

Earliest Asian discoglossid frog from western Liaoning

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Abstract Based on a superbly preserved skeleton, a new anuran taxon has been named and described from the Yixian Formation (Upper Jurassic/Lower Cretaceous), Liaoning Province, northeastern China. This discovery documents the first discoglossid fossil from China, the earliest record of the group in Asia, and the only second Mesozoic discoglossid known from fully articulated material in the world. The family Discoglossidae is widely perceived as a primitive anuran group, but has no definite fossils found in collaboration with their recent distribution in Asia. The new discovery from Liaoning extends the temporal range of the group in Asia back at least 120 million years, and provides valuable fossil material for study of anatomical details of early discoglossids, as well as of historical distribution of this primitive anuran group.

Keywords: Discoglossidae, Anura, Late Jurassic/Early Cretaceous, western Liaoning, systematics and biogeography.

THE Upper Jurassic/Lower Cretaceous lacustrine deposits in western Liaoning Province are world celebrated

for producing exceptionally well-preserved vertebrate fossils. Among the astounding discoveries recently made from the fossil beds are primitive birds and feathered dinosaurs^[1,2], along with mammals^[3] and other important fossils^[4,5]. These beds recently yielded an articulated frog skeleton, which represents the geologically oldest and first definite fossil occurrence of the Discoglossidae in Asia. Here we name and briefly describe this important fossil as pertaining to a new genus and species, then comment on the systematic and biogeographic significance of the fossil.

The family Discoglossidae is a group of primitive frogs that includes the popular midwife toad (*Alytes*), the males of which carry eggs around their legs, and the fire-bellied toad (*Bombina*), the ventral surface of which is brightly colored for aposematic display. Besides Europe and North Africa, extant discoglossids have a fairly wide distribution in East and Southeast Asia, and the Middle East; however, no definite fossils of the group have ever been found in collaboration with their recent distribution in Asia, with the exception of a highly doubtful referral of a partial skull from the Upper Cretaceous of the Gobi desert to the family^[6]. The new frog from Liaoning documents the earliest Asian discoglossid, the only fossil sympatric with the extant range of the Discoglossidae in Asia, and the only second Mesozoic fossil taxon of the group that is known from fully articulated material in the world. Study of this material provides important insights into the early evolution and biogeographic history of the group.

1 Systematic paleontology

Class Amphibia Linnaeus, 1758

Subclass Lissamphibia Haeckel, 1866

Superorder Salientia Laurenti, 1768

Order Anura Rafinesque, 1815

Systematic remarks. The order Anura includes some 4 000 extant species (300 genera in 24 families) and some 100 known fossil species in 50 genera^[7,8]. While the unusual adaptations, behavior, and wide geographical distribution of frogs have drawn special interests to systematic and evolutionary biologists, fossils provide the major source of information for depicting the biogeographic origin and early evolution of this major vertebrate group. The earliest known anurans are represented by two Early Jurassic forms; *Vieraella herbstii* Reig, 1961 from the Roca Blanca Formation of Argentina, and *Prosalirus bitis* Shubin and Jenkins, 1995^[9] from the Kayenta Formation of Arizona^[10].

Family Discoglossidae Günther, 1859

The monophyly of the Discoglossidae is supported by the results of a recent phylogenetic analysis, and the relationships of the extant taxa have been elucidated as: *Alytes* [(*Bombina* + *Barbourula*) + *Discoglossus*]^[1]. The diagnosis of the family includes the following osteological character states: otoccipitals with anterior and posterior margins parallel or only slightly convergent; quadratojugal present, at least 40%—50% length of pterygoid fossa; palatine absent; parasphenoid alae either uniformly shallow or shallow medially, flaring laterally; parahyoid bone present; eight presacral vertebrae, being opisthocelous and stegochordal; Presacrals I and II remain unfused; free ribs present on Presacrals II-IV; anterior end of scapulae overlain by clavicle; cleithrum bifurcate; sacrum having expanded diapophyses and bicondylar articulation with urostyle; urostyle having transverse processes proximally; ilium with dorsal crest and well-defined prominence; humeral condyle large, greater than 66% distal width of the humerus; tibiae and fibulae fused only proximally and distally^{[7,11],1)}.

Genus *Callobatrachus*, gen. nov.

Etymology. kallos + batrachus (Gr.), delicate frog.

Type species. *Callobatrachus sanyanensis*, sp. nov.

Diagnosis. As for the type and only known species (see below).

Callobatrachus sanyanensis, sp. nov.

(figure 1)

1) Clarke, B. T., Evolutionary relationships of the discoglossoid frog, Osteological evidence, unpublished Ph. D. Dissertation, British Museum (Natural History) and City of London Polytechnic, 1988, 1—431.

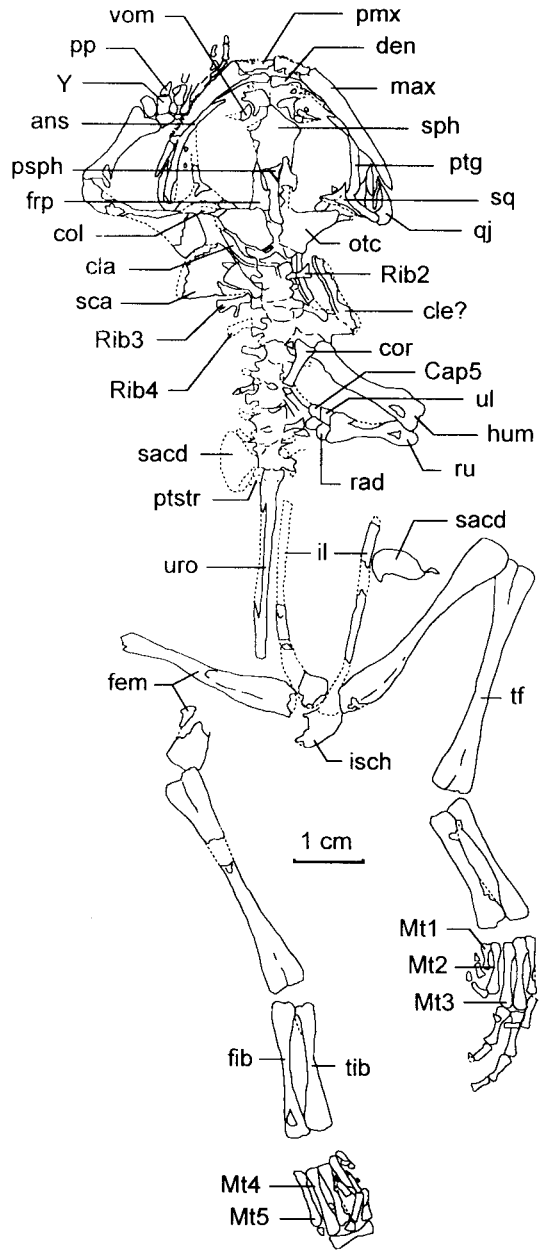


Fig. 1. *Callobatrachus sanyanensis* Wang and Gao gen. et sp. nov. (IVPP V11525, holotype). Photograph (left) and outline (right) of the skeleton in dorsal view (broken lines indicate impressions of bones). ans, Angulosplenial; Cap5, Carpal 5; cla, clavicle; cle, cleithrum; col, columella; cor, coracoid; den, dentary; fem, femur; fib, fibulare; frp, frontoparietal; hum, humerus; il, ilium; isch, ischium; max, maxilla; Mt1-5, Metatarsals I-V; otc, otic capsule; pmx, premaxilla; pp, prepollex; psph, parasphenoid; ptg, pterygoid; ptstr, postsacral transverse process; qj, quadratojugal; rad, radiale; Rib2-4, free ribs on 2nd through 4th presacrals; ru, radioulna; sacd, sacral diapophysis; sca, scapula; sph, sphenethmoid; sq, squamosal; tf, tibiofibula; tib, tibiale; ul, ulnare; uro, urostyle; vom, vomer; Y, Element Y.

Etymology. Sanyan (Chinese Pinyin), ancient place name for Liaoning.

Holotype. Institute of Vertebrate Paleontology and Paleoanthropology specimen number: IVPP V11525, nearly complete skeleton and imprint of bones exposed in dorsal view on a shale slab.

Type locality and horizon. Sihetun, Beipiao, Liaoning Province, northeastern China; lower part of Yixian

Formation (Late Jurassic/Early Cretaceous).

Diagnosis. Differing from other members of the group in having a combination of the following character states: lateral borders of frontoparietal parallel; maxilla anteriorly notched for articulation with premaxilla; marginal teeth slightly compressed longitudinally along tooth row and labiolingually expanded; zygomatic ramus of squamosal not in contact with maxilla; presacral vertebrae nine in number; iliac crest weak, dorsal protuberance absent; tibiofibula slightly longer than femur; proximal tarsal segment longer than one-half length of tibiofibula; proximal tarsal elements remain free from one another.

Description. The specimen was originally preserved as a nearly complete skeleton in volcanoclastic shales, but parts of the skeleton broken away and were lost when the slab was split. Exposed in dorsal view (fig. 1), the specimen includes the cranial and postcranial skeletons with imprints of the missing parts. Most of the skeletal elements are preserved in their original positions, but the pelvic girdle and the hind limbs have been shifted to the right of the cranium and the trunk region.

Skull and mandibles. The skull is short and wide, with a rounded snout. The maximum width of the skull across the otic capsule region is about 35 mm, and the maximum length is about 28 mm from the tip of the snout to the occipital condyles. All cranial elements lack dermal sculptures, differing from pelobatids and some other frogs^[12].

The premaxillae, preserved laterally in articulation with the maxillae, bear labiolingually expanded fine teeth, the number of which cannot be determined as a matter of preservation. The maxilla anteriorly has a well-defined notch for articulation with the premaxilla, and posteriorly articulates with the quadratojugal close to the craniomandibular joint. Like the premaxilla, the maxilla bears fine pedicellate teeth that have a comblike arrangement medially along the ventral edge of the jaw. The quadratojugals are well preserved on both sides, and hooked medially to contact the pterygoid and the squamosal. The nasals are not preserved on the available. The frontoparietal has been broken into several pieces, and whether the element is paired or azygous cannot be determined; however, the parallel lateral borders give a rectangular configuration of the element.

Preserved on the right side, the squamosal is roughly "—"-shaped, as commonly seen in other frogs. The ventral ramus is thin and more or less platelike, extending ventrally to contact the quadratojugal. The otic and zygomatic rami of the squamosal are each about 2.5 mm long and about one-half the length of the ventral ramus. The zygomatic ramus does not contact the maxilla. The otic capsule, consisting of the prootic and the exoccipital, is preserved on both sides between the frontoparietal and the squamosal. The capsule is anteriorly articulated with the well-developed posteromedial process of the pterygoid. A slender columella is well exposed on the left side, but only partially exposed on the right. Such an ossified columella is present in most frog taxa, but it is absent in leiopelmatids^[13].

As the skull is dorsally broken, some palatal and neurocranial elements can be observed in dorsal view. The vomer is laterally notched for the choana, and the well-defined prechoanal and postchoanal processes are oriented laterally. No palatines are identifiable, and they are probably absent as in other discoglossids. The sphenethmoid has a triangular anterior end, wedging between the vomers. The posterior part of the element is largely covered by the fragments of the frontoparietal. Posterior to the triangular portion of the sphenethmoid, the anterior tip of the parasphenoid is exposed. The remainder of the cultriform process and the posterolateral extensions (alae or wings) are covered by other cranial elements. Therefore, the shape of the parasphenoid cannot be observed on the specimen.

The pterygoid, best preserved on the right side, is a triradiate element. The anterior ramus extends to a point slightly posterior to the midlevel of the maxillary tooth row, where it attaches to the medial aspect of the maxilla. The posteromedial process extends medially along the anterior surface of the prootic component of the otic capsule and closely approaches to the lateral border of the frontoparietal. The posterolateral ramus of the pterygoid is about the same length as the posteromedial ramus, but the former laterally contacts the quadratojugal.

The lower jaws are mostly covered by the maxillary arch, but the mandibular symphysis and some other parts are exposed in dorsal view. The dentary is clearly edentulous, having a thin dorsal crest as commonly seen in other frogs. The anterior part of the angulosplenic is slightly detached from the dentary on both mandibles, and is exposed as a spike medial to the dentary.

Vertebral column. The vertebral column consists of nine presacral vertebrae, a single sacrum, and a

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free urostyle that has a bicondylar articulation with the sacrum. The first two presacrals are unfused. The neural arch is incompletely preserved on each of the first three vertebrae, yet it is clear that the arches are strongly imbricated. The neural arch is broken off on each of the more posterior vertebrae. The fourth and the fifth presacral vertebrae show that the centrum is opisthocelous and of the stegochordal type. Three pairs of free ribs, preserved as bony elements or imprints, are present on the second through the fourth presacrals. The transverse processes are short and slant strongly anterolaterally on the seventh through the ninth presacrals, slant less strongly on the second and the sixth presacrals, and are oriented laterally on the third and fifth presacrals. Those on the fourth vertebra, however, are extended posterolaterally.

The sacral vertebra is badly broken. Preserved as an impression, the left diapophysis is broadly expanded anteriorly and posteriorly, the shape of the process corresponds to Clarke's "butterfly-wing type"¹⁾. Anteriorly, the diapophysis contacts the transverse process of the ninth vertebra. The right diapophysis is broken and its distal two-thirds has been displaced laterally along with the pelvic girdle (figure 1).

The urostyle is about 27 mm long, making it about 6 mm shorter than the length of the presacral part of the column. The anterior end of the urostyle has two small cotyles that are aligned horizontally. This condition indicates an articulation with the bicondylar sacrum. The transverse process of the urostyle or postsacral transverse process is preserved as a clear impression on the left side, and is oriented posterolaterally. The process cannot be observed on the right side. A pair of foramina for spinal nerves is present anteriorly on the dorsolateral side of the urostyle.

Pectoral girdle and forelimbs. The pectoral girdle is arciferal type as indicated by the curved clavicle and the strongly oblique coracoid. The scapula is widened distally and is anteriorly overlain by the clavicle; the latter is a diagnostic feature of discoglossids^[7]. The coracoid, well preserved on both sides, is approximately 7 mm long and slightly expanded at both ends. Preserved on both sides, the clavicle is a long curved element, with an apparent groove along the posterior margin. An elongate thin bone is preserved on the right side of the displaced right clavicle; this thin element may represent the displaced right clethrium.

The left arm is folded anteriorly, with the forefoot lying close to the snout. The right arm is folded posteriorly and the forefoot lies underneath the vertebral column. The humerus (20 mm) is substantially longer than the more distal segment of the forelimb (14 mm). The radius and the ulna are completely fused into a single radioulna. The proximal end of the ulna part of the radioulna bears a short olecranon process. The mesopodials exhibit the so-called "Morphology A" pattern^[14] in having moderate-sized radiale and ulnare proximally, relatively large Element Y and Carpal V, and much smaller Carpals II-IV distally. A triangular prepollex lies distolateral to the Element Y. Although slightly overlapping one another as preserved, the metacarpals are better shown on the right side than on the left. The fourth metacarpal is the longest (5 mm) and the fifth is the shortest (3 mm). The phalangeal formula of the forefoot as observed is ?-?-3-3.

Pelvic girdle and hind limbs. The pelvic girdle has been shifted to the right side of the urostyle, but is still in articulation with the hind limbs. The ilium is laterally compressed and dorsally bearing a weak iliac crest. The dorsal protuberance, commonly seen in extant discoglossids and many other frogs, is primitively absent.

The hind limb is slenderly built and strongly elongated, with an estimated total length of some 116 mm. The femur is straight and is approximately 34 mm long, with a slender and constricted shaft. The tibiofibula, slightly longer than the femur at 35 mm, has a groove at the proximal and distal ends marking fusion of the tibia with the fibula. The total length of the femur plus the tibiofibula is about 69 mm, which is about three-quarters (73%) of the snout-vent length.

More proximally, tarsal segment is about 20 mm long. The tibiale (19 mm) and the fibulare (20 mm) contact one another at both ends, but remain unfused. This differs from the fused condition seen in extant discoglossids^[7]. As in other discoglossids, the tarsal elements are poorly ossified, but the prehallux

1) See footnote 1) on page 637.

and distal prehallux on the right hind foot are indicated by clear impressions. The phalangeal formula is 2-2-3-4-3, as shown on the better preserved right hind foot.

2 Systematic and biogeographic significance

The new frog is referred to the Discoglossidae as it shares with other members of the family the following character states: the presacral vertebrae are stegochordal and opisthocoelous; the neural arches are imbricated; Presacrals I and II remain unfused; free ribs are present on anterior presacrals; the sacrum has expanded diapophyses and bicondylar articulation with the urostyle; transverse process is present proximally on the urostyle; pectoral girdle is of arciferal type; anterior end of scapula is overlain by clavicle; and palatine is absent.

Along with the Leiopelmatidae (= Ascaphidae in Estes and Reig, 1973^[15]), the family Discoglossidae has been widely perceived as the most primitive group of extant frogs^[7,15]; hence, study of fossils of discoglossids should be important for elucidating the evolutionary history of anurans. Yet, largely owing to the lack of adequate fossil material, the early history of this primitive family group remains poorly understood. The known fossil records indicate that the family Discoglossidae was established by no later than Middle Jurassic, however, all of the early fossil taxa are only known from fragmentary materials (see refs. [16,17] for review), with the exception of *Eodiscoglossus*. Articulated skeletons of the latter taxon are known from the lithographic limestones at the Sierra del Montech^[15,18,19], and undescribed material from Las Hoyas, Spain^[20]. However, the new frog from Liaoning is morphologically more primitive than *Eodiscoglossus* in having nine presacral vertebrae, retaining maxillary and premaxillary teeth, and transverse processes on the urostyle, and lacking a definite dorsal protuberance on the ilium. In addition, the sacral diapophysis of the new frog is of a butterfly-wing type, contrasting the weakly expanded condition in *Eodiscoglossus*. These structural details give new insights into the anatomy of early discoglossids, and hence, are significant for scrutinizing the evolutionary history of the group.

Biogeographically, the family Discoglossidae is essentially a northern group in both extant and fossil distribution. This distribution pattern is in stark contrast with the Leiopelmatidae, which appears to have originated in and radiated from the Southern Hemisphere^[15]. The divergence of the two primitive groups represents a major biogeographic event in the anuran history, regardless the uncertain area of origin of anurans^[15]. Early discoglossid fossils are known from the Middle to Upper Jurassic beds in Europe and North America^[16,21], but an unanswered question is when the group invaded Asia. With the new discovery from Liaoning, now it is clear that the historical distribution of discoglossids in Asia can be traced back to at least 120 million years ago^[22]. Generally speaking, Mesozoic fossils of early frogs are mostly known from North and South American continents, and Europe. Recent discoveries from western Liaoning (ref. [23] and this note) open a new scope to view the biogeographic history of the major anuran groups.

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References

- 1 Hou Lianhai, Zhou Zhonghe, Martin, L. D. *et al.*, A beaked bird from the Jurassic of China, *Nature*, 1995, 377: 616.
- 2 Ji Qiang, Currie, P. J., Norell, M. A. *et al.*, Two feathered dinosaurs from northeastern China, *Nature*, 1998, 393: 753.
- 3 Hu Yaoming, Wang Yuanqing, Luo Zhexi *et al.*, A new symmetrodont mammal from China and its implications for mammalian evolution, *Nature*, 1997, 390: 137.
- 4 Ji Shu'an, New pterosaurs (Reptilia: Pterosauria) from northeastern China and the geological age problem of *Confuciusornis*, *Journal of Vertebrate Paleontology*, 1998, 18: 54A.
- 5 Gao Keqin, Tang Zhilu, Wang Xiaolin, A long-necked diapsid reptile from the Upper Jurassic/Lower Cretaceous of Liaoning Province, northeastern China, *Vertebrata Palasiatica*, 1999, 37(1): 1.
- 6 Špínar, Z. V., Tatarinov, L. P., A new genus and species of discoglossid frog from the Upper Cretaceous of the Gobi desert,

NOTES

- Journal of Vertebrate Paleontology*, 1986, 6(2): 113.
- 7 Duellman, W. E., Trueb, L., *Biology of Amphibians*, Baltimore and London: Johns Hopkins University Press, 1986. 1—670.
 - 8 Duellman, W. E., Amphibian species of the world: Additions and corrections, *University of Kansas Museum of Natural History Special Publication*, 1993, 21: 1.
 - 9 Shubin, N. H., Jenkins, Jr. F. A., An Early Jurassic jumping frog, *Nature*, 1995, 377: 49.
 - 10 Jenkins, Jr. F. A., Shubin, N. H., *Prosalirus bitis* and the anuran caudopelvic mechanism, *Journal of Vertebrate Paleontology*, 1998, 18 (3): 495.
 - 11 Rocek, Z., Taxonomy and distribution of Tertiary discoglossid (Anura) of the genus *Latonia* v. Meyer, 1843, *Geobios*, 1994, 27(6): 717.
 - 12 Trueb, L., Bones, frogs, and evolution, *Evolutionary Biology of the Anurans: Contemporary Research on Major Problems* (ed. Vial, J. L.), Columbia: University of Missouri Press, 1973, 65—132.
 - 13 Trueb, L., Patterns of cranial diversity among the Lissamphibia, *The Skull*. Volume 2: *Patterns of Structural and Systematic Diversity* (eds. Hanken, J., Hall, B. K.), Chicago: University of Chicago Press, 1993, 255—343.
 - 14 Fabrezi, M., El carpo de los anuros, *Alytes*, 1992, 10: 1.
 - 15 Estes, R., Reig, O. A., The early fossil record of frogs: a review of the evidence, *Evolutionary Biology of the Anurans: Contemporary Research on Major Problems* (ed. Vial, J. L.), Columbia: University of Missouri Press, 1973, 11—63.
 - 16 Evans, S. E., Milner, A. R., Musset, F., A discoglossid frog (Amphibia: Anura) from the Middle Jurassic of England, *Palaeontology*, 1990, 33: 299.
 - 17 Sanchiz, B., Salientia, *Handbuch der Paläoherpetologie* (ed. Wellnhofer, P.), Teil 4, München: Verlag Dr. Friedrich Pfeil, 1998, 1—275.
 - 18 Hecht, M. K., The morphology of *Eodiscoglossus*, a complete Jurassic frog, *American Museum Novitates*, 1970, 2424: 1.
 - 19 Vergnaud-Grazzini, C., Wenz, S., Les discoglossidés du Jurassique supérieur du Montsech (Province de Lérida, Espagne). *Annales de Paléontologie (Vertébrés)*, 1975, 61(1): 19.
 - 20 Evans, S. E., McGowan, G., Milner, A. R. et al., Amphibians. In: II International Symposium on Lithographic Limestones, *Field Trip Guide Book*, 1995, 51—53.
 - 21 Evans, S. E., Milner, A. R., Frogs and salamanders from the Upper Jurassic Morrison Formation (Quarry Nine, Como Bluff) of North America, *Journal of Vertebrate Paleontology*, 1993, 13(1): 24.
 - 22 Swisher, C. C., Wang Yuanqing, Wang Xiaolin et al., $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Lower Yixian Fm, Liaoning Province, north-eastern China, *Chinese Science Bulletin*, 1998, 43 (Supp.): 125.
 - 23 Ji Shu'an, Ji Qiang, The first Mesozoic fossil frog from China (Amphibia: Anura), *Chinese Geology* (in Chinese), 1998, 250: 39.

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