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Authors: Tsubamoto, Takehisa, Egi, Naoko, Takai, Masanaru, ., Thaug-Htike, and ., Zin-Maung-Maung-Thein

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A new genus and species of bunodont artiodactyl from the Eocene Pondaung Formation, Myanmar

TAKEHISA TSUBAMOTO^{1,2}, NAOKO EGI³, MASANARU TAKAI³, THAUNG-HTIKE⁴ AND ZIN-MAUNG-MAUNG-THEIN⁵

¹Hayashibara Museum of Natural Sciences, 4382-4 Shirimi, Oku-cho, Setouchi 701-4212, Japan (e-mail: sorlestes@msc.biglobe.ne.jp)

²Faculty of Biosphere-Geosphere Science, Okayama University of Science, 1-1 Ridai-cho, Kita-ku, Okayama 700-0005, Japan

³Primate Research Institute, Kyoto University, 41-2 Kanrin, Inuyama 484-8506, Japan

⁴Department of Geology, Shwebo University, Shwebo, Myanmar

⁵Department of Geology, Mandalay University, 73rd Road, Mandalay, Myanmar

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Abstract. A new genus and species of small bunodont artiodactyl (Mammalia), *Myanmarius chitseini*, is established on the basis of molar specimens from the upper middle Eocene Pondaung Formation, Myanmar. The specimens consist of upper molars and one m3. The m3 is provisionally referred to this species. *Myanmarius* is characterized by a low crown, bunodont cusps, a wide crushing trigon basin, a large metaconule, a reduced paraconule, a protocone distinctly larger than the other main cusps, an obtuse angled and inverted V-shaped centrocrista, a mesiodistally oriented postprotocrista and premetacristule, a buccally shifted and almost mesiodistally oriented cristid obliqua, no hypocone, no styles, and no lingual separation into two (mesial and distal) lobes of the upper molars. Our cladistic analysis supports the raoellid affinity of *Myanmarius*, which is nested with *Khirtharia*. However, if the m3 is excluded from the hypodigm of *Myanmarius*, the cladistic analysis rather supports the suoid affinity of *Myanmarius*. Therefore, the phyletic position of *Myanmarius* is still unclear.

Key words: Artiodactyla, Eocene, Myanmar, *Myanmarius*, Pondaung Formation, Raoellidae

Introduction

The upper middle Eocene Pondaung Formation (Pondaung Sandstones) of central Myanmar (Cotter, 1914; Aye Ko Aung, 1999) is one of the richest fossiliferous Paleogene deposits in Southeast Asia. Since the first mammalian fossils were described by Pilgrim and Cotter (1916), many vertebrate fossils have been reported in the formation (e.g. Colbert, 1938; Tsubamoto *et al.*, 2006, 2011, 2012, 2013, and references therein; Chaimanee *et al.*, 2012). Although the mammalian fauna of the Pondaung Formation had been considered to be dominated by perissodactyls and anthracotheriid artiodactyls in terms of taxonomic diversity and collection size (Pilgrim and Cotter, 1916; Colbert, 1938), recent discoveries have indicated that many small artiodactyls are part of the Pondaung fauna (Tsubamoto *et al.*, 2003, 2005, 2012, 2013; Métais, 2006; Métais *et al.*, 2007).

Among these small artiodactyls from the Pondaung fauna, the ‘Artiodactyla indeterminate 2’ briefly described by Tsubamoto *et al.* (2005) has attracted the

attention of several paleontologists. Métais *et al.* (2007) and Theodor *et al.* (2007) suggested that this indeterminate artiodactyl likely belongs to the Raoellidae. The Raoellidae Sahni *et al.*, 1981 are a bunodont artiodactyl family (Theodor *et al.*, 2007) and are currently considered to be the stem group of the Cetacea (whales) because a raoellid genus *Indohyus* has a thickened medial lip of the auditory bulla (involucrum) in its skull, which is an autapomorphy of the cetaceans (Thewissen *et al.*, 2007, 2009). Their unambiguous records are only from the lower middle Eocene of the Indian Subcontinent (Thewissen *et al.*, 2001; Theodor *et al.*, 2007). Therefore, the reported raoellid records in the upper middle Eocene Pondaung fauna of Myanmar by Métais *et al.* (2007) and Theodor *et al.* (2007) have impacts on the paleobiogeography and evolution of this stem cetacean group. On the other hand, Orliac and Ducrocq (2012) rejected the raoellid affinity of this artiodactyl based on their cladistic analysis and concluded that outside of the Indian Subcontinent undisputed raoellids only occurred in the middle Eocene of the central part of coastal China.

Therefore, the phyletic position of this indeterminate artiodactyl from the Pondaung fauna can alter our understanding of the paleobiogeography and early evolution of Eocene Asian artiodactyls. However, this artiodactyl is represented only by two isolated teeth and these specimens have been only briefly described (Tsubamoto *et al.*, 2005). The dental morphology of this artiodactyl has not been well documented in detail.

This article provides the precise morphology and comparisons of this artiodactyl and establishes a new genus and species. Three new specimens are also described. To test the phyletic position of the new genus, phylogenetic analyses are performed using the data matrix derived from that by Orliac and Ducrocq (2012).

Dental terminology.—Mostly follows Orliac and Ducrocq (2012). The dental terminology of the upper molars used in this paper are shown in Figure 1.

Dental abbreviations.—M/m, upper/lower molars. P, upper premolars.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA. GSI, Geological Survey of India, Kolkata, India. H-GSP, Howard University collections stored in Geological Survey of Pakistan, Islamabad, Pakistan (Thewissen *et al.*, 2001). IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China. ONG, Oil and Natural Gas Commission, Dehra Dun, India (Ranga Rao, 1971; Kumar and Sahni, 1985). NMMP-KU, specimens catalogued by the Myanmar-Japan (Kyoto University) Joint Fossil Expedition Team (Tsubamoto *et al.*, 2006), which is currently stored in the Department of Archaeology (Ministry of Culture), Yangon, Myanmar; NMMP, National Museum, Myanmar, Paleontology; KU, Kyoto University. PRI, Primate Research Institute, Kyoto University, Inuyama, Japan. UMII, Université Montpellier II (Montpellier, France). VPL, specimens stored in Panjab University, Chandigarh, India (Kumar and Sahni, 1985).

Systematic paleontology

Order Artiodactyla Owen, 1848
Family indeterminate
Genus *Myanmarius* gen. nov.

Type and only known species.—*Myanmarius chitseini* sp. nov.

Distribution.—Pondaung Formation, Myanmar; upper middle Eocene.

Etymology.—Named after Union of Myanmar, where the holotype was found. The gender of the new genus is masculine.

Diagnosis.—Small and bunodont artiodactyl. The molar morphology and size are similar to those of

Khirtharia (Raoellidae). Differs from *Khirtharia* and other raoellids in having a stronger postprotocrista and a more mesially located paraconule, in lacking a bilophodont structure (lacking the buccolingually oriented endocristae/endocristids [= buccolingual lophids/lophids] on the molars), and in that the centrocrista is not mesiodistally straight but is rather inverted V-shaped. Differs from other bunodont artiodactyls except for the raoellids in having a more buccally shifted and almost mesiodistally oriented cristid obliqua. Further differs from primitive suoids, bunodont anthracotheres, and the putative primitive anthracotheriid *Pakkokuhyus* in having a wider crushing trigon basin and a protocone distinctly larger than the other main cusps (paracone, metacone, and metaconule), and in lacking a clear lingual separation into two (mesial and distal) lobes of the upper molars. Further differs from the entelodontids in having a smaller paraconule and in lacking a hypocone. Further differs from other primitive and small bunodont artiodactyls such as the bunodont dichobunoids, helohyids, cebochoerids, and choeropotamids in having the combination of the following upper molar characteristics: a small (reduced) paraconule, a wide crushing trigon basin, a metaconule as large as the paracone and metacone, a centrocrista that is not mesiodistally straight but rather inverted V-shaped, a mesiodistally oriented postprotocrista and premetacristule, no hypocone, and no styles.

Myanmarius chitseini sp. nov.

Figures 1–3, 4A, 5A

Artiodactyla indeterminate 2. Tsubamoto *et al.*, 2005, p. 119–121, fig. 2B–C.

Holotype.—NMMP-KU 1765, right M2 (Figures 1, 2A, 4A; Tsubamoto *et al.*, 2005, p. 119, fig. 2B).

Referred material.—NMMP-KU 1742, right M3 (Figures 2B, 4A; Tsubamoto *et al.*, 2005, p. 119, fig. 2C), which likely belongs to the same individual as the holotype (Tsubamoto *et al.*, 2005).

Provisionally referred material.—NMMP-KU 2208a, right ?M1 (Figure 3A); NMMP-KU 2208b, right ?M2 (Figure 3B), which possibly belongs to the same individual as NMMP-KU 2208a; NMMP-KU 2000, broken right m3 (Figure 2C).

Locality.—NMMP-KU 1765 (holotype), NMMP-KU 1742, NMMP-KU 2208a, and NMMP-KU 2208b are from the Pk12 locality (21°44'56"N, 94°39'14"E [WGS84 datum]) near Paukaung Village. NMMP-KU 2000 is from the OPT1 locality (21°44'46" N, 94°37'40" E [WGS84 datum]) near Bahin Village. Both localities are situated in Myaing Township, Magway Division, central Myanmar (Tsubamoto *et al.*, 2005, 2006).

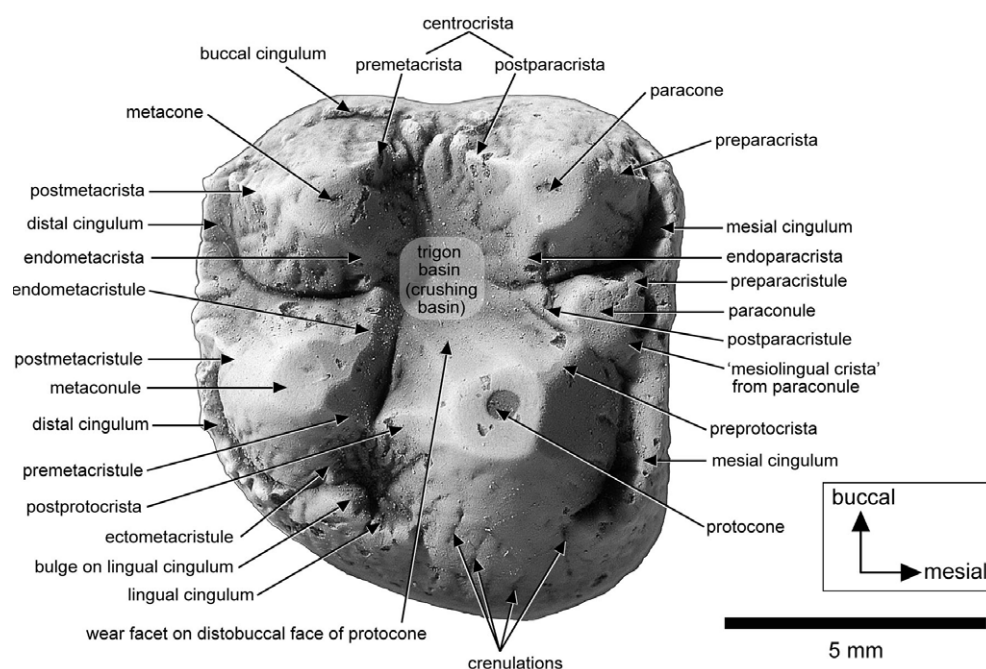


Figure 1. The dental terminology of the upper molars used in this paper, showing the occlusal view of the holotype (NMMP-KU 1765; right M2) of *Myanmarius chitsei* gen. et sp. nov. from the Eocene of Myanmar.

Formation and age.—“Upper Member” of the Pondaung Formation (Pondaung Sandstones) (Cotter, 1914; Aye Ko Aung, 1999); late middle Eocene (Bartonian) (Holroyd and Ciochon, 1994; Tsubamoto *et al.*, 2002b, 2005, 2011).

Etymology.—Named after Dr. Chit-Sein (Department of Geology, Hinthada University, Hinthada, Myanmar), who discovered the holotype.

Diagnosis.—As for the genus.

Description

NMMP-KU 1765 (holotype) and NMMP-KU 1742 were briefly described by Tsubamoto *et al.* (2005). Here, more detailed descriptions of these specimens are provided. Other specimens (NMMP-KU 2000, 2208a, 2208b) are new material. The teeth are bunodont with very low crowns and bulbous cusps. The dental enamel is somewhat crenulated.

The holotype, NMMP-KU 1765 (Figures 1, 2A, 4A), is a right M2 (Tsubamoto *et al.*, 2005). It is basically tetracuspidate with a paracone, metacone, protocone, and metaconule. These four main cusps are separated from one another by valleys. The protocone is distinctly larger than the paracone, metacone, and metaconule. The metaconule is located not distobuccally but distal to the protocone. The metaconule is as large as the paracone

and metacone. The paraconule is reduced and tiny, and is more mesial relative to the paracone and protocone. The styles (parastyle, metastyle, and mesostyle) are absent, but there are enamel crenulations on the central part of the buccal margin of the crown. The hypocone is absent. The trigon basin (central crushing basin) is large. The preparacrista extends mesially, stopping at the mesial base of the paracone. The endoparacrista extends distolingually, linking to the postparacristule. The postparacrista extends distobuccally and is not concave buccally but straight; and the premetacrista extends mesiobuccally and is not concave buccally but straight. Therefore, the centrocrista (= postparacrista + premetacrista) is not straight mesiodistally but is obtuse angled and inverted V-shaped, making the crushing trigon basin relatively wide buccally. The centrocrista is separated from the buccal cingulum. The postmetacrista extends distally, stopping at the distal base of the metacone. The endometacrista extends mesiolingually, connecting to the endometacristule. The preparacristule extends mesiobuccally, linking to the mesial cingulum. There is a mesiolingual crista from the paraconule; this crista links to the mesial cingulum. The preprotocrista extends mesiobuccally, linking to the paraconule. On the distobuccal face of the protocone, a wear facet is developed. The postprotocrista extends distally, linking to the premetacristule. The premetacristule extends mesially. The endometacris-

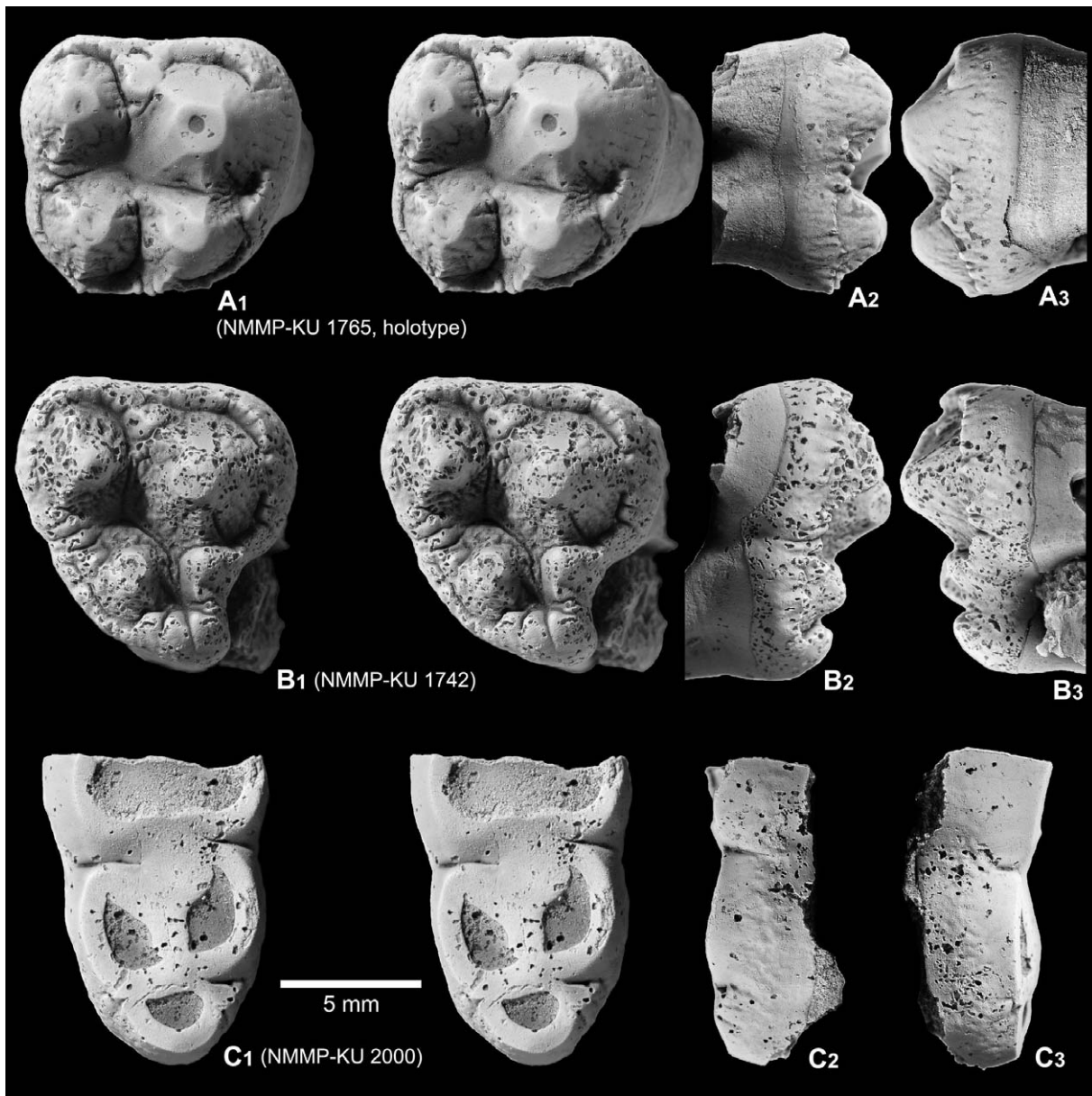


Figure 2. *Myanmarius chitsei* gen. et sp. nov. from the Eocene of Myanmar. **A**, NMMP-KU 1765 (holotype), an epoxy cast of right M2; A₁, occlusal view (stereo pair); A₂, buccal view; A₃, lingual view; **B**, NMMP-KU 1742, an epoxy cast of right M3; B₁, occlusal view (stereo pair); B₂, buccal view; B₃, lingual view; **C**, NMMP-KU 2000, an epoxy cast of right m3; C₁, occlusal view (stereo pair); C₂, buccal view; C₃, lingual view.

tule extends mesiobuccally. The postmetacristule extends distobuccally, connecting to the distal cingulum. The cingulum surrounds the crown except at the lingual base of the protocone and at the buccal base of the paracone. The metaconule has a lingual crista (ectometacristule) extending toward the small bulge on the lingual cingulum at the lingual base of the metaconule. The lingual root consists of one pillar. There is an interstitial wear

facet on the mesial and distal faces of the crown.

NMMP-KU 1742 (Figures 2B, 4A) is a right M3 (Tsubamoto *et al.*, 2005). It has many tiny pits on the surface of the crown. These tiny pits are likely caused by chemical erosion during diagenesis or weathering. It is triangular in occlusal view. The morphology of the mesial part (paracone-paraconule-protocone part) is very similar to that of the holotype (M2) except that the para-

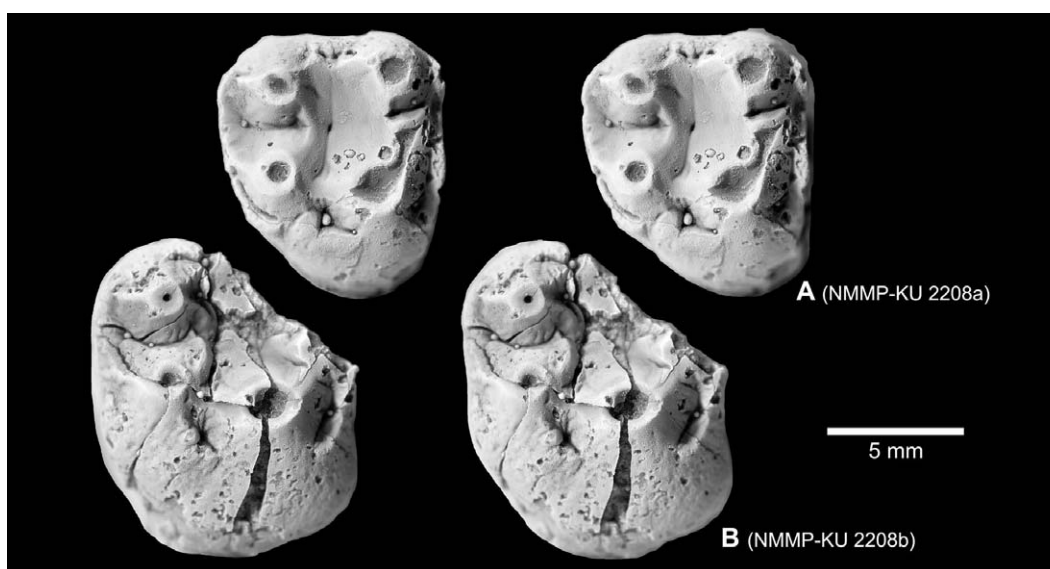


Figure 3. *Myanmarius chitseini* gen. et sp. nov. from the Eocene of Myanmar in occlusal view (stereo pair). **A**, NMMP-KU 2208a, an epoxy cast of right ?M1; **B**, NMMP-KU 2208b, an epoxy cast of right ?M2.

conule is proportionally smaller on M3 than on M2 and the paraconule lacks the ‘mesiolingual crista’ linking to the mesial cingulum. The distal part (metacone-metaconule part) is buccolingually very compressed and much narrower than the mesial part. The metacone is somewhat proportionally smaller than that of M2 and is more lingually located compared to the paracone. The metaconule is proportionally much smaller than that of M2. The metaconule has a lingual crista (= ectometacristule?) that connects to the lingual cingulum. The endocristae cannot be observed. The distal margin of the crown (talon in Tsubamoto *et al.*, 2005) is distally elongated, bearing accessory cusps on the distal margin of the cingulum. There is no interstitial wear facet on the distal face of the crown.

NMMP-KU 2208a (Figure 3A) is tentatively identified as a right M1. Its morphology is basically similar to that of the holotype (M2), except that there is no ‘mesiolingual crista’ from the paraconule connecting to the mesial cingulum. NMMP-KU 2208a is smaller in size and more worn than the holotype (M2). NMMP-KU 2208a has an interstitial wear facet on the mesial and distal faces of the crown.

NMMP-KU 2208b (Figure 3B) is tentatively identified as the right M2. Its mesiobuccal part (around the paracone) is broken away. NMMP-KU 2208b has an interstitial wear facet on the distal face of the crown. It is larger in size and less worn than NMMP-KU 2208a (?M1). It is larger than the holotype (M2) and NMMP-KU 1742 (M3) in size. Its morphology is basically similar to that

of the holotype except that it has a weaker cingulum.

NMMP-KU 2000 (Figures 2C, 5A) is a right m3. The mesial part of the trigonid is broken away. Although the crown is heavily worn, the basic size and morphology of cusps and the orientation of the cristids are visible. The tooth shows no evidence of lophodonty. The crown appears to be very low, although no tips of the cusps are preserved due to wear. The dentine is exposed on the occlusal surface of all the cusps. The trigonid is wider than the talonid. The cristids appear to be weak. The cristid obliqua (= prehypocristid) originates at the buccal part of the distal trigonid wall and extends almost mesiodistally. Therefore, the hypoflexid is very narrow buccolingually and the talonid basin (crushing basin) is wider buccally. The hypoconulid is not so greatly elongated distally. It is centrally positioned between the buccal and lingual margins of the crown and is smaller than the hypoconid and entoconid. There is no cingulum except for the buccal base of the hypoconulid.

On the hypodigm and tooth class

The holotype (NMMP-KU 1765) and NMMP-KU 1742 are identified as M2 and M3, respectively, likely derived from a single individual according to Tsubamoto *et al.* (2005). Therefore, we do not repeat the reasoning here. Although NMMP-KU 1742 is eroded with many tiny pits (Figure 2B), such pits are also observed on the surface of the other specimens of *Myanmarius chitseini* (Figures 1–3).

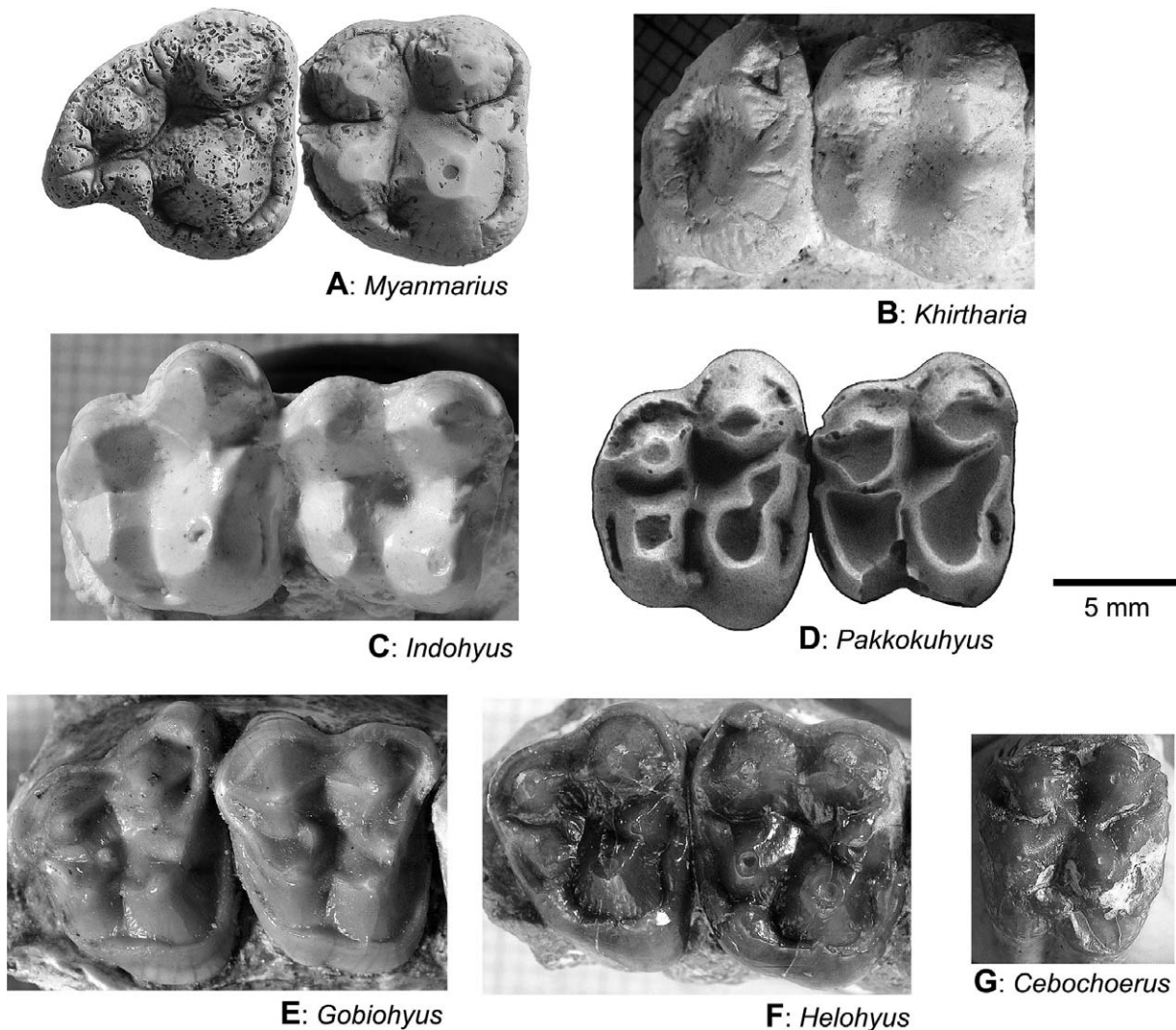


Figure 4. Comparison of the upper molars of *Myanmaricus* with those of *Khirtharia* and *Indohyus* (Raellidae), *Pakkokuhyus* (cf. Anthracotheriidae), *Gobiohyus* and *Helohyus* (Helohyidae), and *Cebochoerus* (Cebochoeridae). All figures are in occlusal view. **A**, *Myanmaricus chitsei* gen. et sp. nov., right M2–M3 (NMMP-KU 1765 and 1742); **B**, *Khirtharia dayi* Pilgrim, right M2–M3 (AMNH 116994: a cast of H-GSP 1979); **C**, *Indohyus indirae* Ranga Rao, right M2–M3 (AMNH 116886: a cast of VPL/K514); **D**, *Pakkokuhyus lahirii* (Pilgrim), right M2–M3 (NMMP-KU 0039 [= Kdw 6]); **E**, *Gobiohyus orientalis* Matthew and Granger, left M2–M3 (reversed) (AMNH 26278); **F**, *Helohyus plicodon* Marsh, left M2–M3 (reversed) (AMNH 12147); **G**, *Cebochoerus helveticus* (Pictet and Humbert), a left upper molar (reversed) (UMII BRT-97).

The buccolingually compressed and distally elongated morphology of the distal part of NMMP-KU 1742 (M3) may be one of the diagnostic characteristics of the species because such a skewed morphology is sometimes observed on normal M3 of some mammals such as several taxa of the suoids. However, this skewed morphology may alternatively indicate that NMMP-KU 1742 is an anomalous M3 specimen, like some anomalous M3 of the living Japanese monkey (*Macaca fuscata*) stored in PRI. Therefore, here, the morphology of the distal part of

M3 is not included in the diagnosis of the new genus and species, although this M3 morphology could be one of the diagnostic characteristics. Additional M3 specimens are necessary to determine the ‘true’ morphology of M3 of *Myanmaricus*.

NMMP-KU 2208a and 2208b are provisionally referred to *Myanmaricus chitsei* and are tentatively identified as M1 and M2, respectively, from the same single individual. Although the occlusal outline of these two specimens is somewhat different from the holotype

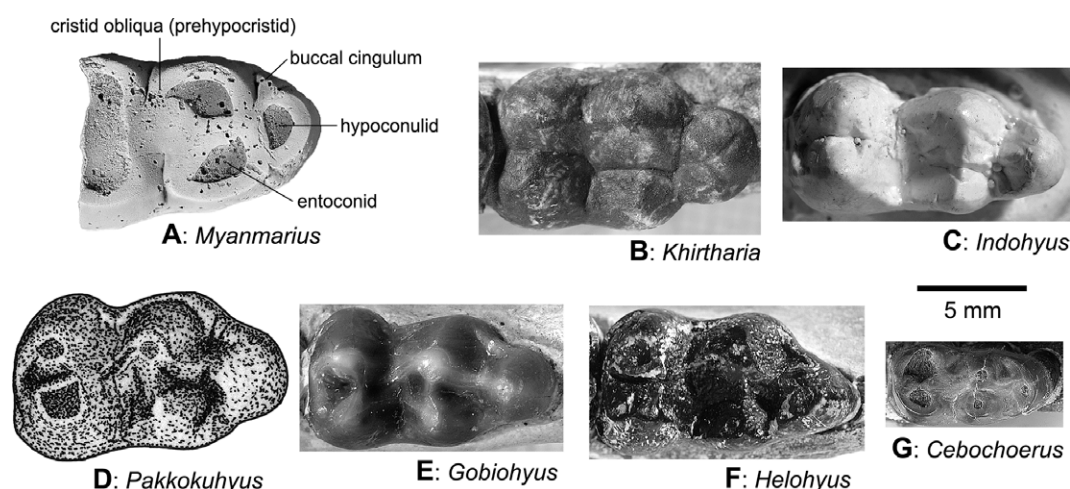


Figure 5. Comparison of m3 of *Myanmarium* with those of *Khirtharia* and *Indoehyus* (Raellidae), *Pakkokuhyus* (cf. Anthracotheriidae), *Gobiohyus* and *Helohyus* (Helohyidae), and *Cebochoerus* (Cebochoeridae). All figures are in occlusal view. **A**, *Myanmarium chitsei* gen. et sp. nov., right m3 (NMMP-KU 2000); **B**, *Khirtharia inflata* (Ranga Rao) (= *Bunodentus inflatus* Ranga Rao), right m3 (AMNH 95456: a cast of ONG/K8); **C**, *Indoehyus indira* Ranga Rao, left m3 (reversed) (AMNH 116884: a cast of VPL/K575); **D**, *Pakkokuhyus lahiri* (Pilgrim), right m3 (GSI B-766); **E**, *Gobiohyus orientalis* Matthew and Granger, right m3 (AMNH 26280); **F**, *Helohyus plicodon* Marsh, left m3 (reversed) (AMNH 12148); **G**, *Cebochoerus robiacensis* Depéret, right m3 (UMII BRT-5155).

(NMMP-KU 1765), the differences are likely caused by their poor preservation and/or by individual (intraspecific) variation. The configuration of cusps and cristae of these two specimens are basically similar to that of the holotype (Figures 2A, 3). NMMP-KU 2208a and 2208b were found in the same small nodule at the PK12 locality. NMMP-KU 2208a and 2208b have an interstitial wear facet on the distal face of the crown, indicating that they are not M3. NMMP-KU 2208b is larger in size and less worn than NMMP-KU 2208a (Figure 3).

NMMP-KU 2000 (m3) is also provisionally referred to *Myanmarium chitsei*. Although it is heavily worn, this lower molar specimen matches the upper molars of this species on the basis of its similar size, bunodont morphology, and configuration of the cusp bases and basins (Figure 2). On the distobuccal corner of the hypoconulid, the wear facet tilts distobuccally (Figure 2C), implying that there is at least a small cusp-like structure distal to the metacone-metaconule on the corresponding M3. The M3 specimen of *Myanmarium* (NMMP-KU 1742) has accessory small cuspules distal to the metacone-metaconule, making the attribution of this m3 specimen (NMMP-KU 2000) to *Myanmarium* plausible.

Comparisons and discussion

As Métails *et al.* (2007) and Theodor *et al.* (2007) suggested, the overall morphology of the upper molars of *Myanmarium* (= ‘Artiodactyla indeterminate 2’ reported

by Tsubamoto *et al.*, 2005) recalls that of the raellid *Khirtharia*. *Khirtharia* is a derived raellid, which has a ‘hyperbunodont’ molar morphology, according to Orliac and Ducrocq (2012). The upper molars of *Myanmarium* and *Khirtharia* share bunodont cusps, a reduced paraconule, no parastyle, a rounded buccal wall, a wide crushing trigon basin (Orliac and Ducrocq, 2012), and no clear lingual separation into two (mesial and distal) lobes (Figure 4A–B). The provisionally referred m3 (NMMP-KU 2000) of *Myanmarium* also recalls the lower molars of the Raellidae in having a buccally shifted and almost mesiodistally oriented cristid obliqua with a wide crushing talonid basin (Orliac and Ducrocq, 2012) (Figure 5A–C). *Myanmarium* is distinguished from *Khirtharia* and also from other raellids in having a more bunodont dentition and a stronger postprotocrista, in lacking the bilophodont structure (the buccolingually oriented endocristiae/endocristids [= buccolingual loph/lophids] on the molars), and in that the paraconule is more mesially located and the centrocrista is not mesiodistally straight but rather inverted V-shaped. It also differs from “? *Khirtharia* cf. *major*” from the middle Eocene Shanguang deposits of coastal China (Orliac and Ducrocq, 2012) in being much smaller and in lacking a bilophodont structure.

However, the assignment of *Myanmarium* to the Raellidae, which was originally suggested by Métails *et al.* (2007) and was agreed on by Theodor *et al.* (2007), is disputable. This is because *Myanmarium* lacks the bilo-

phodont structure, which has been traditionally considered to be one of the most diagnostic characteristics of the family (Figures 4A–C, 5A–C; Sahni *et al.*, 1981; Kumar and Sahni, 1985; Thewissen *et al.*, 1987). Therefore, assigning ‘Artiodactyla indeterminate 2’ of Tsubamoto *et al.* (2005) (= *Myanmarius*) to the Raoellidae, Theodor *et al.* (2007) mentioned that the raoellids have ‘various degrees of lophodonty.’ According to the phylogenetic analysis by Orliac and Ducrocq (2012), on the other hand, the molars of the Raoellidae are characterized by wide crushing trigon and talonid basins, a metaconule located distally to the protocone (misstated as ‘paracone’ in Orliac and Ducrocq, 2012, p. 86, and a buccally shifted cristid obliqua, and by the lack of a parastyle, a paraconid, and a m1–m2 hypoconulid. Orliac and Ducrocq (2012) also suggested that the primitive raoellids have stronger bilophodonty and the derived ones reduced lophodonty. The molar morphology of *Myanmarius* matches this definition of the Raoellidae by Orliac and Ducrocq (2012) and implies that *Myanmarius* might be the most derived representative of the family in having the most reduced lophodonty (Figure 4A–C). However, the phylogenetic analysis by Orliac and Ducrocq (2012) implied that NMMP-KU 1765 (= holotype of *Myanmarius*) is phyletically related not to the Raoellidae but to the Suoidea. *Myanmarius* is represented only by the upper molars with provisionally assigned broken m3, and its premolar dentition is unknown. The raoellids have many diagnostic characteristics also on the premolars, lower molars, and skull (Thewissen *et al.*, 1987; 2007, 2009; Orliac and Ducrocq, 2012). Therefore, the assignment of *Myanmarius* to the Raoellidae is ambiguous due to its unique morphology and to the scarcity of its material.

Gobiohyus yuanchuensis was described from the middle Eocene Heti Formation of central China by Young (1937, as *Gobiohyus yuanchuensis*). It was questionably referred to the raoellid genus *Indohyus* by Coombs and Coombs (1977), but was later removed from the Raoellidae by Thewissen *et al.* (1987). *Myanmarius* differs from *G. yuanchuensis* at least in being smaller and in having a more buccally shifted and almost mesiodistally oriented cristid obliqua, judging from the illustration by Young (1937). The cristid obliqua of m3 of *G. yuanchuensis* originates centrally at the distal trigonid wall. In this character, *G. yuanchuensis* is not comparable to the Raoellidae, although its P4 morphology is likely compatible with that of the family (Orliac and Ducrocq, 2012).

Haqueina haquei was described from the lower middle Eocene Kuldana Formation of Pakistan by Dehm and Oettingen-Spielberg (1958). It is the type species of the genus *Haqueina*. It is based only on m2–m3 and its upper

molars are unknown (Dehm and Oettingen-Spielberg, 1958; Sahni and Khare, 1973; Thewissen *et al.*, 1987, 2001). *H. haquei* was retained in the Raoellidae by Thewissen *et al.* (1987, 2001), but was removed from the family by Theodor *et al.* (2007) and Orliac and Ducrocq (2012). *Myanmarius* differs from *H. haquei* in having a more buccally shifted and almost mesiodistally oriented cristid obliqua. *H. haquei* has a centrally originated cristid obliqua below the notch between the protoconid and the metaconid at the distal trigonid wall, implying that it appears to be not referable to the Raoellidae at least in this character (Thewissen *et al.*, 1987; Orliac and Ducrocq, 2012).

‘*Haqueina*’ *haichinensis* was described from the middle Eocene Khaichin Ula II locality of Mongolia by Vislobokova (2004) as a raoellid. *Myanmarius* differs from ‘*H.*’ *haichinensis* in having a smaller paraconule, weaker cristae, and a weaker cingulum, and in lacking a parastyle. As implied by Orliac and Ducrocq (2012), the molars of ‘*H.*’ *haichinensis* are more similar in morphology to those of *Gobiohyus* (Helohyidae) (Figure 4E), particularly in having a parastyle and a paraconid. On the other hand, the lower molars of *H. haquei* differ from *Gobiohyus* in lacking a paraconid (Dehm and Oettingen-Spielberg, 1958), implying that ‘*H.*’ *haichinensis* may not belong to the genus *Haqueina*.

Myanmarius is distinguished from the suoids by its molar morphology, although the phylogenetic analysis by Orliac and Ducrocq (2012) implied its suoid affinity. *Myanmarius* has a larger protocone compared to the paracone, metacone, and metaconule than the suoids. The postprotocrista of *Myanmarius* is mesiodistally oriented, while that of the suoids (except for some taxa such as *Cynorca*) is distobuccally oriented, if present. *Myanmarius* lacks a clear lingual separation into two (mesial and distal) lobes of the upper molars, which is typical in the suoids. It also lacks a centroconule (= an accessory cusp between the metacone and the protocone), which is typical in the suoids except for some primitive taxa such as *Siamochoerus* and *Huaxiachoerus*. *Myanmarius* has a wider crushing trigon basin than the suoids. In *Myanmarius*, the cristid obliqua is buccally originated at the distal trigonid wall and is almost mesiodistally oriented with a buccolingually very narrow hypoflexid. In the suoids, however, it is more centrally originated and is more diagonally oriented in occlusal view. None of the suoids has a mesiodistally oriented cristid obliqua.

Myanmarius is close in size to the other primitive bunodont artiodactyls from the Pondaung Formation, *Pakkokuhyus lahirii* and Artiodactyla indeterminate 1. *Pakkokuhyus lahirii* (Figures 4D, 5D) is recorded only in the Pondaung Formation (Pilgrim, 1928; Holroyd and Ciochon, 1995; Ducrocq *et al.*, 2000; Tsubamoto *et al.*,

Table 1. Dental measurements (in mm) of *Myanmarius chitseini* gen. et sp. nov. from the Eocene of Myanmar. L, mesiodistal length; W, buccolingual width; W-trd, trigonid width; W-tad, talonid width; *, estimate.

NMMP-KU 1765	L	9.7
(M2; holotype)	W	10.7
NMMP-KU 1742	L	10.8
(M3)	W	10.7
NMMP-KU 2208a	L	8.6
(?M1)	W	10.0
NMMP-KU 2208b	L	10.5*
(?M2)	W	12.5*
NMMP-KU 2000	L	13.0*
(m3)	W-trd	8.2
	W-tad	7.4

2002a) and is likely a very primitive bunodont anthracothere (Pilgrim, 1928; Ducrocq *et al.*, 2000; Tsubamoto *et al.*, 2011). *Myanmarius* is distinguished from *Pakkokuhyus* in having a wider crushing trigon basin, a smaller paraconule, an inverted V-shaped centrocrista (mesiodistally straight in *Pakkokuhyus*), a mesiodistally oriented postprotocrista and premetacristule (no mesiodistally oriented cristae between the protocone and the metaconule in *Pakkokuhyus*), a stronger lingual cingulum of the upper molars, and a more buccally shifted and almost mesiodistally oriented cristid obliqua, and in lacking a clear lingual separation into two (mesial and distal) lobes of the upper molars. On the other hand, Artiodactyla indeterminate 1 was originally described by Tsubamoto *et al.* (2005) based only on a maxillary fragment with an upper molar and was later reexamined by Tsubamoto *et al.* (2012). *Myanmarius* is distinguished from Artiodactyla indeterminate 1 (Tsubamoto *et al.*, 2005) in having less developed cristae and a larger metaconule, and in lacking a hypocone, a parastyle, and buccolingually oriented endocristae.

Myanmarius is generally distinguished from other bunodont artiodactyls except for the raoellids in having a more buccally shifted and almost mesiodistally oriented cristid obliqua (Figure 5). Other artiodactyls except for the raoellids have more lingually shifted and diago-

nally oriented cristid obliqua (Figure 5). *Myanmarius* is further distinguished from the entelodontids in having a smaller paraconule, in lacking a hypocone, and in being smaller. It is further distinguished from bunodont anthracotheres in having a wider crushing trigon basin, a smaller paraconule (except for *Myaingtherium* Tsubamoto *et al.*, 2011), and a mesiodistally oriented postprotocrista and premetacristule, and in lacking a clear lingual separation into two (mesial and distal) lobes of the upper molars.

Myanmarius is further distinguished from other primitive and small bunodont artiodactyls such as the helohyids (Figures 4E–F, 5E–F), cebochoerids (Figures 4G, 5G), choeropotamids, leptocherids, diacodexids, homacodontids, and dichobunids. It differs from the helohyids in having a mesiodistally oriented postprotocrista and premetacristule, an inverted V-shaped centrocrista, and a larger metaconule, and in lacking a hypocone. It differs from the cebochoerids in having a mesiodistally oriented postprotocrista and premetacrista and an inverted V-shaped centrocrista, and in lacking a clear lingual separation into two (mesial and distal) lobes of the upper molars. It differs from the choeropotamids in having less developed cristae, less developed styles, and a protocone distinctly larger than the other cusps. It differs from the leptocherids in having a larger metaconule, a smaller paraconule, a wider crushing trigon basin, and not a triangular but instead a quadrate outline of M1–M2 in occlusal view, and in lacking any trace of the hypocone. It differs from the diacodexids in having a more bunodont protocone, a larger metaconule, and a not triangular but instead a quadrate outline of M1–M2 in occlusal view. The homacodontids and dichobunids have a variety of molar morphologies (Stucky, 1998; Theodor *et al.*, 2007). Nevertheless, *Myanmarius* differs from the bunodont homacodontids and bunodont dichobunids in having the combination of the following upper molar characteristics: a small (reduced) paraconule, a wide crushing trigon basin, a metaconule as large as the paracone and metacone, a centrocrista that is not mesiodistally straight but rather obtuse-angled and inverted V-shaped, a mesiodistally oriented postprotocrista and premetacristule, no hypocone, and no styles.

Phylogenetic analysis

We performed phylogenetic (cladistic) analyses using the data matrix derived from that of Orliac and Ducrocq (2012). Orliac and Ducrocq (2012) performed a phylogenetic analysis for several primitive artiodactyl taxa including the raoellids and the holotype of *Myanmarius* (NMMP-KU 1765) using 37 dental characters. They found eight characters that can be coded for NMMP-KU

Table 2. Characters of which states are known in *Myanmarius* among the 37 characters of Orliac and Ducrocq (2012).

-
1. *Enamel crenulation*: (0) absence; (1) presence.
 8. *Lower molars, cristid obliqua*: (0) mesially pointed towards the center of the tooth; (1) mesially pointed towards the postectoprotocristid.
 9. *Lower molars, accessory internal cristid*: (0) absence; (1) presence.
 11. *Lower molars, lingual cusps*: (0) connection between postectometacristid and ectoentocristid; (1) no connection between postectometacristid and ectoentocristid.
 12. *Lower molars, mesoconulid*: (0) absence; (1) presence.
 15. *Lower molar crown height*: (0) high (deep transverse valley in lateral view); (1) low (wide and shallow transverse valley in lateral view).
 20. *Upper molars, parastyle*: (0) absence; (1) presence.
 21. *Upper molars, endoparaacrista*: (0) absence; (1) presence.
 22. *Upper molars, hypocone*: (0) absence; (1) presence (might be present on M1 only).
 23. *Upper molars, endometacrista and endometacristule forming a transverse crest*: (0) absence; (1) presence.
 24. *Upper molars, ectometacristule connected to lingual cingulum*: (0) absence; (1) presence.
 25. *Upper molars, buccal wall of the cusps of the upper molars*: (0) with two wide fossae; (1) about rounded.
 26. *Upper molars, connection of buccal cristae with buccal cingulum*: (0) absence; (1) presence.
 27. *Upper molars, position of the metaconule*: (0) located on the buccal side of the protocone; (1) located on the distal side of the protocone.
 28. *Upper molars, lingual roots*: (0) one pillar; (1) two pillars (may be joined, clear distal pillar).
-

1765 (Characters 20–27). We added seven character states of *Myanmarius* to their matrix and reanalyzed the revised matrix. The newly indicated character states of *Myanmarius* are as follows: Character 1 = State 1; Character 8 = State 1; Character 9 = State 0; Character 11 = State 1; Character 12 = State 0; Character 15 = State 1; Character 28 = State 0. Character 1 is a character on the postcanine teeth; Characters 8, 9, 10, 11, 12, and 15 are characters on the lower molars; and Character 28 is a character on the upper molars (Orliac and Ducrocq, 2012). In total, 15 characters were able to be coded for *Myanmarius*. These 15 characters are indicated and described in Table 2.

The revised data matrix is composed of 37 characters and 18 taxa (Orliac and Ducrocq, 2012). It was compiled using MacClade version 4.0 (Maddison and Maddison, 2000) and was analyzed using PAUP version 4.0b10 (Swofford, 2002) under the assumption of the minimal model of unweighted parsimony with a branch and bound search. No other constraints have been applied. The robustness of the clades was measured by Bremer support (Bremer, 1994). Two cladistic analyses, Analysis 1 and Analysis 2, were performed as follows. The NEXUS file (for MacClade and PAUP) of Analysis 1 is indicated in Appendix.

Analysis 1

The m3 specimen (NMMP-KU 2000), which is provi-

sionally referred to *Myanmarius*, was treated as a part of the hypodigm of *Myanmarius*. Therefore, the lower molar character states of *Myanmarius* indicated above (Characters 8, 9, 10, 11, 12, and 15) were coded as they are in the matrix. The revised character matrix of *Myanmarius* for Analysis 1 is shown in Table 3.

The result of Analysis 1 recovered 18 equally most parsimonious cladogram trees with a length of 70 steps. All characters were parsimony informative. Each most parsimonious tree has a CI of 0.529, RI of 0.763, RC of 0.403, and HI of 0.471. The strict consensus tree of the 18 equally most parsimonious trees (Figure 6A) indicates that *Myanmarius* is a sister taxon for *Khirtharia* and “*Khirtharia* cf. *major*” and that it is nested within the deepest (most derived) part of the Raoellidae, implying that *Myanmarius* is a derived raoellid. The robustness of all the clades in this tree are actually not so strong (Bremer support 1 and 2) (Figure 6A). The clades of the Raoellidae and [Raoellidae + Cetacea] are supported by Bremer support 1 (Figure 6A). In terms of Bremer support, the robustness of the clade of the Raoellidae is the same as that of the phylogenetic analysis performed by Orliac and Ducrocq (2012), but that of the [Raoellidae + Cetacea] is weaker than the latter.

Analysis 2

The m3 specimen (NMMP-KU 2000) was excluded from the hypodigm of *Myanmarius*. Therefore, the lower

Table 3. Character matrices of *Myanmarius* for Analysis 1 and Analysis 2 (after Orliac and Ducrocq, 2012).

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Analysis 1	1	?	?	?	?	?	?	1	0	?	1	0	?	?	1	?	?	?	?	0
Analysis 2	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0

Character	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
Analysis 1	1	0	0	1	1	0	1	0	?	?	?	?	?	?	?	?	?
Analysis 2	1	0	0	1	1	0	1	0	?	?	?	?	?	?	?	?	?

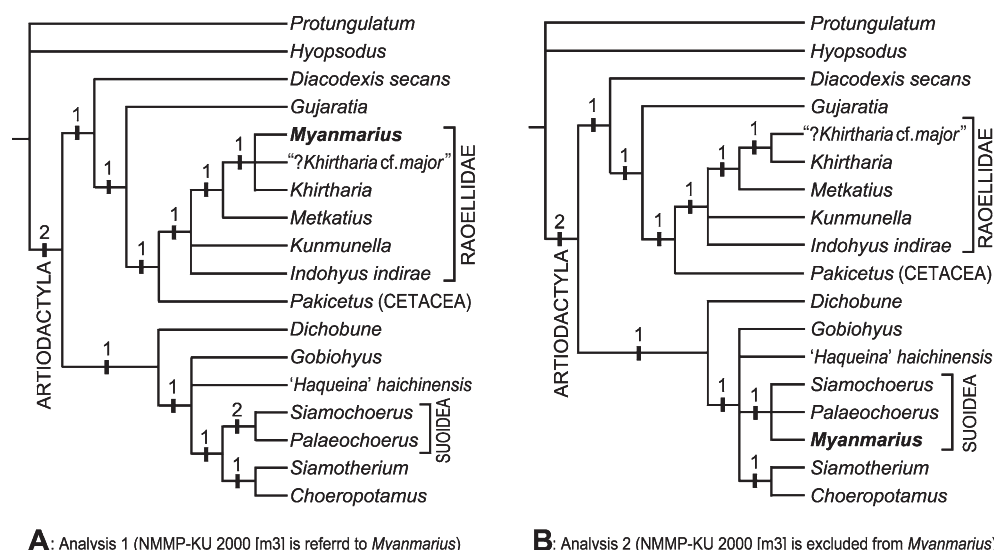


Figure 6. Strict consensus trees of the most parsimonious cladogram trees recovered by the phylogenetic analyses. Numbers indicate Bremer support (Bremer, 1994). **A**, strict consensus tree recovered by Analysis 1 (NMMP-KU 2000 [m3] is referred to *Myanmarius*) (18 most parsimonious trees, tree length = 70, CI = 0.529, RI = 0.763, RC = 0.403, HI = 0.471); **B**, strict consensus tree recovered by Analysis 2 (NMMP-KU 2000 [m3] is excluded from the hypodigm of *Myanmarius*) (36 most parsimonious trees, tree length = 68, CI = 0.544, RI = 0.770, RC = 0.419, HI = 0.456).

molar character states of *Myanmarius* indicated above (Characters 8, 9, 10, 11, 12, and 15) were coded as ‘missing (= ?)’ in the matrix. The revised character matrix of *Myanmarius* for Analysis 2 is shown in Table 3.

The result of Analysis 2 recovered 36 equally most parsimonious cladogram trees with a length of 68 steps. All characters were parsimony informative. Each most parsimonious tree has a CI of 0.544, RI of 0.770, RC of 0.419, and HI of 0.456. The strict consensus tree of the 36 equally most parsimonious trees (Figure 6B) indicates that *Myanmarius* is nested with the suoids, implying that *Myanmarius* is a suoid or is the sister taxon of the suoids. However, the robustness of all the clades within the Artiodactyla is weak (Bremer support 1) (Figure 6B). The robustness of the clades of the Raoellidae and

[Raoellidae + Cetacea] is the same as that of Analysis 1.

Discussion

Both Analysis 1 and Analysis 2 did not strongly imply the phyletic position of *Myanmarius* within the Artiodactyla. They weakly suggested that *Myanmarius* can be related either to the Raoellidae or to the Suoidea (Figure 6). On the other hand, our cladistic analyses indicate that the raoellid affinity hypothesis of *Myanmarius*, which was originally proposed by Métais *et al.* (2007) and was agreed on by Theodor *et al.* (2007), cannot be abandoned yet, although Orliac and Ducrocq (2012) denied the hypothesis. The search for the phyletic position of *Myanmarius* within the Artiodactyla should be investigated by more comprehensive phylogenetic analyses with better

material of *Myanmarius* showing the morphologies of the premolars and lower molars.

Concluding remarks

In conclusion, the phyletic position of *Myanmarius chitseini* gen. et sp. nov. from the upper middle Eocene Pondaung Formation of Myanmar within the Artiodactyla is still unclear due to the scarcity of its material. One of our phylogenetic analyses indicated that *Myanmarius* is a derived raoellid closely related to *Khirtharia* (Figure 6A). However, if m3 (NMMP-KU 2000), which is a provisionally referred specimen, is excluded from the hypothesis of *Myanmarius*, the phylogenetic analysis alternatively implied a suoid affinity of *Myanmarius* (Figure 6B). Nevertheless, *Myanmarius* lacks a bilophodont molar structure, which has been traditionally considered to be one of the most diagnostic characteristics of the Raoellidae, and distinctly differs from the Suoidea mainly in having a larger protocone compared to the other main cusps and a more buccally shifted and almost mesiodistally oriented cristid obliqua, and in lacking a clear lingual separation into two (mesial and distal) lobes of the upper molars. At least our phylogenetic analyses indicate that the raoellid affinity of *Myanmarius*, which was proposed by Métais *et al.* (2007) and was later denied by Orliac and Ducrocq (2012), cannot be abandoned. Better material of *Myanmarius* with more comprehensive phylogenetic analyses will confirm the phyletic position of *Myanmarius* and may alter the definition and diagnosis of the Raoellidae. Therefore, *Myanmarius* is an important and critical taxon to resolve the phyletic relationships among the several artiodactyl (cetartiodactyl) groups such as the Raoellidae, Suoidea, Pakicetidae, Anthracotheriidae, and Helohyidae, and to resolve the paleobiogeography and early evolution of these artiodactyl groups in the Eocene of eastern Eurasia (Métais *et al.*, 2007; Tsubamoto *et al.*, 2011; Orliac and Ducrocq, 2012).

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Appendix. NEXUS file corresponding to the data matrix for Analysis 1 (Figure 6A) (after Orliac and Ducrocq, 2012).

```
#NEXUS
[]
```

```
BEGIN TAXA;
```

```
  DIMENSIONS NTAX=18;
  TAXLABELS
  Protungulatum
  Hyopsodus
  Diacodexis_secans
  Gujaratia
  Dichobune
  Gobiohyus
  ''Haqueina'' haichinensis'
  ''?Khirtharia cf. major''
  Khirtharia
  Metkathius
  Kumnunella
  Indohyus
  Pakicetus
  Siamochorus
  Palaeochorus
  Siamotherium
  Choeropotamus
  Myanmarium;
```

```
END;
```

```
BEGIN CHARACTERS;
```

```
  DIMENSIONS NCHAR=37;
  FORMAT MISSING=? GAP=- ;
  CHARSTATELABELS
```

```
    1 enamel_crenulation / absence presence,
  2 'lower molars, paraconid' / absence presence,
  3 'lower molars, entoconid high' / greatly_reduced_compared_to_hypoconid similar_to_hypoconid,
  4 'lower molars, entoconid surface' / reduced_compared_to_hypoconid only_slightly_smaller_or_same_size,
  5 'lower molars, endoentocristids' / absence presence,
  6 'lower molars, orientation of the endoentocristid' / forward transversal,
  7 'lower molars, endohypocristid' / absence presence,
  8 'lower molars, cristide oblique' / mesially_pointed_toward_the_center_of_the_tooth mesially_pointed_toward_the_
postectoprotocristid,
  9 'lower molars, accessory internal cristid' / absence presence,
  10 'lower molars, postfossids on the mesial cupids' / absent_or_greatly_reduced present_and_deep,
  11 'lower molars, lingual cuspids' / connection_between_postectometacristid_and_ectoentocristid no_connection_
between_postectometacristid_and_ectoentocristid,
  12 'lower molars, mesoconulid' / absence presence,
  13 m2_hypoconulid / absence presence,
  14 m3_hypoconulid_ectohypoconulid / absence presence,
  15 crown_high / 'high_(deep_traverse_valley_in_lateral_view)' 'low_(wide_and_shallow_traverse_valley_in_lateral_
view)',
  16 'p4, mesiostylid (paraconid)' / absent present,
  17 'p4, lingual face inflexion of the basis of the crown' / absence presence,
  18 'p4, metaconid' / absence presence,
  19 'p4, hypoconulid' / absence presence,
  20 'upper molars, parastyle' / absence presence,
  21 'upper molars, endoparacrista' / absence presence,
  22 'upper molars, hypocone' / absence presence,
  23 'upper molars, endometacrista and endometecristule forming a transverse crest' / absence presence,
  24 'upper molars, ectometacristule connected to lingual cingulum' / absence presence,
  25 'upper molars, buccal wall of the cusps of the upper molars' / with_two_wide_fossae about_rounded,
  26 'upper molars, connection of buccal cristae with buccal cingulum' / absence presence,
  27 'upper molars, position of the metaconule' / located_on_the_labial_side_of_the_protocone located_on_the_distal_
side_of_the_protocone,
  28 'upper molars, lingual roots' / one_pillar 'two_pillars_(may_be_joined,_clear_distal_pillar)',
```

29 'P4, postprotocrista' / absence presence,
 30 'P4, endocristids forming an anterior lophe' / absence presence,
 31 'P4, endoparacrista' / absence presence,
 32 'P4, paracone height/protocone' / slightly_higher_than_protocone much_higher_than_protocone,
 33 'P4, paracone height/molar' / same_height_as_paracones_on_the_molars much_higher_than_paracones_on_the_molars,
 34 'P4, assymetrie du paracone' / absence presence,
 35 'P4, constriction between protocone and paracone' / absence presence,
 36 'P3, protocone' / absence presence,
 37 'P3, number of roots' / three two

MATRIX

```
[
      10      20      30      ]
[
      .      .      .      ]
```

```
Protungulatum      01000-0010101101?101010-00001000011??
Hyopsodus          01000-00101011010101010-00-0100001110
Diacodexis_secans 01000-00100011011001111-000000100111?
Gujaratia          01000-00100011011001101-0000001101110
Dichobune          01111110110011010101110-001000?000110
Gobiohyus          1111111011001001110110000010101000010
'''Haqueina''' haichinensis' 111111101?00100????110000010101000010
'''?Khirtharia cf. major''' 101011110100?11????????????????????
Khirtharia         10101111000001101010101010????????
Metkathius         1000???11?000?1??0????????????????
Kumnunella         100011111100010110?0101010011111101
Indohyus           10001111110001001010101010011111101
Pakicetus          11----111--0--00100010--1000--1110101
Siamochorus        1011111011111000011010?11011????????
Palaeochoerus      1011111011111001011000011011000000000
Siamotherium       001110001100100000001000011110001000?
Choeropotamus      0011100011001?01000110000111101000010
Myanmaris          1?????10?10??1?????010011010????????
```

;

END;

BEGIN ASSUMPTIONS;

OPTIONS DEFTYPE=unord PolyTcount=MINSTEPS ;

END;

BEGIN NOTES;

TEXT CHARACTER=22 TEXT= might_be_present_on_M1_only;

END;