# The Luoping biota: exceptional preservation, and new evidence on the Triassic recovery from end-Permian mass extinction

**Shi-xue Hu**[1]**, Qi-yue Zhang**[1]**, Zhong-Qiang Chen**[2]**,**
**Chang-yong Zhou**[1]**, Tao Lü**[1]**, Tao Xie**[1]**, Wen Wen**[1]**,**
**Jin-yuan Huang**[1] **and Michael J. Benton**[3,*]

[1]*Chengdu Institute of Geology and Mineral Resources, Chengdu 610081, China*
[2]*School of Earth and Environment, The University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia*
[3]*School of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK*

The timing and nature of biotic recovery from the devastating end-Permian mass extinction (252 Ma) are much debated. New studies in South China suggest that complex marine ecosystems did not become re-established until the middle–late Anisian (Middle Triassic), much later than had been proposed by some. The recently discovered exceptionally preserved Luoping biota from the Anisian Stage of the Middle Triassic, Yunnan Province and southwest China shows this final stage of community assembly on the continental shelf. The fossil assemblage is a mixture of marine animals, including abundant lightly sclerotized arthropods, associated with fishes, marine reptiles, bivalves, gastropods, belemnoids, ammonoids, echinoderms, brachiopods, conodonts and foraminifers, as well as plants and rare arthropods from nearby land. In some ways, the Luoping biota rebuilt the framework of the pre-extinction latest Permian marine ecosystem, but it differed too in profound ways. New trophic levels were introduced, most notably among top predators in the form of the diverse marine reptiles that had no evident analogues in the Late Permian. The Luoping biota is one of the most diverse Triassic marine fossil Lagerstätten in the world, providing a new and early window on recovery and radiation of Triassic marine ecosystems some 10 Myr after the end-Permian mass extinction.

**Keywords:** end-Permian mass extinction; Triassic recovery; Luoping; China; marine reptiles

## 1. INTRODUCTION

The Triassic period documents recovery from the most devastating mass extinction of all time, the end-Permian event, which killed 80–90% of species [1–3]. The 10–20% of species that survived entered a world of harsh conditions that continued at least through the Early Triassic, a span of some 5 Myr [4], with repeated climatic shocks [5], and this set back the possibility of recovery of life and normal ecosystem functioning until at least the Middle Triassic [6]. It may have taken even longer for diversity dynamics to become re-established among tetrapods on land [7].

There are five types of taxa in the immediate post-extinction world. Three of these are survivors of pre-existing lineages that either (i) retain their pre-extinction ecological roles and persist ('survivors'), (ii) flourish for a short time as 'disaster taxa', or (iii) represent the final remnants of formerly significant clades, but do not flourish and soon disappear ('dead clade walking' [8]). There are also two kinds of survivors that radiate dramatically and create new roles for themselves, either by (iv) replacing roles performed before the extinction by

other, now extinct groups ('replacers'), or (v) adding entirely new roles ('innovators'). Taxa in categories (ii) and (iii) do not contribute to the stable phase of the recovery. Taxa in categories (i), (iv) and (v) drive the recovery and the assembly of new ecosystems. In the case of smaller events, post-extinction ecosystems may resemble those before the crisis [8]: the speed of the bounce-back to similar diversity and food web structure is presumably facilitated by the survival of the outline or skeleton of the pre-extinction ecosystem retained by the chance survivors of the extinction event; species evolve to plug the gaps, and so the pre-extinction ecosystem structure can be rebuilt. However, this is not the case for larger-scale events. The end-Permian event was more profound than all other mass extinctions, and so there were far fewer survivors to provide a skeleton ecosystem structure [2]. In the sea, it is perhaps no surprise that the new ecosystems differed in some profound ways, especially in the addition of new layers of top predators, with the evolution of several clades of marine reptiles (ichthyosaurs, sauropterygians, thalattosaurs, placodonts and prolacertiforms).

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 Earth history from the Middle Permian to the Late Triassic. These
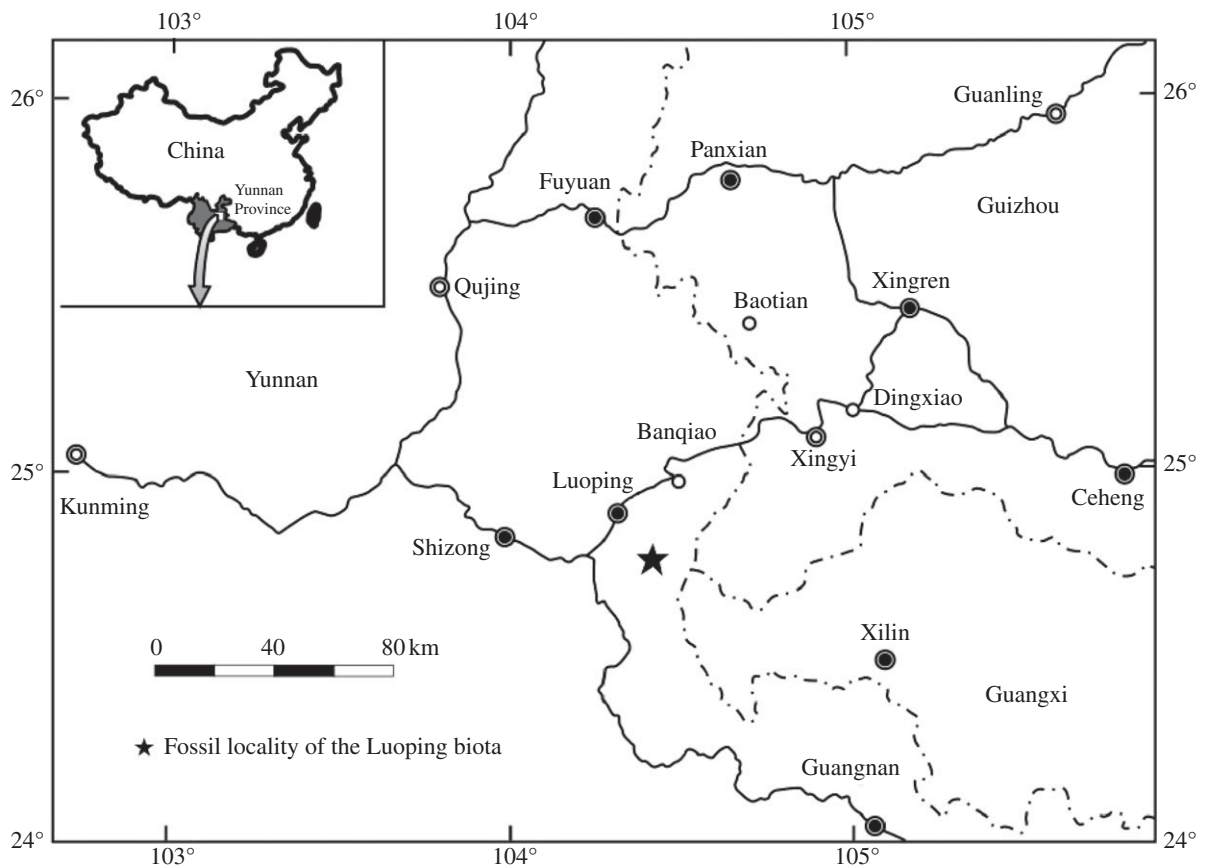
Figure 1. Map of Yunnan Province, southwest China, showing locality of the Luoping biota.

sections have been studied intensively for the past 30 years, and they now offer high-precision dating throughout, in part because the global standard sections for the Permo-Triassic (PT) boundary are there [9], but also because volcanic ash levels provide radiometric dates that can be keyed with a detailed biostratigraphy based on conodonts and ammonoids, and also because certain formations can be correlated laterally over 100s or 1000s of kilometres across South China. The discovery of exceptionally preserved Triassic biotas at Panxing, Luoping, Xingyi and Guanling has provided a mass of remarkable new fossils and a series of intensively sampled snapshots of the recovering marine faunas through the Triassic.

One of these Lagerstätten, Luoping, has been discovered recently, and has so far been reported only briefly [10]. The Luoping biota comes from near Daaozi village, Luoping County, Yunnan Province, southwest China (figure 1). The common fossils in the Luoping Lagerstätte are arthropods, followed by fishes, marine reptiles, bivalves, gastropods, echinoderms, brachiopods, conodonts, foraminifers and plants. Several previously unreported fossil groups, including millipedes, cycloids and belemnoids with preserved arm hooks, hydro-medusae, ammonoids and lingulid brachiopods have been added to the fossil list following recent intensive excavation, led by Q.-Y.Z.

Early and Middle Triassic Lagerstätten are especially significant in documenting stages in the recovery of ecosystems from the devastation of the end-Permian mass extinction, and yet such deposits are rare worldwide. The purpose of this paper is to present the Luoping biota as a new resource for understanding early stages in the rebuilding of marine ecosystems.

## 2. STRATIGRAPHY

The Luoping biota comes from the Guanling Formation, a unit exposed extensively over eastern Yunnan and western Guizhou provinces (figure 1), located in the southwestern part of the Yangtze Platform between the Nanpanjiang Basin and the Yangtze Platform [11]. The Guanling Formation (figure 2) comprises carbonates and clastic rocks, and is subdivided into two members. Member I is 333 m thick, and consists of mainly mudstone and argillaceous dolomite with a volcanic ash bed (green pisolite) at the base. Member II is a 580 m thick succession composed of nodular limestone, silty limestone, micritic limestone and bands of dolomite. The overlying Yangliujing Formation comprises 1204 m of dolostone and dolomitic limestone intercalated with limestone breccias that are characterized by pseudomorphs of gypsum- and evaporite-solution breccias.

The Luoping biota occurs in the middle part of Member II, approximately 16 m thick at Daaozi (figure 2), and delimited at the bottom and top by thick-bedded, massive limestones and silty limestones, with high levels of bioturbation. This unit comprises mainly thinly laminated micritic limestones alternating with thin- to moderately thick-bedded silty limestones. Lower units are dark grey, medium- to thick-bedded laminated micritic limestones with siliceous concretions, interbedded with a few thin ash beds. A diverse fish assemblage has been recovered mainly from these units. This is followed by a 1.5 m thick succession of dark grey medium- to thick-bedded, strongly bioturbated nodular limestone containing numerous cherty concretions. The overlying 2 m-thick unit consists of finely laminated micritic limestone with even bedding planes, containing
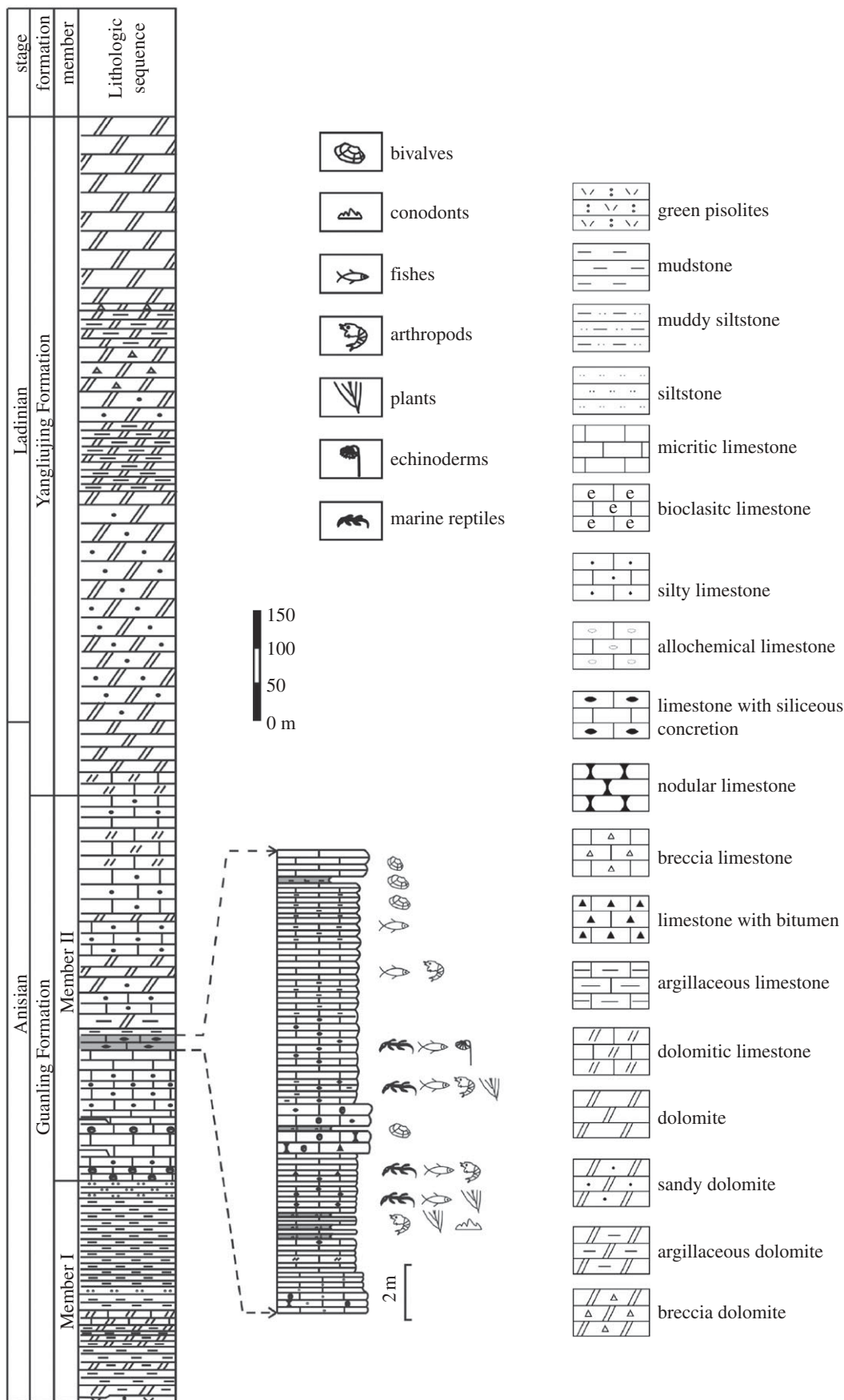
Figure 2. Sedimentary log through the Guanling Formation (Members I and II) and the Yanliujing Formation at the Daaozi locality, showing lithologies, sedimentary structures and key fossiliferous beds. (Modified from Zhang *et al.* [20].)

abundant well-preserved shrimps, isopods, fishes and a few marine reptiles. The succeeding 2 m-thick interval also shows millimetre-scaled lamination, but the surface

of the bedding planes is uneven. Isolated pebbles are commonly observed in these layers, different in lithology from the matrix: they were probably not transported by
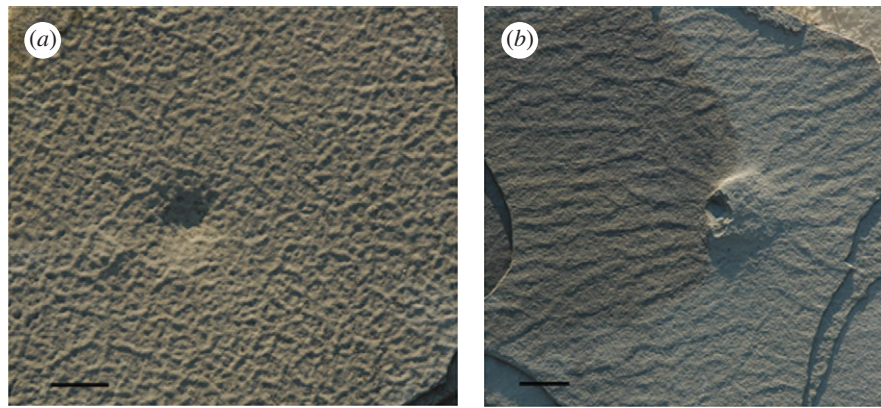
Figure 3. Microbial mats from the Guanling Formation, Luoping locality, near Daaozi village, Yunnan Province. Surfaces of laminae show (*a*) network and (*b*) furrow patterns of wrinkled microbial mat surfaces. Scale bars, 20 mm.

currents, but were most probably released from root masses of plants floating in the water. Upward, the remaining part of the section is thin- to moderately thick-bedded, mainly micritic limestone with relatively higher bioturbation. Exceptionally preserved fossils, including fishes, reptiles, shrimps and xiphosurids, although still recovered from certain layers, are relatively rare. Instead, bivalves and molluscs are commonly found from this part. Although small-scale turbidite layers are common in the fossil-bearing intervals, no exceptionally preserved fossils have been recovered from those event beds.

The highly fossiliferous, dark-coloured micritic limestones of Member II of the Guanling Formation, as seen at Daaozi, have been traced in detail over an area of some 200 km$^2$ through the regional mapping programme of the Chengdu Institute of Geological and Mineral Resources. Several lines of evidence including abundant organic materials in the dark sediments, the presence of tiny pyrite framboids, the near absence of sessile organisms and the low levels of bioturbation, suggest that the exceptionally preserved fossil horizons were deposited in dysoxic to anoxic conditions, as indicated by similar sediments in the Early Triassic of South China [12–14]. Outside the area with exceptional fossil preservation, Member II of the Guanling Formation consists of bioturbated, pale-coloured micritic limestones. Abundant fine horizontal laminae throughout the succession and the absence of bioturbation suggest that the Luoping biota-bearing succession was deposited in a low energy, calm, semi-enclosed intraplatform basin setting. Most fossils are complete (99% of more than 10 000 specimens), but they are flattened, and three-dimensional preservation is extremely rare.

The model for basin evolution and fossil preservation at Luoping involves episodic oxygenation of bottom waters, as indicated by bioturbated layers, with occasional flourishing of benthic organisms. Pelagic groups, however, could survive in the upper part of the water column. Abundant terrestrial plants and rare millipedes indicate nearby land or islands. Microbial mats are extremely common on the upper surfaces of micritic limestones at Luoping (figure 3). Their analogues in modern seas and in the fossil record have been interpreted as the products of cyanobacteria or other microbes [15,16]. Thus, proliferation of the Luoping biota was

probably associated with a bloom of cyanobacteria. Abundant microbes in sea water are crucial for the exceptional preservation of soft tissues and articulated specimens in fossil Lagerstätten, especially through the role of microbial mats (e.g. [17,18]). The 'death mask' model for the preservation of the soft-bodied Ediacaran animals [19] is also a plausible model for the Luoping biota. Microbes sealed rapidly onto the animal bodies and generated microbial coats after the animal's death. The microbial envelopes generated a local, close anoxic environment and thus prevented the decay of soft tissues, devouring by scavengers, and disarticulation of carcasses by current or wave movements. Following the Ediacaran model [19], the external moulds of the Luoping organisms functioned as a sole veneer in early diagenesis. The death mask that arose from bacterial precipitation may have smothered decaying microbial mats and the Luoping organisms.

Abundant conodonts were found in association with the Luoping biota in beds 41 and 43, and they were assigned to the *Nicoraella kockeli* Zone [20], characteristic of the Pelsonian Substage of the Anisian Stage (Middle Triassic) [21]. Thus, the Luoping biota is coeval with the Panxian Fauna (*N. kockeli* Zone [22]) and predates the Guanling Biota (Middle Carnian Xiaowa Formation at Xinpu, Guanling [23]) and the Xingyi Fauna (Late Ladinian Zhuganpo Formation at Dingxiao, Xingyi) from neighbouring Guizhou Province.

## 3. THE LUOPING COMMUNITY
So far, nearly 20 000 individual macrofossils have been identified from the Luoping biota in its main location (figure 4). Arthropods dominate by far, comprising over 90 per cent of the fauna, followed by fishes (4%), then bivalves (2%), and then relatively tiny proportions (less than 1%) of plants, gastropods, marine reptiles and others.

The arthropods include crustaceans, millipedes and limulids (figure 5*k*). Among these, crustaceans are the most common and diverse group, represented by decapods, isopods [24] (figure 5*h*), cycloids (figure 5*e*), mysidiaceans, conchostracans and ostracods. Several specimens of fossil horseshoe crabs show preservation of appendages. Millipedes (figure 5*j*) are extremely rare and only very few specimens have been found.
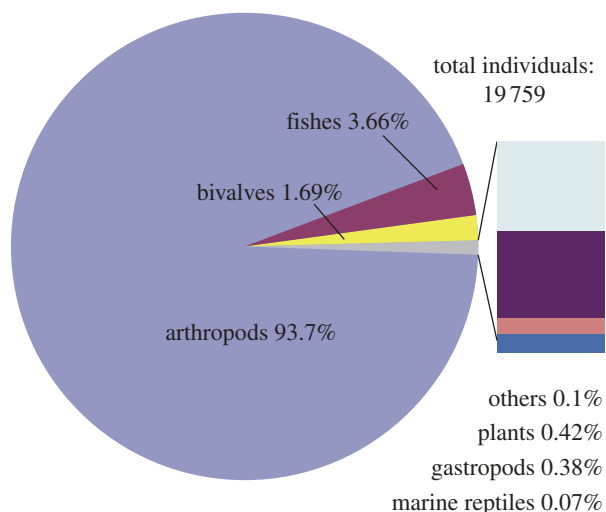
Figure 4. Pie chart showing the relative representation of the main macrofossils from Luoping, based on a count of nearly 20 000 specimens. Rose, fishes; yellow, bivalves; purple, plants; blue, others; grey, arthropods; pink, marine reptiles; light blue, gastropods.

Molluscs in the Luoping biota include bivalves, gastropods, ammonoids and belemnoids. Bivalves and gastropods are relatively abundant, whereas ammonoids and belemnoids are extremely rare. Although only two specimens of belemnoids have been recovered, both show good preservation of beak parts and arm hooks (figure 5g). Such specimens of belemnoids with preserved beaks and arm hooks are rare, with reports only from the Middle Triassic Monte San Giorgio [25], the Early Jurassic Posidonia Shale [26] and the Late Jurassic Nusplingen Limestone [27].

Echinoderms and brachiopods are less diverse and less abundant in the biota than the arthropods and molluscs. Only a few specimens of crinoids, starfishes and sea urchins (figure 5i) have been found, indicating that they were rare in life because of the overall dysoxic to anoxic settings, which are inhospitable for most sessile organisms. Only one lingulid brachiopod genus has been found.

Most of the fossil plants are conifers (figure 5l). Given the relatively complete branches and leaves in the specimens, these plants were presumably transported only a very short distance (*ca* 10 km) into the Luoping basin from nearby coastal areas, indicating that conifer forests flourished during Pelsonian times.

Trace fossils are common in the thick-bedded limestone layers, especially *Arenicolites*, *Rhizocorallium* and *Thalassinoides*. However, most of the fossil-bearing layers are nearly devoid of trace fossils or yield simple, fine, horizontal burrows. In addition, coprolites are commonly observed. Some fish coprolites containing fish scales provide direct evidence of predation.

Among the vertebrates, fishes are an important component of the fauna, including more than 25 taxa, belonging to nine families of basal actinopterygians, the Saurichthyidae, Palaeoniscidae, Birgeriidae, Perleididae, Eugnathidae, Semionotidae, Pholidopleuridae and Peltopleuridae, as well as coelacanths. One new genus of perleidid fish, *Luopingichthys* [28], a basal neopterygian, *Gymnoichthys* [29] and two new species of the saurichthyid *Saurichthys* (figure 5b) [30,31] have also been

reported from Luoping. Many of the remaining Luoping fishes are undescribed taxa. At least three layers with mass occurrences of fishes are found in the lower part. The occurrence of large numbers of well-preserved fishes on single bedding planes suggests that populations were killed off in mass mortality events such as large volcanic eruptions and upwelling of stagnated, poorly oxygenated bottom waters. The former is evidenced by the presence of several layers of volcanic ash beds, while the latter is supported by the alternation of grey, thick-bedded bioclastic limestone and dark, thin-bedded micritic limestone. It should be noted that frequent volcanic eruptions may have triggered anoxia and bloom of cyanobacteria in oceans, as also occurred immediately after the end-Permian mass extinction [32]. Most large fishes from the Luoping biota were carnivorous, as indicated by their dentition consisting of large and striated conical teeth alternating with much smaller ones, and from coprolites (figure 5f).

Finally, well-preserved, diverse marine reptiles are one of the highlights of the Luoping biota, including ichthyosaurs, sauropterygians (pachypleurosaurs), thalattosaurs, rare archosaurs (figure 5d) and prolacertiforms (tanystropheids). The assemblage of marine reptiles is similar to that of the Anisian–Ladinian-aged Monte San Giorgio locality in Switzerland [33–35]. Some reptiles, for instance, ichthyosaurs (figure 5a) represent top predators and so suggest full rebuilding of the ecosystem.

## 4. COMMUNITY STRUCTURE AND RECOVERY
The Luoping biota is one of the most diverse Triassic marine fossil Lagerstätten known in the world [23,33–38]. Although several other faunas have been reported from the Middle and Upper Triassic of southwest China during the last decades, most taxa were described based on a small number of specimens, and thus their diversity is relatively lower. For example, arthropods are absent in the Panxian fauna [22,38] and the Guanling biota [23], and represented by only one taxon of crustacean from the Xingyi biota [39]. This means that the new biota, represented by nearly 20 000 *in situ* specimens, offers the best insights into the first fully complex Triassic marine ecosystems, some 10 Myr after the end-Permian crisis.

The claim that Luoping is a fully recovered ecosystem is based on the diversity of top predators, most notably the fish and reptile taxa, which are much more diverse than all taxa reported from the Early Triassic and comparable with many known pre-extinction vertebrate assemblages in the Permian oceans, where fishes of all kinds were modest components of faunas and reptiles were absent [40,41]. Studies at Luoping have not proceeded far enough to judge the total diversity of invertebrate fossils, and whether they approach the diversities of 130 species achieved in Changhsingian assemblages [42] is yet to be determined. Further, the diversity of fishes and reptiles at Luoping was at a peak that was not subsequently exceeded in later Triassic Lagerstätten.

The full recovery of the ecosystem is also suggested by the complexity of the food web (figure 6). Lower parts of the food chains are dominated by crustaceans, fishes and bivalves, typical of later Triassic marine faunas, and different from preceding Induan and Olenekian faunas. Importantly, the top predators, animals that fed on fishes and small predatory reptiles, such as the
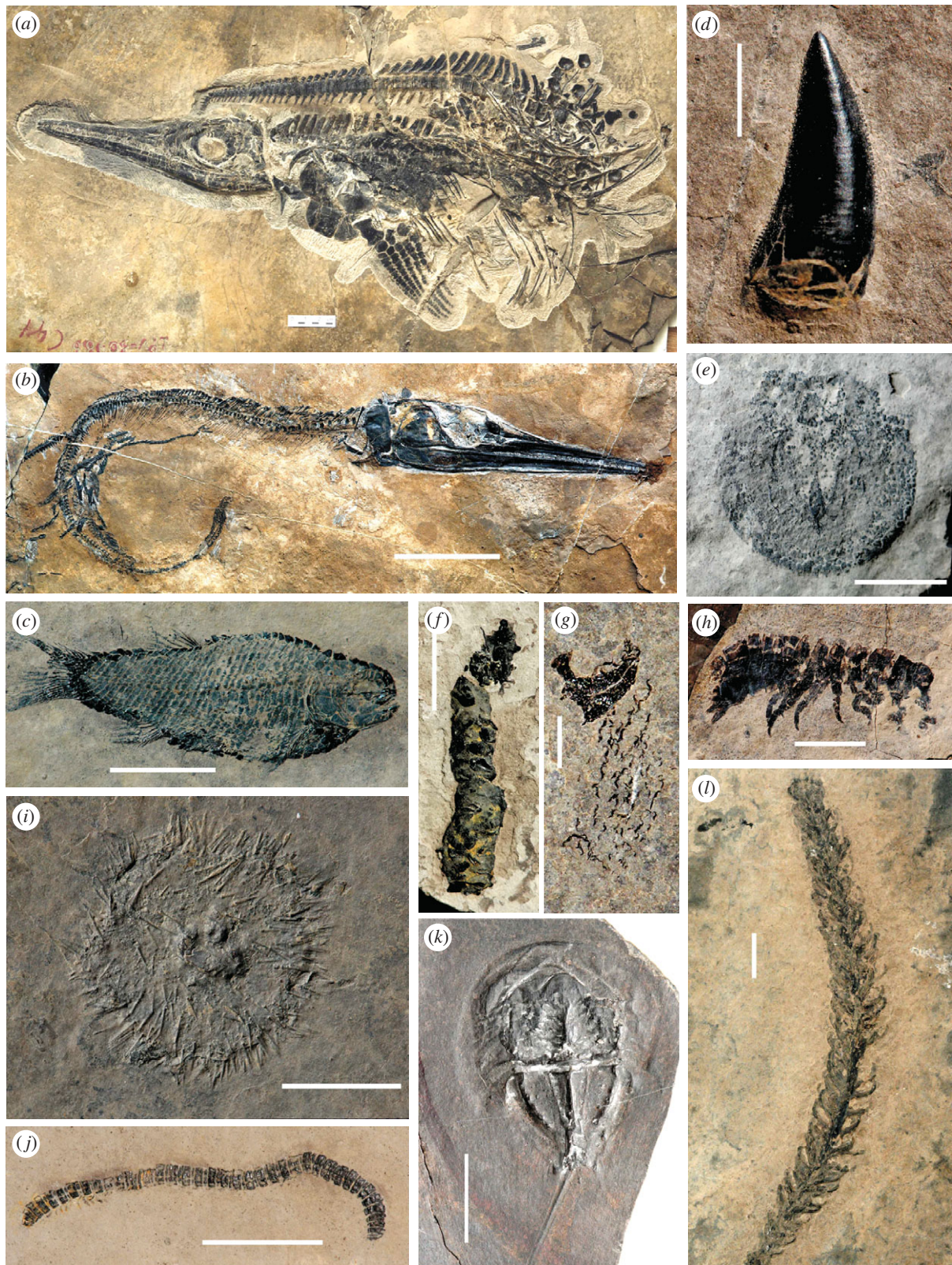
Figure 5. Characteristic faunal elements of the Luoping biota. (*a*) Ichthyosaur (LPV 30986); (*b*) carnivorous fish *Saurichthys yunnanensis* (LPV 20881); (*c*) eugnathid fish (LPV 11846); (*d*) tooth of archosaur (LPV 31411); note serrated margin; (*e*) cycloid arthropod (LPI 32637); (*f*) coprolite containing fish scales (LPI 61753); (*g*) belemnoid with preserved arm hooks (bottom) and beak parts (top) (LPI 61543); (*h*) *Protamphisopus baii*, an isopod arthropod (LPI 61713); (*i*) sea urchin (LPI 61701); (*j*) millipede (LPI 61593); (*k*) *Yunnanolimulus luopingensis*, a xiphosurid arthropod (LPI 61299); (*l*) conifer plant (LPI 60148). Scales bars, (*a*) 4 cm, (*b*) 5 cm (*g*) 2 mm, (*c,i–l*) 1 cm, (*d–f,h,j*) 0.5 cm, respectively. All specimens are deposited at the Chengdu Geological Center (LPI = Luoping invertebrates; LPV = Luoping vertebrates).

long-snouted bony fish *Saurichthys*, the ichthyosaur *Mixosaurus*, the sauropterygian *Nothosaurus* and the prolacertiform *Dinocephalosaurus*, are present for the first time in the Chinese successions at Luoping: they

mark the completion of a typical Mesozoic ecosystem for the first time after the end-Permian mass extinction.

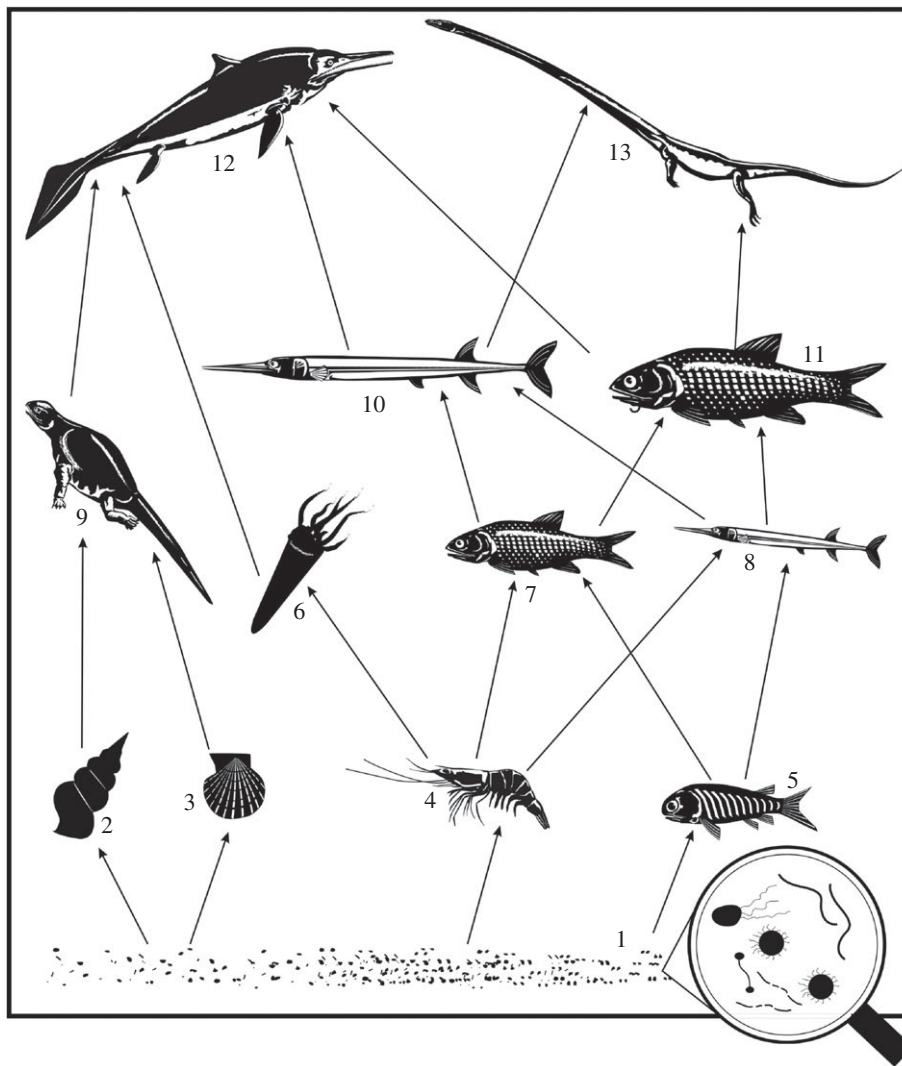The establishment of the top-level predator-dominated trophic structure in the Luoping ecosystem, evidenced

Figure 6. Food web of the Luoping biota, showing assumed interactions among the key components of the marine fauna, based on comparisons with modern taxa, comparisons with other Triassic faunas and direct evidence from rare fossil examples of stomach contents and coprolites. 1, Microbes; 2, gastropods; 3, bivalves; 4, crustaceans; 5, fishes; 6, belemnoids; 7, carnivorous fishes; 8, *Saurichthys* sp. A; 9, placodonts; 10, *Saurichthys* sp. B; 11, large carnivorous fishes; 12, ichthyosaurs; 13, prolacertiforms.

by the abundant and diverse carnivores, suggests that the Mesozoic marine revolution (MMR) [43] may have actually started in the early Middle Triassic, as supported by bivalves [44] and crinoids [45]. The initial MMR was coupled with biotic recovery and restoration of marine ecosystems in the early Middle Triassic. Given its age, further excavation and research of the Luoping biota should shed new light on the recovery and radiation of marine ecosystems after the end-Permian mass extinction.

## REFERENCES

1 Benton, M. J. & Twitchett, R. J. 2003 How to kill (almost) all life: the end-Permian extinction event. *Trends Ecol. Evol.* **18**, 358–365. (doi:10.1016/S0169-5347(03)00093-4)

2 Erwin, D. H. 2006 *Extinction: how life on earth nearly ended 250 million years ago.* Princeton, NJ: Princeton University Press.

3 Knoll, A. H., Bambach, R. K., Payne, J. L., Pruss, S. & Fischer, W. 2007 Paleophysiology and end-Permian mass extinction. *Earth Planet. Sci. Lett.* **256**, 295–313. (doi:10.1016/j.epsl.2007.02.018)

4 Lehrmann, D. J. *et al.* 2006 Timing of recovery from the end-Permian extinction: geochrologic and biostratigraphic constraints from South China. *Geology* **34**, 1053–1056. (doi:10.1130/G22827A.1)

5 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. (doi:10.1126/science.1097023)

6 Chen, Z. Q., Chen, J., Tong, J. & Fraiser, M. L. 2010 Marine ecosystem changes from latest Permian to Middle Triassic in the Qingyan area, Guizhou, southwest China. *J. Earth Sci.* **21**, 125–129.

7 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. (doi:10.1038/nature02950)

8 Jablonski, D. 2001 Lessons from the past: evolutionary impacts of mass extinctions. *Proc. Natl Acad. Sci. USA* **98**, 5393–5398. (doi:10.1073/pnas.101092598)

9 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.

10 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. *Geol. Rev.* **54**, 145–149.

11 Enos, P., Lehrmann, D. J., Wei, J. Y., Yu, Y. Y., Xiao, J. F., Chaikin, D. H., Minzoni, M., Berry, A. K. & Montgomery, P. 2006 Triassic evolution of the Yangtze Platform in Guizhou Province, People's Republic of China. *Geol. Soc. Am. Spec. Pap.* **417**, 1–105.

12 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. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **102**, 215–237. (doi:10.1016/0031-0182(93)90068-T)

13 Chen, Z. Q., Tong, J. N., Kaiho, K. & Kawahata, H. 2007 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. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **252**, 176–187. (doi:10.1016/j.palaeo.2006.11.042)

14 Chen, Z. Q., Tong, J. N., Liao, Z. T. & Chen, J. 2010 Structural changes of marine communities over the Permian–Triassic transition: ecologically assessing the end-Permian mass extinction and its aftermath. *Global Planet. Change* **73**, 123–140. (doi:10.1016/j.gloplacha.2010.03.011)

15 Noffke, N. V. 1998 Multidirected ripple marks rising from biological and sedimentological processes in modern lower supratidal deposits (Mellum Island, southern North Sea). *Geology* **26**, 879–882. (doi:10.1130/0091-7613(1998)026<0879:MRMRFB>2.3.CO;2)

16 Noffke, N. V., Hazenv, R. & Nhleko, N. 2003 Earth's earliest microbial mats in a siliciclastic marine environment (2.9 Ga Mozaan Group, South Africa). *Geology* **31**, 673–676. (doi:10.1130/G19704.1)

17 Wilby, P. R. & Briggs, D. E. G. 1996 Mineralization of soft-bodied invertebrates in a Jurassic metalliferous deposit. *Geology* **24**, 847–850. (doi:10.1130/0091-7613(1996)024<0847:MOSBII>2.3.CO;2)

18 Gall, C. 2001 Role of microbial mats. In *Palaeobiology II* (eds D. E. G. Briggs & P. R. Crowther), pp. 280–284. Oxford, UK: Blackwell Science.

19 Gehling, J. G. 1999 Microbial mats in terminal Proterozoic siliciclastics: Ediacaran death masks. *Palaios* **14**, 40–57. (doi:10.2307/3515360)

20 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. *Sci. China Ser. D Earth Sci.* **52**, 1673–1678. (doi:10.1007/s11430-009-0114-z)

21 Kozur, W. H. 2003 Integrated ammonoid, conodont and radiolarian zonation of the Triassic and some remarks to stage/substage subdivision and the numeric age of the Triassic stages. *Albertiana* **28**, 57–74.

22 Hao, W. C., Sun, Y. L., Jiang, D. Y. & Sun, Z. Y. 2006 Advance in studies of the Panxian Fauna. *Acta Sci. Nat. Univ. Pekinensis* **42**, 817–823.

23 Wang, X. F. *et al.* 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. (doi:10.1111/j.1475-4983.2007.00735.x)

24 Fu, W. L., Wilson, G. D. F., Jiang, D. Y., Sun, Y. L., Hao, W. C. & Sun, Z. Y. 2010 A new species of *Protamphisopus* Nicholls (Crustacea, Isopoda, Phreatoicidea) from Middle Triassic Luoping Fauna of Yunnan Province, China. *J. Paleontol.* **84**, 1001–1011. (doi:10.1666/10-042.1)

25 Rieber, H. 1970 *Phragmoteuthis*? *ticinensis* n. sp., ein Coleoidea-Rest aus der Grenzbitumenzone (Mittlere Trias) des Monte San Giorgio (Kt. Tessin, Schweiz). *Paläontol. Z* **44**, 32–40.

26 Riegraf, W. & Hauff, R. 1983 Belemniten mit Weichkörper, Fangarmen und Gladius aus dem Untertoarcium (Posidonienschiefer) und Unteraalenium (Opalinuston) Südwestdeutschlands. *N. Jb. Geol. Paläontol. Abh.* **165**, 466–483.

27 Klug, C., Schweigert, G., Fuchs, D. & Dietl, G. 2009 First record of a belemnite preserved with beaks, arms and ink sac from the Nusplingen Lithographic Limestone (Kimmeridgian, SW Germany). *Lethaia* **43**, 445–456. (doi:10.1111/j.1502-3931.2009.00203.x)

28 Sun, Z. Y., Tintori, A., Jiang, D. Y., Lombardo, C., Rusconi, M., Hao, W. C. & Sun, Y. L. 2009 A new perleidiform (Actinopterygii, Osteichthyes) from the Middle Anisian (Middle Triassic) of Yunnan, South China. *Acta Geol. Sin.* **83**, 460–470. (doi:10.1111/j.1755-6724.2009.00067.x)

29 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). *Riv. Ital. Paleontol. Strat.* **116**, 161–172.

30 Wu, F. X., Sun, Y. L., Hao, W. C., Hang, D. Y., Xu, G. H., Sun, Z. Y. & Tintori, A. 2009 New species of *Saurichthys* (Actinopterygii: Saurichthyidae) from Middle Triassic (Anisian) of Yunnan Province, China. *Acta Geol. Sin.* **83**, 440–450. (doi:10.1111/j.1755-6724.2009.00056.x)

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

32 Xie, S., Pancost, R. D., Wang, Y., Yang, H., Wignall, P. B., Luo, G., Jia, C. & Chen, L. 2010 Cyanobacterial blooms tied to volcanism during the 5 m. y. Permo–Triassic biotic crisis. *Geology* **38**, 447–450. (doi:10.1130/G30769.1)

33 Kuhn-Schnyder, E. 1974 *Die Triasfauna der Tessiner Kalkalpen*. Zürich, Switzerland: Naturforschenden Gesellschaft.

34 Etter, W. 2002 Monte San Giorgio: remarkable Triassic marine vertebrates. In *Exceptional fossil preservation* (eds D. J. Bottjer, W. Etter, J. W. Hagadorn & C. M. Tang), pp. 221–242. New York, NY: Columbia University Press.

35 Furrer, H. 2003 Der Monte San Giorgio im Südtessin— vom Berg der Saurier zur Fossil-Lagerstätte internationaler Bedeutung. *N Jb. Naturf. Ges. Zürich* **206**, 1–64.

36 Gall, J.-C. & Grauvogel-Stamm, L. 2005 The early Middle Triassic 'Grès à Voltzia' Formation of eastern France: a model of environmental refugium. *C. R. Palevol.* **4**, 637–652. (doi:10.1016/j.crpv.2005.04.007)

37 Shcherbakov, D. E. 2008 Madygen, Triassic Lagerstätte number one, before and after Sharov. *Alavesia* **2**, 113–124.

38 Jiang, D. Y., Motani, R., Hao, W. C., Rieppel, O., 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 Geol. Sin.* **83**, 451–459. (doi:10.1111/j.1755-6724.2009.00047.x)

39 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 fossil 'Mysidaceans'. *J. Paleontol.* **75**, 310–318. (doi:10.1666/0022-3360(2001)075<0310:ANUMTS>2.0.CO;2)

40 Wang, N. Z., Zhu, X. S., Jin, F. & Wang, W. 2007 Chondrichthyan microremains under Permian-Triassic boundary both in Zhejiang and Jiangxi provinces, China. *Vertebr. Palasiat.* **45**, 13–36.

41 Wang, N. Z., Jin, F., Wang, W. & Zhu, X. S. 2007 Actinopterygian fishes from the Permian–Triassic boundary beds in Zhejiang and Jiangxi provinces, South China, and fish mass extinction, recovery and radiation. *Vertebr. Palasiat.* **45**, 307–329.

42 Jin, Y. G., Wang, Y., Wang, W., Shang, Q. H., Cao, C. Q. & Erwin, D. H. 2000 Pattern of marine mass extinction near the Permian–Triassic boundary in South China. *Science* **289**, 432–436. (doi:10.1126/science.289.5478.432)

43 Vermeij, G. J. 1995 Economics, volcanoes, and Phanerozoic revolutions. *Paleobiology* **21**, 125–152.

44 McRoberts, C. A. 2001 Triassic bivalves and the initial marine Mesozoic revolution: a role for predators? *Geology* **29**, 359–362. (doi:10.1130/0091-7613(2001)029<0359:TBATIM>2.0.CO;2)

45 Baumiller, T. K., Salamon, M. A., Gorzelak, P., Mooi, R., Messing, C. G. & Gahn, F. J. 2010 Post-Paleozoic crinoid radiation in response to benthic predation preceded the Mesozoic marine revolution. *Proc. Natl Acad. Sci. USA* **107**, 5893–5896. (doi:10.1073/pnas.0914199107)