Title
Repeated evolution of durophagy during ichthyosaur radiation after mass extinction indicated by hidden dentition.

Permalink
https://escholarship.org/uc/item/03h5t5z8

Journal
Scientific reports, 10(1)

ISSN
2045-2322

Authors
Huang, Jian-Dong
Motani, Ryosuke
Jiang, Da-Yong
et al.

Publication Date
2020-05-08

DOI
10.1038/s41598-020-64854-z

Peer reviewed
Repeated evolution of durophagy during ichthyosaur radiation after mass extinction indicated by hidden dentition

Jian-dong Huang1, Ryosuke Motani2✉, Da-yong Jiang3,4, Xin-xin Ren1, Andrea Tintori5, Olivier Rieppel6, Min Zhou3, Yuan-chao Hu1 & Rong Zhang1

Marine tetrapods quickly diversified and were established as marine top predators after the end-Permian Mass extinction (EPME). Ichthyosaurs were the forerunner of this rapid radiation but the main drivers of the diversification are poorly understood. *Cartorhynchus lenticarpus* is a basal ichthyosauriform with the least degree of aquatic adaptation, holding a key to identifying such a driver. The unique specimen appeared edentulous based on what was exposed but a CT scanning revealed that the species indeed had rounded teeth that are nearly perpendicular to the jaw rami, and thus completely concealed in lateral view. There are three dental rows per jaw ramus, and the root lacks infoldings of the dentine typical of ichthyopterygians. The well-developed and worn molariform dentition with three tooth rows supports the previous inference that the specimen is not of a juvenile. The premaxilla and the corresponding part of the dentary are edentulous. Molariform dentition evolved three to five times independently within Ichthyosauriformes in the Early and Middle Triassic. Convergent exploitation of hard-shelled invertebrates by different subclades of ichthyosauriforms likely fueled the rapid taxonomic diversification of the group after EPME.

Many components of the modern ecosystem emerged in the Triassic, after the EPME. One of them is marine tetrapods, air-breathing vertebrates that invaded the sea from land, such as marine mammals and reptiles1. Marine colonization by tetrapods occurred at least 69 times in the past, 27 of which were in the Mesozoic2. A high concentration of such colonization events is found soon after the EPME in the Early to Middle Triassic, when multiple lineages of marine tetrapods entered marine environments and radiated quickly to achieve high taxonomic and ecological diversity3. Some of these lineages gave rise to the iconic marine reptiles of the Jurassic and Cretaceous, such as ichthyosaurs and plesiosaurs, that occupied niches similar to those of cetaceans and pinnipeds in the modern sea4. However, it is still unclear what may have fueled this rapid early diversification.

Ichthyosaurs are a group of marine reptiles noted for the evolution of fish-shaped body profiles5. Typical fish-shaped ichthyosaurs form the clade Parvipelvia, a subclade within Ichthyosauria, which in turn is a part of Ichthyopterygia6 (Fig. 1). The sister group of ichthyopterygians has been ambiguous but it is now likely that Nasorostra, a recently discovered clade of marine reptiles, is sister to Ichthyopterygia, together belonging to a lineage called Ichthyosauriformes. *Cartorhynchus lenticarpus* was the first nasorostran to be discovered, followed by *Sclerocormus parviceps*7,8. Nasorostra are the only ichthyosauriforms to have a combination of features that are expected in the earliest members of the clade soon after marine invasion, such as the abbreviated snout, short body trunk, and pachyostotic ribs. However, Nasorostra have been known only for four years based on two specimens, so our knowledge of the group is still limited. Yet, they are expected to provide information on the emergence of Ichthyosauriformes because of their basal position within the clade. Additional information on this clade is clearly needed.

1Department of Research, Anhui Geological Museum, Jiahe Road 999, Hefei, Anhui, 230031, China. 2Department of Earth and Planetary Sciences, University of California, One Shields Avenue, 95616, Davis, California, USA. 3Department of Geology and Geological Museum, Peking University, Yiheyuan Street, 5, Beijing, 100871, P.R. China. 4State Key Laboratory of Palaeobiology and Stratigraphy (Nanjing Institute of Geology and Palaeontology), Chinese Academy of Science, Nanjing, 210008, P. R. China. 5Dipartimento di Scienze della Terra, Università degli Studi di Milano, Via Mangiagalli 34-20133, Milano, Italy. 6Center of Integrative Research, The Field Museum, Chicago, IL, 60605-2496, USA. ✉e-mail: rmotani@ucdavis.edu
One of the controversies about the basal ecomorphology of ichthyosaurs, dating back to the previous century, concerns the dentition. It was once believed that rounded posterior teeth are plesiomorphic in this lineage, largely based on the condition found in *Grippia longirostris* that was then believed to be the most basal ichthyosaur, but later discoveries revealed that some other basal members of the clade had conical teeth while *G. longirostris* was not necessarily the most basal ichthyopterygian. Of the four-known basal ichthyopterygians from the Early Triassic, two have rounded posterior teeth and the other two have conical teeth. Ichthyopterygia in this context accords with the first phylogenetic definition explicitly given to the clade, i.e., a clade containing all descendants of the last common ancestor of *Utatsusaurus*, *Grippia*, and *Ichthyosaurus* (Fig. 1). Dental morphology usually reflects diet and other ecological factors and may provide important information on what fueled the early radiation of marine tetrapods in the Early and Middle Triassic. It is therefore important to understand the evolution of dentition in early marine reptiles.

*Cartorhynchus lenticarpus* is known only from a single specimen exposed from the right-dorsal side. The mouth is closed, with up to one millimeter of a gap between the upper and lower jaws depending on the location. No dentition was seen through the gap, so it was initially considered edentulous. An attempt to remove further
matrix through this gap revealed that there was a tooth-like structure, which later turned out to be an isolated
tooth that was not attached to the jaws. The discovery prompted an examination of the hidden left side of the
specimen to test the presence of a dentition. However, the holotype and only known specimen is delicate, so
mechanical preparation from the other side would involve risk of damage. We therefore decided to CT scan this
rare specimen. The purpose of the present paper is to report the anatomical features revealed by CT scanning,
including a unique dentition, and discuss the evolution of tooth morphology and diet in basal ichthyosauriforms
and its bearing on the rapid diversification of the clade after the end-Permian mass extinction.

Results
Preservation. The specimen has severely been compacted to about 7 mm of total thickness. As a result,
boundaries between bones are often unclear in CT images when a bone is preserved on top of another. Unlike the
right side of the skull that is articulated, the left side, which was hidden previously and revealed by CT scanning
for the first time, is disarticulated, although many bones are still located close to the original positions. Thus, it is
likely that the specimen was deposited with the right side facing down and embedded in sediment, while the left
side was exposed for longer and became disarticulated. Some posterior cranial bones are missing, including large
parts of the left angular and surangular and most of the occiput. One possible mandibular element, tentatively
identified as a possible prearticular in Fig. 2b, is found postcranially, overlapping the right clavicle, suggesting dis-
turbance of the left-posterior part of the skull before complete burial.

Tooth orientation and ‘occlusion’. The most unusual feature of the dentition is the orientation of the
teeth. Unlike in most vertebrates, many teeth are perpendicular to the outer walls of the respective jaw rami,
especially posteriorly (Fig. 3), and therefore completely concealed when viewing the ramus perpendicularly from
its outer side. The tooth orientation in natural posture is more horizontal than vertical (Fig. 3), when it is nearly
vertical in most reptiles. The outer walls of the jaw rami are preserved parallel to the bedding plane, with the teeth
approximately vertical to the plane, i.e., compactional bias is unlikely to alter the orientation of the teeth (see
Discussion).

The most-likely inclination of the mandibular rami is presented in Fig. 3 (see Methods). Because of the pecu-
liar tooth orientation, the maxillary and dentary teeth do not contact each other tip to tip, and instead, ‘occlusion’
occurs between the side walls of the tooth crowns of the maxilla and dentary (see Discussion). This strange ‘occlu-
sion’ is also evidenced by the tooth wear. Both maxillary and dentary teeth have been worn from their sides facing
the corresponding dentition, and the worn maxillary dentition seems to fit into a shallow basin of worn dentary
teeth (Fig. 3b–d). The worn teeth lack the thin wall of dense material on the occlusal side, which had most likely
been worn through ‘occlusion’ (yellow brackets in Fig. 4b,e). The tooth wear is not an artifact of preservational
compaction because the teeth outside of the occlusal area are not worn. The upper and lower teeth do not abut
against each other in their preserved postures, so the wear was formed before the burial.

Tooth morphology and arrangements. A total of 21 teeth are recognized on the right dentary, forming
three rows that are approximately parallel to the jaw margin. There are 10, 7, and 4 teeth, respectively, in the labial,
middle, and lingual rows (Fig. 4b; note that two immature teeth are not showing in this cross section, namely the
most posterior tooth of the labial row and the second to the last tooth of the lingual row). The left dentary has 10, 7, and 3 teeth in the labial, middle, and lingual rows, respectively, but the count is less accurate given that they are not exposed on either side of the specimen. The antepenultimate tooth of the labial row of the right dentary is the largest, with the maximum crown diameter of 3.13 mm along the horizontal plane and a crown height of 1.65 mm, as measured from CT slices. The teeth in the more labial row are on average larger than those in the more lingual row, although the difference is minor when excluding the antepenultimate tooth of the labial row. The anterior part of the dentary, approximately corresponding to the premaxilla in the upper jaw, is edentulous.

The right maxilla has 12 teeth in two rows, and a tooth position belonging to the third row. Seven of the teeth are in the labial row and 5 in the middle row. The third-row tooth position is located lingual to the middle row and houses a partly formed tooth crown that is much smaller than the space and tilted about 90 degrees relative to other tooth crowns. The hidden left maxilla seems to have at least 7 and 3 teeth, respectively, in the labial and middle rows, and again there seems to be a single tooth in the lingual row.

The tooth crowns are generally rounded, with the crown apex shape ranging from weakly pointed to completely flattened (Figs. 2 and 4c–e), from anterior to posterior and from lingual to labial within the dentition. Most tooth crowns have disto-mesial elongated cross-sectional shapes, except for a few posterior teeth along the jaw margin that are as wide as long in cross-section. All tooth crowns are swollen at least to some extent (Fig. 4c–e), unlike in more derived ichthyosauriforms where molariform teeth are exclusively found in heterodont dentitions with conical anterior and molariform posterior teeth. Cross-sectional images also reveal that the tooth crowns are unusually thin-walled, as judged by the distribution of dense material that at least contains the enamel (Fig. 4a–e). However, the CT images do not allow clear separation of the dentine from the enamel and the rock matrix, which may have high density depending on the place probably because of concretion. Also, the gray levels in the images seem to be driven by artifacts, such as beam hardening and scattering than the actual density of the material, especially near the boundary of bones and teeth. For example, inside the dense wall, the teeth in Fig. 4c–e are least dense (i.e., dark) near the crown apex and becomes denser toward the bottom but this change unlikely to reflect biological structures. Also, the distributions of the darkest parts are inconsistent across images (compare Fig. 4c with e).

Figure 3. 3D Reconstruction of mandibular posture. (a) Dorsal view of the reconstructed mandible. (b) Medial view of the reconstructed mandible and maxilla. (c) Medio-ventral view of the dentary and maxillary ‘occlusion’. (d) Same from posterior view. Maxilla is colored in purple. Scale bar is 1 cm.
Thus, the “wall” in the current context means the periphery of the teeth with high density. The root is present in most teeth. Many of the teeth are constricted between the root and crown, even in the largest teeth in the postero-labial region (yellow arrows in Fig. 4). The root is approximately cylindrical without any fluting or infoldings that are typically found in ichthyopterygians.

The dentigerous region is 18.9 mm long in the right dentary and 14.3 mm in the right maxilla. Thus, some dentary teeth have no corresponding teeth in the upper jaw. These teeth are found in the most anterior part of the dentary dentition, where the gap between the right and left mandibular rami is narrow. See Discussion.

Relative tooth size and crown shape index. Massare (1987) proposed a combination of two tooth characteristics to divide the feeding guilds of Jurassic and Cretaceous marine reptiles, namely the crown shape index quantified as the ratio between the height and diameter of the largest tooth crown in the dentition, and the relative tooth size, measured as the maximum dimension of the largest tooth crown to the skull width. These two metrics were estimated for the present specimen.

The estimation of the tooth size index involves the skull width, which is ideally measured between the quadrate but may be substituted by the width between the lateral sides of the supratemporals in ichthyosauriforms, where the two values are usually similar to each other. Unfortunately, one each of the quadrate and supratemporal has been displaced, making direct measurements of the skull width unreliable. However, a half of the skull width can be measured on the right side of the skull roof that retains its articulation, providing a value of 15.1 mm between the lateral margin of the supratemporal and the sagittal line, measured perpendicular to the latter. This results in an estimated skull width of 30.2 mm.

The crown shape index based on the largest dentary tooth is 1.90, placing Cartorhynchus in the crushing guild characterized by an index value above 1.0. The relative tooth size is about 0.104, again placing Cartorhynchus in the crushing guild, characterized by values equal to or greater than 0.1.

Jaw symphysis. The tooth orientation and size, together with the morphology of the anterior tip of the dentary, make it difficult for the right and left mandibular rami to form a solid symphysis. The teeth occupy much of the medial surface of the mandible anteriorly, leaving only the very tip of the snout for possible symphysal articulation. Yet, the rostral tip of the mandible is slender and curved upward, without a symphysal surface on the medial side. Therefore, the jaw symphysis, if any, was weak. The jaw symphysis is also weak in Huphsuchia, the sister taxon of Ichthyoauriformes, so the weakness in C. lenticarpus is phylogenetically reasonable.
Cranial morphology. The CT imaging illuminated misidentifications of bone sutures and one misinterpretation of morphology in the original description. The parietal seems to have the parietal ridge and slope based on the CT images. The premaxilla has a short supranasal process that forms the anterior-dorsal margin of the external naris. Also, the right quadrate, which was thought to underlie the right quadratojugal, seems to have been displaced, and most of what was identified as the quadrate is parts of the quadratejugal and squamosal.

Ancestral state reconstruction. Ancestral state reconstruction based on likelihood suggests that common ancestors along the main lineage of Ichthyosaurusiformes likely retained conical teeth, and that rounded teeth most likely evolved five times in ichthyosauriforms (Fig. 1a). The parsimony reconstruction suggests that molariform teeth evolved three to five times in ichthyosauriforms, and that the common ancestors along the main lineage of Ichthyopterygia unambiguously retained conical teeth (Fig. 1b).

Discussion

The new data on the dentition and jaw design in Cartorhynchus lenticarpus provides useful information on the feeding ecology of the species. The presence of rounded teeth implies durophagy, although this does not mean exclusive feeding on hard-shelled invertebrates; durophagous marine reptiles and mammals consume various mixtures of hard and soft prey items. Some mixture of hard and soft prey is therefore likely for C. lenticarpus too. Such a diet does not contradict the suction-feeding habit that was previously inferred for C. lenticarpus based on the co-existence of a robust ceratohyal and short and narrow snout with edentulous tips. For example, among extant marine vertebrates, at least some sparid fishes are known to suction feed despite their molariform teeth and durophagous diet. The prey size of C. lenticarpus is inferred to have been small, given that the edentulous tip of the snout, which is likely used as the opening during suction feeding, is about 6 mm wide. The jaw width at the point where the first tooth becomes visible in Fig. 3a is about 10 mm. The narrowness relative to the skull width further supports the inference of suction-feeding because it allows a high degree of pressure concentration along the skull, as seen in extant suction-feeders. No stomach content is available but small thin-shelled bivalves, together with bivalved-arthropods (Thylacocephala) and small ammonoids, occur abundantly in the strata that yielded the holotype of the species. Also, the first diversification peak of invertebrates, especially bivalves, after the end-Permian mass extinction was recorded in Chinese strata coinciding with the occurrence of C. lenticarpus and other oldest ichthyosauromorphs.

The strange tooth orientation and 'occlusion' seen in the specimen is enigmatic—the teeth are structurally strongest when stressed from the tip, not from the side, while high stress is expected when durophages crush hard-bodied prey. There are two possibilities that may reconcile tooth morphology and tooth mechanics, strongest when stressed from the tip, not from the side, while high stress is expected when durophages crush hard-bodied prey. For example, among extant marine vertebrates, at least some sparid fishes are known to suction feed despite their molariform teeth and durophagous diet. The prey size of C. lenticarpus is inferred to have been small, given that the edentulous tip of the snout, which is likely used as the opening during suction feeding, is about 6 mm wide. The jaw width at the point where the first tooth becomes visible in Fig. 3a is about 10 mm. The narrowness relative to the skull width further supports the inference of suction-feeding because it allows a high degree of pressure concentration along the skull, as seen in extant suction-feeders. No stomach content is available but small thin-shelled bivalves, together with bivalved-arthropods (Thylacocephala) and small ammonoids, occur abundantly in the strata that yielded the holotype of the species. Also, the first diversification peak of invertebrates, especially bivalves, after the end-Permian mass extinction was recorded in Chinese strata coinciding with the occurrence of C. lenticarpus and other oldest ichthyosauromorphs.

The dental morphology of C. lenticarpus resembles that of Omphalosaurus to some extent in that the teeth are rounded. However, unlike in Omphalosaurus, most teeth have the root and there is only one tooth per tooth position in C. lenticarpus—Omphalosaurus is known for vertical overlap of teeth without the root. Thin tooth walls would imply mechanical weakness, which is counter-intuitive given that rounded tooth crowns are often, although not always, used for crushing hard prey. Molariform teeth evolved in many vertebrate clades, especially in aquatic environments with a variety of hard-shelled invertebrate prey but also on land. Of these examples, the best modern analogues for the dentition of Cartorhynchus lenticarpus are found in teleost fishes of the Family Sparidae, whose skull length and tooth size are comparable to those of C. lenticarpus. Some sparids are known for their molariform oral teeth that are arranged in multiple rows per jaw ramus. As with C. lenticarpus, most of the teeth do not protrude beyond the dentigerous margins of the jaw rami and therefore are largely hidden from external view, although the degree of concealment is greater in C. lenticarpus. It may be hypothesized that this concealed placement of the teeth reduces disruption of water movement during suction feeding. Despite the similarities, sparids differ from C. lenticarpus in a few respects. As in Ximiminosaurus, lingual teeth are larger than labial ones, making the tips of the crowns of different tooth rows more leveled. Also, sparids may have anterior prehensile teeth unlike in C. lenticarpus.
Molariform teeth are usually an ontogenetic feature. Juveniles of relevant species have conical or tricuspid teeth that become larger and more rounded with growth, sometimes becoming almost flattened in extreme cases. Such ontogenetic morphological changes are usually associated with dietary shifts. A few exceptions to this rule have been noted in at least two, and possibly three species of fish, where larger juveniles already have at least a few molariform teeth. However, we are not aware of a case where juveniles have three or more tooth rows of molariform teeth per oral jaw ramus, or where the labial teeth of juveniles have already become as large as more lingual teeth as a result of tooth replacement. In species with three rows of mandibular teeth, tooth rows are added from the lingual side and teeth are replaced with growth, while the teeth are not yet molariform in small juveniles. Therefore, it takes time before molariform teeth reach the labial row and become as large as those in more lingual rows. Given the presence of three tooth rows with large teeth in the labial row, and that molariform teeth are an adult feature in most cases, it is most likely that the holotype of *Cartorhynchus lenticarpus* was not of a juvenile, as previously inferred based on skeletal proportions.

Convergent evolution of molariform teeth within a clade is not rare among non-mammalian vertebrates. For example, at least two lineages within monitor lizards (genus *Varanus*) have molariform teeth in adults, namely an African lineage including *V. niloticus* and the Philippine lineage including *V. olivaceus*. Durophagy, associated with oral molariform teeth, evolved ten times independently among moray eels and up to seven times among sparid fishes. Molariform teeth also repeatedly evolved in the pharyngeal jaws of some fish lineages, such as hermaphroditic cichlid fishes where it evolved at least six times. Our inference that molariform teeth evolved three to five times in ichthyosauriforms, whose Linnaean rank is undetermined but should be higher than the Superorder Ichthyoptyeria that it contains, is therefore not exceptionally high, especially for an aquatic lineage.

The evolution of molariform teeth is most likely correlated with that of durophagy. More than half of Early and Middle Triassic ichthyosauriform species had at least a few molariform teeth (Fig. 1), so it is likely that hard-shelled prey formed a substantial proportion of the diet of early ichthyosauriforms. However, it is unlikely that all of them fed on the same prey type through time. For example, molariform ichthyosauriforms in the Early Triassic had small teeth as in *Cartorhynchus*, with the maximum diameter of up to about three millimeters, while those in the Middle Triassic included species with the maximum tooth diameter exceeding 1 cm. The shape of the occlusal surface of the crown varied from round to ridged in the Middle Triassic, while Early Triassic species had uniformly rounded teeth. Therefore, it seems that later ichthyosauriforms consumed larger and more diverse prey than their predecessors. This matches the known pattern of invertebrate diversification after the EPME.

It then appears that ichthyosauriforms exploited the changing communities of hard-shelled prey by repeatedly giving rise to new types of durophages in the Early and Middle Triassic, rather than by a single durophagous lineage adapting to the changes. Therefore, it is likely that the rapid taxonomic diversification of ichthyosauriforms after the EPME was at least partly driven by the evolution of hard-shelled prey.

**Methods**

**Specimen.** The holotype of *Cartorhynchus lenticarpus* was used. It is accessioned at the Anhui Geological Museum under the specimen number AGB 6257. Its field number was MT-II. The first author is in charge of research at the museum and granted permission to study the specimen himself.

**CT scanning.** The holotype of *Cartorhynchus lenticarpus* (AGB 6257) was scanned at the Yinghua testing co. LTD, Shanghai, China, using 250 kV micro CT (VCT 460m3 s). The specimen was scanned with a beam energy of 180 kV and a flux of 150 mA at a detector resolution of 38 μm per pixel. A total of 1200 transmission images were reconstructed in 1588 slices of 1313 × 720 pixels.

**3D rendering from CT slices.** We used a combination of Fiji (ImageJ 2.0), 3D Slicer 4.8.1, and Meshlab for 3D surface reconstruction given in Fig. 2a,b through a method that may be called Sequential Isosurface Trimming. Fiji was used to crop the slices and to apply a weak convolution filter to reduce noises—the slices suffered from streaks of noises even after the best efforts to remove noise by the scanning facility. Slicer was then used to produce 20 isosurfaces at different gray levels. The resulting isosurfaces were converted to polygonal meshes and saved as PLY files, which were then edited in Meshlab to remove noisy areas—noises typically form linear streaks of random lengths that are parallel to X and Z axes of the original CT images and can readily be distinguished from the smooth surfaces of bones. The trimmed surfaces were then examined for redundancy, and when two or more surfaces were redundant, one with the lowest gray level was retained. The remaining trimmed surfaces were merged and faces with low ambient occlusion (i.e., largely concealed from outside) were removed.

This Sequential Isosurface Trimming approach may not be traditional but we used it because our initial trial using a standard approach of CT image segmentation, whereby bone boundaries are subjectively determined on each CT slice to form the basis of 3D reconstruction, turned out to be unfruitful. It was very difficult to segment bones consistently because of a combination of biases, such as inconsistency of gray levels within and between slices caused by the high-density matrix, high level of noises, and severe compaction of the fossil that turned many bones into thin sheets. The resulting 3D images failed to capture many of the small features.

To test whether Sequential Isosurface Trimming led to unintentional elimination of important bone structures, we also volume-rendered the data in ImageVis 3D 3.1.0, using the 2D transfer function option for comparison. Supplementary Fig. S1 is an example of such a rendered image. After trying different combinations of 2D transfer functions, we concluded that the surface reconstruction did not lack any significant part of the skeleton that is present in the CT image slices. The outcome of Sequential Isosurface Trimming is given in Supplementary Fig. S2.
3D arrangement of the mandibular rami. The mandible was reconstructed by combining the 3D mesh of the right mandibular ramus with the mirror image of itself, given that the left ramus is far less complete than the right. The arrangement of the two was made under the following conditions. First, the mandibular width at the jaw joint was kept at the skull width reported in Results. Second, the anterior tips of the two mandibular rami are located as close to the sagittal plane as possible, without diverging laterally—the tips would diverge from the sagittal plane unless the rami are kept in certain postures because of the strong upward curvature of the mandible. Third, the two mandibular rami do not overlap with each other. The jaw rami were allowed to incline relative to the sagittal plane, but it was evident that there was little space for manipulation under these three conditions. For example, if we try to orient the mandible and maxilla so that their respective teeth point at each other tip-to-tip, the right mandibular ramus with the mirror image of itself, given that the left ramus is far less complete than the right. The jaw joint was kept at the skull width reported in Results. Second, the anterior tips of the two mandibular rami are located as close to the sagittal plane as possible, without diverging laterally—the tips would diverge from the sagittal plane unless the rami are kept in certain postures because of the strong upward curvature of the mandible.

Ancestral character state reconstruction. We used a recently published phylogenetic hypothesis of Ichthyosauromorpha and its associated taxon-character matrix for ancestral state reconstruction25. The matrix reflects the dental morphology reported in the present study, as well as the latest findings on basal ichthyosauromorphs. Dental character states for Sclerothorax parviceps are considered ambiguous given that the species may have hidden dentition as in C. lenticarpus. The ancestral state reconstruction was performed based on the strict consensus tree of the most parsimonious trees using Mesquite 3.51. Two reconstruction models, squared-change parsimony and likelihood models, were used. We only examined character 72, which codes the posterior tooth crown shape as (0) conical, (1) rounded, or (2) flat. In parsimony reconstruction, the multistate character was treated as ordered, while the default model of Mesquite was used in likelihood reconstruction. Because the phylogeny is based on parsimony, the exact branch lengths for likelihood reconstruction is unknown. Thus, branch lengths were kept uniform across the tree when calculating likelihood reconstruction.

Data availability
All data used in this study are available in Supplementary Material or in cited references.

Received: 3 February 2020; Accepted: 17 April 2020; Published online: 08 May 2020

References
1. Kelley, N. P. & Pyenson, N. D. Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. Science (80-.). 348, 3716–3716 (2015).
2. Vermeij, G. J. & Motani, R. Land to sea transitions in vertebrates: the dynamics of colonization. Paleobiology 44, 237–250 (2018).
3. 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-Science Rev. 137, 85–128 (2013).
4. Motani, R. The evolution of marine reptiles. Evol. Educ. Outreach 2, 224–235 (2009).
5. Motani, R. Evolution of fish-shaped reptiles (Reptilia: Ichthyopterygia) in their physical environments and constraints. Annu. Rev. Earth Planet. Sci. 33, 395–420 (2005).
6. Motani, R. Phylogeny of the Ichthyopterygia. J. Vertbr. Paleontol. 19, 473–496 (1999).
7. Jiang, D.-Y. et al. A large aberrant stem ichthyosauriform indicating early rise and demise of ichthyosauromorphs in the wake of the end-Permain extinction. Sci. Rep. 6, 26232 (2016).
8. Motani, R. et al. A basal ichthyosauriform with a short snout from the Lower Triassic of China. Nature 517, 485–488 (2015).
9. Mazin, J.-M. Grippia longirostris Wiman, 1929, un Ichthypoterygia primitif du Trias inférieur du Spitsberg. Bull. du Muséum Natl. d’Histoire Nat. 4, 317–340 (1981).
10. Motani, R. Redescription of the dentition of Grippia longirostris (ichthyosauria) with a comparison with Utatsusaurus hataii. J. Vertbr. Paleontol. 17, 39–44 (1997).
11. Motani, R. Redescription of the dental features of an early triassic ichthyosaur, Utatsusaurus hataii. J. Vertbr. Paleontol. 16, 396–402 (1996).
12. Massare, J. A. Tooth morphology and prey preference of Mesozoic marine reptiles. J. Vertbr. Paleontol. 7, 121–137 (1987).
13. Motani, R. et al. Lung feeding in early marine reptiles and fast evolution of marine tetrapod feeding guilds. Sci. Rep. 5, 8900 (2015).
14. Motani, R. The skull and taxonomy of Mixosaurus (Ichthyopterygia). J. Paleontol. 73, 924–935 (1999).
15. Kelley, N. P. & Motani, R. Trophic convergence drives morphological convergence in marine tetrapods. Biol. Lett. 11, 20140709–20140709 (2015).
16. Vandelwalle, P., Saintin, P. & Chardon, M. Structures and movements of the buccal and pharyngeal jaws in relation to feeding in Diplodus sargus. J. Fish Biol. 46, 623–656 (1995).
17. Motani, R. et al. Absence of suction feeding ichthyosaurs and its implications for Triassic mesopelagic palaeoecology. PLoS One 8, e66075 (2013).
18. Ji, C., Tintori, A., Jiang, D.-Y. & Motani, R. New species of Thylacoleocephala (Archthopoda) from the Spatian (Lower Triassic) of Chaohu, Anhui Province of China. Palaeontologische Zeitschrift 91, 171–184 (2017).
19. Fan, J. et al. A high-resolution summary of Cambrian to Early Triassic marine invertebrate biodiversity. Science (80-.). 367, 272–277 (2020).
20. Motani, R., Jiang, D.-Y., Tintori, A., Ji, C. & Huang, J.-D. Pre- versus post-mass extinction divergence of Mesozoic marine reptiles dictated by time-scale dependence of evolutionary rates. Proc. R. Soc. B-Biological Sci. 284, 20170241 (2017).
21. Crofts, S. B. & Summers, A. P. How to best smash a snack: the effect of tooth shape on crushing load. J. R. Soc. Interface 11, 20131053 (2014).
22. Jiang, D.-Y. et al. New primitive ichthyosaurian (Reptilia, Diapsida) from the Middle Triassic of Panxian, Guizhou, southwestern China and its position in the Triassic biotic recovery. Proc. Nat. Sci. Int. 18, 1315–1319 (2008).
23. Merriam, J. C. Preliminary note on a new marine reptile from the Middle Triassic of Nevada. Bull. Dep. Geol. Univ. Calif. Publications Bulletin 0, 71–79 (1906).
24. Sander, P. M. & Faber, C. The Triassic marine reptile Omphalosaurus: Osteology, jaw anatomy, and evidence for ichthyosaurian affinities. J. Vertbr. Paleontol. 23, 799–816 (2003).
25. Motani, R. Is Omphalosaurus ichthyopterygian? A phylogenetic perspective. J. Vertbr. Paleontol. 20, 295–301 (2000).
26. Bemis, K. E. & Bemis, W. E. Functional and developmental morphology of tooth replacement in the Atlantic Wolfish, Anarhichas lupus (Teleostei: Zoarcoidei: Anarchichadidae). Copeia 103, 886–901 (2015).
28. Hulsey, C. D., Roberts, R. J., Lin, A. S. P., Guldberg, R. & Streelman, J. T. Convergence in a mechanically complex phenotype: detecting structural adaptations for crushing in cichlid fish. *Evolution (N. Y.)* 62, 1587–1599 (2008).
29. Grubich, J. Morphological convergence of pharyngeal jaw structure in durophagous perciform fish. *Biol. J. Linn. Soc.* 80, 147–165 (2003).
30. Gidmark, N. I., Taylor, C., Lopresti, E. & Brainerd, E. Functional morphology of durophagy in black carp, *Mylopharyngodon piceus*. *J. Morphol.* 276, 1422–1432 (2015).
31. Elgindy, S. A. A., Alsayf, M. A. M. & Tanekh, M. Morphological characterization of the oral cavity of the gilthead seabream (*Sparus aurata*) with emphasis on the teeth-age adaptation. *Microsc. Res. Tech.* 79, 227–236 (2016).
32. Estes, R. & Williams, E. E. Ontogenetic variation in the molariform teeth of lizards. *J. Verteb. Paleonolt.* 4, 96–107 (1984).
33. Dessem, D. Ontogenetic changes in the dentition and diet of *Trachemys scripta* (Lacertilia: Testudines). *Copeia* 1, 245–247 (1985).
34. D’Amore, D. C. Illustrating ontogenetic change in the dentition of the Nile monitor lizard, *Varanus niloticus*: A case study in the application of geometric morphometric methods for the quantification of shape-size heterodony. *J. Anat.* 226, 403–419 (2015).
35. Fernandez, L., Motta, P. J., Hernandez, I. P. & Motta, F. J. Trophic consequences of differential performance: Ontogeny of oral jaw crushing performance in the sheephead, *Archosargus probatocephalus* (*Teleostei, Sparidae*). *J. Zool.* 243, 737–756 (1997).
36. Huang, M. Y., Ryan, T. M., Stauffer, J. R. & Madsen, H. Does hardness of food affect the development of pharyngeal teeth of the black carp, *Mylopharyngodon piceus* (*Pisces: Cyprinidae*)? *Biol. Control* 80, 156–159 (2015).
37. French, B., Platell, M. E., Clarke, K. R. & Potter, I. C. Ranking of length-class, seasonal and regional effects on dietary compositions of the co-occurring *Pagrus auratus* (*Sparidae*) and *Pseudocaranx georgianus* (*Carangidae*). *Estuar. Coast. Shelf Sci.* 115, 309–325 (2012).
38. Constantinou, P. J., Bush, M. B., Barani, A. & Lawn, R. On the evolutionary advantage of multi-cusped teeth. *J. R. Soc. Interface* 13, 20160374 (2016).
39. Richardson, T. J., Potts, W. M., Santos, C. V. & Sauer, W. H. H. Ontogenetic dietary shift and morphological correlations for *Diplodus capensis* (*Teleostei: Sparidae*) in southern Angola. *African Zool.* 46, 280–287 (2011).
40. Leblanc, A. R. H. & Reisz, R. R. Patterns of tooth development and replacement in captorhinid reptiles: A comparative approach for understanding the origin of multiple tooth rows. *J. Verteb. Paleonolt.*. https://doi.org/10.1080/02724634.2014.919928 (2015).
41. Berkovitz, B. & Shellis, P. Reptiles 2. In *The Teeth of Non-Mammalian Vertebrates* 201–224. https://doi.org/10.1086/97878-0-12-802850-6.00007-2 (2017).
42. Pianka, E. R., King, D. & King, R. A. Varanoid lizards of the world. (Indiana University Press, 2004).
43. Edmund, A. G. Dentition. In *Biologie of the Reptilia*. Volume I: Morphology A. (eds. Gans, C., Bellairs, A. d’A. & Parsons, T. S.) 1, 117–200 (Academic Press, 1969).
44. Chiha, S. N., Iwatsuki, Y., Yoshino, T. & Hanzawa, N. Comprehensive phylogeny of the family *Sparidae* (*Percomorph: Teleostei*) inferred from mitochondrial gene analyses. *Genes Genet. Syst.* 84, 153–170 (2009).
45. Hulsey, C. D. & Darrin Hulsey, C. Function of a key morphological innovation: Fusion of the cichlid pharyngeal jaw. *Proc. R. Soc. B Biol. Sci.* 273, 669–675 (2006).
46. McGowan, C. & Motani, R. Ichthyopterygia. *Handbook of Paleoherpetology 8* (Verlag Dr. Friedrich Pfeil, 2003).
47. Hanel, R. & Sturmbauer, C. Multiple recurrent evolution of trophic types in northeastern Atlantic and Mediterranean seabreams (*Sparidae, Percoidei*). *J. Mol. Evol.* 50, 276–283 (2000).
48. Motani, R. Detailed tooth morphology in a durophagous ichthyosaur captured by 3D laser scanner. *J. Verteb. Paleonolt.* 25, 462–465 (2005).
49. Foster, W. I. & Sebe, K. Recovery and diversification of marine communities following the late Permian mass extinction event in the western Palaeoathysts. *Glob. Planet. Change* 155, 165–177 (2017).
50. Hofmann, R. et al. Recovery of benthic marine communities from the end Permian mass extinction at the low latitudes of eastern Pantalassa. *Palaeontologia* 57, 547–589 (2014).
51. Schindelin, J. et al. Fiji: an open-source platform for biological-image analysis. *Nat. Methods* 9, 676–682 (2012).
52. Fedorov, A. et al. 3D Slicer as an image computing platform for the Quantitative Imaging Network. *Magn. Reson. Imaging* 30, 1323–1341 (2012).
53. Cignoni, P. et al. MeshLab: an open-source mesh processing tool. *Sixth Eurographics Ital. Chapter Conf.*, https://doi.org/10.2312/LocalChapterEvents/ItalChap/ItalianChapConf2008/129-136 (2008).
54. Fogal, T. & Krüger, J. Tuvok, an Architecture for Large Scale Volume Rendering. In *Proceedings of the 15th International Workshop on Vision, Modeling, and Visualization* (2010).
55. Huang, J.-D. et al. The new ichthyosauroid *Chaohusaurus brevifemoralis* (Reptilia, Ichthyosauromorphia) from Majiashan, Chaohu, Anhui Province, China. *PeerJ* 7, e7561 (2019).
56. Maddison, W. P. & Maddison, D. R. Mesquite: a modular system for evolutionary analysis. Version 3.2. http://mesquiteproject.org (2017).
57. Maddison, W. P. Squared-change parsimony reconstructions of ancestral states for continuous-valued characters on a phylogenetic tree. *Syst. Biol.* 40, 304–314 (1991).

Acknowledgements
Geerat J. Vermeij read an earlier version of the manuscript. Fa-yao Huang first noticed the presence of a disarticulated tooth that triggered CT scanning. National Geographic Society Committee for Research and Exploration (#8669–09) to R.M.; Project 41920104001 and 41372016 to D.-Y.J. and Project 41772003 to J.-D.H. from the National Natural Science Foundation of China; Project 123102 from State Key Laboratory of Palaeoecology and Stratigraphy (Nanjing Institute of Geology and Palaeontology, CAS) to D.-Y.J.; Project 2016-k-5 from the Department of Land Resources of Anhui Province to J.-D.H., X.-X.R., Y.-C.H., and R.Z., and Project 201511054 from the Ministry of Land and Resources of China to J.-D.H., X.-X.R., Y.-C.H., R.M. and D.-Y.J.

Author contributions
J.H. conceived the examination of the dentition, as a part of a larger project co-conceived with D.J., A.T., O.R., and R.M., and arranged for C.T. scanning with X.R. and M.Z. R.M. drafted the manuscript, ran phylogenetic analyses and ancestral state reconstruction, and reconstructed 3D models given in Figures 2 and 3, and Supplementary Figures 1 and 2. X.R. reconstructed the teeth using manual segmentation of C.T. images (images not presented; see Methods). J.H., R.M., D.J., X.R., O.R., A.T., M.Z., Y.H., and R.Z. all helped revise the manuscript.

Competing interests
The authors declare no competing interests.
Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41598-020-64854-z.

Correspondence and requests for materials should be addressed to R.M.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher’s note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/.

© The Author(s) 2020