

Similarities and differences in the ilia of Late Cretaceous anurans and urodeles

ZBYNĚK ROČEK¹, JAMES D. GARDNER², JEFFREY G. EATON³ and TOMÁŠ PŘIKRYL⁴

Key-words. – Anura, Cretaceous, Ilium, North America, Postcranial skeleton, Urodela

Abstract. – Screen-washing of matrix from 37 Upper Cretaceous microvertebrate localities in southern Utah, USA, yielded a rich sample of anuran disarticulated bones, including nearly 200 ilia. Because the bones are relatively small and delicate and were subject to pre-mortem transport and unavoidable damage when the fossiliferous matrix was collected and processed, none of the recovered ilia retained intact shafts. This means that features such as the form of the anterior end of the shaft and the presence and form of a dorsal crest cannot be used to identify the fossils. Urodele bones also are known from many of the same localities. When anuran and urodele ilia are isolated and missing much of their shafts, they are superficially similar, so it was important to reliably differentiate ilia of the two groups. Here we provide a list and brief descriptions of some of the features that we found useful for distinguishing between anuran and urodele ilia. These features relate to differences between the two groups in muscle attachments, contacts between pelvic bones, and structure of the acetabula. Because all of the features exhibit some variation, we recommend that they be used in combination when trying to distinguish between anuran and urodele ilia.

Similarités et différences dans les ilions d'anoures et urodèles du Crétacé supérieur

Mots-clés. – Anura, Crétacé, Ilion, Amérique du Nord, Squelette post-crânien, Urodela.

Résumé. – Un lavage-tamisage de sédiments provenant de 36 localités à microvertébrés du Crétacé supérieur du Sud de l'Utah (Etats-Unis) a livré un échantillon conséquent d'ossements désarticulés d'anoures, dont environ 200 ilions. A cause des petites tailles estimées de ces grenouilles (la longueur museau-cloaque estimée de beaucoup d'individus ne dépasse pas 20 mm), du transport post-morten de ces ossements avant leur enfouissement, et de l'inévitable casse lors de la collecte et du traitement des sédiments, aucun des ilions ne présente de diaphyse intacte. Cela implique que des caractères, comme la forme de l'extrémité antérieure de la diaphyse, ou la présence et la forme de la crête dorsale, ne peuvent être utilisés dans l'identification des fossiles. Des urodèles sont également connus dans beaucoup de ces localités. Lorsque des ilions d'anoures et d'urodèles sont isolés et que leur région diaphysaire n'est pas conservée, ils se ressemblent, d'où l'importance de bien différencier les ilions des deux groupes. Pour cela, nous proposons une liste ainsi qu'une brève description de caractères que nous trouvons utiles pour distinguer les ilions d'anoures de ceux des urodèles. Ces caractères sont liés aux différences entre des d'attachements musculaires entre les deux groupes, aux contacts entre les os pelviens, et à la structure de l'acétabulum. Parce que tous ces caractères présentent quelques variations, nous recommandons de les utiliser ensemble lors des tentatives de distinction entre ilions d'anoures et d'urodèles.

INTRODUCTION

Modern amphibians are represented by three different and well discernible crown-groups: Anura, Urodela and Apoda. The earliest anurans are known from the Early Jurassic of Arizona, USA [Shubin and Jenkins, 1995; Curtis and Padian, 1999], whereas the earliest urodeles are known from the Middle-Late Jurassic of England and China [Evans and Milner, 1994; Milner, 2000; Gao and Shubin, 2003]. As regards their distribution, since the very beginning of their existence, anurans have been present on Gondwanan and Laurasian continents and, thus, are considered cosmopolitan. In contrast, disregarding some enigmatic isolated vertebrae recovered from the Late Cretaceous of Niger, Sudan,

and Bolivia [Rage *et al.*, 1993; Evans *et al.*, 1996], poorly preserved skeletons of *Ramonellus longispinus* from the Early Cretaceous of Israel [Nevo and Estes, 1969], and some recent occurrences in northern Africa and northern South America, urodeles have been recorded only on Laurasian continents. The most generalized of the three groups are urodeles, which preserve basic anatomical features of their temnospondyl ancestors, whereas anurans are the most derived, undoubtedly because of their specialized jumping locomotion. Apodans are anatomically specialized for burrowing and they entirely lack limbs and girdles. The pro-apodan *Eocaecilia* (Early Jurassic; Arizona, USA) retains vestigial limbs and girdles [Jenkins and Walsh, 1993; Jenkins *et al.*, 2007]; although reduced, its appendicular

1. Laboratory of Palaeobiology, Institute of Geology, Academy of Sciences of the Czech Republic, Rozvojová 135, CZ-165 00 Prague 6, Czech Republic; Rocek@gli.cas.cz and Department of Zoology, Charles University, Viničná 7, CZ-12844 Prague 2, Czech Republic; Rocek@natur.cuni.cz
2. Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada, T0J 0Y0; James.Gardner@gov.ab.ca
3. Department of Geosciences, Weber State University, 2507 University Circle, Ogden UT 84408-2507, USA; JEaton@weber.edu
4. Department of Palaeobiology, Institut of Geology, Academy of Sciences of the Czech Republic, Rozvojová 135, CZ 165 00 Prague 6, Czech Republic and Department of Palaeontology, Charles University, Albertov 6, CZ 128 43 Prague 2, Czech Republic; Prikryl@gli.cas.cz
Manuscript accepted on April 8, 2012

skeleton otherwise conforms to the basic tetrapod plan. The consensus view [e.g., Schoch and Milner, 2004; Marjanović and Laurin, 2007] is that the three groups of modern amphibians form a monophyletic clade called the Lissamphibia.

The postcranial skeleton of the Urodela, if compared with ancestral temnospondyls, is not very modified [cf., figs. 1A, 2A-D versus figures in Pawley and Warren, 2006; Pawley, 2007]. Because urodeles use all four legs for walking on land or bottom-walking in water, the basic form and position of their ilia is the same as in the earliest terrestrial tetrapods. Their pubis and ischium, which in the piscine ancestors of terrestrial tetrapods were represented by a single, horizontal, puboischiadic plate that did not have a bony connection with the vertebral column, became divided into two bones isolated from one another by a narrow strip of cartilage, with the pubis oriented anteriorly and the ischium oriented posteriorly. A new pelvic bone, the ilium, appeared as a result of adaptation to a terrestrial way of life, which required a firm connection between the hindlimbs and axial skeleton. Originally, the dorsally elongated shaft of the ilium connected the puboischiadic plate with the lateral end of the sacral rib, and all three pelvic bones joined each other in the acetabulum. The puboischiadic plates of the left and right side were co-ossified in fishes, but during the transition onto dry land both halves became separated by a strip of cartilage and the acetabula faced ventrolaterally. The paired ilia were broadly separated from one another by the puboischiadic plates and served as vertical, columnar supports for the rear part of the body. This basic tetrapod pelvic configuration remains essentially unaltered in urodeles.

In anurans, however, the situation is different (figs. 1B, 3A-D). Their iliac shafts are located horizontally along the proximal section of what once was the tail, but which has been transformed into the rod-like urostyle, rather than vertically as in their temnospondyl ancestors and in urodeles. This re-orientation and re-positioning of the ilium required that the acetabulum be shifted posteriorly and dorsally from its original position below the sacral vertebra. This evolutionary process seems to be documented by posterior rotation of the ilium during metamorphosis in extant anurans [Ročková and Roček, 2005]. In extant anurans, the rudimentary halves of the pelvis first appear well separated from one another, but during metamorphosis they move towards the midline until all three pelvic bones contact with their counterparts of the opposite side; the pubes and ischia broadly contact one another, whereas the ilia only contact one another near their posterior ends. It is not important in this context whether the elongate iliac shafts in anurans evolved in conjunction with saltatory locomotion – probably not, because in the Early Triassic proanuran *Triadobatrachus* the iliac shafts are already elongate and in a horizontal, not vertical, position, whereas other adaptations that are functionally critical for hindlimb jumping, such as shortening of the presacral column, fusion of the caudal vertebrae to form the urostyle, and strengthening of the sacral diapophyses by fusion with the sacral ribs, are not yet present in *Triadobatrachus* [Rage and Roček, 1989].

From the above descriptions and accompanying illustrations (figs. 1, 2A-D, 3A-D), it is clear that the pelvic girdles of urodeles and anurans are profoundly different. However, differences between their ilia are not so immediately evident when that bone is extracted from its natural anatomical

context (figs. 2E-T versus 3E-I). Ilia in both groups consist of two parts: a shaft that is elongate, curved, oval or slightly compressed laterally in cross-section, and may taper or expand towards its free end, and an expanded acetabular region that connects the ilium with the rest of the pelvic girdle and laterally houses part of the acetabulum for articulation with the femur. Generally, in both groups the acetabulum is a cup-like depression that also extends onto the ischium and pubis. However, the pubis is mostly cartilaginous in both groups, whereas the ossified ischium is connected to the ilium by a rigid cartilaginous suture in anurans and by a larger mass of cartilage in urodeles. Some of the similarities between anuran and urodele ilia may be due to the fact that their pelvic girdles are underossified to various degrees and, consequently, a more or less substantial portion of their acetabulum (not only the articular surface) is formed by cartilage.

Features of the iliac shaft can be useful for identifying anuran ilia to at least family level [e.g., Rage, 1974] and for differentiating anuran and urodele ilia. Compared to urodeles, anuran iliac shafts typically are longer, oval in cross-section, tapered towards the free end, and may bear a crest or groove along the dorsal surface. However, variational overlap in those features means that shafts alone may not be sufficient for distinguishing anuran and urodele ilia. For instance, the anterior portion of the iliac shafts in the Pipidae are enlarged due to their sliding articulation with the sacral diapophyses [Van Dijk, 2002] and, thus, somewhat resemble the expanded dorsal end of the iliac shaft seen in many urodeles. Isolated fossil ilia usually are missing a substantial portion of the shaft, so for those specimens features of the acetabular region and adjacent part of the shaft need to be considered when attempting to differentiate anuran and urodele ilia.

RESULTS

Our samples from 37 localities of middle Cenomanian to late Campanian age in southern Utah [Roček et al., 2010] involved nearly 200 anuran ilia whose variation suggests a remarkable diversity of these amphibians during the Late Cretaceous in that part of the North American Western Interior. Urodele fossils (mostly vertebrae and jaws, but also rare ilia) are known from many of the same localities [Gardner et al., 2013]. Most of the anuran and urodele ilia are small, with estimated total lengths of 5 mm or less. If the ratio between total ilium length and snout-vent length (SVL) in extant *Ascaphus truei* is used for estimating body size, then the average SVL of the Late Cretaceous anurans in the Utah samples was around 20 mm. The percentage of larger-bodied anurans increased markedly in the Campanian, with the largest individuals having SVLs of about 70 mm. Probably the small size of these anurans and correspondingly delicate build of their bones, plus post-mortem transport and damage of bones before burial and unavoidable damage when the matrix was collected and washed, are why all the ilia in the samples were incomplete and only their acetabular region and adjacent portion of the iliac shaft were preserved. Consequently, although the shape of the tip of the iliac shaft is a potentially informative feature, it could not be used to differentiate anuran and urodele ilia in the samples from Utah. However, on the preserved part

of the ilia there are several features that can be used to distinguish anurans from urodeles. One of the most obvious features is the dorsal tubercle, which is consistently absent in urodeles but is variably present in anurans. Where present in anurans (fig. 3G, I), the dorsal tubercle is located along the dorsal margin of the acetabular region, approximately in line with the anterior margin of the acetabulum, and serves as an area of insertion for the gluteus maximus, ilio-tibialis and ilio-femoralis muscles [Příkryl *et al.*, 2009]. Unfortunately, ilia with a dorsal tubercle were uncommon in the samples from Utah and, at some localities, were completely lacking.

Thus, in the Utah samples, the problem of differentiating between incomplete anuran and urodele ilia was restricted to those ilia without a dorsal tubercle. Among them was a comparatively large group of ilia with an oblique groove (spiral groove of some authors) that crosses over the dorsal margin of the acetabular region from the lateral surface of the bone onto its medial surface. Such a groove, in various modifications (e.g., sometimes accompanied by a parallel groove or crista posteriorly or sometimes appearing only as a faint depression that does not extend onto the medial surface of the bone), occurs in many North American Late Cretaceous anurans. Among extant anurans, similar ilia may be found in *Pelobates* (fig. 3F); in that genus, the oblique groove serves as an area of origin for the inner head of the iliocaudatus muscle [Příkryl *et al.*, 2009], which wraps laterally over the dorsal margin of the iliac shaft to join the outer head of the muscle and insert onto the dorsal surface of the proximal part of the femur. The main function of the muscle is protraction of the femur, which is

important in the preparatory phase of the jump and in the recovery stroke in swimming when the hindlimbs are flexed and retracted back towards the body [Gillis and Biewener, 2000]. Because in urodeles the iliocaudatus muscle originates only by a single head on the lateral surface of the ilium, but never in any sort of an oblique groove on the medial surface of the ilium, we concluded that all ilia in the Utah samples with an oblique groove were from anurans.

This left an assortment of ilia that were more challenging to identify because they had neither a dorsal tubercle nor an oblique groove. Previously investigated North American Jurassic and Cretaceous anurans generally have been assigned to Tertiary-age or extant higher level taxa (e.g., Ascaphidae, Discoglossidae, Palaeobatrachidae, ?Rhinophrynidae and, based on the presence of an oblique groove, to the Pelobatidae [e.g., Estes, 1964, 1969; Estes and Sanchíz, 1982; Evans and Milner, 1993; Henrici, 1998; but see Gardner, 2008]). However, some Cretaceous anurans were described on the basis of skeletal elements that differ from those in extant anurans, which suggests that those Cretaceous taxa could have been somewhat anatomically different from those which occur today. Examples of these enigmatic Cretaceous taxa include: *Theatonius lancensis* Fox, 1976, which lacks teeth on its maxilla and has dense pustular ornamentation on its skull bones; *Scotiophryne pustulosa* ESTES, 1969, which has a maxilla with an unusual medial structure; and *Nezpercius dodsoni* BLOD *et al.*, 2001, which is known only by peculiar ilia. In such cases, although we may rely on anatomical features seen in extant taxa and well-preserved Tertiary fossil skeletons to help distinguish between older anuran and urodele fossils, it is

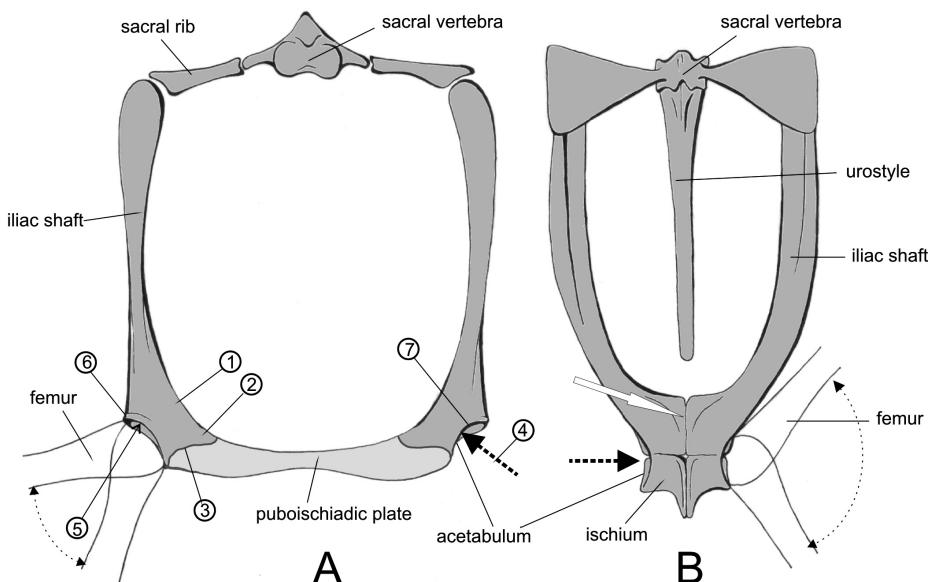


FIG. 1. – Stylized diagrams depicting pelvic girdles of a urodele in posterior view (A) and an anuran in dorsal view (B), to show different positions and contacts of the ilium in both groups. Note that ilia are in vertical orientation in the urodele pelvis (A) versus horizontal orientation in the anuran pelvis (B). Large, broken, black arrows mark different orientations of the acetabula; small, broken, black arrows indicate different limits of movements of the femora; and white arrow (anuran pelvis) points to contact surface (= interiliac suture in fig. 3A, C) between ilia. Bone in pelvic girdle and vertebral column depicted in dark gray; cartilage depicted in light gray. Numbers in circles correspond to features listed in the text.

FIG. 1. – Schéma de la ceinture pelvienne d'un urodele en vue postérieure (A) et d'un anoure en vue dorsale (B), montrant les différentes positions et contacts osseux de l'ilioïde dans les deux groupes. Notez que l'ilioïde est en position verticale chez l'urodele (A) et en position horizontale chez l'anoure (B). Les flèches grasses en pointillé montrent les orientations différentes de l'acétabulum; les flèches fines en pointillé l'amplitude de mouvement du fémur; la flèche blanche (en B) la surface de contact entre les ilios (suture interilioïde voir fig. 3A, C). Les os de la ceinture pelvienne et les vertèbres sont en gris, le cartilage en gris clair. Les numéros entourés correspondent aux caractères listés dans le texte.

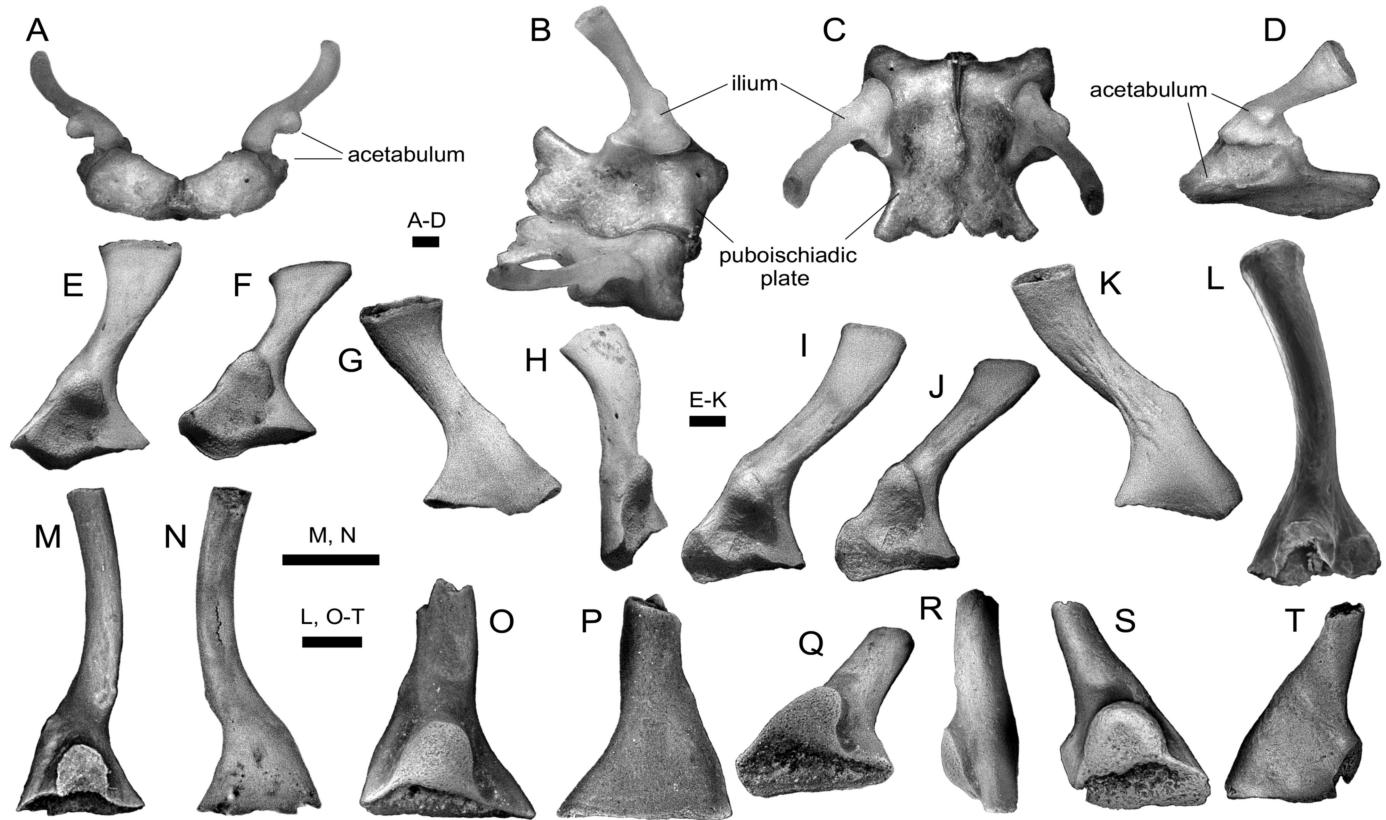


FIG. 2. – Pelvis and ilia of representative extant and fossil urodeles. A-D, Pelvic girdle of metamorphosed, adult *Ambystoma maculatum*, UALVP 14330 (Recent, eastern USA): (A) anterior view; (B) oblique mediiodorsal and slightly anterior view; (C) dorsal view, with anterior end to top of figure; and (D) left lateral view. Note how ilia are broadly separated by puboischiadic plate, are oriented with shaft directed posterodorsally and laterally, and iliac portions of acetabula are directed ventrolaterally. E-H, Left ilium of metamorphosed, adult *Ambystoma tigrinum*, TMP 90.07.217 (Recent, Alberta, Canada): (E) lateral view; (F) oblique ventrolateral view, showing shallowly concave ventral margin for contact with puboischiadic plate; (G) medial view, showing smooth medial surface of acetabular region; and (H) oblique anterolateral view, showing ramp-like dorsal portion of acetabulum. I-K, Left ilium of neotenic, adult *Ambystoma mexicanum*, TMP 2010.30.07 (Recent, captive raised): (I) lateral view; (J) oblique ventrolateral view; and (K) medial view. Note how shaft in this specimen is more elongate than in ilia of metamorphosed *A. maculatum* (D) and *A. tigrinum* (E). L, Left ilium of neotenic, adult *Necturus maculosus*, TMP 2010.30.12 (Recent, purchased specimen, presumably from eastern USA), lateral view. Note that acetabulum in this specimen resembles the figured Cretaceous salamander ilia (M, O, S) in having a subcircular outline, rather than the more oblong, elongate outline seen in the figured (D, E, J) *Ambystoma* ilia. M, N, Nearly complete left ilium (missing only dorsalmost end of shaft) of Urodela indet., NDGS 853 (late Maastrichtian, Hell Creek Formation, North Dakota, USA): (M) lateral view and (N) medial view. O-R, Incomplete left ilium (missing dorsal part of shaft) of Urodela indet., TMP 96.78.199 (late Campanian, Oldman Formation, Alberta, Canada): (O) lateral and slightly ventral view, to emphasize deeply concave ventral margin; (P) medial view, showing smooth medial surface of acetabular region; (Q) oblique lateroventral and slightly posterior view, showing deeply concave ventral margin of the bone, shallowly convex surface of acetabulum, and lack of a raised bony rim around acetabular surface; and (R) posterior view, showing ventrally and laterally directed acetabulum and shallowly convex surface of acetabulum. S, T, Incomplete right ilium (missing dorsal part of shaft and posteroventral corner of acetabular region) of Urodela indet., TMP 96.78.200 (late Campanian, Oldman Formation, Alberta, Canada): (S) lateral and slightly ventral view, to emphasize deeply concave ventral margin, and (T) medial view. Specimens at different magnifications; all scale bars equal 1 mm. Institutional abbreviations/ Abréviations institutionnelles: NDGS - North Dakota Geological Survey, Bismarck, USA; TMP - Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; and UALVP - University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada.

FIG. 2. – *Pelvis et ilions de taxons représentatifs d'urodèles fossiles et actuels. A-D, Ceinture pelvienne d'*Ambystoma maculatum* métamorphosé, adulte, UALVP 14330 (récent, USA) : (A) vue antérieure ; (B) vue oblique antéro-mésio-dorsale ; (C) vue dorsale ; et (D) vue latérale gauche. Notez les ilions, largement séparés par la plaque pubo-ischiatique, orientés avec une diaphyse dirigée postéro-dorso-latéralement ; et les portions iliatiques de l'acétabulum dirigées ventrolatéralement. E-H, ilion gauche d'*Ambystoma tigrinum* métamorphosé, adulte, TMP 90.07.217 (récent, Alberta, Canada) : (E) vue latérale ; vue oblique ventrolatérale montrant un bord ventral légèrement concave pour le contact avec la plaque pubo-ischiatique ; (G) vue médiale montrant la surface médiale lisse de la région acétabulaire ; et (H) vue oblique antérolatérale montrant une portion dorsale de l'acétabulum en forme de rampe. I-K, ilion gauche d'*Ambystoma mexicanum* néoténique adulte, TMP 2010.30.07 (récent, élevé en captivité) : (I) vue latérale ; (J) vue oblique ventrolatérale ; et (K) vue mésiale. Notez la diaphyse plus allongée ici que chez *A. maculatum* métamorphosé (D) et *A. tigrinum* (E). L, ilion gauche de *Necturus maculosus* néoténique adulte, TMP 2010.30.12 (récent, probablement des USA), en vue latérale. Notez l'acétabulum ressemblant à celui figuré (M, O, S) d'une salamandre crétacée par son contour sub-circulaire plutôt qu'oblong ou allongé comme c'est le cas chez *Ambystoma* (D, E, J). M, N, ilion gauche subcomplet (seule l'extrémité la plus dorsale de la diaphyse est absente) d'un urodele indéterminé, NDGS 853 (Maastrichtien terminal, Formation d'Hell Creek, Nord Dakota, USA) : vues latérale (M) et médiale (N). O-R, ilion gauche incomplet (la partie dorsale de la diaphyse manque) d'un urodele indet., TMP 96.78.199 (Campanien terminal, Formation de Oldman, Alberta, Canada) : (O) vue latéro-ventrale montrant le bord ventral très concave ; (P) vue mésiale montrant une surface médiale lisse de la région acétabulaire ; (Q) vue oblique latéro-ventro-postérieure montrant le bord ventral très concave de l'os, la surface légèrement convexe de l'acétabulum, et un bord osseux péri-acétabulaire non élevé ; et (R) vue postérieure montrant l'acétabulum dirigé ventro-latéralement avec une surface légèrement convexe. S, T, ilion droit incomplet (manque la partie dorsale de la diaphyse et la coin postéroventral de la région acétabulaire d'un urodele indet., TMP 96.78.200 (Campanien terminal, Formation Oldman, Alberta, Canada) : (S) vue latéro-ventrale montrant le bord ventral très concave, et (T) vue mésiale. Echelle 1 mm.*

important to bear in mind that there may also be other informative features that occur exclusively in those older taxa. For instance, whereas the maxillae of *Theatonius* and *Scotiophryne* bear reliable evidence that they belong to the anurans, even if they differ in certain features from living taxa, this is not the case with many ilia in our samples because they do not exhibit previously widely recognized anuran features, such as the dorsal tubercle or oblique groove.

Therefore, we focused our attention on those iliac features that clearly reflect the different anatomical positions and contacts of that bone in anurans and urodeles, and which could be used to differentiate ilia of the two groups. At the same time when we were studying the Utah

collections, we were also critically evaluating the affinities of the purported anuran *Nezpercius dodsoni*, which was described based on three enigmatic ilia from the Campanian of Montana, USA [Blob *et al.*, 2001]. For the latter project, we developed an extensive list of similarities and differences between urodele and anuran ilia –most of which had not previously been documented– and concluded that the *Nezpercius* ilia belonged to an indeterminate urodele, not an anuran [Gardner *et al.*, 2010]. Certain of those features proved especially useful for identifying ilia from the Utah localities and are summarized here. These features are indicated by Arabic numerals in the following text and by Arabic numerals within circles in figure 1, and can be seen

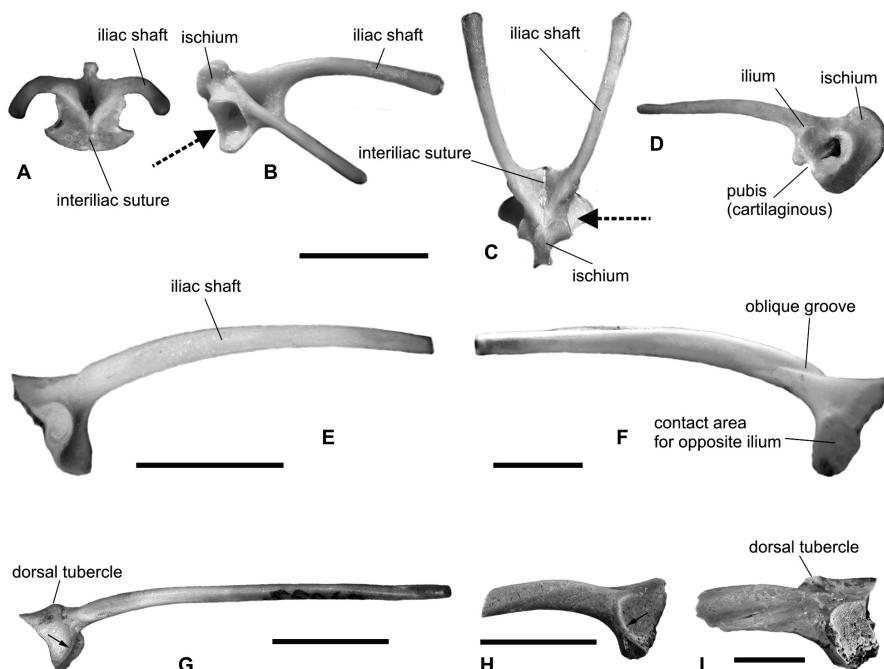


FIG. 3. – Pelvis and ilia of representative extant and fossil anurans. A-D, Pelvic girdle of *Ascaphus truei*, DP FNSP 6537 (Recent, northwestern USA), as an example of a generalized (i.e., primitive) anuran ilium that does not have a dorsal crest, a dorsal tubercle, or an oblique groove: (A) anterior view; (B) oblique right dorsolateral and slightly anterior view; (C) dorsal view, with anterior end to top of figure; and (D) left lateral view. Orientation of the acetabulum (B, C) marked by large, broken, black arrow. Note how the medial surfaces of the acetabular region of the ilia are in direct bony contact across the interiliac suture and how the iliac shafts are oriented horizontally. E-F, Right ilium from two different-sized individuals of *Pelobates fuscus* (Recent, Czech Republic), as examples of anuran ilia with an oblique groove: (E) lateral view of DP FNSP 6333; (F) medial view of DP FNSP 6433. G, Right ilium of *Bombina bombina*, UMMZ 152271 (Recent, Germany), as an example of an anuran ilium with a dorsal tubercle, lateral view. H, Incomplete left ilium (missing anterior part of shaft and damaged along posterior end) of Anura indet., UALVP 40184 (late Campanian, Dinosaur Park Formation, Alberta, Canada), lateral view. Small arrows (G, H) point at laterally-projecting, bony flange forming a distinct rim around ventral and anterior margins of acetabulum. I, Incomplete left ilium (missing anterior part of shaft and damaged along posterior end) of Anura indet., TMP 74.10.88 (late Campanian, Dinosaur Park Formation, Alberta, Canada), lateral view. For examples of similarly incomplete Upper Cretaceous ilia from Utah, see Rocek *et al.* [2010]. Specimens at different magnifications; all scale bars equal 5 mm (top scale bar is for A-D; other images have individual scale bars).

Institutional abbreviations / Abréviations institutionnelles. DP FNSP - Department of Palaeontology, Faculty of Natural Sciences, Prague, Czech Republic. TMP - Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; UMMZ - University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA; and UALVP - University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada.

FIG. 3. – *Pelvis et ilions de taxons représentatifs d'anoures fossiles et actuels*. A-D, ceinture pelvienne d'*Ascaphus truei*, DP FNSP 6537 (récent, USA) considéré comme un exemple d'ilion classique (archaïque) sans crête dorsal, tubercule dorsal ni sillon oblique : (A) vue antérieure ; (B) vue dorso-méso-antérieure ; (C) vue dorsale et (D) vue latérale gauche. L'orientation de l'acétabulum (B, C) est marquée par des flèches en pointillé gras. Notez les surfaces mésiales de la région acétabulaire en contact direct avec la suture inter-iliaque, et les diaphyses iliaques horizontales. E-F, Ilion droit de deux individus de taille différente de *Pelobates fuscus* (récent, Tchéquie), comme exemples d'ilions d'anoure à sillon oblique : (E) vue latérale de DP FNSP 6333 ; (F) vue mésiale de DP FNSP 6433. G, ilion droit de *Bombina bombina*, UMMZ 152271 (récent, Allemagne), comme exemple d'ilion d'anoure à tubercule dorsal, en vue latérale. La petite flèche montre le rebord latéral formant une marge distincte autour des régions ventrale et antérieure de l'acétabulum. H, ilion gauche incomplet (manque la partie antérieure de la diaphyse, et sa partie postérieure est endommagée) d'un anoure indet., UALVP 40184 (Campanien terminal, Formation « Dinosaur Park », Alberta, Canada), en vue latérale. Les petites flèches (G, H) montrent les bord osseux latéraux formant une marge distincte autour des bords ventral et antérieur de l'acétabulum. I, Ilion gauche incomplet (manque la partie antérieure de la diaphyse, et son extrémité postérieure est endommagée) d'un anoure indet., TMP 74.10.88 (Campanien terminal, Formation « Dinosaur Park », Alberta, Canada), en vue latérale. Pour des exemples d'ilions incomplets similaires du Crétacé supérieur de l'Utah, voir Rocek *et al.* [2010]. Echelle 5 mm (en haut pour A-D ; les autres ayant chacune une échelle).

in photographs of pelvic girdles and ilia of urodeles and anurans depicted in, respectively, figures 2 and 3.

The first three features are related to contacts of the ilium. The medial surface of the acetabular region is smooth in urodeles (feature 1; see fig. 2G, K, N, P, T), which occurs because the paired ilia are separated from one another by the broad, horizontal puboischiadic plate (figs. 1A, 2A-C). In anurans, however, the ilia are in direct bony contact ("interiliac suture" in fig. 3A, C) with one another across the medial surfaces of the acetabular region. This bony contact produces a triangular, interiliac "scar" on the medial surface of the acetabular region (fig. 3F). In extreme cases, such as *Palaeobatrachus*, the interiliac "scar" may cover much of the inner surface of the acetabular region and that portion of the bone may also be expanded medially. Another feature, closely related to the previous, is that the medial surface of the acetabular region often is broadly convex in urodele ilia (feature 2; see fig. 2G, K, N, P, R, T). In contrast, the medial surface of the acetabular region is flat in anuran ilia (fig. 3F), because that is where the left and right ilia contact one another. Because urodele ilia are in a more or less vertical position and broadly contact the puboischiadic plate along its dorsolateral margins, the basal or ventral surface of the ilium tends to be broader mediolaterally relative to the condition in anurans and because contact between the ilium and puboischiadic plate in urodeles typically involves a substantial cartilaginous component, the ventral surface of the urodele ilium often is concave from side-to-side (feature 3; see fig. 2F, I, J, M, O, and especially Q and S). By contrast, in anurans the homologous surface is solid and flat, because that is where the ilium is in firm bony contact with the ischium and, if ossified, the pubis.

There also are several differences between the acetabula of anurans and urodeles (see fig. 3B-I versus fig. 2A, D-F, H-J, L, M, O, Q-S). The acetabulum in anurans is oriented laterally (feature 4), whereas in urodeles it is oriented ventrolaterally. The acetabular surface (feature 5) in anurans is deeply concave and bowl-shaped (i.e., concave both parallel and perpendicular to the long axis of the shaft) and at least partially sunk into the lateral surface of the bone. In urodeles, the acetabular surface is never bowl-shaped. Instead, it typically is shallowly concave or sinuous (i.e., saddle-shaped) parallel to the long axis or even nearly flat. As a consequence of how features 4 and 5 are expressed in urodeles, the acetabulum in urodeles tends to be somewhat ramp-like, with its dorsal portion (i.e., closest to base of shaft) projecting laterally (feature 6), whereas in anurans the homologous, anterodorsal portion of the acetabulum (i.e., closest to base of shaft) remains relatively low. Finally, the acetabular margin (feature 7) in anurans is prominently developed as a laterally projecting, bony flange that forms a rim around the acetabulum, especially around the ventral and anterior margins (marked by an arrow in fig. 3G, H), whereas in urodeles the margin is, at best, a low ridge that does not extend any significant distance laterally beyond the articular surface. In many of the Cretaceous urodele ilia we examined (e.g., fig. 2M-T), all of the above-listed acetabular features tend to be even more prominently developed, as follows: the entire acetabulum (not just the dorsal portion) is developed as raised, ramp-like bony pedestal (feature 6), with an acetabular surface that faces ventrolaterally (feature 4) and is flat or even convex

(feature 5) and has no appreciable bony rim around its margins (feature 7). Another curious aspect of many of the North American Cretaceous urodele ilia we examined is that the lateral outline of the acetabulum is subcircular (i.e., anuran-like), whereas in extant urodeles the acetabular outline is more variable, ranging from subcircular to more elongate and oblong or hourglass-shaped in outline (see fig. 2L versus E, I). The same suite of acetabular features are evident in other figured Cretaceous urodele ilia from Middle Asia [Nessov, 1981: Pl. 8, Figs. 6, 14, 15; Pl. 9, Figs. 12, 13] and the North American Western Interior [Gardner et al., 2010: Fig. 5U, V, Y, A] and a probable pro-urodele (*?Marmoroperpeton*) ilium from the Middle Jurassic of Scotland [Evans and Waldman, 1996, Fig. 1B].

Differences between the acetabula of urodeles and anurans are probably due to two main factors. First, there are differences in the relative contributions of the pelvic bones to the acetabulum. In urodeles, much or all of the bony portion of the acetabulum is formed by the ilium, because in many taxa the pubis and ischium components of the puboischiadic plate are largely or exclusively cartilaginous. In anurans, the ischium is always ossified and the bony part of the acetabulum is shared between the ischium and ilium. Second, there are differences in locomotor capabilities, with urodeles retaining a more generalized tetrapod style of walking versus anurans being specialized for hindlimb jumping. Consequently, in urodeles the shape and position of the acetabulum prevent dorsal movements of the thigh exceeding the horizontal plane, whereas in anurans a greater range of motion is needed to permit protraction of the thigh anteriorly to the body flanks when in a crouching position during the preparatory phase of the jump, as well as extensions of the hindlegs posteriorly during the jump.

Each of the above-described features is subject to some variation, the full extent of which is unknown for Mesozoic anurans and urodeles. For instance, the medial surface of the acetabular region in some urodele ilia may be flat, even though those bones are widely separated from each other. Although any one feature alone may not be sufficient, when used in combination the features reported here can be useful for differentiating anuran or urodele ilia, even when those bones are recovered as isolated specimens missing much of their shaft.

CONCLUSIONS

Fossil urodele and anuran ilia typically are recovered as isolated bones that are missing much of the shaft. When preserved in this manner, ilia of the two groups are superficially similar. When used in combination, the following set of features can be useful for differentiating ilia of urodeles and anurans: medial surface of acetabular region (1) smooth in urodeles versus bears triangular interiliac scar in anurans and (2) typically convex in urodeles versus flat in anurans; (3) contact surface of the ilium with the puboischiadic plate typically mediolaterally broad and concave in urodeles versus narrower and flat in anurans; (4) acetabulum faces ventrolaterally in urodeles versus laterally in anurans; (5) acetabulum shallowly concave, saddle-shaped, or nearly flat, often somewhat elongate (but less so in known Cretaceous specimens), and dorsal portion not especially sunk into bone in urodeles

versus deeply concave, bowl-shaped, and at least partially sunk across its entire width into bone in anurans; (6) portion of acetabulum closest to base of shaft often laterally projecting and ramp-like in urodeles versus not laterally projecting in anurans; and (7) acetabular margin at best a weak, bony ridge in urodeles versus a prominent, laterally-projecting, bony flange in anurans. The presence of a dorsal tubercle or an oblique groove (neither feature occurs in

extant or fossil urodeles) also are potentially diagnostic for anuran ilia, but their utility is compromised by the fact that many anurans lack both of those features.

Acknowledgements. – This paper greatly benefited from reviews by Anne-lise Folie and Andrew Milner who provided helpful comments and suggestions. The research was funded by the Ministry of Education, Youth and Sports of the Czech Republic grant No. ME08066 through the American Science Information Center, Prague.

References

- BLOB R.W., CARRANO M.T., ROGERS R.R., FORSTER C.A. & ESPINOZA N.R. (2001). – A new fossil frog from the Upper Cretaceous Judith River Formation of Montana. – *J. Vertebr. Paleontol.*, **21**, 190-194.
- CURTIS K. & PADIAN K. (1999). – An Early Jurassic microvertebrate fauna from the Kayenta Formation of northeastern Arizona: Microfaunal change across the Triassic-Jurassic boundary. – *PalaeoBios*, **19**, 19-37.
- ESTES R. (1964). – Fossil vertebrates from the Late Cretaceous Lance Formation, eastern Wyoming. – *Univ. Calif. Publ. Geol. Sci.*, **49**, 1-180.
- ESTES R. (1969). – A new fossil discoglossid frog from Montana and Wyoming. – *Breviora*, **328**, 1-7.
- ESTES R. & SANCHÍZ B. (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. – *J. Vertebr. Paleontol.*, **2**, 9-20.
- EVANS E. & MILNER A.R. (1993). – Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America. – *J. Vertebr. Paleontol.*, **13**, 24-30.
- EVANS S.E. & MILNER A.R. (1994). – Middle Jurassic microvertebrate assemblages from the British Isles. In: N.C. FRASER & H.-D. SUES, Eds., *In the shadow of the dinosaurs: Early Mesozoic tetrapods*. – Cambridge University Press, New York, 303-321.
- EVANS S.E. & WALDMAN M. (1996). – Small reptiles and amphibians from the Middle Jurassic of Skye, Scotland. – *Mus. N. Arizona Bull.*, **60**, 219-226.
- EVANS S.E., MILNER A.R. & WERNER C. (1996). – Sirenid salamanders and a gymnophionan amphibian from the Cretaceous of the Sudan. – *Palaeontology*, **39**, 77-95.
- FOX R.C. (1976). – An edentulous frog (*Theattonius lancensis*, new genus and species) from the Upper Cretaceous Lance Formation of Wyoming. – *Can. J. Earth. Sci.*, **13**, 1486-1490.
- GAO K-Q. & SHUBIN N.H. (2003). – Earliest known crown-group salamanders. – *Nature*, **422**, 424-428.
- GARDNER J.D. (2008). – New information on frogs (Lissamphibia: Anura) from the Lance Formation (late Maastrichtian) and Bug Creek Anthills (late Maastrichtian and early Paleocene), Hell Creek Formation, USA. In: J.T. SANKEY & S. BASZIO, Eds., *Vertebrate microfossil assemblages: Their role in paleoecology and paleobiogeography*. – Indiana University Press, Bloomington, 219-249.
- GARDNER J.D., EATON J.G. & CIFELLI R.L. (2013). – Preliminary report on salamanders (Lissamphibia; Caudata) from the Late Cretaceous (late Cenomanian-late Campanian) of southern Utah, U.S.A. In: A. TITUS and M.A. LOWEN, Eds., *The Late Cretaceous of southern Utah: Critical window into end Mesozoic ecosystems*. – Indiana University Press, Bloomington, (in press).
- GARDNER J., ROČEK Z., PRÍKRYL T., EATON J., BLOB R.W. & SANKEY J.T. (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. – *J. Vertebr. Paleontol.*, **30**, 1684-1696.
- GILLIS G.B. & BIWENER A.A. (2000). – Hindlimb extensor muscle function during jumping and swimming in the toad (*Bufo marinus*). – *J. Exp. Biol.*, **203**, 3547-3563.
- HENRICI A.C. (1998). – A new pipoid anuran from the Late Jurassic Morrison Formation at Dinosaur National Monument, Utah. – *J. Vertebr. Paleontol.*, **18**, 321-332.
- JENKINS F.A. JR. & WALSH D.M. (1993). – An Early Jurassic caecilian with limbs. – *Nature*, **365**, 246-250.
- JENKINS F.A., WALSH D.M. & CARROLL R.L. (2007). – Anatomy of *Eocaecilia micropodia*, a limbed caecilian of the Early Jurassic. – *Bull. Mus. Comp. Zool.*, **158**, 285-366.
- MARJANOVIC D. & LAURIN M. (2007). – Fossils, molecules, divergence times, and the origin of lissamphibians. – *Syst. Biol.*, **56**, 369-388.
- MILNER A.R. (2000). – Mesozoic and Tertiary Caudata and Albanerpetontidae. In: H. HEATWOLE & R.L. CARROLL, Eds., *Amphibian biology*. Volume 4. *Paleontology: The evolutionary history of amphibians*. – Surrey Beatty and Sons, Chipping Norton, 1412-1444.
- NESSOV L.A. (1981). – “Cretaceous salamanders and frogs of Kyzylkum Desert”. – *Trudy Zoologicheskogo Instituta, Akademiya Nauk SSSR*, **101**, 57-88 and 12 pls. [In Russian.]
- NEVO E. & ESTES R. (1969). – *Ramonellus longispinus*, an Early Cretaceous Salamander from Israel. – *Copeia*, **1969**, 540-547.
- PAWLEY K. (2007). – The postcranial skeleton of *Trimerorhachis insignis* COPE, 1878 (Temnospondyli: Trimerorhachidae): a plesiomorphic temnospondyl from the Lower Permian of North America. – *J. Paleont.*, **81**, 873-894.
- PAWLEY K. & WARREN A. (2006). – The appendicular skeleton of *Eryops megacephalus* COPE, 1877 (Temnospondyli: Eryopoidea) from the Lower Permian of North America. – *J. Paleont.*, **80**, 561-580.
- PRÍKRYL T., AERTS P., HAVELKOVÁ P., HERREL A. & ROČEK Z. (2009). – Pelvic and thigh musculature in frogs (Anura) and origin of anuran jumping locomotion. – *J. Anat.*, **214**, 100-139.
- RAGE J.-C. (1974). – Les batraciens des gisements quaternaires Européens. Determination ostéologique. – *Bull. mens. Soc. Linn. Lyon*, **43**, 276-289.
- RAGE J.-C., MARSHALL L.G. & GAYET M. (1993). – Enigmatic Caudata (Amphibia) from the Upper Cretaceous of Gondwana. – *Geobios*, **26**, 515-519.
- RAGE J.-C. & ROČEK Z. (1989). – Redescription of *Triadobatrachus massinoti* (PIVETEAU, 1936) an anuran amphibian from the Early Triassic. – *Palaeontographica Abt. A*, **206**, 1-16.
- ROČEK Z., EATON J., GARDNER J. & PRÍKRYL T. (2010). – Evolution of anuran assemblages in the Late Cretaceous of Utah. – *Palaeobiodiv. Palaeoenviron.*, **90**, 341-393.
- ROČKOVA H. & ROČEK Z. (2005). – Development of the pelvis and posterior part of the vertebral column in the Anura. – *J. Anat.*, **206**, 17-35.
- SCHOCH R.R. & MILNER A.R. (2004). – Structure and implications of theories on the origin of lissamphibians. In: G. ARRATIA, M.V.H. WILSON & R. CLOUTIER, Eds., *Recent advances in the origin and early radiations of vertebrates*. – Dr. Friedrich Pfeil, Munich, 345-377.
- SHUBIN N.H. & JENKINS F.A. Jr. (1995). – An Early Jurassic jumping frog. – *Nature*, **377**, 49-52.
- VAN DIJK DIJK E. (2002). – Longitudinal sliding articulations in pipid frogs. – *South African J. Sci.*, **98**, 555-556.