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贵州三叠纪海龙类化石一新材料[1)]

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摘要 记述了贵州关岭晚三叠世早期法郎组瓦窑段新的海龙标本：一个基本完整的侧向挤压头骨及下颌(中国科学院古脊椎动物与古人类研究所标本编号 V 11860)。根据图版，它与尹恭正等(2000)建立并归入鱼龙目 Cymbospondylidae 科的孙氏“新铺鱼龙”(*Xinpusaurus suni*)极为相似。但是由于从文章中得不到头部关键性状的描述，并且本文第一作者到贵阳也不被允许观察标本，目前只有依据与正模图版的对比将 V 11860 标本暂定为孙氏新铺龙相似种(*Xinpusaurus* cf. *X. suni*)。由于系统分类位置的改变，建议将该属的中文名称由“新铺鱼龙”改为新铺龙。

迄今为止，在所有海龙类头骨中此标本提供了最多可以观察到的性状，包括脑颅侧面的特征。这是一类小型的海龙，吻部中等长度，微微向腹面倾斜；上颌骨前端背向弯曲，此处牙齿扩大且向前平伏；头骨前部的牙齿(前颌骨、上颌骨前部、齿骨)圆锥形，较突出，而靠后部的牙齿可能较圆钝(保存不完整)；前颌骨与上颌骨牙齿间无明显间隙；犁骨和翼骨具齿；下颌细长，齿骨联合部窄。长的齿骨大约占下颌长度的 2/3。

基于 18 个性状进行了初步的支序分析，结果表明新铺龙与北美的 *Nectosaurus* 关系最近。但受海龙类化石保存所限，提供性状较少，支序分析对此结果的支持较弱。目前只能说海龙类是一个化石发现尚少的广布类群。

关岭动物群目前包括海龙类、鱼龙类及楯齿龙类。其中中国豆齿龙(*Sinocyamodus*)(李淳，2000)是中国第一个楯齿龙类，安顺龙(*Anshunsaurus*)(刘俊，1999)是海龙类在中国的首次发现。

关键词 贵州关岭，晚三叠世，法郎组瓦窑段，海龙目，新铺龙

中图法分类号 Q915.864

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THE SECOND THALATTOSAUR FROM THE TRIASSIC OF GUIZHOU, CHINA

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Abstract A new specimen of *Xinpusaurus* (*Xinpusaurus* cf. *X. suni* Yin) from the Wayao Member, Falang Formation (early Late Triassic) of Guanling, Guizhou Province, southwestern China, is described, and the diagnosis of that taxon is revised. This taxon was originally described as an ichthyosaur, but is in fact a thalattosaur. A preliminary phylogenetic analysis indicates potential trans-Pacific relationships of *Xinpusaurus*.

Key words Guizhou, Late Triassic, Wayao Member of Falang Formation, Thalattosauria, *Xinpusaurus*

1 Introduction

The first thalattosaur discovered in China was recently described by Liu (1999), and its phylogenetic relationships assessed by Rieppel et al. (2000). In the meantime, preparation of new specimens from the collection of marine reptiles from Guizhou kept at the IVPP, was completed, and allowed the identification of the second thalattosaur. The specimens are referred to a taxon that was recently described by Yin (Yin et al., 2000) under the name of *Xinpusaurus suni*, and referred to cymbospondylid ichthyosaurs. The new specimen includes a nearly complete skull, mandible and some vertebrae. It offers more detailed information on skull morphology than any thalattosaur previously described.

2 Systematic Paleontology

Thalattosauria Merriam, 1904

***Xinpusaurus* cf. *X. suni* Yin, 2000**

(figs. 1, 2; pl. I)

Referred specimen An almost complete skull with mandible (IVPP V 11860).

Locality and horizon Xinpu, Guanling County, Anshun Prefecture, Guizhou Province, China; Wayao Member of Falang Formation, lower Upper Triassic.

Known distribution Late Triassic, southern China.

Diagnosis A relatively small claraziid thalattosaur with a moderately long rostrum that is weakly bent ventrad; anterior end of the maxilla curved dorsally carrying enlarged procumbent teeth; anterior teeth (on premaxilla, anterior part of maxilla, and dentary) conical and pointed, more posterior teeth probably blunt (incompletely preserved); no marked diastema between the premaxillary and maxillary teeth; vomer and pterygoid dentigerous; slender mandible with dentary symphyseal region tapering to a narrow tip; dentary about 2/3 of the length of the mandible.

Comments Our diagnosis of the taxon is based on the referred specimen IVPP V 11860, and the preliminary analysis of its phylogenetic relationships. Unfortunately, we were not granted access to the holotype of *Xinpusaurus suni*. Should referral of the specimen IVPP V 11860 to that taxon prove erroneous in future studies, the diagnosis will apply to the taxon of which specimen IVPP V 11860 will be the holotype.

3 Morphological Description

Skull Compared to Askeptosauridae, *Xinpusaurus* is a relatively small thalattosaur: the length from the tip of snout to the posterior tip of the right supratemporal is 136 mm, the length from the tip of the dentary to the posterior end of the left articular is 140mm.

The skull and the mandible are crushed and compressed (fig. 1A, C); ventral skull elements are exposed in left lateral view. The sutures can clearly be identified on the left side of the skull, but the original surface of the bones of the right side is abraded. The jugal, squamosal and quadrate of the left side are lost, exposing the braincase in left lateral view (fig. 1B).

The snout is moderately long, with a preorbital region of the skull that is not distinctly longer than the postorbital region of the skull. The snout is slightly curved ventrad and tapering to a blunt tip. The posterior processes of the premaxillae contact the frontals at a level in front of the anterior margin of the orbit. The external nares are small and retracted, located closely in front of the orbit. The medial (dorsal) margin of the external naris is defined by the premaxilla and the nasal. The lateral (ventral) margin of the external naris is formed by the maxilla. The nasal is a small and triangular element, and it remains separated from the prefrontal by the slender ascending process of the maxilla, which contacts the anterolateral process of frontal. The nasal does not extend backwards to a level behind the anterior margin of orbit. The maxilla is an elongated, essentially triangular bone, extending anteriorly to a level well in front of the external naris. The anterior end of the alveolar margin of the maxilla is sharply curved dorsally. Posteroventrally, the maxilla is drawn out into a short process that follows the anteroventral (anterolateral) margin of the orbit for a short distance.

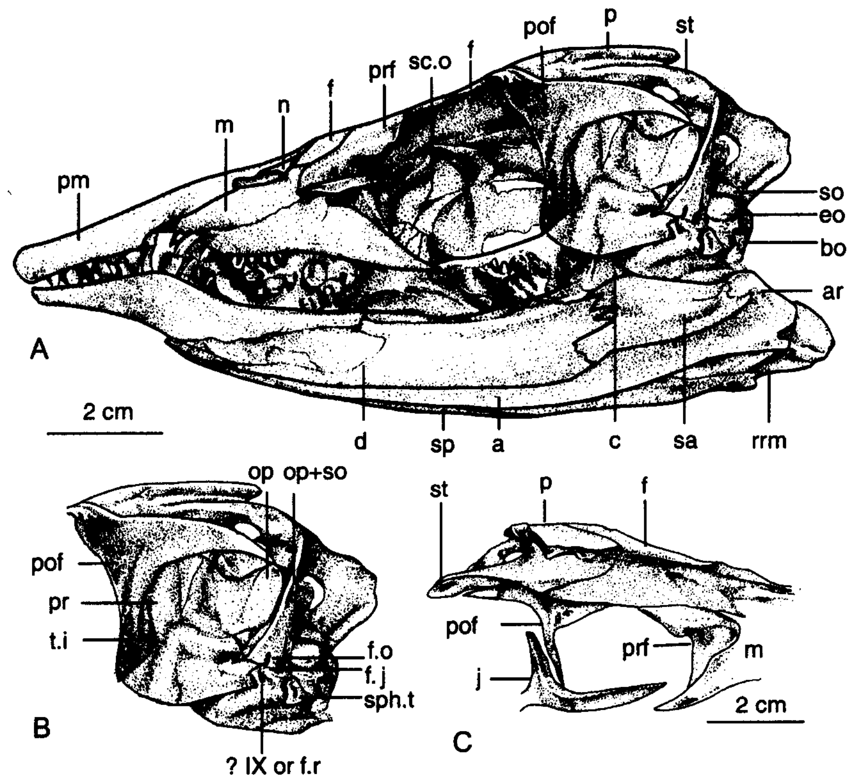

Fig. 1 *Xinpusaurus* cf. *X. suni* (IVPP V 11860)

A. Skull in left view; B. Braincase in left view; C. Skull in right view

简字说明 Abbreviations: a, angular 隅骨; ar, articular 关节骨; bo, basiocciptal 基枕骨; c, coronoid 冠状骨; d, dentary 齿骨; eo, exoccipital 外枕骨; f, frontal 额骨; f.j, jugular foramen 颈静脉孔; f.o, fenestra ovalis 卵圆窗; f.r, fenestra rotundum 圆窗; j, jugal 轭骨; m, maxilla 上颌骨; n, nasal 鼻骨; op, opisthotic 后耳骨; p, parietal 顶骨; pm, premaxilla 前颌骨; pof, postorbitofrontal 眶后一后额骨; pr, prootic 前耳骨; prf, prefrontal 前额骨; q, quadrate 方骨; rrm, right ramus of mandible 下颌右支; sa, surangular 上隅骨; sc.o, scleral ossicles 巩膜骨; so, supraoccipital 上枕骨; sp, splenial 夹板骨; sph.t, sphenoccipital tuber 蝶枕结节; sq, squamosal 鳞骨; st, supratemporal 上颞骨; t.i, trigeminal incisure 三叉神经切迹; IX, nerve IX 第九脑神经孔

Each of the frontals forms an anterolateral and an anteromedial process, both of which taper to a pointed tip. The anterolateral process of the frontal, which is embraced by the nasal and the maxilla, is shorter than the anteromedial process of the frontal. The anteromedial processes of the frontals together embrace the pointed posterior tips of the premaxillae. The frontals meet the parietals in a deeply embayed, V-shaped suture (the apex pointing forwards). Each frontal forms a distinct posterolateral process, as is also seen in *Thalattosaurus* and *Nectosaurus* (Nicholls, 1999), whereas the posterolateral processes in *Anshunsaurus* (Rieppel et al., 2000) and *Clarazia* (Rieppel, 1987) are more slender. In *Xinpusaurus*, the posterolateral process of the frontal extends backwards between the postorbitofrontal and parietal to the level of the anterodorsal corner of the lower temporal fossa. As in *Anshunsaurus* (Liu, 1999; Rieppel et al., 2000), the posterolateral process of the frontal does not contact the anterior process of the supratemporal.

The orbit is relatively large. Scleral ossicles (four or more plates) are preserved in the anteroventral corner of the left orbit. A scleral ring had also been described for *Askeptosaurus* (Kuhn-Schnyder, 1952). The prefrontal is a curved element that defines the anterodorsal margin of the orbit. Its posterodorsal process does not contact the postorbitofrontal along the dorsal (medial) margin of the orbit. The postorbital and postfrontal are fused. The postorbitofrontal forms the posterodorsal and most of the posterior margin of the orbit. Posterodorsally, the postorbitofrontal is drawn out into a long and slender process that extends far back along the lateral margin of the skull roof. The tapering ventral process of the postorbitofrontal meets the jugal in an oblique overlap within the postorbital arch. The jugal is a distinctly triradiate element. Its pointed dorsal process enters the postorbital arch. A long anterior process forms the ventral (lateral) margin of the orbit, meeting the posterior process of the maxilla in the anteroventral (anterolateral) corner of the orbit. The posterior extent of the jugal cannot be assessed due to incomplete preservation of the latter.

The upper temporal fossa is completely obliterated in *Xinpusaurus*, as is also the case in *Anshunsaurus* (Rieppel et al., 2000), as well as in *Clarazia* (Rieppel, 1987). All well preserved specimens of thalattosaurs show this condition, which indeed may be a general character of Thalattosauria as was suggested by Rieppel et al. (2000). Part of the left parietal has been pushed across the right one, partly obscuring the pineal foramen. The pineal foramen is displaced anteriorly, located shortly behind the frontoparietal suture.

The parietal establishes a contact with the posterior process of the postorbitofrontal between the frontal and the supratemporal. Posterolaterally, the parietal is drawn out into an elongate supratemporal process that forms the posterodorsal margin of the deeply excavated occiput. The supratemporal is broadly exposed at the posterolateral corner of the skull table. Its broad posterior part forms the main part of the quadrate suspension. Anteriorly, the supratemporal tapers to a narrow process that extends between the parietal and the postorbitofrontal, but does not reach the frontal.

The squamosal is not preserved on the left side of the skull. Its identification on the right side of the skull remains equivocal. A slender bone just anterior of the right quadrate may represent the squamosal (exposed in dorsal view), or perhaps the epipterygoid. Only the right quadrate is partly exposed in lateral view, but it is displaced anteriorly relative to its original position. The shape of the quadrate corresponds to that seen in *Thalattosaurus alexandrae* (Nicholls, 1999, Fig. 4). The surface of the cephalic condyle is evenly convex, and articulates with the supratemporal and squamosal. The shaft of the quadrate has a convex anterior margin and a concave posterior margin. The mandibular condyle of the quadrate is expanded to form an elongate surface. No quadratojugal can be identified.

The lateral side of the braincase (fig. 1A, B) is exposed due to the loss of the left quadrate and the jugal. The left prootic is complete. It is a large element preserved in its original position. The anterior margin of the prootic is notched as it delineates the trigeminal incisure (exit of cranial nerve V). The prootic shows a transversely oriented crest in its middle part. Posteriorly, it contacts the opisthotic. The fenestra ovalis is located between the ventral parts of these two bones. The ventral margin of the prootic contacts the basisphenoid. Posteroventrally, a large jugular foramen can be identified that transmitted the cranial nerves X, XI and the posterior cerebral vein. There is an opening anteroventral to the jugular foramen, it perhaps is the foramen just for the cranial nerve IX (glossopharyngeal nerve), or the fenestra rotundum. The posterior end of the basisphenoid forms a sphenoccipital tuber, which is located anterolateral to the occipital condyle. The occiput is exposed, although it is somewhat displaced to the left side. The foramen magnum is closed due to compression of the skull. Its margin is formed by the supraoccipital, the basioccipital, and the exoccipitals.

Lower jaw The sutures on the left mandible are more clearly delineated than those on the right one. The description of the lower jaw is therefore primarily based on the left ramus. The mandible is slender, the symphyseal region of the dentary is tapering to a narrow tip. The alveolar margin of the anterior part of the dentary is curved dorsally to match the curved anterior part of the maxilla. As a consequence of this curvature, the anterior dentary teeth point backwards, opposing the anteriorly pointing teeth on the anterior part of the maxilla. The dentary extends backwards along about 2/3 of the whole length of the mandible. It contacts the coronoid posteriorly. The interdigitating suture between the dentary and the surangular is exposed just below the coronoid process. The coronoid is distinct, and forms all of the coronoid process. The posterior extension of the coronoid, as exposed on the lateral surface of the mandible, is short. The angular does not extend as far anteriorly as it does in *Thalattosaurus* (Nicholls, 1999) and *Askeptosaurus* (Kuhn-Schnyder, 1952). The suture between the articular and angular is not clear. The retroarticular process is short and sloping posteroventrally.

Most of the medial side of the mandible is obscured by compression of the skull, but the ventral part of the right ramus is exposed as it emerges from below the left ramus. The splenial is elongated, as it extends posteriorly to a level behind the apex of the coronoid process.

Dentition The teeth or right side of the skull are not as well preserved as those of the left side. The following description is therefore based on the left side of the skull. The premaxilla carries 7 teeth. The teeth are conical, pointed, and vertically oriented. The crown is separated from the root by a distinct constriction, and the enamel is ornamented with vertical striations. There is no marked diastema between the premaxillary and maxillary teeth. The anterior two (three?) teeth on the maxilla are procumbent due to the dorsal curvature of the anterior part of the alveolar margin of the maxilla. The second (third?) maxillary tooth is distinctly enlarged. More posteriorly, the remains of four more broad and blunt teeth can be identified on the maxilla, the tips of which are broken.

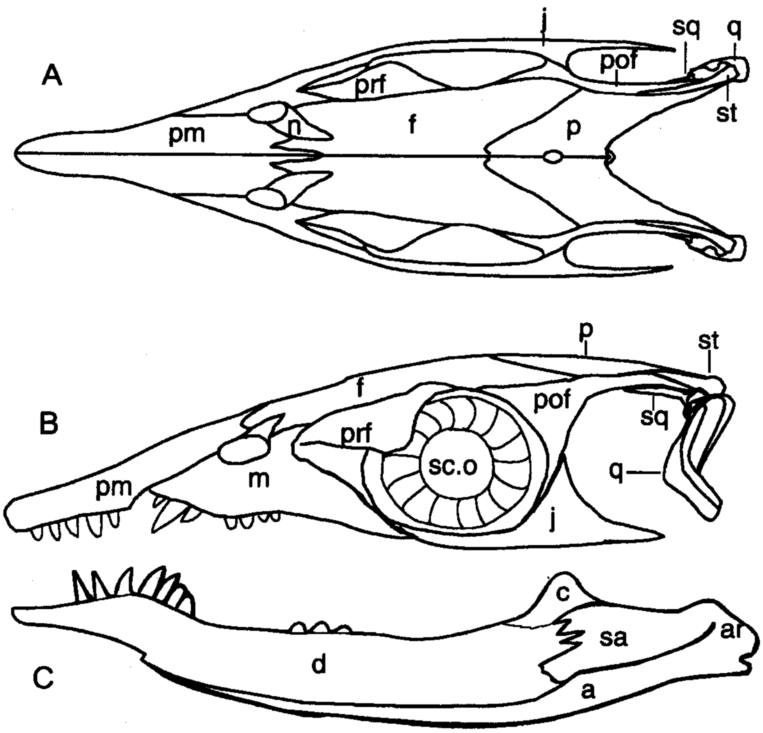

Fig.2 Reconstruction of the skull of *Xinpusaurus* cf. *X. suni* in dorsal view (A), in lateral view (B) and the mandible in lateral view (C), abbreviations as in fig.1

There are 7 conical and pointed teeth on the dentary, but no tooth is found on the most anterior part. The dentary teeth opposing the procumbent teeth in the anterior part of the maxilla are enlarged and reclining posteriorly, the posterior dentary teeth are bulbous and blunt.

Compression of the skull resulted in the lateral exposure of some tooth bearing palatal elements. There are 6 or more large, bulbous and blunt teeth on the vomer, whereas the pterygoid is furnished with numerous small teeth.

4 Discussion

Xinpusaurus is readily distinguished from *Askeptosaurus* and *Anshunsaurus* by its relatively small size, and by its short snout that is weakly bent ventrad (Kuhn-Schnyder, 1952; Rieppel et al., 2000). In thalattosaur genera with a short snout, the tip of the snout is deflected ventrally to a variable degree in *Thalattosaurus* (Nicholls, 1999), *Clarazia* and *Hescheleria*, which resembles the weakly ventral orientation of the rostrum in *Xinpusaurus*. *Xinpusaurus* differs from *Thalattosaurus*, *Clarazia*, and *Hescheleria* by the absence of a marked diastema between the premaxillary and maxillary teeth. By contrast, *Xinpusaurus* resembles *Thalattosaurus* and *Nectosaurus* in the differentiation of the posterolateral process of the frontal. The material of the other three genera of thalattosaurs, viz. *Agkistrognathus*, *Paralonectes*, and *Nectosaurus*, is less well preserved, but *Xinpusaurus* is still readily distinguished from them. The dentary of *Agkistrognathus* is bent ventrally in a sharp curve, and a bony protuberance projects anteriorly from the mandibular symphysis (Nicholls and Brinkman, 1993). *Paralonectes* has relatively larger external nares (Nicholls and Brinkman, 1993), and *Nectosaurus* lacks bulbous and blunt teeth (Nicholls, 1999), and its maxilla extends posteriorly well below the orbit.

The anterior end of the alveolar margin of the maxilla of *Xinpusaurus* is curved dorsally; its anterior teeth consequently are procumbent. This character is also observed in *Paralonectes* and *Nectosaurus* (Nicholls and Brinkman, 1993; Nicholls, 1999), but is absent in other thalattosaurs. This character suggests a close relationship of *Xinpusaurus* with these genera. In order to test this hypothesis, we conducted a preliminary phylogenetic analysis, building on the characters and data matrix used previously by Rieppel et al. (2000). The characters previously used are:

1. Rostrum absent (0); rostrum present but preorbital region of skull not distinctly longer than postorbital region of skull (1) (distance from tip of the snout to anterior margin of orbit shorter than distance from anterior margin of orbit to posterior tip of supratemporal), and rostrum tapering to pointed tip, i.e., with convergent lateral margins in front of external nares; rostrum present but preorbital region of skull distinctly longer than postorbital region of skull (2) (distance from tip of the snout to anterior margin of orbit longer than distance from anterior margin of orbit to posterior tip of supratemporal), and rostrum tapering to blunt tip, i.e., with parallel lateral margins in front of external nares.
2. Tip of snout (rostrum) straight (0), tip of snout (rostrum) deflected ventrally (to a variable degree) (1).
3. Diastema between premaxillary and maxillary teeth absent (0), present (1) (*Agkistrognathus* and *Paralonectes* are coded following Nicholls and Brinkman, 1993).
4. Anteriormost dentary teeth upright (0), procumbent as their implantation curves around anterior end of dentary (1).
5. Posterior dentary and maxillary teeth conical and pointed (0), bulbous and blunt (1).
6. Nasals do not (0), or do (1) extend backwards to level behind anterior margin of orbit.
7. Anterolateral processes of frontal remain broadly separated from external naris, nasal meets prefrontal

(0), anterolateral processes of frontal closely approach or even enter the posterior margin of external naris, nasal separated from prefrontal (1).

8. Nasal in contact with prefrontal (0), nasal separated from prefrontal (1). This character is partially, but not fully, correlated with the previous one.
9. Anteromedial processes of frontals that enter in between nasal and premaxilla are shorter (0), or longer (1) than anterolateral processes of frontal.
10. Posterolateral processes of frontal absent (0), present and not extending far beyond anterior margin of lower temporal fossa (1), present but extending far beyond anterior margin of lower temporal fossa (2).
11. Posterolateral processes of frontal absent (0), present but separate from supratemporal (1), or present and in contact with supratemporal (2).
12. Postfrontal and postorbital separate (0), or fused (1).
13. Upper temporal fenestra present and large (0), reduced and slit-like (1), absent (2). (We code *Nectosaurus* for the absence of an upper temporal fossa (2) on the basis of the figure published by Nicholls (1999, Fig. 16), which shows absolutely straight opposing margins of the frontal and postfrontal.)
14. Posterior end of squamosal without (0), or with ventral process (1).
15. Quadrate without (0), or with (1) distinct anterior flange.
16. Pineal foramen small and located at center or somewhat behind of parietal skull table (0), or large and located in front of midpoint of parietal skull table (1).

To those characters, we here add the following:

17. Posterolateral process of frontal constricted (0) or broad (1) at its base (i.e., fronto-parietal suture interdigitating, oriented transversely for most of its part [0], or deeply embayed in the shape of a broad V, the apex pointing forwards [1]).
18. Anterior part of alveolar margin of maxilla straight (0), or distinctly curved upwards (1).

We coded these characters for *Agkistrognathus*, *Anshunsaurus*, *Askeptosaurus*, *Clarazia*, *Hescheleria*, *Nectosaurus*, *Paralonectes*, *Thalattosaurus*, and *Xinpusaurus* on the basis of the descriptions given by Nicholls (1999), Nicholls and Brinkman (1993), Rieppel (1987), and Rieppel et al. (2000), and rooted the analysis on an all-0-ancestor (data matrix see appendix I). Phylogenetic analysis using parsimony was done by implementation of the exhausted search (all multistate characters unordered) in PAUP version 4.0b4a (Swofford, 2000). Three most parsimonious trees were obtained, with a tree length of 30 steps, an ensemble consistency index of 0.733, and a retention index of 0.692. The strict consensus tree reads (*Askeptosaurus* (*Anshunsaurus* ((*Xinpusaurus*, *Nectosaurus*) (*Agkistrognathus* (*Clarazia*, *Hescheleria*, (*Thalattosaurus*, *Paralonectes*)))))). Deletion of the poorly preserved genera *Agkistrognathus* and *Paralonectes* again resulted in 3 most parsimonious trees, with a tree length of 29 steps, an ensemble consistency index of 0.759, and a retention index of 0.696. The strict consensus tree reads (*Askeptosaurus* (*Anshunsaurus* ((*Xinpusaurus*, *Nectosaurus*) (*Hescheleria*, *Clarazia*, *Thalattosaurus*)))). Given the scarcity of characters, and the poor preservation (*Agkistrognathus*, *Hescheleria*, *Nectosaurus*, *Paralonectes*) or incomplete knowledge (*Anshunsaurus*) of many taxa, it is not surprising that support for the tree topology is weak. With all taxa included, all resolution among thalattosaurs is lost in a tree only one step longer (TL = 31) than the most parsimonious tree.

This preliminary analysis is interesting nonetheless, as it indicates paraphyly of the Askeptosauridae: *Anshunsaurus* is found to be more closely related to "claraziids" than to *Askeptosaurus* on the basis of the synapomorphies 11*(1), 12*(1), 13(2), and 15*(1) (DELTRAN optimization, synapomorphies with a CI = 1 are characterized by an asterisk). This is a potentially important signal that will have to be tested once the postcranial anatomy of *Anshunsaurus* is known. "Claraziids" are monophyletic on the basis of the following synapomorphies: 1(1), 2*(1), 8(1), 10*(1). This signal had been found previously (Thalattosauria of Nicholls, 1999; see also Rieppel et al., 2000). Within "claraziids", *Xinpusaurus* is found to be the sister-taxon of *Nectosaurus* on the basis of the following synapomorphies: 17(1), convergent in *Thalattosaurus*, and 18(1), convergent in *Paralonectes* (DELTRAN optimization). While it is tempting to consider this relationship as a (weak) signal for trans-Pacific relationships, it has to be acknowledged that the overall topology of the thalattosaur tree allows little more than the conclusion that thalattosaurs were a widespread group for which the fossil record remains very incomplete.

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图版 I 说明 (Explanations of Plate I)

Xinpusaurus cf. *X. suni* (IVPP V 11860) ×0.9, A. left lateral view; B. right lateral view

Appendix I Data Matrix for the analysis of thalattosaur interrelationships

Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Askeptosaurus	2	0	0	0	0	1	0	1	1	0	0	0	1	1	0	1	0	0
Thalattosaurus	2	1	1	1	1	0	1	1	1	1	2	1	1	0	1	0	1	0
Anshunsaurus	2	0	?	?	?	1	0	0	1	2	1	1	2	1	1	1	0	0
Clarazia	1	1	1	0	1	0	1	?	1	1	2	1	2	0	1	0	0	0
Hescheleria	1	1	1	0	1	?	?	?	?	?	?	1	2	?	?	?	?	0
Xinpusaurus	1	1	0	0	(01)	0	0	1	0	1	1	1	2	1	1	?	1	1
Nectosaurus	?	?	?	?	0	0	?	1	1	1	?	1	2	?	?	?	1	1
Paralonectes	1	1	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?	1
Agkistrognathus	?	?	1	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?

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