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 annulae. 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.

Susan E. Evans [ucgasue@ucl.ac.uk], Department of Anatomy and Developmental Biology, University College London, Gower Street, London WC1E 6BT, England;
Yuan Wang [wangyuan@ivpp.ac.cn], Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, 142 Xi-Zhi-Men-Wai St, P.O.Box 643, Beijing 100044, 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 Yixian Formation from the basal Lujiatun 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 Yixian Formation, or from the overlying Jiufotang Formation.

Many of the best specimens from the Lujiatun 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

?Carusioidea Gao and Norell, 1998

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.
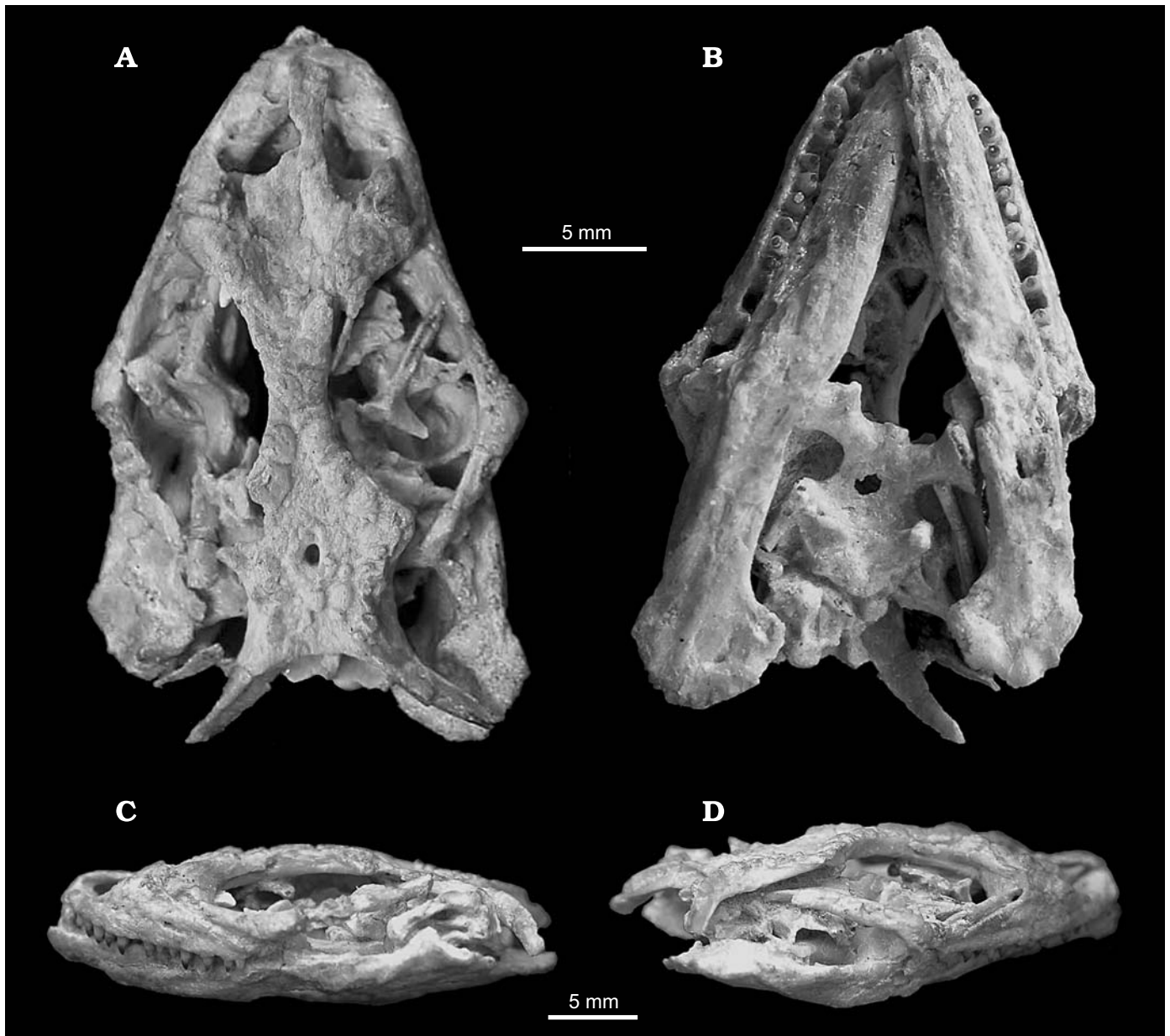
Acta Palaeontol. Pol. 50 (4): 725–742, 2005

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

Fig. 1. *Dalinghosaurus longidigitus.* IVPP V13282, Hauterivian–Barremian, Lujiatun, China. Skull in dorsal (**A**), palatal (**B**), left lateral (**C**), and right lateral (**D**) views. See Fig. 2 for explanation.

Type horizon: Early Cretaceous Yixian Formation Jianshangou Bed.

Referred specimens.—IG-02-7-16-2 (nearly complete postcranial 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 V13865 (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).

Distristribution.—Lower Cretaceous Yixian Formation of north-eastern China from the Lujiatun Bed (c. 128–132 Ma), to the Dawangzhangzi Bed (c. 122 Ma) (Wang and Zhou 2003).

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 medially; 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
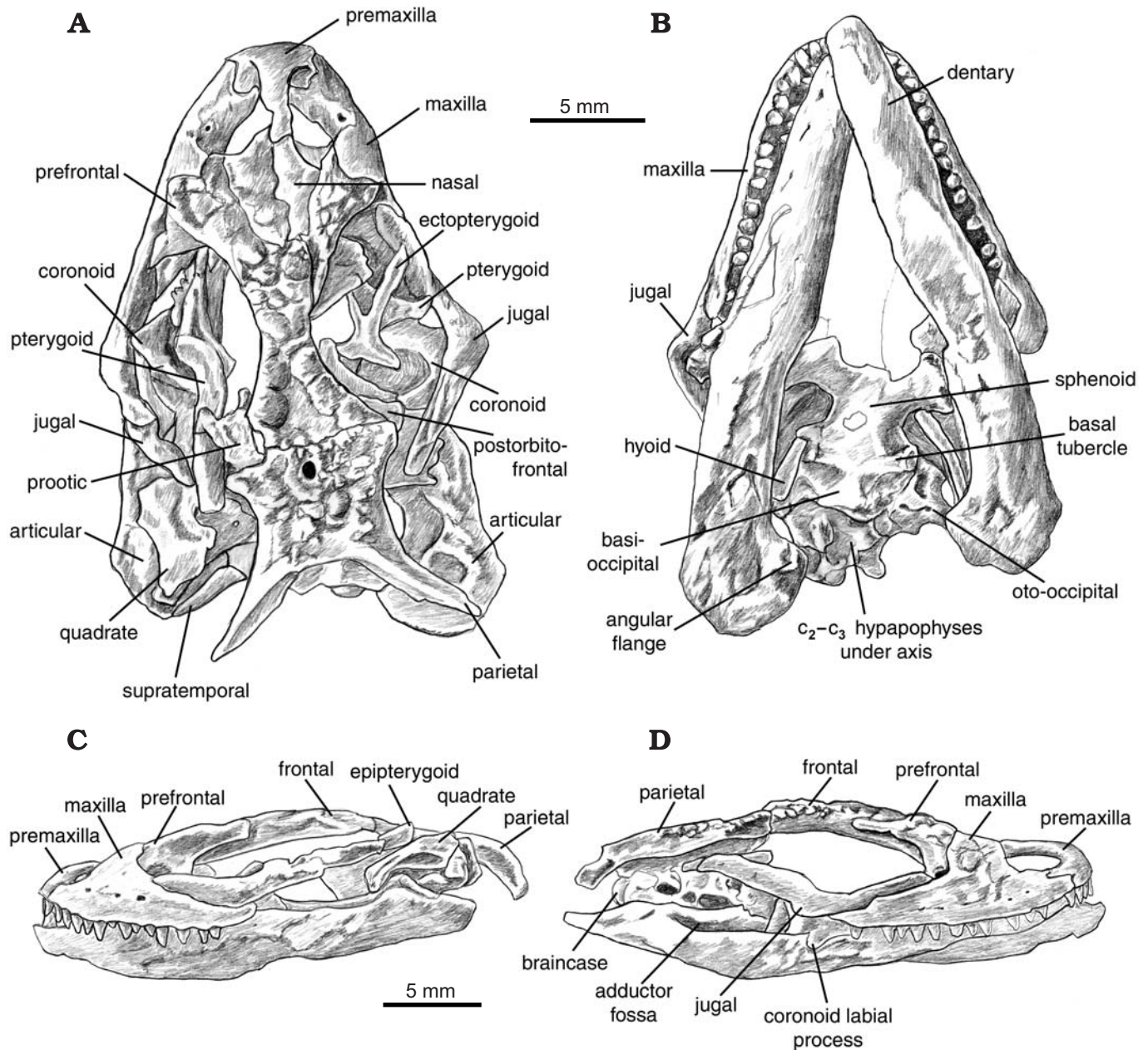
Fig. 2. *Dalinghosaurus longidigitus*. IVPP V13282, explanatory drawings for Fig. 1. Skull in dorsal (**A**), palatal (**B**), left lateral (**C**), and right lateral (**D**) views.

squamosal and bears pustulate sculpture. *Dalinghosaurus* resembles the Late Cretaceous *Carusia* (Borsuk-Białynicka 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 *Bavarisaurus*, 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
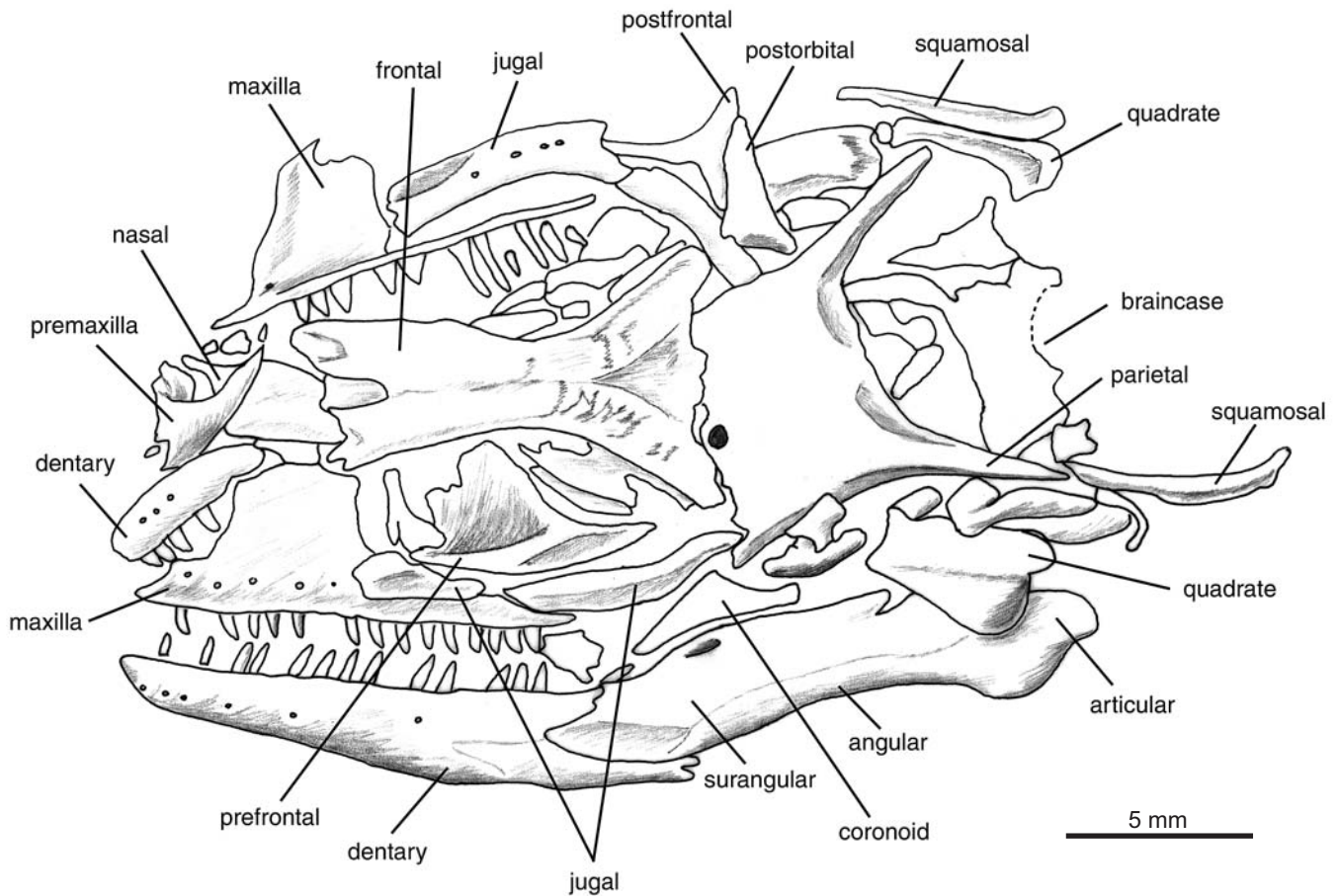
Fig. 3. *Dalinghosaurus longidigitus*. IVPP V13281, Barremian, Hejiaxin, China, immature specimen, skull in dorsal view.

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 nares, 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
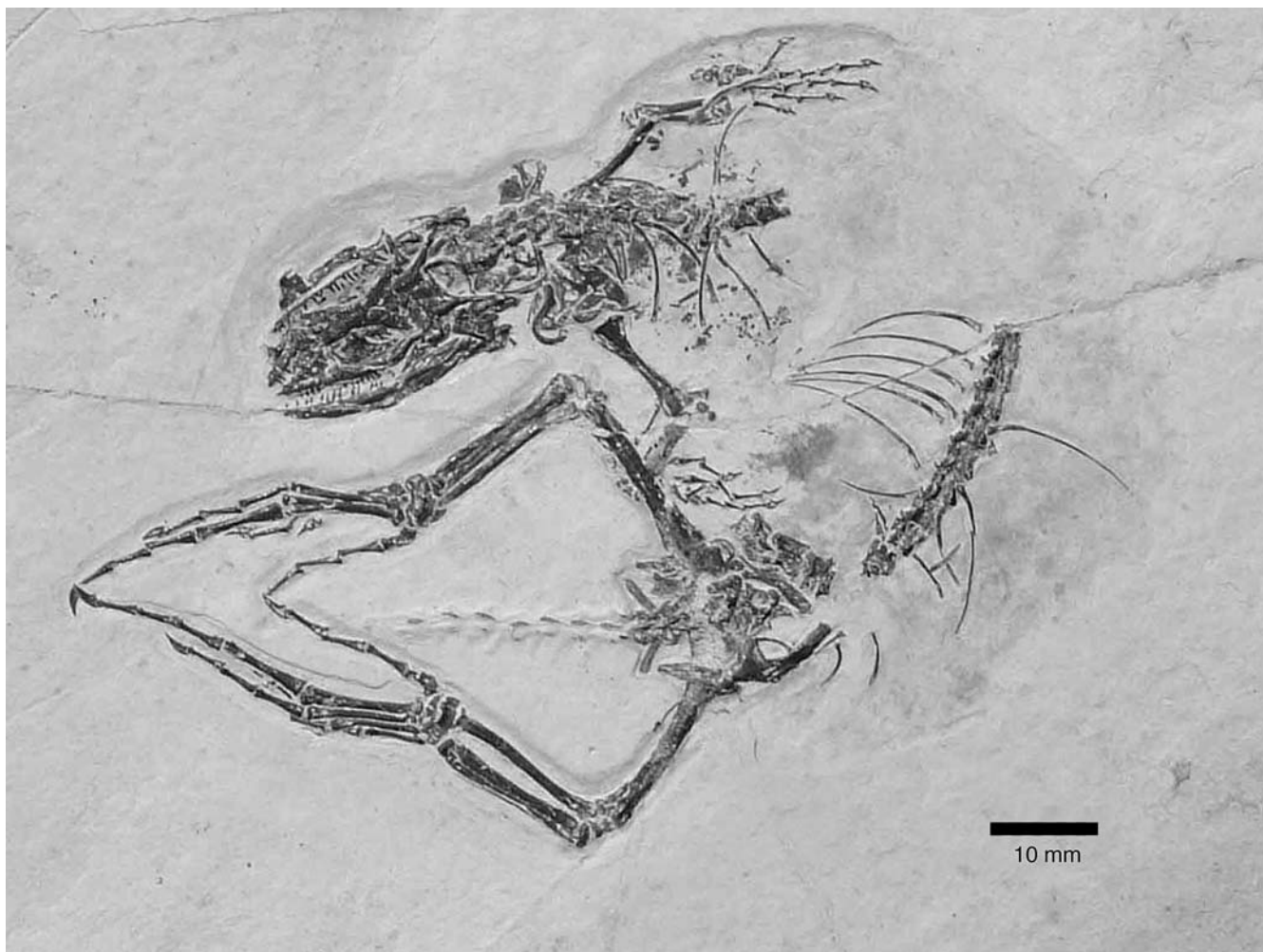
Fig. 4. *Dalinghosaurus longidigitus*. IVPP V13281, Barremian, Hejiaxin, China. Complete skeleton, dorsal view.

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
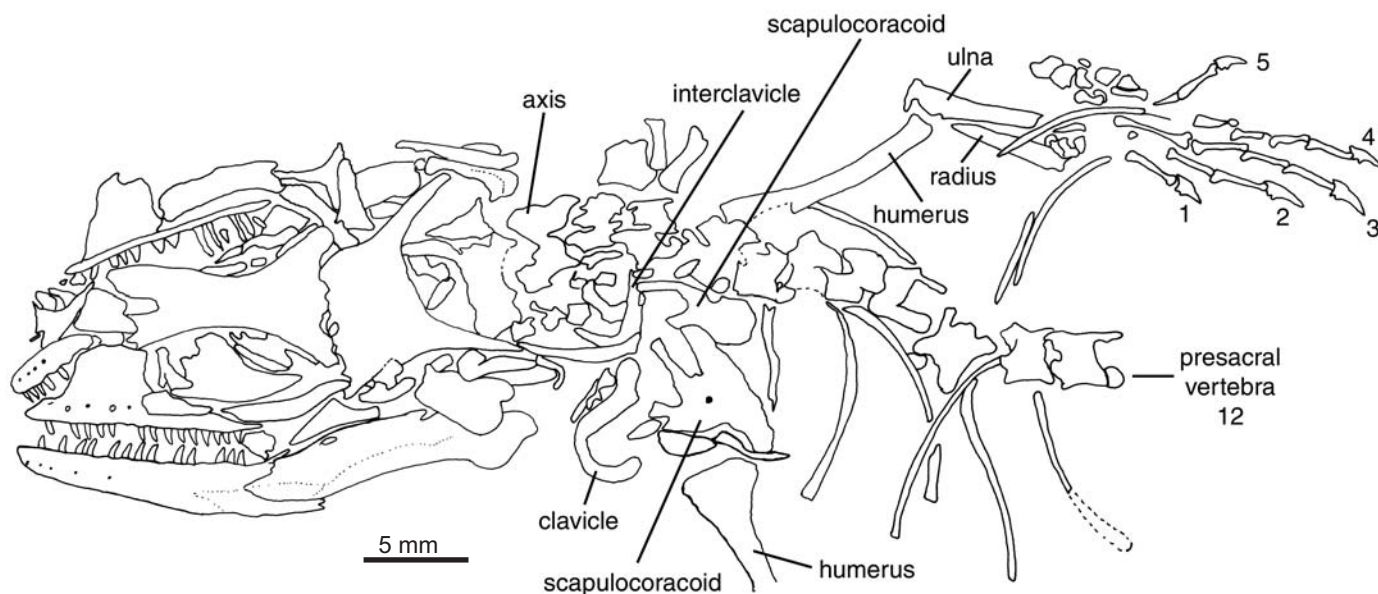
Fig. 5. *Dalinghosaurus longidigitus*. IVPP V13281, Barremian, Hejiaxin, China. Anterior skeleton showing right forelimb and part of pectoral girdle.

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 posteromedially, and the nasal anteromedially, and the maxilla anterolaterally. 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 (none *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 quadratojugal 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 triradiate, 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 anticlockwise, 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 postobital and probably the jugal.
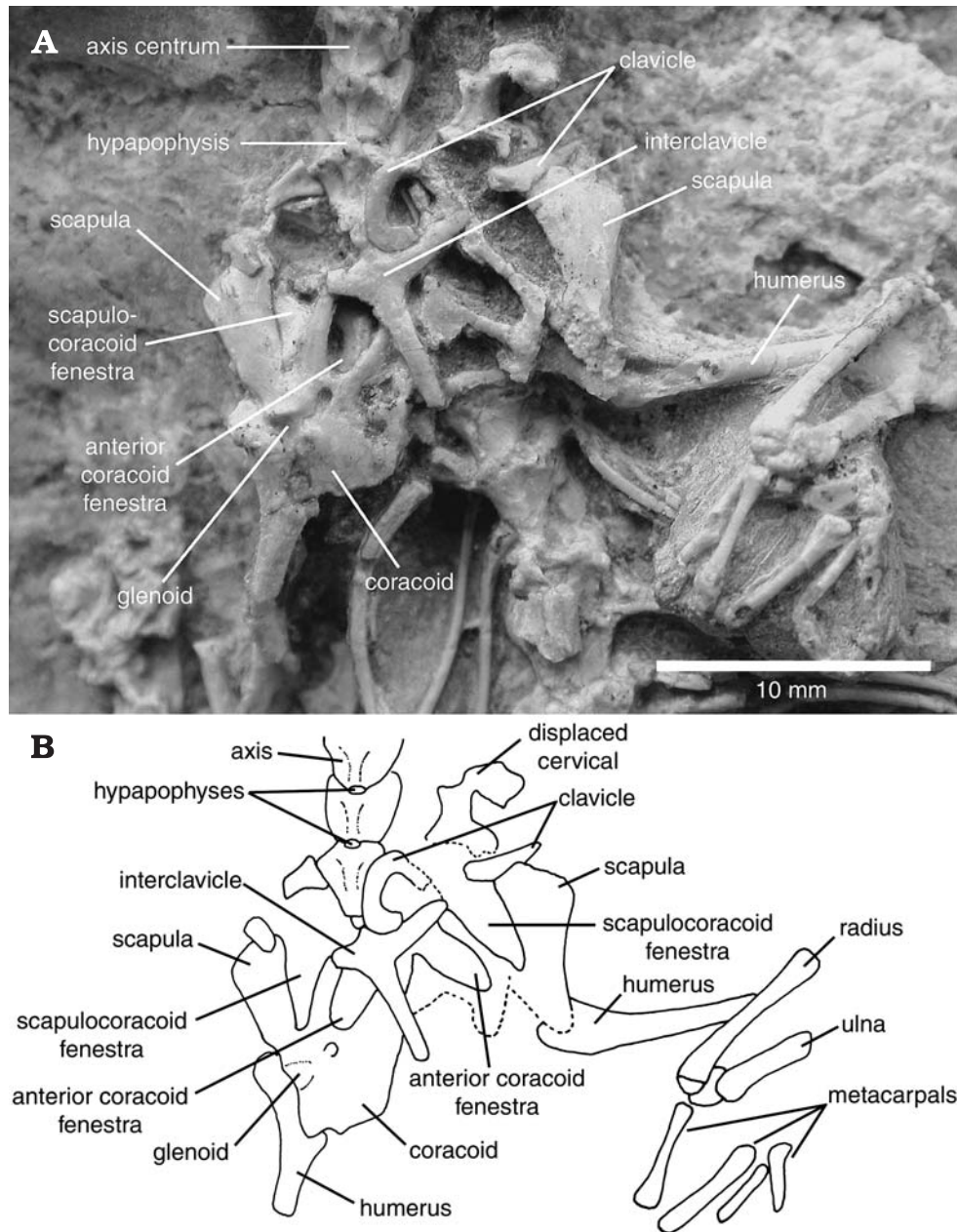
Fig. 6. *Dalinghosaurus longidigitus*. IVPP V14234.1, Hauterivian–Barremian, Lujiatun, China. Pectoral girdle in ventral view (**A**) and explanatory drawing (**B**), not to scale.

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-
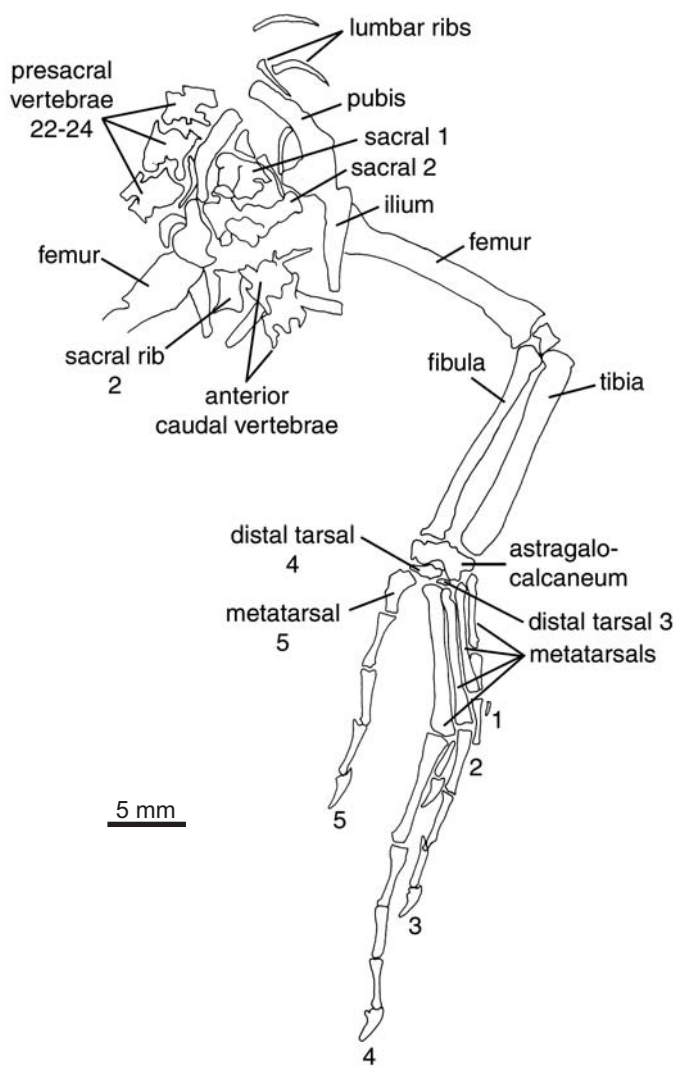
Fig. 7. *Dalinghosaurus longidigitus.* IVPP V13281, Barremian, Hejiaxin, China. Pelvic girdle, sacrum and right hind limb.

foramina that open into large recesses for eye muscle origin. Ventrally, the parasphenoid 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 spheno-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 posterodorsal 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 symphysial 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 posteromedially directed ridge along the margin of the posterior ramus. The surangular forms most of the lateral and ventrolateral faces of the post-dentary 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-

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
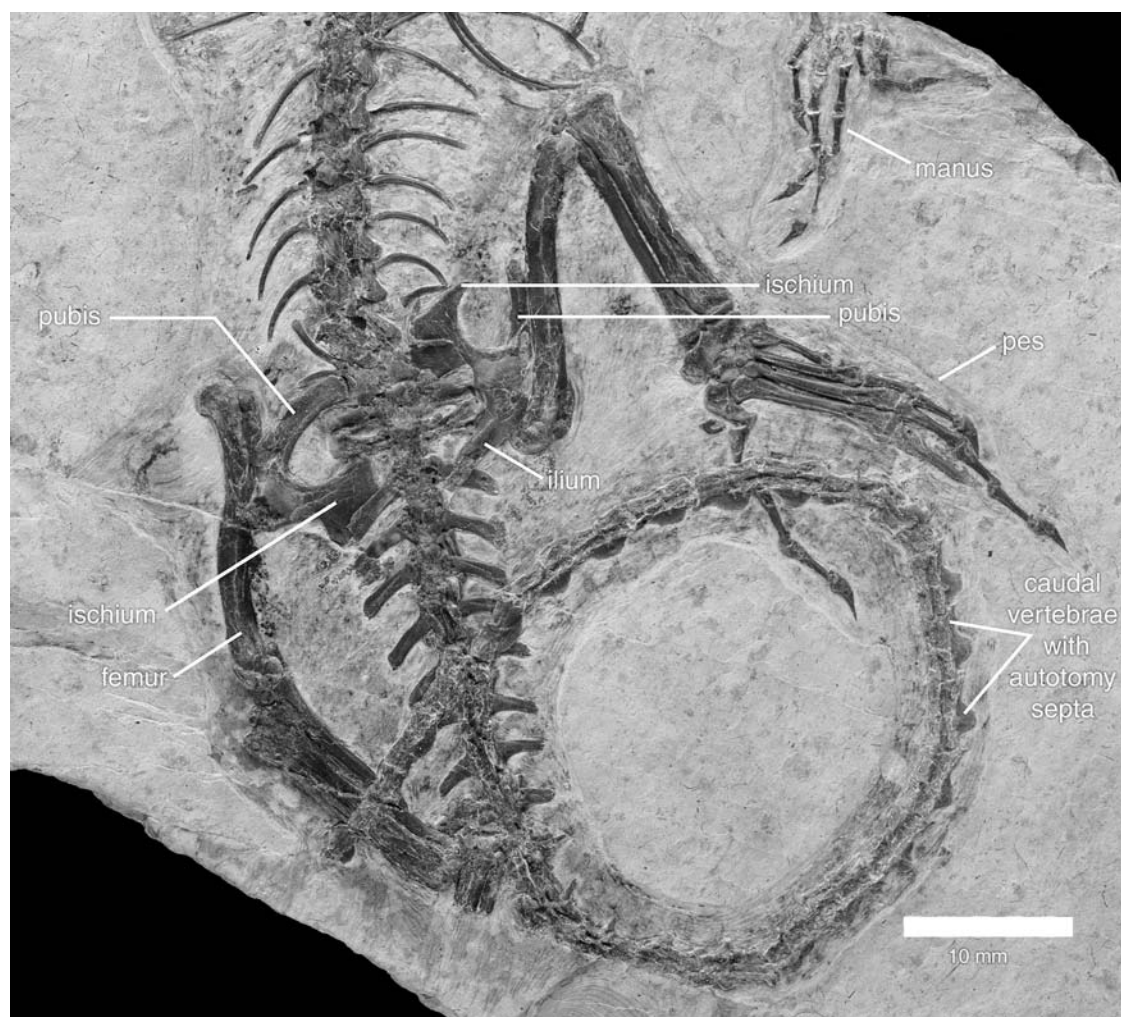
Fig. 8. *Dalinghosaurus longidigitus.* IVPP V14295, Barremian, Sihetun, Beipiao City, China. Pelvic girdle, hind limbs and tail, mainly dorsal view.

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, posteromedially 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 pecto-

ral 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 sacrals, 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 sacrals 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 posteroventral margin. The axis is also preserved associated with the skull in IVPP V13282 and is seen to have attached anterior and posterior hypapophyses (c_2–c_3 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 zygosphene-zygantral accessory articulation. In IVPP V14234.1 and IVPP V14234.2, the dorsal centra are preserved in ventral view. They taper anteroposteriorly 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 autotomous 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 V13865A 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 *Dalinghosaurus*, 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 symphysial 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 anteroventral 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,
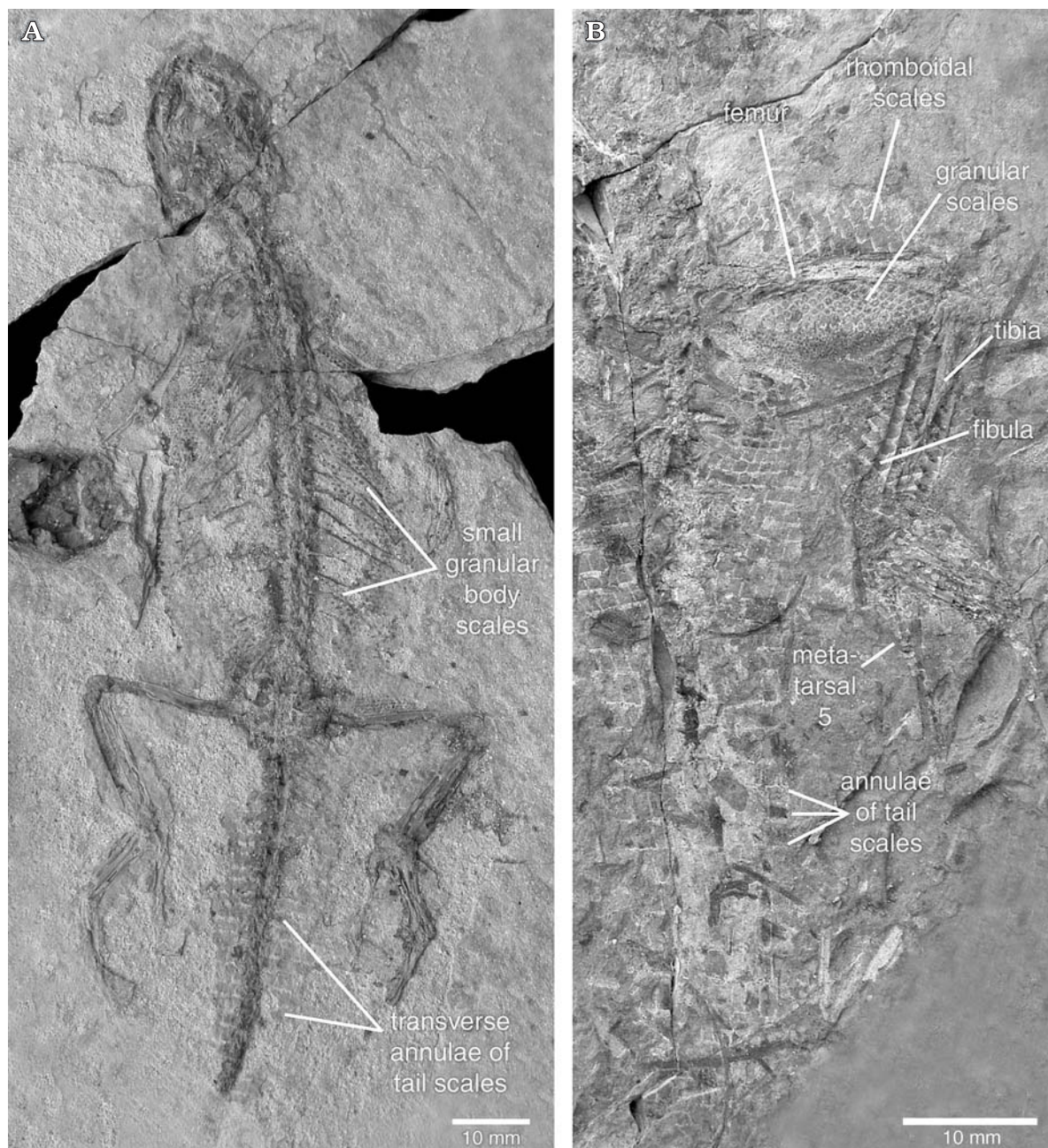
Fig. 9. *Dalinghosaurus longidigitus*, Barremian, Dawangzhangzi, China. Skin preservation. **A**. IVPP V13865B, showing body and tail scales. **B**. IVPP V12586, detail of hind leg and tail with scalation.

like the astragalocalcaneum, it is both wide and also prox-imo-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 to-gether), and strongly asymmetric, with an exceptionally long fourth digit, although digit 5 is quite long. The fourth meta-tarsal (Mt) has the greatest diameter of the metapodial ele-ments, 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 pro-cess 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 pro-cesses. The phalangeal formula of the pes is 2:3:4:5:4.

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 scalation 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 pecularities (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 post-

cranial 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-Białynicka 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-Białynicka 1985). In the extant *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-Białynicka 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 postorbital 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-Białynicka, 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—*Eich-*
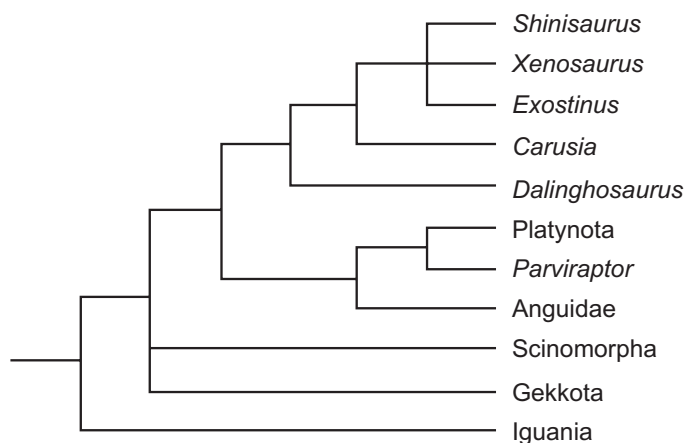

Fig. 10. Cladogram showing the relationships of major squamate lineages, derived using the data matrix of Gao and Norell (1998) with the addition of Gekkota, *Dalinghosaurus* and the Jurassic–Cretaceous anguimorph *Parviraptor*.

staettisaurus (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, Amphisbaenia 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; Paramacellodidae, 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-Białynicka 1985; Gao and Norell 1998). The results of these analyses were inconclusive,
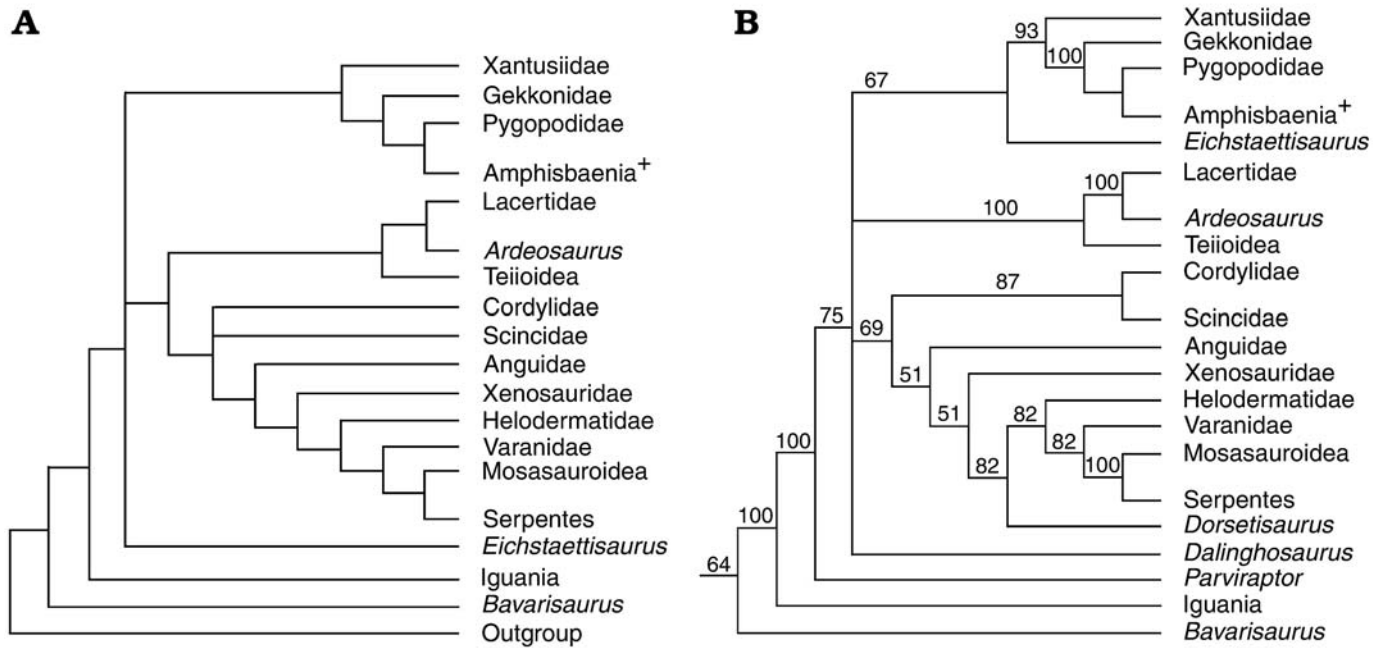
A

B

Fig. 11. Cladograms showing the relationships of major squamate lineages, derived using the data matrix of Lee (1998). **A**. With the addition of the Jurassic genera *Ardeosaurus*, *Bavarisaurus* and *Eichstaettisaurus*. **B**. 50% Majority Rule Consensus tree after addition of *Dalinghosaurus*, *Dorsetisaurus* and *Parviraptor*. Amphisbaenia[+] includes also Dibamidae.

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, Teiiidae, 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 the 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 surround-

ing 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-Białynicka (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 platynotans.

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-
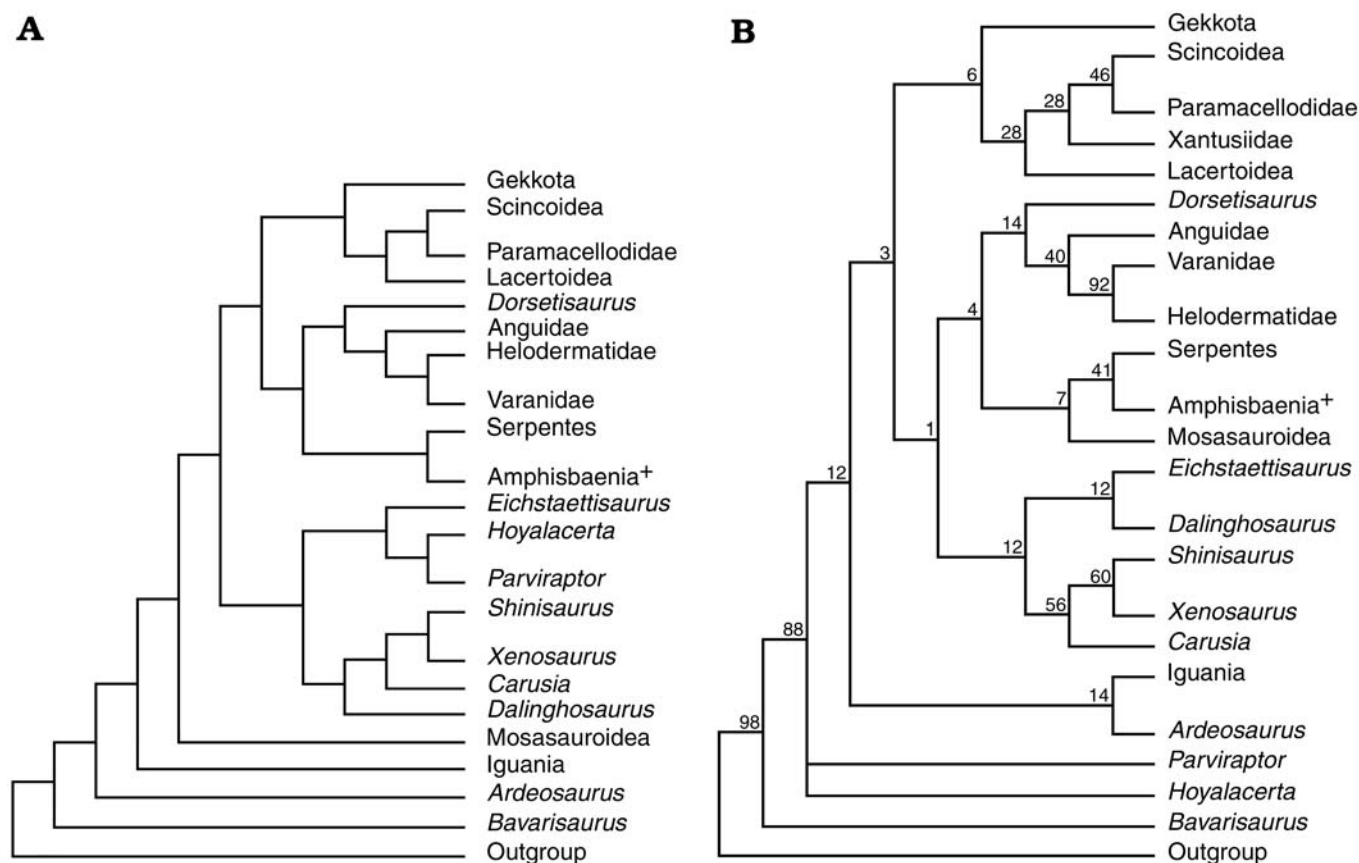
A

B

Fig. 12. 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. Amphisbaenia[+] includes also Dibamidae.

bate because under their traditional definition, "xenosaurs" provide one of several squamate examples of Asian-North American biogeographical links (e.g., polyglyphanodont teiids, 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 2000; Nydam 2002), 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 Nessov 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

shinisaurs and xenosaurs (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-Białynicka 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, shinisaurs, 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.

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

References

Alifanov, V. 1993. Some peculiarities of the Cretaceous and Palaeogene lizard faunas of the Mongolian People's Republic. *Kaupia* 3: 9–13.

Alifanov, V. 2000. Macrocephalosaurs and the early evolution of lizards of Central Asia [in Russian]. *Trudy Paleontologičeskogo Instituta RAN* 272: 1–126.

Arnold, E.N., Azar, D., Ineich, I., and Nel, A. 2002. The oldest reptile in amber: a 120 million year old lizard from Lebanon. *Journal of Zoology* 258: 7–10.

Barrows, S. and Smith, H.M. 1947. The skeleton of the lizard *Xenosaurus grandis*. *The University of Kansas Science Bulletin* 31: 227–281.

Broili, F. 1938. Ein neuer fund von ?*Ardeosaurus* H. von Meyer. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften, München* 1938: 97–114.

Borsuk-Białynicka, M. 1984. Anguimorphans and related lizards from the Late Cretaceous of the Gobi Desert. *Palaeontologia Polonica* 46: 5–105.

Borsuk-Białynicka, M. 1985. Carolinidae, a new family of xenosaurid-like lizards from the Upper Cretaceous of Mongolia. *Acta Palaeontologica Polonica* 30: 151–176.

Borsuk-Białynicka, M. 1986. On the diagnosis of the Xenosauridae (Anguimorpha). *In*: Z. Roček (ed.), Studies in Herpetology. *Proceedings of the European Herpetological Meeting* 1986: 213–218. Societas Europaea Herpetologica, Charles University, Prague.

Caldwell, M.W. 1999. Squamate phylogeny and the relationships of snakes and mosasauroids. *Zoological Journal of the Linnean Society* 125: 115–147.

Conrad, J.L. 2002. First fossil relative of *Shinisaurus* (Anguimorpha, Squamata) and the phylogenetic importance of Shinisauridae. *Journal of Vertebrate Paleontology* 22: 46A.

Conrad, J.L. 2004. Skull, mandible, and hyoid of *Shinisaurus crocodilurus* Ahl (Squamata, Anguimorpha). *Zoological Journal of the Linnean Society* 141: 399–434.

Endo, R. and Shikama, T. 1942. Mesozoic reptilian fauna in the Jehol mountainland, Manchoukuo. *Bulletin of the Central National Museum of Manchoukuo* 3: 1–19.

Estes, R. 1983. *Sauria Terrestria, Amphisbaenia*. *In*: P. Wellnhofer (ed.), *Handbuch der Paläoherpetologie, vol. 10A*, 1–245. Gustav Fischer Verlag, Stuttgart.

Estes, R., Gauthier, J., and de Queiroz, K. 1988. Phylogenetic relationships within Squamata. *In*: R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families: Essays Commemorating Charles L. Camp*, 119–281. Stanford University Press, Stanford.

Evans, S.E. 1994a. The Solnhofen (Jurassic: Tithonian) lizard genus *Bavarisaurus*: new skull material and a reinterpretation. *Neues Jahrbuch für Paläontologie und Geologie, Abhandlungen* 192: 37–52.

Evans, S.E. 1994b. A new anguimorph lizard from the Jurassic and Lower Cretaceous of England. *Palaeontology* 37: 33–49.

Evans, S.E. and Barbadillo, L.J. 1997. Early Cretaceous lizards from las Hoyas, Spain. *Zoological Journal of the Linnean Society* 119: 23–49.

Evans, S.E. and Barbadillo, L.J. 1998. An unusual lizard from the Early Cretaceous of Las Hoyas, Spain. *Zoological Journal of the Linnean Society* 124: 235–265.

Evans, S.E. and Barbadillo, L.J. 1999. A short-limbed lizard from the Early Cretaceous of Spain. *Special Papers in Palaeontology* 60: 73–85.

Evans, S.E. and Chure, D. 1998. Paramacellodid lizard skulls from the Jurassic Morrison Formation at Dinosaur National Monument, Utah. *Journal of Vertebrate Paleontology* 18: 99–114.

Evans, S.E., Lacasa-Ruiz, A., and Erill Rey, J. 1999. A lizard from the Early Cretaceous (Berriasian–Hauterivian) of Montsec. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 215: 1–15.

Evans, S.E., Raia, P., and Barbera, C. 2004. New lizards and sphenodontians from the Early Cretaceous of Italy. *Acta Palaeontologica Polonica* 49: 393–408.

Evans, S.E., Wang, Y., and Li, C. (in press). The Early Cretaceous lizard *Yabeinosaurus* from China: resolving an enigma. *Journal of Systematic Palaeontology*.

Fürbringer, M. 1900. Beitrag zur Systematik und Genealogie der Reptilien. *Jenaischen Zeitschrift für Naturwissenschaften* 34: 596–682.

Gao, K.Q. and Fox, R.C. 1996. Taxonomy and evolution of Late Cretaceous lizards (Reptilia: Squamata) from Western Canada. *Bulletin of Carnegie Museum of Natural History* 33: 1–107.

Gao, K.Q. and Nessov, L.A. 1998. Early Cretaceous squamates from the Kyzylkum Desert, Uzbekistan. *Neues Jahrbüch für Geologische und Paläontologische Abhandlungen* 207: 289–309.

Gao, K.Q. and Norell, M.A. 1998. Taxonomic revision of *Carusia* (Reptilia: Squamata) from the Late Cretaceous of the Gobi Desert and phylogenetic relationships of the anguimorphan lizards. *American Museum Novitates* 3230: 1–51.

Gao, K.Q. and Norell, M. A. 2000. Taxonomic composition and systematics of Late Cretaceous lizard assemblages from Ukhaa Tolgod and adjacent localities, Mongolian Gobi Desert. *Bulletin of the American Museum of Natural History* 249: 1–118.

Gilmore, C.W. 1928. Fossil lizards of North America. *Memoirs of the National Academy of Sciences* 22: 1–201.

Haeckel, E. 1866. *Generelle Morphologie der Organismen. Allgemeine Grundzuge der organischen Formen-Wissenschaft mechanisch begrundet durch die von Charles Darwin reformierte Deszendenz-Theorie*, 2 vols: 1, 574 pp.; 2, 462 pp. Georg Reimer Verlag, Berlin.

Hoffstetter, R. 1964. Les Sauria du Jurassique supérieur et specialement les Gekkota de Bavière et de Mandchourie. *Senckenbergiana Biologie* 45: 281–324.

Hoffstetter, R. 1967. Coup d'oeil sur les Sauriens (= lacertiliens) des couches de Purbeck (Jurassique supérieur d'Angleterre). Résumé d'un Mémoire). *Colloques Internationaux du Centre National de la Recherche Scientifique* 163: 349–371.

Hu, Q., Jiang, Y., and Zhao, E.M. 1984. A study on the taxonomic status of *Shinisaurus crocodilurus*. *Acta Herpetologica Sinica* 3: 1–7.

Jerzykiewicz, T. and Russell, D.A. 1991. Late Mesozoic stratigraphy and vertebrates of the Gobi Basin. *Cretaceous Research* 12: 345–377.

Ji, S.A. 1998. A new long-tailed lizard from the Upper Jurassic of Liaoning, China. *In*: Department of Geology, Peking University (ed.), *Collected Works of International Symposium on Geological Science, Peking University, Beijing, China*, 496–505. Seismological Press, Beijing.

Ji, S.A. and Ji, Q. 2004. Postcranial anatomy of the Mesozoic *Dalinghosaurus* (Squamata): evidence from a new specimen of Western Liaoning. *Acta Geologica Sinica* 78: 897–906.

Ji, S.A., Lu, L.W., and Bo, H.C. 2001. New material of *Yabeinosaurus tenuis* (Lacertilia) [in Chinese]. *Land and Resources* 2001: 41–43.

Ji, S. and Ren, D. 1999. First record of lizard skin fossil from China with description of a new genus (Lacertilia, Scincomorpha). *Acta Zootaxonomica Sinica* 24: 114–120.

Lee, M.S.Y. 1998. Convergent evolution and character correlation in burrowing reptiles: towards a resolution of squamate relationships. *Biological Journal of the Linnean Society* 65: 369–453.

Macey, J.R., Schulte, J.A., Larson, A., Tuniyev, B.S., Orlov, N., and Papenfuss, T.J. 1999. Molecular phylogenetics, tRNA evolution, and historical biogeography in anguid lizards and related taxonomic families. *Molecular Phylogenetics and Evolution* 12: 250–272.

Mateer, N. 1982. Osteology of the Jurassic lizard *Ardeosaurus brevipes* (Meyer). *Palaeontology* 25: 461–469.

McDowell, S.B. and Bogert, C.M. 1954. The systematic position of *Lanthanotus* and the affinities of anguinomorphan lizards. *Bulletin of the American Museum of Natural History* 105: 1–141.

Nessov, L.A. 1985. Rare bony fishes, terrestrial lizards and mammals from the lagoonal zone of the littoral lowlands of the Cretaceous of the Kyzylkum [in Russian]. *Ežegodnik Vsesoûznogo Paleontologičeskogo Obŝestva (Akademiâ Nauk SSSR), Leningrad* 28: 199–219.

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

Nessov, L.A. 1997. *Cretaceous Nonmarine Vertebrates of Northern Eurasia* [in Russian with English summary]. 218 pp. (Posthumous paper ed. by L.B.Golovneva and A.O.Averianov). University of Sankt Petersburg, Institute of Earth Crust, Sankt Petersburg.

Nydam, R.L 2002. Lizards of the Mussentuchit local fauna (Albian–Cenomanian boundary) and comments on the evolution of the Cretaceous lizard fauna of North America. *Journal of Vertebrate Paleontology* 22: 645–600.

Oppel, M. 1811. *Die Ordnungen, Familien und Gattungen der Reptilien, als Prodrom einer Naturgeschichte derselben*. 87 pp. Joseph Lindauer, Munich.

Reynoso V.H. 1998. *Huehuecuetzpalli mixtecus* gen. et sp. nov: a basal squamate (Reptilia) from the Early Cretaceous of Tepexi de Rodríguez, Central México. *Philosophical Transactions of the Royal Society B* 353: 477–500.

Rieppel, O. 1980. The phylogeny of anguimorphan lizards. *Denkschriften der Schweizerischen Naturforschenden Gesellschaft* 94: 1–98.

Snyder, R.C. 1949. Bipedal locomotion of the lizard *Basiliscus basiliscus*. *Copeia* 1949: 129–137.

Snyder, R.C. 1952. Quadrupedal and bipedal locomotion of lizards. *Copeia* 1952: 64–70.

Snyder, R.C. 1954. The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. *American Journal of Anatomy* 95: 1–36.

Swofford, D.L. 1993. *PAUP* (Phylogenetic Analysis Using Parsimony). Version 3.1.1*. University of Illinois, Urbana-Champaign.

Swofford, D.L. 2001. *PAUP* Version 4.06b10 for 32 bit Microsoft Windows*. Sinauer Associates Incorporated, Publishers, Sunderland, Massachusetts.

Townsend, T.M., Larson, A., Louis, E., and Macey, J.R. 2004. Molecular phylogenetics of Squamata: the position of snakes, amphisbaenians, and dibamids, and the root of the squamate tree. *Systematic Biology* 53: 735–757.

Wang, X.L. and Zhou, Z.H. 2003. Mesozoic Pompei. *In*: M.M. Chang, P.J. Chen, Y.Q. Wang, and Y.Wang (eds.), *The Jehol Biota*, 19–35. Shanghai Scientific and Technical Publishers, Shanghai.

Wu, C.H. and Huang, Z.J. 1986. Morphological comparison of *Shinisaurus crocodilurus* and *Xenosaurus grandis*. *Sinozoologica* 4: 41–50.

Young, C.C. 1958. On a new locality of *Yabeinosaurus tenuis* Endo and Shikama. *Vertebrata PalAsiatica* 2: 151–156.

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 raw data 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)

Carusia

```
00010 11?10 0?1?1 01?00 002/300 00000 ?00?? 0?000 00101 100?1 01?10 01110
00?00 00000 02121 00??? ?????  ????? ????? ????? ????? ????? ????? ?????
????? ????1 11111 111?? 2?211  2???? ????? ????? ????? ????? ????? ?????
????? ????1 11221 1111? 0?011  0???? ?2
```

Dalinghosaurus

```
00000 11?10 0011? 01?01 00301 0010? 0?0?? ?01?0 1???? 0???? 00?10 0??10
?02?0 00000 ?1120 00??? 0200? 10011 ??010 ?10?1 1?100 00?2? ????? ?????
????? ????1 11110 111?? 2?1?? 211?? 1???? ?1111 211?? ????? ????? ?????
????? ????? ?1221 11111 030?1 0?012 0?
```

Dorsetisaurus

```
100?0 00000 0???? 01000 01001 ????? ????? ?01?? ?100? 00??0 00010 00010
000?? ???1? 01121 00??? 020?? ????? ????? ????? ????? 0000? ????? ?????
????? ????? 1???? 111?? 2?1?1 2???? 1???? ????? ????? ????? ????? ?????
????? ????? ????? ????? 0?01? 0???? ?2
```

Parviraptor
```
?1??0 00?11 00??? 00002 00??? ?01?? ??1?? 00100 1???? 00012 ????? ?????
????? ????? 02221 00??? 0201? 1?0?? ????? ????? ????? ??00? ????? ?????
????? ????1 11?1? ?11?? ???1? ?11?? ????? ????? ????? ????? ????? ?????
????? ????? 1???? ?1??? 0???? ????? ?2
```

Gao and Norell (1998)

Dalinghosaurus
```
00020 11101 0?010 01?00 00000 00??? 0?100 10000 00100 ?0000 0000? 1020?
??0?? 00?10 121?0 0??0? 001?0 ???0? ????? ????? ????? ?????
```

Gekkota
```
000/101 0/10110 00111 00090 91013 10000 00000 00/1000 00000 00/100/10 01100/1
00010 00119 20010 10000 00000 0000/10/1 100/100 ?0/1000 00/1000 00000
```

Parviraptor
```
??10? 00100 00000 00100 001?1 0???? ??1?? ?0??0 11000 ?10?? 11101
???1? ?1?20 0???? ??0?? ?000? 00??? 1???? ????? ????? ????? ?????
```

Lee (1998)

Ardeosaurus
```
????0 0???? ?0?0? ??10? 0000? 00101 00000 000?0 11011 00?1? 0???? 0????
????? ????? ????? ????? 0???? ????? ????? ????? ??0?? ????1 ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????? ?11?? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
```

Bavarisaurus
```
????0 01??? ?0?0? ??0?? 00000 00000 00001 000?0 10011 00?1? 0???? 0????
????? ????? ????? ????? ????? ????? ????? ????? ??0?? ????1 ????? ?10??
????? ????? ????? ????? ????? 1?000 0???? ?11?? ???0? ?0??? 0???? 0????
????? ????? ???1? ????? ????? ????? ????? ????? ????? ?????
```

Dalinghosaurus
```
??000 00??0 00100 1001? 10001 ?0101 ?0001 000?0 10011 ?0011 0010? 0?000
0?011 ???00 0??01 1???? 0?00? ???0? 00000 ???0? ??001 00?0? 001?? ??100
????0 1?1?0 00?0? 2??00 0?000 10000 00010 00000 00?01 0111? 11000 ??0?0
00000 ?0000 01000 10011 ???00 0002? 00000 00000 2???? ??0?0
```

Dorsetisaurus
```
??00 0?000 00101 00100 1???1 ????1 ?0001 00??? ?00?? ????? ????? 0?000
0?011 000?0 0??01 000?1 010?? ????? ????? ??0?? ????? ?0001 01100 ?0100
10?00 1010? 001?? 0000? 1??1? 11001 0???? ?0000 00??? ????? ????? ?????
????? ????? ????? ????? ??0? ????? 000?? 00??? 2???? ?????
```

Eichstaettisaurus
```
????0 01??? ?0?0? ??01? 10001 00101 10000 01010 10011 00?1? 0???? 0????
????? ????? ????? ????? 0???? ????? ????? ????? ??001 ???01 02??? ??0??
????? ????? ????? ????? ????? 1?000 ????? ?0??? ???0? ??1?? ????? ?????
????? ????? ????? ????? ????? ????? ????? ????? ????? ?????
```

Parviraptor
```
????0 0???? ?0??1 ??100 10??1 ????0 00001 00??0 100?? ???1? ??10? 0?000
????? ????0 0???? ????1 010?? ???0? 01?00 0?100 0?001 ?10?1 00?00 12???
??1?? ????? ????? ????? ????? 20011 ????? ?001? 1??00 01001 ????0 000??
00000 ?00?? ????? ????? ????? ????? ????? ????? 0???? ?????
```

Note added in proof

In a recent paper, Bever et al. (2005) have confirmed the presence of free cranial osteoderms in the living *Shinisaurus*.

Bever, G.S., Bell, C.J., and Maisano, J.A. 2005. The ossified braincase and cephalic osteoderms of *Shinisaurus crocodilurus* (Squamata, Shinisauridae). *Palaeontologia Electronica* 8: 1–36.