Osteology of *Concavispina biseridens* (Reptilia, Thalattosauria) from the Xiaowa Formation (Carnian), Guanling, Guizhou, China

Author(s): Jun Liu , Li-Jun Zhao , Chun Li , and Tao He
Source: Journal of Paleontology, 87(2):341-350. 2013.
Published By: The Paleontological Society
DOI: http://dx.doi.org/10.1666/12-059R1.1
URL: http://www.bioone.org/doi/full/10.1666/12-059R1.1

Journal of Paleontology, 87(2), 2013, p. 341–350

0022-3360/13/0087-341$03.00

OSTEOLOGY OF *CONCAVISPINA BISERIDENS* (REPTILIA, THALATTOSAURIA) FROM THE XIAOWA FORMATION (CARNIAN), GUANLING, GUIZHOU, CHINA

JUN LIU,[1] LI-JUN ZHAO,[2] CHUN LI,[1] AND TAO HE[2]

[1]Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China, <liujun@ivpp.ac.cn>; and [2]Zhejiang Museum of Natural History, Hangzhou 310012, China

ABSTRACT—A thalattosaur taxon, *Concavispina biseridens*, was recently named and briefly described. It is described here in detail and compared with other thalattosaurs, especially *Xinpusaurus. Concavispina* is characterized by a long skull, measuring approximately half the length of presacral portion of the vertebral column, two rows of blunt teeth on the anterior part of the maxilla, and neural spines that have convex anterior or posterior margins and V-shaped notches in their dorsal margins. *Concavispina* differs from all thalattosaurs except *Xinpusaurus* in that the anterior end of the maxilla is curved dorsally, less than five cervical vertebrae are present, and the proximal end of the humerus is wider than the distal end. Phylogenetic analysis of 40 characters suggests that *Miodentosaurus* occupies a basal position within Askeptosauridea, *Paralonectes* is the basalmost member of Thalattosauridea, *Concavispina* may form a clade with *Xinpusaurus*, and Chinese thalattosaurs do not have a close relationship with eastern Pacific forms as suggested by previous studies. *Concavispina* may have been similar to *Xinpusaurus* in overall locomotor style, but probably had a poorer swimming ability. *Concavispina* likely differed from *Xinpusaurus* in diet, for example by depending on softer food.

INTRODUCTION

THE BLACK shale of the Xiaowa Formation (previously known as the Wayao Member of the Falang Formation, or as the Wayao Formation) is a unique Upper Triassic (Carnian) Lagerstätte that has produced abundant well-preserved marine reptiles and crinoids (Wang et al., 2008). Among these marine reptiles, thalattosaurs are the most abundant and diverse group. Hundreds of nearly complete thalattosaur skeletons have been excavated from Guanling, Guizhou, China, and four genera and six species have been named based on these specimens: *Anshunsaurus huangguoshuensis* Liu, 1999; *Xinpusaurus suni* Yin, 2000; *Xinpusaurus bamaolinensis* Cheng, 2003; *Xinpusaurus kohi* Jiang et al., 2004; *Miodentosaurus brevis* Cheng et al., 2007; and *Concavispina biseridens* Zhao et al., 2013. Although it is possible that only one of the *Xinpusaurus* species is valid (Liu, 2013), the Xiaowa Formation of Guanling, Guizhou, China has nevertheless produced the most diverse thalattosaur fauna in the world, surpassing even that of the Early to Middle Triassic Sulphur Mountain Formation of the Wapiti lake region of British Columbia, Canada (Nicholls and Brinkman, 1993). Among thalattosaur taxa, *Concavispina biseridens* is unique in having two rows of maxillary teeth, and neural spines with notched dorsal margins. This species is represented by a nearly complete skeleton, which has the absolute longest skull of any known thalattosaurs. This taxon was only briefly described by Zhao et al. (2013), and in the present paper we provide a detailed description of the only known specimen and discuss its phylogenetic position, locomotion, and diet.

SYSTEMATIC PALEONTOLOGY

Institutional abbreviations include: GMPKU, Geological Museum of Peking University, Beijing, China; Gmr, Geological Survey of Guizhou, Guiyang, China; IVPP, Institute for Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; ZMNH, Zhejiang Museum of Natural History, Hangzhou, China.

Order THALATTOSAURIA Merriam, 1904
Family THALATTOSAURIDAE Merriam, 1904
GENUS CONCAVISPINA Zhao, Liu, Li, and He, 2013

Type species.—By monotypy.

CONCAVISPINA BISERIDENS Zhao, Liu, Li, and He, 2013
Figures 1–4

Diagnosis.—Skull long, around half as long as presacral part of vertebral column; two rows of blunt teeth on anterior part of maxilla; dentary with long posteroventral process and short posterodorsal process; at least 43 presacral vertebrae; fewer than five cervicals; three sacrals; neural spines of dorsal vertebrae with V-shaped notches in their dorsal margins and typically with convex anterior or posterior margins; neural spines of presacrals low, with spine height measuring less than twice anteroposterior spine length; scapula wide with convex anterior margin; clavicle projecting much farther dorsally than scapula; femur with nearly unexpanded proximal end; fibula relatively slender.

Description.—The skull is 50 cm long and is mainly exposed in left lateral view, with the tip of the rostrum missing (Fig. 2). This specimen is the largest known thalattosaur in terms of absolute skull length. The distance from the broken tip of rostrum to the anterior margin of the (left) orbit is 252 mm, whereas the distance from the posterior margin of the (left) orbit to the posterior margin of the quadrate is 107 mm.

The skull is similar to that of *Xinpusaurus suni* in its general shape. Despite the absence of the tip of the rostrum, the preserved part of the rostrum is still longer than the remaining skull. The preserved premaxillae are exposed in ventral and lateral views, and measure approximately 19 cm in length. The sutural boundaries of the premaxilla cannot be clearly identified on the lateral surface of the snout.

Seven slender, pointed teeth are preserved on the right premaxilla, and are less than 7 mm in crown height. No sockets can be observed. The attachment of the teeth superficially appears to be acrodont, but also is probably ankylothecodont.

The preserved anterior part of the maxilla curves dorsally, indicating that the alveolar margin of the upper jaw curves

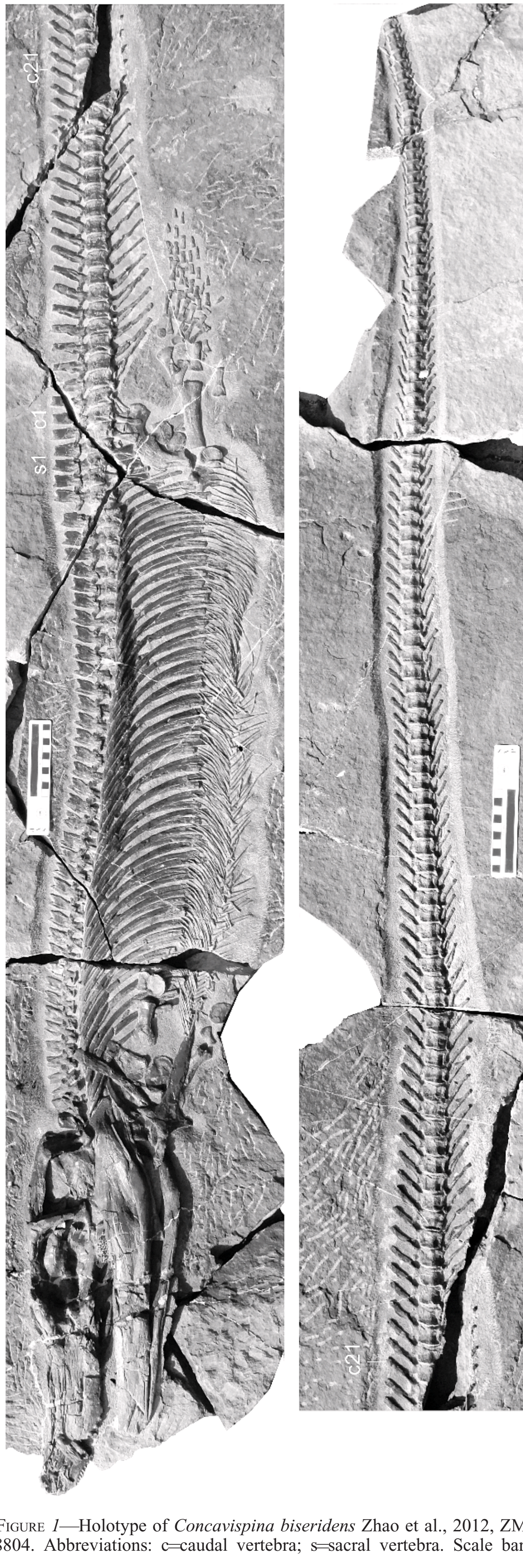

FIGURE 1—Holotype of *Concavispina biseridens* Zhao et al., 2012, ZMNH M8804. Abbreviations: c=caudal vertebra; s=sacral vertebra. Scale bar=10 cm.

anterodorsally near the anterior end of the maxilla as in *Xinpusaurus suni* (Rieppel and Liu, 2006). The dorsal part of the maxilla forms the ventral border of the external naris, and the maxilla contacts the frontal with an apex, the prefrontal along an extensive posterodorsal margin, and the jugal with a sharp posterior tip as in *Xinpusaurus suni* (Rieppel and Liu, 2006). If the maxilla contributes to the ventral border of orbit, its contribution must be rather small.

Seven small, knob-like teeth are preserved on the anterior part of the alveolar margin of the maxilla, far below the level of the external nares. They are superficially attached to the bone, and arranged in two rows: four in the medial row and three in the lateral row. No other teeth are observed on the maxilla.

The triangular prefrontal is large, forming most of the anterior and anterodorsal margins of the orbit, and the lacrimal may be fused with the prefrontal. The dorsal part of the prefrontal forms a shelf-like lateral projection overhanging the recessed ventrolateral surface of the bone. It is separated by the frontal from the postorbitofrontal along the dorsal margin of the orbit. The postorbitofrontal sends a robust ventral process with a blunt distal end to overlap the jugal, forms the major part of the postorbital bar, and bears a long posterodorsal process that extends for approximately the length of the lower temporal fenestra and contacts the supratemporal near the dorsal head of the quadrate.

The orbit is elongated and oval in shape, with a longitudinal diameter of 118 mm on the left side. The preserved left sclerotic ring consists of at least 15 subrectangular scleral ossicles. The left jugal is crushed and displaced medially into the orbit. The posterior process of the left jugal is missing, but the dorsal process of this bone is tall, approaching the skull roof.

The small supratemporal lies on the posterolateral corner of skull roof, and is partially exposed in lateral view. It contacts the squamosal laterally, the postorbitofrontal anterolaterally, and the dorsal head of the quadrate ventrally. The squamosal lies along the posteroventral side of the postorbitofrontal, extends anteriorly to a point near the postorbital bar, and contributes most of the dorsal margin of the lower temporal fenestra. The base of the squamosal is expanded to form a pronounced ventral process, and caps the quadrate dorsolaterally.

The massive left quadrate is preserved in situ. The dorsal condyle contacts the squamosal, the supratemporal, and possibly the parietal. The shaft of the quadrate extends almost vertically, but the ventral portion curves posteriorly and forms an elongated mandibular condyle. The posterolateral surface of the shaft is deeply concave and bounded by two ridges of bone, of which the lateral ridge is more concave than the medial. The pterygoid ramus (anterior flange) of the quadrate is rather large, and it contributes to the posterior portion of the lateral wall of the middle ear chamber. The rostral portion of the anterior flange of the quadrate receives the base of the epipterygoid, which is partially exposed within the lower temporal fenestra posterior to the postorbitofrontal. The posterior margin of the epipterygoid is deeply concave. Both the dorsal head and the ventral foot of this bone are distinctly expanded, although the foot is more so.

The anterior part of the vomer is exposed in ventral view and bounded laterally by the premaxillae (Fig. 2). The toothless palatine is exposed ventrally, and is sutured to the maxilla laterally and the pterygoid posteromedially. The suborbital fenestra lies posterior to the palatine and ventral to the orbit. The ventral surface of the pterygoid is exposed below the suborbital process of the jugal, and the transverse flange bears a durophagous dentition, as seen in many specimens of *Xinpusaurus* (e.g., IVPP V 14372, IVPP V 11860, and Gmr 010).

Mandible.—The anterior tip of the dentary is missing, but the preserved length of this bone still accounts for approximately half

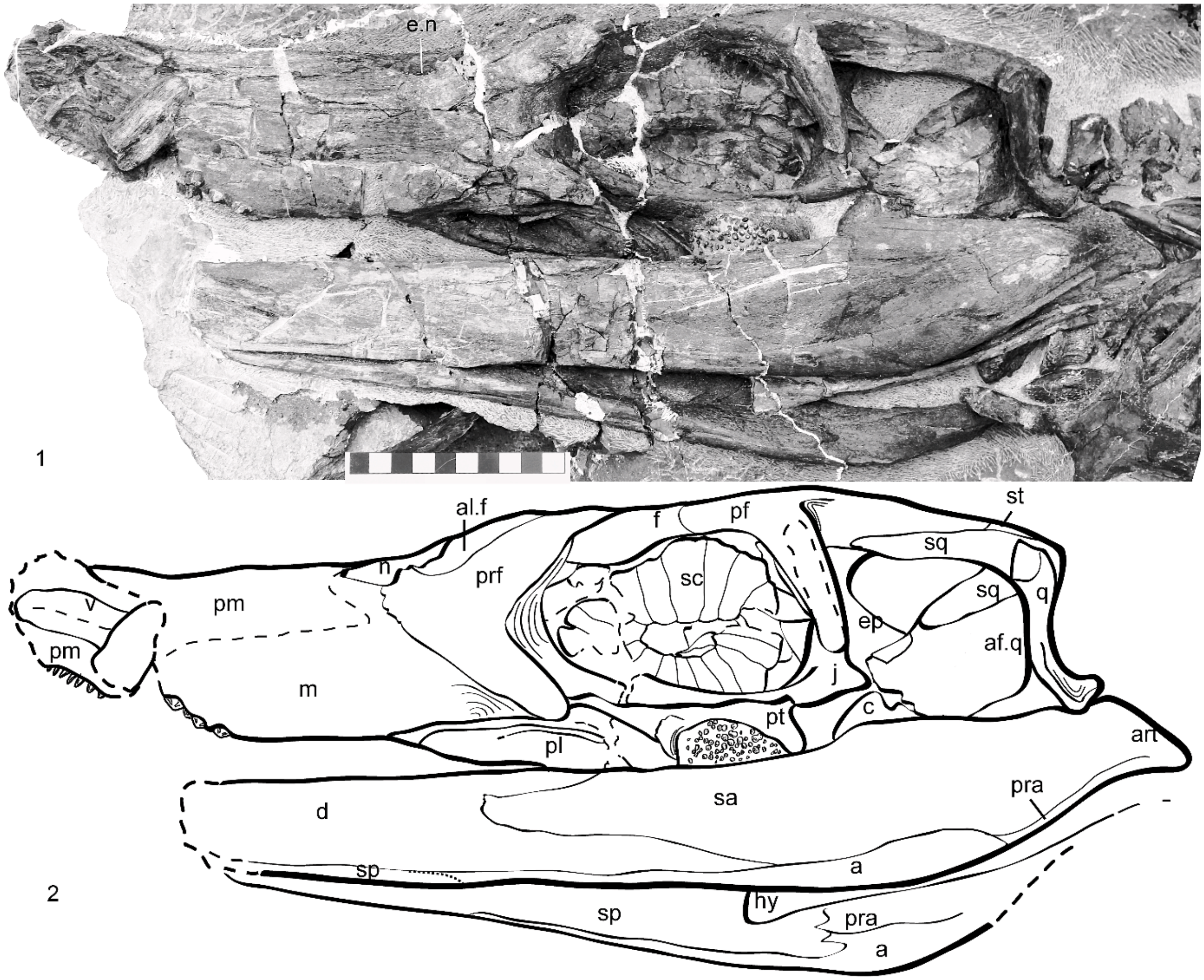

FIGURE 2—*Concavispina biseridens*, skull and mandibles of ZMNH M8804 in lateral view: *1*, photograph; *2*, interpretive drawing. Scale bar=10 cm. Abbreviations: a=angular; af.q=anterior flange of quadrate; al.f=anterolateral process of frontal; art=articular; c=coronoid; d=dentary; ep=epiperygoid; f=frontal; hy=hyoid; j=jugal; m=maxilla; n=nasal; pf=postorbitofrontal; pl=palatine; pm=premaxilla; pra=prearticular; prf=prefrontal; pt=pterygoid; q=quadrate; sa=surangular; sc=scleral ossicle; sp=splenial; sq=squamosal; v=vomer.

the preserved length of the mandible. In lateral view, the dentary bifurcates posteriorly into two processes: a rather short dorsal process that extends slightly posterior to the level of the anterior margin of the orbit, and a relatively long ventral one that approaches the level of the postorbital bar. Accordingly, the suture between the dentary and the surangular is V-shaped, with an anteriorly directed apex, as in *Clarazia* (Rieppel, 1987) and *Miodentosaurus* (Cheng et al., 2007). The surangular is the most conspicuous bone of the mandible in lateral view, being broader than the preserved part of the dentary but similar to it in length. The surangular is bordered ventrally by the angular, and forms posteriorly an unclear boundary with the articular. The coronoid is exposed in lateral view as a triangular prominence above the surangular. The left splenial is narrowly exposed along the ventral margin of the mandible in lateral view, along with the angular. In medial view the right splenial appears rather broad, and can be seen to extend posteriorly to the level of the coronoid (Fig. 2). The right angular is also exposed in medial view, lying ventral to the splenial anteriorly and the prearticular posteriorly.

Hyoid.—A hyoid is exposed medial to the mandibular rami, and has a slightly expanded anterior end that lies close to the level of the pterygoid.

Vertebral column and ribs.—The articulated vertebral column is exposed in lateral view, with 159 vertebrae evident: 42 presacrals, three sacrals, and 114 caudals (Fig. 1). The first fully exposed neural spine (p3 of Fig. 3) lacks the general ax-shape that would be expected in the axial neural spine, and a rather long (>7 cm) rib is preserved in articulation with its corresponding centrum (Fig. 3). Accordingly, this vertebra cannot be identified as the axis, suggesting the specimen bears at least 43 presacral vertebrae. Just anterior to this vertebra, however, is a partially exposed neural spine that is rather low and has a concave posterior margin. The partially exposed neural spine resembles the axial neural spines of *Askeptosaurus* (Müller, 2005) and *Xinpusaurus suni* (IVPP V 14372), and is herein considered to belong to the axis (p2 of Fig. 3). Based on this interpretation, the remaining vertebrae are numbered according to this assumption.

Presacral region.—No sternum is preserved, but in natural anatomical position this element would lie medial to the coracoid. The fifth rib (third exposed rib) reaches the position where a sternum would be expected, suggesting this animal with an

FIGURE 3—*Concavispina biseridens*, anterior portion of postcranial skeleton of ZMNH M8804 in lateral view. Scale bar=10 cm. Abbreviations: (l)=left; cl=clavicle; co=coracoid; g=gastralia; hu=humerus; hy=hyoid; ic=interclavicles; mc=metacarpal; ns=neural spine; p=presacral vertebra; pc=presacral centrum; pr=prezygapophysis; ra=radius; sc=scapula; ul=ulna.

extremely short neck. The third rib (first exposed rib) is clearly much shorter than the more posterior ribs, although its distal end is hidden by the pectoral girdle. The fourth rib is around double the length of the third, and its distal end seems not to reach the sternum. Accepting the first partially exposed vertebra as the axis, the number of cervicals is four.

Most presacrals centra are obscured by the ribs in lateral view, apart from a few posterior dorsal centra and one anterior centrum that is displaced to a position between the mandibles. The exposed dorsal centra are fairly constant in length (~23 mm). The last three presacral centra are fully exposed, and are taller than long.

The neural arches are not fused to the centra: in the anterior vertebrae the neural arches are displaced from the centra, and curved sutures divide them from the centra in the posterior presacrals. The prezygapophyses eclipse most of the postzygapophyses in lateral view, although the postzygapophyses are partially exposed in the anteriormost presacrals. This implies that each postzygapophysis is shorter and more slender than its corresponding prezygapophysis. Each prezygapophysis extends anterodorsally and faces dorsomedially, with a relatively broad base, a nearly straight dorsal edge, and a broad, convex anterior tip. The dorsal edges of the postzygapophyses are nearly horizontal. Below the zygapophyseal articulations between succeeding vertebrae, distinct, oval intervertebral foramina are seen.

The neural spines are rather low. They generally increase in height posteriorly, but their height never exceeds two times their anteroposterior length. The dorsal margin of the third spine (p3) is convex, whereas that of the fifth slants posterodorsally and is rugose. Posterior to the fifth vertebra, the dorsal margins of the presacral neural spines are V-shaped, a condition that appears natural in this specimen although it is unknown in other animals. The notches are shallow near the anterior and posterior ends of the presacral column, but relatively deep in the middle of the series. The apex of the 'V' lies in the anterior half of the neural spine, except in the case of the twenty-fourth vertebra. The anterior and posterior tips flanking the indentation are similar in height in the anterior presacrals, whereas the anterior tips are higher in the middle and posterior presacrals.

The neural spines in the presacral region vary in shape, particularly with respect to the anteroposterior level at which the spine is longest. On the third and fifth vertebrae, the anterior and posterior margins of the spine are nearly vertical, and the dorsal margin of the third neural spine is the longest in the column. From the sixth vertebra to the eighth, the neural spines have elongate bases and taper towards their dorsal margins. Posterior to the eighth vertebra, the neural spines have constricted bases and are longer near the dorsoventral midpoint. Continuing posteriorly, the point of greatest anteroposterior elongation moves towards the dorsal margin of the neural spine. The anterior margins of the neural spines are distinctly convex from the ninth vertebra to approximately the 30th, but in some cases the anterior margin is smoothly curved whereas in others it is more angular and forms a distinct anterior apex. In the presacrals posterior to this region, the anterior margin of the neural spine has a slight convex curvature. The neural spines of the anterior presacrals have nearly straight posterior margins, whereas those of the 18th to 42rd presacrals have posterior margins that are somewhat convex. The convexity is relatively smooth in most cases, except in the18th to 21st, 37th, and 38th presacrals, which have angular posterior margins. The 43rd neural spine has nearly straight anterior and posterior margins, and reaches its maximal anteroposterior elongation close to its dorsal margin. The third to sixth neural spines are closely packed together with little intervening space, although this may be a preservational artifact. The seventh neural spine is anteriorly inclined, whereas the eighth, ninth, and 43rd neural spines are more or less vertical. The 10th to 42nd spines are posteriorly inclined, with the degree of obliquity decreasing posteriorly.

Each diapophysis is located on the anteroventral limit of its corresponding neural arch. The diapophyses are distinctly developed on the anterior vertebrae, but diminish in prominence posteriorly along the column. Posterior to the 33rd vertebra they are no longer discernible. Each parapophysis is a small knob, and, in the posterior vertebrae, they are located on the anterodorsal portion of the centrum. In the last two presacrals the position of the parapophyses is unclear, although in the last presacral the attachment point for the rib seems to lie on the ventral portion of the centrum.

The presacral ribs are robust and slightly curved (Table 1). The heads of the ribs cannot be observed except in the 40th to 43rd ribs, which have single heads that attach to the lower portions of the centra.

A series of gastralia is exposed laterally below the ribs, in the area between the pectoral and pelvic girdles. More than 100 pairs of gastralia are preserved, indicating that there are more than two pairs of gastralia per body segment. The gastralia begin just posterior to the interclavicle. The two gastralia of each pair overlap each other in the ventral midline of the body, except in the posterior third of the series.

Sacral region.—Three sacral vertebrae, similar in shape to the preceding dorsals, can be identified (Fig. 4). In each case the centrum is clearly sutured with the neural arch, and nearly square in lateral view. The prezygapophysis of the first sacral vertebra is similar to that of neighboring dorsal vertebrae , whereas those of the last two sacral vertebrae are more slender. The neural spines are nearly the same height as those of the posterior dorsal and anterior caudal vertebrae, but their bases are elongated and they taper distally. The base of the neural spine is particularly expanded in the anterior two sacral vertebrae, whereas the

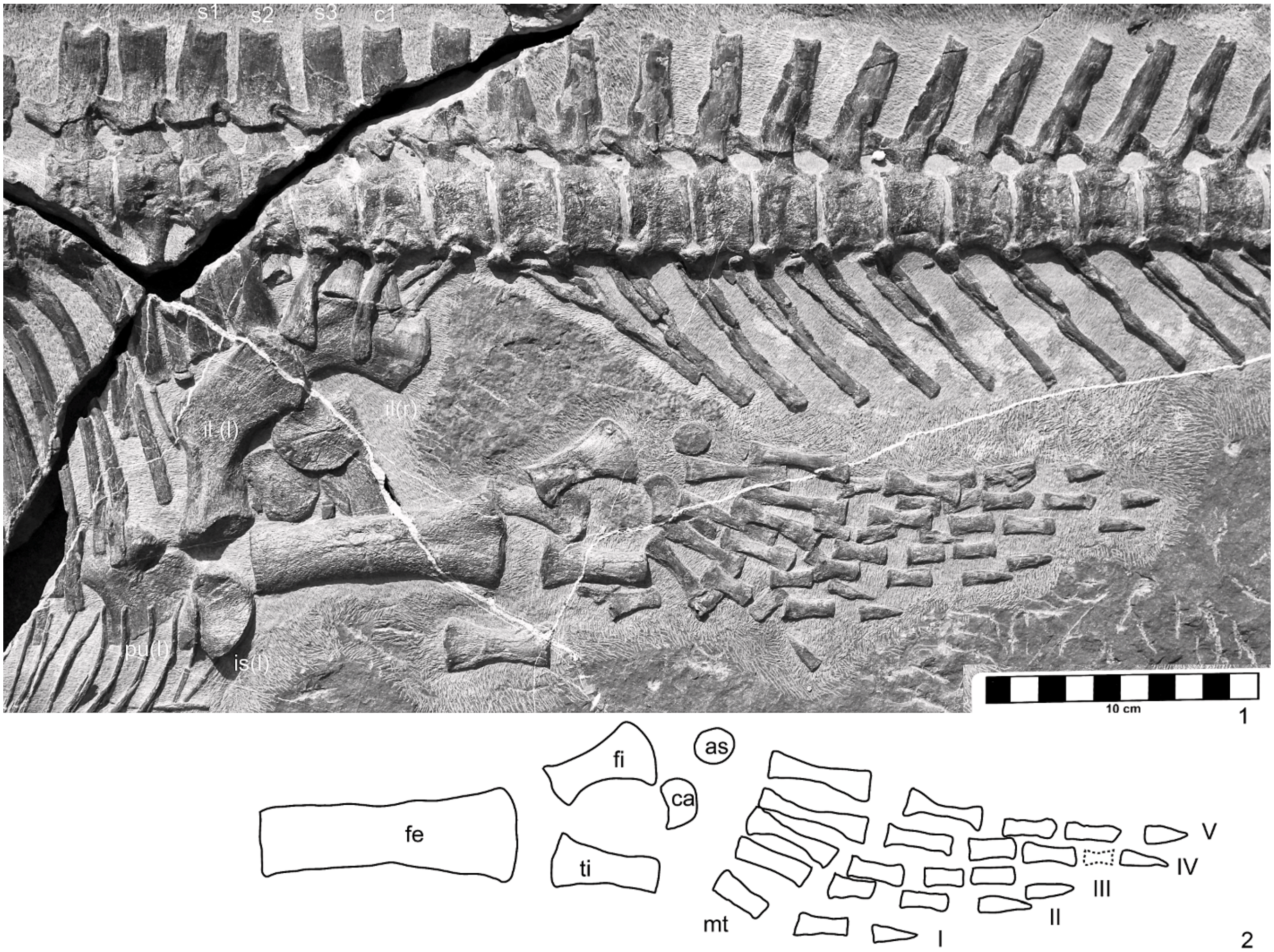

FIGURE 4—*Concavispina biseridens*, partial postcranial skeleton of ZMNH M8804 in lateral view: *1*, photograph showing sacral region, pelvic girdle, and hind limbs; *2*, interpretive drawing of left hind limb. Scale bar=10 cm. Abbreviations: (l)=left; (r)=right; as=astragalus; c=caudal vertebra; ca=calcaneum; fe=femur; fi=fibula; il=ilium; is=ischium; mt=metatarsal; pu=pubis; s=sacral vertebra; ti=tibia; I-V=the digits.

anterior and posterior margins of the neural spine of the third sacral vertebra are nearly vertical. The dorsal margin of each sacral neural spine bears a V-shaped indentation, and the anterior peak is higher than the posterior one. The deepest point of the concavity is positioned in the posterior portion of the neural spine.

The sacral ribs are not fused to the centra, articulating in each case slightly above the lower margin of the centrum. The sacral ribs are short and distally expanded (Table 1).

Caudal region.—The distal tip of the tail is missing, and 114 caudals are preserved (Fig. 1). The anteriormost two caudal vertebrae bear depressions on the ventrolateral margins of their centra and unfused ribs (Fig. 4). The first caudal rib is similar in shape to the sacral ribs, although narrower. The second caudal rib is narrower and shorter (Table 1). The other caudal centra have smooth lateral surfaces that are interrupted near their mid-lengths by vertically oriented depressions, running from the ventrolateral margin of each centrum up to the dorsal edge. The centra gradually decrease in height and length posteriorly, and each centrum is considerably higher than long (Table 2).

The neural arches of the anterior caudal vertebrae are similar to those of the dorsals: comparatively high with stout prezygapophyses and small postzygapophyses. Posterior to the 10th caudal, the neural arches have prominent, elongated, anterodorsally directed prezygapophyses that originate almost directly above the contacts with the centra. By contrast, the postzygapophyses remain very small, and indeed nearly unnoticeable. The neural arches diminish in size posteriorly, and even the prezygapophyses become unnoticeable on the more posterior caudal vertebrae.

The neural spines of the anterior four caudal vertebrae are nearly vertical, but that of the fifth caudal vertebra is deflected posteriorly. From this point the degree of posterior inclination increases posteriorly, and the neural spines of the posteriormost preserved caudal vertebrae are nearly horizontal. The neural

TABLE *1*—Measurements (in mm) of ribs; S=sacral; C=caudal.

No.	3	4	5∼39	40	41	42	43	S1	S2	S3	C1	C2
Length	70	178	∼200–210	173	147	93	57	50	40	39	38	27
Distal width								16	18	15	6.5	4

TABLE *2*—Measurements (in mm) of caudal centra.

No.	1	11	31	41	51	61	71	81	91	101	111
Length	24	22	21	20	19	18	16	15	13	13	12
Height	31	28	28	26	24	23	23	21	18	18	15

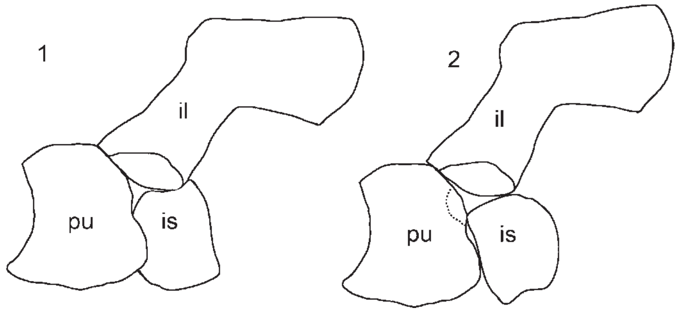

FIGURE 5—Two different reconstructions of the pelvic girdle. Abbreviations: il=ilium; is=ischium; pu=pubis.

spines of the anterior caudal vertebrae have elongated bases and taper towards their dorsal margins. Neural spine height remains approximately constant throughout this part of the column, but the spines become distinctly more slender posteriorly. Posterior to the fifteenth caudal vertebra, the neural spines are slender and rod-like, and they gradually decrease in height and length posteriorly. Although the neural spines remain higher than the corresponding centra throughout the caudal series, neural spine height falls below centrum height in the posteriormost caudals. The dorsal margin is concave in the anteriormost caudal vertebrae, but nearly straight more distally.

Beginning posterior to the second caudal vertebra (Figs. 1, 3), hemal arches are present between successive vertebrae throughout the preserved part of the series. The hemal arches are posteroventrally directed and V-shaped. Each small articular surface of the arch bears a knob-like tips, whereas the ventral tip of each arch is elongated and rectangular. Each hemal arch is higher than the corresponding neural spine, except in the posterior caudal vertebrae. Together with the slightly laterally compressed centra, the elongate neural spines and hemal arches give the tail a laterally compressed appearance.

Pectoral girdle.—The interclavicle is preserved in ventral view (Fig. 3), and has a general arrow shape with an expanded shaft as in other thalattosaurs (Rieppel, 1987; Liu and Rieppel, 2005; Müller, 2005). The anterior process is sharp, and relatively slender. As preserved, the two lateral processes are asymmetric, the left one being longer. Both lateral processes extend laterally rather than posterolaterally as in *Clarazia* (Rieppel, 1987), contrast to *Anshunsaurus* (Liu and Rieppel, 2005; Rieppel et al., 2006) and *Miodentosaurus* (Zhao et al., 2010). The posterior process diminishes in diameter posteriorly over the anterior half of its length, then slightly expands again before finally tapering to a point. The posterior process is approximately four times as long as the anterior process and 1.5 times as long as the span of the lateral processes, and its distal end is covered by gastralia. The interclavicle measures 155 mm in length, and 81 mm in width across the lateral processes.

The left side of the paired pectoral girdle elements is preserved almost in situ and exposed in lateral view, although the left clavicle and coracoid are partially hidden by the interclavicle, whereas the right scapula and coracoid are partially exposed in medial view (Fig. 3). The clavicle lies anterior to the scapula and coracoid, and measures 190 mm in total length. The width of the clavicle varies slightly along its length. The dorsal end of the clavicle extends far beyond the dorsal margin of scapula, a feature unknown in other thalattosaurs. The clavicle is rod-like and similar in shape to that of *Xinpusaurus suni*, but the dorsal portion is slightly curved rather than nearly straight as in *X. suni*. This slight curvature may, however, be an artifact of preservation.

The scapular blade is broad, with a straight dorsal margin, strongly convex anterior and ventral margins, and a posterior margin that is only slightly concave. The supraglenoid buttress is poorly developed. The scapula measures 61 mm in height and 37 mm in width.

The coracoid is broad, with rounded anterior and posterior margins, a dorsal (lateral) margin that is slightly convex and forms a loose articulation with the scapula, and a strongly convex ventral (medial) margin. A small coracoid foramen is situated close to the midpoint of the anterodorsal margin. Posterodorsally, the coracoid thickens and forms a concave area that seems to represent the ventral portion of the glenoid cavity. The bone extends slightly beyond this putative glenoid cavity posteriorly.

Pelvic girdle.—Elements of the pelvic girdle are preserved on both the left and right sides of the body (Fig. 4). The left pelvic girdle is exposed in lateral view, and the right one in medial view. The left ilium covers the ventral part of the right ilium. The right pubis and ischium are distinctly smaller than their left counterparts and differ from them in shape; variations that may be due to incomplete preservation and ossification of the right pubis and ischium. The following description is based mostly on the left pelvis.

The ilium is of typical thalattosaur appearance (Rieppel, 1987; Müller, 2005; Zhao et al., 2010). The elongated posterodorsal process, whose posterodorsal margin is slightly convex, 50 mm long, exceeding the combined length of two sacral centra. Both sides of its posterior portion bear distinct striations. The ventral portion of the ilium is only slightly expanded anteroposteriorly, with a convex ventral margin whose short anterior half contacts the pubis. The ventrolateral portion of the ilium bears a smooth depression that opens posteriorly, representing the dorsal contribution to the acetabulum. The ilium measures 78 mm in height.

The pubis is broad, with an enlarged ventral portion. The posterodorsal margin of the pubis articulates with the ilium, and the short posterior margin contacts the ischium. The posterodorsal corner of the pubis makes a small contribution to the acetabulum. The dorsal margin of the pubis is covered by ribs and may be slightly convex, whereas the anterior margin is distinctly concave and the posterior and ventral margins form a continuous convex arc. A shallow depression lies in the middle of the bone, below the acetabulum and close to the posterior margin. No obturator foramen is visible, but if present this structure would be expected to be situated within the anterior end of the depression.

The ischium is more or less quadrangular in shape. One margin is long and convex, one long and nearly straight, one short and concave, and one short, thick, and convex. In most reptiles, the ventral margin of the ischium lies at approximately the same level as that of the pubis. Following this assumption, we present two possible reconstructions of the pelvis: one in which the thick, convex margin of the ischium is ventrally situated and the pubis overlaps the ischium in lateral view (Fig. 5.1) and one in which the thick, convex edge of the ischium is anterodorsal and the short concave margin is ventral (Fig. 5.2). We prefer the reconstruction shown in Figure 5.1.

Forelimb.—The left and right humeri, radii, and ulnae are present, but a total of three right metacarpals are the only other preserved forelimb elements (Fig. 3). The proximal end of the right humerus is covered by the interclavicle. The humerus is stout and moderately elongate, with a greatly expanded proximal end whose width exceeds that of the distal end. The shaft is slightly constricted, and the distal articular surface is strongly rounded. No foramen can be observed. The left humerus is 65 mm in length, 32 mm in proximal width, and 26 mm in distal width.

Both the radius and the ulna are stout, but the radius is much wider than the ulna. The radius is kidney-shaped, with an anterior margin that is strongly convex and a medial (posterior) margin that is deeply concave. The radius encloses a considerable interosseus space together with the more slender ulna, which is slightly expanded proximally and distally. The shaft of the ulna is constricted, making the lateral and medial margins concave. The proximal and distal ends of the ulna are slightly convex, and the posterior corner of the distal end is thickened. The left radius is 30 mm in length and 23 mm in width, whereas the left ulna is 28 mm in length, 15 mm in proximal width, and 18 mm in distal width.

Three elements from the manus are preserved, and are 13 mm, 14 mm, and 17 mm in length. The shortest one is rather wide, with both ends widened and one end distinctly convex, and can be identified as metacarpal I. The other two are more slender, and each has at least one convex end. They represent two of the other four metacarpals.

Hindlimb.—The left hindlimb is nearly complete, and partially obscures the right (Fig. 4). The femur is elongated and cylindrical, with a slightly constricted shaft and a slightly expanded distal end. The proximal end is weakly convex and two-thirds the width of the distal end, while the distal end is divided into two relatively straight edges in dorsal view. The condyles are poorly developed, and the intercondylar fossa for the triceps tendon is shallow. The left femur has a length of 95 mm, a proximal width of 26 mm, a minimum width along the shaft of 23 mm, and a distal width of 37 mm.

The tibia, a bone that shows little variability among thalattosaurs, retains a primitive cylindrical shape with an expanded proximal end (Rieppel, 1987; Liu and Rieppel, 205; Müller, 2005; Zhao et al., 2010). The fibula is roughly as long as the tibia, but bears a flat, expanded proximal end and a greatly expanded distal end. The distal end is approximately double the width of the shaft. The shaft is markedly concave on both sides. The tibia is 41 mm in length, 21 mm in proximal width, and 14 mm in distal width, whereas the fibula is 40 mm in length, 17.5 mm in proximal width, and 26 mm in distal width.

Two tarsal elements are present and can be identified as the astragalus and calcaneum, as in the holotype of *Xinpusaurus suni* (Yin et al., 2000, pl. 8, fig. 4). The astragalus is broad and roughly kidney-shaped as in other thalattosaurs, and the calcaneum is rounded and displaced from its original position. The five metatarsals are uniformly long and slender with moderately expanded proximal ends, but the first metatarsal is much shorter than the others. The lengths of the first to fifth metatarsals are 21 mm, 35 mm, 35.5 mm, 40.5 mm, and 39 mm, respectively. As preserved, the pes has a phalangeal formula of 2-3-4-4-4. However, the penultimate phalanx of the fourth digit may have been lost, so this animal probably had a typical reptilian phalangeal formula of 2-3-4-5-4.

Type.—ZMNH M8804, a nearly complete skeleton. The holotype is an articulated skeleton with only a few elements missing (Fig. 1). Its preserved length of 364 cm makes *C. biseridens* one of the longest thalattosaurs, exceeded in length only by *Miodentosaurus brevis* (Zhao et al., 2010).

Occurrence.—Xinpu Village, Guanling County, Guizhou Province, China; Xiaowa Formation, Upper Triassic (Carnian).

Remarks.—*Concavispina biseridens* is diagnosed as a distinct taxon within Thalattosauria by a suite of autapomorphies including: skull long, about half as long as presacral part of vertebral column, two series of blunt teeth on anterior part of maxilla; and neural spines of dorsal vertebrae with convex anterior or posterior margins and V-shaped notches on their dorsal margins.

Concavispina is more similar to *Xinpusaurus* than to other thalattosaurs, although the two genera also show some clear differences. Although the skull of *Concavispina* is longer than that of *Xinpusaurus*, there are many shared cranial features: snout moderately elongated, anterior end of maxilla curved dorsally, premaxillary teeth conical and pointed, blunt teeth on maxilla, pterygoid dentigerous, and a slender mandible with a long surangular. However, *Concavispina* has a dentary with a long posteroventral process and a short posterodorsal process, rather than with no posteroventral process and a long posterodorsal process as in *Xinpusaurus* (Liu, 2013).

Concavispina has at least 43 presacral vertebrae, more than are known to exist in any other thalattosaur. Previously recorded presacral counts include 41 or 42 in *Anshunsaurus* (Liu, 2007), at least 38 in *Askeptosaurus* (Müller, 2005), ~30 in *Clarazia* (Rieppel, 1987), and at least 28 in *Endennasaurus* (Müller et al., 2005; Renesto, 1992). *Xinpusaurus* has at least 40 presacral vertebrae, and may have as many as *Concavispina*, but this cannot be confirmed at present. *Concavispina* and *Xinpusaurus* have a very short neck with around four cervical vertebrae, less than even the 7 to 9 deduced to be present in the comparatively short-necked *Clarazia* and *Hescheleria* (Peyer, 1936a, 1936b; Rieppel, 1987). *Concavispina* has three sacral vertebrae whereas most other thalattosaurs have two although in *Xinpusaurus* the number is uncertain (Liu and Rieppel, 2005; Müller, 2005; Peyer, 1936a; Renesto, 1992; Rieppel, 1987).

The neural arches are not fused to the centra in the presacral vertebrae of *Concavispina*, which is represented by an adult specimen, but are fused in the presacral vertebrae of *Xinpusaurus* even in subadults. The neural spines of the posterior cervical and dorsal vertebrae are rather low, with the height measuring less than two times the anteroposterior length, in both *Concavispina* and *Clarazia* (Peyer, 1936a; Rieppel, 1987), but spine height is at least double spine length in *Thalattosaurus* (Merriam, 1905; Nicholls, 1999), *Hescheleria* (Peyer, 1936b), *Nectosaurus* (Merriam, 1908; Nicholls, 1999), and *Xinpusaurus* (Liu, 2001). The proximal caudal neural spines are distinctly elevated and at least three times taller than broad in *Nectosaurus* (Merriam, 1908), the Kössen thalattosaur (Müller, 2007), *Concavispina*, and *Xinpusaurus*.

The scapula is comparatively wide in *Concavispina* but the width of this element is still much less than its height as in other taxa of Thalattosauridea. The anterior margin of the scapula is convex, as in *Clarazia* and *Hescheleria* (Rieppel, 1987) but in contrast to the condition in *Thalattosaurus* (Nicholls, 1999), *Xinpusaurus* (Liu, 2001), and possibly *Nectosaurus halius* (Nicholls, 1999). The clavicle extends much farther dorsally than the scapula in *Concavispina*, a highly unusual condition among thalattosaurs. For example, the clavicle is level with or lower than the dorsal margin of the scapula in *Xinpusaurus* (Liu, 2001) and *Askeptosaurus* (Müller, 2005). The ilium of *Concavispina* is expanded posterodorsally, rather than the unexpanded condition as in *Clarazia* and *Hescheleria* (Rieppel, 1987).

In *Concavispina*, the limbs are shorter in comparison to the length of the presacral vertebral column than is the case in *Xinpusaurus*, and the forelimb/hindlimb and epipodial/propodial length ratios are also smaller in the former taxon. *Concavispina* and *Xinpusaurus* are quite similar in their forelimb morphology, but have quite different hindlimb. In both genera the humerus has a distinctly expanded proximal end, exceeding the distal end in width. This condition has not been explicitly described in other thalattosaurs, but the humerus of *Nectosaurus* sp. (Merriam, 1905, pl. 8, fig. 8) is of similar shape. The distal articular surface of the humerus is convex in *Concavispina* but concave in *Xinpusaurus* (Liu, 2001). The radius is kidney-shaped in *Concavispina*, as in *Xinpusaurus* (Liu, 2001), *Thalattosaurus* (Merriam, 1905), and *Nectosaurus* (Nicholls, 1999). The proximal end of the femur is nearly unexpanded in *Concavispina*, but expanded in other thalattosaurs. The fibula is expanded distally in *Concavispina* as in other thalattosaurs, but its proximal end is not expanded as in

TABLE 3—Taxon-character data matrix for Thalattosauria.

Character number	1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890
Petrolacosaurus kansensis	000-000000	0000000001	0000000000	00010?0000
Youngina capensis	000-000010	0101000000	0??0000000	0000000000
Prolacerta broomi	000-000010	0001000000	0?12000000	0010000000
Agkistrognathus campebelli	1?????????	??????????	10?20100??	??????????
Anshunsaurus huangguoshuensis	0220100110	0100120011	0000000112	0011100001
Anshunsaurus wushaensis	0120100110	010012?011	0000000??2	0011100001
Askeptosaurus italicus	0220100111	0000010111	0000000111	0011101001
Convavispina biseridens	?1?0??1100	1?0?1?001?	?01?0?1?03	00?0111201
Clarazia schinzi	101101010?	1010121110	1000011000	00?01?1112
Endennasaurus acutirostris	0110100100	?1?11??1??	???-2--111	0001?00001
Hescheleria ruebeli	10120101??	????11????	1??3011?00	1010101112
Miodentosaurus brevis	0010100110	0101120011	00000-0111	0011101011
Nectosaurus halius	101201010?	?0?111?11?	??1101000?	11?0?002??
Paralonectes merriami	101??1011?	??????0?1?	1??201100?	??????????
Thalattosaurus alexandrae	1211000101	?011111010	111211100?	1??00?021?
Thalattosaurus borealis	1?110?01??	1?????????	10?21?10??	??????????
Xinpusaurus suni	1210011101	1001120110	1110011003	11?0011212

Clarazia (Peyer, 1936a), *Hescheleria* (Peyer, 1936b), the Kössen thalattosaur (Müller, 2007), and *Xinpusaurus* (Liu, 2001).

To evaluate the phylogenetic position of *Concavispina*, a character list and data matrix containing all 14 thalattosaur species and 40 characters was constructed based on information in the literature. Current character list is mostly based on previous studies by Liu and Rieppel (2005) and Müller (2007) with nine modified characters and four new characters (Appendix 1). The matrix (Table 3) was analyzed using the branch-and-bound search option of PAUP 4.0b10, and all characters are treated as equal weight (Swofford, 2001). With all characters unordered, *Concavispina* lies near the base of Thalattosauridae and does not form a clade with *Xinpusaurus* (Fig. 6.1). While some multistate characters (characters 2, 4, 16, 38, 40) with one state falling between other two states are treated as additive, by contrast, *Concavispina* and *Xinpusaurus* form a clade (Fig. 6.2). In both trees, the only well-supported clades are Askeptosauridea and Thalattosauridea within Thalattosauria, with bootstrap values greater than 50 percent (1,000 replicates) and Bremer support values greater than 2 (Fig. 6). The results slightly differ from previous results. In the present analysis, *Paralonectes* lies on the basal position of Thalattosauridea, *Thalattosaurus* rather than *Xinpusaurus* is closely related to *Nectosaurus*, and no Chinese thalattosaur shows a closer relationship to eastern Pacific species than to western Tethyan species, in contrast to the results of Jiang et al. (2004), Müller (2005, 2007), and Wu et al. (2009). If *Miodentosaurus* really lies on the basal position of Askeptosauridea as in Figure 6.2, the biogeographic origin of thalattosaurs should be out of the western Tethys.

Locomotion.—*Concavispina* is an aquatic animal, with a very short neck as in ichthyosaurs. It has a long tail with a laterally compressed appearance due to the presence of relatively high neural spines and long chevrons. Its limbs are short relative to the body, with short, wide epipodials and a poorly ossified carpus and tarsus. The animal probably relied on lateral undulations of the body axis for propulsion as in *Hovasaurus boulei* (Currie, 1981). The neural spines and chevrons of the body and anterior tail provided sites of attachment for the muscles that drove lateral undulation. In reptiles, the neural spine generally anchors M. semispinalis on the anterior margin and M. multifidus spinae on the posterior margin (Cong et al., 198). The presacral, sacral, and anterior caudal neural spines are lower in *Concavispina* than in *Xinpusaurus*, and have an indented dorsal margin in the former but not in the latter. Although the function of the indented dorsal margin is unknown in *Concavispina*, this feature would provide less surface area to accommodate the aforementioned muscles, resulting in less muscle volume, and therefore less contractile force, as compared to the non-indented neural spines of *Xinpusaurus*. The reduced limbs of *Concavispina* are less developed than those of *Xinpusaurus*, and were probably used for steering rather than propulsion. Furthermore, the body is relatively shorter compared to the head in *Concavispina* than in *Xinpusaurus*, suggesting more limited propulsion power and poorer swimming ability in the former taxon.

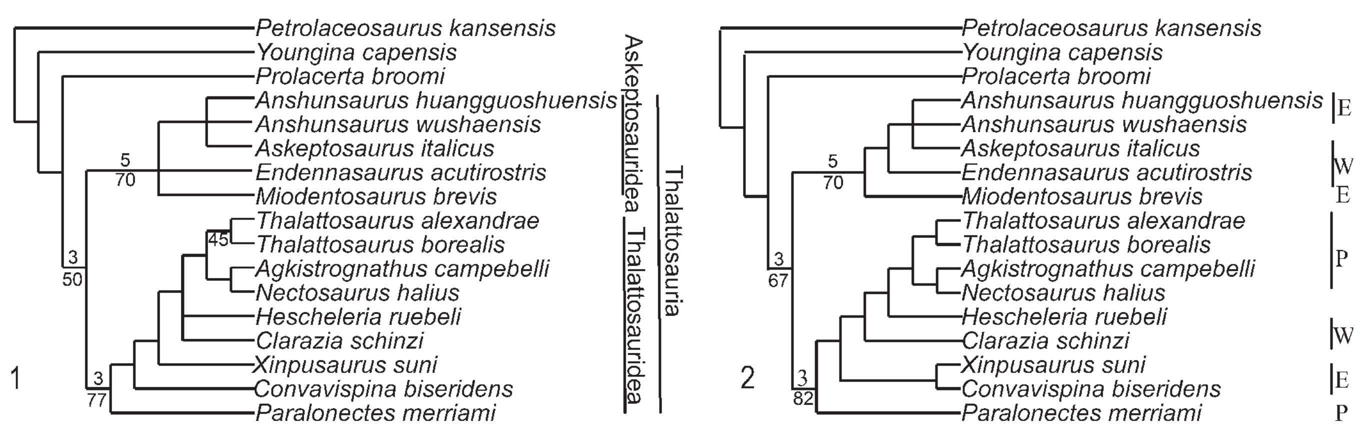

FIGURE 6—Cladograms of thalattosaurian relationships with the distribution of thalattosaurs: *1,* strict consensus of 12 shortest trees generated when all characters are unordered (tree length=89, CI=0.57, RI=0.72); *2,* strict consensus tree of two shortest trees generated when five characters (2, 4, 16, 38, 40) are ordered (tree length=93, CI=0.55, RI=0.72). Bootstrap values above 30% and Bremer support values above 1 are indicated above and below the lines, respectively. Abbreviations: E=eastern Tethys; P=eastern Pacific; W=western Tethys.

Diet.—*Concavispina* and *Xinpusaurus* probably had different diets. In *Xinpusaurus* the anterior teeth are pointed and robust, while the posterior teeth are blunt and broad (Cheng, 2003; Liu and Rieppel, 2001). In *Concavispina* the premaxillary teeth are pointed and slender, while the maxillary teeth are small, blunt, and anteriorly positioned. *Xinpusaurus* probably had the power to crush shells, while *Concavispina* could have eaten softer food such as fish and jellyfish.

ACKNOWLEDGMENTS

We thank Wang S. for preparing the specimen, Wang Y. for helping draw the illustration in Figure 2, C. Sullivan, Wu X.-C., J. Müller, and R. Cuthbertson for comments and improvement on the manuscript. This work is supported by National Science Foundation of China (No. 41172027).

REFERENCES

Cheng, L. 2003. A new species of Triassic Thalattosauria from Guanling, Guizhou. Geological Bulletin of China, 22:274–277. (In Chinese)

Cheng, Y.-N., X.-C. Wu, and T. Sato. 2007. A new thalattosaurian (Reptilian: Diapsida) from the Upper Triassic of Guizhou, China. Vertebrata Palasiatica, 45:246–260. (In Chinese)

Cong, L., L. Hou, X. Wu, and J. Hou. 1998. The gross anatomy of Alligator sinensis Fauvel. Science Press, Beijing, 388 p.

Currie, P. J. 1981. *Hovasaurus boulei*, an aquatic eosuchian from the Upper Permian of Madagascar. Palaeontologia Africana, 24:99–168.

Jiang, D.-Y., M. W. Maisch, Y.-L. Sun, A. T. Matzke, and W.-C. Hao. 2004. A new species of *Xinpusaurus* (Thalattosauria) from the upper Triassic of China. Journal of Vertebrate Paleontology, 24:80–88.

Liu, J. 1999. Sauropterygian from Triassic of Guizhou, China. Chinese Science Bulletin, 44:1312–1316.

Liu, J. 2001. Postcranial skeleton of *Xinpusaurus*, p. 1–7. *In* T. Deng and Y. Wang (eds.), Proceedings of the Eighth Annual Meeting of the Chinese Society of Vertebrate Palaeontology. China Ocean Press, Beijing.

Liu, J. 2007. A Juvenile Specimen of *Anshunsaurus* (Reptilia: Thalattosauria). American Museum Novitates, 3582:1–9.

Liu, J. 2013. On the taxonomy of *Xinpusaurus* (Reptilia: Thalattosauria). Vertebrata Palasiatica, 53(1):17–23.

Liu, J. and O. Rieppel. 2001. The second thalattosaur from the Triassic of Guizhou, China. Vertebrata PalAsiatica, 39:77–87.

Liu, J. and O. Rieppel. 2005. Restudy of *Anshunsaurus huangguoshuensis* (Reptilia: Thalattosauria) from the Middle Triassic of Guizhou, China. American Museum Novitates, 3488:1–34.

Merriam, J. C. 1904. A new marine reptile from the Triassic of California. Bulletin of the Department of Geology at the University of California, 3: 419–421.

Merriam, J. C. 1905. The Thalattosauria: a group of marine reptiles from the Triassic of California. California Academy of Sciences Memoirs, 5:1–38.

Merriam, J. C. 1908. Notes on the osteology of the thalattosaurian genus *Nectosaurus*. University of California Publications, Bull. Depart. Geol., 5: 217–223.

Müller, J. 2005. The anatomy of *Askeptosaurus italicus* from the Middle Triassic of Monte San Giorgio, and the interrelationships of thalattosaurs (Reptilia, Diapsida). Canadian Journal of Earth Sciences, 42(7):1347–1367.

Müller, J. 2007. First record of a thalattosaur from the Upper Triassic of Austria. Journal of Vertebrate Paleontology, 27:236–240.

Müller, J., S. Renesto, and S. E. Evans. 2005. The marine diapsid reptile *Endennasaurus* from the Upper Triassic of Italy. Palaeontology, 48:15–30.

Nicholls, E. L. 1999. A reexamination of *Thalattosaurus* and *Nectosaurus* and the relationships of the Thalattosauria (Reptilia: Diapsida). PaleoBios, 19: 1–29.

Nicholls, E. L. and D. B. Brinkman. 1993. New thalattosaurs (Reptilia: Diapsida) from the Triassic Sulphur Formation of Wapiti Lake, British Columbia. Journal of Paleontology, 67:263–278.

Peyer, B. 1936a. Die Triasfauna der Tessiner Kalkalpen. X. *Clarazia schinzi* nov. gen. nov. sp. Abhandlungen der Schweizerischen Paläontologischen Gesellschaft, 57:1–61.

Peyer, B. 1936b. Die Triasfauna der Tessiner Kalkalpen. XI. *Hescheleria rübeli n*ov. gen. nov. sp. Abhandlungen der Schweizerischen Paläontologischen Gesellschaft, 58:1–48.

Renesto, S. 1992. The anatomy and relationships of *Endennasaurus acutirostris* (Reptilia, Neodiapsida), from the Norian (Late Triassic of Lombardy). Rivista Italiana di Paleontologia e Stratigrafia, 97:409–430.

Rieppel, O. 1987. *Clarazia* and *Hescheleria*, a re-investigation of two problematical reptiles from the Middle Triassic of Monte San Giorgio, Switzerland. Palaeontographica A, 195:101–129.

Rieppel, O. and J. Liu. 2006. On *Xinpusaurus* (Reptilia: Thalattosauria). Journal of Vertebrate Paleontology, 26:200–204.

Rieppel, O., J. Liu, and H. Bucher. 2000. The first record of a thalattosaur reptile from the Late Triassic of southern China (Guizhou Province, PR China). Journal of Vertebrate Paleontology, 20:507–514.

Rieppel, O., J. Liu, and C. Li. 2006. A new species of the thalattosaur genus *Anshunsaurus* (Reptilia: Thalattosauria) from the Middle Triassic of Guizhou Province, southwestern China. Vertebrata Palasiatica, 44:285–296.

Swofford, D. L. 2001. PAUP*. Phylogenetic Analysis Using Parsimony (* and Other Methods). Sinauer Associates, Sunderland, MA.

Wang, X., G. H. Bachmann, H. Hagdorn, P. M. Sander, G. Cuny, X. Chen, C. Wang, L. Chen, L. Cheng, F. Meng, and G. Xu. 2008. The Late Triassic black shales of the Guanling Area, Guizhou Province, South-West China: A unique marine reptile and pelagic crinoid fossil lagerstatte. Palaeontology, 51:27–61.

Wu, X.-C., Y.-N. Cheng, T. Sato, and H.-Y. Shan. 2009. *Miodentosaurus brevis* Cheng et al., 2007 (Diapsida: Thalattosauria): Its postcranial skeleton and phylogenetic relationships. Vertebrata Palasiatica, 47:1–20.

Yin, G. Z., X. G. Zhou, and Z. T. Cao. 2000. A preliminary study on the early Late Triassic marine reptiles from Guanlig, Guizhou. Geology Geochemistry, 28(3):1–23. (In Chinese)

Zhao, L.-J., J. Liu, C. Li and T. He. 2013. A new thalattosaur, *Concavispina biseridens* gen. et sp. nov. from Guanling, China. Vertebrata Palasiatica, 51(1):24–28. (In Chinese)

Zhao, L.-J., T. Sato, J. Liu, C. Li, and X.-C. Wu. 2010. A new skeleton of *Miodentosaurus brevis* (Diapsida: Thalattosauria) with a further study of the taxon. Vertebrata Palasiatica, 48:1–10.

Accepted 29 September 2012

Appendix *1*

Characters used in the phylogenetic analysis of *Thalattosauria*

The data set consists of 40 characters and is based on previous studies by L. Liu and Rieppel (2005) and M. Müller (2007). Four new characters (7, 22, 35, 36) have been added, and the definitions of nine characters (1, 2, 4, 16, 23, 25, 30, 34, 40) have been modified. The analysis was run once with all characters unordered, and once with the characters marked with asterisks treated as ordered.

1) Snout: nearly horizontal (0); turned downwards (1). [*M2*]
2) Snout length: preorbital region short, distance from tip of snout to anterior margin of orbit shorter than distance from anterior margin of orbit to posterior tip of supratemporal (0); preorbital region moderate, distance from tip of snout to anterior margin of orbit longer than distance from anterior margin of orbit to posterior tip of supratemporal but less than twice distance from anterior margin of the orbit to posterior margin of parietal skull table (1); preorbital region elongated, distance from tip of snout to anterior margin of orbit more than twice distance from anterior margin of orbit to posterior margin of parietal skull table (2). [*M40*]*
3) Rostrum: absent (0); present and tapering to pointed tip, i.e. with convergent lateral margins in front of external nares (1); present and tapering to blunt tip, i.e. with parallel lateral margins in front of external nares (2). [L2]
4) Premaxilla: not deflected ventrally (0); moderately deflected ventrally (1); strongly deflected ventrally, with alveolar margin positioned nearly perpendicular to alveolar margin of maxilla (2). [*M3*]*
5) Premaxilla, posteroventral process below naris: present (0); absent (1). [L5]
6) Proportions of maxilla: at least twice as long as high (0); with truncated anterior end and narrow, vertically positioned ascending process, and less than twice as long as high (1). [M4]
7) Anterior part of alveolar margin of maxilla: straight (0); distinctly curved upwards (1).
8) Nasals: contact each other across midline (0); separated by posterior extent of premaxillae (1). [M13]
9) Nasal: does not extend posterior to level of anterior margin of orbit (0); does extend posteriorly beyond this level (1). [L9, M14]
10) Nasal: contacts prefrontal (0); separated from prefrontal (1). [L11, M17]
11) Anterolateral process of frontal: well separated from external naris (0); closely approaches or even enters posterior margin of external naris (1). [L10, M15]
12) Posterolateral process of frontal: does not extend far beyond anterior margin of lower temporal fossa (0); does extend far beyond this margin (1). [L14, M19]
13) Frontal: does not contact supratemporal (0); does contact supratemporal (1). [L13, M20]

14) Frontoparietal suture: interdigitating, oriented transversely for most of its length (0); deeply embayed in shape of broad V, with apex pointing forward (1). [L15, M21]
15) Postfrontal and postorbital: separate (0); fused (1). [L16, M22]
16) Upper temporal fenestra: present and large (0); reduced and slit-like (1); absent (2). [*M23*]*
17) Squamosal, posteroventral process: present (0); absent (1). [L17, M24]
18) Quadrate, expanded medial lamina: present (0); absent (1). [M25]
19) Quadratojugal: present (0); absent (1). [M26]
20) Pineal foramen: small and located at or somewhat behind midpoint of parietal skull table (0); large and located in front of midpoint of parietal skull table (1). [L19, M27]
21) Dorsal margin of dentary symphysis: straight (0); recurved (1). [L20, 24, M8]
22) Dentary, posteroventral process: distinct (0); indistinct or absent (1).
23) Angular, exposure on lateral side of lower jaw: extensive (0); small, much less extensive than lateral exposure of surangular (1). [*L21*]
24) Tooth implantation: subthecodont (0); thecodont (1); ankylothecodont (2); superficial (3). [M5]
25) Premaxilla dentition: present (0); pseudodont projection (1); absent (2). [*L22, M6*]
26) Diastema between premaxillary and maxillary teeth: absent (0); present (1). [L23, M7]
27) Posterior maxillary and dentary teeth: conical and pointed (0); bulbous and blunt (1). [L25, M9]
28) Vomerine dentition: present (0); absent (1). [M12]
29) Pterygoid dentition: present (0); absent (1). [M10, 11]
30) Number of cervical vertebrae: $6\sim10$ (0); $11\sim14$ (1); >14 (2); <6 (3). [*L27*, *M29*, *W29*]
31) Posterior cervical and dorsal vertebrae, neural spine height: less than double neural spine anteroposterior length (0); at least double neural spine anteroposterior length (1). [L28, M30]
32) Proximal caudal vertebrae, neural spine height: less than triple neural spine anteroposterior length (0); distinctly elevated, at least triple neural spine anteroposterior length (1). [L29, M31]
33) Anterior processes on cervical ribs: absent (0); present (1). [M32]
34) Scapula: slender (0); broad, width approximately equal to height (1). [*L30, M33*]
35) Scapular anterior margin: approximately straight or slightly convex (0); strongly convex (1).
36) Humerus, proximal end: not wider than distal end (0); wider than distal end (1).
37) Deltopectoral crest: well developed (0); reduced (1). [L31, M38]
38) Radius: slender (0); distal end slightly expanded (1); whole bone strongly expanded and roughly kidney shaped (2). [L32, *M35, 36*]*
39) Femur, distal end: about equal in width to proximal end (0); markedly wider than proximal end (1). [L33]
40) Fibula: slender (0); slightly expanded (1); broadly mediolaterally expanded (2). [*L34*, *M39*]*