Anuran Ilia from the Upper Cretaceous of Utah – Diversity and Stratigraphic Patterns

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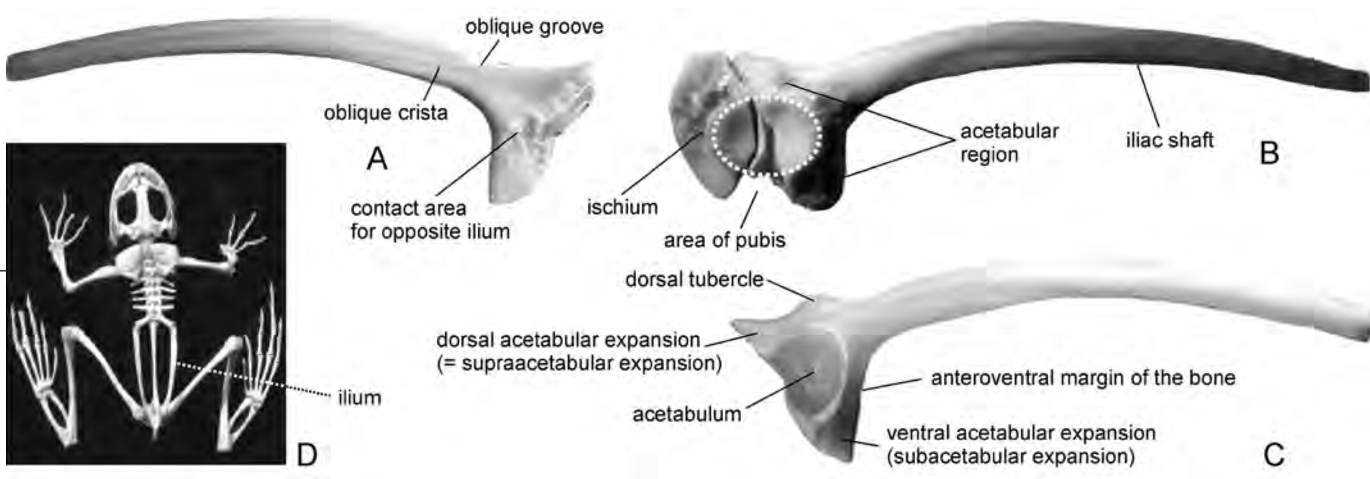
Zbyněk Roček, James D. Gardner, Jeffrey G. Eaton, and Tomáš Přikryl

THANKS TO THEIR RELATIVELY ROBUST BUILD AND DISTINCTIVE structure, isolated ilia are among the most commonly recovered anuran bones from fossil micovertebrate sites. Across the spectrum of known anurans, there is considerable variation in features of the ilium. With some caveats, these features may be useful for assigning anuran ilia to biological taxa or, more conservatively, for estimating taxonomic diversities in fossil assemblages. A stratigraphically extensive sequence of 37 microvertebrate sites, ranging in age from the middle? Cenomanian–late Campanian (i.e., an interval of about 25 million years), in southwestern Utah, U.S.A., has yielded a relatively large sample of about 180 anuran ilia. Three major groups of ilia can be identified in the Utah sequence: those with an oblique groove on the medial surface, those with a dorsal tubercle, and those with neither structure. Within each group, specimens further can be subdivided into morphotypes based on other features (e.g., outline and relative size of acetabulum; extent and path of oblique groove; shape and position of dorsal tubercle). Some of the iliac morphotypes are discrete and easily recognizable, whereas others are less distinct. Certain of the iliac morphotypes (especially the more distinct ones) undoubtedly represent biological species, and the occurrence in many of the sampled localities and horizons of multiple morphotypes implies the presence in those areas of at least moderately diverse anuran assemblages. Only one iliac morphotype with an oblique groove can be assigned to a named genus, *Scotiophryne*, and this extends the temporal range for the genus back from the late Maastrichtian into the late Campanian. Although anuran ilia are not useful for stratigraphic correlations within the Utah sequence, several interesting patterns are evident; for example, the rarity both of specimens with a dorsal tubercle in the early–middle Santonian and middle Campanian and of specimens with an oblique groove in the late Santonian or early Campanian. The Utah ilia are typical for Mesozoic anurans in that none has a dorsal crest and only a minority have a dorsal tubercle; this contrasts with the situation in the Cenozoic, when most anurans have one or both of those iliac structures.

INTRODUCTION

Anurans (frogs) are the most diverse and widespread group of living amphibians, consisting of about 5400 extant species and occurring on every continent except Antarctica (Bossuyt and Roelants, 2009). Anurans also were a characteristic component of Late Cretaceous ecosystems in the North American Western Interior, judging by how common their remains are in nonmarine deposits in that region (Estes, 1964; Sahni, 1972; Estes and Sanchíz, 1982; Brinkman, 1990; Gardner, 2005; Roček et al., 2010). In contrast to the situation elsewhere in the Western Interior, where Late Cretaceous anurans are known from more limited stratigraphic intervals (e.g., Campanian and Maastrichtian of Wyoming and Montana; Santonian and Campanian of Alberta, Canada), in Utah anurans are known from every stage of the Late Cretaceous (Cifelli et al., 1999a, 1999b; Roček et al., 2010). Long-term quarrying by one of us (J.G.E.) of Upper Cretaceous strata in southwestern Utah, and subsequent processing of the rock by wet screen washing, has recovered more than 700 isolated anuran bones from 37 microvertebrate localities of middle? Cenomanian–late Campanian age. This interval is about 25 million years, according to the timescale of Ogg, Agterberg, and Gradstein (2004), and the Utah sequence represents one of the most stratigraphically extensive records of Late Cretaceous anurans from anywhere in the world. Recently we presented a preliminary report on this collection (Roček et al., 2010). Ilia are the most commonly recovered bones and account for about one quarter of the total collection of anuran bones from southwestern Utah. Historically, ilia have been important for identifying fossil anuran species. To cite two examples: first, in the most recent compendium of fossil anurans, about 40% of the listed species had the ilium as their holotype (Sanchiz, 1998:6); and second, four of the five anuran species recognized by Holman (2003) from the North American Late Cretaceous had the ilium as their holotype. In the past decade, justifiable concerns have been raised about the uncritical use of iliac features to differentiate among anuran species (Jones, Evans, and Ruth, 2002; Bever, 2005; Gardner, 2008). Nevertheless, it is evident that across the spectrum of extant and fossil anurans that



12.1. Principal morphological features of the anuran ilium. (A) Right ilium with an oblique groove (group 1 ilia) in medial view, *Pelobates fuscus* (Recent). (B) Pelvis, in right lateral view and with outlines of acetabulum marked by white dotted line, *Pelobates fuscus* (Recent). (C) Right ilium with a dorsal tubercle (group 2 ilia) in lateral view, *Bufo calamita* (Recent). (D) Articulated anuran skeleton showing location of ilium, in dorsal view, *Rana ridibunda* (Recent).

there is considerable variation in the structure of this bone (Lynch, 1971:figs. 36–40; Trueb, 1973:fig. 2–11; Tyler, 1976:fig. 3) and that some of those features are phylogenetically and taxonomically significant. Although it is no longer accepted practice to erect fossil anuran species solely on the basis of subtle differences in iliac structure, especially when known from only one isolated bone, anuran ilia remain useful for estimating or gauging taxonomic diversities in fossil assemblages, especially ones in which isolated bones are the only or a major source of information (Henrici, 1998; Prasad and Rage, 2004; Gardner, 2008). As a follow-up to our 2010 article, here we present more detailed identifications, descriptions, and comparisons of anuran iliac morphotypes from the Upper Cretaceous (middle? Cenomanian–upper Campanian) of southwestern Utah, and we evaluate whether these morphotypes can be used for stratigraphic correlations.

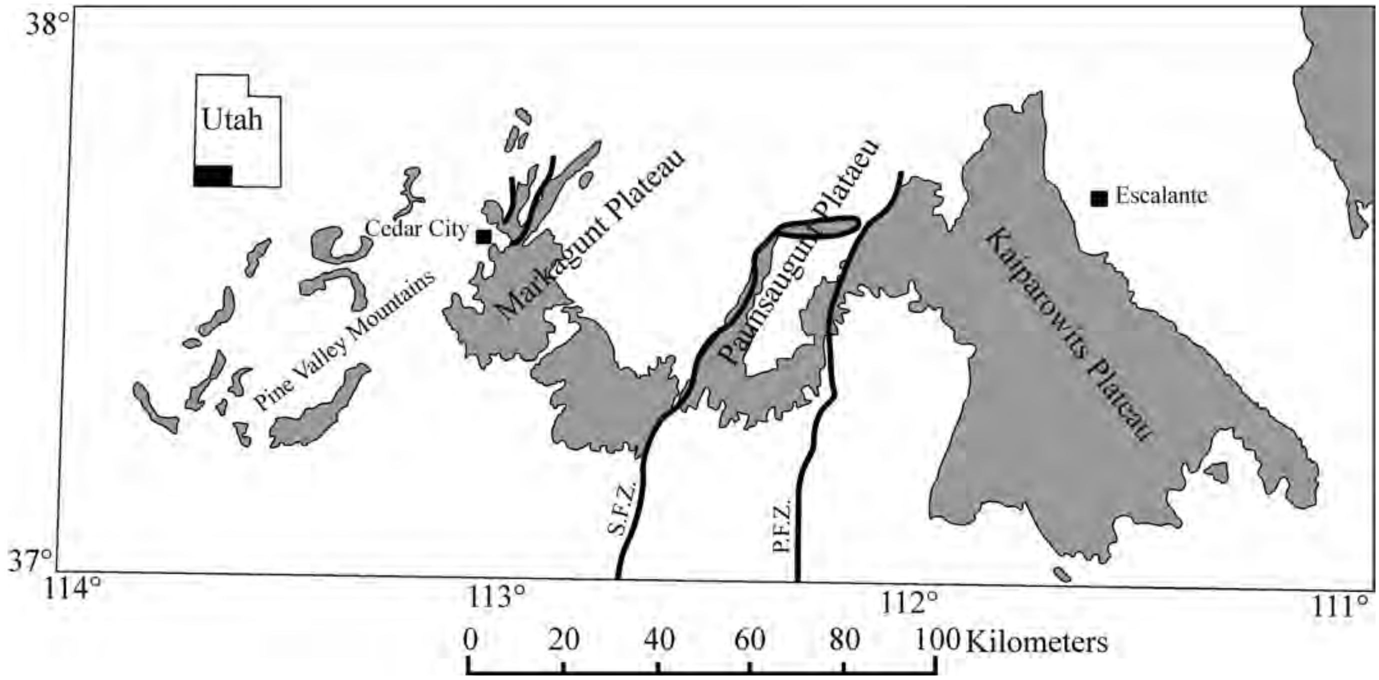
All the ilia collected from southwestern Utah and used for this study are curated in the vertebrate paleontological collections of the Utah Museum of Natural History (UMNH) in Salt Lake City, Utah. The complete list of those specimens and their localities may be found in Roček et al. (2010). Examples of extant anuran ilia and important osteological features are shown in Fig. 12.1.

GEOLOGICAL SETTING

A thick succession of Upper Cretaceous sediments was deposited in the Sevier foreland basin of Utah. The anuran specimens reported here are from three adjacent plateaus in southwestern Utah (Figs. 12.2, 12.3). On these plateaus, the Upper Cretaceous sequence unconformably overlies Jurassic rocks and in turn is overlain unconformably by lower Cenozoic rocks. The youngest unit in the sequence, the Kaiparowits Formation, is found only on the Kaiparowits Plateau. With the exception of the Kaiparowits Formation, the same units found on the Kaiparowits Plateau are found on the next plateau to the west, the Paunsaugunt Plateau. Units that are time equivalent to those on the Paunsaugunt Plateau are present on the westernmost Markagunt Plateau, but on the latter, the lithology is different enough that it has been difficult to use the Paunsaugunt Plateau terminology on the Markagunt sequence. Moore et al. (2004) suggested using the "Formation of Cedar Canyon" for rocks possibly equivalent to the upper part of the Straight Cliffs Formation and the Wahweap Formation until a more secure basis for lithologic correlation has been established. The correlation used for the Markagunt Plateau has been based on mammalian faunas (Eaton, 2006) and radiometric dates (Eaton, Maldonado, and McIntosh, 1999; Eaton et al., 2001). Further details about the anuran-bearing localities and formations can be found in Roček et al. (2010).

GENERAL STRUCTURE OF ANURAN ILIA

The anuran ilium consists of two portions: an expanded acetabular portion and an anteriorly elongate shaft (Fig. 12.1). Compared to the more primitive tetrapod condition, anuran ilia are distinctive in the following ways: (1) the left and right ilia articulate with one another along the medial surface of the acetabular region (primitively the ilia are separated by the ischia and pubes); (2) the ilia and other bones of the pelvic girdle are rotated posteriorward about 90°, so the iliac shaft lies in the horizontal plane (primitively in a more vertical plane); and (3) the iliac shaft is greatly elongate (primitively



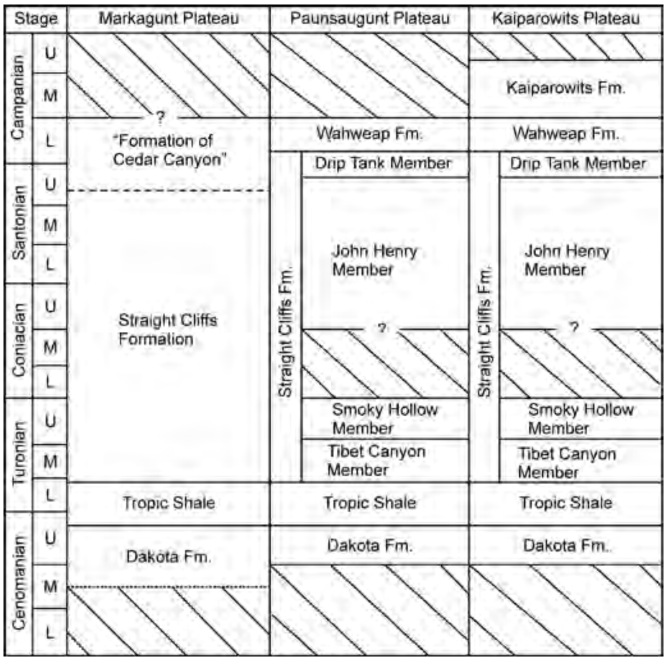
12.2. Location map showing Cretaceous outcrops in southwestern Utah from which anuran fossils were recovered. Most of the anuran specimens were recovered from Cedar Canyon on the west side of the Markagunt Plateau, from Bryce Canyon National Park area on the east side of the Paunsaugunt Plateau, and from the Kaiparowits Plateau, which is within the Grand Staircase–Escalante National Monument. P.F.Z., Paunsaugunt fault zone; S.F.Z., Sevier fault zone.

it is relatively shorter). Thanks to their distinctive structure, anuran ilia can be easily recognized in fossil deposits, even when they are isolated and broken. This is fortunate, because all of the 183 Upper Cretaceous ilia collected to date from southwestern Utah are isolated and incomplete, with each missing part of the shaft and some missing portions of the acetabular region. For a more detailed description of anuran ilia and features that are useful for identifying that bone, see Gardner et al. (2010, and references therein).

The acetabular portion of the anuran ilium articulates by immovable sutures with two other pelvic bones – ventrally with the pubis, which typically is cartilaginous and thus not capable of fossilization (the pubis is ossified in some anurans; e.g., Pipidae) and posteriorly with the ischium. On its lateral surface, the acetabular portion bears the anterior part of a bowl-like cavity, termed the acetabulum, for articulation with the femur; posteriorly, the acetabulum extends onto the ischium. The shape, size, prominence, and position of the acetabulum may differ considerably among species. The posterior part of the acetabular region of the ilium may be strongly extended both dorsally and ventrally, resulting in a fan-like or triangular shape. As a result, when viewed in lateral aspect, a considerable portion of the bone may be visible below the acetabulum (termed the ventral acetabular or subacetabular expansion) and above the acetabulum (termed the dorsal acetabular or supraacetabular expansion). The medial surface of the acetabular portion usually bears a rugosity that is the contact area for attachment with the ilium on the opposite side (Fig. 12.1A). The iliac shaft is anteriorly elongate, and moderately convex dorsally and, to a lesser extent, also laterally. Unlike in more advanced Cenozoic anurans, most Mesozoic taxa have an iliac shaft that is suboval in cross section and lacks a longitudinal dorsal crest.

The transition between the acetabular region and the iliac shaft may be marked by a depression between the dorsal margins of the supraacetabular expansion and the iliac shaft. The dorsal margin of the supra-acetabular expansion slants anteroventrally and continues onto the medial surface of the shaft, thus producing a more or less prominent crista (Fig. 12.1A). As a result, an oblique groove (called the spiral groove by some authors) that is delimited posteroventrally by that crista crosses the dorsal margin of the ilium and extends onto the medial surface, sometimes extending as far as the lower margin of the shaft. On the lateral surface of the ilium, the oblique groove may begin as a horizontal depression above the acetabulum. The oblique groove is a typical feature of many Mesozoic anurans.

In many extant anurans, the dorsal surface of the acetabular portion bears a raised outgrowth called the dorsal tubercle. Although its base may be anteroposteriorly elongate, the top of this tubercle is uniformly located at the level of the anterior margin of the acetabulum. The dorsal tubercle



12.3. Generalized Upper Cretaceous stratigraphic units on the Markagunt, Paunsaugunt, and Kaiparowits Plateaus in southwestern Utah. Diagonal lines indicate missing strata.

is the area of origin for three muscles that are functionally important for the preparatory (crouching) and initial phases of jumping. However, the same muscles also occur in those taxa that lack a dorsal tubercle. In such cases, these muscles originate on the lateral surface of the ilium (Přikryl et al., 2009). It is not known whether the shift in the origin of these muscles is associated with differences in jumping capabilities. It is, however, important to emphasize that ilia with a dorsal tubercle never have an oblique groove crossing their dorsal margin onto the medial surface, so their medial surface is mostly smooth. Some anurans, including some Mesozoic taxa, lack both an oblique groove and a dorsal tubercle on their ilia.

MORPHOTYPIC DIVERSITY OF ILIA IN THE UPPER CRETACEOUS OF SOUTHWESTERN UTAH

To make comparisons easier and try to make some sense of the diverse array of ilia, we created an informal classification based on the morphotypes listed below. Such morphotypes can be used to make limited inferences about the taxonomic diversity of fossil assemblages, without erecting potentially redundant biological taxa on the basis of isolated bones from different parts of the skeleton that may be difficult to associate with each other. (For a similar approach using isolated Upper Cretaceous fish elements, see Brinkman and Neuman, 2002; Brinkman et al., this volume, Chapter 10.) Three principal groups of anuran ilia can be recognized easily in the Utah samples: those with an oblique groove (group 1), those with a dorsal tubercle (group 2), and those with neither structure (group 3). Within each group, many morphotypes could be recognized, mostly on the basis of subtle differences. The main challenge we encountered in identifying and defining those morphotypes was how to handle variation within each of the three principal groups. Especially in the first group, morphotypes that initially seemed to be clearly defined often were bridged, as sample sizes increased, by specimens with intermediate features. For instance, the oblique groove in some ilia is delimited by sharp, prominent cristae and in others by faint, rounded ridges; however, there is a series of specimens that are intermediate between those two extremes. That pattern could suggest extensive or broad individual variation. However, other specimens exhibit minimal or no obvious variation. For example, two group 2 specimens (UMNH VP 13482 and 13494; Fig. 12.9, upper part of middle column) from the Santonian or Campanian Paul's locality in Cedar Canyon (Roček et al., 2010) are right ilia (and therefore from different individuals) that are identical even in minor details.

The first group consists of ilia with an oblique groove but no dorsal tubercle. The oblique groove originates on the lateral surface of the bone, above the dorsal margin of the acetabulum, then it crosses over the dorsal edge of the bone along a shallow depression between the acetabular region and iliac shaft, and continues onto the medial surface of the posterior portion of the shaft where it may extend as far as the ventral margin of the shaft. In *Pelobates* (Fig. 12.1A), *Scaphiopus*, and to a certain degree also *Megophrys*, which are the only extant frogs in which the oblique groove is known, the portion of the groove on the medial surface of the shaft is the area of origin of muscles important for locomotion (Přikryl at al., 2009). The second group consists of ilia that have a dorsal tubercle but no oblique groove. The dorsal tubercle is located on the upper margin of the ilium at the level of the anterior margin of the acetabulum. In extant anurans, the dorsal tubercle serves as the area of origin for muscles responsible for extension and flexion of the hind limb (Přikryl at al., 2009). It should be noted that the earliest anurans (*Prosalirus*; Early Jurassic) lacked the dorsal tubercle, and that in the Early Triassic proanurans (*Triadobatrachus* and *Czatkobatrachus*) there is a similar, prominent tubercle, but it is located more anteriorly relative to the acetabulum. The third group consists of ilia that have neither an oblique groove nor a dorsal tubercle.

In the following accounts, each morphotype is briefly diagnosed, followed by information on stratigraphic occurrences and a list of voucher specimens. To allow for better comparisons, key characters of all morphotypes are

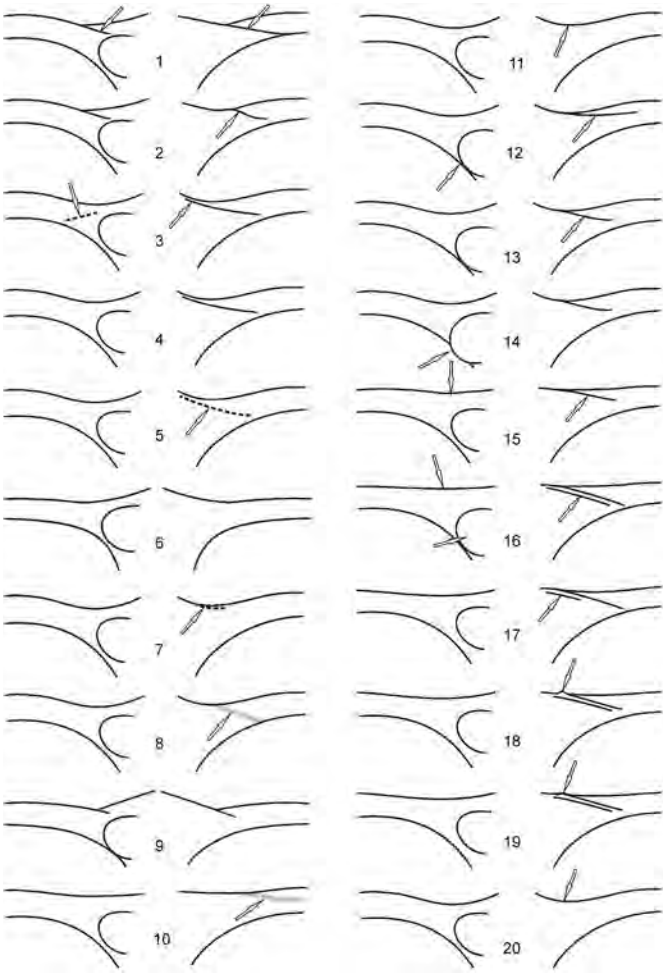


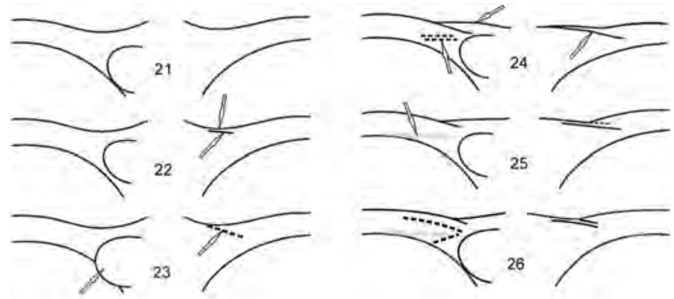
Figure 12.4. Semidiagrammatic line drawings of the first 20 of 26 iliac morphotypes with an oblique groove (group 1 ilia) left ilium in lateral (left) and medial (right) views (continues onto Fig. 12.5. Morphotype numbers are the same as in the text. Key characters are marked by arrows. Full lines within the outlines of the bone denote crests, broken lines denote rounded ridges, gray strips denote a broad shallow groove. See the text for diagnoses and voucher specimens.

illustrated in Figs. 12.4–12.7, and photographs of most of the voucher specimens are presented in approximate stratigraphic sequence in Figs. 12.8–12.11.

GROUP 1: ILIA WITH AN OBLIQUE GROOVE (FIGS. 12.4–12.5; FIGS. 12.8–12.11, LEFT COLUMN)

Morphotype 1

Description The dorsal margin of the pars ascendens extends anteriorly as a distinct, oblique crista onto the medial surface of the ilium and reaches the ventral margin of the shaft; the iliac shaft is markedly convex dorsally, and consequently there is a distinct concavity on the dorsal margin of the bone in lateral view; an oblique groove passes the dorsal



12.5. Semidiagrammatic line drawings of the last six of 26 iliac morphotypes with an oblique groove (group 1 ilia) left ilium in lateral (left) and medial (right) views (continued from Fig. 12.4).

margin of the bone from its lateral surface onto the medial surface on the bottom of this concavity; the groove begins in the horizontal depression above the acetabulum and terminates on the lower margin of the iliac shaft; acetabulum not extending beyond the anteroventral outline of the bone.

Distribution Dakota Formation, middle? Cenomanian: UMNH VP 12936.

Morphotype 2

Description Similar to 1, except the dorsal margin of the pars ascendens continues anteroventrally onto the medial surface of the bone as a prominent but gradually lowering osseous lamina that disappears before reaching the lower margin of the ilia shaft; the lamina may extend in an obtuse point and may be paralleled by a shallow groove posteriorly; the medial surface of the acetabular portion is depressed; acetabulum does not reach the level of the anteroventral outline of the bone. These features correspond to those given by Estes (1969:fig. 1c, d) in his illustration of the holotype ilium of *Scotiophryne pustulosa*.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 18182, 18263, 18283, 18338, perhaps also UMNH VP 18287, 18288, 18140 (the last may be from a juvenile).

Morphotype 3

Description Similar to 1, except the pars ascendens is broad and widely rounded on its dorsal margin, consequently the crista delimiting the oblique groove is shifted onto the medial surface of the bone; the oblique groove is wide and continues onto the medial surface of the shaft, consequently the medial surface of the shaft is horizontally concave or flat; the oblique groove originates on the dorsal margin of the bone, not on its lateral surface; on the lateral surface, a faint oblique mound or groove runs anteroventrally from the supraacetabular region.

Distribution Straight Cliffs Formation, John Henry Member, Coniacian: UMNH VP 19371. Kaiparowits Formation, upper Campanian: UMNH VP 19311.

Morphotype 4

Description Similar to 3, except the lateral surface of the bone is uniformly convex and smooth, because the oblique groove is confined to the medial surface.

Distribution Straight Cliffs Formation, John Henry Member, upper Santonian: UMNH VP 18480.

Morphotype 5

Description Similar to 4, except instead of the crista delimiting the oblique groove posteriorly there is only a faint rounded ridge.

Distribution Straight Cliffs Formation, Smoky Hollow Member, Turonian: UMNH VP 18367. Straight Cliffs Formation, John Henry Member, upper Santonian: UMNH VP 18476. Wahweap Formation, lower–middle Campanian: UMNH VP 18106.

Morphotype 6

Description Similar to 5, except the margins of the acetabular region are markedly divergent from the longitudinal axis of the bone; the shaft is slender; the anteroventral margin of the acetabulum is markedly prominent; the medial surface of the acetabular region is concave, consequently this part of the bone is very thin.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 18104.

Morphotype 7

Description Similar to 5, except the dorsal margin of the pars ascendens joins the dorsal margin of the shaft by a short crista shifted medially, which, however, does not continue onto the medial surface; although this gives an impression that there is a broad oblique groove crossing the dorsal surface of the bone, it does not continue onto either the lateral or medial surfaces.

Distribution Straight Cliffs Formation, John Henry Member, lower Santonian: UMNH VP 18299. Straight Cliffs Formation, John Henry Member, upper Santonian: UMNH VP 18484, 18506.

Morphotype 8

Description Similar to 1, except the oblique groove originates on the dorsal surface of the bone and continues as a broad shallow depression toward the lower margin of the bone.

Distribution Straight Cliffs Formation, John Henry Member, lower Santonian: UMNH VP 18544 (note: spine projecting ventrally from anteroventral margin of the acetabulum is considered a malformation). Kaiparowits Formation, upper Campanian: UMNH VP 19314, 19330.

Morphotype 9

Description Similar to 8, except the tip of the pars ascendens extends dorsally beyond the level of the shaft; the acetabulum is prominent but shallow; the oblique groove deep, with rounded margins; the dorsal part of the shaft is markedly swollen medially.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 18102.

Morphotype 10

Description Similar to 1, except the oblique groove is only a faint depression on the medial surface of the shaft; the lateral surface of the shaft is smooth; the dorsal margins of the shaft and the pars ascendens meet in a shallow concavity.

Distribution Formation uncertain, lower–middle Campanian: UMNH VP 18304.

Morphotype 11

Description Similar to 1, except the oblique groove is developed only in the concavity on the rounded dorsal margin of the bone; the medial surface of the acetabular portion is moderately depressed; the acetabulum is in the middle of the acetabular region.

Distribution Straight Cliffs Formation, John Henry Member, middle Santonian: UMNH VP 18213, perhaps also UMNH VP 18220, 19356. Straight Cliffs Formation, John Henry Member, upper Santonian: UMNH VP 18344. Wahweap Formation, lower–middle Campanian: UMNH VP 18154, 18282.

Morphotype 12

Description Similar to 11, except the oblique groove carries onto the medial surface of the shaft, extends anteriorly and slightly ventrally, and is delimited ventrally by a short, faint ridge; the acetabulum is extremely prominent ventrally.

Distribution Straight Cliffs Formation, John Henry Member, middle Santonian: UMNH VP 18227.

Morphotype 13

Description Similar to 12, except the faint ridge deliminating the ventral margin of the oblique groove extends anteroventrally at a steeper angle and for a shorter distance along the medial surface of the shaft.

Distribution Straight Cliffs Formation, John Henry Member, middle Santonian: UMNH VP 18539.

Morphotype 14

Description Similar to 13, except the acetabulum is extremely large, exceeding the anteroventral margin of the bone.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 18286.

Morphotype 15

Description Similar to 1, except the shaft is only slightly convex and the pars ascendens only moderately declined from the longitudinal axis of the bone; consequently, the dorsal margin of the bone has only a very shallow concavity; the acetabulum is located in the middle of the acetabular region and is not too extensive; lateral surface of the bone is smooth; only a faint ridge runs down from the pars ascendens onto the medial surface of the bone, but is not accompanied by an obvious oblique groove. Although this morphotype lacks an obvious oblique groove, we have retained it in the group 1 ilia because the faint ridge that typically accompanies that groove is present and thus implies that the same muscle inserted in that region.

Distribution Straight Cliffs Formation, John Henry Member, lower Santonian: UMNH VP 18509.

Morphotype 16

Description Similar to 10 in that a shallow oblique groove begins on the dorsal margin of the bone, but the dorsal margin of the bone is straight; the oblique groove on the medial surface of the bone is paralleled by another groove originating on the medial surface of the pars ascendens; the acetabulum is shifted ventrally.

Distribution Straight Cliffs Formation, John Henry Member, lower Santonian: UMNH VP 18293. Straight Cliffs Formation, John Henry Member, upper Santonian: UMNH VP 18395, 18471. Wahweap Formation, lower–middle Campanian: UMNH VP 18180, perhaps also UMNH VP 18183. Formation uncertain, lower–middle Campanian: UMNH VP 18307.

Morphotype 17

Description Similar to 16, except the groove that runs parallel to the main oblique groove is faint and short; the dorsal margin of the bone is shallowly concave; the acetabulum is not extensive, located in the middle of the acetabular region.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 18264.

Morphotype 18

Description Similar to 16, except the posterior margin of the oblique groove is delimited by a prominent crista that may appear, in lateral view, as a dorsal tubercle-like structure; also the ridge coming from the medial surface of the pars ascendens and delimiting the parallel groove on the medial surface of the bone is better pronounced than in 16.

Distribution Straight Cliffs Formation, Smoky Hollow Member, Turonian: UMNH VP 13461.

Morphotype 19

Description Similar to 18, except the cristae are rounded and the dorsal tubercle-like structure is less prominent.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 19345.

Morphotype 20

Description Similar to 11, except the medial surface of the bone is entirely smooth, because the oblique groove does not extend onto that surface.

Distribution Straight Cliffs Formation, John Henry Member, lower Santonian: UMNH VP 18556. Straight Cliffs Formation, John Henry Member, middle Santonian: UMNH VP 19303. Straight Cliffs Formation, John Henry Member, upper Santonian: UMNH VP 18473.

Morphotype 21

Description Similar to 11, except the medial surface of the bone is entirely smooth, because the oblique groove does not extend onto that surface, and the acetabulum is extensive and shifted to the lower part of the acetabular region.

Distribution Straight Cliffs Formation, John Henry Member, lower Santonian: UMNH VP 19270, 19273.

Morphotype 22

Description Similar to 11, except the oblique groove (which is restricted to the dorsal margin of the bone) is accompanied by a similar, short groove posteriorly.

Distribution Straight Cliffs Formation, John Henry Member, upper Santonian: UMNH VP 18396.

Morphotype 23

Description Similar to 20, except the acetabulum extends beyond the anteroventral margin of the bone; a rounded ridge runs down from the medial surface of the dorsal margin of the acetabular region onto the medial surface of the iliac shaft, where it soon disappears.

Distribution Formation uncertain, upper Santonian or lower Campanian: UMNH VP 13480. Wahweap Formation, lower–middle Campanian: UMNH VP 18103.

Morphotype 24

Description Similar to 1 in that the dorsal margin of the shaft arises on the lateral margin of the bone above the anterior margin of the acetabulum, and that a shallow concavity between the shaft and the pars ascendens continues onto the medial surface of the bone, delimited posteriorly by a faint ridge; the shaft is widely convex dorsally; however, the pars ascendens is low, producing a moderate convexity and not terminating in a posterodorsally directed point; the lateral surface of the proximal section of the shaft bears faint, anteroventrally directed grooves and longitudinal elevations; a posteroventrally directed crista splits off from the anteroventral margin of the acetabulum and the ventral margin of the acetabulum continues posteriorly and even posterodorsally; consequently, a triangular field occurs between the crista and margin of the acetabulum. (Note that although this crista is a distinctive structure, it is too small to be depicted in the corresponding drawing in Fig. 12.5.)

Distribution Straight Cliffs Formation, Smoky Hollow Member, Turonian: UMNH VP 18366.

Morphotype 25

Description Similar to 24, except the oblique groove is only on the dorsal margin of the bone, delimited posteriorly by a rounded ridge coming from the margin of the pars ascendens; posteriorly, the oblique groove is paralleled by another groove, delimited by a crista; on the lateral surface of the bone is a shallow horizontal depression.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 18247.

Morphotype 26

Description Similar to 25, except the acetabulum is large and shifted ventrally, with its anteroventral margin markedly prominent; a horizontal mound derives from the dorsal portion of the acetabulum, and another, less prominent mound is directed anteroventrally; a distinct depression is developed between them; the crista delimiting posteroventrally the oblique groove is rather prominent, accompanied by a parallel groove that is delimited by only a faint ridge.

Distribution Kaiparowits Formation, upper Campanian: UMNH VP 18435.

GROUP 2: ILIA WITH A DORSAL TUBERCLE (FIG. 12.6; FIGS. 12.8–12.11, MIDDLE COLUMN)

Morphotype 1

Description The iliac shaft is moderately convex and its dorsal margin widely rounded; the dorsal margin of the pars ascendens is continuous with the dorsal margin of the shaft; the dorsal tubercle is mediolaterally compressed, triangular in lateral view, with its upper part widely rounded and slightly declined anteriorly; the dorsal margin of the acetabulum is markedly prominent; consequently, the dorsal surface of the pars ascendens is horizontal or even concave; a broad mound runs from the anterior margin of the acetabulum anteriorly; a broad shallow groove extends from the base of the tubercle onto the posterior section of the shaft where it disappears.

Distribution Straight Cliffs Formation, Smoky Hollow Member, Turonian: UMNH VP 13459. Formation uncertain, upper Santonian or lower Campanian: UMNH VP 13488, 13496.

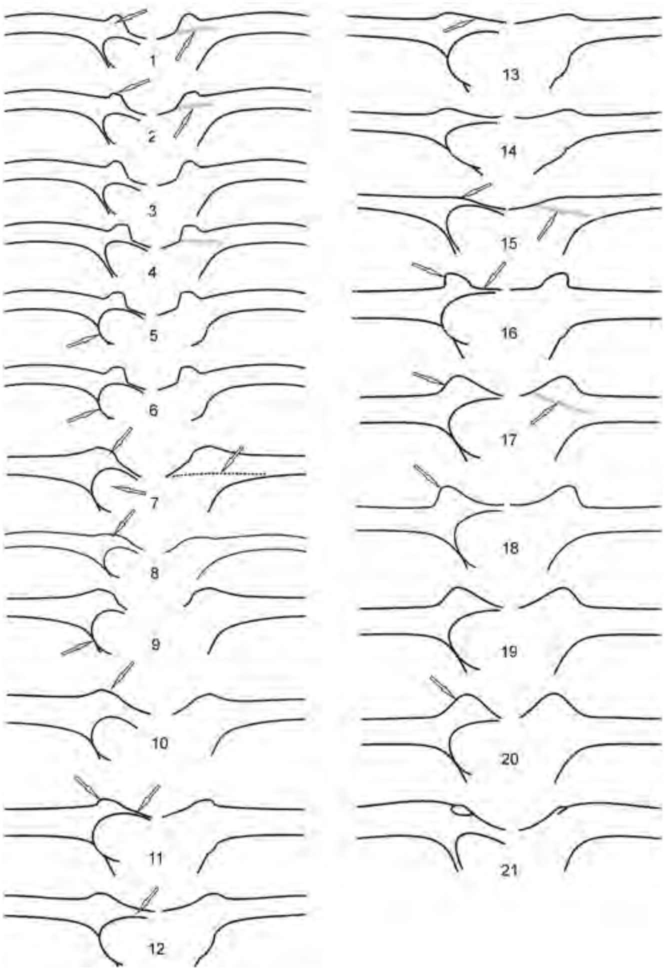
Morphotype 2

Description Similar to 1, except the dorsal tubercle is knoblike, not compressed mediolaterally, and is slightly squarish in lateral outline.

Distribution Straight Cliffs Formation, John Henry Member, upper Santonian: UMNH VP 18483. Formation uncertain, upper Santonian or lower Campanian: UMNH VP 13500, 13504.

Morphotype 3

Description Similar to 1, except the dorsal tubercle is knoblike, not compressed mediolaterally, and the medial surface of the bone is smooth.



12.6. Semidiagrammatic line drawings of the 21 iliac morphotypes with a dorsal tubercle (group 2 ilia) left ilium in lateral (left) and medial (right) views. Symbols are the same as in Fig. 12.4.

Distribution Dakota Formation, upper Cenomanian: UMNH VP 13159. Straight Cliffs Formation, Smoky Hollow Member, Turonian: UMNH VP 18355.

Morphotype 4

Description Similar to 1, except the dorsal tubercle is rather quadrangular in lateral view and the acetabulum is prominent but shallow; because of the prominent dorsal margin of the acetabulum, there is a groove between the acetabulum and the dorsal tubercle.

Distribution Straight Cliffs Formation, Smoky Hollow Member, Turonian: UMNH VP 13460.

Morphotype 5

Description Similar to 4, except the acetabulum is deeply concave with a raised edge along the entire margin and it extends from the level of the dorsal margin of the pars ascendens to beyond the anteroventral margin of the bone; the medial surface of the bone is smooth.

Distribution Straight Cliffs Formation, Smoky Hollow Member, Turonian: UMNH VP 13458.

Morphotype 6

Description Similar to 4, except the dorsal tubercle is not compressed laterally and the dorsal margin of the acetabulum is not prominent.

Distribution Formation uncertain, upper Santonian or lower Campanian: UMNH VP 13483.

Morphotype 7

Description The posterior section of the iliac shaft is straight;; the dorsal tubercle has an anteroposteriorly extended base but is low, with its upper part rather swollen; in cross section, the dorsal surface of the pars ascendens is a broadly rounded, nearly horizontal plane extending onto the dorsal margin of the acetabulum; the acetabulum extends from nearly the level of the dorsal surface of the pars ascendens almost to the anteroventral margin of the bone; the medial surface of the bone is flat and almost smooth, except for a faint crista running from the medial surface of the pars ascendens to the lower margin of the iliac shaft.

Distribution Dakota Formation, upper Cenomanian: UMNH VP 13158.

Morphotype 8

Description Similar to 7, except the dorsal tubercle is a low, anteroposteriorly elongate crista; the iliac shaft is moderately convex dorsally; the medial surface of the bone is smooth.

Distribution Dakota Formation, upper Cenomanian: UMNH VP 13156. Wahweap Formation, lower–middle Campanian: UMNH VP 18112.

Morphotype 9

Description Similar to 7 in size and lateral shape of the tubercle; however, the upper part of the tubercle is sharp (not swollen) and its lateral surface slants down toward the prominent dorsal margin of the acetabulum; the medial surface of the tubercle is vertical, continuous without any distinct border with the flat and smooth medial surface of the bone; the anteroventral margin of the acetabulum reaches the level of the bone; the iliac shaft is straight.

Distribution Straight Cliffs Formation, John Henry Member, middle Santonian: UMNH VP 19355.

Morphotype 10

Description Similar to 7, except the dorsal tubercle is more extensive anteroposteriorly, and slightly declined anteriorly; the medial surface of the bone is smooth.

Distribution Straight Cliffs Formation, John Henry Member, upper Santonian: UMNH VP 18474.

Morphotype 11

Description Similar to 7, except the dorsal tubercle is small and declined anteriorly; the acetabulum extends to the dorsal margin of the bone.

Distribution Straight Cliffs Formation, John Henry Member, upper Santonian: UMNH VP 18394.

Morphotype 12

Description Similar to 7, except the acetabulum extends beyond the anteroventral margin of the bone.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 18114, 18122.

Morphotype 13

Description Similar to 12, except the dorsal margin of the pars ascendens is above the level of the dorsal margin of the iliac shaft.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 18099.

Morphotype 14

Description Similar to 13, except the dorsal margin of the pars ascendens is slightly concave and the acetabular region of the bone is low.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 18098.

Morphotype 15

Description Similar to 11, except the dorsal tubercle is only a faint though extensive elevation; a shallow groove extends on the medial surface of the bone as in morphotype 1.

Distribution Formation uncertain, upper Santonian or lower Campanian: UMNH VP 13497.

Morphotype 16

Description Similar to 11, except the dorsal tubercle is comparatively large and prominent; the dorsal margin of the pars ascendens is horizontal, continuous with that of the iliac shaft.

Distribution Formation uncertain, upper Santonian or lower Campanian: UMNH VP 13481.

Morphotype 17

Description Similar to 1, except the dorsal tubercle is a triangular, comparatively thin lamella with its rounded tip slightly declined anteriorly; the tubercle is well delimited, both laterally and medially, from the surrounding horizontal surface of the bone.

Distribution Formation uncertain, upper Santonian or lower Campanian: UMNH VP 13482, 13494, 13499.

Morphotype 18

Description Similar to 17, except the dorsal tubercle is more prominent; the medial surface of the bone is smooth.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 18095, 18100, 18113.

Morphotype 19

Description Similar to 17, except the medial surface of the dorsal tubercle is continuous with the medial surface of the bone, the latter of which is smooth.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 18101.

Morphotype 20

Description Similar to 10, except the dorsal tubercle is comparatively large, triangular in lateral view, compressed mediolaterally either only in its posterior part or in the whole of its extent, with a rugosity in its lateral side; the medial surface of the tubercle is continuous with the medial surface of the bone, which is flat and smooth; the acetabulum extends up to the dorsal margin of the bone.

Distribution Formation uncertain, upper Santonian or lower Campanian: UMNH VP 13501. Wahweap Formation, lower–middle Campanian: UMNH VP 18108, 18121.

Morphotype 21

Description Large ilium; the dorsal margin of the pars ascendens is declined posteroventrally from the longitudinal axis of the bone; the acetabulum is comparatively small and shifted ventrally; the iliac shaft is strongly compressed mediolaterally but not bearing a dorsal crest; the dorsal tubercle is small, declined dorsolaterally, separated from the dorsal edge of the shaft by a shallow depression; both the lateral and medial surfaces of the bone are smooth.

Distribution Formation uncertain, upper Santonian or lower Campanian: UMNH VP 13551.

Group 3: Ilia Lacking an Oblique Groove and a Dorsal Tubercle (Fig. 12.7; Figs. 12.8–12.11, Right Column)

Morphotype 1

Description Between the pars ascendens and shaft is only a very faint concavity on the dorsal surface of the bone; the acetabulum is cup-like, located in the middle of the acetabular region; on the lateral surface of the posterior section of the shaft are longitudinal, anteroventrally directed elevations, well delimited posteroventrally; the medial surface of the acetabular portion is depressed.

Distribution Straight Cliffs Formation, John Henry Member, Coniacian: UMNH VP 19366.

Morphotype 2

Description Similar to 1, except the lateral surface bears a moderately well-developed (i.e., not too prominent) crista.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 18139.

Morphotype 3

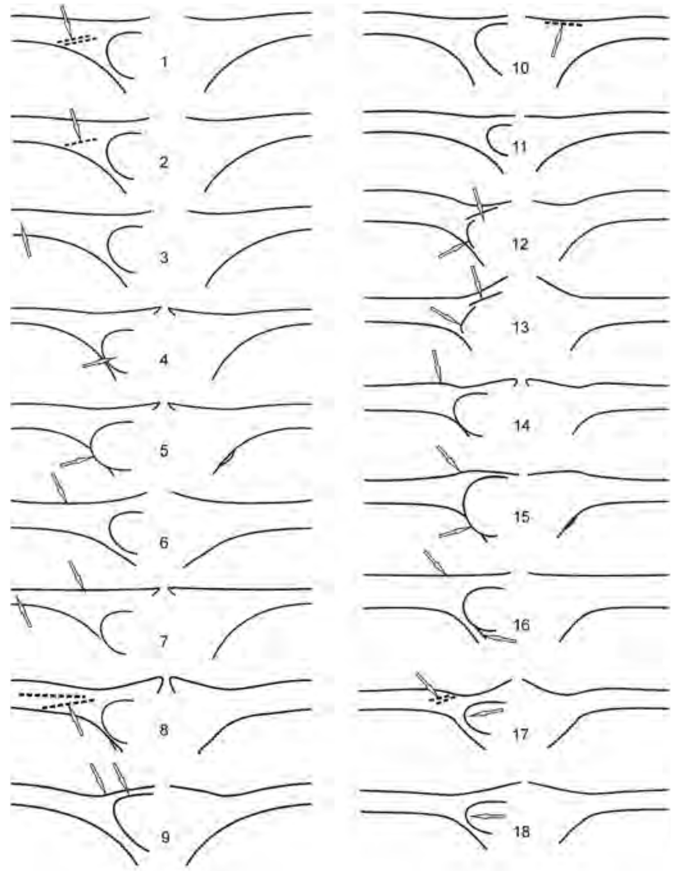
Description Similar to 1, except the lateral surface of the shaft bears no elevations.

Distribution Straight Cliffs Formation, John Henry Member, middle Santonian: UMNH VP 18211, 18218. Straight Cliffs Formation, John Henry Member, upper Santonian: UMNH VP 18475. Formation uncertain, ?Campanian: UMNH VP 18554, possibly also UMNH VP 18555. Wahweap Formation, lower–middle Campanian: UMNH VP 18134.

Morphotype 4

Description Similar to 1, except there are no longitudinal elevations on the lateral surface of the shaft; the pars ascendens is extensive and produces a robust posterodorsal point; the posterior section of the shaft is comparatively slender; the acetabulum is shifted ventrally.

Distribution Straight Cliffs Formation, John Henry Member, middle Santonian: UMNH VP 18228, 18233; Formation uncertain, upper Santonian or lower Campanian: UMNH VP 13484, 13495, possibly also 13498 and 19293. Formation uncertain, ?Campanian: UMNH VP 18552.



12.7. Semidiagrammatic line drawings of the 18 iliac morphotypes lacking both an oblique groove and a dorsal tubercle (group 3 ilia) left ilium in lateral (left) and medial (right) views. Morphotypes 17 and 18 are cf. *Nezpercius* sp. (Caudata) each depicted with long axis rotated about 90° from life orientation (i.e., iliac shaft would have extended vertically) to emphasize similarities between isolated ilia of anurans and caudates. Symbols are the same as in Fig.12.4.

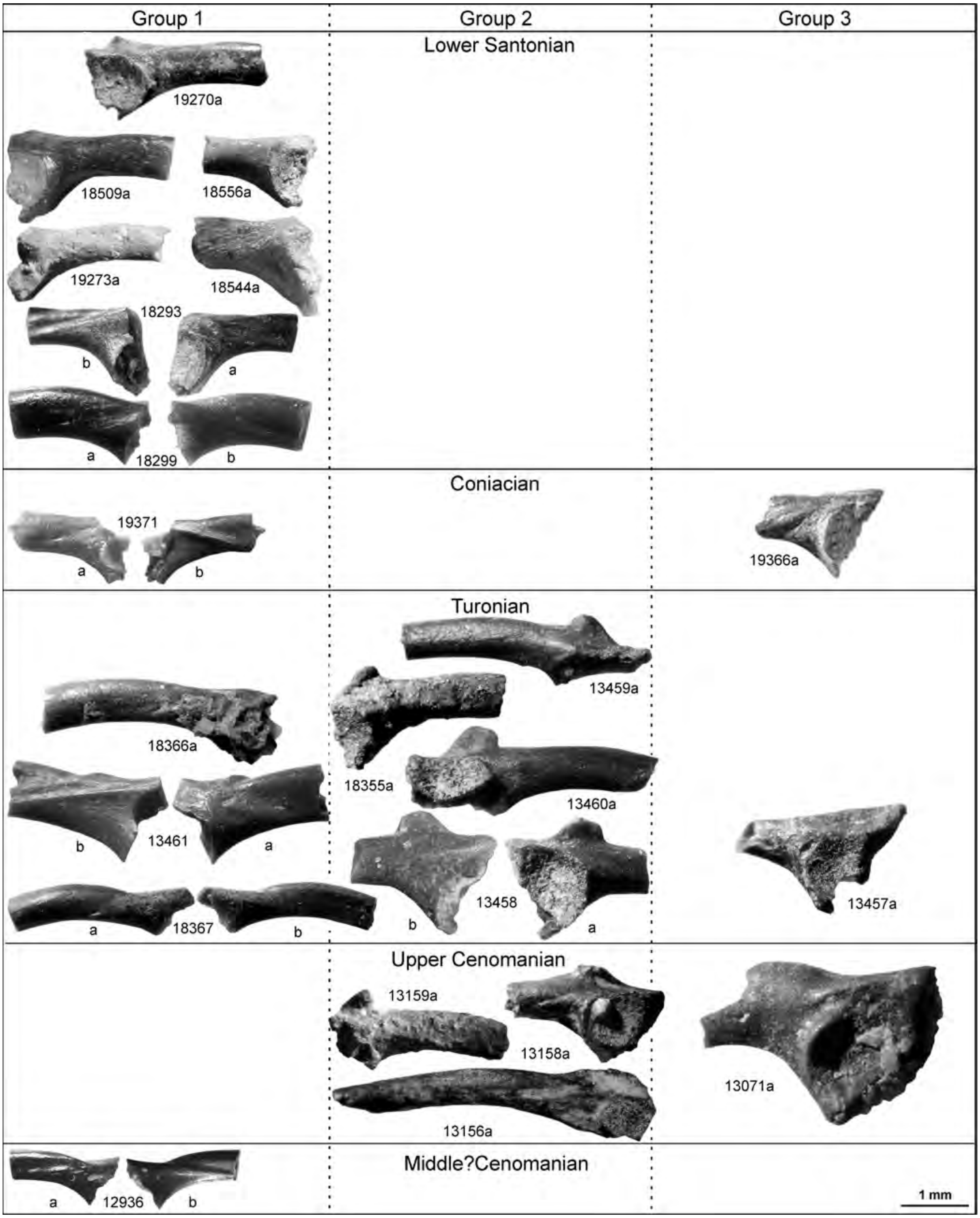
Morphotype 5

Description Similar to 4, except the posterior section of the shaft is not slender; the acetabulum is large, exceeding the anteroventral margin of the bone.

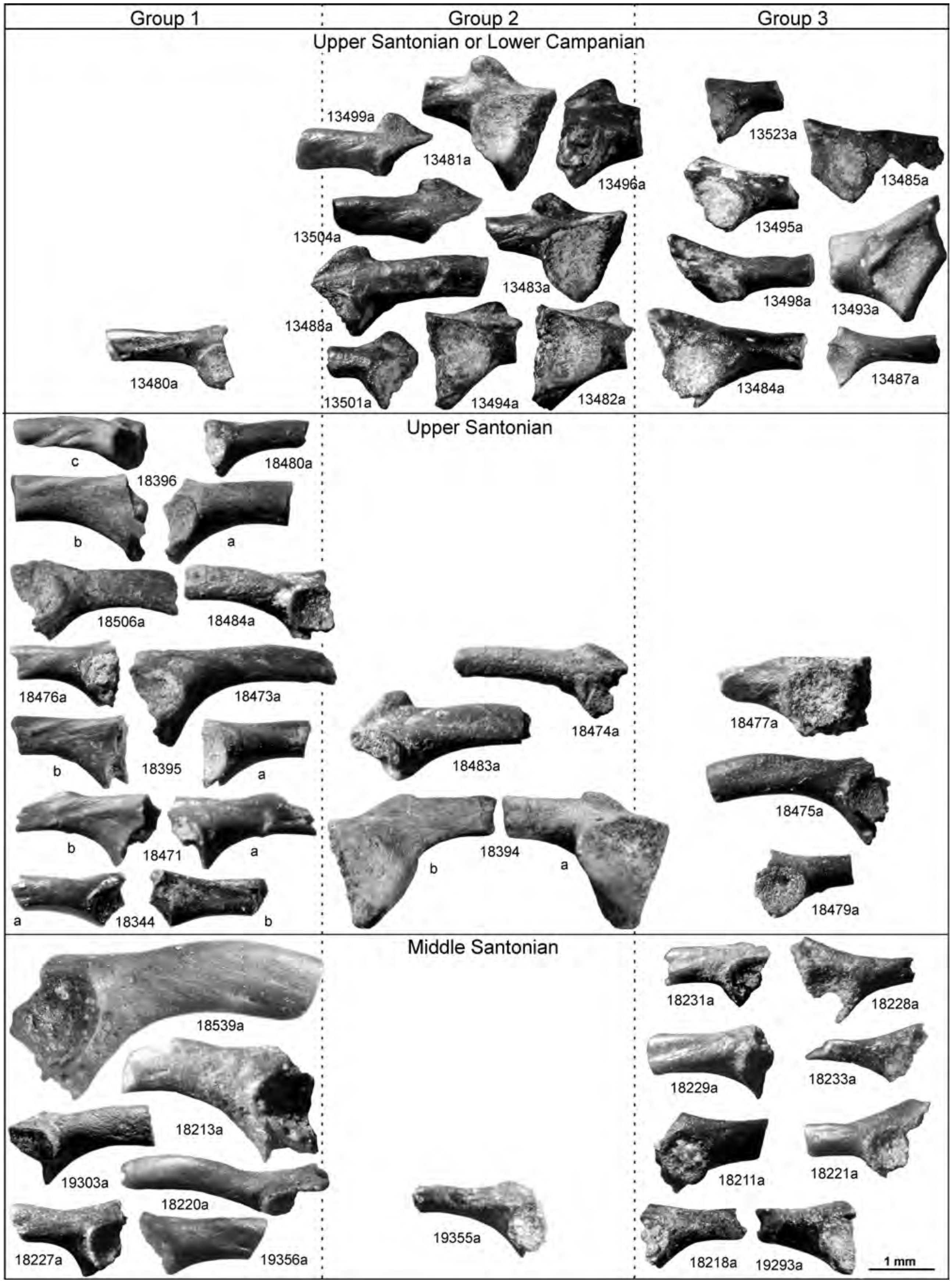
Distribution Straight Cliffs Formation, John Henry Member, upper Santonian: UMNH VP 18479. Perhaps also Wahweap Formation, lower–middle Campanian: UMNH VP 18088, 18320.

Morphotype 6

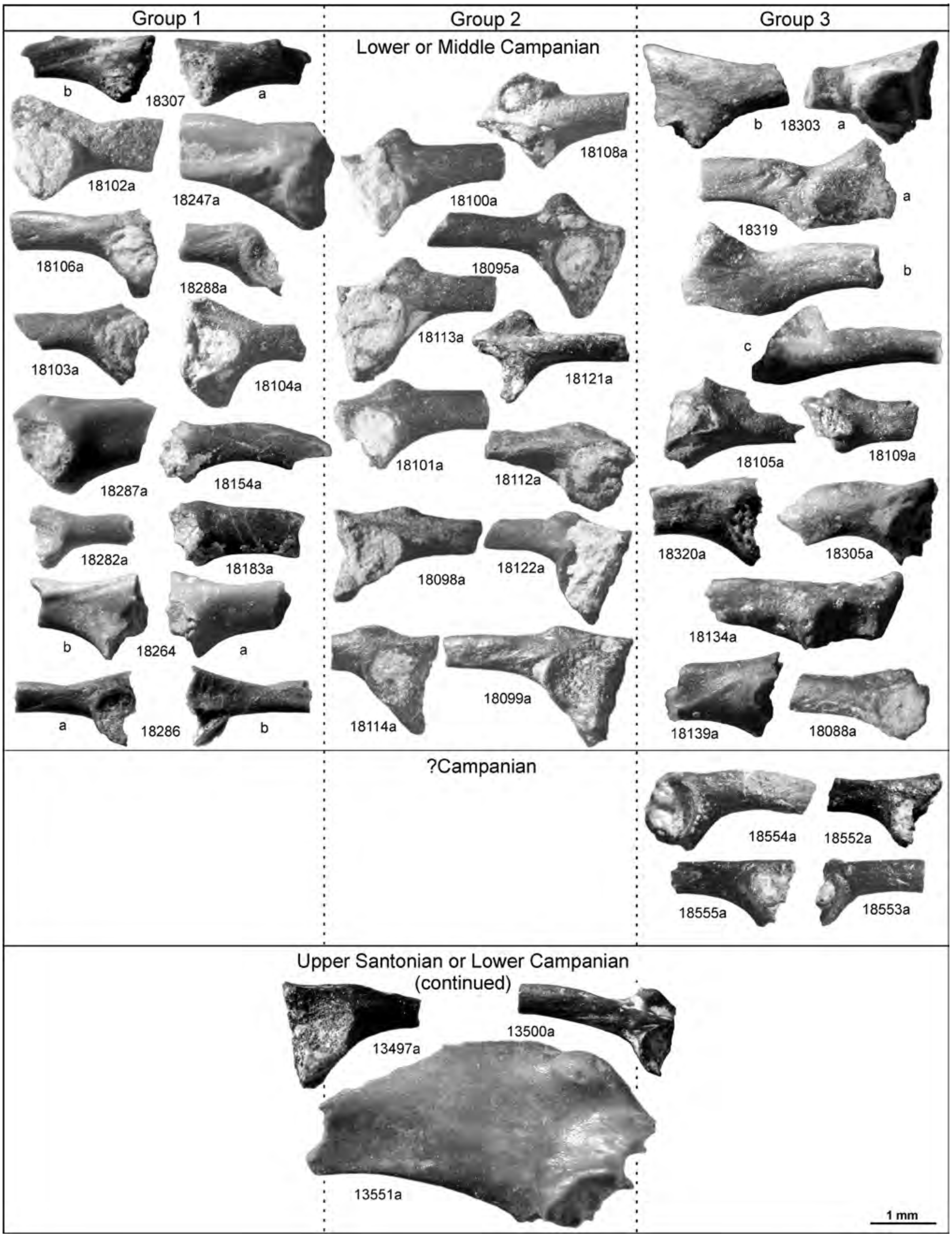
Description Similar to 4, except the margins of the acetabular portion are moderately divergent; the dorsal margin of the shaft is straight and meets the dorsal margin of the pars



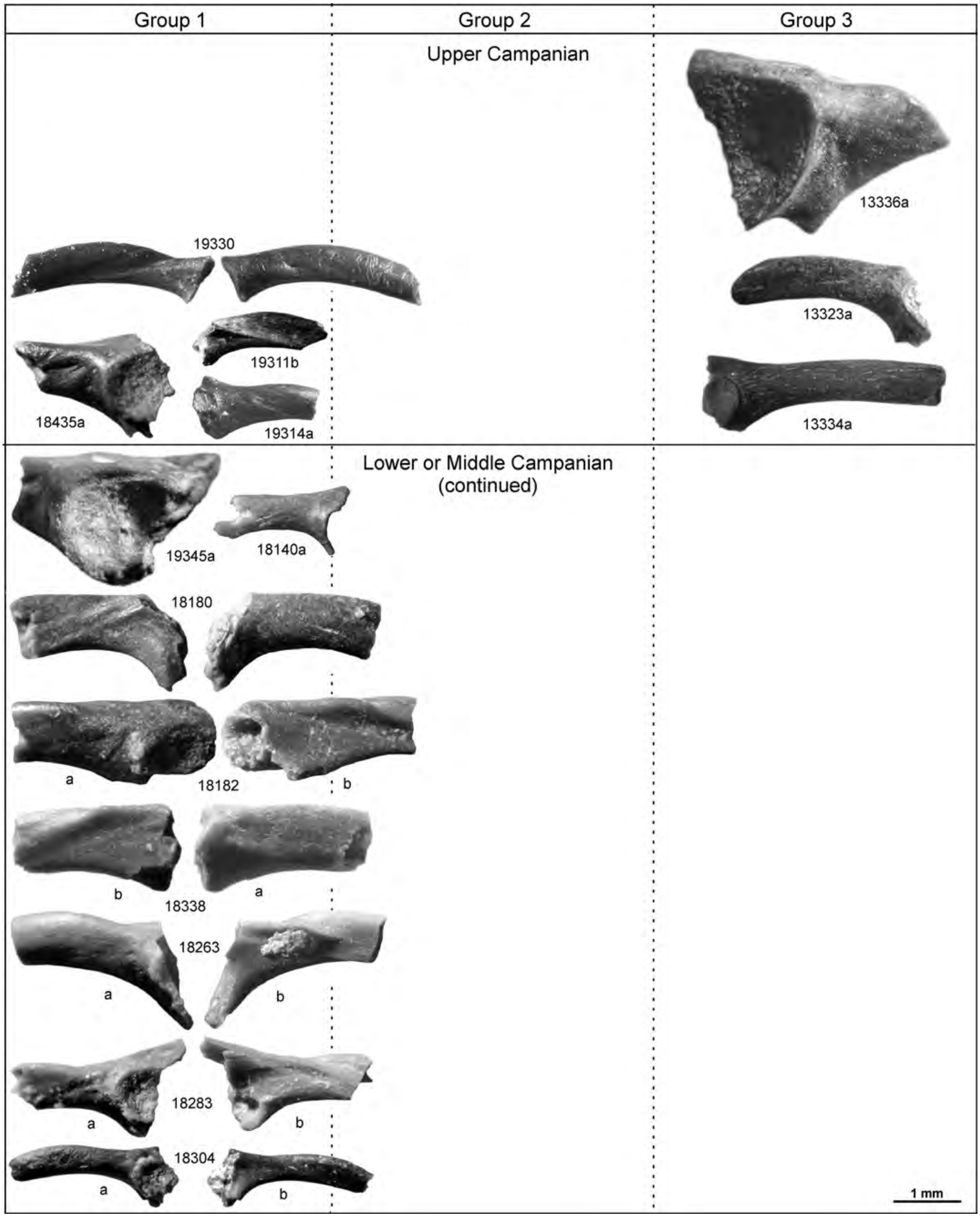
12.8. Stratigraphic distribution of representative anuran ilia from middle? Cenomanian through lower Santonian localities in south–western Utah (continues onto Figs. 12.9–12.11). Left column is group 1 ilia (with an oblique groove); center column is group 2 ilia (with a dorsal tubercle); and right column is group 3 ilia (lacking both an oblique groove and a dorsal tubercle). Most of the voucher specimens listed in the text are depicted here. For each specimen, the accompanying five-digit number is its formal UMNH catalog number; a, b, and c indicate lateral, medial, and dorsal views, respectively. Specimens shown at same magnification (see scale bar at lower right).



12.9. Stratigraphic distribution of representative anuran ilia from middle Santonian through upper Santonian or lower Campanian localities in southwestern Utah (continued from Fig. 12.8; see Fig. 12.8 caption for details).



12.10. Stratigraphic distribution of representative anuran and caudate ilia from upper Santonian or lower Campanian through lower or middle Campanian localities in southwestern Utah (continued from Figs. 12.8 and 12.9; see Fig. 12.8 caption for details). Four examples of group 3 ilia (UMNH VP 18303, 18319, 18105, and 18109; all in upper right) are cf. *Nezpercius* sp. (Caudata) each depicted with long axis rotated about 90° from life orientation (i.e., iliac shaft would have extended vertically) to emphasize similarities between isolated ilia of anurans and caudates.



12.11. Stratigraphic distribution of representative anuran ilia from lower or middle Campanian through upper Campanian localities in southwestern Utah (continued from Figs. 12.8–12.10; see Fig. 12.8 caption for details).

ascendens in a shallow depression; the acetabulum is prominent but shallow; the medial surface of the bone is concave and smooth.

Distribution Formation uncertain, upper Santonian or lower Campanian: UMNH VP 13487, 13523.

Morphotype 7

Description Similar to 4, except the dorsal margin of the bone is straight.

Distribution Straight Cliffs Formation, Smoky Hollow Member, Turonian: UMNH VP 13457.

Morphotype 8

Description Similar to 4, except there are two elongate and anteriorly divergent mounds on the lateral surface of the posterior section of the shaft; the medial surface of the pars ascendens is concave.

Distribution Straight Cliffs Formation, John Henry Member, middle Santonian: UMNH VP 18221, 18229, possibly also UMNH VP 18231.

Morphotype 9

Description Acetabulum large, extending closer to the dorsal margin of the acetabular region than to the ventral one; on the dorsal margin of the bone, the transition between the pars ascendens and the iliac shaft is marked by a moderate indentation; the shaft seems to be comparatively slender; the medial surface of the bone is flat or even slightly concave posteriorly.

Distribution Kaiparowits Formation, upper Campanian: UMNH VP 13336.

Morphotype 10

Description Acetabulum small, its anterodorsal part is a mere depression in the bone; the shaft is comparatively robust; a prominent though rounded ridge runs horizontally on the dorsal part of the medial surface.

Distribution Kaiparowits Formation, upper Campanian: UMNH VP 13334.

Morphotype 11

Description Similar to 10, except the acetabulum is well delimited and located in the middle of the acetabular region; the acetabular region is comparatively small; the shaft is only moderately convex dorsally; the medial surface of the acetabular region is smooth and flat.

Distribution Kaiparowits Formation, upper Campanian: UMNH VP 13323.

Morphotype 12

Description The dorsal margin of the pars ascendens is declined posterodorsally and its posterior tip is swollen and slightly declined laterally above the acetabulum; the iliac shaft is laterally compressed; the posterior section of the dorsal margin of the iliac shaft is widely convex; consequently, it meets the dorsal margin of the pars ascendens in a shallow concavity; an oblique rounded ridge splits from the dorsal margin of the pars ascendens and runs down anteroventrally onto the lateral surface of the shaft where it terminates abruptly at the level of the anterior margin of the acetabulum; the acetabulum is a mere depression in the bone, except for a well-delimited anterior part that is prominent; the medial surface of the bone is moderately convex and smooth.

Distribution Dakota Formation, upper Cenomanian: UMNH VP 13071. Formation uncertain, lower or middle Campanian: UMNH VP 18305.

Morphotype 13

Description Similar to 12, except the margins of the acetabular region are strongly divergent from the longitudinal axis of the bone; the shaft is relatively stout; the acetabulum is a mere depression in the bone, except for the anterior margin, which is slightly prominent; a rounded ridge coming from the dorsal margin of the pars ascendens terminates abruptly above the anterior acetabular margin; the medial surface of the bone is moderately convex and smooth.

Distribution Formation uncertain, upper Santonian or lower Campanian: UMNH VP 13493.

Morphotype 14

Description The iliac shaft is convex in its posterior section, whereas its anterior part is straight; the acetabulum is a mere depression with rounded margins; the medial surface of the bone is moderately convex and smooth.

Distribution Formation uncertain, upper Santonian or lower Campanian: UMNH VP 13485.

Morphotype 15

Description The pars ascendens is not developed, consequently the dorsal margin of the acetabulum extends to the dorsal margin of the bone; the acetabulum is large, exceeding beyond the anteroventral margin of the bone; the shaft is comparatively slender; a very shallow convexity is present on the dorsal surface of the acetabular region, above the anterior margin of the acetabulum (although this convexity occurs in the same position as the dorsal tubercle, we hesitate to identify it as such because it is very shallow and it is not prominently developed as the knob- or ridge-like structure seen in most group 2 ilia); the medial surface of the acetabular portion is concave.

Distribution Straight Cliffs Formation, John Henry Member, upper Santonian: UMNH VP 18477.

Morphotype 16

Description The dorsal margin of the bone is straight; the acetabulum is small but markedly prominent; a posteroventrally directed crista splits from the anteroventral margin of the acetabulum.

Distribution Formation uncertain, ?Campanian: UMNH VP 18553.

Morphotype 17

Description The posterior part of the acetabular portion is strongly extended both dorsally and ventrally so it has a fanlike, triangular shape; the posterior, articular surface of the bone is thick but concave (it was probably filled with cartilage in the living animal); the anterior part of the acetabulum is convex and extremely prominent, so the acetabulum is strongly declined posteriorly and very shallow; the acetabulum does not reach the level of the anteroventral outline of the bone; the medial surface of the acetabular portion is smooth; there is a distinct rugosity on the lateral surface of the iliac shaft. Those features are similar (but not all identical) to those of *Nezpercius dodsoni* (Blob et al., 2001), so referral to *Nezpercius* is justified.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 18319.

Morphotype 18

Description Same as in 17 (and also referable to *Nezpercius*), except there is no rugosity on the lateral surface of the iliac shaft. The surface of the anterior, convex margin of the acetabulum may be abraded.

Distribution Wahweap Formation, lower–middle Campanian: UMNH VP 18105, 18109, 18303.

STRATIGRAPHIC OCCURRENCES OF ILIA IN THE UPPER CRETACEOUS OF SOUTHWESTERN UTAH

Group 1 ilia

For the first group of ilia, namely those with an oblique groove, we defined our morphotype 1 on the basis of a typical ilium with an oblique groove (UMNH VP 12936) from the lowest locality in our stratigraphic sequence (middle? Cenomanian). On the basis of its stratigraphic occurrence, this morphotype can be postulated as the basic or most primitive iliac morphotype, from which others in the same group could have been derived. Interestingly, morphotype 1 or its slight modifications persisted throughout the entire stratigraphic sequence, as indicated by morphotype 8 (represented by UMNH VP 19330, which differs from morphotype 1 only in that there is a shallow depression instead of a groove) in the upper Campanian portion of the sequence.

Morphotype 2 could have been derived from morphotype 1. It also is one of the few morphotypes in our samples that corresponds with ilia from elsewhere in the Western Interior that have been assigned to a named anuran species. Estes (1969) chose an ilium having an oblique groove delimited posteriorly by an expanded crista from the Bug Creek Anthills (mixed upper Maastrichtian and lower Paleocene), Hell Creek Formation of Montana, as the holotype of *Scotiophryne pustulosa*. Estes (1969) also referred to the species some distinctive skull bones (maxillae and squamosals), humeri, and several ilia in which the oblique groove was less strongly marked than in the holotype. Gardner (2008) described additional, isolated bones and presented a revised diagnosis for *S. pustulosa*. Because the holotype ilium (Estes, 1969:fig. 1c, d) of *S. pustulosa* appears virtually identical to our morphotype 2 ilium, we assign the Utah specimens to *Scotiophryne*. In our samples, this morphotype occurs in the lower–middle Campanian Wahweap Formation, at both the Campbell Canyon and White Flats Road localities. These Utah occurrences extend the range for *Scotiophryne* from the late Maastrichtian/early Paleocene (Estes, 1969; Gardner, 2008) back to the early–middle Campanian.

Morphotype 3 mainly differs from the previous two in that its crista delimits a broad depression in the medial surface of the iliac shaft and bears an oblique depression on its lateral surface. It was recorded by only two specimens, one (UMNH VP 19371) from the Coniacian and one (UMNH VP 19311) from the upper Campanian. Morphotype 4, represented by UMNH VP 18480 from the upper Santonian, is similar and differs only in that its lateral surface is smooth. If these differences express individual variation and morphotypes 3 and 4 belong to a single taxon, then its stratigraphic range is from the Coniacian to late Campanian.

Morphotypes 5, 7, and 8 are also similar to each other and vary only in different expressions of the oblique groove. Considering that the oblique groove is an area for attachment of the medial head of the iliacus externus muscle (Přikryl et al., 2009), variation in the groove may indicate differences in how well developed this muscle was in individuals of the same or closely related taxa. These three morphotypes were recorded from the Turonian to the uppermost level (upper Campanian) in our stratigraphic sequence. This lengthy stratigraphic range supports the view that morphotypes 1–5, 7, and 8 are generalized ilia with an oblique groove, from which only morphotype 2 is markedly derived by its peculiar morphology of having a prominent lamina delimiting the groove posteriorly, which is a feature that substantiates the taxonomic distinctiveness of the genus *Scotiophryne* (Estes, 1969). Morphotypes 10, 11, and 15 may also be derived from the generalized scheme, as are morphotypes 1–5, 7, and 8, in that their oblique groove is poorly developed (i.e., very shallow or entirely absent). Morphotypes 10, 11, and 15 have a more restricted range and are known from the middle Santonian through middle Campanian.

In contrast to the previously discussed ilia, morphotype 6 (UMNH VP 18104) differs in that the margins of its pars ascendens and pars descendens are strongly divergent from the longitudinal axis of the bone (they form an angle of more than 90°) and that its shaft is straight and comparatively slender. The only example of this morphotype was recovered from the lower–middle Campanian Barker Reservoir Road locality.

Morphotype 9 (UMNH VP 18102) also is markedly different in having a massive pars ascendens and an acetabulum that is shifted to the anteroventral margin of the acetabular region and is markedly prominent from the surface of the bone, but with a flat acetabular surface. It also was recovered only from the lower–middle Campanian Barker Reservoir Road locality.

Nine morphotypes (12–14, 16–19, 20, and 21) still maintain the basic morphology of the oblique groove, especially on the medial surface of the bone; however, there is some variation, especially in the position and size of their acetabula.

Morphotypes 12 and 13 are characterized by their large and ventrally shifted acetabula, which resembles the condition in morphotype 9. However, morphoptypes 12 and 13 are older (middle Santonian) and thus provide the earliest evidence for expansion and ventral shift of the acetabulum in ilia with an oblique groove from Utah. Otherwise, the two morphotypes are typical for ilia with an oblique groove and differ from each other only in minor details, most notably the course of the oblique groove on the medial surface of the bone. Morphotype 14 could also be included with the previous two morphotypes, but it differs from them in having a larger acetabulum and a stratigraphically higher (lower Campanian) occurrence.

Morphotypes 16 through 19 share two features: (1) the oblique groove is paralleled posteriorly by another groove arising on the medial surface of the pars ascendens, and (2) the nearly straight dorsal margin of the bone. Morphotype 16 is characterized by a large and ventrally shifted acetabulum; its stratigraphic occurrence is lower Santonian through lower–middle Campanian. Morphotypes 17 through 19 differ from morphotype 16 and resemble one another in having the acetabulum smaller and located in the middle of the acetabular region, but they differ from each other in how prominently developed is the crista that posteriorly delimits the oblique groove. In morphotype 18, represented by UMNH VP 13461, this crista is so prominent that where it crosses the dorsal margin of the bone it resembles a small tubercle. However, because morphotype 18 occurs in the Turonian and the similar morphotype 19 (UMNH VP 19345) occurs much later in the lower–middle Campanian, it appears that these two morphotypes (and probably also other morphotypes with two parallel grooves) are just variations of the basic morphotype with a single oblique groove and, judging by their stratigraphic occurrence, they have no stratigraphic value.

Morphotypes 20 and 21 are characterized by having the oblique groove restricted to the dorsal margin of the bone and by the smooth medial surface of the bone. These morphotypes differ from one another only in the position of their acetabula. Both occur only in the Santonian.

The remaining two morphotypes, 23 and 26, are notable for their large and ventrally located acetabula. Besides UMNH VP 13480 from the upper Santonian or lower Campanian Pinto Flats locality; this is the only example of an ilium with an oblique groove recovered from this locality, even though the other two principal groups of ilia are well represented at that locality.

Although ilia with an oblique groove have a continuous distribution throughout the stratigraphic sequence in southern Utah and we have recognized 26 different morphotypes, we were not able to recognize correlations between any particular morphotype and stratigraphic intervals. Even if there were morphotypes restricted to certain stratigraphic units, those would be difficult to recognize on the basis of our small sample sizes, which, in some cases, constituted only a single specimen for a particular morphotype. Moreover, because the morphotypes in this group of ilia generally differ only subtly from one another, it is difficult to decide whether those differences are taxonomically significant or simply reflect individual variation; regardless, most of the morphotypes appear to have no stratigraphic value. The only exception seems to be morphotype 2 (*Scotiophryne*), which is clearly defined by a prominent lamina that posteriorly delimits the oblique groove and, in the Utah samples, is stratigraphically restricted to the lower–middle Campanian. Elsewhere in the Western Interior, *Scotiophryne* is known from the late Maastrichtian and early Paleocene of Montana and Wyoming (Estes, 1969; Gardner, 2008).

Group 2 ilia

The second principal group consists of ilia with a dorsal tubercle. The most generalized morphotype (morphotype 1) is characterized by having a slightly convex shaft, by a dorsal tubercle that is triangular, laterally compressed, has a rounded apex and is slightly declined anteriorly, and by the prominent dorsal margin of the acetabulum. This morphotype occurs in the Turonian and upper Santonian or, possibly, lower Campanian.

Morphotype 3 is similar, except its dorsal tubercle is not laterally compressed. It occurs in the upper Cenomanian and Turonian. The relatively early (Turonian) co-occurrence and the overall similarity of morphotypes 1 and 3 might suggest that the generalized morphotype for this group of ilia was one in which the dorsal tubercle could vary in its mediolateral compression. In other words, it could include ilia with both compressed and knob-like dorsal tubercles. If this is correct, then morphotypes 1 and 3 could both represent the generalized morphotype for this group of ilia.

Morphotype 2 from the upper Santonian or lower Campanian is similar to morphotypes 1 and 3, except the outline of its dorsal tubercle tends to be a more squarish and it is not laterally compressed. A squarish outline of the dorsal tubercle is also characteristic of morphotypes 4, 5, and 6; these vary only in the shape and location of their acetabula. However, they occur in the Turonian (UMNH VP 13458 and 13460 in Fig. 12.8) and upper Santonian or lower Campanian (UMNH VP 13483 in Fig. 12.9). It is unknown why there is a gap between these stratigraphic occurrences and whether the squarish outline of the dorsal tubercle indicates the ilia are from closely related taxa. If the squarish outline of the dorsal tubercle arose independently more than once, then at least some of the ilia with that feature might be from unrelated taxa.

Morphotype 7 differs from the previous six in that its acetabular region is declined ventrally (i.e., the dorsal margin behind the tubercle is declined posteroventrally, whereas the dorsal margin of the shaft is located horizontally; consequently, the dorsal tubercle is a protuberance located at the point where both meet together). It is represented by a single specimen (UMNH VP 13158) from the upper Cenomanian.

Morphotype 8 is similar, except its dorsal tubercle is compressed laterally and elongated anteroposteriorly, so it is more a crista than a tubercle. This morphotype is very characteristic, and therefore it is rather surprising that examples occur in the upper Cenomanian (UMNH VP 13156 in Fig. 12.8) and Campanian (UMNH VP 18112 in Fig. 12.10).

Morphotype 9 possibly could be related to morphotype 7 (there are only minor differences between them); however, they are separated by a large stratigraphic gap (upper Cenomanian versus middle Santonian). On the other hand, morphotype 9 likely is related to morphotypes 10, 11, and 12, represented by UMNH VP 18474, 18394, and 18114 and 18122, respectively. All (including morphotype 9) are from the middle Santonian to lower or middle Campanian and all are characterized by a massive acetabular region that is declined posteroventrally from the longitudinal axis of the shaft. Morphotype 13, which also is from the lower or middle Campanian, differs from morphotype 12 only by having the posterior margin of its dorsal tubercle being confluent with the dorsal margin of the pars ascendens. Consequently, the dorsal tubercle is only slightly prominent.

Morphotypes 14 and 15 (represented by UMNH VP 18099 and 18098, respectively) are similar to each other in their acetabular region being shallow and slender, and their dorsal tubercle is not prominent. These two morphotypes are also restricted to the upper Santonian or lower Campanian (morphotype 15) and lower–middle Campanian (morphotype 14).

Morphotype 16 is characterized by an extensive acetabular region (the dorsal margin of which is continuous with the dorsal margin of the shaft) and by a prominent dorsal tubercle. It occurs in the upper Santonian or lower Campanian.

Morphotypes 17–20 are all characterized by a dorsal tubercle that is large and triangular in lateral aspect and by an extremely large acetabulum. All are restricted to the upper Santonian–middle Campanian.

Morphotype 21 strongly deviates from all other ilia in that the dorsal margin of the shaft is a comparatively sharp edge. This morphotype is similar to ilia of *Enneabatrachus hechti* Evans and Milner, 1993, from the Upper Jurassic Morrison Formation, in that the dorsal tubercle is declined laterally and that its shaft has a medially declined dorsal crest. However, in UMNH VP 13551 from the upper Santonian or lower Campanian, the dorsal tubercle is separated from the dorsal crest by a deep depression, which argues against assigning this specimen to *Enneabatrachus*.

To sum up the situation in the group of the ilia with a dorsal tubercle, one can conclude that although there are intriguing irregularities in the occurrences of this type of ilia (e.g., their complete absence or relative scarcity in the lower and middle Santonian and in the upper Campanian), it is not possible to recognize any morphotypes that can be correlated with a particular stratigraphic interval. Even those morphotypes that seemingly are well defined (i.e., those with squarish tubercle, such as morphotypes 2, 4, 5, and 6) occur in the upper Santonian or lower Campanian, but also in the Turonian. If differences in the size and shape of the dorsal tubercle are ignored, one might argue that ilia with an enlarged acetabular region (morphotypes 11–20) are typical of the upper Santonian–middle Campanian.

Group 3 ilia

Within the third group – ilia lacking both the oblique groove and dorsal tubercle – morphotypes 1 to 3 differ from each other only in presence or absence of rounded ridges on the lateral surface of the iliac shaft. Their shafts are rather stout. However, their stratigraphic range spans the Coniacian to lower–middle Campanian. Morphotype 8 from the middle Santonian is similar in general proportions, but differs in having two rounded and slightly divergent mounds on the lateral surface of the iliac shaft.

Morphotype 5 is similar to the previous four in general shape of the bone; however, it differs in the relatively larger size of its acetabulum. It was recorded from the upper Santonian and lower–middle Campanian.

Morphotype 4 is clearly different from morphotypes 1–3 in its slender shaft and in having the acetabulum shifted toward the anteroventral margin of the bone. It is restricted to the middle Santonian through lower Campanian.

Morphotype 6 is similar to morphotypes 1–3, but differs in that its acetabular region is symmetrical, with the acetabulum in the middle. Its stratigraphic record is from the upper Santonian or lower Campanian.

Morphotype 7 is well distinguished from all others in this group by a thin shaft, a straight dorsal margin terminated by a point, and by its ventrally shifted acetabulum. It was recorded from the Turonian.

Morphotype 9 clearly differs from all others (irregardless of the size of the bone) by its large acetabulum extending almost to the dorsal margin of the bone and by its slender iliac shaft. Unfortunately, it is represented by only a single specimen (UMNH VP 13336), from the upper Campanian. This specimen is also notable because it documents the presence of large anurans in the upper Campanian.

Morphotypes 10 and 11 resemble one another, and differ only in the size and position of the acetabulum and in the presence or absence of a horizontal rounded ridge. Both are from the upper Campanian.

Morphotypes 12 and 13 are similar to one another in the shape of the anterodorsal margin of the acetabulum, which is unusual in being discontinuous. Morphotype 12 is known from the upper Cenomanian (UMNH VP 13071) and also the lower or middle Campanian (UMNH VP 18305). UMNH VP 13493 (morphotype 13) is from the upper Santonian or lower Campanian and it differs in the shape of the acetabular region and the iliac shaft.

Morphotype 14 is based on one fragmentary specimen, UMNH VP 13485, but it is distinct in having a dorsal margin that is moderately depressed at the level of the anterior margin of the iliac shaft. It was recovered from the upper Santonian or lower Campanian Paul's locality.

Morphotype 15, although also based on a fragmentary specimen (UMNH VP 18477), is profoundly different from all others in having an extremely large acetabulum and by the unusual shape of its acetabular region. It is known only from the upper Santonian.

Morphotype 16 is dubious, but it seems to be characterized by its straight and horizontal dorsal margin. It is from the upper Santonian or lower Campanian Pinto Flats locality.

The remaining two morphotypes (17 and 18) generally resemble the other morphotypes, but differ in that the acetabular surface closest to the iliac shaft is broadly convex, but the rest of the surface is steeply declined in the opposite direction. Such an acetabular morphology is characteristic of *Nezpercius*, as described by Blob et al. (2001) from the Campanian age Judith River Formation in Montana. One of the Utah morphotypes (17) bears an elevated rugosity on the dorsolateral side of its shaft, which is a key diagnostic character of *Nezpercius*. All our specimens referable to these two morphotypes (and thus to the genus *Nezpercius*) are from the lower or middle Campanian, which is in agreement with the stratigraphic occurrence of the three specimens described by Blob et al. (2001). Although *Nezpercius* was described as an anuran, its distinctive ilia (which are the only bones known for the taxon) have recently been reinterpreted as belonging to a caudate amphibian (Gardner et al., 2010). We have retained the *Nezpercius*-like ilia from Utah here to highlight their presence in the Utah sequence and to emphasize that these problematic ilia are similar in many respects to, and thus may easily be mistaken for, ilia of unequivocal anurans. For a more detailed list of similarities and differences between ilia of anurans and caudates, see Gardner et al. (2010).

DISCUSSION

The collection used in this study from the Upper Cretaceous of southwestern Utah is the largest sample of anuran ilia yet reported from a comparable area and stratigraphic interval in North America. Even a cursory glance at Figs. 12.4–12.7 and 12.8–12.11 indicates a diversity of ilia were recovered. The question naturally arose whether these ilia could be used for stratigraphic correlations. Unfortunately, this is not feasible at present. Although we have identified 65 iliac morphotypes among the nearly 200 specimens used in this study, there are several problems with using those morphotypes for biostratigraphic correlation. Many of the morphotypes differ only subtly from one another. From a practical standpoint, these morphs may be challenging for nonspecialists to identify in their screen-wash samples. Equally importantly, some of these morphotypes may simply be variants within a broader range of biologically distinct taxa. What we have recognized here as different morphotypes could conceivably be some combination of ontogenetic, sexually dimorphic, temporal, or individual variants of a lesser number of temporally longer-ranging species. The very real possibility that some of those iliac morphotypes are from conspecific individuals is difficult to evaluate, because many of the morphotypes are known by just one or only a few specimens and from only one or a few localities. It is possible that certain iliac morphotypes had a broader stratigraphic range than what is suggested by our current, relatively small samples. Some morphotypes admittedly are more distinctive (e.g., group 3, morphotypes 14 and 15), yet their utility remains limited because they are known by a single specimen each from just one locality. Fortunately, collecting and processing of previously sampled and new microvertebrate localities in the study area continues. As sample sizes of anuran ilia increase, it should be possible to refine identifications of anuran iliac morphotypes (perhaps even assign some of those to biological taxa) and better resolve their stratigraphic ranges.

At a general morphological level, however, we were able to record some potentially interesting patterns in the stratigraphic occurrences of the three groups of ilia. The most remarkable is the relatively poor record of the ilia with a dorsal tubercle in the lower and middle Santonian and in the upper Campanian. Another peculiarity is the relative absence of ilia with an oblique groove in the upper Santonian or lower Campanian. Although these patterns may accurately reflect the presence or absence (or relative abundances) of taxa at different times, they may simply be an artifact of sample sizes (which generally were small; i.e., less than a dozen ilia per locality) or particular depositional conditions in the localities.

The predominance of ilia without a dorsal tubercle in Mesozoic anurans is surprising, and it contrasts with the situation in the Cenozoic when most anurans have a dorsal tubercle. It is interesting that almost all known Mesozoic frogs also lack a dorsal crest on the iliac shaft (in life, this crest separates the origins of the iliacus externus and coccygeoiliacus muscles from each other; Přikryl et al., 2009). A notable exception from North America is *Paradiscoglossus americanus* Estes and Sanchíz, 1982, which is known by two ilia from the upper Maastrichtian Lance Formation of Wyoming that each bear a relatively tall and anteriorly elongate dorsal crest (Estes and Sanchíz, 1982; Gardner, 2008); no examples of this kind of ilia were identified from any of our older Utah localities. It is not clear whether the dorsal tubercle and the dorsal crest appeared at the same or different times during the evolution of anurans as a consequence of a shift in locomotor behavior or whether the widespread occurrence of these structures in Cenozoic anurans is associated with the appearance and diversification during the Paleogene and Neogene of more derived groups (e.g., Bufonidae, Ranidae, and Hylidae) that now dominate most contemporary anuran faunas (Rage and Roček, 2003). We do not even know whether the dorsal tubercle in the Early Triassic proanurans *Triadobatrachus* and *Czatkobatrachus* (Rage and Roček, 1989; Evans and Borsuk-Białynicka, 2009) is homologous with those in true anurans. Additional material is needed to resolve these kinds of problems. Further collection and study of specimens from stratigraphically extensive sequences of localities – such as the sequence in southwestern Utah used for this study – should help establish when key iliac features appeared during the evolution of anurans and may allow us to better understand how significant those novelties might have been to the success of particular anuran groups.

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