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SHORT COMMUNICATION

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A juvenile ankylosaur from China

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Abstract Juvenile ankylosaur specimens are very rare. A new ankylosaur, *Liaoningosaurus paradoxus* gen. et sp. nov., is described based on a beautifully preserved juvenile ankylosaur specimen from the famous Yixian Formation of Liaoning, China. *Liaoningosaurus* has a large bony plate (somewhat shell-like) shielding the abdomen. This discovery represents the first record of such a structure among dinosaurs. Although it has a number of distinct features seen in the family Ankylosauridae, a cladistic analysis placed *Liaoningosaurus* in the sister-family Nodosauridae. The 'intermediate' status of this taxon between the two ankylosaur families further supports the monophyly of Ankylosauria. This finding also documents the smallest known ankylosaur specimen and first complete nodosaurid specimen from Asia.

Ornithischia

Ankylosauria

Nodosauridae

Liaoningosaurus paradoxus gen. et sp. nov

Etymology. Generic name refers to Liaoning Province; specific name refers to the surprising characteristics of this animal.

Holotype. IVPP V12560, a nearly complete skeleton (Fig. 1).

Type locality and horizon. WangJiagou, Yixian, Liaoning Province, China; Yixian Formation, Lower Cretaceous.

Diagnosis. An ankylosaurian that differs in having: shell-like ventral armour, trapezoidal sternum with slender and distally pointed posterolateral process and short medial articular margin, and pes more than twice as long as manus.

Description. IVPP V12560 represents a juvenile individual, as indicated by the unfused centra and neural arches of vertebrae. It is less than 34 cm in length and represents the smallest ankylosaur specimen reported to date.

The maxilla is excavated posteriorly, suggesting the possible existence of the antorbital fossa and fenestra. The dentary is a stout, rough bone, possibly with a straight ventral margin. The external mandibular fenestra appears to be present. Premaxillary teeth are present as in some primitive nodosaurids (Carpenter 1982, 1997) and the ankylosaurid *Gargoyleosaurus* (Carpenter et al. 1998), and they are slender and have fewer denticles (Fig. 2g). There are about 10 maxillary teeth. The cheek teeth are morphologically similar to those of nodosaurids in having a shelf-like cingulum at their bases, a laterally compressed, palmate crown bearing vertical flutes coincident with the notches between marginal cusps (Hayakawa and Carpenter 1996; Carpenter 1997; Fig. 2h). The cheek teeth are very large for the skull size, while in other adult ankylosaurs they are proportionally much smaller (Coombs and Maryanska 1990).

In contrast to other ankylosaurs except *Gargoyleosaurus* (Coombs and Maryanska 1990; K. Carpenter, personal communication), the proximal caudal centra have a diameter about equal to their length. The prezygapophyses and postzygapophyses of the distal caudals are long, and the distal chevrons articulate with each other in an interdigitating way as in some ankylosaurines (Coombs 1978; Coombs and Maryanska 1990; Fig. 2a), but no ossified hypaxial tendons on distal caudals and tail club were observed, as seen in adult ankylosaurids.

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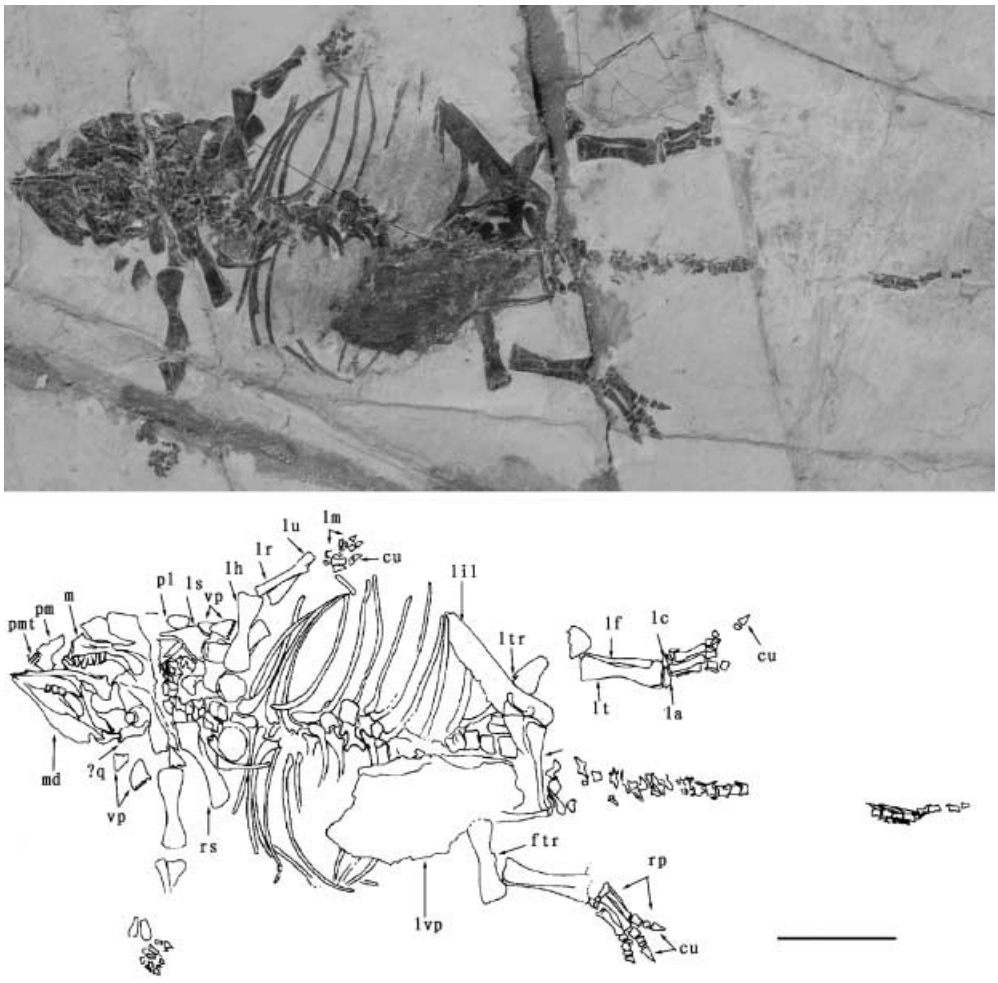

Fig. 1a, b *Liaoningosaurus paradoxus* (IVPP V12560, holotype). **a** photograph, **b** line-drawing of the holotype. Abbreviations: *cu* clawlike ungual, *ftr* fourth trochanter, *la* left astragalus, *lc* left calcanium, *lf* left fibula, *lh* left humerus, *lic* left ischium, *lil* left ilium, *lm* left manus, *lr* left radius, *ls* left sternum, *lt* left tibia, *ltr* lesser trochanter, *lu* left ulna, *lvp* large ventral plate, *m* maxilla, *md* mandible, *pl* plate, *pm* premaxilla, *pmt* premaxillary teeth, *q* quadrate, *rp* right pes, *rs* right scapula, *vp* vertical plate. *Scale bar* = 4 cm

The sternum is similar to that of nodosaurids in having a sub-trapezoidal main body but differs in that the posterolateral process is very slender and distally pointed to some extent (Fig. 2b). It has a straight medial margin as in ankylosaurids; however, the medial margin of ankylosaurids is much longer and its main body is subtriangular in outline (Coombs and Maryanska 1990). The scapula is slender, with a posteroventrally oriented scapular glenoid, a narrow scapular base, and possibly an obliquely directed (toward the glenoid) scapular spine as in nodosaurids (Coombs and Maryanska 1990; Sereno 1999; Fig. 2c).

The humerus has a combination of both nodosaurid and ankylosaurid features. It is relatively slender, with the deltopectoral crest extending less than half the length of the shaft, as in nodosaurids, but the deltopectoral crest and transverse axis through distal humeral condyles are in the same plane, as in ankylosaurids, and the radial condyle is less developed, also as in ankylosaurids (Coombs 1978). The olecranon process of the ulna is moderately developed. The manus is short, and the manual phalangeal formula is 2-3-3-2. All unguals are claw-shaped, laterally grooved, and longer than they are wide.

The preacetabular process of the ilium is long, and strongly deflected laterally, as in other ankylosaurs (Maryanska 1977), and its anatomically lateral surface is twisted to face ventrally, as in nodosaurids (Coombs 1978). The preacetabular process is enlarged as in other ankylosaurs (Coombs 1979). The acetabulum is closed, and ventromedially a crest is present which connects the ischial and pubic peduncles. Unlike other ankylosaurs, the postacetabular process faces more laterally (Fig. 2d). The pubis is strongly reduced, and the ischium is straplike, relatively straight, and with a convex acetabular margin as in some ankylosaurids (Coombs and Maryanska 1990; Sereno 1999; Fig. 2e)

The femur is similar to that of ankylosaurids in having a less distinctive femoral head but also similar to that of nodosaurids in having the crest-shaped fourth trochanter located proximally to the mid-length of the shaft. The tibia is as long as the femur and appears to lack a strongly-twisted appearance as in other dinosaurs (Charig 1972) (Fig. 2f). The calcaneum is proportionally larger than in most other ornithischians. The pes is long (about 230% as long as the manus). Metatarsals II–IV are elongate and closely associated in an arrangement that is approximately similar to that seen in *Scelidosaurus* (Coombs et al. 1990). Metatarsals I and V are rudimentary and splint-like elements. A relatively slender metatarsus has been reported in basal ankylosaurid *Tianchi-*

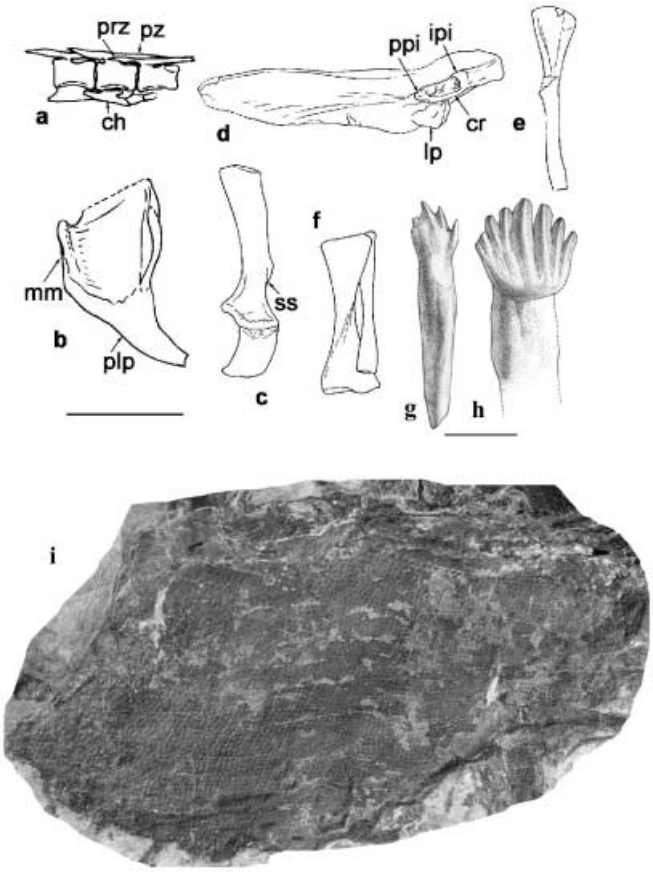

Fig. 2a–i *Liaoningosaurus paradoxus* (IVPP V12560, holotype). **a** line-drawing of three distal caudals in lateral view; **b** right sternum, *scale bar* = 1 cm; **c** reconstructed scapula and coracoid in medial view based on both the right and left scapulas and coracoids; **d** line-drawing of right ilium in ventral view; **e** line-drawing of right ischium; **f** line-drawing of right tibia and fibula, *scale bar* =2 cm; **g** a premaxillary tooth; **h** a maxillary tooth, *scale bar* = 1 cm; **i** close-up of the large ventral plate. Abbreviations: *ch* chevron, *cr* crest, *ipi* ischial peduncle of ilium, *lp* left pubis, *mm* medial margin, *plp* posterolateral process, *ppi* pubic peduncle of ilium, *prz* prezygapophysis, *pz* postzygaphophysis, *ss*, scapula spine

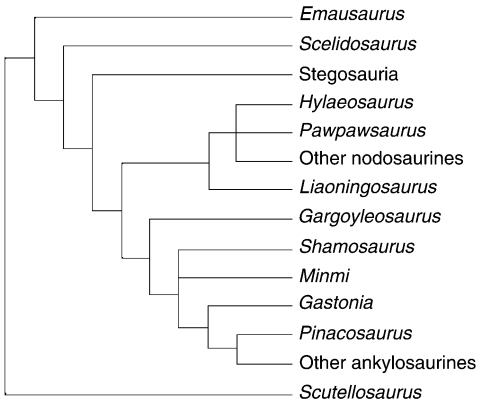

Fig. 3 Cladogram showing the phylogenetic position of *Liaoningosaurus*. Using branch-and-bound option of PAUP 3.11, we produced a 50% majority-rule consensus of 24 equally most parsimonious trees (tree length = 123; consistency index = 0.772; retention index = 0.844). Synapomorphies for each node were determined by accelerated transformation (ACCTRAN). *Liaoningosaurus* was referred to Nodosauridae mainly based on the characters related to the modification of shoulder girdle, including characters 63(1), 64(1), 65(1) and 66(1), and a few other characters, i.e., characters 57(1), 58(1) and 59(1). The topology of the trees remained unchanged when coding those possible juvenile features of *L. paradoxus* as unknown

saurus (Dong 1993). The pedal phalangeal formula is 0-3-4-5-0 and the pedal unguals are all clawlike, and much longer than they are wide.

There are a few sub-triangular plates preserved close to the shoulder girdle, which appear to have been vertical as in stegosaurs (Galton 1997). Ventral to the right pelvic girdle, a large bony plate is preserved (Figs. 1, 2i). The medial edge of this plate is broken, and the external surface of the plate is sculptured by numerous rhombic and hexagonal tubercles with a diameter of about 0.5 mm. The plate is thin laterally and anteriorly, but much thicker medially. The impression reveals a similar plate (or the other half of the illustrated plate) ventral to the left side of the pelvic girdle and similar plates covering the anterior body.

A cladistic analysis placed *Liaoningosaurus* in Nodosauridae (Fig. 3, see Electronic Supplementary Material). However, this result is not strongly supported by the analysis. *Liaoningosaurus* has an unusual combination of characters and it might (for example) represent a third ankylosaur lineage. The twofold division of the Ankylosauria has been also questioned recently, based on study of the polacanthine ankylosaurs from the Early Cretaceous of eastern Utah (Kirkland 1998). The possible juvenile features of *Liaoningosaurus* include fewer large-sized maxillary teeth (comparable to the tooth number in most other adult ankylosaurs), postacetabular process of the ilium facing somewhat laterally, olecranon process moderately developed, pubic peduncle present, distinct finger-like lesser trochanter, tibia as long as femur, and all manual and pedal unguals claw-shaped. Considering the distribution of these characters in basal thyreophorans and other ankylosaurs (juvenile and adult), it is possible that ontogenetic shifts in developmental timing (viz. peramorphosis) played an important role in ankylosaurian evolution.

Liaoningosaurus is unique among ankylosaurs in displaying a large, ventral abdominal plate. Ankylosaurs show evidence of some ventral dermal armour (Lambert 1993); however, this is, in all other known examples (such as *Minmi*), restricted to small unfused elements that do not form a large plate or shield-like structure.

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Supplementary information for:

A juvenile ankylosaur dinosaur from China

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Cladistic Analysis. We determined the phylogenetic position of *L. paradoxus* from an analysis of a dataset modified from Sereno (1999) dataset 2. We used *Scutellosaurus, Emausaurus, Scelidosaurus,* Stegosauria as outgroups, *Hylaeosaurus, Pawpawsaurus,* other nodosaurines, *Gargoyleosaurus, Shamosaurus, Minmi, Gastonia, Pinacosaurus,* other ankylosaurines, and *L. paradoxus* as ingroups, and used characters 1-28, 52-118 from Sereno (1999)'s dataset 2.

Character list

1. Jugal orbital ramus, depth versus transverse breadth: deeper (0); broader (1).
2. Parasagittal row of keeled scutes to each isde of the midline on the dorsal aspect of the trunk: absent (0); present (1)
3. Lateral rows of scutes on the dorsal aspect of the trunk: absent (0); present (1)
4. Dentary tooth row (and anterior edentulous margin), form (lateral view): straight (0) sinuous (1)
5. Palpebral shape: rod-shaped (0); plate-shaped (1)
6. Metacarpals I and V length: substantially shorter than (0), or subequal to (1), metacarpal III.
7. Manual and pedal unguals: claw-shaped (0), hoof-shaped (1)
8. Antorbital fossa size: large (0); small (1); absent (2).
9. Palpebral articulation, form: mobile contact with prefrontal (0); interdigitating contact with prefrontal, frontal and postorbital (1).
10. Quadrate condyle, shape: symmetrical (0); medial side larger (1).
11. Pterygovomerine keel, maximum depth: less (0) or more (1), than 50% of snout depth.
12. Basisphenoid length: longer (0), or subequal to or shorter (1), than the basioccipital.
13. Anterior and posterior supraorbitals: absent (0); present (1).
14. Quadrate condyle, inclination of articular surface (posterior view): horizontal (0); ventromedially inclined at approximately 45 degrees (1).
15. Quadrate condyle lateral raumus: present (0); absent (1)
16. Pterygovomerine keel, length: less (0), or more (1), than 50% of palate length.
17. Dentary symphysial ramus, width: more (0), or less (1), than half of the maximum depth of the mandibular ramus.
18. Premaxillary tooth count: 6(0); 5(1); 7(2).
19. Atlantal neural arch and intercentrum, articulation: open (0); coossified (with maturity) (1).
20. Scapular blade shape: distally expanded (0); parallel-sided.

21. Iliac preacetabular process length: less (0), or more (1), than 50% of the length of the iliac blade.
22. Iliac preacetabular process, lateral deflection: 10-20 degrees (0); 45 degrees (1).
23. Ischial blade shape: distally expanded (0); distally tapering (1)
24. Femoral fourth trochanter, form: pendant (0); crest-shaped (1).
25. Femoral anterior trochanter: separated by narrow cleft (0), coossified with greater trochanter in the adult (1).
26. Pedal digit IV phalangeal number: 5 (0); 4 or less (loss of at least one nonterminal phalanx) (1).
27. Metatarsal arrangement: compact (0); spreading (1).
28. Metapodial length: more (0), or less (1), than 30% of propodial length.
29. Occiput, maximum width; less (0), or more (1), than maximum height.
30. Antorbital fenestra: present, open (0); absent, closed by maxilla, lacrimal, and jugal (1).
31. Supratemporal fenestra: present, open (0); absent, closed by postorbital, squamosal and parietal (1).
32. Jugal-postorbital bar, width; narrower (0), or broader (1), than laterotemporal fenestra.
33. Quadratojugal, orientation of external surface: lateral (0); posterior (1)
34. Nasal septum dividing narial passage: absent (0); present (1).
35. Quadrate shaft, orientation: approximately vertical (0); inclined approximately 45 degrees anteroventrally (1).
36. Pteygovomerine keel, ventral margin: above (0), or level eith (1), amxillary alveolar margin.
37. Pteygoquadrate ramus, depth: deep (0); narrow (1).
38. Space between palate and braincase: open (0) very constricted or clsoed (1).
39. Accessory ossification separating antorbital andorbital spaces: absent (0); present (1).
40. Fusion and dermal sculpturing of skull roof (except ventral margin of premaxilla and maxilla and posterior portion of the quadratojugal): absent (0); present (1)
41. Jaw articulation, position: posterior (0), or medial (1), to adductor fossa.
42. Elongate, keeled mandibular osteoderm: absent (0); present (1).
43. Predentary ventral process, length: prong-shaped (0); rudimentary eminence (1).
44. Maxillary/dentary corwns, band-shaped cingulum: absent (0); present (1).
45. Atlantal neural arches, median contact above neural canal: absent (0); present (1).
46. Three sacrodorsals with long ribs attaching to the ventral aspect of the iliac preacetabular process: absent (0); present (1).
47. Anterior caudal vertebrae, length of transverse processes: subeaual to (0), or approximately twice (1), the height of the neural spine.
48. Distal chevron shape, mutual contact: tongue-shaped, isolated (0); inverted T-shaped, ends in contact (1).
49. Sternum with shaft-shaped posterolateral process: absent (0), present (1).
50. Scapular acromion, orientation: coplanar with blade (0); everted (1).
51. Acetabular fenestra: open (0); closed (1).
52. Postpubic porcess, length: more (0), or less (1), than 50% of ischial length.
53. Postpubic process, shape: rod-shaped (0); strap-shaped (1).
54. Two U-shaped cervical collars composed of contiguous keeled scutes: absent (0); present (1).
55. Moszic of small osteoderms between larger osteoderms and on the ventral surfaces of the neck, trunk, and proximal portions of the limbs: absent (0); present

(1).

56. Snout low: maximum preorbital depth less (0), or more (1), than twice maxmum preorbital length.
57. Premaxillary palate, shape: subtriangular (0); oval (1); subquadrate (2)
58. Occipital condyle, form: crescentic (0); hemispherical (Ventrally deflected) (1).
59. Occipital condyle, composition: basioccipital and exoccipitals (0); basioccipital onely (1).
60. Posterior margin of pterygoid, position: anterior to (0), or in transverse alignment with (1), the ventral margin of the pterygoid ramus of the quadrate.
61. Scute pattern on dorsal skull roof: large median interorbital and interorbital and internarial scutes (0); paired interorbital and internarial scutes (1).
62. Dentary ventral margin: straight (0); sinuous (1).
63. Scapular blade, anteroposterior width of base: subequal to (0), or at least 25% less than (1), proximal width at glenoid.
64. Scapular glenoid, orientation: facing posteroventrally and laterally (0); facing posteroventrally (1).
65. Coracoid shape: subquadrate (0); subrectangular (1).
66. Coracoid glenoid, size: subequal to (0), or approximately half of (1), scapular glenoid.
67. U-shaped pectoral collar composed of contiguous keeled scutes: absent (0); present (1).
68. Interpremaxillary notch: absent (0); present (1).
69. Accessory dermal ossifications forming lateral margin of external nares: absent (0); present (1).
70. Accessory dermal ossifications on posterodorsal and posteroventral corners of the skull roof: absent (0); present (1).
71. Skull width: less than (0), equal to (1), or greater than (2), maximum skull length.
72. Snout width lateral sinus: absent (0); present (1).
73. Premaxillary teeth: present (0); absent (1).
74. Hypaxial ossifed tendons on distal caudals: absent (0); present (1).
75. Tail club composed of 2 pairs of large ossifications (anterior pair largest): absent (0); present (1).
76. Snout profile: level with (0), or arching above (1), the posterior skull table.
77. Premaxillary posteroventral rim: poorly developed (0); obscures anteriormost maxillary teeth (lateral view) (1).
78. Premaxillary rim, position of posterior end : in line with (0), or shifted lateral to (1), the maxillary tooth row.
79. Maxillary tooth rows, anteiror separation: narrow (0); broad (1).
80. Respiratory passage, shape: straight (0); S-shaped (10.
81. Postocular (jugal-postorbital)wall: absent (0); present (1).
82. Posteroventral dermal plate, position: posterior (0), or posteroventral (1), to orbit.
83. Cranial acessory dermal plates, isze: moderate (0); hypertrophied (1).
84. Dentary ramus, location of maximum depth: posterior end (0); mid length (1).
85. Coronoid height: moderate (0); low (1).
86. Posteriormost caudal pre- and postzygapophyses, length: extend over less (0), or more (1), than half of the adjacent centrum.
87. Distal caudal postzygapophyses, form: short, wedge-shaped (0); long, tongue-shaped (1).
88. Distal hemal arches, mutual contact: absent (0); present (1).
89. Sternal plates, median contact: open (0); coossified (1).

90. Humeral deltopectoral crest, orientation: anteriorly curved (0); transverse (1)
91. Iliac postacetabular process, length: longer (0), or shorter (1), than acetabular diameter.
92. Ischial acetabular margin, form: concave (0); convex (1).
93. Ischial shaft orientation: posteroventral (0); subvertical (1).
94. Pubis size, participation in acetabulum: small, participates (0); rudimentary, nearly exluded (1).
95. Tibia, maximum distal width: less (0), or greater (1), than mximum width of proximal end.

Matrix

Scutellosaurus
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Emausaurus
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