

# *Diandongosaurus acutidentatus* Shang, Wu & Li, 2011 (Diapsida: Sauropterygia) and the relationships of Chinese eosauropterygians

TAMAKI SATO\*†, YEN-NIEN CHENG‡§, XIAO-CHUN WU¶ & HSI-YIN SHAN‡§

\*Tokyo Gakugei University, 4-1-1 Nukui Kita Machi, Koganei City, Tokyo 184-8501, Japan

†National Museum of Natural Science, No.1 Kuan Chien Road, Taichung, Taiwan 40453

§Department of Earth Sciences, National Cheng Kung University, No.1 University Road, Tainan, Taiwan 701

¶Canadian Museum of Nature, PO Box 3443 STN 'D', Ottawa, ON K1P 6P4, Canada

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**Abstract** – *Diandongosaurus acutidentatus* Shang, Wu & Li, 2011 is restudied on the basis of a new specimen. The new specimen provides further information on the palate of the skull, the shoulder girdle, the gastralia and hind limbs, and permits revision of the diagnosis. Newly added or modified diagnostic characters include the presence of a few small vomerine teeth, the presence of an ectopterygoid, lateral elements of gastralia distally swollen and curving dorsally, boomerang-shaped interclavicle and clavicle with a distinct anterolateral process. Slight variations in the vertebral counts, girdle morphology, and phalangeal formulae are attributed to the intraspecific variations. A revised phylogenetic analysis demonstrates that *Diandongosaurus* is closely related to the Nothosauroidae and that certain Chinese taxa (e.g. *Keichousaurus*) previously affiliated with the Pachypleurosauridae are more closely related to the Nothosauroidae. The effect of inclusion or exclusion of fragmentary taxa in the phylogenetic analysis is observed in the branching pattern of the cladogram, but it has little effect on the morphological characterization of the major clades.

Keywords: Triassic, China, marine reptiles, fragmentary taxa.

## 1. Introduction

The Sauropterygia were a successful group of Mesozoic marine reptiles with a fossil record extending from late Early Triassic to latest Cretaceous times (Rieppel & Hagdorn, 1997; Welles, 1943). The interrelationships of many of its Triassic-aged members, including pachypleurosaurs, nothosaurs, and certain Chinese taxa (*Keichousaurus* Young, 1958, *Hanosaurus* Young, 1972, *Wumengosaurus* Jiang *et al.* 2008, *Dianopachysaurus* Liu *et al.* 2011) have been subject to debate.

This conflict is partly the consequence of uncertainty as to the taxonomic content of the Pachypleurosauridae and Pachypleurosauria and the resulting disagreements regarding the definition of the clade names. We employ the phylogenetic definitions of the clade names in Rieppel (2000) and Liu *et al.* (2011) in this contribution in an attempt to avoid this problem (see Table 1), although the large number of taxa in the definition of the Pachypleurosauridae and Pachypleurosauria is certainly arguable because of the implicit assumption of their monophyly. Despite considerable taxonomic uncertainty within pachypleurosaurs (*sensu* Rieppel (2000) and Liu *et al.* (2011)), the European pachypleurosaurs (*Neusticosaurus*, *Serpianosaurus*, *Dactylosaurus* and *Anarosaurus*) have consistently formed a clade separate from the Nothosauroidae and the Chinese forms in recent studies; in this contribution, the term 'European pachypleurosaurs' is used to refer to these four genera.

Rieppel (2000) regarded the Nothosauroidae as the sister taxon of the Pistosauroidae within the Eusauropterygia, and the Pachypleurosauridae as the sister taxon of the Eusauropterygia. Liu *et al.* (2011) presented a cladogram in which three Chinese taxa (*Keichousaurus*, *Dianopachysaurus* and *Wumengosaurus*) were more closely related to the European pachypleurosaurs than to the Eusauropterygia, and regarded the three Chinese taxa as members of the Pachypleurosauridae. A different view was presented by Holmes, Cheng & Wu (2008), Shang, Wu & Li, (2011) and Wu *et al.* (2011) in which *Keichousaurus* is more closely related to the Nothosauroidae than to the European pachypleurosaurs, and *Wumengosaurus* is a stem taxon of the lineage leading to the clade consisting of the Nothosauroidae and the European pachypleurosaurs. Cheng *et al.* (2012) reached a similar conclusion finding that none of the three Chinese taxa in question belongs to the Pachypleurosauridae.

*Diandongosaurus acutidentatus* Shang, Wu & Li, 2011 is a recently described member of the Eosauropterygia from the middle Anisian Guanling Formation in eastern Yunnan, China. The holotype displays a combination of traits seen in nothosauroids such as *Simosaurus* and *Nothosaurus*, and the European pachypleurosaurs. For example, characters such as an unconstricted snout, a preorbital region longer than the postorbital region and a supratemporal fenestra smaller than the orbit are common features among the European pachypleurosaurs, whereas the enlarged and procumbent teeth in the premaxilla and anterior portion of the dentary, and the fang-like maxillary teeth suggest nothosauroid affinity. The strict consensus

†Author for correspondence: tsato@u-gakugei.ac.jp

Table 1. Phylogenetic definitions of the clade names used in this contribution

Clade name	Definition
Eosauropterygia (in Rieppel, 2000)	A monophyletic taxon including the Pachypleurosauria, Nothosauroida and the Pistosauroida
Pachypleurosauria (in Liu <i>et al.</i> 2011)	A monophyletic taxon including the most recent ancestor of <i>Wumengosaurus</i> , <i>Keichousaurus</i> , <i>Dianopachysaurus</i> , <i>Anarosaurus</i> , <i>Dactylosaurus</i> , <i>Neusticosaurus</i> and <i>Serpianosaurus</i> , and all of its descendants
Pachypleurosauridae (in Rieppel, 2000)	A monophyletic taxon including the genera <i>Anarosaurus</i> , <i>Dactylosaurus</i> , <i>Hanosaurus</i> , <i>Keichousaurus</i> , <i>Neusticosaurus</i> , and <i>Serpianosaurus</i>
Eusauropterygia (in Rieppel, 2000)	A monophyletic taxon including the Nothosauroida and the Pistosauroida
Nothosauroida (in Rieppel, 2000)	A monophyletic taxon including <i>Simosaurus</i> and <i>Nothosaurus</i>
Nothosauridae (in Rieppel, 2000)	A monophyletic taxon including the genera <i>Nothosaurus</i> and <i>Lariosaurus</i>
Pistosauroida (in Rieppel, 2000)	A monophyletic taxon including the Cymatosauridae, Pistosauria, and the Jurassic and Cretaceous crown-clades (Plesiosauria)

of the phylogenetic analysis by Shang, Wu & Li (2011) recovered *Diandongosaurus* among the basal polytomy of the Eosauropterygia, whereas the majority consensus placed this taxon as the basal-most member of the lineage leading to the clade consisting of the European pachypleurosaurs, the Nothosauroida and *Wumengosaurus*.

One problem with the holotype, and until recently the only specimen of *Diandongosaurus*, is the lack of information on the ventral side of the skull; the neck is twisted in its middle portion and although the postcranial elements are exposed in ventral view, the skull is preserved in dorsal aspect. The new specimen described here not only reveals the ventral view of the skull, but also intraspecific variation of the postcranial skeleton, which leads to a revised diagnosis of the taxon. The phylogenetic analysis is also revised to re-examine the relationship of the Pachypleurosauridae, Nothosauroida and Chinese eosauropterygian taxa such as *Keichousaurus*, *Wumengosaurus*, *Hanosaurus*, and *Dianopachysaurus*.

*Institutional abbreviations.* IVPP – Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; NMNS – National Museum of Natural Science, Taichung, Taiwan.

## 2. Systematic palaeontology

SAUROPTERYGIA Owen 1860  
 EOSAUROPTERYGIA Rieppel, 1994a  
 [sensu Rieppel, 2000]  
*Diandongosaurus* Shang, Wu & Li, 2011  
*Diandongosaurus acutidentatus* Shang, Wu & Li, 2011

*Holotype.* IVPP V 17761, a complete skeleton with the skull in dorsal and the postcranial skeleton in ventral views.

*Referred specimen.* NMNS-000933-F03498, a nearly complete skeleton preserved in ventral view, lacking only the posterior-most section of the tail.

*Locality and horizon.* Luoping County, Yunnan Province, China; Member II of the Guanling Formation, lower Middle Triassic (Anisian).

*Remarks.* The occurrence data in the specimen label does not specify a stratigraphic level and age, but it is inferred from the literature data (Zhang *et al.* 2009).

*Emended diagnosis.* A small to medium-sized eosauropterygian with the following characters: enlarged and fang-like premaxillary and anterior dentary teeth; maxilla with one or two fangs and distinctly smaller conical teeth; short snout without constriction; supratemporal fenestra smaller than orbit; broad interorbital bridge; posterolateral process approaching the supratemporal fenestra; presence of a few small vomerine teeth; parietal foramen anterior to supratemporal fenestra; frontal excluded from orbit by prefrontal-postfrontal contact; postorbital excluded from infratemporal fenestra by jugal–squamosal contact; descending process of squamosal reaching lateral side of articular condyle of quadrate; quadratojugal present; ectopterygoid present; distinct trough on the dorsal surface of retroarticular process; vertebral column consisting of about 20 cervical, 18 dorsal, 3 or 4 sacral and 39 caudal vertebrae; anterior caudal ribs 3 to 8 elongate and distally truncated; lateral elements of gastralia distally swollen and curving dorsally; clavicle with a distinct anterolateral process; boomerang-shaped interclavicle (may develop a weak posterior projection); entepicondylar foramen absent; ungual phalanges of pes extremely expanded dorso-ventrally; phalangeal formula 2-4-5-6-3 for manus and 2-3-4-(6/5)-(5/4/3) for pes.

## 3. Description

We refer NMNS-000933-F03498 to *D. acutidentatus* based on the following characteristics shared with the holotype: anterolateral process of the clavicle, transverse processes of anterior caudal vertebrae slender and distally truncated, lateral elements of gastralia distally swollen and turned upwards, and ungual phalanges of the pes extremely expanded in dorso-ventral direction.

See Table 2 for the measurements. The new specimen is larger than the holotype, the latter being about 85% of the former in the trunk length, and retains 27 caudal vertebrae (Fig. 1a). If the original number of caudals was the same as that in the holotype (39), the new specimen is missing 12 caudals; based on this assumption, the total length of the NMNS specimen is estimated to be about 340 mm. In the following text, the description will focus primarily on the structures not described by, or unavailable to, Shang, Wu & Li (2011), as well as on the comparison with the European pachypleurosaurs and nothosauroids.

Table 2. Selected measurements of NMNS00093-F034398, the referred specimen of *Diandongosaurus acutidentatus* Shang, Wu & Li, 2011

Dimension	Length (mm)
Skull (anterior tip to occipital condyle)	26
Mandible (anterior tip to retroarticular process)	32
Presacral vertebral length (without skull)	170
Sacral vertebrae	14
Tail (missing posterior portion)	111
Humerus	20 (L)
Radius	10.5 (L)
Ulna	10
Femur	26.5 (R), 26 (L)
Tibia	14 (L)
Fibula	14.5 (L)

R – right; L – left

### 3.a. Skull

The skull of NMNS-000933-F03498 is exposed in ventral view, showing much of the palate between the occluded mandibular rami. The palate anterior to the internal naris mainly consists of the palatal portion of the premaxilla with smaller contributions of the maxilla and vomer (Fig. 1b, c). The premaxilla meets its counterpart along the ventral midline; it is largely covered by the mandibular symphysis anteriorly, and excluded from the internal naris by the vomer–maxilla contact posteriorly. The latter condition is shared with *Nothosaurus* (Rieppel, 2000: figs. 55B, 58B, 59B, 60B) but differs from the European pachypleurosaurs and *Keichousaurus* in which the premaxilla enters the anterior border of the internal naris (Sander, 1989: fig. 11a; Carroll & Gaskill, 1985: fig. 14c; Holmes, Cheng & Wu, 2008: fig. 3B). The internal nares are damaged but the right one is nearly complete; they are oval and slightly oblique relative to the midline.

The vomer is well-preserved but detached from the counterpart, exposing the ventral view of the dorsal portion of the premaxilla along the midline (Fig. 1b, c). Each vomer takes a narrow triangular shape with a pointed posterior end, and forms much of the septum separating two internal nares. The sutures with the premaxilla and maxilla are highly interdigitated, but the suture with the pterygoid is nearly straight. There are small teeth or denticles on the ventral surface of the vomer, at least one on the left and two on the right.

The outline of the palatine is unclear owing to cracks at the maxillary suture, but its suture with the pterygoid is nearly straight. The ventral surface is weakly concave and bears very fine ridges. The bone may meet the vomer just posteromedial to the internal naris, although the contact is not confirmed due to damage (Fig. 1b, c).

The pterygoids form most of the palate. A peculiar median opening here referred to as the ‘anterior interpterygoid vacuity’ (Fig. 1b, c) is located in the bottom of a shallow central depression; the nature of this opening and the ‘posterior interpterygoid vacuity’ described below will be discussed in Section 5.b.2.

There is a pair of ridges symmetrically extending from the sides of this opening onto the transverse processes towards the ectopterygoid, although this feature appears to have been emphasized by the collapse of the postorbital bar onto the dorsal surface of the palate. The pterygoids are indistinguishably fused anterior to the opening, but the midline suture is open posterior to it, leaving an irregular opening referred to here as the ‘posterior interpterygoid vacuity’ anterior to the basioccipital. The anterior ends of pterygoids taper into a sharp process that inserts between the vomers. The quadrate ramus of the pterygoid extends posterolaterally, and broadly contacts the pterygoid ramus of the quadrate lateral to the occipital region.

The ectopterygoid is a nearly square small bone (Fig. 1b, c). It is sutured to the anterolateral side of the transverse process of the pterygoid, and meets the palatine anteriorly; it appears to have lost a contact with the maxilla and jugal laterally. On the right side, this element is detached from the neighbouring elements and displaced. The ectopterygoid has not been confidently identified in many non-pistosauroid eosauropterygians excluding the Nothosauroida (Carroll & Gaskill, 1985; Sander, 1989; Rieppel, 1989; Lin & Rieppel, 1998; Holmes, Cheng & Wu, 2008; Wu *et al.* 2011).

Two elements of the braincase, the epipterygoid and basioccipital, can be positively identified. The right epipterygoid is a narrow rod with an expanded base, obviously bent laterally, and sandwiched between the squamosal and the pterygoid. The base of the basioccipital is partially exposed along the midline fissure between the pterygoids; sediments fill this fissure anterior to the basioccipital, suggesting the displacement of the basisphenoid. The posterior surface of the occipital condyle is concave.

The mandible is complete, and individual elements in the right ramus are mostly distinguished (Fig. 1a, b). The dentary occupies at least two-thirds of the ramus. Its ventral surface is slightly concave and bears fine longitudinal ridges. The mandibular symphysis is robust, and longer than those in the European pachypleurosaurs and *Keichousaurus* (Carroll & Gaskill, 1985; Sander, 1989; Rieppel, 1989; Lin & Rieppel, 1998; Holmes, Cheng & Wu, 2008). The angular forms the base of the adductor chamber and the ventrolateral edge of the retroarticular process (Fig. 1a, b).

The splenial lines the ventromedial wall of the mandible anterior to the adductor chamber, and contributes to the posterior quarter of the mandibular symphysis. The coronoid is a thin strap of bone forming the coronoid process; the bone contacts the surangular posterolaterally above the anterior edge of the adductor chamber. The articular is entirely covered by the prearticular and angular in ventral view. The prearticular is a large element that forms the medial wall of the adductor chamber anteriorly; posteriorly, it supports the mandibular articulation and forms the short and stout retroarticular process.



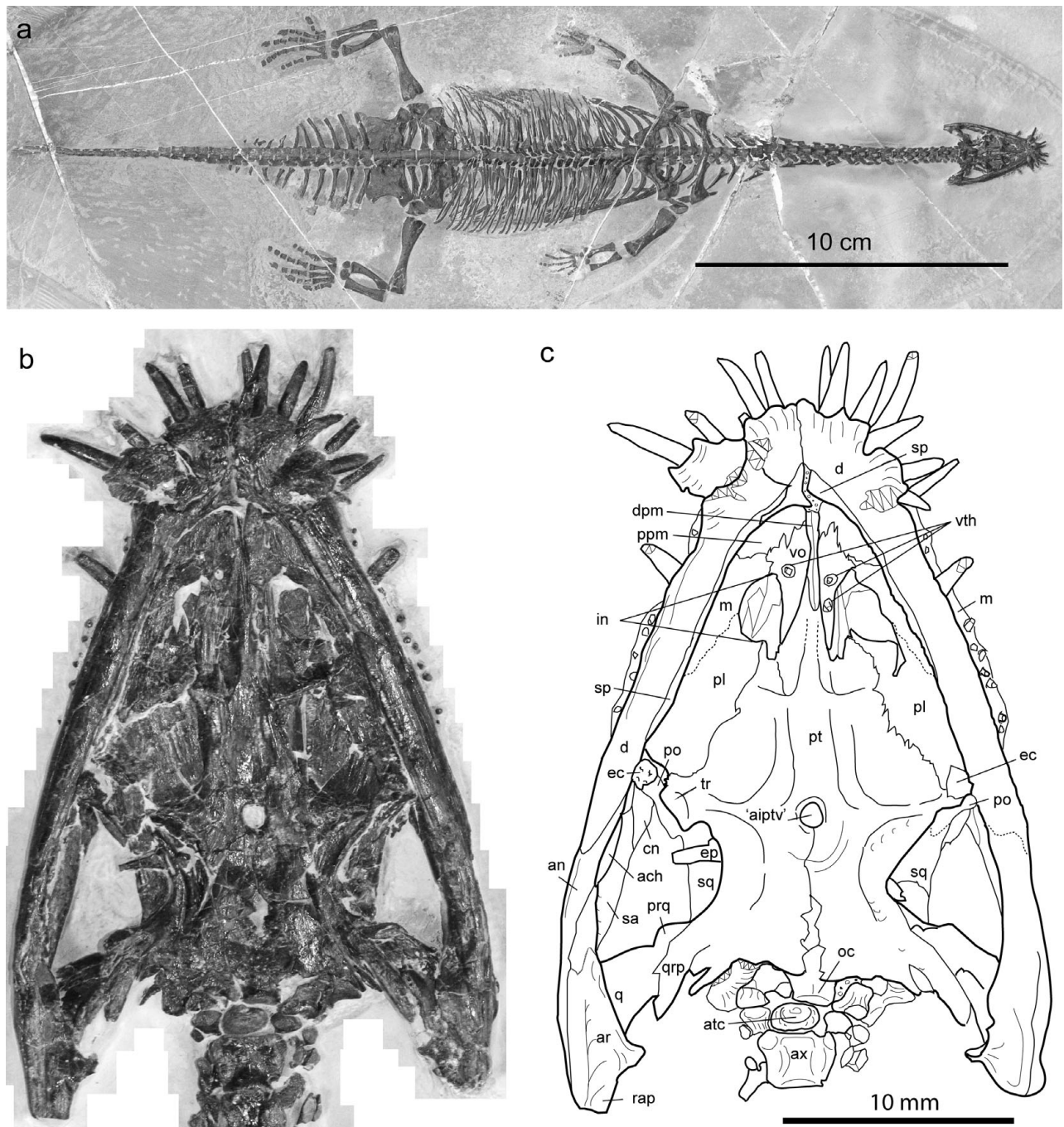


Figure 1. Referred specimen of *Diandongosaurus acutidentatus* Shang, Wu & Li, 2011 (NMNS00093-F034398). (a) Skeleton in ventral view; (b) skull and mandible in ventral view; (c) camera lucida line drawing of the skull and mandible in ventral view. Abbreviations: ach – adductor chamber; ‘aiptv’ – ‘anterior interpterygoid vacuity’; an – angular; apcl – anterolateral process of clavicle; ar – articular; as – astragalus; atc – atlantal centrum; ax – axis; cal – calcaneum; cd – caudal rib; cl – clavicle; cn – coronoid; co – coracoid; cof – coronoid foramen; cr – cervical rib; cv – cervical vertebra; d – dentary; dl – distal end of lateral element of gastral rib; dpm – dorsal portion of premaxilla; dr – dorsal rib; dsc – dorsal blade of scapula; dv – dorsal vertebra; ec – ectopterygoid; ep – epipterygoid; fcl – facet for clavicle; fco – facet for coracoid; fi – fibula; ficl – facet for interclavicle; gsc – glenoid portion of scapula; h – humerus; icl – interclavicle; in – internal naris; m – maxilla; mpcl – medial process of clavicle; mt – metatarsal; oc – occipital condyle; pl – palatine; ppm – palatal portion of premaxilla; po – postorbital; prq – pterygoid ramus of quadrate; pt – pterygoid; q – quadrate; qrp – quadrate ramus of pterygoid; rap – retroarticular process; r – rib; sa – surangular; sc – scapula; sp – splenial; spcl – scapular process of clavicle; sq – squamosal; ti – tibia; tp – transverse process; tr – transverse ridge; vo – vomer; v – vertebra; vth – vomerine teeth.

The ventromedial surface of this bone is noticeably concave.

The marginal teeth are essentially the same as those of the holotype; the five maxillary teeth are large and procumbent, and include two large fangs or caniniform

teeth. However, the contrast in size of the fangs and other maxillary teeth is more pronounced than in the holotype. There are two small teeth anterior to the fang, but the large space between the fang and the last premaxillary tooth suggests that there

might have been one or two additional maxillary teeth.

### 3.b. Axial skeleton

The anterior end of the vertebral column is disturbed and individual components of the atlas could not be identified, but there were probably 20 cervical vertebrae present. The posterior portion of the tail is missing, but the rest of the column is preserved in articulation (Fig. 1). The estimated number of presacral vertebrae (38) is the same in NMNS00093-F034398 and the holotype.

There are about 20 cervicals and 18 dorsals in *Diandongosaurus*. Various features, such as the position and number of rib heads, rib length, or the position of the pectoral girdle, have been used in previous studies to approximate the location of the cervical–dorsal boundary (e.g. Carroll & Gaskill, 1985; Sander, 1989; Shang, Wu & Li, 2011), leaving the division somewhat arbitrary. A gradual transition of morphology, as well as the presence of an overlapping pectoral girdle, also obscures the boundary. In the holotype, the 19<sup>th</sup> vertebra is the last one located anterior to the pectoral girdle and in which the double-headed rib was confirmed. The rib becomes gradually longer posteriorly in the proximal portion of the neck (near the shoulder), and this trend continues to the 20<sup>th</sup> rib; the 21<sup>st</sup> ribs are the most anterior ones with a truncated distal end, suggesting cartilaginous connection to the ventral element(s). In the referred NMNS specimen, the 20<sup>th</sup> vertebra is just anterior to the pectoral girdle, and the anterior process of the rib is lost but the distal end is still pointed. The distal portions of the 21<sup>st</sup> ribs of the referred specimen are covered by the coracoids and the morphology of the distal end cannot be confirmed; the 22<sup>nd</sup> ribs are the first with a confirmed truncated end.

The atlantal centrum is exposed between the occipital condyle and the axial centrum (Fig. 1b, c); the atlantal intercentrum appears to be missing. Judging by the orientation, the atlantal centrum was not fused with the axis. It is short and spherical, with a concavity on its anterior surface. The axial centrum is approximately as long as wide, only about two-thirds of the following centrum in length, and the ventral surface is slightly concave. In the cervical series, lateral constriction of the centrum is more prominent in anterior vertebrae than in posterior vertebrae (Fig. 2a, b); the ventral midline ridge is only weakly developed. Most of the dorsal vertebrae are covered with gastralia, but exposed ones show less constricted, cylinder-shaped centra.

Two vertebrae are confirmed to have ribs that directly articulate with the ilium. The vertebra anterior to and posterior to these articulating ones bear ribs that angle towards the ilium, but their distal ends are covered by the overlying pubis or ischium, and the presence of iliac articulations cannot be confirmed. The holotype has at least three sacral vertebrae (Shang, Wu & Li, 2011), and intraspecific variation of sacral count is

common among Triassic eosauroptrygians (Sander, 1989; Lin & Rieppel, 1998; Rieppel, 1998b); the sacral count of *Diandongosaurus* is probably three, if not four. Anterior caudals are slightly tilted to the right and show parts of neural spines and caudal rib facets at the neurocentral suture. The first caudal ribs are directed posterolaterally, and the distal ends are pointed. The caudal ribs are similar in length until the 6<sup>th</sup> caudal, then becoming progressively shorter to the 13<sup>th</sup> caudal, posterior to which ribs are absent (Fig. 3a, b). The most posterior caudal vertebra with ribs is the 15<sup>th</sup> in the holotype. This difference is attributed to intraspecific variation (c.f. Carroll & Gaskill, 1985).

There are 26 rows of gastralia corresponding to 13 dorsal vertebrae. This pattern (two gastralia for each vertebra) is also known in some European pachypleurosaurids and pistosauroids (Sander, 1989; Storrs, 1991). Each gastralium consists of one medial element and four lateral elements (two per each side). The distal end of the most lateral element becomes swollen and curves; it was probably directed dorsolaterally in life. The same features are observed in the holotype (Fig. 2c, d).

### 3.c. Appendicular skeleton

The pectoral girdle elements remain articulated in NMNS00093-F034398, providing more accurate topological information than those in the holotype. The pectoral girdle as a whole, excluding the anterior process of the clavicle, was obviously wider than long in life. Minor differences in the morphology of the interclavicle (Fig. 2f, h) can be attributed to the intraspecific variation also known in other eosauroptrygians (e.g. Rieppel, 1989). Shang, Wu & Li (2011) described the interclavicle of the holotype as ‘arrowhead-shape’, but there is a weak projection on the midline at the anterior and posterior edge, and our re-examination revealed that the lateral ends are actually slightly damaged in the holotype. In the NMNS specimen, the interclavicle is boomerang-shaped, and the posterior edge is smoothly concave without the midline projection; the condition of the anterior projection is unknown due to damage.

Shang, Wu & Li (2011) considered that the clavicle of the holotype was disarticulated from the interclavicle and scapula, but the NMNS specimen demonstrates that it is not the case (Fig. 2e–h). There is a prominent, characteristic spike near the anterolateral corner of the clavicle (misidentified as a ‘scapular process’ in Shang, Wu & Li, 2011), although it is more slender than that in the holotype. What was identified as the dorsal blade of the scapula in the holotype by Shang, Wu & Li (2011) actually represents the posterolateral extension of the clavicle which overlies the dorsal surface of the scapula. It remains unclear whether or not the narrow medial process of the clavicle met its counterpart to exclude the interclavicle from the anterior edge of the pectoral girdle.



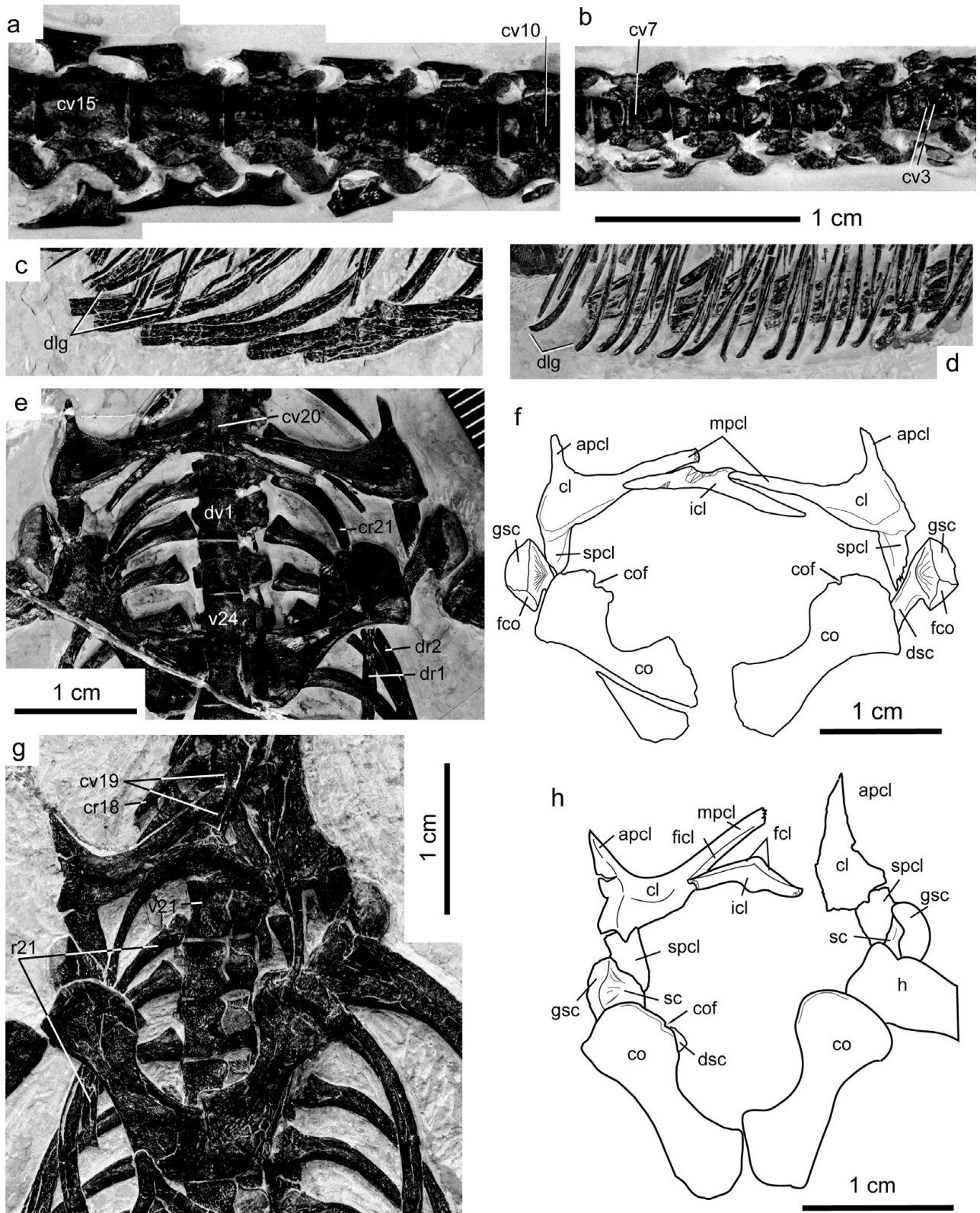


Figure 2. *Diandongosaurus acutidentatus* Shang, Wu & Li, 2011. (a, b) Cervical vertebrae in ventral view (NMNS00093-F034398); (c, d) lateral elements of some gastral sets from both the holotype (c) and NMNS00093-F034398 (d) in ventral view, showing their distal ends that are swollen and curving dorsally. (e–h) Elements of pectoral girdle of NMNS00093-F034398 (e, f) and the holotype (g, h) in ventral view. See Figure 1 for abbreviations.

The scapula consists of a ventral portion and a dorsal blade. The dorsal blade is long and the distal end is truncated; scapulae with such characteristics are known in the nothosauroid *Simosaurus* (Rieppel, 1994a), but

not in the European pachypleurosaurs. The coracoid foramen is marked as a notch on the edge of pectoral fenestra in the NMNS specimen, but this feature is poorly developed in the holotype.

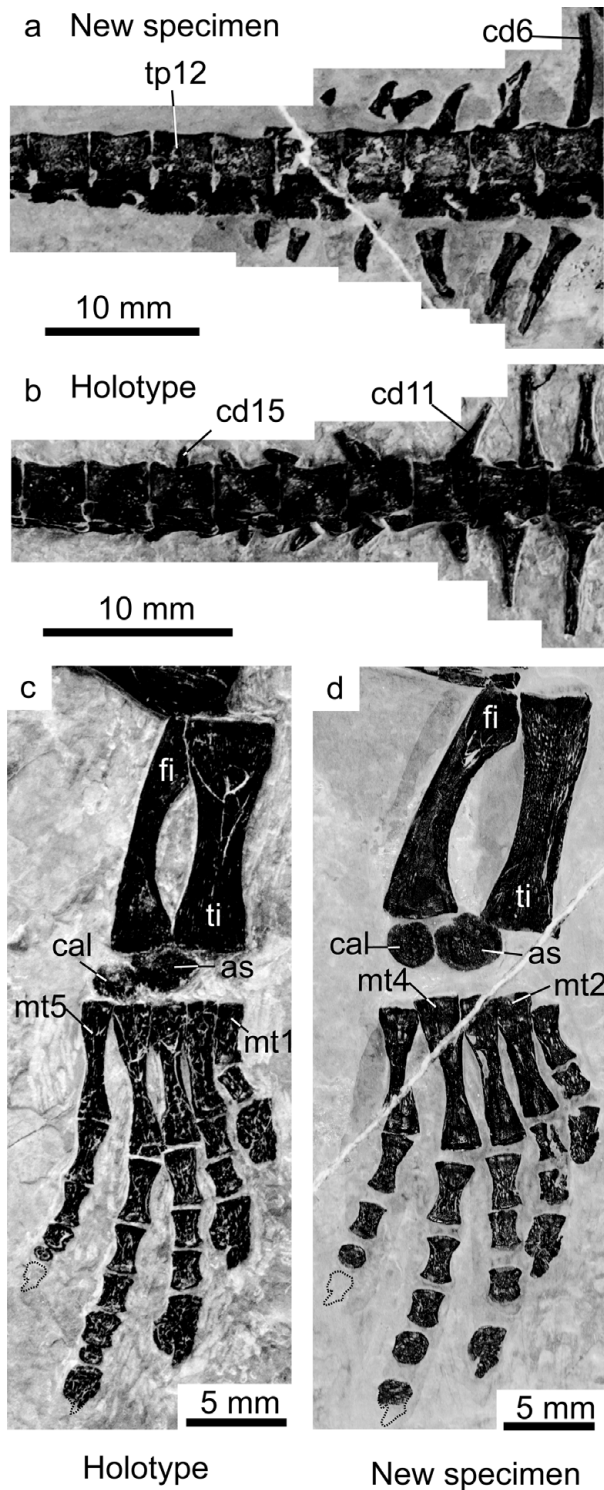


Figure 3. *Diandongosaurus acutidentatus* Shang, Wu & Li, 2011. (a, b) Caudal vertebrae from both NMNS00093-F034398 (a) and the holotype (b), showing different numbers of the transverse processes between the specimens; (c, d) lower part of the hind limbs from both the holotype (c) and NMNS00093-F034398 (d), showing variation in the phalanx formula between the specimens. See Figure 1 for abbreviations.

There are no notable differences in the morphology of the forelimb between the two specimens. There are one or two fewer manual phalanges per digit in the NMNS specimen, but this can be attributed to the preservation.

*Diandongosaurus* is characterized by a unique foot morphology with peculiar claws; Shang, Wu & Li (2011) considered 2-3-4-6-5 to be the pedal phalangeal formula of this taxon. The basic foot structure is the same in the NMNS specimen, but it provides further details of the claw morphology and suggests intraspecific variation of phalangeal formula (Fig. 3c, d). The ungual phalanges of first to fourth digits are larger than the penultimate phalanx, and those in second to fourth are distally pointed. The penultimate phalanges of the fourth and fifth digit are round and smaller than the other phalanges. None of the fifth digits of the two specimens retains a claw, and the fifth digit likely lacked such a claw in life. The morphology and size of the most distal phalanges of the fourth and fifth digits preserved in the NMNS specimen does not correspond well to those in the holotype. The minimum pedal phalangeal formula of the NMNS specimen is 2-3-4-5-3, although the count for the fourth and fifth digits is slightly higher in the holotype. Intraspecific variation of phalangeal formula is a common phenomenon among eosauropterygian taxa (Rieppel, 1989; Sander, 1989; Wu *et al.* 2011) and it is likely to be the case in *Diandongosaurus* as well.

#### 4. Phylogenetic relationships

As mentioned in the Introduction above, the cladistic analysis by Shang, Wu & Li (2011) essentially supported the results of Holmes, Cheng & Wu (2008) and Wu *et al.* (2011) in which the European pachypleurosaur and the Nothosauroida formed a clade, and *Wumengosaurus* was the sister taxon of this clade; *Keichousaurus* and *Hanosaurus* Young, 1972 (a pachypleurosaurid in Rieppel, 1998a, 2000) were more closely related to the Nothosauroida than to the European pachypleurosaur. Shang, Wu & Li's (2001) majority consensus found *Diandongosaurus* to be the most basal stem taxon of this lineage. These results do not conform to the phylogenies by Rieppel (2000) or Liu *et al.* (2011) in which *Keichousaurus* and *Wumengosaurus* were closely related to the European pachypleurosaur.

We reran the analysis with additional information provided by NMNS00093-F034398 and two recently described eosauropterygian taxa from China not included in Shang, Wu & Li (2011): *Dianopachysaurus* Liu *et al.* 2011 and *Qianxisaurus* Cheng *et al.* 2012. We revised the data matrix of Cheng *et al.* (2012) by incorporating the information in Holmes, Cheng & Wu (2008), Sato *et al.* (2010), Liu *et al.* (2011), Shang, Wu & Li (2011) and Li *et al.* (2011); note that our new data matrix includes the Thalattosauria, a possible sauropterygian sister taxon not included in Shang, Wu & Li (2011). The new data matrix scored 18 more characters for *Diandongosaurus*, leaving only nine missing entries for this taxon (see Appendix S1 in the online Supplementary Material



available at <http://journals.cambridge.org/geo>). The revised data matrix was analyzed using PAUP\* 4.0 beta 10 (Swofford, 2002), with all characters unordered and equally weighed.

Two additional analyses (hereafter referred to as second and third analyses) were performed to test the effect of fragmentary taxa. Fragmentary taxa with abundant missing data have been sometimes excluded in previous phylogenetic analyses, and their exclusion may improve the resolution of the cladogram but affects the branching pattern (e.g. Sato *et al.* 2010). In the second analysis, *Kwangsisaurus*, *Sanchiaosaurus* and *Chinchenia* (Rieppel, 1999) are excluded because of the high percentage of missing data (79.9%, 64.75% and 72.66%, respectively). The third analysis excluded *Hanosaurus* (49% missing data; Rieppel, 1998a) as well.

In the first analysis, with all taxa included, a heuristic search produced 12 most parsimonious trees (MPTs), with tree length (TL) of 497 steps, CI = 0.3763, and RI = 0.6837. In the strict consensus tree of the 12 MPTs (Fig. 4a), the phylogenetic relationships of *Diandongosaurus* with non-pistosauroid eosauropterygians differed considerably from those in Shang, Wu & Li (2011). The genus was found to be closely related to the Nothosauroidae, being grouped together with three fragmentary taxa (*Sanchiaosaurus*, *Kwangsisaurus*, and *Chinchenia*) to form the sister-group of the Nothosauroidae (clade B in Fig. 4a). The status of the three fragmentary taxa has been problematic, but they have been often regarded as pistosauroids in recent studies (e.g. Rieppel, 1999, 2000; Sato *et al.* 2010) and their nothosauroid affinity in this study and Cheng *et al.* (2012) was unexpected. *Keichousaurus*, *Dianopachysaurus*, the European pachypleurosaurs (clade A), *Qianxisaurus*, *Wumengosaurus* and *Hanosaurus* are successive outgroups of clade C containing the Nothosauroidae and *Diandongosaurus* with the three fragmentary taxa. The Pistosauroidae splits from the lineage of the above-mentioned taxa (clade I) at the base of the Eosauropterygia. The Eosauropterygia and the placodonts form the Sauropterygia for which the Thalattosauria is the sister taxon.

In the second analysis without *Chinchenia*, *Kwangsisaurus*, and *Sanchiaosaurus*, a heuristic search yielded 8 MPTs with TL = 487, CI = 0.3840, and RI = 0.6865. Their strict consensus does not differ much from that of the first analysis in terms of the relationships among the European pachypleurosaurs, Nothosauroidae and Pistosauroidae, but the relationships of *Keichousaurus*, *Diandongosaurus*, *Dianopachysaurus*, *Qianxisaurus*, *Wumengosaurus* and *Hanosaurus* change drastically (Fig. 4b). *Hanosaurus* appeared to be most closely related to the Nothosauroidae, and a clade consisting of *Keichousaurus*, *Diandongosaurus*, and *Dianopachysaurus* is the sister taxon of the Nothosauroidae + *Hanosaurus* clade. *Qianxisaurus* and *Wumengosaurus* remain as outgroups of the clade including the Nothosauroidae and the European pachypleurosaurs, but their order is altered so that *Qianxisaurus* is more

basal. Exclusion of the three fragmentary taxa affects tree topology outside the Sauropterygia–Thalattosauria clade as well; turtles, Lepidosauromorpha (represented by Kuehneosauridae, Rhynchocephalia and Squamata) and Archosauromorpha formed a series of successive sister taxa towards the Sauropterygia–Thalattosauria clade.

In the third analysis in which *Hanosaurus* was also excluded in addition to the three aforementioned taxa, a heuristic search also produced 8 MPTs with TL = 478, CI = 0.3912 and RI = 0.6904. The strict consensus of the 8 MPTs (Fig. 5) retained the same relationships of the European pachypleurosaurs, Nothosauroidae, and Pistosauroidae seen in the first and second analyses, whereas the relationships among the Nothosauroidae, *Diandongosaurus*, *Keichousaurus*, *Dianopachysaurus*, *Wumengosaurus* and *Qianxisaurus* differ only in that the last two forms switched their positions.

A bootstrap analysis of the first data set (all taxa included) was performed to test the confidence level of the branching pattern (Fig. 4a). The Sauropterygia and Eosauropterygia survived the analysis, but most eosauropterygian taxa form a polytomy; only the sister-taxon relationship of *Nothosaurus* and *Lariosaurus*, the monophyly of *Placodus* and *Paraplacodus*, and the monophyly and relationship among four pistosauroids, i.e. ((*Pistosaurus*, *Augustasaurus*), *Plesiosaurus*, *Yunguisaurus*), were recovered.

In summary, NMNS00093-F034398 improves the scoring of *Diandongosaurus* for the phylogenetic analysis, but the results of three analyses do not differ substantially from those of Cheng *et al.* (2012) in which only the holotype was scored. *Diandongosaurus*, *Keichousaurus*, and *Dianopachysaurus* are more closely related to the Nothosauroidae than to European pachypleurosaurs, and *Wumengosaurus* and *Qianxisaurus* are basal members of the clade of non-pistosauroid eosauropterygians. Removal of fragmentary taxa results in certain changes within and outside the Sauropterygia–Thalattosauria clade, but a nesting pattern of ((European pachypleurosaurs, Nothosauroidae), Pistosauroidae) within the Eosauropterygia is maintained in MPTs of the three analyses, although the confidence level of the eosauropterygian relationship was demonstrated to be low in the bootstrap analysis.

## 5. Discussion

### 5.a. Phylogenetic relationships

The strict consensus of our analysis with all taxa included (first analysis, Fig. 4a) indicates a close relationship of *Diandongosaurus* to the Nothosauroidae. The sister-taxon relationship between the clade of *Diandongosaurus* plus the three most fragmentary taxa (*Chinchenia*, *Kwangsisaurus*, *Sanchiaosaurus*) and the nothosauroid clade was supported by ten synapomorphies including three unequivocal characters under ACCTRAN optimization (Appendix



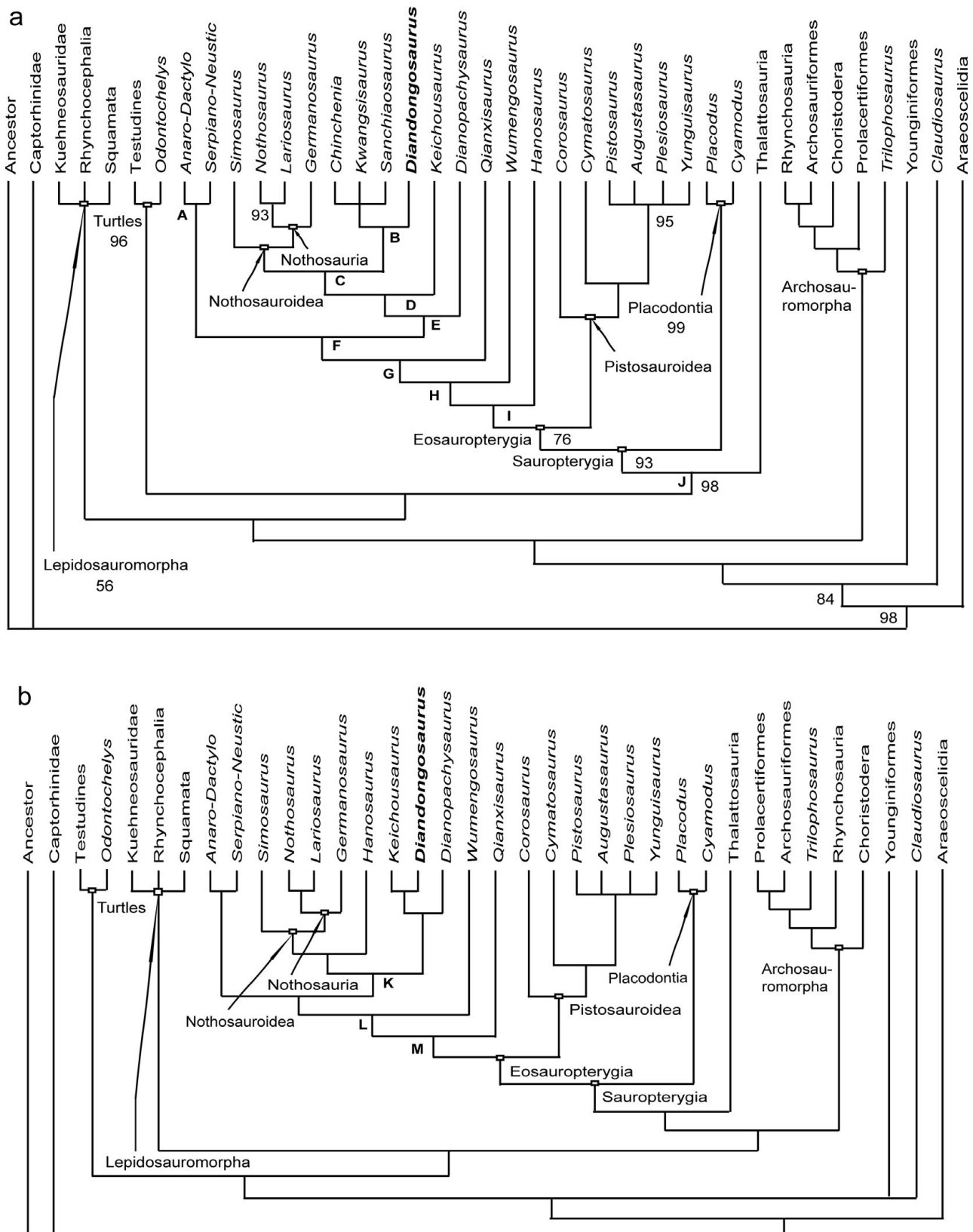


Figure 4. Strict consensus trees of (a) 12 MPTs of the first analysis with all taxa included, and (b) 8 MPTs of the second analysis without *Kwangsisaurus*, *Sanchiaosaurus* and *Chinchenia*. Arabic numbers in (a) indicate the bootstrap support values; nodes without numbers have a bootstrap support value lower than 50%. See text and Table 3 for node-based clades labeled with capital letters. Abbreviations: *Anaro* – *Anarosaurus*; *Serpiano* – *Serpianosaurus*.

S2 in the online Supplementary Material available at <http://journals.cambridge.org/geo>: the parietal skull table weakly constricted [19 (1)], the pachyostosis

of the dorsal ribs absent [72 (0)] and the bone in dermatocranium distinctly sculptured [138(0)]. Among the seven equivocal synapomorphies, fang-like teeth in

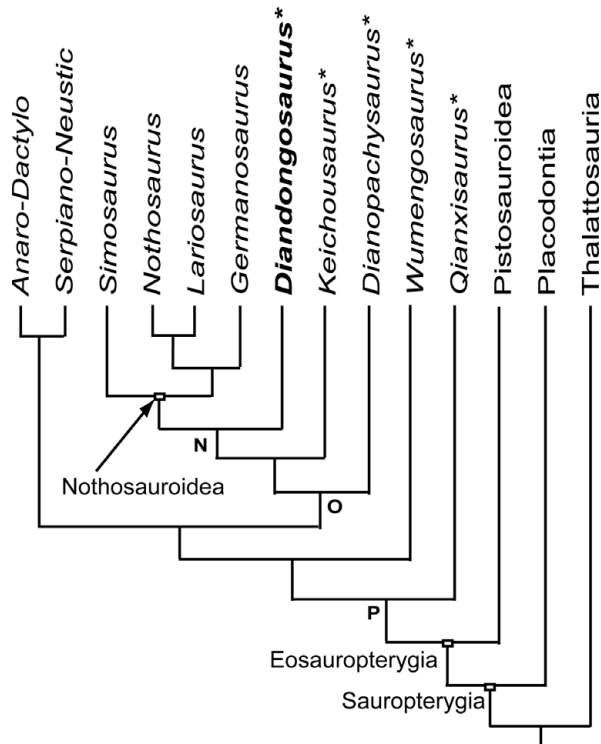


Figure 5. Part of strict consensus tree of 8 MPTs derived from the third analysis without *Hanosaurus*, *Kwangsisaurus*, *Sanchiaosaurus*, and *Chinchenia*. See Figure 4b for the interrelationships of other groups. See Figure 4 for abbreviations.

the premaxilla and anterior dentary are common in pistosauroids as well.

Successive removal of fragmentary taxa in the second and third analyses changed branching patterns of the cladograms and resulted in a rather puzzling contrast in the strict consensus trees. Removal of *Chinchenia*, *Kwangsisaurus*, and *Sanchiaosaurus* in the second analysis changed the relationships among *Diandongosaurus*, *Keichosaurus* and *Dianopachysaurus* drastically with the latter three forming a clade. In contrast, further removal of *Hanosaurus* in the third analysis essentially brought back the pattern observed in the first analysis. It is also noted that the nesting relationship of (((Nothosauroida, *Diandongosaurus*), *Keichosaurus*), *Dianopachysaurus*) is demonstrated in MPTs of the first and third analyses.

Meanwhile, comparison of synapomorphies of major clades in the three analyses suggests that influence of fragmentary taxa is limited in terms of morphological characterization of the clade despite the change of internal branching pattern (Appendix S2 in the online Supplementary Material available at <http://journals.cambridge.org/geo>). The set of synapomorphies supporting clade E of the first analysis is nearly identical to those of clade K of the second and clade O of the third analysis. The internal branching patterns of those three clades differ, but all unite the Nothosauroida with *Diandongosaurus*, *Keichosaurus* and *Dianopachysaurus* to form the sister taxon of the European pachypleurosaurs. Another

example is shown in the comparison of clades C in the first analysis and L in the second; synapomorphies differ little between the two clades, indicating the minimal role of the three fragmentary taxa (*Chinchenia*, *Kwangsisaurus*, and *Sanchiaosaurus*). Finally, sets of synapomorphies of the clades I in the first analysis, M in the second, and P in the third analysis largely overlap despite the radically different locations or absence/presence of *Hanosaurus*, indicating that this taxon has little influence on the distribution of derived character states.

Based on the consideration above, we conclude that *Diandongosaurus*, *Keichosaurus* and *Dianopachysaurus* are more closely related to the Nothosauroida than to the European pachypleurosaurs, although their exact relationships are sensitive to the inclusion of fragmentary taxa. *Wumengosaurus* and *Qianxisaurus* are outgroups of the clade including all of the above, but their order is influenced by the fragmentary taxa as well. Inclusion or exclusion of the four fragmentary taxa in this study affect branching pattern sometimes considerably, but had only limited influence in the morphological characterization of major clades.

### 5.b. Characters of possible phylogenetic significance

The presence of vomerine teeth of *Diandongosaurus* is unique among the Sauropterygia, whereas the presence of median interptergoid vacuities, maxillary fangs, lateral elements of gastralia with broadened and curved distal ends, and the anterior spike of the clavicle are variably known among the Eosauropterygia. Their possible phylogenetic significance is discussed below.

#### 5.b.1. Vomerine teeth

Vomerine teeth are common among primitive reptiles, including early diapsids such as *Petrolacosaurus*, *Youngina*, *Claudiosaurus* and *Proterosuchus* (Carroll, 1981; Reisz, 1981; Cruickshank, 1972), but are lost in many later lineages. Among the taxa related to the Sauropterygia, thalattosaurs (e.g. *Thalattosaurus*, *Nectosaurus* and *Xinpusaurus*; Nicholls, 1999; Liu & Rieppel, 2001) and primitive turtles (*Odontochelys* and *Proganochelys*; Gaffney, 1990; Li *et al.* 2008) retain them. Within the Sauropterygia, many placodonts have large palatine teeth but none on the vomers (e.g. Rieppel, 2000). Romer (1997: p. 460) mentions palatal dentition in *Lariosaurus* but we were unable to trace the source of this information. Palatal dentition is unknown in other eosauropterygians. The presence of vomerine teeth in *Diandongosaurus* is reasonably regarded as autapomorphic within the Sauropterygia.

#### 5.b.2. Openings in the palate

One of the most puzzling features of *Diandongosaurus* is the presence of two openings in the middle of the palate between the pterygoids. We referred them to as 'anterior and posterior interpterygoid vacuities'



but in quotation marks, because their homology with those in the plesiosaurs (derived pistosauroids) is quite doubtful because of their remote phylogenetic relationships. In addition, morphology of the ‘anterior interpterygoid vacuity’ differs from that in pistosauroids. Most pistosauroids have only one oval vacuity that exposes the basisphenoid and parasphenoid (e.g. Sues, 1987), and corresponds to the posterior interpterygoid vacuity in some short-necked plesiosaurs with two (i.e. anterior and posterior) openings (e.g. Williston, 1903; Andrews, 1911; Cruickshank, 1994). The morphology and location (a round pit in the middle of palate) of the ‘anterior interpterygoid vacuity’ of *Diandongosaurus* are not comparable with those in these short-necked plesiosaurs. Therefore, the ‘anterior interpterygoid vacuity’ of *Diandongosaurus* is considered to be an autapomorphy of this taxon.

Although the location of the ‘posterior interpterygoid vacuity’ of *Diandongosaurus* matches that of pistosauroids, the current phylogeny implies that it is an apomorphy of the former, because a well-defined vacuity occurs only in derived pistosauroids (*Yunguisaurus*, *Augustasaurus*, *Pistosaurus* and plesiosaurs) within the Sauropterygia, whereas it is absent in the basal pistosauroid *Cymatosaurus* (Rieppel, 1997) and in various placodonts (Rieppel, 2000). Furthermore, the small size and irregular shape of this vacuity in *Diandongosaurus* suggest that it could be the result of postmortem displacement or incomplete ossification, and more specimens are needed to confirm its taxonomic significance.

#### 5.b.3. Epipterygoid

Although the morphology of the epipterygoid has been documented in only a limited number of sauropterygians, considerable variation is known to exist. The narrow, rod-like epipterygoid of *Diandongosaurus* differs from the large, flat element in *Nothosaurus*, whereas this element is absent in *Simosaurus* (Rieppel, 1994a). Carroll & Gaskill (1985) regarded a similarly narrow rod in the skull of *Neusticosaurus edwardsi* as an epipterygoid, but Rieppel (1994b) questioned their identification. This element remains essentially unknown in other non-pistosauroid eosauropterygians such as *Wumengosaurus* and *Keichousaurus*. Outside the lineage leading to the European pachypleurosaurs and nothosauroids, the epipterygoid has a wide base among the pistosauroids, but the dorsal portion could be wide (e.g. *Augustasaurus*; Rieppel, Sander & Storrs, 2002) or narrow (e.g. *Pistosaurus*; Sues, 1987), whereas this element in *Placodus* is a distinct wide element attached to the prootic (Rieppel, 1995). Although the epipterygoid of *Diandongosaurus* adds information on the morphological variability of this element within the Sauropterygia, the variation and patchiness of information in related taxa do not give a clear pattern or trend within the group yet.

#### 5.b.4. Maxillary fangs

The presence of maxillary caniniform teeth is a characteristic of the Nothosauridae (Rieppel, 2000). *Simosaurus* lacks this feature (Rieppel, 1994a). Their presence in *Diandongosaurus* and *Keichousaurus* (Holmes, Cheng & Wu, 2008) complicates the polarity decision, and their absence in *Simosaurus* could turn out to be autapomorphic. It is difficult to confirm their condition in *Germanosaurus* and *Dianopachysaurus* for which only dorsal views of the skull are available (e.g. see alternative interpretation of the absence of maxillary fangs in *Germanosaurus* in Rieppel (1997), p.20). Distribution of this character in more basal forms and pistosauroids (e.g. absent in *Wumengosaurus* and *Corosaurus*, present in *Cymatosaurus* and *Augustasaurus*; Storrs, 1991; Rieppel, 1997; Rieppel, Sander & Storrs, 2002; Wu *et al.* 2011) suggests that this character is highly homoplastic.

#### 5.b.5. Gastralium

A single gastralium of most sauropterygians including *Diandongosaurus* consists of five elements (one medial and two pairs of lateral elements), whereas gastralium comprising three elements has been reported only in the European pachypleurosaurs *Neusticosaurus* (Carroll & Gaskill, 1985; Sander, 1989). The presence of five elements is likely to represent a plesiomorphic condition among the Sauropterygia.

The distal end of the most lateral element of the gastralium is curved and distally broadened in *Diandongosaurus*, and reminiscent of that in the European pachypleurosaurs *Serpianosaurus* (Rieppel, 1989). Only a limited number of nothosauroid taxa have comparable published information, but the presence of lateral elements with broadened and/or curved distal ends has been documented at least in *Nothosaurus jagisteus* and *Lariosaurus xingyiensis* (Rieppel, 2001; Rieppel, Li & Liu, 2003), suggesting that such gastralium might be common within this lineage. However, they are often slender, straight and taper into a pointed end in *Wumengosaurus* (Wu *et al.* 2011), pistosauroids *Corosaurus* and *Yunguisaurus* (Storrs, 1991; pers. obs.) and some thalattosaurs (Müller, Renesto & Evans, 2005; Wu *et al.* 2011), whereas they are either curved or angulated among the placodonts (Rieppel, 2000). Mapping of these states onto proposed phylogenies suggests their homoplastic nature within the Sauropterygia.

#### 5.b.6. Clavicle

The clavicle of *Diandongosaurus* is characterized by its narrowness relative to other pectoral girdle elements, the narrow medial process, and the long and pointed anterior process. The first two features are comparable to that of the holotype of *Paranothosaurus amsleri* Peyer 1939 (later synonymized with *Nothosaurus giganteus*; Rieppel, 2000), although the latter lacks the distinct

anterior process. There is a prominent anterior process in the clavicles of *Simosaurus* and some species of *Nothosaurus* and *Lariosaurus* (Rieppel, 1994a, 1998b, 2001), but they are positioned more medially and not as sharp or long as those in *Diandongosaurus*. Although the distinct morphology of sharp, long anterior process is an autapomorphy of *Diandongosaurus*, the presence of an anterior process among nothosauroid taxa may serve as additional evidence of the nothosauroid affinity of *Diandongosaurus*.

The clavicle is much larger than the scapula, and its anterolateral edge forms a corner in *Diandongosaurus*. The European pachypleurosaurs *Dactylosaurus* and *Anarosaurus* (Sues & Carroll, 1985; Rieppel & Lin, 1995; Klein, 2012), the pistosauroids *Corosaurus* and *Augustasaurus* (Storrs, 1991; Sander, Rieppel & Bucher, 1997) and placodonts (Rieppel, 2000) also have large and somewhat square clavicles. This contrasts with the condition in the European pachypleurosaurs *Neusticosaurus* and *Serpianosaurus* (Carroll & Gaskill, 1985; Rieppel, 1989; Sander, 1989), *Keichousaurus* (Lin & Rieppel, 1998), and plesiosaurs in which the ventral portion of the scapula is relatively large and the clavicle lacks the anterolateral corner. The first type may represent a primitive condition within the lineage to the European pachypleurosaurs and Nothosauroida because of its presence in placodonts and basal pistosauroids. Meanwhile, taxa with the latter type are not closely related in current and previous phylogenetic studies, and their similarities are interpreted as homoplasy.

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