

A juvenile lizard specimen with well-preserved skin impressions from the Upper Jurassic/Lower Cretaceous of Daohugou, Inner Mongolia, China

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Abstract Lizards are now relatively well known from the Yixian Formation of northeastern China. In this study, we describe a juvenile lizard from a fossil horizon at Daohugou, Inner Mongolia. These beds predate the Yixian Formation, and are probably Late Jurassic or earliest Cretaceous in age. The new specimen thus documents the first lizard material from the Daohugou locality and is the earliest lizard skeleton from China. Comparisons with developmental stages of modern lizards suggest the Daohugou lizard is a hatchling. Although tiny, the specimen is notable in preserving exquisite skin impressions showing the variation in scalation across the body, the shape and position of the cloacal outlet, and details of the manus and pes. These are the earliest recorded lepidosaurian skin traces. In its general proportions and the possession of paired frontals, the small Daohugou lizard resembles both the Yixian taxon *Yabeinosaurus tenuis* and the questionable *Jeholacerta formosa*, but it differs from the latter in scalation and, based on other characters, may be distinct from both.

Keywords Lizard · Late Jurassic/Early Cretaceous · China · Scalation · Ontogeny

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Introduction

The deposits of the Lower Cretaceous Yixian and Jiufotang formations of the Jehol Group, northeastern China (Liaoning, Hebei, Inner Mongolia) are justly famous for their extensive and well-preserved flora and fauna (the Jehol Biota, Chang et al. 2003; Zhou et al. 2003). According to most scholars, and based on isotopic dating techniques (e.g., Smith et al. 1995; Swisher et al. 1999; Zhou et al. 2003) the Jehol Group ranges from Valanginian (Lujiatun Bed, Yixian Formation) to Aptian (Jiufotang Formation) in age. To date, the Yixian Formation has yielded material of two distinct lizard taxa, *Yabeinosaurus tenuis* (Endo and Shikama 1942; Ji et al. 2001; Evans et al. 2005) and the smaller *Dalinghosaurus longidigitus* (Ji 1998; Evans and Wang 2005). *Y. tenuis* is known from the lower to upper horizons of the Yixian Formation (Jianshangou, Dawangzhangzi, and Jingangshan beds) and also from the overlying Jiufotang Formation (Evans et al. 2005). A second species, *Yabeinosaurus youngi*, was named by Hoffstetter (1964), but the specimen on which it is based (IVPP V961) is too poorly preserved to be sure of either its generic or specific attribution. *Dalinghosaurus*, on the other hand, is known only from the lower and middle horizons of the Yixian Formation (Lujiatun, Jianshangou, and Dawangzhangzi beds [Evans and Wang 2005]). The lizard *Pachygenysthlastesa* Gao and Cheng 1999, from Shandong, China, is probably equivalent in age to the lizards of the Jehol Group, as is the supposedly Upper Jurassic *Mimobecklesisaurus gansuensis* Li 1985, from Gansu Province (Wang, personal communication, July 2005).

In this paper, we describe a small lizard specimen (IVPP V14386A, B) from the Inner Mongolian locality of Daohugou. Although the age of the fossiliferous horizon

at this site has yet to be confirmed, it is generally agreed to predate the Yixian Formation (Wang 2004; Wang et al. 2005), making this the oldest known lizard skeleton from China (fragmentary jaw and vertebral material exists from the Middle Jurassic, but has yet to be described [Wang, work in progress]). It is also the earliest recorded lepidosaur with well-preserved skin traces, and yields details of scale morphology in different regions of the body. Several geologically younger Jehol lizards also preserve skin traces, but outside China such soft tissue remains are limited to a partial lizard preserved in amber from the Early Cretaceous (Neocomian–Aptian) of the Lebanon (Arnold et al. 2002), and a Late Cretaceous (Cenomanian) marine lizard in fine-grained limestone, again from Lebanon (Caldwell and Dal Sasso 2004; Caldwell 2006).

Geology and materials

The fossiliferous Daohugou bed comprises freshwater shales interbedded with tuffs. It was first recognized near the village of Daohugou, Inner Mongolia, but is also known from neighboring Lingyuan, Liaoning Province (e.g., at the locality of Wubaiding, Wang et al. 2005; Wang and Evans 2006a,b). In combination, deposits of the Daohugou bed have yielded a diverse assemblage of insects (Ren and Yin 2002; Zhang 2002), conchostracans (Shen et al. 2003), salamanders (*Chunerpeton*, Gao and Shubin 2003; *Jeholotriton*, Wang 2000; Wang and Rose 2005; *Liaoxitriton daohugouensis*, Wang 2004; *Pangerpeton*, Wang and Evans 2006b), one anuran tadpole (Yuan et al. 2004), small, feathered theropods (*Epidendrosaurus*, Zhang et al. 2002; *Pedopenna*, Xu and Zhang 2005), rhamphorhynchid (*Pterorhynchus*, Czerkas and Ji 2002) and anurognathid (*Jeholopterus*, Wang et al. 2002) pterosaurs, and a docodontan mammal (Ji et al. 2006). The geology of Daohugou is complex and the dating is problematic. Invertebrate researchers generally favour a Middle Jurassic age, equivalent to the Jiulongshan Formation (Ren and Yin 2002; Shen et al. 2003). Others have argued that some of the tetrapods from Daohugou (salamanders, pterosaurs, dinosaurs, Wang 2004; Zhou 2004; Wang et al. 2005) are closer to those of the Jehol Biota (and the salamander genus *Liaoxitriton* is known from both assemblages), although some key Jehol taxa (e.g., *Ephemeropsis*, *Lycoptera*) are missing. Wang et al. (2005) recently reviewed both the stratigraphy and faunal assemblage of the Daohugou fossil bed. They rejected a Middle Jurassic age and concluded that the Daohugou bed probably belongs to the same cycle of volcanism and sedimentation as the Yixian Formation, but is lower in the sequence. Its assemblage may therefore represent a fauna that was a precursor to the typical Jehol Biota. Discussion of the age of this horizon is ongoing, but

for the interim, we accept Wang et al.'s interpretation of the assemblage as pre-Yixian and of earliest Cretaceous or possibly Late Jurassic age.

Description

The lizard specimen (IVPP V14386A, B) is preserved mainly as skeletal impressions with ventral and dorsal views on the part and counterpart, respectively, and with well-preserved skin traces showing scale morphology on different parts of the body including the manus and pes (Fig. 1). The right forelimb is folded under the body, but otherwise all parts of the skeleton are clearly exposed. The animal is 43.9 mm in snout–pelvis length (SPL). From the weak state of development of the skeleton, it is clear that it is juvenile (see also “Discussion” section). The skull is rounded with large eyes and has been compressed, partially disarticulating the thin, weakly sutured bones (Fig. 1). In the vertebral column, only isolated centra are visible (suggesting that the neurocentral sutures were open) and the sacral and caudal ribs appear to be separate from the vertebral bodies. Vertebral condyles are not visible, but this is probably due to immaturity. The elements of the pectoral girdle are poorly defined and those of the pelvis are not coossified. In the limbs, the ends of the long bones are straight without ossified epiphyses or obvious joint surfaces, but some bear the impressions of cartilaginous ends. The carpus seems to be mostly unossified and in the ankle, only one rounded tarsal element is present.

Because the original specimen is preserved in impression, high fidelity peels were made to examine the detailed structure and, unless otherwise noted, the description that follows is based mainly on the peels, which show the “bone” rather than its impression. One of these peels (part) was gold coated for scanning electron microscopy.

Skull

The skull (Figs. 1 and 2) is compressed asymmetrically so that the part preserves the ventral and right ventrolateral surfaces, and the counterpart has a partial dorsal/dorsolateral view. The part preserves the left and right dentaries, framing the skull region (Fig. 2a). The left maxilla is preserved in medial view, with a triangular facial process. The right maxilla is preserved in a partial lateral view. Its anterior end is drawn out into a slender premaxillary process and its posterior end is overlain by the biradial right jugal (Figs. 1e and 2). The latter has a short anterior ramus and a slightly longer postorbital ramus. A small right prefrontal is preserved posterodorsal to the right maxilla. In this specimen, at least, the jugal does not meet the prefrontal and the maxilla may have entered the orbital

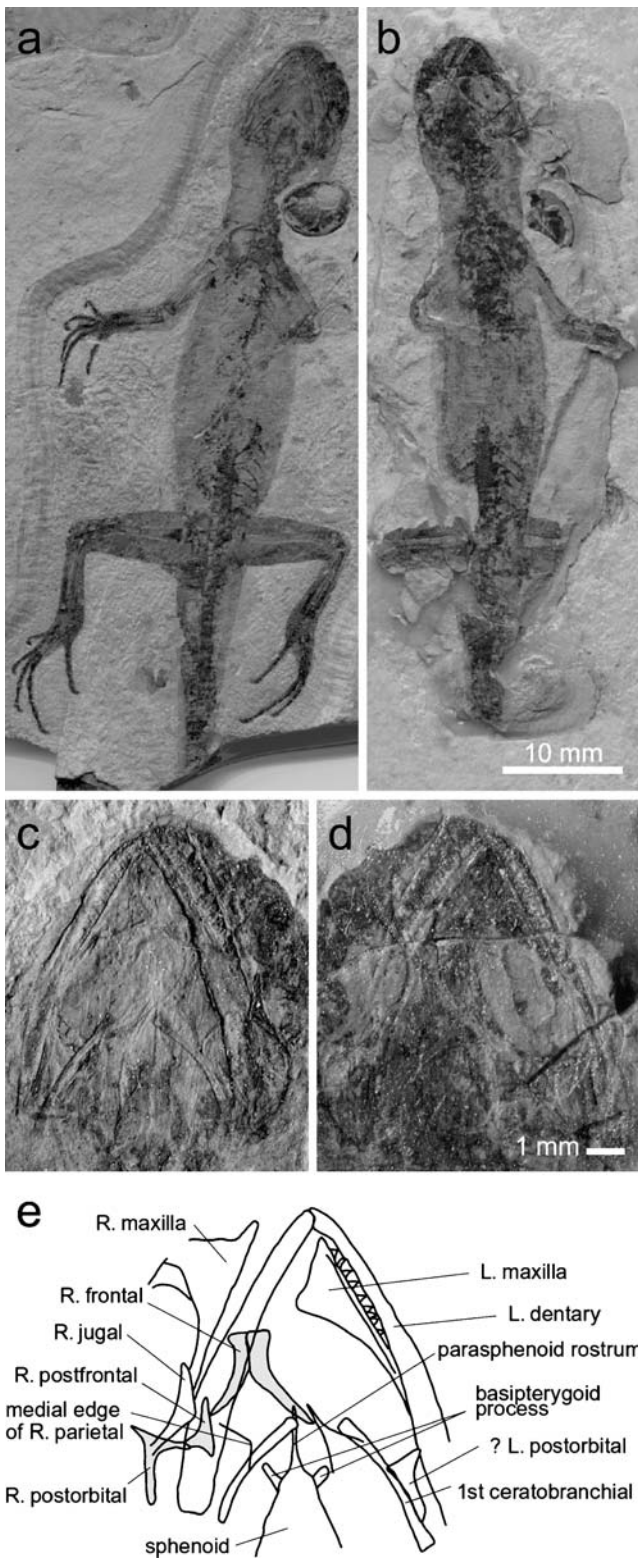


Fig. 1 Daohugou lizard V14386. **a** Part; **b** counterpart; **c** skull of part; **d** skull of counterpart; **e** outline drawing of skull (based on high fidelity peels) with bone traces on the counterpart (*grey infill*) superimposed on those of the part. Note that the ovoid structure adjacent to the neck in **a** and **b** is a conchostracan

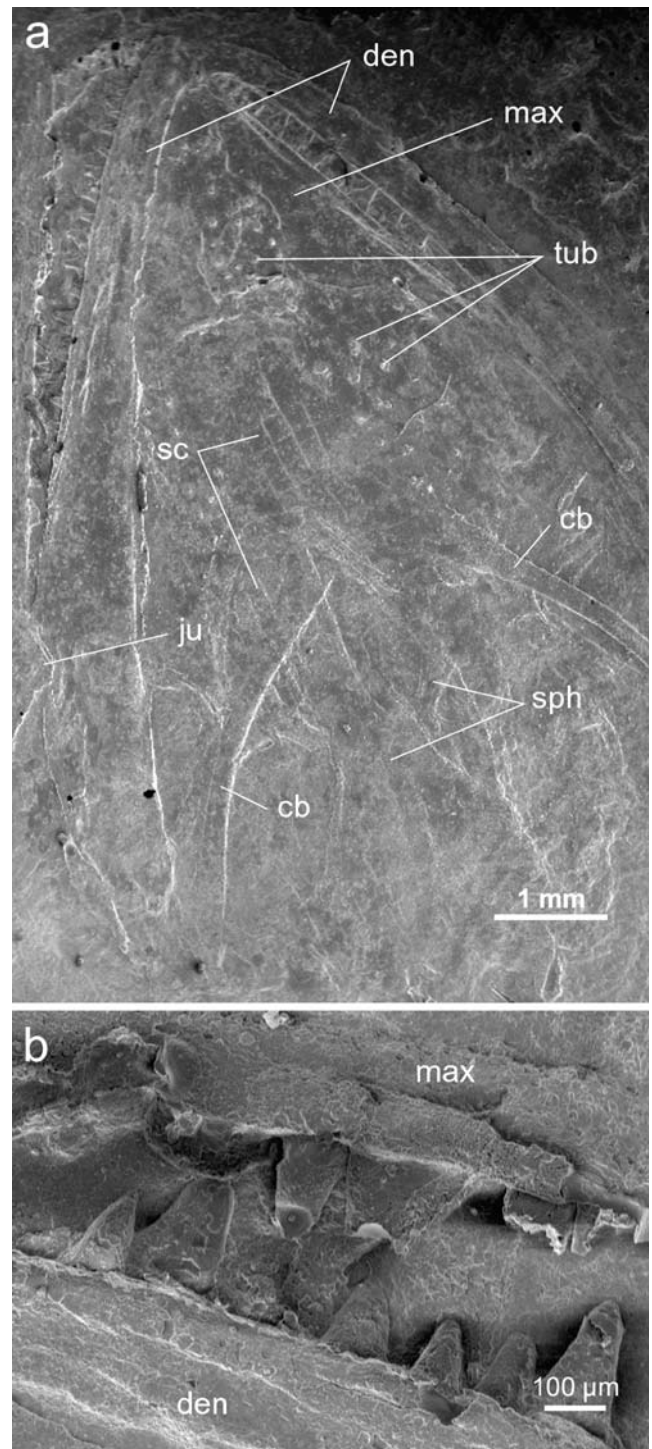


Fig. 2 Daohugou lizard V14386. **a** Scanning electron microscope image of the skull on the part block (using a coated high fidelity peel of the original). **b** Scanning electron microscope image of the dentition (taken from a peel as in **a**). **cb** Ceratobranchial element, **den** dentary, **ju** jugal, **max** maxilla, **sc** scales, **sph** sphenoid, **tub** tubercles on underside of head

margin. There is no evidence of a lacrimal, but given the preservation, its absence is not certain. The counterpart bears paired frontals that meet between the orbits but are separated posteriorly by a large, unossified gap (Fig. 1e). Behind them, the parietal region is marked by very weak impressions and the two-halves of the parietal are separate. Given the immaturity of the specimen, there is no way of knowing whether either frontals or parietals remained paired in the adult. The right postfrontal and the right postorbital are seen as separate elements posterolateral to the right frontal. As preserved, the postfrontal is a triangular element, the longest edge of which lies against the frontal and parietal. The narrow lateral tip meets a triradiate postorbital with a long posterior squamosal ramus. When the part and counterpart skull elements are superimposed, the ventral process of the postorbital overlies the dorsal ramus of the jugal. In this juvenile lizard, at least, the upper temporal fenestra is fully open. A possible left postorbital lies adjacent to the left dentary; anteromedial to it is a bone edge that may belong to the left postfrontal. The basicranium is exposed on the main part. The sphenoid has a long slender parasphenoid rostrum and short, anterolaterally directed basiptyergoid processes (Figs. 1e and 2a). The main body of the bone is triangular, flaring posteriorly to its junction with the basioccipital (not visible). Paired hyoid elements (first ceratobranchials) lie on either side of the sphenoid, but superficial to it. The mandibles are preserved on both sides and meet anteriorly in a short symphysis. They preserve little detail and the sutures between the constituent parts are unclear. The maxillary and dentary dentition is preserved on both sides. The teeth are small and conical (Fig. 2b) with no distinguishing characters, except that the maxillary teeth are clearly pleurodont in their implantation.

Vertebrae

It is impossible to make an accurate vertebral count because many of the vertebrae and ribs are not visible. The column is clearest towards the pelvis, where the isolated centra are exposed. These are short and roughly hour-glass shaped with no development of posterior condyles, but given the age of the specimen this is probably not significant. There are two sacrals and more than nine caudals.

Limbs and girdles

Very little of the pectoral girdle can be seen, barring a T-shaped interclavicle with a long posterior stem and a curved element on the left side of the animal that may be a clavicle (Fig. 3a). Presumably the endochondral elements were only partially ossified. In the arm, the humerus (5.4 mm), radius (4.15 mm) and ulna are clearly preserved but they form

simple cylinders without joint surfaces or processes (Fig. 3a,b). The carpus seems to be completely unossified although two small rounded structures (Fig. 3b) may be partially mineralized carpals. The small bones of the hand are clearly preserved giving a phalangeal formula of 2–3–4–5–3. The hand is quite strongly asymmetrical, with long penultimate phalanges and small slender unguals.

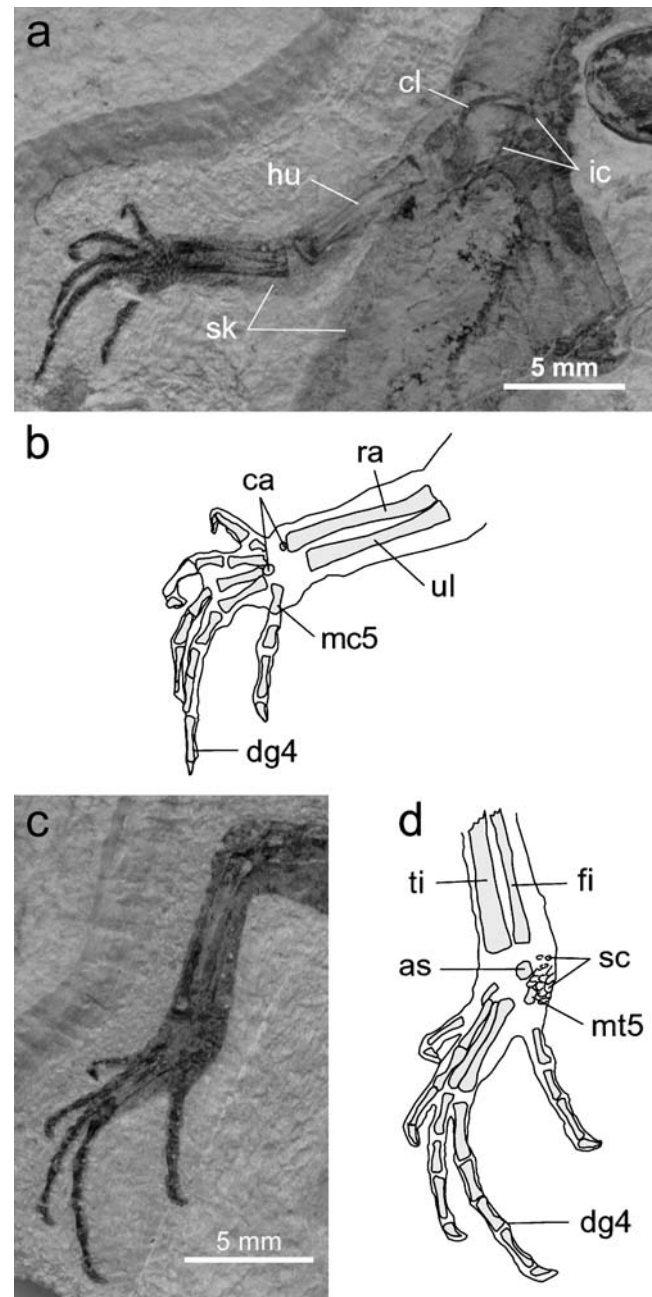


Fig. 3 Daohugou lizard V14386. **a** The part block, forelimb and pectoral girdle; **b** detail of the hand; **c** the part block, hind limb showing metatarsal traces; **d** detail of foot showing the enclosure of metatarsals 1–4 in a common skin sheath. *as* Astragalus, *ca* carpals, *cl* clavicle, *dg4* digit 4, *fi* fibula, *hu* humerus, *ic* interclavicle, *mc5* fifth metacarpal, *mt5* fifth metatarsal, *ra* radius, *sc* small scales, *sk* skin traces, *ti* tibia, *ul* ulna

The pelvis is seen faintly on each peel. The counterpart preserves an ilium with a tapering blade; the part preserves an ischium with a strong posterior process and, anterior to it, a poorly defined mass that may be part of the pubis. The shafts of the femur (7.65 mm), tibia (6.5 mm), and fibula are well ossified but there is no mineralization of the epiphyses. The fibula is much more slender than the tibia. On each side, the tarsal region contains a single round ossification and a more geometrically shaped element that seems to be the developing fifth metatarsal (Fig. 3d). By reference to developmental papers by Rieppel (1992a,b, 1994a,b) and Maisano (2001), the rounded element is probably the astragalus, the first tarsal to ossify. The bones of the pes are also clear, with long metatarsals on the third and fourth toes, and a strongly divergent fifth digit (Fig. 3c, d). The foot is asymmetrical with a long fourth digit (9.35 mm) and the phalangeal formula is 2–3–4–5–4.

Skin and soft tissues

The skin is well preserved, with the outlines of individual scales on the dorsal and ventral parts of the body, on the head and neck region, and on the limbs. The dorsal scales are, for the most part, small and rounded, giving a granular appearance. The squamation is not visible on the dorsum of the head, but ventrally, in the midportion of the intermandibular region, the scales are square and form anteroposterior rows (Fig. 2a). Further laterally, near the posterior ends of the mandibles, they become smaller and more circular (Fig. 4a), like those of the dorsum. The scales on the ventral surface of the neck are small and square (Fig. 4b) but those over the pectoral region are larger and become circular to hexagonal, overlapping like roofing tiles (Fig. 4c). Behind the level of the arms, the scales become more rectangular and form distinct transverse rows from the level of the forelimbs to the level of the pelvis (Fig. 4d; a precise row count is not possible, but it is in the range of 60–70). Judging from the length of the vertebral centra, there are three transverse scale rows for each body segment, but in an animal with fully ossified centra, the count would be higher. At the lateral edges of the body, the transition between dorsal and ventral scales is visible, with two dorsal rows to each ventral one. However, on the venter, the bilateral boundaries of the individual scales are visible only in the anterior region; behind this, the scale rows are marked by undivided transverse bands. A similar condition is present in a specimen of *Lacerta schreiberi* (Natural History Museum London, 1906-10-30-14) where some of the keratin scales have fallen off.

There is a sharp change in scale morphology roughly two vertebrae behind the sacrum where the scales become very small and circular and form a wide U-shaped band (posteriorly convex, Fig. 4e) that reflects the position of the

cloacal outlet. Caudal to this, the scales return to a transverse row arrangement, of roughly the same size as those on the belly but with distinct individual boundaries. Only the proximal part of the tail is preserved. The scales of the hand are small and circular or subcircular, sheathing each finger separately. The pedal scales are similar in shape, but the first four metatarsals are clearly encased in a single

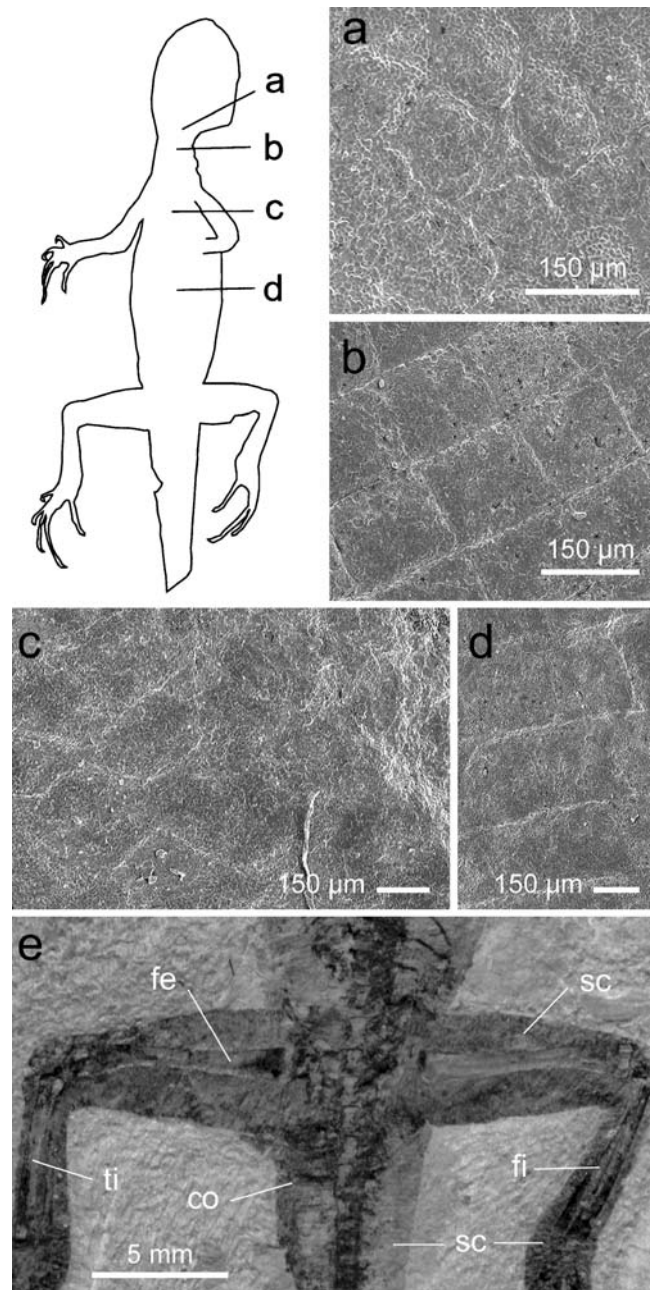


Fig. 4 Daohugou lizard V14386, scanning electron microscope images of scales from the part block (using a high fidelity peel). **a** Between the head and neck, and similar to those on the dorsum; **b** on the underside of the neck; **c** over the pectoral girdle; **d** across the underside of the body; **e** pelvic region and proximal tail, showing the curved line marking the cloacal outlet and the beginning of the tail. *co* Cloacal outlet, *fe* femur, *fi* fibula, *sc* scales, *ti* tibia

skin sheath, the digits separating only at the level of the proximal phalanx (Fig. 3c,d). The fifth digit, however, is separate, reflecting the divergence of the fifth digit that is typical for lepidosaurs. Claw sheaths are visible over the ungual phalanges, deepening and strengthening the rather slender bony elements, but there is no evidence of any specialization of the digital scales (by comparison with the climbing pads of many gekkotans and some iguanians).

On the underside of the head, there are a number of elongate tubercles (Fig. 2a, *tub*). These do not have a distinct pattern but seem to be associated with the epidermis rather than deeper layers (i.e., they are not exposed palatal teeth). Nothing similar is found elsewhere on the body. Scanning electron microscopy of these structures affords no unequivocal interpretation but it is possible that they either represent pathology or some form of post mortem intrusion.

Discussion

The ontogenetic age of the specimen

According to Maisano (2001) at least one tarsal element (the astragalus) is present in all neonatal (hatchling) lizards, and most have more than this (the exceptions, among living taxa studied, being agamids, xantusiids, and some anguids [Maisano 2001]). As the Daohugou lizard has only a single tarsal bone, it is likely a “neonate” (there is no trace of an egg or yolk sac, so it is probably not a prehatching stage). Even for a neonate, the Daohugou lizard is relatively weakly ossified in having a single tarsal, delayed ossification of the carpals, the absence of any ossification centres in the epiphyses of the limbs, and a very small fifth metatarsal (suggesting that the unossified epiphyses were large).

Comparison

The divergent fifth pedal digit, the shape of the pelvis, the skin type and pattern of scalation, and the visible characters of the skull (incomplete lower temporal bar, pleurodont tooth implantation, hyoid, and braincase structure) all indicate that this small reptile is a lepidosaur. The pleurodont tooth implantation, tooth shape, slender jaw symphysis, absence of a posterior jugal process, and absence of gastralia suggests that this is a squamate and not a rhychocephalian.

Three lizards have been named from the Jehol Biota of China, *Yabeinosaurus* (Endo and Shikama 1942; Young 1958), *Dalinghosaurus* (Ji 1998) and *Jeholacerta formosa* (Ji and Ren 1999). New work on *Yabeinosaurus* (Evans et al. 2005) has shown that it reached large adult size and is robustly built, with a morphology poorly reflected by the

very young individuals previously attributed to it. The adult skull is heavily sculptured, the frontals remain paired, there is a complex interdigitating frontoparietal suture, and the parietal is posteriorly extended. The second Yixian genus, *Dalinghosaurus*, does not grow to such large size, but even the smallest (probably hatchling) specimens (e.g., IVPP 14234.3) have the frontals already fused (though also unossified posteromedially) (Evans and Wang 2005; Evans, Wang, and Jones, submitted manuscript). *Jeholacerta* (Ji and Ren 1999) is based on a single specimen of a juvenile lizard that, like the Daohugou lizard, has good skin impressions but no diagnostic characters. The skull is interpreted as though it is in dorsal view, but judging from the accompanying figures and the description itself, this is, at best, speculative. Whether it is really a distinct genus, or simply a juvenile of *Yabeinosaurus*, cannot be resolved without adult material.

The Daohugou lizard differs from similar-sized specimens of *Dalinghosaurus* in having frontals that are still paired. The hind limb of the Daohugou lizard is also markedly shorter than that of *Dalinghosaurus* (hind limb 57% SPL vs 72–88%) with the foot more notably so (foot 21% SPL vs 29–39%; foot/femur 122 vs 140–200%) (Table 1). This is the opposite of what would be expected if the Daohugou lizard was a hatchling of *Dalinghosaurus*. In modern lizards, the distal limb elements are negatively allometric in relation to body size (e.g., Irschick and Jayne 2000; Hsieh 2003), and we have established that the same is true of *Dalinghosaurus*, based on a series of specimens of different ontogenetic age (Evans, Wang, and Jones, submitted manuscript). There is also a difference in the hand, where the phalangeal formula is 2–3–4–5–3 in the Daohugou lizard and 2–3–4–5–4 in *Dalinghosaurus*, with far greater elongation of the digits in the latter taxon.

The paired frontals of the Daohugou lizard resemble those of *Yabeinosaurus*, but this character is too widespread (especially in juveniles) to form the basis of an attribution. The postfrontal and postorbital are fused or nearly fused in adult *Yabeinosaurus*, contrary to the condition in the Daohugou lizard. However, this region is not clearly preserved in the youngest specimens of *Yabeinosaurus*, nor is the back of the lower jaw, characterized in the adult by a prominent, hook-shaped angular process. The Daohugou lizard differs from the smallest recorded *Yabeinosaurus* (the neotype YFM-R002, c. 80 mm SPL, Ji et al. 2001) in having proportionally longer hind limbs (57 vs 45% SPL) and forelimbs (38 vs 28.5% SPL) (Table 1), a proportionally longer tibia (85% femoral length vs 71%, 13.7 vs 8.5% SPL); and a slightly longer femur (16 vs 12.5% SPL) (Table 1). Certainly, many of these differences could be related to growth (hind limb elements becoming smaller relative to SPL with growth, Irschick and Jayne 2000; Hsieh 2003), but if this is the case, it is odd that the foot of

Table 1 Comparative limb proportions in Chinese Mesozoic lizards

	Daohugou V14386	Ya Neotype YFM-R002	Ya V13284	Da V13281	Da V13865	Da V12345	Da V14234.1	Da V14234.2	Je GMV2114
SPL (mm)	43.7	80.6	180	142	92	115	88	87	45.5
FL/HL (%)	67	63	63	43.9	50	50	43	–	65
HL/SPL (%)	57.4	45	45%	73	76	88	82	72	53.8
FL/SPL (%)	38	28.5	28	32	37.6	41	37.4	–	35
Ft/Fe (%)	123	159	150	200	140	146	174	175	204.7
Ti/Fe (%)	85	70.6	62.5	95	90	90	91	88	80
Hu/Fe (%)	70.1	75.7	79	63	60	65	71	–	86
Ft/HL (%)	37.4	43	43	48	38	38	45	48	53
Fe/HL (%)	31	33	29	24	29	29	26	27	26
Fe/SPL (%)	16	12.5	13.3	16.9	21.7	25	22.3	19.8	14.1
Ti/SPL (%)	13.7	8.5	8.3	16	19.5	22.8	19.5	18.1	11.2
Fe/Hd (%)	80.5	51	53	72	120	100	87	79	50
Ft/SPL (%)	21.5	21	20	34	29	37	39	34.4	29

DaDalinghosaurus, *JeJeholacerta*, *YaYabeinosaurus*, GMV Geological Museum of China, *Fe* femur, *FL* forelimb length, *Ft* foot, *H* humerus, *Hd* head, *HL* hind limb length, *L* length, *SPL* snout-pelvis length, *Ti* Tibia, *V* vertebrate specimen number of IVPP (Institute of Vertebrate Paleontology and Paleoanthropology), *YFM* Yizhou Fossil Museum.

the Daohugou lizard does not follow the same trend. Given that lizard feet become relatively shorter with maturity, the foot of the hatchling Daohugou specimen should be longer than that of the two older juveniles in Table 1 (as is that of *Jeholacerta*), not the same length. Generally the proportions of the Daohugou lizard are most closely similar to the similar-sized (SPL 45.5 mm) type specimen of *J.formosa* (Ji and Ren 1999) except that the head and foot of the former are considerably shorter (Table 1).

The scalation of the Daohugou lizard (granular dorsal scales, more rhomboid or rectangular ventral scales) broadly matches that described for *D.longidigitus* (Evans and Wang 2005), but the scalation of *Yabeinosaurus* is incompletely known. Ji and Ren (1999) describe body scales for *Jeholacerta* but it is not clear that the dorsal and ventral surfaces of the body have been correctly interpreted. They describe rhomboid “trunk” scales, without saying whether these are dorsal or ventral. By comparison with the smaller scales around the neck and limbs; however, it is likely that the preserved trunk scales are those of the ventral surface, with the smaller, rounded scales on the dorsum. For *Jeholacerta*, Ji and Ren (1999) give a count of 41–43 transverse rows (i.e., from front to back between forelimbs and hind limbs ventrally) and 21–22 longitudinal rows (across the body). The longitudinal rows cannot be counted in the Daohugou lizard, but it has a far higher count of transverse rows (60–70). This makes it unlikely that *Jeholacerta* and the Daohugou lizard represent the same taxon, but without similar details for *Yabeinosaurus*, comparison is limited.

In iguanians and gekkotans, the dorsal and ventral surfaces of the body are generally covered by small scales of similar morphology, and this has generally been

considered the primitive pattern (e.g., Camp 1923). In contrast, among scincomorphs and most anguimorphs (*Autarchoglossa* in traditional classification, e.g., Estes et al. 1988; but see Townsend et al. 2004), the belly scales are often larger and more regular in their arrangement. This matches the condition in the Daohugou lizard (and *Jeholacerta*) where the belly scales are at least twice the size of the dorsal scales, are rectangular rather than circular, and run across the ventral surface in distinct rows separated by straight lines. However, the living rhynchocephalian *Sphenodon* also shows a disparity in size, shape, and alignment between dorsal and ventral scales (SE personal observation) so the polarity of these scale characters remains ambiguous. Apart from standard scale counts, very little comparative literature exists for scale patterns in lizards.

Conclusions

On the basis of frontal morphology and limb proportions, the small Daohugou lizard is clearly distinct from the Yixian *Dalinghosaurus*. Proportionally, it more closely resembles *Yabeinosaurus* and the questionably valid *Jeholacerta*, but it differs from the latter in scalation and in relative head and foot lengths despite closely similar size. Allowing for the effects of allometric growth, the Daohugou lizard could be a juvenile of *Yabeinosaurus*, but this would require a rather unusual growth curve for the foot. Without material of comparable age for *Yabeinosaurus*, or adult specimens from Daohugou, the systematic position of this small lizard must remain unresolved. Nonetheless, it contributes to our knowledge of Mesozoic lizards in three

ways. Firstly, it demonstrates the presence of lizards at the important salamander locality of Daohugou, in a horizon that is significantly lower than that of previous Jehol lizard finds. With further excavation at Daohugou, there is the potential for the discovery of adult material. Secondly, it provides the earliest and most complete record of scalation in a Mesozoic lizard, data that will aid the discussion of lepidosaurian scale characters in future analyses. Finally, it highlights the need to consider ontogenetic age in descriptions and interpretations of fossil taxa.

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