

A new frog (Amphibia: Anura) from the Lower Cretaceous of western Liaoning, China

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Received 1 October 2003; accepted in revised form 29 June 2004

Available online 28 August 2004

Abstract

Based on a nearly complete skeleton, an archaic frog is described from the Early Cretaceous Yixian Formation near Yixian, western Liaoning Province, China. The new frog shows several peculiar morphologies including the presence of a co-ossified parahyoid bone with a V-shaped configuration. Such a parahyoid was previously known only for the problematic taxon *Neusibatrachus* from the Lower Cretaceous of Spain. A phylogenetic analysis was performed with the inclusion of the new taxon and *Neusibatrachus*. This analysis suggests that the new taxon is a primitive archaeobatrachian closely related to *Notobatrachus* and *Vieraella*, while *Neusibatrachus* is placed as a basal member of the Pipoidea. The suggested relationships of the new frog with South American forms reveal a biogeographic enigma that cannot be resolved until there is more fossil evidence and current phylogenetic hypotheses are further evaluated.

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Keywords: Archaeobatrachian frog; Early Cretaceous; Yixian Formation; Western Liaoning; Anuran phylogeny

1. Introduction

Among the three major groups of living amphibians, anurans (frogs and toads) are the most successful, as they have the greatest taxonomic diversity and widest geographic distribution in comparison to salamanders and caecilians. The Anura include some 4500 species and are found on all continents except Antarctica. They live in diverse habitats including tropical rain forests, rivers, lakes and ponds, high mountains and even deserts (Hofrichter, 2000).

Compared to salamanders and caecilians, anurans have a fairly good fossil record extending back to the Early Jurassic (Shubin and Jenkins, 1995; Sanchiz,

1998), or even earlier if the closely related proanurans *Triadobatrachus* from the Lower Triassic of Madagascar and *Czatkobatrachus* from the Lower Triassic of Poland (Evans and Borsuk-Białynicka, 1998) are taken into account. The most extensive record of the group is, however, from the Cenozoic, with only six or seven out of 24 extant families having a record extending into the Mesozoic; these are Leiopelmatidae, Discoglossidae, Palaeobatrachidae, Pipidae, Pelobatidae, Leptodactylidae (see Sanchiz, 1998: fig. 153) and possibly Rhinophrynidae (Henrici, 1998).

An Early Cretaceous frog from the locality of Hejiaxin near Yixian (Fig. 1) in western Liaoning Province, China, is described in this paper. The fossil beds at Hejiaxin belong to the Yixian Formation (Wang et al., 2003), the lacustrine deposits that are well known for yielding fossils of feathered dinosaurs and primitive birds. Previous reports of fossil frogs from the Yixian

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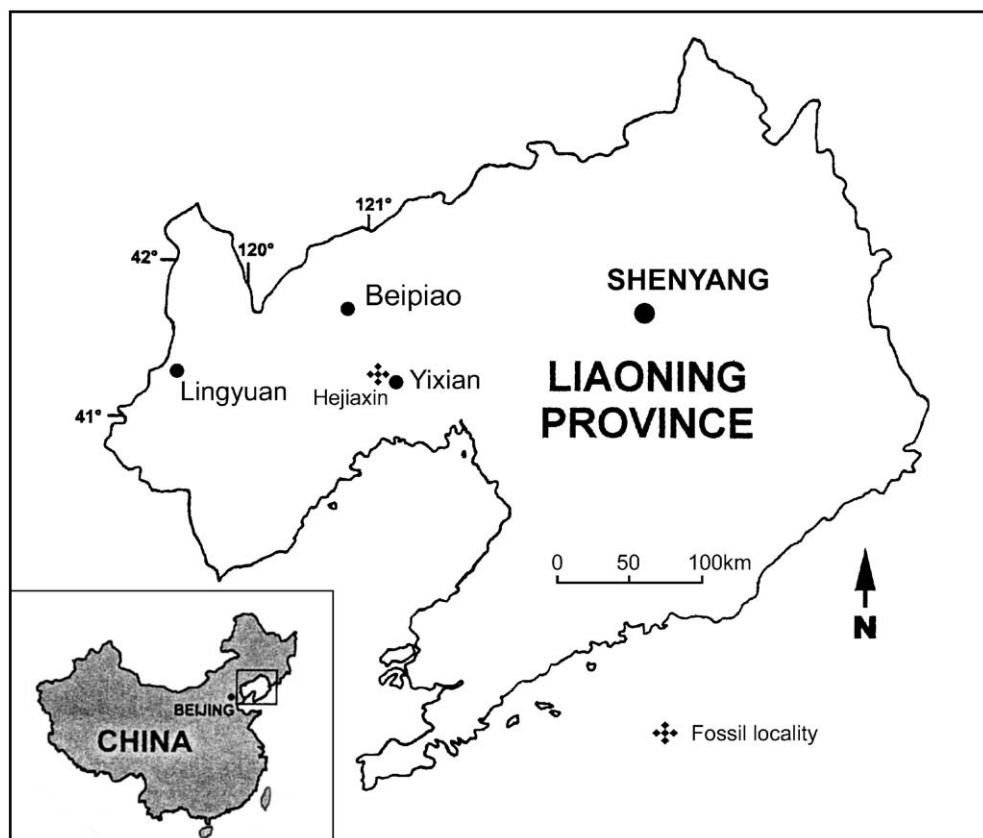


Fig. 1. Map showing the location of Hejiaxin in relation to two other fossil localities, Beipiao and Lingyuan, in western Liaoning Province, China.

Formation were based on occurrences at two localities, Sihetun and Heitizigou near Beipiao (Wang and Gao, 1999; Gao and Wang, 2001). This paper adds another record from the same formation at a different locality. There are no radiometric age determinations available from the Hejiaxin site, but fossiliferous beds in the same formation near Sihetun have yielded a date of 125 Ma (Swisher et al., 1999; also see Lo et al., 1999 for a different date), suggesting a Barremian age for the formation (Gradstein et al., 2004).

2. Systematic palaeontology

Class: Amphibia Linnaeus, 1758
 Superorder: Salientia Laurenti, 1768
 Order: Anura Rafinesque, 1815
 Family: incertae sedis
 Genus *Yizhoubatrachus* gen. nov.

Derivation of name. Yizhou, ancient name for Yixian.

Type species. *Yizhoubatrachus macilentus* sp. nov.

Generic diagnosis. As for the type and only known species.

Yizhoubatrachus macilentus sp. nov.

Figs. 2, 3

Derivation of name. Latin, *macilentus*, thin or lean.

Holotype. M8621, Zhejiang Museum of Natural History, a nearly complete but compressed skeleton preserved in volcanic shales.

Type locality and horizon. Fossil site near Hejiaxin village, approximately 15 km west of Yixian; Yixian Formation, Early Cretaceous.

Diagnosis. The new species can be distinguished from all other extant and fossil anuran species by the unique combination of the following character states: postero-medial process of parasphenoid absent; parahyoid co-ossified showing V-shaped configuration; frontoparietal shelf present; presacral vertebrae opisthocelous and nine in number; clavicle sickle shaped with well-developed anterolateral process; sacral diapophysis moderately expanded; tibiale and fibulare remain free from one another; no mesopodium ossified in both fore- and hind limbs.

Distinguished from *Mesophryne* and *Callobatrachus* in having a unique configuration of pterygoid with anterior and posterior processes forming a straight bar

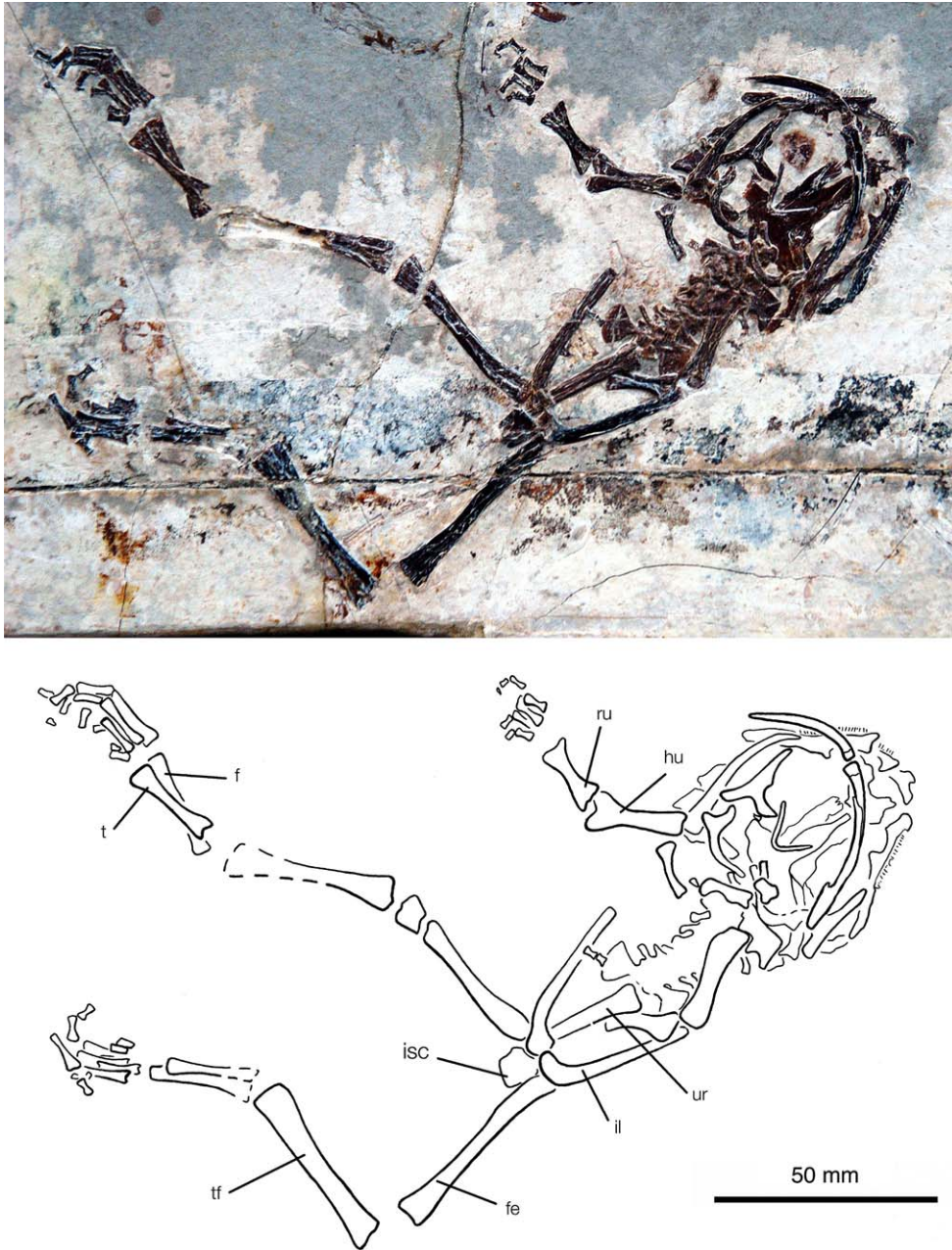


Fig. 2. Holotype specimen (ZMNH M8621) of *Yizhoubatrachus macilentus* gen. et sp. nov., nearly complete skeleton in ventral view. Abbreviations used in this and other figures: angs, angulosplenial; cla, clavicle; cle, cleithrum; col, columella; cor, coracoid; den, dentary; fe, femur; frpa, frontoparietal; hu, humerus; il, ilium; isc, ischium; max, maxilla; na, nasal; parh, parahyoid; ptg, pterygoid; pmx, premaxilla; ps, parasphenoid; qj, quadratojugal; ru, radioulna; sc, scapula; tf, tibiofibula; vom, vomer.

and medial process branching from the bar at a right angle; having a well-ossified parahyoid; having longer and laterally directed transverse processes on posterior presacral vertebrae; lacking transverse processes on urostyle; and lacking ossification of carpal elements.

3. Anatomical description

The holotype and only known specimen, ZMNH M8621, consists of an articulated and nearly complete

skeleton, representing a lightly built frog. The specimen is dorsoventrally compressed and preserved in pale-grey shales of volcanic ash. In common with other vertebrates from the Liaoning beds, the specimen is preserved on part and counterpart slabs (Fig. 2), but impressions of the skeleton on the counterpart slab provide little information on the morphology of this frog.

Skull and mandible. The skull is exposed in palatal view, allowing the ventral aspect of some roofing elements to be observed. These include the premaxilla,

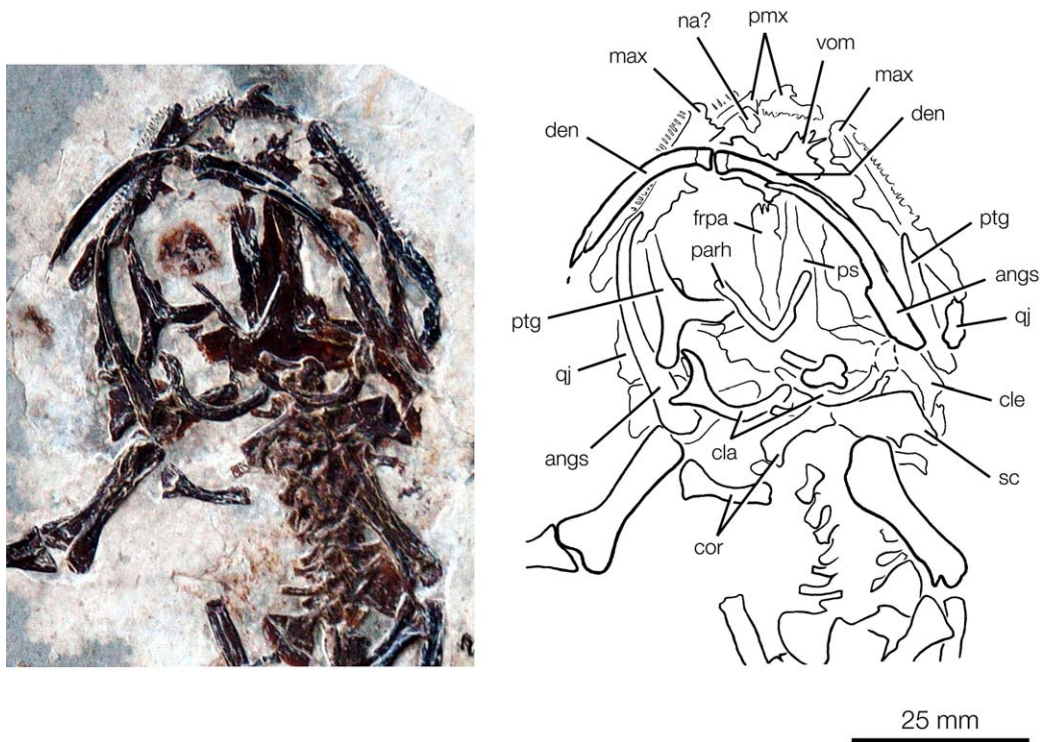


Fig. 3. Holotype (ZMNH M8621) of *Yizhoubatrachus macilentus* gen. et sp. nov., skull and pectoral girdle of holotype in ventral view.

maxilla, quadratojugal, and the frontoparietal. No part of the squamosal is exposed; thus the shape of this element cannot be ascertained. Both the premaxilla and the maxilla are toothed (see description of dentition below). The right premaxilla is exposed in lingual view, while the left element is seen in labial view (Fig. 2). The left premaxilla bears 11 teeth, while the right bears ten. The teeth are slender, simple cones, but whether the teeth are pedicellate or not cannot be ascertained. Lingually, the premaxilla has a simple dental shelf, but lacks a palatine process. Distally, it ends with a small posterolateral process that fits into a facet on the maxilla. The dorsal or alary process of the premaxilla is short and narrow, located anteromedially near the joint of the maxillary arch. Slightly posterior to the right premaxilla, a fragment may represent part of nasal, but this element cannot be identified with certainty due to poor preservation.

The maxilla on both sides is exposed in lingual view. The right maxilla is partly obscured by the right dentary and angulosphenial; the left maxilla is nearly complete, bearing approximately 20 teeth. As in the premaxilla, the maxillary teeth are simple cones but it is difficult to determine whether they are pedicellate or not. Anteriorly the maxilla develops a facet for a small posterolateral process of the premaxilla. The maxilla has a well-defined dental shelf, the medial border of which curves smoothly along with the curvature of the maxillary arch. Above the shelf is a low lateral wall, which bears a prominent dorsal process at the midlevel

of the tooth row. The lateral wall anterior to this process is notched to form the lower border of the external narial opening, while the wall posterior to the dorsal process has a curved border forming part of the rim of the orbit. Posteriorly at the end of the dental shelf, the maxilla displays a facet that receives the anterior process of the quadratojugal. Posterior to the maxilla, the quadratojugal can be observed on both sides of the skull.

The frontoparietal is exposed on both sides of the cultriform process of the parasphenoid. Because it is medially obscured by the parasphenoid, whether the frontoparietal is paired or azygous cannot be ascertained; however, a fontanelle can be seen extending to the midlevel of the frontoparietal. The lateral borders of the frontoparietal are elaborated to form a well-defined shelf turning ventrally towards the palate. As shown on the left side, the posterolateral process of the frontoparietal is well developed as a more or less wing-like structure. The prootic-occipital region is concealed by ventral elements, hence the formation of this region cannot be determined.

In the palate, the vomer is incompletely preserved, but a notch can be identified on both sides as marking the position for the choana (Fig. 3). The choana is bordered anteriorly by a slender process and posterolaterally by a stronger process of the vomer. Medial to the choana are several small swellings that may represent the vomerine teeth. Posteriorly, the parasphenoid is an inverted T-shaped element, with the

pointed tip of the cultriform process anteriorly and the widened alae directed laterally. Although the posterior end of the parasphenoid is partly obscured by a vertebra and a clavicle, the exposed part shows that it lacks a clearly defined posteromedial process. Neither the sphenethmoid nor the palatine can be identified due to poor preservation.

Both the left and the right pterygoids are completely preserved. The left pterygoid is in articulation with the lateral ala of the parasphenoid, although it is partly obscured by the left mandible. The right pterygoid has been slightly shifted away from the parasphenoid, but is well exposed. As a diagnostic feature of this fossil form, the anterior and posterior processes of the pterygoid form an essentially straight bar, with the medial process branching from the bar at a right angle; therefore, the pterygoid is distinctive in its shape (Figs. 2, 3). The anterior process is approximately twice as long as the length of either the posterior or the medial process. Although slightly displaced, the anterior process of the pterygoid on both sides is nearly in position for articulation with the poorly developed palatal process the maxilla.

Behind the medial process of the right pterygoid is a small columella (= stapes of some other authors) with a slightly expanded medial end. The left columella cannot be observed owing to the state of preservation. Among extant frogs, a columella is present in most family groups with the exception of leiopelmatids (*Ascaphus* and *Leiopelma*), rhinophrynids, and some neobatrachians (Trueb, 1993).

A notable feature of the palate of this frog is the ossification of the slenderly built parahyoid as a V-shaped bone (Fig. 3). Such a configuration of the parahyoid is unique among extant and known fossil frogs with the exception of *Neusibatrachus* from the Lower Cretaceous of Spain (Seiffert, 1972; considered to be a junior synonym of *Eodiscoglossus* by Sanchiz, 1998; but see Roček, 2000 contra Sanchiz, 1998). By comparison, the parahyoid of the latter taxon is more narrowly V-shaped and has a posteriorly directed base differing from the condition in the Liaoning form.

Both mandibles are preserved but have been displaced from their association with the maxillary arch. The dentaries are almost in articulation at the symphysis, with a small and thickened tip that can be identified as the mentomeckelian bone. The dentary is edentate (best shown on the right side), with a dorsal crest as seen in many other anurans. The dentary is proportionally large, covering the anterior two-thirds of the external aspect of the jaw. The posterior extension of the dentary ends as a pointed process. However, the angulosplenial is the largest element in the lower jaw, forming the posterior one-third of its external surface, and extending anteriorly along the inner surface of the dentary to a point close to the mandibular symphysis.

Vertebral column. The vertebral column includes nine presacrals, a single sacral, and a free urostyle. The four anterior presacral vertebrae as preserved are disarticulated and scattered behind the skull. The posterior five vertebrae are, however, in straight-line articulation with each other. As a result of distortion, the first two and the fourth vertebrae are more or less in a transverse position along the midline, whereas the third is straight on the right-hand side of the midline. The atlas bears no transverse process and is not fused to the second vertebra. The remaining presacrals have a short centrum that is probably opisthocoelous, as shown on the sixth and seventh presacrals. Differing from *Callobatrachus* from the Yixian Formation, the diapophyses of the posterior presacrals are long and slender, and laterally directed. The last presacral vertebra bears the longest process. The sacral vertebra has moderately expanded diapophyses, which can be characterized as “broadly hatchet-shaped”, differing from the “butterfly wing-shape” in some other primitive frogs (e.g., pelobatids and pipids).

The urostyle is 19 mm long, which is 78.7% of the length of the femur (24 mm). Having undergone slight rotation, the urostyle is exposed on the right-hand side in lateral view. It shows a well-developed dorsal crest, and a groove extends along the lateral surface of the rod. Anteriorly, a small condyle is visible on the right side, indicating a bicondylar articulation with the sacrum. The urostyle lacks transverse processes.

Pectoral girdle and forelimb. The clavicles on both sides are well developed and strongly curved as sickle-shaped bones. As shown on the right element, the lateral end of the clavicle develops a strong process curving anterolaterally, and this process laterally bears a thin crest that provided an extensive articulation with the scapula. Both coracoids are preserved, but are slightly dislocated from their original position. The coracoid has a slender shaft, and the medial and lateral ends are roughly the same width. The right scapula is partly obscured by the posterior tip of the mandible, while the left scapula is well exposed and in articulation with the humerus. The scapula is short and wide, a more or less rectangular plate except for the notch of the glenoid fossa. The anterior border of the bone is straight, resembling the condition as seen in the Discoglossidae and some other groups (see Appendix for coding of character 48). The cleithrum is partly ossified with a thickened anterior border, but whether the cleithrum is forked or not cannot be ascertained because of the incomplete preservation. The pectoral girdle is of arciferal type, as indicated by the strongly curved clavicles and the oblique position of the coracoids.

Both forelimbs are preserved in articulation with the scapulae. The humerus is 12 mm long and the fused radioulna is 8 mm long. Proximally on the humerus, the

crista ventralis is weakly developed and extends distally to connect with the better-developed crista lateralis. The radioulna has a weakly developed olecranon process, the poorly defined fossa indicating the poor ossification of the humeral condyle (eminentia capitata). Distally on the left element, a longitudinal sulcus marks the fusion of the radius and ulna. No carpal elements, including the prepollex, are ossified on the specimen (see discussion below). The four metacarpals are completely preserved on the right-hand side, while those on the left are mostly preserved as impressions. The longest, metacarpal III, is 4 mm, while the shortest, metacarpal V, is only 2 mm long. Although other digital elements are preserved, the phalangeal formula of the forefoot cannot be determined because of poor preservation.

Pelvic girdle and hind limb. The pelvis is well preserved, although it has been slightly distorted and displaced from its articulation with the sacral vertebra. The iliac shaft is 18 mm long from the anterior tip to the anterior rim of the acetabulum. It lacks a dorsal crest and a dorsal protuberance. The acetabulum has a prominent anterior rim, while the ischium contributes to form the posterior rim. The ischium is roughly triangular in shape. The right ischium is exposed in lateral view and obscures the left element as preserved.

Both hind limbs are preserved in articulation with the pelvis. The femur is 24 mm long, and the tibiofibula is 22 mm long. The femur has a weak sigmoid curvature, while the tibiofibula is virtually straight. The proximal tarsal segment (12.5 mm) is slightly longer than half the length of the tibiofibula. Both the tibiale and the fibulare are slender bones, with the fibulare (12.5 mm) slightly longer than the tibiale (11 mm). The two bones are free from one another as evidenced by their condition on both sides of the specimen. As in the forefoot, no distal tarsal elements are ossified. More distally, five metatarsals are well preserved on both sides, with the fourth being the longest. The phalangeal formula is ?-?-3-4-3, as observed from the right foot.

4. Comparison and taxonomic discussion

Yizhoubatrachus macilentus shows several morphological features that are phylogenetically significant. One of these features is the single ossification of the V-shaped parahyoid. Such a configuration of the parahyoid is unknown for extant anurans, but is known for the fossil taxon *Neusibatrachus wilferti* from the Lower Cretaceous of Spain (Seiffert, 1972). The taxonomic status and the relationships of the latter taxon are still in dispute. The original author (Seiffert, 1972) considered *Neusibatrachus wilferti* to be an ancestor of the Palaeobatrachidae and Ranidae whereas Estes and Reig (1973) regarded it as a definitive member of the

Palaeobatrachidae. More recently, Sanchiz (1998) treated *Neusibatrachus wilferti* as the junior synonym of *Eodiscoglossus santonjae*, and thus hinted at a discoglossid relationship for this Cretaceous frog. However, this conclusion is in marked disagreement with several key characters of the taxon, including the single ossification of the frontoparietal, the parasphenoid lacking posterior alae, and the presence of procoelous vertebrae (Vergnaud-Grazzini and Wenz, 1975). After reviewing the current evidence, Roček (2000) concluded that in the absence of a thorough taxonomic revision the relationships of *Neusibatrachus wilferti* must remain uncertain.

Yizhoubatrachus macilentus shares with *Neusibatrachus wilferti* the ossification of the V-shaped parahyoid, but is clearly different from the latter taxon in having opisthocelous vertebrae and other features including a parasphenoid with well-defined posterolateral alae. These significant differences indicate that the V-shaped parahyoid in the two different forms is homoplastic in origin.

Another feature of *Yizhoubatrachus macilentus* is the unfused tibiale and fibulare. These two elements are completely separate from each another in primitive frogs, including *Prosalirus* and *Notobatrachus* (Shubin and Jenkins, 1995; Roček, 2000), whereas in most other frogs the two elements are fused at both proximal and distal ends, with the exception of pelodytids and centrolenids in which they are completely fused (Duellman and Trueb, 1986). Another primitive frog, *Eodiscoglossus*, is described as having two unfused elements (see Roček, 2000), but in this Cretaceous discoglossid they are better described as being fused at both ends (Gao and Wang, 2001: character 60). The two elements in *Yizhoubatrachus macilentus* are unfused at both ends, indicating a primitive morphology.

The third such feature is the absence of the ossified mesopodium on both fore- and hind limbs. The size of the specimen (snout-vent length ca. 115 mm), especially the ossification of the parahyoid element, indicates that it represents a mature individual. This interpretation is reinforced by evidence of a well-ossified columella and mentomeckelian bone, which are among the last bones to be ossified during ontogeny (Duellman and Trueb, 1986). Therefore, the lack of ossification of the mesopodium is not an ontogenetic feature, but is taxonomically significant for this specimen.

Overall, the general morphology of *Yizhoubatrachus macilentus* indicates that it represents a primitive archaeobatrachian frog. Its relationships with other known forms are further explored below.

5. Phylogenetic analysis and results

A cladistic analysis was performed using a taxon-character matrix from Gao and Wang (2001) with the

inclusion of the new taxon and the problematic *Neusibatrachus*. Incorporation of the latter in this analysis is justified following a recent review of the Mesozoic record of anurans (Roček, 2000), which concluded that the relationships of *Neusibatrachus* remain uncertain. Character coding for *Neusibatrachus* is based on data presented in Seiffert (1972), Vergnaud-Grazzini and Wenz (1975), and Roček (2000). Among the 65 characters in the original data matrix, 26 can be scored for *Yizhoubatrachus macilentus*, and 16 for *Neusibatrachus* based on the data from Seiffert (1972). The modified data set was analyzed using PAUP version 3.1.1 (Swofford, 1993) on a Macintosh Powerbook G4, using the Branch-and-Bound search option. All characters were unordered and equally weighted, and ACCTRAN tree optimization was used to minimize the possibility of parallelisms. The trees were rooted using the Caudata as the out-group.

This phylogenetic analysis found 540 Most Parsimonious Trees (MPTs) with a tree length of 181 steps, CI 0.541 and RI 0.698. Strict consensus of the 540 MPTs shows a *Yizhoubatrachus*-*Notobatrachus*-*Vieraella* polytomy (Fig. 4A), while the 50% majority consensus weakly supports the grouping of *Yizhoubatrachus*-*Notobatrachus* as sister groups (Fig. 4B). The three taxa involved in the polytomy share the following derived character states: dorsal exposure of frontoparietal fontanelle 50% of the frontoparietal length or less (8-1); formation of prootic-occipital region by prootic-exoccipital without fusion (11-1; missing data for

Yizhoubatrachus); and postchoanal processes of vomer present, forming a wide angle with anterior portion of vomer (24-1). The *Yizhoubatrachus*-*Notobatrachus* sister group relationship is supported by two character states: the presence of a frontoparietal shelf (10-1) and the medial ramus of the pterygoid in contact with the parasphenoid (30-1). Such phylogenetic relationships (whether the *Yizhoubatrachus*-*Notobatrachus*-*Vieraella* polytomy or the *Yizhoubatrachus*-*Notobatrachus* sister group relationship) present a biogeographic enigma because *Yizhoubatrachus* is linked with South American forms. The resolution of this enigma requires further evaluation of the current phylogenetic hypothesis, and the recovery of more fossil evidence of closely related forms from different continents.

In both the strict consensus and the 50% majority consensus trees, the problematic *Neusibatrachus* was placed as the basal member of the Pipoidea. Based on data from Seiffert (1972) and Roček (2000), *Neusibatrachus* unambiguously shares with the Pipoidea the following derived character states: frontoparietal in adult stage azygous (7-1; unique); posterolateral alae of parasphenoid absent (27-2; unique); transverse process on postsacral complex absent (46-2; convergent in *Yizhoubatrachus*). In addition, the derived state of one character in the number of tarsalia (reduced to two elements; 61-1) is known for all pipoids but is unknown for *Neusibatrachus*. In tree comparisons, moving *Neusibatrachus* to group with Discoglossidae would significantly increase tree length by five steps;

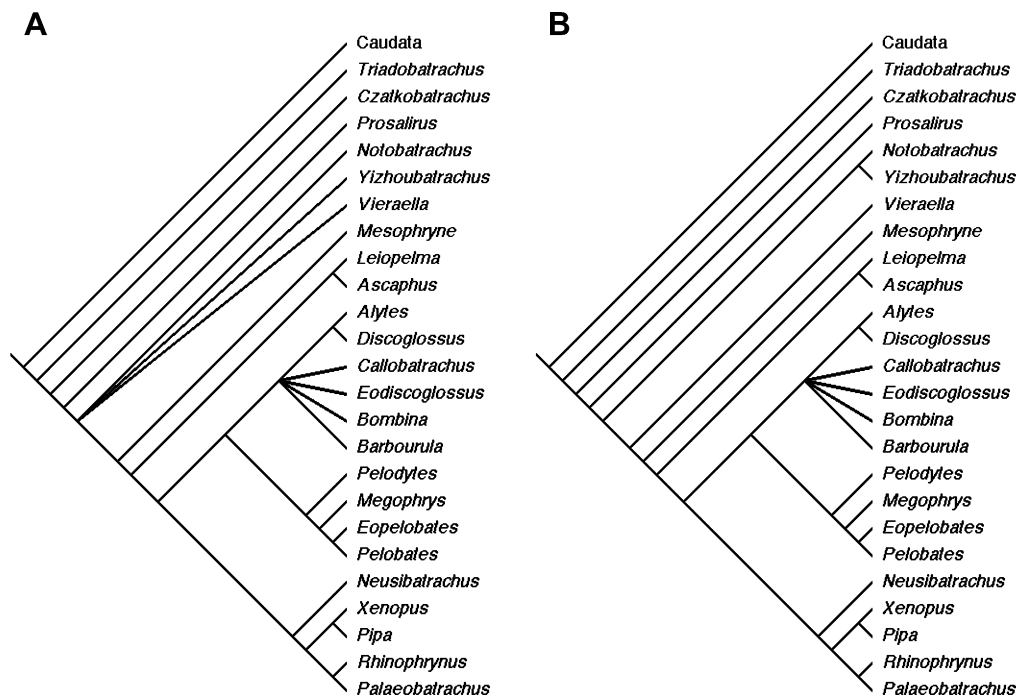


Fig. 4. Phylogenetic relationships of *Yizhoubatrachus* with other archaeobatrachian frogs: strict consensus tree (A) and 50% majority consensus tree (B). For description of characters, see Gao and Wang (2001).

thus, the phylogenetic results reject the hypothesized discoglossid relationship of *Neusibatrachus*.

6. Conclusions

Our study of a new frog specimen from the Early Cretaceous Yixian Formation in western Liaoning has led us to the following conclusions: (1) the specimen represents a new genus and species of archaeobatrachian frog; (2) it shows several peculiar morphologies, including the presence of a co-ossified parahyoid with a V-shaped configuration: such a parahyoid is known for only one other Cretaceous frog (*Neusibatrachus wilferti*), but our analysis suggests that this similarity is a result of homoplasy; (3) our phylogenetic analysis indicates a close relationship between the new frog and South American *Notobatrachus* and *Vieraella* within the Archaeobatrachia and, hence, reveals a biogeographic enigma; (4) the problematic *Neusibatrachus* is hypothesized as a basal member of the Pipoidea, a relationship that is supported unambiguously by three derived characters and equivocally by one character that is coded as unknown for *Neusibatrachus*.

Acknowledgements

We thank Professor R.C. Fox (University of Alberta, Canada) for help with improving the manuscript, and Kapi Monoyois (University of Chicago) for preparation of the drawings. Gao's research is supported by the National Natural Science Foundation of China (40272006) and the Research Fund for the Doctoral Program of Higher Education (RFDP), Chinese Ministry of Education. Chen's research is supported by the Zhejiang Museum of Natural History, Hangzhou, China.

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Appendix

Taxon-character data matrix used in phylogenetic analysis (see Gao and Wang, 2001 for character description and explanation). Character coding for *Neusibatrachus* based on data presented in Seiffert (1972), Vergnaud-Grazzini and Wenz (1975), and Roček (2000).

	5					10					15					20				
Caudata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triadobatrachus	0	0	0	?	?	?	?	?	0	0	0	0	?	?	?	?	0	0	0	0
Czatkobatrachus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Prosalirus	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?
Ascaphus	0	1	1	1	1	0	2	1	0	1	0	0	1	1	1	1	1	0	0	0
Leiopelma	0	1	1	1	1	0	2	1	0	2	0	0	1	1	1	1	1	0	0	0
Alytes	0	1	0	0	1	1	0	2	1	0	2	1	1	0	1	2	0	1	0	0
Barbourula	0	1	0	0	0	1	0	0	1	0	2	1	0	0	1	2	0	1	0	0
Bombina	0	1	0	0	0	1	0	2	1	0	2	1	1	0	1	3	0	1	0	0
Discoglossus	0	1	0	0	0	1	0	1/2	1	0	2	1	1	0	1	2	0	1	1	0
Eodiscoglossus	0	1	0	0	0	1	0	?	1	0	1	?	1	0	?	2	0	1	0	0
Notobatrachus	0	0	0	0	0	1	0	1	0	1	0	1	0	0	1	1	1	0	0	0
Vieraella	1	?	0	?	0	1	0	1	0	0	1	?	?	0	1	?	?	1	0	0
Callobatrachus	0	1	0	?	0	1	0	?	?	0	2	?	?	0	?	2	0	1	0	0

<i>Mesophryne</i>	0	1	0	?	0	1	?	?	?	2	?	0	0	?	?	0	1	1	0
<i>Pelobates</i>	0	0	0	0	0	1	0	1	0	1	1	2	1	1	0	1	2	0	1
<i>Eopelobates</i>	0	0	0	1	0	1	0	0	1	1	?	?	?	?	?	2	0	1	1
<i>Megophrys</i>	0	1	0	0	0	1	0	0	1	1	2	?	1	0	1	2	0	1	0
<i>Pelodytes</i>	0	0	1	1	0	1	1	0	2	1	0	2	?	0	0	1	2	0	1
<i>Pipa</i>	0	1	0	1	1	1	0	1	0	2	2	0	1	0	1	1	3	0	0
<i>Xenopus</i>	0	1	1	2	1	0	1	1	0	1	0	2	3	0	1	0	1	1	3
<i>Rhinophrynus</i>	1	1	0	0	0	1	1	0	1	1	2	1	0	0	1	1	0	2	0
<i>Palaeobatrachus</i>	1	1	0	0	0	1	1	0	1	0	2	1	0	0	0	2	0	1	1
<i>Yizhoubatrachus</i>	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Neusibatrachus</i>	0	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?

					25					30						35					40
<i>Caudata</i>	0	0	0	0	0	0	?	?	?	?	0	?	?	?	0	0	0	0	?	?	0
<i>Triadobatrachus</i>	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Czatkobatrachus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Prosalirus</i>	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Ascapus</i>	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
<i>Leiopelma</i>	1	0	1	2	1	0	1	1	1	1	0	1	0	1	1	2	0	0	1	2	2
<i>Alytes</i>	1	1	1	2	1	1	1	1	1	0	1	0	0	1	3	0	1	1	0	2	
<i>Barbourula</i>	1	1	1	2	1	1	1	1	1	0	1	0	0	1	3	0	1	0	0	2	
<i>Bombina</i>	1	1	1	2	1	1	1	1	1	0	1	0	0	1	3	0	1	0	0	2	
<i>Discoglossus</i>	1	1	1	2	1	1	1	1	1	0	1	0	0	1	3	0	1	0	0	2	
<i>Eodiscoglossus</i>	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Notobatrachus</i>	1	0	0	1	1	0	0	0	0	1	0	0	0	1	2	?	?	?	?	?	
<i>Vieraella</i>	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Callobatrachus</i>	1	1	1	2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Mesophryne</i>	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Pelobates</i>	1	1	1	1	0	1	1	1	1	1	2	0	0	1	3	0	2	0	0	4	
<i>Eopelobates</i>	1	1	?	1	?	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	
<i>Megophrys</i>	1	1	?	1	1	1	1	1	1	?	2	0	0	1	3	0	2	0	0	4	
<i>Pelodytes</i>	1	1	?	1	0	1	1	1	1	0	1	0	0	1	3	1	2	0	0	4	
<i>Pipa</i>	1	2	?	?	?	1	0	2	1	1	1	2	0	1	1/2	3	1	1	0	3	
<i>Xenopus</i>	1	2	?	?	?	1	0	2	1	1	0	2	0	1	1	3	0	1	0	2	
<i>Rhinophrynus</i>	1	1	1	1	1	0	2	1	0	2	0	1	1	2	3	0	1	0	0	4	
<i>Palaeobatrachus</i>	1	1	1	?	?	1	0	2	1	0	0	0	0	1	3	1	2	0	2	3	
<i>Yizhoubatrachus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Neusibatrachus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	

					45					50						55					60
<i>Caudata</i>	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Triadobatrachus</i>	0	0	0	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Czatkobatrachus</i>	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Prosalirus</i>	?	1	0	1	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Ascapus</i>	1	1	1	2	0	0	1	1	1	0	0	1	1	1	1	1	0	?	?	?	
<i>Leiopelma</i>	1	1	1	2	0	0	1	0	0	0	1	?	?	?	?	?	?	?	?	?	

<i>Alytes</i>	1	1	1	2	1	0	1	1	1	1	2	1	1	1	1	1	2	1	1	
<i>Barbourula</i>	1	1	2	2	2	0	1	1	1	1	2	1	1	1	1	1	0	1	1	
<i>Bombina</i>	1	1	2	2	2	0	1	1	1	1	2	1	1	1	1	1	0	0	1	
<i>Discoglossus</i>	1	1	1	2	1	0	1	1	1	1	2	1	1	1	1	1	1	2	1	
<i>Eodiscoglossus</i>	1	1	2	2	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Notobatrachus</i>	0	1	0	1	0	0	1	0	0	0	1	0	1	0	1	0	1	0	2	
<i>Vieraella</i>	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Callobatrachus</i>	1	1	1	2	1	0	1	1	1	1	0	?	?	?	?	?	?	?	?	
<i>Mesophryne</i>	0	1	2	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Pelobates</i>	1	1	2	2	2	1	1	0	0	0	?	?	?	?	?	?	?	?	?	
<i>Eopelobates</i>	1	1	2	2	2	1	0	0	0	0	?	?	?	?	?	?	?	?	?	
<i>Megophrys</i>	1	1	2	2	1	1	1	0	0	0	?	?	?	?	?	?	?	?	?	
<i>Pelodytes</i>	1	1	2	2	2	0	1	0	1	0	0	?	?	?	?	?	?	?	?	
<i>Pipa</i>	1	1	2	2	3	2	1	0	1	0	1	?	?	?	?	?	?	?	?	
<i>Xenopus</i>	1	1	2	2	3	2	1	1	2	1	1	?	?	?	?	?	?	?	?	
<i>Rhinophrynus</i>	1	1	2	2	1	2	1	0	1	0	2	2	1	1	1	1	1	2	1	
<i>Palaeobatrachus</i>	0	1	1	2	1	2	1	1	1	1	0	1	1	1	0	1	1	?	?	
<i>Yizhoubatrachus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	
<i>Neusibatrachus</i>	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	

																					65
<i>Caudata</i>	0					0				0					0						
<i>Triadobatrachus</i>	?					?				?					?						
<i>Czatkobatrachus</i>	?					?				?					?						
<i>Prosalirus</i>	?					?				?					?						
<i>Ascapus</i>	0					1				0					1						
<i>Leiopelma</i>	0					1				1					1						
<i>Alytes</i>	0					1				1					0						
<i>Barbourula</i>	0					1				1					0						
<i>Bombina</i>	0					1				1					0						
<i>Discoglossus</i>	0					1				1					0						
<i>Eodiscoglossus</i>	?					1				?					?						
<i>Notobatrachus</i>	?					?				?					?						
<i>Vieraella</i>	?					?				?					?						
<i>Callobatrachus</i>	?					1				?					0						
<i>Mesophryne</i>	?					?				?					0						
<i>Pelobates</i>	1					2				2					2						
<i>Eopelobates</i>	0					?				?					?						
<i>Megophrys</i>	1					2				2					0						
<i>Pelodytes</i>	0					1				2					0						
<i>Pipa</i>	1					1				2					0						
<i>Xenopus</i>	1					1				2					1						
<i>Rhinophrynus</i>	1					1				2					0						
<i>Palaeobatrachus</i>	1					1				?					?						
<i>Yizhoubatrachus</i>	?					?				?					0						
<i>Neusibatrachus</i>	?					?				?					?						