Brief report

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Lower jaw morphology of the last surviving tritylodontid *Fossiomanus sinensis* from the Early Cretaceous Jehol Biota, Liaoning Province, China

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Tritylodontids are close relatives of mammals with specialized teeth adapted for herbivory. Despite their diversification during the Jurassic, the fossil record of this clade suggests they declined significantly in the Cretaceous when they are mainly represented by fragmentary dental remains. The exception is the Early Cretaceous taxon *Fossiomanus sinensis* Mao et al., 2021. Here we describe a new mandible of this species from the same locality as the holotype specimen. The new specimen provides more complete information on mandible shape and tooth morphology, filling a knowledge gap for this iconic Cretaceous tritylodontid, given that cranial morphology in the holotype of *F. sinensis* remains insufficiently studied. Additionally, the fossil record of *F. sinensis* represents the youngest known tritylodontid (~119 Ma, Aptian) and the latest non-mammaliaform cynodont, shedding light on the evolutionary history of early mammalian relatives.

Introduction

Tritylodontids are a group of mammaliamorphs that were predominantly specialized herbivores (Kalthoff et al. 2019), characterized by multi-cusped cheek teeth (postcanines). It is generally accepted that this clade is closely related to mammaliaforms due to dental morphological similarities (complexity in cusp pattern and occlusal configuration), although their exact phylogenetic position, whether as the sister clade to mammaliaforms or another related group, remains debated (Rowe 1988; Angielczyk and Kammerer 2018; Abdala 2021). Tritylodontids were among the most derived and diverse cynodonts, with a wide geographic distribution and an extensive temporal range, from the Late Triassic to the Early Cretaceous (Kühne 1956; Fedak et al. 2015; Matsuoka et al. 2016; Velazco et al. 2017; Angielczyk and Kammerer 2018; Mao et al. 2021). The unequivocal record of this clade in the Triassic is sparse, e.g., *Oligokyphus* discovered in the Upper Triassic (Rhaetian) Scots Bay Member of the McCoy Brook Formation at Wasson Bluff in the Fundy rift basin in Nova Scotia and NewBrunswick, Canada (Fedak et al. 2015). Tritylodonts flourished during the Early Jurassic, but experienced a sharp decline by the end of the Jurassic (Kühne 1956; Sues 1985b, 1986b; Matsuoka and Setoguchi 2000; Matsuoka et al. 2016). The Early Cretaceous tritylodontids have been reported from Siberia (Tatarinov and Matchenko 1999), central Japan (Matsuoka et al. 2016), and northeastern China (Mao et al. 2021). Most of these fossil remains are only dentition, with the exception of *Fossiomanus sinensis* Mao et al., 2021, which is represented by a complete skeleton (Mao et al. 2021). However, in the holotype of *F. sinensis*, the crania and mandible are poorly preserved, obscuring the details of the morphology of this iconic tritylodontid taxon. Here, we report a new mandible of this taxon discovered in Liaoning Province from the Jiufotang Formation, the late stage of the Early Cretaceous Jehol Biota (Zhou et al. 2021; Yu et al. 2023).

Institutional abbreviations.—CVEB, Centre for Vertebrate Evolutionary Biology, Yunnan University, Kunming, China; JZPM, Jinzhou Paleontological Museum; ZMNH, Zhejiang Museum of Natural History, Hangzhou, Zhejiang Province, China.

Material and methods

The specimen, ZMNH M31795, was discovered in the same locality as the holotype: in the Jiufotang Formation at the Lamadong site, Jianchang County, Chaoyang City, Liaoning Province, China. It is currently housed in the Zhejiang Museum of Natural History, Hangzhou, Zhejiang Province. High-resolution micro-computed tomography (micro-CT) was conducted at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing using a GE V|Tome|xm dual tube. The mandible was scanned at a resolution of 15.734 μm (160 kV, 110 μA). The software package VGStudio Max 3.0 was used for virtual segmentation and visualization. The 3D files for the lower jaws are deposited in figshare (https://figshare.com/s/bff16d85764872847655). The cusp terminology of lower cheek teeth used in this study follows Watabe et al. (2007), in which cusps are labelled as the buccal (b) and lingual (l) rows and numbered mesiodistally as cusp 1 and cusp 2 in each cusp row. The measurements of the lower jaws and teeth were taken digitally in ImageJ.

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Systematic palaeontology

Genus *Fossiomanus* Mao et al., 2021

Type locality: Lamadong, Jianchang County, Liaoning province, China; Aptian, Lower Cretaceous.

Fossiomanus sinensis Mao et al., 2021

Fig. 1.

Type material: ZGY0052, a nearly complete skeleton.

Type locality: Lamadong, Jianchang County, Liaoning province, China.

Type horizon: Aptian, Lower Cretaceous Jiufotang Formation.

Material.—Holotype and the new specimen (ZMNH M31795), a partial mandible discovered from the Jiufotang Formation at Lamadong site.

Description (mandible only).—The mandible, ZMNH M31795, is mainly represented by the dentaries, and the tooth row is badly damaged except for the lower incisors and one displaced left postcanine (Fig. 1A_1, A_2). The dentaries are slightly compressed dorsoventrally. The length of the mandible is 51.3 mm. The mandibular symphysis is transversely broad and not fused with a longitudinal suture in the anterior portion between the left and right dentaries. The suture exhibits an interlocking connection on the posteroventral portion of the symphysis, likely suggesting a partial fusion between the dentaries. On the ventral side of the symphysis, a zig-zag suture is present (Fig. 1A_4). The posterior margin of the symphyseal facets is anteriorly concave and extends posteriorly to the level of the anterior-most part of the tooth row. The ventral margin of the dentaries is rounded and broad in the symphysis region. In lateral view, a mental foramen is visible on the lateral surface of the left dentary dorsal to the anterior part of the tooth row (Fig. 1A_3).

Only one lower incisor is present in each dentary of the mandible, characterized by an enlarged and procumbent crown (Fig. 1A_2, B). No additional small or developing lower incisors are present near this tooth locus on each side. The apical portion of the lower incisors is linguolabially compressed, featuring a longitudinal ridge along the midline of the crown, with sharp medial and lateral margins (Fig. 1B_4). The basal portion of the lower incisors is more robust and rounded, and the roots appear to be open as indicated by the incomplete outline observed in the distal region. The lower canine is absent, as in all tritylodontids, and a distinct diastema separates the lower incisor from the postcanine row on each side. The diastema has a ridged dorsal margin. The postcanine rows run relatively straight along the length of each dentary with minimal twisting between the anterior and posterior teeth. A distinct internal groove is present on the medial surface of each dentary (Fig. 1A_3).

One left lower postcanine is preserved, though slightly displaced (Fig. 1A_2, C). The tooth measures 2.5 mm in length, 1.6 mm in width, and 4.4 mm in height (including both the crown and root). The postcanine tooth exhibits a cusp formula of 2:2, consisting of two longitudinal rows of equal-sized cusps (Fig. 1C_1). The cusps are distally concave and separated by a deep, open groove. The postcanine tooth has two roots, mesial and distal, which are fused in their proximal half and only separate in their distal half (Fig. 1C_2, C_3). The tip of the mesial root curves mesially, while the tip of the root shows damage to the distal region.

Remarks.—We assign this specimen to the recently reported species *Fossiomanus sinensis* based on the similarities of dental morphology and shared locality of discovery. The curvature, fusion of roots, and the cusp formula of lower postcanines closely resembles that of the holotype of *F. sinensis*, JZMP 2107500093. The preserved lower postcanine of ZMNH M31795 (2.5 mm in length) is much smaller than that of the holotype (approximately 4.5 mm in length, as measured from figures) (Mao et al. 2021: extended fig. 3E). The replacement pattern of postcanines in tritylodontids is featured by teeth moving anteriorly, with oldest teeth lost at the anterior end of the postcanine row and newly erupted teeth being added at the posterior end of the postcanine row, so-called the "conveyor belt" system (Kühne 1956; Matsuoka and Setoguchi 2000; Panciroli et al. 2017). Given that intraspecific variation in postcanine size is distinct in tritylodontids due to ontogenetic differences (e.g., Panciroli et al. 2017), the size difference of lower postcanines between these two specimens suggests that ZMNH M31795 likely represents a younger individual of *F. sinensis*. The lower postcanine in ZMNH M31795 is likely an anteriorly implanted, soon-to-be lost tooth. *Fossiomanus sinensis* with the preserved dentary length of 51.3 mm in ZMNH M31795, represents a medium-sized tritylodontid. This size of the mandible within the clade ranges from small taxa like *Lufengia* (CVEB 12001, dentary length about 23 mm, cranium length estimated about 31 mm) (Liu et al. 2022) to large-sized taxa like *Kayentatherium* (skull length over 220 mm) (Sues 1986b). The mandibular symphysis in *Fossiomanus* is transversely wider than in most Jurassic taxa, such as *Oligokyphus*, *Dinnebitodon*, and *Kayentatherium* (Kühne 1956; Sues 1985a, 1986a, b). A zig-zag suture of the mandibular symphysis was noted in the holotype of *F. sinensis* by Mao et al. (2021), whereas the new specimen exhibits a longitudinally oriented suture in the anterior portion of the symphysis. In addition, the posteroventral portion of the symphysis tends to be partially fused with an interlocking suture in dorsal view. Recent studies in fossorial rodents suggest that compared to the cranium, mandible morphology is more adaptable to functional selective pressures (McIntosh and Cox 2019). The fossorial adaptation to scratch-digging of *Fossiomanus*, as reflected by its postcranial morphology (Mao et al. 2021), might also be enhanced by the shovel-like lower incisor and the broad, partially fused mandibular symphysis, which likely contributes to the stability of the mandible and the efficiency of penetrating and soil-grasping of the lower incisors, a similar mechanism as shown in fossorial rodents (Kley and Kearney 2007; Van Wassenbergh et al. 2017; Mclntosh and Cox 2019).

Only one pair of lower incisors is present in *Fossiomanus* (Fig. 1A_2, B), similar to *Bienotherium* (Young 1947; Cui and Sun 1987), and *Kayentatherium* (Sues 1986b), but different from *Bienotherodes* (Sun 1984; Cui and Sun 1987; Watabe et al. 2007) and *Lufengia* (two pair of lower incisors; Liu et al. 2022), and *Oligokyphus* (three pair of lower incisors; Kühne 1956). In lower

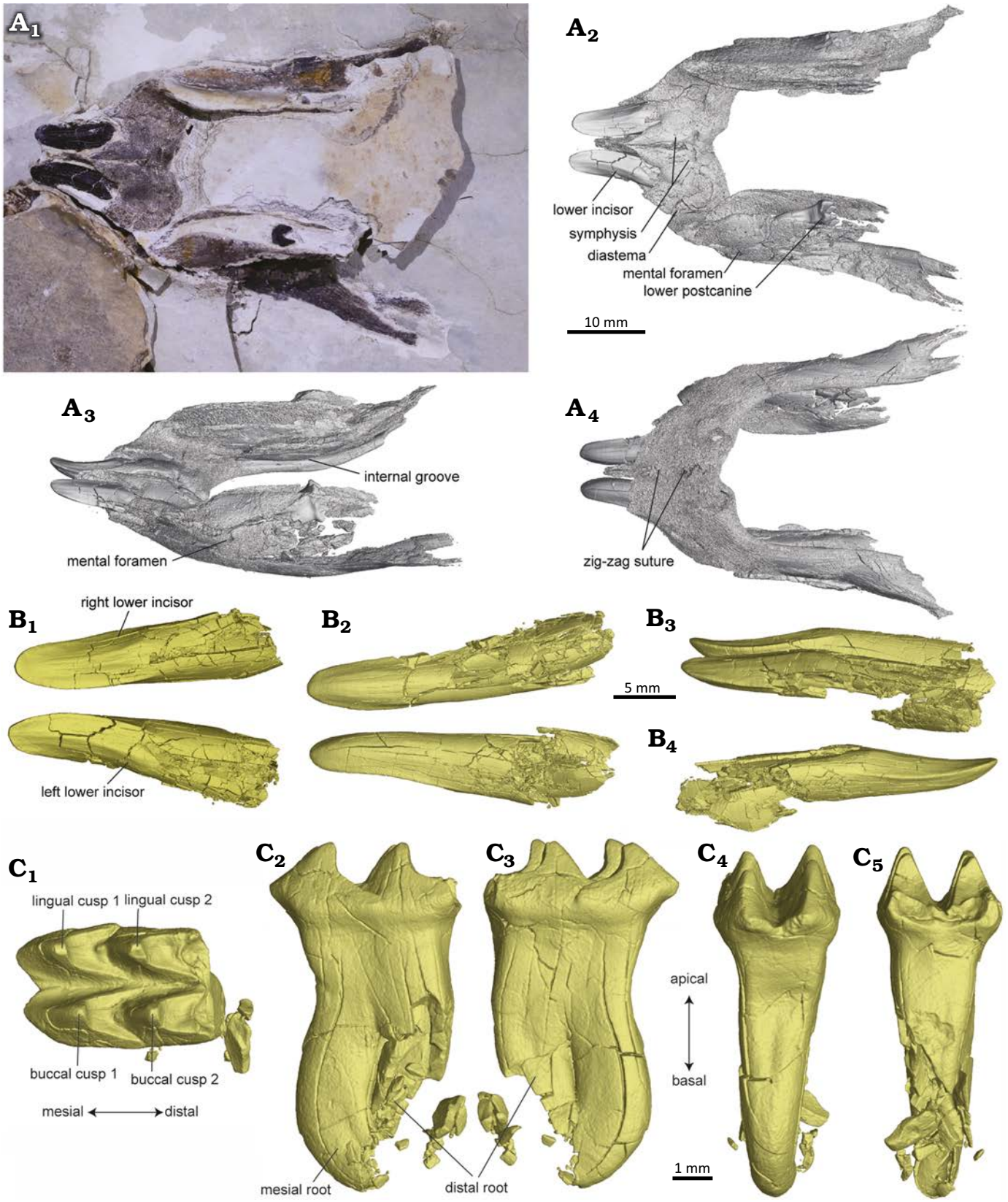

Fig. 1. The mandible of tritylodontid mammal *Fossiomanus sinensis* Mao et al., 2021, from Aptian, Lower Cretaceous Jiufotang Formation at the Lamadong site, with two lower incisors preserved in their alveoli and one lower postcanine displaced (ZMNH M31795) from the Jiufotang Formation at the Lamadong site. **A**. The new specimen preserved in the slab in dorsal view (A_1), segmented mandible based on CT data in dorsal (A_2), dorsolateral (A_3), and ventral (A_4) views. **B**. Lower incisors in occlusal (B_1), ventral (B_2), left lateral (B_3), and right lateral (B_4) views. **C**. Lower left postcanine in occlusal (C_1), buccal (C_2), lingual (C_3), mesial (C_4), and distal (C_5) views.

incisors, the tooth crown is more laterally compressed, and the root is open posteriorly in *Fossiomanus*, different from that of the Early Cretaceous *Montirictus* from central Japan (Matsuoka et al. 2016). Tritylodontids exhibit a pattern of horizontal tooth replacement, with the addition of newly erupting postcanines at the distal end of the tooth row (Kühne 1956; Matsuoka and Setoguchi 2000; Jasinoski and Chinsamy 2012). Differences in tooth morphology are an important aspect in evolutionary morphology of tritylodontids, and distinct variations have been observed in height, number, fusion, and curvature of postcanine roots (e.g., Cui and Sun 1987; Averianov et al. 2017; Panciroli et al. 2017; Liu et al. 2022). The curvature of the roots in the lower postcanines increases anteriorly, whether the roots of lower postcanines are fused or not. In *Fossiomanus*, the double-rooted and partially fused condition of the lower postcanine roots differs from the long, separate, and distinctly curved condition in *Bienotherium* (Cui and Sun 1987) and from the slighter shorter and less curved condition in *Lufengia* (Liu et al. 2022). The fusion of the proximal root in the lower postcanine of *Fossiomanus* is intermediate between that seen in the Middle Jurassic *Stereognathus* and Early Cretaceous *Montirictus* (Matsuoka et al. 2016; Averianov et al. 2017). The fusion of lower postcanine roots tends to be more developed in some specimens of the Middle Jurassic derived *Stereognathus* sp. (with nearly fully fused roots; Averianov et al. 2017) and *Bienotheroides* (single-rooted with complete fusion; Cui and Sun 1987).

Stratigraphic and geographic range.—Aptian, Lower Cretaceous Jiufotang Formation in Liaoning Province, China.

Concluding remarks

Fossiomanus represents the latest survival tritylodontid taxon and the youngest record of a non-mammaliaform cynodont. Among the few Early Cretaceous tritylodontid localities, the Ilek Formation in western and central Siberia is currently considered to date from Barremian to Aptian stages (Tatarinov and Matchenko 1999; O'Connor et al. 2014). The Kuwajima Formation in central Japan is estimated between 130.7 Ma and 121.2 Ma by zircon U-Pb ages, indicating that the Kuwajima Formation formed between late Hauterivian and early Aptian. The lower part of the Kuwajima Formation yields a zircon U-Pb age of 130.7 ± 0.8 Ma (Matsuoka and Setoguchi 2000; Matsuoka et al. 2016), while a LA-ICP-MS zircon U-Pb date of 121.2 ± 1.1 Ma was obtained from the tuff of the overlying Akaiwa Formation (Matsuoka et al. 2016; Sakai et al. 2019), providing a minimum age estimate for the Kuwajima Formation (Matsuoka et al. 2016; Sakai et al. 2019). Recently, a series of zircon U-Pb ages have been reported for the Jiufotang Formation, which represents the later stage of the Early Cretaceous Jehol Biota, from two main sections: the Sanmendian section and the Xiaotaizi section (Yu et al. 2021, 2023) using secondary ion mass spectroscopy (SIMS). One tuff from the Sanmendian section, nearly the lowest part of the Jiufotang Formation, constrains the lower limit of the depositional age to an (SIMS) age of 122.0 ± 0.9 Ma. Additional age constraints are also available, including U-Pb ages of 118.9 ± 0.8 Ma, 118.8 ± 0.6 Ma, and 118.6 ± 1.1 Ma for the Jiufotang Formation at the Xiaotaizi section (Yu et al. 2021). Additionally, an age constraint of 120.3 ± 0.7 is reported for the Shangheshou section of the Jiufotang Formation based on $^{40}Ar/^{39}Ar$ dating (He et al. 2004). These results suggest that the depositional age of Jiufotang Formation is approx. 123–119 Ma (He et al. 2004; Yu et al. 2021, 2023). *Fossiomanus*, discovered at the Lamadong site, can be estimated in age by the geological dating in the Xiaotaizi section, i.e., approx. 119 Ma (Aptian) (Gale et al. 2020; Yu et al. 2021). The young age of *Fossiomanus* makes it a significant taxon for understanding the evolutionary history of tritylodontids, and of cynodonts as a whole. Tritylodontids is one of the most successful clades in the evolutionary history of cynodonts, which can be attributed to their wide dietary range, efficient mastication, fossorial adaptation, and reproduction and growth pattern (Hoffmann and Rowe 2018; Kalthoff et al. 2019; Mao et al. 2021). Current evidence indicates a dramatic decline of this clade in the Early Cretaceous, coinciding with the rise of multituberculates, another group of specialized herbivores with more derived life history strategies (Hoffmann and Rowe 2018; Wang et al. 2019; Weaver et al. 2022). This suggests that the diversification of multituberculates, along with other small vertebrates occupying similar ecological niches, may have intensified competition for resources and ecological space, ultimately leading to the extinction of tritylodontids.

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