

中国化石两栖类和有鳞类研究 进展:过去15年回顾¹⁾

王 原¹ 苏珊·E·埃文斯²

(1 中国科学院古脊椎动物与古人类研究所 北京 100044)

(2 伦敦大学学院解剖与发育生物学系 伦敦 WC1E 6BT)

摘要:过去15年中,我国的化石两栖类和两栖类研究取得了加速进展。共报道了16种两栖类和22种有鳞类,其中15种两栖类和11种有鳞类为新种,包括我国最古老的四足动物宁夏晚泥盆世的潘氏中国螈,湖北中三叠世的大型全椎两栖类宽头远安鲩,东北晚侏罗世/早白垩世的多种滑体两栖类(如无尾类三燕丽蟾和北票中蟾,有尾类奇异热河螈和东方塘螈),华北古近纪的蜥蜴类(如浙川短齿蜥和垣曲响蜥),以及内蒙古晚白垩世的多种蜥蜴类等。部分旧属种被修订,多与热河生物群的种类有关,如细小矢部龙过去依据幼年个体被认为是一种小型细弱的蜥蜴,新材料显示它实为大型强壮的种类。一批新的两栖类和两栖类重要化石点被发现,如辽宁北票市四合屯、陆家屯和葫芦岛市水口子,河北丰宁县炮仗沟以及内蒙古宁城县道虎沟和乌拉特后旗巴彥满达呼。我国晚侏罗世/早白垩世两栖类和两栖类对研究滑体两栖类和两栖类相关类群的起源和早期演化提供了重要信息,但系统发育研究工作尚处于初级阶段。

关键词:中国,两栖类,蜥蜴类,化石,分类学,系统发育

中图法分类号:Q915.863 文献标识码:A 文章编号:1000-3118(2006)01-0060-14

ADVANCES IN THE STUDY OF FOSSIL AMPHIBIANS AND SQUAMATES FROM CHINA: THE PAST FIFTEEN YEARS

WANG Yuan¹ Susan E. EVANS²

(1 Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing 100044)

(2 Department of Anatomy and Developmental Biology, University College London London WC1E 6BT)

Abstract The past fifteen years have witnessed an acceleration in the study of Chinese fossil amphibians and squamates. Sixteen (15 new) amphibian and twenty-two (11 new) squamate species have been reported across China, including the oldest Chinese tetrapod *Sinostega pani* from the Late Devonian of Ningxia Hui Autonomous Region, the large stereospondyl amphibian *Yuanansuchus laticeps* from the Middle Triassic of Hubei Province, Late Jurassic/Early Cretaceous lissamphibians (e.g., the anurans *Callobatrachus sanyanensis* and *Mesophryne beipiaoensis*), the caudates *Jeholotriton paradoxus* and *Laccotriton subsolanus*) from Northeast China, Paleogene lizards (e.g., *Brevidensilacerta xichuanensis* and *Tinosaurus yuanquensis*) from North China, and numerous lizards from the Late Cretaceous of Nei Mongol

1) 国家自然科学基金项目(编号:40302008, 40121202)、英国皇家学会与国家基金委国际合作项目和中国科学院知识创新工程重要方向项目(编号:KZCX3-SW-142)资助。

收稿日期:2005-10-20

(Inner Mongolia) Autonomous Region. Some previously described taxa have been revised, especially those of the Jehol Biota (e. g., *Yabeinosaurus tenuis*, long considered a small gracile lizard, but shown to be a large robust genus with all previous specimens juvenile). New important paleoherpetological localities have been discovered, such as Sihetun, Lujiatun of Beipiao City and Shuikouzi of Huludao City in Liaoning Province, Paozhanggou of Fengning County in Hebei Province, and Daohugou of Ningcheng County and Bayan Mandahu of Urad Houqi in Nei Mongol Autonomous Region. Late Jurassic/Early Cretaceous amphibians and lizards from China have provided important information on the origin and early evolution of relevant groups, but phylogenetic studies on these taxa are at a preliminary stage.

Key words China, amphibians, lizards, fossil, systematics, phylogeny

1 Introduction

The study of fossil non-mammalian tetrapods, including amphibians, squamates, and several other groups, has been of increasing interest to vertebrate paleontologists in China over the past fifteen years. This is associated with the recovery of exquisite fossils from several important new localities, such as Sihetun in western Liaoning Province, and Daohugou and Bayan Mandahu in Nei Mongol (Inner Mongolia) Autonomous Region (Chang et al., 2003; Gao and Hou, 1996; Gao and Norell, 2000). Sun and others (1992) published a comprehensive review of Chinese fossil amphibians, reptiles and birds, but the information contained therein dated no later than 1991 when the book was in press. From 1991 to now, a large number of amphibian and reptile fossils have been described, and most have resulted in the establishment of new taxa. This paper aims to provide a brief review of work during the past fifteen years, and to serve as a relatively complete reference for future systematic and phylogenetic studies.

2 Systematic paleontology

2.1 New amphibian taxa reported

No new material of fossil amphibians was described from China between 1991 and 1998, but sixteen new species have been named in the past eight years. They were collected from 10 new localities (see a locality map in Fig. 1). These taxa are briefly introduced here in roughly cladistic sequence from the base crownward.

Sinostega pani Zhu et Ahlberg, 2002, represented by an incomplete left mandible from Ningxia Hui Autonomous Region, was the first stem-group tetrapod reported from China. This Late Devonian (Famennian) ichthyostegid most closely resembles the Greenland genus *Acanthostega*, but differs in having a smaller denticulated field on the prearticular.

Li and Cheng (1999) described three new amphibian taxa from the Upper Permian of Gansu Province: *Ingentidens corridoricus* and *Phratochronis qilianensis* of the family Chroniosuchidae (Anthracosauria), and *Anakamacops petrolicus* of the family Dissorophidae (Temnospondyli). These taxa are represented by fragmentary jaw or skull material, and are comparable to Russian species of the same age.

Yuanansuchus lateiceps Liu et Wang, 2005 was recently reported from a Middle Triassic (Anisian) locality in Hubei Province, and is represented by a nearly complete skull. This temnospondyl amphibian was referred to the mastodonsauroids, but differs from all other mastodonsauroids in its truncated skull shape, with a width greater than the length. Phylogenetic analysis places *Yuanansuchus* as the sister-taxon of the *Eocyclotosaurus-Quasicyclotosaurus* clade, a result consistent with traditional biostratigraphical studies.

Jeholotriton paradoxus Wang, 2000 was reported from the Daohugou locality of Nei Mongol, and a detailed description has been provided based on new fossil finds (Wang and Rose, 2005). Recent phylogenetic analysis suggests that this neotenic caudate may lie at the base of crown-group Urodela, either just within it, or just outside (Wang and Evans, in press).

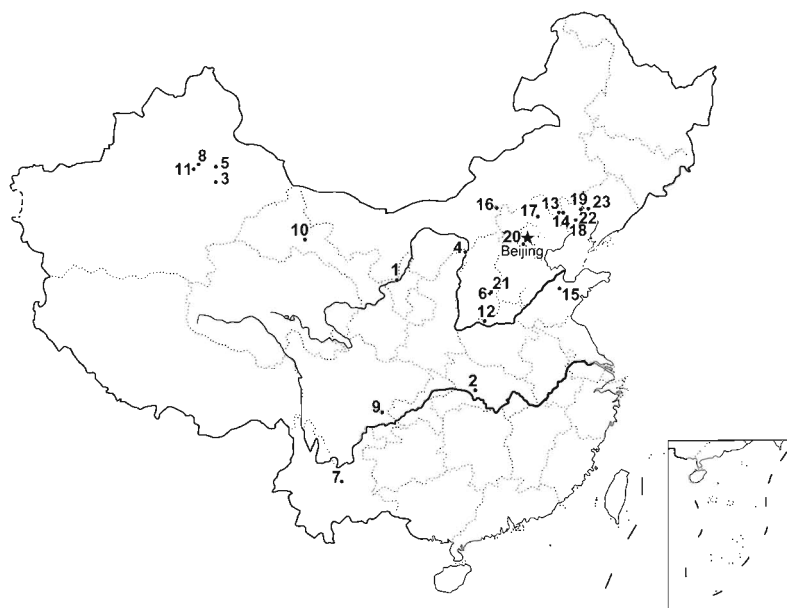


Fig. 1 Locality and geological age of fossil amphibians in China (New localities found after the year 1991 are marked by an asterisk)

*1. Zhongning County, Ningxia Hui Autonomous Region: *Sinostega pani*, Late Devonian; *2. Maopingchang, Yuan'an County, Hubei Province: *Yuanansuchus laticeps*, Middle Triassic; 3. Taoshuyuanzi, Turpan City, Xinjiang Uygur Autonomous Region: *Parotosuchus turfanensis*, Middle Triassic; 4. Fugu County, Shaanxi Province: Mastodonsauroidea indet., Early Triassic; 5. Jimsar County, Xinjiang Uygur Autonomous Region: Mastodonsauroidea indet., Early Triassic; 6. Wuxiang County, Shanxi Province: Mastodonsauroidea indet., Middle Triassic; 7. Heiguopeng, Lufeng County, Yunnan Province: Mastodonsauroidea indet., Early Jurassic; 8. Quanshuigou, Fukang City, Xinjiang Uygur Autonomous Region: *Bogdania fragmenta*, Late Triassic; 9. Dashanpu, Zigong City, Sichuan Province: *Sinobrachyops placenticephalus*, Middle Jurassic; *10. Dashankou, Yumen City, Gansu Province: *Anakamacops petroliticus*, *Ingentidens corridoricus*, *Phratochronis qilianensis*, Late Permian; 11. Liudaowan, Urumqi City, Xinjiang Uygur Autonomous Region: *Urumqia liudaowanensis*, Late Permian; 12. Dayu, Jiyuan City, Henan Province: *Bystrorwiana sinica*, Labyrinthodontia indet., Late Permian; *13. Daohugou, Ningcheng County, Nei Mongol Autonomous Region: *Chunerpeton tianyiensis*, *Jeholotriton paradoxus*, *Liaoxitriton daohugouensis*, Anura indet., Late Jurassic/Early Cretaceous; *14. Wubaiding, Lingyuan City, Liaoning Province: *Chunerpeton tianyiensis*, Caudata gen. et sp. nov., Late Jurassic/Early Cretaceous; 15. Shanwang, Linqu County, Shandong Province: Anura indet., *Bufo linquensis*, *Macropelobates cratus*, *Rana basaltica*, *Procynops miocenicus*, middle Miocene; 16. Ertemte, Huade County, Nei Mongol Autonomous Region: *Rana hipparionum*, ? *Triturus* sp., late Miocene/early Pliocene; *17. Paozhanggou, Fengning County, Hebei Province: *Lacotriton subsolanus*, *Sinerpeton fengshanensis*, Early Cretaceous; *18. Shuikouzi, Huludao City, Liaoning Province: *Liaoxitriton zhongjiani*, Early Cretaceous; *19. Sihetun, Beipiao City, Liaoning Province: *Collobatrachus sanyanensis*, *Liaobatrachus grabaui*, Early Cretaceous; 20. Zhoukoudian (Choukoutien), Fangshan District, Beijing City: *Bufo bufo* cf. *B. b. asiaticus*, *B. raddei*, *Rana asiatica*, *R. nigromaculata*, middle Pleistocene; 21. Zhangcun, Yushe County, Shanxi Province: *Rana yushensis*, early Pliocene; *22. Heitzigou, Beipiao City, Liaoning Province: *Mesophryne beipiaoensis*, Early Cretaceous; *23. Hejiaxin, Yixian County, Liaoning Province: *Yizhoubatrachus macilentus*, Early Cretaceous

Chunerpeton tianyiensis Gao et Shubin, 2003 was the second caudate described from the Daohugou locality of Nei Mongol. Among the six reported Chinese Mesozoic salamanders, *Chunerpeton* is the only taxon that can be classified at familial level. Its referral to the living family Cryptobranchidae also makes it one of the earliest crown-group salamanders in the world.

Liaoxitriton zhongjiani Dong et Wang, 1998 was reported from the Shuikouzi locality in Liaoning Province. This locality has yielded several hundred salamander fossils. The fossil bed was originally documented as the Lower Cretaceous Jiufotang Formation, but it may be representative of the underlying Yixian Formation (c. 125 Ma; Swisher et al., 1999, 2002). This crown-group salamander is similar to modern hynobiids in the morphology of the vomerine tooth row and hyobranchial apparatus.

A second species of *Liaoxitriton*, *L. daohugouensis* Wang, 2004, was established on the basis of two well-preserved skeletal impressions (Wang, 2004a) from the Daohugou locality, Nei Mongol. It differs from *L. zhongjiani* in several aspects, most notably the anterolaterally extended vomerine tooth rows, 16 presacral vertebrae, and an unexpanded Metacarpal II. This is the third caudate taxon from Daohugou, and emphasizes the diversity of the Late Jurassic/Early Cretaceous amphibian fauna in this area.

Laccotriton subsolanus Gao et al., 1998 was the first Mesozoic lissamphibian reported from China. Represented by numerous articulated skeletons, this salamander, together with *Sinerpeton fengshanensis* Gao et Shubin, 2001 from the same quarry in Hebei Province, was undoubtedly a member of the Jehol Biota that flourished in the Early Cretaceous of East Asia. Both are similar to modern hynobiids.

Mesophryne beipiaoensis Gao et Wang, 2001 was established on the basis of an articulated skeleton from the Yixian Formation in Liaoning Province. Osteological characters, e. g., the presence of nine presacrals, three pairs of free ribs, an expanded proximal end of the coracoid, and the retention of an intermedium, suggest that this is a primitive frog, and recent phylogenetic analyses have placed it as a sister taxon to the archaeobatrachian clade (Gao and Wang, 2001; Wang, 2001, 2002).

Gao and Liu (2004) named a new frog, *Dalianbatrachus mengi*, from a locality close to that of *Mesophryne beipiaoensis*. Based on shared osteological characters (e. g., proportionally large skull, squamosal/maxillary contact, greatly shortened vertebral column, nine presacral vertebrae and three pairs of free ribs), it should be a junior synonym of the latter taxon.

Yizhoubatrachus macilentus Gao et Chen, 2004 was described on the basis of a nearly complete but compressed skeleton from the Yixian Formation at Hejiaxin in Yixian County, Liaoning Province. Numerous specimens of the aquatic hyphalosaurs (Reptilia: Choristodera) were recovered from the same site. Some of the diagnostic characters of this Early Cretaceous frog are questionable and are discussed in the revision section below.

Liaobatrachus grabaui Ji et Ji, 1998, represented by an incomplete skeleton from the Yixian Formation in Liaoning Province, was the first Mesozoic frog reported from China. Its referral to the family Pelobatidae in the original paper is based on several questionable characters, such as the presence of procoelous presacrals, the lack of free ribs, and the fusion of the frontoparietals, none of which can be confirmed due to poor preservation. The systematic position of this frog remains to be investigated.

Callobatrachus sanyanensis Wang et Gao, 1999 was erected on the basis of a nearly complete fossil skeleton from the Yixian Formation in Liaoning Province. It documented the first fossil discoglossid from China, and is also by-far the most primitive member of the family Discoglossidae in the world (Wang et al., 2000; Wang, 2001).

2.2 New squamate taxa reported

Twenty-two squamate species have been reported from twelve new localities across China since Sun et al. (1992)'s comprehensive review (see a locality map in Fig. 2). These include newly established taxa as well as known taxa represented by new material that were not included in Sun et al. (1992). They are briefly introduced here in the order of stratigraphic age and fossil locality, rather than systematic position, in order to keep members of the same faunal assemblage together.

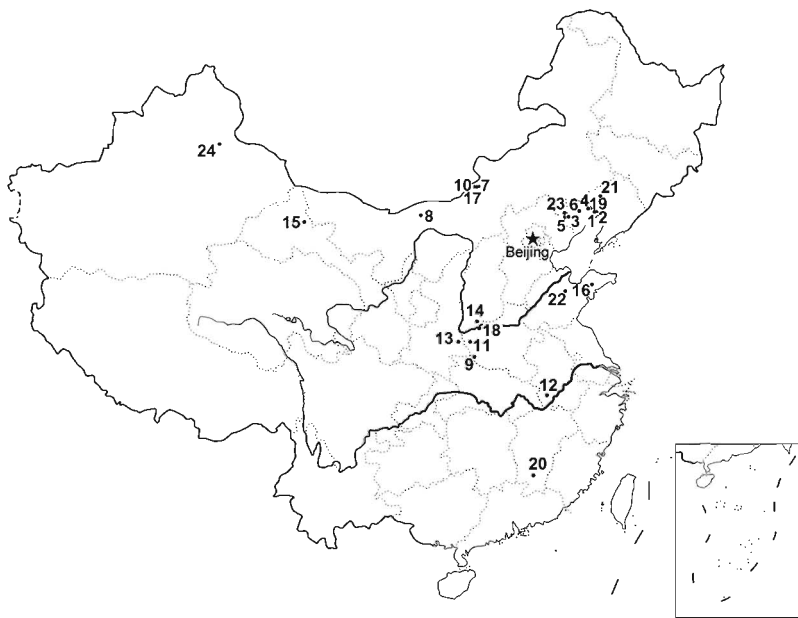


Fig. 2 Locality and geological age of fossil squamates in China (New localities found after the year 1991 are marked by an asterisk)

1. Zaocishan (Tsaotzushan), Yixian County, Liaoning Province: *Yabeinosaurus tenuis*, Early Cretaceous; *2. Jingangshan, Yixian County, Liaoning Province: *Yabeinosaurus tenuis*, Early Cretaceous; 3. Gezidong (Ketzutung), Lingyuan City, Liaoning Province: '*Yabeinosaurus*' *youngi*, ? Middle Jurassic; *4. Sihetun, Beipiao City, Liaoning Province: *Dalinghosaurus longidigitus*, *Yabeinosaurus tenuis*, Early Cretaceous; *5. Dawangzhangzi, Lingyuan City, Liaoning Province: *Dalinghosaurus longidigitus*, *Yabeinosaurus tenuis*, Early Cretaceous; *6. Dapingfang, Chaoyang City, Liaoning Province: *Yabeinosaurus tenuis*, Early Cretaceous; 7. Twin Oboes, Erlianhot City, Nei Mongol Autonomous Region: *Arretosaurus ornatus*, late Eocene; *8. Bayan Mandahu, Urad Houqi, Nei Mongol Autonomous Region: *Adamisaurus magnidentatus*, *Anchaurosaurus gilmorei*, *Bainguis* sp. (cf. *B. parvus*), *Carusia intermedia*, *Conicodontosaurus djadochtaensis*, *Gobiderma pulchrum*, *Isodontosaurus gracilis*, *Mimeosaurus crassus*, *Pleurodontagama aenigmatodes*, *Priscagama gobiensis*, *Sineoamphisbaena hexatabularis*, *Xihaina aquilonia*, Agamidae genus and species indeterminate, Necrosauridae genus and species undetermined, ? Varanidae genus and species undetermined A and B, Genus and species undetermined A, B and C, Late Cretaceous; *9. Xichuan County, Henan Province: *Brevidensilacerta xichuanensis*, *Creberidentat henanensis*, *Tinosaurus* cf. *T. lushihensis*, middle Eocene; 10. North Mesa, Erlianhot City, Nei Mongol Autonomous Region: *Tinosaurus asiaticus*, middle Eocene; 11. Lushi County, Henan Province: *Tinosaurus lushihensis*, middle Eocene; 12. Qianshan County, Anhui Province: ? *Agama sinensis*, *Anhuisaurus huainanensis*, *Anqingosaurus brevicephalus*, *Changjiangosaurus huananensis*, *Qianshanosaurus huangpuensis*, *Tinosaurus doumuensis*, late Paleocene; *13. Luonan County, Shaanxi Province: *Conicodontosaurus qinlingensis*, *Tinosaurus luonanensis*, ? mid-late of early Pleistocene; *14. Yuanqu County, Shanxi Province: *Hemishinisaurus latifrons*, *Tinosaurus yuanquensis*, ? Scincomorpha gen. et sp. indet., late Eocene; 15. Subei County, Gansu Province: *Mimobecklesisaurus gansuensis*, Early Cretaceous; *16. Laiyang City, Shandong Province: *Pachygenys thlastesa*, Early Cretaceous; 17. Baron Sog, Erlianhot City, Nei Mongol Autonomous Region: *Placosaurus mongoliensis*, middle Eocene; 18. Mianchi County, Henan Province: *Placosaurus mongoliensis*, *P.* cf. *P. nodosus*, middle Eocene; *19. Lujiatun, Beipiao City, Liaoning Province: *Dalinghosaurus longidigitus*, Early Cretaceous; 20. Ganxian (Kanhshien) County, Jiangxi Province: *Conicodontosaurus kanhsienensis*, Late Jurassic/Early Cretaceous; 21. Fuxin City, Liaoning Province: *Teihardosaurus carbonarius*, Early Cretaceous; 22. Shanwang, Linq County, Shandong Province: *Mionatrix ditomus*, middle Miocene; *23. Daohugou, Ningcheng County, Nei Mongol Autonomous Region: Squamata gen. et sp. indet., Late Jurassic/Early Cretaceous; *24. Wucaiwan, Changji City, Xinjiang Uygur Autonomous Region: Squamata gen. et sp. nov., Middle/Late Jurassic

The holotype of *Dalinghosaurus longidigitus* Ji, 1998 is a partial post-cranial skeleton, preserving only the hind legs and tail, from the Yixian Formation at the famous Sihetun fossil site in Liaoning Province. Recently, a new locality at Lujiatun (Liaoning) has yielded a few hundred specimens of this species, with good three-dimensional preservation, and it would seem that many individuals were buried together. *Dalinghosaurus* is clearly a scleroglossan lizard (Ji and Ji, 2004), but its skull morphology remained undescribed until recently, with the publication of Evans and Wang (2005)'s revision of this species (see below).

Based on a juvenile specimen with well-preserved skin impressions, Ji and Ren (1999) established a new lizard species, *Jeholacerta formosa*, from the Yixian Formation in Pingquan, Hebei Province. However, this species may be a junior synonym of the common Jehol (Yixian Formation) lizard *Yabeinosaurus tenuis* Endo et Shikama, 1942, since it has the same body and limb proportions, similar cranial characters (including the wide paired frontals), and is at a similar level of skeletal development as juvenile *Yabeinosaurus* of the same size. A revision of the latter taxon by Evans et al. (2005) is summarised below.

Pachygenys thlastesa Gao et Cheng, 1999 is a possible scincomorph recovered from the Early Cretaceous Doushan Formation in Shandong Province. This taxon is currently represented only by lower jaw material, making it difficult to compare with other lizard skull material from China.

The Upper Cretaceous Djadokhta Formation in Bayan Mandahu, Nei Mongol has yielded a large number of lizard fossils. It is the most proliferous lizard fossil locality in China, with descriptive work started by Gao and Hou in 1995. To date, the following eleven lizard taxa have been recognized from this horizon: the iguanid lizards *Anchaurosaurus gilmorei* Gao et Hou, 1995 and *Xihaina aquilonia* Gao et Hou, 1995, the acrodontan iguanians *Priscagama gobiensis* Borsuk-Białynicka et Moody, 1984 (Gao and Hou, 1995), *Pleurodontagama aenigmatodes* Borsuk-Białynicka et Moody, 1984 (Gao and Hou, 1995) and *Mimeosaurus crassus* Gilmore, 1943 (Gao and Hou, 1995), the pleurodont iguanian *Isodontosaurus gracilis* Gilmore, 1943 (Gao and Hou, 1996), the polyglyphanodontid teioid *Adamisaurus magnidentatus* Sulimski, 1972 (Gao and Hou, 1996), the anguid *Bainguis* sp. (cf. *B. parvus*) Borsuk-Białynicka, 1984 (Gao and Hou, 1996), the carusiid anguimorph *Carusia intermedia* Borsuk-Białynicka, 1987 (Gao and Hou, 1996), the helodermatid *Gobiderma pulchrum* Borsuk-Białynicka, 1984 (Gao and Norell, 2000), and the indeterminate lizard *Conicodontosaurus djadochtaensis* Gilmore, 1943 (Estes, 1983). The Djadokhta Formation also yielded the enigmatic squamate *Sineoamphisbaena hexatabularis* Wu et al., 1993, identified as an amphisbaenian in the original paper, but regarded as a macrocephalosaurid teioid by other workers (e. g., Kearney, 2003). The systematic position of this taxon remains to be resolved.

Li (1991a) described two new lizards *Brevidensilacerta xichuanensis* and *Creberidentat henanensis* from the middle Eocene Hetaoyuan Formation in Xichuan, Henan Province. This locality is also an important Paleogene mammal site. Both lizards are represented by incomplete skull material. The former was referred to the Agamidae and the latter may be a member of the Anguidae (Li, 1991a). A broken jaw fragment with three teeth from the same locality was referred to *Tinosaurus* cf. *T. lushihensis* by Li (1991a).

Tinosaurus yuanquensis Li, 1991 is represented by incomplete skull bones with conical lower teeth and tricuspid upper check teeth. It was reported from the late Eocene Hedi Formation in Yuanqu, Shanxi Province, a famous Paleogene mammal site. An incomplete frontal and a pair of prefrontals from the same locality belong to another lizard *Hemishinisaurus latifrons* Li, 1991. This species is characterised by a wide interorbital region, and was referred to the family Xenosauridae (Li, 1991b). However, this requires reexamination, because other shinisaurs and xenosaurs are characterised by extremely narrow frontals.

Tinosaurus luonanensis Li et Xue, 2002, from the ? middle-upper part of the lower Pleistocene

in Luonan, Shaanxi Province documented the first occurrence of this genus in the Quaternary strata in China. It is represented by a right maxilla and a left mandible, both with teeth.

Conicodontosaurus qinlingensis Li et al., 2004, represented by a right dentary, was reported from the middle Pleistocene (493 ± 55 ka B. P.) in Luonan, Shaanxi Province. It is the third species of the genus reported from China, though material of *C. kanhsienensis* Young, 1973 is now referred to *Squamata incertae sedis*. Other lizard material has been reported from the same cave fauna, including the scincids *Eumeces* sp. and *Eremias* sp., and the agamid *Tinosaurus luonanensis*.

2.3 Revisions to previously established amphibian and squamate taxa

Chinese temnospondyls (mainly mastodontosauroids, sensu Damiani, 2001) are mostly poorly preserved and fragmentary, precluding revision at the current time. This should change as further work is done on recent new discoveries from the Jurassic of Northwest China.

For the remaining Chinese fossil amphibians, the revisions are mainly of Mesozoic lissamphibian taxa only recently reported from the Jehol Biota and associated fauna. To date, five frogs and six salamanders have been named. Among these, the frog taxon *Dalianbatrachus mengi* is a junior synonym of *Mesophryne beipiaoensis*, as they share the same body proportions and osteological characters (e. g. large skull and short vertebral column, nine presacral vertebrae and three pairs of free ribs, presence of squamosal/maxilla contact, transverse processes on posterior presacrals laterally oriented).

The recently reported Jehol anuran *Yizhoubatrachus macilentus* Gao et Chen, 2004 can be revised in two respects. Firstly, the following features can be added to the original diagnosis: maxilla with a prominent pre-orbital process; coracoid of roughly same width at both ends and without an anterior expansion at the proximal end; and ilium with no dorsal protuberance or dorsal crest. Secondly, the snout-pelvis length of the holotype was described as 115 mm (a large frog) in Gao and Chen (2004). But on the basis of the figure and its scale, this measurement should be around 62 mm (a small frog), so the original diagnostic character, "no mesopodium ossified in both fore- and hind limbs", might be a subadult feature, and should be used with caution. A revised measurement of all Jehol anurans is provided here (see Table 1).

The basal caudate *Jeholotriton paradoxus* was briefly reported in Wang (2000). Recently, a full description and a revised diagnosis were made by Wang and Rose (2005) in which the neotenic state of this animal was confirmed. The presacral number was revised from 17 to 15 ~ 16, a more primitive number in caudate evolution.

Chunerpeton tianyiensis was a neotenic cryptobranchid salamander. With a large number of new specimens in the IVPP collection, its original diagnosis can be extended as follows: presacral number 15 or 16 (15 in holotype); phalangeal formula of manus 2-2-3-2; mesopodium unossified; hypobranchial I and II, and ceratobranchial II ossified; three pairs of external gills with gill rakers; scapulocoracoid with slightly expanded and roughly rhomboid coracoid end.

Table 1 Comparative measurements of the holotypes of Chinese

Mesozoic anurans (revised from Wang, 2004b)

(mm)

	<i>Liaobatrachus grabau</i>	<i>Callobatrachus sanyanensis</i>	<i>Mesophryne beipiaoensis</i>	* <i>Yizhoubatrachus macilentus</i>
Snout-pelvis length (snout tip to end of pelvis)	70*	93*	70*	62 ⁺¹⁾
Skull length at midline/width across otic capsules	22*/32*	28.7/35	24*/34*	-/-
Vertebral column length including (urostyle)	46* (22*)	58.7 (27)	43* (21*)	- (19)
* transverse/longitudinal length of sacral diapophysis	5.5/6	5.8/8.3*	5/8	-/-
* Clavicle length	9	>9	>7	-
Length of humerus/radioulna	22/13	20/14	20/14	12/8
* Length/anterior width of pelvic girdle/ilium length	23/12.5/22*	35/16/31	29/17/26	-/-/ >18
Length of femur/tibiofibula/tibiale/fibulare	29/29/14/16	34/35/18.5/20	30*/29/16/17.4	24/22/11/12.5

1) The value was wrongly estimated as 115 mm in the original paper, see text for discussion. * new category; + estimated value.

The Hebei urodele *Sinerpeton fengshanensis*, described as a neotenic salamander in the original paper (Gao and Shubin, 2001), is probably a young adult of the metamorphosed *Laccotriton subsolanus* from the same site. In the original paper on *S. fengshanensis*, Gao and Shubin (2001) revised the phalangeal formula of the manus in *Laccotriton* from 2-3-4-3 to 2-2-3-2, and added some diagnostic characters, but these were not sufficient to justify generic distinction, especially in contemporaries from the same locality. According to Wang (in press), *Laccotriton* seems to have a slender ceratobranchial bone, expanded second metacarpal, and similar carpal, cranial, and pectoral girdle characters to *Sinerpeton* (from the same site) and to *Liaoxitriton* (of roughly the same age). It is therefore possible that *Laccotriton* is a senior synonym of the latter two taxa; but a revised description of *Laccotriton* is needed to complete more detailed comparisons and a fuller discussion of its systematic status.

Based on biostratigraphic studies, Wang and Gao (2003) and Wang (2004b) referred the horizon bearing *Laccotriton subsolanus* and *Sinerpeton fengshanensis* at Paozhanggou to the Dadianzi Formation (equivalent to the lower part of the Yixian Formation), with an Early Cretaceous, not Late Jurassic age as Gao et al. (1998) and Gao and Shubin (2001) originally proposed. More fieldwork is being carried out to resolve this problem.

Two species of the urodele *Liaoxitriton*, *L. zhongjiani* and *L. daohugouensis* have been described from two different fossil horizons. A revised diagnosis of the genus, with a differential diagnosis of the two species, can be found in Wang (2004a). Wang (in press) revised the presacral number of *L. zhongjiani* to 15 (16 in Dong and Wang, 1998) after further preparation of the holotype and observation of new specimens; the phalangeal formula of the pes of this species is also quite variable. This genus has provided some biostratigraphic information for the comparison of fossil horizons and the age of the associated fauna (Wang, 2004b). A character comparison of Chinese Mesozoic salamanders is provided in Table 2, with revised characters in bold face.

In Sun et al. (1992), the Early Triassic *Santaisaurus yuani* Koh, 1940 was regarded as one of the earliest squamates in the world. It was first assigned to the Paliguanidae of Romer's (1956) *Eosuchia*, but later transferred to the anapsid Procolophonidae (Romer, 1966; Carroll, 1988). Judging from the snout and palate morphology, in combination with T-shaped interclavicle and amphicoelous vertebra, *Santaisaurus* is more similar to procolophonoids and is not a lizard. Further study is needed to resolve its precise systematic position.

With the advances in the study of the Jehol Biota, two poorly understood Jehol lizards were recently reviewed and revised on the basis of new fossil finds. Since its establishment *Yabeinosaurus tenuis* Endo et Shikama, 1942 was considered to be a small gracile, weakly ossified lizard, possibly related to the lightly built gekkotans (e. g. Estes, 1983). However a new study, based on a larger sample of specimens, revealed that both the lost holotype and the newly erected neotype (Ji et al., 2001) were very young juvenile specimens, explaining the weak ossification. The adult is characterized by coarse cranial sculpture, a complete jugal arch (*contra* Endo and Shikama, 1942; Estes, 1983), a hooklike angular process on the articular, and a proximally broad fifth metatarsal with strong outer process. *Yabeinosaurus* was a large robust lizard with conservative body proportions. The contemporaneous *Dalinghosaurus* (Ji, 1998; Ji and Ji, 2004) differs in having smaller adult size, shorter forelimbs and very long feet.

Dalinghosaurus longidigitus was established on the basis of a partial postcranial skeleton comprising only the hind limbs and tail (Ji, 1998). Evans and Wang (2005) provided a revised diagnosis for this lizard based on numerous well-preserved articulated skeletons. It is a small lizard with heavy pustulate sculpture on the dermal skull bones (adult only), and is distinguishable from *Yabeinosaurus* in many osteological characters, such as very long tail and feet, fifth metatarsal with little development of the outer process and a flared rather than hook-like angular process on the lower jaw (Evans and Wang, 2005).

With respect to the diverse lizard assemblage in Bayan Mandahu, amended diagnoses can

be found in Gao and Hou (1996) and Gao and Norell (1998, 2000).

Table 2 Comparison of osteological characters of Chinese Mesozoic caudates

	<i>Laccotriton subsolanus</i>	<i>Sinerpeton fengshanensis</i>	<i>Liaoxitriton zhongjiani</i>	<i>Liaoxitriton daohugouensis</i>	<i>Jeholotriton paradoxus</i>	<i>Chunerpeton tianyiensis</i>
Snout-pelvis length	40 ~ 50 mm	47 mm*	70.4 mm*	75 mm*	72 mm*	—
Total body length	—	—	~120 mm*	>140 mm*	~140 mm*	~180 mm*
Skull length/width	—	—	19.9/20 mm*	19/21 mm*	21/22 mm*	—
Phalangeal formula in manus	2-2-3-2	1-2-3-2*	2-2-3-(2/3)	2-2-3-2	2-2-3-2	2-2-3-2
Phalangeal formula in pes	2-2-3-4-2	1-2-3-4-2*	2-2-4-5-(3/4), 2-2-3-4-(2/3), ?-3-4-5-3, 2-2-3-5-4	2-2-3-4-2	(1/2)-2-3-3-2	2-2-3-(3/4)-3
Mesopodial ossification	At least partial ossification	At least partial ossification	At least partial ossification	At least partial ossification	none	none
Number of presacrals	16	16 ~ 17	15 (~ ?16)	16	15 ~ 16	15 ~ 16
Caudal rib	At least 5 pairs	At most 4 pairs	2 pairs	3 pairs	None?	2 or 3 pairs
Metacarpal II	Expanded	Expanded*	Expanded	Unexpanded	Unexpanded	Unexpanded
Orientation of vomerine tooth row	Transverse	Transverse	Transverse, with distal end extending posterolaterally	Transverse, with distal end extending anterolaterally	Large tooth patch anteriorly, with a dentigerous bar extending posteriorly	Close and parallel to the maxillary arcade
Orientation of the anterior ramus of pterygoid	Directed to the posterior end of the maxilla	Directed to the posterior end of the maxilla*	Directed to the posterior end of the maxilla	Directed to the posterior end of the maxilla	Directed anteromedially and extending to the middle of the vomer	First extending anterolaterally, then curving in, tapering, and directed to lateral end of vomer
Ossification of hyobranchial apparatus	Stated as none in the original paper, but needs reexamination	At least one pair of ceratobranchials is ossified*	Ossified 2nd pair of hypobranchials, 2nd pair of ceratobranchials, and 2nd basibranchial	Ossified 2 nd pair of hypobranchials, 2 nd pair of ceratobranchials, and 2 nd basibranchial	Partially ossified, but weak ossification precludes further examination	Ossified 1st and 2nd pairs of hypobranchials, and 2nd basibranchial, having gill rakers
Scapulocoracoid	Coracoid end expanded, nearly rectangular in shape*	Coracoid end relatively expanded, nearly rectangular in shape*	Coracoid end expanded, nearly rectangular in shape	Coracoid end greatly expanded, nearly rectangular in shape	Coracoid end slightly expanded, round in shape	Coracoid end slightly expanded, rhomboid in shape

* denotes data from the holotype. Bold-faced characters refer to revisions or supplements to the original paper.

3 Phylogeny

The phylogeny of Chinese fossil amphibians and squamates has not been well studied. This was mainly due to the rarity of fossil material, the fragmentary nature and incomplete character preservation of the fossils and, especially, the lack of early (basal) members that could provide important information on character polarity. Over the past fifteen years, a large number of better-preserved fossils have been unearthed, especially from late Mesozoic strata. These new finds permit a more detailed discussion of phylogeny, most notably with respect to basal anurans (Wang et al., 2000; Gao and Wang, 2001; Wang, 2002; Gao and Chen, 2004; Wang, in press) and, less comprehensively, the major caudate families (Gao and Shubin, 2001; Wang and Evans, in press) and main lizard groups (Evans and Wang, 2005; Evans et al., 2005).

The Late Jurassic/Early Cretaceous lissamphibians from China represent early stages in the radi-

tion of frogs and salamanders, and are thus phylogenetically important in elucidating the relationships of basal taxa (Wang, in press). Based on previous phylogenetic analyses of basal anurans (Ford and Cannatella, 1993; Báez and Basso, 1996; Wang et al., 2000; Wang, 2002; Gao and Chen, 2004), Wang (in press) conducted a new analysis including all known Mesozoic frogs from East Asia, except for *Liobatrachus*, the original description of which is questionable. The result (see Fig. 3) confirms the monophyly of the family Discoglossidae, with *Callobatrachus* as the most basal member. The 50% majority-rule consensus tree supports the sister-group relationship of *Prosalirus* and *Notobatrachus* as suggested by Gao and Wang (2001) and Wang (2002), but rejected by Gao and Chen (2004). The newly established *Yizhoubatrachus* from the Jehol Biota forms a tetrachotomy with *Mesophryne*, the Japanese Tetori frog (Evans and Manabe, 1998), and the archaeobatrachian clade (node C), suggesting a primitive position for the first three taxa among basal anurans. This result differs from that of Gao and Chen (2004), which placed *Yizhoubatrachus* and *Notobatrachus* as sister taxa and thus created a biogeographic enigma by affiliating an Asian frog with a South American one. The new analysis presented here shows that the “enigma” is artificial, probably resulting from errors in character coding (Wang, in press).

Despite many analyses, there is no consensus on the phylogenetic relationships of caudates and sharply different hypotheses have been proposed (Hillis, 1991; Trueb and Cloutier, 1991; Trueb, 1973; Hay et al., 1995). Because early salamanders are usually represented by fragmentary material, they have rarely been included in a phylogenetic analysis. The well-preserved Chinese Mesozoic fossils may partially fill in this gap. Gao and Shubin (2001)'s analysis included *Laccotriton* and *Sinerpeton* from the Jehol Biota, as well as some important fossil taxa from outside China, such as the Late Jurassic *Karaurus* from Kazakhstan and the Early Cretaceous Spanish *Valdotriton*. Recently, Wang and Evans (in press) completed a more comprehensive analysis, including taxa such as *Liaoxitriton*, *Jeholotriton* and the Late Jurassic *Iridotriton*

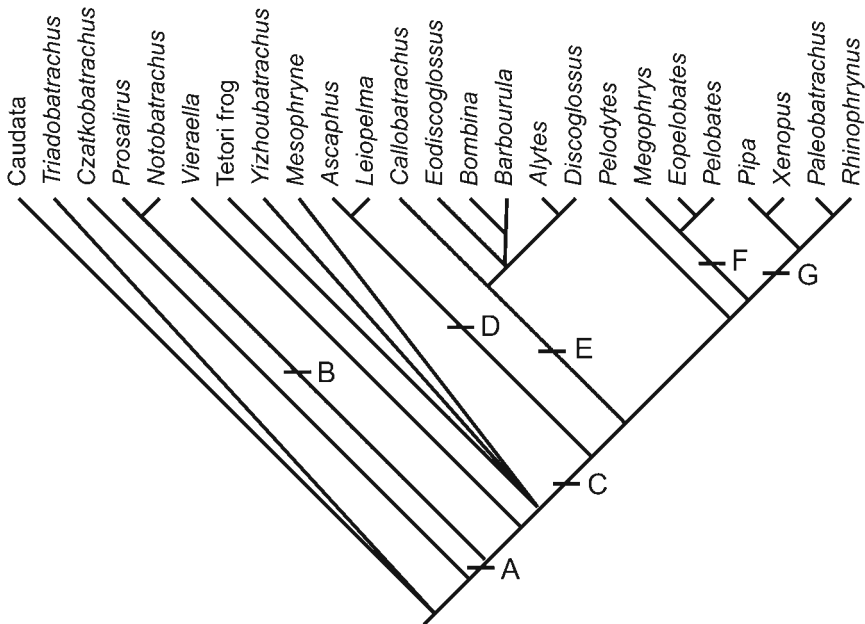


Fig. 3 Phylogeny of basal anurans (redrawn from Wang, in press, fig. 2b)
 A. Anura (apomorphy-based taxon, same below); B. Notobatrachidae; C. Archaeobatrachia; D. Leiopelmatidae; E. Discoglossidae; F. Pelobatidae; G. Pipoidea [See text and Wang (in press) for further explanations]

from the USA. However, neither study produced a definitive result because the characters used in these analyses were still not adequate to reveal the inter-group relationships. With the help of the exquisite Chinese fossils, further work is ongoing to investigate the early evolution and phylogeny of caudate groups.

There is a greater degree of consensus with respect to squamate phylogeny, although the relationships of some groups (e. g. xantusiids, amphisbaenians, snakes) are still disputed (Estes et al. , 1988; Evans and Chure, 1998; Lee, 1998; Gao and Norell, 1998). To date, relatively few Chinese fossils have been included in squamate phylogenetic analyses, the exceptions being *Carusia* (Gao and Norell, 1998), *Dalinghosaurus* (Evans and Wang, 2005) and *Yabeinosaurus* (Evans et al. , 2005). The genus *Carusia*, recovered from the Upper Cretaceous in both Mongolia and Nei Mongol, was fully revised by Gao and Norell (1998), with a phylogenetic analysis placing it within Anguimorpha, not Scincomorpha as originally suggested (Borsuk-Białynicka, 1987). Similarly, a recent study (Evans and Wang, 2005) also placed the Yixian *Dalinghosaurus* within Anguimorpha, as a possible relative of *Carusia*. *Yabeinosaurus*, on the other hand, was placed as a basal squamate (Evans et al. , 2005). As such, it is a relict taxon, representing a stage of squamate evolution reached by the Late Triassic or early Jurassic.

4 Conclusions

1) Sixteen amphibian (*Anakamacops petrolicus*, *Callobatrachus sanyanensis*, *Chunerpeton tianyiensis*, *Dalianbatrachus mengi*, *Ingentidens corridoricus*, *Jeholotriton paradoxus*, *Laccotriton subsolanus*, *Liaobatrachus grabaui*, *Liaoxitriton daohugouensis*, *L. zhongjiani*, *Mesophryne beipiaoensis*, *Phratochronis qilianensis*, *Sinerpeton fengshanensis*, *Sinostega pani*, *Yizhoubatrachus macilentus*, *Yuanansuchus laticeps*) and twenty-two squamate (*Adamisaurus magnidentatus*, *Anchaurosaurus gilmorei*, *Bainguis* sp. (cf. *B. parvus*), *Brevidensilacerta xichuanensis*, *Carusia intermedia*, *Conicodontosaurus djadochtaensis*, *C. qinlingensis*, *Creberidentat henanensis*, *Dalinghosaurus longidigitus*, *Gobiderma pulchrum*, *Hemishinisaurus latifrons*, *Isodontosaurus gracilis*, *Jeholacerta formosa*, *Mimeosaurus crassus*, *Pachygenys thlastesa*, *Pleurodontagama aenigmatodes*, *Priscagama gobiensis*, *Sineoamphisbaena hexatabularis*, *Tinosaurus luonanensis*, *Tinosaurus* cf. *T. lushihensis*, *T. yuanquensis*, *Xihaina aquilonia*) species have been reported since Sun et al. (1992)'s comprehensive review. Among these, fifteen amphibians and eleven squamates are valid new species.

2) Recent revisions of Chinese fossil amphibians and lizards mainly concern taxa from the Jehol Biota, due to the large number of new, well-preserved specimens.

3) Several important new paleoherpetological localities were discovered, including the frog and lizard locality of Sihetun (Liaoning), the salamander localities of Daohugou (Nei Mongol), Shuikouzi (Liaoning) and Paozhanggou (Hebei), and the lizard localities of Lujiatun (Liaoning) and Bayan Mandahu (Nei Mongol). Fossils from these localities are mostly well preserved.

4) The Late Jurassic/Early Cretaceous amphibians and lizards from China have provided important information on the origin and early evolution of relevant groups of lissamphibians and squamates, but phylogenetic research on many of these taxa is at a preliminary stage.

Acknowledgements This work was supported by grants from the National Natural Science Foundation of China (40302008, 40121202), a Royal Society of London/National Natural Sciences Foundation of China Joint Projects program, and the Chinese Academy of Sciences (KZCX3-SW-142). Thanks are given to Fucheng Zhang for providing an edited blank map of China for figures 1 and 2, and Jinling Li for kindly reviewing early versions of the manuscript.

References

- Báez A M, Basso N G, 1996. The earliest known frogs of the Jurassic of South America: review and cladistic appraisal of their relationships. *Münchner Geowiss Abh, Reihe A*, **30**: 131 ~ 158
- Borsuk-Białynicka M, 1984. Anguimorphans and related lizards from the Late Cretaceous of the Gobi Desert, Mongolia. *Palaeont Pol*, **46**: 5 ~ 105
- Borsuk-Białynicka M, 1987. *Carusia intermedia*, a new name for the Later Cretaceous lizard *Carolina* Borsuk-Białynicka, 1985. *Acta Palaeont Pol*, **32**: 153
- Borsuk-Białynicka M, Moody S M, 1984. Priscagaminae, a new subfamily of the Agamidae (Sauria) from the Late Cretaceous of the Gobi Desert. *Acta Palaeont Pol*, **29**: 51 ~ 81
- Carroll R L, 1988. *Vertebrate Paleontology and Evolution*. New York: W H Freeman and Company. 1 ~ 698
- Chang M M, Chen P J, Wang Y Q et al., 2003. The Jehol Biota: The Emergence of Feathered Dinosaurs, Beaked Birds and Flowering Plants. Shanghai: Shanghai Sci Tech Publ. 1 ~ 208
- Damiani R J, 2001. A systematic revision and phylogenetic analysis of Triassic mastodonsauroids (Temnospondyli: Stereospondyli). *Zool J Linn Soc*, **133**(4): 379 ~ 482
- Dong Z M (董枝明), Wang Y (王原), 1998. A new urodele (*Liaoxitriton zhongjiani* gen. et sp. nov.) from the Early Cretaceous of western Liaoning Province, China. *Vert Palasiat (古脊椎动物学报)*, **36**(2): 159 ~ 172 (in Chinese with English summary)
- Endo R, Shikama T, 1942. Mesozoic reptilian fauna in the Jehol mountainland, Manchoukuo. *Bull Central Nat Mus Manchoukuo*, **3**: 1 ~ 19
- Estes R, 1983. Sauria Terrestria, Amphisbaenia. In: Wellnhofer P ed. *Handbuch der Paläoherpetologie*. Volume 10A. Stuttgart & New York: Gustav Fischer Verlag. 1 ~ 245
- Estes R, Gauthier J, de Queiroz K, 1988. Phylogenetic relationships within Squamata. In: Estes R, Pregill G eds. *Phylogenetic Relationships of the lizard families: essays commemorating Charles L. Camp*. Stanford: Stanford Univ Press. 119 ~ 281
- Evans S E, Chure D, 1998. Paramacellodid lizard skulls from the Jurassic Morrison Formation at Dinosaur National Monument, Utah. *J Vert Paleont*, **18**(1): 99 ~ 114
- Evans S E, Manabe M, 1998. Early Cretaceous frog remains from the Okurodani Formation, Tetori Group, Japan. *Paleont Res*, **2**(4): 275 ~ 278
- Evans S E, Wang Y, 2005. The Early Cretaceous lizard *Dalinghosaurus* from China. *Acta Paleont Pol*, **50**(4): 725 ~ 742
- Evans S E, Wang Y, Li C, 2005. The Early Cretaceous lizard genus *Yabeinosaurus* from China: resolving an enigma. *J Sys Palaeont*, **3**(4): 319 ~ 335
- Ford L S, Cannatella D C, 1993. The major clades of frogs. *Herpet Monogr*, **7**: 94 ~ 117
- Gao C L (高春玲), Liu J Y (刘金远). 2004. A new taxon of Anura from Beipiao of Liaoning in China. *Global Geol (世界地质)*, **23**(1): 1 ~ 5 (in Chinese with English abstract)
- Gao K Q, Chen S H, 2004. A new frog (Amphibia: Anura) from the Lower Cretaceous of western Liaoning, China. *Cretaceous Res*, **25**(5): 761 ~ 769
- Gao K Q, Cheng Z W, 1999. A new lizard from the lower Cretaceous of Shandong, China. *J Vert Paleont*, **19**(3): 456 ~ 465
- Gao K Q (高克勤), Cheng Z W (程政武), Xu X (徐星), 1998. First report of a Mesozoic urodele from China. *Chinese Geol (中国地质)*, (250): 40 ~ 41 (in Chinese)
- Gao K Q, Hou L H, 1995. Iguanians from the Upper Cretaceous Djadochta Formation, Gobi Desert, China. *J Vert Paleont*, **15**(1): 57 ~ 78
- Gao K Q, Hou L H, 1996. Systematics and taxonomic diversity of squamates from the Upper Cretaceous Djadochta Formation, Bayan Mandahu, Gobi Desert, People's Republic of China. *Can J Earth Sci*, **33**: 578 ~ 598
- Gao K Q, Norell M A, 1998. Taxonomic revision of *Carusia* (Reptilia: Squamata) from the Late Cretaceous of the Gobi Desert and phylogenetic relationships of the anguimorph lizards. *Am Mus Novit*, (3230): 1 ~ 51

- Gao K Q, Norell M A, 2000. Taxonomic composition and systematics of Late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. *Bull Am Mus Nat Hist*, **249**: 1 ~ 118
- Gao K Q, Shubin N H, 2001. Late Jurassic salamanders from northern China. *Nature*, **410**: 574 ~ 577
- Gao K Q, Shubin N H, 2003. Earliest known crown-group salamanders. *Nature*, **422**: 424 ~ 428
- Gao K Q, Wang Y, 2001. Mesozoic anurans from Liaoning Province, China, and phylogenetic relationships of archaeobatrachian anuran clades. *J Vert Paleont*, **21**(3): 460 ~ 476
- Gilmore C W, 1943. Fossil lizards of Mongolia. *Bull Am Mus Nat Hist*, **81**: 361 ~ 384
- Hay J M, Ruvinsky I, Hedges S B et al., 1995. Phylogenetic relationships of amphibian families inferred from DNA sequences of mitochondrial 12S and 16S ribosomal RNA genes. *Mol Biol Evol*, **12**: 928 ~ 937
- Hillis D M, 1991. The phylogeny of amphibians: current knowledge and the role of cytogenetics. In: Green D M, Sessions S K eds. *Amphibian Cytogenetics and Evolution*. San Diego, London: Academic Press. 7 ~ 32
- Ji S A, 1998. A new long-tailed lizard from Upper Jurassic of Liaoning, China. In: Department of Geology, Peking University ed. *Collected works of international symposium on Geological Science held at Peking University, Beijing, China*. Beijing: Peking Univ Press. 496 ~ 505
- Ji S A (姬书安), Ji Q (季强), 1998. The first Mesozoic frog fossil from China (Amphibia; Anura). *Chinese Geol (中国地质)*, (250): 39 ~ 42 (in Chinese with English abstract)
- Ji S A, Ji Q, 2004. Postcranial anatomy of the Mesozoic *Dalinghosaurus* (Squamata): evidence from a new specimen of western Liaoning. *Acta Geol Sin*, **78**(4): 897 ~ 906
- Ji S A (姬书安), Lu L W (卢立伍), Bo H C (薄海臣), 2001. New material of *Yabeinosaurus tenuis* (Lacertilia). *Land and Resources (国土资源)*, **2001**(3): 41 ~ 43 (in Chinese)
- Ji S A, Ren D, 1999. First record of lizard skin fossil from China with description of a new genus (Lacertilia, Scincomorpha). *Acta Zootaxon Sin*, **24**(1): 114 ~ 120
- Kearney M, 2003. The phylogenetic position of *Sineoamphisbaena hexatabularis* reexamined. *J Vert Paleont*, **23**(2): 394 ~ 403
- Koh T P, 1940. *Santaisaurus yuani* gen. et sp. nov. ein neues Reptil aus dem unteren Trias von China. *Bull Geol Soc China*, **20**: 73 ~ 92
- Lee M S Y, 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. *Biol J Linn Soc*, **65**: 369 ~ 453
- Li J L (李锦铃), 1991a. Fossil reptiles from Hetaoyuan Formation, Xichuan, Henan. *Vert PalAsiat (古脊椎动物学报)*, **29**(3): 190 ~ 203 (in Chinese with English summary)
- Li J L (李锦铃), 1991b. Fossil reptiles from Zhaili Member, Hedi Formation, Yuanqu, Shanxi. *Vert PalAsiat (古脊椎动物学报)*, **29**(4): 276 ~ 285 (in Chinese with English summary)
- Li J L (李锦铃), Cheng Z W (程政武), 1999. New anthracosaur and temnospondyl amphibians from Gansu, China—The fifth report on Late Permian Dashankou lower tetrapod fauna. *Vert PalAsiat (古脊椎动物学报)*, **37**(3): 234 ~ 247 (in Chinese with English summary)
- Li Y X (李永项), Xue X X (薛祥煦), 2002. The first appearance of *Tinosaurus* fossil in the Quaternary. *Vert PalAsiat (古脊椎动物学报)*, **40**(1): 34 ~ 41 (in Chinese with English abstract)
- Li Y X (李永项), Xue X X (薛祥煦), Liu H J (刘护军), 2004. Fossil lizards of Qinling Mountains. *Vert PalAsiat (古脊椎动物学报)*, **42**(2): 171 ~ 176 (in Chinese with English abstract)
- Liu J, Wang Y, 2005. The first complete mastodonsauroid skull from the Triassic of China: *Yuanansuchus laticeps* gen. et sp. nov. *J Vert Paleont*, **25**(3): 725 ~ 728
- Romer A S, 1956. *Osteology of the Reptiles*. Chicago: Univ Chicago Press. 1 ~ 772
- Romer A S, 1966. *Vertebrate Paleontology* (3rd edition). Chicago: Univ Chicago Press. 1 ~ 468
- Sulimski A, 1972. *Adamisaurus magnidentatus* n. gen., n. sp. (Sauria) from the Upper Cretaceous of Mongolia. *Palaeont Pol*, **27**: 33 ~ 40
- Sun A L, Li J L, Ye X K et al., 1992. *The Chinese Fossil Reptiles and Their Kins*. Beijing: Science Press. 1 ~ 260

- Swisher III C C, Wang Y Q, Wang X L et al. , 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature*, **400**: 58 ~ 61
- Swisher III C C, Wang X L, Zhou Z H et al. , 2002. Further Support for a Cretaceous age for the feathered-dinosaur beds of Liaoning, China: New $^{40}\text{Ar}/^{39}\text{Ar}$ dating of the Yixian and Tuchengzi Formations. *Chinese Sci Bull*, **47**(2): 135 ~ 138
- Trueb L, 1973. Bones, Frogs, and Evolution. In: Vial J L ed. *Evolutionary Biology of the Anurans: Contemporary Research on Major Problems*. Columbia: Univ Missouri Press. 65 ~ 132
- Trueb L, Cloutier R, 1991. A phylogenetic investigation into the inter- and intrarelationships of the Lissamphibia (Amphibia: Temnospondyli). In: Schultze H P, Trueb L eds. *Origins of the Higher Groups of Tetrapods: Controversy and Consensus*. Ithaca: Cornell Univ Press. 175 ~ 188
- Wang Y (王原), 2000. A new salamander (Amphibia: Caudata) from the Early Cretaceous Jehol Biota. *Vert Palasiat* (古脊椎动物学报), **38**(2): 100 ~ 103 (in Chinese with English abstract)
- Wang Y, 2001. Advances in the study of Mesozoic lissamphibians from China. In: Deng T, Wang Y eds. *Proceedings of the Eighth Annual Meeting of the Chinese Society of Vertebrate Paleontology*. Beijing: China Ocean Press. 9 ~ 19
- Wang Y (王原), 2002. Fossil Lissamphibians from the Jehol Group and Phylogenetic Study of Basal Anurans. Unpublished Ph. D. Dissertation. Beijing: Graduate School of the Chinese Academy of Sciences. 1 ~ 153 (in Chinese with English summary)
- Wang Y, 2004a. A new Mesozoic caudate (*Liaoxitriton daohugouensis* sp. nov.) from Inner Mongolia, China. *Chinese Sci Bull*, **49**(8): 858 ~ 860
- Wang Y, 2004b. Taxonomy and stratigraphy of late Mesozoic anurans and urodeles from China. *Acta Geol Sin*, **78**(6): 1169 ~ 1178
- Wang Y (in press). Phylogeny and early radiation of Mesozoic lissamphibians from East Asia. In: Rong J Y, Fang Z J, Zhou Z H et al. eds. *Originations, Radiations and Biodiversity Changes—Evidence from the Chinese Fossil Record*. Beijing: Science Press.
- Wang Y, Evans S E (in press). A new short-bodied salamander from the Upper Jurassic/Lower Cretaceous of Liaoning, China. *Acta Paleont Pol*.
- Wang Y, Gao K Q, 1999. Earliest Asian discoglossid frog from western Liaoning. *Chinese Sci Bull*, **44**(7): 636 ~ 642
- Wang Y, Gao K Q, 2003. Amphibians. In: Chang M M, Chen P J, Wang Y Q et al. eds. *The Jehol Biota: the Emergence of Feathered Dinosaurs, Beaked Birds and Flowering Plants*. Shanghai: Shanghai Sci Tech Publ. 76 ~ 85
- Wang Y, Gao K Q, Xu X, 2000. Early evolution of discoglossid frogs: new evidence from the Mesozoic of China. *Naturwissenschaften*, **87**(9): 417 ~ 420
- Wang Y, Rose C S, 2005. *Jeholotriton paradoxus* (Amphibia: Caudata) from the Lower Cretaceous of southeastern Inner Mongolia, China. *J Vert Paleont*, **25**(3): 523 ~ 532
- Wu X C, Brinkman D B, Russell A P et al. , 1993. Oldest known amphisbaenian from the Upper Cretaceous of Chinese Inner Mongolia. *Nature*, **366**: 57 ~ 59
- Young C C (杨钟健), 1973. On a Mesozoic lizard from Kanhsien, Kiangsi. *Vert Palasiat* (古脊椎动物学报), **11**(1): 44 ~ 45 (in Chinese)
- Zhu M, Ahlberg P E, Zhao W J et al. , 2002. First Devonian tetrapod from Asia. *Nature*, **420**: 760 ~ 761