A new short-bodied salamander from the Upper Jurassic/Lower Cretaceous of China

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Abundant well-preserved salamander fossils have recently been recovered from localities across northeastern China. *Pangerpeton sinensis* gen. et sp. nov. is represented by a nearly complete skeletal impression of a postmetamorphosed salamander from the Late Jurassic/Early Cretaceous locality of Wubaiding, Liaoning Province. It is characterised by a short wide skull and only 14 presacral vertebrae. Associated soft tissue impressions suggest a warty skin and a broad body outline. Phylogenetic analysis indicates a basal position within Caudata, either just within or just outside crown-group Urodela.

Introduction

The Late Jurassic to Early Cretaceous deposits of northeastern China (Liaoning, Hebei, Inner Mongolia), have yielded a diverse fossil assemblage, including many exquisitely preserved salamanders. To date five genera and six species have been described: *Laccotriton subsolanus* Gao, Cheng, and Xu, 1998; *Liaoxitriton zhongjiani* Dong and Wang, 1998; *L. daohugouensis* Wang, 2004a; *Jeholotriton paradoxus* Wang, 2000; *Sinerpeton fengshanensis* Gao and Shubin, 2001; and *Chunerpeton tianyiensis* Gao and Shubin, 2003. In conjunction with specimens from Central Asia, Europe and North America (e.g., Ivakhnenko 1978; Evans et al. 1988, 2005; Nessov 1988; Evans and Milner 1996), these important Chinese fossils are shedding new light on a poorly known period of salamander evolution.

A new locality at Wubaiding, Lingyuan, Liaoning Province has recently yielded further salamander specimens (Wang 2004b). Most belong to the cryptobranchid *Chunerpeton* Gao and Shubin, 2003, but one specimen is strikingly different in body proportions from all other Mesozoic salamander taxa. This new genus forms the basis of the current paper. Biostratigraphic and lithologic evidence suggests that Wubaiding is contemporaneous with the Daohugou locality of Inner Mongolia (Wang 2004b; Wang et al. 2005). However, there have been three different opinions on the age of the Daohugou beds: Middle Jurassic Jiulongshan Formation (Ren et al. 2002), Late Jurassic Daohugou Formation (Zhang 2002), and Early Cretaceous Jehol Group (Wang et al. 2005). Invertebrate researchers generally favour the first option, especially those that maintain a Late Jurassic age for the Yixian Formation (e.g., Ren et al. 1997) despite Early Cretaceous isotopic dates (ca. 125 Ma; Swisher et al. 1999). The tetrapods from Daohugou (salamanders, pterosaurs, dinosaurs; Wang et al. 2005) are closer to those of the Jehol Biota, although some key taxa (e.g., *Ephemeropsis*, *Lycoptera*) are missing. Reference simply to the "Daohugou fossil bed" seems preferable until the debate is settled. The age is probably Late Jurassic, but could be basal Cretaceous.

Lissamphibia Haeckel, 1866

Caudata Scopoli, 1777 (usage *sensu* Milner 1988)

Family indet.

Genus *Pangerpeton* nov.

Type species: *Pangerpeton sinensis* sp. nov.

Derivation of name: From the Chinese, Pang, meaning fat, an allusion to the short, broad body, and the Greek, *herpeton*, a crawling thing.

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

Pangerpeton sinensis gen. et sp. nov.

Derivation of name: from the Latin, *Sine*, meaning Chinese.

Holotype: IVPP V14244, a nearly complete skeletal impression (Fig. 1), collections of the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, Beijing.

Type locality: Wubaiding Village, Lingyuan City, Liaoning Province, China.

Type horizon: Probably contemporaneous with the salamander-bearing horizon at Daohugou, Inner Mongolia, Late Jurassic/Early Cretaceous (Wang 2004a, b).

Diagnosis.—A postmetamorphosed salamander with a short wide head and only 14 presacral vertebrae; longitudinal arrangement of vomerine teeth with at least two rows centrally; anterolateral pterygoid process short and tapering; short rib-bearers with single-headed ribs. Differs from *Chunerpeton* and *Jeholotriton* in lacking teeth on the palatopterygoid, and having longitudinal vomerine tooth rows rather than a row parallel to the marginal dentition (*Chunerpeton*) or a tooth patch (*Jeholotriton*); further differs from *Jeholotriton* in having the anterior process of the pterygoid directed anterolaterally rather than anteromedially, and the presence of ossified hyoid elements (unossified in *Jeholotriton*); differs from *Liaoxitriton, Laccotriton* and *Sinerpeton* in the longitudinal rather than transverse arrangement of the vomerine teeth and in lacking ossified carpals and tarsals; differs from all other known Mesozoic salamander genera in the significantly shorter head and presacral series, and the presence of two ossified ceratobranchials (Estes 1981; Milner 2000).

Description.—IVPP V14244 preserves a ventral impression of the skeleton with associated skin traces showing the body outline. The specimen is almost complete, missing only the left hind foot and part of the tail (Fig. 1A). The head is proportionally short and wide (Fig. 1B, C, Table 1), with the lower jaws together forming a semicircle. The snout-pelvis length (midline of premaxillae to the rear of the ischiadic plate) is 39.4 mm. The individual is postmetamorphic as the bone surfaces are finished and there are no traces of external gills. The description that follows is based on a high-fidelity cast taken from the impression.

Each premaxilla has a slender tooth-bearing alveolar portion and a short alary process with a distinct lateral curvature. Judging from the

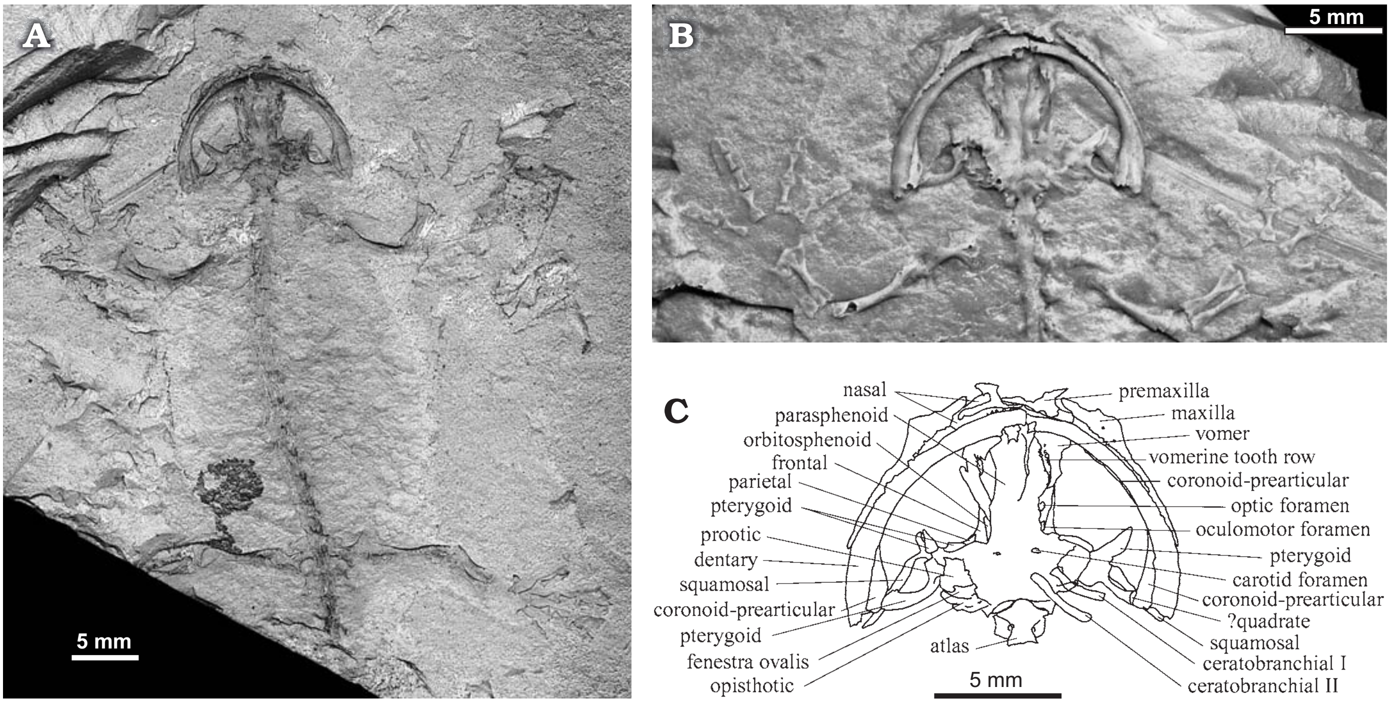

Fig. 1. *Pangerpeton sinensis* gen. et sp. nov. **A**. Holotype specimen (IVPP V14244) from Wubaiding Village, Lingyuan City, Liaoning Province, China, probably contemporaneous with the salamander-bearing horizon at Daohugou, Inner Mongolia, Late Jurassic/Early Cretaceous, showing ventral impression of a nearly complete skeleton. **B**. High-fidelity cast of holotype showing skull, forelimbs and pectoral girdle. **C**. Line drawing of skull and atlas, taken from cast.

length and breadth of the alary processes, they probably overlapped the nasal anteriorly, although the articulation is not preserved. Each maxilla is long (*c*. three-quarters of lower jaw length) with a long, low facial portion, small teeth, and a slender premaxillary process. The palate is dominated by a broad, parallel-sided parasphenoid that expands posteriorly into short wings, each of which is perforated by an internal carotid foramen. In the anterior margin, just behind the jaw symphysis, is a depressed area that may be a membrane-filled fenestra, whereas on either side of the parasphenoid are anteroposteriorly elongated vomers. These are divided into two portions, most clearly seen on the right side. The anterior part is toothless, with an incurved medial expansion. Further back are at least two rows of teeth, although this is difficult to image as the vomer is tilted inwards. The more lateral row is continued some distance along the posterior bar of the vomer. The triradiate pterygoid has a long, curved posterolateral process, a shorter tapering anterolateral process, and a smaller anteromedial process. The anterolateral process is well separated from the end of the maxilla. Between the tip of the left posterolateral process and the coronoid-prearticular flange of the lower jaw, there is a rounded mass that may be an ossified or partially ossified quadrate. This would place the jaw articulation roughly on a line with the atlanto-occipital joint. Some of the dorsal skull bones are visible above the vomers and parasphenoid – notably frontals forming the orbital margins, orbitosphenoids between the frontals and parasphenoid, and short parietals above the expanded parasphenoid wings. On the left, anterior and posterior foramina perforate the orbitosphenoid, probably the optic and oculomotor foramina respectively (Fig. 1C). The squamosals lie above and parallel to the posterolateral processes of the pterygoids. The right bone is more exposed and reveals a short anterior ramus and a long slender ventral ramus. Elements of the braincase are clearest on the right and do not appear co-ossified. The prootic meets the anterior part of the parasphenoid wing, separated from the opisthotic by a cleft that represents the fenestra ovalis. The exoccipital condyles are widely separated, with their articular surfaces directed posteromedially.

The lower jaw is composed mainly of the elongated dentary. This bears tiny conical teeth (6–7 per mm), but it is not clear whether or not they are pedicellate. The long coronoid-prearticular has a smooth continuous dorsomedial edge, in contrast to the bilobed condition in *Chunerpeton* and *Liaoxitriton*. On each side, the flange is perforated by a small foramen, but unlike *Jeholotriton*, it bears no teeth. On the

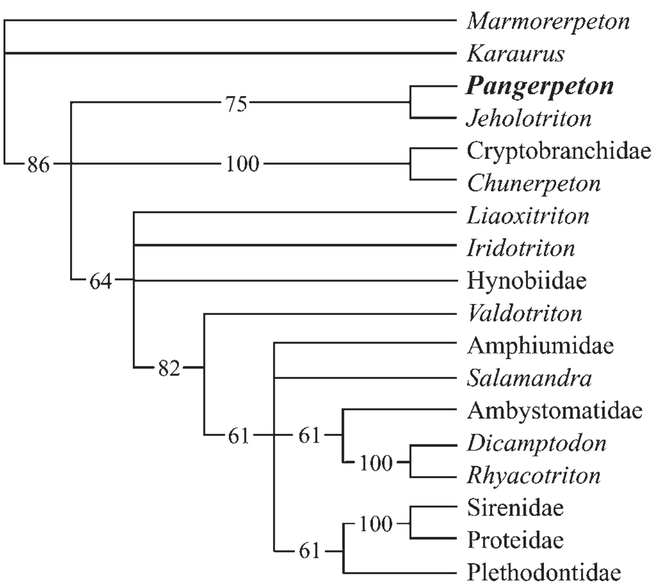

Fig. 2. Fifty percent Majority Rule Consensus of 28 most parsimonious trees resulting from a phylogenetic analysis using PAUP* (see character description in http://spaces.msn.com/members/ywangivpp, and matrix of taxon and character states in Table 2).

Table 1. Comparative measurements (in mm) of *Pangerpeton* and three other Chinese Mesozoic salamanders. L, length; W, width; proportion A, skull width/one vertebra length; proportion B, skull length/one vertebra length. Specimens of IVPP collection.

	Pangerpeton	*Jeholotriton*		*Chunerpeton*		*Liaoxitriton*	
	V14424	V12623 adult	V11943A juvenile	V13343B adult	V13374 juvenile	V13393 adult	V14062 juvenile
Skull W	13.35	23.50	16.25	29.30	14.30	20.60	17.25
Skull L	7.85	18.05	12.85	21.55	15.20	17.55	15.15
Skull W / L	1.69	1.30	1.27	1.35	0.93	1.18	1.14
Average vertebra L	2.03	3.05	2.33	3.18	2.05	3.45	3.28
Proportion A	6.59	7.7	6.99	9.23	6.98	5.97	5.28
Proportion B	3.88	5.9	5.53	6.79	7.5	5.08	4.63

Table 2. Matrix of taxon and character states used in the phylogenetic analysis of caudates in Fig. 2; multistate characters shown as ( ) are variable within the relevant taxon, whereas { } denotes possible alternative states. A = (01); B = {01}; C =(02) D = (12); E = {12}; F ={23}; G = (012) [see text and character description for further explanation].

Liaoxitriton	010?0?1?0? ??11??0000 ?1???????E 000E0????0 1????????? ?????11110 001??0???? ??
Jeholotriton	011?0?1?20 0??1???130 ?1?00????1 0000000??? ?????????? ??????1110 000??2???? ??
Chunerpeton	010?0?1010 0?01???030 ?1???????1 1201000??? ?????????? ?????11111 000??1???? ??
Valdotriton	010?0?1201 0?111??000 ?0210????2 0000011??? ?????????? ?????B1110 0010?0???? ??
Iridotriton	0000???101 0?01???000 ?1E10????2 00??011??? ???1?????? ??????1?1? 10?0?0???? ??
Pangerpeton	010?B?1000 ??11??0000 ?1???????? ?0?00????? ?????????? ??????1?1? 100??2???? ??
Sirenidae	04D1111031 1210101120 ?023010111 1122100?1? ????111110 00000?110- 2?22020000 00
Hynobiidae	010000A001 00A1010000 ?120000002 01010?1?0? ????0000A0 10001?1110 ??10AC0000 00
Cryptobranchidae	0101011011 00011A0000 ?120000011 1211000?0? ????000000 10001?1111 2110110000 00
Ambystomatidae	020011120A 0011A01000 ?02301100D 02010A1?0? ????221001 11110?1110 ??1BA01111 11
Salamandra	0301111201 0011001001 1023111012 0100011201 1111220A00 1101021110 B010020111 01
Dicamptodon	0200001000 0010001000 1022011002 0102001?0? ????221001 11010?1110 2011000111 ?1
Plethodontidae	A2CAD11241 A2111010A1 ?A23A11002 00A0A11?1? ????221110 01010?111A G?2B1C0111 11
Rhyacotriton	0200201000 0011001000 ?02201100? 000011?0? ????221111 01010?1111 ???0000111 11
Karaurus	010?000?00 0?01???000 00200????0 00000000?? ?????????? ??????1110 0100?0???? ??
Amphiumidae	1201111030 0011101000 ?02101011? 0001000?1? ????220000 01000?1110 2120120011 01
Marmorerpeton	010??????? ???????000 0A000????0 ?0???????? ?????????? ????????1? ?0?0?0???? ??
Proteidae	0221211130 12101010F0 ?020010112 0222111?1? ????22A110 11010?111- 2?2B010111 11

left, the coronoid-prearticular flange is separated for a short distance from a thin sliver of bone that is exposed along the anteromedial aspect of the dentary. This sliver may be an anterior extension of the coronoid-prearticular, but this is uncertain.

Overlying the parasphenoid on the anatomical left side are two short ossified rods interpreted as the first and second hyoid ceratobranchials. These are not clearly discernable on the right.

There are 14 amphicoelous presacrals, one sacral, and up to five anterior caudals. The atlas is roughly the same length as succeeding vertebrae. It is hourglass shaped ventrally but appears to expand dorsally into flared lateral wings that are perforated in the narrowest region by pits or foramina. The anterior border forms a smooth curve, the apex of which is the interglenoid prominence. The remaining vertebrae are featureless, with no evidence of either a ventral keel or basapophyses. The rib bearers are short and support single-headed ribs with proximal and distal ends of similar width. The strongest ribs, supporting the pectoral girdle, are those of the third and fourth vertebrae, but the following two are longer. The ribs become noticeably shorter towards the sacrum, with the last being little more than a triangular stub. The sacral vertebra is similar in size to the presacrals, but the free ribs are angled backwards to support the pelvis. The first two or three caudal vertebrae are obscured by the ischiadic plate. The next two are visible but it is not possible to determine whether they had either free ribs or haemal arches. The rest of the tail is lost.

Both forelimbs are complete. The scapulocoracoid is a relatively small, flask-shaped bone composed of a rounded coracoid plate and a longer, narrower scapula with a slight proximal expansion. The proximal and distal heads of the humerus are only slightly expanded, with little development of a proximal crista ventrolateralis and no ossified joint surfaces. The radius and ulna are short (humerus, 5.7 mm; ulna, 3.6 mm) and the carpus is unossified. The manus consists of four widely spread digits with a phalangeal formula of 2:3:3:2 on the left and 2:2:3:2 on the right.

Each pelvis consists of a short, dumb-bell shaped ilium that is expanded proximally, and a longer, more massive ischiadic plate that is notched laterally in its midsection. A gap between the anteroventral edge of the ilium and the corresponding ischium suggests the presence in life of a cartilaginous pubic plate. The femur (6.2 mm) is slightly longer than the humerus but is of similar width. The tibia and fibula are short (tibia, 3.6 mm), the tarsals are unossified and the pes has a phalangeal formula of ?:2:3:3:2.

The skeletal impression is surrounded by a soft tissue outline that reveals a broader body shape than the skeleton would suggest, with short, stumpy limbs and wide digits. The lateral edge of the body outline and parts of the surface are slightly irregular and the skin may have been warty.

Discussion.—We compared the body proportions of *Pangerpeton* with those of other well-preserved Chinese Mesozoic salamanders

(Table 1). Skull width/skull length for *Pangerpeton* is 1.7, a higher value than that of other taxa. Thus *Chunerpeton*, *Jeholotriton* and *Liaoxitriton* all have proportionally narrower skulls than the smaller *Pangerpeton*. This cannot be an effect of small size or immaturity because younger representatives of each of the major Chinese taxa have proportionally longer, narrower skulls than full adults. The difference in proportions raises the question as to whether the skull is unusually short or unusually wide, or both. A comparison of skull proportions against a standard (one vertebral length) (Table 1) shows that it is skull length (i.e., proportion B, Table 1) rather than skull width (proportion A, Table 1) that is significantly different in *Pangerpeton*. Thus skull width in *Pangerpeton* is within the range of other taxa, but the skull is significantly shorter. Unfortunately, the material referred to *Sinerpeton* and *Laccotriton* does not permit detailed measurements, but the published figures (Gao and Shubin 2001) suggest the skulls have similar proportions to those of *Liaoxitriton* and thus also differ from *Pangerpeton*.

In order to determine the phylogenetic relationships of *Pangerpeton* with respect to other caudates, we constructed a data matrix (Table 2) of 18 taxa and 72 characters (using mainly the characters listed by Gao and Shubin, 2003, and derived mainly from Duellman and Trueb 1986; Larson and Dimmick 1993; and Trueb 1993; see http://spaces.msn.com/members/ywangivpp for character descriptions). In addition to modern families and Chinese fossil salamanders, we included two basal caudates, *Marmorerpeton* (Middle– Upper Jurassic, Europe, Evans et al. 1988) and *Karaurus* (Upper Jurassic, Central Asia, Ivakhnenko 1978), and two more derived taxa, *Valdotriton* (Lower Cretaceous, Spain, Evans and Milner 1996) and *Iridotriton* (Upper Jurassic, North America, Evans et al. 2005). We ran an analysis using PAUP* Version 4.0b10 for 32-bit Microsoft Windows (Swofford 2001) on a PC computer. All characters were unordered and equally weighted, with DELTRAN tree optimization used to minimize reversals. The basal caudate *Marmorerpeton* was used as the outgroup taxon. A Branch-and-Bound search option resulted in 28 most parsimonious trees (TL = 167, CI = 0.6048, RI = 0.5823). As shown in the 50% Majority Rule Consensus Tree (Fig. 2), *Pangerpeton* emerged as a possible sister taxon of the roughly contemporaneous *Jeholotriton*, and this clade forms an unresolved trichotomy with cryptobranchids on the one hand and all other included crown-group salamanders on the other. *Pangerpeton* is thus close to the base of crown-group Urodela (*sensu* Milner 1988; Evans and Milner 1996) either just outside it or just within. Further resolution requires more information on the skull and ear region. The only caudates lying basal to the trichotomy are the Jurassic *Karaurus* and *Marmorerpeton*.

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References

Dong, Z. and Wang, Y. 1998. A new urodele (*Liaoxitriton zhongjiani* gen. et sp. nov.) from the Early Cretaceous of western Liaoning Province, China. *Vertebrata PalAsiatica* 36: 159–172 [Chinese 159–165; English 166–172].

Duellman, W.E. and Trueb, L. 1986. *Biology of Amphibians.* 670 pp. Johns Hopkins University Press, Baltimore.

Estes, R. 1981. Gymnophiona, Caudata. *In*: P. Wellnhofer (ed.), *Encyclopedia of Paleoherpetology, Part 2*, 1–115. Gustav Fischer Verlag, Stuttgart.

Evans, S.E., Milner, A.R., and Mussett, F. 1988. The earliest known salamanders (Amphibia: Caudata): a record from the Middle Jurassic of England. *Geobios* 21: 539–552.

Evans, S.E. and Milner, A.R. 1996. A metamorphosed salamander from the Early Cretaceous of Las Hoyas, Spain. *Philosophical Transactions of Royal Society of London B* 351: 627–646.

Evans, S.E., Lally, C., Chure, D., Elder, A., and Maisano, J. 2005. A Late Jurassic salamander (Amphibia: Caudata) from the Morrison Formation of North America. *Zoological Journal of the Linnean Society* 143: 599–616.

Gao, K. and Shubin, N. 2001. Late Jurassic salamanders from northern China. *Nature* 410: 574–577.

Gao, K. and Shubin, N. 2003. Earliest known crown-group salamanders. *Nature* 422: 424–428.

Gao, K., Cheng Z., and Xu, X. 1998. First report of a Mesozoic urodele from China [in Chinese]. *Chinese Geology* 250: 40–41.

Haeckel, E. 1866. *Generelle Morphologie der Organismen. I, Allgemeine Anatomie der Organismen*. 574 pp. Georg Reimer, Berlin.

Ivakhnenko, M.F. [Ivahnenko, M.F.] 1978. Caudates from the Triassic and Jurassic of Middle Asia [in Russian]. *Paleontologičeskij žurnal* 3: 84–89.

Larson, A. and Dimmick, W.W. 1993. Phylogenetic relationships of the salamander families: an analysis of congruence among morphological and molecular characters. *Herpetological Monographs* 7: 77–93.

Milner, A.R. 1988. The relationships and origin of living amphibians. *In*: M.J. Benton (ed.), *The Phylogeny and Classification of the Tetrapods. Volume 1, Amphibians, Reptiles, Birds*, 59–102. Clarendon Press, Oxford.

Milner, A.R. 2000. Mesozoic and Tertiary Caudata and Albanerpetontidae. *In*: H. Heatwole and R.L. Carroll (eds.), *Amphibian Biology, Volume 4, Palaeontology: The Evolutionary History of Amphibians,* 1412–1444. Surrey Beatty and Sons, Chipping Norton, Australia.

Nessov, L.A. 1988. Late Mesozoic amphibians and lizards of Soviet Middle Asia. *Acta Zoologica Cracoviensia* 31: 475–486.

Ren, D., Guo, Z., Lu, L., Ji, S., Tang, F., Jin, R., Fang, X., and Ji, Q. 1997. A further contribution to the knowledge of the Upper Jurassic Yixian Formation in western Liaoning. *Geological Review* 43: 449–459.

Ren, D., Gao, K., Guo, Z., Ji, S., Tan, J., and Song, Z. 2002. Stratigraphic division of the Jurassic in the Daohugou area, Ningcheng, Inner Mongolia. *Geological Bulletin of China* 21: 584–591. [Chinese 584–590; English 591].

Scopoli, G.A. 1777. *Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae.* 506 pp. Wolfgang Gerle, Prague.

Swisher, C. C., Wang, Y., Wang, X., Xu, X., and Wang, Y. 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature* 400: 58–61.

Swofford, D.L. 2001. *PAUP* (Version 4.0b10 for 32-bit Microsoft Windows).* Sinauer Associates, Incorporated. Sunderland, Massachusetts.

Trueb, L. 1993. Patterns of cranial diversity among the Lissamphibia. *In*: J. Hanken and B.K. Hall (eds.), *The Skull. Volume 2, Patterns of Structural and Systematic Diversity*, 255–243. The University of Chicago Press, Chicago.

Wang, X., Zhou, Z., He, H., Jin, F., Wang, Y., Zhang, J., Wang, Y., Xu, X., and Zhang, F. 2005. Stratigraphy and age of the Daohugou Bed in Ningcheng, Inner Mongolia. *Chinese Science Bulletin* 50: 2369–2376.

Wang, Y. 2000. A new salamander (Amphibia: Caudata) from the Early Cretaceous Jehol Biota [in Chinese with English abstract]. *Vertebrata PalAsiatica* 38: 100–103.

Wang, Y. 2004a. A new Mesozoic caudate (*Liaoxitriton daohugouensis* sp. nov.) from Inner Mongolia, China. *Chinese Science Bulletin* 49: 858–860.

Wang, Y. 2004b. Taxonomy and stratigraphy of late Mesozoic anurans and urodeles from China. *Acta Geologica Sinica* 78: 1169–1178.

Zhang, J. 2002. Discovery of Daohugou Biota (pre-Jehol Biota) with a discussion on its geological age. *Journal of Stratigraphy* 26: 173–178. [Chinese 173–177; English 177–178].

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