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A gigantic nothosaur (Reptilia: Sauropterygia) from the Middle Triassic of SW China and its implication for the Triassic biotic recovery

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The presence of gigantic apex predators in the eastern Panthalassic and western Tethyan oceans suggests that complex ecosystems in the sea had become re-established in these regions at least by the early Middle Triassic, after the Permian-Triassic mass extinction (PTME). However, it is not clear whether oceanic ecosystem recovery from the PTME was globally synchronous because of the apparent lack of such predators in the eastern Tethyan/western Panthalassic region prior to the Late Triassic. Here we report a gigantic nothosaur from the lower Middle Triassic of Luoping in southwest China (eastern Tethyan ocean), which possesses the largest known lower jaw among Triassic sauropterygians. Phylogenetic analysis suggests parallel evolution of gigantism in Triassic sauropterygians. Discovery of this gigantic apex predator, together with associated diverse marine reptiles and the complex food web, indicates global recovery of shallow marine ecosystems from PTME by the early Middle Triassic.

The Permian-Triassic mass extinction (PTME) was the largest biodiversity crash of the Phanerozoic, witnessing the death of almost all life on earth[1,2]. The timing of biotic recovery in the sea from this mass extinction has been puzzling. It is known that some taxa such as ammonites[3,4], conodonts[4,5] and benthic foraminifera[6] had a higher recovery rate than other marine taxa, and species numbers in some transient biotas recovered to the pre-extinction level within a very short interval[7–9]. Furthermore, some transient metazoan reefs even appeared shortly after the catastrophe[10]. More recently, a survey of marine vertebrate predators has shown that multi-level food webs had already become established very shortly after the PTME[11]. On the other hand, the traditional view is that complete recovery of life in the sea was much delayed until the rebuilding of stable and complex ecosystems some 5–10 million years after PTME, likely the result of a combination of intrinsic causes, primarily the severity of the extinction and destruction of key life modes such as reefs, as well as extrinsic causes, primarily repeated periods of global warming, ocean acidification and anoxia linked to volcanic activity throughout the Early Triassic[12–15].

Although devastating to the pre-existing biota, recovery from the PTME facilitated emergence of several entirely new groups, most strikingly, the appearance of Mesozoic marine reptiles[13]. The earliest Mesozoic marine reptiles–nothosaurs, pachypleurosaurs, ichthyosaurs, hupehsuchids and probably thalattosaurs–appeared in the late Early Triassic, and further new groups, including placodonts, saurosphargids and probably some archosauromorphs, emerged soon after, in the early Middle Triassic[11,16,17]. These predators roamed in the shallow epicontinental seas and intraplatform basins around the supercontinent Pangea, and explored many different diets, ranging from cephalopods and other invertebrates to fishes, while the placodonts specialized in crushing hard-shelled invertebrates, and the larger marine reptiles, such as some ichthyosaurs and nothosaurs, may have expanded their diet to include small marine reptiles[11,18].
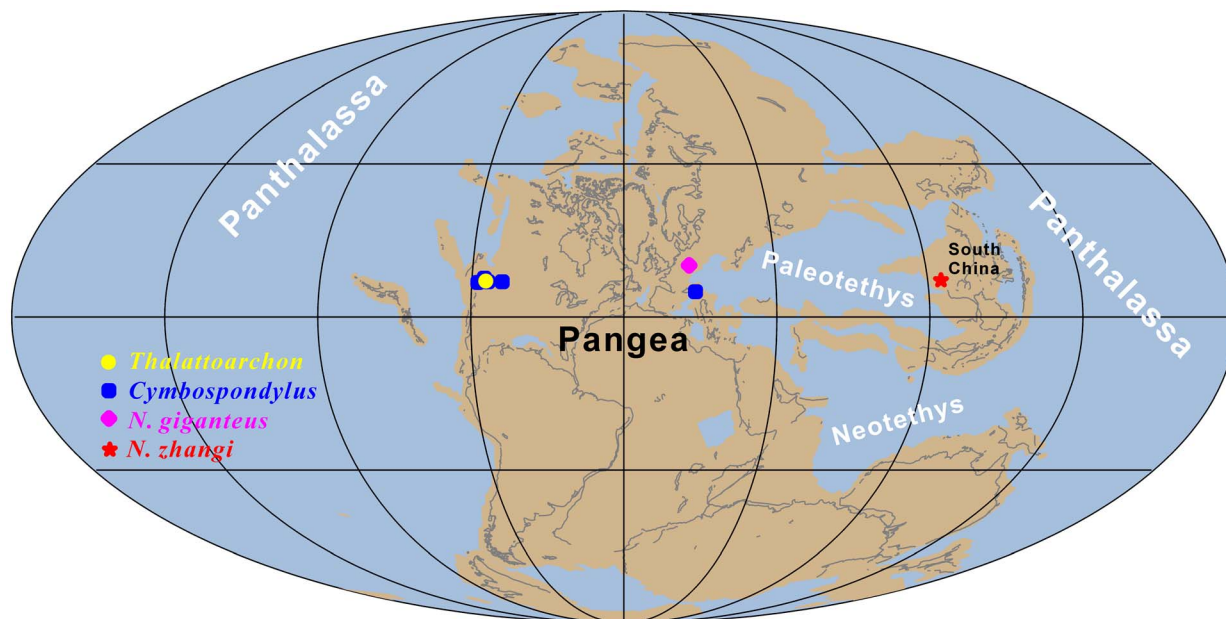
Figure 1 | Palaeogeographic reconstruction (244 Ma) showing the global distribution of Anisian gigantic apex predators in the sea (Generated from http://fossilworks.org/). The underlying source of the data is the Paleobiology Database.

The first diversity peak of marine reptiles occurred in the Anisian[16,19]. Interestingly, the first appearance of gigantic apex predators (defined here as those having body size > 5 m long) in the sea from the eastern Panthalassic and western Tethyan provinces (Fig. 1) coincides with this diversity peak. The appearance of such gigantic apex predators, together with associated complex food webs, has been taken as an indicator of the full recovery of marine ecosystems from the PTME[20]. Surprisingly, Middle Triassic gigantic apex marine predators have not yet been recorded from the eastern Tethyan/western Panthalassic province, where several Lagerstätten with beautifully preserved fossils have been intensively sampled in recent decades[21]. The lack of gigantic apex predators in the Middle Triassic of this region could imply significant diachronic timing of recovery in different parts of the Triassic ocean, as often suggested by research on invertebrates[6–10]. Here we report a gigantic nothosaur and associated diverse marine reptiles from the Middle Triassic Luoping biota[22,23] in the eastern Tethyan province, which indicates that the appearance of such apex predators and complex food webs in the sea was globally synchronous after the devastating PTME, rejecting the hypothesis of diachronous ecosystem recovery across different parts of the Triassic ocean.

Results

Systematic Palaeontology.
Sauropterygia Owen, 1860
Nothosauria Baur, 1889
Nothosauridae Baur, 1889
Nothosaurus Münster, 1834
Nothosaurus zhangi sp. nov.

Holotype. LPV 20167, a complete lower jaw associated with partial postcranial skeleton (Fig. 2), catalogued at the Chengdu Center, China Geological Survey.

Type Locality and horizon. The holotype and only known specimen was collected from Bed 165 of the Dawazi section[24] in Luoping County, Yunnan Province, by Qiyue Zhang and his mapping team in 2008. Dawazi is the nominal location of the Luoping biota[22,23]. The fossiliferous horizons of the Luoping biota are contained within the upper member of the Guanling Formation, and conodont study suggests dating to the Pelsonian substage of the Anisian[24].

Etymology. The species name is in honour of Qiyue Zhang who discovered the Luoping biota.

Diagnosis. A gigantic species of Nothosauria whose size approached or slightly exceeded that of *Nothosaurus giganteus*, the largest known Triassic sauropterygian. The new species differs from *N. giganteus* by the presence of a short mandibular symphysis, a relatively higher neural spine, a distinct medial expansion of the prearticular (autapomorphy among Sauropterygia), and a distinctly short retroarticular process (autapomorphy among Nothosauria).

Description and comparisons. The lower jaw is prepared in ventral view. Although broken into two pieces, the right mandibular ramus is nearly complete, only lacking some fragments along the inner broken edge (Fig. 2a,b). Its length along the midline is about 65 cm, while the width is about 45 cm, comparable to the largest known specimens of *Nothosaurus giganteus*[25]. The lower jaw is strongly constricted at a level just posterior to the mandibular symphysis (Fig. 2c).

The mandibular symphysis is very short, a primitive character among Nothosauria. Dividing the length of the symphysis by the width of the lower jaw in the constriction yields a ratio of 0.64, much smaller than all known mandibular symphyses of *Nothosaurus baruthicus* (synonymized with *N. giganteus*) which yield ratios between 1.0 and 1.3 (ref. 25). Many small pits are present on the surface of the symphysis. The mandibular symphysis is almost completely fused, leaving only the trace of a suture line in the posterior half of the mandible. The splenial is excluded from the formation of the symphysis.

Both the splenial and the dentary extend posteriorly for two-thirds of the length of the mandible. In the posteriormost part of the left mandible, the surangular and prearticular form the lateral and medial margins respectively. The lateral ridge of the surangular is present. The prearticular is expanded medially to a degree not seen in other Nothosauria. The posterior margin of the prearticular is smoothly concave. Part of the articular is exposed posteromedial to the prearticular. The retroarticular process is distinctly short, a morphology that is known among Nothosauria only from a specimen reported as *Nothosaurus* cf. *giganteus* from the Middle Triassic of Makhtesh Ramon in Israel[26].
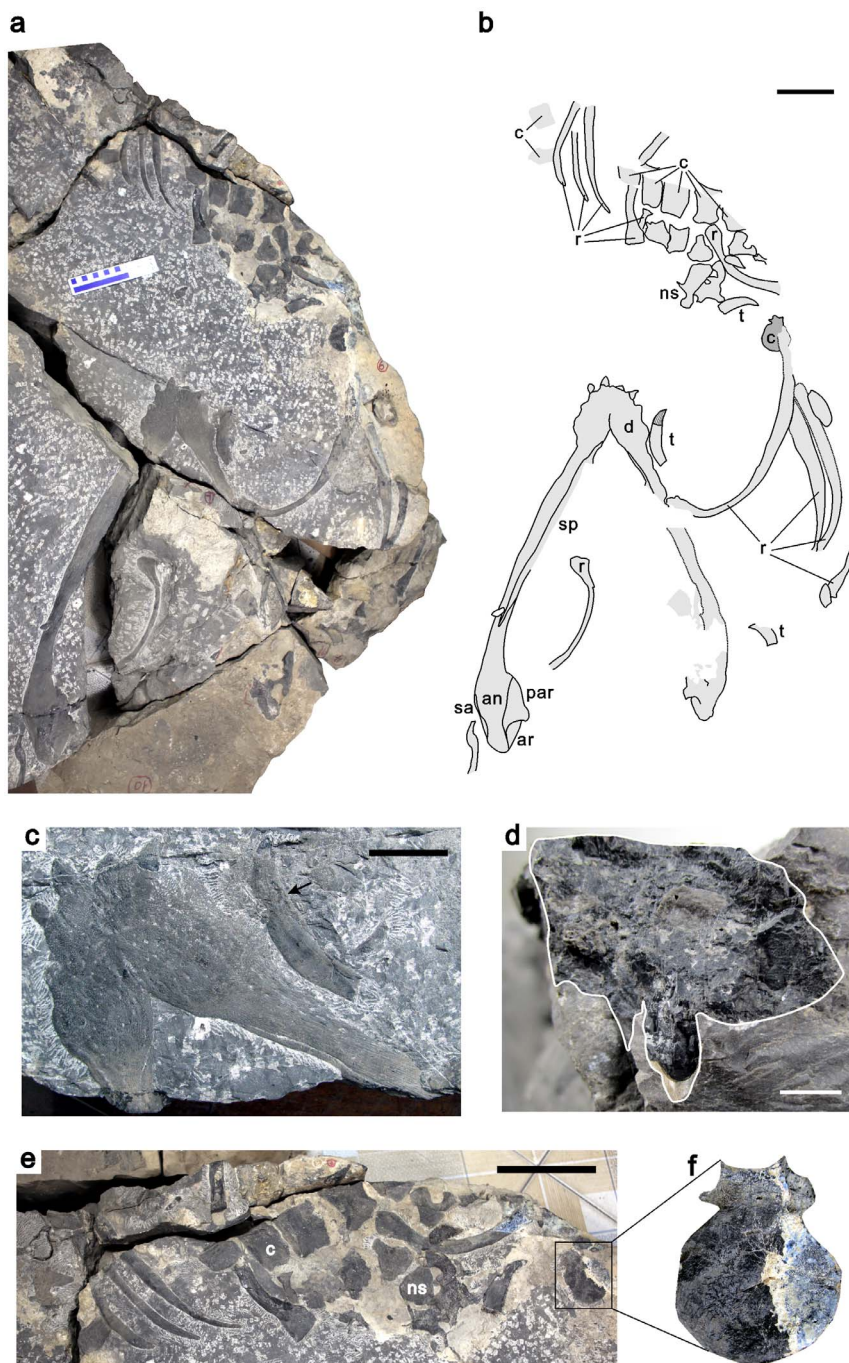
Figure 2 | Holotype of *Nothosaurus zhangi* (LPV 20167). (a) Photo of the skeleton. (b) Line drawing. (c) Mandibular symphysis and a dislocated tooth; the black arrow indicates the rough position of crown/root boundary. (d) Cross section of the left dentary and an associated small functional dentary tooth with tooth wear. (e) Postcranial skeleton. (f) Anteroposteriorly exposed centrum. Scale bar equals 10 cm in b and e, 5 cm in c, and 5 mm in d. Abbreviations: an, angular; ar, articular; c, centrum; d, dentary; ns, neural spine; par, prearticular; r, rib; sa, surangular; sp, splenial; t, tooth.

Four anteriormost dentary teeth are exposed. Judging from the shape of the symphysis, there were at least four dentary fangs present on either side. These fang-like teeth are procumbent and implanted in deep sockets in the dentary. The crown surface is striated. Three dislocated fangs are scattered on the surface of the blocks. All three fangs are strongly curved. One of them is completely preserved, with a striated crown surface and a smooth root. The crown of this tooth is about 34 mm long while the root measures 56 mm. There is no constriction between root and crown. The crown has a conical shape, while the root seems more compressed.

The broken surface of the left dentary exposes the sagittal section of a small functional dentary tooth just posterior to the mandibular symphysis, which indicates that the bottom of the tooth root is firmly attached to the dentary bone (Fig. 2d). The crown is represented only by an impression and is slightly curved inward. The lingual (inner) side of the crown has an apparent constriction slightly below the level where the pulp cavity extends (Fig. 2d), a character unknown in all other nothosaurs, but likely caused by wear.

There are five articulated centra preserved and exposed in ventro-lateral view, as well as an anteroposteriorly exposed centrum (Fig. 2e). All preserved centra are platycoelous. The anteroposteriorly exposed centra show that the vertebrae are non-notochordal (Fig. 2f). The main part of this centrum is round. The dorsal part that connects with the neural arches develops an articular facet for the rib. The

dorsal margin of this centrum is concave, forming the floor of the neural canal. All of the centra are slightly constricted, but still retain parallel edges. Small nutritive foramina are found on the ventral surface of the centra. However, they are by no means comparable to those found in pistosauroid sauropterygians, where the subcentral foramina are relatively large and symmetrically paired.

One isolated neural arch is also preserved (Fig. 2e). The neural spine is relatively low compared with those found in *Nothosaurus mirabilis*, *N. haasi* or *N. tchernovi*, but relatively higher than a typical *N. giganteus* neural spine[25].

The articular head of the dorsal ribs is unicipital and expanded. It becomes thinner along the curved shaft, but expanded again at the distal end. The cross sections of the dorsal ribs are oval in shape. No groove is found on any of the dorsal ribs.

There is one partly preserved rib with a rectangular articular head, which is different from all other preserved rib heads that have a more rounded articular head. This rectangular-headed rib may belong to the posterior dorsal region.

Phylogenetic relationships. *Nothosaurus zhangi* shares a set of derived characters with other Nothosauria, including the well developed lateral ridge of the surangular, the elongated and "scoop"-like mandibular symphysis, strongly procumbent and fang-like teeth in the anterior region of jaws, and platycoelous centra with parallel lateral edges. Phylogenetic analysis based on a new species-level data matrix (Supplementary Note) recovered *N. zhangi* as one of the most primitive taxa within Nothosauria. This is relatively well supported by the Decay index (also known as Bremer support), although the relationship with several other basal taxa remains unresolved (Fig. 3). Bootstrap values (1000 replications) across the tree are generally low, mainly because of the fragmentary nature of *Germanosaurus* and many European *Nothosaurus* species, and the new taxon introduced here, which can be only scored with ca. 12% of all characters. Only the clades consisting of (*N. jagisteus* (*N. mirabilis*, *N. tchernovi*)) have bootstrap values more than 50%.

One of the important results of this phylogenetic analysis is the collapse of the monophyly of traditionally recognized *Nothosaurus* and *Lariosaurus*. To force the monophyly of *Nothosaurus* and *Lariosaurus* as traditionally recognized clades would require 16 additional steps, clear evidence that the two genera, as generally constituted, are not monophyletic. This is, however, not a surprise as some recent Chinese taxa have shown many mixed morphologies[27,28] intermediate between *Nothosaurus* and *Lariosaurus*. Systematic revision of these two genera will be presented elsewhere. We adopt the conservative approach of referring this new species to *Nothosaurus*, with the acknowledgement that this genus requires further clarification in light of the phylogenetic results presented here.

Discussion

Among Triassic sauropterygians, *N. giganteus* from Central Europe achieved the largest skull size. The largest complete skull of *N. giganteus* reached a length of ca. 61 cm, while the largest complete lower jaw is 59 cm[25]. In the type of *N. zhangi*, the lower jaw measures 65 cm long, representing the largest jaw ever reported in a Triassic sauropterygian. Although *N. zhangi* is similar to *N. giganteus* in size, it differs significantly from the latter in morphological details, as recovered in the phylogenetic analysis (Fig. 3). This result demonstrates parallel evolution of gigantism in Triassic sauropterygians.

Estimating the body size of an extinct organism from incomplete remains is fraught with difficulty, and it is easy to exaggerate. In this case, however, the close relationship of *Nothosaurus zhangi* to other nothosauroid sauropterygians, and close similarity of skull and vertebral proportions among them suggests that a direct comparison might be possible. Among the more complete specimens from Europe, the ratio of skull: body length ranges from about 0.12 in

N. giganteus to about 0.09 in *Lariosaurus*[29]. The length from the tip of the snout to the jaw articulation of *N. zhangi* measures about 60 cm, which gives a rough estimate of a 5–7 m total body length in *N. zhangi*.

Biotic recovery after the PTME in the sea was a protracted process lasting 5–10 million years, probably slowed down by the harsh environment in the Early Triassic, with repeated global warming and environmental crises and destruction of key habitats such as reefs[12–15]. Immediately after the catastrophe, most marine communities[13], if not all[11], were characterized by primary producers and opportunistic consumers, followed by the addition of meso-consumers. Predatory invertebrates and vertebrates appeared later. Gigantic apex predators, however, did not evolve until the establishment of a complex and stable ecosystem, as evidenced by the occurrence of the ichthyosaurs *Thalattoarchon* and *Cymbospondylus* in western USA, eastern Panthalassic province, and *Cymbospondylus* and *Nothosaurus giganteus* in central Europe, western Tethyan province, both in the mid-late Anisian[20,25] (Fig. 1).

Recently, Scheyer et al.[11] reported a huge ichthyopterygian humerus supposedly from the Lower Triassic of western USA. The body size of this animal, by extrapolation, is around 11 m long[11]. However, this new specimen was collected from the surface of private land[11], so its stratigraphic provenance needs to be confirmed by further scientific excavation. In addition, gigantic size alone does not necessarily indicate the existence of a long food chain. For example, the largest marine mammals, the baleen whales, mainly feed on zooplankton and small schooling fish[30]. The whale shark and the basking shark, the only two living shark species with body length over 10 m, are both planktivorous[31]. Such gigantic marine vertebrates all have very low trophic levels[31–33]. Therefore, if a gigantic ichthyosaur with body length of around 11 m was indeed present in the Early Triassic, it is possible that this ichthyosaur fed on small organisms by batch feeding[34] like the gigantic Late Triassic shastasaurid ichthyosaurs[35,36], baleen whales[30], and whale and basking sharks[31]. Whereas such planktivory has been suggested in giant ichthyosaurs, there is no evidence that sauropterygians, including nothosaurs, ever adopted such a diet. Therefore, a large ichthyosaur bone might indicate an apex predator or planktivore, whereas a giant nothosaur was almost certainly an apex predator. This is confirmed in the case of our specimen, and the other giant Middle Triassic nothosaurs, by their elongate, predatory teeth[25].

In the eastern Tethyan province, gigantic apex predators were previously unknown in the Middle Triassic, not appearing until their occurrence in the Carnian Guanling biota in South China[21,37]. Considering the intensive sampling in several beautifully preserved fossil Lagerstätten in South China in recent decades[21], this might have implied that ecosystem recovery in the eastern Tethyan region was somehow slower than in the western Tethyan and the eastern Panthalassic region. Now, the discovery of *Nothosaurus zhangi* in the Luoping biota fills this spatio-temporal gap and indicates a globally synchronous complete biotic recovery of shallow marine ecosystems after the PTME. The diversity of marine reptiles (Fig. 4 and Table 1) and the reconstructed complex community structure in the Luoping biota (Fig. 5) also supports the ecological recovery evidenced by the occurrence of the gigantic nothosaur.

Among the marine reptiles in the Luoping community, ichthyosaurs dominate the fauna. They are exclusively composed of medium- to large-sized (see ref. 21 for definition of size classes in Triassic marine reptiles) mixosaurid ichthyosaurs. Mixosaurs are inferred to have been widely foraging predators that actively searched for their prey[38]. At least two forms could be differentiated among the Luoping mixosaurs. One is *Phalarodon atavus*[38], characterized by a largely homodont dentition adapted for externally soft prey (Fig. 4a). The other (Fig. 4b) is a taxon that resembles *Mixosaurus panxianensis*, for which the heterodont dentition suggests a broad spectrum of prey[39,40].
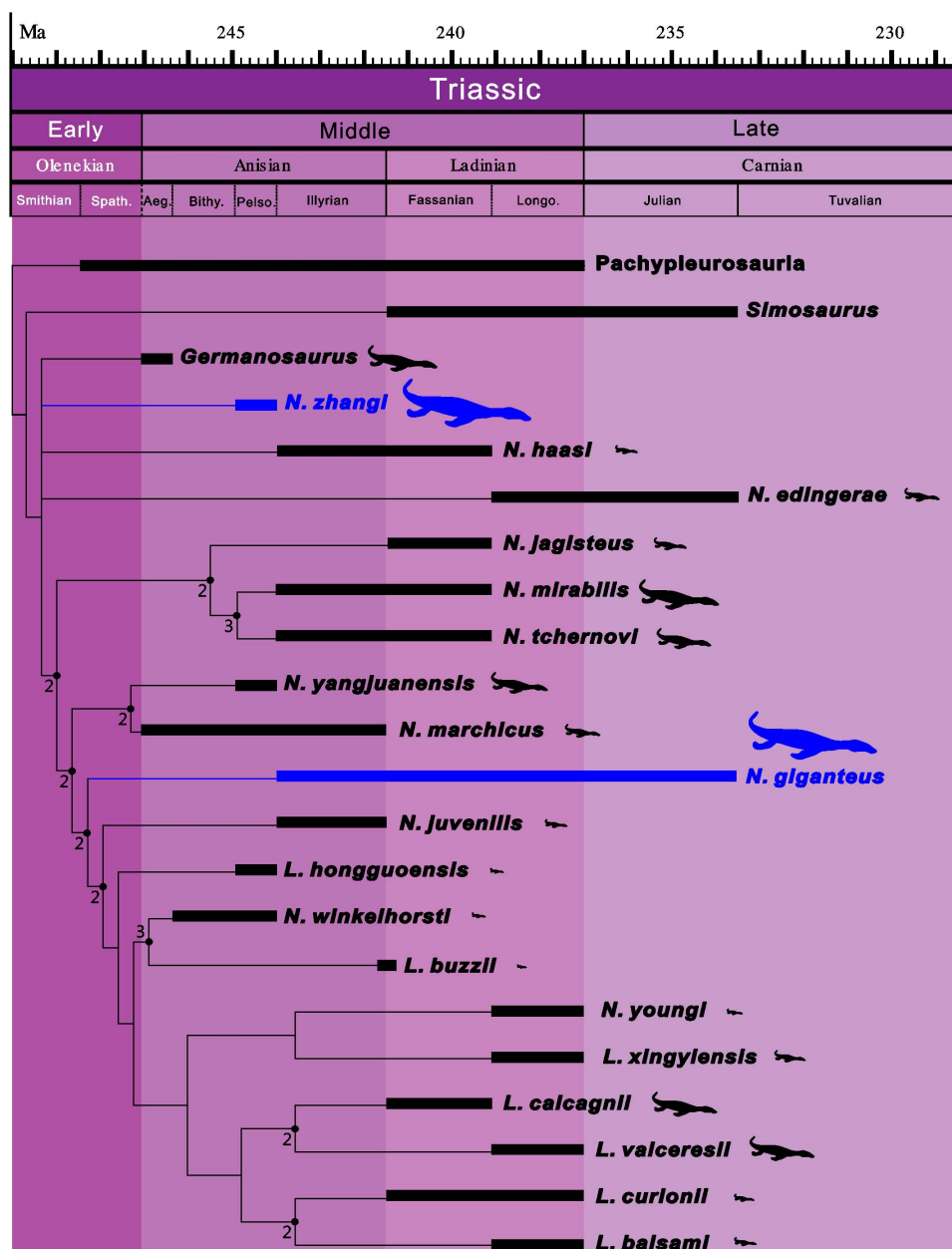
Figure 3 | Phylogenetic relationships and stratigraphic occurrences of Nothosauria. Consensus of the seven most parsimonious trees (TL = 234, CI = 0.3761, HI = 0.6239, RI = 0.4931, RC = 0.1854). Time scale was generated using TSCreator 6.1 (Available free at https://engineering.purdue.edu/Stratigraphy/tscreator/index/index.php). Schematic body outlines are scaled on the maximum size of individual species. Taxa with gigantism are highlighted with blue. Numbers beside nodes indicate Decay indices.

A recently described large-sized marine reptile, *Atopodentatus unicus*, a possible relative of the sauropterygians[41], has been interpreted as a bottom-living filter feeder that consumed microorganisms or benthic invertebrates such as sea worms (Fig. 4c). Two medium-sized saurosphargids[42,43] (Fig. 4d) might have been omnivorous[41] but given their body plan likely fed on slow-moving or benthic prey. Among sauropterygians from Luoping, eosauropterygians include two small-sized pachypleurosaurs[44–46] (Fig. 4e,f), a yet undescribed medium-sized *Lariosaurus* (Fig. 4g), and the gigantic *Nothosaurus zhangi* (Fig. 4h), all characterized by fang-like and conical teeth in the anterior region of the jaws, and these all specializing in pincering their prey.

Archosauromorphs from Luoping comprise archosaurs and protorosaurs. Archosaurs are represented by scattered teeth (Fig. 4i), in which the serrated margin is a typical feature of the clade. From the time-equivalent Panxian fauna, *Qianosuchus* has been reported[47], a

large-sized marine predator with dagger-like teeth, which could catch any prey available with a forceful strike. It is probable that archosaurian teeth from Luoping may come from the same species or a closely related taxon. Considering the fragmentary nature of the material from Luoping, however, discovery of more complete specimens is needed to confirm the presence of *Qianosuchus*-like predators in the Luoping community. Another large-sized archosauromorph from Luoping is the protorosaur *Dinocephalosaurus* (Fig. 4j), characterized by an elongated neck that presumably helped it to catch its prey with a rapid strike before the prey had even detected it[48].

With its gigantic skull and the presence of large and conical canine teeth, *Nothosaurus zhangi* must have occupied the top level of the food web in Luoping (Fig. 5). Although the postcranial skeleton of *N. zhangi* is incomplete, its phylogenetic placement and the generally conservative postcranial anatomy of nothosaurs suggests that this
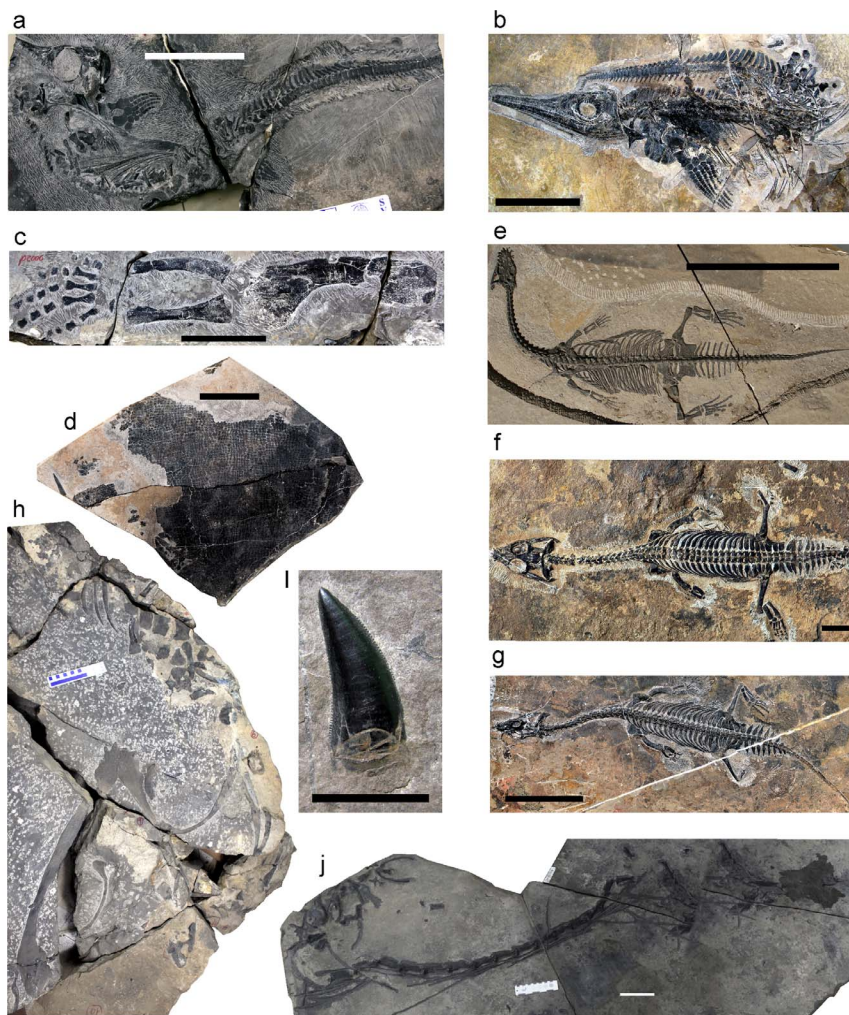
Figure 4 | Marine reptiles from Luoping biota. (a) *Phalarodon atavus* (LPV 30872)[38]. (b) *Mixosaurus* cf. *panxianensis* (LPV 30986)[40]. (c) *cf. Atopodentatus* (LPV 30172)[41]. (d) *Sinosaurosphargis yunguiensis* (LPV uncatalogued)[42]. (e) *Diandongosaurus acutidentatus* (IVPP V 17761)[45]. (f) *Dianopachysaurus dingi* (LPV 31365)[44]. (g) *Lariosaurus* sp. (LPV 301881). (h) *Nothosaurus zhangi* (LPV 20167). (i) cf. *Qianosuchus* (LPV 31411). (j) *Dinocephalosaurus* cf. *orientalis* (LPV 30174). Scale bar equals 1 cm in f and i, and 10 cm in all others.

species may have had a similar body shape to other nothosauroids, which were probably ambush predators[49] using their forelimbs as the primary propulsive organs[50,51]. Nothosauroid sauropterygians in general were well adapted to prey on fish and cephalopods[52], and occasionally, the preservation of rare gastric contents[53] and coprolites[54] provides direct evidence that small marine reptiles were part of their diets. Thus, *N. zhangi* could prey on large fish and other marine reptiles from Luoping and attack their prey with a quick strike and pierce them with its large fang-like teeth. The discovery of *N. zhangi* at Luoping thus provides direct evidence that a complex and stable ecosystem in the ocean had been established globally by the early Middle Triassic, after the devastating PTME.

Although biotic recovery after the PTME has generally been thought to have been slow in the sea[13], some recent discoveries have

Table 1 | Ecological guilds of marine reptiles from Luoping biota

Feeding Guild	Widely Foraging Predators	Ambush Predators
Cut		cf. *Qianosuchus* (large)
Pierce II		*Lariosaurus* sp. (medium) *Nothosaurus zhangi* (gigantic)
Pierce I		*Dianopachysaurus dingi* (small) *Diandongosaurus acutidentatus* (small) *Dinocephalosaurus* cf. *orientalis* (large)
Smash	*Phalarodon atavus* (medium-large) *Mixosaurus* cf. *panxianensis* (medium)	
Crunch	*Mixosaurus* cf. *panxianensis* (medium) *Sinosaurosphargis yunguiensis* (medium) *Largocephalosaurus polycarpon* (medium)	
Filter	*Atopodentatus unicus* (large)	

Guild and size division follows ref. 21. The filter feeding guild is added following ref. 41. Marine reptiles mainly eating immobile organisms are classified as widely foraging predators because of the nature of their prey. *Mixosaurus* cf. *panxianensis* is placed in two guilds reflecting heterodont dentition.
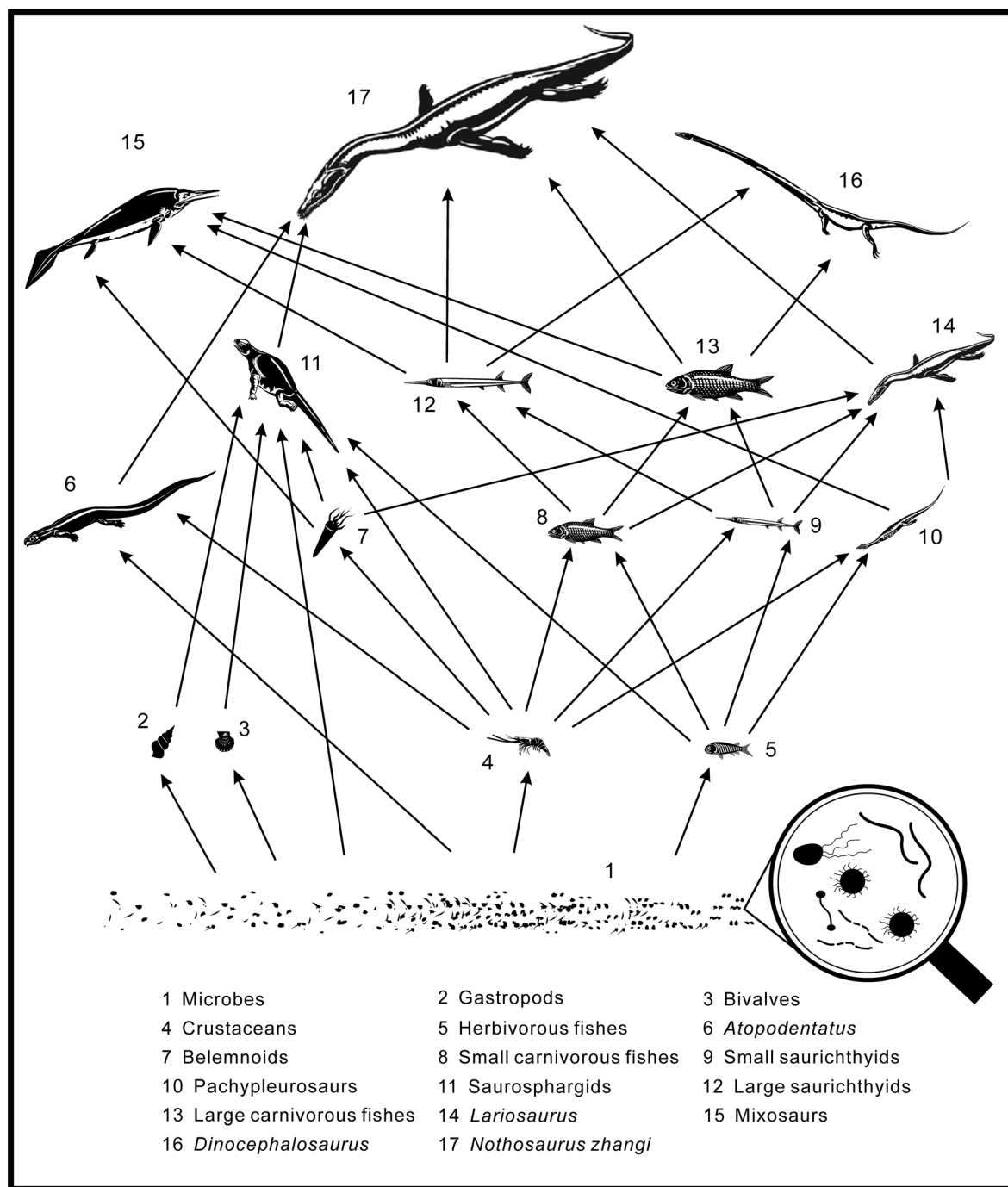
Figure 5 | Hypothesized food web of Luoping biota, updated from ref. 23. Silhouettes 6, 10, 14 and 17 were adapted and revised from ref. 17, which were the original artwork of B. Scheffold (Zurich).

challenged this hypothesis. For example, some marine clades such as ammonites[3] and conodonts[5] diversified rapidly within a short interval after the catastrophe, leading to the suggestion that post-extinction recovery may not have been as slow as previously envisioned. However, the diversity of most other groups remained relatively low until the Middle Triassic[13]. In addition to the generally low diversity, the Early Triassic ocean was also characterized by a harsh and unstable environment, as evidenced by large fluctuations of carbon[12] and oxygen isotopes[14,15], sharp warming episodes, episodic widespread oceanic anoxia, the coral gap[13], and the lack of rich and diverse marine faunas across the globe hosting gigantic apex predators. Thus, it is unlikely that healthy and stable marine ecosystems could have become globally re-established

before the environment had stabilized. The appearance of gigantic marine reptile predators across the Panthalassic and Tethyan regions in the Middle Triassic represents an important indicator of climax recovery.

Methods

To clarify the phylogenetic relationships of *Nothosaurus zhangi*, we constructed a new species-level data matrix (Supplementary Note), which is a combination of phylogenetically informative characters for resolving the phylogenetic interrelationships of *Nothosaurus*[55] and *Lariosaurus*[27], as well as 20 new morphological characters that have not been used previously. These new characters are Characters 7, 9, 14, 16, 19, 23, 25, 32, 34, 36, 38, 39, 40, 41, 42, 43, 44, 46, 59 and 66 listed in the Supplementary Note. Thus, there are 74 informative morphological characters in total. Informative proportional characters from previous analyses[27,55] were retained.

However, many states were redefined for those proportional characters based on gap coding.

Based on several recent global phylogenetic analyses of sauropterygians[17,44], Pachypleurosauria and *Simosaurus* were selected as successive outgroups for the analysis of interrelationships of Nothosauria. All currently recognized species of Nothosauria were included in the data matrix, except for *Micronothosaurus stensioi*, *Nothosaurus cymatosauroides*, and *Ceresiosaurus lanzi*, which are less well known. In addition, coding of *N. winterswijkensis* was combined with *N. marchicus* based on recent revisionary work[56,57].

PAUP Version 4.0 Beta 10 for Windows[58] was used to analyze the data matrix. Heuristic search (ADDSEQ = RANDOM, NREPS = 1000, HOLD = 100, with other settings default) was performed to search the most parsimonious trees. The character list and data matrix were constructed using NDE Version 0.5.0 (available free at http://taxonomy.zoology.gla.ac.uk/rod/NDE/nde.html).

1. Benton, M. J. Diversification and extinction in the history of life. *Science* **268**, 52–58 (1995).
2. Alroy, J. *et al.* Phanerozoic trends in the global diversity of marine invertebrates. *Science* **321**, 97–100 (2008).
3. Brayard, A. *et al.* Good genes and good luck: ammonoid diversity and the end-Permian mass extinction. *Science* **325**, 1118–1121 (2009).
4. Stanley, S. M. Evidence from ammonoids and conodonts for multiple Early Triassic mass extinctions. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 15264–15267 (2009).
5. Orchard, M. J. Conodont diversity and evolution through the latest Permian and Early Triassic upheavals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **252**, 93–117 (2007).
6. Song, H. *et al.* Recovery tempo and pattern of marine ecosystems after the end-Permian mass extinction. *Geology* **39**, 739–742 (2011).
7. Twitchett, R. J., Krystyn, L., Baud, A., Wheeley, J. R. & Richoz, S. Rapid marine recovery after the end-Permian mass-extinction event in the absence of marine anoxia. *Geology* **32**, 805–808 (2004).
8. Beatty, T. W., Zonneveld, J.-P. & Henderson, C. M. Anomalously diverse Early Triassic ichnofossil assemblages in northwest Pangea: A case for a shallow-marine habitable zone. *Geology* **36**, 771–774 (2008).
9. Hautmann, M. *et al.* An unusually diverse mollusc fauna from the earliest Triassic of South China and its implications for benthic recovery after the end-Permian biotic crisis. *Geobios* **44**, 71–85 (2011).
10. Brayard, A. *et al.* Transient metazoan reefs in the aftermath of the end-Permian mass extinction. *Nat. Geosci.* **4**, 693–697 (2011).
11. Scheyer, T. M., Romano, C., Jenks, J. & Bucher, H. Early Triassic marine biotic recovery: the predators' perspective. *PLoS ONE* **9**, e88987 (2014).
12. Payne, J. L. *et al.* Large perturbations of the carbon cycle during recovery from the end-Permian extinction. *Science* **305**, 506–509 (2004).
13. Chen, Z.-Q. & Benton, M. J. The timing and pattern of biotic recovery following the end-Permian mass extinction. *Nat. Geosci.* **5**, 375–383 (2012).
14. Sun, Y. D. *et al.* Lethally hot temperatures during the Early Triassic greenhouse. *Science* **338**, 366–370 (2012).
15. Romano, C. *et al.* Climatic and biotic upheavals following the end-Permian mass extinction. *Nat. Geosci.* **6**, 57–60 (2013).
16. Kelley, N. P., Motani, R., Jiang, D.-Y., Rieppel, O. & Schmitz, L. Selective extinction of Triassic marine reptiles during long-term sea-level changes illuminated by seawater strontium isotopes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **400**, 9–16 (2014).
17. Neenan, J. M., Klein, N. & Scheyer, T. M. European origin of placodont marine reptiles and the evolution of crushing dentition in Placodontia. *Nat. Commun.* **4**, 1621 (2013).
18. Motani, R. The evolution of marine reptiles. *Evo. Edu. Outreach* **2**, 224–235 (2009).
19. Benson, R. B. J., Butler, R. J., Lindgren, J. & Smith, A. S. Mesozoic marine tetrapod diversity: mass extinctions and temporal heterogeneity in geological megabiases affecting vertebrates. *Proc. Roc. Soc. B* **277**, 829–834 (2010).
20. Fröbisch, N. B., Fröbisch, J., Sander, P. M., Schmitz, L. & Rieppel, O. Macropredatory ichthyosaur from the Middle Triassic and the origin of modern trophic networks. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 1393–1397 (2013).
21. Benton, M. J. *et al.* Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. *Earth-Sci. Rev.* **125**, 199–243 (2013).
22. Zhang, Q. Y. *et al.* Discovery and significance of the Middle Triassic Anisian biota from Luoping, Yunnan Province. *Geological Review* **54**, 523–526 (2008).
23. Hu, S. X. *et al.* The Luoping biota: exceptional preservation, and new evidence on the Triassic recovery from end-Permian mass extinction. *Proc. R. Soc. B* **278**, 2274–2282 (2011).
24. Zhang, Q. Y. *et al.* A conodont-based Middle Triassic age assignment for the Luoping Biota of Yunnan, China. *Science in China Series D: Earth Sciences* **52**, 1673–1678 (2009).
25. Rieppel, O. & Wild, R. A revision of the genus *Nothosaurus* (Reptilia: Sauropterygia) from the Germanic Triassic, with comments on the status of *Conchiosaurus clavatus*. *Fieldiana (Geology) n.s.* **34**, 1–82 (1996).
26. Rieppel, O., Mazin, J. & Tchernov, E. Sauropterygia from the Middle Triassic of Makhtesh Ramon, Negev, Israel. *Fieldiana (Geology) n.s.* **40**, 1–85 (1999).
27. Rieppel, O., Li, J. L. & Jun, L. *Lariosaurus xingyiensis* (Reptilia: Sauropterygia) from the Triassic of China. *Can. J. Earth Sci.* **40**, 621–634 (2003).
28. Ji, C. *et al.* A new specimen of *Nothosaurus youngi* from the Middle Triassic of Guizhou, China. *J. Vert. Paleontol.* **34**, 465–470 (2014).
29. Storrs, G. W. Anatomy and relationships of *Corosaurus alcovensis* (Diapsida: Sauropterygia) and the Triassic Alcova Limestone of Wyoming. *Bull., Peabody Mus. Nat. Hist.* **44**, 1–151 (1991).
30. Bannister, J. L. in *Encyclopedia of Marine Mammals (Second Edition)* (eds William F. Perrin, Bernd Würsig, & Thewissen, J. G. M.) 80–89 (Academic Press, 2009).
31. Cortés, E. Standardized diet compositions and trophic levels of sharks. *ICES J. Mar. Sci.* **56**, 707–717 (1999).
32. Pauly, D., Trites, A. W., Capuli, E. & Christensen, V. Diet composition and trophic levels of marine mammals. *ICES J. Mar. Sci.* **55**, 467–481 (1998).
33. Romanuk, T. N., Hayward, A. & Hutchings, J. A. Trophic level scales positively with body size in fishes. *Global Ecol. Biogeogr.* **20**, 231–240 (2011).
34. Heithaus, M. R. & Dill, L. M. in *Encyclopedia of Marine Mammals (Second Edition)* (eds William F. Perrin, Bernd Würsig, & Thewissen, J. G. M.) 414–423 (Academic Press, 2009).
35. Motani, R. *et al.* Absence of suction feeding ichthyosaurs and its implications for Triassic mesopelagic paleoecology. *PLoS ONE* **8**, e66075 (2013).
36. Sander, P. M., Chen, X., Cheng, L. & Wang, X. Short-snouted toothless ichthyosaur from China suggests Late Triassic diversification of suction feeding ichthyosaurs. *PLoS ONE* **6**, e19480 (2011).
37. Wang, X. F. *et al.* 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 (2008).
38. Liu, J. *et al.* The first specimen of the Middle Triassic *Phalarodon atavus* (Ichthyosauria: Mixosauridae) from South China, showing postcranial anatomy and peri-Tethyan distribution. *Palaeontology* **56**, 849–866 (2013).
39. Jiang, D. Y., Schmitz, L., Hao, W. C. & Sun, Y. L. A new mixosaurid ichthyosaur from the Middle Triassic of China. *J. Vert. Paleontol.* **26**, 60–69 (2006).
40. Liu, J. *et al.* New mixosaurid ichthyosaur specimen from the Middle Triassic of SW China: further evidence for the diapsid origin of ichthyosaurs. *J. Paleontol.* **85**, 32–36 (2011).
41. Cheng, L., Chen, X.-H., Shang, Q.-H. & Wu, X.-C. A new marine reptile from the Triassic of China, with a highly specialized feeding adaptation. *Naturwissenschaften* **101**, 251–259 (2014).
42. Li, C., Rieppel, O., Wu, X.-C., Zhao, L.-J. & Wang, L.-T. A new Triassic marine reptile from southwestern China. *J. Vert. Paleontol.* **31**, 303–312 (2011).
43. Li, C., Jiang, D. Y., Cheng, L., Wu, X. C. & Rieppel, O. A new species of *Largocephalosaurus* (Diapsida: Saurosphargidae), with implications for the morphological diversity and phylogeny of the group. *Geol. Mag.* **151**, 100–120 (2014).
44. Liu, J. *et al.* A new pachypleurosaur (Reptilia, Sauropterygia) from the lower Middle Triassic of SW China and the phylogenetic relationships of Chinese pachypleurosaurs. *J. Vert. Paleontol.* **31**, 292–302 (2011).
45. Shang, Q. H., Wu, X. C. & Li, C. A new eosauropterygian from Middle Triassic of eastern Yunnan Province, southwestern China. *Vertebrata PalAsiatica* **49**, 155–171 (2011).
46. Sato, T., Zhao, L.-J., Wu, X.-C & Li, C. *Diandongosaurus acutidentatus* Shang, Wu & Li, 2011 (Diapsida: Sauropterygia) and the relationships of Chinese eosauropterygians. *Geol. Mag.* **151**, 121–133 (2014).
47. Li, C., Wu, X. C., Cheng, Y. N., Sato, T. & Wang, L. T. An unusual archosaurian from the marine Triassic of China. *Naturwissenschaften* **93**, 200–206 (2006).
48. Li, C., Rieppel, O. & LaBarbera, M. C. A Triassic aquatic protorosaur with an extremely long neck. *Science* **305**, 1931–1931 (2004).
49. Massare, J. A. in *Mechanics and physiology of animal swimming* (eds Maddock, L., Bone, Q. & Rayner, J.M.V.) 133–149 (Cambridge University Press, 1994).
50. Storrs, G. W. Function and phylogeny in sauropterygian (Diapsida) evolution. *Am. J. Sci.* **293A**, 63–90 (1993).
51. Zhang, Q. *et al.* Nothosaur foraging tracks from the Middle Triassic of southwestern China. *Nat. Commun.* **5**, 3973 (2014).
52. Rieppel, O. Feeding mechanics in Triassic stem-group sauropterygians: the anatomy of a successful invasion of Mesozoic seas. *Zool. J. Linn. Soc.* **135**, 33–63 (2002).
53. Tschanz, K. *Lariosaurus buzzii* n. sp. from the Middle Triassic of Monte San Giorgio (Switzerland) with comments on the classification of nothosaurs. *Palaeontogr. Abt. A* **208**, 153–179 (1989).
54. Sander, P. M. The pachypleurosaurids (Reptilia: Nothosauria) from the Middle Triassic of Monte San Giorgio (Switzerland) with the description of a new species. *Phil. Trans. R. Soc. B* **325**, 561–666 (1989).
55. Rieppel, O. A new species of *Nothosaurus* (Reptilia: Sauropterygia) from the upper Muschelkalk (lower Ladinian) of southwestern Germany. *Palaeontogr. Abt. A* **263**, 137–161 (2001).
56. Klein, N. & Albers, P. C. H. A new species of the sauropsid reptile *Nothosaurus* from the Lower Muschelkalk of the western Germanic Basin, Winterswijk, The Netherlands. *Acta Palaeontol. Pol.* **54**, 589–598 (2009).
57. Albers, P. C. H. New *Nothosaurus* skulls from the Lower Muschelkalk of the western Lower Saxony Basin (Winterswijk, the Netherlands) shed new light on the status of *Nothosaurus winterswijkensis*. *Neth. J. Geosci.* **90**, 15–21 (2011).

58. Swofford, D. L. *PAUP*: Phylogenetic Analysis Using Parsimony (* and Other Methods), Version 4.0 b10.* 142 (Sinauer Associates, 2002).

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