[Original report]

Dental morphology of an enigmatic artiodactyl from the Eocene Pondaung Formation, Myanmar

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Abstract

The upper molar morphology of an enigmatic indeterminate artiodactyl (Mammalia), Artiodactyla indeterminate 1 (Tsubamoto *et al.*, 2005, *Acta Palaeontol. Pol.* **50**, 117-138), from the middle Eocene Pondaung Formation of Myanmar is described in detail and is compared with an enigmatic artiodactyl *Aksyiria* from the middle Eocene of Kazakhstan. This upper molar is characterized by bunodont cusps, a square occlusal outline, a hypocone, non-selenodont conules, a parastyle, and a straight ectoloph. This indeterminate artiodactyl is distinct from *Aksyiria* at the genus level in having a stronger parastyle, a large hypocone, non-selenodont conules without link to the cingulum, and a more mesially located protocone, and in being much larger. Although it represents a new genus and species because of its unique upper molar morphology, new taxa are not established here because of the scarcity and heavily damaged nature of the material.

Key words: Artiodactyla, Eocene, Myanmar, Pondaung Formation, upper molar

Introduction

The upper middle Eocene Pondaung Formation of central Myanmar yields several primitive artiodactyl mammals whose phyletic positions within the Artiodactyla have not been solved (Holroyd and Ciochon, 1995; Ducrocq et al., 2000; Tsubamoto et al., 2002, 2003, 2005; Métais, 2006; Métais et al., 2007). Among these enigmatic artiodactyls from the Pondaung Formation, Métais et al. (2007, 2008) suggested that Artiodactyla indeterminate 1 briefly described by Tsubamoto et al. (2005) may be referable to the genus Aksyiria. Artiodactyla indeterminate 1 in Tsubamoto et al. (2005) is an enigmatic artiodactyl based only on a fragmentary specimen, which has a unique upper molar morphology. Aksyiria is a small

and enigmatic dichobunid artiodactyl described and recorded only from the lower middle Eocene lower Obayla 'Subsvita' of eastern Kazakhstan by Gabunia (1973). This genus is represented by one species, *Aksyiria oligostus*, which is based on an isolated upper molar (Gabunia, 1973). If this indeterminate artiodactyl from the Pondaung Formation is really referable to the genus *Aksyiria*, it would be of interest paleobiogeographically because it would extend the geographic and chronological range of the genus (Métais *et al.*, 2007, 2008) and would suggest a direct faunal link between Southeast Asia and northern Asia during the middle Eocene. However, because this indeterminate artiodactyl was only briefly described and mentioned (Tsubamoto *et*

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al., 2005), its precise morphology has not been documented yet.

The purpose of this report is to reveal the precise dental morphology of this indeterminate artiodactyl (Figs. 1, 2A) from the Pondaung Formation and to compare it with *Aksyiria*. The dental terminology used here mostly follows Orliac and Ducrocq (2012) and is indicated in Fig. 2.

Dental abbreviations.—M, upper molars.

Institutional abbreviations.—AN GSSR, Academy of Sciences of the Georgian SSR, Tbilisi, Georgia. NMMP–KU, specimens catalogued by the Myanmar-Japan (Kyoto University) Joint Fossil Expedition Team (Tsubamoto *et al.*, 2005, 2006), which are currently stored in Department of Archaeology (Ministry of Culture), Yangon, Myanmar. Liv, specimens from La Livinière (Eocene) of France, which are stored in Université Montpellier II, Montpellier, France.

Description

Artiodactyla indeterminate 1 in Tsubamoto *et al.* (2005) is based on a single specimen, NMMP-KU 1556 (Tsubamoto *et al.*, 2005, p. 199-120, fig. 2A). NMMP-KU 1556 was discovered in the upper middle Eocene Pondaung Formation at the Pk5 locality near Paukkaung village, Myaing Township, Magway Division, central Myanmar (Tsubamoto *et al.*, 2005). It is a left maxillary fragment with an upper molar (Figs. 1, 2A), which was provisionally interpreted as M2 by Tsubamoto *et al.* (2005).

The upper molar (length = 10.5 mm; width = 10.8 mm) is bunodont and brachyodont with conical cusps. The enamel of the crown is heavily damaged and covered with many pits probably caused by chemical etching during diagenesis or weathering. In occlusal view, the crown has a square outline. There are three large main cusps, the paracone, metacone, and protocone. The metaconule is smaller than these three main cusps. The parastyle and hypocone are

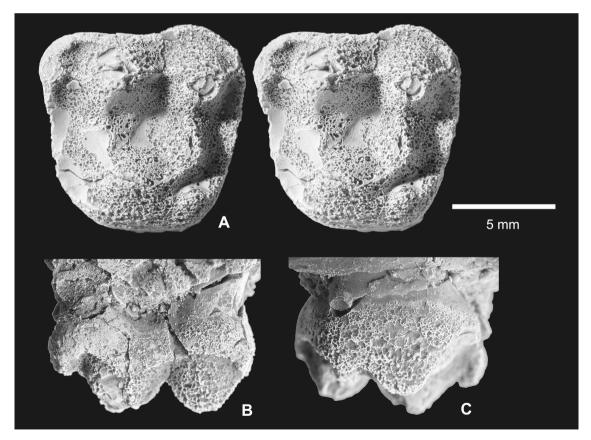


Fig. 1. An epoxy cast of left ?M2 of Artiodactyla indeterminate 1 (NMMP-KU 1556; Tsubamoto *et al.*, 2005) from the Eocene Pondaung Formation of Myanmar. A, occlusal view (stereo pair). B, buccal view. C, lingual view.

smaller than the metaconule. The paraconule appears to the smallest cusp, although it is worn more heavily than the other cusps. The mesostyle and metastyle are absent. The metacone is slightly smaller than the paracone and is as lingual as the paracone. The parastyle is located just mesial to the paracone. The ectoloph (preparacrista + postparacrista + premetacrista + postmetacrista) is mesiodistally straight, connecting to the parastyle and to the distal cingulum. The ectoloph has no connection to the buccal cingulum. The endoparacrista is located slightly mesial to the tip of the paracone and extends lingually, linking to the paraconule. The endoparacristule possibly exists, although it is not

confirmed due to the wear and poor preservation. The postparacristule is absent. The preparacristule is absent or is worn away; and there is no link between the paraconule and the mesial cingulum. The protocone is distal to the paracone; however, it is not centrally located mesiodistally on the crown but is located slightly mesially to the mesiodistal center of the crown. The preprotocrista extends mesiobuccally, connecting to the paraconule. The postprotocrista extends distobuccally, connecting to the metaconule. The metaconule does not show a selenodont morphology. The premetacristule and postmetacristule are absent. The endometacristule extends buccally, linking to the lingual base of the

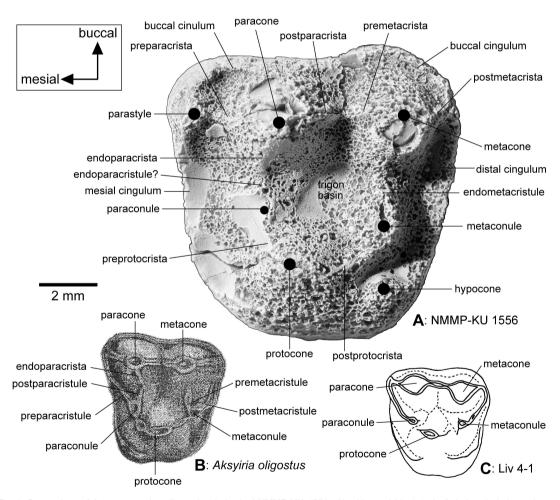


Fig. 2. Comparison of the upper molars (in occlusal view) of NMMP-KU 1556, Aksyiria, and Liv 4-1. A, Artiodactyla indeterminate 1 from the Eocene Pondaung Formation of Myanmar, left ?M2 (length = 10.5 mm; width = 10.8 mm) of NMMP-KU 1556. B, Aksyiria oligostus Gabunia from the Eocene of Kazakhstan, AN GSSR No. 25, right M1 or M2 (length = 4.2 mm; width = 4.4 mm) (reversed) (after Gabunia, 1973). C, Dichobunidae indeterminate from La Livinière (Eocene) of France, Liv 4-1, a right upper molar (length = 3.4 mm; width = 4.0 mm) (reversed) (after Sudre, 1978).

metacone. The hypocone is distolingually located to the tip of the protocone and is located just lingual to the metaconule. The hypocone is well separated from the other cusps by a groove. A cingulum surrounds the crown except at the lingual base of the protocone, bearing a parastyle and a hypocone. The trigon basin is large and deep.

Comparisons and discussion

NMMP-KU 1556 (Figs. 1, 2A) is assigned to the Artiodactyla on the basis of its enlarged metaconule and is referable to the dichobunoids in retaining a hypocone and a paraconule, in the relatively poor development of the styles and cristae. and in the relatively central position of the protocone (Tsubamoto et al., 2005; Métais et al., 2007). It is distinguished from the entelodonts in having a larger parastyle, stronger cristae, and less conical and less bunodont cusps (Tsubamoto et al., 2005). It is somewhat reminiscent of the upper molars of the raoellids in having buccolingually displaced cristae between the paracone and the protocone and between the metacone and the metaconule (Sahni et al., 1981). NMMP-KU 1556 and the raoellids also share a wide crushing trigon basin (Orliac and Ducrocq, 2012). However, NMMP-KU 1556 is distinguished from the raoellids in having sharper cristae, a parastyle, a hypocone, and less bulbous cusps.

Aksyiria is represented only by a single right upper molar (M1 or M2), AN GSSR No. 25 (Fig. 2B; Gabunia, 1973). As Métais et al. (2007) suggested, the upper molars of NMMP-KU 1556 and Aksyiria share the following characteristics: a square occlusal outline, similar sizes and locations of the three main cusps and conules, a similar development of the cingulum, and a straight ectoloph (Fig. 2A-B). However, the upper molar of NMMP-KU 1556 is distinguished from that of Aksyiria in the following morphologies (Fig. 2 A-B). NMMP-KU 1556 has a larger parastyle and hypocone, while Aksyiria has no (or very small) parastyle and hypocone (Métais et al., 2007). In NMMP-KU 1556, the protocone is somewhat mesially displaced rather than centrally located, while in Aksyiria, it is centrally placed mesiodistally on the crown. In NMMP-KU 1556, the endoparacrista is slightly mesially shifted, while in Aksyiria, it is rather distally displaced. The paraconule and metaconule of NMMP-KU 1556 show no selenodont

morphology lacking pre- and post-cristules. They are separated from the cingula in NMMP-KU 1556. In contrast, those of Aksyiria are somewhat selenodont with the pre- and post-cristules. The preparacristule and postmetacristule of Aksyiria connect to the mesial and distal cingula, respectively. The metaconule is larger than the paraconule in NMMP-KU 1556, while the former is as large as the latter in Aksyiria (Métais et al., 2007). NMMP-KU 1556 has an endometacristule and possibly an endoparacristule which are distinct from the pre- and post-cristules. In contrast, the buccally oriented cristae of the paraconule and metaconule in Aksviria would better be named the postparacristule and premetacristule, respectively. rather than the endoparacristule and endometacristule. respectively, judging from the selenodont morphology of the conules. Finally, NMMP-KU 1556 is nearly twice as big as Aksyiria in the molar size (Métais et al., 2007). Therefore, the dental morphological differences between NMMP-KU 1556 from Myanmar and Aksyiria from Kazakhstan are great enough to distinguish one from the other at the genus level.

Sudre (1978) and Métais *et al.* (2007) mentioned some resemblances of *Aksyiria* to an indeterminate dichobunid (Liv 4-1) from La Livinière (middle Eocene) of southern France described by Sudre (1978). Liv 4-1 (Fig. 2C) is a right upper molar (Sudre, 1978), which is smaller than the upper molar of *Aksyiria* (Fig. 2B). Apart from its smaller size, Liv 4-1 is distinguished from the upper molar of NMMP-KU 1556 in having a somewhat selenodont paraconule and metaconule, a postmetacristule linking to the distal cingulum, and a smaller parastyle, and in lacking a hypocone and endocristae/endocristules (Fig. 2A, 2C). Liv 4-1 is also distinct morphologically from NMMP-KU 1556 at the genus level.

Concluding remarks

In conclusion, although Métais *et al.* (2007, 2008) suggested that NMMP-KU 1556 from the Pondaung Formation may be referable to the genus *Aksyiria*, our dental comparisons lead us to reject this hypothesis. The two are distinct from one another in the upper molar morphology at least at the genus level, although they might be phyletically related. NMMP-KU 1556 is morphologically distinct from all other artiodactyl genera and it represents a

new genus and species because of its unique upper molar morphology, although its affinity within the Artiodactyla is still unclear. However, better material is necessary in order to establish a new genus and species for NMMP-KU 1556 because the only preserved tooth is heavily damaged. The affinity of Artiodactyla indeterminate 1 in Tsubamoto *et al.* (2005) should be resolved by the discovery of better material.

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