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记贵州关岭生物群中的大型鱼龙 *Shastasaurus*[1)]

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摘要：贵州关岭三叠纪法郎组瓦窑段除产出大量保存完整的海百合化石外，还产出多门类海生爬行动物化石。迄今为止，关岭生物群已报道的中-大型鱼龙类有 6 属 6 种，包括邓氏贵州鱼龙（*Guizhouichthyosaurus tangae*）、蔡胡氏典型鱼龙（*Typicusichthyosaurus tsaihuae*）、梁氏关岭鱼龙（*Guanlingsaurus liangae*）、亚洲杯椎鱼龙（*Cymbospondylus asiaticus*）、美丽盘江龙（*Panjiangsaurus epicharis*）和卧龙岗卡洛维龙（*Callawayia wolonggangense*）。一些种属的存在长期以来争议较大，目前多数观点倾向将 *Cymbospondylus asiaticus* 和 *Panjiangsaurus epicharis* 归并于 *Guizhouichthyosaurus tangae*，将 *Typicusichthyosaurus tsaihuae* 归并于 *Guanlingsaurus liangae*。*Guanlingsaurus* 以具有较短的吻部和较多的荐前椎数目而与 *Guizhouichthyosaurus* 有明显的不同（Maisch et al., 2006）。虽然 Maisch et al.（2006）对 *G. tangae* 进行了重新研究，但他们的研究重点是头部骨骼，有限的头后骨骼信息来自一具未经充分修理的骨架（GNP-d41），一些特征未能清晰揭示。头后骨骼材料的缺乏限制了对该种分类位置的判断（Maisch et al., 2006）。在中、晚三叠世大型鱼龙中，肩带和腰带骨骼的形态、前肢和后肢骨骼的特征常具有非常重要的系统分类学意义。本文通过对关岭生物群的一具保存完整的大型鱼龙骨骼化石的详细研究，对 *Guizhouichthyosaurus tangae* 的归属进行了重新修订。研究标本（IVPP V 11853）产于贵州省关岭县新铺乡法郎组瓦窑段。修理后的骨架全长 5.2 m，以腹面向上保存，尾部后部以右侧面向上保存。除前、后肢部分残缺外，其他部位均保存完整，肩带骨骼和腰带骨骼均原位保存。头骨背腹向压扁，仅右侧角的上颞骨有部分破损。新材料的头后骨骼特征表明该种应该属于萨斯特鱼龙科（Shastasauridae）的萨斯特鱼龙属（*Shastasaurus*）。

Shastasaurus 是一个广为人知的晚三叠世大型鱼龙化石属，最初建立于美国加利福尼亚州的 Shasta 地区，包括 5 个种（Merriam, 1895, 1902, 1908）。由于建立这些种的化石材料均保存不好，尤其是模式种仅建立于几块背椎、背肋和两块耻骨之上，导致有关萨斯特鱼龙属和萨斯特鱼龙科的一些特征定义不明确。后人倾向于将已建立的种进行归并，即将 *Shastasaurus alexandrae*、*S. altispinus* 和 *S. osmonti* 划归模式种 *S. pacificus*，将 *S. careyi* 另归入 *Shonisaurus* sp.。虽然萨斯特鱼龙类的其他属，如 *Shonisaurus*、*Besanosaurus*、*Metashastasaurus*、*Pessosaurus* 等，在加拿大、墨西哥、意大利、瑞士等地的中、晚三叠世地层中被陆续发现和报道，但除美国加利福尼亚州的材料外，其他地区发现的萨斯特鱼龙属的化石均未得到广泛认可。

本文将 *G. tangae* 归入萨斯特鱼龙属主要依据对该种模式标本（Gmr 009）的重新观察和

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对该种一新材料(IVPP V 11853)头后骨骼的深入研究。两骨架的头后部分尤其是前肢和肩带均表现出与已知的萨斯特鱼龙属各种的极大相似性,具体包括:椎体稍短;颈肋近端双头;尾椎腹侧 Y 型人字骨发育;锁骨细长,中部向后弯;乌喙骨斧状,中部收缩形成前后缘不对称的“茎”;肩胛骨呈宽的镰刀状,前缘强烈外展;肱骨、桡骨、尺骨均较短;肱骨和桡骨前缘具凹缺;桡骨明显大于尺骨,桡骨后缘和尺骨前缘略凹入;相对较大的桡腕骨等。腰带和后肢特征与萨斯特鱼龙类其他属差别不大。除头后骨骼特征外,关岭材料的头骨特征也与萨斯特鱼龙属惟一的一个保存有部分头骨骨骼的 *S. alexandrae* 的特征大体相符,如具有大的、前后略拉长的眼眶,相对较窄的颊部,横向伸展的鼻骨和额骨的接触面,颞孔稍小于眼眶等。同时,通过与萨斯特鱼龙类其他各属化石的对比研究发现,虽然一些研究者认为萨斯特鱼龙属的荐前椎数目在 55 个左右,且指(趾)骨为 3 指(趾),但鉴于已经发现同属于萨斯特鱼龙类的 *Shonisaurus*、*Besanosaurus*、*Metashastasaurus* 等属或者具有超过 60 的荐前椎数,或者指(趾)骨为 4 指(趾),同时迄今为止尚无完整的萨斯特鱼龙属的化石标本被发现,有关其荐前椎数目和指(趾)骨列数仅是推测,因此基于中国贵州关岭的标本,本文认为萨斯特鱼龙属很可能具有超过 60 的荐前椎数,同时指骨(趾骨)是 4 指(趾)。在观察和对比了众多产于关岭的大型鱼龙骨骼化石的基础上,将邓氏贵州鱼龙、亚洲杯椎鱼龙和美丽盘江龙重新厘定为邓氏萨斯特鱼龙,并对该种的头后骨骼特征进行了详细描述。这是萨斯特鱼龙属的分子第一次在中国被确认,为了解该属鉴定特征和古地理分布提供了新的信息。

关键词:贵州关岭生物群,晚三叠世,萨斯特鱼龙(*Shastasaurus*)

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ON THE OCCURRENCE OF THE ICHTHYOSAUR *SHASTASAURUS* IN THE GUANLING BIOTA (LATE TRIASSIC), GUIZHOU, CHINA

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Abstract A completely articulated ichthyosaur skeleton from the Guanling biota, Guizhou is described. The well preserved postcranial skeleton demonstrates that *Guizhouichthyosaurus tangae*, a large Triassic ichthyosaurid species previously described from Guizhou, should be referred to *Shastasaurus*. Enough materials were found to make possible a satisfactory determination of the systematic position of the large Guanling ichthyosaur species, although both the genus *Shastasaurus* and the family Shastasauridae have long been hard to define due to the fragmentary nature of the type specimens. The postcranial characters of *Shastasaurus tangae* are described in detail based on the new skeleton, the holotype of *Guizhouichthyosaurus tangae* and other associated Guanling large ichthyosaur materials. The trunk is very long, with more then 60 presacral vertebrae and a ventrally bent tail. The scapula is broad and sickle-shaped. The humerus is anteriorly notched with a short shaft. The radius is nearly rectangular, with a small notch in the anterior edge, and a very slightly concave posterior edge. The ulna is much smaller than the radius, with a slightly concave anterior edge and bluntly rounded posterior and distal edge. The forefin and hindfin have four principal digits.

Key words Guizhou, Guanling biota, Late Triassic, *Shastasaurus*

1 Introduction

Shastasaurid ichthyosaurs are widely distributed in Middle and Late Triassic strata. Specimens have been reported from the United States (Merriam, 1895, 1902, 1908), Canada (Camp, 1980; McGowan, 1994), Mexico (Callaway and Massare, 1989), Austria (Huene, 1925), Italy (Dal Sasso and Pinna, 1996), Switzerland (Maish and Matzke, 1997), Germany

(Sander, 1997), Spitzbergen (Wiman, 1910, 1916) and China (Young and Dong, 1972; Yin et al., 2000; Maisch et al., 2006; Chen et al., 2007). However, the referral of specimens to *Shastasaurus*, apart from material originating at the type locality in Shasta County, California, remains dubious. A reported occurrence of *Shastasaurus carinthiacus* in the Austrian Alps (Huene, 1925) is doubtful because it was based on inadequate material (McGowan, 1994). A specimen from Mexico was originally identified as *S. altispinus* (Callaway and Massare, 1989) but later assigned to *Shonisaurus* (Motani, 1999a; McGowan and Motani, 2003). The holotype of *Shastasaurus neubigi* from the German Muschelkalk (Sander, 1997) is too fragmentary to be diagnostic (Motani, 1999a; Nicholls and Manabe, 2001) and *S. neoscapularis* from Canada (McGowan, 1994) was ultimately reassigned to a different genus *Metashastasaurus* or *Callawayia* (Maisch and Matzke, 2000; Nicholls and Manabe, 2001; McGowan and Motani, 2003).

Although *Shastasaurus* has a long taxonomic history and is a well known Triassic ichthyosaur taxon, both the genus itself and the broader family Shastasauridae are hard to delimit due to the fragmentary nature of the type material, as pointed out by McGowan (1994), Maisch (2000), Nicholls and Manabe (2001), and McGowan and Motani (2003). Of five species of *Shastasaurus* from Shasta County, California described by Merriam (1895, 1902), the type species *S. pacificus* (Merriam, 1895) was established based on only a few posterior dorsal vertebrae, ribs, and two pubes; *S. altispinus* and *S. careyi* consist only of vertebrae and ribs; and only *S. alexandrae* and *S. osmonti* are based on adequate material, the former showing some cranial characters. After further research, *S. careyi* was reassigned to *Shonisaurus* sp. (Motani, 1999a), and the other three species of *Shastasaurus* were referred to the type species *S. pacificus* (McGowan and Motani, 2003). Since Merriam's work no complete skeleton of *Shastasaurus* has been found at the type locality. The status of the genus is undermined by the inadequacy of the material available for the type species (McGowan and Motani, 2003). The absence of good material precludes the erection of a new taxon, and also makes it difficult to assign newly discovered specimens to this genus.

Abundant ichthyosaur material has been discovered within the Guanling biota of Guanling County, Guizhou Province, China since 1998, in the course of excavations intended primarily to recover fossil crinoids. The early Late Triassic marine reptile fauna of Guanling (including thalattosaurs, placodonts and ichthyosaurs) is remarkable for the large quantity, perfect preservation, and high diversity of available fossils (see Li, 2006 for a review). At present, six genera and species of large ichthyosaur have been named based on Guanling specimens. They include *Guizhouichthyosaurus tangae*, *Typicusichthyosaurus tsaihuae*, *Guanlingsaurus liangae* (Yin et al., 2000), *Cymbospondylus asiaticus* (Li and You, 2002), *Panjiangsaurus epicharis* (Chen and Cheng, 2003), and *Callawayia wolonggangense* (Chen et al., 2007). However, the taxonomic assignments of some species are problematic. Maisch et al. (2006) studied some large ichthyosaur materials from Guanling and considered two taxa, *Guizhouichthyosaurus tangae* and *Guanlingsaurus liangae*, to be valid; they proposed that *Cymbospondylus asiaticus* and *Panjiangsaurus epicharis* are junior synonyms of *Guizhouichthyosaurus tangae*, and that *Typicusichthyosaurus tsaihuae* is a junior synonym of *Guanlingsaurus liangae*. Their work mainly focused on the cranial morphology of *Guizhouichthyosaurus tangae*. Postcranial information on this species exclusively from a nearly unprepared skeleton (GNG dq-41 or GNP-d41), and details of the postcranial anatomy of the skeleton studied by Maisch et al. is in general. Meanwhile, Pan et al. (2006) discussed *G. tangae* and provided more information on the postcranium of the same skeleton. As noted by Maisch et al. (2006), the poor preparation of the material constrained discussion of the phylogenetic position of *G. tangae*.

Though the type specimen (Gmr 009) of *G. tangae* is rather well preserved, the pectoral and pelvic girdles are mostly obscured by matrix because the skeleton is exposed in dorsal view.

Furthermore, the caudal portion has been lost and the tail structure remains unknown. A nearly complete and well-preserved specimen exposed in ventral view (IVPP V 11853) largely compensates for the deficiencies of Gmr 009. Postcranial evidence from the new material demonstrates that the large ichthyosaur *G. tangae* from the Triassic of Guizhou belongs to the genus *Shastasaurus*.

The purpose of this paper is to provide a detailed description of the postcranial characters of *Shastasaurus tangae*, based on IVPP V 11853, Gmr 009, and other associated large ichthyosaur materials from Guanling, and to discuss its reassignment to *Shastasaurus*. The well-preserved Guanling material may possibly be used as a basis for diagnosing both the genus *Shastasaurus* and the family Shastasauridae.

Abbreviations GNG(GNP): specimen described by Maisch et al. (2006) and Pan et al. (2006) and housed at the Guanling National Geopark, Guanling County, Guizhou Province, People's Republic of China; Gmr: specimens described by Yin et al. (2000) and housed at the Geological Survey of Guizhou Province, Guiyang, People's Republic of China; IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, People's Republic of China; TR: specimen described by Chen and Cheng (2003) and housed at the Yichang Institute of Geology and Mineral Resources, Hubei Province, People's Republic of China.

2 Description

IVPP V 11853 is a well preserved and nearly complete skeleton, lacking only parts of the forefins and right hindfin. It reaches more than 5.2 meters in total length, with the skull and mandibles almost complete (the skull has been fully prepared). The trunk has been prepared in ventral view, but the posterial portion of the tail preserved in right lateral view. The pectoral and pelvic girdles are preserved in their original positions. The specimen was recovered from the Wayao Member of the Falang Formation of Xinpu, Guanling County, Guizhou Province, China. It dates to the Carnian Age of the Late Triassic (Wang et al., 2001).

Skull The snout is very long, with isodontous dentition. The length ratio of the snout to the skull is 68% in IVPP V 11853 (Fig. 1), compared to 67% in Gmr 009 and 66% in IVPP V 11865. The premaxilla extends posteriorly to the level of the posterior narial margin and has no subnarial process. The maxilla has a long processus postnarialis. The nasal narrows anteriorly but extends as far anteriorly as the maxilla. It extends posteriorly to the level of the middle of the orbit and meets the frontal along a jagged suture, also contacting the postfrontal lateroposteriorly. The large orbit is slightly anteroposteriorly elongated. The postorbital region is poorly preserved in IVPP V 11853, and constitutes 11% of the length of the skull. The large supratemporal fenestra extends over nearly 15% of the skull length (14% in Gmr 009 and IVPP V 11865). It is bordered by the parietal, supratemporal, postfrontal, and frontal. The anterior terrace of the supratemporal fenestra is moderately sculptured over its area of exposure on the skull roof. The high parietal sagittal crest is bifurcated both anteriorly and posteriorly. Anteriorly, the crest separates the area of the parietal foramen from the anterior terrace of the supratemporal fenestra; posteriorly, it forms a low ridge along the fenestra's posteromedial edge. The supratemporal bone forms the posterior and lateral edges of the supratemporal fenestra.

Mandible The mandibular rami are united in a symphysis that accounts for about one-third of the length of the mandibles in IVPP V 11853 (Fig. 1), and the anterior ends of the splenials are included in the symphysis. As in *Cymbospondylus* (Merriam, 1908), the elongated dentary extends backward almost to the level of the posterior border of the orbit, and the narrowed anterior ends of the angular and surangular extend forward almost as far as the anterior end of the maxilla. The splenial extends posteriorly to a point below the coronoid region.

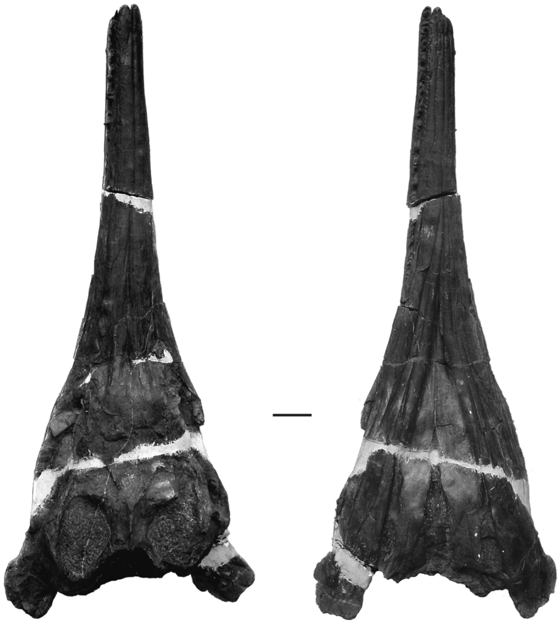

Fig. 1 Skull of *Shastasaurus tangae*, IVPP V 11853, in dorsal (left) and ventral (right) views scale bar = 5 cm

Vertebrae and ribs The vertebral column is continuous from the atlas-axis complex to the tip of the tail in IVPP V 11853, with a moderate tail-bend in the middle to posterior part of the caudal region (Fig. 2). The dorsalventraly flattened trunk of IVPP V 11853 is about 200 cm long and the widest part is 40 cm, the tail is about 220 cm long. The whole body is very slender and has a body plan closely resembling the stem plan that introduced by McGowan and Motani (2003).

All cervical vertebrae are exposed ventrally and show slightly expanded anterior and posterior articular ends. Each centrum is about 24 mm long, with a flattened width of about 50 mm. The centra bear double rib-articulations as in *Shastasaurus osmonti* (Merriam, 1902, pl. 8, fig. 1). Nine cervical vertebrae can be counted in front of the interclavicle, but the atlantal intercentrum is not evident in IVPP V 11853. The parapophysis is clear on the 11th vertebra, but is greatly reduced on the 12th vertebra of IVPP V 11853. The 18th to 30th vertebral centra are anteroposteriorly longer than the cervicals, with a height/length ratio of approximately 2.3. Because ribs and gastralia ventrally covered the vertebral column from 31st vertebra, it is hard to count precisely the presacral vertebrae of IVPP V 11853. However, an estimate can be produced based on the total length of the covered part and the average length of the individual dorsal vertebra centra. Because the covered part of the dorsal vertebral column is 107 cm long, and each dorsal vertebral centrum measures about 3.4 cm, the number of covered dorsal vertebrae is approximately 32. Together with the three posteriorly exposed dorsals, the total presacral vertebral count is approximately 65 in IVPP V 11853, compared to 69 in TR 00001 (Chen and Cheng, 2003) and more than 62 in Gmr 009 (personal observation). The neural spines cannot be observed in IVPP V 11853. Their height is about 60 mm in Gmr 009 (personal observation), and 60 ~ 70 mm in TR 00001 (Chen and Cheng, 2003). Both the centra and the neural spines of these specimens are similar in proportional size to those of *S. osmonti* (Merriam, 1902:95).

The cervical ribs are double-headed and increase in size posteriorly in IVPP V 11853. The trunk ribs are rather robust, bearing posterior grooves and high, anteroposteriorly flattened heads. The length of the ribs remains nearly constant throughout the middle portion of the trunk, but is reduced in the posterior dorsal region. A large number of slender gastralia are exposed and arranged tightly on the ventral surface of the trunk. The median element of each gastralial row is V-shaped with a short anterior process, which rests on the trunk midline. The lateral elements are about 10 ~ 15 cm long, extending posterolaterally to the edges of the trunk.

We believe that the first sacral vertebra can be recognized by the position of the proximal end of the right ilium, and the left rib of the vertebra at this point in the column contacts the pelvic girdle as would be expected for a sacral rib. There are probably two sacral vertebrae, as suggested for *Shonisaurus popularis* (Camp, 1980) and *Besanosaurus leptorhynchus* (Dal Sasso and Pinna, 1996). The single identifiable sacral rib is flat, and is 4 cm long. Its rounded distal end is wider than the proximal end.

Fig. 2　Trunk（ventral view）and tail（partly lateral view）of *Shastasaurus tangae*，IVPP V 11853
（the skull presented in this photo is a cast; areas inside of dotted line are reconstructed）; scale bar = 10 cm

A continuous series of about 170 vertebrae represents the structure of the caudal region. A pronounced posteroventral directed bend in the distal region is present as in *Cymbospondylus* (Merriam, 1908). Posterior to the bend, the vertebral centra decrease in size, show a degree of lateral compression. All caudal vertebral centra show a well developed ventral keel, which differentiates them from the cervicals and dorsals. Some of the caudal neural spines have been displaced from the tail and scattered. The caudal neural spines are low and distally swollen, with a slight posterior curvature. The hemal arches of the caudal region are united ventrally to form long-stemmed chevrons, which are preserved intact in most of the caudals of IVPP V 11853. These chevrons are similar in form to those of *Shastasaurus osmonti* (Merriam, 1908, pl. 17, fig. 1) and *Besanosaurus leptorhynchus* (Dal Sasso and Pinna, 1996). In *Cymbospondylus petrinus* facets for hemal arches are present on the caudal centra, but chevrons have been observed only in the region posterior to the downward bend of the tail (Merriam, 1908:117).

Pectoral girdle All elements of the pectoral girdle are well preserved and exposed in ventral view in IVPP V 11853 (Fig. 3). Their shapes are extremely similar to those of the corresponding bones in *Shastasaurus alexandrae* (Merriam, 1902, pl. 12).

The clavicles are long and slender, with a groove on the ventral side. They are close to the midline, and separated by a small median gap. The medial ends of the clavicles are expanded, and conjoined with the interclavicle, so that all three elements share a continuous anterior margin. The distally narrowing shaft of each clavicle curves posteriorly to reach the glenoid region. The rod-like clavicle is very similar in shape to those of *S. alexandrae* (Merriam, 1902, pl. 12), *Shonisaurus popularis* (Camp, 1980) and *Besanosaurus leptorhynchus* (Dal Sasso and Pinna, 1996). In *Cymbospondylus petrinus* the middle portion of each clavicle is significantly expanded, and the ends are narrow (Merriam, 1908:119).

The interclavicle is a very small and delicate element relative to the other elements of the pectoral girdle. It is a T-shaped bone with a thin, short stem, its anterior part transversely expanded for the articulation with the clavicles. The length of the stem is only 50 mm in IVPP V 11853. Its posterior tip does not reach the intercoracoid juncture, in contrast to the condition in post-Triassic forms like *Ichthyosaurus communis* (McGowan and Motani, 2003).

The coracoids are paired and meet along the mid-line. Each coracoid is rounded proximally and narrows distally to form a distinct asymmetrical neck. The distal ends are stout. The maximum proximodistal length of coracoid is nearly equal to its anteroposterior length. The intercoracoidal facets are long, and the anterolateral corner of the distal end of the coracoid bears a fairly straight facet for the scapula. The remaining portion of the distal end bears a much large elliptical facet that contributes to the glenoid cavity, which represents the thickest part of the coracoid. Both facets are set off from one another at an obtuse angle. The coracoid is similar in shape and size to those of *Shastasaurus osmonti* (Merriam, 1902, pl. 10, fig. 2), *S. alexandrae* (Merriam, 1902, pl. 12), *Metashastasaurus neoscapularis* (McGowan, 1994, fig. 6; Nicholls and Manabe, 2001, fig. 9) and *Shonisaurus popularis* (Camp, 1980, fig. 39). The coracoids of *Mixosaurus*, *Besanosaurus*, and *Ichthyosaurus* are also similar in general outline, but are shorter proximodistally.

The right scapula is fully visible, whereas the distal portion of the left scapula is missing in IVPP V 11853. The scapula is a broad sickle-shaped element with an anteriorly expanded blade. The anterior edge is joined by a continuous curve to the distal margin of the scapula and the posterior edge is concave. A relatively straight facet for the coracoid is set off from the middle of the thickened proximal end of the scapula, and the rest of the proximal end contributes to the glenoid cavity. The anterior edge of the right scapula bears a notch anterior to the coracoid facet, resembling the condition in *Shastasaurus osmonti* (Merriam, 1902, pl. 10, fig. 4) and *S. alexandrae* (Merriam, 1902, pl. 12). However, this notch does not exist on the left scapula, the margins of whose blade are smooth as in *Besanosaurus leptorhynchus* (Dal Sasso and Pin-

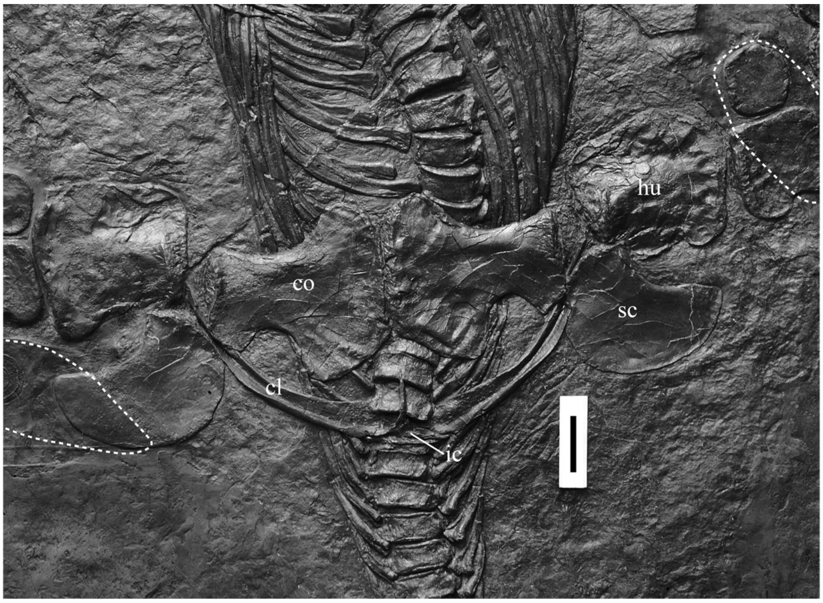

Fig. 3　Pectoral girdle of *Shastasaurus tangae*, IVPP V 11853, in ventral view
Abbreviations: cl. clavicle 锁骨; co. coracoid 乌喙骨; hu. humerus 肱骨; ic. inter clavicle 间锁骨; sc. scapula 肩胛骨; scale bar = 5 cm

na, 1996, fig. 17). The right scapula of Gmr 009 is similar to the left of IVPP V 11853 in that there is no indentation of the blade margin. The anterior indentation in the right scapula of IVPP V 11853 may be an artifact of preparation or a result of incomplete ossification.

The precise nature of the joints among the scapula, coracoid and clavicle in IVPP V 11853 allows the probable life positions of these elements to be clearly discerned. For example, the shaft of the clavicle is curved posterolaterally so that the distal end lies far posterior to the proximal end. The scapular facet and coracoid facet are closely articulated, and the glenoid cavity has the clear outline of a right-angled triangle. The widely expanded blade edge of the scapula faced forward.

Pelvic girdle　All the pelvic girdle elements of IVPP V 11853 are also preserved close to their natural positions (Fig. 4). The proximal end of the ilium rests within the angled cavity formed by the proximal ends of the pubis and ischium, and the three bones all contribute to the acetabulum.

The pubis is considerably broader distally than proximally, being widely flared anteroposteriorly. The proximal (acetabular) end is thickened, with a rather straight proximal margin in external view and a facet developed on its vertical aspect. The convex posterior margin has a deep, narrow obturator notch. The anterior margin of the ischium is regularly convex, and curves smoothly into the proximal and distal margins. The posterior margin is slightly concave. The proximal end is thickened, and contributes to the acetabulum, while the distal part of the ischium carries a thin posterior blade. The distal ends of both the pubes and ischia fail to meet along the median line in IVPP V 11853, and a ventral mass of cartilage may have intervened between the left and right halves of the pelvis. The ilium is bar-like element. The proximal end is expanded, and bears a large and robust elliptical facet that participates in the acetabulum. The distal end is flattened and slightly widened (anteroposteriorly) in comparison to the proximal end. The anterior curvature is larger than the posterior and the proximal end lies posterior

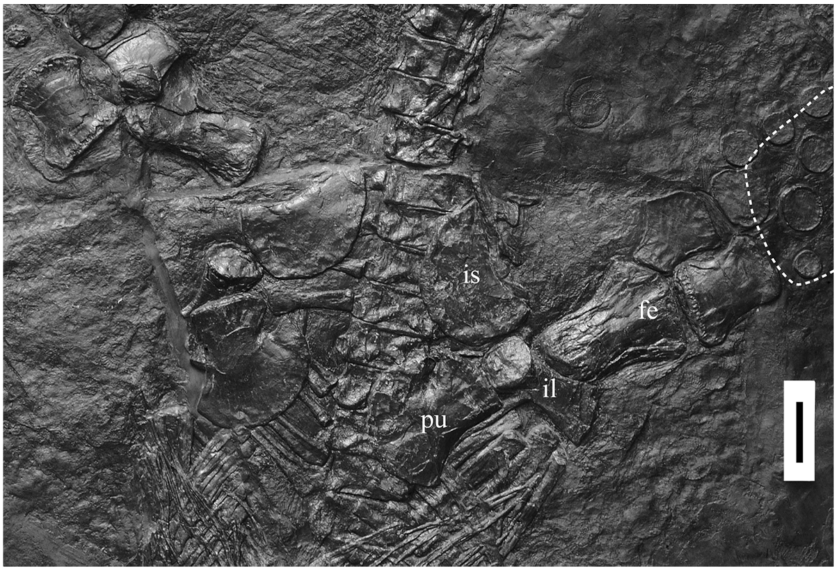

Fig. 4 Pelvic girdle of *Shastasaurus tangae*, IVPP V 11853, in ventral view
Abbreviations: fe. femur 股骨; il. ilium 髂骨; is. ischium 坐骨; pu. pubis 耻骨; scale bar = 5 cm

to the distal end. This corresponds to the anterodorsal direction of the ilia illustrated by Merriam (1908, fig. 70, 72, 73) and Dal Sasso and Pinna (1996, fig. 21). In all its major features, the pelvic girdle of IVPP V 11853 is very similar to those of *Shastasaurus osmonti* and *S. alexandrae* as described by Merriam (1902, 1908), and somewhat similar to those of *Californosaurus perrini* (Merriam, 1902, pl. 5, fig. 1, 3, 4), *Shonisaurus popularis* (Camp, 1980, fig. 51) and *Besanosaurus leptorhynchus* (Dal Sasso and Pinna, 1996, fig. 17C).

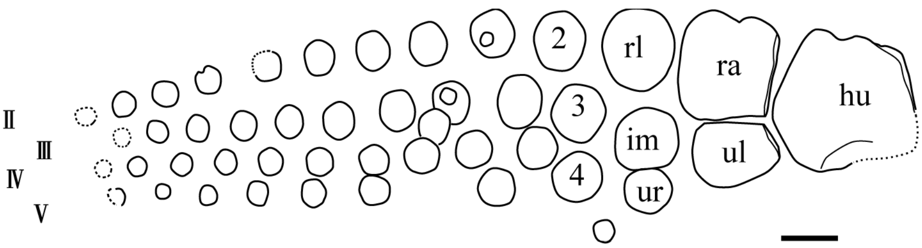

Fig. 5 Left forefin of *Shastasaurus tangae*, Gmr 009, in dorsal view
Abbreviations: hu. humerus 肱骨; im. intermedium 中间腕骨; ra. radius 桡骨; rl. radiale 桡腕骨; ul. ulna 尺骨; ur. ulnare 尺腕骨; 2–4. distal carpals 远端腕骨; II–V. digits 指骨; scale bar = 5 cm

Forefin The forefins are incomplete in IVPP V 11853, but are well preserved in Gmr 009 (Fig. 5). The humerus is a fairly short and broad bone, with a notch in the middle of its anterior edge. The proximal end is robust, and much of the articular surface is inclined anteriorly to match the glenoid facet of the scapula. The distal end is flattened and has two facets, of which the anterior facet for the radius is marginally longer than the ulnar facet. The ventral aspect of IVPP V 11853 shows that, a prominent deltopectoral crest arises from the proximal end of the humerus, but does not extend much further distally than the mid-shaft region. In most of

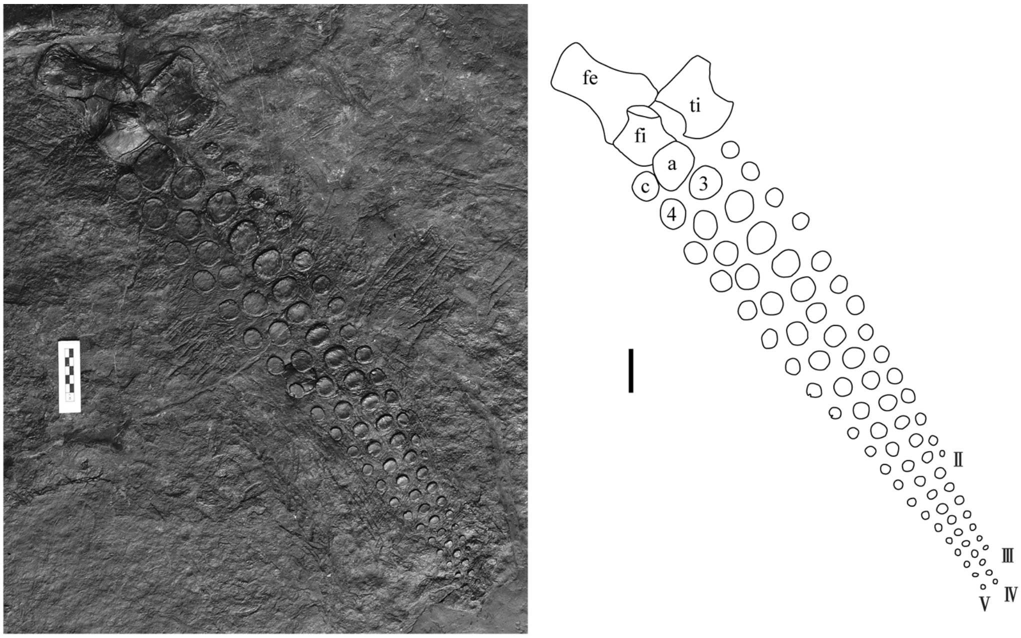

Fig. 6　Left pelvic fin of *Shastasaurus tangae*, IVPP V 11853, in ventral view
Abbreviations: a. astragalus 距骨; c. calcaneum 跟骨; fe. femur 股骨; fi. fibula 腓骨; ti. tibia 胫骨; 3, 4. distal tarsals 远端跗骨; II–V. digits 趾骨; scale bar = 5 cm

these features the humerus corresponds to that of *Shastasaurus osmonti* as described by Merriam (1902, pl. 11, fig. 1). No complete radius or ulna is preserved in IVPP V 11853, but the features of these elements can be adequately observed in the type species Gmr 009 and other associated Guanling large ichthyosaur materials. The radius is short and quadrangular, with a notch in the middle of its anterior border, and its posterior border is relatively straight or slightly concave. The ulna is very much smaller than the radius, and its width is less than its length. Its proximal and anterior margins are relatively straight or slightly concave, but its posterior and distal margins are bluntly rounded.

Though the forefins in IVPP V 11853 are incomplete, they clearly possess three proximal carpals and four digits as in Gmr 009 and TR 00001. The radiale, intermedium and ulnare are rounded and from radiale to ulnare the size decreased. As in *S. osmonti* (Merriam, 1908, pl. 15, fig. 1a) the size of radiale is nearly equal to the size of ulna. Digit II is the longest in the manus. Digit V is the smallest, and the two proximalmost phalanges are missing. A very small phalanx lies beside (behind) the ulnare. In contrast to Gmr 009, v-shaped notch presented in the anterior margin of phalanx of radial digit (digit II) in IVPP V 11853 and TR 00001. All of the phalanges are separated from one another, and are oval to circular in shape. The number of elements in the longest digit appears to be 20 in Gmr 009. Maisch et al. (2006) and Pan et al. (2006) redescribed the *Guizhouichthyosaurus tangae*, but stated that there were only three digits based on the GNP-d41.

Hindfin　IVPP V 11853 preserves a complete left hindfin (Fig. 6), and a partially disarticulated right hindfin. The hindfin shares the slender built of the forefin, but is substantially smaller.

The femur is heavy and massive, with the trochanter joining the rounded head. The shaft is constricted proximally, but widens abruptly toward the distal end. The tibial facet is thick and

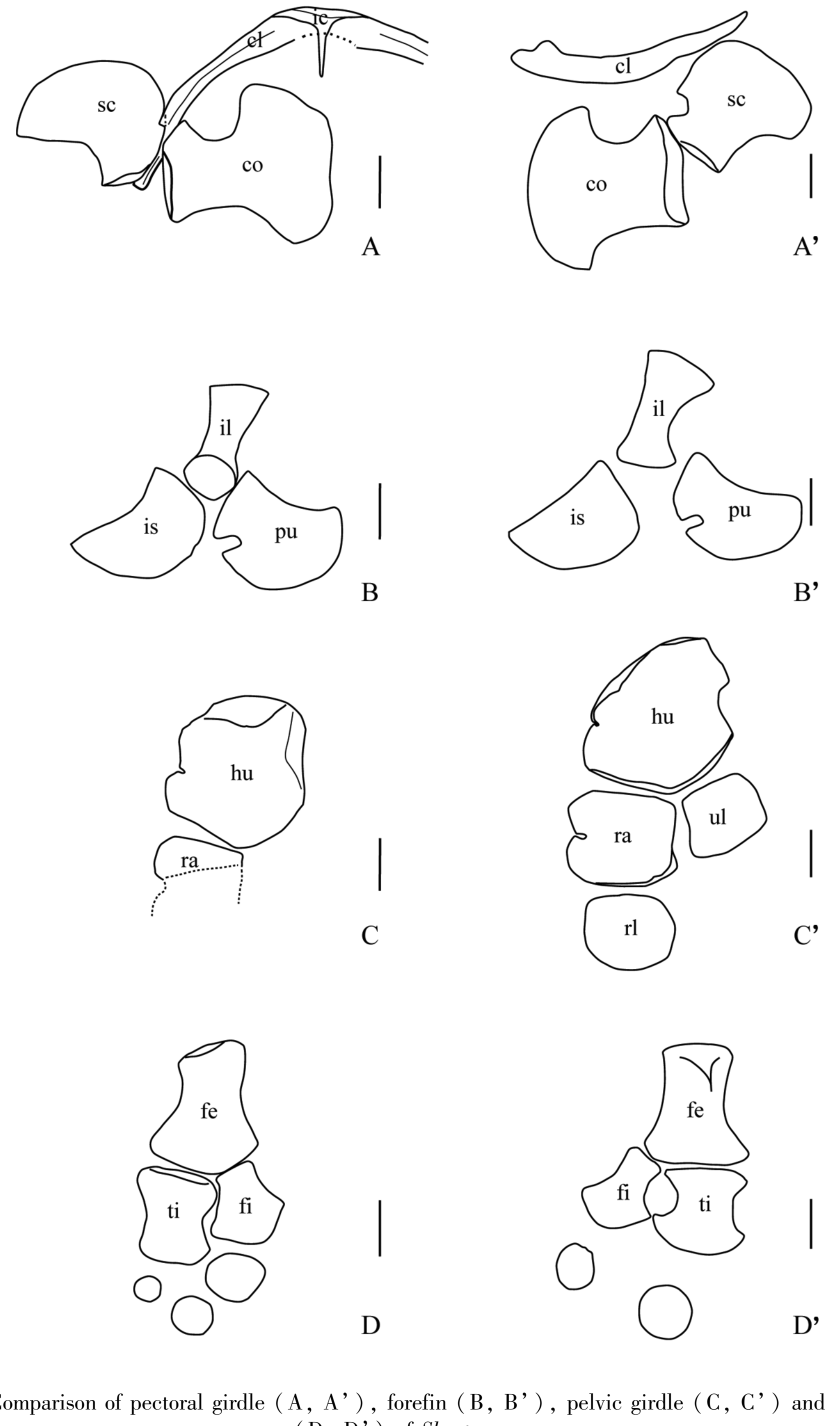

Fig. 7 Comparison of pectoral girdle (A, A'), forefin (B, B'), pelvic girdle (C, C') and pelvic fin (D, D') of *Shastasaurus*

A, B, C, D are IVPP V 11853 of right side, in ventral view; A' is *Shastasaurus alexandrae*, after Merriam, 1902, pl. 12, right side, in dorsal view; B', C', D' are *S. osmonti*, after Merriam, 1908, pl. 15, 16; for abbreviations see Figs. 3-6; scale bar = 5 cm oval, and roughened for cartilaginous attachment. It forms an obtuse angle with the small fibular facet. The tibia is larger than the fibula and is constricted in the midshaft region with a straight-edged proximal end that is slightly wider than the rounded distal end. The fibula is expanded distally as in *Shastasaurus osmonti* (Merriam, 1908, fig. 73), *Besanosaurus leptorhynchus* (Dal Sasso and Pinna, 1996, fig. 17D) and *Californosaurus perrini* (Merriam, 1902, pl. 6, fig. 4), but the proximal end is barely wider than the middle of the shaft.

There are two proximal tarsals, of which the astragalus is larger than the calcaneum. There are four principal digits in both IVPP V 11853 and Gmr 009, and we identify them as digits II, III, IV and V (Fig. 7). Digit IV is the longest, and contains about 20 individual elements in IVPP V 11853. All of the pedal phalanges are unnotched.

3 Comparisons

Middle and Late Triassic large ichthyosaurs mostly belong to two families, Cymbospondylidae and Shastasauridae. Several pectoral girdle and forefin characters visible in the large ichthyosaurs from Guanling, especially the hatchet-shaped coracoid and the sickle-shaped scapula, clearly differ from the cymbospondylid condition but are reminiscent of shastasaurids.

A comparison of IVPP V 11853 with two well-known species of *Shastasaurus*, *S. alexandrae* and *S. osmonti* (Merriam, 1902, 1908), indicates that IVPP V 11853 closely related with the *Shastasaurus* (Fig. 7). Characters shared by *Shastasaurus* and IVPP V 11853 include the following: vertebral centra relatively short, bicipital ribs present in cervical region only, short caudal ribs, Y-shaped chevrons present on caudal vertebrae, long and slender clavicle with deep groove on ventral surface, coracoid rounded proximally and narrowing distally to a distinct asymmetrical neck, scapula convex anteriorly, pubis and ischium expanded distally, pubis with posteriorly open obturator notch, humerus and radius anteriorly notched, humerus with a short shaft and its proximal end strongly inclined anteriorly, posterior epipodials (ulna, fibula) very much smaller than their anterior counterparts (radius, tibia), radius of subrectangular shape with very slightly concave posterior edge, relatively large radiale. Most of these characters are also present in Gmr 009. These similarities support the reassignment of *Guizhouichthyosaurus tangae* to the genus *Shastasaurus*. Postcranially, *Shastasaurus tangae* differs from the Shasta county species of *Shastasaurus* (Merriam, 1902, 1908) only in the anterior contour of the scapula and the relatively straight posterior margin of the humerus. The scapula of *S. alexandrae* and *S. osmonti* (Merriam, 1902, 1908) presents a distinct anterior hook in the broad anterior blade. In *S. tangae* the anterior margin is not cut out so as to produce an anterior hook.

Following the revision proposed by McGowan and Motani (2003), the Shastasauridae contains the genera *Shastasaurus*, *Himalayasaurus* (Dong, 1972) and *Shonisaurus* (Camp, 1980). *Metashastasaurus* (*Callawayia* of Maisch & Matzke, 2000) may represent a fourth shastasaurid genus (Nicholls and Manabe, 2001). The most distinct postcranial difference separating *Shastasaurus tangae* from *Shonisaurus* and *Metashastasaurus* lies in the shape of the scapula. In *S. tangae* the scapula is broad, but in *Metashastasaurus* (Nicholls and Manabe, 2001) and *Shonisaurus* (Camp, 1980) it is elongated. *Shonisaurus* also possesses very short vertebral centra in the dorsal region, with an H/L ratio of about 3.0 (Camp, 1980). The vertebral centra of IVPP V 11853 have a H/L ratio of 2.0 in the cervical region and 2.3 in the anterior dorsal region, and these values are closely matched in the Shasta county material. Only limited information on the postcranial skeleton of *Himalayasaurus* is available, but this genus differs from *Shastasaurus tangae* in having swollen teeth implanted in a groove. *Besanosaurus leptorhynchus* (Dal Sasso and Pinna, 1996) is the only species not assigned to *Shastasaurus* that can be regarded as closely similar to *S. tangae*. McGowan and Motani (2003) suggested that the *Besanosaurus* might belong to a distinct family, Besanosauridae. Most elements of the pectoral and pelvic girdles of *S. tangae*, particularly the scapula, bear a close resemblance to their counterparts in *B. leptorhynchus*. However the humerus and ulna in *B. leptorhynchus* are much more rounded than in *S. tangae*. In *B. leptorhynchus* the coracoid is relatively short proximodistally, the pubis has an obturator notch and the ilium is relatively large (Dal Sasso and Pinna, 1996). McGowan and Motani (2003) have suggested a relationship between the large ichthyosaurs of Guanling and the species *Pessosaurus polaris* from Switzerland, but the humerus of *P. polaris* (Wiman, 1910, pl. 7, fig. 2b) seems more rounded than that of *S. tangae* and the coracoid of the former species seems shorter proximodistally (Wiman, 1910, pl. 7, fig. 2).

The similarity of the type specimen of *S. tangae* (Gmr 009) to previously identified *Shastasaurus* material was mentioned by Yin et al. (2000). However, Yin et al. (2000) ultimately excluded Gmr 009 from *Shastasaurus* because its parapophyses are relatively low on the vertebrae, because its ribs, epipodials and neural spines are short, and because it possesses four digits on the manus. They accordingly proposed the erection of a new genus, *Guizhouichthyosaurus*. As a general rule, however, variations in vertebral and rib morphology are quite common in shastasaurids. Furthermore, the proportions of the anterior epipodials in Gmr 009 are the same as in *Shastasaurus osmonti* (Merriam, 1902, pl. 11, fig. 1), according to our own observations. Short epipodials in fact represent a conspicuous character of *Shastasaurus*.

4 Discussion

The exceptionally well-preserved material from Guanling considerably extends current knowledge of the genus *Shastasaurus*. As Dal Sasso and Pinna (1996) pointed out, several mistakes are present in previous description of *Shastasaurus*. One concerns the vertebral number, which was reported to be low in most of the known shastasaurid genera. The total number of presacral vertebrae was estimated to be 50–55 in *Shonisaurus popularis* (Camp, 1980), about 54 in *Metashastasaurus neoscapularis* (Nicholls and Manabe, 2001), and close to 45 in *Californosaurus perrini* (Merriam, 1902:132). In the meantime, many researchers believed that the genus *Shastasaurus* characterized by 50–55 presacral vertebrae (Callaway and Massare, 1989; Massare and Callaway, 1990; McGowan and Motani, 2003). Only the genus *Cymbospondylus* was initially described as possessing a high number of presacral vertebrae (Merriam, 1908), and indeed the highest number (67 prescral vertebrae) in any ichthyosaur (Sander, 1989). However, a revision of the skeletal anatomy of *Shonisaurus popularis* estimated that there were 64 presacral vertebrae (Kosch, 1990) and 60 presacral vertebrae were found in *Besanosaurus leptorhynchus* (Dal Sasso and Pinna, 1996). As pointed out by Dal Sasso and Pinna (1996), it is possible that the incompleteness of most of the type specimens of these taxa led to erroneous vertebral counts. Thus, most of the genera included in Shastasauridae could in fact have more than 55 presacral vertebrae. There is a high probability that *Shastasaurus* had more than 60 presacral vertebrae, because no *Shastasaurus* skeleton from a locality other than Guanling has ever been reported to have a complete vertebral column. In IVPP V 11853, the trunk is long, with approximately 65 presacral vertebrae, and the total number of presacrals is estimated at more than 60 in Gmr 009.

The phalangeal region of the limbs of *Shastasaurus* from Shasta County has not been seen in its natural arrangement in connection with the remainder of the limb. The much larger radius and the large sized radiale are the main evidences for Merriam (1908) to consider that the space for the posterior digits of *Shastasaurus* is narrower than the *Californosaurus* (*Delphinosaurus* of Merriam, 1908). Because the latter have been considered tridactyl, Merriam (1908:72) consider that two well developed digits and a rudimentary third were present in *Shastasaurus* . Callaway and Massare (1989) then diagnosed *Shastasaurus* as having a reduced forefin with 2–3 digits. Motani (1999a, b) used the presence of only two digits as a defining character of

Shastasaurus and the family Shastasauridae, and McGowan and Motani (2003) used three digits. As a result, the number of forefin digits was an important piece of diagnostic evidence that helped exclude "*Guizhouichthyosaurus*" *tangae* (Yin et al., 2000) and *Panjiangsaurus epicharis* (Chen and Cheng, 2003) from the genus *Shastasaurus*, since both of these Guanling taxa are characterized by four digits.

As mentioned above, *Shastasaurus* from Guanling presents the much large sized radius and radiale as in *S. osmonti* (Merriam, 1908, pl. 15, fig. 1a), but shows clearly tetradactyl. The *S. neoscapularis* (McGowan, 1994) was considered to have three digits first, then Nicholls and Manabe (2001) reassigned *S. neoscapularis* to *Metashastasaurus* and diagnosed the genus as having four digits in the forefin and possibly three digits in the hindfin later. The *Besanosaurus* has four digits and the tetradactyl hindfin was considered as an important feature of *Besanosaurus* to distinguish with the tridactyl diagnosed *Shastasaurus* (Dal Sasso and Pinna, 1996). Paralleling the situation for the presacral vertebrae, it is highly probable that *Shastasaurus* is characterized by more than three digits. The distinct tetradactyl condition of the Guanling specimens supports this interpretation.

Three monotypic large ichthyosaur genera were erected by Yin et al. (2000). One of them, *Guizhouichthyosaurus*, is referred to *Shastasaurus* in this paper. Of the others, *Guanlingsaurus* is unique in having a very high presacral count and very short snout. It is certainly quite distinct from *Shastasaurus*. The status of *Typicusichthyosaurus* is obscure. After a reassessment of the type specimen (Gmr 015), we agree with Maisch et al.'s (2006) conclusion that it is most likely referable to *Guanlingsaurus* or a closely related form, because of its small head and high presacral vertebral count. Most of the apparent hindfin morphology of Gmr 015 actually represents preparational artifacts, and cannot be used to characterize the taxon. The forefin and pelvic fin of TR 00001 closely resemble those of Gmr 009 and IVPP V 11853, and it is reasonable to conclude that *Panjiangsaurus epicharis* is a synonym of *S. tangae*. Examination of the skull of the holotype of *Cymbospondylus asiaticus* (Li and You, 2002) reveals a high degree of similarity to the skulls of Gmr 009 and IVPP V 11853. We regard *C. asiaticus* is a synonym of *S. tangae*, confirming the earlier interpretations of Maisch et al. (2006) and Chen et al. (2007).

5 Systematic paleontology

Order Ichthyosauria Blainville, 1835
Family Shastasauridae Merriam, 1902
Genus *Shastasaurus* Merriam, 1895

Type species *Shastasaurus pacificus* Merriam, 1895.

Revised diagnosis Posterior epipodials (ulna, fibula) very much smaller than their anterior counterparts (radius, tibia); humerus and radius anteriorly notched; posterior edge of radius and anterior edge of ulna very slightly concave; posterior and distal edges of ulna bluntly rounded; probably more than 60 presacral vertebrae and four principal digits.

***Shastasaurus tangae* (Cao & Luo, in Yin et al., 2000)**

Guizhouichthyosaurus tangae Cao & Luo, in Yin et al., 2000, p. 15, pl. VI
Cymbospondylus asiaticus Li & You, 2002, p. 9, figs. 1-2
Panjiangsaurus epicharis Chen & Cheng, 2003, p. 229, pl. I, figs. 1-3
Guizhouichthyosaurus tangae Maisch et al., 2006, p. 588, figs. 2-4
Guizhouichthyosaurus tangae Pan et al., 2006, p. 698, fig. 1

Holotype Gmr 009, a generally well-articulated skeleton lacking the pelvis, the left hindfin and most of the tail. The specimen officially belongs to the collections of the Geological

Survey of Guizhou Province and is available for limited comparative studies.

Referred material IVPP V 11853, V 11865 (Li and You, 2002), V 11869 (Li and You, 2002), TR 00001 (Chen and Cheng, 2003), SPCV 30014 (Chen and Cheng, 2003), GNG dq-41 (Maish et al., 2006; Pan et al., 2006), GNG dq-46 (Maish et al., 2006), GNG dq-22 (Maish et al., 2006).

Diagnosis Medium-sized to very large ichthyosaur with the following combination of characters: long snout; premaxilla without subnarial process; moderately developed anterior terrace of supratemporal fenestra; high parietal sagittal crest bifurcated both anteriorly and posteriorly; relatively short postorbital skull region; approximately 65 presacral vertebrae; two sacral vertebrae; long tail with caudal bend; T-shaped interclavicle with very small, thin stem; broad sickle-shaped scapula with smooth convex anterior blade, and without anterior hook, posterior edge of humerus relatively straight.

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