The Early Cretaceous lizard *Dalinghosaurus* from China

SUSAN E. EVANS and YUAN WANG


The Early Cretaceous lizard genus *Dalinghosaurus* from the Yixian Formation of Liaoning, China, was originally described on the basis of a partial postcranial skeleton characterised by extremely long slender hind feet and a long tail. The skull has remained unknown and the systematic position is undetermined. Here we describe the skeletal anatomy of this lizard in detail based on a series of new specimens in the collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing. The adult animal is small, with a well-ossified skull having a characteristic pattern of pustulate sculpture on the roofing bones and an expanded angular flange on the lower jaw. Skin impressions show a pattern of fine granular dorsal scales, rhomboidal ventral scales, and elongate tail scales arranged in annulæ. In many features, the skull resembles that of the living *Xenosaurus* and *Shinisaurus*, as well as *Carusia* from the Late Cretaceous of Mongolia and China. Phylogenetic analysis using three different data sets provides some support for that interpretation. The postcranial skeleton is characterised by long hind limbs and short forelimbs, but the delicacy of the long pes and the slender claws suggest this animal may have been a climber rather than a facultative bipedal runner.

Key words: Lepidosauria, Squamata, lizard, Cretaceous, Jehol Biota, China.

Introduction

To date, three lizard genera have been described from the Early Cretaceous Yixian Formation of China: *Yabeinosaurus* (Endo and Shikama 1942; Young 1958; Hoffstetter 1964; Ji et al. 2001), *Jeholacerta* (Ji and Ren 1999) and *Dalinghosaurus* (Ji 1998; Ji and Ji 2004). Of these, the status of *Jeholacerta* is doubtful, since the holotype skeleton is clearly juvenile and shows a close resemblance to juvenile specimens of the common Jehol lizard, *Yabeinosaurus* (Evans et al. in press). *Dalinghosaurus* clearly differs from *Yabeinosaurus* in having extremely elongated hind feet, but the original description is based on a partial skeleton preserving only the hindlimbs and tail. This made phylogenetic discussion impossible. Recently, Ji and Ji (2004) have described further details of the postcranial skeleton, but the skull remains unknown.

The collections of the Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China, include a series of eleven specimens referable to *Dalinghosaurus*. These include both juvenile and adult individuals, and many of the specimens preserve the skull and postcranial skeleton in association. One remarkable specimen (IVPP V14234) contains the skeletons of at least ten immature individuals. Together, the specimens of *Dalinghosaurus* span the lower range of the Xixian Formation from the basal Lujiazuang Bed, through the Jianshangou Bed, and into the Dawangzhangzi Bed, a period of roughly 10 Ma (Wang and Zhou 2003). The genus has yet to be reported from the Jingangshan Bed at the top of the Xixian Formation, or from the overlying Jiufotang Formation.

Many of the best specimens from the Lujiazuang Bed, including the finely preserved isolated skull, IVPP V13282, are preserved in 3-dimensions in a reddish-brown silty mudstone. IVPP V13282 was prepared mechanically using fine needles.

Institutional abbreviations.—GMV, Geological Museum of China, Beijing; IG, Institute of Geology, Chinese Academy of Geological Sciences, Beijing; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing.

Systematic palaeontology

Lepidosauria Haeckel, 1865
Scleroglossa Estes, Gauthier, and de Queiroz, 1988
?Anguimorpha Fürbringer, 1900

Genus *Dalinghosaurus* Ji, 1998

Type species: *Dalinghosaurus longidigitus* Ji, 1998.

*Dalinghosaurus longidigitus* Ji, 1998
Figs. 1–9.

Holotype: GMV2127.

Type locality: Sihetun Village, Beipiao City, western Liaoning Province, China.
**Type horizon:** Early Cretaceous Yixian Formation Jianshangou Bed.

**Referred specimens.**—IG-02-7-16-2 (nearly complete postcranium skeleton, Ji and Ji, 2004); IVPP V12345 (part and counterpart of associated skeleton); IVPP V12586 (posterior skeleton with skin traces); IVPP V12643 (part and counterpart of poorly preserved associated skeleton); IVPP V13281 (associated skeleton, immature/subadult); IVPP V13282 (skull, adult); IVPP V13864 (part and counterpart of associated skeleton); IVPP V14069 (immature skull); IVPP V14234 (block with at least ten associated skeletons); IVPP V14262 (poorly preserved associated skeleton; and IVPP V14295 (posterior half of postcranial skeleton).


**Revised diagnosis.**—A lizard with small adult size (c. 150 mm snout-pelvis length) distinguished from most Mesozoic lizards but resembling carusioids (*sensu* Gao and Norell 1998) in the following combination of derived characters: pustulate sculpture on dermal skull bones (mature adult); maxillary facial process narrow dorsally and inturned medi-ally; frontals fused, with deep cristae cranii and orbital constriction; parietal foramen within parietal but close to anterior margin; jugal large with tall postorbital ramus that meets...
squamosal and bears pustulate sculpture. *Dalinghosaurus* resembles the Late Cretaceous *Carusia* (Borsuk-Bialynicka 1985; Gao and Norell 1998) in the strong development and pattern of the skull ornamentation (double interorbital row of large pustules that diverge posteriorly along the orbital margin), the loss/fusion of the lacrimal, and the presence of a small coronoid notch on the rear of the dentary, but differs in dental structure (tightly packed teeth in *Carusia*, fewer conical teeth in *Dalinghosaurus*) and in having a longer snout; it resembles *Shinisaurus*, but differs from *Carusia* and *Xenosaurus*, in having an anteriorly extended prefrontal that separates the maxilla from the nasal, and differs from all three in the posterior extension of the nares and the possession of a strongly flared angular flange on the lower jaw. The postcranial skeleton of *Carusia* is unknown, but *Dalinghosaurus* differs from both *Xenosaurus* and *Shinisaurus* (and from most Mesozoic lizards except the Upper Jurassic *Bavariosaurus*, Evans 1984a) in having a pes that is equal in length to the femur and tibia combined.

Specimens used in the description.—IVPP V13282 is an almost complete, fully articulated skull (Figs. 1, 2) that provides the basis for the description of cranial anatomy, with additional information from IVPP V13281 (an immature specimen of roughly 70–80% of the size of IVPP V13282, Figs. 3–5), IVPP V13864 (a complete skeleton with a disarticulated and incomplete skull), and two individuals on
IVPP V14234 (V14234.1, V14234.2). Postcranial information comes mainly from IVPP V13281 (Figs. 5, 7), with additional information from IVPP V14234.1 (Fig. 6), IVPP V14234.2, and IVPP V14295 (Fig. 8).

Skull.—The skull of IVPP V13282 is 28 mm long and preserves most of the dorsal and lateral surfaces, the braincase, the lower jaws and part of the palate (Figs. 1, 2). In general, the skull is characterised by its large narial openings and its robust jaws and dentition. The dorsal surface of the adult skull bears distinctive pustulate sculpture, but this is less developed on anterolateral elements. The sculpture appears to be derived from the interaction of the dermal bone and the skin; there is no evidence that this results from the attachment of separate osteoderms. The skull of IVPP V13281 (Fig. 3) is smaller, with only weak development of the sculpture, unfused premaxillae, and more gracile circumorbital and postorbital bones.

The premaxilla is single in the adult, but fusion occurred late in ontogeny (as shown by IVPP V13281). The alveolar portion is “U”-shaped but without a strong palatal flange. It bears seven small teeth. The ventral aspect of the bone is obscured by the dentary symphysis, so that the presence or absence of an incisive process cannot be confirmed. Dorsally, the nasal process is quite short, overlying the tips of the nasals but barely separating them; there are no conspicuous perforating foramina on the dorsolateral margins. The premaxilla is clasped firmly on each side by the maxillae.

The maxillae are triradiate bones that extend back just beyond the midpoint of the orbit, but are excluded from the ventral orbital margin by the jugal and prefrontal. The premaxillary process is relatively long, contributing to a large narial opening. The process bifurcates anteromedially where it clasps the premaxilla, the posterior limb extending medially behind the premaxilla but not reaching the midline. Behind the nasals, the maxilla ascends more steeply to form a tall facial process, the narrow apex of which curves over onto the dorsal surface of the skull. Here it meets the prefrontal rather than the nasal (see below). Medially, the facial process has a strong overlapping suture with the prefrontal and then decreases in height gradually to its meeting with the jugal. It bears around 16–18 large conical teeth. Laterally, a series of neurovascular foramina open from the superior alveolar canal; these carried branches of the maxillary nerve and blood vessels. The main canal has its exit foramen at the medial junction of the facial process with the premaxillary process. The medial surface of the bone is preserved in IVPP V13281, showing an unexpanded medial palatal shelf and a concavity for the nasal region.

The nasals are small and subrectangular, with an anteromedian premaxillary process and an oblique (and slightly
curved) anterolateral narial margin. Laterally, the nasal appears to have been separated from the maxilla by the enlarged prefrontal. Medially, the two nasals meet along the entirety of their suture, the two bones overlapping the frontal without the intervention of an anteromedian frontal process. The posterior ends of the nasals are partially obscured by overlaps in IVPP V13282, but the isolated right nasal of IVPP V13281 shows the edge to have been bifurcated into a short lateral and longer medial process.

The frontal is single and probably became so at an early stage of development since the smallest skull (IVPP V14069) already lacks a median suture. In IVPP V13282 (Figs. 1, 2), the frontal bears heavy pustulate sculpture that is particularly well developed on the posterior part, with the “pustules” forming an inverted “V” (a small central interorbital boss with further “pustules” running down each edge but an unsculptured area in the centre). In the smaller IVPP V13281 (Fig. 3) the pustules are not developed. Instead the bone bears weak sculpture but the “V” pattern is still present with a central depressed and unsculptured area. This feature helps to link the two skulls despite the ontogenetic differences between them. The frontal is long and slender, with a sharp orbital constriction. The anterior edge of the bone is covered by the nasals in IVPP V13282, but in IVPP V13281, the nasals have disarticulated. Anteriorly, the frontal appears bifurcate, with paired lateral facets separated by a central recess. Judging from the morphology of the adjacent nasal in IVPP V13281, these frontal facets accommodated the posterolateral and posteromedial ends of the nasals. Anterolaterally, the frontal has a long contact with the prefrontal. Posterior to the orbit, the frontal expands again into its suture with the parietal (roughly twice the width of the frontonasal suture). Here the frontal bears a lateral facet for the postfrontal or postorbitofrontal, this bone clasping the lateral frontoparietal angle. The posterior border is almost straight (but slightly irregular) in the adult, and more “U”-shaped in the subadult (as is usually the case, the thickened lateral margins ossifying first). Ventrally, the bone bears strong cristae cranii (partially visible in the lateral views, Fig. 2C, D) but these do not approach in the midline or form strong descending orbitonasal processes. They rather reinforce the orbital rim.

The parietal of IVPP V13282 has a small anteriorly-shifted parietal foramen that lies just behind the frontoparietal suture and is surrounded by a raised edge. The dorsal

Fig. 4. *Dalinghosaurus longidigitus*, IVPP V13281, Barremian, Hejiaxin, China. Complete skeleton, dorsal view.
sculpture is more developed anteriorly than posteriorly. The ventral surface is not exposed in any specimen, but none shows any evidence of a descending process for the epipterygoid. The parietal is short anteroposteriorly, with shallow embayed lateral margins, no major adductor crests, and long divergent postparietal processes that become blade-like towards their tips. The anterior parietal margin meets the frontal as described above. The presence or absence of ventral tabs extended forward under the frontal cannot be determined. The posterior margin is a wide open “U” shape between the postparietal processes, with recesses to either side of the midline for epaxial neck muscles. In cross-section, the postparietal processes are triangular, the apex formed by a sharp dorsal crest that separates the lateral surface from the posteromedial surface. The end of the lateral face bears a facet for the supratemporal. In IVPP V13282, the squamosals are missing and only a fragment of the left supratemporal is preserved. In IVPP V13281, the squamosal is also preserved although the bones are disarticulated backward.

The prefrontal is a large bone with a long narrow frontal process and a broad main body. It meets the frontal postero-medially, and the nasal anteromedially, and the maxilla antero-laterally. Somewhat unusually, it seems to be fully interposed between the maxilla and nasal and enters the dorsal narial margin for a short distance. The orbitonasal flange is broad dorsally but narrows ventrally. It meets the palatine and is embayed laterally for the lacrimal canal, the lateral border being provided by the maxilla. There is no trace of a lacrimal and no specimen shows any indication of the presence of a palpebral (non in situ, and no suggestion of a notch or tubercle on the prefrontal to which it might have been attached).

The jugal is preserved in several specimens. It is roughly L-shaped, but with both limbs approximately the same length and enclosing an angle of c. 120 degrees. The ventral ramus extends along the dorsal margin of the maxilla up to the lacrimal opening, thus excluding the maxilla from the orbital margin. The dorsal ramus bears pustulate sculpture like that on the skull roof and appears to have formed much of the posterior orbital margin. Even allowing for some displacement, the dorsal tip of the jugal reaches a level well behind the anterior margin of the parietal. Given the length of the displaced squamosal in IVPP V13281, it is likely that the jugal and squamosal met. At the ventral junction of the dorsal and ventral jugal rami, there is a small posterior tubercle but no strong quadratejugal process. Together, the maxilla and jugal provided a surface of articulation for the ectopterygoid, although the position of the facet is not clear on existing specimens.

The area between the jugal and skull roof in IVPP V13282 is damaged on both sides. The postorbital/postfrontal complex has been lost on the left, but on the right is displaced under the parietal as a single mass. The postorbital component is triangular, with a slender posterior process that bears a ventrolateral facet for the jugal and, presumably, a dorsal one for the squamosal, although this is obscured. In IVPP V13281, the postfrontal and postorbital bones are preserved on both sides as separate elements. The postfrontal in this specimen is tri-radiate, with a strongly bifurcated medial margin that clasped the frontoparietal suture and a short ventrolateral process that met the postorbital. The postorbital has been rotated anti-clockwise, but shows a short thickened orbital margin and a longer, relatively broad posterior process. Its contribution to the posterior orbital margin thus seems to have been small, with most of this margin being formed by the jugal.

The squamosal is preserved in IVPP V13281 but not IVPP V13282. It is a long slender bone without a dorsal process and only a slight ventral hook, although these features may have been more pronounced in the adult. The bone tapers anteriorly where it met the postorbital and probably the jugal.
On all of our specimens, the palate is more poorly preserved than the rest of the skull and cannot be clearly figured. The anterior region is largely obscured by the mandibles in IVPP V13282, but some of this is exposed in IVPP V14234.1 and IVPP V14234.2. The vomer is visible in one of the latter animals as a short bone fully separated from the maxilla by the elongate choana. In this individual, at least, there is no division of the choana into anterior (vomeronasal) and posterior (choanal) parts, although this may have changed in a fully mature animal. The palatines are quite large (IVPP V13865A) and retained at least some teeth (IVPP V13282). IVPP V14234.2 shows that they were fully, or almost fully, separated in the midline by the interpterygoid vacuities and had short deep choanal grooves. The pterygoids are also large and bore a long cluster of teeth along the pterygoid plate (IVPP V13282, IVPP V13865A, IVPP V14234.1). There is a long, narrow palatal process, and a short pterygo-palatine suture. The posterior process is long and slender, tapering towards its meeting with the quadrate. The medial recess for the basipterygoid process of the sphenoid is deep and bordered ventrolaterally by a crest. It seems to have formed an open surface for sliding rather than a distinct fossa (IVPP V13282, IVPP V14234.1). The right ectopterygoid is preserved in IVPP V13282 but has been rotated so that its lateral head faces posteromedially. It has a typical lepidosaurian configuration, with a small concave lateral head that proba-
bly met both jugal and maxilla, and a bifurcate medial head that clasped, and interlocked with, the pterygoid flange.

The quadrate is present in several specimens, and is most clearly seen on the left side of IVPP V13282. It has a relatively small ventral joint surface for the articular and a slightly larger, elongated, dorsal head with no obvious trace or either a foramen or notch. The lateral conch is narrow, and there is a distinct medial pterygoid lappet (out of view in Fig. 2C). Epipterygoids were present, but their dorsal and ventral articulations cannot be reconstructed with any confidence.

IVPP V13282 preserves the braincase in three-dimensions: sphenoid, basioccipital, prootic and opisthotic, and the ventral elements are also visible in IVPP V14234.1. Only the supraoccipital is obscured. The sphenoid has short basipterygoid processes that project laterally and slightly anteriorly. Their distal ends are strongly expanded. Between them is a deep dorsum sellae, perforated bilaterally by abducens foramina that open into large recesses for eye muscle origin. Ventrally, the paraphenoid rostrum is either broken or unossified, probably the latter since the same condition is seen in several individuals. The anterior and posterior openings of the vidian canals are obscured, but there are no accessory cristae ventrolaterales and the body of the sphenoid is quite narrow. The sphenoid-occipital suture is fully closed in IVPP V13282, but is visible on IVPP V14234.1. The sphenoid has a triradiate posterior margin. A small triangular flange overlaps the basioccipital in the midline while longer lateral processes contribute to the well-developed basal tubera. The basioccipital is short with a single occipital condyle. Dorsally, the basal tubera contribute to large occipital recesses. The prootic is obscured by the medially displaced postorbital elements but a well-developed alary process projects anteriorly. IVPP V13282 also shows a distinct medial recess for the floccular lobe of the cerebellum. The opisthotic is well-preserved and has a long, slender paroccipital process. The fenestra vestibuli is large and is separated from the more posterior vagus foramen by a weak interfenestral crest. The lateral opening of the recessus scala tympani is extended ventrally and posteriorly by a well-developed occipital recess and a strong crista tuberalis. The braincase is also partially preserved in IVPP V13281, disarticulated backwards from the rear of the skull and so exposing a wide supraoccipital.

The mandible is represented by the dentary, splenial, coronoid, surangular, angular and articular-prearticular. The dentary is laterally quite shallow, but the surface is damaged in IVPP V13282 and the teeth are hidden. The following description is therefore based mostly on IVPP V13281, IVPP V13864A and IVPP V13865A. The dentary has 16–19 tooth positions. It bifurcates posteriorly into a short posteroventral process that meets the small lateral flange of the coronoid, and a small ventral process that extends below the anterior tip of the angular, with the angular and surangular wedging into the triangular gap between. This surangular notch is deep, so that the angular extends forward (IVPP V13281) to the level of the last preserved tooth. Above the surangular notch, however, IVPP V13281 shows a very small additional notch. A small line of neurovascular foramina runs along the lateral surface of the bone. No specimen shows a clear medial view of the dentary, partly because a large splenial covers the surface from the sphenomaxillary region to the level of the coronoid process (IVPP V13282). The coronoid is tall, with a small lateral flange, and a strong dorsal process. Medially it is bifurcate, with a smaller anterior ramus and a longer posterior ramus. Seen from above, the medial surface of the coronoid is strongly concave, due mainly to a posteromediocally directed ridge along the margin of the posterior ramus. The surangular forms most of the lateral and ventrolateral faces of the postdental region, extending forward to a level in front of the coronoid eminence, and has a large lateral foramen anterodorsally. Medially the bone contributes to the lateral wall of the adductor fossa. The angular makes a narrow contribution to the ventral margin of the jaw. It meets the splenial anteromedially but its posterior extension is unclear because the su-

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Fig. 7. Dalanghosaurus longidigitus, IVPP V13281, Barremian, Hejiaxin, China. Pelvic girdle, sacrum and right hind limb.
ture with the surangular is indistinct. The articular-prearticular is robust. The surface for the quadrate (IVPP V13282) is anteroposteriorly short but broad, with a small anterior boss to prevent forward slippage of the quadrate condyle. Medially, a strong angular process is embedded in a broad prearticular flange. Posteriorly, there is a short, postero-medially directed retroarticular process (broken in IVPP V13282). The prearticular component is mostly obscured by overlying bones.

Dentition.—The dentition consists of robust homodont teeth with labiolingually compressed tips. The tooth count varies between specimens but there are around 16–18 maxillary teeth, 16–19 dentary teeth, and 7 premaxillary teeth. The implantation is strongly pleurodont and tooth replacement occurs from the lingual surface by erosion of the tooth base.

Postcranial skeleton.—Of the IVPP specimens, the postcranial skeleton is best preserved in IVPP V13281 (Figs. 4, 5, 7), IVPP V14234.1 (Fig. 6), IVPP V14234.2, and IVPP V14295 (Fig. 8). The skeleton of IVPP V13281 broke into three pieces post mortem. The first section includes the skull, the first twelve presacral vertebrae and their ribs, and the pectoral girdle and forelimbs; the second part consists of nine dorsal vertebrae and their ribs; and the third part consists of the last five presacrals, the sacral, the caudal series (only partially visible), the pelvic girdle and the hind limbs. IVPP V14234.1 and IVPP V14234.2 provide supplementary information on ventral anatomy (most notably of the vertebral structure, pectoral girdle, and pelvis), whereas IVPP V14295 shows details of the pelvic girdle and tail. All the complete specimens of *Dalinghosaurus* show the same basic features and proportions, but the robusticity of the bones varies with ontogenetic age, and many individuals are young (as demonstrated by the lack of fusion of long bone epiphyses).

Vertebral column.—In IVPP V13281 there are five or six cervical vertebrae (CV), 19–20 dorsals (DV), two sacral and an unspecified number of caudals. A similar count can be made on IVPP V14234.1 and IVPP V14234.2, but there is uncertainty as to the total presacral number (at least 27, Ji and Ji 2004; 26 this paper). The tail is composed of around 10 anterior caudals and a long series of autotomous posterior caudals. In his short nomenclatural paper, Ji (1998) gave a count of 55 for the caudal series. All vertebrae are procoelous.
with rounded condyles that are slightly oblique (larger dorsally than ventrally). There are no free intercentra in the trunk region, but IVPP V14234.1 and IVPP V14234.2 have small intercentral hypapophyses between the cervicals (Fig. 6). These may have been larger in adults.

IVPP V13281 preserves the left atlantal arch behind and to the side of the braincase. The axis lies immediately behind the skull, rotated slightly so that it is seen in left lateral view. The spine of the axis is large and is longer than the centrum. Posteriorly, it is drawn into a hook-like posterior process with a curved posterodorsal margin. The axis is also preserved associated with the skull in IVPP V13282 and is seen to have attached anterior and posterior hypapophyses (c2–c3 hypapophyses, Fig. 2B). The bodies of the cervical vertebrae are shorter than those of the dorsal series (IVPP V14234.1, Fig. 6); the neural spines are not well preserved but they were clearly taller in the anterior part of the series. The dorsal vertebrae show little or no development of neural spines. In IVPP V13281, most dorsals are preserved in lateral view and show elongated posterior zygapophyses, suggesting strong contacts between adjacent elements. Only one vertebra (presacral 10) is preserved in dorsal view on IVPP V13281 and this has no trace of a zygosphenon-zygapophyseal articulation. In IVPP V14234.1 and IVPP V14234.2, the dorsal centra are preserved in ventral view. They taper antero-posteriorly towards the small posterior condyle. The sacral ribs are quite gracile with little expansion, and no bifurcation in the second sacral rib. There is, however, a groove in the distal part of the second sacral rib that opens from a small more proximal foramen (not figured). The caudal vertebrae of IVPP V13281 are mostly covered by matrix, but at least eleven anterior caudals are preserved, of which nine have long, posterolaterally directed transverse processes. The processes are also visible in IVPP V13865, and are well-preserved in IVPP V14295 (Fig. 8). They do not taper and are rather blunt-ended. Anteriorly, each caudal neural arch bears a low mid-dorsal ridge that extends posteriorly as a small median process. Further posteriorly, the spine becomes more pronounced as the transverse processes decrease in length. These posterior spines are more clearly seen in IVPP V14295. They form long, low dorsal blades with rounded dorsal margins (Fig. 8). Ji (1998) and Ji and Ji (2004) record the caudal vertebrae as being autogenous from about caudal 11 or 12 backwards, and our specimens show a similar morphology. Haemal arches are present and attach to the posterior end of the centrum.

The ribs are single headed throughout, very slender, and without any accessory processes. In IVPP V13281, there is a short rib associated with CV4 (it may be incomplete), but the condition of CV3 is unclear. The anterior dorsal vertebrae bear long slender ribs, but there is a sharp decrease in length from presacral nineteen backward, producing a set of posterior dorsal vertebrae with short “lumbar” ribs, although these are not fused to the centra. Judging from IVPP V13281, IVPP V14234.1, and IVPP V14234.2, all dorsal vertebrae bear ribs.

Forelimbs and pectoral girdle.—The pectoral girdle is rather jumbled in IVPP V13281 (Fig. 5), but is also preserved in IVPP V13865 and is clearest in IVPP V14234.1 (Fig. 6). It is characterised by clavicles that have an expanded, hook-like medial component; a cruciform interclavicle with a small anterior process and a long tapering stem (IVPP V13865A, IVPP V14234.1); and a scapulocoracoid with scapulocoracoid and anterior coracoid fenestrae. The scapular blade is long and slender. Scapula and coracoid are already sutured in IVPP V13281 and in IVPP V14234.1, but the coracoid plate looks unfinished and has a rim of cartilage. Ji and Ji (2004) describe an ossified sternum in their specimen of Dalinghosauroidea, but there is no trace of such a structure in any of the IVPP specimens and it is likely to be a misidentification. The sternum is cartilaginous in squamates.

The forelimb is about 50% of the length of the hind limb (Figs. 4, 5). The humerus is short, with a large proximal head and a slightly narrower distal end containing an ectepicondylar foramen. Ji and Ji (2004) describe an incomplete ectepicondylar foramen in their specimen, a juvenile feature. In IVPP V13281, the epiphyses are not fused to the humeral shaft and they appear to be calcified cartilage rather than bone (lightly coloured, porous). The radius and ulna are shorter than the humerus, and the ulna olecranon is not ossified. The carpus is preserved in several specimens (but not well) and has at least seven separate elements, probably more (i.e., radiale, ulnare, intermedium, centrale, pisiform, and several distal carpals). Ji and Ji (2004) describe (and figure) the same arrangement. All metacarpals are of similar diameter, with the third being longer than the fourth. The hand is relatively long, compared to the humerus and epipodials, but it is small by comparison with the foot. The phalanges are very slender with well-formed joints; in all digits, the penultimate phalanx is the longest. The unguals are long and very pointed, with a distinct flexor tubercle and a pit for muscle or ligament attachment. The phalangeal formula of the manus is 2:3:4:5:4.

Hind limbs and pelvic girdle.—The elements of the pelvic girdle are already conjoined in the immature IVPP V13281, but not in IVPP V14234.2. The ilium has a relatively long, slender blade with a slight anterior tuberosity. It is small in relation to the femoral head. The pubis is slender and elongate, with an anteromedially projecting ramus that has only a short symphysis surface, and a large proximal obturator foramen. The ischium is seen most clearly in IVPP V14234.2 and IVPP V14295 (Fig. 8). It is waisted proximally, but expands distally into a quadrangular plate that has a small posterior angle and a curved anterodorsal extension.

The femur is elongate with strong proximal and distal heads. The tibia and fibula are slightly shorter, and lightly built, without any marked proximal or distal expansions. In IVPP V13281, the epiphyses are just fusing to the ends of the long bones so that the epiphysial line is still visible. The tarsus is well preserved in this specimen. There is a broad, but proximo-distally short astragalocalcaneum with a distinct proximal notch between tibial and fibular surfaces. Distally, the recess for distal tarsal 4 (Dt4) is shallow. Dt4 is large but,
like the astragalocalcaneum, it is both wide and also proximo-distally short. It meets both metatarsal 4 and metatarsal 5. There is a small Dt3 but no Dt2. Ji and Ji (2004) describe a large Dt5, but from its position and size, this is probably a detached portion of the astragalocalcaneum.

The foot is beautifully preserved in IVPP V13281 (Fig. 7). It is very elongate (longer than the femur and tibia together), and strongly asymmetric, with an exceptionally long fourth digit, although digit 5 is quite long. The fourth metatarsal (Mt) has the greatest diameter of the metapodial elements, and, at 10.5 mm, is of similar length to the humerus. Mt3 is narrower, but only slightly shorter (9.5 mm), while Mt2 (8 mm) and then Mt1 (5.2 mm) become both markedly shorter and narrower. Mt5 is the shortest (4 mm) and is clearly hooked, but with little development of the outer process and thus limited proximal expansion. The phalanges of the foot resemble those of the hand in general structure, but become progressively shorter towards the tip of each digit. Like its metatarsal, the proximal phalanx of digit four is very robust. As in the hand, the unguals are long, slender and bear a strongly curved proximal articular surface suggesting they could be strongly flexed to give a firm grip. This is supported by the presence of well-developed extensor and flexor processes. The phalangeal formula of the pes is 2:3:4:5:4.

Fig. 9. Dalinghosaurus longidigitus, Barremian, Dawangzhangzi, China. Skin preservation. A. IVPP V13865B, showing body and tail scales. B. IVPP V12586, detail of hind leg and tail with scalation.
Soft tissue preservation.—Several IVPP specimens of *Dalinghosaurus* preserve clear traces of the scales on both the body and the tail, most notably IVPP V13865 (Fig. 9A) and IVPP V12586 (Fig. 9B). The tail shows a pattern of proximodistally elongated overlapping rectangular scales arranged in distinct transverse rows, or annulae (Fig. 9A, B), except on the proximal end where the scales are more granular in appearance. The body scales are also well-preserved (Fig. 9A, B). IVPP V12586 shows that there is a distinct difference between dorsal and ventral surfaces. One surface had large rhomboid scales, the other had smaller, rounded granular scales. In IVPP V12585A, the large rhomboid scales seem to lie under the scapulocoracoid, suggesting they are ventral, while the counterpart block looks up into the dorsal surface of the body and seems to have more of the granular scales. Thus *Dalinghosaurus* appears to have had small rounded granular scales on the dorsum, larger rhomboid scales on the underside, and enlarged caudal scales arranged in transverse rows. This pattern of caudal sculation is found in many scincomorphs and anguimorphs (Autarchoglossa), and a small number of iguanians (Arnold et al. 2002).

**Discussion**

**Reference of the specimens to *Dalinghosaurus***.—The holotype specimen of *Dalinghosaurus longidigitus* (GMV2127) is restricted to the posterior part of the body (tail, pelvis, and hind limbs), while a more recently described skeleton (Ji and Ji 2004) preserves the pectoral region as well, but not the skull. The IVPP material consists mostly of fully associated skeletons (skulls and postcrania), and there is sufficient well-preserved postcranial material to be confident that we are dealing with the same genus described by Ji (1998). Despite variation in their level of preservation, all specimens show the typically elongated hind limbs and long feet, combined with a suite of clavicular, tarsal and phalangeal peculiarities (expanded perforated clavicle, wide short astragalocalcaneum, unexpanded mt5, slender digits around a massive fourth digit, elongate narrow claws). The association of the skull, IVPP V13282, is based on its resemblance to the skulls of IVPP V13281 (morphology of individual bones but allowing for difference in maturity, and hence sculpture), IVPP V13864A (frontal morphology and pustulate sculpture, jaw morphology), IVPP V14234.1 and IVPP V14234.2 (jaw morphology and postcranium). Since IVPP V13281 is not greatly different in overall size to IVPP V13282 (c. 70–80%), it might be argued that the lack of heavy sculpture could indicate a second, closely related species. This is possible, of course, but although age and size are linked, other factors (e.g., sexual dimorphism) can affect this. IVPP V13281 is clearly not fully mature, as shown by the incomplete ends to the limb bones, and, on current evidence, immaturity provides the most plausible explanation for the less developed sculpture and unfused premaxillae. Since there is a suite of characters providing links between the different specimens, we are confident that the long-limbed postcranial skeleton of *Dalinghosaurus* can be associated with a distinctive skull having strong pustulate ornamentation in the mature adult and a broad angular flange on the prearticular.

**Phylogenetic position of *Dalinghosaurus***.—In the original report on *Dalinghosaurus*, Ji (1998) noted possible similarities with the Late Jurassic *Bavarisaurus* (Evans 1994a), but otherwise left the phylogenetic position open. More recently, Ji and Ji (2004) suggested scleroglossan affinity, based on a small subset of postcranial characters listed by Estes et al. (1988). Identification of the skull of *Dalinghosaurus*, together with a large sample of specimens, permits a more detailed analysis of relationship.

In general appearance, the skull of *Dalinghosaurus* bears a strong resemblance to that of another fossil lizard from the Sino-Mongolian Cretaceous, namely the Late Cretaceous *Carusia*. *Carusia* was originally attributed to the Scincomorpha (Borsuk-Bialynicka 1985), but on the basis of new material, Gao and Norell (1998) argued that it lay on the stem of Xenosauridae, erecting the name Carusioidea to encompass the stem and crown. From their analysis, they diagnosed Carusioidea on the basis of seven synapomorphies: fused frontals; lateral borders of frontals constricted between orbits; postorbital branch of jugal sculptured; surangular extends anteriorly slightly beyond the level of the coronoid eminence; presence of a jugal-squamosal contact on the upper temporal bar; anterior tapering of surangular reduced; presence of cranial osteoderms with vermiculate rugosities. These taxa also share an inturned dorsal portion of the maxilla (Gao and Norell 1998), an anteriorly placed parietal foramen that lies just behind the frontoparietal suture, and a tendency for the surangular to fuse with the articular-prearticular. *Dalinghosaurus* shows almost all of these characters, except the anterior reduction of the surangular. *Xenosaurus* and *Shinisaurus* (the postcranium of *Carusia* is not known), like *Dalinghosaurus*, lack ventral osteoderms (unlike anguids and many scincomorphs) and the dorsal osteoderms are either very reduced (*Shinisaurus*) or virtually absent (*Xenosaurus*). The issue of cranial osteoderms is more problematic. In none of the carusioids, as defined, are the cranial osteoderms separable from the skull, and the condition is usually described as an osteodermal incrustation (e.g., Borsuk-Bialynicka 1985). In the extent *Xenosaurus*, the osteodermal nature of the pustulate cranial sculpture is clear; in *Shinisaurus* and the fossil taxa it is less so, and Wu and Huang (1986) concluded that *Shinisaurus* lacked osteoderms. In the most recent account of *Shinisaurus* skull morphology, Conrad (2004) mentions only sculpture. It may be that the different conditions are developmental variants of the same character (Borsuk-Bialynicka 1984) but we left the coding of this character unchanged for the “carusioid” taxa (changing *Shinisaurus* to ? made no difference to the results), and coded *Dalinghosaurus* as (?) for this feature in subsequent data matrices.

For *Dalinghosaurus*, the obvious first point of comparison is with *Carusia*. Although the skulls are broadly similar in shape and external appearance, and share the loss/fusion...
of the lacrimal and the presence of a very small coronoid notch on the rear of the dentary (IVPP V13281), they differ in several important ways. One of the most notable differences is in the dentition, where Carusia has a tightly packed row of slender teeth but Dalinghosaurus has fewer conical teeth. A second major difference is in the structure of the snout region. Dalinghosaurus resembles Shinisaurus in that the prefrontal is anteriorly expanded and separates the nasal and maxilla, entering the narial margin. The latter morphology may be convergent however, resulting from snout shortening in Shinisaurus but narial extension in Dalinghosaurus (Magdalena Borsuk-Białynicka personal communication, February 2005). Shinisaurus and Dalinghosaurus also have a similar dentition and sculpture pattern, but Dalinghosaurus differs from mature Shinisaurus (and Xenosaurus) in parietal shape, mandible shape, the pattern of pterygoid dentition, and in having separate postfrontal and postorbitals bones, although these bones are discrete in immature individuals of Shinisaurus (Evans personal observation).

In order to explore the phylogenetic position of Dalinghosaurus in more detail, we coded it into three different published squamate matrices (a combined matrix using elements of Evans and Barbadillo 1997, 1998, 1999 and Evans and Chure 1998; Gao and Norell 1998; Lee 1998), and ran analyses using either PAUP version 3.1.1. (Swofford 1993) (Heuristic search option, large matrices) or PAUP* version 4.0b10 for Windows (Swofford 2001) (Branch and Bound option, for smaller matrix subsets).

We began by adding Dalinghosaurus to the anguimorph matrix of Gao and Norell (1998) that was used to explore the relationships of Carusia (Appendix 1). Like the original authors, we omitted some fossil anguimorph taxa for which there was a lot of missing data, but we added Gekkota to increase the representation of other squamate groups (only Iguania and Scincomorpha in the original data set) and the Middle Jurassic to Early Cretaceous Parviraptor (Evans 1994b) to determine the effect, if any, of other fossil taxa. In each of 12 most parsimonious trees (Branch and Bound analysis: TL = 286; CI, 0.504; RC, 0.373), Dalinghosaurus emerged as the sister taxon of a clade corresponding to the Carusioidea of Gao and Norell (1998), which fell at the base of Anguimorpha (Fig. 10). This clade, as defined (Gao and Norell 1998), includes the extant Xenosaurus (Mexico, Guatemala) and Shinisaurus (China), and the extinct Exostinus (Late Cretaceous to Oligocene, USA), as well as Carusia (Late Cretaceous, Mongolia and China: Borsuk-Bialynicka, 1985; Gao and Norell, 1998) and, tentatively the poorly known Restes (Paleocene–Eocene, USA) (Estes, 1983) (not shown in Fig. 10). This result supports the more traditional comparison made above.

As the Gao and Norell matrix focuses on anguimorphs, we also included Dalinghosaurus in two more general squamate matrices to determine whether at least the general placement of Dalinghosaurus (within Scleroglossa, within Anguimorpha) was supported. The results were less clear-cut.

We first used the matrix of Lee (1998), repeating his ordering and adding three Jurassic–Cretaceous taxa—Eichstaettisaurus (Late Jurassic–Albian, Germany, Spain, Italy, Broili 1938; Evans et al. 1999, 2004), Bavarisaurus (Late Jurassic, Germany, Evans, 1994a), and Ardeosaurus (Late Jurassic, Germany, Mateer 1982) (Appendix 1). Addition of these taxa did not disrupt the topology of Lee’s tree (Lee 1998: fig. 2): i.e., with xantusiids joining a clade comprised of Gekkota, Amphibiaenia and Dibamidae that stands as the sister taxon to the remaining scleroglossans including snakes (Fig. 11A). Interestingly, the result placed Ardeosaurus with lacertids, and Eichstaettisaurus in an unresolved trichotomy with other scleroglossans, both positions more crownward than in other recent analyses (e.g., Evans and Barbadillo 1998; Reynoso 1998; Evans et al. 2004), but discussion of these taxa is beyond the scope of the present study. We then sequentially added the Jurassic–Cretaceous Parviraptor (Evans 1994b) and Dorsetisaurus (Hoffstetter 1967), both generally considered as anguimorphs, and Dalinghosaurus. Fig. 11B shows the 50% Majority Rule tree derived from the final addition of Dalinghosaurus (61 trees). Dorsetisaurus remains grouped with anguimorphs but Dalinghosaurus is unresolved at the base of Scleroglossa, and Parviraptor has dropped below it. Support for these groups was weak, however, and bootstrap analysis reduced most of Scleroglossa to a polytomy.

We constructed a third matrix using a combination of data from Evans and Barbadillo (1997, 1998, 1999) and from Evans and Chure (1998), and thus including a range of other Jurassic and Early Cretaceous taxa (Ardeosaurus, Dorsetisaurus, Eichstaettisaurus, Hoyalacerta, Evans and Barbadillo 1999; Paramacelldloidae, Evans and Chure 1998; Parviraptor) (Appendix 1). Because of problems regarding the monophyly of the Xenosauridae (see below), we coded Xenosaurus (Barrows and Smith 1947; Rieppel 1980; Evans personal observation) and Shinisaurus (Hu et al. 1984; Wu and Huang 1986; Evans personal observation) separately, and added Carusia (Borsuk-Bialynicka 1985; Gao and Norell 1998). The results of these analyses were inconclusive, resulting in a polytomy.
yielding trees of very different topology depending on the addition or removal of individual fossil taxa. Tree statistics were generally poor (CI in the range of 0.4–0.5; RC in the range of 0.2–0.3). 

Xenosaurus, Shinisaurus, and Carusia always formed a well-supported clade (so there was enough signal in the matrix to bring these together), but the position of this clade varied. Fig. 12A shows one of four equally parsimonious trees resulting from a heuristic search with 32 taxa and 212 characters (TL = 587), in which Xenosaurus, Shinisaurus, and Carusia combine with several Jurassic and Early Cretaceous taxa to form a clade that is the sister taxon of all other scleroglossans except mosasauroids. Fig. 12B shows the results of a Bootstrap analysis of the same four trees. This brings the Xenosaurus–Shinisaurus–Carusia clade to the base of Anguimorpha. In both analyses, Dalinghosaurus emerged as a sister taxon to the Xenosaurus–Shinisaurus–Carusia clade (with or without Eichstaettisaurus). However, the weakness of support is clearly demonstrated by the extremely low bootstrap values at most nodes. To test this result further, we ran a Branch and Bound search of a subset of taxa (Kuehneosauridae, Rhynchocephalia, Iguania, Gekkota, Anguidae, Helodermatidae, Varanidae, Serpentes, Cordylidae, Teiidae, Xantusiidae, and the fossil taxa Eichstaettisaurus, Bavarisaurus, Ardeosaurus, and Dalinghosaurus). The analysis yielded two most parsimonious trees (TL = 642, CI = 0.76, RI = 0.46) in which Dalinghosaurus emerged as a sister group of the Xenosaurus–Shinisaurus–Carusia clade + Eichstaettisaurus, as in some of the heuristic search trees. Ardeosaurus and Bavarisaurus lay on the squamate stem.

Resolution of the systematic position of Dalinghosaurus is made more difficult by the current controversy surrounding the status of Xenosauridae. McDowell and Bogert (1954) in their major review of anguimorph relationships brought Shinisauridae (Shinisaurus) within Xenosauridae, a conclusion backed by Rieppel (1980), Estes (1983), Borsuk-Bialynicka (1986), Estes et al. (1988), Gao and Norell (1998), and Lee (1998), amongst others. However, several more recent workers, notably Hu et al. (1984), Wu and Huang (1986), Caldwell (1999), Macey et al. (1999), Conrad (2002, 2004) and Townsend et al. (2004), have split Xenosauridae once again, with the most recent authors arguing for a placement of Shinisaurus closer to platygnathes. All the analyses indicate that Dalinghosaurus was a scleroglossan lizard. The comparisons outlined above, and the analyses using both the focused matrix of Gao and Norell (1998) and the general matrix of Evans and Chure (1998), suggest a relationship between Dalinghosaurus and a clade composed of Carusia, Xenosaurus, and Shinisaurus. Analysis using Lee’s (1998) matrix, however, leaves the position of Dalinghosaurus unresolved, and this simply highlights current problems with many aspects of the squamate phylogeny. Better resolution requires more data for both modern and fossil taxa. With respect to Dalinghosaurus, this should be helped by ongoing new work on Shinisaurus (Jack Conrad, University of Chicago), and the description and analysis of new Tertiary shinisaur material (Conrad 2002). It would also be assisted by the recovery of postcranial material of Carusia, more details of the palate and braincase of Dalinghosaurus, and new material of the North American Restes and Exostinus.

Biogeography.—Discussion of biogeography depends ultimately on the resolution of the Shinisaurus–Xenosaurus de-
bate because under their traditional definition, “xenosaurs” provide one of several squamate examples of Asian−North American biogeographical links (e.g., polyglyphanodont teids, dibamids, helodermatids). The living genus *Xenosaurus* is restricted to Mexico and Guatemala, but fossil “xenosaurs” are recorded in North America from the Campanian onwards (e.g., Gilmore 1928; Estes 1983; Gao and Fox 1996; Nydam 2002). In Asia, *Shinisaurus* is currently found only in Guangxi Province, China (Hu et al. 1984; Wu and Huang 1986) and Vietnam (Conrad 2004), but fossil “xenosaurs” have a longer recorded history. They have been reported from Campanian and Maastrichtian age localities in China and Mongolia (Jerzykiewicz and Russell 1991; Alifanov 2000; Gao and Norell 1998, 2000), with more fragmentary remains recorded from the Early Cretaceous of Mongolia (Alifanov 1993, 2000) and Uzbekistan, Central Asia (Oxia, Nessov 1985, 1988, 1997; Gao and Jessop 1998). This has led to the idea that Asia was the centre of origin for “xenosaurs” (e.g., Alifanov 2000; Nydam 2002), with representatives entering North America via the Bering Bridge later in the Cretaceous. However, identification of the fragmentary early specimens as “xenosaurs” relied mainly on the absence of anguid or varanoid characters rather than the possession of clear-cut “xenosaur” autapomorphies. If shinisaur and xenosaur (sensu stricto) are not closely related, then correct attribution of the fossil taxa becomes particularly important. *Dalinghosaurus* from the Lower Cretaceous of China and *Carusia* from the Upper Cretaceous (Campanian) of Mongolia and China (Borsuk-Bialynicka 1985; Gao and Norell 1998, 2000) provide a firmer basis for the comparison of fragmentary specimens and, if correctly interpreted, support the hypothesis that xenosaurs, shinisaur, or both, were present in Asia from an early date.

**Lifestyle**—*Dalinghosaurus* was a small gracile lizard with an exceptional long tail and pes, and hind limbs that were markedly longer than the forelimbs. Typically, modern lizards with this morphology are either swift terrestrial runners that become bipedal at speed, and/or climbers. On this basis, Ji and Ji (2004) proposed that *Dalinghosaurus* was a ground-living, bipedal runner, but like many extant iguanians, it may have combined locomotor styles. Modern bipedal lizard cursors generally have an enlarged anterior process at the front of the ilium (e.g., Snyder 1949, 1952, 1954; Brian Ruth, UCL, personal communication June 2004), and this feature appears to be only weakly developed in *Dalinghosaurus*. In addition, the ungual phalanges are extremely slender, suggesting that *Dalinghosaurus* may have climbed more than it ran.

![Cladograms showing the relationships of major squamate lineages, derived using a data matrix based on Evans and Chure (1998) with additional data from Evans and Barbadillo (1997, 1998, 1999). A. One of four resulting maximum parsimony trees. B. Result of Bootstrap Analysis with bootstrap values added to nodes. Amphibiaenia+ includes also Dibamidae.](http://app.pan.pl/acta50/app50-725.pdf)
Conclusions

The recovery of new material of the Early Cretaceous Chinese genus *Dalinghosaurus* shows that the long hind limbs (as known from the holotype specimen) are combined with relatively short forelimbs and an ornamented skull resembling that of living and extinct xenosaur-like lizards. Xenosaur (or shinisaur) affinity is broadly, but not categorically, supported by phylogenetic analysis and would strengthen the view that East Asia was an important centre for the evolution of these lizards in the Early Cretaceous.

Acknowledgments

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References


Appendix 1

Three different character lists and three data matrices were used in the analyses; they are not reproduced here due to their overall length. The relevant character lists can be found in Evans and Chure (1998), Gao and Norell (1998), and Lee (1998), with most of the details for individual taxa. Below we list the codings for the taxa that have been added to each matrix in this analysis.

Evans and Chure (1998)

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http://app.pan.pl/acta50/app50-725.pdf
Parviraptor

Gao and Norell (1998)

Dalinghosaurus

Gekkota

Parviraptor

Lee (1998)

Ardeosaurus

Bavarisaurus

Dalinghosaurus

Dorsetisaurus

Eichstaettisaurus

Parviraptor

Note added in proof