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New information on the dentition of *Chaohusaurus zhangjiawanensis* (Reptilia, Ichthyosauriformes) from the Early Triassic of Yuan'an, Hubei Province, China

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Abstract

Chaohusaurus is an early ichthyosauriform represented by three species known from the Early Triassic of Chaohu, Anhui Province, China, with a fourth species—*Chaohusaurus zhangjiawanensis*—known from the Nanzhang-Yuan'an region of Hubei Province. In contrast to the *Chaohusaurus* species from Chaohu, *Chaohusaurus zhangjiawanensis* remains poorly known, hindering our understanding of early ichthyosauriform evolution. Here, we report a new specimen of *Chaohusaurus zhangjiawanensis*, which provides new information on its dentition. The new specimen confirms that *Chaohusaurus zhangjiawanensis* had heterodont dentition consisting of pointed anterior teeth and robust, rounded posterior teeth, indicating a generalist diet. The posterior teeth of *Chaohusaurus zhangjiawanensis* are more robust (broader and larger) than the posterior dentition of *Chaohusaurus chaoxianensis* and *Chaohusaurus brevifemoralis* from Chaohu. This suggests differences in hard-shelled prey preference between species of *Chaohusaurus* from Chaohu and Nanzhang-Yuan'an, with *Chaohusaurus zhangjiawanensis* likely capable of feeding on harder and larger prey than *Chaohusaurus brevifemoralis* and *Chaohusaurus chaoxianensis*. In turn, this probably reflects differences in durophagous prey availability between the shallow-marine palaeoecosystem of Nanzhang-Yuan'an and the deeper, slope-basin palaeoecosystem of Chaohu. The posterior dentition and forefin of *Chaohusaurus zhangjiawanensis* are strikingly similar to those of *Chaohusaurus geishanensis*, the rarest species of *Chaohusaurus* from the Chaohu fauna. The scarcity of *Chaohusaurus geishanensis* in the Chaohu fauna, and its morphological similarity to *Chaohusaurus zhangjiawanensis*, possibly indicate that *Chaohusaurus geishanensis* was closely related with *Chaohusaurus zhangjiawanensis* and that it was also a shallow-marine species that was not a typical component of the Chaohu fauna. It probably occasionally wandered out into the deeper waters of Chaohu from a nearby coastal environment.

Keywords Ichthyosaur, Heterodont dentition, Feeding ecology, Nanzhang-yuan'an fauna, Chaohu fauna

Introduction

The Permo-Triassic Mass Extinction (PTME) was the most severe extinction event in the history of the Earth, occurring around 252 million years ago and causing the extinction of up to 90% of all marine species (Benton, 2015). Biotic recovery from the PTME began in its immediate aftermath in the Early Triassic and some reptile groups rapidly adapted to life in the marine environment as a result of the arising ecological opportunities (Cheng

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et al., 2019; Ezcurra & Butler, 2018; Qiao et al., 2022; Scheyer et al., 2014; Simões et al., 2022; Vermeij & Motani, 2018; Wolniewicz et al., 2023). Ichthyosauromorphs were a clade of diapsid reptiles that may have originated in the Early Triassic and achieved a high level of adaptation to life in the marine realm relatively quickly (Moon & Stubbs, 2020; Motani et al., 2015a, 2017; Nakajima et al., 2022; Sander et al., 2021; Ye et al., 2024; but see Kear et al., 2023). According to the recent phylogenetic analyses (Fang et al., 2024; Liu et al., 2024; Qiao et al., 2022), ichthyosauromorphs comprise the highly endemic Hupehsuchia, a group of edentulous, suspension feeding reptiles known only from the Early Triassic of Nanzhang-Yuan'an, Hubei Province, China (Carroll & Dong, 1991; Chen et al., 2014a, 2014b, 2014c, 2015; Cheng et al., 2019; Fang et al., 2023; Liu et al., 2024; Qiao et al., 2020, 2023; Wang, 1959; Wu et al., 2003, 2011; Young & Dong, 1972) and the geographically widespread Ichthyosauriformes. The latter include the durophagous Omphalosauridae (=Nasorostra) (Huang et al., 2020; Jiang et al., 2016; Motani et al., 2015a; Qiao et al., 2022; Sander & Faber, 2003), and a clade consisting of *Chaohusaurus* (Chen, 1985; Chen et al., 2013; Huang et al., 2019; Maisch, 2001; Motani, 1996; Motani & You, 1998a, 1998b; Motani et al., 2014, 2015b, 2015c, 2018; Yin et al., 2021; Young & Dong, 1972; Zhou et al., 2017) and the Ichthyopterygia ('true' ichthyosaurs) (McGowan & Motani, 2003; Motani, 2005). The earliest ichthyosauriforms are represented by several taxa known from the Early Triassic of South China, Thailand, Russia, Japan, Svalbard, and western North America (see Ye et al., 2024 for a recent review). However, the genus *Chaohusaurus* from South China is of particular importance for our understanding of the early evolution of ichthyosaurs because it is recovered as the sister-group to Ichthyopterygia and is known from abundant fossil material that has allowed palaeontologists to obtain a detailed understanding of its skeletal and soft tissue anatomy, swimming style, sexual dimorphism, and reproduction mode (Huang et al., 2019; Motani, 1996; Motani & You, 1998a, 1998b; Motani et al., 2014, 2018; Zhou et al., 2017). However, the diet of *Chaohusaurus* is still poorly known.

Chaohusaurus is represented by three species known from the Early Triassic of Chaohu, Anhui Province—*Ch. geishanensis* (type species) (Young & Dong, 1972), *Ch. chaoxianensis* (Chen, 1985; Motani et al., 2015c), and *Ch. brevifemoralis* (Huang et al., 2019; Motani et al., 2018; Yin et al., 2021; Zhou et al., 2017), and a single species—*Ch. Zhangjiawanensis*—from the Early Triassic of Nanzhang-Yuan'an, Hubei Province (Chen et al., 2013; Zhao et al., 2022; Zou et al., 2020). All currently known species of *Chaohusaurus* were generalist predators, as revealed by their conical and pointed anterior dentition and robust

and rounded posterior dentition (Gu et al., 2024; Huang et al., 2019; Maisch, 2001; Young & Dong, 1972; Zhao et al., 2022; Zhou et al., 2017). However, in contrast to the species of *Chaohusaurus* from the Chaohu fauna, which inhabited a deep-water (slope-basin) palaeoenvironment (Du et al., 2023; Feng et al., 1997; Qiao et al., 2022; Tong et al., 2003), *Ch. zhangjiawanensis* lived in a shallow-marine ecosystem (Chen et al., 2014a; Li & Liu, 2020; Wolniewicz et al., 2023; Yan et al., 2021) and possibly represents a very early step of aquatic adaptation in the lineage leading to ichthyosaurs (Motani & Vermeij, 2021). Therefore, a detailed understanding of its morphology, phylogenetic position and palaeoecology are crucial for understanding the origins and earliest evolution of ichthyosaurs. Nonetheless, even though *Ch. zhangjiawanensis* is known from a well-preserved holotype and three referred specimens, their anatomy has not been comprehensively described and figured in the literature (Chen et al., 2013; Zhao et al., 2022; Zou et al., 2020). Consequently, the phylogenetic position of *Ch. zhangjiawanensis* relative to other species of *Chaohusaurus* remains unresolved (Huang et al., 2019). Furthermore, the holotype and paratype specimens lack snouts and dentition (the presence of two blunt maxillary teeth was reported in the holotype, but they were not described in detail nor figured; Chen et al., 2013) and even though one of the referred specimens preserves the skull with dentition, it was not described and figured in great detail (Zhao et al., 2022). This hinders our understanding of the feeding ecology of *Ch. zhangjiawanensis*.

Here, we report a new specimen of *Ch. zhangjiawanensis* from the uppermost part of the third member of the Lower Triassic Jialingjiang Formation of Zhangjiawan quarry, Nanzhang-Yuan'an, Hubei Province, China (Fig. 1). The new specimen is described and figured in detail and its dentition is comprehensively compared with that of other species of *Chaohusaurus* in an aim to better understand the dietary diversity within the genus.

Institutional abbreviations

AGM (AGB) Anhui Geological Museum, Hefei, Anhui, China; GMPKU Geological Museum of Peking University, Beijing, China; HFUT Geological Museum of Hefei University of Technology, Hefei, Anhui, China; IVPP Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China; NGM Nanjing Geological Museum, Nanjing, Jiangsu, China; WGSC (WHGMR) Wuhan Centre of China Geological Survey (formerly Wuhan Institute of Geology and Mineral Resources), Wuhan, Hubei, China; YGM Yuan'an Geological Museum, Yichang, Hubei, China.

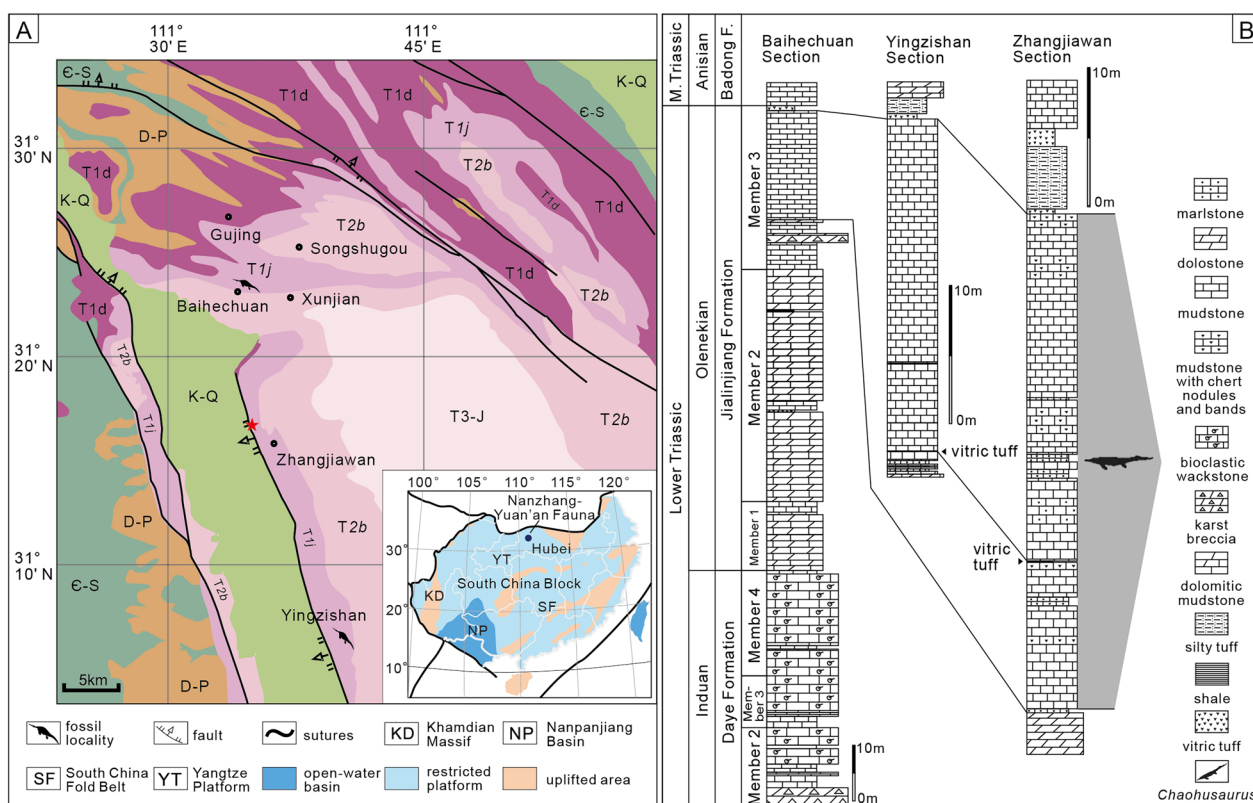


Fig. 1 Locality and horizon of the new *Chaohusaurus zhangjiawanensis* specimen HFUT YAV-10-08 (updated from Wolniewicz et al., 2023). **A** The geological map of the Nanzhang-Yuan'an region with Zhangjiawan quarry, the locality of HFUT YAV-10-08, marked with a red star; inset shows a paleogeographic map of the South China Block in the Triassic, with the location of the Nanzhang-Yuan'an fauna highlighted. **B** Stratigraphic column showing the horizon from which HFUT YAV-10-08 was collected. E-S, Cambrian-Silurian; D-P, Devonian-Permian; K-Q, Cretaceous-Quaternary; T1d, Daye Formation, Lower Triassic; T1j, Jialingjiang Formation, Lower Triassic; T2b, Badong Formation, Middle Triassic; T3-J, Upper Triassic-Jurassic

Materials and methods

The new specimen HFUT YAV-10-08 (Fig. 2) was collected from Zhangjiawan quarry, the type locality of *Ch. zhangjiawanensis* (Chen et al., 2013), in Yuan'an County, Hubei Province, China. The specimen was collected in 2008 when the quarry was still active for limestone mining. It is housed in the collections of the Geological Museum of Hefei University of Technology (HFUT), where it was prepared under a binocular microscope with pneumatic scribes. The specimen consists of the anterior part of the rostrum and associated dentition, impressions of the posterior part of the rostrum, including impressions of posterior maxillary and dentary teeth, a single preserved posterior maxillary tooth crown, and abraded fragments of indeterminate skull bones (Figs. 2, 3, 4, 5, 6 and 7). A mould of the specimen was made from silicone dental impression material to visualise the morphology of the bones and teeth from the preserved impressions (Fig. 5). Photographs of the specimen were made using a Nikon D720

camera with a macro lens and interpretative diagrams were drawn using Adobe Illustrator CS6 software.

Tooth measurements were taken to the nearest 0.01 mm using a Leica S9i trinocular microscope and LAMOS Engineer×64 software. The following tooth measurements were taken following Motani (1996) and Kelley et al. (2016): (1) exposed tooth height (distance from tip of crown to jaw margin); (2) proximal tooth width (mesio-distal width of the root at the jaw margin); (3) crown height (the distance between the crown-root interface and the tip of the crown) (the crown-root boundary in HFUT YAV-10-08 was determined on the basis of the extent of crown ornamentation and/or the position of a basal constriction; see Figs. 4, 6, 7); (4) crown width (the widest mesio-distal width of the crown); and (5) tooth spacing (the distance between the centers of two adjacent teeth). The following indices and ratios were calculated from the collected tooth measurements, following Motani (1996) and Kelley et al. (2016): (1) crown shape index (crown height

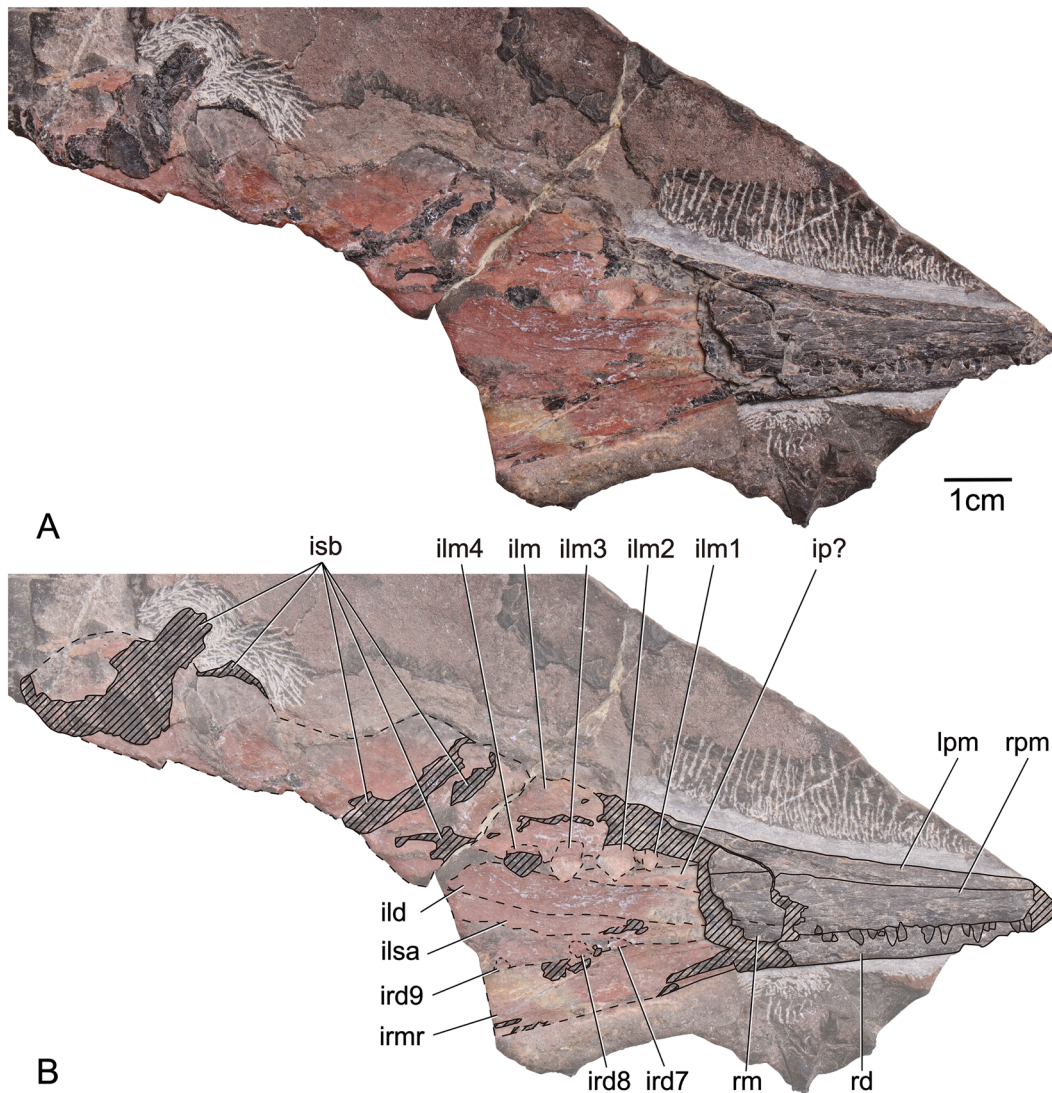


Fig. 2 A partial skull of *Chaohusaurus zhangjiawanensis* (HFUT YAV-10-08) (A) and interpretative diagram (B). ird7–9, impressions of right dentary teeth 7–9; ild, impression of left dentary; ilm, impression of left maxilla; ilsa, impression of left surangular; ilm1–4, impressions of left maxillary teeth 1–4; ip?, possible impression of palatal bone; irmr, impression of right mandibular ramus; isb, indeterminate skull bones; lpm, left premaxilla; rd, right dentary; rm, right maxilla; rpm, right premaxilla. Note that tooth numbers indicate their position in the preserved parts of the jaws from anterior to posterior direction, not their exact position along the tooth row. Dashed lines indicate inferred bone and tooth margins, hatching indicates broken bone surface

divided by crown basal width); (2) crown ratio (crown height divided by the exposed tooth height).

Systematic palaeontology

Reptilia Laurenti, 1768

Diapsida Osborn, 1903

Ichthyosauromorpha Motani et al., 2015a

Ichthyosauriformes Motani et al., 2015a

Chaohusaurus Young & Dong, 1972

Chaohusaurus zhangjiawanensis Chen et al., 2013

Diagnosis (modified after Chen et al., 2013; Zhao et al., 2022; Zou et al., 2020).

Small ichthyosauriform about 1 m in adult length; orbit large and with irregular anterodorsal margin formed by a lateral shelf of the prefrontal; postfrontal-prefrontal contact present; dentition heterodont, with slender and pointed anterior teeth and robust and rounded posterior teeth (revised character state); anterior tooth crowns ornamented with sparse apicobasal enamel ridges, posterior tooth crowns ornamented with

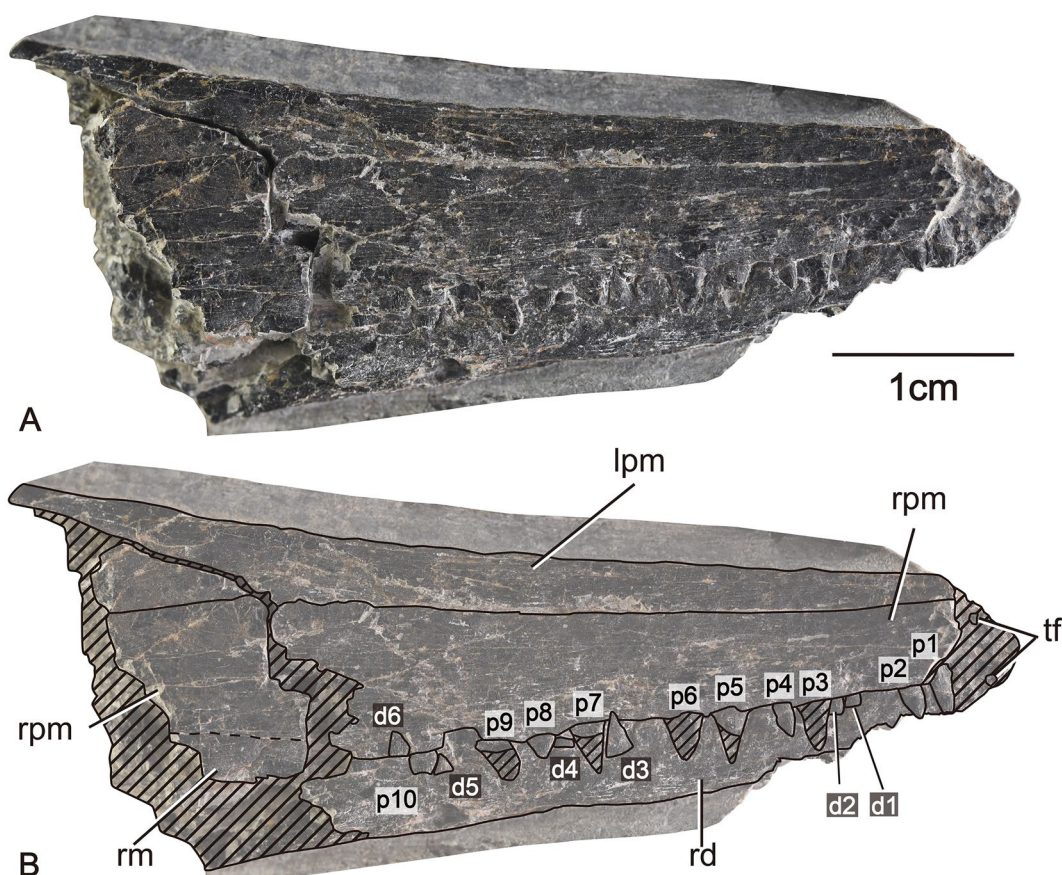


Fig. 3 Close-up of the anterior portion of the snout and associated dentition of a partial skull of *Chaohusaurus zhangjiawanensis* (HFUT YAV-10-08) (A) and interpretative diagram (B). d1–6, dentary teeth 1–6; lpm, left premaxilla; p1–10, premaxillary teeth 1–10; rd, right dentary; rm, right maxilla; rpm, right premaxilla; tf, tooth fragment. Note that tooth numbers indicate the position of the teeth in the preserved parts of the dentigerous bones from anterior to posterior direction, not their exact position along the tooth row. Dashed lines indicate inferred bone margins, hatching indicates broken bone or tooth surface

ridges forming an anastomosing pattern (revised character state); plicidentine present at least in posterior teeth (new character state); maxilla anterior process much longer than posterior process; two pairs of sacral ribs, with only the first pair being distally expanded and the second pair being similar to, but smaller, than the adjacent caudal ribs; caudal peak present; forelimb elements tightly packed; proximal carpals completely ossified; manual pisiform present; distal carpal I unossified/absent; intermedium pentagonal; dorsal process of femur well-developed.

Referred specimen

HFUT YAV-10-08, the anterior part of the snout with associated dentition, impressions of the posterior portions of the upper and lower jaws and posterior maxillary and dentary teeth, a single preserved posterior maxillary

tooth crown, and abraded fragments of indeterminate skull bones (Fig. 2).

Type horizon

Uppermost part of the third member of the Jialingjiang Formation, Olenekian (Spathian), Lower Triassic (see Wolniewicz et al., 2023 for a more detailed discussion of the stratigraphy).

Type locality

Zhangjiawan quarry, Yuan'an County, Hubei Province, China.

Description

Skull. The preserved length of the skull measures 146 mm and is comparable in size to an almost complete skull of *Ch. zhangjiawanensis* reported by Zhao et al. (2022), which measures 151.22 mm in length. The anterior part of the snout is exposed in right dorsolateral view (Fig. 2).

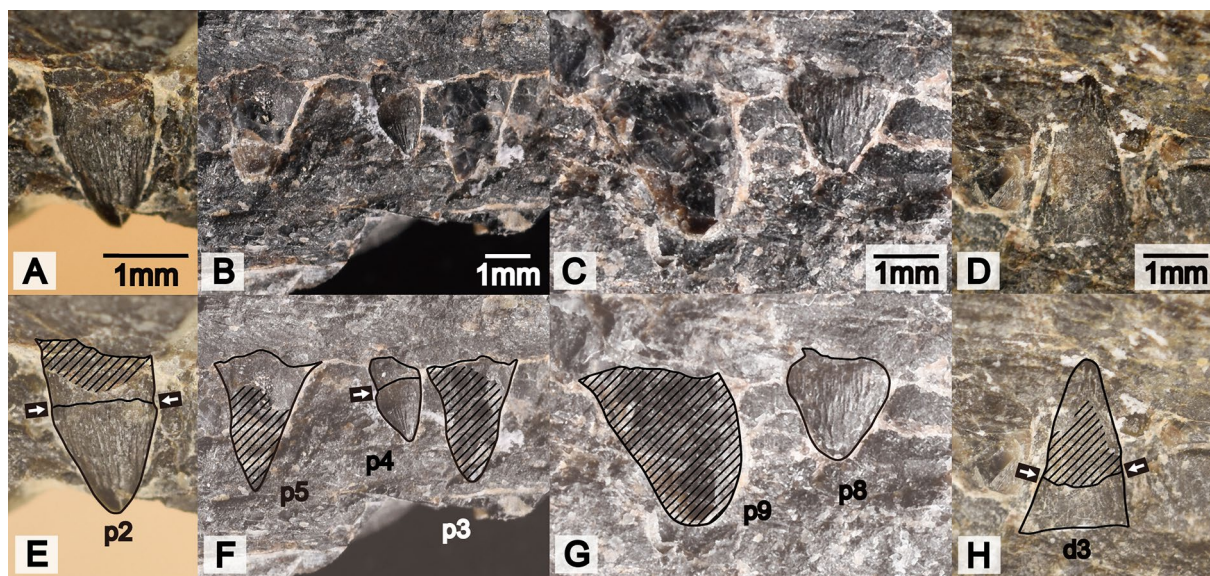


Fig. 4 Magnified views of premaxillary teeth p2 (A), p3–p5 (B), p8 and p9 (C), and a dentary tooth (d3) (D) of *Chaohusaurus zhangjiawanensis* (HFUT YAV-10-08) and corresponding interpretative diagrams (E–H) (see Fig. 2 for exact position of selected teeth within jaws). White arrows indicate the position of the crown-root boundary. Broken tooth surfaces are marked with hatching. p, premaxillary tooth; d, dentary tooth

The premaxillae are partially preserved, with their anterior tips as well as their posterior portions missing, but they are articulated and form a clearly visible inter-premaxillary suture. Only the anteriormost part of the right maxilla is preserved, whereas the left maxilla is heavily abraded, and the bone is preserved mostly as an impression in the rock matrix. The anterior portion of the right dentary is preserved in semi-occlusion with the right premaxilla. As revealed by surface striations and suture lines visible in the mould of the specimen, the posterior portions of the jaws are represented by the impressions of the left dentary and left surangular exposed in lateral view, and the right mandibular ramus exposed in medial view (Fig. 2 and 5). Several heavily abraded and indeterminate skull bone fragments are preserved in the posterodorsal part of the specimen.

Dentition—general morphology. The dentition of *Ch. zhangjiawanensis* is heterodont, as demonstrated by specimens HFUT YAV-10-08 (this work) and YGM-Y4701 (Zhao et al., 2022) (crushing posterior teeth were also reported in the holotype of *Ch. zhangjiawanensis*, but were only briefly described and were not figured; Chen et al., 2013). The anterior premaxillary and dentary teeth are conical and pointed, whereas the posterior maxillary and dentary teeth are robust and rounded (Figs. 3, 4, 5, 6 and 7). The morphological transition from conical to rounded teeth occurs in the anterior part of the maxilla, as seen in YGM-Y4701 (Zhao et al., 2022). This transitional region is also partially preserved in HFUT YAV-10-08, but the transitional teeth themselves

are not preserved. The mode of tooth implantation of the premaxillary teeth is not possible to determine with confidence. The maxillary teeth are set within alveoli (Fig. 6), like in *Ch. brevifemoralis*, but the presence of a shallow dental groove could not be confirmed (Gu et al., 2024). It is unknown whether an additional tooth row, like the one reported in *Ch. brevifemoralis* (Gu et al., 2024; Yin et al., 2021), was present lingually to the only exposed maxillary tooth row. Root impressions indicate the presence of deep, vertical grooves on root surfaces in the posterior dentition, which implies the presence of plicidentine (Maxwell et al., 2011). Selected measurements of the dentition are given in Table 1 and Supplementary Table 1.

Anterior (conical) dentition. The anterior teeth of HFUT YAV-10-08 include ten premaxillary teeth (p1–10) and six dentary teeth (d1–6) (Figs. 3 and 4). The teeth are conical and terminate in a pointed tip (e.g., tooth p2; Fig. 4A). The crown surfaces are ornamented with sparse apicobasal (longitudinal) ridges (e.g., teeth p2, p4, and p8; Fig. 4). The roots seem to lack grooves on their surfaces (e.g., teeth p3, p5, and d3; Fig. 4B, D). A slight constriction seems to be present at the crown-root boundary in some of the conical teeth (e.g., teeth p2 and p4; Fig. 4A, B).

Ten teeth form a single row in the right premaxilla and around five vacant tooth positions are visible among them—between teeth p2 and p3 (two vacant tooth positions), between p6 and p7 (two vacant positions) and between p9 and p10 (one vacant position) (Fig. 3). This indicates a total tooth count of 15 teeth for the preserved

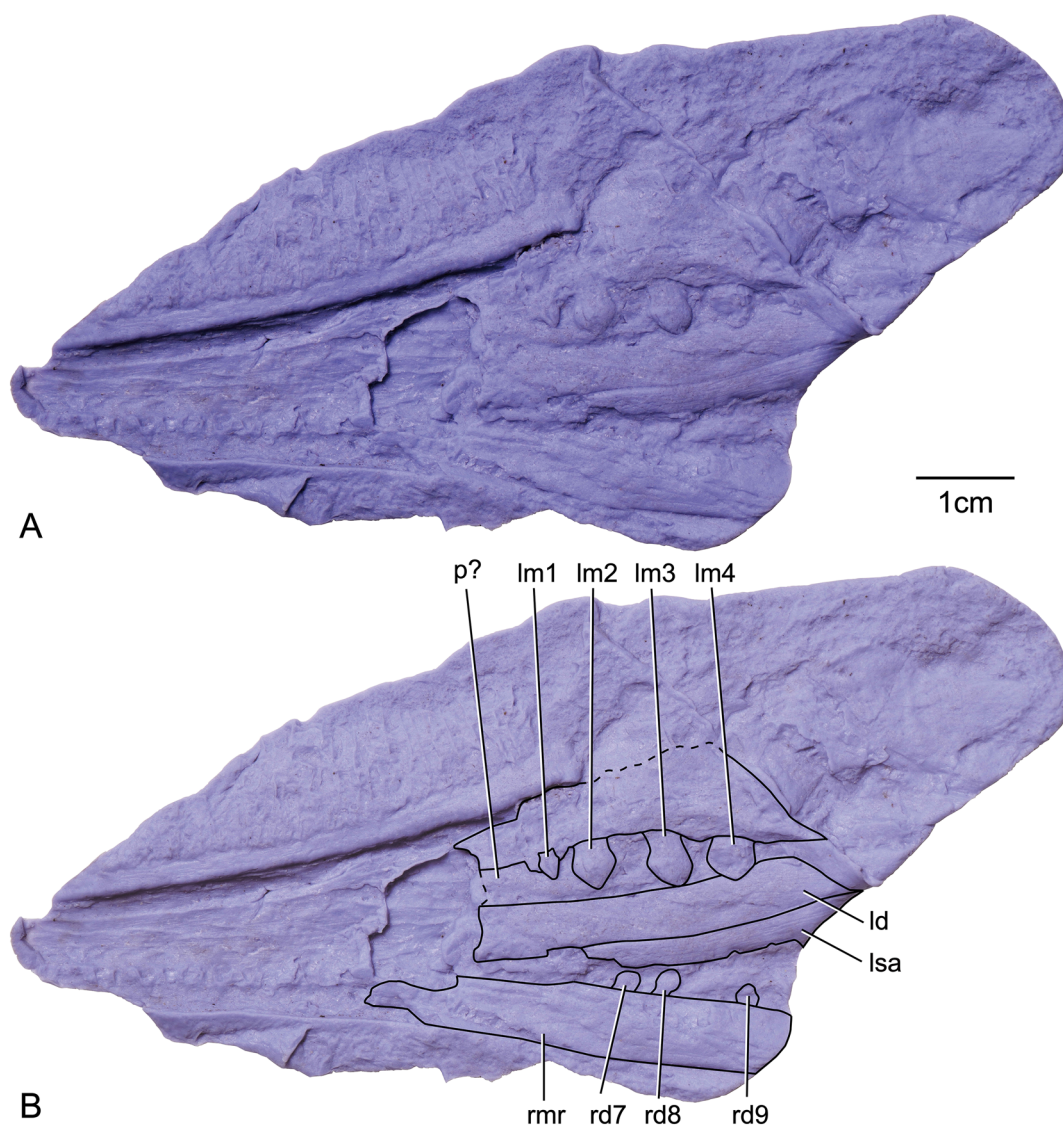


Fig. 5 Mould of the posterior part of the jaws and dentition of *Chaohusaurus zhangjiawanensis* (HFUT YAV-10-08) (A) and interpretative diagram (B). rd7–9, right dentary teeth 7–9; ld, left dentary; lsa, left surangular; lm1–4, left maxillary teeth 1–4; p?, possible palatal bone; rmr, right mandibular ramus. Note that tooth numbers indicate the position of the teeth in the preserved parts of the dentigerous bones from anterior to posterior direction, not their exact position along the tooth row

part of the right premaxilla. Tooth spacing ranges from 1.59 to 3.15 mm (full data available in Supplementary Table 1), but the maximum tooth spacing value of 3.15 mm (between teeth p4 and p5) is likely overestimated, since p4 represents a replacement tooth, which has not reached its maximum size (Fig. 4B, F). In general, tooth size increases posteriorly along the jaw length. Teeth p4 and p8 likely represent replacement teeth, because they are much smaller than the remaining premaxillary teeth. Even though some premaxillary teeth are abraded, details of tooth microanatomy (such as the morphology of the pulp cavity and the presence of infolded

dentine) are not preserved due to extensive damage (e.g., teeth p6 and p7, Fig. 3; teeth p3 and p9, Fig. 4). The right dentary preserves only six teeth; tooth d3 (Fig. 4D, H) is the best-preserved one. The anterior dentary teeth are only very partially exposed, but they share the same general morphology with the anterior premaxillary teeth, being slightly smaller in size (Fig. 3; Table 1).

Posterior dentition. The posterior teeth of HFUT YAV-10-08 are represented by impressions left by four left maxillary teeth (Figs. 5 and 6) and three left dentary teeth (Figs. 5 and 7). They are rounded with a blunt or slightly pointed (e.g. i/lm 2; Figs. 5 and 6) crown tip. Their crown

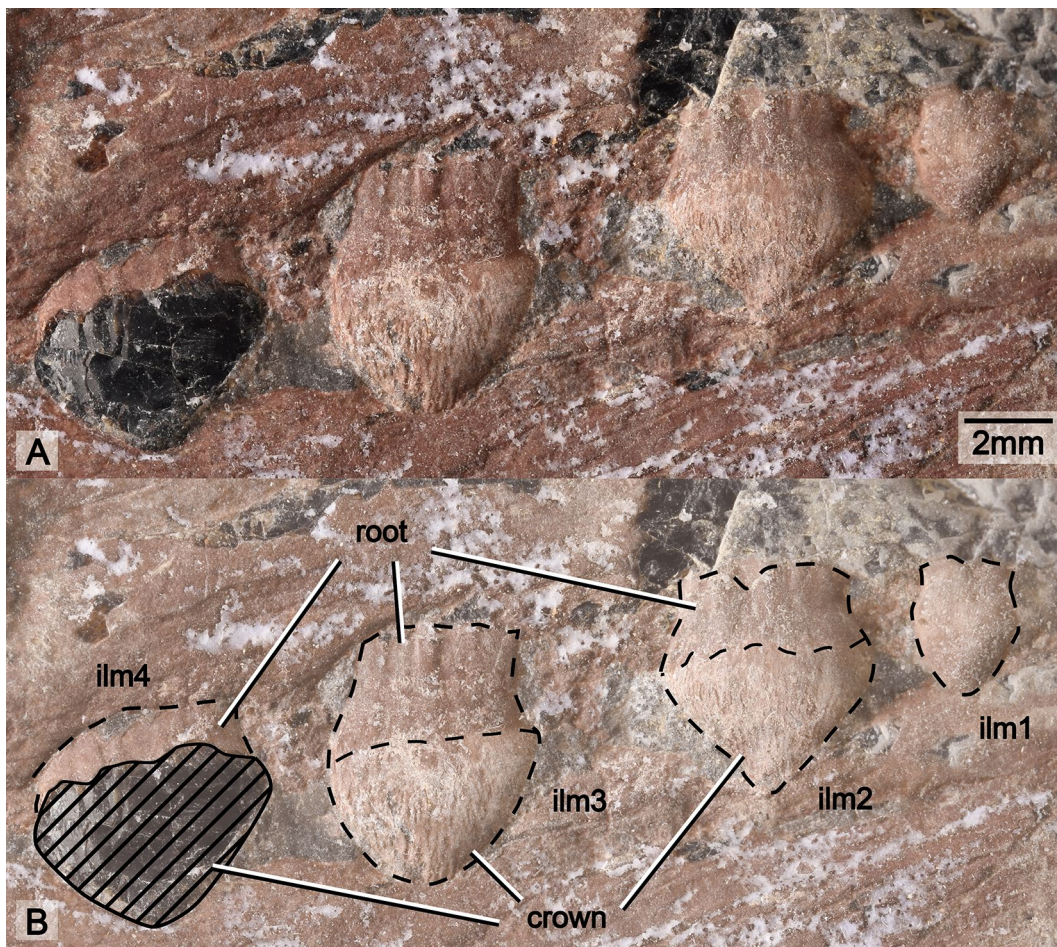


Fig. 6 Detail of maxillary tooth impressions of *Chaohusaurus zhangjiawanensis* (HFUT YAV-10-08) (A) and interpretative diagram (B). ilm1–4, impressions of left maxillary teeth 1–4. Note that tooth numbers indicate their position in the preserved parts of the jaws from anterior to posterior direction, not their exact position along the tooth row. Dashed lines indicate inferred bone tooth margins, hatching indicates broken tooth surface

surfaces are ornamented with ridges forming a vermiform (anastomosing) pattern, superficially similar to that present in the posterior teeth of the early-diverging durophagous ichthyosaurs *Tholodus* and *Xinminosaurus* (Mulder & Jagt, 2019). The widely exposed roots of the maxillary teeth bear clearly visible vertical grooves (Figs. 6 and 7).

The impressions demonstrate that the maxillary teeth were set in shallow sockets, similar to the condition in *Ch. brevifemoralis* (Gu et al., 2024). However, it is not possible to determine if a shallow dental groove was present along the maxillary tooth row.

The maxillary teeth become more robust posteriorly. Tooth lm1 is the smallest preserved maxillary tooth and likely represents a replacement tooth (Fig. 6). Tooth lm4 is the only maxillary tooth that has its crown partially preserved, although it is heavily abraded (Fig. 6). The crown shape index of tooth m4 has a value of 0.51, indicating that it has the most robust crown out of all

preserved maxillary teeth and tooth impressions. The impression of tooth rd8 indicates that the posterior dentary teeth were also rounded. Its root is well exposed and ornamented with sparse, broad, vertical grooves (Fig. 7). Teeth rd7 and rd9 only left partial impressions of their crowns. The vermiform (anastomosing) pattern of crown ornamentation is clearly visible in all the preserved impressions of dentary teeth (Fig. 7). There is a large empty space present between the impressions of teeth d8 and d9, indicating vacant tooth positions for likely two additional dentary teeth.

Discussion

Referral of HFUT YAV-10-08 to *Ch. zhangjiawanensis*

The holotype of *Ch. zhangjiawanensis* (WHGMR V26001) was reported by Chen et al. (2013:674) as having “two blunt crushing broken teeth preserved in the most posterior part of the left maxilla” and Zhao et al. (2022:775) mentioned that these two crushing teeth

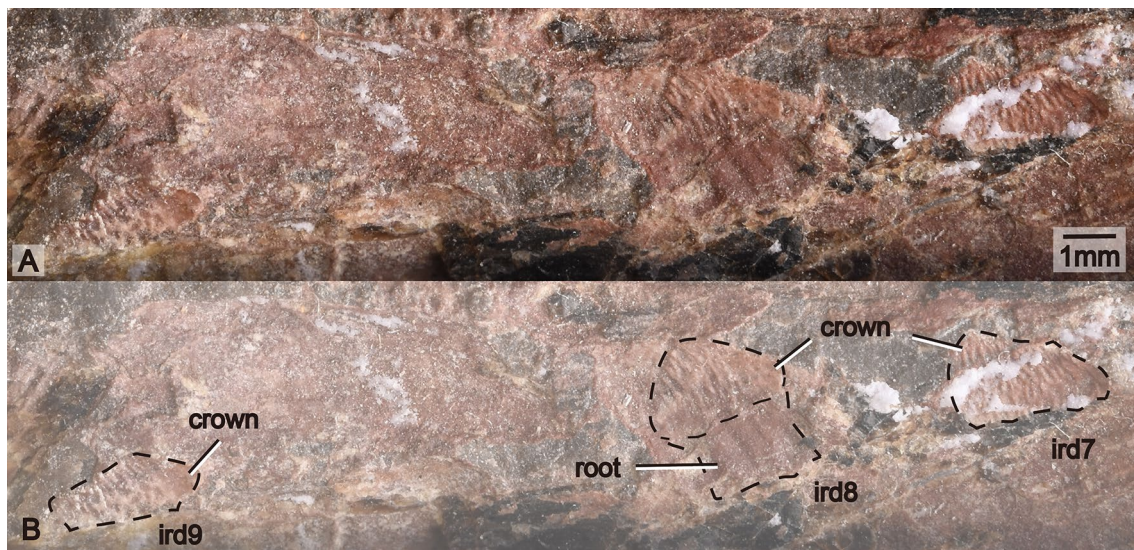


Fig. 7 Detail of posterior dentary tooth impressions of *Chaohusaurus zhangjiawanensis* (HFUT YAV-10-08) (A) and interpretative diagram (B). ird7–9, impressions of right dentary teeth 7–9. Note that tooth numbers indicate their position in the preserved parts of the jaws from anterior to posterior direction, not their exact position along the tooth row. Dashed lines indicate inferred tooth margins

Table 1 Summarized tooth measurements of the dentition of *Chaohusaurus zhangjiawanensis* (HFUT YAV-10-08)

HFUT YAV-10-08		Exposed height (mm)	Proximal width (mm)	Crown height (mm)	Crown width (mm)	Crown shape index	Crown ratio
Premaxillary teeth	Max.	3.02	2.33	1.44	1.50	1.31	1.00
	Min.	1.13	1.06	0.82	1.05	0.56	0.52
	Mean	2.08	1.68	1.15	1.26	0.94	0.73
Anterior (conical) dentary teeth	Max.	2.31	1.54	1.34	1.13	1.26	1.00
	Min.	0.97	0.89	1.27	1.06	1.12	0.58
	Mean	1.30	1.14	1.31	1.10	1.19	0.79
Anterior (conical) teeth (premaxillary + dentary)	Max.	3.02	2.33	1.44	1.50	1.31	1.00
	Min.	0.97	0.89	0.82	1.05	0.56	0.52
	Mean	1.79	1.48	1.20	1.22	1.01	0.75
Impressions of fully-erupted maxillary teeth	Max.	5.58	4.46	3.47	5.49	0.80	0.63
	Min.	4.80	3	2.81	4.33	0.51	0.58
	Mean	5.06	3.65	3.10	4.87	0.65	0.61
Impressions of posterior (rounded) dentary teeth	Max.	3.03	3.18	2.25	3.08	0.73	1.00
	Min.	1.33	1.70	1.33	2.28	0.53	0.52
	Mean	2.20	2.47	1.72	2.61	0.65	0.84

All values are in mm except for crown shape index and crown ratio, which are unitless. See Supplementary Table 1 for the complete set of measurements

possessed “dense and deep longitudinal striations on the enamel surface”. Furthermore, Zhao et al. (2022) described and figured the dentition of a referred specimen of *Ch. zhangjiawanensis* (YGM-Y4701), which demonstrated the dentition of the species was heterodont with conical anterior teeth and rounded posterior teeth, a morphology also clearly visible in HFUT YAV-10-08. However, despite the generally good preservation of

the dentition in YGM-Y4701 (Zhao et al., 2022: Fig. 4), many of the anatomical features of the teeth were not described nor figured in detail. Zhao et al. (2022: Fig. 4b, c) described the crowns of the premaxillary teeth as conical and bearing longitudinal striations, and the crowns of maxillary teeth as constricted at the base and ornamented with dense and longitudinal striations. However, based on HFUT YAV-10-08, the crown surface of

the premaxillary teeth in *Ch. zhangjiawanensis* can be more precisely described as bearing sparse longitudinal (apicobasal) ridges, not striations (Figs. 3 and 4). Furthermore, the impressions of preserved posterior maxillary teeth of HFUT YAV-10-08 clearly demonstrate that even though the maxillary tooth crowns are indeed constricted at their base, their surface enamel texture should be described more appropriately as vermiform or anastomosing (a morphology also consistent with that visible in photos published by Zhao et al. [2022: Fig. 4]). Zhao et al. (2022) were unable to confidently determine the mode of tooth implantation of *Ch. zhangjiawanensis* based on YGM-Y4701. However, on the basis of HFUT YAV-10-08 it is possible to determine that the maxillary teeth were set in sockets, like in *Ch. brevifemoralis* (Gu et al., 2024), although it is unknown if a dental groove was also present.

HFUT YAV-10-08 was collected from Zhangjiawan quarry, the type locality of *Ch. zhangjiawanensis* (Chen et al., 2013) and its tooth morphology and skull size are consistent with those previously reported for YGM-Y4701, a specimen clearly referable to the species (Zhao et al., 2022). In addition, *Ch. zhangjiawanensis* is the only ichthyosauriform reported from the Nanzhang-Yuan'an fauna to date. As a consequence, we refer HFUT YAV-10-08 to *Ch. zhangjiawanensis*.

Comparisons of the dentition of *Ch. zhangjiawanensis* with other species of *Chaohusaurus*

Premaxillary teeth

The premaxillary teeth of YGM-Y4701 (*Ch. zhangjiawanensis*; Zhao et al., 2022: Fig. 4b) and GMPKU-P-3188 (referred to *Ch. chaoxianensis* by Gu et al., 2024; Zhou et al., 2017: Fig. 8a) appear apicobasally high in comparison with the premaxillary teeth of HFUT YAV-10-08. Zhao et al. (2022) mentioned that the exposed height of the fifth premaxillary tooth of YGM-Y4701 (pt5 in Zhao et al., 2022: Fig. 4b) measures 5.12 mm and its basal width is 2.03 mm, giving a tooth shape index (apicobasal height divided by basal width of the tooth; after Jiang et al., 2006) of 2.52. This value closely matches that in *Ch. brevifemoralis* (GMPKU-P-3086) (shape index of the most posterior premaxillary tooth is about 2.6; Zhou et al., 2017). Moreover, the shape index of the most posterior premaxillary tooth of *Ch. chaoxianensis* is 2.3 (GMPKU-P-3188, Zhou et al., 2017). Calculating a similar tooth shape index for some premaxillary teeth of HFUT YAV-10-08 (p2, the best preserved functional premaxillary tooth—1.49, p3—1.32, p6—1.22, and p7—1.45; see Fig. 3) gives values which are much smaller than those in YGM-Y4701, GMPKU-P-3086 and GMPKU-P-3188. However, some premaxillary teeth (e.g., pt3, pt4, and pt5 in Zhao et al., 2022: Fig. 4b) of YGM-Y4701

bear vertical ridges that disappear before reaching the base of the exposed teeth, indicating the basal portions of the teeth that are not ornamented with vertical ridges are likely the exposed roots. This demonstrates that the relatively high premaxillary tooth shape indices in YGM-Y4701, GMPKU-P-3086 and GMPKU-P-3188 likely indicate true tooth morphology, whereas the low tooth shape index in HFUT YAV-10-08 is likely a preservational artefact caused by exposure of the skull in dorsolateral view, specimen compression, and damage.

Maxillary teeth

In the referred specimen of *Ch. zhangjiawanensis* (YGM-Y4701, Zhao et al., 2022), the anterior maxillary teeth are conical, similar to the premaxillary teeth, but they are larger in size and have rounded, instead of pointed, tips. In contrast, the posterior maxillary teeth are rounded and robust (Zhao et al., 2022). The transition between these two types of teeth is gradual and can be observed in the maxilla of YGM-Y4701 (Zhao et al., 2022), but the teeth from this transitional region are not preserved in HFUT YAV-10-08. In a referred specimen of *Ch. geishanensis* (GMPKU-P-3267; Gu et al., 2024: Fig. 1d), the transition of tooth morphology from conical to rounded also seems to occur gradually anterior to the last 6 rounded teeth in the right maxilla (Gu et al., 2024; see also Fig. 8B). On the other hand, the transition between conical teeth with pointed tips and robust teeth with rounded crowns is abrupt in *Ch. chaoxianensis* and *Ch. brevifemoralis* (Huang et al., 2019; Zhou et al., 2017).

The crown shape indices of the rounded maxillary teeth range from about 0.80 to 1.31 in *Ch. brevifemoralis* (calculated from the seven posteriormost teeth in each maxilla of GMPKU-P-3086; Gu et al., 2024: Figs. 2c, d and 3c), from 0.56 to 1.02 in *Ch. geishanensis* (calculated from the six posteriormost teeth in the right maxilla of GMPKU-P-3267; Gu et al., 2024: Figs. 1d and 3d) and from 0.51 to 0.80 in *Ch. zhangjiawanensis* (this work, ilm2—0.63; ilm3—0.80 and ilm4—0.51) (the crown shape indices of *Ch. chaoxianensis* are not available, but its dentition is identical in proportions to that of *Ch. brevifemoralis*; Huang et al., 2019). This indicates that the maxillary teeth of *Ch. zhangjiawanensis* were more robust (broader and larger) in comparison with those of *Ch. chaoxianensis* and *Ch. brevifemoralis*, but similar in proportions to those of *Ch. geishanensis* (Fig. 8). This probably indicates differences in diet between the species (see below).

Dentary teeth

The transition between the conical and rounded dentary tooth morphologies in *Ch. zhangjiawanensis* occurs in the same region as the transition between both types of teeth in the upper jaw (see above). The

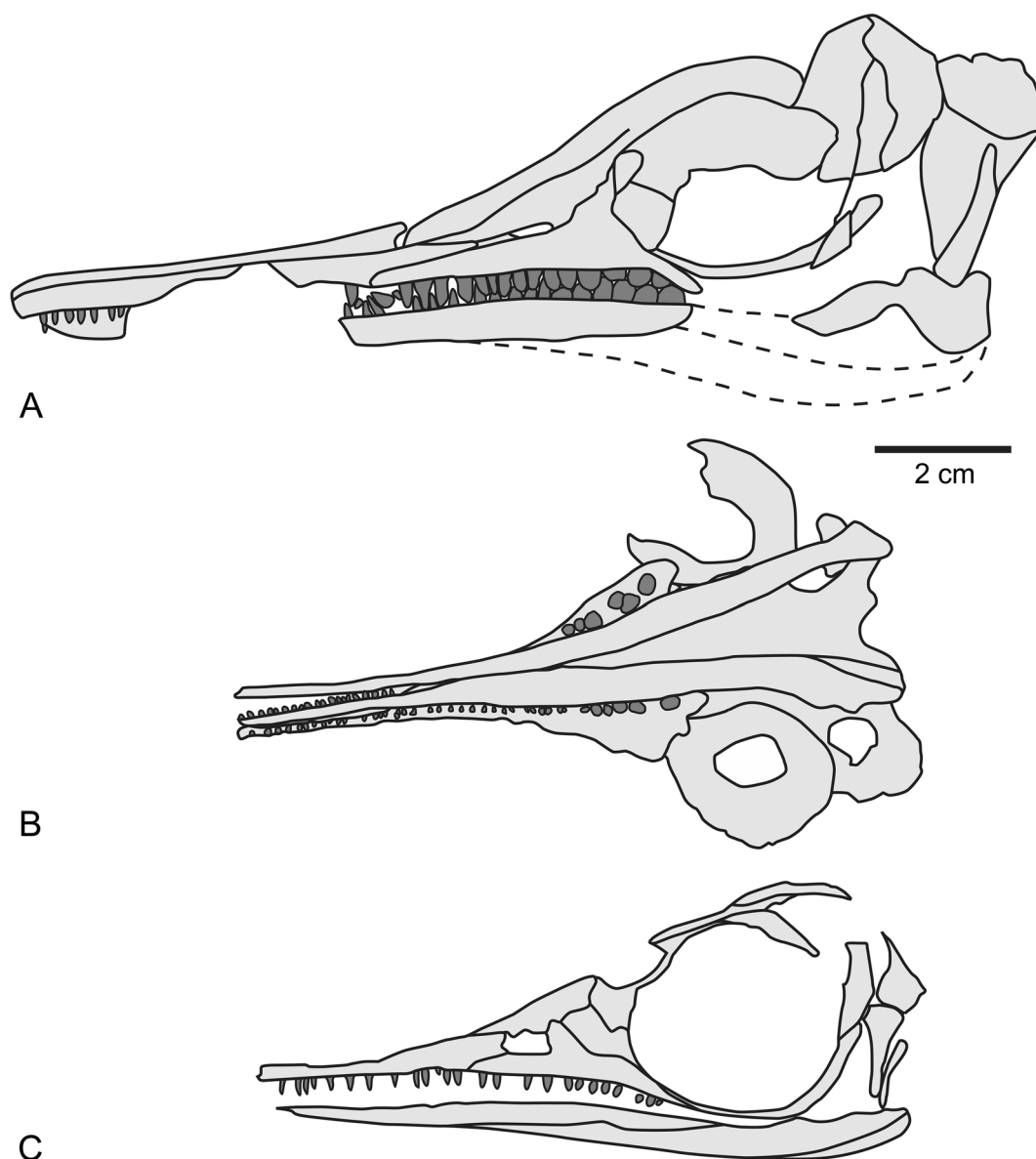


Fig. 8 Comparisons of skulls and dentitions of species of *Chaohusaurus*. **A** *Chaohusaurus zhangjiawanensis* (YGM-Y4701) (redrawn from Zhao et al., 2022), **B** *Chaohusaurus geishanensis* (GMPKU-P-3267) (redrawn from Gu et al., 2024), and **C** *Chaohusaurus chaoxianensis* (GMPKU-P-3188) (redrawn from Zhou et al., 2017). *Ch. brevifemoralis* was not figured, but its dentition is identical in proportions to that of *Ch. chaoxianensis* (Huang et al., 2019)

anterior dentary teeth likely have a similar morphology to the corresponding anterior premaxillary teeth, but this cannot be firmly established because no anterior-most dentary teeth are preserved in any of the currently known *Ch. zhangjiawanensis* specimens (Chen et al., 2013; Zhao et al., 2022; this work). The anterior dentary teeth preserved in HFUT YAV-10-08 are conical; coarse longitudinal ridges ornament the whole crown surface from the base to the tips, but this is difficult to observe due to severe damage and incomplete exposure of most of the anterior dentary tooth crowns (Fig. 4D,

H). These teeth have a similar morphology to the ones from the corresponding premaxillary region, but are slightly smaller in size. The morphology of the posterior dentary teeth is also consistent with that of the corresponding posterior maxillary teeth (see above). Zhao et al. (2022) indicated that the four most posterior dentary teeth of YGM-Y4701 were rounded, but slightly smaller in size compared to the corresponding posterior premaxillary teeth. This can also be observed in HFUT YAV-10-08, in which three impressions of posterior rounded dentary teeth are preserved. The

most complete of them (i/rd 8; Figs. 5 and 7) is smaller in size compared to the impressions left by the posterior maxillary teeth (except for the replacement tooth lm1; Fig. 6).

In *Ch. brevifemoralis*, the anterior dentary teeth are slender and conical and the posterior teeth are robust and rounded. Huang et al. (2019) described the transition between the two tooth types as abrupt (based on AGB7403), whereas Zhou et al. (2017) noted that the tips of four conical teeth are no longer pointed (become slightly rounded) anterior to the first fully rounded tooth (based on GMPKU-P-3086; Zhou et al., 2017). In contrast, in *Ch. zhangjiawanensis* (YGM-Y4701; Zhao et al., 2022) the transition from conical to rounded dentary teeth is more gradual and occurs over a region containing at least 14 teeth (Zhao et al., 2022). These transitional teeth are conical but no longer pointed (with slightly rounded tips), and share the same tooth morphology as the four most posterior teeth described by Zhou et al. (2017) in GMPKU-P-3086.

In *Ch. chaoxianensis*, the anterior and middle dentary teeth were described as pointed and conical, the more posterior dentary teeth as conical with rounded tips, and the five posteriormost dentary teeth as more rounded (based on NGM P45- H85-21; Maisch, 2001). This morphology in general corresponds to the morphology of dentary teeth and their transition described for *Ch. brevifemoralis* by Zhou et al. (2017) (GMPKU-P-3086; see above). Furthermore, the rounded posterior teeth were described by Maisch (2001:316) as having crowns ornamented with “very distinct, widely spaced apicobasal striations” and roots with “labyrinthodont” infolding (plicidentine). Whether the crown striations are actually more consistent with the vermiform pattern of ornamentation in the posterior dentary teeth observed in *Ch. zhangjiawanensis* requires further study. However, the maxillary tooth root impressions preserved in HFUT YAV-10-08 (Figs. 6 and 7) confirms the presence of plicidentine in *Ch. zhangjiawanensis*.

The diet of *Chaohusaurus*

It was hypothesized that *Ch. geishanensis*—the type species of *Chaohusaurus*—had a benthic foraging strategy, and was able to probe the sea floor in search of food, consisting of molluscs (Young & Dong, 1972). The other species of *Chaohusaurus* from the Chaohu fauna—*Ch. chaoxianensis* and *Ch. brevifemoralis*—were inferred to have preyed on ammonoids, bivalves, arthropods, and fish, based on their dentition (Gu et al., 2024). The Chaohu fauna preserves a large number of fish and invertebrates (Ji et al., 2017, 2021; Sun et al., 2013; Tintori et al., 2014; Xiong & Ji, 2023; Zhang et al., 2014, 2016), but no fish or macroinvertebrate fossils have been

recovered from the Nanzhang-Yuan’an fauna to date (Li & Liu, 2020). Furthermore, no stomach contents of *Chaohusaurus* have been reported to date, neither from the Chaohu fauna, nor from the Nanzhang-Yuan’an fauna. As a result, it is difficult to determine the specific diet of *Chaohusaurus*.

Grippia longirostris, an early-branching ichthyopterygian from the Early Triassic of Svalbard, had heterodont dentition similar to that of *Chaohusaurus*, with anterior conical teeth and posterior rounded teeth (Mazin, 1981; Mazin & Sander, 1993; Motani, 1997a, 1997b; Wiman, 1928). *Grippia longirostris*, *Ch. geishanensis*, and *Ch. brevifemoralis* were all inferred to represent the “crunch” feeding guild of Massare (1987), suggesting preference for armoured fish and thin-shelled invertebrates (Gu et al., 2024; Motani, 1997a, 1997b). In addition, gut contents comprising cephalopod hooklets and possible polychaete remains were reported in an ichthyosaur specimen from the Early Triassic of Svalbard possibly representing *Grippia* by Buchy et al. (2004). Furthermore, coleoid cephalopods, scales of actinistian and actinopterygian fish, and vertebral centra probably representing shark remains have been discovered in the stomach contents of *Mixosaurus* (Renesto et al., 2020), a Middle Triassic ichthyosaur similar in size to *Chaohusaurus*, with heterodont dentition comprising conical anterior teeth and rounded posterior teeth. Therefore, it is possible that *Chaohusaurus* had a diet similar to that of *Grippia* and *Mixosaurus*. In the Chaohu fauna, *Chaohusaurus* may have used its pointed anterior teeth to grasp prey items, whereas the rounded posterior teeth were used for crushing the scales of fish (e.g. *Chaohuperleidus*; Sun et al., 2013), and the shells of bivalved arthropods (e.g. *Ankitokazocaris chaohuensis*; Ji et al., 2017), thin-shelled bivalves (Zhang et al., 2014, 2016), and small ammonoids (Ji et al., 2015; Tong et al., 2004).

The high abundance of marine reptiles, but the low abundance or even complete absence of fish and macroinvertebrates in the Nanzhang-Yuan’an fauna was argued to reflect the natural composition of this assemblage (Li & Liu, 2020), consistent with the idea of rapid recovery of nektonic predators in the immediate aftermath of the PTME (Song et al., 2018). However, it cannot be completely ruled out that the lack of fish and macroinvertebrate fossils in the Nanzhang-Yuan’an fauna is the result of a preservation bias. Therefore, it is possible that *Ch. zhangjiawanensis* could have fed on other marine vertebrates and invertebrates, such as shrimps, and its diet was similar to that of other species of *Chaohusaurus*, *Grippia* and *Mixosaurus*.

As pointed out earlier, *Ch. zhangjiawanensis* and *Ch. geishanensis* had more robust posterior teeth compared to those in *Ch. chaoxianensis* and *Ch. brevifemoralis*. A detailed comparison of body size in all known species of

Chaohusaurus is difficult to perform, because only *Ch. chaoxianensis* and *Ch. brevifemoralis* are known from complete skeletons, whereas *Ch. geishanensis* and *Ch. zhangjiawanensis* are known from partial specimens the size of which is difficult to compare directly. However, based on comparisons of relative skull size of published specimens with mostly complete skulls, *Ch. zhangjiawanensis* was the largest species of *Chaohusaurus* (Fig. 8). The differences in the size of crushing teeth have been previously proposed as an indicator of dietary differences between ichthyosaur taxa (Huang et al., 2020). Thus, it is very likely that *Ch. zhangjiawanensis* was able to feed on harder and larger prey items than any of the *Chaohusaurus* species from the Chaohu fauna. Further studies of the composition of the Nanzhang-Yuan'an fauna and additional fossils of *Ch. zhangjiawanensis* with preserved stomach contents are needed to more reliably infer the diet of this species.

Palaeoecology of *Ch. zhangjiawanensis* and *Ch. geishanensis*

Ch. geishanensis is the least abundant of the *Chaohusaurus* species occurring at Chaohu. Only four specimens have been recovered until now, including the holotype (Young & Dong, 1972) and three referred specimens (Gu et al., 2024; Jiang et al., 2023; Motani et al., 2015b, 2015c), but the holotype is incomplete and badly preserved, and the referred specimens have not been described in detail. As a consequence, the morphology of the species is poorly known. However, *Ch. geishanensis* shares some striking similarities with *Ch. zhangjiawanensis*, which clearly differentiate both taxa from *Ch. chaoxianensis* and *Ch. brevifemoralis* from Chaohu. First, the posterior (maxillary) dentition of *Ch. geishanensis* is more robust (smaller crown shape indices) than the dentition of *Ch. chaoxianensis* and *Ch. brevifemoralis*, and seems similar in proportions to that of *Ch. zhangjiawanensis* (see above). Furthermore, the forefin architecture of *Ch. geishanensis* with well-ossified and tightly packed carpals is more similar to that of *Ch. zhangjiawanensis* than to the poorly ossified forefins of *Ch. chaoxianensis* and *Ch. brevifemoralis*, in which the carpal elements are small and broadly separated from each other (Chen et al., 2013; Motani et al., 2015b).

The morphological similarities between *Ch. geishanensis* and *Ch. zhangjiawanensis* indicate that the two taxa could be closely related. However, the available material for both species is currently too incomplete to test this hypothesis conclusively through phylogenetic analysis (Huang et al., 2019). The similar morphological features demonstrate that both species may have also shared a similar feeding ecology and inhabited a similar environment. The robust posterior dentition of *Ch. zhangjiawanensis* possibly reflects high availability of benthic prey

with hard shells in the shallow-marine palaeoenvironment of Nanzhang-Yuan'an. On the other hand, the relatively weaker posterior dentition of *Ch. chaoxianensis* and *Ch. brevifemoralis* was probably related with a diet consisting mostly of prey with shells that were only weakly sclerotized, such as thin-shelled bivalves and bivalved arthropods that occur in the Chaohu fauna (Ji et al., 2021). Massare and Callaway (1990) noted that in coastal habitats, the availability of both pelagic and hard-shelled benthic prey is high, but in the open ocean the range of prey is reduced to only pelagic forms. In the open ocean, rounded crushing teeth are less useful compared to sharp grasping teeth when dealing with prey without shells. The relatively weaker posterior rounded teeth of *Ch. chaoxianensis* and *Ch. brevifemoralis* compared to *Ch. geishanensis* and *Ch. zhangjiawanensis* may therefore be interpreted as an adaptation to an open-ocean environment for the two latter species. Consequently, the robust dentition of *Ch. geishanensis* may indicate a diet consisting of relatively hard-shelled prey and suggests it could have inhabited a shallow-marine, rather than open ocean, environment, with a relatively high availability of hard-shelled prey. However, this robust dentition could also be an adaptation to feeding on pelagic prey with the hardest shells within the Chaohu fauna. The currently available fossil material of *Ch. geishanensis* does not allow for a confident distinction between these two hypotheses.

The relative abundance of *Ch. geishanensis* in the Chaohu fauna also indicates its possible shallow-marine lifestyle. To date, only four specimens of *Ch. geishanensis* have been reported from the Chaohu fauna, compared with over 20 skeletons each reported for *Ch. chaoxianensis* and *Ch. brevifemoralis* (Huang et al., 2019; Motani & You, 1998a, 1998b; Motani et al., 2015b, 2015c, 2018; Zhou et al., 2017). The sauropterygian *Majiashanosaurus discoracoidis* is known from a single skeleton discovered from the Chaohu fauna (Jiang et al., 2014). Recent phylogenetic analyses have recovered it as an early-diverging member of the eosauroptrygian lineage (Li & Liu, 2020; Wolniewicz et al., 2023) and its pachypleurosauro- or nothosaur-like body plan is consistent with it representing a shallow-marine, rather than open ocean, species (Motani & Vermeij, 2021). Therefore, it is likely that *Majiashanosaurus* was not a typical representative of the Chaohu fauna, but that it only occasionally ventured out into deeper water from a nearby coastal environment. Furthermore, it was recently demonstrated that the rare stem turtle *Odontochelys semitestacea* (known from only three specimens), the remains of which are known exclusively from the open ocean Guanling fauna (Carnian, Late Triassic) of South China, was probably also primarily a shallow marine species (Goedert et al., 2023; Li et al., 2008). It is possible that a similar phenomenon explains

the presence of *Ch. geishanensis* in the Chaohu fauna. Taking all of the available evidence into consideration, i.e. the robust rounded posterior dentition of *Ch. geishanensis*, and the low relative abundance of *Ch. geishanensis* in the Chaohu fauna, we propose that it was possibly a shallow-marine species that did not live in the Chaohu fauna, but occasionally swam into deeper waters from a more coastal environment. Additional, well-preserved skeletons of *Ch. geishanensis* and *Ch. zhangjiawanensis* and histological studies of the marine reptiles of the Chaohu fauna are needed to further test this hypothesis.

Conclusions

This study provides new information on the dentition of *Ch. zhangjiawanensis* from the Nanzhang-Yuan'an fauna and a detailed interspecific comparison of tooth morphology within the genus *Chaohusaurus*. The anterior teeth of *Ch. zhangjiawanensis* are conical with sparse, apicobasal ridges, whereas the posterior teeth are rounded and ornamented with ridges forming a vermiform (anastomosing) pattern of surface ornamentation. *Ch. zhangjiawanensis* has slightly more robust posterior dentition than those of *Ch. chaoxianensis* and *Ch. brevifemoralis* from the Chaohu fauna. Therefore, *Ch. zhangjiawanensis* was probably capable of feeding on prey with relatively harder shells than the two species from Chaohu. The differences in tooth morphology between *Ch. zhangjiawanensis* from Nanzhang-Yuan'an and *Ch. chaoxianensis* and *Ch. brevifemoralis* from Chaohu might reflect the differences in hard-shelled prey availability between the shallow-marine palaeoecosystem of Nanzhang-Yuan'an and the deeper, slope-basin palaeoecosystem of Chaohu. In addition, similarities between the dental morphology of *Ch. zhangjiawanensis* and *Ch. geishanensis* and the rarity of the latter in the Chaohu fauna suggest that *Ch. geishanensis* was possibly also a shallow-marine species and was not a typical component of the Chaohu fauna. However, considering that *Ch. geishanensis* is known from only a few specimens, further studies are needed to test these hypotheses.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13358-024-00331-8>.

Additional file 1: Table 1. Complete measurements of the dentition preserved in a partial skull (HFUT YAV-10-08) of *Chaohusaurus zhangjiawanensis*. All values are in mm except for crown shape index and crownratio, which are unitless. d, dentary tooth; ird, impression of right dentary tooth; ilm, impression of left maxillary tooth; p, premaxillary tooth; v, vacant tooth position.

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Author contributions

JL designed the research and led the fieldwork. LAG made the mould of the fossil specimen and all authors examined the morphology of the fossil specimen and the mould. LAG prepared the figures and tables and drafted the manuscript with substantial input from ASW. All authors read, revised and approved the final version of the manuscript.

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Availability of data and materials

All generated data are provided in the text, figures and tables. Specimen HFUT YAV-10-08 is housed in the Geological Museum of Hefei University of Technology and available for comparative studies upon request to JL. No datasets were generated or analysed during the current study.

Declarations

Ethics approval and consent to participate

The authors declare that they have no competing interests.

Competing interests

The authors declare no competing interests.

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