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A New Troodontid Dinosaur from the Lower Cretaceous Yixian Formation of Liaoning Province, China

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Abstract: A new troodontid dinosaur, *Daliansaurus liaoningensis* gen. et sp. nov., is erected based on a nearly complete specimen from the Lower Cretaceous Yixian Formation of Beipiao City, Liaoning Province, China. This well preserved skeleton provides important new details of the anatomy for Liaoning troodontids, and gives new insight into their phylogenetic relationships and evolution. *Daliansaurus* is distinguished from other troodontids by an enlarged ungual on pedal digit IV, which is approximately the same size as the sickle-shaped second ungual, and is differentiated from other Liaoning troodontids by a number of characters of the skull, manus, pelvis, and hindlimb. A phylogenetic analysis recovers *Daliansaurus* within a subclade of Liaoning troodontids that also includes *Sinovenator*, *Sinusonasus*, and *Mei*. We erect a name for this group—Sinovenatorinae—and argue that it reflects a localized radiation of small-bodied troodontids in the Early Cretaceous of eastern Asia, similar to previously recognized radiations of Liaoning dromaeosaurids and avialans. As more Liaoning theropods are discovered, it is becoming apparent that small, feathered paravians were particularly diverse during the Early Cretaceous, and future work is needed to clarify how this diversity arose, which species coexisted, and how these numerous species partitioned niches.

Key words: Troodontids, *Daliansaurus liaoningensis*, Early Cretaceous, Yixian Formation, Liaoning

1 Introduction

Troodontidae is a group of small, feathered non-avian theropod dinosaurs known primarily from the Middle Jurassic to Late Cretaceous of Asia and North America (Varricchio, 1997; Makovicky and Norell, 2004; Xu and Norell, 2006; Goswami et al., 2013). They are widely regarded as some of the closest relatives of birds (e.g., Gauthier, 1986; Norell et al., 2001; Turner et al. 2012; Brusatte et al. 2014). Thus far, at least 11 troodontid genera have been reported from China. They include *Sinornithoides* (Russell and Dong, 1993), *Sinovenator* (Xu et al., 2002), *Mei* (Xu and Norell, 2004), *Sinusonasus* (Xu and Wang, 2004), *Jinfengopteryx* (Ji et al., 2005), *Anchiornis* (Xu et al., 2008), *Xixiasaurus* (Lü et al., 2010), *Linhevenator* (Xu et al., 2011a), *Xiaotingia* (Xu et al., 2011b), *Philovenator* (Xu et al., 2012) and *Eosinopteryx* (Godefroit et al., 2013b).

The Chinese troodontids are particularly important. Unlike the vast majority of troodontids from North America and Mongolia (except for *Gobivenator*), the Chinese specimens are often nearly complete and naturally articulated, so they provide comprehensive information on troodontid phylogeny and the relationship between troodontids and birds (Avialae). Many previous phylogenetic analyses have recovered troodontids as the sister group to dromaeosaurids within a clade called Deinonychosauria, which in turn forms the sister group to Avialae. The deinonychosaurian-avialan group is referred to as Paraves (Xu et al., 2002; Hu et al., 2009; Senter et al., 2012; Turner et al., 2012; Godefroit et al., 2013b; Xu

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et al., 2014). However, some recent studies have indicated that troodontids might be are more closely related to Avialae than to dromaeosaurids (Brusatte et al. 2014; Cau et al., 2015), and other studies suggest even more radical phylogenetic rearrangements (e.g., Agnolin and Novas, 2013; Chatterjee, 2015). Clearly, the phylogenetic relationship of troodontids are more complex than previously thought, which makes the discovery and description of articulated, well-preserved new material critically important.

Herein we report a new troodontid *Daliansaurus liaoningensis* gen. et sp. nov. from the Lower Cretaceous Yixian Formation of Beipiao City, Liaoning Province, China. *Daliansaurus* has an unusual combination of primitive features, which are similar to those of coeval troodontids from western Liaoning and shares some features with troodontids from the Cretaceous deposits of the Gobi regions of Inner Mongolia and Mongolia. The new discovery not only adds a new member to the troodontid fauna of western Liaoning, but also provides new insights into the evolution and phylogeny of troodontids more generally.

2 Geological Setting

The skeleton of the new troodontid was found in the Cretaceous deposits of the Yixian Formation, in the Fuxin-Yixian Basin, Lujiatun, of western Liaoning Province. These deposits are situated in the eastern part of the Yanshan fold and thrust belt, the North China Craton (Fig. 1). The Fuxin-Yixian Basin is one of many small volcanic-sedimentary basins that formed in this region during Late Mesozoic. The strata are mainly formed by Middle-Upper Jurassic to Lower Cretaceous deposits, whereas Paleozoic sediments are absent. The Lower Cretaceous beds lies upon the Archean basement unconformably or are in contact with the older beds by faulting (Zhang et al., 2005). The Lower Cretaceous lithostratigraphic units of the Fuxin-Yixian Basin are in ascending stratigraphic order, the: Yixian, Jiufotang, Shahai, Fuxin and Sunjiawan formations (Zhang et al, 2005). The Yixian Formation is composed of volcanic rocks including several layers of lacustrine facies (BGMRLP, 1989). The vertebrate fossils from the Yixian Formation include, among many other dinosaurs: ceratopsids, basal ornithischians, basal oviraptorosaurs and the troodontids *Sinovenator* (Xu et al., 2002), *Mei* (Xu and Norell, 2004) and *Sinusonasus* (Xu and Wang, 2004).

3 Systematic Paleontology

Theropoda Marsh, 1881

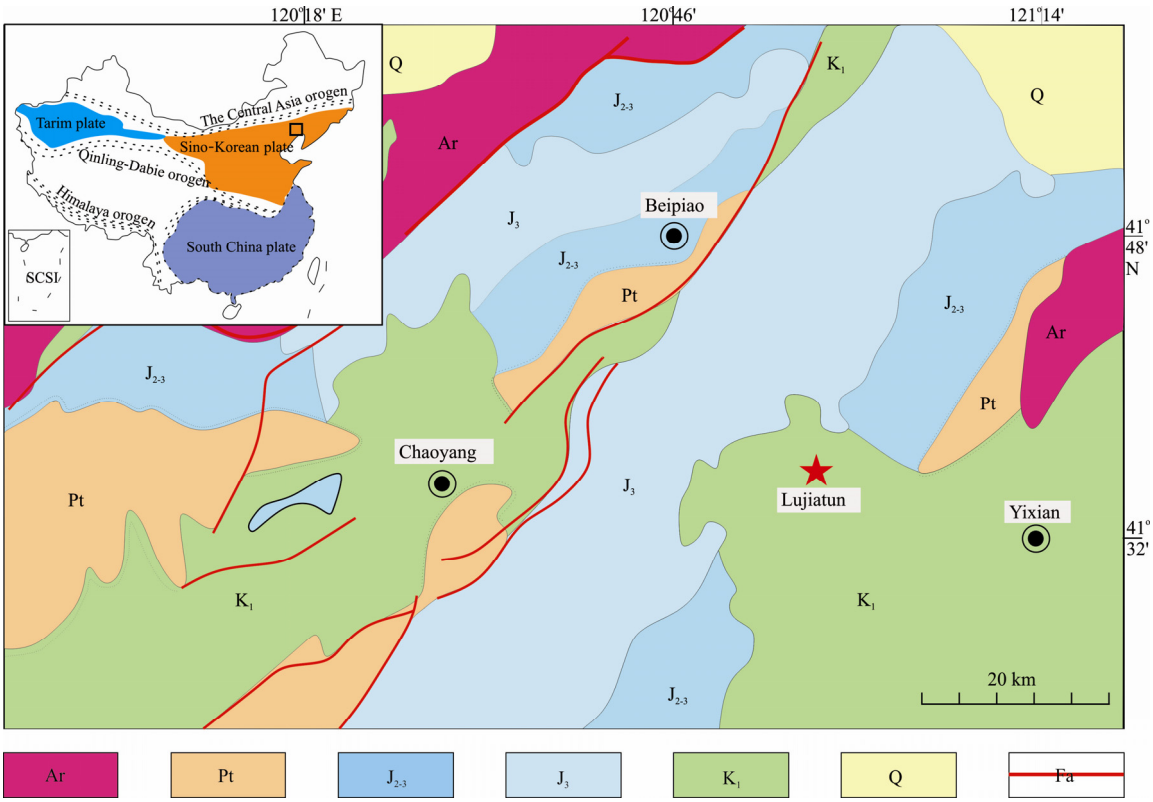

Fig. 1. Generalized tectonic map of the Beipiao area, Liaoning Province (modified from He et al., 2007) showing the locality (asterisk) of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885).
Abbreviations: Ar, Archean; Pt, Proterozoic; J_{2-3}, Middle-Upper Jurassic; J_3, Upper Jurassic; K_1, Lower Cretaceous; Q, Quaternary; Fa, Fault.

Maniraptora Gauthier, 1986
Troodontidae Gilmore, 1924
Sinovenatorinae subfamily nov.

Definition: The most inclusive clade including *Sinovenator changii* but not *Troodon formosus*, *Saurornithoides mongoliensis*, *Anchiornis huxleyi*, *Archaeopteryx lithographica*, *Gallus gallus*, *Unenlagia comahuensis*, or *Dromaeosaurus albertensis*.

Diagnosis: Based on our phylogenetic analysis, this clade can be diagnosed with the following combination of characters (for further discussion, see below): a premaxilla whose anteroposterior length is less than 10% of the length of the maxilla along the ventral margin of the upper jaw; a premaxillary maxillary process that contacts the nasal ventral to the external naris; some maxillary and dentary teeth that lack serrations on the mesial carina; unfused zygapophyses on the sacral vertebrae; an antitrochanter that is posterodorsal to the acetabulum; and a metatarsal IV that is mediolaterally wide and flattened in cross section.

Included species: Based on our phylogenetic analysis, this clade currently includes *Sinovenator changii*, *Sinusonasus magnodens*, *Mei long*, and *Daliansaurus liaoningensis* gen. et sp. nov.

Daliansaurus liaoningensis gen. et sp. nov. (Fig. 2a, b)

Etymology: The generic name refers to the city of Dalian in the south of Liaoning province. The specific name "*liaoningensis*" refers to the province in which the specimen was discovered.

Holotype: A nearly complete skeleton (DNHM D2885) with an estimated total body length of 1 meter. The posterior region of the cranium, posterior to the maxillae, is either missing or covered by cervical vertebrae. The bones around the orbit and lateral temporal fenestra have been reconstructed, and these portions of the specimen are not genuine. The lower jaws are preserved back to the region surrounding the external mandibular fenestra, but their posterior-most portions (much of the surangular and articular) are reconstructed. The left and right scapulae and coracoids are missing, and the left humerus is hidden under the matrix. Most parts of the pelvis are not exposed, except for the ilia and part of one ischium. The right hindlimb is missing and the distal caudal vertebrae are covered by the matrix. The specimen is housed at the Dalian Natural History Museum, Liaoning Province, China.

Locality and horizon: Lujiatun, Beipiao City, Liaoning Province; Yixian Formation, Lower Cretaceous.

Diagnosis: *Daliansaurus* possesses the following autapomorphy among sinovenatorines, and troodontids more generally: the ungual of pedal digit IV is robust, dorsoventrally deep, and approximately the same size as that of pedal digit II. Another possible autapomorphy among troodontids is the presence of uncinate processes on the dorsal ribs (see discussion below). *Daliansaurus* differs from other sinovenatorines (*Sinovenator*, *Sinusonasus*, *Mei*) in that metatarsal IV lacks a prominent longitudinal flange, and in that the ventral surface of the postacetabular process of the ilum is strongly concave in lateral view (not nearly straight as in *Sinovenator* and *Mei*, condition unknown in *Sinusonasus*). *Daliansaurus* differs from *Sinovenator* and *Sinusonasus* in that metatarsal II is so short that it terminates before the trochlea of metatarsal IV begins (instead of terminating further distally than the start of the mt IV trochlea), and in that metacarpal II is slightly shorter than metacarpal III (instead of longer). Other comparative differences with other sinovenatorines are expanded on in the Comparisons section below.

Description: The specimen is three-dimensionally preserved, and many bones (particularly of the hands and feet) exhibit fine detail. The skull and neck are arched backward, and the tail is curled forward on the right side of the body. The right arm is tucked inwards towards the body, whereas the left arm is extended underneath the body. The neural arches are fused to the centra in dorsal vertebrae, which is typical for mature individuals (Russell and Dong, 1993; Currie and Dong, 2001). The measurements of the skeleton are summarized in Table 1.

Most of the skull is exposed on its left side, although the right maxilla is exposed in medial view. The skull is triangular in shape (Fig. 2), and the external naris is nearly ovoid in shape. The slender, strip-like nasal process of the premaxilla extends posterodorsally. The junction between the posterior portion of the premaxilla and the nasal is unclear due to poor preservation, and thus it is difficult to determine whether the premaxilla participates in the margin of the external naris, although this appears to be the case based on the overall similarity of this region to that in *Sinovenator* and *Sinusonasus*, where the nasal and premaxilla make contact. The nasal process of the premaxilla is wide and flat dorsoventrally in lateral view, which contrasts with the more rounded cross- section in *Sinovenator* (Xu et al., 2002). The nasal process forms the major part of the internarial bar as in other troodontids (Norell et al., 2009), as well as some other theropods, like ornithomimosaurs (Ji et al., 2003) and alvarezsaurus (Chiappe et al., 1998). Another process of the premaxilla, the slender subnarial process projects straight posteriorly in lateral view (Fig.3, 4a). This condition similar to that in *Sinusonasus*, but differs from *Sinovenaor*, in which the subnarial process curves dorsally as it extends posteriorly,

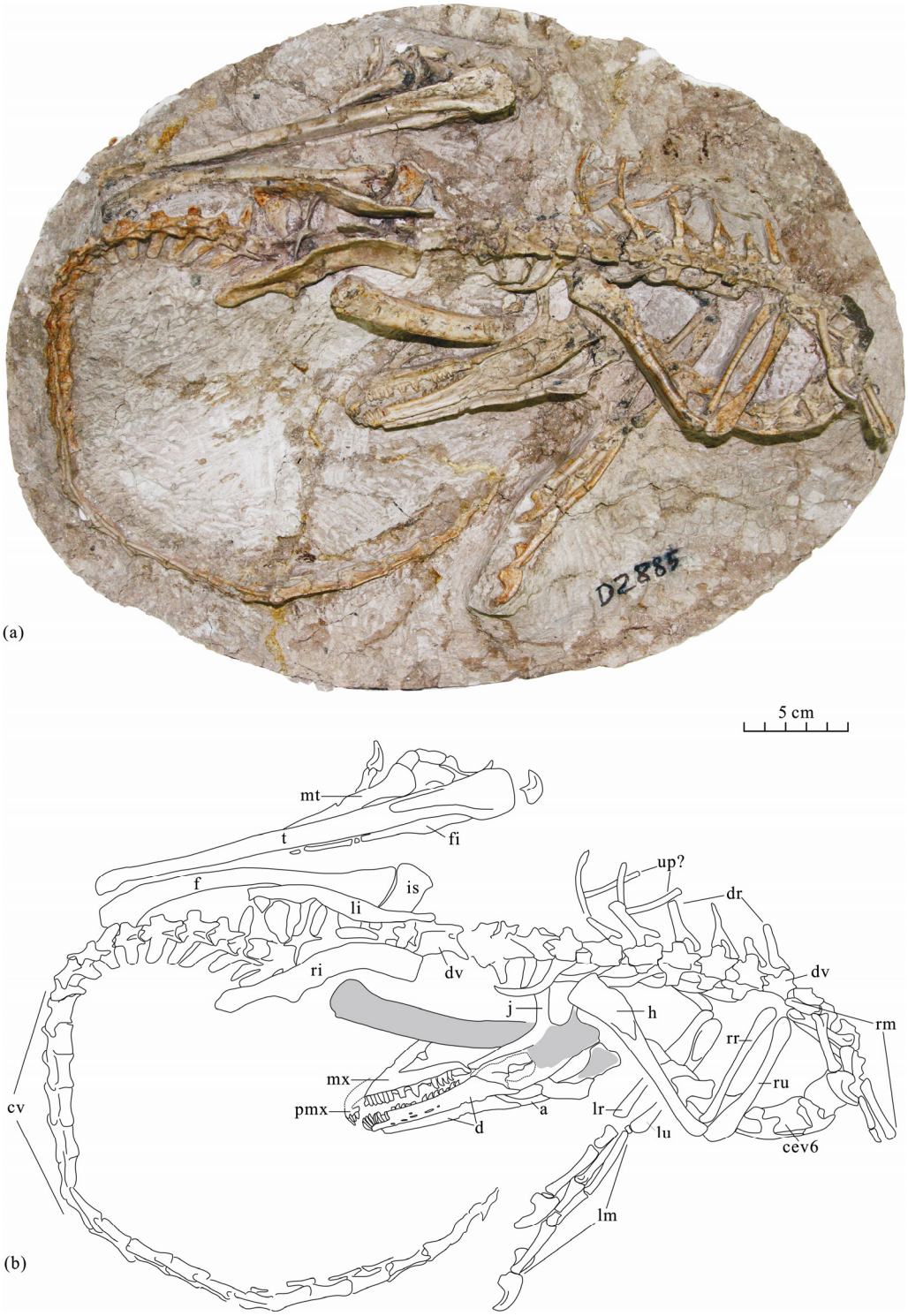

Fig. 2. Photograph (a) and line drawing (b) of the holotype of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885).

Abbreviations: a, angular; cev 6, sixth cervical vertebrae; cv, caudal vertebrae; d, dentary; dr, dorsal rib; dv, dorsal vertebrae; f, femur; fi, fibula; h, humerus; j, judgal; li, left ilium; lm, left manus; lr, left radius; lu, left ulna; is, ischium; mt, metatarsal; mx, maxilla; pmx, premaxilla; rm, right manus; rr, right radius; ru, right ulna; up?, uncinate process.

such that it is strongly convex dorsally.

The right maxilla is positioned immediately posterior to the left premaxilla. At first glance, it appears as if the premaxilla and maxilla are in contact, and that the maxilla is therefore the left maxilla in lateral view. However, the large palatal shelf, the exposure of the alveoli, and the broken wall of the maxillary antrum reveal that the bone is, in fact, the right maxilla in medial view. The maxilla

Table 1 Measurements (in mm) of the main bones of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885)

	Left	Right
Skull	138*	
Premaxillar	9.3*	
Maxillar	74	
Dentary	71.6	71.2
Humerus	-	82.9
midshaft diam.		6.09
Ulna	65.0	64.7
Ulna, anteroposterior midshaft diam.	-	3.84
Radius	65.2	65.7
Radius, anteroposterior midshaft diam.	2.85	2.85
Space between radius and ulna	8.19	-
Metacarpal I	15.7	14.1
Metacarpal II	30.5	31.5
Metacarpal III	31.0*	32.0
Manual phalanx I-1	28.7	31.1
Manual phalanx I-2	16.6	25.4
Manual phalanx II-1	20.5*	23.2
Manual phalanx II-2	27.5	27.8
Manual phalanx II-3	20.8	19.9
Manual phalanx III-1	-	7.5
Manual phalanx III-2	-	8.7
Manual phalanx III-3	-	19.2
Manual phalanx III-4	19.7	19.1
Ilium	82.3	92.8
Preacetabular blade, max depth	24.5	25.2
Preacetabular process	29.7	30.4
Postacetabular process		30.6
Acetabular, interior		18.8
Acetabular, outside		29.7
Femur	130.8	-
Femur, anteroposterior midshaft diam.	8.6	-
Tibia	190.1	-
Tibia, anteroposterior midshaft dima.	8.8	
Metatarsal II	98.1	
Metatarsal IV	110.1	
Pedal phalanx I-1	11.3	
Pedal phalanx I-2	13.3	
Pedal phalanx II-1	20.1	
Pedal phalanx II-2	14.7	
Pedal phalanx II-3	22.7	
Pedal phalanx IV-1	15.9	
Pedal phalanx IV-2	14.8	
Pedal phalanx IV-3	13.3	
Pedal phalanx IV-4	11.3	
Pedal phalanx IV-5	20.8	

* indicates estimated measurement

has a discrete anterior ramus that is separated from the ascending ramus by a step, and the ascending ramus is thin, broad anteroposteriorly, and fans out dorsally. Part of the premaxillary fenestra can be seen through the broken wall of the maxillary antrum; it is a large, dorsoventrally elongate, tear-drop shaped opening positioned at the anterior end of the antorbital fossa, as in *Sinovenator*. The anterior end of the maxillary fenestra is preserved, and it was an enormous, anteroposteriorly elongate oval as in other troodontids.

The dentary is a long bone that expands in dorsoventral depth as it extends posteriorly. It is straight ventrally and slightly concaved dorsally, as in some troodontids such as *Sinovenator*, *Sinornithoides* and *Mei*. However, it differs from *Sinusonasus*, which has a distinctly convex ventral margin of the dentary (although this may be exaggerated by crushing). A deep neurovascular groove is incised onto the lateral surface of the dentary, as in other troodontids (Makovicky and Norell, 2004). This groove is dorsoventrally narrow and deeply inset into the bone anteriorly, but it becomes dorsoventrally taller and more shallowly inset posteriorly. It extends dorsoventrally and parallels the upper margin of the alveolar row. There are two rows of nutrient foramina on the lateral surface of the dentary. The upper row is inside the groove and is especially prominent in the anterior part of the dentary. Whereas, the foramina forming the lower row are exposed below the groove. The foramina in the upper row are round in the anterior part of the dentary and oval further posteriorly (Fig. 3); the ventral foramina are more conspicuous than those of the upper row. Part of the medial surface of the right dentary can be observed. Here, there is a deep and slender Meckelian groove that projects posteroventrally. It appears that the groove fails to reach the dentary-splenial contact. A large part of the splenial is

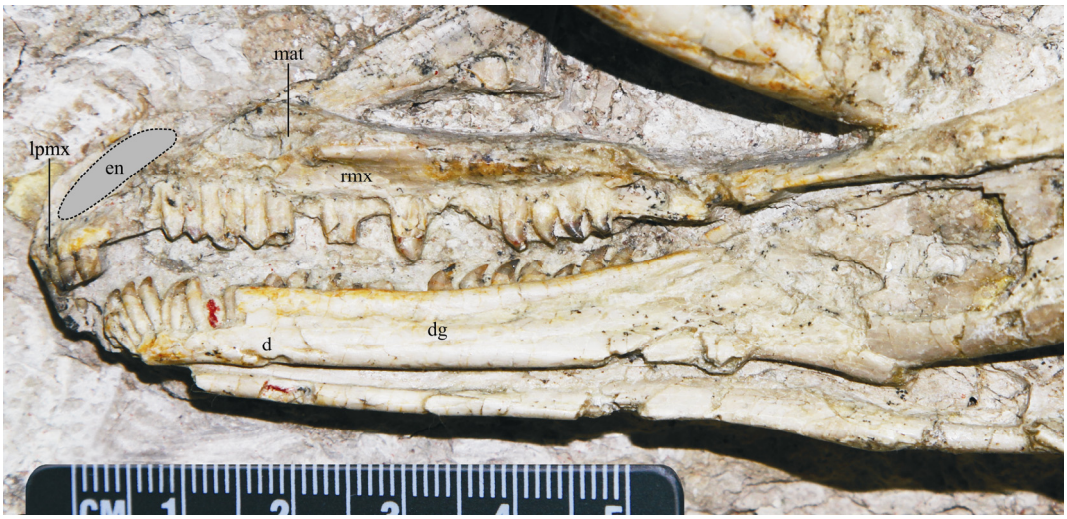

Fig. 3. Photograph of lateral portion of the skull of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885).
Abbreviations: d, dentary; dg, dentary groove; en, external narial; mat, maxillary antrum; rmx, right maxilla; lpmx, left premaxilla.

exposed in lateral view, where it meets the dentary along a diagonal suture.

There are four unserrated teeth preserved in the left premaxilla. The teeth are erupted perpendicular to the ventral margin of the premaxilla, have a D-shaped in longitudinal section (Fig. 4a). However, in other troodontids (Xu et al., 2011a), the premaxillary teeth are recurved both on the labial and lingual surfaces, and thus have a reaphook-like shape in longitudinal section.

There are at least seventeen tooth positions exposed on the right maxilla (Fig. 3). The anterior teeth are rounded in cross-section and the posterior ones are slightly compressed laterally. The middle maxillary teeth are somewhat larger than the anterior and posterior ones. Four well-preserved posterior maxillary teeth have serrations on the distal carinae, but lack serrations on the mesial carinae (Fig. 5a). Only the roots of the anterior and middle maxillary teeth are preserved.

There are twenty-four tooth positions on the left dentary (Fig. 3), which is fewer than in *Troodon* (35; Makovicky and Norell, 2004), *Saurornithoides* (31; Norell et al., 2009), *Zanabazar* (35; Norell et al., 2009), *Sinovenator* (27; Xu, 2002) and *Urbacodo*n (32; Averianov and Sues, 2007). The anterior teeth are more closely packed than those in the middle and posterior parts of the tooth row. As in other troodontids, the dentary teeth are constricted between the root and crown (Makovicky and Norell, 2004). The crowns are more recurved in the posterior portion of the tooth row than are the opposing maxillary teeth (Fig. 4b). The 15th dentary tooth, which is 2.9 mm long, is the longest in the series: it has a fore–aft basal length (FABL) of 2.0 mm. The opposing 10th maxillary tooth is 3.1 mm long and has a FABL of 2.3 mm. Serrations are present on the distal carinae as in *Sinovenator*, but unlike other troodontids with unserrated dentary teeth, such as *Byronosaurus* (Makovicky et al., 2003), *Jinfengopteryx* (Ji et al., 2005), *Urbacodon* (Averianov and Sues, 2007), *Anchiornis* (Xu et al., 2008), *Xixiasaurus* (Lü et al., 2010), *Eosipnopteryx* (Godefroit et al., 2013) and *Gobivenator* (Tsuihiji et al., 2014). The serrations of the anterior dentary teeth of *Daliansaurus* are small and inconspicuous, but they become larger and more prominent in the posterior dentary teeth. These blunt serrations are perpendicular to the distal carina and differ from those in *Troodon*, which are apically hooked (Currie, 1987). Compared to *Troodon* (Currie, 1987), *Saurornithoides* (Norell et al., 2009) and unnamed troodontids from Russia and Uzbekistan (Averianov and Sues, 2007) with large serrations, the serrations are relatively small in *Daliansaurus*.

There are at least nine cervical vertebrae preserved in *Daliansaurus*. The 6th cervical vertebra is well exposed in

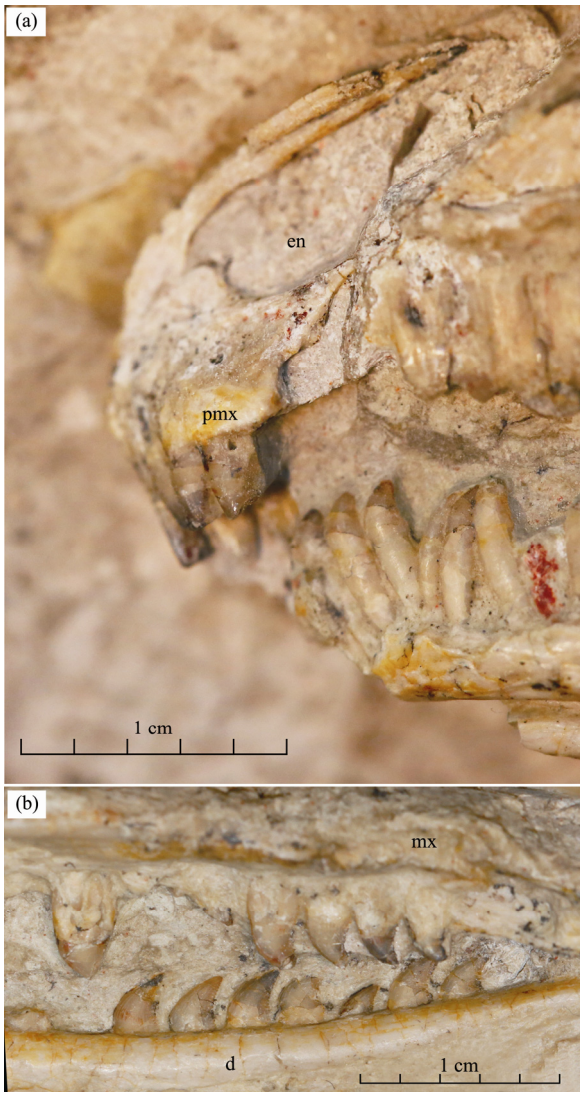

Fig. 4. Close up of the anterior teeth (a) and posterior teeth (b) of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885).
Abbreviations: d, dentary; en, external narial opening; mx, maxilla; pmx, premaxilla.

lateral view (Fig. 6a). The pre- and postzygapophysis of this vertebra project to the same level dorsally. In dorsal view, the pre- and postzygapophyses extend laterally, to give the vertebra an X-shape; the prezygapophyses extend farther away from the midline of the centrum than do the postzygapophyses. The transverse process of the 6th cervical forms a thin osseous lamina paralleling the centrum, as in some troodontids (Currie and Dong, 2001) and ornithomimids (Barsbold and Osmolska, 1990). The lateral surface of the centrum is concave and bears a single pneumatic opening (pleurocoel). The corresponding cervical rib is large. The rib capitulum is fused to the centrum. The rib shaft is strap-like and extends anteroposteriorly to follow the ventral contours of the centrum. Although anterior and posterior cervical

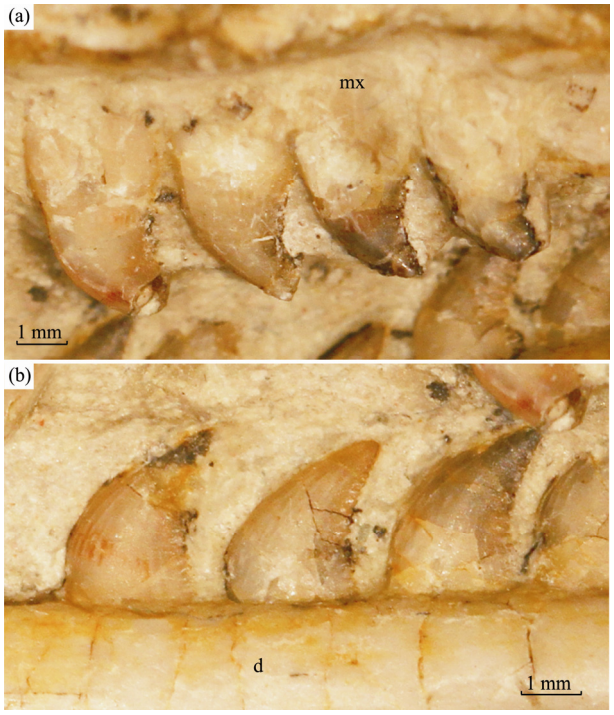

Fig. 5. Close up of denticles of posterior maxillary teeth (a) and dentary teeth (b) of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885).

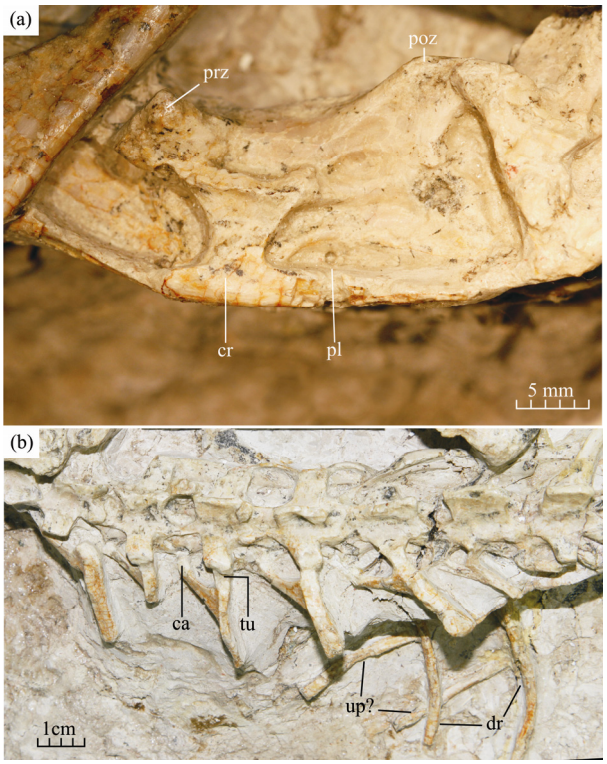

Fig. 6. Photograph of the 6th cervical vertebra (a) and the dorsal vertebrae (b) of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885).
Abbreviations: ca, capitulum; cr, cervical rib; dr, dorsal rib; pl, pleurocoel; poz, postzygapophysis; prz, prezygapophysis; tu, tuberculum; up?, uncinate process ?.

vertebrae are poorly preserved, it is clear that their centra are shorter than those of the middle part of the neck. The ventral surfaces of all cervical centra are concave.

The presence of thirteen dorsal vertebrae is inferred. Compared to the last cervical vertebra, the 1st dorsal vertebra has a distinct hypapophysis. The transverse process of the 2nd dorsal vertebra is wide and narrow posteriorly, and exhibits a thick distal margin oriented posteriorly. Starting from the 9th dorsal vertebra, the transverse processes are oriented laterally and extended posteriorly (Fig. 6b). The neural spines of the dorsal vertebrae are higher than these of the cervical vertebrae. In lateral view, the centra of the dorsal vertebrae are quadrangular in shape, as in other troodontids.

Eight right dorsal ribs are well preserved, as are the proximal portions of seven left dorsal ribs. In the anterior dorsal ribs, the capitula and tubercula are clearly separated by an average distance of 8.17 mm. The capitula are longer and more robust than the tubercula, and the two structures meet at an angle of 130°. In more posterior ribs, the capitula and tubercula become gradually shorter and less prominent, reaching equal lengths in the posterior dorsal vertebrae (Fig. 6b).

There are four overlapping rod-like bones situated just ventral to the dorsal vertebrae (Fig. 6b). Two of them are embedded in the matrix, and they probably represent dorsal ribs. The two other bones, which curve ventrally, each bear a rod-like ossification that is interpreted here as an uncinate process. It is unclear, however, whether the uncinate processes are fused to the ribs, because of poor preservation. Uncinate processes have not previously been reported in troodontids, but they have been recognized in some avialans, dromaeosaurids, and other theropods. In avialans, these processes have a laminar shape, whereas they are rod-like in the dromaeosaurids *Velociraptor* (Norell and Makovicky, 1999) and *Linheraptor* (Xu et al., 2010), and the oviraptorid *Heyuannia* (Lü, 2002). If our interpretation of this feature is correct, then the uncinated processes of *Daliansaurus* probably helped to reinforce the rib cage and may have increased the effectiveness of muscles involved in breathing, similar to the condition in birds (Codd, 2008).

There are five sacral vertebrae in *Daliansaurus*. The neural spines are fused in the first two sacrals, whereas the neural spines of the remaining three vertebrae are incomplete and poorly preserved. The transverse processes of the first two sacral vertebrae are equally long, while the transverse processes of the 3rd through 5th sacral vertebrae gradually extend dorsally. In dorsal view, the transverse process of the 5th sacral vertebra is wider and fan-shaped than the others, and its anterior margin is slightly concave. This is in contrast to the 5th sacral vertebra of *Sinovenator*,

whose transverse process is moderately extended distally and deeply concave on the anterior margin (Xu et al., 2002). The width between the anterior parts of the left and right ilia is narrow (from the 1st to 2nd sacral vertebrae), and gets much wider posteriorly (at the level of the 3rd through 5th sacral vertebrae) (Figs. 2, 10b). This is contrast to much wider separation between the the 3rd to 5th sacral vertebrae in *Mei* (Xu and Norell, 2004; Gao et al., 2012).

There are twenty-eight caudal vertebrae preserved. As in other troodontids, the caudal centra become gradually elongated while the transverse processes get progressively shorter posteriorly along the tail (Makovicky and Norell, 2004). Proximal caudals have a discrete neural spine, but it is replaced by a groove on the dorsal surface of the centrum from the 14th caudal onwards. The transition point is situated between the 9th and 10th caudals. The first caudal vertebra is small and short anteroposteriorly, and it connects to the last sacral vertebra tightly. The postzygapophysis is located higher than that of the prezygapophysis. The transverse process is oriented at about 30° to the central horizontal axis. The 2nd caudal vertebra bears a significantly longer prezygapophysis, and the neural spine is slightly higher than in the previous caudal. The transverse process of the 2nd caudal vertebra is posteriorly oriented, narrow distally, and is oriented at 40° with the horizontal axis of the centrum. From the 3rd to the 6th caudal vertebrae, the transverse processes are posterolaterally oriented and become gradually longer and wider. The prezygapophyses of the 4th-6th caudal vertebrae are situated close to the midline, forming a well-developed groove between the prezygapophyses (Fig. 7a). The transverse processes from the 6th to 9th caudals vertebrae are short and form a right angle with the horizontal axis of the centra. The transverse process of the 10th caudal is reduced into a small tuber on the lateral surface of the centrum. The neural spine is low and the centrum is elongated. From the 11st to 14th caudal vertebrae, the neural spines are distinctly longer. The corresponding neural arches are low and weekly developed, and project over the rectangular centra, which have concave lateral surfaces. The pre- and postzygapophysis of the 11st caudal vertebra are thicker and longer than these in more anterior vertebrae. The 14th cadual bears the pre- and postzygapophysis that fuse to form a rod-like ridge along the dorsal edge of the centrum, which can be seen in lateral view (Fig. 7b). This ridge becomes gradually more slender distal to the 20th caudal vertebrae.

There are seven chevrons appressed to the 3rd through the 9th caudal vertebrae. The chevrons are constricted at the midshaft, and exhibit expanded articular facets. As in *Sinornithoides* (Currie and Dong, 2001), the distal ends of these chevrons are plate-like, elongate, and posteriorly oriented. Chevrons of the 23rd-27th caudal vertebrae (Fig. 7c, d) are elongated, compressed laterally, flattend dorsoventrally, and slender and rod-like in lateral view.

The humerus is relatively long, about 63% of the femur length (Fig. 8), and the deltopectoral crest is almost 24% of the total length of the humerus. These values are generally similar to other troodontids such as *Sinovenator* and *Sinornithoides*, but contrast with those in *Linhevenator* (40% and 50%, respectively: Xu et al., 2011a). Laterally, a large triangle depression on the proximal surface of the humerus resembles the conditions in some troodontids and dromaeosaurids (Xu et al., 2011a; Ostrom, 1969). The distal end of the bone expands mediolaterally.

The ulna is slightly curved, and is 79% of the length of the humerus. The lateral surface of the proximal end is compressed (Fig. 8) and the corresponding articular surface is expanded. The radius is slender, curved, and expanded at its distal end. The distance between the radius and ulna is about 8.1 mm in the middle.

Both the left and right metacarpals are well preserved. The distal end of metacarpal I is ginglymoid with a weak lateral ligament pit. The shaft of metacarpal I is sharply curved dorsoventrally, more so than in *Sinornithoides*. The mid-shaft of metacarpal II is 3.28 mm wide mediolaterally. Its distal articular facet is divided into the two condyles that are separated by a groove; the medial condyle is larger than the lateral one. The medial ligament pit is pronounced and larger than that on the lateral side. Metacarpal III is slightly longer than metacarpal II, and it is 2.92 mm thick mediolaterally at the mid-shaft. Metacarpal II is tightly appressed to metacarpal III. Metacarpal III is moderately curved (Figs. 8, 9), and it is not ginglymoid.

The phalanges of both hands are also well preserved. Phalanx I-1 is slightly curved, arch-shaped, and is the longest and more roubst of all the phalanges of manus. The phalanx projects substantially beyond the distal end of metacarpal II. The ungual phalanx I-2 is laterally compressed and exhibits a well-developed flexor tubercle ventrally on the proximal end. A distinct and deep groove is present on lateral surface of the phalanx I-2, whereas the corresponding groove that occurs on the medial surface is shallow. The proximal articular surface of phalanx II-1 is compressed mediolaterally and extended dorsoventrally. The shaft tapers to its minimum diameter at the proximal end of the distal articular surface, where there is a shallow lateral ligament pit. Phalanx II-2 is similar to II-1 i in overall morphology. However, phalanx II-2 is markedly longer than the latter. Laterally, phalanx II-2 is slightly curved and with expanded articular surface on the end of proximal end, whereas the dorsal margin of the distal

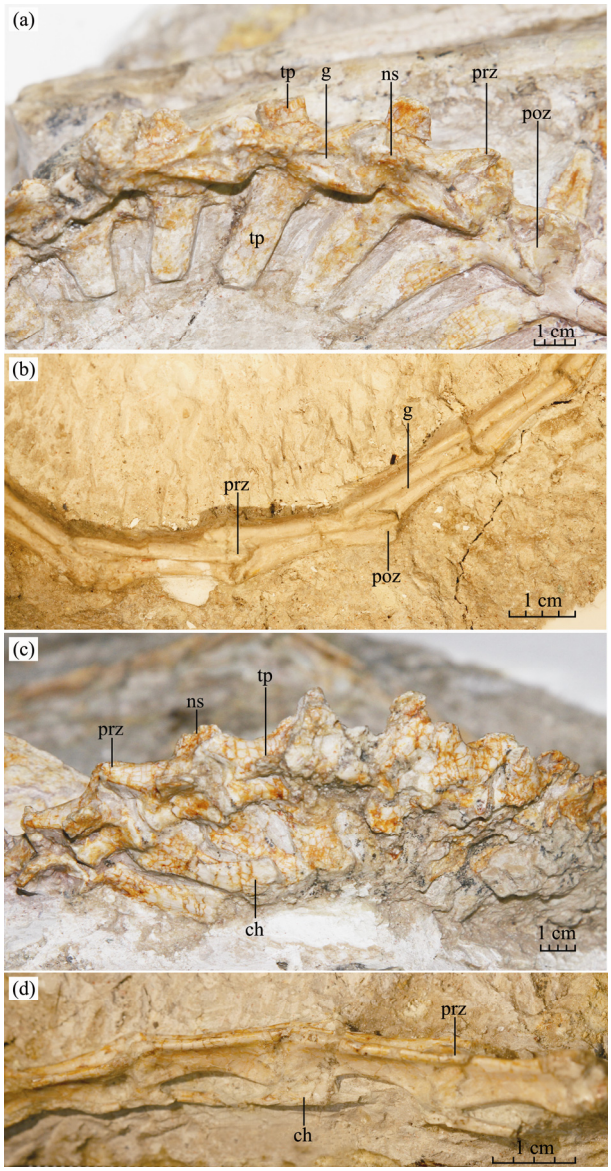

Fig. 7. Close up of the anterior caudal vertebrae (a); middle caudal vertebrae (b); chevrons of proximal caudal vertebrae (c); chevrons of distal caudal vertebrae (d) of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885).
Abbreviations: ch, chevorn; g, groove; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; tp, transverse process.

Fig. 8 Photograph of the left forelimb of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885).
Abbreviations: h, humerus; mcI, metacarpal I; mcII, metacarpal II; mcIII, metacarpal III; I-1, I-2, II-1, II-2, II-3, III-3, III-4, corresponding manual digit and phalanx; r, radius; u, ulna.

articular surface is straight and extended ventrally. The ungual phalanx II-3 is smaller than phalanx II-2. The flexor tubercle is well-developed on the ventral surface of the proximal end. Phalanx III-1 is short, and fused to phalanx III-2. The ungual phalanx III-4 is shorter than other manusal claws, and bears a small flexor tubercle.

The ilium is about 63% the length of the femur. This ratio is larger than in other troodontids, such as *Sinornithoides* (52%; Rusell and Dong, 1993), *Mei* (54%; Gao et al., 2012) and *Anchiornis* (56%; Hu et al., 2009). The acetabulum is located at the middle of the ilium. The rectanglular preacetabular process is large, and its lateral surface is concave (Fig. 10a). In dorsal view, the preacetabular processes of the left and right ilia are parallel. At the level of the 3rd sacral vertebra, the ilia became distinctly separated from each other (Fig. 10b) as in *Mei* (Xu and Norell, 2004; Gao et al., 2012); however, the distance between the ilia is wider in *Mei* than in *Daliansaurus*. The postacetabular process is large, and it tapers in depth posteriorly. Its ventral surface is deeply concave, contrasting with *Sinovenator*, in which this margin is nearly straight. A deep fossa on the proximal portion of the lateral surface of the postacetabular process serves for attachment of the iliofemoralis muscle (Rowe, 1986). The cuppedicus fossa is not visible in lateral view. The ischial peduncle is small and triangular, and there is a large antitrochanter in the region where the peduncle meets the iliac body. The public peduncle is larger than the iliac peduncle. There is a supracetabular crest that overhangs the acetabulum laterally, but it is weakly developed.

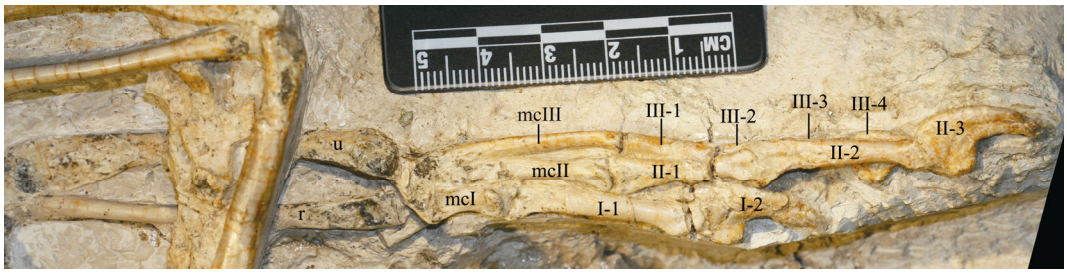

Fig. 9. Photograph of the right manus of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885).
Abbreviations: mcI, metacarpal I; mcII, metacarpal II; mcIII, metacarpal III; I-1, I-2, II-1, II-2, II-3, III-2, III-3, III-3, III-4, corresponding manus digit and phalanx; r, radius; u, ulna.

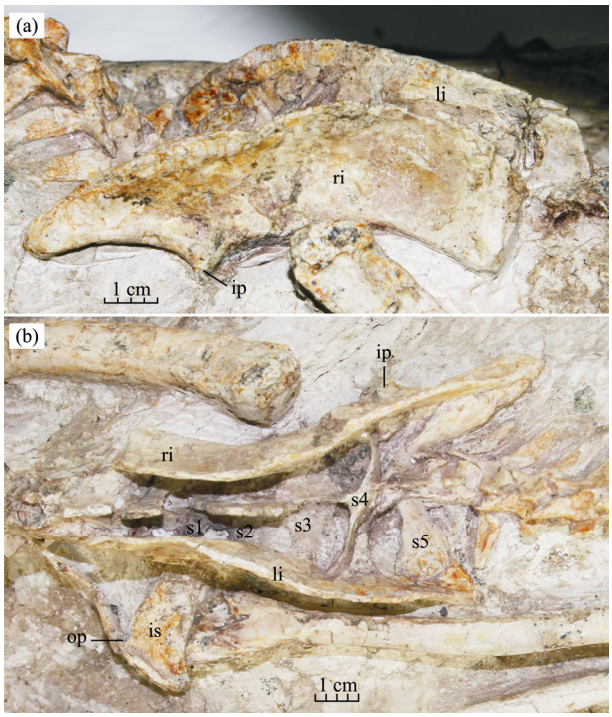

Fig. 10. Close up of the ilium of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885) in right lateral (a) and dorsal views (b).
Abbreviations: li, left ilium; ip, ischium process; is, ischium; op, obturator process; ri, right ilium; s1-s5, sacral vertebrae 1-5.

Fig. 11 Photograph of the hindlimb bones of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885) in lateral view.
Abbreviations: f, femur; fi, fibular; gt, great trochanter; lcc, lateral cnemial crest; lr, lateral ridge; lrd, lateral ridge near distal end; ltr, lesser trochanter; pt, posterior trochanter; t, tibia.

The distal end of an ischium is preserved. The anterior margin of the bone is almost straight, but it has a concave posterior margin. There is a small obturator process, which projects from the distal portion of the bone (Fig. 10b). The ischium lacks a distalodorsal ridge on the shaft, which is also the case in some primitive troodontids (Xu et al., 2002; Xu et al., 2011b). However, this ridge is prsent in derived troodontids, such as *Saurornithoides* and *Talos* (Norell et al., 2009; Zanno et al., 2011).

The femur is distinctly bowed in lateral view (Fig. 11). The lesser trochanter is fused to the greater trochanter, thus forming an anteroposteriorly extended trochanteric crest as in some derived troodontids (Makovicky and Norell, 2004; Tsuihiji et al., 2014; Norell et al., 2009; Xu et al., 2012) and dromaeosaurids (Norell and Makovicky, 1999). The lateral crest is positioned lower than the posterior trochanter (Fig. 11), differing from other

troodontids, for example *Sinornithoides* (Rusell and Dong，1993) and *Linhevenator* (Xu et al., 2011a), in which the lateral crest and posterior trochanter project to the same level. The distal lateral condyle of the femur is wider than the medial condyle. As in some derived troodontids (Xu et al., 2012; Xu et al., 2011a), a short longitudinal ridge appears on the distal end of the lateral surface of the femoral shaft (Fig. 11).

The tibia is long, straight, and approximately 145% the length of the femur. It is proportionally longer than that of *Sinovenator* (125%; Xu, 2002), but similar to that of *Sinornithoides* (140%; Rusell and Dong, 1993). The proximal end of the tibia is anteroposteriorly expanded. The mid-shaft of the bone is square shaped in cross-section (Fig. 11). The tibia bears a well-developed crest and a deep depression that extends 52.3 mm towards the proximal end, as in primitive troodontids (Xu, 2002). A fusiform tuber on the proximal part of the fibula is interpreted as the attachment of the iliofibularis muscle (Xu, 2002). The shaft of the fibula is slender and circular in cross-section.

Daliansaurus has longer metatarsals relative to femur length than in other troodontids (Table 2), which may suggest elaborated more corresponds with elaborated cursorial type of locomotion (Godefroit et al., 2013). In *Daliansaurus*, the lateral condyle of the distal end of metatarsal I is larger than the medial condyle as is the case in the unnamed troodontid MPC-D 100/44 (originally cited as SPS 100/44) (Barsbold et al., 1987) and *Sinovenator* (Xu, 2004). When in articulation with the rest of the foot, The metatarsal I projects posteriorly and deviates from the other metatarsals. The lateral ligament pit is not as well-developed in *Daliansaurus* as in some other troodontids (Russell, 1969; Norell et al., 2009). Metatarsal II is much shorter than metatarsals III and IV, this condition differs from that of MPC-D 100/44, in which metatarsal III is longer than metatarsal II. In Posterior view, the proximal portion of metatarsal II is extended midolaterally and articulates with the proximal end of metatarsal IV (Fig. 12). This condition resembles that of some derived troodontids, for example *Tochisaurus* (Kurzanov and Osmólska., 1991). As in *Borogovia* (Osmólska, 1987), metatarsals II and IV of *Daliansaurus* are contact each other closely at their distal end. Metatarsal III is partly exposed in posterior view, unlike the condition in *Tochisaurus* in which metatarsal III is widely visible posteriorly. The condition in *Daliansaurus*, however, may be partially due to crushing, as the proximal end of the metatarsus is compressed. With that said, extending the trend of metatarsals II and IV in the posterior view and the identification of a weak suture in the proximal end may indicate that this configuration is natural. Metatarsal IV projects laterally at its distal articular surface, and its shaft lacks a prominent lateroventral flange in the lateral view. This is unlike the condition in *Sinovenator* and *Sinusonasus*, in which metatarsal IV bears a distinct lateroventral flange. The lateral ligament pit is not well-developed in metatarsal IV. Finally, metatarsal IV is much longer than metatarsal II in *Daliansaurus*. Metatarsal II is so short that it terminates before the trochlea of metatarsal IV begins. This differs from *Sinovenator* and *Sinusonasus*, in which metatarsal II terminates further distally than the start of the metatarsal IV trochlea.

The phalanges of the left foot are well preserved (Fig. 13). the shaft of phalanx I-2 is compressed dorsoventrally, and projects distally as a the ginglymoid surface. The lateral ligament pit is large and shallow. Phalanx I-2, the ungual, is smaller than other unguals as in basal deinonychosaurs (Makovicky and Norell, 2004), but unlike the case in *Linhevenator* where bone is longer than pedal ungula IV (Xu et al., 2011a). The proximal articular surface of phalanx I-2 is convex laterally, bearing a distinct sheath groove at the distal end of the bone.

Phalanx II-1 is longer than the phalanx II-2. The distal articular surface of phalanx II-1 extends dorsally and exhibits a deep and large lateral ligament pit. Phalanx II-2 is short and thick, about 73% of the length of the phalanx II-1, this ratio is smaller than in *Philovenator* and *Borogovia* (Xu et al., 2012; Osmolska, 1987). The “heel”

Table 2 Comparisons of important length ratios between *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885) and other troodontids in mm

	Metetarsal IV/Femur	Humerus/ Femur	Skull/ Femur	Radius/ Humerus	Metacarpal I/II	Ilium/ Femur	Tibia/ Femur	Ulna/ Humerus	Data Source
Daliansaurus	0.84	0.63	1.06	0.79	0.51	0.67	1.45	0.78	
Sinornithoides	0.79	0.59*	1.09	0.71	0.30	0.52	1.40	0.78	Russell and Dong, 1993
Sinovenator	0.69	0.68	0.77	-	0.42	0.6*	1.25		Xu, 2004
Jinfengopteryx	-	0.7	0.96	0.86	0.41	-			Ji et al., 2005
Mei	0.75	0.52	0.69–0.75	0.95	0.31	0.54		0.86–0.9	Xu and Norell, 2004; Gao et al., 2012
Anchiornis	0.83	0.96–1.04	0.96	0.78	0.37	0.61-0.56			Hu et al., 2009
Xiaotingia	-	0.85	0.74*	0.89	-	0.62			Xu et al., 2011b
Linhevenator	0.63	0.56	0.91						Xu et al., 2011a
philovenator	1.25								Xu et al., 2012
Troodon	0.67	0.47	-	-	-	-			Russell, 1969

* indicates estimated measurement

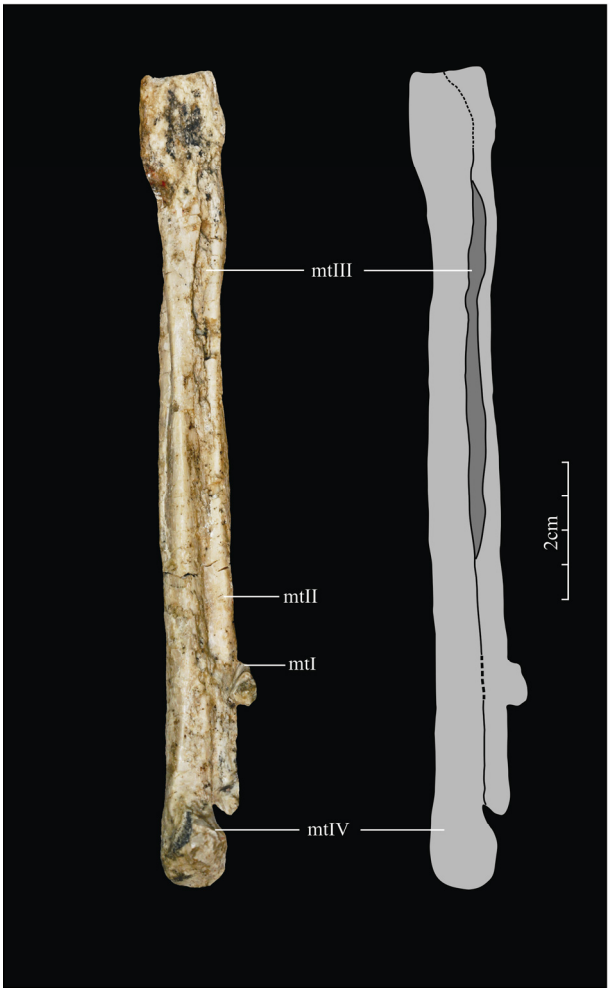

Fig. 12. Photograph and reconstruction of the metatarsi of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885) in posterior of view.
Abbreviations: mt I, metatarsal I; mt II, metatarsal II; mt III, metatarsal III; mt IV, metatarsal IV.

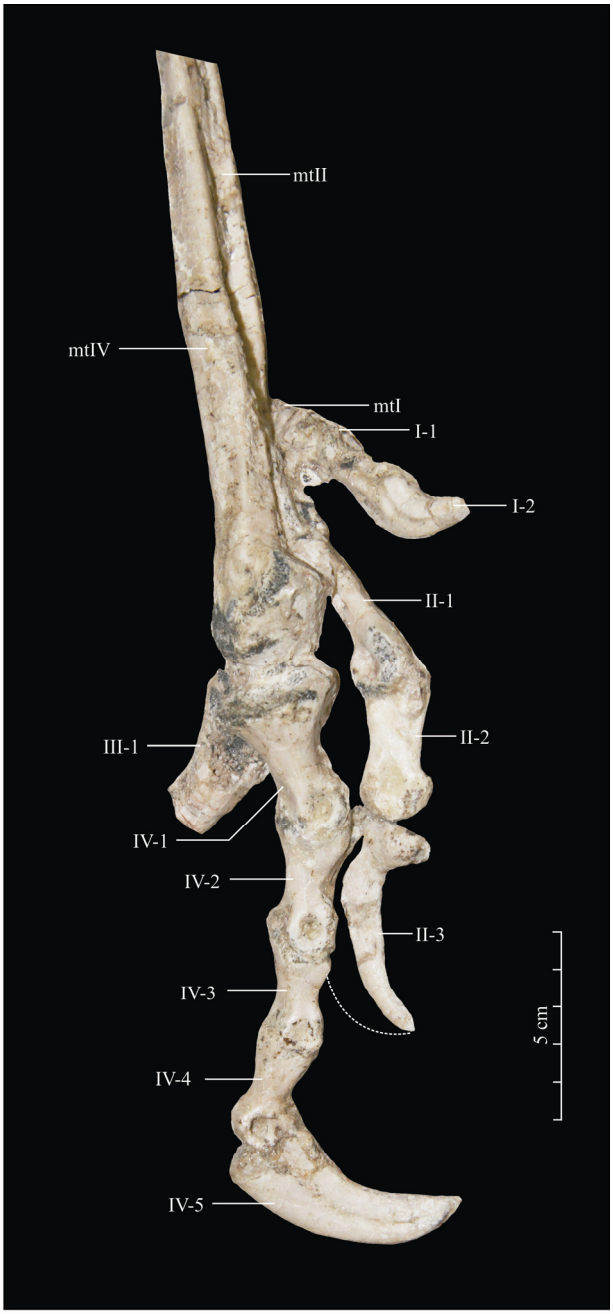

Fig. 13. Photograph of the pedal anatomy of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885) in lateral view.
Abbreviations: mt I, metatarsal I; mt II, metatarsal II; mt III, metatarsal III; mt IV, metatarsal IV; I-1, I-2, II-1, II-2, II-3, III-1, IV-1, IV-2, IV-3, IV-4, IV-5, corresponding pedal digit and phalanx.

on the proximal articular surface of phalanx II-2 is not well-developed in *Daliansaurus*, which may be an artefact of poor preservation. The ungual of the sickle-shaped digit II is partly preserved. It is asymmetrical in ventral view. In lateral view, the proximal part of the ventral articular surface bears a large flexor tubercle.

Only the proximal portion of digit III is exposed. The articular surface of phalanx III-1 projects dorsoventrally.

All of digit IV is present. The proximal articular surface of phalanx IV-1 is smooth and curved, implying the absence of a ginglymoid morphology on the distal end of the metatarsal IV. The shaft of phalanx IV-1 tapers to a minimum diameter at the proximal end of the distal articular surface. The "heel" of phalanx IV-2 is well-developed, straight dorsoventrally in lateral view, and extends ventrally on the distal articular surface. Phalanges IV-1 and IV-2 are equal in length, and are longer and more robust than phalanges IV-3 and IV-4. Phalanx IV-3 is shorter than phalanx II-1, as in some derived troodontids (Zanno et al., 2011). The morphology of phalanx IV-3 is similar to that of the phalanx IV-4, although the ligament pit of phalanx IV-4 is much deeper than that of phalanx IV-3. The ungual phalanx (IV-5) is enormous. It is nearly the same length as the ungual of pedal digit II, and is considerably more robust. This is a highly unusual feature, as in other troodontids the second ungual is much longer than the fourth (e.g., Russell and Dong, 1993). The flexor

tubercle of the fourth ungual is not well-developed, but the sheath groove is distinct and similar in size to that of the second ungual.

4 Phylogenetic Analysis

We included *Daliansaurus* in a modified version of the largest and most comprehensive phylogenetic dataset for coelurosaurian theropods—the most recent version of the Theropod Working Group (TWiG) matrix, published by Brusatte et al. (2014). We took the original dataset, which includes 152 taxa scored for 853 characters, and modified it by adding in *Daliansaurus* and *Sinusonasus*. Our scores for *Sinusonasus* were generously provided by TWiG member Rui Pei, who studied the material first hand (we made a few slight changes to the scores provided by Dr Pei), and our scores for *Daliansaurus* were based on our study of the holotype specimen we are describing in this paper.

We analyzed the dataset in TNT following the same protocols used by Brusatte et al. (2014). The analysis returned 10,000+ most parsimonious trees (Length=3380, CI=0.320, RI=0.777), the strict consensus of which is shown in Figure 14. The strict consensus topology recovers *Daliansaurus* as a deeply-nested member of Troodontidae, within a clade of Yixian taxa that also includes *Mei*, *Sinovenator*, and *Sinusonasus*. Within this clade, *Daliansaurus* and *Sinusonasus* are placed as sister taxa.

The clade of Yixian troodontids is united by one unambiguous synapomorphy: a metatarsal IV that is mediolaterally wide and flattened in cross section (character 204; scored as ? in *Daliansaurus*). The subclade of *Daliansaurus*, *Sinovenator*, and *Sinusonasus* is united by five unambiguous synapomorphies: a premaxillary maxillary process that contacts the nasal ventral to the external naris (character 20); some maxillary and dentary teeth that lack serrations on the mesial carina (character 81); unfused zygapophyses on the sacral vertebrae (character 109); an antitrochanter that is posterodorsal to the acetabulum (character 400); and a premaxilla whose

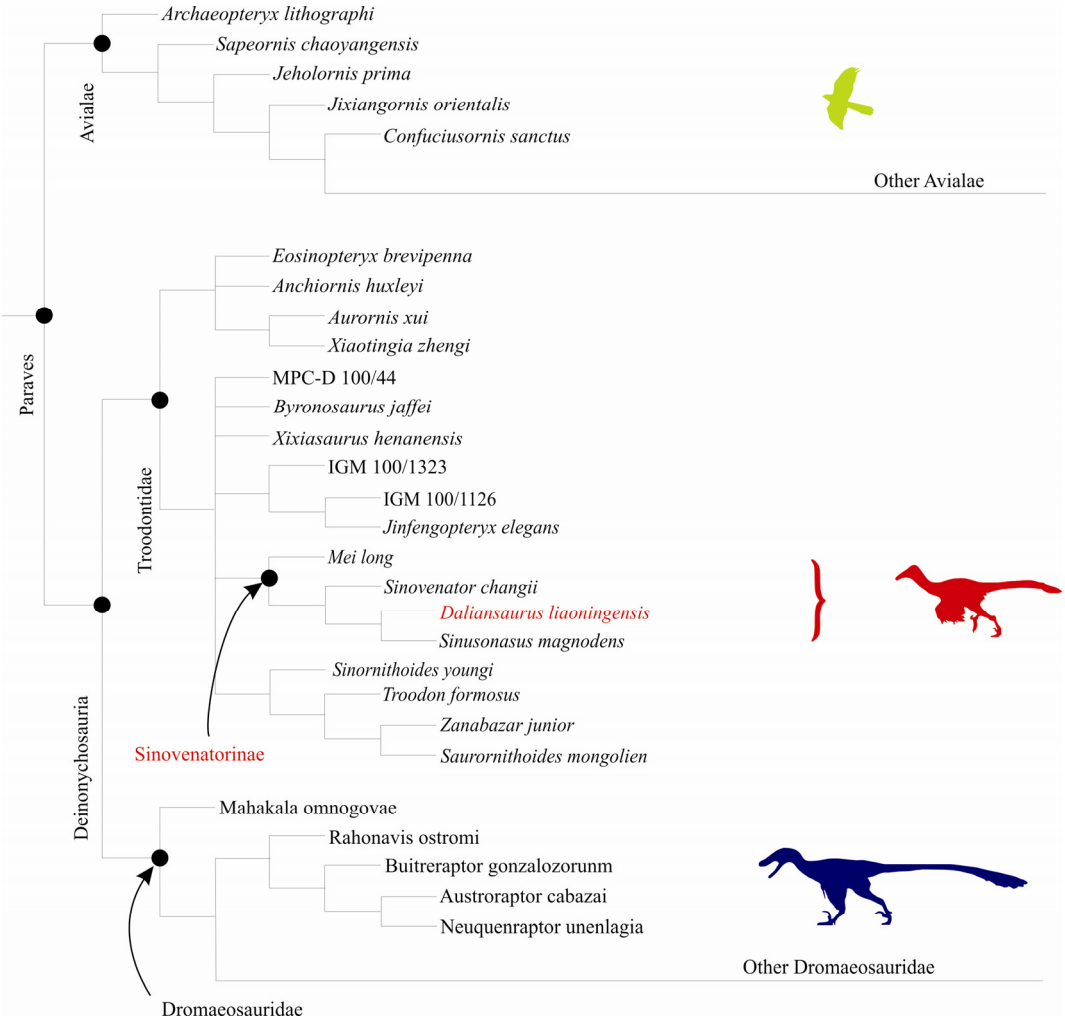

Fig. 14. A simplified cladogram showing the phylogenetic relationships of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D2885) among the Troodontidae. The novel clade of Sinovenatorinae is in red.

anteroposterior length is less than 10% of the length of the maxilla along the ventral margin of the upper jaw (character 826). Finally, the sister taxon pair of *Daliansaurus* and *Sinusonasus* is united by two unambiguous synapomorphies: chevrons in the distal tail that bifurcate at both ends (character 121) and greater and lesser trochanters of the femur that are completely fused into a trochanteric crest (character 181).

5 Comparisons and Discussion

Daliansaurus can clearly be assigned to the Troodontidae based on the results of the phylogenetic analysis and its possession of the following key characters of the clade: numerous (dental formulas: 4+17*/24) and closely packed teeth; a dorsoventrally flat internarial bar; a deep groove on the lateral surface of dentary; grooves replacing the neural spines on the dorsal surfaces of the distal caudal vertebrae; and an asymmetric foot (with metatarsal IV much more robust than metatarsal II); (e.g. Varricchio, 1997; Makovicky and Norell, 2004).

Daliansaurus is most similar to the other troodontid taxa from Liaoning, namely *Mei*, *Sinovenator*, and *Sinusonasus*. These troodontids are placed in their own clade by the phylogenetic analysis. Several shared, derived characters support this grouping, as outlined above. Nevertheless, *Daliansaurus* exhibits several differences from these taxa. First, *Daliansaurus* has some autapomorphies that diagnose it relative to all other troodontids, which are described in the diagnosis section above. Second, there are several additional differences between *Daliansaurus* and these Liaoning troodontids, which are summarized here.

Daliansaurus differs from *Sinovenator* (Xu et al, 2002; Xu, 2002) in that the premaxillary ascending process is long and flat dorsoventrally, contrasting with the more rod-like process of *Sinovenator*. The transverse process of the 5th sacral vertebra of *Daliansaurus* is the widest of all sacral vertebrae, and the anterior margin of this transverse process is slightly concave. This contrast with *Sinovenator*, in which the 3rd sacral transverse process is the widest, and in which the anterior margin of 5th transverse process is strongly concave (Xu et al., 2002). The holotype of *Sinovenator* (Xu, 2002) and *Daliansaurus* are both are seemingly mature individuals (based on vertebral fusion), and therefore ontogenetic variation is not a likely explanation for the differences in sacral morphology. Moreover, the metatarsal III of *Daliansaurus* is constricted for most of the proximal length in posterior view, and metatarsals II and IV extend and connect proximally. However, the distal metatarsal III of *Sinovenator* is constricted for most of its length, and metatarsals II and IV are not connected proximally in posterior view (Xu, 2002).

Daliansaurus differs from *Sinusonasus* (Xu and Wang, 2004) in several features. In *Daliansaurus*, the ventral margin of the dentary is slightly convex, the unguals of pedal digit I is distinctly curved ventrally, and the unguals of pedal digit II and IV are equal in size. In *Sinusonasus*, on the other hand, the ventral margin of the dentary is prominently convex, the first pedal ungual is straight ventrally, and the the second pedal ungual is much larger than the fourth.

Daliansaurus differs from *Mei* (Xu and Norell, 2004) in that the anterior end of the maxilla is short and deep, whereas it is long and shallow in *Mei*. The external naris of *Daliansaurus* is relatively smaller than that of *Mei*. The skull of *Daliansaurus* is relatively large, about 96% the length of femur, whereas this ratio is about 69% in the holotype of *Mei* (IVPP V12377) and 75% in a referred specimen (DNHM D2154) (Gao et al., 2012). In addition, the ratio of ulna-radius/humerus length is 79% in *Daliansaurus*, but 95% (IVPP V12377, radius/humerus) and 94% (DNHM D2154, ulna/ humerus) in *Mei* (Gao et al., 2012). It is worth noting, however, that some of these differences could be ontogenetic in nature, as some of the specimens of *Mei* may belong to very young individuals.

Daliansaurus also exhibits differences with other troodontids, from other parts of the world. These are briefly summarized here.

Daliansaurus differs from *Sinornithoides* (Currie and Dong, 2001) in that the pre- and postacetabular processes of the ilium are equally long, whereas the preacetabular process is shorter than the postacetabular process in *Sinornithoides*. Posteriorly, metatarsals II and IV of *Daliansaurus* are in contact and metatarsal III is strongly constricted and not exposed in proximal view. Although the proximal part of metatarsal III is slender in *Sinornithoides*, the bone is fully exposed in posterior view, which is different from the condition in *Daliansaurus*. In addition, the shaft of the humerus in *Daliansaurus* is straight and the head region is expanded anteroposteriorly, giving the bone a fan-shaped outline. However, in *Sinornithoides*, the humerus shaft is bowed and the proximal region is not expanded, giving it a rectangular shape in outline.

Daliansaurus differs from *Jinfengopteryx* (Ji et al., 2005; Ji and Ji, 2007) in that it possesses serrated teeth (whereas the teeth of *Jinfengopteryx* are unserrated) and a much greater number of the maxillary teeth and dentary teeth (17/24, compared to 14/18 in *Jinfengopteryx*).

Daliansaurus differs from *Byronosaurus* (Makovicky et al., 2003), *Urbacodon* (Averianov and Sues, 2007), *Anchiornis* (Xu et al., 2008), *Xixiasaurus* (Lü et al., 2010),

Eosipnopteryx (Godefroit et al., 2013) and *Gobivenator* (Tsuihiji et al., 2014) in having serrated maxillary and dentary teeth, whereas these other taxa exhibit unserrated teeth. In addition, the body size and skeleton ratios are considerably different in these troodontid dinosaurs, although in some cases this may reflect ontogenetic or individual variation rather than a phylogenetic signal.

Daliansaurus differs from *Saurornithoides* (Barsbold, 1974; Currie, 1987) and *Troodon* (Russell, 1948) by its smaller number of dentary teeth (n = 24), versus 31 in *Saurornithoides* (Norell et al., 2009), 35 in *Zanabazar* (Norell et al., 2009) and 35 in *Troodon* (Makovicky and Norell, 2004). The tooth serrations are markedly smaller in *Daliansaurus* than in *Saurornithoides* and *Troodon*, which have large, hooked denticles that point towards the tip of the crown.

Daliansaurus differs from *Linhevenator* (Xu et al., 2011a) in having a much longer humerus. *Daliansaurus* differs from *Philovenator* (Xu et al., 2012) from Inner Mongolia in that the length of the metatarsus is shorter than the length of the femur in *Daliansaurus*, whereas the metatarsus is substantially longer than the femur in *Philovenator*.

Daliansaurus differs from the unnamed troodontid MPC-D 100/44 (Barsbold et al., 1987) in that metacarpal III is longer than metacarpal II in *Daliansaurus*, whereas metacarpal III is shorter than metacarpal II in MPC-D 100/44. *Daliansaurus* differs from *Borogovia* (Osmólska, 1987) in that pedal phalanx II-2 is distinctly much longer in *Daliansaurus*. *Daliansaurus* also differs from *Tochisaurus* (Kurzanov and Osmólska, 1991) in that metatarsal III of *Daliansaurus* is constricted distally in posterior view, whereas the entire metatarsal III is visible posteriorly in *Tochisaurus*.

The discovery of *Daliansaurus* helps to further clarify the anatomy, phylogeny, and evolution of troodontids, a group that is particularly important for understanding the origin of birds and the development of the avian bauplan (Fig. 15). The well-preserved holotype of *Daliansaurus* includes much of the skull, vertebral column, and limbs in three dimensions, and in natural articulation. Therefore, it provides critical new anatomical information on Liaoning troodontids, particularly as two Liaoning taxa—*Sinovenator* and *Sinusonasus*—have been only briefly described in the literature.

Our phylogenetic analysis recovers *Daliansaurus* within a troodontid subclade that also includes other Liaoning taxa: *Mei*, *Sinovenator*, and *Sinusonasus*. This clade is

Fig. 15. The living scene of *Daliansaurus liaoningensis* gen. et sp. nov. (DNHM D 2885) (drawn by Zhao Chuang)

united by several synapomorphies that are not present in other troodontids, and all members are relatively small-bodied animals. We provide a name for this group—Sinovenatorinae. The recognition of this subclade indicates that Liaoning troodontids were undergoing a localized evolutionary radiation during the Early Cretaceous in eastern Asia. This is similar in scope to the local radiation of microraptorine dromaeosaurids, which include at least six genera that lived in the same general area, and at the same general time, as the sinovenatorines (e.g., Xu et al. 1999, 2000, 2003; Zheng et al. 2010; Han et al. 2014; Lü and Brusatte, 2015)

All four current members of Sinovenatorinae are similar in their overall morphology, but each possesses unique characters that differentiate it from the other group members. It remains possible that future studies—based on much larger samples of these still-rare dinosaurs, and perhaps using bone histology—may find that some of these sinovenatorines belong to the same species, and that their differences are due to individual or ontogenetic variation. However, at this point in time, we argue that the distinctive morphologies of the holotypes of the four species are best interpreted as signs of taxonomic separation. This is not surprising, given that there are several species of Liaoning dromaeosaurids—some of the closest relatives of troodontids—that differ from each other in subtle ways that are nonetheless taxonomically informative (Xu, 2002).

6 Conclusions

It appears that small-bodied, feathered, winged paravian theropods from Liaoning—dromaeosaurids, avialans, and troodontids—were exceptionally diverse. Each group experienced its own local Early Cretaceous diversification, which produced a number of species that either coexisted or, perhaps more likely, replaced each other over time or partitioned niches and geographic ranges so that they did not extensively overlap in space. The discovery of *Daliansaurus* also demonstrates that Liaoning continues to produce new dinosaur taxa, and remains one of the world's most productive sites for understanding paravian evolution, more than two decades after the first feathered dinosaurs were reported.

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Appendix 1: Scores for *Daliansaurus* and *Sinusonasus* for the phylogenetic dataset of Brusatte et al. (2014)

Daliansaurus liaoningensis

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