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Guanling Biota: A Marker of Triassic Biotic Recovery from the end-Permian Extinction in the Ancient Guizhou Sea

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Abstract After a slow recovery from the end-Permian extinction during the Early Triassic and rapid radiation in the Middle Triassic, evolution of organisms reached a new peak phase in the Late Triassic. The Guanling Biota from the Wayao Member (conodont *Paragondolella polygnathiformis* Zone), Falang Formation, Xinpu, Guanling County, Guizhou Province, southwestern China corresponds to this peak that marks the full recovery from the end-Permian extinction of marine ecosystems. The biota is of high diversity, containing well preserved and completely articulated skeletons of vertebrates comprising marine reptiles, fishes, and invertebrates including crinoids, ammonites, bivalves, and other fossils, and is one of the best examples of marine ecosystem records in life history. The fossil marine reptiles and crinoids are most significant in this biota, especially the marine reptiles, which provide an important link between the Triassic Pacific and Tethys, and between Triassic basal forms and the Jurassic-Cretaceous marine top predators. The most remarkable fossils are the large completely articulated ichthyosaur skeletons up to and more than 10 m, and the first recorded thalattosaurs and placodonts in China. Following our review, of the 17 named reptilian taxa the eight listed here are considered to be valid: three ichthyosaurs (*Qianichthyosaurus zhoui* Li, 1999; *Guizhouichthyosaurus tangae* Cao and Luo in Yin et al., 2000, *Guanlingsaurus liangae* Yin in Yin et al., 2000), three thalattosaurs (*Anshunsaurus huangguoshuensis* Liu, 1999, *Xinpusaurus suni* Yin in Yin et al., 2000, *Xinpusaurus kohi* Jiang et al., 2004), and two placodonts (*Sinocyamodus xinpuensis* Li, 2000, *Psephochelys polyosteoderma* Li and Rieppel, 2002). *Mixosaurus guanlingensis* Cao in Yin et al., 2000 might be a junior synonym of *Qianichthyosaurus zhoui* Li, 1999, and *Cymbospondylus asiaticus* Li and You, 2002 and *Panjiangsaurus epicharis* Chen and Cheng, 2003 might be junior synonyms of *Guizhouichthyosaurus tangae* Cao and Luo in Yin et al., 2000. It needs to re-describe the holotypes after a complete preparation for clarifying the taxonomic status of *Typicusichthyosaurus tsaihuae* Yu in Yin et al., 2000, *Xinpusaurus bamaolinensis* Cheng, 2003, *Neosinosaurus hoangi* (Zhou in Yin et al., 2000), *Wayaosaurus geei* Zhou in Yin et al., 2000, *Wayaosaurus bellus* Zhou in Yin et al., 2000 and *Placochelys ? minutus* Yin and Luo in Yin et al., 2000.

Key words: Guanling Biota, marine reptiles, Late Triassic, Carnian, Guizhou, China

1 Introduction

The Guanling Biota is characterized by abundant, well-preserved Late Triassic fossils notably marine reptiles and crinoids, and especially complete articulated ichthyosaur skeletons of large-size up to more than 10 m and the first Chinese thalattosaurs and placodonts. This fauna is attracting more and more interest from scientists all over the world and thus the time is right for a review of the taxonomic diversity.

Mu's (1949) description of several crinoid species from Guanling can be considered as the first scientific report of the Guanling Biota. However, it was not until the late 1990s that the extent of the biota was fully recognized, following excavations of numerous marine reptile fossils by local farmers. Li (1999) and Liu (1999) first reported marine reptiles from the Guanling Biota. Since then, several international research groups, including the Institute of Vertebrate Paleontology and Paleoanthropology of the Chinese Academy of Sciences (IVPP), Department of Geology and Geological Museum of Peking University (GMPKU), and the Yichang Institute of Geology and Mineral Resource, have been excavating and studying the fossil taxa and biodiversity, stratigraphy and sedimentary geology, paleoenvironment and paleogeography of this biota. The fossils were excavated from the Wayao Member of the Falang Formation at Xinpu in Guanling County, Guizhou Province, southwestern China (Fig. 1; Wang et al., 2000; Wang et al., 2001; Sun et al., 2003; Jiang et al., 2004a), where the Guanling National Geopark of Fossil

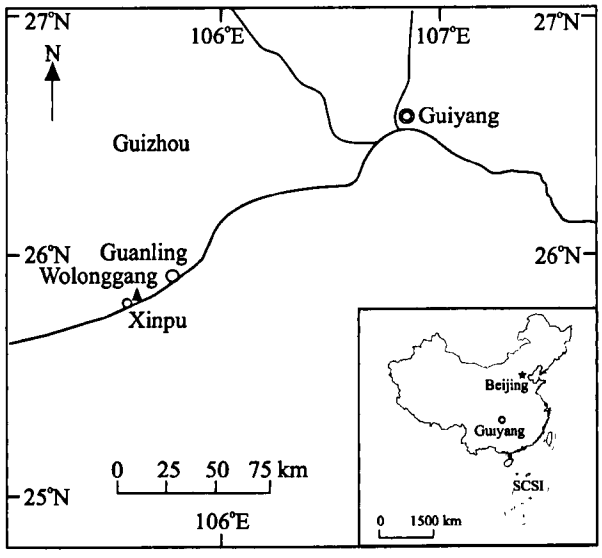

Fig. 1. Locality of the Guanling Biota in South China.

Biota is being constructed.

There are two other important marine reptile faunas in Guizhou Province, namely the Middle Triassic (Ladinian) Xingyi Fauna dominated by nothosauroids (Li et al., 2002; Li and Jin, 2003; Li and Rieppel, 2004) and the Middle Triassic (Anisian) Panxian Fauna comprising mixosaurid ichthyosaurs, placodonts, tanystropheiids, and nothosaurs (Fig. 2; Jiang et al., 2003; Jiang et al., 2004b; Jiang et al., 2005; Li, 2003; Li et al., 2004). The Guanling Biota is the most remarkable of the Triassic biota known around the world in terms of its faunal diversity, preservation and body size of individual reptiles. Other biota include Monte San Giorgio, Switzerland and the Germanic Basin in central Europe; Nevada and British Columbia in the North America; and Spitsbergen in arctic Norway (e.g. Motani, 1999; Maisch and Matzke, 2000; Rieppel, 2000; McGowan and Motani, 2003) (Fig. 3).

2 Age of the Guanling Biota

The Wayao Member of the Falang Formation is characterized by grayish yellow to dark gray, thin- to medium-bedded marl, argillaceous limestone and limestone with some intercalations of black shale and siltstone. There are several fossil layers yielding abundant marine reptiles, crinoids and other fossils in the lower part, mainly in the bed about 8 m above the base of the Wayao Member, which can be ascribed to the conodont *Paragondolella polygnathiformis* Zone (Sun et al., 2003).

Three chronostratigraphic levels for the Guanling Biota have been proposed:

1) Middle Carnian of the Late Triassic by Chen and Wang (2002), Sun et al. (2003) and Chen and Cuny (2003) on the basis of conodont and elasmobranch ichthyolith biostratigraphic correlation.

2) Early or late period of early Carnian of the Late Triassic by Hao et al. (2003) and Xu et al. (2003) on the basis of cephalopod stratigraphic correlation.

3) Late period of late Ladinian of the Middle Triassic based on bivalve (e.g., Hsü, 1944); the view is still held by some researchers.

The two most recently proposed levels of the above three agree that the Guanling Biota represents a part of the Late Triassic Carnian and this view is adopted here. There is no age dating by radiogenic isotopes for the Guanling Biota available. From the Geological Time Scale 2004 of the International Commission of Stratigraphy (Gradstein et al., 2005), the range of the Carnian is taken as 230–216 Ma. We presume that the age of the Guanling Biota is around 225 Ma given its early Carnian or middle Carnian level.

3 Taxa in the Guanling Biota

3.1 Marine reptiles

The most remarkable animals in the Guanling Biota are the marine reptiles, including ichthyosaurs, thalattosaurs, placodonts and possibly other sauropterygians. Li and Jin (2003) gave a brief comment on this fauna. The study of the marine reptiles of the Guanling Biota is still at its beginning. Till now, 17 endemic taxa of marine reptiles have been erected; of these some should be re-studied and comparison made in detail with those elsewhere, and the taxonomic status of others needs to be confirmed. Given this complicated situation, we temporarily use the term of taxonomic name, instead of taxon, in this paper.

Ichthyosaurs

Ichthyosaurs are a group of fish-shaped diapsid reptiles that first appeared in the late Early Triassic; they became especially adapted to live in Mesozoic marine environments.

Taxonomic names 1, 2 (It does not mean they are true synonyms. For more information see description in the text.)

Ichthyosauria De Blainville, 1835

Toretocnemidae Maisch and Matzke, 2000
Qianichthyosaurus Li, 1999
Qianichthyosaurus zhoui Li, 1999

Mixosauridae Baur, 1887
Mixosaurus Baur, 1887
Mixosaurus guanlingensis Cao in Yin et al., 2000

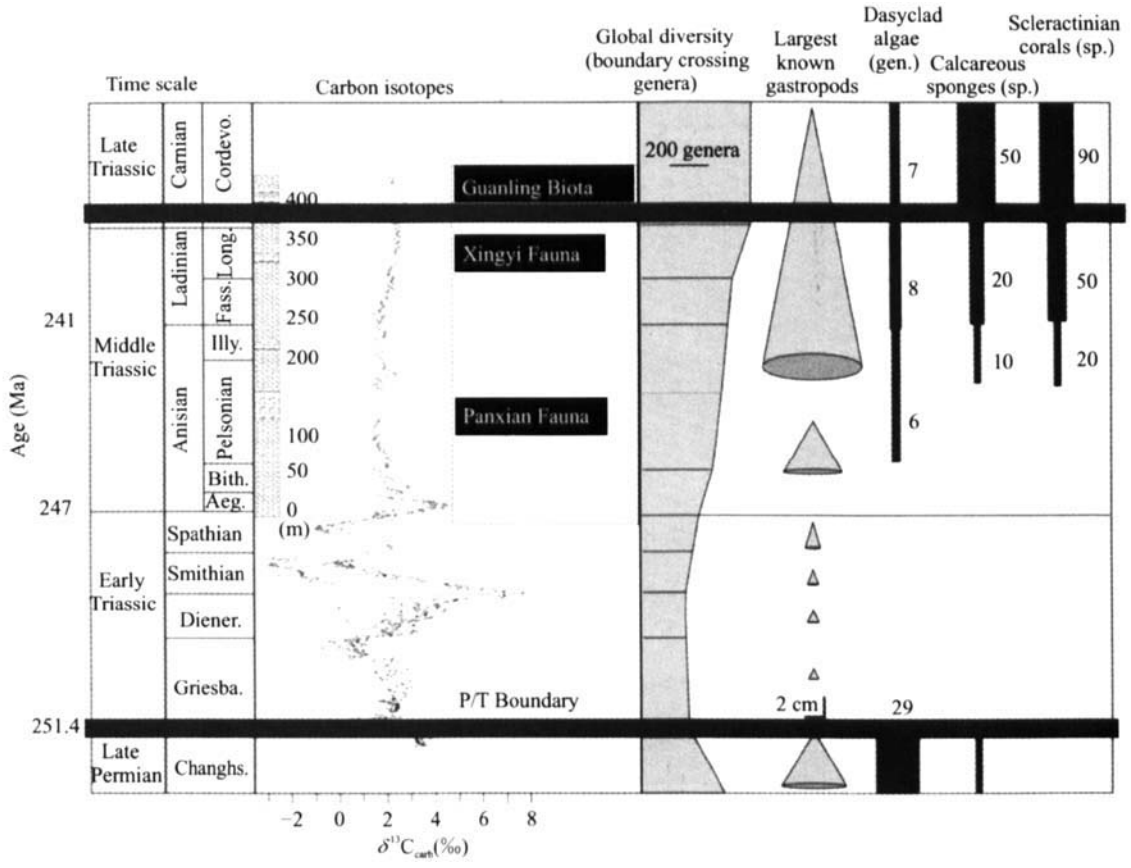

Fig. 2. Stratigraphic horizons of the Guanling Biota, Xingyi Fauna and Panxian Fauna in the biotic recovery from the end-Permian extinction.

Modified with permission from Fig. 3 of Payne et al. (2004), original copyright 2004 by the American Association for the Advancement of Science.

Li (1999) first reported a new genus and species in the Guanling Biota: *Qianichthyosaurus zhoui* Li, 1999 (Plate I-1), a small ichthyosaur specimen of less than 2 m long. Yin et al. (2000) briefly recognized additional referred specimens in size from 0.5 m to 2 m. Nicholls et al. (2002) re-described and presented detailed anatomical information, and agreed with Maisch and Matzke (2000) to unite *Qianichthyosaurus zhoui* Li, 1999 with *Toretocnemus californicus* Merriam, 1903 from the Carnian in California, North America in the family Toretocnemidae. Furthermore, they inferred that *Qianichthyosaurus* is more derived than *Toretocnemus*.

Cao in Yin et al. (2000) assigned a small ichthyosaur specimen of 1.27 m long to a new species *Mixosaurus guanlingensis*. Its taxonomic status remains uncertain, but most probably it is not a mixosaur because no synapomorphy of *Mixosaurus* can be distinguished and might be a junior synonym of *Qianichthyosaurus zhoui*.

Taxonomic names 3, 4, 5

Ichthyosauria De Blainville, 1835
Merriamosauria Motani, 1999
Shastasauridae Merriam (1902)
Guizhouichthyosaurus Cao and Luo in Yin et al., 2000
Guizhouichthyosaurus tangae Cao and Luo in Yin et al., 2000

Cymbospondylus Leidy, 1868
Cymbospondylus asiaticus Li and You, 2002

Panjiangsaurus Chen and Cheng, 2003
Panjiangsaurus epicharis Chen and Cheng, 2003

Many large ichthyosaur specimens with various total lengths from 5 m to more than 10 m have been excavated from Guanling. They represent the most remarkable members of the Guanling Biota. Three species were erected, namely *Guizhouichthyosaurus tangae* Cao and Luo in Yin et al., 2000, *Cymbospondylus asiaticus* Li and You, 2002 (Plate I-2; Li and You, 2002), and *Panjiangsaurus epicharis* Chen and Cheng, 2003 (Chen and Cheng, 2003). The three species have long snouts, and their presacral vertebral count when known is about 62–65. Distinguishing characters among the three have not been clarified, and therefore a possibility exists that the latter two might be

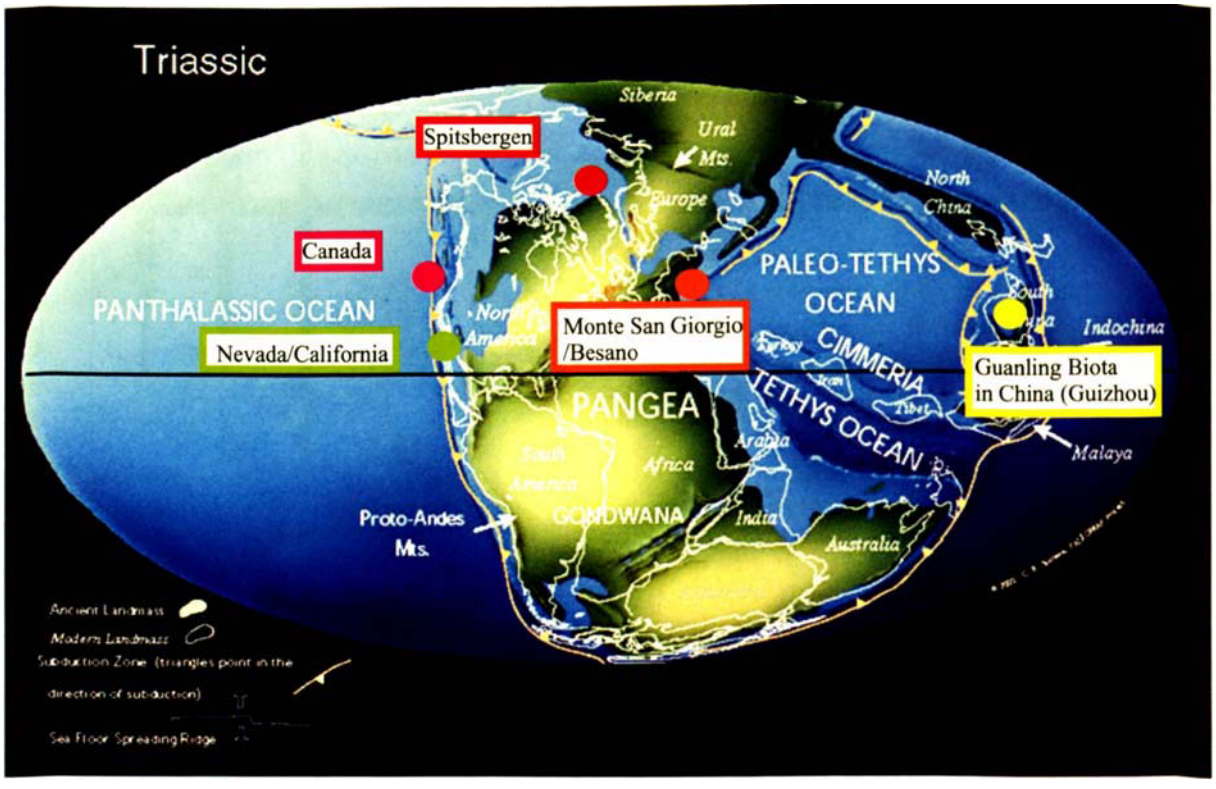

Fig. 3. Paleogeographic position of the Guanling Biota.
Paleogeographic map from Scotese (2001) and see also Scotese, C.R., 2002., http://www.scotese.com (PALEOMAP website).

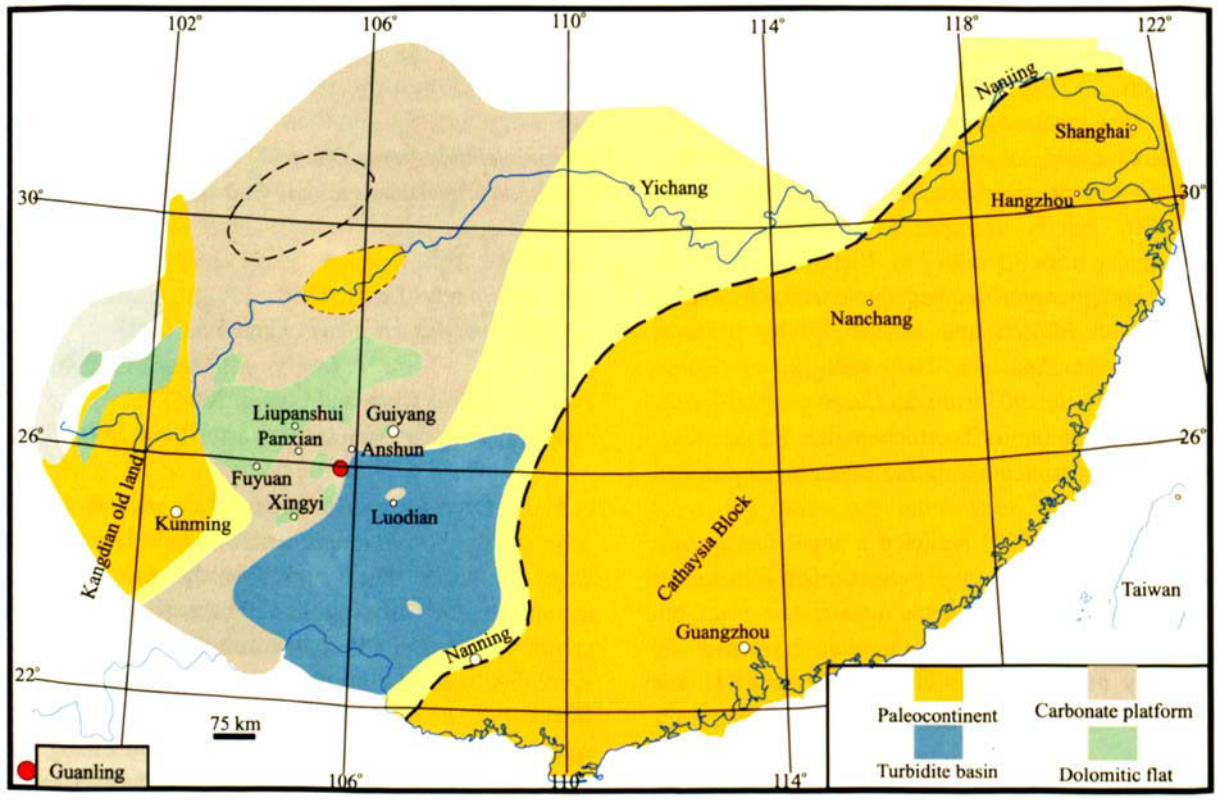

Fig. 4. Lithofacies paleogeographic position of the Guanling Biota in southern China.
Dark yellow area: old land; yellow area: clastic deposit platform; light blue area: carbonate platform; dark blue area: deeper basin.
Lithofacies Paleogeographic map from Feng et al., 1997, Appendix figure 4.

junior synonyms of *G. tangae*. Given that the two skulls of *C. asiaticus* were described in detail by Li and You (2002), it is imporant to redescribe the type specimens of *G. tangae* and *P. epicharis*. A detailed comparison can be then made to solve the taxonomic problem.

Taxonomic names 6, 7
Ichthyosauria De Blainville, 1835
Merriamosauria Motani, 1999
Shastasauridae Merriam (1902)

Guanlingsaurus Yin in Yin et al., 2000
Guanlingsaurus liangae Yin in Yin et al., 2000

Typicusichthyosaurus Yu in Yin et al., 2000
Typicusichthyosaurus tsaihuae Yu in Yin et al., 2000

Guanlingsaurus liangae, with more than 80 presacral vertebrae, appears to be a distinct type of large ichthyosaur and different from *Guizhouichthyosaurus tangae* because it presents more presacral vertebrae than latter. *Typicusichthyosaurus tsaihuae* is a third genus and species of large ichthyosaur described in Yin et al. (2000), which was reported to have about 68 presacral vertebrae. Its taxonomic status can only be clarified through further research.

Thalattosaurs

Thalattosaurs are a group of lizard-shaped diapsid reptiles with a long tail, which were formerly known only from the Middle-Upper Triassic of Europe and North America, with a possible occurrence from the Lower Triassic of Canada.

Taxonomic name 8
Thalattosauria Merriam, 1904
Askeptosauridae Kuhn-Schnyder, 1952
Anshunsaurus Liu, 1999
Anshunsaurus huangguoshuensis Liu, 1999

Liu (1999) reported the first specimen of this mysterious group from Guanling, reaching nearly 3 m in total length, but he described it as a pistosaurid sauropterygian (Plate I-5). Rieppel et al. (2000) re-described this taxon and clarified its status as a thalattosaur and suggested a close relationship to the Middle Triassic basal thalattosaur *Askeptosaurus italicus* from Europe.

Taxonomic names 9, 10, 11
Thalattosauria Merriam, 1904
Thalattosauridae Merriam, 1905
Xinpusaurus Yin in Yin et al., 2000

Xinpusaurus suni Yin in Yin et al., 2000

Xinpusaurus bamaolinensis Cheng, 2003

Xinpusaurus kohi Jiang et al., 2004a

Yin in Yin et al. (2000) reported a new taxon *Xinpusaurus suni* and briefly described it from four articulated skeletons with a size range of 1.41–2.38 m, but attributed it to the ichthyosaurian family Cymbospondylidae. Liu (2001), Liu and Rieppel (2001, Plate I-6), and Luo and Yu (2002) re-described and attributed the species to Thalattosauria. Liu and Rieppel (2001) also presented a phylogenetic analysis of thalattosaur relationships. Cheng (2003) briefly reported a second species of the genus *Xinpusaurus*, *X. bamaolingensis* with a very long snout. Jiang et al. (2004a) described the third species of this genus, *X. kohi* (Plate I-7), and analyzed thalattosaurian interrelationships based on 30 cranial and postcranial characters. Their phylogenetic tree corroborated a sister-group relationship between *Xinpusaurus* and *Nectosaurus* from the Carnian of California, USA.

Taxonomic names 12, 13, 14
Neosinosaurus hoangi (Zhou in Yin et al., 2000)

Wayaosaurus geei Zhou in Yin et al., 2000

Wayaosaurus bellus Zhou in Yin et al., 2000

Zhou in Yin et al. (2000) erected the three taxa above and assigned them to a new family of pachypleurosauriod sauropterygian, Sinasauridae (Neosinasauridae in Yin and Zhou, 2000). Preliminary observations suggest that they may indeed be thalattosaurs, and more detailed preparation and descriptions are needed to clarify their taxonomic status.

Sauropterygians

Placodont sauropterygians, a group of Triassic marine reptiles with characteristic crushing teeth, were formerly only known from the western Tethys.

Taxonomic names 15, 16, 17
Sauropterygia Owen, 1860
Placodontia Cope, 1871
Cyamodontoidea Nopcsa, 1923

Family incertae sedis
Sinocyamodus Li, 2000

Sinocyamodus xinpuensis Li, 2000

Placochelysidae Romer, 1956
Psephochelys Li and Rieppel, 2002
Psephochelys polyosteoderma Li and Rieppel, 2002

Placochelys ? *minutus* Yin and Luo in Yin et al., 2000

The turtle-shaped *Sinocyamodus xinpuensis* (Plate I-3) was the first placodont discovered in China and outside the western Tethys (Li, 2000). Li and Rieppel (2002) reported another taxon of placodont, *Psephochelys polyosteoderma* (Plate I-4), and discussed the idea that "*Placochelys*? *minutes*" named by Yin and Luo in Yin et al. (2000) was not clearly a member of the genus *Placochelys*, and in addition, that its relationship with *Sinocyamodus xinpuensis* was not clear.

3.2 Fossil fishes

There are also abundant fossil fishes with well-preserved and completely articulated skeletons of up to and more than 1 m in the Guanling Biota. No description on these fish has yet been published.

Chen and Cuny (2003) reported abundant elasmobranch ichthyoliths (microscopic shark teeth and dermal denticles) across the horizon containing the Guanling Biota, including a single tooth possibly of a shark of the family Hybodontidae as well as seven paragenera and paraspecies of dermal denticles.

3.3 Crinoids

Another remarkable group in the Guanling Biota is the crinoids, represented by numerous well-preserved fossils. Mu (1949, 1957) recognized six taxa: *Traumatocrinus hsui*, *T. uniformis*, *T. kweichouensis*, *T. hsui* var. *enormis*, *T.* aff. *T. timorensis*, and *T.* sp. Yu et al. (2000) erected a new species: *T. guanlingensis*, and recognized *T. hsui* and *T. uniformis*. Wang et al. (2002) reported another new species: *T. xinpuensis*. Wang et al. (2003) argued that all crinoid specimens in the Guanling Biota should be assign to a single species, *Traumatocrinus hsui* Mu 1949, and that "the juvenile *Traumatocrinus hsui* lived a pseudoplanktonic life".

3.4 Cephalopods

From the Zhuganpo and Wayao members of the Falang Formation at Guanling, a cephalopod sequence has been discerned. Hao et al. (2003) recognized four genera and eight species of ammonites and one genus and species of nautiloid, including *Protrachyceras*? sp., *Trachyceras* sp. A, *T.* sp. B, *T. multituberculatum* Hsü, 1940, *T. uraniae* Mojsisovics, 1893, *Arctosirenites canadensis* Tozer, 1961, *Arctosirenites columbianus* Tozer, 1994, *Austrotrachyceras triadicum* (Mojsisovics, 1893), and *Enoploceras*? sp. Xu et al. (2003) reported cephalopods in 11 families, 19 genera and 37 species, including three new species. They listed five ammonoid zones in ascending order as: the *Xenop rotrachyceras primum* Zone, the *Protrochyceras deprati* Zone, the *Protrochyceras costulatum* Zone, the *Trachyceras multituberculatum* Zone, and the *Sirenites* cf. *senticosus* Zone, and attributed the horizon containing the Guanling Biota to the *Trachyceras multituberculatum* Zone, which they correlated with the early Early Carnian *Trachyceras aon* Zone in Europe.

3.5 Bivalves

The "*Halobia* Bed", named after the enclosed bivalve fossils by Hsü (1944), was previously used to represent the strata of the Falang Formation. The bivalves in the Guanling Biota mainly form the *Halobia*-"*Daonella*" assemblage.

3.6 Conodonts

Conodonts survived from the end-Permian extinction, but finally became extinct at the end of the Triassic. Conodonts are important in determining the age of the Guanling Biota. Wang (2000), Chen and Wang (2002), and Sun et al. (2003) reported conodonts from Guanling, including *Paragondolella polygnathiformis*, *P. tadpole*, *P. navicula navicula*, *P. foliata foliata*, *P. jiangyouensis*, *P. foliata inclinata*, and *P. maantangensis*, which can be ascribed to the conodont *Paragondolella foliata inclinata* Zone, *Paragondolella polygnathiformis* Zone and *Paragondolella tadpole* Zone in ascending order.

3.7 Other fossils

There are also fossils of brachiopods, holothurian sclerites (Chen et al., 2003), heterochthonous terrestrial plants (Meng et al., 2002) in the Guanling Biota.

4 Paleogeographic position of the Guanling Biota

After the end-Permian extinction, the biosphere started to recover slowly during the Early Triassic (Erwin, 1994), when the environment was unstable as indicated by the large perturbations of the carbon cycle preserved in marine sediments (Payne et al., 2004). The marine ecosystem stabilized in the Middle Triassic, and then the organisms radiated rapidly (Payne et al., 2004). The Panxian and Xingyi faunas represent this time period (Fig. 2). In the early Late Triassic, global diversity reached its highest in the Triassic (Payne et al., 2004; Fig. 2). The Guanling Biota

(Fig. 3) corresponds to this peak phase that marks a full recovery of marine organismal diversity from the end-Permian extinction. Reptiles became the top predators in the marine realm just as dinosaurs began to dominate on land.

Wang et al. (2000) briefly discussed the scientific significance of the Guanling fauna fossils, and its lithofacies and tectonic position. Rieppel et al. (2000), Li (2000) and Nicholls et al. (2002) discussed the paleogeographic significance of the Guanling Biota. Ichthyosaurs in the Guanling Biota show closer relationship with those from the Carnian of North America (*Qianichthyosaurus* with *Toretocnemus*, and *Guizhouichthyosaurus* with *Shonisaurus* or *Shastasaurus*). Of thalattosaurs, *Xinpusaurus* appears as a sister group of *Nectosaurus* from North America (Jiang et al., 2004a), whereas *Anshunsaurus* shows close relationship to the Middle Triassic basal thalattosaur *Askeptosaurus italicus* from Europe (Rieppel et al., 2000). Of placodonts, they expanded their geographic distribution from the western Tethys to China, indicating a close relationship with the western Tethys (Li, 2000). The Guanling Biota was a transitional biota between the eastern Pacific and western Tethys, and located in the carbonate platform near by the margin of a deeper basin (Figs. 3, 4, and Feng et al. 1997). Lehrmann et al. (2005) also pointed out that the paleogeographic position of Guanling was in the interior of the Yangtze Platform and away from the Nanpanjiang Basin.

5 Prospects for the Future Research on the Guanling Biota

Among the 17 taxa described from the Guanling Biota, three ichthyosaurs (*Qianichthyosaurus zhoui*, *Guizhouichthyosaurus tangae*, *Guanlingsaurus liangae*), three thalattosaurs (*Anshunsaurus huangguoshuensis*, *Xinpusaurus suni*, *Xinpusaurus kohi*), and two placodonts (*Sinocyamodus xinpuensis*, *Psephochelys polyosteoderma*) are currently accepted to stand on their taxonomic status, although all need further study.

The Guanling Biota undoubtedly surpasses other Late Triassic faunas in abundance, preservation quality and diversity of fossils. Especially noteworthy are the complete skeletons of marine reptiles. The study on this biota will greatly expand our knowledge of Triassic marine reptiles, when they were in their early evolutionary stage. Limited numbers of well-preserved specimens had previously been known for thalattosaurs and placodonts; the well-preserved specimens of these two groups in the Guanling Biota will greatly enhance our understanding of these mysterious animals, which only lived in the Triassic sea. The large ichthyosaurs in the Guanling Biota will help us fill the gap between Triassic and Jurassic forms, and help complete the link in the evolutionary line. Furthermore, the Guanling Biota will provide more data to discuss Triassic paleogeography, paleoenviroments and its coevolutionary relationship with the biota.

As described above, the Guanling Biota is unique, well preserved, and scientifically important. To fully expose the potential of this natural treasure, it is first critical to protect the biota from destruction and exploitation. At the same time, it is important to systematically collect scientific data through excavations, detailed stratigraphic investigations, and specimen preparation. These basic activities will ultimately form the basis of all future research.

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Explanation of Plate

Plate I

1. *Qianichthyosaurus zhoui* Li, 1999: paratype, IVPP V 11838. Scale bar: 10 cm.
2. *Guizhouichthyosaurus tangae* Cao and Luo in Yin et al., 2000: paratype of *Cymbospondylus asiaticus* Li and You, 2002, IVPP V 11869. scale bar: 10 cm
3. *Sinocyamodus xinpuensis* Li, 2000: holotype, IVPP V 11872. Scale bar: 10 cm.
4. *Psephochelys polyosteoderma* Li and Rieppel, 2002: holotype, IVPP V 12442; 4a: skull, 4b: carapace. Scale bar: 5 cm.
5. *Anshunsaurus huangguoshuensis* Liu, 1999: holotype, IVPP V 11835. Scale bar: 10 cm.
6. *Xinpusaurus suni* Yin in Yin et al., 2000: IVPP V 11860. Scale bar: 5 cm.
7. *Xinpusaurus kohi* Jiang et al., 2004: holotype, GMPKU-P-1005 (former GMPKU 2000/005); 7a: skull, 7b: skeleton. Scale bar: 15 cm.

Plate I