Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction

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ABSTRACT

The Triassic was a time of turmoil, as life recovered from the most devastating of all mass extinctions, the Permo-Triassic event 252 million years ago. The Triassic marine rock succession of southwest China provides unique documentation of the recovery of marine life through a series of well dated, exceptionally preserved fossil assemblages in the Daye, Guanling, Zhuganpo, and Xiaowa formations. New work shows the richness of the faunas of fishes and reptiles, and that recovery of vertebrate faunas was delayed by harsh environmental conditions and then occurred rapidly in the Anisian. The key faunas of fishes and reptiles come from a limited area in eastern Yunnan and western Guizhou provinces, and these may be dated relative to shared stratigraphic units, and their palaeoenvironments reconstructed. The Luoping and Panxian biotas, both from the Guanling Formation, are dated as Anisian (Pelsonian) on the basis of conodonts and radiometric dates, the former being slightly older than the latter. The Xingyi biota is from the Zhuganpo Formation, and is Ladinian or early Carnian, while the Guanling biota is from the overlying Xiaowa Formation, dated as Carnian. The first three biotas include extensive benthos and burrowing in the sediments, and they were located in restricted basins close to shore. Further, even though the Luoping and Panxian biotas are of similar age, their faunas differ significantly, reflecting perhaps palaeogeographically isolated basins. Between the time of the Xingyi and Guanling biotas, there was a major transgression, and the Guanling biota is entirely different in character from the other three, being dominated by pelagic forms such as large floating crinoids attached to logs, very large ichthyosaurs and thalattosaurs, and pseudoplanktonic bivalves, with no benthos and no burrowing. Phylogenetic study of the fishes and marine reptiles shows apparently explosive diversification among 20 actinopterygian lineages very early in the Early Triassic, but a later expansion of marine reptile groups, in the late Olenekian and early Anisian. This offset in diversification patterns is matched by comparisons of feeding guild categories and body size data. New research tools will shed considerable light on the phylogenetic and ecological implications of recovery of mairne vertebrates in the Triassic.

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Contents

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1. Introduction

The Triassic, 252–201 Ma, was a time of unusual diversification of life, the period during which the foundations of modern ecosystems were established both in the sea and on land. This claim is based on the fact that the Permo-Triassic mass extinction (PTME) marked a fundamental divide in the Phanerozoic history of life in the oceans (Sepkoski, 1984; Van Valen, 1984), with the rise of the so-called 'modern fauna', in the Triassic. Further, although the Mesozoic marine revolution (Vermeij, 1977) has often been dated as beginning in the Jurassic, in fact most of the new-style predators that apparently drove the major changes in morphology and life modes were already established in the Triassic in the aftermath of the PTME, such as pred-atory gastropods, decapods, light and fast neopterygian fishes, and marine reptiles (Chen and Benton, 2012). The same is true on land, where the PTME marked the end of formerly key groups such as pareiasaurs and gorgonopsians, and it was the trigger for the rise of basal forms of modern groups such as turtles, crocodylomorphs, liz-ard ancestors, mammals, and dinosaurs (and their descendants, the birds), all of which emerged in the Middle Triassic and around the be-ginning of the Late Triassic, some 10–20 Myr after the PTME (Sahney and Benton, 2008; Brusatte et al., 2011; Irmis and Whiteside, 2012). Note that we refer to the mass extinction as the PTME, rather than end-Permian mass extinction (EPME) as the major extinction epi-sodes straddled the Permo-Triassic boundary (Song et al., 2013).

The Triassic began with a devastated world, in which only about 10% of species had survived through the most severe mass extinction ever, at the end of the preceding Permian Period. The PTME was prob-ably caused by a series of massive eruptions of the Siberian Traps, great outpourings of basalt lava that occurred repeatedly from 252.6 to 250.3 Ma, and with late-stage eruptions up to 243 Ma (Saunders and Reichow, 2009; Shen et al., 2011). The eruptions led to a series of consequences that have been identified worldwide by sedimentol-ogy and isotope geochemistry, including: atmospheric and oceanic warming by 5–10 °C, anoxia in the oceans, and acid rain leading to massive killing of forests and consequent stripping of soils on land (Wignall and Twitchett, 1996; Benton, 2003; Benton and Twitchett, 2004; Erwin, 2006; Knoll et al., 2007; Algeo and Twitchett, 2010; Sun et al., 2012). Key killing agencies appear to have been acidifica-tion and anoxia in the seas (Knoll et al., 2007) and acid rain and aridification on land (Benton and Newell, in press).

These grim conditions continued at least through the Early Triassic, a span of some 5 Myr, with repeated intense and rapid phases of global warming (Payne et al., 2004; Retallack, 2012; Sun et al., 2012), and this set back the possibility of recovery of life and normal ecosystem functioning at least into the Middle Triassic. Documenting the patterns of the Triassic recovery of life, and hence the foundations of modern ecosystems and modern biodiversity, has been fraught with problems (Chen and Benton, 2012), not least because of the im-precise dating of fossil-bearing formations, uncertainties about the quality of the fossil data, and the need to place taxa on sound phylo-genetic trees.

The South China basin, some 3000 km wide and 1500 km from north to south, documents, in many continuous rock sequences, over 70 Myr of the Earth's history from the Middle Permian to the Late Triassic. These sections have been studied intensively for the past 30 years, and they now offer high-precision dating throughout, not least because the global standard sections for the Permo-Triassic boundary (PTB) are there (Yin et al., 2001; Shen et al., 2011).

The aim of this review is to synthesise the mass of new data that has emerged in the past 20 years, to place the South Chinese fossil vertebrate biotas in stratigraphic and regional context, to compare them with contemporaneous faunas elsewhere in the world, most no-tably in central Europe, and to point to some of the wider indications they give about the nature of the Triassic recovery of marine life.

1.1. Nomenclatural note

Place names and names of people and stratigraphic systems may be transliterated from the Chinese in different ways. The current stan-dard is the pinyin (= 'spelled-out words') system, adopted by the Chinese government in 1958 and revised several times since. Before 1950, various systems of transliteration from Chinese characters to Western spelling were used. Here, we generally use pinyin transliter-ation, but retain some older forms (e.g. Khamdian, Yangtze), where they are common in the literature.

1.2. Repository abbreviations

CIGMR, Chengdu Institute of Geology and Mineral Resources (also known as Chengdu Center, China Geological Survey), Chengdu, China; CMR, Museum of China University of Geosciences, Beijing, China; GMPKU, Geological Museum, Peking University, Beijing, China; Gmr, Weiwei Paleontological Research Center, Guizhou Province, China; IVPP, Institute for Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; LPV, Luoping Vertebrate

Collection, Chengdu Institute of Geology and Mineral Resources, Chengdu, China; NGMC, National Geological Museum of China, Beijing, China; NIGP, Nanjing Institute of Geology and Palaeontology, Nanjing, China; NMNS, National Museum of Natural Science, Taiwan, China; SPC, Wuhan Center, China Geological Survey, Wuhan, China; YIGMR, the former Yichang Institute of Geology and Mineral Resources (now known as Wuhan Center, China Geological Survey), Wuhan, China; ZMNH, Zhejiang Museum of Natural History, Hangzhou, China.

2. The Early to Middle Triassic construction of ecosystems

Current estimates for the timing of the Triassic recovery of life in the sea range from as little as 1–3 Myr and up to 10–15 Myr, and the differences depend partly on which definition of 'recovery' is intended (Chen and Benton, 2012). There are perhaps three phases of recovery of life in the Triassic, and these might be common to the times after all mass extinctions: (1) initial diversification of disaster taxa, (2) replacement of disaster taxa by more 'normal' groups, those that remain as key elements of ecosystems in the long-term, and (3) emergence of long-lasting ecosystem structures. These terms are for recovery of ecosystems, and most authors would probably accept stage (2) as the recovery of life. Recovery modes and times differ by taxa, with some clades such as ammonoids recovering fast, other such as bivalves and tetrapods recovering more slowly, and others such as foraminifera somewhere between (e.g. Song et al., 2011).

As for the initial diversification of disaster taxa, most palaeontologists would agree that this does not constitute the full recovery of life. However, many ecosystems achieved pre-extinction diversity levels, if numbers of species are simply added up, by the Smithian, some 2 Myr after the crisis. For example, ammonoids had actually achieved higher diversities by that time than before the mass extinction (Brayard et al., 2009). Further, the PTME had little effect on conodonts, which showed a stepwise increase in diversity through the entire Early Triassic, although they suffered setbacks at the ends of the Smithian and Spathian (Orchard and Krystyn, 2007). Among echinoderms, crinoids disappeared for most of the Early Triassic and rebounded at the end-Spathian, while ophiuroids experienced diversity increase and geographic expansions immediately after the PTME (Chen et al., 2010).

The longer recovery period of some 10–15 Myr is perhaps more plausible for two reasons: (1) it reflects the establishment of long-lasting fully Mesozoic-style ecosystems, not something short-lived, and (2) it includes the 'coral gap' in the sea, over 10 Myr with no corals or reefs, and the 'coal gap' on land, a time when no coal was laid down, indicating an absence of forests. To claim that life had recovered before reefs and forests had re-emerged might seem rather odd. The 10–15 Myr recovery period allows for the re-establishment of full trophic pyramids with top predators (Chen et al., 2009; Chen and Benton, 2012). It may have taken even longer for ecosystem diversity dynamics to become re-established among tetrapods on land (Benton et al., 2004; Irmis and Whiteside, 2012; Retallack, 2012; Benton and Newell, in press).

Recovery was almost certainly slow, partly because of the devastating scale of the PTME, but also because of poor environmental conditions in the Early Triassic (Hallam, 1991; Payne et al., 2004; Sun et al., 2012). These poor conditions are indicated by unusual biosedimentary features, such as microbialites, wrinkle structures and seafloor carbonate precipitates, which reflect the absence of metazoans devastated by the PTME, combined with episodes of low oxygen and high chemical precipitation (Schubert and Bottjer, 1992; Algeo et al., 2011; Chen and Benton, 2012). Further, there were several negative excursions in carbon isotope ratios, indicating repeated greenhouse crises at least four times during the 6 Myr of the Early Triassic and early Anisian (Payne et al., 2004; Retallack, 2012).

The repopulating of the world in the Triassic was not simply a matter of recovery of the few surviving stragglers of formerly significant groups; some entirely new groups appeared which performed ecological roles not seen before. For example, in the oceans, the first substantial radiation of marine reptiles occurred, the ichthyosaurs, sauropterygians, and thalattosaurs. In the Permian, there had been a short-lived radiation of unrelated marine reptiles, the mesosaurs, in southern oceans, but the rapid appearance of five or six lineages of predatory reptiles, ranging from 0.1 to 5 m in length, was something entirely new in the Triassic (Rieppel, 2000; McGowan and Motani, 2003). Lower in the food chain, new groups of fishes, echinoderms, molluscs, arthropods, and scleractinian corals replaced previously dominant, but now vanished, groups such as brachiopods, trilobites, and rugose and tabulate corals.

On land, the formerly significant groups of tetrapods disappeared, and were eventually replaced by new forms. Some re-established their former roles, such as the dicynodonts, important herbivores in the Late Permian, and again a significant group by the Middle Triassic. But others, such as cynodonts and archosaurs, which had been present in modest numbers in the latest Permian, had a dramatic opportunity to achieve major ecological roles that might not have occurred had the extinction not happened (Brusatte et al., 2011). Extinctions and recoveries among plants and insects on land were more complex (reviewed, Benton and Newell, in press).

3. Historical background

The research history of Triassic fossil Lagerstätten in SW China dates back to the middle of the 20th century, when the first articulated crinoid, *Traumatocrinus* hsui from the Guanling area, was described by Mu (1949). In 1957, the first marine reptile was found by Chengzhi Hu from the National Geological Museum of China at Lüying Village, Dingxiao, Xingyi City, Guizhou Province, and it was named *Keichousaurus hui* by Zhongjian Yang (= Chung-Chien Young) in the following year (Young, 1958). Three taxa of fishes were reported from the same locality in 1959 (Su, 1959). In the next three decades, Triassic marine reptiles were recovered widely over south China. Fossil localities include those from Guizhou, Yunnan, Hubei, Tibet, and Guangxi provinces, and these range stratigraphically from Olenekian to Carnian (Young, 1965b, 1972a,b; Young and Dong, 1972; Dong, 1972; Young, 1978; Chen, 1985; see below). These earlier papers were published in China, and mainly in Chinese, and some (other than those by Young) had minimal English-language translations. Regional geological mapping at the scale of 1:200,000 was finished in those provinces by local geological teams during this time, so providing a basic stratigraphic framework for further work.

The situation changed dramatically with reports of new fossil fishes and reptiles from the marine Triassic of SW China (Li, 1999; Liu, 1999). Abundant fossil reptiles and fishes have now been excavated from the Triassic of Guizhou Province and neighbouring, eastern parts of Yunnan Province. Besides the already known Xingyi biota (Li and Jin, 2003), several new biotas with exceptionally preserved fossils were recovered from different horizons and localities, including the Anisian Panxian biota (Hao et al., 2006; Motani et al., 2008; Jiang et al., 2009), the Carnian Guanling biota (Wang et al., 2003a,b; Jiang et al., 2005a,b,c; Wang et al., 2008), and the Anisian Luoping biota (Zhang et al., 2008; Hu et al., 2011). These discoveries attracted increased attention from both scientists and the public.

Several research groups with vertebrate specialists from China and overseas are currently working on Chinese Triassic fossils. Consequently several groups of marine reptiles, including ichthyosaurs, prolacertiforms, sauropterygians, thalattosaurs, and archosaurs, have been reported and these are well studied. Nearly all major clades of Triassic marine reptiles known worldwide have been recovered from this area, indicating that SW China might be a centre of radiation for some of these forms (Li, 2006). Despite numerous discoveries and

publications on marine reptiles, study of fishes and invertebrates has been much slower (Jin, 2001). Meanwhile, stratigraphic correlation, sedimentology and taphonomy of these exceptionally preserved Lagerstätten have also been carried out, especially for the Guanling biota (Wang et al., 2008). However, the full spectrum of the faunal composition, age determination, and furthermore, the implications of these exceptionally preserved fossils for our understanding of the recovery of marine ecosystems, still remain poorly understood.

4. The Triassic of the South China Block

The South China Block (Fig. 1), composed of the Yangtze Platform and the South China Fold Belt, is bounded to the north by the large North China Block, and to the southwest by the Simao Block and the Indochina Block. Palaeomagnetic and sedimentary evidence suggests that the South China Block formed a united plate since the Late Proterozoic or Early Palaeozoic (Lehrmann et al., 2005; Shen et al., 2006). From the Late Proterozoic to the end of the Middle Triassic, the Yangtze Platform was characterised by shallow-water carbonate deposition (Liu and Xu, 1994; Feng et al., 1997; Ma et al., 2009) up to a thickness of more than 4000 m from the Permian through the middle–late Triassic (Wang, 1985). The Nanpanjiang Basin, with some smaller isolated platforms

such as the Great Bank of Guizhou and the Chongzuo–Pingguo Platform, both of which developed during the Triassic (Lehrmann et al., 1998, 2007), was located at the southwestern margin of the Yangtze Platform. The South China Block joined with the Simao and Indochina blocks along suture belts that represented former oceans, probably during the Triassic Indosinian orogeny (Lepvrier and Maluski, 2008).

The Indosinian orogeny created the topography for Triassic deposition, at a time when sea levels were high. Five substantial blocks of continent, termed 'old land' by Chinese geologists because much of it dated back to the Precambrian, were uplifted, the Khamdian (Kangdian) continent to the west, which had been a stable massif since the late Proterozoic (Liu and Xu, 1994; Ma et al., 2009), the Jiangnan continent in the centre, the Yunkai continent to the south, and a series of smaller islands extending northwards to Cathaysia in the far east. Between the Khamdian and Jiangnan islands lay the Nanpanjiang Basin (also named the Youjiang depression in some Chinese references) of Guizhou (Wang, 1985), characterised by relatively deep-water carbonate and turbite sequences in the Triassic (Lehrmann et al., 2003, 2007, 2009). This and neighbouring intraplatform basins (Fig. 1) provided a suitable environment for the preservation of fossil Lagerstätten including the Luoping (Hu et al., 2011), Panxian (Motani et al., 2008; Jiang et al., 2009), and Xingyi and Guanling biotas (Wang et al., 2008).
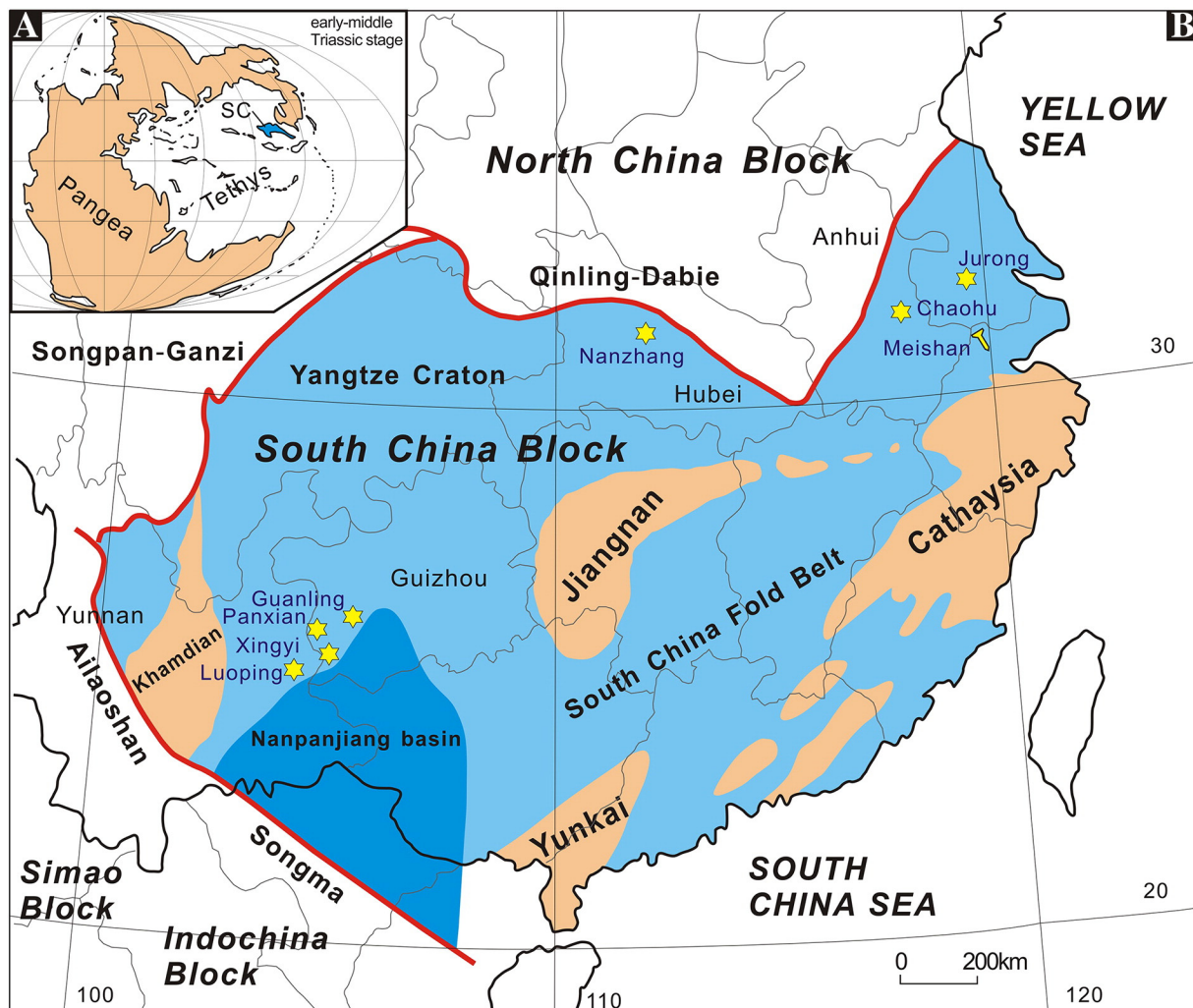
Fig. 1. Geology of South China in the Triassic. (A) General location of the South China Block in an Early–Late Triassic palaeogeographic map of the world. (B) Tectonic map illustrating major blocks of South China, interpreted suture zones and extent of the Nanpanjiang Basin and Yangtze Platform (= Craton), with sites of named localities and biotas (yellow stars). 'Old land' is brown, shallow seas pale blue, and deep marine basins dark blue.
A, From Ron Blakey, http://jan.ucc.nau.edu/~rcb7/globaltext2.html; B, with tectonic blocks modified from Sun et al. (1989) and palaeogeography from Liu and Xu (1994) and Lehrmann et al. (2009).

Triassic sediments are widely distributed in the South China Block (Fig. 1), and yet most of the exceptional biotas are located in eastern Yunnan and western Guizhou provinces, in the southwestern Yangtze Platform, between the Nanpanjiang Basin and the Yangtze Platform (Lehrmann et al., 2003, 2007), although some Early Triassic marine fish and reptile fossils have also been reported from other areas of the Yangtze Platform (see below). In order to determine the relative

and exact ages of these biotas it is not necessary to consider the stratigraphy of all successions across the larger series of basins in South China, so we focus on the portions of the basin that preserve fossil vertebrates.

The 1 km succession of Middle and Upper Triassic limestones and marls seen in eastern Yunnan and western Guizhou provinces has had a long history of study, dating back to the 1930s and 1940s. During
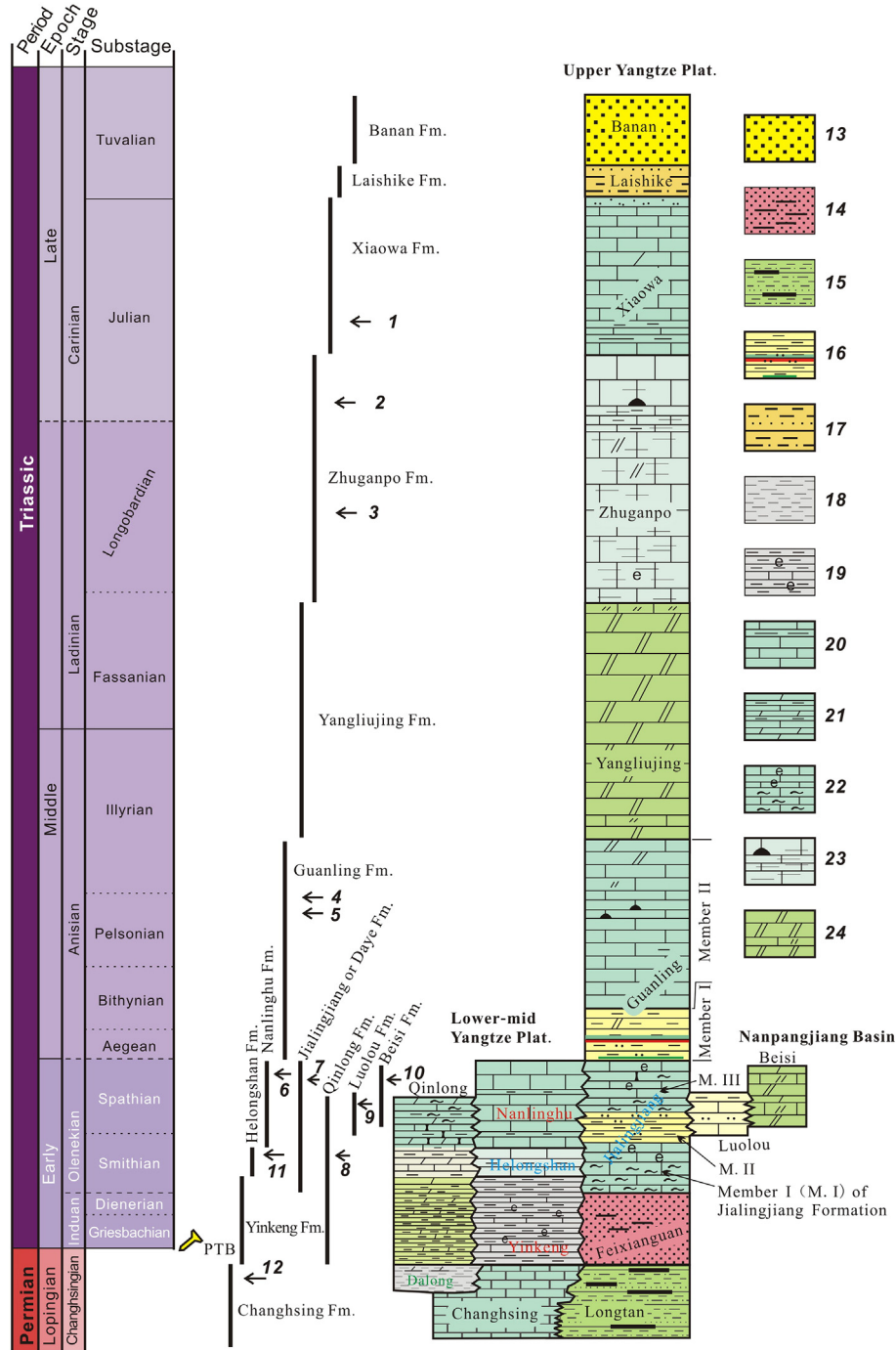
Fig. 2. Schematic stratigraphic column illustrating the Permian and Triassic formations of the Yangtze Platform. The different formations and biotas are dated according to biostratigraphy and radiometric dates, all compared with the international geological column. Numbered vertebrate-bearing units, from 1 to 12, are 1, Guanling biota; 2, Xingyi biota; 3, reptile layers below the Xingyi biota; 4, Panxian biota; 5, Luoping biota; 6, fishes and reptiles from the Nanlinghu Formation in Chaohu; 7, fishes from the Daye Group in Huangshi, and reptiles from the Jialingjiang Formation in Nanzhang and Yuanan, Hubei Province; 8, fishes from the Qinglong Formation in Jiangsu; 9, fishes from the upper Luolou Group in Guangxi Province; 10, reptiles from the Beisi Formation in Guangxi; 11, fishes from Helongshan Formation in Chaohu; 12, fishes from the upper Changhsing Formation in Meishan. Major lithologies, numbered 13–24, are 13, siliciclastics; 14, siliciclastics with mudstone; 15, siliciclastics with mudstone and coal; 16, mudstone, silt and fine sandstone with colourful mudstone and silt sandstone interbeded; 17, mudstone and silt sandstone with shale; 18, mudstone; 19, mudstone with limestone intercalated; 20, limestone with mudstone interbedded; 21, limestone and marl with mudstone interbedded; 22, worm limestone and limestone with bioclastics; 23, medium- and thick-bedded limestones with chert nodules and laminated or bedded; and 24, dolomite with dolomitic limestone interbedded.

Table 1
Summary of the vertebrate-bearing rock units of the Triassic of China. All these formations, except the Beisi, have yielded fish remains; those marked with * have also yielded reptiles. The four biotas, sites of exceptional fossil preservation are highlighted in bold. Note that most lithological units of the Yangtze Platform are diachronous, and the time range they represent varies from place to place. We give ages specific to the localities noted.

Formation	Locality	Province	Age
Yinkeng	Meishan	Zhejiang	Griesbachian (early–late)
Qinglong (upper lower)	Qingshan	Jiangsu	Griesbachian–Spathian
Qinglong (lower upper)	Simashan	Anhui	Spathian
Helongshan (upper)	Chaohu	Anhui	Smithian (late)
Nanlinghu (upper)*	Chaohu	Anhui	Spathian (late)
Jialingjiang (3rd Member)*	Huangshi	Hubei	Spathian (late)
Luolou (upper)	Fengshan/Tiandong	Guangxi	Spathian (early)
Beisi*	Wuming	Guangxi	Spathian (late)
Guanling (2nd Member)*	**Luoping**	Yunnan	Anisian (mid-Pelsonian)
Guanling (2nd Member)*	**Panxian**	Guizhou	Anisian (mid-Pelsonian)
Zhuganpo (upper)*	**Xingyi**	Guizhou	late Ladinian - early Carnian
Xiaowa (Lower Member)*	**Guanling**	Guizhou	Carnian (early)

that time, the nomenclature has evolved substantially, and we follow the current scheme, reviewed by Wang et al. (2008). Here (Fig. 2), there are 14 formations, some in the Early Triassic coeval with each other, but then five main fossiliferous formations that follow in sequence, with maximum thicknesses indicated: Guanling Formation (up to 2000 m, early–middle Anisian), Yangliujing Formation (490 m, upper Anisian–Ladinian), Zhuganpo Formation (75 m, upper Ladinian–lower Carnian), Xiaowa Formation (137 m, Carnian), and Laishike Formation (810 m, upper Carnian). These five formations may be traced for hundreds of kilometres across much of Guizhou and Yunnan provinces, showing matching successions and shared key biostratigraphic indicators, and boundaries between pairs of formations show that they succeed each other without major regional-scale gaps. Further, the validity of the biostratigraphic assignments and the lateral correlations are confirmed by a growing number of radiometric dates (e.g. Lehrmann et al., 2006; Ovtcharova et al., 2006; Galfetti et al., 2007).

The key vertebrate biotas occur in three formations, the Guanling Formation (Luoping and Panxian biotas), the Zhuganpo Formation (Xingyi biota), and the Xiaowa Formation (Guanling biota), which are dated as broadly Anisian, Ladinian–Carnian, and Carnian, respectively. Even though there are no fossil Lagerstätten from the Early Triassic (Induan and Olenekian stages) of South China, there are several fossiliferous localities of that age.

4.1. Early Triassic stratigraphy

Vertebrate remains, especially fishes, have been reported from many stratigraphic units across China, and these formations are noted in approximate stratigraphic sequence, starting with the PTB succession at Meishan. Because of the complexity of the nomenclature of stratigraphic units, and their estimated ages, these are summarised also in Table 1 and Fig. 2.

At Meishan, the global stratotype for the PTB, the well-exposed succession comprises the Changhsing and Yinkeng formations below and above, respectively (Fig. 3A). The basal Triassic Yinkeng Formation is
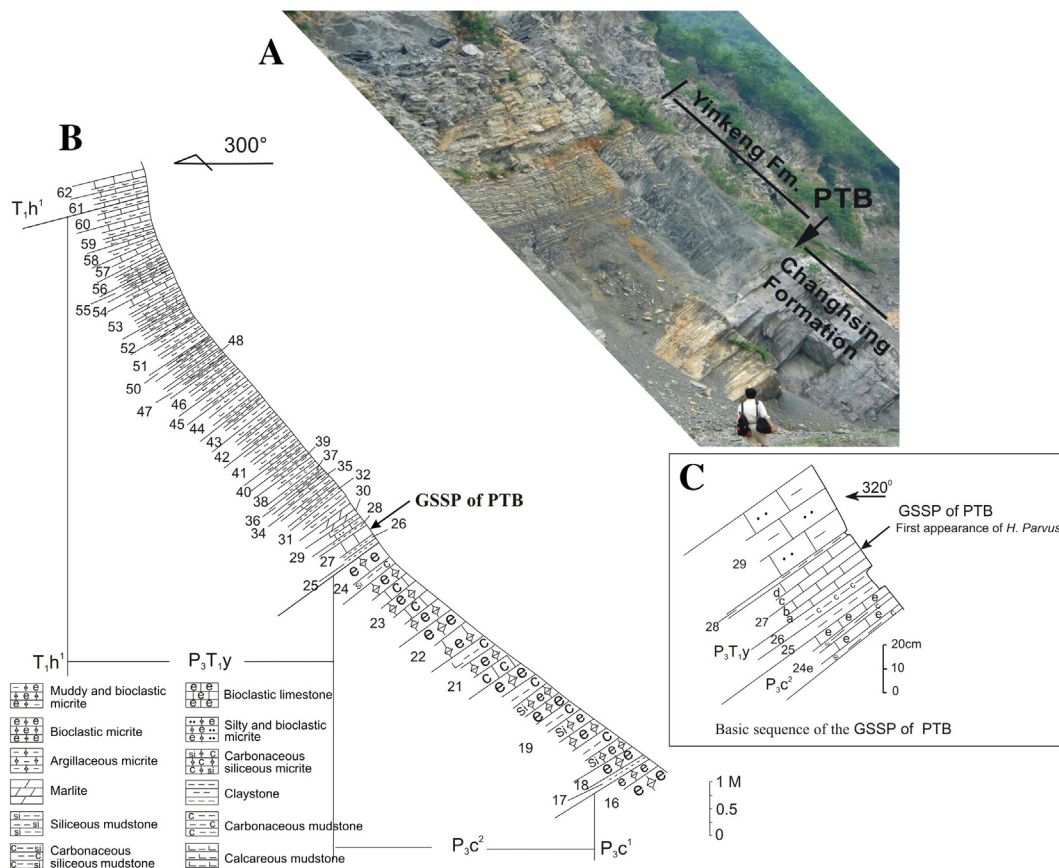
Fig. 3. The international stratotype of the Permo-Triassic boundary at Meishan, Zheijian Province. (A) Field photograph of the section across the boundary, showing the main geological formations. (B) Summary stratigraphic section, with standard bed numbering, with the PTB within bed 27, and the main mass extinction horizon within bed 25. (C) Detail of the section below and above the GSSP of the PTB. Abbreviations: GSSP, Global Stratotype Section and Point; PTB, Permo-Triassic boundary; P_3c^1, P_3c^2, Permian (upper), Changhsing Formation lower (1) and upper (2); P_3T_1y, Permian (upper), Triassic (lower), Yinkeng Formation; T_1h^1, Triassic (lower), Helongshang Formation, lower (1).
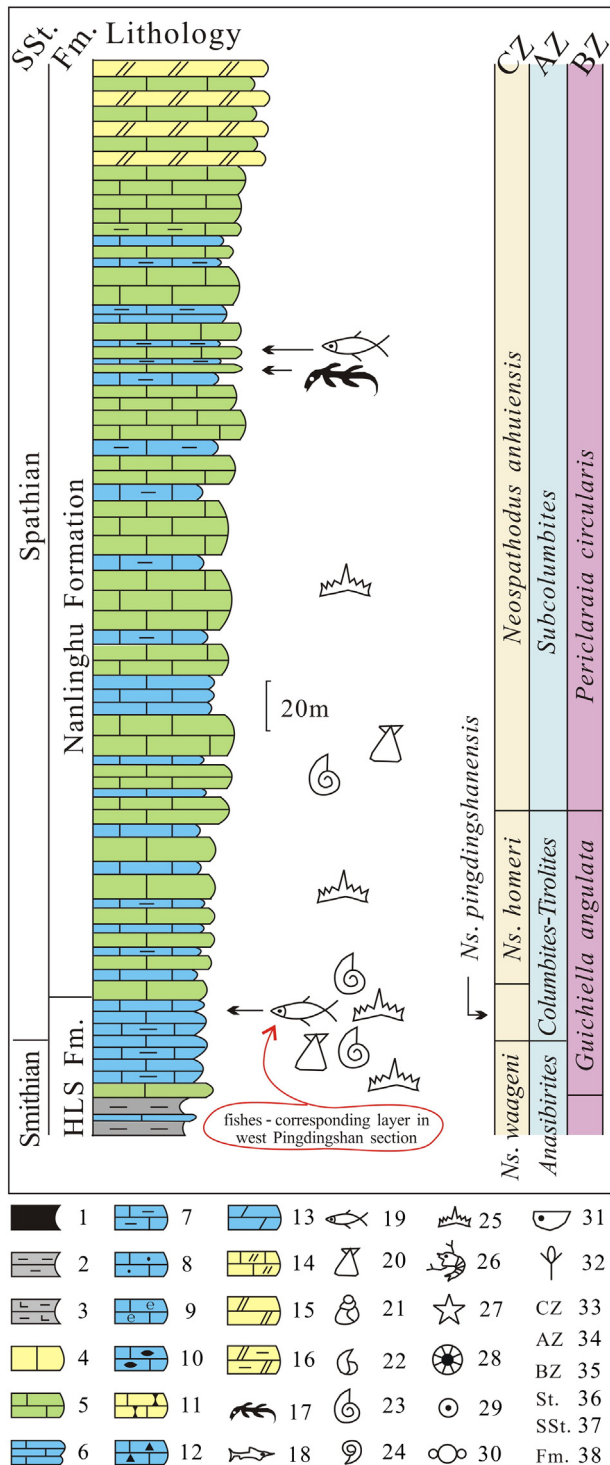
Fig. 4. Stratigraphic sections at the Majiashan and Pingdinshan sections at Chaohu, Anhui Province, showing the complete Early Triassic succession, and the vertebrate-bearing horizons in the late Spathian Nanlinghu Formation. Abbreviations: HLS, Helongshan; 1, bentonite; 2, mudstone; 3, calcareous mudstone; 4, thick limestone; 5, micritic limestone; 6, lamellar or thin limestone; 7, muddy limestone; 8, sandy limestone; 9, bioclastic limestone; 10, limestone intercalated with siliceous concretions; 11, nodular limestone; 12, limestone with bitumen; 13, marl; 14, dolomitic limestone; 15, dolomite; 16, muddy dolomite; 17, marine vertebrate; 18, ichthyosaur; 19, fish; 20, bivalve; 21, gastropod; 22, brachiopod; 23, ammonoid; 24, other cephalopod; 25, conodont; 26, arthropod; 27, star fish; 28, holothurian sclerites; 29, crinoid; 30, foraminifer; 31, ostracod; 32, plant fragments; 33, conodont zone; 34, ammonoid zone; 35, bivalve zone; 36, stage; 37, substage; 38. Formation. Modified from Chen et al. (2011). These symbols are used in this figure, and throughout the paper.

typified by alternating black shale, greenish grey mudstone, and grey marls in the lower part and interbeds of grey calcareous mudstone and pale muddy limestone in the upper part (Chen et al., 2002; Fig. 3A). This mudstone-dominated succession has been interpreted as the result of sedimentation in a relatively deep offshore setting (Wignall and Hallam, 1993; Z.Q. Chen et al., 2007). The finely laminated black shale and greenish grey mudstone of the lower Yinkeng Formation indicate anoxic sedimentation, while the marlstone or limestone of the upper Yinkeng Formation suggests a dysoxic environment (Wignall and Hallam, 1993). The combination of palaeontological, sedimentary and geochemical data reveals an increase in benthic biodiversity, an up-shallowing depositional cycle and sea floor changing from anoxic to oxygenated up-section (Z.Q. Chen et al., 2007). Apart from the *Hindeodus parvus* conodont zone, the *Isarcicella staeschei*, *I. isarcica* and *Neogondolella tulongensis–N. carinata* conodont zones are proposed for Beds 27d–28, Beds 29–51 and Beds 52–62, respectively (Fig. 3B).

Subsequent Early Triassic fishes are known from eight localities in South China. The most abundant and diverse Early Triassic fishes have been reported from the Qinglong Formation of Qingshan Quarry of Jurong City, Jiangsu Province (Figs. 1, 2). Here, the fossil fishes were collected from the black muddy limestone and calcareous mudstone, which belong to the upper part of the Lower Qinglong Formation (Liu et al., 2002a). The Qinglong Formation comprises alternating thin-bedded muddy limestone, calcareous mudstone and limestone, and is widely exposed in the Jurong area and adjacent Nanjing areas (Ming et al., 1981; Chen et al., 1988). Abundant ammonoids and bivalves are characteristic of the upper part of the Lower Qinglong Formation, and these were assigned to the *Anasibirites* Zone of late Smithian age (early Olenekian) by Chen et al. (1988). The age has been disputed, and the conodonts suggest a Dienerian age (Wang, 1991; Liu et al., 2002a). However, the Lower Qinglong Formation in Jiangsu is long and it is equivalent to both the Yinkeng Formation (Griesbachian to early Smithian) and Helongshan Formation (late Smithian) at Chaohu (see below; Chen et al., 2011). The fish-bearing strata at Jiangsu are identical to the lithology of the Helongshan Formation, which consists of dark grey or black mudstone and thin- to medium-bedded muddy limestone. They are very different from the lower part of the Lower Qinglong Formation, which comprises an alternation of thin-bedded greenish or yellowish mudstone and thin-bedded muddy limestone (sometimes calcareous mudstone with uneven calcareous nodules). Thus, the fish horizons are definitely in the upper part of the Lower Qinglong Formation, and equivalent to the Helongshan Formation. For the present, the Smithian (likely late Smithian) age assignment is most probable for the fish-bearing beds in the upper Lower Qinglong Formation of Jiangsu.

The Upper Qinglong Formation was assigned to the Spathian (late Olenekian) based on the presence of the *Neospathodus homeri* conodont zone and the *Columbites* ammonoid zone (Chen et al., 1988). Another fish assemblage has been reported from the lower part of the Upper Qinglong Formation at Simashan in Hexian, about 50 km east of Chaohu city, Anhui Province (Su, 1981). The Hexian fish assemblage is therefore also Spathian (late Olenekian) in age.

The famous fish and reptile assemblage from the Lower Triassic of the Chaohu area, Anhui Province, South China (Figs. 1, 4; Tong et al., 2006) comes from the extensive exposures on the Pingdingshan and Majiashan hills. There are three formations, in ascending order, the Yinkeng, Helongshan and Nanlinghu (Figs. 2, 4), spanning from the base of the Triassic (Griesbachian) to late Spathian. The bony fish assemblage was derived from the muddy limestone and calcareous mudstone of the upper Helongshan Formation in the Pingdingshan–Majiashan sections. In addition, Chen (1985) reported that some *Saurichthys* coexisted with ichthyosaurs from the upper Nanlinghu Formation in the southern Majiashan section of the same area.

In the Pingdingshan section (Fig. 4), the Yinkeng Formation, as at Meishan, comprises greenish/black shale interbedded with marlstone (Beds 3–37). Lower portions are dated as Griesbachian by the *Hindeodus typicalis* and *Neogondolella krystyni* conodont zones, the

Ophiceras–Lytophiceras ammonoid zone, and the *Claraia stachei–C. aurita* bivalve assemblage (Tong et al., 2003, 2004; Zhao et al., 2007; L.S. Zhao et al., 2008; Chen et al., 2010). Upper portions of the Yinkeng Formation are dated as Dienerian by the *Neospathodus kummeli* and *Ns. dieneri* conodont zones, the *Prionolobus–Gyronites* ammonoid zone, and the lower part of the *Eumorphotis inaequicostata–E. huancangensis* bivalve assemblage (Tong et al., 2004; Zhao et al., 2007; L.S. Zhao et al., 2008).

The Helongshan Formation in the Pingdingshan section (Fig. 4) is characterised by thin-bedded dolomitic limestone interbedded with calcareous mudstone (Beds 38–53), and dated as Smithian by the *Ns. waageni ecowaageni* and *Ns. waageni waageni* conodont zones and the *Flemingites–Euflemingites* and *Anasibirites* ammonoid zones. The overlying Nanlinghu Formation (Chen et al., 2011), comprising medium-bedded limestone interbedded with mudstone (Beds 54–58) is dated as lower Spathian by the *Ns. pingdingshanensis* and *Ns. homeri* conodont zones and the *Columbites–Tirolites* ammonoid zone (Tong et al., 2003, 2004; Zhao et al., 2007; L.S. Zhao et al., 2008).

The complete Spathian sequence is exposed in the southern Majiashan section (Fig. 4), where the Helongshan and lower Nanlinghu formations correlate well with their counterparts in the West Pingdingshan section. Apart from the *Ns. pingdingshanensis* and *Ns. homeri* conodont zones, the *Ns. anhuiensis* zone was also established for the Nanlinghu Formation (Zhao et al., 2007). The *Columbites–Tirolites* and *Subcolumbites* ammonoid zones are also present in Majiashan (Tong et al., 2004; Zhao et al., 2007; Chen et al., 2011). These biozones constrain the Nanlinghu Formation as Spathian in age (Tong et al., 2003, 2004). As a result, the Helongshan fish assemblage from Chaohu is late Smithian to early Spathian in age, while the Nanlinghu fish and reptile assemblage is late Spathian in age.

Zhangia yangtzensis (Su and Li, 1983) has been described from the 4th division of the Daye Group of Huangshi City, Hubei Province. This stratigraphical unit has been re-assigned to the Jialingjiang Formation, which is equivalent to the Nanlinghu Formation of the Anhui Province (Tong, 2005). Thus, the Huangshi fish assemblage is Spathian (late Olenekian) in age.

Lower Triassic fishes have also been reported from the upper Luolou Group of the Fengshan and Tiandong areas, Guangxi Province (Liu, 1964; Yang et al., 1984; Wang et al., 2001), and these were dated locally as early Spathian (Wang et al., 2001).

Reptiles are reported from the marine beds of South China from three localities dated as late Spathian. *Chaohusaurus geishanensis* was described from the Nanlinghu Formation of the Chaohu area, Anhui Province (Young and Dong, 1972; Fig. 4). A relatively diverse reptile assemblage has been described from the Lower Triassic of the Nanchang and Yuanan counties of western Hubei Province (Wang, 1959; Young, 1965a,b; 1972a,b; Carroll and Dong, 1991; Rieppel, 1998a,b; Wu et al., 2003). Their detailed fossil horizons however have long been disputed (Wang, 1959; Young and Dong, 1972; Carroll and Dong, 1991). Li et al. (2002a) re-investigated these fossil localities in western Hubei and clarified that these Hubei reptiles were derived from the upper Daye/lower Jialingjiang formations, the latter of which comprises three members. Of these, the third member is characterised by alternating thin-bedded muddy limestone, oolitic limestone and bioclastic limestone and contains conodonts from the *Neospathodus triangularis–N. homeri* Zone and ammonoids of the *Tirolites* Zone, and thus is equivalent to the upper Nanlinghu Formation of late Spathian (late Olenekian) age (Tong, 2005).

A Lower Triassic reptile has also been reported from the Beisi Formation of the Wuming area of Laibin City, Guangxi Province (Young, 1959). The Beisi Formation (Fig. 1) is 300 m thick and comprises alternations of dolomite, dolomitic limestone and thin-bedded muddy limestone. Its upper part is characterised by the presence of the ammonoid *Tirolites* sp. and thus is assigned to the late Spathian (late Olenekian) (Lehrmann et al., 2007).

4.2. Middle Triassic stratigraphy

The Guanling Formation (Fig. 2) follows conformably above the Jialingjiang Formation, and comprises carbonates and clastic rocks. It is subdivided into two members (thicknesses refer to the type area). The first member is 333 m thick, and consists of calcareous silty mudstone and mudstone intercalated with muddy dolomite, interpreted to reflect a transition from restricted-evaporitic tidal flat to shallow marine facies. A coarse-grained volcanic ash bed (green pisolite) is seen at the base. The second member is a 580-m-thick succession composed of dark nodular micritic limestone, muddy limestone and cherty micritic limestone with bands of dolomite. The overlying Yangliujing Formation comprises 1204 m of peritidal facies dolostone and dolomitic limestone intercalated with limestone breccias that are

Fig. 5. The Middle Triassic Guanling Formation (second member) at Daaozi, south of the county seat of Luoping, source of the Luoping biota. The quarry was excavated systematically by members of the Chengdu Institute of Geology and Mineral Resources, led by QYZ.

characterised by pseudomorphs of gypsum- and evaporite-solution breccias.

The Luoping biota (Zhang et al., 2008, 2009; Hu et al., 2011) occurs in the middle part of the second Member of the Guanling Formation over a wide area in eastern Yunnan (Figs. 1, 2), but the best occurrences (Fig. 5) are near the village of Daaozi (= Dawazi), in a 16-m-thick succession of richly fossiliferous beds, delimited at the bottom and top by bioturbated limestone and silty limestone, respectively. The fossiliferous horizons consist mainly of thinly laminated micritic limestone alternating with thin- to moderately thick-bedded silty limestone. Lower units (Beds 2–66) are dark grey, medium- to thick-bedded, laminated micritic limestones with siliceous concretions (Fig. 6). A 40-mm-thick light grey claystone (Bed 15) and a 5-cm-thick grey-yellow, thin-bedded silty mudstone (Bed 24) are pronounced in the lower units. A highly diverse fish assemblage has been recovered mainly from Beds 33 and 44. Most saurichthyid fish fossils

Fig. 6. Sedimentary log through the through part of Member II of the Guanling Formation containing the Luoping biota, at the Daaozi locality, showing lithologies, sedimentary structures, and key fossiliferous beds. Lithologies and symbols explained in caption of Fig. 4.
Modified from Hu et al. (2011).

are found in Bed 48. Beds 57 and 61 yield marine reptiles, associated with shrimps, crinoids, and plant fossils. These units are followed by a 1.4-m-thick succession of dark grey medium- to thick-bedded nodular limestone intercalated with cherty concretions (Beds 67–74). The overlying 2.9 m of dark-grey to yellowish-grey laminated muddy limestone (Beds 75–110) contains rare siliceous concretions. Numerous marine reptiles along with rare shrimps occur in Beds 78–81 and 106 (Fig. 6).

The Luoping biota (Figs. 7, 8) is extensive and spectacular, including arthropods as the commonest fossils, followed by fishes, marine reptiles, bivalves, gastropods, echinoderms, brachiopods, conodonts, foraminifers, and plants. Recent finds include millipedes, cycloids, belemnoids with preserved arm hooks, hydromedusae, ammonoids, and lingulid brachiopods. So far, nearly 20,000 individual macrofossils have been identified from the Luoping biota in its main location (Fig. 5). Arthropods dominate by far, comprising over 90% of the fauna, followed by fishes (4%), then bivalves (2%), and then relatively tiny proportions (<1%) of plants, gastropods, marine reptiles, and others (Hu et al., 2011). The dominant arthropods include remarkable materials of crustaceans, millipedes, and horseshoe crabs (Fig. 7). The majority are crustaceans, including decapods (lobsters and shrimps), isopods, cycloids, mysidiaceans, conchostracans, and ostracods. In restoration (Fig. 8), fishes dominate, with medium-sized marine reptiles of all major clades.

The highly fossiliferous, dark-coloured micritic limestones of the second member of the Guanling Formation, as seen at Daaozi (Figs. 5, 6), have been traced in detail over an area of some 200 km² through the regional mapping programme of the Chengdu Institute of Geological and Mineral Resources. Outside the Luoping area, the second member of the Guanling Formation consists of the bioturbated, pale-coloured micritic limestones seen in the basal and top members at Luoping. This is interpreted to suggest that the Luoping biota is preserved within a semi-enclosed intraplatform basin, showing some anoxia, whereas more typical, well-oxygenated contemporaneous sediments were being deposited at the same time around the edges of this semi-enclosed basin.

Abundant conodonts found in association with the Luoping biota were assigned to the *Nicoraella kockeli* Zone (Zhang et al., 2009), characteristic of the Pelsonian Substage of the Anisian Stage (Middle Triassic) (Kozur, 2003). Preliminary radiometric dating (ZQC, unpublished), confirms this date.

The Panxian biota (Motani et al., 2008; Jiang et al., 2009) also occurs in the Guanling Formation, but in the upper part of Member II, and it is slightly younger than the Luoping biota. The fossils were found first at Yangjuan Village, Xinmin District, Panxian County, where the second member of the Guanling Formation is well exposed (Fig. 9). This unit consists of grey to dark grey, thin- and medium-bedded to massive, marly limestones and limestones with muddy bands and chert concretions intercalated with dolomitic limestone and bentonite layers.

Motani et al. (2008) noted that fish and reptile specimens had been collected around Panxian by professionals and amateurs over many years, and exact horizons were rarely recorded. These workers carried out bed-by-bed excavations in 2006, and were able to log four stratigraphic sections, and record the exact horizons of individual fossil finds (Fig. 9). There are two stratigraphic terminologies, a system of bed numbers, from Cy29 to Cy0 (Sun et al., 2006), and a system of numbered horizons from 0 to 100+ (Motani et al., 2008; Jiang et al., 2009): we indicate equivalents in both systems.

The lower part of the succession (Fig. 9) consists of 35 m of interbedded limestones and marls, with occasional finer-grained and bentonitic clay bands, termed Beds Cy29–Cy14. These include limestones with chert, dolomitic limestones, and limestones with oncolites that probably match those at Luoping, and these confirm lithostratigraphically that the Panxian biota is younger than the Luoping biota, with the age difference represented by some 50 m of limestone accumulation (QYZ, unpublished).
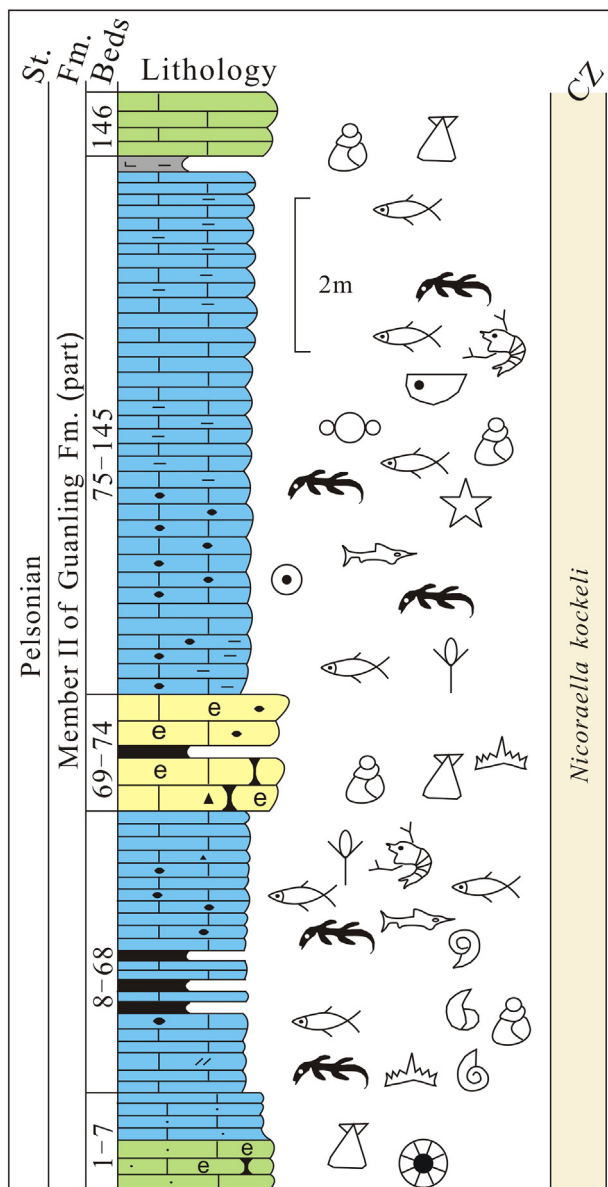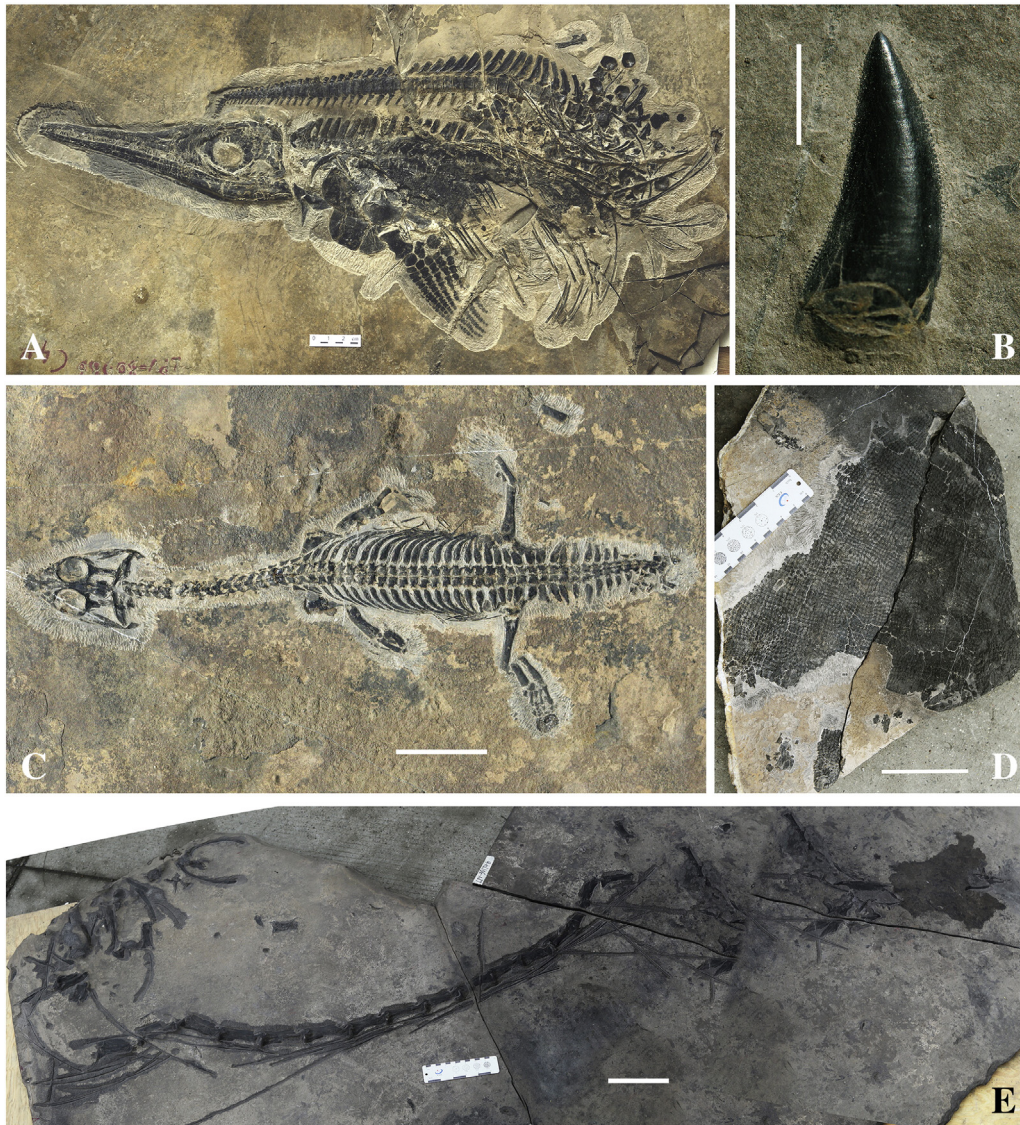
Fig. 7. Reptiles from the Luoping biota. (A) *Mixosaurus* cf. *panxianensis*. (B) Tooth of archosaur; note serrated margin. (C) *Dianopachysaurus dingi*. (D) *Sinosaurosphargis yunguiensis*. (E) *Dinocephalosaurus* sp. Scales in A, B, C are 4 cm, 0.5 cm and 2 mm, respectively; scales in D and E, are 10 cm.

The vertebrate-bearing portion of the section, layers 77–100 (Beds Cy13–10) is only 5 m thick, but comprises 23 distinguishable layers, and these are described in more detail, highlighting the finds of fishes and reptiles, by Motani et al. (2008) and Jiang et al. (2009). Traditionally, the Panxian locality is said to have three reptile horizons, a lower, middle and upper. There are in fact eight vertebrate-bearing beds (Motani et al., 2008), and these have previously been lumped as follows: Lower Reptile Horizon (layers 77 and 79), Middle Reptile Horizon (layers 81, 84, 85), and Upper Reptile Horizon (layers 87, 89, 90).

Layers 77–78 (Bed Cy13) consist of a lower unit of grey, medium-bedded limestone, 0.2–0.3 m thick (layer 77), the source of numerous marine reptiles, including the mixosaurid ichthyosaurs *Phalarodon* cf. *fraasi* and *Mixosaurus panxianensis*, the primitive ichthyosaur *Xinminosaurus catactes*, the placodont *Placodus inexpectatus*, and the nothosaur *Lariosaurus hongguoensis*, together with a rich bivalve fauna (Jiang et al., 2009). Overlying layer 78 is 0.05–0.10 m of dark grey, thin-bedded limestone.

Layers 79–87 (Bed Cy12) have yielded marine vertebrate fossils at five levels. The basal unit, layer 79, consists of 0.20–0.29 m of grey, medium-bedded limestone that has apparently yielded the same fauna as layer 77, according to Jiang et al. (2009, p. 454): the mixosaurid ichthyosaurs *P*. cf. *fraasi* and *M. panxianensis*, the primitive ichthyosaur *X. catactes*, the placodont *P. inexpectatus*, and the nothosaur *L. hongguoensis*, together with a rich fauna of small bivalves. Overlying layer 80 is 0.005–0.015 m of reddish-yellow-coloured bentonite.

The next horizon, layer 81, consists of a further 0.36–0.40 m of grey, medium-bedded limestone that has yielded the nothosaurid *Nothosaurus yangjuanensis* and the crurotarsan archosaur *Qianosuchus mixtus*, as well as the mixosaurid ichthyosaur *M. panxianensis*. This is overlain by layer 82, 0.17–0.20 m of black-grey, laminated, marly limestone, and layer 83, 0.11–0.15 m of black-grey, thin-bedded limestone.

Three vertebrate-bearing horizons occur in close succession in layers 84–87 (Bed Cy12). The third, layer 84, consists of 0.05–0.15 m of black-grey, laminated marly limestone, the source of abundant and complete skeletons of saurichthyid and other actinopterygian fishes, and the mixosaurid *M. panxianensis*. This is overlain by the fourth vertebrate-bearing horizon, layer 85, 0.15–0.18 m of black-grey, thin- to medium-bedded limestone with a few muddy bands that have
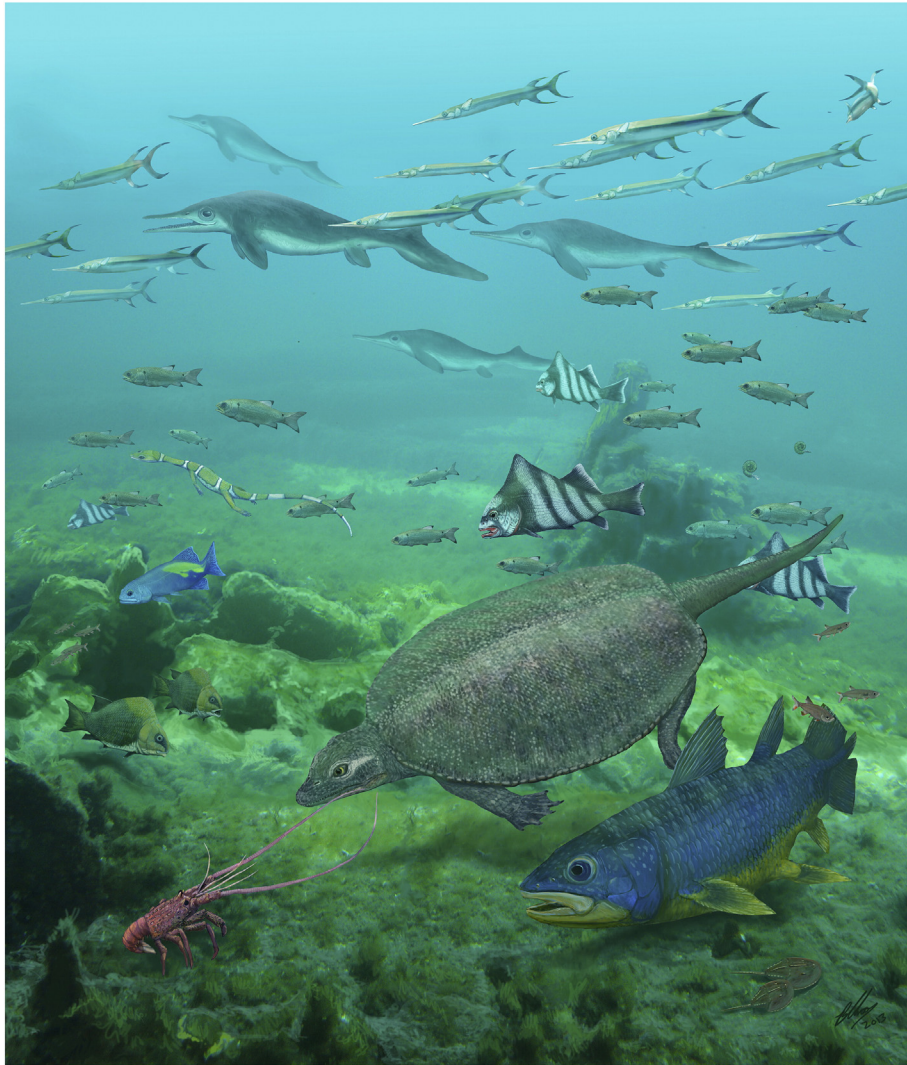
Fig. 8. Lobster lunch of Luoping; over a muddy seabed during the Middle Triassic (Ansian) at the future site of Luoping County, Yunnan. In the foreground, an early rock lobster (*Yunnanopalinura schrami*) attracts the unwanted attention of the coelacanth *Luopingcoelacanthus eurylacrimalis* and the armoured reptile *Sinosaurosphargis yunguiensis*, allowing a pair of horseshoe crabs (*Yunnanolimulus luopingensis*) to scuttle away unnoticed. Behind them cruise other aquatic reptiles: the ichthyosaurs *Mixosaurus* cf. *panxianensis* and the little pachypleurosaur *Dianopachysaurus dingi*. Swarming around is a diverse community of actinopterygians: ubiquitous *Sangiorgioichthys sui* (numerous fish with black-tipped fins), sleek *Sinosaurichthys longimedialis* (thin with long snout), tiny *Marcopoloichthys ani* (very small with red-spotted fins), scaleless *Gymnoichthys inopinatus* (blue with yellow back) and the deep-bodied *Kyphosichthys grandei* (brown and yellow) and *Luoxiongichthys hyperdorsalis* (black and white). Painting by Brian Choo © 2013.

yielded the nothosaurid *N. yangjuanensis* and the archosaur *Q. mixtus*, together with the seemingly ubiquitous mixosaurid ichthyosaur *M. panxianensis*. Layer 86 comprises 0.005–0.012 m of yellow-coloured bentonite, overlain by layer 87, the fifth vertebrate-bearing horizon, 0.14–0.16 m of dark grey, thin- to medium-bedded marly limestone with muddy bands, and the source of abundant skeletons of the mixosaurid *M. panxianensis* and fragmentary fossil fish remains, as well as remains of the pachypleurosaurs *Keichousaurus* sp. and *Wumengosaurus delicatomandibularis*.

The overlying layer 88 (Bed Cy11) consists of one layer only, 0.05–0.10 m of yellowish white-coloured bentonite, followed by layers 89–100 (Bed Cy 10). The basal unit, layer 89, is 0.07–0.14 m of grey, laminated marly limestone, source of remains of the mixosaurid *M. panxianensis*. The overlying layer 90, 0.12–0.16 m of light reddish-grey, thin-bedded limestone, was the source of the prolacertiform *Dinocephalosaurus orientalis* (Motani et al., 2008). Layer 91 above is 0.2–0.3 m of reddish-grey, thin-bedded dolomitic limestone, and layers 92–100 consist of 0.6–0.8 m of interbedded grey and light grey, thin-bedded dolomitic limestones.

The remainder of the Panxian section (Fig. 9) is 50 m of predominantly marly limestone, with units of limestone with chert and dolostone, but without reported vertebrate fossils (Jiang et al., 2009).

Apart from the fish and reptile fossils, the Panxian biota includes brachiopods, bivalves, and ostracods, but none of the other arthropod groups, including the abundant crustaceans, that have been found at Luoping.

The Panxian succession has yielded the conodonts *Nicoraella germanicus* (Beds Cy29–22), *N. kockeli* (Beds Cy6–21), *Paragondolella bifurata* (Beds Cy2 (bottom)–5), and *Neogondolella constricta* (Beds Cy0–2 (top)) (Jiang et al., 2009). These identify a complete Anisian succession, from Bithynian at the base to Illyrian at the top of the sequence, but the fossil vertebrates come from the middle of the Pelsonian succession (Member II of the Guanling Formation), just slightly younger than the Luoping biota. Sun et al. (2006) established that the Upper Member of the Guanling Formation that is exposed in the area corresponds to the Anisian (Bithynian to Illyrian). They also indicated that reptile beds were found in their Cy12 and 13, where the conodonts *N. kockeli* and *N. germanicus* coexisted. The horizon
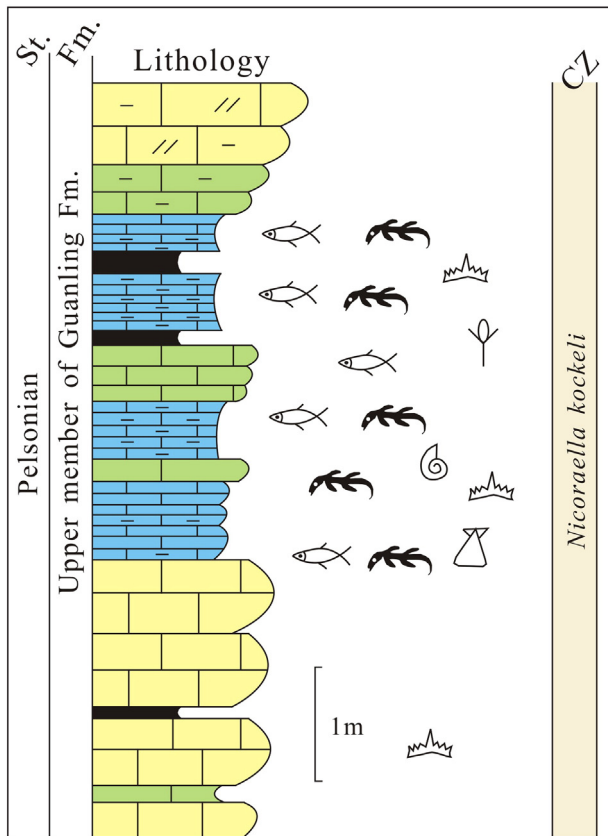
Fig. 9. Sedimentary log through the interval containing the Panxian biota in the Guanling Formation near Xinmin, Guizhou Province, showing the vertebrate-bearing horizons of the Panxian biota.

corresponds to the lower part of the *kockeli* Zone, and therefore represents the middle Pelsonian (Sun et al., 2006).

4.3. Latest Middle Triassic to early Late Triassic stratigraphy

There has been some confusion in defining fossil vertebrate occurrences higher in the Middle Triassic, namely those from the Yangliujing and Zhuganpo Formations (Fig. 2), and the stratigraphy requires further work. Some of the first finds were reported from the Yangliujing Formation, and similar, and sometimes identical, taxa have also been identified from the overlying Zhuganpo Formation, and these are assigned to the Xingyi biota.

Liu et al. (2002c) reported the marine reptile *Dingxiaosaurus luyinensis* from the upper Yangliujing Formation of the Dingxiao area, Xingyi, Guizhou Province. As mentioned by Liu et al. (2002c), the layer with *D. luyinensis* is from the upper part of the Yangliujing Formation, which is dominated by dolomitic limestone, lithologically different from the massive dolomite of the lower part below the fossil layer (Fig. 2). Sun et al. (2005b,c) also reported a thalattosaur and a lariosaur from the upper part of the Gejiu Formation at Niubudai Village, Banqiao Town, Luoping County. The layer containing the reptiles is composed of slightly grey, thin bedded, well-laminated dolomitic limestone, just 20 m below the layer with abundant *K. hui*. Our field examination of the two localities confirmed that both the layers with *D. luyinensis* from Xingyi and the thalattosaur and lariosaur from Luoping should be assigned to the lower part of the Zhuganpo Formation. As suggested by Chen and Wang (2009), the definition of the Yangliujing Formation should be constrained to the massive dolomites, and exclude the overlying laminated dolomitic limestone. Chen and Wang (2009) reported abundant conodonts from dolomites in the lower part of the Yangliujing Formation and detected the *N. constricta cornuta–N. constricta postcornuta* conodont evolutionary lineage.

These authors placed the Anisian–Ladinian boundary in the lower part of the Yangliujing Formation. Accordingly, the Dingxiao reptile assemblage is middle to late Ladinian in age, older than the Xingyi biota.

The Xingyi biota comes from the upper part of the Zhuganpo Formation in the Dingxiao and Wusha districts of Xingyi City in Guizhou Province, as well as the Banqiao (Changdi) district of Luoping County and Jiyangshan in Fuyuan County, Yunnan Province (Fig. 1). The fossils occur in a set of dark grey laminated muddy limestones, exposed in various shallow quarries around the city. The Zhuganpo Formation is c. 75 m thick in its type area, between the villages of Zhuganpo and Wayao, about 4 km southwest of the town of Yongning, and it is chiefly composed of grey and dark grey medium- and thick-bedded argillaceous limestones, marlites, bioclastic limestones, dolomitic limestones and siliceous mudstones (Figs. 2, 10).

The fossils are preserved in dark grey thin-bedded marlites and argillaceous limestones near the top of the unit. Many bedding planes of the laminated muddy limestone are densely covered with bivalves and ammonites, including the bedding plane that yields the reptilian skeletons. Fossils include marine reptiles (*K. hui* Young, 1958; *Glyphoderma kangi* Zhao et al., 2008a; *Nothosaurus youngi* Li and Rieppel, 2004; *Lariosaurus xingyiensis* Li et al., 2002b; *Yunguisaurus liae* Cheng et al., 2006b; *Anshunsaurus wushaensis* Rieppel et al., 2006; see also Young and Dong, 1972; Chen, 1985), the shrimp *Schimperella acanthocercus* Taylor et al., 2001, the bivalves *Daonella* (Gu et al., 1976), ammonites (*Protrachyceras* sp.; Wang et al., 1998), crinoids (*Traumatocrinus hsui*; Mu et al., 1949), fishes (*Sinoeugnathus kueichowensis* Su, 1959, *Peltopleurus orientalis* Su, 1959, and *Asialepidotus shingyiensis*; Su, 1959), conodonts (*Paragondolella polygnathiformis*, *P. foliata*, *P. navicula*, *P. inclinata*, and *P. maantangensis*; Tian et al., 1983), and autochthonous plant remains. Together, these provide rich information on the marine ecosystem (Fig. 11).
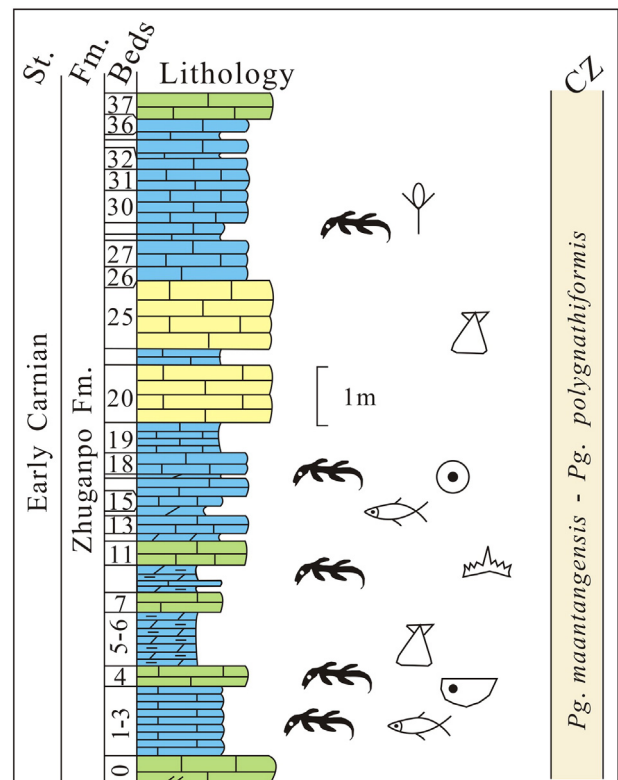

Fig. 10. Stratigraphy of the interval containing the Xingyi biota in the Zhuganpo Frmation at Nimaigu village, near Wusha town, about 15 km north-west of Xingyi, Guizhou Province, showing the location of the vertebrate-bearing layers. Bed numbers after Wang et al. (1998).

Fig. 11. Keichosaur killer of Xingyi; on a shallow reef in the latest Middle Triassic (Ladinian) of Xingyi, Guizhou. The deadly *Nothosaurus youngi* grabs its smaller relative, the abundant *Keichousaurus hui*, ducking beneath the incredible neck of *Tanystropheus* cf. *longobardicus* to do so. Other reef denizens flee in terror: swarms of shrimps (*Schimperella acanthocercus*) and the fishes *Peltopleurus orientalis* (numerous small brown fishes), *Guizhoubrachysoma minor* (short blue), *Guizhouamia bellula* (slender with orange stripe) and *Asialepidotus shingyiensis* (brown with vertical bands). Ammonoids (*Protrachyceras* sp.) and the wing-finned *Potanichthys xingyiensis* hover unconcerned in the surface waters. Large open-water predators cruise in the distance: the serpentine *Anshunsaurus wushaensis* and a pair of long-necked *Yunguisaurus liae*. Painting by Brian Choo © 2013.

The age of the Zhuganpo Formation, and the Xingyi biota, has been debated. It has been said to be entirely Middle Triassic or entirely Carnian, but we prefer an age range from late Ladinian to early Carnian. Earlier work that focused on bivalves and ammonites had suggested an early Ladinian age (Zhao et al., 1982; Wang and Duan, 1990; Wang et al., 1998). On the other hand, the conodonts all suggest a Carnian age: *Metapolygnathus polygnathiformis* is found in the lower Upper Zhuganpo Formation (Sun et al., 2005a), together with *Metapolygnathus navicula*, *M. foliata inclinata* and *M. parafoliata* (Chen and Wang, 2002; Wang et al., 2003a). *Metapolygnathus nodosus* occurs in the uppermost Zhuganpo Formation together with the above-mentioned conodonts of the *M. polygnathiformis* Zone, and ranges up into the Xiaowa Formation. These conodonts are all typical of the early Carnian, confirming wider studies of the upper Zhuganpo Formation (Wang et al., 1998; Lehrmann et al., 2005; Wang et al., 2008).

The Guanling biota has perhaps been most studied of the various South Chinese Triassic marine vertebrate assemblages, with fossil finds of giant crinoids dating back to 1940 (Wang et al., 2008). Fossil localities yielding the Guanling biota are distributed in the border

area between Yunnan and Guizhou provinces, about 160 km south-west of Guiyang and 40 km south-west of Guanling, seat of Guanling County, and covers an area of at least 200 km^2 (Fig. 12A). The best exposures, where most discoveries have been made, are located in Guanling County at Wolonggang (Lying Dragon Hill) near the village of Xiaowa, along the small creek, Shiao He, downstream of the village of Bamaolin near the town of Xinpu, at the villages of Maowa, Huangtutang and Zhuganpo, at the village of Baiyan near the town of Gangwu, and at the village of Liangshui in adjacent Qinglong County.

The fossils come from the Xiaowa Formation (formerly Wayao Member of the Falang Formation), a succession of 140 m of carbonates and marls, all of Carnian age (Xu et al., 2003). The fossils occur in the Lower Member of the Xiaowa Formation, often termed the 'Lower Xiaowa Formation' (Fig. 12B), which is exposed in a large number of quarries operated by local farmers for fossil collecting.

The Lower Member of the Xiaowa Formation is 12 m thick, and can be subdivided into two units (Fig. 12B; Wang et al., 2008). The lower, 5-m-thick unit consists of medium- to thick-bedded, grey bioclastic micrites with yellow-green shale interbeds. The micrites
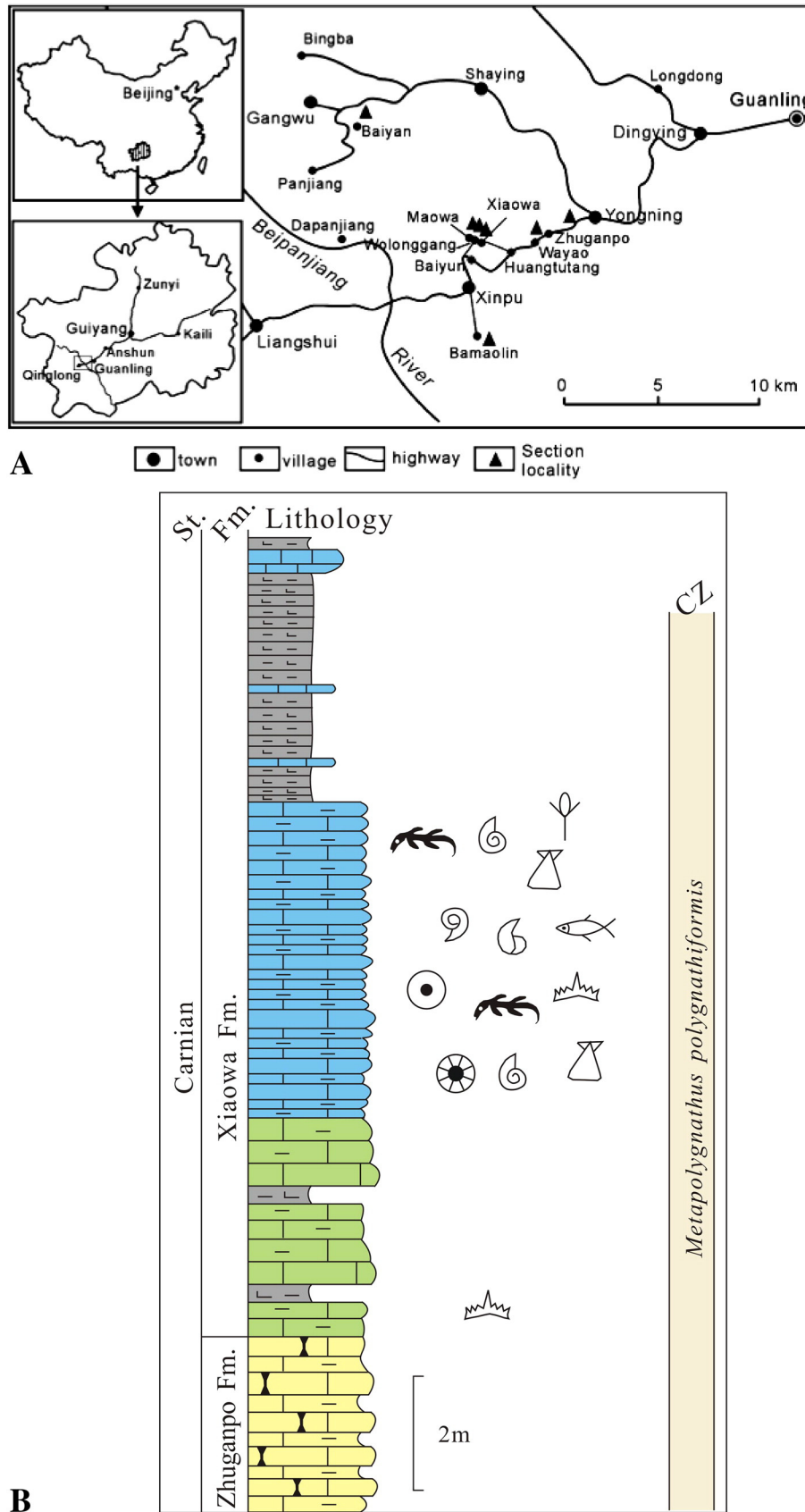
Fig. 12. Occurrence of the Zhuganpo Formation and Xiaowa Formation sections at Guanling, Guizhou Province, containing the Guanling biota. (A) Map showing the main fossiliferous localities. (B) Section showing the location of the vertebrate-bearing layers.
Modified from Wang et al. (2008, 2009).

commonly have sharp bases and pass upwards gradationally into dm-thick grey to dark grey laminated marlstones. The limestones are generally either biopelmicrites or biomicrites containing rare marine reptiles. Isolated *Traumatocrinus* ossicles and the bivalves *Halobia subcomata* and *Daonella bifurcata* are abundant. The conodonts *M. nodosus* and *M. polygnathiformis* are relatively rare. Ammonoids include *Protrachyceras deprati*, *P. costulatum*, *P.* cf. *douvillei* and *Clionites* cf. *zeilleri*, which are mainly found in the lowermost 3 m of the formation. Other fossils found are ostracods and diverse elasmobranch ichthyoliths (Chen and Cuny, 2003). The depositional environment of the limestones was quiet and deeper than during deposition of the Zhuganpo Formation, but still with generally oxygenated bottom waters. The interbedded, dark grey, laminated marlstones are thought to represent times of more reduced oxygenation and carbonate productivity (Wang et al., 2008).

The upper unit is 7 m thick and consists of greyish to black, thin- to medium-bedded laminated mudstone with argillaceous limestone interbeds containing crinoids (Fig. 11). It begins with c. 1 m of thick-bedded, dark grey, marly, laminated micritic limestones. Most of the well-preserved articulated marine vertebrate and *Traumatocrinus* skeletons and the driftwood logs for which the biota is famous occur on the bedding planes. The next 2 m are characterised by conspicuously dark grey to black shaly marlstones and marly shales that are rich in *Halobia* and *Daonella*, and the ammonoids *Trachyceras multituberculatum*, *T.* cf. *aon*, *Paratrachyceras* cf. *hofmanni*, *P. douvillei* and *Hauerites* cf. *himalayanus*. The uppermost 3.5–4 m of the upper unit of the Lower Member consist of dark grey laminated marlstones with the conodonts *M. nodosus* and *M. polygnathiformis*. The upper unit represents anoxic conditions with much reduced carbonate productivity. The black shaly interval seems to represent the greatest water depth.

The Middle Member of the Xiaowa Formation is separated by a sharp boundary from the Lower Member (Fig. 12). It is c. 140 m thick and consists of medium- to thick-bedded, laminated, grey limestones interbedded with medium to thick grey laminated marlstones. The lamination is highlighted by thin layers of quartz silt. The basal part of the unit frequently shows synsedimentary slumping.

Fig. 13. Among the floating lily fields of Guanling; Guanling, Guizhou during the Late Triassic (Carnian). A diverse open-water community flourishes in the sunlit surface waters, far above a deep anoxic seabed. Great colonies of the crinoid *Traumatocrinus hsui* hang from floating logs, providing shelter for numerous smaller animals, which in turn attract marauding ocean predators. The dominant reptiles are the slender thalattosaurs (large *Miodentosaurus brevis* in the background, small *Xinpusaurus bamaolinensis* in the left foreground) and the fish-like ichthyosaurus (giant *Shastasaurus/Guanlingsaurus liangae* in the background, small *Qianichthyosaurus zhoui* in the foreground). Foraging among the giant sea-lillies are smaller armoured reptiles, the turtle-like placodont *Psephochelys polyosteoderma* (left foreground) and the early genuine turtle *Odontochelys semitestacea* (right foreground). Flitting around them are coiled ammonoids (*Trachyceras multituberculatus*) and a variety of fishes, including large predators (hybodont shark, *Guizhoucoelacanthus guanlingensis*, *Birgeria* sp.), the slender shoaling *Pholidopleurus xiaowaensis*, pursued by *Miodentosaurus* in the background, and the diminutive *Peltopleurus brachycephalus*. Painting by Brian Choo © 2013.

The Upper Member of the Xiaowa Formation, c. 30 m thick, consists of laminated limestones with few marl interbeds, but increasing amounts of silt and fine sand towards the top of the section. The laminated limestones contain some dm-thick deformed intervals. The laminae consist of mm-thick layers of quartz silt commonly with sharp bases and tops. The silty laminae are sometimes indistinctly graded and occasionally rippled. *Halobia* sp. and the ammonoids *Buchites* cf. *aldrovandii*, *Protrachyceras* sp., *Sirenites* cf. *senticosus* and *Trachyceras* sp. are found in the uppermost part of the Middle Member in the Xiaowa section (Xu et al., 2003), suggesting a late early Carnian age. Fossils, such as *Halobia* sp. and ammonoids, are rare in the Upper Member. There is no bioturbation. The laminated silty limestones are considered to be deposits of relatively deep and anoxic waters (Wang et al., 2008).

The Guanling biota is well known for its marine reptiles (see Section 6.3) and rare fishes (see Section 5.4), and they include teeth and other remains of sharks as well as a diversity of actinopterygians, but none of them longer than 1 m. The most notable invertebrates are the giant crinoids, *Traumatocrinus*, which grew stems many metres in length and commonly attached themselves to floating logs (Fig. 13). Other invertebrates (Jiang et al., 2005a,b,c; Wang et al., 2008) include ceratite ammonoids, nautiloids, the bivalves *Halobia* and *Daonella*, brachiopods, holothurian sclerites, conodonts, and washed-in plant debris.

4.4. Latest Triassic stratigraphy

In most areas of Guizhou and Yunnan, the Permian to Triassic marine successions terminate in the mid to late Carnian with the Xiaowa Formation. This coincides with uplift of the South China Block in the Norian and deformation by the intra-continental collision caused by the Indosinian Orogeny. Throughout the southwestern portion of the Yangtze Platform and the Nanpanjiang Basin, there are no marine deposits of latest Carnian or early Norian age. However, coastal swamp deposits of late Norian and Rhaetian age occur widely in association with isolated coal-bearing basins in southwestern Yunnan, but with isolated fully marine basins, with ammonites.

5. Fishes from the marine Triassic of South China

The effects of the PTME on the evolution of fishes, primarily sharks and rays (Chondrichthyes) and bony fishes (Actinopterygii), have long been uncertain: little has been published on the subject, and previous attempts to compile and plot data have been limited and previous attempts to compile and plot data have been limited and incomplete (Friedman and Sallan, 2012; Benton and Newell, in press). Pitrat (1973) found that marine fishes declined in diversity sharply at the end of the Permian, just like other marine animals, but that freshwater and eurhyaline fishes experienced their main extinctions earlier in the Permian. Thomson (1977) and Blieck (2011) found little evidence for any extinction at all. Benton (1989a,b), on the other hand, identified an extinction rate of 44% for all families of fishes through the Late Permian, but with most of the losses occurring in the mid-Permian. The picture is obscured by the patchiness of the fish fossil record in the Permian: most Late Permian data come from the Kupferschiefer of Germany, and lateral equivalents in the UK and Poland, in contrast to the many fish Lagerstätten in the Triassic. Data compilations so far have been far from complete, and many clades require substantial taxonomic revision before accurate counts of species or genera can be obtained. Further of course, many chondrichthyan groups are known only from teeth, and their taxonomy is much debated and probably diversity counts would be impossible to compare with other clades. Friedman and Sallan (2012) suggest that there may have been selective extinction of marine fishes in general, and particularly durophages, during the PTME, whereas non-durophages, as well as euryhaline elasmobranchs and actinopterygians were largely unaffected.

Triassic fishes are abundant in both North and South China (Fig. 1). Freshwater fishes have been found in the continental sediments of the Tarim Basin, Junggar Basin, Ordos Basin and Sichuan Basin and marine fishes from marine beds in the Yangtze region, Youjiang region and Himalaya region. Triassic fishes in China range in age from the PTB to the Upper Triassic, forming a rather continuous sequence. This record has rarely been reviewed (Sun et al., 2012; supplement).

5.1. Fishes near the PTB

It is enormously frustrating that fish Lagerstätten are absent from the latest Permian and earliest Triassic in China. This means that ichthyologists have to rely on isolated finds to try to understand the impact of the PTB, and yet such clues cannot be ignored (Table 2). Microteeth are abundant near the PTB in South China, especially in Zhejiang and Jiangxi provinces Wang and Jin (2007).

Below the PTB, the teeth are dominated by chondrichthyans including Hybodontidae, Ctenacanthidae, Acrodontidae, Polyacrodontidae and Neoselachii, as well as some actinopterygians. In the Changhsing Formation at Meishan (Figs. 2, 3), the Baoqing Member yields shark teeth, scales and one platysomid, *Sinoplatysomus baoqingensis* Wang, 1986, as well as the chondrichthyans *Changxingselache wangi*

Table 2
Fishes, based mainly on teeth and other microremains, from the lowest Triassic (Induan) of South China, immediately above the PTB. Abbreviations: Actinopt., Actinopterygian; Fm., Formation; Mem., Member.

Epoch	Stage	Substage	Fm.	Mem.	Locality		
					Zhejiang		Jiangxi
					Microfossils	Macrofossils	Microfossils
Triassic	Induan	Dienerian Griesbachian	Yingkeng Fm.		*Baoqingichthys microdontus* Perleididae indet.	*Paraperleidus changxingensis*	
Permian		Changhsingian	Changhsing Fm.	Meishan	*Baoqingichthys microdontus* *Zhengjiangichthys zhaoi* *Baoqingichthys* sp. *Sinohelicoprion changhsingensis* *Meishanselache liui* *Changxingselache wangi* *Sinacrodus donglingensis* Hybodontidae indet.	*Sinoplatysomys meishanensis* *Eosaurichthys chaoi* *Youngichthys xinhuainsis* *Changxingia aspratilis* *Changxingia weii*	*Sinacrodus donglingensis* *Lissodus xiushuiensis* *Polyacrodus jiangxiensis* *Zhengjiangichthys zhaoi* *Baoqingichthys microdontus* Hybodontoid scale type-1 Actinopt. tooth type-1 Neoselachian scale type-1 Neoselachian tooth type-1 cf. *Caturus*
				Baoqing	*Changxingselache wangi* Ctenacanthidae indet. Hybodontidae indet. Neoselachian scale type1	*Sinoplatysomus baoqingensis*	

Wang et al., 2007a, Ctenacanthidae indet., Hybodontidae indet., and neoselachian scale type-1 (Wang et al., 2007a). Fossils of the Meishan Member include one platysomid, one saurichthyid, three coelacanthids, and five different forms of shark teeth. Macrofossils (Wei, 1977; Wang and Liu, 1981; Liu and Wei, 1988; Jin, 1997; Wang et al., 2007a) are *Sinoplatysamys meishanensis* Wei, 1977, *Eosaurichthys chaoi* Liu and Wei, 1988, *Changxingia aspratilis* Wang and Liu, 1981 (Fig. 14B), *Changxingia weii* Jin, 1997 and *Youngichthys xinhuainsis* Wang and Liu, 1981, and microfossils are *Meishanselache liui* Wang et al., 2007a, *C. wangi* Wang et al., 2007a, Hybodontidae indet. (Wang et al., 2007a), *Sinacrodus donglingensis* Wang et al., 2007a, and *Sinohelicoprion changhsingensis* Liu and Zhang, 1963 (Fig. 14C; Liu, 1994; Liu and Wang, 1994), *Sinohelicoprion qomulongma* Zhang, 1976, and *Sinohelicoprion macrodentus* Lei, 1983. Most important among these latest Permian fishes are complete specimens of *E. chaoi*, whose scales cover the whole body, and which may be close to the ancestor of the Triassic saurichthyids (Liu and Wei, 1988).

Other latest Permian fish fossils include teeth of actinopterygians from Meishan Section Z: *Baoqingichthys microdontus* Wang et al., 2007b, *Baoqingichthys* sp., *Zhejiangichthys zhaoi* Wang et al., 2007b, and Perleididae indet. (Wang et al., 2007b), perhaps the oldest record of perleidid fishes (Li and Jin, 2009). In fossiliferous beds at Xiushui and Xinfeng in Jiangxi Province equivalent to the Meishan Member, chondrichthyan and actinopterygian teeth were found, including Acrodontidae, Polyacrodontidae, Neoselachii, Actinopterygii, and Hybodontidae (Wang et al., 2007a,b) (Table 2).

In the earliest Triassic, the oldest complete fish fossil from South China is a single specimen of *Paraperleidus changxingensis* from the lower part of the Yinkeng Formation (Figs. 14A, 15A; Zhao and Lu, 2007). ZQC also found some fragmented fish specimens from Beds 31–33 and 57 of the same section (Fig. 3B; Z.Q. Chen et al., 2007b). Among the 15 microfossil and macrofossil species found in the Changhsingian, only *B. microdontus* survived through the PTME (Table 2), so yielding the very high extinction rate for fish species of 93% (Wang et al., 2007b).

5.2. Fishes from the Early Triassic

Localities that yield Early Triassic fishes are located in both North and South China. In line with the tectonic and palaeogeographic outline, "sea in the south and land in the north", the fishes from northern localities are fresh-water, and those from southern areas are marine (Jin, 2006). The northern localities include the Ordos Basin and the Tarim Basin. There are eight main localities for marine fishes in South China, and these are widely distributed in the Yangtze region and Youjiang region (see above, Section 4.1), and a small number of fishes have been found in the Himalaya region.
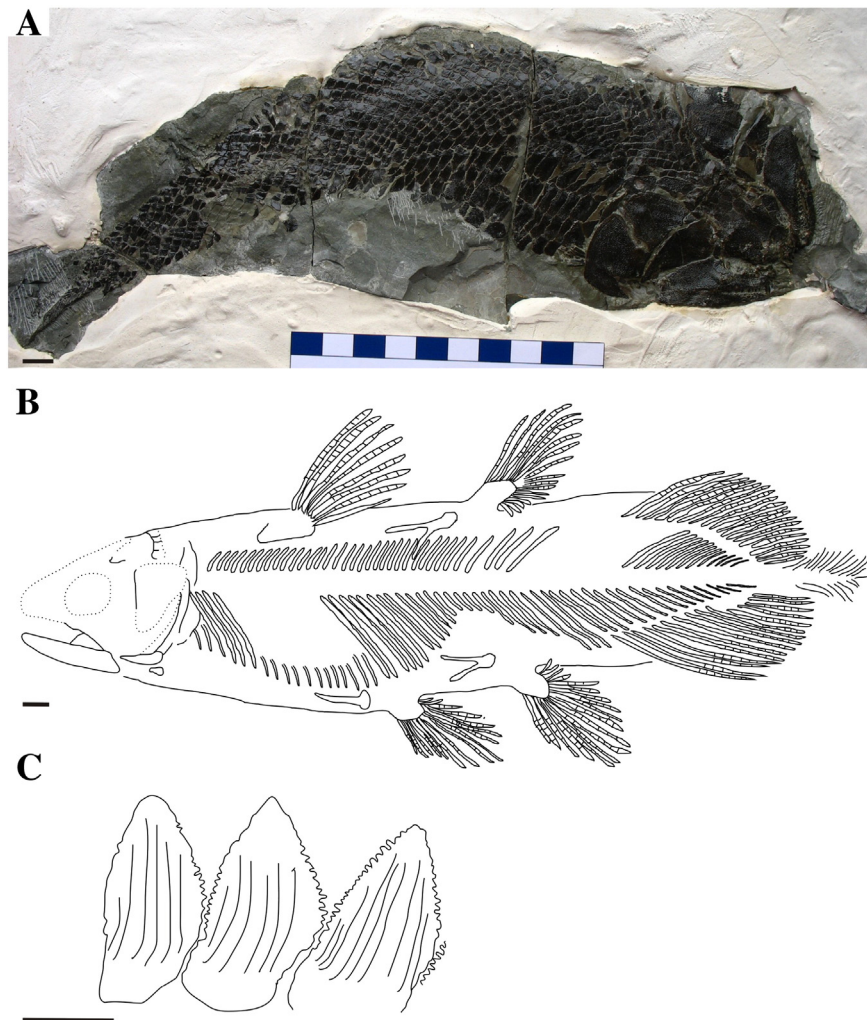
Fig. 14. Fishes of the PTB/Earliest Triassic. (A) *Paraperleidus changxingensis* (ZMNH M1401). (B) Reconstruction of *Changxingia aspratilis*. (C) Drawing of several teeth of *Sinohelicoprion changhsingensis*. Scale bar is 10 mm.
Panel B is redrawn from Wang and Liu, (1981). Panel C is redrawn from Liu and Wang (1994).
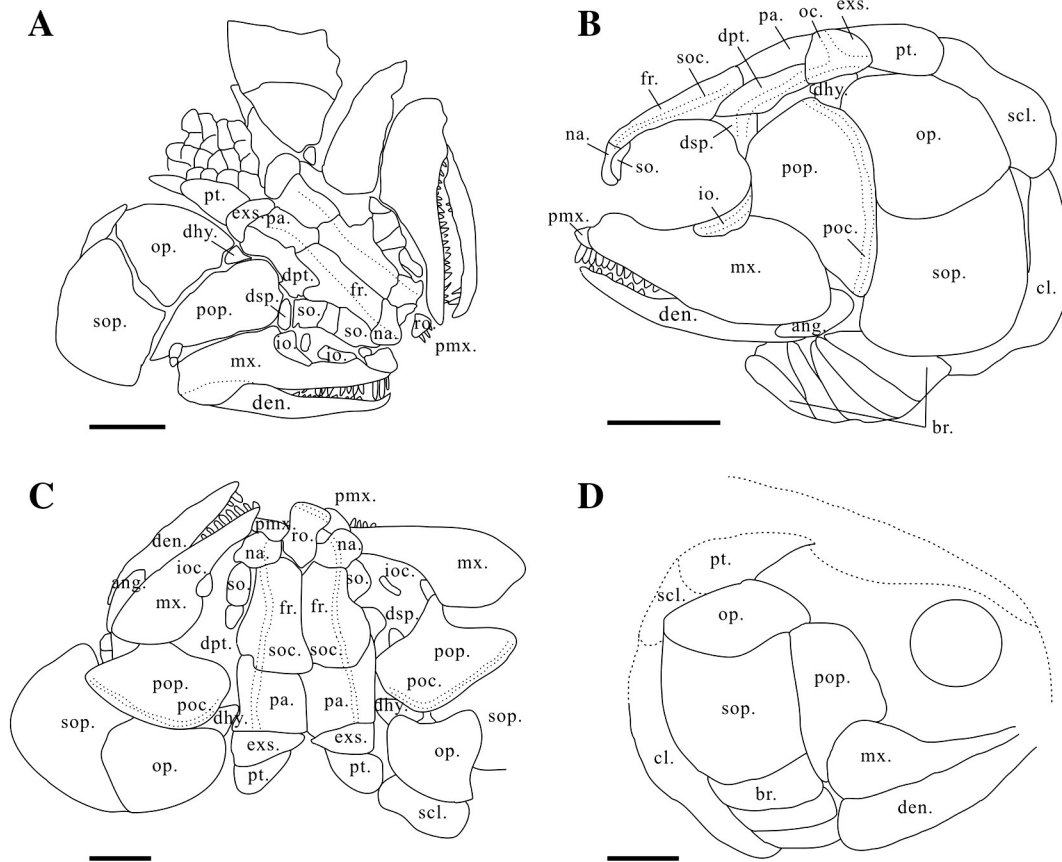
Fig. 15. Fishes of the later Early Triassic, drawings of skull remains. (A) *Paraperleidus changxingensis*. (B) *Plesioperleidus yangtzensis*. (C) *Plesioperleidus jiangsuensis*. (D) *Plesioperleidus dayeensis*. Abbreviations: ang, angular; ant, antorbital; bop, branchiopercle; br, branchiostegal ray; cl, cleithrum; den, dentary; dhy, dermohyal; dpt, dermopterotic; dsp, dermosphenotic; exs, extrascapular; fr, frontal; io, infraorbital; ioc, infraorbital canal; iop, interopercle; l, lacrimal; md, mandible; mx, maxilla; na, nasal; oc, orbital canal; op, opercle; pa, parietal; pcl, postcleithrum; pmx, premaxilla; po, postinfraorbital; poc, preopercular canal; pop, preopercle; pt, posttemporal; ro, rostral; scl, supracleithrum; so, subinfraorbital; soc, supraorbital canal; sop, subopercle; sph, sphenotic. Scale bar is 10 mm.

The most diverse Early Triassic fishes in China come from the Middle and Lower Yangtze regions, especially in Jurong, Jiangsu Province and Chaohu, Anhui Province (Fig. 1), dated as Smithian (early Olenekian). Perleididae, Parasemionotidae, Semionotidae, Saurichthyidae, and Coelacanthidae have been described there (Table 3).

Table 3
Fish taxa from various Early Triassic formations of South China.

Province	Locality	Formation	Olenekian	
			Smithian	Spathian
Jiangsu	Jurong	Qinglong	*Plesioperleidus yangtzensis*	
			Plesioperleidus jiangsuensis	
			Stensionotus dongchangensi	
			Jurongia fusiformis	
			Qingshania cercida	
			Suius brevis	
			Lepidotes jurongensis	
			Peia jurongensis	
	Nanjing			*Saurichthys* sp.
Hubei	Huangshi	Daye		*Plesioperleidus dayeensis*
Anhui	Hexian	Qinglong		*Plesioperleidus yangtzensis*
	Chaohu	Nanlinghu		*Saurichthys* sp.
		Helongshan	*Plesioperleidus dayeensis*	
			Plesioperleidus yangtzensis	
			Plesioperleidus jiangsuensis	
			Jurongia fusiformis	
			Qingshania cercida	
			Suius brevis	
			Chaohuichthys majiashanensis	
			Coelacanth indet.	
Guangxi	Tiandong	Luolou		*Hybodus zuodengensis*
				Hybodus yohi
				Polyacrodus tiandongensis
	Fengshan			*Sinicoelacanthus fengshanensis*

The Perleididae was the first fish family to radiate after the PTME (Wang et al., 2007b). Chinese palaeontologists have named many species based on well-preserved specimens: *Perleidus yangtzensis* (Fig. 15B) from Hexian, Anhui Province (Su, 1981), *Plesioperleidus dayeensis* (Fig. 15D) from Tieshan, Huangshi, Hubei Province (Su and Li, 1983), *Perleidus jiangsuensis* (Fig. 15C) from the Lower Qinglong Formation, Jurong, Jiangsu Province (Qian et al., 1997), which also yielded *Zhangina cylindrica*, *Perleidus piveteaui*, "*Perleidus*" *eurylepidotrichia* and *Perleidus madagascariensis*, named by Liu and Feng (2002a). Jin (2003, 2006) concluded that only *P. jiangsuensis*, *P. yangtzensis*, *Zhangina jiangsuensis*, and *Zhangina yangtzensis* were valid species. *Z. cylindrica* and *P. piveteaui* were included in *Z. jiangsuensis*, "*P.*" *eurylepidotrichia* in *Z. yangtzensis*, and *P. madagascariensis* was regarded as non-perleidid. Further, *Z. yangtzensis* should be reattributed to *Plesioperleidus* (Jin et al., 2003; Jin, 2006; Zhao and Lu, 2007; Li and Jin, 2009).

The only semionotid fish reported in Jurong (Qian et al., 1997), *Lepidotes jurongensis*, was thought to be a parasemionotid (Li and Jin, 2009). Four genera of Parasemionotidae, *Stensionotus dongchangensi*, *Jurongia fusiformis*, *Qingshania cercida*, and *Suius brevis*, were erected by Liu (2002a). *Peia jurongensis* is a parasemionotid-like fish from Jurong (Li, 2009), perhaps the only valid parasemionotid fish from the locality.

The best-preserved Early Triassic fish fossils were found at Chaohu City, Anhui Province, in the Smithian Helongshan Formation (Fig. 2). These include three Perleididae, all of them species of *Plesioperleidus* (Tong et al., 2006), three Parasemionotidae, all given the same names as those from Jurong, and one Coelacanthidae (*Chaohuichthys majiashanensis*; Fig. 16), as well as some undetermined actinopterygians

and coelacanths. The overlying Nanlinghu Formation has yielded *Saurichthys* sp. (Tong et al., 2006).

Spathian fishes are limited. Some material of *Saurichthys* has been reportedly found in the Upper Qinglong Formation in the Nanjing area (Su and Li 1983). Two Spathian-age quarries in Guangxi Province include Fengshan, which yields *Sinocoelacanthus fengshanensis* from the Luolou Group (Liu, 1964), the first coelacanth reported from China. However, the holotype is just the caudal fin, and its lower lobe is larger than the upper. The other quarry is Tiandong, which has yielded *Hybodus zuodengensis*, *H. yohi* and *Polyacrodus tiandongensis* (Wang et al., 2001). These are the youngest hybodonts from China, and it is remarkable that they were originally thought to be two kinds of conodont.

In summary, the main part of the Early Triassic, after the immediate aftermath of the PTME, is marked by a distinctive fish fauna (Wang et al., 2007b): the *Sinoplatysomys–Sinacrodus* assemblage of the Late Permian of South China was replaced by the *Zhangina–Hybodus* assemblage of the Early Triassic, actually the *Plesioperleidus–Hybodus* assemblage.

5.3. Fishes from the Middle Trassic

During the Middle Triassic, primitive actinopterygians such as Perleididae and Saurichthyidae still comprised a large proportion of the ichthyofauna. However, neopterygians began to radiate to some extent. These forms share a number of derived characters: ossified endoskeleton, maxilla no longer hinged with preopercular, preopercular with narrow dorsal limb, interopercular, pectoral fins and pelvic fins segment distally, each radial supporting one lepidotrichium, and tail
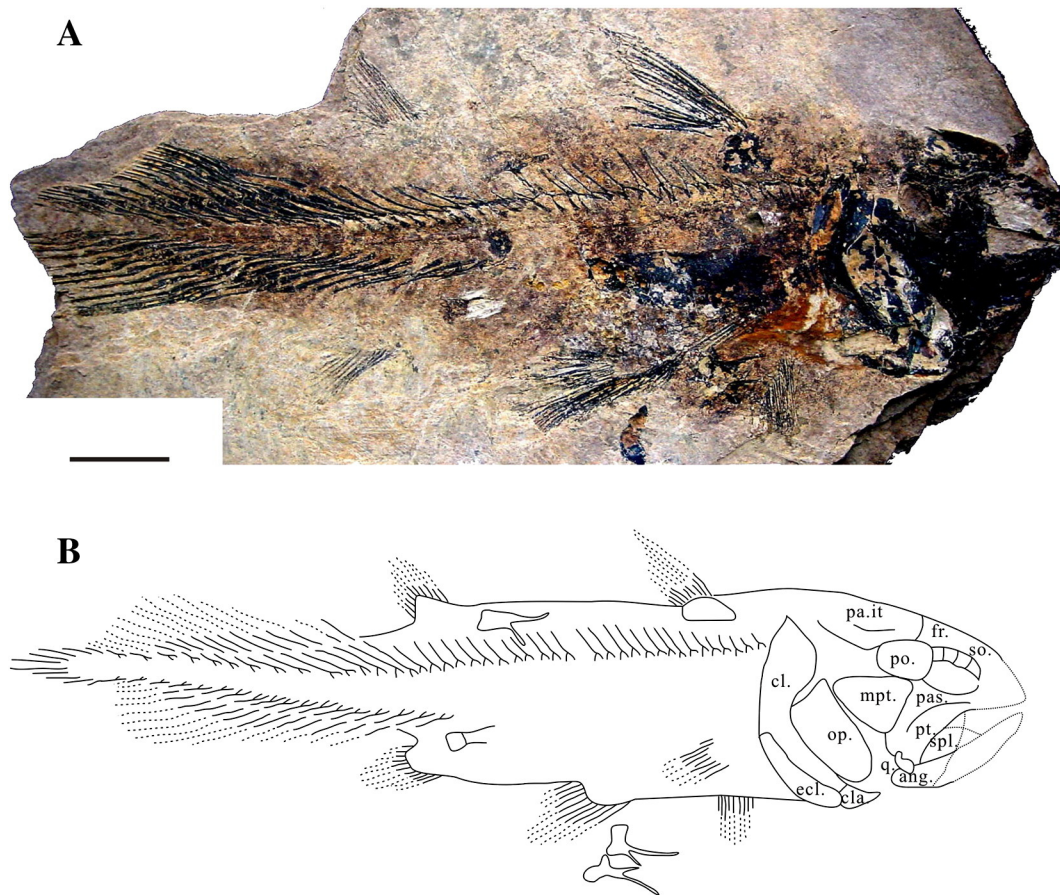
Fig. 16. *Chaohuichthys majiashanensis* Tong et al., 2006 from the Early Triassic (Olenekian) of Chaohu, holotype CMR 701, photograph (A) and drawing (B). Abbreviations as in Fig. 18, plus: ang, angular; cla, clavicle; ecl., extracleithrum; it, intertemporal; fr, frontal; mpt, metapterygoid; op, opercular; pa, parietal; pas, parasphenoid; pt, pterygoid; so, subinfraorbital; spl, splenial. Scale bar is 10 mm.
Redrawn from Tong et al. (2006).

hemiheterocercal or homocercal (Gardiner et al., 2005; Hurley et al., 2007). Sarcopterygians comprise a small proportion.

Fish fossils are known mainly from Yunnan and Guizhou provinces of the Yangtze region. The Luoping biota is worthy of mention as being particularly rich. This is an exquisite lagerstätte yielding well-preserved invertebrates and vertebrates, including numerous fishes. This famous ichthyobiota (Figs. 17, 18) is composed mostly of actinopterygian fishes, and coelacanths are relatively rare. Initial identifications indicate more than nine families of actinopterygian fishes, and 14 new species have been named: *Marcopoloichthys ani* Tintori et al., 2007, *Luopingichthys bergi* Sun et al., 2009, *Saurichthys dawaziensis* Wu, 2009, *Saurichthys yunnanensis* Zhang, 2010, *Gymnoichthys inopinatus* Tintori et al., 2010, *Sinosaurichthys longimedialis* Wu et al., 2011a, *Sinosaurichthys minuta* Wu et al., 2011a, *Sangiorgichthys sui*

López-Arbarello et al., 2011, *Perleidus sinensis* Lombardo et al., 2011, *Habroichthys broughi* Lin et al., 2011, *Kyphosichthys grandei* Xu and Wu, 2012, *Luopingperleidus sui* Geng et al., 2012, *Luoxiongichthys hyperdorsalis* Wen et al., 2012, and *Diandongperleidus denticulatus* Geng et al., 2012 (Table 4). Two new species of coelacanths have been named from Luoping, *Luopingcoelacanthus eurylacrimalis* and *Yunnancoelacanthus acrotuberculata* (Wen et al., 2013). It is notable that two embryos were found in the holotype of *L. eurylacrimalis*, the oldest record of ovoviviparity in a coelacanth (Fig. 18G).

Based on the specimens we collected from Daaozi quarry, Saurichthyiformes and Peltopleuriformes are the main clades of primitive actinopterygians. *Saurichthys* species are diverse in the Luoping biota (Zhang et al., 2010), comprising two genera and more than
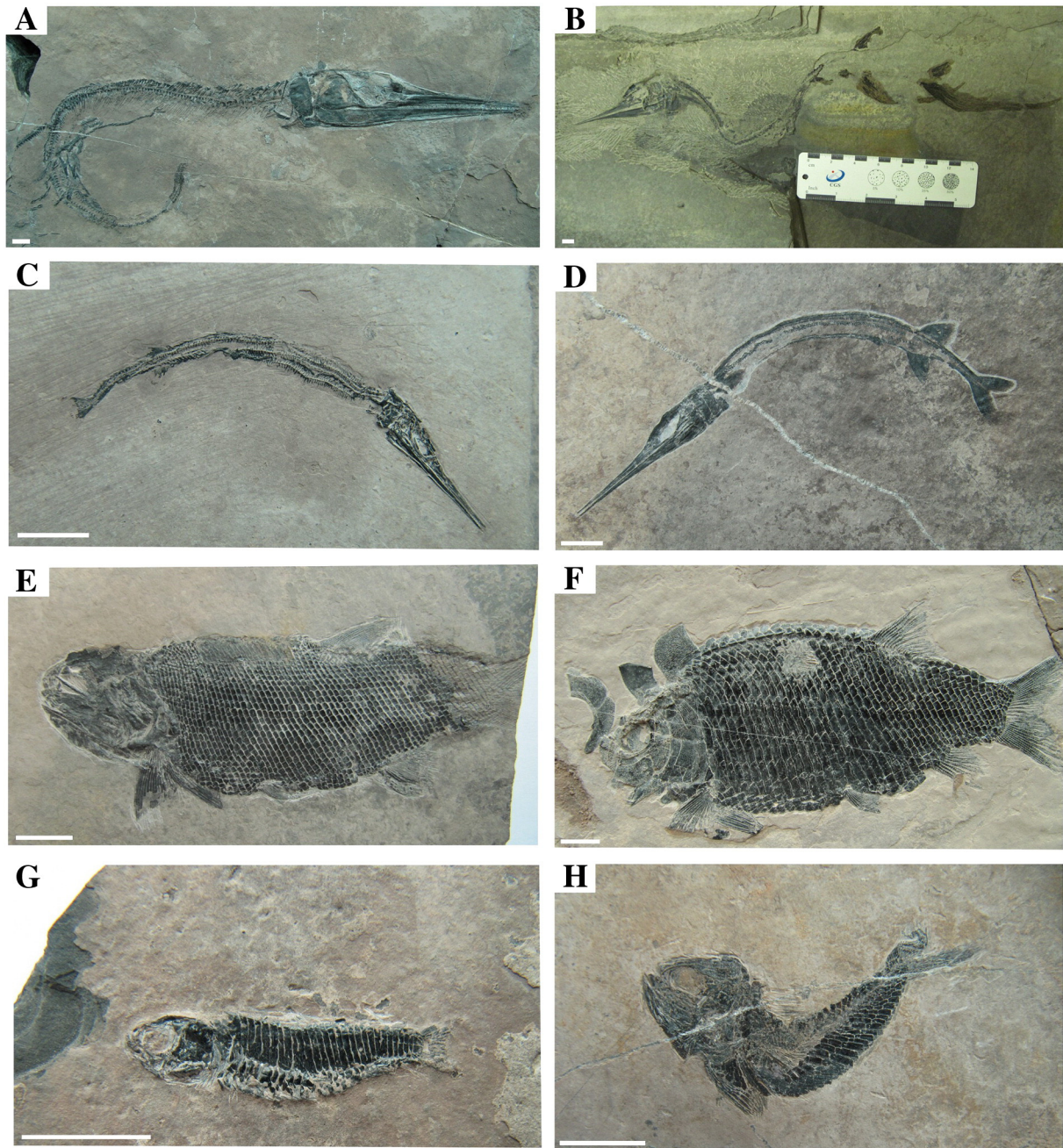
Fig. 17. Fishes from the Middle Triassic (Anisian) of Luoping, part 1. (A) *Saurichthys yunnanensis* (Holotype LPV-20881). (B) *Sinosaurichthys longimedialis* (LPV-3583). (C) *Saurichthys* sp. (LPV-20585). (D) *Sinosaurichthys minuta* (LPV-21108). (E) Palaeonisciform (LPV-11788). (F) *Luopingichthys bergi* (LPV-10196). (G) *Habroichthys broughi* (LPV-10107). (H) *Placopleurus* (LPV-11207). Scale bar is 10 mm.
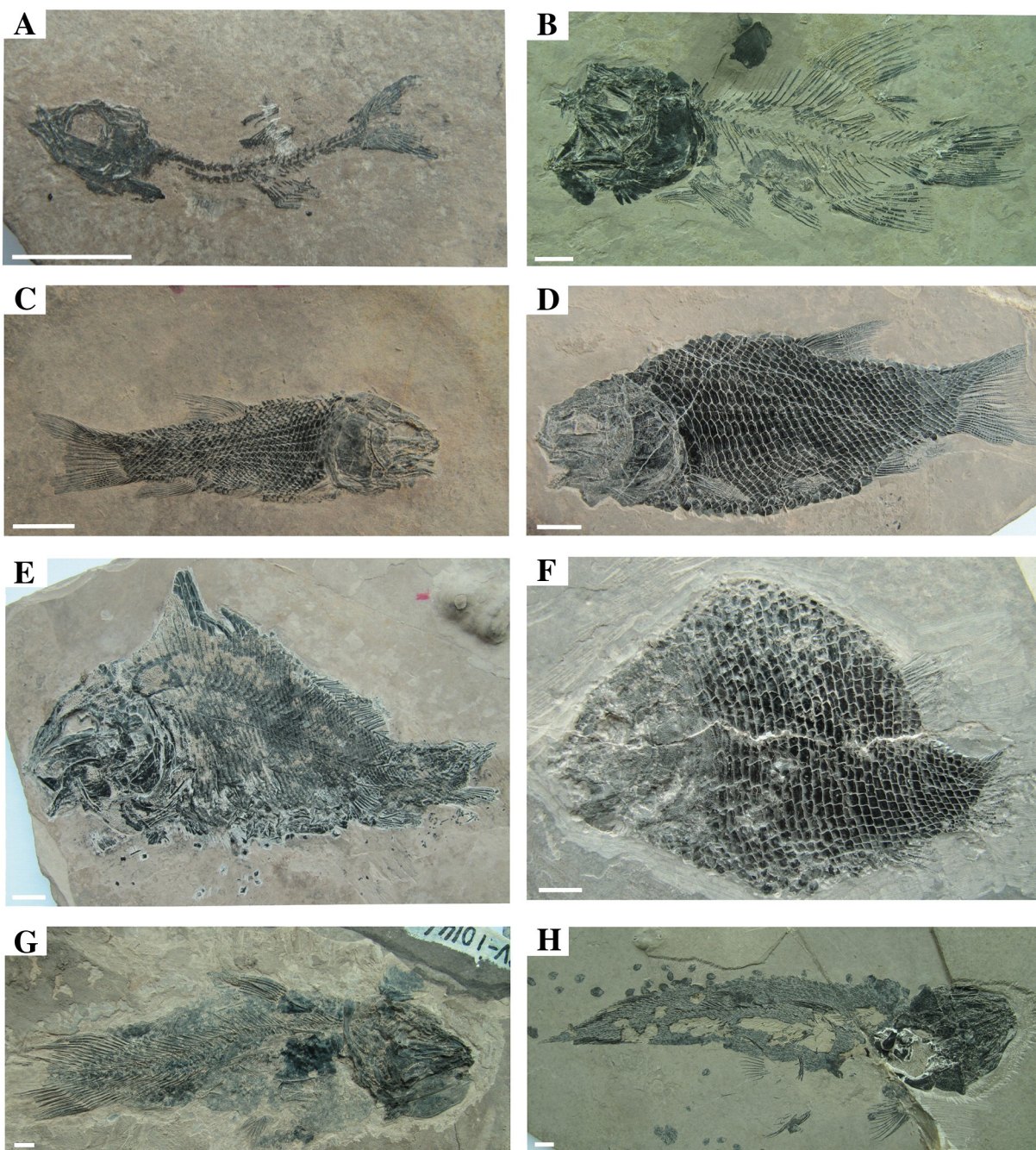
Fig. 18. Fishes from the Middle Triassic (Anisian) of Luoping, part 2. (A) *Marcopoloichthys ani* (LPV-11182). (B) *Gymnoichthys inopinatus* (LPV-10143). (C) *Sangiorgioicthys sui* (LPV-10001). (D) *Sangiorgioichthys sui* (LPV-133-1). (E) *Luoxiongichthys hyperdorsalis* (Holotype LPV-10144). (F) *Kyphosichthys grandei* (LPV-11303). (G) *Luopingcoelacanthus eurylacrimalis* (Holotype LPV-10146). (H) *Yunnancoelacanthus acrotuberculatus* (Holotype LPV-12748). Scale bar is 10 mm.

eight species in coexistence. *Sinosaurichthys* differs from *Saurichthys* (Fig. 17A–D) in its boot-shaped cleithrum, the position of the pectoral fin, the absence of branchiostegals, the wider mid-dorsal scales, and the anterior position of the medial fin (F.X. Wu et al., 2011). *M. ani* is a unique naked small neopterygian (Fig. 18A). It has a modified teleost-like jaw system, "L"-shaped preopercle and modified support of the medial fin (Tintori et al., 2007). *G. inopinatus* is another naked basal neopterygian (Fig. 18B) with a single row of small scales along the lateral line. *Sangiorgioichthys* (Fig. 18C, D) has unique circumorbital bones. It is the most abundant neopterygian in the Luoping biota, with more than 20 specimens of *Sangiorgichthys* on average per square metre on layer 30 of Daaozi quarry (Zhang et al., 2008). *Luoxiongichthys*

and *Kyphosichthys* have similar deep bodies (Fig. 18E, F) and have many similarities in their skulls. However, they differ in the pectoral girdle and medial fin, and their interrelationships require further dicussion. In addition to these taxa, the Luoping biota includes further actinopterygians, including species of *Saurichthys*, *Peltoperleidus*, *Peripeltopleurus*, *Placopleurus*, *Helmolepis*, palaeoniscids and Eugnathidae, all of which are currently under study by W.W.

The Panxian biota includes a variety of fish fossils, including Saurichthyidae and *Birgeria* among the basal palaeopterygians, *Colobodus* (Fig. 19A) and *Peltopleurus* and *Placopleurus* among the subholosteans, and semionotids among the neopterygians (Jin, 2006; Sun et al., 2008). However, only two forms have been published, namely

Table 4
Fish taxa from various Middle and Late Triassic formations of South China.

Stage	Locality	Macrofossils	
Carnian	Guanling	*Birgeria guizhouensis*	*Pholidopleurus xiaowaensis*
		Birgeria sp.	*Guizhoueugnathus largus*
		Peltopleurus brachycephalus	*Guizhoucoelacanthus guanlingensis*
Ladinian	Fuyuan	*Fuyuanperleidus dengi*	
		Guizhoucoelacanthus guanlingensis	
	Changdi	*Birgeria liui*	
		Actinopterygian indet.	
	Xingyi	*Peltopleurus orientalis Sinoeugnathus kueichowensis*	*Guizhouniscus microlepidus*
		Asialepidotus shingyiensis	*Xingyia gracilis*
		Guizhoubrachysomus minor	*Guizhouamia bellula*
		Marcopoloichtys	*Potanichthys xingyiensis*
		Habroichthys	
		Peripeltopleurus	
Anisian	Panxian	*Birgeria* sp.	*Colobodus baii* Semionotid
		Sinosaurichthys longipectoralis	
		Placopleurus	
	Luoping	Chondrosteans:	*Luopingperleidus sui*
		Saurichthys dawaziensis	*Diandongperleidus denticulatus*
		Saurichthys yunnanensis	*Helmolepis* sp.
		Sinosaurichthys longimedialis	Halecomorphi:
		Sinosaurichthys minuta	*Marcopoloichthys ani*
		Saurichthys sp.	*Gymnoichthys inopinatus*
		Subholosteans:	Ginglymodi:
		Habroichthys broughi	*Luoxiongichthys hyperdorsalis*
		Placopleurus sp.	*Kyphosichthys grandei*
		Luopingichthys bergi	*Sangiorgioichthys sui*
		Perleidus sinensis	Coelacanths:
			Yunnancoelacanthus acrotuberculata
			Luopingcoelacanthus eruylacrimalis

Colobodus baii Sun et al., 2008 and *Sinosaurichthys longipectoralis* Wu et al., 2011 (Fig. 19B). Although both the Luoping and Panxian biotas are of similar age, they differ from each other in preservation quality and fish taxa (Tintori, 2010).

Among the Middle Triassic fishes from South China, it is interesting that large taxa such as *Saurichthys*, *Birgeria* and *Colobodus*, as well as some small actinopterygians such as *Marcopoloichthys*, *Placopleurus*, *Habroichthys*, and *Sangiorgioichthys* have been found both on the western and eastern coasts of Palaeotethys. This has suggested to some (Tintori et al., 2007; Lombardo et al., 2011) that these taxa could migrate from the east to the west of that ocean.

### 5.4. Fishes from the latest Middle Triassic to Late Triassic

In the Late Triassic, as the primitive actinopterygians declined, holosteans became more significant.

The first Late Triassic fish fossils from South China were found in 1957 by Mr. Cao of Guizhou Museum in the *K. hui* layers of the Zhuganpo Formation at Dingxiao, Xingyi (Yang and Liu, 1995; Liu et al., 2003). These five specimens were identified as *P. orientalis*, *S. kueichowensis* (Fig. 20A), and *A. shingyiensis* by Su (1959). Further fish fossils of this age were not found until the 1980s when specimens were uncovered from Dingxiao and Wusha in Guizhou Province, and Changdi and Fuyuan in Yunnan Province (Liu et al., 2003; Jin, 2006). Liu et al. (2002b, 2003) named these as *Guizhouamia bellula* from Dingxiao, *Guizhouniscus microlepidus*, *Guizhoubrachysomus minor* and *Guizhoueugnathus analilepida* from Wusha, and *Xingyia gracilis* from Dingxiao (Fig. 20B–E; Table 4). *Marcopoloichtys*, *Habroichthys* and *Peripeltopleurus* were found during a new excavation in Wusha.

A unique primitive actinopterygian fish, *Birgeria liui*, was found in Changdi, Luoping, Yunnan Province (Jin, 2001), from a horizon that is nearly the same as that of the Xingyi biota. Though only the caudal region was preserved, it is the first *Birgeria* found in China (Fig. 20H). We also found some medium-sized actinopterygians at Changdi (Fig. 20F, G).

Many fish fossils have been collected in the Zhuganpo Formation, Fuyuan, Yunnan Province since 1999. These include actinopterygians as well as a coelacanth (*Guizhoucoelacanthus guanlingensis*) from

Jiyangshan and Shibalianshan (Geng et al., 2009). Further, one new form of Perleididae has been named, *Fuyuanperleidus dengi* Geng et al., 2012. A new flying fish, *Potanichthys xingyiensis* Xu et al., 2013,
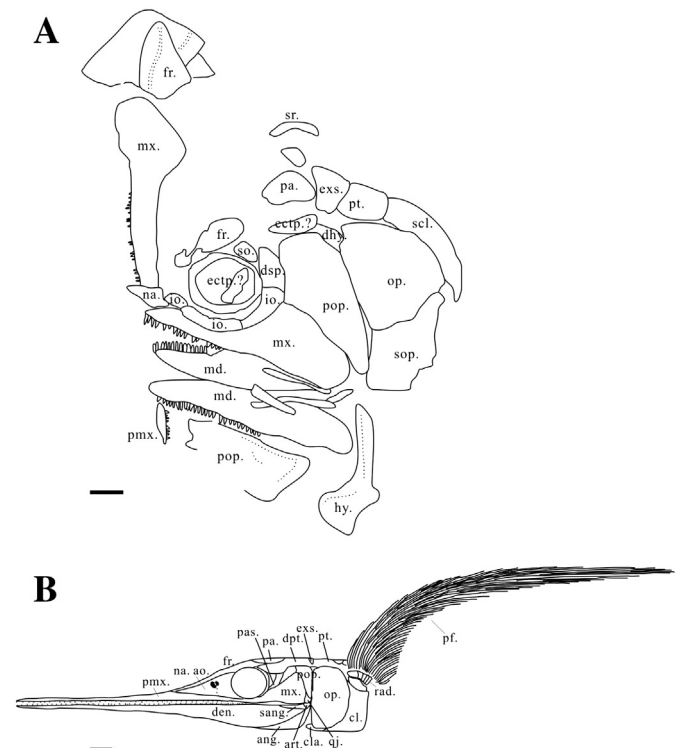
Fig. 19. Fishes from the Middle Triassic (Anisian) of Panxian. (A) Skull of *Colobodus baii*. (B) Reconstruction of skull of *Sinosaurichthys longipectoralis*. Abbreviations: as for Fig. 18, plus: ao, antorbital fenestra; art, articular; cla, clavicle; ectp, ectopterygoid; hy, hyoid; pf, pectoral fin; rad, radials; sang, surangular. Scale bar is 10 mm.
Panel A is redrawn from Sun et al. (2009). Panel B is redawn from F.X. Wu et al. (2011).
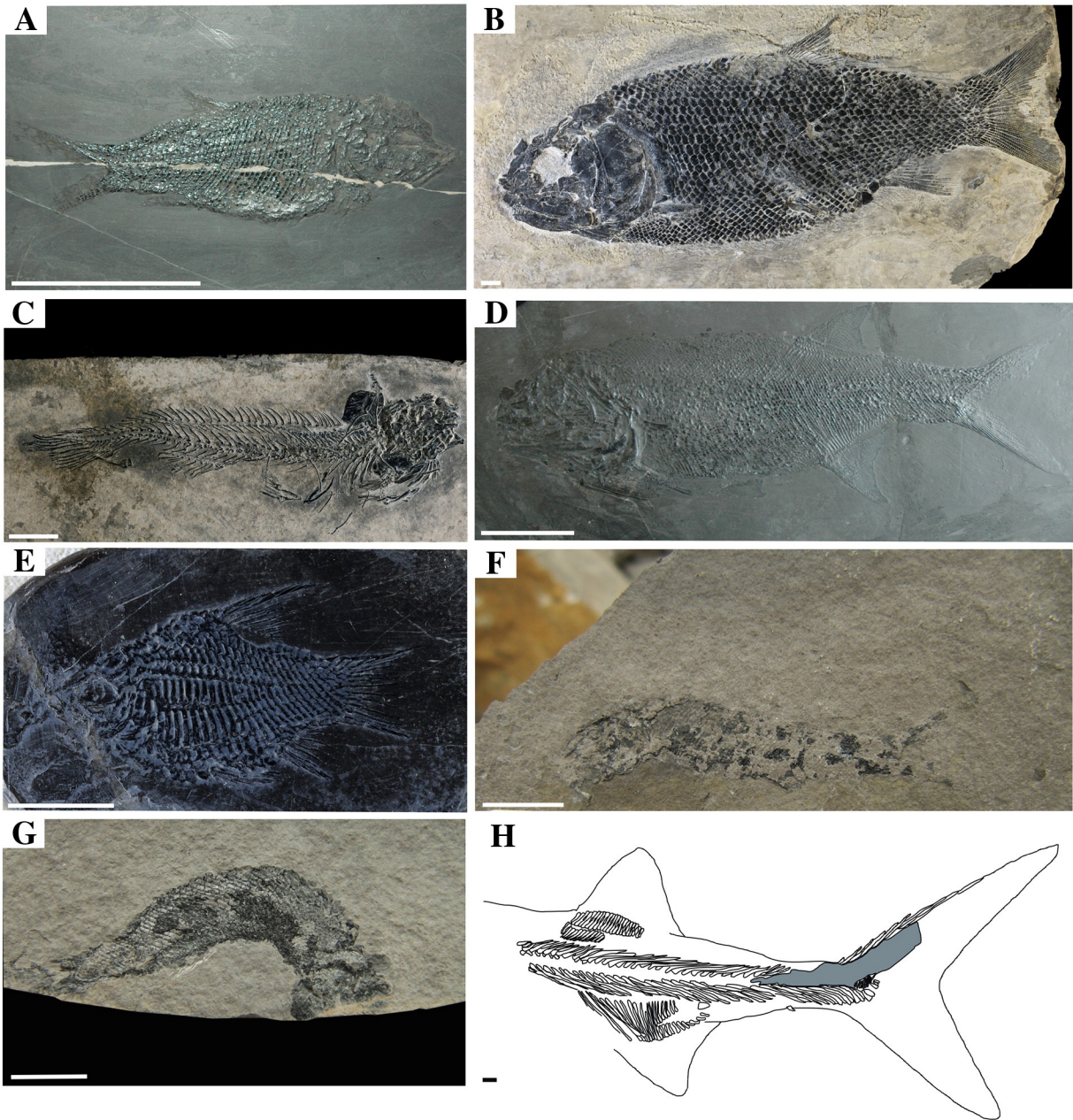
Fig. 20. Fishes from the Middle Triassic (Ladinian) of Xingyi and Changdi, Ladinian. (A) *Sinoeugnathus kueichowensis* (specimen from Xingyi Museum). (B) *Guizhoueugnathus analilepida* (Holotype NIGP-136040). (C) *Guizhouamia bellula* (Holotype NIGP-124837). (D) *Guizhouniscus microlepidus* (specimen from Xingyi Museum). (E) *Guizhoubrachysomus minor* (Holotype NIGP-136039). (F, G) Actinopterygians from Changdi (CIGMR specimens). (H) *Birgeria liui*. Scale bar of A–D is 50 mm, and scale bar of E–G is 10 mm. Panel H is redrawn from Jin (2001).

extends the earliest record of Thoracopteridae from the Late Triassic back to the Middle Triassic.

One of the Zhuganpo Formation fishes, *G. bellula* (Fig. 20C), was claimed by Liu et al. (2002b) as the first amiid (bowfin), which would be a remarkable record if true — the first representative of an extant clade that was thought to have originated in the Late Jurassic (Grande and Bemis, 1998). However, Tintori and Lombardo (2005) indicate that *Guizhoamia* is similar to European '*Caturus*', a basal amiiform, and non-amiid amiiforms are indeed known elsewhere also from the Early and Middle Triassic.

After observation of many Eugnathidae from Xingyi, we found that there are no real differences between *Guizhoueugnathus* (Fig. 20B) and *Asialepidotus shigyiensis*. Both their preopercula are slender, and the lower limb extends forward slightly, which is different from *S. kueichowensis* (Fig. 20A). The coronoid mentioned by Liu

et al. (2003) in the skull of *G. analilepida* cannot be identified. Besides these forms, some new materials, including Acrolepidae, *Saurichthys*, *Peripeltopleurus*, *Eosemionotus*, *Archaeosemionotus*, Macrosemiidae, Caturidae, and Pholidophoridae are mentioned by Jin (2006).

The Guanling biota is famous for its abundant large reptiles and crinoids, but fishes also occur. Actinopterygians are restricted to the lower Xiaowa Formation of Xinpu and Gangwu villages, and they are rare when compared to the reptiles (Jin, 2006; Wang et al., 2008, 2009). Some of them have been identified, with representatives of five families described by Liu et al. (2006), including the holostean families Pholidopleuridae, Peltopleuridae and Eugnathidae (*Pholidopleurus xiaowaensis*, *Peltopleurus brachycephalus*, *Guizhoueugnathus largus*; Fig. 21A–C; Table 4), and rare Birgeriidae. Coelacanthidae are also rare, among which *G. guanlingensis* (Fig. 21D) was assigned to the Whiteiidae
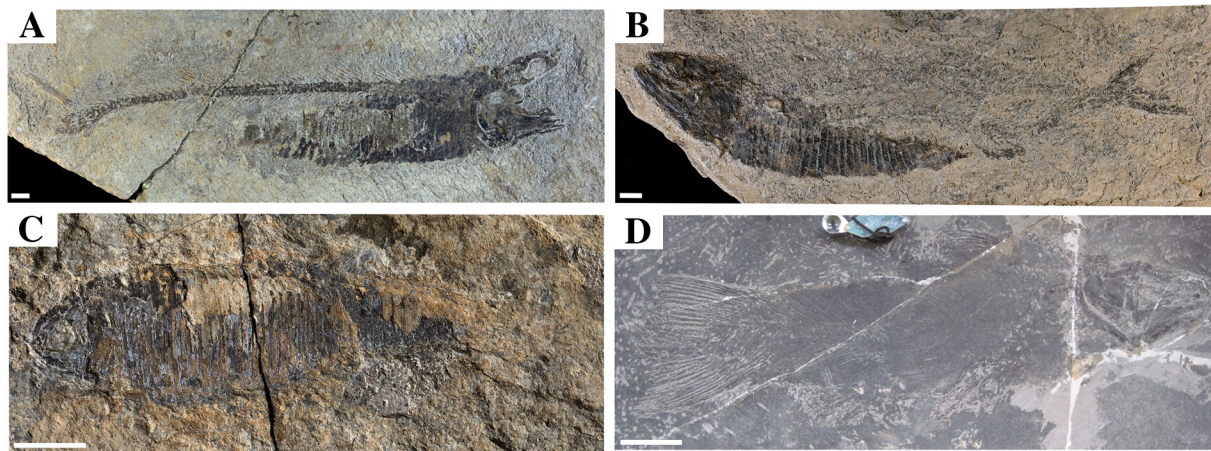
Fig. 21. Fishes from the Late Triassic (Carnian) of Guanling. (A) *Pholidopleurus* (Holotype, NIGP-139726). (B) *Pholidophorus xiaowaensis* (Paratype, NIGP-139727). (C) *Peltopleurus brachycephalus* (Holotype, NIGP-129729). (D) *Guizhoucoelacanthus guanlingensis* (specimen from Xingyi Museum). Scale bar of A–C is 10 mm, and scale bar of D is 50 mm.

by Geng et al. (2009). Some new materials should belong to *Colobodus* (Jin, 2006).

Elasmobranch ichthyoliths are abundant in the Guanling biota (Wang et al., 2003a). Chen (2002) reported six genera from Guanling, while Chen and Cuny (2003) noted a possible hybodontid tooth and some elasmobranch ichthyoliths from Xinpu in the Guanling area. Teeth of *Polyacrodus contrarius* were reported from the Yangliujing and Zhuganpo formations, Lonchidiidae (? *Parvodus*) from the Yanliujing Formation, and Neoselachii? and aff. *Arctacanthus* from the Zhuganpo Formation in the Guanling area. In addition, some actinopterygian teeth have also been found (L.D. Chen et al., 2007). Later, more materials of dermal denticles were found in the Zhuganpo Formation at Zhengfeng, Guizhou Province, whose age is equivalent to that of the Xingyi biota (Zhang et al., 2012a,b).

6. Reptiles from the marine Triassic of South China

There were substantial extinctions of tetrapods on land during the PTME, with annihilation of the complex latest Permian ecosystems dominated by herbivorous pareiasaurs and dicynodonts and carnivorous gorgonopsians, and their replacement by new clades of archosaurs (crurotarsans, dinosauromorphs) and synapsids (cynodonts) (Benton et al., 2004; Brusatte et al., 2011). Current data suggest a loss of four out of 11 families of amphibians (36%) and 17 out of 32 families of amniotes (53%) at the end of the Changhsingian (Benton and Newell, in press). Such figures cannot be estimated for marine tetrapods as there were no exclusively marine tetrapods in the Late Permian, the marine mesosaurs having been restricted to much older Permian units.

The Chinese Triassic marine reptiles represent new clades, with as yet no Permian precursors, all presumably diapsids of one sort or another, and so emerging from a clade that had originated in the mid-Carboniferous, but was never particularly diverse or abundant either on land or in the sea through the Late Carboniferous and Permian. Marine diapsids (ichthyosaurs, thalattosaurs, sauropterygians) emerged in the Olenekian and Anisian ages and added new top trophic levels, adding the finishing touches to a typical Mesozoic, or even 'modern', ecosystem (Rieppel, 2000; McGowan and Motani, 2003; Motani et al., 2008; Jiang et al., 2009; Chen and Benton, 2012). For a long time, the best Triassic marine reptiles came from the Germanic Basin (especially Germany and Switzerland) and from western Canada and the United States, but now the south Chinese marine reptile Lagerstätten or biotas are taking over as the source of some of the richest faunas, and certainly the most continuous over a long span of time.

Study of Chinese Triassic marine reptiles began from the description of *K. hui* in 1958 by C.C. Young, a pioneering vertebrate palaeontologist in China. Since then, numerous marine reptiles have been reported

and described from China. To date, 71 Triassic marine reptile taxa have been reported from 14 localities in the South China basins (Fig. 1). We recognise 51 valid species from these top marine predators and give a brief review below, arranged in stratigraphic sequence of the finds.
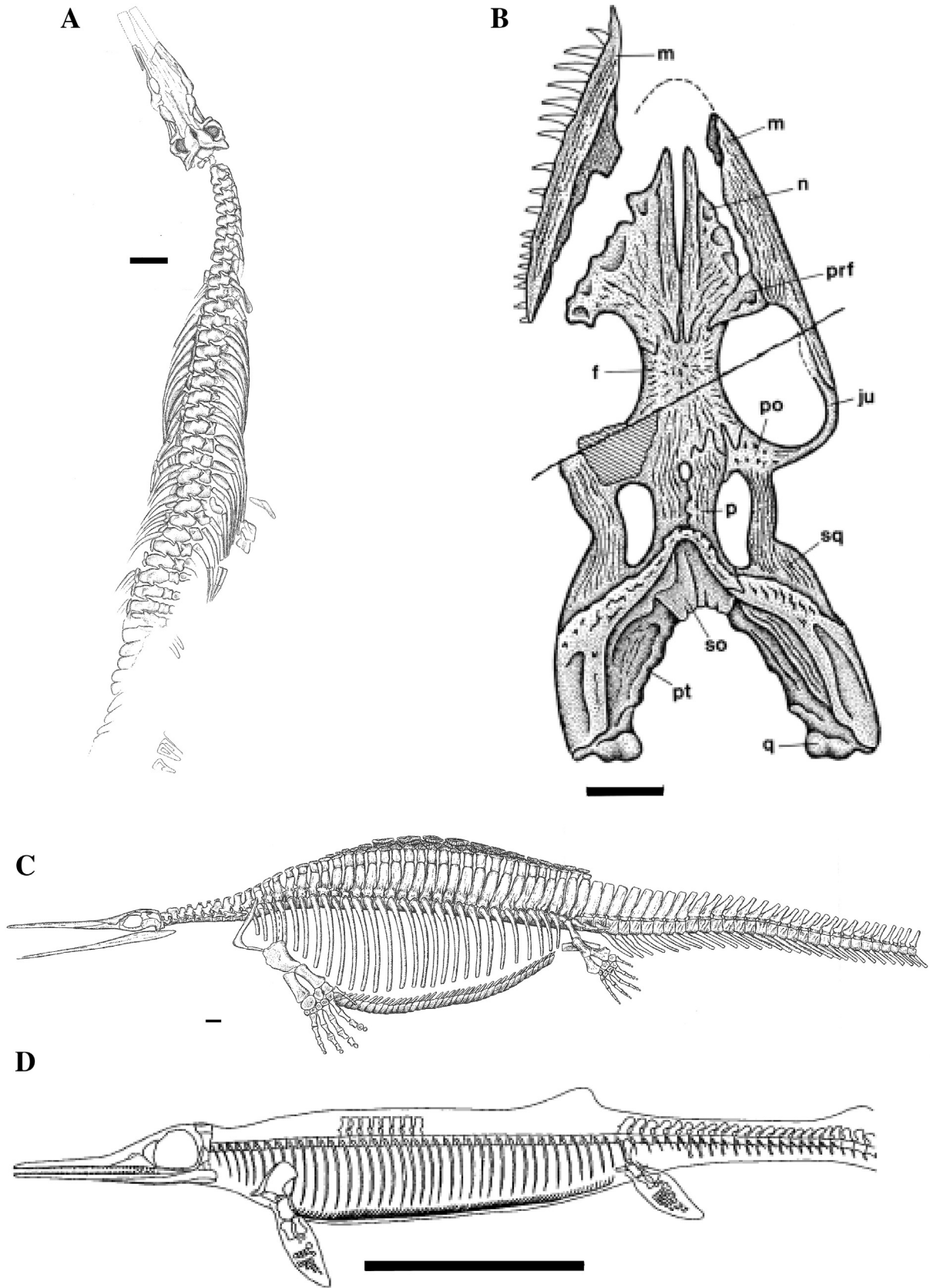
6.1. Reptiles from the Early Triassic

Four Early Triassic marine reptiles have been reported from Nanzhang and Yuanan counties in Hubei Province, Chaohu City in Anhui Province, and Wuming County in Guangxi Province. To date, nine taxa including three sauropterygian species, three ichthyopterygian species, and three species of Hupehsuchia have been described. In addition to one unnamed species, we recognise another five valid taxa among them (Fig. 23; Appendix 1).

The Jialingjiang Formation in Nanzhang and Yuanan counties (see Section 4.1) yields a diverse marine reptile fauna, which is probably the earliest occurrence of marine reptiles in China (Li et al., 2002a). In addition to one unnamed species of Nanchangosauridae (Carroll and Dong, 1991; Wu et al., 2003), four species have been described and named, including *Nanchangosaurus suni* Wang, 1959 (Fig. 22A), *Keichousaurus yuananensis* Young, 1965, *Hanosaurus hupehensis* Young, 1972 (Fig. 22B), and *Hupehsuchus nanchangensis* Young, 1972 (Fig. 22C). Among them, only *K. yuananensis* was originally reported from Yuanan, whereas the other four species were all reported from Nanzhang. Our fieldwork, however, confirms the occurrence of all these taxa in the quarry at Yuanan where the holotype of *K. yuananensis* was discovered. In addition, the occurrence of ichthyosaurs in Yuanan has also been confirmed during our fieldwork, which is being studied by colleagues from the Wuhan Center of the China Geological Survey. *K. yuananensis* has been assigned as a nomen dubium (Rieppel, 2000), whereas the other three named species are all recognised as valid taxa (Appendix 1).

The Beisi Formation of Wuming, representing an isolated platform surrounded by the Nanpanjiang Basin (Lehrmann et al., 2007), yields another Early Triassic reptile taxon, *Kwangsisaurus orientalis* Young, 1959. The Nanlinghu Formation of Chaohu (see Section 4.1) also yields one valid reptile taxon, the ichthyosaur *C. geishanensis* Young and Dong, 1972 (Fig. 22D; Appendix 1). *Chaohusaurus* has received repeated attention from vertebrate palaeontologists (Motani et al., 1996; Motani and You, 1998; Maisch, 2001). It is a small-sized ichthyosaur and most probably adopted an anguilliform swimming mode, as demonstrated by Motani et al. (1996). Its heterodont dentition together with the body shape indicates that it could capture and consume any invertebrate or fish it met with a quick attack.

Fig. 22. Early Triassic marine reptiles from China. (A) *Nanchangosaurus suni* Wang, 1959. (B) *Hanosaurus hupehensis* Young, 1972. (C) *Hupehsuchus nanchangensis* Young, 1972. (D) *Chaohusaurus geishanensis* Young and Dong, 1972. Scale bar of A–C is 10 mm, and scale bar of D is 100 mm.
Panel A is from Carroll and Dong (1991). Panel B is from Rieppel (1998b). Panel C is from Carroll and Dong (1991). Panel D is from Maisch (2001).
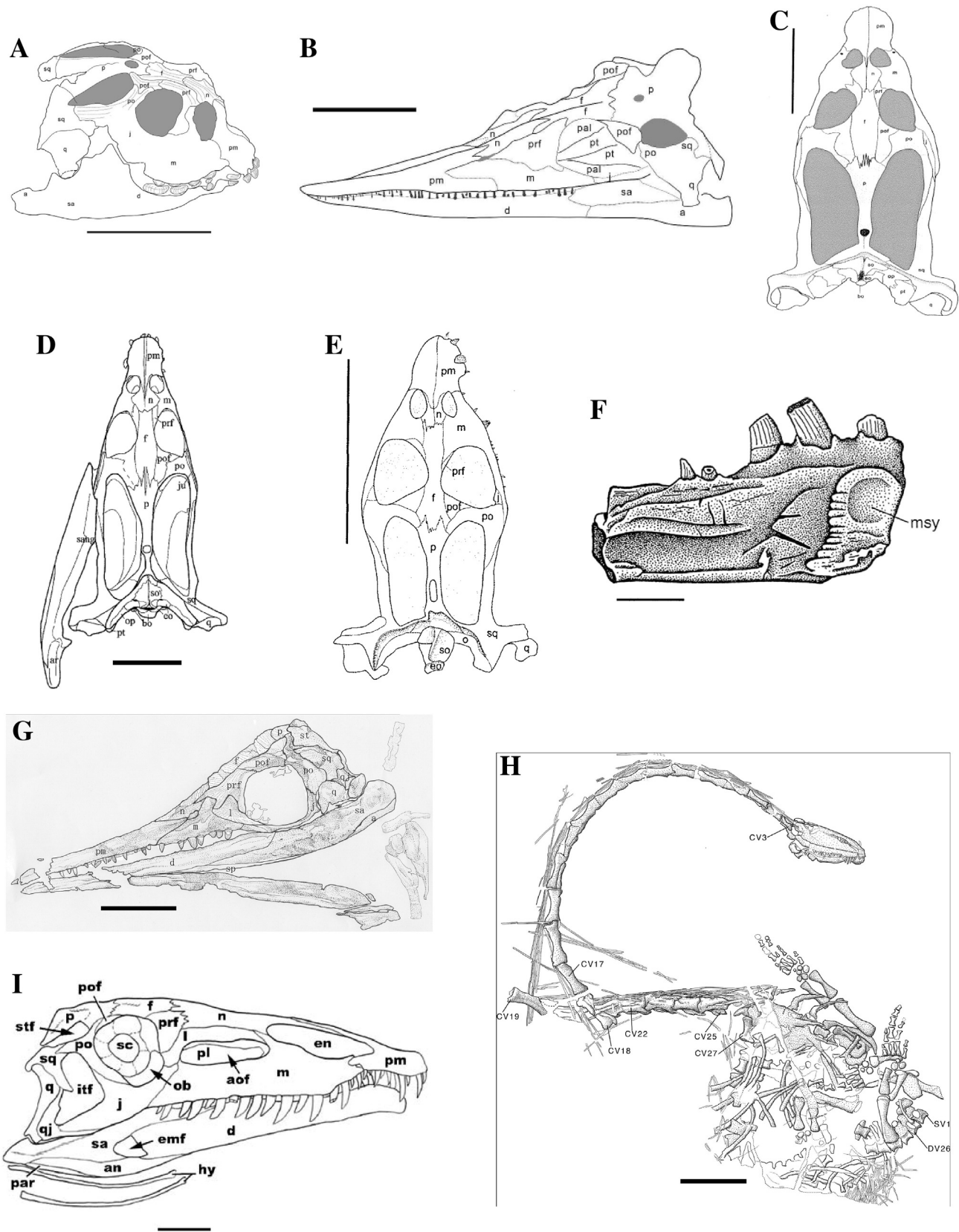
Fig. 23. Middle Triassic marine reptiles from South China, from the Panxian biota (A–E, G–I) and Member 1 of the Guanling Formation at Qingzhen and Guiyang in Guizhou Province (F). (A) *Placodus inexpectatus* Jiang et al., 2008b. (B) *Wumengosaurus delicatomandibularis* Jiang et al., 2008d. (C) *Nothosaurus yangjuanensis* Jiang et al., 2006a. (D) *Nothosaurus rostellatus* Shang, 2006. (E) *Lariosaurus hongguoensis* Jiang et al., 2006b. (F) *Chinchenia sungi* Young, 1965. (G) *Mixosaurus panxianensis* Jiang et al., 2006c. (H) *Dinocephalosaurus orientalis* Li, 2003. (I) *Qianosuchus mixtus* Li et al., 2006. Scale bar of A and C is 100 mm, scale bar of B is 20 mm, scale bar of D–G and I is 50 mm, and scale bar of H is 150 mm. Panel A is from Jiang et al. (2008b). Panel B is from Jiang et al. (2008d). Panel C is from Jiang et al. (2006a). Panel D is from Shang (2006). Panel E is from Jiang et al. (2006b). Panel F is from Rieppel (1999). Panel G is from Jiang et al. (2006c). Panel H is from Rieppel et al. (2008). Panel I is from Li et al. (2006).
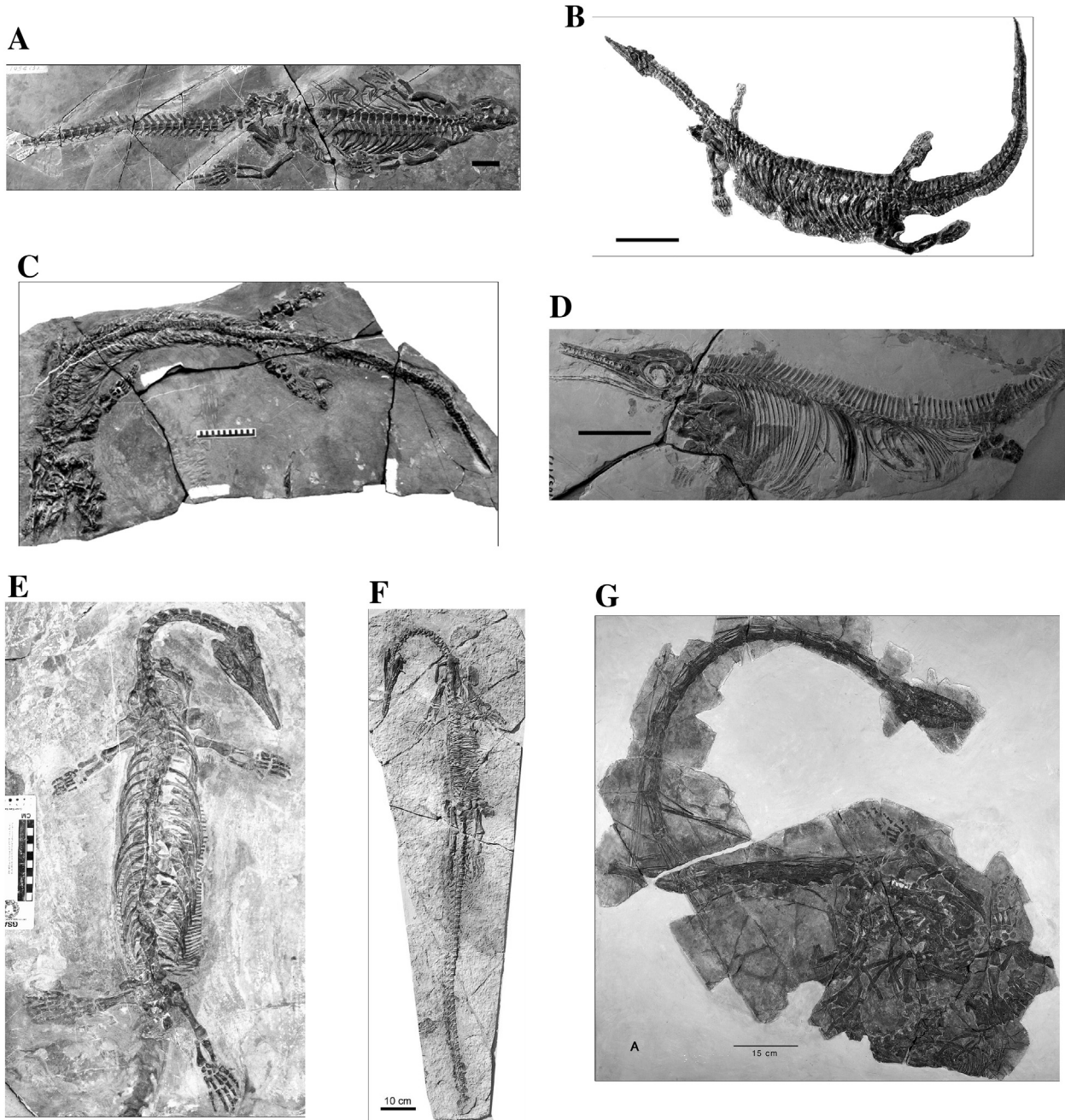
Fig. 24. Photos showing the excellent preservation of Triassic marine reptiles from South China, from the Panxian (A–D. G), Xingyi (E), and Guanling (F) biotas. (A) *Placodus inexpectatus* Jiang et al., 2008b (GMPKU-P-1054, holotype). (B) *Wumengosaurus delicatomandibularis* Jiang et al., 2008b (GMPKU-P-1210, holotype). C. *Xinminosaurus catactes* Jiang et al., 2008c (GMPKU-P-1071, holotype). (D) *Mixosaurus panxianensis* Jiang et al., 2006c (GMPKUP-1039, paratype). (E) *Anshunsaurus wushaensis* Rieppel et al., 2006, a juvenile specimen (KM512). (F) *Anshunsaurus huangguoshuensis* Liu, 1999, a complete and articulated specimen (IVPP V11834). (G) *Dinocephalosaurus orientalis* Li, 2003 (IVPP V13898, referred specimen). Scale bar of A, B, and D–F is 100 mm, scale bar of C is 200 mm, and scale bar of G is 150 mm.
Panel A is from Jiang et al. (2008b). Panel B is from Jiang et al. (2008d). Panel C is from Jiang et al. (2008c). Panel D is from Jiang et al. (2006c). Panel E is from Liu (2007). Panel F is from Liu and Rieppel (2005). Panel G is from Rieppel et al. (2008).

6.2. Reptiles from the Middle Triassic

To date, twenty-six marine reptile taxa have been reported from the Middle Triassic of South China, of which 17 have been recognised as valid taxa (Fig. 23; Appendix 2). Localities yielding these marine reptiles are distributed at Renhuai, Qingzhen, Guiyang, and Panxian in Guizhou Province and Luoping in Yunnan Province (Fig. 1).

Member I of the Guanling Formation at Qingzhen and Guiyang in Guizhou Province yields two sauropterygian taxa, namely *Chinchenia sungi* Young, 1965b (Fig. 23F) and *Sanchiaosaurus dengi* Young, 1965b. Member II of the Guanling Formation in Panxian County, Guizhou Province and

Luoping County, Yunnan Province yields two highly diversified marine reptile faunas, the Luoping and the Panxian biotas.

The marine reptiles from the Panxian biota are highly diversified (Figs. 23A–E, G–I, 24A–D, G; Motani et al., 2008; Jiang et al., 2009). Eleven species (Table 5) and eight ecological guilds (Table 7) of marine reptiles are identified from this biota. Recognised marine reptiles from the Panxian biota include five sauropterygians, three ichthyosaurs, one archosaur, one prolacertiform, and one phylogenetically undetermined taxon (Tables 5, 7; Appendix 2). In addition, Liu and Yin (2008) reported three species of *Mixosaurus* from the Panxian biota. However, none of these was correctly identified, as pointed

Table 5
Summary of numbers of species of major reptile groups from the major marine vertebrate biotas of South China. Numbers are based on the summary of valid taxa (Appendix).

	Chaohu	Luoping	Panxian	Xingyi	Guanling
Ichthyosaurs	1	2	3	0	3
Thalattosaurs	0	0	0	2	5
Nothosaurs	0	0	2	3	0
Pachypleurosaurs	0	2	2	2	0
Placodonts	0	0	1	1	2
Archosauromorphs	0	0	2	0	0
Turtles	0	0	0	0	1
Indeterminate	0	1	1	0	0
Totals	1	5	11	8	11

out by Jiang et al. (2008a), and further preparation is needed to decide their species classification. Chen and Cheng (2010) named *Mixosaurus xindianensis* from Puan County, Guizhou Province, and its type locality and type horizon are actually very close to the type locality of the Panxian biota. The description of *M. xindianensis* is brief, and Chen and Cheng (2010) stated that the only recognised

difference from *M. panxianensis* (Fig. 23G) is the presence of a posterior notch of the ulna, which, however, is also present in *Phalarodon callawayi* (Schmitz et al., 2004). Since there are apparently no diagnostic characters, and the specimens are not currently available for examination, it is taken as species inquirendae here.

One of the most remarkable findings from the Panxian biota is the marine archosaur *Q. mixtus* Li et al., 2006 (Figs. 23I, 24D). The mixture of both aquatic and terrestrial morphological features suggests that this animal lived in a coastal-island environment. The discovery of *Q. mixtus* documents the earliest invasion of the sea by archosaurs. The dagger-like teeth and large size of *Q. mixtus* suggest that it could catch any prey available with a forceful strike.

The Luoping biota has a similar faunal composition to the Panxian biota regarding the reptiles (Liu et al., 2010). Reported marine reptiles from the Luoping biota include one thalattosaur, three sauropterygians and three ichthyosaurs, as well as the same phylogenetically undetermined taxon which also occurrs in the Panxian biota. Five of them are recognised as valid species here (Table 5; Appendix 2), which could be identified into three ecological guilds (Table 7).
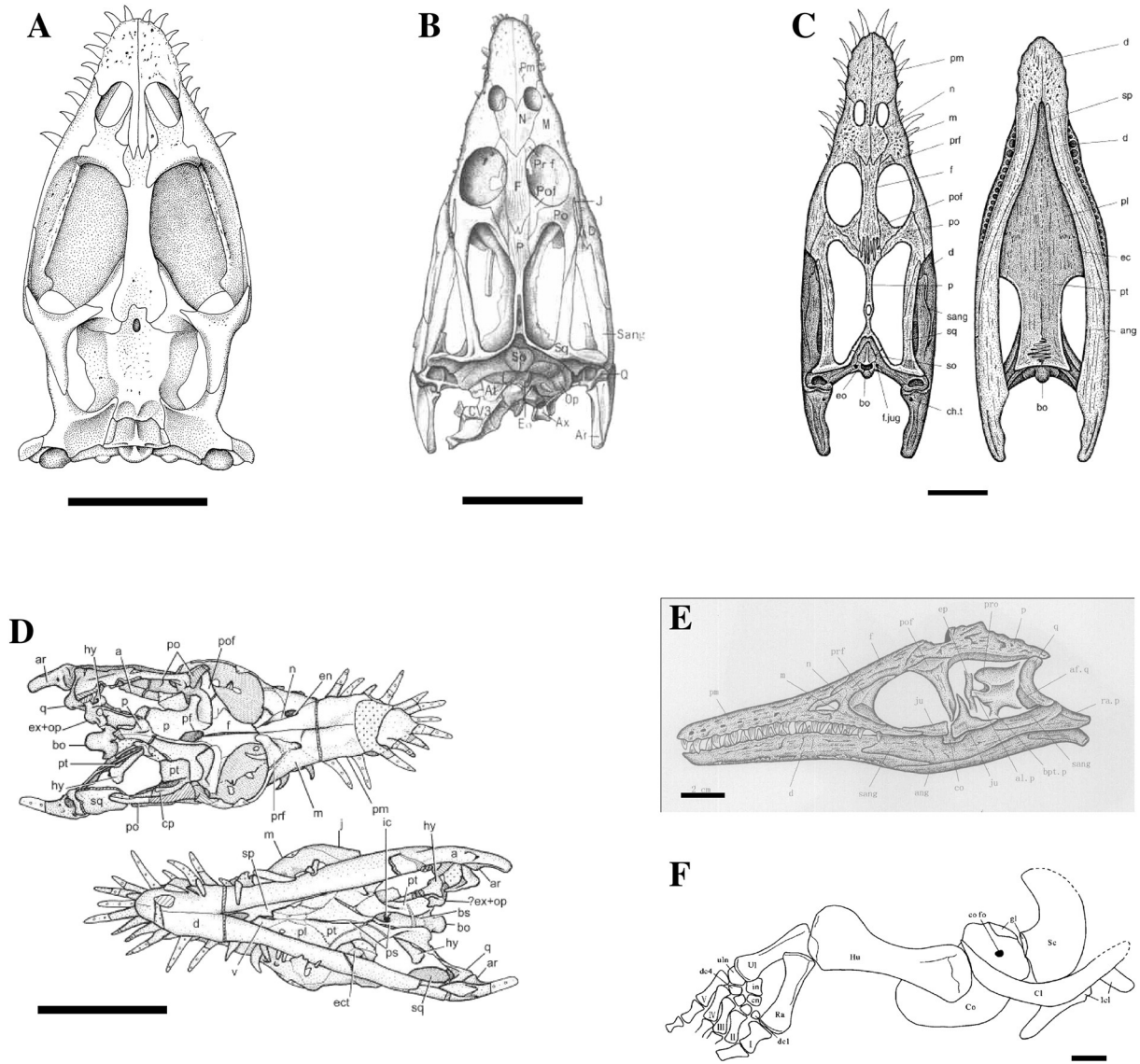
Fig. 25. Latest Ladinian–earliest Carnian marine reptiles from South China, from the Xingyi biota and equivalents. (A) *Keichousaurus hui* Young, 1958. (B) *Nothosaurus youngi*, Li and Rieppel, 2004. (C) *Lariosaurus xingyiensis* Li et al., 2002b. (D) *Yunguisaurus liae* Cheng et al., 2006. (E) *Anshunsaurus wushaensis* Rieppel et al., 2006. (F) *Anshunsaurus huangnihensis* L. Cheng et al., 2007. Scale bar of A, B and D is 50 mm, and scale bar of C, E and F is 20 mm.
Panel A is from Holmes et al. (2008). Panel B is from Li and Rieppel (2004). Panel C is from Rieppel et al. (2003). Panel D is from Y.N. Cheng et al. (2006b). Panel E is from Rieppel et al. (2006). Panel F is from L. Cheng et al. (2007).

Mixosaurus maotaiensis Young, 1965a was also reported from the Guanling Formation at Yueliangtian, Xinqiao, Maotai, Renhuai County, Guizhou Province, although the exact horizon yielding this animal is ambiguous. It was recently revisited and recognised as a valid taxon by Maisch et al. (2003) and Jiang et al. (2005a). However, Jiang et al. (2006c) have most recently demonstrated that *M. maotaiensis* is not diagnostic at species level.

D. luyinensis Liu et al., 2002c was reported from the Middle Triassic Yangliujing Formation at Luying Village, Dingxiao, Xingyi City, Guizhou Province. It was originally described as a potential ichthyosaur by Liu et al. (2002c). It was most recently mentioned by Cheng et al. (2006b) as a possible pistosauroid and identified as a nomen dubium because of the poor preservation of the only known specimen.

6.3. Reptiles from the latest Middle Triassic to Late Triassic

Four localities at Xingyi in Guizhou Province, and Fuyuan, Luxi and Luoping in Yunnan Province have yielded marine reptiles, members of the Xingyi biota, all coming from the Zhuganpo Formation. Sixteen taxa of reptiles from the Xingyi biota have been reported, of which eight are recognised as valid taxa (Figs. 24E, 25; Table 5; Appendix 3) and could be identified into four ecological guilds (Table 7).

The Zhuganpo Formation at Xingyi City in Guizhou Province and Fuyuan County in Yunnan Province yields many well-preserved marine reptiles (Fig. 25). Reported reptile taxa from the Zhuganpo Formation in Fuyuan and Xingyi include seven sauropterygians, two thalattosaurs, and two prolacertiforms, but only eight of them
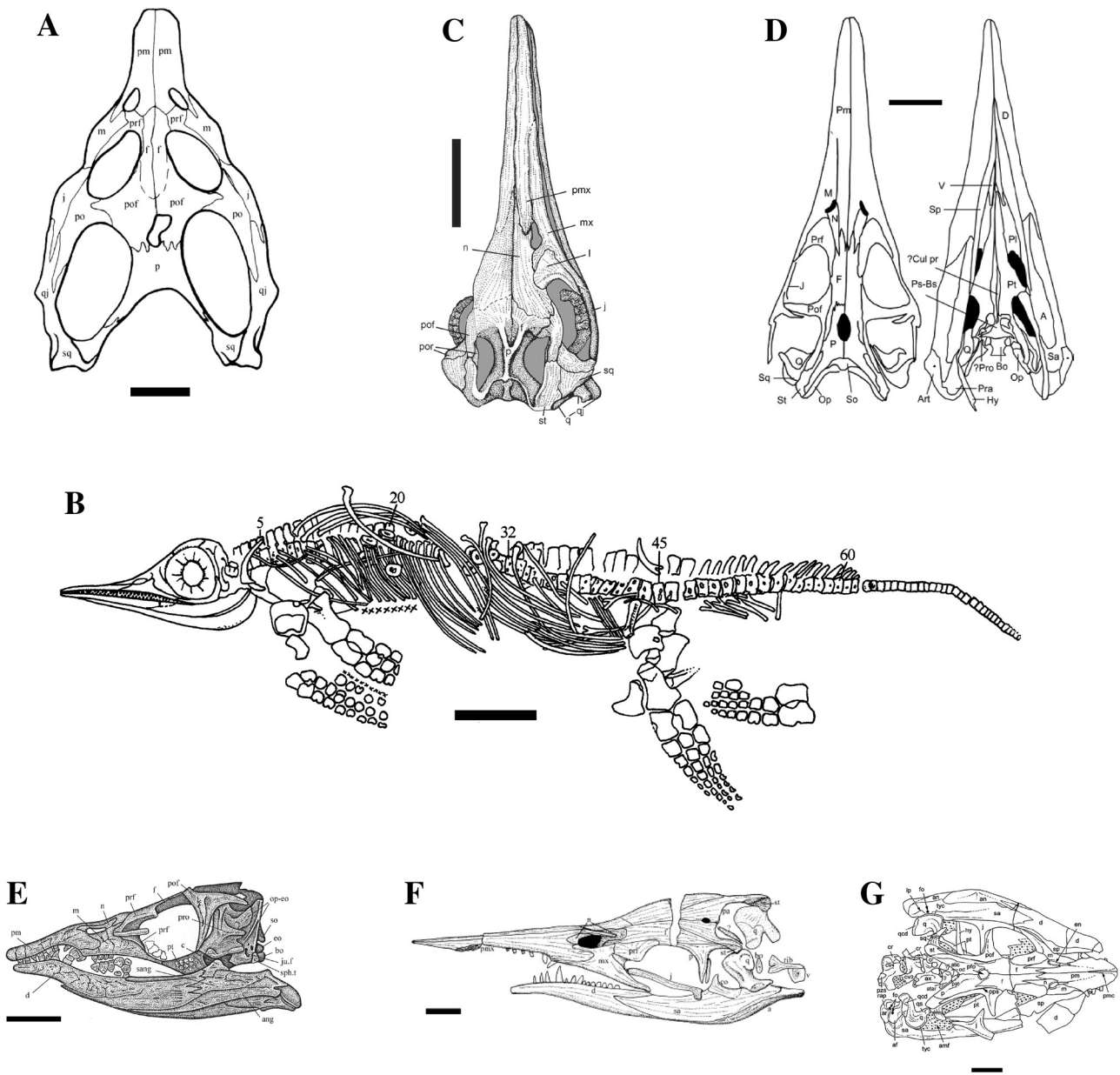
Fig. 26. Late Triassic marine reptiles from South China. (A) *Psephochelys polyosteoderma* Li and Rieppel, 2002. (B) *Qianichthyosaurus zhoui* Li, 1999. (C) *Guizhouichthyosaurus tangae* Cao and Luo in Yin et al., 2000. (D) *Anshunsaurus huangguoshuensis* Liu, 1999. (E) *Xinpusaurus suni* Yin in Yin et al., 2000. (F) *Xinpusaurus bamaolinensis* Cheng, 2003. (G) *Miodentosaurus brevis* Y.N. Cheng et al., 2007. Scale bar of A is 20 mm, scale bar of B is 100 mm, scale bar of C is 200 mm, scale bar of D, E and G is 50 mm, and scale bar of F is 10 mm.
Panel A is from Li and Rieppel (2002). Panel B is from Nicholls et al. (2003). Panel C is from Maisch et al. (2006). Panel D is from Liu and Rieppel (2005). Panel E is from Rieppel and Liu (2006). Panel F is from Jiang et al. (2004). Panel G is from Y.N. Cheng et al. (2007).

could be identified to the species level (Appendix 3). The most spectacular discovery from the Xingyi biota is the large, long-necked prolacertiform *Tanystropheus* (Rieppel et al., 2010). The specimen from South China is indistinguishable from larger specimens of *Tanystropheus longobardicus* from western Tethys. The discovery of these similar semi-terrestrial animals so far apart demonstrates a close faunal affinity between the eastern and western Tethys Ocean realms.

Sun et al. (2005b,c) reported a late Ladinian marine reptile assemblage from Niubudai Village, Banqiao, Luoping County, Yunnan Province. The fossil-bearing stratum was recorded as the fourth member of the Gejiu Formation, which corresponds to the Zhuganpo Formation in Guizhou Province. Ammonoid assemblages support a late Ladinian age for this fauna (Sun et al., 2005b,c). Known reptile taxa from this fauna include cf. *Askeptosaurus*, *Lariosaurus* sp., and *Keichousaurus* sp., all of which cannot be differentiated from reported taxa in Guizhou Province (Appendix 3).

The famous Guangling biota from the Carnian Xiaowa Formation is known for its large and well-preserved marine reptiles (Jiang et al., 2005a, 2005b, 2005c; Wang et al., 2008). To date, three placodonts, seven ichthyosaurs, and ten thalattosaurs have been reported, of which 11 have been recognised as valid taxa (Figs. 24F, 26; Table 5; Appendix 4) and they could be identified into eight ecological guilds (Table 7). These marine reptiles include numerous complete, articulated, large ichthyosaur skeletons more than 10 m in length, and the first Chinese thalattosaurs and placodonts to be reported. One ichthyosaur from Guanling, *Qianichthyosaurus zhoui* Li, 1999, (Fig. 26B) is however, much smaller, ranging in length from 0.5 to 2 m, and very similar, if not identical, with *Toretocnemus californicus* Merriam, 1903, from the Carnian of the western United States (Nicholls et al., 2003). The larger ichthyosaurs, from 5 to 10 m long, have been assigned to the genera *Guizhouichthyosaurus* and *Guanlingsaurus* (Sander et al., 2011; Ji et al., 2013). The thalattosaurs *Anshunsaurus* (Fig. 24E, 26D) and *Xinpusaurus* (Fig. 26E, F) are 1.4–2.4 m long, and appear superficially ichthyosaur-like, with their long, narrow snouts, but their heads are relatively small and their bodies somewhat serpentine, when compared to the ichthyosaurs. Another thalattosaur, the short-snouted *Miodentosaurus brevis* Cheng et al., 2007b, is more than 4 m long and shares a close affinity with the *Askeptosaurus* from western Tethys (X.C. Wu et al., 2009). Two species of *Wayaosaurus*, established by Zhou in Yin et al. (2000), were confirmed as thalattosaurs by X.C. Wu et al. (2009), but their true taxonomic status cannot be clarified without further preparation of the type material. Guanling sauropterygians comprise the turtle-shaped placodonts *Sinocyamodus xinpuensis* Li, 2000 and *Psephochelys polyosteoderma* Li and Rieppel, 2002, but other taxa, such as pachypleurosaurs and nothosaurs, are absent.

One of the most remarkable recent finds was the world's oldest turtle, *Odontochelys semitestacea*, which predates the previously oldest forms by some 5–10 Myr, and shows a partially intermediate stage in evolution (Li et al., 2008). *Odontochelys* has a fully developed ventral plastron, but the dorsal carapace consists of neural plates only. The dorsal ribs are expanded, and osteoderms are absent. The *Odontochelys* specimen shows that the plastron evolved before the carapace and that the first step of carapace formation is the ossification of the neural plates coupled with a broadening of the ribs. This had been predicted from embryological studies of developing turtle embryos. Further, the carapace shape, and the nature of the forelimbs suggest that *Odontochelys* inhabited 'stagnant or small bodies of water'.

7. Evolution of the vertebrate-bearing sedimentary basins of the South China Triassic

The Guizhou–Yunnan marine basin showed considerable palaeogeographic evolution through the Middle and Late Triassic. During the Anisian, Ladinian, and early Carnian (Fig. 27A), the Nanpanjiang Basin was centred on a deep-water portion, surrounded by shallow marine shelf areas from 100 to 300 km wide, and land to east and west. There was a substantial transgression between early and late Carnian, and the Nanpanjiang Basin contracted substantially, and especially the surrounding shelf zones to east, north and west (Fig. 27B). These substantial palaeogeographic shifts changed the modes of deposition and affected the marine life and modes of preservation seen in the pre- and post-regression exceptional biotas.

The basins with exceptional fossil preservation share the general absence of bioturbation in the fossil layers, and the common occurrence of slump structures, presumably associated with movement of unconsolidated sediments along a gentle slope during earthquake activity. These basins are similar to each other in their restricted circulation, density stratification of the water column, and dysoxic to anoxic bottom water, but they differ in size, sedimentary dynamics, and faunal assemblages. These were restricted basins, and the bottom became dyaerobic or anoxic because of restricted circulation associated with a drop in sea level, and the anoxic condition of the bottom water preserved the carcasses. A rise in relative sea level might have caused intermittent reoxygenation of the basin or finally terminated the restricted circulation in the depressions and closed the taphonomic window that led to the exceptional preservation of the vertebrates.

In the Luoping basin, the lower units (Beds 2–66) with dark grey, medium- to thick-bedded, laminated micritic limestones, are enriched in fossil fishes, arthropods, and plants. It should be noted that conodonts are common in the lower unit, but none has been found from the upper unit (Beds 75–110), which consists of dark-grey to yellowish-grey laminated muddy limestones. Since conodonts are typical elements of open marine envinroments, it is reasonable to assume that the Luoping basin became restricted and stagnant, changing from a semi-enclosed basin at the time of the lower unit, after a short time of reoxygenation indicated by the bioturbated limestone of the middle unit, to a deep, relatively
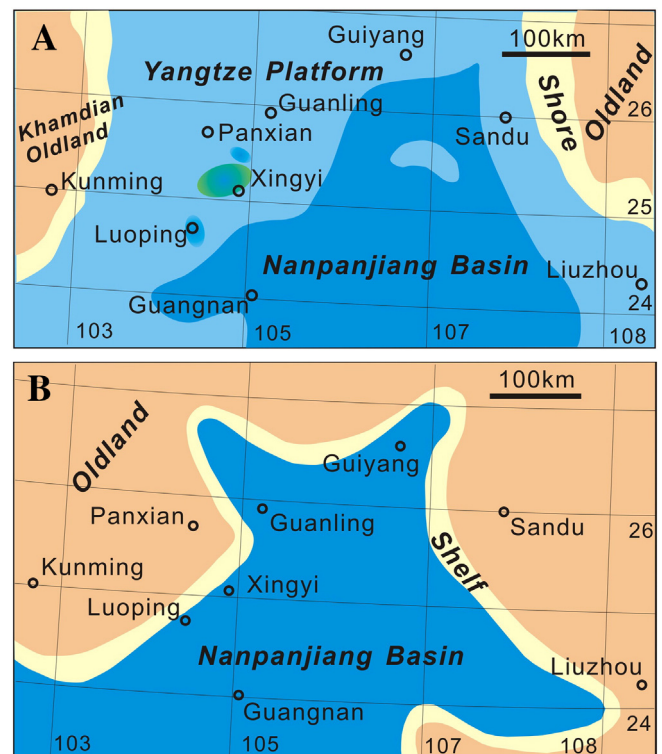

Fig. 27. Palaeogeography of southwest China in the Middle to Late Triassic, showing an extensive marine basin in the Middle Triassic to early Carnian (A), then much reduced in size following a major regression, during the late Carnian (B). Based on Liu and Xu (1994).

stagnant basin at the time of the upper unit. The occurrence of conifer debris and terrestrial animals (e.g. millipedes) indicates a location close to land. The overlying massive limestone indicates a normal platform environment and the end of the restricted basin. Apart from the bioturbated layer in the upper unit, there were several episodes with oxygenated bottom waters. The middle bioturbated limestone probably represents a regional transgressive episode that lasted long enough to allow benthic organisms such as bivalves and arthropods to mine the substrate and disturb the sediments. Other reoxygenation events, perhaps caused by extraordinary storms, were much shorter and did not allow enough time for the establishment of a mature community, only for some shallow burrowers.

The Luoping basin can be traced over an area of some 200 km^2. Recent work by a team from the Chengdu Institute of Geology and Mineral Resources has led to the discovery of a new, contemporary basin south of Luoping, namely the Luxi basin. Preliminary work shows similar faunal assemblages in both basins, but further work is needed to compare their faunas and lithologies.

The Panxian basin is slightly younger than the Luoping basin (see Section 4.2). The known extent of the basin is about 6.55 km^2, much smaller than the Luoping basin. The interval containing exceptional fossils is only 4 m in thickness, consisting of mainly bituminuous shales and a few layers of micritic limestones. However, it is not straightforward to compare the succession between Luoping and Panxian since the succession in the latter is much condensed. The fossil assemblage in Panxian is less diverse than that of Luoping, consisting of marine reptiles and fishes, bivalves, brachiopods, gastropods, ammonoids, conodonts, and plants. So far, no arthropods have been recovered. It is worthy of note that there are no bioturbated layers within the fossil-bearing interval, indicating the absence, or no records, of episodic oxygenation events and the continuation of stagnant and anoxic environments until the end of the existence of the restricted basin. Compared to Luoping, the Panxian basin is much restricted and stagnant, with a minor influence of turbidity or storm currents. The role of microbial sealing in exceptional preservation remains unclear although it cannot be excluded.

The intervals representing the Xingyi basin can be traced in outcrop for several tens of kilometres, extending some 100 km from Xingyi in the east, to Fuyuan–Luoping in the west. Whether this indicates a single large basin or several separated small basins is unclear, and further investigation is needed. The fossil-containing interval is in the upper part of the Zhuganpo Formation. The lower part of the Zhuganpo Formation in western Guizhou and eastern Yunnan is characterised by laminated micritic limestones, whereas the upper part with the Xingyi biota consists of mainly intercalation of micritic limestones and bituminuous shales. Exceptionally preserved fossils are recovered mostly from the shales and rarely from the micritic limestones. In some quarries such as Nimaigu near Xingyi and Changdi near Luoping, the fossil-containing intervals are well exposed, with a thickness of 6–7 m. The fossil assemblage of the Xingyi biota is mainly dominated by fishes and marine reptiles, associated with less common bivalves, brachiopods, gastropods, ammonoids, conodonts, and plants, as well as rare echinoderms and arthopods. Arthropods are represented by a single mysidian taxon. The occurrence of some terrestrial reptiles (Li et al., 2007) implies nearby land or islands.

The development of the Guanling basin is different from those mentioned above, having occurred in a much-reduced marine basin (Fig. 27B). It was a shelf basin rather than an intraplatform basin, formed in an anoxic offshore environment following rapid transgression. The fossil intervals are composed of mainly marl or calcareous shales, from the lower part of the Xiaowa Formation. As the depocentre during the stage, the thickness of the Xiaowa Formation in Guanling area is over 100 m (Wang et al., 2008), whereas the thickness is normally less than 20 m in other areas of Guizhou and Yunnan. Characteristic fossils include large ichthyosaurs and

abundant articulated crinoids. Wang et al. (2008) suggested a basin stagnation model to explain the fossil preservation. According to their model, the bottom water was anoxic, so benthic organisms are absent. The bivalves and crinoids perhaps lived at the surface of the water column with a pseudoplanktonic lifestyle.

The exceptional preservation of the Panxian, Xingyi, and Guanling biotas has been attributed to anoxia (Wang et al., 2008, 2009), but anoxia alone cannot stop scavenging (Briggs, 2003). Hu et al. (2011) suggested that the exceptional preservation of the Luoping biota resulted from anoxia and microbial sealing rather than rapid burial. Microbial mat structures (wrinkle marks) are commonly observed from the fossil layers in Luoping (Hu et al., 2011); an energy dispersive X-ray analysis on fossil fragments and their groundmass (Luo et al., in press) indicated that microbial mats also played an important role in the phosphatization of fossil components of the Luoping biota. Such microbial mats have not been reported from Panxian, Xingyi, or Guanling. However, it is probable that they occur but have been missed or overlooked; we have noted abundant microbial mat structures during recent work in a quarry yielding the Xingyi biota from near Chajiang Town on the border of Yunnan and Guizhou provinces, implying the important role of microbial sealing in exceptional preservation of these biotas.

Perhaps the only region comparable to the SW Chinese Middle and Late Triassic is the southern Alps in Europe, which was located in western Tethys. Several basins have been reported (Tintori, 1992; Jadoul et al., 1994; Furrer, 1995, 2003), extending temporally from the Grenzbitumenzone (late Anisian), through the Kalkschieferzone (late Ladinian), to the Zorzino Limestone (Norian), and spatially from Lombardy and Perledo (North Italy), Ducan (Davos, Switzerland) to Monte San Giorgio (Meride, Italian–Swiss border).

## 8. Marine ecosystem rebuilding in the Triassic

8.1. Influence of physical environmental change

Organismal diversity is in part controlled by the physical environment. For example, the total diversity of life in the sea, which is essentially life on the continental shelf, is dependent on sea level (Newell, 1952; Peters, 2005; Benton, 2009): at times of transgression, diversity rises as the shelf area expands, and at times of regression diversity diminishes. For marine reptiles, while the fossil record of open ocean forms is influenced by sampling bias, especially the artificial diversity boosts of fossil Lagerstätten, shallow marine forms show strong correlation of diversity and sea level (Benson and Butler, 2011), suggesting a common cause effect (Peters, 2005). For the Triassic, Kelley et al. (2013) noted a correlation of marine reptile diversity with the strontium isotope curve, a measure of the volume of land-derived sediment entering the sea, and so correlated with tectonically controlled sea level change. They found that the rate of sea-level change, rather than the absolute magnitude of sea level or the flooded shelf area, played a role in shaping patterns of ecological diversification and ecologically selective extinction during the Triassic. The only mismatch is for the Early Triassic, a time of high sea level but low marine reptile diversity, but this marked the time of initial diversification of the marine reptile groups.

During post-PTME times, there is broad consensus that global environmental conditions did not quickly settle back to the pre-extinction norm. Indeed, repeated carbon crises indicate that there were three or four bursts of sudden global warming after the PTB, during the 5–6 Myr of the Early to early Middle Triassic, associated with consequent atmospheric heating, acid rain, landscape stripping, ocean acidification, and seabed anoxia (Payne et al., 2004; Retallack, 2012; Sun et al., 2012). Indeed Sun et al. (2012) presented several lines of evidence that global temperatures rose rapidly to exceptionally high values at the PTB, and these high temperatures continued with several extreme peaks through the Early Triassic. This is shown

by phosphate oxygen isotope curves, as well as by the loss of calcareous algae, the near-absence of fish in equatorial Tethys, and the dominance of small taxa of invertebrates during the thermal maxima. Further, the high temperatures drove most Early Triassic plants and terrestrial animals out of equatorial terrestrial ecosystems and they were probably a major cause of the end-Smithian crisis.

Further work is required to discriminate the timing, scale, and effects on the recovery of life of each of these early Triassic carbon crises. If these crises dealt repeated blows to life on land and in the sea, as seems likely, then it might be hard to determine the relative roles of extrinsic and intrinsic controls on diversification and ecosystem rebuilding because the extrinsic crises would potentially
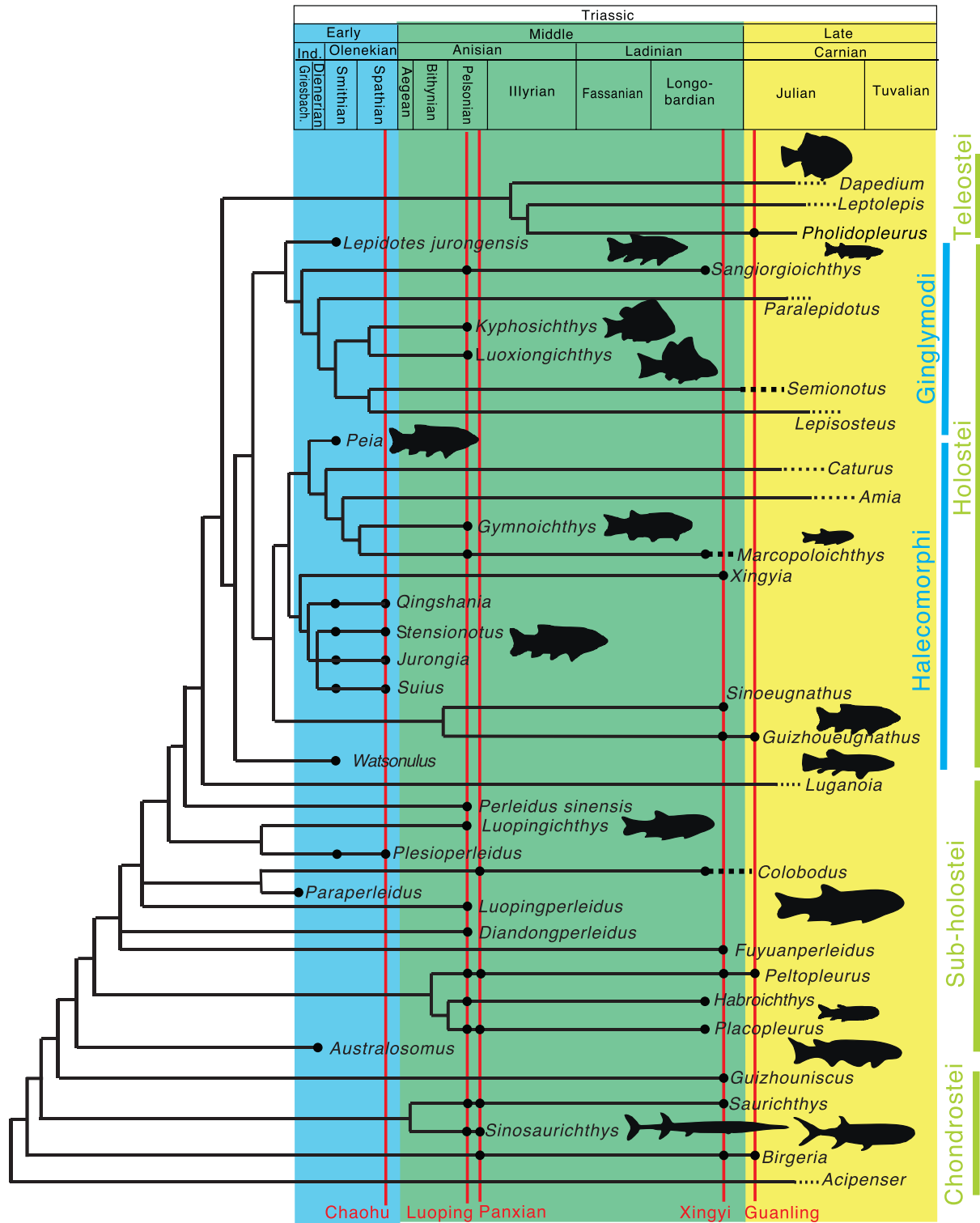
Fig. 28. Phylogeny of the main actinopterygian genera from the Triassic of South China. The phylogeny is based on a cladistic analysis of 31 taxa chosen from representatives of the five key Lagerstätten (Chaohu, Luoping, Panxian, Xingyi, Guanling) and ten other typical Triassic genera from elsewhere in the world. Abbreviations: Griesbach., Griesbachian; Ind., Induan. Each fish genus was coded for 60 characters adopted from Xu and Wu (2012). Characters 32 (maxillary shape) and 45 (preoperculum) were modified from Hurley et al. (2007). Some characters states were taken from Gardiner et al. (1996).

swamp or conceal the effects of species interactions (competition, predation).

Debates hitherto over the timing of recovery, whether it was fast or slow, might be immaterial. Certainly, some taxa such as foraminifera, ammonites, and fishes diversified within the first 1–2 Myr of the Early Triassic (e.g. Brayard et al., 2009; Song et al., 2011), but the long durations of the so-called coral gap and chert gap in the sea and the coal gap on land, amounting to 10–15 Myr, suggests that ecosystems were far from normal for a very long time. The South China basins offer the potential to disentangle the recovery of marine ecosystems at fine scale (Chen and Benton, 2012).

8.2. Macroevolutionary patterns

From a wider perspective, the episodes following mass extinctions have long been seen as special, times when normal ecosystem regulation had broken down, and in particular when competition was supposed to be weak (Erwin, 2001; Solé et al., 2002, 2010). In the broadest sense, Erwin (2001) noted that 'although mass extinctions probably account for the disappearance of less than 5% of all extinct species, the evolutionary opportunities they have created have had a disproportionate effect on the history of life.' However, given the harsh environmental conditions of the Early Triassic, it is instructive
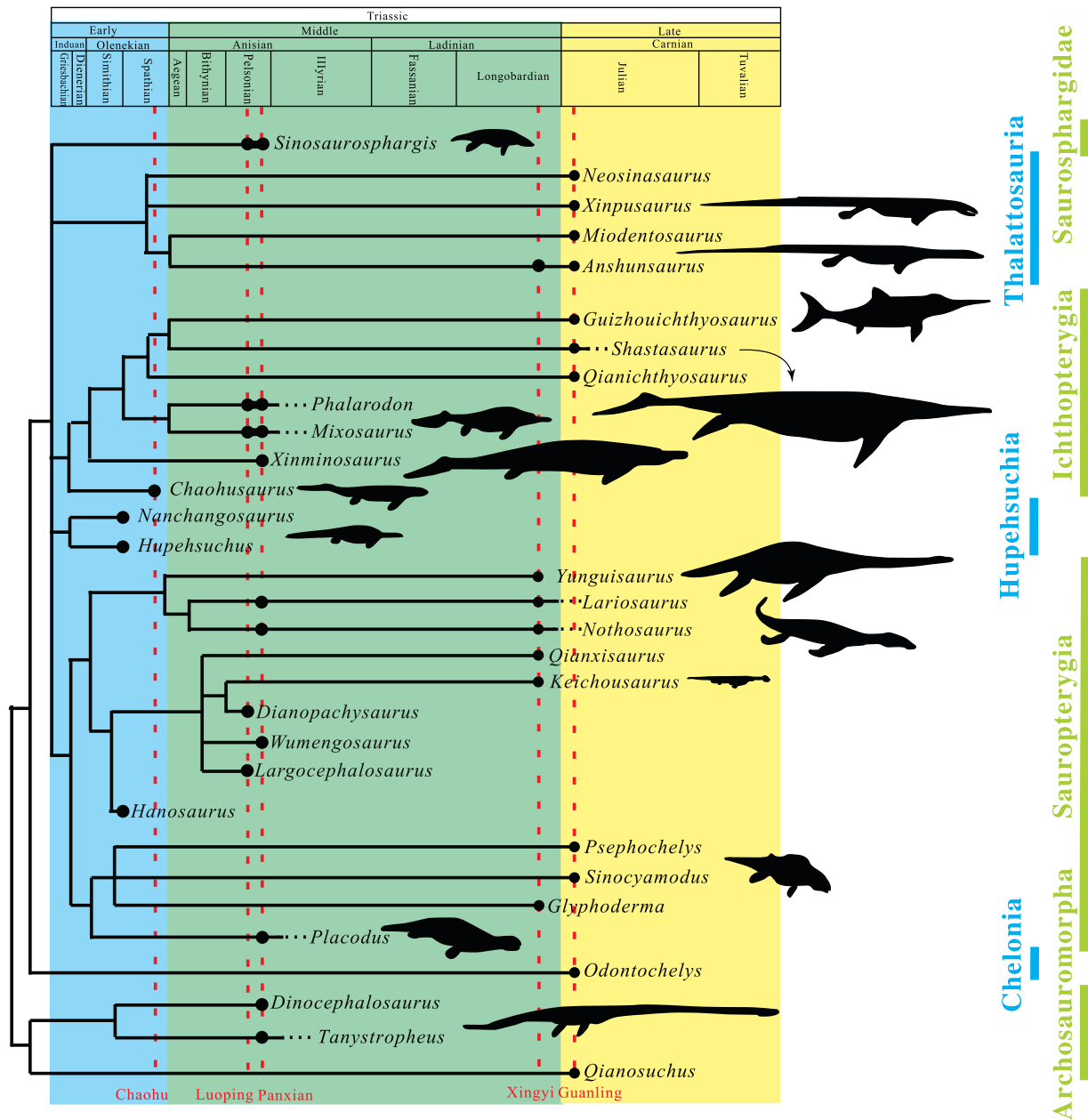
Fig. 29. Phylogeny of all valid reptilian genera from the five key Lagerstätten (Chaohu, Luoping, Panxian, Xingyi, Guanling) in the Triassic of South China and the well preserved biota from Yuanan and Nanzhang counties in Hubei Province. Abbreviations as in Fig. 31.
The basic topology is adapted from Li et al. (2011). Specific topologies for sauropterygians, ichthyosaurs and thalattosaurs follow Liu et al. (2011a,b), Sander et al. (2011), and X.C. Wu et al. (2009), respectively. Reconstruction of external morphology of major marine reptile clades is adapted from Kelley et al. (2013).

to see how the record of recovery is manifest in the South China Lagerstätten.

We focus here on the establishment of marine vertebrates in Early and Middle Triassic ecosystems — sharks and bony fishes were to an extent recovering, in the sense that they were evolving into feeding guilds that may have been vacated during the PTME (although the severity of the PTME in terms of putative fish extinctions is debated; Friedman and Sallan, 2012). Marine reptiles, on the other hand, were new in the Triassic, and so were largely or wholly establishing themselves in new niches or new trophic guilds, unless a case can be made that some of them were usurping roles previously taken in the Middle or Late Permian by predatory sharks or bony fishes.

Actinopterygii, the bony fishes, showed a major diversification in the latest Early and Middle Triassic of South China (Fig. 28), with sequential expansion of the 'subholosteans', primarily perleids, in the Early Triassic, and then the Chondrostei and Holostei (Halecomorphi and Ginglymodi) in the Middle Triassic (Anisian). The Holostei became the most diverse of all fish clades in the Luoping and Panxian biotas. The Teleostei originated with three common genera in the later Middle Triassic (Ladinian) and Late Triassic of the Xingyi and Guanling biotas. Among other fish groups, chondrichthyan diversity is hard to assess because the fossils (mainly teeth) are sporadic and hard to classify. Although the fossil record shows a late Olenekian expansion of taxa, the phylogeny (Fig. 28) demonstrates that at least 19 lineages spanned the Early Triassic, 12 of which (Teleostei, Caturidae, *Luganoia*, *Perleidus*, *Luopingperleidus*, *Diandongperleidus*, *Fuyuanperleidus*, Peltopleuridae, *Guizhouniscus*, Saurichthyidae, Birgeriidae, Acipenseridae) had no Early Triassic record. Without better documentation of latest Permian fossils, it cannot be said how many of these 19 lineages also crossed the PTB. Only one can be documented for sure, the Saurichthyiae, represented by fossils in the Chinese Late Permian. The basal amiiform *Caturus* has been reported from the Changxing Formation in Jiangxi, and is also known from the Triassic. At present, it cannot be determined whether there was indeed an explosive diversification of bony fishes in the Early and Middle Triassic (Fig. 28), or whether this is exaggerated by a poor Late Permian and Early Triassic record.

Coelacanths were present in the Chaohu, Luoping, Fengshan, and Guanling assemblages, always at low diversity (1–2 species; Tables 4, 5). Nonetheless, the apparently continuous occurrence of coelacanths throughout the Triassic, and especially their globally very high diversity in the Early Triassic suggests that they might have been favoured in some way by marine conditions in the Early and Middle Triassic. Wen et al. (2013) suggest the relatively high diversity of coelacanths in the Early Triassic, and adaptations of living *Latimeria* to low-oxygen conditions, might suggest that the group included 'disaster taxa' that benefited from anoxic and dysoxic oceanic conditions in the aftermath of the PTME.

Several clades of marine reptiles (Ichthyosauria, Thalattosauria, Sauropterygia, Archosauromorpha) radiated in the late Early and early Middle Triassic (late Olenekian to Anisian). These are sampled by the five major marine faunas (Fig. 29; Table 5), showing that ichthyosaurs were first to originate and then maintained a relatively steady diversity of three species per biota, except for the Xingyi biota, which lacks ichthyosaurs, perhaps for environmental reasons. Thalattosaurs started rare, with no examples from Chaohu or Panxian, and one from Luoping, but then diversified to two species in the Xingyi biota and five in the Guanling biota, being the dominant group of large marine predators there. The sauropterygians also diversified, from no species in the Chaohu fauna, to five and seven, a mix of pachypleurosaurs and nothosaurs, and one placodont, in the Luoping and Panxian biotas, respectively, six in the Xingyi biota, and only two placodonts in the Guanling biota. Other marine groups include single examples of prolacertiforms and archosaurs in the Luoping, Panxian, and Xingyi biotas, and the first turtle, *Odontochelys*, in the Guanling biota. Taxon numbers are low and it is impossible to determine whether variations in numbers might represent broader

aspects of the relative success of different groups through time, or perhaps a substantial component of environmental and preservational variations between the biotas.

Comparison of the fish and reptile cladograms confirms an offset in timing of diversification of actinopterygian fishes and the various marine reptile clades. The delay in reptilian diversification may have been a combination of ecological (higher elements in food chains emerge after their prey) and phylogenetic reasons (all evidence suggests the various marine reptile groups emerged only after the PTB). Although there were many undiscovered fish clades in the Early Triassic, their relative abundances might have remained low, and hence fossils are rare, during the poor environmental conditions of the first 5 Myr of the Triassic.

8.3. The Triassic recovery and ecosystem rebuilding

The changing diversity of vertebrates through the Triassic documents some aspects of their recovery in the South China seas after the PTME. The best indications of change probably do not come from raw counts of taxa (e.g. Tables 2–5) because local diversity records a mix of regional diversity and local environmental and facies effects. Counts of major clades and feeding guilds may be more informative. Among the fishes, we can count chondrichthyans, coelacanths, and actinopterygians (divided further into chondrosteans, sub-holosteans, halecomorph
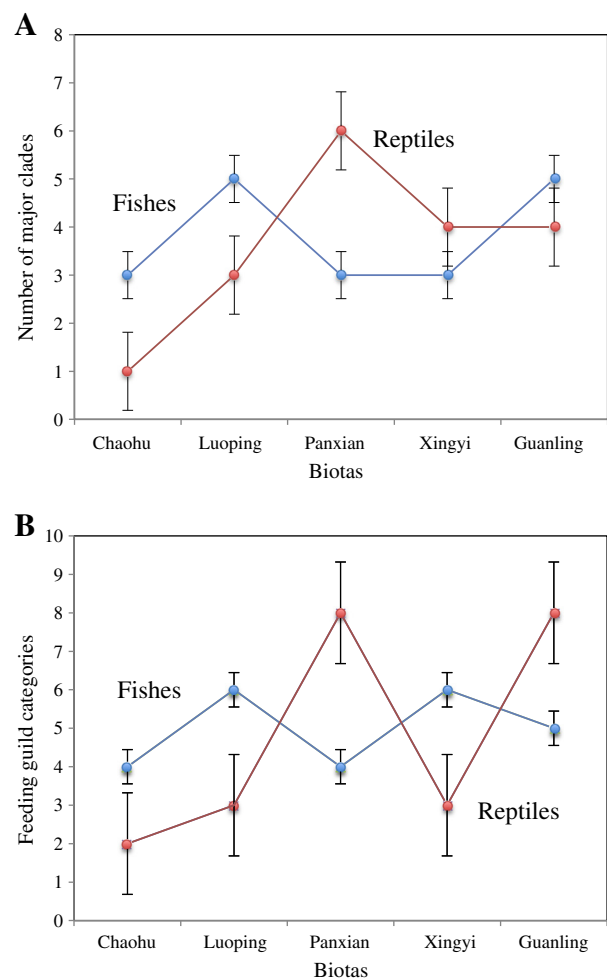
Fig. 30. Evolution of marine vertebrates through the Triassic of South China, documented for the Chaohu (late Early Triassic), Luoping (early Middle Triassic), Panxian (early Middle Triassic), Xingyi (late Middle Triassic), and Guanling (early Late Triassic) biotas. (A) The number of major clades of fishes and reptiles (data from Tables 2–5). (B) The number of feeding guild categories of fishes and reptiles (data from Tables 6, 7). Confidence intervals are standard errors.

holosteans, ginglymodan holosteans, and teleosts), and among the reptiles ichthyosaurs, thalattosaurs, sauropterygians (nothosaurs, pachypleurosaurs, placodonts), archosauromorphs (prolacertiforms, archosaurs), and turtles. As noted, these clades did not all appear at once, but in succession (Fig. 30A): the number of fish clades ranged between three and five, with no clear temporal trend, but the number of reptile clades rose from one in Chaohu to three in Luoping and six in Panxian, and fell to four in Xingyi and Guanling.

When the fishes are divided into feeding guilds (Table 6) and the reptiles into feeding guilds and body size categories (Table 7), there are some trends of change through the Triassic. The numbers of fish feeding guilds vary between four and six, and so there is no evident trend of increase through time, whereas reptile guild numbers rose from two and three in the Chaohu and Luoping biotas, respectively, to eight in the Panxian and Guanling biotas (Fig. 30B). It should be noted, however, that the rise is not clearcut and simple: the younger Xingyi biota shows only three reptilian feeding guilds, and the approximately coeval Luoping and Panxian biotas show very different values: three and eight, respectively. The contrast between Luoping and Panxian suggests that there are major environmental controls on the numbers of reptile specimens and the diversity of feeding guilds represented, but the Luoping taxa require further study to be sure.

When the fish and reptile species are assigned to broader guild categories and the reptiles to size categories (Tables 6, 7), there do appear to be some generalised temporal trends (Fig. 31). In terms of the pursuit and ambush predatory categories, fishes show absolute declines from the Chaohu and Luoping biotas through the Panxian, Xingyi, and Guanling (Fig. 31A). Reptiles, on the other hand, show

absolute increases in numbers of species assigned to the pursuit and ambush feeding categories through those three younger biotas. In summary, whereas reptile species make up 18% of vertebrate taxa at Chaohu, they make up 77% at Guanling.

Rough body size categories highlight a similarly marked change among the marine reptiles through the Triassic in South China, with only small-sized forms at Chaohu, only small and medium at Luoping, and increases in the proportions of medium- and large-sized taxa at Panxian and later (Fig. 31B). It is important to note that the critical switch-over appears to happen between Luoping and Panxian, and could be partly a real temporal change as ecosystems became more complex at a time of maximum recovery (Hu et al., 2011; Chen and Benton, 2012), but also could represent some facies and environmental effects in light of the closeness of age between Luoping and Panxian.

9. Conclusions

The Triassic of South China offers one of the most impressive series of fossiliferous sediments that span the PTB and document, in many parallel sections, rich marine faunas from a variety of sedimentary settings through the Early, Middle, and early Late Triassic. In this review, we have focused on the vertebrates, and we have documented the current situation, in which enormous advances have been made in the past twenty years to improve stratigraphic acuity and correlation, and understanding of taxonomy and phylogeny of the fishes and reptiles. Further work has to be done to identify the true diversity of species, with large samples of undescribed materials from new Early Triassic sites and from Luoping and Xingyi. In addition, the species lists have to be

Table 6
Classification of the Triassic fishes from South China into major feeding guilds.

	Feeding guild	Pursuit predators	Ambush predators
Chaohu biota	Catch and grind	*Plesioperleidus yantzensis*	
		Plesioperleidus jiangsuensis	
		Plesioperleidus dayeensis	
	Pierce		*Saurichthys* sp.
	Grasp	*Peia jurongensis*	*Chaohuichthys majiashanensis*
		Jurongia fusiformis	
		Qingshania cercida	
		Suius brevis	
	Suction		
Luoping biota	Catch and grind	*Luopingichthys bergi*	
		Perleidus sinensis	
		Luopingperleidus sui	
		Diandongperleidus denticulatus	
	Pierce	*Sinosaurichthys longimedialis*	*Saurichthys yunnanensis*
		Sinosaurichthys minuta	*Saurichthys dawaziensis*
			Saurichthys sp.
	Grasp	*Sangiorgioichthys sui*	*Luopingcoelacanthus eurylacrimalis*
		Gymnoichthys inopinatus	*Yunnancoelacanthus acrotuberculata*
			Luoxiongichthys hyperdorsalis
			Kyphosichthys grandei
	Suction	*Habroichthys broughi*	
		Marcopoloichthys ani	
		Placopleurus sp.	
Panxian biota	Catch and grind	*Colobodus baii*	
	Pierce	*Sinosaurichthys longipectoralis*	*Birgeria* sp.
	Grasp		
	Suction	*Placopleurus* sp.	
Xingyi biota	Catch and grind	*Fuyuanperleidus dengi*	
		Xingyia gracilis	
		Guizhoueugnathus analilepida	
	Pierce	*Guizhouniscus microlepidus*	*Birgeria liui*
			Saurichthys sp.
	Grasp	*Sinoeugnathus kueichouensis*	
		Potanichthys xingyiensis	
	Suction	*Peltopleurus orientalis*	*Guizhoubrachysomus minor*
Guanling biota	Catch and grind	*Guizhoueugnathus largus*?	
	Pierce		*Birgeria guizhouensis*
	Grasp	*Pholidopleurus xiaowaensis*	*Guizhoucoelacanthus guanlingensis*
	Suction	*Peltopleurus brachycephalus*	

Table 7

Classification of the Chinese Triassic marine reptiles into major guilds. Mollusc-eating marine reptiles whose body morphology might suggest an ambush predator mode are classed as puruit predators because of the nature of their main prey. Body sizes are given arbitrarily as small (total length < 1 m), medium (total length 1–2 m), and large (total length > 2 m).

The classification of feeding types follows Massare (1997), and the division into pursuit and ambush predators follows Massare (1988). The Suction-feeding guild is added following Sander et al. (2011). Reptiles with heterodont dentitions are placed in different feeding guilds, as Massare (1997) suggested.

	Feeding guild	Pursuit predators	Ambush predators
Chaohu biota	Cut		
	Pierce II		
	Pierce I		
	Smash		*Chaohusaurus geishanensis* (small)
	Crunch		*Chaohusaurus geishanensis* (small)
	Crush		
	Suction		
Luoping biota	Cut		
	Pierce II		
	Pierce I		*Dianopachysaurus dingi* (small)
	Smash	*Phalarodon atavus* (medium)	
		Mixosauridae indet. (medium)	
	Crunch	*Sinosaurosphargis yunguiensis* (medium),	
		Largocephalosaurus polycarpon (medium)	
	Crush		
	Suction		
Panxian biota	Cut		*Qianosuchus mixtus* (large)
	Pierce II		*Nothosaurus yanjuanensis* (large),
			Lariosaurus hongguoensis (medium)
	Pierce I		*Dinocephalosaurus orientalis* (large),
			Keichousaurus sp. (small)
	Smash	*Mixosaurus panxianensis* (medium),	*Xinminosaurus catactes* (large)
		Phalarodon cf. *fraasi* (medium)	
	Crunch	*Sinosaurosphargis yunguiensis* (medium),	*Wumengosaurus delicatomandibularis* (medium),
		Mixosaurus panxianensis (medium),	*Xinminosaurus catactes* (large)
		Phalarodon cf. *fraasi* (medium)	
	Crush	*Placodus inexpectatus* (large),	
		Phalarodon cf. *fraasi* (medium),	
		Xinminosaurus catactes (large)	
	Suction		
Xingyi biota	Cut		
	Pierce II		*Nothosaurus youngi* (medium),
			Lariosaurus xingyiensis (medium),
			Anshunsaurus wushaensis (medium),
			Tanystropheus sp. (large)
	Pierce I		*Keichousaurus hui* (small),
			Yunguisaurus liae (large)
	Smash		*Qianxisaurus chajiangensis* (small)
	Crunch		
	Crush	*Glyphoderma kangi* (small)	
	Suction		
Guanling biota	Cut		
	Pierce II		*Anshunsaurus huangguoshuensis* (large),
			Xinpusaurus suni (medium),
			Xinpusaurus bamaolinensis (medium),
			Miodentosaurus brevis (large),
			Neosinasaurus hoangi (large)
	Pierce I		*Xinpusaurus bamaolinensis* (medium)
	Smash	*Qianichthyosaurus zhoui* (medium),	*Xinpusaurus suni* (medium),
		Guizhouichthyosaurus tangae (large)	*Xinpusaurus bamaolinensis* (medium)
	Crunch	*Odontochelys semitestacea* (small)	*Xinpusaurus suni* (medium),
			Xinpusaurus bamaolinensis (medium)
	Crush	*Sinocyamodus xinpuensis* (small),	
		Psephochelys polyosteoderma (small),	
		Xinpusaurus suni (medium),	
		Xinpusaurus bamaolinensis (medium)	
	Suction	*Guanlingsaurus liangae* (large)	

reconsidered, by comparisons among collections and with faunas elsewhere in the world. In addition, such comparative work will lead to further improvements in phylogenetic understanding, and new studies are required of the morphometrics and ecologies of the fish and reptile taxa.

The ecological results (Tables 6, 7; Figs. 30, 31) are preliminary and based on limited assessment of the faunas. Ongoing research on each of the Chinese biotas should allow further exploration of changes in disparity (variance in form assessed from cladistic and continuous morphometric data) and guild occupancy associated

with food web reconstructions. Overall, the current data confirm the standard view of a prolonged time of recovery after the PTME, with vertebrate faunas building up from rather limited representation in the Early Triassic, to more complex ecosystems, with additional higher trophic levels, in the Anisian. In our analysis, we have omitted conodonts, and yet these should be added as small-sized predatory chordates, together with other predatory forms such as gastropods and malacostracans, in future attempts to understand the shapes of recovering Triassic marine ecosystems.
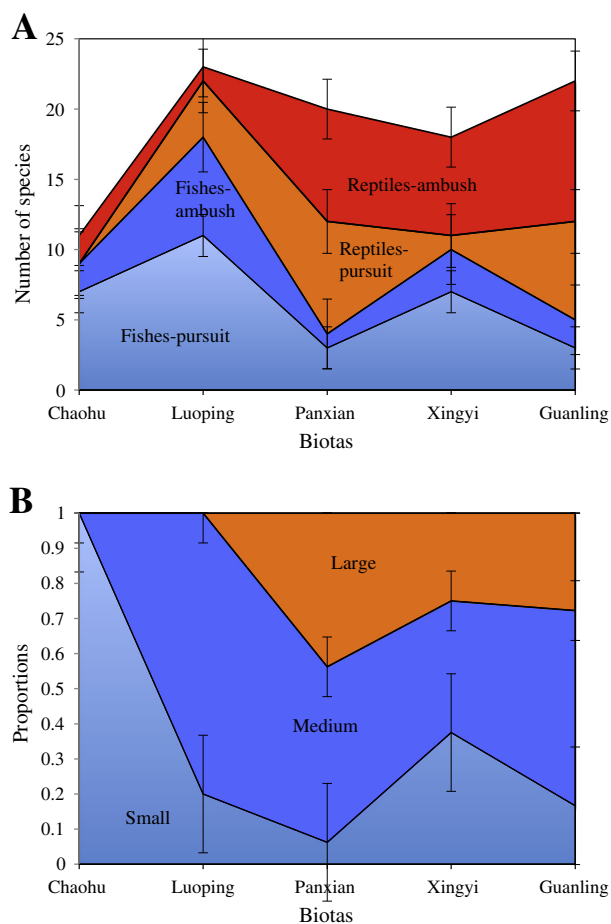
Fig. 31. Evolution of marine vertebrates through the Triassic of South China, documented for the Chaohu (late Early Triassic), Luoping (early Middle Triassic), Panxian (early Middle Triassic), Xingyi (late Middle Triassic), and Guanling (early Late Triassic) biotas. (A) Number of species assigned to major feeding guild categories (data from Tables 6, 7). (B) Proportions of species of marine reptiles assigned to different body size categories (data from Table 7). Confidence intervals are standard errors.

Palaeobiological work in South China and elsewhere should in the future shed light on the biological impacts of mass extinctions, both in terms of killing models, but importantly also in terms of the recovery. Current unresolved debates (Chen and Benton, 2012) concern the timing of recovery, models for ecosystem reconstruction, the roles of intrinsic and extrinsic factors in the recovery, and the long-term significance of the Triassic recovery in shaping later and modern biodiversity.

Appendix 1. Systematic summary of currently valid marine reptilian taxa from the Early Triassic of South China

Sauropterygia
Family Hanosauridae Young and Dong, 1972
Hanosaurus hupehensis Young and Dong, 1972 (Fig. 23B)
Holotype: IVPP V3231, skull and partial postcranial skeleton.
Type locality: Songshugoulaowan, Xunjian, Nanzhang County, Hubei Province, China.
Type horizon: Jialingjiang Formation, Lower Triassic.
Comments: *Hanosaurus hupehensis* was originally described as a thalattosaur (Young and Dong, 1972). Later revision (Rieppel, 1998b) established its pachypleurosaurian affinity. Young (1965b) reported another pachypleurosaur, "*Keichousaurus yuananensis*", from Wangchengang (now known as Yingzishan), Yuanan County, Hubei Province. The holotype and only described specimen cannot be located currently (Rieppel, 2000). The description (Young, 1965b) is not enough to diagnose it at species level and consequently its species validity has been doubted (Rieppel, 2000). During fieldwork by one of us (JL), a pachypleurosaur specimen was collected from the original quarry where the only known specimen of "*Keichousaurus yuananensis*" had been found; this specimen shows no difference with *Hanosaurus hupehensis*. Further study of new pachypleurosaurian material from this locality may confirm that "*Keichousaurus yuananensis*" is conspecific with *Hanosaurus hupehensis*.
Pistosauroidea fam. indet.
Kwangsisaurus orientalis (Young, 1959).
Holotype: IVPP V2338 (currently catalogued at Anhui Provincial Museum), part of the postcranial skeleton.
Type locality: Fupingtun, Dengliu, Wuming County, Guangxi Province, China.
Type horizon: Beisi Formation, Olenekian, Lower Triassic.
Comments: The only known specimen has been most recently restudied by Rieppel (1999). The holotype was discovered in the Olenekian Beisi Formation, not the Luolou Group of the Beisi Formation (fide Rieppel, 1999). The Luolou Group is the basinal equivalent of the shallow marine Majiaoling and Beisi Formations.

Ichthyopterygia
Family Grippidae Wiman, 1929
Chaohusaurus geishanensis Young and Dong, 1972 (Fig. 23D)
Holotype: IVPP V4001, an articulated and nearly complete skeleton lacking part of the snout and tail.
Type locality: Chaohu City, Anhui Province, China.
Type horizon: Nanlinghu Formation, upper Olenekian, Lower Triassic.
Comments: *Chaohusaurus geishanensis* was originally described by Young and Dong (1972). Chen (1985) reported two new ichthyosaurian species from the well-studied Majiashan Section of Chaohu, namely *Anhuisaurus chaoxianensis* and *A. faciles*. Mazin et al. (1991) replaced the generic name *Anhuisaurus* with *Chensaurus* because they found that the generic name *Anhuisaurus* was preoccupied. Motani et al. (1996) proposed an anguilliform swimming mode for early ichthyosaurs based on a nearly complete specimen of *Chensaurus* with partly preserved skin impression. Later revision by Motani and You (1998) demonstrated that the differences between *Chaohusaurus* and *Chensaurus* are caused by ontogenetic variations and consequently, *Chensaurus* is synonymized with *Chaohusaurus*. Maisch (2001) revisited two specimens of *Chaohusaurus* originally described by Chen (1985) and provided some additional information about the anatomy of this taxon.

Hupehsuchia
Family Nanchangosauridae Wang, 1959
Nanchangosaurus suni Wang, 1959 (Fig. 23A)

Holotype: NGMC V646, an articulated skeleton lacking limbs and part of the snout and tail.

Type locality: Yinpo, Gujing (now known as Jiaojiawan), Liangshuiquan (now known as Leiping), Xunjian, Nanzhang County, Hubei Province, China.

Type horizon: Uppermost Daye Formation or lowermost Jialingjiang Formation.

Comments: *Nanchangosaurus suni* was originally reported by Wang (1959) and briefly redescribed by Carroll and Dong (1991).

Hupehsuchus nanchangensis Young and Dong, 1972 (Fig. 23C)

Holotype: IVPP V3232, a nearly complete and articulated skeleton.

Type locality: Tuling, Baihechuan, Xunjian, Nanzhang County, Hubei Province, China.

Type horizon: Jialingjiang Formation.

Comments: This taxon has been most recently restudied by Carroll and Dong (1991).

Nanchangosaurid gen. indet.

Comments: An unnamed species of Hupehsuchia from Nanzhang was briefly described by Carroll and Dong (1991). It was most recently revised by Wu et al. (2003) based on a nearly complete new specimen from Yuanan County, Hubei Province.

Appendix 2. Systematic summary of currently valid marine reptilian taxa from the Middle Triassic of South China

Saurosphargidae Li et al., 2011

Sinosaurosphargis yunguiensis Li et al., 2011

Holotype: IVPP V 17040, a nearly complete skeleton exposed in dorsal view, lacking postero-left part.

Type locality: Yangmazhai, Luoping County, Yunnan Province, China.

Type horizon: Member 2, Guanling Formation, Pelsonian, Anisian, Middle Triassic.

Sauropterygia

Family Placodontidae Cope, 1871

Placodus inexpectatus Jiang et al., 2008b (Figs. 24A, 25A)

Holotype: GMPKU-P-1054, a nearly complete skeleton exposed in right lateral view.

Type locality: Yangjuan Village, Xinmin District, Panxian County, Guizhou Province, China.

Type horizon: Member 2, Guanling Formation, Pelsonian, Anisian, Middle Triassic.

Pachypleurosauria fam. indet.

Wumengosaurus delicatomandibularis Jiang et al., 2008b (Figs. 24B, 25B)

Holotype: GMPKU-P-1210, a complete and articulated skeleton exposed in left lateral view.

Type locality: Yangjuan Village, Xinmin District, Panxian County, Guizhou Province, China.

Type horizon: Member 2, Guanling Formation, Pelsonian, Anisian, Middle Triassic.

Comments: F.X. Wu et al. (2011) and X.C. Wu et al. (2011) describe additional material of this species from the type locality and provide complementary anatomical information previously unavailable from the two type specimens.

Family Keichousauridae Young, 1965b

Keichousaurus sp.

Comments: An unnamed species of Pachypleurosauria from Panxian biota has been tentatively identified as *Keichousaurus* sp. (Motani et al., 2008; Jiang et al., 2009).

Dianopachysaurus dingi Liu et al., 2011b

Holotype: LPV-31365, a complete and articulated skeleton exposed in dorsal view.

Type locality: Daaozi Village, Luoping County, Yunnan Province, China.

Type horizon: Member 2, Guanling Formation, Pelsonian, Anisian, Middle Triassic.

Comments: Shang et al. (2011) described *Diandongosaurus acutidentatus* from Luoping. These two species are from the same locality and share a general morphology. When naming the new species *D. acutidentatus*, Shang et al. (2011) did not provide any comparison with *Dianopachypleurosaurus dingi*. Considering *Diandongosaurus* shares a unique frontal morphology with *Dianopachypleurosaurus* as well as many other similarities, the former is likely a junior synonym of the latter. Further study is needed to determine the validity of this taxon.

Eosauropterygia fam. indet.

Largocephalosaurus polycarpon L. Cheng et al., 2012

Holotype: Wuhan Institute of Geology and Mineral Resources (WIGM) SPC V1009, a nearly complete and articulated skeleton (more than 1.13 m long), with most of the tail missing.

Type locality: Luoping County, Yunnan Province, China.

Type horizon: Member 2, Guanling Formation, Pelsonian, Anisian, Middle Triassic.

Comments: Cheng et al. (2012) described the new species and synonymised another specimen previously described as a thalattosaur by Cheng et al. (2010). This taxon shares a unique synapomorphy with other pachypleurosaurs among sauropterygians, i.e. a much reduced upper temporal fenestra.

Largocephalosaurus qianensis Li et al., 2013

Holotype: IVPP V15638, a nearly complete skeleton in ventral view, with posteriormost section of the tail missing.

Type locality: Xinmin District, Yunnan Province, China.

Type horizon: Member 2, Guanling Formation, Pelsonian, Anisian, Middle Triassic.

Comments: Li et al. (2013) described this new species based on three specimens, that differs from *L. polycarpon* in various characters of the skull, ribs, and vertebrae.

Family Nothosauridae Baur, 1889

Nothosaurus yangjuanensis Jiang et al., 2006a (Fig. 24C)

Holotype: GMPKU-P-1080, a complete skull exposed in both dorsal and ventral views.

Type locality: Yangjuan Village, Xinmin District, Panxian County, Guizhou Province, China.

Type horizon: Member 2, Guanling Formation, Pelsonian, Anisian, Middle Triassic.

Comments: The palatal anatomy of this species was first established by Jiang et al. (2005b) before it was formally named by Jiang et al. (2006a). In the same year, Shang (2006) named another species of *Nothosaurus*, *N. rostellatus* (Fig. 24D), from the same locality. This species presents no diagnostic characters compared to *N. yangjuanensis* (pers. obs., J. L.). Although Klein and Albers (2009) included both *Nothosaurus yangjuanensis* and *N. rostellatus* as valid species, further study may confirm that the latter is a junior synonym of *N. yangjuanensis*.

Lariosaurus hongguoensis Jiang et al., 2006b (Fig. 24E)

Holotype: GMPKU-P-1011, a nearly complete skeleton exposed in ventral view.

Type locality: Yangjuan Village, Xinmin District, Panxian County, Guizhou Province, China.

Type horizon: Member 2, Guanling Formation, Pelsonian, Anisian, Middle Triassic.

Nothosauroidea fam. Indet.

Sanchiaosaurus dengi Young, 1965b

Holotype: IVPP V3228, a natural mould of skull and lower jaw and partial postcranial skeleton.

Type locality: Zhuerqiao, ~ 400 m southwest of Jinzhong Bridge, Sanqiao, in the suburb of Guiyang City, Guizhou Province, China.

Type horizon: Member 1, Guanling Formation, lower Anisian, Middle Triassic.

Comments: This taxon has been most recently restudied by Rieppel (1999).

Pistosauroidea fam. Indet.

Chinchenia sungi Young, 1965b (Fig. 24F)

Lectotype: IVPP V3227, anterior tip of left mandible.

Type locality: Shangpu, Cangxi Bridge, seven km west of the county seat of Qinzhen County, Guizhou Province, China.

Type horizon: Member 1, Guanling Formation, lower Anisian, Middle Triassic.

Comments: Young's (1965b) original description did not designate a holotype. Rieppel (1999) has most recently revised this taxon and selected a lectotype among syntypes.

Ichthyopterygia

Ichthyosauria fam. indet.

Xinminosaurus catactes Jiang et al., 2008c (Fig. 25C)

Holotype: GMPKU-P-1071, a nearly complete and articulated skeleton.

Type locality: Yangjuan Village, Xinmin District, Panxian County, Guizhou Province, China.

Type horizon: Member 2, Guanling Formation, Pelsonian, Anisian, Middle Triassic.

Family Mixosauridae Baur, 1887

Mixosaurus panxianensis Jiang et al., 2006c (Figs. 24G, 25D)

Holotype: GMPKU-P-1033, a nearly complete skull and partial postcranial skeleton.

Type locality: Yangjuan Village, Xinmin District, Panxian County, Guizhou Province, China.

Type horizon: Member 2, Guanling Formation, Pelsonian, Anisian, Middle Triassic.

Comments: Material of *Mixosaurus panxianensis* was first described and identified as *Barracudasaurus maotaiensis* by Jiang et al. (2005a). Later, the holotype of *B. maotaiensis* was thought undiagnostic at species level and consequently, the newly introduced genus name was abandoned by Jiang et al. (2006c). The material originally described by Jiang et al. (2005a) was referred to *M. panxianensis* by Jiang et al. (2006c).

Phalarodon cf. *P. fraasi* Merriam, 1910

Comments: Jiang et al. (2003) reported a mixosaurid specimen from the Panxian biota as *Phalarodon* sp. Later, Jiang et al. (2007) admitted that the referred specimen was inappropriately prepared and the generic assignment is problematic. Jiang et al. (2007) described a further mixosaurid specimen from the Panxian Fauna as *Phalarodon* cf. *P. fraasi*.

Phalarodon atavus (Quenstedt, 1852)

Lectotype: GPIT/RE/411, complete left maxilla and lacrimal.

Type locality: Calw-Althengstett, Lower Muschelkalk, Germany.

Comments: Liu et al. (2013) reported an almost complete and articulated specimen of *Phalarodon atavus* from the Luoping biota, the first example discovered outside of Germanic Basin.

Mixosauridae gen. and sp. indet.

Comments: Liu et al. (2011a) reported a mixosaurid specimen from the Luoping biota, which provides further evidence for the diapsid origin of ichthyosaurs. This specimen can be easily differentiated from the *Phalarodon atavus* specimen from Luoping by the presence of double notches on the anterior margin of radius, a derived character shared with *Mixosaurus panxianensis* (Jiang et al., 2006c). Chen and Cheng (2009) reported the ichthyosaur *Mixosaurus kuhnschnyderi* Brinkmann, 1998 in the Luoping biota, but our examination of this material reveals that their specimen also shares a synapomorphy with *M. panxianensis* among mixosaurid ichthyosaurs: two notches on the leading edge of the radius. This specimen might belong to either a new species that is closely related to *M. panxianensis* or a local population of *M. panxianensis* with consistent anatomical differences. The reported alternation of conical and mound-shaped teeth in the posterior jaw of this specimen is a taphonomic alteration, rather than a natural situation. Further study may demonstrate that the specimen described as *M. kuhnschnyderi* by Chen and Cheng (2009) is conspecific with the specimen reported by Liu et al. (2011a).

Prolacertiformes/Protorosauria

Prolacertiformes fam. indet.

Dinocephalosaurus orientalis Li, 2003 (Figs. 24H, 25G)

Holotype: IVPP V13767, a nearly complete skull and lower jaw exposed from left laterodorsal view plus some cervical elements.

Type locality: Xinmin, Panxian County, Guizhou Province, China.

Type horizon: Member 2, Guanling Formation, Pelsonian, Anisian, Middle Triassic.

Comments: A second specimen of this taxon was reported by Li et al. (2004). The skeletal anatomy of this taxon has been most recently redescribed in detail by Rieppel et al. (2008).

Archosauria

Crurotarsi fam. indet.

Qianosuchus mixtus Li et al., 2006 (Fig. 24I)

Holotype: IVPP V13899, a nearly complete skeleton lacking distal part of forelimbs and posterior end of the tail.

Type locality: Xinmin, Panxian County, Guizhou Province, China.

Type horizon: Member 2, Guanling Formation, Pelsonian, Anisian, Middle Triassic.

Appendix 3. Systematic summary of currently valid marine reptilian taxa from the late Ladinian to early Carnian Zhuganpo Formation, and lateral equivalents, of South China

Sauropterygia

Family Placochelyidae Romer, 1956

Glyphoderma kangi Zhao et al., 2008a

Holotype: ZMNH M8729, a nearly complete and articulated skeleton.

Type locality: Fuyuan, Yunnan Province, China.

Type horizon: Zhuganpo Formation, Cordevolian, Carnian, Upper Triassic.

Family Keichousauridae Young, 1965b

Keichousaurus hui Young, 1958 (Fig. 26A)

Holotype: IVPP V952, a skull and 21 cervical vertebrae.

Type locality: Dingxiao, Xingyi City, Guizhou Province, China.

Type horizon: Zhuganpo Formation, Cordevolian, Carnian, Upper Triassic.

Comments: The morphology of *Keichousaurus hui* was restudied in detail by Lin and Rieppel (1998) and Holmes et al. (2008). Reproductive mode and sexual dimorphism in this taxon have been investigated by Cheng et al. (2004, 2009). An unnamed species of *Keichousaurus* was reported from late Ladinian fourth Member of the Gejiu Formation at Niubudai Village, Banqiao, Luoping County, Yunnan Province (Sun et al., 2005b,c). Further study, however, may demonstrate that this taxon is the same as *K. hui*.

Eosauropterygia fam. indet.

Qianxisaurus chajiangensis Cheng et al., 2012

Holotype: NMNS-KIKO-F044630, a nearly complete skeleton with the tip of the tail and the right hind limb missing.

Type locality: Xingyi City, Guizhou Province, China.

Type horizon: Zhuganpo Formation, Cordevolian, Carnian, Upper Triassic.

Comments: This taxon shares a unique synapomorphy with other pachypleurosaurs among sauropterygians, i.e. a much reduced upper temporal fenestra.

Family Nothosauridae Baur, 1889

Nothosaurus youngi Li and Rieppel, 2004 (Fig. 26B)

Holotype: IVPP V13590, a nearly complete skull and lower jaw and most of the postcranial skeleton.

Type locality: Xingyi City, Guizhou Province, China.

Type horizon: Zhuganpo Formation, Cordevolian, Carnian, Upper Triassic.

Comments: "*Shingyisaurus unexpectus*" was originally described as a simosaurid by Young (1965b) from Dazai, Dingxiao, Xingyi City. Later revision by Rieppel (1998a) reassigned it as a species of *Nothosaurus*

or a taxon closely related with *Nothosaurus*, because severe distortion of the only known specimen means this taxon is not diagnostic at species level and therefore, the species name is a nomen dubium.

Lariosaurus xingyiensis Li et al., 2002b (Fig. 26C)

Holotype: IVPP V11866, a nearly complete skeleton.

Type locality: Xingyi City, Guizhou Province, China.

Type horizon: Zhuganpo Formation, Cordevolian, Carnian, Upper Triassic.

Comments: The only known specimen has been restudied in detail by Rieppel et al. (2003). Sun et al. (2005b) described a partial postcranial skeleton from the late Ladinian fourth member of the Geijiu Formation at Niubudai Village, Banqiao, Luoping County, Yunnan Province and identified it as *Lariosaurus* sp. The published description is not enough to diagnose this taxon as a new species. *Kwangsisaurus lusiensis* Young, 1978 was reported from thin-layered limestones of the late Middle Triassic Zhuganpo Formation (formerly called the Falang Group) at Jujiu Village, ~50 km southeast of the county seat of Luxi County, Yunnan Province, the exact horizon of which is not clear, but is equivalent to the Zhuganpo Formation in Guizhou Province. The only described specimen cannot be located currently and the illustration by Young (1978) showed that it might represent a taxon closely related to *Lariosaurus* (Rieppel, 2000).

Pistosauroidea fam. indet.

Yunguisaurus liae Y.N. Cheng et al., 2006 (Fig. 26D)

Holotype: NMNS 004529/F003862, a nearly complete and articulated skeleton, missing the distal part of the tail.

Type locality: Near Huangnihe River, Chajiang, about 10 km northwest of Xingyi City, Guizhou Province, China.

Type horizon: Falang Group, Carnian, Upper Triassic.

Comments: Sato et al. (2010) provide a full morphological description of the holotype. Zhao et al. (2008b) described the skull, and Sato et al. (2013) the skeleton, of another nearly complete specimen of *Yunguisaurus* from the Zhuganpo Formation on the western side of the Huangnihe River, Fuyuan County, Yunnan Province, and tentatively identified it as *Yunguisaurus* cf. *liae* based on some anatomical differences between this smaller specimen and the holotype of *Y. liae* that cannot be explained by ontogenetic variation.

Thalattosauria

Family Askeptosauridae Kuhn-Schnyder, 1952

Anshunsaurus wushaensis Rieppel et al., 2006 (Figs. 25E, 26E)

Holotype: IVPP V13782, an almost complete skeleton.

Type locality: Wusha, Xingyi City, Guizhou Province, China.

Type horizon: Zhuganpo Formation, Cordevolian, Carnian, Upper Triassic.

Comments: A second specimen was described by Liu (2007) as a juvenile representative of this species. *Anshunsaurus huangnihensis* L. Cheng et al., 2007 was reported from the same locality with *A. wushaensis*. The only difference between *A. huangnihensis* and *A. wushaensis* given by L. Cheng et al. (2007) is the number of tarsal ossifications, which is most probably an ontogenetic variation, based on Liu (2007). Further study may demonstrate that *A. huangnihensis* is a subjective junior synonym of *A. wushaensis*, although Cheng et al. (2011), in a redescription of the skull, argue for its validity. Sun et al. (2005c) described a partial postcranial skeleton from the late Ladinian fourth member of the Geijiu Formation at Niubudai Village, Banqiao, Luoping County, Yunnan Province and identified it as cf. *Askeptosaurus*, which is also difficult to differentiate from *A. wushaensis*.

Prolacertiformes/Protorosauria

Family Tanystropheidae Gervais, 1858

Tanystropheus sp.

Comments: Li (2007) reported a juvenile specimen of a tanystropheid from the Zhuganpo Formation at Chajiang of Xingyi City and identified it as *Tanystropheus* sp. Rieppel et al. (2010) described another adult specimen of *Tanystropheus* also from the Zhuganpo Formation, which probably belongs to the same species with the one by Li (2007).

Appendix 4. Systematic summary of currently valid marine reptilian taxa from the Carnian Xiaowa Formation at Guanling, Guizhou Province, China

Testudines

Family Odontochelyidae Li et al., 2008

Odontochelys semitestacea Li et al., 2008

Holotype: IVPP V15639

Type locality: Guanling County, Guizhou Province, China.

Type horizon: Lower Member, Xiaowa Formation, Tuvalian, Carnian, Late Triassic.

Sauropterygia

Cyamodontoidea fam. indet.

Sinocyamodus xinpuensis Li, 2000

Holotype: IVPP V11872, a complete skeleton.

Type locality: Xinpu, Guanling County, Guizhou Province, China.

Type horizon: Lower Member, Xiaowa Formation, Tuvalian, Carnian, Late Triassic.

Placochelyidae Romer, 1956

Psephochelys polyosteoderma Li and Rieppel, 2002 (Fig. 27A)

Holotype: IVPP V12442, a complete skull and carapace, and partial appendicular skeleton.

Type locality: Xinpu, Guanling County, Guizhou Province, China.

Type horizon: Lower Member, Xiaowa Formation, Tuvalian, Carnian, Late Triassic.

Comments: Yin et al. (2000) reported another placochelyid, *Placochelys*? *minutus* shortly after the description of the first Chinese placodont, *Sinocyamodus xinpuensis*. *Placochelys*? *minutus* was taken as a nomen dubium by Zhao et al. (2008a) because the only known specimen is currently in a private collection and poorly preserved.

Ichthyopterygia

Family Toretocnemidae Maisch and Matzke, 2000

Qianichthyosaurus zhoui Li, 1999 (Fig. 27B)

Holotype: IVPP V11839, a complete and articulated skeleton exposed from lateral view.

Type locality: Huangtutang, Xinpu, Guanling County, Guizhou Province, China.

Type horizon: Lower Member, Xiaowa Formation, Tuvalian, Carnian, Late Triassic.

Comments: Shortly after the description of *Qianichthyosaurus zhoui*, Yin et al. (2000) reported "*Mixosaurus guanlingensis*" also from Xinpu. This taxon has been synonymized with *Q. zhoui* by Maisch et al. (2008). *Q. zhoui* was further redescribed in detail by Nicholls et al. (2003) and Maisch et al. (2008).

Family Shastasauridae Merriam, 1902

Guizhouichthyosaurus tangae Cao and Luo in Yin et al., 2000 (Fig. 27C)

Holotype: YIGMR 009, currently in the possession of Guanling County Government, a well preserved skeleton lacking the tail, most of the pelvis and the hindlimbs.

Type locality: Guanling County, Guizhou Province, China.

Type horizon: Xiaowa Formation, Tuvalian, Carnian, Late Triassic.

Comments: A further two medium-sized ichthyosaurs, *Cymbospondylus asiaticus* Li and You, 2002, and *Panjiangsaurus epicharis* Chen and Cheng, 2003 from the Guanliang area were briefly described after the report of *Guizhouichthyosaurus tangae*. These two taxa, however, have both been synonymized with *G. tangae* by Pan et al. (2006) and Sander et al. (2011). The cranial and postcranial morphology of *G. tangae* have been restudied by Maisch et al. (2006) and Pan et al. (2006) respectively. The stomach content of "*Panjiangsaurus epicharis*" has been studied by Cheng et al. (2006a) and Cheng and Chen (2007).

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

Holotype: YIGMR 014, currently in the possession of Guanling County Government, a nearly complete and articulated skeleton.

Type locality: Gongjipo, Xinpu, Guanling County, Guizhou Province, China.

Type horizon: Xiaowa Formation, Tuvalian, Carnian, Late Triassic.

Comments: This taxon was originally assigned to genus *Guanlingsaurus* in the new family Guanlingosauridae by Yin et al. (2000), but Sander et al. (2011) reassigned the species to the well-known genus *Shastasaurus*, and compared it closely with North American taxa such as *S. pacificus*. Most recently, however, Ji et al. (2013) have maintained the generic status of *Guanlingsaurus* based a new phylogenetic analysis. Another large ichthyosaur from Guanling County, *Typicusichthyosaurus tsaihuae* Yin in Yin et al. (2000), shares an unusually small head with *Guanlingsaurus liangae*. Differences listed by Yin et al. (2000) to differentiate the two genera are apparently preparational artefacts (Maisch et al., 2006). *T. tsaihuae* is listed as species inquirenda by McGowan and Motani (2003), and it might be a subjective synonym of *Guanlingsaurus liangae*.

Thalattosauria Merrian, 1905

Askeptosauridae Kuhn-Schnyder, 1952

Anshunsaurus huangguoshuensis Liu, 1999 (Figs. 25F, 27D)

Holotype: IVPP V11835, a skeleton composed of seven parts and lacking most of the hind limbs and tail.

Type locality: Huangtutang, Xinpu, Guanling County, Guizhou Province, China.

Type horizon: Xiaowa Formation, Tuvalian, Carnian, Late Triassic.

Comments: Liu (1999) originally reported *Anshunsaurus huangguoshuensis* as a sauropterygian. Later revision by Rieppel et al. (2000) reassigned it to Thalattosauria. This taxon has been most recently restudied by Liu and Rieppel (2005) based on a new perfectly preserved and articulated specimen.

Xinpusaurus suni Yin in Yin et al., 2000 (Fig. 27E)

Holotype: YIGMR010, a nearly complete skeleton.

Type locality: Guanling County, Guizhou Province, China.

Type horizon: Lower Member, Xiaowa Formation, Tuvalian, Carnian, Late Triassic.

Comments: Yin in Yin et al. (2000) reported *Xinpusaurus suni* based on four articulated skeletons and briefly described it as a pachypleurosaur. Shortly after the description, Yin and Zhou (2000) recognised the thalattosaurian affinity of this taxon. Liu and Rieppel (2001) studied a new skull of *Xinpusaurus* and referred it as *Xinpusaurus* cf. *suni*. Liu (2001) described postcranial morphology of *Xinpusaurus* based on another specimen. Luo and Yu (2002) restudied the skull anatomy of *Xinpusaurus suni* based on further preparation of the holotype of *X. suni* and another well preserved skull, and referred Liu and Rieppel's (2001) material to *X. suni*. Rieppel and Liu (2006) gave a further account of *X. suni* based on a perfectly preserved new skull of this species.

Xinpusaurus bamaolinensis Cheng, 2003 (Fig. 27F)

Holotype: SPC (Wuhan Center, China Geological Survey, Wuhan, China) V 30015, a nearly complete skull and lower jaw, and partial postcranial skeleton.

Type locality: Bamaolin, Xinpu, Guanling County, Guizhou Province, China.

Type horizon: Lower Member, Xiaowa Formation, Tuvalian, Carnian, Late Triassic.

Comments: Jiang et al. (2004) described a new species of *Xinpusaurus* and named it as *Xinpusaurus kohi*, which is a junior synonym of *Xinpusaurus bamaolinensis* (Rieppel and Liu, 2006).

Askeptosauroidea fam. indet.

Miodentosaurus brevis Cheng et al., 2007b (Fig. 27G)

Holotype: NMNS 004727/F003960, a nearly complete skeleton lacking the posteriormost part of the tail.

Type locality: Guanling County, Guizhou Province, China.

Type horizon: Xiaowa Formation, Tuvalian, Carnian, Late Triassic.

Type horizon: Cheng et al. (2007b) firstly named this new species based on the skull of the holotype. The postcranial skeleton was prepared and described subsequently by F.X. Wu et al. (2009) and X.C. Wu et al. (2009). This taxon has been most recently revised by Zhao et al. (2010) based on a new beautifully preserved skeleton.

Neosinosauridae Zhou in Yin and Zhou, 2000

Neosinosaurus hoangi Zhou in Yin and Zhou, 2000

Holotype: YIGMR001, an articulated and nearly complete skeleton lacking only part of the forelimb.

Type locality: Maowa, Xinpu, Guanling County, Guizhou Province, China.

Type horizon: Xiaowa Formation, Tuvalian, Carnian, Late Triassic.

Comments: *Neosinosaurus hoangi* was originally named as *Sinasaurus hoangi* by Zhou in Yin et al. (2000) and described as a pachypleurosaur. Yin and Zhou (2000) subsequently found that the name *Sinasaurus* was pre-occupied by a dinosaur and renamed it *Neosinosaurus*. The thalattosaur affinity of this taxon was confirmed by X.C. Wu et al. (2009) after their examination of the type material.

References

Algeo, T.J., Twitchett, R.J., 2010. Anomalous Early Triassic sediment fluxes due to elevated weathering rates and their biological consequences. Geology 38, 1023–1026.

Algeo, T.J., Chen, Z.Q., Fraiser, M.L., Twitchett, R.J., 2011. Terrestrial marine teleconnections in the collapse and rebuilding of Early Triassic marine ecosystems. Palaeogeography Palaeoclimatology Palaeoecology 308, 1–11.

Benson, R.B.J., Butler, R.J., 2011. Uncovering the diversification history of marine tetrapods: ecology influences the effect of geological sampling biases. In: McGowan, A.J., Smith, A.B. (Eds.), Comparing the Geological and Fossil Records: Implications for Biodiversity Studies. Geological Society, London, Special Publications, 358, pp. 191–208.

Benton, M.J., 1989a. Patterns of evolution and extinction in vertebrates. In: Allen, K.C., Briggs, D.E.G. (Eds.), Evolution and the Fossil Record. Belhaven, London, pp. 218–241.

Benton, M.J., 1989b. Mass extinctions among tetrapods and the quality of the fossil record. Philosophical Transactions of the Royal Society of London, Series B 325, 369–386.

Benton, M.J., 2003. When Life Nearly Died: The Greatest Mass Extinction of All Time.Thames and Hudson, London (340 pp.).

Benton, M.J., 2009. The Red Queen and the Court Jester: species diversity and the role of biotic and abiotic factors through time. Science 323, 728–732.

Benton, M.J., Newell, A.J., 2013. Impacts of global warming on Permo-Triassic terrestrial ecosystems. Gondwana Research (in press).

Benton, M.J., Twitchett, R.J., 2004. How to kill (almost) all life: the end-Permian extinction event. Trends in Ecology & Evolution 18, 358–365.

Benton, M.J., Tverdokhlebov, V.P., Surkov, M.V., 2004. Ecosystem remodelling among vertebrates at the Permian–Triassic boundary in Russia. Nature 432, 97–100.

Blieck, A., 2011. From adaptive radiations to biotic crises in Palaeozoic vertebrates: a geobiological approach. Geologica Belgica 14, 203–227.

Brayard, A., Escarguel, G., Bucher, H., Monnet, C., Brühwiler, T., Goudemand, N., Galfetti, T., Guex, J., 2009. Good genes and good luck: ammonoid diversity and the end-Permian mass extinction. Science 325, 1118–1121.

Briggs, D.E.G., 2003. The role of decay and mineralization in the preservation of soft-bodied fossils. Annual Review of Earth and Planetary Sciences 31, 275–301.

Brusatte, S.L., Benton, M.J., Lloyd, G.T., Ruta, M., Wang, S.C., 2011. Macroevolutionary patterns in the evolutionary radiation of archosaurs (Tetrapoda: Diapsida). Earth and Environmental Science Transactions of the Royal Society of Edinburgh 101, 367–382.

Carroll, R.L., Dong, Z.M., 1991. *Hupehsuchus*, an enigmatic aquatic reptile from the Triassic of China, and the problem of establishing relationships. Philosophical Transactions of the Royal Society of London, Series B 331, 131–153.

Chen, L.Z., 1985. Ichthyosaurs from the Lower Triassic of Chao County, Anhui. Regional Geology of China 15, 139–146 (in Chinese).

Chen, L.D., 2002. New data of Middle–Late Triassic elasmobranch ichthyoliths from "Falang Formation" in Guanling, Guizhou. Acta Micropalaeontologica Sinica 19, 276–287.

Chen, Z.Q., Benton, M.J., 2012. The timing and pattern of biotic recovery following the end-Permian mass extinction. Nature Geoscience 5, 375–383.

Chen, X.H., Cheng, L., 2003. A new species of large-sized and long-body ichthyosaur from the Late Triassic Guanling biota, Guizhou, China. Geological Bulletin of China 22, 228–235 (in Chinese with English abstract).

Chen, X.H., Cheng, L., 2009. The discovery of *Mixosaurus* (Reptilia: Ichthyopterygia) from the Middle Triassic of Luoping, Yunnan Province. Acta Geologica Sinica 83, 1214–1220 (in Chinese with English summary).

Chen, X.H., Cheng, L., 2010. A new species of *Mixosaurus* (Reptilia: Ichthyosauria) from the Middle Triassic of Puan, Guizhou, China. Acta Palaeontologica Sinica 49, 251–260.

Chen, L.D., Cuny, G., 2003. Discovery of the Middle–Late Triassic elasmobranch ichthyoliths from the Guanling area, Guizhou, SW China. Geological Bulletin of China 22, 236–247 (in Chinese with English abstract).

Chen, L.D., Wang, C.Y., 2002. Conodonts from the uppermost Zuganpo Formation and lowermost Wayao Formation of Guanling, Guizhou Province. Acta Palaeontologica Sinica 41, 349–360 (in Chinese with English abstract).

Chen, L.D., Wang, C.Y., 2009. Conodont-based age of the Triassic Yangliujing Formation in SW Guizhou, China. Journal of Stratigraphy 33, 98–103 (in Chinese with English abstract).

Chen, C., Wang, Y., Wang, Z., Huang, B., 1988. Triassic biostratigraphy of the southern Jiangsu Province. In: Academy of Geological Sciences, Jiangsu Bureau of Petroleum Prospecting and Nanjing Institute of Geology and Palaeontology, Academia Sinica (Eds.), Sinian–Triassic Biostratigraphy of the Lower Yangtze

Peneplatform in Jiangsu Region. Nanjing University Press, Nanjing, pp. 315–368 (in Chinese with English summary).

Chen, Z.Q., Shi, G.R., Kaiho, K., 2002. A new genus of rhynchonellid brachiopod from the Lower Triassic of South China and implications for timing the recovery of Brachiopoda after the end-Permian mass extinction. Palaeontology 45, 149–164.

Chen, L.D., Cuny, G., Wang, X.F., 2007a. The chondrichthyan fauna from the Middle–Late Triassic of Guanling (Guizhou province, SW China). Historical Biology 19, 291–300.

Chen, Z.Q., Tong, J., Kaiho, K., Kawahata, H., 2007b. Onset of biotic and environmental recovery from the end-Permian mass extinction within 1–2 million years: a case study of the Lower Triassic of the Meishan section, South China. Palaeogeography, Palaeoclimatology, Palaeoecology 252, 176–187.

Chen, Z.Q., Tong, J.N., Zhang, K.X., Yang, H., Liao, Z.T., Song, H.J., Chen, J., 2009. Environmental and biotic turnover across the Permian–Triassic boundary on a shallow carbonate platform in western Zhejiang, South China. Australian Journal of Earth Sciences 56, 775–797.

Chen, Z.Q., Tong, J., Liao, Z., Chen, J., 2010. Structural changes of marine communities over the Permian–Triassic transition: ecologically assessing the end-Permian mass extinction and its aftermath. Global and Planetary Change 73, 123–140.

Chen, Z.Q., Tong, J., Fraiser, M.L., 2011. Trace fossil evidence for restoration of marine ecosystems following the end-Permian mass extinction in the Lower Yangtze region, South China. Palaeogeography, Palaeoclimatology, Palaeoecology 299, 449–474.

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

Cheng, L., Chen, X.H., 2007. Gut contents in the Triassic ichthyosaur *Panjiangsaurus* from the Guanling biota in Guizhou. Geology in China 34, 61–65 (in Chinese with English abstract).

Cheng, Y.N., Wu, X.C., Ji, Q., 2004. Triassic marine reptiles gave birth to live young. Nature 432, 383–386.

Cheng, L., Wings, O., Chen, X.H., Sander, P.M., 2006a. Gastroliths in the Triassic ichthyosaur *Panjiangsaurus* from China. Journal of Paleontology 80, 583–588.

Cheng, Y.N., Sato, T., Wu, X.C., Li, C., 2006b. First complete pistosauroid from the Triassic of China. Journal of Vertebrate Paleontology 26, 501–504.

Cheng, L., Chen, X.H., Wang, C.S., 2007a. A new species of Late Triassic *Anshunsaurus* (Reptilia: Thalattosauria) from Guizhou Province. Acta Geologica Sinica 81, 1346–1351.

Cheng, Y.N., Wu, X.C., Sato, T., 2007b. A new thalattosaurian (Reptilia: Diapsida) from the Upper Triassic of Guizhou, China. Vertebrata PalAsiatica 45, 246–260.

Cheng, Y.N., Holmes, R., Wu, X.C., Alfonso, N., 2009. Sexual dimorphism and life history of *Keichousaurus hui* (Reptilia: Sauropterygia). Journal of Vertebrate Paleontology 29, 401–408.

Cheng, L., Chen, X.H., Zhang, B.M., Wang, X.F., 2010. A new material of Thalattosauria (Reptilia: Diapsida) from the Middle Triassic of Luoping, Yunnan Province. Earth Science. Journal of China University of Geosciences 35, 507–511.

Cheng, L., Chen, X.H., Zhang, B.M., Cai, Y.J., 2011. New study of *Anshunsaurus huangnihensis* Cheng, 2007 (Reptilia: Thalattosauria): revealing its transitional position in Askeptosauridae. Acta Geologica Sinica 85, 1231–1237 (in Chinese with English abstract).

Cheng, L., Chen, X.H., Zeng, X., Cai, Y., 2012a. A new eosauropterygian (Diapsida: Sauropterygia) from the Middle Triassic of Luoping, Yunnan Province. Journal of Earth Science 23, 33–40.

Cheng, Y.N., Wu, X.C., Sato, T., Shan, H.Y., 2012b. A new eosauropterygian (Diapsida, Sauropterygia) from the Triassic of China. Journal of Vertebrate Paleontology 32, 1335–1349.

Dong, Z.M., 1972. An ichthyosaur from the region of Qomolangma Feng, Tibet, China. Mem IVPP Acad Sin 9, 7–10 (in Chinese).

Erwin, D.H., 2001. Lessons from the past: biotic recoveries from mass extinctions. Proceedings of the National Academy of Sciences of the United States of America 98, 5399–5403.

Erwin, D.H., 2006. Extinction: How Life on Earth Nearly Ended 250 Million Years Ago.Princeton University Press, Princeton (296 pp.).

Feng, Z.Z., Bao, Z.D., Li, S., 1997. Lithofacies Paleogeography of Middle and Lower Triassic of South China.Petroleum Industry Press, Beijing (222 pp. (in Chinese with English abstract)).

Friedman, M., Sallan, L.C., 2012. Five hundred million years of extinction and recovery:a Phanerozoic survey of large-scale diversity patterns in fishes. Palaeontology 55, 707–742.

Furrer, H., 1995. The Kalkschieferzone (Upper Meride Limestone; Ladinian) near Meride (Canton Ticino, Southern Switzerland) and the evolution of a Middle Triassic intraplatform basin. Eclogae Geologicae Helvetiae 88, 827–852.

Furrer, H., 2003. Der Monte San Giorgio im Südtessin—vom Berg der Saurier zur Fossil-Lagerstätte internationaler Bedeutung. Neujahrsblatt der Naturforschenden Gesellschaft Zürich 206, 1–64.

Galfetti, T., Bucher, H., Ovtcharova, M., Schaltegger, U., Brayard, A., Brühwiler, T., Goudemand, N., Weissert, H., Hochuli, P.A., Cordey, F., Guodun, K., 2007. Timing of the Early Triassic carbon cycle perturbations inferred from new U–Pb ages and ammonoid biochronozones. Earth and Planetary Science Letters 258, 593–604.

Gardiner, B.G., Maisey, J.G., Littlewood, D.T.J., 1996. Interrelationships of basal neopterygians. In: Stiassney, M.L.J., Parenti, L.R., Johnson, G.D. (Eds.), Interrelationships of Fishes. Academic Press, San Diego, pp. 117–146.

Gardiner, B.G., Schaeffer, B., Masserie, J.G., 2005. A review of lower actinopterygian phylogeny. Zoological Journal of the Linnean Society 144, 511–525.

Geng, B.H., Zhu, M., Jin, F., 2009. A revision and phylogenetic analysis of *Guizhoucoelacanthus* (Sarcopterygii, Actinistia) from the Triassic of China. Vertebrata Palasiatica 47, 165–177.

Geng, B.H., Jin, F., Wu, F.X., Wang, Q., 2012. New perleidid fishes from the Middle Triassic strata of Yunan Province. Geological Bulletin of China 31, 915–927.

Grande, L., Bemis, W.E., 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. Memoir of the Society of Vertebrate Paleontology 4, 1–679.

Gu, Z.W., Huang, B.Y., Chen, C.Z., Wen, S.X., Ma, Q.H., Lan, X., Xu, J.T., Liu, L., Wang, S.M., Wang, D.Y., Qiu, R.Z., Huang, Z.Q., Zhang, Z.M., Chen, J.H., Wu, P.L., 1976. Fossil Bivalves of China.Science Press, Beijing (pp. 221–223. (in Chinese with English summary)).

Hallam, A., 1991. Why was there a delayed radiation after the end-Palaeozoic extinctions? Historical Biology 5, 257–262.

Hao, W.C., Sun, Y.L., Jiang, D.Y., Sun, Z.Y., 2006. Advance in studies of the Panxian Fauna. Acta Scientiarum Naturalium Universitatis Pekinensis 42, 817–823 (in Chinese with English abstract).

Holmes, R., Cheng, Y.N., Wu, X.C., 2008. New information on the skull of *Keichousaurus hui* (Reptilia: Sauropterygia) with comments on sauropterygian interrelationships. Journal of Vertebrate Paleontology 28, 76–84.

Hu, S.X., Zhang, Q.Y., Chen, Z.Q., Zhou, C.Y., Lü, T., Xie, T., Wen, W., Huang, J.Y., Benton, M.J., 2011. The Luoping biota: exceptional preservation, and new evidence on the Triassic recovery from end-Permian mass extinction. Proceedings of the Royal Society, Series B 278, 2274–2282.

Hurley, I.A., Mueller, R.L., Dunn, K.A., Schmidt, E.J., Friedman, M., Ho, R.K., Prince, V.E., Yang, Z., Thomas, M.G., Coates, M.I., 2007. A new time-scale for ray-finned fish evolution. Proceedings of the Royal Society of London, Series B 274, 489–498.

Irmis, R.B., Whiteside, J.H., 2012. Delayed recovery of non-marine tetrapods after the end-Permian mass extinction tracks global carbon cycle. Proceedings of the Royal Society, Series B 279, 1310–1318.

Jadoul, F., Maserti, D., Cirilli, S., Berra, F., Claps, M., Frisia, S., 1994. Norian–Rhaetian stratigraphy and paleogeographical evolution of the Lombardy Basin (Bergamasc Alps). Excursion 81 — 15th IAS Regional Meeting, Ischia, Italy (38 pp.).

Ji, C., Jiang, D.-Y., Motani, R., Hao, W.-C., Sun, Z.-Y., Cai, T., 2013. A new juvenile specimen of *Guanlingsaurus* (Ichthyosauria, Shastasauridae) from the Upper Triassic of southwestern China. Journal of Vertebrate Paleontology 33, 340–348.

Jiang, D.Y., Hao, W.C., Sun, Y.L., Maisch, M.W., Matzke, A.T., 2003. The mixosaurid ichthyosaur *Phalarodon* from the Middle Triassic of China. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 2003, 656–666.

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

Jiang, D.Y., Hao, W.C., Maisch, M.W., Matzke, A.T., Sun, Y.L., 2005a. A basal mixosaurid ichthyosaur from the Middle Triassic of China. Palaeontology 48, 869–882.

Jiang, D.Y., Maisch, M.W., Hao, W.C., Pfretzschner, H.-U., Sun, Y.L., Sun, Z.Y., 2005b. *Nothosaurus* sp. (Reptilia, Sauropterygia, Nothosauridae) from the Anisian (Middle Triassic) of Guizhou, southwestern China. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 2005, 565–576.

Jiang, D.Y., Motani, R., Lu, C., Hao, W.C., Sun, Y.L., Sun, Z.Y., Schmitz, L., 2005c. Guanling biota: a marker of riassic biotic recovery from the end-Permian extinction in the ancient Guizhou sea. Acta Geologica Sinica 79, 729–738.

Jiang, D.Y., Maisch, M.W., Hao, W.C., Sun, Y.L., Sun, Z.Y., 2006a. *Nothosaurus yangjuanensis* n. sp. (Reptilia, Sauropterygia, Nothosauridae) from the middle Anisian (Middle Triassic) of Guizhou, southwestern China. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 2006, 257–276.

Jiang, D.Y., Maisch, M.W., Sun, Z.Y., Sun, Y.L., Hao, W.C., 2006b. A new species of *Lariosaurus* (Reptilia, Sauropterygia) from the Middle Anisian (Middle Triassic) of southwestern China. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 242, 19–42.

Jiang, D.Y., Schmitz, L., Hao, W.C., Sun, Y.L., 2006c. A new mixosaurid ichthyosaur from the Middle Triassic of China. Journal of Vertebrate Paleontology 26, 60–69.

Jiang, D.Y., Schmitz, L., Motani, R., Hao, W.C., Sun, Y.L., 2007. The mixosaurid ichthyosaur *Phalarodon* cf. *P. fraasi* from the Middle Triassic of Guizhou Province, China. Journal of Paleontology 81, 602–605.

Jiang, D.Y., Hao, W.C., Motani, R., Schmitz, L., Sun, Y.L., Sun, Z.Y., 2008a. Middle Triassic mixosaurids of Panxian, Guizhou and problems of "*Mixosaurus yangjuanensis* Liu and Yin, 2008". Acta Palaeontologica Sinica 47, 377–384.

Jiang, D.Y., Motani, R., Rieppel, O., Schmitz, L., Hao, W.C., Sun, Y.L., Sun, Z.Y., 2008b. First record of Placodontoidea (Reptilia, Sauropterygia, Placodontia) from the Eastern Tethys. Journal of Vertebrate Paleontology 28, 904–908.

Jiang, D.Y., Motani, R., Rieppel, O., Hao, W.C., Schmitz, L., Sun, Y.L., Sun, Z.Y., 2008c. New primitive ichthyosaurian (Reptilia, Diapsida) from the Middle Triassic of Panxian, Guizhou, southwestern China and its position in the Triassic biotic recovery. Progress in Natural Science 18, 1315–1319.

Jiang, D.Y., Rieppel, O., Motani, R., Hao, W.C., Sun, Y.L., Schmitz, L., Sun, Z.Y., 2008d. A new Middle Triassic eosauropterygian (Reptilia, Sauropterygia) from Southwestern China. Journal of Vertebrate Paleontology 28, 1055–1062.

Jiang, D.Y., Rieppel, O., Motani, R., Hao, W.C., Sun, Y.L., Tintori, A., Sun, Z.Y., Schmitz, L., 2009. Biodiversity and sequence of the Middle Triassic Panxian marine reptile fauna, Guizhou Province, China. Acta Geologica Sinica 83, 451–459.

Jin, X.S., 1997. New species of coelacanth from Changxing Formation of Zhejiang. Bulletin of Science and Technology 13, 143–147.

Jin, F., 2001. Notes on the discovery of *Birgeria* in China. Vertebrata Palasiatica 39, 168–176.

Jin, F., 2006. An overview of Triassic fishes from China. Vertebrata Palasiatica 44, 28–42.

Jin, F., Wang, N.Z., Cai, Z.Q., 2003. A revision of the perleidid fishes from the Lower Yangtze region of South China—second report on the fish sequence study near the Permian–Triassic boundary in South China. Vertebrata Palasiatica 41, 169–184.

Kelley, N.P., Motani, R., Jiang, D.Y., Rieppel, O., Schmitz, L., 2013. Selective extinction of Triassic marine reptiles during long-term sea-level changes illuminated by seawater strontium isotopes. Palaeogeography, Palaeoclimatology, Palaeoecology. http://dx.doi.org/10.1016/j.palaeo.2012.07.026.

Klein, N., Albers, P.C.H., 2009. A new species of the sauropsid reptile *Nothosaurus* from the Lower Muschelkalk of the western Germanic Basin, Winterswijk, The Netherlands. Acta Palaeontologica Polonica 54, 589–598.

Knoll, A.H., Bambach, R.K., Payne, J.L., Pruss, S., Fischer, W.W., 2007. Paleophysiology and the end-Permian mass extinction. Earth and Planetary Science Letters 256, 295–313.

Kozur, H.W., 2003. Integrated ammonoid, conodont and radiolarian zonation of the Triassic and some remarks to Stage/Substage sub-division and the numeric age of the Triassic stages. Hallesches Jahrbuch Geowissenschaften, B 25, 49–79.

Lehrmann, D.J., Wei, J.Y., Enos, P., 1998. Controls on facies architecture of a large Triassic carbonate platform: the Great Bank of Guizhou, Nanpanjiang Basin, South China. Journal of Sedimentary Research 68, 311–326.

Lehrmann, D.J., Payne, J.L., Felix, S.V., Dillett, P.M., Wang, H., Yu, Y., Wei, J., 2003. Permian–Triassic boundary sections from shallow-marine carbonate platforms of the Nanpanjiang Basin, South China. Palaios 18, 138–152.

Lehrmann, D.J., Enos, P., Payne, J.L., Montgomery, P., Wei, J., Yu, Y., Xiao, J., Orchard, M.J., 2005. Permian and Triassic depositional history of the Yangtze platform and Great Bank of Guizhou in the Nanpanjiang basin of Guizhou and Guangxi, South China. Albertiana 33, 149–168.

Lehrmann, D.J., Ramezani, J., Bowring, S.A., Martin, M.W., Montgomery, P., Enos, P., Payne, J.L., Orchard, M.J., Wang, H., Wei, J., 2006. Timing of recovery from the end-Permian extinction: geochronologic and biostratigraphic constraints from south China. Geology 34, 1053–1056.

Lehrmann, D.J., Payne, J.L., Pei, D., Enos, P., Ellwood, B., Orchard, M.J., Zhang, J., Wei, J., 2007. Record of the end-Permian extinction and Triassic biotic recovery in the Chongzuo–Pingguo platform, southern Nanpanjiang basin, Guangxi, south China. Palaeogeography Palaeoclimatology Palaeoecology 252, 200–217.

Lehrmann, D.J., Minzoni, M., Enos, P., Yu, Y., Wei, J., Li, R., 2009. Triassic depositional history of the Yangtze Platform and Great Bank of Guizhou in the Nanpanjiang Basin of South China. Journal of Earth Sciences and Environment 31, 344–367.

Lei, Y.C., 1983. A new *Sinohelicoprion* (helicopriond, shark) from Late Permian of Hunan, South China. Vertebrata Palasiatica 21, 347–351.

Lepvrier, C., Maluski, H., 2008. The Triassic Indosinian orogeny in East Asia. Comptes Rendus Geosciences 340, 75–82.

Li, C., 1999. Ichthyosaur from Guizhou, China. Chinese Science Bulletin 44, 1329–1333.

Li, C., 2000. Placodont (Reptilia: Placodontia) from Upper Triassic of Guizhou, southwest China. Vertebrata PalAsiatica 38, 314–317 (in Chinese with English summary).

Li, C., 2003. First record of protorosaurid reptile (Order Protorosauria) from the Middle Triassic of China. Acta Geologica Sinica 77, 419–423.

Li, J.L., 2006. A brief summary of the Triassic marine reptiles of China. Vertebrata PalAsiatica 44, 99–108.

Li, C., 2007. A juvenile *Tanystropheus* sp. (Protorosauria, Tanystropheidae) from the Middle Triassic of Guizhou, China. Vertebrata PalAsiatica 45, 37–42 (in Chinese with English summary).

Li, Q.G., 2009. A new parasemionotid-like fish from the Lower Triassic of Jurong, Jiangsu Province, South China. Palaeontology 52, 369–384.

Li, J.L., Jin, F., 2003. New advances of the research on *Keichousaurus* reptile fauna. Progress in Natural Sciences 13, 796–800.

Li, J.L., Jin, F., 2009. A Travel in the Sea 20 Million Years Ago—Triassic Marine Reptile and Environment of South China.Science Press, Beijing 99–121.

Li, C., Rieppel, O., 2002. A new cyamodontoid placodont from Triassic of Guizhou, China. Chinese Science Bulletin 47, 403–407.

Li, J.L., Rieppel, O., 2004. A new nothosaur from Middle Triassic of Guizhou, China. Vertebrata PalAsiatica 42, 1–12 (in Chinese with English summary).

Li, C., You, H.L., 2002. *Cymbospondylus* from the Upper Triassic of China. Vertebrata PalAsiatica 40, 9–16 (in Chinese with English summary).

Li, J.L., Liu, J., Li, C., Huang, Z.X., 2002a. The horizon and age of the marine reptiles from Hubei Province, China. Vertebrata PalAsiatica 40, 241–244 (in Chinese with English summary).

Li, J.L., Liu, J., Rieppel, O., 2002b. A new species of *Lariosaurus* (Sauropterygia: Nothosauridae) from Triassic of Guizhou, southwest China. Vertebrata PalAsiatica 40, 114–126 (in Chinese with English summary).

Li, C., Rieppel, O., LaBarbera, M.C., 2004. A Triassic aquatic protorosaur with an extremely long neck. Science 305, 1931–1931.

Li, C., Wu, X.C., Cheng, Y.N., Sato, T., Wang, L.T., 2006. An unusual archosaurian from the marine Triassic of China. Naturwissenschaften 93, 200–206.

Li, C., Wu, X.C., Rieppel, O., Wang, L.T., Zhao, L.J., 2008. An ancestral turtle from the Late Triassic of southwestern China. Nature 456, 497–501.

Li, C., Rieppel, O., Wu, X.C., Zhao, L.J., Wang, L.T., 2011. A new Triassic marine reptile from southwestern China. Journal of Vertebrate Paleontology 31, 303–312.

Li, C., Jiang, D.Y., Cheng, L., Wu, X.C., Rieppel, O., 2013. A new species of *Largocephalosaurus* (Diapsida: Saurosphargidae), with implications for the morphological diversity and phylogeny of the group. Geological Magazine. http://dx.doi.org/10.1017/S001675681300023X (online ahead of print).

Li, C., Zhao, L.J., Wang, L.T., 2007. A new species of Macrocnemus (Reptilia: Protorosauria) from the Middle Triassic of southwestern China and its palaeogeographical implication. Science in China Series D: Earth Sciences 50, 1601–1605.

Lin, K., Rieppel, O., 1998. Functional morphology and ontogeny of *Keichousaurus hui* (Reptilia, Sauropterygia). Fieldiana (Geology) 39, 1–39.

Lin, H.Q., Sun, Z.Y., Tintori, A., Lombardo, C., Jiang, D.Y., Hao, W.C., 2011. A new species of *Habroichthys* Brough, 1939 (Actinopterygii; Peltopleuriformes) from the Pelsonian (Anisian, Middle Triassic) of Yunan Province, South China. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 262, 79–89.

Liu, X.T., 1964. Discovery of a coelacanth from the Lower Triassic of Guangxi Province of China. Vertebrata Palasiatica 8, 211–212 (in Chinese with English summary).

Liu, Z.H., 1994. New material of helicopriond in Lianyuan, Hunan province. Vertebrata Palasiatica 32, 127–133 (in Chinese with English summary).

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

Liu, J., 2001. Postcranial skeleton of *Xinpusaurus*. In: Deng, T., Wang, Y. (Eds.), Proceedings of the Eighth Annual Meeting of the Chinese Society of Vertebrate Paleontology. China Ocean Press, Beijing.

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

Liu, J., Rieppel, O., 2001. The second thalattosaur from the Triassic of Guizhou, China. Vertebrata PalAsiatica 39, 77–87 (in Chinese with English summary).

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

Liu, G.B., Wang, Q., 1994. New material of *Sinohelicoprion* from Changxing, Zhejiang province. Vertebrata Palasiatica 32, 244–248.

Liu, X.T., Wei, F., 1988. A new saurichthyid from the Upper Permian of Zhejiang, China. Vertebrata Palasiatica 26, 77–89 (in Chinese with English summary).

Liu, B.J., Xu, X.S. (Eds.), 1994. Paleogeography and Lithofacies Atlas of South China (Sinian–Triassic). The Series of Paleogeography and Lithofacies of South China. Science Press, Beijing (192 pp. (in Chinese)).

Liu, G.B., Yin, G.Z., 2008. Preliminary researches for mixosaurid fossils from Middle Triassic Guanling Formation in Panxian of Guizhou. Acta Palaeontologica Sinica 47, 73–90 (in Chinese with English summary).

Liu, X.T., Zhang, M.M., 1963. Discovery of Helicoprionidae in China. Vertebrata Palasiatica 7, 123–131 (in Chinese with English summary).

Liu, G.B., Feng, H.Z., Wang, J.X., Wu, T.M., Zhai, Z.H., 2002a. Early Triassic fishes from Jurong, Jiangsu. Acta Palaeontologica Sinica 41, 27–52 (in Chinese with English summary).

Liu, G.B., Yin, G.Z., Wang, X.H., 2002b. On the most primitive amiid fish from Upper Triassic of Xingyi, Guizhou. Acta Palaeontological Sinica 41, 461–463.

Liu, G.B., Yin, G.Z., Wang, X.H., Wang, S.Y., Huang, L.Z., 2002c. On a new marine reptile from Middle Triassic Yangliujing Formation of Guizhou, China. Geological Journal of China Universities 8, 220–226 (in Chinese with English summary).

Liu, G.B., Yin, G.Z., Wang, X.H., Luo, Y.M., Wang, S.Y., 2003. New discovered fishes from *Keichousaurus* bearing horizon of Late Triassic in Xingyi of Guizhou. Acta Palaeontologica Sinica 42, 346–366 (in Chinese with English summary).

Liu, G.B., Yin, G.Z., Luo, Y.M., Wang, X.H., Wang, S.Y., 2006. Preliminary examination of fish fossils from Upper Triassic Wayao Member of Falang Formation in Guanling of Guizhou. Acta Palaeontologica Sinica 45, 1–20 (in Chinese with English summary).

Liu, J., Jiang, D.Y., Montani, R., Rieppel, O., Benton, M.J., Aitchison, J.C., Hu, S.X., Zhang, Q.Y., Zhou, C.Y., 2010. A preliminary review of the diversity of marine reptiles from Luoping Fauna. International Symposium on Triassic and Later Marine Vertebrate Faunas Program and Abstracts Book, p. 62.

Liu, J., Aitchison, J.C., Sun, Y.Y., Zhang, Q.Y., Zhou, C.Y., Lv, T., 2011a. New mixosaurid ichthyosaur specimen from the Middle Triassic of SW China: further evidence for the diapsid origin of ichthyosaurs. Journal of Paleontology 85, 32–36.

Liu, J., Rieppel, O., Jiang, D.Y., Aitchison, J.C., Motani, R., Zhang, Q.Y., Zhou, C.Y., Sun, Y.Y., 2011b. A new pachypleurosaur (Reptilia, Sauropterygia) from the lower Middle Triassic of SW China and the phylogenetic relationships of Chinese pachypleurosaurs. Journal of Vertebrate Paleontology 31, 292–302.

Liu, J., Motani, R., Jiang, D.Y., Hu, S.X., Aitchison, J.C., Benton, M.J., Rieppel, O., Zhang, Q.Y., Zhou, C.Y., 2013. The first specimen of *Phalarodon atavus* from South China, showing the postcranial anatomy and peri-Tethyan distribution. Palaeontology 56, 849–866. http://dx.doi.org/10.1111/pala.12021.

Lombardo, C., Sun, Z.Y., Tintori, A., Jiang, D.Y., Hao, W.C., 2011. A new species of the genus *Perleidus* (Actinopterygii: Perleidiformes) from the Middle Triassic of Southern China. Bollettino della Società Palaeontologica Italiana 50, 75–83.

López-Arbarello, A., Sun, Z.Y., Sferco, E., Tintori, A., Xu, G.H., Sun, Y.L., Wu, F.X., Jiang, D.Y., 2011. New species of *Sangiorgioichthys* Tintori and Lombardo, 2007 (Neopterygii, Semionotiformes) from the Anisian of Luoping (Yunnan Province, South China). Zootaxa 2749, 25–39.

Luo, Y., Yu, Y., 2002. The restudy on the skull and mandible of *Xinpusaurus suni*. Guizhou Geology 19, 71–75 (in Chinese with English abstract).

Luo, M., Chen, Z.Q., Hu, S.X., Zhang, Q.Y., Benton, M.J., Zhou, C.Y., Wen, W., Huang, J.Y., 2013. Carbonate reticulated ridge structures from the early middle triassic of Luoping area, Yunnan, Southwest China: geobiologic features and implications for exceptional preservation of the Luoping biota. Palaios (in press).

Ma, Y.S., Chen, H.D., Wang, G.L. (Eds.), 2009. Atlas of Tectonics and Sequence Lithofacies Palaeogeography in Southern China (Sinian–Neogene). Science Press, Beijing (301pp.).

Maisch, M.W., 2001. Observations on Triassic ichthyosaurs. Part VII: new data on the osteology of *Chaohusaurus geishanensis* Young and Dong, 1972 from the Lower Triassic of Anhui (China). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 219, 305–327.

Maisch, M.W., Matzke, A.T., Jiang, D.Y., 2003. Observations on Triassic ichthyosaurs. Part XI: the taxonomic status of *Mixosaurus maotaiensis* Young, 1965 from the Middle Triassic of Guizhou, People's Republic of China. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 2003, 428–438.

Maisch, M.W., Pan, X.R., Sun, Z.Y., Cai, T., Zhang, D.P., Xie, J.L., 2006. Cranial osteology of *Guizhouichthyosaurus tangae* (Reptilia: Ichthyosauria) from the Upper Triassic of China. Journal of Vertebrate Paleontology 26, 588–597.

Maisch, M.W., Jiang, D.Y., Hao, W.C., Sun, Y.L., Sun, Z.Y., Stöhr, H., 2008. A well-preserved skull of *Qianichthyosaurus zhoui* Li, 1999 (Reptilia: Ichthyosauria) from the Upper Triassic of China and the phylogenetic position of the Toretocnemidae. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 248, 257–266.

Massare, J.A., 1988. Swimming capabilities of Mesozoic marine reptiles: implications for method of predation. Paleobiology 14, 187–205.

Massare, J.A., 1997. Faunas, behavior, and evolution: introduction. In: Callaway, J.M., Nicholls, E.L. (Eds.), Ancient Marine Reptiles. Academic Press, New York, pp. 401–421.

Mazin, J.M., Suteethorn, V., Buffetaut, E., Jäger, J.J., Helmcke-Ingavat, R., 1991. Preliminary description of *Thaisaurus chonglakmanni* n. g., n. sp., a new ichthyopterygian (Reptilia) from the Early Triassic of Thailand. Comptes Rendus de l'Académie des Sciences, Série II 313, 1207–1212.

McGowan, C., Motani, R. (Eds.), 2003. Ichthyopterygia. Handbook of Paleoherpetology, 8. Friedrich Pfeil, München (175 pp.).

Ming, Q., Zhou, G., Jiang, F., Chen, C., Wen, S., Zhang, Z., 1981. Reinvestigation of the Triassic System in Nanjing district. Journal of Stratigraphy 5, 1–9.

Motani, R., You, H.L., 1998. Taxonomy and limb ontogeny of *Chaohusaurus geishanensis* (Ichthyosauria), with a note on the allometric equation. Journal of Vertebrate Paleontology 18, 533–540.

Motani, R., You, H.L., McGowan, C., 1996. Eel-like swimming in the earliest ichthyosaurs. Nature 382, 347–348.

Motani, R., Jiang, D.Y., Tintori, A., Sun, Y.L., Hao, W.C., Boyd, A., Hinic-Friog, S., Schmitz, L., Shin, J.Y., Sun, Z.Y., 2008. Horizons and assemblages of Middle Triassic marine reptiles from Panxian, Guizhou, China. Journal of Vertebrate Paleontology 28, 900–903.

Mu, A.T., 1949. On the discovery of the crown of *Traumatocrinus*. Bulletin of the Geological Society of China 29, 85–92.

Newell, N.D., 1952. Periodicity in invertebrate evolution. Journal of Paleontology 26, 371–385.

Nicholls, E.L., Wei, C., Manabe, M., 2003. New material of *Qianichthyosaurus* Li, 1999 (Reptilia, Ichthyosauria) from the Late Triassic of Southern China, and implications for the distribution of Triassic ichthyosaurs. Journal of Vertebrate Paleontology 22, 759–765.

Orchard, M., Krystyn, L., 2007. Conodonts from the Induan-Olenekian boundary interval at Mud, Spiti. Albertiana 35, 30–34.

Ovtcharova, M., Bucher, H., Schaltegger, U., Galfetti, T., Brayard, A., Guex, J., 2006. New Early to Middle Triassic U–Pb ages from South China: calibration with ammonoid biochronozones and implications for the timing of the Triassic biotic recovery. Earth and Planetary Science Letters 243, 463–475.

Pan, X.R., Jiang, D.Y., Sun, Z.Y., Cai, T., Zhang, D.P., Xie, J.L., 2006. Discussion on *Guizhouichthyosaurus tangae* Cao and Luo in Yin et al., 2000 (Reptilia, Ichthyosauria) from the Late Triassic of Guanling County, Guizhou. Acta Scientiarum Naturalium Universitatis Pekinensis 42, 697–703.

Payne, J.L., Lehrmann, D.J., Wei, J., Orchard, M.J., Schrag, D.P., Knoll, A.H., 2004. Large perturbations of the carbon cycle during recovery from the end-Permian extinction. Science 305, 506–509.

Peters, S.E., 2005. Geologic constraints on the macroevolutionary history of marine animals. Proceedings of the National Academy of Sciences of the United States of America 102, 12326–12331.

Pitrat, C.W., 1973. Vertebrates and the Permo-Triassic extinction. Palaeogeography, Palaeoclimatology, Palaeoecology 14, 249–264.

Qian, M.P., Zhu, S.P., Zhao, F.M., Zhou, X.D., Su, R., Gu, G.H., Zhai, Z.H., 1997. Discovery of Early Triassic fish fossils and its significances in Jurong, Jiangsu Province. Jiangsu Geology 21, 65–71 (in Chinese with English summary).

Retallack, G.J., 2012. Permian and Triassic greenhouse crises. Gondwana Research. http://dx.doi.org/10.1016/j.gr.2012.03.003 (online first).

Rieppel, O., 1998a. The status of *Shingyisaurus unexpectus* from the Middle Triassic of Kweichou, China. Journal of Vertebrate Paleontology 18, 541–544.

Rieppel, O., 1998b. The systematic status of *Hanosaurus hupehensis* (Reptilia, Sauropterygia) from the Triassic of China. Journal of Vertebrate Paleontology 18, 545–557.

Rieppel, O., 1999. The sauropterygian genera *Chinchenia, Kwangsisaurus*, and *Sanchiaosaurus* from the Lower and Middle Triassic of China. Journal of Vertebrate Paleontology 19, 321–337.

Rieppel, O., 2000. Sauropterygia I. Encyclopedia of Paleoherpetology, 12A. Verlag Dr. Friedrich Pfeil, Munich (134 pp.).

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

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

Rieppel, O., Li, J.L., Jun, L., 2003. *Lariosaurus xingyiensis* (Reptilia: Sauropterygia) from the Triassic of China. Canadian Journal of Earth Sciences 40, 621–634.

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

Rieppel, O., Li, C., Fraser, N.C., 2008. The skeletal anatomy of the Triassic protorosaur *Dinocephalosaurus orientalis* Li, from the Middle Triassic of Guizhou Province, southern China. Journal of Vertebrate Paleontology 28, 95–110.

Rieppel, O., Jiang, D.Y., Fraser, N.C., Hao, W.C., Motani, R., Sun, Y.L., Sun, Z.Y., 2010. *Tanystropheus* cf. *T. longobardicus* from the early Late Triassic of Guizhou Province, southwestern China. Journal of Vertebrate Paleontology 30, 1082–1089.

Sahney, S., Benton, M.J., 2008. Recovery from the most profound mass extinction of all time. Proceedings of the Royal Society, Series B 275, 759–765.

Sander, P.M., Chen, X.F., Cheng, L., Wang, X.F., 2011. Short-snouted toothless ichthyosaur from China suggests Late Triassic diversification of suction feeding ichthyosaurs. PLoS One 6 (5), e19480. http://dx.doi.org/10.1371/journal.pone.0019480.

Sato, T., Cheng, Y.N., Wu, X.C., Li, C., 2010. Osteology of *Yunguisaurus* Cheng et al., 2006 (Reptilia; Sauropterygia), a Triassic pistosauroid from China. Paleontological Research 14, 179–195.

Sato, T., Zhao, L.J., Wu, X.C., Li, C., 2013. A new specimen of the Triassic pistosauroid *Yunguisaurus*, with implications for the origins of Plesiosauria (Reptilia, Sauropterygia). Paleontology (online ahead of print).

Saunders, A., Reichow, M., 2009. The Siberian Traps and the end-Permian mass extinction: a critical review. Chinese Science Bulletin 54, 20–37.

Schmitz, L., Sander, P.M., Storrs, G.W., Rieppel, O., 2004. New Mixosauridae (Ichthyosauria) from the Middle Triassic of the Augusta Mountains (Nevada, USA) and their implications for mixosaur taxonomy. Palaeontographica Abteilung A 270, 133–162.

Schubert, J.K., Bottjer, D.J., 1992. Early Triassic stromatolites as post-mass extinction forms. Geology 20, 883–886.

Sepkoski Jr., J.J., 1984. A kinetic model of Phanerozoic taxonomic diversity. Paleobiology 10, 246–267.

Shang, Q.H., 2006. A new species of *Nothosaurus* from the early Middle Triassic of Guizhou, China. Vertebrata PalAsiatica 44, 237–249.

Shang, Q.H., Wu, X.C., Li, C., 2011. A new eosauropterygian from Middle Triassic of eastern Yunnan Province, southwestern China. Vertebrata PalAsiatica 49, 155–171.

Shen, Z.Y., Ding, J.H., Ye, C.H., Wen, J.W., Wang, Z.L., Chen, Z.F., 2006. New Early Triassic paleomagnetic data from Huangben section, Guangdong and its tectonic implications. Chinese Science Bulletin 51, 1894–1902.

Shen, S.Z., Crowley, J.L., Wang, Y., Bowring, S.A., Erwin, D.H., Sadler, P.M., Cao, C.Q., Rothman, D.H., Henderson, C.M., Ramezani, J., Zhang, H., Shen, Y., Wang, X.D., Wang, W., Mu, L., Li, W.Z., Tang, Y.G., Liu, X.L., Liu, L.J., Zeng, Y., Jiang, Y.F., Jin, Y.G., 2011. Calibrating the end-Permian mass extinction. Science 334, 1367–1372.

Solé, R.V., Montoya, J.M., Erwin, D.H., 2002. Recovery from mass extinction: evolutionary assembly in large-scale biosphere dynamics. Philosophical Transactions of the Royal Society of London, Series B 357, 697–707.

Solé, R.V., Saldañya, J., Montoya, J.M., Erwin, D.H., 2010. Simple model of recovery dynamics after mass extinction. Journal of Theoretical Biology 267, 193–200.

Song, H.J., Wignall, P.B., Chen, Z.Q., Tong, J.N., Bond, D.P.G., Lai, X., Zhao, X., Jian, H., Yan, C., Niu, Z., Chen, J., Yang, H., Yang, Y., 2011. Recovery tempo and pattern of marine ecosystems after the end-Permian mass extinction. Geology 39, 739–742.

Song, H.J., Wignall, P.B., Tong, J.N., Yin, H.F., 2013. Two pulses of extinction during the Permian–Triassic crisis. Nature Geoscience 6, 52–56.

Su, D.Z., 1959. Marine Triassic fish fossils from Xingyi, Guizhou Province. Paleovertebrata et Paleoanthropologia 1, 205–210 (in Chinese).

Su, D.Z., 1981. A new species of *Perleidus* from Anhui. Vertebrata Palasiatica 19, 107–112.

Su, D.Z., Li, Z.C., 1983. A new Triassic perleidid fish from Hubei, China. Vertebrata PalAsiatica 21, 9–16.

Sun, S., Li, J.L., Chen, H.H., Peng, H.P., Hsü, K.J., Shelton, J.W., 1989. Mesozoic and Cenozoic Sedimentary History of South China. American Association of Petroleum Geologists Bulletin 73, 1247–1269.

Sun, Z.Y., Hao, W.C., Jiang, D.Y., 2005a. Conodont biostratigraphy near the Ladinian–Carnian boundary interval in Guanling of Guizhou. Journal of Stratigraphy 29, 259–262 (in Chinese with English abstract).

Sun, Z.Y., Hao, W.C., Maisch, M.W., Pfretzschner, H.U., Jiang, D.Y., 2005b. A lariosaur (Reptilia: Sauropterygia) from the Middle Triassic (Ladinian) Gejiu Formation of Yunnan, China. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 2005, 431–448.

Sun, Z.Y., Maisch, M.W., Hao, W.C., Jiang, D.Y., 2005c. A Middle Triassic thalattosaur (Reptilia: Diapsida) from Yunnan (China). Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 2005, 193–206.

Sun, Z.Y., Sun, Y.L., Hao, W.C., Jiang, D.Y., 2006. Conodont evidence for the age of the Panxian fauna, Guizhou. Acta Geologica Sinica 80, 621–630.

Sun, Z.Y., Tintori, A., Lombardo, C., Jiang, D.Y., 2008. A new species of the genus *Colobodus* Agassiz, 1844 (Osteichthyes, Actinopterygii) from the Pelsonian (Anisian, Middle Triassic) of Guizhou, South China. Rivista Italiana di Paleontologia e Stratigrafia 114, 363–376.

Sun, Z.Y., Tintori, A., Jiang, D.Y., 2009. A new perleidiform (Actinopterygii, Osteichthyes) from the Middle Anisian (Middle Triassic) of Yunnan, South China. Acta Palaeontologica Sinica 83, 460–470.

Sun, Y.D., Joachimski, M.M., Wignall, P.B., Yan, C.B., Chen, Y.L., Jiang, H.S., Wang, L.D., Lai, X.L., 2012. Lethally hot temperatures during the Early Triassic Greenhouse. Science 338, 366–370.

Taylor, R.S., Schram, F.R., Shen, Y.B., 2001. A new upper Middle Triassic shrimp (Crustacea: Lophogastrida) from Guizhou, China, with discussion regarding other "mysidaceans". Journal of Paleontology 75, 310–318.

Thomson, K.S., 1977. The pattern of diversification among fishes. In: Hallam, A. (Ed.), Patterns of Evolution as Illustrated by the Fossil Record. Elsevier, Amsterdam, pp. 377–404.

Tian, C.Y., Dai, J.Y., Tian, S.G., 1983. Triassic conodonts. In: Chengdu Institute of Geology and Mineral Resources (Ed.), Paleontological Atlas of Southwest China: Microfossils. Geological Publishing House, Beining, pp. 345–397 (in Chinese with English abstract).

Tintori, A., 1992. Fish taphonomy and Triassic anoxic basins from the Alps: a case history. Rivista Italiana di Paleontologia e Stratigrafia 97, 393–408.

Tintori, A., Lombardo, C.R.S., 2005. Tethyan Triassic fishes from Europe to China. Journal of Vertebrate Paleontology 25, 122A (Supplement).

Tintori, A., Sun, Z.Y., Lombardo, C., Jiang, D.Y., Sun, Y.L., Hao, W.C., 2007. New specialized basal neopterygians (Actinopterygii) from Triassic of the Tethys Realm. Geologia Insubrica 10, 13–20.

Tintori, A., Sun, Z.Y., Lombardo, C., Jiang, D.Y., Sun, Y.L., Hao, W.C., 2010. A new basal neopterygian from the Middle Triassic of Luoping County (South China). Rivista Italiana di Paleontologia e Stratigrafia 116, 161–172.

Tong, J.N., 2005. Triassic. In: Wang, X., Chen, X. (Eds.), Stratigraphical Subdivision and Correlations of Geological Times in China. Geological Publishing House, Beijing, pp. 343–390 (in Chinese with English summary).

Tong, J.N., Zakharov, Y.D., Orchard, M.J., Yin, H., Hansen, H., 2003. A candidate of the Induan–Olenekian boundary stratotype in the Tethyan region. Science in China Series D: Earth Sciences 46, 1182–1200.

Tong, J.N., Zakharov, Y.D., Wu, S.B., 2004. Early Triassic ammonoid succession in Chaohu, Anhui Province. Acta Palaeontologica Sinica 43, 192–204.

Tong, J.N., Zhou, X., Erwin, D.H., Zuo, J., Zhao, L., 2006. Fossil fishes from the Lower Triassic of Majiashan, Chaohu, Anhui Province, China. Journal of Paleontology 80, 146–161.

Van Valen, L., 1984. A resetting of Phanerozoic community evolution. Nature 307, 50–52.

Vermeij, G.J., 1977. The Mesozoic marine revolution; evidence from snails, predators and grazers. Paleobiology 3, 245–258.

Wang, K.M., 1959. Discovery of a new reptile from fossil from Hubei, China. Acta Palaeontologica Sinica 7, 367–378 (in Chinese with English abstract).

Wang, H.Z. (Ed.), 1985. Atlas of the Palaeogeography of China. Cartographic Publishing House, Beijing (281 pp.).

Wang, A.D., 1986. A new species of Sinoplatysomus from Changxing Formation, Zhejiang. Geology of Zhejiang 2, 1–6.

Wang, C.Y., 1991. Triassic conodont biostratigraphy in China. Journal of Stratigraphy 15, 311–312 (in Chinese with English abstract).

Wang, Z.H., Duan, Z., 1990. Triassic conodont biostratigraphy of different facies realms in eastern Yunnan, western Guizhou and northern Guangxi. Journal of Stratigraphy 14, 15–35 (in Chinese with English abstract).

Wang, N.Z., Jin, F., 2007. Actinopterygian fishes from the Permian–Triassic Boundary beds in Zhejiang and Jiangxi provinces, South China and fish mass extinction, recovery and radiation. Vertebrata PalAsiatica 45, 307–329 (in Chinese with English summary).

Wang, N.Z., Liu, X.T., 1981. Coelacanth fishes from the marine Permian of Zhejiang, South China. Vertebrata Palasiatica 19, 305–312.

Wang, C.Y., Kang, P.Q., Wang, Z.H., 1998. Conodont-based age of the Keichousaurus hui Yang, 1958. Acta Micropalaeontologica Sinica 15, 196–198 (in Chinese with English abstract).

Wang, N.Z., Yang, S.R., Jin, F., 2001. Early Triassic Hybodontoidae from Tiandong of Guangxi, China—first report on the fish sequence study near the Permian–Triassic boundary in South China. Vertebrata Palasiatica 39, 251–265.

Wang, X.F., Chen, X.H., Chen, L.D., Wang, C.S., 2003a. Study of the Guanling biota in Guizhou: progress and problems. Geological Bulletin of China 22, 221–227 (in Chinese with English summary).

Wang, X.F., Chen, X.H., Chen, L.D., Wang, C.S., 2003b. The Guanling biota—a unique "Fossillagerstätte" in the world. Geology in China 30, 20–35.

Wang, N.Z., Zhu, X.S., Jin, F., 2007a. Chondrichthyan microremains under Permian–Triassic boundary both in Zhejiang and Jiangxi provinces, China — fifth report on the fish sequence study near the Permian–Triassic boundary in South China. Vertebrata Palasiatica 45, 13–36.

Wang, N.Z., Jin, F., Wang, W., 2007b. Actinopterygian fishes from the Permian–Triassic boundary beds in Zhejinag and Jiangxi province, South China and fish mass extinction, recovery and radiation. Vertebrata Palasiatica 45, 307–329.

Wang, X.F., Bachmann, G.H., Hagdorn, H., Sander, P.M., Cuny, G., Chen, X.H., Wang, C.S., Chen, L.D., Cheng, L., Meng, F.S., Xu, G.G., 2008. The Late Triassic black shales of the Guanling area, Guizhou Province, south-west China: a unique marine reptile and pelagic crinoid fossil Lagerstätte. Palaeontology 51, 27–61.

Wang, X.F., Chen, X.H., Chen, L.D., Wang, C.S., Bachmann, G.H., Sander, M., Hargdorn, H., 2009. Sedimentary and palaeoecological environments of the Guanling and related biotas. Acta Palaeontologica Sinica 48, 509–526 (in Chinese with English abstract).

Wei, F., 1977. On the occurrence of platysomid in the Changsing (Changxing) limestone of Zhejiang. Acta Palaeonotologica Sinica 16, 293–296.

Wen, W., Zhang, Q.Y., Hu, S.X., Zhou, C.Y., Xie, T., Huang, J.Y., Chen, Z.Q., Benton, M.J., 2012. A new genus of basal actinopterygian fish from the Anisian (Middle Triassic) of Luoping, Yunnan Province, Southwest China. Acta Palaeontologica Polonica 57, 149–160.

Wen, W., Zhang, Q.Y., Hu, S.X., Benton, M.J., Zhou, C.Y., Xie, T., Huang, J.Y., Chen, Z.Q., 2013. Coelacanths from the Middle Triassic Luoping biota, Yunnan, South China, with the earliest evidence of ovoviviparity. Acta Palaeontologica Polonica 8, 175–193. http://dx.doi.org/10.4202/app. 2011.0066.

Wignall, P.B., Hallam, A., 1993. Griesbachian (earliest Triassic) palaeoenvironmental changes in the Salt Range, Pakistan and southeast China and their bearing on the Permo-Triassic mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology 102, 215–237.

Wignall, P.B., Twitchett, R.J., 1996. Oceanic anoxia and the end Permian mass extinction. Science 272, 1155–1158.

Wu, X.C., Li, Z., Zhou, B.C., Dong, Z.-M., 2003. Palaeontology: a polydactylous amniote from the Triassic period. Nature 426, 516.

Wu, F.X., Sun, Y.L., Hao, W.C., Hang, D.Y., Xu, G.H., Sun, Z.Y., Tintori, A., 2009a. New species of Saurichthys (Actinopterygii: Saurichthyidae) from Middle Triassic (Anisian) of Yunnan Province, China. Acta Geologica Sinica 83, 440–450.

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

Wu, F.X., Sun, Y.L., Xu, G.H., Hao, W.C., Jiang, D.Y., Su, Z.Y., 2011a. New saurichthyid actinopterygian fishes from the Anisian (Middle Triassic) of southwestern China. Acta Palaeontologica Polonica 56, 581–614.

Wu, X.C., Cheng, Y.N., Li, C., Zhao, L.J., Sato, T., 2011b. New information on Wumengosaurus delicatomandibularis Jiang et al., 2008 (Diapsida: Sauropterygia),
with a revision of the osteology and phylogeny of the taxon. Journal of Vertebrate Paleontology 31, 70–83.

Xu, G.H., Wu, F.X., 2012. A deep-bodied ginglymodian fish from the Middle Triassic of eastern Yunnan Province, China, and the phylogeny of lower neopterygians. Chinese Science Bulletin 57, 111–118.

Xu, G.G., Niu, Z.J., Chen, H.M., 2003. Triassic cephalopods from the Zhuganpo and Xiaowa formations in Guanling, Guizhou with a discussion on the age of the Guanling biota. Geological Bulletin of China 22, 254–265 (in Chinese with English abstract).

Xu, G.H., Zhao, L.J., Gao, K.Q., Wu, F.X., 2013. A new stem-neopterygian fish from the Middle Triassic of China shows the earliest over-water gliding strategy of the vertebrates. Proceedings of the Royal Society, Series B 280, 20122261. http://dx.doi.org/10.1098/rspb. 2012.2261.

Yang, S.R., Liu, J., 1995. Conodonts from the "Falang Formation" of southwestern Guizhou and their age. Journal of Stratigraphy 19, 162–170.

Yang, S.R., Wang, X.P., Hao, W.C., 1984. New knowledge on the Lower Triassic of Zuodeng, Tiandong County, Guangxi. Selected Papers for the Commemoration of Professor Yue Senxun engaged in Geological Education for 60 Years. Geological Publishing House, Beijing, pp. 105–117.

Yin, G.Z., Zhou, X.G., 2000. The Early Triassic marine reptile Neosinasaurus nom. nov. from Guanling, Guizhou, China. Geology–Geochemistry 28, 107–108 (in Chinese with English summary).

Yin, G.Z., Zhou, X.G., Cao, Z.T., Yu, Y.Y., Luo, Y.M., 2000. A preliminary study on the early Late Triassic marine reptiles from Guanling, Guizhou, China. Geology–Geochemistry 28, 1–23 (in Chinese with English summary).

Yin, H.F., Zhang, K.X., Tong, J.N., Yang, Z.Y., Wu, S.B., 2001. The global stratotype section and point (GSSP) of the Permian–Triassic boundary. Episodes 24, 102–114.

Young, C.C., 1958. On the new pachypleurosauroidea from Keichow, South-West China. Vertebrata PalAsiatica 2, 69–81 (in Chinese with English summary).

Young, C.C., 1959. On a new Nothosauria from the Lower Triassic beds of Kwangsi. Vertebrata PalAsiatica 3, 73–78.

Young, C.C., 1965a. On a revised determination of a fossil reptile from Jenhui, Kweichou with note on a new ichthyosaur probably from China. Vertebrata PalAsiatica 9, 368–376 (in Chinese with English summary).

Young, C.C., 1965b. On the new nothosaurs from Hupeh and Kweichou, China. Vertebrata PalAsiatica 9, 315–356 (in Chinese with English summary).

Young, C.C., 1972a. A marine lizard from Nanchang, Hupeh Province. Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropology. Academia Sinica 9, 17–28 (in Chinese).

Young, C.C., 1972b. Hupehsuchus nanchangensis. Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropology. Academia Sinica 9, 28–34 (in Chinese).

Young, C.C., 1978. Kwangsisaurus lusiensis from Yunnan. Vertebrata PalAsiatica 16, 222–224 (in Chinese with English summary).

Young, C.C., Dong, Z.M., 1972. Aquatic Reptiles from the Triassic of China. Academia Sinica, Institute of Vertebrate Paleontology and Paleoanthropology, Memoir, 9 (Beijing).

Zhang, M.M., 1976. A new species of helicoprionid shark from Xizang. Chinese Journal of Geology 10, 332–336 (in Chinese with English abstract).

Zhang, Q.Y., Zhou, C.Y., Lü, T., Bai, J.K., 2010. Discovery of Middle Triassic Saurichthys in the Luoping area, Yunnan, China. Geological Bulletin of China 29, 26–30.

Zhang, Q.Y., Zhou, C.Y., Lü, T., Xie, T., Lou, X.Y., Liu, W., Sun, Y.Y., Jiang, X.S., 2008. Discovery and significance of the Middle Triassic Anisian biota from Luoping, Yunnan Province. Geological Review 54, 523–526 (in Chinese with English summary).

Zhang, Q.Y., Zhou, C.Y., Lü, T., Xie, T., Luo, X.Y., Liu, W., Sun, Y.Y., Huang, J.Y., Zhao, L.S., 2009. A conodont-based Middle Triassic age assignment for the Luoping biota of Yunnan, China. Science in China Series D: Earth Sciences 52, 1673–1678.

Zhang, B.M., Chen, X.H., Cheng, L., Zhang, M., 2012a. Middle Triassic (Ladinian) elasmobranch scales from the southwest Guizhou, China. Acta Micropalaeontologica Sinica 29, 52–61.

Zhang, K., Tong, J., Lai, X., He, W., Jiang, H., Luo, G., 2012b. Stratigraphic unit and GSSP: concept, nomenclature, regulation and example. Geological Science and Technology Information 31, 23–42 (in Chinese with English abstract).

Zhao, L.J., Lu, L.W., 2007. A new genus of Early Triassic perleidid fish from Changxing, Zhejiang, China. Acta Palaeontologica Sinica 46, 238–243 (in Chinese with English summary).

Zhao, J.K., Chen, C.Z., Wang, Y.G., He, G.X., Chen, J.H., 1982. Problems on subdivision and correlation of the marine Triassic strata in China. Stratigraphic Correlation Chart in China, With Explanatory Text. Science Press, Beijing, pp. 191–205.

Zhao, L.S., Orchard, M.J., Tong, J.N., Sun, Z.M., Zuo, J.X., Zhang, S.X., Yun, A.L., 2007. Lower Triassic conodont sequence in Chaohu, Anhui Province, China and its global correlation. Palaeogeography, Palaeoclimatology, Palaeoecology 252, 24–38.

Zhao, L.J., Li, C., Liu, J., He, T., 2008a. A new armored placodont from the Middle Triassic of Yunnan Province, southwestern China. Vertebrata PalAsiatica 46, 171–177.

Zhao, L.J., Sato, T., Li, C., 2008b. The most complete pistosauroid skeleton from the Triassic of Yunnan, China. Acta Geologica Sinica 82, 283–286.

Zhao, L.S., Tong, J.N., Zhang, S.X., Sun, Z.M., 2008c. An update of conodonts in the Induan–Olenekian boundary strata at West Pingdingshan section, Chaohu, Anhui Province. Journal of China University of Geosciences 19, 207–216.

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