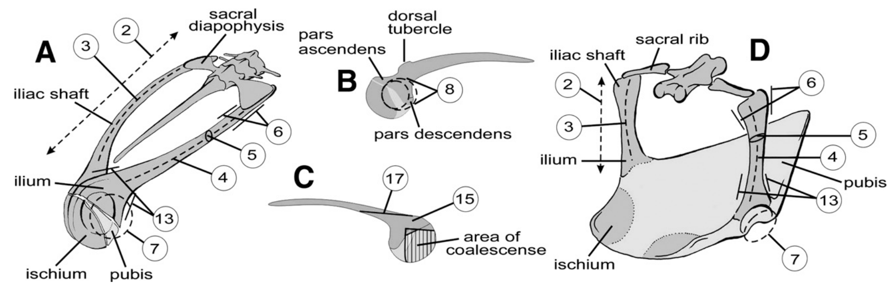


FIGURE 2. Stylized diagrams of representative anuran and urodele pelvic girdles. **A**, Anuran pelvic girdle, right lateral and dorsoposterior view. **B**, **C**, Anuran right ilium: **B**, lateral view; **C**, medial view. **D**, Urodele pelvic girdle, right lateral and dorsoposterior view. Urodele pelvic girdle based on extant *Necturus*, which has the ventral puboischiadic plate comprised of small, ossified ischia and larger, cartilaginous pubes; cf. more extensively ossified puboischiadic plate in *Ambystoma* (Fig. 3A–F). Bone depicted as dark gray and cartilage depicted as light gray. Numbers in circles correspond to features listed in Appendix 1.

elongate and hollow iliac shafts are especially prone to breakage. Where this occurs, a suite of features that describe the relative length (2), curvature (3 and 4), cross-sectional shape (5), and lateral outline (6) of the shaft and, if present, lateral structures (20) may be compromised. Feature 2 requires essentially the entire shaft, whereas features 3–6 and 20 may be informative if enough remains of the proximal and median portions of the shaft to determine the general trend of a given feature (e.g., for feature 6, if enough of the shaft is preserved to see that it expands distally, even though its distalmost end is missing). Features located more proximally on the shaft often are easier to assess because, for example, where present in anurans the oblique groove (17) and dorsal crest (19) extend proximally onto the acetabular region. Damage to the acetabular region is not uncommon, especially to the proximal edge and adjacent surfaces, and this damage may affect any of the features (7–18) associated with that region.

Many of the features listed in Appendix 1 overlap between urodeles and anurans and vary within each clade. This is

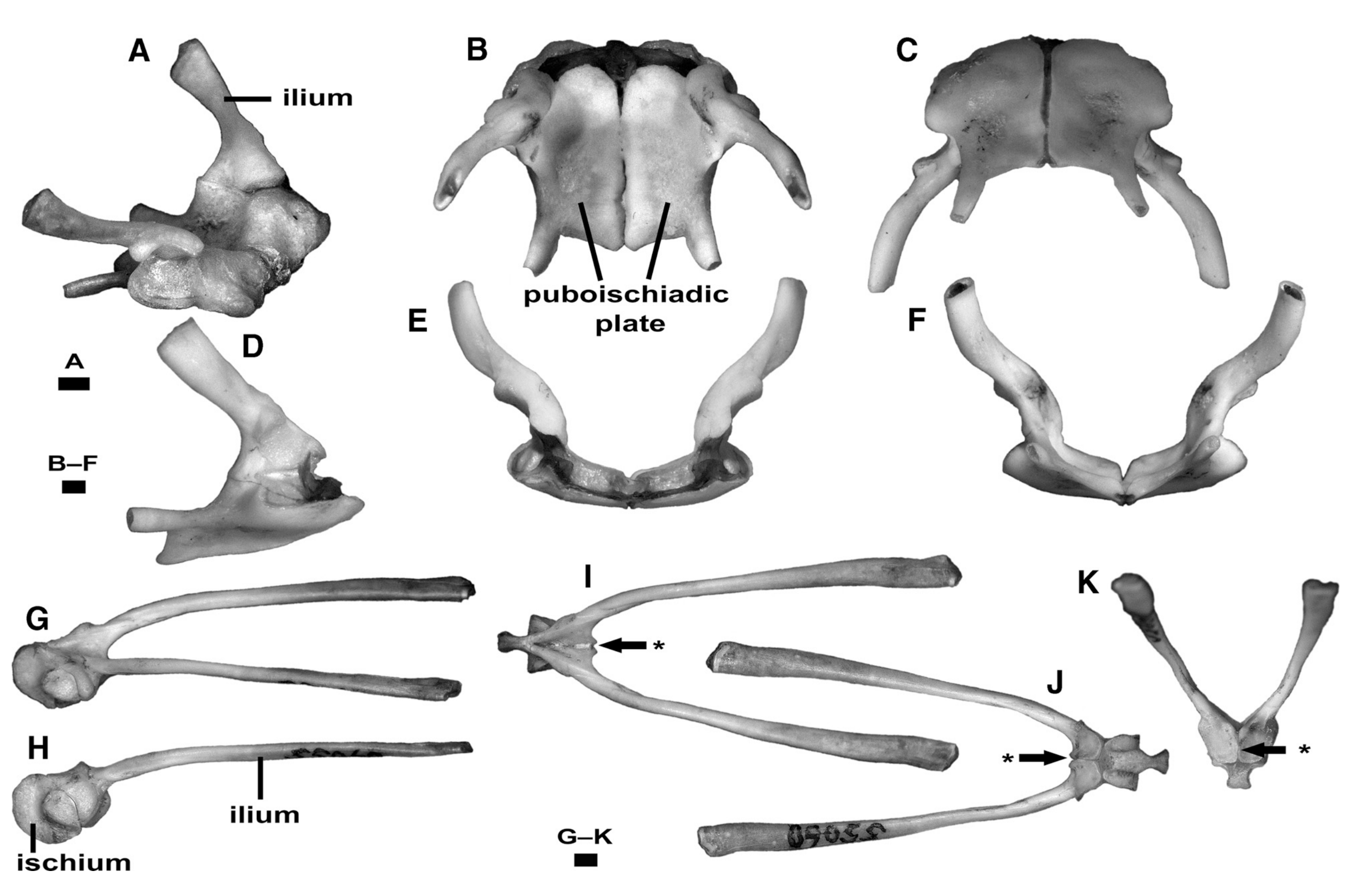


FIGURE 3. Photographs of representative urodele and anuran pelvic girdles. **A**–**F**, Urodele pelvic girdles, as exemplified by extant *Ambystoma* (Ambystomatidae): **A**, *Ambystoma maculatum*, purchased specimen (presumably from eastern U.S.A.), transformed individual, UALVP 14331, right lateral and anterodorsal view; **B**–**F**, *Ambystoma mexicanum*, captive-raised, neotenic individual, TMP 2010.30.04: **B**, dorsal view, with anterior end towards top of page; **C**, ventral and slightly posterior view, with anterior end towards to top of page; **D**, right lateral view; **E**, anterior view; **F**, posterior view. Note puboischiadic plate is thicker and more robust in the transformed individual than in the neotenic individual (cf., **A** versus **B**–**F**). **G**–**K**, Anuran pelvic girdle, as exemplified by extant *Bombina bombina* (Bombinatoridae), Recent, Germany, UMMZ 152271: **G**, right lateral and dorsal view; **H**, right lateral view; **I**, dorsal view, with anterior end towards right; **J**, ventral view, with anterior end towards left; **K**, anterior and slightly ventral view. Arrow and asterisk point to broad inter-iliac contact between ventral portion of medial surfaces of acetabular regions of left and right ilia in the anuran pelvic girdle; compare with broadly separated ilia in the figured urodele pelvic girdles. Images at different magnifications; all scale bars equal 1 mm.

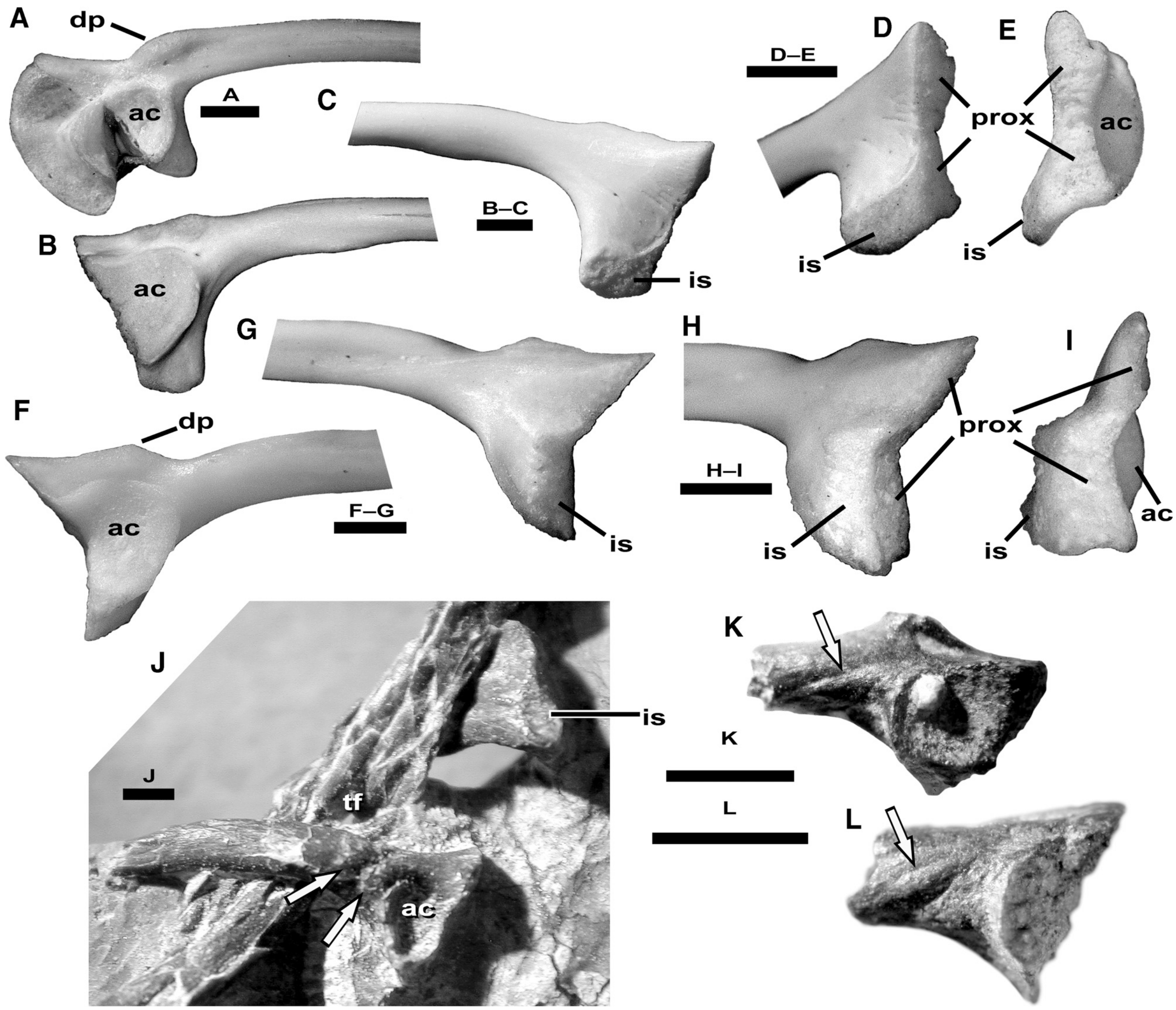


FIGURE 4. Photographs of representative extant and fossil anuran ilia. **A**, *Discoglossus pictus* (Alytidae), Recent, Spain, UMMZ 152280, close-up of acetabular portion of right ilium + ischium, lateral view. **B–E**, *Ascaphus truei* (Leiopelmatidae), Recent, Washington, U.S.A., USNM 62450, close-up of proximal three-fifths of right ilium: **B**, lateral view; **C**, medial view; **D**, oblique medioproximal and ventral view; **E**, proximal (= posterior) view. **F–I**, *Bombina orientalis* (Bombinatoridae), Recent, captive raised specimen, TMP 2010.30.21, close up of proximal half of right ilium: **F**, lateral view; **G**, medial view; **H**, oblique medioproximal and slightly dorsal view; **I**, proximal (= posterior) view. **J**, *Prosalirus bitis* (Prosaliridae), Lower Jurassic (Pliensbachian), Kayenta Formation, Arizona, U.S.A., MCZ 8725, block containing disarticulated assemblage of bones from at least two individuals (Jenkins and Shubin, 1998), close-up of three incomplete bones: left ilium (lower left), lateral view, with arrows pointing at pair of short, oblique ridges on lateral surface of base of iliac shaft; right ilium (upper right), medial view, showing small inter-iliac scar along ventroposterior corner of medial surface of acetabular region; and crushed tibiofibula extending diagonally through center of image. For less magnified view of same block, see Jenkins and Shubin (1998:fig. 3D). **K**, **L**, Anura indet., left ilia, lateral views, each missing distal part of shaft and with arrow pointing at oblique ridge on lateral surface of base of iliac shaft; Upper Cretaceous, Utah, U.S.A.: **K**, UMNH 13158, Dakota Formation (upper Cenomanian); **L**, UMNH 19366, Straight Cliffs Formation (Coniacian); both adapted from raw images used by Roček et al. (in press:figs. 5k and 7b, respectively). **Abbreviations**: **ac**, acetabulum; **dp**, dorsal process; **is**, inter-iliac scar; **prox**, proximal surface; **tf**, tibiofibula. Images at different magnifications; all scale bars equal 1 mm.

especially evident for features describing the relative length and form of the shaft (2–6), shape and size of the acetabulum (7 and 8), form of the acetabular region (12–14), form of the medial and proximal articular surfaces (15 and 16), presence or absence of an oblique groove, dorsal tubercle, and iliac crest (17–19), and nature of lateral structures on the iliac shaft (20). Depending on the specimen, any one of those features may or may not be informative; for example, feature 12 (outline of acetabular region) would not be informative for an ilium with a triangular acetabular region, because that condition occurs in urodeles and many anurans, but it would be informative if the acetabular region had a squarish outline, because that condition only occurs in some anurans. Because the utility of any one of those features will vary depending on the specimen being examined, as many features as possible need to be considered when trying to determine whether a particular ilium pertains to an anuran or a urodele.

Variation in some of the above-listed features is continuous, and their different conditions may be subtle and somewhat subjective (e.g., feature 7: outline of acetabulum ranges from semi-circular, to subtriangular, to oblong). Other features have discrete conditions that are easier to recognize (e.g., feature 19: dorsal crest is either present or absent). Individual variation also complicates matters. To cite two examples, the relative size of the acetabulum (feature 8) varies ontogenetically in some anurans (Jones et al., 2002) and the presence and form of muscle attachment structures along the lateral surface of the iliac shaft (feature 20) vary in at least some urodele species (see below). Despite these limitations, it is worth emphasizing that for most of the features listed in Appendix 1 the 'typical' condition for anurans is distinctly different from that of urodeles. For example, the outline of the acetabulum (feature 7) is subtriangular in some anurans and urodeles, but typically it is semi-circular in anurans versus oblong or hourglass-shaped in urodeles.

Two features (9 and 10) describing the form of the margin and the surface of the acetabulum differ consistently between anuran and urodele specimens that we have examined. The distinctive anuran acetabulum (i.e., concave and bowl-shaped; partially sunk into the acetabular region; surrounded by a laterally projecting, flange-like bony rim) clearly is derived relative to the more generalized urodele acetabulum. Although we are not aware of any studies that have considered variation in the form and size of the anuran acetabulum in relation to different modes of locomotion, its distinctive structure presumably provides a strong, but highly flexible joint for anchoring the femur within the acetabulum during various locomotory modes, such as jumping or swimming. Urodeles are not specialized for jumping or swimming by means of their hind limbs and, thus, retain a more generalized acetabulum.

Following from the above remarks and given that the three specimens of *Nezpercius* collectively preserve virtually all the acetabular region and a moderate amount of the shaft, up to 16 features (3–5, 7–10, 12–20) from Appendix 1 potentially are useful for assessing whether *Nezpercius* is an anuran or a urodele.

RE-ASSESSMENT OF THE THREE SPECIMENS OF *NEZPERCIUS DODSONI*

Brief Description of the Specimens of *Nezpercius*

Blob et al. (2001:190–191, figs. 2, 3) presented a concise and generally accurate description of the three *Nezpercius dodsoni* ilia, based mostly on the holotype (FMNH PR 2078), and provided drawings of the holotype in multiple planar views and of both referred specimens (FMNH PR 2079 and 2080) in lateral view. Our Figure 1 provides scanning electron micrograph images of each specimen in multiple views. The three specimens are incomplete and small. The iliac shafts are broken distally in each specimen: FMNH PR 2079 preserves only the base of the shaft, whereas about twice as much of the shaft (accounting for ca. 55% of the total preserved length of each specimen) is preserved in FMNH PR 2078 and 2080. All three specimens preserve most of the acetabular region: FMNH PR 2078 lacks the posteroproximal corner, whereas FMNH PR 2079 and 2080 are missing only small pieces along the proximal margins of the bone. The acetabulum is intact in each of the three specimens. Approximate dimensions (first value = maximum preserved width across proximal end; second value = maximum preserved length) are as follows: FMNH PR 2078 (1.5 and 3.0 mm), FMNH PR 2079 (3.5 and 3.0 mm), and FMNH PR 2080 (2.5 and 4.0 mm). Based on proximal widths, the holotype would have been about two-thirds the size of FMNH PR 2080 and one-third the size of FMNH PR 2079 when complete. Subtle differences among the three specimens in the outline and surface of the acetabulum, relative concavity of the proximal end, and form of the tuberosity on the lateral surface of the shaft and of the ridge along the anterior margin of the acetabular region ("ventrolateral tuberosity" and "dorsal prominence," respectively, of Blob et al. [2001]) may be size related.

New Interpretation of the Life Orientations of the Specimens of *Nezpercius*

Based on their interpretation that the three specimens were anuran ilia, Blob et al. (2001:figs. 2, 3) oriented each specimen with the shaft extending horizontally and the low ridge, which they interpreted as the "dorsal prominence," along one margin of the acetabular region facing upwards. Oriented as such, FMNH PR 2078 and 2079 were interpreted as right ilia and FMNH PR 2080 was interpreted as a left ilium. Although we agree with Blob et al. (2001) that the three specimens of *Nezpercius* are ilia (contra Holman, 2003), as will become evident in our assessment of anuran and urodele iliac features later in this section, we interpret the specimens as being from a urodele. Our new interpretation requires that the specimens be rotated approximately 90°, so that their shafts are directed dorsally and slightly posteriorly, and flipped horizontally, so that FMNH PR 2078 and 2079 become left ilia and FMNH PR 2080 becomes a right ilium (cf., Blob et al., 2001:figs. 2A, 3A, B versus here: Fig. 1A, G, L). Our decisions about which side of the body each specimen came from are based on the observations that in extant urodeles (1) the anterior margin of the acetabular region (see feature 13) is more nearly in line with the long axis of the iliac shaft; (2) where present, the low ridge (= "dorsal prominence" of Blob et al. [2001]; see below, feature 18) lies along the anterior margin of the acetabular region; and (3) where present, the attachment structure or scar for thigh muscles (see below, feature 20) is located midway across or slightly more posteriorly on the lateral surface of the iliac shaft.

Anuran versus Urodele Features of the Specimens of *Nezpercius*

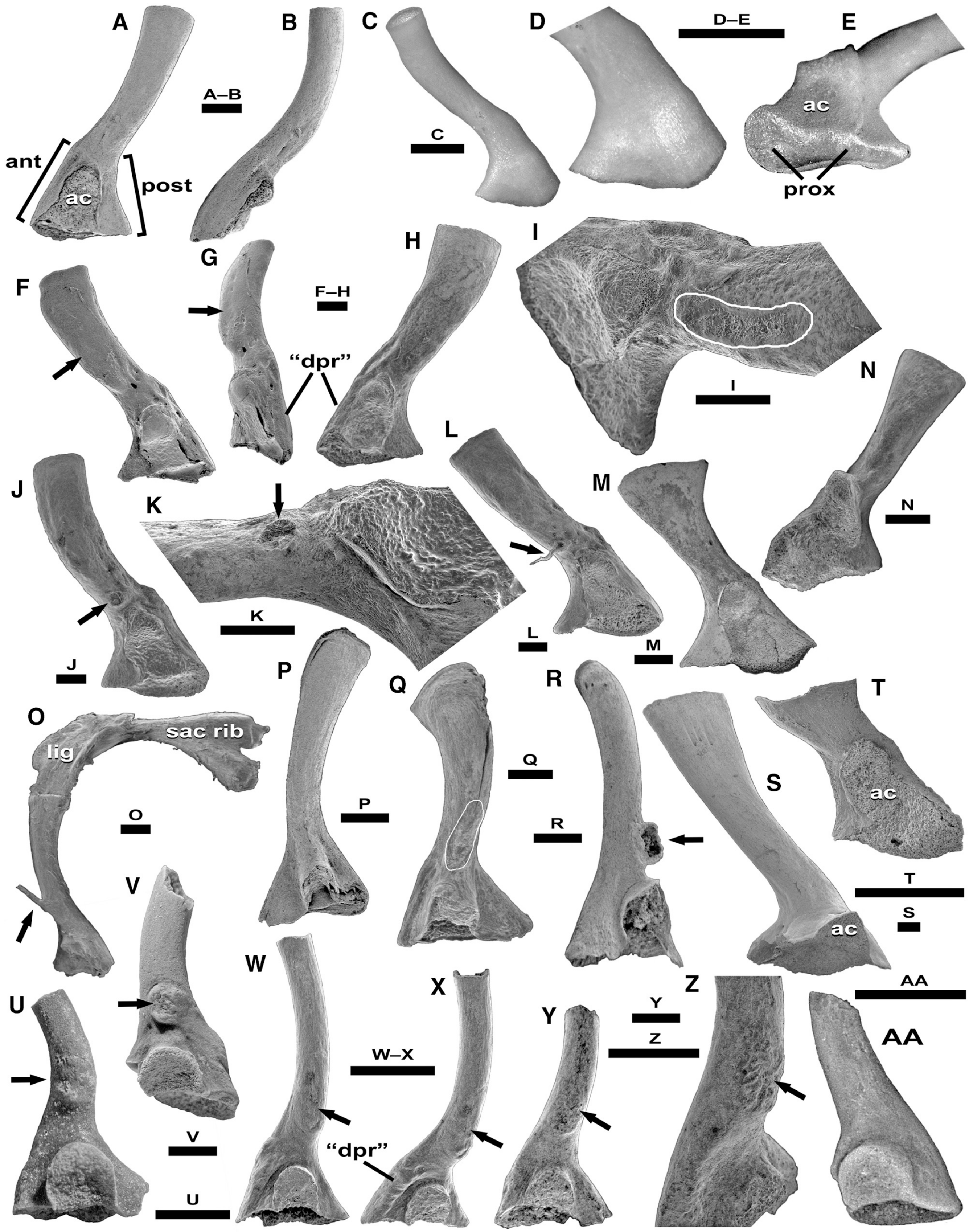
Below we consider the 16 features identified earlier in this paper to assess whether *Nezpercius dodsoni* is an anuran or a urodele.

Feature 3, Curvature of Iliac Shaft in Lateral View—FMNH PR 2079 preserves too little of the shaft to determine whether it was curved. In lateral view, the preserved portions of the shaft in FMNH PR 2078 and 2080 both have a shallowly concave anterior margin; the posterior margin in the former is essentially straight, whereas in the latter it is shallowly convex. These observations imply—although admittedly do not prove—that the shaft in both specimens was weakly curved anteriorly, which is the urodele condition. Curvature of the shaft in FMNH PR 2080 was emphasized in Blob et al.'s (2001:fig. 3B) drawing by the use of dashed lines extending forward from the broken distal end. Their depiction of the shaft as being shallowly convex ventrally (they oriented the specimen with the shaft horizontally) is at odds with their interpretation that the specimen is an anuran ilium, because in anurans the iliac shaft is either straight or dorsally convex in lateral view.

Feature 4, Lateral Curvature of Iliac Shaft—As with the previous feature, only FMNH PR 2078 and 2080 preserve enough of the shaft to evaluate this feature. The preserved portion of the shaft is shallowly curved laterally in both specimens; this curvature is more pronounced along the medial edge, whereas the lateral edge appears essentially straight. Because a shallowly laterally curved shaft occurs in both anurans and urodeles, this feature is not informative for *Nezpercius*.

Feature 5, Cross-sectional Outline of Iliac Shaft—This feature is equivocal for resolving the identity of *Nezpercius*, because in all three specimens the shaft is subcircular in outline and that condition occurs in both anurans and urodeles.

Feature 7, Outline of Acetabulum in Lateral View—All three specimens have an intact acetabulum. In the two smallest ilia, FMNH PR 2078 and PR 2080, the acetabulum is somewhat semicircular: the width across the proximal edge is slightly greater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than the maximum proximal–distal length and the anterior, dorsal, and posterior margins are broadly rounded. In the largest ilium, FMNH PR 2079, the acetabulum is distinctly subtriangular: the width across the proximal edge is less than the maximum proximal–distal length, the acetabulum is narrower anteriorly, and the anterior and posterior margins are less convex. Although we have not seen identical acetabula in any of the extant urodele ilia we examined, acetabula similar to those in *Nezpercius* do occur in some other Upper Cretaceous urodele ilia (Fig. 5U–AA; see also Nessov, 1981:pl. 9, figs. 12, 13; Peng et al., 2001:pl. 5, fig. 32). Even so, the condition in *Nezpercius* must be regarded as uninformative, because similar outlines occur in both urodeles and anurans.

Feature 8, Relative Size of Acetabulum—The acetabulum in all three specimens is fully enclosed within the acetabular region. This condition occurs in urodeles and many anurans, so it is not informative for *Nezpercius*.

Feature 9, Form of Acetabular Margins—The anterior, dorsal, and posterior margins of the acetabulum are indistinct in all three specimens of *Nezpercius*. Typically the margins are nothing more than an extremely shallow ridge formed by the junction between the surface and outer walls of the acetabulum; in all three specimens this ridge is slightly more prominent along the dorsal portion (i.e., adjacent to the base of the shaft). In the largest specimen, FMNH PR 2079, the dorsoanterior portion of the margin follows the acetabular surface (see next feature) where it curves medially across the wall of the acetabulum. Even where most prominently developed, the acetabular margin in *Nezpercius* in no way resembles the raised, flange-life rim characteristic of anurans; instead, it is typical of urodeles.

Feature 10, Form of Acetabular Surface—In all three specimens of *Nezpercius*, the acetabular surface is elevated laterally on a bony, ramp-like pedestal that is highest dorsally (i.e., adjacent to base of shaft) and lowest proximally; consequently, the acetabular surface is tilted proximally. In the smallest specimen, FMNH PR 2078, the acetabular surface is extremely shallowly concave to nearly flat across the entire face. In FMNH PR 2080, the surface is flat to extremely shallowly convex, with the convexity becoming slightly more pronounced across the dorsoanterior portion of the face. In the largest specimen, FMNH PR 2079, the acetabular surface is sigmoidal: it is shallowly concave proximally, becoming flatter across the dorsal portion and convex across the anterodorsal portion where it ultimately wraps medially across the wall of the pedestal. The form of the acetabular surface in *Nezpercius* is typical of urodeles, not anurans.

Feature 12, Outline of Acetabular Region in Lateral View—The acetabular region is intact enough in all three specimens of *Nezpercius* to show that the region is triangular in outline. This condition is typical of urodeles and many anurans, so it is not informative for *Nezpercius*.

Feature 13, Outline of Anterior and Posterior Margins of Acetabular Region in Lateral View Relative to Long Axis of Shaft—Relative to the long axis of the shaft, when viewed in lateral aspect the anterior edge of the acetabular region diverges only slightly in all three specimens, whereas the posterior edge diverges at about 50° in FMNH PR 2078 and at about 40° in FMNH PR 2079 and 2080. Based on our re-assessment of which sides of the body the *Nezpercius* ilia came from, the pattern observed in these specimens is typical of urodeles. Anurans exhibit the opposite configuration—the edge of the pars ascendens (homologous to the posterior part of the acetabular region in urodeles) deviates at a shallower angle than does the pars descendens (homologous to the anterior part of the acetabular region in urodeles).

Feature 14, Relative Sizes and Proximal Extent of Bone in Acetabular Region Outside of Acetabulum—FMNH PR 2079 and 2080 preserve enough of the acetabular region to show that the

← FIGURE 5. Photographs and scanning electron micrographs of representative extant and fossil urodele ilia. **A–L**, *Ambystoma mexicanum* (Ambystomatidae), all Recent, captive-raised, and neotenic individuals: **A**, **B**, TMP 2010.30.06, left ilium: **A**, lateral view; **B**, anterior and slightly dorsal view; **C–E**, TMP 2010.30.01, left ilium: **C**, entire bone, medial view; **D**, close-up of proximal portion, medial view, showing smooth and shallowly convex medial surface; **E**, close-up of proximal portion, ventral (= proximal) and slightly lateral view, showing concave proximal surface for contact with puboischiadic plate; **F**, **G**, TMP 2010.30.10, right ilium, with swollen, broad, and elongate ridge (arrow) in approximate position of "ventrolateral tuberosity": **F**, lateral view; **G**, anterolateral and slightly dorsal view; **H**, **I**, TMP 2010.30.03, left ilium, with elongate scar having a slightly wrinkled texture (circled in close-up view) in approximate position of "ventrolateral tuberosity": **H**, entire bone, lateral view; **I**, close-up of proximal two-thirds of bone, rotated clockwise with distal end towards right, dorsolateral and slightly anterior view; **J**, **K**, TMP 2010.30.02, right ilium, with slightly raised, circular, and concave-bottomed pit (arrow) in approximate position of "ventrolateral tuberosity": **J**, entire bone, lateral view; **K**, close-up of proximal two-thirds of bone, rotated counter clockwise with distal end towards left, posterolateral and slightly ventral view; **L**, TMP 2010.30.05, right ilium, with ligament (arrow) attached in approximate position of "ventrolateral tuberosity," lateral view. **M**, *Ambystoma tigrinum* (Ambystomatidae), Recent, Alberta, Canada, transformed individual, TMP 90.07.217, right ilium, lateral view. **N**, *Ambystoma maculatum* (Ambystomatidae), Recent, purchased specimen (presumably from eastern U.S.A.), transformed individual, UALVP 14330, left ilium, lateral and slightly posterior view. **O–R**, *Necturus maculosus* (Proteidae), all Recent and neotenic individuals, purchased specimens (presumably from eastern U.S.A.): **O**, TMP 2010.30.12, right ilium + sacral rib, with ligament (arrow) attached in approximate position of "ventrolateral tuberosity," anterolateral view; **P**, TMP 2010.30.13, right ilium dissected out of preserved individual shown in Figure 6, with indistinct (not visible in this image), low, and elliptical prominence in approximate position of "ventrolateral tuberosity," lateral view; **Q**, TMP 2007.30.10, left ilium, with elliptical scar (circled) in approximate position of "ventrolateral tuberosity," lateral view; **R**, TMP 2007.30.11, right ilium, with raised, steep-sided, and circular pit (arrow) in approximate position of "ventrolateral tuberosity," anterolateral view. **S**, *Cryptobranchus alleganiensis* (Cryptobranchidae), Recent, purchased specimen (presumably from eastern U.S.A.), TMP 2007.30.17, right ilium, lateral view. **T**, *Plethodon jordani* (Plethodontidae), Recent, purchased specimen (presumably from eastern U.S.A.), UALVP 14354, right ilium, lateral view. **U**, **V**, Urodela indet., Upper Cretaceous (upper Campanian), Oldman Formation, Alberta, Canada, each with a raised, subcircular prominence (arrows) in approximate position of "ventrolateral tuberosity": **U**, TMP 96.78.228, from TMP locality L1137, left ilium missing distal part of shaft, with prominence best developed at its proximal and distal ends and shallower across its median portion, lateral view; **V**, TMP 96.78.198, from TMP locality L1134, right ilium, missing distal part of shaft and posteroproximal corner of acetabular region, with more strongly developed prominence having a rugose surface, lateral view. **W–Z**, Urodela indet., Upper Cretaceous (upper Maastrichtian), U.S.A., each with an elongate and slightly raised prominence having a wrinkled texture (arrows), in approximate position of "ventrolateral tuberosity": **W**, **X**, NDGS 853, left ilium missing distalmost end of shaft, Hell Creek Formation, NDGS locality 02–02 (= Pioneer Trails Regional Museum locality V88018), North Dakota: **W**, lateral view; **X**, lateral and slightly anterodorsal views; **Y**, **Z**, AMNH 27012, Lance Formation, Bushy Tailed Blowout, Wyoming, left ilium missing more of distal end of shaft: **Y**, entire specimen, lateral view; **Z**, close-up of base of shaft and adjacent part of acetabular region, lateral and anterodistal view. **AA**, Urodela indet., Upper Cretaceous (upper Cenomanian), Dakota Formation, MNA locality 1067, Utah, U.S.A., MNA V10305, right ilium missing distal end of shaft and lacking any raised structure or roughened surface in approximate position of "ventrolateral tuberosity," lateral view. **Abbreviations**: **ac**, acetabulum; **ant**, anterior acetabular expansion; **"dpr"**, "dorsal prominence" of Blob et al. (2001); **lig**, ligament connecting distal ends of ilium and sacral rib; **post**, posterior acetabular expansion; **prox**, proximal surface, **sac rib**, sacral rib. Images at different magnifications; all scale bars equal 1 mm.

areas anterior and posterior to the acetabulum are roughly equivalent in size and that their proximal limits are essentially in line with the proximal edge of the acetabulum. FMNH PR 2078 is missing the proximal portion of the region behind the acetabulum, but the bone anterior to the acetabulum is intact and conforms to the pattern seen in the other two specimens. The condition in *Nezpercius* is typical of urodeles and some anurans, so it is not informative.

Feature 15, Medial Surface of Acetabular Region—Anuran ilia typically have an inter-iliac scar on the medial surface of the acetabular region; primitively this scar is confined to the proximal and ventral portion of the medial face, as in *Ascaphus* and *Prosalirus* (Fig. 4C–E and J, respectively). The inter-iliac scar may expand to cover more (e.g., *Bombina*, Fig. 4G–I) or virtually all (e.g., *Hungarobatrachus* [Szentesi and Venczel, 2010:fig. 2] and Palaeobatrachidae) of the medial surface of the acetabular region. In anuran ilia, the medial surface also is flat to shallowly concave. By comparison, in urodeles the medial surface of the acetabular region is flat to convex and no inter-iliac scar is present (Fig. 5C, D). The three *Nezpercius* ilia exhibit the urodele condition. FMNH PR 2078 lacks the posterior corner of the acetabular region; the rest of the medial surface is flat to extremely shallowly convex and smooth, with no indication of an inter-iliac scar (see Blob et al., 2001:fig. 2C). The medial surface of the acetabular region is intact in FMNH PR 2079 and 2080 (Fig. 1M). In both specimens the medial surface is smooth and no inter-iliac scar is present; the medial surface is shallowly convex in FMNH PR 2079 and more nearly flat in FMNH PR 2080

Feature 16, Proximal Surface of Acetabular Region—In most of the extant urodele ilia we examined, the proximal surface of the bone is excavated and mediolaterally concave along its entire anteroposterior length (Fig. 5E). This concavity may be asymmetrical from side-to-side, with the medial rim projecting farther than the lateral rim. In one extant *Plethodon jordani* skeleton we examined, however, the proximal surface of the ilium is relatively flat. In all extant anuran skeletons we examined, the proximal end of the ilium is thicker and the proximal surface is fully finished in bone, flat, and roughened for contact with the other pelvic elements (Fig. 4E, I). Each of the three specimens of *Nezpercius* preserves enough of the acetabular region to show that they have the typical urodele condition—the proximal surface is concave along its entire anteroposterior length and the medial rim projects slightly farther than does the lateral rim.

Feature 17, Oblique Groove—There is no trace of an oblique groove in any of the specimens of *Nezpercius*. An oblique groove is absent in all urodeles and most anurans, so its absence in *Nezpercius* is not informative.

Feature 18, Dorsal Prominence and Dorsal Tubercle—In many anurans, the dorsal margin of the ilium at the junction between the acetabular region and shaft bears a low, ridge-like structure called the "dorsal prominence." On top of the dorsal prominence there may be a knob-like process called the "dorsal tubercle." These structures serve as attachment points for muscles (see Přikryl et al., 2009). Homologous structures do not occur in urodeles at the anatomically equivalent position (i.e., posterior margin) on the ilium. Each of the *Nezpercius* ilia has a low ridge extending for a short distance along the less divergent margin (see above, feature 13) of the acetabular region; this ridge is best developed in the largest specimen, FMNH PR 2079. Blob et al. (2001:figs. 2, 3) interpreted this ridge as the "dorsal prominence." Some extant and fossil urodele ilia have a poorly developed, unnamed ridge that structurally resembles the "dorsal prominence" of *Nezpercius* and also lies along the less divergent margin of the acetabular region. In unequivocal urodeles, however, that ridge is on the opposite side (i.e., anterior margin, which is homologous to the ventral margin in anurans) from where the dorsal prominence occurs in anurans. If the ilia of *Nezpercius* were from a urodele, the ridge along the less divergent margin (i.e., anterior) of the acetabulum cannot be homologous with the dorsal prominence of anurans.

Feature 19, Dorsal Crest—All three specimens of *Nezpercius* preserve enough of the bone to establish that no dorsal crest was present. The lack of a dorsal crest is not informative, because that condition occurs in all urodeles and variably in anurans. Interestingly, a dorsal crest is absent in most Mesozoic anurans.

Feature 20, Lateral Structures on Iliac Shaft—According to Blob et al. (2001), the key diagnostic feature of *Nezpercius dodsoni* was a structure that they called the "ventrolateral tuberosity." This structure is intact in FMNH PR 2078 and 2080, whereas only the proximal end is preserved in FMNH PR 2079. The ventrolateral tuberosity is a proximodistally elongate, ovoid prominence that is located slightly distal to the acetabulum on the lateral surface of the iliac shaft; it is best developed proximally and grades distally into the shaft. The ventrolateral tuberosity lies midway across the lateral surface of the shaft (i.e., perpendicular to long axis) in FMNH PR 2080, whereas in the other two specimens it is offset slightly and lies closer to what Blob et al. (2001) interpreted as the ventral margin of the shaft. The surface of the ventrolateral tuberosity is smooth in the two smallest specimens, but slightly roughened in FMNH PR 2079. Blob et al. (2001) regarded the ventrolateral tuberosity of *Nezpercius* as being autapomorphic among known anurans and suggested that it likely served as the point of origin for one of the hind limb muscles. Some unequivocal anurans do have bony structures along the lateral surface of the iliac shaft, but the form, orientation, and position of those structures differ from the ventrolateral tuberosity of *Nezpercius*. Examples of non-comparable lateral structures on anuran iliac shafts include (1) a laterally projecting crest extending along much of the length of the shaft in extant pipids (e.g., Cannatella and Trueb, 1988:fig. 11D, E) or along the anterior two-thirds of the shaft in the extant microhylid *Melanophryne carpish* (Lehr and Trueb, 2007:fig. 20D); (2) the so-called "lamina calamita" (sensu Sanchiz, 1977), which is a weakly developed and moderately elongate flange located well in front of the acetabulum along the ventrolateral-most portion of the shaft in extant *Bufo calamita* (see Holman, 1989:fig 1, top; Bailon, 1999:fig. 19M) and variably in extant *Bufo bufo* (J.-C. Rage, pers. comm., 2009, to J.D.G.); (3) a pair of short, parallel ridges extending dorsoposteriorly–ventroanteriorly along the lateral surface of the base of the shaft in the Lower Jurassic *Prosalirus* (Fig. 4J); and (4) one short ridge extending dorsoposteriorly–ventroanteriorly along the lateral surface of the base of the shaft in indeterminate ilia from the Upper Cretaceous of Utah (e.g., Fig. 4K, L) and, according to Báez and Rage (1998:684), in pipid ilia from the Upper Cretaceous of Niger.

Although not previously reported, some extant and fossil urodele ilia have structures that resemble the ventrolateral tuberosity of *Nezpercius*. Some *Ambystoma mexicanum* individuals have an elongate, low bony ridge, with a slightly roughened texture, that extends along the posterolateral surface of the iliac shaft (Fig. 5F, G). A similar structure, but with a more elliptical outline and wrinkled texture, is seen in some but not all fossil urodele ilia (Fig. 5W–Z). In the same position, some other urodele ilia bear an elongate and roughened, scar-like surface (Fig. 5H, I, Q), a subcircular and concave-bottomed pit (Fig. 5J, K), a subcircular and raised bony patch with a roughened surface (Fig. 5U, V), or a subcircular and raised bony rim with a hollow interior (Fig. 5R). These features are not, however, universally present in all urodeles (Fig. 5A, B, M, N, S, T, AA). There appears to be both taxonomic differences in the presence or absence of these structures (e.g., not seen in extant *Cryptobranchus* and *Plethodon*; Fig. 5S and T, respectively) and intraspecific differences in the presence and form of the structure. For example, in the specimens of *A. mexicanum* we examined, some individuals do not have any structure on the lateral surface of the iliac shaft (e.g., Fig. 5A, B) and, in those that do, the structure

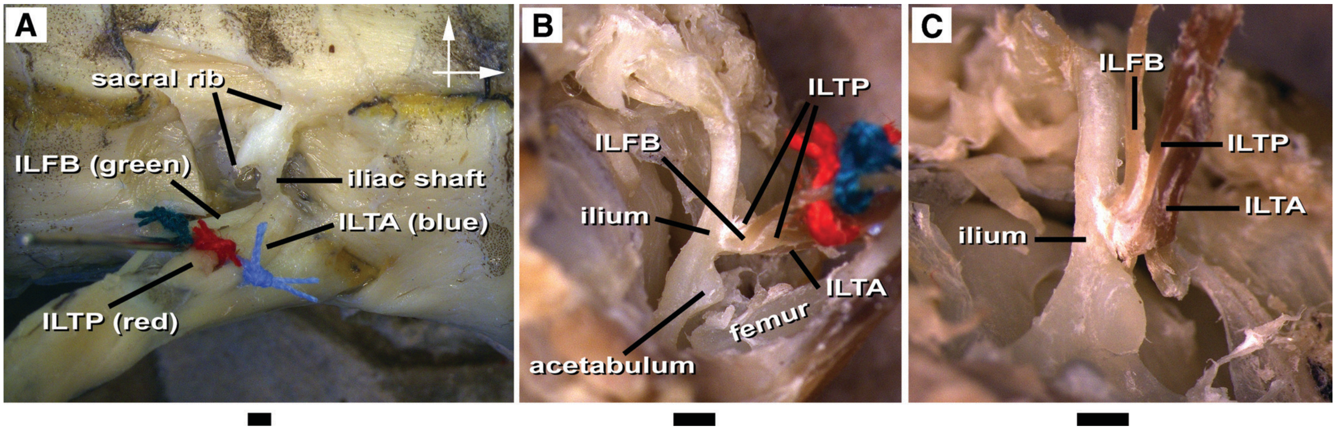

FIGURE 6. Photographs of sequential dissection of right pelvic and hind limb region in an extant individual of *Necturus maculosus*, TMP 2010.30.13, showing three thigh muscles that attach to proximal portion of iliac shaft just above acetabulum. From posterior to anterior, the three thigh muscles (muscle names and abbreviations follow Ashley-Ross, 1992:157–158) are as follows: **ILFB**, M. iliofibularis; **ILTP**, M. extensor iliotibialis, pars posterior; **ILTA**, M. extensor iliotibialis, pars anterior. Origins of ILFB and ILTP are in similar positions to where the "ventrolateral tuberosity" is located on *Nezpercius* ilia (see Fig. 1) and where various raised structures or roughened surfaces are located on some extant and fossil urodele ilia (see Fig. 5). **A**, Superficial dissection, in lateral view, with hind limb extending posteriorly (i.e., to left side of figure) and trunk muscles in pelvic region partially removed to expose iliac shaft and sacral rib (see Fig. 5O for image of right ilium + sacral rib dissected out from another *Necturus* individual). Trunk muscles tied off with different colored threads and pin used to demonstrate that ILFB is separate along much of its length from other thigh muscles, except proximally where it is partially attached to proximal portion of posterior surface of ILTP. Perpendicular arrows in upper right indicate anterior and dorsal directions. **B**, Deep dissection, in posterior view, with femur partly disarticulated from acetabulum and thread removed from ILFB. **C**, Deep dissection, in lateroposterior and slightly ventral view, with femur completely disarticulated from pelvic girdle and threads removed from all thigh muscles. Right ilium subsequently was dissected out, de-fleshed, and photographed (see Fig. 5P). Images at different magnifications; all scale bars equal 1 mm.

varies (cf., Fig. 5F, I, K). Despite this variation, the "ventrolateral tuberosity" is a structure that is restricted to urodeles and, thus, its presence argues against assigning *Nezpercius* to the Anura.

Blob et al. (2001) suggested that the "ventrolateral tuberosity" in *Nezpercius* served as an attachment point for a muscle; we agree that this is the most likely function for such a process and for the comparable structures reported in the previous paragraph. While macerating the specimens of *Ambystoma mexicanum* used in this study, we recovered an ilium (Fig. 5L) with a ligament firmly attached to the posterolateral surface of the proximal portion of the iliac shaft, in the approximate position of the "ventrolateral tuberosity," which clearly indicates that some kind of soft tissue attached to the bone at that point. This led us to dissect several preserved specimens of *Necturus* and one specimen of *Andrias* with the goal of identifying which muscle(s) might connect to that ligament. Based on those dissections, plus information gleaned from published dissections for *Necturus* (e.g., Stuart, 1940; Gilbert, 1973; Wischnitzer, 1993; Přikryl et al., 2009) and for other urodeles (e.g., *Ambystoma*: Ashley-Ross, 1992; Přikryl et al., 2009; *Dicamptodon*: Ashley-Ross, 1992; *Pseudoeurycea*: Baird, 1951; *Salamandra*: Francis, 1934; *Taricha*: Walthall and Ashley-Ross, 2006), we found that two thigh muscles—M. iliofibularis and M. extensor iliotibialis, pars posterior—attach to the ilium in the same place as the "ventrolateral tuberosity" and the other above-mentioned structures (Fig. 6).

DISCUSSION AND CONCLUDING REMARKS

To summarize, of the 16 features that we were able to evaluate for *Nezpercius*, five (numbers 9, 10, 15, 16, and 20 in Appendix 1) are seen in urodeles, but not anurans. The remaining features are consistent with *Nezpercius* being a urodele, but none of those is decisive because for each feature a similar condition occurs in some anurans. We have not identified any features in any of the three specimens of *Nezpercius* that are exclusive to anurans. In our opinion, the available evidence indicates that *Nezpercius* is a urodele, not an anuran as originally proposed by Blob et al. (2001).

Holman (2003) previously suggested that *Nezpercius* was not an anuran—although he did not go so far as to formally exclude the genus from the Anura—and also questioned whether the three specimens described by Blob et al. (2001) were even ilia. His objection to the specimens being ilia centered largely on what he described as "an ovoid cotyle" (Holman, 2003:46) forming the proximal end of each specimen. As shown here, an excavated proximal surface can occur in ilia, but in urodeles not anurans. Other attributes, most notably the presence of an acetabulum and what obviously is the base of a shaft, also clearly point to those specimens being ilia. Our work supports Holman's (2003) contention that three features (form of the proximal surface and the acetabulum; presence of a ventrolateral tuberosity) do not support assigning *Nezpercius* to the Anura, and goes further in showing that those features instead support assigning *Nezpercius* to the Urodela. Holman's (2003) suggestion that the circular transverse outline of the shaft also excluded *Nezpercius* from being an anuran can be disregarded, because that condition is typical of basal anurans (e.g., Trueb, 1973:107).

Aside from differences in absolute size and minor variation in several features (i.e., relative depth of the concave proximal end, outline of the acetabulum, and development of the ridge along the leading edge of the anterior acetabular region and of the "ventrolateral tuberosity"), the three *Nezpercius dodsoni* ilia are similar enough that we agree with Blob et al.'s (2001) original interpretation that the specimens are from conspecific individuals. Although we regard these specimens as being from a urodele, we cannot assign them to any urodele family or synonymize the name *N. dodsoni* with any urodele genus and species. Three urodele families (Sirenidae, Scapherpetontidae, and Batrachosauroididae) are known from the Campanian of the North American Western Interior (e.g., Estes, 1981; Gardner, 2005), but their constituent genera and species are represented almost exclusively by isolated vertebrae and skull bones that cannot reliably be associated with, or meaningfully compared to, any of the three *Nezpercius* ilia. We thus remove *Nezpercius dodsoni* Blob et al., 2001, from the Anura and transfer to it the Urodela, as Urodela incertae sedis.

Using the criteria we have presented here for differentiating urodele and anuran ilia, it is evident that isolated urodele ilia are not uncommon in microvertebrate localities. Here we illustrate examples (Fig. 5U–AA) from four units of Cenomanian, Campanian, and Maastrichtian ages in the North American Western Interior that differ in features such as overall size, shape, and presence/absence and form of thigh muscle attachment structures on the shaft. Nessov (1981) illustrated several Upper Cretaceous urodele ilia from Uzbekistan that differ from fossil specimens illustrated here in having shafts that are more mediolaterally compressed and expanded distally. Two examples of Upper Cretaceous (lower or middle Campanian) urodele ilia from Utah have been figured as "cf. *Nezpercius dodsoni*" and "cf. *Nezpercius* sp." by Roček et al. (in press:fig. 14p and r, respectively). One of our figured specimens, MNA V10305 (Fig. 5AA) from the Dakota Formation (Cenomanian) of Utah, resembles the three *N. dodsoni* ilia in size and overall form, but lacks a "ventrolateral tuberosity." Extant and fossil specimens reported here demonstrate that there is considerable variation in urodele ilia. With a better understanding of patterns of iliac variation among extant urodeles and larger samples of fossil ilia, it may be possible to begin recognizing distinct fossil iliac morphs and identify those to at least family level.

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APPENDIX 1. Features potentially useful for differentiating ilia of anurans and urodeles.

Feature	Anurans	Urodeles
Iliac shaft:		
1. Orientation in lateral view.	Projects anteriorly to slightly dorsoanteriorly.	Projects dorsally to posterodorsally.
2. Relative proximal–distal length.	Elongate (i.e., typically accounts for at least three-quarters total anterior–posterior length of bone).	Relatively shorter (i.e., typically accounts for less than three-quarters total dorsal–ventral height of bone).
3. Curvature in lateral view.	Nearly straight to shallowly convex dorsally.	Nearly straight to shallowly convex posteriorly.
4. Lateral curvature.	Nearly straight to shallowly convex laterally, when seen in dorsal or ventral aspect.	Shallowly to broadly convex laterally, when seen in posterior or anterior aspect.
5. Cross-sectional outline (i.e., perpendicular through long axis) ca. midway along shaft, excluding dorsal crest.	Subcircular to oval.	Subcircular, oval, or mediolaterally flattened.
6. Outline in lateral view.	Uniform along shaft or tapers distally.	Uniform along shaft or expands distally.
Acetabulum (= acetabular fossa):		
7. Outline in lateral view.	Semi-circular or subtriangular (with distal end tapered); margins typically convex.	More variable; typically distally elongate and oblong to hourglass-shaped or shorter, broader, and subtriangular; semi-circular in many Upper Cretaceous specimens.
8. Relative size.	Varies from small (i.e., fully enclosed within acetabular region) to larger (i.e., ventral and anteroventral margins extend beyond edges of acetabular region).	Small to moderate (i.e., always fully enclosed within acetabular region).
9. Form of margins.	Distinct margin: low along dorsal portion, but developed as a laterally projecting rim or flange along ventroanterior and ventral portions.	Weakly developed as a low ridge that does not extend laterally any significant distance beyond level of acetabular surface.
10. Form of acetabular surface.	Deeply concave, bowl-shaped, and partially sunk into bone.	Varies from saddle-shaped or sinuous (i.e., dorsal portion nearly flat to shallowly convex and ventral portion concave) to shallowly concave or nearly flat; may be shallowly sunk along ventral and middle portions into acetabular region or elevated laterally on a ramp-like, bony pedestal.
11. Orientation of acetabular surface.	Directed laterally and slightly posteriorly.	Directed laterally and ventrally.
Lateral surface of acetabular region, exclusive of acetabulum:		
12. Outline in lateral view.	Typically triangular, but squarish in some.	Triangular.
13. Outlines of margins in lateral view relative to long axis of iliac shaft.	Dorsal margin of pars ascendens and ventral margin of pars descendens may be strongly divergent; latter typically more divergent than former.	Posterior and anterior margins less strongly divergent; posterior margin typically more divergent than anterior.
14. Sizes and proximal extent of areas dorsal and ventral (anurans) or posterior and anterior (urodeles) to acetabulum.	Pars ascendens often larger than pars descendens and may project beyond proximal edge of acetabulum.	Posterior and anterior regions subequal in size or former slightly larger; neither region projects beyond proximal edge of acetabulum.
Medial and proximal surfaces of acetabular region:		
15. Medial surface.	Bony contact between paired ilia typically produces triangular scar (inter-iliac scar) on medial surface of acetabular region; this contact surface may project medially as an inter-iliac tubercle and may expand dorsally and anteriorly to cover much of medial surface of acetabular region. Remainder of medial surface smooth and flat to shallowly concave.	No bony contact between paired ilia, thus no scar on medial surface. Medial surface smooth, varies from flat to convex.
16. Proximal surface.	Proximal (posterior in life) end of ilium articulates dorsally with ossified ischium and ventrally with cartilaginous or ossified pubis. Proximal end of ilium mediolaterally thickened, proximal face complete, flattened to shallowly convex, and distinct from acetabular surface, usually with sharp posterolateral edge separating the proximal and lateral surfaces.	Articular surface with ischium component of puboischiadic plate extends along entire proximal (ventral in life) end of ilium. Proximal end of ilium not thickened, proximal face typically concave (infilled in life by cartilage), and may be asymmetrically concave with lateral edge more excavated and grading into acetabulum.
Grooves and processes:		
17. Oblique (= spiral) groove.	Many Mesozoic and some extant anurans (e.g., *Pelobates*) have an oblique groove extending from the lateral surface of the pars ascendens, wrapping across the dorsal surface of the ilium, and carrying anteriorly onto the medial surface of the shaft.	Comparable structure not known.
18. Dorsal prominence and dorsal tubercle (= tuber superius).	Many anurans have a raised ridge (dorsal prominence), often topped with a dorsal tubercle (knob-like process) on the dorsal surface of the acetabular region.	Comparable structure not known.
19. Dorsal crest (crista dorsalis).	Mediolaterally compressed, blade- or ridge-like crest extending anteriorly along dorsal surface of iliac shaft variably present in anurans.	Comparable structure not known.
20. Lateral structures on iliac shaft.	Typically absent, except as follows: some Mesozoic anurans have one or two short, oblique ridges extending along lateral surface of shaft in front of acetabular region; some extant European *Bufo* spp. have a moderately elongate ridge extending anteroposteriorly along ventrolateral surface of shaft well in front of acetabular region; and some taxa (e.g., pipids) have a prominent lateral or dorsolateral crest extending anteroposteriorly along shaft.	Lateral surface either smooth or proximal portion may bear a moderately elongate, low ridge or scar or a subcircular scar, pit, or raised knob.