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THE FIRST RECORD OF A THALATTOSAUR REPTILE FROM THE LATE TRIASSIC OF SOUTHERN CHINA (GUIZHOU PROVINCE, P.R. CHINA)

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ABSTRACT—The first thalattosaur from the marine Middle Triassic of Guizhou Province, southern China, is described, and its phylogenetic relationships analyzed. The taxon, *Anshunsaurus huangguoshuensis*, was found to be the sister-taxon of *Askeptosaurus italicus* from the southern Alpine Triassic. The paleobiogeography of thalattosaurs, now known from the Middle and Late Triassic of China, Europe, and North America, is discussed.

INTRODUCTION

Thalattosaurs are a monophyletic clade of Triassic marine reptiles (Nicholls, 1999) of possible lepidosauromorph affinities (Rieppel, 1987, 1998), known from the Middle and Late Triassic of Europe and North America (Anisian-Ladinian boundary of the southern Alps [Rieppel, 1987]; Ladinian of northwestern Spain [Rieppel and Hagdorn, 1998]; Ladinian of the Germanic Triassic [*Bletzingeria*: Fraas, 1896]; Carnian of the Julian Alps [Dalla Vecchia, 1993]; Late Triassic of northern California [Merriam, 1904, 1905, 1908]; Anisian and Carnian of northwestern Nevada [Storrs, 1991; Sander et al., 1994]; Middle [perhaps even Early: Nicholls and Brinkman, 1993] as well as Late [Storrs, 1991] Triassic of British Columbia). The only putative thalattosaur ever described from the Middle Triassic of southern China (Hubei Province) is *Hanosaurus hupehensis* Young, 1972, but this taxon was recently shown to be a pachypleurosaur sauropterygian (Rieppel, 1998). Here, we report the first occurrence of a thalattosaur from the Late Triassic of Guizhou Province, P.R. China, and analyze its phylogenetic and paleobiogeographic relationships.

SYSTEMATIC PALEONTOLOGY

THALATTOSAURIA Merriam, 1904
ASKEPTOSAURIDAE Kuhn-Schnyder, 1952
ANSHUNSAURUS Liu, 1999

Etymology—Named after the Anshun area, Guizhou Province, southwestern China.

Type and Only Known Species—*Anshunsaurus huangguoshuensis* Liu, 1999.

Known Distribution—Late Triassic, southern China

ANSHUNSAURUS HUANGGUOSHUENSIS Liu, 1999
(Figs. 1, 2)

Etymology—The specific name refers to Huangguoshu, a famous touring place known for the waterfall, near which the fossil locality is located.

Holotype—Institute of Vertebrate Paleontology and Paleoanthropology, IVPP V11835; almost complete skeleton (Fig. 1).

Locality and Horizon—Wayao Member, Falang Formation, Ladinian or Carnian (upper Middle or lower Upper Triassic), Xinpu, Guanlin County, Anshun area, Guizhou Province, southern China.

Diagnosis—An askeptosaurid thalattosaur which differs from

Askeptosaurus by fusion of the postorbital and postfrontal; posterolateral process of frontal narrowly approaches but does not contact supratemporal; upper temporal fenestra closed; long and slender ventral ramus of the squamosal extends to lower margin of cheek; posterior process of jugal elongate.

Comments—The species is known from an almost complete skeleton, nearly 3 meters in length. Today, only the dorsal view of the skull of the holotype is prepared, but it provides enough anatomical information to allow the identification of a new species, and given the incompleteness of other thalattosaur material, it is also possible to analyze its phylogenetic relationships. Because no schedule for further preparation can be determined at this time, we provide a preliminary report of this important taxon, and an account of its phylogenetic and paleobiogeographic relationships.

Stratigraphic Provenience—*Anshunsaurus* was collected from the Wayao Member of the Falang Formation. The Falang Formation was considered Ladinian by Wang (1981), but has later been considered to include at least part of the Carnian, with the Ladinian-Carnian boundary at the base of the Wayao Member (Wang, 1983; Dong, 1997). Ammonites associated with the fossil could not be unequivocally identified, but may be *Protrachyceras* (Ladinian) or *Trachyceras* (lower Carnian). The stratigraphic provenience of *Anshunsaurus*, and of other reptiles from the same beds, thus remains somewhat indeterminate, and will have to be further investigated in the future.

Description—*Anshunsaurus huangguoshuensis* (Table 1; Figs. 1–3) shares thalattosaur synapomorphies such as an elongated and tapering premaxillary rostrum, retracted nares, a contact of the premaxilla with the frontal, a reduced upper temporal fossa (slit-like in other thalattosaurs, completely closed in *Anshunsaurus huangguoshuensis*), a deeply concave occiput with the occipital condyle located well in front of the mandibular articulations, and an incomplete lower temporal arch (Rieppel, 1987; Nicholls, 1999). In *Anshunsaurus huangguoshuensis*, the rostrum is relatively long, which results in the preorbital region of the skull being distinctly longer than the postorbital region. In front of the external nares, the rostrum gradually assumes straight and parallel lateral margins, before it terminates in a blunt tip.

The external nares are retracted, lying rather closely in front of the orbits. Their posterior margin is distinct, but their anterior margin is obscured through breakage on both sides of the skull. It is conceivable, though, that the anterior margin of the external naris was formed by the premaxilla. The left side of the



FIGURE 1. The skull of *Anshunsaurus huangguoshuensis* (holotype, IVPP V11835), in dorsal view. Scale bar equals 40 mm.

skull shows the premaxillary—maxillary suture to trend from the anteroventral (anterolateral) margin of the external naris in an anterolateral direction.

The preorbital elements of the dermatocranium meet each other in a complex interdigitating pattern at the level of the anterior margin of the orbit. Each of the frontals forms an anterolateral and an anteromedial process, both of which taper to a pointed tip. In *Anshunsaurus huangguoshuensis*, the anteromedial process of the frontal is longer than the anterolateral process. The anteromedial processes of the frontals together embrace the pointed posterior tips of the premaxillae. The anterolateral process of the frontal enters between the nasal and the prefrontal.

The nasal is a slender and elongated element, which forms the posterior and dorsal (medial) margin of the external naris.

Laterally, the nasal meets the maxilla and the prefrontal in a more or less straight, anterolaterally trending suture. Medially, the nasal meets the premaxilla and the frontal. The pointed posterior tip of the nasal is embraced by the anterolateral and anteromedial processes of the frontal.

The maxilla extends anteriorly to a level well in front of the external naris before it tapers out along the lateral (ventral) margin of the rostrum. It forms most of the ventral (lateral) margin of the external naris, and between the latter and the orbit it expands into a distinct ascending process. This ascending process of the maxilla forms the anteroventral (anterolateral) margin of the orbit, and meets the nasal and prefrontal in a suture that describes an obtuse angle. Posteroventrally, the maxilla is drawn out into a short process which follows the anteroventral (anterolateral) margin of the orbit for a short distance.

The prefrontal is a curved element which defines the anterodorsal (anteromedial) margin of the orbit. It closely approaches but fails to contact the postorbitofrontal along the dorsal (medial) margin of the orbit. The postorbital and postfrontal are fused. The postorbitofrontal forms the posterodorsal (posteromedial) and most of the posterior margin of the orbit. Posterodorsally, the postorbitofrontal is drawn out into a long and slender process which extends far back within the skull roof. The tapering ventral process of the postorbitofrontal obliquely overlaps the dorsal process of the jugal within the postorbital arch.

As in all thalattosaurs, 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 an oblique suture at the anteroventral (anterolateral) margin of the orbit. Unfortunately, the exact relations of the prefrontal to the maxilla and jugal within the anterior wall of the orbit cannot be established, nor can the lacrimal foramen be identified. *Anshunsaurus huangguoshuensis* differs from all other thalattosaurs by a very long posterior process of the jugal, which forms a secondary ventral margin of the lower temporal fenestra. Due to dislocation of the bones, it is not possible to determine whether the posterior process of the jugal met the ventral process of the squamosal. However, if such a contact was absent, the two elements certainly approached each other very closely.

The frontals meet the parietals in a complex interdigitating suture at the level of the postorbital arch. Each frontal forms a slender posterolateral process, which extends backwards between the postorbitofrontal and parietal to a level well behind the anterior margin of the upper temporal fossa. In *Anshunsaurus huangguoshuensis*, the posterolateral process of the frontal does not meet the anterior process of the supratemporal, a contact which is present in other thalattosaurs such as *Clarazia* (Rieppel, 1987), or *Thalattosaurus* (Nicholls, 1999). The parietal contacts the posterior process of the postorbitofrontal in between the frontal and the supratemporal. The upper temporal fossa is completely obliterated in *Anshunsaurus huangguoshuensis*, as is also the case in *Clarazia* (Rieppel, 1987). The skull of *Anshunsaurus huangguoshuensis* is beautifully preserved in three dimensions, and documents the complete obliteration of the upper temporal fenestra beyond all doubt. Given the severe dorsoventral compression of the skulls of *Askeptosaurus* (Kuhn-Schnyder, 1952, 1971), the question remains as to whether this genus is also characterized by a complete obliteration of the upper temporal fenestra, or whether it indeed retained a small, slit-like opening as reconstructed by Kuhn-Schnyder (1952, 1971).

The parietals enclose a large pineal foramen which is displaced anteriorly, located shortly behind the frontoparietal suture. Posterolaterally, the parietal is drawn out into elongate supratemporal processes which form the posterior margin of the deeply excavated occiput. The supratemporal is broadly ex-

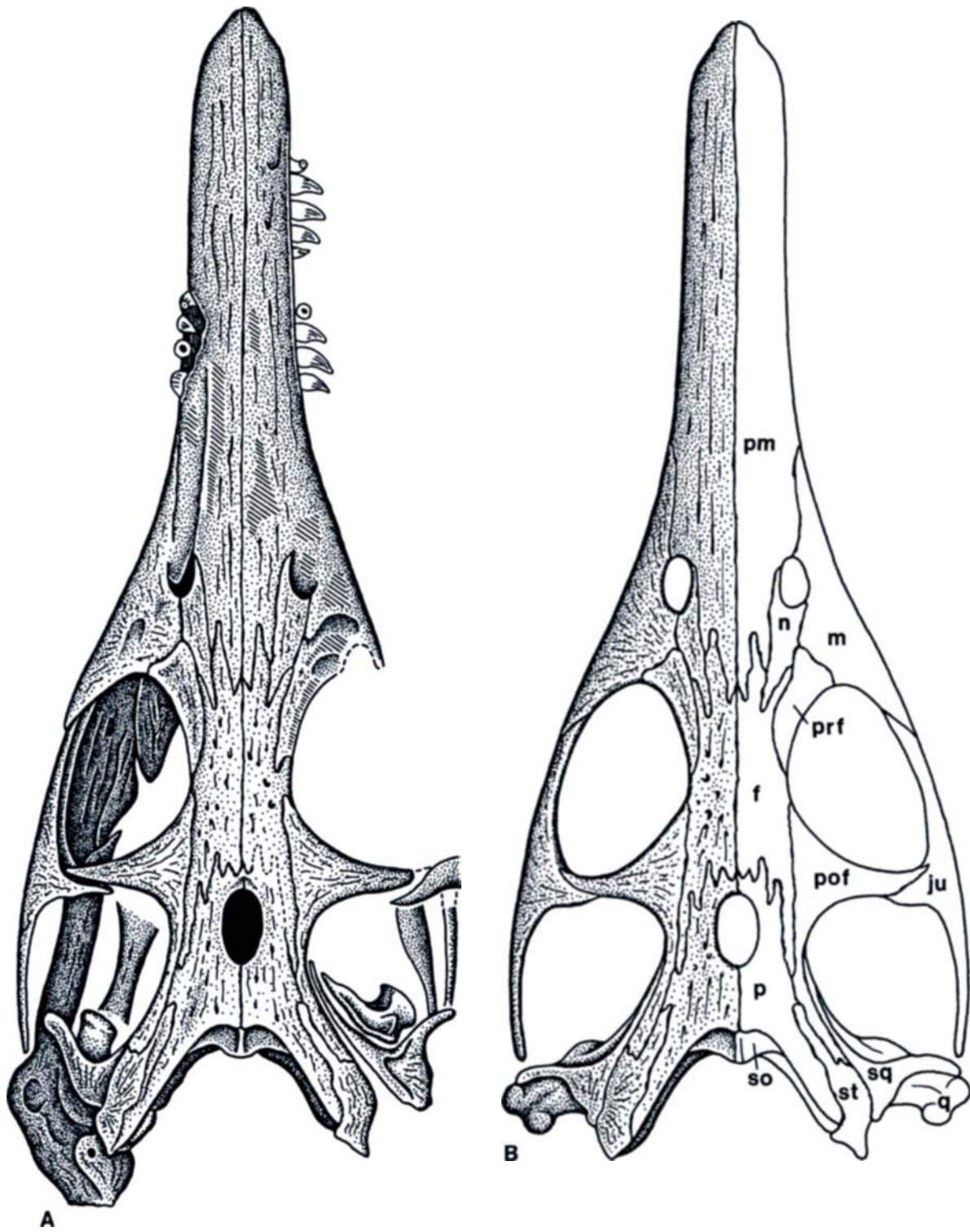


FIGURE 2. *Anshunsaurus huangguoshuensis* (holotype, IVPP V11835). The skull in dorsal view (A); reconstruction of the skull in dorsal view (B). Abbreviations: f, frontal; m, maxilla; n, nasal; ju, jugal; p, parietal; pm, premaxilla; pof, postfrontal; prf, prefrontal; so, supraoccipital; sq, squamosal; st, supratemporal. Scale bar equals 50 mm.

posed at the posterolateral corner of the skull table. Its broad posterior part has a ventrolaterally inclined surface. Anteriorly, the supratemporal is reduced to a narrow process which extends between the parietal and the postorbitofrontal. The squamosal is autapomorphic in *Anshunsaurus huangguoshuensis* in that it

again is a roughly triradiate element. The posterior end is relatively broad, and must have been positioned lateral to the posterior end of the jugal. A slender anterior process follows the lateral margin of the skull table, tapering to a pointed tip at a level in front of the midpoint of the longitudinal diameter of

TABLE 1. Measurements taken on the skull of *Anshunsaurus huangguoshuensis* (holotype, IVPP V11835).

Distance from tip of snout:			
1. —to anterior margin of orbit	left	236.0 mm	
	right	232.5 mm	
2. —to anterior margin of upper temporal fossa	left	309.5 mm	
	right	309.0 mm	
3. —to posterior margin of parietal skull table		345.0 mm	
4. —to posterior margin of supraoccipital		355.5 mm	
5. —to posterior tip of supratemporal	left	394.0 mm	
	right	397.0 mm	
6. Width of skull across posterior tips of supra-temporal		96.5 mm	
7. Longitudinal diameter of orbit	left	63.3 mm	
	right	62.8 mm	
8. Longitudinal diameter of upper temporal fossa	left	69.0 mm	
9. Distance from posterior margin of external naris to anterior margin of orbit	left	32.5 mm	

the lower temporal fenestra. A very distinct and slightly recurved ventral process, not known from other thalattosaurs, must have lined the lateral edge of the posteriorly concave shaft of the quadrate, extending to the ventral margin of the cheek and possibly contacting the posterior tip of the jugal. The quadrates are poorly exposed on both sides of the skull, but the right quadrate shows the cephalic condyle to be drawn out into an anterior process which must have formed the dorsal margin of an extensive anterior quadrate flange.

The braincase is very poorly exposed. The supraoccipital is seen to project from below the posterior margin of the parietals, carrying a low sagittal crest. Below the supraoccipital and the supratemporal processes of the parietal, the posterior margin of the posterolaterally trending paroccipital processes is exposed.

The left mandibular ramus is preserved in articulation. Parts which are difficult to identify are exposed in the floor of the orbit. These may include a coronoid bone. The surangular is exposed in the area of the lower temporal fossa, lateral to the dorsal exposure of the quadrate ramus of the pterygoid. The mandibular articulation is transversely expanded, and the chorda tympani foramen is exposed just behind it on the posteroventrally sloping base of the retroarticular process. More distal parts of the retroarticular process, which is usually elongate in thalattosaurs (Nicholls, 1999), are missing.

PHYLOGENETIC ANALYSIS

An analysis of thalattosaur interrelationships was recently presented by Nicholls (1999) and our attempt to place *Anshunsaurus huangguoshuensis* in this phylogeny has raised several problems. Nicholls (1999) used 39 characters to resolve the relationships among eight in-group taxa. The eight multistate characters were treated as ordered. However, upon unordering the multistate characters, 22 characters were found to be uninformative; ordering the multistate characters rendered five of them informative reducing the number of uninformative characters to 17. Of the 19 skull characters, 13 are uninformative with unordered multistate characters. Running the data matrix compiled by Nicholls (1999) with all multistate characters unordered severely reduces resolution among terminal taxa. The relationships among *Agkistrognathus*, *Clarazia*, *Hescheleria*, *Nectosaurus* and *Paralonectes* remain unresolved. These genera were included within the Thalattosauria by Nicholls (1999), the monophyly of which is preserved. *Askeptosaurus* and *Endennasaurus* were found to be the successive sister-groups of this clade. The relationships between *Askeptosaurus* and *Endennasaurus* remain unresolved in Nicholls' (1999) original analysis, but in the re-analysis of her data matrix with the multistate

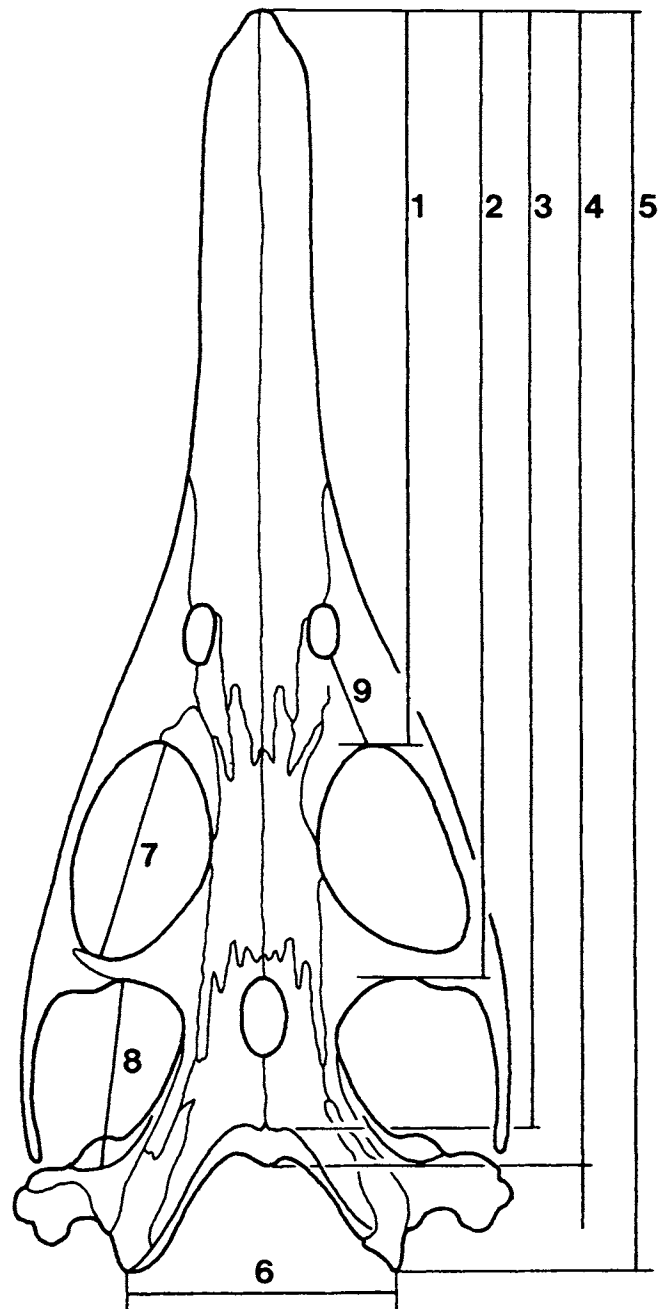


FIGURE 3. Measurements taken on the skull of *Anshunsaurus huangguoshuensis* (holotype, IVPP V11835) as reported in Table 1.

characters unordered, *Askeptosaurus* groups with other thalattosaurs to the exclusion of *Endennasaurus* on the basis of two characters: prefrontal separated from nasal (unknown for *Endennasaurus*), and premaxillae separating nasals from one another. Indeed, the skull of *Endennasaurus* is very incomplete, and the thalattosaur relationships of this genus are poorly supported (Renesto, 1991). It is impossible to identify an unequivocal synapomorphy shared by *Endennasaurus* and thalattosaurs, and the genus should be placed incertae sedis among diapsids (Carroll, 1988).

It is only by ordering the multistate characters that the tree published by Nicholls (1999) is obtained. Yet ordering multistate characters always implies ad hoc assumptions about the direction of evolutionary changes, and some of the multistate

characters imply unlikely instances of reversal if ordered, such as pterygoid and vomerine teeth first being lost and then reappearing (characters 26 and 27).

In order to analyze the relationships of *Anshunsaurus huangguoshuensis* with other thalattosaurs, we have therefore constructed a data matrix (Appendix I) for 16 characters (enumerated below) and five in-group taxa (*Anshunsaurus*, *Askeptosaurus* [Kuhn-Schnyder, 1952, 1971], *Clarazia* [Rieppel, 1987], *Hescheleria* [Rieppel, 1987], and *Thalattosaurus* [Nicholls, 1999]). We do not include other thalattosaur genera in our analysis because of their very incomplete preservation. Inclusion of very incomplete material in a phylogenetic analysis usually results in a loss of resolution (Novacek, 1992; Rieppel, 1994).

The characters used in the analysis of thalattosaur interrelationships are the following:

- (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 (1).
- (3) Diastema between premaxillary and maxillary teeth absent (0), present (1).
- (4) Anterior dentary and premaxillary teeth upright (0), procumbent (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 which enter in between nasal and maxilla 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 upper temporal fossa (1), present but extending far beyond anterior margin of upper 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).
- (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).

The in-group was rooted on an all-0-ancestor (same as *Youniiformes* in Nicholls, 1999), and the branch-and-bound search option implemented (all characters informative, all multistate

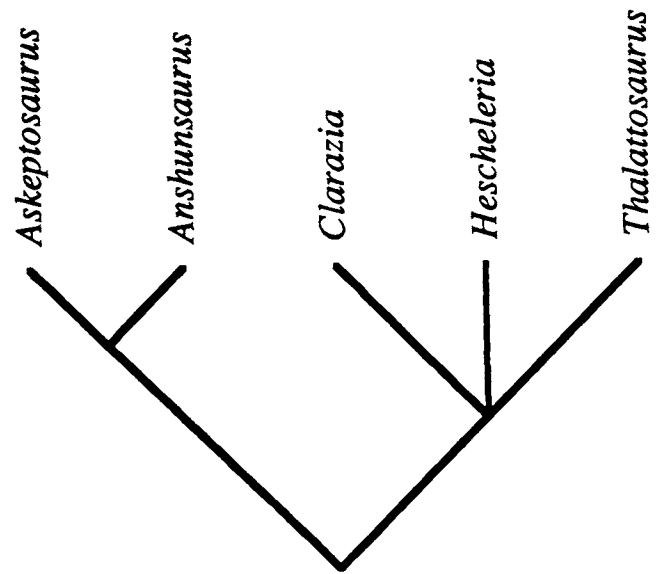


FIGURE 4. Phylogenetic interrelationships of the better known thalattosaur genera. For further details see discussion in text.

characters unordered). Two most parsimonious trees were found, with a Tree Length of 26 steps, a Consistency Index of 0.769, and a Retention Index of 0.647. The relationships among *Clarazia*, *Hescheleria*, and *Thalattosaurus* remain unresolved (Fig. 4). The strict consensus tree reads (*Anshunsaurus*, *Askeptosaurus*) (*Clarazia*, *Hescheleria*, *Thalattosaurus*), and hence reproduces the basal dichotomy between *Askeptosauroida* Kuhn-Schnyder, 1971, and *Thalattosauroida* Merriam, 1904, that had previously been identified (Kuhn-Schnyder, 1971; Rieppel, 1987; Nicholls, 1999).

Based on DELTRAN character optimization, shared derived characters of the *Askeptosauroida* (*Anshunsaurus* and *Askeptosaurus*) are: rostrum elongated with parallel edges and a blunt anterior tip; nasals extending backwards to a level distinctly behind the anterior margin of the orbit; anteromedial process of the frontal longer than anterolateral process; posterior end of the squamosal with a ventral process (distinctly larger in *Anshunsaurus* than in *Askeptosaurus*); and large pineal foramen located in front of the midpoint of the parietal skull table. Shared derived characters of the *Thalattosauroida* (*Clarazia*, *Hescheleria*, *Thalattosaurus*) are: rostrum relatively shorter, with convergent lateral margins and pointed anterior tip; tip of snout deflected ventrally; diastema separating premaxillary from maxillary teeth present; posterior dentary and maxillary teeth bulbous and blunt; anterolateral process of frontal closely approaching the posterior margin of the external naris; posterolateral process of frontal not extending far beyond the level of the anterior margin of the upper temporal fenestra; posterolateral process of frontal contacting the supratemporal; postorbital and postfrontal fused (convergent in *Anshunsaurus*); and quadrate with anterior flange (convergent in *Anshunsaurus*).

PALEOBIOGEOGRAPHIC CONSIDERATIONS

Most recently, the Middle Triassic deposits of Guizhou Province have yielded a large number of marine reptiles, such as ichthyosaurs, sauropterygians, and the thalattosaur described above. Of these, the (Triassic stem-group) sauropterygians and thalattosaurs remained restricted, on a global scale, to shallow epicontinental seas or nearshore habitats such as intraplatform basins. In contrast to ichthyosaurs, the postcranial anatomy of stem-group sauropterygians and thalattosaurs is little modified

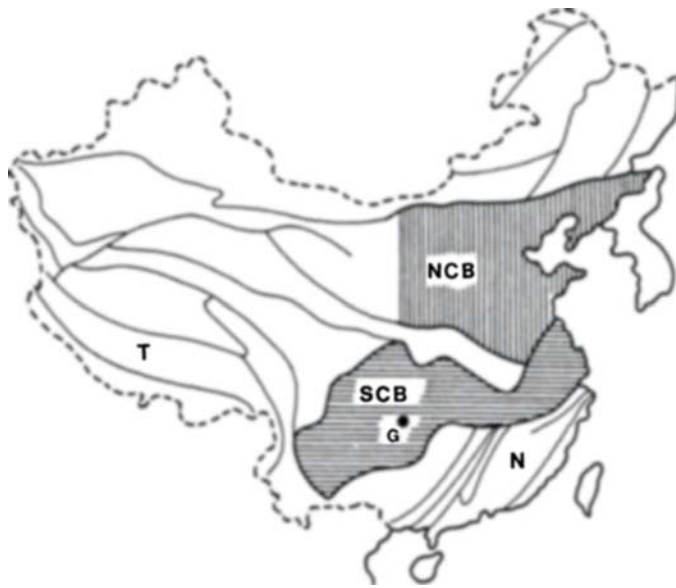


FIGURE 5. A simplified rendering of the tectonic composition of China. **Abbreviations:** N, Nipponides; G, Guiyang, Guizhou Province; NCB, North China Block; SCB, South China Block; T, Tethyside collage (redrawn after Chen, 1988, fig. 4).

in adaptation to an aquatic mode of life, and does not suggest obligatory pelagic habits.

The distribution of marine reptiles in southern China (Dong, 1980), including the new material, corresponds to their occurrence on the South China Block (Yin and Nie, 1996; Ziegler et al., 1996), which during Middle and Late Triassic times was located in the warm temperate zone (Ziegler et al., 1996). The South China Block is also referred to as the South China Plate with the Yangzi Paraplatform as its nucleus (Cheng, 1988), or as the Yangtze Platform (Sengör and Natal'in, 1996). The South China Block (SCB) itself formed by the amalgamation of the western SCB (the Yangtze terrane) and the eastern SCB (the Huanan terrane) in the latest Precambrian, and it remained separated from the North China Block (NCB) by intervening oceans throughout the Paleozoic (Xiong and Coney, 1985; Yin and Nie, 1996). Collision of the SCB and NCB (Fig. 5) is believed to have started in the late Permian and then progressed from east to west. Collision is claimed to have been complete in the late Triassic, as sediments on the SCB change from shallow marine to terrestrial (Yin and Nie, 1996). Despite the fact that the SCB lacks paleopole constraints for the Late Triassic time interval, paleomagnetic data suggest instead that the scissors-like collision between the SCB and NCB was completed around the Middle to Late Jurassic, and that the docking of the two amalgamated blocks against Eurasia is of Cretaceous age (Gilder and Courtillot, 1997).

The South China Block is bordered to the West by a Tethyside collage (Fig. 5) which is composed of continental blocks that separated from Gondwana and moved in an northeastern direction to unite with Laurasia (Sengör and Natal'in, 1996). To the East, the South China Block is bordered by Nipponides (Southeast China Arc) as part of the Circum-Pacific Super-Orogenic Complex (Sengör and Natal'in, 1996). Paleomagnetic constraints obtained from the Fujian Province (Gilder et al., 1996) furthermore suggest that the Early Triassic rocks of the coastal provinces were deposited far off from the SCB.

The SCB is thus located on the boundary between the eastern Tethyan and the western Pacific domains. Xiong and Coney (1985) refer the Yangzi-Hunan superterrane to the western Pa-

cific domain, assuming it was carried to its present position in a northwestward direction by "Pacific" plates, when in fact the SCB moved northwards if at all (Yin and Nie, 1996; Ziegler et al., 1996, found that the SCB did not move into collision, but sutured to the southward-moving Eurasian continent). By contrast, Cheng (1988) characterized the marine Triassic deposits of southern and southwestern China as typically Tethyan, which may result from insufficient consideration of marine Triassic invertebrate faunas from the western United States. Because the Tethyan faunas benefited from earlier investigations than those of the North American Cordillera, many authors have underlined Tethyan affinities of the ammonoid faunas from southern China. However, assessment of the paleobiogeographic significance of the marine Triassic faunas of the SCB and juxtaposed terranes requires the analysis of paleobiogeographic patterns at a larger, indeed global, scale. As far as ammonoids and pseudoplanktonic bivalves are concerned, the recognition of a "Tethyan" biogeographic domain is not that clear, and may vary over relatively short time intervals such as one or several consecutive biozones. For the Triassic Tethys and Pacific oceans, the predominant biogeographic pattern is that of a latitudinal distribution of open marine ammonoid faunas with low, middle and high paleolatitude faunas as recognized by Tozer (1982) for the eastern Pacific. Among the few exceptions to the latitudinal pattern are faunas of Griesbachian and of latest Smithian age, both of which are cosmopolitan and Early Triassic in age. The comparison of the plate-bound, low latitude faunas from the North American Cordillera (Nevada, California, Idaho, and Utah) with those of Tethyan provenance suggest a greater uniformity than previously thought. As the low latitude faunal sequence of the eastern Pacific is becoming documented in greater detail (Bucher, 1992a, b, and unpublished data), the distinctive character of the Tethyan realm is significantly decreasing, and we believe that gaps and insufficient sampling in both records are largely responsible for such biased paleobiogeographic interpretations. For organisms with high capabilities of trans-oceanic dispersion like ammonoids and pseudoplanktonic bivalves, sea surface temperature and surface currents appear to have been the main factors regulating their paleogeographic distributions. Therefore, the strictly low paleolatitude (or pantropical) invertebrate faunas known from the SCB may not be appropriate in discriminating between Tethyan or Pacific influences.

Located on the boundary between the eastern Tethyan and the western Pacific, the SCB may be expected to share dual faunal affinities. Indeed, trans-Pacific relationships (based on cladistic analysis) were found (if very weakly supported due to the fragmentary nature of the material) for previously described Triassic sauropterygians from southern China and Wyoming (Rieppel, 1999). By contrast, *Anshunsaurus* from Guizhou Province is found to be the sister-taxon of *Askeptosaurus* from the *Grenzbitumen*-horizon (Anisian-Ladinian boundary) of the southern Alps (Monte San Giorgio, Switzerland). This sister-group relationship is taxonomically congruent with correspondingly described western Tethyan sister-group relationships of other previously described marine reptiles from the Middle Triassic of southern China, such as the sauropterygian pachypleurosaur genera *Hanosaurus* and *Kyeichousaurus* (Rieppel and Lin, 1995; Rieppel, 1998).

But whereas *Askeptosaurus* is found to be the sister-taxon of *Anshunsaurus*, other thalattosaurs from the western Tethyan faunal province (*Clarazia*, *Hescheleria*) fall into a monophyletic clade with thalattosaurs from the eastern Pacific faunal province (*Thalattosaurus*). This pattern of relationships is again taxonomically congruent with sauropterygians, i.e., with the sister-group relationship of *Pistosaurus* from the Germanic Triassic with *Augustasaurus* from northwestern Nevada (Sander et al., 1997). Similar patterns of faunal relationships are also sug-

gested by ammonoids (Bucher, 1992a, b). Given the absence of a northern marine connection between the western Tethyan and the Pacific (Panthalassan) realm during the Triassic (Ziegler, 1988; Doré, 1991; Ricou, 1996), as well as climatic differentiation along a north-south gradient as indicated by ammonoid provincialism, dispersal of thalattosaurs (or sauropterygians) around northern Pangean coastlines seems unlikely. Implementation of the Brooks Parsimony Analysis (BPA; see Brooks and McLennan [1991] for a general review) on our cladogram of thalattosaur relationships did not result in a resolved area cladogram. The conclusion must be that known taxa of thalattosaurs (as well as pistosaurs) are related to (derived from) as yet unknown, widespread taxa, a hypothesis which in turn implies biogeographic refuges (guyots, volcanic arcs, and larger terranes) straddling the equatorial or inter-tropical Pacific Ocean.

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APPENDIX 1. Data matrix for the analysis of thalattosaur interrelationships. The definition of characters and the search procedures implemented are discussed in the text.

Taxon	Characters			
	12345	57891	11111	1
		0	12345	6
<i>Ancestor</i>	00000	00000	00000	0
<i>Askeptosaurus</i>	20000	10110	00110	1
<i>Thalattosaurus</i>	21111	01101	21101	0
<i>Anshunsaurus</i>	20???	10012	11211	1
<i>Clarazia</i>	11101	01?11	21201	0
<i>Hescheleria</i>	11111	?????	?1???	?

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