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## A new lizard (Reptilia: Squamata) with exquisite preservation of soft tissue from the Lower Cretaceous of Inner Mongolia, China

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The Early Cretaceous Jehol Biota of China includes seven named lizard taxa: *Yabeinosaurus tenuis* and *Dalinghosaurus longidigitus*; the gliding *Xianglong*; more fragmentary remains referred to the genera *Pachygenys* and *Mimobecklesisaurus*; and the undiagnostic juvenile skeletons *Jeholosaurus* and *Liaoningolacerta*. Here we describe new lizard remains from the Yixian Formation at Liutiaogou, Ningcheng County, Inner Mongolia. The eight specimens vary in size and ontogenetic development, but appear to pertain to a single species. Several specimens show unparalleled preservation of soft tissue impressions including scalation and pigmentation, claw sheaths, sternal and extrastapedial cartilages, as well as rarely preserved skeletal elements like orbitosphenoids and postcloacal bones. The combination of characters precludes attribution to known taxa both within and outside China, and the new lizard is named *Liushusaurus acanthocaudata* gen. et sp. nov. Cladistic analysis supports the placement of *Liushusaurus* within the Scincogekkonomorpha, as the sister group of Scleroglossa.

**Key words:** *Liushusaurus*; scalation; Jehol Biota; Scleroglossa; new taxon

### Introduction

Deposits of the Jehol Group of northeastern China have yielded numerous lizard remains, most of which can be attributed to one of two taxa: *Yabeinosaurus tenuis* Endo & Shikama, 1942 (Ji *et al.* 2001; Evans *et al.* 2005) and *Dalinghosaurus longidigitus* Ji, 1998 (Ji & Ji 2004; Evans & Wang 2005; Evans *et al.* 2007). Three other genera have been named on the basis of juvenile specimens: *Jeholacerta* Ji & Ren, 1999, *Liaoningolacerta* Ji, 2005 and *Xianglong* Li *et al.*, 2007. Although its skull is poorly preserved, *Xianglong* can be distinguished on the basis of the elongate gliding ribs. Unfortunately, the same is not true for either *Jeholacerta* or *Liaoningolacerta*. The type and only specimen of the first is immature and consists of a skin impression with a few problematically interpreted skull impressions. The diagnosis lacks any derived features to distinguish *Jeholacerta* from known taxa or to form the basis of a referral of new material. *Liaoningolacerta* is almost equally problematic. The type and only specimen appears to preserve some skeletal remains, but its extreme immaturity renders the existing interpretation of cranial morphology problematic, and the diagnosis is a mixture of ontogenetic observations (e.g. unfused astragalus and calcaneum) and generalised lizard characters (moderate expansion of scapula), making attribution of adult specimens to the same genus impossible.

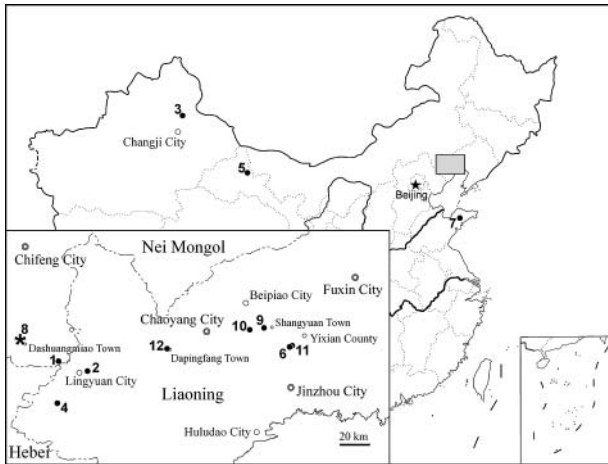
Both *Jeholacerta* and *Liaoningolacerta* must be regarded as *nomina dubia*. Two further lizards have been named on the basis of fragmentary remains from deposits that may be contemporaneous with the Jehol Biota (Wang & Evans 2006a, 2006b; Wang & Li 2008). These are *Mimobecklesisaurus* Li, 1985, based on a partial skull and osteoderms from Gansu, and *Pachygenys* Gao & Cheng, 1999 from Shandong (lower jaw specimens).

Here we describe new lizard material from the Yixian Formation at Liutiaogou, Nei Mongol (Inner Mongolia) (Fig. 1). There are eight individuals, ranging in age from near-hatchling to mature. Allowing for ontogenetic variation, body shape, limb proportions, scalation and skull morphology suggest they represent a single new taxon.

### Geological background

All of the material described here comes from a locality close to Liutiaogou Village, Dashuangmiao Town, Ningcheng County, Chifeng City, Nei Mongol (Inner Mongolia) (Fig. 1). The beds are referred to the Yixian Formation, Jehol Group, Lower Cretaceous (Wang *et al.* 2000). This locality has also yielded new gomphaeschnid dragonflies (B. L. Zhang *et al.* 2008) and chresmodid insects (X. W. Zhang *et al.* 2008), exceptionally well-preserved

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**Figure 1.** Localities (in alphabetical order) of Jurassic and Early Cretaceous lizards in China. \* denotes locality of *Liushusaurus acanthocaudata* (8, Liutiaogou). An enlargement of the grey area is shown in the lower left corner. Jurassic localities: 1. Daohugou, Ningcheng County, Nei Mongol (Inner Mongolia): Squamata gen. et sp. indet. 1 (Evans & Wang 2007) & 2 (Evans & Wang 2009), ?Late Jurassic (YW); 2. Gezidong (Ketzutung), Lingyuan City, Liaoning: ‘*Yabeinosaurus*’ *youngi* (Hoffstetter 1964; regarded as questionable by Wang & Li 2008), ?Middle Jurassic; 3. Wucuiwan, Changji City, Xinjiang: Squamata gen. et sp. nov. (YW, work in progress), Middle/Late Jurassic. Localities of the Lower Cretaceous Yixian Formation: 4. Dawangzhangzi, Lingyuan City, Liaoning: *Dalinghosaurus longidigitus*, *Yabeinosaurus tenuis* (Evans & Wang 2005; Evans *et al.* 2005); 5. Hongliugedajing, Subei County, Gansu: *Mimobecklesisaurus gansuensis* (Li 1985); 6. Jingangshan, Yixian County, Liaoning: *Yabeinosaurus tenuis* (Ji *et al.* 2001; Evans *et al.* 2005); 7. Laiyang City, Shandong: *Pachygenys thlastesa* (Gao & Cheng 1999), Doushan Formation (lateral equivalent of Yixian Formation, personal communication with Wang X. L.); 8. Liutiaogou, Ningcheng County, Nei Mongol (Inner Mongolia): *Liushusaurus acanthocaudata* (this paper); 9. Lujiatun, Beipiao City, Liaoning: *Dalinghosaurus longidigitus* (Evans *et al.* 2007); 10. Sihetun, Beipiao City, Liaoning: *Dalinghosaurus longidigitus*, *Yabeinosaurus tenuis* (Evans & Wang 2005; Evans *et al.* 2005); 11. Zaocishan (Tsaotzushan), Yixian County, Liaoning: *Yabeinosaurus tenuis* (specimen lost, Endo & Shikama 1942; Wang & Li 2008). Locality of the Lower Cretaceous Jiufotang Formation: 12. Dapingfang, Chaoyang City, Liaoning: *Yabeinosaurus tenuis* (Evans *et al.* 2005).

material of a new lamprey (Chang *et al.* 2006), a juvenile pterosaur (Lü 2009), as yet undescribed bird and mammal material, and more typical elements of the Yixian biota including the fish *Lycoptera* and acipenseriforms (*Peipiaosteus* and *Protosphephurus*). Precise correlation of the horizon with those in Liaoning has yet to be made, but it is thought to be equivalent to either the Jianshangou or Dawangzhangzi bed (*c.* 124–122 Ma) of the Yixian Formation (X. L. Wang, pers. comm., July 2006).

## Systematic palaeontology

Squamata Oppel, 1811

Genus *Liushusaurus* gen. nov.

**Type species.** *Liushusaurus acanthocaudata* gen. et sp. nov.

**Diagnosis.** As for type species.

**Derivation of name.** *Liushu*, Chinese, willow tree (derived from “Liutiao”, willow leaf, of Liutiaogou, meaning “willow leaf valley” where the fossils were excavated); *sauros*, Greek, reptile.

**Occurrence.** As for type species.

*Liushusaurus acanthocaudata* sp. nov.  
(Figs 2–10)

**Diagnosis.** A medium-sized (SPL = 66 mm in holotype) Early Cretaceous lizard. Differs from the Yixian lizards *Yabeinosaurus* (e.g. Evans *et al.* 2005) and *Dalinghosaurus* (Ji 1998; Ji & Ji 2004; Evans & Wang 2005) in having relatively longer forelimbs; differs from *Dalinghosaurus* in having more than six cervical vertebrae; differs from *Yabeinosaurus* in reaching skeletal maturity at a smaller size, in having expanded, hook-like (perforate) clavicles, and in having a proportionally shorter presacral region; differs from *Xianglong* (Li *et al.* 2007) in lacking elongated gliding ribs; differs from the Japanese Early Cretaceous *Kuwajimalla* (Evans & Manabe 2008) in lacking multicuspoid teeth; and differs from both *Yabeinosaurus* and the Japanese Early Cretaceous *Sakurasaurus* (Evans & Manabe 2009) in lacking co-ossification of the postorbital and postfrontal and restriction of the upper temporal fenestra. Resembles *Yabeinosaurus* (Evans *et al.* 2005) and differs from *Dalinghosaurus longidigitus* (Evans & Wang 2005) and Late Jurassic German *Bavarisaurus* (Evans 1994a) in having proportionally shorter feet; differs from *Mimobecklesisaurus* (Early Cretaceous, China, Li 1985) and other Jurassic-Cretaceous paramacellodids (Hoffstetter 1967; Evans & Chure 1998) in lacking a body covering of rectangular osteoderms; differs from *Jeholacerta* (Ji & Ren 1999), *Yabeinosaurus*, and from the Early Cretaceous Lebanese *Baabdassaurus* (Arnold *et al.* 2002) in the elongate, spiky scales on the tail; differs from the Italian Early Cretaceous *Chometokadmon* (Evans *et al.* 2006) in having a much shorter parietal and a relatively shorter presacral body length; resembles the Late Jurassic German *Ardeosaurus* (Mateer 1982; Estes 1983) and differs from the Jurassic-Cretaceous *Eichstaettisaurus* (Evans *et al.* 1999, 2004) and the Early Cretaceous Iberian *Meyasaurus* (Evans & Barbadillo 1997) in having a slightly restricted upper temporal fenestra, loss of parietal foramen, and fewer teeth in the maxilla; resembles the Late Cretaceous Mongolian ‘mongolochampopines’ (Alifanov 2000) in having paired frontals, loss/reduction of the parietal foramen, and a short parietal, but differs in having proportionally shorter frontals and therefore a shorter, more rounded antorbital skull; differs from *Meyasaurus*, *Dicrodon* and

*Bicuspidon* (Nydam & Cifelli 2002a, mid-Cretaceous, USA), *Atokosaurus* (Nydam & Cifelli 2002b, mid-Cretaceous, USA), and the ‘mongolochamopines’ *Mongolochamops* and *Altanteius* (Alifanov 2000, Upper Cretaceous, Mongolia) in having conical rather than cuspidate teeth; differs from the Early Cretaceous Spanish *Hoyalacerta* (Evans & Barbadillo 1999) in having fewer, larger teeth and proportionally longer limbs; differs from the Early Cretaceous Mexican *Huehucuetzpalli* (Reynoso 1998) in the retention of a large free postfrontal, the absence of a parietal foramen, paired rather than fused frontals, and the absence of an elongated premaxilla; differs from *Bavarisaurus* (Evans 1994a) and the Spanish Early Cretaceous *Scandensia* (Evans & Barbadillo 1998) in having well-developed vertebral condyles, and from the latter in having a cruciform rather than rhomboid interclavicle and in rib morphology (narrow *vs* expanded ribs); differs from the Late Jurassic German *Ardeosaurus* (Mateer 1982), British Early Cretaceous *Parasaurillus* (Evans & Searle 2002), and *Dalinghosaurus* (Evans & Wang 2005) in lacking obvious sculpture on the skull bones, even in mature specimens; differs from the Jurassic–Cretaceous *Parviraptor* (Evans 1994b) in having a short single parietal, rather than paired elongate bones, and in lacking a parietal foramen; and differs from the Early Cretaceous *Dorsetisaurus* (Hoffstetter 1967) in lacking well-developed sculpture and in tooth morphology. Comparison with *Pachygenys* (Gao & Cheng 1999) is difficult as the latter is represented only by two, albeit very distinctive, lower jaws with eight teeth clustered in the anterior part of the dentary. The lower jaw dentition is not clearly visible in any of the *Liushusaurus* specimens, but the presence of 13 maxillary teeth distributed evenly along the bone renders it unlikely that they occluded with a lower jaw dentition like that of *Pachygenys*. Comparison with other taxa based on dentary specimens is similarly problematic, but *Liushusaurus* differs from the British Early Cretaceous *Pseudosaurillus* (Hoffstetter 1967; Evans & Searle 2002) in having larger teeth (very small in relation to jaw height in *Pseudosaurillus*) and from the Jurassic–Cretaceous Euramerican *Saurillodon* (Seiffert 1973) in jaw and tooth proportions (short robust dentary, larger recurved teeth in *Saurillodon*).

**Derivation of name.** From: *acanthus*, Latin, spine; *cauda*, Latin, tail, in reference to the appearance of the tail scalation.

**Holotype.** IVPP V15587A/B (vertebrate collection number of Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing), part and counterpart of a young adult specimen, snout–pelvic length *c.* 66 mm (Fig. 2).

**Paratype.** IVPP V14715A/B (partial skull and postcranium, Fig. 3B), showing well-preserved scale pattern,

notably the tail scalation that forms the basis of the specific name.

**Other material.** IVPP V14716 (incomplete postcranial skeleton with skin traces and post-autotomy tail replacement, Fig. 3D); IVPP V14746A/B (part and counterpart of incomplete postcranial skeleton, Fig. 3F); IVPP V15507 A/B (isolated hind limb with fine scalation, Fig. 9A, B); IVPP V15508 A/B (complete skeleton of very young, hatchling or near hatchling, animal, Fig. 3C); IVPP V15011 (adult individual, Fig. 3A); IVPP V15586A/B (skeleton and fine skin impressions from subadult individual, with post-autotomy tail replacement, Fig. 4). All specimens are from the type locality.

**Occurrence.** Liutiaogou Village, Dashuangmiao Town, Ningcheng County, Chifeng City, Nei Mongol (Inner Mongolia) (Fig. 1); Lower Cretaceous, Jehol Group, Yixian Formation.

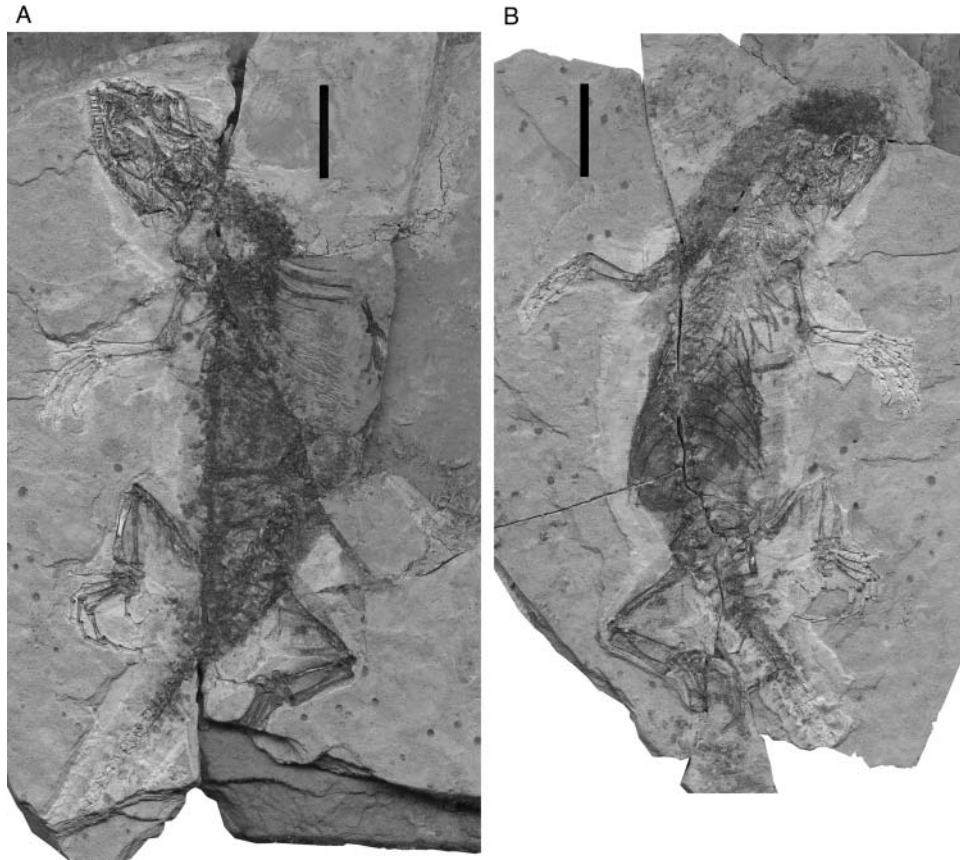
**Remarks.** Two juvenile lizard skeletons (Evans & Wang 2007, 2009) have recently been described from the Daohugou fossil bed of Inner Mongolia and neighbouring areas, associated with a diverse caudate fauna (Wang 2004; Wang & Rose 2005; Wang & Evans 2006b). The bed is probably of Upper Jurassic age based on composite lithological and palaeontological data, although J<sub>2</sub>, J<sub>3</sub>, and K<sub>1</sub> ages have all been proposed and there is currently no consensus. *Liushusaurus* differs from the first Daohugou lizard (Evans & Wang 2007) in having proportionally longer forelimbs (relative to the hind limbs), shorter hind limbs (relative to snout–pelvis length, SPL) and a shorter tibia (relative to the femur). This is also true for the second Daohugou lizard (Evans & Wang 2009), which also has a markedly longer femur, tibia and foot (to SPL) (Table 1). *Liushusaurus* further differs from the second Daohugou lizard in having broader body shape and shorter preorbital region, in contrast to the slender body and relatively longer preorbital region of the latter.

## Description

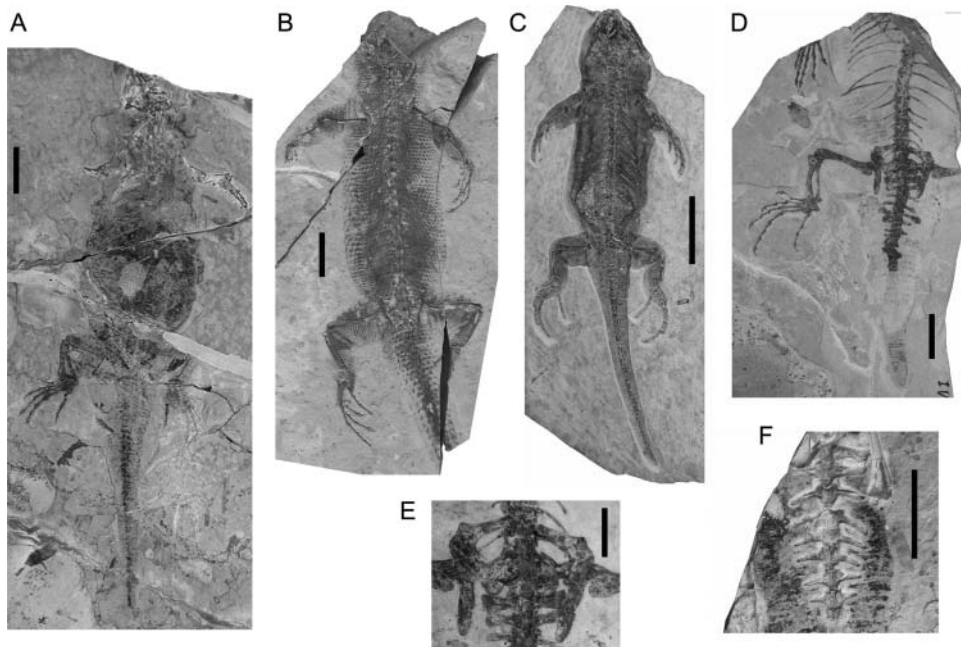
### Skull

The skull of *Liushusaurus* is complete only on IVPP V15586 and V15587 (Fig. 5A, B), but IVPP V14715, V15011 and the juvenile IVPP V15508 provide supplementary information (Figs 3, 6). However, much of the skeleton is preserved in impression and the description that follows is based primarily on high definition peels. This limits the level of fine detail available, but larger specimens suggest the presence of weak sculpture on the frontals and parietals.

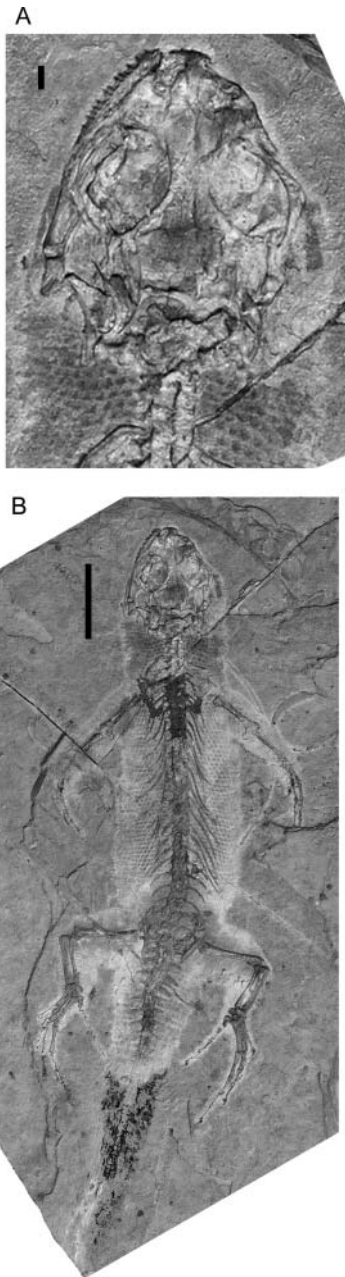
The nasals are paired and short, making the skull short and rather rounded in the antorbital region. The prefrontal is large. The frontals are parallel-sided for the anterior



**Figure 2.** Holotype specimen (IVPP V15587) of *Liushusaurus acanthocaudata* gen. et sp. nov., from the Liutiaogou locality, Inner Mongolia. **A**, part and **B**, counterpart. Scale bars = 10 mm.



**Figure 3.** Additional specimens of *Liushusaurus acanthocaudata* gen. et sp. nov. from the type locality. **A**, IVPP V15011; **B**, IVPP V14715; **C**, IVPP V15508; **D**, IVPP V14716; **E**, IVPP V14716, detail of pelvis; **F**, IVPP V14746, detail of vertebrae. All scale bars = 10 mm, except E = 5 mm.



**Figure 4.** *Liushusaurus acanthocaudata* gen. et sp. nov., IVPP V15586, main block. **A**, skull; **B**, whole skeleton. Scale bars 1 mm and 10 mm respectively.

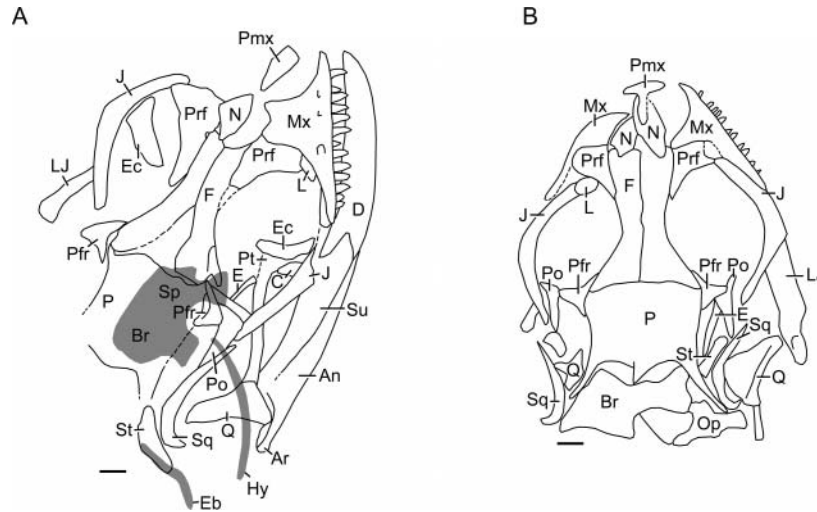
two-thirds of their length and then expand at the frontoparietal suture. That suture appears straight in young adults like IVPP V15586, but in larger specimens (e.g. IVPP V15011) is more irregular. The parietal is unpaired and lacks a parietal foramen. Its shape varies between immature (e.g. IVPP V15586, short and broad, with emarginations on either side of the midline) and mature (e.g. IVPP V15011, V15587, longer, more U-shaped posterior margin). The postparietal processes lengthen with maturity and are long and divergent in IVPP V15587. The pit for the processus ascendens of the braincase lies forward of posterior parietal margin. The premaxilla is not well-preserved in any specimen but IVPP V15586 (Fig. 5B) shows that it is single, broad in its alveolar portion, and has a narrow nasal process. The maxilla is rather short (~13 teeth) with a tall anterior facial process and a short posterior process that is excluded from the orbit by the prefrontal and the jugal. The latter biramous bone reaches the anterior margin of the orbit, forms its ventral rim, and then ascends to form most of the postorbital margin, restricting the entry of the postorbital. Between the jugal and the prefrontal in both IVPP V15586 and V15587 (Fig. 5A, B) there is a small fragment of bone that is probably a lacrimal. The postfrontal and postorbital are separate, with the postfrontal spanning the frontoparietal junction. The postorbital has a small orbital component and a longer posterior extension. This is excluded from the margin of the lower temporal fenestra by a contact between the jugal and the squamosal. The latter is slender and classically ‘hockey-stick shaped’ (Robinson 1967), with a curved posteroventral tip that met the quadrate. Behind the squamosal in IVPP V15587 is a shorter, blade-like bone that we interpret as the supratemporal. The quadrate has a well-developed lateral conch and its tympanic crest is notched dorsally for a ventral squamosal peg. In IVPP V15587, the lateral conch is broken away revealing the medial pterygoid wing with a distinct pterygoid lappet. Ventrally the bone tapers to a narrow mandibular condyle. The epipterygoid is columnar.

No specimen has the skull preserved in palatal view, so nothing is known of this region except that the slender quadrate rami of the pterygoids contact the quadrates.

The braincase is not well preserved in any specimen. In IVPP V15586, the braincase lies behind the parietal and has partially disarticulated on the right side, with the opisthotic being slightly displaced. Rather short paroccipital processes

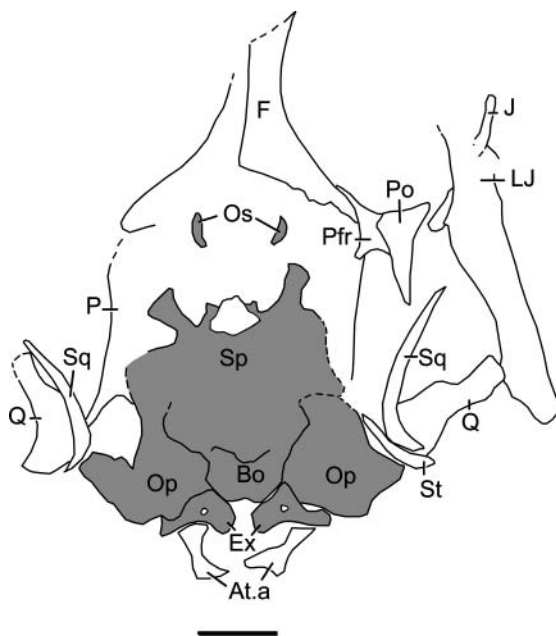
**Table 1.** Comparative limb proportions in two specimens of *Liushusaurus acanthocaudata* gen. et sp. nov. (V15587, V15508) and two Daohugou lizards (V14386, V13747). DHG, Daohugou lizard; Fe, femur; FL, forelimb length; Ft, foot; Hd, head; HL, hind limb length; Hu, humerus; SPL, snout-pelvic length; Ti, tibia. SPL in mm; others in % proportions.

	SPL	FL/HL	HL/SPL	FL/SPL	Ft/Fe	Ti/Fe	Hu/Fe	Ft/HL	Fe/HL	Fe/SPL	Ti/SPL	Ft/SPL
V15587 subadult	66	92.1	40.1	37.3	121	74.6	81.3	50	41.3	16.8	12.5	20.3
V15508 hatchling	38.1	79	47.2	37.3	162	71.6	93.9	46	28.4	13.4	9.6	21.7
V14386 DHG 1	43.7	67	57.4	38	123	85	70.1	37.4	31	16	13.7	21.5
V13747 DHG 2	60.1	63	66	42	134	82.9	67	41.7	31.8	21	17.7	28



**Figure 5.** *Liushusaurus acanthocaudata* gen. et sp. nov., skull morphology drawn from silicon peels of **A**, IVPP V15587A and **B**, IVPP V15586A. The grey areas in **(A)** (basicranium and hyoid elements) have been superimposed from the counterpart block. Scale bars = 1 mm. Abbreviations: An, angular; Ar, articular; Br, braincase; C, coronoid; D, dentary; E, epipterygoid; Eb, epibranchial; Ec, ectopterygoid; F, frontal; Hy, hyoid; J, jugal; L, lacrimal; LJ, lower jaw; Mx, maxilla; N, nasal; Op, opisthotic; P, parietal; Pfr, postfrontal; Pmx, premaxilla; Po, postorbital; Prf, prefrontal; Pt, pterygoid; Q, quadrate; Sp, sphenoid; Sq, squamosal; St, supratemporal; Su, surangular.

meet the suspensorium bilaterally, and in IVPP V15011, the tips of elongate prootic alary processes extend forward to about half the length of the parietal body. The sphenoid (parasphenoid+basisphenoid), preserved in impression in IVPP V15587 (Fig. 5A) and in the juvenile IVPP V15508



**Figure 6.** *Liushusaurus acanthocaudata* gen. et sp. nov. Skull of IVPP V15508, juvenile, with dorsal and ventral impressions superimposed. Braincase in grey. Scale bar = 1 mm. Abbreviations as in Fig. 5 and: At.a, atlantal arches; Bo, basioccipital; Ex, exoccipital; Op, opisthotic; Os, orbitosphenoid.

(Fig. 6), is wide with divergent basiptyergoid processes, and is roughly equal in length to the basioccipital. IVPP V15508 also preserves small, comma-shaped orbitosphenoids *in situ* (Fig. 6, Os). These delicate bones, supporting the sides of the cartilage-membrane braincase, are rarely preserved in fossils.

In the lower jaw, the dentary is short and strongly bifurcated posteriorly, accommodating a large surangular. The sutures between the surangular, angular and articular are not clear on the casts, but there is certainly a separate angular and the articular has a strong retroarticular process. The hyoid apparatus is represented by a slender element that is probably a first ceratobranchial and, in the region of the supratemporal (IVPP V15587, Fig. 5A), a second cartilaginous element that could be an epibranchial.

### Axial skeleton

There were 26 presacral vertebrae of which the first seven or eight are cervicals, but it is not clear which rib is the first to attach to the sternum. The vertebrae are all procoelous, with well-developed rounded condyles that lack any trace of waisting at the contact with the centrum (contra varanoids) (Fig. 3F). The neural spines are low, the zygapophyses are broad and rather strongly angled (especially in the dorsal region) and there are well-developed zygosphenoidal surfaces. All rib attachments are single. The small atlantal arches are typically disarticulated (e.g. Fig. 6) and the atlantal intercentrum lies between the axis and the braincase. Cervical vertebrae are slightly shorter than the dorsals, with mid-ventral keels and keeled hypapophyses between

at least the first four vertebrae in the series (e.g. IVPP V15586). The two sacral ribs are of roughly equal size and make contact distally. The second sacral ribs lack any trace of a posterior process or flange. The anterior five to nine caudal vertebrae bear long, laterally directed transverse processes, followed by another four with shorter processes. The first caudal is shorter than those following and its transverse processes are deeply grooved. In IVPP V14715 the caudal fracture plane occurs on or about caudal eight, but posterior caudals are poorly preserved. Two specimens (IVPP V14716, V15586) have truncated tails with traces of the unossified regrowth (Figs 3D, 4). A haemal arch is visible on some tail vertebrae of IVPP V14715, lying in an intercentral, or posterior central, position.

The ribs are slender and single-headed. The first rib is on the fourth cervical vertebra as shown in IVPP V15586 (Fig. 4). This and the following two ribs are short and thick, with expanded ends for muscles attaching the pectoral girdle to the axial skeleton; rib four (cervical vertebra seven) is longer, more slender, and strongly curved, as are the next few in the series. All bear traces of the terminal costal cartilages but it is not clear which of these is the first to reach the sternum. The remaining presacral vertebrae all bear slender free ribs, although the last six are markedly shorter than those preceding them. Rib curvature decreases through the body. In the two larger specimens (IVPP V14716 and V14746), in particular, there are several pairs of long thoracoabdominal ribs that show little curvature and seem to span a body that was either unusually wide or rather flattened, suggesting an adult shape like that of the living iguanian *Sauromalus*.

### Pectoral girdle and forelimb

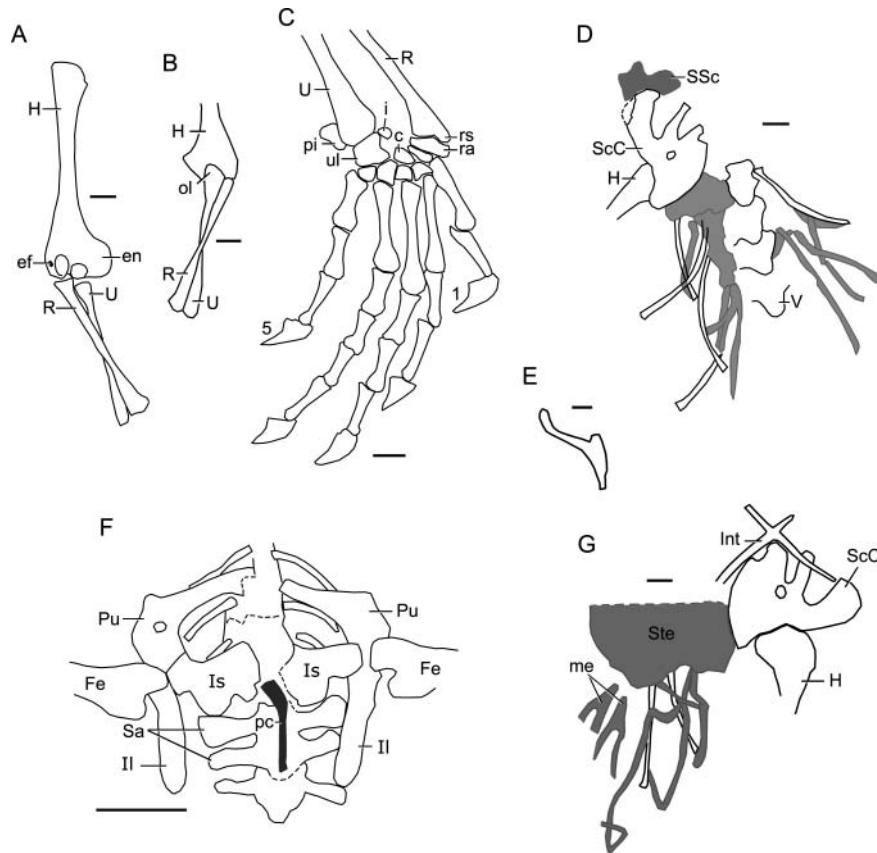
The pectoral girdle is divided between the part and counterpart blocks in the holotype specimen, and the ventral elements are obscured by the vertebral column. A cruciform interclavicle is preserved in IVPP V15587A, with a short anterior process and a longer posterior stem (Fig. 7G). Clavicles are not well preserved on any specimen, but the main block of V14715 has a right clavicle that is almost complete and has a hooked medial head (interpreted as a perforate clavicle without a complete posteromedial rim) and a short tapering dorsal process. The left clavicle lies adjacent to it, under the first right cervical rib, but only the hook-like medial part is visible (Fig. 7E). In the young IVPP V15508, the clavicles are sigmoid and unexpanded medially. The scapulocoracoids are preserved on several specimens (Fig. 7D, G). The component parts are fully co-ossified in IVPP V14715 and V15587, but not in IVPP V15586, indicating immaturity. The scapula part is relatively short with a small dorsal expansion but no scapular fenestra; the coracoid part is larger. Scapulocoracoid and anterior (primary) coracoid fenestrae are present, and there is a small posterior (secondary) coracoid notch. A shallow suprascapular cartilage is preserved above the scapula in

IVPP V14715 (Fig. 7D), its vertebral border showing clear traces of the notching seen in many living taxa. The cartilaginous sternum (presternum of Russell & Bauer 2008) is preserved in IVPP V14715 and V15587 (Fig. 7D, G) and appears to have been a wide rhomboid, like that of many living taxa. The posterolateral margins angle towards the midline, with three direct attachment points for ribs and, on either side of the midline, attachment of a bifurcate mesosternal element (*sensu* Russell & Bauer 2008) to which two further costal cartilages attach (Fig. 7G). All of the cartilage traces are thin; none shows any evidence of mineralization. It is not possible to say whether or not sternal fontanelles were present.

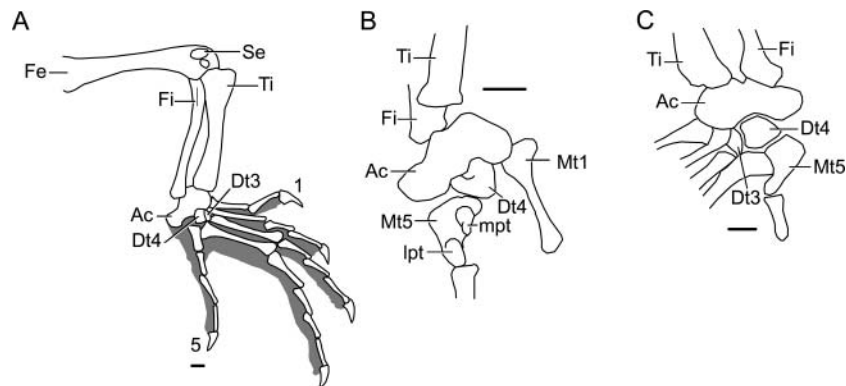
The humeri are preserved as clear impressions in IVPP V14715 (Fig. 7A). The joint surfaces are fully formed, with ossified and attached epiphyses. The proximal end of the bone is relatively narrow and lacks a strong deltopectoral crest. The shaft is long (humerus 79% of femoral length) and rather slender. Distally, the bone expands asymmetrically, the ectepicondyle remaining small (with an enclosed ectepicondylar foramen) and the entepicondyle flaring out into a large flexor muscle expansion. Both radial and ulnar condyles are well rounded. The radius and ulna of IVPP V14715 are in articulation, again with complete joint surfaces and a short wide ossified olecranon (ulna, Fig. 7A, B). Like the humerus, they are comparatively long (forearm roughly 85% of crural length). Distally the ulna is expanded into a hemispherical condyle for articulation with the carpus whereas the radius develops a distinct styloid process (Fig. 7C). The carpus is preserved on several specimens but with different degrees of mineralization. It is well-preserved in the holotype (Fig. 7C). There are nine elements, including a distal series of five bones, either distal carpals 1–5 (Fabrezi *et al.* 2007; Russell & Bauer 2008) or the medial centrale and distal carpals 2–5 (Romer 1956; Maisano 2001). Three more proximal carpals are interpreted as ulnare, radiale and centrale (= lateral centrale of some authors, e.g. Romer 1956), and there is a large pisiform. The size of this bone, in conjunction with the expansion of the entepicondylar region, suggests the flexor carpi ulnaris muscle may have been strong. A small element associated with the ulnare is probably an intermedium (IVPP V15587, Fig. 7C).

The manus is 63% of pedal length, with metacarpal (Mc) three significantly longer than Mc4, and a phalangeal formula of 2:3:4:5:3. Mc1 and Mc5 are somewhat more robust than Mc2–4. Although the third digit has one less phalanx than the fourth, it is of roughly the same overall length. This is partly due to the longer third metacarpal but also because the second, third and fourth phalanx of the fourth digit are short (Fig. 7C). The fifth digit is also only slightly longer than digit one. Overall, therefore, although the hand is quite long, the digits have a rather symmetrical arrangement. The penultimate phalanges are longer than those preceding them, and the unguals are long and curved,

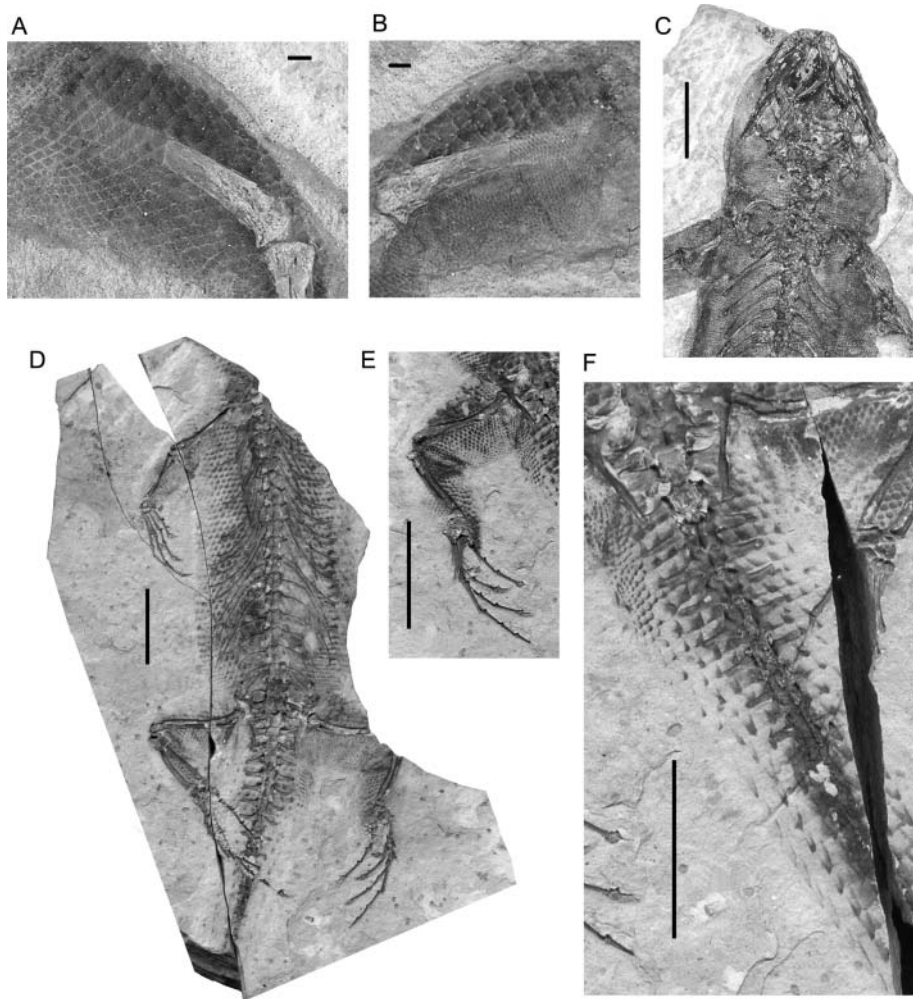




**Figure 7.** *Liushusaurus acanthocaudata* gen. et sp. nov., details of the postcranial skeleton. **A**, IVPP V14715B, humerus, radius and ulna, flexor surface; **B**, IVPP V14715A, partial humerus, radius and ulna, extensor surface; **C**, IVPP V15587A, manus, drawn from peel; **D**, IVPP V14715B, pectoral girdle, showing cartilaginous regions in grey; **E**, IVPP V14715A, detail of left clavicle, drawn from peel; **F**, IVPP V14716, pelvis with postcloacal bone in grey; **G**, IVPP V15587B, pectoral girdle, with cartilaginous sternum and sternal rib attachments in grey. All scale bars = 1 mm, except F = 5 mm. Abbreviations: c, centrale; ef, ectepicondylar foramen; en, entepicondyle; Fe, femur; H, humerus; i, intermedium; Il, ilium; Int, interclavicle; Is, ischium; me, mesosternum; ol, olecranon process; pc, possible postcloacal bone; pi, pisiform; Pu, pubis; R, radius; ra, radiale; rs, radial styloid process; Sa, sacrum; ScC, scapulocoracoid; SSc, suprascapula; Ste, sternum; U, ulna; ul, ulnare; V, vertebra; 1,5, digit numbers.



**Figure 8.** *Liushusaurus acanthocaudata* gen. et sp. nov., details of hind limb and foot. **A**, IVPP V14716 foot, drawn from peel, grey area shows extent of pedal soft tissues; **B**, IVPP V14715B, ankle region; **C**, IVPP V15587B, ankle region, drawn from peel. All scale bars = 1 mm. Abbreviations: Ac, astragalocalcaneum; Dt3,4, distal tarsals; Fe, femur; Fi, fibula; lpt, lateral plantar tubercle; mpt, medial plantar tubercle; Mt1,5, metatarsals; Se, sesamoid; Ti, tibia; 1,5, digit numbers.



**Figure 9.** *Liushusaurus acanthocaudata* gen. et sp. nov., scalation. **A** and **B**, part and counterpart of IVPP V15507, an isolated hind limb showing rhomboid ventral scales (**A**) and rhomboid scales above the femur and fine dorsal scales below it (**B**); **C**, IVPP V15508B showing dorsal scalation (small granular scales); **D–F**, IVPP V14715, showing ventral scalation; **D**, counterpart block (IVPP V14715B); **E**, hind limb from main block (IVPP V14715A); **F**, tail on IVPP V14715A, showing elongate spiny scales. Scale bars: A, B = 1 mm; C = 5 mm; D–F = 10 mm.

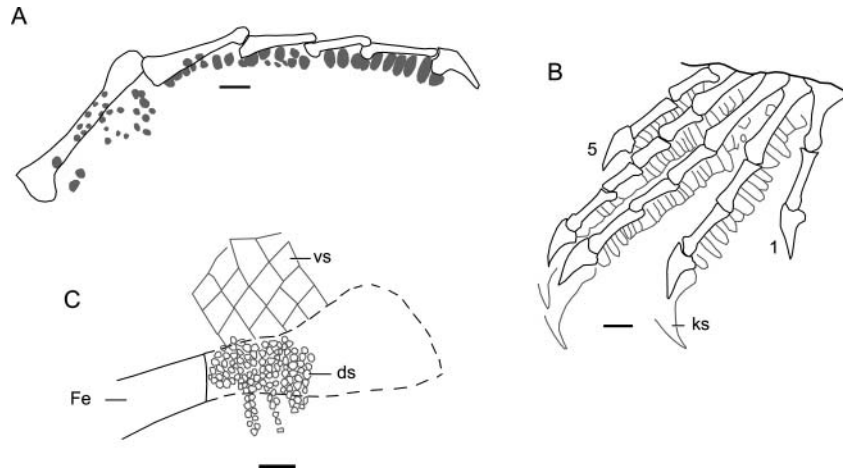
with a pronounced flexor tubercle. Keratin claw sheaths are visible on both V14715 and V14716, and where fully exposed, they are sharp and at least twice as long as the underlying unguis phalanx (Fig. 10B).

### Pelvic girdle and hind limb

Like the scapulocoracoid, the pelvic elements can be separate, sutured or fused depending on the size/age of the individual. The ilium is long and slender, with an apparently horizontal dorsal edge, a short preacetabular process and a prepubic process. The pubis and ischium are best preserved on the counterpart block of IVPP V14715, on IVPP V14716 (Figs 3E, 7F), and IVPP V14746. They frame a large thyroid fenestra. The pubis is relatively elongate with a slender distal portion that is oriented anteromedially and ends with a narrow, moderately elongated but anteromedially directed

symphyseal process. The obturator foramen is proximal in position, as is the small, slightly incurved lateral pubic process. The ischia are flask-like, with a distinct posterior angle (posterior edges damaged in the specimen shown, Fig. 7F) and short symphyseal process. Altogether, the puboischiadic plate is only half as long as it is wide. It lies anterior to the level of the first sacral rib due to the posterior position of the sacroiliac attachment, well behind the level of the acetabulum.

IVPP V14716 and V14746 both preserve a long, asymmetric, rod-like element, expanded anteriorly and tapering posteriorly (Fig. 7F). This underlies the sacral region, but is quite distinct from the pubis and ischium and is most reasonably interpreted as a postcloacal or hemipenial bone, on the assumption that only one of the pair has been preserved in each case.



**Figure 10.** *Liushusaurus acanthocaudata* gen. et sp. nov., scalation. **A**, IVPP V14716, pes, fourth digit, drawn from peel, subdigital scales in grey; **B**, IVPP V14716, manus with outlines of subdigital scales and keratin claw sheaths, drawn from peel; **C**, IVPP V15507B, detail of femoral region showing size difference between small dorsal and large ventral scales. All scale bars = 1 mm. Abbreviations: ds, dorsal scales; Fe, femur; ks, keratin claw sheath; vs, ventral scales; 1, 5, digit numbers.

The mature femur is long, robust and sigmoid. At its distal end there may be one or more sesamoid bones (Fig. 8A). The tibia and fibula are shorter, with the tibia the stouter of the two, although even in the large specimens (e.g. IVPP V. 14716, Fig. 8A) there is only a slight development of a cnemial crest. The distal end is not clearly preserved in any specimen but it appears to be notched in IVPP V14715 and V14746. The fibula meets the side of the lateral femoral condyle and bears a weak proximal crest in the largest specimens (e.g. IVPP V14746). Distally it has a convex epiphysis. Both elements meet the astragalocalcaneum in a relatively broad articulation. The three-dimensional structure of the tibio-talar joint is difficult to reconstruct, but it is at least incipiently sellar. The astragalus and calcaneum are fully co-ossified in the adult but, like the pectoral girdle and pelvis, progress from fully separated, to sutured, to fully co-ossified in individuals of different ontogenetic age. The adult bone is relatively short and wide with a distinct rounded calcaneal tuber (e.g. IVPP V14715, V14716, V14746, Fig. 8). Distally it meets a large fourth distal tarsal (Dt4) in a complex articulation whereby Dt4 has a tongue-like process that fits under the edge of the astragalocalcaneum but the latter bone, in turn, seems to fit into a notch on the proximal surface of Dt4. There is also a smaller distal tarsal three. The metatarsals (Mt) increase in size from Mt1 to Mt4, although Mt4 is only slightly longer than Mt3. Mt5 is short and hooked, with equally pronounced plantar tubercles separated only by a narrow groove for the long flexor tendon. Proximally, Mt5 meets Dt4 but it is uncertain whether or not it contacted the astragalocalcaneum in life. The pedal phalangeal formula is usually 2:3:4:5:4 (2:3:4:5:3 in IVPP V15011). In IVPP V14715, the pedal digits are like those of the hand in being relatively slender; in IVPP V14716 they are more robust

and therefore appear shorter. The unguals are long and curved, with a distinct flexor tubercle. Where preserved and exposed, the keratin claws are more than twice the length of the underlying ungual phalanges.

#### Soft tissue preservation and scalation

IVPP V14715, V14716, V15508, V15011, and V15587 show clear body outlines. Most specimens represent a rather stocky lizard with short sturdy legs, but IVPP V14716 is remarkably broad, both in the body and in the proximal parts of the legs and tail. Its body outline extends beyond the wide rib cage and the legs and tail appears thick. None of the body or tail impressions, either dorsally or ventrally, shows any trace of osteoderms.

IVPP V14715 and IVPP V15587 are notable in preserving much of the cartilaginous parts of the skeleton (as described in the sections above) and also for the exquisite preservation of the body scales, although scalation is preserved to different degrees in most specimens. Depending on the original position of interment, either the dorsal or the ventral body scales are better preserved. These dorsal and ventral scales differ in size and in shape. The dorsal scales are visible only on the edges of the trunk in IVPP V14715 but the ventral scales are also imprinted onto the counterpart block, obscuring the dorsal layer (Fig. 9D–F). IVPP V14716 and V15508 (Fig. 9C) preserves this dorsal layer and shows that the dorsal scales are much smaller than those of the venter. On the venter, the scales are rhomboidal and overlapping. These continue onto the neck but the scales seem to become smaller on the head, at least on the side of the head that is exposed in the main part of IVPP V14715. Each of the ventral scales has a light base and a dark free edge (Fig. 9D, E), but the amount of colour along the free edge varies from a thin strip to almost complete

coverage. Whether this is representative of the original pigment pattern is uncertain. The darkest scales are on the middle of the belly, with the remaining scales grading in colour from medial to lateral, although the darkly pigmented edge always faces towards the midline. There are 43–48 scale rows (c. 4 per segment) between the front and hind limbs (allowing for the difficulty of locating the axillary position precisely), and roughly 28–30 scales across the body. The large rhomboid ventral scales continue onto the underside of the limbs, but on the dorsal surface the scales are again smaller and rounded, the diameter decreasing dorsally and distally. IVPP V15507 is the part and counterpart of an incomplete leg, attributed to the new species only on scalation pattern (Figs 9A, B, 10C). It is significant only in the exquisite preservation of the dorsal and ventral scalation, with a stark contrast between the large rhomboid ventral scales and the tiny granular dorsal scales (>0.5 mm diameter).

In the foot, the first four metatarsals are bound together in a single sheath of skin, but the fifth is divergent. On the plantar surfaces of the manus and pes, some of the scale impressions become much deeper and this is particularly marked on the undersides of the digits (Figs 10A, B). These deep depressions reflect the presence of wide tuberculous plantar scales, a common feature in modern lizards (Arnold *et al.* 2002). The penultimate phalanges bear a ventral median row of 5–6 of these wide scales (Fig. 10A), each tubercle separated from the next by a thin band of skin. This structure is particularly clear in V14716.

On the ventral side of the tail (Fig. 9F), the anterior scales are like those of the body but further distally, they elongate and taper, so that the tail seems to have been covered in a sheath of longitudinal spines. From the base of the tail to the level of the fifth caudal vertebrae, however, the lateral flanking scales and the dorsal scales are smaller and rounded, like those on the dorsum of the legs. Further distally the flanking scales take the form of the ventral scales and become spiky. The more dorsal scales are visible in IVPP V14716 and on IVPP V14746. They seem to be smaller and have a more annular arrangement, with a slight size alternation between rows (e.g. IVPP V14746).

The head scales are small with no development of the enlarged, plate-like scales seen in many scincomorph and anguimorph lizards. Unusually, IVPP V14715 preserves the ear region. The area immediately in front of the quadrate is covered by small scales; these resume behind the jaw, but there is an uncovered area immediately behind the quadrate that marks the position of the tympanic membrane.

## Discussion

### Phylogenetic position

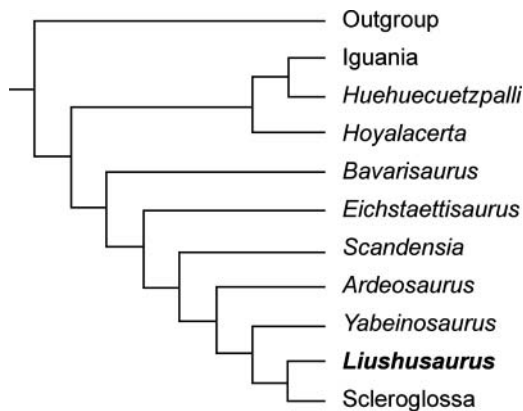
*Liushusaurus* is a squamate, as demonstrated by the columnar epipterygoid, the streptostylic quadrate, reduced

squamosal, procoelous vertebrae and fenestrate scapulocoracoid. As outlined in the diagnosis, it can be differentiated from other valid Yixian and Yixian equivalent lizards, and from well-preserved lizard specimens from other contemporaneous, or roughly contemporaneous, localities worldwide.

The retention of a relatively large postfrontal argues against iguanian affinity, as does the absence of a distinct mid-dorsal scale row (Estes *et al.* 1988). A bifurcated postfrontal that clasps the fronto-parietal suture has been listed as a scleroglossan synapomorphy (Estes *et al.* 1988, but see Townsend *et al.* 2004; Vidal & Hedges 2005), as has the presence of perforate clavicles (although this is present in some iguanians, e.g. *Gambelia wislizeni*, *Basiliscus*, Russell & Bauer 2008), of a cruciform interclavicle with a long anterior process, and of a notched (sellar) distal tibial epiphysis (Estes *et al.* 1988). Alternation in the size of tail scales has been cited as an autarchoglossan trait (Arnold *et al.* 2002), as has a marked difference in dorsal and ventral scale patterns (Camp 1923), although gekkotan skin patterns might be secondary (and the iguanian *Sceloporus* comes close to scleroglossan scalation, SEE pers. obs.).

The absence of body osteoderms precludes attribution to Scincidae, Cordylidae or Anguidae, or to the extinct Paramacellodidae. The absence of plate-like head scales differentiates *Liushusaurus* from Lacertidae, Gymnophthalmidae, Teiidae, Xantusiidae, Cordyliformes, or Scincidae, and many anguimorph lineages. Small regular head scales are found in iguanians, gekkotans and some anguimorphs (xenosaurs, shinisaurs or platynotans) and presumably represent the primitive squamate condition. The simple vertebral condyles preclude a varanoid relationship, whereas among recent genera, postcloacal bones are found in some gekkotans (Kluge 1982) and xantusiids (Rieppel 1976), and occasionally in *Varanus* (Smith 1935). *Liushusaurus* resembles lacertiforms (*sensu* Estes *et al.* 1988) generally in having a pterygoid lappet on the quadrate, a retroarticular process with a dorsal pit, and well-developed vertebral zygosphenes (Estes *et al.* 1988), and teioids more closely in the absence of the parietal foramen, the shape of the parietal (long posterior processes, no lateral parietal flanges, no extended squamosal/parietal contact: Conrad 2008; Evans 2008), the absence of strong dermal rugosities or osteoderms, and the presence of a posterior coracoid emargination. However, teioids lack an ectepicondylar foramen on the humerus and have fused frontals, although these are paired in the related boreoteioids (*sensu* Nydam *et al.* 2007).

This mosaic of scale and skeletal characters complicates systematic assignment, but is suggestive of a closer relationship to Scleroglossa than to Iguania. This was tested by phylogenetic analysis, using the data set of Conrad (2008) with 131 living and extinct genera representative of all major squamate clades (having limited all genera to single



**Figure 11.** Tree showing hypothesis of relationship for *Liushusaurus acanthocaudata* gen. et sp. nov. within Squamata, based on a simplified strict consensus of three equally parsimonious trees ( $L = 3687$ ) from a heuristic search using TNT (Goloboff *et al.* 2008) and the full data matrix of Conrad (2008).

representatives, and limited mosasauroids to a representative sample). The matrix was run first on PAUP 4.0b10 (Swofford 2002), completely unordered and then using the ordering of Conrad (2008), multistate taxa were treated as uncertainty, and Kuehneosauridae, *Marmoretta* and Rhynchocephalia were the designated outgroups. A preliminary heuristic analysis on unordered characters yielded 6 equally parsimonious trees (Tree length [ $L$ ] = 2536; Consistency Index [CI] = 0.331; Rescaled Consistency Index [RC] = 0.188), the Strict Consensus of which placed *Liushusaurus* on the stem of Scleroglossa. We then re-ran the heuristic analysis using the ordering of Conrad (2008) (20 characters ordered) obtaining 3055 equally parsimonious trees ( $L = 2580$ ; CI = 0.193; RC = 0.126) in which *Liushusaurus* was again placed as a stem scleroglossan, within the wider clade that Conrad (2008) refers to as Scincogekkonomorpha (effectively: Scleroglossa + those taxa closer to Scleroglossa than to Iguania). Allowing one additional step ( $L = 2581$ ) collapsed the topology at the base of the tree, leaving *Liushusaurus* with an unresolved scincogekkonomorph placement. The matrix is too large for a full Branch and Bound analysis in PAUP, but we ran *Liushusaurus* in a smaller analysis (18 taxa) against representatives of living lizard clades; it again emerged in an unresolved scincogekkonomorph position. We then ran the analysis using the

full Conrad data set in the programme TNT (Goloboff *et al.* 2008), using Conrad's settings. It yielded three trees ( $L = 3687$ ) which placed *Liushusaurus* as the sister group of Scleroglossa (Fig. 11).

Whether this placement as a stem scleroglossan truly reflects the phylogenetic position of *Liushusaurus*, or is indicative of our limited ability to differentiate between early members of major squamate clades using morphological characters, is uncertain. Placement of other Jurassic–Early Cretaceous genera like *Parviraptor*, *Eichstaettisaurus*, *Ardeosaurus* and *Scandensia* has been equally problematic.

### Lifestyle

The body outline, particularly in IVPP V14716, suggests that the adult *Liushusaurus* was either a rather flattened lizard (like the Malagasy gecko *Uroplatus* or the African cordylid *Platysaurus*), or was broad-bodied like the North American iguanine *Sauromalus*. The relatively short scapula and short suprascapular cartilage are consistent with a depressed body shape, as are the long, thin, weakly curved posterior ribs. Body flattening in lizards can serve to maximise surface area exposed to the sun (e.g. the cordylid *Platysaurus*), aid crevice dwelling (e.g. *Platysaurus*), help to disguise the body outline (e.g. the Malagasy gekkotan *Uroplatus*), and/or permit a semi-controlled fall (e.g. the 'Butterfly lizard', *Leiolepis*) (Losos *et al.* 1989). The long, slender tapering claws of *Liushusaurus* would be consistent with a climber on rough surfaces (rock or vegetation) (Zani 2000), as are the relatively long forelimbs, absence of marked asymmetry in the manus and pes, and well-developed tubercular plantar digital scales (Arnold *et al.* 2002). The simple conical teeth suggest a diet of insects or other small invertebrates.

### Sexual dimorphism

Two specimens (IVPP V14716, IVPP V14746) bear a ventral pelvic element that we interpret as a possible post-cloacal bone, a sexually dimorphic (male) feature found in some living lizards (notably gekkotans). They are the 1st and 3rd largest specimens in the collection (the 2<sup>nd</sup> largest specimen, V15507, is preserved in dorsal view so the presence or absence of post-cloacal bones cannot be determined) (Table 2), hinting at size dimorphism as in many living taxa.

**Table 2.** Tibia length (mm) in eight available specimens of *Liushusaurus acanthocaudata* gen. et sp. nov. (in mm, all from IVPP collection).

	V14746	V15507	V14716	V15587 (Holotype)	V15011	V14715 (Paratype)	V15586	V15508
Tibia length	11.85	11.43	10.22	8.38	8.06	7.61	6.86	3.62

### Ontogenetic variation

As for *Yabeinosaurus* (Evans *et al.* 2005) and *Dalinghosaurus* (Evans *et al.* 2007), *Liushusaurus* shows age related variation (e.g. in the co-ossification of elements, the shape of the parietal, the frontoparietal suture, the shape of the clavicle). This variation highlights the problems that arise when juvenile skeletons are used as holotypes, especially if they lack diagnostic features. The morphology and phylogenetic position of *Yabeinosaurus* (e.g. Estes 1983) was misunderstood for several decades because the holotype chosen was a juvenile, a problem compounded by the selection of an equally juvenile specimen as a neotype (Ji *et al.* 2001).

Among the eight available specimens of *Liushusaurus*, only the tibia/fibula length can be measured in all specimens. It ranges from 3.62 to 11.85 mm and thus shows a considerable size variation (Table 2). As IVPP 15587 is the largest specimen that has a skull and it provides diagnostic skull information, we selected it as the holotype to minimize possible bias due to ontogenetic variation. As shown in Table 1, *Liushusaurus* has proportionally shorter forelimbs and longer hind limbs in small individuals, and proportionally shorter feet but longer femora and tibiae in larger ones.

### Conclusions

The deposits of the Yixian Formation of northeastern China continue to produce exquisite fossils of a wide range of groups. Squamates are well represented in this assemblage, with at least six diagnosable genera including the new *Liushusaurus*. Of these, two (*Mimobecklesisaurus*, *Yabeinosaurus*) seem to be surviving representatives of essentially Jurassic lineages and may therefore be relicts of a once wider Laurasian or Eurasian distribution. The phylogenetic analysis suggests *Liushusaurus* may fall into the same category. *Dalinghosaurus* on the other hand (as a relative of the shinisaurs, Evans & Wang 2005; Conrad 2008) and the contemporaneous Japanese *Kuwajimalla* (as an early relative of the boreoteioids, Evans & Manabe 2008) probably represent squamate lineages that evolved within Asia. The same may be true of *Pachygenys* and the gliding *Xianglong*, but additional material of each is needed to determine their relationships.

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## Appendix

### Data matrix for *Liushusaurus*

The principle phylogenetic analysis described in the text used the data matrix of Conrad (2008). Listed below are the 364 character codings for *Liushusaurus*. A = states 0 & 1; B = 0 & 2; C = 1 & 2.

1000?	00011	120?0	0?A00	0000?	??000	??000	00010	3-??0	01100
01110	02000	????0	??0?1	001?0	?3?00	00?00	00010	00100	01001
0????	?????	?????	?????	?????	?0??0	0?00?	?????	?????	?10?0
?????	??210	?0000	?????	?????	??000	??211	00???	?????	?????
?0??0	00??0	0A0B0	00000	??200	0??21	20001	10-??	0A0?0	10000
0A000	00011	11110	01010	0?0?0	00001	000A1	11000	C1??0	0?1–1
00000	00000	000??	?????	?????	?????	?????	?????	?????	?????
?????	?????	??28							