

# 云南东部中三叠世始鳍龙类一新属种<sup>1)</sup>

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**摘要:**根据一保存完整的骨骼(包括头骨、下颌和全部头后骨骼)建立了鳍龙类的一新属新种——利齿滇东龙(*Diandongosaurus acutidentatus* gen. et sp. nov.)。标本采自云南省罗平县中三叠世安尼期关岭组上段。新属种既具有肿肋龙类(包括 *Dactylosaurus*, *Anarosaurus*, *Serpianosaurus* 和 *Neusticosaurus*) 吻部两侧不收缩、眶前区域长于眶后区域、眼眶大于上颞孔等典型特征,同时又具有幻龙类(包括 *Simosaurus* 和 nothosaurians) 前颌和下颌前部犬齿型齿发育、上颌具1或2个犬齿型齿等典型特征。新种的额骨和顶骨均愈合,额骨两后外侧支的末端后延超过上颞孔前缘,轭骨和鳞骨相交将眶后骨排除于下颞孔之外,方轭骨发育,锁骨前外侧缘具一突起,3对荐肋以及最前部尾肋的外侧端均未见明显收缩。这些特征也多表现出肿肋龙类和幻龙类的混合特征。此外,新种还具有一些较为独特的特征,包括前额骨和后额骨沿眼眶背缘相交,第3至第8对尾肋的长度超过荐肋,后肢末端发育异常膨大的爪趾骨。系统关系分析表明,滇东龙既不是肿肋龙类也不是幻龙类;它可能与由乌蒙龙、幻龙类和传统的肿肋龙类所构成的分支亲缘关系最近,为始鳍龙类基干类群。

**关键词:**云南罗平,中三叠世安尼期,始鳍龙类

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## A NEW EOSAUROPTERYGIAN FROM MIDDLE TRIASSIC OF EASTERN YUNNAN PROVINCE, SOUTHWESTERN CHINA

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**Abstract** A new eosauropterygian, *Diandongosaurus acutidentatus* gen. et sp. nov., is described based on a skeleton from the Upper Member of Guanling Formation (Middle Anisian) of Luoping County, Yunnan Province, southwestern China. This new species displays a combination of traits seen in nothosauroids (*Simosaurus* and nothosaurians) and pachypleurosaurs (*Dactylosaurus*, *Anarosaurus*, *Serpianosaurus*, and *Neusticosaurus*). It has an unconstricted snout, preorbital region longer than the postorbital region, and a supratemporal fenestra smaller than the orbit, as in the pachypleurosaurs. On the other hand, it bears enlarged and procumbent teeth in the premaxilla and the anterior dentary, and one or two fang-like maxillary teeth, as in the nothosaurs. In this new species, the frontals and the parietals are fused, the posterolateral process of the frontal extends posteriorly over the anterior margin of the supratemporal fenestra, the postorbital is excluded from the infratemporal fenestra by the jugal-squamosal contact, the quadratojugal is present, the clavicle has an anterolateral projection, and the three

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sacral and anterior caudal ribs are distally pinched off but not constricted. Unlike in most of other stem eosauropterygians, the prefrontal and the postfrontal meets each other along the dorsal margin of the orbit, the descending ramus of the squamosal reaches the articular condyle of the quadrate, caudal ribs 3 to 8 are elongate and longer than sacral ribs, and the ungual phalanxes of the pes are extremely dorsoventrally expanded. Our phylogenetic analysis suggests that *Diandongosaurus* is neither a pachypleurosaur nor a nothosauroid; it might be the sister group of the clade consisting of *Wumengosaurus*, the nothosauroids and those taxa traditionally considered as pachypleurosaurs.

**Key words** Luoping, Yunnan; Anisian, Middle Triassic; eosauropterygian

The marine Triassic deposits in southwestern China have yielded rich vertebrate fossils which are mainly represented by three successive faunas: the earliest Panxian fauna (middle Anisian), the middle Xingyi fauna (late Ladinian), and the late Guanling fauna (early Carnian) (Li, 2006). Most common members of those vertebrate faunas are ichthyosaurians, sauropterygians, thalattosaurians, and fishes. Among the sauropterygians, many eosauropterygians were reported from the Xingyi fauna (Young, 1958; Rieppel, 1998a; Li et al., 2002; Li and Rieppel, 2004; Lin and Rieppel, 1998; Rieppel et al., 2003; Cheng et al., 2004, 2006; Zhao et al., 2008) and the Panxian fauna (Jiang et al., 2005, 2006a, b, 2008; Shang, 2006). Scattered remains were also known from other sites (Young, 1965, 1978). Recently, diverse vertebrate fossils have been discovered from the Guanling Formation of Luoping County, southeast Yunnan Province (Zhang et al., 2008). It is contemporary with the Panxian fauna, about 110 km southwest of Panxian. This fauna is dominated by fishes but also includes reptiles and possible amphibian remains (Zhang et al., 2009). The new eosauropterygian described here was excavated from this site; its skeleton was collected from the limestone interbedded with marls of Anisian age in Da'aozi of Luoping County. Although this new eosauropterygian is known from a single skeleton, the excellent nature of its preservation provides a solid basis for its taxonomic identification and phylogenetic relationships.

Since *Keichousaurus* formerly included in the Pachypleurosauroidea (Rieppel and Lin, 1995) is closely related to the Nothosauroidea (Holmes et al., 2008; Wu et al., in press), the terms Pachypleurosauria and pachypleurosaurs in the following text will be restricted to the European taxa of *Serpianosaurus*, *Neusticosaurus*, *Dactylosaurus*, and *Anarosaurus*.

**Superorder Sauropterygia Owen, 1860**  
**Order Eosauropterygia Rieppel, 1994**  
**Family incertae sedis**  
**Genus *Diandongosaurus* gen. nov.**

**Type species** *Diandongosaurus acutidentatus* gen. et sp. nov.

**Diagnosis** Same as the only known species.

***Diandongosaurus acutidentatus* gen. et sp. nov.**

**Holotype** IVPP (Institute of Vertebrate Paleontology and Paleoanthropology) V 17761, a complete skeleton with the skull articulated.

**Etymology** The generic name is derived from "Diandong", meaning the eastern Yunnan where the fossil site is located. The specific name is derived from the Latin *acutidens* for sharp teeth.

**Type locality and horizon** Da'aozi Village, Luoping County, Yunnan Province, P. R. China. The Upper Member of the Guanling Formation in the conodont *Nicoraella kockeli* Zone; Pelsonian, middle Anisian, Middle Triassic (Zhang et al., 2009).

**Diagnosis** A small sized eosauropterygian differs from others in the combination of following characters. Premaxillary and anterior dentary teeth enlarged and fang-like; maxilla with one

or two fangs followed by a distinctly smaller conical teeth; snout short with no constriction; supratemporal fenestra smaller than orbit; prefrontal contacting postfrontal along dorsal orbital margin, excluding fused frontal from orbit; interorbital bridge broad; posterolateral process of frontal extending posteriorly over anterior margin of supratemporal fenestra; pineal foramen more anteriorly positioned than supratemporal fenestra; jugal and squamosal meeting each other to exclude postorbital from infratemporal fenestra; descending ramus of squamosal reaching articular condyle of quadrate; quadratojugal present; distinct trough on dorsal surface of retroarticular process; vertebral column consisting of 19 cervical, 19 dorsal, three sacral, and about 40 caudal vertebrae; distal end of anterior caudal ribs not tapering off and caudal ribs 3 to 8 elongate, longer than sacral ribs; clavicle with an abrupt anterolateral process; entepicondylar foramen absent; two ossified carpals; two ossified tarsals; pes unguis phalanx extremely expanded; manual phalangeal format 2-4-5-6-3; and pes phalangeal format 2-3-4-6-5.

**Morphological description** IVPP V 17761 is a complete and well preserved skeleton (Fig. 1). It is relatively small in size (Table 1). The total length of V 17761 is 285 mm from the tip of the snout to the end of the tail. The skull is exposed in dorsal view, the cervical to anterior dorsal series of the vertebral column is exposed in left lateral view, and the other parts of the skeleton are exposed in ventral view.

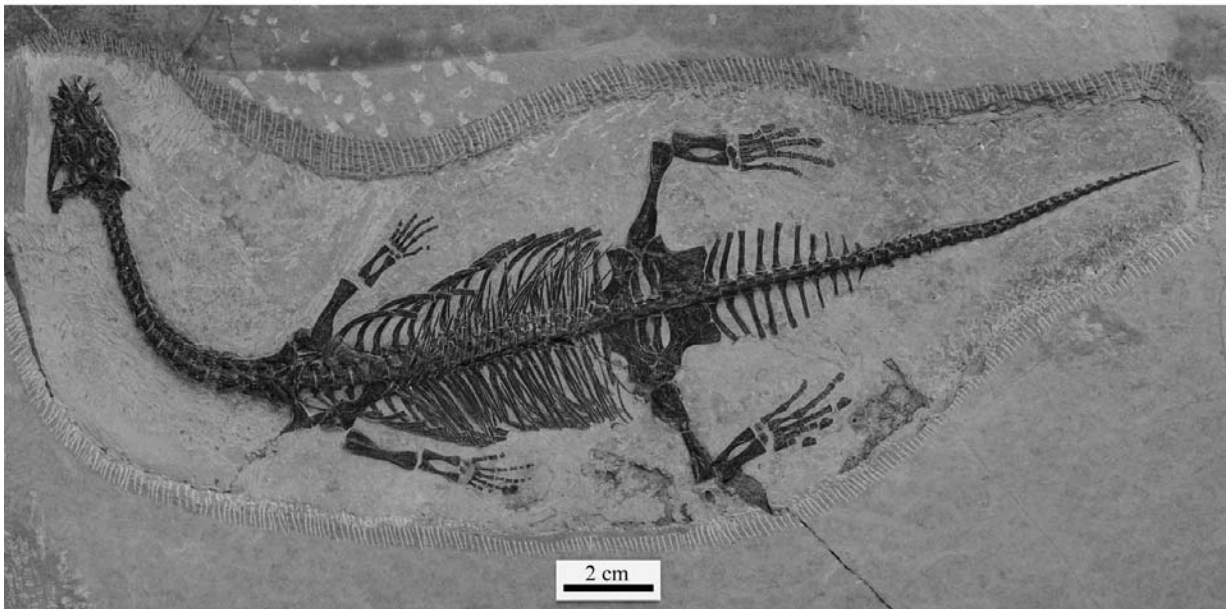


Fig. 1 Skeleton of *Diandongosaurus acutidentatus* gen. et sp. nov. (holotype, IVPP V 17761)

**Skull** The skull of V 17761 is occluded with the lower jaw (Fig. 2). It is dorsoventrally flattened and distorted toward the right side so that some of the skull elements of that side were damaged. The external naris, the orbit and the supratemporal fenestra are all oval-shaped. As in the pachypleurosaurs, the orbit is larger than the supratemporal fenestra, and the preorbital region of the skull is distinctly longer than the postorbital region (Table 1). However, the relative size of the postorbital arch is narrower than in the most genera of the Pachypleurosauridae (Rieppel, 2000), indicating a relatively large supratemporal fenestra. The ventrally opened infratemporal fenestra is the largest among the skull openings, with its posterior margin nearly vertical in orientation. The pineal foramen is oval in outline and almost shifted to the anterior half of the parietal, with its anterior edge somewhat exceeding the supratemporal fenestra.

The premaxillary portion of the rostrum is short and blunt, as is the case in the pachypleurosaurs, except for *Serpianosaurus* (Rieppel, 1989). The premaxillae are paired bones with larger nasal processes between the external nares. The nasal processes extend posteriorly beyond

the anterior margin of the orbit and insert into the frontal. The premaxilla forms the anterior and dorsal borders of the external naris. The premaxilla meets the maxilla at the anterolateral corner of the external naris.

**Table 1 Selected skeletal measurements of the holotype (IVPP V 17761) of *Diandongosaurus acutidentatus* gen. et sp. nov. (mm)**

skull and mandible			
length from the tip of the snout to		length of retroarticular process	>2
anterior margin of external naris	4	width across (with measurement error due to the	
anterior margin of orbit	10.5	distorted compression)	
anterior margin of supratemporal fenestra	16.7	widest before external naris	6
occipital ridge	19	widest behind orbit	12.5
lower jaw articulation	24	articulation of lower jaw	16.8
length between external naris and orbit	2.8	minimal width of bony bridge between	
length from orbit to supratemporal fenestra	0.9	external nares	1.6
length of mandible from symphysis to end of		orbits	3
retroarticular process	27	supratemporal fenestra	1.5
postcranial elements			
length of neck	65	distance from proximal end of humerus to	
length of trunk	85	distal end of 4 <sup>th</sup> digit	41
length of tail	112	length of ulna	8
distance from glenoid to acetabulum	73	length of radius	9.1
width between glenoids	20	length of 4 <sup>th</sup> metacarpal	4.2
width between acetabulae	27	length of 4 <sup>th</sup> digit	9
length of posterior cervical centrum	3.9	distance from proximal end of femur to	
length of anterior dorsal centrum	4	distal end of 4 <sup>th</sup> toe	60.5
length of sacral centrum	4	length of femur	23
width of sacral centrum	2.7	length of tibia	11.6
length of anterior caudal centrum	4	length of fibula	12
width of anterior caudal centrum	2.6	length of 4 <sup>th</sup> metatarsal	7.5
length of humerus	16	length of 4 <sup>th</sup> toe	12.5

The maxilla is a large bone. It forms the ventral and posteroventral margins of the external naris. The ascending process of the maxilla meets the nasal posterior to the external naris and forms an oblique suture with the prefrontal anterior to the orbit. Posteroventrally, the maxilla forms a tapering process that extends backwards to a level below the posterior margin of the orbit and underlies the jugal (Fig. 2).

The nasals are fully separated from each other by the posterodorsal processes of the premaxillae, as in *Keichousaurus* (Holmes et al., 2008). It is a small bone, with an anterior end narrow and a posterior end broad. The bone only enters the posterodorsal corner of the external naris. Posteriorly, the nasal contacts the frontal and prefrontal through a zigzagged edge.

The frontals are fused into one, butterfly-like in dorsal view, The bone does not enter the orbit because of the contact of the prefrontal with the postfrontal along the dorsal orbital margin, a peculiar character that does not appear to be closely related to the relatively large orbits atypical of the pachypleurosaurs. Posterolaterally, the frontal forms a stout process that extends between parietal and postfrontal and does not enter the anteromedial margin of the supratemporal fenestra, a similar situation seen in the pachypleurosaurs and the pistosauroid *Corosaurus* (Storrs, 1991), but well beyond the anterior margin of the pineal foramen as in *Wumengosaurus* (Wu et al., in press).

The parietals are partly fused; they are sutured anteriorly to the pineal foramen. The bone is anteriorly narrow and tapers off, inserting into the frontal. The anterolateral process of parietal contacts the postorbital along the anterior margin of the supratemporal fenestra. Posteriorly,



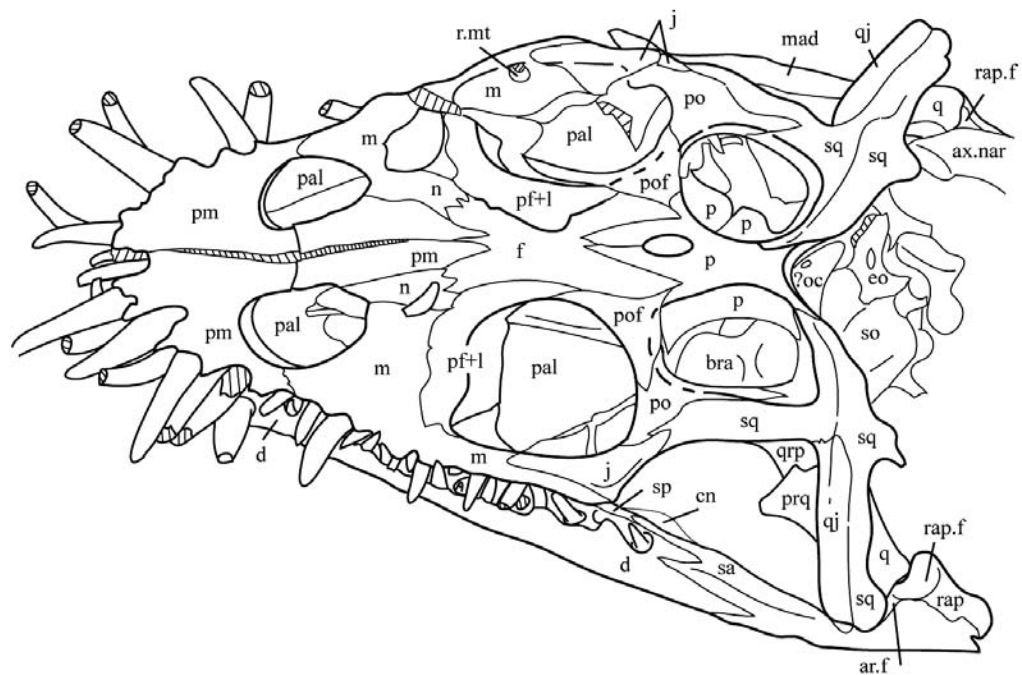
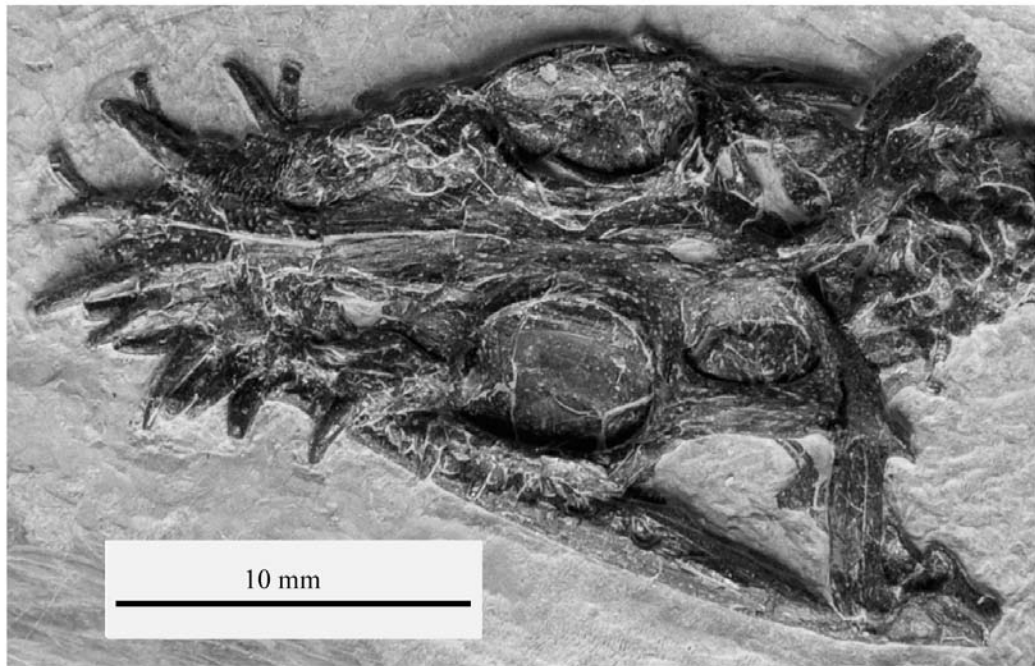


Fig. 2 Skull and mandible of *Diandongosaurus acutidentatus* gen. et sp. nov. (IVPP V 17761)

Photo and outline of the photo in dorsal view

Abbreviations: ar. f. articular fossa 关节窝; ax. nar. axial neural arch 枢椎神经弓; bra. braincase 脑颅; cn. coronoid 冠状骨; d. dentary 齿骨; eo. exoccipital 外枕骨; f. frontal 额骨; j. jugal 颞骨; m. maxilla 上颌骨; mad. mandible 下颌骨; n. nasal 鼻骨; oc. occipital condyle 枕髁; p. parietal 顶骨; pal. palatine 腭骨; pf+l. prefrontal+lacrimal 前额骨+泪骨; pm. premaxilla 前颌骨; po. postorbital 眶后骨; pof. postfrontal 后额骨; prq. pterygoid ramus of quadrate 方骨翼骨支; q. quadrate 方骨; qj. quadratojugal 方颞骨; qrp. quadrate ramus of pterygoid 翼骨方骨支; rap. retroarticular process 反关节突; rap. f. fossa on retroarticular process 反关节突上的窝; r. mt. root of a maxillary tooth 上颌齿根部; sa. surangular 上隅骨; so. supraoccipital 上枕骨; sp. splenial 夹板骨; sq. squamosal 鳞骨

the parietal is constricted between the supratemporal fenestrae and forms a curved occipital edge in dorsal view. The skull table is narrower than known species of pachypleurosaurs. The posterolateral processes is short, contacting the medial process of the squamosal. The parietal forms the entire medial portion of the fossa of the supratemporal fenestra. The contribution of the parietal, with the squamosal, to the occiput is set off from the skull table by a ridge that extremely concaved and marks the facet for the insertion of the epiaxial muscles of the neck region.

The prefrontal is most probably fused with the lacrimal. Its dorsal and dorsolateral portions are slightly expanded, showing an inflated appearance, whereas its ventral portion, forming the anterior margin of the orbit as it curves down towards the palate, is somewhat set off. Posterodorsally, the prefrontal forms a tapering process to contact the postfrontal bone at the midway of the dorsal margin of the orbit (Fig. 2), as in the pistosauroid *Cymatosaurus* (Rieppel, 1997). The contact of the prefrontal with the postfrontal, in association with the frontal, makes a broad interorbital bridge, relatively much wider than that in the pachypleurosaurs and nothosauroids.

The postfrontal constructs the dorsal part of the narrowed postorbital arch and forms a tapering anterodorsal process to meet the prefrontal along the posterodorsal margin of the orbit. In contrast to the situation of the most pachypleurosaurs, the postfrontal is excluded by the contact of the anterolateral process of the parietal with the postorbital from the central opening but not the fossa of the supratemporal fenestra. The postfrontal-frontal suture is convex laterally and the postfrontal-postorbital suture is sharply curved medially. Posteriorly, the postfrontal meets the parietal within the supratemporal fossa.

The postorbital is roughly a triradiate bone. The anteroventral process forms the posterior margin of the orbit and is distally overlapped by the jugal. The anteromedial process forms the lateral half of the postorbital arch. The posterior process is elongate and forms most of the lateral margin of the supratemporal fenestra, as in *Anarosaurus* (Carroll, 1981), *Dactylosaurus* (Sues and Carroll, 1985) and *Keichousaurus* (Young, 1958; Lin and Rieppel, 1998). Posteriorly, the process tapers into a pointed tip to imbed in the squamosal.

The jugal is 'L'-shaped in lateral view, setting on the posterior process of the maxilla and defining the posteroventral margin of the orbit and the anteroventral border of the infratemporal fenestra. It extends anteriorly up to a level shortly beyond the midpoint of the ventral margin of the orbit. The ascending process of the bone forms the lower half of the postorbital bar; it contacts the postorbital and overlaps the anterior tip of the squamosal dorsally as in the specimen NME 480000130 of *Anarosaurus heterodontus* (Klein, 2009).

The squamosal is a large, irregular element, with four processes of different length. The anterior process embraces the posterior process of the postorbital and defines the dorsal margin of the infratemporal fenestra; its anteroventrally curved tip extends to a level exceeding the anterior margin of the supratemporal fenestra and meeting the jugal to exclude the postorbital from the infratemporal fenestra. The posteromedial process forms the most part of the posterior margin of the supratemporal fenestra and distally tapers off and meets the posterolateral process of the parietal. The descending process of the squamosal is elongate and extends ventrally to reach the lateral side of the articular condyle of the quadrate, unlike in the pachypleurosaurs where the process is short and tapers off before reaching the quadrate condyle (Carroll and Gaskill, 1985; Rieppel, 1989; Sander, 1989). The short posteromedial process of the squamosal extends ventrally and possibly participates in the formation of the occiput.

The quadratojugal is a strap-like bone. It is situated vertically against the anterior side of the descending process of the squamosal and forms the entire posterior margin of the infratemporal fenestra as in the pachypleurosaurs (Carroll and Gaskill, 1985; Rieppel, 1989; Sander, 1989).

The quadrate is limitedly exposed, with only the ventromedial part of the body and the

pterygoid ramus seen in lateral view (Fig. 2). As in the pachypleurosaurs, the mandibular condyle of the quadrate extends into a posteriorly projection, a trait that is associated with the suspension of a tympanum. In contrast to the condition of *Serpianosaurus* (Rieppel, 1989) and *Neusticosaurus* (*Pachypleurosaurus*, Carroll and Gaskill, 1985), no distinct posterior quadrate notch present, but with an excavation on the dorsal surface of the quadrate posterior projection. The tympanum, if present, may have attached to the posterior edge of the descending process of the squamosal. Anteromedially, the pterygoid ramus overlaps the quadrate ramus of the pterygoid.

The braincase is represented by the supraoccipital and the exoccipital only. They were articulated with one another and somewhat displaced towards the left side. This displacement exposed the part of the occipital condyle (Fig. 3). The supraoccipital is a broad bone in occipital view, with its dorsal part slightly narrower than the ventral part. Its occipital surface is convex, with a low but broad middle ridge. It is clear that the concave ventral edge of the bone forms the dorsal margin of the foramen magnum, as in other eosauropterygians, such as the pachypleurosaurs and *Keichousaurus*.

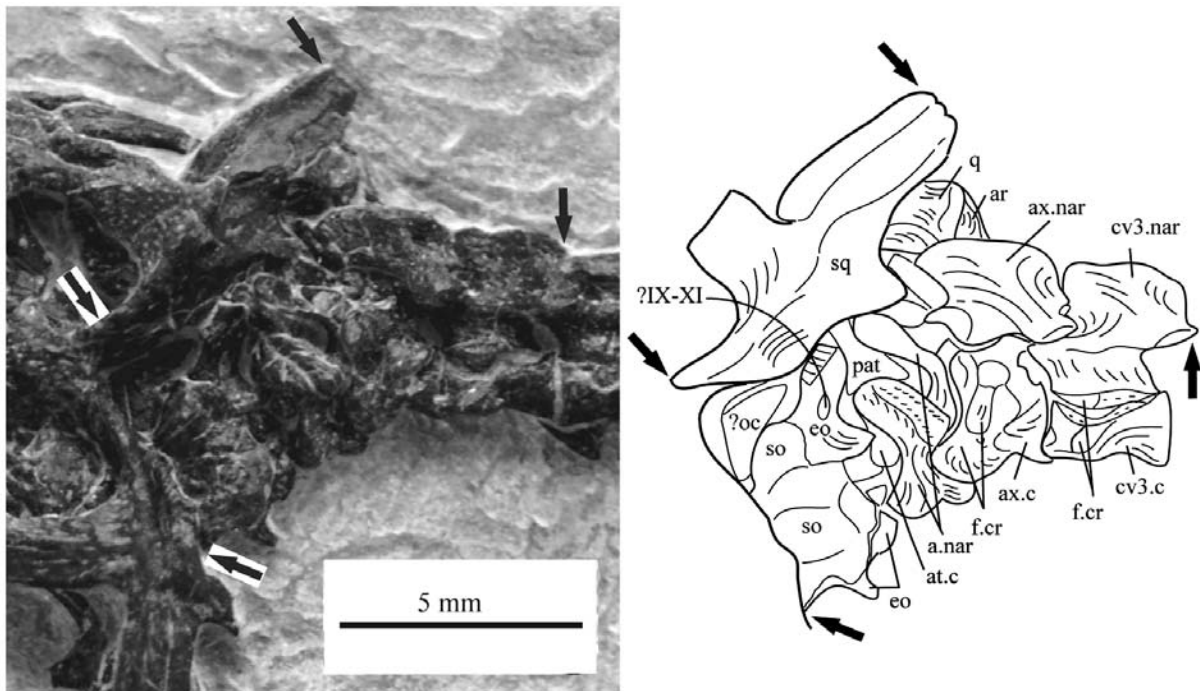


Fig. 3 Photo and outline of the photo of some elements of the braincase and the first three cervical vertebrae of *Diandongosaurus acutidentatus* gen. et sp. nov. (IVPP V 17761) in dorsal view  
Abbreviations: a. nar. atlantal neural arch 环椎神经弓; ar. articular 关节骨; at. c. atlantal centrum 环椎椎体; ax. c. axial centrum 枢椎椎体; ax. nar. axial neural arch 枢椎神经弓; cv3. c. centrum of the 3<sup>rd</sup> cervical vertebra 第三颈椎椎体; cv3. nar. neural arch of the 3<sup>rd</sup> cervical vertebra 第三颈椎神经弓; eo. exoccipital 外枕骨; f. cr. articular facet for cervical rib 颈肋关节面; ? oc. ? occipital condyle ? 枕髁; pat. proatlas 前环椎; q. quadrate 方骨; so. supraoccipital 上枕骨; sq. squamosal 鳞骨; ? IX-XI. foramen for the 9<sup>th</sup> to 11<sup>th</sup> cranial nerves ? 第九-第十一脑神经孔; arrows indicating the equivalent positions between the photo and line drawing

The exoccipital is an irregular bone. It is strongly constricted at the middle portion and broadens at both the medial and lateral ends. The occipital surface of the bone is concave-convex. Medially, the bone becomes thick and forms the lateral margin of the foramen magnum. Laterally, the paroccipital process is somewhat damaged. Only one foramen is confirmed, which is relatively large and possibly for the exit of cranial nerves IX-XI.

**Mandible** The mandible is partly exposed on the left side (Fig. 2). Its anterior portion is entirely covered by the upper jaw and its elements are largely obscured by the way of preservation. The dentary is relatively longer than in the European pachypleurosaurs, such as *Serpianosaurus* and *Neusticosaurus* (Sander, 1989; Rieppel, 1989). It extends backwards to a level exceeding the midpoint of the infratemporal fenestra as in *Keichousaurus* (Holmes et al., 2008). The bone appears anteriorly shallow and posteriorly deep, with a forked posterior end which differs from that of the pachypleurosaurs and *Keichousaurus*. The posterodorsal process of the fork is much shorter than the posteroventral one, the former inserting into the surangular and the latter into the angular. The dentary sutures with the surangular and angular forming therefore a sharply zigzagged line.

The surangular extends anteriorly through a narrow process along the dorsal margin of the mandible to the medial side of the last dentary tooth where it is abut the medially positioned coronoid (Fig. 2). Posteriorly, the surangular forms the lateral wall of the articular fossa and extends to the posterior end of the retroarticular process. The dorsal margin of the bone is slightly convex. The surangular-angular suture is not clear but distinguishable. For the angular, only its most dorsal portion is exposed on the lateral side.

The articular is still articulated with the quadrate, its retroarticular process is well exposed. The process is stout and posteriorly truncated, much shorter than in the pachypleurosaurs and *Keichousaurus* in which the process terminates by a pointed end. There is a fossa just posterior to the articular fossa on the dorsal surface of the process (Fig. 2), as in the aforementioned taxa but relatively smaller.

The coronoid is partly visible on the medial side of the mandible; it appears strap-like, with a convex ventral margin and does not form a pronounced dorsal process (Fig. 2). No further information is observable owing to the way of preservation.

**Dentition** As in the nothosauroids *Lariosaurus* and *Nothosaurus* (Rieppel, 2000), each premaxilla carries a total of five teeth, which are enlarged, fang-like, strongly procumbent, and with vertical striations on the crown. The 1<sup>st</sup>, 3<sup>rd</sup>, and 5<sup>th</sup> right and the 2<sup>nd</sup> and 4<sup>th</sup> left premaxillary teeth are fully grown, functional teeth. As in a *Nothosaurus* species (Shang, 2007), the tooth replacement of the premaxilla possibly occurred in the manner of an alternate and asynchronous order.

One or two caniniform teeth present on the maxilla. It is large, with vertical striations on the crown as in the premaxillary teeth. The precanine maxillary teeth and postcanine maxillary teeth are small and same in size. They are closely implanted, forming a dense palisade as in a *Nothosaurus* species (Shang, 2007). The exact number of the maxillary teeth cannot be determined because of the mandibular occlusion, there are possible 3 precanine and 10 postcanine maxillary teeth.

As in the premaxillae, the anterior dentary fangs are distinctly enlarged. The dentary tooth row extends backward to a level well beyond the anterior margin of the infratemporal fenestra.

**Vertebrae and ribs** There are 38 presacrals, three sacrals and approximately 40 caudals in the new taxon. As preserved, there are 19 vertebrae anterior to the interclavicle, of which the 19<sup>th</sup> bears a short, double headed rib. The rib of the 20<sup>th</sup> vertebra is much longer than that of the 19<sup>th</sup>. Although the proximal portion of the 20<sup>th</sup> rib is covered by the shoulder girdle, it appears that the transition of the double-headed cervical ribs to the single-headed dorsal ribs takes place at the 20<sup>th</sup>. Based on the rib length, the first 19 vertebrae are considered as belonging to the cervical series.

The atlas is represented by its neural arches which are disarticulated and slightly displaced (Fig. 3). The arch is strongly waisted and bowed laterally, with the ventral portion thickened to articulate the atlantal centrum. The spine portion of the arch is broadened, with a dorsomedian tip to approach the counterpart from the other side. It is clear that two arches do not physically



meet each other. Anterior to the left neural arch is the intercentrum which is partly exposed. Anterior to the two arches is a triangle-shaped bone, which is identified as the proatlas.

The axis is well exposed. Its suture between the neural arch and centrum is open. The axial centrum is laterally compressed and bears a facet for the rib near its anterolateral margin. The facet is deeply concave and extends from the centrum over to the base of the neural arch. The neural arch is characterized by a broad, ax-like spine. The odontoid process of the axis is entirely covered by displaced atlantal arches.

The cervical centra are constricted medially and the length of the centra decreases progressively. The length of the neural spine also decreases progressively anterior to the base of the neck. They are rhomboidal and tilt posteriorly. Toward the base of the neck the parapophyses become more prominent. The anterior margin of the base of the neural spine fits into the posterior margin of the more anterior vertebrae between flat and wide zygapophyses.

The dorsal centra are consistent and constricted medially also. The parapophyses are not abruptly lost in the trunk region, as in *Neusticosaurus* (Carroll and Gaskill, 1985; Sander, 1989). In the anterior dorsal region, both centrum and arch contributed to the transverse process, and the arch contributing progressively more to the latter. The neurocentral suture passes through the transverse process in the anterior dorsal vertebra centra (the 21<sup>st</sup> to 23<sup>rd</sup>). In the 26<sup>th</sup> vertebra, the articular facet of the rib moves entirely up onto the neural arch. The transverse processes are broad at the base and form bluntly rounded articular surfaces facing laterally. They extend well beyond the centrum in the anterior trunk vertebrae, and appear to become shorter more posteriorly.

The sacral vertebrae continue the pattern of the dorsals, with the neural arch to contribute to the transverse processes mainly.

The caudal centra are progressively diminish in size backwards. In the middle part of the caudal region, there are longitudinal keels on the ventral surfaces of the centra. Although the neural arch continues to contribute to the transverse processes in the anterior caudals, these processes progressively shift down on to the centrum more posteriorly. The transverse processes also diminish in size from front to back. The 14<sup>th</sup> caudal vertebra is the last to bear a transverse process.

As in the pachypleurosaurs, cervical ribs developed a distinct anterior process close to the articular heads. Throughout the trunk, the dorsal ribs are single-headed, having ventrally directed shaft and flat rib end. Pachyostosis is absent in dorsal rib, as in *Anarosaurus* and *Dactylosaurus* (Rieppel and Lin, 1995) and most nothosaurs (Rieppel, 2000). The sacral ribs are partly covered by the pubis and ischium. There are three pairs of the ribs converging to the acetabulum, as in the pachypleurosaurs and *Keichousaurus*, indicating at least three sacral vertebrae were present in life. The sacral ribs are not ankylosed to the sacral vertebrae, and show slightly expanded distal and proximal heads.

The length of the caudal ribs increases from the first to third caudal vertebrae. The 4<sup>th</sup> through 6<sup>th</sup> caudal ribs are of nearly constant size, whereas the 7<sup>th</sup> to 11<sup>th</sup> caudal ribs decrease rapidly in length. The anterior caudal ribs are of similar character to the sacral ribs, but they are flatter, longer, and with distal end less expanded than the proximal end. As in the trunk and sacral region, no pachyostosis appeared in the caudal ribs.

The gastralia are well-preserved. Each gastral set consists of five elements, the 'V'-shaped median one and two slender lateral ones, which correspond in structure to those of the pachypleurosaurs or *Keichousaurus*. As in *Anarosaurus* and *Serpianosaurus* (Rieppel, 1989), there are two gastral ribs per vertebral segment.

**Pectoral girdle and forelimb** The morphology of the pectoral girdle conforms to the general pattern of sauropterygians (Fig. 4). The interclavicle is preserved in ventral view; it is weakly developed and roughly arrowhead-like in outline. It is anteriorly very convex and poste-

riorly strongly concave, with a posterior stem much reduced and just knob-like. The anterior margin is entirely occupied by the clavicle facet which meets its counterpart of the other side. This indicates that two clavicles meet each other along the midline anterior to the interclavicle, as in some of the pachypleurosaurs such as *Neusticosaurus* (Sander, 1989).

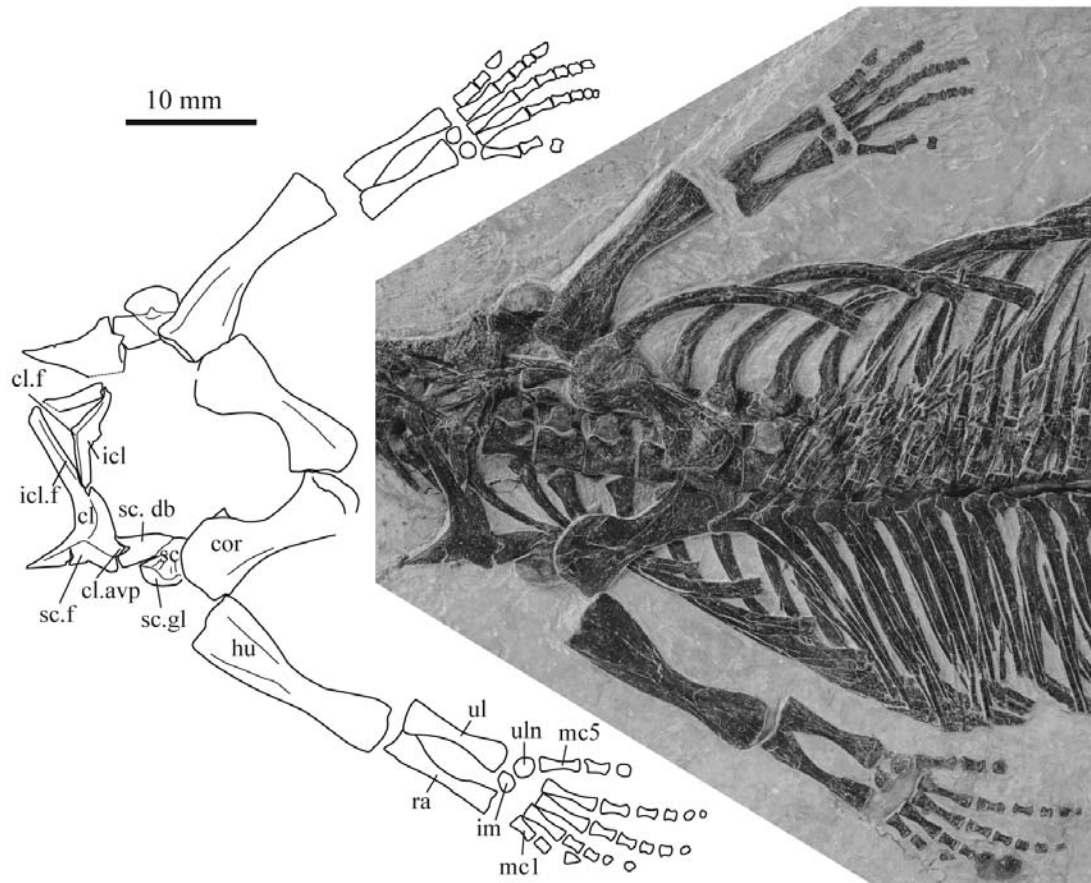


Fig. 4 Photo and outline of the photo of pectoral girdle and forelimb of *Diandongosaurus acutidentatus* gen. et sp. nov. (IVPP V 17761) in ventral view

Abbreviations: cl. clavicle 锁骨; cl. avp. anteroventral process of clavicle 锁骨前腹侧突; cl. f. facet for clavicle 锁骨关节面; cor. coracoid 乌喙骨; hu. humerus 肱骨; icl. interclavicle 间锁骨; icl. f. facet for interclavicle 间锁骨关节面; im. intermedium 中间腕骨; mc1. metacarpal 1 第一掌骨; mc5. metacarpal 5 第五掌骨; ra. radius 桡骨; sc. scapular 肩胛骨; sc. db. dorsal blade of scapular 肩胛骨背突; sc. f. facet for scapular 肩胛骨关节面; sc. gl. glenoid on scapular 肩胛骨肩臼部; ul. ulna 尺骨; uln. ulnare 尺腕骨

The right clavicle is almost complete, with an 'L'-shaped outline, similar to that of *Serpianosaurus* (Rieppel, 1989:fig. 8a). It was disarticulated with the interclavicle and the scapular. The clavicle is exposed in posteromedial view so that its scapular process points anteriorly (Fig. 4). The scapular process is shorter but broader than the ventral process that articulates the interclavicle. The ventral process is slender, relatively narrower than that of *Serpianosaurus*. There is a small process, anteroventral process, from the anterior edge of the junction of the two processes, which is not present in any of the pachypleurosaurs and *Keichousaurus*. In the nothosauroid *Simosaurus gaillardoti*, a similar small process projecting from the anterior margin of the clavicle had been reported (Rieppel, 1994). Facets for the scapular and interclavicle are clearly marked along the lateral margin of the scapular process and the posteromedial edge of the ventral process.

The scapular is preserved in ventral and slightly medial view on both sides, with the posterodorsal blade directing anteriorly (Fig. 4). The glenoid portion is expanded and stout, and

the narrow coracoid facet is covered by the coracoid (right) or humerus (left). The posterodorsal blade underlies the anteroventral process of the clavicle. As a whole, the scapular appears similar in morphology to that of *Wumengosaurus* (Jiang et al., 2008; Wu et al., in press).

The coracoid is well exposed on both sides. It is a characteristically ‘waisted’ bone, with a strongly concave anteromedial margin opposing the less distinctly concave posterolateral margin. Both the proximal and distal ends are roughly equally expanded. It is much longer than broad, more similar to that of *Serpianosaurus* (Rieppel, 1989; fig. 8c) when compared with those of other pachypleurosaurs. The coracoid foramen is not clear, which is possible located at the coracoid-scapular suture, as in many other eosauroptrygians.

The fore-limb is well-preserved in ventral view (Fig. 4). The humerus is shorter than the femur (Table 1). It is only weakly curved. Both the proximal and distal ends are expanded although the latter is to a less degree. The shaft is slightly concave on the radial side but very so on the ulnar side. The articular surface of the distal head is smoothly convex and evenly slightly angulated to separate the contact areas with the radius and the ulna. As in the general sauroptrygians, the antebrachium was held at a very low angle from the humerus. The entepicondylar foramen that usually presents in the pachypleurosaurs is absent.

The ulna and radius are relatively gracile, as in *Dactylosaurus* (Rieppel and Lin, 1995) and *Neusticosaurus* (Sander, 1989). The ulna is slightly shorter than the radius. Both ends of the ulna are equally expanded, and both lateral and medial sides of the shaft are nearly symmetrically concave. The distal articular surface is convex. The lateral (outer) margin of the radius is less concave than the ulnar margin, and the proximal end, which is partly overlapped by the ulna, is broader than the distal end and even broader than that of the ulna.

There are two ossified elements in the carpus, as in the pachypleurosaur *Serpianosaurus*, *Neusticosaurus peyeri* and *N. pusillus* (Sander, 1989). They are flat and rounded in outline. The larger and laterally positioned one is the ulnare and the other is the intermedium.

The metacarpals are well-preserved on both sides. As in *Neusticosaurus* (Sander, 1989), metacarpal 1 is much shorter than the others, the metacarpals 3 and 4 are of nearly equal length, and metacarpal 5 is slightly shorter than metacarpal 2. The interosseous space between metacarpals 4 and 5 is broadest, and as in *Keichousaurus* (Lin and Rieppel, 1998), the metacarpals 2 and 3 bow toward the ulnar side, and the fifth bows toward the opposite direction.

The phalangeal elements are complete in digits 1 to 3 although the unguis phalanx of digit 3 is damaged. Digit 4 on both sides has five phalanges preserved and is ended by a small round element; the latter is comparable to the penultimate of digit 4 of the pes. This indicates that the unguis phalanx of digit 4 of the manus was lost. Digit 5 has two phalanges preserved on both sides, with the ungula element of the left side and the second phalanx of the right side missing, respectively. As a whole, the forelimb most probably had a phalangeal formula of 2 – 4 – 5 – 6 – 3. The unguis phalanx is best preserved in digits 1 and 2, which is mediolaterally compressed and dorsoventrally expanded, blade-like in shape (Fig. 4). Metacarpals 3 and 4 are similar in length but their first phalanx is not the case, being evidently shorter in the former than in the latter.

**Pelvic girdle and hind limb** The pelvic girdle has a standard sauroptrygian (especially pachypleurosaur) plan (Romer, 1956), with a small ilium and a large plate-like pubis and ischium (Fig. 5). For the ilium, its thickened ventral side is only exposed on the right side, showing facets that have different orientations, serving for contacting the pubis and the ischium.

The pubis is nearly symmetrically constricted at its middle portion and expanded towards its extremities. The proximal end articulates with the ilium and ischium. The obturator foramen is a narrow slit opening at the facet for the ischium. It is relatively medially positioned than in most pachypleurosaurs such as *Neusticosaurus* and *Serpianosaurus* (Sander, 1989; Rieppel, 1989).

The ischium is waisted in the proximal portion, from which it expands to a flattened rhom-

boidal distal plate. The proximal margin of the ischium is thickened and weakly angulated into two facets for the ilium (the wider one) and the pubis (the narrower one). The medial margin of the distal plate is straight, meeting the counterpart from the opposite side along the midline, whereas the posteromedial portion of the distal plate is slightly convex. The thyroid fenestra is a large oval area. As a whole, the ischium is morphologically more comparable to that of *Neusticosaurus peyeri* (Sander, 1989:fig. 22a).

The left femur is complete; its shaft is nearly symmetrically constricted, with the expanded proximal and distal ends. A horizontal extension near the posterior proximal end may have served for the insertion of the muscle, iliofemoralis, as in *Serpianosaurus* (Rieppel, 1989) and *Neusticosaurus* (Sander, 1989). Again as in the aforementioned pachypleurosauroids, the distal articular surface is oriented distally only, excluding the possibility of the ventral articulation of the lower hind limb.

The tibia and fibula is well-preserved on both sides; the former is somewhat overlapped by the latter at the proximal end. The two bones closely resemble their counterparts in *Neusticosaurus* (Carroll and Gaskill, 1985; Sander, 1989). The fibula is longer and more pronouncedly

curved than the ulna, while the latter is stouter than the former (Fig. 5). The shaft of the tibia is constricted nearly symmetrically; its proximal end is slightly more expanded than the distal end. The proximal end of the fibula is possibly as broadly expanded as the distal; its shaft is laterally convex and medially very concave.

The astragalus and calcaneum are only the ossified elements of the tarsus and the former is bigger than the latter (Fig. 5). The facets of the astragalus for the articulation with the tibia and fibula are flat. The other margins of the astragalus are convex, forming an oval outline in ventral view. The calcaneum is of an essentially circular outline.

The metatarsals increase in length from the metatarsal 1 to 4, and metatarsal 5 is of about the length of metatarsal 2 but its shaft is slightly slenderer (Fig. 5), as in *Neusticosaurus peyeri* (Sander, 1989:fig. 23B, C). The proximal ends of adjacent metatarsals are overlapped one another. Unlike in the pachypleurosaurs *Neusticosaurus* (Carroll and Gaskill, 1985; Sander, 1989) and *Serpianosaurus* (Rieppel and Lin, 1995), there is no distinct expansion occurred at the proximal end of the first metatarsal (c. f. the right pes).

The pes on both sides are nearly complete and all digital elements are well-preserved except for digit 5. It is peculiar that the phalanx (penultimate) just proximal to

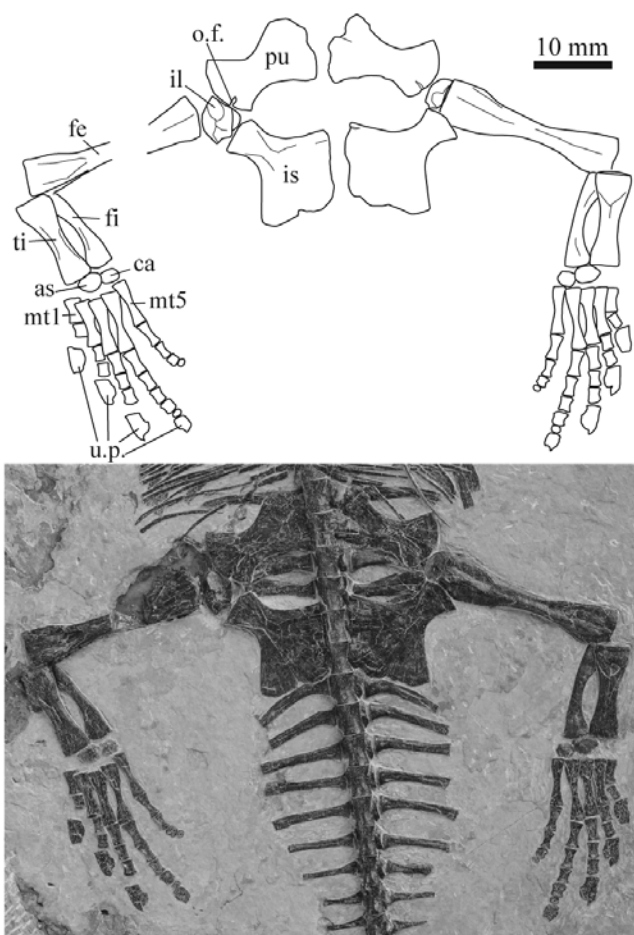


Fig. 5 Photo and outline of the photo of pelvic girdle and hind limb of *Diandongosaurus acutidentatus* gen. et sp. nov. (IVPP V 17761) in ventral view

Abbreviations: as. astragalus 距骨; ca. calcaneum 跟骨; fe. femur 股骨; fi. fibula 腓骨; il. ilium 肠骨; is. ischium 坐骨; mt1. metatarsal 1 第一趾骨; mt5. metatarsal 5 第五趾骨; o. f. obturator foramen 闭孔; pu. pubis 耻骨; ti. tibia 胫骨; u. p. unguis phalange 爪趾骨



the ungual is much smaller than the others and is pisiform in outline in digit 4. The preserved distal most phalanx of digit 5 is about the same as to the penultimate of digit 4 in both size and outline; this suggests that this phalanx should have articulated an ungual that was lost in digit 5. In this case, the phalangeal count of the pes is 2-3-4-6-5, different from that of any pachypleurosaur or *Keichousaurus*. The ungual phalanges appear similar to those of the manus but relatively much more massive; they are better exposed than in the manus. The blade-like ungual is much larger than the phalanx just proximal to it and terminates by a curved nail-like end. Again, such an ungual of the pes has not been seen in other sauropterygians.

**Phylogeny** In order to establish the phylogenetic relationship of *Diandongosaurus*, a cladistic analysis (Appendix 1) was performed based on data matrix derived from Wu et al. (in press) which was based on Rieppel et al. (2002) and Holmes et al. (2008). With the addition of the new taxon and *Hanosaurus* formerly a pachypleurosaur (Rieppel, 1998b), the data matrix includes 35 taxa and 137 characters. The data matrix was analyzed using PAUP\* (version 4.0b10; Swofford, 2002). Multistate characters were treated as unordered and all characters were equally weighted. A heuristic search yielded 120 shortest trees with 441 steps, a CI of 0.408, and a RI of 0.693. The strict consensus and 50% majority-rule consensus of 120 trees are given in Fig. 6.

The results of our analysis is largely comparable to those of Holmes et al. (2008) and Wu et al. (in press), not supporting that the Eusauroptrygia is a monophyletic group and the Pachypleurosauria includes just the European taxa. Further more, the nothosauroid affinity of *Keichousaurus*, which was first suggested by Holmes et al. (2008) and later supported by Wu et al. (in press), is again the case here. *Wumengosaurus* which was considered to be closely related to the pachypleurosaur (Jiang et al., 2008) is a basal member of a monophyletic group including the Pachypleurosauria and Nothosauroida (the Pachy-Nothosaur clade for convenience hereafter), as recently hypothesized by Wu et al. (in press). For *Diandongosaurus*, it is clear that the new species is an eosauroptrygian, which is supported by 15 synapomorphies including eight unequivocal characters: 28(0), 47(1), 64(1), 65(1), 84(1), 95(1), 99(2), and 105(1). However, its relationships with the Pachy-Nothosaur clade and other remain taxa are unsolved. As suggested by the 50% majority rule consensus tree, *Diandongosaurus* might have a close relationship with the Pachy-Nothosaur clade. The present analysis does not support that *Hanosaurus* is a pachypleurosaur but a nothosauroid, possibly occupying the basal most position within the Nothosauroida if not *Keichousaurus*. This is defined by eleven derived characters including seven unequivocal ones: 12(0), 14(1), 17(2), 18(3), 37(0), 96(1), and 115(1).

The monophyly of the Pistosauroida is not established as in Wu et al. (in press) but is the case in Holmes et al. (2008). Three poorly represented Chinese taxa: *Chinchenia*, *Kwangsisaurus*, and *Sanchiaosaurus* had different phylogenetic positions in previous studies (Rieppel, 1999; Holmes et al., 2008; Wu et al., in press) and have been never grouped together. This is the case again here, although the relationships among the pistosauroid taxa appear to be solved in the 50% majority rule consensus tree.

**Discussion** As addressed in the description, there are a number of the characters that are peculiar for *Diandongosaurus*, which include the prefrontal-postfrontal contact, the jugal-squamosal contact; the descending ramus of the squamosal reaching the articular condyle of quadrate, the pineal foramen more anteriorly positioned than the supratemporal fenestra; the elongate anterior caudal ribs, and the extremely expanded ungual phalanx. These autapomorphies form the key part of the diagnosis of the new eosauroptrygian.

*Diandongosaurus* is also a morphological mixture, displaying a combination of nothosaurian and pachypleurosaur features (Table 2). This new species shared many similarities with the pachypleurosaur, such as the preorbital region of the skull longer than the postorbital region,

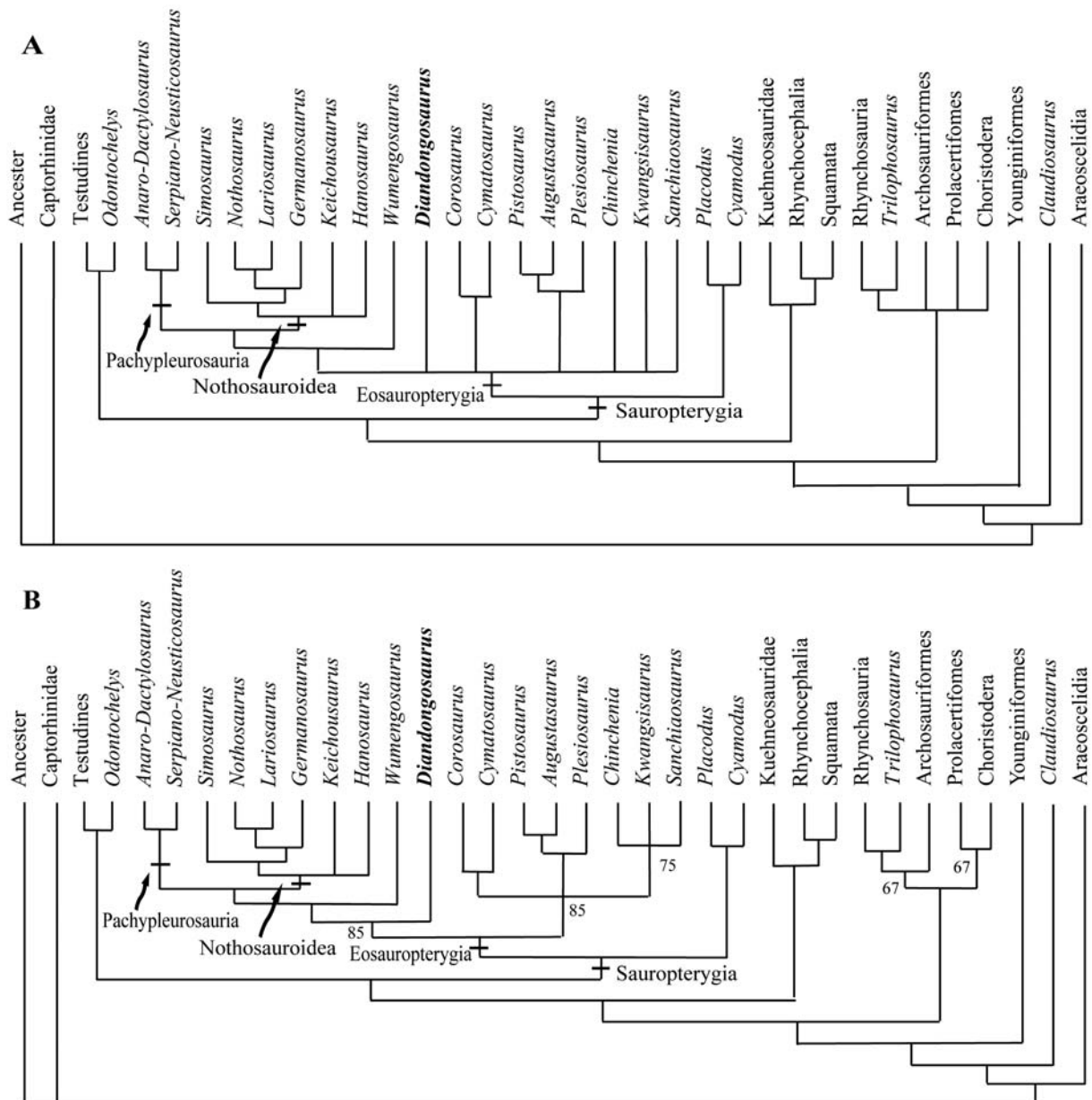


Fig. 6 Cladograms depicting the phylogenetic relationships of *Diandongosaurus acutidentatus*

A. strict consensus of 120 equally shortest trees; B. 50% majority-rule consensus of 120 equally shortest trees

Abbreviations: Anaro, *Anarosaurus*; Serpiano, *Serpianosaurus*

the supratemporal fenestra distinctly smaller than the orbit, the distinct trough/fossa on the dorsal surface of the retroarticular process. On the other hand, *Diandongosaurus* is comparable to the Nothosauroida in some other characters, such as the anterior premaxillary and dentary teeth strongly procumbent, the presence of one or two maxillary caniniform teeth, the fused frontals and parietals, the parietal skull table weakly constricted, and the absent of the zygapophyseal pachyostosis. However, in addition to the autapomorphies, *Diandongosaurus* is also distinguishable from the pachypleurosaurs and the nothosaurs in some other features as recognized by the present analysis. *Diandongosaurus* lacks a set of the three synapomorphies of the Pachypleurosauria, including two unequivocal characters: 46(0) and 99(3) and a set of 11 synapomorphies of the Nothosauroida, including seven unequivocal characters: 12(0)— it shows a derived state from state(0) to state(2) in nothosaurs, 14(1)— the fused frontal is hypothesized here to be independently gained in *Diandongosaurus*, 17(2), 18(3)— it shows state(1) de-

rived from state(3) in nothosaurs, 37(0), 96(1), and 115(1).

**Table 2 Comparisons of the features in *Diandongosaurus* with the pachypleurosaurs and the nothosaurs**

Characters	pachypleurosaurs	nothosaurs
premaxillary and anterior dentary teeth enlarged and fang-like	× (-)	○
maxilla with one or two fangs followed by a distinctly smaller conical teeth	×	○
snout short and with no constriction	○	×
preorbital region of the skull longer than postorbital region	○	×
supratemporal fenestra smaller than the orbit	○	×
interorbital region broad than the interfenestral region	×	-
prefrontal and postfrontal contacted along dorsal orbital margin	×	×
frontals and parietals fused	×	○
frontal with posterolateral process	○	×
pineal foramen shifted anteriorly	-	×
descending ramus of squamosal reaching articular condyle of quadrate	×	×
quadratojugal present	○	×
distinct trough/fossa on the dorsal surface of the retroarticular process	○	×
ribs without “pachyostotic”	× (-)	○ (-)
distal end of anterior caudal ribs not tapering off	×	×
caudal ribs 3 to 8 elongate, longer than sacral ribs	×	×
clavicle with a anterolateral project	×	-
pes with extremely expanded ungual phalanx	×	×

Note: ○. present, ×. absent, - variable.

The only know small eosauroptrygian from China is *Keichousaurus* Young, 1958. *Diandongosaurus* clearly differs from *Keichousaurus* in the postcranial skeleton. In the latter, there are 25–26 cervical and 18–19 dorsal vertebrae, the cervical region is longer than the trunk region, the ribs are “pachyostotic”, the ulna is distinctly broadened, and there are five carpals in the adult. For the skull, *Diandongosaurus* is also distinguishable from *Keichousaurus* in those features: the shape of the prefrontal, the postfrontal, and the quadrate and the length of the quadratojugal and the descending process of the squamosal. The eosauroptrygian *Wumengosaurus* (Jiang et al., 2008; Wu et al., in press) is from the Anisian deposit of southwest China too, but its remarkably elongate rostrum and peculiar tooth morphology exclude a close affinity of the taxon with *Diandongosaurus*.

It has to be emphasized that the pachypleurosaurs status of *Keichousaurus*, *Hanosaurus*, and *Wumengosaurus* from China are further disapproved here and the interrelationship of *Diandongosaurus* remains uncertain within the Eosauroptrygia. It has no doubt that any new or more complete materials of the poorly known taxa (such as *Hanosaurus*, *Sanchiaosaurus*, *Kwangsisaurus*, and *Chinchenia*) will be helpful to verify the results drawn from our study.

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**Appendix 1** Coding for *Diandongosaurus* (the new taxa described here) and *Hanosaurus* added to the analysis of Wu et al. (in press) for characters 1 through 137

<i>Hanosaurus</i> (Characters 1 ~ 119 mainly based on Rieppel, 1998; characters 120 ~ 137 mainly based on IVPP V 3231)						
??00100020	003110?301	11000?20??	?01?10????0	???????????	??0?010??0	1?????1???
?1???11?00	?????02??	0?????????0	10?1121111	0011100?10	0?00?000??	0?????0?
<i>Diandongosaurus</i>						
1000010221	0131111011	1100012001	?0?????11?0	?????????100	??01112?1?	1111100000
1011011111	?02??0211	01111?11?0	1111111110	001120000?	0000?0000?	0110002