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短吻贫齿龙(双孔亚纲:海龙目)的新材料及补充研究[1)]

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摘要:记述了产自贵州关岭法郎组瓦窑段(上三叠统)短吻贫齿龙一新材料。新标本头后骨骼十分完整,使我们对该海龙的全身骨骼形态有了一个完整的认识,尤其是澄清了其肩带及前、后肢的解剖学特征。短吻贫齿龙牙齿稀少且局限于上、下颌的前端,以及末端指/趾骨(爪)扁平等性状表明,该种不是纯粹的肉食动物。依据新材料,短吻贫齿龙在局部形态上存在个体变异,并确认后肢趾趾式(2-3-4-5-5)可作为该海龙的特征之一。

关键词:海龙目,贫齿龙,骨架,个体变异
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A NEW SKELETON OF *MIODENTOSAURUS BREVIS* (DIAPSIDA: THALATTOSAURIA) WITH A FURTHER STUDY OF THE TAXON

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Abstract A new thalattosaurian skeleton from the Upper Triassic Wayao Member of the Falang Formation, Guanling area, Guizhou Province, China can be referred to *Miodentosaurus brevis*. The postcranial skeleton of the specimen is well-preserved and so complete that it is worthy to be described. This new specimen provides a full knowledge of the osteology of the thalattosaurian, especially the anatomy of the pectoral girdle and both the fore- and hind-limbs. The presence of a few teeth restricted to the anterior ends of both the upper and lower jaws and dorsoventrally flattened ungual phalanges indicate that *M. brevis* is not a pure carnivore. With new information, some individual variations are recognized and the digital formula (2-3-4-5-5) of the pes can be identified as one of the diagnostic features for the thalattosaurian.

Key words Thalattosauria, *Miodentosaurus*, skeleton, individual variation

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1 Introduction

The type of *Miodentosaurus brevis* (Cheng et al., 2007; Wu et al., 2009) is a relatively complete skeleton but some elements of the girdles are obscured due to postmortem damage (e.g., the scapula), the tail is missing the posterior third, and the zeugopodium and manus/pes of the forelimbs/hindlimbs are incomplete. A new thalattosaurian skeleton (Fig. 1) was collected from the same lower Upper Triassic Wayao Member of the Falang Formation in the Guanling area, Guizhou Province, China. Although the skull of this specimen is preserved in ventral view, it is evidently referable to *Miodentosaurus brevis* on the basis of the combination of the following features: no more than six teeth in the premaxilla, the short snout, the edentulous maxilla, the open and elongate interpterygoid vacuity, the internal carotid foramen on the ventral surface of the basisphenoid, and the interclavicle becoming much narrower distally than proximally. The new specimen is so complete that it can be used to clarify the anatomy of the areas that are not well-preserved or missing in the type.

The new specimen of *Miodentosaurus brevis* is housed in Zhejiang Museum of Natural History (ZMNH), with a catalogue number of ZMNH M8742. It is articulated and very complete except for the palm of the right forelimb and tarsus of the left hindlimb. The skull is preserved in ventral but the postcranial skeleton is mainly in lateral views. The whole skeleton is about 440 cm in total length, with a precaudal length of approximately 181.5 cm.

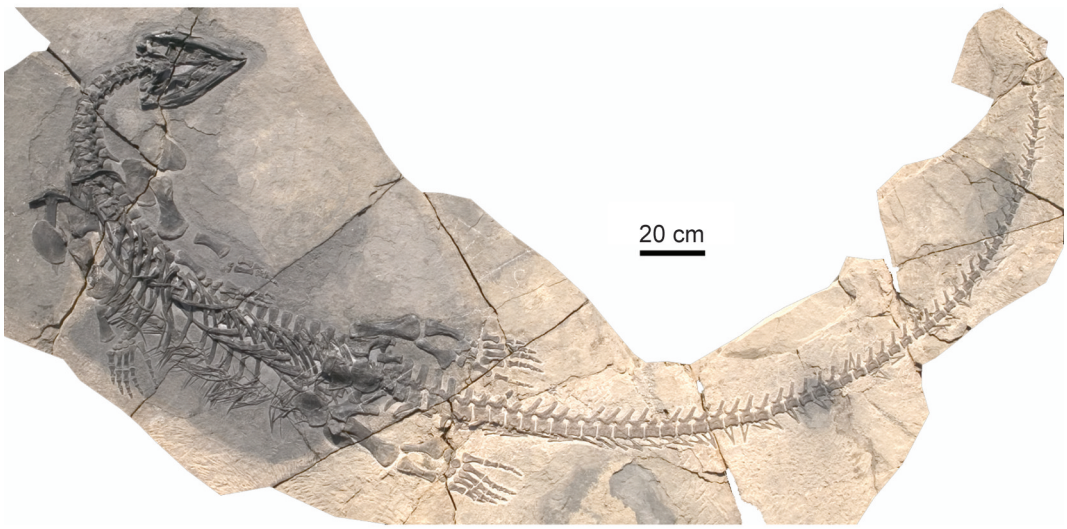

Fig. 1 The new skeleton of *Miodentosaurus brevis* (ZMNH M8742)
The skull and mandible in ventral view and the postcranial mainly in lateral view

2 Description and comparison

Skull and mandible The skull is similar in length to that of the type, which is based on the length from the anterior margin of the choana to the posterior end of the occipital condyle (18.2 cm in the new specimen and 18.4 cm in the type). The exposed ventral surface of the skull morphologically differs little from that of the type, and the mandible shows no significant anatomical difference as well. The nearly intact skull further indicates that the internal choana is small and oval in outline; the two pterygoids do not meet along the midline and their slightly curving medial margin indicates an open and long vacuity between them; and the internal caro-

tid foramen is located on the ventral surface of the basisphenoid (Fig. 2). As in the type, the palatal elements do not have any teeth or denticles on the ventral surface.

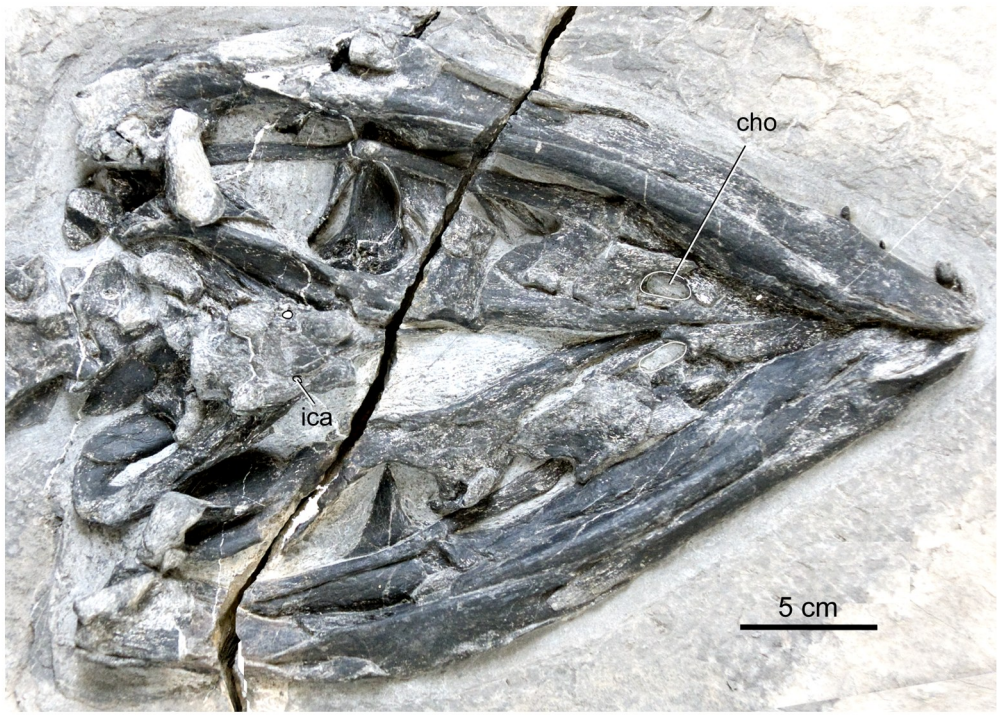

Fig. 2　A close-up of the skull of *Miodentosaurus brevis* (ZMNH M8742) in ventral view
Abbreviations: cho. choana 内鼻孔; ica. foramen for internal carotid artery 内颈动脉孔

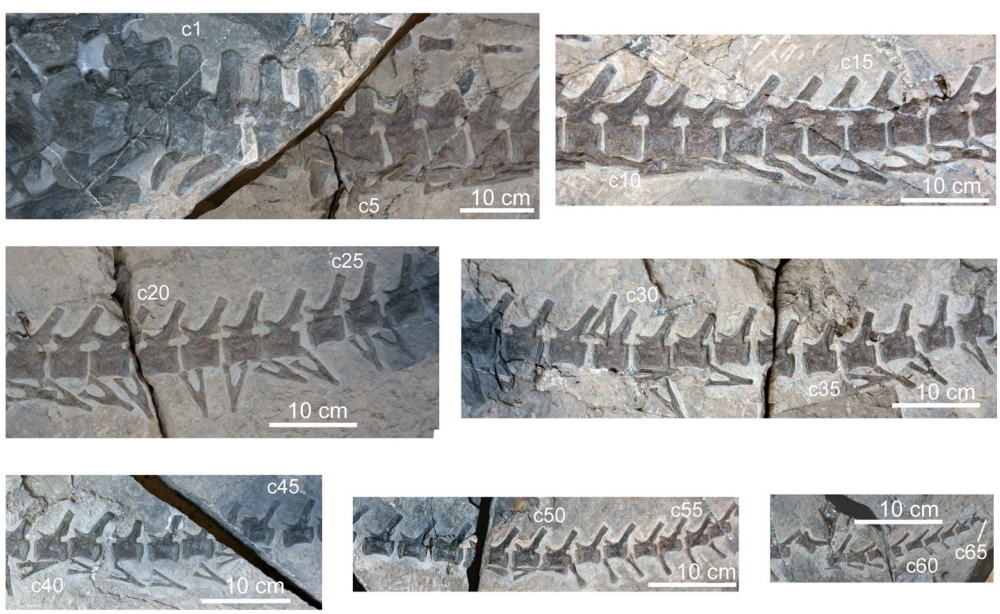

Fig. 3　The 65 caudal vertebrae of *Miodentosaurus brevis* (ZMNH M8742) in lateral view
Abbreviation: c. caudal vertebrae 尾椎

Axial skeleton The complete vertebral column consists of 105 vertebrae, of which there are 13 cervical, 25 dorsal, 2 sacral, and 65 caudal vertebrae (Fig. 3). The number of each vertebral section of the precaudal vertebral column is same as in the type. The posterior dorsal vertebrae are obscured by the overlapping of the elements of the pelvic girdle in the type, which are well exposed in ZMNH M8742. Morphologically, those dorsals are not different much from the anterior dorsals, with a neural spine that is constricted at the base. As a whole, there are only a few size-related differences in the vertebral column between the new specimen and the type, of which the most obvious is in the sacral and first two caudal vertebrae relative to the dorsals (see Table 1). These may reflect individual variations within the thalattosaurian.

Table 1 Measurements of selected elements of the type (from Wu et al., 2009) and the new specimen (ZMNH M8742 in the second line) (mm)

	Axis	C6	C9	D2	D12	S2	Ca2
Length of centrum	30.3	35.8	35.5	38.8	38.1	36.1	43
	26^	34.5	35	38	39.5	42	40.5
Height of centrum	—	32.5	34.2	35.5	32.5	32.9	37.5
	29.5	34	33	34	34	45	43
Height of whole vertebra	49	74.5	82.4	85.8	109	106.9	108.6
	52.5	70	81	85	—	122	128
Maximal width of spine	46	18.7	22.2	30	34.5	19.5	22.5
	30	19.5	25.5	30	26	24.5	24

		Hu	Ra	Ul	Fe	Fi	Ti
Length	(R)	186	114	87	210.6	96.2*	94.5*
		—	110	—	210	131	121
	(L)	188	103*	105	—	—	—
		195	110	115	212	130	122
Proximal width	(R)	62.5	36	—	49.2	28.5	50.5
		68	42.5	—	49.5	28	48.5
	(L)	61.9	37	33	—	—	—
		67	43	40	48	29	50
Distal width	(R)	68.8*	45.5	36.8	80.4	—	—
		91	51	—	78	67	31
	(L)	86	47.2	36	—	—	—
		95	51.5	36	77	66	30

	MCI	MCII	MCIII	MCIV	MCV	MTI	MTII	MTIII	MTIV	MTV
Length (R)	47	59.4	60	61.5	52.5	56.4	68.7	72.5	—	63
	45	42	50	60	55	50	64	68	72	67.5

Abbreviations: C. cervical 颈椎; Ca. caudal vertebrae 尾椎; D. dorsal 背椎; Fe. femur 股骨; Fi. fibula 腓骨; Hu. humerus 肱骨; MC. metacarpal 掌骨; MT. metatarsal 跖骨; Ra. radius 桡骨; S. sacral 荐椎; Ti. tibia 胫骨; Ul. ulna 尺骨.

* preserved length or exposed width 保存的长度或暴露的宽度; ^ not including the odontoid process 不包含齿突.

The type has the first 47 caudal vertebrae preserved, of which, however, the 3rd to 5th and the 12th and 13th are missing. There is no obvious morphological difference in the first two caudals between ZMNH M8742 and the type, with no chevron facets along the posteroventral edge of the centrum of the two caudals. Caudal vertebrae 3–5 in the new specimen also have a nearly vertically oriented neural spine, as in the first two. As in the type, the neural spine (shown by the impression) of the 6th caudal starts to direct posterodorsally (to a greater degree in the further posterior caudals) and the distal end of the neural spine is narrower than the base. It is clear that the caudal rib is sutured but not fused to the transverse process until the 8th caudal, one more posterior than in the type. The chevron stars to occur from the 4th caudal vertebra and is present through others to the 62nd.

Fig. 4　The pectoral girdle and forelimbs of *Miodentosaurus brevis* (ZMNH M8742)
A. elements of the pectoral girdles in internal view and the left humerus in posterior (ventral) view; B. the left radius and ulna in posterior view; C. the left manus in ventral view
Abbreviations: avf. anteroventral flange 前腹翼; cl. clavicle 锁骨; cn. centrale 中央腕骨; co. coracoid 乌喙骨; cof. coracoid foramen 乌喙孔; h. humerus 肱骨; icl. interclavicle 间锁骨; in. intermedium 中间腕骨; ra. radius 桡骨; sc. scapula 肩胛骨; ul. ulna 尺骨; unl. ulnare 尺腕骨; I, III, V. the 1st, 3rd, 5th metacarpal 第一, 第三和第五掌骨; 1, 3. the 1st, 3rd distal carpal 第一和第三远侧腕骨

No difference is significant in the first 47 caudal vertebrae between ZMNH M8742 and the type. After the 47th, the further posterior caudal vertebrae still keep a similar morphology, except for the size reducing. They retain a narrow, tall, and obliquely oriented neural spine before the last caudal. The latter is slightly displaced, with its anterior end pointing backward. It is about half-sized and has no neural spine at all.

Two sacral ribs are well-preserved in both the type and ZMNH M8742. The 1st shows little difference between the two specimens. However, the 2nd is rod-like and with both ends slightly expanded in ZMNH M8742 (Fig. 5A). This rib has a distal end much broader than the proximal end in the type (see fig. 7A, B in Wu et al., 2009).

Pectoral girdle All elements of the pectoral girdle are well exposed except for the scapula in the type (Wu et al., 2009). The right scapula is complete in ZMNH M8742. It is characterized by a thin and broad anteroventral flange (Fig. 4). In contrast to a plate-like shape seen in most other thalattosaurians, the scapula remains a shaft although very short. The dorsal blade of the scapula does not expand much. In general, the scapula is most comparable to that of *Anshunsaurus huangguoshuensis* but the bone in the latter has a relatively narrower and taller shaft (see fig. 5 in Liu and Rieppel, 2005). The scapula of *Thalattosaurus alexandrae* (see fig. 10A in Nicholls, 1999) is slightly damaged but it shows the presence of the anteroventral flange. The scapula of this species even has an evident shaft with an expanded dorsal blade, very similar to that of a terrestrial reptile.

A small embayment just posterior to the glenoid seen in the coracoid of the type is not present in ZMNH M8742. This is evidently an individual variation in *Miodentosaurus brevis*. The interclavicle is preserved in external view in the type, which is in internal view in ZMNH M8742. The internal surface of the interclavicle is flat and smooth in most part of the bone; it is strongly concave close to the arrowhead-like anterior end.

Pelvic girdle The ilium bears a nearly straight dorsal blade with a slightly broadened distal tip in the type (Wu et al., 2009), 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). However, the right ilium of ZMNH M8742 (Fig. 5A) shows that the shaft of the dorsal blade is curved posterodorsally and distally not broadened, as in *Anshunsaurus huangguoshuensis* (see fig. 6 in Liu and Rieppel, 2005), although the shaft is not as strongly curved as in *A. italicus*, and *E. acutirostris*. This is an individual variation within *Miodentosaurus brevis*.

The right ischium is nearly complete in external view in the type (Wu et al., 2009). It was described that the posteriorly directed process was not as sharply pointed as in most other thalattosaurians such as *Anshunsaurus huangguoshuensis*, *Askeptosaurus italicus*, and *Endennasaurus acutirostris*. In ZMNH M8742, the well-preserved left ischium shows a similar morphology as seen in *A. huangguoshuensis* (see fig. 10 in Liu and Rieppel, 2005), with a posteriorly directed moderate process (Fig. 5A). This process clearly differs from that of *A. italicus* in which it is much strong and continues from the posteromedial margin of the bone (see fig. 10 in Müller, 2005) and that of *E. acutirostris* in which it is pronounced and very sharp, projecting posteriorly from a nearly straight posterior margin (see fig. 8A in Renesto, 1992). It is obvious that the entire shape of this process in the type was obscured because of the damage along the margins of the bone.

Forelimbs Most elements of the zeugopodium and manus are either incomplete or disarticulated in both forelimbs in the type (Wu et al., 2009). The radius (in posterior/ventral view) and ulna (in dorsal/anterior view) of the left side and the manus of the right side are well-preserved in ZMNH M8742 (Fig. 4B, C). As previously described (Wu et al., 2009), the new radius differs little from that of *Anshunsaurus huangguoshuensis* [but see *A. wushaensis* (the type specimen, IVPP V 13782 or the juvenile in fig. 5 in Liu, 2007)], with the distal

Fig. 5　The pelvic girdle and hindlimbs of *Miodentosaurus brevis* (ZMNH M8742)

A. elements of the right pelvic girdle and femur in medial view and elements of the left pelvic girdle and femur in lateral view; B. the right fibula and tibia and pes in posterior (ventral) view; C. the left fibula and tibia and pes in posterior (ventral) views

Abbreviations: as. astragalus 距骨; ca. calcaneum 跟骨; cr. caudal rib 尾肋; f. femur 股骨; fi. fibula 腓骨; fpu. facet for pubis 耻骨关节面; gl. glenoid portion of ischium 坐骨髋臼部; il. ilium 肠骨; is. ischium 坐骨; mem. medial margin of ischium 坐骨内缘; otf. obturator foramen 闭孔; pdm. posterodorsal margin of ischium 坐骨后背缘; pu. pubis 耻骨; sr. sacral rib 荐肋; ti. tibia 胫骨. I, V. the 1st, 5th metatarsal 第一和第五跖骨; 1, 4. the 1st, 4th distal tarsal 第一和第四远侧跗骨

end which is slightly broader than the proximal end. The lateral edge of the radius is nearly straight and the ulnar edge is concave. The proximal articular surface is flat whereas the distal articular surface is convex.

The exposed right ulna is proximally incomplete and the complete left one is extensively covered by the gastralia in the type (Wu et al., 2009). The left ulna of ZMNH M8742 shows that both ends of the bone are similarly expanded. The shaft is nearly symmetrically constricted as in *Anshunsaurus huangguoshuensis*. The dorsal surface of the proximal end is slightly concave-convex and the ventral surface of the bone is slightly concave.

The carpals of the left side are articulated and only the ulnare is covered by the rib end in ZMNH M8742 (Fig. 4C). There are 7 carpals as in *Askeptosaurus italicus* and *Endennasaurus acutirostris*. Of the carpals, the intermedium is the largest, with a roughly rectangular shape; the centrale is the smallest, with a shape asymmetrically pentagonal. Among the four distal carpals, the 1st and 2nd are similar in size and nearly square in shape; the distal carpal 3 is bigger than the 1st and 2nd carpals and with a shape nearly rectangular; and the distal carpal 4 is the largest among the four distals, with a shape similar to the 3rd. In the type, distal carpal 2 is the smallest and with an unusual shape, which may have been obscured by the overlap of the metacarpals.

As described in Wu et al. (2009), the five metatarsals of ZMNH M8742 show no significant morphological but length difference from those of the type (Fig. 5C; Table 1). The 4th metatarsal is the longest and the 1st is the shortest but most robust. The 3rd and 5th metatarsals are same in length, and the 2nd is slightly shorter than the former two. In the type, the 2nd metatarsal is longer than the 5th; once more, an individual variation within the taxon.

The phalangeal formula of the forelimb could not be established in the type because of the disassociation and incompleteness of the phalanges (Wu et al., 2009). According to the almost intact right palm of ZMNH M8742, the formula is 2-3-4-4-4, as in *Anshunsaurus huangguoshuensis* (Liu and Rieppel, 2005). The formula is either 2-3-3-4-3 or 2-3-4-4-3 in *Askeptosaurus italicus* (Müller, 2005) and 2-3-4-4-3 in *Endennasaurus acutirostris* (Müller et al., 2005) and *Anshunsaurus wushaensis* (Rieppel et al., 2006). The ungual phalanges (claws) are dorsal-ventrally flat, neither bilaterally compressed nor sharply curved as in other askeptosauroids. This indicates that *Miodentosaurus brevis* was not a pure carnivore.

Hindlimbs The fibula and tibia are incomplete on both right and left sides in the type (Wu et al., 2009), which are well-preserved in both hindlimbs of ZMNH M8742 (Fig. 5B, C). In detail, the fibula resembles that of *Anshunsaurus huangguoshuensis* (see fig. 12 in Liu and Rieppel, 2005) more than other askeptosauroids although its shape does not change much among those taxa. It has a narrow proximal half, which is column-like, and an evidently broadened distal half, which is fan-shaped. In *Askeptosaurus italicus* (Müller, 2005) and *Endennasaurus acutirostris* (Müller et al., 2005), the distal portion does not expand as much as in ZMNH M8742 or *A. huangguoshuensis*.

The tibia shows a broadened proximal end and a narrow distal end as in other askeptosauroids. It has a nearly straight lateral side and a concave fibular side. In detail, it is more similar to that of *E. acutirostris* in that the proximal end expands to a greater degree when compared to that of other askeptosauroids.

All tarsals are missing except for one that was identified as distal tarsal 5 in the type (Wu et al., 2009). As in *Anshunsaurus huangguoshuensis* (see fig. 12 in Liu and Rieppel, 2005) and *Askeptosaurus italicus* (see fig. 13B in Müller, 2005), there are six tarsals in ZMNH M8742, including a calcaneum, an astragalus, four distal ones (Fig. 5B, C). The astragalus is the largest among the tarsals and irregularly hexagonal in outline. It is similar to that of *A. italicus*, stouter than that of *A. huangguoshuensis*. The calcaneum is the second largest and nearly round in shape although five sides are recognizable (it is not complete in the left pes). Among

the four distal tarsals, the 4th is the largest, just slightly smaller than the calcaneum in size. It is irregularly quadrangle, articulating the 4th and 5th metatarsals distally. The other three distal tarsals are also irregularly quadrangle; they contact the metatarsals 3 to 5. The one that was identified as distal tarsal 5 in the type (Wu et al., 2009) should be distal tarsal 4. A centrale seen in *Endennasaurus acutirostris* (see fig. 7C in Müller et al., 2005) is not present in ZMNH M8742.

Metatarsals I–III and V are preserved but disassociated with one another in the type (Wu et al., 2009). All five metatarsals are well-preserved in both hindlimbs in ZMNH M8742. The longest is the 4th metatarsal and the shortest is the 1st (see Table 1). It is obvious that metatarsal V is longer than metatarsal II, which is opposite in other askeptosauroids where the pes is known. According to the left pes, the length order of the five metatarsals (from the longest to the shortest) is metatarsals IV, III, V, II, and I. Metatarsal I is shortest as in other thalattosaurians but not as robust as in the latter, such as *Anshunsaurus huangguoshuensis* (see fig. 12 in Liu and Rieppel, 2005) and *Askeptosaurus italicus* (see fig. 13B in Müller, 2005).

The phalangeal formula of the hindlimb which was unknown in the type (Wu et al., 2009) is 2–3–4–5–5. It differs from that of other askeptosauroids, being 2–3–4–5–4 in *Anshunsaurus* species (Liu and Rieppel, 2005; Rieppel et al., 2006), 2–3–4–5–4 in *Endennasaurus acutirostris* (Müller et al., 2005), and 2–3–4–4–4 in *Askeptosaurus italicus* (Müller, 2005). As in the forelimb, the ungual phalanges (claws) are not highly curved and bilaterally compressed as in other askeptosauroids but dorsoventrally flat as in herbivorous reptiles such as ceratopsian dinosaurs (Weishampel et al., 2004).

3　Discussion

3.1　Individual variation

Although a number of complete skeletons of different thalattosaurians have been described/reported from the Triassic marine limestone of China (see Cheng et al., 2007; Wu et al., 2009), ZMNH M8742 is the best one in view of both scientific research and museum display because it is not only so complete but also fully and beautifully prepared by an experienced technician team. The study of this specimen leads us to have a better understanding of *Miodentosaurus brevis*, especially in the individual variation of certain structures.

The most obvious of those individual variations are recognized in the coracoid, ilium, and metacarpals. The variations are emphasized here. 1) The coracoid has a narrow embayment immediately posterior to the glenoid in the type. This is, as previously described, unique within the Thalattosauria. The relevant part is well-preserved in both coracoids of ZMNH M8742. However, no such an embayment but a round edge of the bone is present, as in other thalattosaurians. 2) The iliac blade is more straight in orientation than in other thalattosaurians and has a broadened distal end in the type, which was considered by Wu et al. (2009) as one of diagnostic features of *Miodentosaurus brevis*. The morphology of the ilium in ZMNH M8742 does not match the condition seen in the type but is similar to that of the species of *Anshunsaurus*. 3) Both the type and ZMNH M8742 are similar in size. In the type, the 2nd metatarsal is longer than the 5th, while the 5th is longer than the 2nd in ZMNH M8742. In addition to the aforementioned variations, the 2nd sacral rib is morphologically different between the type and the new specimen and the sacral and first two caudal vertebrae show some differences in total height or the spine width between the type and the new specimen.

3.2　Revised diagnosis of *Miodentosaurus brevis*

Cheng et al. (2007) established a set of diagnostic characters of *Miodentosaurus brevis* based on the study of the skull and mandible. Later, Wu et al. (2009) emended the diagnosis

of the species after the description of the postcranial skeleton. New information drawn from ZMNH M8742 indicates that some of the previously recognized diagnostic characters related to the coracoid and the ilium vary within the taxon (see above) and some features from the limbs (such as the phalangeal formula of the pes) is unique among the askeptosauroids so far known. Therefore, the diagnosis of *M. brevis* is further 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 a crest along the 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 a slender anterolateral process to wrap posterolateral process of frontal; 7) dentary having no more than six conical teeth implanted in the rostral portion; 8) surangular suddenly broadens ventrally at posterior third of its length; 9) interclavicle becoming much narrower distally than proximally; and 10) phalangeal formula of pes 2-3-4-5-5.

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