Middle Eocene ungulate mammals from Myanmar: A review with description of new specimens

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Tsubamoto, T., Egi, N., Takai, M., Sein, C., and Maung, M. 2005. Middle Eocene ungulate mammals from Myanmar: A review with description of new specimens. *Acta Palaeontologica Polonica* 50 (1): 117–138.

We review an ungulate mammalian fauna of the Eocene Pondaung Formation, central Myanmar, and herein describe new dental specimens. The taxa newly recognized in the Pondaung Formation are two indeterminate bunodont artiodactyls, two small "eomoropid" perissodactyls (*Eomoropus* sp. cf. *E. minimus* and an indeterminate "eomoropid"), and a new deperetellid perissodactyl genus, *Bahinolophus*, which is established for *Deperetella birmanica* from the Pondaung Formation. The Pondaung ungulate fauna consists of 29 species (14 families and 18 genera): one species of an indeterminate small ungulate, 12 species (six genera in six families) of artiodactyls, and 16 species (11 genera in seven families) of perissodactyls. Although both Pondaung artiodactyls and perissodactyls are abundant and taxonomically diverse, the former are less diversified in generic numbers than the latter, but are nearly equal to the latter in abundance. Anthracotheriid artiodactyls and brontotheriid and amynodontid perissodactyls are the most abundant elements in the fauna. The estimated paleoecologies of the included taxa, the geologic and geographic evidence, and cenogram analysis suggest that the paleoenvironment of the Pondaung fauna was forested/woodland vegetation with humid/subhumid moisture and large rivers, which were located not far from the eastern Tethyan Sea. The age of the Pondaung fauna is independently correlated with the latest middle Eocene only on the basis of the stratigraphic, microfossil, and radiometric evidence, yielding a result consistent with mammalian faunal correlations. On the other hand, the Pondaung fauna includes many artiodactyl taxa compared to other middle Eocene faunas of East Asia and shows relatively high endemism at the generic level, implying that the Pondaung fauna is not formally included in the Eocene Asian Land Mammal "Ages" system.

Key words: Ungulata, *Bahinolophus*, cenogram, Eocene, Pondaung Formation, Myanmar.

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Introduction

The Eocene Pondaung Formation of Myanmar (former Burma) is one of the richest Paleogene fossil-bearing deposits of terrestrial mammals in Southeast Asia. The mammalian fossils from this formation were first described by Pilgrim and Cotter (1916), and in the first half of the 20th century, primate, artiodactyl, and perissodactyl mammals were described (Pilgrim 1925, 1927, 1928; Matthew 1929; Colbert 1937, 1938). In the 1970s and 1980s, some primate fossil specimens were reported (Ba Maw et al. 1979; Ciochon et al. 1985). In the late 1990s and 2000s, numerous fossils of mammals as well as other vertebrates (Hutchison and Holroyd 1996; Pondaung Fossil Expedition Team 1997; Hutchison et al. 2004; Stidham et al. in press; Head et al. in press) and micro-fossils (Swe Myint 1999; Hla Mon 1999; Thet Wai 1999) were reported.

Among the Pondaung mammalian fossils, in particular, two primate genera *Pondaungia* and *Amphipithecus* have been attracting the attention of many paleontologists, primatologists, and anthropologists because they show several primitive anthropoid ("higher primate"-like) features (e.g., Pilgrim 1927; Colbert 1937, 1938; Ba Maw et al. 1979; Ciochon et al. 1985). Recent discoveries of many new primate fossil specimens in the Pondaung Formation are also attracting the attention of many researchers in terms of the anthropoid origins debate (Pondaung Fossil Expedition Team, 1997; Jaeger et al. 1998, 1999; Chaimanee et al. 2000; Takai et al. 2000, 2001, 2003, in press; Ciochon et al. 2001; Gebo et al. 2002; Gunnell et al. 2002; Shigehara et al. 2002; Marivaux et al. 2003; Egi, Soe Thura Tun, et al. 2004; Egi, Takai, et al. 2004; Kay et al. 2004; Shigehara and Takai 2004; Takai and Shigehara 2004).

There are only a few studies on Pondaung creodonts, carnivores, and rodents because these mammalian taxa have been

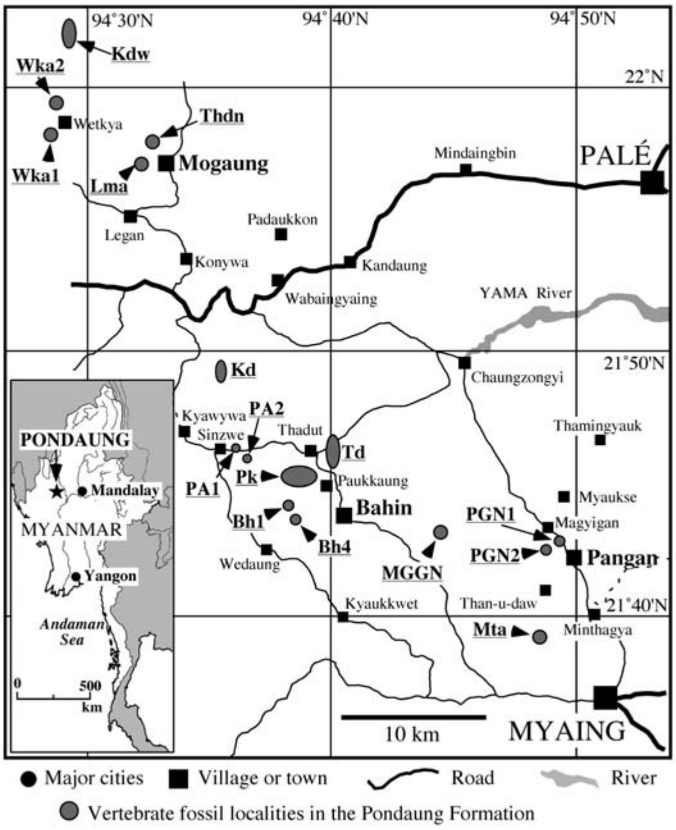

Fig. 1. Geographical map of the Pondaung area of central Myanmar showing several vertebrate fossil localities in the Pondaung Formation.

discovered by recent fossil expeditions (Pondaung Fossil Expedition Team, 1997; Egi and Tsubamoto 2000; Tsubamoto, Egi, et al. 2000; Dawson et al. 2003; Egi, Holroyd, et al. 2004; Marivaux et al. in press).

On the other hand, there were several studies on the Pondaung ungulates in the early 20th century, as mentioned above. Also, there are several recent studies by Myanmar, Japanese, French, and American researchers on the Pondaung ungulates (Holroyd and Ciochon 1995, 2000; Pondaung Fossil Expedition Team, 1997; Ducrocq, Aung Naing Soe, Aye Ko Aung, et al. 2000; Ducrocq, Aung Naing Soe, Bo Bo, et al. 2000; Métais et al. 2000; Tsubamoto, Egi, et al. 2000; Tsubamoto, Holroyd, et al. 2000; Tsubamoto, Takai, Egi, et al. 2002; Tsubamoto et al. 2003; Holroyd et al. in press). The Pondaung ungulates have been used in studies of mammalian correlation in the Eocene of East Asia (e.g., Russell and Zhai, 1987; Holroyd and Ciochon 1994; Tsubamoto et al. 2004).

The Pondaung ungulate assemblage is one of the most important faunas for understanding the evolution of Eocene mammals in East Asia. Among the Pondaung mammals, artiodactyls and perissodactyls dominate the fauna (e.g., Colbert 1938), as they often do in many Eocene mammalian faunas of East Asia (e.g., Russell and Zhai 1987; Meng and McKenna 1998: fig. 3). Furthermore, the Pondaung Formation has been dated by fission-track analysis (Tsubamoto, Takai, Shigehara, et al. 2002), whereas most Eocene terrestrial mammalian faunas in East Asia have not been well-dated (Li and Ting 1983; Russell and Zhai 1987; Ducrocq 1993; Holroyd and Ciochon 1994; Meng and McKenna 1998).

Since 1998, Kyoto University field parties with Myanmar researchers have continued fossil expeditions in the Pondaung Formation. In this article, we provide an updated mammalian faunal list of the Pondaung Formation, a description of newly recognized taxa of artiodactyl and perissodactyl ungulates, a discussion on the paleoenvironment and age of the Pondaung fauna, and a faunal comparison of the ungulates.

Institutional and dental abbreviations.—BMNH, The Natural History Museum (previously British Museum of Natural History), London, United Kingdom; CM, Carnegie Museum of Natural History, Pittsburgh, USA; DMR, Department of Mineral Resources, Bangkok, Thailand; GSI, Geological Survey of India, Kolkata, India; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; NMMP-KU, National Museum-Myanmar-Paleontology-Kyoto University (stored in the National Museum, Yangon, Myanmar); NSM, National Science Museum, Tokyo, Japan; PMUM, Paleontological Museum, Uppsala University, Uppsala, Sweden; PU, Princeton University (specimens now in the Yale Peabody Museum, New Haven, USA—Lucas and Schoch 1989); PSS, Geological Institute of the Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; M/m, upper/lower molars; P/p, upper/lower premolars.

Geologic setting

The Eocene Pondaung Formation is distributed in the western part of central Myanmar (Fig. 1) and constitutes a part of the Central Irrawaddy Lowland, which is mainly composed of Cenozoic deposits (Cotter 1914; Ba Than Haq 1981; Aye Ko Aung 1999). The Pondaung Formation consists of terrestrial deposits and is about 2,000 m thick at the type section (Aye Ko Aung 1999). Its thickness decreases toward the south (Stamp 1922). It consists of alternating terrestrial mudstones, sandstones, and conglomerates, and is subdivided into "Lower" and "Upper" Members (Aye Ko Aung 1999). The "Lower Member" is about 1,500 m thick at the type section and is dominated by greenish sandstones and conglomerates (Aye Ko Aung 1999). The "Upper Member" is about 500 m thick in the type section and is dominated by yellowish sandstones and variegated claystones (Aye Ko Aung 1999).

The "Upper Member" of the Pondaung Formation yields vertebrate fossils in its lower half (Colbert 1938; Aye Ko Aung 1999, 2004), and is interpreted as fluvio-deltaic deposits (Aung Naing Soe et al. 2002). Currently known fossil sites

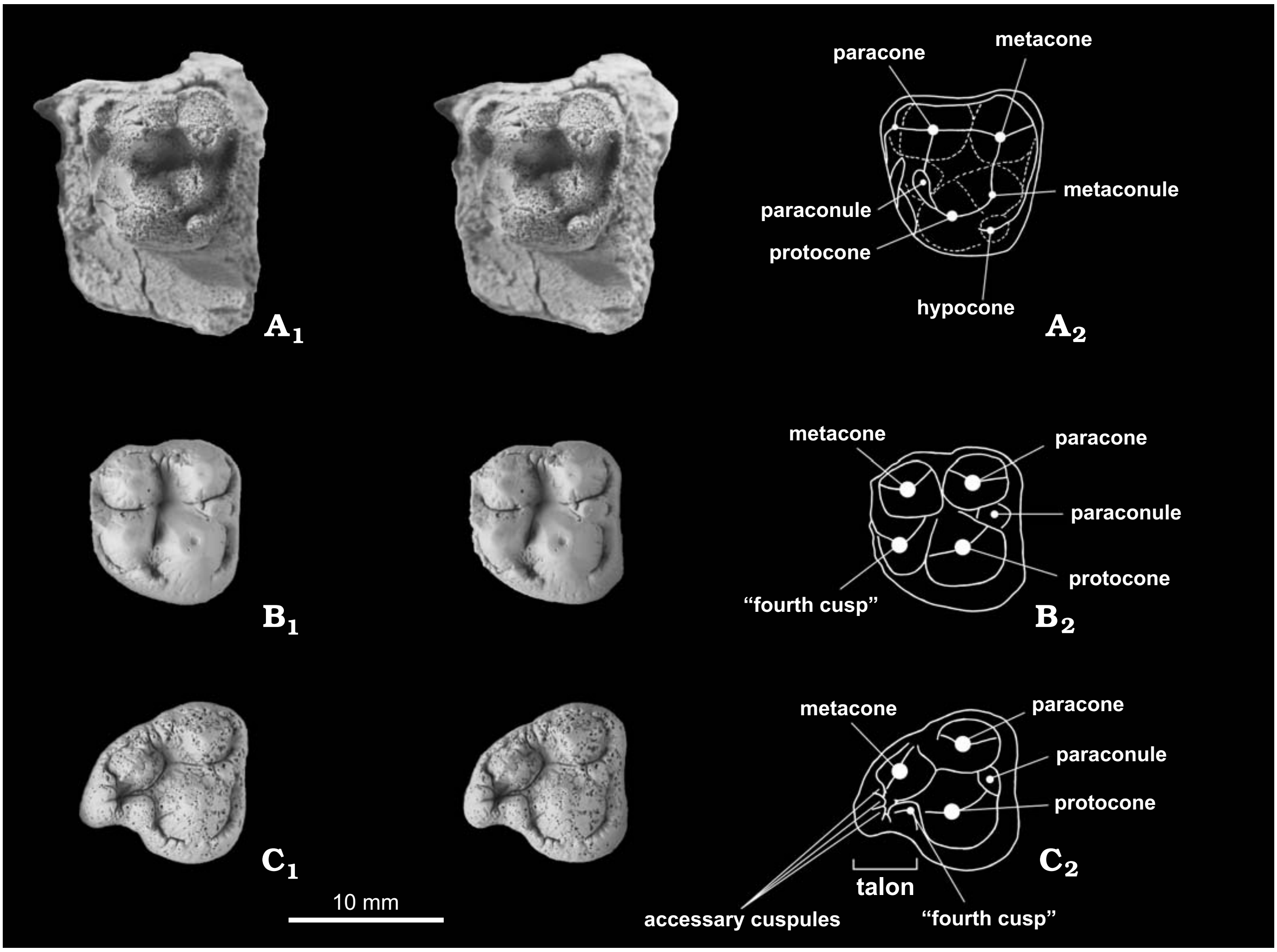

Fig. 2. **A**. Artiodactyla indeterminate 1, NMMP-KU 1556, a left maxillary fragment with ?M2, occlusal view: A_1, stereo pair; A_2, schematic drawing of ?M2. **B**, **C**. Artiodactyla indeterminate 2. **B**. NMMP-KU 1765, a right M2; B_1, stereo pair; B_2, schematic drawing. **C**. NMMP-KU 1742, a right M3; C_1, stereo pair; C_2, schematic drawing.

for Pondaung mammals are distributed at the west side of the Chindwin River extending about 50 km from northwest to southeast (Fig. 1; Colbert 1938: fig. 6). Most of the vertebrate fossils come from mudstones of swale-fill sediments and some of them come from sandy fluvial channels and/or crevasse channels (Aung Naing Soe et al. 2002). Although fossils have been collected predominantly by surface prospecting, enough materials remain in place to indicate their original distributions in the sediment matrix.

Systematic paleontology

We describe and comment on several ungulate taxa from the Pondaung Formation. All the new ungulate specimens described below were discovered in the "Upper Member" of the Pondaung Formation and are stored in the National Museum of Myanmar in Yangon.

The basic dental terminology mostly follows those of Bown and Kraus (1979). We use the term "fourth cusp" to stand for the "hypocone" of suoid artiodactyls. We follow the chalicotherioid dental terminologies by Coombs (1978: fig. 2) except that we use "paraconule" instead of "protoconule" and use "metacone-metastylar region" instead of "metacone" and "metastyle." We follow the tapiroid dental terminologies of Hooker (1989).

Order Artiodactyla Owen, 1848

Artiodactyla indeterminate 1

Fig. 2A.

Material.—NMMP-KU 1556, a left maxillary fragment with ?M2.

Locality.—The Pk5 locality (21°45´20˝N; 94°38´33˝E) in Myaing Township, western part of central Myanmar (Fig. 1; Tsubamoto, Egi, et al. 2000).

Dental measurements.—M2 length = 10.5 mm; M2 width = 10.8 mm.

Description.—The preserved upper molar is bunodont and brachyodont, with seven distinct cusps (paracone, metacone, protocone, hypocone, paraconule, metaconule, and parastyle). 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 is weak and straight. The protocone is slightly distal to the paracone. The preprotocrista and postprotocrista extend to the paracone and metacone, respectively, bearing a paraconule and metaconule, respectively. The paraconule is worn more than the other cusps. The metaconule is larger than the paraconule and hypocone and is smaller than the paracone, metacone, and protocone. The hypocone is lingual to the protocone and is located just lingual to the metaconule. A cingulum surrounds the crown except for the lingual margin, bearing the parastyle and hypocone.

The present specimen preserves two (buccal and lingual) broken alveoli mesial to the preserved tooth. The lingual alveolus is located as distal as the buccal one, suggesting that the tooth for these alveoli is not P4 but M1 and that the preserved tooth is probably M2.

Discussion.—This specimen (NMMP-KU 1556) is assigned to the Artiodactyla on the basis of its enlarged metaconule. It is referable to such primitive bunodont artiodactyls as dichobunids or primitive entelodonts in having a brachyodont crown, conical cusps, a small hypocone, and a small paraconule. However, this upper molar differs from upper molars of primitive dichobunids such as *Diacodexis* and *Eolantianius* in being larger and in lacking V-shaped para- and metaconule cristae. It differs from upper molars of primitive entelodonts such as *Brachyhyops* (= *Eoentelodon*) in having a larger parastyle, more distinct cristae, and less conical and less bunodont cusps. This specimen is morphologically unique and provides poor information, so its affinity among artiodactyls is unclear. Nevertheless, this specimen is not assignable to any mammalian species reported from the Pondaung Formation so far, suggesting an occurrence of an additional artiodactyl species in the Pondaung fauna.

Artiodactyla indeterminate 2

Fig. 2B, C.

Material.—NMMP-KU 1765, a right M2; NMMP-KU 1742, a right M3.

Locality.—The Pk12 locality (21°44′56″N; 94°39′14″E) in Myaing Township, western part of central Myanmar (Fig. 1).

Dental measurements.—M2 length = 9.7 mm; M2 width = 10.7 mm; M3 length = 10.8 mm, M3 width = 10.7 mm.

Description.—M2 (NMMP-KU 1765; Fig. 2B) shows the upper molar morphology of primitive bunodont artiodactyls such as helohyids and raoellids. The protocone is the largest cusp. The cusps are conical with weak cristae. The paraconule is tiny but distinct. The fourth cusp (metaconule or hypocone) is enlarged: it is nearly as large as the paracone and metacone but smaller than the protocone. There are no styles but there is enamel crenulation at the position of mesostyle. The cingulum is visible except at the lingual base of the protocone and the buccal base of the paracone. The dental enamel is somewhat wrinkled.

M3 (NMMP-KU 1742; Fig. 2C) shows somewhat strange morphology and is triangular in occlusal view. The morphology of the mesial part (paracone-paraconule-protocone) is very similar to that of the present M2 although the paraconule is proportionally smaller on M3 than on M2. In the distal part (talon), the metacone is somewhat proportionally smaller than that of M2 and is more lingually located compared to the paracone. The fourth cusp is proportionally much smaller than that of M2, and seems to be located on a cingulum. The talon is distally elongated, bearing accessory cuspules on the distal margin of the cingulum.

Comparison and discussion.—We judged that NMMP-KU 1765 (Fig. 2B) is a right M2 and NMMP-KU 1742 (Fig. 2C) is a right M3, both of which probably belong to the same single individual. The two molars were found at the same locality. At the mesial margin of M3, there is an interstitial wear facet, which seems to match the distal interstitial wear facet of M2. There is no interstitial wear facet on the distal margin of M3. The two molars are very similar to each other in size, in morphology of the mesial part (paracone-paraconule-protocone), and in enamel and root colors. The M3 tooth wear is less progressed than the M2 tooth wear. The distal part of M3 is skewed compared to that of M2, and such a skewed distal part of M3 is often seen in M3 of various mammals.

Although the present upper molars are similar in morphology and size to those of helohyids and raoellids, the former differs from the latter two taxa in having buccolingually much more narrowed and distally much more elongated M3 talon. The present specimens further differ from those of *Pakkokuhyus* (Helohyidae) from the Pondaung Formation in having a lingual cingulum at the base of the fourth cusp and more wrinkled enamel, and in lacking weak but distinct proto- and metacristae directed mesiodistally.

The distally elongated M3 talon of the present specimen is reminiscent of that of several suoids such as *Hyotherium*, but the present molars seem not to be assignable to the Suoidea. The M3 differs from that of suoids in that the fourth cusp (metaconule or hypocone) is much smaller. A really distally elongated talon is an advanced character, and is not usually found in primitive Eocene suoids from Thailand, southern China, and North America (Scott, 1940; Tong and Zhao 1986; Ducrocq 1994; Ducrocq et al. 1998; Liu 2001). Although M3 of an Eocene suoid *Eocenchoerus* from southern China (Liu 2001) has a somewhat distally elongated talon with distal accessory cusps, its fourth cusp is much better developed than that of the present M3. Also, the M2 differs from that of suoids in having a smaller fourth cusp and a lingual cingulum at the base of the fourth cusp, and in lacking clear lingual separation into two (mesial and distal) lobes and an accessory cusp between the metacone and protocone.

These present specimens are also not assignable to any mammalian species reported from the Pondaung Formation so far, suggesting an occurrence of another additional artiodactyl species in the Pondaung fauna.

Order Perissodactyla Owen, 1848

Family Brontotheriidae Marsh, 1873

Genus cf. *Sivatitanops* Pilgrim, 1925

Cf. *Sivatitanops rugosidens* Pilgrim, 1925

Sivatitanops (?) *rugosidens* Pilgrim, 1925: 11, pl. 2: 6, 7; Colbert 1938: 303–304.

Discussion.—We change the name of *Sivatitanops* (?) *rugosidens* into cf. *Sivatitanops rugosidens* because locating the question mark in parentheses between the generic and specific names is not used in recent literature. On the other hand, this species is based only on a few fragmentary teeth (Pilgrim 1925). These materials of cf. *S. rugosidens* are too poor to establish a new species (Colbert 1938), so that they might represent an individual variation of the other species of the Pondaung *Sivatitanops*.

Genus cf. *Metatelmatherium* Granger and Gregory, 1938

Discussion.—Among the Pondaung brontotheres, two species have been questionably assigned to the genus *Metatelmatherium*, and named as *Metatelmatherium* (?) *browni* (Pilgrim, 1925) and *Metatelmatherium* (?) *lahirii* Colbert, 1938, respectively (Colbert 1938). Here, we change the names of the two species into cf. *Metatelmatherium browni* and cf. *Metatelmatherium lahirii*, respectively, for the same reason as in the case of cf. *Sivatitanops rugosidens*.

Colbert (1938) did not differentiate cf. *M. browni* from cf. *M. lahirii*. In fact, cf. *M. lahirii* is based on fragmentary materials, so that it is difficult to find any critical characteristics distinguishing cf. *M. lahirii* from cf. *M. browni*. The two species are very similar to each other in dental size and overall dental morphology, so there is a possibility that cf. *M. browni* may be synonymous with cf. *M. lahirii*.

Superfamily Chalicotherioidea Gill, 1872

Family "Eomoropidae" Matthew, 1929

Comments.—Recent cladistic studies have noted that the "Eomoropidae" is most likely paraphyletic within chalicotherioids (e.g., Coombs 1998). Here, we conventionally use the term "Eomoropidae".

Genus *Eomoropus* Osborn, 1913

Type species: *Eomoropus amarorum* (Cope, 1881) (= *Eomoropus annectens* Peterson, 1919).

Included species: *Eomoropus quadridentatus* Zdansky, 1930; *Eomoropus minimus* Zdansky, 1930.

Eomoropus sp. cf. *E. minimus* Zdansky, 1930

Fig. 3A.

Material.—NMMP-KU 0708, a right maxillary fragment with M3.

Locality.—PA1 locality (21°46′24″N; 94°36′04″E), Myaing Township, western part of central Myanmar (Fig. 1).

Dental measurements.—Shown in Table 1.

Table 1. Dental measurements (in mm) of M3 of the Pondaung "eomoropids", *Eomoropus*, and *Grangeria*. Data of *E. minimus* are taken from Hu (1959: 127), and those of *E. amarorum*, *E. quadridentatus*, and *Grangeria* are taken from Lucas and Schoch (1989: table 23.1). *, estimate.

Specimens	M3 length	M3 width
Pondaung "eomoropids"		
NMMP-KU 0708	11.4	13.9
NMMP-KU 1270	12.1	14.8
Eomoropus minimus		
IVPP V2403.2	11.0	12.5
Eomoropus amarorum		
CM 3109	17.4	20.0
PU 18067	19.2*	20.1*
Eomoropus quadridentatus		
PMUM 3451	15.8	18.6
PMUM 3451b	15.9	18.7
PMUM 6000	16.2*	18.2
PMUM 6001	14.9	18.2
Grangeria anarsius		
USNM 21097	21.2	25.0*
Grangeria canina		
PMUM 3458	22.6*	27.9*

Description.—The preserved M3 is brachyodont and wider than long, and shows typical small "eomoropid" M3 morphology. The paracone is the largest and tallest cusp. The metacone cannot be identified, but it appears to be located right at the junction of the metaloph and postparacrista as in other basal chalicotheres. The parastyle is large and isolated. The mesostyle is enlarged and is located at the distobuccal corner of the crown. The mesostyle is proportionally larger than that in *E. amarorum* and *E. quadridentatus*. The metacone-metastylar region is smaller than the mesostyle and is located just distal to the junction of the postparacrista, mesostyle, and metaloph. The ectoloph is incompletely W-shaped. The protoloph is incomplete with a relatively large paraconule. The metaloph is complete without a metaconule. The mesial cingulum originates from the tip of the parastyle and disappears at the mesiolingual base of the protocone. There are no distinct lingual, distal, and buccal cingula.

"Eomoropidae" gen. et sp. indet.

Fig. 3B.

Material.—NMMP-KU 1270, a left M3.

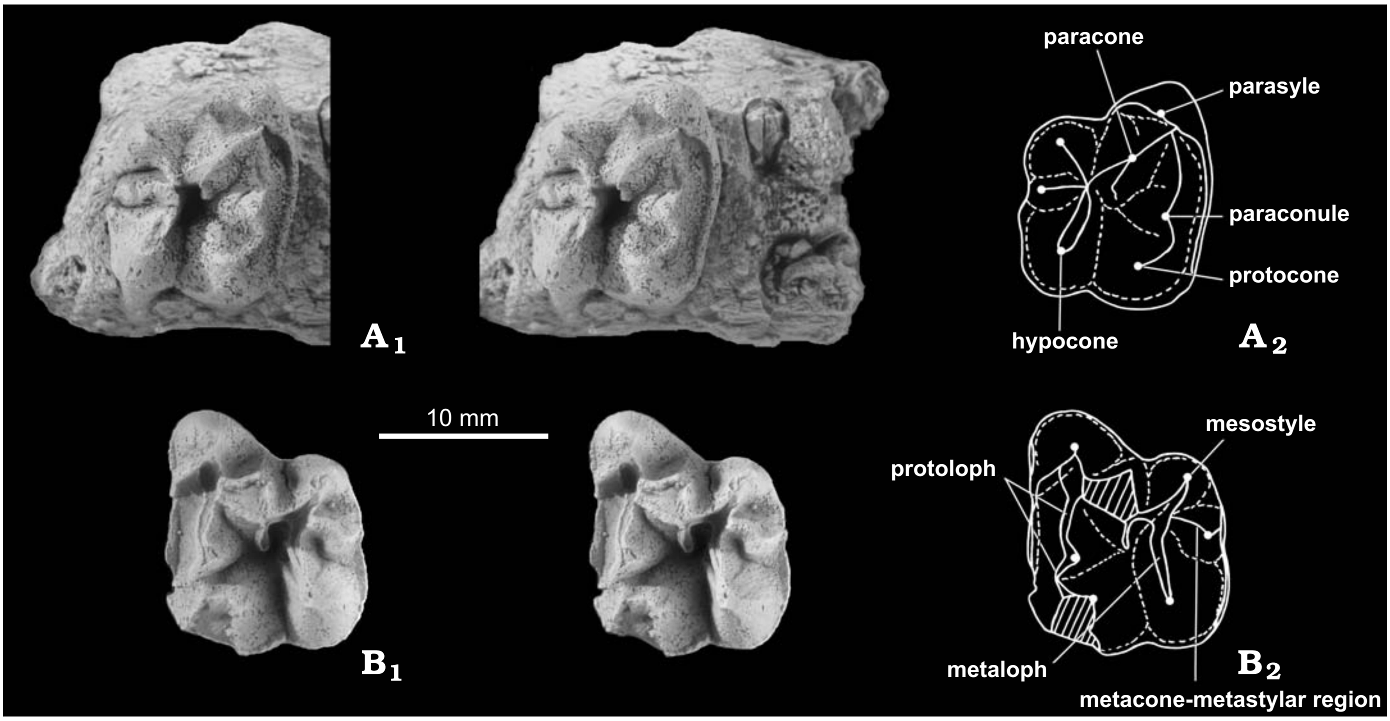

Fig. 3. **A**. *Eomoropus* sp. cf. *E. minimus* Zdansky, 1930, NMMP-KU 0708, a right maxillary fragment with M3, occlusal view; A_1, stereo pair; A_2, schematic drawing of M3. **B**. "Eomoropidae" gen. et sp. indet., NMMP-KU 1270, a left M3, occlusal view; B_1, stereo pair; B_2, schematic drawing.

Locality.—The Kd1 locality (21°49′25″N; 94°35′24″E) in Myaing Township, western part of central Myanmar (Fig. 1).

Dental measurements.—Shown in Table 1.

Description and comments.—This M3 is very similar to M3 of NMMP-KU 0708 in morphology and size. The former differs from the latter in that it has a more mesiobuccally prominent parastyle, slightly stronger metacone-metastylar region, and slight lingual and distal cingula.

Comparison and discussion of the Pondaung "eomoropids".—To date, seven genera of "eomoropids" have been reported (McKenna and Bell 1997). Among these genera, however, two genera, *Paleomoropus* Radinsky, 1964 and *Lophiaspis* Depéret, 1910, have been placed not in this family but in the Lophiodontidae by several authors (Fischer 1977; Lucas and Schoch 1989; Prothero and Schoch 1989; Coombs 1998); *Danjiangia* Wang, 1995 was considered a primitive brontothere by Beard (1998: 27) and Hooker and Dashzeveg (2003: 491); and *Lunania* Chow, 1957 is represented only by mandibular fragments with lower molars (Chow 1957; Huang 2002) and might be a phenacolophid condylarth (Lucas and Schoch, 1989). Therefore, only the three genera (*Eomoropus* Osborn, 1913; *Grangeria* Zdansky, 1930; and *Litolophus* Radinsky, 1964) have been recognized with confidence in the "Eomoropidae" by most researchers (Lucas and Schoch 1989; Coombs 1998).

The present M3 specimens show typical "eomoropid" M3 morphology in having an incomplete protoloph with retained paraconule, complete metaloph with no metaconule, isolated and large parastyle, developed mesostyle, and incompletely W-shaped ectoloph. They are morphologically similar to M3 of *Eomoropus* and *Grangeria* and are distinct from those of *Litolophus* in that they lack the distobuccal rotation of the M3 metaloph and the distal end of the ectoloph, have a much larger M3 mesostyle, and are proportionally shorter and wider (Radinsky 1964; Chow et al. 1974; Lucas and Schoch 1989).

Eomoropus and *Grangeria* are relatively similar in morphology to each other. They are distinguished from each other mainly by their mandibular and anterior dental characteristics and also by the following features: *Eomoropus* is smaller than *Grangeria* and has less mesiobuccally prominent upper molar parastyles (Radinsky 1964; Lucas and Schoch 1989). Lucas and Schoch (1989: 424, left column, line 2 from the bottom) mentioned that *Eomoropus* is distinguished from *Grangeria* by the less prominent upper molar "metastyles," but we judged that the word "metastyles" was used mistakenly in this context and should be "parastyles".

The present M3s are similar in size to each other. They can be assigned to *Eomoropus* rather than to *Grangeria* because of their size (Table 1; Lucas and Schoch 1989: table 23.1). M3 of NMMP-KU 0708 has a less mesiobuccally prominent parastyle, which is one of the diagnostic characters of *Eomoropus*. Therefore, NMMP-KU 0708 is assigned to *Eomoropus*. On the other hand, NMMP-KU 1270 has a more prominent parastyle, which is one of the diagnostic characters of *Grangeria*. Therefore, we describe NMMP-KU 1270 as an indeterminate "eomoropid" in this paper.

However, the possibility that the present two specimens can be assigned to a single species of *Eomoropus* cannot be eliminated because of their similar size and morphology, their occurrence in the same formation, and the poor fossil record of the "Eomoropidae" in the Pondaung Formation. If these specimens truly belong to the same species, the diagnoses of *Eomoropus* and *Grangeria* concerning parastylar development by Lucas and Schoch (1989) would need to be reconsidered.

On the basis of molar size (Table 1), M3 of the Pondaung *Eomoropus* is referable to that of *E. minimus* (IVPP V2403.1 and V2403.2), the smallest species of *Eomoropus*, which was discovered in the middle Eocene Rencun Member of the Heti Formation (central China) and was described and figured by Hu (1959: pl. 1: 2a, b), though the Pondaung form is slightly larger than the Heti form. The Pondaung form is much smaller than the other two species of *Eomoropus*, *E. amarorum* and *E. quadridentatus* (Table 1). On the other hand, Radinsky (1964) and Lucas and Schoch (1989) considered that the holotype of *E. minimus* from the Heti Formation described by Zdansky (1930) as M1 is DP4 and that *E. minimus* is synonymous with *E. quadridentatus*. However, the upper molar material described as *E. minimus* by Hu (1959) and that of the Pondaung *Eomoropus* are much smaller than molars of *E. quadridentatus*, suggesting that they can be distinguished from *E. quadridentatus*. We identify the Pondaung *Eomoropus* specimen as *Eomoropus* sp. cf. *E. minimus* in order to avoid confusion between specific names in this paper.

Zong et al. (1996) described a left maxillary fragment with M1–M3 (IVPP V9911) discovered in the middle Eocene Xiangshan Formation of the Lijiang basin (southern China), and identified it as *E. minimus*. However, M3 in V9911 has a much smaller mesostyle than that in *Eomoropus* and *Grangeria*, and is proportionally longer and narrower than M3 of the latter. These characteristics of M3 in V9911 suggest that V9911 is referable not to *Eomoropus* but to *Litolophus*.

Superfamily Tapiroidea Gray, 1825

Family Deperetellidae Radinsky, 1965

Type genus: *Deperetella* Matthew and Granger, 1925a (including *Cristidentinus* Zdansky, 1930 and *Diplolophodon* Zdansky, 1930).

Included genera: *Teleolophus* Matthew and Granger, 1925b (including *Pachylophus* Tong and Lei, 1984) and *Bahinolophus* gen. nov. Tsubamoto.

Revised diagnosis.—Tapiroids with full placental dentition and strongly bilophodont and relatively high-crowned molars. Upper molars with developed protoloph and metaloph joined by U-shaped and buccally convex ectoloph, weak postmetacrista, metaloph not interrupted by postmetacrista, no distinct molar metacone, no or very weak buccal ridge on paracone, and no distinct posthypocrista. Lower molars with developed protolophid and hypolophid and no or extremely reduced paralophid and cristid obliqua. Hypoconulid of m3 reduced to a cingular bulge. Molar protoloph/protolophid and metaloph/hypolophid are parallel to each other, respectively.

Discussion of taxon content and synonymy.—Seven genera (*Deperetella*, *Teleolophus*, *Cristidentinus*, *Diplolophodon*, *Haagella*, *Pachylophus*, and *Irdinolophus*) of the Deperetellidae have been reported to date (McKenna and Bell 1997; Dashzeveg and Hooker 1997). However, only two genera (*Deperetella* and *Teleolophus*) among these seven are now recognized as belonging in the Deperetellidae.

Three of the remaining five genera (*Cristidentinus*, *Diplolophodon*, and *Pachylophus*) have been synonymized with other deperetellid genera by previous researchers. *Cristidentinus* and *Diplolophodon*, which were discovered from the middle Eocene Heti Formation of central China and described by Zdansky (1930), were synonymized with *Deperetella* by Radinsky (1965) and Tsubamoto, Holroyd, et al. (2000). *Diplolophodon* was also reported from the middle Eocene Dongjun and Lumeiyi Formations from southern China (Ding et al. 1977; Russell and Zhai 1987). *Pachylophus*, which was discovered from the middle Eocene Hetaoyuan Formation of central China and described by Tong and Lei (1984), was synonymized with *Teleolophus* by Dashzeveg and Hooker (1997).

Haagella, which was discovered from the lower Oligocene of Germany and described by Heissig (1978) as belonging in the Deperetellidae, was excluded from the Deperetellidae by Dashzeveg and Hooker (1997). This genus is more likely to be related to *Colodon*, a helaletid tapiroid (Dashzeveg and Hooker 1997).

In this paper, *Irdinolophus* is excluded from the Deperetellidae. *Irdinolophus* was established for *Desmatotherium mongoliense* Osborn, 1923 (= *Helaletes mongoliensis*) and was assigned to the Deperetellidae by Dashzeveg and Hooker (1997). However, *Irdinolophus* lacks deperetellid characteristics such as a high crown and very weak molar postmetacrista. It is distinct from deperetellids in having a slight posthypocrista, much stronger molar postmetacrista, less lophodont lower premolars, and much lower dental crown. Also, the molar metaloph of *Irdinolophus* is interrupted by a strong postmetacrista, making the upper molar lophs incompletely U-shaped. These characteristics of *Irdinolophus* are more similar to those of the Helaletidae than to those of the Deperetellidae.

Genus *Bahinolophus* nov. Tsubamoto

Type and only known species: *Bahinolophus birmanicus* (Pilgrim, 1925) comb. nov.

Distribution.—The "Upper Member" of the Eocene Pondaung Formation, central Myanmar.

Etymology.—*Bahino*-, from Bahin Village, where good specimens of the upper and lower dentition of this genus were discovered (the Bh4 locality; Fig. 1); *lophus*, referring to the lophodont teeth of this animal. The gender of the new genus is masculine.

Diagnosis.—Small- to medium-sized deperetellid with premolar series nearly as long as molar series and with developed bilophodonty on P2–P4. Differs from other deperetellids (*Deperetella* and *Teleolophus*) in having more buccally located molar postmetacrista, less straight molar protoloph and metaloph, less buccally prominent molar ectoloph, less squared and proportionally less wide crown aspect of molars in the occlusal view, and a single-rooted p1, and in lacking a distinct cingulum at the distobuccal corner of the crown on upper postcanine dentition. Differs from *Deperetella cristata* and *Deperetella khaitchinulensis* in having a shorter premolar series, less mesiodistally elongated p2, and much weaker buccal and lingual cingula, and in being smaller. Further differs from *D. cristata* in having parallel protoloph and metaloph on P2. Further differs from *Deperetella similis* in being slightly larger and in having a much lingually narrower mesial (protoloph) part compared to the distal (metaloph) part on P2. Differs from *Teleolophus* in that the protoloph and metaloph on P2–P4 are higher, parallel to each other, and lingually separated by a groove, and in having a weaker molar parastyle and much weaker buccal and lingual cingula.

Bahinolophus birmanicus (Pilgrim, 1925) comb. nov.

Figs. 4, 5.

Chasmotherium (?) *birmanicum* Pilgrim, 1925: 25–28, pl. 2: 9.
Chasmotherium birmanicum; Matthew 1929: 514–515, fig. 38.
Deperetella (?) *birmanicum*; Colbert 1938: 348–350, fig. 40 [sic].
Deperetella birmanicum; Radinsky 1965: 227; Tsubamoto, Egi, et al. 2000: 60, pl. 93 [sic].
Diplolophodon birmanicum; Ding et al. 1977: 44–45.
Deperetella birmanica; Tsubamoto, Holroyd, et al. 2000 (in part): 185–187, figs. 3, 4C, D.

Holotype: GSI C348 (a left mandibular corpus with heavily worn p4–m3) and BMNH M12756 (a right mandibular corpus with heavily worn p4–m3), which belong to the same single individual (Fig. 5C, D; Pilgrim 1925).

Type locality: 2.4 km southwest of Thadut Village (= at or near the Pk5 locality), Myaing Township, central Myanmar (Fig. 1; Pilgrim 1925).

Referred material.—NMMP-KU 0005 and 0006 (Tsubamoto, Egi, et al. 2000; Tsubamoto, Holroyd, et al. 2000).

New material.—NMMP-KU 1046, a left maxillary fragment with complete P1, somewhat broken P2–P4, and complete M1–M2; NMMP-KU 1199, broken left mandibular fragments including symphysis part with p2 and other broken postcanine teeth of a single individual (NMMP-KU 1199 probably belongs to the same individual as NMMP-KU 1046 does); NMMP-KU 1558, a right P3; NMMP-KU 1662, a distal part of a right upper cheek tooth; NMMP-KU 1795, a talonid of a right ?p3.

Locality of the new material.—NMMP-KU 1046 and 1199 are from the Bh4 locality (21˚43´39˝N; 94˚38´30˝E), NMMP-KU 1558 is from the Pk5 locality (21˚45´20˝N; 94˚38´33˝E), NMMP-KU 1662 is from the PGN2 locality (21˚42´32˝N; 94˚48´46˝E), and NMMP-KU 1795 is from the Pk12 locality (21˚44´56˝N; 94˚39´14˝E), all of which are located in Myaing Township, western part of central Myanmar (Fig. 1; Tsubamoto, Egi, et al. 2000).

Diagnosis.—As for genus.

Dental measurements of the new material.—NMMP-KU 1046: P1 length = 10.4 mm, P1 width = 9.7 mm, P2 length = 11.6 mm, P2 width (estimate) = 13.9 mm, P3 length = 12.8 mm, P3 width (estimate) = 16.3 mm, P4 length (estimate) = 14.3 mm, P4 width (estimate) = 16.9 mm, M1 length = 15.1 mm, M1 width = 17.0 mm, M2 length = 17.4 mm, M2 width = 18.4 mm; NMMP-KU 1199: p2 length = 12.1 mm, p2 trigonid width = 7.6 mm, p2 talonid width = 8.1 mm; NMMP-KU 1558: P3 length = 11.1 mm, P3 width = 15.0 mm; NMMP-KU 1662: maximum width of the preserved part = 15.4 mm; NMMP-KU 1795: talonid width of ?p3 = 8.4 mm.

Description.—The upper dentition of the new material (Fig. 4) shows a strong bilophodont structure with a relatively high crown, mesial and distal cingula, and no or very weak buccal and lingual cingula. The cingulum is much more weakly developed than that in *Deperetella* and *Teleolophus*. In NMMP-KU 1046 (Fig. 4A), P1 and M1 are moderately worn, P2–P4 and M2 are almost unworn, and M3 is probably not erupted or in eruption, indicating that P1 and M1 erupt earlier than the other adult postcanine teeth in *Bahinolophus* and that this individual is a subadult.

P1 is somewhat mesiodistally elongated, longer than it is wide, and triangular-shaped from the occlusal view. There are a tall and large paracone, a very low protoloph, and a very low metaloph. The protoloph and metaloph are not parallel to each other, but lingually converge. The metaloph is stronger than the protoloph.

P2–P4 are wider than they are long. The protoloph and metaloph are parallel to each other, extending buccolingually. The two lophs are lingually separated by a deep transverse groove. Slight dental crenulations are observed at the middle part of the mesial face of the metaloph. The P2 protoloph is lower and less lingually extended than the P2 metaloph, making the crown of P2 trapezoidal rather than rectangular from the occlusal view. The P3 crown is higher than the P2 crown. The P3 protoloph is nearly as high and lingually extended as the P3 metaloph. P2 < P3. On NMMP-KU 1558 (P3), a distinct parastyle and lingually and buccally ridged paracone are observed (Fig. 4B). The P4 crown is higher than the P3 crown. The mesial part of P4 in NMMP-KU 1046 is broken.

M1–M2 also have parallel protoloph and metaloph. The two lophs are slightly diagonal to the tooth row and slightly convex mesially, being joined buccally by the U-shaped and buccally convex ectoloph. The ectoloph is less buccally projected than it is in *Deperetella* and *Teleolophus*. The paracone is identified with slightly conical aspects, though the metacone is difficult to identify. The parastyle is located mesial to the paracone. There is neither mesostyle nor metastyle. The postmetacrista extends mesiodistally, being located as buccal as the paracone, and is less developed than in

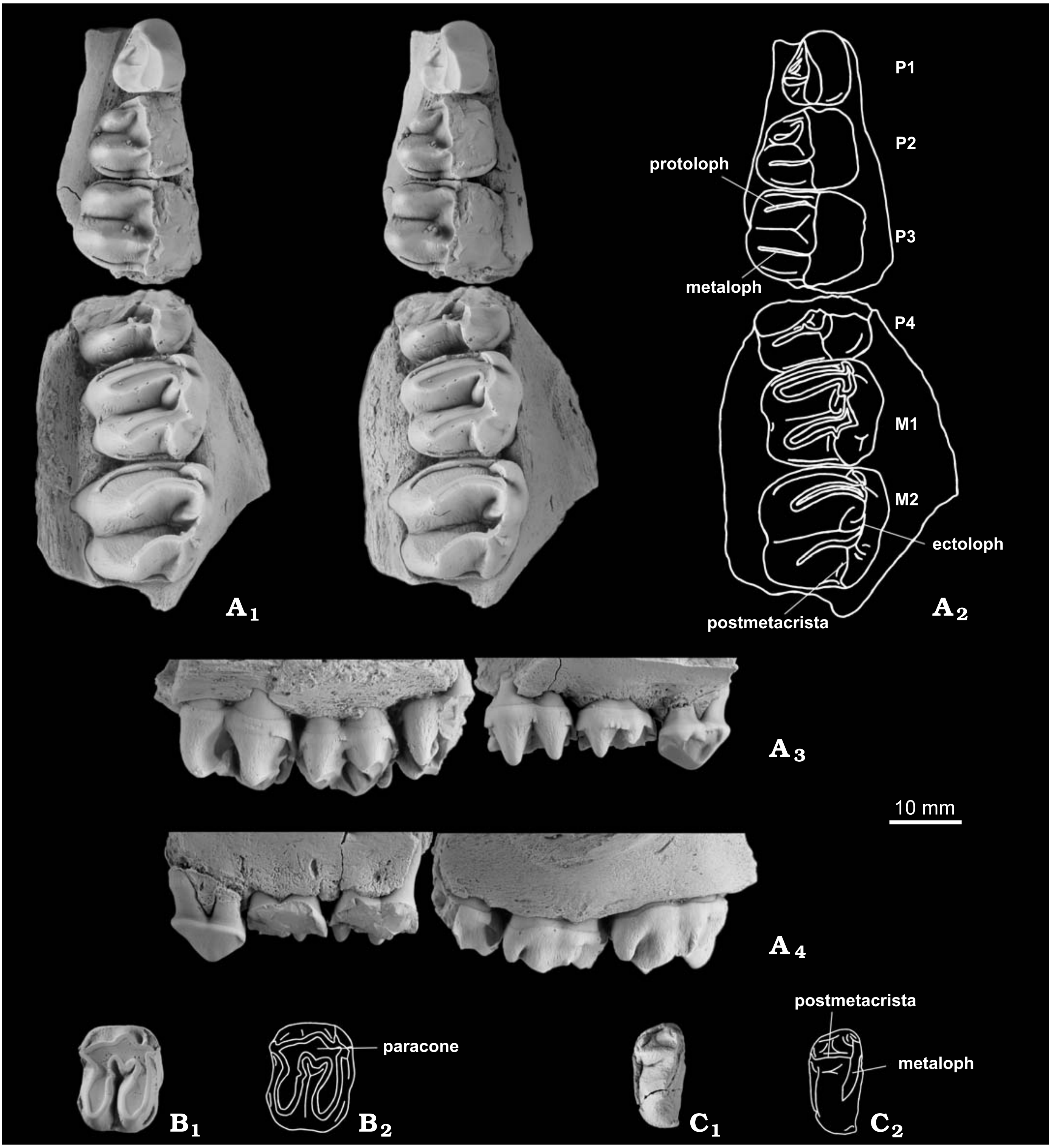

Fig. 4. New specimens of the upper dentition of *Bahinolophus birmanicus* (Pilgrim, 1925) comb. nov. **A**. NMMP-KU 1046, a maxillary fragment with P1–M2; A_1, occlusal view (stereo pair); A_2, schematic drawing of the occlusal view; A_3, lingual view; A_4, buccal view. **B**. NMMP-KU 1558, a right P3; B_1, occlusal view; B_2, schematic drawing of the occlusal view. **C**. NMMP-KU 1662, a distal part of a right upper cheek tooth; C_1, occlusal view; C_2, schematic drawing of the occlusal view.

other Eocene tapiroids. The crown in occlusal view is less squared and proportionally less wide than that in *Deperetella* and *Teleolophus*. M1<M2.

NMMP-KU 1662, a distal half of an upper postcanine tooth (Fig. 4C), is so fragmentary that its tooth class cannot be identified.

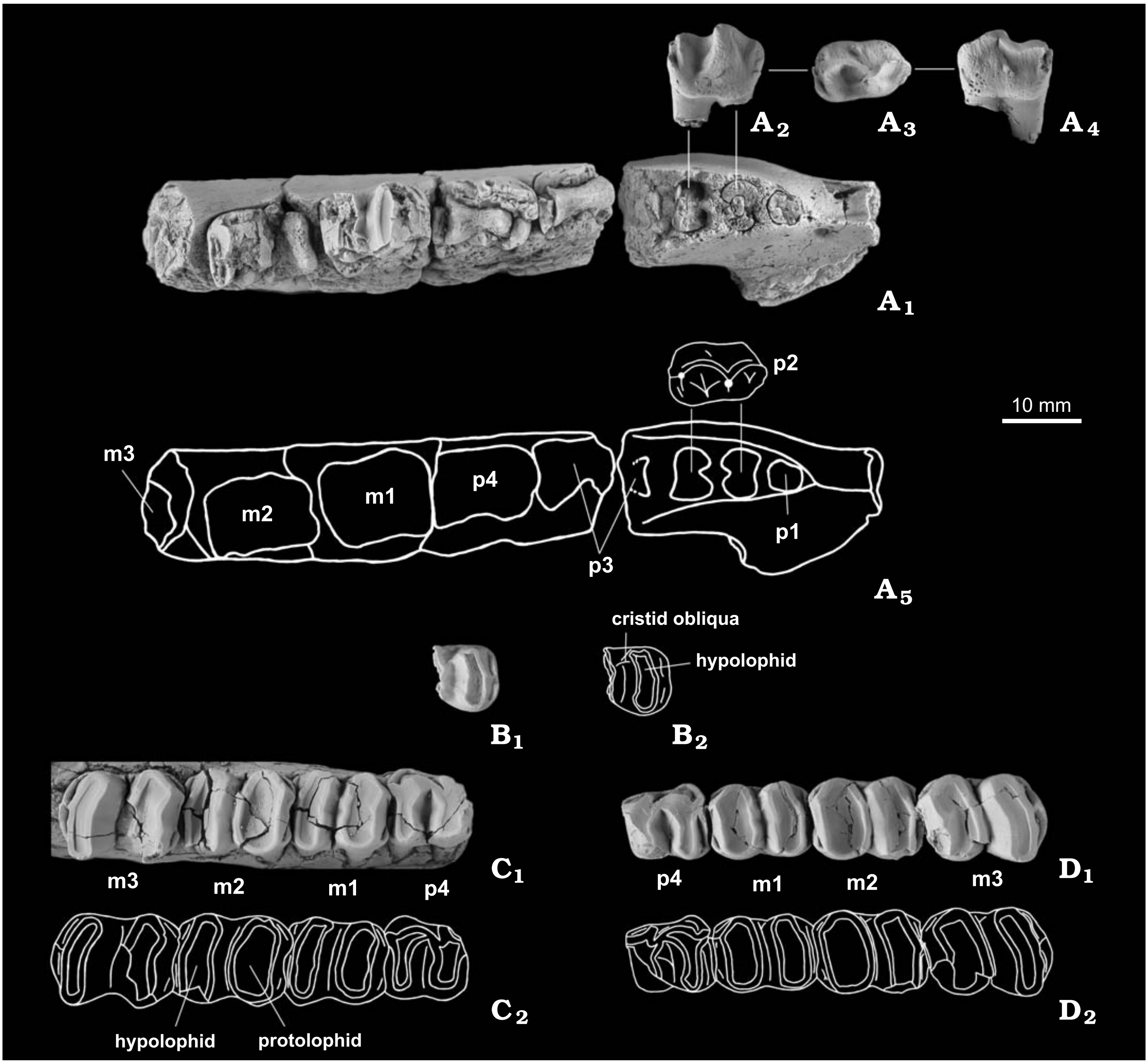

Fig. 5. Lower dentition of *Bahinolophus birmanicus* (Pilgrim, 1925) comb. nov. **A**. NMMP-KU 1199, a left mandibular corpus with p2 and heavily broken other postcanine teeth (new specimen); A_1, occlusal view of the mandible; A_2, lingual view of p2; A_3, occlusal view of p2; A_4, buccal view of p2; A_5, schematic drawing of the occlusal view. **B**. NMMP-KU 1795, a talonid of a right ?p3 (new specimen); B_1, occlusal view; B_2, schematic drawing of the occlusal view. **C**, **D**. The type specimens, left and right lower mandibular fragments with left and right p4–m3. **C**. GSI C348, left p4–m3; C_1, occlusal view; C_2, schematic drawing of the occlusal view. **D**. BMNH M12756, right p4–m3; D_1, occlusal view; D_2, schematic drawing of the occlusal view.

We judge that NMMP-KU 1199 (Fig. 5A), a heavily broken new lower dental specimen, is from the same individual as NMMP-KU 1046. This lower dental specimen was discovered at exactly the same locality as the upper dentition, NMMP-KU 1046. Although the teeth are badly broken, they are very similar in morphology and size to the lower dental material (type specimen) of *Deperetella birmanica* previously described by Pilgrim (1925). A very small fragment of the most mesial part of m3 is observed in the mandible of this specimen, indicating that m3 is unerupted or in eruption. Therefore, this specimen, like NMMP-KU 1046, is from a subadult.

In NMMP-KU 1199, the mandibular symphysis extends below the mesial root of p2. There is a long diastema between the canine (not preserved) and p1 (only root is preserved). The first lower premolar (p1) is single-rooted, and the p1 root is slightly longer than it is wide. The second premolar (p2) (Fig. 5A) is mesiodistally elongated and has mesiodistally elongated lophids that form shearing blades, a weak and low hypolophid, and neither lingual nor buccal cingulids. The p2 talonid is slightly wider than the p2 trigonid. The length of the lower premolar series of NMMP-KU 1199 is estimated to be about 43 mm. It is nearly as long as the length of the lower molar series of the type specimen. Therefore, the premolar series is estimated to be nearly as long as the molar series in *Bahinolophus*.

NMMP-KU 1795 (Fig. 5B) is a talonid of a right lower molariform tooth. It has a well-developed and buccolingually oriented hypolophid like that seen in p4–m3 of this species, so it is distinct from p2. It is smaller than p4–m3 and is nearly as wide as the distal part of p2. We tentatively identified this tooth as a right p3.

Comparison and discussion.—The morphology and size of the upper premolars and lower postcanine dentition of the new materials are very similar to those of the previously described dentition of the deperetellid species, *Deperetella birmanica* (Pilgrim 1925; Tsubamoto, Egi, et al. 2000; Tsubamoto, Holroyd, et al. 2000) from the Pondaung Formation, indicating that the new materials belong to this species. However, the upper molar morphology of the present materials is distinct from that of *Deperetella cristata* and *Deperetella similis* (= *Diplolophodon similis*) from China, indicating that it is generically not referable to *Deperetella*. The upper molar morphology of the new materials is also distinct from that of the other known deperetellid, *Teleolophus*, and from that of other tapiroids. Therefore, we establish a new genus, *Bahinolophus*, for the Pondaung species.

Bahinolophus is assigned to the family Deperetellidae based on its bilophodont dentition, a relatively high crown, parallel molar protoloph and metaloph joined buccally by U-shaped and buccally convex ectoloph, a weak molar postmetacrista, a molar metaloph not interrupted by the postmetacrista, no distinct molar metacone, no distinct posthypocrista on the upper postcanine dentition, and a m3 hypoconulid reduced to a cingular bulge (Figs. 4, 5).

Bahinolophus differs from other Eocene tapiroids including the other deperetellids in lacking distinct cingulum at the distobuccal corner of the crown on the upper postcanine dentition, and in having a more buccally located molar postmetacrista. Other Eocene tapiroids have at least a small distobuccal cingulum connecting to the postmetacrista on the upper molars. In addition, on the upper molars of other tapiroids, the metacone is much more lingually located than the paracone. In contrast, on the upper molars of *Bahinolophus*, the estimated metacone region is not so lingually located, and is, instead, nearly as buccal as the paracone.

Bahinolophus is further distinct from the other deperetellids (*Teleolophus* and *Deperetella*) in having a slightly less straight molar protoloph and metaloph, a less sharp molar postmetacrista, a less buccally prominent molar ectoloph, and less squared and proportionally less wide crown aspect of molars in the occlusal view. It further differs from *Teleolophus* in having a relatively longer premolar series, a more developed bilophodonty and higher crown on the premolars, much weaker buccal and lingual cingula, a weaker molar parastyle, and a weak but distinct p2 hypolophid. It further differs from *Deperetella cristata* from northern China and *Deperetella khaitchinulensis* from Mongolia in having a relatively shorter premolar series, much weaker buccal and lingual cingula, and a less mesiodistally elongated p2, and in being smaller. It further differs from *D. cristata* in having a parallel protoloph and metaloph on P2.

Bahinolophus is also distinct from *Deperetella similis* from central and southern China. *D. similis* has been considered to be phyletically closely related to *Deperetella birmanica* (= *Bahinolophus birmanicus*) from the Pondaung Formation (Radinsky 1965; Ding et al. 1977; Dashzeveg and Hooker 1997; Tsubamoto, Holroyd, et al. 2000). Tsubamoto, Holroyd, et al. (2000) synonymized *D. similis* with *D. birmanica* on the basis of upper premolar and lower dental morphology. However, as mentioned above, the Pondaung form is distinct from *Deperetella*, including *D. similis*, in its upper molar morphology. Although the upper premolar morphology of *Bahinolophus* is very similar to that of *D. similis*, as mentioned by Tsubamoto, Holroyd, et al. (2000), the P2 protoloph in *D. similis* is much more lingually extended (as lingually extended as the P2 metaloph) than that in *Bahinolophus*. This difference implies that p2 of *D. similis* is proportionally wider than that of *Bahinolophus*, although the p2 morphology of *D. similis* is not yet known. Furthermore, the upper molars of *D. similis* have a more lingually located postmetacrista, more developed distobuccal cingulum, and more buccally projected ectoloph, all of which are characteristic of the genus *Deperetella*. Therefore, *D. similis* is a distinct species of *Deperetella*, and is distinguishable from *D. birmanica* (= *B. birmanicus*).

Among the Deperetellidae, *Bahinolophus* has both derived and primitive characteristics. The derived characteristics are the very slight but distinct P1 bilophodonty with protoloph and metaloph, and strongly developed P2–P4 bilophodonty with a high crown. The primitive characteristics are a less buccally projected ectoloph and a less elongated anterior premolar dentition.

The anterior premolar and upper molar morphologies suggest that *Deperetella* and *Teleolophus* are closer to each other than to *Bahinolophus*. *Deperetella* and *Teleolophus* have a double-rooted p1, whereas *Bahinolophus* has a single-rooted p1. *Deperetella* and *Teleolophus* have a straighter molar protoloph and metaloph, a more lingually located postmetacrista, and a more distinct and stronger distobuccal molar cingulum than does *Bahinolophus*.

However, posterior premolar morphology suggests that *Deperetella* and *Bahinolophus* are closer to each other than to *Teleolophus*. *Deperetella* and *Bahinolophus* have more developed bilophodonty and a higher crown on the posterior premolars than does *Teleolophus*.

On the other hand, *Bahinolophus* has intermediate characteristics between those of *Deperetella* and *Teleolophus* in terms of the relative length of the premolar series. As mentioned above, the length of the premolar series of *Bahinolophus* is estimated to be nearly as long as the molar series. In contrast, the length of the premolar series of *Deperetella* is longer than the molar series, and that of *Teleolophus* is shorter than the molar series (Radinsky 1965).

Dashzeveg and Hooker (1997) described a deperetellid left mandibular fragment with p3–p4 (PSS.27-31) from the Sevkhul Member of the upper Eocene Ergilin Formation (Mongolia) as *Deperetella* sp. cf. *D. birmanica*. Although p4 of this specimen (PSS.27-31) is similar in morphology and size to that of the type specimen of *Deperetella birmanica* (= *Bahinolophus birmanicus*) as suggested by Dashzeveg and Hooker (1997), the former is slightly larger in size than the latter: p4 of PSS.27-31 is 13.8 mm long by 11.9 mm wide (Dashzeveg and Hooker 1997), and that of the type of *D. birmanica* is 11.7 mm long by 9.7 mm wide (Pilgrim 1925). The phyletic relationships of this Mongolian specimen (PSS.27-31) to *Bahinolophus* are unclear because *Bahinolophus* is characterized mainly by its upper dentition and because the upper dentition of the species of PSS.27-31 is as yet unknown.

The Pondaung fauna

The Pondaung mammal fauna now includes six orders (Primates, Creodonta, Carnivora, Rodentia, Artiodactyla, and Perissodactyla) and an indeterminate ungulate, consisting of 22 families, 33 genera, and 48 species (Table 2). The Pondaung ungulates consist of 29 species (14 families and 18 genera): one species of indeterminate ungulate (*Hsanotherium parvum*), 12 species (six genera and six families) of the Artiodactyla, and 16 species (11 genera and seven families) of the Perissodactyla. So, more than half of the mammalian species recorded so far in the Pondaung fauna consists of artiodactyl and perissodactyl ungulates.

In the Pondaung fauna, only a few small-sized mammals (anomalurid rodents and eosimiid and indeterminate primates) have been discovered so far. This can be explained by sampling bias. Most of the Pondaung fossil materials have been collected by field surface prospecting, which is biased against small faunal elements (Winkler 1983; Gunnell 1994). In some Eocene faunas of East Asia such as Shanghuang and Heti faunas of central China and in North American Eocene faunas, small mammals such as rodents dominate the fauna (Savage and Russell 1983; Russell and Zhai 1987; Tong 1997; Tsubamoto et al. 2004). Therefore, rodents and other small mammals would be much more abundant and diverse than artiodactyls and perissodactyls in a true picture of the Pondaung fauna.

On the other hand, the sampling and taphonomic biases among the Pondaung ungulates are considered to be minimized. All the Pondaung ungulates are medium- to large-sized mammals and have relatively low crowned and robust teeth, so that their habitats are considered to be ecologically close to each other. Such ungulate assemblages would not be so strongly biased by the surface-prospecting sampling method (Winkler 1983; Gunnell 1994) or by sedimentological and chemical biases.

Both artiodactyls and perissodactyls are very abundant in the recorded Pondaung mammalian fauna representing more than 90 % of taxonomically identifiable dental specimens at the familial/ordinal levels (Table 3). The two are similar to each other in abundance (Table 3), but perissodactyls are taxonomically more diversified at the generic level than artiodactyls (Table 2).

About 40 percent of identifiable dental specimens of mammals from the Pondaung fauna labeled under NMMP-KU serial numbers were referred to anthracotheriid artiodactyls (Table 3), and anthracotheres constitute the major part of the recorded Pondaung mammal fauna (Pilgrim and Cotter 1916; Colbert 1938; Tsubamoto, Egi, et al. 2000). Pondaung anthracotheriid species were traditionally classified into three genera, *Anthracohyus*, *Anthracothema*, and *Anthracokeryx*, and as many as 13 species (Pilgrim 1928; Colbert 1938; Russell and Zhai 1987). However, Tsubamoto, Takai, Egi, et al. (2002) studied the Pondaung anthracotheres and concluded that the all Pondaung anthracotheriids are assigned to a single genus, *Anthracotherium*, and that they consist of four species. All four species of Pondaung *Anthracotherium* are very primitive within the genus, are morphologically very similar to one another, and have a high degree of morphological variation, suggesting that the genus *Anthracotherium* might have originated and radiated throughout the Pondaung area during the middle Eocene (Pilgrim 1928, 1941; Ducrocq 1999; Tsubamoto, Takai, Egi, et al. 2002).

Most of the dental collections of perissodactyls in the Pondaung fauna belong to brontotheres or amynodontids (Table 3). In addition, the perissodactyls are, as a whole, larger in estimated body size than the artiodactyls in the Pondaung fauna.

Paleoenvironment

The paleoenvironment of the Pondaung fauna is estimated to be forested/woodland vegetation with humid/subhumid moisture and large rivers, which were located not far from the coast of the eastern Tethyan Sea.

Most herbivorous mammals of the Pondaung fauna have brachyodont teeth, which are adapted to a diet of soft plants, such as buds, young leaves, and fruits, suggesting that their habitats were not open lands but a forested/woodland environment. There are no herbivorous species with complete hypsodonty (as in living horses), which is regarded to be an adaptation to a diet of hard and abrasive plants, such as grasses, found in open lands. The amphipithecid primate postcranial specimens from the Pondaung Formation suggest that the amphipithecids were arboreal quadrupedalists (Ciochon et al. 2001; Marivaux et al. 2003), also implying forested environment. The Pondaung fauna is located at a

Table 2. Mammalian list of the Pondaung Formation on the basis of previous studies (Pilgrim and Cotter 1916; Pilgrim 1925, 1927, 1928; Matthew 1929; Colbert 1937, 1938; Jaeger et al. 1998, 1999; Holroyd and Ciochon 1995, 2000; Ducrocq, Aung Naing Soe, Aye Ko Aung, et al. 2000; Ducrocq, Aung Naing Soe, Bo Bo, et al. 2000; Egi and Tsubamoto 2000; Métais et al. 2000; Tsubamoto, Egi, et al. 2000; Tsubamoto, Holroyd, et al. 2000; Takai et al. 2001, in press; Gebo et al. 2002; Gunnell et al. 2002; Tsubamoto, Takai, Egi, et al. 2002; Dawson et al. 2003; Tsubamoto et al. 2003; Egi, Holroyd, et al. 2004; Holroyd et al. in press), this study, and our recent discovery.

- Mammalia
- Primates
    - Family indet.
        - Gen. et sp. indet.
    - ?Sivaladapidae
        - Gen. et sp. indet.
    - Anthropoidea
        - Eosimiidae
            - *Bahinia pondaungensis*
            - Cf. *Eosimias* sp. nov.
            - Cf. *Eosimias* sp.
    - ?Anthropoidea
        - Amphipithecidae
            - *Amphipithecus mogaungensis*
            - *Pondaungia cotteri*
            - *Pondaungia savagei*
            - *Myanmarpithecus yarshensis*
- Creodonta
    - Hyaenodontidae
        - Proviverrinae
            - *Yarshea cruenta*
            - Gen. et sp. nov. 1
            - Gen. et sp. nov. 2
            - Gen. et sp. indet.
        - Hyaenailourinae
            - "*Pterodon*" *dahkoensis*
- Carnivora
    - Miacidae
        - Cf. *Vulpavus* sp.
    - Family indet.
        - Gen. et sp. indet.
- Rodentia
    - Anomaluridae
        - *Pondaungimys anomaluropsis*
        - Anomaluridae sp. 1
        - Anomaluridae sp. 2
- Ungulata
    - Order indet.
        - Family indet.
            - *Hsanotherium parvum*
- Artiodactyla
    - Family indet. 1
        - Gen. et sp. indet. 1
    - Family indet. 2
        - Gen. et sp. indet. 2
    - Dichobunidae
        - Homacodontinae
            - *Asiohomacodon myanmarensis*
            - Cf. *Asiohomacodon myanmarensis*
        - Helohyidae
            - *Pakkokuhyus lahirii*
    - Anthracotheriidae
        - *Anthracotherium pangan*
        - *Anthracotherium crassum*
        - *Anthracotherium birmanicum*
        - *Anthracotherium tenuis*
- Ruminantia
    - Family indet.
        - *Indomeryx cotteri*
        - *Indomeryx arenae*
        - Cf. *Indomeryx cotteri*
- Perissodactyla
    - Brontotheriidae
        - *Sivatitanops cotteri*
        - *Sivatitanops birmanicus*
        - Cf. *Sivatitanops rugosidens*
        - Cf. *Metatelmatherium lahirii*
        - Cf. *Metatelmatherium browni*
        - *Bunobrontops savagei*
        - *Bunobrontops* sp.
- Ancylopoda
    - Chalicotherioidea
        - "Eomoropidae"
            - *Eomoropus* sp. cf. *E. minimus*
            - Gen. et sp. indet.
    - Tapiromorpha
        - Indolophidae
            - *Indolophus guptai*
    - Ceratomorpha
        - Family indet.
            - Gen. et sp. indet.
    - Rhinocerotoidea
        - Rhinocerotidae
            - Cf. *Teletaceras* sp.
        - Amynodontidae
            - Gen. et sp. indet.
    - Amynodontinae
        - Metamynodontini
            - *Paramynodon birmanicus*
            - *Paramynodon cotteri*
    - Tapiroidea
        - Deperetellidae
            - *Bahinolophus birmanicus*

relatively low latitude (around 20°N at present), implying a warm or hot climate. Aung Naing Soe et al. (2002) suggested that there was a climatic seasonality on the basis of occurrence of calcareous nodules at the fossil localities. Although the presence of soil carbonate nodules may indicate seasonality, however, these nodules form in a variety of ways and are indicative of well-drained habitats that are likely to be local phenomena. Therefore, there is no strong evidence of seasonality for the Pondaung fauna.

The "Upper Member" of the Pondaung Formation consists mostly of fluvial sediments (Aung Naing Soe et al. 2002) and yields chondrichthyan and siluriform fishes and aquatic turtles and crocodiles (Hutchison and Holroyd 1996)

Table 3. Percentages of the numbers of the identified NMMP-KU dental material of the Pondaung mammal fauna. Total = 1027 dental materials.

Taxa	%
Artiodactyla	48.0
(Anthracotheriidae)	(42.5)
(Ruminantia)	(3.4)
(Dichobunidae)	(1.4)
(Other artiodactyls)	(0.7)
Perissodactyla	45.4
(Amynodontidae)	(25.4)
(Brontotheriidae)	(15.5)
(Amynodontidae or Brontotheriidae)	(2.0)
(Other perissodactyls)	(2.5)
Hsanotherium	0.8
Creodonta	3.0
Primates	1.4
Rodentia	1.1
Carnivora	0.3

as well as ungulate mammals of semi-aquatic habits like modern hippos such as metamynodontinie amynodontids and anthracotheriids (Wall 1989, 1998; Kron and Manning 1998), indicating occurrences of large rivers and well-drained flood plain (Hutchison et al. 2004). The formations lying above and below the Pondaung Formation, that is, the Yaw and Tabyin Formations, are marine deposits (Bender, 1983; Aye Ko Aung 1999), and the southern part of the "Pondaung Sandstones" (Cotter, 1914) consists of brackish to marine deposits (Colbert, 1938; Bender, 1983), suggesting that Pondaung vertebrates lived near the coast of the eastern Tethyan Sea.

Cenogram analysis

A cenogram is a graph which describes a mammalian community using the body-size distribution of species within the community (Legendre and Hartenberger 1992). It was originally proposed by Valverde (1964, 1967) and developed by Legendre (1986, 1989) and Legendre and Hartenberger (1992). The graph is constructed by plotting the natural logarithm of the mean body mass of each mammal species, except for bats and carnivorous species (carnivores, creodonts, and carnivorous condylarths). The estimated body weights are plotted on the Y-axis, and the species are ranked in decreasing-size order on the X-axis.

It has been documented that among the extant faunas on every continent the distributional pattern of body sizes is related to their vegetational and climatic environments (Legendre 1986, 1989; Legendre and Hartenberger 1992): (1) in open environments, medium-sized species (body mass ranging from 500 g to 8 kg) are so rare that there is a gap at the middle range of the cenogram, whereas in more closed or forest environments, medium-sized animals are normally present, so that the graph curve is smooth without a gap; (2) in arid environments, large-sized species (weighing over 8 kg) are so rare that the graph curve decreases steeply, whereas in humid environments, large-sized animals are so common that the graph curve decreases smoothly. Many researchers have applied cenogram analyses to fossil faunas of North America, Europe, and East Asia, and estimated their paleoenvironments (e.g., Legendre 1989; Gingerich 1989; Legendre and Harten-

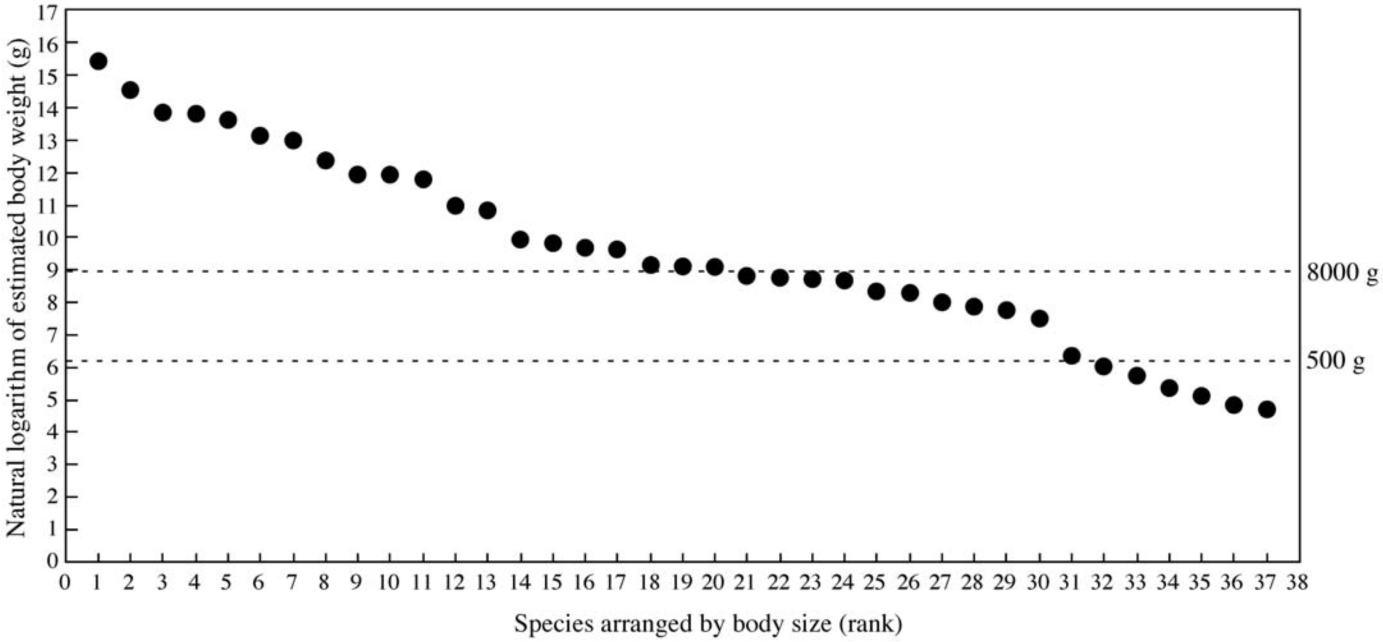

Fig. 6. Cenogram of the Pondaung fauna.

Table 4. Estimated mean body weights of the mammals of the Pondaung fauna used in the cenogram analysis. They are calculated on the mean m1 area (i.e., mesiodistal length X buccolingual width) of each mammal using regression parameters taken from Legendre (1989: table 1), except for primates. The estimated mean body weights of the Pondaung primates were from Egi, Takai, et al. (2004) and Gebo et al. (2002). The m1 sizes of the taxa whose m1 is unknown were estimated by comparing the sizes of the molar specimens with those of related mammals of each species.

Rank	Taxa	Body weight (g)
1	*Sivatitanops birmanicus*	5110000
2	*Sivatitanops cotteri*	2080000
3	*Paramynodon cotteri*	1010000
4	*Bunobrontops savagei*	987000
5	cf. *Metatelmatherium browni*	815000
6	*Bunobrontops* sp.	512000
7	*Paramynodon birmanicus*	441000
8	*Anthracotherium pangan*	237000
9	Amynodontidae indet.	154000
10	cf. *Teletaceras* sp.	152000
11	*Anthracotherium crassum*	131000
12	*Anthracotherium birmanicum*	59400
13	*Bahinolophus birmanicus*	51600
14	*Indolophus guptai*	20700
15	"Eomoropidae" indet.	18400
16	*Anthracotherium tenuis*	16100
17	*Eomorops* sp. cf. *E. minimus*	15200
18	Artiodactyla indet. 2	9470
19	*Pakkokuhyus lahirii*	8940
20	*Pondaungia savagei*	8800
21	*Amphipithecus mogaungensis*	6800
22	*Asihomacodon myanmarensis*	6330
23	cf. *Asihomacodon myanmarensis*	6050
24	*Pondaungia cotteri*	5900
25	cf. *Indomeryx cotteri*	4120
26	*Indomeryx cotteri*	3930
27	?Sivaladapidae indet.	2990
28	*Hsanotherium parvum*	2630
29	*Indomeryx arenae*	2320
30	*Mynammarpithecus yarshensis*	1800
31	*Bahinia pondaungensis*	570
32	cf. *Eosimias* sp. nov. Takai et al. in press	410
33	Primates indet.	310
34	Anomaluridae sp. 1	209
35	*Pondaungimys anomaluropsis*	164
36	Anomaluridae sp. 2	124
37	cf. *Eosimias* sp. Gebo et al. 2002	111

berger 1992; Gunnell 1994, 1997; Gunnell and Bartels 1994; Maas and Krause 1994; Ducrocq et al. 1995; Morgan et al. 1995; Dashzeveg et al. 1998; Wilf et al. 1998).

In order to perform a cenogram analysis of the Pondaung fauna, we estimated the mean body weights of the Pondaung ungulates and rodents on the basis of the m1 area (i.e., mesiodistal length X buccolingual width) of each mammal, using the regression parameters taken from Legendre (1989: table 1). Body mass estimation of the taxa whose m1 area has been unknown was obtained by comparison of molar size with that of known taxa. The estimated mean body weights of the Pondaung primates were taken from Egi, Takai, et al. (2004) and Gebo et al. (2002). Four species (cf. *Metatelmatherium lahirii*, cf. *Sivatitanops rugosidens*, an indeterminate ceratomorph, and Artiodactyla indeterminate 1) are not included in this cenogram analysis because these species are based on such poor materials that their body mass is difficult to estimate in detail. However, at least we can conclude that these four species are large-sized (over 8 kg) mammals based on comparing the dental sizes with those of other related taxa. Exclusion of these species from the cenogram analysis will not bias our interpretation of the analysis. The estimated mean body weights of the Pondaung mammalian species (except for creodonts and carnivores) ranged from about 100 g for the smallest species (cf. *Eosimias* sp. Gebo et al. 2002), to about 5000 kg for the largest (*Sivatitanops birmanicus*) (Table 4).

The cenogram of the Pondaung fauna (Fig. 6) suggests forested/woodland environment with humid/subhumid moisture for the fauna. This cenogram decreases smoothly from the large-sized through the medium-sized species without any major distinct gap, although a small gap can be observed within the medium-sized species, that is, between *Myanmarpithecus* (1.8 kg; rank 30) and *Bahinia* (570 g; rank 31) (Fig. 6; Table 4). There are many large-sized and medium-sized species in the Pondaung fauna. The slope for medium-sized mammals is 0.2022. This slope of the Pondaung fauna is consistent with that for modern faunas of humid to subhumid and forested or closed environments (Legendre 1989; Gingerich 1989: table 31; Gunnell 1994: fig. 17A, 1997: fig. 9). Although the cenogram analysis has recently been criticized by several researchers (e.g., Rodríguez 1999; Alroy 2000), the results of the cenogram analysis of the Pondaung fauna is consistent with its paleoenvironment estimate based on the estimated paleoecologies of the mammalian species and on the geologic and geographic evidence.

The offset score between the medium-sized and small-sized species in the cenogram is also related to vegetation regime (Gingerich 1989; Gunnell 1994, 1997), but it is difficult to enter this parameter into the interpretation of the cenogram of the Pondaung fauna. The offset score between the medium-sized and small-sized species varies depending on the estimated body mass of *Bahinia*. Egi, Takai, et al. (2004) estimated the body mass of *Bahinia* as 570 g. Using this value, the offset between the medium-sized and small-sized species is between the rank 31 (*Bahinia*) and 32 (cf. *Eosimias* sp. nov. Takai et al. in press: 410 g). This offset score is low (about 0.34 ln mass [g]) and is consistent with modern rainforest (Legendre 1989; Gingerich 1989: table 31; Gunnell 1994: fig. 17B). However, Jaeger et al. (1999) estimated the body mass of *Bahinia* as 400 g, while Ciochon et al. (2001) estimated it as 630–1000 g. If we use the Jaeger et al.'s (1999) estimation, the offset score (between *Myanmarpithecus* and cf. *Eosimias* sp. nov. Takai et al. in press) will be high (about 1.5 ln mass [g]), which is comparable to modern scrub/open habitat; if we use the Ciochon et al.'s (2001) estimation, the offset (between *Bahinia* and cf. *Eosimias* sp. nov. Takai et al. in press) will be about 0.67 ln mass [g], which is comparable to modern woodland/rainforest habitat (Gingerich 1989: table 31; Gunnell 1994: fig. 17B). On the other hand, the Pondaung fauna is probably biased against small faunal elements as mentioned above, so that the offset between medium-sized and small-sized species of this fauna can also be biased. Therefore, the small gap of the cenogram of the Pondaung fauna might indicate a seasonality as suggested by occurrence of pedogenic carbonate concretions (Aung Naing Soe et al. 2002), but possibly suggests sampling bias against smaller-sized mammals due to use of the surface-prospecting method in the Pondaung Formation.

Age of the Pondaung fauna

The age of the Pondaung fauna is correlated with the latest middle Eocene on the basis of stratigraphic, micropaleontological, and radiometric evidence, not using the faunal comparison of mammals. The Pondaung Formation overlies and partially interfingers with the Tabyin Formation, and is conformably overlain by the Yaw Formation (Stamp 1922; Bender 1983; Aye Ko Aung 1999). Both the Tabyin and Yaw Formations are composed mainly of marine claystones. The Tabyin Formation, which yields nummulites (benthic foraminifera) (Stamp 1922; Bender 1983), has been correlated with the Khirthar Stage of India, which is correlated with the Lutetian (lower middle Eocene) (Eames 1951; Gingerich and Russell 1990; Holroyd and Ciochon 1994). The Yaw Formation has been correlated with the Priabonian (upper Eocene) on the basis of foraminiferan and molluscan faunas (Stamp 1922; Cotter 1938; Bender 1983). However, the biozone of a foraminiferan from the Yaw Formation, *Discocyclina sella* D'Archiac (= *Discocyclina dispansa sella*), listed by Bender (1983) is now correlated with the Shallow Benthic Zones (SBZs) 15–18, which correspond to the upper part of the middle Lutetian to the upper Bartonian (about 43.5–37 Ma; middle Eocene) (Serra-Kiel et al. 1998: fig. 5). Therefore, at least the lower part of the Yaw Formation can be correlated with the uppermost Bartonian (= uppermost middle Eocene), and in that case, the Pondaung Formation is automatically correlated with the middle Eocene. The uppermost Bartonian correlation of the Yaw Formation is also suggested by Holroyd and Ciochon (1994, 1995), on the basis of the correlation of the Yaw Formation with the Nanggulan Formation of Java. On the other hand, nannoplankton assemblages of the vertebrate-fossil-bearing "Upper Member" of the Pondaung Formation at the vertebrate fossil sites suggests a middle Eocene age (Hla Mon 1999). The fission-track age of the "Upper Member" was determined as 37.2±1.3 Ma (around the middle–late Eocene boundary; Berggren et al. 1995) by Tsubamoto, Takai, Shigehara, et al. (2002). On the basis of these evidence, the "Upper Member" of the Pondaung Formation is correlated with the upper Bartonian (= uppermost middle Eocene).

The precise age determination of the Pondaung fauna by geological and microfossil evidence is very important for the study of Paleogene mammals in East Asia. As discussed above, this age determination is not based on the mammalian fauna. In contrast, most of the Paleogene terrestrial mammalian faunas of East Asia are dated only by comparison of the included mammalian taxa with fossil mammals of North America and Europe (e.g., Li and Ting 1983; Russell and Zhai 1987). Although some faunas are dated by the magnetostratigraphy, radiometric dating, and/or isotope stratigraphy (Meng and McKenna 1998: fig. 2; Benammi et al. 2001; Bowen et al. 2002), their datings are also based on mammalian faunal correlations. The Pondaung fauna is the only East Asian Paleogene mammalian fauna precisely dated not using mammalian comparison. The late Bartonian age (latest middle Eocene) of the Pondaung Formation corresponds to the age of the Pondaung fauna determined by the ungulate mammalian faunal comparison by previous researchers (e.g., Pilgrim and Cotter 1916; Pilgrim 1928; Colbert 1938; Russell and Zhai 1987; Holroyd and Ciochon 1994; Ducrocq 1999), suggesting that such comparison of mammalian faunas is useful for determining the age of Eocene mammal-bearing terrestrial deposits of East Asia when done carefully.

Comparison and correlation of ungulate faunas in East Asia

The Pondaung ungulate fauna appears to be endemic at the generic and specific levels among the middle Eocene faunas of East Asia, although the fauna is not endemic at the familial level.

At the familial level, the Pondaung fauna includes many artiodactyl and perissodactyl families widely common with other middle Eocene faunas of East Asia, such as the Helohyidae, Anthracotheriidae, Brontotheriidae, "Eomoropidae", Amynodontidae, and Deperetellidae.

At the generic level, on the other hand, the Pondaung ungulate fauna shows a high degree of endemism. Among the 13 identified genera (named genera and unnamed new genera) of Pondaung ungulates, seven genera (*Hsanotherium*, *Asiohomacodon*, *Pakkokuhyus*, *Sivatitanops*, *Bunobrontops*, *Indolophus*, and *Bahinolophus* gen. nov.) are endemic to the fauna. In addition, the two indeterminate artiodactyls from the Pondaung Formation described above show characteristic morphology distinct from other artiodactyl genera, and are considered to be endemic for the fauna at the generic level. Although *Paramynodon* is recorded in three (Dongjun, Upper Lumeiyi, and Naduo) faunas of Eocene southern China (Li and Ting 1983; Russell and Zhai 1987), the *Paramynodon* materials from these faunas are so poor (Xu 1961, 1966; Ding et al. 1977; Tang and Qiu 1979) that the generic identification of these materials is doubtful.

At the specific level, only four to five species may be in common with other Eocene East Asian faunas. Most of these species are from southern China. *Indomeryx cotteri* is also recorded from the Naduo (= Nadu) fauna of southern China (Tang et al. 1974; Guo et al. 1999). Cf. *Metatelmatherium* sp. cf. *M. browni* is recorded from the Tientong beds (= ?Naduo Formation) of southern China (Chow 1957; Li and Ting 1983). *Eomoropus minimus* is recorded from the Huangzhuang and Rencun (Upper Heti) faunas of central China (Zdansky 1930; Hu 1959; Shi 1989). Some species of *Anthracotherium* (including *Anthracothema* and *Anthracokeryx*) are common between the Pondaung fauna and the Naduo fauna (Russell and Zhai 1987; Tsubamoto, Takai, Egi, et al. 2002). However, a newly reported specimen of *Anthracotherium birmanicum* (= *Anthracokeryx birmanicus*) from the Naduo fauna by Li and Chen (2001) shows a huge and enlarged canine (IVPP V12718; Li and Chen 2001: pl. 1). Although many *Anthracotherium* specimens have been found in the Pondaung Formation, such a huge anthracotheriid canine has never been found in the formation, suggesting that the Naduo *Anthracotherium* species is not identical on the basis of the canine morphology to the Pondaung *Anthracotherium* species.

The Pondaung ungulate fauna has been correlated with the Shara Murun fauna of northern China and to the Heti (Rencun and Zhaili) fauna of central China, both of which are considered to be Bartonian (late middle Eocene) in age (Pilgrim and Cotter 1916; Pilgrim 1928; Colbert 1938; Russell and Zhai 1987; Ducrocq 1993; Holroyd and Ciochon 1994; McKenna and Bell 1997; Meng and McKenna 1998). This correlation is based mainly on the faunal comparison of ungulates such as brontotheriids, amynodontids, anthracotheriids, and primitive ruminants.

Despite some overlap, the generic similarity between the Pondaung ungulate fauna and the middle to late Eocene faunas of Mongolia and northern and central China is very low. Only a few genera of Pondaung ungulates (*Eomoropus* and possibly *Metatelmatherium* and *Teletaceras*) are shared with Mongolian and northern/central Chinese faunas (Table 2; Russell and Zhai 1987; Antoine et al. 2003). The anthracotheres from the Pondaung fauna were previously assigned to the same genera as those of the Heti fauna and were are considered to be closely related (Russell and Zhai 1987; Holroyd and Ciochon 1994). However, the Pondaung anthracotheres are generically distinct from those from the Heti fauna on the basis of the selenodonty of molars and p4 morphology (Tsubamoto, Takai, Egi, et al. 2002), although they are similar to each other in terms of "evolutionary stages." The deperetellid from the Pondaung fauna was previously assigned to the genus *Deperetella*, which is widely distributed in the middle to late Eocene of East Asia (Colbert 1938; Radinsky 1965; Tsubamoto, Holroyd, et al. 2000), but it is now assigned to the new genus (*Bahinolophus*) as discussed above. The generic dissimilarity between the Pondaung fauna and Eocene faunas of Mongolia and northern and central China suggests that the Pondaung fauna is not formally included in the Eocene Asian Land Mammal "Ages" system (Romer 1966), which is based mainly on the Mongolian and northern Chinese faunas (Tsubamoto et al. 2004), although comparison of the "evolutionary stages" of mammals between the Pondaung fauna and other Eocene faunas of East Asia may be still useful for mammalian faunal correlation.

Another feature of the Pondaung ungulate fauna is the relative dominance of artiodactyls compared to middle Eocene faunas of Mongolia and northern/central China. In most middle Eocene faunas of East Asia, perissodactyls such as brontotheriids, amynodontids, and deperetellids are much more diverse at the generic level and probably also in abundance than artiodactyls (Russell and Zhai 1987; Meng and McKenna 1998; Tsubamoto et al. 2004). In the Pondaung fauna, although artiodactyls are less taxonomically diverse than perissodactyls, they consists of six families and six genera (Table 2) and are more diverse compared to other middle Eocene faunas of East Asia (Russell and Zhai 1987; Tsubamoto et al. 2004). Besides, Pondaung artiodactyls are as abundant as perissodactyls (Table 3).

Among the southern East Asian (southern Chinese and Southeast Asian) faunas, the Pondaung fauna is closest to the Naduo fauna (Bose and Yongle basins, Guangxi Province, southern China) in geologic age and geographic location, although the similarity is not great. The Pondaung and Naduo faunas share five genera (*Anthracotherium*, *Indomeryx*, and *Eomoropus*, and questionably cf. *Metatelmatherium* and *Paramynodon*) (Table 2; Li and Ting; 1983; Russell and Zhai 1987; Tsubamoto, Takai, Egi, et al. 2002). However, the Pondaung fauna seems to be slightly older in age than the Naduo fauna. The Naduo fauna includes several more progressive artiodactyls such as suoids (tayassuids and suids) and tragulids than typical middle Eocene artiodactyls, such as dichobunids and helohyids (Li and Ting 1983; Russell and Zhai 1987). Besides, the species of *Anthracotherium* (= *Anthracokeryx*) from the Naduo fauna have a huge canine (Li and Chen 2001), which is more progressive than the much smaller canine of species of *Anthracotherium* found in the Pondaung fauna. Therefore, the Naduo fauna seems to be early late Eocene in age.

Faunal conclusions

The Eocene Pondaung fauna of Myanmar includes 29 ungulate mammalian species: one indeterminate small ungulate, 12 artiodactyls (six families incorporating six genera), and

16 perissodactyls (seven families incorporating 11 genera). Although both artiodactyls and perissodactyls are abundant and diverse, the former are less diversified at the generic level than the latter, but the two are similar in abundance. Anthracotheriid artiodactyls and brontotheriid and amynodontid perissodactyls are highly dominant in terms of collection size. The paleoenvironment of the Pondaung fauna was presumed to be forested/woodland vegetation with humid/subhumid moisture and large rivers, which were located not far from the eastern Tethyan Sea. The age of the Pondaung fauna is independently correlated with the latest middle Eocene on the basis of stratigraphic, microfossil, and radiometric evidence, yielding a result consistent with mammalian faunal correlations. However, the Pondaung ungulate fauna includes many artiodactyl taxa compared to other middle Eocene faunas of East Asia and shows relatively high endemism at the generic level, so that the fauna is not formally included in the Eocene Asian Land Mammal "Ages" system, which is based mainly on the Mongolian and northern Chinese faunas.

Acknowledgments

We are grateful to Brigadier General Than Tun and Major Bo Bo (International Affairs and Research Department, Office of the Chief of Military Intelligence, Ministry of Defense, Myanmar), to the personnel of the Myanmar-Japan (Kyoto University) Joint Fossil Expedition Team, and to the curators of the National Museum of Myanmar for their guidance and help in the field and museum. Thanks are also due to Drs. Jin Meng (AMNH), K. Christopher Beard (CM), Mary R. Dawson (CM), Patricia A. Holroyd (UCMP), Yaowalak Chaimanee (DMR), D. Haldar (GSI), and Yukimitsu Tomida (NSM), all of whom helped us in working at their institutions, to Prof. Nobuo Shigehara (Kyoto University, Japan) for his financial support, and to Dr. Haruo Saegusa (Museum of Nature and Human Activities, Hyogo, Japan) for providing a cast of specimen in the BMNH. We are also grateful to Drs. Jan van der Made (Museo Nacional de Ciencias Naturales, Spain), Philip D. Gingerich (University of Michigan, USA), and K. Christopher Beard for their discussion and critical reading of some parts of the manuscript. This manuscript was improved by two referees, Gregg F. Gunnell (University of Michigan, USA) and Margery C. Coombs (University of Massachusetts Amherst, USA). Researchers from several Myanmar and Japanese universities have been helped us with geological information on the Pondaung area, particularly Drs. Aye Ko Aung, Soe Thura Tun, Thaung Htike, Zin Maung Maung Thein, Hisashi Suzuki, Hiroaki Ugai, and Takeshi Nishimura. Financial supports were provided by the MEXT Overseas Scientific Research Fund (09041161, 14405019, 16405018) and by the MEXT Grant-in-Aid for COE Research (10CE2005), for the 21st Century COE Program (A14 to Kyoto University), and for JSPS Fellows (15004836, 15004748).

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