TOOTH MICROWEAR AND OCCLUSAL MODES OF EUHARAMIYIDANS FROM THE JURASSIC YANLIAO BIOTA REVEAL MOSAIC TOOTH EVOLUTION IN MESOZOIC ALLOTHERIAN MAMMALS

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Abstract: 'Haramiyidans' are extinct mammaliaforms often clustered with Multituberculata as Allotheria, and with a fossil record extending from the Upper Triassic to possibly the Upper Cretaceous. For many decades, 'haramiyidans' were known only from isolated teeth, and their relationships to other mammaliaforms remain unclear. With the discovery of several euharamiyidans represented by skeletal specimens from the Jurassic Yanliao Biota, north-western China, our knowledge of this group has significantly advanced. Nonetheless, much morphology, including dentition and occlusal patterns, has only been briefly described for most taxa, and phylogenetic reconstruction and interpretation of the biology of the group still remain unclear or controversial. Here we provide systematic descriptions of the dental wear of shenshouids (Qishou and Shenshou) from the Yanliao Biota. We reconstruct the occlusal mode of shenshouids and compare it with those of other taxa based on our observation of specimens of most known 'haramiyidan' taxa. Several occlusal patterns are recognized. In particular, that of Thomasia, Haramiyavia and Maiopatagium is similar to the multituberculate M1/m1 occlusal relationship and probably represents the primitive occlusal condition in 'haramiyidans'. The occlusal mode of shenshouids resembles the multituberculate M2/m2 occlusion. The double-engaged mode in Arboroharamiya and Vilevolodon, as well as that of Eleutherodon, represents a more advanced occlusal pattern. The diverse dental occlusions suggest diverse diet adaptations and resource partitioning from co-existing taxa in the Jurassic forests; they also reflect mosaic evolutionary transformations and complicated phylogenetic relationships within the group. Some aspects of the dental evolution remain challenging and require further vigorous testing.

Key words: microwear, occlusion, mastication, feeding ecology, Yanliao Biota, Mesozoic.

ALLOTHERIA is an extinct group of mammaliaforms (Kielan-Jaworowska et al. 2004), including Multituberculata (Cope, 1884), 'Haramiyida' (Hahn et al. 1989) and probably Gondwanatheria (Krause et al. 2014). 'Haramiyidans' and multituberculates are characterized by the allotherian dental morphology in which each upper or lower molar has at least two longitudinal rows of multiple cusps, the tooth occlusion is bilateral, and the jaw movement in chewing consists of a palinal (posterior) component but very little or no transverse movement. Because of their early occurrence and unique tooth morphology, allotherians were thought to be derived from other mammals early in mammalian evolution (Simpson 1945; Butler & MacIntyre 1994; Butler 2000; Butler & Hooker 2005; Hahn & Hahn 2006). The phylogenetic relationships within allotherians and that of each allotherian subgroup

within mammaliaforms have not been resolved and remain a highly controversial issue related to divergence time and higher-level phylogenies of mammals.

Among allotherians, multituberculates have a diverse fossil record, often represented by cranial and postcranial material. In contrast, 'haramiyidans' have been known mainly from isolated teeth for many decades since their first report (Pleininger 1847; Owen 1871; Hennig 1922; Simpson 1928; Pabbington 1947; Peyer 1956; Hahn 1973; Clemens 1980, 2007; Sigogneau-Russell et al. 1986; Sigogneau-Russell 1989; Butler & MacIntyre 1994; Heinrich 1999; Butler & Hooker 2005; Maisch et al. 2005; Martin et al. 2010; Averianov et al. 2011; Clemens & Martin 2014; Debuysschere 2016). Haramiyavia clemmenseni was based on fragmentary jaws with partial dentitions and some postcranial remains (Jenkins et al. 1997; Luo et al.

2015; FM & JM pers. obs.) Recently, seven genera and nine species of 'haramiyidans', represented by skeletal material, have been reported from the Jurassic Yanliao Biota, China (Zheng et al. 2013; Zhou et al. 2013; Bi et al. 2014; Han et al. 2017; Luo et al. 2017; Meng et al. 2017; Mao & Meng in 2019a). These newly discovered specimens have revealed a rich suite of osteological features that show adaptation to forest life and gliding locomotion; they also provided evidence for the evolution of mammalian middle ear. Moreover, they present diverse tooth occlusal patterns, as interpreted by various authors in the aforementioned studies.

It has been recognized that mammalian dental morphologies reflect genetic differences as well as effect of the environmental factors, such as food (Butler 1983). In general, tooth morphology and tooth wear can be used to interpret the evolutionary adaptation of mammals and changes in the environment in which they lived (Fortelius & Solounias 2000; Sponheimer et al. 2003; Merceron et al. 2010; DeMiguel et al. 2011; Davis & Pineda-Munoz 2016). In particular, tooth microwear texture is one of the features that is commonly used to understand dietary specializations and feeding ecology in mammals (Ungar 2010, 2015). The dentitions of Morganucodon and Kuehneotherium have shown the earliest trophic diversification in basal mammaliaforms (Gill et al. 2014), and, compared to them, the dentition of 'haramiyidans' could represent a truly distinctive feeding and dietary specialization at the beginning of the mammalian radiation, which has since undergone significant modification during their evolution.

To understand the dietary adaptations of fossil mammals, quantitative methods, such as orientation patch count and multi-proxy dental morphology analysis, have been developed and applied to various mammals, including allotherians (Evans & Sanson 2003; Evans et al. 2007; Wilson et al. 2012; Pineda-Munoz et al. 2017). However, all these inferences and quantitative analyses rely on how much we know about the dental morphology, occlusal relationship of teeth and the resultant wear facets of a mammal group. Unfortunately, detailed descriptions of tooth morphologies and wear are yet to be documented for most Yanliao euharamiyidans. A systematic treatment of the occlusal patterns within 'haramiyidans' has not been conducted, despite different interpretations of occlusal patterns in various taxa, some of which are controversial.

Following up the description of the tooth morphology of Qishou (Mao & Meng 2019a) and enamel microstructures and tooth replacements of euharamiyidans (Mao et al. 2017, 2019), here we provide a detailed description of tooth wear of shenshouids (Qishou and Shenshou) with the assistance of SEM and CT-scan images. The goal of the study is to establish the dental occlusal pattern of shenshouids based on convincing evidence of tooth morphology and wear. With published data and our personal observations on specimens of other taxa, including Thomasia, Theroteinus, Haramiyavia, Eleutherodon, Sineleutherus, Kirtlingtonia, Arboroharamiya, Shenshou and Xianshou, we compare various occlusal modes known in 'haramiyidans' and discuss their possible evolutionary transformations. These patterns might indicate fundamental phylogenetic divergence and mosaic evolutionary trend within the group, and are probably related to an improvement in processing different kinds of food.

MATERIAL AND METHOD

Material

The primary specimens used for this study are the holotype specimen of Qishou jizantang (JZT-D061) and the specimen assigned to Qishou sp. (JZT-CK005, Mao & Meng 2019a), with additional data of Shenshou lui (LDN HMF2001, Bi et al. 2014). The specimens assigned to Qishou have been further prepared to reveal their detail dental features (Mao & Meng 2019a). JZT-D061 and JZT-CK005 are housed in the Jizantang Paleontological Museum, Chaoyang County, Liaoning Province, China. JZT-D061 represents a full adult individual and JZT-CK005 is from an old individual animal, perhaps the oldest known of the euharamiyidan specimens from the Yanliao Biota. Thus, distinct wear and striations are well preserved in the two specimens and furnish convincing evidence for interpreting the occlusal mode of these euharamiyidans. The wear pattern of the holotype specimen of S. lui (LDN HMF2001; Bi et al. 2014) has also been revisited.

Terminology

We follow Butler (2000) for cusp terminology (Fig. 1; see also Meng et al. 2014 and Mao & Meng 2019a) and Koenigswald et al. (2013) for general tooth wear terminology. Because individual wear mechanisms do not act alone but interact with each other (Addey & Shellis 2006), the tooth wear terminology may not be precisely applicable to the teeth of all 'haramiyidans'. Following Koenigswald et al. (2013), abrasional facets are those formed by abrasion resulting from friction of food materials between tooth crowns, that is, tooth–food contact during chewing, and these facets may reflect physical properties of the food being processed. Attritional facets are planar, showing marginal separation to the surrounding enamel, and often bear orientated striations; the wear facets best reflect contact and occlusal relationships of teeth, whereas the striations indicate the relative movement of teeth. The attritional facets and striations are created by tooth–tooth contacts during the power stroke and developed during
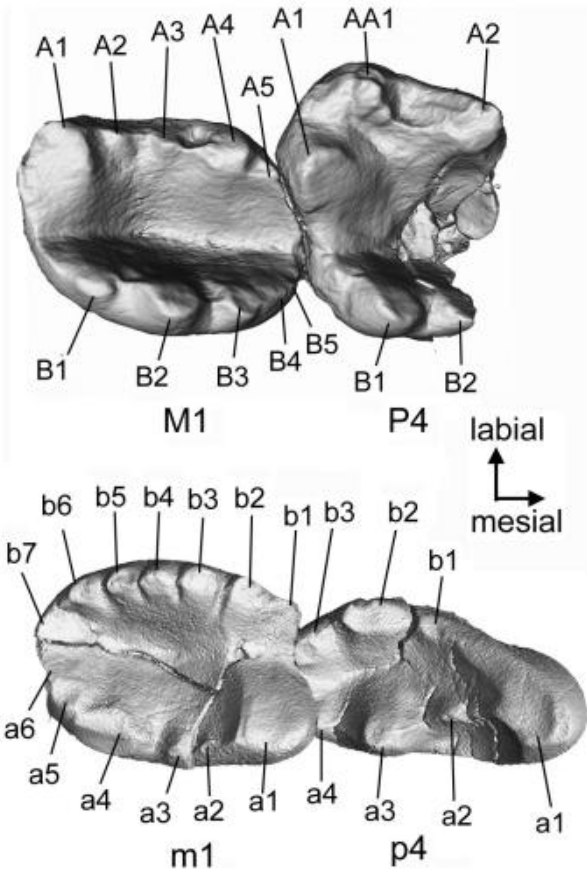
FIG. 1. Terminology of upper and lower tooth cusps used in this study. On upper cheek teeth, the two rows of cusps are termed row-A (labial) and row-B (lingual) with the cusps numbered from distal to mesial. The two rows of cusps on the lower molar are termed row-a (lingual) and row-b (labial) and the cusps are numbered from mesial to distal. The terminology follows Butler (2000) but also see Meng et al. (2014) and Mao & Meng (2019a).

normal mastication (see also Maier & Schneck 1982; Butler 1983; Mills 1963, 1967). General wear facets and their distribution on various teeth are shown in Figure 2.

Imaging

All facilities we used for the study are installed in the Key Laboratory of Evolutionary Systematics of Vertebrates, Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), CAS. We took optical images using a Canon digital camera with a macro lens and a Zeiss microscope (SteREO Discovery V. 20) with a digital imaging system (AxioVision SE64 Rel. 4.9). These optical images show the general morphology and condition of specimen preservation.

For SEM imaging, the specimens were uncoated and imaged using a Hitachi S4700 scanning electron microscope. Most of the SEM photographs were taken at 3–5 kV voltage with magnifications of 10–30⊘ for the general shape of the tooth and 100–500⊘ for tooth wear and striation. The SEM images reveal the details of tooth wear and striations that form the primary data for interpreting tooth occlusion and movement.

The X-ray micro computerized tomography (CT) scanning was carried out using the 225 kV micro-computerized tomography and scanned with beam energy of 120 kV and a flux of 120 l A at a resolution of 28.46 l m per pixel for the lower jaw (JZT-D061), 4.70 l m per pixel for the lower teeth (JZT-D061), 9.72 l m per pixel for the upper teeth (JZT-D061) and 4.70 l m per pixel for the lower teeth (JZT-CK005); these were done using a 360° rotation with a step size of 0.5° and an unfiltered alini reflection target. A total of 720 transmission images were reconstructed in a 2048 by 2048 matrix of 1536 slices using a two-dimensional reconstruction software developed by the Institute of High Energy Physics, CAS. The CT images provide various views of dentitions that are difficult to obtain using other imaging methods, show the morphology and wear facets in a homogenous tone for dark specimen, and allow us to produce a 3D tooth model print.

The X-ray micro computed laminography (CL) scanning was done with a beam energy of 70 kV and a flux of 70 l A at a resolution of 5.58 l m per pixel for the upper teeth of JZT-CK005 using a 720° rotation with a step size of 0.5°. A total of 720 image slices with a size of 2048 ⊘ 2048 pixels were reconstructed using a modified Feldkamp algorithm developed by the Institute of High Energy Physics, CAS. The CT/CL data were rendered to produce three-dimensional reconstructions of specimens using VGstudio Max 3.02 (Volume Graphics). The CL images can extract 3D tooth morphology from specimen preserved in large slabs that is not suitable for CT scan.

RESULTS

Tooth wear morphologies

Qishou jizantang. The upper incisors in JZT-D061 are preserved on a sizable slab and cannot be separated without destruction so the tooth wear cannot be properly imaged.
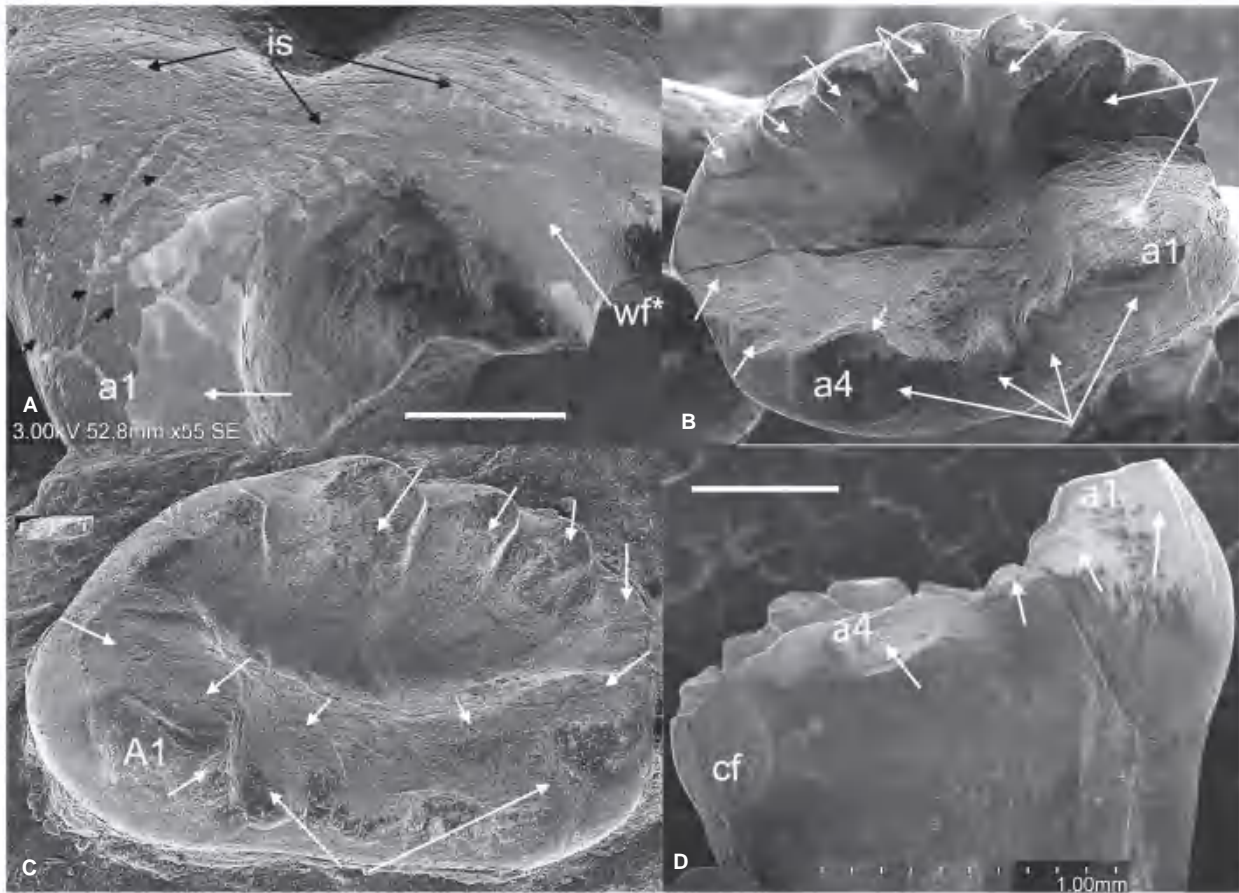
FIG. 2. General wear facets on teeth of Qishou jizantang (JZT-D061). A, lingual view of left p4. B, occlusal view of left m1. C, occlusal view of left M2. D, lingual view of left m1. White arrows point to wear facets. Short black arrows point to vertical or inclined orientated scratch grooves on the surface of a1, indicating orthal movement of the tooth in chewing (see also Mao & Meng 2019b, fig. S2C). Abbreviations: cf, contact facet; is, irregular striations; wf* indicates wear facet that is covered by glue. Scale bars represents 0.5 mm (A, D); B and C are at the same scale.

P3 is not preserved. We infer that the wear on the upper incisor and P3 are similar to those of Qishou sp. (see below). Two-thirds of the distal left P4 is preserved, whereas M1–2 on both sides are intact (Fig. 3). On P4, each of the two B cusps bears a wear facet on the tip, and the facet tilts buccally toward the central basin; there is no wear on the lingual side of row-B cusps (Figs 3, 4). A1 of P4 is worn on the tip and both the lingual and buccal sides, with the lingual side being more heavily worn. The labial-most cusp, mesiolabial to A1, bears wear on its lingual side, indicating that this cusp is positioned labial to b cusps of p4 in occlusion. By its position and wear, this cusp has been identified as AA1, following the terminology of Butler (2000) and Mao & Meng (2019a). Differing from both A1 and AA1, cusp A2 is worn on its tip. It seems that A2 of P4 cannot bite into the central basin of the narrow p4 but has a tip-to-tip contact with b cusps of p4.

The cusp rows of M1 and M2 are mesiodistally aligned (Fig. 3), as in other 'haramiyidans'; this cusp orientation differs from multituberculates in which the ultimate upper molar (M2) is one cusp row lingual to M1 (Krause & Hahn 1990). The general shape of the tooth indicates that the labial edge of each upper molar is relatively straight, and the lingual edge is curved (Figs 3, 4). This relationship is reversed in the lower molar, where the lingual edge is straight, and the labial edge is curved (Fig. 5). The tooth crown configuration reflects the occlusal mode of shenshouids in which the lingual cusps (row-a) of the lower molar bite into the central basin of the upper molar and the labial cusps (row-A) of the upper molar bite in the central basin of the lower molar; the straight arrangement of A/a cusps allows palinal movement of the lower teeth. Reflecting such an occlusal relationship, labial cusps of the upper molars, particularly A1 and A4, bear distinct wear facets and striations on the lingual and labial sides (Fig. 4; Mao & Meng 2019b, fig. S1). On the upper molars, row-B cusps bear a wear facet only on the labial side (Figs 3, 4). Wear striations were present
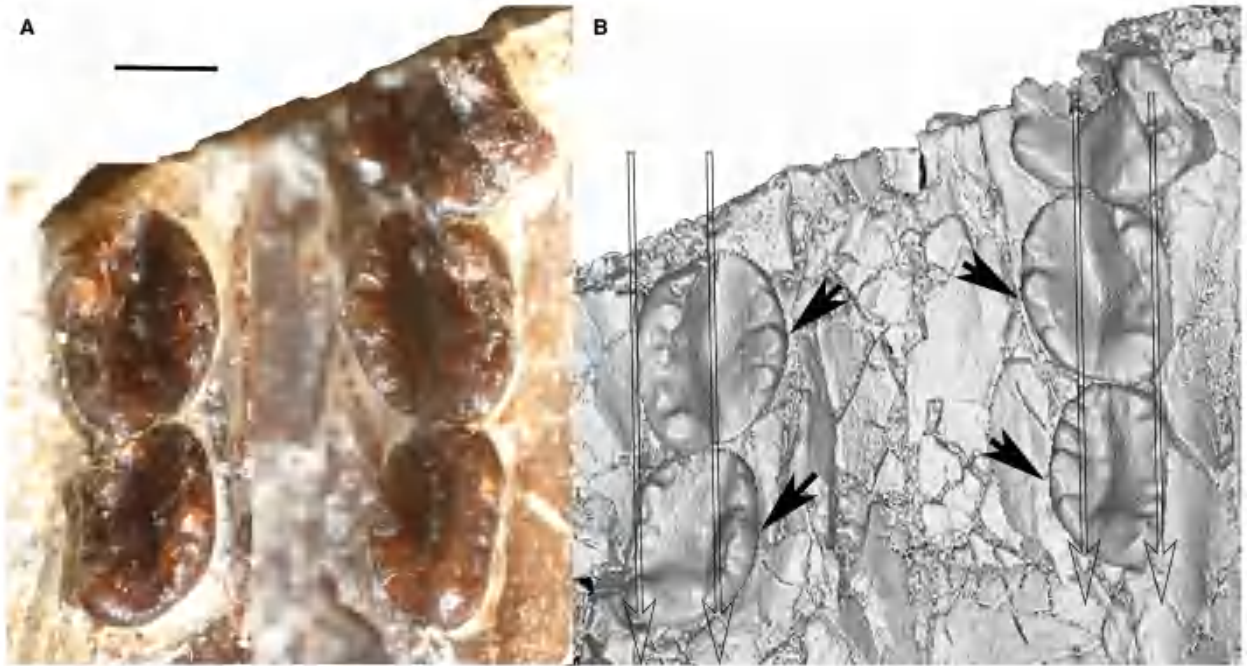
FIG. 3. Upper cheek tooth rows of *Qishou jizantang* (JZT-D061). A, optical photograph showing the occlusal view of the distal portion of the left P4 and M1–2 on both sides. B, CT-scan reconstruction of the dentition in the same view; the empty long arrows show functional areas for palinal move (in contact with cusps of lower teeth) and indicate the mesiodistal alignment of cusp rows in M1 and M2; note the straight labial side of each molar, in contrast to the curved lingual edge, as indicated by black arrow. Scale bar represents 1 mm.

in the basin, orientated parallel to the long axis of the tooth (Fig. 4; Mao & Meng (2019b, fig. S1).

The lower incisor is procumbent with its tip slightly bending distally (Fig. 5A). In lateral view, the sharp tip shows no sign of wear, but a wear facet is clear on the dorsal (distal) side of the tip (Fig. 5B, C). The wear indicates contact with the mesioventral side of the upper incisor, consistent with the wear of the upper incisor in *Qishou* sp. (JZT-CK005; Fig. 5D).

Cusp a1 of p4 is large and bears distinct wear that can be divided into two parts: the lingual part tilting slightly lingually and the labial part facing slightly labially and extending more ventrally on the cusp (Fig. 6A, B). The enamel on the lingual part appears thicker than the labial one. On the wear facet, striations are visible and orientated roughly in parallel to the longitudinal axis of the tooth (Figs 6; Mao & Meng 2019b, fig. S2). If the tooth cusp shape and occlusal relationship are also considered, it is clear that the power stroke in the chewing movement is generally palinal (posterior), but the chewing cycle must be constrained by the uneven tooth topology and cusp orientation. In addition, striations on the facet (Mao & Meng 2019b, fig. S2A) and vertical grooves on the mesial surface of a1 tip (Mao & Meng 2019b, fig. S2C) indicate that an orthal phase could be present and is followed by the palinal phase during chewing (See Discussion, below).

Similar to the upper molars but in a reversed orientation, the lingual and labial surfaces of row-a cusps of the lower molars bear wear facets; the lingual wear is particularly clear on a1 and a4 (Fig. 6). Striations on the wear facets are orientated roughly in parallel to the longitudinal axis of the tooth (Mao & Meng 2019b, fig. S2). Cusps b1 and b2 of m1 bear a confluent wear facet on the lingual side, opposite to the labial wear facet on a1; these two facets define a trough that has an open V-shape in mesial view. At the distal end of m1, cusps a6 and b7 are heavily worn, indicating contact with an upper tooth cusp (presumably A1 of M2) during the palinal grinding, while the cusps at the distal end of m2 do not have distinct wear facet. Wear varies in degree on the lingual side of other row-b cusps but there is no wear on the labial side of any b-row cusp (Figs 6; Mao & Meng 2019b, fig. S2). The longitudinally long central basin provides a guidance for palinal tooth movement during chewing, but the guidance could be reduced with progressive wear due to relief flattening, as in old individuals of other mammals (Koenigswald et al. 2013). The tooth morphology, cusp arrangement, and wear facets show no evidence for transverse movement of the teeth during tooth contact in the chewing cycle.

In addition to striations on the attritional facets, we recognize another kind of striations that are found primarily on the lateral side of a cusp or between adjacent
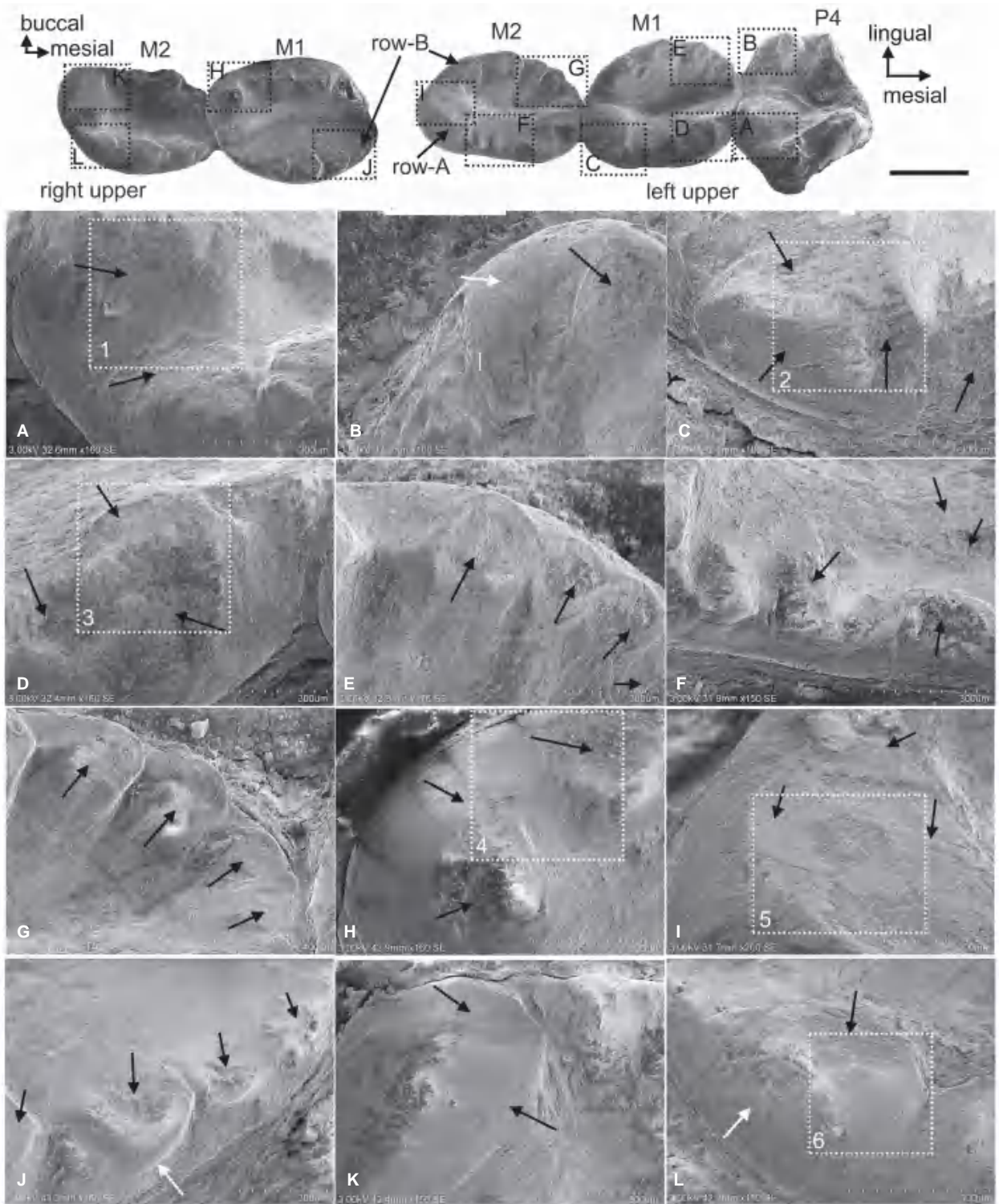
FIG. 4. Wear facets on upper teeth of Qishou jizantang (JZT-D061). A–L correspond to boxed areas shown on the dentition (top). Black arrows point to wear facets at various places of P4-M2. White boxes 1–6 on A, C, D, H, I and L correspond to figure S1A–F in Mao & Meng (2019b). Note that there are wear facets on both the lingual and buccal sides of row-A (buccal) cusps and on buccal sides of row-B (lingual) cusps, but not on the lingual sides of the latter (as indicated by white arrows in B, J and L). Scale bar represents 1 mm (top).
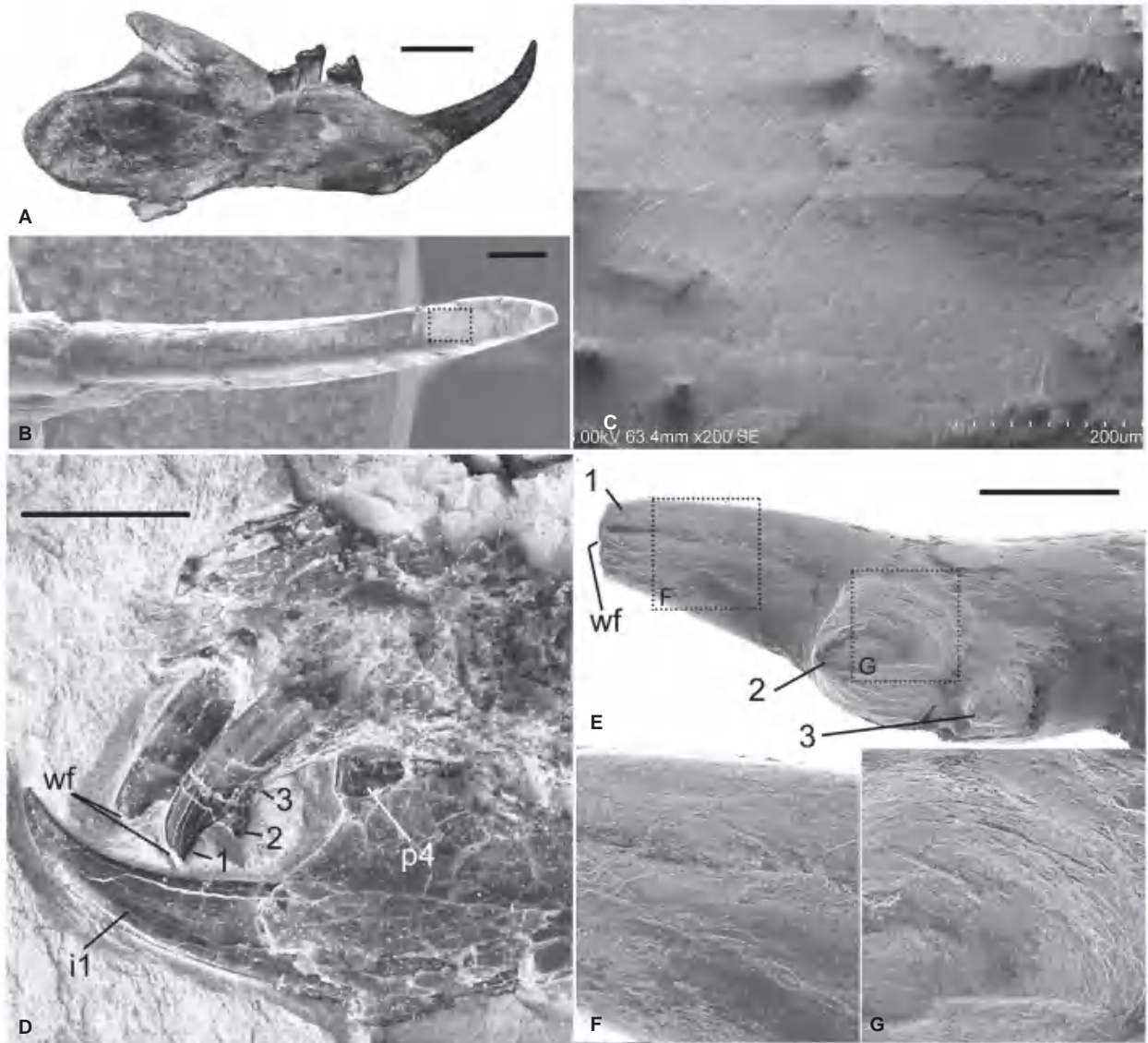
FIG. 5. Incisor condition of Qishou. A, medial view of the left lower jaw of Qishou jizantang (JZT-D061). B, dorsal (distal) view of the lower incisor showing the wear facet on the tip. C, close-up view corresponding to the boxed area on the tip of the lower incisor in B, showing the wear and striations in mesiodistal orientation. D, medial view of the right lower incisor and medial and lateral views of the right and left upper incisors of Qishou sp. in preserved condition (JZT-CK005); note that the main cusp (cusp 1) was worn on its tip. E, SEM image of the left upper incisor crown in ventral (distal) view. F–G, close-up views of the boxed areas in E showing scratched striations. Scale bars represent: 5 mm (A, D); 1 mm (B, E).

cusps (Mao & Meng 2019b, fig. S1F). We interpret these as being caused by scratches of food material across the tooth surface as they usually show irregular orientations. The tooth contact and lower jaw movement direction cannot be deduced from these irregular striations. In addition, there are some grooves that are occasionally observed on various teeth. These are usually in a vertical orientation and are thicker than the striations (Fig. 2A; Mao & Meng 2019b, fig. S2C). The size and orientation of these grooves suggest that they were probably created during the orthal movement of lower teeth while pressing against hard food particles, but this interpretation calls for further evidence.

Qishou sp. The general dental morphology of the specimen is similar to the holotype of Qishou jizantang, but this specimen represents an old individual with the dental morphology obscured by deep wear that hampers its precise identification (Mao & Meng 2019a). The mesial (main) cusp of the upper incisor bears a distinct wear
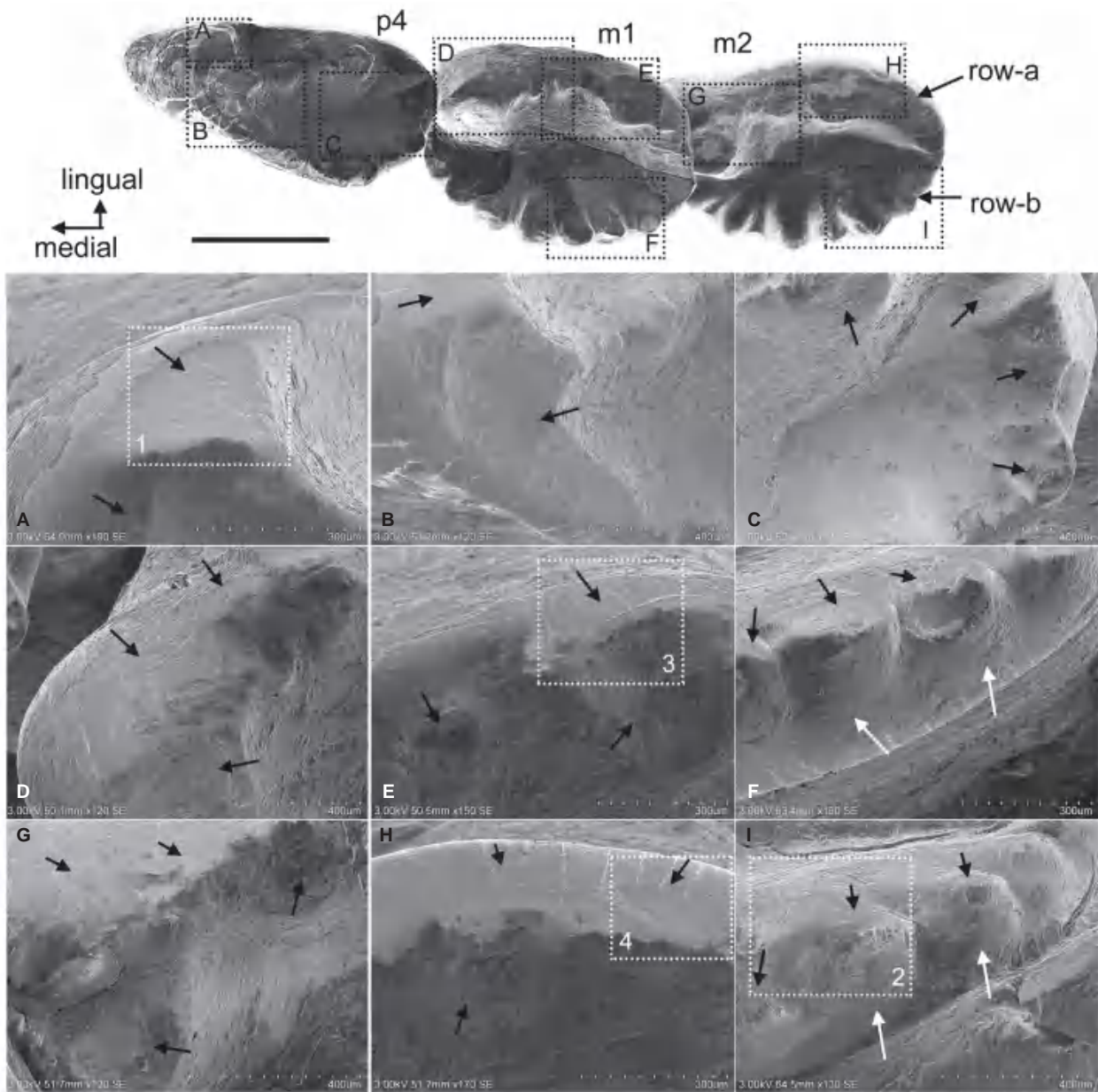
FIG. 6. Wear facets on lower left teeth of Qishou jizantang (JZT-D061). A–I correspond to boxed areas shown on the dentition (top). Black arrows point to wear facets at various places on p4–m2. White boxes 1–4 on A, E, H and I correspond to figure S2A–D in Mao & Meng (2019b). Note that wear facets on the lingual and buccal sides of row-a (lingual) cusps and on lingual sides of row-b (buccal) cusps, but not on the buccal sides of the latter (as indicated by white arrows in F and I). Scale bar represents 1 mm (top).

facet on its tip, whereas the tip of the lower incisor is sharp in lateral or medial view (Fig. 5D), similar to that of Q. jizantang. It is clear that the lower incisor did not contact the upper incisor in a tip-to-tip manner. The inclined facet on the upper incisor suggests that it is caused by grinding against the distal surface of the lower incisor. This is confirmed by the wear facet on the dorsal (distal) side of the lower incisor tip of Q. jizantang that has mesiodistally oriented striations (Fig. 5B, C). There is a wear facet on the tip of cusp 2, facing distoventrally.

Striations are denser on the lateral side than on other areas of the incisor (Fig. 5E–G). These striations are irregular in size and orientation, not planar, although a general ventrodorsal trend is discernible; it is most likely that they are caused by scratches from food particles.

The left upper cheek teeth are illustrated in Figure 7. Because the dentition is preserved in slab, it is impossible to take SEM images of the specimen. CL images have been obtained, but the method cannot supply sufficient data to reconstruct the dentition in its entirety. Nevertheless, it is
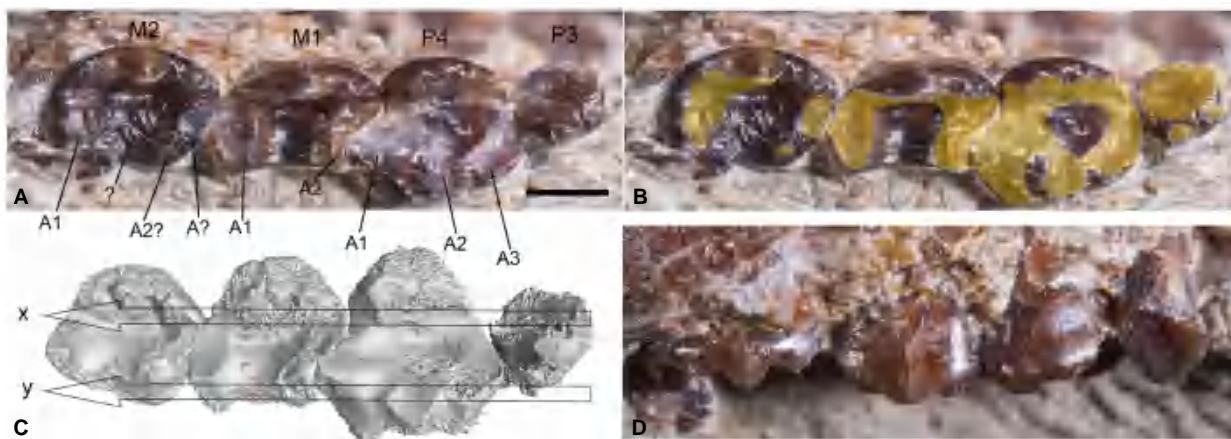
FIG. 7. Left upper cheek teeth of Qishou sp. (JZT-CK005). A, occlusal (crown) view, slightly more toward the lingual side. B, crown view with wear facets marked with yellow. C, CL image of the teeth, with the empty arrows x and y indicating the wear tracks and direction of move for the lower molars relative to the upper ones. D, lingual view of the left upper cheek teeth, showing the wear on P3 and the intact surface of P4–M2. Scale bar represents 1 mm.

clear that P3 has a large wear facet that inclines ventrolingually and facets on the tips of the two small labial cusps. This is the only upper tooth that has the lingual side significantly worn, contrasting with the condition in P4–M2 in which the lingual sides of row-B cusps are intact (Fig. 7D). However, the P3 wear facet on the lingual side is immediately aligned mesially to the wear facet on the labial side of the lingual cusp of P4, created by contact with the lingual side of a1 of p4 (Fig. 7B, C).

Row-A cusps of P4 are heavily worn (Fig. 7A–C). The labial and lingual wear are distinct on A1, and continues distally with wear facets on cusp A2 of M1. The central basin is open mesially and distally, and confluent distally with the mesial basin of M1. Distinct striations are present on all wear facets, indicating a palinal movement of lower teeth in chewing. The centre of the basin appears less worn than its surrounding area, which suggests that a1 of p4 may not have reached the deepest centre of the basin after it became blunt with wear (Fig. 8B). Although there are three row-A cusps, no cusp that is comparable to the one denoted as AA1(C1) in the holotype of Qishou jizantang (JZT-D061). A2 of P4 in JZT-CK005 is worn on its labial and lingual sides, whereas in JZT-D061 only the lingual side of C1 is worn; the condition in the former does not seem to be formed by deeper wear.

M1 is less worn than P4 but more so than M2. Cusps A1 and A2 are worn on the lingual and labial sides. Row-B cusps are heavily worn on the labial side to form a vertical and flat facet, contrasting the unworn and thus convex lingual surface. Because of the wear, row-B cusps become ridge-like with sharp edges. Similar to P4, the basin centre of M1 between A1 and A2 is less worn than its surrounding area, and that of M2 appears little worn so that fine enamel ridges are present. The wear pattern

of the upper cheek teeth indicates again that it is the row-A cusps occluded with the central basin of the lower teeth, whereas row-B cusps must have been positioned lingually to row-a cusps of the lower teeth in occlusion.

The lower premolar (p4) is deeply worn (Figs 8, 9). Cusp a1 bears wear on its lingual and labial sides (Figs 8A, B; 9). The lingual facet is small and tilts dorsolingually (Fig. 9). The large labial facet faces dorsolabially, extending distolabially to the middle of the labial cusp row, then turns distolingually to the floor of the central basin (Figs 8B; 9). This indicates that when a1 of p4 passed through the basin between row-A and row-B of P4, the labial side of a1 had an extensive contact with the lingual side of the large cusp A1 of P4. The wear on cusp a1 shows a typical character of attritional facets, with a flat surface and marginal boundaries (Fig. 9). Because of wear, cusp a1 has become blunt. Two distal row-a cusps, presumably a2 and a3, also bear wear (Fig. 8B). Row-b cusps have been completely erased by contact or grinding against the large cusp A1 and A2 (or AA) of P4 (Figs 8C, 9). This could be because p4 is narrow and the wear facet on row-b continues distally with the facet on the lingual side of row-b cusps of m1 (Fig. 8B). Striations on a1 facets along the basin are distinct; they are parallel and generally orientated mesiodistally, showing palinal movement (Fig. 9). Because of the deep wear, the central basin of p4 has almost disappeared.

Row-a cusps of m1 have been completely erased so that the lingual view of the tooth shows only a low, flat platform of row-a (Fig. 8D). In occlusal view, row-a has been reshaped as a rounded and mesiodistally confluent wear surface with its lingual side facing dorsolingually (Fig. 8A, B). Cusp a1 is not distinguishable and partly broken, probably owing to the weakness of this area
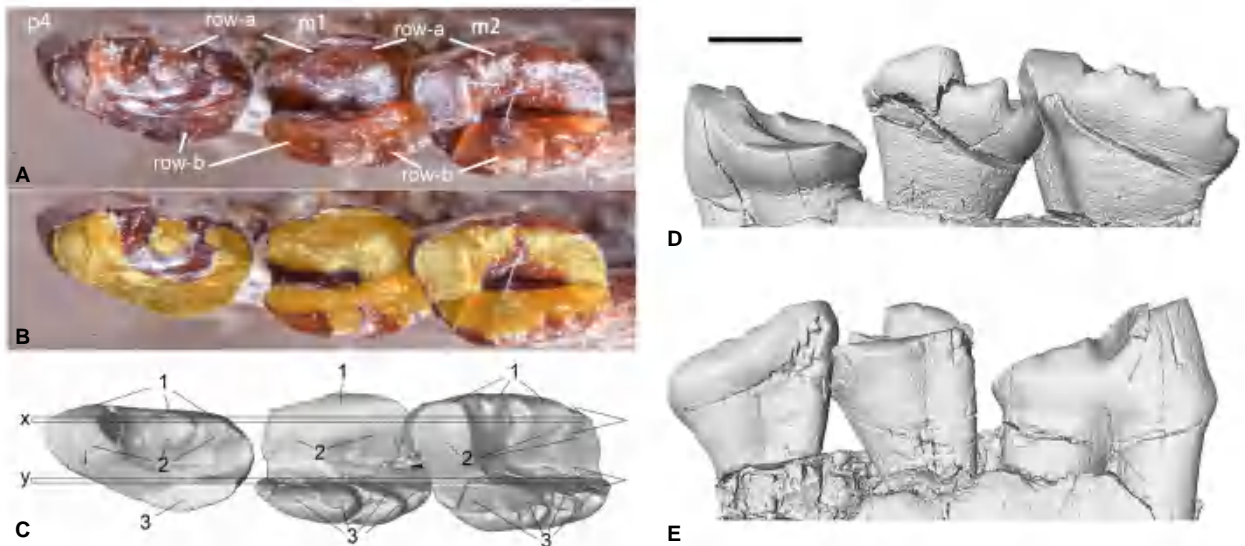
FIG. 8. Lower left cheek teeth of Qishou sp. (JZT-CK005). A, optical photograph of the teeth in occlusal view. B, wear facets on the crown surface in yellow. C–E, reconstructed CT images of the teeth in occlusal, labial and lingual view, respectively. The empty arrows x and y in C indicate wear tracks and movement direction of the lower teeth in chewing, corresponding to those on the upper teeth. 1, wear on the lingual side of row-a; 2, wear on the labial side of row-a; 3, wear on the lingual side of row-b. Note the unworn labial surface of row-b cusps on m1–2 and the heavily worn row-a cusps. Scale bar represents 1 mm.

caused by wear. In contrast, row-b is still high, with its lingual side bears steep wear facets, created by contact with the labial surface of row-A cusps of the upper molar, whereas the labial side of row-b remains unworn. Because of the wear, the central basin becomes shallow and its two ends are wide open. Striations are distinct on all wear facets; however, because of the glue on the crown to protect the cracked tooth, details of the striations in some areas are masked (Fig. 9C).

Distinct attritional facets are on the usual positions of m2, mostly on the basin-ward sides of row-a and row-b cusps. It is worthwhile emphasizing again that wear facets are present on the lingual side of row-a, distributed from a1 to a4 (Fig. 9), which forms the evidence that row-a has occluded in the central basin of the upper molar. Similar to p4 and m1, distinct striations are present on all attritional facets of m2 and show a horizontal movement of the tooth. The central basin is open on its mesial and distal end; its floor is uneven with its center being the deepest. The unevenness could be reduced if tooth wear had continued, as noted in other mammals by Koenigswald et al. (2013).

Shenshou lui. The dental morphology of S. lui have been briefly reported, and because the holotype of S. lui is preserved on a large slab, it is difficult to obtain SEM and CT images so that only general tooth wear is described (Fig. 10; Bi et al. 2014).

The holotype of Shenshou lui (LDN HMF2001) represents an individual that is slightly older than that of

JZT-D061 but certainly younger than JZT-CK005. M1 was broken but the tooth shape and wear are clear. The wear facets are on the labial and lingual sides of row-A cusps. In particular, wear facets on the labial side of row-A cusps of M1 become confluent to form a large facet that extends mesiolabially (Fig. 10A). This clearly shows that row-A cusps had occluded in the central basin of the lower molar. The wear facets on the labial sides of row-B cusps are also extensive that they become confluent to form a single flat facet. Striations are visible on these attritional facets. Again, there is no wear facet on the lingual side of row-B. M2 is complete and less worn than M1. Each of its row-A cusps, including the small middle ones, bears wear facet on the labial side. The labial sides of row-B cusps are worn, but the adjacent facets are separated by a narrow groove.

On the lower teeth, cusp a1 of p4 has a distinct abrasional facet at its tip, suggesting its puncture–crushing function. A small facet also exists on the lingual side of a1 (Fig. 10B). The basin-ward sides of other cusps bear wear facets with various degrees of wear. On m1, the wear facets are distinct on the lingual and labial sides of row-a cusps and the wear on the lingual side extends from a1 to the distolingual cusp, indicating that row-a cusps occluded in the basin of M1 in chewing (Fig. 10B, C). The lingual side of row-b bears three distinct wear facets that are separated by narrow grooves; further wear would make them confluent as one large facet; there is no wear on the labial side (Fig. 10D). As in other euharamiyidans, m2 is less worn than m1. Only a1 has a wear facet on the
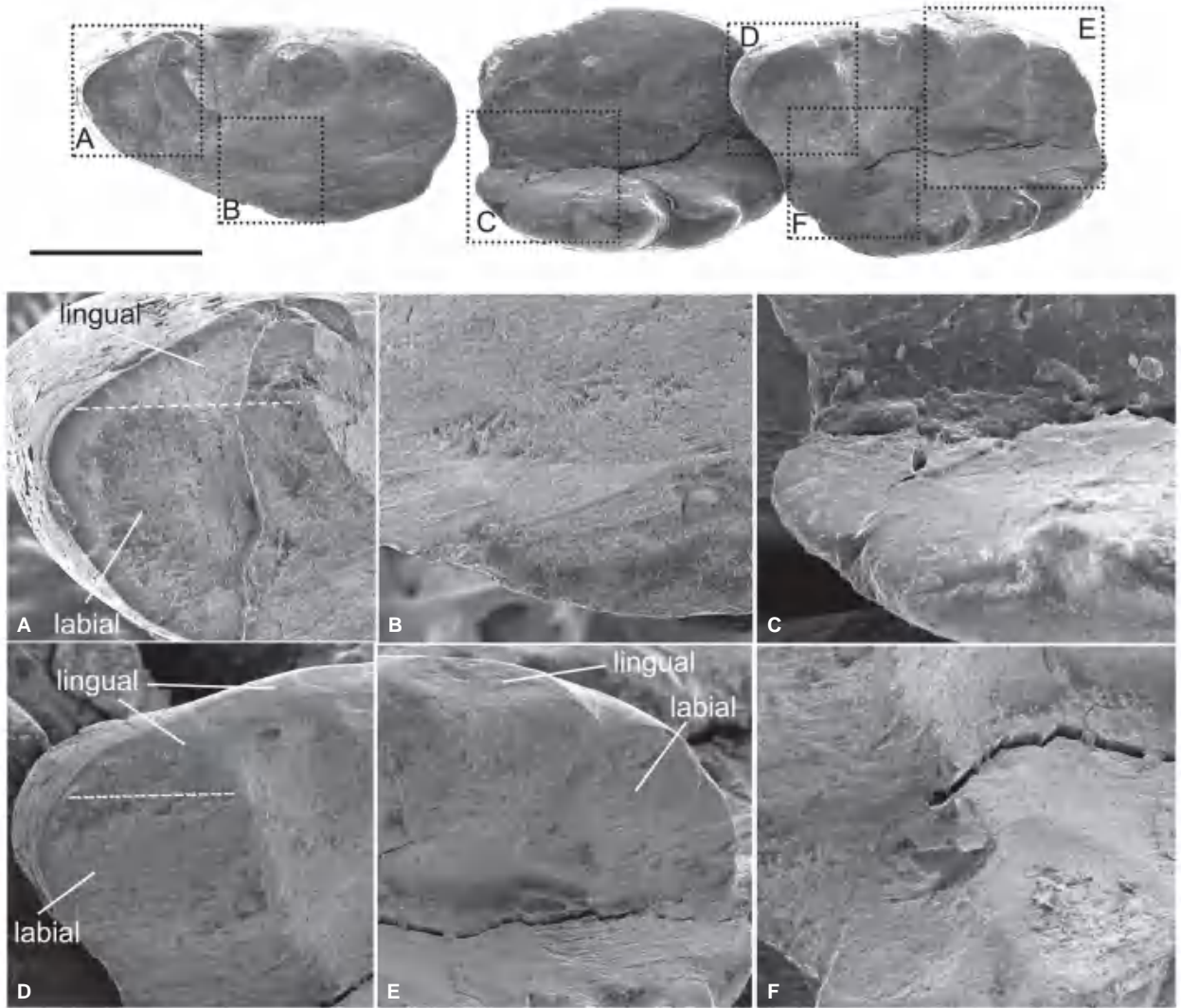
FIG. 9. Scanning electron microscopy (SEM) images of lower cheek teeth of Qishou sp. (JZT-CK005). The top image is the occlusal (crown) view of the left lower cheek teeth. A–F, close-up views corresponding to the boxed areas in the top image. The dashed line in A and D shows the boundary between the lingual and labial wear facets on a1 of p4 and m2, respectively. Scale bar represents 1 mm.

lingual side, although wear is on the basin-ward surfaces of both row-a and row-b cusps.

Summary remarks

The wear patterns of Qishou jizantang, Qishou sp. and Shenshou lui are similar in that row-A of upper molars and row-a of lower molars are the primary cusp rows engaged in tooth–tooth contact in chewing; each of them occlude in the central valley of the opposite tooth. The holotype of Q. jizantang is unique in having cusp AA1 on P4 and an extra wear facet on the lingual side of AA1. The specimen assigned to Qishou sp. has the deepest tooth wear that has erased much of the cusp structure, which is the primary reason that the specimen was not

identified to species level (Mao & Meng 2019a). The holotype of S. lui has relatively simple wear facets because the molars have fewer cusps.

Because of the unevenness of the cusp heights, abrasional facets are commonly present on the tip of the highest cusp of a tooth, best shown on A1/a1 in euharamiyidans; these facets are often rounded, not planar, and do not bear distinct and regular boundaries and striations. Attritional facets are predominant on teeth of shenshouids (Qishou and Shenshou). The attritional facets and striations are created by tooth–tooth contacts during the power stroke and developed during normal mastication (Maier & Schneck 1982; Butler 1983; Mills 1963, 1967). As pointed out by Koenigswald et al. (2013), attritional facets best reflect contact and occlusal relationships of teeth, whereas the striations indicate the relative
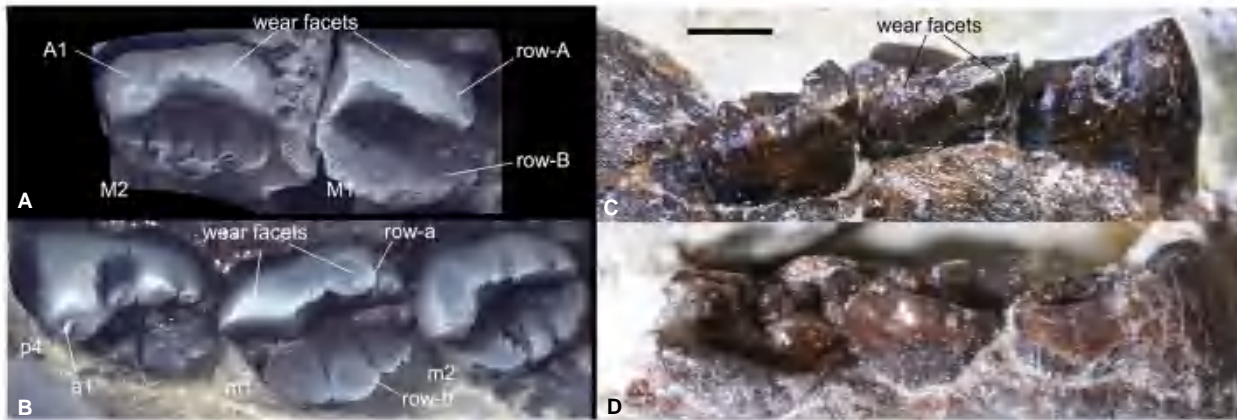
FIG. 10. Cheek teeth of Shenshou lui (LDN HMF2001). A, right M1–M2 in occlusal view (M1 was broken and photographically joined). B, lower left cheek teeth (p4–m2) in occlusal (slightly lingual) view. The specimen was coated with ammonium chloride to enhance contrast. C, left lower cheek teeth in lingual view. D, labial view of the right lower cheek teeth. Note the unworn labial surface of the teeth. Scale bar represents 1 mm.

movement of teeth. In shenshouids, wear facets of upper teeth are present on the labial side of row-B (lingual) cusps and on both lingual and buccal sides of row-A (buccal) cusps. In the lower teeth, distributions of wear facets are reversed: they are on the lingual side of row-b (buccal) cusps and on both lingual and buccal sides of row-a (lingual) cusps. Flat attritional facets are present on various cusps, representing a consistent and lasting contact relationship between the upper and lower teeth in chewing. The striations on these facets are primarily horizontal and parallel to the straight side of the tooth (the lingual cusps row-a of the lower molar and the labial cusps row-A of the upper molar), which indicates a palinally occlusal motion.

The moderate tooth wear in the holotype of Qishou jizantang indicates that the individual is probably in the individual dental age stage 3 (IDAS 3; Anders et al. 2011), which is most suitable for motion analysis of occlusion (Koenigswald et al. 2013). In contrast, the teeth of Qishou sp. (JZT-CK005) are deeply worn and can be assigned to senile age stages, either IDAS 4 or IDAS 5 (Anders et al. 2011). Deep wear can lead to flattening of the occlusal surface and less precise chewing movements of teeth because the guiding structures are reduced (Koenigswald et al. 2013). Thus, differences of functional structures preserved on teeth from individuals with different ages should be viewed with caution.

DISCUSSION

General remarks

Simpson (1926; see also Ungar 2010, 2015) recognized three types of food processing in mammal teeth: (1) shearing, wherein tooth crests in opposing slide past one another with vertical jaw movements; (2) crushing, wherein cusps are pressed into basins with vertical movements; and (3) grinding, wherein cusps slide across basins with horizontal movements. These mastication types can be inferred from tooth morphology, orientation and tooth wear (Koenigswald et al. 2013).

For many decades, occlusal relationships in 'haramiyidans' were inferred from isolated teeth; this is highly challenging for such a unique group that has no analogue to compare it with. Nonetheless, the pioneers in the research of 'haramiyidans' laid down the foundation in proposing various occlusal patterns based on tooth wear, on which the current studies build. Unequivocal wear facets were known in Thomasia (= Haramiya; Sigogneau-Russell 1989, 1990; Butler & MacIntyre 1994; Clemens & Martin 2014), Eleutherodon (Kermack et al. 1998; Butler & Hooker 2005), Theroteinus (Sigogneau-Russell et al. 1986; Hahn et al. 1989; Debuysschere 2016), Sineleutherus uyguricus (Maisch et al. 2005; Martin et al. 2010), Arboroharamiya jenkinsi (Zheng et al. 2013; Meng et al. 2014), Shenshou lui, Xianshou (Bi et al. 2014), Maiopatagium (Meng et al. 2017) and Q. jizantang (this study). Tooth wear on P3 is clearly present in the exposed tooth of A. allinhopsoni (Han et al. 2017) and may be so in Vilevolodon (Luo et al. 2017) but wear on the other teeth needs to be confirmed in both taxa; this is partly due to the fact that in these two taxa most cheek teeth are in occlusal position, which prevents examination of the detailed wear facets and striations. Wear striations were known in Theroteinus (Sigogneau-Russell et al. 1986), Thomasia (Butler & MacIntyre 1994), Eleutherodon (Kermack et al. 1998) and A. jenkinsi (Meng et al. 2014); the latter provides the matching wear facets and striations from upper and lower teeth of the same individual. Wear condition

has been presented in Haramiyavia (Luo et al. 2015) but the wear in Haramiyavia is equivocal based on our observation of the type specimens of Haramiyavia (NHMD 236380 (= MCZ 7/G95) and NHMD 236381 (= MCZ 10/ G95)).

The newly discovered skeletal specimens provided more reliable evidence on the occlusal relationship of 'haramiyidans'. In these specimens, upper and lower teeth are preserved in occlusion, such as in Xianshou linglong (Bi et al. 2014), Vilevolodon diplomylos (Luo et al. 2017) and Arboroharamiya allinhopsoni (Han et al. 2017); if not in occlusion, the teeth from the same individuals, such as A. jenkinsi (Zheng et al. 2013; Meng et al. 2014), X. songae, Shenshou lui (Bi et al. 2014) and Q. jizantang (Mao & Meng 2019a; this study), allow us to infer the occlusal relationship with confidence. In fact, because the tooth occlusal relationship may have altered in preservation, the most reliable evidence for tooth occlusion is a combination of dental morphology from a single individual, wear facets, and striations on the teeth of the animal. The general tooth morphology and cusp shape and arrangement of upper and lower molars show that shearing, if present at all, is minimal in food processing of shenshouids (Shenshou and Qishou) and other 'haramiyidans'; this is further confirmed by tooth wear facets and striations.

Centric occlusion

Centric occlusion had been briefly used in some studies on 'haramiyidans', thus general discussion about centric occlusion in mammals is provided in Mao & Meng (2019b). What would be the centric occlusion in 'haramiyidans' appears to be difficult to define for the reason that tooth occlusal patterns are different, or at least interpreted to be so, in various taxa of 'haramiyidans'. For instance, in Haramiyavia (Jenkins et al. 1997; Luo et al. 2015) and Maiopatagium (Meng et al. 2017), it is the labial cusps of the lower molar that occlude into the central basin of the upper molar, whereas in Arboroharamiya (Zheng et al. 2013; Meng et al. 2014; Han et al. 2017) and Vilevolodon (Luo et al. 2017), it is the lingual cusps that occlude into the central basin of the upper molar. To keep it consistent and convenient when we discuss the occlusal patterns below, we propose the following definition for the centric occlusion in 'haramiyidans': the relation of opposing cheek teeth as a unit with their cusps reaching the maximal interdigitation contact. We want to emphasize the cheek teeth as a unit because the centric occlusion has to involve all the cheek teeth and cannot to be a condition represented by individual teeth. Even though for those taxa that are based on isolated teeth, occlusal condition inferred is still informative. In addition, 'cusps' are not specified; they could be

the lingual cusps, labial cusps, or both. Moreover, for those that have the extra cusps, such as Haramiyavia and Eleutherodon discussed below, whether those cusps involved in occlusion is unclear or controversial. We would assume that the centric occlusion is transitory and occurs at the end of the occlusal phase of the power stroke when the stroke has involved tooth–tooth contact, as in tribosphenic dentition (Crompton & Hiiemae 1969, 1970). For specimens that we have access to, the centric occlusion can be estimated with confidence by fitting the opposing teeth against each other, as in Arboroharamiya jenkinsi (Meng et al. 2014), or manipulating 3D printed casts of the upper and lower teeth, as in Qishou (this study); in both cases, the premise is that the upper and lower teeth are from the same individual.

Occlusal modes

Multituberculates. To understand various occlusal patterns in 'haramiyidans', it is helpful to use the tooth occlusal relationship of multituberculates as a reference because the latter is now well known and extensively studied. The basic or primitive form of multituberculate molars is that there are two rows of multiple cusps in both upper and lower molars. In addition, M2 is positioned one cusp row lingual to M1. When the upper and lower molars are in occlusion, the labial cusps of m1 occlude in the central furrow of M1, whereas the lingual cusps of m2 bite into the furrow of M2 (Fig. 11). This pattern has been demonstrated to be unique and
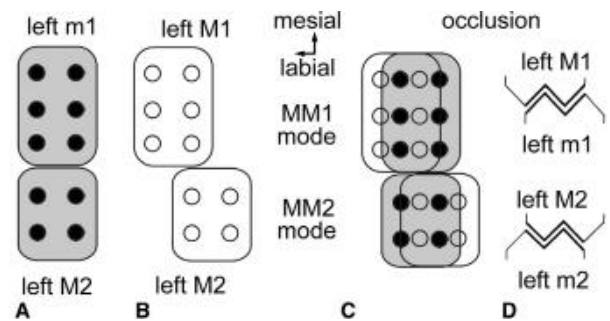

FIG. 11. Diagrammatic expression of multituberculate occlusal patterns of molars. A, left lower molar shaded with cusps represented by black dots. B, left upper teeth unshaded with cusps represented by open circles (this is dorsal view of the right upper molars). C, occlusal relationship of the upper and lower molars. D, occlusal relationship in cross-sectional view. MM1 mode represents the occlusal relationship of the M1 and m1 in multituberculates, and MM2 mode for M2 and m2. Note that in MM1 the labial cusps of m1 bite in the central basin of M1, whereas in MM2 mode the lingual cusps of m2 bite in the central basin of M2. The diagram is based on but horizontally flipped from Krause & Hahn (1990).

universally present in multituberculates (Krause & Hahn 1990). In some advanced forms, primarily cimolodontans, an additional ridge or cusp row has developed on the lingual side of M1 and the buccal side of M2.

In this study, for convenience in discussion, we denote the multituberculate M1/m1 occlusal relationship as MM1 mode, and the multituberculate M2/m2 occlusal relationship as MM2 mode (Fig. 11). It should be pointed out that previous studies on the tooth occlusal relationship of multituberculates have commonly been focused on the ultimate premolars and the mesial molar (M1/m1) (Lazzari et al. 2010), and that of the M2/m2 has unfortunately often been overlooked (Kielan-Jaworowska et al. 2004; Lazzari et al. 2010; Yuan et al. 2013; Luo et al. 2015). For instance, one of the diagnostic features of allotherians proposed by Kielan-Jaworowska et al. (2004, p. 249) is: 'mammals in which the upper and lower molariform teeth have basically two longitudinal rows of cusps, which occlude so that the labial lower row bites into the basin between the upper rows (additional rows may develop on upper teeth)'. This is incorrect for the M2/m2 occlusion of multituberculates, as already demonstrated by Krause & Hahn (1990; Fig. 11).

As currently interpreted, 'haramiyidans' differ from multituberculates in having either MM1 or MM2 occlusal mode, but not simultaneously. Nonetheless, The MM2 mode is unique among mammaliaforms and shared by euharamiyidans (except for Maiopatagium) and multituberculates, which may hold the key to understanding the evolution of allotherian molars and occlusal patterns (Meng 2014).

Shenshouids. Shenshouids include Shenshou lui, Qishou jizantang and Qishou sp. (Mao & Meng 2019a). The holotype of Q. jizantang and the specimen assigned to Qishou sp. have the left upper and lower dentitions preserved, making it possible for us to follow Charles et al. (2007) and Koenigswald et al. (2013) in using the motion of the left lower jaw as the standard point of view. Dentally, shenshouids are more derived than Haramiyavia, Thomasia and Theroteinus, but more primitive than those with the double-engaged (DE) occlusal mode (see below) including Arboroharamiya, Vilevolodon and probably Xianshou.

The lower jaw and tooth movements can be inferred from the morphology of jaw joint, attachment sites of masticatory muscles, tooth occlusion relationship (tooth shape that provides the guidance), wear facets and striations. In particular, the attritional facets and striations on these facets are the main source for occlusal relationship and motion directions (Koenigswald et al. 2013); this is particularly important for extinct species, such as 'haramiyidans'. The transversely narrow but dorsoventrally extended mandibular condyle, located in the glenoid fossa that lacks the postglenoid process (Mao & Meng 2019a), provides the first constraint for jaw movement in shenshouids. With such a joint, the jaw can open to a considerable extent and moves palinally in chewing. As in multituberculates and rodents, the pterygoid and masseteric fossae are anteriorly extended so that the masticatory muscles could provide power and control for the lower jaw during chewing (Kielan-Jaworowska et al. 2004).

As we reported above, a distinctive feature of shenshouids is that row-A and row-a cusps are aligned relatively straight so that they can fit in the central basin of the opposite tooth and allow palinal movement of the lower teeth in chewing. In contrast, row-B and row-b cusps are arranged in curved outline, and cusps on these rows are relatively small; these cusps are worn only on their basin-ward sides. Based on tooth shape, cusp orientation, and wear facets and striations, the occlusal mode of shenshouids can be reconstructed (Fig. 12; Mao & Meng 2019b, fig. S3).

Compared to those that have the DE mode (Fig. 13), such as Arboroharamiya, Vilevolodon and possibly Xianshou, the cheek teeth of shenshouids are proportionally small and the premolars are not so inflated (see also Mao et al. 2019; Mao & Meng 2019a). P3 and P4 are not basined and have no enamel flutings or ridges; they do not form a 'flexure' in the maxilla (Luo et al. 2017); instead, they are aligned horizontally with the molars in lingual or labial view. As shown by the distinct wear facet on P3 in JZT-CK005 (Fig. 7), it is clear that cusp a1 of p4 must have bitten against P3 as the initial contact of the upper and lower teeth at the end of the orthal (puncture–crushing) phase during mastication. This initial contact provides a reference point with which the relative positions of other teeth at the same chewing stage can be identified (Figs 12C; Mao & Meng 2019b, fig. S3A–B). For instance, at the same time as a1 of p4 is in contact with P3, a1 of m1 must be positioned in the basin between A1 and B1 of P4, and A1 of P4 in the mesial end of the m1 central basin, immediately distal to cusp a1 of m1. At the same stage, A4 of M1 is in the midpoint of the central basin of m1, whereas A1 of M1 is in mesial end of the m2 central basin, immediately distal to a1 of m2.

During the palinal phase of chewing stroke, a1 of p4 would pass distally and 'stop' in the basin of P4 (Fig. 12). Similarly, a1 of m1 would pass through the P4–M1 junction and stop in the basin center of M1, and a1 of m2 would pass the M1–M2 junction and stop in the basin of M2. Correspondingly, A1 of M1 and M2 would stop in the basin centre of m1 and m2, respectively. This position represents the maximal cuspal interdigitation and is interpreted as the centric occlusion in shenshouids. From the centric occlusion, the lower teeth disengage from the uppers and start a new chewing cycle. In addition, using a1 of m1 as the exemplar, the travel distance of the palinal
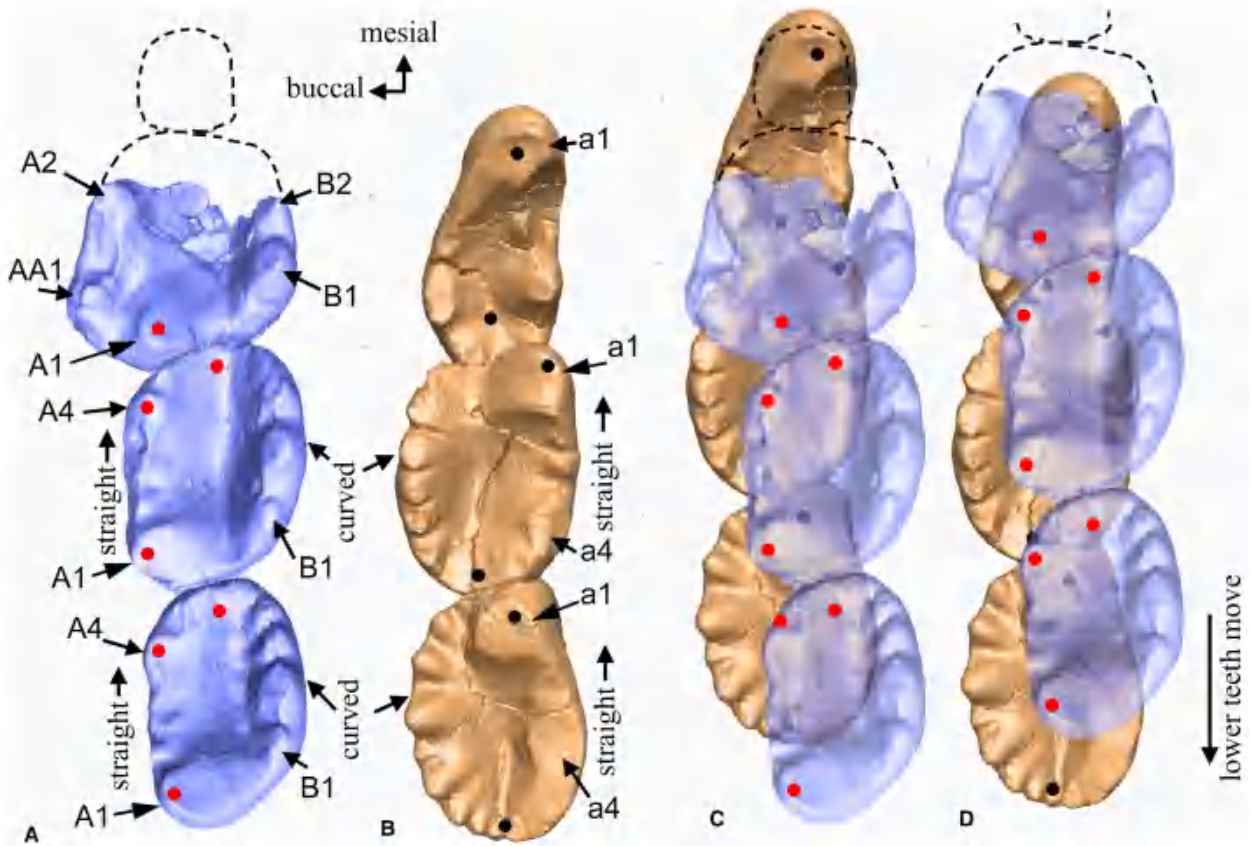
FIG. 12. Tooth occlusal relationship of shenshouids. A, occlusal view of the left P4–M2 (for the purpose of showing their matching relationship in occlusion, the upper teeth are photographically flipped horizontally). B, occlusal view of the left p4–m2. C, the upper and lower teeth are in occlusal relationship, presumably at the end of the puncture–crushing phase. D, the upper and lower teeth are in centric occlusion, presumably at the end of the grinding (palinal move) phase. The red and black dots are reference points on upper and lower teeth, respectively. In C and D, the upper teeth are displayed semi-transparently to show the occlusal relationship with the lower teeth. Additional views of the tooth occlusion are provided in Mao & Meng (2019b).

phase can be estimated, which is about two-thirds of the tooth length. As guided by the uneven cusp height and basin floor with its centre being the deepest, the travel path of the lower molar would be first distoventrally and then distodorsally to reach the centric occlusion. These may be considered as the incursive and excursive occlusal phases of the power stroke. When tooth wear deepens with aging, the relief of the tooth will be reduced, and the travel path of the lower molar will become even.

Compared to molar occlusion, P4/p4 occlusion, at least in *Qishou jizantang* (JZT-D061), has an extra valley between A1 and AA1; thus, a unique feature in the occlusion of *Q. jizantang* is that the extra valley would receive b-cusps, at least b2, of p4 (Fig. 12). This is quite different from the P4/p4 occlusion in other euharamiyidans. Again, the cusp arrangement of P4 in JZT-D061 is highly similar to that of M1 in *Haramiyavia*, although the tooth occlusal mode has been interpreted differently (Jenkins *et al.* 1997; Luo *et al.* 2015; Figs 13, 14).

Compared with other Jurassic 'haramiyidans', cusps a1 on the lower molars and A1 on the upper molars are relatively small in shenshouids in which the mesial extension of a1 on lower molars is not significant, relative to row-b cusps, and A1 on upper molars is not so distally extended. In addition, a4 on the lower molar is the second largest cusp, whereas the corresponding cusp in *Arboroharamiya*, *Xianshou*, *Vilevolodon*, *Eleutherodon* and *Sineleutherus* has been reduced. We have shown that wear facets are present on the lingual side a4 of the lower molar and the labial side of A4 of the upper molar in shenshouids. This wear pattern indicates that row-a cusps, not only a1, of the lower molar, occluded into the basin of the opposite upper molar, whereas row-A cusps, not only A1, of the upper molar, bit into the basin of the corresponding lower molar (Fig. 12). This occlusion is similar to the M2/m2 occlusion of multituberculates (Fig. 11), which is unique among mammaliaforms.
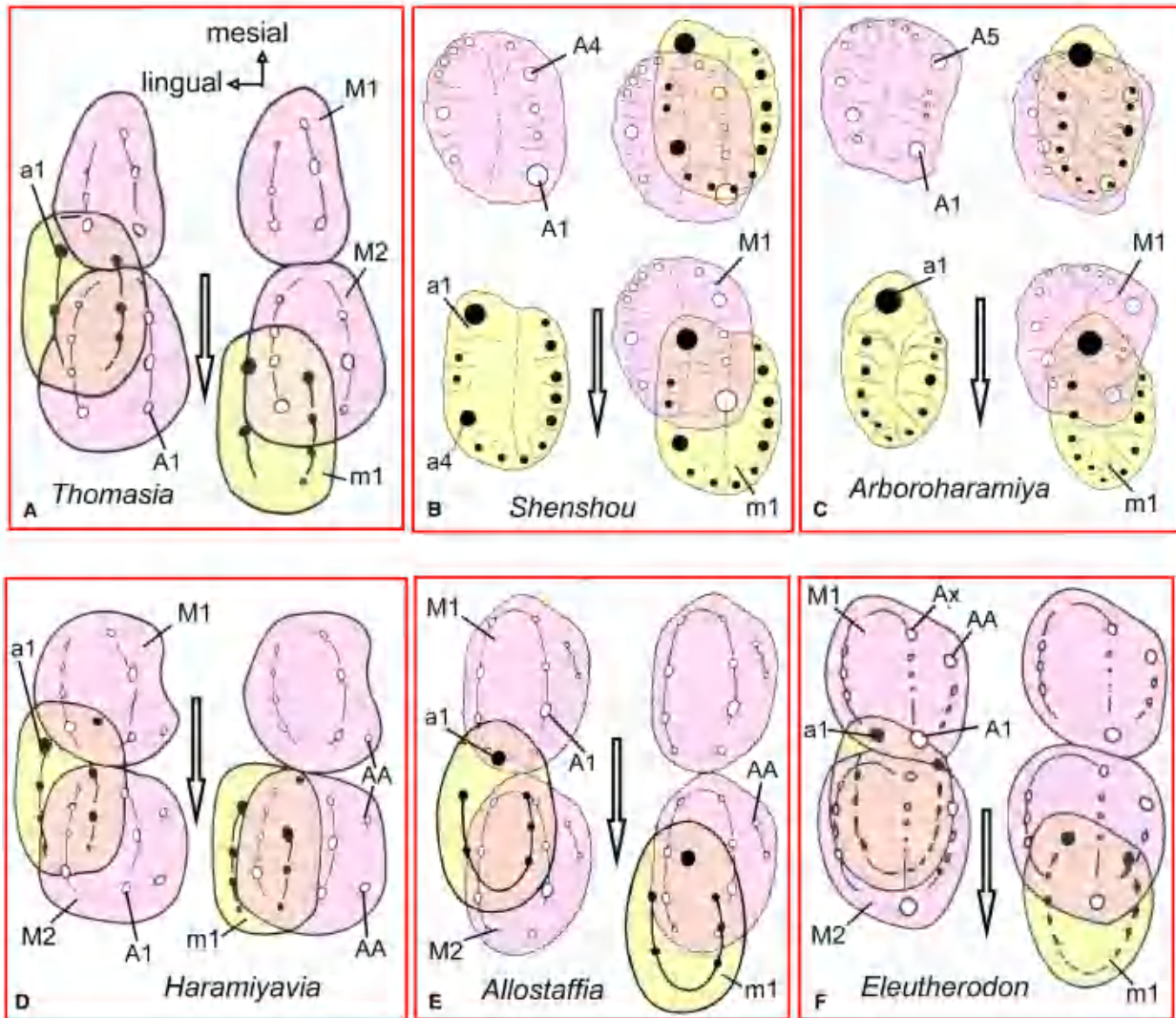
FIG. 13. Diagrams of upper and lower molars showing occlusal modes in 'haramiyidans'. A, MM1 mode as represented by Thomasia. B, MM2 mode as represented by Shenshou and Qishou. C, DE mode as represented by Arboroharamiya. D, occlusal mode of Haramiyavia. E, occlusal mode of Allostaffia as interpreted originally, but see the discussion for an alternative. F, occlusal mode of Eleutherodon in which the tooth orientation and cusp identification have been reinterpreted following Meng et al. (2014). Lower molar is in yellow with cusps shown as solid black dots; the upper molars are in pink with cusps shown as empty circles. Empty arrow in each panel indicates chewing movement direction of the lower molar. Figures are redrawn based on Butler (2000) for Thomasia, Haramiyavia, and Eleutherodon; Meng et al. (2014) for Arboroharamiya; Heinrich (2001) for Allostafia. The drawing of Eleutherodon was horizontally flipped.

Comparison of occlusal modes

Figure 13 summarizes various occlusal modes interpreted for various taxa of 'haramiyidans', some of which have been discussed by Butler (2000). The occlusal mode of Thomasia, Haramiyavia and Maiopatagium, if interpreted correctly, is MM1 and represents the primitive occlusal mode of 'haramiyidans'. The occlusal mode of shenshouids is similar to that of the M2/m2 occlusion of multituberculates (MM2), in which the lower molar is one cusp row more labial in relation to the upper molar compared to the occlusal mode in Thomasia, Haramiyavia

and Maiopatagium. The DE occlusal mode in Arboroharamiya and Vilevolodon is a derived condition in which a1 is hypertrophied, becoming the primary functional cusp, and row-b cusps are greatly reduced on lower molars. Similarly, A1 is the main functional cusp in the upper molar. Because of these changes, the mesiolabial cusp (A5 in Arboroharamiya, for instance; Fig. 13C) no longer bite in the central basin of the lower molar. In Eleutherodon and probably in Allostaffia the tooth occlusal modes are different in that additional AA cusps are developed so that extra wear facets exist on the lingual side of AA cusp. A detailed comparison and discussion on these
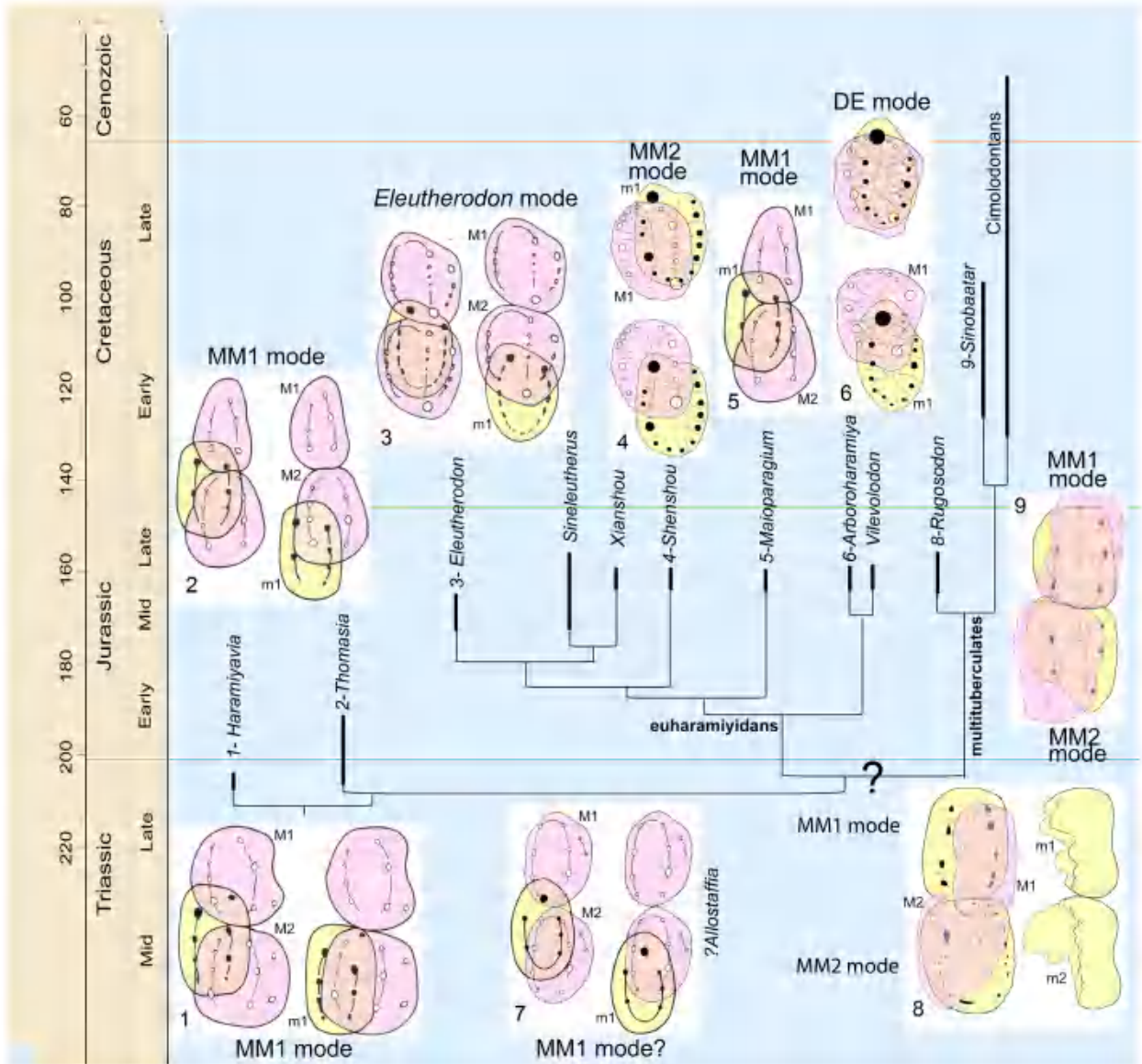
FIG. 14. Occlusal modes of 'haramiyidans' mapped on a simplified phylogeny with those of multituberculates. The phylogenetic framework is based on Han et al. (2017) and Luo et al. (2017) for 'haramiyidans', but Allostaffia (7) was not included in those analyses and so is left out of the phylogeny. 'Haramiyidans' were separated from multituberculates and placed outside of Mammalia by Luo et al. (2017), so we have placed a question mark in the cladogram to indicate an alternative hypothesis. Following Luo et al. (2017), Maiopatagium has the MM1 mode; Arboroharamiya and Vilevolodon have the DE mode. Figures are redrawn based on Butler (2000) for Thomasia, Haramiyavia and Eleutherodon; Meng et al. (2014) for Arboroharamiya; Heinrich (2001) for Allostafia; Yuan et al. (2013) for Rugosodon; Kusuhashi et al. (2009) for Sinobaatar.

occlusal modes are provided in the Mao & Meng (2019b).

Transformation of occlusal modes in 'haramiyidans'

We map the occlusal modes on a simplified phylogenetic tree for comparison and contrast them with those of multituberculates (Fig. 14). In the tooth evolution of

mammals, determining the precursor that gave rise to the allotherian tooth pattern is a fundamental question. Although a hypothesis concerning its evolution from a triconodont pattern has been postulated (Meng 2014), the subject is beyond the scope of this study. Our discussion below will focus on the possible evolutionary transformation of the occlusal modes in 'haramiyidans'. We are aware of competing phylogenies presented in recent studies (Zheng et al. 2013; Zhou et al. 2013; Bi et al. 2014;

Luo et al. 2015, 2017; Han et al. 2017; Huttenlocker et al. 2018) and the phylogenetic framework we choose should be viewed with caution. Nonetheless, the general problem in the transformation of occlusal patterns remains regardless of the phylogeny chosen.

Based on the working hypotheses on occlusal modes discussed above, the MM1 mode in the Late Triassic Thomasia and Haramiyavia may be considered to be the most primitive one among 'haramiyidans'. The MM1 mode was also present in the Late Jurassic Maiopatagium (Meng et al. 2017; Figs 13, 14) and possibly the Late Jurassic Allostaffia (Heinrich 2001, 2004). The condition in Maiopatagium may be regarded as a primitive retention. Whether the MM1 mode in the Late Triassic forms had given rise to others, such as the MM2 mode in shenshouids, is unknown. An obstacle for such a transformation is that from MM1 to MM2 mode, the tooth occlusal relationship has to 'jump' one cusp row, with the lower molar being positioned one cusp row more labial in relation to cusp rows of the upper molar. Although it may not be impossible, there seems no evidence to support such an abrupt transformation. It is also an unusual situation that the MM1 mode of Maiopatagium co-existed with the MM2 mode of shenshouids and the DE modes of Arboroharamiya and Vilevolodon in the Yanliao Biota; this is especially so given that the general tooth morphologies of these taxa are similar.

We propose that the DE mode was most probably derived from the MM2 mode, or from the condition present in shenshouids, or the former is a specialized version of the latter. In both DE and MM2 modes, a1 of the lower molar and A1 of the upper molars have wear facets on their lingual and buccal sides because each of them bites into the central basin of the opposite tooth. However, a critical difference is that there is wear on the labial side of the large mesiobuccal cusp, such as A4 in Qishou, but this wear is absent in those with the DE mode, such as Arboroharamiya jenkinsi (Zheng et al. 2013; Meng et al. 2014; Fig. 13C). This is because in A. jenkinsi row-b cusps are greatly reduced in size and distally retreated in relation to the inflated and mesially extended a1, so that the mesiobuccal cusp (A5 in A. jenkinsi) is buccal to a1 of the lower molar in occlusion. The transformation from MM2 mode as in shenshouids to DE mode was possible with the following dental structure changes. First, cusp a1 of the lower molar extremely inflates; it extends mesially and labially and forms the primary functional cusp for crushing and grinding. Secondly, row-b cusps reduce in size and retreat distally in relation to cusp a1. Thirdly, the distolingual cusp of the lower molar (a4 in Qishou jizantang) reduces in size and its function for grinding. Finally, cusp A1 of the upper molar proportionally expanded and cusps between the two main buccal cusps

reduce in size. The formation of the DE mode is not because the tooth orientation changed, it is because of the modification of cusps on both upper and lower teeth, resulting in a 'twisted' double-engaged occlusal relationship.

The DE mode in molars is also associated with enlargement of P4/p4 and the specialized premolar occlusion, which is also derivable from the premolars of shenshouids by inflation of cusp a1 of the lower premolar and reducing the distal cusps in number and size. In relation to the modification of the lower premolars, P3–4 have widened to become broadly basined with cusps positioned marginally and secondary cusps developed within the basin.

The occlusal mode of Eleutherodon is generally comparable to and derivable from either the MM2 or DE mode, depending on how the cusp homology is interpreted. The wear facet on the lingual side of AA cusp must be created by contact with the row-b cusps of the lower molar. The wear facet on the labial side of A1 (denoted as wear facet 13 by Kermack et al. 1998, fig. 2) and the facet on the lingual side of A1 indicate that A1 must have fitted into the basin of the lower molar; the extensive wear on the lingual side of row-Ax must be created by contact with the labial surface of row-a of the lower molar. Comparing this occlusal relationship with that of shenshouids, it seems better to homologize row-Ax of Eleutherodon with row-A of shenshouids.

It is also possible that the occlusal mode of Eleutherodon is derived from the DE mode. In the specimens reported by Butler & Hooker (2005; FM & JM pers. obs.), the upper molars (M46832, M46821) have a very weak Ax row, or no cusp row at all. These small cusps bear little or no wear. Thus, the distinct AA cusp seems to be better interpreted as being homologous to cusp A5 of Arboroharamiya (Fig. 13) because cusp AA does not occlude in the basin of the lower molar but is positioned labially to the row-b of the lower molar.

AA cusps are present in Haramiyavia, Allostaffia and Eleutherodon, and BB cusps were present in Theroteinus and Megaconus. Whether the AA cusps are homologous in these forms remains unknown. As interpreted by Jenkins et al. (1997; see also Luo et al. 2015), the AA cusps of Haramiyavia are not functional so that they are probably not homologous with those of Eleutherodon. It has been postulated that evolution of tooth complexity represents a balance between structural integrity and food manipulation, and a multi-cusp configuration presumably allows for enhanced food manipulation (Constantino et al. 2016). It may be inferred that the development of extra cusps in some 'haramiyidans' may provide enhanced food manipulation. However, the current competing phylogenetic relationships (Luo et al. 2017; Han et al. 2017) complicate interpretations of the cusp

homology and transformation of occlusal modes in 'haramiyidans'.

Finally, it is worth noting that a critical dental feature commonly used to distinguish multituberculates from 'haramiyidans' is that molars of multituberculates have longitudinal rows of low cusps of the same height, except for paulchoffatiids (Butler 2000; Kielan-Jaworowska et al. 2004). Instead of regarding the paulchoffatiid condition as an exception, we postulate that the uneven cusp height, particularly a large mesiolingual cusp on the lower molar of paulchoffatiids such as Rugosodon (Yuan et al. 2013; Fig. 14), could be a shared feature between early multituberculates and 'haramiyidans'. The even cusp height of the molar may well be a derived condition evolved in more advanced multituberculates. Furthermore, the MM2 occlusal mode that multituberculates share with euharamiyidans is unique among mammaliaforms. Although Thomasia, Haramiyavia and Maiopatagium were interpreted as having the MM1 mode, this interpretation is equivocal in our view; all hypotheses about tooth occlusal patterns and their evolutionary transformation within 'haramiyidans' require vigorous testing and additional evidence.

CONCLUSIONS

Detailed dental wear of shenshouids is documented, helping us to understand the occlusal pattern and chewing movement of 'haramiyidans'. We compare the shenshouid occlusal mode with several other occlusal modes currently known in 'haramiyidans'. Based on the interpretations of the tooth morphologies and occlusions, it seems that the occlusal modes of 'haramiyidans' are diverse, which may reflect diverse diets, such as granivorous, omnivorous (Zheng et al. 2013) and/or herbivorous (Luo et al. 2017), suggesting resource partitioning among 'haramiyidans'. This dietary diversification must have been present by at least the Late Triassic. The tooth occlusal modes also reflect a mosaic evolutionary transformation and complicated phylogenetic relationships within the group. The most challenging issues raised by recent discoveries from the Jurassic Yanliao Biota, and still to be resolved, include: how did the MM1 mode in Thomasia jump to the MM2 condition of shenshouids and other later taxa (except for Maiopatagium) during the evolution of 'haramiyidans'? Why did Maiopatagium retain the MM1 mode while coeval taxa, such as Arboroharamiya and Vilevolodon, demonstrate the derived DE mode? How should we interpret the similarity and dissimilarity between the occlusal modes of 'haramiyidans' and those of multituberculates? To answer these questions, more evidence, such as the detailed documentation of tooth morphology and wear structures we report here for shenshouids, are needed for other taxa in the group.

DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.c65b4j5

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SUPPORTING INFORMATION

Tooth microwear and occlusal modes of euharamiyidans from the Jurassic Yanliao Biota reveal mosaic tooth evolution in Mesozoic allotherian mammals

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I. INSTITUTIONAL ABBREVIATIONS

BDUC, Biology Department, University College, London, UK; JZT, Jizantang Paleontological Museum, Chaoyang, Liaoning, China; MCZ, Museum of Comparative Zoology, Harvard, USA; MNHN, Muséum National d'Histoire Naturelle, Paris, France; NHMUK (BMNH), The Natural History Museum, London, United Kingdom; NHMD, Natural History Museum of Denmark, University of Copenhagen, Denmark.

II. SUPPLEMENTARY FIGURES
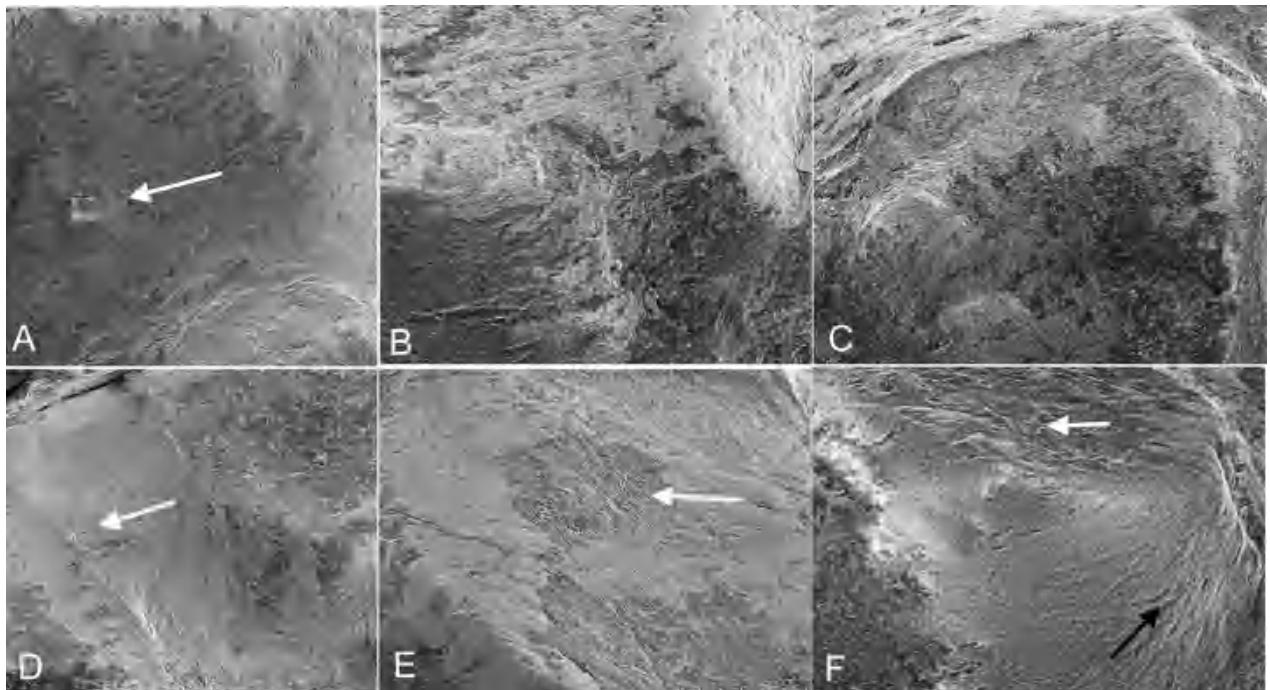
Figure S1: Close-up views of wear facets and striations on upper teeth of *Qishou jizantang* (JZT-D061). A-F correspond to boxed areas 1-6 in Figure 4. Panels B and C show abrasional facets that are not planar and do not have distinct and directional striations, in contrast to attritional facets in other panels. In panel F, the attritional facet bears striations (white arrow) and scratching striations by tooth-food contact on the mesiolingual base of a cusp (pointed by the black arrow).
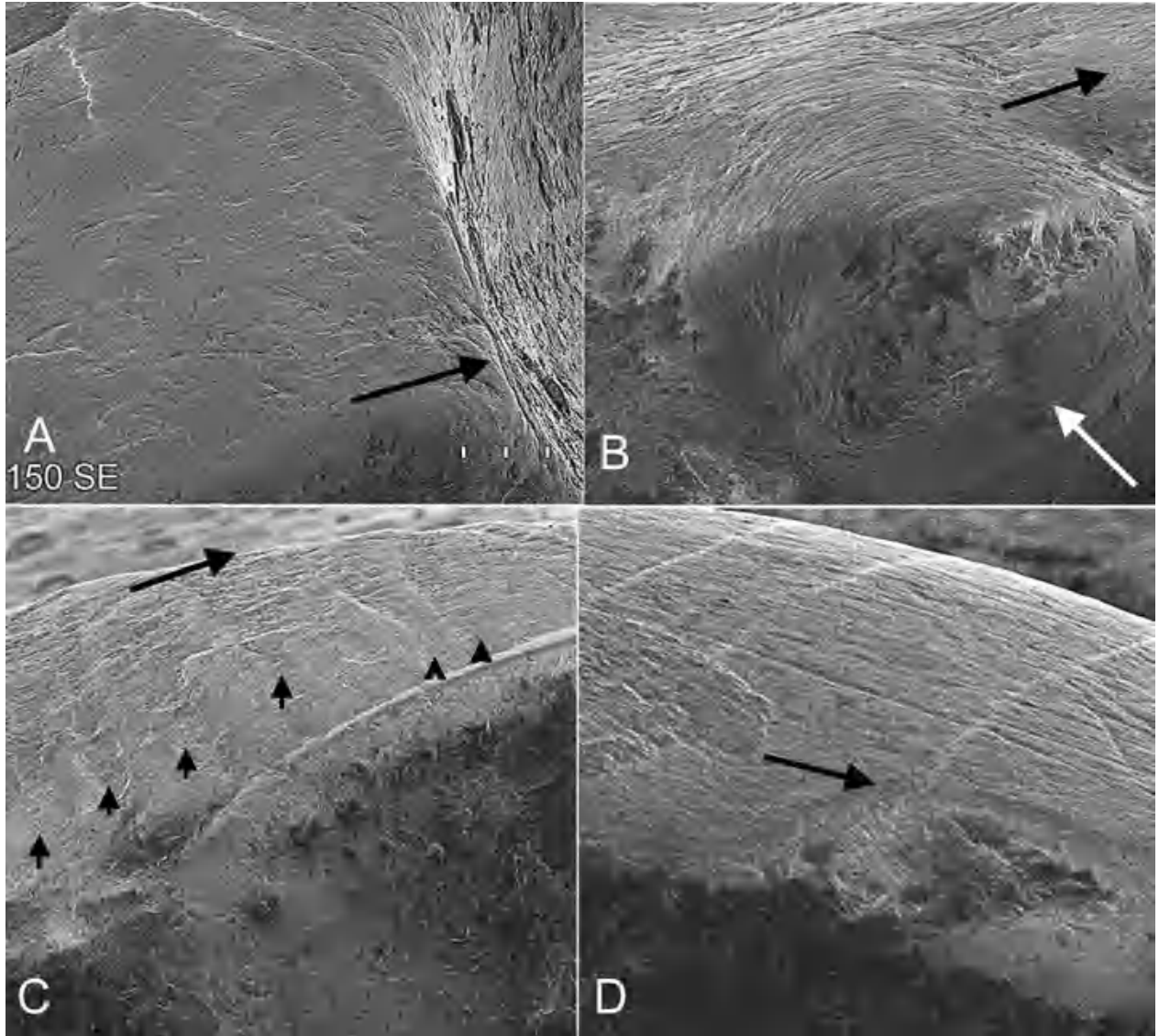
Figure S2: Close-up views of striations on lower teeth of *Qishou jizantang* (JZT-D061). A-D correspond to boxed areas 1-4 in A, I, E and H in Figure 6. Long black arrows indicate general directions of striations, which demonstrate a palinal chewing movement. Short black arrows in c indicate vertical grooves that are interpreted as formed in the orthal phase of chewing (see text). A, C and D show wear facets and striations on the lingual sides of row-a cusps, whereas panel B shows a row-b cusp on which the wear and striations are clear on the lingual side but absent on the labial side (as indicated by the white arrow).
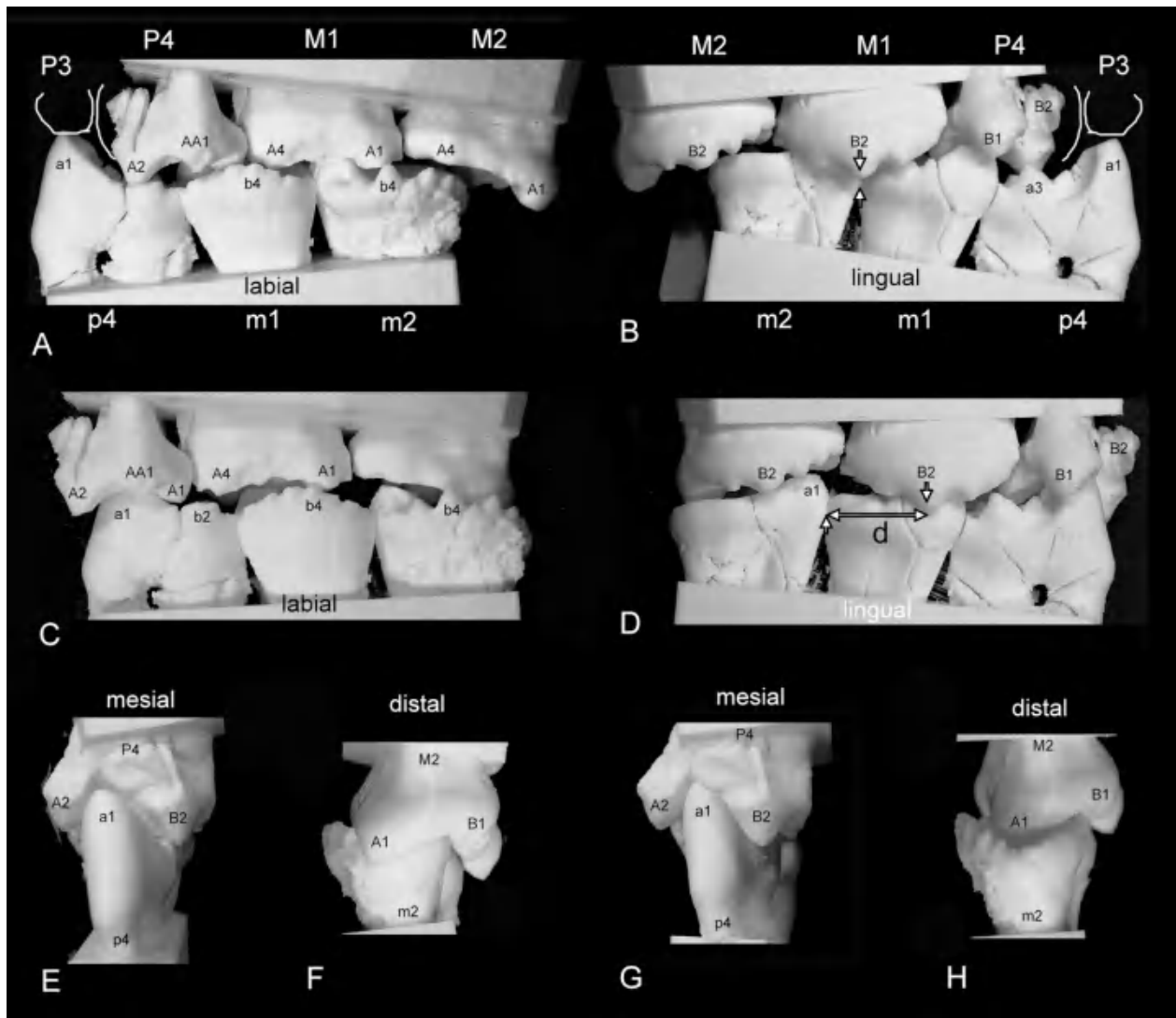
Figure S3: 3D casts for upper and lower cheek teeth of *Qishou jizantang* (JZT-D061) showing the occlusal relationship. A, Labial view showing the end position of the orthal phase and beginning position of the palinal phase in which a1 of p4 is in contact with P3; B, Lingual view of the same relationship in A; C, Labial view of teeth in centric position; D, Lingual view of the same relationship in C; E and F, Mesial and distal views of teeth in the same stage of A and B; G and H, Mesial and distal views of teeth in the same stage of C and D. Arrows in B and D show reference points and the moving distance (d) of the palinal movement. See Figure 12 for the crown view relationship of the tooth occlusion.

III. GENERAL DISCUSSION ON CENTRIC OCCLUSION

To understand the occlusal pattern in 'haramiyidans', we want to clarify the usage of "centric occlusion" in 'haramiyidans'. The term 'centric occlusion' used for mammals was derived from dental occlusion of human (Mills 1967; Crompton & Hiiemae 1969, 1970). However, the meaning or definition of the term, along with others such as 'occlusion relation', was not clear then and still remain confusing today (Türp *et al.* 2008). The general definition of 'centric occlusion' for human is 'the relation of opposing occlusal surfaces which provide the maximum intercuspation and/or planned contact' (see Crompton & Hiiemae 1970: 41), but in human the centric occlusion can be achieved for both sides of the mouth simultaneously and with the lower jaw more or less symmetrically placed about the midline. For mammals with tribosphenic molar, such as *Didelphis*, Crompton & Hiiemae (1970: 23) stated: "the term 'centric occlusion' is restricted to the condition where the protocone is tightly locked into the talonid basin of the lower molar". The authors realized that centric occlusion or maximal cuspal interdigitation in *Didelphis* can only be achieved on one side of the mouth at any one time, and when the teeth of one side are in centric occlusion, the molars of the other side lie medial to the position of centric occlusion for that side; thus, the centric occlusion in mammals with tribosphenic teeth must be unilateral, existing either in the right side or the left side of the mouth, but not simultaneously and symmetrically on both sides. This unique aspect of chewing results from the fact that the mandible is usually narrower than the maxilla, a condition called anisognathy (Ungar 2010). In addition, the centric occlusion "occurs at the end of the occlusal phase of the power stroke when the stroke has involved tooth-tooth contact" (Crompton & Hiiemae 1970: 33) and, as part of the chewing cycle, it is transitory.

The term of centric occlusion, without giving a definition, has been briefly used in some studies on 'haramiyidans' in which it is applied to occlusion (Luo *et al.* 2017) or phylogeny

(Debuysschere 2016). Debuysschere (2016: 2) pointed out that in some classifications of 'haramiyidans', *Theroteinus* was regarded as to be more basal than other forms upon one main feature that "in centric occlusion, one tooth of *Theroteinus* is in contact with two opposite teeth ('one-to-two' occlusion). This feature is shared by other mammaliaforms such as morganucodonts and kuehneotheriids but not by other 'haramiyidans', which are characterized by an occlusal mode where one tooth is in contact with only one opposite tooth in centric occlusion ('one-to-one' occlusion)." However, in the Jurassic euharamiyidan *Vilevolodon*, it appears to be a 'one-to-two' condition when the centric position is reached (Luo *et al.* 2017: extended data fig. 6). In *Eleutherodon* (Kermack *et al.,* 1998; Butler, 2000), the centric occlusion appears in a 'one-to-two' condition. Apparently, the centric occlusion in 'haramiyidans' is fundamentally different from what has been defined for tribosphenic dentition by Crompton & Hiiemae (1970), that is, the protocone of the upper molar is tightly locked into the talonid basin of the lower molar.

IV. OCCLUSAL MODES IN OTHER 'HARAMIYIDANS'

Thomasia. The occlusal mode of *Thomasia* was reconstructed by Butler (2000). This occlusal mode is similar to the MM1 mode. Reconstruction of this occlusal pattern is primarily based on the wear facets of isolated teeth (Butler & MacIntyre 1994) as well as a comparison with that of *Haramiyavia* (Butler 2000). The tooth morphology of *Thomasia* is highly diverse (Meng *et al.* 2014; personal observation on specimens in MNHN (by FM & JM). We noted that wear facets on cheek teeth are commonly on tips of cusps and attritional facets are commonly not so distinct that the occlusal relationships of many isolated teeth are difficult to ascertain. A systematic study of these teeth is needed to clarify the kinds of tooth morphology and to clearly show their wear facets and occlusal relationships. Before conclusive evidence is available, we regard the occlusal

pattern of *Thomasia* by Butler (2000) as the working hypothesis, on which our discussion about the occlusion of *Thomasia* will be based.

Maiopatagium. *Maiopatagium* was also interpreted as having the MM1 mode, similar to *Thomasia*. Although the lower teeth are unknown in *Maiopatagium*, Meng *et al.* (2017: Supplementary Information) recognized a few unambiguous features from the upper molars and concluded that "These features suggest that the lingual-most cusp row of lower molars occluded lingual (medial) to the upper molars, and the labial cusp row of upper molars occludes outside the lower molars." The tooth morphology of *Maiopatagium* was considered to be most similar to *Shenshou lui* in several aspects (Meng *et al.* 2017), but the occlusal mode of *Maiopatagium* is fundamentally different from those of *Shenshou* and *Qishou*.

Haramiyavia. *Haramiyavia* was interpreted as having the MM1 mode (Jenkins *et al.* 1997; Butler 2000; Luo *et al.* 2015; Figs 13D, 14). However, the upper molars of *Haramiyavia* differ from those of *Thomasia* in possessing extra cusps labial to row-A, denoted as C cusps (Jenkins *et al.* 1997) or AA cusps (Butler 2000). The occlusal relationship interpreted for *Haramiyavia* would result in that a significant labial portion of the upper tooth crown is not used for food processing, which is unusual among mammaliaforms. As already questioned by Meng *et al.* (2014; see also Han *et al.* 2017: SI, 54), there are several reasons to postulate that *Haramiyavia* may actually have an MM2 occlusal mode. Luo *et al.* (2015) have presented a detailed analysis of the tooth occlusion of *Haramiyavia*, but the wear depicted on the teeth are unclear, if present at all, and striations, if any, are randomly distributed. We have carefully observed the specimens (NHMD 236380 [= MCZ 7/G95], NHMD 236381 [=MCZ 10/G95]) under microscope and using SEM, but we did not find any convincing attritional facets on the

teeth. Because the teeth are covered with glue, our SEM imaging failed to reveal convincing striations. Our observation echoes that of Butler (2000: 323): "Unfortunately the single specimen of *Haramiyavia* is little worn and no wear scratches have been reported."

In addition, when initially reported (Jenkins *et al.* 1997), the maxilla with upper teeth has a separate catalog number, and the upper teeth (identified as M1-M3) are significantly larger than the lower ones. In reconstructing the occlusal relationship of *Haramiyavia*, Luo *et al.* (2015: E7107) stated: "Using 3D models printed from CT scans, we found that rescaling the referred and larger upper molars (MCZ10/G95) to 83% made the best match to the lower teeth (MCZ7/G95)." If the referred specimens came from the same species, the 17% size difference between the upper and lower teeth suggests that the specimens may belong to more than one individual. Based on our observation of the original specimens, we think that the alternative occlusal pattern of *Haramiyavia* (Meng 2014; Meng *et al.* 2014) still remains a possibility. In the current study, however, we regard the occlusal mode (Jenkins *et al*. 1997; Luo *et al.* 2015); as the working hypothesis, and consider it as a mode different from that of *Thomasia* because of its possession of extra AA(C) cusps.

Double-engaged occlusal mode. The double-engaged (DE) occlusal mode was first recognized in *Arboroharamiya jenkinsi* (Zheng *et al.* 2013; Meng *et al.* 2014; Fig. 13C). As described by Zheng *et al.* (2013: 200):

"The cusp shape and arrangement, wear pattern and occlusal match of M1 and m1 show that, during mastication, a1 of the lower molar must have bit orthally in the basin of the upper molar in the puncture-crushing cycle and then moved palinally within the basin in a grinding cycle. In a reversed symmetry, A1 of the upper molar bit into the central basin of the lower molar and 'moves' mesially in the valley of the lower molar. This

'double engaged' occlusion prevents both proal and transverse chewing motion; it creates wear in the tooth basin at the distal V-notch and on the buccal side of A1–3, but not the lingual side of M1. It also creates wear on the lingual and buccal sides of a1 in lower molars. This occlusal pattern is unique among mammals and differs from what has been interpreted for both haramiyids and multituberculates."

Meng *et al.* (2014) further described this unique occlusal mode and specifically emphasized that it was termed as 'double engaged' occlusal pattern. The same occlusal relationship was also found in *Vilevolodon* and termed as 'dual mortar–pestle occlusion' (Luo *et al.* 2017: fig. 2k). The DE mode is possibly present in *Xianshou* (Bi *et al.* 2014), but because the teeth in the holotypes are in occlusion, the occlusal relationship in *Xianshou* cannot be conclusive.

Differing from the MM2 mode, a1 of the lower molar with the DE mode is greatly enlarged and more labially positioned near the longitudinal axis of the tooth, whereas other row-a cusps are reduced. Along with the modification of row-a cusps, row-b cusps are reduced, particularly the mesial ones, and distally positioned in relation to the mesially extended a1. As a result of these changes, the mesiolabial cusp of the upper molar no longer bites in the central basin of the lower molar in occlusion (A5 in Fig. 13C); thus, its labial surface does not have wear.

In addition to the occlusion of molars, the premolar occlusion is also distinctive in the DE mode. The hypertrophied a1 appears to be the primary, if not the only, functional cusp in p4. Wear facets and striations show that it travels orthally to crush and then palinally to grind food items against the broadly basined P3 and P4 in which exist small cusps with flutings. As described above, the premolar configuration in DE mode best reflects the idea of how opposing teeth function against tooth breaking and efficiently process food (Ungar 2015). Ungar (2015:

29) wrote: "A point or cusp tip makes a good model to concentrate forces required. A blunt or hemispherical tip is best to buffer the tooth itself against breaking. Besides, a sharper tip might cause a food item to deform plastically. The opposing surface can be flat (think of a hammer and anvil), or concave (think of a mortar and pestle). The advantage to a concave surface is that it prevents spread or movement of food that would result in loss of energy during the fracture process. A basin, or spaces between staggered opposing cusps, often does the job (Lucas 2004; Ungar 2010)." In the DE mode, the upper premolar does not only form a basin, but also bears cusps along the tooth margin as well as develops small cusps in the basin floor; these cusps are further decorated with enamel ridges (flutings). Such a configuration is not a normal "mortar" but an enhanced one; the cusps surrounding the tooth margin and within the basin help to hold the food and prevent spread or movement of food particles while the food is being fractured. The function of such teeth is similar to a mill and represents a more efficient way of grinding food. We consider the DE mode as a highly derived and unique condition in tooth morphology and function within mammaliaforms.

Allostaffia. The occlusal pattern in *Allostaffia* from the Upper Jurassic of Tanzania has been controversial. The holotype of *Allostaffia* (MB.Ma 48080) was originally identified as a right lower posterior premolar or possibly an anterior molar (Heinrich 1999, 2001), and Butler & Hooker (2005) interpreted it as m1. Based on comparison with dentitions of euharamiyidans from the Yanliao Biota, Mao & Meng (2019) concurred the original identification of the tooth as p4 by Heinrich. Heinrich (2001: 251) postulated that, owing to the tooth morphologies, primarily the inflated a1 that is positioned near the longitudinal axis of the tooth, "cusp a1 might have been able to travel, with the cusps of row-b, along the central basin of the opposing upper molar, suggesting a functional shift of the main cusp a1 from a cutting to a crushing and grinding

action" (Fig. 13E). This view was disagreed with by Butler in a personal communication (Heinrich 2001). Butler suggested that cusp a1 identified by Heinrich might be b2 (Butler 2000), so that a1 "jumping" across the upper row-B cusps in occlusion would be unnecessary.

Our study supports the general interpretation on the tooth occlusion of *Allostaffia* by Heinrich (2001) in which a1 is the primary functional cusp that occluded, in crushing and grinding action, in the central basin between row-B and row-A of the upper molar. However, we think a modified interpretation is that a1 did not function along with row-b cusps in chewing; instead, *Allostaffia* probably has either an MM2 or a DE mode, as we discussed above. Nonetheless, the fragmentary nature of *Allostaffia* specimens hampers a precise identification of its occlusal pattern. Given that cusps AA1 and AA2 are developed on the labial side of row-A of the upper molar (MB.Ma.50070, tentatively identified as a left M2 by Heinrich 2001), it is probable that all row-a cusps traveled through the main central basin between row-B and row-A, whereas the small row-b cusps passed through the space between row-A and row-AA cusps in chewing movement. This interpretation would be consistent with the occlusal patterns present in the Jurassic euharamiyidans.

Eleutherodon. *Eleutherodon*, probably *Sineleutherus* as well (the upper molar is unknown in *Sineleutherus*), has an occlusal mode that probably represents another type of tooth and chewing specialization among 'haramiyidans'. On the upper molar, an extra cusp row ("BB") has developed and cusp "B1" (denoted as cusp A in Kermack *et al.* 1998) is enlarged and distally extended (Kermack *et al.* 1998; Butler 2000; Butler & Hooker 2005; Fig. 13F). In the study of *Vilevolodon*, Luo *et al.* (2017: Suppl. Info.) stated that "we can now corroborate the original proposed model of occlusal relationship of upper and lower molars for *Eleutherodon* by Kermack and colleagues [Kermack *et al.* 1998: fig. 23; Butler 2000: fig. 5]." Based on tooth

morphology and wear in *Arboroharamiya*, Meng *et al.* (2014) had pointed out that the occlusal relationship of *Eleutherodon*, originally proposed by Kermack *et al.* (1998: fig. 23) and Butler (2000: fig. 5), was probably reversed or flipped. Here we restate the alternative interpretation of Meng *et al.* (2014): The right upper molar of *Eleutherodon* (for instance, M46832 and M46821, in Butler & Hooker 2005: fig. 1A, 1B) should be interpreted as the left upper molar, and accordingly, the cusp denoted as B1 should be A1. Similarly, the left lower molar (for instance, M46851) should be a right lower molar, and the cusp denoted as b2 is actually a1. The alternative interpretation applies to the holotype specimen (BDUC J.460; note that specimens were renumbered under BMNH in Butler & Hooker [2005]) and paratypes of *Eleutherodon oxfordensis* (Kermack *et al.* 1998). For instance, the holotype was identified as an upper right molar, but we interpret it as a left upper molar. With the alternative orientation, cusps denoted as BB and Bx for *Eleutherodon* (Butler 2000; Butler & Hooker 2005) are here considered as AA and Ax (Fig. 13F). Along the same line, "b2" of *Sineleutherus* (Martin *et al.* 2010; Averianov *et al.* 2011), also identified as "b1" (Zhou *et al.* 2013), should be a1 (Meng *et al.* 2014).

The alternative interpretation means that the labial side of the tooth originally interpreted should now be the lingual side. More specifically, the largest cusp on the lower molar of *Eleutherodon* is a1 and positioned at the mesiolingual corner of the tooth, consistent with that of *Haramiyavia*, whereas the largest cusp on the upper molar is A1 at the distolabial corner of the tooth. Because of the tooth orientation, Kermack *et al.* (1998: fig. 2b) recognized wear facets mainly on the labial side of the lower molar in *Eleutherodon*. It is clear now that the wear is on the lingual cusp row, which indicates that a1 bites in the central basin of the upper molar, whereas A1 occludes in the basin of the lower molar. This occlusal relationship has also been echoed by another study (Luo *et al.* 2017: fig. 2).

Based on the published data (Kermack *et al.* 1998; Butler & Hooker 2005) and our

observations of the *Eleutherodon* specimens housed in the Museum of Natural History, London, as well as comparison with those from the Yanliao Biota, we think the occlusal relationship of *Eleutherodon* has the following characteristics: cusp a1of the lower molar would be the main cusp that bites in the main basin (between Ax-row and B-row in our usage), whereas b-row cusps bite in the secondary basin between Ax-row and AA-row (Fig. 13F). A1 of the upper molar is the primary functional cusp that bites in the basin of the lower molar. Similar to the DE mode, cusp AA will be positioned on the labial side of row-b cusps in occlusion. The centric occlusion is when cusp A1 and a1 are lodged in the basin center of the opposing tooth, as diagramed by Butler (2000: fig. 5). Because the extra cusps and basin increase the contact surface of the tooth crowns, the occlusal mode of *Eleutherodon* appears to be a derived condition and is more efficient in processing food.

Theroteinus. *Theroteinus* has teeth with low crowns and blunt cusps; its upper molars developed an extra BB row on the lingual side (Butler 2000). Butler (2000: fig. 4) presented a diagram to show the occlusal relationship and recognized that in *Thomasia*, probably in *Haramiyavia* as well, a palinal movement was present in chewing, but it was absent in *Theroteinus*; this was considered as a primitive feature of *Theroteinus* (Debuysschere 2016). Because of its unique tooth morphology and small sample size, the occlusal mode of *Theroteinus* is difficult for us to reconstruct. In his review work on *Theroteinus*, Debuysschere (2016) did not explore the occlusal pattern of *Theroteinus* either, but intended to deal with it in detail in later studies. Debuysschere (2016: 24) did mention that "Indeed, *Theroteinus* is the only haramiyid for which the wear pattern does not highlight a horizontal movement of the jaw during mastication (Sigogneau-Russell *et al.* 1986 and see above). Such a wear pattern and the small size of the

basins support an essentially vertical masticatory movement." We consider that *Theroteinus* possesses yet another occlusal mode different from those of other taxa (Figs 13, 14).

Hahnodontids. The family Hahnodontidae includes the type genus *Hahnodon* from the Lower Cretaceous of Morocco (Sigogneau-Russell 1991) and *Cifelliodon* from the Lower Cretaceous of North America (Huttenlocker *et al.* 2018). *Hahnodon* is known by a single tooth, interpreted as m2 by Sigogneau-Russell (1991), and its taxonomic placement in either multituberculates or 'haramiyidans' has been controversial (Butler & Hooker 2005; Hahn & Hahn 2006). Huttenlocker *et al.* (2018) placed *Cifelliodon* in Hahnodontidae and considered the unerupted postcanine tooth (PC4) to be similar to the holotype of *Hahnodon* and suggested a chewing pattern with an orthal stroke and a palinal stroke for hahnodontids.

Megaconus. *Megaconus* was considered as a member of Eleutherodontidae (Zhou *et al.* 2013), but its morphology and taxonomy are contentious (Meng *et al.* 2014). The occlusal mode of *Megaconus* has been reconstructed as to be the MM1 mode, similar to that of *Haramiyavia* and *Maiopatagium* (Luo *et al.* 2017). However, *Megaconus* has extra cusps developed on the lingual side of the upper molars, which should be BB cusps following the terminology of Butler (2000). In contrast, extra cusps are present on the labial side of the upper molar of *Haramiyavia*, which are AA cusps (Butler 2000).

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