

# 记内蒙古宁城道虎沟上侏罗统/ 下白垩统一具有长肢的蜥蜴<sup>1)</sup>

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**摘要:**道虎沟化石层分布于内蒙古宁城县道虎沟以及毗邻的河北北部和辽宁西部等地,已报道4种有尾类、1个无尾类蝌蚪、1个幼年蜥蜴、3种带原始羽毛的兽脚类恐龙、2种翼龙、3种哺乳动物以及双壳类、叶肢介、昆虫和植物等化石(有学者称之为“前热河生物群”)。该层位比热河群义县组低,但地层划分存在争议;中侏罗统九龙山组、上侏罗统道虎沟组和下白垩统热河群均有报道。本文研究的道虎沟蜥蜴是该地点发现的第2个蜥蜴化石,其身体细长,为一幼年个体;前颌骨、顶骨和额骨均成对;上颌骨的面突高;后额骨和后眶骨不愈合;后额骨较大,但可能未进入上颞孔;后眶骨具宽的后突;牙齿小而尖锐,结构简单且可能为侧生;头骨的眶前区较长;具27个荐前椎;虽然未成年但个体较大;未见真皮骨板;手掌和四肢较长。上述特征组合区别于所有现生蜥蜴类,四肢比例也与其他蜥蜴有较大区别。欧美中侏罗世-早白垩世的小盗蜥(*Parviraptor*)和蒙古早白垩世的一个幼年个体(可能属于壁虎型类)与道虎沟标本比较相似。头骨特征和较大的荐前椎数目显示道虎沟标本可能属于硬舌蜥类(*scleroglossan*)。但因标本为幼年个体,本文暂将它归入有鳞类属种未定(*Squamata gen. et sp. indet.*)。测量数据显示,道虎沟标本的手掌和前肢相对较长;该特征常见于适应攀爬的蜥蜴种类,似可显示攀爬习性。但肢体比例可能会随身体增长而发生变化,所以此生活习性并非定论。

**关键词:**内蒙古宁城道虎沟,上侏罗统/下白垩统,前热河生物群,蜥蜴

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## A LONG-LIMBED LIZARD FROM THE UPPER JURASSIC/LOWER CRETACEOUS OF DAOHUGOU, NINGCHENG, NEI MONGOL, CHINA

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**Abstract** Lizards are now relatively well known from the Jehol Group of northeastern China, seven taxa having been named from the group or equivalent horizons. Here we describe a lizard specimen from a

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fossil horizon at Daohugou of Ningcheng, Nei Mongol, which predates the Yixian Formation of the Jehol Group. This is the second lizard from this locality. Comparisons with ontogenetic series of modern lizards show that the new Daohugou lizard is a juvenile. The specimen is notable in having a slender body and relatively long limbs and extremities. Even allowing for immaturity, its proportions differ markedly from those of previously described Jehol Biota lizards. Comparison with modern lizards suggests the new Daohugou lizard may have been at least partly scansorial. Its phylogenetic placement is problematic given its immaturity and preservation, but skull characters and vertebral number preclude attribution to Iguania and it may be a scleroglossan.

**Key words** Daohugou, Nei Mongol, China; Late Jurassic/Early Cretaceous; pre-Jehol Biota; lizard

## 1 Introduction

The Jehol Group (Dabeigou, Yixian and Jiufotang formations) of northeastern China has yielded a spectacular fossil assemblage with a wide range of plants and animals (Chang et al., 2003). The best known Jehol Biota lizard taxa are *Yabeinosaurus* (Endo and Shikama, 1942; Ji et al., 2001; Evans et al., 2005) and the smaller *Dalinghosaurus* (Ji, 1998; Ji and Ji, 2004; Evans and Wang, 2005). *Dalinghosaurus* is known only from the Yixian Formation (Evans and Wang, 2005), whereas *Yabeinosaurus tenuis* has been recorded from both the Yixian Formation and the overlying Jiufotang Formation (Evans et al., 2005). A second species of *Yabeinosaurus*, *Y. youngi*, was named by Hoffstetter (1964), but the specimen on which it is based (IVPP V 961) is too poorly preserved to be secure of either its generic or specific attribution. A third Yixian Formation genus, *Jeholacerta*, was described by Ji and Ren (1999), but the type and only specimen is a skin impression without diagnostic characters. It could be a juvenile of *Yabeinosaurus* or belong to a distinct taxon, but there is insufficient information in the designated holotype to permit determination. Dong and Chen (2000) briefly reported a new pleurodont lizard as a prey in the stomach of *Sinosauropteryx*, a feathered dinosaur from the Yixian Formation, but no detailed description has been given. Ji (2005) named *Liaoningolacerta brevirostra* on the basis of a specimen with scale impressions from the Yixian Formation, but, like *Jeholacerta*, the designated holotype is an indeterminate juvenile specimen with a generic diagnosis consisting of juvenile traits (e. g. unfused astragalus and calcaneum) and generalised squamate features. Most recently a juvenile specimen of a long-ribbed gliding lizard, *Xianglong zhaoi*, was described from the Yixian Formation at Zhuanchengzi near Yizhou, Liaoning Province (Li et al., 2007). Two other fragmentary lizard specimens, *Pachygenys* Gao & Cheng, 1999 (Doushan Formation, Qingshan Group, Shandong Province) and *Mimobecklesisaurus* Li, 1985 (Chijinbu Group, Gansu Province) are from horizons that are probably contemporaneous with those of the Jehol Group (X L Wang, pers. comm. July 2005). No lizard remains have been recovered from the lowermost part of the Jehol Group, the Dabeigou Formation.

The fossiliferous Daohugou bed (Wang et al., 2000) comprises freshwater shales interbedded with tuffs. It was first recognised near the village of Daohugou, Ningcheng County, Nei Mongol, but is also known from neighbouring Lingyuan City, Liaoning Province (e. g. at the locality of Wubaiding, Wang et al., 2005; Wang and Evans, 2006a,b). In combination, deposits of the Daohugou bed have yielded a spectacular collection of early salamanders (*Chunerpeton*, Gao and Shubin, 2003; *Jeholotriton*, Wang, 2000, Wang and Rose, 2005; *Liaoxitriton daohugouensis*, Wang, 2004a; *Pangerpeton*, Wang and Evans, 2006b), but also plants (Zhou et al., 2007), bivalves (Jiang, 2006), conchostracans (Shen et al., 2003), insects (Ren and Yin, 2002; Zhang, 2002, 2004a,b, 2006a,b; Zhang and Kluge, 2007), an anuran tadpole (Yuan et al., 2004), a juvenile lizard (Evans and Wang, 2007), small, feathered theropods (Zhang et al., 2002; Xu and Zhang, 2005; Zhang et al., 2008), rhamphorhynchid (Czerkas and Ji, 2002) and anurognathid (Wang et al., 2002) pterosaurs, and three mammals, a docodont

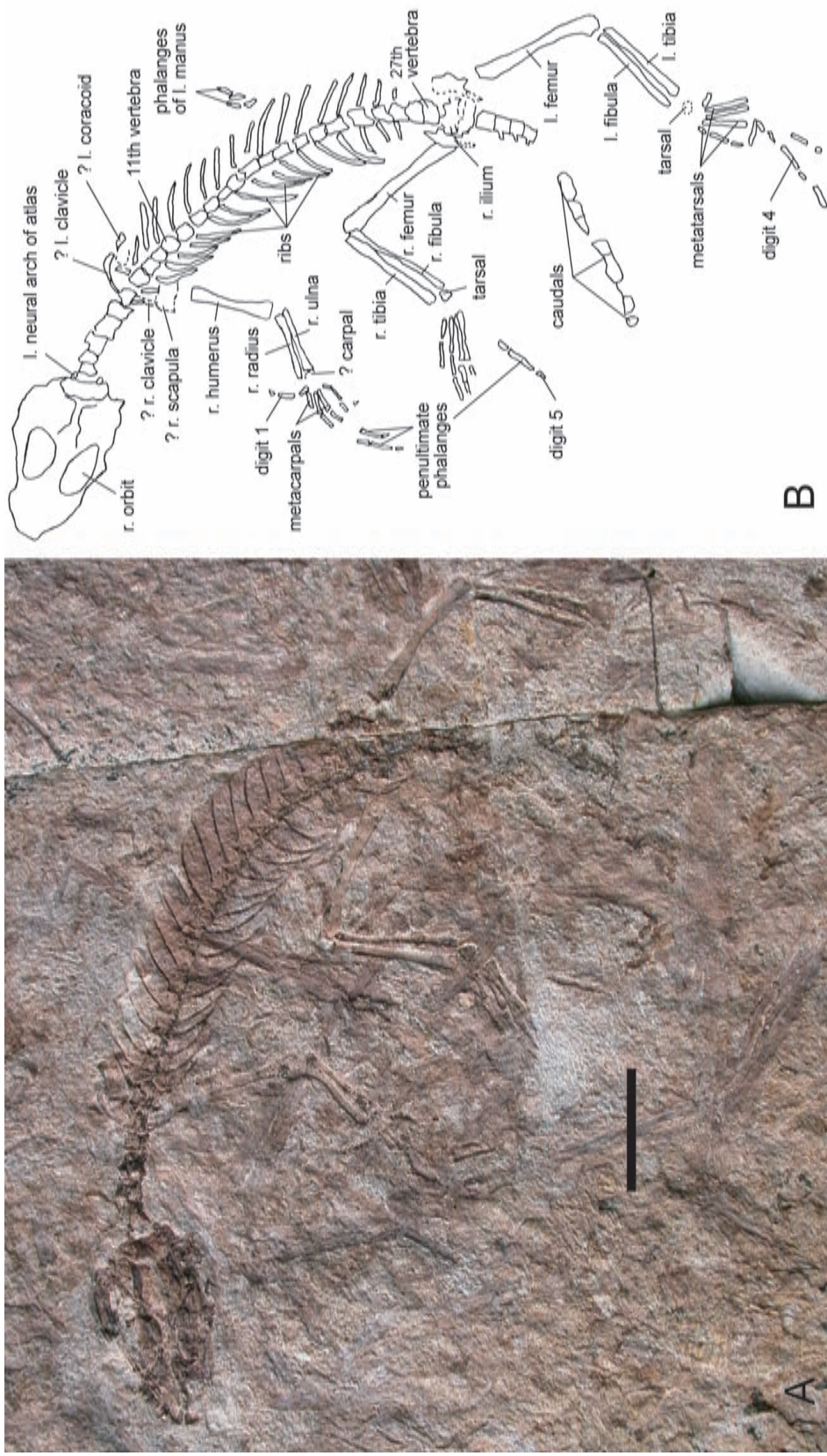


Fig. 1 New Daohugou lizard (Squamata gen. et sp. indet., IVPP V 13747) in ventral view  
 A. photo of specimen; B. outline drawing of skeleton; scale bar = 1 cm; abbreviations: l. left; r. right

(Ji et al., 2006), a flying form (Meng et al., 2006), and one with highly derived pseudo-tri-bosphenic molars (Luo et al., 2007). To date, however, no fish and no aquatic reptiles have been recovered, a sharp contrast with the assemblages of the younger Jehol Group.

The geology of the Daohugou bed is complex and the dating is problematic. The horizon has been equated with the Middle Jurassic Jiulongshan Formation (Ren and Yin, 2002; Shen et al., 2003), the Late Jurassic Daohugou Formation (Zhang, 2002), and the Early Cretaceous Jehol Group (Wang et al., 2000). Invertebrate researchers generally favour a Middle Jurassic age, equivalent to the Jiulongshan Formation (Ren and Yin, 2002; Shen et al., 2003) and this has formed the basis for proposed Middle Jurassic occurrences of crown-group salamanders (e. g. Gao and Shubin, 2003). However, others have argued that some of the tetrapods from Daohugou (salamanders, Wang, 2004a; pterosaurs, Wang et al., 2005) are closer to those of the Early Cretaceous Jehol Biota (and the salamander genus *Liaoxitriton* is known from both assemblages), although some key Jehol taxa (e. g. *Ephemeropsis*, *Lycoptera*) are missing. Wang et al. (2005) recently reviewed both the stratigraphy and faunal assemblage of the Daohugou fossil bed. They rejected a Middle Jurassic age and concluded that the Daohugou bed probably belonged to the same cycle of volcanism and sedimentation as the Yixian Formation, but lower in the sequence. Its assemblage may therefore represent a fauna that was a precursor to the typical Jehol Biota. Discussion of the age of this horizon is ongoing, but for the interim we accept Wang et al.'s interpretation of the assemblage as pre-Yixian and of earliest Cretaceous or, more likely, Late Jurassic age.

Terrestrial tetrapods are not rare in the Daohugou bed but only two lizards have been recovered to date. One, a hatchling with good skin impressions, is described elsewhere (Evans and Wang, 2007). In this paper we describe a second lizard (IVPP V 13747), distinguished by a slender body and relatively long limbs (Fig. 1).

Abbreviation: "IVPP V" is the catalogue designation for vertebrate specimens in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing.

## 2 Systematic paleontology

### Squamata genus and species indet.

#### 2.1 Description

The lizard specimen (IVPP V 13747) is fully articulated but is preserved mainly as a skeletal impression with some very thin bone traces (Fig. 1). It has therefore been challenging to prepare. Overall, the body appears narrow and rather laterally compressed, and the limbs are relatively long. The skeleton is in ventral view, but most of the ventral bones are lost, exposing the ventral side of some dorsal bones, especially on the skull. The skeleton, skull in particular, is not very stable and we deemed the specimen unsuitable for casting. The lizard was clearly juvenile (but post-hatchling) as shown by the unfinished ends to the limb bones, the limited mineralization of the carpus and tarsus, and the weak ossification of the skull bones. As preserved, the snout-pelvis length is 60.1 mm, with a skull length of 15.7 mm. The adult lizard was probably at least twice this size.

**Skull** Much of the skull is preserved (Fig. 2) but without detail of bone surfaces. Most clearly exposed is the underside of the skull roof. The antorbital region of the skull is relatively long given the immaturity of the specimen and is likely to have been even longer in the adult. Premaxillae, nasals, frontals and parietals are all paired, with an unossified gap in the midline at the frontoparietal junction. As in the juveniles of living lizards (e. g. Rieppel, 1992a, b; 1994a), each parietal shows a relatively thick lateral margin and a very thin, barely ossified, central region. It is not clear whether or not a parietal foramen was present, and nor whether the premaxillae, frontals or parietals were ultimately fused in the adult. In any event, by com-



parison with modern taxa, fusion would have occurred post-hatching and would have been relatively late in occurrence.

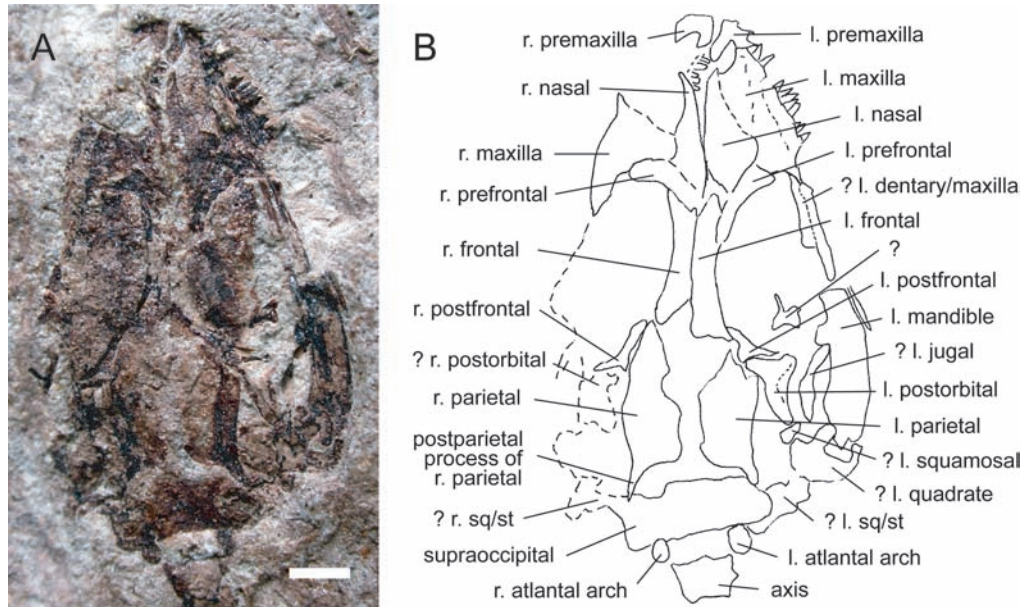


Fig. 2 Skull of the Daohugou lizard (Squamata gen. et sp. indet., IVPP V 13747) in ventral view

A. photo of skull region; B. outline drawing of skull; scale bar = 2 mm

Abbreviations: l. left; r. right; sq/st. squamosal/supratemporal

As preserved, the premaxillae are rather small with nasals processes that intervened between the tips of the long nasals, although the tips of the processes are not preserved. The right maxilla has a tall facial process that meets the nasal but seems to be separated from the frontal by the prefrontal, although the precise relationship of the maxilla and prefrontal is not clear. The frontals are paired and show no unusual features. As preserved, the parietals have straight lateral margins and rather short postparietal processes, but the parietal is an element that can show considerable ontogenetic change, and the adult shape may be quite different (Evans, 2008). At the lateral edges of the frontoparietal contact, there are small triangular postfrontals, and posterolateral to these are larger postorbitals. The left postorbital is better preserved, with a broad posterior process and a dorsomedial process that may have excluded the postfrontal from the upper temporal fenestra. The squamosals and the supratemporals are not clearly identified, but a posterolateral mass distal to the postorbital is probably part of a large quadrate. Behind the parietals is the braincase, with a large conspicuous supraoccipital. Part of the left mandible is preserved between the end of the maxilla and the quadrate/braincase region, but provides no details.

**Dentition** The left maxilla bears several small pointed teeth that are probably, but not certainly, pleurodont. Several associated teeth are preserved between the anterior tips of the two nasals and they may belong to the broken and displaced anterior part of the right maxilla.

**Postcranial skeleton** The vertebral column has around 27 presacral vertebrae and an unknown number of caudals. Given the poor preservation of the pectoral girdle, it is difficult to gauge cervical number (7–8). The two unfused neural arches of the atlas are widely separate and are preserved as two oval impressions behind the supraoccipital (Fig. 2B). The preservation of individual vertebrae is poor but there is no evidence of vertebral condyles. Whether these

were late developing (as in the Jurassic-Cretaceous lizard *Parviraptor*, Evans, 1994a) or the vertebrae remained amphicoelous is unclear. A small number of caudal vertebrae lie between the hind limbs but they are too poorly preserved to determine whether or not they are autotomous (Fig. 1B).

The ribs are slender and single headed. They are clearly visible on the 7<sup>th</sup> to 25<sup>th</sup> presacrals in pairs, but are not clearly identified in the cervical region or on the posterior presacrals. Based on their shape and position, the 28<sup>th</sup> and 29<sup>th</sup> vertebrae are probably the sacrals, but are not determinate due to poor preservation of the region. The sacral diapophyses are not well preserved, nor are the transverse process on the caudals, except that short transverse process can be seen on 31<sup>st</sup>-33<sup>rd</sup> vertebrae (probably 2<sup>nd</sup> to 4<sup>th</sup> caudal) on the right hand side.

**Limbs and girdles** Parts of the pectoral girdle are preserved, probably representing the scapulae, the coracoids and the clavicles, but the identification is uncertain (Fig. 1B). The right forelimb is seen in impression and the bones were unfinished. However, it is almost complete with a robust humerus (8.5 mm), radius (6.8 mm), ulna (6.7 mm) and parts of the manus. A stained impression distal to the ulna may represent unossified proximal carpal(s), but no detail is visible due to poor preservation. As preserved, the manus is large (10.1 mm at least), but is also unusual in having relatively short metacarpals, long penultimate phalanges, and robust unguals (Fig. 1B). The phalangeal formula cannot be reconstructed. Most of the left forearm is lost (presumably on the counterpart) but traces of the phalanges are preserved adjacent to the rib cage.

The pelvis preserves little detail but part of the right ilium overlies the proximal end of the femur. Both hind limbs are visible in impression, with all joint surfaces unfinished. The femora are long (12.4 mm right, 12.7 mm left), as are the crural elements (right/left tibia 10.65/10.4 mm; right/left fibula 10.1/9.4 mm), with the tibia being unusually slender, though wider than the associated fibula. Only one tarsal bone is ossified on each side, but it is large and irregular in shape. By reference to modern taxa (Rieppel, 1992a,b, 1994a,b; Maisano, 2001), the element is probably the astragalus, the first tarsal to ossify. Neither pes is complete, but the left is the better preserved (at least 16.8 mm in length). As in the manus, the metatarsals are relatively short (in marked contrast to the Yixian *Dalinghosaurus*), but the penultimate phalanges (preserved on the fifth toe of the right pes) are elongated.

## 2.2 Discussion

**The ontogenetic age of the specimen** This specimen, like the other small lizard from Daohugou (Evans and Wang, 2007), is skeletally immature. This is shown in the weak ossification of the skull roofing bones, the gaps between skull bones, the unfinished ends of the limb bones, and the limited mineralisation of the carpus and tarsus. According to Maisano (2001) at least one tarsal element (the astragalus) is present in all neonatal (hatchling) lizards, and most have more than this (the exceptions, amongst living taxa studied, being agamides, xantusiids and some anguids, Maisano, 2001). In the skull, the bones are not fully ossified and the central areas of each bone are very thin or unfinished.

The new Daohugou specimen thus represents a juvenile, probably in the first year, and the first season, of its life. However, it is relatively large for a lizard of this ontogenetic age. In extant lizards, juveniles in their first year of life typically reach around 30% ~ 35% of adult size (Dunham et al., 1994; Bauwens and Diaz-Uriarte, 1997), although there is considerable variation. The adult of IVPP V 13747 may therefore have been 150 ~ 200 mm in snout-pelvis length, representing a lizard larger than *Dalinghosaurus*, but smaller than *Yabeinosaurus*.

**Systematic comparison** IVPP V 13747 is certainly a reptile (vertebral column, ribs, skull morphology) and clearly not an archosaur (iliac morphology, skull). The combination of pleurodont teeth, an open lower temporal region, and a large expanded quadrate, suggests that

this specimen is probably a lizard. The only other known taxa with a similar body shape would be rhynchocephalians, non-lepidosaurian lepidosauromorphs like the Jurassic *Marmoretta* (Evans, 1991), and basal choristoderes. The preserved skull morphology of V 13747 precludes attribution to the aquatic Choristodera, which are derived in having the prefrontals separating the nasals and frontals, and in having a complete lower temporal bar. The pleurodont teeth of V 13747 also preclude attribution to rhynchocephalians (except the most basal forms), but comparison with *Marmoretta* is more difficult as this genus has subpleurodont teeth, an open temporal region, and paired frontals in the juvenile. The postcranial skeleton of *Marmoretta* is also poorly known. *Marmoretta* has never been recorded outside Europe (Britain, Portugal), but the persistence of non-lepidosaurian lepidosauromorphs into the Late Jurassic of western Laurasia leaves open the possibility of such relict forms occurring amongst the Daohugou biota. Nonetheless, *Marmoretta* differs from V 13747 in having a large squamosal holding the quadrate, a specialised parietal with descending flanges and a mid-dorsal keel, and a low facial process of the maxilla. By contrast, V 13747 has the tall facial process of the maxilla typically found in lepidosaurs. Thus on the basis of existing evidence, V 13747 is probably a squamate. However, its immaturity and the weak ossification of the skeleton limit comparison to the following features of this animal:

- 1) paired parietals post-hatching;
- 2) separate postfrontal and postorbital;
- 3) postfrontal relatively large but probably excluded from upper temporal fenestra;
- 4) postorbital with wide posterior process;
- 5) paired frontals post-hatching;
- 6) paired premaxillae post-hatching;
- 7) small, sharp, acuminate teeth;
- 8) relatively elongate antorbital skull;
- 9) 27 presacrals;
- 10) relatively large size given immaturity;
- 11) no evidence of osteoderms;
- 12) long manus;
- 13) relatively long limbs compared to estimated snout-pelvis length.

On morphological grounds, living squamates are usually divided into two sister-clades, Iguania and Scleroglossa (Estes et al., 1988; Conrad, 2008; but see Townsend et al., 2004). In iguanians (pleurodont and acrodont), the frontals fuse in the embryo and the postfrontal is reduced or absent (Estes et al., 1988). Acrodont iguanians have a maximum of 25 presacral vertebrae (Hoffstetter and Gasc, 1969) and pleurodont iguanians only rarely go above this number. Thus on cranial and vertebral characters, the Daohugou lizard is unlikely to be an iguanian. Presacral counts of 27+ are more commonly found in scleroglossans. Amongst scleroglossans, paired parietals occur in most gekkotans and some xantusiids, but the post-temporal bar is always incomplete in the former group. Most, but not all, gekkotans have fused frontals, but they can be paired in xantusiids, scincids, lacertids, cordyliforms and anguids (Evans, 2008). Some gekkotans (eublepharines, some diplodactylines) and scincids have paired premaxillae in post-hatchlings, but amongst anguimorphs, they occur only in some *Ophisaurus* (Evans, 2008). Thus no living lizards are recorded as having a post-hatchling stage with a complete postorbital bar in association with paired premaxillae, frontals and parietals (allowing for the fact that few studies have been made on post-hatchling skull development in this group).

To date, seven lizards have been named from the Early Cretaceous Jehol Biota or its equivalents in China: *Yabeinosaurus* (Endo and Shikama, 1942; Young, 1958; Ji et al., 2001; Evans et al., 2005), *Mimobecklesisaurus* (Li, 1985), *Dalinghosaurus* (Ji, 1998; Ji and Ji, 2004; Evans and Wang, 2005), *Jeholacerta* (Ji and Ren, 1999), *Pachygenys* (Gao and Cheng, 1999), *Liaoningolacerta* (Ji, 2005) and *Xianglong* (Li et al., 2007). New work on *Yabeinosaurus* (Evans et al., 2005) has shown that it reached large adult size and is robustly built, with a morphology poorly reflected by the very young individuals previously used to characterise it. However, even in young individuals, the parietal is single and has a strong interdigitating suture with the frontals. Limb proportions are also very different from those of V 13747 (Table 1), with *Yabeinosaurus* having shorter hands and feet and no elongation of the penultimate phalanx in each digit.

**Table 1 Comparison of limb proportions for the new Daohugou lizard with juvenile and subadult representatives of other contemporary Chinese lizard fossils**

	DHG 2 (V 13747)	DHG 1 (V 14386)	<i>Yabeinosaurus</i> (YFM-R002)	<i>Dalinghosaurus</i> (V 14234.1)	" <i>Jeholacerta</i> " (GMV 2114)	" <i>Liaoningolacerta</i> " (GMV 1580)	<i>Yabeinosaurus</i> (V 13284)	<i>Dalinghosaurus</i> (V 13281)
SPL(mm)	60.1	43.9	80.6	88.0	45.5	33.4	180.0	142.0
FL/HL(%)	63	67	63	43	65	59	63	44
FL/SPL(%)	42	38	29	37	35	37	28	32
HL/SPL(%)	66	57	45	82	54	57	45	73
Hu/Fe(%)	67	70	76	71	86	75	79	63
Ra/Ti(%)	86	64	83	52	73	71	90	57
Hd/Ft(%)	74	72	67	33	—	—	51	36
Hd/SPL(%)	21	15	15	15	15	16	13	14
Ft/SPL(%)	28	21	21	39	29	33	20	38
Hd/FL(%)	50	42	58	37	44	45	44	40
Fe/SPL(%)	21	16	13	22	14	16	13	17
Hd/PSC	7.4	5.7	4.4	3.9	3.9	4.6	4.3	5.1
Ra/PSC	4.1	3.4	2.5	2.9	2.1	2.3	2.3	2.9
Hu/PSC	4.9	4.3	3.6	3.9	2.9	3.3	3.8	4.1
Fe/PSC	7.6	5.4	4.8	5.8	3.6	4.4	5.0	6.6
Ti/PSC	6.3	4.9	3.3	5.6	2.8	3.2	3.2	6.1

Abbreviations: DHG. Daohugou lizard; Fe. femur; FL. forelimb; Ft. foot; Hd. hand; HL. hind limb; Hu. humerus; PSC. presacral centrum length; Ra. radius; SPL. snout-pelvis length; Ti. tibia.

*Dalinghosaurus* does not grow to such large size but even the smallest specimens (e. g. IVPP V 14234.3) have the frontals already fused (though also unossified posteromedially) (Evans and Wang, 2005; Evans et al., 2007). The feet are remarkably long and are characterised by longer metatarsals, whereas the forelimbs are proportionally shorter.

*Xianglong* (Li et al., 2007) is distinguished by elongated ribs that supported expanded gliding surfaces. *Mimobecklesisaurus* is a fragmentary specimen from Gansu Province (Li, 1985), but unlike the Daohugou juvenile, it has associated osteoderms like those of Laurasian scincomorph paramacellodids. *Pachygenys* (Gao and Cheng, 1999) from Shandong Province is represented by isolated jaw material that precludes comparison with the Daohugou specimen. The remaining two named taxa, *Jeholacerta* (Ji and Ren, 1999) and *Liaoningolacerta* (Ji, 2005), are highly problematic, as outlined in the introduction. Both are based on single juvenile specimens represented by skin impressions but little skeletal morphology (and that of uncertain interpretation). Their diagnoses are a mix of juvenile traits (e. g. small size, unfused proximal tarsals) and generalised morphological observations (e. g. "scapula of moderate height"), none of which is adequate for differential diagnosis. Based on scalation and general proportions, they could both belong to the same taxon, to one or more new taxa, or to *Yabeinosaurus*. Both *Jeholacerta* and *Liaoningolacerta* must be regarded as *nomina dubia* as it would be impossible to refer any new specimen to either "taxon" with any degree of assurance. Nonetheless, the proportions of V 13747 are different from either of these Jehol juveniles (Table 1), and also from the only other lizard recorded from the Daohugou locality (Evans and Wang, 2007), also a juvenile. This first specimen, IVPP V 14386, is smaller overall (43.9 mm snout pelvis length as against 60.1 mm), having relatively shorter hands and feet, and a very short antorbital skull—as is more typical for juvenile animals. Even allowing for V 14386 to be ontogenetically younger (early hatchling) than V 13747, the two Daohugou juveniles represent different taxa. Thus on the basis of the known skull characters and postcranial proportions, V 13747 is distinct from known Jehol lizards and from the only other lizard recorded from Daohugou. However, given the immaturity of the specimen, we decline to use it as the basis of a new taxon. This must await the recovery of a more mature specimen.



Fossil lizards are known from many other Mesozoic localities, although relatively few have yielded articulated specimens (Estes, 1983). The combination of simple, acuminate teeth and a relatively generalised body form in V 13747 rules out several specialised taxa, and the absence of any trace of osteoderms preclude attribution to the widespread paramacellodids. *Meyasaurus* (Lower Cretaceous, Spain, Evans and Barbadillo, 1997), *Palaeolacerta* (Upper Jurassic, Germany, Estes, 1983), *Chometokadmon* (Lower Cretaceous, Italy, Evans et al., 2004), and *Bavarisaurus* (Upper Jurassic, Germany, Estes, 1983, Evans, 1994b) are described as having only 25 presacral vertebrae (against 27 in the Daohugou lizard), although *Bavarisaurus*, a basal squamate, shares the paired parietals and premaxillae (Evans, 1994b). The body proportions of IVPP V 13747 (fore- and hind limbs relatively long in relation to snout-pelvis length) differ from those of *Hoyalacerta* (Lower Cretaceous, Spain, Evans and Barbadillo, 1999), *Eichstaettisaurus* and *Ardeosaurus* (Upper Jurassic, Germany, Estes, 1983, SEE pers. obs.), and *Euposaurus* (Upper Jurassic, France, Evans, 1994c). IVPP V 13747 also differs from *Scandensia* (Lower Cretaceous, Spain, Evans and Barbadillo, 1998) in having relatively shorter forelimbs (FL/HL, 62.8% as compared to 86.2% in *Scandensia*; see Table 2) and lacking the expanded ribs. The single specimen of *Scandensia* is more mature skeletally than the Daohugou juvenile, but smaller. The closest similarities are with the Jurassic/Lower Cretaceous *Parviraptor* (UK, Portugal, Evans, 1994a) and an unnamed juvenile skull from the Lower Cretaceous of Mongolia attributed to Gekkonomorpha (Conrad and Norell, 2006). *Parviraptor* has paired frontals and parietals into at least post-hatchling life (premaxillae unknown) and appears to have reached skeletal maturity slowly as the vertebral centra are amphicoelous in juveniles, becoming procoelous later (Evans, 1994a). Unfortunately as yet, nothing is known of skeletal proportions. The Mongolian skull is also juvenile, with paired frontals and parietals (premaxillae unknown), separate postfrontals and postorbitals, and a complete postorbital bar.

In summary, the new Daohugou specimen appears to be distinct from any previously described lizards from Jehol, or Jehol-associated localities, but the combination of post-hatchling skull traits makes it difficult to place systematically with any confidence. It shows similarities to the Middle Jurassic-Early Cretaceous Euramerican *Parviraptor* (variously placed as a basal varanoid (Evans, 1994a; Nydam, 2000) or basal scleroglossan (Conrad and Norell, 2006)) and a juvenile skull from the Lower Cretaceous of Mongolia (Conrad and Norell, 2006), but further material of all of these taxa would be needed to determine whether these similarities have any systematic significance.

**Lifestyle** We compared the limb proportions of V 13747 with a range of modern lizards, ground living, part-scansorial, and arboreal (Table 2). Compared with a generalised tetrapodal lizard (e. g. *Gekko*, *Eumeces*), V 13747 has a forelimb that is short relative to the hind limb (63%), but relatively long in relation to snout-pelvis length (42%); a manus that is long relative to forelimb length (50%) and snout-pelvis length (21%); a radius that is long relative to the humerus (78%) and the forelimb as a whole (28%); and pedal penultimate phalanges that are long relative to the foot (18%) and the femur (24%). The large manus and relatively long forelimbs seem to be the most distinctive features. In comparison with extant lizards:

1) The long manus is most like those of the iguanians *Aphaniotis*, *Calotes*, *Phrynocephalus*, and *Plica* of which all but *Phrynocephalus* are arboreal climbers.

2) The relatively long forelimbs (FL/SPL; see Table 2) are shared with climbers (*Anolis*, *Aphaniotis*, *Calotes*, *Corytophanes*, *Enyaloides*, *Lophognathus*, *Plica*, *Rhacodactylus*), ground-livers (*Leiocephalus*, *Leiolepis*, *Phrynocephalus*), and those with mixed habits (*Lacerta*, *Sceloporus*).

3) Long penultimate phalanges are shared with *Scandensia*, interpreted as a climber, and also with the extant *Lacerta*, *Rhacodactylus*, and *Sceloporus*, of which only *Rhacodactylus* is strictly arboreal.

**Table 2 Measurements and comparisons of limb proportions for the new Daohugou lizard with the Early Cretaceous Spanish *Scandensia*, and representatives of modern lizards** (from the collections of the Natural History Museum, London) (mm)

	SPL	FL	Hu	Ra	Hd	HL	Fe	Ti	Ft	PuFt	FL/HL (%)	Hd/FL (%)	Hd/SPL (%)	FL/SPL (%)	Ft/SPL (%)	PuFt/Ft (%)	PuFt/Fe (%)
Daohugou 2	60.1	25.1	8.5	6.8	12.5	40.0	12.7	10.4	16.8	3.0	62.8	49.8	20.8	41.8	28.0	17.9	23.6
<i>Scandensia</i>	26.0	13.3	4.6	3.3	5.3	15.4	5.0	3.6	6.9	1.3	86.2	39.8	20.4	51.2	26.5	18.8	26.0
<i>Agama</i>	105.0	58.8	23.0	18.0	17.5	65.0	23.0	19.0	23.0	3.0	90.5	29.8	16.7	56.0	21.9	13.0	13.0
<i>Anolis</i>	115.0	54.2	19.5	17.0	18.0	81.5	25.0	21.5	35.0	4.0	66.5	33.2	15.7	47.1	30.4	11.4	16.0
<i>Aphanizis</i>	62.5	44.0	16.5	13.0	14.5	66.3	25.5	23.0	17.5	—	66.4	33.0	23.2	70.4	28.0	—	—
<i>Calotes</i>	119.0	69.0	24.5	19.5	24.0	90.5	29.5	25.0	36.0	4.5	76.2	34.8	20.2	58.0	30.3	12.5	15.3
<i>Corytophanes</i>	107.0	53.3	19.5	15.5	18.0	95.0	34.0	28.0	33.0	4.5	56.1	33.8	16.8	49.8	30.8	13.6	13.2
<i>Ctenosaura</i>	136.0	62.0	23.0	15.0	24.0	99.5	27.0	22.5	50.0	4.0	62.3	38.7	17.6	45.6	36.8	8.0	14.8
<i>Enyaloides</i>	115.0	51.0	17.5	14.5	19.0	90.5	25.5	25.0	40.0	4.0	56.4	37.3	16.5	44.3	34.8	10.0	15.7
<i>Eremias</i>	—	30.0	9.5	7.5	13.0	34.0	12.0	9.5	13.0	2.0	88.2	43.3	—	—	—	15.4	16.7
<i>Eumeces</i>	178.0	57.3	22.0	14.0	21.0	65.0	24.0	16.0	25.0	3.0	88.2	36.6	11.8	32.2	14.0	12.0	12.5
<i>Gekko</i>	143.0	56.3	21.0	15.0	19.0	69.3	27.0	19.0	23.0	3.0	81.2	33.7	13.3	39.4	16.1	13.0	11.1
<i>Lacerta</i>	132.0	49.0	18.0	13.0	18.0	77.5	23.0	17.5	37.0	4.5	63.2	36.7	13.6	37.1	28.0	12.2	19.6
<i>Leiocephalus</i>	135.0	61.0	23.0	15.0	23.0	94.5	28.5	25.0	41.0	4.5	64.6	37.7	17.0	45.2	30.4	11.0	15.8
<i>Leiolepis</i>	142.0	63.5	19.0	19.0	25.0	93.0	25.5	25.5	42.0	4.5	68.3	39.4	17.6	44.7	29.6	10.7	17.6
<i>Lophognathus</i>	102.0	52.8	18.0	15.5	19.0	92.5	28.5	26.0	38.0	4.5	57.1	36.0	18.6	51.8	37.3	11.8	15.8
<i>Phrynocephalus</i>	99.0	63.3	22.5	18.0	22.0	80.0	27.5	26.0	26.0	4.5	79.1	34.8	22.2	63.9	26.3	17.3	16.4
<i>Plica</i>	107.0	68.0	22.0	19.0	27.0	90.0	29.5	25.0	35.0	5.0	75.6	39.7	25.2	63.6	32.7	14.3	16.9
<i>Pogona</i>	219.0	92.0	34.5	28.0	30.0	106.5	38.5	31.5	37.0	4.0	86.4	32.6	13.7	42.0	16.9	10.8	10.4
<i>Rhacodactylus</i>	141.0	57.0	19.0	15.0	23.0	68.0	23.5	16.5	28.0	5.0	83.8	40.4	16.3	40.4	19.9	17.9	21.3
<i>Sceloporus</i>	112.0	50.5	18.0	12.5	20.0	59.0	21.0	16.0	22.0	4.0	85.6	39.6	17.9	45.1	19.6	18.2	19.0
<i>Varanus</i>	182.0	56.5	17.0	14.0	25.0	72.0	22.0	15.0	35.0	5.0	78.5	44.2	13.7	31.0	19.2	14.3	22.7

Abbreviations as in Table 1 plus PuFt, penultimate phalange of digit 4 on foot.

Thus V 13747 shows limb proportions (most notably the long hands) suggestive of a climbing habit, though not necessarily in trees, but this is open to interpretation and relative proportions may have changed with growth.

### 3 Conclusions

On the basis of skull morphology, IVPP V 13747 is probably a lizard. The relatively high presacral vertebral count suggests it may be a scleroglossan but, on current knowledge of post-hatchling development, the combination of paired premaxillae, frontals and parietals and a complete postorbital bar precludes attribution to any living family. A combination of skull and postcranial morphology indicates that it is distinct from all described Jehol Biota lizards and from the other juvenile lizard previously reported from Daohugou (Evans and Wang, 2007). IVPP V 13747 can also be distinguished from most other described Jurassic and Early Cretaceous lizards on body proportions and cranial features, but there are similarities with the incompletely known *Parviraptor* (Evans, 1994a) and an unnamed possible gekkonomorph from the Lower Cretaceous of Mongolia (Conrad and Norell, 2006). IVPP V 13747 undoubtedly represents a new lizard record from China, but more mature specimens are needed to permit comprehensive comparisons. Nonetheless, the recovery of two distinct juvenile lizard specimens from Daohugou not only indicates the presence of squamates at this important salamander locality, but also hints at their unexpected diversity. With further excavation, the site has the potential to yield more phylogenetically informative adult material. The limb proportions of this animal (especially long manus) suggest it may have been a climber in life.

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