A New Crown-Group Frog (Amphibia: Anura) from the Early Cretaceous of Northeastern Inner Mongolia, China

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A New Crown-Group Frog (Amphibia: Anura) from the Early Cretaceous of Northeastern Inner Mongolia, China

KE-QIN GAO[1] AND JIANYE CHEN[2]

ABSTRACT

Based on 12 well-preserved skeletons of postmetamorphic individuals, a new crown-group frog taxon is named and described from the Lower Cretaceous Guanghua (upper part of Longjiang) Formation (stratigraphic equivalent of the world-famed Yixian Formation) exposed in Dayangshu Basin, Hulunbuir, in the far northeast of Inner Mongolia, China. The new taxon, *Genibatrachus baoshanensis*, documents another Early Cretaceous anuran having reduction of the presacral vertebrae to eight in number, similar to several frog taxa of roughly the same age from Spain and Brazil. The new frog also displays several features that are ontogenetically and phylogenetically informative, including ontogenetic fusion of the palatine to the sphenethmoid, and ontogenetic fusion of ribs to the diapophyses of the posterior trunk vertebrae. In addition, the new discovery extends the geographic range of Early Cretaceous frogs of the Jehol Biota northward to near the 50th parallel north in East Asia.

INTRODUCTION

The amphibian order Anura includes more than 6600 extant species of frogs and toads, distributed on all continents except Antarctica (AmphibiaWeb, 2016; Frost, 2016). As a clade, they are characterized by their highly specialized skull morphology and tailless body plan, distinct from either caecilians or salamanders, the other two major clades of modern amphib-

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ians. Fossil frogs, especially those from the Mesozoic, provide direct evidence on how these morphological specializations were gradually acquired in deep time.

The earliest stem frogs are known from the Early Triassic of Madagascar (*Triadobatrachus massinoti* Piveteau, 1936) and southern Poland (*Czatkobatrachus polonicus* Evans and Borsuk-Bialynicka, 1998). The skulls of these two Triassic frogs already resemble those of modern frogs, but their postcranial morphologies are still plesiomorphic in retaining a nonshortened vertebral column and a tail. The Jurassic is marked by the first occurrence of crown-group frogs, a wider geographic distribution of fossil frogs, and the stabilization of postcranial morphology typical of modern frogs (Roček, 2000). The best-known examples of Jurassic frogs (see Roček, 2000) include *Prosalirus bitis* from the Early Jurassic of the United States (Shubin and Jenkins, 1995), *Vieraella herbsti* and *Notobatrachus degiustoi* from the Middle-Late Jurassic of Argentina (see Roček, 2000), *Eodiscoglossus oxoniensis* from the Middle Jurassic of England (Evans et al., 1990), and *Rhadinosteus parvus* from the Late Jurassic of the United States (Henrici, 1998). The Cretaceous witnessed the first radiation of modern frog families (e.g., Discoglossidae and Ceratophryidae; Villalta, 1956; Wang and Gao, 1999; Evans et al., 2008) and the first occurrence of fossil frogs in Asia. The most significant radiation of extant families of frogs took place after the K-Pg transition (Sanchiz, 1998: fig. 152; Roček and Rage, 2000a).

In East Asia, the geologically oldest fossil frogs are known from the Early Cretaceous Yixian Formation (Barremian/Aptian) of Liaoning Province, northern China. They include *Callobatrachus* from Sihetun near Beipiao (Wang and Gao, 1999), *Mesophryne* from the nearby Heitizigou locality (Gao and Wang, 2001), and *Yizhoubatrachus* from the Hejiaxin locality near Yixian (Gao and Chen, 2004). A purported "tadpole" fossil (CAGS-IG01-705), previously reported from the Middle Jurassic Daohugou beds, Inner Mongolia, China (Yuan et al., 2004), has been reinterpreted as an incomplete insect specimen (Huang, 2013). In addition, *Dalianbatrachus* (Gao and Liu, 2004), based on a single specimen exposed on part-and-counterpart shale slabs (D2166, D2167) from the Yixian Formation, has been synonymized with *Mesophryne* (Wang and Evans, 2006). Another nominal taxon (*Liaobatrachus* Ji and Ji, 1998) from the Yixian Formation is here treated as a nomen dubium (but see Dong et al., 2013), because the poorly preserved holotype specimen (GMV 2126) provides insufficient information to permit recognition of this as a distinct species. Dong et al. (2013) provided a taxonomic revision of the Jehol fossil frogs, in which the three taxa (*Callobatrachus*, *Mesophryne*, and *Yizhoubatrachus*) were grouped collectively in a single genus and were synonymized with *Liaobatrachus*. This revision, however, remains contentious and is not supported by a recent phylogenetic analysis (Chen et al., 2016). Here we treat the three Jehol frogs as independent taxa and keep their original names.

This paper describes a new frog based on material from Lower Cretaceous beds exposed at the Pigeon Hill locality, near Taipingqiao village, Morin Dawa Daur Autonomous Banner, Hulunbuir, Inner Mongolia, in the far north of northeastern China (fig. 1). The fossil beds exposed at the Pigeon Hill locality pertain to the Lower Cretaceous Guanghua Formation, lacustrine volcanic ash deposits occurring in the Dayangshu Basin along the south slope of the Great Khingan Range (e.g., Sun et al., 2005; Liu et al., 2008). The geological unit Guanghua Formation was named and described by the Heilongjiang Bureau of Geology and Mineral

FIGURE 1. Area map showing the location of Taipingqiao locality (Inner Mongolia) in relation to other Early Cretaceous frog fossil localities near Chaoyang in western Liaoning Province, China (area shaded dark grey indicates the former "Jehol Province" after which the "Jehol Biota" was named).

Resources (1993), based on volcanic rocks that were previously treated as the upper part of the Longjiang Formation (Compiling Group for Heilongjiang Regional Stratigraphic Scale, 1979). The name Guanghua Formation has been adopted in regional geological maps and followed by some authors (Heilongjiang Bureau of Geology and Mineral Resources, 1997; Zhang, 2010; Li W. et al., 2011; Zhou et al., 2013). Although some other authors recently advocated reverting to the former usage of the Longjiang Formation (sensu lato) and discarding the name Guanghua Formation (e.g., Li Y. et al., 2013), both the Guanghua and Longjiang formations are used in current literature. The Guanghua (or upper part of Longjiang) Formation has been dated at 125 Ma, making it a temporal equivalent of the world-famed Yixian Formation in western Liaoning Province (Heilongjiang Institute of Geological Survey, 2005; Li Y. et al., 2013). No anuran fossils have previously been described from the Guanghua Formation; thus, this paper documents the first record of Lower Cretaceous frog fossils from the unit, far to the north of the typical Jehol area in western Liaoning and vicinity.

Anatomical terminology follows Duellman and Trueb (1986), unless otherwise explained, and the nomenclatural terminology follows Ford and Cannatella (1993). We use "juvenile" (from the Latin word *juvenis*, meaning "young") strictly to refer to newly metamorphic individuals before reaching the adult stage, and restrict the term "larvae" to those individuals of premetamorphic development stage (although we have no larval specimens from the new site).

ABBREVIATIONS

The following institutional abbreviations are used: **CAGS-IG**, Institute of Geology, Chinese Academy of Geological Sciences, Beijing, China; **D**, Dalian Natural History Museum, Dalian, China; **GMV**, Geological Museum, Beijing, China; **PKUP**, Peking University Paleontological Collections, Beijing, China.

The following anatomical abbreviations are used: **ang**, angulosplenial; **cen**, centrale; **cla**, clavicle; **cle**, clethrum; **col**, columella; **cor**, coracoid; **fe**, femur; **fibl**, fibulare; **frpa**, frontoparietal; **hu**, humerus; **il**, ilium; **iul**, intermedium+ulnare; **isc**, ischium; **max**, maxilla; **na**, nasal; **pal**, palatine; **par**, parasphenoid; **pm**, premaxilla; **ptg**, pterygoid; **qj**, quadratojugal; **r**, rib; **rad**, radiale; **ru**, radioulna; **sc**, scapula; **sm**, septomaxilla; **sq**, squamosal; **tf**, tibiofibula; **tibl**, tibiale; **uro**, urostyle; **vo**, vomer.

SYSTEMATIC PALEONTOLOGY

Class Amphibia Linnaeus, 1758

Superorder Salientia Laurenti, 1768

Order Anura von Waldheim, 1813

Family incertae sedis

Genibatrachus, gen. nov.

Etymology: Geni (Pinyin) + *batrachos* (Greek), meaning Geni River frog. The generic name refers to the Geni River, a major tributary of the Nenjiang River that flows southward close to the type locality near Taipingqiao village.

Type Species: *Genibatrachus baoshanensis,* sp. nov.

Genibatrachus baoshanensis, sp. nov.

Figures 2–6

Etymology: The species epithet refers to the Baoshan township near the type locality.

Holotype: PKUP V0401, an incomplete adult skeleton preserved in volcanic shales, exposed in part-and-counterpart slabs.

Referred Specimens: PKUP V0402–V0412; all specimens are preserved in volcanic shales, exposed in part-and-counterpart slabs. PKUP V0410–V0412 are juvenile individuals based on their smaller body size, whereas the remaining specimens are adults.

Type Locality and Horizon: Pigeon Hill (N48°66′43.38″/E123°87′28.85″), near Taipingqiao village, approximately 18 km northwest of Baoshan township, Morin Dawa Daur Autonomous Banner, Hulunbuir, Inner Mongolia, China; Lower Cretaceous Guanghua (= upper part of Longjiang) Formation (?Barremian-Aptian).

FIGURE 2. Photograph of the holotype of *Genibatrachus baoshanensis,* gen. et sp. nov. (PKUP V0401): incomplete skeleton exposed on part-and-counterpart shale slabs. **A,** skull and postcranial skeleton exposed in dorsal view; **B,** impressions of the skull and postcranial skeleton exposed in counterpart slab of A.

Diagnosis: A new fossil belonging to the Pipanura (a clade consisting of the Pipoidea, Pelobatoidea, and Neobatrachia) based on the combination of the following characters: palatine present; eight presacral vertebrae; centrum procoelous; separate ribs present on the presacral II–IV; ribs V–VIII fused to the transverse processes of the presacral. It is distinguished from all other taxa within the Pipanura with the combination of the following characters: alary process of premaxilla bifurcated; nonimbricate presacral neural arches; transverse processes of presacral V–VIII laterally oriented; unexpanded sacral diapophysis.

DESCRIPTION

The holotype (PKUP V0401) and the 11 referred specimens are all dorsoventrally compressed, preserved as fairly complete and fully articulated skeletons embedded in pale-grey volcanic ash shales. However, all specimens were damaged to various degrees from splitting of the shale slabs during collection. The holotype has most of the skeleton preserved in one slab, whereas the counterpart slab displays impressions of the dorsal aspect of the skeleton (figs. 2, 3). Adult specimens are of medium body size, and the preserved skin impressions show a plump body outline. The holotype has a skull length of 23 mm and a snout-vent length (SVL) of 70 mm, whereas several other specimens reach an SVL of 80 mm. The collection also includes three juvenile specimens (PKUP V0410–V0412), characterized by their small size

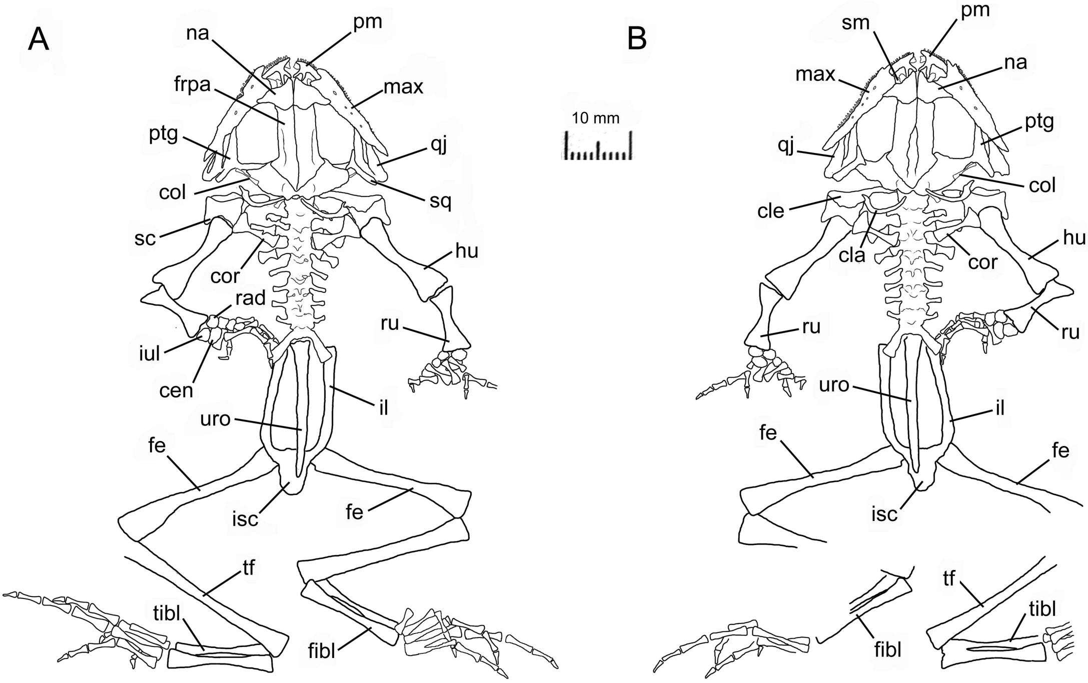

FIGURE 3. Holotype of *Genibatrachus baoshanensis,* gen. et sp. nov. (PKUP V0401): line drawing of the incomplete skeleton and impressions of the skeleton in dorsal view, as exposed on part-and-counterpart shale slabs.

(SVL of 30–45 mm), incomplete ossification of some skull elements (e.g., nasals, frontoparietals), and no ossification of the mesopodia in either fore- or hind limbs (fig. 4).

Skull Roof and Cheek Region: The skull is slightly wider than long, and the dermal skull roof is smooth, without sculpture. The holotype skull is exposed in dorsal view, with a skull length of 23 mm and a maximum width of 29 mm. As observed from several specimens including the holotype, the premaxilla has a robust alary process ascending from the midlength of the pars dentalis. The dorsal end of the alary process is bifurcated (figs. 2, 3), but in life, because of its vertical orientation, the process seems to be free of contact with the nasal bone. The pars palatina of the premaxilla is partly exposed in the holotype in dorsal view, displaying a triangular palatal process at the medial end of the premaxilla. The process has a straight medial border for articulation with the counter element. The pars dentalis of the premaxilla bears at least 15 teeth as observed from several specimens including the holotype. The teeth are slender and columnar, closely spaced, and pedicellate (as observed from several specimens that show the jaws in medial view). The tooth crowns are bicuspid, with the medial cusp obviously more crestlike than the laterally located accessory cusp (best shown in the holotype, PKUP V0401).

A septomaxilla is identified in several specimens including the holotype. The element is ossified as a small dermal bone within the narial opening, attached to the inner side of the maxilla at the posterior rim of the opening, as occurs in all living frogs (Duellman and Trueb, 1986). Ossification of this element is also seen in small postmetamorphic individuals (e.g., PKUP V0410), indicating that it probably ossified at metamorphosis as in salamanders (Rose, 2003).

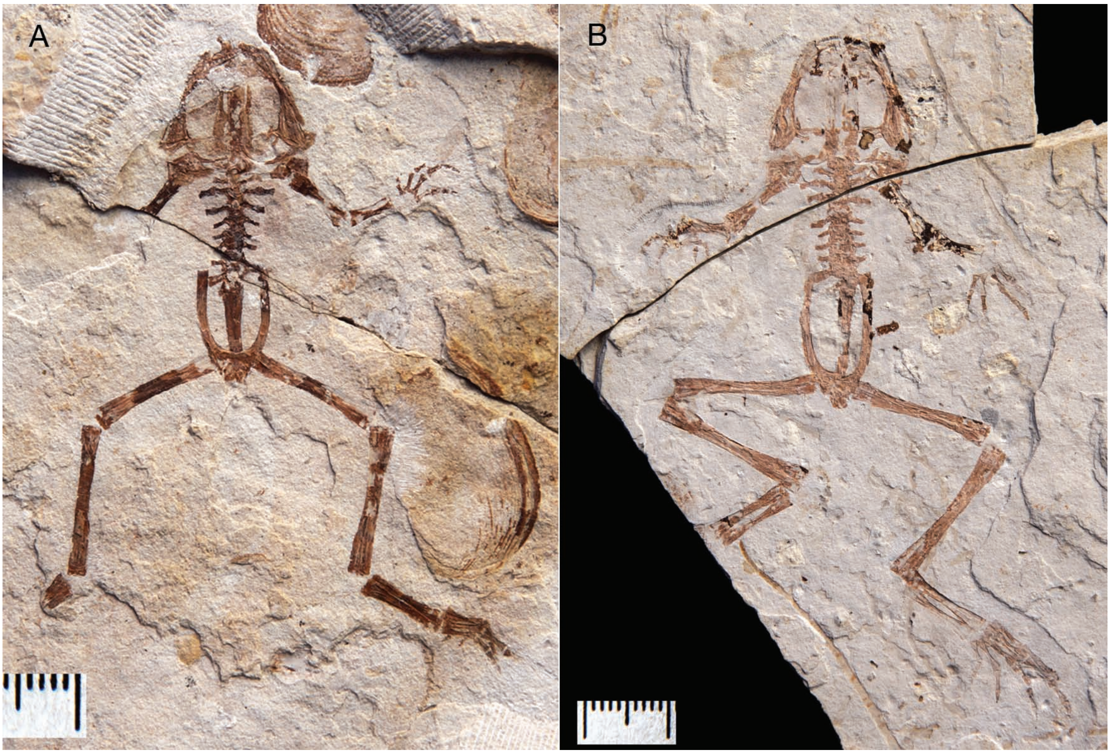

FIGURE 4. Referred specimens of *Genibatrachus baoshanensis,* gen. et sp. nov. (juvenile individuals): **A,** PKUP V0411 in dorsal view; **B,** PKUP V0412 in ventral view.

The paired nasals are well ossified and meet along the midline in large specimens, but in some juvenile specimens a fontanelle may occur posteriorly between the nasals and the frontoparietals owing to incomplete ossification (fig. 4). In its fully developed form, the nasal is wider than long, and more or less triangular shaped. The dorsal surface of the nasal is domed at the center of the bone marking the position of the nasal capsule below. The domed surface is ornamented with several small bony bumps, whereas the flat part surrounding the dome has a smooth surface. A short rostral process contacts the alary process of the premaxilla anteriorly, and the anterolateral border of the bone is slightly notched for the narial opening. The nasal contacts the maxilla by a lateral process and along the anterolateral border of the process as well. Posteriorly, the nasal has a more or less transverse sutural articulation with the frontoparietal.

The frontoparietals are paired, having a smooth dorsal surface without ornamentation. A frontoparietal fontanelle is present at variable sizes in juvenile specimens, but is closed in the fully grown adult stage. The frontoparietal on each side has a straight lateral edge that borders the orbit, and has a small posterolateral process (margo prootica) in articulation with the prootic. The posterior half of the orbital border is flanged for attachment of the pterygoideus muscle. At the level behind the orbits, the posterior projections of the frontoparietals form a triangular process that wedges between the prootic-exoccipitals, but does not extend to overhang the craniopostcranial articulation.

The maxilla on both sides of the holotype is exposed in external view (figs. 2, 3). The maxilla is deep and long, extending to the level of the posterior border of the orbit. The anterior border of the maxilla is slightly notched for articulation with the premaxilla. The pars dentalis of the maxilla bears a minimum number of 40 teeth, as observed in the holotype. The toothrow extends posteriorly to surpass the midlevel of the orbit, but does not reach the posterior extremity of the bone. The maxilla has a low facial process in articulation with the nasal in large specimens. In small specimens (PKUP V0410–V0412), however, the maxilla has an essentially straight dorsal margin, indicating that the facial process is developed and ossified at a much later ontogenetic stage, as in the common frog *Rana temporaria* (Parker, 1871). Above the maxillary toothrow, a series of small alveolar foramina arranged horizontally in a linear fashion penetrate the lateral surface of the bone. Posteriorly, the maxilla gradually decreases in height and terminates as a tapered process that articulates medially with the quadratojugal to form a complete maxillary arcade.

The quadratojugal can be observed on both sides of the skull in several specimens, including the holotype. In dorsal view, the quadratojugal forms a slightly curved splint, but in lateral view it is an elongated plate anteriorly in contact with the maxilla and posteriorly in contact with the pterygoid and squamosal (fig. 3). The presence of a maxilla-quadratojugal articulation is considered a plesiomorphic condition in batrachians (Parker, 1871), whereas the absence of the quadratojugal in Ascaphidae, Leiopelmatidae and Pipidae is a derived condition within Anura (Trueb, 1993).

The squamosal is triradiate with a roughly T-shaped configuration. The anteriorly directed zygomatic ramus is a short spike that does not contact the maxilla. The posteriorly directed otic ramus is an even shorter process in contact with the prootic. The ventral ramus is a straight bar ventrally in articulation with the pterygoid and quadratojugal at the jaw suspensorium.

Braincase and Palate: The prootic and exoccipital are fused dorsally to cover the otic capsule and posteriorly to articulate with the atlas. No gap or clear suture can be identified at the midline behind the frontoparietals; thus, the foramen magnum of this new frog is dorsally bound by the midline contact of the exoccipitals. As observed in the holotype and other specimens in which the prootic-exoccipital complex is exposed, the columella (stapes) is ossified as a slender stylus (fig. 3), extending below the prootic from the otic capsule to the cheek, where the tympanic ring was located in life. A columella is present in most extant frogs, except for *Ascaphus*, *Leiopelma*, rhinophrynids, and some neobatrachians (Trueb, 1993).

The palatal part of the skull is largely concealed in the holotype, but it can be observed in several other specimens (e.g., PKUP V0412) that have the skull exposed in ventral view. As observed from PKUP V0412, the pars palatina of the premaxilla along much of its length is a narrow shelf, but the shelf medially bears a palatal process as described above. The narrow shelf is in contact with the vomer (PKUP V0412), whereas the palatal process of the shelf is free from contacting the vomer (fig. 5).

The vomers meet medially. The vomer has a well-defined anterolateral process and a postchoanal process; between the two processes is a notch that marks the position of the internal choana (fig. 5). Medial to the choana is a small patch of vomerine teeth (best shown in PKUP

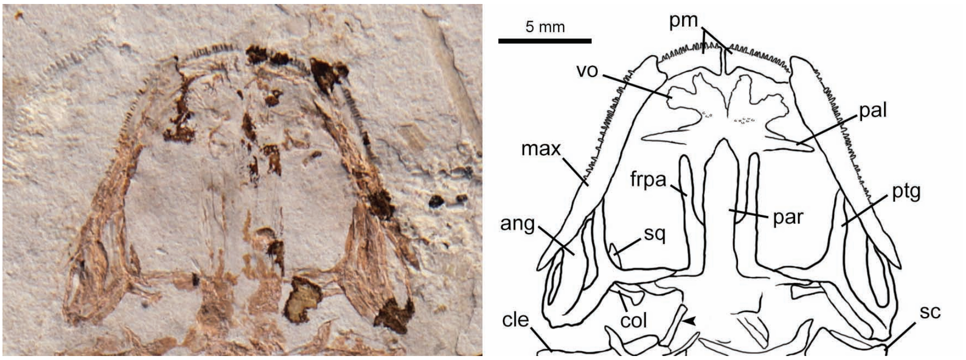

FIGURE 5. Palatal structures of *Genibatrachus baoshanensis,* gen. et sp. nov. (PKUP V0412). Arrow points to the ossified posteromedial process of the hyoid.

V0412). The palatine (neopalatine of Trueb, 1993) is ossified as a slender bar as observed from both juvenile and adult specimens (fig. 5). The medial end of this slender bar is in articulation with either the vomer or sphenethmoid in juvenile specimens, but is apparently free from contacting the maxilla laterally (PKUP V0412). Presence of a palatine (neopalatine) is considered an apomorphic feature for neobatrachians (Trueb, 1993: table 6.3), but the palatine is known as a discrete element in *Triadobatrachus* (Roček and Rage, 2000b), fused with the vomer in *Vieraella* (Báez and Basso, 1996), or fused to the vomer or to the palatal process of the maxilla in many other frogs (Roček, 2000). For Early Cretaceous anurans, the presence or absence of this element in *Eodiscoglossus* and *Neusibatrachus* is a matter of debate (Vergnaud-Grazzini and Wenz, 1975; Roček, 2000; Báez and Sanchiz, 2007).

The sphenethmoids are fully fused to form an azygous element in the palate. Lateral to the cultriform process of the parasphenoid, the posterior extension of the sphenethmoid terminates at the midlevel of the orbit. The parasphenoid displays an inverted T-shaped configuration as commonly seen in other frogs except pipoids. The cultriform process has parallel lateral borders, and has a blunt tip anteriorly in articulation with the sphenethmoid. The anterior extension of the parasphenoid articulates with the sphenethmoid, but fails to reach the vomers. Posteriorly, the parasphenoid has well-developed subotic alae that form the posterolateral wings in contact with the medial process of the pterygoid. Whether a posteromedial process of the parasphenoid is present or absent cannot be ascertained because no specimen shows a complete posterior border of the bone.

The pterygoid is typically triradiate, as commonly seen in other frogs. The anterior ramus extends to the midlevel of the orbit, with a tapering end laterally in articulation with the maxilla. The slenderer medial ramus extends below the anterior border of the prootic, and its medial end attaches to the anterior rim of the lateral ala of the parasphenoid. The posterolateral ramus is only half the length of the anterior ramus, and its distal end articulates with the quadratojugal and squamosal.

A pair of posteromedial processes of the hyoid is ossified and preserved in several specimens (e.g., PKUP V0401, V0402) as short barlike structures diverging posterolaterally and partly exposed lateral to the atlas (figs. 2, 3). Such a pair of hypobranchial elements are invariably ossified in extant frogs (Trueb, 1993). The presence of these elements in small specimens (PKUP V0410–V0412) indicates that the process ossified before maturity in this Early Cretaceous frog (fig. 5). No specimen shows a bony parahyoid, and the hyoid plate likely was entirely cartilaginous.

Mandible: The mandibles are largely concealed in the holotype, and are poorly preserved in other specimens (e.g., PKUP V0402, V0405, V0410–V0412). Based on the available information, the dentary is edentate with a smooth dorsal crest as seen in most other anurans. The dentary covers the anterior two-thirds of the external aspect of the lower jaw. None of the available specimens has the anterior end of the mandible well exposed; thus, whether a mentomeckelian is present or absent cannot be determined. The angulosplenial is larger than the dentary. It extends anteriorly along the inner side of the dentary to a point close to the mandibular symphysis, but also forms the posterior one-third of the external surface of the mandible.

Vertebral Column: The vertebral column consists of eight presacrals (including the atlas), a single sacrum, and a free urostyle. The neural arches of the presacrals are not significantly imbricated. The nonimbrication of the presacrals is similar to the condition in modern *Ascaphus*, *Leiopelma*, *Alytes*, and some neobatrachians, but differs significantly from pipoids and pelobatoids. Several specimens (e.g., PKUP V0404, V0406, V0411) display the ventral view of the presacral series, which shows the procoelous type of centrum. The atlas (presacral I) displays no transverse processes, indicating no possible fusion of the atlas with presacral II. The dual cotyles of the atlas are close to each other but not confluent.

Large specimens show that presacrals II–IV bear free ribs in adults, whereas small specimens show free ribs articulated with the transverse processes on all presacrals except the atlas (figs. 4, 6). In adult specimens, the first pair of ribs has a hooked process at the distal end and the second pair has a small spike posteriorly, close to the base of the rib (termed uncinate processes). Uncinate processes are present on ribs in basal anurans, and are considered functionally associated with the origin of pectoral muscles (Ritland, 1955). In the new frog *Genibatrachus baoshanensis*, the ribs associated with vertebrae III and IV are more or less dumbbell shaped, and the ribs of vertebra III are the most robust. Having free ribs restricted to the vertebrae II–IV in the adult stage is a derived condition in comparison with Jurassic stem anurans, but a plesiomorphic condition within crown-group anurans (see text below). Posteriorly, the new frog has the short transverse processes of presacrals V–VII directed more or less laterally, in contrast to the anterolaterally directed condition typical of pipoids and pelobatoids.

The sacral vertebra is roughly the same size as the trunk vertebrae. The prezygapophyses are well developed and in articulation with the last presacral, whereas the postzygapophyses are entirely absent, as in extant anurans (Duellman and Trueb, 1986). The diapophysis of the sacral is essentially unexpanded, and is oriented posterolaterally. The nonexpanded condition is probably plesiomorphic in frog evolution, similar to that in living *Ascaphus* and *Leiopelma* and the Jurassic frogs such as *Prosalirus* (Jenkins and Shubin, 1998), *Vieraella,* and *Notobatrachus* (Estes and Reig, 1973; Bàez and Basso, 1996), but differs from the condition in pipoids and pelobatoids, in which the sacral diapophysis is strongly dilated. The sacral vertebra posteriorly has two condyles for a bicondylar articulation with the urostyle.

The length of the urostyle is similar to or slightly shorter than the combined length of the trunk series. The urostyle bears one pair of transverse processes anterolaterally. In the holotype,

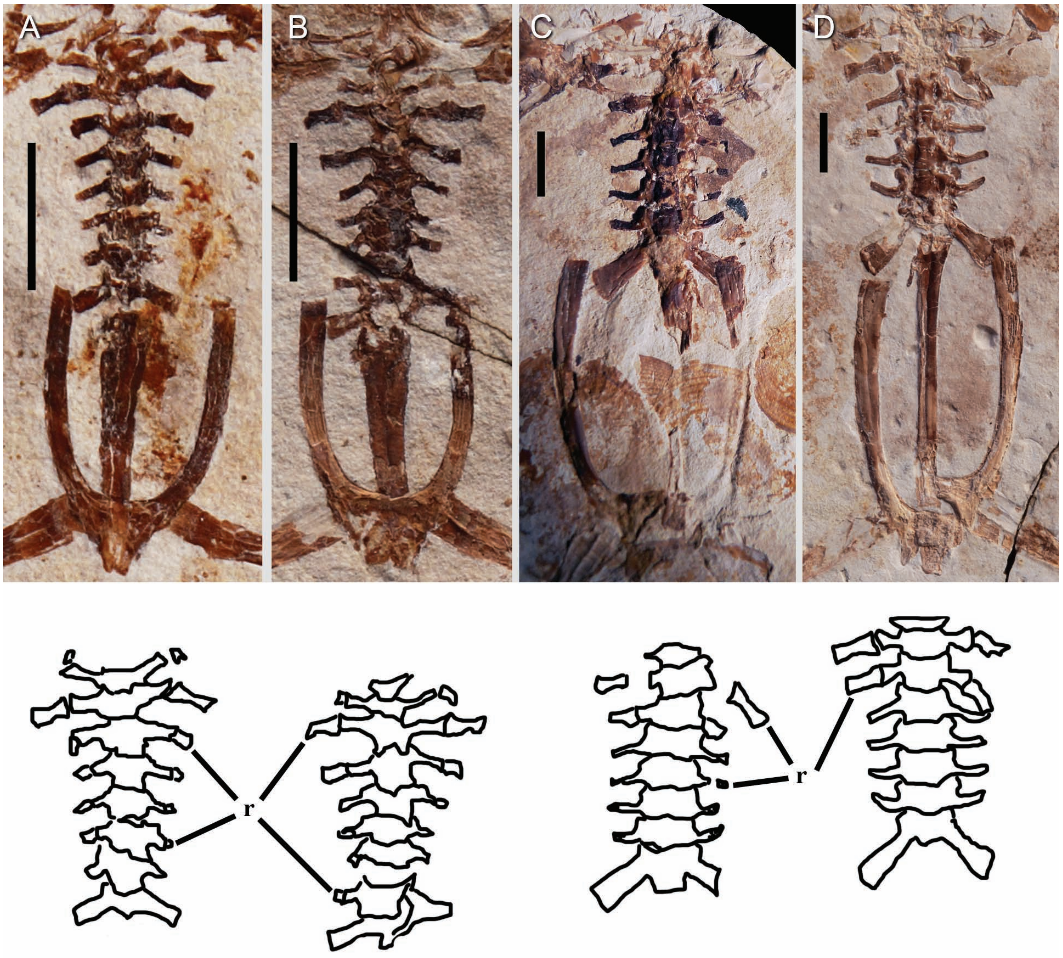

FIGURE 6. Ontogenetic fusion of ribs to transverse process of the vertebra: **A,** PKUP V0410 (juvenile); **B,** PKUP V0411 (juvenile); **C,** PKUP V0406 (young adult); **D,** PKUP V0404 (fully grown adult). Scale bars = 5 mm. Note that PKUP V0410 and V0411 show all trunk vertebrae with free ribs articulated with the transverse process, PKUP V0406 shows a transitional stage of fusion of the ribs on posterior trunk vertebrae, whereas PKUP V0404 shows fully fused ribs to the transverse process on the posterior trunk vertebrae.

the transverse processes are still imbedded in the matrix, but several other specimens including the juvenile individuals have the processes exposed (fig. 4). The urostyle is dorsally smooth and lacks a dorsal crest, but has a groove running ventrally along its long axis. Posteriorly the urostyle reaches the ischiac arch, where the tapering tip of the urostyle sits in the V-shaped ischiac arch.

Pectoral Girdle and Forelimb: The pectoral girdle is likely of arciferal type, as indicated by the oblique position of the coracoid in relation to the clavicle. The curved clavicle is roughly sickle shaped, and the two elements appear to have an abutting contact at the midline. The lateral end of the clavicle has a spikelike process, with its concave posterior border wrapping around the anteromedial edge of the scapula. The coracoid has a slender shaft, but it is expanded at both its medial and lateral ends, with the lateral expansion slightly wider than the medial sternal end. The two coracoids are widely set apart medially, without direct contact at their sternal ends. This morphology of the coracoids, in keeping with the sickle-shaped clavicles, indicates an arciferal type of pectoral girdle (Cope, 1864, 1865; Kaplan, 2004). The scapula is short and stout, at no more than one-third the length of the humerus. The leading edge of the scapula is weakly concave, whereas its posterior border is concave to a greater degree. The medial or glenoid end of the scapula lacks a notch or cleft; thus, there is no clear distinction between the pars acromialis and pars glenoidalis. The cleft and uncleft conditions of the scapula seem to be highly variable in fossil and extant frogs (Ritland, 1955; Kluge and Farris, 1969; Worthy, 1987), and the phylogenetic significance of the character needs to be more fully investigated. The cleithrum is ossified as a thin and widened plate at its base, and a tonguelike process extends toward the midline. The cleithrum is penetrated by several tiny foramina at its base and the medial process.

The humerus in large specimens has well-ossified proximal and distal ends, whereas the same element in small individuals shows incomplete ossification at both ends. As observed from adult specimens, the expanded proximal end carries a rounded humeral condyle for articulation with the scapula, and a clearly defined crest (cresta ventralis) anteroventrally extends to the midlevel of the shaft for the attachment of pectoral muscles. At the distal end of the humerus, a well-ossified ventral head (eminentia capitata of Gaupp, 1896) articulates with the radioulna.

The radioulna is fully fused into a single bone, which has a short shaft constricted between the expanded proximal and distal ends. An olecranon process is recognizable as a small projection, dorsal to which lies the fossa for articulation with the ventral head of the humerus. Toward the distal end of the radioulna, a longitudinal sulcus marks the fusion of the two elements, but the two condyles are still distinguishable from one another at the end of the bone.

Large specimens show a variable number of ossified carpals, whereas small individuals show no ossification of mesopodial elements. Six carpal elements are observed in the left hand of the holotype: radiale, fused intermedium-ulnare, a large centrale, and distal carpals 2, 3, and 4 (fig. 3). Distal carpals 3 and 4 are dislocated because of preservational distortion, but other elements are essentially in their natural position. The presence of only two proximal carpals indicates that the intermedium is probably fused with the ulnare. Distal carpal 5 is probably fused with distal carpal 4, as indicated by the large size of the latter element. A prepollex is absent in the holotype and all other specimens. Among the metacarpals (Mc) preserved in the holotype, Mc II is the shortest (3 mm long in the holotype). Mc III and IV are roughly equal in length (4 mm in the holotype), whereas Mc V is slightly shorter (3.5 mm long). Mc I has a smooth lateral border, showing no trace of a possible nuptial tubercle, which occurs in some frogs. *Genibatrachus baoshanensis* has a phalangeal formula of 2-2-3-3 in the manus, as observed in all specimens with this part of the limb preserved. Judging from multiple specimens, digit 1 is in a normal position, showing no sign of inward rotation; thus, the new frog lacks carpal torsion.

PELVIC GIRDLE AND HINDLIMB: The ilium has a cylindrical shaft that lacks a clearly defined dorsal crest. The dorsal tubercle (tuber superior) is present as a small process rather than a distinct protuberance anterodorsal to the supraacetabulum crest (PKUP V0402–V0404, and V0407), for the attachment of m. gluteus magnus (Duellman and Trueb, 1986). In living frogs, the dorsal tubercle is either absent or low, but the lack of a distinct dorsal tubercle is a plesiomorphic condition for Anura, as evidenced by the condition in the Jurassic stem anurans *Prosalirus* and *Notobatrachus* (Shubin and Jenkins, 1995; Báez and Nicoli, 2008). The supraacetabulum crest is present, but not noticeably high. The two ilia are in sutural contact posteroventrally to form an iliac symphysis (synchondrosis). The ischium has a dorsal expansion above the acetabulum and a posterior projection in dorsal view.

The femur is straight in small specimens (fig. 4), but is weakly sigmoid in large individuals (fig. 3). The fused tibiofibula is straight, having a slender shaft and slightly expanded proximal and distal ends. The tibiofibula is slightly longer than the femur as observed in both small and large specimens that have the long bones completely preserved.

The tibiale and fibulare are unfused, but contact one another at both ends, leaving a narrow, fissurelike gap between the two bones. Both elements are slender and elongate, with the fibulare slightly longer than the tibiale (16 mm vs. 15 mm in the holotype). As observed in both large and small specimens, the length of the tarsal segment is slightly greater than half the length of the tibiofibula, indicating that the proportions of the tarsal segment in relation to the tibiofibula are not variable ontogenetically. No distal tarsals are ossified in the holotype and other large specimens, indicating that ossification of the hind foot is ontogenetically postponed in relation to the forefoot. Among the metatarsals (Mt) observed in the holotype, Mt IV is the longest (9 mm), followed by Mt III (8 mm). Mt II and V are roughly equal in length (7.5 mm), whereas the shortest metatarsal, Mt I, is only 4 mm long. The phalangeal formula of the pes is 2-2-3-4-3, a typical pattern for most frogs. Digit 1 is the shortest, and digit 4 the longest, in keeping with the relative length of the corresponding metatarsals. No prehallux nor any trace of cartilaginous impressions has been identified in any available specimens, indicating that the prehallux was probably absent.

PHYLOGENY AND COMPARISON WITH OTHER EARLY CRETACEOUS FROGS

The new frog named and described in this paper is based on multiple specimens from the Early Cretaceous of far northern China. The well-preserved fossils show several noticeable morphological features that can be incorporated into a phylogenetic analysis. We sampled 97 morphological characters across 57 fossil and living taxa (see appendix 1 and Morphobank.org Project 2501 for detailed coding), and nine mitochondrial, ribosomal and nuclear gene sequences (16S, 28S, CXCR4, CYTB, H3A, NCX1, RAG1, Rhodopsin, SIA, see appendices 2–10) for 37 living taxa, resulting in a combined matrix of 62 terminals coded for morphological and molecular data for the analyses. The morphological matrix was modified from Chen et al. (2016). Gene sequences were downloaded from Genbank (Benson et al., 2004) and aligned using the default settings in MUSCLE (Edgar, 2004). The analysis was performed under maximum parsimony criterion using POY 4.1.2 (Varon et al., 2010). All morphological characters were unordered and weighted equally. Both substitution and indel costs for gene sequence transformations were set to one. The "Search" command is used (appendix 11), which uses a combination of methods including tree building, swapping using TBR (perturbation using ratchet and tree fusing) to find the most parsimonious trees (MPTs). The total run time was set to two hours. The search ended up evaluating 18 independent repetitions with ratchet and fusing for 190 generations. Jackknife value was calculated with a deletion of 36% characters for 100 iterations in POY 4.1.2.

Results of the combined phylogeny confirmed *Genibatrachus baoshanensis* as a basal member of the Pipanura with a low jackknife value of 0.18 (fig. 7), with unresolved relationships with the Pipoidea and Acosmanura (Pelobatoidea + Neobatrachia). The new frog shares with the Pipanura eight presacral vertebrae and the procoelous type of vertebral centrum. In modern frogs, the presence of eight presacral vertebrae is seen in the Pipanura and "Discoglossidae" (recovered as paraphyletic), but not in the Leiopelmatoidea (with nine presacrals). A procoelous centrum occurs only in the Pipanura, whereas "Discoglossidae" have an opisthocoelous and Leiopelmatoidea have an amphicoelous type of centrum. The new fossil taxon retains plesiomorphic morphologies within the Pipanura, such as the presence of free ribs on presacral II–IV and nonimbricate neural arches, preventing it from being included in either of the crown clades in the phylogenetic analysis of this study.

Previously, Early Cretaceous frog fossils from northern China came solely from several localities near Chaoyang within the Jehol area (fig. 1). These frogs (*Callobatrachus*, *Mesophryne*, and *Yizhoubatrachus*) were recovered as occupying paraphyletic positions at the base of the "Discoglossidae" + Pipanura (fig. 7), retaining plesiomorphic morphologies such as the presence of nine presacrals and an amphicoelous centrum. *Genibatrachus baoshanensis* was recovered from a new locality far north of the Jehol area (fig. 1). Despite its similarity in age, the new fossil taxon is clearly different from those previously known Jehol frogs in its combination of the following characters: alary process of premaxilla bifurcated; procoelous presacral vertebrae eight in number; anterior trunk vertebrae II–IV bearing free ribs; sacral diapophysis nonexpanded and posterolaterally oriented; urostyle bearing a single pair of transverse processes; clavicle sickle shaped and closely approaching or in contact with the counter element; tibiofibula slightly longer than femur; tarsal segment slightly longer than half the length of tibiofibula in adult stage; fibulare slightly longer than tibiale; phalangeal formula 2-2-3-3 in manus and 2-2-3-4-3 in pes.

A number of well-preserved fossil frogs have been found from Early Cretaceous beds of Spain (Sanchiz, 1998; Roček, 2000; Báez and Sanchiz, 2007; Báez, 2013). The age of these fossils was thought to be Late Jurassic or Early Cretaceous (Hecht, 1970; Vergnaud-Grazzini and Wenz, 1975), but has been revised to Early Cretaceous (Ansorge, 1993: Barremian to Aptian; Martín-Closas and López-Morón, 1995: late Hauterivian to early Barremian; Báez and Sanchiz, 2007: late Berriasian to early Valanginian). *Eodiscoglossus santonjae* and a recently described taxon *Iberobatrachus angelae* are both discoglossidlike, characterized by the opisthocoelous type of centrum, which differs from the procoelous centrum in *Genibatrachus baoshanensis*. These three frogs (*Eodiscoglossus*, *Iberobatrachus*, and *Genibatrachus*), however, all retain the

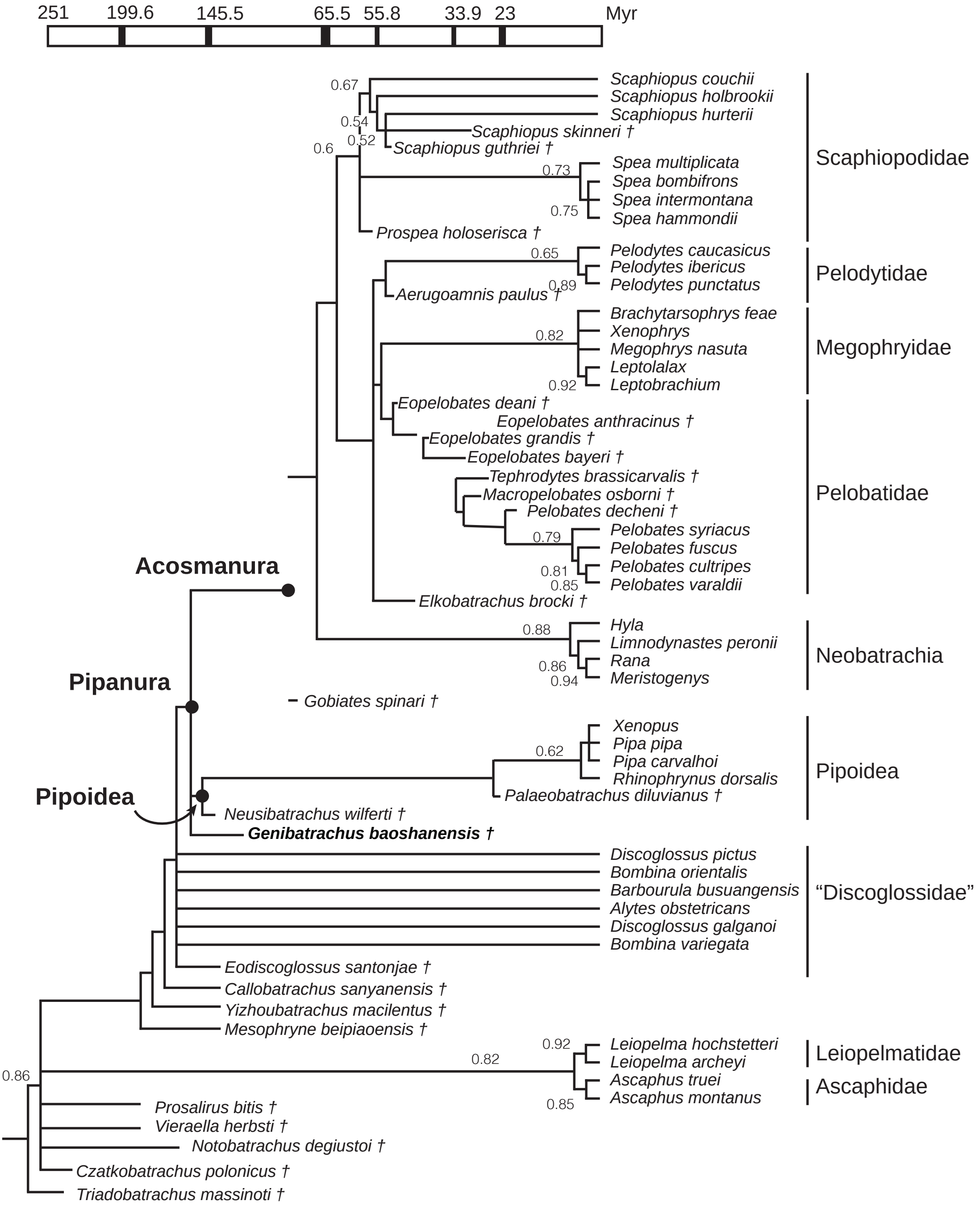

FIGURE 7. Relationships (strict consensus) of *Genibatrachus baoshanensis* with other living and fossil frogs. The tree is calibrated with the ages of fossil taxa. The new fossil taxon is highlighted in **boldface**. The numbers next to the branches represent the jackknife supporting value (only supporting value higher than 0.5 is shown).

plesiomorphic condition of having free ribs in presacrals II–IV. Early Cretaceous *Neusibatrachus wilferti* and *Gracilibatrachus avallei* from Spain, on the other hand, clearly belong to the specialized clade Pipoidea, most notably characterized by azygous frontoparietal, absence of posterolateral wing of parasphenoid, and long transverse processes on presacral II–V indicating rib fusion (Báez and Sanchiz, 2007; Báez, 2013). The new frog *Genibatrachus baoshanensis* lacks any of these specializations, and is not closely related to the Pipoidea.

The Early Cretaceous Crato Formation (Aptian–Albian) of northeastern Brazil is also known for well-preserved fossil frogs, representing one of the best Gondwanan Cretaceous frog fossil assemblages (Báez et al., 2009). Three fossil species, *Arariphrynus placidoi*, *Euricephalilla alcinae* and *Cratia gracilis*, were identified and included in the clade Neobatrachia, representing the earliest neobatrachians known worldwide (Báez et al., 2009). *Genibatrachus baoshanensis* shares with these frogs the presence of the palatine, nonimbricate neural arches, and nonexpanded and posterolaterally directed sacral diapophysis. However, the new frog differs in retaining the plesiomorphic condition of free ribs in presacral II–IV, which is absent in all three Brazilian fossil taxa.

Comparing the Early Cretaceous frogs of northern China, Spain, and northeastern Brazil comes to the conclusion that each represents completely different lineages of evolution. The previously known fossil frogs from China (*Mesophryne*, *Callobatrachus*, and *Yizhoubatrachus*) represent basal taxa of crown anurans. The discovery of *Genibatrachus baoshanensis* shows that basal pipanurans were also present in East Asia by the Early Cretaceous. The fossil frogs from Spain represent discoglossidlike forms (*Eodiscoglossus* and *Iberobatrachus*) and basal pipoids (*Neusibatrachus* and *Gracilibatrachus*). The Gondwanan fossil frogs from the Early Cretaceous of Brazil, in sharp contrast to those from the Laurasian faunas, were closely related to modern neobatrachians. The large diversity and wide geographic distribution of Early Cretaceous crown-group frogs on three different continents indicate an early diversification radiation of crown anurans paired with a high degree of endemism.

DISCUSSION ON EVOLUTION OF EARLY FROG BODY PLAN

The new frog described in this paper displays several postcranial characters that are of ontogenetic and phylogenetic importance: presacral vertebrae eight in number; free ribs present in association with presacrals II–IV; ribs associated with presacrals V–VIII fused with transverse processes through ontogeny; neural arches nonimbricate; and sacral diapophysis nonexpanded. Compared with the other early fossil frogs and results from our combined phylogeny as a framework (fig. 7), here we discuss how the body plan of frogs was modified through time and across lineages.

Shortening of Vertebral Column: Reduction in the number of trunk vertebrae is a major trend in anuran evolution (Griffiths, 1963; Kluge and Farris, 1969; Lynch, 1973; Shubin and Jenkins, 1995). Most living frogs have no more than eight presacral vertebrae, with the exception of the Leiopelmatidae (*Ascaphus* and *Leiopelma*) having nine. The Triassic proanuran *Triadobatrachus* has as many as 14 presacral vertebrae (Rage and Roček, 1989), whereas the number of vertebrae is unknown for the closely related *Czatkobatrachus* from the Triassic of Poland (Evans and Borsuk-Bialynicka, 1998). One Jurassic stem anuran, *Vieraella*, has 10 presacrals, and *Notobatrachus* has nine (Báez and Basso, 1996; Báez and Nicoli, 2008). The Early Jurassic *Prosalirus* from North America is based on a composite of isolated elements from different individuals; thus, the actual number of presacral vertebrae cannot be determined (Shubin and Jenkins, 1995). Among all known Jurassic anurans, *Rhadinosteus* from Utah is the only taxon reliably known to have eight presacrals (Henrici, 1998).

All previously known Early Cretaceous frogs from the Jehol Biota in China (*Callobatrachus*, *Mesophryne*, *Yizhoubatrachus*) have nine presacrals, although they lived roughly at the same time as the new frog *Genibatrachus baoshanensis* from the far north of Inner Mongolia. The Early Cretaceous *Neusibatrachus* from Spain also has nine presacrals, with presacral I and II fused (Báez and Sanchiz, 2007). Estes and Reig (1973) considered the possession of nine presacral vertebrae in extinct and extant frogs as a fixed condition for a long interval in anuran history. Because Jurassic-Cretaceous and some extant forms (*Ascaphus* and *Leiopelma*) have nine presacral vertebrae, reduction of the trunk vertebrae to eight is a character transformation that clearly took place within the crown anurans, probably somewhere near the base of the "Discoglossidae" + Pipanura. Analysis of the new frog *Genibatrachus*, as well as of the Early Cretaceous fossil frogs from Spain and Brazil, shows that the reduction of presacral vertebrae to eight occurred before the Early Cretaceous; further support for this hypothesis may be found in the Late Jurassic *Rhadinosteus* from Utah (Henrici, 1998).

Loss of Ribs by Fusion with Transverse Process: Another major trend in frog evolution is the reduction and ultimately the loss of free ribs, in association with the shift from coelom-driven respiration to buccal-pump respiration (Duellman and Trueb, 1986). This trend of evolution is corroborated by evidence from both ontogenetic and paleontological studies. According to Pugener et al. (2003: char. 41), extant leiopelmatids and discoglossids are the only groups that have three (or occasionally four) pairs of free ribs in their larval and adult stages. In contrast, extant pipoids have free ribs in the larval stage, but the ribs are fused to the transverse processes around metamorphosis. Developmental studies have documented that rib rudiments are also present in larval stage of some neobatrachians (*Hyla* and *Rana*) and pelobatoids (*Pelobates*), but are subsequently lost in adults (Blanco and Sanchiz, 2000). It is unclear whether the loss was due to resorption or fusion, according to Blanco and Sanchiz (2000).

In the fossil record, the Early Triassic proanuran *Triadobatrachus* has all of its trunk vertebrae bearing free ribs (Sanchiz, 1998). In addition, *Triadobatrachus* also has ribs unfused to the sacral vertebra, and at least the first caudal vertebra bears free ribs. The Early Jurassic stem anuran *Prosalirus* and the Late Jurassic *Notobatrachus* are both known to have four to five pairs of free ribs associated with their anterior trunk vertebrae (Shubin and Jenkins, 1995; Bàez and Basso, 1996), and the Early Jurassic *Vieraella* has three pairs of free ribs (Roček, 2000). The rib condition for the Late Jurassic *Rhadinosteus* is still unknown (Henrici, 1998).

Among the Early Cretaceous frogs, the European *Neusibatrachus* probably has four pairs of free ribs (Báez and Sanchiz, 2007), whereas *Eodiscoglossus* from Spain and all frogs previously known from the Jehol Biota of China have three pairs of free ribs associated with the trunk vertebrae II–IV (Sanchiz, 1998; Gao and Wang, 2001; Gao and Chen, 2004). Neogene *Palaeobatrachus* from Central Europe has five pairs of free ribs during development, but these are fused with the transverse processes of presacral vertebrae II–VI in adults (Špinar, 1972; Roček, 2003). In view of the fossil record and knowledge from extant anurans, possession of three pairs of free ribs should be regarded as a derived condition compared with Jurassic stem anurans, but a plesiomorphic condition in relation to crown-group anurans. The complete loss of adult ribs in frogs probably occurred along the stem of the Pipanura crownward of *Genibatrachus*, as the new fossil taxa still retains ribs II–IV in adults.

Comparative study of juvenile and adult specimens of *Genibatrachus* also reveals ontogenetic information regarding the fusion of ribs, corroborating the developmental patterns in extant groups (Blanco and Sanchiz, 2000; Pugener et al., 2003). All large specimens have ribs articulated with the transverse processes of the trunk vertebrae II–IV. However, juvenile specimens have free ribs associated with all trunk vertebrae (figs. 4, 6A, B). As observed from three juvenile specimens (PKUP V0410–V0412), the anterior trunk vertebrae II–IV bear free ribs as seen in adult specimens, but the trunk vertebrae V–VIII also have short ribs articulated with the transverse processes (fig. 6A, B). Because these small specimens have a SVL of 30–45 mm, substantially shorter than that of the holotype (70 mm) and the other large specimens (maximum 80 mm), the presence of free ribs associated with all trunk vertebrae obviously displays a juvenile feature, which is evidently different from the condition in adults. More interesting is a specimen (PKUP V0406) with an SVL estimated as ~65 mm, as it displays what is probably the final stage of rib fusion to the transverse process on posterior trunk vertebrae (fig. 6C). In this specimen, the suture between the transverse process and the rib is barely distinguishable, but the colors of the two parts are still different, reflecting the recent independence of ribs from the vertebrae just prior to fusion. Because the specimen is substantially larger than the juveniles but slightly smaller than the other large specimens, it is interpreted as a subadult yet reached the full adult stage.

Type of Centrum: Three types of vertebral centrum occurs in extant frogs. The amphicoelous centrum is the plesiomorphic condition for frogs, as evidenced by the condition in the proanuran *Triadobatrachus* and some basal crown anurans (*Ascaphus* and *Leiopelma*). In other frogs, two independent apomorphic conditions occur. Discoglossids (*Alytes*, *Bombina*, *Barbourula,* and *Discoglossus*) and pipoids (*Pipa*, *Xenopus*, and *Rhinophrynus*) have an opisthocoelous type of centrum, which is convex anteriorly and the concave posteriorly. The Pelobatoidea and Neobatrachia, on the other hand, have a procoelous type of centrum, which is concave anteriorly and convex posteriorly.

In the fossil record, the Jurassic taxa *Prosalirus*, *Vieraella*, and *Notobatrachus* all have the plesiomorphic condition of amphicoelous centrum (Roček, 2000), similar to the proanuran *Triadobatrachus*. The Jehol frogs *Yizhoubatrachus* and *Callobatrachus* were originally reported to have opisthocoelous centra (Gao and Wang, 2001; Gao and Chen, 2004), whereas *Mesophryne* express procoelous centra (Gao and Wang, 2001). Dong et al. (2013) considered all these three Jehol frogs to have amphicoelous centra, but no clear evidence supports such speculations. *Eodiscoglossus* and *Iberobatrachus* from the Early Cretaceous of Spain possesses opisthocoelous centra, a character shared by other discoglossids (Roček, 2000; Báez, 2013). Interestingly, the basal pipoids *Neusibatrachus*, *Paleobatrachus*, and *Gracilibatrachus*, unlike their living relatives with opisthocoelous centra, all possess procoelous centra (Roček, 2000; Báez and Sanchiz, 2007; Báez, 2013). The new frog *Genibatrachus*, as a basal member of the Pipanura, also possesses a procoelous centrum. Optimizing this character in the phylogeny indicates that the procoelous centrum is a shared derived character of the Pipanura. Modern pipoids further evolved into the opisthocoelous state from a procoelous condition.

Imbrication of Neural Arches: *Genibatrachus* shares with leiopelmatids (*Ascaphus* and *Leiopelma*) and some neobatrachians the apomorphic condition of nonimbricate neural arches, whereas in most "archaeobatrachian" frogs the neural arches are weakly (Discoglossidae) or strongly (Pipoidea and Pelobatoidea) imbricated, with the arches roofing over the spinal cord. However, based on results of our combined phylogeny (fig. 7), the occurrences of the derived condition in leiopelmatids and some but not all neobatrachians are probably homoplastic. Furthermore, this character may be correlated with mode of locomotion, with "hoppers" more likely to have nonimbricate and "crawlers" imbricate neural arches. Further work is needed to evaluate the phylogenetic significance of this character.

Modification of Pelvic Region: As the most speciose group of modern amphibians, anurans have evolved a highly specialized pelvic region along with the evolution of a unique type of hopping/jumping locomotion. Four traits have been highlighted in discussing the phylogenetic and functional aspects of the frog pelvis (Emerson, 1979; Shubin and Jenkins, 1995; Reilly and Jorgensen, 2011): the expansion of the sacral diapophysis, the dorsal ridge on the ilium, the type of sacral-urostyle articulation, and the dorsal ridge on the urostyle. The pelvic region of the Early Triassic proanuran *Triadobatrachus* is still significantly different from that of modern frogs, with a salamanderlike sacrum, presence of sacral ribs, short ilium, and presence of six caudal vertebrae instead of a fused urostyle. The rigid ilio-sacral articulation of *Triadobatrachus* suggests the incapacity of jumping locomotion (Shubin and Jenkins, 1995). The modern frog pelvis appeared first in the Jurassic *Prosalirus* and *Notobatrachus* (Shubin and Jenkins, 1995; Báez and Nicoli, 2008), characterized by a nonexpanded sacral diapophysis directed posterolaterally, smooth dorsal surface of ilium and urostyle without a ridge, and a bicondylar sacral-urostyle articulation. This set of characters is also seen in the most primitive living frogs *Ascaphus* + *Leiopelma*, all Early Cretaceous fossil discoglossids and pipoids from Spain (Báez and Sanchiz, 2007; Báez, 2013), and the Early Cretaceous fossil neobatrachians from Brazil (Báez et al., 2009). All the three previously known Jehol frogs are characterized by moderately expanded and hatchet-shaped sacral diapophysis, bicondylar sacral-urostyle articulation, and smooth ilia and urostyle (Gao and Wang, 2001; Gao and Chen, 2004). In sharp contrast, the new frog *Genibatrachus* displays a nonexpanded sacral diapophysis, although it retains a smooth dorsal surface in ilia and urostyle. Modern pipids (*Pipa* and *Xenopus*), adapted to a swimming lifestyle, have a specialized pelvic morphology of greatly expanded sacral diapophysis, and fusion of the sacrum with urostyle. Modern Pelobatoidea are also known to have a moderately or greatly expanded sacral diapophysis, but the sacrum and urostyle are either fused or bear a monocondylar articulation, which was considered to be related to their crawling style of locomotion (Reilly and Jorgensen, 2011). Specialized long-distance jumpers evolved multiple times in the Neobatrachia (Reilly and Jorgensen, 2011), characterized by the combination of nonexpanded, rodlike sacral diapophysis, with the ilium and/or urostyle bearing a dorsal ridge.

The polarity of the sacral diapophysis morphology was controversial in previous studies. Based on outgroup comparison and fossil evidence, we treat the nonexpanded condition as plesiomorphic, and both hatchet-shaped and butterfly wing-shaped conditions as derived conditions. This interpretation of the character evolution concurs with that of some previous authors (e.g., Estes and Reig, 1973), but differs from others (e.g., Tihen, 1965; Reilly and Jorgensen, 2011), who thought that the evolutionary transition was from the dilated to the nondilated condition (see also Lynch, 1973).

CONCLUSIONS

In this paper, we described a new fossil frog from the Early Cretaceous Guanghua Formation of Inner Mongolia, China. It extends the geographic distribution of Jehol frogs from western Liaoning to the far north of China, close to the 50th parallel north. The unique combination of plesiomorphic and derived morphologies places the new frog as a stem member of the Pipanura, which include modern Pipoidea, Pelobatoidea, and Neobatrachia. Comparisons of this new frog with other Early Cretaceous frogs from China, Spain, and Brazil reveal a high diversity of frog species coupled with a high degree of endemism. The new fossil provides novel information on the early evolution of modern frog body plans related to the reduction of vertebral column, fusion of ribs, acquisition of procoelous centrum, imbrication of neural arches, and modification of the pelvic region. The presence of both juvenile and adult specimens provides rare ontogenetic evidence of the pattern and pathway of rib fusion in a fossil frog of Early Cretaceous age.

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APPENDIX 1

Morphological Matrix

For the morphological character list, see supplementary material of Chen et al. (2016).

Triadobatrachus massinoti
000??0?1000000????0?0?0000?????0?00000000?0??0?0000?00000000???000?00??0??000001000?0
?000????????

Czatkobatrachus polonicus
???0?0???10??????????1????????010??1?00??????????????

Prosalirus bitis
???????1??00???11?????????1??????0?0????0??0???0?0???10{12}???0???1?0???1?????01??1?20?1??0?
????????

Vieraella herbsti
1?0?01?1011001???001??1001101101?010?????00??1?00?{12}?0?0?0?0?0????0?001?0???01??1??0?
1?0??????????

Notobatrachus degiustoi
000000?101{12}?11001000111001?001010000?1?00000?2?0021?0101000{12}0??1000001?0??00
10?1020?1??0?????????

Ascaphus truei
00111?010220?10?01?111100100?0?1011100001000?2001220010200000001011001?002011101
0?00111101?000000

Leiopelma hochstetteri
00111?010220?20?01?1111001001201011101001000?20012200102100000001000001?003011101
0200111101?100000

Alytes obstetricans
00001?010210?21?10?1201001101201111100010000?30110200112?10?01010110000103111101
1200120101?1000?0

Barbourula busuangensis
000000010010021000012010011012011111001000000?301002?0112?20?0001011?10?103111101
0100100101?1000?0

Bombina orientalis
00000101021012101001301001101201111100001000030100200112?2000001011100?10311110
10{01}00100101?1000?0

Discoglossus pictus
000000010{12}1012101001201101101201111100110000030100200112110?010101110001031111011210120101?1000?0

Eodiscoglossus santonjae
000001?1001001??100?201001?0????????????0?00?3010?2?01{01}2110?0????1??00?1????11?102?01?01?1???????

Callobatrachus sanyanensis
000?0??10?20?2??100?201001101201???????0000?2010?2?0112110?0??1011??0?0???111?1?2??1?01?1??0????

Mesophryne beipiaoensis
000?0??1?????2?0000??01101?0?????11?0?0?000??2020?2?01120?0????10??0010????110?1?2?01?01?0??0?0??

Pipa pipa
10011{01}{12}11021022101101130011 1???10211111201{01}1?31100321122132?1011001{01}010102?111010021100111?201000

Xenopus
{01}021000110201231011011300 11{12}???102111012010103{01}102321122132?10110120100102?111010021110111?201000

Rhinophrynus dorsalis
100000?11021?21?0011102001101 1?10210020011110301004?1102?12??001101?01?2001111011200100111?210010

Palaeobatrachus diluvianus
10000??110?0?21?00102{01}10011?1??10210?0?00001?312023?0112?12????1?11??1?1??011{01}?1?2??1?0111???????

Neusibatrachus wilferti
0??????11??0????1?0??0?????01??1021??0?00?0??31202{34}20102112?0???0111000?????1??1????1????????????

Hyla
{01}0011?010220?21?10?12010101011001111?1020?01?312024?0112112?{01}1011001010001?11121010?100111?210011

Limnodynastes peronii
10010?0101?0?21?10?12010011011001111?1020101?312114{12}0102112?110110000101{01}1?11121021?1001{01}1?210011

Yizhoubatrachus macilentus
00???0101?1???1010??0?????0????001?01?0000??2?1????0112?12?0???0111001????11??1????1??0????0????

Pelodytes caucasicus
0011110100101 2?10001201001101201110100010001030200411122?2??01011001011?1??1111111001002?1?210100

Pelodytes punctatus
0010000102201 2?1000120100110120111110001000103020141112 2?2??0101010101 1?1??11?1111001002?1?210100

Pelodytes ibericus
0011100102201 2?1000120100110120111110001000103020141112 2?2??0101010101 1?1??11?1111001002?1?210100

Aerugoamnis paulus
101001010?{12}012?1?00120100110???1?????{01}??0?01?30?104111120201 0??100010??1???11??1?2001?00?{01}???????

Tephrodytes brassicarvalis
010000?1001?02???001201111?????????????0?01130200411122?{12}2?0???1001?????111??1?10?1??2?{01}???????

Megophrys nasuta
00010?0100?1?2??10?12010101011011111 0?020001130200410 1?2?{03}1?0201100?01?01??11101?1?0100111?21000?

Elkobatrachus brocki
?0?10??10210?2?010??2????10????1100????01130?0?411112120?0??1101001?011?11??1???01?00?1??1????

Prospea holoserisca
10010??102111{12}???0012?100110???1?11?010???01?3020?{34}11122021?0??1??01001?01111?01?20?1??1?22?1????

Spea multiplicata
0001002102111 2??101121200110121111110102000 1?30200411112 03{12}001011001001101?1110112001001122?10100

Spea hammondii
00110?2102?112??10?121200110?211?1?1010?00011302004111120310010110010 01?01?11?01?200100??22?10100

Spea intermontana
0001002101211 2??1011212001101211011101020001130200411112032001011001001?01?1110112001001122?10100

Spea bombifrons
00110121021112?0101121200110121111110102000113020041111203100101100100 1?01?1110112001001122?10100

Scaphiopus hurterii
02010021002102??10012111111012111111010200011302004 11?120??001011001001?01?11?01
?200100??21?10100

Scaphiopus holbrookii
02010021001102??10012111111012111111010200011302004111120320010110010 01?01?11?0
11200100??21?10100

Scaphiopus couchii
02010021001102??10112111111012111111010200011302004111120320010110010 01?01?11?0
1?200100??21?10100

Scaphiopus skinneri
02011121002102?010012111111012111111010?0?0?13020???1112?32?0???10???0???????????????
????????????

Scaphiopus guthriei
0210??21002102????0?21111110?{12}111111011???0?1???????????????????100????????????????????
??????????

Macropelobates osborni
010????1001112??????20111110?????1??0?0?0?01?3020?4?1122022?0??11????1?????11??112011?
00?21?1????

Pelobates decheni
010000?1001102???00?201110??????????????????130?0?41?122022?0??1???????0???11??1?2?01??0
?????????

Pelobates varaldii
01000?2110?102??10?120111010100111110?020001130200411122032001011001011?11?11?01
?200100??21?10100

Pelobates cultripes
01000121100102?0100120111010100111110102000113020041112 20{23}20010110?1011011?11
10112{01}01001?21?10100

Pelobates fuscus
01000?211011021?100120111{01}101001111101?22001130200411122032001011001011011?11
1011200100{01}121210100

Pelobates syriacus
01000?2110?102??10?1201110101001111101?22001130200411122032001011001011?11?11?01
1200100??21?10100

Gobiates spinari
02000021021011?0??00201111110?0?111?101???0??13000?2?1112110?0??111010??????1??1?0?0
1????0???????

Eopelobates anthracinus
00010?21001102???00?20111110?10?111101020?0?13020?4?11220{23}2?0??1110??1?{01}1??11?
?102??1?0000???????

Eopelobates bayeri
01010021102102???00?201111101????????1????0??3020?4111220{23}200??111?1????1???1??1???
?1?00?{01}???????

Eopelobates deani
1011100100{12}112?1100120110110?????????????????302{01}?41112201200??111?????011?11??1
????1?00?0???????

Eopelobates grandis
010111?1002102????0?211111101?????????????01?3020?4111?2?{12}?00??111??????11?11??1??10
1?0{01}?0???????

Gennibatrachus baoshanensis
00000001001002?01000201001101 1?011??010?0?01130210200102110 00??10011000{01}0?1111
21010?1?00?0??0????

APPENDIX 2

Sampling for 16S Genes

All sequences downloaded from Genbank (Benson et al., 2004) and aligned using the default setting in MUSCLE (Edgar, 2004).

Leptolalax pelodytoides	AY236797	*Brachytarsophrys feae*	AY236799	*Xenophrys lateralis*	AY236800
Pelobates cultripes	AY236801	*Pelobates fuscus*	AY236805	*Pelobates syriacus*	AY236807
Pelobates varaldii	AY236808	*Pelodytes caucasicus*	AY236811	*Pelodytes ibericus*	AY236812
Pelodytes punctatus	AY236814	*Spea bombifrons*	AY236818	*Spea intermontana*	AY236819
Spea hammondii	AY236820	*Spea multiplicata*	AY236823	*Scaphiopus couchii*	AY236825
Scaphiopus holbrookii	AY236827	*Scaphiopus hurterii*	AY236828	*Ascaphus truei*	AY236829
Ascaphus montanus	AY236830	*Discoglossus galgano*	AY236831	*Rana iberica*	AY236832

APPENDIX 3

Sampling for 28S Genes

All sequences downloaded from Genbank (Benson et al., 2004) and aligned using the default setting in MUSCLE (Edgar, 2004).

Hyla cinerea	AY844241	*Rhinophrynus dorsalis*	DQ283507	*Pelodytes punctatus*	DQ283509
Pelobates fuscus	DQ283511	*Ascaphus truei*	DQ283514	*Meristogenys orphnocnemis*	DQ283538
Scaphiopus couchii	DQ283541	*Scaphiopus holbrookii*	DQ283547	*Spea hammondii*	DQ283566
Leiopelma archeyi	DQ283588	*Leiopelma hochstetteri*	DQ283589	*Leptobrachium hasseltii*	DQ283605
Discoglossus galganoi	DQ283609	*Bombina variegata*	DQ283612	*Pipa carvalhoi*	DQ283613
Xenophrys major	DQ283692	*Leptolalax bourreti*	DQ283696	*Rana sylvatica*	DQ283702
Bombina orientalis	DQ283741	*Discoglossus pictus*	DQ283744	*Xenopus gilli voucher*	DQ283750

APPENDIX 4

Sampling for CXCR-4 Genes

All sequences downloaded from Genbank (Benson et al., 2004) and aligned using the default setting in MUSCLE (Edgar, 2004).

Hyla meridionalis	AY523687	*Leptobrachium montanum*	AY523688	*Leptolalax arayai*	AY523689
Brachytarsophrys feae	AY523690	*Xenopus sp.*	AY523691	*Scaphiopus hurterii*	AY523692
Bombina variegata	AY523693	*Ascaphus truei*	AY523695	*Leiopelma hochstetteri*	AY523696
Xenopus tropicalis	AY523697	*Ascaphus montanus*	AY523698	*Rhinophrynus dorsalis*	AY523699
Leiopelma archeyi	AY523700	*Spea multiplicata*	AY523701		

APPENDIX 5

SAMPLING FOR CYTB GENES

All sequences downloaded from Genbank (Benson et al., 2004) and aligned using the default setting in MUSCLE (Edgar, 2004).

Discoglossus galganoi	AF128897	*Leptolalax pelodytoides*	AY236764	*Xenophrys lateralis*	AY236766
Pelobates cultripes	AY236767	*Pelobates fuscus*	AY236771	*Pelobates syriacus*	AY236773
Pelobates varaldii	AY236774	*Pelodytes caucasicus*	AY236777	*Pelodytes ibericus*	AY236778
Pelodytes punctatus	AY236780	*Spea bombifrons*	AY236784	*Spea intermontana*	AY236785
Spea hammondii	AY236786	*Spea multiplicata*	AY236789	*Scaphiopus couchii*	AY236791
Scaphiopus hurterii	AY236793	*Ascaphus truei*	AY236794	*Ascaphus montanus*	AY236795
Rana iberica	AY236796				

APPENDIX 6

SAMPLING FOR H3A GENES

All sequences downloaded from Genbank (Benson et al., 2004) and aligned using the default setting in MUSCLE (Edgar, 2004).

Hyla cinerea	DQ284057	*Rhinophrynus dorsalis*	DQ284156	*Pelodytes punctatus*	DQ284157
Pelobates fuscus	DQ284159	*Ascaphus truei*	DQ284162	*Meristogenys orphnocnemis*	DQ284187
Scaphiopus holbrookii	DQ284194	*Leiopelma archeyi*	DQ284246	*Leiopelma hochstetteri*	DQ284247
Leptobrachium hasseltii	DQ284265	*Discoglossus galganoi*	DQ284270	*Limnodynastes peronii*	DQ284272
Bombina variegata	DQ284274	*Pipa carvalhoi*	DQ284277	*Megophrys nasuta*	DQ284331
Xenophrys major	DQ284360	*Leptolalax bourreti*	DQ284367	*Rana sylvatica*	DQ284373
Discoglossus pictus	DQ284412	*Xenopus gilli*	DQ284418		

APPENDIX 7

Sampling for NCX-1 Genes

All sequences downloaded from Genbank (Benson et al., 2004) and aligned using the default setting in MUSCLE (Edgar, 2004).

Alytes obstetricans	AY523703	*Meristogenys kinabaluensis*	AY523704	*Bombina variegata*	AY523705
Pelobates cultripes	AY523707	*Discoglossus pictus*	AY523708	*Pelodytes punctatus*	AY523709
Hyla meridionalis	AY523710	*Pipa pipa*	AY523711	*Leptolalax arayai*	AY523714
Bombina orientalis	AY523715	*Xenopus sp.*	AY523716	*Scaphiopus hurterii*	AY523720
Xenopus tropicalis	AY523721	*Rhinophrynus dorsalis*	AY523722	*Leiopelma archeyi*	AY523723
Spea multiplicata	AY523724	*Brachytarsophrys feae*	AY523725	*Ascaphus montanus*	AY523730
Ascaphus truei	AY523731	*Leiopelma hochstetteri*	AY523734		

APPENDIX 8

SAMPLING FOR RAG-1 GENES

All sequences downloaded from Genbank (Benson et al., 2004) and aligned using the default setting in MUSCLE (Edgar, 2004).

Alytes obstetricans	AY364200	*Pelobates cultripes*	AY364201	*Discoglossus pictus*	AY364202
Pelodytes punctatus	AY364203	*Pipa pipa*	AY364204	*Meristogenys kinabaluensis*	AY364206
Bombina orientalis	AY364207	*Xenopus sp.*	AY523743	*Scaphiopus hurterii*	AY523744
Xenopus tropicalis	AY523745	*Ascaphus montanus*	AY523746	*Rhinophrynus dorsalis*	AY523747
Leiopelma archeyi	AY523748	*Spea multiplicata*	AY523749	*Bombina variegata*	AY523750
Ascaphus truei	AY523751	*Leiopelma hochstetteri*	AY523753		

APPENDIX 9

Sampling for Rhodopsin Genes

All sequences downloaded from Genbank (Benson et al., 2004) and aligned using the default setting in MUSCLE (Edgar, 2004).

Pelobates cultripes	AY364386	*Hyla cinerea*	AY844597	*Pipa pipa*	DQ283781
Rhinophrynus dorsalis	DQ283822	*Pelodytes punctatus*	DQ283824	*Pelobates fuscus*	DQ283826
Meristogenys orphnocnemis	DQ283847	*Scaphiopus couchii*	DQ283850	*Scaphiopus holbrookii*	DQ283852
Spea hammondii	DQ283870	*Leiopelma archeyi*	DQ283895	*Leptobrachium hasseltii*	DQ283911
Discoglossus galganoi	DQ283915	*Limnodynastes peronii*	DQ283917	*Bombina variegata*	DQ283919
Pipa carvalhoi	DQ283922	*Megophrys nasuta*	DQ283969	*Leptolalax bourreti*	DQ284000
Rana sylvatica	DQ284004	*Bombina orientalis*	DQ284032	*Discoglossus pictus*	DQ284034

APPENDIX 10

Sampling for SIA Genes

All sequences downloaded from Genbank (Benson et al., 2004) and aligned using the default setting in MUSCLE (Edgar, 2004).

Hyla cinerea	AY844816	*Pipa pipa*	DQ282660	*Rhinophrynus dorsalis*	DQ282681
Pelodytes punctatus	DQ282682	*Meristogenys orphnocnemis*	DQ282703	*Scaphiopus couchii*	DQ282706
Scaphiopus holbrookii	DQ282710	*Spea hammondii*	DQ282728	*Leiopelma hochstetteri*	DQ282755
Leptobrachium hasseltii	DQ282767	*Discoglossus galganoi*	DQ282770	*Limnodynastes peronii*	DQ282772
Pipa carvalhoi	DQ282774	*Megophrys nasuta*	DQ282818	*Leptolalax bourreti*	DQ282844
Rana sylvatica	DQ282849	*Discoglossus pictus*	DQ282889		

APPENDIX 11

Script for Calculating the Most Parsimonious Trees and Jackknife Supporting Value in POY 4.1.2.

```
read (“morphology.nex”, prealigned:(“/Users/zbcjx/*.afa”,tcm:(1,1)))
set (root:”Triadobatrachus”)

report (“terminal”,cross_references)
report (“data”,data)

set (log:”analysis-log”)
search (max_time:0:2:0)
select ()

report (“frog-tree”,trees:(total))
report (“frog-consensus”, consensus)
report (“frog-tree-graphconsensus”,graphconsensus)

calculate_support (jackknife:(resample:100),build(),swap(tbr,5))
report (“jackknife-frog”,graphsupports:jackknife)
calculate_support (bootstrap:100,build(trees:5),swap(trees:1))
report (“bootstrap-frog”,graphsupports:bootstrap)
set (nolog)
```

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