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Reevaluation of some ungulate mammals from the Eocene Pondaung Formation, Myanmar

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Abstract. We reevaluate some fossil specimens of ungulate mammals from the uppermost middle Eocene Pondaung Formation (central Myanmar), describing some new materials. The taxa studied in this paper are *Hsanotherium parvum* (Ungulata), *Asiohomacodon myanmarensis* gen. et sp. nov. (Artiodactyla; Dichobunidae; Homacodontinae), *Indomeryx* (Artiodactyla; Ruminantia), *Indolophus guptai* (Perissodactyla; Tapiromorpha; Indolophidae), and Ceratomorpha fam., gen. et sp. indet. (Perissodactyla). (1) The lower molars of *Hsanotherium* show a similarity to those of *Gobiohyus pressidens* (Artiodactyla; Helohyidae), and its mesiodistally elongated and trilobed dP_4 morphology recalls that of artiodactyls and macroscelideans. However, the unique molar and P_4 morphologies of *Hsanotherium* indicate that *Hsanotherium* cannot confidently be classified into any present ungulate order, although it can be identified as belonging to the Ungulata because of its large, elongated, and posteriorly projecting hypoconulid on M_3. (2) The molar size and morphology of *Asiohomacodon* recall primitive protoreodontine agriochoerids (Oreodontoidea) such as *Protoreodon parvus* and derived and agriochoerid-like homacodontine dichobunids such as *Pentacemylus*, both of which occur in Eocene North America. *Asiohomacodon* is classified not into the Protoreodontinae but into the Homacodontinae because of the lack of molar metastylid. The lower molar morphology of *Asiohomacodon* also resembles that of an unusual and agriochoerid-like anthracotheriid, *Atopotherium*, from Eocene Thailand, although the affinity between these two genera cannot be tested because of the lack of the P_4 material of *Asiohomacodon*. (3) The Pondaung *Indomeryx* consists of large and small species, *I. cotteri* (including *I. pilgrimi*) and *I. arenae* (including *I. minus*). Dental morphology in each species of the Pondaung *Indomeryx* indicates relatively high variation, and the two species are not separable based on their dental morphology. *Indomeryx* shows many primitive characteristics among ruminants and lacks any critical derived features referable to any ruminant family. (4) *Indolophus* is referable to primitive tapiromorphs in having a somewhat lophodont dentition and in lacking lingual and buccal cingula and molar metaconule, paraconule, and metastylid. It differs from other tapiromorphs in having a smaller parastyle on the upper dentition and a unique P^{2-4} morphology with large protocone, high and acute preprotocristid, and no postprotocristid. (5) Although the material of the indeterminate ceratomorph is poorly preserved, its preserved tooth is not identical to any other ceratomorph from the Pondaung Formation, indicating an occurrence of an additional ceratomorph species in the Pondaung fauna.

Key words: *Asiohomacodon myanmarensis*, Eocene, *Hsanotherium*, *Indolophus*, *Indomeryx*, Pondaung Formation

Introduction

The Pondaung Formation of Myanmar is one of the richest Eocene fossil-bearing deposits of terrestrial mammals in Southeast Asia. The mammalian fossils from this formation were first described by Pilgrim and Cotter (1916), and since then numerous fossils of mammals (Pilgrim, 1925, 1927, 1928; Matthew, 1929; Colbert, 1937, 1938; Ba Maw *et al.*, 1979; Ciochon *et al.*, 1985, 2001; Holroyd and Ciochon, 1995, 2000; Pondaung Fossil Expedition Team,

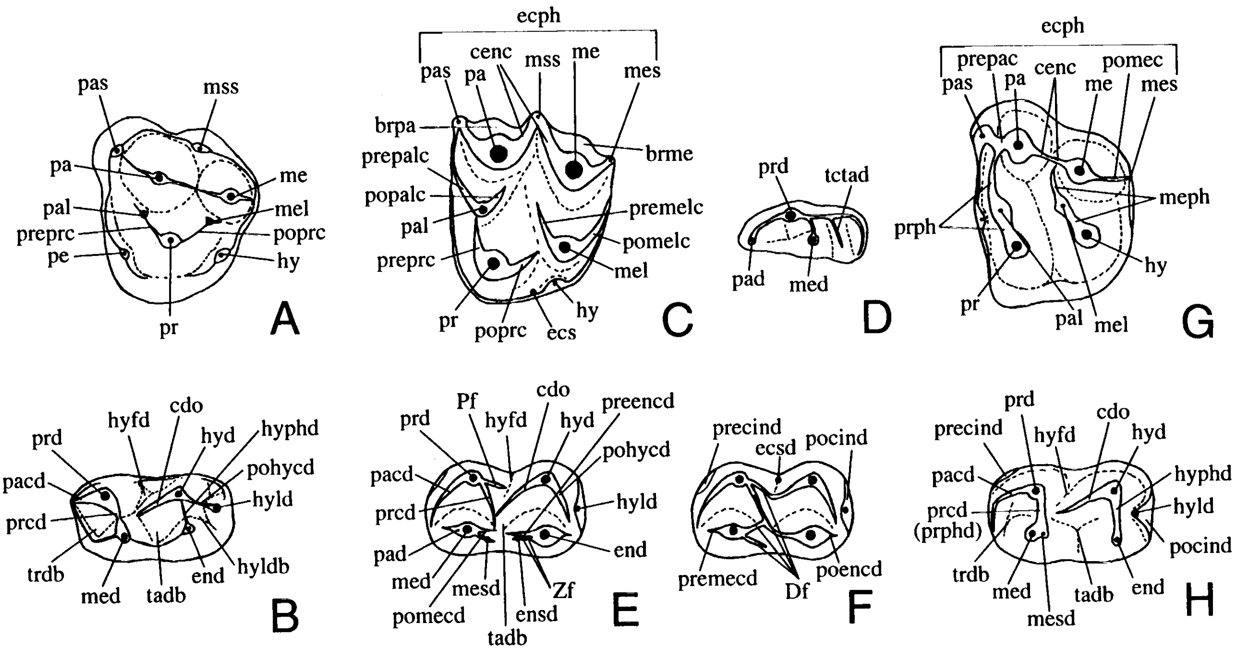


Figure 1. Several dental terminologies. **A–B**. *Hsanotherium.* **C–F**. Primitive artiodactyl (modified from Gentry and Hooker, 1988). **G–H**. Primitive perissodactyl (modified from Hooker, 1989). A, C, G, left upper molar; B, E, F, H, right lower molar; D, right P_4. Abbreviations: brme, buccal ridge of metacone; brpa, buccal ridge of paracone; cdo, cristid obliqua; cenc, centrocrista; Df, *Dorcatherium*-fold; ecph, ectoloph; ecs, ectostyle; ecsd, ectostylid; end, entoconid; ensd, entostylid; hy, hypocone; hyd, hypoconid; hyld, hypoconulid; hyldb, hypoconulid basin; hyfd, hypoflexid; hyphd, hypolophid; me, metacone; med, metaconid; mel, metaconule; meph, metaloph; mes, metastyle; mesd, metastylid; mss, mesostyle; pa, paracone; pacd, paracristid (preprotocristid); pad, paraconid; pal, paraconule (protoconule); pas, parastyle; pe, pericone; Pf, *Palaeomeryx*-fold; pocind, postcingulid; poencd, postentocristid; pohycd, posthypocristid; pomec, postmetacrista; pomecd, postmetacristid; pomelc, postmetaconulecrista; popalc, postparaconulecrista; poprc, postprotocrista; pr, protocone; prcd, protocristid (postprotocristid); prd, protoconid; precind, precingulid; preencd, preentocristid; premecd, premetacristid; premelc, premetaconulecrista; prepac, preparacrista; prepalc, preparaconulecrista; preprc, preprotocrista; prph, protoloph; prphd, protolophid; tadb, talonid basin; tctad, transverse crest on talonid; trdb, trigonid basin; Zf, *Zhailimeryx*-fold.

1997; Jaeger *et al.*, 1998, 1999; Takai *et al.*, 1999, 2000, 2001, 2003; Chaimanee *et al.*, 2000; Ducrocq *et al.*, 2000a, b; Egi and Tsubamoto, 2000; Métais *et al.*, 2000; Tsubamoto *et al.*, 2000a, b, 2001, 2002a; Shigehara *et al.*, 2002; Gunnell *et al.*, 2002; Gebo *et al.*, 2002), lower vertebrates (Hutchison and Holroyd, 1996), and microfossils (Swe Myint, 1999; Hla Mon, 1999; Thet Wai, 1999) have been reported.

In the present work, we reevaluate some fossil material of ungulate mammals from the Pondaung Formation, describing several new specimens. Most of the fossil materials figured in this paper were also figured and mentioned by Tsubamoto *et al.* (2000a). However, the quality of the pictures of fossils in that reference is poor, and the paper contains only preliminary results. Therefore, we refigure the informative fossil materials reported by Tsubamoto *et al.* (2000a) with some new materials and revised discussion.

Abbreviations

AMNH = American Museum of Natural History, New York, USA. **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. **LK** = Pondaung fossil specimens catalogued by the French paleontologists (Métais *et al.*, 2000). **NMMP-KU** = National Museum, Myanmar, Paleontology-Kyoto University (Japan). **NSM** = National Science Museum, Tokyo, Japan. **UCMP** = Museum of Paleontology, University of California, Berkeley, USA.

Geologic setting and age

The Pondaung Formation is distributed in the western part of central Myanmar (Tsubamoto *et al.*, 2000a, fig. 1, 2002a, fig. 1). It is a freshwater deposit associated with meandering rivers, marshes, and delta plains, and is subdi-

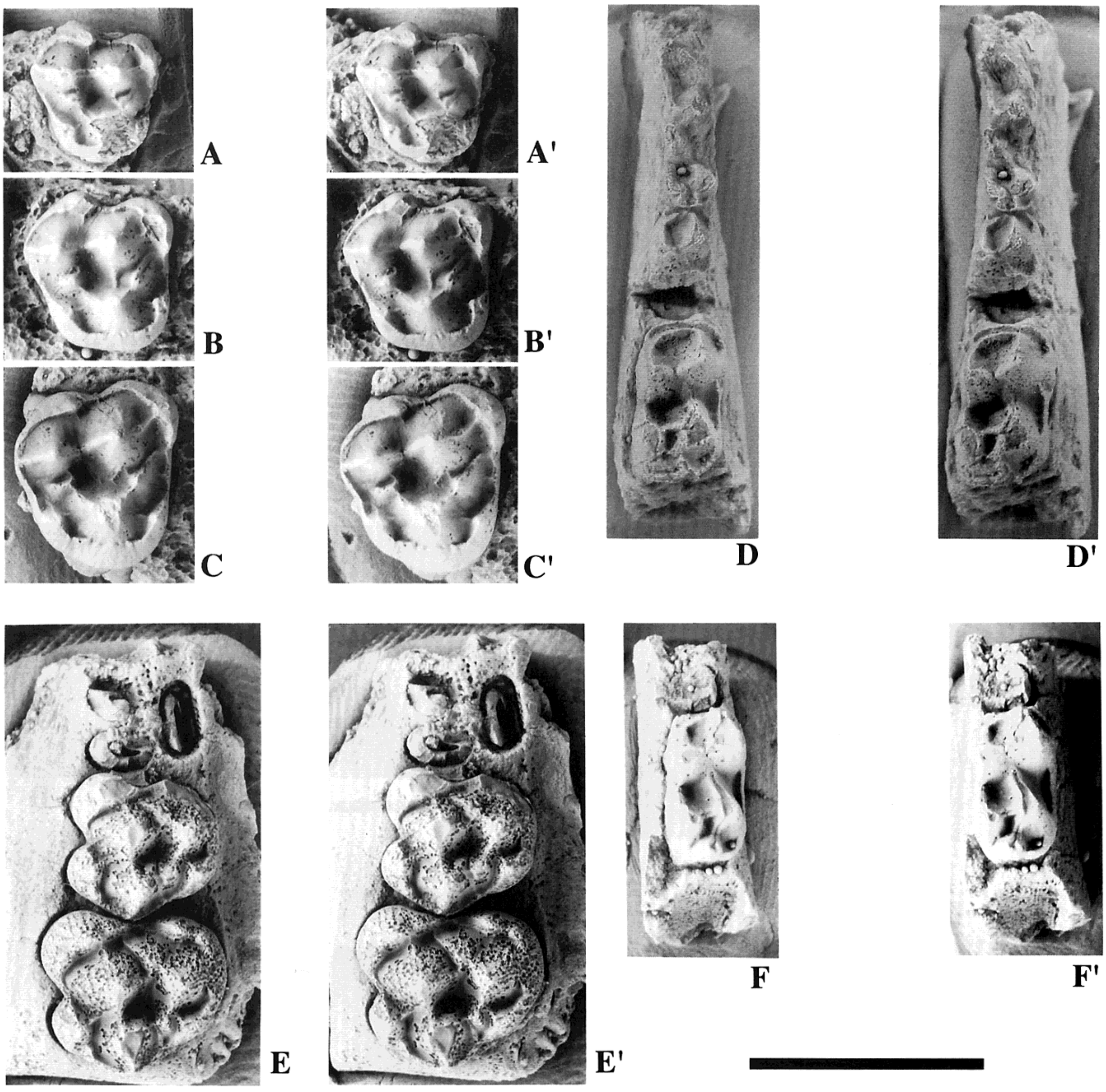
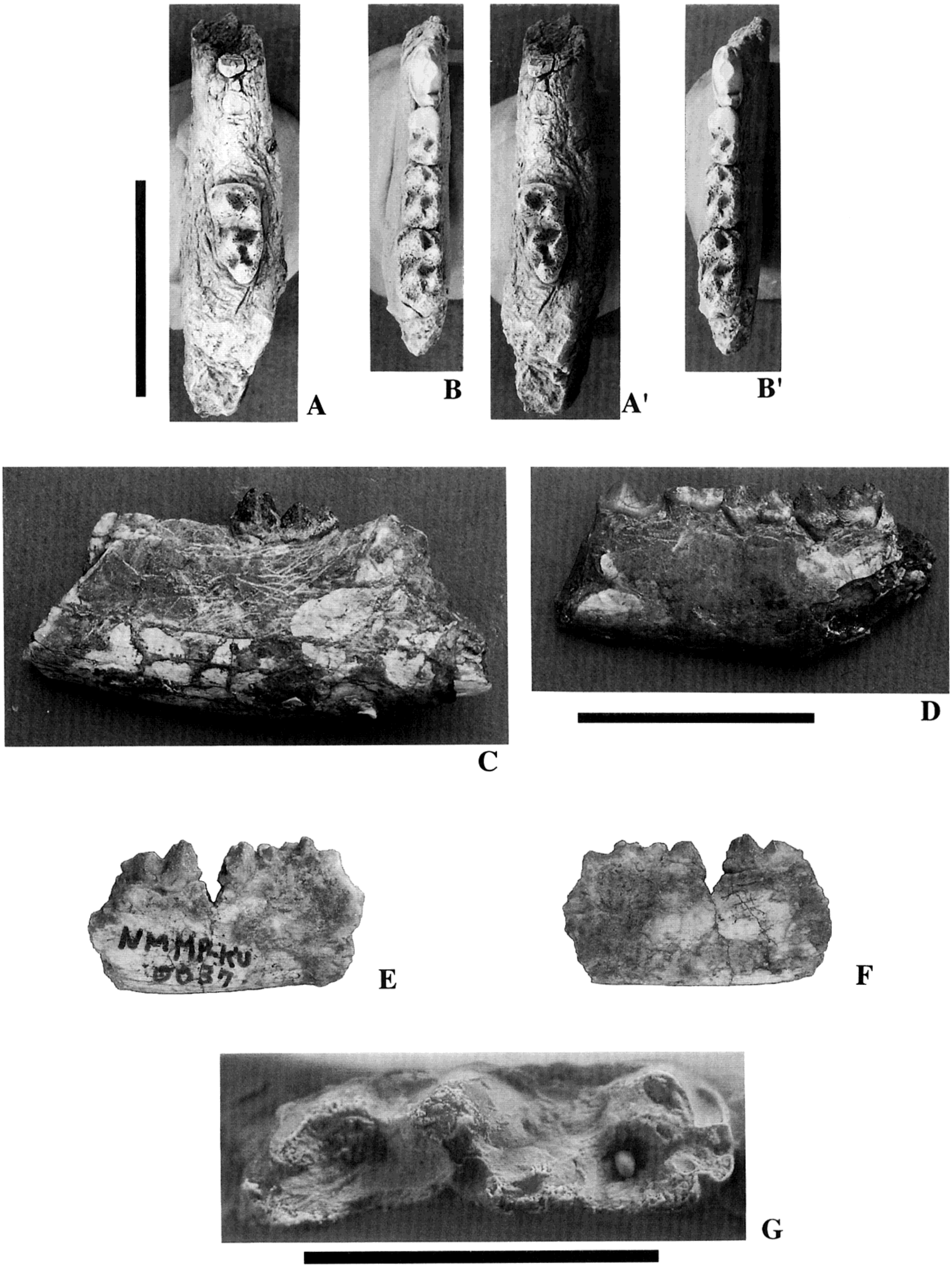


Figure 2. *Hsanotherium parvum* Ducrocq *et al.*, in occlusal view. **A–C, A'–C'**. NMMP-KU 0035 (Bhn 10; Holotype), a right maxillary fragment with M^{1-3}: A, A', M^1 (stereo pair); B, B', M^2 (stereo pair); C, C', M^3 (stereo pair). **D, D'**. NMMP-KU 0037, a right mandibular fragment with dP_4M_{1-2} (stereo pair). **E, E'**. NMMP-KU 0031 (Bhn 11), a right maxillary fragment with M^{2-3} (stereo pair). **F, F'**. NMMP-KU 0033, a right mandibular fragment with M_2 (stereo pair). Scale bar = 1 cm.

vided into the "Lower" and "Upper" Members (Aye Ko Aung, 1999; Aung Naing Soe, 1999; Aung Naing Soe *et al.*, 2002). All of the mammalian fossils occur in the lower half of the "Upper Member" (Stamp, 1922; Colbert, 1938; Bender, 1983; Aye Ko Aung, 1999).

The mammalian faunal correlation (Pilgrim and Cotter, 1916; Pilgrim, 1925, 1928; Colbert, 1938; Holroyd and Ciochon, 1994), nannoplankton assemblage (Hla Mon, 1999), and biostratigraphic relationships with adjacent marine units (Holroyd and Ciochon, 1994) indicate that most of the Pondaung Formation is Bartonian equivalent, which is now correlated to the upper middle Eocene (Berggren


A
B
A'
B'
C
D
NMMP-KU
0037
E
F
G

et al., 1995). In addition, the fission-track date of the "Upper Member" has been given as 37.2 ± 1.3 Ma (around middle-late Eocene boundary) by Tsubamoto *et al.* (2002b). Therefore, the age of the mammalian fossils from the Pondaung Formation is most likely the latest middle Eocene (Tsubamoto *et al.*, 2003).

Systematic paleontology

The basic dental terminologies mostly follows those of Bown and Kraus (1979), Janis and Scott (1987), Gentry and Hooker (1988), and Hooker (1989). Several dental terminologies are indicated in Figure 1. Dental measurements of the NMMP-KU materials are shown in the Appendix.

Grandorder Ungulata Linnaeus, 1766
Order and family indeterminate
Genus **Hsanotherium** Ducrocq *et al.*, 2000b

Type and only known species.—*Hsanotherium parvum* Ducrocq *et al.*, 2000b.

Revised diagnosis.—Primitive and very small ungulate with low-crowned teeth. Upper molars with three main cusps (paracone, metacone, and protocone), four smaller cusps (parastyle, mesostyle, hypocone, and pericone), and two much smaller cusps (paraconule and metaconule) (metastyle absent). P_4 simple premolariform and mesiodistally elongated with large protoconid, one distal cusp (hypoconulid?), and no talonid basin. DP_4 mesiodistally elongated showing trilobed aspect. Lower molars with protoconid, metaconid, hypoconid, entoconid, hypoconulid (paraconid absent), large trigonid and talonid basins, three cristids descend from hypoconulid (cristid obliqua linking to trigonid, hypolophid linking to entoconid, and posthypocristid linking to hypoconulid), and hypoconulid basin (a basin surrounded by hypoconulid, posthypocristid, hypoconid, hypolophid, and entoconid). $M^1/M_1 < M^2/M_2 < M^3/M_3$.

Hsanotherium parvum Ducrocq *et al.*, 2000b

Figures 2–3

Ungulata indet. D, Tsubamoto *et al.*, 2000a, p. 39–42, 73–75, pls. 2-4.
Hsanotherium parvum Ducrocq *et al.*, 2000b, p. 727, fig. 2.

Holotype.—NMMP-KU 0035 (Bhn 10), a right upper jaw fragment with M^{1-3}.

Type locality.—Bh1 (Yarshe Kyitchaung) locality, near Bahin Village, Myaing Township, central Myanmar (Tsubamoto *et al.*, 2000a, fig. 5; Ducrocq *et al.*, 2000b).

Referred material.—NMMP-KU 0031 (Bhn 11), 0032, 0033, 0034, 0036, 0037. (Tsubamoto *et al.*, 2000a; Ducrocq *et al.*, 2000b)

Diagnosis.—As for genus.

Description of dP_4.—DP_4 (in NMMP-KU 0037) (Figures 2D, D', 3E–G) is mesiodistally elongated and shows trilobed structure: posterior talonid, central "trigonid," and anterior lobe. Talonid is roughly similar to that of molars in morphology, having hypoconid, hypoconulid, and entoconid. The presence/absence of hypoconulid basin is unknown due to the poor preservation on that part. Hypoflexid is deeper than that of molars. In central "trigonid" there is a large protoconid. At metaconid region, there appears to be three small tubercles, making a single bulge. There is a lobe anterior to central "trigonid." This anterior lobe makes a shallow and mesiodistally elongated basin. This basin is encircled by a low paracristid. There appear to be three tiny cuspules at the anterior margin of the anterior lobe (at paraconid region). These three capsules are much lower than the other cusps. Dental enamel is thinner than that of molars.

Discussion.—The upper molar dentition, NMMP-KU 0035 (Bhn 10) and NMMP-KU 0031 (Bhn 11), was originally described with the lower dentition and assigned to an indeterminate taxon within the Ungulata by Tsubamoto *et al.* (2000a). Based only on these examples of upper dentition, Ducrocq *et al.* (2000b) erected a new genus and species, *Hsanotherium parvum*, but they did not mention the lower dentition.

Ducrocq *et al.* (2000b) placed *Hsanotherium* among the most primitive anthracobunids (Ungulata; Tethytheria) because the following dental characteristics are shared by *Hsanotherium* and other anthracobunids: an increase in molar size from M^1 to M^3; the buccal notch of the upper molars between parastyle and mesostyle; the existence of six distinct cusps (paracone, metacone, protocone, hypocone, paraconule, and metaconule); the arrangement of the anterior cusps (paracone, paraconule, and protocone) in a somewhat convex curve; the lack of ectoloph; and the relatively great anterior breadth of the molars. Based on these characteristics, Ducrocq *et al.* (2000b) denied the relationship of *Hsanotherium* with artiodactyls, perissodactyls, phenacolophids (Condylarthra), and other condylarths.

Nevertheless, further comparison of the upper molar

← **Figure 3.** *Hsanotherium parvum* Ducrocq *et al.*, **A, A', C.** NMMP-KU 0032, a left mandibular fragment with M_3: A, A', occlusal view (stereo pair); C, buccal view. **B, B', D.** NMMP-KU 0036, a left mandibular fragment with P_4-M_3: B, B', occlusal view (stereo pair); D, buccal view. **E–G.** NMMP-KU 0037, a right mandibular fragment with dP_4M_{1-2}: E, buccal view; F, lingual view; G, occlusal view of dP_4. Upper and middle scale bars = 2 cm (upper scale corresponds to A–B, A'–B', and middle scale corresponds to C–F). Lower scale bar = 5 mm (corresponds to G).

dentitions of *Hsanotherium* with those of anthracobunids casts doubt on the classification of *Hsanotherium* as a member of the Anthracobunidae. Although the upper molars of *Hsanotherium* resemble those of anthracobunids in the characteristics mentioned by Ducrocq *et al.* (2000b), the roughly triangular occlusal outline of the upper molars of *Hsanotherium* is reminiscent of that of P^4 of anthracobunids, rather than of their upper molars (Ducrocq *et al.*, 2000b). The upper molars of anthracobunids are more squared (Ducrocq *et al.*, 2000b), have much larger paraconule and metaconule than those of *Hsanotherium*, and lack pericone. Therefore, the assignment of *Hsanotherium* to the Anthracobunidae is not definitive.

On the other hand, the upper molars of *Hsanotherium* are distinct from those of any other ungulate mammals. They are distinguished from those of perissodactyls and phenacolophids in lacking the pi (π) shaped arrangement of the six cusps (Ducrocq *et al.*, 2000b). *Hsanotherium* has a molar metaconule so tiny that it cannot be assigned to the Artiodactyla, whose molar metaconule is large. The upper molars of *Hsanotherium* somewhat resemble those of *Ectoconus*, a periptychid condylarth, in having a similar arrangement of seven cusps (paracone, metacone, protocone, hypocone, pericone, paraconule, and metaconule), as well as in having two large styles with lobes. However, the parastylar lobe in *Ectoconus* extends buccally to paracone, while that in *Hsanotherium* does so mesiobuccally. Furthermore, the other stylar lobe in *Ectoconus* is located buccally to metacone, while that in *Hsanotherium* (i.e., mesostylar lobe) is located between paracone and metacone. *Hsanotherium* also lacks the lingually expanded protocone base, which is one of the diagnostic characteristics of periptychids (Archibald, 1998). Moreover, in condylarths, including periptychids, M^3 is smaller than M^2 and the posterior part of M^3 is reduced buccolingually, while in *Hsanotherium*, M^3 is larger than M^2 and the posterior part of M^3 is not reduced (Ducrocq *et al.*, 2000b). Therefore, *Hsanotherium* is not assigned to either the Periptychidae or the Condylarthra.

The lower dental materials (NMMP-KU 0032, 0033, 0034, 0036, 0037) described with the type specimen of *Hsanotherium parvum* by Tsubamoto *et al.* (2000a) are assigned to this species. They come from the Bahin area of the Pondaung Formation, where the upper dental materials of this species were found (Tsubamoto *et al.*, 2000a; Ducrocq *et al.*, 2000b). The molar size and morphology of these lower dentitions provide a good match to the upper dentitions of *H. parvum*: the configurations of the pericone, protocone, and hypocone on the upper molars fit the trigonid, talonid, and hypoconulid basins of the corresponding lower molars, respectively. Because of this high correspondence, we have identified these lower dental materials as belonging to *H. parvum*. The lower dental morphology provides new evidence for the phyletic relationships of *Hsanotherium*.

The lower dentition of *Hsanotherium* is distinct from that of anthracobunids. The lower molars of *Hsanotherium* have a large trigonid basin, and their metaconid and entoconid are distal to protoconid and hypoconid, respectively. In contrast, the lower molars of anthracobunids have no or only a very narrow trigonid basin, and their metaconid and entoconid are located almost buccally to protoconid and hypoconid, respectively, creating a bilophodont structure. *Hsanotherium* has a molar posthypocristid linking to the hypoconulid, while anthracobunids have no such molar posthypocristid. P_4 of *Hsanotherium* is simple and premolariform, lacking both paraconid and metaconid. In contrast, that of anthracobunids is more molariform, having distinct paraconid and metaconid, triangular trigonid in occlusal view, and wider talonid.

The lower dentition of *Hsanotherium* is distinct from that of condylarths, whose lower molars lack not only the hypolophid linking hypoconid and entoconid directly, but also lacks the hypoconulid basin on M_{1-2}. Furthermore, condylarths generally have a much more molariform P_4 and a less elongated hypoconulid on M_3 than those of *Hsanotherium*.

The lower dentition of *Hsanotherium* is distinct from that of perissodactyls, although the lower molars of *Hsanotherium* and primitive perissodactyls such as *Hyracotherium* share hypolophid and large and mesiolingually open trigonid. The molar hypoconulid of primitive perissodactyls is much lower than the hypoconid and entoconid, while that of *Hsanotherium* is as tall as the hypoconid and entoconid. Perissodactyls lack hypoconulid basin on M_{1-2}, and furthermore, they have a much more molariform P_4 than that of *Hsanotherium*, showing large metaconid and large talonid basin.

The lower dentition of *Hsanotherium* is also distinct from that of primitive artiodactyls, such as *Diacodexis*. P_4 of primitive artiodactyls has a small and shallow talonid basin, which is lacking in *Hsanotherium*, and it does not have such a large distal cuspid (hypoconulid?) as that of *Hsanotherium*. The lower molars of primitive artiodactyls also have a small paraconid appressed to the large and conical metaconid and no or only a very narrow trigonid basin, again unlike *Hsanotherium*. Additionally, M_{1-2} of primitive artiodactyls lack a hypoconulid basin.

Despite such a unique lower dental morphology, the lower molars of *Hsanotherium* are similar to those of *Gobiohyus pressidens* Matthew and Granger, 1925 (AMNH 20247) (Artiodactyla; Helohyidae). The molar trigonid of *G. pressidens* shows a paracristid that extends down mesially, and then turns distolingually, and finally extends up distally to the tip of the metaconid, forming a relatively large and lingually opened trigonid basin and a wide trigonid angle, like that of *Hsanotherium*. On M_2 of *G. pressidens*, we also find posthypocristid and hypolophid, forming a kind of hypoconulid basin.

However, the dental morphology of *Hsanotherium* is also distinct from that of *G. pressidens*. In the lower molars of *G. pressidens*, there is a tiny paraconid appressed to a metaconid, and metaconid is located just lingually to a protoconid, while in those of *Hsanotherium*, there is no trace of paraconid, and metaconid is distal to protoconid. Moreover, in the lower molars of *G. pressidens*, both talonid and hypoconulid basins are open lingually, and cristid obliqua is very low, unlike those of *Hsanotherium*. Hypoconulid on M_3 is much larger in *G. pressidens* than in *Hsanotherium*. Additionally, P_4 of *Gobiohyus* is more molariform, having a large metaconid, and its upper molars are distinct from those of *Hsanotherium* in having much larger metaconule and in lacking pericone.

The most interesting morphology of *Hsanotherium* is its dP_4 structure (Figure 3G). The mesiodistally elongated and trilobed dP_4 morphology of *Hsanotherium* is reminiscent of that of artiodactyls and macroscelideans (Luckett and Hong, 1998). First, the trilobed dP_4 morphology of artiodactyls has been well known since the 19th century, and has been treated as one of the diagnostic characters of the order (Cuvier, 1822; Blainville, 1839-1864; Weber, 1928; Sudre *et al.*, 1983; Tobien, 1985; Gentry and Hooker, 1988; Sudre and Erfurt, 1996; Luckett and Hong, 1998). However, dP_4 of *Hsanotherium* differs from that of a very primitive artiodactyl, *Diacodexis*, in having mesiodistally much longer anterior lobe and three cuspules at the metaconid region (Luckett and Hong, 1998, fig. 5). It also differs from dP_4 of more derived artiodactyls, such as anthracotheres and haplobunodonts, in having and three cuspules at the metaconid region and in lacking better-derived and large two cusps (protoconid- and metaconid-like, respectively) on the anterior lobe (Tobien, 1985, fig. 4; Luckett and Hong, 1998, fig. 3). Second, the mesiodistally elongated dP_4 of macroscelideans was mentioned by Butler (1969, 1984) and Luckett and Hong (1998). In particular, dP_4 of *Hsanotherium* somewhat resembles that of the Miocene macroscelidean genus *Hiwegicyon* (Butler, 1969, fig. 4B, 1984, fig. 8A) in having anteriorly elongated trigonid and three cuspules at the paraconid region. However, it differs from that of *Hiwegicyon* and other macroscelideans in having three cuspules at the metaconid region and much smaller and lower cuspules at the paraconid region (Butler, 1969, figs. 2D, 3D, 4B, 1984, fig. 8A). It further differs from *Hiwegicyon* in having more tapered anterior margin (Butler, 1969, fig. 4B; Luckett and Hong, 1998). In addition, the P_4 and molar morphologies of *Hsanotherium* are distinct from those of macroscelideans: *Hsanotherium* has simple premolariform P_4, and large and unreduced $M^3/_3$, whereas macroscelideans have molariform P_4 and reduced $M^3/_3$ (Figures 1-2; Butler, 1969, figs. 2-3, 1984, figs. 2-7; Hartenberger, 1986; Simons *et al.*, 1991, figs. 1-3, 5). On the other hand, the mesiodistally elongated dP_4 can be also seen in *Desmostylus* (Tethytheria; Desmostylidae) (Uno, 2000, figs. 2, 10), although the dental morphology of *Hsanotherium* is quite different from that of *Desmostylus*. DP_4 of anthracobunids shows bilobed morphology like lower molars (West, 1980, pl. 4, fig. 5), so that it is distinct from that of *Hsanotherium*.

In sum, the dental morphology of *Hsanotherium* strongly suggests that *Hsanotherium* is not an anthracobunid and cannot confidently be classified into any present ungulate order, although it can be identified as belonging to the Ungulata because of its large, elongated, and posteriorly projecting hypoconulid on M_3 (Prothero *et al.*, 1988; Prothero, 1993; Nessov *et al.*, 1998). Although the dental morphology of *Hsanotherium* is quite unique, its lower molars show a similarity to those of *Gobiohyus pressidens* (Artiodactyla; Helohyidae), and its mesiodistally elongated dP_4 morphology resembles that of artiodactyls and macroscelideans. Nevertheless, the overall unique dental morphology of *Hsanotherium* is distinguished from that of these two orders.

Order Artiodactyla Owen, 1848
Family Dichobunidae Turner, 1849
Subfamily Homacodontinae Marsh, 1894
Genus ***Asiohomacodon*** gen. nov.

Type and only known species.—Asiohomacodon myanmarensis sp. nov.

Diagnosis.—One of the most derived homacodonts with bunoselenodont dentition and small but distinct molar paraconule. Dental size and morphology similar to those of *Protoreodon parvus* (a primitive protoreodontine agriochoerid oreodont) and *Pentacemylus* (a derived and protoreodontine-like homacodont). Differs from protoreodontines in having larger molar paraconule, more erect molar paracone and metacone, weaker styles, less inflated molar mesostyle, more mesiodistally compressed molar talonid, and molar postmetacristid and preentocristid both of which link straight to each other in occlusal view, and in lacking molar metastylid. Differs from *Pentacemylus* in having more selenodont dentition, weaker molar parastyle, more mesiodistally compressed lower molars, sharper molar preentocristid, and M^3 whose posterior part is much less reduced. Differs from other homacodonts in having more selenodont dentition and in lacking any trace of molar hypocone and paraconid. Differs from *Atopotherium* (an agriochoerid-like anthracotheriid) in being smaller, and in having shallower mandibular corpus and less mesiodistally compressed molar trigonid and talonid.

Etymology.—Asio-: Asia, where the type specimen was

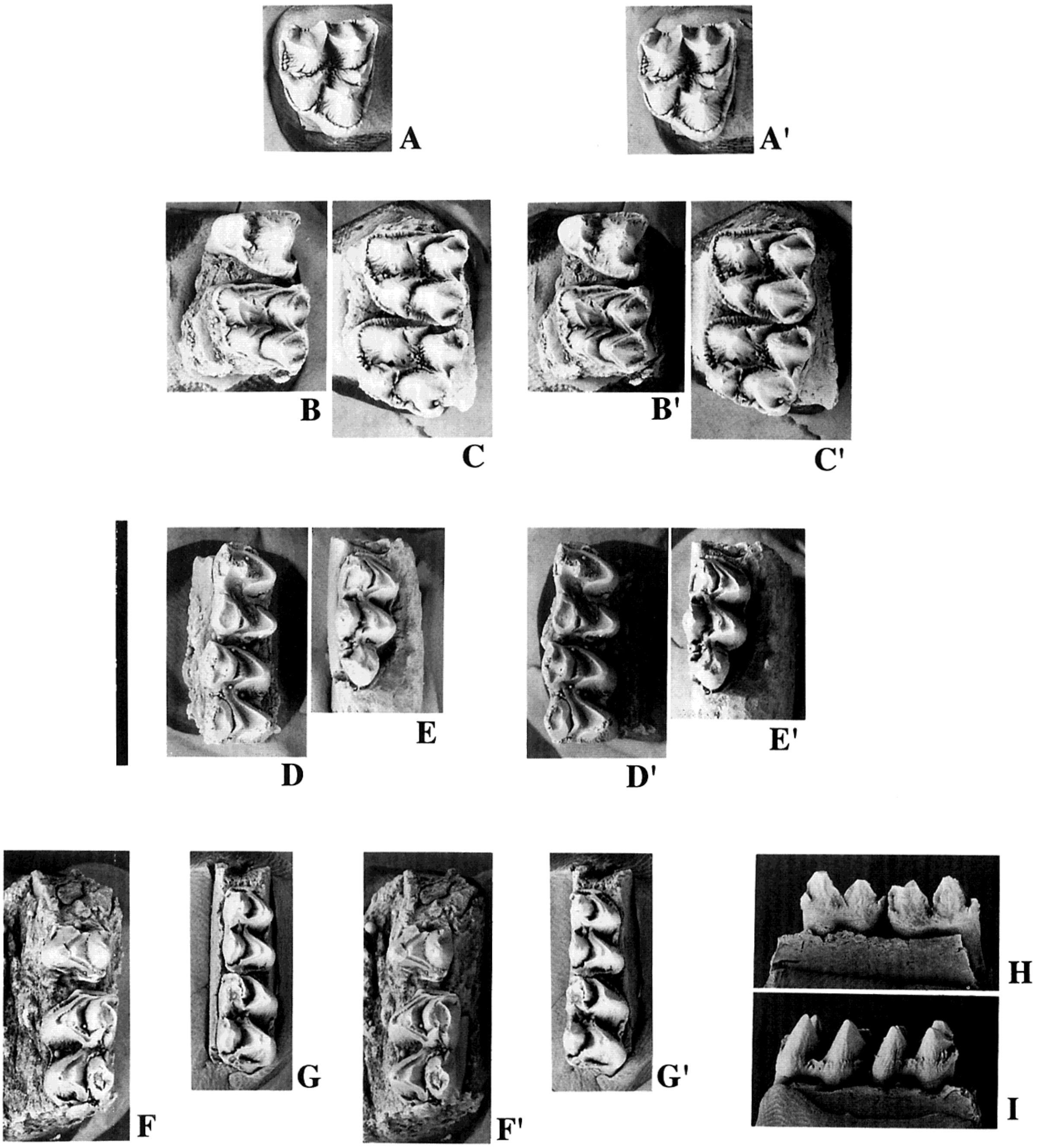


Figure 4. *Asiohomacodon myanmarensis* gen. et sp. nov. **A**, **A'**. NMMP-KU 0026, a right M^3, in occlusal view (stereo pair). **B**, **B'**, **C**, **C'**. NMMP-KU 0713 (Holotype), a left maxillary fragment with P^4-M^3, in occlusal view: B, B', P^{4}M^1 (stereo pair); C, C', M$^{2-3}$ (stereo pair). **D**, **D'**. NMMP-KU 0027, a right mandibular fragment with M$_{2-3}$, in occlusal view (stereo pair). **E**, **E'**. NMMP-KU 0028, a right mandibular fragment with M$_3$, in occlusal view (stereo pair). **F, F'**. NMMP-KU 0264, a left mandibular fragment with M$_{2-3}$, in occlusal view (stereo pair). **G**, **G'**, **H**, **I**. NMMP-KU 0029, a right mandibular fragment with M$_{1-2}$: G, G', occlusal view (stereo pair); H, lingual view; I, buccal view. Scale bar = 2 cm.

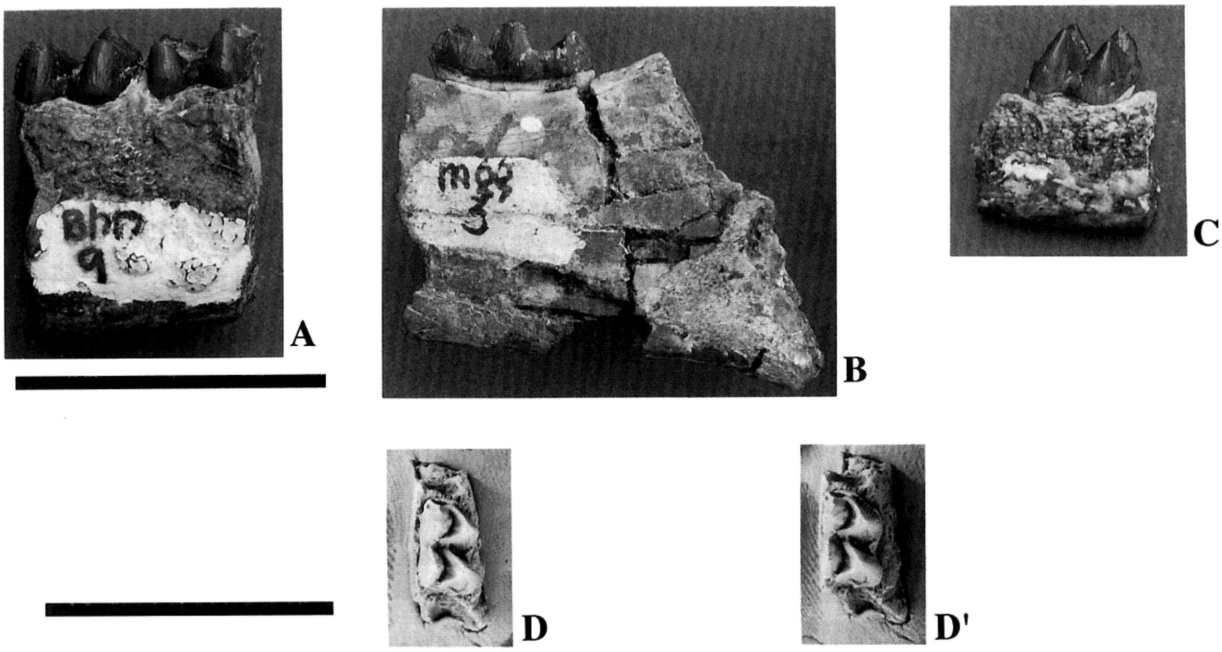


Figure 5. **A, B.** *Asiohomacodon myanmarensis* gen. et sp. nov. A, NMMP-KU 0027, a right mandibular fragment with $M_{2\text{-}3}$, in buccal view; B, NMMP-KU 0028, a right mandibular fragment with M_3, in lingual view. **C, D, D'.** Cf. *Asiohomacodon myanmarensis* gen. et sp. nov., NMMP-KU 0030, a right mandibular fragment with $M_{1?}$: C, buccal view; D, D', occlusal view (stereo pair). Scale bars = 2 cm (upper scale corresponds to A–C, lower scale corresponds to D, D').

collected; -homacodon: homacodonts, in which this genus is included.

Asiohomacodon myanmarensis sp. nov.

Figures 4, 5A, B

?Agriochoeridae indet. E, Tsubamoto *et al.*, 2000a, p. 45–48, 80–81, pls. 9, 10 A–C.

Holotype.—NMMP-KU 0713, a left upper jaw fragment with P^4-M^3 (new material).

Type locality.—Kd2 locality (21°49′24.0′′N, 94°35′25.2′′E), Kyudaw (near Thidon Village in Bahin area), Myaing Township, central Myanmar (Tsubamoto *et al.*, 2000a, fig. 4).

Referred material.—NMMP-KU 0026, 0027, 0028, 0029, 0068, 0264 (Tsubamoto *et al.*, 2000a).

New material.—NMMP-KU 0714, a right mandibular fragment with broken M_3 (this specimen probably belongs to the same individual as NMMP-KU 0713).

Locality of new material.—As for the holotype.

Diagnosis.—As for genus.

Etymology.—Named after the Union of Myanmar, the country where the type specimen was collected.

Description.—The dental materials show small, primitive, brachyodont, and bunoselenodont artiodactyl condition. Mandible is as deep as in *Pentacemylus* (Dichobunidae; Homacodontinae) and *Protoreodon* (Agriochoeridae; Protoreodontinae), and is much deeper than those of primitive ruminants, such as *Indomeryx* and *Archaeomeryx.* Dental enamel is somewhat wrinkled.

P^4 is premolariform, bearing two distinct cusps, paracone and protocone, and an incipient trace of hypocone at the distobuccal base of the protocone. Crown is triangular in occlusal view and is wider than long. Paracone is much larger and taller than protocone. Paracrista is distinct and somewhat selenodont shaped. Metastyle is small but distinct. Parastylar region is only weakly developed. Cingulum extends from the distolingual base of the metastylar region and surrounds the distal and lingual margins of the crown, disappearing at the mesial base of the protocone.

Upper molars are quadrilateral in occlusal view, bearing large paracone, metacone, protocone, and metaconule, and small but distinct paraconule (there is no trace of hypocone). $M^{1\text{-}3}$ are very similar to one another in morphology, although metaconule on M^3 is proportionally only slightly smaller and lower than that on $M^{1\text{-}2}$. Upper molar sizes are: $M^1 < M^2 = M^3$. Paracone and metacone are of nearly equal size and are conical and erect. Paracone has strong buccal ridge, while metacone has weaker one. Ectoloph is distinct and somewhat W-shaped in occlusal view. Parastyle is small but distinct. A strong crista from tip of parastyle extends down distally, disappearing at buccal face of paracone. Mesostyle and metastyle are only weakly developed. Lingual margin of metaconule is much more buccally located than that of protocone. Postprotocrista reaches mesial wall of metaconule, making protocone incompletely selenodont. A cingulum that originates below the mesiolingual base of the parastyle is continuous through the mesial and lingual base of the crown, disappearing at the distal base of the metaconule. Ectostyle is absent. In NMMP-KU 0713 (type), a weak buccal cingulum exist on the buccal face of the metacone, linking mesostyle and metastyle.

Lower molars show primitive selenodont morphology. M_1 and M_2 are almost identical in morphology, although M_1 is only slightly less mesiodistally compressed than M_2. M_3 is also almost identical to M_2 in morphology, except for having posteriorly elongated hypoconulid. The molar sizes increase gradually from M_1 to M_3. Trigonid is as wide as, roughly as long as, and nearly as tall as talonid. Metaconid and entoconid are somewhat buccolingually compressed, and the latter is more compressed than the former. Paraconid, metastylid, and entostylid are absent. Protocristid extends down lingually and then extends up to tip of metaconid, making a V-shaped notch between protoconid and metaconid. Cristid obliqua originates below the notch between protoconid and metaconid. Posthypocristid extends lingually, and then turns distolingually at the distobuccal base of entoconid, linking to hypoconulid. Preentocristid extends down mesially and links to postmetacristid, making a V-shaped talonid notch. Postentocristid extends down distally and stops at distal base of entoconid: it connects neither to hypoconulid nor to posthypocristid. Precingulid extends from mesial base of metaconid, disappearing at mesiobuccal base of protoconid. Buccal cingulum occurs between protoconid and metaconid, but ectostylid is absent. Lingual cingulum is absent. Postcingulid extends from distolingual base of entoconid and disappears at distal base of hypoconid on M_{1-2}, bearing tiny hypoconulid. On M_3, hypoconulid is large and posteriorly elongated, and bears single cusp and single hypoconulid loop. The inner cristid of hypoconulid loop stops just distal to postentocristid, making crenulation there. Its outer cristid connects to posthypocristid.

Discussion. — The overall dental morphology of *Asiohomacodon* recalls those of a derived homacodont, *Pentacemylus* (Bunomerycini), and *Asiohomacodon* is classified with the Homacodontinae. *Asiohomacodon* and *Pentacemylus* share the following characteristics: similar dental size, bunoselenodont dentition, incipient trace of hypocone on P^4, small but distinct molar paraconule and mesostyle, enlarged molar metaconule, no trace of molar hypocone, no molar paraconid, neither molar metastylid nor entostylid, mesiodistally compressed molar trigonid and talonid, and deeper mandibular corpus than that of primitive ruminants. Based on these characteristics, *Asiohomacodon* can be referred to one of the derived homacodonts. Homacodonts have been found mostly in Eocene North America, and one genus has been recorded from Eocene Europe (McKenna and Bell, 1997). A new homacodont was recently found in the Eocene Shanghuang fauna of central China (Qi *et al.*, 1996), but it has not been described yet.

Asiohomacodon is distinct from all other homacodonts. It differs from *Pentacemylus* in having a more selenodont dentition, slightly weaker molar parastyle, more mesiodistally compressed lower molars, sharper molar preentocristid, P^4 whose lingual part (protocone part) is mesiodistally much shorter than the buccal part (paracone part), and M^3 whose posterior part is almost unreduced (i.e., M^3 metaconule is nearly as large as that of M^2, and the posterior part of M^3 is nearly as wide as that of M^2). *Asiohomacodon*, with its more selenodont dentition, may be more similar to the new homacodont genus B of Stucky (1998) than to *Pentacemylus*, judging from Stucky's short description (1998, p. 368). In any case, *Asiohomacodon* differs from the new homacodont genus B in lacking any trace of molar metastylid and ectostylid. On the other hand, it differs from the other homacodonts, such as *Homacodon*, in having more selenodont dentition and in lacking molar hypocone and paraconid.

It is believed that *Pentacemylus*-like homacodonts gave rise to the Protoreodontinae (Oreodontoidea; Agriochoeridae), which occurs only in Eocene North America (Lander, 1998), so that the dental morphology of *Asiohomacodon* might suggest a transitional morphology from homacodonts to protoreodontines. In fact, the dental morphologies of *Asiohomacodon*, *Pentacemylus*, and the new homacodont genus B (Stucky, 1998, p. 368) are also similar to that of primitive protoreodontines such as *Protoreodon parvus*. However, both *Asiohomacodon* and *Pentacemylus* differ from protoreodontines in having less selenodont upper molars and smaller molar paraconule, and in lacking molar metastylid. The lack of molar metastylid in *Asiohomacodon* and *Pentacemylus* specifically indicates that these two genera are more primitive than protoreodontines and therefore cannot be assigned to the Protoreodontinae. In this respect, the new genus B, which has an incipient molar metastylid (Stucky, 1998, p. 368), is more derived and more protoreodontine-like than *Asiohomacodon* and *Pentacemylus*. Compared to *Pentacemylus*, *Asiohomacodon* is more derived and more protoreodontine-like in having more selenodont dentition and much less reduced M^3 metaconule but is more primitive in having slightly smaller molar parastyle.

It is interesting to note that, in its lower molar morphology, *Asiohomacodon* also resembles an agriochoerid-like anthracotheriid, *Atopotherium bangmarkensis*, from the upper Eocene Krabi basin of Thailand (Ducrocq *et al.*, 1996). *Atopotherium* is based only on the single specimen, lower mandibular fragments with right P_2-M_2 and left P_4 (DMR TF 2908) (Ducrocq *et al.*, 1996). Both mammals have selenodont lower molars with mesiodistally compressed trigonid and talonid. Compared to *Asiohomacodon*, however, *Atopotherium* is much larger, and has a much deeper mandibular corpus and more mesiodistally compressed molar trigonid and talonid. *Atopotherium* has been assigned to the Anthracotheriidae on the basis of its P_4 morphology, although *Atopotherium* and agriochoerids are similar to each other in their lower molar morphology (Ducrocq *et al.*, 1996). The affinity of these two genera cannot be tested because of the lack of the P_4 material of *Asiohomacodon*.

Cf. ***Asiohomacodon myanmarensis*** sp. nov.

Figure 5C, D, D'

Cf. ?Agriochoeridae indet. E, Tsubamoto *et al.*, 2000a, p. 48, 81, pl. 10 D–F.

Material.—NMMP-KU 0030 (Tsubamoto *et al.*, 2000a).

Discussion. — As mentioned by Tsubamoto *et al.* (2000a), the dental size and morphology of the preserved molar in NMMP-KU 0030 is nearly identical to that of M_1 of *Asiohomacodon myanmarensis*. However, it differs in the following features from *A. myanmarensis*: the mandibular is much more slender (it is as slender as that of primitive ruminants); the molar protocristid extends down lingually and stops at the distal base of the metaconid, whereas that of *A. myanmarensis* extends down lingually and then extends up to the tip of the metaconid, making a V-shaped notch.

Suborder Ruminantia Scopoli, 1777
Family indeterminate
Genus ***Indomeryx*** Pilgrim, 1928

Type species.—Indomeryx cotteri Pilgrim, 1928.

Referred species.—Indomeryx arenae Pilgrim, 1928.

Revised diagnosis.—Small and very primitive ruminant with brachyodont and bunoselenodont dentition. Upper molars with weak styles and no distinct ectostyle. Short diastema between P_2 and P_3. P_4 relatively simple having metaconid twinned with protoconid and small talonid basin, and lacking transverse crest on talonid. Lower molars with tiny paraconid twinned with metaconid in some specimens, paracristid and slight premetacristid both not so projecting anteriorly, *Zhailimeryx*-fold (double preentocristid; entoconidian groove), and lingually closed hypoconulid loop on M_3, and without ectostylid, *Palaeomeryx*-fold, distinct metastylid, and distinct *Dorcatherium*-fold. Differs from *Archaeomeryx*, *Gelocus*, *Gobiomeryx*, *Notomeryx*, and *Prodremotherium* in having *Zhailimeryx*-fold, less anteriorly projecting molar paracristid and premetacristid, and P_4 metaconid twinned with protoconid, and in lacking transverse crest on P_4 talonid. Further differs from the latter three genera (Prodremotheriidae) in having smooth and undepressed distal face of molar entoconid, and in lacking distinct molar metastylid and ectostylid and sharp molar postentocristid. Further differs from *Gobiomeryx* in lacking accessory cusp on M_3 hypoconulid. Further differs from *Archaeomeryx* in having lingually closed and larger hypoconulid loop on M_3. Differs from lophiomerycids in having much weaker molar styles, P_4 metaconid twinned with protoconid, and molar premetacristid, and in lacking lingually opened and large molar trigonid basin. Differs from tragulids in having P_4 metaconid and in lacking distinct *Dorcatherium*-fold. Further differs from the basal tragulid, *Archaeotragulus*, in having molar trigonid as wide as talonid and in lacking anteriorly projecting and stronger paracristid, and in lacking lingually opened and large molar trigonid basin. Differs from *Xinjiangmeryx* in having less developed upper molar cingulum and styles, and less molariform P_4.

Classification of the Pondaung species.—To date, four species of *Indomeryx* from the Pondaung Formation have been described. Pilgrim (1928) elected the genus *Indomeryx* and described two species from the Pondaung Formation: the first, *Indomeryx cotteri* (the type species), based on a mandibular fragment with P_4-M_3 (GSI B768); and the second, *Indomeryx arenae*, based only on a mandibular fragment with M_3 talonid (GSI B769) (Pilgrim, 1928). Pilgrim (1928) distinguished *I. arenae* from *I. cotteri* by the following four features: (1) its smaller size; (2) a lesser degree of concavity of the lower border of the mandibular corpus behind M_3; (3) the absence of buccal cingulum on M_3; and (4) molar preentocristid showing a double ridge (*Zhailimeryx*-fold; Figure 1; Guo *et al.*, 2000). On the other hand, Colbert (1938) considered *I. arenae* to be possibly synonymous with *I. cotteri* by the following reasons: (1) the size differences between the specimens were not large enough to separate them into two species; (2) the difference in the shapes of the lower border of the corpus of the two species could be attributed to the difference between immature material (*I. cotteri*) and fully adult material (*I. arenae*); and (3) the difference in the degree of cingular development could be a result of individual variation. According to Colbert (1938), the only significant difference between *I. arenae* and *I. cotteri* is the molar preentocristid showing a double ridge (*Zhailimeryx*-fold) in

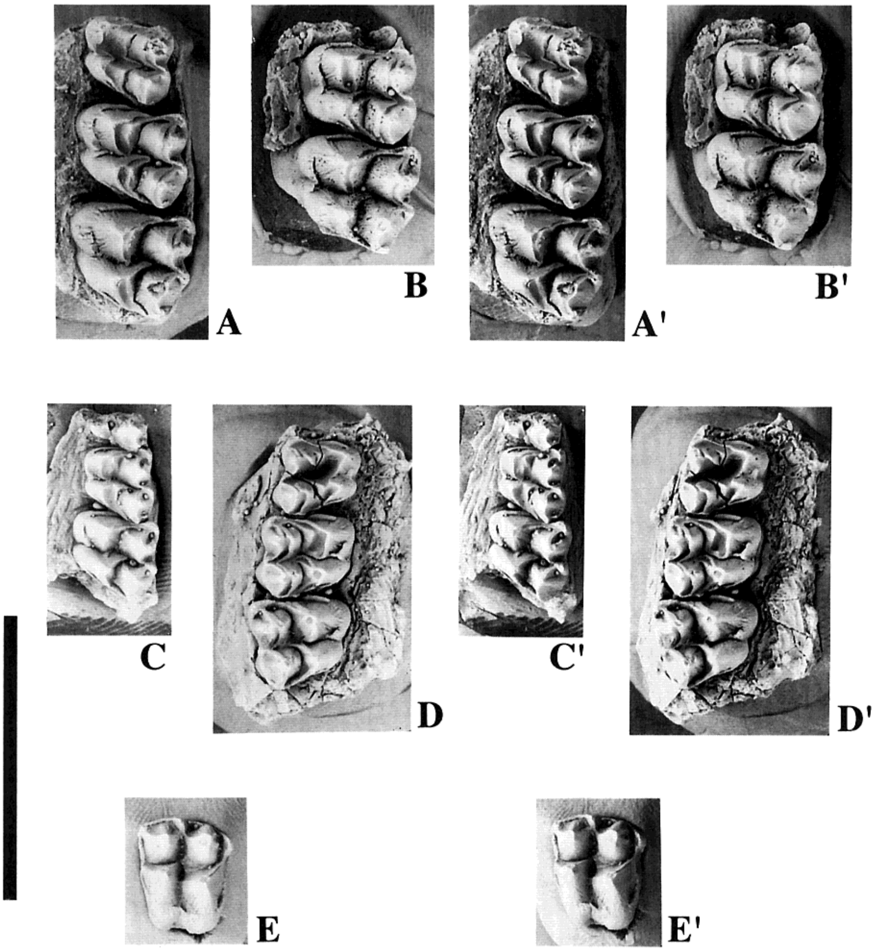


Figure 6. **A–C, A'–C'**. *Indomeryx cotteri* Pilgrim, in occlusal view: A, A', NMMP-KU 0008 (Mgg 2), a left maxillary fragment with M^{1-3} (stereo pair); B, B', NMMP-KU 0009 (Mgg 14), a left maxillary fragment with M^{2-3} (stereo pair); C, C', NMMP-KU 0010, a left maxillary fragment with $dP^{3-4}M^{1}$ (stereo pair). **D, D'**. *Indomeryx arenae* Pilgrim, NMMP-KU 0007 (Bhn 1115), a right maxillary fragment with M^{1-3}, in occlusal view (stereo pair). **E, E'**. Cf. *Indomeryx cotteri*, NMMP-KU 0025, a right $M^{2?}$, in occlusal view (stereo pair). Scale bar = 2 cm.

the case of the former. Métais *et al.* (2000) has recently described two new species of *Indomeryx* from the Pondaung Formation, *Indomeryx pilgrimi* and *Indomeryx minus*. According to them, *I. pilgrimi* differs from *I. cotteri* in its larger size, retention of molar paraconid, a groove on the mesial side of molar entoconid (*Zhailimeryx*-fold), weak *Dorcatherium*-fold, and stronger postcingulum on M_{1-2}; while *I. minus* differs from *I. cotteri* in its smaller size, *Zhailimeryx*-fold, and weak *Dorcatherium*-fold, and differs from *I. pilgrimi* again in its smaller size, thin buccal cingulum on the lower molars, and in lacking molar paraconid.

The new materials and a reexamination of previously described materials (Figures 6–8) lead us to conclude that there is no distinct dental morphology, except for differences in M_1 size, between the four species of the Pondaung *Indomeryx*. Our reasons are summarized in the following five paragraphs:

(1) The double-ridged preentocristid (*Zhailimeryx*-fold), one of the diagnoses of *I. arenae* cited by Pilgrim (1928) and of *I. pilgrimi* and *I. minus* by Métais *et al.* (2000), exists on M_{1-3} of all well preserved lower dental materials of the Pondaung *Indomeryx* including *I. cotteri* (Figure 7). This structure is also seen in *I. cotteri* from the upper Eocene Naduo Formation of China, so that it is one of the identifying characteristics of this genus.

(2) As for the morphology of the mandibular corpus of *I. arenae* mentioned by Pilgrim (1928), the suggestion by Colbert (1938) is appropriate: the difference found between *I. cotteri* and *I. arenae* is due to the expected difference between immature material (*I. cotteri*) and fully adult material (*I. arenae*). Moreover, there is individual variation in the

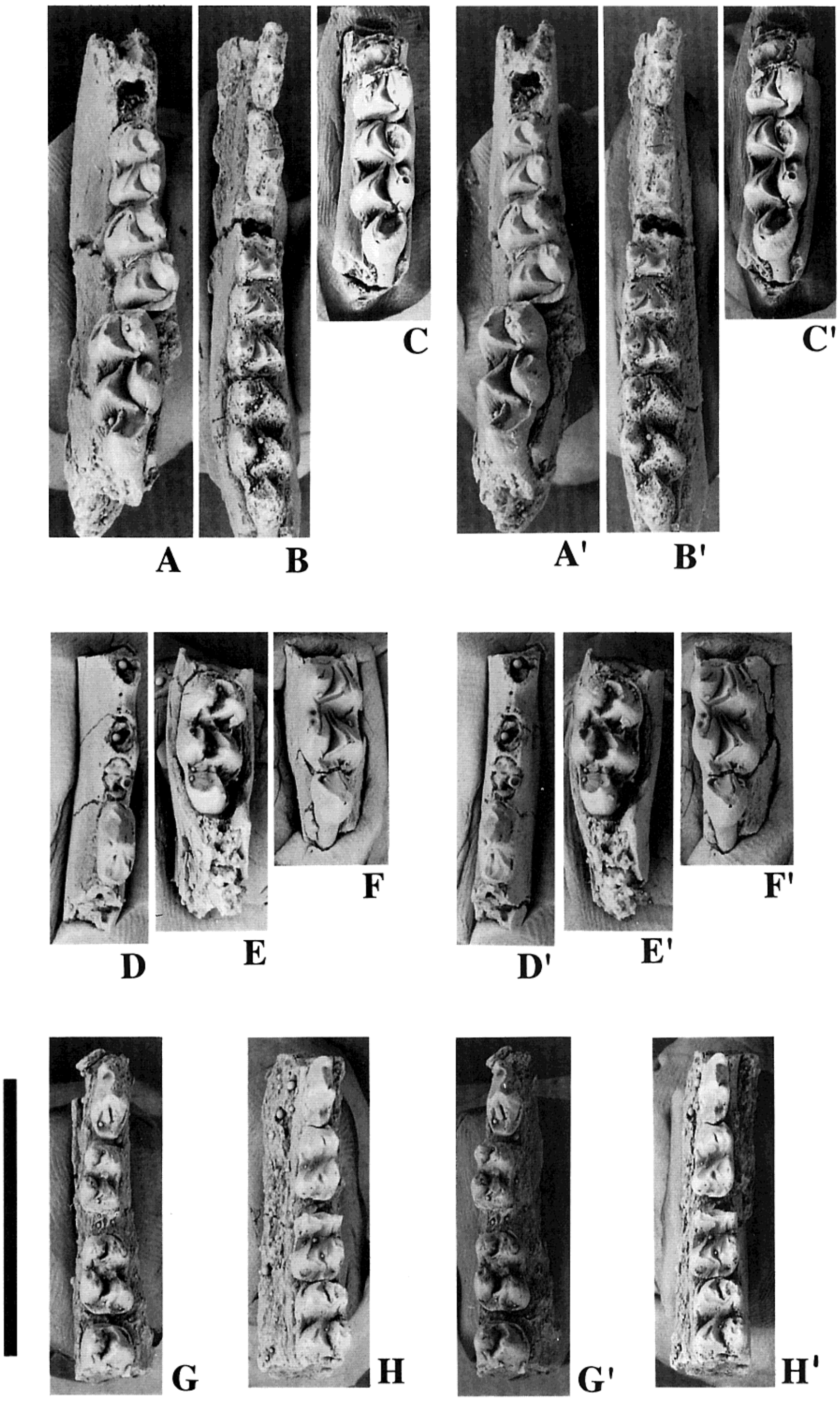


Figure 7. **A–F, A'–F'**. *Indomeryx cotteri* Pilgrim, in occlusal view: A, A', NMMP-KU 0015 (Bhn 911, the type of *Indomeryx pilgrimi* Métais *et al.*), a left mandibular fragment with $M_{1\text{-}3}$ (stereo pair); B, B', NMMP-KU 0019, a right mandibular fragment with P_3-M_3 (stereo pair); C, C', NMMP-KU 0018, a left mandibular fragment with $M_{2\text{-}3}$ (stereo pair); D, D', NMMP-KU 0021, a right mandibular fragment with P_4 (stereo pair); E, E', NMMP-KU 0289, a right mandibular fragment with M_3 (stereo pair); F, F', NMMP-KU 0017 (Mgg 5), a right mandibular fragment with M_3 (stereo pair). **G, G', H, H'**. *Indomeryx arenae* Pilgrim, in occlusal view: G, G', NMMP-KU 0013, a right mandibular fragment with P_4-M_3 (stereo pair); H, H', NMMP-KU 0011 (Bhn 3, the type of *Indomeryx minus* Métais *et al.*), a left mandibular fragment with P_4-M_3 (stereo pair). Scale bar = 2 cm.

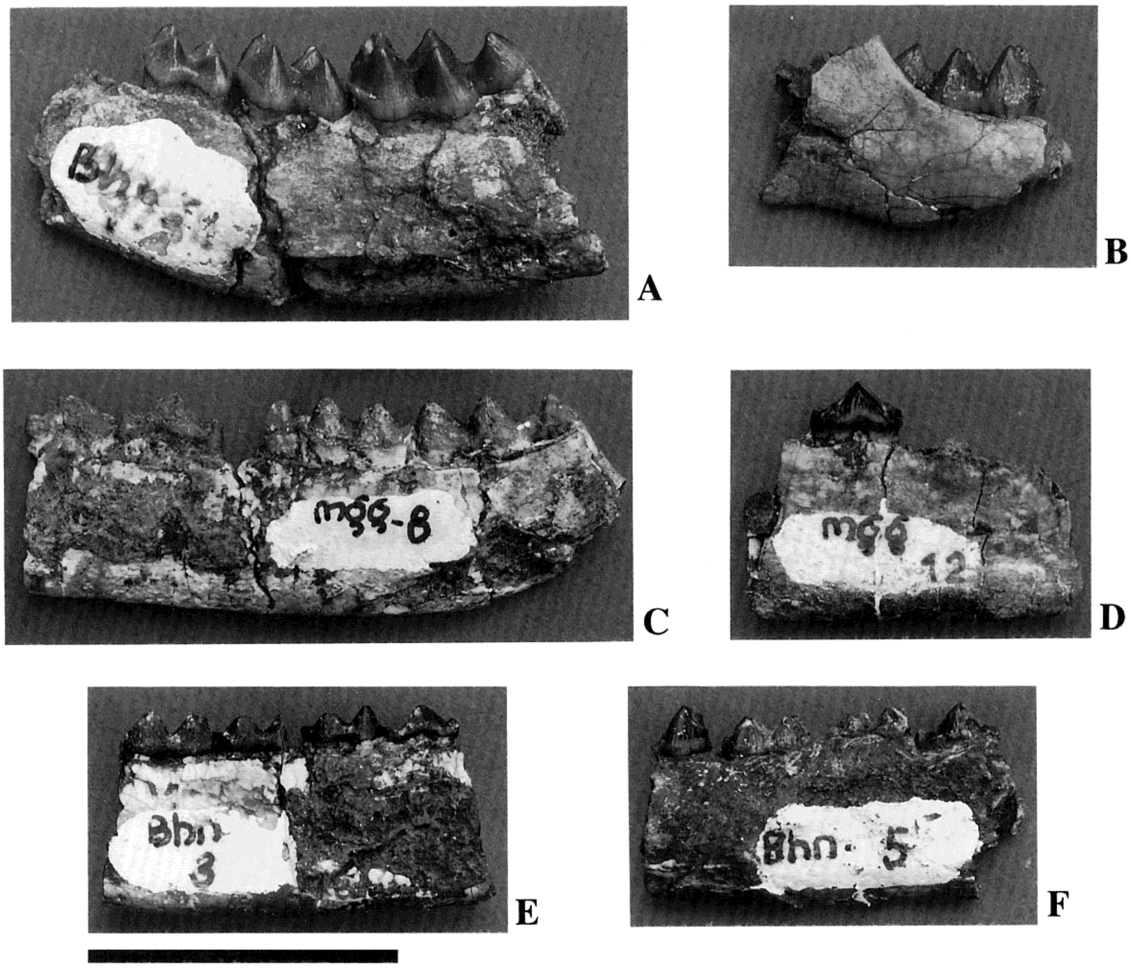


Figure 8. **A–D**. *Indomeryx cotteri* Pilgrim. A, NMMP-KU 0015 (Bhn 911), a left mandibular fragment with M_{1-3}, in buccal view; B, NMMP-KU 0289, a right mandibular fragment with M_3, in buccal view; C, NMMP-KU 0019, a right mandibular fragment with P_3-M_3, in lingual view; D, NMMP-KU 0021, a right mandibular fragment with P_4, in buccal view. **E–F**. *Indomeryx arenae* Pilgrim. E, NMMP-KU 0011 (Bhn 3), a left mandibular fragment with P_4-M_3, in lingual view; F, NMMP-KU 0013, a right mandibular fragment with P_4-M_3, in buccal view. Scale bar = 2 cm.

degree of concavity of the lower border of the mandibular corpus among the Pondaung *Indomeryx* (Figure 8).

(3) Colbert (1938) is also correct in his evaluation of the development of the cingulum in *I. arenae* (and also in *I. pilgrimi* and *I. minus*): its difference results from individual variation (Figure 7).

(4) The presence or absence of molar paraconid of *Indomeryx* mentioned by Métais *et al.* (2000) is also considered to depend on individual variation. Most of the *Indomeryx* materials lack a molar paraconid, however, in NMMP-KU 0015 (the type of *I. pilgrimi*), a very tiny molar paraconid can be observed on M_1, though not on M_2. On its M_3, the mesiobuccal part of the tip of the metaconid is broken, so that it is unclear whether or not there is a paraconid. In some other materials as well, such as M_3 of NMMP-KU 0013 and of AMNH 20023, a very tiny paraconid can be observed.

(5) The presence or absence of *Dorcatherium*-fold and metastylid of *Indomeryx* mentioned by Métais *et al.* (2000) is also considered to depend on individual variation. Most of the *Indomeryx* materials seem to lack both distinct molar *Dorcatherium*-fold and metastylid, however, in some materials, such as M_{1-2} of NMMP-KU 0015 and M_2 of NMMP-KU 0013, there are structures which might be treated as incipient *Dorcatherium*-fold and metastylid. However, the structure is so indistinct that it is unclear whether it is a true *Dorcatherium*-fold or not.

On the other hand, the dental sizes of lower molars of the Pondaung *Indomeryx* materials are also variable (Figure 9). However, the M_1 size can be readily divided into two groups, large (*I. cotteri* and *I. pilgrimi*) and small (*I. arenae* and *I. minus*). Because M_1 has been considered to express

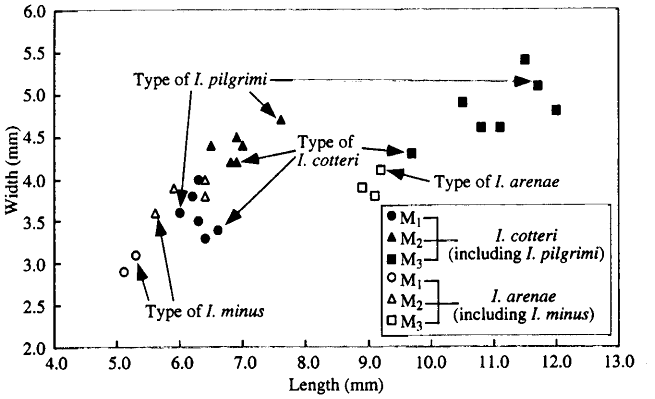


Figure 9. Size distribution of the lower molars of the Pondaung *Indomeryx*.

less size variation and to correlate very closely to the body size of mammals compared to other tooth classes (Tsubamoto *et al.*, 2002a), the dental size distribution (Figure 9) suggests that the Pondaung *Indomeryx* can be grouped into two size categories.

In conclusion, there is no distinct dental morphology by which to distinguish the species of the Pondaung *Indomeryx*. The M_1 sizes indicate that they can be grouped into two (large and small) categories. Although Colbert (1938) and Tsubamoto *et al.* (2000a) suggested that the two groups probably indicate the sexual dimorphism of a single species, it is difficult to determine this issue without knowing the morphological and size variation of the canines, so that we tentatively consider that the two categories are indicative of two species in this paper. The larger species is referred to as *I. cotteri* Pilgrim, 1928 (including *I. pilgrimi* Métais *et al.*, 2000), while the smaller one is referred to as *I. arenae* Pilgrim, 1928 (including *I. minus* Métais *et al.*, 2000).

Phyletic position.—The classification and phyletic relationships of primitive ruminants are complicated (e.g., Scott and Janis, 1993), so that the familial position of *Indomeryx* has been, and remains, controversial. Pilgrim (1928) erected the genus *Indomeryx* and tentatively assigned it to the Tragulidae. Colbert (1938) and Qiu (1978), on the other hand, assigned it to the Hypertragulidae, while Sudre (1984) and Holroyd and Ciochon (1995) treated it as a representative of the Gelocidae, which is now considered to be a polyphyletic taxon (Janis, 1987; Janis and Scott, 1987, 1988). McKenna and Bell (1997) assigned *Indomeryx* to the Leptomerycidae. Guo *et al.* (1999) described *Indomeryx* from the upper Eocene Naduo Formation of China and classified *Indomeryx* into a new family Prodremotheriidae (Pecora; Ruminantia) together with *Prodremotherium*, *Notomeryx*, and *Gobiomeryx*. Métais *et al.* (2000) assigned *Indomeryx* to an undetermined family within the Pecora.

Among ruminants, *Indomeryx* is very primitive in having bunoselenodont dentition, brachyodont teeth, relatively conical cusps, relatively simple P_4, and very tiny molar paraconid in some samples. The existence of *Zhailimeryx* -fold distinguishes *Indomeryx* from all other ruminants except for primitive lophiomerycids, such as *Zhailimeryx* and *Krabimeryx*, and primitive tragulids, such as *Archaeotragulus*, *Dorcatherium*, *Dorcabune*, and *Siamotragulus* (Guo *et al.*, 2000; Tsubamoto *et al.*, 2000a; Métais *et al.*, 2000, 2001). *Indomeryx* is phyletically close neither to *Zhailimeryx* from Eocene China nor to *Krabimeryx* from Eocene Thailand and is not assigned to the Lophiomerycidae because it lacks a lingually opened and large trigonid basin, one of the identifying characteristics of the Lophiomerycidae. Also, it is distinguished from the tragulids in having P_4 metaconid and in lacking distinct *Dorcatherium*-fold. It is further distinguished from the basal tragulid from Eocene Thailand, *Archaeotragulus*, in having molar trigonid as wide as talonid and in lacking anteriorly projecting and stronger paracristid, and in lacking lingually opened and large molar trigonid basin (Métais *et al.*, 2001). Therefore, *Indomeryx* is not referable to the Tragulidae. According to Métais *et al.* (2000, 2001), *Zhailimeryx*-fold is also a symplesiomorphic characteristic among Asian primitive ruminants such as lophiomerycids and tragulids. The only derived feature of *Indomeryx* among ruminants is a lingually closed hypoconulid loop and relatively large hypoconulid on M_3, but this characteristic is seen in many primitive ruminant taxa.

Although *Indomeryx* shows a certain resemblance to primitive ruminants, such as *Gelocus*, *Archaeomeryx*, *Gobiomeryx*, *Prodremotherium*, and *Notomeryx*, in both size and dental morphology (Pilgrim, 1928; Colbert, 1938; Guo *et al.*, 1999), it nevertheless remains distinct from these ruminants. *Indomeryx* is distinct from *Prodremotherium*, *Notomeryx*, and *Gobiomeryx*, in lacking enlarged and more distally located P_4 metaconid, transverse crest on $P_{3\text{-}4}$ talonid, depressed distal face of molar entoconid (double-ridged postentocristid in *Notomeryx*), sharp molar postentocristid, and distinct molar metastylid and ectostylid. Because of having these characteristics, these latter three genera can be grouped as the Prodremotheriidae (Guo *et al.*, 1999). According to Guo *et al.* (1999), the Chinese *Indomeryx* (*Indomeryx cotteri*, the same species as one of the Pondaung *Indomeryx*) has some of those characteristics of the Prodremotheriidae and is referable to this family. However, as mentioned above, the Pondaung *Indomeryx* lacks those distinct prodremotheriid characteristics and is so primitive that it cannot be referred to the family with confidence. On the other hand, *Indomeryx* is distinguished from *Archaeomeryx* in having a lingually closed hypoconulid loop on M_3, and therefore the former is more derived than the latter on that point. However, *Indomeryx* is more primitive than *Archaeomeryx* and also *Gelocus*, *Notomeryx*, *Prodremotherium*, and pecorans in lacking a transverse crest on P_{3-4} talonid and enlarged and more distally located P_4 metaconid. The dental morphology of *Indomeryx* shows many primitive characteristics among ruminants and lacks any critical derived features referable to any ruminant family.

Indomeryx cotteri Pilgrim, 1928

Figures 6A-C, A'-C', 7A-F, A'-F', 8A-D

Indomeryx cotteri Pilgrim, 1928, p. 33-35, pl. 4, figs. 7, 7a, 9, 9a; Colbert, 1938, p. 393-397, figs. 55-56; Tsubamoto *et al.*, 2000a (in part), p. 49-53, 82-85, pls. 11A-C, G-I, 12G-I, 13, 14B-D.

Undescribed ruminant, Matthew, 1929, p. 516, fig. 40.

Indomeryx pilgrimi Métais *et al.*, 2000, p. 808-810, fig. 2A-C.

Holotype.—GSI B768, a right mandibular corpus with P_4-M_3.

Type locality.—Seven furlongs E.S.E. of Sinzwe Village (in Bahin area), Myaing Township, central Myanmar (Pilgrim, 1928; Tsubamoto *et al.*, 2000a, figs. 4-5).

Referred material.—AMNH 20023, 32521; NMMP-KU 0008 (Mgg 2), 0009 (Mgg 14), 0010, 0015 (Bhn 911), 0016, 0017 (Mgg 5), 0018, 0019, 0020, 0021, 0022, 0024, 0201, 0266, 0289, 0290; LK 6. (Colbert, 1938; Tsubamoto *et al.*, 2000a; Métais *et al.*, 2000)

New material.—NMMP-KU 0716, a left mandibular fragment with M_{1-2}, upper and lower molar fragments, and bone fragments; NMMP-KU 0720, right and left maxillary fragments with right and left M^{1-2}.

Locality of new material.—NMMP-KU 0716 is from Kd2 locality (21°49′24.0″N, 94°35′25.2″E), Kyudaw (near Thidon Village in Bahin area), Myaing Township, central Myanmar; NMMP-KU 0720 is from PA1 locality (21°46′24.0″N; 94°36′30.8″E) near Sinzwe Village (in Bahin area), Myaing Township, central Myanmar (Tsubamoto *et al.*, 2000a, figs. 4-5).

Revised diagnosis.—Body size larger than *I. arenae* based on the size of M_1.

Discussion.—Qiu (1978, p. 9, line 13 from the bottom) mentioned that the lower dental materials of *Indomeryx cotteri* described and figured by Colbert (1938, p. 394, fig. 55), AMNH 20023 and 32521, belong to *Notomeryx besensis* (Ruminantia), which was originally described from the upper Eocene Naduo Formation of south China. However, the sizes and dental morphologies of AMNH 20023 and 32521 are identical to that of *I. cotteri*, and definitively differ from those of *Notomeryx* from China (Tsubamoto *et al.*, 2000a). On the other hand, AMNH 32521 was described as a left mandibular fragment with M_{1-2} of *Indomeryx cotteri* by Colbert (1938). However, the posterior part of its posterior molar is broken, so that it is difficult to determine whether the posterior molar is M_2 or M_3 based only on its morphology. On the basis of size the two molars preserved in AMNH 32521 are M_2 and M_3.

Cf. ***Indomeryx cotteri*** Pilgrim, 1928

Figure 6E, E'

Cf. *Indomeryx cotteri* Pilgrim, 1928. Tsubamoto *et al.*, 2000a, p. 53-54, 85, pl. 14E.

Material.—NMMP-KU 0025 (Tsubamoto *et al.*, 2000a).

Discussion.—As described by Tsubamoto *et al.* (2000a), the size and morphology of NMMP-KU 0025 are nearly identical to those of M^2 of *Indomeryx cotteri*, except that: paracone and metacone are more conical; overall shape in occlusal view is less diagonal and somewhat wider; and a distinct buccal cingulum buccal to metacone exists. Also, in this specimen, ectoloph is less developed, and protocone and metaconule are more distally located (just lingually to protocone and metacone, respectively) compared to *Indomeryx cotteri*.

Indomeryx arenae Pilgrim, 1928

Figures 6D, D', 7G, G', H, H', 8E-F

Indomeryx arenae Pilgrim, 1928, p. 35-36, pl. 4, figs. 10, 10a; Colbert, 1938, p. 393-397, fig. 55-56.

Indomeryx cotteri Pilgrim, 1928 (in part). Tsubamoto *et al.*, 2000a (in part), p. 49-53, 82-83, 85, pls. 11D-F, J-L, 12A-F, 14A.

Indomeryx minus Métais *et al.*, 2000, p. 810, fig. 2D-F.

Holotype.—GSI B769, a left mandibular fragment with talonid of M_3.

Type locality.—0.25 mile west of Pangan Village (probably PGN2), Myaing Township, central Myanmar (Pilgrim, 1928; Tsubamoto *et al.*, 2000a, fig. 6).

Referred material.—NMMP-KU 0007 (Bhn 1115), NMMP-KU 0011 (Bhn 3), 0012 (Bhn 4), 0013, 0014 (Bhn 6), 0222; LK 3. (Tsubamoto *et al.*, 2000a; Métais *et al.*, 2000)

New material.—NMMP-KU 0669, a left mandibular fragment with M_{2-3}.

Locality of new material.—Bh1 (Yarshe Kyitchaung) locality, near Bahin Village, Myaing Township, central Myanmar (Tsubamoto *et al.*, 2000a, fig. 5).

Revised diagnosis.—Body size smaller than *I. cotteri* based on the size of M_1.

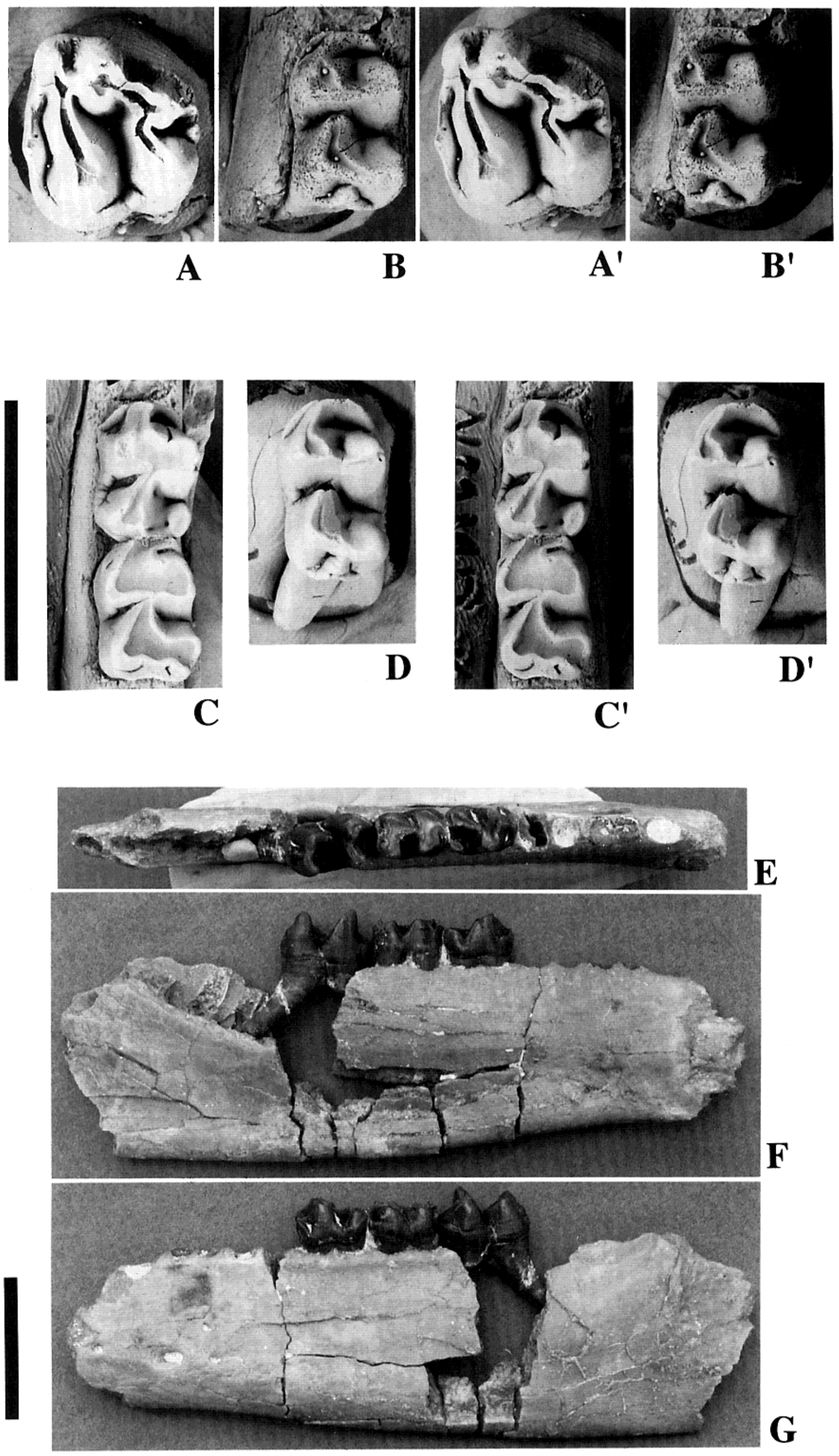


Figure 10. *Indolophus guptai* Pilgrim. **A, A'**. NMMP-KU 0265, a left M^3, in occlusal view (stereo pair). **B, B'**. NMMP-KU 0040, a left mandibular fragment with M$_2$, in occlusal view (stereo pair). **C–G, C'–D'**. NMMP-KU 0623, a left mandible with P$_4$-M$_2$: C, C', P$_4$M$_1$, in occlusal view (stereo pair); D, D', M$_2$, in occlusal view (stereo pair); E, occlusal view; F, lingual view; G, buccal view. Scale bars = 2 cm (upper scale corresponds to A–D, A'–D', lower scale corresponds to E–G).

Order Perissodactyla Owen, 1848
Suborder Tapiromorpha Haeckel, 1866
sensu Froehlich, 1999
Family Indolophidae Schoch, 1984

Genus **Indolophus** Pilgrim, 1925

Type and only known species. — *Indolophus guptai* Pilgrim, 1925.

Revised diagnosis. — Medium-sized and primitive tapiromorph. P^{2-4} with triangular aspect in occlusal view, large and subconical paracone and metacone, large and centrally placed protocone with high and acute preprotocrista, and very small parastyle, and lacking postprotocrista, metaconule, and hypocone: P^2 longer than wide with conical protocone and an incipient paraconular bulge; P^{3-4} wider than long with large, buccolingually flattened, and posteriorly elongated protocone, and lacking paraconule. Upper molars with conical paracone and metacone, somewhat lophodont protocone and hypocone, small parastyle, straight centrocrista, and low and weakly developed ectoloph, lacking paraconule and metaconule. M^3 posterior part reduced buccolingually with somewhat reduced metacone. Four lower premolars with a diastema between C_1 and P_1. P_1 one-rooted. P_4 nearly as large as M_1. Lower molars with small hypoconulid on M_{1-2}, distinct hypolophid, and distinct cristid obliqua originating below the notch between protoconid and metaconid, lacking metastylid. Differs from other tapiromorphs in having smaller parastyle on the upper dentition and very large and centrally placed P^{2-4} protocone with a strong and sharp preprotocrista and without postprotocrista. Further differs from ceratomorphs and *Kalakotia* in having less lophodont dentition, more conical cusps, and low and weak molar ectoloph. Differs from primitive hippomorphs (such as *Hyracotherium* and *Propalaeotherium*) and further differs from basal tapiromorphs (*Orientolophus*, *Cymbalophus*, and *Systemodon*) in having more developed molar protolophid and hypolophid, and smaller hypoconulid on M_{1-2}, and in lacking lingual and buccal cingulum and molar paraconule, metaconule, and metastylid.

Indolophus guptai Pilgrim, 1925

Figure 10

Indolophus guptai Pilgrim, 1925, p. 22–25, pl. 2, figs. 8a–8d; Matthew, 1929, p. 515, fig. 39; Colbert, 1938, p. 346–348, fig. 39; Radinsky, 1965, p. 235–236, fig. 22, pl. 4, fig. 6; Tsubamoto *et al.*, 2000a, p. 56–59, 92, pl. 21.

Holotype.—GSI C347, a left maxilla with P^2-$^4M^1$.

Type locality.—1.25 miles north of Konywa Village (in Mogaung area), Palé Township, central Myanmar (Pilgrim, 1925; Tsubamoto *et al.*, 2000a, fig. 4).

Referred material. — NMMP-KU 0040, 0041, 0265 (Tsubamoto *et al.*, 2000a).

New material.—NMMP-KU 0623, a left mandible with P_4-M_2.

Locality of new material.—Pk2 locality, near Paukkaung Village, Myaing Township, central Myanmar (Tsubamoto *et al.*, 2000a, fig. 5).

Diagnosis.—As for genus.

Description of new material.—NMMP-KU 0623 is a subadult specimen, of which M_3 (this tooth was not collected) was probably unerupted. Mandible is slightly more slender than that of NMMP-KU 0040. Five alveoli are preserved anterior to P_4, indicating one rooted P_1 and two rooted P_{2-3}. There is a diastema between C_1 and P_1. This diastema seems to be relatively long, judging from the broken anterior margin of the mandible and broken alveolus for C_1. P_1 alveolus is oval in occlusal view, elongating distolingually. P_2 alveoli are conical in occlusal view, suggesting P_2 is premolariform. Anterior P_3 alveolus is conical, and posterior one is somewhat widened buccolingually, suggesting that P_3 talonid is somewhat molariform. Judging from preserved anterior part of mandible, posterior margin of mandibular symphysis seems to be anterior to P_1 alveolus. There are four mental foramina: the largest one is located below anterior P_2 alveolus; two are located below the posterior P_2 alveolus; and remaining one is located near anteriormost part of the preserved mandible.

P_4 is nearly as large as M_1 and is molariform but is distinct from M_1 in having mesiodistally oriented (more buccally oriented) paracristid and lower entoconid, and in lacking hypoconulid and hypolophid.

M_{1-2} shows a typical primitive tapiromorph structure with some lophodonty and without paraconid and metastylid. Metaconid and entoconid are distal to protoconid and hypoconid, respectively. Small hypoconulid exists on postcingulid and links neither to hypoconid nor to entoconid. Paracristid extends down mesiolingually from protoconid. Protocristid (protolophid) makes a notch between protoconid and metaconid. Trigonid basin is open lingually. Posterior trigonid wall is nearly perpendicular to the mandibular extension in occlusal view, and vertically diagonal in lateral view. Talonid is as wide as trigonid. Cristid obliqua originates below the notch between protoconid and metaconid. Hypolophid is not notched and extends slightly distolingually. Talonid basin is open lingually. Lingual and buccal cingulids are absent. Precingulid extends from mesial base of trigonid, disappearing at mesiobuccal base of protoconid. M_2 is larger than M_1.

Identification of NMMP-KU materials.—The morphology of M^3 specimen, NMMP-KU 0265, is almost identical to that of M^1 of the type of *Indolophus guptai*: conical paracone and metacone, straight and low centrocrista, lophodont protocone and hypocone, relatively small parastyle, no paraconule, and no metaconule. This M^3 material is slightly larger in size than M^1 of *Indolophus guptai* and this is congruent with the primitive perissodactyl condition. The morphology of the lower dental materials, NMMP-KU 0040, 0041, and 0623, is referable to primitive tapiromorphs, such as *Isectolophus* and *Orientolophus*, and their size is congruent with the upper dentition of *Indolophus guptai*. The cusp morphology and lophid configuration of these lower dental materials provide a good match to the upper dentitions of *Indolophus guptai*: the cusps display a slightly conical aspect and the directions of protolophid and hypolophid are congruent with those of protoloph and metaloph, respectively. Because of these high correspondences, we have identified these NMMP-KU materials as belonging to *Indolophus guptai*.

Phyletic position.—The phyletic position of *Indolophus* has been uncertain because of the unique morphology of its upper dentition (Pilgrim, 1925; Matthew, 1929; Colbert, 1938; Radinsky, 1963, 1965, 1969; Schoch, 1984, 1989). Pilgrim (1925) assigned *Indolophus* into the Tapiridae, while Matthew (1929) and Colbert (1938) assigned it to the Isectolophidae (= Parisectolophidae). Both of these researchers believed that *Indolophus* was closely related to the North American isectolophids, such as *Homogalax* and *Isectolophus*. Radinsky (1963, 1965, 1969) reported that the differences between *Indolophus* and the isectolophids were great enough to remove *Indolophus* from the Isectolophidae. He also mentioned that *Indolophus* resembled cf. *Breviodon acares* (AMNH 81751) (Lophialetidae) from the middle Eocene of China, although the phyletic relationship between them was uncertain (Radinsky, 1965). In any case, all these researchers considered *Indolophus* to be a primitive "tapiroid" (= primitive tapiromorph). On the other hand, Schoch (1984, 1989) considered *Indolophus* to be not a tapiromorph but a hippomorph, and Schoch (1984) erected a new family Indolophidae for *Indolophus*.

Indolophus is a tapiromorph (*sensu* Hooker, 1984, 1989, and Froehlich, 1999), not a hippomorph. Schoch (1984, 1989) suggested that the M^1 metaloph of *Indolophus* is very low at the ectoloph and this characteristic is referable to the hippomorphs. However, this characteristic is also seen in the type specimen of the basal tapiromorph, *Orientolophus* (Ting, 1993, fig. 4A). Therefore, Schoch's (1984, p. 16, 1989, p. 312–313) suggestion of a hippomorph affinity for *Indolophus* is invalid. *Indolophus* differs from primitive hippomorphs, such as *Hyracotherium* and *Propalaeotherium*, in having more buccally oriented P_4 paracristid and more developed molar lophs and lophids, and in lacking lingual and buccal cingulum and molar paraconule, metaconule, and metastylid. Judging from these characteristics (Ting, 1993), *Indolophus* is assigned into the Tapiromorpha.

Among tapiromorphs, *Indolophus* displays relatively primitive characteristics in having rather conical cusps, straight and low centrocrista, small parastyle, and distinct and diagonally oriented cristid obliqua. Therefore, *Indolophus* lacks any derived features of primitive ceratomorphs, such as helaletids, lophialetids, and deperetellids, and is not assigned to the Ceratomorpha (*sensu* Froehlich, 1999). However, *Indolophus* is more derived than the basal tapiromorphs (*Orientolophus*, *Cymbalophus*, and *Systemodon*) (Ting, 1993; Froehlich, 1999; Maas *et al.*, 2001) in having larger size, more developed molar protolophid and hypolophid, and smaller hypoconulid on M_{1-2}, and in lacking lingual and buccal cingulum and molar paraconule, metaconule, and metastylid.

Indolophus is distinct from other tapiromorphs in having smaller parastyle on the upper dentition and a unique P^{2-4} morphology: paracone and metacone are very large and conical; protocone is centrally placed with distinct and strong preprotocrista lacking postprotocrista; protocone is relatively large and conical on P^2 and is very large, buccolingually flattened, and posteriorly elongated on P^{3-4} (Radinsky, 1965). These characteristics indicate that *Indolophus* is not assignable into the North American isectolophids (Radinsky, 1963, 1965; Schoch, 1989). Among primitive tapiromorphs, however, the upper premolar dentition of *Orientolophus* from China is not known (Ting, 1993), so that the possibility of a close phyletic relationship between *Indolophus* and *Orientolophus* still remains.

The molar morphology of *Indolophus* shows a mosaic structure with reference to the primitive tapiromorphs. In lacking molar paraconule and metaconule, it is more derived than that of some isectolophids [*Cardiolophus*, *Homogalax*, *Sastriolophus*, *Karagalax*, and unnamed isectolophid from the Wutu basin of China (Tong and Wang, 1998)], a questionable very primitive lophialetid from China (*Ampholophus* Wang and Tong, 1996), and basal tapiromorphs. In lacking metastylid, it is also more derived than *Cardiolophus*, *Homogalax*, and basal tapiromorphs. On the other hand, in having less sharp and low molar ectoloph with no or only slightly developed postmetacrista, it is more primitive than that of some isectolophids (*Isectolophus*, *Sastriolophus*, and *Karagalax*), *Kalakotia* (including *Aulaxolophus*) from Indo-Pakistan (Ranga Rao, 1972), and ceratomorphs. Such mosaic characteristics make it difficult to determine the phyletic position of *Indolophus* among tapiromorphs.

Hooker (1989) performed a cladistic analysis of primitive tapiromorphs and indicated that the isectolophids are placed at the base of the tapiromorph lineage, more basally so than the ancylopods (chalicotherioids and lophiodonts). Froehlich (1999) also performed a cladistic analysis of the

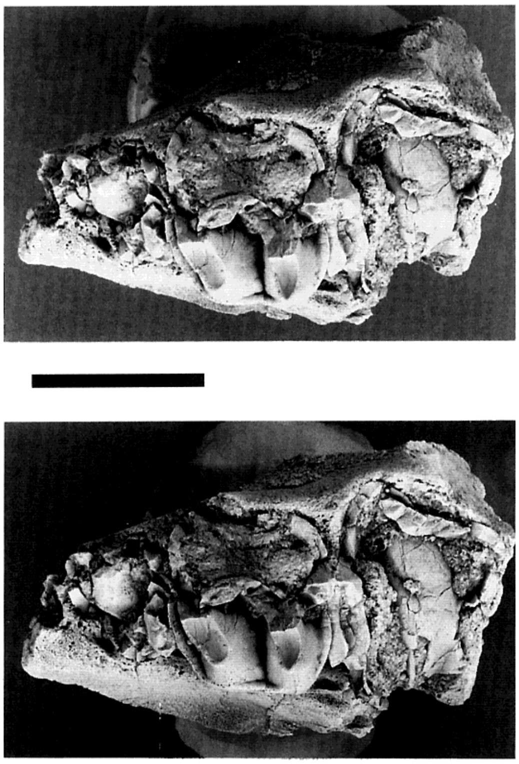


Figure 11. Ceratomorpha fam., gen. et sp. indet., NMMP-KU 0058, a left maxillary fragment with a tooth which is assumed here as P^3, in occlusal view (stereo pair). Scale bar = 2 cm.

primitive tapiromorphs and further indicated that isectolophids are paraphyletic. However, Hooker (1989) did not include some important primitive Asian Eocene tapiromorphs such as *Sastrilophus* from Indo-Pakistan (Sahni and Khare, 1971), *Homogalax wutuensis* from China (Chow and Li, 1965), and *Indolophus* from Myanmar (and also the later-described taxa including *Orientolophus* Ting, 1993 from China); while Froehlich (1999) also did not include *Sastrilophus*, *Homogalax wutuensis*, *Indolophus*, and other important Asian Eocene tapiromorphs such as *Kalakotia* from Indo-Pakistan, *Ampholophus* from China, lophialetids, and deperetellids [and also the later-described taxa such as *Karagalax* Maas *et al.*, 2001, unnamed isectolophid from China (Tong and Wang, 1998), and unnamed primitive tapiromorph from the Akasaki Formation of Japan (Miyata and Tomida, 1998)] (Maas *et al.*, 2001). We could determine the phylogenetic relationship of *Indolophus* among the primitive tapiromorphs by undertaking a cladistic analysis combining all the known anatomical characteristics of the above-mentioned primitive tapiromorphs, but the lack of materials representing important characteristics for some taxa, such as M_3 of *Indolophus* and premolar dentition of *Orientolophus*, might obstruct a determination of the phyletic position of *Indolophus*.

Infraorder Ceratomorpha Wood, 1937
sensu Froehlich, 1999

Ceratomorpha fam., gen. et sp. indet.

Figure 11

Material.—NMMP-KU 0058, a left maxillary fragment with a lingual half of a tooth (P^3?).

Locality.—Pk2 locality, near Paukkaung Village (in Bahin area), Myaing Township, central Myanmar (Tsubamoto *et al.*, 2000a, fig. 5).

Description.—Only a lingual part of a tooth is preserved in this left maxillary fragment. We will assume this preserved tooth to be P^3 here for the purpose of description. Judging from P^3 and preserved alveoli for other broken teeth, there were originally at least two teeth anterior to P^3 without diastema and there were also at least two teeth posterior to it: P^2 is narrower and shorter than P^3, and P^1 is much narrower than P^2; and P^4 is wider and longer than P^3. Infraorbital foramen is located just above the anterior part of P^3.

P^3 is wider than long and shows bilophodont structure with complete protoloph and metaloph, which is reminiscent of ceratomorph molars. Both lophs are separated lingually by a groove, and not perpendicular but somewhat diagonal to the tooth row. Protoloph is slightly more diagonal to the tooth row than metaloph at the lingual part. Mesial cingulum exists and continuous to lingual cingulum, disappearing at mesiolingual base of metaloph. Distal cingulum originates at distolingual base of metaloph. Buccal structure cannot be described because this part is broken.

Discussion.—Although the present material is poorly preserved, the dental morphology and size of the preserved tooth is not identical to any other ceratomorph species described from the Pondaung Formation to date. This material indicate an occurrence of an additional ceratomorph species in the Pondaung fauna.

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Appendix. Dental measurements (in mm) of the NMMP-KU specimens studied in this paper. Abbreviations: L, anteroposterior length; W, buccolingual width; TRW, trigonid with; TAW, talonid width; *, estimate.

Taxa	NMMP-KU	dP^{3}	dP^{4}	dP^{4}	P^{3}	P^{4}	P^{4}	M^{1}	M^{1}	M^{2}	M^{2}	M^{3}	M^{3}
	number	W	L	W	L	L	W	L	W	L	W	L	W
Upper dentition													
Hsanotherium parvum	0031									6.3	6.5	7.4	7.8
Hsanotherium parvum	0035							5.4	5.7	6.3	6.7	6.9	7.9
Asiohomacodon myanmarensis	0026											7.8	9.5
Asiohomacodon myanmarensis	0713					6.3	7.2	7.1	8.0	8.1	9.1	8.0	9.4
Indomeryx cotteri	0008							6.0	6.2	6.6	7.6	7.5	8.5
Indomeryx cotteri	0009									6.7	7.6	7.7	8.5
Indomeryx cotteri	0010	4.1	5.4	4.8				6.1	6.2				
Indomeryx cotteri	0720 (right)							6.4	6.4	7.4	7.6		
Indomeryx cotteri	0720 (left)							6.4	6.4	7.5	7.7		
cf. *Indomeryx cotteri*	0025									6.6	7.9		
Indomeryx arenae	0007							5.4	5.7	5.8	6.6	6.4	7.3
Indolophus guptai	0265											12.8	14.5
Ceratomorpha indet.	0058				20.6*								

		dP$_{4}$	dP$_{4}$	dP$_{4}$	P$_{3}$	P$_{3}$	P$_{4}$	P$_{4}$	P$_{4}$	P$_{4}$	M$_{1}$	M$_{1}$	M$_{1}$	M$_{2}$	M$_{2}$	M$_{2}$	M$_{3}$	M$_{3}$	M$_{3}$
		L	TRW	TAW	L	W	L	W	TRW	TAW	L	TRW	TAW	L	TRW	TAW	L	TRW	TAW
Lower dentition																			
Hsanotherium parvum	0032																9.3	4.8	4.5
Hsanotherium parvum	0033													6.8	3.6	3.6			
Hsanotherium parvum	0034																		4.1
Hsanotherium parvum	0036						5.9	2.9			5.4	2.8	3.1	6.0	3.7	3.6	7.8	4.5	4.2
Hsanotherium parvum	0037	7.5	2.2	2.3							5.4*	2.9		7.0	4.0	4.1			
Asiohomacodon myanmarensis	0027													7.7	5.2	5.4		6.0	5.6
Asiohomacodon myanmarensis	0028																10.7	5.0	5.0
Asiohomacodon myanmarensis	0029										7.0	4.0	4.3	7.4	4.9	4.9			
Asiohomacodon myanmarensis	0068																	5.8	5.5
Asiohomacodon myanmarensis	0264															5.7		6.0	5.5
Asiohomacodon myanmarensis	0714																		5.0
cf. *Asiohomacodon myanmarensis*	0030										6.8	4.2	4.3						
Indomeryx cotteri	0015										6.0	3.4	3.6	7.6	4.3	4.7	11.7	5.0	5.1
Indomeryx cotteri	0016												3.3	7.0	4.0	4.4	10.8	4.5	4.6
Indomeryx cotteri	0017																12.0	4.8	4.8
Indomeryx cotteri	0018															4.3	10.8	4.6	4.6
Indomeryx cotteri	0019				6.4	2.2	6.9	2.7					3.3	6.8	4.1	4.2	11.1	4.7	4.6
Indomeryx cotteri	0021						6.0	2.7											
Indomeryx cotteri	0022						6.0	2.7											
Indomeryx cotteri	0024										6.4*	3.2	3.3						
Indomeryx cotteri	0201										6.3	3.0	3.5	6.9	3.9	4.5		4.5	
Indomeryx cotteri	0266										6.3	3.5	4.0		4.2				
Indomeryx cotteri	0268																		4.6
Indomeryx cotteri	0289																10.5	4.8	4.9
Indomeryx cotteri	0290													6.5	3.5				4.3
Indomeryx cotteri	0716										6.2	3.4	3.8		4.2				
Indomeryx arenae	0011						5.0	2.2			5.3	2.8	3.1	5.6*	3.3	3.6		3.6	3.9
Indomeryx arenae	0012																8.9	4.0	3.9
Indomeryx arenae	0013						5.4	2.7			5.1	2.6	2.9	5.9	3.5	3.9		3.9	
Indomeryx arenae	0014																8.9	3.7	3.9
Indomeryx arenae	0222													6.4	3.8	3.8	9.1	4.0	3.8
Indomeryx arenae	0669													6.4	3.5	4.0		4.2	4.4
Indolophus guptai	0040													13.6	7.9	7.7			
Indolophus guptai	0041										10.6	7.1	7.8						
Indolophus guptai	0623						10.0		6.5	7.1	10.2	7.0	6.9	13.1	7.7	7.1			