
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

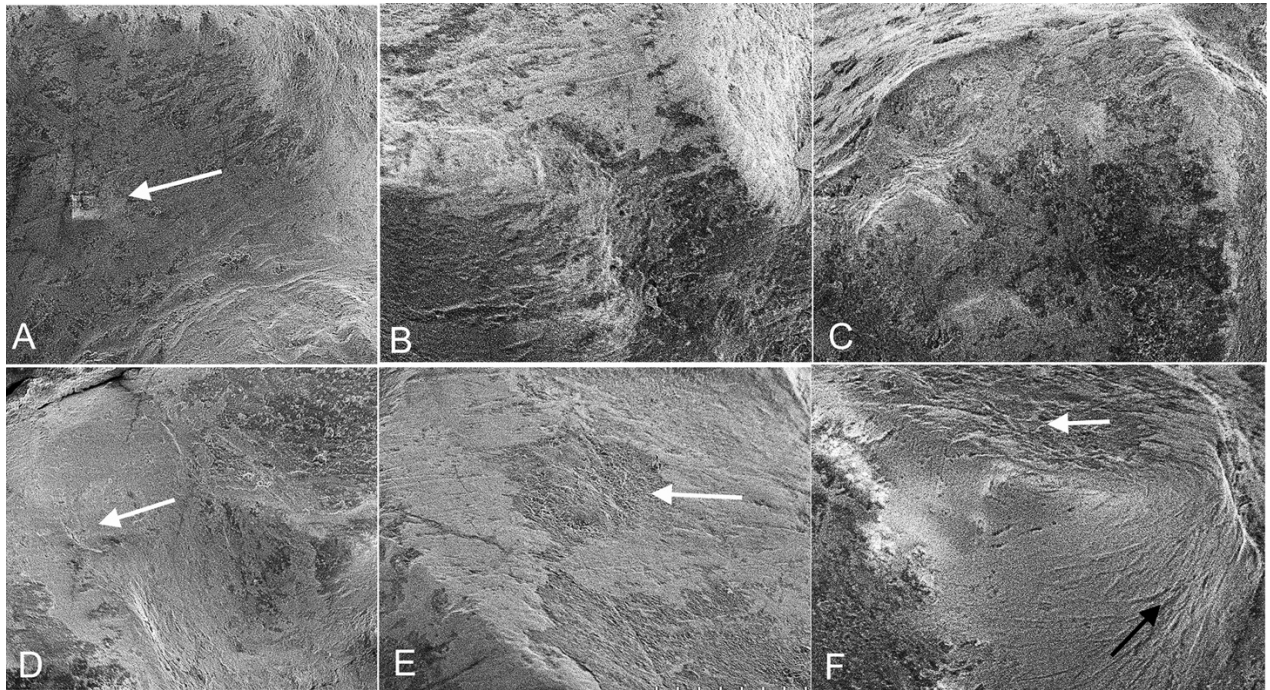


Figure S1: Close-up views of wear facets and striations on upper teeth of *Qishou jizantang*

(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).

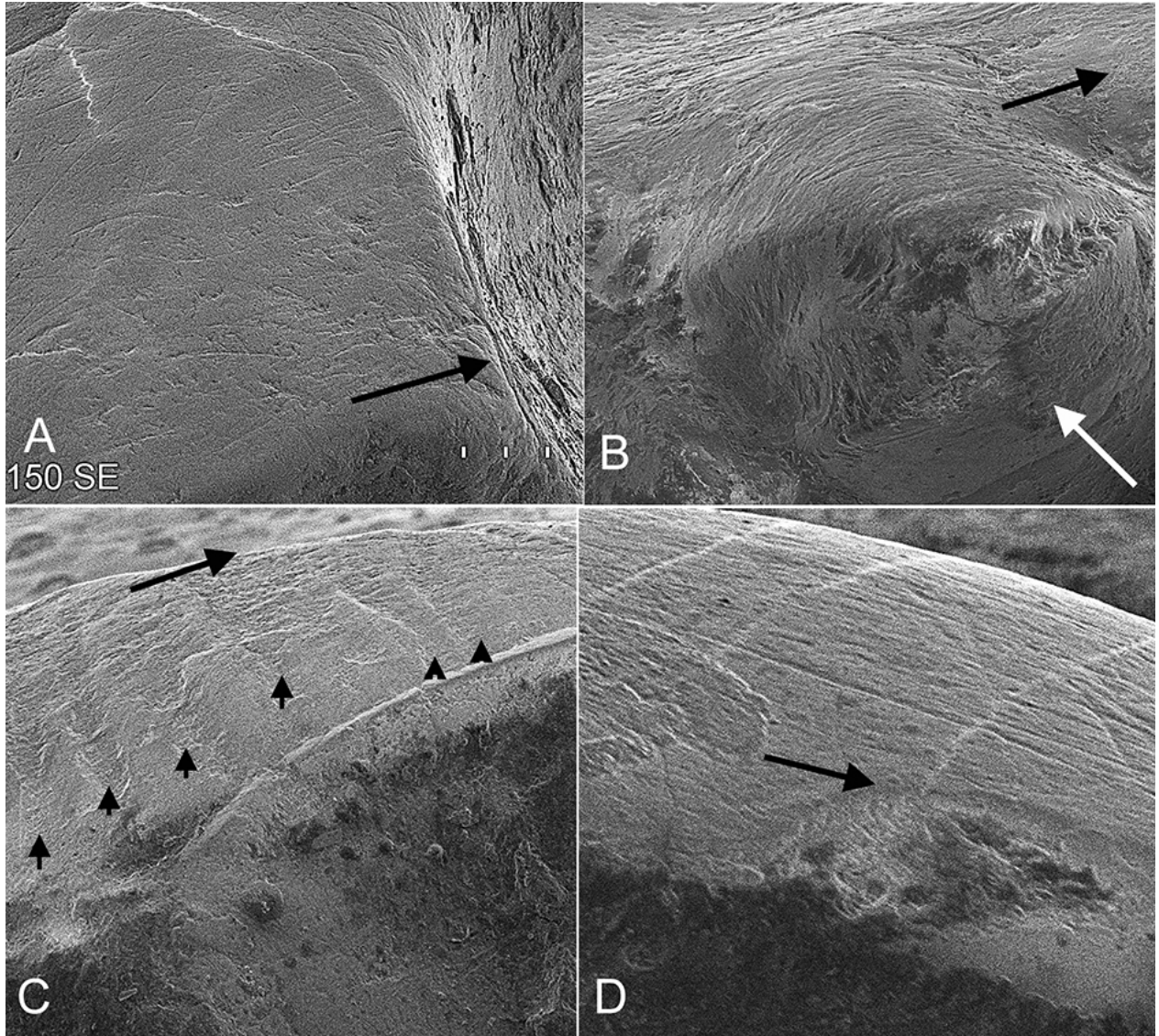


Figure S2: Close-up views of striations on lower teeth of *Qishou jizantang* (JZT-D061). A-D correspond to boxed areas 1-4 in A, I, E and H in Figure 6. Long black arrows indicate general directions of striations, which demonstrate a palinal chewing movement. Short black arrows in c indicate vertical 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).

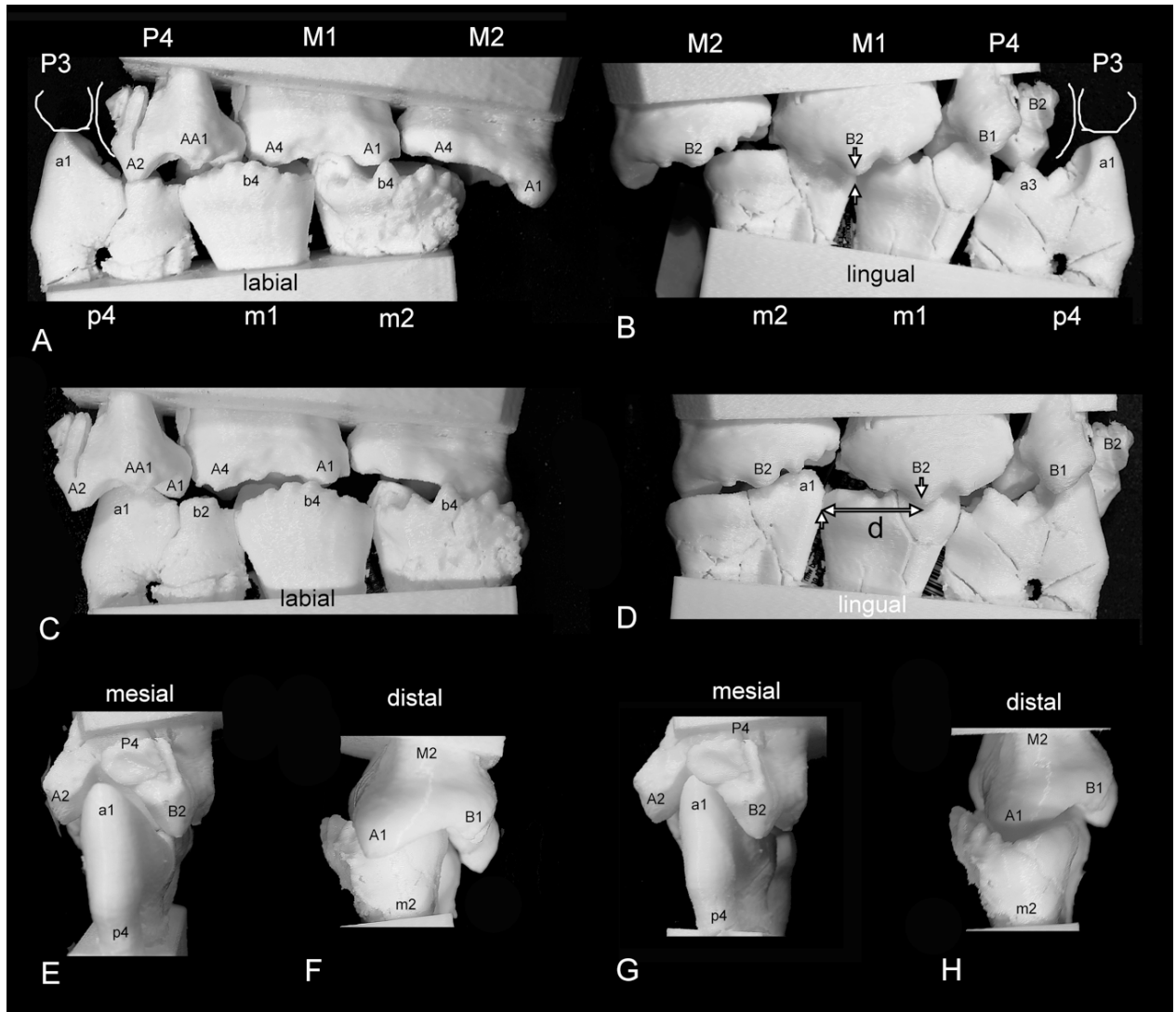


Figure S3: 3D casts for upper and lower cheek teeth of *Qishou jizantang* (JZT-D061) showing the occlusal relationship. A, Labial view showing the end position of the orthal phase and beginning position of the palinal phase in which a1 of p4 is in contact with P3; B, Lingual view of the same relationship 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 anisognathia (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 a1 of 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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