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Taxonomy and Stratigraphy of Late Mesozoic Anurans and Urodeles from China

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Abstract Three anurans (*Callobatrachus sanyanensis, Liaobatrachus grabaui, Mesophryne beipiaoensis*) and six urodeles (*Laccotriton subsolanus, Liaoxitriton zhongjiani, Jeholotriton paradoxus, Sinerpeton fengshanensis, Chunerpeton tianyiensis, Liaoxitriton daohugouensis*) are reported from the late Mesozoic tuff-interbedded lacustrine deposits (mostly of the Jehol Group) in northeastern China. They document the first discovery of Chinese Mesozoic lissamphibians, and their old geological age, superb preservation condition, and large taxonomic diversity are unique compared with other findings worldwide. The anurans occupy a higher evolutionary position than typical Jurassic taxa, supporting a post-Late Jurassic age of the fossil horizons. The urodeles all have unicapitate ribs, suggesting an evolutionary grade at the cryptobranchoid level, and are advanced in osteological features over non-urodeles from the Middle and Upper Jurassic in England and Central Asia. Some urodeles (*Jeholotriton* and *Chunerpeton*) exhibit neotenic features, representing the earliest occurrence among such findings. Six fossil horizons are recognized for the known Chinese Mesozoic anurans and urodeles: the Daohugou fossil bed, the Dabeigou Formation, the Lujiatun Bed, Jianshangou Bed and Dawangzhangzi Bed of the Yixian Formation, and the Jiufotang Formation. As implied from the osteological and phylogenetical studies, the geological age of these anurans and urodeles is the Early Cretaceous.

Key words: anurans, urodeles, taxonomy, stratigraphy, Late Mesozoic, China

1 Introduction

The early evolution of lissamphibians (including frogs, salamanders, and caecilians) is one of the research highlights of paleoherpetologists (Duellman and Trueb, 1986; Milner, 1988; Carroll, 2000). However, lissamphibian fossils are generally poorly preserved and sparsely distributed, especially are of the Mesozoic forms that can play an important role in elucidating the origin and evolutionary process of modern amphibian groups (Sanchiz, 1998; Milner, 2000). Thus it is significant that a large number of well-preserved fossil skeletons, representing nearly ten new taxa of anurans and urodeles, were recovered recently from the late Mesozoic tuff-interbedded lacustrine deposits in northeastern China. These discoveries have provided a good supplementary to the poor document of the early history of lissamphibians.

Before the discoveries, fossil lissamphibians from China were rather limited in both quantity and taxonomic diversity, and all the material was from the Cenozoic strata (Wang, 2001). Therefore, when well-preserved skeletons of Mesozoic anurans and urodeles first appeared since late 1990s from Liaoning, Hebei, and Inner Mongolia in the distribution range of the renowned Jehol Group that contains the Biota (locality map see Fig. 1), they have not only represented the first document of Mesozoic lissamphibians from China, but also provided crucial information on the origin and early evolution of several major anuran and urodele groups. Furthermore, these amphibians are of old geological age, superb preservation condition, and large taxonomic diversity that are unique compared with other findings worldwide, and they are also useful in discussing the long-disputed stratigraphic correlation and geological age of the Jehol Group.

In this paper, systematic reviews will be conducted on these important amphibians, some of which with revised diagnosis and/or measurements for the first time. The biostratigraphical and geochronological significance of these taxa will also be discussed based on the osteological studies and analysis on the evolutionary stages of relevant groups. Osteological terminology follows Duellman and Trueb (1986) and Estes (1981). Abbreviations: IVPP V, specimen number for vertebrate fossils of the Institute of Vertebrate Paleontology and Paleoanthropology; GMV, specimen number for vertebrate fossils of the Geological Museum of China; LPM, Liaoning Paleontological Museum.

2 Systematic Paleontology

Nine lissamphibian taxa have been described from the Mesozoic of China, including three anurans

Plate I

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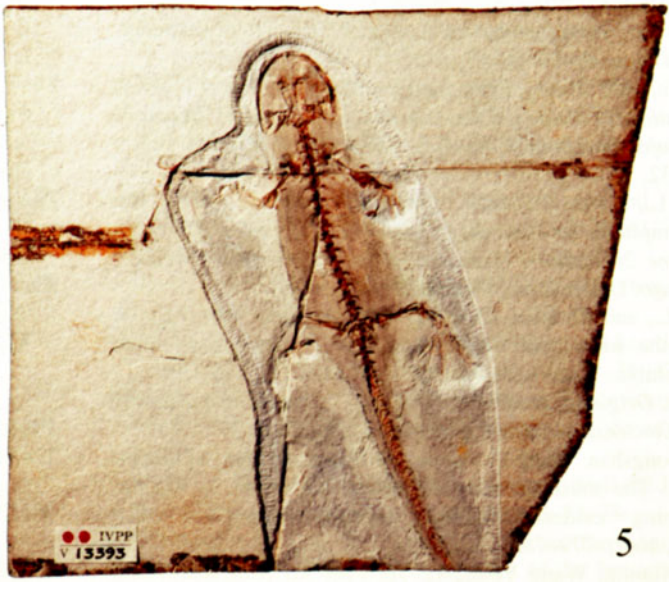

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Table 2 Comparative measurements of the holotype of *Callobatrachus*, *Liaobatrachus*, and *Mesophryne* (in mm)

	Callobatrachus IVPP V 11525	*Liaobatrachus* GMV 2126	*Mesophryne* LPM 0030
Snout-pelvis L	93+	70+	70+
Skull L/W	28.7/35	22+/32+	24+/34+
Vertebral column (urostyle) L	58.7(27)	46+(22+)	43+(21+)
Humerus L	20	22	20
Radioulna L	14	13	14
Femur L	34	29	30+
Tibiofibula L	35	29	29
Tibiale L	18.5	14	16
Fibulare L	20	16	17.4
Hind limb Digit IV L	27+	–	27.5

Note: Measurements on *Liaobatrachus* were taken by the author, some of which are different from those in the original paper. +, estimated; –, character not preserved; L, length; W, width.

Gao [1999] and Gao and Wang [2001]).

Callobatrachus documents not only the earliest Asian discoglossid frog, but also the only fossil form sympatric with the extant range of Discoglossidae in Asia (Wang and Gao, 1999). As a basal discoglossid, *Callobatrachus* is valuable in examining the early character evolution of the group. The type of centra (opisthocoely), presence of free ribs (three pairs), and shape of coracoid (elongate, not anteriorly expanded at proximal end) are proved to be diagnostic of the discoglossids; whereas part of the familial diagnosis should be revised after the adding of *Callobatrachus*, such as the number of presacrals (8–9) and the shape of the distal end of cleithrum (nonbifurcate or bifurcate). It is noted that a formerly used diagnostic feature of the discoglossids, "the presence of a developed dorsal protuberance on ilium" (Evans et al., 1990; Evans and Milner, 1993), should be used with caution, as it is now regarded a plesiomorphic feature in primitive anurans.

Liaobatrachus grabaui Ji et Ji, 1998

The holotype and only specimen (Table 2; Pl. I-2) was an incomplete skeleton with the skull elements disarticulated and partially lost. *Liaobatrachus grabaui* was the first Mesozoic frog described from China. The original diagnosis was in Chinese and is translated here for future reference: "A medium-sized anuran (snout-pelvis length estimated 75 mm), skull wide, maxillae with closely arranged tiny comb-like teeth, frontoparietals fused, presacrals nine in number, most centra procoelous, transverse processes on Vertebrae II to IV relatively long, sacral diapophyses wide and fan-shaped, urostyle longer than total length of presacrals, with transverse process on its anterior portion, pectoral girdle arciferal with strongly curved clavicle, pelvic girdle long, forelimbs short and robust, hind limbs long, tibiofibula same length to the femur, proximal tarsal segments longer than half length of the tibiofibula" (translated from Ji and Ji [1998]).

The taxonomic status of this animal remains to be investigated, as the referral of it to the family Pelobatidae (Ji and Ji, 1998) was based on several characters in question, such as the presence of procoelous presacrals and the lack of free ribs, and the fuse of frontoparietals, which cannot be confirmed due to poor preservation. The real systematic position of this animal needs further work, which is also counted on better-preserved material to be found.

Mesophryne beipiaoensis Gao et Wang, 2001

The holotype (Table 2; Pl. I-3) was a nearly complete skeleton split on part and counterpart of shale. This frog differs from *Callobatrachus* in having proportionally large skull, shortened vertebral column, procoelous central type, enlarged prepollex, tibiofibula shorter than femur, and Digit IV in pes proportionally much longer in relation to the length of the tibiofibula. A full description of the frog was provided in the naming paper, which, with a comprehensive phylogenetic analysis on archaeobatrachian frogs, referred it to an unknown basal anuran clade (Gao and Wang, 2001). Whether this new clade should be named at familial level is not yet decided; however, this anuran does show several distinct primitive features such as the presence of nine presacrals, anteriorly expended proximal end of the coracoids, and retaining of free ribs and an intermedium. So, it is not surprising that the taxon occupies a more basal position than the discoglossid clade, and is regarded as the sister group of the suborder Archaeobatrachia (Gao and Wang, 2001; see a revised analysis in Wang [2002]).

Chunerpeton tianyiensis Gao et Shubin, 2003

The salamander was described based on four catalogued specimens, with the largest (total length approximately 180 mm) assigned as the holotype. All the material was collected from the same locality and of the same preservative condition (natural mould/impression of articulated skeleton) of a pervious reported urodele, *Jeholotriton paradoxus*, though the naming paper did not mention. The urodele was diagnosed based on the comparisons with living cryptobranchoids and cryptobranchids. No comparisons were made concerning the four previously found Chinese Mesozoic urodeles (i.e., *Laccotriton, Liaoxitriton, Jeholotriton, Sinerpeton*); however, the taxon can still be justified with its distinct characteristics. Among the six reported Chinese Mesozoic salamanders, *Chunerpeton* is the only taxon that is classified at familial level. Its referral to the extant family Cryptobranchidae also makes it one of the earliest crown-group salamanders in the world (Gao and Shubin, 2003); whereas its geological age is still controversial, and will be discussed in the later section of this paper.

Jeholotriton paradoxus Wang, 2000

This taxon was established based on a holotype (Pl. I-4) and three paratype specimens. Most of its known material are preserved as impressions of articulated skeleton, an

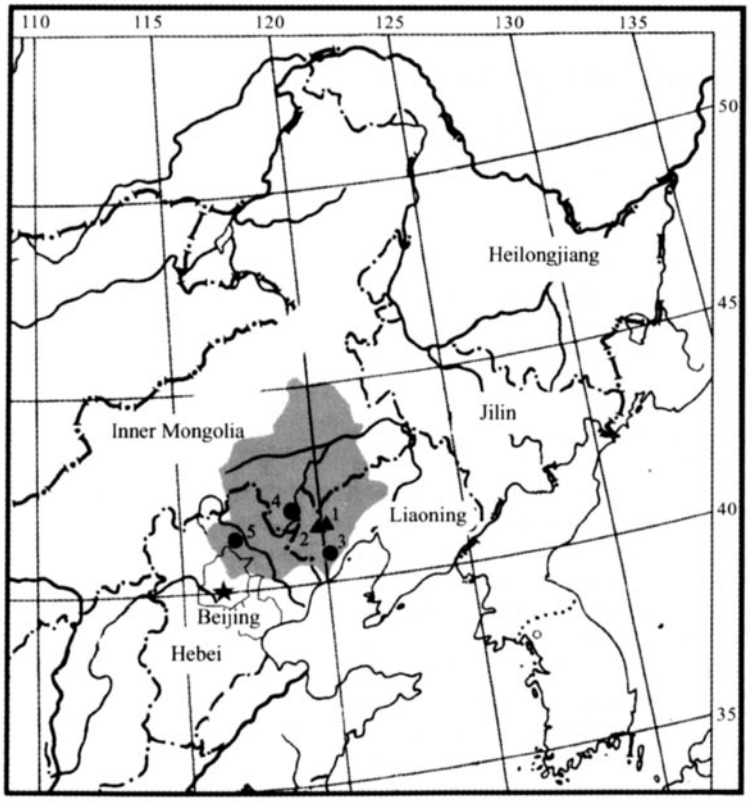

Fig. 1. Map of localities of Mesozoic anurans and urodeles from China.
The gray area shows the range of the "Jehol Province" of China in the 1920s, based on which the biota was named. Triangles denote anuran localities; dots urodele. 1: Sihetun, Shangyuan, Beipiao, Liaoning; 2: Heitizigou, Zhangjiying, Beipiao, Liaoning; 3: Shuikouzi, Xintaimen, Huludao, Liaoning; 4: Daohugou, Ningcheng, Chifeng, Inner Mongolia; 5: Paozhanggou, Fengshan, Fengning, Hebei.

(*Callobatrachus sanyanensis*, *Liaobatrachus grabaui*, *Mesophryne beipiaoensis*) and three urodeles (*Laccotriton subsolanus*, *Sinerpeton fengshanensis*, *Liaoxitriton zhongjiani*) from the Jehol Group, and three urodeles (*Jeholotriton paradoxus*, *Chunerpeton tianyiensis*, *Liaoxitriton daohugouensis*) from a slightly lower horizon; there are also some unstudied materials from new localities and horizons (Table 1). These taxa will be reviewed in systematic and alphabetic sequences in the following paragraphs.

Callobatrachus sanyanensis Wang et Gao, 1999

This anuran taxon was erected based on a nearly complete skeleton (Table 2; Pl. I-1), with its full description in Wang and Gao (1999) and Gao and Wang (2001). Phylogenetic analysis shows that it is the most basal member of the family Discoglossidae (Wang Yuan et al., 2000; see a revised analysis in Wang, 2002). A revised diagnosis is given here: Early Cretaceous discoglossid differing from all other members of the family in having nine presacral vertebrae, and in having a combination of the following characters: 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; cleithrum non-bifurcated distally; iliac crest weak, dorsal protuberance absent; tibiofibula slightly longer than femur; proximal tarsal segment longer than one-half length of tibiofibula. Compared with other well-established fossil and extant discoglossid taxa, *Callobatrachus* 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 (revised from Wang and

Table 1 Material of Mesozoic anurans and urodeles from China

Taxon	Material	Locality and Horizon	Reference
Anura			
Anura indet. 1	An incomplete skeleton	Yixian, Liaoning; Jiufotang Fm.	This paper
Anura indet. 2	Dozens of incomplete skeletons	Beipiao, Liaoning; Lujiatun Bed, Yixian Fm.	This paper
Anura indet. 3	Two nearly complete skeletons	Yixian, Liaoning; Dawangzhangzi Bed, Yixian Fm.	This paper
Callobatrachus sanyanensis	Two nearly complete skeletons	Sihetun, Liaoning; Jianshangou Bed, Yixian Fm.	Wang and Gao, 1999
Liaobatrachus grabaui	An incomplete skeleton	Sihetun, Liaoning; Jianshangou Bed, Yixian Fm.	Ji and Ji, 1998
Mesophryne beipiaoensis	One nearly complete skeleton	Heitizigou, Liaoning; Jianshangou Bed, Yixian Fm.	Gao and Wang, 2001
Urodela			
Chunerpeton tianyiensis	Four cataloged skeletal moulds	Daohugou, Inner Mongolia; Daohugou fossil bed	Gao and Shubin, 2003
Jeholotriton paradoxus	Dozens of skeletal impressions	Daohugou, Inner Mongolia; Daohugou fossil bed	Wang, 2000
Laccotriton subsolanus	Four cataloged skeletons	Paozhanggou, Hebei; Fengshan fossil bed, Yixian Fm.	Gao et al., 1998
Liaoxitriton daohugouensis	Two skeletal impressions	Daohugou, Inner Mongolia; Daohugou fossil bed	Wang, 2004
Liaoxitriton zhongjiani	Dozens of incomplete skeletons	Shuikouzi, Liaoning; Jiufotang Fm.	Dong and Wang, 1998
Sinerpeton fengshanensis	Five cataloged incomplete skeletons	Paozhanggou, Hebei; Fengshan fossil bed, Yixian Fm.	Gao and Shubin, 2001
Urodela indet. 1	One incomplete skeleton	Weichang, Hebei; Dabeigou Fm.	This paper
Urodela indet. 2	One incomplete skull	Luanping, Hebei; Dabeigou Fm.	Young, 1979; This paper
Urodela indet. 3	One nearly complete skeleton	Lingyuan, Liaoning; Daohugou fossil bed	This paper

Table 3 Osteological measurements of *Jeholotriton paradoxus* (in mm)

	11944 (H)	11946 (P)	11984 (P)	11943 (P)	12623	13389	11969	12622	12610	11947	12515	11948
Snout-pelvis L	72	–	67	53	70	–	–	58	–	53+	52	40
Skull L	21	21	19	15	20	20	–	17+	–	16	16	13+
Humerus L	8	7.5	8	5	7.5	7.5	6.8	6.8	7	5.8	6	3.5
Forelimb L	23+	21.5	22.5	15	21.5+	21.5+	19+	20+	–	17+	17+	12+
Femur L	7.5	–	7.5	5	7.5+	–	7.5	6	5.5	5	5.5	2.2
Hind limb L	23+	–	23	16	23+	–	–	18+	–	–	15+	11.5

Note: +, estimated; –, character not preserved; L, length; H, holotype; P, paratype. All specimens are catalogued IVPP V.

unusual condition for Mesozoic urodeles worldwide. With more specimens found, eight catalogued fossils are added as referred material (Table 3), though over a hundred unsorted specimens may be referred to the species (Wang, 2002).

Recent study has confirmed the neotenic feature of *Jeholotriton*, as indicated by a combination of both larval and adult features on this animal. A revised diagnosis is provided here: A Mesozoic salamander showing a combination of larval and adult features that indicate neoteny or incomplete metamorphosis. The larval features include the presence of external gills, a tooth-bearing coronoid, larval shaped pterygoid, and a short maxillary arcade with underdeveloped maxilla. The adult features include extensive medial contact of the two nasals and the presence of a posteriorly directed tooth row in the palate. It differs from other Mesozoic salamanders in having the following combination of character states: 16 (or 17?) presacrals, vertebrae with short transverse processes, ribs unicapitate and proximally expanded, pterygoid directed to the middle part of the skull base rather than to the posterior end of the maxilla, vomer with a large tooth patch anteriorly and a longitudinal dentigerous bar posteriorly, nasals large with no anterior notch, frontal with no anterolateral extension, alary process of premaxilla prominent and of about 2/5 the width of the premaxilla, hyobranchial elements not well ossified, carpals and tarsals unossified, and phalangeal formulae of 2-2-3-2 for manus and 2-2-3-3-2 for pes (revised from Wang [2000] and Wang and Rose [in press]).

Concerning its systematic affinity, *Jeholotriton* may be related to modern cryptobranchoids (including cryptobranchids and hynobiids), with the sharing of one derived character: the presence of unicapitate ribs. However, it still cannot be referred to any of the three extant salamander families (Cryptobranchidae, Hynobiidae, Salamandridae) in China, and the familial arrangement remains to be investigated by further phylogenetic analysis on basal caudates.

Laccotriton subsolanus Gao, Cheng et Xu, 1998

The taxon was established based on four catalogued skeletons (Gao et al., 1998), though a few hundred unnumbered specimens from the type locality may also be included into the type and only species (Gao and Shubin, 2001). The naming paper was in Chinese with no English abstract, so, the original diagnosis is translated here for future reference: "A urodele with widened skull and rounded snout; differing from all neotenic salamanders including sirenids in having well-developed maxillae and nasals, single ossification (scapulocoracoid) of pectoral girdle and fully ossified limb bones with no degeneration phenomenon; differing from advanced cryptobranchids, sirenids and amphiumids in lacking anterolateral extension of the frontals into the nasal region; differing from *Valdotriton* in lacking intravertebral spinal foramen on caudal vertebrae and having a phalangeal formula of 2-3-4-3 in the manus" (translated from Gao et al. [1998]).

Laccotriton represents a small metamorphosed urodele as indicated by well-developed maxillary arcade and nasals. The snout-pelvis length of most specimens ranges in 40–50 mm (Gao et al., 1998). A brief re-description of the salamander was given in Gao and Shubin (2001), in which the authors revised the phalangeal formula of the manus from 2-3-4-3 to 2-2-3-2, and provided some new diagnostic characters (see Gao and Shubin [2001]). The familial referral of *Laccotriton* is still unresolved, while a refined phylogenetic study is undertaken by the present author.

Liaoxitriton daohugouensis Wang, 2004

This new species (Pl. I-5) of *Liaoxitriton* is recently established with two specimens that are preserved as skeletal impressions. Wang (2004) provided a revised diagnosis of the genus for the first time since *Liaoxititon zhongjiani*, the type species, was named. New diagnostic features of the genus include: "…nasals abutted at the midline; frontals without, parietals with anterolateral extension; prefrontals and lacrimals retained; …with a palatal fenestra; …anterior ramus of pterygoid robust, directing to the end of maxilla; prearticular and articular retained; hyobranchial apparatus with three ossifications: paired Hypobranchial II and Ceratobranchial II slender, single Basibranchial II anchor-shaped…; scapulocoracoid notably expanded at proximal end; presacrals 15–16 in number; …postsacral ribs 2–3 pairs; mesopodials partially ossified." A differentiation of the new species from *L. zhongjiani* is also provided by Wang (2004). It is noted that *Liaoxitriton* has similar osteological characteristics with some extant hynobiids, e.g. unicapitate ribs, hyobranchial morphology, and the transverse extension of vomerine tooth rows, though its phylogenetic position remains to be investigated.

***Liaoxitriton zhongjiani* Dong et Wang, 1998**

This fossil salamander was represented by several dozen articulated skeletons that are in various preservation condition on fragile slabs of mudstone. With new fossils found and further studies, a revised diagnosis of the species is provided here: Species of *Liaoxitriton* that differs from *L. daohugouensis* by narrower rostrum, posterolaterally extended vomerine tooth row, lower coronoid flange, less developed articular, smaller proximal end and longer distal bar of scapulocoracoid, presence of 15 presacrals, stick-shaped ribs on second presacral with no obvious distal expansion, two pairs postsacral ribs, expanded Metacarpal II, phalangeal formula 2-2-3-(2/3) for the manus and 2-2-4-5-(3/4) for the pes (revised from Dong and Wang [1998]).

***Sinerpeton fengshanensis* Gao et Shubin, 2001**

This taxon was named based on five cataloged and numerous unnumbered specimens, all preserved as articulated skeletons in various preservation condition. The naming paper regarded it a neotenic urodele by having ossified mesopodium (indicating adulthood) and paired ossified ceratobranchials (indicating presence of external gills). However, the slender ceratobranchials on *Sinerpeton* are too weak to be a real support of external gills (same situation in some living salamanders, pers. commun. with Dr. C. Rose), so, the neoteny statement is still open to question. Also the holotype of the species is very similar in osteological morphology to juvenile material of *Liaoxitriton zhongjiani*, thus whether the species is actually a junior synonym to the later taxon awaits further study.

A phylogenetic analysis was provided by Gao and Shubin (2001), trying to resolve the caudate phylogeny with the new discoveries of *Sinerpeton* and *Laccotriton*. The two taxa are "bushed" with the cryptobranchoids and more advanced urodeles, suggesting an unresolved phylogeny of the basal caudates, so, the two taxa are still referred as "Family incertae sedis". However, the analysis reveals that these Asian taxa lie at the base in the phylogenetic tree of Caudata. The basal position of the two Chinese taxa with the superfamily Cryptobranchoidea suggests that "basal salamanders initially radiated in Asia, and later spread to North America and Europe" (Gao and Shubin, 2001). It can be inferred that extant urodeles may have an Asian origin as observed from the fossil evidence.

Undescribed anuran and urodele material

Though nine taxa have been named and described, more new material of anurans and urodeles is to be studied, some of which may represent new taxa. Among these, the anuran material include an incomplete skeleton from Yixian (Table 1, Anura indet. 1) that obviously represent an previously unknown advanced frog, dozens of three-dimensional anuran skeletons from Beipiao (Table 1, Anura indet. 2) and several skeletons from Yixian (Table 1, Anura indet. 3) that may represent new species and document new horizons of the genus *Mesophryne*; the urodele material include one from a new locality in Lingyuan that resembles *Chunerpeton* in Ningcheng (Table 1, Urodela indet. 1); and some incomplete specimens from two localities in Hebei (Table 1, Urodela indet. 2, 3), both of which may represent basal urodeles as other known Mesozoic salamanders from China.

3 Discussion on the Stratigraphy and Geological Age of the Fossil Horizons

Most Chinese Mesozoic anurans and urodeles were found in relation with the Jehol Group. The Jehol Group and its associate biota have been in the highlight of paleontological study in recently years (Chang et al., 2003; Zhou et al., 2003). Though debates remains on the stratigraphic correlation of the fossil horizons and the deposition time of the group (Jin, 1996; Chen, 1999; Chang et al., 2003). The amphibians may be of help to the discussion of some related issues.

The holotype of *Callobatrachus sanyanensis* was collected at the Sihetun locality. The lithological characteristics can relate the specimen to Level 27 (Wang et al., 1998) of the excavation section at this site. The whole section has been correlated to the lower part of the Yixian Formation (namely "Jianshangou Bed", Wang et al., 1999). Tuff samples collected from Level 18, about 2.5 m above Level 27, have provided an isotopic dating of 125 Ma (Swisher III et al., 1999, 2002; Wang et al., 2001). This age is Valanginian according to the stratigraphic chart (with J/K boundary at 135 Ma) of Ramane et al. (1998). *Liaobatrachus grabaui* was from the same site, and possibly Level 28 as known from field investigation. *Mesophryne beipiaoensis* was reported from the Heitizigou locality, about 2.5 km southwest to the Sihetun locality; the strata are correlated also to the lower part of the Yixian Formation (Wang et al., 1998). The horizon and age of the three Chinese Mesozoic anurans are of little debate. Most people accept the isotopic dating result (125 Ma) from the Sihetun site. "Late Jurassic" age for the fossil horizon was once proposed based on a different isotopic dating (Lo et al., 1999), but it has been proved to be flawed in its sampling (Swisher III et al., 2002) and the dating result is not well accepted. It is noteworthy that some new anuran material were discovered recently from the Lujiatun Bed (Anura indet. 2, see Table 1) and Dawangzhangzi Bed (Anura indet. 3, see Table 1) of the basal and middle Yixian Formation, respectively, and the Jiufotang Formation (Anura indet. 1, see Table 1); thus, by now, four horizons have been recognized for the Chinese Mesozoic anurans.

The number of presacrals, the type of centrum, and the number of free ribs on the presacrals are three most

Table 4 Comparisons of Chinese Mesozoic anurans to Jurassic taxa of the world

	Presacral #	Centrum Type	Free rib #
Prosalirus	?	notochordal	?
Notobatrachus	9	notochordal	4 pairs
Vieraella	10	notochordal	3 pairs
Mesophryne	9	procoelous	3 pairs
Callobatrachus	9	opisthocoelous	3 pairs

important characters in the phylogenetic reconstruction of frogs. The larger number of presacrals, the amphicoelous or notochordal types of centrum, and the greater number of free ribs are regarded primitive in the anuran character evolution (Trueb, 1973; Báez and Basso 1996; Gao and Wang, 2001; Wang, 2002). As shown from the comparisons (Table 4), *Mesophryne* and *Callobatrachus* (note: *Liaobatrachus* is not included because its characteristics are still in question) are advanced in these characters over all the three known Jurassic taxa, the Early Jurassic *Prosalirus* of the US (Shubin and Jenkins, 1995), the Early Jurassic *Vieraella* of Argentina (Reig, 1961) and the Middle to Late Jurassic Argentine frog *Notobatrachus* (Báez and Basso, 1996). As indicated by a new phylogenetic analysis, the Chinese Mesozoic anurans occupy a higher evolutionary position than these Jurassic taxa (see Fig. 2). This implies that the fossil horizon of the known Chinese Mesozoic anurans is most likely of post-Jurassic age, which gives additional supports to the Early Cretaceous age acquired from isotopic dating method.

The stratigraphic correlation and geological age of Chinese Mesozoic urodeles are under hot debates. The fossil locality of *Liaoxitriton zhongjiani* was documented as "Shajiaocheng" in the original naming paper (Dong and Wang, 1998), but further fieldwork by the present author recovered the exact locality is at Shuikouzi of Wangbaoshan Village in Huludao City. This urodele-bearing bed was correlated to the Lower Cretaceous Jiufotang Formation based on the opinion from Mr. Chang Zhenglu, a geologist and early collector of material of *L. zhongjiani*. He also found *Ephemeropsis trisetalis*, a typical Jehol insect, from the fossil horizon, and referred the bed to the Jiufotang Formation based on the fact that no lava or volcanic interbeds can be found in this area. However, A recent fieldwork by him and the present author have found basalt deposit under the fossil horizon in this region. So, the possibility that the fossil bed is in the Yixian Formation cannot be ruled out. Further work is needed to solve this problem.

Material of the two Hebei taxa, *Laccotriton subsolanus* and *Sinerpeton fengshanensis*, was discovered from Paozhanggou, Fengshan Town, Fengning County of Hebei Province, and was collected in a small quarry of no more than 10 m^2 (Gao and Shubin, 2001). The naming paper of *Laccotriton* referred the fossil horizon to the "Xiguayuan Formation of Late Jurassic" (Gao et al., 1998). But in a later paper that reported *Sinerpeton*, the fossil horizon was described as: "Late Jurassic fossil beds that overlay the Zhangjiakou Formation (Tithonian)" (Gao and Shubin, 2001). It is noted that Ren et al. (1996) correlated the Xiguayuan Formation to the lower part of the Yixian Formation, while some other scholars regard it comparable to the Jiufotang Formation (Hao et al., 2000). Both correlations cannot provide a "Late Jurassic" age of the fossil bed, if the isotopic result on the lower part of the Yixian Formation (125 Ma; Swisher III et al., 2002; Wang et al., 2001) is to be accepted. By now, with the report of the "E.-E.-L. fauna" associated with the two salamanders (Gao et al., 1998), the Fengshan fossil bed is most likely referable to the Dadianzi Formation established in Hebei. Jin (1996) suggested that the Dadianzi Formation, as well as the underlying Dabeigou Formation, may be comparable to the lower part of the Yixian Formation in western Liaoning, a view also hold by Wang Xiaolin et al. (2000). It is noted here that the new salamander fossil horizon in Luanping (Urodela indet. 2, see Table 1) of Hebei may be a more significant finding. It was first

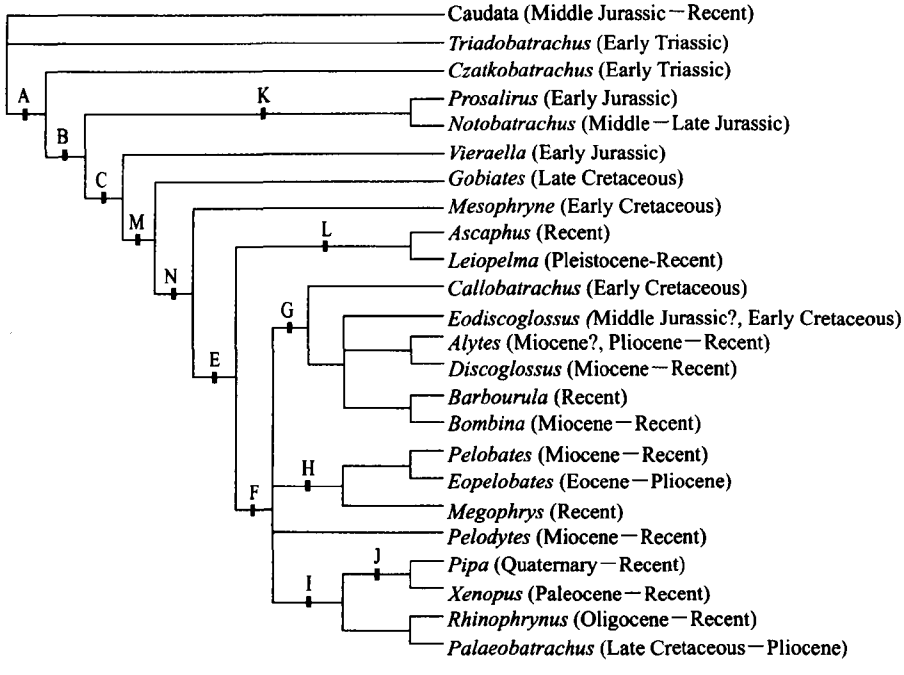

Fig. 2. Cladogram based on a phylogenetic analysis of 24 taxa across 62 characters, showing the phylogenetic relationships of basal anurans.
Temporal range of fossil record is denoted in the parenthesis after each taxon (from Wang, 2002; Fig. 4-1-6).

mentioned by Young Chungchien when he described a footprint from the same locality (Young, 1979). Reportedly, it is from level 2 of the Dabeigou Formation. If the stratigraphic identification is true, it should represent the lowest urodele horizon in the Jehol Group. Urodela indet. 1 (see Table 1) from Weichang, Hebei may also from the Dabeigou Formation as the Luanping salamander. Further studies on these specimens are undergoing.

The three urodeles, *Jeholotriton paradoxus*, *Chunerpeton tianyiensis* and *Liaoxitriton daohugouensis*, recovered from Daohugou Village, Ningcheng County, Chifeng City of Inner Mongolia have also raised great controversies over their horizon correlation and age. Wang (2000) reported the former taxon, and correlated the fossil bed to the lower part of the Yixian Formation based on a stratigraphic study by Wang Xiaolin and his colleagues (Wang Xiaolin et al., 2000). However, "Late Jurassic pre-Jehol Biota" (Zhang, 2002, 2003) and "Middle Jurassic Jiulongshan Formation" (Ren and Oswald, 2002; Ren et al., 2002) were also proposed. Gao and Shubin (2003) adopted the "Middle Jurassic" age when they reported the cryptobranchid *Chunerpeton tianyiensis*, and entitled the finding as "the earliest crown-group salamander" based on this stratigraphic correlation, which expands the previously earliest Paleocene record of the cryptobranchids into the Middle Jurassic. However, it is noted that most advocators of the "Middle Jurassic" age are paleoentomologists, who generally hold an older age of the fossil horizons when studying the Jehol Group. For example, they regard the age of the Yixian Formation as Late Jurassic (Ren et al., 1995, 1997), which is younger than isotopic dating results (125 Ma, middle Early Cretaceous). Nonetheless, the feature of the associate plant flora at the Daohugou locality is indeed relatively primitive (Zhang, 2002), so, it should be of interest to explore this issue from the aspect of urodele evolution.

By osteological characteristics, not only the three Daohugou urodeles, but also all the six known Mesozoic urodeles from China are advanced over *Karaurus sharovi*, a basal caudate from the Late Jurassic Karabastou Formation of Kazakhstan. *Karaurus sharovi* is a medium-sized primitive salamander, differing from all other salamanders by the presence of a distinct quadratojugal, and its occiput does not project beyond the skull roof (Ivachnenko, 1978; Estes, 1981; Milner, 2000). The primitive features of this taxon have made it the most basal member of the salamander group, and the taxon is regarded as a non-urodele, distinguishing from other crown-group salamanders (Milner, 1988; Trueb and Cloutier, 1991; Trueb, 1993). The Chinese Mesozoic urodeles all have unicapitate ribs, and lack the quadratojugal bone and the heavy sculptures on the skull roof. The bearing of bicapitate ribs, retaining of the quadratojugal bone and having heavy cranial sculptures that resemble its temmospondyl ancestors have made *Karaurus* a more primitive form than the Daohugou and other Mesozoic urodeles of China. Thus, the geological age of the Daohugou fossil bed and other Mesozoic urodeles horizons of China is more likely to be of post-Jurassic. This argument is further supported by a recent stratigraphic study, which regarded the Daohugou fossil bed comparable to the Dabeigou Formation in northern Hebei (Chang et al., 2003).

The earliest known fossil salamanders were discovered from the Middle Jurassic (Bathonian) of England (*Marmorerpeton*; Evans et al., 1988) and Kirgizstan (*Kokartus*; Nessov, 1988). They were represented by isolated vertebrae, skull and limb bones. *Marmorerpeton* is more primitive than any other known salamanders by the lack of intravertebral spinal nerve foramina in the atlantal centrum (Evans et al., 1988). *Kokartus* is similar to *Karaurus* by having heavily sculptured skull roof (Nessov, 1988). These Middle Jurassic caudates bears little resemblance to the Chinese taxa. They should represent earlier diversifications in the caudate evolution. Further examination shows that, all the six known Chinese Mesozoic salamanders are characterized by the presence of unicapitate ribs, a feature only seen in cryptobranchoids of all salamanders, suggesting a possible close relationship with the group. In a recent phylogenetic analysis, *Laccotriton* and *Sinerpeton* were put with cryptobranchoids and more advanced salamanders in an unresolved tetrachotomy (Fig. 4 of Gao and Shubin, 2001), but crown-ward to *Karaurus* from the Late Jurassic. In combination of the osteological and phylogenetical studies, the Chinese Mesozoic salamanders should occupy a post-Late Jurassic stage in the urodele evolution, and the implied age of these salamander fossil horizons should be Early Cretaceous, with the Daohugou fossil bed the lowest by now.

Two of the six Chinese Mesozoic urodeles (i.e. *Jeholotriton paradoxus* and *Chunerpeton tianyiensis*) have exhibited neotenic features. This not only represents the earliest geological age among such findings in fossil salamanders, but also implies that neoteny is a common phenomenon and an important mechanism in the early evolution of salamanders (actually, of all modern amphibians from their temnospondyl ancestors; Zybněk Roček, pers. comm.). This is in accordance to some other studies on the paedomorphy of amphibians (Estes, 1981; Sanz et al., 1988; Roček and Rage, 2000).

4 Conclusions

Three anurans and six urodeles have been described from the late Mesozoic tuff-interbedded lacustrine deposits in northeastern China. They are correlated to the following three horizons: (1) the Daohugou fossil bed (for *Jeholotriton Chunerpeton, Liaoxitriton*); (2) the Jianshangou Bed of the lower part of the Yixian Formation

(for *Callobatrachus, Liaobatrachus* and *Mesophryne*), and the Dadianzi Formation (for *Laccotriton* and *Sinerpeton*) of Hebei, which may be comparable to the lower part of the Yixian Formation; and (3) the Jiufotang Formation (for *Liaoxitriton*). Undescribed anuran materials are found from the Lujiatun Bed of the basal Yixian Formation, the Dawangzhangzi Bed of the middle Yixian Formation, and the Jiufotang Formation. New urodeles specimens are referred to the Daohugou fossil bed in Lingyuan, the Dabeigou Formation and the Dadianzi Formation in Hebei. Inferred from osteological studies and phylogenetic analysis on the evolutional grades of the early anurans and urodeles, the geological age of these amphibian-bearing horizons is Early Cretaceous.

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Plate I

1. *Callobatrachus sanyanensis* Wang et Gao, 1999 (Hototype)
2. *Liaobatrachus grabaui* Ji et Ji, 1998 (Hototype)
3. *Mesophryne beipiaoensis* Gao et Wang, 2001 (Hototype, Slab A)
4. *Jeholotriton paradoxus* Wang, 2000 (Hototype, Slab A)
5. *Liaoxitriton daohugouensis* Wang, 2004 (Hototype)