

The earliest herbivorous marine reptile and its remarkable jaw apparatus

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Newly discovered fossils of the Middle Triassic reptile *Atopodentatus unicus* call for a radical reassessment of its feeding behavior. The skull displays a pronounced hammerhead shape that was hitherto unknown. The long, straight anterior edges of both upper and lower jaws were lined with batteries of chisel-shaped teeth, whereas the remaining parts of the jaw rami supported densely packed needle-shaped teeth forming a mesh. The evidence indicates a novel feeding mechanism wherein the chisel-shaped teeth were used to scrape algae off the substrate, and the plant matter that was loosened was filtered from the water column through the more posteriorly positioned tooth mesh. This is the oldest record of herbivory within marine reptiles.

INTRODUCTION

The recovery of the trophic structure in both terrestrial and marine biota following the end-Permian mass extinction has recently been a topic of intense discussion (1–4). Here, we report the first herbivorous filter-feeding marine reptile known, from the early Middle Triassic of China. Relative to the heavily built trunk skeleton, the skull is remarkably small (skull length is approximately 18% of trunk length), which calls for an efficient foraging mechanism that is uniquely specialized in this new form.

Atopodentatus unicus was originally described (5) as a putative sauropterygian filter feeder with a downturned rostrum, supposedly used to stir up invertebrates in soft sediment in a flamingo-like manner. Here, we describe two new specimens of *Atopodentatus* from the Guanling Formation (Member II, Anisian) of Luoping County, Yunnan Province, that require a very different interpretation of skull morphology and provide evidence for an even more remarkable feeding strategy. The new specimens clearly demonstrate that rather than being downturned, the rostrum was developed into a “hammerhead” with pronounced lateral processes formed by the premaxillae and maxillae in the upper jaw and mirrored by the dentary in the lower jaw. We confirm the presence of fine and densely packed needle-shaped teeth in the ramus of the dentaries and maxillae, but the premaxillary teeth are arranged along the anterior edge of the element and are more robust and peg-like in form.

RESULTS

The new specimens (V20291 and V20292, Figs. 1 and 2) are unquestionably referable to *A. unicus*. IVPP (Institute of Vertebrate Paleontology and Paleoanthropology) V20291 is exposed in dorsal view, and apart from the distinct hammerhead, it exhibits dermal skull roofing elements that broadly follow the pattern described in the holotype (5), including the narrow L-shaped maxillae with a short anteriorly placed ascending process; needle-shaped teeth; the presence of very large nasals; prefrontals and postfrontals sharing a broad contact, thereby excluding the frontal from the orbital margin; a robust jugal; and a much reduced lower temporal fenestra that forms a weak embayment at the

ventral margin of the otherwise closed cheek region. The slight variability in the arrangement of the articulation of the frontal with the parietal is readily attributable to individual variation and/or preservational differences. Furthermore, the postcranium also closely resembles the holotype, with anterior dorsals bearing distinctly tall and rounded neural spines, a moderately elongate neck, and large and robust forelimbs. The new specimens of *Atopodentatus* provide no further insights into the phylogenetic relationships of this taxon that, presently, must still be considered an aberrant sauropterygian (5).

The second specimen of *Atopodentatus* at our disposal, IVPP V20292, is the only one that displays the skull in ventral view. The transversely oriented premaxillae have separated from one another. The spatulate teeth are preserved in situ on the right premaxilla; tooth attachment is pleurodont, and in some positions, at least two teeth are ankylosed to each dental groove, thereby forming a rudimentary battery of teeth slightly reminiscent of a hadrosaur jaw. No teeth are preserved on the left premaxilla. At its anterior end, the dentary forms a medial transverse process that engages in the formation of the symphysis and a lateral transverse process to match the width of the premaxilla. Exposed in ventromedial and ventrolateral view, respectively, an extensive and deep splenial is also exposed in the right mandible, whereas prominent surangular and angular are apparent in the left mandible. Between the mandibles, the right side of the dermal palate is exposed, with the posterior end of the left pterygoid emerging from below the left mandible. The pear-shaped internal naris is located in an anterolateral position, with its narrow anterior margin lying slightly behind the anterior margin of the external naris. The broad posterior margin of the external naris is formed by the anterior margin of the palatine. Medial to the right internal naris, there seem to be paired elements that might represent the vomers, separating the internal nares from one another (the left one concealed by the left mandible).

The dermal palate is extensively developed, mainly through a conspicuous enlargement of the pterygoids, which form broad and elongate, plate-like elements obliterating the interpterygoid vacuity and underlying much of the base of the braincase. From the posteromedial margin of the left pterygoid, protruding from below the left mandible, projects a bulbous flange that seems to form the pterygoid notch that in turn would have received the basiptyergoid process. If our interpretation is correct, it would imply that the palatobasal articulation was not fused, in spite of the development of a closed dermal palate. Behind the right internal naris lies the palatine, a relatively slender but elongate element,

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extending back alongside the pterygoid. Both the pterygoid and the palatine are covered by a densely set shagreen of minute denticles. Near the posterolateral corner of the right pterygoid, the ectopterygoid embraces the posterior end of the palatine. The posterior end of the ectopterygoid is partially concealed by matrix. The paired hyoids are conspicuous rod-like elements: the left one overlying the left pterygoid and the right one lying just behind what we consider to be the right ectopterygoid.

Behind the skull, and oriented at a sharp angle relative to the long axis of the skull, lies a string of four cervical vertebrae and associated cervical ribs. The anterior-most of these cervical vertebrae displays a broad, crescent-shaped neural spine, indicating that it represents the axis. The atlas centrum is preserved right in front of it, apparently without any cervical ribs in association with it. The right cervical ribs associated with the axis and the succeeding cervicals overlap and thus obscure both the posterior margin of the dermal palate and the contact of the pterygoids with the quadrate.



Fig. 1. Prepared skulls referred to the Middle Triassic marine reptile *A. unicus*. (A) IVPP V20291 exposed in dorsal view. (B) IVPP V20292 exposed in ventral view. Scale bar, 2.0 cm. [Photo Credit: W. Gao, Institute of Vertebrate Paleontology and Paleoanthropology]

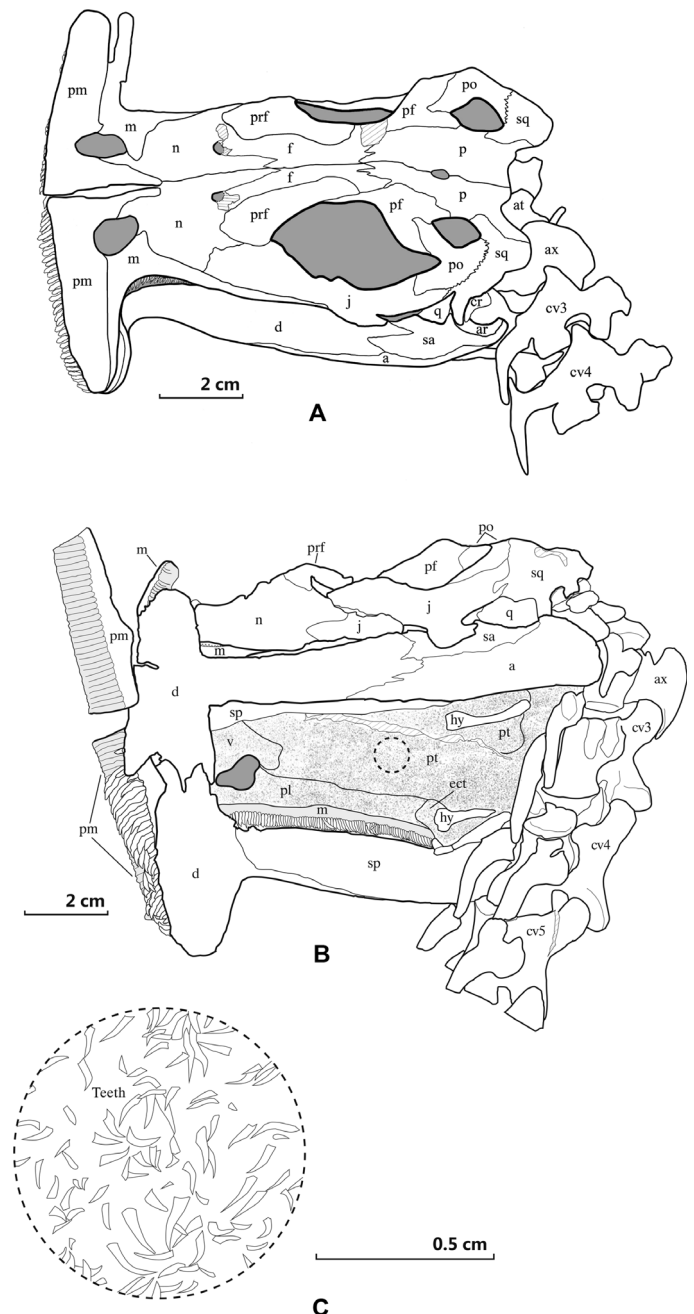


Fig. 2. Interpretative drawings of the skulls of *A. unicus*. (A) IVPP V20291 in dorsal view. (B) IVPP V20292 in ventral view, with detail of the shagreen of palatal teeth highlighted. a, angular; ar, articular; at, atlas; ax, axis; cr, cervical rib; cv, cervical vertebra; d, dentary; ect, ectopterygoid; f, frontal; hy, hyoid; in, internal naris; j, jugal; mx, maxilla; n, nasal; p, parietal; pal, palatine; pf, post-frontal; pm, premaxilla; po, postorbital; prf, prefrontal; pt, pterygoid; q, quadrate; sa, surangular; sp, splenial; sq, squamosal; v, vomer. [Illustration: X. Guo, Institute of Vertebrate Paleontology and Paleoanthropology]



Fig. 3. Artist's restoration of *A. unicus* depicting it as a herbivore grazing on marine plants growing on a hard substrate in the eastern Tethyan Sea during Middle Triassic times. Using batteries of spatulate teeth lining the hammerhead expansions of both the upper and lower jaws, it would have been able to scrape off numerous pieces of plant matter into suspension in the water. This could then be sucked in and filtered by the long, thin, and closely packed needle-shaped teeth lining the main jaw rami. [Illustration: Y. Chen, Institute of Vertebrate Paleontology and Paleoanthropology]

With the new specimens on hand, closer examination of the holotype WIGM SPC V1107 shows that, in essence, the dentary is of a pronounced T shape [Fig. 2, A and B, of (5)]. In addition to the lateral process, the dentary also turns sharply inward to form the symphysis with its counterpart. The teeth on the dentary appear to have been arranged in a single row, extending from the symphysis along the entire anterior edge of the bone to the extremity of the lateral process before flexing back along the posterior margin of the process and then extending posteriorly along the main anteroposterior axis of the skull. As a consequence, the dentary has a double row of teeth on the lateral hammerhead process as can be seen in the holotype. The teeth on the maxilla extend as a single row along the entire lateral process and then turn sharply backward. The portion of the maxillary tooth row on the hammerhead process thus occluded between the two dentary tooth rows on the counterpart process.

We reconstruct the premaxillae as overhanging the dentary, with the combined rows of teeth on both sides forming a single raking “comb.” From this very peculiar tooth arrangement and jaw structure, we infer that *Atopodentatus* used the premaxillary teeth to scrape soft plant material (algae) off the substrate underwater (Fig. 3). Subsequent rapid opening of the broad mouth would have created a significant suction force, drawing the watery mix into the buccal cavity. On closing the mouth, the tongue, supported by the hyoid skeleton, was involved in forcing water out through the mesh formed by the maxillary and dentary teeth, thereby filtering out plant matter. It could be argued that

Atopodentatus filtered small invertebrates in suspension, but such a feeding mode would not explain the peculiar morphology and arrangement of the premaxillary teeth.

DISCUSSION

Herbivory in marine reptiles is exceptional, yet herbivory evolved a second time, during the Triassic recovery phase, in the unrelated placodont *Henodus* from the Gipskeuper of Tübingen (Carnian, Upper Triassic) (6). *Henodus* is only known from a marginal marine environment. The skull of *Henodus* lacks the remarkable hammerhead (7), but it is still flattened and square in outline with a broad and straight transversely oriented rostrum formed by the premaxillae. The ventral margin of the overhanging premaxillary edge is furnished with a palisade of spatulate denticles (8), interpreted to have had a plant-scraping function. The broad flat skull again identifies *Henodus* as an efficient suction feeder that filtered the plant material thus acquired, not through teeth, but possibly by baleen-like structures (9, 10). Both *Atopodentatus* and *Henodus* lack the morphological characteristics that are otherwise functionally correlated with true suspension feeding (11). This early convergence in herbivory in *Atopodentatus* and *Henodus* is remarkable because no other case of herbivorous adaptation has been recorded for marine reptiles for the rest of the Mesozoic, with the possible exception of some Late Cretaceous marine turtles. The sauropod dinosaur *Nigersaurus* (12) sports a similar, rather spatulate and very blunt snout bearing transversely orientated rows of teeth, but it lacked the array of intermeshing teeth in the main quadrant of each jaw. In *Nigersaurus*, wear facets on the peg-like teeth indicate their use for cropping soft vegetation close to the ground, possibly in a riparian environment (12).

In addition to *Sphyrna*, the extant hammerhead shark, a number of vertebrates have evolved a hammerhead-shaped skull. The freshwater *Diplocaulus* from the Permian and the Triassic *Gerrothorax* have similar lateral extensions on the rostrum, albeit more boomerang-shaped. The function of the rostral modification in these forms varies: In *Diplocaulus*, for instance, it likely served a hydrodynamic function, providing lift to the head, whereas in *Sphyrna*, with its eyes at the ends of the extensions and with an array of electroreceptors, it also provides an increased sensory function. *Atopodentatus* is unique in having a hammerhead adaptation for underwater grazing.

Atopodentatus is the earliest marine reptile to have evolved herbivory. Convergence in *Henodus* shows that herbivory evolved in the photic zone of near-shore shallow water habitats. The predator-prey pyramid reestablished quickly after the end-Permian extinction (2, 3). Herbivory adds a new dimension to the diversity of feeding styles reported for the recovery of the marine biota. This documentation is coeval with the first occurrence of a macropredatory ichthyosaur (4), serving to underscore the concept that a complete restitution of trophic networks had occurred by the Anisian.

MATERIALS AND METHODS

Two new specimens of Middle Triassic (Anisian) tetrapods were collected from outcrops of the Guanling Formation in Luoping County, Yunnan Province. They were prepared mechanically using air scribes together with fine needles and pin vises at the IVPP preparation laboratories at Xiaotangshan, Beijing. They were examined under an Olympus

SZX7 binocular microscope and photographed using a Pentax 645D camera with a 120-mm fixed focus lens under fiber-optic lights. Drawings were made using a camera lucida.

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