Paleontological Research, vol. 6, no. 4, pp. 363–384, December 31, 2002

The Anthracotheriidae (Mammalia; Artiodactyla) from the Eocene Pondaung Formation (Myanmar) and comments on some other anthracotheres from the Eocene of Asia

TAKEHISA TSUBAMOTO[1], MASANARU TAKAI[1], NAOKO EGI[1], NOBUO SHIGEHARA[1], SOE THURA TUN[2], AYE KO AUNG[3], AUNG NAING SOE[2] AND TIN THEIN[4]

[1]*Primate Research Institute, Kyoto University, Inuyama, Aichi, 484–8506, Japan (e-mail: tsuba@pri.kyoto-u.ac.jp)*

[2]*Department of Geology, University of Pathein, Pathein, Myanmar*

[3]*Department of Geology, Dagon University, Yangon, Myanmar*

[4]*Department of Geology, University of Yangon, Yangon, Myanmar*

Received May 9, 2002; Revised manuscript accepted October 7, 2002

Abstract. We reevaluate the classifications of the anthracotheres (Mammalia; Artiodactyla) from the latest middle Eocene Pondaung Formation (central Myanmar), mentioning other anthracotheres from the Eocene of Asia. The three anthracotheriid genera previously known from the Pondaung Formation, *Anthracothema*, *Anthracokeryx*, and *Anthracohyus*, are synonymized into *Anthracotherium*. As many as 13 species had been recognized in the Pondaung anthracotheres, but they are summarized into four species (*Anthracotherium pangan*, *Anthracotherium crassum*, *Anthracotherium birmanicum*, and *Anthracotherium tenuis*), based on the difference of M_1 size (~ body size). Dental morphology in each species indicates high variation, and the four species are not separable based on their dental morphology. The dental morphology of the Pondaung *Anthracotherium* species is distinct from that of other species and is the most primitive. In addition, the Pondaung *Anthracotherium* species are the oldest of the genus. The genus *Anthracotherium* might have originated and rapidly radiated around the Pondaung area during the latest middle Eocene. *Siamotherium pondaungensis* described from the Pondaung Formation as an anthracotheriid is synonymized to *Pakkokuhyus lahirii* (Artiodactyla; Helohyidae).

Key words: Anthracotheriidae, *Anthracotherium*, Eocene, Myanmar, Pondaung Formation, systematics

Introduction

The Anthracotheriidae is an extinct group of browsing suiform artiodactyls that achieved wide distribution across Eurasia, parts of Africa, and North America from the Eocene to Plio-Pleistocene periods (Black, 1978; Ducrocq, 1997; Kron and Manning, 1998). Their body size ranges from small, terrier-sized animals to beasts approaching the size of a hippopotamus (Black, 1978). Typical early anthracotheres have complete dentition and bunodont or bunoselenodont molars, five cusped upper molars without hypocone and four cusped lower molars without paraconid (Ducrocq *et al.*, 1996). Their low-crowned teeth and frequent occurrence in paleochannel deposits suggest habits and habitat similar to those of modern hippos (Kron and Manning, 1998).

The fossil record of anthracotheres is abundant and diverse throughout the world. In East Asia, they appeared from the middle Eocene and survived until the Plio-Pleistocene (Colbert, 1938; Ducrocq, 1997). In Europe, they appeared during the late Eocene and became extinct in the Miocene. In Africa, they evolved from the late Eocene to the Plio-Pleistocene (Black, 1978; Ducrocq, 1994a, 1997). In North America, they are recorded from the late middle Eocene to the early Miocene, but the fossil record of North American anthracotheres is neither particularly abundant nor very diverse (Kron and Manning, 1998).

In regard to the anthracotheres' phyletic relationships, traditionally, most researchers have considered that anthracotheres might have originated from a helohyid stock (Pilgrim, 1928, 1940, Coombs and Coombs, 1977; Ducrocq *et al.*, 1997) or from diacodexoid forms (Ducrocq, 1994b), and that they might have been the ancestors of extant hippos because some types of anthracotheres are considered to have had a hippopotamid mode of life and a body structure similar to hippos (Black, 1978; Colbert, 1935; Gentry and Hooker, 1988; Thewissen *et al.*, 2001). According to molecular data (e.g., Nikaido *et al.*, 1999), hippopotamids comprise a monophyletic clade with cetaceans, so that anthracotheres might have originated from a stock of the [Cetacea + Hippopotamidae] clade (Rose, 2001). On the other hand, a few researchers (Pickford, 1983; but see Ducrocq, 1994b for discussion) suggested that hippopotamids could have originated not from an anthracothere stock but from a peccary one (Ducrocq, 1997).

In regard to regional origin, many researchers have considered that anthracotheres might have originated in East Asia during the Eocene (e.g., Pilgrim, 1928; Suteethorn *et al.*, 1988; Ducrocq, 1994a, 1999), because Eocene anthracotheres of East Asia are abundant and well diversified and because they show a primitive bunodont condition (Ducrocq, 1999).

The anthracotheres from the Eocene Pondaung Formation (Myanmar) are the first mammalian taxa in this formation to have been described (Pilgrim and Cotter, 1916). They are among the oldest anthracotheres in East Asia and consist of three genera and as many as 13 species (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938). Therefore, many studies have viewed the Pondaung anthracotheres in relation to the origin and early radiation of this group (e.g., Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938; Coombs and Coombs, 1977; Ducrocq, 1999).

Despite the richness of the fossil collections, the classification of the Pondaung anthracotheres has been problematic (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938; Holroyd and Ciochon, 1991). The taxonomic confusion on the Pondaung anthracotheres is likely to be due to their highly varied and primitive dental morphology.

In this paper, we reevaluate the classification of the Pondaung anthracotheres based on previously described fossil materials (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938) and new collections. We then also discuss classifications of some other Eocene anthracotheres of East Asia in relation to the revision of the classification of the Pondaung anthracotheres.

Institutional abbreviations

AMNH = American Museum of Natural History, New York, USA; **CM** = Carnegie Museum of Natural History, Pittsburgh, USA; **BMNH** = The Natural History Museum (formerly British Museum of Natural History), London, United Kingdom; **DMR** = Department of Mineral Resources, Bangkok, Thailand; **GSI** = Geological Survey of India, Kolkata, India; **IVPP** = Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; **NSM** = National Science Museum, Tokyo, Japan; **UCMP** = Museum of Paleontology, University of California, Berkeley, USA.

Materials

The new collections of Pondaung anthracotheres used here were discovered in 1997 by Myanmar researchers (Pondaung Fossil Expedition Team, 1997; Takai *et al.*, 1999), and in 1998 (November) and 1999 (November) by Myanmar-Japan joint team (Takai *et al.*, 2000, 2001; Egi and Tsubamoto, 2000; Tsubamoto *et al.*, 2000a, b, 2001, 2002; Shigehara *et al.*, 2002; Gebo *et al.*, in press). These new fossil materials are stored in the National Museum of the Union of Myanmar (Yangon, Myanmar). They are serially catalogued under **NMMP-KU** specimen numbers. NMMP stands for National Museum, Myanmar, Paleontology; and KU for Kyoto University (Japan). The dental measurements used here are listed in the Appendix.

Geologic setting

The Pondaung Formation is distributed in the western part of central Myanmar (Figure 1). The Pondaung Formation overlies and partially interfingers with the middle Eocene Tabyin Formation, and is conformably overlain by the late Eocene Yaw Formation (Stamp, 1922; Bender, 1983; Aye Ko Aung, 1999). The Pondaung Formation consists of alternating mudstone, sandstone, and conglomerate, and is subdivided into the "Lower" and "Upper" Members (Aye Ko Aung, 1999). The "Lower Member" is dominated by greenish pebbly sandstone and mudstone and contains only a few fossil leaf fragments in its upper part (Aye Ko Aung, 1999). The "Upper Member" is dominated by fine- to medium-grained sandstone and variegated mudstone and contains many terrestrial mammalian and other vertebrate fossils that indicate a freshwater environment (Colbert, 1938; Bender, 1983; Aye Ko Aung, 1999; Aung Naing Soe, 1999; Aung Naing Soe *et al.*, 2002). Its mammalian fauna and the fission-track age of the "Upper Member" (37.2 ± 1.3 Ma) indicate a latest middle Eocene age (Tsubamoto *et al.*, 2002).

Previous studies on Pondaung anthracotheres

Pilgrim and Cotter (1916) first described three genera (*Anthracohyus*, *Anthracotherium*, and *Anthracokeryx*) and seven species of anthracotheres from the Pondaung Formation. Pilgrim (1928) revised the Pondaung anthracotheres into three genera (*Anthracohyus*, *Anthracothema*, and *Anthracokeryx*) and 13 species, describing new

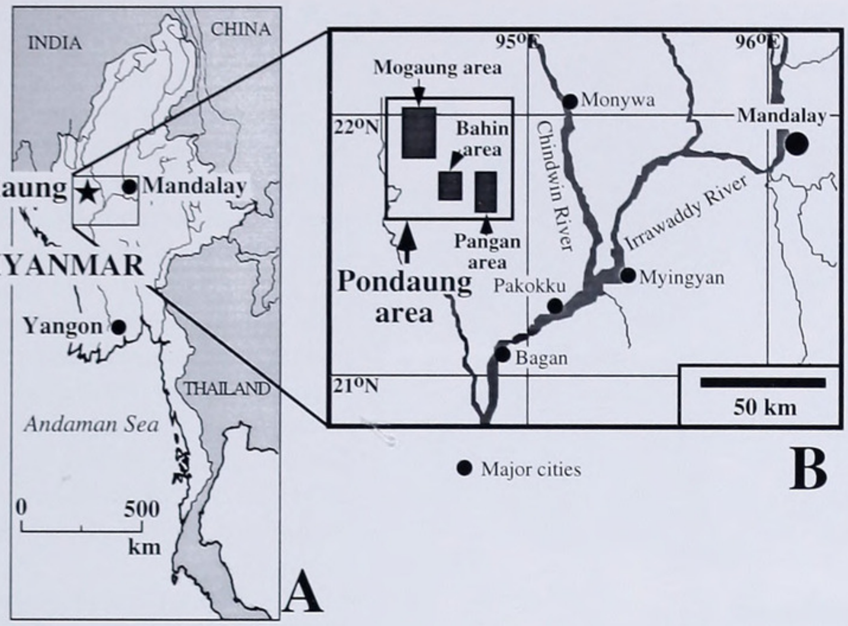


Figure 1. A. Map of Myanmar showing the location of the Pondaung area. B. Map of the Pondaung area showing the location of the three main regions of fossil localities.

materials. Colbert (1938) reviewed the Pondaung anthracotheres, and recognized the same three genera as Pilgrim (1928) and seven to nine species, also describing new materials. Thus, in the Pondaung Formation, the three anthracothere genera *Anthracohyus*, *Anthracothema*, and *Anthracokeryx* have been traditionally recognized. All these three genera were established based on the material from the Pondaung Formation. Most of the anthracothere materials collected from the Pondaung Formation have been assigned to *Anthracothema* or *Anthracokeryx*, whereas remains of *Anthracohyus* have been very rare.

Anthracohyus was established by Pilgrim and Cotter (1916) and was characterized particularly by the absence or very feeble development of the styles on the upper molars. Originally, this genus included three species, that is, *Anthracohyus choeroides*, *Anthracohyus rubricae*, and *Anthracohyus palustris*. Subsequently, the latter two species were moved to a new genus *Anthracothema* as determined by Pilgrim (1928). This classification is followed by Colbert (1938). The only remaining species in the genus *Anthracohyus*, *A. choeroides*, was characterized by the conical cusps on its molars, by the absence or very feeble development of the molar styles, and by the mesiodistal diameter of the upper molar being shorter on the buccal side than on the lingual side (Colbert, 1938).

Anthracothema was established by Pilgrim (1928). Four species of the Pondaung anthracotheres described by Pilgrim and Cotter (1916) were referred to this genus: *Anthracohyus rubricae*, *Anthracohyus palustris*, *Anthracotherium pangan*, and *Anthracotherium crassum*. All these species were renamed by Pilgrim (1928) as *Anthracothema rubricae*, *Anthracothema palustre*, *Anthracothema pangan*, and *Anthracothema crassum*, respectively. Afterwards, *A. palustre* and (questionably) *A. crassum* were synonymized to *A. pangan* by Colbert (1938). Therefore, two (or three) species of the Pondaung *Anthracothema* were still recognized by him. The genus *Anthracothema* was characterized by its larger size, weaker molar styles, and its more conical molar cusps than those of *Anthracokeryx* from the Pondaung Formation (Pilgrim, 1928; Colbert, 1938). Recently, *Anthracothema* was synonymized to *Anthracotherium* by Ducrocq (1999).

Anthracokeryx was erected by Pilgrim and Cotter (1916). They described two species of *Anthracokeryx*, *Anthracokeryx birmanicus* and *Anthracokeryx tenuis*. Pilgrim (1928) then described six more species of this genus, namely *Anthracokeryx hospes*, *Anthracokeryx bambusae*, *Anthracokeryx myaingensis*, *Anthracokeryx ulnifer*, *Anthracokeryx moriturus*, and *Anthracokeryx*? *lahirii*. Colbert (1938) later on recognized four to six species of the Pondaung *Anthracokeryx*. The genus *Anthracokeryx* was characterized by its smaller size, better marked molar styles, and its more crescentic (selenodont) molar cusps than *Anthracothema* and *Anthracohyus* from the Pondaung Formation (Pilgrim, 1928; Colbert, 1938). On the other hand, the taxonomic validity of keeping *Anthracokeryx*? *lahirii* in the Anthracotheriidae was discussed by both Pilgrim (1928) and Colbert (1938). Recently, this species was referred to the Helohyidae (Artiodactyla) and renamed *Pakkokuhyus lahirii* by Holroyd and Ciochon (1995).

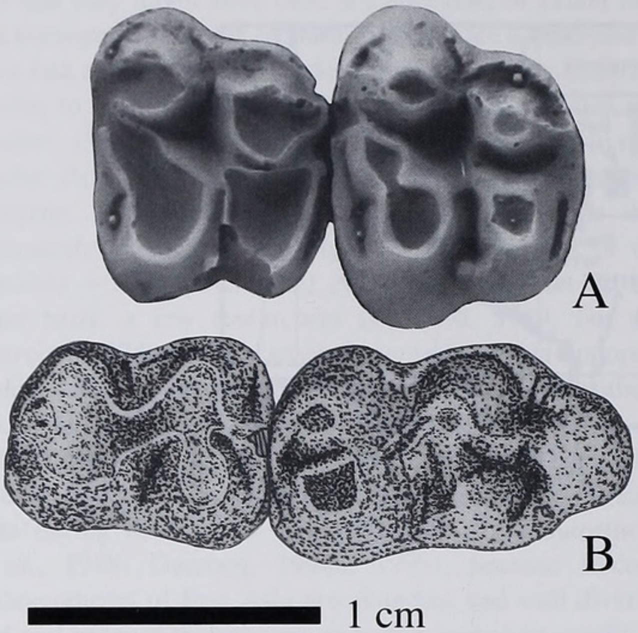


Figure 2. Comparison of *Siamotherium pondaungensis* and *Pakkokuhyus lahirii*. **A**. M^{2-3} of the type of *Siamotherium pondaungensis* [NMMP-KU 0039 (Kdw 6): a right maxillary fragment with M^{2-3}] in occlusal view (reversed). **B**. M_{2-3} of the type of *Pakkokuhyus lahirii* (GSI B-766: a right mandibular fragment with M_{1-3}) in occlusal view.

On *Siamotherium pondaungensis*

Based on a right maxillary fragment with M^{2-3} (Kdw 6 = NMMP-KU 0039; Figure 2A) from the Pondaung Formation, *Siamotherium pondaungensis* was described by Ducrocq *et al.* (2000) as a new species of *Siamotherium* (Anthracotheriidae). *Siamotherium* was known only from the Krabi basin, the late Eocene of Thailand (Suteethorn *et al.*, 1988; Ducrocq, 1999). However, the dentition displayed by the unique material of *S. pondaungensis* matches that of *Pakkokuhyus lahirii* (Helohyidae) (Figure 2B) described from the Pondaung Formation by Pilgrim (1928) and Holroyd and Ciochon (1995) based on a right mandibular fragment with M_{1-3}. Ducrocq *et al.* (2000) did not compare *S. pondaungensis* with *P. lahirii*. Although the upper dentition of *P. lahirii* has never been described, we believe that this upper dental material described as *S. pondaungensis* should be referred to *P. lahirii* rather than to another taxon because (1) the upper molars of *S. pondaungensis* are conical, bunodont, and brachyodont molars, like the lower molars of *P. lahirii*; (2) the sizes and cusp configurations of M^2 and M^3 of *S. pondaungensis* well match those of M_2 and M_3 of the type of *P. lahirii* (GSI B-766), respectively (e.g., M^2 protocone, M^3 protocone, and M^3 metaconule match M_2 talonid basin, M_3 talonid basin, and M_3 hypoconulid basin, respectively) (Figure 2); (3) the upper dental morphology of *S. pondaungensis* is similar to that of helohyids, such as *Helohyus*, in having similar dental size, bunodont and conical cusps with enlarged metaconule, and no or vestigial styles; and additionally, (4) both *S. pondaungensis* and *P. lahirii* have been found only in the Pondaung Formation. Further discoveries of better materials are necessary to settle the classification, but following our observations on the dental materials, we treat *Siamotherium pondaungensis* as a junior synonym of *Pakkokuhyus lahirii* (Helohyidae) in this paper.

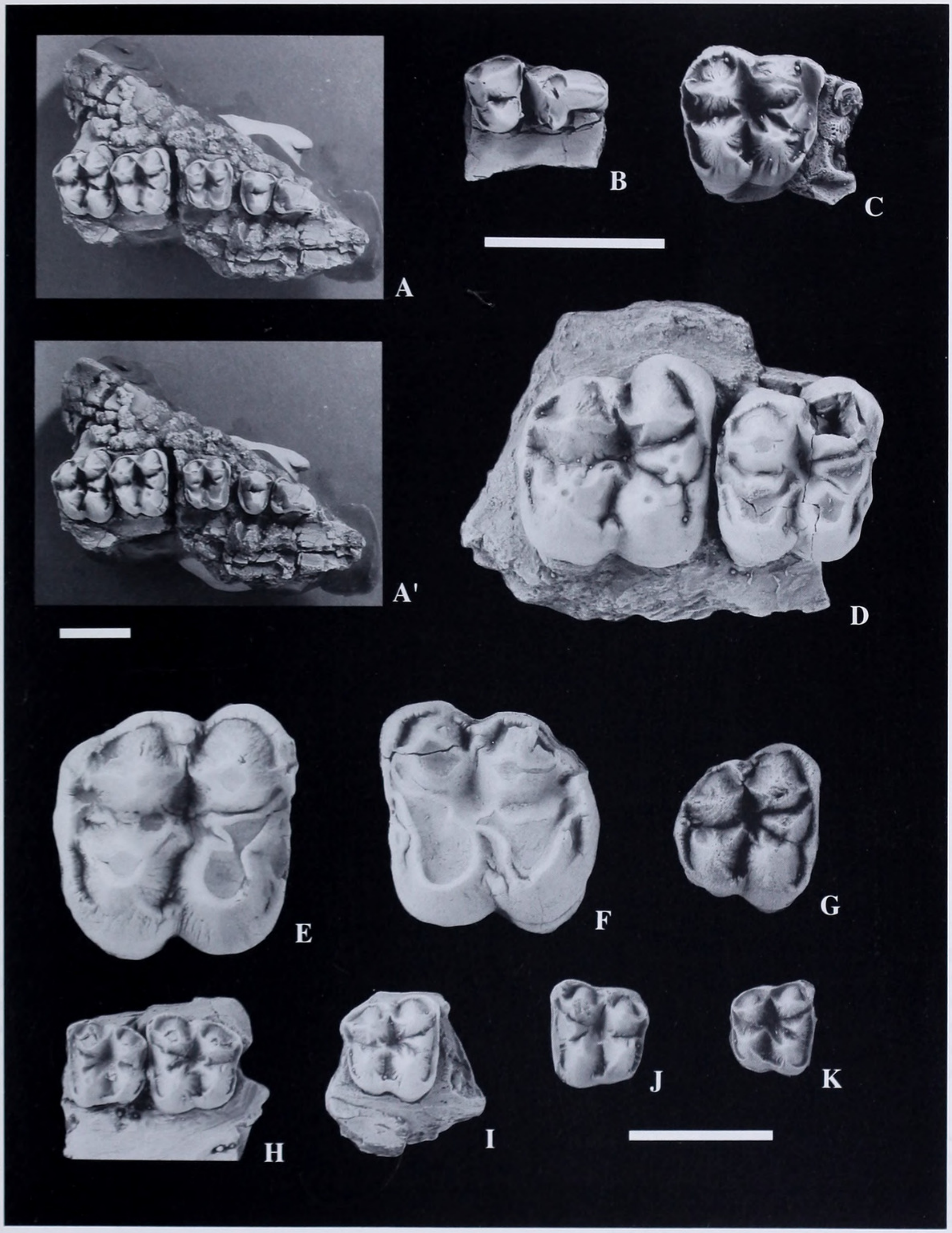
Dental morphology and size variation of Pondaung anthracotheres and their classification

Generic status of *Anthracothema* and *Anthracokeryx*

As mentioned above, after the review of Colbert (1938), the Pondaung anthracotheres have been classified into three genera, *Anthracohyus*, *Anthracothema*, and *Anthracokeryx*, and into as many as 13 species. This is because Colbert (1938) and earlier researchers (Pilgrim and Cotter, 1916; Pilgrim, 1928) recognized various dental morphologies among the Pondaung anthracotheres.

However, the differences in dental morphologies between two of the genera, *Anthracothema* and *Anthracokeryx*, in the Pondaung Formation are very subtle compared to other anthracotheriid taxa. In addition, these two genera have variations in selenodonty (crista development) and style development on the upper molars, which were the diagnostic characters for distinguishing them (Figures 3–5; Pilgrim and Cotter, 1916, plates 2–5; Pilgrim, 1928, plates 1–4; Colbert, 1938, figs. 41–52). Although *Anthracokeryx*, the smaller anthracothere group, generally has rather selenodont molars with better developed molar styles compared to *Anthracothema*, and although *Anthracothema*, the larger anthracothere group, generally has rather bunodont molars with less-developed styles compared to *Anthracokeryx*, the development of selenodonty and styles is variable. We examined all previously described materials of the Pondaung anthracotheres stored in AMNH and GSI, and recently collected materials in the National

➡ **Figure 3.** New upper dental materials of the Pondaung anthracotheres (*Anthracotherium*) in occlusal view (1). **A, A'**. NMMP-KU 0053, an right upper jaw with P^3-M^3 (stereo pair). **B**. NMMP-KU 0455, a right maxillary fragment with P^{3-4}. **C**. NMMP-KU 0327, a right mandibular fragment with dP^4. **D**. NMMP-KU 0056, a right maxillary fragment with M^{2-3}. **E**. NMMP-KU 0404, a right M^3. **F**. NMMP-KU 0411, a left maxillary fragment with M^3. **G**. NMMP-KU 0070, a right M^3. **H**. NMMP-KU 0382, a left maxillary fragment with M^{2-3} (or M^{1-2}). **I**. NMMP-KU 0326, a right maxillary fragment with $M^{3\,(or\,2)}$. **J**. NMMP-KU 0379, a left $M^{3?}$. **K**. NMMP-KU 0384, a right $M^{1\,(or\,2)}$. Scale bars = 2 cm (left middle scale corresponds to A, A', central upper scale corresponds to B–C, and right lower scale corresponds to D–K).


A
A'
B
C
D
E
F
G
H
I
J
K

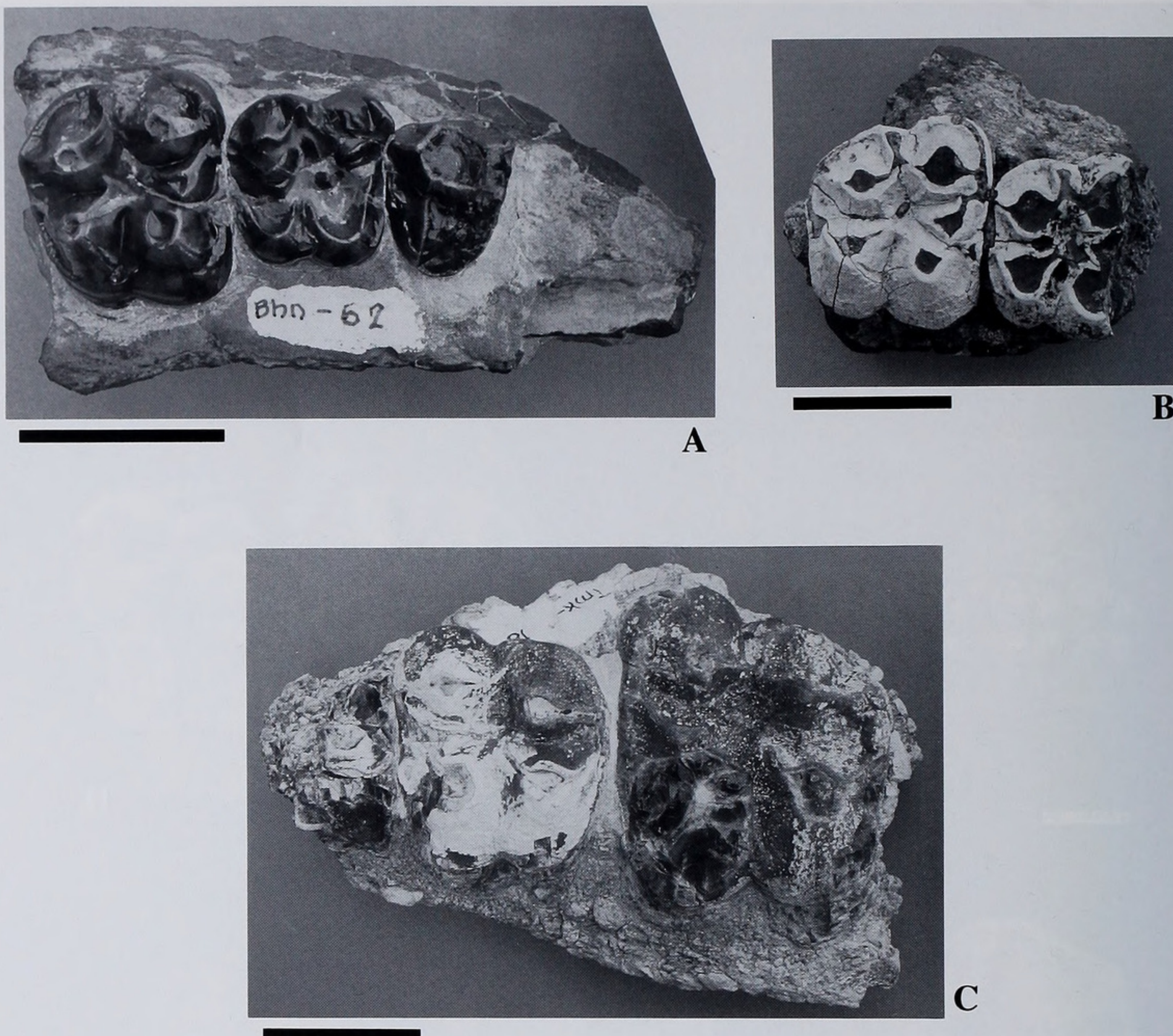
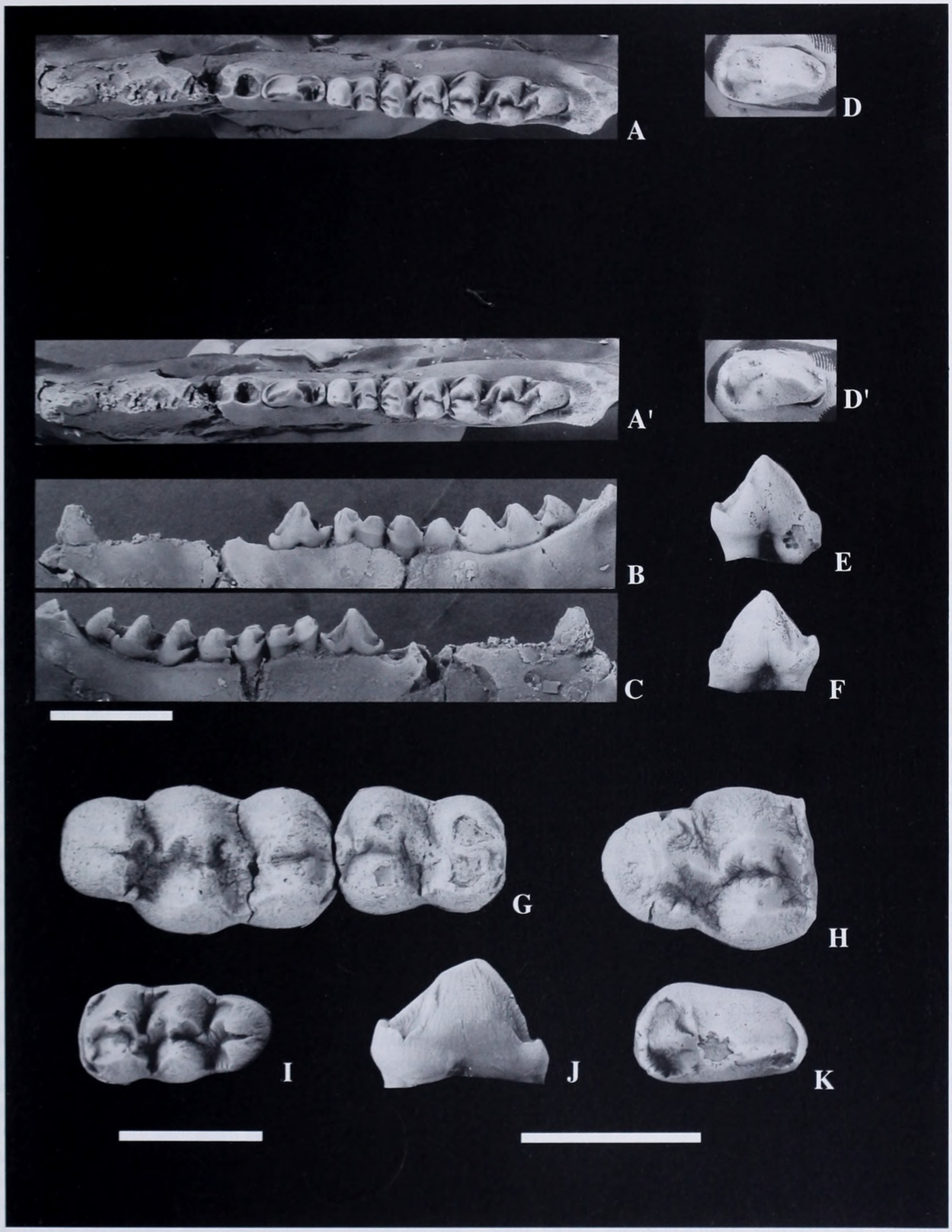


Figure 4. New upper dental materials of the Pondaung anthracotheres (*Anthracotherium*) in occlusal view (2). **A**. NMMP-KU 0413, a right maxillary fragment with P^4M^{1-2}. **B**. NMMP-KU 0216, a right maxillary fragment with M^{2-3}. **C**. NMMP-KU 0329, a left maxillary fragment with M^{1-3}. Scale bars = 2 cm.

Museum of Myanmar. We did not find any critical differences in selenodonty and style development between the Pondaung *Anthracothema* and *Anthracokeryx*. Furthermore, we did not recognize any dental characteristics separating these two Pondaung anthracotheriid genera. For example, NMMP-KU 0056, a right maxillary fragment with M^{2-3} (Figure 3D), has large dental size suggesting that it is referable to *Anthracothema*. However, the molar styles of this material are developed as well as or more than the small molar materials in Figure 3G–K, which may be referable to *Anthracokeryx*. Therefore, we conclude that the two genera are identical to each other.

➡ **Figure 5.** New lower dental materials of the Pondaung anthracotheres (*Anthracotherium*). **A, A', B–C**. NMMP-KU 0052, a right mandibular fragment with P_1P_4–M_3: A, A', occlusal view (stereo pair); B, lingual view; C, buccal view. **D, D', E–F**. NMMP-KU 0086, a left P_4: E, E', occlusal view (stereo pair); F, lingual view; G, buccal view. **G**. NMMP-KU 0330, a left mandibular fragment with M_{2-3}, in occlusal view. **H**. NMMP-KU 0419, a talonid part of left M_3, in occlusal view. **I**. NMMP-KU 0332, a right mandibular fragment with M_3, in occlusal view. **J, K**. NMMP-KU 0433, a right P_4; J, lingual view; K, occlusal view. Scale bars = 2 cm (left middle scale corresponds to A–C, A', and left lower scale corresponds to D–K, D', and right lower scale corresponds to J–K).


A
D
A'
D'
B
E
C
F
G
H
I
J
K

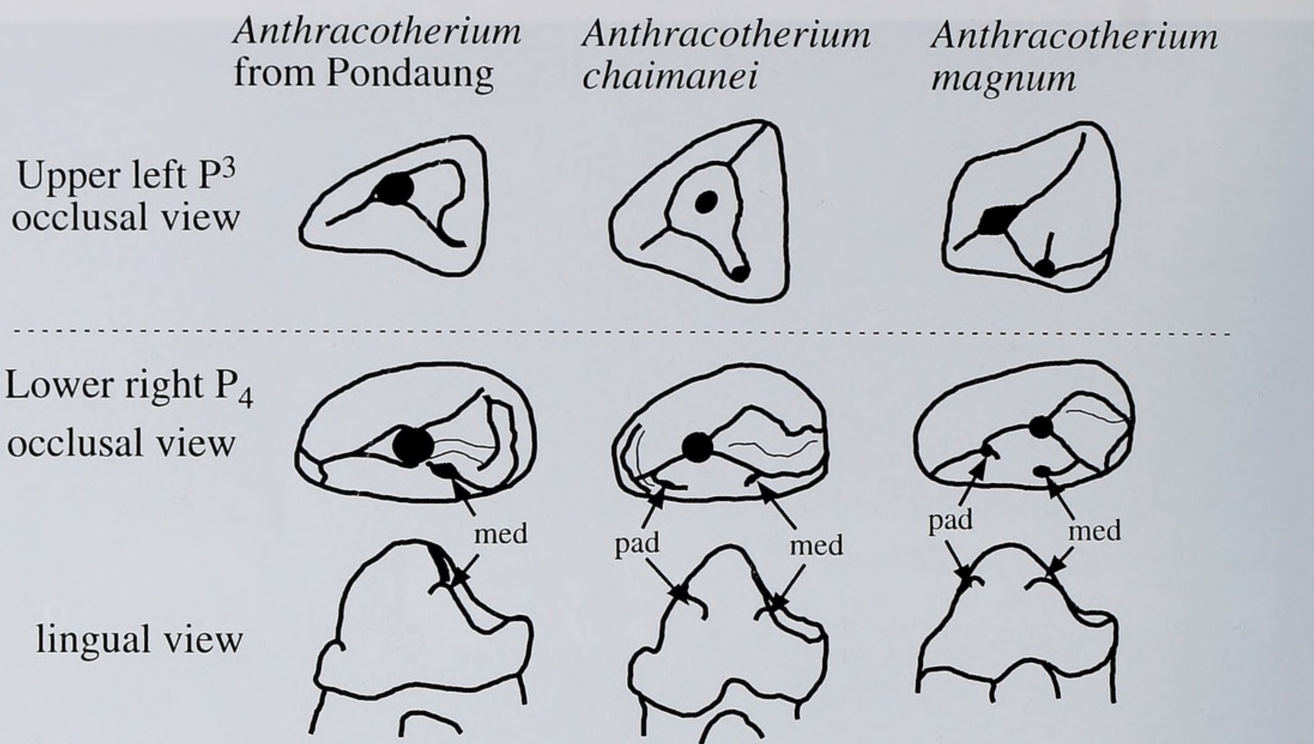


Figure 6. Schematic drawings of left P^3 and right P_4 of the Pondaung *Anthracotherium*, *Anthracotherium chaimanei*, and *Anthracotherium magnum*. Abbreviations: pad, paraconid; med, metaconid.

Furthermore, these two genera, *Anthracothema* and *Anthracokeryx*, are also similar to the genus *Anthracotherium* in regard to dental morphology (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938). Describing a new species of *Anthracotherium* from the late Eocene Krabi basin of Thailand, Ducrocq (1999) synonymized *Anthracothema* to *Anthracotherium*. He mentioned that the graduation observed in the style development of P^4–M^3, in the robustness and orientation of P^3, and in the development of the lingual crests on the lower premolars among *Anthracothema pangan* from Pondaung, *Anthracotherium* chaimanei from Krabi, and *Anthracotherium monsvialense* from Europe probably indicates a direct relationship among these three taxa. We concur with Ducrocq's (1999) conclusion. In addition, we also synonymize *Anthracokeryx* to *Anthracotherium* in this paper because *Anthracokeryx* and *Anthracothema* are not separable from each other, as mentioned above. All these three genera have bunodont dentition, quite similar upper and lower molar morphologies to one another, and mesiodistally elongated simple P_4. No distinct characteristics of dental morphology distinguish the three genera.

Specific identification

Among the species of the genus *Anthracotherium*, definitive characteristics in upper and lower posterior premolars distinguish the Pondaung *Anthracotherium* species from more progressive *Anthracotherium* species, such as *Anthracotherium chaimanei* from the late Eocene Krabi basin of Thailand and European *Anthracotherium* (e.g., *Anthracotherium magnum* from the Oligocene). These premolar characteristics indicate that the Pondaung *Anthracotherium* species resemble each other in their dental morphology more than they do any other species of this genus (Figures 3, 5, 6). The P^3 in all materials of the Pondaung *Anthracotherium* has a mesiodistally elongated triangular outline in occlusal view with pre- and postprotocrista extending mesiodistally; whereas the P^3 of *A. chaimanei* has a more mesiodistally compressed trianglar outline with the pre- and postprotocrista running more diagonally, and that of *A. magnum* has a trapezoidal outline in occlusal view with pre- and postprotocrista running more diagonally (Figure 6; Ducrocq, 1999). The P_4 in all materials of the Pondaung *Anthracotherium* has a vestigial metaconid but does not have any trace of paraconid, whereas *A. chaimanei* and *A. magnum* have both tiny paraconid and metaconid (Figure 6). The P^4 in all materials of the Pondaung *Anthracotherium* is less selenodont and has much weaker styles than those in the P^4 of *A. magnum* and *A. chaimanei*, as mentioned by Ducrocq (1999). Also, the development of the lingual crests on the lower premolars of the Pondaung *Anthracotherium* is weaker (Ducrocq, 1999). In such premolar morphologies, there are no critical characteristics that distinguish any group

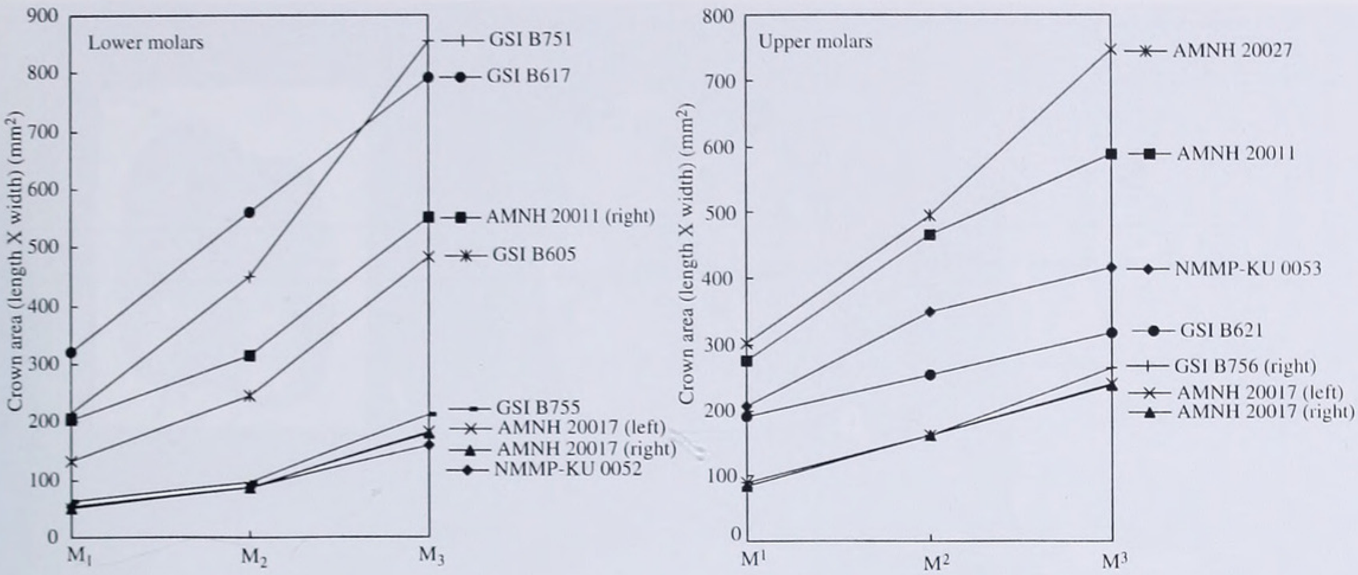


Figure 7. Size change (line chart) of upper and lower molars of the Pondaung anthracotheres in each individual.

among the Pondaung *Anthracotherium*. In addition, although there are individual variations, the Pondaung *Anthracotherium* species are distinct from other *Anthracotherium* species in having such molar morphologies as weaker selenodonty and weaker development of styles (Figures 3–5). These characteristics indicate that the Pondaung *Anthracotherium* species possess the most primitive dentition within the genus (Ducrocq, 1999).

Similar to the case of the dental morphology, the dental sizes of the Pondaung anthracotheres are highly variable. Figure 7 shows the line chart of the molar areas (width X length) in individuals of the Pondaung anthracotheres. The size of $M^1/_1$ relative to $M^2/_2$ and $M^2/_2$ relative to $M^3/_3$ in a single individual is not constant among the Pondaung anthracotheres. For example, M_1 in GSI B751 is much smaller than in GSI B617, while M_3 in the former is rather larger than in the latter. This kind of variation shown in Figures 7 can be explained by individual variation and cannot be attributed to specific differences, as mentioned below.

The dental sizes of each tooth class of all the Pondaung anthracothere materials are also highly variable (Figures 8, 9). For example, the size of smallest M^3 is about 15 mm in width and 14 mm in length, while that of largest M^3 is about 45 mm in width and 39 mm in length (Figure 8). Such size differences do not support the idea that the Pondaung anthracotheres consist of one species. However, this distributional pattern of the dental size supports the argument that these animals belong to the same taxonomic category (that is, genus) because the scatter plots of the mesiodistal length and buccolingual width of $P^3/_3$–$M^3/_3$ are easily fitted to a straight-line by simple regression (Figures 8, 9).

Among the dental size distributions (Figures 8, 9), it is noteworthy that the M_1 size can be more readily divided into four groups than the other tooth classes. In general, the first molars are the first of the adult dentition to erupt and express less size variation among the adult dentition. A number of extant herbivores, including both browsing and grazing forms and certain species of hippos and suids, compensate for tooth wear by sequential or delayed tooth eruption (Kron and Manning, 1998). As the anterior teeth (and/or teeth erupting earlier) wear out, the emerging last molars (typically enlarged) take a progressively greater role in food comminution, resulting in no net loss of feeding efficiency (Kron and Manning, 1998). Thus, the teeth erupting later (posterior molars and premolars) are considered to express much wider dental size variations than do first molars in each species. In particular, lower first molars (M_1) have been considered to express less size variation compared to upper first molars (M^1), and to correlate very closely to the body size of mammals compared to other tooth classes (Gingerich, 1974; Gingerich and Schoeninger, 1979; Legendre, 1986, 1989; Conroy, 1987; Legendre and Roth, 1988; Dagosto and Terranova, 1992; Bown *et al.*, 1994).

Therefore, the distributional pattern of M_1 size ($\sim$ body size) in the Pondaung anthracotheres (Figure 9) suggests that the Pondaung anthracotheres can be divided into four subgroups within a single taxonomic group, that is, four species within a single genus, although a very high degree of size variation exists particularly in the posterior molars.

In relation to the specific classification of the Pondaung anthracotheres, we should mention here one dental charac-

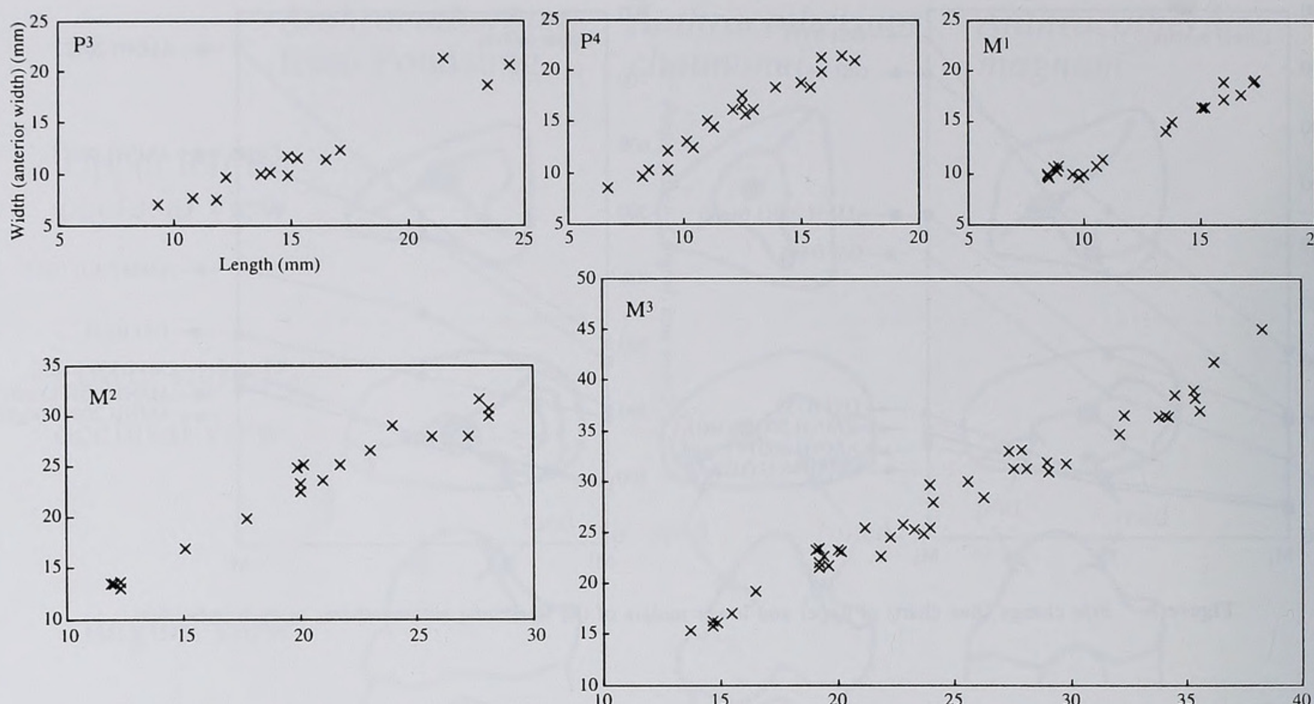


Figure 8. Size distribution of P^{3-4} and upper molars of the Pondaung anthracotheres.

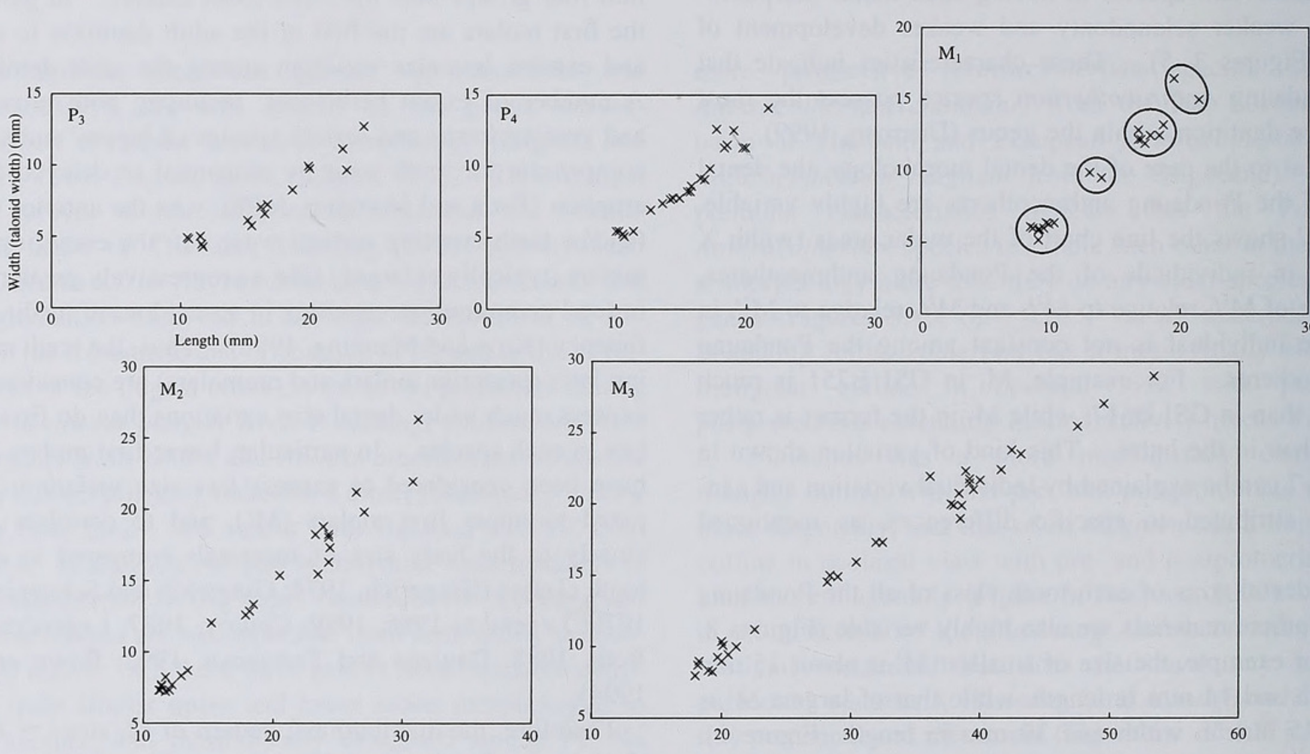


Figure 9. Size distribution of P_{3-4} and lower molars of the Pondaung anthracotheres.

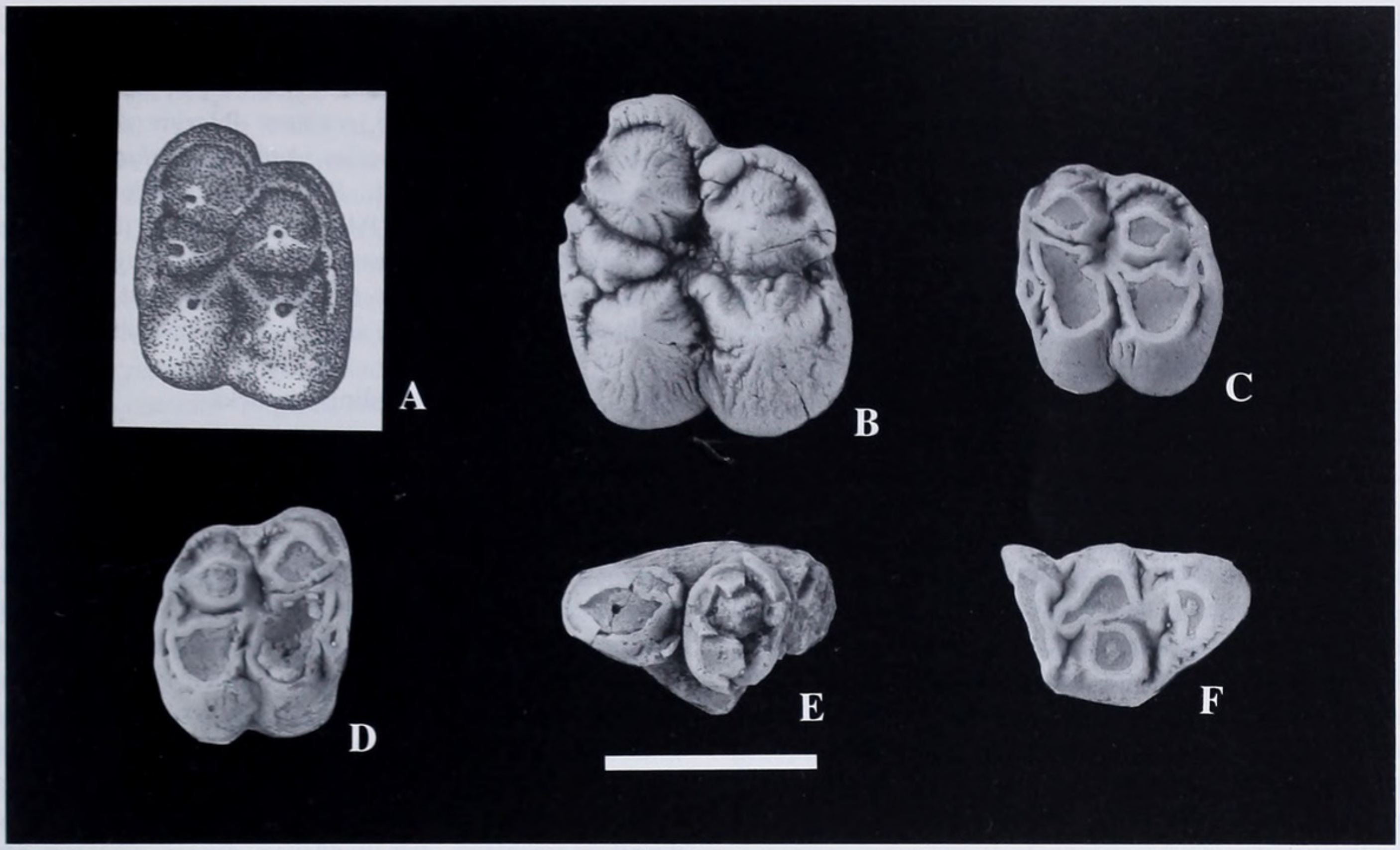


Figure 10. The Pondaung anthracothere materials of *Anthracohyus*-type in occlusal view. **A**. GSI B603 (holotype of *Anthracohyus choeroides*), a left M^3. **B**. NMMP-KU 0452, a left M^3. **C**. NMMP-KU 0454, a left M^3. **D**. NMMP-KU 0453, a right M^3. **E**. NMMP-KU 0500, a left maxillary fragment with P^{3-4}. **F**. NMMP-KU 0475, a right M_3. Scale bar = 2 cm.

teristic of M_3. Pilgrim (1928) distinguished the two small Pondaung anthracotheres, *Anthracokeryx ulnifer* and *Anthracokeryx myaingensis*, from one another on the basis of the morphology of the hypoconulid on M_3; the former has a single cusp at the hypoconulid region on M_3, whereas the latter has a double cusp. Although most of the Pondaung anthracotheres have a double cusp at the hypoconulid region on M_3, the buccal of which is always larger and more distinct than the lingual one, the development of the lingual one is highly variable among all the examples of M_3 in the Pondaung anthracotheres. For example, the lingual cusp in the hypoconulid on M_3 is almost as large as the buccal one in NMMP-KU 0330 (Figure 5G), whereas it is very small and faint in NMMP-KU 0419 (Figure 5H). We consider this difference to be individual variation, not a specific characteristic.

Status of *Anthracohyus*

We also synonymize the remaining genus among the Pondaung anthracotheres, *Anthracohyus*, to *Anthracotherium*. Although *Anthracohyus* has unique dental structures in the upper molars (GSI B603, Figure 10A) (Pilgrim and Cotter, 1916; Pilgrim, 1938; Colbert, 1938), the basic structures of its upper molars are referable to those of the Pondaung *Anthracotherium* (Figures 3, 4). Furthermore, the lower dental material of *Anthracohyus choeroides*, GSI B605 (a right mandibular fragment with complete dentition) (Pilgrim and Cotter, 1916, pl. 2, figs. 3, 3a-e, 4, 4a-e), is identical to that of *Anthracokeryx birmanicus* from the Pondaung Formation (Pilgrim, 1928, pl. 4, fig. 5; Colbert, 1938, fig. 45); there is no morphological or size distinction among the lower dental materials of the two species.

On the other hand, there are a few new specimens whose dental morphologies seem to be identical to that of *Anthracohyus* (Figure 10B-F): NMMP-KU 0452 (a left M^3), 0453 (a right M^3), 0454 (a left M^3), 0475 (a right M_3), and 0500 (a left maxillary fragment with P^{3-4}) [the latter four specimens (NMMP-KU 0453, 0454, 0475, and 0500) probably belong to the same individual]. The upper molars amomg these (NMMP-KU 0452, 0453, 0454) have characteristics of *Anthracohyus*: very conical cusps, no or very vestigial styles on the upper dentition, and mesiodistally shorter buccal margins than the lingual one on the upper molars. The three examples of M^3, GSI B603 (type of *Anthracohyus choeroides*) (length: 21.2 mm;

width: 25.4 mm), NMMP-KU 0452 (length: 27.9 mm; width: 33.0 mm), and NMMP-KU 0453 (length: 19.6 mm; width: 21.8 mm), are separately scattered in the same linear size-distributional pattern prevalent among the Pondaung anthracotheres (Figure 6). Although these three specimens are not M_1 and are considered to have relatively great size variation, they may be referred to the second largest, largest, and second smallest groups among the four groups of the Pondaung anthracotheres mentioned above, respectively, according to their sizes. Therefore, this size-distributional pattern also suggests that these *Anthracohyus* -type materials express one of the variations among the Pondaung anthracotheres, that is, species of *Anthracotherium*.

In conclusion, taking the variations of molar morphology (particularly development of upper molar styles) and size of the Pondaung anthracotheres into consideration (Figures 3-5), we interpret the dental morphology of *Anthracohyus* as one of the unusual individual variations of the Pondaung *Anthracotherium*. Otherwise, a multiplicity of species (of *Anthracothema*, *Anthracokeryx*, and *Anthracohyus*) which are morphologically and phyletically very close to one another, have to be maintained in a single fossil fauna (the Pondaung fauna). Such a situation seems unreasonable.

Classification

To review, we synonymize all the genera of the Pondaung anthracotheres (*Anthracothema* Pilgrim, 1928, *Anthracokeryx* Pilgrim and Cotter, 1916, and *Anthracohyus* Pilgrim and Cotter, 1916) to *Anthracotherium* Cuvier, 1822. We group the Pondaung *Anthracotherium* materials into four species on the basis of M_1 size (~ body size). Materials lacking M_1 are tentatively assigned to one of the four species based on the sizes of available teeth (Appendix).

There is a possibility that the larger two and smaller two of the four species might in fact be sexual dimorphic pairs as implied by Holroyd and Ciochon (1991). Most anthracotheres show a moderate amount of sexual dimorphism, but it is expressed by the canines: the individuals adjudged to have been male have larger canines than do the females (Kron and Manning, 1998). However, the fossil materials of the Pondaung anthracotheres are too poor to evaluate distribution of canine size, so there is no evidence to confirm that the larger two and smaller two represent male-and-female of sexually dimorphic species. Also, no critical difference in canine size relative to M_1 is observed among the currently available materials. Therefore, we treat these four groups of the Pondaung *Anthracotherium* as four species in this paper.

Although the specific nomenclature of the Pondaung anthracotheres has been very complicated as mentioned above (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938), the following four species names can be retained based on the rule of priority: largest species, *Anthracotherium pangan* Pilgrim and Cotter, 1916; second largest species, *Anthracotherium crassum* Pilgrim and Cotter, 1916; second smallest species, *Anthracotherium birmanicum* (Pilgrim and Cotter, 1916); and smallest species, *Anthracotherium tenuis* (Pilgrim and Cotter, 1916). The possibility remains that the larger two (*A. pangan* and *A. crassum*) and smaller two (*A. birmanicum* and *A. tenuis*) might each be combinable as a sexually dimorphic species.

Concluding remarks

The dental morphological comparisons in this study indicate that the Pondaung anthracotheres consist of four species of one genus (*Anthracotherium*). Their dental morphology, such as selenodonty, development of styles, and premolar shapes, suggest that the four species are much more similar to one another than to any other species of *Anthracotherium* from other deposits, although the dental morphology trend seems to be highly variable within the Pondaung *Anthracotherium*. In addition, the group of Pondaung *Anthracotherium* species has the other following features: (1) it is the oldest among the genus; (2) in basic dental morphology, the Pondaung *Anthracotherium* are likely to be the most primitive among the genus; and (3) their fossil materials predominate in collections of the Pondaung mammal fauna, suggesting a dominant population size (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938; Tsubamoto, 2001). Therefore, it is suggested that: (1) the genus *Anthracotherium* originated and rapidly radiated around the Pondaung area during the latest middle Eocene, and (2) *Anthracotherium* migrated from southern East Asia to Europe during the latest middle to late Eocene (Ducrocq, 1995).

Systematic paleontology

Order Artiodactyla Owen
Family Anthracotheriidae Leidy
Genus ***Anthracotherium*** Cuvier, 1822

Synonyms.—*Anthracohyus* Pilgrim and Cotter, 1916; *Anthracokeryx* Pilgrim and Cotter, 1916; *Anthracothema* Pilgrim, 1928.

Type species.—*Anthracotherium magnum* Cuvier, 1822.

Included species from Europe. — *Anthracotherium monsvialense* De Zigno, 1888; *Anthracotherium alsaticum* Cuvier, 1822; *Anthracotherium seckbachense* Kinkelin, 1884; *Anthracotherium illyricum* Teller, 1886; *Anthracotherium bumbachense* Stehlin, 1910; *Anthracotherium cuvieri* Gaudry, 1873; *Anthracotherium hippoideum* Rütimeyer, 1857; *Anthracotherium valdense*

Kowalevski, 1876; *Anthracotherium dalmatinum* von Meyer, 1854. (after Ducrocq, 1999)

Included species from Asia.—*Anthracotherium bugtiense* Pilgrim, 1907 (*sensu* Pickford, 1987); *Anthracotherium silistrense* Pentland, 1828 (*sensu* Pickford, 1987); *Anthracotherium changlingensis* Zhao, 1993; *Anthracotherium chaimanei* Ducrocq, 1999; *Anthracotherium thailandicus* (Ducrocq, 1999) new combination; *Anthracotherium gungkangensis* (Qiu, 1977) new combination; *Anthracotherium verhoeveni* (von Koenigswald, 1967); *Anthracotherium pangan* Pilgrim and Cotter, 1916; *Anthracotherium crassum* Pilgrim and Cotter, 1916; *Anthracotherium birmanicum* (Pilgrim and Cotter, 1916) new combination; *Anthracotherium tenuis* (Pilgrim and Cotter, 1916) new combination.

Revised diagnosis.—Large- to small-sized bunodont and primitive anthracothere. Differs from selenodont and bunoselenodont anthracotheres, such as *Elomeryx* and *Bothriogenys*, in having much simpler premolars and less developed selenodonty. Differs from *Siamotherium* in having double premetacristid on the lower molars (there is no distinct outer metacristid on those of *Siamotherium*), much better developed molar styles, less lingually located molar metacone in relation to paracone, much less mesiodistally compressed M^3, and much better developed protocone compared to paracone on P^{3-4}. Differs from *Anthracosenex* in having mesially or mesiobuccally oriented outer premetacristid rather than buccally oriented in *Anthracosenex*. Differs from *Heptacodon* in having less developed P_4 cristids, and in lacking such strongly developed and prominent styles on the upper molars as in *Heptacodon*, and molar postentocristid that runs distobuccally and links to posthypocristid making a V-shaped notch. Differs from *Microbunodon* in having more bunodont cusps, less developed cingulum, rather straight (not V-shaped) ectoloph on P^{3-4}, and mesiodistally longer P^3.

Anthracotherium pangan Pilgrim and Cotter, 1916

Anthracotherium pangan Pilgrim and Cotter, 1916, p. 59–60, pl. 4, figs. 1-3.

Anthracothema pangan (Pilgrim and Cotter, 1916). Pilgrim, 1928, p. 10–13, pl. 1, figs. 1–7; Colbert, 1938, p. 353–355, figs. 41–42.

Anthracohyus rubricae Pilgrim and Cotter, 1916 (in part), p. 55–57, pl. 2, fig. 5–6, pl. 3, fig. 1–2.

Anthracothema rubricae (Pilgrim and Cotter, 1916) (in part). Pilgrim, 1928, p. 14; Colbert, 1983, p. 356–358.

Anthracotherium crassum Pilgrim and Cotter, 1916 (in part), p. 60–61, pl. 4, fig. 4–5, 5a.

Anthracothema crassum (Pilgrim and Cotter, 1916) (in part). Pilgrim, 1928, p. 16–18; Colbert, 1938, p. 355–356.

Anthracohyus palustris Pilgrim and Cotter, 1916, p. 58, pl. 3, figs. 7–9.

Anthracothema palustre (Pilgrim and Cotter, 1916). Pilgrim, 1928, p. 14–16, pl. 2, figs. 8–10; Colbert, 1938, p. 355.

Lectotype.—GSI B619, a left maxillary fragment with M^{2-3} (Colbert, 1938).

Revised diagnosis.—Large-sized and one of the most primitive *Anthracotherium* species. The dental morphology is almost identical to other Pondaung *Anthracotherium* species (i.e., *A. crassum*, *A. birmanicum*, and *A. tenuis*). Differs from the other Pondaung *Anthracotherium* species in having larger M_1. Differs from more progressive *Anthracotherium*, such as *A. magnum*, *A. monsvialense*, *A. bugtiense*, and *A. chaimanei*, in having slightly less selenodont cusps, less developed styles, mesiodistally elongated triangular outline of P^3 in occlusal view having mesiodistally (not diagonal to the tooth row) extending paracrista, less developed lower premolar cristids, and less molariform P_4 lacking a trace of paraconid. Differs from *A. thailandicus* in having slightly lower tooth crown in the lower dentition, less selenodonty, and metaconid on P_4, and lacking paraconid on P_4. Differs from *A. silistrense* in having larger size and slightly lower P_{3-4}. Differs from *A. gungkangensis* in having larger size, slightly less developed selenodonty and styles, more rounded outline of upper molars in occlusal view, and slightly wider and shorter upper molars. Differs from *A. verhoeveni* in lacking hypertrophied metastyle on the distal face of M^3. Differs from *A. changlingensis* in being smaller.

Anthracotherium crassum Pilgrim and Cotter, 1916

Anthracotherium crassum Pilgrim and Cotter, 1916 (in part), p. 60–61, pl. 5, fig. 1.

Anthracothema crassum (Pilgrim and Cotter, 1916) (in part). Pilgrim, 1928, p. 16–18; Colbert, 1938, p. 355–356.

Anthracohyus rubricae Pilgrim and Cotter, 1916 (in part), p. 55–57, pl. 2, fig. 7, pl. 3, figs. 3–6, 5a.

Anthracothema rubricae (Pilgrim and Cotter, 1916) (in part). Pilgrim, 1928, p. 14, pl. 2, figs. 1–7; Colbert, 1983, p. 356–358, figs. 43–44.

Anthracohyus choeroides Pilgrim and Cotter, 1916 (in part), p. 52–55, pl. 2, figs. 1–2.

Anthracokeryx moriturus Pilgrim, 1928, p. 32, pl. 4, figs. 1–3; Colbert, 1938, p. 376–379, figs. 51–52.

Holotype.—GSI B615, a left maxillary fragment with M^{2-3}.

Revised diagnosis. — Second largest (medium-sized) Pondaung *Anthracotherium*. Differs from *A. pangan* in having smaller M_1. Differs from *A. birmanicum* and *A. tenuis* in having larger M_1.

Anthracotherium birmanicum (Pilgrim and Cotter, 1916)

Anthracokeryx birmanicus Pilgrim and Cotter, 1916 (in part), p. 61–62, pl. 5, figs. 2, 4; Pilgrim, 1928, p. 18–19, pl. 4, figs, 5, 5a; Colbert, 1938, p. 360–362, fig. 45.

Anthracokeryx hospes Pilgrim, 1928, p. 29–30; Colbert, 1938, p. 362–363.

Anthracohyus choeroides Pilgrim and Cotter, 1916 (in part), p. 52–55, pl. 2, figs. 3–4, 3a–3e, 4a–4e.

Holotype.—GSI B621, a right maxillary fragment with P^3–M^3.

Revised diagnosis. — Second smallest (medium-sized) Pondaung *Anthracotherium*. Differs from *A. pangan* and *A. crassum* in having smaller M_1. Differs from *A. tenuis* in having larger M_1.

Anthracotherium tenuis (Pilgrim and Cotter, 1916)

Anthracokeryx tenuis Pilgrim and Cotter, 1916, p. 62–63, pl. 5, figs. 6–8; Colbert, 1938, p. 364.

Anthracokeryx birmanicus Pilgrim and Cotter, 1916 (in part), p. 61–62, pl. 5, figs. 3, 5.

Anthracokeryx bambusae Pilgrim, 1928, p. 29; Colbert, 1938, p. 363.

Anthracokeryx myaingensis Pilgrim, 1928, p. 30–31, pl. 3, figs. 4–7; Colbert, 1938, p. 364–365.

Anthracokeryx ulnifer Pilgrim, 1928, p. 19–29, pl. 3, figs. 1–3, pl. 4, fig. 6; Colbert, 1938, p. 365–375, figs. 46–50.

Holotype.—GSI B625 (a left maxillary fragment with M^{1-2}) and GSI B626 (a left mandibular fragment with M_1 and posterior part of dP_4).

Revised diagnosis. — Smallest (small-sized) Pondaung *Anthracotherium*. Differs from other Pondaung *Anthracotherium* species in having smaller M_1. Further differs from *A. thailandicus* in lacking the high and ventrally salient mandibular symphysis under P_1, and in having longer diastema between P_2 and P_3. Further differs from *A. silistrense* in having longer diastema in the anterior premolar dentition.

Family Helohyidae Marsh

Genus ***Pakkokuhyus*** Holroyd and Ciochon, 1995

Pakkokuhyus lahirii (Pilgrim, 1928)

Anthracokeryx? *lahirii* Pilgrim, 1928, p. 32–33, pl. 4, figs 4, 4a; Colbert, 1938, p. 379.

Pakkokuhyus lahirii (Pilgrim, 1928). Holroyd and Ciochon, 1995, p. 178–180, fig. 1A, B.

Siamotherium pondaungensis Ducrocq *et al.*, 2000, p. 756, fig. 2.

Holotype.—GSI B766, right mandibular fragment with M_{1-3}.

Revised diagnosis.—A helohyid having bunodont and conical cusps, lacking hypocone at least on M^{2-3} and paraconid at least on M_{2-3}. Differs from *Gobiohyus* and *Helohyus* in having more bunodont and conical cusps, a basally inflated crown, larger metaconule on M^3, entoconid slightly posterior to hypoconid and less pronounced ectoflexid on the lower molars, a continuous labial cingulid on M_3, shorter and less distinct hypoconulid loop on M_3, stronger labial cingulids on M_{1-2}, and absolutely and relatively greater mandibular depth, and in lacking trace of molar hypocone, lingual cingulum and stylar cusps on the upper molars, and molar paraconid. Further differs from *Gobiohyus* in having relatively higher crowns and from *Helohyus* in having a stronger hypoconulid on the distal cingulid and in lacking accessory cuspulids on the hypoconulid loop. Differs from *Progenitohyus* in having smaller dental size, larger hypoconulid on M_3, and labial cingulid on M_3, and in lacking paraconid on M_2. Differs from the possible raoellid *Haqueina* in having entoconid slightly posterior to hypoconid, a stronger hypoconulid on the distal cingulid, and weaker hypolophid and cristid obliqua, a weaker and less constricted hypoconulid loop and a single hypoconulid on M_3. Differs from anthracotheriids in having smaller dental size, more conical (less selenodont) cusps, straight hypolophid on the lower molars, and shorter hypoconulid loop on M_3, and in lacking a double premetacristid on the lower molars.

Comments on some other Eocene anthracotheres from Asia

We reappraise several Eocene anthracotheres from Asia in relation to the revision of the Pondaung anthracotheres. *Anthracothema* and *Anthracokeryx* have been also reported from other deposits in the Eocene of Asia. Because the Pondaung *Anthracothema* and *Anthracokeryx* are the types of the two genera and the two were referred to *Anthracotherium*, all species of *Anthracothema* and *Anthracokeryx* are referred to *Anthracotherium*, except for *Anthracokeryx sinensis* (including *Anthracokeryx dawsoni* and *Anthracothema minima*), *Anthracokeryx litangensis*, and *Anthracothema lijiangensis*.

Anthracokeryx birmanicus, *Anthracokeryx moriturus*, *Anthracokeryx* sp. (= *Anthracokeryx* sp. cf. *bumbusae*), and *Anthracothema rubricae*, which are conspecific with one or another of the Pondaung anthracotheres, are recorded from the late Eocene Naduo Formation, Bose and Yongle basins, Guangxi, southern China (Chow, 1957; Tang *et al.*, 1974; Qiu, 1977; Russell and Zhai, 1987). The materials of these species are poor, so that for the time being we tentatively refer these materials to the same species as

Anthracotherium from the Pondaung Formation. We refer *Anthracothema rubricae* and *Anthracokeryx moriturus* to *Anthracotherium crassum*, *Anthracokeryx birmanicus* to *Anthracotherium birmanicum*, and *Anthracokeryx* sp. to *Anthracotherium* sp.

Anthracokeryx gungkangensis and *Anthracokeryx kwangsiensis* are recorded from the late Eocene Gongkang Formation, which overlies the Naduo Formation (Qiu, 1977). *Anthracokeryx kwangsiensis* is also recorded from the Naduo Formation (Zhao, 1993). Ducrocq (1999) mentioned that these two species likely correspond to only one form in terms of their very similar morphology and dimensions. Following his suggestion, we treat *Anthracokeryx kwangsiensis* as a junior synonym of *Anthracokeryx gungkangensis*. Therefore, both of these species are referred to *Anthracotherium gungkangensis*.

Anthracokeryx sinensis is recorded from the Heti (Yuanchu basin), Xiangshan (Lijiang basin, Yunnan), and Huangzhuang (Qufu, Shandong) formations of the middle Eocene of China (Zdansky, 1930; Xu, 1962; Shi, 1989; Zhong *et al.*, 1996). We think that *Anthracokeryx sinensis* is not a bunodont but a primitive bunoselenodont anthracothere, so that this species is not referable to *Anthracotherium* (bunodont anthracothere). The P_4 of *Anthracokeryx sinensis* (Zdansky, 1930, pl. 1, fig. 18; Xu, 1962, p. 241, fig. 1-3a) is much more molarized than that of progressive *Anthracotherium* species, such as *Anthracotherium magnum*. It has a somewhat triangle-shaped trigonid in occlusal view and resembles that of bunoselenodont or selenodont anthracotheres. Also, the upper molars of *Anthracokeryx sinensis* reveal stronger selenodonty than those of *Anthracotherium*. In particular, the paraconule of the upper molars of *A. sinensis* is much more selenodont than that of *Anthracotherium*. The selenodonty of the upper molars of *A. sinensis* also appears similar to that of bunoselenodont anthracotheres, such as *Bothriogenys*. Therefore, we consider that it is better to establish a new genus for *Anthracokeryx sinensis*.

We suspect that it is better to synonymize both *Anthracokeryx dawsoni* and *Anthracothema minima* to *Anthracokeryx sinensis*. First, *Anthracokeryx dawsoni* was described by Wang (1985) from the late middle Eocene Zhaili Member of the Heti Formation (Yuanchu basin, central China), which also yields *Anthracokeryx sinensis*. The material of *Anthracokeryx dawsoni* consists of a skull with upper dentition. This material (IVPP V7915) has very similar dental morphology and size to *Anthracokeryx sinensis* except for a few dental differences (Xu, 1962, pl. 1, fig. 2-3, 8, 2A-3A, pl. 2, fig. 2, 2A; Wang, 1985, p. 58, pl., 1); such subtle differences seem to be within the range of intraspecific variation. Second, *Anthracothema minima* was described by Xu (1962, p. 233, 244, pl. 1, fig. 1, 1A) from the late middle Eocene Rencun Member of the Heti Formation, which also yields *Anthracokeryx sinensis*. *Anthracothema minima* consists of only one upper molar (IVPP V2661), which has conical cusps like that of the Pondaung *Anthracothema* and *Anthracohyus*. However, its overall dental morphology and size are similar to that of *Anthracokeryx sinensis*. Taking the case of the Pondaung anthracotheres mentioned above into consideration, it may be better to consider that *Anthracothema minima* is also not a distinct species but one of the variations of *Anthracokeryx sinensis*.

Anthracokeryx litangensis was described from the late Eocene to early Oligocene Gemusi basin of Litang County (Sichuan, China), based on a right mandibular fragment with P_4M_1 and an astragalus by Zhong *et al.* (1996). Although its only preserved lower molar (M_1) is heavily worn (Zhong *et al.*, 1996, p. 265, pl. 21, fig. 3), the lower molar is rather selenodont than bunodont, having more lingually oriented preparacristid and cristid obliqua than *Anthracotherium* and *Anthracokeryx sinensis*. Its P_4 is mesiodistally elongated and with well-developed cristids, suggesting it is referable neither to *Anthracotherium* nor to *Anthracokeryx sinensis*. The dental morphology of *Anthracokeryx litangensis* is rather similar to that of selenodont anthracotheres, such as *Bothriodon*.

Anthracokeryx thailandicus was described from the late Eocene Krabi basin of Thailand by Ducrocq (1999). We refer this species to the genus *Anthracotherium* and introduce for it the new combination *Anthracotherium thailandicus*.

Ducrocq (1999, p. 125, pl. 14G) described an anthracotheriid left M^3 (DMR TF2662) from the Krabi basin as Anthracotheriinae gen. *et* sp. indet. This material is morphologically similar to that of *Anthracohyus* from the Pondaung Formation (Ducrocq, 1999) and is similar to *Anthracotherium thailandicus* in size. Thus, DMR TF2662 might be one of the individual variations of *A. thailandicus*.

Anthracokeryx sp. from the middle Eocene Lizhuang Formation (Henan, central China) was described by Wang and Zhou (1982) based on a broken right upper molar. Although this material was not illustrated, Wang and Zhou (1982) mentioned its morphological similarity to upper molars of *Anthracokeryx sinensis*. Here, we tentatively refer this material to cf. *Anthracokeryx sinensis*.

Cf. *Anthracokeryx* sp. was cited in the early to early middle Eocene Kuldana Formation (Indo-Pakistan) by Gingerich *et al.* (1979) and Russell and Zhai (1987). It is only represented by BMNH 32168, a left M_3, which was referred to *Lammidhania wardi* (Anthracobunidae) by Gingerich (1977). However, the dental morphology of BMNH 32168 is identical M_3 of bunoselenodont anthracotheres, such as *Bothriogenys*, and is definitely not referable to *Anthracokeryx* (= *Anthracotherium*). Besides, BMNH 32168 may be from the overlying Murree Formation (Russell and Zhai, 1987). Therefore, the existence of an *Anthracokeryx* (*Anthracotherium*)-like anthracothere in the Kuldana Formation is highly doubtful.

Cf. *Anthracokeryx* sp. was cited also in the late middle Eocene Shara Murun Formation (Inner Mongolia, northern China) by Russell and Zhai (1987). The sole specimen of this form, AMNH 22090 (a right mandibular fragment with M_3), was originally described as *Gobiohyus robustus* (Helohyidae) by Matthew and Granger (1925). The M_3 of the specimen has three large and distinct cusps at the hypoconulid region and reveals a bilophodont structure, which have never been seen in anthracotheres. Therefore, the existence of an *Anthracokeryx* (*Anthracotherium*)-like anthracothere in the Shara Murun Formation is also highly doubtful.

Anthracothema lijiangensis was described from the middle Eocene Xiangshan Formation (Lijiang basin, Yunnan, southern China) by Zong *et al.* (1996). This species differs from *Anthracotherium* in having straight (not V-shaped) hypolophid, mesiodistally rather than mesiolingually oriented cristid obliqua, and no buccal premetacristid directed mesiobuccally on the lower molars (Zong *et al.*, 1996, p.279, pl. 35, fig. 2). These characteristics demand rejection of a reference of *Anthracothema lijiangensis* to *Anthracotherium*. It may be better to establish a new genus for this species (*Anthracothema lijiangensis* is distinguished from *Anthracokeryx sinensis*). On the other hand, although the material of *Anthracothema lijiangensis* was referred to the Anthracotheriidae by Zong *et al.* (1996) and Huang (1999), this familial position of *A. lijiangensis* is also doubtful because the species have straight hypolophid and no trace of mesiobuccally-directed premetacristid on the lower molars, both which are not appropriate to the anthracotheriid diagnosis (Holroyd and Ciochon, 1995).

Anthracotherium chaimanei was originally reported as *Anthracothema* sp. cf. *A. pangan* from the Krabi basin of Thailand by Ducrocq *et al.* (1992). It was formally described by Ducrocq (1999).

Anthracotherium verhoeveni was originally described from Timor (Indonesia) (but see Ducrocq, 1996, p.765) as *Anthracothema verhoeveni* by von Koenigswald (1967). It was referred to the genus *Anthracotherium* by Ducrocq (1999).

Anthracotherium? spp. were cited in the middle middle Eocene Lushi Formation (Henan, central China) by Chow *et al.* (1973). However, this report contained no illustration of their material. In addition, the mammalian fauna of the Lushi Formation, which was referred to the middle middle Eocene (Irdinmanhan East Asian Land Mammal Age) (Russell and Zhai, 1987), is much older than the latest middle Eocene Pondaung Formation including the oldest positive *Anthracotherium* species. Therefore, the presence of the genus *Anthracotherium* in the Lushi Formation is doubtful (Russell and Zhai, 1987).

Heothema is recorded from the late Eocene Naduo and Gongkang Formations (Bose and Yongle basins, Guangxi) and lower part of Yongning Formation (late Eocene or early Oligocene; Nanning basin, Guangxi) of southern China (Tang, 1978; Zhao, 1981, 1983, 1993). Although the genus *Heothema* was synonymized to *Anthracotherium* by Ducrocq (1999), this genus may be valid because: (1) the molars and P^4 of *Heothema* are more selenodont than those of *Anthracotherium*; (2) crests on the lingual face of lower premolars in *Heothema* (Tang, 1978, pl. 3, fig. 1, 1A) are stronger than those in *Anthracotherium*; and (3) P_4 of *Heothema* seems to be more molariform than that of *Anthracotherium*, having a somewhat triangularly-shaped trigonid outline in occlusal view (Tang, 1978, pl. 3, fig. 1). Judging from these morphological points, *Heothema* might be one of the primitive bunoselenodont anthracotheres. For specific division of *Heothema*, we follow the grouping by Ducrocq (1999, p. 121), who recognized two species, *Heothema bellia* and *Heothema chengbiensis*.

Huananothema imparilica was described as a new genus and species of the Anthracotheriidae by Tang (1978) based on an upper molariform tooth from the late Eocene Naduo Formation, which also yields *Heothema*. According to Tang (1978), the type and unique material of *Huananothema imparilica* (IVPP V4964) is an upper molar, and therefore this species is identified by its upper molar having an anterior buccolingual width less than its posterior buccolingual width, in contrast to other anthracotheres (in the upper molars of all other anthracotheres, the anterior buccolingual width is greater than the posterior buccolingual width). However, this feature in IVPP V4964 is a typical dP^4 morphology of large anthracotheres as seen in DMR TF 2901, a right dP^4 of *Anthracotherium chaimanei* from the Krabi basin of Thailand (Ducrocq, 1999, pl. 5, fig. B), and also in NMMP-KU 0327, an upper dental specimen of the Pondaung *Anthracotherium* (Figure 3C). Therefore, IVPP V4964 is dP^4, so that the diagnosis of *Huananothema imparilica* by Tang (1978) is invalid. By comparing its size and morphology with those of anthracotheres from the Naduo Formation, we consider that IVPP V4964 is a dP^4 of *Heothema chengbiensis*. Therefore, we synonymize both the genus *Huananothema* and species *Huananothema imparilica* to genus *Heothema* and species *Heothema chengbiensis*, respectively.

The materials of *Probrachyodus* are poor. Russell and Zhai (1987, p. 130) mentioned that this genus may be inseparable from *Anthracokeryx* (that is, *Anthracotherium* or the same genus as *Anthracokeryx sinensis*). However, the upper molars of *Probrachyodus* show bunoselenodonty, so that this species differs from *Anthracotherium*, which comprises bunodont anthracotheres. *Probrachyodus* is distinct from *Anthracokeryx sinensis* and also further from *Anthracotherium* in having more lingually procumbent molar paracone and metacone. Therefore, we consider this genus a valid one. *Probrachyodus panchiaoensis* was described from the middle Eocene Lumeiyi Formation (Yunnan, Lunan basin, southern China) by Xu (1962). *Probrachyodus*? sp. nov. was cited in the middle Eocene Dongjun Formation (Guangxi, southern China) by Ding *et al.* (1977).

Acknowledgments

We would like to express our sincere gratitude to Brigadier General Than Tun, Major Bo Bo and other personnel of the Office of the Chief of Military Intelligence (formerly Office of Strategic Studies), Ministry of Defence, Union of Myanmar for their guidance and help in the field and museum. Thanks are also due to the curators of the National Museum of the Union of Myanmar who helped us in working at that institution. P. A. Holroyd (UCMP), M. C. McKenna (AMNH), J. Alexander (AMNH), K. C. Beard (CM), D. Haldar (GSI), and Y. Chaimanee (DMR) helped us in working at their respective institutions, and offered comments. The following people also helped us with critical discussions: J.-J. Jaeger and S. Ducrocq (University of Montpellier, France); and T. Setoguchi, F. Masuda, A. Yamaji, H. Kamiya, H. Matsuoka, H. Maeda, and T. Sakai (Department of Geology and Mineralogy, Graduate School of Science, Kyoto University, Japan). Y. Tomida (NSM) helped us in collecting references. This manuscript was improved by two referees, S. Ting (Louisiana State University) and P. A. Holroyd. This research was supported by Overseas Scientific Research Funds (No. 14405019 to N. Shigehara) and the Grants-in-Aid for COE Research (No. 10CE2005) and for JSPS Fellows (No. 9714 to T. Tsubamoto) from the Ministry of Education, Culture, Sports, Science and Technology of Japan.

References

Aung Naing Soe, 1999: Sedimentary facies of the upper part of the Pondaung Formation (in central Myanmar) bearing late Middle Eocene anthropoid primates. *In*, Pondaung Fossil Expedition Team *ed.*, *Proceedings of the Pondaung Fossil Expedition Team*, p. 152–178. Office of Strategic Studies, Ministry of Defence, Yangon.

Aung Naing Soe, Myitta, Soe Thura Tun, Aye Ko Aung, Tin Thein, Marandat, B., Ducrocq, S. and 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*, vol. 1, p. 153–160.

Aye Ko Aung, 1999: Revision on the stratigraphy and age of the primates-bearing Pondaung Formation. *In*, Pondaung Fossil Expedition Team *ed.*, *Proceedings of the Pondaung Fossil Expedition Team*, p. 131–151. Office of Strategic Studies, Ministry of Defence, Yangon.

Bender, F., 1983: *Geology of Burma*, viii + 293 p. Gebrüder Borntraeger, Berlin.

Black, C.C., 1978: Anthracotheriidae. *In*, Maglio, V.J. and Cooke, H.B.S. *eds.*, *Evolution of African Mammals*, p. 423–434. Harvard University Press, Cambridge.

Bown, T.M., Holroyd, P.A. and Rose, K.D., 1994: Mammal extinctions, body size, and paleotemperature. *Proceedings of the National Academy of Sciences of the United States of America*, vol. 91, p. 10403–10406.

Chow, M., 1957: On some Eocene and Oligocene mammals from Kwangsi and Yunnan. *Vertebrata PalAsiatica*, vol. 1, no. 3, p. 201–214, pls. 1–2.

Chow, M., Li, C. and Chang, Y., 1973: Late Eocene mammalian faunas of Honan and Shansi with notes on some vertebrate fossils collected therefrom. *Vertebrata PalAsiatica*, vol. 11, no. 2, p. 165–181. (*in Chinese with English summary*)

Colbert, E.H., 1935: Siwalik mammals in the American Museum of Natural History. *Transactions of the American Philosophical Society, New Series*, vol. 26, p. i–x, 1–401.

Colbert, E.H., 1938: Fossil mammals from Burma in the American Museum of Natural History. *Bulletin of the American Museum of Natural History*, vol. 74, p. 255–436.

Conroy, G.C., 1987: Problems of body-weight estimation in fossil primates. *International Journal of Primatology*, vol. 8, no. 2, p. 115–137.

Coombs, W.P. and Coombs, M.C., 1977: The origin of anthracotheres. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, Heft 10, p. 584–599.

Cuvier, G., 1822: *Recherches sur les ossemens fossiles. Nouvelle édition*, vol. 3, p. 398–403. d'Ocagne, Paris.

Dagosto, M. and Terranova, C.J., 1992: Estimating the body size of Eocene primates: A comparison of results from dental and postcranial variations. *International Journal of Primatology*, vol. 13, no. 3, p. 307–344.

De Zigno, A., 1888: Anthracoterio di Monteviale. *Memorie del Real Istituto Veneto di Scienze, Lettere ed Arti*, vol. 23, p. 1–35.

Ding, S., Zheng, J., Zhang, Y. and Tong, Y., 1977: The age and characteristic of the Liuniu and the Dongjun Faunas, Bose basin of Guangxi. *Vertebrata PalAsiatica*, vol. 15, no. 1, p. 35–45, pls. 1–2. (*in Chinese with English summary*)

Ducrocq, S., 1994a: Les Anthracothères paléogènes de Thaïlande: Paléogéographie et phylogénie. *Comptes Rendus de l'Academie des Sciences*, tome 318, ser. II, p. 549–554.

Ducrocq, S., 1994b: An Eocene peccary from Thailand and the biogeographical origins of the artiodactyl family Tayassuidae. *Palaeontology*, vol. 37, part 4, p. 765–779.

Ducrocq, S., 1995: The contribution of Paleogene anthracotheriid artiodactyls in the paleobiogeographical history of Southern Europe. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, 1995, Heft 6, p. 355–362.

Ducrocq, S., 1996: The Eocene terrestrial mammal from Timor, Indonesia. *Geological Magazine*, vol. 133, no. 6, p. 763–766.

Ducrocq, S., 1997: The anthracotheriid genus *Bothriogenys* (Mammalia, Artiodactyla) in Africa and Asia during the Paleogene: Phylogenetical and paleobiogeographical relationships. *Stuttgarter Beiträge zur Naturkunde, Serie B* (*Geologie und Paläontologie*), vol. 250, p. 1–44.

Ducrocq, S., 1999: The late Eocene Anthracotheriidae (Mammalia, Artiodactyla) from Thailand. *Palaeontographica Abt. A*, vol. 252, p. 93–140, pls. 1–14.

Ducrocq, S., Aung Naing Soe, Aye Ko Aung, Benammi, M., Bo Bo, Chaimanee, Y., Than Tun, Tin Thein and Jaeger. J.-J., 2000: A new anthracotheriid artiodactyl from Myanmar, and the relative ages of the Eocene anthropoid primate-bearing localities of Thailand (Krabi) and Myanmar (Pondaung). *Journal of Vertebrate Paleontology*, vol. 20, no. 4, p. 755–760.

Ducrocq, S., Buffetaut, E., Buffetaut-Tong, H., Helmcke-Ingavat, R., Jaeger, J.-J., Jongkanjanasoontorn, Y. and Suteethorn, V., 1992: A Lower Tertiary vertebrate fauna from Krabi (South Thailand). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, vol. 184, P. 101–122.

Ducrocq, S., Chaimanee, Y., Suteethorn, V. and Jaeger. J.-J., 1996: An unusual anthracotheriid artiodactyl from the late Eocene of Thailand. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, Heft 7, p. 389–398.

Ducrocq, S., Chaimanee, Y., Suteethorn, V. and 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'Academie des Sciences, Paris, Sciences de la Terre et des planètes/Earth and Planetary Sciences*, vol. 325, p. 367–372.

Egi, N. and Tsubamoto, T., 2000: A preliminary report on carnivorous mammals from Pondaung fauna. *In, Oversea Research Report of Studies on Origin and Evolution of Hominoids in East Asia*, p. 103–114. 1997–99 Grant-in-Aid for Scientific Research Reports for Oversea Scientific Survey, Asian Paleoprimatology, vol. 1, 2000. Primate Research Institute, Kyoto University, Japan.

Gaudry, M.A., 1873: Sur l'*Anthracotherium* trouvé à Saint-Menoux (Allier). *Bulletin de la Société géologique de France*, vol. 2, p. 36–40.

Gebo, D.L., Gunnell, G.F., Ciochon, R.L., Takai, M., Tsubamoto, T. and Egi, N., in press: *Eosimias* from Myanmar. *Journal of Human Evolution*.

Gentry, A.W. and Hooker, J.J., 1988: The phylogeny of the Artiodactyla. *In*, Benton, M.J. *ed.*, *The Phylogeny and Classification of the Tetrapods, Volume 2: Mammals*, p. 235–272. Clarendon Press, Oxford.

Gingerich, P.D., 1974: Stratigraphic record of Early Eocene *Hyopsodus* and the geometry of mammalian phylogeny. *Nature*, vol. 248, p. 107–109.

Gingerich, P.D., 1977: A small collection of fossil vertebrates from the middle Eocene Kuldana and Kohat formations of Punjab (Pakistan). *Contributions from the Museum of Paleontology, the University of Michigan*, vol. 24, no. 18, p. 190–203.

Gingerich, P.D., Russell, D.E., Sigogneau-Russell, D. and Hartenberger J.-L., 1979: *Chorlakkia hassani*, a new middle Eocene dichobunid (Mammalia, Artiodactyla) from the Kuldana formation of Kohat (Pakistan). *Contributions from the Museum of Paleontology, the University of Michigan*, vol. 25, no. 6, p. 117–124.

Gingerich, P.D. and Schoeninger, M.J., 1979: Patterns of tooth size variability in the dentition of Primates. *American Journal of Physical Anthropology*, vol. 51, p. 457–465.

Holroyd, P.A. and Ciochon, R.L., 1991: A reappraisal of Burmese anthracotheriid artiodactyls. *Journal of Vertebrate Paleontology*, vol. 11, no. 3, p. 35A.

Holroyd, P.A. and Ciochon, R.L., 1995: A new artiodactyl (Mammalia) from the Eocene Pondaung Sandstones, Burma. *Annals of Carnegie Museum*, vol. 64, no. 3, p. 177–183.

Huang, X., 1999: Middle Eocene mammals of Lijiang Basin, Yunnan. *In*, Wang, Y. and Deng, T. *eds.*, *Proceedings of the Seventh Annual Meeting of the Chinese Society of Vertebrate Paleontology*, p. 125–138. China Ocean Press, Beijing.

Kinkelin, F., 1884: Ueber Fossilien aus Braunkohlen der Umgebung von Frankfurt a/M. *Bericht über die senckenbergische naturforschende Gesellschaft in Frankfurt am Main*, pp. 165–182.

Koenigswald, G.H.R. von, 1967: An upper Eocene mammal of the family Anthracotheriidae from the Island of Timor, Indonesia. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Series B*, vol. 70, p. 529–533.

Kowalevski, W., 1876: Monographie der Gattung *Anthracotherium* und Versuch einer natürlichen Klassifikation der fossilen Huftiere. *Palaeontographica*, vol. 22, p. 131–347.

Kron, D.G. and Manning, E., 1998: Anthracotheriidae. *In*, Janis, C.M., Scott, K.M. and Jacobs, L.L. *eds.*, *Evolution of Tertiary Mammals of North America. Volume 1: Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals*, p. 381–388. Cambridge University Press, Cambridge.

Legendre, S., 1986: Analysis of mammalian communities from the late Eocene and Oligocene of southern France. *Palaeovertebrata*, vol. 16, fasc. 4, p. 191–212.

Legendre, S., 1989: Les communautés de mammifères du Paléogène (Eocène supérieur et Oligocène) d'Europe occidentale: structures, milieux et évolution. *Münchner Geowissenschaftliche Abhandlungen* (*Reihe A, Geologie und Paläontologie*), vol. 16, p.1–110.

Legendre, S. and Roth, C., 1988: Correlation of carnassial tooth size and body weight in Recent carnivores (Mammalia). *Historical Biology*, vol. 1, p. 85–98.

Matthew, W.D. and Granger, W., 1925: New mammals from the Irdin Manha Eocene of Mongolia. *American Museum Novitates*, no. 198, p. 1–10.

Meyer, H. von, 1854: *Anthracotherium dalmatinum* aus der Braunkohle des Monte Promina und andere Anthracotherien. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, p. 47–49.

Nikaido, M., Rooney, A.P. and Okada, N., 1999: Phylogenetic relationships among cetartiodactyls based on insertions of short and long interspersed elements: hippopotamuses are the closest extant relatives of whales. *Proceedings of the National Academy of Sciences of the United States of America*, vol. 96, p. 10261–10266.

Pentland, J.B., 1928: Description of fossil remains of some animals from the north-east border of Bengal. *Transactions of the Geological Society of London*, vol. 2, no., 2, p. 394–395.

Pickford, M., 1983: On the origins of Hippopotamidae together with descriptions of two new species, a new genus and a new subfamily from the Miocene of Kenya. *Geobios*, vol. 16, fasc. 2, p. 193–217, pls. 1–2.

Pickford, M., 1987: Révision des Suiformes (Artiodactyla, Mammalia) de Bugti (Pakistan). *Annales de Paléontologie* (*Vert.-Invert.*), vol. 73, fasc.4, p. 289–350.

Pilgrim, G.E., 1907: Description of some new Suidae from the Bugti Hills, Baluchistan. *Records of the Geological Survey of India*, vol. 36, p, 45–56.

Pilgrim, G.E., 1928: The Artiodactyla of the Eocene of Burma. *Palaeontologia Indica, New Series*, vol. 13, p. 1–39, pls. 1–4.

Pilgrim, G.E., 1940: Middle Eocene mammals from north-west India. *Proceedings of the Zoological Society of London, Ser. B*, vol. 109, p. 127–152.

Pilgrim, G.E. and Cotter, G. de P., 1916: Some newly discovered Eocene mammals from Burma. *Records of the Geological Survey of India*, vol. 47, p, 42–77, pls. 1–6.

Pondaung Fossil Expedition Team, 1997: *Report on Work Achieved by the Pondaung Fossil Expedition Team.* Office of Strategic Studies, Ministry of Defence, Yangon. (*in Burmese, partly in English*)

Qiu, Z., 1977: Note on the new species of *Anthracokeryx* from Guangxi. *Vertebrata PalAsiatica*, vol. 15, no. 1, p. 54–58, pl. 1. (*in Chinese*)

Rose, K.D., 2001: The ancestry of whales. *Science*, vol. 293, p.2216–2217.

Russell, D.E. and Zhai, R., 1987: The Paleogene of Asia: mammals and stratigraphy. *Mémoires du Muséum National d'histoire Naturelle, Ser. C, Sciences de la Terre*, tome 52, p. 1–488.

Rütimeyer, 1857: Ueber *Anthracotherium magnum* und *hippoideum*. *Neue Denkschriften der Schweizerischen Naturforschenden Gesellschaft*, vol. 18, no. 8, p. 1–32.

Shi, R., 1989: Late Eocene mammalian fauna of Huangzhuang, Qufu, Shandong. *Vertebrata PalAsiatica*, vol. 27, no. 2, p. 87–102, pls. 1-3. (*in Chinese with English summary*)

Shigehara, N., Takai, M., Kay, R. F., Aye Ko Aung, Aung Naing Soe, Soe Thura Tun, Tsubamoto, T. and Tin Thein, 2002: New dental and facial remains of the middle Eocene primate *Pondaungia cotteri* from Central Myanmar. *Journal of Human Evolution*, vol. 43, no. 2, p. 143–166.

Stamp, L. D., 1922: An outline of the Tertiary geology of Burma. *The Geological Magazine*, vol. 59, p. 481–501.

Stehlin, H.G., 1910: Zur Revision der europäischen Anthracotherien. *Verhandlungen der Naturforschenden Gesellschaft in Basel*, vol. 40, no. 2, p. 599–625.

Suteethorn, V., Buffetaut, E., Helmcke-Ingavat, R., Jaeger, J.-J. and Jongkanjanasoontorn, Y., 1988: Oldest known Tertiary mammals from South East Asia: middle Eocene primate and anthracotheres from Thailand. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, 1988(9), p. 563–570.

Takai, M., Shigehara, N., Aye Ko Aung, Soe Thura Tun, Aung Naing Soe, Tsubamoto, T. and Tin Thein, 2001: A new anthropoid from the latest middle Eocene of Pondaung, central Myanmar. *Journal of Human Evolution*, vol. 40, no. 5, p. 393–409.

Takai M., Shigehara, N., Tsubamoto, T., Egi, N., Aye Ko Aung, Tin Thein, Aung Naing Soe and Soe Thura Tun, 2000: The latest middle Eocene primate fauna in the Pondaung area, Central Myanmar. *In, Oversea Research Report of Studies on Origin and Evolution of Hominoids in East Asia*, p. 7–28. 1997–99 Grant-in-Aid for Scientific Research Reports for Oversea Scientific Survey, Asian Paleoprimatology, vol. 1, 2000. Primate Research Institute, Kyoto University, Japan.

Takai, M., Tsubamoto, T., Kunimatsu, Y. and Shigehara, N., 1999: Pondaung primates and its geological age: late Eocene mammal fauna in Myanmar. *Primate Research*, vol. 15, p. 17–38. (*in Japanese with English summary*)

Tang, Y., 1978: Two new genera of Anthracotheriidae from Kwangxi. *Vertebrata PalAsiatica*, vol. 16, no. 1, p. 13–21, pls. 1–3. (*in Chinese*)

Tang, Y., You, Y., Xu, Q, Qiu, Z. and Hu, Y., 1974: The Lower Tertiary of the Baise and Yungle basins, Kwangsi. *Vertebrata PalAsiatica*, vol. 12, no. 4, p. 279–290, pls. 1–2. (*in Chinese with English summary*)

Teller, F., 1886: Neue Anthracotherienreste aus Südsteiermark und Dalmatien. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients*, vol. 4, p. 45–133.

Thewissen, J.G.M., Williams, E.M., Roe, L.J. and Hussain, S.T., 2001: Skeletons of terrestrial cetaceans and the relationship of whales to artiodactyls. *Nature*, vol. 413, p. 277–281.

Tsubamoto, T., 2001: *The Pondaung Mammal Fauna: an Analysis of a Terrestrial Mammal Fauna in the Latest Middle Eocene of Central Myanmar (Southeast Asia)*, 112 p., 20 pls., 4 appendices. Doctoral Dissertation in the Department of Geology and Mineralogy, Graduate School of Science, Kyoto University, Japan.

Tsubamoto, T., Egi, N., Takai, M., Shigehara, N., Aye Ko Aung, Tin Thein, Aung Naing Soe and Soe Thura Tun, 2000a: A preliminary report on the Eocene mammals of the Pondaung fauna, Myanmar. *In, Oversea Research Report of Studies on Origin and Evolution of Hominoids in East Asia*, p. 29–101. 1997–99 Grant-in-Aid for Scientific Research Reports for Oversea Scientific Survey, Asian Paleoprimatology, vol. 1, 2000. Primate Research Institute, Kyoto University, Japan.

Tsubamoto, T., Holroyd, P. A., Takai, M., Shigehara, N., Aye Ko Aung, Tin Thein, Aung Naing Soe and Soe Thura Tun, 2000b: Upper premolar dentitions of *Deperetella birmanica* (Mammalia: Perissodactyla: Deperetellidae) from the Eocene Pondaung Formation, Myanmar. *Paleontological Research*, vol. 4, no. 3, p. 183–189.

Tsubamoto, T., Suzuki, H., Egi, N., Takai, M. and Shigehara, N., 2001: Excavation of mammalian fossils in Myanmar. *Journal of the Geological Society of Japan*, vol. 107, no. 9, p. XVII–XVIII. (*in Japanese*)

Tsubamoto, T., Takai, M., Shigehara, N., Egi, N., Soe Thura Tun, Aye Ko Aung, Maung Maung, Danhara, T. and Suzuki, H., 2002: Fission-track zircon age of the Eocene Pondaung Formation, Myanmar. *Journal of Human Evolution*, vol. 42, no. 4, p. 361–369.

Wang, B. and Zhou, S., 1982: Late Eocene mammals from Pingchangguan basin, Henan. *Vertebrata PalAsiatica*, vol. 20, no. 3, p. 203–215, pl. 1. (*in Chinese with English summary*)

Wang, J., 1985: A new species of *Anthracokeryx* from Shanxi. *Vertebrata PalAsiatica*, vol. 23, no. 1, p. 52–59, pl. 1. (*in Chinese with English summary*)

Xu, Y., 1962: Some new anthracotheres from Shansi and Yunnan. *Vertebrata PalAsiatica*, vol. 6, no. 3, p. 232–250, pls. 1–2. (*in Chinese with English summary*)

Zdansky, O., 1930: Die alttertiären Säugetiere Chinas nebst stratigraphischen Bemerkungen. *Palaeontologia Sinica, Ser. C*, vol. 6, fasc. 2, p. 1–87, pls. 1–5.

Zhao, Z., 1981: The vertebrate fossils and lower Tertiary from Nanning basin, Guangxi. *Vertebrata PalAsiatica*, vol. 19, no. 3, p. 218–227, pls. 1–2. (*in Chinese with English abstract*)

Zhao, Z., 1983: A new species of anthracothere from Nanning basin, Guangxi. *Vertebrata PalAsiatica*, vol. 21, no. 3, p. 266–270, pl. 1. (*in Chinese with English abstract*)

Zhao, Z., 1993: New anthracothere materials from the Paleogene of Guangxi. *Vertebrata PalAsiatica*, vol. 31, no. 3, p. 183–190, pl. 1. (*in Chinese with English summary*)

Zong, G., Chen, W., Huang, X. and Xu, Q., 1996: *Cenozoic Mammals and Environment of Hengduan Mountains Region*, 279 p. China Ocean Press, Beijing. (*in Chinese with English abstract*)

Appendix. Dental measurements (in mm) of the Pondaung *Anthracotherium* used in this paper (Figures 7–9). Abbreviations: L, anteroposterior length; W, buccolingual width; *, estimate; [ ] (square bracket), the data are from the literature (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938).

Upper dentition

Specimen number	Taxa	P3/ L	P3/ W	P4/ L	P4/ W	M1/ L	M1/ W	M2/ L	M2/ W	M3/ L	M3/ W
NMMP-KU 0053	*A. birmanicum*	14.1	10.1	10.4	12.5	13.8	15.0	17.7	19.8	19.2	21.6
NMMP-KU 0056	*A.* sp. cf. *A. crassum*							23.0	26.6	28.1	31.2
NMMP-KU 0066	*A. tenuis*					10.8	11.4				
NMMP-KU 0067	*A.* sp. cf. *A. crassum*			12.1	16.1						
NMMP-KU 0070	*A. birmanicum*									20.2	23.2
NMMP-KU 0071	*A.* sp. cf. *A. crassum*					15.1	16.4				
NMMP-KU 0074	*A.* sp. cf. *A. pangan*			13.9	18.3						
NMMP-KU 0081	*A. birmanicum*									19.2	23.4
NMMP-KU 0082	*A. birmanicum*									19.4	22.6
NMMP-KU 0083	*A. birmanicum*									19.1	23.3
NMMP-KU 0103	*A. pangan*			15.9	21.2						
NMMP-KU 0105	*A.* sp. cf. *A. crassum*			11.0	15.0						
NMMP-KU 0106	*A.* sp. cf. *A. birmanicum*	13.7	9.9								
NMMP-KU 0122	*A.* sp. cf. *A. birmanicum*	17.1*	12.2	12.5	16.6	15.2	16.5				
NMMP-KU 0128	*A.* sp. cf. *A. birmanicum*									21.9	22.7*
NMMP-KU 0215	*A.* sp. cf. *A. birmanicum*	14.9	11.6								
NMMP-KU 0216	*A.* sp. cf. *A. crassum*									24.1	28.0
NMMP-KU 0275	*A. pangan*									38.3	45.0
NMMP-KU 0284	*A.* sp. cf. *A. birmanicum*									23.3	25.3
NMMP-KU 0325	*A. tenuis*					10.5	10.7				
NMMP-KU 0328	*A. pangan*									35.6	37.0
NMMP-KU 0329	*A. pangan*							27.7	31.6	36.2	41.8
NMMP-KU 0379	*A. tenuis*									13.7	15.3
NMMP-KU 0380	*A. tenuis*					8.5	9.7				
NMMP-KU 0385	*A. tenuis*					8.4	9.8				
NMMP-KU 0387	*A. tenuis*					9.5	10.0				
NMMP-KU 0388	*A. tenuis*					10.0	10.0				
NMMP-KU 0389	*A. tenuis*					10.5	10.7				
NMMP-KU 0401	*A.* sp. cf. *A. birmanicum*									22.8	25.8
NMMP-KU 0403	*A.* sp. cf. *A. crassum*									29.1	30.9
NMMP-KU 0404	*A.* sp. cf. *A. pangan*									34.2	36.4
NMMP-KU 0407	*A.* sp. cf. *A. pangan*									34.1	36.5
NMMP-KU 0408	*A. pangan*							28.1	30.0		
NMMP-KU 0409	*A.* sp. cf. *A. crassum*									27.4	32.9
NMMP-KU 0410	*A.* sp. cf. *A. crassum*							20.2	25.1*	24.0	29.6
NMMP-KU 0411	*A.* sp. cf. *A. crassum*									29.8	31.7
NMMP-KU 0412	*A. pangan*									35.3	38.9
NMMP-KU 0413	*A. crassum*			12.6	15.7	16.8	17.7	21.0	23.6		
NMMP-KU 0414	*A.* sp. cf. *A. crassum*					17.4	19.1	25.7	28.0		
NMMP-KU 0452	*A.* sp. cf. *A. crassum*									27.9	33.0
NMMP-KU 0453	*A. birmanicum*									19.2	22.1
NMMP-KU 0454	*A. birmanicum*									19.6	21.8
NMMP-KU 0455	*A. tenuis*	9.3	7.0	6.7	8.5						
NMMP-KU 0459	*A.* sp. cf. *A. crassum*									25.6	29.9
NMMP-KU 0463	*A.* sp. cf. *A. birmanicum*									22.3	24.5*
NMMP-KU 0476	*A.* sp. cf. *A. pangan*			15.4	18.4						
NMMP-KU 0480	*A. pangan*			17.3	21*						
NMMP-KU 0500	*A. birmanicum*	12.2	9.7	10.1	13.1						
AMNH 20011	*A. crassum*	16.5*	11.3	11.3	14.5	16.0	17.3	20.0	23.3	23.7	24.8
AMNH 20015	*A. birmanicum*									20.0	23.3
AMNH 20017 (right)	*A. tenuis*					8.4	10.0	12.0	13.5	14.7	16.3
AMNH 20017 (left)	*A. tenuis*	10.8	7.6	8.2*	9.6	8.8	10.2	11.9	13.5	14.9	16.1
AMNH 20024	*A. crassum*							20.0*	22.5*	24.0*	25.5
AMNH 20027	*A. crassum*			12.5*	17.6	16.0	18.9	19.9	24.9	26.3	28.4
AMNH 32525	*A. crassum*			13.0	16.2	17.3*	18.9				
AMNH 32526	*A. pangan*							[24]	[29]	32.3	36.5

Specimen number	Taxa	P3/ L	P3/ W	P4/ L	P4/ W	M1/ L	M1/ W	M2/ L	M2/ W	M3/ L	M3/ W
GSI B603	*A. crassum*									21.2	25.4
GSI B604	*A. crassum*	15.6	11.2								
GSI B608	*A. pangan*	24.6	20.4								
GSI B609	*A. pangan*									32.8	34.8
GSI B610	*A. pangan*							26.3	30.3		
GSI B611	*A. crassum*			14.4	18.8						
GSI B615	*A. crassum* (type)							21.7	25.1	27.6	31.2
GSI B616	*A. pangan*			15.9	19.9						
GSI B618	*A. pangan*	24.2	19.3								
GSI B619	*A. pangan* (type)							27.1	30.0*	34.0	36.4
GSI B621	*A. birmanicum* (type)	14.6	9.6	9.3*	11.8	13.0*	14.0*	15.0	16.8	16.7	19.0
GSI B622	*A. tenuis*							12.1	12.9	14.6	15.6
GSI B625	*A. tenuis* (type)					9.7	9.5				
GSI B748	*A. pangan*	21.5*	21.2*	16.2	22.3						
GSI B750	*A. pangan*							[28.1]	[30.8]	36.4	38.4
GSI B752	*A. pangan*									33.4	39.8
GSI B756 (right)	*A. tenuis*	11.6	7.2	8.9	10.4	8.5	10.7	11.9	13.5	15.6	17.0
GSI B756 (left)	*A. tenuis*			9.2	10.4	8.9	10.7	12.3	13.5		
GSI B763	*A. crassum*									27.6*	30.0*

Lower dentition

Specimen number	Taxa	P/3 L	P/3 W	P/4 L	P/4 W	M/1 L	M/1 W	M/2 L	M/2 W	M/3 L	M/3 W
NMMP-KU 0052	*A. tenuis*			10.6	5.1	9.1	5.8	12.0	7.3	19.0	8.3
NMMP-KU 0062	*A.* sp. cf. *A. crassum*							27.1	19.8		
NMMP-KU 0063	*A. tenuis*					9.1	5.9				
NMMP-KU 0077	*A.* sp. cf. *A. crassum*									43.1	23.5
NMMP-KU 0079	*A.* sp. cf. *A. birmanicum*	16.2	7.0								
NMMP-KU 0086	*A.* sp. cf. *A. crassum*			15.5	8.2						
NMMP-KU 0087	*A.* sp. cf. *A. crassum*									38.8*	22.3
NMMP-KU 0093	*A. tenuis*									18.2	8.7
NMMP-KU 0107	*A. tenuis*	11.5	5.0								
NMMP-KU 0113	*A. tenuis*			10.5	5.3						
NMMP-KU 0116	*A.* sp. cf. *A. birmanicum*			14.8	7.8			18.2*	12.9		
NMMP-KU 0125	*A. birmanicum*	15.5	5.7	13.5	7.4			17.9	12.6		
NMMP-KU 0263	*A. tenuis*									20.1	10.1
NMMP-KU 0267	*A. tenuis*					9.2	5.9	11.2	7.3		
NMMP-KU 0274	*A. crassum*	19.9	9.7	18.5	11.5	17.7*	12.5*				
NMMP-KU 0306	*A.* sp. cf. *A. pangan*	22.8	9.6								
NMMP-KU 0307	*A.* sp. cf. *A. pangan*			18.3	11.3						
NMMP-KU 0330	*A. crassum*							24.3	18.2	39.2	21.5
NMMP-KU 0331	*A. crassum*							24.4	17.3		
NMMP-KU 0332	*A. birmanicum*									28.2	14.5
NMMP-KU 0399	*A. tenuis*									19.3	8.2
NMMP-KU 0415	*A.* sp. cf. *A. crassum*									42.4	23.8
NMMP-KU 0417	*A.* sp. cf. *A. crassum*									40*	21.7
NMMP-KU 0418	*A. pangan*							31.2	26.3		
NMMP-KU 0421	*A. crassum*					17.3	11.9				
NMMP-KU 0422	*A. tenuis*							11.7	8.2	20.0*	10.4
NMMP-KU 0423	*A. tenuis*									18.3	9.0
NMMP-KU 0424	*A. crassum*									38.5	19.9
NMMP-KU 0426	*A. crassum*							23.3*	18.2*	39.5*	21.0*
NMMP-KU 0427	*A.* sp. cf. *A. crassum*									41.6	22.4
NMMP-KU 0429	*A. crassum*							24.3	16.3	37.7	20.0
NMMP-KU 0430	*A. birmanicum*	16.5	6.6	14.3	7.8						
NMMP-KU 0432	*A.* sp. cf. *A. crassum*			15.7	8.2						
NMMP-KU 0433	*A. pangan*			19.9	11.3						

Specimen number	Taxa	P/3 L	P/3 W	P/4 L	P/4 W	M/1 L	M/1 W	M/2 L	M/2 W	M/3 L	M/3 W
NMMP-KU 0434	*A. pangan*			17.7	12.6						
NMMP-KU 0435	*A. crassum*			16.8	9.1						
NMMP-KU 0457	*A. crassum*									38.4	19.0
NMMP-KU 0458	*A. tenuis*					9,9*	6.3	13.4	8.7		
NMMP-KU 0465	*A. tenuis*									22.6	11.2
NMMP-KU 0466	*A. tenuis*							12.2	7.7		
NMMP-KU 0468	*A. crassum*					18.4	12.5				
NMMP-KU 0470	*A. tenuis*							11.3	7.3	20.5	9.4
NMMP-KU 0478	*A. birmanicum*					10.3	6.4	12.9	8.3		
NMMP-KU 0505	*A.* sp. cf. *A. crassum*			15.8	8.6						
AMNH 20006	*A. pangan*									49.5*	27.0
AMNH 20011 (right)	*A. crassum*	16.7	7.2	16.5	9.2	16.8*	12.2	20.5	15.4	31.9	17.3
AMNH 20011 (left)	*A. crassum*									32.4	17.3
AMNH 20015 (right)	*A. birmanicum*									29.0*	14.9
AMNH 20015 (left)	*A. birmanicum*									28.4	15.0
AMNH 20017 (right)	*A. tenuis*	10.5*	4.9	10.2*	5.5	8.4	6.1	11.4*	7.7	20.0	9.0
AMNH 20017 (left)	*A. tenuis*	10.6	4.8	10.0	5.5	8.6	6.0	11.4	7.6	19.7	9.3
AMNH 20028	*A. crassum*	18.6	8.2	17.2	9.8						
AMNH 20029	*A. crassum*									37.9	19.9
AMNH 32522	*A. crassum*					18.7	13.2	23.5*	15.5*		
GSI B605	*A. birmanicum*	[14.9]	[5.8]	14.3	7.7	14.0	9.5	18.0	13.4	29.7	16.0
GSI B607	*A. pangan*									52.7	29.7
GSI B612	*A. crassum*				[10.8]	[16.7]	[11.8]	[23.7]	[17.4]		
GSI B613	*A. crassum*									38.2	20.5
GSI B614	*A. crassum*	21.3	9.8								
GSI B617	*A. pangan*			19.3	12.4	19.5*	16.5*	26.1	21.9	36.7	22.2
GSI B620	*A. pangan*									47.7	24.5
GSI B626	*A. tenuis*					9.2	6.0				
GSI B627	*A. tenuis*							11.7	7.4	18.0	8.7
GSI B745	*A. pangan*	24.1	12.7	21.7	14.1	21.5*	15.0*	30.8	21.9		
GSI B751	*A. crassum*	19.8	9.9	19.7	11.3	16.8	12.9	23.9	18.8	39.2	21.8
GSI B755	*A. tenuis*	[11.7]	[4.3]	11.3	5.6	9.3	6.4	11.6	8.1	21.0	9.4
GSI B760	*A. tenuis*					[9.1]	[5.2]				
GSI B761	*A. tenuis*	11.9	3.9								
GSI B767	*A. birmanicum*			12.9	7.0	12.9	9.9	15.5	11.8		