Taxonomic diversity, stratigraphic range, and exceptional preservation of Juro-Cretaceous salamanders from northern China1

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Taxonomic diversity, stratigraphic range, and exceptional preservation of Juro-Cretaceous salamanders from northern China[1]

Ke-Qin Gao, Jianye Chen, and Jia Jia

Abstract: Since the late 1990s, eight localities in volcanic shale-rich lacustrine deposits of Middle Jurassic through Early Cretaceous age in northern China (western Liaoning Province, northern Hebei Province, and southern Inner Mongolia) have yielded thousands of exceptionally well-preserved salamander specimens. With 10 species published and several new taxa yet to be named and described, the fossil samples from northern China represent the most species-diverse, individually abundant, and exquisitely preserved salamander fossil assemblage known from the Mesozoic Era. The stratigraphic range of the fossil record covers a geologic time span of roughly 40–45 million years from the Middle Jurassic (Bathonian) through the Early Cretaceous (Aptian). In contrast to the well-known stem-group salamanders *Karaurus* and *Kokartus* from the Middle to Late Jurassic of Middle Asia, the Chinese record contains the earliest known crown-group salamanders, including Jurassic representatives of both Cryptobranchoidea and Salamandroidea. The Chinese Mesozoic record includes numerous examples of virtually complete larval, juvenile, young adult, and fully grown adult individuals that collectively provide key information on the life histories and developmental patterns of the earliest known crown-group salamanders. Many specimens show preservation of soft tissue structures, including body outline, eye, liver, and external gill filaments. This kind of soft tissue preservation is unusual for fossil salamanders, so the Chinese Mesozoic specimens are important for furnishing otherwise unavailable information on the life history, diversity, and ecological adaptations of early crown-group salamanders.

Résumé : Depuis la fin des années 1990, huit localités dans des dépôts lacustres riches en shale volcanique d'âge jurassique moyen à crétacé précoce du nord de la Chine (province de Liaoning occidentale, province de Hebei septentrionale et sud de la Mongolie intérieure) ont produit des milliers de spécimens de salamandres exceptionnellement bien préservés. Les échantillons de fossiles du nord de la Chine, qui comprennent notamment 10 espèces publiées et plusieurs nouveaux taxons n'ayant pas encore été nommés ni décrits, constituent l'assemblage de salamandres mésozoïques présentant la plus grande diversité spécifique, la plus forte abondance individuelle et la meilleure préservation. La répartition stratigraphique de ces fossiles couvre une période géologique d'environ 40 à 45 millions d'années, du Jurassique moyen (Bathonien) au Crétacé précoce (Aptien). Comparativement à *Karaurus* et *Kokartus,* des groupes-souches bien connus de salamandres du Jurassique moyen à tardif de l'Asie centrale, l'assemblage chinois renferme le groupe-couronne connu de salamandres le plus ancien, dont des représentants jurassiques des Cryptobranchoïdés et des Salamandroïdés. L'assemblage mésozoïque chinois comprend de nombreux spécimens essentiellement complets d'individus larvaires et juvéniles, de jeunes adultes et d'adultes matures qui, collectivement, fournissent des renseignements clés sur les cycles vitaux et les patrons de développement des salamandres du plus ancien groupe-couronne connu. Dans de nombreux spécimens, des structures de tissus mous sont préservées, dont le contour du corps, les yeux, le foie et les lamelles branchiales externes. Une telle préservation de tissus mous, inhabituelle dans les fossiles de salamandres, souligne également l'importance de cet assemblage pour ce qui est de fournir des données par ailleurs non disponibles sur le cycle vital, la diversité et les adaptations écologiques des salamandres d'un groupe-couronne précoce.

[Traduit par la Rédaction]

Introduction

The Urodela, commonly known as newts and salamanders, form one of the three major groups of modern amphibians (Lissamphibia), along with Anura (frogs) and Gymnophiona (caecilians) (Duellman and Trueb 1986; Trueb and Cloutier 1991; Cannatella and Hillis 1993; Hay et al. 1995; Feller and Hedges 1998; Frost et al. 2006). Compared with the more highly specialized frogs and caecilians, salamanders show extreme morphological conservatism in having a generalized

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skull pattern, in retaining normal proportions of the body and (usually) two pairs of equal-sized limbs, and in possessing a post-anal tail. Because of their generalized body form, salamanders have been employed as a model group for studies in different fields of biological sciences, including systematics, ecology, and developmental biology. For example, the diversity of salamander limb structures has been established as a model system for the analysis of the role of development in evolution (Alberch and Gale 1985; Hanken 1985; Shubin et al. 1995; Shubin and Wake 2003). In addition, salamander phylogeny and biogeography have been used as examples of patterns of geographic distribution in relation to biological diversification (Milner 1983, 1988).

Extant salamanders include more than 618 species (AmphibiaWeb 2012) classified in 10 families (Duellman and Trueb 1986; Frost et al. 2006; Frost 2011). Prior to major fossil discoveries from China, all but two extant salamander families had their fossil records confined to the Cenozoic (Estes 1981). The two exceptions were the Amphiumidae and Sirenidae, which have records extending back into, respectively, the latest Maastrichtian and the Campanian (Estes 1981; Gardner 2003); both families are geographically confined in North America. Some other Mesozoic salamanders from North America and Europe cannot be assigned to any of the known salamander families. Among these, *Iridotriton*, based on a partial skeleton from the Upper Jurassic Morrison Formation (Evans et al. 2005), was originally interpreted as a salamandroid but recently has been recognized as a possible cryptobranchoid (Gao and Shubin 2012). In Europe, *Marmorerpeton* is based on fragmentary material from the Middle Jurassic Forest Marble Formation at Kirtlington, England, and is regarded as a stem-group salamander (Evans et al. 1988); several other unnamed salamanders also are known from Kirtlington and from Skye, Scotland (Evans and Milner 1994, 1996; Milner 2000; Evans et al. 2005). Another European genus, *Valdotriton*, is based on articulated material from the Lower Cretaceous La Huérguina Formation in Spain; it originally was classified in Neocaudata (Evans and Milner 1996) but recently was assigned to the suborder Salamandroidea (Gao and Shubin 2012). In addition, several problematic taxa were reported in the literature as possible sirenids from Gondwana, but those identifications have been refuted or disputed in later studies. Among these, an unnamed taxon based on fragmentary dentary material from the Lower Jurassic of India was originally referred to the Sirenidae (Yadagiri 1986) but has been shown to be nondiagnostic for either a sirenid or a urodele (Milner 1993; Evans et al. 1996). *Kababisha,* based on fragmentary jaws and vertebrae from the Cenomanian of Sudan (Evans et al. 1996), and *Noterpeton*, based on vertebral material from the Maastrichtian of Bolivia (Rage et al. 1993), were referred to or transferred to the Sirenidae (Evans et al. 1996), but assignment of these genera to the Sirenidae has been disputed (Gardner 2003).

The paucity of well-preserved Mesozoic fossils has hampered studies of the early evolutionary history of salamanders. Fortunately, major fossil discoveries since the late 1990s in northern China have substantially improved our knowledge of Mesozoic salamanders and have provided many informative specimens for documenting and interpreting the early diversity and evolution of this long-lived amphibian group. These new samples consist of exceptionally preserved, articulated salamander fossils collected through extensive field expeditions to lacustrine deposits of Middle Jurassic – Early Cretaceous age that are exposed in northern Hebei Province, western Liaoning Province, and southern Inner Mongolia (Fig. 1). At many of the localities, salamander specimens are preserved in dense concentrations, numbering in the hundreds (e.g., Fengshan) or even thousands (e.g., Guancaishan) of specimens. Based on these fossils, 10 species in nine genera have been named and described in publications (summarized in Table 1), and a few more new taxa have yet to be named and described. The fossils from China represent the most species-diverse, individually abundant, and exquisitely preserved salamander fossil assemblage known from the Mesozoic Era. Taxonomic diversity of the fossil forms reflects a significant early radiation of Juro-Cretaceous salamanders in northern China, and the exceptional preservation of many specimens, which often are embedded in volcanic shale deposits, provides rare opportunities to study anatomical details of these early salamanders as they related to their life histories and ecological adaptations. This paper reviews the Mesozoic salamander record from northern China, particularly the taxonomic diversity and stratigraphic range of known taxa, and the exceptional preservation of the fossils from western Liaoning Province and the nearby areas.

Institutional abbreviations

IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; PKUP, Peking University Paleontological Collection, Beijing, China.

Material and methods

Since the late 1990s, several thousand salamander fossils have been collected from Juro-Cretaceous beds in northern China. The fossil material is from 10 localities distributed among three different stratigraphic horizons of Middle Jurassic, Late Jurassic, and Early Cretaceous age (Figs. 1, 2). Salamander fossils from these localities and horizons are catalogued in collections of several institutions, including the IVPP and PKUP; the latter collection includes some 2000 specimens. Most specimens are fully articulated, although some show a minor amount of distortion, with some bony elements being slightly dislocated from their original position. The material consists of specimens that preserve skeletal structures and, in many cases, soft anatomical details, as well as a size range of larval, juvenile, subadult, and adult individuals that are informative for documenting ontogenetic changes, life histories, and ecology. Specimens were hand quarried by splitting shales and then were manually prepared under a microscope to expose anatomical details for comparative and phylogenetic studies. Geological ages of the fossils were estimated using stratigraphic correlations and radiometric dates of the fossil beds, as presented in previous studies. Specimens shown in this paper were photographed with a digital camera under tungsten light or under a microscope equipped with a digital camera.

Stratigraphic range of the Mesozoic salamander record in northern China

The stratigraphic range of Juro-Cretaceous salamander occurrences in northern China extends from 165 to 122 Ma or

Fig. 1. Map showing major localities for Chinese Mesozoic salamander fossils in western Liaoning Province, northern Hebei Province, and southern Inner Mongolia. Jurassic localities are denoted with black diamonds, and Cretaceous localities are denoted with solid triangles. See also Table 1.

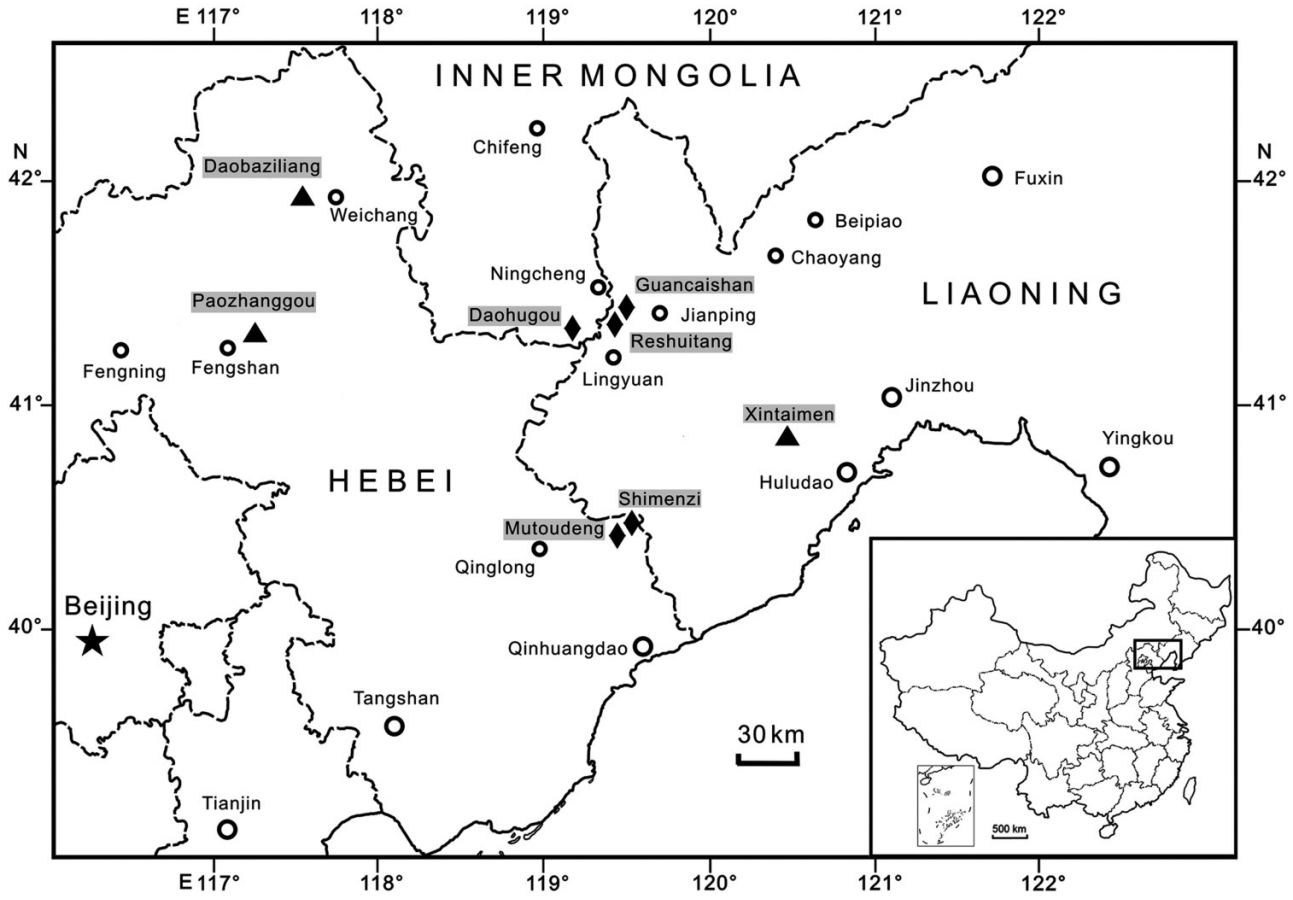


Table 1. Taxonomic diversity of Middle Jurassic to Early Cretaceous crown-clade salamanders from northern China.

Taxa and publication date	Fossil horizon and region	Locality and age
Suborder Cryptobranchoidea Dunn, 1922		
Chunerpeton tianyiensis Gao and Shubin, 2003	Haifanggou Fm., Inner Mongolia	Daohugou, M. Jurassic
Chunerpeton sp.	Tiaojishan Fm., Liaoning Prov.	Reshuitang, M. Jurassic
Jeholotriton paradoxus Wang, 2000	Haifanggou Fm., Inner Mongolia	Daohugou, M. Jurassic
Liaoxitriton daohugouensis Wang, 2004	Haifanggou Fm., Inner Mongolia	Daohugou, M. Jurassic
Pangerpeton sinensis Wang and Evans, 2006	Tiaojishan Fm., Liaoning Prov.	Reshuitang, M. Jurassic
"*Voldotriton*" *sinensis* Zhang and Fan, 2001	Haifanggou Fm., Inner Mongolia	Daohugou, M. Jurassic
Laccotriton orientalis Gao et al., 1998	Dabeigou Fm., Hebei Prov.	Paozhanggou, E. Cretaceous
Sinerpeton fengshanensis Gao and Shubin, 2001	Dabeigou Fm., Hebei Prov.	Paozhanggou, E. Cretaceous
Liaoxitriton zhongjiani Dong and Wang, 1998	Yixian Fm., Liaoning Prov.	Xintaimen, E. Cretaceous
Regalerpeton weichangensis Zhang et al., 2009	Huajiying Fm., Hebei Prov.	Daobaziliang, E. Cretaceous
Suborder Salamandroidea Noble, 1931		
Beiyanerpeton jianpingensis Gao and Shubin, 2012	Tiaojishan Fm., Liaoning Prov.	Guancaishan, L. Jurassic
Genus and species unnamed A	Tiaojishan Fm., Liaoning Prov.	Guancaishan, L. Jurassic
Genus and species unnamed B	Tiaojishan Fm., Liaoning Prov.	Guancaishan, L. Jurassic
Genus and species unnamed C	Tiaojishan Fm., Liaoning Prov.	Guancaishan, L. Jurassic

Note: E., Early; Fm., Formation; L., Late; M., Middle; Prov., Province.

Bathonian to Aptian (Liu et al. 2006; Gradstein et al. 2005; Chang et al. 2009*a*, 2009*b*; Fig. 2). The geologically oldest known record is from the Middle Jurassic Haifanggou (Jiulongshan) Formation, exposed at the Daohugou locality (see later in the text) near Ningcheng, in southern Inner Mongolia, and the youngest record is from the Lower Cretaceous Yixian Formation, exposed at the Xintaimen locality near Huludao, in western Liaoning Province (Figs. 1, 2).

Fig. 2. Composite sections showing stratigraphic occurrences and regional correlations of some Chinese Mesozoic salamander fossil localities in western Liaoning Province, northern Hebei Province, and southern Inner Mongolia. Stratigraphic data and isotopic dates compiled from various sources: Jurassic formations from Chang et al. (2009*b*), Liu et al. (2006), and Wang et al. (2004) and Cretaceous formations from Bi and Yang (1992), Chang et al. (2003), Chang et al. (2009*a*), He et al. (2006), Ke and Guo (1997), and Niu and Tian (2008). Form., Formation; Ma, million years.

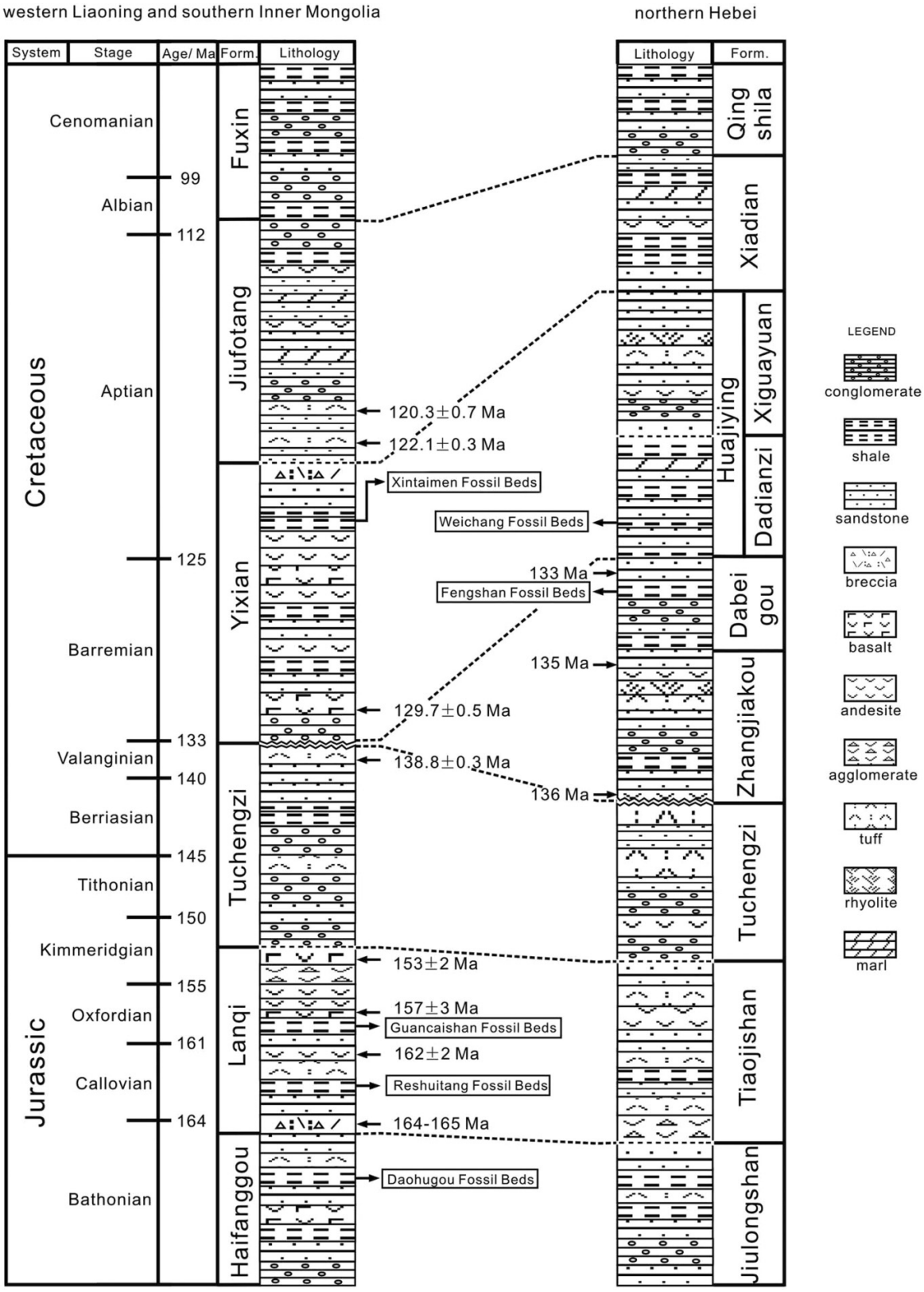
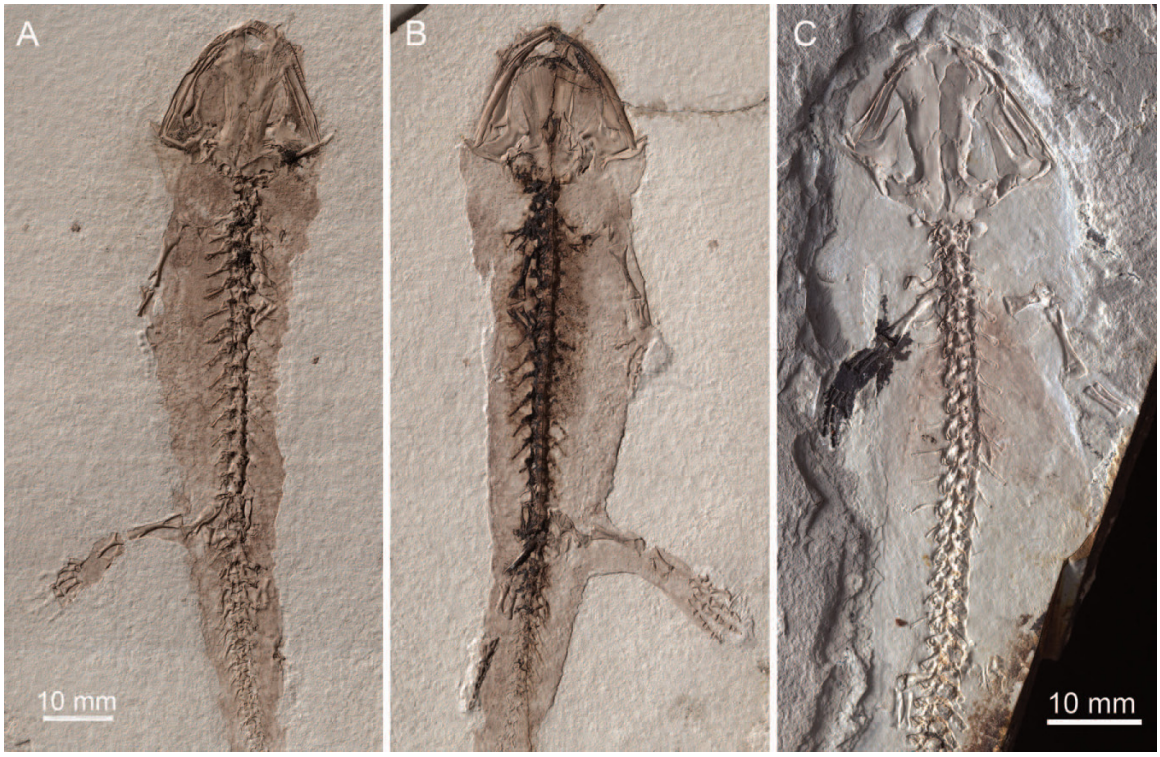


Fig. 3. Middle Jurassic salamander fossils from Daohugou (Haifanggou Formation), southern Inner Mongolia: A, B, part and counterpart of a referred skeleton of *Chunerpeton tianyiensis* (PKUP V0211); C, referred skeleton of *Jeholotriton paradoxus* (PKUP V0213) exposed in dorsal view. Note that the fully dissolved skeletons, which are typical preservation at this locality, left only a high-fidelity natural mould in the fine-grained volcanic shale slabs; positive photographic images of the moulds were created by using low-angled light photography.



Middle Jurassic salamanders

The fossil beds exposed at the Daohugou locality (N41°18′50″/E119°13′45″), in southern Inner Mongolia, consist of pale grey tuffaceous shales and mudstones interbedded with tuffs (Liu et al. 2004, 2006; Gao and Ren 2006). The Daohugou fossil beds originally were interpreted as part of the Lower Cretaceous Yixian Formation (Wang et al. 2000; Wang and Rose 2005) but have been re-interpreted as belonging to the Middle Jurassic Haifanggou (Jiulongshan) Formation, the age of which is supported by a radiometric date of 164–165 Ma from rock samples collected from a horizon about 20 m above the fossil-bearing shales (Chen et al. 2004; Liu et al. 2006; Gao and Ren 2006; Yang and Li 2008). Because the rock samples were collected from the bottom horizon of the overlying Tiaojishan (Lanqi) Formation (Zhang Lijun personal communication 2012; Fig. 2), the actual age of the Daohugou beds in the underlying Haifanggou Formation is estimated here as Bathonian, based on the geological time scale of Gradstein et al. (2005).

Along with other vertebrate, abundant invertebrate, and plant fossils, the Daohugou locality has yielded exceptionally well-preserved fossils of several salamander taxa. Among these, the neotenic salamander *Chunerpeton* (Figs. 3A, 3B) is reported as the earliest known record so far for the Cryptobranchidae (Gao and Shubin 2003). *Jeholotriton* (Fig. 3C) is another neotenic salamander but of uncertain affinities at the familial level (Wang and Rose 2005). A third taxon from the Daohugou locality, *Liaoxitriton daohugouensis* (Wang 2004), is known by two specimens, both catalogued in the IVPP collections. It was reported as a small metamorphosed salamander congeneric with *L. zhongjiani* (see later in the text) from the Lower Cretaceous Yixian Formation of Xintaimen, western Liaoning Province (Wang 2004), but we suggest that more diagnostically informative specimens are needed to verify the taxonomic identity of *L. daohugouensis*.

A fourth problematic taxon, "*Voldotriton* [sic] *sinensis*", was named and described based on a single specimen from the Daohugou beds (Zhang and Fan 2001). Although the specimen is well preserved, many anatomical structures were misidentified in the original publication, and the species was referred to the European genus *Valdotriton* without justification. "*Voldotriton* [sic] *sinensis*" is here treated as a *nomen dubium*, pending a thorough redescription and evaluation of its taxonomic affinities.

Constrained by a radiometric date of 164–165 Ma (Chen et al. 2004; Liu et al. 2006; Yang and Li 2008) from the overlying beds in the Tiaojishan (Lanqi) Formation, the salamanders from the Daohugou beds in the Haifanggou Formation are the earliest known crown-group or true salamanders. Depending on the actual ages of *Kokartus* and *Karaurus* from, respectively, Kyrgyzstan and Kazakhstan (Ivachnenko 1978; Nesov 1988; Nesov et al. 1996; Averianov et al. 2008; Skutschas and Martin 2011), the crown-group salamanders from the Daohugou beds (Bathonian) may well be the same age or even slightly older than the stem-group salamanders from Middle Asia. In Europe, salamander remains of Bathonian age are known from Kirtlington, England, and Skye, Scotland; most of that material consists of isolated, incomplete

Fig. 4. Middle Jurassic salamander fossil (*Pangerpeton sinensis*) from Reshuitang (Tiaojishan Formation), western Liaoning Province: part and counterpart of referred skeleton (PKUP V0218). Note that all skeletal elements have been dissolved as a taphonomic artifact.

cranial and postcranial elements that have been regarded as belonging to stem-group rather than crown-group salamanders (Evans et al. 1988; Evans and Milner 1994). Also from the Kirtlington beds, a single form (salamander B) is mentioned in the literature as a possible crown-group salamander, but it has yet to be named and described (Milner 2000). In North America, a crown-group salamander, *Iridotriton*, has been named and described based on articulated material from the Upper Jurassic Morrison Formation (Evans et al. 2005). The Morrison Formation has been dated as 148–150 Ma (Kowallis et al. 1998), an age slightly younger than the Daohugou beds.

Salamander fossils of slightly younger age than those from the Daohugou beds have been found at the nearby Reshuitang (meaning "hot spring") locality, approximately 15 km northeast of Daohugou and approximately 13 km north of the city of Lingyuan, in western Liaoning Province. This locality has been reported in the literature as "Reshuitang" by some authors (Zhang and Wang 2004; Liu et al. 2006) and as "Wubaiding" by others (Wang and Evans 2006; the correct spelling is Wubaidingyingzi). Here we advocate "Reshuitang" as the proper name for the locality, because north of the village of Wubaidingyingzi there are exposures of the Lower Cretaceous Yixian Formation; thus, using the names "Wubaiding locality" or "Wubaiding beds" for the Middle Jurassic salamander-bearing beds could lead to confusion with the Lower Cretaceous beds outside that village. Fossil beds in the lower part of the Tiaojishan (Lanqi) Formation exposed at the Reshuitang locality (N41°22′03″/E119°23′27″) consist of pale grey volcanic shales and have been dated at 164 Ma using the sensitive high-resolution ion microprobe (SHRIMP) zircon U–Pb method (Liu et al. 2006). Salamander fossils from this locality are preserved as natural moulds of skeletons with soft-tissue impressions, which is the same mode of preservation as at the nearby Daohugou locality (Fig. 3). Most of the specimens from the Reshuitang beds are *Chunerpeton*-like forms, but *Pangerpeton* (Fig. 4) is a small salamander that

Fig. 5. Late Jurassic salamander fossils (*Beiyanerpeton jianpingensis*) from Guancaishan (Tiaojishan Formation), western Liaoning Province: A, holotype skeleton (PKUP V0601); B, referred skeleton (PKUP V0602); both expose the ventral view of the body and palatal view of the skull.

shows quite different skull and body proportions from all other salamanders known from the same horizon (Wang and Evans 2006). The *Chunerpeton*-like specimens are currently under study to scrutinize their taxonomic status and phylogenetic relationships with other salamanders (Gao et al. in preparation).

Late Jurassic salamanders

Salamanders of Late Jurassic age have recently been found at the Guancaishan locality (N41°24′32″/E119°27′13″), approximately 6.5 km northeast of the Reshuitang locality and 14 km west of the county town of Jianping, western Liaoning Province (Fig. 1). The fossil beds exposed at this locality consist of dark grey, tuffaceous shales belonging to the upper part of the Tiaojishan (Lanqi) Formation. Trachyandesite rock samples from approximately 35 m above the fossil beds have yielded a SHRIMP zircon U–Pb date of 157 ± 3 Ma (Liu et al. 2006), which corresponds to the Oxfordian stage (Gradstein et al. 2005). Salamander fossils from the Guancaishan locality include the recently named and described *Beiyanerpeton* (Fig. 5). *Beiyanerpeton* is the geologically oldest record of the Salamandroidea (Gao and Shubin 2012) and, thus, is important for estimating the timing of the split between the Salamandroidea and Cryptobranchoidea, which was a major cladogenetic event in salamander evolution. Besides *Beiyanerpeton*, there are other salamander fossils from the Guancaishan locality that pertain to new but as yet unnamed taxa; these specimens are currently under study (Gao and Shubin in preparation).

The newly discovered localities of Shimenzi (N40°31′52″/E119°29′11″) and Mutoudeng (N40°28′35″/E119°23′54″) in Qinglong County, easternmost Hebei Province (Fig. 1), have yielded hundreds of salamander fossils. Like at Guancaishan, specimens from Shimenzi and Mutoudeng are preserved as fossilized skeletons, with soft anatomical structures rarely preserved. The age of the fossil beds exposed at the two localities is still uncertain, although a Late Jurassic age is

Fig. 6. Early Cretaceous salamander fossils (*Liaoxitriton zhongjiani*) from Xintaimen (Yixian Formation), northern Hebei Province: *left*, nearly complete referred skull exposed in dorsal view (PKUP V0300); *right*, incomplete referred skull of a subadult exposed in dorsal view (PKUP V0301).

suggested based on preliminary stratigraphic correlation with the Tiaojishan (Lanqi) Formation. The fossils are currently under study, and at least two different taxa are recognizable (Gao et al. in preparation).

Early Cretaceous salamanders

In northern Hebei Province, salamander fossils have been reported from the Fengshan and Weichang areas (Fig. 1). From the Paozhanggou locality (N41°14′40″/E117°16′29″) approximately 7 km northeast of Fengshan, two fossil taxa have been named and described: *Laccotriton orientalis* and *Sinerpeton fengshanensis* (Gao et al. 1998; Gao and Shubin 2001). The fossil horizon at this locality was first reported as part of the Xiguayuan Formation (Gao et al. 1998) but subsequently was regarded as part of the Dabeigou Formation (Pang et al. 2006). The age of the fossil horizon previously was regarded as Late Jurassic based on geological data then available (Gao et al. 1998; Gao and Shubin 2001; Pang et al. 2006), but an isotopic date of 133 Ma subsequently obtained from a different section within the same formation (Yang and Li 2008; Chang et al. 2009*a*) indicates an Early Cretaceous (Valanginian–Hauterivian) age. This revised age estimate places the Fengshan horizon stratigraphically below the Yixian Formation (see later in the text), which has a geologic range of 122–129 Ma (Chang et al. 2009*a*).

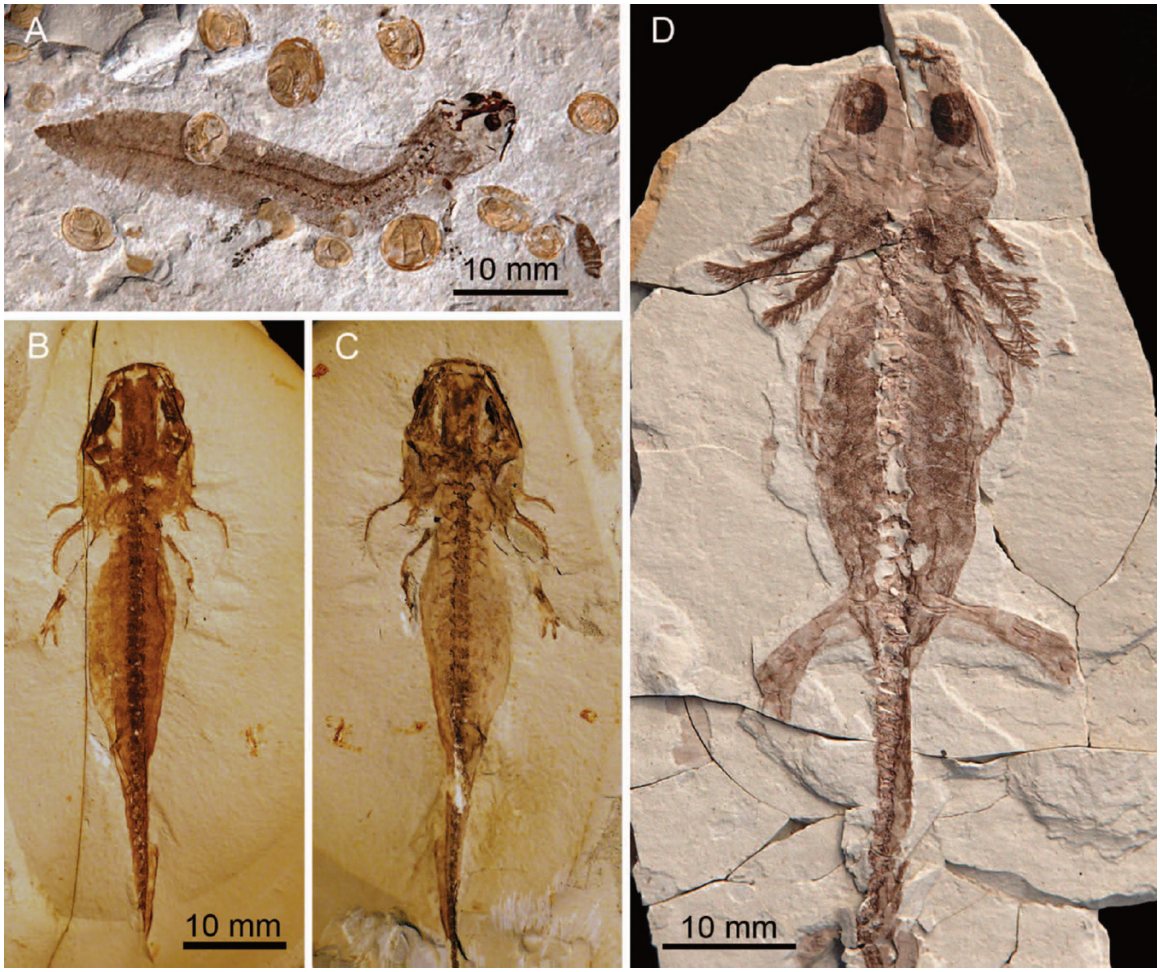
Regalerpeton was named and described based on a single specimen from Daobaziliang (N41°58′23″/E117°33′25″), near Weichang in northern Hebei Province (Zhang et al. 2009). The fossil beds at Daobaziliang were reported to be part of the Huajiying Formation and were correlated with the Yixian Formation farther to the east in Liaoning Province (Zhang et al. 2009). However, the Huajiying Formation has been dated as 133 Ma (Li 1988), which is older than the dates of 122–129 Ma (Chang et al. 2009*a*) for the Yixian Formation; thus, the fossil beds at Daobaziliang are probably older than the Yixian Formation and may well be stratigraphically equivalent to the Dabeigou Formation (Fig. 2).

The geologically youngest record of Mesozoic salamanders in China comes from the Xintaimen locality (N40°50′17″/E120°25′56″) near Huludao, in western Liaoning Province (Fig. 1). The salamander fossil-bearing beds at this locality consist of organic-rich, dark shales that are lithologically different from the tuffaceous shales at other localities and horizons, and thus, indicate a normal lacustrine environment not directly in association with volcanic activities. The Xintaimen fossil beds were first reported as part of the Upper Cretaceous Jiufotang Formation (Dong and Wang 1998), then later reinterpreted as part of the Yixian Formation (Zhang et al. 2004). Although no isotopic date is available for the fossil beds, the age of the Xintaimen beds can be estimated as 122–125 Ma based on stratigraphic correlation with the Yixian Formation (Zhang et al. 2004; Zhang Lijun personal communication 2012). Most of the fossils from this locality and horizon are preserved as articulated skeletons and can be referred to a single genus and species, namely *Liaoxitriton zhongjiani* (Dong and Wang 1998; Fig. 6). *Liaoxitriton* is a metamorphosed salamander that may represent the earliest known record of the cryptobranchoid family Hynobiidae (Chen and Gao 2009).

Taxonomic diversity and life histories of Mesozoic salamanders from China

Since 1998, 10 species in nine genera have been named and described based on salamander fossils from northern China. Several other new taxa have been recognized but have yet to be named and described (Table 1). The named taxa include early representatives of both the Cryptobranchoidea and Salamandroidea, two major suborders within the order Urodela, or crown-group salamanders (Duellman and Trueb 1986). Among these early fossil salamanders, *Chunerpeton* has been assigned to the family Cryptobranchidae (Gao and Shubin 2003), *Liaoxitriton zhongjiani* may represent a basal member of the family Hynobiidae (Chen and Gao 2009), and the other taxa remain as "family *incertae sedis*". Nonetheless, with the exception of *Beiyanerpeton*, most of the described taxa share the presence of unicapitate ribs with extant cryptobranchoids and, thus, can be classified in the suborder Cryptobranchoidea. The recently named taxon *Beiyanerpeton jianpingensis* is based on fossil specimens from the Guancaishan locality, and it has been recognized as a basal member of the suborder

Fig. 7. Exceptional preservation of Middle Jurassic salamander larvae from northern China and examples of the two types of larval morphs that can be recognized. A, Pond-type larva, Urodela indet. (PKUP V0214), from Daohugou (Haifanggou Formation), southern Inner Mongolia; B, C, part and counterpart of a stream-type larva, Urodela indet. (PKUP V0220), from Reshuitang (Tiaojishan Formation), western Liaoning Province; D, a half-grown subadult, Urodela indet. (PKUP V0221), from Reshuitang (Tiaojishan Formation), western Liaoning Province.



Salamandroidea (Gao and Shubin 2012). The latter group differs from cryptobranchoids in having nasals separated by an anterodorsal fenestra without a midline contact; the presence of a parietal–prefrontal contact medially above the orbit; angular and articular bones in the mandible fused to the prearticular; and double-headed ribs associated with dorsal vertebrae (Gao and Shubin 2012).

Many salamander fossils from different localities show different ontogenetic stages, ranging from very small larval to fully grown adult individuals (Fig. 7). As is the case with extant salamanders, fossil larval specimens are characterized by a combination of their small body size, incomplete ossification of cranial and postcranial skeletons, and a configuration of the skull that differs from that of adults. Many larval specimens preserve clear impressions of external gills and caudal fins, providing evidence of the aquatic environments they inhabited. For extant salamanders, two types of larvae can be distinguished from one another based on the size of their external gills and the shape of their caudal fin (Valentine and Dennis 1964). Pond-type larvae, which live in relatively quiet and less well-oxygenated water, tend to have large external gills and a high caudal fin, whereas stream-type larvae, which live in flowing and more highly oxygenated water, tend to have short external gills and a low caudal fin (Duellman and Trueb 1986). Both pond-type and stream-type larvae can be recognized among the Chinese fossil samples (Fig. 7). For example, pond-type larval specimens are found at Daohugou (Fig. 7A) and stream-type larval specimens are found at Reshuitang (Figs. 7B, 7C). Occurrences of different larval types at the Daohugou and Reshuitang localities indicate that different aquatic conditions prevailed at those two localities during the Middle Jurassic.

Adult specimens, in contrast to larval forms, are large (at least within the same species) and show extensive ossification of the dermal skull roof, hyobranchial apparatus, and limb bones. Adult salamanders known from the Mesozoic of northern China document two different types of life-history strategies or developmental patterns: neotenic adults are characterized by the retention of larval features at sexual maturity (Gould 1977), whereas metamorphosed adults are

characterized by loss of larval features, remodelling of the skull roof and palate (Rose 2003), and extensive ossification of the mesopodium. Examples of mature, neotenic salamanders are found at three localities — Daohugou, Reshuitang, and Guancaishan — all of which are Jurassic in age. From the Daohugou beds (Inner Mongolia), large specimens of neotenic *Chunerpeton* have been reported to reach total lengths of 500 mm (Dong et al. 2012). Many large specimens of that genus in the PKUP collections show clear impressions of external gills but lack ossified mesopodial elements in the limbs (Figs. 3A, 3B). Besides *Chunerpeton*, other neotenic salamanders known from the Mesozoic of China include *Jeholotriton* and *Beiyanerpeton*. As reported in a recent paper by Gao and Shubin (2012), because of the mode of preservation at the Guancaishan locality, none of the *Beiyanerpeton* specimens show impressions of external gills, but they do preserve mineralized branchial denticles (or gill rakers) indicating the retention of that larval feature in the adult stage. Several specimens with a snout–pelvic length of 100 mm also show a well-ossified septomaxilla. Considering that ossification of the septomaxilla is delayed until close to the onset of sexual maturity in extant salamanders and their possible fossil relatives (e.g., Schoch 2002; Rose 2003), the presence of that bone in the *Beiyanerpeton* specimens indicates that they likely were fully mature at death.

In contrast to the neotenic salamanders, metamorphosed salamanders undergo a dramatic morphological change from the larval to adult stage, including loss of gill structures and ossification of mesopodial elements. Most of the metamorphosed Mesozoic salamanders (*Liaoxitriton*, *Laccotriton*, *Sinerpeton,* and *Regalerpeton*) are known from Lower Cretaceous localities (Fengshan, Xintaimen, and Weichang), although two taxa (*Pangerpeton* and *Liaoxitriton*) are also known from Middle Jurassic beds. Among these, *Sinerpeton* was originally interpreted as a neotenic form based on the presence of ossified ceratobranchials in the holotype (Gao and Shubin 2001). However, it is now known that ossification of the ceratobranchials can occur in both neotenic and metamorphosed extant salamanders (Rose 2003), which means the presence of ossified ceratobranchials cannot be used as an indication of external gills. The presence of well-ossified mesopodial elements instead suggests that *Sinerpeton* is likely a metamorphosed salamander. Both *Regalerpeton* and *Pangerpeton* lack evidence of gill structures, and the holotype of the former taxon clearly shows ossification of the mesopodium (Zhang et al. 2009). *Pangerpeton* is likely a small, metamorphosed salamander as originally described (Wang and Evans 2006), although lack of mesopodial ossification in the holotype and only known specimen suggests that it was a newly postmetamorphosed individual that died before its limbs had fully ossified. Compared with adult neotenics, adults of metamorphosed salamanders tend to be smaller, with snout–pelvic lengths no more than 100 mm (see Gao and Shubin 2001; Wang and Rose 2005). Metamorphosed salamanders at the adult stage also are characterized by remodelling of skull elements, especially the palatal bones (Rose 2003), and many of these features can be directly observed in the fossil specimens from China. The fossil record of both metamorphosis and neoteny in these early crown-group salamanders has great significance in studying the evolutionary developmental biology of salamanders. Also, neotenic and metamorphosed salamanders generally inhabit quite different environments. With little or no modification of the external gills, neotenic salamanders are fully aquatic and permanent water dwellers during all stages of their life (Duellman and Trueb 1986). On the other hand, metamorphosed forms, having relatively strong limbs with ossified mesopodia for supporting their body weight and the ability to feed and breathe out of water, are fully capable of living in a terrestrial environment, providing there is ample free moisture, such as in areas near water bodies. Both aquatic and terrestrial adaptations in salamanders are documented in the Mesozoic record from China.

Exceptional preservation of salamander fossils

The salamander fossils from the Juro-Cretaceous beds of northern China are characterized by exceptional preservation of anatomical details. Resulting from different taphonomic settings, two types of fossil preservation can be clearly distinguished. In the first type (here called Type A mode of preservation; Figs. 3, 4, 7), all bony structures have been entirely dissolved away in the course of fossilization, leaving only a natural mould of the skeleton. This complete dissolution of bony tissues may occur when the buried skeletons come into extended contact with ground water containing highly toxic sulfuric acid sourced from volcanic ash (Yang and Li 2008). When split into part and counterpart slabs, one slab shows the dorsal and the other the ventral impressions of the skull, trunk vertebrae, and limb bones. The tail typically is rotated or twisted relative to the rest of the body, which means that the part and counterpart slabs preserve impressions of either side of the tail.

This type of preservation occurs in specimens from the Middle Jurassic deposits exposed at the Daohugou (Haifanggou Formation) and the nearby Reshuitang (Tiaojishan Formation) localities. Interestingly, a similar type of preservation is also seen once from the Early Cretaceous, namely in the only known specimen of *Regalerpeton* from Weichang, in the Huajiying Formation in northern Hebei Province (Fig. 1). Fossil beds at these Jurassic and Cretaceous localities are all pale grey tuffaceous shales, formed by fine-grained sediments derived from pyroclastic eruptions. Although the bony skeletons are fully dissolved, anatomical details of soft-tissue structures are superbly preserved in the specimens from the Daohugou and Reshuitang localities (Figs. 7A, 7D). Among neotenic forms such as *Chunerpeton* and *Jeholotriton*, clear impressions of branchial denticles or gill rakers (mineralized internal gill structure) and external gill filaments are preserved both in small larvae and large individuals; the latter are identified as fully grown adults based on their well-ossified dermal skull roof, hyobranchial apparatus, and limb bones (Rose 2003). As in extant salamanders, individual denticles of the gill rakers are arranged alternatively in a linear fashion and are lined up as three pairs of parallel rows on each side. Also like in extant salamanders, external gill filaments are three in number on each side of the gill region. No neotenic forms from these localities show ossification of carpal and tarsal elements, which is another clear indication of their obligate aquatic lifestyle.

A second type of preservation (here called Type B mode of preservation) is characterized by having the bony skeletons preserved but with impressions of soft-tissue structures only variably preserved (Figs. 5, 6). Depending on the nature of the rock matrix, fossilized bone can be as dark coloured as the surrounding rock matrix, or the bones may be whitish and con-

trast sharply with the rock matrix. Type B preservation is known for specimens from the Guancaishan locality near Jianping (Liaoning Province), the Paozhanggou locality near Fengshan (Hebei Province), and the Xintaimen locality near Huludao (Liaoning Province). The ages of the fossil beds at these localities vary from Late Jurassic to Early Cretaceous (see earlier in the text).

Regardless of whether they exhibit Type A or Type B mode of preservation, salamander fossils from the Juro-Cretaceous beds in northern China are often found in great densities, and specimens are fully articulated, with no sign of scavenging or transportation. Disarticulated body parts are rare, and incomplete specimens are, in most cases, the result of pieces being lost when slabs were split in the field. Almost all the specimens are dorso-ventrally compressed, although it is uncertain in most cases whether they were preserved lying dorsal side up or down, because that information typically is not recorded when specimens are collected. Although Type A preservation occurs only in volcanic ash deposits (Daohugou, Reshuitang, and Weichang), Type B preservation occurs in both volcanic ash (Guancaishan and Paozhanggou) and normal lake or pond deposits (Xintaimen). In these Mesozoic deposits in northern China, the lack of a nearby source for sulfuric acid appears to be a critical factor for allowing superb preservation of bony skeletons.

Preservation of soft-anatomical details is rare in the fossil record of salamanders, which makes the fossil material from China truly exceptional in this regard. Body outlines, gill rakers and external gill filaments, caudal fins, eyes and other organs such as the liver, and even intestinal contents can be preserved as either clear impressions or mineralized structures in fossil specimens from several localities and horizons. This material provides the most extensive record of soft anatomical features for Mesozoic salamander fossils from anywhere in the world. Soft anatomical features are extremely informative for interpretations of salamander life histories and ecological adaptations to particular habitats. For example, as discussed earlier, the pond-type larvae from Daohugou indicate a calm-water environment within a Middle Jurassic (Bathonian) pond, whereas the stream-type larvae from Reshuitang provide evidence for mountain streams during Callovian time. Discoveries of exceptionally well-preserved salamander fossils from China provide otherwise impossible opportunities to study the life histories and ecological features of the earliest known crown-group salamanders.

Conclusions

In contrast to previously known fossil records of Mesozoic salamanders, which typically consist of sparse and often disarticulated material, recent discoveries of a rich record of Juro-Cretaceous salamander fossils from multiple localities and horizons in northern China provide key material for documenting and interpreting the early evolution of crown-group salamander clades. The study of this material has led us to the following conclusions:

1. The Mesozoic salamanders from northern China document a significant early radiation of crown-group salamanders. The rich fossil record includes 10 species in nine genera that have been named and described, and a few more taxa yet to be published.
2. The fossil record from China covers a geologic range from the Middle Jurassic (approximately 165 Ma) to the Early Cretaceous (approximately 120 Ma), documenting an evolutionary history of approximately 40–45 million years, within a relatively small region, for several clades of crown-group salamanders.
3. The rich fossil record includes both larval and adult forms and offers significant information on growth series, reveals a diversity of life-history features, and includes both neotenic and metamorphosed forms.
4. Depending on the taphonomic settings, virtually complete fossil specimens often display exceptional preservation of soft-tissue structures, including body outlines, gill rakers, impressions of eyes, external gill filaments, internal organs such as the liver, and contents of the digestive tract.
5. Fossil specimens from the Juro-Cretaceous beds in northern China are individually abundant (numbering in the hundreds to thousands of specimens at some localities), taxonomically diverse, and exceptionally well preserved. Thus, these collections provide an unmatched opportunity to conduct multidimensional research on the phylogeny, life-history features, and paleoecology of early salamanders.

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