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New remains of *Siamochoerus banmarkensis* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998 (Artiodactyla: Suidae) from the late Eocene of Thailand

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Siamochoerus banmarkensis Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998, buccal and lingual views of the mandibles (BM-04-09-30-1).

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New remains of *Siamochoerus banmarkensis* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998 (Artiodactyla: Suidae) from the late Eocene of Thailand

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ABSTRACT
We report here new craniodental remains from the late Eocene Krabi coal mine in Thailand that can be attributed to the suoid *Siamochoerus banmarkensis* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998. This material that includes the complete lower dentition and isolated upper molars provides new information on the dental morphology of this species and makes *S. banmarkensis*, together with *Egatochoerus jaegeri* Ducrocq, 1994 from Krabi, the second best documented early suoid in the Eocene of Asia. A few dental features that can be observed on these new remains suggest that *S. banmarkensis* might be more closely related to Suidae Gray, 1821, but it also illustrates the difficulty to attribute a precise taxonomic position to Eocene taxa.

KEY WORDS
Suoidea,
Eocene,
Asia,
Thailand,
Siamochoerus,
systematics.

RÉSUMÉ

Nouveaux restes de Siamochoerus banmarkensis *Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998 (Artiodactyla: Suidae) de l'Eocène supérieur de Thaïlande.*

Nous décrivons dans ce travail de nouveaux restes crânio-dentaires provenant de la mine de lignite de Krabi d'âge Eocène supérieur en Thaïlande et pouvant être attribués au suoïde *Siamochoerus banmarkensis* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998. Ce matériel, qui inclue la dentition inférieure complète et des molaires supérieures isolées, permet de préciser la morphologie dentaire pour cette espèce et fait de *S. banmarkensis*, tout comme *Egatochoerus jaegeri* Ducrocq, 1994 de Krabi, le second suoïde primitif le mieux documenté dans l'Eocène d'Asie. Quelques caractères dentaires, pouvant être observés sur ces nouveaux restes, suggèrent que *S. banmarkensis* pourrait être plus étroitement apparenté aux Suidae Gray, 1821, mais cela illustre également la difficulté d'attribuer une position taxonomique précise aux formes éocènes.

MOTS CLÉS
Suoidea,
Eocène,
Asia,
Thailande,
Siamochoerus,
systématique.

INTRODUCTION

The early evolution of Suoidea Gray, 1821 is documented since the middle Late Eocene in Asia by several species. All of these taxa, however, are represented by fragmentary remains and their affinities have thus long been debated mostly because of their primitive condition (Tong & Zhao 1986; Ducrocq 1994; van der Made 1997, 2010; Ducrocq *et al.* 1998; Liu 2001; Orliac *et al.* 2010, 2011).

The first fossil suoid that was described from the Paleogene of Asia is *Odoichoerus uniconus* Tong & Zhao, 1986 (Late Eocene, China). First considered as a suoid by Tong & Zhao (1986), it was then tentatively referred to the Suidae by Ducrocq (1994) until van der Made (1997) and then Orliac *et al.* (2011) suggested that it is the earliest representative of the taucanamine suoids. *Egatochoerus jaegeri* Ducrocq, 1994 from the Late Eocene of Thailand was then described and considered as a tayassuid (Ducrocq 1994), but Orliac *et al.* (2011) analyzed additional material attributed to this species and concluded that it should be referred to the Suoidea. *Siamochoerus banmarkensis* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998 from the late Eocene of Thailand is the third Paleogene suoid reported from Asia (Ducrocq *et al.* 1998) and was known so far only by its lower p3-m3 and damaged upper M2-M3. This taxon has been attributed to the Suidae by Ducrocq *et al.* (1998), an opinion that was followed by van der Made (2010), whereas Liu (2003) placed it in "Suoidea indet." and Harris & Liu (2007) in "primitive suoids". Orliac *et al.* (2011) then considered it as a primitive suid. Liu (2001) described fragmentary remains of several other primitive suoids in the Late Eocene of China (a new species of *Siamochoerus* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998 that she included into the Palaeochoeridae Matthew, 1924 [a family name that was re-introduced by van der Made in 1996a for "Old World peccaries"], and *Huaxiachoerus* Liu, 2001 and *Eocenchoerus* Liu, 2001 attributed to the Palaeochoeridae and the Suidae respectively). However, recent papers by Pickford (2016, 2018) on the systematics of early European suoids added confusion concerning the characters used to distinguish Palaeochoeridae from Suidae (van der Made 2023). The diversity of suoid taxa in the Eocene of Asia and the uncertainties about their phylogenetic relationships thus illustrate the complex evolutionary history of the group and the confusion that characterizes its systematics.

We describe here new material from the late Eocene Bang Mark lignite pit (Krabi coal mine, Thailand) that can be attributed to *Siamochoerus banmarkensis*. Bang Mark is one of the three pits (together with Bang Pu Dam and Wai Lek) present in the Krabi coal mine from which lignite was extracted by the Electricity Generating Authority of Thailand (EGAT). The Bang Mark coal deposit is elongated along a north northwest to south southeast axis, and it covers 1.5 square kilometers (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 lignite pits that are thus considered as contemporaneous (Ducrocq *et al.* 1992, 1995, 1997; Benammi *et al.* 2001). The fossil record of Bang Mark has been recently extended to about twenty mammal taxa including rodents, primates, carnivores, artiodactyls and perissodactyls (Ducrocq *et al.* 2021) which makes this locality one of the richest and most diversified in the Krabi fauna and in South Asia. The new fossil remains described here include four lower jaws (two of them preserve the complete dentition) and several isolated upper molars.

MATERIAL AND METHODS

The dental terminology used here follows Orliac *et al.* (2011).

Measurements

For lower incisors, we measured the mesio-distal diameter (corresponds to Length in Table 1), the bucco-lingual diameter (corresponds to Width f in Table 1) and the height at the lingual side (Hli); for lower canines, we measured the length of the lingual side of the crown (corresponds to Length in Table 1) and the width of the distal side of the crown (corresponds to Width f in Table 1); for premolars and molars, we measured the mesio-distal length of the crown and due to the preservation of lower premolars, we could only measure the width of the second lobe; for molars, we measured the length of the tooth, the width of the first lobe and second lobe for m1/M1 and m2/M2 and the width of the third lobe for m3 (see van der Made 1996b: figs 16-18 for measurement protocol, including mandible depth).

Abbreviations

Institutional abbreviations

All fossils described here are housed in the Department of Mineral Resources, Bangkok, Thailand:

BM	Bang Mark Collections at the Department of Mineral Resources, Bangkok;
TF	Thai Fossil Collections at the Department of Mineral Resources, Bangkok.

Other Abbreviations

c	lower canine;
i	lower incisor;
l	left;
m	lower molar;
M	upper molar;
p	lower premolar;
r	right.

SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Owen, 1848
Superfamily Suoidea Gray, 1821
Family Suidae Gray, 1821

Genus *Siamochoerus* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998

Type species. — *Siamochoerus banmarkensis* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998.

Included species. — *Siamochoerus viriosus* Liu, 2001.

Material examined. — **Holotype. Thailand.** Fragmentary lower jaw with left p4-m3, TF 2905.

Referred material. — Right lower jaw with i1-i3, c, p1-m3 associated with left lower jaw with i1-i3, c, p2-m3 (BM-04-09-30-1); left lower jaw with p2 and m1-m3 (BM-06-08-03-5.1); right lower jaw with p2 and m1-m3 (BM-06-08-03-5.2); left m3 (BM-04-07-26-1b); right M3 (BM-04-07-26-1a); right M3 (BM-06-08-04-2); left M3 (BM-06-08-04-3); right M1 (BM-06-08-04-5).

Emended diagnosis. — Primitive suid close to *Palaeochoerus typus* Pomel, 1847 in size with small verrucosic lower canine (buccal side wider than the distal side), very short diastemata between c-p1 and p1-p2, p1-p3 without accessory cusps, p4 with a small metaconid and a moderately developed hypoconid. Lower molars with the mesial lobe wider than the distal lobe, and almost absent mesoconulid. Upper molars with a distinct centroconule and a small paraconule slightly mesial to the paracone and protocone, and divergent roots. Differs from *Siamochoerus viriosus* Liu, 2001 in being smaller, in having mesial lobe wider than the distal one on m1 and m2, and in having buccal cuspids in line with the lingual ones. Differs from *Eocenchoerus savagei* Liu, 2001 by its less distally developed M3 with a centroconule. Differs from *Huaxiachoerus guangxiensis* Liu, 2001 in being larger and in having a centroconule on upper molars.

Type locality and horizon. — Bang Mark lignite pit, Krabi coal mine (southern Thailand), late Eocene.

Description

The better-preserved mandibles (BM-04-09-30-1) still exhibit a complete dentition, and the horizontal ramus that displays a rather constant depth from p2 to m3 (depth under p2: 23.5 mm; under p4: 21.8 mm; under m3: 23.5 mm). In dorsal view, it is swollen buccally beneath the molars with a shallow lingual fossa (Fig. 1B). The shallow and almost horizontal symphysis extends to the back of the p2. The two symphyses do not seem to be fused (Fig. 2A, C). The root of the ascending ramus rises behind the back of the m3, and the distal part of the coronoid apophysis that is still preserved on BM06-08-03-5.1 is vertical (Fig. 3). Two mental foramina are visible at mid-height of the ramus, one beneath the mesial root of the p2 and one beneath the p4 on BM-04-09-30-1 (Fig. 1A), and only one foramen is visible under p2 on BM-06-08-03-5.2 (Fig. 4A).

The three incisors are forwardly protruding, spatulate and mesiodistally short, the i1 being the longest with a horizontal apex. Its buccal face is convex and its lingual face is concave with a longitudinal central ridge extending from the cervix to about 3 mm under the apex. The i2 is slightly shorter than the i1 and displays a similar shape except for its oblique apex higher mesially than distally. It also exhibits a central longitudinal ridge on its lingual face that extends from the cervix to about 4 mm under the apex. The i3 is the smallest incisor with a shorter and oval-shaped crown in buccal view. It is a smaller version of the i2 rather than a triangular tooth in lateral view. The buccal face is convex and the concave lingual face also displays a central ridge that ends on a very slight enamel swelling above the cervix. There is no diastema between the incisors (Figs 1A-C; 2A, B).

On BM-04-09-30-1 the small and slender lower canine (not much larger than the p1) is separated from the i3 by a short diastema (about 4 mm). It is slightly laterally splaying, its apex is broken about 6 mm above the root and the crown has a verrucosic section. The distal face is straight to slightly concave (Fig. 1A-C). It is difficult to attribute BM-04-09-30-1 to a male or a female on the basis of the canine size because it is the only known mandible that preserve this tooth and sexual dimorphism is thus unknown. In addition, the size of male and female canines might have been smaller in primitive suoids than in younger taxa.

There is a very short diastema (3 mm) between the canine and the p1. The p1 is a small and very simple tooth with only one root preserved. It is triangular in lateral view. The buccal face is convex and the lingual face is concave. The apex is broken but two mesial and distal cristids can be distinguished on the crown (Fig. 1A).

The p2 is separated from the p1 by a diastema of about 3 mm. It is a triangular narrow tooth with two roots and the apex above the gap between both roots. The mesial half of the crown is damaged on BM-04-09-30-1 (Fig. 1A) but on the specimens that are better preserved (BM-06-08-03-5.1 and BM-06-08-03-5.2 that very likely belong to the same individual) two slight mesial and distal cristids are present

Fig. 1. — *Siamochoerus banmarkensis* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998 from Bang Mark lignite pit, Krabi coal mine, late Eocene: **A**-**C**, right and left lower jaw (BM-04-09-30-1) in buccal (**A**), occlusal (**B**) and lingual (**C**) views. Scale bar: 1 cm.

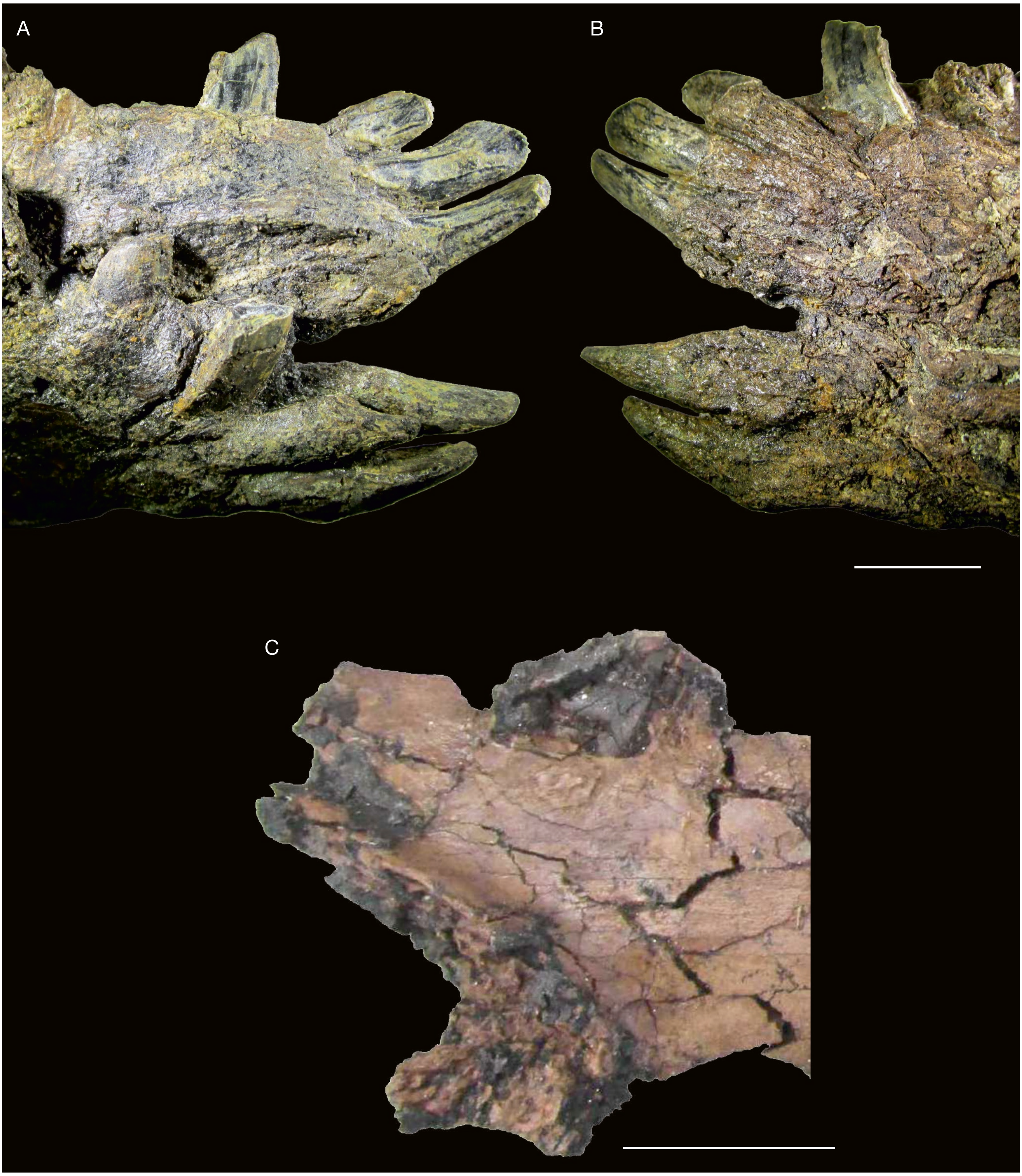

Fig. 2. — *Siamochoerus banmarkensis* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998 from Bang Mark lignite pit, Krabi coal mine, late Eocene: **A**, **B**, lower incisors, canine and mandibular symphysis (BM-04-09-30-1) in lingual (**A**) and buccal (**B**) views; **C**, mandibular symphysis of right lower jaw (BM-06-08-03-5.2) in lingual view. Scale bars: 1 cm.

that connect the apex and the mesial and distal end of the crown respectively (Figs 3; 4). There is no extended talonid distally, but a very small enamel spur meets the distal cristid. The buccal face is convex and the lingual face is concave.

The lower p3-p4 and molars have been described in detail in Ducrocq *et al.* (1998), and only variations in their morphology and additional characters that were not observed because of the preservation of the original material will be added here.

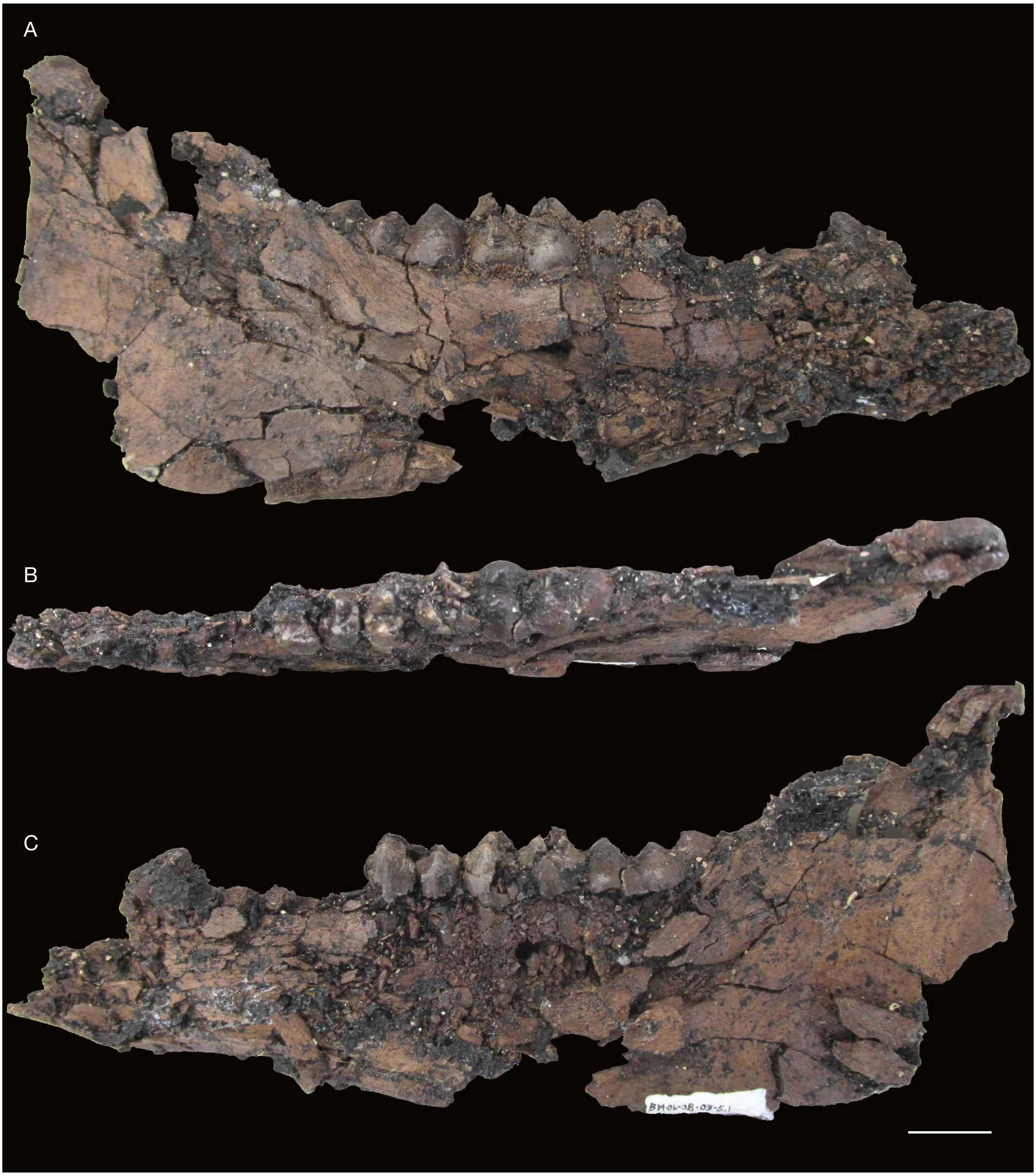

FIG. 3. — *Siamochoerus banmarkensis* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998 from Bang Mark lignite pit, Krabi coal mine, late Eocene: **A**-**C**, left lower jaw (BM-06-08-03-5.1) in lingual (**A**), occlusal (**B**) and buccal (**C**) views. Scale bar: 1 cm.

The p3 and p4 on BM-04-09-30-1 exhibit a triangular crown, a convex buccal face and a concave lingual face, and a small metaconid on the lingual face of the p4 slightly distal to the main cuspid. The talonid part is weakly developed and there is no distinct paraconid, but a very slight mesiodistal enamel swelling at the end of the preprotocristid (Fig. 1A-C).

The lower molars of the new specimens are also similar in morphology and size to those of the holotype TF 2905 (Ducrocq *et al.* 1998). The m3 BM-04-07-26-1b however, displays a few minor differences compared with the holotype, such as its less well developed preprotocristid and postprotocristid, but the wear facet on the distal face of the protoconid

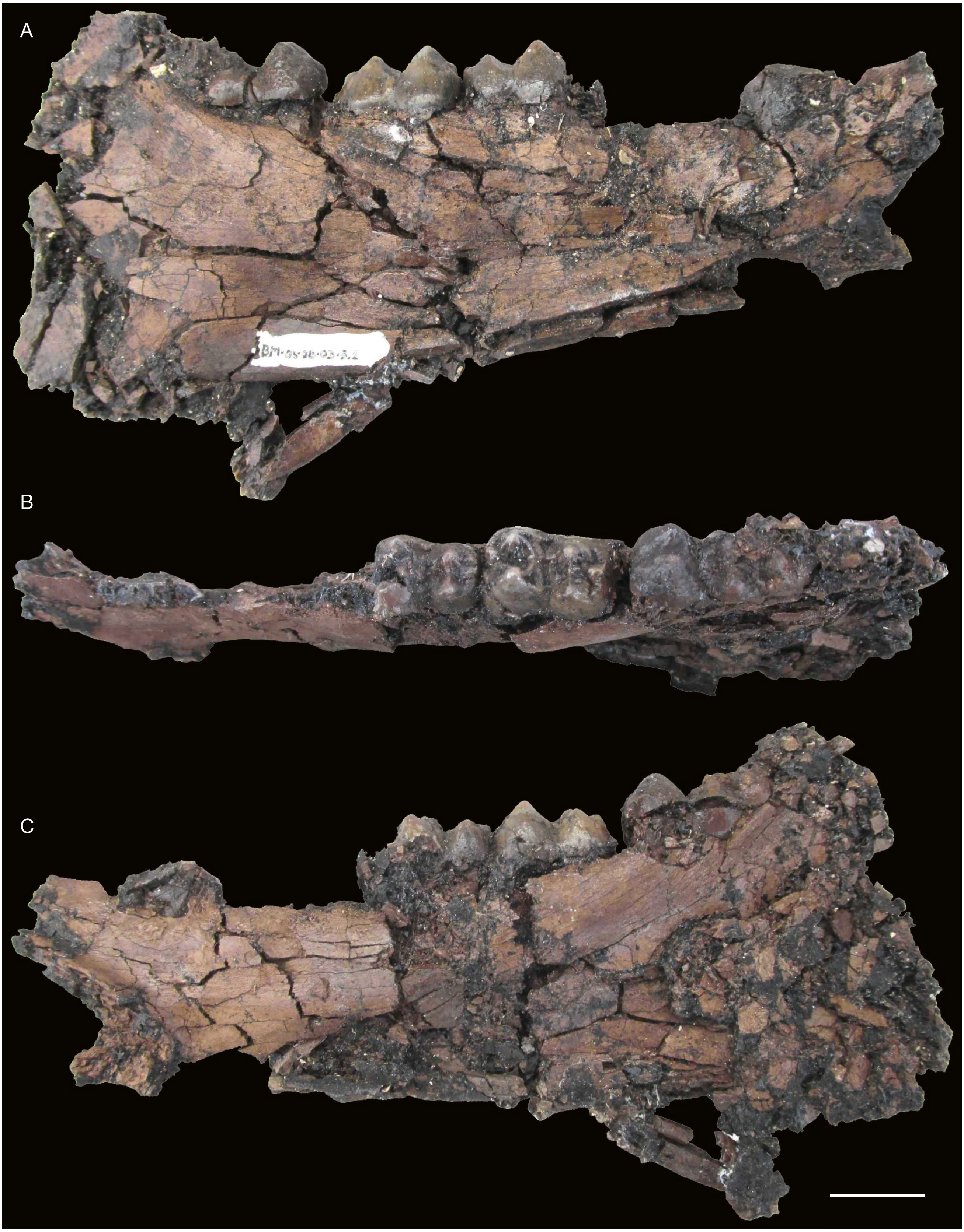

FIG. 4. — *Siamochoerus banmarkensis* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998 from Bang Mark lignite pit, Krabi coal mine, late Eocene: **A**-**C**, right lower jaw (BM-06-08-03-5.2) in buccal (**A**), occlusal (**B**) and lingual (**C**) views. Scale bar: 1 cm.

TABLE 1. — *Siamochoerus banmarkensis* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998. Measurements (mm) of dental remains from Bang Mark lignite pit. Length: mesio-distal diameter for lower incisors, length of lingual side of the crown for lower canines, mesio-distal length for premolars and molars. Abbreviations: **Hli**, height of incisor at lingual side (see van der Made 1996b for measurement method); **Width f**, bucco-lingual diameter for lower incisors, width of distal side of the crown for lower canines, width of the first lobe for molars; **Width s**, width of the second lobe for premolars and molars; **Width t**, width of the third lobe of m3. *****, indicates estimated measurement of damaged tooth.

Catalogue No.	Tooth	Length	Width f	Width s	Width t	Hli
BM-06-08-04-3	l M3	13.2	14.7	–	–	–
BM-06-08-04-2	r M3	13.1	14.3	10.8	–	–
BM-04-07-26-1a	r M3	13.8	13.7	12.0	–	–
BM-06-08-04-5	r M1	11.5	–	11.2	–	–
BM-04-07-26-1b	l m3	–	9.5	8.6	–	–
BM-06-08-03-5.2	r p2	10.7*	3.5*	–	–	–
	r m1	12.5*	9.3	7.7	–	–
	r m2	14.3	10.3	9.3	–	–
	r m3	18.7	9.9*	7.7	6.5*	–
BM-06-08-03-5.1	l p2	9.8*	5.3	–	–	–
	l m1	12.3*	8.2*	7.5	–	–
	l m2	14.8*	10.3*	8.9*	–	–
	l m3	19.1	10.6	8.4	6.3	–
BM-04-09-30-1	l i1	4.2	4.5	–	–	10.3
	l i2	5.0	3.3	–	–	11.4
	l i3	4.7	4.4	–	–	7.5
	l c	5.1	4.2	–	–	–
	l p2	9.7*	5.3*	–	–	–
	l p3	12.3*	–	–	–	–
	l p4	10.6*	8.9*	–	–	–
	l m1	13.7*	–	–	–	–
	l m2	14.2	–	–	–	–
	l m3	17.8	11.0*	8.8	6.1	–
	r i1	4.7	5.1	–	–	11.4
	r i2	4.9	4.1	–	–	10.0
	r i3	4.9	5.0	–	–	7.0
	r c	5.4	3.6	–	–	–
	r p1	5.7	–	–	–	–
	r p2	9.6	5.7	–	–	–
	r p3	10.2*	–	–	–	–
	r p4	10.8*	–	–	–	–
	r m1	11.2	–	–	–	–
	r m2	13.7	–	9.5	–	–
	r m3	19.2	10.5	9.0	6.4	–

might be responsible for the less distinct development of the postprotocristid (Fig. 5K).

The upper molars of *S. banmarkensis* that were first described (Ducrocq *et al.* 1998) are longitudinally cracked and their morphology is thus not known with accuracy. For example, it was noticed that there were no well-defined accessory cusps. The new material is thus described here in more detail. Three M3's and a possible M1 are present in the new material. The M3 is narrower distally than mesially with the buccal cusps more mesially situated than the lingual ones. The paracone is the largest cusp and a small centroconule is present mesiobuccally to the metaconule (this cusp was not visible on TF 2907 due to the preservation of the molars). A very small paraconule occurs slightly mesial to the paracone and the protocone and is merged in the preparacrista, but tends to disappear with wear. A cingulum is present mesially and distally and is variably developed under the metaconule (strong on BM-06-08-04-2 and weak on BM-06-08-04-5 and BM-04-07-26-1a). The distal part on the M3 is represented by a small distostyle that is often connected to the distal end of the postmetacristule (Fig. 5A-H). The M1 is morphologically similar to the M3 (Fig. 5G-H) except for its more square occlusal outline. A very tiny entostyle is present at the lingual end of the transverse valley of the M1 (BM-06-08-04-5) and this structure is much less developed on the M3 (Table 1). Ducrocq *et al.* (1998) mentioned that the roots of the upper molars of TF 2907 are unfused, but it is unclear. In buccal view, the upper parts of the roots are separated and seem to be divergent (Fig. 5I). In lingual view, the roots of M2 are embedded in the bone but they seem to be separated and divergent at their junction with the crown (Fig. 5J).

DISCUSSION

When *Siamochoerus banmarkensis* was first described, other primitive Eocene suoids were unknown in Asia, and it could be compared only with *Odoichoerus uniconus* (Tong & Zhao 1986) from China, *Egatochoerus jaegeri* (Ducrocq 1994) from Thailand and Paleogene western Europe taxa (Ducrocq *et al.* 1998). Since then, several new suoids have been reported from the late Eocene of China (Guangxi Province) by Liu (2001): *Siamochoerus viriosus*, *Eocenchoerus savagei* and *Huaxiachoerus guangxiensis*, all of them being represented by fragmentary material (upper and/or lower cheek teeth).

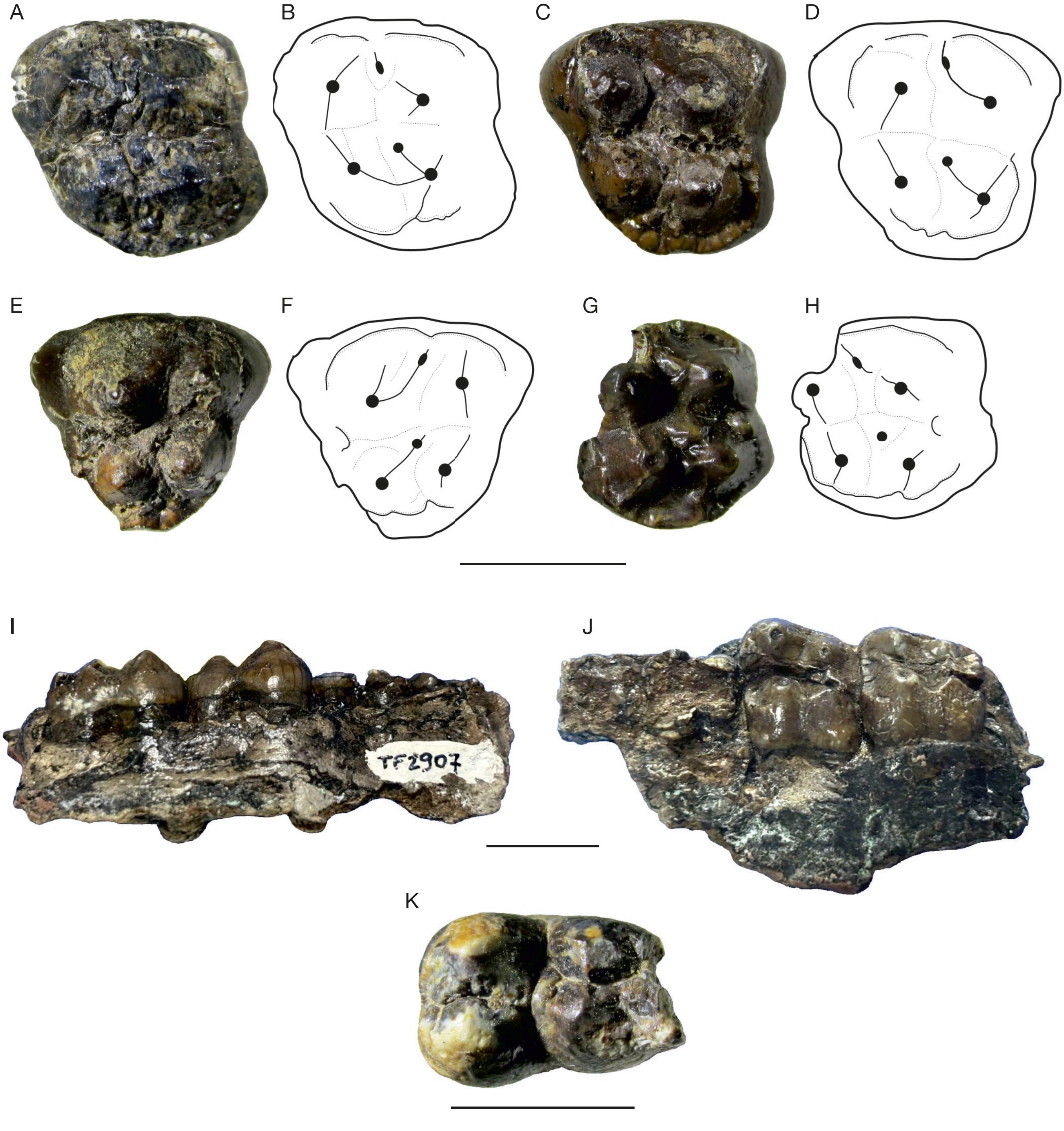

Fig. 5. — *Siamochoerus banmarkensis* Ducrocq, Chaimanee, Suteethorn & Jaeger, 1998 from Bang Mark lignite pit, Krabi coal mine, late Eocene: **A**, **B**, right M3 (BM-04-07-26-1a) in occlusal view; **C**, **D**, right M3 (BM-06-08-04-2) in occlusal view; **E**, **F**, left M3 (BM-06-08-04-3) in occlusal view; **G**, **H**, right M1 (BM-06-08-04-5) in occlusal view; **I**, **J**, left fragmentary maxilla with M2-M3 (TF 2907) in buccal (**I**) and occluso-lingual (**J**) views; **K**, left m3 (BM-04-07-26-1b) in occlusal view. Scale bars: 1 cm.

Siamochoerus viriosus has been described based on of three isolated lower molars (right m1-m3) that are considered to belong to the same individual (Liu 2001). Although both species of *Siamochoerus* exhibit a similar morphology, *S. viriosus* is much larger than *S. banmarkensis*. On the m1 of *S. viriosus*, the buccal cuspids are more mesially situated than the lingual ones, whereas they are in line on the m1 of *S. banmarkensis*. The m2 of *S. viriosus* also displays a trigonid and a talonid of roughly the same width contrary to *S. banmarkensis* where the trigonid is clearly wider than the talonid. The distostylid (or hypoconulid) on the m1 and m2 of *S. viriosus* is also better developed than in *B. banmarkensis* and the premetacristid is lower and weaker in the latter.

Eocenchoerus savagei is known only by an isolated M3 and P4. The M3 of *Eocenchoerus* mainly differs from that of *Siamochoerus* in being slightly longer and by its better developed talon in buccal position, its much more buccally salient paracone and by the absence of a centroconule and of a distal cingulum.

Huaxiachoerus guangxiensis is a third suoid known only by its M2 and M3. It is smaller than *S. banmarkensis* and contrary to the latter its M2 is smaller than its M3. In addition, the upper molars of *H. guangxiensis* do not exhibit a centroconule, the buccal crest of its metaconule (endometacristule) does not connect the lingual wall of the metacone as in *S. banmarkensis*, and the mesial cingulum does not extend mesiolingually under the protocone in the Thai genus.

The lower molars and p3-p4 of *Siamochoerus* have been extensively compared with those of *Egatochoerus jaegeri* by Ducrocq *et al.* (1998) and Orliac *et al.* (2011), but the upper molars of *Siamochoerus* were still fragmentarily known because of their poor preservation, and its anterior lower dentition had not been recovered yet. The new material from Bang Mark allows more precise comparisons. For example, we agree with Orliac *et al.* (2011) that the upper molars of both genera share a similar structure with a distinct centrocrista, but they also share a centroconule connected to the metaconule by a premetacristule (not visible on TF 2907) and a paraconule slightly mesial to the paracone and the protocone. On the other hand, *Siamochoerus* does not exhibit a buccal cingulum as developed as in *Egatochoerus*, the entostyle on its M1 is more distinct and its upper molar roots are divergent. The lower jaw of *Egatochoerus* also differs from that of *Siamochoerus* in being much deeper with a marked angular process, it has a stronger vertical canine, it lacks a p1, and its p2 has only one root.

Odoichoerus uniconus has been compared in detail with *Siamochoerus banmarkensis* by Ducrocq *et al.* (1998) and the new material only confirms the differences that can be observed in both taxa. Indeed, *Odoichoerus* Tong & Zhao, 1986 differs from *Siamochoerus* by its smaller size, shallower mandibular ramus, much smaller hypoconulid lobe on m3, sharper and more simple p4 without accessory cuspid and with a better developed and higher distal cristid (postprotocristid).

The fossil record of Paleogene suoids in Europe is not documented before the Oligocene, and their taxonomic content and familial status remain contentious (Orliac *et al.* 2010). It is not our aim here to rediscuss the number of families and subfamilies and their content. Yet, it is interesting to notice that the morphology of upper molar roots has been first used by Stehlin (1899-1900) to distinguish between different groups of suoids, and van der Made (1996a) used this feature to differentiate Suidae and Palaeochoeridae. Pickford (2016, 2018) then proposed a classification for *Propalaeochoerus* Stehlin, 1899-1900, *Doliochoerus* Filhol, 1882 (Doliochoeridae, often referred to as Old World peccaries) and *Palaeochoerus* Pomel, 1847 (Suidae). However, van der Made (2023) convincingly demonstrated that the conclusions of Pickford (2016, 2018) were based on erroneous observations and interpretations, and he proposed a classification (van der Made 2023: fig. 1) that is followed here.

According to Pickford (2016), *Propalaeochoerus* and *Doliochoerus* are morphologically very similar and can be distinguished mainly by features of the skull and upper teeth that cannot be observed on our material. *Doliochoerus* and *Propalaeochoerus* are about the same size as *S. banmarkensis* but they differ from the Thai species by their somewhat deeper horizontal ramus, their much larger lower canines, their more massive p4 that exhibits better developed metaconid, paraconid and talonid, their lower molars with a trigonid and talonid of similar width, and their m3 with a wider hypoconulid. The upper molars of both European genera also display better developed accessory cusplets and their M3 is less triangular in occlusal outline than that of *S. banmarkensis*.

Palaeochoerus mainly differs from *Siamochoerus* by its slightly narrower p4 with a larger metaconid, a tiny paraconid, a taller talonid part and a less convex lingual face, by its lower molars with a trigonid almost as wide as the talonid that exhibit an endometaconulid, a stronger mesoconulid and prehypocristid and a more complete preprotocristid, by its m3 with a more massive hypoconulid lobe, by its upper molars with a less developed centrocista, a stronger preprotocrista and by its M3 that is less triangular in occlusal outline.

The late Eocene *Perchoerus* Leidy, 1869 from North America is the oldest suoid known outside of Eurasia. It is commonly considered as a New World tayassuid (for example Prothero 2021), but Orliac *et al.* (2010) placed it within suoids of uncertain phylogenetic position. The jugal teeth of *Siamochoerus* are about the same size as those of *P. minor*. However, the North American genus differs from *Siamochoerus* by its much stronger and vertical lower canine, the presence of longer diastema between c and p1 and between p1 and p2, its p4 with much better developed metaconid, talonid and cingulids, its somewhat more waisted lower molars with a shorter talonid and a more massive and simpler hypoconulid lobe of m3, its upper molars with a stronger centroconule and thicker mesial and distal cingula.

The systematics of suoids is still actively debated as recently demonstrated for example by Orliac *et al.* (2010) or van der Made (1997, 2010, 2023) with much disagreement as to families that are not accepted by different authors and even the content of families or subfamilies that greatly varies in different studies. In addition, the Asian Eocene taxa that have been included in Orliac *et al.* (2010) analyses might have artificially biased the results about their phylogenetic position given their much more fragmentary dental anatomy compared to that of Neogene genera. Furthermore, Orliac *et al.* (2010) stated that the upper dentition provides most of the characteristics for suoids and these features are poorly preserved or fragmentary in Asian Eocene forms.

Liu (2001) tentatively attributed *Eocenchoerus* to the Suidae, and *Siamochoerus* and *Huaxiachoerus* to the Palaeochoeridae, a group of primitive Suoidea that was considered as the stem group of suoids (e.g. Ginsburg 1974; Pickford 1988; Hellmund 1992). Later, Harris & Liu (2007) considered that *Siamochoerus* and *Huaxiachoerus* were primitive suoids and *Eocenchoerus* a primitive suid. van der Made (2010) followed Liu (2001) in referring *Huaxiachoerus* to the Palaeochoeridae, but he moved *Eocenchoerus* to the same family, and he assigned *Siamochoerus* to a primitive suid based on its unfused upper molar roots, a feature that was noticed by Ducrocq *et al.*

(1998). He also suggested that *S. viriosus* had affinities with the Suidae because of its separate roots below the anterior lobe of m2. On the other hand, Orliac *et al.* (2010) considered that the phylogenetic position of all Paleogene Asian suoids was uncertain. There are only few features on our new material that might help to reassess the systematic attribution of *Siamochoerus*. As noted above, Stehlin (1899-1900) and then van der Made (1996a) stressed out the taxonomic importance of upper molar root condition, and van der Made (1996a) pointed out that palaeochoerids were characterized by their upper molars with lingual roots fused together to the contrary of suids where the upper molars had their lingual roots unfused. Unfortunately, except on the fragmentary maxilla TF 2907 where the lingual roots are divergent and maybe not fused, it is not possible to observe that feature on the new material because only the enamel caps of the upper molars are preserved. The mesial position of the anterior accessory cusplet (paraconule or protoconule in van der Made 1996a) on the upper molars of *Siamochoerus* is also a character used by van der Made (1996a) to distinguish Palaeochoeridae (fused to the protocone) and Suidae (fused to the mesial cingulum). Pickford (2018) later used that same feature, but in different terms ("anterior accessory cusplet" between the protocone and the paracone in doliochoerids vs. mesial to the protocone and paracone in *Palaeochoerus typus*). However, the small paraconule in *Siamochoerus* is neither fused to the cingulum or fused to the protocone, which might suggest a primitive suid condition. It is interesting to note that van der Made (2010) observed that the paraconule (protopreconule according to him) is fused to the protocone in both *Eocenchoerus* and *Huaxiachoerus*. Also, the lower jaw BM-06-08-03-5-1 which has the better-preserved posterior part exhibits a rather straight ventral border and does not seem to display an angular process or a marked vascular groove, which is the case in suids contrary to other suoids (like *Perchoerus* and *Egatochoerus*) where this structure is well developed. Finally, the horizontal ramus of *Siamochoerus* is somewhat laterally expanded under the molars, as usually observed in suids. On the other hand, the horizontal rami of *S. banmarkensis* do not show any evidence of fusion at the symphysis level, which is probably a plesiomorphic feature, and the diastemata between the lower incisors, canine and anterior premolars are very reduced which suggests a more primitive condition compared to later forms. Although only the upper molars (no skull or anterior upper dentition) are known for *Siamochoerus*, there is some evidence that suggests that this genus might be referred to the Suidae rather than to the Palaeochoeridae.

Pickford (2018) advocated an origin of Suidae between 25 and 20 Ma (MP 27-28 to MN1-2) in western Europe from Doliochoeridae, the earliest suids known from Indo-Pakistan (Colbert 1933) and China (Liu *et al.* 2002) being not as primitive as *Palaeochoerus typus*. In his argument however, he did not consider Asian Paleogene suoids that might have played a still unclear role in the early history of the group. This matter has been discussed in detail by van der Made (2023). The late Eocene *Siamochoerus* appears to display some features that suggest a systematic position closer to suids. If this is the case, the new material documents a possible origination of Suidae and the divergence of the family with the Tayassuidae at least during the late Eocene and maybe even earlier in Asia.

CONCLUSIONS

Among the five known suoids in the Eocene of Asia, *Egatochoerus jaegeri* from Krabi was the best documented taxon so far with upper and lower permanent and decidual teeth, a fragmentary lower jaw and some foot bones (Ducrocq 1994; Orliac *et al.* 2011). The affinities of *Egatochoerus* with one suoid family or another are still unclear according to Orliac *et al.* (2011). The other suoid from the late Eocene of Bang Mark (Krabi), *Siamochoerus banmarkensis*, is now the second representative of the Eocene Asian Suoidea known by its complete lower dentition and upper molars. Although no skull remains or anterior upper dentition is known for *Siamochoerus* so far that might help to clarify its relationships, the new material described here displays some features that suggest that this genus is closer to the Suidae than to any other suoid family. This also highlights the difficulty to clearly define the different families and to tentatively solve the phylogenetic relationships that are still debated by different authors.

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