

MESOZOIC ANURANS FROM LIAONING PROVINCE, CHINA, AND PHYLOGENETIC RELATIONSHIPS OF ARCHAEOBATRACHIAN ANURAN CLADES

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ABSTRACT—Two Jurassic–Cretaceous anurans are described based on well-preserved specimens from the lower part of the Yixian Formation, western Liaoning Province, northeastern China. One specimen, from the Heitizigou site, documents a new genus and species, and the second, from the Sihetun site, is the holotype and only known specimen for the recently named *Callobatrachus sanyanensis*. Phylogenetic relationships of the major archaeobatrachian anuran clades are investigated with incorporation into the analysis of selected (well-established) early fossil taxa. The new taxon named and described in this paper is placed as the representative of a distinct archaic anuran clade, and *Callobatrachus* is considered to be an ingroup member of the Discoglossidae, constituting the earliest record of the family from Asia. The oldest known fossil anuran, *Prosalirus* from the Early Jurassic of Arizona, is grouped with *Notobatrachus* as sister taxa, and the two together form the most basal clade of Anura. Contradicting the widely accepted Leiopelmatidae–Discoglossidae sistergroup relationship, new evidence places the Leiopelmatidae as the most basal extant familial group and the sister group to other archaeobatrachian clades. The relationships and classification of the major archaic anuran clades are discussed, based on the phylogenetic results of this study.

INTRODUCTION

Frogs and toads are lissamphibians that are classified in the order Anura, superorder Salientia (Duellman and Trueb, 1986; see also Trueb, 1993 for comments). The superorder Salientia, as recently defined, includes the Early Triassic Proanura (*Triadobatrachus* from Madagascar) and the taxonomically diverse Anura (Duellman and Trueb, 1986; Milner, 1988; but see also Evans and Borsuk-Bialynicka, 1998 for a different definition of Anura). The recent discovery of *Czatkobatrachus* from Poland (Evans and Borsuk-Bialynicka, 1998) has added a second Triassic salientian, which is more derived than *Triadobatrachus* (see phylogenetic discussion below). Taxonomically, the Order Anura includes some 4,400 extant species in more than 300 genera among 24 families, and approximately 100 fossil species in 50 genera that are known from the Early Jurassic through Neogene (data from Duellman and Trueb, 1986; Glaw and Köhler, 1998; Sanchiz, 1998; Köhler et al., 2000).

As a major lissamphibian group, the order Anura holds an important position in vertebrate history, although the fossil records of many anuran clades are poorly documented (Trueb and Cloutier, 1991a, b; Sanchiz, 1998). The evolutionary history of anurans can be traced back to the Early Jurassic, documented by two genera and species: *Prosalirus bitis* Shubin and Jenkins, 1995 from the Kayenta Formation of Arizona (see also Jenkins and Shubin, 1998); and *Vieraella herbstii* Reig, 1961 from the Roca Blanca Formation of Argentina. The former represents the oldest anuran recognized, and was assigned to the monotypic family Prosaliridae with uncertain relationships to other families (Shubin and Jenkins, 1995). The latter taxon was classified in different groups by different authors (Casamiquela, 1965, Notobatrachidae; Estes and Reig, 1973, possibly Ascaphidae; Báez and Basso, 1996, a basal member of Salientia; Sanchiz, 1998, family incertae sedis; but see phylogenetic discussion in this paper). Besides these, only two other Jurassic frogs are represented by fairly well preserved and articulated specimens: *Notobatrachus degiustoi* Reig, 1955 from the Middle–Late Jurassic La Matilde Formation of Argentina (Reig, 1957; Estes and Reig, 1973; Báez and Basso, 1996), and the pipoid *Rhadinoosteus parvus* Henrici, 1998 from the Late Jurassic Morrison Formation of Utah (Henrici, 1998). Following the Jurassic,

there is a great shortage of anuran fossils of various familial groups during the Early Cretaceous (see Sanchiz, 1998; Roček, 2000). *Eodiscoglossus santonjae* from the late Berriasian or early Valanginian beds of Spain (formerly reported as Late Jurassic; see Villalta, 1957; Hecht, 1970; Estes and Sanchiz, 1982; Evans et al., 1995) and three genera of pipids from Israel (see Sanchiz, 1998) are the only Early Cretaceous frogs that are known from articulated material. Discovery of additional fossils of this age would greatly clarify early anuran evolution.

Recent discoveries from western Liaoning Province, China, include two articulated anuran specimens from this important interval. The Jurassic–Cretaceous fossil beds, from which these specimens originate, are located in the Sihetun area, near Beipiao (Fig. 1). The age of the fossil beds was dated as 124.6 Ma by Swisher et al. (1999) and 147.1 Ma by Lo et al. (1999). Herein, we describe the two specimens and provide an assessment of their relationships with other archaeobatrachians. One specimen represents a new genus and species belonging to a distinct archaic anuran clade, and the other documents an early discoglossid recently named and briefly described as *Callobatrachus sanyanensis* (Wang and Gao, 1999). Both specimens were collected from the lower part of the Yixian Formation, in association with the well-known feathered dinosaur and primitive bird fossils (Wang et al., 1998). The age of the formation has been regarded as either Late Jurassic or Early Cretaceous (Jin, 1996; Ren et al., 1997; Ji et al., 1999; Wang, 1990, 1998) based on biostratigraphic correlation, but recent radiometric dating of rock samples of the formation has yielded conflicting results (Swisher et al., 1999; Lo et al., 1999). Historically, the early reports of vertebrate fossils from western Liaoning Province begin in the early 1940s, and Endo (1940) published a faunal list that included the anuran “*Jeholobatrachus intermedius* Endo (M. S.)” Although this represents the first literature record of fossil amphibians from western Liaoning, the name never was validated by publication of the manuscript, and the specimen seems to have been lost during the World War II, together with other important fossils, including the holotypes of the diapsid *Monjurosuchus* and the mammal *Endotherium*. Nonetheless, the two new specimens described here from Liaoning are so far the best-preserved Mesozoic anuran fossils

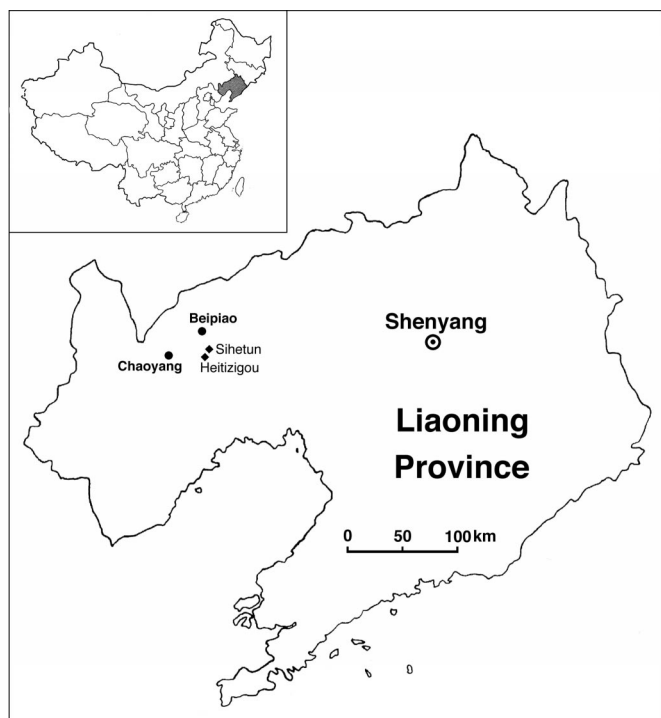


FIGURE 1. Area map showing the frog fossil localities in western Liaoning Province, northeast China.

from China, and study of them has significant phylogenetic and biogeographic implications.

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; GMV, vertebrate fossils in the collections of the National Geological Museum of China, Beijing, China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Anatomical Abbreviations—angs, angulosplenic; carp, carpal; cla, clavicle; cle, cleithrum; col, columella; cora, coracoid; den, dentary; fem, femur; fibl, fibulare; frpa, frontoparietal; hum, humerus; il, ilium; im, intermedium; isch, ischium; max, maxilla; na, nasal; otc, otic capsule; pmx, premaxilla; pp, prepollex; pro, prootic; psph, parasphenoid; ptg, pterygoid; qj, quadratojugal; rad, radiale; radu, radioulina; sacd, sacral diapophysis; scap, scapula; sph, sphenethmoid; sq, squamosal; supsc, suprascapula; tibf, tibiofibula; tibl, tibiale; ul, ulnare; uro, urostyle; vom, vomer; Y, Element Y.

SYSTEMATIC PALEONTOLOGY

Class AMPHIBIA Linnaeus, 1758
 Subclass LISSAMPHIBIA Haeckel, 1866
 Superorder SALIENTIA Laurenti, 1768
 Order ANURA Rafinesque, 1815

Taxonomic Remarks—The Anura are considered to be a major salientian group that includes some 24 extant and one extinct tailless amphibian families (e.g., Köhler et al., 2000; Sanchiz, 1998). Ford and Cannatella (1993:99) provided a node-based definition of the Anura: “the ancestor of living frogs and all of its descendants.” The stem-based name Anura used in this paper refers to a higher group that includes not only all living anurans, but also several fossil taxa that are more closely related to living frogs than to proanurans (see phylogenetic discussion below).

Family incertae sedis
 Genus *MESOPHRYNE*, gen. nov.

Etymology—*Mesos* and *phryne* (Gr.), meaning “middle toad,” in reference to the Mesozoic age of the anuran from the “Middle Kingdom,” China.

Type Species—*Mesophryne beipiaoensis*, sp. nov.

Diagnosis—As for the type and only known species.

Known Distribution—Known only from the type locality and horizon.

MESOPHRYNE BEIPIAOENSIS, sp. nov.
 (Figs. 2–4)

Etymology—Beipiao (place name), referring to the city approximately 25 km north of the type locality.

Holotype—IVPP V11721, nearly complete skeleton with impressions exposed as part and counterpart on shale slabs.

Type Locality and Horizon—Heitizigou, approximately 25 km south of Beipiao City, Liaoning Province; lower part of the Yixian Formation (Wang et al., 1998).

Diagnosis—A primitive anuran differing from other anurans in having the following combination of character states: Skull large in relation to size of body; squamosal/maxillary contact present; vertebral column greatly shortened, but having nine presacrals; free ribs present in association with Presacrals II–IV; urostyle short, only slightly longer than half length of femur; prepollex strongly expanded.

This taxon differs from *Callobatrachus* in having squamosal/maxillary contact; procoelous vertebral centra; short urostyle approximately 60% of length of femur; transverse processes on posterior presacrals laterally oriented; ilial crest absent; prepollex enlarged; tibiofibula shorter than femur; and Digit IV in pes proportionally much longer (91.7%) in relation to the length of the tibiofibula.

Description

The holotype and only known specimen (IVPP V11721) is a nearly complete skeleton exposed as part and counterpart (Figs. 2, 4). The skeleton has a snout–vent length of 69 mm, and is dorsoventrally compressed, as commonly seen in other vertebrate specimens from the same horizon. Most elements of the skeleton remain in their original positions, but the skull is slightly distorted and some elements of the pectoral girdle are slightly displaced.

Skull—The skull is proportionally short and wide, having the maximum width (across the otic capsules) approximately 142% of the total length (34 mm vs. 24 mm). No dermal sculpture can be seen on the lateral surface of the maxillae or on the squamosals.

The premaxillae are incompletely preserved, and due to crushing, are medially separated by the anterior end of the left dentary. No palatine process of the premaxilla is developed, and the posterior aspect of the element bears a simple shelf as shown on V11721A. The distal end of the premaxilla fits into the notch of the maxilla, and no posterolateral process is developed. Each premaxilla is about 6 mm wide, and bears slender and conical teeth. Sixteen teeth are present on the incomplete left element, and six are exposed on the right element.

Only the left nasal is preserved, but it is incomplete and the condition of its anterolateral margin (concave or straight) is uncertain. The medial contact of the nasals, the nasal-premaxillary contact, and the condition of the rostral process of the nasal are also uncertain due to poor preservation of the area. The frontoparietal is exposed lateral to the cultriform process of the parasphenoid on the ventral face (Fig. 4). The exposed anterior portion shows no dermal sculpture on the dorsal surface, resembling in that respect the lateral surfaces of the max-



FIGURE 2. *Mesophryne beipiaoensis*, gen. et sp. nov. (IVPP V11721A, holotype), nearly complete skeleton and impressions in dorsal view.

illa and the squamosal. Whether the frontoparietal is paired or azygous cannot be determined, nor can the condition of the dorsal exposure of the frontoparietal fontanelle.

The maxillae, exposed in dorsolateral view, are proportionally short and thick in relation to the overall dimensions of the skull. In life, the posterior end of the maxilla would have articulated medially with the anterolateral surface of the quadratojugal, but the latter element (exposed on the right side on V11721A slab) as preserved has been slightly detached from the maxilla. A small but well-defined triangular postorbital process of the maxilla is exposed posterodorsally and is still in articulation with the zygomatic ramus of the squamosal (V11721B slab; Fig. 4).

The prootic and exoccipital probably are fused. The left columella is identifiable, although it has been slightly displaced. It has a circular footplate and a short, slightly bent shaft. The squamosal is triradiate with a clearly defined zygomatic ramus (5 mm long) contacting the maxilla. The ventral ramus is slightly longer (7 mm) and extends to meet the quadratojugal. Although the tip of the otic ramus is broken, it is obviously short and slenderly built, as observed from the right squamosal. Medially, the squamosal has likely lost its contact with the skull table as in other anurans, although the skull table is not exposed on the specimen.

The palatal aspect of the skull is best shown on the V11721B slab (Fig. 4). Both vomers are mostly broken, and are difficult to restore to their original configuration. Medially, two small pieces of bone may represent the broken tips of the prechoanal processes of the vomers; the conditions of the other parts of these bones (position of the anterior process of vomer, vomer-

choana relationship, postchoanal process of vomer, dentigerous process of vomer) as well as the vomerine dentition cannot be determined. The presence or absence of a palatine bone cannot be ascertained. The sphenethmoid is a single element with a notched posterior border, where both the dorsal and ventral parts of the element are exposed on the specimen.

The triradiate pterygoids are well preserved on both sides, but have been slightly displaced from their original positions. The anterior ramus (7 mm long) extends to contact the posteromedial part of the maxilla. The medial ramus (5 mm long) extends medially along the anterior surface of the otic capsule. The relationships between the medial ramus of the pterygoid and the parasphenoid is uncertain owing to the distortion of this part of the skull. The posterior ramus (6 mm long) is thinner than the other two, and extends posterolaterally to the quadratojugal.

The parasphenoid has its anterior tip and the right ala broken; otherwise it is complete. This bone has an inverted "T" configuration, as commonly seen in other anurans, with the crossbar of the "T" in a posterior position. The ventral surface of the parasphenoid is generally smooth and ventrally convex, but the distal end of the left ala is weakly striated. The ala is laterally oriented, crossing the width of the otic capsule. The anteroposterior width of the ala is narrower than one-third of the distance between the lateral ends, and no posterolateral notch is developed on the parasphenoid alae. Because of breakage, neither the anterior extent of the cultriform process (to or behind the level of the vomers) nor the morphology of the posteromedial process of the parasphenoid can be determined.

Mandible—The mandibles are mostly preserved on the

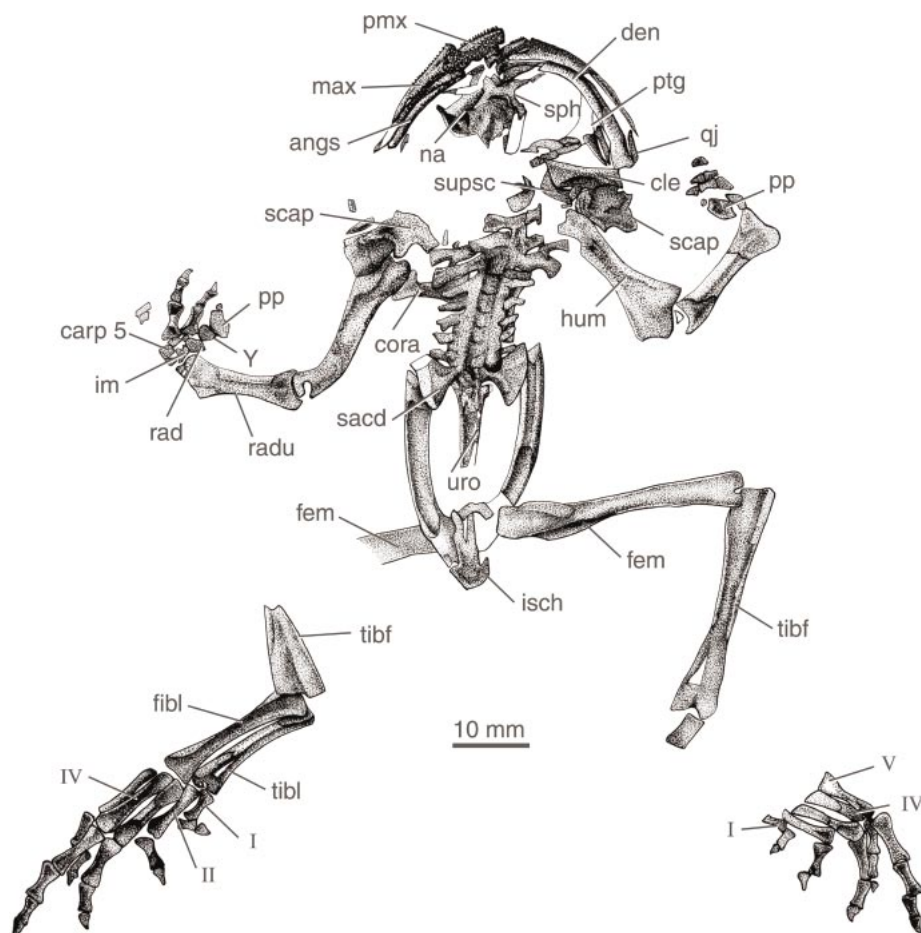


FIGURE 3. *Mesophryne beipiaoensis*, gen. et sp. nov., line drawing of IVPP V11721A (holotype).

V11721A slab, and are exposed in dorsal view (Figs. 2, 3). Although nearly covered by the maxillary arch, the slightly expanded anterior end of the mandible represents a well-ossified mentomeckelian bone near the mandibular symphysis. Because of crushing of the skull, the two mandibles are disarticulated at

the symphysis and separated by the right premaxilla. The dentary has a thin crest that is edentate. The angulosplenic is strong and thick, with its anterior part attaching to the medial surface of the dentary. Posteriorly, the angulosplenic is slightly expanded, and the craniomandibular joint is located lateral to the otic capsule.

Vertebral Column—The vertebral column is composed of at least nine presacral vertebrae, a single sacral vertebra, and a urostyle. The presacral vertebral series is proportionally short (about 23 mm long) in relation to the snout-vent length of the frog. Eight presacrals are exposed on the specimen. The anteriormost presacral exposed, however, obviously is not the atlas, because it lacks cotyles but bears a pair of free ribs. This probably is the Presacral II, which is unfused to the atlas as evidenced by the smooth anterior surface of the centrum. The atlas itself probably was broken off or crushed into the skull. The presacral vertebrae are procoelous, and in this feature, *Mesophryne* differs from *Callobatrachus* (opisthocelous) from the same area and horizon. The neural arches are imbricated and roof the spinal canal, as seen in other primitive anurans except *Alytes* and leiopelmatids.

The transverse processes of Presacral II are short and laterally oriented, whereas those on Presacrals III–VII are directed posterolaterally. The longest pair of processes is associated with the Presacral V. The last two presacrals have spikelike transverse processes extending horizontally (the processes on the right side of the specimen are anterolaterally directed due to distortion). Three pairs of free ribs are present in association with Presacrals II–IV (Figs. 2, 3). The first pair of ribs is hatch-

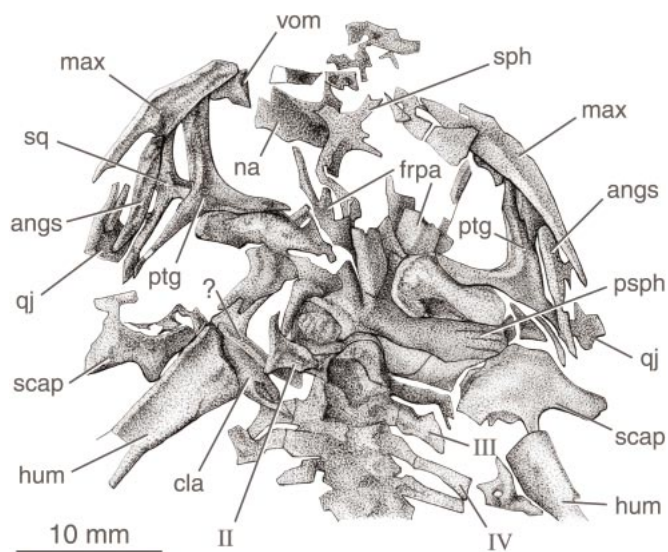


FIGURE 4. *Mesophryne beipiaoensis*, gen. et sp. nov., line drawing of skull and pectoral girdle in ventral view (IVPP V11721B, holotype).

et-shaped, best shown on the right side of the specimen. The second pair is relatively long and bifurcated, with a small and posterolaterally extending branch (best shown on the left side). The third pair is short and robust, having a slightly expanded lateral end. The sacral diapophysis is broadly expanded, the "butterfly-wing" type of Clarke (1988). The angles of the leading and trailing edges of the diapophyses to the midline are approximately 45° and 60°, respectively.

The urostyle is mostly preserved on the V11721A slab, but a small posterior portion is preserved on the V11721B slab. The urostyle is proportionally short, having a length of 18 mm, which is approximately 60% of the length of the femur. The condylar pattern of the urostyle cannot be observed as the urostyle is still in articulation with the sacrum. However, a vestigial postsacral transverse process can be observed on the right side of the proximal end of the urostyle, and a foramen for a spinal nerve opens dorsally at the base of the transverse process.

Pectoral Girdle and Forelimb—The pectoral girdle is of arciferal type, as indicated by the curved right clavicle that is preserved on the V11721B slab (Fig. 4). The lateral end of the clavicle is slightly expanded for articulation with the scapula, but the remaining portion shows the curved nature of the element. A slender bone (unidentified) obliquely crosses the clavicle lateral to the first free rib. With an expanded medial end, the left coracoid is incompletely preserved on V11721A slab. The element is preserved as a horizontal bone, but it likely has been slightly rotated from its original oblique position in keeping with the slight dislocation of the left forelimb (Figs. 2, 3).

The scapula is preserved on both part and counterpart slabs. It has a concave posterior border, while the leading edge is obscured by other bones. The scapula is approximately 9 mm long and is 6 mm wide at the distal end. The right cleithrum is preserved on the V11721A slab, anterior to the right scapula (Fig. 3). It is compressed, together with the suprascapula, onto the dorsal plane, and hence the dorsolateral surface of the bone is exposed. The cleithrum is elongated, having a straight anterior border; however, whether or not it is distally bifurcated cannot be determined. The right suprascapula is partly exposed beneath the right cleithrum. It is well ossified, but its general shape cannot be restored because the bone is badly broken.

Both humeri are well preserved, and each shows a robust crista ventralis proximally. Distally, the humeral condyle is well ossified, although the actual size and morphological details cannot be observed on either side. The fused radioulna is approximately two-thirds of the length of the humerus (15 mm vs. 22 mm). The olecranon process is well defined.

There are seven ossified carpal elements preserved in the wrist of the left forelimb. Following the terminology of Fabrezi and Alberch (1996), we identified these as: a free intermedium, element Y, radiale, ulnare, and carpals 2, 3, and 5. Two digits and two prepollical elements are preserved in the wrist of the left forelimb (Figs. 2, 3). Identification of the prepollex is based on its position medial to Digit II and its association with a small distal segment. The prepollex is broadly expanded, with a small distal prepollical segment. Each of the two digits preserved on the left side has two phalanges in the complete finger, and these apparently represent Digits II and III as evidenced by their phalangeal formula and positions. The tips of the terminal phalanges are pointed and claw-shaped.

Pelvic Girdle and Hind Limb—The pelvis is preserved in articulation with the vertebral column and the hind limbs, without significant distortion. The length of the ilial shaft (20 mm) is slightly shorter than that of the preserved eight presacrals (21 mm). The ilial shaft lacks a dorsal crest, but having an extremely weakly developed dorsal protuberance close to the acetabulum. The acetabular region is well exposed on the right side on V11721B. A well-defined supra-acetabular fossa is present dorsal to the acetabulum. The preacetabular angle (i.e., the angle

between the ilial shaft and the preacetabular margin) is about 56°. The dorsal acetabular expansion is weakly developed, but a ventral acetabular expansion is best shown by the impressions of the right ilium. In dorsal view, the ischia are posteriorly fused to form an inverted triangle, but are anteriorly bifurcated to form two narrowly separated bars (Figs. 2, 3). No ossified pubis or epipubis is identifiable.

The hind limb (best preserved on the V11721A slab) in its entirety is longer than that in *Callobatrachus sanyanensis*, but the tibiofibula (30 mm long) is slightly shorter than the femur (31 mm long). The fibulare (18 mm) is slightly longer than the tibiale (17 mm), and hence, the proximal tarsal segment of this new form is 60% of the length of the tibiofibula. The tibiale and the fibulare are fused at their proximal and distal ends, leaving an extremely narrow gap between the two elements. The pes has the typical anuran phalangeal formula of 2-2-3-4-3, and the relative length of the digits is $I < II < V < III < IV$. The longest Digit IV is approximately 91.7% of the length of the tibiofibula. No ossified tarsal or prehallal elements can be identified on either limb, and these elements were probably absent as bony structures.

Comparison and Discussion

As described above, the new taxon *Mesophryne beipiaoensis* differs from *Callobatrachus sanyanensis* (from a nearby site; see below) primarily in having procoelous vertebral centra, an urostyle of the same length as the proximal tarsal segment, a tibiofibula shorter than the femur, and proportionally a much longer fourth pedal digit (91.7%) in relation to the length of the tibiofibula. Compared to other known anurans, the new taxon is morphologically distinct in having: a large skull in relation to body size, greatly shortened vertebral column (although still consisting of nine presacrals), strongly expanded prepollex, and a proportionally short urostyle that is only 60% of length of femur.

In terms of the evolution of anurans, one interesting feature of this early frog is the presence of free ribs in association with Presacrals II–IV. Free ribs are only present in several primitive anuran clades, including extant leiopelmatids and discoglossids. In addition, free ribs occur in extant pipids and extinct palaeobatrachids at subadult stages but ankylose to the transverse processes in adults (see Špinar, 1972; Duellman and Trueb, 1986). The ossification of the Mentomeckelian and columella bones indicates that the holotype of *Mesophryne* is a fully developed adult that bears free ribs. The distribution pattern of this character among anurans, in keeping with the ontogenetic evidence from pipids and palaeobatrachids, shows a strong evolutionary trend towards reduction in the number, and eventually loss, of ribs (see Lynch, 1973; Trueb, 1973).

Family DISCOGLOSSIDAE Günther, 1859

Taxonomic Remarks—The Discoglossidae are a group of primitive frogs that include 17 living species in five genera and a number of fossil taxa (Duellman and Trueb, 1986; Duellman, 1999). The familial status of the group is recognized by most authors (e.g., Estes and Sanchiz, 1982; Frost, 1985; Duellman and Trueb, 1986; Clarke, 1988; Báez and Basso, 1996; Sanchiz, 1998), but is rejected by others (e.g., Slabbert and Maree, 1945; Cannatella, 1985; Ford and Cannatella, 1993). Dubois (1987) discussed the nomenclatural problems of this taxonomic group, and the monophyly of the group is discussed below.

Genus CALLOBATRACHUS Wang and Gao, 1999

Type Species—*Callobatrachus sanyanensis* Wang and Gao, 1999.

Diagnosis—As for the type and only known species.

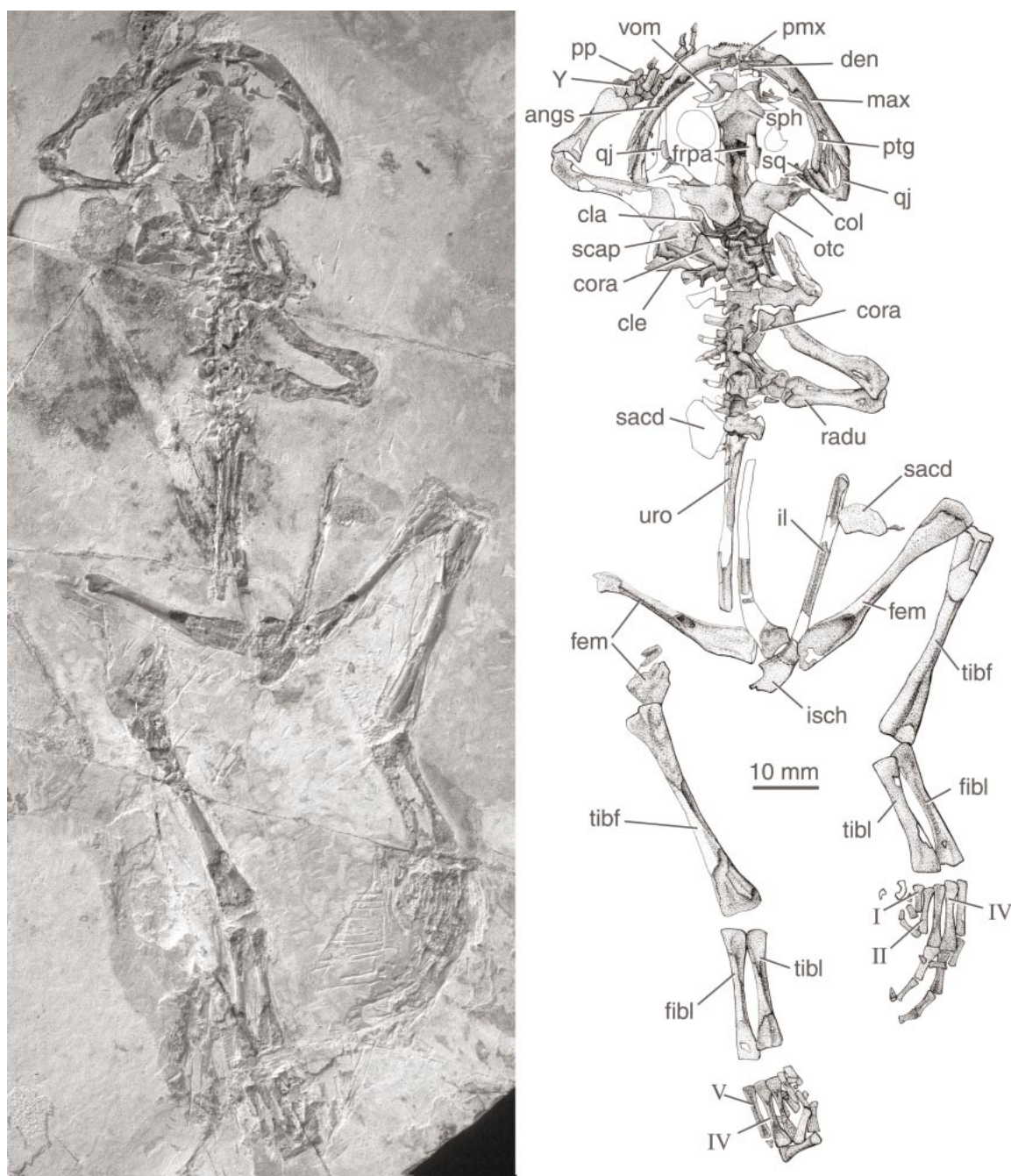


FIGURE 5. *Callobatrachus sanyanensis* (IVPP V11525, holotype), nearly complete skeleton and impressions of bones exposed in dorsal view.

Known Distribution—Known only from the type locality and horizon.

CALLOBATRACHUS SANYANENSIS Wang and Gao, 1999
(Fig. 5)

Holotype—IVPP V11525, nearly complete skeleton and impressions of bones exposed in dorsal view on a shale slab.

Type Locality and Horizon—Site near Sihetun, Beipiao City, Liaoning Province, northeastern China; lower part of the Yixian Formation (Wang et al., 1998).

Diagnosis (Revised from Wang and Gao, 1999)—Sharing with extant discoglossids derived character states including: presacral vertebrae stegochordal and opisthocoelous; leading

edge of scapula straight; anterior margin of scapula overlain by clavicle; and coracoid elongate, with rounded sternal end. Differing from other discoglossids in having a combination of the following character states: frontoparietal having parallel lateral borders; presacral vertebrae nine in number; cleithrum nonbifurcate; proximal tarsal segment longer than one-half length of tibiofibula.

Description

Only a brief description of *Callobatrachus sanyanensis* was provided by Wang and Gao (1999) in order to validate the taxonomic name. Herein, an explicit description of the holotype and the only known specimen for the taxon is provided.

Exposed in dorsal view, the specimen as preserved includes the cranial and postcranial skeleton, with impressions of the missing parts (Fig. 5). Most of the skeletal elements are preserved in their original positions, but the pelvic girdle and the hind limbs are shifted to the right of the rest of the skeleton. The total body length (snout-vent) is estimated as approximately 94 mm (100 mm as preserved with slight dislocation of the pelvis and hind limbs), and the specimen obviously represents a fully developed, adult individual as indicated by its ossification of the Mentomeckelian and columella bones (see below).

Skull—The skull is short and wide, with a broadly rounded snout. Compressed dorsoventrally, the maximum width of the skull across the otic capsule region is 125% of the total length (35 mm vs. 28 mm) from the tip of the snout to the occipital condyles. All of the cranial elements lack dermal sculpture, differing in this respect from some pelobatids and many other anurans (Trueb, 1973), including certain fossil taxa that have been referred to the Discoglossidae (Sanchiz, 1998).

Both premaxillae are preserved, and each laterally articulates with the notched anterior end of the maxilla. The alary processes of the premaxillae are broken off. The pars dentalis of each premaxilla bears 18–20 slender and conical teeth, which are slightly expanded linguolabially. The medial aspect of the premaxilla is not exposed; therefore, whether a palatal process is present cannot be determined.

The maxillae are incompletely preserved on both sides, and the dorsal process of each is largely missing. Each maxilla anteriorly has a well-defined notch for articulation with the premaxilla, and posteriorly becomes narrow and pointed, articulating with the quadratojugal. Like the premaxilla, the maxilla bears fine pedicellate teeth (approximately 40–50) that have the pedicels slightly expanded linguolabially and compressed along the tooth row. The quadratojugal (preserved on both sides) articulates with the maxilla to form a complete maxillary arcade. By comparison, in *Leiopelmatidae* and *Pipidae*, the quadratojugal is missing and the arcade is incomplete (Trueb, 1993). The posterior end of the quadratojugal is hooked anteromedially in IVPP V11525 to form the articulation with the pterygoid and the squamosal.

The nasals (preserved as impressions) are paired elements with a midline contact, and each has a short rostral process anteromedially. The configuration of the anterior border of the nasal is unknown owing to poor preservation. The posterolateral process of the nasal does not contact the maxilla, but it does form most of the anterior margin of the orbit.

The frontoparietals are probably paired as indicated by the straight medial border of the right element. Although incompletely preserved, the parallel lateral borders give a rectangular configuration to this part of the skull. As in other discoglossids, the frontoparietal lacks a supraorbital flange. The frontoparietal fontanelle is present, but the extent of its exposure is uncertain (contra Wang and Gao, 1999). Also, the condition of the posterolateral process of the frontoparietal cannot be determined because of breakage.

Preserved on the right side, the squamosal is T-shaped and has no contact with the maxilla or the skull table. The ventral ramus is thin, meets the quadratojugal ventrally. The otic and zygomatic rami of the squamosal are short, each about 2.5 mm long or about half the length of the ventral ramus.

The otic capsule is incompletely preserved on both sides, but the prootic and exoccipital are apparently fused. The capsule articulates anteriorly with the well-developed posteromedial process of the pterygoid. The columella (or the stapes of other authors) is well exposed on the left side, while the right element is partially exposed (Fig. 5). This element is present in most frog taxa but is absent in *leiopelmatids* and *rhinophrynids* (Trueb, 1993). The columella of *Callobatrachus* is short, rod-

like, laterally extends from the otic capsule (fenestra ovale) to the posterior of the squamosal where the tympanum was positioned in life.

Because the skull roof is broken, some palatal and neurocranial elements are exposed in dorsal view. The vomer is incompletely preserved on both sides, with the anterior process lying posterior to the premaxilla-maxillary articulation. The vomer lacks contact with the maxillary arch, and has well-defined prechoanal and postchoanal processes; the latter forms a narrow angle with the anterior part of the vomer. Vomerine teeth cannot be observed, because the element is exposed in dorsal view. No palatines are identifiable, and they are probably absent, as in discoglossids and many other anuran groups.

The sphenethmoid is single and has a triangular anterior end between the vomers. The posterior part of the element is covered by the frontoparietals. The optic foramen, which normally opens between the sphenethmoid and the prootic, cannot be observed, as this part of the skull is exposed in dorsal view. Posterior to the triangular portion of the sphenethmoid, the anterior tip of the parasphenoid is exposed. The remainder of the cultriform process and the posterolateral extensions (alae or wings) are covered by other cranial elements.

The pterygoid is triradiate, with its anterior ramus attaches to the medial aspect of the maxilla at a point slightly posterior to the midlevel of the maxillary tooth row. This contact is best shown on the right side of the specimen, while the left pterygoid has been separated from the maxilla by the slightly dislocated dentary (Fig. 5). The medial ramus is about half the length of the anterior ramus, and articulates with the anterior wall of the otic capsule; its relationship to the parasphenoid cannot be determined. The posterolateral ramus of the pterygoid is slightly shorter than the medial ramus, but it extends posterolaterally and contacts the squamosal.

Mandible—The mandibular elements are mostly obscured by the maxillary arch, but the symphysis and some other parts are exposed in dorsal view. The edentate dentary has a thin dorsal crest as commonly seen in other anurans. The mentomeckelian bone is a small, rectangular element, which is slightly expanded at the symphysis. The anterior part of the angulosplenic as preserved is slightly detached from the dentary on both sides of the specimen, and is exposed as a slender spike medial to the dentary. The craniomandibular joint is located lateral to the otic capsule (see Báez and Púgener, 1998 for evaluation of this character).

Vertebral Column—The vertebral column consists of nine presacral vertebrae, a single sacral vertebra, and a free urostyle that has a bicondylar articulation with the sacrum. The first two presacrals are unfused, typical of other discoglossids. The neural arch is incompletely preserved on each of the first three vertebrae, while on the others it is mostly broken off. The arches on the first three presacrals are strongly imbricated. The centra of last two presacrals (VIII and IX) are opisthocelous. Three pairs of free ribs, preserved as bony elements or impressions, are present in association with Presacrals II–IV. The first pair of ribs is hatchet-shaped, the second pair has a well-defined uncinat process, and the third pair is simply a short bar. The transverse processes are consistently short and slant strongly anterolaterally on the Presacrals VII–IX, slant less strongly anterolaterally on the Presacrals II and VI, and are oriented laterally on Presacrals III and V.

The sacral vertebra is badly broken. The left diapophysis (preserved only as an impression) is broadly expanded antero-posteriorly, the shape of which is more of a “butterfly-wing” type than “hatchet-shaped” (terms of Clarke, 1988). Anteriorly, the diapophysis contacts the transverse process of Presacral IX, which is also preserved as an impression. The right diapophysis is broken at the base with its distal part displaced lateral to the right ilium (Fig. 5).

The urostyle (27 mm long) is approximately 80% of the length of the femur. The anterior end of the urostyle has two small cotyles aligned horizontally, indicating a bicondylar articulation with the sacrum. A transverse process of the urostyle, or postsacral transverse process, is preserved as a clear impression on the left side and is oriented posterolaterally. The opposite process cannot be observed, and may be still imbedded in the matrix. A pair of small foramina for spinal nerves is present anteriorly on the dorsolateral side of the urostyle.

Pectoral Girdle and Forelimb—The pectoral girdle is of the arciferal type as indicated by the curved clavicle and the strongly oblique coracoid. The scapula is slightly shorter than one half of the length of the humerus, and has a straight leading edge as in extant discoglossids. Anteriorly, the scapula is overlain by the clavicle. The latter feature is considered to be a diagnostic feature of discoglossids (Duellman and Trueb, 1986; but see discussion below). Best shown on the left side, both the cleithrum and the suprascapula are well ossified (Fig. 5). Differing from the condition in extant discoglossids, the cleithrum is nonbifurcate, having a bladeliike distal border. The coracoid is moderately elongated (approximately 7 mm long) and has a medial end that is narrower than the lateral end. The curved clavicle is at least 9 mm long, and has a grooved posterior margin for articulation with the epicoracoid cartilage.

The left forelimb is folded anteriorly, with the forefoot close to the snout. The right forelimb is folded posteriorly, and the forefoot lies underneath the vertebral column (Presacrals V–VII). The humerus is approximately 20 mm long, substantially longer than the more distal segment of the forelimb, which is 14 mm long. The humeral condyle is not exposed on either side, and its actual condition (single or double condyles) cannot be determined. Proximally, the radioulna bears a short and well-ossified olecranon process, and distally it is expanded to a slightly greater width than the proximal end (5 mm vs. 4 mm).

The mesopodials of the forelimb exhibit the so-called “Morphology A” (Fabrezi, 1992) pattern, having a moderate-sized radiale and ulnare proximally, a relatively large Element Y and carpal 5, and much smaller carpals 2–4 distally. No free intermedium is present. A triangular prepollex lies distolateral to Element Y. Although slightly overlapping one another as preserved, the metacarpals are better shown on the right side than on the left. The Metacarpal IV is the longest (5 mm) and V the shortest (3 mm). Because only two digits are exposed, the relative length of the digits cannot be determined except that Digit IV is longer than Digit V. The phalangeal formula of the forefoot as observed is ?-?-3-3.

Pelvic Girdle and Hind Limb—As preserved, the pelvic girdle is shifted to the right side of the urostyle, but is still in articulation with the hind limbs. The ilium is laterally compressed and bears a weakly developed iliac crest dorsally. It lacks a conspicuous dorsal protuberance, a feature commonly seen in extant discoglossids and many other anurans. The pubis is probably unossified as in other anurans generally. The right ischium is exposed in articulation with the ilium, while the left element is probably obscured underneath.

Both hind limbs are nearly completely preserved, with the left femur broken distally. The hind limb is slenderly built and has an estimated length of approximately 116 mm. The nearly straight femur has a slender shaft. Both ends of the femur are slightly expanded, with the distal end being slightly wider than the proximal end (6 mm vs. 5 mm). The tibiofibula has a sulcus at the proximal and distal ends marking the fusion of the tibia with the fibula. The total length of the femur (34 mm) plus the tibiofibula (35 mm) is about 69 mm, which are about 73% of the snout–vent length. The proximal tarsal segment is about 20 mm long (tibiale 19 mm; fibulare 20 mm). The tibiale and fibulare are fused at both ends, leaving a narrow space between the two elements. The tarsal elements were probably unossified,

but the prehallux on the right hind foot is indicated by clear impressions. The hind foot has a phalangeal formula of 2-2-3-4-3 (best shown on the right side), with the longest Digit IV (27 mm), being approximately 77% of the length of the tibiofibula.

Comparison and Discussion

The referral of *Callobatrachus sanyanensis* to the Discoglossidae requires a stem-based definition of the family Discoglossidae. This early fossil taxon shares with other discoglossids four unequivocal character states: (1) postchoanal process of the vomer present, forming a narrow angle with anterior portion of vomer; (2) the leading edge of the scapula straight; (3) presence of anterior overlap of clavicle on scapula; and (4) the coracoid slenderly built with little expansion at its medial end. Two other character states also support a monophyletic Discoglossidae, but cannot be scored for *Callobatrachus*: the single humeral condyle is enlarged, with diameter greater than 60% of distal width; and the trigeminal and facial foramina separated by prefacial commissure (see below). *Callobatrachus* differs from all other known discoglossids in retaining primitive character states such as possession of nine rather than eight presacrals, and a nonbifurcated cleithrum.

The discovery of the early discoglossid from the Liaoning beds is biogeographically significant. Besides Europe and North Africa, extant discoglossids have a fairly wide distribution in Asia (East and Southeast Asia, and the Middle East); however, no definite fossils of the group have been known that correspond to their Recent distribution in Asia. Early fossil discoglossids are known by fragmentary material from the Middle and Late Jurassic beds in Europe and North America (Evans et al., 1990; Evans and Milner, 1993), but an unanswered question continued to be when did the group invade Asia as they had no Asian record. With the discovery of *Callobatrachus sanyanensis* from Liaoning, it is now clear that the historical distribution of discoglossids in Asia can be traced back to Late Jurassic or Early Cretaceous, 124.6–147.1 Ma (Swisher et al., 1999; Lo et al., 1999) before the present.

PHYLOGENETIC ANALYSIS AND RESULTS

Construction of Character-Taxon Matrix

To resolve the phylogenetic relationships of the two frogs from the western Liaoning fossil beds with other archaic anuran clades, a data matrix containing 65 characters across 23 taxa was constructed (Appendices 1, 2). Most of the characters were taken from Báez and Basso (1996), with modifications explained in Appendix 1. New characters added to the original data set are denoted with an asterisk in the character list (Appendix 1).

Among the ingroup taxa in our data matrix, several families (Rhinophrynidae, Palaeobatrachidae, Pelodytidae) are each represented by a single genus, while other families are represented by more than one selected genera. Because the monophyly of Discoglossidae has been questioned (e.g., Ford and Cannatella, 1993), we included the major representative genera of the group to test the monophyly of the family. As explained below, several purported members of the Discoglossidae are excluded from the analysis because of their doubtful taxonomic status or morphological ambiguity. Until the taxonomy and morphology of these problematic taxa is clarified, they should not be included in the data set to avoid generating misleading phylogenetic hypotheses.

Gobiates Špinar and Tatarinov, 1986 is highly problematic taxonomically. It includes as many as 11 nominal species (see Sanchiz, 1998 for species list) based on extremely fragmentary material from the Kyzylkum Desert and slightly better pre-

served material from the Gobi Desert. Many of these species are based on anatomically noncomparable parts (e.g., *Gobiates asiaticus* based on a squamosal fragment, *Gobiates parvus* on a fragment of right maxilla), and hence, have been recognized as “nomina inquirenda” (Sanchiz, 1998). Some other congeneric species are named based on inadequate material, and these fall in the “nomen dubium” category (Sanchiz, 1998). Two nominal species (*Gobiates khermeentsavi* and *Gobiates leptocolaptus*) are based on slightly better preserved skull material from the same locality and horizon in the Gobi (Khermeen Tsav); however, in reviewing these specimens, Sanchiz (1998: 20) concluded that “a phylogenetic relationship of the Mongolian *Gobiates* with the pelobatoids is a possibility that deserves future studies.” Gubin (1999) reviewed the taxonomy of the Gobiatidae and noted the similarities of some gobiatids to *Palaeobatrachus* in morphology and possible mode of life.

Wealdenbatrachus Fey, 1988, based on fragmentary material, is another problematic taxon that was referred to the Discoglossidae. In Sanchiz’s (1998) review, it is ambiguously described as “very similar to *Eodiscoglossus*” but having an “elongated *Leiopelma*-like scapula,” and the morphology of the vertebral centra (amphicoelous or opisthocoelous) cannot be confirmed. From the available information, we see no evidence to support a referral of this problematic taxon to the Discoglossidae, and to include such taxon in our data set can only render confusion.

Latonia von Meyer, 1843 is a large anuran known from the Tertiary of Europe. The type species (*Latonia seyfriedi*) is based on articulated skeletons that were only exposed in ventral view, while the other two nominal species (*L. gigantea* and *L. ragei*) were based on disarticulated material that morphologically cannot be compared with the holotype of the type species; therefore, the taxonomic status of the latter two species is still an open question (Roček, 1994). The taxonomic position of *Latonia* has been shifted from Ranidae, to Pelobatidae, Latoniidae, and Discoglossidae (see Roček, 1994 for citations). This Tertiary anuran has eight opisthocoelous presacra, and three pairs of free ribs in association with Presacra II–IV. It is probably based on these features that some authors (e.g., Roček, 1994; Sanchiz, 1998) placed this taxon in Discoglossidae. However, it must be pointed out that these are actually the plesiomorphic features that *Latonia* shares not only with discoglossids but with pipoids as well (Appendix 1). The skull of *Latonia* is bizarre in having heavy osteodermal incrustations on its dorsal roofing elements, and the zygous frontoparietal with a well-developed lateral flange shows no resemblance to any known discoglossids.

Liaobatrachus grabaui Ji and Ji, 1998 from the Liaoning fossil beds is known from an incomplete skeleton (GMV 2126). The basic morphology of this frog is poorly understood, and the referral of it to the Pelobatidae is not supported by the available evidence from the specimen. For example, the assumed frontoparietal is not an actual structure or impressions of a structure but an artifact; the vertebral centra are described as procoelous, but this morphology cannot be verified; it is described as lacking free ribs, but several ribs are indicated by impressions on the specimen. Because of these anatomical uncertainties, such a nominal taxon should not be included in a phylogenetic analysis before its morphology and taxonomic status are clarified.

Analysis of the Data Set

The data set was analyzed using PAUP version 3.1.1 (Swoford, 1993) on a Macintosh PowerBook 3400c, using the Branch-and-Bound search option. Tracing of character evolution was performed using MacClade version 3.01 (Maddison and Maddison, 1992). All characters were unordered and equally weighted, and ACCTRAN tree optimization was used to min-

imize possibilities of parallelisms. Besides using a different computer program, our analysis differs from Báez and Basso’s (1996) in several other aspects:

1. Uninformative characters. Báez and Basso (1996) included all uninformative characters, in which the derived state is autapomorphic for a single taxon in their matrix. In this study, three uninformative characters (6, 34, 56; see Appendix 1) were excluded from the actual analysis (see Yeates, 1992; Bryant, 1995 for discussion).

2. Outgroup rooting. Báez and Basso (1996) included two non-lissamphibian dissorophoids (*Apateon* and *Doleserpeton*) as more basal outgroups than Caudata. Because it is well understood that anurans are lissamphibians within the Salientia, we choose to use the basal salientian *Triadobatrachus* and Caudata as successive outgroups.

3. Character coding. Where subsets of certain characters are obviously related to the same anatomical structure and the features can be combined, we have chosen to use fused coding of single, multistate characters to avoid risks of homoplasy bias (but see Pleijel, 1995; Lee and Bryant, 1999 for discussion).

Phylogenetic Position of *Czatkobatrachus*

Described by Evans and Borsuk-Bialynicka (1998), *Czatkobatrachus* is the second Triassic salientian besides the Madagascan *Triadobatrachus*. The taxon is known from disarticulated material, including the holotype ilium (ZPAL Ab. IV/7) and other referred specimens from Early Triassic (Scythian) fissure deposits at the Czatkowice locality in Poland. The original authors discussed character evolution, and placed *Czatkobatrachus* as the second most basal salientian clade. The results of this study concur with those of Evans and Borsuk-Bialynicka (1998) in that *Czatkobatrachus* holds a more derived position than *Triadobatrachus*, as the sister group with the stem-based taxon Anura (Fig. 6).

Characterization of the Stem-based Anura

Diagnosis or characterization of the Anura has been provided by previous authors (e.g., Duellman and Trueb, 1986; Milner, 1988; Trueb and Cloutier, 1991a). Among the osteological characters that were included in the data set, the following character states characterize (diagnose) the stem-based Anura (Clade A): otic-occipital region composed of prootic and exoccipital (11-1; see Duellman and Trueb, 1986; Báez and Basso, 1996; phylogenetic discussion below); prefrontal lost (16-1); squamosal triradiate with anteriorly projecting zygomatic ramus (18-1); squamosal not in contact with dermal bones of the skull table (21-1); postchoanal processes of vomer present, forming wide or narrow angles with anterior portion of vomer (24-1); palatine absent owing to fusion with vomer (25-1); reversal in Pelobatidae; vertebral column shortened, with no more than ten presacral vertebrae (35-1); free ribs greatly reduced in number and eventually lost on all vertebrae (40-1-4); presence of rodlike urostyle with or without free postsacral vertebrae (44-1-2); scapula shortened to less than half length of humerus (47-1); epipodial elements fused to form compound bones (radioulna and tibiofibula) (54-1); dorsal tubercle of ilium low or absent (58-1; reversal in Pipidae); and hind limbs lengthened with significant elongation of proximal tarsal elements (59-1).

Phylogenetic Positions of Several Basal Anuran Clades

Prosalirus and *Notobatrachus*—The earliest known anuran *Prosalirus bitis* is represented by disarticulated material from the Early Jurassic Kayenta Formation in northeastern Arizona (Shubin and Jenkins, 1995). The family Prosaliridae was proposed by Shubin and Jenkins (1995), whereas Sanchiz (1998) listed *Prosalirus* as family incertae sedis together with *Vieraella*

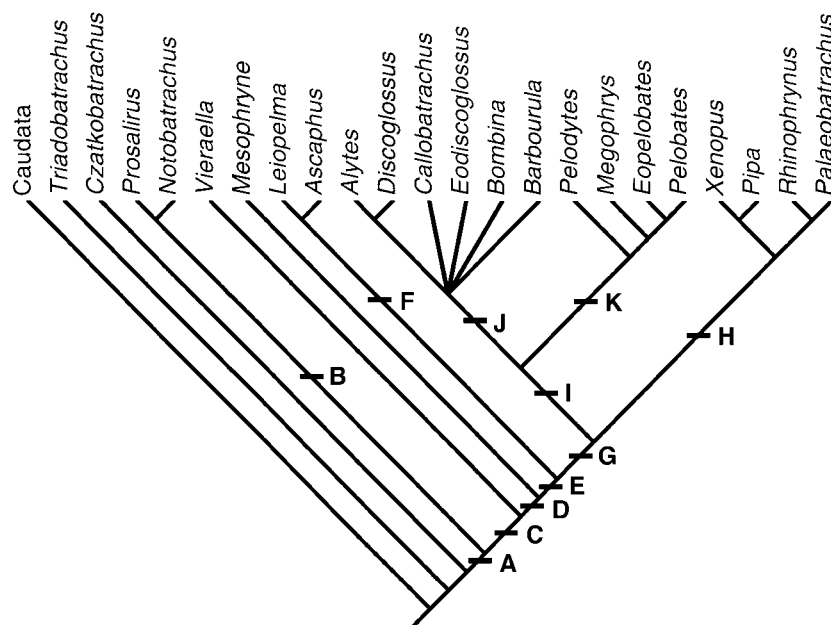


FIGURE 6. Phylogenetic hypotheses based on analysis of 65 characters across 23 taxa (see Appendices 1, 2). Strict consensus of eight shortest trees (TL = 168, CI = 0.577, RI = 0.718): A, Anura (stem-based taxon); B, Notobatrachidae (weakly supported taxon); C, unnamed clade 1; D, unnamed clade 2; E, Archaeobatrachia; F, Leiopelmatidae; G, unnamed clade 3; H, Pipoidea; I, unnamed clade 4; J, Discoglossidae; K, Pelobatoidea.

and several other taxa. In this study, strict consensus of the five equally parsimonious trees found suggests a *Prosalirus*–*Notobatrachus* sistergroup relationship, and tracing character evolution shows that this group (Clade B: Notobatrachidae) is weakly supported by a single character state: palatine process of premaxilla well developed (13-1). Such a palatine process of the premaxilla has independent occurrences within the Discoglossidae (*Alytes*, *Bombina*, and *Discoglossus*), in pelobatids, and in some neobatrachians.

Vieraella—Reig (1961) suggested the possibility of naming a monotypic family Vieraellidae, whereas Casamiquela (1965) placed *Vieraella* in the family Notobatrachidae. Estes and Reig (1973) discussed similarities of *Vieraella* with Ascaphidae (now Leiopelmatidae) and Discoglossidae, and referred both *Vieraella* and *Notobatrachus* to their Ascaphidae (see also Duellman and Trueb, 1986). More recently, Báez and Basso (1996:131) viewed *Vieraella* as “the most basal known member of Salientia, except the Early Triassic *Triadobatrachus* from Madagascar.”

The phylogenetic results of this study revealed that *Vieraella* is an ingroup member of the Anura. It shares with other anurans a large number of derived character states: Formation of prootic-occipital region by prootic-exoccipital (11-1); squamosal triradiate and T-shaped (18-1); squamosal not in contact with dermal bones of skull table (21-1); postchoanal processes of vomer present, forming wide angle with anterior portion of vomer (24-1); palatine absent owing to fusion with vomer or maxilla (25-1); epipodial elements fused to form single element (54-1); hind limb proportionally long with great elongation of proximal tarsals (59-1). These character states are among those supporting the Clade A in the resulting cladogram (Fig. 6).

Within the Anura, *Vieraella* holds a more derived position than the *Prosalirus*–*Notobatrachus* clade, and is placed as the sister group of a more derived clade that includes *Mesophryne* and other known anuran groups. This placement is supported by four character states: Premaxilla-nasal contact lost with separation of the two elements (15-1); position of anterior process of vomer lying near premaxilla-maxilla articulation (23-1); pos-

terolateral notch of parasphenoid alae absent (28-1). These character states support the Clade C in the resulting cladogram (Fig. 6). *Vieraella* is more primitive than other anurans in having a greater number of presacral vertebrae (35-1); however, congruence with other characters does not place this taxon as the most basal member of the stem-based Anura.

Mesophryne—As shown in the cladogram (Fig. 6), this new taxon represents a distinct archaic anuran clade, which is in a more derived position than *Vieraella*. It shares with the archaeobatrachian and more derived anurans several character states, including: Sculpture on dermal skull roof absent (2-1); formation of prootic-occipital region by fused prootic-exoccipital (11-2); sacral diapophysis widely expanded as butterfly wing-shaped structure (43-2); postsacral vertebrae uniformly modified into a single urostyle (44-2); humeral condyle well ossified (53-1); proximal tarsals fused at proximal and distal ends (60-1). However, *Mesophryne* lacks several other derived character states of the Archaeobatrachia: e.g., transverse process of posterior presacral vertebrae anterolaterally oriented (41-1), free intermedium in carpus absent (55-1), and prehallux present (62-1). Lack of these derived character states, in congruence with other characters in the data set, places *Mesophryne* as the sister group rather than an ingroup member of the Archaeobatrachia (Fig. 6: Clade D).

Monophyly of Discoglossidae

The diagnosis of the family provided by previous authors (Duellman and Trueb, 1986; Clarke, 1988; Roček, 1994) was based on a combination of plesiomorphic and derived character states. The most often used osteological character states include: eight stegochordal, opisthocoelous presacral vertebrae; Presacrals I and II unfused; presence of free ribs on Presacrals II–IV; and sacrum having expanded diapophyses and bicondylar articulation with urostyle (e.g., Duellman and Trueb, 1986).

Because these are not discoglossid synapomorphies, Ford and Cannatella (1993) suggested dropping the family name Discoglossidae. However, the phylogenetic analysis in this study found

four synapomorphies that support a monophyletic Discoglossidae (Fig. 6: Clade J): postchoanal processes of vomer present, forming narrow angle with anterior portion of vomer (24-2; also in *Leiopelma*); presence of anterior overlap of clavicle on scapula (49-1; independent occurrences in *Ascaphus* and some pipoids); coracoid elongate with little expansion of its medial end (50-1; independent occurrence in *Xenopus*); and trigeminal and facial foramina separated by prefacial commissure (63-1; also in *Leiopelma*).

Analysis of the data set shows the results as follows: *Alytes* and *Discoglossus* were grouped as sister taxa; however, the interrelationships of other genera were not fully resolved, as indicated by a four-taxon polytomy (*Bombina*, *Barbourula*, *Eodiscoglossus* and *Callobatrachus*). Resolution of this polytomy depends on developing a more extensive survey of characters among the family members, but such a task is beyond the scope of this study.

Taxonomic Status of Mesobatrachia Laurent, 1979

Laurent (1979) grouped Pipoidae and Pelobatoidea together in his Mesobatrachia (see Dubois, 1983 with a similar grouping but using a different subordinal name, Pipoidae). Ford and Cannatella (1993) defined the Mesobatrachia as: "the most recent common ancestor of the living Pelobatoidea and Pipoidae." Their purported synapomorphies for the Mesobatrachia include: closure of the frontoparietal fontanelle by juxtaposition of the frontoparietal bones; partial closure of the hyoglossal sinus by the ceratohyals; and a developmental feature: absence of the taenia tecti medialis and absence of the taenia tecti transversum (Sokol, 1981; Cannatella, 1985).

This study reveals the following character states that support the grouping of Discoglossidae with the Pelobatoidea as sister taxa (Fig. 6: Clade I): nasal forms most of the anterior margin of the orbit (16-2); cultriform process of parasphenoid does not reach the level of the vomers (26-1); parahyoid bone present and paired (31-1); and single humeral condyle enlarged with diameter greater than 60% of distal width (52-2). On the other hand, constraint grouping of the Pelobatoidea with the Pipoidae, as Laurent (1979) suggested, increases the tree length by three steps (171 vs. 168). This reveals the possibility of the suborder Mesobatrachia being a paraphyletic group, and the interrelationships of the three groups involved (Discoglossidae, Pelobatoidea, Pipoidae) merit further investigation.

Interrelationships and Higher Level Classification of Archaeobatrachian Clades

Widely accepted classification schemes for anurans have been proposed by Duellman (1975), Laurent (1979), and Dubois (1983). Duellman's classification recognized three superfamilies (Discoglossoidae, Pipoidae, and Pelobatoidea) within the suborder Archaeobatrachia Reig, 1958. The other two authors proposed a similar grouping of the families but used slightly different superfamily or suborder names. All three authors classified Discoglossidae and Leiopelmatidae in a "superfamily Discoglossoidae," whereas Ford and Cannatella (1993) pointed out the paraphyly of this superfamily. The suborder Archaeobatrachia, as used in this paper, contains the following subclades: [Leiopelmatidae + (Discoglossidae + Pelobatoidea) + Pipoidae].

Within the Archaeobatrachia, although the Discoglossidae and Leiopelmatidae share several plesiomorphic character states (e.g., presence of free ribs), our phylogenetic analysis found no evidence to support a sistergroup relationship of the two families; instead, the strict consensus of eight shortest trees places the Leiopelmatidae as the most basal archaeobatrachian clade and the sistergroup of other extant families. Furthermore, constrained grouping of the two families as sister taxa entails an

increase of tree length by five steps more than the shortest tree found (173 vs. 168 steps).

Notobatrachidae—This is a weakly supported family group that includes *Notobatrachus* and *Prosalirus*. As mentioned above, the grouping of the two genera into the same family is supported by a single character state (13-1), and the robustness of this hypothesis merits further investigation.

Vieraella and Mesophryne—As shown in the cladogram, neither of these two taxa can be grouped with any of the other archaic anuran clades. Therefore, in this paper each of these taxa is treated as an individual genus that represents an independent clade. Although a family name Vieraellidae (Reig, 1961) has been coined, we see no need to use it at this point because of its redundancy in relation to the generic name.

Besides the Discoglossidae discussed above, the following groups are well supported as monophyletic:

Leiopelmatidae—The grouping of *Ascaphus* and *Leiopelma* in the Leiopelmatidae (Ascaphidae of other authors) is widely accepted, but Ford and Cannatella (1993) discussed the possibility of grouping *Leiopelma* with their Bombinanura. In this study, the monophyly of the Leiopelmatidae (Fig. 6: Clade F) is supported by as many as 11 synapomorphies: nasals widely separated medially (3-1; also in *Pelodytes*); anterolateral margin of nasal essentially straight (4-1; also in *Eopelobates* and pipids); rostral process of nasal absent (5-1; also in *Alytes*, *Pelodytes*, and *Pipa*); dorsal exposure of frontoparietal fontanelle more than 50% of its length (8-2; *Pelodytes* and most discoglossids); slender and long posterior process of premaxilla present for premaxilla-maxilla articulation (14-1; also in pipids); quadratojugal absent (17-1; also in pipids and *Notobatrachus*); columella absent (32-1; also in rhinophrynids); neural arch of presacral vertebrae not imbricated, with spinal canal partially exposed (38-1; also in *Alytes*); atlantal cotyles confluent as a single articular surface (39-2; also in *Notobatrachus*, *Xenopus*, and *Palaeobatrachus*); sacral diapophysis moderately dilated, hatchet-shaped (43-1; also in *Palaeobatrachus* and some discoglossids); and prepubic elements present in pelvis (64-1; also in *Xenopus*).

Although most of these characters have independent occurrences in some other groups in the data set, this long list of synapomorphies shows that the Leiopelmatidae are a well-supported monophyletic clade.

Pipoidae—This anuran clade more or less corresponds to what Cope (1889) has called the Aglossa, which included the Pipidae, Xenopidae, and Palaeobatrachidae. Recent studies (e.g., Ford and Cannatella, 1993; Báez and Púgener, 1998) added the Rhinophrynidae to this superfamily group. The analysis of our data set shows that the grouping of the three families in the Pipoidae (Fig. 6: Clade H) is supported by the following character states: frontoparietal azygous in adults (7-1; convergent in some pelobatids); posterolateral alae of parasphenoid absent (27-2; unique); free ribs present on Presacrals II–IV until subadult stage (40-3; further derived condition in rhinophrynids); transverse process on postsacral complex absent (46-2; also in neobatrachians); cleithrum present and forked (51-1); and presence of two tarsalia (61-1; convergent in some pelobatids).

Pelobatoidea—Consisting of the Pelobatidae and Pelodytidae (Fig. 6: Clade K), this superfamilial group is widely accepted at present (see Duellman, 1975; Laurent, 1979; Dubois, 1983; Ford and Cannatella, 1993; Maglia, 1998).

This study reveals that the grouping of the Pelobatidae and the Pelodytidae as the Pelobatoidea is weakly supported by the following character states: centrum of presacral vertebrae procoelous (37-2; also in *Mesophryne* and most neobatrachians); and free ribs on presacral vertebrae absent in both subadults and adults (40-4; also in *Rhinophrynus* and neobatrachians). However, because the two character states (37-2, 40-4) are

shared with neobatrachians, the homology of these character states and the monophyly of the Pelobatoidea need to be further tested by developing a more global analysis based on more extensive data.

CONCLUSIONS

This study comes to the following conclusions:

1. The new fossil material from the Jurassic–Cretaceous deposits in western Liaoning Province, northeastern China, documents two anuran taxa: a new taxon, *Mesophryne*, represents a distinct archaic anuran clade, and a second taxon, *Callobatrachus*, represents the earliest fossil record of discoglossids from Asia.

2. Phylogenetic analysis of 65 characters across 23 taxa provides important insights into the interrelationships of the major archaic anuran clades. All of the three Jurassic forms (*Prosalirus*, *Vieraella*, and *Notobatrachus*) are ingroup members of the stem-based Anura, and *Prosalirus* and *Notobatrachus* can be grouped in the same family, Notobatrachidae.

3. A revised classification scheme is proposed for Archaeobatrachia on the basis of the results of the phylogenetic analysis. Recognized monophyletic groups include a weakly supported Notobatrachidae, Leiopelmatidae, Pipoidea, Discoglossidae, and Pelobatoidea.

4. The Discoglossidae and Leiopelmatidae are not sister groups, and the Discoglossidae as previously defined is probably an artificial taxon. New evidence supports the grouping of the Discoglossidae with the Pelobatoidea, and the suborder Mesobatrachia as previously defined is probably a paraphyletic group.

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APPENDIX 1

Characters used in phylogenetic analysis (modified from Báez and Basso, 1996), with new characters from other sources denoted with an asterisk.

1. General shape of the skull: skull wider than long (0); or roughly as long as wide (1). In *Triadobatrachus* and the remaining taxa studied, the skull is wider than long. The skull is as long as wide in *Vieraella*, *Rhinophrynus*, and *Palaeobatrachus*.

*2. Sculpture on dermal skull roof: present (0); or absent (1). Modified from Henrici (1994). *Triadobatrachus* has low rugosities on skull roof (Rage and Roček, 1989). Outgroup comparison indicates that presence of dermal sculpture is a primitive condition among anurans.

3. Medial contact of nasals: contact present (0); nasals widely separated medially (1); or nasals fused medially (2). Among the taxa included in the analysis, the (1) condition occurs in leiopelmatids and pelodytids independently and the (2) condition is unique for *Xenopus*.

*4. Anterolateral margin of nasal: concave (0); or essentially straight (1). See Trueb (1993) and Henrici (1994) for discussion. Considerable variation in size and shape of the nasals can be seen in different anuran groups, but primitive anurans generally have the nasal with a concave anterior margin, while most “mesobatrachians” and neobatrachians have the nasal with a more or less straight anterior margin.

5. Rostral process of nasal: present (0); or absent (1). In caudates, the nasals project anteriorly to contact the alary processes of the premaxillae. The nasals of *Vieraella*, *Notobatrachus*, and all discoglossids but *Alytes* bear rostral processes extending forward along the cranial midline. In *Ascaphus* and *Leiopelma*, the nasals lack a distinct rostral process (Stephenson, 1951).

6. Fusion of frontal and parietal: frontal and parietal remain separate (0); or fused to form frontoparietal (1). The frontals and parietals are discrete dermal roofing bones in caudates. In *Triadobatrachus* and other salientians, the two elements are fused to form the frontoparietals either paired or azygous. The derived state is a salientian synapomorphy (Miller, 1988).

7. Frontoparietal in adults: paired (0); or azygous (1). Although this can be combined with character 6, we treat this character as separate because of the uncertain condition in *Czatkobatrachus*, *Prosalirus* and *Mesophryne*. Coding the paired condition for *Triadobatrachus* follows Roček and Rage (2000). Some *Barbourula* have the frontoparietals partially fused posteriorly (Clarke, 1987), but we have coded the primitive paired condition for the taxon.

8. Dorsal exposure of frontoparietal fontanelle: fontanelle not exposed (0); exposed 50% of its length or less (1); fontanelle exposed more than 50% of its length (2). The absence of exposure of the frontoparietal fontanelle in adults occurs in caudates and *Triadobatrachus* as a primitive condition. See Báez and Basso (1996) for comments.

9. Posterolateral process of frontoparietal: well developed and wing-like (0); poorly developed or absent (1). The primitive state occurs in basal caudates, *Triadobatrachus* (Rage and Roček, 1989), and *Prosalirus* (Jenkins and Shubin, 1998). Coding of *Notobatrachus* and *Vieraella* is based on Báez and Basso (1996:135, 139). *Pelobates* and *Scaphiopus* have a small posterolateral process (Roček, 1981), but definitely not wing-like.

10. Frontoparietal shelf: absent (0); or present (1). The lateral border of the frontoparietal is elaborated to form a narrow orbital shelf in *Notobatrachus*. Such a shelf is absent in caudates, in which the frontal and parietal are separate bones, but it occurs also in rhinophrynids and pelobatids.

11. Formation of prootic-occipital region: by prootic-exoccipital-osthotic complex (0); by prootic-exoccipital without fusion (1); or by fused prootic-exoccipital (2). The prootic and exoccipital are fused during ontogeny in most living anurans. A separate exoccipital has been described in *Triadobatrachus* (Rage and Roček, 1989). Discrete exoccipitals occur in *Vieraella*, *Notobatrachus*, *Ascaphus* (Van Eeden, 1951), and *Leiopelma*, although in adults of the latter genus these bones

may eventually fuse to the prootics (Worthy, 1987). The exoccipital is indistinguishably fused to the prootic in *Bombina*, *Alytes*, and *Discoglossus*. Coding (1) for *Eodiscoglossus* is according to Hecht (1970).

12. Perilymphatic foramen: double foramina open on medial capsular wall (0); double foramina present on posterior wall of otic capsule (1); only superior perilymphatic foramen present (2); or only inferior foramen present (3). In urodeles, the perilymphatic foramina are absent on the posterior wall of the otic capsule (open on the medial wall, instead). A similar condition is seen in *Ascaphus* and *Leiopelma* (Van Eeden, 1951). A single foramen in *Notobatrachus* is interpreted as the jugular foramen (Báez and Basso, 1996). Coding this character for *Pipa* concurs with Báez and Pügener's (1998:appendix 3) data matrix but contradicts their incorrect description that both foramina are absent in pipines. Paterson (1960) identified a single foramen (superior perilymphatic foramen) in pipids.

13. Palatine process of premaxilla: absent or barely present (0); or well developed (1). The pars palatina of the premaxilla forms a distinct palatine process in *Notobatrachus* and most discoglossids (Báez and Basso, 1996). Such a process is barely present in *Ascaphus* and *Leiopelma* (Jurgens, 1971), and is lacking in the premaxilla in caudates. The actual condition of this process is unknown for *Vieraella* and *Triadobatrachus* because of poor preservation.

14. Premaxilla-maxilla articulation: posterior process of premaxilla absent (0); or present (1). In *Leiopelma* and *Ascaphus* (Trueb, 1993:fig. 6.2 and 6.18), the pars palatina of the premaxilla projects posteriorly into an elongate and pointed “process” for the articulation with the maxilla. In *Triadobatrachus*, the frontal region of the skull is not preserved and the character is unknown. This elongate shape of the posterior (or lateral) end of the pars palatina of the premaxilla also occurs in *Pipa* and *Xenopus* among the other taxa studied.

15. Premaxilla-nasal contact: articulation or contact present (0); or contact lost with separation of the two elements (1). The contact condition is known for *Notobatrachus* (Báez and Basso, 1996), but the actual condition of the appropriate region is unknown for *Triadobatrachus*, *Czatkobatrachus*, and *Prosalirus*. The derived condition occurs in all other anurans but *Palaeobatrachus* that represents a character reversal.

16. Prefrontal and anterior margin of the orbit: prefrontal present, maxilla and nasal excluded from the anterior margin of the orbit (0); prefrontal lost with maxilla and nasal forming the anterior margin of the orbit (1); nasal forming most of the anterior margin of the orbit (2); or anterior ramus of pterygoid excludes maxilla from the anterior margin of the orbit (3). A prefrontal is plesiomorphically retained in caudates and *Triadobatrachus*, while it is absent in all the anuran taxa that can be scored. Pending knowledge of the actual condition in *Czatkobatrachus*, *Prosalirus*, and *Vieraella*, loss of the prefrontal could be a synapomorphy for the anurans (e.g., Trueb, 1993; Báez and Basso, 1996).

17. Quadratojugal: present (0); or absent (1). A quadratojugal is probably present in *Triadobatrachus* (Piveteau, 1937; Estes and Reig, 1973; but see also Rage and Roček, 1989). Among anurans, the derived condition occurs in *Notobatrachus*, *Ascaphus*, *Leiopelma*, and pipids (Trueb, 1993). As the condition is uncertain in *Vieraella* (see Estes and Reig, 1973; Báez and Basso, 1996), we have coded it as unknown.

18. Shape of squamosal: as a simple horizontal bar (0); triradiate and T-shaped (1); nontriradiate with loss of zygomatic ramus (2); or funnel-shaped and in fusion with tympanic annulus (3). Both caudates and *Triadobatrachus* have a simple squamosal that is not distinctly triradiate. Most anurans have a typically triradiate squamosal with variations involving expansion/reduction of the zygomatic or otic processes, or curving of the quadrate process (see Trueb, 1993 for discussion).

19. Squamosal-maxilla contact: absent (0); or contact present (1). As the presence of a squamosal-maxilla contact is directly related to the size of the zygomatic ramus of the squamosal, this character can be polarized by comparison with the character above. The derived state is probably a pelobatine synapomorphy with independent occurrences in *Discoglossus*, *Mesophryne*, and some neobatrachians.

20. Expansion of otic ramus of squamosal in lateral view: not expanded (0); or otic ramus expanded and deep (1). Among all of the taxa included in the matrix, the derived state of this character diagnoses the Pelobatidae.

21. Medial articulation of squamosal: squamosal medially in contact with dermal skull roof (0); or squamosal not in contact with dermal skull roof (1). Although stated “both squamosals lost their contact with the frontoparietals,” Rage and Roček (1989:text-fig. 4) restored a con-

tact for *Triadobatrachus*, and this restoration was followed by Sanchez (1998).

22. Sphenethmoid: bilaterally paired (0); or single (1); or fused to parasphenoid ventrally (2). Modified from Báez and Basso (1996:character 17). The sphenethmoid ossification is bilaterally paired in the adults of *Notobatrachus* (Báez and Basso, 1996). A similar condition occurs in leiopelmatids and most microhylids (Van Eeden, 1951; Trueb, 1993); however, Trueb (1993:313) explained that "the apparent division is the result of incomplete medial replacement of cartilage by bone." The sphenethmoid is single in most anurans, but is fused to the parasphenoid in pipids.

23. Position of anterior process of vomer: anterior process of vomer lying immediately behind premaxilla (0); or lying near premaxilla-maxilla articulation (1). In the primitive caudate *Karaurus*, the anterior part of the vomer lies adjacent to the premaxilla anteriorly, whereas in urodeles it broadly contacts the premaxilla and maxilla. The condition in *Triadobatrachus* is unknown because the appropriate region is not preserved. In *Notobatrachus*, the anterior plate-like portion of the vomer (anterior process) lies close to the premaxilla, and is more or less parallel to the cranial midline. In all of the other ingroup taxa, the anterior portion of the vomer, if well developed, lies adjacent to the premaxilla-maxilla articulation.

24. Postchoanal processes of vomer: absent (0); or present, forming wide angle with anterior portion of vomer (1); present, forming narrow angle with anterior portion of vomer (2). Modified from Báez and Basso (1996:character 21). The postchoanal process of the vomer forms a rather wide angle (about 90–110°) with the anterior process in *Vieraella* and *Notobatrachus*. In *Leiopelma*, *Bombina*, *Alytes*, *Barbourula*, and *Discoglossus*, this angle is significantly narrower (about 45°). *Ascaphus* lacks anterior and postchoanal processes on the vomer, which is reduced to the dentigerous portion (Van Eeden, 1951). In *Triadobatrachus*, the condition of this region is unknown.

*25. Palatine: present as separate element (0); or absent or fused with vomer or maxilla (1). The palatine is retained as a separate element in many urodele taxa (Trueb, 1993), in *Triadobatrachus* (Rage and Roček, 1989), but is absent in *Vieraella* and *Notobatrachus* (Estes and Reig, 1973; Báez and Basso, 1996). The condition of this character is unknown for *Czatkobatrachus* and *Prosalirus* (Evans and Borsuk-Bialynicka, 1998; Jenkins and Shubin, 1998).

26. Cultriform process of parasphenoid: extending anteriorly to the level of the vomers (0); or not reaching the level of the vomers (1). The anterior terminus of the cultriform process of the parasphenoid extends forward to reach the level of the posteromedial portion of the vomers in *Notobatrachus*, *Ascaphus*, and *Leiopelma* (Jurgens, 1971). The cultriform process does not reach so far forward in other taxa, including *Bombina*, *Alytes*, and *Discoglossus*. Báez and Basso (1996) ambiguously stated "it is impossible to assess the anterior extent of the process" but coded it as (1) for *Vieraella*; we coded the character as unknown for the taxon. The condition in *Triadobatrachus* cannot be determined as preserved, but the character can be polarized, as the primitive state is known for caudates.

27. Posterolateral alae of parasphenoid: anteroposterior width of alae equal or greater than one-third distance between lateral ends (0); width narrower than one-third distance between lateral ends (1); or alae absent (2). The primitive state is known for *Triadobatrachus*, *Vieraella*, *Notobatrachus*, and *Prosalirus*. All other taxa show the (1) condition, with the exception of pipoids, which lack posterolateral alae of the parasphenoid.

28. Posterolateral notch of parasphenoid alae: present (0); or absent (1). The posterolateral corner of the parasphenoid alae is deeply indented in both *Triadobatrachus* (Rage and Roček, 1989) and *Notobatrachus* (Báez and Basso, 1996). The latter authors considered the similarity as superficial. As in both taxa, the notch is functionally related to the auditory capsule, we choose to code them (0).

29. Posteromedial process of parasphenoid: absent (0); or present (1). A distinct, narrow process on the posterior margin of the parasphenoid is absent in *Triadobatrachus*, *Vieraella*, *Notobatrachus*, and *Prosalirus*. Among other ingroup taxa, it occurs in all groups that can be scored with the exception of *Palaeobatrachus* and *Rhinophrynus*.

30. Medial ramus of pterygoid: not contacting parasphenoid (0); or contacting parasphenoid (1); or medial ramus absent (2). Modified from Báez and Basso (1996:character 28). The medial process of the pterygoid does not contact or overlap the parasphenoid ala in *Triadobatrachus* (Rage and Roček, 1989). We coded unknown for *Vieraella* because of the uncertain condition of this taxon (Báez and Basso, 1996). Rhin-

ophrynids are unique in having no medial ramus of the pterygoid (Trueb, 1993).

*31. Parahyoid bone: present and single (0); or present and paired (1); or absent (2). Single parahyoid is present in *Triadobatrachus* (Rage and Roček, 1989), *Notobatrachus* (Báez and Basso, 1996), leiopelmatids, rhinophrynids (Trueb, 1993), and palaeobatrachids (Estes and Reig, 1973); paired in discoglossids including *Bombina* and *Barbourula* (Trueb, 1993; Clarke, 1987), and pelodytids; absent in pipids, pelobatids, and neobatrachians. The "Y"-shaped parahyoid in *Alytes* is considered to be a modified paired condition.

*32. Columella: well-ossified columella present (0); or absent (1). Trueb (1993:315) discussed the uncertain polarity of this character; however, given the distribution of the character among extant and fossil anurans in comparison to *Triadobatrachus* and Caudata, it is clear that the absent condition is a derived condition. The derived state is known for leiopelmatids (*Ascaphus* and *Leiopelma*), rhinophrynids, and some neobatrachians (Trueb, 1993).

*33. Mentomeckelian bone: present (0); or absent (1). An ossified mentomeckelian bone is present in caudates and most anurans, but the derived condition is known for pipids and rhinophrynids (see Trueb, 1993).

34. Marginal teeth: both upper and lower dentition present (0); or lower dentition absent (1); or both upper and lower dentition absent (2). The dentary is edentulous in *Triadobatrachus* and this condition is considered a synapomorphy of Salientia (Milner, 1988). *Prosalirus* has an upper dentition, while the condition of its lower dentition is unknown; therefore, we coded unknown for this taxon.

35. Number of presacral vertebrae: 14 or more (0); ten presacral vertebrae (1); normally nine presacral vertebrae (2); normally eight or fewer (3). See Lynch (1973) for discussion on extant taxa. *Triadobatrachus* has 14 presacral vertebrae (Rage and Roček, 1989). The number of presacrals is ten in *Vieraella* and nine in *Notobatrachus* (Báez and Basso, 1996).

*36. Fusion of Presacrals I and II: fusion absent (0); or fusion present (1). From Duellman and Trueb (1986). The derived condition occurs in the Pelodytidae and several other taxa that are included in the data matrix: *Pipa*, *Palaeobatrachus*, some neobatrachians including some bufonids, and some ranids (Duellman and Trueb, 1986).

37. Centrum of presacral vertebrae: vertebral centra amphicoelous or notochordal (0); or opisthocoelous (1); or procoelous (2). The primitive state is known for *Triadobatrachus*, *Czatkobatrachus*, *Prosalirus*, *Vieraella*, *Notobatrachus*, *Ascaphus*, and *Leiopelma* (Rage and Roček, 1989; Báez and Basso, 1996; Evans and Borsuk-Bialynicka, 1998; Jenkins and Shubin, 1998). Coding of *Eodiscoglossus* based on the original photographs of the holotype, in which the last three presacrals have an opisthocoelous centrum.

38. Neural arch of presacral vertebrae: completely or weakly imbricated roofing of spinal canal (0); or not imbricated with spinal canal partially exposed (1). The derived state is known for *Ascaphus*, *Leiopelma*, and *Alytes*. *Czatkobatrachus* and *Prosalirus*, based on disarticulated material, are coded as unknown, although at least the latter taxon may have the imbricated condition (Jenkins and Shubin, 1998). The derived state also occurs in some neobatrachians (Trueb, 1973).

39. Morphology of atlantal cotyles: cotyles mostly ventral and narrowly separated by notochordal fossa (0); cup-like cotyles displaced laterally and widely separated from one another (1); cotyles confluent as a single articular surface (2). See discussion in Trueb (1973). In Báez and Basso's (1996) original data set, two states (ventral and lateral positions of the cotyles) were recognized. Since the ventrally located cotyles can be either apart from one another or confluent, we choose to separate the two states following Lynch (1969).

40. Free ribs on presacral vertebrae: free ribs present on all presacral vertebrae (0); ribs present on Presacrals II–V or II–VI (1); or ribs restricted to Presacrals II–IV (2); present at least on Presacrals II–IV till subadult stage (3); free ribs absent in both subadults and adults (4). *Vieraella* is coded as unknown because of the uncertain condition on posterior presacrals (Báez and Basso, 1996). In *Prosalirus*, free ribs are definitely present on some presacral vertebrae, but the actual number cannot be determined (Jenkins and Shubin, 1998). Palaeobatrachids have free ribs on Presacrals II–VI in subadults, but these ribs are ankylosed to the transverse processes in adults; similarly, young pipids have free ribs on Presacrals II–IV but they are ankylosed to the transverse processes in adults.

41. Transverse process of posterior presacral vertebrae: laterally oriented (0); or anterolaterally oriented (1). The derived condition is seen in all archaebatrachians with the exception of the palaeobatrachids.

*42. Fusion of sacral ribs: remain free from sacral vertebra (0); or fused to transverse process of sacral (1). The primitive state is known for *Triadobatrachus* (Rage and Roček, 1989), while all other taxa including *Czatkobatrachus* and *Prosalirus* have the sacral ribs fused to the vertebra (Evans and Borsuk-Bialynicka, 1998; Jenkins and Shubin, 1998).

43. Dilation of sacral diapophysis: diapophysis slender and no dilation (0); or moderately dilated and hatchet-shaped (1); or widely expanded as butterfly wing-shaped (2). Description of the transformation series follows Clarke (1988). Coding the (2) condition for *Eodiscoglossus santonjae* is based on observation of the original photographs of the type specimen, which clearly show the impressions that indicate expanded diapophyses on both sides (contra Hecht, 1970). Among extant discoglossids, state (2) is seen in *Barbourula* and *Bombina*, while the moderately expanded "hatchet-shaped" condition is seen in *Alytes* and *Discoglossus* (Clarke, 1988).

44. Postsacral vertebrae: caudal vertebrae remain unfused (0); or urostyle present in association with discrete caudal between sacrum and urostyle (1); or all postsacral vertebrae uniformly modified into single urostyle (2). *Triadobatrachus* has at least six caudals bearing transverse processes. *Notobatrachus* normally has a discrete caudal between the sacrum and urostyle, but all other anurans have a highly modified urostyle only. *Prosalirus* has a urostyle, which could be either the (1) or (2) condition (Jenkins and Shubin, 1998).

45. Sacrococcygeal articulation: cartilaginous joint (0); bicondylar (1); monocondylar (2); or simply fused (3). In *Notobatrachus*, *Ascaphus* (Ritland, 1955), and *Leiopelma* (Stephenson, 1952, 1960), there is a cartilaginous joint between the sacrum and urostyle, similar to that between successive presacral vertebrae. A bony monocondylar joint is formed between the sacrum and the urostyle in *Bombina* and *Barbourula*, whereas a bicondylar joint is present in *Alytes* and *Discoglossus*. A cartilaginous joint between the sacral vertebra and the following vertebra is present in *Triadobatrachus*.

*46. Transverse process on postsacral complex: present (0); or fused to a bony web of sacral diapophysis (1); or absent (2). See Lynch (1973) for discussion. The postsacral complex refers to either the discrete vertebrae as in *Triadobatrachus* or the urostyle as in other salientians. *Czatkobatrachus* may have caudal vertebrae that bear no transverse processes (Evans and Borsuk-Bialynicka, 1998); we code the character (?) as the urostyle is unknown for the taxon.

47. Length of scapula: at least half length of humerus (0); or less than half length of humerus (1). The primitive state is known for *Triadobatrachus* (Rage and Roček, 1989). *Prosalirus* has a scapula that is slightly shorter than one-half length of the humerus (Jenkins and Shubin, 1998). Although described as having a relatively long scapula and coded (0) for *Vieraella* (Báez and Basso, 1996), the actual condition is uncertain as both humeri are incomplete on the holotype and only known specimen; therefore, we coded the character as unknown for the taxon.

48. Leading edge of scapula: leading edge concave (0); or straight (1). The leading edge of the scapula is anteriorly concave in *Triadobatrachus*, *Prosalirus*, *Vieraella*, *Notobatrachus*, and *Leiopelma*. The edge is straight in discoglossids, and a similar condition is also seen in *Ascaphus*, *Xenopus*, and *Palaeobatrachus*.

*49. Anterior overlap of clavicle on scapula: overlap absent (0); or overlap present (1); or two elements fused (2). Overlapping occurs in *Ascaphus*, discoglossids, palaeobatrachids, pipids, and rhinophrynids (see Lynch, 1973). Coding of pelodytids is based on Henrici (1994). The condition in *Triadobatrachus*, *Czatkobatrachus*, and *Prosalirus* is unknown, but this character can be polarized by the primitive condition observed in caudates.

50. Coracoid shape: medial end of coracoid expanded anteriorly (0); or coracoid elongate, medial end little expanded anteriorly (1). The medial (sternal) end of the coracoid is expanded anteriorly in *Vieraella* and *Notobatrachus*. A similar anterior expansion of the medial end of this bone also occurs in *Leiopelma* and *Ascaphus*, whereas in *Bombina*, *Alytes* and *Discoglossus*, the coracoid has a rounded sternal end. The shape of the coracoid in *Triadobatrachus* cannot be determined because of incomplete preservation (Rage and Roček, 1989). The medial end of the coracoid in *Prosalirus* is strongly expanded (Jenkins and Shubin, 1998:fig. 4C), while the structure in *Czatkobatrachus* is unknown (Evans and Borsuk-Bialynicka, 1998).

*51. Cleithrum: present and unforked (0); present and forked (1); or cleithrum fused to suprascapula (2). The unforked condition of the cleithrum is known for *Triadobatrachus* (Rage and Roček, 1989), *Vieraella*, and several extant groups, including leiopelmatids and pelobatids. The forked condition is seen in pipids, and all discoglossids

but *Callobatrachus*. The fused condition is known for rhinophrynids and brachycephalids (Trueb, 1973).

52. Humeral condyle: double humeral condyles present (0); or single condyle with small diameter less than 60% of distal width (1); or single condyle enlarged with diameter greater than 60% of distal width (2). The condyle has a diameter of 54% of the distal width in *Czatkobatrachus*; the condition cannot be determined in *Prosalirus*, *Mesophryne*, and *Callobatrachus*.

53. Ossification of humeral condyle: condyle unossified (0); or condyle ossified (1). The derived condition is known for *Ascaphus* and all other archaebatrachians; cartilaginous condition is known for *Triadobatrachus*, *Prosalirus*, *Vieraella*, and *Notobatrachus*.

54. Epipodial elements: remaining as separate elements (0); or fused to form single element (1). The derived condition is an unambiguous synapomorphy for the Anura (see Milner, 1988). The primitive state is known for *Triadobatrachus* (Rage and Roček, 1989) and *Czatkobatrachus* (Evans and Borsuk-Bialynicka, 1998). *Prosalirus* has the derived condition as in other anurans (Jenkins and Shubin, 1998).

55. Free intermedium in carpus: present (0); or absent (1). The primitive state is known for *Triadobatrachus*, *Notobatrachus*, and the new taxon *Mesophryne*. The condition is unknown for *Prosalirus* and *Vieraella* because of preservation. The derived condition is known for all modern anuran groups (Trueb, 1973).

56. Length and orientation of ilium: short ilium essentially dorsally directed (0); or elongate shaft of ilium anteriorly directed (1). The derived state is known for *Triadobatrachus*, *Czatkobatrachus*, *Prosalirus*, and *Vieraella* as in other salientians. This is an unambiguous synapomorphy for Salientia (Milner, 1988).

57. Dorsal acetabular expansion of ilium: not extending to dorsal limit of ischium (0); or extending to dorsal limit of ischium (1). The derived state is known for *Alytes* and *Discoglossus* (Clarke, 1988), *Rhinophrynus*, and pelobatoids except for *Eopelobates* (Estes, 1970).

*58. Dorsal prominence of ilium: strongly developed as a high tubercle (0); or tubercle low or absent (1). Degree of development of this structure is highly variable among anurans, and description of the dorsal prominence (dorsal protuberance of other authors) in the literature is confusing (e.g., Estes and Sanchiz, 1982; Evans and Milner, 1993). *Triadobatrachus* and *Czatkobatrachus* clearly has a conspicuous tubercle (Rage and Roček, 1989:text-fig. 3; Evans and Borsuk-Bialynicka, 1998:fig. 1), while in *Prosalirus* and *Notobatrachus* the dorsal prominence is barely developed (Jenkins and Shubin, 1998:fig. 2).

*59. Hind limb proportions: normal length (0); or proportionally long with great elongation of proximal tarsals (1). The derived state is positively known for all anurans except *Czatkobatrachus*. The hind limb of *Vieraella* is incompletely preserved, but an elongated femur gives positive evidence for hind limb elongation as in other anurans.

*60. Fusion of proximal tarsals: fusion absent (0); or fused at proximal and distal ends (1); or completely fused to form a single bone (2). Modified from Henrici (1994:character 22). The unfused condition is known for primitive anurans including *Prosalirus* and *Notobatrachus*, while the condition is unknown for *Vieraella*. Most other anurans have the (1) condition, but complete fusion of the tibiale and fibulare is known for pelodytids and centrotenids (Duellman and Trueb, 1986).

*61. Number of tarsalia: three or more free elements (0); or only two elements present (1). For discussion of the character, see Lynch (1973), Duellman and Trueb (1986), and Henrici (1994).

*62. Prehallux: absent (0); or present as small hind foot element (1); or modified as bony spade (2). Modified from Henrici (1994:character 24). The primitive condition is seen in *Mesophryne*, and the derived condition is scored for all the modern anuran groups according to Trueb (1973).

*63. Consolidation of Cranial Nerve V and VII: three separate foramina occur (0); or trigeminal and facial foramina separated by pre-facial commissure (1); or commissure absent, nerves exit via single prootic foramen (2). From Trueb (1973:84): (0) condition in primitive anuran *Ascaphus* and salamanders; (1) condition in *Leiopelma* and discoglossids; and (2) condition in all other anurans.

*64. Prepubic elements: absent (0); or present (1). The derived condition is known for leiopelmatids, *Xenopus*, and *Pseudhymenochirus* (Duellman and Trueb, 1986).

*65. Posture of manus: medial inturning of manus absent (0); or inturning present (1). This character corresponds to the condition that has been termed "carpal torsion" by Estes and Reig (1973), and "brachiocarpal rotation" by Báez and Basso (1996); see also discussion in Jenkins and Shubin (1998).

