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SHORT COMMUNICATION

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Early evolution of discoglossid frogs: new evidence from the Mesozoic of China

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The Anura hold an important position in the history of the vertebrates as a major lissamphibian group. Although Cenozoic anuran record is fairly well documented from North America and Eurasia, Mesozoic fossils of the group are too inadequate to be illuminative of the early evolution of the group (Estes and Reig 1973; Sanchiz 1998). Among extant anurans, the family Discoglossidae is a primitive group which, together with Leiopelmatidae, was regarded as the most basal clade of living anurans (Estes and Reig 1973; Duellman and Trueb 1986; Sanchiz 1998). However, the taxonomic composition and the monophyly of the Discoglossidae are quite controversial (Cannatella 1985; Clarke 1988; Ford and Cannatella 1993a; Báez and Basso 1996), and no phylogenetic analyses have included both extant and the fossil taxa that have been attributed to the family.

Recently, a well-preserved specimen was recovered from the famous *Confuciusornis*-feathered dinosaur fossil beds at Sihetun, western Liaoning Province, China (Wang and Gao 1999). This discovery documents the earliest and sole definite discoglossid fossil from Asia, and only the second fully articulated specimen of the Mesozoic age known for the group from elsewhere. Based on congruence of primitive and derived characters in a phylogenetic analysis, *Callobatrachus* is placed as the most basal member of the Discoglossidae. This placement and the distribution pattern of early discoglossid fossils provide considerably significant insights into the biogeographic history of the group, and completeness of the specimen from Liaoning reveals pivotal anatomical details of an early discoglossid, otherwise not available from disarticulated material.

Electronic Supplementary Material Appendix I
Character description for matrix in Table 1 (see our homepage at: http://link.springer.de/journals/nawi)

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Systematics

Order Anura Rafinesque, 1815; Family Discoglossidae Günther, 1859; *Callobatrachus sanyanensis* Wang and Gao, 1999.

Holotype

A nearly complete skeleton; Institute of Vertebrate Paleontology and Paleoanthropology, IVPP V11525 (Fig. 1).

Locality and horizon

Sihetun, western Liaoning, China; lower part of Yixian Formation, Early Cretaceous (124.6 Ma) (Swisher et al. 1999).

Diagnosis

Early Cretaceous discoglossid differing from all other members of the family in having the frontoparietals with parallel lateral borders, presacral vertebrae nine in number, and cleithrum nonbifurcated distally. It further differs from *Eodiscoglossus* in lacking a dorsal protuberance but having a weak dorsal crest on ilium; from *Bombina* and *Barbourula* in having bicondylar sacro-urostylar articulation; and from *Latonia* in lacking dermal sculptures on skull roof, and having expanded sacral diapophyses.

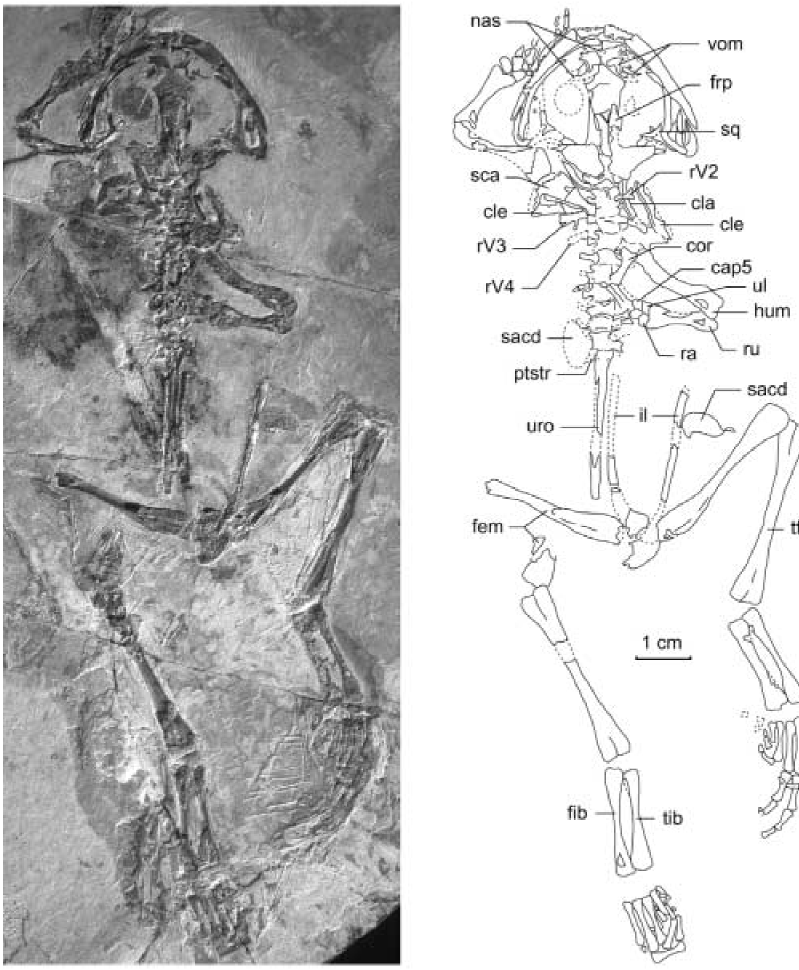

Fig. 1 *Callobatrachus sanyanensis*. Photograph (*left*) and outline (*right*) of the skeleton in dorsal view (*broken lines* indicate impressions of bones). *Cap5*, carpal 5; *cla*, clavicle; *cle*, cleithrum; *cor*, coracoid; *fem*, femur; *fib*, fibulare; *frp*, frontoparietal; *hum*, humerus; *il*, ilium; *ptstr*, postsacral transverse process; *ra*, radiale; *rV2–4*, free ribs on 2nd through 4th presacrals; *ru*, radioulna; *sacd*, sacral diapophysis; *sca*, scapula; *sq*, squamosal; *tf*, tibiofibula; *tib*, tibiale; *ul*, ulnare; *uro*, urostyle; *vom*, vomer

The family Discoglossidae is regarded as a monophyletic group by some authors (Duellman and Trueb 1986; Báez and Basso 1996; Sanchiz 1998), but as paraphyletic by others (Cannatella 1985; Ford and Cannatella 1993a,b). It is also debatable on whether the Central Asian gobiatines should be referred to the family (Sanchiz 1998). The discovery of the well-preserved skeleton of *Callobatrachus sanyanensis* makes it possible to re-examine the interrelationships of the taxa that have been attributed to the family, and to consider the early evolution of the osteological characters of the group. A phylogenetic analysis, based on 54 characters across 17 taxa, was conducted to elucidate the relationships of discoglossids and the group with other early anurans. Both extant and well-preserved fossil discoglossids were included in the analysis. The result is given in Fig. 2. The data matrix is provided as Table 1.

The phylogenetic analysis shows that some osteological characters are particularly informative in elucidating the early evolution of discoglossids. The number of presacral vertebrae and the type of centra are systematically important characters amongst anurans (Trueb 1973). Eight presacrals were considered the normal count for all discoglossids before the discovery of the *Callobatrachus* species, although an abnormal count of either seven or nine presacrals occurs rarely in the living *Bombina* spp. (Madej 1965). On the other hand, a presacral count of more than eight is common in other basal anurans (e.g. *Vieraella*, *Notobatrachus*, and *Asca-*

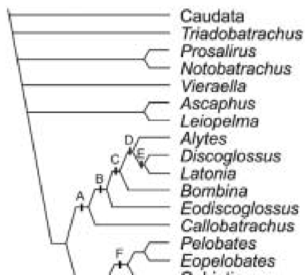

Fig. 2 The most parsimonious tree resulting from a phylogenetic analysis using PAUP3.1.1 (Swofford 1993) based on the data matrix given in Table 1 (all characters unordered and unweighted, Branch & Bound Search, ACCTRAN optimization, Caudata and *Triadobatrachus* as outgroups). TL = 105, CI = 0.676, RI = 0.748. Synapomorphies supporting each node: *A* (Discoglossidae): 2(1), 13(2); *B* 46(1), 47(1); *C* 8(1); *D* 40(1), 52(1);*E* 16(1); *F* 16(1), 17(1), 30(1). This tree supports the monophyly of the Discoglossidae, and regards *Callobatrachus* as the most basal member of the family. Gobiatinae are excluded from Discoglossidae and are referred to pelobatoids

Table 1 Matrix of taxon and characters and states which were used in the phylogenetic analysis in Fig. 2. *A* = 0/1, *B* = 1/2

	11111111112222222222333333333344444444445555 123456789012345678901234567890123456789012345678901234
Caudata	000A0000000000000000000000????0?0?????00?0????0?00?00
Triadobatrachus	000??000????0000001???????0000000?000000000000100000?
Prosalirus	?1????1??11???????1???????0?0?????0?0??0???100??01??0?
Notobatrachus	000001100100111001010011000001002?0021001001000101000?
Vieraella	1?0?0100??01??1001111011??010???1?00?200????000?01????
Ascaphus	1?1112000011111100101–10–1011100120012B102001–001111011
Leiopelma	0?111201001111100101102100111101200123102001000 1?11011
Alytes	01001201110120100011?10210111100030110211210111121111111
Discoglossus	01000B01110120111111?10210111101030100211210111121111111
Latonia	0000?001?A0?2011?111?0210?111?1?30100211210111?211111?
Bombina	01000201110130100011?102101111010301002122201111 2111011
Eodiscoglossus	010001?0??01201001?????????????030?0021?210?111?111?11
Callobatrachus	010?0?????0?20100111102????????0201002122101?00??11?1?
Pelobates	000000?1?1001011111010?1011111203020?412221?000??11?12
Eopelobates	000100?????0?011111?????011111?03?20?412221?00???1??1?
Gobiatinae	000??2?0?????011111??????11111??300004?021000?0?11????
Pelodytidae	0A0111????01101001?1?02??1111010312004122220????111?21

phus). The possibility that the nine presacrals in *Callobatrachus sanyanensis* occurs as an isolated variation can simply be ruled out based on other primitive features that it bears. Thus the count of nine presacrals in *C. sanyanensis* may represent a primitive state in the evolutionary history of discoglossids, with a trend towards a decrease in the number of vertebrae in more advanced taxa. Opisthocoelous centra are known for all discoglossids except some amphicoelous vertebrae that have been misattributed to the family (Spinar and Tatarinov 1986; Fey 1988; Evans et al. 1990; Evans and Milner 1994). Since the amphicoelous centrum is primitive in anuran evolution, the opisthocoelous centra of *C. sanyanensis* show the derived condition, in spite of its basal position in the clade. The presence of forked cleithra, anterolaterally directed transverse processes on the posterior presacrals, and free ribs on presacrals II–IV are used as important diagnostic features of all discoglossids (Rocek 1994) Although the presence of free ribs is primitive in relation to more advanced frogs, the *Callobatrachus* species possesses the latter two characteristics, but shows a clearly non-forked cleithrum, as seen in other basal anurans (e.g., *Notobatrachus*, *Ascaphus*, and *Leiopelma*). This provides further evidence for the basal status of *Callobatrachus* within Discoglossidae. The coracoid with an expanded medial end is common in basal anurans, and can therefore be regarded as a primitive character (Báez and Basso 1996) of *Callobatrachus*; whereas the coracoid in all other discoglossids is elongate with little expansion. Outgroup comparison reveals that the lack of dermal sculptures on the skull roof of *Callobatrachus sanyanensis* should be regarded as a derived character. However, in the scope of Discoglossidae, dermal sculptures were secondarily acquired in species of the Tertiary genus *Latonia*.

Characteristics of the ilium (especially the well-developed dorsal protuberance) are frequently used as diagnostic characters for early discoglossids when represented by isolated material (Evans and Milner 1993; Sanchiz 1998). However, the development of a pronounced dorsal protuberance on the ilium seems to represent a primitive state based on outgroup comparison with other basal anurans. Representatives of *Triadobatrachus* (sister taxon to all anurans), *Czatkobatrachus* (an Early Triassic stem-group frog from Poland), and *Notobatrachus*, all bear a dorsal protuberance (Báez and Basso 1996; Evans and Borsuk-Bialynicka 1998; Sanchiz 1998). The iliac impression of *Callobatrachus sanyanensis* suggests it that lacks a dorsal protuberance, a derived condition within discoglossids. Although *Alytes* and *Discoglossus* species have a well-defined dorsal protuberance, *Bombina* species have a weak one. The condition in *Eodiscoglossus* is unknown from the type specimen. We would suggest this character should be used with caution. Fossil taxa previously attributed to the discoglossids based on this character, including all Jurassic forms (Evans et al. 1990; Evans and Milner 1993), deserve further investigation.

Callobatrachus shows several derived characters that support its attribution to the Discoglossidae (see above), but also some primitive features in relation to other discoglossids, such as having nine presacrals, a non-forked cleithrum, and a coracoid with an anteriorly expanded medial end. Although the Early Cretaceous (late Berriasian or early Valanginian) *Eodiscoglossus santonjae* is slightly older than *Callobatrachus sanyanensis* in terms of geological age, several derived features of *Eodiscoglossus* relative to *Callobatrachus* place it higher than the Chinese form. These features include the presence of eight presacrals, a distally forked cleithrum, and a slenderly built coracoid (Hecht 1970; Vergnaud-Grazzini and Wenz 1975). Apparently, the discrimination of character distribution and temporal range between the two earliest definite discoglossids, *Eodiscoglossus* and *Callobatrachus*, suggest that the family Discoglossidae should have had a pre-Cretaceous origin.

Callobatrachus sanyanensis documents the first discoglossid fossil from China, and the earliest record of the group in Asia. Because the Central Asian gobiatines are more closely related to pelobatoids than to Discoglossidae as revealed by our analysis, *Callobatrachus* also represents the only known record of Mesozoic discoglossids in Asia. The discovery from Liaoning shows that the history of discoglossid frogs in Asia can be traced back to at least 125 million years ago, and it is probable that early discoglossids entered Asia prior to its separation from Europe in the Late Jurassic. The mosaic of primitive and derived characters found in *Callobatrachus* places it as the most basal taxon in the clade, and shows that the taxon had diverged early from the stem, and had evolved separately as a distinct lineage in East Asia by the Early Cretaceous. The recent anuran discoveries in China (Ji and Ji 1998; Wang and Gao 1999), coupled with isolated Early Cretaceous anuran materials (135 Ma) recovered from Japan (Evans and Manabe 1998), indicate that East Asia could have been an important place for the early diversification of anurans.

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