缅甸始新世邦唐组一新的石炭兽类偶蹄类动物

锷本武久[1]　ZIN-MAUNG-MAUNG-THEIN[2,3]　江木直子[2]
西村刚[2]　THAUNG-HTIKE[4]　高井正成[2]

（1 日本株式会社林原生物化学研究所古生物学研究中心　冈山　700–0907）
（2 日本京都大学灵长类研究所　犬山　484–8506）
（3 缅甸曼德勒大学地质学系　曼德勒）
（4 缅甸瑞冒学位学院地质学系　瑞冒）

摘要：描述了缅甸中始新统上部邦唐组发现的一种新的丘齿形石炭兽 *Myaingtherium kenyapotamoides* gen. et sp. nov. 。标本为破碎的上下颌骨。*Myaingtherium* 是一种基干石炭兽类，其大小和基本形态可以与邦唐一种小的石炭兽 *Anthracokeryx tenuis* 相对比。然而，*Myaingtherium* 因具有更丘型化的齿列而与 *Anthracotherium* 和 *Anthracohyus* 在牙齿形态上更相似。在丘型齿石炭兽类中，*Myaingtherium* 以臼齿前小尖非常退化为特点。*Myaingtherium* 的一些牙齿特征，如具有退化的臼齿前小尖的丘型齿列和下臼齿上具有一个中间附尖，与 Kenyapotaminae（最原始的化石河马）以及非洲中新世类似河马的石炭兽 *Kulutherium* 的牙齿特征相似，暗示 *Myaingtherium* 在谱系上可能与 Kenyapotaminae 有关。尽管需要更多的证据来检验 *Myaingtherium* 的谱系关系，但这个发现强化了邦唐石炭兽类在检验和理解河马–石炭兽支系的谱系关系和早期演化方面的重要性。

关键词：缅甸，始新世，邦唐组，偶蹄目，石炭兽科，*Myaingtherium*

A NEW ANTHRACOTHERIID ARTIODACTYL FROM THE EOCENE PONDAUNG FORMATION OF MYANMAR

TSUBAMOTO Takehisa[1]　ZIN-MAUNG-MAUNG-THEIN[2,3]　EGI Naoko[2]
NISHIMURA Takeshi[2]　THAUNG-HTIKE[4]　TAKAI Masanaru[2]

（1 *Center for Paleobiological Research*, *Hayashibara Biochemical Laboratories*, *Inc.*
　Okayama 700–0907, Japan　sorlestes@ msc. biglobe. ne. jp）
（2 *Primate Research Institute*, *Kyoto University* Inuyama 484–8506, Japan）
（3 *Department of Geology*, *University of Mandalay* Mandalay, Myanmar）
（4 *Department of Geology*, *Shwebo Degree College* Shwebo, Myanmar）

Abstract　We describe a new bunodont anthracothere (Mammalia; Artiodactyla), *Myaingtherium kenyapotamoides* gen. et sp. nov., discovered from the upper middle Eocene Pondaung Formation of Myanmar. The specimens consist of upper and lower dentitions with fragmentary jaws. *Myaingtherium* is one of the basal anthracotheres and is comparable in size and overall morphology to a small-sized Pondaung

anthracothere, *Anthracokeryx tenuis*. However, *Myaingtherium* is more similar in dental morphology to *Anthracotherium* and *Anthracohyus* rather than to *Anthracokeryx* in having more bunodont dentition. *Myaingtherium* is characterized particularly by having a very reduced molar paraconule among bunodont anthracotheres. Some dental characteristics of *Myaingtherium*, such as a reduced molar paraconule with bunodont dentition and a median accessory cusplet on the lower molars, are reminiscent of those of the Kenyapotaminae (most primitive fossil hippopotamuses) and hippo-like anthracotheriid *Kulutherium* from the Miocene of Africa, implying a possibility that *Myaingtherium* might be phyletically related to the Kenyapotaminae. Although more evidences are necessary to test the phyletic relationships of *Myaingtherium*, this discovery reinforces that the Pondaung anthracotheres are an important fauna for testing and understanding the phyletic relationships and early evolution of the hippo-anthracothere clade.

Key words   Myanmar, Eocene, Pondaung Formation, Artiodactyla, Anthracotheriidae, *Myaingtherium*

1   Introduction

The anthracotheres (family Anthracotheriidae) are one of the major groups of fossil artiodactyls (Mammalia), which are recorded in the middle Eocene to Plio-Pleistocene of Eurasia, in the middle Eocene to early Miocene of North America, and in the late Eocene to late Miocene of Africa (Lihoreau and Ducrocq, 2007). They have long been believed to have habits and habitats similar to those of modern hippopotamuses (Kron and Manning, 1998), but according to Lihoreau (2003), they were adapted to several kinds of environments and had more diversified habits and habitats than was thought. The typical early anthracotheres have bunodont or bunoselenodont molars with a large paraconule; and later advanced anthracotheres have selenodont molars without a paraconule. The anthracotheres have been considered to be phyletically related to the Hippopotamidae (Falconer and Cautley, 1836; Lydekker, 1876; Colbert, 1935a, b; Pilgrim, 1941; Gentry and Hooker, 1988; Boisserie et al., 2005a, b, 2010; Boisserie and Lihoreau, 2006; Boisserie, 2007), although this hypothesis is still debated (Pickford, 1983, 1989, 1993, 2005, 2007b, 2008; Pickford and Morales, 1989).

The upper middle Eocene Pondaung Formation (Pondaung Sandstones) of Myanmar (Cotter, 1914; Aye Ko Aung, 1999) is one of the fossiliferous Paleogene deposits in Southeast Asia. Since first mammalian fossils were described by Pilgrim and Cotter (1916), many vertebrate fossils have been reported in the formation (Tsubamoto et al., 2006 and references therein; Marivaux et al., 2006, 2008a, b; Métais et al., 2006b, 2007; Egi et al., 2007; Beard et al., 2007, 2009; Peigné et al., 2007; Rosenberger and Hogg, 2007; Adnet et al., 2008; Gunnell and Ciochon, 2008). In the Pondaung mammal fauna, the anthracotheres are dominant in terms of collection size (Pilgrim and Cotter, 1916; Tsubamoto et al., 2005). The Pondaung anthracotheres are morphologically close to one another but have a wide variation in dental morphology (Tsubamoto et al., 2002a). In the Pondaung Formation, many species of primitive bunodont anthracotheres have been described (Pilgrim and Cotter, 1916; Pilgrim, 1928; Colbert, 1938); and the classification of the Pondaung anthracotheres have been debated (Colbert, 1938; Holroyd and Ciochon, 1991, 1995; Holroyd, 1994; Ducrocq, 1999; Ducrocq et al., 2000; Tsubamoto, 2001; Tsubamoto et al., 2002a; Holroyd et al., 2006; Lihoreau and Ducrocq, 2007). The Pondaung anthracotheres are very primitive and are one group of the oldest anthracotheres, so that they are often discussed in the context of the origin of the family (Pilgrim and Cotter, 1916; Pilgrim, 1928, 1940, 1941; Colbert, 1938; Coombs and Coombs, 1977; Holroyd, 1994; Ducrocq, 1999; Ducrocq et al., 2000; Tsubamoto et al., 2002a).

In this article, we describe a new enigmatic anthracothere discovered from the Pondaung Formation. This is a small-sized and bunodont anthracothere and interestingly has several dental characteristics similar to those of primitive fossil hippopotamids (Kenyapotaminae) and hippo-like putative anthracotheriid *Kulutherium* from the Miocene of Africa, implying a possible relationship between the new anthracothere and primitive hippopotamids. The basic dental termino-

logies mostly follow those of Bown and Kraus （1979）. Additional dental terminologies are compiled from Hershkovitz （1971）, Pickford （1983, 2007a, b）, Holroyd （1994）, Lihoreau and Ducrocq （2007）, and Boisserie et al. （2010）. Several dental terminology used here are shown in Fig. 1. Concerning the generic taxonomy of the bunodont anthracotheres from the Paleogene of Asia, we generally follow the classification by Lihoreau and Ducrocq （2007）, although it is still debated （Holroyd and Ciochon, 1991; Tsubamoto et al., 2002a; Holroyd et al., 2006）.
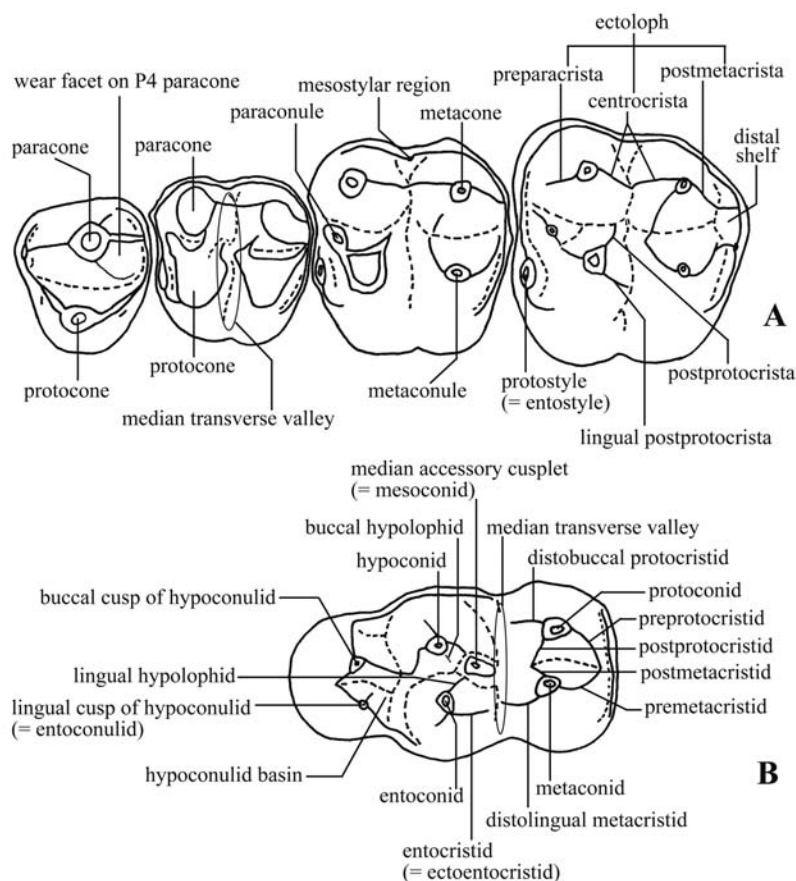
Fig. 1　Dental terminology used in this paper, showing the schematic drawings of the dentition of the type
（NMMP-KU 2245）of *Myaingtherium kenyapotamoides* gen. et sp. nov. in occlusal view
A. Left P4-M3; B. Left m3

Abbreviations　AMNH, American Museum of Natural History, New York, USA. DMR, Department of Mineral Resources, Bangkok, Thailand. GSI, Geological Survey of India, Kolkata, India. KNM, National Museums of Kenya, Nairobi, Kenya. NMMP-KU, specimens catalogued by the Myanmar-Japan Joint Fossil Expedition Team （Tsubamoto et al., 2000, 2005, 2006）stored in the National Museum of Myanmar （Yangon, Myanmar）, Yangon University （Yangon, Myanmar）, and Department of Archaeology （Ministry of Culture, Yangon, Myanmar）："NMMP" means National Museum, Myanmar, Paleontology and "KU" means Kyoto University （Japan）.

2　Geological setting and age

The new fossil specimens described here was collected from the "Upper Member" of the Pondaung Formation （Aye Ko Aung, 1999）in the Chindwin-Irrawaddy Basin of the western part of central Myanmar （Fig. 2）. The Pondaung Formation stratigraphically lies between the marine deposits （Fig. 3; Cotter, 1914; Stamp, 1922; Bender, 1983）. The Pondaung Forma-

tion consists of terrestrial deposits and is subdivided into the "Lower" and "Upper" members (Aye Ko Aung, 1999, 2004; Aung Naing Soe, 1999; Aung Naing Soe et al., 2002). All of the Pondaung vertebrate fossils come from the "Upper Member." The vertebrate fauna of the "Upper Member" includes fishes, terrestrial and aquatic reptiles (such as turtles, snakes, agamid lizards, and crocodiles), an ibis-like bird, and terrestrial mammals, such as primates, dermopterans, hyaenodontids, carnivorans, rodents, insectivorans, artiodactyls, and perissodactyls (Tsubamoto et al., 2005, 2006; Métais, 2006; Marivaux et al., 2006). The "Upper Member" is correlated to the upper middle Eocene (Bartonian) on the basis of its mammalian fauna, fission-track age, stratigraphic relationships, and paleomagnetostratigraphy (Fig. 3; Holroyd and Ciochon, 1994; Tsubamoto et al., 2002b, 2004, 2005; Benammi et al., 2002).
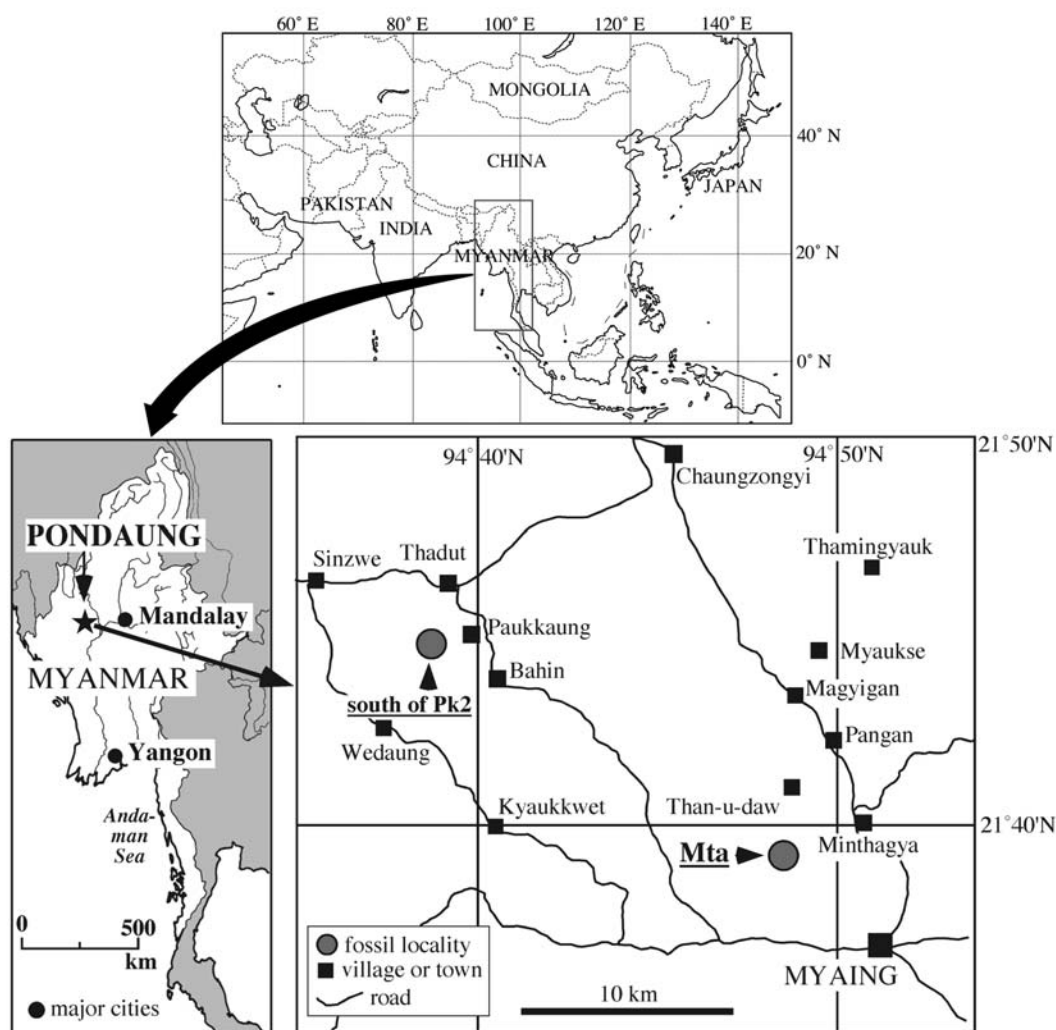

Fig. 2 Geographical map showing the two fossil localities of *Myaingtherium kenyapotamoides* gen. et sp. nov. in central Myanmar

In this paper, the age of the Pondaung fauna is considered to be the middle part of the Bartonian (ca. 39 ~ 38 Ma) based on recently analyzed radiometric data (Tsubamoto et al., 2009; Suzuki et al., 2010) and magnetostratigraphy (Benammi et al., 2002) (Fig. 3). Tsubamoto et al. (2002b) reported a fission-track zircon age, 37. 2 ± 1. 3 (1 sigma) Ma, of the tuff bed at the Pk1 fossil locality (Tsubamoto et al., 2000) of the "Upper Member." Tsubamoto et al. (2009) have newly reported a fission-track zircon age, 38. 8 ± 1. 4 (1 sigma) Ma, of the tuff bed at the Pk5 fossil locality (Tsubamoto et al., 2000) of the "Upper Member." Because the tuff beds of the Pk1 and Pk5 localities are considered to be located at the same hori-

zon (Maung Maung et al., 2005), the fission-track zircon age of the tuff bed distributed at the Pk1 and Pk5 localities is averaged as around 38 Ma (Tsubamoto et al., 2009). Suzuki et al. (2010) also newly reported a fission-track zircon age, 38.6 ± 1.1 (1 sigma) Ma, of the tuff bed at the Kd1 fossil locality (Tsubamoto et al., 2006) of the "Upper Member." On the other hand, Benammi et al. (2002) reported a magnetostratigraphy of the "Upper Member" and concluded that the "Upper Member" is assigned to a normal polarity remanent magnetization from the bottom to the top. The relatively long normal polarity chron near 38 Ma is the Polarity Chron C18n.1n, which ranges from 38.975 Ma to 38.032 Ma (Ogg and Smith, 2004). On the basis of these evidence, the age of the "Upper Member" (i. e., the age of the Pondaung fauna) is correlated to the Polarity Chron C18n.1n (ca. 39 ~ 38 Ma), which is the middle part of the Bartonian (Luterbacher et al., 2004).

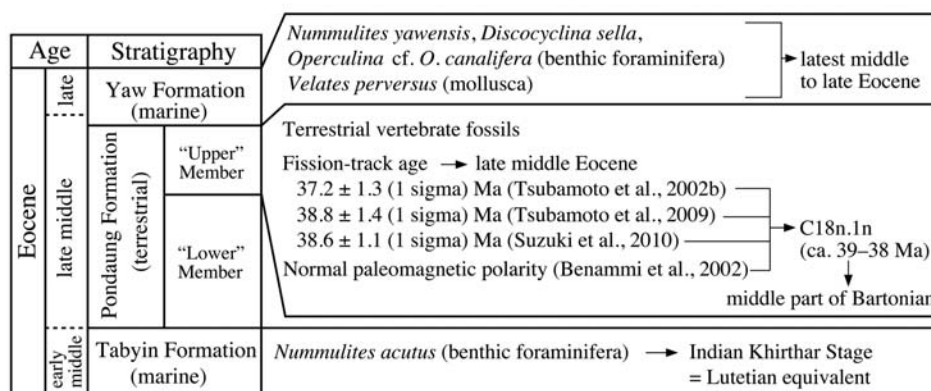| Age	Stratigraphy		Fossils & Dating	
Eocene — late middle (late)	Yaw Formation (marine)		*Nummulites yawensis*, *Discocyclina sella*, *Operculina* cf. *O. canalifera* (benthic foraminifera) *Velates perversus* (mollusca)	→ latest middle to late Eocene
Eocene — late middle	Pondaung Formation (terrestrial)	"Upper" Member	Terrestrial vertebrate fossils Fission-track age → late middle Eocene 37.2 ± 1.3 (1 sigma) Ma (Tsubamoto et al., 2002b) 38.8 ± 1.4 (1 sigma) Ma (Tsubamoto et al., 2009) 38.6 ± 1.1 (1 sigma) Ma (Suzuki et al., 2010) Normal paleomagnetic polarity (Benammi et al., 2002)	→ C18n.1n (ca. 39–38 Ma) ↓ middle part of Bartonian
		"Lower" Member		
Eocene — early middle	Tabyin Formation (marine)		*Nummulites acutus* (benthic foraminifera)	→ Indian Khirthar Stage = Lutetian equivalent

Fig. 3   General stratigraphy of the Pondaung Formation, central Myanmar (after Stamp, 1922; Bender, 1983; Holroyd and Ciochon, 1994; Aye Ko Aung, 1999; Tsubamoto et al., 2002b, 2005, 2009; Benammi et al., 2002; Suzuki et al., 2010)

3   Systematic paleontology

Order Artiodactyla Owen, 1848 (*sensu* Cetartiodactyla Montgelard et al., 1997)

Comments   We use the term Artiodactyla (including cetaceans) instead of the term Cetartiodactyla. The term Cetartiodactyla was established by Montgelard et al. (1997) to include the artiodactyls and cetaceans because they found that the cetaceans are sister group of the hippopotamids and are cladistically included in the artiodactyls based on their study of molecular biology (mitochondrial cytochrome b and 12S rRNA sequences). Further studies on the molecular phylogeny of the artiodactyls and cetaceans revealed that the cetaceans are deeply nested within the Artiodactyla cladistically (e. g., Shimamura et al., 1997; Gatesy et al., 1999; Nikaido et al., 1999; Murphy et al., 2001; Beck et al., 2006). Therefore, the cetaceans are not the sister group of the artiodactyls but are deeply included in the artiodactyls. In other words, the cetaceans are actually the artiodactyls: the term Cetartiodactyla actually represents the same meaning as the term Artiodactyla cladistically. Because the term Artiodactyla Owen, 1848 has the priority on the nomenclature to the term Cetartiodactyla Montgelard et al., 1997 and has long been used traditionally in biology and paleontology, we consider that the Cetartiodactyla is a junior synonym of the Artiodactyla.

Family Anthracotheriidae Leidy, 1869
Genus *Myaingtherium* gen. nov.

Type and only known species   *Myaingtherium kenyapotamoides* sp. nov.
Distribution   Pondaung Formation, Myanmar; late middle Eocene.

Etymology *Myaing*: from the Myaing Township of Myanmar, where the type specimen of the type species was found; *therium*: wild beast in Latin. The gender of the new genus is neuter.

Generic diagnosis Small-sized bunodont anthracothere with a reduced molar paraconule somewhat shifted mesially, no distinct molar styles on the buccal part, a mesiodistally-oriented molar ectoloph without a connection to the mesostylar region, a large molar protostyle, P4 with more rounded outline, pre- and postprotocristae on P4 continuous with cingulum, a short diastema between c1 and p1, double-rooted p1, a single premetacristid on the lower molars, a median accessory cusplet on the cristid obliqua of the lower molars, a relatively large hypoconulid on m1−m2, and a large and double-cuspid hypoconulid on m3.

Differential diagnosis The size and overall dental morphology are comparable to those of *Anthracokeryx tenuis* (= *Anthracokeryx ulnifer*); however, the dental morphology is more comparable to that of *Anthracotherium* and *Anthracohyus* rather than to that of *Anthracokeryx* in having more bunodont dentition. Differs from most of other bunodont anthracotheres (such as *Anthracotherium*, *Anthracokeryx*, *Anthracohyus*, *Heptacodon*, *Microbunodon*, *Prominatherium*, *Siamotherium*, and *Pakkokuhyus*) in having a much smaller paraconule on the upper molars and a median accessory cusplet on the lower molars. Differs from *Bugtitherium* in being much smaller and in having a median accessory cusplet on the lower molars. Differs from *Kulutherium* in being much smaller and in having weaker cingulum on the upper dentition, proportionally shorter and wider M1−M2, a single-cuspid P4 protocone, and in lacking accessory cusps that are located on the lingual and distal regions of the upper molars.

Myaingtherium kenyapotamoides sp. nov.
(Figs. 1, 4−12; Table 1)

Holotype NMMP-KU 2245, associated mandibular and maxillary fragments with upper and lower dentitions (right and left P4−M3, right i1, right p1−m3, and left p3−m3), which belong to a single individual.

Type locality Mta locality (GPS data [WGS 84 datum] of the specimen site: 21°39′12″N and 94°49′13″E), near Minthagya Village, Myaing Township, Magway Division, western part of central Myanmar (Fig. 2; Tsubamoto et al., 2000, 2006).

Repository of the type specimen Department of Archaeology, Ministry of Culture of Myanmar, Yangon, Myanmar.

Type formation and age The "Upper Member" of the Pondaung Formation; late middle Eocene (Bartonian).

Referred material NMMP-KU 1723, left M1.

Locality of the referred material South of the Pk2 locality (GPS data [WGS 84 datum] of the Pk2 locality: approx. 21°45′15″N and 94°39′13″E), near Paukkaung Village, Myaing Township, Magway Division, western part of central Myanmar (Fig. 2; Tsubamoto et al., 2000, 2006).

Repository of the referred specimen Department of Geology, Yangon University, Yangon, Myanmar (Tsubamoto et al., 2006).

Formation and age of the referred material As for the type specimen.

Etymology Named after its kenyapotamine-like dental morphology.

Diagnosis As for the genus.

Dental measurements Shown in Table 1. Measurements were made using digital calipers.

Description The present specimens preserve P4−M3, i1, roots of i2−i3, alveolus of lower canine, and p1−m3. The dental morphology shows a brachyodont and basic bunodont anthracotheriid morphology. The dental size is comparable to that of small-sized anthracotheres. In the left upper jaw of the type specimen (NMMP-KU 2245), a part of the internal choane is preserved, indicating that the choane is located at the level of M3 (Fig. 4A).
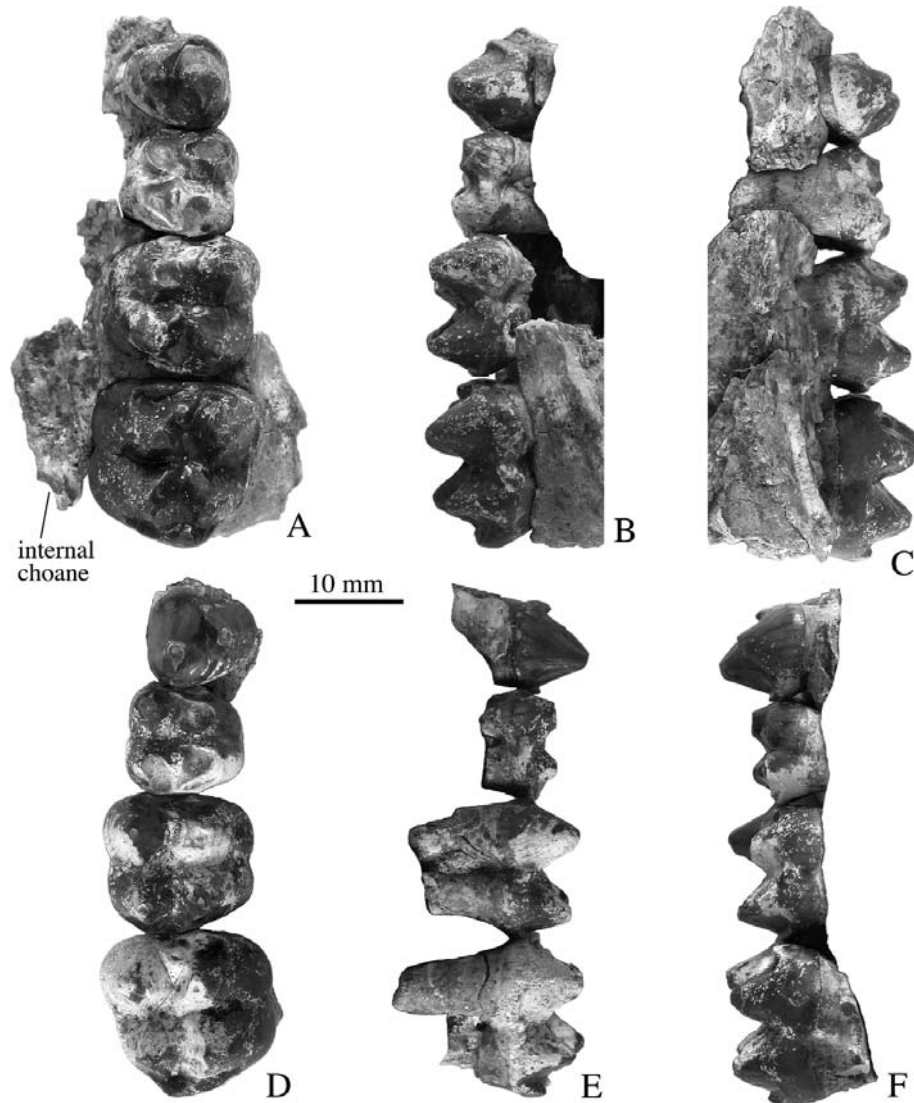
Fig. 4 Upper dentition of the type（NMMP-KU 2245）of *Myaingtherium kenyapotamoides* gen. et sp. nov.
A－C. Left maxillary fragment with P4－M3（A. occlusal view；B. buccal view；C. lingual view）；
D－F. Right P4－M3（D. occlusal view；E. buccal view；F. lingual view）

Table 1　Dental measurements of *Myaingtherium kenyapotamoides* gen. et sp. nov.
（NMMP-KU 2245〔= holotype〕and 1723）from the Eocene Pondaung Formation of Myanmar　（mm）

NMMP-KU	i1 L	i1 W	p1 L	p1 W	p2 L	p2 W	p3 L	p3 W	p4 L	p4 W
2245 left	—	—	—	—	—	—	—	5.0	10.3	6.7
2245 right	4.0	3.3	6.3	2.9	9.0	4.0	10.4	5.6	10.5 *	6.4

NMMP-KU	m1 L	m1 W-tr	m1 W-ta	m2 L	m2 W-tr	m2 W-ta	m3 L	m3 W-tr	m3 W-ta
2245 left	11.4	7.4	8.0	—	9.6	—	21.7	11.5	11.4
2245 right	11.5 *	7.3	7.9	14.2	9.3	9.8	—	—	10.8

NMMP-KU	P4 L	P4 W	M1 L	M1 W-m	M1 W-d	M2 L	M2 W-m	M2 W-d	M3 L	M3 W-m	M3 W-d
2245 left	8.8	10.1	10.4	10.5	11.0	13.1	14.3	13.8	15.4	16.1	14.7
2245 right	8.7	10.2	10.5	10.5	10.9	13.0	14.3	13.9	15.6	16.1	14.9
1723 left	—	—	10.4	11.1	11.1	—	—	—	—	—	—

Abbreviations：L. mesiodistal length；W. buccolingual width；W-tr. trigonid width；W-ta. talonid width；W-m. width of the mesial part of upper molar（paracone-protocone）；W-d. width of the distal part of upper molar（metacone-metaconule）；* estimate.

Fig. 5 Casts of the left upper dentition of *Myaingtherium kenyapotamoides* gen. et sp. nov. in occlusal view (stereo pair)
A. Left P4–M3 of NMMP-KU 2245 (type);
B. Left M1 of NMMP-KU 1723

P4 has three isolated roots and rounded outline in occlusal view (Figs. 1A, 4, 5A, 6). The paracone and protocone are also somewhat rounded. The paracone has the pre- and postparacristae and weak fossae (*sensu* Boisserie et al., 2010). The pre- and postparacristae extend mesiodistally and stop at the mesial and distal cingula, respectively. There is a broad wear facet on the distolingual face of the paracone. This wear facet occludes that of the mesiobuccal face of the m1 trigonid. The protocone is smaller and lower than the paracone and is mesial to the paracone. The protocone is separated from the paracone by a mesiodistal groove. The pre- and postprotocristae extend mesiobuccally and distobuccally, respectively, and are continuous with the mesial and distal cingula, respectively. The mesial cingulum disappears at the mesiobuccal base of the paracone. The distal cingulum disappears at the distobuccal base of the paracone. There is neither buccal nor lingual cingula. There are faint and dimple-like cingula mesial and distal to the protocone: these faint cingula are isolated from the buccal part of the mesial and distal cingula, respectively. There are no styles, although there are faint swellings at the para- and metastylar regions of the cingula, which are located mesial and distal to the para-

cone, respectively.

The upper molars are bunodont and three-rooted (Figs. 1A, 4, 5, 6). They are almost tetracuspidate: there are a large paracone, protocone, metacone, and metaconule with a very small, reduced, and somewhat mesially-shifted paraconule. The paracone, metacone, and paraconule are conical; and the protocone and metaconule shows a slight degree of selenodonty. The cristae are relatively weak. The cingulum is relatively weak and surrounds the mesial, buccal, and distal margin of the crown. It becomes very faint or disappears in some parts. There is no distinct lingual cingulum, although on M3 there is a tiny cusplet between the bases of the protocone and the metaconule. The paracone and metacone are mesial to the protocone and metaconule, respectively. The ectoloph (preparacrista + centrocrista + postmetacrista) is mesiodistally oriented. The centrocrista is isolated from the mesostylar region: there is no crista linking the centrocrista to the mesostylar region. The paraconule is located more mesial to the line going through the tips of the paracone and protocone. The preparaconule crista extends mesiobuccally and is sometimes connected to the mesial cingulum at the mesiolingual base of the paracone. There is no postparaconule crista. The preprotocrista extends mesiobuccally, connecting to the paraconule. The postprotocrista extends distobuccally, stopping at the distolingual

base of the paracone. The lingual postprotocrista is weaker than the postprotocrista and extends distally or distolingually, stopping at the median transverse valley. It does not interrupt the median transverse valley. The premetaconule crista extends mesiobuccally, stopping at the mesiolingual base of the metacone. The postmetaconule crista extends distobuccally, linking to the distal cingulum. The lingual metaconule crista (= third metacristule = ecto-metacristule) is absent in most of the teeth, but a weak structure is observed on right M3 of NMMP-KU 2245 (Fig. 6). There is a large protostyle on the mesial cingulum, which is located mesially to the tip of the protocone. There are neither distinct para-, meso-, nor meta-styles, although sometimes there is a small enamel crenulation or swelling at the mesostylar region. The median transverse valley is straight and is open buccally and lingually. The metacone is smaller relative to the other main cusps on M3 than on M1–M2. On M3, there is

Fig. 6   Casts of right upper P4–M3 of the type
(NMMP-KU 2245) of *Myaingtherium kenyapotamoides*
gen. et sp. nov. in occlusal view (stereo pair)

a distal shelf on the distal cingulum. This distal shelf has a wear facet that occludes with the distal face of the m3 hypoconulid. There can be observed a possible incipient trilobed wear facet on the protocone and metaconule of M1. On M1 of the type specimen (NMMP-KU 2245), there is a wear facet on the distolingual face of the metacone. This wear facet occludes with the mesiobuccal face of the m2 trigonid. This wear facet is not developed on M1 of the referred specimen (NMMP-KU 1723). M1 < M2 < M3.

    The preserved part of the right mandibular corpus is relatively shallow (Fig. 7, 8). It shallows anteriorward. The mandibular symphysis is unfused and shallow. It is anteroposteriorly elongated, extending beneath the anterior root of p3. The mandible appears to be slightly compressed transversally behind the canine (Fig. 7). There are three incisor loci without diastema (Fig. 9). The alveolus of right i1 is adjacent to the symphysis and does not preserve the root, suggesting that the preserved isolated incisor (Figs. 7, 8A–B, 10C–F) is right i1. The alveoli of i2 and i3 preserve the roots, which are round-shaped in the cross section (Fig. 9). There is a short diastema between i3 and c1 (Fig. 7, 9). Judging from the broken alveolus, the lower canine is moderately large: its estimated mesiodistal diameter (length) is about 7 mm. There is a diastema (ca. 6 mm) between c1 and p1 (Fig. 7). There appears to be no diastema between p1 and p2, although this part is somewhat dislocated due to the breakage (Fig. 7). There is a very short diastema (1.5 mm) between p2 and p3. The p3–m3 are crowded (Figs. 7, 8).

    The lower i1 has a spatulate crown (Figs. 7, 8, 10). The crown is triangular in lingual and buccal views. The mesial margin of the crown is higher than the distal margin. There is a notch between the mesial tip and the distal tip of the crown, with a shallow lingual groove. The root is twice as long as the crown height.

    The lower p1 is triangular in lateral view and is two-rooted (Figs. 7, 8, 10). It has only
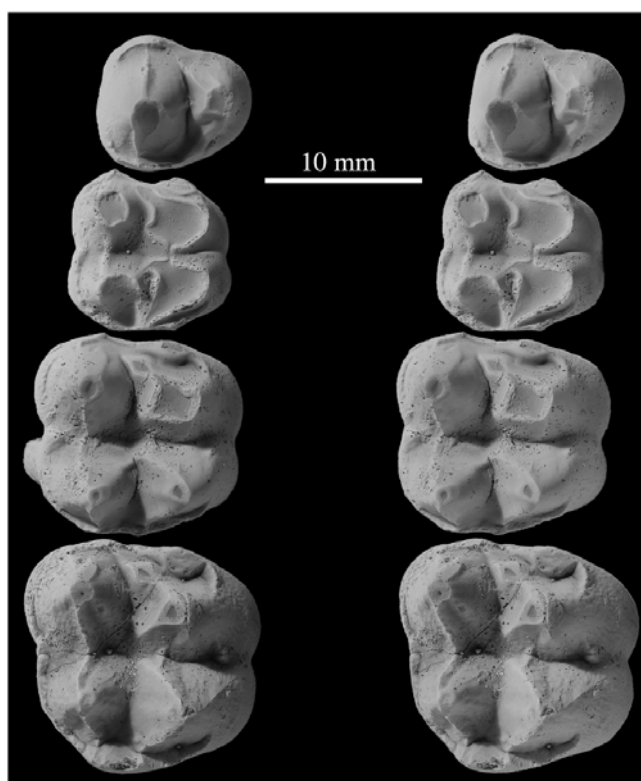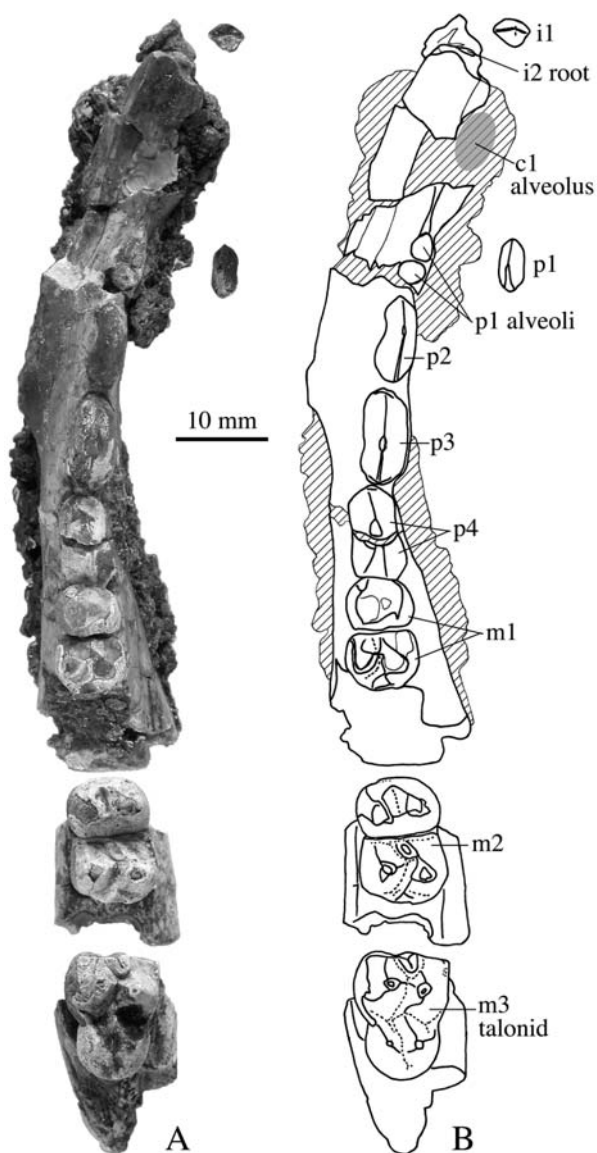
Fig. 7 Right mandibular fragment and lower dentition
of the type (NMMP-KU 2245) of *Myaingtherium*
kenyapotamoides gen. et sp. nov. in occlusal view
A. Photo; B. Schematic drawing

one cusp, the protoconid. The pre- and postprotocristids are mesiodistally oriented. The preprotocristid is shorter than the post-protocristid. There is a bulge at the distal margin of the crown connected to the post-protocristid. There is no cingulum. The two roots are closely located with each other.

The lower p2 has almost the same morphology as p1 (Figs. 7, 8, 10). However, it is larger, taller, longer, and wider than p1 and has a weak distal cingulum connected with the postprotocristid. Separation between the two roots is larger in p2 than in p1.

The lower p3 has almost the same morphology as p2 (Figs. 7, 8, 10, 11, 12). However, it is larger, taller, longer, and wider than p2. It has a weak mesial cingulum and a stronger distal cingulum, which are connected with pre- and postprotocristids, respectively. There are no buccal and lingual cingula.

The lower p4 has roughly the same morphology as p3 (Figs. 7, 8, 10, 11, 12). It is mesiodistally as long as p3, is buccolingually wider than p3, and is roughly as tall as p3. It has stronger mesial and distal cingula. There is an additional cristid that originates from the tip of the protoconid and is located lingual to the postprotocristid. This cristid extends distally and disappears before reaching the distal cingulum.

The lower molars (Figs. 1B, 7, 8, 10, 11, 12) are bunodont and with four main cusps (protoconid, metaconid, hypoconid, and entoconid) on m1 – m2. There is no trace of a paraconid. The metaconid has only one mesial cristid (single premetacristid).

The preprotocristid extends mesiolingually and the premetacristid extends mesiobuccally. The two cristids meet at the center of the mesial face of the crown between the protoconid and the metaconid, where a notch is observable, making a paracristid. The postprotocristid and post-metacristid extend rather transversally, meet at the notch which is located at the center of the distal trigonid wall, making a protocristid. A cristid from the tip of the protoconid (= distobuccal protocristid) extends distally and disappears at the base of the trigonid wall, making a shallow groove lingual to the cristid. Similarly, a cristid from the tip of the metaconid (= distolingual metacristid) extends distally and disappears at the median transverse valley, making a shallow groove buccal to the cristid. These two cristids and protocristid make a weak M-shaped ridge at the distal trigonid wall in the distal view. The cristid obliqua hits the distal trigonid wall below the notch of the protocristid. There is a median accessory cusplet (= mesoconulid) on the cristid obliqua. Although this part is moderately worn on m1, there is a bulge at the central
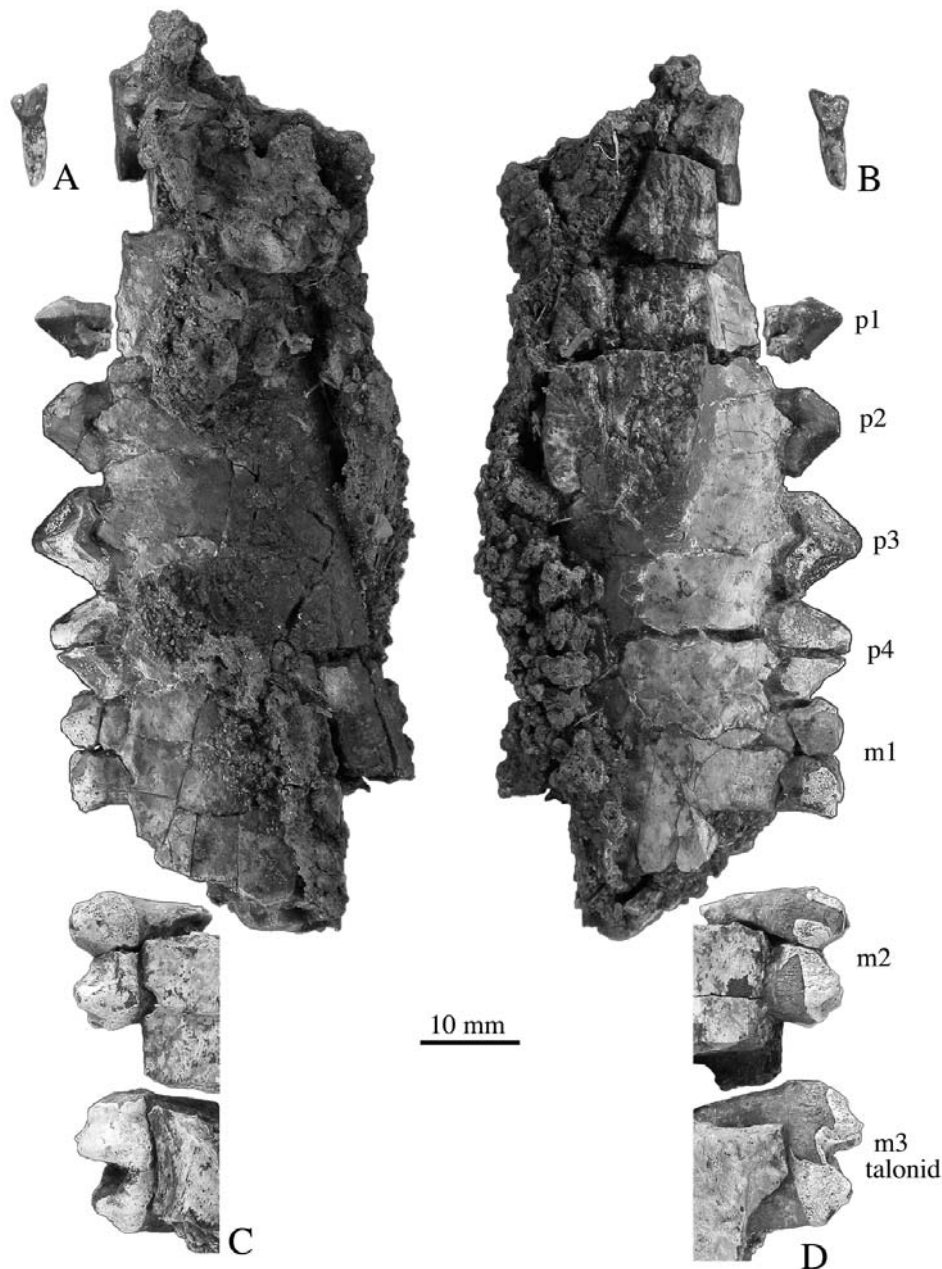
Fig. 8　Right mandibular fragment and lower dentition（i1 and p1－m3）of the type（NMMP-KU 2245）
of *Myaingtherium kenyapotamoides* gen. et sp. nov.
A－B. Right i1（A. buccal view；B. lingual view）；C－D. Mandibular fragment with p1－m3
（C. buccal view；D. lingual view）

part of the cristid obliqua, indicating a presence of the median accessory cusplet even on m1. The median accessory cusplet does not block the center of the median transverse valley. The entoconid is mesial to the hypoconid. The entocristid（= mesiolingual entocristid）extends mesially and disappears at the median transverse valley. The lingual hypolophid connects to the median accessory cusplet or stops at the distolingual base of the median accessory cusplet. On right m3, however, the lingual hypolophid is continuous with the buccal hypolophid with a deep notch between them. In other molars, there is no distinct buccal hypolophid. There is no distinct postentocristid. The posthypocristid extends distolingually and links to the hypoconulid. On m1－m2, the hypoconulid（= cingulum spur）is on the distal cingulum and is relatively large. On m3, the hypoconulid is very large, is distally elongated, and is buccolingually wid-

Fig. 9 Incisor region of the right mandible of the type (NMMP-KU 2245) of *Myaingtherium kenyapotamoides* gen. et sp. nov.

ened with two cusps, the buccal and lingual (= entoconulid) ones. The mesial cristid of the buccal cusp of the m3 hypoconulid links to the posthypocristid with a notch between them. The buccal and lingual cusps of the m3 hypoconulid are separated by a deep groove and are linked by a notched cristid distally. The mesial cristid of the lingual cusp of the m3 hypoconulid extends mesiolingually and disappears at the distolingual base of the entoconid, making the hypoconulid basin somewhat closed lingually. On m1–m2, there are mesial and distal cingula, no lingual cingulum, and a buccal cingulum between the pro-

Fig. 10 Casts of the right lower dentition of the type (NMMP-KU 2245) of *Myaingtherium kenyapotamoides* gen. et sp. nov.
A. Right p1–m1 (occlusal view, stereo pair); B. Right m2 and talonid of m3 (occlusal view, stereo pair); C–F. Right i1 (C. lingual view; D. buccal view; E. distal view; F. mesial view)

toconid and the hypoconid. On m3, there is a precingulid (mesial cingulum), no distal and lingual cingula, and buccal cingula between the protoconid and the hypoconid and between the hypoconid and the buccal cusp of the hypoconulid. The buccal cingulum is continuous to the buccal cristid of the buccal cusp of the m3 hypoconulid. The talonid is wider than the trigonid on m1 − m2 and is as wide as the trigonid on m3 (Table 1). The m1 trigonid is heavily worn and has a mesiobuccal wear facet that occludes the distolingual face of the P4 paracone. The m2 protoconid also has a mesiobuccal wear facet that occludes the distolingual face of the M1 metacone. m1 < m2 < m3.

4 *Myaingtherium* as a variation of the Pondaung anthracotheres

In the mammalian fauna of the Pondaung Formation, the anthracotheres are most abundant in terms of collection size: half of the mammalian dental specimens from the formation are attributed to the anthracotheres (Tsubamoto et al., 2002a, 2005). The Pondaung anthracotheres
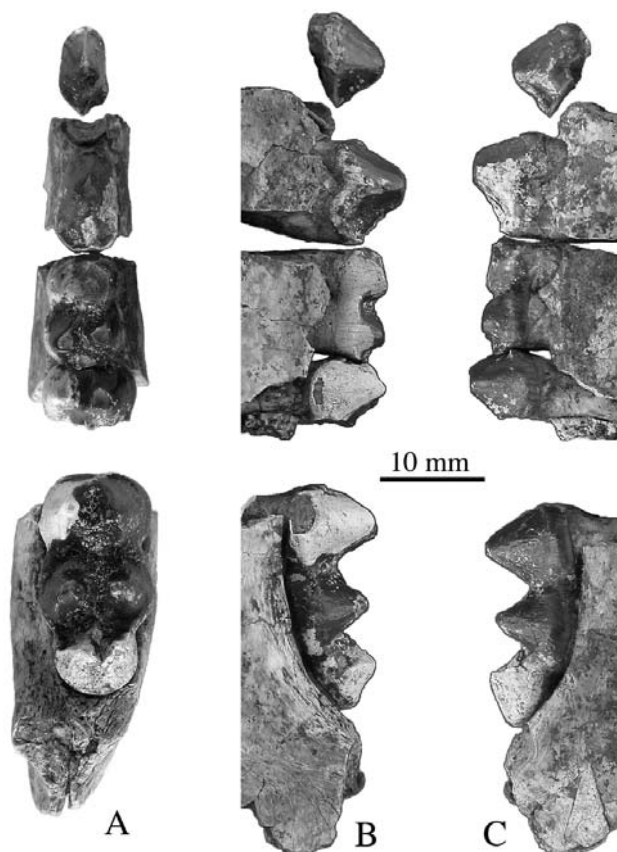

Fig. 11   Left mandibular fragment and lower dentition (p3−m3) of the type (NMMP-KU 2245) of *Myaingtherium kenyapotamoides* gen. et sp. nov.
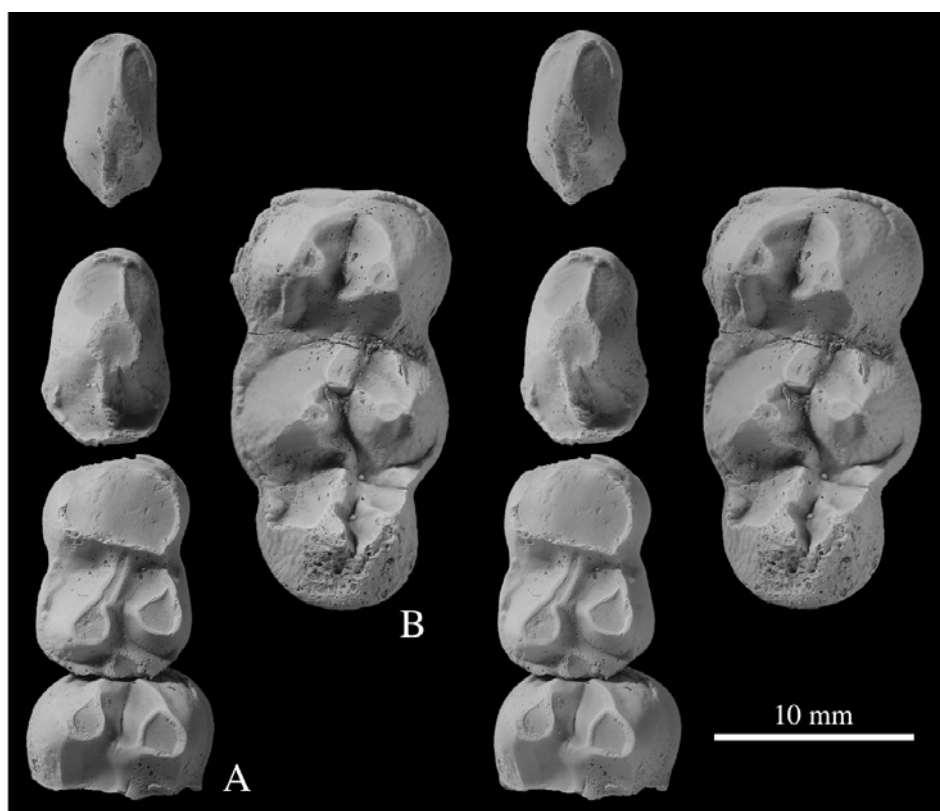A. Occlusal view; B. Buccal view; C. Lingual view

currently consist of four genera besides the present new genus (*Myaingtherium*), although their generic and specific taxonomies are still controversial (Colbert, 1938; Holroyd and Ciochon, 1991; Ducrocq et al., 2000; Tsubamoto et al., 2002a; Holroyd et al., 2006). All of these four genera are primitive bunodont anthracotheres. Two are common genera with abundant fossil specimens and many described species; and the other two are rare in terms of collection size. The common genera are *Anthracotherium* and *Anthracokeryx*. *Anthracotherium* is lager and more bunodont than *Anthracokeryx*, although Tsubamoto et al. (2002a) considered that the two genera are not distinguishable except for size in the Pondaung Formation. The rare genera are *Anthracohyus* and *Pakkokuhyus*. *Anthracohyus* is a medium/large-sized and enigmatic bunodont anthracothere, although Tsubamoto et al. (2002a) considered *Anthracohyus* to be synonymous with *Anthracotherium*. *Pakkokuhyus*, which was originally described as the Helohyidae by Holroyd and Ciochon (1995), is a very small-sized and putative bunodont anthracothere (Holroyd et al., 2006). Tsubamoto et al. (2002a) considered that the material of *Siamotherium pondaungensis* Ducrocq et al., 2000 from the Pondaung Formation is synonymous with *Pakkokuhyus lahirii* and that the genus *Siamotherium* is endemic to the late Eocene of Krabi; we follow this synonymy here.

Myaingtherium is basically similar in morphology to these Pondaung *Anthracotherium*, *Anthracokeryx*, and *Anthracohyus* (= the "Pondaung *Anthracotherium*" in Tsubamoto et al., 2002a). It is similar to *Anthracokeryx* in dental size, is much larger than *Pakkokuhyus*, and is much smaller than *Anthracotherium* and *Anthracohyus*: the m1 size is intermediate between those of large *Anthracokeryx* (= *Anthracokeryx birmanicus* = "*Anthracotherium birmanicum*" in Tsu-

Fig. 12　Casts of the left lower dentition of the type（NMMP-KU 2245）of *Myaingtherium kenyapotamoides*
gen. et sp. nov. in occlusal view（stereo pair）
A. Left p3（distal most part is broken）, p4, m1, and trigonid of m2; B. Left m3

bamoto et al. 2002a）and small *Anthracokeryx*（= *Anthracokeryx tenuis* = *Anthracokeryx ulnifer* = "*Anthracotherium tenuis*" in Tsubamoto et al. 2002a）; and the m2 and m3 sizes approach those of small *Anthracokeryx*（Fig. 13）. However, it is morphologically more similar to *Anthracotherium* and *Anthracohyus* than to *Anthracokeryx* in having more bunodont dentition（Fig. 14）.

　　Compared to the other four genera of the Pondaung anthracotheres（*Anthracotherium*, *Anthracokeryx*, *Anthracohyus*, and *Pakkokuhyus*）, *Myaingtherium* is characterized by a very reduced paraconule on the upper molars and by a median accessory cusplet on the cristid obliqua of the lower molars. The other four genera have a large molar paraconule with developed pre- and postparaconule cristae and lack the median accessory cusplet on the lower molars, although some specimens of *Anthracotherium* have enamel crenulation at this position（Fig. 14）.

　　Myaingtherium is distinguished from the other four genera of the Pondaung anthracotheres in other precise dental morphologies by the combination of the following characteristics（Fig. 14）. *Myaingtherium* has a developed protostyle on the upper molars, which is shared with *Anthracotherium* and *Anthracohyus*. *Anthracokeryx* and *Pakkokuhyus* have no or weak protostyle. *Myaingtherium* has no or only a very faint styles on the buccal part of the upper molars, which is shared with *Anthracohyus* and *Pakkokuhyus*. *Anthracotherium* and *Anthracokeryx* have variously developed but distinct styles on the buccal part（parastyle, mesostyle, and metastyle）and/ or a more developed buccal cingulum. *Myaingtherium* has a mesiodistally-oriented ectoloph on the upper molars, which is shared with *Anthracohyus*, *Pakkokuhyus*, and some specimens of *Anthracotherium*. *Anthracokeryx* and other specimens of *Anthracotherium* have a W-shaped ectoloph connected with the buccal styles. Even in *Anthracohyus* and some specimens of *Anthracotherium*, the centrocrista is connected with the mesostyle or mesostylar region by a crista. In *Myaingtherium*, the centrocrista is completely isolated from the mesostylar region as in *Pakkokuhy-*
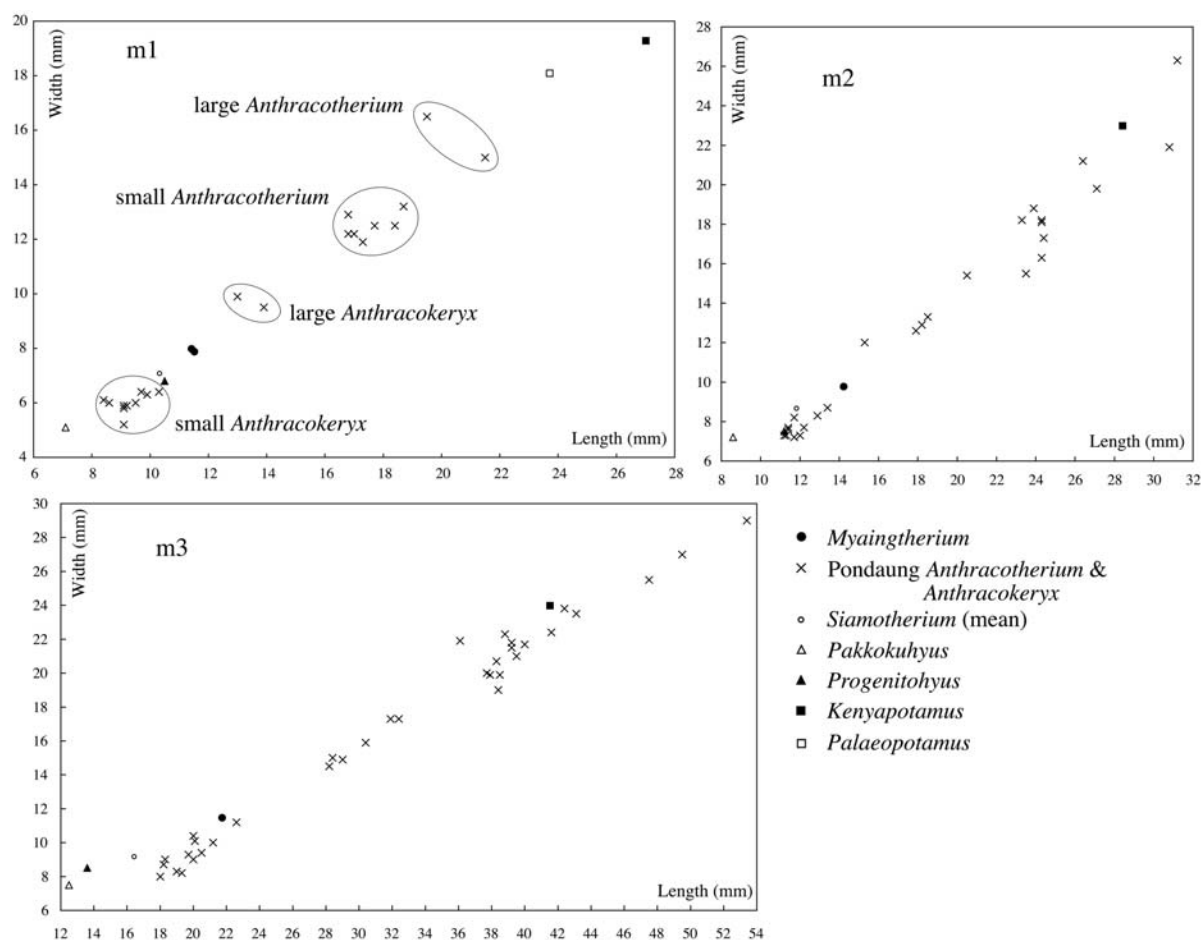
Fig. 13   Bivariate plots of the lower molar dimensions (in mm) of *Myaingtherium*, Pondaung *Anthracokeryx* and *Anthracotherium*, *Siamotherium*, *Pakkokuhyus*, *Progenitohyus*, *Kenyapotamus*, and *Palaeopotamus*
The data of Pondaung *Anthracokeryx* and *Anthracotherium* are from Tsubamoto et al. (2002a); the data of *Siamotherium* (mean) are from Ducrocq (1999); the data of *Pakkokuhyus* are from Holroyd and Ciochon (1995); the data of *Progenitohyus* (? Helohyidae) are from Ducrocq et al. (1997); the data of *Kenyapotamus* (= *Kenyapotamus coryndonae*) and *Palaeopotamus* (= *Kenyapotamus ternani*) (Hippopotamidae; Kenyapotaminae) are from Pickford (1983) and Pickford (2007b), respectively

us. *Myaingtherium* lacks a distinct mesiolingual crista on the molar metaconule (third metacristule); this character is shared with *Anthracohyus*. Many (but not all) specimens of *Anthracotherium* and *Anthracokeryx* have a distinct mesiolingual crista on the metaconule. The presence/ absence of this crista in *Pakkokuhyus* is not clear. *Myaingtherium* has a single premetacristid, which is shared with *Pakkokuhyus*. *Anthracotherium* and *Anthracokeryx* have a double premetacristid (Holroyd and Ciochon, 1995). *Myaingtherium* has a large, wide, and double-cuspid hypoconulid on m3, which is shared with *Anthracotherium*. *Anthracokeryx* and *Pakkokuhyus* have a smaller, narrower, and single-cuspid hypoconulid on m3. However, *Anthracotherium* occasionally has an almost-single-cuspid hypoconulid on m3; and *Anthracokeryx* occasionally has a double-cuspid hypoconulid on m3 in the Pondaung Formation (Pilgrim and Cotter, 1916, pl. 5, fig. 8; Colbert, 1938:377, fig. 52; Holroyd, 1994; Tsubamoto et al., 2002a:369, fig. 5I). Therefore, this character (single- or double-cuspid hypoconulid on m3) may not be a critical diagnostic character among the Pondaung *Anthracotherium* and *Anthracokeryx*. *Myaingtherium* has a relatively larger hypoconulid (= cingulum spur) on m1–m2 than *Anthracotherium*, *Anthracokeryx*, and *Pakkokuhyus*. *Myaingtherium* has a relatively mesiodistally longer M3 with
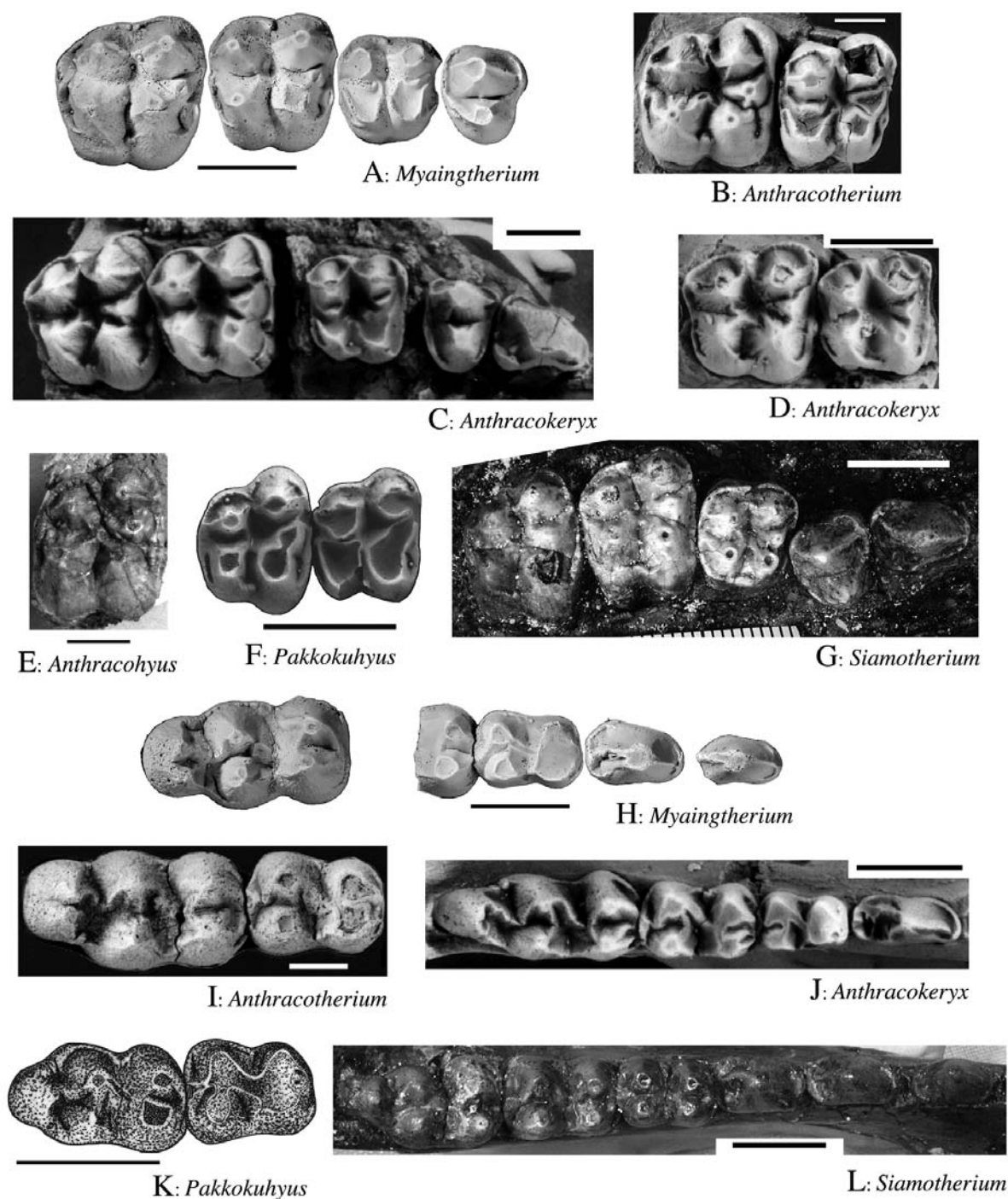
Fig. 14 Comparison of the dentitions of *Myaingtherium* with those of the Pondaung anthracotheres (*Anthracokeryx*, *Anthracotherium*, *Anthracohyus*, and *Pakkokuhyus*) and *Siamotherium* (from the late Eocene of Thailand) in occlusal view

A. Right P4−M3 of *Myaingtherium kenyapotamoides* (NMMP-KU 2245); B. Right M2−M3 of Pondaung *Anthracotherium* (NMMP-KU 0056); C. Right P3−M3 of Pondaung *Anthracokeryx* (NMMP-KU 0053); D. Left M2−M3 of Pondaung *Anthracokeryx* (NMMP-KU 0382) (reversed); E. Left M3 of *Anthracohyus choeroides* (GSI B603) (reversed); F. Right M2−M3 of *Pakkokuhyus lahirii* (NMMP-KU 0039 [Kdw 6]); G. Right P3−M3 of *Siamotherium krabiense* (DMR TF2333. 1); H. Left p3−m3 of *Myaingtherium kenyapotamoides* (NMMP-KU 2245); I. Left m2−m3 of Pondaung *Anthracotherium* (NMMP-KU 0330); J. Right p4−m3 of Pondaung *Anthracokeryx* (NMMP-KU 0052) (reversed); K. Right m2−m3 of *Pakkokuhyus lahirii* (GSI B766) (reversed); L. Right p2−m3 of *Siamotherium krabiense* (DMR TF2333. 2) (reversed); scale bars = 10 mm

a distal shelf; *Anthracotherium* and *Anthracokeryx* occasionally have this character, but *Anthracohyus* and *Pakkokuhyus* have proportionately shorter and wider M3 without a distal shelf. The cusps of *Myaingtherium* are conical like *Anthracotherium* and *Anthracohyus*; they are less conical than those of *Pakkokuhyus* and are more conical than those of *Anthracokeryx*. *Myaingtherium* differs from *Anthracotherium* and *Anthracokeryx* in having a more rounded P4 outline and a proportionally smaller P4 protocone, in that the pre- and postprotocristae on P4 are continuous with the mesial and distal cingula, respectively, and in that there are only a small and dimple-like cingula mesial and distal to the P4 protocone, which are isolated from the buccal part of the mesial and distal cingula, respectively. Normally, the mesial and distal cingula on P4 of *Anthracotherium* and *Anthracokeryx* are continuous respectively from the buccal parts to the lingual parts and are not interrupted by the pre- and postprotocristae.

In spite of the characteristics of *Myaingtherium* discussed above, there is a possibility that *Myaingtherium* might be an individual variation of the "Pondaung *Anthracotherium*" (*sensu* Tsubamoto et al., 2002a) and might be not assigned to a new genus and species because the "Pondaung *Anthracotherium*" have a very wide individual variation on their dental morphology (Tsubamoto et al., 2002a). Although the very reduced molar paraconule in *Myaingtherium* is very unique, a specimen of *Anthracokeryx moriturus* from the Pondaung Formation described by Colbert (1938:376, fig.51), AMNH 20011 (right P3-M3), has a relatively small paraconule, too. Nevertheless, the molar paraconule in *Myaingtherium* is much smaller than that in AMNH 20011 and this character is very unique among the bunodont anthracotheres. *Myaingtherium* also differs from other bunodont anthracotheres as discussed below. Therefore, we establish a new genus and species to the present specimens. *Myaingtherium* shows further taxonomic and dental morphological variations among the Pondaung anthracotheres.

5   Comparison with other bunodont anthracotheres

Myaingtherium is distinguished from the other bunodont anthracotheres except for *Kulutherium* in having very reduced molar paraconule. This character is probably a derived character in the Anthracotheriidae because all other plesiomorphic anthracotheres including basal anthracotheres (such as *Siamotherium*, *Anthracotherium*, *Anthracokeryx*, and *Heptacodon*), putative primitive anthracothere *Pakkokuhyus*, and also plesiomorphic bothriodontines (such as *Bothriogenys* and *Elomeryx*) have a large molar paraconule. It is also distinguished from the other bunodont anthracotheres except for some specimens of *Anthracotherium* in having a median accessory cusplet on the cristid obliqua of the lower molars.

Myaingtherium further differs from *Anthracotherium*, *Anthracokeryx*, *Heptacodon*, *Microbunodon*, and *Prominatherium*, in having a mesiodistally oriented molar ectoloph without a connection to the mesostylar region, a much weaker buccal cingulum on the upper molars, and a single molar premetacristid, and in lacking a parastyle, metastyle, and distinct mesostyle on the upper molars. These latter genera generally have distinct styles and/or stronger cingulum on the buccal side of the upper molars, a W-shaped ectoloph with a connection to the mesostyle or mesostylar region, and a double premetacristid. *Myaingtherium* further differs from *Anthracotherium* in its much smaller size (Fig.13). It further differs from *Microbunodon* and *Anthracokeryx* in having a larger molar protostyle and a double-cuspid hypoconulid on m3. It further differs from "*Anthracothema minima*" (late middle Eocene of central China; Xu, 1962), which is represented only by M3, in having a much larger molar metaconule and a less developed cingulum and in lacking a molar parastyle. It further differs from "*Anthracothema*" *lijiangensis* (middle Eocene of southern China; Zong et al., 1996), which is represented only by m1-m3, in being smaller and in having stronger cristids, a more lingually shifted cristid obliqua at the distal trigonid wall on the lower molars, and a double-cuspid hypoconulid on m3. The distal shelf on
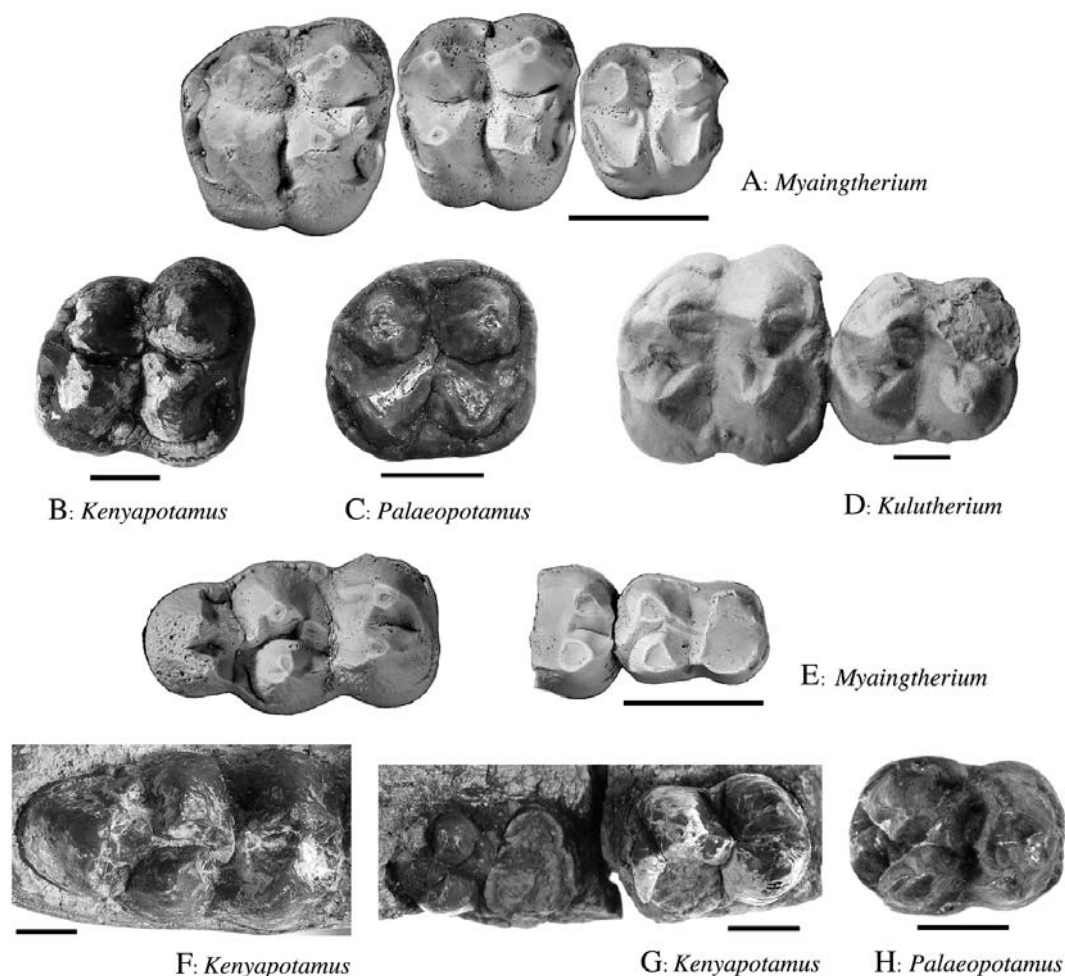
Fig. 15　Comparison of the molars of *Myaingtherium* with those of the Kenyapotaminae and *Kulutherium*（from the Miocene of Africa）in occlusal view

A. Right M1−M3 of *Myaingtherium kenyapotamoides*（NMMP-KU 2245）; B. Right M3 of *Kenyapotamus coryndonae*（KNM BN1321）; C. Right M1 of *Palaeopotamus ternani*（= *Kenyapotamus ternani*）（KNM FT3634）; D. Left M1−M2 of *Kulutherium kenyensis*（R773'49）（reversed）; E. Left m1−m3 of *Myaingtherium kenyapotamoides*（NMMP-KU 2245）; F. Right m3 of *Kenyapotamus coryndonae*（KNM NA246）（reversed）; G. Left m1 −m2 of *Kenyapotamus coryndonae*（KNM SH14792）; H. Left m1 of *Palaeopotamus ternani*（= *Kenyapotamus ternani*）（Bar1186'99）; scale bars = 10 mm

M3 of *Myaingtherium* is reminiscent of that of "*Anthracothema*" *verhoeveni*（? late Eocene of Indonesia; von Koenigswald, 1967）, however the former is less developed and less distally protruded than the latter.

　　Myaingtherium further differs from *Siamotherium*（Fig. 14G, L; late Eocene of Thailand; Suteethorn et al., 1988; Ducrocq, 1999）, which is supposed to be the most primitive anthracothere（Lihoreau and Ducrocq, 2007）, in having a larger molar protostyle, a molar centrocrista isolated from the mesostylar region, proportionately longer and narrower M3, a diastema between c1 and p1, double-rooted p1（*Siamotherium* has a single-rooted p1）, a relatively lager hypoconulid（= cingulum spur）on m1−m2, and a much larger and double-cuspid hypoconulid on m3（*Siamotherium* has a single-cuspid hypoconulid on m3）. On the other hand, they share several characteristics: a rounded outline of P4 crown, a proportionately smaller protocone on P4, P4 pre- and postprotocristae continuous with the cingula, no or very weak molar styles（on the buccal part）, and a single premetacristid on the lower molars.

　　Myaingtherium differs from an enigmatic possible anthracothere *Bugtitherium*（late Oligo-

cene of Pakistan；Pilgrim，1907，1908；Métais et al., 2006a），whose rostral structure of the skull has some similarities with that of archaeocete cetaceans，in being much smaller and in having a median accessory cusplet on the lower molars，although they share a double-cuspid hypoconulid on m3. The upper molar dentition of *Bugtitherium* has been unknown.

Myaingtherium have some dental similarities with the hippo-like anthracothere *Kulutherium* （Fig. 15D；early Miocene of Kenya；Pickford，2007a）in having a bunodont and almost tetracuspidate upper molar with a very small paraconule shifted mesially，no or vestigial molar mesostyle，and a mesiodistally-oriented molar ectoloph isolated from the mesostylar region，and in lacking a molar parastyle and metastyle. However，it is distinguished from *Kulutherium* in being much smaller and in having a weaker cingulum on the upper dentition，proportionately shorter and wider M1–M2，a large protostyle on the upper molars （*Kulutherium* lacks a molar protostyle but have an elevation of the middle part of the mesial cingulum almost connected to the paraconule on the upper molars），a single-cuspid P4 protocone，and in lacking accessory cusps that are located on the lingual and distal regions of the upper molars.

6 Phylogenetic analysis

We performed cladistic analyses to test the phyletic position of *Myaingtherium*. Cladistic analyses of the anthracotheres have been attempted by several previous studies. We performed four cladistic analyses using the data sets by Lihoreau et al. （2004），Lihoreau and Ducrocq （2007），Holroyd （1994），and Boisserie et al. （2010）. A consensus tree of the most parsimonious trees discovered by each analysis is shown in Figs. 16–19.

6.1 Analysis 1

The cladistic analysis 1 was performed using the data set by Lihoreau et al. （2004），concerning relationships among bunodont anthracotheres. We added the data matrix of *Myaingtherium* to the matrix represented by Lihoreau et al. （2004：110, table 4）. The added data matrix of *Myaingtherium* is as follows：

?0(01)010???1(01)(01)011001

We revised some character states shown in Lihoreau et al. （2004：110, table 4）. The states
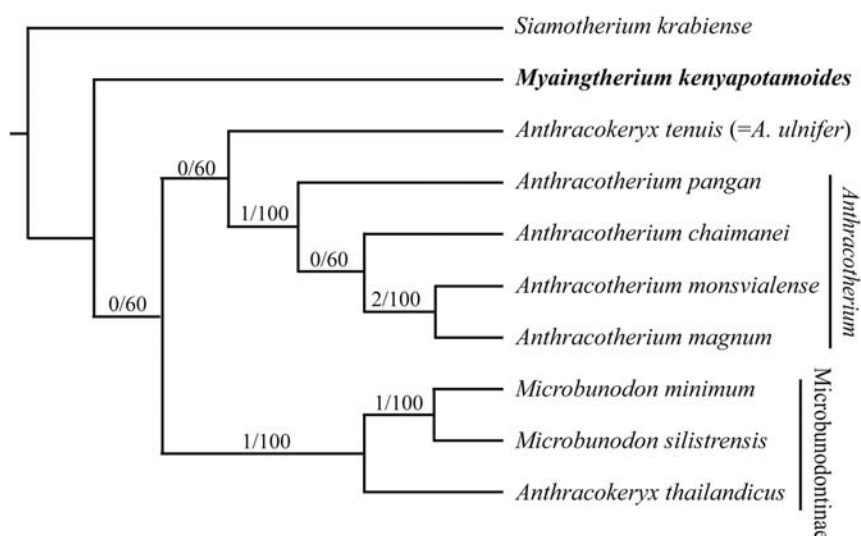

Fig. 16   50% majority-rule consensus tree of the five equally most parsimonious cladogram trees recovered by
the cladistic analysis 1 （using the data set modified from that by Lihoreau et al., 2004）
Numbers indicate Bremer support/frequencies of occurrence

of the character 1（on the P3 "protocone"）of *Anthracokeryx tenuis* (= *A. ulnifer*) and *Anthra-cokeryx thailandicus* were changed from "0" to "1" because *Anthracokeryx* have an accessory lin-gual cusp（protocone）on P3 as implied by Lihoreau et al.（2004：98）. Also, the states of the character 10（on the m3 entoconulid ［ = lingual cusp of hypoconulid］）of *Anthracokeryx tenuis* and *Anthracotherium pangan* (= *Anthracothema pangan*) were changed from "0"（former）and "1"（latter）, respectively, to "（01）" because the entoconulid on m3 variously exists/lacks in *Anthracokeryx* and *Anthracotherium* from the Pondaung Formation（Holroyd, 1994; Tsubamoto et al., 2002a）. *Microbunodon milaensis* was removed form the analysis following Lihoreau et al. （2004）. The data matrix（10 taxa and 18 characters）was compiled using MacClade version 4.0 （Maddison and Maddison, 2000）and analyzed using PAUP4.0b10（Swofford, 2002）with branch-and-bound search option, using *Siamotherium* to represent an outgroup to the other an-thracotheres. All characters were corded as unordered and unweighted. Multi-state taxa were in-terpreted as polymorphism. All characters were parsimony-informative. This analysis recovered five equally most parsimonious trees with a length of 33 steps. Each most parsimonious tree has a consistency index（CI）of 0.7273, homoplasy index（HI）of 0.4242, retention index（RI）of 0.7805, and rescaled consistency index（RC）of 0.5676.

6.2　Analysis 2

The cladistic analysis 2 was performed using the data set by Lihoreau and Ducrocq（2007）, concerning relationships among an extensive number of anthracotheres. We added the data matrix of *Myaingtherium* to the matrix represented by Lihoreau and Ducrocq（2007：103, table 7.1）. The added data matrix of *Myaingtherium* is as follows：

0?00????0000100?011（01）00001（01）（01）000? 01100000?0?????????0

The same revisions of the character states as in the analysis 1 were made on the character 16 （on P3）of *Anthracokeryx tenuis* and *Anthracokeryx thailandicus* and on the character 25（on m3）of *Anthracokeryx tenuis* and *Anthracotherium pangan*. The data matrix（28 taxa and 51 charac-ters）was analyzed in the same procedure as in the analysis 1. This analysis recovered 45 equally most parsimonious trees with a length of 118 steps. Each most parsimonious tree has a CI（exclu-ding uninformative characters）of 0.6293, HI（excluding uninformative characters）of 0.3707, RI of 0.8497, and RC of 0.5400.

6.3　Analysis 3

The cladistic analysis 3 was performed using the data set by Holroyd（1994）, concerning re-lationships among Old World Paleogene anthracotheres and relationships with helohyids. We add-ed the data matrices of *Myaingtherium* and also putative anthracothere *Pakkokuhyus* from the Pon-daung Formation to the matrix represented by Holroyd（1994：289, table 6.3）. The added data matrices are as follows：

Myaingtherium：11?00（13）000010101121110112112（12）1131（12）0110000
Pakkokuhyus：1???0?1002200001200?????1100113110110?00

The character 35（lower molar trigonid to talonid width）was removed from the analysis be-cause the width of the molar trigonid to that of the talonid varies depending on tooth class. The data matrix（16 taxa and 39 characters）was analyzed generally in the same procedure as in Hol-royd（1994）with branch-and-bound search option, using *Pentacemylus* to represent an outgroup. Multi-state taxa were interpreted as polymorphism. This analysis recovered one most parsimonious tree with a length of 116 steps. The most parsimonious tree has a CI（excluding uninformative characters）of 0.5652, HI（excluding uninformative characters）of 0.4348, RI of 0.6711, and RC of 0.3818.

6.4　Analysis 4

The cladistic analysis 4 was performed using the data set by Boisserie et al.（2010）, con-
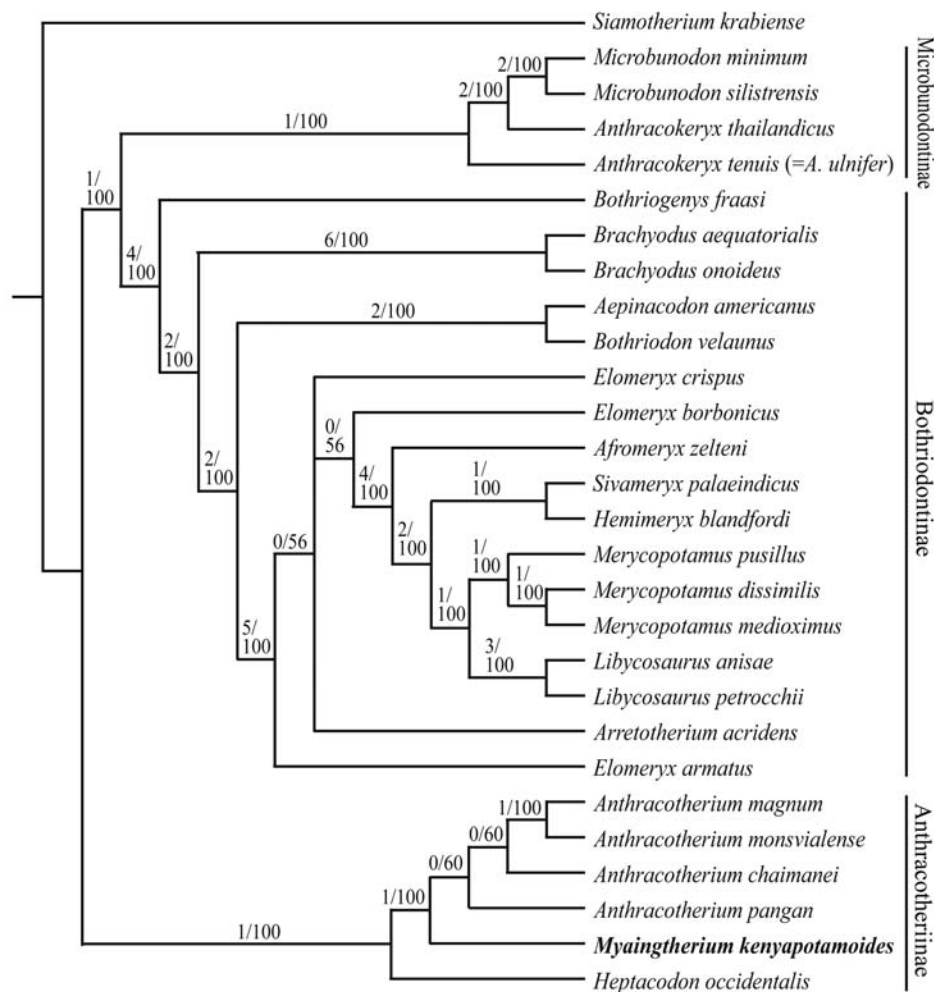
Fig. 17   50% majority-rule consensus tree of the 45 equally most parsimonious cladogram trees recovered by the cladistic analysis 2（using the data set modified from that by Lihoreau and Ducrocq，2007）
Numbers indicate Bremer support/frequencies of occurrence

cerning hippos，anthracotheres，some suoids，and some other primitive artiodactyls. We added the data matrix of *Myaingtherium* to the matrix represented by Boisserie et al.（2010：365，appendix 3）. The added data matrix of *Myaingtherium* is as follows：

? 0? 000100100 ????????????? 1001101111002000010100100010000011000000010110100010021 ??????

The data matrix（25 taxa and 87 characters）was analyzed generally in the same procedure as in Boisserie et al.（2010）. This analysis recovered six equally most parsimonious trees with a length of 297 steps. Each most parsimonious tree has a CI（excluding uninformative characters）of 0. 4595, HI（excluding uninformative characters）of 0. 5405, RI of 0. 7193, and RC of 0. 3318.

6. 5   Discussion

The phylogenetic tree obtained by the analysis 1（Fig. 16）indicates that *Myaingtherium* is positioned at the very basal part of the family，between *Siamotherium*（designated as outgroup）and the other bunodont anthracotheres. The analysis 1 supports the Microbunodontinae Lihoreau and Ducrocq，2007 excluding *Anthracokeryx tenuis*（ = *A. ulnifer*），and shows that *Anthracokeryx tenuis* is a sister taxon of the genus *Anthracotherium*. The tree obtained by the analysis 2（Fig. 17），however，indicates that *Myaingtherium* is positioned within the Anthracotheriinae（*sensu* Li-
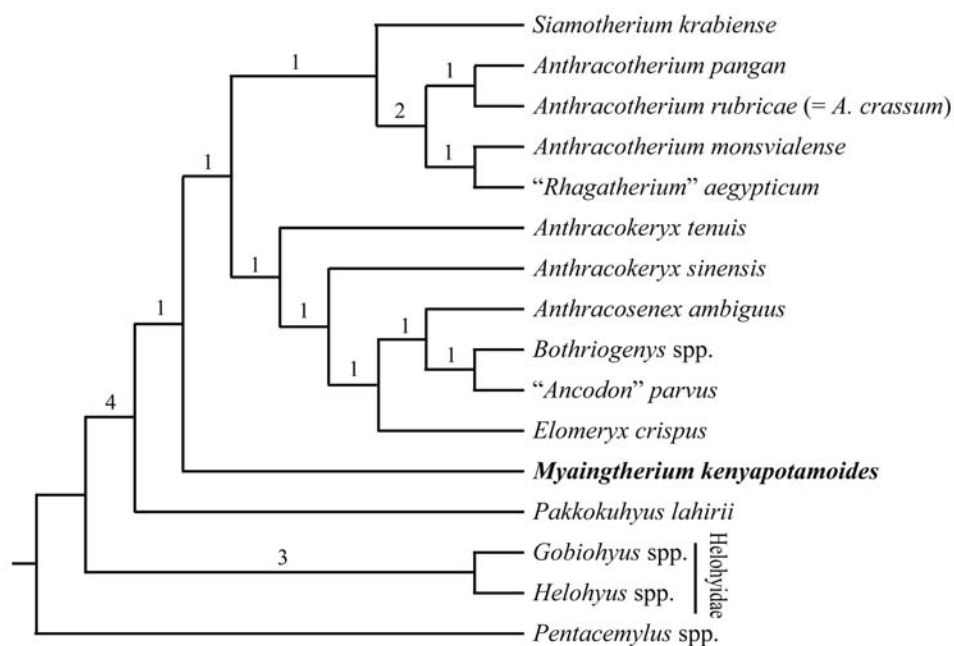
Fig. 18   The most parsimonious cladogram tree recovered by the cladistic analysis 3
（using the data set modified from that by Holroyd，1994）
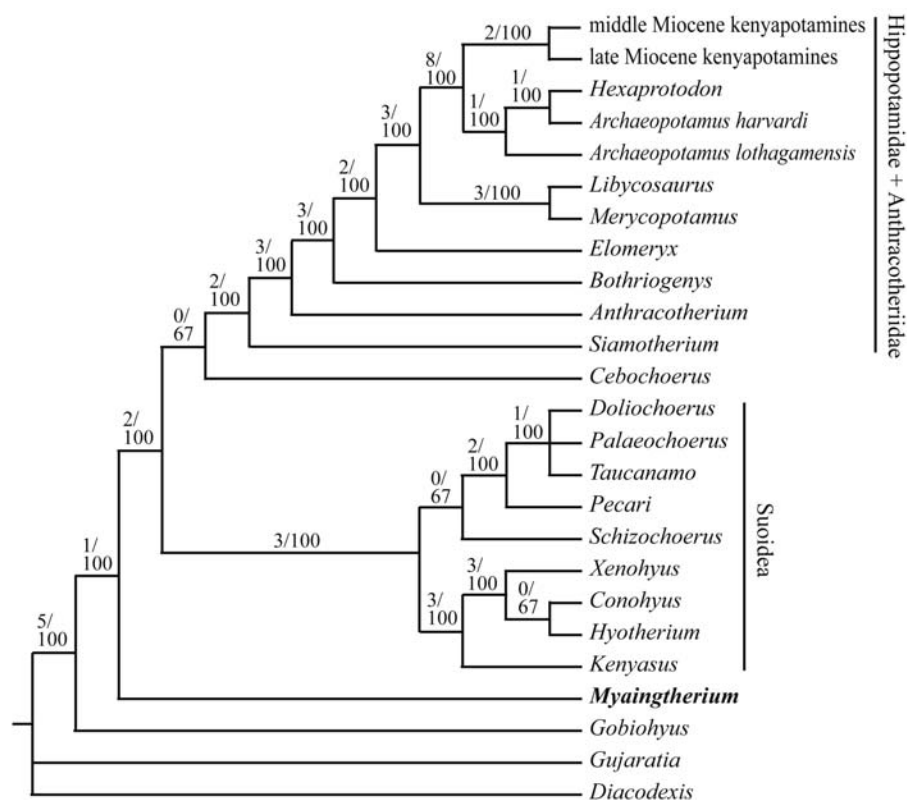Numbers indicate Bremer support

Fig. 19   50% majority-rule consensus tree of the six equally most parsimonious cladogram trees recovered
by the cladistic analysis 4（using the data set modified from that by Boisserie et al., 2010）
Numbers indicate Bremer support/frequencies of occurrence

horeau and Ducrocq，2007），between *Heptacodon* and *Anthracotherium*，and is one of the basal anthracotheriine species. This tree supports the monophyly of the Anthracotheriinae，but not

strongly (Bremer support 1). This tree also supports the monophyly of the Microbunodontinae including *Anthracokeryx tenuis* (Bremer support 1). The tree obtained by the analysis 3 (Fig. 18) indicates that *Myaingtherium* is a basal anthracothere which is positioned more basal than *Siamotherium*. This tree strongly indicates that *Pakkokuhyus* is the sister taxon of the other anthracotheres including *Myaingtherium* (Bremer support 4), implying its inclusion within the Anthracotheriidae rather than within the Helohyidae, as suggested by Ducrocq et al. (2000) and Holroyd et al. (2006). The analyses 1–3 emphasize that *Myaingtherium* is a very primitive and one of the basal and oldest bunodont anthracotheres. On the other hand, the cladogram by the analysis 4 (Fig. 19) indicates that *Myaingtherium* is positioned outside of the hippo-anthracothere clade and is located more basal within the Artiodactyla, albeit a basal anthracothere *Siamotherium* is included in the hippo-anthracothere clade. This may be caused by the fragmentary nature of the currently available material of *Myaingtherium*, resulting in many missing data in the matrix, but may alternatively imply a need for further reconsideration of the character selection and coding of the data matrix to test the phyletic relationships of the anthracotheres among the Artiodactyla.

7   Similarity with primitive hippos and possible implication for the hippo origins

Interestingly, several dental characteristics of *Myaingtherium* are reminiscent of those of the Kenyapotaminae (primitive Hippopotamidae) from the middle to late Miocene of Africa and the hippo-like anthracothere *Kulutherium* (known only on the upper dentition) from the early Miocene of Africa (Fig. 15). Although *Myaingtherium* is much smaller in size than the latter (Figs. 13, 15), it is comparable to the kenyapotamines and *Kulutherium* in the following molar characteristics (Fig. 15): a bunodont dentition, an almost tetracuspidate upper molar with a very small paraconule shifted mesially, lack of a molar parastyle and metastyle, no or vestigial molar mesostyle, a mesiodistally-oriented molar ectoloph, a centrally (not lingually) positioned and well-defined notch between the preprotocristid and the premetacristid on the lower molars, an M-shaped ridge at the distal trigonid wall on the lower molars, and a median accessory cusplet on the lower molars. Besides, the configuration of the cusps and cristids of the lower molars in the kenyapotamines is comparable to that in *Myaingtherium* (Fig. 15E–H). Among these similarities, however, there are only two potential synapomorphies, a reduced molar paraconule and median accessory cusplet on the lower molars, among *Myaingtherium*, the Kenyapotaminae, and *Kulutherium*. Most of other similarities are considered to be symplesiomorphies because they are generally common among the early primitive Eocene artiodactyls.

The origin of the Hippopotamidae has long been debated (Pilgrim, 1941; Gentry and Hooker, 1988; Boisserie et al., 2005a, 2010; Pickford, 1989, 2008, and references therein). Several possible ancestors of the family have been elected, such as anthracotheres, suoids, and cebochoerids (Pickford, 1989, 2008). As summarized by Boisserie et al. (2005a, 2010), at present, there are two major hypotheses on the origin of the Hippopotamidae, the advanced selenodont anthracotheriid (bothriodontine) origin hypothesis (Falconer and Cautley, 1836; Lydekker, 1876; Colbert, 1935a, b; Boisserie et al., 2005a, b, 2010; Boisserie and Lihoreau, 2006; Boisserie, 2007) and the palaeochoerid (= Old World tayassuid) origin hypothesis (Pickford, 1989, 1993, 2005, 2007b, 2008; Pickford and Morales, 1989). The advanced selenodont anthracotheriid origin hypothesis is well supported by cladistic analyses (Boisserie et al., 2005a, b, 2010), but the problem is the molar morphology. The advanced anthracotheres have a strongly selenodont dentition, but conversely the primitive hippos (kenyapotamines) have a bunodont dentition. On the other hand, the palaeochoerid (Suoidea) origin hypothesis agrees with the molar morphology, but it disagrees with the molecular phylogeny. This hypothesis implies that the suoids and hippos are closely related, but the molecular phylogeny strongly suggests that the hippos are closely related not to the suoids but to the cetaceans and then ruminants (Gatesy et al., 1999; Nikaido et al.,

1999; Murphy et al., 2001; Marcot, 2007). If we consider that *Myaingtherium* (primitive buno-dont anthracothere) is phyletically related to kenyapotamines (and *Kulutherium*) as implied by Gentry and Hooker (1988), this agrees with the molar morphology and at the same time it is not incongruent with the molecular phylogeny. Although the cladistic analysis (the analysis 4; Fig. 19) does not indicate a close relationship between *Myaingtherium* and kenyapotamines, this might be caused by the poor fossil record of these taxa and a large temporal gap (ca. 20 Ma) be-tween them. Actually, the close phyletic relationship between *Kulutherium* and the kenyapota-mines has been recently suggested by Orliac et al. (2009). Therefore, the discovery of *Mya-ingtherium* indicates that the further resolution on the hippo origin requires the discovery of data on poorly known Paleogene and early Miocene bunodont anthracotheres from Asia and Africa, such as *Myaingtherium*, *Kulutherium*, "*Rhagatherium*" *aegypticum*, and *Bugtitherium* (Holroyd, 1994; Métais et al., 2006a; Pickford, 2007a).

8   Concluding remarks

The new anthracotheriid specimens from the upper middle Eocene Pondaung Formation of Myanmar described here (Figs. 1, 4–12) are assigned to a new genus and species, *Myaingthe-rium kenyapotamoides*. *Myaingtherium* is a primitive and bunodont anthracothere and has overall dental similarity with Pondaung *Anthracotherium*, *Anthracohyus*, and *Anthracokeryx*. It is more comparable in dental morphology to the larger Pondaung anthracotheres, *Anthracotherium* and *An-thracohyus*, in having more bunodont dentition, rather than to *Anthracokeryx*; however, it is more comparable in dental size to a small-sized Pondaung anthracothere, *Anthracokeryx tenuis*. It dif-fers from the Pondaung and other bunodont anthracotheres (except for Miocene African *Kuluthe-rium*) particularly in having very reduced molar paraconule, which is a unique character among the bunodont anthracotheres. The present specimens add further taxonomic and dental morphologi-cal variations among the Pondaung anthracotheres. The cladistic analyses indicated that *My-aingtherium* is one of the basal and oldest anthracotheres and is likely included in the Anthracoth-eriinae (*sensu* Lihoreau and Ducrocq, 2007).

Interestingly, *Myaingtherium* has some dental similarities, such as a reduced molar para-conule with bunodont dentition, with the Kenyapotaminae (primitive hippopotamids) and *Kulu-therium* (hippo-like putative anthracothere), filling the gap of the superficial molar morphology between the Anthracotheriidae and the primitive Hippopotamidae. This implies a possibility that *Myaingtherium* (primitive bunodont anthracothere) might be related to *Kulutherium* and ken-yapotamines, that is, primitive hippos, as implied by Gentry and Hooker (1988). It is also in-teresting to note that the Pondaung fauna includes a possible raoellid artiodactyl (Tsubamoto et al., 2005; Métais et al., 2007; Theodor et al., 2007). The raoellids are an early to early middle Eocene bunodont artiodactyl family recorded in the lower to lower middle Eocene of northern Indo-Pakistan and have been recently considered to be the sister group of cetaceans (Thewissen et al., 2001, 2007; Theodor et al., 2007; Geisler and Theodor, 2009; Spaulding et al., 2009). Therefore, possible hippopotamid ancestors (most primitive anthracotheres including *Myaingthe-rium*) and a possible raoellid (sister group of cetaceans) coexisted in the middle Eocene Pon-daung fauna. This is consistent with the results of the molecular biology that the cetaceans and hippopotamids are in a sister-taxon relationship (Gatesy et al., 1999; Nikaido et al., 1999; Murphy et al., 2001; Marcot, 2007). Although more evidences are necessary to test the precise phyletic relationships of *Myaingtherium*, this discovery reinforces that the Pondaung anthracotheres are an important group for testing and confirming the phyletic relationships among the Anthracotheriidae, Hippopotamidae, Cetacea, Raoellidae, and Suoidea, and for understanding the early evolution of these artiodactyl groups (Pilgrim and Cotter, 1916; Pilgrim, 1928, 1940, 1941).

References

Adnet S, Cappetta H, Beard K C et al., 2008. First myliobatiform teeth (Elasmobranchii, Neoselachii) from the Pondaung Formation (late Middle Eocene) of central Myanmar. Neues Jahrb Geol Paläont Abh, **247**(3)：335–340

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. Yangon：Office of Strategic Studies, Ministry of Defence. 152–178

Aung Naing Soe, Myitta, Soe Thura Tun et al., 2002. Sedimentary facies of the late Middle Eocene Pondaung Formation (central Myanmar) and the paleoenvironments of its anthropoid primates. C R Palevol, **1**：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. Yangon：Office of Strategic Studies, Ministry of Defence. 131–151

Aye Ko Aung, 2004. The primate-bearing Pondaung Formation in the upland area, northwest of central Myanmar. In：Ross C, Kay R F eds. Anthropoid Origins：New Visions. New York：Kluwer Academic/Plenum Press. 205–217

Beard K C, Marivaux L, Chaimanee Y et al., 2009. A new primate from the Eocene Pondaung Formation of Myanmar and the monophyly of Burmese amphipithecids. Proc R Soc B, **276**：3285–3294

Beard K C, Marivaux L, Soe Thura Tun et al., 2007. New sivaladapid primates from the Eocene Pondaung Formation of Myanmar and the anthropoid status of Amphipithecidae. Bull Carnegie Mus Nat Hist, **39**：67–76

Beck R M D, Bininda-Emonds O R P, Cardillo M et al., 2006. A higher-level MRP supertree of placental mammals. BMC Evol Biol, **6**：93, doi：10. 1186/1471–2148–6–93

Bender F, 1983. Geology of Burma. Berlin: Gebrüder Borntraeger. 1–293

Benammi M, Aung Naing Soe, Than Tun et al., 2002. First magnetostratigraphic study of the Pondaung Formation: implications for the age of the Middle Eocene anthropoids of Myanmar. J Geol, **110**: 748–756

Boisserie J-R, 2007. Family Hippopotamidae. In: Prothero D R, Foss S E eds. The Evolution of Artiodactyls. Baltimore: Johns Hopkins University Press. 106–119

Boisserie J-R, Lihoreau F, 2006. Emergence of Hippopotamidae: new scenarios. C R Palevol, **5**: 749–756

Boisserie J-R, Lihoreau F, Brunet M, 2005a. Origins of Hippopotamidae (Mammalia, Cetartiodactyla): towards resolution. Zool Script, **34**(2): 119–143

Boisserie J-R, Lihoreau F, Brunet M, 2005b. The position of Hippopotamidae within Cetartiodactyla. Proc Natl Acad Sci USA, **102**(5): 1537–1541

Boisserie J-R, Lihoreau F, Orliac M et al., 2010: Morphology and phylogenetic relationships of the earliest known hippopotamids (Cetartiodactyla, Hippopotamidae, Kenyapotaminae). Zool J Linn Soc, **158**: 325–366

Bown T M, Kraus M J, 1979. Origin of the tribosphenic molar and metatherian and eutherian dental formulae. In: Lillegraven J A, Kielan-Jaworowska Z, Clemens W A eds. Mesozoic Mammals: The First Two-Thirds of Mammalian History. Berkeley: University of California Press. 172–181

Colbert E H, 1935a. Distributional and phylogenetic studies on Indian fossil mammals. IV. The phylogeny of the Indian Suidae and the origin of the Hippopotamidae. Am Mus Novit, (799): 1–24

Colbert E H, 1935b. Siwalik mammals in the American Museum of Natural History. Trans Am Philos Soc, New Ser, **26**: 1–401

Colbert E H, 1938. Fossil mammals from Burma in the American Museum of Natural History. Bull Am Mus Nat Hist, **74**: 259–434

Coombs W P, Coombs M C, 1977. The origin of anthracotheres. Neues Jahrb Geol Paläont Monatsh, **10**: 584–599

Cotter G de P, 1914. Some newly discovered coal-seams near the Yaw River, Pakokku District, Upper Burma. Rec Geol Surv India, **44**: 163–185

Ducrocq S, 1999. The Late Eocene Anthracotheriidae (Mammalia, Artiodactyla) from Thailand. Palaeontogr Abt A, **252**(4–6): 93–140

Ducrocq S, Aung Naing Soe, Aye Ko Aung et al., 2000. A new anthracotheriid artiodactyl from Myanmar, and the relative ages of the Eocene anthropoid primate-bearing localities of Thailand (Krabi) and Myanmar (Pondaung). J Vert Paleont, **20**(4): 755–760

Ducrocq S, Chaimanee Y, Suteethorn V et al., 1997. First discovery of Helohyidae (Artiodactyla, Mammalia) in the Late Eocene of Thailand: a possible transitional form for Anthracotheriidae. C R Acad Sci, Paris, Sci Terre Planèt/Earth Planet Sci, **325**: 367–372

Egi N, Tsubamoto T, Takai M, 2007. Systematic status of Asian "*Pterodon*" and early evolution of hyaenaelurine hyaenodontid creodonts. J Paleont, **81**(4): 770–778

Falconer H, Cautley P T, 1836. Note on the fossil *Hippopotamus* of the Siwalik Hills. Asiat Res, Calcutta, **19**: 39–53

Gatesy J, Milinkovitch M, Waddell V et al., 1999. Stability of cladistic relationships between Cetacea and higher-level artiodactyl taxa. Syst Biol, **48**(1): 6–20

Geisler H H, Theodor J M, 2009. *Hippopotamus* and whale phylogeny. Nature, **458**: E1–E4, doi:10.1038/nature07776

Gentry A W, Hooker J J, 1988. The phylogeny of the Artiodactyla. In: Benton M ed. The Phylogeny and Classification of the Tetrapods, Volume 2: Mammals, Systematics Association Special Volume No. 35B. Oxford: Clarendon Press. 235–272

Gunnell G F, Ciochon R L, 2008. Revisiting primate postcrania from the Pondaung Formation of Myanmar. In: Fleagle J G, Gilbert C C eds. Elwyn Simons: A Search for Origins. New York, Springer. 211–228

Hershkovitz P, 1971. Basic crown patterns and cusp homologies of mammalian teeth. In: Dahlberg A A ed. Dental Morphology and Evolution. Chicago: The University of Chicago Press. 95–150

Holroyd P A, 1994. An Examination of Dispersal Origins for Fayum Mammalia. Ph. D. Dissertation. Durham: Duke University. 1–328

Holroyd P A, Ciochon R L, 1991. A reappraisal of Burmese anthracotheriid artiodactyls. J Vert Paleont, **11**(suppl 3)：35A

Holroyd P A, Ciochon R L, 1994. The relative ages of Asian primate-bearing deposits. In：Fleagle J G, Kay R F eds. Anthropoid Origins. New York：Plenum Press. 123–141

Holroyd P A, Ciochon R L, 1995. A new artiodactyl (Mammalia) from the Eocene Pondaung Sandstones, Burma. Ann Carnegie Mus, **64**(3)：177–183

Holroyd P A, Ciochon R L, Gunnell G F, 2006. Phylogenetic relationships among late Middle Eocene to Early Oligocene Old World anthracotheriids. J Vert Paleont, **26**(suppl 3)：78A

Koenigswald G H R von, 1967. An upper Eocene mammal of the family Anthracotheriidae from the Island of Timor, Indonesia. Proc K Ned Akad Wet, Ser B, **70**：529–533

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

Leidy J, 1869. The extinct mammalian fauna of Dakota and Nebraska including an account of some allied forms from other localities, together with a synopsis of the mammalian remains of North America. J Acad Nat Sci Philadelphia, Ser 2, **7**：1–472

Lihoreau F, 2003. Systématique et Paléoécologie des Anthracotheriidae (Artiodactyla；Suiformes) du Mio-Pliocène de l'Ancien Monde：Implications Paléobiogéographiques. Poitiers：Thèse Pour l'obtention du Grade de Docteur de l'Universite de Poitiers. 1–395

Lihoreau F, Blondel C, Barry J et al., 2004. A new species of the genus *Microbunodon* (Anthracotheriidae, Artiodactyla) from the Miocene of Pakistan：genus revision, phylogenetic relationships and palaeobiogeography. Zool Script, **33**(2)：97–115

Lihoreau F, Ducrocq S, 2007. Family Anthracotheriidae. In：Prothero D R, Foss S E eds. The Evolution of Artiodactyls. Baltimore：Johns Hopkins University Press. 89–105

Luterbacher H P, Ali J R, Brinkhuis H et al., 2004. The Paleogene Period. In：Gradstein F M, Ogg J G, Smith A G eds. A Geologic Time Scale 2004. Cambridge：Cambridge University Press. 384–408

Lydekker R, 1876. Notes on the osteology of *Merycopotamus dissimilis*. Rec Geol Surv India, **9**：114–153

Maddison W P, Maddison D R, 2000. MacClade Version 4.0. Sunderland：Sinauer Associations, Inc

Marcot J D, 2007. Molecular phylogeny of terrestrial artiodactyls：conflicts and resolution. In：Prothero D R, Foss S E eds. The Evolution of Artiodactyls. Baltimore：Johns Hopkins University Press. 4–18

Marivaux L, Beard K C, Chaimanee Y et al., 2008a. Anatomy of the bony pelvis of a relatively large-bodied strepsirrhine primate from the late Middle Eocene Pondaung Formation (central Myanmar). J Hum Evol, **54**：391–404

Marivaux L, Beard K C, Chaimanee Y et al., 2008b. Proximal femoral anatomy of a sivaladapid primate from the late Middle Eocene Pondaung Formation (central Myanmar). Am J Phys Anthrop, **137**：263–273

Marivaux L, Bocat L, Chaimanee Y et al., 2006. Cynocephalid dermopterans from the Palaeogene of South Asia (Thailand, Myanmar and Pakistan)：systematic, evolutionary and palaeobiogeographic implications. Zool Script, **35**(4)：395–420

Maung Maung, Thaung Htike, Tsubamoto T et al., 2005. Stratigraphy of the primate-bearing beds of the Eocene Pondaung Formation at the Paukkaung area, central Myanmar. Anthrop Sci, **113**(1)：11–15

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**(1)：51–67

Métais G, Antoine P-O, Baqri S R H et al., 2006a. New remains of the enigmatic cetartiodactyl *Bugtitherium grandincisivum* Pilgrim, 1908, from the upper Oligocene of the Bugti Hills (Balochistan, Pakistan). Naturwissenschaften, **93**：348–355

Métais G, Aung Naing Soe, Ducrocq S, 2006b. A new basal tapiromorph (Perissodactyla, Mammalia) from the Middle Eocene of Myanmar. Geobios, **39**：513–519

Métais G, Aung Naing Soe, Marivaux L et al., 2007. Artiodactyls from the Pondaung Formation (Myanmar)：new data and re-evaluation of the South Asian Faunal Province during the Middle Eocene. Naturwissenschaften, **94**：759–768

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

Murphy J W, Eizirik E, O'Brien S J et al., 2001. Resolution of the early placental mammal radiation using Bayesian phylogenetics. Science, **294**: 2348−2351

Nikaido M, Rooney A P, Okada N, 1999. Phylogenetic relationships among cetartiodactyls based on insertions of short and long interspersed elements: hippopotamuses are the closest extant relatives of whales. Proc Natl Acad Sci USA, **96**: 10261−10266

Ogg J G, Smith A G, 2004. The geomagnetic polarity time scale. In: Gradstein F M, Ogg J G, Smith A G eds. A Geologic Time Scale 2004. Cambridge: Cambridge University Press. 63−86

Orliac M, Lihoreau F, Boisserie J-R et al., 2009: Revision of the African Palaeochoerids: implications for the relationships of Hippopotamidae (Cetartiodactyla, Mammalia). J Vert Palaeont, **29**(suppl 3): 159A

Owen R, 1848. Description of teeth and portions of jaw of two extinct anthracotherioid quadrupeds (*Hyopotamus vectianus* and *Hyop. bovinus*) discovered by the Marchioness of Hastings in the Eocene deposits of the N. W. coast of the Isle of Wight: with an attempt to develop Cuvier's idea of the classification of Pachyderms by the number of their toes. Quart J Geol Soc London, **4**: 103−141

Peigné S, Morlo M, Chaimanee Y et al., 2007. New discoveries of hyaenodontids (Creodonta, Mammalia) from the Pondaung Formation, Middle Eocene, Myanmar—paleobiogeographic implications. Geodiversitas, **29**(3): 441−458

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, **16**(2): 193−217

Pickford M, 1989. Update on hippo origins. C R Acad Sci, Sér II, **309**: 163−168

Pickford M, 1993. Old World suoid systematics, phylogeny, biogeography and biostratigraphy. Paleont Evol, **26−27**: 237−269

Pickford M, 2005. The anterior dentition of *Libycosaurus anisae* and *Kenyapotamus coryndoni* from Beglia, Tunisia: implications for the affinities of anthracotheres and hippopotamids. Notes Serv Géol Tunisie, **73**: 5−49

Pickford M, 2007a. A new suiform (Artiodactyla, Mammalia) from the Early Miocene of East Africa. C R Palevol, **6**: 221−229

Pickford M, 2007b. Suidae and Hippopotamidae from the Middle Miocene of Kipsaraman, Kenya and other sites in East Africa. Paleont Res, **11**(1): 85−105

Pickford M, 2008. The myth of the hippo-like anthracothere: the eternal problem of homology and convergence. Rev Esp Paleont, **23**(1): 31−90

Pickford M, Morales J, 1989. On the tayassuid affinities of *Xenohyus* Ginsburg, 1980, and the description of new fossils from Spain. Estud Geol, **45**: 233−237

Pilgrim G E, 1907. Description of some new Suidae from the Bugti Hills, Baluchistan. Rec Geol Surv India, **36**: 45−56

Pilgrim G E, 1908. The Tertiary and Post-Tertiary freshwater deposits of Baluchistan and Sind with notices of new vertebrates. Rec Geol Surv India, **37**: 139−167

Pilgrim G E, 1928. The Artiodactyla of the Eocene of Burma. Palaeont Indica, New Ser, **13**: 1−39

Pilgrim G E, 1940. Middle Eocene mammals from north-west India. Proc Zool Soc London, Ser B, **110**: 127−152

Pilgrim G E, 1941. The dispersal of the Artiodactyla. Biol Rev, **16**: 134−163

Pilgrim G E, Cotter G de P, 1916. Some newly discovered Eocene mammals from Burma. Rec Geol Surv India, **47**: 42−77

Rosenberger A L, Hogg R, 2007. On *Bahinia pondaungensis*, an alleged early anthropoid. PaleoAnthropology, **2007**: 26−30

Shimamura M, Yasue H, Ohshima K et al., 1997. Molecular evidence from retroposons that whales form a clade within even-toed ungulates. Nature, **388**: 666−670

Spaulding M, O'Leary M A, Gatesy J, 2009. Relationships of Cetacea (Artiodactyla) among mammals: increased taxon sampling alters interpretations of key fossils and character evolution. PLoS ONE, **4**(9): e7062(1−14), doi:10.1371/journal.pone.0007062

Stamp L D, 1922. An outline of the Tertiary geology of Burma. Geol Mag, **59**: 481−501

Suteethorn V, Buffetaut E, Helmcke-Ingavat R et al., 1988. Oldest known Tertiary mammals from South East Asia: Middle Eocene primate and anthracotheres from Thailand. Neues Jahrb Geol Paläont Monatsh, **9**: 563−570

Suzuki H, Tsubamoto T, Thaung-Htike et al., 2010. Geologic age of the Pondaung fauna: fission-track age of acidic tuff from the Kyudaw area, central Myanmar. In: the Palaeontological Society of Japan ed. Abstracts with Programs, the 159th Regular

Meeting, the Palaeontological Society of Japan (January 29–31, 2010, Kusatsu, Shiga Prefecture). Tokyo：the Paleontological Society of Japan. 49(in Japanese)

Swofford D L, 2002. PAUP*：Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4.0b10. Sunderland：Sinauer Associations, Inc

Theodor J M, Erfurt J, Métais G, 2007. The earliest artiodactyls：Diacodexeidae, Dichobunidae, Homacodontidae, Leptochoeridae, and Raoellidae. In：Prothero D R, Foss S E eds. The Evolution of Artiodactyls. Baltimore：Johns Hopkins University Press. 32–58

Thewissen J G M, Cooper L N, Clementz M T et al., 2007. Whales originated from aquatic artiodactyls in the Eocene epoch of India. Nature, **450**：1190–1194

Thewissen J G M, Williams E M, Hussain S T, 2001. Eocene mammal faunas from northern Indo-Pakistan. J Vert Paleont, **21**(2)：347–366

Tsubamoto T, 2001. The Pondaung mammal fauna：an analysis of a terrestrial mammal fauna in the latest Middle Eocene of central Myanmar (Southeast Asia). D. Sc. Dissertation. Kyoto：Kyoto University. 1–112

Tsubamoto T, Egi N, Takai M et al., 2005. Middle Eocene ungulate mammals from Myanmar：a review with description of new specimens. Acta Palaeont Pol, **50**(1)：117–138

Tsubamoto T, Egi N, Takai M et al., 2000. A preliminary report on the Eocene mammals of the Pondaung fauna, Myanmar. Asian Paleoprimat, **1**：29–101

Tsubamoto T, Egi N, Takai M et al., 2006. A summary of the Pondaung fossil expeditions. Asian Paleoprimat, **4**：1–66

Tsubamoto T, Takai M, Egi N, 2004. Quantitative analyses of biogeography and faunal evolution of Middle to Late Eocene mammals in East Asia. J Vert Paleont, **24**(3)：657–667

Tsubamoto T, Takai M, Egi N et al., 2002a. The Anthracotheriidae (Mammalia；Artiodactyla) from the Eocene Pondaung Formation (Myanmar) and comments on some other anthracotheres from the Eocene of Asia. Paleont Res, **6**(4)：363–384

Tsubamoto T, Takai M, Shigehara N et al., 2002b. Fission-track zircon age of the Eocene Pondaung Formation, Myanmar. J Hum Evol, **42**(4)：361–369

Tsubamoto T, Zin-Maung-Maung-Thein, Suzuki H et al., 2009. Fission-track ages of the "Upper Member" of the Pondaung Formation, Paukkaung area, central Myanmar. In：the Geological Society of Japan ed. Abstracts of the 116th Annual Meeting of the Geological Society of Japan, 2009. Tokyo：the Geological Society of Japan. 203(in Japanese)

Xu Y X, 1962. Some new anthracotheres from Shansi and Yunnan. Vert PalAsiat, **6**(3)：232–250(in Chinese with English summary)

Zong G F, Chen W Y, Huang X S et al., 1996. Cenozoic Mammals and Environment of Hengduan Mountains Region. Beijing：China Ocean Press. 1–279(in Chinese with English abstract)