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SHORT COMMUNICATION

A new marine reptile from the Triassic of China, with a highly specialized feeding adaptation

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Abstract The Luoping fauna (Anisian, Middle Triassic) is probably the oldest of Triassic faunas in Guizhou–Yunnan area, China. The reptilian assemblage is comprised of ichthyosaurs, a number of sauropterygians (pachypleurosaur-like forms), saurosphargids, protorosaurs, and archosauriforms. Here, we report on a peculiar reptile, newly found in this fauna. Its dentition is fence or comb-like and bears more than 175 pleurodont teeth in each ramus of the upper and lower jaws, tooth crown is needle-like distally and blade-shaped proximally; its rostrum strongly bends downward and the anterior end of its mandible expands both dorsally and ventrally to form a shovel-headed structure; and its ungual phalanges are hoof-shaped. The specializations of the jaws and dentition indicate that the reptile may have been adapted to a way of bottom-filter feeding in water. It is obvious that such delicate teeth are not strong enough to catch prey, but were probably used as a barrier to filter microorganisms or benthic invertebrates such as sea worms. These were collected by the specialized jaws, which may have functioned as a shovel or pushdozer (the mandible) and a grasper or scratcher (the rostrum). Our preliminary analysis suggests that the new reptile might be more closely related to the Sauropterygia than to other marine reptiles.

Keywords Diapsida · Bottom-filter feeding · Middle Triassic · Yunnan · China

Introduction

The exceptionally preserved Luoping fauna, recently discovered in the east-most Yunnan Province of China, is mainly comprised of a mixture of marine animals, including arthropods (crustaceans, millipedes and limulids), fishes, reptiles, bivalves, gastropods, belemnoids, ammonoids, echinoderms, brachiopods, conodonts, and foraminifers (Hu et al. 2011). It is one of the best-preserved Triassic marine fossil treasures known in the world and has been considered to be coeval in age with the Panxian fauna, about 90 km northeast, in southwest-most Guizhou Province of China on the basis of the *Nicoraella kockeli* Zone of conodonts (Hao et al. 2006; Zhang et al. 2009; Hu et al. 2011; also see Fig. S1.1 in Electronic Supplementary Material (ESM)). As for vertebrate assemblages, especially the reptilian members in Luoping or Panxian fauna, it is comparable to that known in Europe (such as in Monte san Giorgio) but much more diverse than that in North America (such as in Nevada), including ichthyosaurs (Jiang et al. 2009; Hu et al. 2011), pachypleurosaur-like forms (Jiang et al. 2009; Liu et al. 2011; Wu et al. 2011; Shang et al. 2011), saurosphargids (Li et al. 2011, 2013), archosauriforms (Li et al. 2006; Hu et al. 2011), protorosaurs (Li et al. 2004; Hu et al. 2011), nothosaurs (Jiang et al. 2009), and placodonts

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(Jiang et al. 2009); the latter two groups have not been reported yet in the Luoping fauna. The faunal diversity is also reflected by the variety of feeding mechanisms evolved among those reptilian groups. As suggested by tooth morphology, adult mixosaur ichthyosaurs and placodonts were durophagous, eosauropterygians (nothosaurs and some pachypleurosaur-like forms) were pincering carnivores (with fang-like and conical teeth), while some other pachypleurosaur-like forms such as *Wumengosaurus* (Wu et al. 2011) were definitely different in diet (with coarse denticles on the margin of the delicate crowns), dinocephalosaur protorosaurs were sucking-pincering animal (with fang-like and conical teeth), saurosphargids might be omnivorous (with a large tooth crown labially convex and lingually concave), and archosauriforms were vicious predators (with dagger-like teeth). As implied in Hu et al. (2011), further excavation and research would expand the biodiversity, stratigraphic presence, and paleogeographic distribution of the Luoping (or Panxian) fauna after the end-Permian mass extinction. A new marine reptile, *Atopodentatus unicus* gen. et sp. nov. that was most recently discovered in the Luoping fauna shows an unusual morphology incomparable to that of any known reptile. We provide here a brief description, functional speculation on its feeding habits, and a preliminary analysis of its phylogeny.

Description of specimen

Taxonomy

Diapsida Osborn 1903
Atopodentatus unicus gen. et sp. nov.

Etymology

Generic name is derived from the Latin *Atopo-* for the peculiar dentition and *dentatus* for teeth; the specific name is derived from the Latin *unicus* for its unique morphology.

Holotype

Wuhan Institute of Geology and Mineral Recourses (WIGM) SPC V 1107, a nearly complete skeleton with the left lateral side of the skull poorly preserved.

Locality and horizon

It is found near Daaozi (Dawazi) village, Luoping County, Yunnan, China; Guanling Formation (Member II), Middle Triassic (Anisian).

Diagnosis

A medium-sized marine reptile differing from all other diapsid reptiles in the following combination of derived characters: high and laterally compressed skull small, about 1/23 of total body length, which is 275 cm; pleurodont dentition fence- or comb-like, consisting of more than 175 and 190 delicate teeth in each ramus of upper and lower jaws, respectively; tooth crown needle-like distally and blade-like basally; maxilla and premaxilla forming a vertical rostrum; prefrontal–postfrontal contact excluding frontal from orbit; postfrontal entering supratemporal fenestra; ventrally opening infratemporal fenestra small; massive mandible with a shovel-headed anterior end; coronoid process considerably posterior in position, approaching jaw joint; stout retroarticular process with a deep fossa dorsally; 36 presacral, two sacral, and 47 caudal vertebrae; margins of flat scapula strongly convex anteriorly and very concave posteriorly; clavicle with a well-developed posterolateral process; flat coracoid oval in outline, with a curved ridge at anterior centre; ischium deeply notched anteriorly; humerus much larger than femur but manus smaller than pes; possibly two carpals and two tarsals; ungual phalanges hoof-shaped.

Description

A. unicus is a diapsid, although its supratemporal fenestra (STF) and infratemporal fenestra are rather small (Fig. 1). It is most probably an aquatic or a semi-aquatic animal judging from its tight sacro-pelvic connection (see below) that are clearly different from those of obligatorily aquatic sauropterygians such as nothosaurs (Rieppel 2000) or pachypleurosaur-like forms (Shang 2011; Wu et al. 2011). *A. unicus* is characterized mainly by a vertical rostrum (VR), a shovel-headed anterior end of the mandible (SHAEM), and a fence-like dentition (FLD) (Figs. 1b, c and 2a, b). The VR is formed by the strongly downward bending of the premaxilla and maxilla, and is proportionally large (minimally 4.5 cm in depth) relative to the 12-cm-long skull. It lies posteroventrally against the SHAEM when jaws are occluded or semi-closed and narrows into a blunt end distally. In anterior view, the VR shows a very narrow profile and the two premaxillae do not meet each other along most of their heights. In other words, there is a vertical gap between them in anterior view. The presence of the gap is also indicated by the articular facet for the opposite premaxilla, which occupies only on the dorsal portion of the medial side (Fig. 2d–f; also see Fig. S1.1 in ESM). The teeth of both premaxillae are implanted perpendicular to the medial edge (dental margin) and therefore point medially to fence the vertically oriented midline gap in front of the SHAEM in life (Fig. 2g).

The SHAEM is formed by the dorsal and ventral extensions of the anterior end of the dentary and is mainly vertical in orientation (Fig. 2a, b). The lateral surface of the SHAEM is broad and slightly concave and faces more laterally than

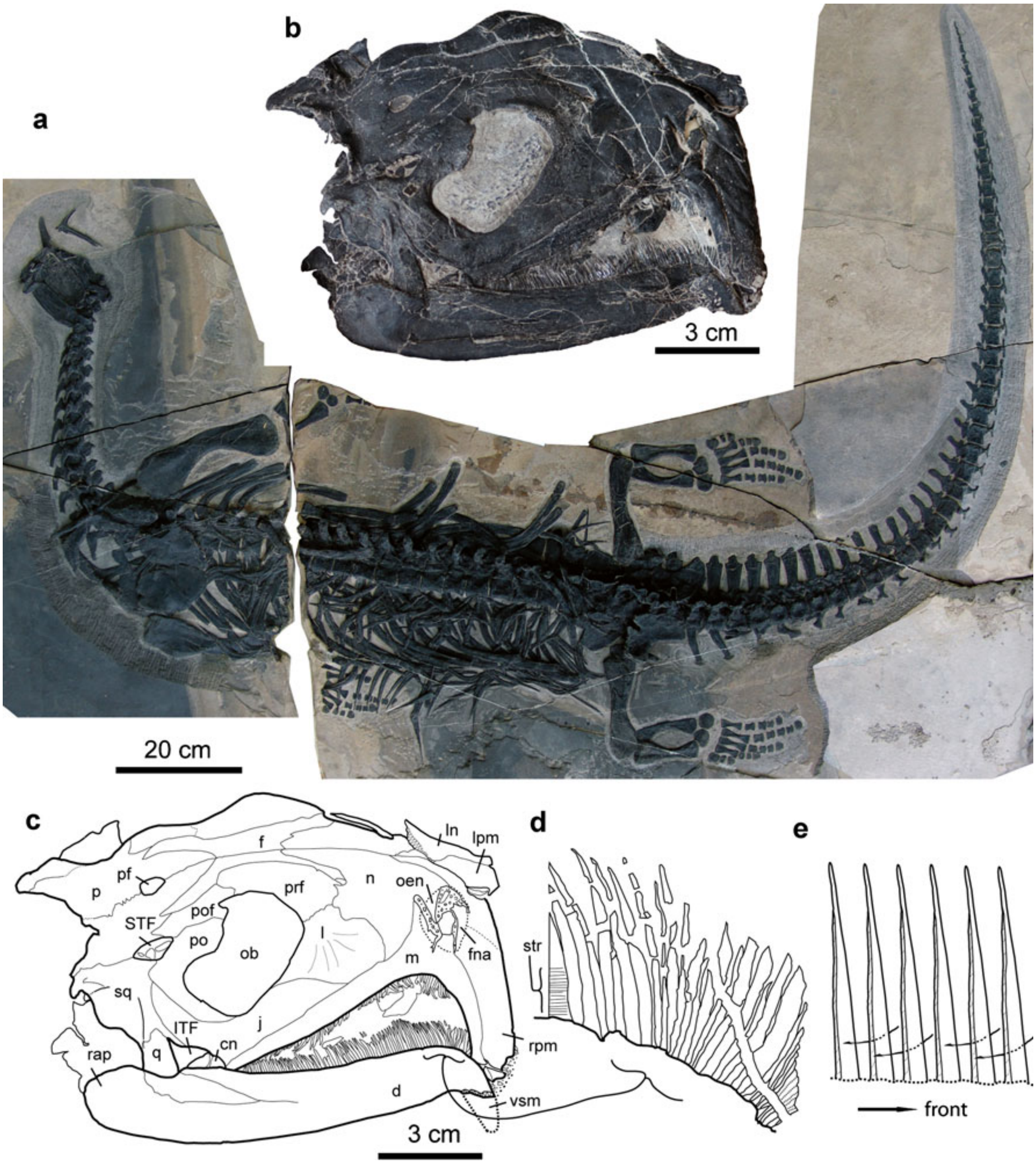

Fig. 1 Skeleton of *A. unicus* gen. et sp. nov. (the holotype, WIGM SPC V 1107). **a** Whole skeleton in left lateral and ventrolateral (trunk) views. **b**, **c** Skull in right lateral view. **d** A close-up of the anterior teeth of the horizontal portion of the mandibular dentition (the needle-shaped tips of the anterior-most teeth were missing). **e** A schematic outline drawing indicating the way of tooth implantation and the directions of water currents from the mouth in posterolateral view, *dotted line* along the base of the teeth indicating the spaces between teeth are purposely widened (the teeth are originally overlap each other in lateral view). Abbreviations: *cn*, coronoid; *d*, dentary; *f*, frontal; *fna*, fossa around the external naris; *ITF*; infratemporal fenestra; *j*, jugal; *l*, lacrimal; *ln*, left nasal; *lpm*, left premaxilla; maxilla; *n*, nasal; *ob*, orbit; *oen*, opening of the external naris; *p*, parietal; *pf*, parietal foramen; *po*, postorbital; *pof*, postfrontal; *prf*, prefrontal; *q*, quadrate; *rap*, retroarticular process; *rpm*, right premaxilla; *sq*, squamosal; *STF*, supratemporal fenestra; *str*, fine striations; *vsm*, ventral portion of shovel-headed anterior end of mandible. [planned for page width]

anteriorly, which was probably exaggerated by preservation. With no flattening, the lateral surface would have been narrower but more concave and therefore faced more anteriorly than laterally in life. In other words, the mandible would have been more shovel-like in lateral view.

There are at least 35 small needle-like teeth in the premaxilla, about 140 small needle-like teeth in the maxilla (at least 100 in the horizontal portion and around 35 in the vertical portion), and more than 190 teeth in the dentary (about 100 in the horizontal portion and 90 in the shovel-headed anterior

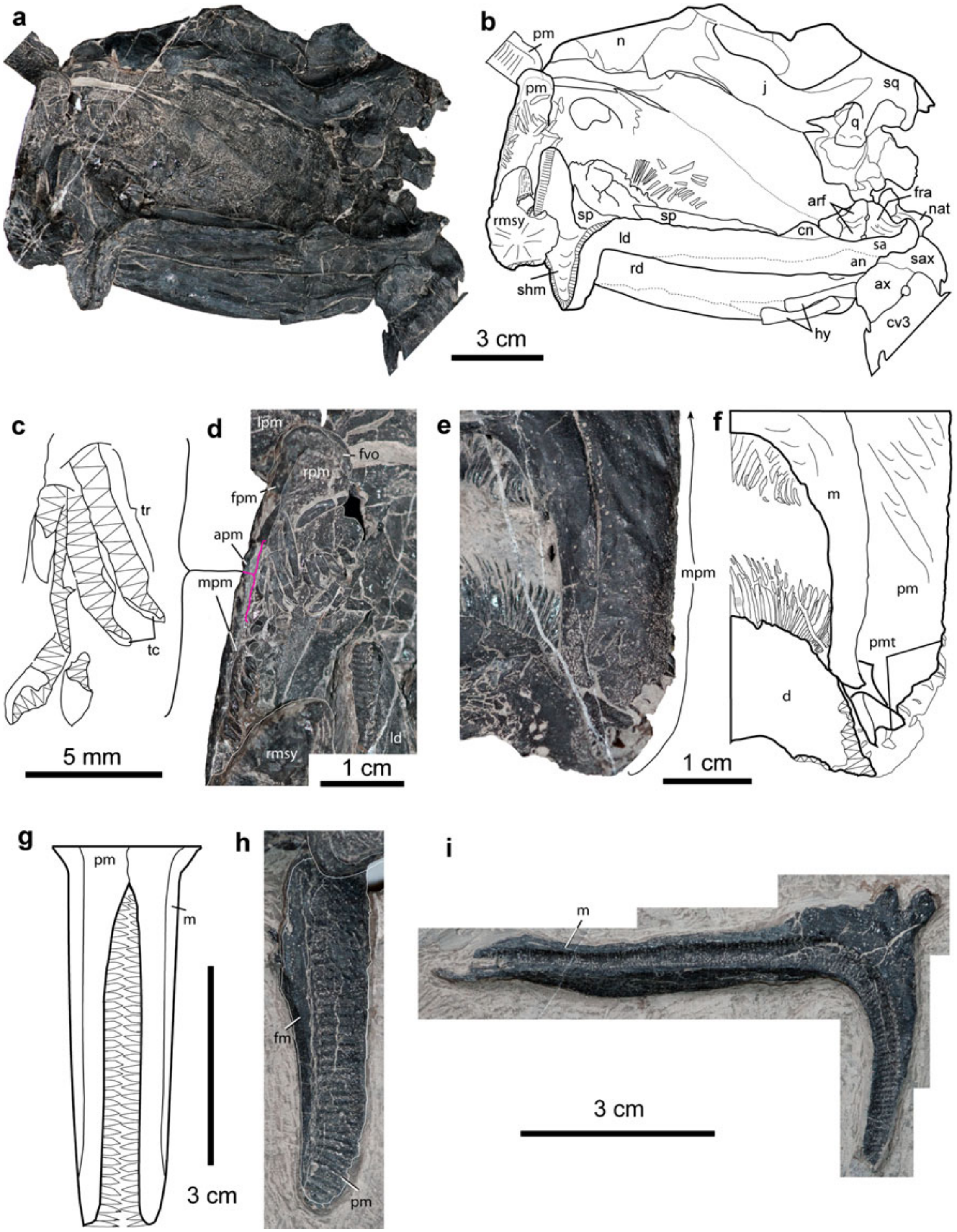

Fig. 2 Skull with the mandible and the dentition of *A. unicus* gen. et sp. nov. (the holotype, WIGM SPC V 1107). **a**, **b** Skull and mandible in left lateral view. **c** A close-up of some premaxillary teeth, showing a short crown. **d** Right premaxilla in lingual view, indicating the thinned medial (dental) margin of the rostral portion, with a limited facet on the dorsal portion for the left element. **e**, **f** A close-up of the rostrum with the incomplete shovel-headed anterior end of the right ramus of the mandible in lateral view, showing some teeth pointing medially. **g** A schematic outline drawing, showing the vertical rostrum with dentition in anterior view. **h** Rostral portion of the left premaxilla in lingual view. **i** Left maxilla in lingual view. Abbreviations as in Fig. 1 plus *an*, angular; *arf*, articular fossa; *apm*, anterior side of premaxilla; *ax*, axis; *cv*, cervical vertebra; *fm*, facet for maxilla; *fpm*, facet for the left premaxilla; *frar*, fossa on the retroarticular process; *fvo*, facet for vomer; *hy*, hyoid; *ld*, left dentary; *mpm*, medial (dental) margin of premaxilla, with no facet for counterpart; *nat*, neural arch of atlas; *pm*, premaxilla; *pmt*, premaxillary teeth; *rd*, right dentary; *rpm*, right premaxilla; *rmsy*, right mandibular symphysis (not complete); *sa*, surangular; *sax*, spine of axis; *shm*, shovel-headed anterior end of mandible; *sp*, splenial; *tc*, premaxillary tooth crown; *tr*, premaxillary tooth root. [planned for page width]

end). The teeth are covered by a layer of enamel (see Fig. S1.2 for more details in ESM). They are extremely slender and closely implanted. As indicated by the detached left premaxilla and the SHAEM in which all teeth were missing, those teeth may have been shaded easily. Tooth crowns are compressed and bladed basally, and taper to needle-like points apically. The tallest tooth crowns approaches 10 mm in height. Their blade-shaped bases are, however, less than 1 mm broad, which is about 1/10 of their height. The very pointed distal tip of all tooth crowns is thinner than the thickness of the basal cross section (Fig. 1e). As exposed, the tallest tooth crowns of the dentary are twice to three times as tall as those in the horizontal part of the upper jaw, and the tooth crowns in the VR and SHAEM are the shortest (Fig. 2c–f). The premaxillary teeth are thickest, with a density of 7.5 teeth per cm, while more slender teeth are packed in the dentary and maxilla with densities between 12.5 and 15 teeth in 1 cm (Fig. 2h, i; also see Fig. S1.1c, d in ESM). In lateral view, the proximal portions of the dentary tooth crowns bear fine striations vertical to the tooth long axis and overlap each other such that the anterior teeth overlap the posterior ones (Fig. 1d; also see Fig. S1.2 in ESM). We do not know whether such an overlapping pattern and those striations also applied to the upper dentition, owing to poor preservation. We think that the teeth were separate from each other in posterolateral view in life. As suggested by the asymmetrical tooth sockets (see Fig. S1.1c, d in ESM), the compressed crown bases are diagonal to the long axis of the jaw and left a gap between them in life, as magnified in Fig. 1e where the arrows point in the direction of the inter-tooth water currents inferred during feeding.

The skull of *A. unicus* is about 12 cm long along the dorsal midline, which is proportionally small (about 1/23) relative to the animal's total length of 275 cm, relatively much smaller than that of the so called small-headed *Helveticosaurus zollingeri* (from the marine middle Triassic of Europe) in which this ratio is about 1/8 as indicated by the length of the complete right ramus (over 25 cm) of the mandible and the estimated total length (about 200 cm) of the holotype (Rieppel 1989). The skull is high and laterally compressed, judging from the laterally and slightly dorsally faced orbit and external naris. The antorbital region is much longer than the postorbital region. The anteriorly positioned external naris is poorly preserved; it is surrounded by a fossa and located near the anterodorsal margin of the latter. The elongated posterodorsal processes of the premaxillae extend caudally beyond the external naris as in *Diandongosaurus*, a sauropterygian (Shang et al. 2011). The nasal and lacrimal are relatively large compared with those of sauropterygians (Rieppel 2000). The prefrontal and postfrontal meet each other to exclude the frontal from the orbit. The postfrontal enters the STF. The jugal bears a small posterior process and its ascending process joins the formation of the supratemporal arcade posterodorsally (Figs. 1b, c and 2a, b). The squamosal does not extend ventrally to cover the whole quadrate. The mandible is massive and sutures between mandibular elements are obscured due to fusion. The modestly developed coronoid process is rather posteriorly located and close to the jaw joint. The stout retroarticular process is deeply excavated dorsally. The left splenial is broken and joins the formation of the mandibular symphysis anteriorly (Fig. 2a, b).

The vertebral column consists of 15 cervical, 21 dorsal, 2 sacral, and 47 caudal vertebrae. The identification of the sacrals is based on the shortness, stoutness, and distal expansion of the sacral ribs (Fig. 3e; also see Fig. S1.3 in ESM). The cervical ribs are three-headed, including an anterior process. The neural spines of most cervical and first 10 caudal vertebrae have a process from the dorsal margin (Fig. 3a, b). The chevrons articulate with the posteroventral surface of the caudal centra and direct posteroventrally but are horizontally oriented, showing a reversed T-shaped profile in those vertebrae after the 10th caudal vertebra (Fig. 1a), as in the middle and posterior caudals of *Placodus* (Jiang et al. 2008). The flat scapula is very convex anteriorly and strongly concave posteriorly (Fig. 3c). The flat coracoid is roughly oval in outline and has a ridge curving anteriorly at the anterior center in ventral view (Fig. 3d). A notch at the articular margin with the scapula represents the position of the coracoid foramen. The clavicle is characterized by a pronounced posterolateral process and laterally articulated with the anterolateral surface of the scapula. As indicated by articular facets, the two clavicles meet each other in front of the interclavicle (Fig. 3d). The latter is roughly triangular and lightly concave posteriorly. The ilium retains a moderately developed post-acetabular process (Fig. 3e). The incomplete pubis is flat. The similarly flat ischium is distinct in that its anterior margin is deeply notched. The humerus is longer (225 mm) than the femur (172 mm), while the manus is shorter than the pes, as indicated by the lengths of the longest metacarpal (41.5 mm) and metatarsal (49.6 mm). The humerus is strongly concave posteriorly; its deltopectoral crest is well-developed (Fig. 1a). The femoral shaft is nearly straight, with a pronounced fourth trochanter (Fig. 3g). The curved fibula (100.4 mm) is slightly shorter and thinner than the hourglass-shaped tibia (106 mm). Two tarsals are ossified and, as preserved, only two carpals were possibly ossified (Fig. 1a). The ungual phalanges are hoof-shaped in both the manus and pes (Fig. 3g–i), which is unique among the contemporaneous aquatic reptiles.

Discussion

Functional morphology

The most striking specializations of *A. unicus* are the FLD, the VR, and the SHAEM. Obviously, all of these are related to the feeding adaptation of the animal. As mentioned earlier, the

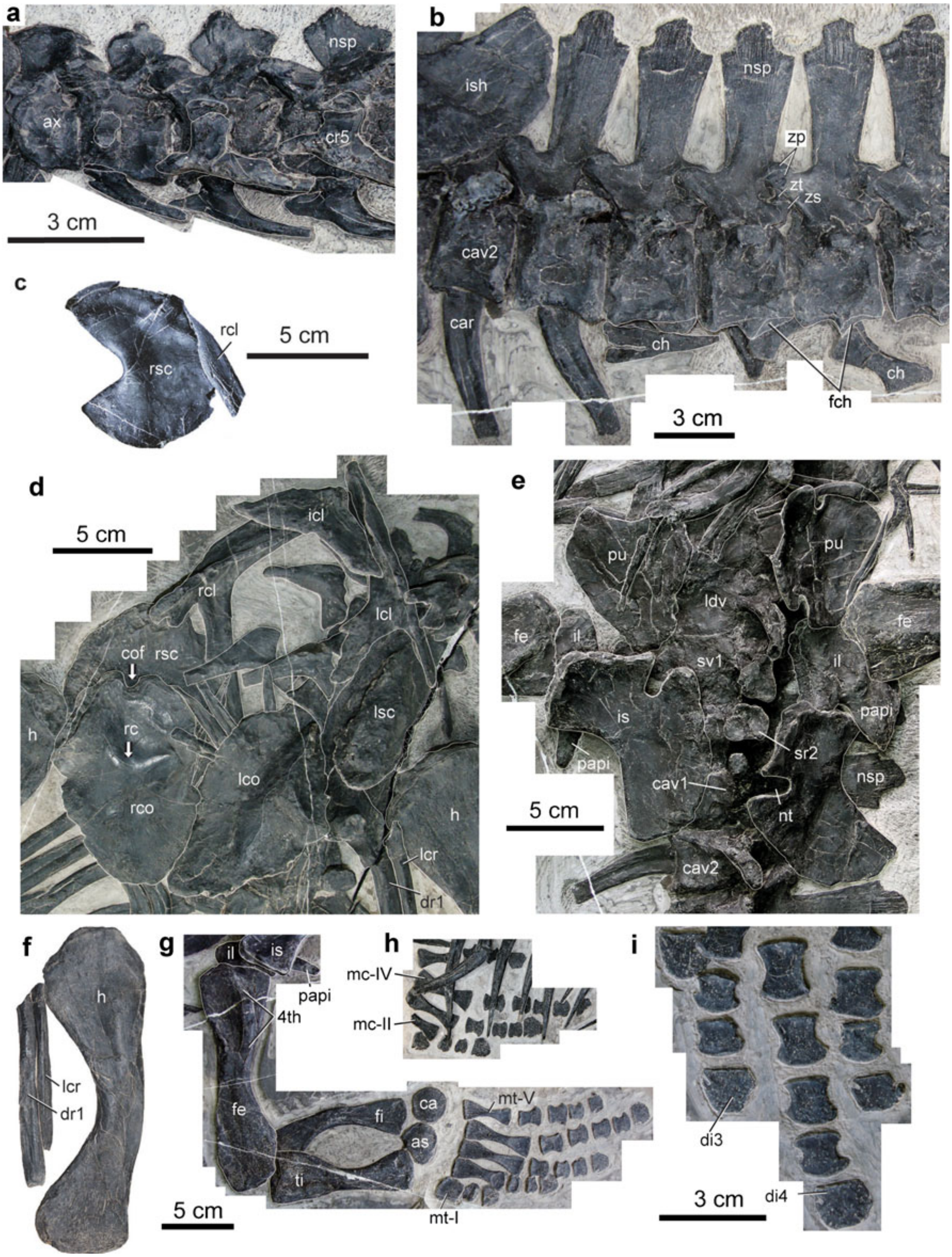

Fig. 3 Selected parts of the postcranial skeleton of *A. unicus* gen. et sp. nov. (the holotype, WIGM SPC V 1107). Note that the last dorsal rib is not expanded distally; it is thinner and much longer than the two sacral ribs. **a**, **b** Cervical vertebrae 2 to 5 and caudal vertebrae 1 to 6 in lateral view, respectively. **c** Right scapula in lateral view. **d**, **e** Pectoral and pelvic girdles in ventral view, respectively. **f** Left humerus in lateral view. **g** Right hindlimb in posteroventral view. **h** Right hand in ventral view. **i** A close-up of the distal portion of digits 3 to 5, showing hoof-like unguals. Abbreviations as in Fig. 1 plus *as*, astragalus; *ca*, calcaneum; *car*, caudal rib; *cav*, caudal vertebrae; *ch*, chevron; *cof*, coracoid foramen; *cr*, cervical rib; *di*, digit; *dr*, dorsal rib; *fch*, facet for chevron; *fe*, femur; *fi*, fibula; *h*, humerus; *icl*, interclavicle; *il*, ilium; *is*, ischium; *lcl*, left clavicle; *lco*, left coracoid; *lcr*, last cervical rib; *ldv*, last dorsal vertebra; *lsc*, left scapula; *mc*, metacarpal; *mt*, metatarsal; *nsp*, neural spine; *nt*, notch; *papi*, post-acetabular process of ilium; *pu*, pubis; *rc*, ridge of coracoid; *rcl*, right clavicle; *rco*, right coracoid; *rsc*, right scapula; *sr*, sacral rib; *sv*, sacral vertebra; *ti*, tibia; *zp*, zygapophyses; *zs*, zygosphene; *zt*, zygantrum; 4^{th}, the fourth trochanter. [planned for page width]

dentary teeth are tall and very delicate. To our knowledge, no fossil or living examples had/have such delicate teeth for biting. Filter-feeding pterosaurs in the Late Jurassic to Early Cretaceous had numerous delicate teeth (Wellnhofer 1978; Chiappe and Chinsamy 1996; Jouve 2004), of which the dentary teeth of *Ctenochasma* are most comparable in both size and shape but they were spatially implanted and did not overlap each other in lateral view. The Permian *Mesosaurus* also had numerous teeth and was once considered as a filter feeder (Carroll 1982). However, the elongate and needle-like tooth crowns of this mesosaur did not overlap each other and conspicuously procumbent anteriorly although the posterior teeth gradually become more vertically orientated (Modesto 2006).

As a whole, the VR is comparable to the beak-like rostrum of some rhynchosaurs (a group of Triassic land herbivores) such as *Rhynchosaurus* or *Hyperodapedon* (Benton 1990). It has been suggested that the beak-like rostrum of those rhynchosaurs may have had functioned in digging (Benton 1990). In contrast to the powerful beak-like rostrum mainly formed by the massive and stout incisors in the rhynchosaurs, the toothed VR of *A. unicus* is a lightly built structure that, paired with the toothed SHAEM, should have functioned very differently. On the other hand, the mandible of *A. unicus* is massive, especially relative to the delicate dentition, which indicates that a strong force should have been applied to it during feeding. It is unexpected that the adductor musculature of *A. unicus* was probably very small, as indicated by a small distance from the peak of the coronoid process to the jaw joint (even shorter than the length of the retroarticular process) as well as a narrow/short temporal region of the skull. Such a jaw-closing apparatus would not have been mechanically able to produce a strong force to the mandible (see Fig. S2.1 for details in ESM). On the contrary, the presence of a large and deep fossa on the dorsal surface of the modestly sized retroarticular process suggests a well-developed depressor muscle, *depressor mandibulae* in *A. unicus*; this muscle not only opens the jaws but also holds, with the adductor musculature, the mandible from moving backwards (Cong et al. 1988). It appears that all available evidence implies that the mandible may have been subjected to powerful longitudinal rather than vertical bite forces, which may have been produced by the mandible functioning as a shovel when the animal was foraging for food along the bottom of the water floor. Judging from the delicateness of the FLD, we think that *A. unicus* was most probably a bottom filter feeder, comparable, to a certain degree, to extant flamingos (Zweers et al. 1995) and some Mesozoic pterosaurs such as *Pterodaustro* and *Ctenochasma* (Wellnhofer 1978; Chiappe and Chinsamy 1996; Jouve 2004). As for *Mesosaurus*, a recent study (Modesto 2006) argued against the suggestion that this mesosaur used their conspicuous dental apparatus as a straining device for filter feeding. However, the short snout with a highly specialized rostrum and a stout mandible with a shovel-headed end suggest that *A. unicus* was certainly different in the way of catching food. Unlike flamingos, *A. unicus* could not bend its neck backward because its cervical vertebrae are morphologically similar to those of other marine retiles such as nothosaurs and pachypleurosaur-like forms. Both *Pterodaustro* and *Ctenochasma* have an extremely long snout and delicate jaws and have been considered as surface filter feeders (Wellnhofer 1978). *A. unicus* may have used its VR and SHAEM as a corresponding pair of shovel or pushdozer and grasper or scratcher functioning on the surface of the sea floor and may have more-or-less resembled bottom-feeding gray whales that consume benthic invertebrates filtered out from the muddy bottom of shallow waters (Fadeev 2005). As introduced earlier (see Hu et al. 2011), the rock that yielded the specimen of *A. unicus* is also rich in invertebrates and microorganisms. *A. unicus* may have foraged on the bottom of shallow water such as near shore areas or lagoons and turned the laterally compressed head on its side, and then used the mandible as a shovel or scoop to gather muddy deposits, the vertical rostrum as a collector to scratch or grasp the piles into the mouth, and the fence-like dentition as a barrier to sift and filter food as it crept forwards using its strong hoof-toed limbs. This kind of passive feeding may be also reflected by a small weak tongue, as suggested by a short hyoid, in *A. unicus* (Fig. 2a, b). It has been hypothesized that the extensive hyoid of *Rhynchosaurus* (over 40 % of the skull length) indicates a large powerful tongue that may have been used in manipulating food items (Benton 1990). The hyoid is short, about 20 % of the length of the small skull in *A. unicus*, which is also not comparable to those of the carnivorous *Qianosuchus* (44 %), a Triassic marine archosaur (Li et al. 2006), or *Miodentosaurus* (45 %), a Triassic thalattosaur (Wu et al. 2009). In addition, *A. unicus* is not, as a whole, proportional in appearance; it bears a small head but a massive body and strong limbs. As hypothesised for large sauropod dinosaurs (Colbert 1993), *A. unicus* may have had to spend most time to search food in life.

As mentioned earlier, *A. unicus* was aquatic or semi-aquatic and was, thus, capable of walking on land or tidal flats and sandy islands in the intertidal zone. It has been argued that the presence of a kinetic pelvis (the sacral ribs lose firm articulation with either the vertebral column or the pelvis) may be used to determine if an aquatic reptile is fully or semi-aquatic (Cheng et al. 2004; Ji et al. 2010). A kinetic pelvis was clearly absent in *A. unicus*, in that the two stout sacral ribs are structurally fused to the vertebral column and their distal ends are expanded for articulating the ilium (Fig. 3e), a situation similar to that seen in some semi-aquatic lizards, such as the extant *Amblyrhynchus* (USNM 65832 in the US National Museum of Natural History) that can walk on land. However, the similarly poor ossification of the carpus and tarsus as in some placodonts such as *Placodus* (Jiang et al. 2008) and

Psephoderma (Renesto and Tintori 1995) indicate that the limbs could have provided only a limited support to the body during walking on land. In addition, the hoof-toed manus and pes are not common in aquatic animals but morphologically comparable to those of *Psephoderma* in which the preserved unguals are discoid and wider than long (see Fig. 4 in Renesto and Tintori 1995). Thus, as suggested for *Psephoderma* (Renesto and Tintori 1995), *A. unicus* may also have had to spend most of its time in water in life although it may have been, as indicated by a solid sacro-pelvic complex, capable of walking in shallow water or even on land.

Phylogenetic analysis

Our preliminarily phylogenetic study, based on an existing data matrix (Li et al. 2013; also see S3 and S4 for details in ESM), indicates that *A. unicus*, together with the Eosauropterygia and Placodontia, forms a trichotomy within a clade, suggesting that it may have had a close relationship with the Sauropterygia (see Fig. S5.1 for details in ESM). However, a low bootstrap value implies that such a relationship is not strongly supported and may alter when a detailed study on its anatomy is available. It is noteworthy that the newly established Saurosphargidae (Li et al. 2011), Thalattosauria, and Ichthyopterygia are successively close in relationship to the Sauropterygia in this study, which is also the case in Li et al. (2013) and Neenan et al. (2013).

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