中国三叠纪海生爬行类综述

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摘要：三叠纪海生爬行类化石广泛分布于中国南方的安徽、湖北、贵州、云南、广西和西藏。它们不仅包括有世界性分布的鱼龙类、鳍龙类、海龙类、原龙类等，而且还有仅出现于扬子海区的湖北鳄类。简单回顾了中国三叠纪海生爬行类的研究历史。根据化石的地史分布确认了自早三叠世晚期至晚三叠世早期的7个海生爬行类组合带。它们是奥伦尼克期的Chaohusaurus-Keichousaurus-Hupehsuchus组合带，安尼期的Chinchenia-Sanchiaosaurus组合带和Dinoccephalosaurus-Mixosaurus组合带，拉丁期的Dingxiaoasaurus带和Keichousaurus-Nothosaurus组合带，卡尼期的Anshunsaurus-Qianichthyosaurus-Sinocycamodus组合带和诺利期的Himalayasaurus带。

对化石的古地理环境分析表明，中国早三叠世晚期的海生爬行类主要分布于扬子海区东部（安徽、湖北）的浅海开阔台地和局限台地。中三叠世由于东部地区的抬升，鱼龙类和鳍龙类向西扩散，在扬子区西部（贵州、云南）辐射发展，在拉丁期达到个体数量和种类的高峰。晚三叠世卡尼期动物的数量依然很多，个体有增大的趋势，但高级分类阶元的数量减少，它们埋藏于海水相对较深的浊积岩相中。晚三叠世诺利期的化石发现于西藏的定日和聂拉木，这是中国惟一属于冈瓦那特提斯区的三叠纪海生爬行类组合带，仅含大型的鱼龙类。受动物的生存环境和埋藏条件的影响，中国三叠纪海生爬行类化石记录并不完整。目前尚有相当数量的化石未经研究，已记述的化石也需要在研究程度上进一步深化。

关键词：中国南方，三叠纪，鱼龙类，鳍龙类，海龙类，原龙类，湖北鳄

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to an endemic group, hupehsuchids, they include all other forms known from the Western Tethys Province and the East Pacific Region, such as ichthyosaurs, cosauropterygians, placodonts, thalattosaurus and protorosaurs. Up to now, 33 species belonging to 28 genera have been described from this region, although some of their taxonomic status remains disputable on generic or species level, which will be discussed below. The marine reptiles occur in the deposits ranging from the upper Lower Triassic to the lower Upper Triassic in this region, and are distributed in Anhui, Hubei, Guizhou, Yunnan provinces, Guangxi Zhuang Autonomous Region and Xizang (Tibet) Autonomous Region (Fig. 1).

Fig. 1 Map of the South China showing the localities bearing Triassic marine reptiles
● Early Triassic; ▲ Middle Triassic; △ Late Triassic

2 Early research history

Study of the Triassic marine reptiles in China can be dated back to the fifties of last century, when Keichousaurus hui was discovered and described by C. C. Young in 1958. As a pioneer Chinese vertebrate paleontologist, mainly engaged in lower tetrapods, Young continued his research on marine reptiles since then. Subsequently, he further recognized 5 genera and 6 species of sauropterygians (Keichousaurus yuanyanensis Young, 1965a, Shingysaurus unexpectus Young, 1965a, Chinchena suni Young, 1965a, Sanchiansaurus dengi Young, 1965a, Kwangisaurus orientalis Young, 1959, Kwangisaurus lusiensis Young, 1978), 3 genera 3 species of ichthyosaurs (Mixosaurus maotaensis Young, 1965b, Chaohusaurus geishanensis Young et Dong, 1972, Tibetosaurus tingsiensis Young et al., 1982), one questionable thalattosaur (Hanosaurus hupehensis Young, 1972a), and one enigmatic aquatic reptile (Hupehsuchus nanchangensis Young, 1972b). In addition, 2 genera and 3 species of ichthyosaurs (Himalayasaurus tibetensis Dong, 1972, Chensaurus chaoxianensis (Chen, 1985), Chensaurus faciles (Chen, 1985)) and a genus (Nanchangousaurus suni Wang, 1959) closely related to Hupehsuchus were described by other students during the same period. All these important discoveries led to a preliminary division of biostratigraphic zonations and interpretation of the Triassic palaeoenvironments in South China.

It is worthy to mention that significant revisions had been made on Chinese sauropterygians, hupehsuchids and ichthyosaurs by both Chinese and foreign paleontologists in the nineties of last century. Carroll and Dong (1991) redescribed the type specimens of Hupehsuchus nanchangensis and Nanchangousaurus suni, and considered the two genera as representing a previously unrecog-
nized assemblage of Triassic aquatic reptiles, probably sharing a common ancestor with ichthyosaurs. Motani and You (1998) restudied three ichthyosaurs from the Lower Triassic of Chaohu, Anhui, and considered both *Chensaurus chaoxianensis* and *Chensaurus faciles* as synonyms of *Chaohusaurus geishanensis*. Rieppel (1998a, b, 1999) restudied several taxa of sauropterygian erected by Young. He assigned *Shingysaurus unexpectus* to Nothosaurs, referred *Hanosaurs huphenensis* to the Pachypleurosauroidea, *Chinchenia suni* and *Kwangsisaurus orientalis* to Pistosauroida, and considered *Kwangsisaurus lusiensis* as a taxon close to *Lariosaurus*.

3 Progress in recent years

3.1 New record of marine reptiles including the first placodont, thalattosaur and protorosaur found in South China

Since the end of the last century, study of Triassic marine reptiles in China has entered into a new era along with many discoveries of perfectly preserved skeletons. Fossils of these reptiles include new genera of not only ichthyosaurs and sauropterygians, but also thalattosaurs, placodonts and protorosaurs, which are new records in China. They include 2 genera and 2 species of nothosaurs (*Lariosaurus xingyiensis* Li et al., 2002, *Nothosaurs youngi* Li et Rieppel, 2004); 3 genera and 3 species of placodont (*Sinocyamodus xinpuensis* Li, 2000, *Psephochelys polyosteodera* Li et Rieppel, 2002, *Plachochelys minutius* Yin et Luo, 2000 (in Yin et al., 2000)); 2 genera and 4 species of thalattosaurs (*Anshunsaurus huangguoshuensis* Liu, 1999, *Xinpusaurus suni* Yin, 2000 (in Yin et al., 2000), *X. bamaolinensis* Cheng, 2003 and *X. kohi* Jiang et al., 2004); 8 genera 8 species of ichthyosaurs (*Qianichthyosaurus zhoui* Li, 1999, *Cymbospondylus asiaticus* Li et You, 2002, *Panjiangsaurus epicharis* Chen et Cheng, 2003, *Guanlingsaurus liangae* Yin, 2000 (in Yin et al., 2000), *Guizhouichthyosaurus tangan* Cao et Luo, 2000 (in Yin et al., 2000), *Typicusichthyosaurus tsaihuai* Yu, 2000 (in Yin et al., 2000), *Mixosaurus guanlingensis* Cao, 2000 (in Yin et al., 2000) and *Phalarodon* sp. (Jiang et al., 2003)); one genus and species of protorosaur (*Dinocephalosaurus orientalis* Li, 2003). The new discoveries are characterized by both abundant specimens and a significant taxonomic diversity, showing that all the major groups of the Triassic marine reptiles known from the West Tethys Province and the East Pacific Region, including Eosauropterygia, Placodontia, Ichthyosauria, Thalattosauria and Protosauria, are also present in the Triassic of the South China. The discovery of many marine reptiles in the Triassic of South China is also important for biostatigraphic zonation and correlation, and the interpretation of their palaeoenvironments.

3.2 The biozones of marine reptile fossils in South China

Marine deposits of the Triassic age are extensively distributed in South China. Up to now, 7 biozonations of marine reptiles have been recognized from upper Lower Triassic to lower Upper Triassic (Fig. 2). A brief introduction to their geological and stratigraphical distribution, composition of reptile assemblages and links with other marine reptile faunas of the same age will be given as follows.

3.2.1 The assemblage of Chaohusaurus-Keichousaurus-Hupehsuchus

**Horizon and age**
Jialingjiang Formation (Hubei Prov.), Nanlinghu Formation (Anhui Prov.) and Beisi Formation (Guangxi Autonomous Region)

Olenekian, Early Triassic

**List of fossils**
Ichthyosauria
Grippididae

*Chaohusaurus geishanensis* Young et Dong, 1972
Sauropterygia

Pachypleurosauridae

*Keichousaurus yuananensis* Young, 1965

*Hanoraurus hupehensis* Young, 1972

Pistosauroidea

*Kwangsisaurus orientalis* Young, 1959

Hupehsuchia

Nanchangosauridae

*Hupehsuchus nanchangensis* Young, 1972

*Nanchangosaurus sunti* Wang, 1959

**Geographical distribution**

Chaoxian, Anhui Province

Yuan'an and Nanzhang, Hubei Province

Wuming, Guangxi Zhuang Autonomous Region

3.2.2 The assemblage of *Chinchenia-Sanchiasaurus*

**Horizon and age**

Member I of Guanling Formation

Early Anicinian, Middle Triassic

**List of fossils**

Sauropterygia

Pistosauroidea incertae sedis

*Chinchenia sunti* Young, 1965

Nothosauria incertae sedis

*Sanchiasaurus dengi* Young, 1965

**Geographical distribution**

Qingzhen and Guiyang, Guizhou Province

3.2.3 The assemblage of *Dinocephalosaurus-Mixosaurus*

**Horizon and age**

Member II of Guanling Formation

Late Anicinian, Middle Triassic

**List of fossils**

Protorosauria

Family incertae sedis

*Dinocephalosaurus orientalis* Li, 2003

Ichthyosauria

Mixosauridae

(*Mixosaurus maotaiensis* Young, 1965

—*a nomen dubium* (see Motani, 1999))

*Phalarodon* sp. (see Jiang et al., 2003)

Sauropterygia

Nothosauridae

*Nothosaurus* sp. (undescribed specimens)

**Geographical distribution**

Panxian and Renhuai, Guizhou Province

3.2.4 The biozonation of *Dingxiaosaurus*

**Horizon and age**

Yangliuqing Formation

1) Including a footprint of *Chirotherium* from Zhenfeng, Guizhou Province (see Wang and Ma, 1989; Zhen et al., 1996).
Early Ladinian, Middle Triassic

**List of fossils**

**Sauropterygia**

**Pistosauridae**

* Dingxiaosaurus luyinensis* Liu et al., 2002

**Geographical distribution**

Dingxiao, Guizhou Province

3.2.5 The assemblage zone of *Keichousaurus-Nothosaurus*

**Horizon and age**

Zhuganpo Member of Falang Formation
Late Ladinian, Middle Triassic

**List of fossils**

**Sauropterygia**

**Pachypleurosauridae**

* Keichousaurus hui* Young, 1958

**Nothosauridae**

* Lariosaurus xingyiensis* Li et al., 2002

* Nothosaurus youngi* Li et Rieppel, 2004

( *Shingyisaurus unexpectus* Young, 1965

= *Nothosaurus* sp. (see Rieppel, 1998a))

("Kwangsisaurus" lusiensis* Young, 1978

—might represent a taxon close to *Lariosaurus* (Rieppel, 1998c))

**Placodontia**

Undescribed specimens

**Thalattosaurusia**

Undescribed specimens

**Ichthyosauria**

Undescribed specimens

**Protorosauria**

Undescribed specimens

**Geographical distribution**

Xingyi, Dingxiao and Anlong, Guizhou Province

Luoping and Fuyuan, Yunnan Province

Luxi, Guangxi Zhuang Autonomous Region

3.2.6 The assemblage zone of *Anshunsaurus-Qianichthyosaurus-Sinocycamodus*

**Horizon and age**

Wayao Member of Falang Formation

Carnian, Late Triassic

**List of fossils**

**Thalattosaurusia**

**Askeptosauridae**

* Anshunsaurus huangguoshuensis* Liu, 1999

**Thalattosaurusidae**

* Xinpusaurus suni* Yin, 2000 (in Yin et al., 2000)

* X. bamaolinensis* Cheng, 2003

( *X. kohi* Jiang et al., 2004

— a synonym of *X. bamaolinensis* (Rieppel and Liu, in press))

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1) "Wayao Member of Falang Formation" was newly named as "Xiaowa Formation" by Wang et al. (2003).
Ichthyosaura
Shastosauridae
_Panjiangsaurs epicharis_ Chen et Cheng., 2003
Cymbospondylidae
_Cymbospondylus asiaticus_ Li et You, 2002
Guanlingsuridae
_Guanlingsaurus liangae_ Yin, 2000 (in Yin et al., 2000)
Family incertae sedis
_Qianichthysaurus zhous_ Li, 1999
— a synonym of _Qianichthysaurus zhous_ (Jiang and Li, in press)
(Guizhouichthysaurus tanguae Cao et Luo, 2000 (in Yin et al., 2000) and_Typicusichthysaurus tsaihuae_ Yu, 2000 (in Yin et al., 2000), both are species inquirendae according to McGowan and Motani (2003))
Placodontia
Family incertae sedis
_Sinocyamodus xinpuensis_ Li, 2000
Placochelyidae
_Psephochelys polyosteootherma_ Li et Rieppel, 2002
— a nomen dubum

Geographical distribution
Guanling, Guizhou Province
Probably Qinglong and Xingyi, Guizhou Province
3.2.7 The biozonation of _Himalayasaurus_

Horizon and age
Qulonggongba Formation\(^1\)
Norian, Late Triassic

List of fossils
Ichthyosaura
Shastosauridae
_Himalayasaurus tibetensis_ Dong, 1972
(Tibetosaurus tingjiangensis Young et al., 1982
—a nomen nudum for poorly preserved specimens)

Geographical distribution
Nyalam and Tingri, Xizang (Tibet) Autonomous Region

4 The analysis of palaeobiogeography

Early Triassic It is considered that the Early Triassic is the earliest interval that reptiles invaded into marine environment on a global scale. A shallow-water marine environment prevailed in the Yangtze Sea Region of South China during the Early Triassic. Although marine reptiles found in upper Lower Triassic occur sporadically and in very small number, the assemblage of _Chaohusaurus-Keichousaurus-Hupehsuchus_ is important for biostratigraphic zonation, correlation and the interpretation of palaeoenvironments. Fossils of this assemblage were mainly discovered in the east part of the Yangtze Region, i.e., _Chaohusaurus_ from the Nanlinghu Formation

Fig. 2  Stratigraphy of the Triassic in the South China and the temporal distribution of marine reptiles

<table>
<thead>
<tr>
<th>Age</th>
<th>Stratigraphical and Geographical distribution</th>
<th>Biozonation</th>
<th>pachypleurosaurians</th>
<th>caenothepetofyrians</th>
<th>placodonts</th>
<th>thalattosaurians</th>
<th>ichthyosaurs</th>
<th>huphsuchus</th>
<th>protorosaurs</th>
<th>archosaurs</th>
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<td>Hubei</td>
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<td>Late Triassic</td>
<td>Notan</td>
<td>Cenoman</td>
<td>Falang Fm</td>
<td>Wayao</td>
<td>Qianhe</td>
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<td>Zhanggao Fm</td>
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of Chaoxian, approximately 30 km from the Huaiyang Block Mass in the Lower Yangtze Region, and the other 4 genera, *Keichousaurus*, *Hanosaurus*, *Huphsuchus* and *Nanchangousaurus* from the Jialoujiang Formation of Yuan’an and Nanzhang in east part of the Upper Yangtze Region. There are minor differences in sedimentation environment between the two regions. The Nanlinghu Formation of Chaoxian represents deposition of open platform\(^1\), but the Jialoujiang Formation of Yuan’an and Nanzhang comprises sediments of restricted platform\(^2\). *Kwangisia* is the only exception that was found in restricted or semi-restricted platform sediments of the Baiji Formation in the southern Yangtze Region. It is worthy of notice that, so far, there is no marine reptile known in the west part of the Yangtze Region—Yongningzhen Formation, which is also Olenekian in age and deposited in restricted platform\(^3\).

**Middle Triassic**  The east part of the Yangtze Region seemed to start an intermittent uplift and subsidence at the beginning of the middle Triassic age, and the deposits of the Badong Formation consist alternatively of marine and terrestrial beds, which contain some terrestrial archosaurs (Zhang, 1975) and amphibians (Liu and Wang, 2005). The appearance of abundant marine reptile fossils in the Middle Triassic of Guizhou and Yunnan provinces along with the occurrence of marine regression in the eastern Yangtze Sea, probably suggests that early marine

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reptiles, ichthyosaurs and pachypleurosaurans migrated westwards, settled down and flourished in the west part of the Yangtze region. As listed above, four assemblage zones are recognized in Members I and II of the Guanling Formation, Yangliuqing Formation and the Zhuangpo Member of Falang Formation, respectively.

Member I of the Guanling Formation, Early Anicinian in age, yielded no ichthyosaurs, but two sauropeterygians—Chinchenia and Sanchiacoelurus. The footprint of Chirotherium found also in this horizon indicates a near shore shallow-water sedimentary environment.

Up to now, one protorosaur, Dinocephalosaurus, and two ichthyosaurs, Mixosaurus and Phalarodon have been recorded from Member II of the Guanling Formation, which comprises deposition of partially enclosed shallow sea at the Late Anicinian age. Some undescribed specimens indicate that nothosaurs, pistosaurs, and even archosaurs may also be members of the fauna.

The Yangliuqing Formation, Early Ladinian in age, is represented by a series of gray thin-bed to massive or brecciated dolomite and a small amount of limestone, which indicate an evaporate sedimentation in semi-restricted platform. Such an environment seems to be unfavourable to the marine reptiles, and only one taxon, Dingxiaosaurus was reported.

Late Ladinian of the Middle Triassic is a period of great prosperity for marine reptiles. Almost all groups of marine reptiles at the period left their trace in the Upper Yangtze Region. The Zhuangpo Member of the Falang Formation comprise a thick sequence of micritic limestone and verrucose limestone, a deposition of open platform that contains the most abundant and diversified fauna of fossil reptiles. Although only one pachypleurosaur, Keichousaurus, and two nothosaurs, Lariosaurus and Nothosaurus have been reported, a considerable number of undescribed fossils of placodonts, thalattosaurs, ichthyosaurs and protorosaurs have also been collected in the Zhuangpo Member.

Late Triassic A marine regression started at the beginning of Carnian age in the Yangtze Sea, but in some areas, such as Guanling, Xingren, Zhenfeng etc. marine water deepened. In Guanling the Wayao Member of Falang Formation comprises a series of turbidite rocks composed of marl, calcareous and sandy claystone, bioclastic limestone and micritic limestone, which represent a deposition of deep-water shelf facies. The fauna of marine reptiles in the Wayao Member is abundant in individual number as that of underlying Zhuangpo Member, but less diverse in high rank taxa. It contains no pachypleurosaurans, nothosaurs or protorosaurs that usually lived in shallow-water environment, but contains some large-sized ichthyosaurs, thalattosaurs and placodonts. It is easy to understand that large-sized ichthyosaurs being pelagic reptiles left their bodies in deposition of deep water, but the appearance of thalattosaurs and placodonts in the Wayao Member suggest that Anshuniasaurus and Xiphusaurus might also be living in open sea, and Sinocamptosaurus and Psephochelys as bentonic placodonts can tolerate an environment of comparative deep sea.

The stratigraphical and geographical distribution of Himalayasaurus, a large ichthyosaur represented by a broken skull and some postcranial bones, has some important implications. It was collected from the Quonggongba Formation (Norian in age) of Xizang (Tibet), and represents the latest member of Triassic marine reptiles ever found in China and the only occurrence in Gondwanan Tethyan region, rather than East Tethyan region.

5 Conclusion

Despite the remarkable discoveries in recent years the record of the Triassic marine reptiles

of China is far from complete due to their unique palaeoenvironment, taphofacies and the insufficient study of the collected fossils. Based on the fact that the earliest ichthyosaur (*Chaohusaurus*) and sauopterygians (*Keichousaurus* and *Hanousaurus*) appeared in the east part of the Yangtze Sea, a westwards spread of marine reptiles is suggested.

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