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Anthracotherium pangan buccal view of the right lower jaw (KYN-08) from Kyargan, Myanmar. Credits: photo by O. Chavasseau; photo editing by S. Ducrocq.

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New mammal remains from the Pondaung Formation (late middle Eocene, Myanmar)

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ABSTRACT
We describe several mammal remains from the late middle Eocene Kyargan locality (Pondaung Formation) in which only primate and two ungulate remains had been reported so far. Besides the identification of two anthracotheriids, a homacodontid and a brontotheriid that are already known in other Pondaung localities, dental material is attributed to a dermopteran whose morphology suggests that the Pondaung dermopteran might have been related to the New World plagiomenids. Moreover, two upper molars attributed to a small dichobunoid artiodactyl might represent the first evidence of the upper dentition of *Pakkokuhyus lahirii* Holroyd & Ciochon, 1995, a species scarcely known in Pondaung.

KEY WORDS
Pondaung,
middle Eocene,
Dermoptera,
Artiodactyla,
Pakkokuhyus.

RÉSUMÉ

Nouveaux restes de mammifères de la formation de Pondaung (fin Eocène moyen, Myanmar).

Nous décrivons un assemblage de mammifères provenant de la localité de Kyargan (fin Eocène moyen, Formation de Pondaung) dans laquelle seuls des restes de primates et de deux ongulés avaient été reportés jusqu'à présent. Outre l'identification de deux anthracotheridés, d'un homacodontidé et d'un brontotheriidé déjà connus dans d'autres localités de Pondaung, du matériel dentaire est attribué à un dermoptère dont la morphologie suggère que le dermoptère de Pondaung pourrait avoir été apparenté aux plagiométidés du Nouveau Monde. D'autre part, deux molaires supérieures attribués à un petit artiodactyle dichobunoïde pourraient constituer les premiers éléments de la dentition supérieure de *Pakkokuhyus lahirii* Holroyd & Ciochon, 1995, une espèce connue de manière très fragmentaire à Pondaung.

MOTS CLÉS
Pondaung,
Eocène moyen,
Dermoptera,
Artiodactyla,
Pakkokuhyus.

INTRODUCTION

The Pondaung Formation in central Myanmar includes more than 30 fossil localities for which a late middle Eocene age (about 40 Ma) has been radiometrically obtained (Khin Zaw *et al.* 2014). A rich and diversified mammal fauna has been collected since about one century including dermopterans (Marivaux *et al.* 2006), rodents (Marivaux *et al.* 2005), primates (e.g., Colbert 1938; Ba Maw *et al.* 1979; Ciochon *et al.* 1985; Jaeger *et al.* 1999, 2019, 2020; Chaimanee *et al.* 2000, 2012; Takai *et al.* 2001, 2005; Gebo *et al.* 2002; Shigehara *et al.* 2002; Beard *et al.* 2005, 2009), creodonts (e.g., Egi *et al.* 2005; Peigné *et al.* 2007), perissodactyls (Colbert 1938; Holroyd & Ciochon 2000; Tsubamoto *et al.* 2000, 2005; Holroyd *et al.* 2006; Métais *et al.* 2006) and artiodactyls (Colbert 1938; Ducrocq *et al.* 2000, 2001, 2016, 2020, 2021, 2022, 2023; Métais *et al.* 2000; Tsubamoto *et al.* 2002, 2003, 2011, 2012, 2013a; Aung Naing Soe *et al.* 2017; Ducrocq 2019).

Although most Pondaung localities have yielded a wide variety of fossil mammal remains, attention has been paid mainly to those where primates fossils have been found. For example, dental and postcranial elements of the amphipithecid primate *Myanmarpithecus yarshensis* Takai, Shigehara, Aye Ko Aung, Soe Thura Tun, Aung Naing Soe, Tsubamoto & Tin Thein, 2001 have been described from Kyargan Kyitchaung in Bahin area (also named Paukkaung Kyitchaung 12, or Pk 12; Egi *et al.* 2006). However, several remains of other mammal groups have been collected there but never published, with the exception of the indeterminate artiodactyl *Myanmarius chitseini* Tsubamoto, Egi, Takai, Thaung-Htike & Zin-Maung-Maung-Thein, 2013 and the deperetellid *Bahinolophus birmanicus* Tsubamoto, Egi, Takai, Chit Sein & Maung Maung, 2005 (Tsubamoto *et al.* 2005, 2013a).

The Kyargan, or Pk 12 locality (21°44'56"N, 94°39'12"E), is situated about 500 m south of Paukkaung 2 locality, and NNW of Bahin village in Myaing Township (Fig. 1). According to Egi *et al.* (2006) and Suzuki *et al.* (2006), the fossiliferous deposits of Kyargan might be slightly younger than those that yielded other fossil primate remains in the Bahin area. However, the amphipithecid *M. yarshensis* has also been decribed from two other localities (Yarshe Kyitchaung and Paukkaung Kyitchaung 2, both in Bahin area; Takai *et al.* 2001; Ciochon & Gunnell 2002) and no significant morphological difference has been pointed out between dental elements reported from each locality, which might suggest that the age difference between Kyargan and the other localities is not significant.

The material described here consists of fragmentary lower jaws and isolated teeth that have been obtained by surface findings or by screen-washing techniques. Some of these remains provide new information on some poorly known taxa already described from Pondaung but for which the precise taxonomic status is still unclear.

MATERIAL AND METHODS

The dental terminology used here follows Boisserie *et al.* (2010). Measurements correspond to the maximum length and width of each tooth.

Abbreviations

Institutional abbreviations

All fossils are housed in the Paleontology Collections of the National Museum, Ministry of Culture in Naypyitaw, Myanmar.

AMNH	American Museum of Natural History, New York;
GSI B	Geological Survey of India Collections, Calcutta;
KYN	Kyargan Kyitchaung Collections at the Myanmar Ministry of Culture, Naypyitaw;
NMMP-KU	National Museum Myanmar Paleontology, Kyoto University;
Pk 2	Paukkaung Kyitchaung 2 Collections at the Myanmar Ministry of Culture, Naypyitaw;
Pk 12	Paukkaung Kyitchaung 12 Collections at the Myanmar Ministry of Culture, Naypyitaw;
YSE	Yarshe Kyitchaung Collections at the Myanmar Ministry of Culture, Naypyitaw.

Other abbreviations

i	lower incisor;
I	upper incisor;
l	left;
m	lower molar;
M	upper molar;
p	lower premolar;
P	upper premolar;
r	right.

SYSTEMATIC PALEONTOLOGY

Order DERMOPTERA Illiger, 1811

Dermoptera indet.
(Fig. 2A, B; Table 1)

MATERIAL REFERRED. — KYN-01, left i1.

DESCRIPTION

The tooth from Kyargan (KYN-01) is very probably a left first lower incisor. It has a single long buccolingually compressed root broken at its end where a small pulp canal is visible, and a crown that consists of two distincts laterally compressed cusps. The mesial oval-shaped one is longer and taller than the more triangular distal one. The buccal face of the crown is convex whereas its lingual face is more concave. Each cusp exhibits a slight vertical lingual rib that extends from the apex to the base of the crown. A moderately developed cingulid is present along the lingual face of the tooth, and a very slight buccal cingulid occurs at the base of the distal cusp. A tiny wear surface corresponding to the occlusion with the upper incisor can be seen at the base of the distal side of the distal cusp that shows a moderately thick enamel. The enamel is slightly ridulated on both faces of the crown.

COMPARISONS AND REMARKS

A few mammals possess bilobed or pectinate front teeth but this is not the case in artiodactyls or perissodactyls except giraffids that have bilobed lower canines. Some hyraxes also have lower incisors that are usually hyper-pectinate. However, both of these groups are unknown in Pondaung. Other mammals that exhibit bilobed lower teeth are the sanguivorous bats (vapire bats) and some macroscelidids (e.g., the elephant shrew *Petrodromus* Peters, 1846). Vampire bats have lower incisors with two pegs of similar size, whereas *Petrodromus* has lower incisors with small and large lobes. Nevertheless vampire bat fossil remains are unknown before the Plio-Pleistocene in South America and those of macroscelidids are exclusively African. Scarce dermopteran remains (a left lower canine and a right m2) have been described from Pondaung in the nearby Paukkaung Kyitchaung 2 (or Pk 2) locality (Marivaux *et al.* 2006), but no lower incisor has been reported so far that could be compared with the Kyargan tooth. In addition, the very limited fossil record of dermopterans in the Paleogene of Asia (late middle Eocene of Myanmar, late Eocene and late Oligocene of Thailand, and early Oligocene of Pakistan; Ducrocq *et al.* 1992; Marivaux *et al.* 2006) makes comparisons with the new material very difficult. An i3 is known only for *Dermotherium chimaera* Marivaux, Bocat, Chaimanee, Jaeger, Marandat, Srisuk, Tafforeau, Yamee & Welcomme, 2006 from the late Oligocene of Nong Ya Plong (Thailand) but it exhibits a morphology very different from that of the corresponding tooth from Kyargan with a pectination showing six tines similar to that of *Galeopterus*. The incisor from Kyargan displays a morphology rather different from the i1 of the extant dermopterans *Cynocephalus volans* and *Galeopterus variegatus* that have a more developed pectinate crown (Berkovitz & Shellis 2008). The more simple structure of the Kyargan tooth reminds that of the i1 of the plagiomenid *Plagiomene multicuspis* Matthew, 1918 from the early Eocene of North America (Rose 1973; Rose & Simons 1977). Indeed, in *Plagiomene multicuspis* the difference in size between the mesial and the distal lobe increases from i1 to i3, and the morphology of KYN-01 with the mesial lobe significantly larger than the distal one is more similar to that of the i1 of *P. multicuspis*. The material from Kyargan cannot be attributed to any of the two families included in the Dermoptera (Plagiomenidae and Cynocephalidae). However, Marivaux *et al.* (2006) showed that the lower molar from Paukkaung Kyitchaung 2 had possible affinities with the cynocephalid *Dermotherium* Ducrocq, Buffetaut, Buffetaut-Tong & Jaeger, 1992. If the Kyargan incisor belongs to the same taxon than that of Paukkaung Kyitchaung 2, this might suggest that the primitive condition of the front dentition of early dermopterans in Asia was similar to that of North American plagiomenids.

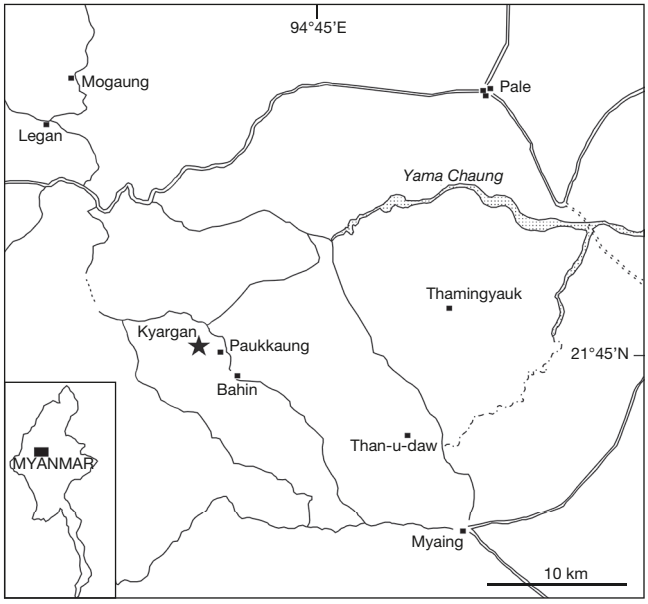

FIG. 1. — Location map of the Pondaung area. The **star** indicates Kyargan Kyitchaung. Credits: S. Ducrocq.

Order ARTIODACTYLA Owen, 1848
Superfamily DICHOBUNOIDEA Gill, 1872
Family HOMACODONTIDAE Marsh, 1894
Genus *Asiohomacodon* Tsubamoto., Soe Thura Tun, Egi, Takai, Shigehara, Aung Naing Soe, Aye Ko Aung & Tin Thein, 2003

Asiohomacodon myanmarensis Tsubamoto, Soe Thura Tun, Egi, Takai, Shigehara, Aung Naing Soe, Aye Ko Aung & Tin Thein, 2003
(Fig. 2C; Table 1)

Asiohomacodon myanmarensis Tsubamoto, Soe Thura Tun, Egi, Takai, Shigehara, Aung Naing Soe, Aye Ko Aung & Tin Thein, 2003: 227.

TABLE 1. — Measurements (mm) of dental remains from Kyargan Kyitchaung. Length: mesio-distal length for upper and lower incisors, premolars and molars; Width: bucco-lingual width for upper and lower incisors, premolars and molars. * indicates estimated measurement of damaged tooth.

Catalogue no.	Tooth	Taxon	Length	Width
KYN-01	l i1	Dermoptera	4.1	2.1
KYN-02	l M1	*Asiohomacodon myanmarensis* Tsubamoto, Soe Thura Tun, Egi, Takai, Shigehara, Aung Naing Soe, Aye Ko Aung & Tin Thein, 2003	6.8*	7.6*
KYN-03	l M1/2	Dichobunoidea indet.	6.4	6.8
KYN-04	r M1/2	Dichobunoidea indet.	6.2	7.5
KYN-05	r P4	*Sivatitanops birmanicum* (Pilgrim & Cotter, 1916)	28.8*	37.9*
KYN-06	r p2	*Anthracokeryx tenuis* (Pilgrim & Cotter, 1916)	8.5	4.9
KYN-07	r I3	*Anthracokeryx tenuis*	7.2	4.8
KYN-08	r p3	*Anthracotherium pangan* (Pilgrim & Cotter, 1916)	24.0	10.5
	r p4	*Anthracotherium pangan*	22.0	11.5
	r m1	*Anthracotherium pangan*	20.5	14.5
	r m2	*Anthracotherium pangan*	28.0	21.5
	r m3	*Anthracotherium pangan*	47.0	22.5
KYN-09	l m1	*Anthracotherium pangan*	19.0	13.5
	l m2	*Anthracotherium pangan*	27.0	19.5
	l m3	*Anthracotherium pangan*	44.0	20.5

MATERIAL REFERRED. — KYN-02, left M1.

DESCRIPTIONS AND REMARKS

Only one damaged upper molar (KYN-02) can be assigned to that taxon. It is probably a left M1 according to the estimated dimensions of the tooth. The buccal and distal parts of the molar are missing, but the general morphology of the upper molar of *Asiohomacodon* is clearly visible: selenodont cusps, protocone more lingually protruding than the metaconule, distinct paraconule, well developed mesial and lingual cingulum. The only other selenodont ungulate known in Pondaung is the archaeomerycid *Indomeryx* Pilgrim, 1928, but it clearly differs from KYN-02 mainly by the absence of a paraconule and by a weaker cingulum on its upper molars. Two other archaeomerycids for which the upper molars are known are *Thandaungia tinti* Métais, 2006 and *Paukkaungmeryx minutus* Ducrocq, Aung Naing Soe, Chavasseau, Chit Sein, Chaimanee, Lazzari & Jaeger, 2020. However, they both are more bunodont, and *Paukkaungmeryx* Ducrocq, Soe, Chavasseau, Sein, Chaimanee, Lazzari & Jaeger, 2019 is smaller, it lacks a paraconule, its metaconule is more lingually protruding and its protocone has a buccal protocrista. *Thandaungia* Métais, 2006 also exhibits a weaker cingulum and a lingually salient metaconule.

Superfamily DICHOBUNOIDEA Turner, 1849

Dichobunoidea indet.
(Fig. 2D, E; Table 1)

MATERIAL REFERRED. — KYN-03, left M1 or M2; KYN-04, right M1 or M2.

DESCRIPTION

The crown of both teeth is subtriangular, with four main cusps. The mesial part of the teeth is slightly wider than the distal part. The paracone and metacone are conical, with the paracone somewhat larger than the metacone. The more selenodont protocone is the largest cusp (it is slightly more developed in KYN-03), it occupies most of the lingual part of the crown and its apex is slightly distal to that of the paracone. A small metaconule is located in the distal half of the crown lingually to the metacone. The crests connecting the cusps are very weak. A very short preparacrista extends from the mesial face of the paracone to a small parastyle, and a very slight postmetacrista reaches the buccodistal corner of the tooth but no metastyle is visible. The centrocrista (postparacrista + premetacrista) is moderately expressed and a deep valley separates the lingual cusps. The posprotocrista connects with the mesiolingual face of the metaconule whereas the preprotocrista is much shorter and ends mesiolingually to the paracone without reaching the mesial cingulum. The distobuccal crest of the metaconule (postmetacristule) extends to the cingulum distally to the metacone. A very weak and almost absent premetacristule is discernible on KYN-03 but not on KYN-04. The cingulum is present all around the crown. It is stronger mesially and lingually except at the base of the protocone. Buccally, it almost fades under the paracone and the metacone. A distinct hypocone raises from the distolingual cingulum lingually to the metaconule. It is more mesiolingually elongated in KYN-03, whereas it is more cusp-like in KYN-04.

COMPARISONS AND REMARKS

The most abundant and diversified artiodactyls in Pondaung are the anthracotheres (see for example Aung Naing Soe *et al.* 2017). However, both molars described here clearly differ from representatives of the family mainly because of their more triangular crown that lacks a paraconule and that displays a hypocone, an enlarged protocone and reduced metaconule. Similarly, the Pondaung ruminants for which the upper molars are known (*Indomeryx*, *Thandaungia* and *Paukkaungmeryx*) markedly differ from KYN-03 and KYN-04 because of their more selenodont crown with much better developed crests and metaconule and that lack a hypocone.

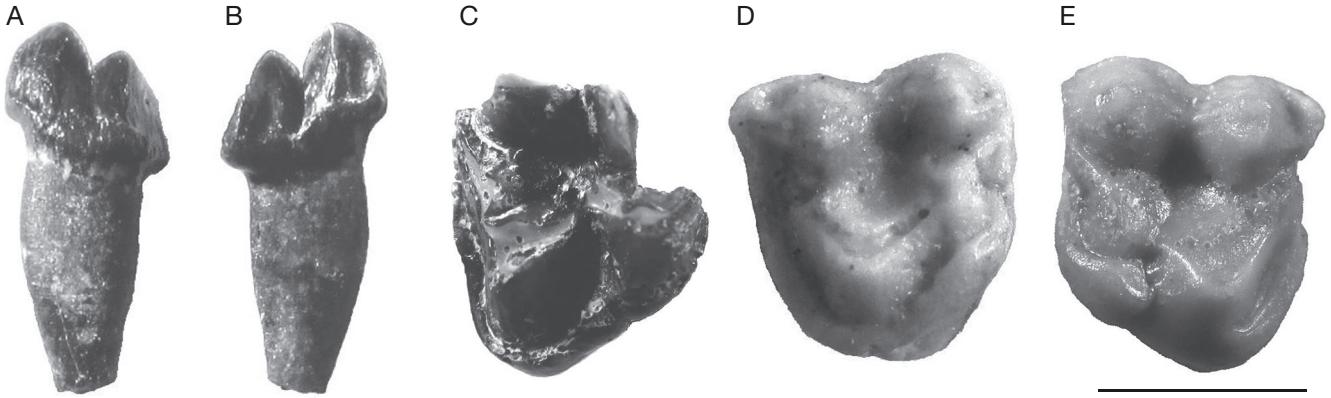

Fig. 2. — Dental remains of mammals from Kyargan: **A**, **B**, Dermoptera indet., KYN-01, left i1 in buccal (**A**) and lingual (**B**) views; **C**, *Asiohomacodon myanmarensis* Tsubamoto, Soe Thura Tun, Egi, Takai, Shigehara, Aung Naing Soe, Aye Ko Aung & Tin Thein, 2003: KYN-02, left M1 in occlusal view; **D**, **E**, Dichobunoidea indet.: **D**, KYN-03, left M1 or M2 in occlusal view; **E**, KYN-04, right M1 or M2 in occlusal view. Scale bar: 5 mm. Credits: S. Ducrocq.

The beginning of the Eocene is known to have been a time of diversification for early ungulates in Asia, which might explain their significant number reported from Pondaung. Dichobunoid artiodactyls are particularly abundant and diversified there with about ten distinct taxa (see Ducrocq *et al.* 2020, 2022). Among them, the homacodontid *Asiohomacodon myanmarensis* exhibits upper molars with sizes similar to those of KYN-03 and KYN-04 but that are much more selenodont with a paraconule, a larger metaconule, well developed styles, and that lack a hypocone. Similarly, the diacodexeid *Magwetherium burmense* Ducrocq, Aung Naing Soe, Chit Sein, Lazzari, Chaimanee, Valentin & Jaeger, 2016 has a similar size, but its upper molars are more triangular and selenodont and they exhibit a paraconule, a pericone and a smaller hypocone.

Representatives of the Pondaung Dichobunidae for which upper molars are known are morphologically more similar with the new material from Kyargan, although they all display distinct features that distinguish them. Contrary to the homacodontids and diacodexeids, they are usually more bunodont with somewhat reduced metaconule and styles, and a more or less developed hypocone. For example, *Hsanotherium parvum* Ducrocq, Aung Naing Soe, Bo Bo, Benammi, Chaimanee, Than Tun, Tin Thein & Jaeger, 2000 can be clearly distinguished by its enlarged paracone, huge parastyle, its mesostyle, pericone, small metaconule and hypocone and reduced cingula.

The indeterminate artiodactyl *Myanmarius chitseini* is closer to the Kyargan upper molars in its general morphology (Tsubamoto *et al.* 2013a) except for its paraconule, lack of a hypocone and its almost straight buccal face (more waisted in KYN-03 and KYN-04).

Several ungulate isolated upper molars have been described from Pondaung as indeterminate Dichobunoidea or even indeterminate Artiodactyla, but they are also morphologically different from the Kyargan taxon. The indeterminate Dichobunoidea upper molar reported by Métais (2006) is more triangular in occlusal outline, it lacks a hypocone, its parastyle is smaller and the buccal face of the metacone is flattened. The inderterminate Dichobunoidea described by Tsubamoto *et al.* (2013b) has a narrower lingual part with more selenodont crests, its parastyle and cingula are less developed and it lacks a hypocone. Finally, the upper molar attributed to an indeterminate Artiodactyla by Tsubamoto *et al.* (2012) is more quadratic, it has a paraconule, a more massive parastyle and less developed cingula.

Although they can be distinguished by their upper molar structure, several Dichobunidae described from Asia (Pakistan and Kazakhstan) also need to be compared with the new Pondaung material because of their similar spatiotemporal occurrence. For example, *Haqueina* Dehm & Oettingen-Spielberg, 1958 and *Chorlakkia* Gingerich, Russell, Sigogneau-Russell & Hartenberger, 1979 both from the middle Eocene of Pakistan lack a hypocone and have a paraconule on their upper molars. *Haqueina* further displays a larger size, a smaller metaconule, a weaker buccal cingulum and no postprotocrista, whereas *Chorlakkia* exhibits stronger cingula and a better developed premetacristule. *Dulcidon* Van Valen, 1965 from the early middle Eocene of Pakistan has smaller and a more triangular upper molar that lacks a hypocone (although Bai *et al.* [2024] stated that *Dulcidon* has a swollen incipient hypocone rising from the postcingulum), with a paraconule, a paracone and a metacone equal in size and a weaker cingula. According to Thewissen *et al.* (1987), *Dulcidon* might be congeneric with *Chorlakkia*, whereas Theodor *et al.* (2007) consider that the tribosphenic pattern of *Dulcidon* upper molar suggests closer affinities with the diacodexeid *Gujaratia* Bajpai, Kapur, Das, Tiwari, Saravanan & Sharma, 2005. *Aksyiria oligostus* Gabunia, 1973 from the early-middle Eocene of Georgia has a more quadratic and larger upper molar with a paraconule, a distinct premetacristule, and that lacks a hypocone. Finally, *Irdinodon* Bai, Theodor, Wang & Meng, 2024 is a small dichobunid recently described from the middle Eocene of northeast China (Bai *et al.* 2024) that is smaller, with more square upper molars that exhibit a paraconule, a smaller protocone, and much more developed parastyle and lingual cingulum, and a more distobuccally oriented postmetacristule.

A few other Asian dichobunids known only by their lower teeth include *Pakibune* Thewissen, Gingerich & Russell, 1987 from the early middle Eocene of Pakistan, and *Cadutherium* Métais, Aung Naing Soe, Marivaux & Beard, 2007 and *Pakkokuhyus* Holroyd & Ciochon, 1995 from Pondaung. However, *Pakibune* is much larger than KYN-03 and KYN-04, whereas *Cadutherium* and *Pakkokuhyus* have lower molars that might correspond in size to the upper molars from Kyargan, but the lower teeth of *Cadutherium* have more selenodont buccal cuspids that do not correspond to the upper molar structure of the Kyargan dichobunid. *Pakkokuhyus* on the other hand, is more bunodont and its right m1 (GSI B-766) occludes well with the right upper molar KYN-04. Tsubamoto *et al.* (2000) attributed a fragmentary maxilla (NMMP-KU 0039) to *Pakkokuhyus*. However, Ducrocq *et al.* (2001) described that same specimen as belonging to the anthracotheriid *Siamotherium pondaungensis* Ducrocq, Aung Naing Soe, Aye Ko Aung, Benammi, Bo Bo, Chaimanee, Than Tun, Tin Thein & Jaeger, 2001. Later, Aung Naing Soe *et al.* (2017) demonstrated that NMMP-KU 0039 cannot be referred to the Helohyidae but indeed belongs to an anthracothere. There is no further clue that the upper molars from Kyargan could be referred to *Pakkokuhyus*, but should it be the case it would confirm that *Pakkokuhyus* is a dichobunid and not a helohyid (Ducrocq 2019), and the material from Kyargan might represent the first upper molars that could be attributed to this genus.

Although the material described here is fragmentary, it displays an upper molar morphology that cannot be referred to any of the dichobunoids known in the Pondaung Formation or in southern Asia. The peculiar distolingual position of the small hypocone, distal to the protocone, on both molars is not really unusual in artiodactyls: a similar condition can be observed for example in the Asian dichobunids *Irdinodon* or *Lantianius* Chow, 1964 (although less developed than in the Kyargan molars). Both indeterminate dichobunoid upper molars YSE 8 (Métais 2006) and NMMP-KU 2182 (Tsubamoto *et al.* 2013b) exhibit a very similar morphology, and Tsubamoto *et al.* (2013b) suggested that they might belong to the same species. However, NMMP-KU 2182 seems to have more selenodont cusps than YSE 8, and no postmetacristule. These two molars are morphologically closer to KYN-03 and KYN-04 notably by their occlusal outline, simple structure and lack of a paraconule. Yet, the latters have more bunodont and mesiolingually more developed crowns with a small hypocone, and no mesiobuccal crest (premetacristule) of the metaconule. This implies that KYN-03 and KYN-04 likely represent a taxon distinct from all of those for which upper molars that have been described as indeterminate dichobunoids so far. Alternatively, there is still a possibility that the two upper molars might belong to *Pakkokuhyus* because of the correspondance in size and occlusion between them, but it will be crucial to discover associated upper and lower teeth remains to test this hypothesis, and to further discuss the attribution of the Kyargan upper molars to the Dichobunoidea.

Family ANTHRACOTHERIIDAE Leidy, 1869
Genus *Anthracotherium* Cuvier, 1822

Anthracotherium pangan Pilgrim & Cotter, 1916
(Fig. 3A-F; Table 1)

Anthracotherium pangan Pilgrim & Cotter, 1916: 59.

MATERIAL REFERRED. — KYN-08, right lower jaw preserving p3-m3; KYN-09, left lower jaw preserving m1-m3.

DESCRIPTION

The crowns of the teeth are relatively well preserved. The molars are bunodont with short and blunt cristids, their distal lobe wider than the mesial one on m1-2. The hypoconulid lobe of m3 is wide, simple and in line with the crown. The premolars are triangular in lateral view, with a moderately developed talonid part, and without accessory cuspids. They exhibit only a pre- and postprotocristid. Their crown is slightly convex buccally and flat to slightly concave lingually. There is only a very short diastema between the sockets of p1 and p2 and a somewhat longer one between the lower canine socket and that of the p1. The horizontal ramus has a rather constant depth and is slightly curved beneath the molars. The anterior part of the coronoid process is vertical and is separated from the m3 by a short retromolar space. The dimensions (Table 1) and general structure of the teeth on KYN-08 and KYN-09 and the important increase of size from m1 to m3 indicate that this material better correspond to *Anthracotherium pangan*, the largest anthracothere known in Pondaung.

Genus *Anthracokeryx* Pilgrim & Cotter, 1916

Anthracokeryx tenuis Pilgrim & Cotter, 1916
(Fig. 3G-K; Table 1)

Anthracokeryx tenuis Pilgrim & Cotter, 1916: 62.

MATERIAL REFERRED. — KYN-06, right p2, KYN-07, right I3.

DESCRIPTION AND REMARKS

KYN-06 is a very simple tooth with an oval rather than a more triangular occlusal outline, which indicates that it is a lower premolar. Its laterally compressed crown is triangular with the apex somewhat slanted backwardly. The buccal face is slightly convex whereas the lingual face is almost flat. Two very weak cristids occur mesially and distally. No cingulid or talonid is visible. The morphology of this lower premolar indicates that it is a right p1 or p2. It is too large to belong to the small *Siamotherium pondaungensis* Ducrocq, Aung Naing Soe, Aye Ko Aung, Benammi, Bo Bo, Chaimanee, Than Tun, Tin Thein & Jaeger, 2001 and too small to be referred to the larger species of *Anthracotherium*.

Although similar in size, the p1 of *A. birmanicus* Pilgrim & Cotter, 1916 is reduced, lower and more laterally compressed, whereas the p2 of *A. tenuis* displays the same morphology as KYN-06. We therefore believe that this premolar should more likely be referred to the latter species.

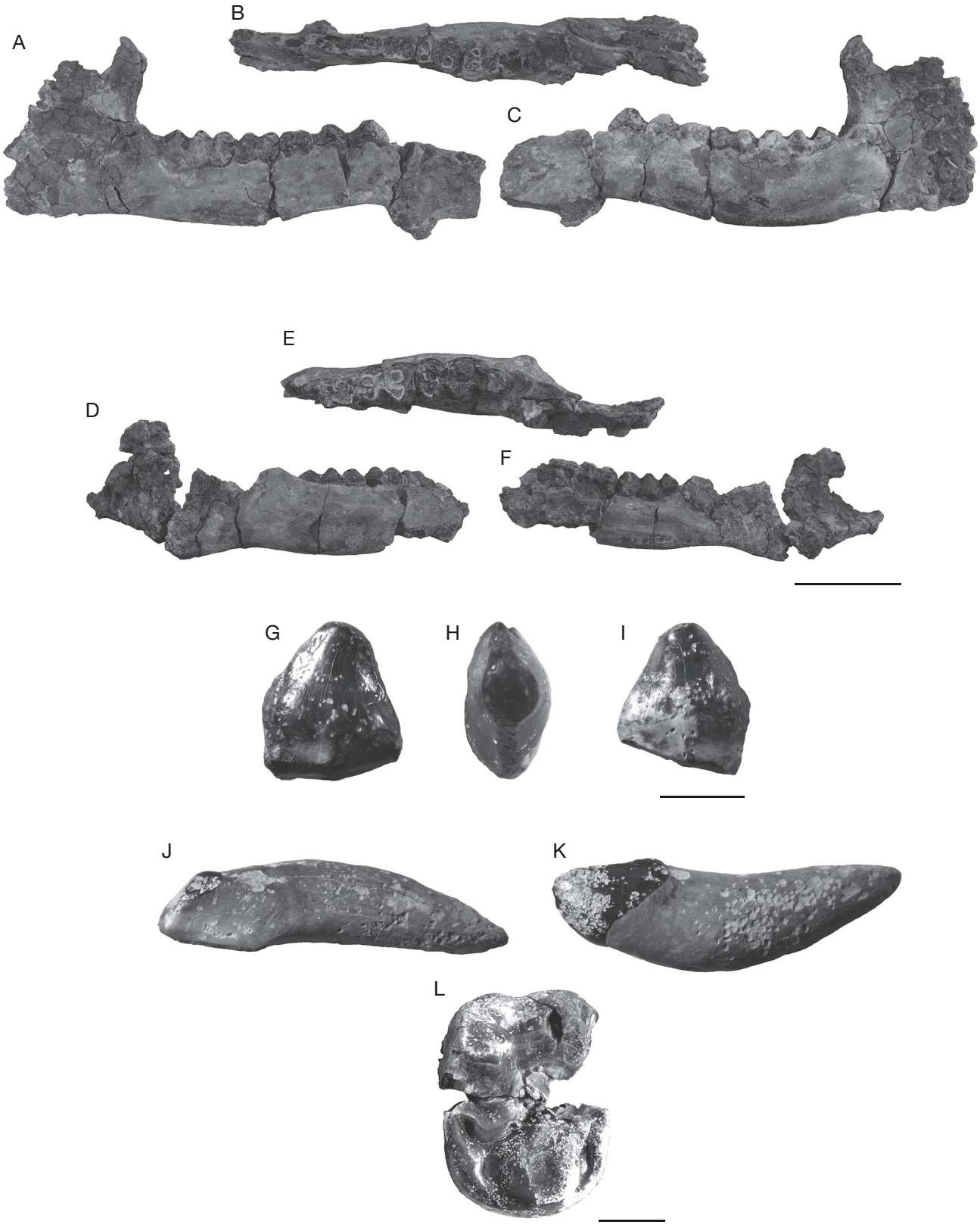

Fig. 3. — Dental remains of mammals from Kyargan: **A**-**F**, *Anthracotherium pangan* (Pilgrim & Cotter, 1916): **A**-**C**, KYN-08, right lower jaw with p3-m3 in buccal (**A**), occlusal (**B**) and lingual (**C**) views; **D**-**F**, KYN-09, left lower jaw with m1-m3 in lingual (**D**), occlusal (**E**) and buccal (**F**) views; **G**-**K**, *Anthracokeryx tenuis* (Pilgrim & Cotter, 1916): **G**-**I**, KYN-06, right p2 in lingual (**G**), occlusal (**H**) and buccal (**I**) views; **J**, **K**: KYN-07, right I3 in buccal (**J**) and lingual (**K**) views; **L**: ?*Sivatitanops birmanicum* (Pilgrim & Cotter, 1916), right P4 in occlusal view. Scale bars: A-F, 5 cm; G-K, 5 mm; L, 1 cm. Credits: A-F, photos by O. Chavasseau and photo editing by S. Ducrocq; G-L, S. Ducrocq.

The upper incisor (KYN-07) is triangular and laterally compressed with its buccal face slightly convex and its lingual face more flat. A very faint crest occurs mesially, and there is a small wear facet mesiolingually (from the contact with the i3) and a longer one distolingually (from contact with the lower canine) that extends from the apex of the crown to part of the root. The root is massive and oval in section and it makes an angle of about 50° with the crown. No cingulum is visible.

The size of the incisor root corresponds to that of the socket for I3 on the skull AMNH 20017 of *Anthracokeryx tenuis* (Colbert 1938), and the dimensions and shape of the distolingual wear facet fits well with that on the mesiobuccal one of its lower canine.

Order PERISSODACTYLA Owen, 1848
Family Brontotheriidae Marsh, 1873

?***Sivatitanops birmanicum*** Pilgrim & Cotter, 1916
(Fig. 3L; Table 1)

Sivatitanops cotteri Pilgrim, 1925: 65.

MATERIAL REFERRED. — KYN-05, fragmentary right P4.

DESCRIPTION

The tooth preserves part of the buccal half with the paracone, metacone and parts of the parastyle and metastyle. The buccal face of the paracone is somewhat convex without a prominent rib and that of the metacone is almost flat. The metacone is also more lingually slanted than the paracone. The distal half of the ectoloph is almost straight contrary to the mesial one that displays a more selenodont outline. There is no buccal cingulum except a very slight enamel shelf mesiobuccally to the parastyle. The central mesial part of the tooth is missing, but no swelling of the enamel in this region suggests that a paraconule was present. The lingual half of the crown indicates that the tooth was lingually square. It displays a large protocone and a much smaller hypocone. The protocone is very worn but a slight preprotocrista seems to extend mesiobuccally to the paracone. The small hypocone is separated from the protocone by a shallow groove. The lingual cingulum is absent under the protocone and is very slightly developed between the protocone and the hypocone, and is stronger mesially to the protocone with a small cingular cusp. The enamel of the tooth is smooth.

COMPARISONS AND REMARKS

Three brontotheriid genera have been reported from Pondaung: *Metatelmatherium*, *Sivatitanops* and *Bunobrontops* (Pilgrim & Cotter 1916; Pilgrim 1925; Colbert 1938; Holroyd & Ciochon 2000). However, Mihlbachler (2008) considered that only *Bunobrontops savagei* Holroyd & Ciochon, 2000 is a valid species, all others species of *Metatelmatherium* and *Sivatitanops* being *nomen dubium* and should probably be referred to Asian (*Rhinotitan*) or European (*Brachydiastematherium*) genera.

The Kyargan tooth exhibits features that are not observed in *Bunobrontops savagei*, mainly because of its smooth enamel, more straight ectoloph, absence of strong buccal ribs and very probably of a paraconule. The morphology of this premolar is much more similar to that of the right P4 (AMNH 141258) from the late Eocene of Bulgaria (Nikolov & Heissig 1985) attributed to *Sivatitanops birmanicum*, and the left P4 (NMMP-KU 0320) from Pondaung attributed to a brontotheriid by Tsubamoto *et al.* (2000). The characters shared by these specimens and the Kyargan premolar include a straighter ectoloph, flat buccal wall of the metacone, lingual outline, lingual cingulum interrupted at the protocone, small mesiolingual cingular cusp, and a small hypocone (that of KYN-05 being somewhat more reduced). Although Mihlbachler (2008) does not accept *Sivatitanops birmanicum* as a valid genus and species, we attribute the Kyargan premolar to *S. birmanicum* pending a more complete revision of the Pondaung material.

DISCUSSION AND CONCLUSIONS

The Kyargan locality does not differ from other Pondaung localities in its faunal composition. Although the amount and diversity of taxa identified there do not reach those of some other localities where a significant assemblage of primates and ungulates have been collected, most taxa (*Anthracotherium pangan*, *Anthracokeryx tenuis*, *Asiohomacodon myanmarensis* and *Sivatitanops birmanicum*) are also known from several other Pondaung localities in Bahin, Moggaung and Pangan areas. This seems to further challenge the hypothesis of Egi *et al.* (2006) and Suzuki *et al.* (2006) according to which the fossiliferous deposits of Kyargan might be slightly younger than those of other localities in Bahin area.

The only non-ungulate specimen in Kyargan that can be identified is a lower incisor of a dermopteran. This group is only known by an isolated lower canine and m2 in Pondaung. Although Marivaux *et al.* (2006) showed that the m2 was more reminiscent of that of the Cynocephalidae *D. major* from the late Eocene of Krabi (Thailand), the i1 from Kyargan, however, exhibits a morphology very close to that of the i1 of *Plagiomene multicuspis* from the early Eocene of North America. If our interpretation of KYN-01 is correct, this suggests that the Cynocephalidae might have been phylogenetically related with the New World Plagiomenidae. Marivaux *et al.* (2006) reviewed the phylogenetic relationships of extant dermopterans among eutherians. The status of Plagiomenidae differs according to different authors: they are considered as *incertae sedis* within the Eutheria (for example MacPhee *et al.* 1989) or linked to the Cynocephalidae (Silcox 2001). It is obviously necessary to recover additional and more complete material that can be attributed to the species described from Pk 2 (Marivaux *et al.* 2006). This might help to further discuss a possible alliance of plagiomenids with cynocephalids advocated by Silcox (2001). Alternatively, the Kyargan incisor might represent a taxon distinct from that already known in Pondaung but related to *Plagiomene*. Ducrocq (2019) showed that despite

faunal exchanges were possible between North America and Asia during most of the Paleogene, some ungulates groups of North American origin did not reach Asia. However, a hypothetical dispersal of plagiomenids into Asia might have been possible at least during the middle Eocene.

As in several other Pondaung localities, the fossil record of Kyargan also illustrates the diversity of primitive ungulates. The two upper molars described here can be distinguished from those of all other dichobunoids that have been identified in Pondaung so far. About ten distinct dichobunoids have been described in Pondaung, all of them known only by fragmentary maxilla or lower jaws or even isolated teeth (Ducrocq *et al.* 2020, 2022). However, it is likely that some upper and lower molars that have been separately described might belong to the same taxon. Indeed, *Pakkokuhyus* seems to be a very rare taxon in the Pondaung assemblage and only an isolated m3 referred to it has been recognized (Ducrocq 2019) since *Pakkokuhyus* was first described three decades ago. However, the important diversity of dichobunoids in Pondaung described from fragmentary material makes it plausible that one or several of the indeterminate isolated upper molars can be associated with the lower teeth of *Pakkokuhyus*. There is no strong evidence that supports this hypothesis except for the size of the dental material and the occlusal matching pattern between the Kyargan upper molars and the lower molars of the type specimen of *Pakkokuhyus*. A thorough review of the small indeterminate ungulate material from Pondaung is thus necessary.

Although the diversity of dental remains that can be identified is low in Kyargan, they provide further information that might help to better understand the morphology and evolutionary history of poorly known taxa. This also illustrates the importance to focus on collecting small and micro-remains of vertebrates through screen-washing techniques, because the very small taxa in Pondaung are often poorly documented or even misinterpreted.

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