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New fossil remains from Bang Mark locality, Krabi Basin, southern Thailand

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DUCROCQ ET AL.–NEW LATE EOCENE MAMMALS FROM BANG MARK

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ABSTRACT—We describe several mammal taxa from the poorly known late Eocene locality of Bang Mark, Krabi Basin in southern Thailand. Most of them were unknown in that locality that now includes nineteen distinct taxa. The new material corresponds to dental remains that can be attributed to a carnivore, a dichobunid, ruminants, anthracotheres and perissodactyls. These remains provide information on the affinities of several genera that were uncertain so far. *Archaeotragulus* might be more closely related to *Siamotragulus* from the Miocene of Southeast Asia, Pakistan and East Africa, and the tragulid status of *Krabitherium* is supported by the morphology of its p4. We also describe the smallest known anthracothere, *Geniokeryx nanus* sp. nov., and a new species of eomoropid chalicothere, *Eomoropus meridiorientalis* sp. nov., that represents the first record of that family in the Krabi fauna. This work also supports the contemporaneity of Bang Mark with Wai Lek and Bang Pu Dam.

INTRODUCTION

The Krabi Basin in southern Thailand has yielded one of the most diverse vertebrate fauna dated from the late Eocene and is considered as a reference fauna in the Paleogene of Asia (Ducrocq et al., 1995; Ducrocq, 1999; Benammi et al., 2001). All fossils have been collected from three pits (Wai Lek, Bang Pu Dam and Bang Mark) in the Krabi coal mine (Fig. 1) from which lignite was extracted by the EGAT (Electricity Generating Authority of Thailand). These coal pits are elongated along a 5 km long NNW-SSE axis (Udomkan et al., 2003). Most of the vertebrate remains come from the main lignite seam, and the same associations of fossil mammals have been found in the three mines which are thus considered as of same age/contemporaneous (Ducrocq et al., 1992, 1995, 1997b). This has been then confirmed by magnetostratigraphic analyses (Benammi et al., 2001). The fossil record of Bang Mark has long been much less diversified than that of Wai Lek and Bang Pu Dam and

the taxa that were described included a rodent, three primates, two suoids and two anthracotheres. We report here additional mammal remains collected from the Bang Mark pit. They can be attributed to a small caniformia, the dichobunid *Progenitohyus*, the tragulids *Archaeotragulus* and *Krabitherium*, the lophiomerycid *Krabimeryx*, the anthracotheriids *Geniokeryx thailandicus* and *Anthracotherium chaimanei*, and the rhinocerotid *Guixia simplex*. We also report the first occurrence of a new species of chalicotheriid perissodactyl in the Krabi Basin (and thus in the late Eocene of southern Asia), of a new genus and species of rhinocerotoid, and a new diminutive anthracothere is identified.

METHODS

Dental Terminology—The dental terminology used here follows Boisserie et al. (2010).

Institutional Abbreviations—**BM**, Bang Mark Collections at the Department of Mineral Resources, Bangkok, Thailand; **SDM**, Shandong Museum Collections, Shandong Provincial Museum, Shandong Province, China; **TF**, Thai Fossil Collections at the Department of Mineral Resources, Bangkok, Thailand.

Additional Abbreviations—**L**, length; **W**, width.

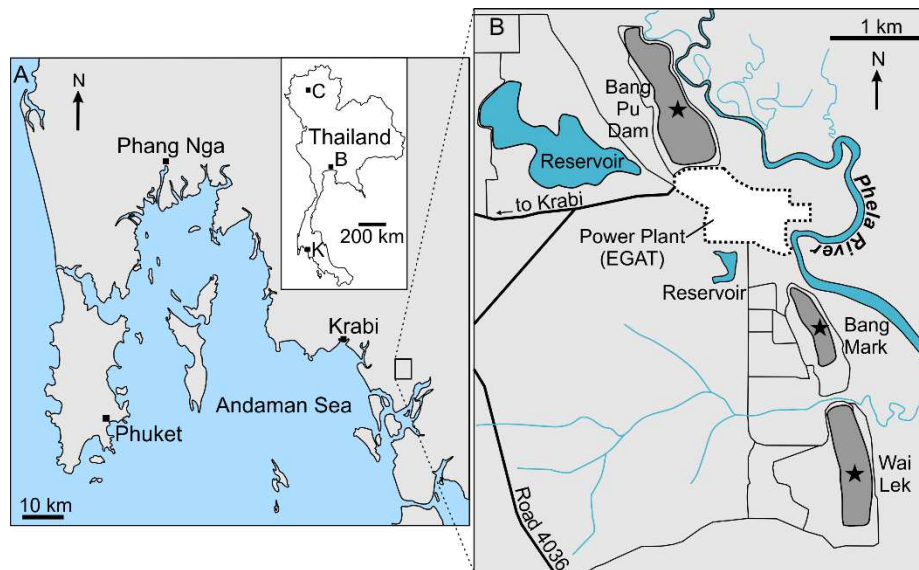


FIGURE 1. **A**, location map of the Krabi Mine in southern Thailand. **Abbreviations: B**, Bangkok; **C**, Chiang Mai; **K**, Krabi. **B**, location map of the Bang Pu Dam, Bang Mark and Wai Lek coal mines. [planned for 2/3 of page width]

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich, 1821

Suborder CANIFORMIA Kretzoi, 1943

CANIFORMIA indet.

(Fig. 2A, C)

Material—Right P3, BM 08-12-17-1.

Description—The two-rooted tooth is triangular in lateral view ($L = 10.8$ mm, $W = 4.9$ mm), the largest cusp being in a medial position. Two mesial and distal cristids extend from its apex. The mesial crest ends at a small enamel spur on the end of the crown and is bordered

by a thin and short mesiolingual cingulum. An accessory cusp occurs on the middle of the distal crest and the latter extends to the distal end of the crown where two small cusplets occur. Short and narrow distolingual and distobuccal cingula are present. The lingual face of the tooth is slightly more convex than its buccal face because the former bears a basal bulge corresponding to the trace of a vestigial protocone/third root. The enamel shows vertical wrinkles along the crown.

Comparisons—The retention of a tiny vestige of protocone/third root could indicate that this tooth is a P3 of carnivorans. The morphology of BM 08-12-17-1 is different from that of the two carnivoramorphan families reported from the Krabi Basin, “Miacidae” and Nimravidae; “Miacidae” have much smaller and sharper upper premolars and Nimravidae have a different configuration of the distal accessory cusp of P3, where the distal crest of the cusp connects directly with the distal border of the tooth in a straight line. Compared to the Paleogene carnivoran fossil record of Asia, this tooth is too large to belong to the small-bodied viverravids and mustelids (*Palaeogale*, *Plesictis*). Other larger carnivoran taxa from the Paleogene of Asia with known upper teeth (from Asia and/or Europe) include a few aeluroids (*Palaeoprionodon*, *Stenoplesictis*, *Stenogale*) and several caniforms “Amphicyonodontidae” (*Amphicyonodon*, *Amphicticeps*), Ursidae (Cephalogalini), and Amphicyonidae (*Amphicyon*, possible *Cynodictis*). All of them have either a less developed, or an absent distal accessory cusp on P3. Overall, the Bang Mark tooth seems lower-crowned and less sharp than in most feliforms and it is possible that it belongs to a new taxon of Caniformia that is not yet reported in Asia. However further material is needed to clarify its taxonomic attribution.

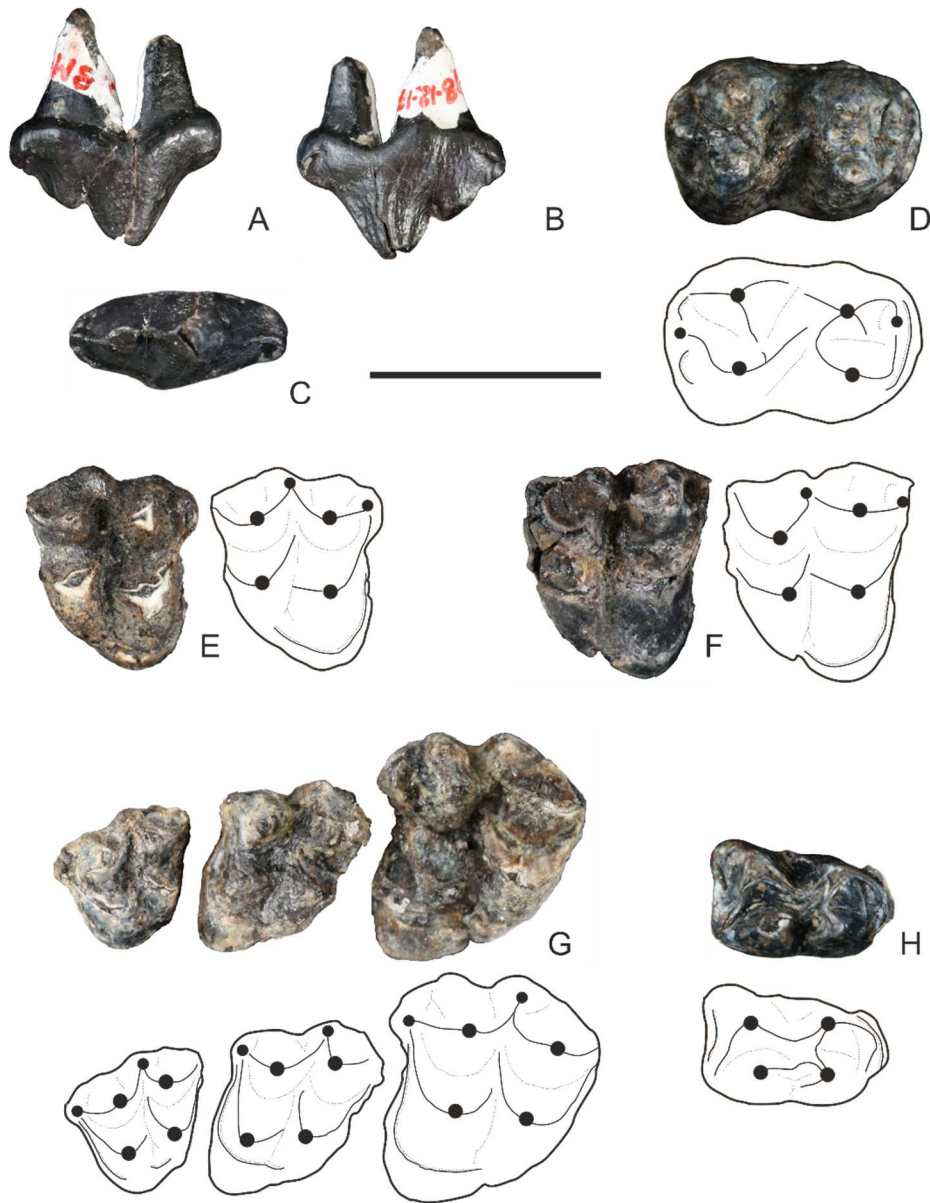


FIGURE 2. **A–C**, *Caniformia* indet., BM 08-12-17-1, right P2 or P3, **A**, buccal view; **B**, lingual view; **C**, occlusal view; **D**, *Progenitohyus thailandicus*, BM 08-01-31-17, right m1; **E–H**, *Archaeotragulus krabiensis*, **E**, BM 08-01-29-16, right M2; **F**, BM 08-01-29-19, right M2; **G**, BM 08-04-25-15, left M1-3; **H**, BM 08-01-30-7, left m2. Scale bar equals 10 mm.

[planned for 2/3 of page width]

Superorder CETARTIODACTYLA Montgelard, Catzeflis, and Douzery, 1997

Superfamily DICHOBUNOIDEA Gill, 1872

Family DICHOBUNIDAE Turner, 1849

PROGENITOHYUS Ducrocq, Chaimanee, Suteethorn, and Jaeger, 1997a

PROGENITOHYUS THAILANDICUS Ducrocq, Chaimanee, Suteethorn, and Jaeger, 1997a

(Fig. 2D)

Type Locality and Horizon—Bang Pu Dam lignite pit, Krabi coal mine (southern Thailand), late Eocene.

Type Specimen—Fragmentary lower jaw with left m1–m3, TF 2668.

Referred Material—Right m1, BM-08-01-31-17.

Emended Diagnosis—Medium-sized dichobunid characterized by $m1 < m2 < m3$, with a paraconid on m1 and a vestigial one on m2, weak and straight preentocristid, a reduced hypoconulid lobe on m3 and lacking a buccal cingulid. Differs from Helohyidae (Foss, 2007) in lacking a well-developed paraconid on m2–3 (*Helohyus*, *Achaenodon*, *Dyscritochoerus*), a metastylid and a buccal cingulid on lower molars (*Achaenodon*), in having a simple reduced hypoconulid lobe on m3 (*Helohyus*, *Achaenodon*), and a trigonid is narrower than the talonid on m1–2 (*Parahyus*). Differs from other Asian dichobunids (Theodor et al., 2007) in being larger, more bunodont (*Haqueina*), in lacking a paraconid on m2–3 (*Haqueina*, *Pakibune*, *Wutuhyus*) and a buccal cingulid (*Haqueina*, *Paraphenacodus*, *Pakibune*), in having a more reduced and simple hypoconulid lobe on m3, mesial cusps close to each other, a shorter trigonid (*Wutuhyus*), and a nonreduced entoconid (*Pakibune*). Differs from Diacodexidae and Homacodontidae by its more bunodont molars that lack a paraconid on m2–3, with a much more reduced hypoconulid lobe on m3, and in having a better developed preentocristid between the entoconid and hypoconid.

Description—The structure of the m1 (L = 10.8 mm; W = 6.9 mm) is identical to that of the lower molars of the holotype (TF 2668), and it provides additional information about the structure of the mesial part of the tooth which is damaged on TF 2668. The trigonid is well preserved and the tooth is not worn. The metaconid displays four crests. The premetacristid is mesially directed and ends at a small paraconid that is mesial to the metaconid. An endometacristid extends mesiobuccally to the bottom of the trigonid valley. The postmetacristid connects lingually with the postprotocristid to close the trigonid distally. The postectometacristid is distally directed and ends in the lingual end of the transverse valley. There is a shallow groove between the postectometacristid and the postmetacristid. The preprotocristid is mesially directed and curves lingually to reach the paraconid from which it is separated by a slight groove. The prehypocristid is mesiolingually oriented and reaches the distobuccal side of the metaconid. The entoconid has an ectoentocristid that extends in the lingual end of the transverse valley, a very slight postectoentocristid that connect the distal cingulid, and a transverse preentocristid that joins a short endohypocristid on the mesial face of the hypoconid. A distolingual posthypocristid connects with the distostyle. As on the lower molars of the holotype, only lingual and distal cingulids are present.

In the taxonomic revision of *Progenitohyus*, Ducrocq (2019) stated that *P. thailandicus* does not have a paraconid on m2 but a slight swelling of enamel on the premetacristid. The new material attributed to *Progenitohyus* indicates that a paraconid was present on m1, but was vestigial on the m2 and absent on m3. In addition, the postectometacristid (named postmetacristid in Ducrocq, 2019) observed on the isolated m1 was probably obliterated with wear very early, which explains why this structure is absent on the worn teeth of the holotype.

Suborder RUMINANTIA Scopoli, 1777

Family TRAGULIDAE Milne-Edwards, 1864

ARCHAEOTRAGULUS Métais, Chaimanee, Jaeger, and Ducrocq, 2001

ARCHAEOTRAGULUS KRABIENSIS Métais, Chaimanee, Jaeger, and Ducrocq, 2001

(Fig. 2E–H)

Type Locality and Horizon—Wai Lek lignite pit, Krabi coal mine (southern Thailand), late Eocene.

Type Specimen—Fragmentary lower jaw with left p2–m2, TF 2997.

Referred Material—Right M2, BM 08-01-29-16; left M1–3, BM 08-04-25-15; right M2, BM 08-01-29-19; left m2, BM 08-01-30-7.

Emended Diagnosis—Small primitive and selenodont ruminant characterized by its simple lower premolars, its p4 lacking a metaconid, its lower molars displaying a complete M structure and a developed and lingually open trigonid, and its upper molars triangular with buccally salient mesostyle, buccally displaced metaconule and developed lingual cingulum. Differs from *Krabitherium* by its smaller size (Table 1), its selenodont lower molars with a enlarged and lingually open trigonid, complete M structure, less lingually oriented cristid obliqua and weaker mesial and distal cingulids, its upper molars with better developed styles and buccally salient mesostyle, developed lingual cingulum and lacking an entostyle. Differs from *Stenomeryx* by its larger size, and by its less elongated lower molars with a developed and lingually open trigonid, a complete M structure, a *Zhailimeryx* fold, and lacking an ectostylid. Differs from *Siamotragulus*, *Dorcatherium* and *Dorcabune* by its smaller size, its cusps more transversely compressed (*Dorcatherium*, *Dorcabune*), the presence of an ectostylid (*Dorcatherium*, *Siamotragulus*), of a *Zhailimeryx* fold (*Dorcatherium*, *Siamotragulus*), and by its upper molars with a better-developed parastyle and a more buccally salient mesostyle.

TABLE 1. Measurements (length x width in mm) of the dental material attributed to *Archaeotragulus krabiensis*

Specimen	m2	M1	M2	M3
BM 08-01-30-7	7.9 x 4.5	-	-	-
BM 08-04-25-15	-	6.5 x 6.2	6.8 x 8.5	9.2 x 9.9
BM 08-01-29-16	-	-	7.1 x 8.4	-
BM 08-01-29-19	-	-	8.1 x 9.3	-

Description—The M1 is almost square and the M2 and M3 are triangular with four cusps. The upper molars increase in size from M1 to M3. The metaconule is more mesiodistally compressed than the protocone. The paracone is strongly ribbed and has a buccally convex wall, whereas the buccal wall of the metacone is ribbed and flat. There is a strong mesial parastyle and a buccally salient mesostyle, and the distal extension of the postmetacrista does not end with a metastyle. The preparacrista is mesially directed and connects with the parastyle, the postparacrista and the premetacrista are distobuccally and mesiobuccally oriented respectively and they both joins the mesostyle. The metaconule is slightly more buccal than the protocone. The preprotocrista extends along the mesial face of the crown and connects with the parastyle. The postprotocrista is distally oriented on M1-2 and ends against the mesial face of the metaconule, and it is distobuccally directed on M3 where it extends in the transverse valley. The premetacristule joins the mesial face of the metacone and the postmetacristule extends along the distal rim of the crown and connects with the metastyle. A thick cingulum occurs mesially and lingually under the protocone. The

morphology of the isolated lower molar is identical to that of the lower teeth described by Métais et al. (2001), and it only exhibits a small ectostylid that was not observed on the holotype.

Comparisons—The new material from Bang Mark provides the first report on the morphology of *Archaeotragulus* upper molars. These teeth are selenodont, very simple, and they display a morphology that is expected to observe for a primitive tragulid. Very few comparisons can be made because the Paleogene fossil record of Tragulidae is very scarce and only includes *Stenomeryx* from the late middle Eocene of Pondaung for which upper molars are unknown so far (but comparisons between lower teeth of *Archaeotragulus* and *Stenomeryx* have been made by Ducrocq et al., 2020), and *Krabitherium* from the late Eocene of Krabi that is larger and more bunodont. Additional features that differentiate *Archaeotragulus* from *Krabitherium* include slightly more elongated and compressed lower premolars that are more bent lingually, lower molars with a more mesially developed and lingually open trigonid, with a complete M structure and a posthypocristid that extends lingually behind the entoconid, and more triangular upper molars with a more lingual metaconule, buccally salient styles, a better developed lingual cingulum and that lack an entostyle.

The Neogene tragulids *Dorcabune* and *Dorcatherium* strongly differ from *Archaeotragulus* by their larger size (except *Dorcatherium minimus*) and wrinkled enamel. In addition, the lower molars of these Neogene genera exhibit a developed premetacristid that closes the trigonid, a deeper *Zhailimeryx* fold, and a less transversely compressed hypoconulid on m3, and their upper molars have a less reduced metaconule, a less lingually protruding protocone, a weaker mesostyle and a bifurcated postprotocrista (*Dorcabune*). Despite their different chronological occurrence, *Archaeotragulus* and *Siamotragulus* from the middle Miocene of Thailand (Thomas et al., 1990) are both small-sized and display a

rather similar morphology including selenodont lower and upper molars, narrow and elongated simple lower premolars. However, the main differences between both genera concern the lower molars of *Archaeotragulus* that exhibit a longer and lingually open trigonid, thicker mesial and distal cingulids, less transversely compressed lingual cusps, and distinct *Zhailimeryx* fold and ectostylid. The upper molars of the Krabi species also have weaker ribs on the buccal cusps, more salient and slightly stronger mesostyle, mesial and distal cingula. If *Archaeotragulus* is more closely related to *Siamotragulus* than to any other known tragulid (contrary to Métais et al., 2001 who suggested that the Krabi species was closer to *Dorcatherium*), the changes in dental morphology involved might include the loss of the *Zhailimeryx* fold (which would be a plesiomorphic feature, as Métais et al., 2007 suggested), the development of the premetacristid and subsequent closing of the trigonid, the enlargement of buccal ribs on upper molars and the weakening of the mesostyle and of the mesial and distal cingula.

KRABITHERIUM Métais, Chaimanee, Jaeger, and Ducrocq, 2007

KRABITHERIUM WAILEKI Métais, Chaimanee, Jaeger, and Ducrocq, 2007

(Fig. 3A–H)

Type Locality and Horizon—Bang Pu Dam lignite pit, Krabi coal mine (southern Thailand), late Eocene.

Type Specimen—Fragmentary lower jaw with left m2–m3, TF 2680.

Referred Material—Left M3, BM 09-12-01-1; left M3, BM 08-12-17-2; left M3, BM 07-07-29-4; right M1?, BM 08-07-15-32; right m2, BM 08-07-15-33; left lower jaw with p4–m3, BM 07-07-28-6.

Emended Diagnosis—Primitive ruminant characterized by its bunoselenodont molars, simple p4 that lacks a metaconid, lower molars with incomplete M structure, a *Zhailimeryx* fold and an ectostylid. Differs from *Archaeotragulus* in being larger (Table 2), in lacking a complete M structure, in having a more lingually oriented cristid obliqua, better mesial and distal cingulids, a less salient parastyle and mesostyle, a more mesiodistal postprotocrista and in lacking a lingual cingulum and a metastyle. Differs from *Stenomeryx* in being larger and more bunoselenodont, in having a better-developed cingulid, a more lingually oriented cristid oblique and an ectostylid. Differs from the Miocene *Dorcabune*, *Dorcatherium*, and *Siamotragulus* in being more bunodont (*Dorcatherium* and *Siamotragulus*), in lacking a complete M structure, in having better developed cingulids and ectostylid, less salient upper molar styles, a distinct entostyle, a less developed lingual cingulum, and a more mesiodistally oriented postprotocrista. Further differs from the extant *Hyaemoschus* and *Tragulus* in having more bunodont molars with less salient styles, and in lacking the well-marked and characteristic crests and folds on lower molars.

Description—The fragmentary lower jaw preserves damaged p4–m1. It is not possible to observe whether a metaconid was present on the premolar because most of the lingual part of the crown is broken away, but there is no swelling on what is left of the lingual face of the tooth that might indicate that an accessory cusp was absent. Two cristids originate from the tip of the protoconid. The buccal one is distally directed and extends to the distolingual part of the talonid, and the lingual cristid is shorter and curves buccally at mid-height of the crown before reaching the talonid. The buccal face of the premolar is flat. The lower molars (BM 07-07-28-6 and BM 08-07-15-33) display a structure similar to that of the holotype (Métais et al., 2007), but the *Zhailimeryx* fold is much less expressed on the entoconid of the m3 (the only molar where this cusps is preserved on BM 07-07-28-6). The upper molars are quadrangular with four rather bunodont cusps. The crests of the paracone and metacone are mesiodistally

oriented. The premetacrista slightly curves buccally to join the small mesostyle whereas the postparacrista is distally oriented and ends in the transverse valley without reaching the mesostyle. The paracone rib is slightly more developed than the metacone rib, and both cusps are buccally convex. The parastyle is mesial and larger than the pillar-like mesostyle that is not buccally salient, and the metastyle is weak. The metaconule is slightly compressed mesiodistally and more buccal than the protocone. The preprotocrista reaches the parastyle and the postprotocrista is mesiodistal and end against the mesial wall of the metaconule. There is no trace of a bifurcated postprotocrista, even on the most fresh molar (BM 07-07-29-4). The premetacristule is mesiobuccally directed and ends in the transverse valley mesially or mesiolingually to the metaconule but it does not reach the mesostyle. The postmetacristule extends along the distal side of the crown and connects with the metastyle. The cingulum is weakly developed on the mesial face of the protocone and on the distal face of the metaconule. There is a very slight entostyle on all molars.

Comparisons—The main feature observed on the new material that supports an attribution of *Krabitherium* to the Tragulidae is the simple structure of the p4 with a single main cusp that very likely does not exhibit a metaconid or a swelling on its lingual face.

Krabitherium significantly differs from the two most primitive known Paleogene Tragulidae *Stenomeryx* from the late middle Eocene of Pondaung (Ducrocq et al., 2020) and *Archaeotragulus* from Krabi (Métais et al., 2001) in being larger and bunoselenodont. As stressed by Métais et al. (2007), the tragulid morphologically most similar to *Krabitherium* is *Dorcabune* Pilgrim, 1910 from the Miocene of Asia. Indeed, the bunoselenodonty, the upper molars with not protruding and moderately developed styles, a postparacrista that does not reach the mesostyle, the simple and narrow p4 that lacks a metaconid, and the lower molars with a mesially directed premetacristid, a *Zhailimeryx* fold, developed cingulids and ectostylid are features shared by both taxa. On the other hand, the Thai species differs from *Dorcabune*

by its smaller size, its upper molars that lack a lingual cingulum and a bifurcated postprotocrista, and its lower molars that exhibit an incomplete M structure. However, the very similar general structure of lower and upper teeth in both genera illustrated by the new material and their molar morphology clearly distinct from that of other tragulids supports Métais et al. (2007) hypothesis that *Krabitherium* might have been an early representative of a bunodont lineage that led to *Dorcabune*.

TABLE 2. Measurements (length x width in mm) of the dental material attributed to *Krabitherium waileki*.

Specimen	p4	m1	m2	m3	M1	M3
BM 07-07- 28-6	8.4 x 4.5	9.2 x 6.4	9.9 x 7.2	14.3 x 7.3	-	-
BM 08-07- 15-33	-	-	9.8 x 6.7	-	-	-
BM 08-07- 15-32	-	-	-	-	8.8 x 9.9	-
BM 09-12- 01-1	-	-	-	-	-	10.7 x 12.2
BM 08-12- 17-2	-	-	-	-	-	10.1 x 11.8
BM 07-07- 29-4	-	-	-	-	-	10.6 x 12.2

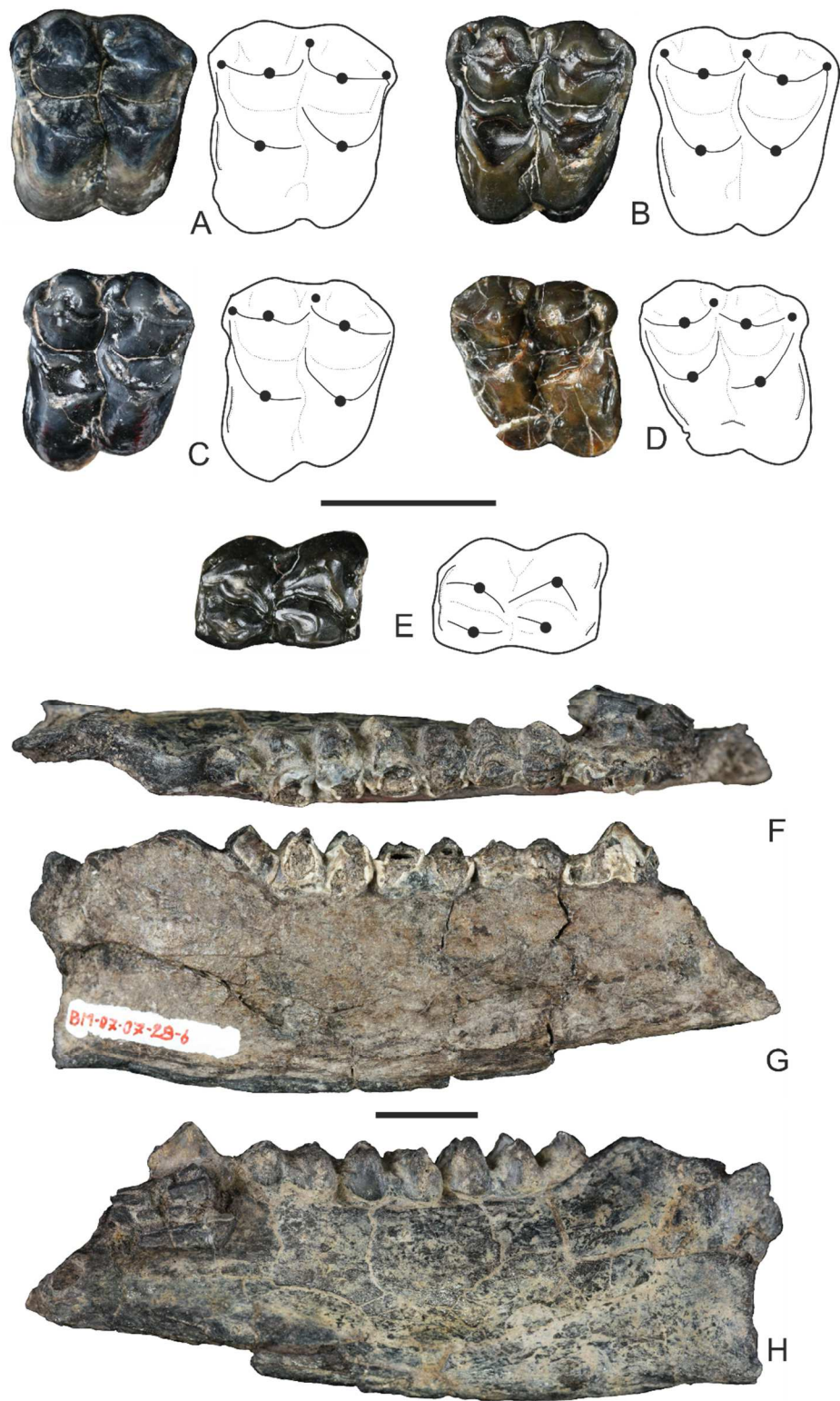


FIGURE 3. *Krabitherium waileki*. **A**, BM 07-07-29-4, left M3; **B**, BM 09-12-01-1, left M3; **C**, BM 08-12-17-2, left M3; **D**, BM 08-07-15-32, right M2 or M1; **E**, BM 08-07-15-33, right

m2; **F–H**, BM 07-07-28-6, left lower jaw with p4-m3, **F**, occlusal view; **G**, buccal view; **H**, lingual view. Scale bars equal 10 mm. [planned for 2/3 of page width]

Family LOPHIOMERYCIDAE Janis, 1987

KRABIMERYX Métais, Chaimanee, Jaeger, and Ducrocq, 2001

KRABIMERYX PRIMITIVUS Métais, Chaimanee, Jaeger, and Ducrocq, 2001

(Fig. 4A–D)

Type Locality and Horizon—Wai Lek lignite pit, Krabi coal mine (southern Thailand), late Eocene.

Type Specimen—Fragmentary lower jaw with left p4–m3, TF 2676.

Referred Material—Fragmentary lower jaw with talonid of left m1 and isolated left m2, BM 04-06-3-4a; isolated right m2, BM 04-06-3-4b.

With the exception of the talonid part of the m1 that displays the same morphology than that of the m2, the new material from Bang Mark listed here does not provide any additional information on the dental morphology of the Krabi species.

Dimensions (in mm)—Left m1: L = ?, W = 4.3, left m2: L = 8.3, W = 5.2, right m2: L = 8.0, W = 5.6.

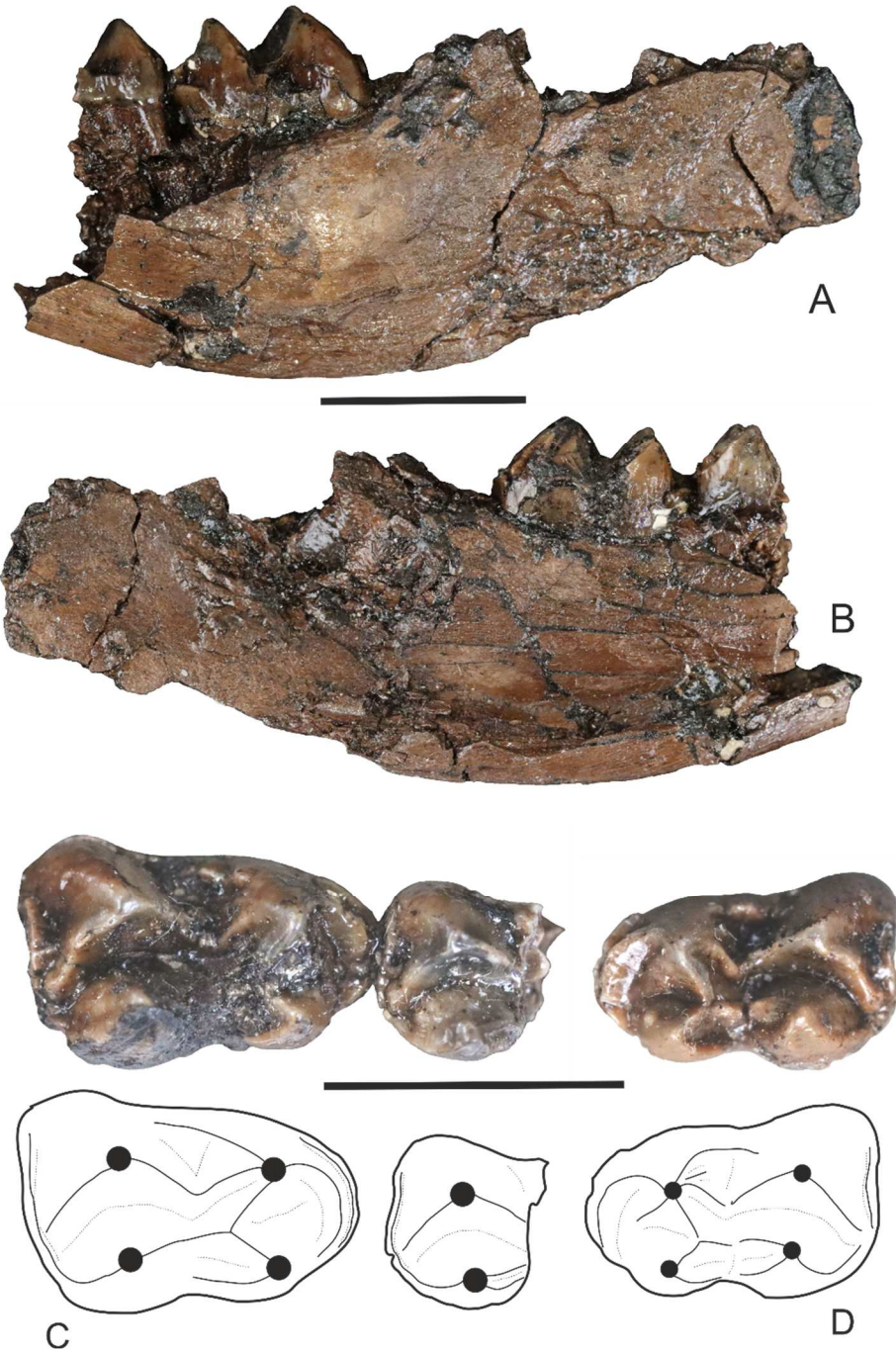


FIGURE 4. A–D, *Krabimeryx primitivus*. A–C, BM 04-06-3-4a, fragmentary left lower jaw with talonid of m1 and m2, A, buccal view; B, lingual view; C, occlusal view; D, BM 04-06-3-4b, isolated right m2. Scale bars equal 10 mm. [planned for 2/3 of page width]

Superfamily HIPPOPOTAMOIDEA Gray, 1821

Family ANTHRACOTHERIIDAE Leidy, 1869

Subfamily MICROBUNODONTINAE Lihoreau and Ducrocq, 2007

GENIOKERYX Ducrocq, 2020

GENIOKERYX NANUS sp. nov.

(Fig. 5A–C)

Holotype—Left lower jaw with p1–m3, BM 02-08-20-1.

Locality and Horizon—Bang Mark coal mine, Krabi Basin, southern Thailand, late Eocene.

Etymology—From the Greek 'nanos', meaning 'dwarf', in reference to the very small size of the species.

Diagnosis—Very small anthracothere characterized by its ventrally protruding unfused symphysis, caniniform p1, simple triangular lower premolars, and bunoselenodont molars with small distostylids. Differs from *Anthracokeryx* species by its shorter and deeper symphysis, lack of diastema between p2 and p3, more simple lower premolars, shorter lower molars with more bunodont lingual cusps and weaker endometacristids and postectometacristids. Differs from *Microbunodon* in being much smaller, in having a deeper and shorter symphysis, narrower and more simple lower premolars, less selenodont lower molars with a less developed hypoconulid lobe. Differs from the larger *G. thailandicus* by its shorter and slightly less ventrally protruding symphysis, its slightly narrower lower premolars, and molars with a weaker endometacristid and narrower hypoconulid lobe on m3

Description—The very small-sized lower jaw exhibits the complete row of bunoselenodont jugal teeth (p1 to m3) and is preserved from the front part of the symphysis to the base of the coronoid apophysis behind m3. The unfused symphysis is ventrally protruding

and its posterior end reaches under the mesial half of the p1. All lower premolars are triangular in lateral view with a flat lingual face and a slightly convex buccal face. A short diastema (about 2.5 mm) occurs between the caniniform p1 and the p2. The p2 is simple with a preprotocristid and a postprotocristid that extend from the apex of the crown. There is no paraconid or cingulid and a very faint talonid basin occupies the distal end of the crown. The p3 is larger than p2 and slightly taller than p4, and it displays the same structure as p2 with somewhat better expressed pre- and postprotocristids and a small spur that occurs on the middle of the postprotocristid. The talonid and distolingual and distobuccal cingulid are slightly more developed. The p4 is the widest premolar. It displays two short lingual and buccal cristids on each side of the postprotocristid. Both cristids originate from the apex of the tooth and they extend to the distal end of the crown. The postprotocristid ends as a very slight hypoconid on the talonid. The cingulid is present only on the distal end of the crown. The trigonid is almost as wide as the talonid on lower molars, and the buccal cusps are more selenodont than the lingual ones. The preprotocristid and the premetacristid are mesially directed and they curve lingually and buccally respectively to connect on the front part of the crown to close the trigonid above a low mesial cingulid. A slight endometacristid extends mesiobuccally from the apex of the metaconid to the center of the trigonid basin. The short postmetacristid and postprotocristid connect to close the trigonid distally. The trigonid wall is slightly slanted mesially. A slight postectometacristid extends from the apex of the metaconid to the lingual end of the transverse valley where it connects with a weak ectoentocristid. The entoconid is slightly mesial to the hypoconid. A short and low prehypocristid extends mesiolingually from the tip of the hypoconid to the lingual part of the protoconid distal wall. The hypoconid and entoconid are connected by a short and transverse preentocristid. The distal face of the entoconid is rounded and does not exhibit any cristid, and the posthypocristid is distally to distolingually oriented and reaches a tiny distostylid on m1-2. On

m3, the posthypocristid is distally oriented and connects with the ectohypocristulid that extends from the apex of the hypoconulid. The posthypocristulid reaches the base of the distal wall of the entoconid. A faint buccal cingulid occurs on all lower molars between the protoconid and the hypoconid. The lower jaw has a rather constant depth (about 12.8 mm under m2; around 13.5 mm under m3). *Geniokeryx nanus* was a very small anthracothere with a body mass estimate of around 4.0 kg, based on regression of body mass on m1 area (Legendre, 1989).

Dimensions (in mm)—The teeth measurements are as follows: p1: L = 3.9, W = 1.7; p2: L = 6.6, W = 2.4; p3: L = 6.8, W = 2.8; p4: L = 6.8, W = 3.2; m1: L = 6.0, W = 3.7; m2: L = 6.3, W = 4.2; m3: L = 9.6, W = 4.6.

Comparisons and Discussion—The very small size of this specimen might suggest affinities with dichobunoid basal ungulates (*sensu* Theodor et al., 2007). However, these taxa are usually smaller (except *Limeryx* and *Haqueina*), they have broader and more complex lower premolars (Asian dichobunids), more selenodont molars with better expressed crests (diacodexeids, homacodontids), that often exhibit a paraconid (diacodexeids, dichobunids, some homacodontids), a more oblique prehypocristid (diacodexeids, dichobunids, homacodontids), a m3 hypoconulid connected to the hypoconid and the entoconid (diacodexeids) or that can be reduced with several cusplets (Asian dichobunids). The general premolar and molar structure (combination of simple lower premolars, bunoselenodont molar cusps, preentocristid connecting the hypoconid and entoconid, endometacristid, distal face of entoconid rounded, well developed hypoconulid connected to the hypoconid on m3) rather reminds that of Paleogene anthracotheres. The smallest anthracotheres known in the Eocene of Southeast Asia are *Siamotherium pondaungensis* and *Anthracokeryx tenuis* from the late middle Eocene of Myanmar (Ducrocq et al., 2000; Aung Naing Soe et al., 2017; Pilgrim, 1928), and *Anthracokeryx naduungensis* from the late Eocene of Vietnam (Ducrocq et al.,

2015). However, all of these taxa are larger and markedly differ from the Bang Mark taxon by several important features. The lower teeth of *Siamotherium pondaungensis* are unknown but the Pondaung species exhibits an upper dental morphology very similar to that of the younger and larger *S. krabiensis* from the late Eocene of Thailand (Suteethorn et al., 1988) which is known by its almost complete dentition. The Thai species is more bunodont than the Bang Mark species, it does not have diastema in the premolar row, its premolars are broader and its p1 is not caniniform, its lower molars have a better developed distostylid and lack a postectometacristid, its m3 has a more massive and shorter hypoconulid lobe, and its symphysis is shallower and not ventrally salient. *Anthracokeryx tenuis* has a long, shallow and fused symphysis, a shallower horizontal ramus, diastema between p2 and p3, more complex premolars, and more elongated lower molars with a more open and longer lingual end of the transverse valley. The Vietnamese *A. naluongensis* also has a less developed and not ventrally protruding symphysis and lower molars with more transversely compressed lingual cusps and better developed endometacristids and postectometacristids. The symphysis, premolar and molar structures of the Bang Mark species are strikingly much more similar to those of the much larger *Geniokeryx thailandicus* from Krabi (Ducrocq, 2020). Indeed, both species displays a ventrally protruding symphysis, a caniniform p1 separated from p2 by a diastema, simple premolars, and bunoselenodont molars with reduced distostylids. The main differences that can be observed are the more massive horizontal ramus in *G. thailandicus*, the distal extension of the symphysis (under p2 in *G. thailandicus* and under p1 in the Bang Mark form), the comparatively slightly broader lower premolars, and the lower molars with a somewhat better expressed endometacristid and a slightly wider hypoconulid lobe on the m3 in *G. thailandicus*.

Despite the significant difference in size, the morphology and structure of the symphysis and lower teeth are very similar in the small species and *Geniokeryx*, which

suggests that the Bang Mark anthracothere can be attributed to that genus. It represents the smallest known anthracothere, and the smallest ungulate known in the Krabi fauna as well, with a body weight similar to that of the greater Indo-Malayan chevrotain *Tragulus napu* (Meijaard, 2011). Contrary to the slightly larger and more selenodont *Archaeotragulus* and *Krabimeryx*, *G. nanus* probably had a diet that included softer elements (berries, small invertebrates) than the Krabi ruminants. The occurrence of *G. nanus* in the late Eocene Krabi Basin also extends the number of representatives of the family to seven species, which makes of this anthracothere association the most important and diversified known during the Paleogene of Asia. No upper teeth collected from any of the three Krabi localities can be attributed to *G. nanus*, but it is very likely that when they are identified, they will probably exhibit a morphology very close to those of *G. thailandicus*.

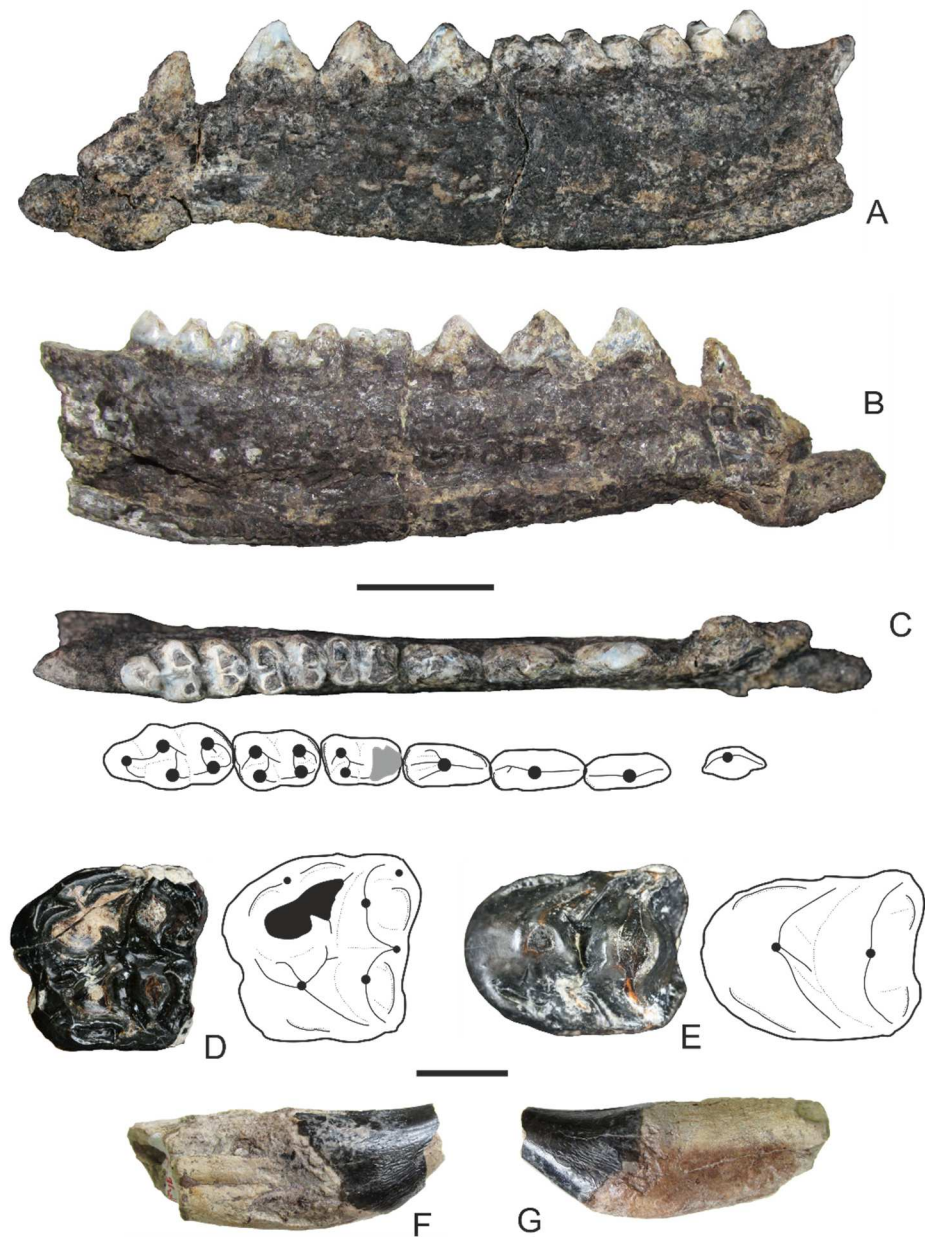


FIGURE 5. **A–C**, *Geniokeryx nanus* sp. nov., BM 02-08-20-1, right lower jaw with p1-m3, **A**, lingual view; **B**, buccal view; **C**, occlusal view. **D**, *Geniokeryx thailandicus*, BM 08-07-15-28, left M3; **E–G**, *Anthracotherium chaimanei*, **E**, BM 08-07-15-27, left P4, **F–G**, BM 08-07-15-31, left upper canine, **F**, buccal view; **G**, lingual view. Scale bars equal 10 mm. [planned for 2/3 of page width]

GENIOKERYX THAILANDICUS (Ducrocq, 2020)

(Fig. 5D)

Type Locality and Horizon—Wai Lek lignite pit, Krabi coal mine (southern Thailand), late Eocene.

Type Specimen—Sub-complete cranium with left and right P3–M3, TF 2638.

Referred Material—Left M3, BM 08-07-15-28. Collected from the green clay layer that underlies the main coal bed.

The worn molar (L = 18.3 mm, W = 19.3 mm) exhibits a morphology and dimensions almost identical to those of the holotype of *Geniokeryx thailandicus*, with the exception of a very slight and short mesiolingual crest of the metaconule and a slightly less developed metastylar region. In his recent taxonomic revision of the genus, Ducrocq (2020) stated that one of the features that distinguishes *Geniokeryx* from *Anthracokeryx* is the lack of an ectometacristule on upper molars. The occurrence of a very weak crest on the metaconule on the Bang Mark molar that might correspond to an incipient ectometacristule (it is absent in all other upper molars of the genus) suggests that this unusual structure, when observable, was variable within the genus. All of the material previously attributed to *Anthracokeryx thailandicus* by Ducrocq (1999) is now included into *Geniokeryx thailandicus* (Ducrocq, 2020).

Subfamily ANTHRACOTHERIINAE Leidy, 1869

ANTHRACOTHERIUM Cuvier, 1822

ANTHRACOTHERIUM CHAIMANEI Ducrocq, 1999

(Fig. 5E–G)

Type Locality and Horizon—Wai Lek lignite pit, Krabi coal mine (southern Thailand), late Eocene.

Type Specimen—Sub-complete cranium with left C–M3 and right P1–M3, TF 2636.

Referred Material—Left P4, BM 08-07-15-27; left upper canine, BM 08-07-15-31.

Collected from the clay layer that underlies the main coal bed.

Description—The P4 exhibits dimensions (L = 18.7 mm, W = 25.6 mm) and morphology that closely match those of the P4 of *Anthracotherium chaimanei*. The paracone and protocone are about the same size. The preparacrista connects with a strong mesiobuccal parastyle and the postparacrista joins a moderately developed distostyle. The thick preprotocrista extends along the mesial side of the crown and connects with the parastyle, and the short postprotocrista ends in the middle of the distal face and thickens as an enamel bulge. A third and very short crest extends distobuccally from the tip of the protocone to the longitudinal valley. A cingulum occurs only mesially and distally. The only differences that can be noticed are a parastyle mesiobuccally slightly stronger and a lingual wall of the protocone slightly more rounded in the Bang Mark specimen (Fig. 5E).

The upper canine has a short crown compared with the massive and long root (L = 17.8 mm, W = 12.5 mm). The tip of the crown is broken away but the wear facet with the lower canine is still visible. A slight keel occurs along the distal face of the crown, and the buccal face is very slightly more convex than the lingual face (Fig. 5F–G).

Geniokeryx thailandicus and *Anthracotherium chaimanei* were known only from the localities of Wai Lek and Bang Pu Dam so far. The fossil material attributed here to both of these species has been collected from a clay level directly under the main coal bed, but no difference in size or morphology can be observed between the specimens from Wai Lek, Bang Pu Dam and Bang Mark, which suggests that the main coal bed and the underlying clay level are contemporaneous or that there is no significant difference in age between both deposits.

Order PERISSODACTYLA Owen, 1848

Superfamily CHALICOTHERIOIDEA Gill, 1872

Family EOMOROPIDAE Matthew, 1929

Genus *EOMOROPUS* Osborn, 1913

EOMOROPUS MERIDIORIENTALIS sp. nov.

(Fig. 6A, B)

Holotype—Left M3, BM 08-07-15-30.

Etymology—The species name means ‘Southeast’ in Latin and refers to the Southeast Asian origin of the taxon.

Locality and Horizon—Bang Mark coal pit of Krabi Basin, collected from the green clay layer that underlies the main coal bed, late Eocene.

Diagnosis—Species of *Eomoropus* slightly larger than *E. amarorum* (Cope, 1881). M3 characterized by sharp lophes, a reduced paraconule, a buccally positioned parastyle connected to the ectoloph, a nearly flat and lingually tilted buccal wall of paracone, a narrow second lobe, transverse protoloph and metaloph, a sharp mesostyle, and a slightly distolingually oriented, sharp and protruding metastyle. Differs from *E. amarorum* (Middle Eocene, USA) by sharper lophes, transverse protoloph and metaloph, narrow second lobe, flatter and more lingually tilted buccal wall of paracone, reduced paraconule, parastyle connected to ectoloph, and by its ectoloph more flexed buccally between the paracone and the metacone. Differs from *E. pawnyunti* Rémy et al., 2005 (late Middle Eocene, Myanmar) by its much larger size, sharper lophes, narrower second lobe, more distally protruding metastyle, and by its flatter buccal wall of paracone. Differs from *E. quadridentatus* Zdansky, 1930 (late Middle Eocene, China) by a more transverse metaloph, a reduced paraconule, a narrower second lobe, a smaller parastyle connected to the ectoloph and more buccally positioned, and by a sharper

mesostyle. Differs from *E. minimus* Zdansky, 1930 (late Middle Eocene, China) by its much larger size. Differs from *Eomoropus anarsius* Gazin, 1956 (late Eocene, USA) by its much smaller parastyle, a smaller paraconule, and by a flat buccal wall of paracone. Differs from *Grangeria canina* Zdansky, 1930 (late Middle Eocene, China) by its smaller size. Differs from *Litolophus gobiensis* (Colbert, 1934) (Early Eocene, China) in having a more mesially positioned protocone, a more buccally protruding parastyle, a mesostyle, and no distolingual rotation of the ectoloph and metaloph. Differs from *Paleomoropus* Radinsky, 1964 (Early Eocene, USA) in having a mesostyle, a flat and lingually tilted buccal wall of paracone and a connection between the parastyle and the ectoloph.

Description—The M3 is well preserved except for minor damage on the parastyle, the paraconule, and on the tip of the protocone and hypocone. It is very lightly worn, with only small wear facets appearing on the mesial side of the protoloph and the metaloph, as well as along the ectoloph. The crown is low (10.69 mm), slightly broader than long (L = 18.9 mm, W = 21.1 mm) with a second lobe much narrower than the first one (buccolingual length between mesostyle and hypocone = 14.8 mm). The lophs are sharp and the paracone is the tallest cusp. This cusp is not inflated, only a small paracone rib being visible buccally. The buccal wall of the paracone is lingually slanted. A short and distolingually oriented crest departs from the summit of the paracone. The protocone is the lowest and the most basally inflated cusp. The paracone and the protocone are connected by a transverse and distally concave protoloph. The paraconule is reduced, being only a small bulge along the protoloph. In mesial view, the protoloph shows a small summit at the level the paraconule. Two faint grooves delimitate the paraconule on the distal side of the protoloph. The parastyle is massive, connected to the ectoloph, much more buccally protruding than the paracone, and it thus represents the buccalmost part of the crown. This style is only slightly more mesial than the protocone and the paracone. The ectoloph is not distinctly flexed buccally between the

paracone and the metacone. The mesostyle is much less lingual than the parastyle, it is smaller but sharp and markedly protruding buccally. The hypocone and the metacone are connected by a transverse and distally concave metaloph. This loph is shorter than the protoloph due to a more lingually placement of the metacone relative to the paracone. The metastyle is oriented distally and very slightly lingually, sharp, and well protruding distally. A deep, distobuccally oriented valley separates the ectoloph from the metaloph at the level of the mesostyle. A moderately thick cingulum is present mesially. A low and thin cingulum also occurs buccally between the parastyle and the mesostyle, and lingually between the protocone and the hypocone that partly closes the central valley. A small cingulum is present distal to the hypocone but it does not close the distal basin which exhibits a mesiodistally oriented valley.

Comparisons—The morphology of BM 08-07-15-30 is typical of chalicotherioid in displaying a low crown, a W-shaped ectoloph with a strong mesostyle, a fully developed metaloph uninterrupted by a metaconule, in retaining a paraconule (Radinsky, 1964), and in possessing a distally recurved parastyle (Hooker and Dashzeveg, 2004). The protoloph in mesial position and the low mesostyle (in comparison with the condition observed in chalicotheriids) conform with the anatomical definition of the paraphyletic family Eomoropidae (Remy et al., 2005). Among eomoropids, BM 08-07-15-30 is markedly different from *Litolophus gobiensis* from the Early Eocene of China. This species possesses for instance upper molars that lack a mesostyle and a connection between the parastyle, and distolingually oriented ectoloph and metaloph on M3. Other genera of Early Eocene chalicotherioids from North America, Europe and Asia sometimes referred to the Eomoropidae (*Paleomoropus*, *Protomoropus*, *Lophiaspis*) also markedly differ from BM 08-07-15-30 in lacking upper molar mesostyles and in showing more bulbous paracone and a more vertical paracone buccal wall on M3 (Radinsky, 1964; Hooker and Dashzeveg, 2004). The putative chalicotherioid *Lunania youngi* Chow, 1957 from the late Eocene of China is

only known by m2-m3 and cannot be directly compared with *E. meridionalis*. However, the lower molars of *Lunania youngi* are much smaller to correspond to the Bang Mark species. *Grangeria canina* is mainly diagnosed by its large canines and deep mandible with short symphysis (Radinsky, 1964). The upper molars of this species are unfortunately unknown, which prevents direct comparisons. However, the length of upper molar series in *G. canina* was estimated from roots at 64 mm by Zdansky (1930). According to this measurement, an estimated M3 length of ~25 mm can be estimated from Zdansky illustration, which is much larger than that of BM 08-07-15-30.

The genus *Eomoropus* best fits the morphology of BM 08-07-15-30, most of its features being observed in the Thai specimen. BM 08-07-15-30 displays more resemblance with *E. pawnyunti* and *E. quadridentatus* in sharing with them moderately developed styles, transverse protoloph and metaloph, well lingually titled paracone buccal walls, reduced paracone rib (especially with *E. quadridentatus*) and well buccally flexed ectoloph between the paracone and the metacone. A few derived or supposedly derived features distinguish *E. meridionalis* from the other species of *Eomoropus*, such as sharper lophes, mesostyle and metastyle, less cuspidate paraconule, a higher degree of integration merging of the parastyle into the ectoloph, and a marked distal narrowing of M3 crown. The latter feature is also observed on the specimen SDM 84006 (late Eocene, Shandong province, China), first identified as *E. quadridentatus* by Shi (1989), but that likely corresponds to a distinct species of *Eomoropus* phylogenetically closer to the Chalicotheriidae according to Bai et al. (2010). The M3 of SDM 84006 is clearly different from BM 08-07-15-30 in its oblique protoloph and metaloph and is more bulbous paracone.

The upper dentition of *Eomoropus ulterior* Chow, 1962 (late Eocene, China), a species similar in size with *E. meridionalis*, is unknown. Although both species cannot be directly compared, the lower dentition of *Eomoropus ulterior* reveals affinities with *E. amarorum*

(Chow, 1962; Bai et al., 2010) contrary to BM 08-07-15-30, which is morphologically closer to *E. pawnnyunti* and *E. quadridentatus* and likely represents a more derived species of *Eomoropus*. Thus, it seems unlikely that BM 08-07-15-30 belongs to *Eomoropus ulterior*.

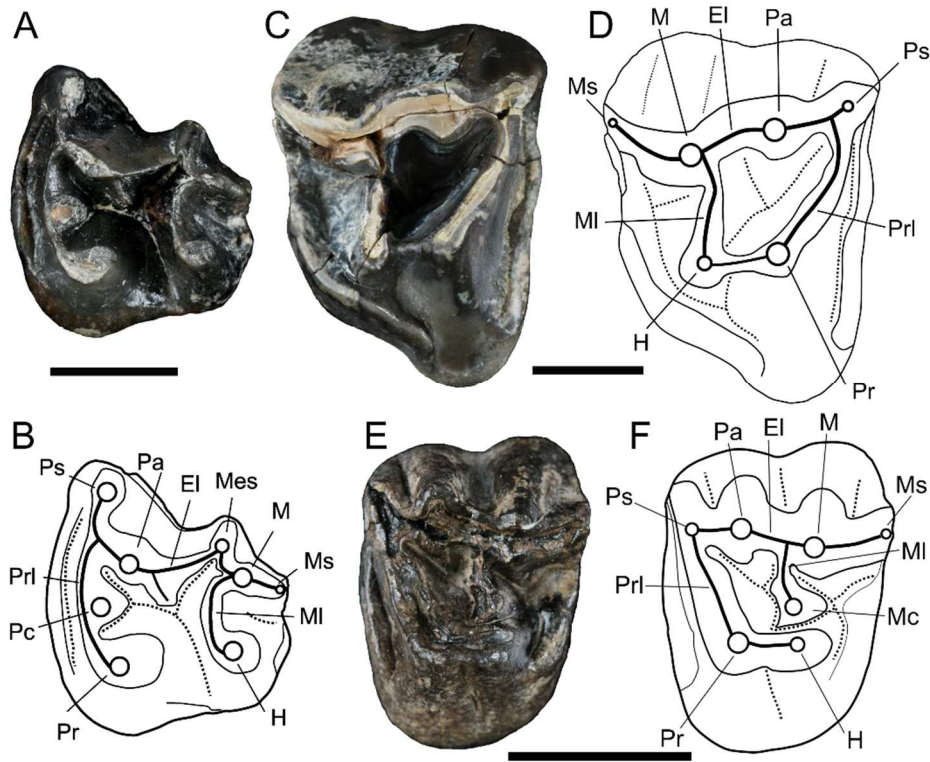


FIGURE 6. **A–B**, *Eomoropus meridiorientalis* sp. nov., BM 08-07-15-30, left M3; **C–D**, *Guixia simplex*, BM 04-10-22-2, right P4; **E–F**, Rhinocerotoida indet., BM 06-12-4-4, left P4. Scale bars equal 10 mm. **Abbreviations:** **El**, ectoloph; **H**, hypocone; **M**, metacone; **Mc**, metaconule; **Mes**, mesostyle; **Ms**, metastyle; **MI**, metaloph; **Pa**, paracone; **Pc**, paraconule; **Ps**, parastyle; **Pr**, protocone; **Prl**, protoloph. [planned for 2/3 of page width]

Superfamily RHINOCEROTOIDEA Gray, 1821

Family RHINOCEROTIDAE Gray, 1821

GUIXIA You, 1977

GUIXIA SIMPLEX You, 1977

(Fig. 6C, D)

Type Locality and Horizon—Bose Basin, Naduo Fm. (Guangxi province, China), late Eocene.

Type Specimen—Fragmentary lower jaw with left p4–m3, IVPP V 5004.

Referred Material—Left m2, TF 2657 and left m3, TF 2658, from a single individual (Antoine et al., 2003).

New Material—Right P4, BM 04-10-22-2.

Description—The P4 has a low crown (L = 24.4 mm, W = 32.9 mm, height = 20.3 mm). This semimolariform tooth is identified as a P4 because its crown is wider than long and possesses a trapezoidal outline. The enamel is finely wrinkled. The protoloph is oblique and connects the parastyle and the protocone. The protocone is located as mesially as the paracone. The protocone is not constricted and it extends far lingually. Its lingual wall is tilted buccally. The hypocone is small and much lower than the protocone. These two cusps are distinct, being about as distant from each other as the paracone and the metacone, and they are connected by a lingual bridge that closes the central valley (semimolariform *sensu* Heissig, 1989). The metaloph is transverse, narrow, and straight. The lingual cingulum is not complete and is interrupted around the protocone. The ectoloph is straight with a moderately developed parastyle mesial to the paracone. The paracone fold and the parastylar groove are weak. The metacone fold is weak and the metastyle is short. A very low buccal cingulum is present on the distal half of the tooth. There is no crochet. The postfossa is large, deep and closed distally. Its distal wall is markedly notched so that this basin should become open distally at an advanced stage of wear.

Discussion—The lophodont pi pattern with a strong and straight ectoloph of BM 04-10-22-2 indicates that it belongs to a rhinocerotoid. The combination of a P4 with a trapezoid outline, a lingually expanded protocone with a buccally tilted wall, and an interrupted lingual

cingulum does not correspond well to the morphology of hyracodontids and amynodontids. In these families, the P4 is either square-shaped or presents a rounded lingual wall, the lingual wall of the protocone is more vertical, and there is most often a complete lingual cingulum. In addition, the upper premolars of amynodontids have much stronger paracone folds. The P4 of Paleogene Rhinocerotidae are more similar to BM 04-10-22-2 in often displaying comparable P4 outlines (e.g., *Subhyracodon*, *Epiaceratherium*, *Mesaceratherium*, *Protaceratherium*, *Molassitherium*, *Amphicaenopus*, *Guixia*) and protocone structure on P3-P4 (e.g., *Subhyracodon*, *Mesaceratherium*, *Guixia*). In addition, Paleogene rhinocerotids generally displays complete lingual cingula on upper posterior premolars (*Trigonias*, *Penetrigonias*, *Amphicaenopus*, *Subhyracodon*, *Diceratherium*, *Molassitherium*, *Ronzotherium*, *Epiaceratherium*, *Protaceratherium*, *Mesaceratherium*). Among Paleogene taxa, only *Teletaceras* (Middle/Late Eocene of North America and Asia) and *Guixia* display a partial lingual cingula on P3-P4 (You, 1977; Hanson, 1989). However, *Teletaceras* can be distinguished by its P4 with a more parabolic lingual wall, poorly developed metaloph and large paracone and metacone ribs (Hanson, 1989:fig. 20.4). The upper premolars of *Guixia*, only known in the species *G. youjiangensis*, conform in all aspects with BM 04-10-22-2. In addition to the previously cited shared characters between *Guixia* and the Bang Mark specimen, the P3-P4 of *G. youjiangensis* further share with BM 04-10-22-2 a premolariform pattern with a connection between the protocone and hypocone, oblique protoloph, rather weak paracone/metacone ribs and parastylar fold, no crochet, and a wide and weakly distally enclosed postfossa.

The size and morphology of BM 04-10-22-2 correspond well to the rhinocerotid from the Wai Lek mine of Krabi Basin identified as ?*Guixia* sp. cf. *G. simplex* by Antoine et al. (2003) based on associated m2 and a m3. The lower molars display morphological affinities with those of *Guixia* and match in size with *G. simplex* but not with the larger *G.*

youjiangensis (Antoine et al., 2003). New information provided by BM 04-10-22-2 indicate that the Krabi rhinocerotid can be firmly allocated to *Guixia*. At the specific level, Antoine et al. (2003) noted that *G. youjiangensis* was likely distinct from the Krabi specimens according to its much larger size. BM 04-10-22-2 confirms this assertion in being much smaller than the P4 of the Chinese species (L = 38 mm, W = 50 mm). The paracone and metacone ribs and the parastylar fold are more pronounced in BM 04-10-22-2 than in *G. youjiangensis* and correspond well to the condition observed on the M1 of *G. simplex*. Although BM 04-10-22-2 is smaller than the M1 from Bose Basin (You, 1977:pl. 1, fig. 3), we consider that the size and morphology of the material from Bose and Krabi Basins are overall sufficiently close to attribute it to the same species.

Superfamily RHINOCEROTOIDEA Gray, 1821

RHINOCEROTOIDEA indet.

(Fig. 6E, F)

Referred Material—Left P4, BM 06-12-14-4.

Description—The P4 is moderately worn. The crown is low (height = 8.3 mm), rectangular and transversely elongated (L = 12.0 mm, W = 16.8 mm). The paracone and metacone are well spaced and show important buccal ribs. The buccal wall also presents a pronounced groove between these cusps. The metacone is more lingual than the paracone and higher than it. The ectoloph is straight but not very sharp. A strong parastyle is present mesially to the paracone and is separated from it by a buccal groove. A smaller metastyle appears at the distal extremity of the ectoloph. A protoloph connects the protocone and the parastyle mesially. The protocone is in mesial position and aligned with the paracone. A mesiodistal endoprotocrista (Holbrook, 2015) departs from the protocone. A hypocone is emerging from this crest against the protocone. Both cusps are only separated by a lingual

groove. A rounded distolingual posthypocrista is visible. The mesial wall is less vertical than the buccal one. A transverse metaloph departs from a point mesial to the metacone along the ectoloph and reaches a metaconule located against the hypocone. The metaloph is not confluent with the hypocone, the metaconule being separated from the hypocone by a small groove. A metaconule appears along the metaloph against the hypocone. Short mesial and distal cingula are present but no cingula occur lingually and buccally.

Discussion—Brontotherioid perissodactyls differ from BM 06-12-14-4 in their more trenchant premolar ectoloph and isolated protocone. Chalicotherioids can be distinguished from the Bang Mark premolar by their more central protocones and their less molarized premolars without hypocone. The Asian Paleogene Tapiroidea with submolariform premolars (Helaletidae and early Tapiridae) possess distinguishing features compared with BM 06-12-14-4. These perissodactyls have most often equally developed protoloph and metaloph, a metaloph without metaconule, no or a small lingual shift of the metacone relative of the paracone, and a shorter and smaller metastyle. Other Paleogene tapiroid families can also be discarded: the Lophialelidae often have non-molarized upper premolars and flatter buccal cusps, and the Deperetellidae display fully molariform and lophodont upper premolars.

The strong ectoloph with a pronounced metastyle and the lingual shift of the metacone relative to the paracone better correspond to the premolars of rhinocerotoids. Arynodonts can be discarded because of their flatter metacone buccal wall. BM 06-12-14-4 might either correspond to a conservative lineage of rhinocerotids or hyracodontids. These two families include small-sized representatives (e.g., *Teletaceras radinskyi* for rhinocerotids, *Prohyracodon meridionale* for hyracodontids; Chow and Xu, 1961; Hanson, 1989) with rather similar occlusal patterns associated with reduced lingual cingula on posterior premolars (although not achieving the cingulum reduction of the Bang Mark specimen). Only further material (e.g., molars) will resolve the identification of this taxon. BM 06-12-14-4 is clearly

different in size and morphology from the P4 of *Guixia simplex* (BM 04-10-22-2), which indicates the existence in the Bang Mark fauna of two rhinocerotoids.

DISCUSSION AND CONCLUSIONS

All of the taxa described here were never recorded from Bang Mark so far, and they were only known in Wail Lek and/or Bang Pu Dam localities or are new for the Krabi fauna. A few species were already shared between Bang Mark and Wai Lek (*Siamopithecus eocaenus*, *Baluchimys krabiense*, *Egatochoerus jaegeri*) or between Bang Mark and Bang Pu Dam (*Egatochoerus jaegeri*, *Bothriogenys orientale*), but the occurrence of several additional taxa that occur in all three localities thus supports their contemporaneity. The faunal list of Bang Mark now includes 19 taxa, which makes of this locality the richest one after Wai Lek (Table 3). Although no anthracothere in the Paleogene of Asia seems to have been closely related to *Geniokeryx*, the identification of a new small anthracothere species in the late Eocene of Southeast Asia also confirms that this region played a critical role in the diversity and evolution of the group during the Paleogene. The new remains that could be attributed to the ruminants from Krabi also provide additional information on their affinities that were still speculative so far. The morphology of the upper molars that belong to the basal tragulid *Archaeotragulus* suggests that this genus might have been more closely related to the Miocene *Siamotragulus* than to any other Neogene tragulid, and the dental material attributed to the alleged Tragulidae *Krabitherium* includes a p4 that supports its tragulid affinities. In addition, we agree with Métais et al. (2007) who suggested that *Krabitherium* was likely an early part of a bunodont radiation closely related to *Dorcabune*, because *Krabitherium* displays more bunodont teeth that are unlike the dental material of any other known tragulid.

TABLE 3. Updated faunal list of the localities of Wai Lek, Bang Pu Dam and Bang Mark (late Eocene, Krabi Basin, southern Thailand).

Taxa		Wai Lek	Bang Pu Dam	Bang Mark
Reptilia		Colubridae	Colubridae	
		Crocodylidae		
		Alligatoriidae		
		Chelonia		
Dermoptera		<i>Dermotherium</i> <i>major</i>		
Insectivora		Family indet.		
Megachiroptera		Pteropodidae indet.		
Rodentia	Baluchimyinae	<i>Baluchimys</i> <i>krabiense</i>		<i>Baluchimys</i> <i>krabiense</i>
		Family indet. 1 and 2		
Primates	Amhipithecidae	<i>Siamopithecus</i> <i>eocaenus</i>		<i>Siamopithecus</i> <i>eocaenus</i>
		Amhipithecidae indet.		<i>Krabilia minuta</i>
	Sivaladapidae	<i>Wailekia</i> <i>orientale</i>		

	Adapiform			<i>Muangthanhinus</i> <i>siami</i>
		Tarsiidae indet.		
Carnivora	Miacidae	<i>Miacis</i> <i>thailandicus</i>		
	Nimravidae	<i>Nimravus</i> cf. <i>intermedius</i> <i>Hoplophoenus</i> sp.		
				Family indet.
Cetartiodactyla	Dichobunidae		<i>Progenitohyus</i> <i>thailandicus</i>	<i>Progenitohyus</i> <i>thailandicus</i>
	Tayassuidae	<i>Egatochoerus</i> <i>jaegeri</i>	<i>Egatochoerus</i> <i>jaegeri</i>	<i>Egatochoerus</i> <i>jaegeri</i>
	Suidae			<i>Siamochoerus</i> <i>banmarkensis</i>
	Lophiomerycidae	<i>Krabimeryx</i> <i>primitivus</i>	<i>Krabimeryx</i> <i>primitivus</i>	<i>Krabimeryx</i> <i>primitivus</i>
	Tragulidae	<i>Krabitherium</i> <i>waileki</i> <i>Archaeotragulus</i> <i>krabiensis</i>	<i>Krabitherium</i> <i>waileki</i>	<i>Krabitherium</i> <i>waileki</i> <i>Archaeotragulus</i> <i>krabiensis</i>
	Entelodontidae	<i>Entelodon</i> aff. <i>E.</i> <i>gobiensis</i>		

Anthracotheriidae	<i>Siamotherium</i>	<i>Siamotherium</i>	
	<i>krabiense</i>	<i>krabiense</i>	
	<i>Anthracotherium</i>		<i>Anthracotherium</i>
	<i>chaimanei</i>		<i>chaimanei</i>
	<i>Geniokeryx</i>	<i>Geniokeryx</i>	<i>Geniokeryx</i>
	<i>thailandicus</i>	<i>thailandicus</i>	<i>thailandicus</i>
			<i>Geniokeryx</i>
			<i>nanus</i> sp. nov.
		<i>Anthracohyus</i>	
		sp.	
		<i>Bothriogenys</i>	<i>Bothriogenys</i>
		<i>orientale</i>	<i>orientale</i>
			<i>Atopotherium</i>
			<i>bangmarkensis</i>
Perissodactyla	Eomoropidae		<i>Eomoropus</i>
			<i>meridiorientalis</i> sp.
			nov.
	Rhinocerotoidae	<i>Siamolophus</i>	
		<i>krabiense</i>	
			Family indet., gen.
			nov.
	Rhinocerotidae	<i>Guixia simplex</i>	<i>Guixia simplex</i>

The ‘ungulate’ component of the Krabi fauna has been traditionally viewed as dominated by cetartiodactyls, which are well diversified and represented by dichobunoids, ruminants, anthracotheres, entelodonts and suoids. On the contrary, perissodactyls have been much scarce so far, being only represented by a rhinocerotid and the enigmatic ceratomorph *Siamolophus* Ducrocq et al., 2006. The new remains from Bang Mark significantly increase the diversity of the Krabi perissodactyls by documenting two new species belonging to a small-sized plesiomorphic rhinocerotoid and a chalicothere. Chalicotheres were never abundant in the Paleogene fossil record of Asia, and although the Bang Mark species is represented by a single upper molar, its presence in the late Eocene of Thailand represents the most meridional occurrence of the superfamily in Asia, and it might contribute to a better understanding of the early evolution of this group in Asia. Despite these new data, we note that the specific diversity of perissodactyls in the Krabi fauna is still much lower than in other late Eocene localities in Asia or in the late Middle Eocene Pondaung Formation of Myanmar (radiometrically dated from 40.31 to 40.22 Ma by Khin Zaw et al., 2014). Several common groups of perissodactyls in contemporaneous Asian localities, such as brontotheres, tapiroids or amynodont rhinocerotoids, are absent from the Krabi fauna. In addition, we observe that the four species of perissodactyls are documented in Krabi by few fossils likely belonging to only five individuals. We can hypothesize that the paleoecological adaptations of the perissodactyls contributed to their underrepresentation in the Krabi localities. Another possible reason would be the consequence of competition for resources by anthracotheres that are much more abundant and diversified in Krabi. Most of the perissodactyls from Bang Mark are indicative of biogeographic affinities between Southeast Asia and China during the late Eocene. This is best demonstrated by the common occurrence of the rhinocerotid *Guixia simplex* in the Krabi and Bose faunas. The Bang Mark chalicothere *Eomoropus meridiorientalis*, which is morphologically close to *E. quadridentatus* (late Middle Eocene

Heti Formation of the Yuanqu basin, Henan Province of China) might also indicate affinities with Chinese perissodactyls. This is not the case, however, for the cetartiodactyls from Krabi. Only four out of 13 taxa present in Krabi (the suid *Siamochoerus banmarkensis* Ducrocq et al., 1998, the anthracotheres *Anthracotherium chaimanei* Ducrocq, 1999 and *Bothriogenys orientale* Ducrocq, 1999, and the entelodont *Entelodon* aff. *E. gobiensis*) display morphological affinities with taxa known from the late Eocene and early Oligocene of southern Asia. Most of other Krabi cetartiodactyls are either closer to taxa from the late middle Eocene of Pondaung (*Progenitohyus thailandicus*, *Siamotherium krabiense* Suteethorn et al., 1988, *Anthracohyus* sp.), or to Neogene genera from Thailand, Pakistan or China (*Archaeotragulus krabiensis*, *Krabitherium waileki*). A bias in the fossil collecting might also explain this discrepancy, and when additional perissodactyl remains are discovered in Krabi, it is possible that they display a pattern of affinities similar to that of cetartiodactyls. Indeed, this study demonstrates that late Eocene localities from Thailand continue to yield fossil remains that will document the community structure of one of the most significant late Eocene fauna of southeast Asia and that will allow a better understanding of the phylogenetic affinities for several ungulate taxa.

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