doi:10.1017/S001675681400003X

RAPID COMMUNICATION

The Triassic U–Pb age for the aquatic long-necked protorosaur of Guizhou, China

YANBIN WANG*‡†, DETING YANG*‡, JUAN HAN§, LITING WANG¶, JIANXIN YAO* & DUNYI LIU*‡

*Institute of Geology, Chinese Academy of Geological Sciences, Beijing 100037, China
‡Beijing SHRIMP Center, Chinese Academy of Geological Sciences, Beijing 100037, China
§Beijing Research Institute of Uranium Geology, Beijing 100029, China
¶Geological Survey of Guizhou Province, Guiyang 550005, China

(*Received* 12 August 2012; *accepted* 16 January 2013; *first published online* 27 February 2014)

Abstract

The ancient marine limestone beds of the upper part of the Guanling Formation, Panxian County, Guizhou Province, SW China, yielded a wide range of high-diversity well-preserved marine reptiles such as the fully aquatic protorosaur with an extremely long neck *Dinocephalosaurus orientalis*, the oldest mixosaurid ichthyosaurs and lariosaurs. However, there is no precise isotopic age to study the intriguing origin, evolution and emigration history of the important fauna. We report a sensitive high-resolution ion microprobe (SHRIMP) U–Pb zircon age for a volcanic tuff bed within the upper part of the Guanling Formation. The result indicates that the age of the fossil horizon is 244.0 ± 1.3 Ma, 14 Ma earlier than the previously estimated age based on conodont evidence. We consider that the marine reptiles had a relatively rapid evolution during Middle Triassic time, some 8 Ma after the end-Permian mass extinction.

Keywords: SHRIMP U–Pb zircon geochronology, volcanic tuff, Panxian Fauna, fully long-necked protorosaur, Middle Triassic.

1. Introduction

The end-Permian mass extinction (252 Ma) was the most devastating extinction event in Earth's history (Erwin, 1993, 1994) with nearly 96 % of the marine species and some 70 % of the terrestrial vertebrate genera becoming extinct (Bowring *et al.* 1998; Benton, 2005; Sahney & Benton, 2008). After the end-Permian mass extinction, the biosphere began to recover slowly in the drastically unstable environment during Early Triassic time. The organisms rapidly evolved during Middle Triassic time when the marine ecosystem became stable (Payne *et al.* 2004; Jiang *et al.* 2005). The fauna in Panxian County, Guizhou Province is the physical marker of a rapid radiation of the biosphere during Middle Triassic time (Jiang *et al.* 2005).

Many amazing marine reptile fossils have recently been discovered in Panxian County, Guizhou Province, SW China. Among these are the unusual archosaurian *Qianosuchus mixtus* (Li *et al.* 2006), the mixosaurid ichthyosaurian *Phalarodon cf. P. fraasi* (Jiang *et al.* 2007), the sauropterygians *Placodus inexpectatus* (Jiang *et al.* 2008*a*) and the *Wumengosaurus delicatomandibularis* (Jiang *et al.* 2008*b*). In particular, there occur some important species never before reported from the eastern Tethyan province such as the oldest mixosaurid ichthyosaur *Mixosaurus panxianensis* (Jiang *et al.* 2006*c*), the oldest lariosaurs *Lariosaurus hongguoensis* (Jiang *et al.* 2006*a*), the *Nothosaurus yangjuanensis* (Jiang *et al.* 2006*b*) and the fully aquatic protorosaur *Dinocephalosaurus orientalis* (Li, Rieppel & Labarbera, 2004). The bizarre creature *Dinocephalosaurus orientalis* (which means 'terrible headed lizard from the Orient') was found in 2002 (Li, 2003). It is the first reported fully marine member of the protorosaurids, different from the giraffe-necked protorosaurid reptile *Tanystropheus* which was discovered in the Monte San Giorgio Grenzbitumenzone Fauna (Besano Formation, Anisian–Ladinian boundary, northern Italy, the representative fauna in the western Tethyan Fauna province). The Grenzbitumenzone Fauna is located on the southern shores of Lake Lugano in the Alps which contains reptiles, fishes, bivalves, ammonites, echinoderms and crustaceans (Bürgin *et al.* 1989; Sander, 1989). Similarly, in the marine limestone beds of the Guanling Formation, there are well-preserved completely articulated skeletons of fishes and invertebrates including brachiopods, cephalopods, bivalves and some as yet undescribed taxa (Hao *et al.* 2006).

This well-preserved assemblage of fossils provides new insights into their origin, evolution and migration. Despite the importance of this fossil assemblage, its geological age has not been precisely determined. Palaeontologists focusing on the age of the fossil assemblage have so far only considered the conodont evidence. As a useful tool, conodonts have played an effective role in defining the age of marine reptile fauna (Sun, Hao & Jiang, 2003; Sun *et al.* 2006). However, their precise correlation with the global Triassic time scale has been problematic, mainly due to an uncalibrated biostratigraphy (Li, Rieppel & Labarbera, 2004; Sun *et al.* 2006). The age of this sequence therefore still requires independent isotopic age control. U–Pb isotopic dating of zircon, using the sensitive high-resolution ion microprobe (SHRIMP) II ion microscope of volcanic tuff layers intercalated within fossil-bearing marine sediments provides one of the best means of geochronologic control. We selected zircon grains from volcanic tuff layers of the upper Guanling Formation and applied the SHRIMP dating method to obtain a reliable radiometric age.

†Author for correspondence: wangyanbin@bjshrimp.cn

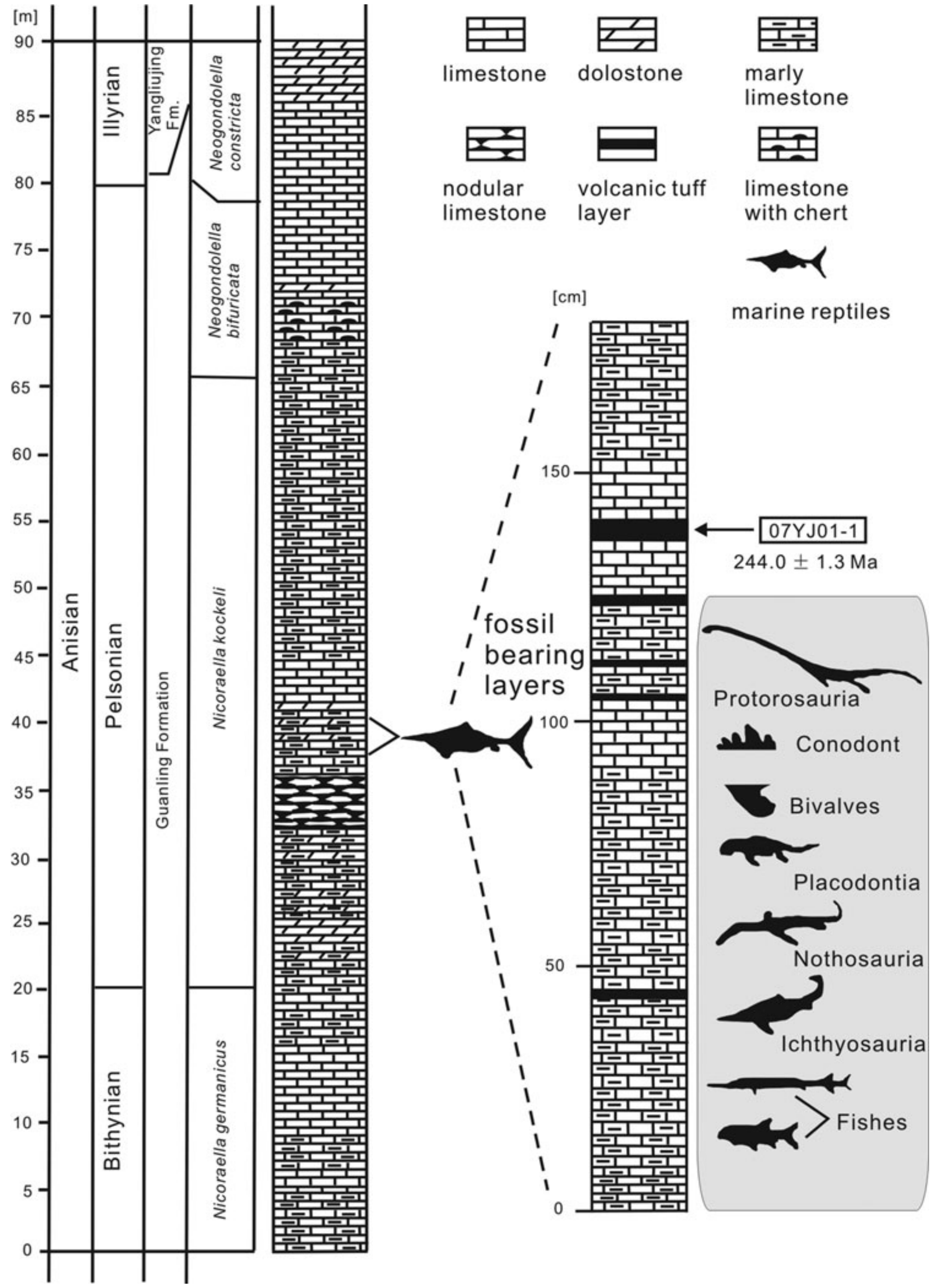

Figure 1. Stratigraphic section of the Middle Triassic Upper Guanling Formation at Yangjuan village. Vertebrate-bearing beds and index fossils of the section are indicated. Arrow shows stratigraphic location of dated tuff sample 07YJ01–1 (the stratigraphic section was modified and updated from Hao *et al.* 2006; Sun *et al.* 2006).

2. Geological setting and sampling

The marine reptile fossils from the upper part of the Guanling Formation are found in a small region surrounding the village of Yangjuan, located nearly 60 km SE of the city of Panxian, Guizhou Province (Fig. S1, available at http://journals.cambridge.org/geo). The upper member of the Guanling Formation, with a thickness of *c.* 80 m, forms the lower section and consists of alternating thinly bedded bituminous limestone, marly limestone, dolostone, nodular limestone and limestone with chert (Fig. 1). Its sedimentary environment is interpreted as shallow marine and partly hypersaline (Wang *et al.* 2008).

Based on the character of the conodont assemblages, four conodont biozones were recognized in the upper member of the Guanling Formation, namely: the *Nicoraella germanicus* zone; *Nicoraella kockeli* zone; *Paragondolella bifurcate* zone; and *Neogondolella constricta* zone (Sun *et al.* 2006). All marine reptile fossils in this area were excavated from a horizon of *c.* 3 m thickness, enlarged on the right in Figure 1. The fossil assemblage has been interpreted as being of Middle Triassic age and Anisian stage, corresponding to the *Nicoraella kockeli* zone. The strata containing the fauna is stratigraphically continuous and contains five volcanic tuff beds (each *c.* 3–5 cm in thickness) which are intercalated within the sediments. The genera of marine reptiles discovered in these strata are Protorsauria, Placodontia, Nothosauria, Ichthyosauria and some undescribed taxa. Motani *et al.* (2008) suggested that most of these fossils occurred at three different levels. The *Lariosaurus*, *Placodus*,

https://doi.org/10.1017/S001675681400003X Published online by Cambridge University Press

Table 1. SHRIMP U–Pb zircon analyses

Spot	$^{206}Pb_c$ (%)	U ($\times 10^{-6}$)	Th ($\times 10^{-6}$)	$^{232}Th/^{238}U$	$^{206}Pb^*$ ($\times 10^{-6}$)	$^{207}Pb^*/^{235}U$	1σ± (%)	$^{206}Pb^*/^{238}U$	1σ± (%)	$^{207}Pb^*/^{206}Pb^*$	1σ± (%)	$^{206}Pb/^{238}U$ Ma	1σ±
1	1.72	136	83	0.63	4.68	0.254	11	0.03932	1.9	0.0468	11	248.6	4.5
2	2.93	144	64	0.46	4.96	0.269	17	0.03902	1.7	0.0501	17	246.8	4.1
3	0.83	305	214	0.73	9.95	0.250	4.5	0.03771	1.3	0.0480	4.3	238.6	2.9
4	–	341	221	0.67	11.0	0.2820	2.4	0.03768	1.2	0.0543	2.1	238.5	2.8
5	0.27	421	287	0.70	14.0	0.2683	3.6	0.03871	1.2	0.0503	3.4	244.9	2.9
6	0.01	187	89	0.49	6.05	0.303	6.0	0.03770	1.4	0.0583	5.9	238.6	3.2
7	1.01	268	143	0.55	8.96	0.253	6.8	0.03854	1.3	0.0477	6.6	243.8	3.1
8	1.76	235	113	0.50	7.85	0.217	9.2	0.03821	1.3	0.0411	9.1	241.8	3.2
9	–	449	263	0.60	14.9	0.2854	1.9	0.03853	1.2	0.05371	1.5	243.7	2.8
10	0.44	344	221	0.66	11.8	0.275	5.8	0.03975	1.3	0.0501	5.7	251.3	3.1
11	0.30	305	182	0.62	9.97	0.275	5.0	0.03792	1.3	0.0526	4.8	240.0	3.0
12	–	276	163	0.61	9.27	0.3012	2.3	0.03917	1.2	0.0558	1.9	247.7	3.0
13	0.06	532	371	0.72	16.8	0.2620	3.0	0.03679	1.2	0.0517	2.7	232.9	2.8
14	0.58	332	222	0.69	11.0	0.263	5.5	0.03832	1.4	0.0498	5.3	242.4	3.4
15	0.31	613	406	0.68	20.5	0.2702	3.2	0.03882	1.2	0.0505	3.0	245.5	2.8
16	0.50	337	205	0.63	11.2	0.274	6.1	0.03854	1.3	0.0515	6.0	243.8	3.0
17	–	894	570	0.66	30.0	0.2852	1.8	0.03911	1.1	0.05288	1.3	247.3	2.8
18	1.56	169	71	0.43	5.70	0.229	13	0.03867	1.5	0.0430	13	244.6	3.6
19	0.67	525	79	0.16	17.8	0.2554	3.7	0.03923	1.2	0.0472	3.5	248.0	2.9
20	1.34	261	153	0.61	8.53	0.217	10	0.03756	1.4	0.0419	9.9	237.7	3.2
21	–	362	231	0.66	12.5	0.3035	2.2	0.04019	1.2	0.0548	1.8	254.0	3.1
22	0.53	541	404	0.77	18.1	0.2599	3.3	0.03867	1.2	0.0487	3.0	244.6	2.8
23	0.71	327	198	0.63	11.0	0.260	5.9	0.03909	1.3	0.0482	5.8	247.2	3.1
24	0.22	531	124	0.24	18.0	0.2777	2.9	0.03930	1.2	0.0513	2.6	248.5	2.9
25	0.85	303	184	0.63	10.00	0.232	6.1	0.03822	1.3	0.0440	6.0	241.8	3.1
26	1.01	402	276	0.71	13.8	0.243	6.3	0.03963	1.2	0.0446	6.1	250.5	3.0
27	1.58	354	235	0.68	11.8	0.233	9.7	0.03814	1.4	0.0444	9.6	241.3	3.4
28	0.96	275	165	0.62	9.28	0.248	6.5	0.03889	1.3	0.0462	6.3	245.9	3.1
29	0.57	350	214	0.63	11.4	0.261	4.5	0.03775	1.3	0.0502	4.3	238.9	3.0
30	0.79	339	199	0.61	11.2	0.251	6.4	0.03803	1.3	0.0478	6.3	240.6	3.0
31	0.44	372	232	0.64	12.4	0.290	4.9	0.03867	1.3	0.0544	4.7	244.6	3.1
32	0.69	204	107	0.54	6.73	0.269	9.2	0.03813	1.4	0.0512	9.1	241.2	3.4
33	0.13	669	510	0.79	22.4	0.2715	1.7	0.03890	1.2	0.05063	1.3	246.0	2.8
34	0.49	247	149	0.62	8.38	0.278	4.9	0.03926	1.3	0.0513	4.7	248.2	3.2
35	0.72	288	160	0.57	9.34	0.2645	2.5	0.03747	1.3	0.0512	2.2	237.2	3.0
36	0.33	317	177	0.58	10.6	0.2733	3.1	0.03881	1.3	0.0511	2.9	245.4	3.0

Errors are 1σ; Pb_c and Pb^* indicate the common and radiogenic portions, respectively.
Error in standard calibration was 0.24 % (not included in above errors but required when comparing data from different mounts).
Common Pb corrected using measured ^{204}Pb.

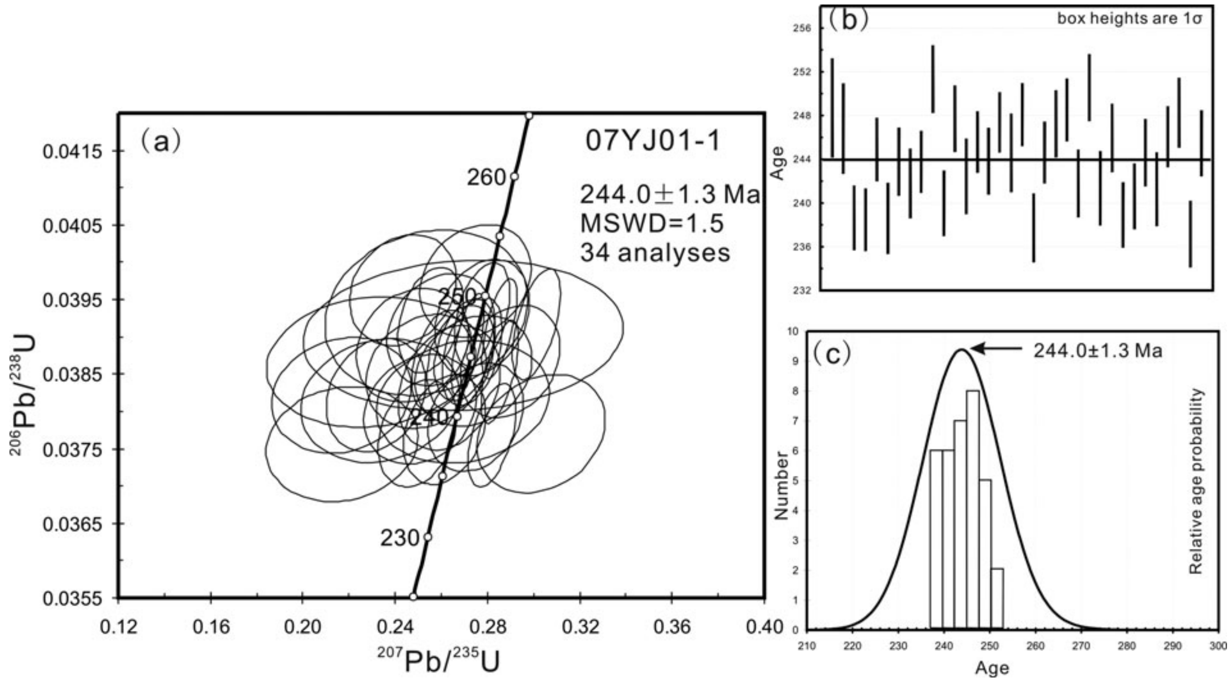

Figure 2. Zircon dating results. **(a)** Concordia plot for zircon grains from sample 07YJ01–1. (**b**) Corresponding distribution of weighted averages of $^{206}Pb/^{238}U$ ages. **(c)** Age probability diagram for analysed zircons from the volcanic tuffs sample (see Table 1 for details).

Phalarodon and undescribed *Ichthyosaur* occurred in the Lower Reptile Horizons, the *Mixosaurus*, *Nothosaurus* and *Qianosuchus* were found in the Middle Reptile Horizons and the *Mixosaurus*, *Dinocephalosaurus* and undescribed *Pachypleurosaur* were unearthed in the Upper Reptile Horizons.

We focus on the middle–upper part of the Guanling Formation. Sample 07YJ01–1 (N 25° 31′ 27″, E 104° 53′ 56″) was collected from the uppermost and thickest volcanic tuff layer in the fossil-bearing strata (Fig. 1). Given the proximity of the tuff to the fossiliferous layer, dating of this tuff is the most effective means to resolve the age of the fossils of the upper Guanling Formation (Stockar, Baumgartner & Condon, 2012). Zircon is considered to be the only suitable mineral for isotopic dating in these tuffs (Mundil *et al.* 2004).

3. Analytical method and results

Sample 07YJ01–1 was processed by conventional heavy liquid and magnetic separation techniques and purified by hand-picking under a binocular microscope. Zircons were mounted together with a fragment of zircon standard SL13 (U = 238 ppm; Williams *et al.* 1998) and grains of the standard zircon Temora 1 (417 Ma; Black *et al.* 2003). The internal structure of the unknown zircons was examined using cathodoluminescence (CL) imaging prior to isotopic analyses.

Measurements of U, Th and Pb isotopes were performed using the SHRIMP II ion microprobe at Curtin University, Perth, Australia through the Remote Operation System at the Beijing SHRIMP Center, Chinese Academy of Geological Sciences. Detailed operating and analytical procedures were similar to those described by Williams (1998). Uranium concentrations were determined by normalizing to zircon SL13 (Williams, 1998). U–Pb ratios were corrected for bias associated with sputtering by using a power law relationship between [$^{206}Pb/^{238}U$]–[$^{238}U^{16}O/^{238}U$] (Claoué-Long *et al*. 1995) and normalizing to the Temora 1 reference zircon (417 Ma; Black *et al*. 2003). Measured compositions were corrected for common Pb using the non-radiogenic ^{204}Pb. Uncertainties for each individual analysis are reported at the 1σ level; weighted mean ages of pooled analyses are quoted at the 95 % confidence interval. Data reduction was carried out using Isoplot 3.0 (Ludwig, 2003). The analytical data are presented in Table 1.

Zircons from sample 07YJ01–1 are mostly euhedral, prismatic, transparent and colourless, range from 100 to 250 μm in length, and have length to width ratios between 1:1 and 3:1 (Fig. S2, available at http://journals.cambridge.org/geo). Most zircon grains have concentric oscillatory zoning under CL, and some have inherited cores (Fig. S2, available at http://journals.cambridge.org/geo). U concentrations range from 136 to 894 ppm, Th from 64 to 570 ppm and Th/U ratios vary between 0.16 and 0.79, evidently of igneous origin (>0.1). With the exception of spot 13 (232.9 ± 2.8 Ma, the minimum age) and spot 21 (254.0 ± 3.1 Ma, the maximum age), 34 of the 36 spots analysed have indistinguishable $^{207}Pb/^{235}U$ and $^{206}Pb/^{238}U$ isotopic ratios within analytical uncertainties (Table 1) and plot as a coherent group close to concordia (Fig. 2a). They provide a weighted mean $^{206}Pb/^{238}U$ age of 244.0 ± 1.3 Ma (1σ, MSWD = 1.5) (Fig. 2b) that is interpreted as reflecting the zircon crystallization age of sample 07YJ01–1 and the best estimate of the depositional age of the tuff layer intercalated within the Guanling Formation. U–Pb isotopic results (Table 1) are presented in a relative age probability diagram (the peak is 244.0 ± 1.3 Ma; Fig. 2c).

4. Discussion and conclusions

Li, Rieppel & Labarbera (2004) reported that the aquatic long-necked protorosaur *Dinocephalosaurus orientalis* lived some 230 Ma ago. Our zircon age of 244.0 ± 1.3 Ma (1σ) for the tuff layer in the upper part of the Guanling Formation provides an absolute age constraint on the Triassic marine reptile fauna. It demonstrates that the age of the fauna is Middle Triassic, Anisian stage, at least 14 Ma earlier than the age of *c.* 230 Ma based on conodont evidence (Li, Rieppel & Labarbera, 2004; Sun *et al.* 2006).

During Middle Triassic time, many marine reptiles inhabited shallow epicontinental seas and intraplatform basins along the margins of Pangea (Li, Rieppel & Labarbera, 2004; Li *et al.* 2006). The Panxian fauna in the eastern Tethys province and the Grenzbitumenzone Fauna (Monte San Giorgio, northern Italy) in the western Tethys province are the two typical faunas of this period. The diversity of vertebrate faunal assemblages recorded in the Grenzbitumenzone fauna has long been recognized. Monte San Giorgio provides the principal point of reference, relevant to new discoveries of marine Triassic remains throughout the world. Dating of zircon grains contained in a layer of volcanic ash has established a time interval of *c.* 4 Ma (239–243 Ma; Stockar, Baumgartner & Condon, 2012). Many palaeontological studies have shown that the marine reptiles of the two faunas have apparent affinities (Rieppel 1999; Hao *et al.* 2006; Jiang *et al.* 2008*a*). Our new age permits a better comparison of the Panxian Fauna with the Monte San Giorgio Grenzbitumenzone Fauna (Rieppel, 1999; Stockar, Baumgartner & Condon, 2012). It is obvious from our results that the Panxian Fauna is slightly older than the Grenzbitumenzone Fauna (Hao *et al.* 2006; Stockar, Baumgartner & Condon, 2012), or nearly contemporaneous, which indicates that there is an important relationship in the evolution of marine reptiles between the eastern and western Tethys fauna (Rieppel, 1999; Li, 2003).

The Middle Triassic marine reptile fauna has received considerable attention in recent years. These fossils provide important clues to the modes of origin as well as subsequent radiation and diversification of marine reptiles. The new age data, in combination with the revised Middle Triassic time scale, provides a picture of relatively rapid evolution of early marine reptiles during Middle Triassic time, some 8 Ma after the end-Permian mass extinction, and the evolution occurred essentially contemporaneously throughout SW China and Europe. More systematic and high-quality geochronological data from the eastern Tethys and other Triassic marine-reptile-bearing successions are required to unravel the global patterns in the evolution of Triassic marine reptiles.

Supplementary material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S001675681400003X

Acknowledgement. This study was supported by the Geological Survey Project of Geological Survey of China (No. 1212011121066) and the Natural Science Foundation Project (No. 41073014). We thank Dirk Frei and an anonymous reviewer for their useful criticisms and comments which led to the improvement of the manuscript and Alfred Kroner, Mainz, Germany for his help with language. We also thank Andy Whitham and Susie Bloor for editorial handling.

References

Benton, M. J. 2005. *When Life Nearly Died: The Greatest Mass Extinction of All Time*. London: Thames & Hudson. ISBN 0-500-28573-X.

Black, L. P., Kamo, S. L., Allen, C. M., Aleinikoff, J. N., Davis, D. W., Korsch, R. J. & Foudoulis, C. 2003. TEMORA 1: a new zircon standard for Phanerozoic U-Pb geochronology. *Chemical Geology* **200**, 155–70.

Bowring, S. A., Ewrin, D. H., Jin, Y. G., Martin, M. W., Davidek, K. & Wang, W. 1998. U/Pb Zircon geochronology and tempo of the end-permian mass extinction. *Science* **280**, 1039–45.

Bürgin, T., Rieppel, O., Sander, P. M. & Tschanz, K. 1989. The fossils of Monte San Giorgio. *Scientific American* **260**, 64–81.

Claoué-Long, J. C., Compston, W., Roberts, J. & Fanning, C. M. 1995. Two carboniferous ages: a comparison of SHRIMP zircon dating with conventional zircon ages and $^{40}Ar/^{39}Ar$ analysis. In *Geochronology, Time Scales and Global Stratigraphic Correlation* (eds W. A. Berggren, D.V. Kent, M. P. Aubry & J. Hardenbol), SEPM (Society for Sedimentary Geology) **4**, 3–21.

Ewrin, D. H. 1993. *The Great Paleozoic Crisis*. New York: Cambridge University Press.

Ewrin, D. H. 1994. The Permo-Triassic extinction. *Nature* **367**, 231–6.

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**, 817–23 (in Chinese with English abstract).

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

Jiang, D. Y., Maisch, M. W., Hao, W. C., Sun, Y. L. & Sun, Z. Y. 2006*b*. Nothosaurus *yangjuanensis* n. sp. (Reptilia, Sauropterygia, Notho-sauridae) from the middle Anisian (Middle Triassic) of Guizhou. *Neues Jahrbuch für Geologie und Palaöntologie Monatshefte* **2006**, 257–76.

Jiang, D. Y., Motani, R., Li, C., Hao, W. C., Sun, Y. L., Sun, Z. Y. & Schmitz, L. 2005. Guanling biota: a marker of triassic biotic recovery from the end-permian extinction in the ancient guizhou sea. *Acta Geologica Sinica* **79**, 729–38.

Jiang, D. Y., Motani, R., Hao, W. C., Rieppel, O., Sun, Y. L., Schmitz, L. & Sun, Z. Y. 2008*a*. First record of placodontoidea (Reptilia, Sauropterygia, Placodontia) from the eastern Tethys. *Journal of Vertebrate Paleontology* **28**, 904–8.

Jiang, D. Y., Rieppel, O., Motani, R., Hao, W. C., Sun, Y. L., Schmitz, L. & Sun, Z. Y. 2008*b*. A new middle Triassic Eosauropterygian (Reptilia, Sauropterygia) from southwestern China. *Journal of Vertebrate Paleontology* **28**, 1055–62.

Jiang, D. Y., Schmitz, L., Hao, W. C. & Sun, Y. L. 2006*c*. 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**, 602–5.

Li, C. 2003. First Record of Protorosaurid Reptile (Order Protorosauria) from the Middle Triassic of China. *Acta Geologica Sinica* **77**, 419–23.

Li, C., Rieppel, O. & Labarbera, M. C. 2004. A Triassic aquatic protorosaur with an extremely long neck. *Science* **305**, 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**, 200–6.

Ludwig, K. R. 2003. *Isoplot 3.00. A Geochronological Toolkit for Microsoft Excel*. Berkley Geochronological Centre, Special Publication no. 4.

Motani, R., Jiang, D. Y., Tintori, A., Sun, Y. L., Hao, W. C., Boyd, A., Frlog, S. H., 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**, 900–3.

MUNDIL, R., LUDWIG, K. R., METCALFE, I. & RENNE, P. R. 2004. Age and timing of the Permian Mass Extinctions: U/Pb dating of closed-system zircons. *Science* **305**, 1760–3.

PAYNE, J. L., LEHRMANN, D. J., WEI, J. Y., 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**, 506–9.

RIEPPEL, O. 1999. Phylogeny and paleobiogeography of Triassic Sauropterygia: problems solved and unresolved. *Palaeogeography, Palaeoclimatology, Palaeoecology* **153**, 1–15.

SAHNEY, S. & BENTON, M. J. 2008. Recovery from the most profound mass extinction of all time. *Proceedings of the Royal Society: Biological* **275**, 759–65.

SANDER, P. M. 1989. The pachypleurosaurids (Reptilia: Nothosauria) from the Middle Triassic of Monte san Giorgio (Switzerland), with the description of a new species. *Philosophical Transactions of the Royal Society of London, Series B* **325**, 561–670.

STOCKAR, R., BAUMGARTNER, P. O. & CONDON, D. 2012. Integrated Ladinian bio-chronostratigraphy and geochrononology of Monte San Giorgio (Southern Alps, Switzerland). *Swiss Journal of Geoscience* **105**, 85–108.

SUN, Z. Y., HAO, W. C. & JIANG, D. Y. 2003. Conodont stratigraphic evidence for the age of the Guanling fauna, Guizhou Province, China. *Acta Scientiarum Naturalium Universitatis Pekinensis* **39**, 118–25 (in Chinese with English abstract).

SUN, Z. Y., SUN, Y. L., HAO, W. C. & JIANG, D. Y. 2006. Conodont evidence for the age of the Panxian Fauna, Guizhou, China. *Acta Geologica Sinica* **80**, 621–30.

WANG, X. F., BACHMANN, G. H., HAGDORN, H., SANDER, P. M., CHEN, L. D., CHENG, L., MENG, F. S. & XU, G. H. 2008. The late Triassic black shales of the Guanling area, Guizhou Province, southwestern China: a unique marine reptile and pelagic crinoid fossil lagerstätte. *Palaeontology* **51**, 27–61.

WILLIAMS, I. S. 1998. U-Th-Pb Geochronology by Ion Microprobe. In Applications of microanalytical techniques to understanding mineralizing processes (eds M. A. McKibben, W. C. Shanks & W. L. Ridley). *Reviews in Economic Geology* **7**, 1–35.