

## 短吻贫齿龙(双孔亚纲:海龙目): 头后骨骼及系统关系研究<sup>1)</sup>

吴肖春<sup>1,2</sup> 程延年<sup>2</sup> 佐藤环<sup>3</sup> 单希瑛<sup>2</sup>

(1 加拿大自然博物馆 渥太华 ON K1P 6P4)

(2 中国台湾自然科学博物馆 台中 40453)

(3 日本东京学艺大学 东京 184-8501)

**摘要:**短吻贫齿龙是根据一保存较完整的头骨和下颌标本建立的;标本采自贵州关岭地区三叠系法郎组灰岩。对其头后骨骼进行了详细描述。短吻贫齿龙在肩带的乌喙骨和间锁骨及腰带的肠骨显示了与众不同的特征,例如:紧靠肩臼后方乌喙骨有一明显的凹,间锁骨后半部比前部要窄很多,及肠骨背突末端加宽等。头骨进一步细修表明,其中一些部位需要进行重新记述。依据头后骨骼和头骨中的新信息,对短吻贫齿龙的特征作了修订。系统关系分析表明,贫齿龙是个 askeptosaurid,其下颌宽大于长的反关节突和肱骨缩小的三角-胸大肌嵴表明它与产自瑞士和意大利的 *Askeptosaurus* 关系最近。

**关键词:**贵州关岭,三叠纪,海龙目贫齿龙,头后骨骼,系统关系

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### ***MIODENTOSAURUS BREVIS* CHENG ET AL., 2007 (DIAPSIDA: THALATTOSAURIA): ITS POSTCRANIAL SKELETON AND PHYLOGENETIC RELATIONSHIPS**

WU Xiao-Chun<sup>1,2\*</sup> CHENG Yen-Nien<sup>2</sup> SATO Tamaki<sup>3</sup> SHAN Hsi-Yin<sup>2</sup>

(1 *Canadian Museum of Nature* Ottawa ON K1P 6P4, PO Box 3443 STN "D", Canada \* Corresponding author: xcwu@mus-nature.ca)

(2 *Museum of Natural Science* Taichung 40453, 1, Kuan Chien RD, Taiwan, China)

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

**Abstract** *Miodentosaurus brevis* was first established on the basis of the skull and mandible of a fairly preserved skeleton from the Triassic Falang Formation, Guanling area, Guizhou Province. The description of the postcranial skeleton reveals that *M. brevis* is also distinct in the morphology of its girdle elements, such as the coracoid with a small embayment just posterior to the glenoid, interclavicle becoming much narrower posteriorly than anteriorly, and the ilium having a dorsal blade with an expanded distal end. With a further preparation, some of the skull anatomy are redescribed. Based on new information from both skull and the postcranial skeleton, the diagnosis of the taxon is revised. A phylogenetic analysis suggests that *M. brevis* is an askeptosauroid, closely related to *Askeptosaurus* from Switzerland and Italy on the basis of two unequivocal synapomorphies, a retroarticular process broader than long and a reduced deltopectoral crest in the humerus.

**Key words** Guanling, Guizhou; Triassic; Thalattosauria, *Miodentosaurus*; postcranial skeleton; phylogeny

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## 1 Introduction

The holotype specimen (housed in National Museum of Natural Science, with a catalogue number of NMNS 004727/F003960) of *Miodentosaurus brevis* Cheng et al., 2007 was collected from the Falang Formation (upper Middle to lower Upper Triassic) of Guanling area, Guizhou Province, China. Its skull and mandible was first described by Cheng et al. (2007) while its postcranial skeleton was still in the matrix. Now the latter is fully prepared and described here. Before the postcranial description, an anatomical revision of the skull and mandible is made on the basis of a further preparation using Sand Bluster. With information drawn from the postcranial skeleton, the diagnosis of *M. brevis* is revised and its phylogenetic relationships among thalattosaurians are analysed. *M. brevis* is an askeptosauroid (see the text below) and the morphological comparison is made mainly with the taxa of the Askeptosauroida (sensu Liu and Rieppel, 2005).

*Neosinasaurus hoangi* Zhou, 2000 (Zhou in Yin & Zhou, 2000) (= *Sinasaurus hoangi* Zhou, 2000 (Zhou in Yin et al., 2000)), *Wayaosaurus geei* Zhou, 2000 (Zhou in Yin et al., 2000), and *Wayaosaurus bellus* Zhou, 2000 (Zhou in Yin et al., 2000) were originally described as pachypleurosauroids on the basis of unprepared specimens. Our examination of the true specimens indicates that both genera are thalattosaurians. The original description of the two genera was not accurate or wrong in many places; it is, for instance, obvious that both have only two rather than five sacral vertebrae. *N. hoangi* (Gmr001, type specimen) appears to be similar to *Miodentosaurus brevis* but clearly differs from the latter in that the neural spine of dorsal vertebrae is not constricted around their base and the humerus is nearly symmetrically incurved on both sides. The paratype skull (Gmr002) of *N. hoangi* bears a median ridge along the dorsal mid-line of the premaxillae as in *M. brevis* but the neural spine of its dorsal vertebrae shows no constriction around the base. Any taxonomic verification of *N. hoangi* has to wait for a full preparation of the specimens. It is possible that the type and paratype of the taxon could represent two different thalattosaurians. *W. bellus* and *W. geei* are separately based on a specimen preserved in ventral view. The specimen of *W. bellus* was not accessible but the relatively long symphysis of its mandible (see fig. 2, 4 in Plate II in Zhou, 2000 (in Yin et al., 2000)) is not comparable to that of *M. brevis*. There is no doubt that the specimen of *W. geei* (Gmr004) is not referable to *M. brevis* because its mandibular symphysis is even relatively longer than that of *W. bellus*. Again, the true taxonomic status of the two species of *Wayaosaurus* can be clarified until their specimens are fully prepared.

## 2 Description and comparison

**Revision of the skull and mandibular anatomy** Fine preparation of the skull using Sand Bluster shows that some skull elements were not properly described or even inaccurately interpreted in Cheng et al. (2007), which are clarified here. 1) The maxillary-jugal relationship along the ventral margin of the orbit was figured in the previous study as that the maxilla extends posteriorly medial to the jugal (see fig. 2A in Cheng et al., 2007). This is not the case but the opposite is true (Fig. 1), as in other thalattosaurians. 2) The frontal resembles that of most thalattosaurians in possessing a posterolateral process, but it is very peculiar in that the bone forms the anterior margin of the pineal foramen (Fig. 1). This is unique among thalattosaurians. 3) The parietal is also very distinctive in having a slender anterolateral process that wraps the posterolateral process of the frontal. Again, this is unique among thalattosaurians. 4) The ventral edge of the surangular of the mandible is not as straight as figured in the study of Cheng et al. (2007) but abruptly convex at the posterior third of the bone; in other words, the surangular suddenly broadens ventrally at the place so that the surangular/angular suture turns downward (Fig. 2). This appears to be unique for *Miodentosaurus brevis*. The surangular/angular suture also turns downward in *Thalattosaurus alexandrae* (see fig. 2 in Nicholls, 1999) but it is much weaker and more anteriorly positioned.

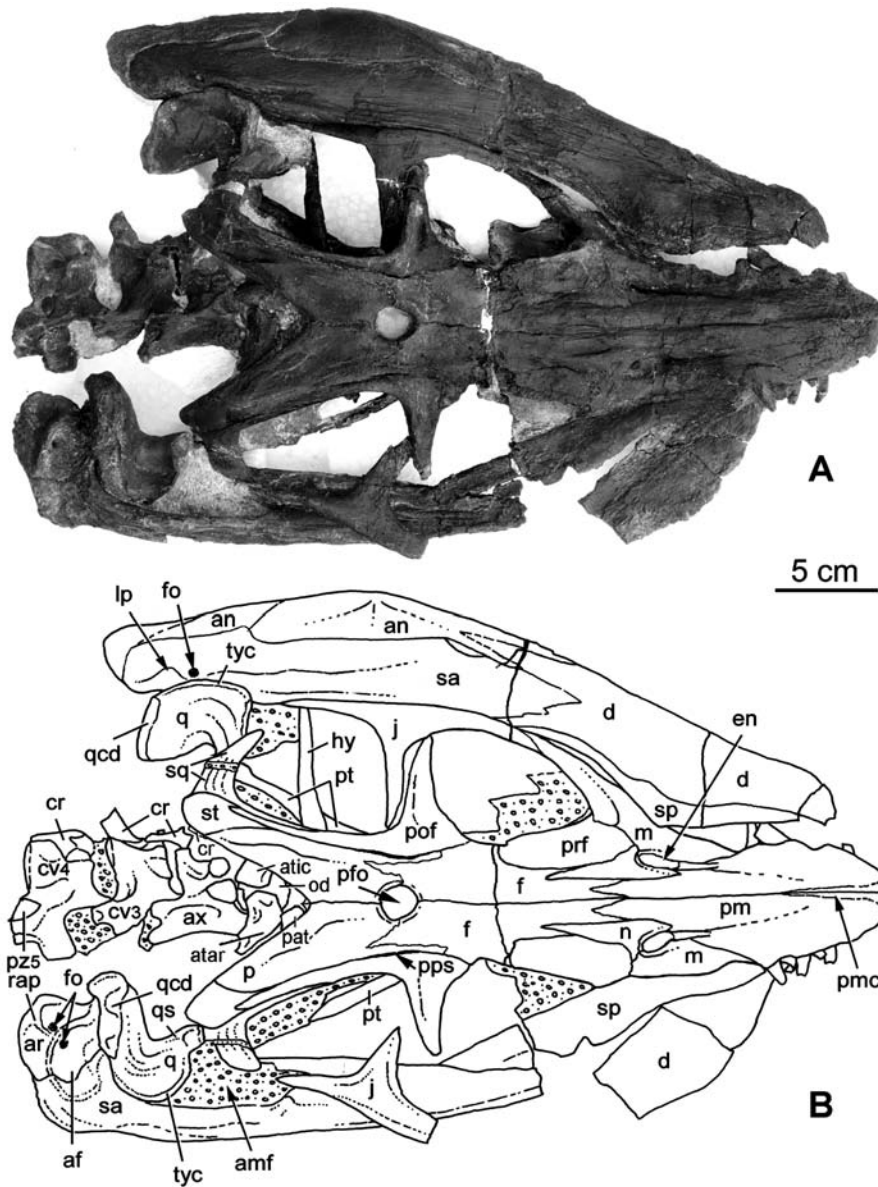


Fig. 1 Photo (A) and outline of the photo (B) of the skull, mandible, and the first four cervical vertebrae of *Miodentosaurus brevis* Cheng et al., 2007 in dorsal (the skull and right ramus of the mandible) and lateral (the left ramus of the mandible and the four cervicals) views

Abbreviations: af. articular fossa 关节窝; amf. adductor mandibular fossa 下颌收肌窝; an. angular 隅骨; ar. articular 关节骨; atar. atlantal neural arch 环椎神经弓; atic. atlantal intercentrum 环椎间椎体; ax. axis 枢椎; cr. cervical rib 颈肋; cv. cervical vertebra 颈椎; d. dentary 齿骨; en. external naris 外鼻孔; f. frontal 额骨; fo. foramen 孔; hy. hyoid 舌骨; j. jugal 轭骨; lp. lateral process of surangular 上隅骨外侧突; m. maxilla 上颌骨; n. nasal 鼻骨; od. odontoid process of axis 环椎齿突; p. parietal 顶骨; pat. proatlans 前环椎; pfo. pineal foramen 松果孔; pm. premaxilla 前颌骨; pmc. premaxillary crest 前颌骨嵴; pof. postfrontal 后额骨; pps. slit-like postfrontal/parietal suture, indicating the position of the supratemporal fenestra 狭长切口样的后额骨/顶骨缝, 表明原来上颞孔的位置; prf. prefrontal 前额骨; pt. pterygoid 翼骨; pz5. left prezygapophysis of cervical vertebra 5 第五颈椎后关节突; q. quadrate 方骨; qcd. quadrate condyle 方骨髁; qs. quadrate shaft 方骨杆; rap. retroarticular process 反关节突; sa. surangular 上隅骨; sp. splenial 夹板骨; sq. squamosal 鳞骨; st. supratemporal 上颞骨; tyc. tympanic crest 鼓膜附嵴

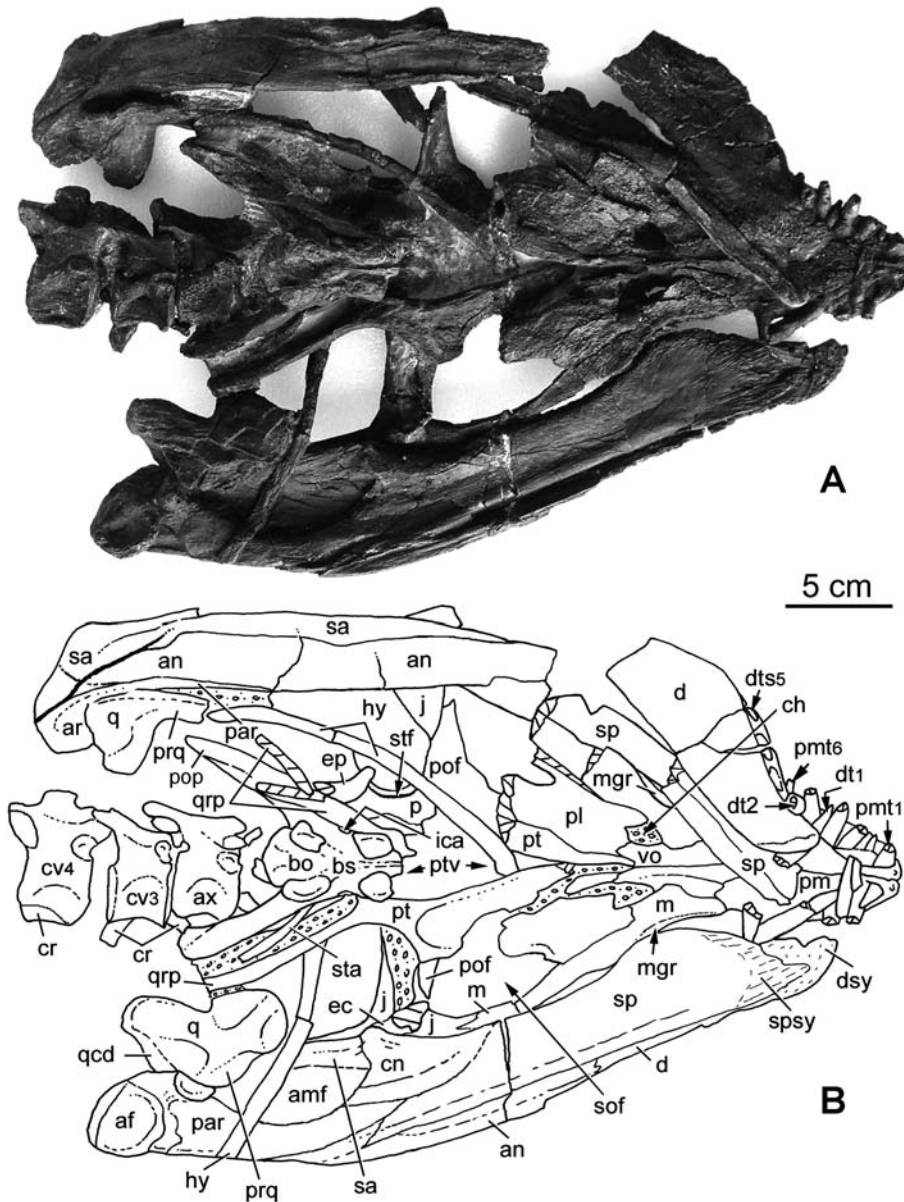


Fig. 2 Photo (A) and outline (B) of the skull, mandible, and the first four cervical vertebrae of *Miodontosaurus brevis* Cheng et al., 2007 in ventral (the skull and right ramus of the mandible), medial (the left ramus of the mandible), and lateral (the four cervicals) views

Abbreviations as in Fig. 1 plus bo. basioccipital 基枕骨; bs. basisphenoid 基蝶骨; ch. choana 内鼻孔; cn. coronoid 冠状骨; dsy. dentary symphyseal facet 齿骨联合面; dt. dentary tooth 齿骨齿; dts. dentary tooth socket 齿骨齿窝; dts5. socket for dentary tooth 5 第五齿骨齿窝; ec. ectopterygoid 外翼骨; ep. epipterygoid 上翼骨; ica. internal carotid artery 内颈动脉孔; mgr. groove-like trough in maxillary 上颌骨沟状槽; par. prearticular 前关节骨; pl. palatine 腭骨; pmt. premaxillary tooth 前颌骨齿; pop. paroccipital process 副枕突; prq. pterygoid ramus of quadrate 方骨翼骨支; ptv. pterygoid vacuity 翼骨间窝; qrp. quadrate ramus of pterygoid 翼骨方骨支; sof. suborbital fenestra 眶下孔; spsy. splenial symphyseal facet 夹板骨联合关节面; sta. stapes 镫骨; stf. trace of supratemporal fenestra 上颞孔遗迹; vo. vomer 犁骨

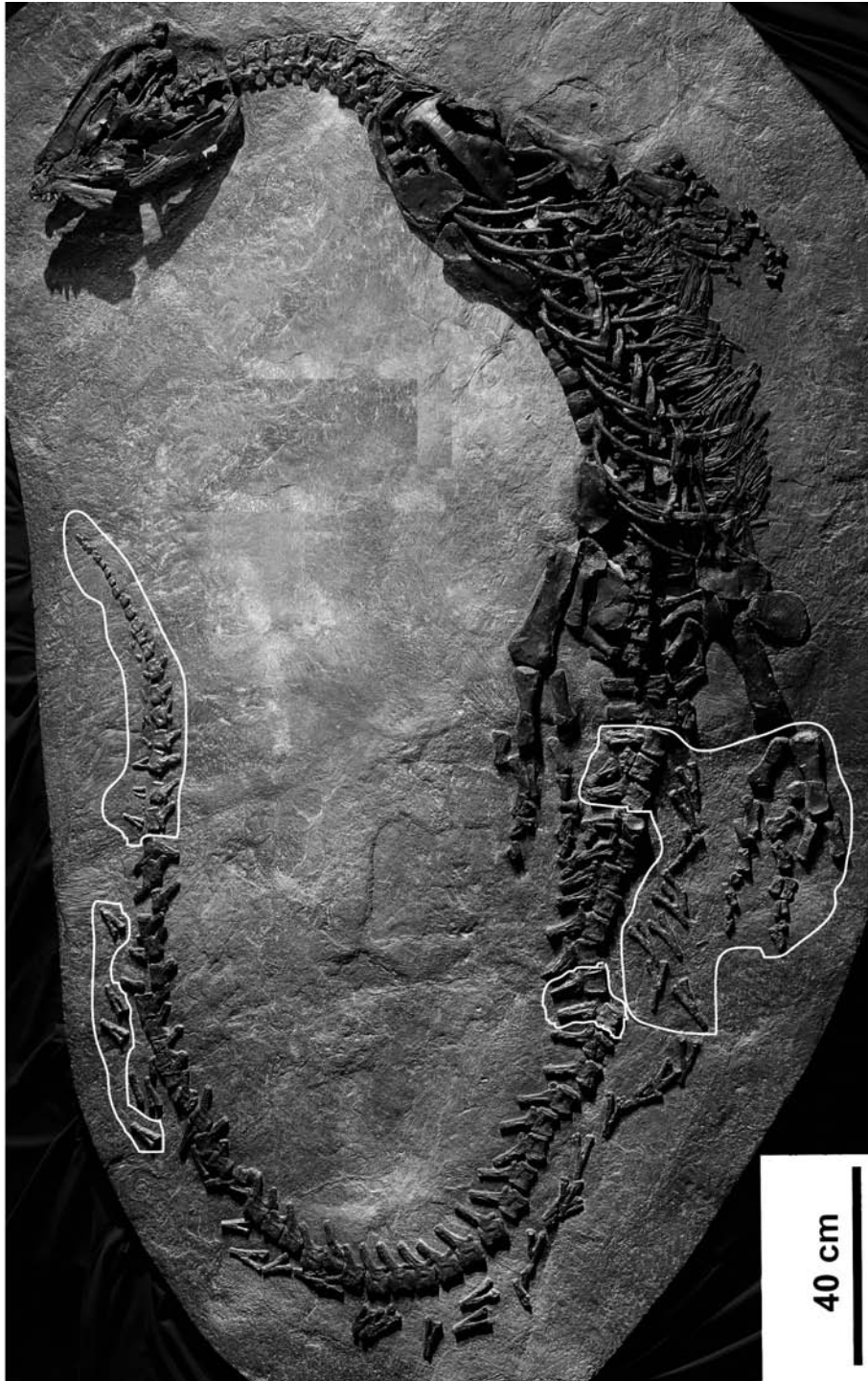


Fig. 3 Skeleton of *Miodentosaurus brevis* Cheng et al., 2007 in ventral (the skull and right ramus of the mandible), medial (the left ramus of the mandible), and lateral (the postcranial skeleton) views (circled areas are reconstructed)

**Axial skeleton** With the skull and mandible, the postcranial skeleton of *Miodentosaurus brevis* is articulated and well preserved although the zeugopodium, the manus of the left hindlimb, and some caudal vertebrae (3–5, 12, 13, about 20 of the posterior most section) are missing (Fig. 3). There are 87 vertebrae preserved, consisting of 38 presacrals (13 cervicals and 25 dorsals), two sacrals, and 47 caudals. The cervicals are fewer in number than 15 or 16 of an askeptosauroid, *Anshunsaurus* species from south-western Guizhou, the number of the latter was recently clarified in a juvenile specimen (Liu, 2007). All but the atlas-axis complex are amphicoelous. Sutures between the neural arches and centra are visible in all cervical and the first five dorsal vertebrae, and evident in the posterior half of the other pre-caudal vertebrae. Most of cervical and all preserved caudal, except for the first several, vertebrae are laterally compressed during fossilization.

The atlas-axis complex is better exposed on the left side. The atlas is represented by its intercentrum and left neural arch, which are in their original position (Fig. 4A). The intercentrum shows the left ventrolateral side, which is convex and has a thickened lateral margin. The neural arch is slightly detached from the intercentrum. It is anteriorly convex, posteriorly concave, ventrally massive, and dorsally narrows into the neural spine. The broken surface suggests that the spine is missing its distal end. The lateral surface of the neural arch is bulged out but becomes concave close to its ventral margin; its anterior portion is thickened but the arch thins posteriorly. The thick ventral side of the arch is convex, with two facets; the anterior one for the atlantal intercentrum and the posterior one probably for the atlantal rib. A piece of bone anterior to the atlantal neural arch is probably the proatlas. A stout and round bone medial to the atlantal neural arch may be the odontoid process of the axis.

The right side of the axis is well exposed (Fig. 4B). The axial centrum is laterally compressed due to postmortem deformation and approximately as long as tall; it should have been longer than high in life although not as elongate as in *Anshunsaurus huangguoshuensis* (Liu and Rieppel, 2005) and *Askeptosaurus italicus* (Müller, 2005). The lateral and ventral surfaces of the axial centrum are significantly concave. The longitudinal keel along the ventral midline might be exaggerated by the strongly lateral compression of the centrum. The rib facet is slightly damaged; it projects laterally and is positioned across the neural arch-central suture at the anterior end of the centrum. The prezygapophysis and postzygapophysis are very large, the latter is larger than the former. The prezygapophysis faces more dorsally than laterally, and it extends slightly beyond the anterior edge of the centrum. The postzygapophysis faces ventrolaterally, with its facet overhanging the posterior edge of the centrum. There is a prominent epipophysis dorsal to the postzygapophysis. The neural spine is low and longitudinally broad, extending more posteriorly than the postzygapophysis. It is higher posteriorly than anteriorly, in contrast with the straight in the species of *Anshunsaurus* (Liu and Rieppel, 2005; Liu, 2007) or convex dorsal margin in *Askeptosaurus italicus*.

In the post-axial cervical vertebrae, the centrum is relatively longer, the neural spine is significantly taller, and the prezygapophysis is more massive than those of the axis (Fig. 4B, C), as in other thalattosaurians. The ventral surface of the centrum is covered with the ribs in those cervicals. The prezygapophysis faces dorsomedially and extends well over the anterior edge of the centrum. The postzygapophysis extends beyond the posterior edge of the centrum but to a lesser degree than in the axis. The epipophyses become smaller in the posterior cervicals and entirely disappear in the eighth cervical. The concave lateral surface of the centrum is further depressed, which is less so in the last two cervicals. The diapophyses become more pronounced in the posterior cervicals, and those of the last (13<sup>th</sup>) cervical are nearly as large as those of the first dorsal. The parapophyses move dorsally in the posterior cervicals, close to the diapophysis in the last cervical. The neural spine, complete only in cervicals 4 and 6, is square-like in the first four post-axial cervicals. The neural spine of the cervical 7 is complete,

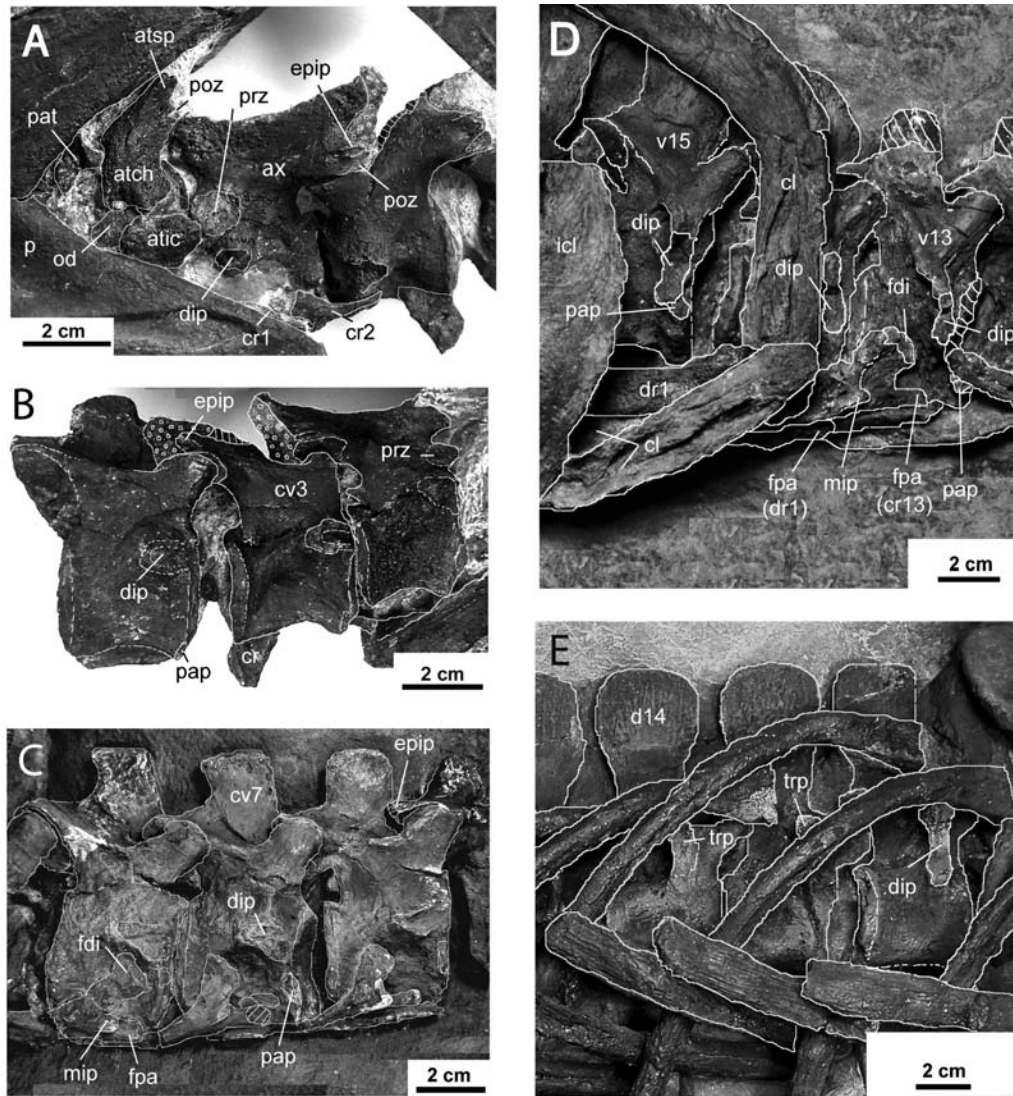


Fig. 4 Some vertebrae of *Miodentosaurus brevis* Cheng et al., 2007 in lateral views

A–C. cervical vertebrae; D. the last cervical and the first two dorsal vertebrae (vertebrae 13 to 15);

E. dorsal vertebrae 12 to 14 (vertebrae 25 to 27)

Abbreviations as in Fig. 1 plus atch. atlantal neural arch 环椎神经弓; atsp. atlantal neural spine 环椎神经棘; cl. clavicle 锁骨; dip. diapophysis 椎弓横突; d14. the 14<sup>th</sup> dorsal vertebra 第十四背椎; dr. dorsal rib 背肋; epip. epipophysis 后关节上突; fdi. rib facet for diapophysis 肋骨关节椎弓横突的面; fpa. rib facet for parapophysis 肋骨关节椎体横突的面; icl. interclavicle 间锁骨; mip. middle process of cervical rib 颈肋中央突; pap. parapophysis 椎体横突; poz. postzygapophysis 后关节突; prz. prezygapophysis 前关节突; trp. transverse process 横突; v. vertebra 椎体

with a dorsal edge projecting further posteriorly than in the first four post-axial cervicals. The neural spine is reconstructed for those posterior to the 7<sup>th</sup> and it in the last cervical may have been as tall as that of the first dorsal.

The 14<sup>th</sup> vertebra is considered as the 1<sup>st</sup> dorsal on the basis of the size of the diapophysis, which is similar to that of the 15<sup>th</sup>, obviously larger than the cervical vertebrae (Fig. 4D). In comparison with the cervicals, the 25 dorsal vertebrae differs in that the centrum is longer, the

neural spine is much taller (compared with that of the 7<sup>th</sup> cervical), and the lateral surface of the centrum is less depressed. The diapophysis and parapophysis are merged into a single transverse process in all dorsals but the first dorsal in which the parapophysis is still separated from the diapophysis as a distinct process, as indicated by the presence of the ventral head of the 1<sup>st</sup> dorsal rib. The parapophysis is represented by a small facet facing dorsomedially in the transverse process in the other dorsals (Fig. 4D). The centrum is relatively shorter in the anterior few and the posterior most dorsals. The neural spines (partly seen in the first four or five dorsals but not exposed in the last two dorsals because of the overlapping of the girdle elements) are strongly constructed around the ventral portion. This situation is also seen in the anterior dorsals of the species of *Anshunsaurus* (see fig. 5 in Liu and Rieppel, 2005 or fig. 1 in Liu, 2007) although the spine is relatively taller than in *Miodentosaurus*. The ventral surface of all dorsal vertebrae is smooth and lacks any ridges.

The two sacral vertebrae are characterized by the large facet for the sacral rib and the centrum longer than in the last two dorsals (Fig. 5A). The facet of the 1<sup>st</sup> sacral is taller than long, and expands nearly to the anterior edge of the centrum, whereas the facet of the 2<sup>nd</sup> is much larger than that of the 1<sup>st</sup>, longer than tall, and expands nearly to the posterior edge of the centrum. The morphology and location of the sacral rib facet in the 2<sup>nd</sup> sacral vertebra contrasts with those in *Endennasaurus acutirostris* in which the facet is nearly round in outline and positioned near the mid-point of the centrum (see fig. 3C in Müller et al., 2005; fig. 3C in Renesto, 1992). The lateral surface of the centrum is significantly concave and the ventral surface is smooth. The sacral neural spine is as tall as those in the dorsals, but the constriction at the base is weak and the spine is relatively taller than in *E. acutirostris* and *Anshunsaurus huangguoshuensis* (see fig. 6 in Liu and Rieppel, 2005).

The first two caudals are longer and slightly taller than the sacral vertebrae (Fig. 5B). Their neural spine is nearly vertical and relatively taller than in other askeptosauroids such as *Anshunsaurus* and *Askeptosaurus*, and lacks the basal constriction seen in the most dorsals. The rib facet is located close to the ventral edge of the centrum as in other thalattosaurians. There are no chevron facets along the posteroventral edge of the centrum in the first two caudals. Caudal vertebrae 3–5 are not preserved. The 6<sup>th</sup> caudal differs from the first two in the following features. The neural spine is posterodorsally directed, which is more so in the further posterior caudals; the distal end of the neural spine is narrower than the base (Fig. 5C); and there are a pair of chevron facets on the posteroventral side of the centrum. The rib facets become smaller in posterior caudals and entirely disappear in the 10<sup>th</sup> caudal. It is clear that the caudal rib is sutured but not fused to the transverse process until the 7<sup>th</sup> caudal.

Cervical ribs are nearly complete except for the first four cervicals in which the ribs are incomplete or covered with the vertebrae. The posterior portion of the 1<sup>st</sup> rib is rod-like (Fig. 4A). The rest of cervical ribs are similar to those of other thalattosaurians in having two heads and a process: a massive dorsal head for the diapophysis, a slender ventral head for the parapophysis, and a short middle process between the two (Fig. 4C, D). The middle process is small and not as pronounced as in many archosaurs (such as a crocodylian *Stangerochampsia* (Wu et al., 1996)). It slightly projects anterolaterally beyond the union of the dorsal and ventral heads in the anterior cervicals, but it is more posteriorly located in the posterior cervical ribs. The rib shaft gradually elongates in the posterior cervical region. The last cervical rib is only partly exposed, and transition to the dorsal rib is unclear. The dorsal and ventral heads become closer in position while their middle processes become smaller in the posterior cervical ribs.

Most dorsal ribs are complete and exposed in right lateral view (Figs. 3, 6, 7A, B). The proximal head of the first three ribs is covered by the pectoral girdles, except for the first rib which has a small ventral head for the parapophysis of the centrum as in the cervical ribs (Fig.



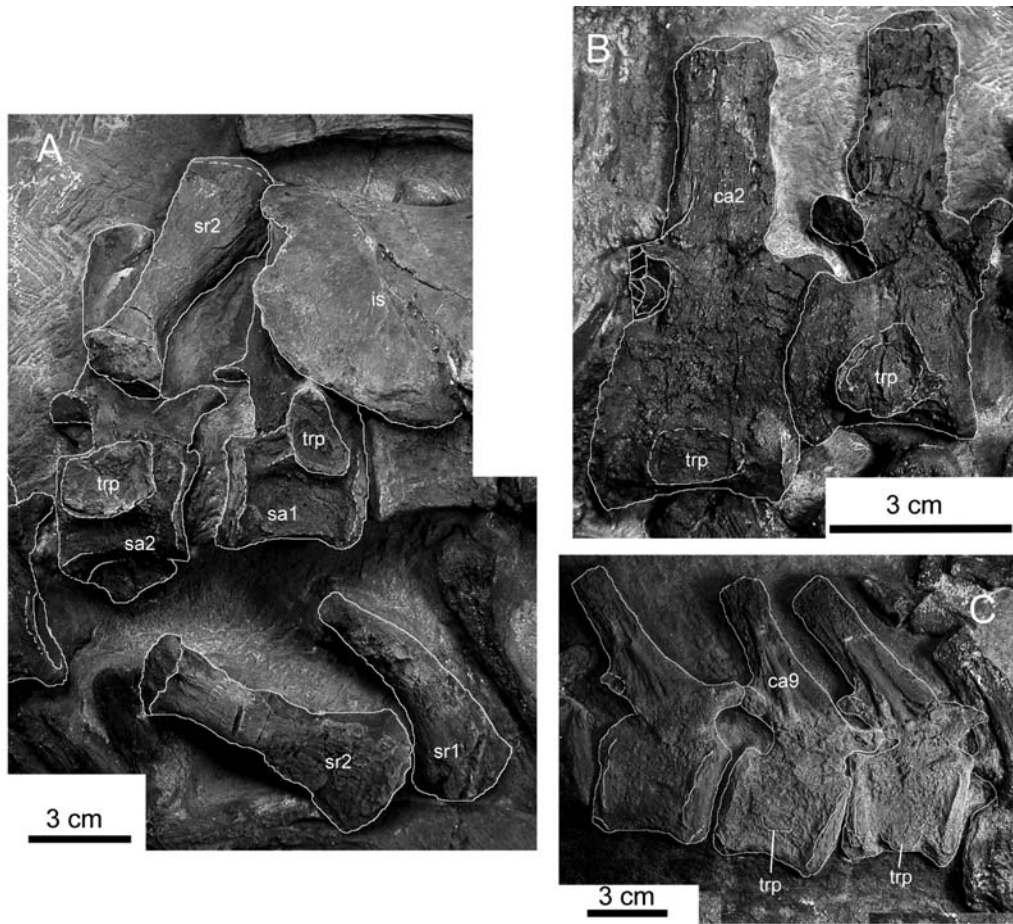


Fig. 5 Sacral and anterior caudal vertebrae of *Miodontosaurus brevis* Cheng et al., 2007 in lateral views  
 A. sacral vertebrae and ribs; B. the 1<sup>st</sup> and 2<sup>nd</sup> caudal vertebrae; C. the 8<sup>th</sup> to 10<sup>th</sup> caudal vertebrae  
 Abbreviations as in Fig. 4 plus ca. caudal vertebra 尾椎; is. ischium 坐骨; sa. sacral vertebrae 荐椎;  
 sr. sacral rib 荐肋

4D). The dorsal ribs are strongly arched in life, with an expanded proximal head, a rod-like shaft, a slightly broadened distal end, and a shallow groove along the proximal half of the lateral surface (Fig. 4E). In a number of the dorsal ribs, the distal end is flattened during fossilization. The most evident differences among the dorsal ribs are that the proximal head is broader and the lateral groove is deeper in the anterior ribs than in the posterior ones.

The two sacral ribs are very distinctive, significantly shorter and much more massive than any dorsal one (Fig. 5A). The first sacral rib is comparable to that of *Anshunsaurus huangguoshuensis* in having a dorsoventrally broadened head and a horizontally broadened distal end, although the distal end is narrower (see fig. 6 in Liu and Rieppel, 2005). The second sacral rib is more massive than the 1<sup>st</sup> and its two broadened ends are situated in the same horizontal plane, as in *Anshunsaurus* but not *Endennasaurus* in which the distal end of the second sacral rib is thinner than the 1<sup>st</sup> (see fig. 3 in Müller et al., 2005). The distal end of the 2<sup>nd</sup> rib is wider than the head as in many other thalattosaurians but *Askeptosaurus* in which the distal end is much broader than (about three times as wide as) the head (see fig. 8E in Müller, 2005).

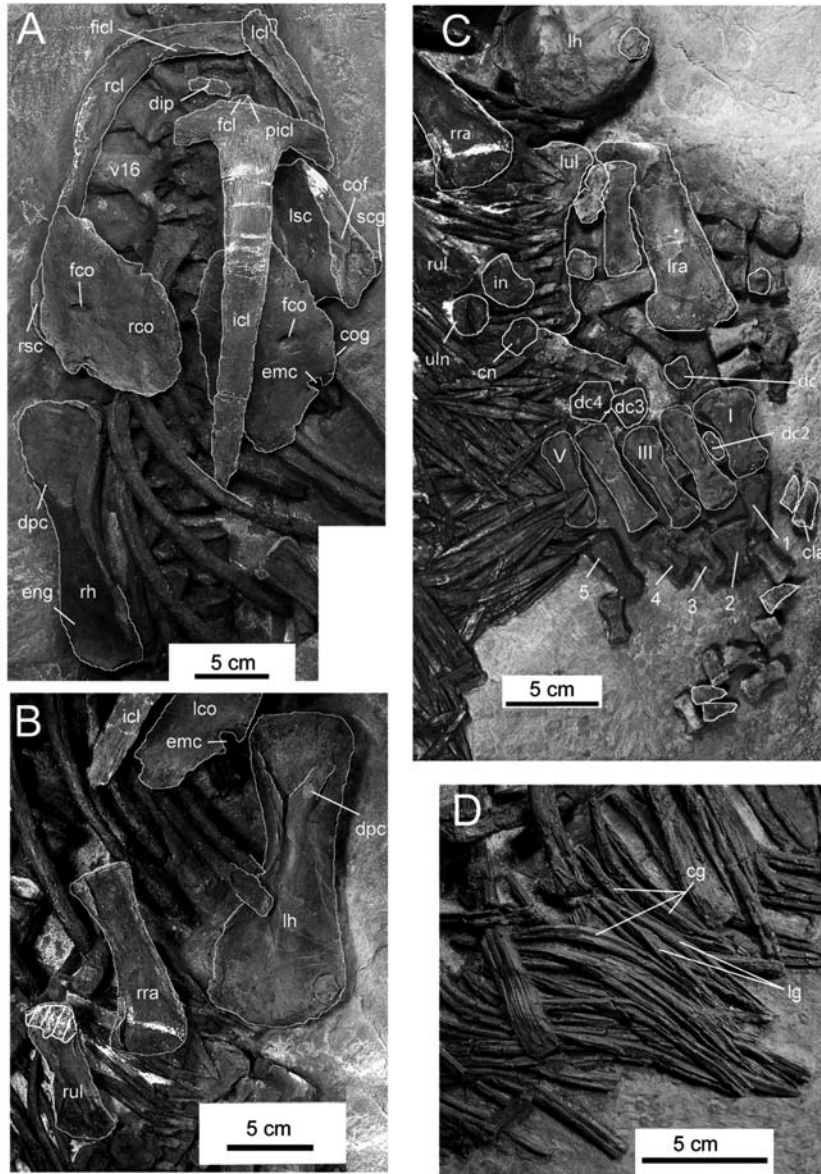


Fig. 6 Pectoral girdle, forelimbs, and gastralia of *Miodontosaurus brevis* Cheng et al., 2007

A. elements of the pectoral girdles in outer view and the right humerus in ventral view; B. the left humerus, radius, and ulna in ventral view; C. the radius, ulna, and manus of the left forelimb in ventral view; D. elements of gastralia  
 Abbreviations as in Fig. 4 plus cg. central element of gastralia 腹肋中央段; cla. claw (ungual) 爪; cn. centrale 中央腕骨; cof. coracoid facet on scapula 肩胛骨上乌喙骨关节面; cog. glenoid on coracoid 乌喙骨的肩臼部; dc. distal carpal 远侧腕骨; dpc. deltopectoral crest 三角肌—胸大肌嵴; emc. embayment on coracoid 乌喙骨凹弯; eng. entepicondylar groove 内髁沟; fcl. facet for clavicle 关节锁骨的面; fco. foramen on coracoid 乌喙孔; fiel. facet for interclavicle 关节间锁骨的面; in. intermedium 中间腕骨; lcl. left clavicle 左锁骨; lco. left coracoid 左乌喙骨; lg. lateral element of gastralia 腹肋外侧段; lh. left humerus 左肱骨; lra. left radius 左桡骨; lsc. left scapula 左肩胛骨; lul. left ulna 左尺骨; picl. anterior process of interclavicle 间锁骨前突; rcl. right clavicle 右锁骨; rco. right coracoid 右乌喙骨; rh. right humerus 右肱骨; rra. right radius 右桡骨; rsc. right scapula 右肩胛骨; rul. right ulna 右尺骨; scg. glenoid on scapula 肩胛骨的肩臼部; uln. ulnare 尺骨; I, II, V. the 1<sup>st</sup>, 3<sup>rd</sup>, 5<sup>th</sup> metacarpals/metatarsals 第一, 二和五掌骨及第一, 三和五跖骨; 1-5. the 1<sup>st</sup> to 5<sup>th</sup> digits of manus/foot 第一到第五指/趾

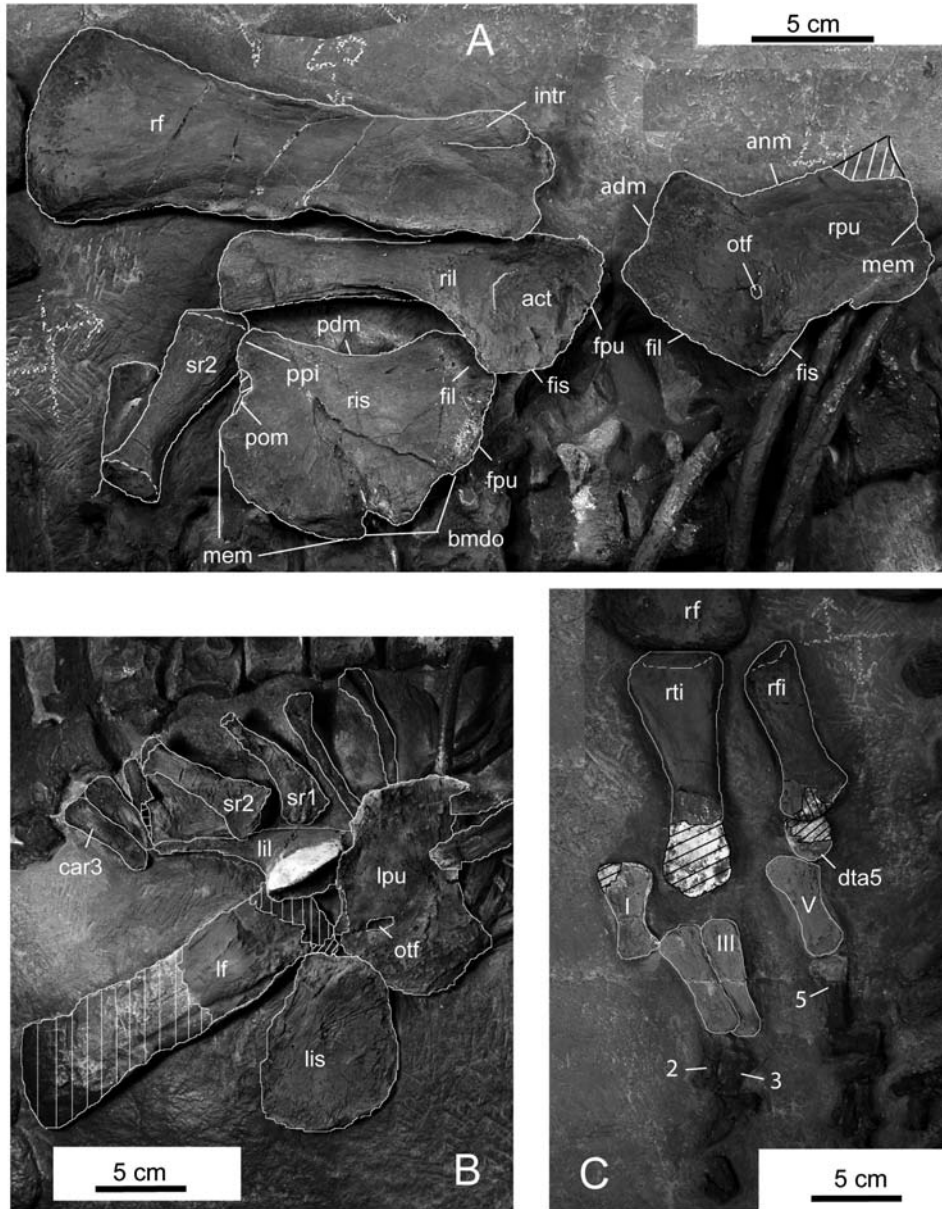


Fig. 7 Pelvic girdle and hindlimbs of *Miodontosaurus brevis* Cheng et al., 2007

A. right pelvic girdle in outer view and right humerus in ventral view; B. left pelvic girdle in dorsal view;

C. right tibia, fibula, and foot elements in ventral view

Abbreviations as in Figs. 5 and 6 plus act. acetabulum 髌臼; adm. anterodorsal margin 前背缘; anm. anterior margin 前缘; bmdo. opening between the pubic symphysis and ischial symphysis 耻骨联合和坐骨联合间孔; car. caudal rib 尾肋; dta. distal tarsal 远侧跗骨; fil. facet for ilium 关节肠骨的面; fis. facet for ischium 关节坐骨的面; fpu. facet for pubis 关节耻骨的面; intr. internal trochanter 小转子; lf. left femur 左股骨; lil. left ilium 左肠骨; lis. left ischium 左坐骨; lpu. left pubis 左耻骨; mem. medial margin 内缘; of. obturator foramen 闭孔; pdm. posterodorsal margin 后背缘; pom. posterior margin 后缘; ppi. posterior process of ischium 坐骨后突; rf. right femur 右股骨; rfi. right fibula 右腓骨; ril. right ilium 右肠骨; ris. right ischium 右坐骨; rpu. right pubis 右耻骨; rti. right tibia 右胫骨

There are only five right caudal ribs preserved, of which the 3<sup>rd</sup> is complete (Fig. 7B). The complete caudal rib is very short and has a slightly broadened head and somewhat pointed distal end. The rib facets suggest there are 9 caudal ribs, of which the first three are separated from the transverse process on the ventrolateral side of the centrum. The size of the transverse process indicates that the ribs become shorter posteriorly and eventually fused with the small transverse process.

Chevrons (haemal arches) are scattered around the mid-portion of the tail but more than 25 of them are fairly preserved (Fig. 3). The chevrons are Y-shaped, with an articular facet on each side facing dorsomedially, as in most other thalattosaurians. The forked portion in the complete chevrons is shorter than the distal portion, similar to the condition seen in *Anshunsaurus huangguoshuensis*, but the forked portion is U-shaped rather than V-shaped in the latter (see those around the 13<sup>th</sup> caudal vertebrae in IVPP V 11834). In an indeterminate thalattosaurian (= thalattosauriform) from the Upper Triassic of Austria (Müller, 2007), the forked proximal portion is much shorter (less than half) than the distal portion (see fig. 1 in Müller, 2007). Three chevrons are illustrated for *Askeptosaurus italicus*, showing that the forked proximal portion is U-shaped and much longer (about twice) than the distal portion if these three are complete (see fig. 8F in Müller, 2005).

Many gastralia are well preserved although not in original arrangement (Fig. 3). Each row of the gastralia may have consisted of three elements, one medial and two laterals. The proximal end of the medial element curves forward and meets the counterpart from the opposite side along the midline (Fig. 6D). Distally, the medial element has a long articular facet on the anterior side for receiving a lateral element. The latter is spindle-shaped but very narrow, with its proximal portion more pointed than its distal portion. The exact number of gastralia rows is unknown owing to the postmortem displacement.

**Pectoral girdle** All elements of the pectoral girdle are well-exposed except for the scapula (Figs. 3, 6A). The right scapula is almost entirely covered by the coracoid and the left is nearly vertical in orientation and its distal expansion is obscured. The articular facet for the coracoid is triangular in outline, and the posterior portion close to the glenoid is much broader than the anterior portion. The scapula has a broad dorsal plate, with a concave posterior edge and a convex anterior edge, probably similar to that of *Askeptosaurus italicus*.

The coracoid is oval and the overall morphology is similar to that of *Anshunsaurus huangguoshuensis*, *Askeptosaurus italicus*, and *Endennasaurus acutirostris*. It has a long and straight medial edge to articulate with the interclavicle. The scapular facet appears to be wider and the coracoid foramen is more posteriorly positioned than in the aforementioned taxa. There is a small embayment just posterior to the glenoid, which is absent in other askeptosauroids such as the aforementioned three taxa. The dorsal surface of the coracoid is not observable.

The interclavicle is nearly complete and well-exposed, and the outline is similar to that of *Anshunsaurus huangguoshuensis* (see fig. 9 in Liu and Rieppel, 2005) and *Endennasaurus acutirostris* (see fig. 4 in Müller et al., 2005). It is characterized by a small anterior process (unknown in *E. acutirostris*) and very elongate posterior shaft (Fig. 6A). The lateral process is missing the distal tip on the left side, but it is suggested to be similar to that of the above two taxa in life. The posterior portion of the shaft is much narrower than the anterior portion, in contrast to the situation seen in *A. huangguoshuensis*, *E. acutirostris* and *Askeptosaurus italicus*. In anterior view, the facet for the clavicle is a deep groove that widens dorsoventrally; the small anterior process is the septum between the grooves from each side.

The right clavicle is well-preserved in posteromedial view, with its distal tip covered with the right coracoid and the proximal portion with the left clavicle (Fig. 6A). It is roughly L-shaped, as in *Anshunsaurus huangguoshuensis*, with a thickened transverse (proximal) portion inserting into the groove-like facet on the interclavicle and a slender vertical (distal) portion

meeting the scapula. The anterolateral margin is thin whereas the posteromedial margin is thick. The posteroventral surface is smooth and concave and the anterodorsal surface is not exposed.

**Pelvic girdle** The elements of the pelvic girdle are preserved in outer view on the right side and in inner view on the left side (Fig. 7A, B). The ilium bears a nearly straight dorsal blade with a slightly broadened distal tip, unlike the ilia in *Askeptosaurus italicus*, and *Endennasaurus acutirostris* in which the dorsal blade is more strongly curved posteriorly and distally narrowed (see fig. 10 in Müller, 2005; fig. 6 in Müller et al., 2005). In *Anshunsaurus huangguoshuensis*, the shaft of the dorsal blade is also curved and distally not broadened (see fig. 6 in Liu and Rieppel, 2005). The dorsal blade of *Hescheleria ruebeli* is also distally broadened but has a pointed tip (see fig. 8m in Rieppel, 1987). As in other askeptosauroids, the ventral portion of the ilium is much broader than the dorsal blade; the iliac acetabulum is very broad and concave, the facet for the pubis is wider than that for the ischium, and the medial surface is convex. The articular facets for the two sacral ribs are still covered by the matrix.

The pubes are nearly complete (Fig. 7A, B). As a whole, the pubis resembles that of *Anshunsaurus huangguoshuensis* (see fig. 10 in Liu and Rieppel, 2005). It is a polygonal plate as in other thalattosaurians, with a curved anterior margin, a straight anterodorsal margin, and a slightly bulged medial margin. The articular facet for the ischium is as large as that for the ilium. The obturator foramen is located closer to the posterodorsal rather than the anterodorsal margin. The ventral (outer) surface is convex and the dorsal (inner) surface is concave. The pubic portion of the acetabulum is not well defined because of surface erosion.

The right ischium is nearly complete in ventral view. It is a plate-like bone that has a concave posterodorsal, a slightly concave posteroventral, and a convex medial margin (Fig. 7A). The posteriorly directed process between the posterodorsal and posteroventral margins is not as sharply pointed as in most other thalattosaurians such as *Anshunsaurus huangguoshuensis* (see fig. 10 in Liu and Rieppel, 2005), *Askeptosaurus italicus* (see fig. 10 in Müller, 2005), and *Endennasaurus acutirostris* (see fig. 8A in Renesto, 1992). The anteromedial margin is convex (but not complete), which certainly indicates that there was a median opening between the pubic symphysis and ischial symphysis in life. There is no evidence to suggest an opening or foramen present between the pubis and ischium, which is seen in *E. acutirostris* (see fig. 6 in Müller et al., 2005).

**Forelimbs** Both forelimbs, except for the left zeugopodium and manus, are preserved in ventral (posterior) view although disarticulated (Figs. 3, 6A–C). Most of the limb elements are measurable (Table 1) although they were flattened during fossilization. The humerus is a massive bone with a slightly broadened head, a thick shaft, and an expanded distal end (Fig. 6A, B). The expansion of the distal end is certainly exaggerated by dorsoventral compression, which is indicated by the difference in the width of two humeri. As in the species of *Anshunsaurus*, the proximal head does not form a pronounced articular prominence seen in *Endennasaurus acutirostris* (see fig. 5A in Müller et al., 2005 (the humerus should be the left one rather than the right)). The humerus is relatively short and stout in comparison with that of other askeptosauroids such as *E. acutirostris* and *Askeptosaurus italicus*. In ventral (posterior) view, the deltopectoral crest is weakly developed when compared with that of *Anshunsaurus huangguoshuensis* (see fig. 9 in Liu and Rieppel, 2005). The ectepicondyle and entepicondyle are not well-developed. There is an entepicondylar groove along the distomedial margin of the shaft. The concavity of the ventral surface of the distal portion is exaggerated during preservation.

The right radius is complete and well-exposed. As in *Anshunsaurus huangguoshuensis* (but see *A. wushaensis* (see the type specimen, IVPP V 13782 or the juvenile in fig. 5 in Liu, 2007)), the distal end is slightly broader than the proximal end (Fig. 6B). The outer edge of the radius is nearly straight and the ulnar edge is concave. The concavity on the ventral surface

of the bone is exaggerated during fossilization. The proximal articular surface is flat whereas the distal articular surface is convex.

**Table 1** Measurements of selected elements of *Miodentosaurus* (mm)

		Axis	C6	C9	D2	D12	S2	Ca2			
Length of centrum		30.3	35.8	35.5	38.8	38.1	36.1	43			
Height of whole vertebra		49	32.5	34.2	35.5	32.5	32.9	37.5			
Height of centrum		—	74.5	82.4	85.8	109	106.9	108.6			
Maximal width of spine		46	18.7	22.2	30	34.5	19.5	22.5			
		Hu	Ra	Ul	Fe	Fi	Ti				
Length	(R)	186	114	87	210.6	96.2*	94.5*				
	(L)	188	103*	105	—	—	—				
Proximal width	(R)	62.5	36	—	49.2	28.5	50.5				
	(L)	61.9	37	33	—	—	—				
Distal width	(R)	68.8 <sup>#</sup>	45.5	36.8	80.4	—	—				
	(L)	86	47.2	36	—	—	—				
		MCI	MCH	MC III	MCIV	MCV	MTI	MTH	MT III	MTIV	MTV
Length/R		47	59.4	60	61.5	52.5	56.4	68.7	72.5	—	63

\* preserved length; # exposed width.

The right ulna is entirely exposed although its proximal end is incomplete. The complete left ulna is extensively covered with the gastralia (Fig. 6B,C). Both ends of the ulna are similarly expanded, but the proximal end is incomplete or partly covered (see Table 1 for measurements). The shaft is nearly symmetrically constricted as in *Anshunsaurus huangguoshuensis*. The radial side of the ulna is more curved than the outer side in *Askeptosaurus italicus* and *Endennasaurus acutirostris*. The concave ventral surface of the bone is exaggerated by the dorsoventral compression.

The manus is disarticulated but many of its elements are preserved. The ulnare is nearly round and has a concave ventral surface. The intermedium is roughly rectangular in outline and has a concave dorsomedial side. The centrale is asymmetrically pentagonal in shape (Fig. 6C). The four distal carpals and five metacarpals are closely associated. Distal carpal 2 is the smallest and the hexagonal distal carpal 4 is the largest. Distal carpal 1 is smaller than distal carpal 3 as in *Anshunsaurus huangguoshuensis* but the opposite is true in *Askeptosaurus italicus* and *Endennasaurus acutirostris*.

As in some other askeptosauroids, metacarpal I is the shortest but most massive among the five elements, with a proximal end much broader than the distal end (Fig. 6C). It is relatively slender in *Endennasaurus acutirostris* (see fig. 5 in Müller et al., 2005). Metacarpals II, III, and IV are of approximately same length (59.4, 60, and 61.5 mm, respectively), which is comparable with those in the species of *Anshunsaurus*. Metacarpal V is longer than metacarpal I, whereas the opposite is the case for *E. acutirostris* and *Clarazia schinzi* (see fig. 5 in Rieppel, 1987).

The first phalanx is closely associated with the corresponding metacarpal in each digit (Fig. 6C). There is a phalanx close to the first of digit 1, which does not belong to this digit; it is in the opposite direction, suggesting that it may have been displaced from a different digit. In this case, it is most likely that digit 1 had two phalanges including the terminal claw (ungual), as in other thalattosaurians. There are number of phalanges scattered around but it is difficult to determine their original location; thus, the phalange formula of the forelimb cannot be established.

**Hindlimbs** The right hindlimb is more complete than the left (Fig. 3). The right femur

is exposed in ventral view, and longer (about 112%) than the humerus. The head is slightly damaged but shows no evident expansion (Fig. 7A). The distal end is complete and expanded. The posterior edge of the femoral shaft is nearly straight but the anterior (medial) edge is concave. The internal trochanter is well-developed, located at the proximomedial (anterior) edge near the articular head as in *Anshunsaurus huangguoshuensis* (IVPP V 11834, see Liu and Rieppel, 2005:23). The fourth trochanter seen in *Endennasaurus acutirostris* (see fig. 7 in Müller et al., 2005) is not evident here. The shaft is flat but it is exaggerated by dorsoventral compression during preservation. There is a depression on the proximoventral surface, and it may have been enhanced by compression. The distoventral surface of the femur is slightly convex, and the distal end has a narrow condyle with which the fibula articulates.

The right tibia is nearly complete but it was superficially damaged in its distodorsal portion (Fig. 7C). As in the species of *Anshunsaurus*, the proximal end is much wider than the distal end. The inner (fibular) margin of the shaft is concave but the outer margin is nearly straight, as in other thalattosaurians.

The right fibula is preserved in ventral view but the proximal and distal ends are damaged (Fig. 7C). It should have been posterolateral to the tibia in life, but it is now located anteromedial to the tibia due to the postmortem displacement. The distal end is wider than the proximal end, as in other thalattosaurians. The constriction of the fibular shaft is nearly symmetrical.

All tarsals are missing except for one which is identified as distal tarsal 5 (Fig. 7C). The surface is damaged but the round outline remains.

Metatarsals I–III and V are preserved. The latter three were displaced from the posterolateral side to the anteromedial side (Fig. 7C), possibly along with the displaced fibula mentioned above. Metatarsal I is the shortest but most massive among the four. It resembles that of *Anshunsaurus* species and *Askeptosaurus italicus* in that its outer side is shorter and more incurved than its inner side and its proximal end is much more expanded than its distal end. Metatarsals II and III are morphologically similar to each other although the latter is slightly longer than the former. Their shaft does not constrict as much as in the aforementioned two taxa and *Endennasaurus acutirostris* (see fig. 11 in Renesto, 1992). As in other thalattosaurians, metatarsal V is more massive but shorter than metatarsals II and III. Its proximal surface for the articulation with the fifth distal tarsal is oblique internally as in *E. acutirostris*.

There are 16 phalanges including five claws (Fig. 7C). The first phalanges of digits 2, 3, and 5 are identified on the basis of their close association to the corresponding metatarsal. The others are scattered around, and the foot phalangeal formula is unknown.

### 3 Revised diagnosis of *Miodentosaurus brevis* Cheng et al., 2007

Cheng et al. (2007) provided a set of diagnostic characters of *Miodentosaurus brevis* based on the study of the skull and mandible. Comparison of the postcranial anatomy reveals that several postcranial features are not common for the Thalattosauria and considered as extra diagnostic characters of *M. brevis*. The most striking of those characters come from the girdle elements, including the coracoid, interclavicle, ilium, and ischium. In addition, the morphology of the frontal, parietal, and surangular clarified here is also distinctive within the Thalattosauria. Therefore, the diagnosis of *M. brevis* is revised as: 1) straight snout very short, nearly as short as post-snout region (from anterior edge of orbit to posterior edge of skull table); 2) presence of crest along anterior third of dorsal midline of premaxillae; 3) premaxilla having six conical teeth; 4) maxilla edentulous; 5) frontal forming anterior border of pineal foramen; 6) parietal possessing slender anterolateral process to wrap posterolateral process of frontal; 7) dentary having no more than six conical teeth implanted in rostral portion; 8) surangular suddenly broadens ventrally at posterior third of its length; 9) coracoid possessing small embayment just

posterior to glenoid; 10) interclavicle becoming much narrower distally than proximally; and (11) iliac blade with expanded distal end.

#### 4 Phylogenetic relationships

Recently, a number of phylogenetic analyses of the Thalattosauria have been published (Nicholls, 1999; Liu and Rieppel, 2001, 2005; Jiang et al., 2004; Müller, 2005, 2007; Müller et al., 2005; also see Appendix 1). With a number of new thalattosaurians newly discovered from China, most recent analyses have suggested that the Thalattosauria consists of two major groups, the Thalattosauroida and Askeptosauroida (Liu and Rieppel, 2005; Müller, 2005, 2007). In the study of the cranial morphology, Cheng et al. (2007) mentioned that the features of the snout and palate suggest a close relationship of *Miodentosaurus* with askeptosauroids although no detailed phylogenetic analysis was carried out because the postcranial skeleton was not available for the study then. The phylogenetic relationships of *Miodentosaurus* are established here on the basis of a cladistic analysis that employs the data matrix derived from the studies of Müller (2007). The new data matrix (Appendixes 2, 3) consists of 42 characters and 15 taxa including *Miodentosaurus* and *Anshunsaurus wushaensis* Rieppel et al., 2006. The definition of the characters are not modified at all from those of Müller (2007) except for character 29, which is now redefined as a tri-state character: cervical vertebrae < 10 (0), > 10 (1), or  $\geq 15$  (2). The analysis (using the branch-and-bound search option of PAUP\* 4.0b10 (Swofford, 2002), all characters unordered, multiple character states treated as polymorphism) produces three shortest trees, with a tree length of 72, CI of 0.625, and RI of 0.738. In all three trees, the included thalattosaurians form two monophyletic groups, the Askeptosauroida and Thalattosauroida (Fig. 8A), as in Liu and Rieppel (2005) and Müller (2005, 2007). The monophyly of the Askeptosauroida is unequivocally supported by five synapomorphies, characters 11, 12, 19, 27, and 29 while the monophyly of the Thalattosauroida is supported by six unequivocal synapomorphies (characters 2, 4, 17, 30, 35, and 37) and four equivocal characters (5, 21, 33, and 36) from ACCTRAN character optimization. *Miodentosaurus* and *Anshunsaurus wushaensis* are unequivocally grouped within the clade Askeptosauroida. Within this clade, a monophyletic Askeptosauridae including *Anshunsaurus*, *Miodentosaurus*, and *Askeptosaurus* is supported as in Liu and Rieppel (2005) and Müller (2005, 2007). *Anshunsaurus wushaensis* is the sister group of *A. huangguoshuensis*, supporting the study of Rieppel et al. (2006), and *Miodentosaurus* has a closer relationship to *Askeptosaurus* than to *Anshunsaurus*. The close relationship between *Miodentosaurus* and *Askeptosaurus* is unambiguously supported by two synapomorphies, i. e., character states 28 (presence of a small retroarticular process, wider than long (a reversal)) and 38 (a reduced deltopectoral crest). The close relationship of the two species of *Anshunsaurus* is supported by state 2 of character 29 (there are more than 15 cervical vertebrae). Our result was exactly same as the analyses of Müller (2005, 2007), in terms of the branching pattern of the Thalattosauroida (his Thalattosauria). As in previous analyses, the bootstrap support is not very strong for many clades (Fig. 8B), much weaker than in Müller's analyses (2005, 2007). With the addition of *M. brevis* and *A. wushaensis*, the monophyly of the Thalattosauroida has a strong support in 100 bootstrap replicates (84%), although it is not the case for the clades within this group. The bootstrap support for the monophyly of the Askeptosauridae is lower than 50%, while the support for the monophyly of the Askeptosauroida is only 53%. There are two taxa (Kössen-Form and *Agkistrognathus*) that have only 4 or 5 characters out of the 42 are scored. This may have affected the results of the analyses, but the tree(s) from an analysis without these two taxa is/are also poorly resolved. This may indicate that the members of the Askeptosauroida might not be so closely related with one another.



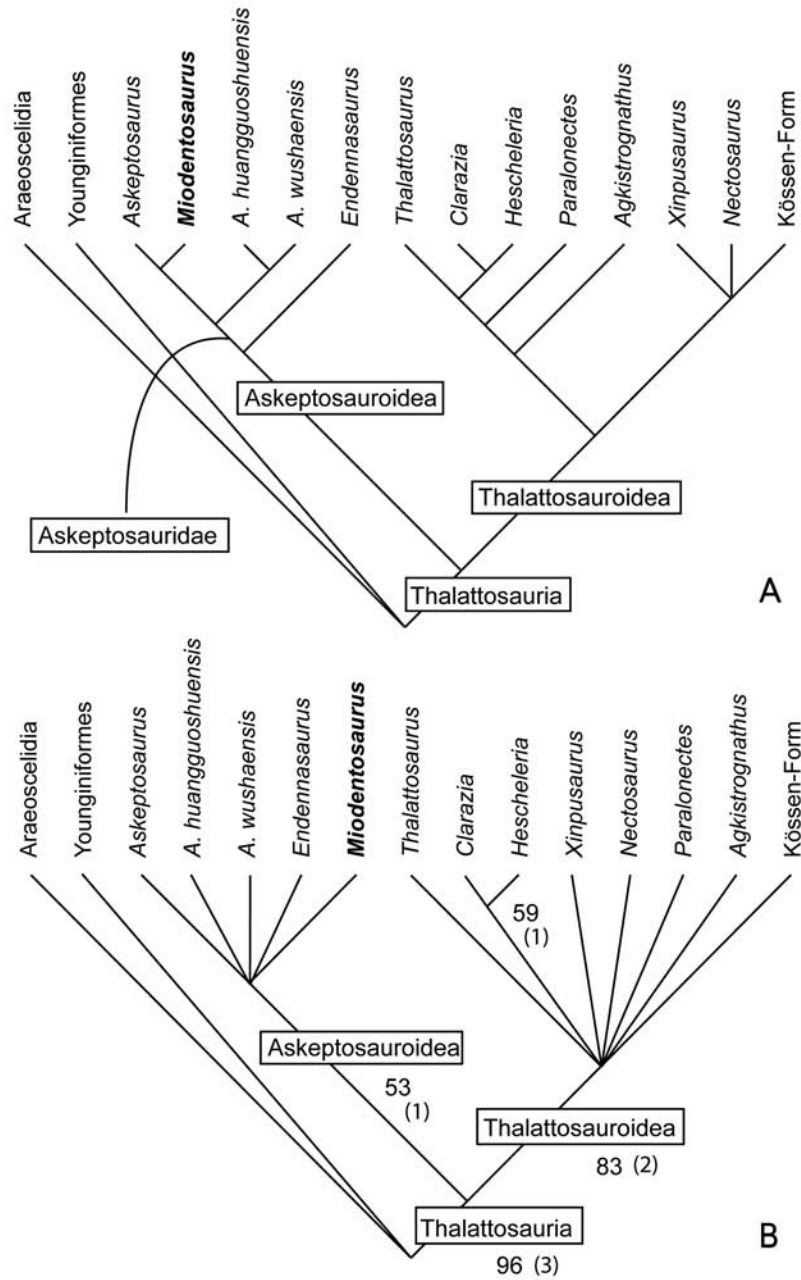


Fig. 8 Cladograms showing phylogenetic relationships of *Miodontosaurus brevis* Cheng et al., 2007  
 A. strict consensus of three shortest trees, with tree length of 72, CI of 0.625, and RI of 0.735; B. bootstrap 50% majority-rule consensus tree, with bootstrap values > 50% indicated; numbers blocked indicate decay index

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### Appendix 1 Specimens and literatures for the character-state data matrix

Araeoscelidia (*Petrolacosaurus kansensis* (Reisz, 1981))  
 Younginiformes (*Y. capensis* (Gow, 1975; Carroll, 1981))  
*Agkistrognathus campebelli* (Nicholls and Brinkman, 1993)  
*Askeptosaurus italicus* (Kuhn-Schnyder, 1971; Müller, 2005)  
*Thalattosaurus* (*T. alexandrae* (Nicholls, 1999), *T. borealis* (Nicholls, 1999; Rieppel et al. 2005))  
*Anshunsaurus huangguoshuensis* (IVPP V 11834 and V 11835; Rieppel et al., 2000; Liu and Rieppel, 2005)  
*Anshunsaurus wushaensis* (IVPP V 13782; Rieppel et al., 2006; Liu, 2007)  
*Clarazia schinzi* (Rieppel, 1987; Rieppel et al., 2005)  
*Hescheleria ruebeli* (Rieppel, 1987)  
*Xinpusaurus* (*X. bamaolinensis* including *X. kohi* Jiang et al., 2004 (Cheng, 2003; Jiang et al., 2004) and *X. suni* (IVPP V 11860 and V 14372; Liu and Rieppel, 2001; Luo and Yu, 2002; Rieppel and Liu, 2006))  
*Nectosaurus halius* (Nicholls, 1999; Rieppel et al., 2005)  
*Paralonectes merriami* (Nicholls and Brinkman, 1993)  
*Endennasaurus acutirostris* (Renesto, 1992; Müller et al., 2005)  
 Kössen-Form (Müller, 2007)  
*Miodentosaurus brevis* (NMNS-004742/F003960; Cheng et al. 2007; this study)

### Appendix 2 Characters for the phylogenetic analysis of *Miodentosaurus* (derived from the data matrix of Müller (2007), with the modification of character 29)

1. Rostrum: absent (0); present (1).
2. Rostrum morphology: straight (0); deflected ventrally (1).
3. Rostrum profile: straight (0); premaxilla moderately turned downwards (1); premaxilla strongly turned downwards, its alveolar margin positioned nearly vertical relative to the alveolar margin of the maxilla (2).
4. Proportions of maxilla: at least twice as long as high (0); with truncated anterior end and narrow, vertically positioned ascending process (1).
5. Tooth implantation: subtheodont (0); thecodont (1); ankylotheodont (2); teeth superficially attached to the bone (3).
6. Premaxilla dentition: present (0); absent (1)(State 1 includes also pseudodont projections).
7. Diastema between premaxillary and maxillary teeth: absent (0); present (1).
8. Anterior most dentary teeth: upright (0); procumbent as their implantation curves around anterior end of dentary (1).
9. Posterior dentary and maxillary teeth: conical and pointed (0); bulbous and blunt (1).
10. Pterygoid transverse flange dentition: present (0); absent (1).
11. Pterygoid palatal ramus dentition: present (1); absent (1).
12. Vomerine dentition: present (0); absent (1)
13. Nasals, medial contact: meet each other medially (0); separated because of the posterior extent of the premaxilla (1).
14. Nasals, posterior extent: do not (0), or do (1) extend backwards to level behind anterior margin of orbit. Character coding has been changed for *Paralonectes* (1).
15. Anterolateral processes of frontal: broadly separated from external naris (0); closely approach or even enter the posterior margin of external naris (1).

16. Anteromedial process of frontal; broadly separated from external naris (0); closely approaching external naris (1).
17. Nasal-prefrontal contact; nasal in contact with prefrontal (0); nasal separated from prefrontal (1).
18. Posterolateral processes of frontal; absent (0); present (1).
19. Posterolateral processes of frontal, posterior extent; not extending far beyond anterior margin of lower temporal fossa (0); extending distinctly beyond anterior margin of lower temporal fossa (1).
20. Frontal-supratemporal contact; frontal separate from supratemporal (0); frontal in contact with supratemporal (1).
21. Posterolateral process of frontal constriction; constricted (0); broad (1) (i. e., fronto-parietal suture interdigitating, oriented transversely for most of its part (0), or deeply embayed in the shape of a broad V with apex pointing forward (1)).
22. Postfrontal and postorbital; separate (0); fused (1).
23. Upper temporal fenestra; present and large (0); absent or reduced and slit-like (1).
24. Squamosal; with (0), or without (1) posteroventral process.
25. Quadrate; with (0), or without (1) distinct medial lamina.
26. Quadratojugal; present (0); absent (1).
27. Pineal foramen; small and located at center or somewhat behind of parietal skull table (0); large and located in front of midpoint of parietal skull table (1).
28. Retroarticular process; small or absent (0); present and distinct (1).
29. Number of cervical vertebrae: < 10 (0); > 10 (1); ≥ 15 (2) (modified).
30. Neural spine height of posterior cervicals and thoracals; relatively low (0); at least two times taller than broad (1).
31. Proximal caudal neural spine height; relatively low (0); distinctly elongated and at least three times taller than broad (1).
32. Cervical ribs; without (0), or with (1) anterior process.
33. Scapula; broad and rounded (0); slender and elongate (1).
34. Humerus; long and slender (0), or stout and short (1), relative to the trunk.
35. Radius; slender (0); expanded (1).
36. Radius expansion; only slightly expanded (0); strongly expanded and roughly kidney-shaped (1).
37. Fibula; slender (0); expanded (1).
38. Deltpectoral crest; well developed (0); reduced (1).
39. Fibula expansion; slightly expanded (0); broadly expanded mediolaterally (1).
40. Snout elongation; distance from the anterior margin of the orbit to the anterior tip of the rostrum less (0), or more (1), than twice the distance from the anterior margin of the orbit to the posterior margin of the parietal skull table.
41. Tip of snout; lateral edges of snout terminating in a blunt tip (0); converging and terminating in a pointed tip (1).
42. Shape of snout; lateral edges of snout converging (0); parallel (1).

**Appendix 3** Character-taxon matrix for the phylogenetic analysis of *Miodontosaurus* (derived from that of Muller (2007) with the addition of *Miodontosaurus* and *Anshunsaurus wushaensis*)

<i>Araeoscelidia</i>	00?000000	00000000??	0000000000	00000?00?0	00
Younginiformes	00?000000	0001000100	0000000000	00000?00?0	00
<i>Askeptosaurus</i>	10?0000001	11110110--	0010111010	01010?01?1	01
<i>Thalattosaurus</i>	1100211111	0010101101	1111010??1	??1111?0?1	10
<i>Anshunsaurus-h</i>	1000000001	1111000110	0110011120	0101000001	01
<i>Anshunsaurus-w</i>	100000000?	??1?0?????	?11?011120	01?1000000	01
<i>Clazzia</i>	1101301111	001010?101	0111110100	0?0?101100	10
<i>Hescheleria</i>	1111301111	0?1???????	?11????101	0101101100	??
<i>Xinpusaurus</i>	1101?000?0	0010001100	111011?101	1?11111011	10
<i>Nectosaurus</i>	?11110??01	0010??110?	111?11?1?1	1?1111?0?0	??
<i>Paralonectes</i>	1111201111	0011??????	???0?1?1??	??????????	??
<i>Agkistrognathus</i>	????2?100?	?0????????	??????????	??????????	??
<i>Endennasaurus</i>	10?0?1???1	1110?1011?	01??1??110	0000??00?1	10
Kössen-Form	??????????	??????????	??????????	1????11?1?	??
<i>Miodontosaurus</i>	10000-0-1	1111000110	0110011010	0101000100	01

*Anshunsaurus-h* = *Anshunsaurus huangguoshuensis*; *Anshunsaurus-w* = *Anshunsaurus wushaensis*; “-” = inapplicable, which is treated as “?” in analyses.