

Artiodactyls from the Pondaung Formation (Myanmar): new data and reevaluation of the South Asian Faunal Province during the Middle Eocene

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Abstract Although Asia is thought to have played a critical role in the radiation of artiodactyls, the fossil record of stem selenodonts (“dichobunoids”) remains dramatically poor in tropical Asian regions. In this study, we report a new dichobunid genus and species *Cadutherium kyaukmagyii* and a new basal ruminant genus and species *Irrawadymeryx pondaungi*, from the late Middle Eocene Pondaung Formation, Central Myanmar. Although the scarcity of the present material prevents any attempts to investigate the phylogenetic relationships of *Cadutherium* with contemporaneous forms from other Holarctic landmasses, this new form shed new light on the diversity of these small rabbit-like ungulates during a key period of their evolutionary history. Reexamination of the small-bodied artiodactyls from Pondaung leads us to propose new identifications of certain published specimens and, in turn, to investigate the temporal and geographic distribution of taxa recognized in the Pondaung Formation. Although fragmentary, these potential new taxa reveal an unsuspected diversity of small forms among artiodactyls of Pondaung. This addition to the Eocene record of dichobunoids and early ruminants provides further insight

in the diversity of dental patterns among small artiodactyls from the Pondaung Formation and attests to the antiquity of these groups in Southeast Asia.

Keywords Artiodactyla · Dichobunoid · Eocene · Pondaung Formation · Myanmar

Introduction

Artiodactyls are among the most common small and medium-sized mammals in the Middle and Late Eocene of Europe and North America. However, their fossil record in southern Asia for the same period of time remains extremely limited. The Middle Eocene Pondaung Formation in central Myanmar (Fig. 1) is one of the few Eocene formations of south Asia (including the Indian subcontinent and Southeast Asia) yielding fossil mammals. The mammalian fauna of the Pondaung Formation has been described in a series of papers including Pilgrim and Cotter (1916), Pilgrim (1928), and Colbert (1938) who provided an extensive review of the fauna. In the past decade, the Pondaung fauna has been intensively reinvestigated, and many new fossil mammals were recovered and studied (Tsubamoto et al. 2006). Artiodactyl remains are the most abundant in the Pondaung Formation, and most belong to anthracotheriids, which were primarily studied by Pilgrim (1928). Smaller and non-anthracothere artiodactyls remain poorly documented, although a helohyid (Holroyd and Ciochon 1995), early ruminants (Colbert 1938; Métais 2006), and a possible homacodontid (Tsubamoto et al. 2003) have also been reported in the Pondaung Formation.

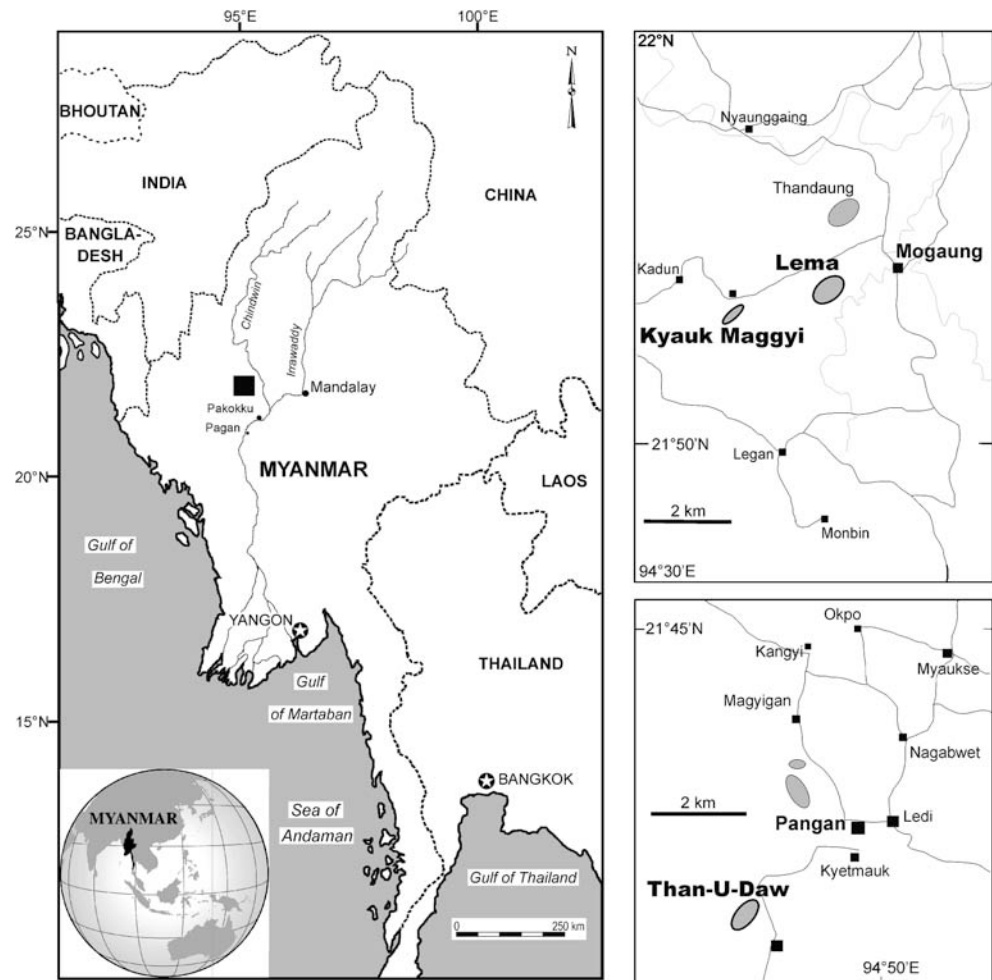
The Pondaung Formation is sandwiched between the overlying Upper Eocene (Priabonian) shallow marine Yaw Formation and the deep marine clays of the underlying

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Fig. 1 Location map showing the area where the Middle Eocene Pondaung Formation is exposed, on the western edge of the Chindwin–Irrawaddy Basin. The enlargement of the Moggaung and Pangan areas indicate the location of the fossiliferous localities (*gray bubbles* on the figure) that have yielded the material described in this work



Lutetian Tabyin Formation (Stamp 1922; Bender 1983). The 2,000-m thick Pondaung Formation consists of successions of mudstone, sandstone, and conglomerates subdivided into two distinct lithologic units (Aung 1999, 2003). The lower member consists of unfossiliferous sandstones and claystones interbedded with pebble to cobble conglomerates deposited in high-energy fluvial-dominated deltaic conditions. The Upper Member is approximately 500 m thick and primarily consists of fine- to medium-grained sandstones and variegated clays. The Pondaung Formation is widely exposed in the western part of the central Irrawaddy lowland, where it forms badlands-like relief partly covered by vegetation. The fossil localities are distributed at the west side of the Chindwin River, northwest of Myaing. Fossil vertebrates generally occur within the lowest 150 m of the Upper Member, and they are found in muddy and sandy fluvial channels corresponding to a mosaic of fluvio-deltaic environments (Soe et al. 2002). The age of the Pondaung Formation has been much debated and was originally considered to be Late Eocene (Colbert 1938). Holroyd and Ciochon (1994) argued that most of the Pondaung Formation is probably correlative to the Sharamurian Asian Land Mammal Age (ALMA) and Duchesnean North American Land Mammal Age (NALMA) based

on the mammal assemblage. Magnetostratigraphic studies (Benammi et al. 2002) and a fission-track age of 37.2 Ma \pm 1.3 Ma (Tsubamoto et al. 2002) further constrain the age of the Pondaung Formation.

In this study, we report a new dichobunoid artiodactyl and basal ruminants based on fossils collected near the village of Moggaung and a new basal ruminant based on a lower jaw collected in the locality Than-U-Daw (Fig. 1). Although still poorly documented, these taxa provide important data on the diversity of small artiodactyls in southern Asia during the late Middle Eocene. Their affinities are briefly discussed in the context of the Pondaung fauna as a whole, and two enigmatic forms recently reported from the same formation (Tsubamoto et al. 2005) are also discussed. This reexamination of the small dichobunoid artiodactyls from Pondaung has implications for southern Asian paleogeography and faunal evolution during the Early–Middle Eocene.

Systematic paleontology

Order Cetartiodactyla Montgelard et al. 1997

Suborder Selenodontia Gentry and Hooker 1988

Family Dichobunidae Turner 1849

Genus *Cadutherium* gen. nov.

Type and only known species: *Cadutherium kyaukmagyii* sp. nov.

Diagnosis—Small-sized ungulate, approximately equivalent in size to the extant ruminant *Tragulus napu*. Bunodont and low-crowned lower molars with the labial cuspids slightly crescentiform and the lingual cuspids substantially inflated. Differs from *Indomeryx* in being more bunodont, in lacking both the strong shelf-like posterior cingulid and the *Zhailimeryx* fold. Differs from *Asiohomacodon* in the lesser development of crests, less crescentic labial cuspids, its lingual cuspids distinctly inflated and less transversely compressed. Differs from the helohyid *Gobiohyus* in its smaller size, its lesser development of cingulids, and its m3 hypo-conulid transversely compressed. *Cadutherium* differs from other dichobunids in lacking a paraconid and in having more crescentic external cuspids than in any European dichobunid.

Etymology—from the Latin *Cadus*, in reference to the barrel shape of the cuspids on the lower molars, *therium* for “wild beast.”

C. kyaukmagyii sp. nov.

Diagnosis—Same as for genus

Etymology—Refers to Kyauk Magyi, name of the locality where the holotype was discovered.

Holotype and only known specimen—Right lower jaw with the talonid of m2 and m3 (KM73). Collections of the National Museum of Myanmar, Yangon, Myanmar.

Locality and horizon—Grayish beds situated at the base of the main purple unit (Aung 2003), Kyauk Magyi, about 5 km southwest of Moggaung Village, Pale Township, Pondaung Formation, central Myanmar (Fig. 1).

Description—The type and only known specimen of *C. kyaukmagyii* consists of a right mandible with alveoli for p4-m2 trigonid, m2 talonid, and complete m3 (Fig. 2a). Although none of the premolars are present, the alveoli indicate that the p4 was double rooted and had a long and narrow crown. The molar teeth are relatively low crowned and bunodont, the labial cuspids being only incipiently crescentic. The cuspids are noticeably inflated giving the molars a characteristic barrel shape in occlusal view. The trigonid consists essentially of the subequal protoconid and metaconid; no trace of paraconid is apparent. The pre-protocristid and pre-metacristid are short and join each other to close up the trigonid mesially. The mesio-lingual side of the entoconid displays a distinct notch, whereas its posterior side is rounded. The cristid obliqua is short, and it contacts the base of the relatively flat posterior side of the trigonid. The post-hypocristid reaches the postero-lingual corner of the tooth. A wide and deep transverse valley extends between the trigonid and the talonid. A thick distal cingulid obliqua in posterior view is linked to the extremity

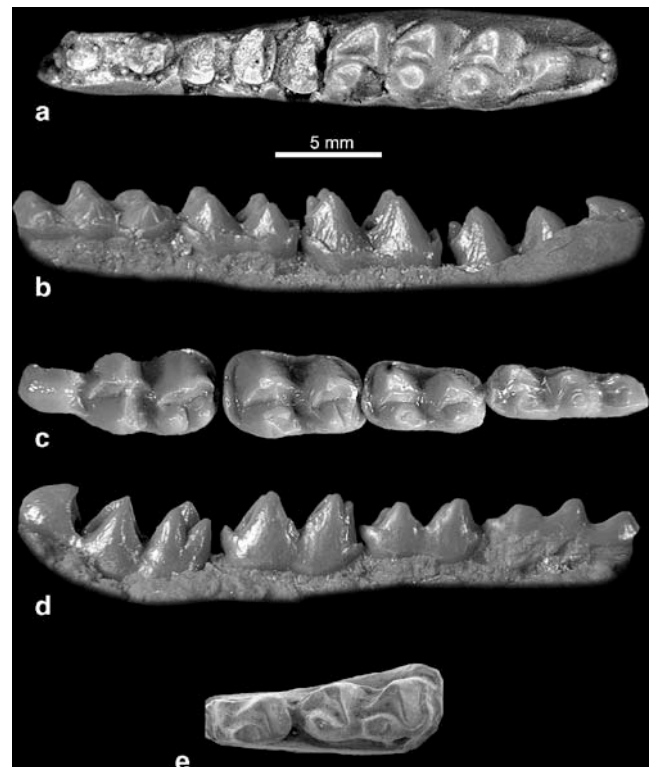


Fig. 2 a *C. kyaukmagyii* gen. and sp. nov., occlusal view of holotype (KM73), fragmentary right lower jaw preserving m3 and the talonid of m2. b–d *I. pondaungi* gen. and sp. nov., labial (b), occlusal (c), and lingual (d) views of the holotype (TUDW-20061), fragmentary left lower jaw preserving dp4–m3. e cf. *Indomeryx* sp., occlusal view of MGG33, fragmentary right lower jaw preserving m2 and the talonid of m1

of the post-hypocristid. A short basal cingulid exists labially between the trigonid and the talonid; a thick cingulid extends mesio-labially and mesially; a cingulid is also present between the second and third lobe on m3. Measurements are given in Table 1.

Discussion—As noted above, the lower molars of *Cadutherium* present a unique combination of low-crowned, bunodont teeth, possessing slightly crescentic labial cuspids and lacking paraconid and hypolophid. *Cadutherium* can be excluded from the Anthracotheriidae because it lacks a paraconid, hypolophid, and accessory cuspids. Moreover,

Table 1 Measurements of the fossil material discussed in this work

Taxon	Specimen	Position	Length	Width
<i>Irrawadymeryx pondaungi</i>	TUDW-20061	dp4	7.1	2.6
		m1	6.1	3.2
		m2	7.0	4.0
		m3	9.3	4.3
<i>Cadutherium kyaukmagyii</i>	KM-1	m2	–	4.15
		m3	9.6	4.6
cf. <i>Indomeryx</i> sp.	MGG-33	m1	–	2.3
		m2	6.7	2.85

Values are in mm

the bunodont molars, inflated cuspids, and lack of accessory folds on the metaconid or entoconid preclude the assignment of *Cadutherium* to any of the ruminants known from the Pondaung Formation. This lesser development of crests would rather favor an inclusion of *Cadutherium* within dichobunids, as *C. kyaukmagyii* does not exhibit the accessory cuspids, which usually occur on the lower molars of Suidae or Tayassuidae (Ducrocq 1994). Likewise, comparisons of *Cadutherium* with the Asian helohyids *Gobiohyus* Matthew and Granger 1925b from Irдин Manha, Inner Mongolia, *Pakkokuhyus* Holroyd and Ciochon 1995 from Pondaung, and *Progenitohyus* Ducrocq et al. 1997 from Krabi, southern Thailand, reveal several differences including the lack of labial cingulid and hypo-conulid on m3. These dental features are the most significant to consider as unlikely close phylogenetic relationships between *Cadutherium* and helohyids.

In its bunodonty and enlarged m3 hypo-conulid, *Cadutherium* shows dental features exhibited by dichobunoids, although those are probably plesiomorphic for artiodactyls. The term “dichobunoids” employed below should be understood in the sense of stem Asian artiodactyls, but their relationship to contemporaneous forms from Europe and North America is still poorly understood. In fact, the concept of “dichobunoids” designates a wide and probably paraphyletic (if not polyphyletic) assemblage of basal artiodactyls that were common tragulid-like ungulates in the mammal communities of the Early and Middle Eocene. Dichobunoids are usually considered as the stem group of selenodont artiodactyls that diversified later in the Eocene. While dichobunoids are rather well known in Europe and North America, their fossil record in Asia remains dramatically poor and mostly restricted geographically to northwestern India and Pakistan (Thewissen et al. 1987). The early Middle Eocene dichobunids *Chorlakkia* and *Pakibune* from the Early Eocene of the Kuldana Formation (Pakistan) display strongly bunodont lower molars (Gingerich et al. 1979; Thewissen et al. 1987), and the m3 hypo-conulid is clearly shorter in *Chorlakkia*. Aside from the dichobunids from the Indo-Pakistani region, Zdansky (1930) reported a fragmentary lower jaw from the Middle Eocene Heti Formation (Yuanqu Basin, Henan Province, China), which was doubtfully referred to *?Dichobune* sp. This specimen is now included in the material referred to the putative homacodontid *Limeryx* Métais et al. 2005 from the Shanghuang Fissure D (Irдинmanhan ALMA). *Limeryx* is much larger than *Cadutherium* and may be easily distinguished from the Burmese form by its more acute, less bunodont and more crescent-shaped cuspids, the presence of a distinct hypolophid, and a well-developed medially displaced hypo-conulid.

In Europe, several essentially endemic families developed a bunoselenodont molar pattern during the Middle and Late Eocene, including dichobunids and choeropotamids. Small

choeropotamids such as *Cuisitherium* (Early Eocene), *Amphirhagatherium*, and *Haplobunodon* (Middle to Late Eocene) show dental resemblances with *Cadutherium* mostly because of the similar bunoselenodont molar pattern. However, European taxa such as *Amphirhagatherium* (Hooker and Thomas 2001) generally differ from *Cadutherium* in lacking inflated cuspids and by the distal structure of the trigonid, which is mostly composed of parts of a post-protocristid. We provisionally refer *Cadutherium* to the family Dichobunidae, which typically contains bunodont to bunoselenodont artiodactyls known in Europe during the Middle and Late Eocene. Asian dichobunids probably underwent a flourishing adaptative radiation during the Early–Middle Eocene in Asia, as is observed both in Europe and North America. Accordingly, and given the lack of knowledge about basal artiodactyls in Asia, we provisionally refer this genus to a bunoselenodont branch of Asian dichobunoids. Therefore, until more complete material becomes available in Asia, *Cadutherium* might represent the first occurrence of dichobunids in Southeast Asia.

Infraorder Ruminantia Scopoli 1777

‘Archaeomerycidae’ Simpson 1945

Genus *Irrawadymeryx* gen. nov.

Type and only known species: *Irrawadymeryx pondaungi* sp. nov.

Diagnosis—Small-sized ruminant with lower molars morphologically close to those of *Indomeryx*. *Irrawadymeryx* differs from *Indomeryx* in retaining a paraconid that increases in size from m2 to m3, but is absent on m1; in the presence of a well-marked *Dorcatherium* fold on the posterior side of the metaconid on m1-2 (this fold is absent on m3), and of incipient low transverse cristids that tend to connect the entoconid and hypo-conid on m2-3; in the presence of a continuous labial cingulid and less crescentic labial cuspids on lower molars. Further differs from early lophiomerycids and tragulids in the absence of the characteristic lingually open trigonid. *Irrawadymeryx* differs from *Archaeomeryx* and *Notomeryx* in retaining a paraconid on m2-3 and in showing either a *Dorcatherium* or a *Zhailimeryx* fold (or both) and incipient transverse cristids connecting the entoconid and hypo-conid on lower molars.

Etymology—From the Irrawaddy River, Myanmar’s largest drainage basin in which the Pondaung Formation deposited. The Greek suffix *meryx* is for ruminant.

I. pondaungi sp. nov.

Diagnosis—Same as for genus

Etymology—Refers to the Pondaung Formation where the holotype was discovered.

Holotype and only known specimen—Left lower jaw with dp4-m3 (TUDW-20061). Collections of the National Museum of Myanmar, Yangon, Myanmar.

Locality and horizon—Grayish beds situated at the base of the main purple unit (Aung 2003), Than-U-Daw, about

3 km southwest of Pangan Village, Pondaung Formation, central Myanmar (Fig. 1).

Description—The type specimen of *I. pondaungi* consists of a left mandible preserving dp4-m3 (Fig. 2b–d). This mandible belonged to a young individual because the dp4 is somewhat heavily worn, and there is very little wear on m2 and m3, which is not completely erupted. The dp4 is hexacuspoid, elongated mesio-distally, narrow transversely, and bears a continuous labial cingulid; it consists of three lobes equally developed in length; the distal lobe is the widest; the mesial lobe has a large transverse wear facet anteriorly, a lingual paraconid, and a basin open posterolingually; the central lobe consists of a labial protoconid and a lingual metaconid slightly mesial to the protoconid; the distal lobe (talonid) includes a crescentic hypoconid connected posteriorly to a strong distal cingulid and lingually to a well-developed and subconical entoconid. The molar teeth are relatively low crowned, bunoselenodont, and increase in length from m1 to m3 (Table 1). The cingulids are particularly well developed and continuous on the mesial, labial, and distal part of the lower molars. The trigonid is the most variable structure of the molars because the paraconid is absent on m1, reduced and twinned with the metaconid on m2, and well developed on the unworn m3; the paraconid is closely appressed to and slightly lower than the metaconid on m2, it is well separated and almost as well developed as the metaconid on m3. The pre-protocristid connects medially to a short pre-metacristid on m1, and to a short pre-paracristid on m2-3; the lingual flank of the ‘*Dorcatherium* groove’ (= *Dorcatherium* fold, see Métais et al. 2001) is connected to the post-protocristid. The talonid also displays a distinct general structure from m1 to m3; the talonid of m1 is the most ‘*Indomeryx*-like’ with the well-developed *Zhailimeryx* fold (= entoconidian groove) on the mesial side of the entoconid which is more transversely compressed in *Indomeryx*; the hypoconid is crescentic, and the post-hypocristid does not reach the posterior side of the entoconid. On m2-3, the pre-hypocristid bifurcates with one branch connecting to the base of the protoconid, and another poorly expressed branch extending transversely to connect a barely visible labial extension of the entoconid. The configuration of m3 differs in showing a connection between the transverse branch of the pre-hypocristid and the labial flank of the *Zhailimeryx* fold. The hypoconulid lobe of m3 is similar to that observed in *Indomeryx*. The enamel is slightly wrinkled. Measurements are provided in Table 1.

Discussion—Retention of a paraconid on m2-3, and the presence of both a *Dorcatherium* fold and a *Zhailimeryx* fold, and the well-developed cingulids on lower molars set *Irrawadymeryx* apart from all the early ruminants reported so far in the Paleogene of Eurasia and North America. *I. pondaungi* is intermediate in size between *Indomeryx cotteri* and *Indomeryx arenae* (Pilgrim 1928; Tsubamoto et al.

2003) and displays the greatest morphological affinities with *Indomeryx*, which is known in the Pondaung Formation (Pilgrim 1928) and southern China (Qiu 1978; Guo et al. 1999). Métais et al. (2000) demonstrated the presence of a residual paraconid almost fused with the metaconid on the m2-3 of *Indomeryx*, but this character was subsequently considered as reflecting individual variation among the material allocated to this genus (Tsubamoto et al. 2003). Development of the molar paraconid in *Irrawadymeryx* certainly indicates a primitive feature that is not observed in *Indomeryx* or any other basal ruminant (for which the lower dentition is known) from the Pondaung Formation. Another unusual character reported only in *Irrawadymeryx* is the presence of a transverse crest joining up low in the talonid of m2-3. We suspect that this character is only visible on unworn, newly erupted teeth, and may disappear after upper molars occlusion in a later adult stage. The presence of a *Dorcatherium* fold in *Irrawadymeryx* is an important dental feature, which is also reported in early lophiomerycids (Guo et al. 2000) and tragulids Métais et al. (2001), but usually absent (or very weak) on *Indomeryx* lower molars. The trigonid of *Irrawadymeryx* molars does not show the ‘M structure’ that is present in early tragulids and possibly basal lophiomerycids Métais et al. (2001). The lower molars of *Irrawadymeryx* are larger than and morphologically distinctive (presence of folds and distinct labial cingulid, retention of a paraconid) from those of *Xinjiangmeryx parvus* Zheng 1978 from the late Middle Eocene Liankan Formation (Xinjiang, China), *Archaeomeryx optatus* Matthew and Granger 1925a from the late Middle Eocene Shara Murun Formation (Inner Mongolia, China), and *Notomeyx besensis* Qiu 1978 from the Naduo Formation (Guangxi, southern China). The occurrence of *Irrawadymeryx* in the Pondaung Formation attests to the diversity of basal ruminants in southern Asia during the late Middle Eocene. As noted above and although our knowledge of *Irrawadymeryx* remains incomplete, its lower molars clearly exhibit a primitive pattern within Ruminantia. The systematics and phylogenetic relationships within early ruminants remain poorly understood, and we provisionally refer *Irrawadymeryx* to the ‘Archaeomerycidae,’ which certainly represent a paraphyletic assemblage of basal Middle–Late Eocene Asian ruminants (Métais and Vislobokova 2007).

cf. *Indomeryx* sp.

Referred and only known specimen—MGG 33, right lower molar, presumed m2, and talonid of the preceding m1 (Fig. 2e).

Locality and horizon—Just above the red sandy clay level (Aung 2003), Lema Kyitchaung, about 2.5 km southwest of Moggaung Village, Pale Township, Pondaung Formation, central Myanmar (Fig. 1).

Description—Only a small, posterior fragment of mandible with the talonid of m1 and a complete m2 are

preserved. The lower molar is low crowned and mesio-distally elongated. Four cuspids are present, and the labial ones are crescentic. The protoconid is located slightly distal to the metaconid, and the post-protocristid is nearly transversely oriented. The pre-protocristid extends mesio-lingually and joins a short pre-metacristid medially. Although the tip of the entoconid is broken, the trigonid is clearly higher than the talonid. The talonid is significantly displaced mesially, and the pre-entocristid extends mesially to join the connection between the post-protocristid and the weak post-metacristid. The hypoconid is crescentic and significantly displaced distally relative to the entoconid. A thick posterior cingulid (that becomes thinner labially) is connected to the posterior side of the entoconid. A labial cingulid and ectostylid are absent.

Discussion—MGG 33 is provisionally referred to *Indomeryx* due to its overall morphology, but the elongation of the lower molars is unusual, not having been observed among the material previously referred to this genus. The ratio of length to width of the m2 preserved on MGG 33 is 2.35, whereas the mean value of the same ratio does not exceed 1.8 in specimens referred to *Indomeryx* from the Pondaung Formation or from other localities of southern China where the genus has been reported (Qiu 1978; Guo et al. 1999). In some aspect of its dental morphology, MGG 33 is more reminiscent of the smallest specimen referable to *I. arenae* than to any other ruminants hitherto reported in the Pondaung Formation. The most distinctive feature is the thick posterior cingulid, which is variably developed in *Indomeryx*, but always present. Other discriminating features of MGG 33 are the distal displacements of the protoconid and hypoconid relative to the metaconid and entoconid, respectively. This combination of characters is unique among the ruminants from Pondaung and has not been reported in other basal ruminants in Asia or North America. Additional material is needed to identify more confidently this form and to determine its relationships to other early ruminants from Asia.

Diversity of dental patterns and uncertain taxonomy among small artiodactyls from the Pondaung Formation

Most of the fossil mammals recovered from the Pondaung Formation have been collected by surface prospecting, thus introducing a bias against small species, with the exception of Primates for which small species (body mass < 2 kg) are well represented (Tsubamoto et al. 2005). A recent increase in screen washing has greatly enhanced the sample of small mammals, and this effort should provide critical new data about the Pondaung microfauna. This bias is particularly true for classic small elements of the fauna such as rodents and insectivores, which are extremely underrepresented in the Pondaung fauna, but probably also affects the repre-

sentation of small ungulates, including small dichobunoids and ruminants. Anthracotheriids represent the majority of artiodactyls that remains recovered in the Pondaung Formation, and they have been widely used for bio-chronologic correlations, although their systematics is still controversial (Holroyd et al. 2006). Dichobunoids reported thus far include the possible homacodontid *Asiohomacodon myanmarensis* Tsubamoto et al. (2003), and probably *Hsanotherium parvum* Ducrocq et al. (2000), which was originally described as an anthracobunid, although there are no special dental characters that justify this identification. *Hsanotherium* probably lies closer to primitive European dichobunids such as *Protodichobune* or *Aumelasia*, but reevaluation of the ordinal affinities of this genus is beyond the scope of the present paper.

Tsubamoto et al. (2005) reported two additional forms of artiodactyls based on isolated upper molars from Paukkaung that were temporarily identified as “Artiodactyla indeterminate 1 and 2,” respectively. Although fragmentary, this new material is very interesting and could be further discussed inasmuch as most of the diagnostic familial characters of early artiodactyls are to be found in the upper molars. Moreover, given the paucity of data concerning dichobunoids in Asia, this material clearly deserves more extensive comparisons with sub-contemporaneous Holarctic artiodactyls faunas, especially those, although clearly older in age (Thewissen et al. 2001), from India and Pakistan. The unique specimen (NMMP-KU 1756) questionably designated as a left m2 was referred to “Artiodactyla indeterminate 1” by Tsubamoto et al. (2005, Fig. 2a). This molar exhibits characters such as the development of the hypocone emerging from a thick postero-lingual cingulum, retention of conules with prominence of the metaconule, and the central position of protocone associated with the relative poor development of crests and styles that are characteristic dental features of dichobunids. Although significantly larger, NMMP-KU 1756 is strongly reminiscent of the holotype of *Aksyiria oligostus* from the Middle Eocene lower Obayla Subsvita in the Zaissan Depression, Eastern Kazakhstan (Gabunia 1973), in its essentially square occlusal outline, size and location of the different cusps, the voluminous and central protocone, the straight shape of the ectoloph, and the development of cingula. However, the holotype and unique specimen of *A. oligostus* differs in the lesser development of the parastyle and hypocone, but the overall morphology of NMMP-KU 1756 suggests that it belongs to a new larger species referable to the genus *Aksyiria*. If correct, this would extend the geographic and chronological range of the genus, which is restricted to its type locality to the late Middle Eocene of Southeast Asia. Gabunia (1973) considered that *Aksyiria* is a small dichobunid close to *Diacodexis*, but in the absence of additional evidence, the affinities of *Aksyiria* are still enigmatic. Thewissen et al. (1987) suggested that this unique

molar might be a deciduous tooth, and Sudre (1978) claimed some resemblance with an indeterminate dichobunid from La Livinière (MP 15), southern France. The specimen from La Livinière (Liv 4-1, collections of the University Montpellier II, France) is partly damaged but morphologically very similar, although smaller than the type specimen of *Aksyria*. Although little can be stated about the systematic position of this genus until more complete remains are discovered, the molar pattern of *Aksyria* (especially the central position of large size of the protocone, the similar development of conules, and the lack of a true hypocone) rather suggests close affinities with diacodexoids. The specimen NMMP-KU 1756 from the Pondaung Formation clearly appears more derived than *Aksyria* in possessing a hypocone, a well-developed parastyle, and metaconule slightly larger than the paraconule, but the general morphology of the molar suggests this specimen may be referable to *Aksyria*, although evidence are required to test this hypothesis.

The second form figured and described in Tsubamoto et al. (2005, Fig. 2b,c) consists of two specimens [one m2 (NMMP-KU 1765) and a possible m3 (NMMP-KU 1742)] from another fossiliferous locality near the village of Paukkaung, which are referred to “Artiodactyla indeterminate 2.” We concur with Tsubamoto et al. (2005) that these dental remains are not assignable to any species known in the Pondaung Formation. However, the upper molars (at least NMMP-KU 1765) referred to “Artiodactyla indeterminate 2” certainly show some resemblance with the raoellid molar pattern, although the molars from Pondaung do not display any trend toward a bilophodont dental pattern, which characterizes the Raoellidae (Sahni et al. 1981). Nevertheless, the bunolophodonty is not equally developed within raoellids, *Indohyus* showing strongly bilophate upper molars, whereas at the other morphological extremity, *Khirtharia* possesses markedly bunodont upper molars with only incipient lophs. Thewissen et al. (1987) diagnosed raoellid upper molars as bilophodont (or incipiently bilophodont); anterior cusp and lophs stronger than posterior ones; post-protocrista absent; paraconule weak or absent. All these dental features are present on NMMP-KU 1765, with the notable exception of the (even incipient) lophodonty. The m2 from Paukkaung somewhat resembles the type specimen of *Khirtharia aurea* identified by Thewissen et al. (2001) as a left m3. In admitting that the holotype of *K. aurea* is not m3 but m2, it becomes very close in size and morphology to the specimen from the Pondaung Formation, although its paracone is not as prominent as in *Khirtharia*.

The morphology of NMMP-KU 1742, considered by Tsubamoto et al. (2005) as a m3 of the “Artiodactyla indeterminate 2,” shows a fairly unusual morphology within artiodactyls. The metaconule (“fourth cusp” of Tsubamoto et al. 2005) is strongly reduced giving the tooth

a sub-triangular outline. The reduced posterior lobe exhibits three distinct, small accessory cusps emerging from a distolabially situated cingulum. Moreover, the metacone is noticeably reduced, and the cingulum surrounding the tooth appears stronger than on the corresponding m2. Such morphology of m3 has never been reported in raoellids hitherto, which usually display a less marked reduction in the posterior lobe of their m3. However, Walsh (2000) pointed out similar transversal reduction in the posterior lobe of m3 in a specimen from the early Uintan Friars Formation (California) referred to the helohyid *Parahyus* sp. At this point, it appears premature to state whether this feature can be considered as a typical character of the Helohyidae. Likewise, such a trend toward reduction in the posterior of m3 can also be observed in European choeropotamids and at a lesser degree in cebochoerids, although this character is never as marked as in NMMP-KU 1742. Despite this atypical morphology of m3, the specimen NMMP-KU 1765 designated as a right m2 definitely displays several diagnostic characters of raoellids: marked bunodont pattern with a trend variably expressed toward a bunolophodont pattern; prominence of cingula; anterior cusps (paracone and protocone) stronger than posterior cusps (metacone and metaconule); lack or very faint post-protocrista, retention of a small but distinct paraconule. Should this inference be confirmed by additional material, it would corroborate the large geographic distribution of raoellids in Asia during the Middle Eocene as suggested by Vislobokova (2004) and thus refute their purported endemism to the Indo-Pakistan region.

Faunal provincialism in Asia during the Middle Eocene

Assessment of the biogeography of Asian mammals during the Middle Eocene is impeded by the relative scarcity of localities in this giant landmass. With the exception of Mongolia, China, and part of Indo-Pakistan, which all have yielded critical faunas, the rest of Asia remains poorly known. The largely isolated assemblages are often inadequate in terms of the number of taxa sampled to allow reliable bio-chronologic correlations and may also be hampered by provincialism. Tsubamoto et al. (2004) attempted to compile faunal data for eastern Asia during the Middle and Late Eocene. They recognized three main biogeographic regions in eastern Asia that essentially rest on the latitudinal distribution of faunas during the Middle to Late Eocene. This latitudinal zonation reflected by mammal assemblages is consistent with paleobotanical data available in the Eocene of China (Sun and Wang 2005), but these direct indicators of vegetation or pollen evidence remain poorly investigated in the rest of Asia. Superimposed upon the pattern imposed by latitudinal gradient may be a pattern

of longitudinal faunal differentiation, although this hypothesis is presently difficult to test given the scarcity of mammal localities in central and southwestern Asia. Their study also suggests that faunal endemism increased during the late Middle Eocene, which would be congruent with the presumed endemism of the Pondaung fauna at the generic level (Tsubamoto et al. 2005). Although more than half of the mammal genera of the Pondaung Formation appear geographically restricted to the Chindwin–Irrawaddy Basin, the apparent endemic character of the Pondaung fauna may simply reflect lack of data for the rest of southern Asia during this interval and does not necessarily indicate geographic isolation of the area due to hypothesized physiographic barriers (Tsubamoto et al. 2004). The Middle Eocene of Southeast Asia is poorly documented and rests largely on the Pondaung fauna and a few local faunas of southern China, which form the basis of the Naduan ALMA (Tong et al. 1995).

The Chindwin–Irrawaddy Basin may have played the role of “crossroads” between faunas of the Indian subcontinent and those of Southeast Asia (including southern China). Although evidence supporting the existence of a well-differentiated south Asian faunal province is still weak, the northern margin of the Paleo-Tethys may have formed a homogenous region in terms of climate and possibly vegetation during the Middle Eocene. The uniqueness of the early Middle Eocene faunas from Indo-Pakistan probably needs to be further tested with additional data from Central Asia and Eastern Europe.

The hiatus between the early Middle Eocene faunas from the Kuldana/Subathu Formations of Pakistan and India and the Early Oligocene faunas of the Chitarwata Formation is approximately 20 Ma and significantly limits meaningful comparisons between southwestern and southeastern Asian faunas during the late Middle Eocene. However, mammals recovered from the Early Oligocene of Paali (lower Chitarwata Formation, Pakistan) are closer to those of the Pondaung fauna than to mammals from the late Middle Eocene faunas of Mongolia and central China. These observations suggest, albeit somewhat weakly, the existence of a southern Asian faunal province that may have been relatively stable in terms of faunal composition during the Eocene–Oligocene transition. The Eocene–Oligocene transition is marked by a profound faunal turnover at higher latitudes in Asia (Meng and McKenna 1998), as well as in Europe (Stehlin 1909) and North America (Prothero and Emry 1996).

Should our identifications of the enigmatic artiodactyls reported by Tsubamoto et al. (2005) prove to be correct, the Chindwin–Irrawaddy Basin may have formed the eastern part of a wider south Asian tropical biogeographic province that also included the Indian subcontinent and probably the western margin of the Paleo-Tethys. Reevaluation of Pondaung material referred to the dichobunoids does not

support the supposed endemism of the Pondaung fauna (Tsubamoto et al. 2005). The current state of knowledge concerning Eocene mammals in southern Asia is insufficient to demonstrate the endemism of the Pondaung fauna, especially when considering the probable collecting/taphonomic bias against certain elements of the fauna (including small vertebrates).

As evidenced in Europe and North America, the late Middle Eocene corresponds to a major phase in the radiation of selenodont artiodactyls, probably related to an increasingly drier climate in the Holarctic continents (Janis 1993). The gradual deterioration of climate was first suggested in North America where major extinctions occurred in the Duchesnean NALMA, although a later wave of extinctions also occurred at the end of the Eocene (Janis 1997). Stucky (1998) suggested that the radiation of selenodont artiodactyls (represented today by camels and ruminants, but including several extinct groups) may have taken place slightly earlier in North America than in Europe. This event marks major change in the structure of mammal communities.

The Pondaung fauna documents the late Middle Eocene in southern Asia, where the timing of this radiation of selenodonts remains poorly understood. An important factor would be to document exactly how global climatic deterioration affected tropical ecosystems during the Middle–Late Eocene transition and whether climatic changes (if any) favored the radiation of ruminants and related groups in the area (Métais et al. 2001; Métais 2006). The faunal data available for the Middle and Late Eocene of Asia show replacement of faunas dominated by perissodactyls by faunas dominated by artiodactyls (Tsubamoto et al. 2004), but this general trend probably reflects decline of perissodactyls in term of abundance and taxonomic diversity and not necessarily a sudden increase in the taxonomic diversity among artiodactyls.

Conclusion

Despite the fragmentary nature of the material described above, they document an array of dental morphologies among small- and medium-sized artiodactyls hitherto unexpected in the Pondaung Formation. The affinities of the new dichobunoid *C. kyaukmagyii* are still poorly understood and reflect the primitive stage of knowledge concerning these small stem artiodactyls in Asia. Allocation of this new genus to the Dichobunoidea is tentative pending collection and additional material, and an alternative assignment could also be rationally supported. *I. pondaungi* displays a combination of primitive ruminant features such as the retention of a paraconid on m2-3 or the presence of accessory cristids (or folds) on its lower molars. Allocation

of this new genus requires additional fossil data investigation, and it is tentatively placed in the Archaeomerycidae, which presently represents a heterogeneous and certainly paraphyletic assemblage of basal Ruminantia. The occurrence of basal ruminants and dichobunoids provide important information for understanding the early evolution of stem selenodont artiodactyls in Asia and their phylogenetic relationships with those from Central Asia, Europe, and North America. This study emphasizes the importance of the Pondaung fauna for better understanding the Middle–Late Eocene transition in southern Asia and, in turn, the biotic and abiotic factors related to the emergence of the ruminant clade. Ruminants are taxonomically and ecologically the most diversified group of ungulate mammals in the present ecosystems.

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References

- Soe AN, Myitta, Tun ST, Aung AK, Thein T, Marandat B, Ducrocq S, Jaeger J-J (2002) Sedimentary facies of the late Middle Eocene Pondaung Formation (central Myanmar) and the palaeoenvironments of its Anthropoid Primates. *Comptes Rendus Palevol* 1:153–160
- Aung AK (1999) Revision on the stratigraphy and age of the primate-bearing Pondaung Formation. In: Pondaung Fossils Expedition Team (ed) Proceedings of the Pondaung Fossils Expedition Team. Office of Strategic Studies, Ministry of Defence, pp 131–151
- Aung AK (2003) The primate-bearing Pondaung Formation in the upland area, north-west of Central Myanmar. In: Ross C, Kay RF (eds) Anthropoid origins: new visions. Kluwer, New York, pp 33–47
- Benammi M, Soe AN, Tun T, Bo B, Chaimanee Y, Ducrocq S, Thein T, Wai S, Jaeger J-J (2002) First magnetostratigraphic study of the Pondaung Formation: implications for the age of the Middle Eocene anthropoids of Myanmar. *J Geol* 110:748–757
- Bender F (1983) The geology of Burma. Gebrüder Borntraeger, Berlin, p 293
- Colbert EH (1938) Fossil mammals from Burma in the American Museum of Natural History. *Bull Am Mus Nat Hist* 74:255–434
- Ducrocq S (1994) An Eocene Peccary from Thailand and the biogeographical origins of the Artiodactyl family Tayassuidae. *Palaeontology* 37:765–779
- Ducrocq S, Chaimanee Y, Suteethorn V, Jaeger J-J (1997) First discovery of Helohyidae (Artiodactyla, Mammalia) in the Late Eocene of Thailand: a possible transitional form for Anthracotheriidae. *Comptes Rendus de l'Académie des Sciences de Paris, Series IIA: Earth and Planetary Science* 325:367–372
- Ducrocq S, Soe AN, Benammi M, Chaimanee Y, Tun T, Thein T, Jaeger J-J (2000) First record of an Anthracobunidae (Mammalia, ?Tethytheria) from the Eocene of the Pondaung Formation, Myanmar. *Comptes Rendus de l'Académie des Sciences de Paris, Series IIA: Earth and Planetary Science* 330:1–6
- Gabunia L (1973) On the presence of the Diacodexinae in the Eocene of Asia. *Bulletin of the Academy of Sciences of the Georgian SSR* 71:741–744
- Gentry AW, Hooker JJ (1988) The phylogeny of the Artiodactyla. In: Benton MJ (ed) The phylogeny of the tetrapods. Clarendon, Oxford, pp 235–272
- Gingerich PD, Russell DE, Sigogneau-Russell D, Hartenberger J-L (1979) *Chorlakkia hassani*, a new Middle Eocene dichobunid (Mammalia, Artiodactyla) from the Kuldana Formation of Kohat (Pakistan). Contribution from the Museum of Paleontology, the University of Michigan, vol 25, pp 117–124
- Guo J, Qi T, Sheng H-J (1999) A restudy of the Eocene ruminants from Baise and Yongle Basins, Guangxi, China, with a discussion of the systematic positions of *Indomeryx*, *Notomeryx*, *Gobiomeryx* and *Prodromotherium*. *Vertebrata Palasiatica* 37:18–39
- Guo J, Dawson MR, Beard KC (2000) *Zhailimeryx*, a new lophiomerycid artiodactyl (Mammalia) from the late Middle Eocene of Central China and the early evolution of ruminants. *J Mamm Evol* 7:239–258
- Holroyd PA, Ciochon RL (1994) Relative ages of Eocene Primate-bearing deposits of Asia. In: Fleagle JG, Kay RF (eds) Anthropoid origins. Plenum, New York, pp 123–141
- Holroyd PA, Ciochon RL (1995) A new artiodactyl (Mammalia) from the Eocene Pondaung sandstones, Burma. *Ann Carnegie Mus* 64:177–183
- Holroyd PA, Ciochon RL, Gunnell GF (2006) Phylogenetic relationships among late Middle Eocene to Early Oligocene Old World anthracotheriids. *J Vertebr Paleontol* 26:78A
- Hooker JJ, Thomas KM (2001) A new species of *Amphirhagatherium* (Choeropotamidae, Artiodactyla, Mammalia) from the Late Eocene Headon Hill Formation of southern England and phylogeny of endemic European 'anthracotherioids.' *Palaeontology* 44:827–853
- Janis CM (1993) Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Ann Rev Ecol Syst* 24:467–500
- Janis CM (1997) Ungulate teeth, diets, and climatic changes at the Eocene/Oligocene boundary. *Zoology* 100:203–220
- Matthew WD, Granger W (1925a) New mammals from the Shara Murun Eocene of Mongolia. *Am Mus Novit* 196:1–11
- Matthew WD, Granger W (1925b) New mammals from the Irдин Manha Eocene of Mongolia. *Am Mus Novit* 198:1–10
- Meng J, McKenna MC (1998) Faunal turnovers of Palaeogene mammals from the Mongolian Plateau. *Nature* 394:364–367
- Métais G (2006) New basal selenodont artiodactyls from the Pondaung Formation (late Middle Eocene, Myanmar) and the phylogenetic relationships of early ruminants. *Ann Carnegie Mus* 75:51–67
- Métais G, Vislobokova IA (2007) Basal ruminants. In: Prothero DR, Foss SE (eds) The evolution of the artiodactyls. John Hopkins University Press, Baltimore (in press)
- Métais G, Benammi M, Chaimanee Y, Jaeger J-J, Tun T, Thein T, Ducrocq S (2000) Discovery of new ruminant dental remains from the Middle Eocene Pondaung Formation (Myanmar): reassessment of the phylogenetic position of *Indomeryx*. *Comptes Rendus de l'Académie des Sciences de Paris, Series IIA: Earth and Planetary Science* 330:805–811
- Métais G, Chaimanee Y, Jaeger J-J, Ducrocq S (2001) New remains of primitive ruminants from Thailand: evidence of the early evolution of the Ruminantia in Asia. *Zool Scr* 30:231–249

- Métais G, Qi T, Guo J, Beard KC (2005) A new bunoselenodont artiodactyl from the Middle Eocene of China and the early record of selenodont artiodactyls in Asia. *J Vertebr Paleontol* 25:994–998
- Montgelard C, Catzeflis F, Douzery E (1997) Phylogenetic relationships of Artiodactyls and Cetaceans as deduced from the comparison of Cytochrome b and 12s rRNA mitochondrial sequences. *Mol Biol Evol* 14:550–559
- Pilgrim GE (1928) The Artiodactyla of the Eocene of Burma. *Palaeontol Indica* 8:1–39
- Pilgrim GE, Cotter GP (1916) Some newly discovered Eocene mammals from Burma. *Rec Geol Surv India* 47:42–77
- Prothero DR, Emry RJ (1996) The terrestrial Eocene–Oligocene transition in North America. Cambridge University Press, p 688
- Qiu Z (1978) Late Eocene Hypertragulids of Baise Basin, Kwangsi. *Vertebrata Palasiatica* 16:7–12
- Sahni A, Bhatia SB, Hartenberger J-L, Jaeger J-J, Kumar K, Sudre J, Vianey-Liaud M (1981) Vertebrates from the Subathu Formation and comments on the biogeography of Indian subcontinent during the Early Paleogene. *Bull Soc Géol Fr* 23:689–695
- Scopoli GA (1777) *Introductio ad historiam naturalem sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae.* Gerie, Prag, pp 1–506
- Simpson GG (1945) The principles of classification and a classification of mammals. *Bull Am Mus Nat Hist* 85:1–350
- Stamp LD (1922) An outline of the Tertiary geology of Burma. *Geol Mag* 59:481–501
- Stehlin HG (1909) Remarques sur les faunules de mammifères de l’Eocène et de l’Oligocène du Bassin de Paris. *Bull Soc Géol Fr* 9:488–520
- Stucky RK (1998) Eocene bunodont and bunoselenodont Artiodactyla (“dichobunids”). In: Janis CM, Scott KM, Jacobs LL (eds) *Evolution of Tertiary mammals of North America*. Cambridge University Press, Cambridge, pp 358–374
- Sudre J (1978) Les Artiodactyles de l’Eocène moyen et supérieur d’Europe Occidentale; systématique et évolution. *Université des Sciences et Techniques du Languedoc, Montpellier*, p 257
- Sun X, Wang P (2005) How old is the Asian monsoon system? Palaeobotanical records from China. *Palaeogeogr Palaeoclimatol Palaeoecol* 222:181–222
- Thewissen JGM, Gingerich PD, Russell DE (1987) Artiodactyla and Perissodactyla (Mammalia) from the Early–Middle Eocene Kuldana Formation of Kohat (Pakistan). *Contributions from the Museum of Paleontology, University of Michigan*, vol 27, pp 247–274
- Thewissen JGM, Williams EM, Hussain ST (2001) Eocene mammal faunas from Northern Indo-Pakistan. *J Vertebr Paleontol* 21:347–366
- Tong Y, Zheng S, Qiu Z (1995) Cenozoic mammal ages of China. *Vertebrata Palasiatica* 33:290–314
- Tsubamoto T, Takai M, Shigehara N, Egi N, Tun ST, Aung AK, Maung M, Danhara T, Suzuki H (2002) Fission-track zircon age of the Eocene Pondaung Formation, Myanmar. *J Hum Evol* 42:361–369
- Tsubamoto T, Tun ST, Egi N, Takai M, Shigehara N, Soe AN, Aung AK, Thein T (2003) Reevaluation of some ungulate mammals from the Eocene Pondaung Formation, Myanmar. *Paleontol Res* 7:219–243
- Tsubamoto T, Takai M, Egi N (2004) Quantitative analyses of biogeography and faunal evolution of Middle to Late Eocene mammals in East Asia. *J Vertebr Paleontol* 24:657–667
- Tsubamoto T, Egi N, Takai M, Sein C, Maung M (2005) Middle Eocene ungulate mammals from Myanmar: a review with description of new specimens. *Acta Palaeontol Pol* 50:117–138
- Tsubamoto T, Egi N, Takai M, Shigehara N, Suzuki H, Nishimura T, Ugai H, Maung-Maung, Sein C, Tun ST, Soe AN, Aung AK, Thein T, Htike T (2006) A summary of the Pondaung fossil expeditions. *Asian Paleoprimatology* 4:1–66
- Turner HN (1849) On the evidences of affinity afforded by the skull in the ungulate Mammalia. *Proc Zool Soc Lond* 17:147–158
- Vislobokova IA (2004) A new representative of the family Raoellidae (Suiformes) from the Middle Eocene of Khaichin-Ula 2, Mongolia. *Paleontol J* 38:102–107
- Walsh SL (2000) Bunodont artiodactyls (Mammalia) from the Uintan (Middle Eocene) of San Diego County, California. *Proc S Diego Soc Nat Hist* 37:1–27
- Zdansky O (1930) Die alttertiären Säugetiere Chinas nebst stratigraphischen Bemerkungen. *Palaeontol Sin* 6:5–84
- Zheng J (1978) Description of some Late Eocene mammals from Lian-Kan Formation of Turfan Basin, Sinkiang. *Memoirs of the Institute of Vertebrate Paleontology and Paleoanthropology Academia Sinica* 13:115–125