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First report of the lower dentition of *Siamotherium pondaungensis* (Cetartiodactyla, Hippopotamoidea) from the late middle Eocene Pondaung Formation, Myanmar

Stéphane Ducrocq, Yaowalak Chaimanee, Aung Naing Soe, Chit Sein, Jean-Jacques Jaeger, and Olivier Chavasseau

Abstract: The anthracothere *Siamotherium pondaungensis* from the late middle Eocene Pondaung Formation in Myanmar was known only from its upper dentition. Recent field work in the Pondaung deposits has led to the discovery of a juvenile fragmentary mandible preserving d3-4, m1-2 and erupting p3-4. The morphology, structure and dimensions of these lower teeth (including simple and bunodont lower premolars with weakly developed talonids, lower molar trigonids and talonids of similar width, entoconid that lacks a postectoentocristid and slightly distal to the hypoconid) confirm their attribution to *S. pondaungensis* which is now documented by its almost complete dentition, and further demonstrate that this species clearly differs from all known dichobunoids, including *Pakkokuhys lahirii*. *Siamotherium pondaungensis* is one of the Pondaung anthracotheres for which most complete cranial and dental material is known, and a phylogenetic analysis supports the basal-most position of *Siamotherium* within the hippopotamoids.

Key words: Myanmar, Pondaung, late middle Eocene, Anthracotheriidae, *Siamotherium pondaungensis*

1. Introduction

The late middle Eocene Pondaung Formation in Myanmar is known for its numerous ungulate and primate fossil remains (COLBERT 1938; JAEGER et al. 1999, 2019; CHAIMANEE et al. 2000, 2012; DUCROCQ et al. 2000, 2016, 2020; TAKAI et al. 2001, 2005; BEARD et al. 2007, 2009; AUNG NAING SOE 2008; AUNG NAING SOE et al. 2017; TSUBAMOTO et al. 2011). Particularly, the primitive anthracothere assemblage is one of the most diversified in the Paleogene of Southeast Asia with five genera and seven species commonly recognized in the Pondaung fauna (LIHOREAU & DUCROCQ 2007; AUNG NAING SOE 2008; TSUBAMOTO et al. 2011). The diversity of this group in Myanmar, as well as in Krabi (Thailand) where the second basal-most anthracothere *S. krabiense* is known, have led to suggest that the group originated in Southeast Asia and differentiated from other ungulates by the beginning of the middle Eocene (PILGRIM 1941; BEARD 1998; DUCROCQ 1999; LIHOREAU & DUCROCQ 2007). The small and primitive anthracothere *Siamotherium pondaungensis* was originally described from a fragmentary maxillary from the Kyadaw kyitchaung locality (DUCROCQ et al. 2000), and later AUNG NAING SOE et al. (2017) attributed an almost complete skull to this species, but no lower teeth could be referred so far to *S. pondaungensis*. This is mainly because small size dental material usually belongs to other small Pondaung anthracotheres (*Anthracokeryx*), bunoselenodont basal ruminants or dichobunoid taxa, and *S. pondaungensis* might not have been abundant in the mammal community. We report here a fragmentary mandible preserving right m1-2 and erupting p3-4 associated with isolated right d3 and d4 that were recently recovered from the Paukkaung kyitchaung 2 locality (Fig. 1) known to have yielded a diversified mammalian assemblage (DUCROCQ et al. 2020). These remains are attributed to *S. pondaungensis* on the basis of their dimensions and peculiar structure, and as such they represent the first lower teeth that can be referred to the smallest anthracothere from Pondaung.

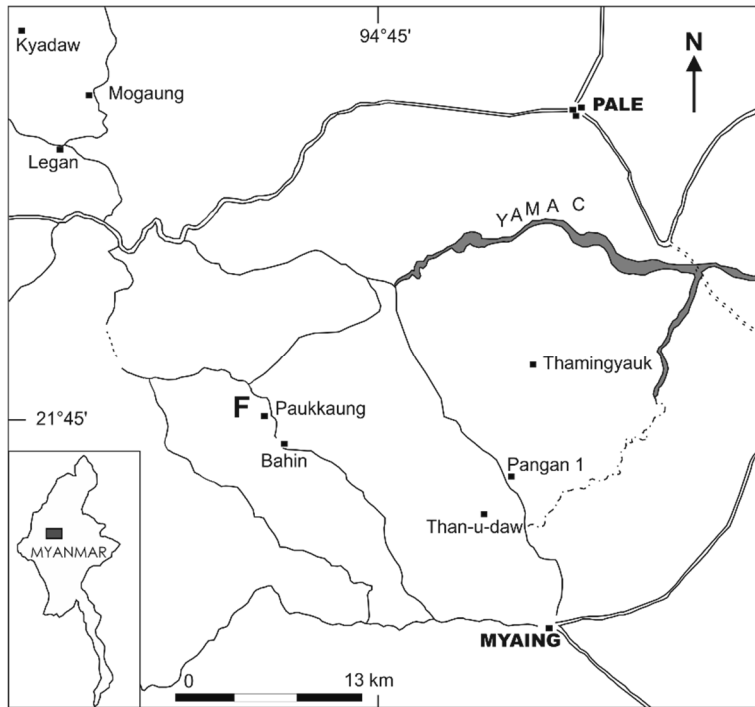


FIGURE 1. Location map of the Pondaung area showing the three localities (Kyadaw, Pangan 1 and Paukkaung 2) where remains of *S. pondaungensis* have been found. 'F' indicates the Paukkaung kyitchaung 2 locality. Most of the taxa from Paukkaung kyitchaung 2 are also known in other Pondaung localities, and no lithological or U-Pb zircon age (KHIN ZAW et al. 2014) difference can be observed between the studied localities (MAUNG MAUNG et al. 2005; BEARD et al. 2007; LICHT 2013).

2. Material and methods

The anthracothere dental terminology used here follows BOISSERIE et al. (2010). c: lower canine, d: lower decidual premolar, p: lower premolar, P: upper premolar, m: lower molar, M: upper molar.

X-ray microtomography: The specimen was scanned using an EasyTom HR-microtomograph with a voxel size of 15.99 μm . Scan parameters: X-ray voltage = 100 kV, current = 100 μA , number of projections = 3936, filter = Tukey, framerate = 4 frame s^{-1} .

Institutional abbreviations: Kdw – Kyawdaw kyitchaung Collections at the Myanmar Ministry of Culture, Nay Pyi Taw, Myanmar. MFP-PK2 – Myanmar French Paleontology, Paukkaung kyitchaung 2 Collections at the Myanmar Ministry of Culture, Nay Pyi Taw, Myanmar.

3. Systematic paleontology

Superorder CETARTIODACTYLA MONTGELARD et al., 1997

Superfamily HIPPOPOTAMOIDEA GRAY, 1821

Family ANTHRACOTHERIIDAE LEIDY, 1869

Genus *SIAMOTHERIUM* SUTEETHORN et al., 1988

Type species: *Siamotherium krabiense* Suteethorn et al., 1988

Type locality: Wai Lek lignite pit, Krabi coal mine (southern Thailand), late Eocene.

Emended diagnosis: Small anthracotheres with short rostrum and complete upper dental formula, bunodont five-cusped molars that show only incipient selenodonty, small to very small styles, no diastema in upper and lower tooth rows except a very short one between P2 and P3, simple upper and lower premolars without accessory cusps, small rounded canines, very strong facial crest, short postglenoid process, and vascular grooves of the supraorbital foramina that end more anteriorly than in Anthracotheriinae and Microbunodontinae. Differs from Anthracotheriinae by their smaller size, smaller canines, upper molars lacking a mesiostyle on the mesial cingulum, with much smaller styles, more slender and simple premolars, lower molars lacking a mesiostylid, and lower m3 with narrow and simple hypoconulid without accessory cuspids. Differs from Microbunodontinae by their shorter skull, shorter and rounded upper canines, less selenodont molars, absence of diastema, more

simple lower premolars with weaker cristids, and absence of constriction on the mandible at the c–p1 level. Differs from Bothriodontinae by their much shorter rostrum, smaller or rounded and not premolariform canines, absence of diastema, much more bunodont upper molars with very weakly developed mesostyles, well-developed paraconule on upper molars (*Arretotherium*, *Telmatodon*, *Afromeryx*, *Hemimeryx*, *Merycopotamus*, and *Libycosaurus*), more simple premolars lacking accessory cusps, and m3 hypoconulid not transversely compressed.

Siamotherium pondaungensis DUCROCQ et al., 2000

(Fig. 2 and 3)

Holotype: Kdw 6, fragmentary maxilla with right M2-M3 from Kyawdaw kyitchaung (Pondaung Fm.).

Referred material: NMMP-PGN-293, subcomplete skull from Pangan-1 kyitchaung (Pondaung Fm.)

New material: MFP-PK2 2018-02-17-1, fragmentary juvenile right mandible with d3, d4, erupting p3-4 and m1-m2 from Paukkaung-2 kyitchaung (Pondaung Fm.).

Emended diagnosis: A species of *Siamotherium* about 20% smaller than *S. krabiense*. Differs from *S. krabiense* in its slightly wider upper molars with weaker lingual cingulum, parastyle, and mesostyle, slightly more rounded P3 and P4 with weaker buccal ribbing and cingulum, P3 shorter than P4, and shorter and more transversely compressed P2. Infraorbital foramen above distal root of P2 (above mesial root of P3 in *S. krabiense*). Further differs from *S. krabiense* by its narrower p3 and p4 with weaker talonid parts and cristids, its lower molars with the trigonid somewhat taller than the talonid and of similar width, the hypoconid slightly more mesially situated than the entoconid that lacks a postectoentocristid, and less expressed

prehypocristid and ectoentocristid. Anterior part of the skull widens significantly at the level of the facial crests.

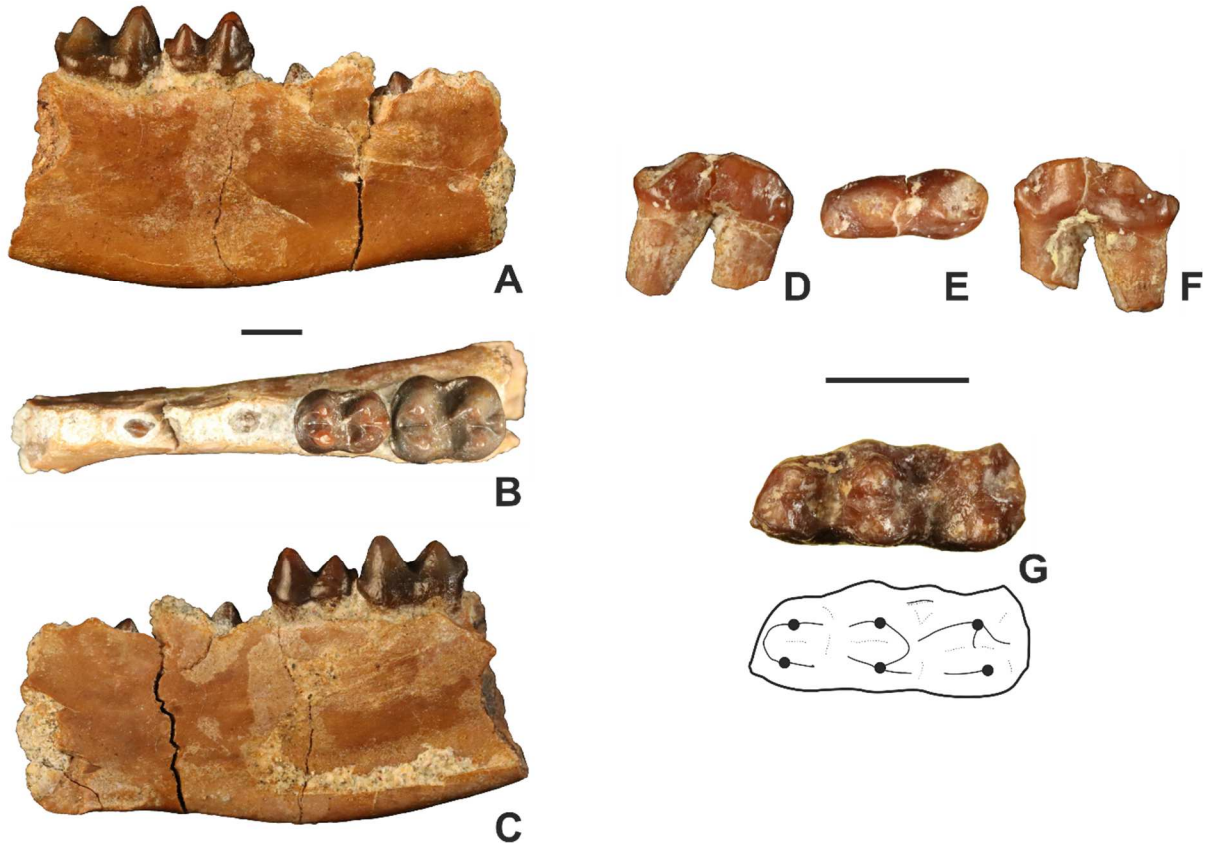


FIGURE 2. A-C – Right mandible (MFP-PK2 2018-02-17-1) of *Siamotherium pondaungensis* in buccal (A), occlusal (B) and lingual (C) views. D-F – right d3 of *Siamotherium pondaungensis* in buccal (D), occlusal (E) and lingual (F) views. G – right d4 of *Siamotherium pondaungensis* in occlusal view. Scale bars equal 5 mm.

Description. The preserved portion of the mandible extends from the distal part of the unfused mandibular symphysis under p2 to the back of the m2. The horizontal ramus is deeper under the lower molars than under the premolars and it is ventrally convex under the molars. Two mental foramina can be observed, one under the alveolus for p2 and the second one under the p3-p4. The specimen is a juvenile because the permanent premolars did not

erupt yet and only the tips of p3-p4 are visible. Although the anterior premolars are lacking, there is no diastema between the preserved alveoli for decidual teeth, and as a consequence the mandible was probably short (Fig. 2A–C).

The d2 is not preserved but it had two roots judging from the two deep alveoli that can be observed in the horizontal ramus mesially to the sockets for the d3 (Fig. 3D–E). There was no diastema between the d2 and the d3. The two-rooted d3 has an elongated and narrow crown with a mesial (protoconid) and a distal cusp (hypoconid) of similar size. A small mesiostylid occurs mesiolingually and a short distostylid occupies the distal rim of the crown that seems to form a short and narrow talonid shelf. The mesiostylid is connected to the protoconid by a very short preprotocristid, unlike in microbunodontines and bothriodontines that display a clearly longer cristid on their d3 (GOMES RODRIGUES et al. 2020). There is no lingual or buccal cingulid (Fig. 2D–F). The d4 is worn but its typically trilobed structure with two cusps on each lobe can be observed. The mesial lobe displays a lingual cusp slightly larger and more mesial than the buccal one. The two posterior lobes are a smaller image of the m1. Three roots are present on the d4, one mesial, one distal and a smaller mediobuccal one under the protoconid distinct from the mesial root (Fig. 2G). The p3 is a simple triangular tooth with one main central cuspid and two mesiodistally oriented cristids: a preprotocristid that mesially connects on a minute enamel spur, and a postprotocristid that ends in a reduced talonid basin. There is no accessory cuspid on these cristids, and a weak and low cingulid occurs distally around the short talonid basin and mesially on each side of the enamel spur (Fig. 3I–K). The p4 is triangular in lateral view, with its widest part in the middle of the crown. It is slightly longer than the p3. The protoconid is central, and two cristids extend from its apex: a preprotocristid that slightly curves mesiolingually and a postprotocristid almost mesiodistally oriented. A small and low mesiostylid occupies the mesial end of the preprotocristid, and a tiny hypoconid is present at the distal end of the postprotocristid. A very

slight endoprotocristid seems to occur on the distolingual part of the protocristid and it ends on the distolingual corner of the crown. The preprotocristid is lingually lined by a very shallow groove that does not reach the base of the crown. A shallow basin occupies the distal part of the premolar and is surrounded by a thin and low cingulid. A mesiobuccal cingulid is present (Fig. 3F–H).

The m1 is markedly smaller than the m2, but the structure of both molars is identical. There is no significant difference in width between the lower molar trigonids and talonids, although the trigonid is somewhat taller than the talonid. The protoconid and the metaconid are in line, and the entoconid is slightly more distally situated than the hypoconid. The preprotocristid and the premetacristid are short, mesiolingually and mesiobuccally oriented respectively and they connect medially low on the mesial face of the crown above the mesial cingulid. A very short and slight ectoentocristid occurs on the mesial face of the entoconid but it does not close the lingual valley. The cristid obliqua (prehypocristid) connects the medial part of the distal wall of the trigonid. A short and low endohypocristid is present in the talonid between the hypoconid and the entoconid. The posthypocristid is short and distolingually oriented then it abruptly curves distally to reaches the median distostylid. Cingulids occur mesially, distally and buccally between the protoconid and the hypoconid at the buccal end of the transverse valley (Fig. 2A–C, 3A–C). There is no contact facet for the m3 on the distal cingulid of m2, which indicates that the m3 very likely erupted after the p4 (GOMES RODRIGUES et al. 2019).

Measurements (in mm): d3: L = 5.5 mm, W = 2.3 mm; d4: L = 8.7 mm, W = 3.5 mm; p3: L = 6.5 mm, W = 2.7 mm; p4: L = 7.1 mm, W = 3.7 mm; m1: L = 7.0 mm, W = 4.7 mm; m2: L = 8.7, W = 6.4

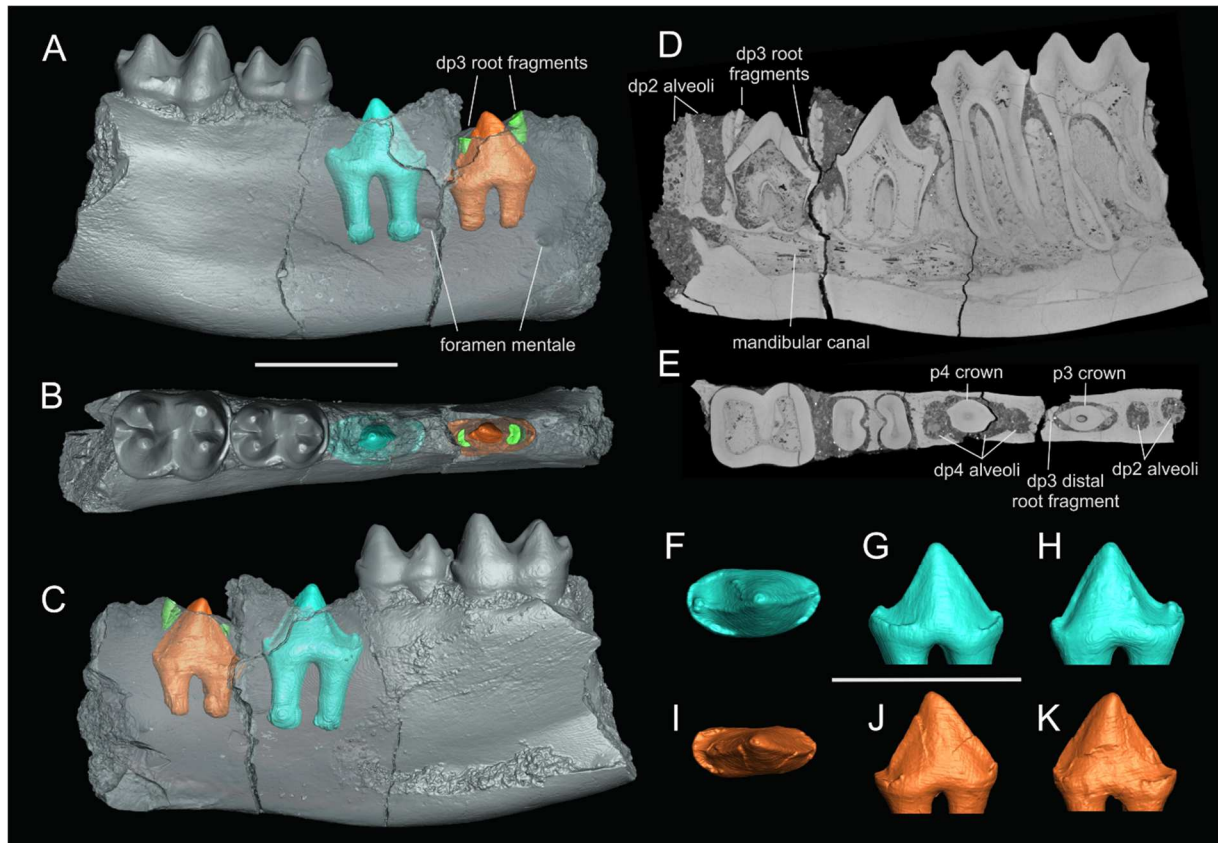


FIGURE 3. A-C – 3D rendering showing manually segmented crowns and/or roots of d3, p3-p4 and m1-m2 crowns of the right mandible (MFP-PK2 2018-02-17-1) of *Siamotherium pondaungensis* in buccal (A), occlusal (B) and lingual (C) views. D – longitudinal virtual section showing roots and p3-p4 crowns. E – horizontal virtual section showing roots of d3 and p3-p4 crowns. F-H – virtually extracted p4 in occlusal (F), buccal (G) and lingual (H) views. I-K – virtually extracted p3 in occlusal (I), buccal (J) and lingual (K) views. Scale bars equal 10 mm. All virtual sections and 3D renderings were produced with Avizo 8.0 (Visualization Sciences Group, <http://www.vsg3d.com/>).

Comparisons. TSUBAMOTO et al. (2002, 2011, 2013) claimed that the holotype of *Siamotherium pondaungensis* (a fragmentary maxilla preserving right M2-3; DUCROCQ et al. 2000) should be synonymized with the helohyid *Pakkokuhyus lahirii*, which is known only

from lower molars. AUNG NAING SOE et al. (2017) then described an almost complete skull attributed to *S. pondaungensis* and they demonstrated that the upper teeth of *S. pondaungensis* cannot be referred to the Helohyidae. In addition, DUCROCQ (2019) recently proved that *Pakkokuhyus* is not a helohyid but a dichobunid, and that helohyids were present only in North America. Although the fragmentary mandible described here displays molars that are roughly similar in size with those of *Pakkokuhyus*, the latter has a deeper mandible, proportionally wider m1-m2 (m1 = 7.1 x 5.1 mm; m2 = 8.6 x 7.2 mm) with the talonid clearly wider than the trigonid. *Pakkokuhyus* further displays m1–2 with mesial cusps closer to each other and thus a narrower trigonid basin, a mesial end of the cristid obliqua slightly more lingually located, a more transverse connection between the preentocristid and the endohypocristid (this connection is V-shaped in *S. pondaungensis*), thicker cristids, a better expressed ectoentocristid, more lingually slanted buccal walls of the protoconid and hypoconid, and stronger and more laterally extended distal cingulids. All of these features that distinguish *Pakkokuhyus* and MFP-PK2 2018-02-17-1 thus demonstrate that the latter is a distinct taxon.

The dichobunoid ungulates from Eurasia (Diacodexidae, Dichobunidae, Homacodontidae and Raoellidae according to THEODOR et al. 2007) display a dental morphology close to that of MFP-PK2 2018-02-17-1, but they all markedly differ from it by several features. Their lower premolars are usually more complex with better expressed cristids and accessory cusps, their lower molars are more bunoselenodont (diacodexids, homacodontids, dichobunid) or more bunodont (raoellids, some dichobunids) with less developed crests (raoellids), more elongated (diacodexids) and have their trigonid narrower than their talonid (diacodexids, homacodontids, dichobunids), often with a paraconid (diacodexids, homacodontids, dichobunids), a reduced metaconid, an ectoentocristid lined with a postectoentofossid on the mesial face of the entoconid and a more distolingually

directed posthypocristid (homacodontids). Asian dichobunids that have an uncertain taxonomic status (according to THEODOR et al. 2007) and for which lower teeth are known include *Haqueina* DEHM & OETTINGEN-SPIELBERG, 1958 from the middle Eocene of Pakistan, *Paraphenacodus* GABUNIA, 1971 from the middle Eocene of Kazakhstan, *Chorlakkia* GINGERICH et al., 1979 and *Pakibune* THEWISSEN et al., 1987 both from the early-middle Eocene of Pakistan, *Wutuhyus* TONG & WANG, 2006 from the early Eocene of China, and a dichobunid indet. described by THEWISSEN et al. (1987). Although they are poorly documented, these taxa are interesting to compare with MFP-PK2 2018-02-17-1 because of their paleogeographical and chronological occurrence. All of them, however, display a peculiar morphology that can be distinguished from that of the Pondaung mandible. They are smaller, their lower premolars are shorter with reduced cingulids (*Chorlakkia*) or enlarged and inflated (*Wutuhyus*), their molar trigonid is narrower (*Haqueina*, *Chorlakkia*, *Pakibune*) or longer than the talonid (*Wutuhyus*), they exhibit a paraconid (*Pakibune*, *Wutuhyus*, dichobunid indet.), a more broadly basined talonid (*Chorlakkia*, *Pakibune*), stronger mesial and buccal cingulids (*Paraphenacodus*, *Pakibune*), a smaller hypoconulid (*Haqueina*, *Chorlakkia*, *Pakibune*) that can be twinned with the entoconid (*Chorlakkia*, *Pakibune*), and a smaller and more distal entoconid (dichobunid indet.). Although they are unknown in Asia, the middle Eocene to early Oligocene North American Leptochoeridae (another family included into the Dichobunoidea according to THEODOR et al. 2007) also differ from MFP-PK2 2018-02-17-1 by their more elongated, massive and complex lower premolars, their lower molars usually bearing a paraconid (except *Leptochoerus*) with an enlarged distostylid (*Ibarus*), a small and crescentic entoconid (*Laredochoerus*), and more complex lower premolars. Similarly, the middle-late Eocene to early Oligocene European Cebochoeridae are smaller (except *Cebochoerus*), with more complex lower premolars, more massive lower

molars sometimes with a paraconid, much more bunodont metaconid, and a weak to absent distostylid (*Gervachoerus*).

The general structure of the premolars (single triangular cusp with weak cristids and no accessory cusps) and molars (absence of a paraconid, protoconid and metaconid in line, short but distinct endohypocristid, transverse valley open lingually, small and median distostylid) of MFP-PK2 2018-02-17-1 is more similar to that of bunodont anthracotheres. Among the small taxa known in the Eocene of southern Asia, *Anthracokeryx tenuis* PILGRIM, 1928 is markedly larger than MFP-PK2 2018-02-17-1, and has more elongated and slender lower premolars with sharper cristids, more selenodont and more elongated lower molars with the talonid slightly wider than the trigonid, weaker buccal cingulid, a distinct endometacristid, more flattened lingual wall of the crowns, and diastema between the lower premolars. The bunodont small *Anthracotherium crassum* PILGRIM & COTTER, 1916 is much larger than MFP-PK2 2018-02-17-1, its lower premolars are more elongated with stronger mesiostylid and talonid part, and its lower molars also exhibit a talonid markedly wider than the trigonid, molar cusps more slanted inwardly, a less developed buccal cingulid, a distinct endometacristid, an inflated cristid obliqua, and a better developed ectoentocristid.

Myaingtherium kenyapotamoides TSUBAMOTO et al., 2011 is also larger than MFP-PK2 2018-02-17-1, its p3 is somewhat more lingually waisted, its p4 is more triangular in occlusal outline with a shorter and wider talonid, its lower molars have a talonid wider than the trigonid and an accessory cusplet on the mesial end of the cristid obliqua, a postectoprotocristid (= distobuccal cristid of the protoconid), and a weaker buccal cingulid.

Siamotherium pondaungensis is the smallest anthracothere known in the Pondaung Formation. Although no lower tooth has been attributed to this species so far, its upper dentition is morphologically very close to that of the slightly younger *S. krabiense* from the

late Eocene of Thailand (AUNG NAING SOE et al. 2017). It is thus interesting to compare the lower teeth of the Thai species and those of MFP-PK2 2018-02-17-1. The lower teeth of *S. krabiense* are similar to those of the Pondaung species, although a few differences can be observed. The Thai species is markedly larger and the p3 and p4 of both species are morphologically close, although the p3 of *S. krabiense* is slightly wider, the p4 has a better developed talonid part, somewhat better expressed postprotocristid and endoprotocristid, a tiny hypoconid distolingually shifted (although the presence of this structure seems to be variable in *S. krabiense*), and a short mesiolingual cingulid. Its lower molars display a prehypocristid slightly more inflated, an ectoentocristid somewhat better expressed, a weak postectoentocristid, and an entoconid and hypoconid more in line. The lower molars of *S. pondaungensis* are also more primitive in having a trigonid somewhat taller than the talonid compared to the corresponding teeth of *S. krabiense* (the ratios lingual height of talonid / lingual height of trigonid are 0.70 for m1 and 0.81 for m2; in the holotype of *S. krabiense*, the corresponding ratios are 0.86 for m1 and 0.98 for m2). The m1 clearly smaller than the m2 in MFP-PK2 2018-02-17-1 reflects the similar difference in size between the M1 and the M2 (AUNG NAING SOE et al. 2017), and the dimensions and structure of the lower molars confirm that they properly occluded with the upper ones. This thus supports an attribution of the Pondaung specimen to *S. pondaungensis*. Furthermore, the absence of a contact facet for m3 on the distal cingulid of m2 also indicates that the m3 very likely erupted after the premolars, a pattern that is commonly observed in anthracotheres, suoids and choeropotamids, but not in most dichobunoids (GOMES RODRIGUES et al. 2019). The general morphology of the d4 is also very similar in both species of *Siamotherium* (DUCROCQ 1999). However, further comparisons between the decidual teeth of both species of *Siamotherium* are more difficult because the scarce known dental material is worn and does not exhibit its detailed morphology. PICKFORD (2018) recently stated that the root morphology on the d4 of

artiodactyls might reflect their phylogenetic relationships. Indeed, he noticed that several anthracotheres belonging to the subfamilies Anthracotheriinae and Bothriodontinae display a three-rooted d4 with a protoconid root well separated from the paraconid root. This configuration is also observed on the d4 of *Siamotherium*. On the other hand, according to PICKFORD (2018) there are only one mesial and one distal roots in the only Diacodexidae that he observed (*Diacodexis morrissi*), and the mediobuccal root is coalescent with the mesial root in the only Dichobunidae (*Dichobune leporina*) included into his study. The root morphology in MFP-PK2 2018-02-17-1 is thus in agreement with the attribution of the Pondaung lower jaw to the anthracotheres rather than to the dichobunoids. However, it is necessary to be careful and to not generalize the type of root morphology on the d4 for every taxon in each family because only very few genera have been observed, and decidual teeth are usually less abundant than permanent teeth in the fossil record and thus unknown for numerous species. Variation in the d4 roots might also occur within each ungulate family (especially the root under the d4 protoconid according to GOMES RODRIGUES et al. 2020), and only a much more thorough investigation would provide reliable phylogenetic information. Similarly, the very short preprotocristid that connects the mesiostylid and the protoconid on the d3 of *S. pondaungensis* might correspond to an anthracotheriine or even a basal anthracothere plesiomorphic feature, because this crest is usually better developed in microbunodontines and bothriodontines (GOMES RODRIGUES et al 2020).

4. Discussion

Although its status was challenged by Tsubamoto et al. (2002, 2011, 2013), *Siamotherium pondaungensis* is the smallest (predicted adult body mass estimate of around 7.5 kg, based on regression of body mass on m1 area, LEGENDRE 1989) and most primitive anthracothere in Pondaung, and it was known only from its upper dentition during two decades. We suspected

that its lower teeth might have been morphologically similar to those of *S. krabiense*, and the material described here confirms this hypothesis. Indeed, the lower premolars and molars of *S. pondaungensis* exhibit a slightly more primitive morphology than that of the younger *S. krabiense* (smaller premolars with narrower talonids, weaker cristids and almost absent mesiolingual cingulid, smaller lower molars with trigonid somewhat taller than the talonid, less expressed cristids, and entoconid and hypoconid less in line). The posterior part of the mandible of *S. pondaungensis* is unfortunately unknown, and it is not possible to infer if the attachment areas for the masseter muscles were developed on the coronoid apophysis, as it is expected from the peculiar skull morphology (AUNG NAING SOE et al. 2017), but the robustness and shortness of the mandible suggest that it might have been the case.

Siamotherium pondaungensis cannot be synonymized with the dichobunid *Pakkokuhyus lahirii* from the Pondaung Fm. and it definitely does not belong to or is related to the Helohyidae, a family that might very likely have occurred only in North America (DUCROCQ 2019). This further challenges the hypothesis that the Helohyidae were the sister-group of anthracotheres (COOMBS & COOMBS 1977), and it supports an origin of anthracotheres within a distinct group of cetartiodactyls which is still unknown.

Two maximum parsimony analyses were performed using a matrix including 57 fossil taxa and 164 morphological dentognathic characters based on the character-taxon matrix of AUNG NAING SOE et al. (2017). Compared with the original taxonomic sample, we have discarded the anthracotheriid *Bothriogenys andrewsi* because of its poorly known dentition and we added the better documented anthracotheriid *Anthracokeryx birmanicus*. In order to further evaluate the phylogenetic relationships of *Siamotherium pondaungensis*, the two rare dichobunids from the Eocene of Southeast Asia, *Pakkokuhyus lahirii* HOLROYD & CIOCHON, 1995 and *Progenitohyus thailandicus* DUCROCQ et al., 1997 were added to the matrix. The

coding of *Siamotherium pondaungensis* was completed according to the newly available mandible and lower teeth characters. About 72% of the features are now documented for this rare species (118 out of 164 characters). The coding of the anthracotheres *Siamotherium krabiense*, *Geniokeryx thailandicus* (formerly *Anthracokeryx thailandicus*; renamed following DUCROCQ 2020) and *Anthracokeryx tenuis* has been slightly revised compared with that of AUNG NAING SOE et al. (2017).

The 57 taxa of the data matrix comprise 31 hippopotamoids (27 anthracotheriids and 4 hippopotamids), 24 species sampling the main families of non-ruminant cetartiodactyls represented in the Paleogene fossil record (exclusive of cetaceans), and two basal ruminants (a lophiomericyd and an archaeomerycid). *Homacodon vagans* (Homacodontidae), *Bunophorus grangeri* and *Gujaratia pakistanensis* (Diacodexidae) were selected as outgroups for this analysis. We noticed topological instability in the trees recovered from our first tests, mostly concerning a clade comprising non-ruminant cetartiodactyls endemic to Europe. For this reason, we have used a small backbone tree based on the results of LIHOREAU et al. (2015), who performed a phylogenetic analysis of cetartiodactyls with an earlier version of the present data matrix. The constraint tree is: ((*Khirtaria*, *Indohyus*), (*Mixtotherium*, (*Perchoerus*, (*Anthracotherium magnum*, *Hexaprotodon*))))). The most parsimonious trees compatible with this constraint were obtained using PAUP 4.0b10 (SWOFFORD, 2003) after performing a heuristic search with 1000 replications of random addition of the taxa. All characters were considered as unordered and unweighted.

In the first analysis, we have decided to test the phylogenetic position of *Siamotherium pondaungensis* without the rare and poorly known *Pakkokuhyus* and *Progenitohyus*. 43 most parsimonious trees of 1002 steps have been found. Similarly to the phylogenetic analysis of LIHOREAU et al. (2015), the retrieved topologies (Fig. 4A) are highly homoplastic (Consistency Index = 0.22) but retain a good amount of synapomorphies (Retention Index =

0.61). The Hippopotamoidea (= Anthracotheriidae + Hippopotamidae) are retrieved as a monophyletic group supported by 5 non-ambiguous synapomorphies: 51(1) (absent preentocristid on lower molars), 64(1) (shallow and constant cingulid in front of the transverse valley on lower molars), 67(2) (ectohypocristulid joining the summit of hypoconulid on m3), 111(1) (distostyle at the level of the metacone on upper molars), and 134(0) (M3/ larger than M2/). Five additional characters support this clade under the ACCTRAN character state optimization: 61(1) (endohypocristid present on lower molars), 102(0) (mesiodistal ribs of the labial cusps of upper molars forming almost half of the molar length), 106(1) (premetacristule divided in two mesial arms on upper molars), 108(0) (postmetafossule absent), 143(0) (no p1-p2 diastema). The hippopotamoids are supported by one additional character under the DELTRAN character state optimization: 85(1) (P3 root pattern with one mesial root and two unfused distal roots). The genus *Choeropotamus* (Choeropotamidae) is the sister-group to all hippopotamoids. This result is consistent with those obtained by LIHOREAU et al. (2015, 2019), AUNG NAING SOE et al. (2017), BOISSERIE et al. (2017) and GOMES RODRIGUES et al. (2019).

The phylogenetic position obtained for *Siamotherium pondaungensis* is identical to that found by AUNG NAING SOE et al. (2017) and confirms this species as the sister-group of *S. krabiense* and a representative of the basal-most clade of hippopotamoids. This clade is not robust (Bremer index of 1) contrary to the results of AUNG NAING SOE et al. (2017) but supported by 5 unambiguous characters: 88(0) (postprotocrista absent on P4), 92(0) (P4 protocone rounded), 101(1) (height of lingual cingulum reaching half of the protocone height on upper molar), 122(0) (parastyle as an enamel knob), 127(0) (mesostyle as an enamel knob). In ACCTRAN optimization, two additional characters support the *Siamotherium* clade: 62(1) (posthypofossid present on lower molars) and 137(0) (no diastema between c and p1). In DELTRAN optimization, an additional character supports this clade: 86(0) (P4 paracone

simple with crest). While PAUP treats all the unambiguous character changes supporting the *Siamotherium* clade as reversals, one could also interpret the shared features between *S. krabiense* and *S. pondaungensis* as symplesiomorphies.

Within hippopotamoids, the Anthracotheriinae (*Anthracotherium*, *Heptacodon*, *Myaingtherium*) and the Microbunodontinae (*Microbunodon*, *Anthracokeryx*, *Geniokeryx*) are found successively crownward to *Siamotherium* in the 50% majority-rule consensus tree. These two subfamilies of anthracotheres are monophyletic, unlike in previous maximum parsimony analyses (for example LIHOREAU et al. 2015, 2019; AUNG NAING SOE et al. 2017; BOISSERIE et al. 2017) in which the Microbunodontinae were paraphyletic. This change can be likely explained by the inclusion of an additional microbunodontine in the taxon sample (*Anthracokeryx birmanicus*). A Bothriodontinae + Hippopotamidae group is the most crownward clade within Hippopotamoidea. This clade is also one of the most robust of the tree with a Bremer index of 4.

The second analysis was carried out with the 57 taxa of the data matrix. 37 trees of 1009 steps were found. The retrieved topologies are less resolved, and the nodes possess overall lower Bremer index values than in the first analysis. However, the topology of the 50% majority-rule consensus tree (Fig. 4B) is close to that of the first analysis, most of the unresolved nodes in the strict consensus tree having high frequencies among the most parsimonious trees (84-95%). In the 50% majority-rule consensus tree, the dichobunid *Pakkokuhyus* forms a clade with *Gobiohyus* and the choeropotamids *Hallebune* and *Amphirhagatherium*. Unlike in our first analysis, *Choeropotamus* is not the sister-group to all hippopotamoids and is positioned rootward of a *Cebochoerus* + *Suoidea* clade. Although the position of *Choeropotamus* varies between our two analyses, we note that the choeropotamids are constantly polyphyletic. A similar result was obtained in a recent study focusing on the phylogenetic relationships of basal cetartiodactyls from Europe (LUCCISANO et al. 2020).

Progenitohyus is positioned crownward of raellids and rootward of a clade comprising all hippopotamoids, suoids and *Pakkokuhyus*. Thus, our analysis does not support the hypothesis of close phylogenetic relationships between *Progenitohyus* and *Pakkokuhyus*. Furthermore, these two genera are also phylogenetically distant from the hippopotamoids. Hence, this result supports the morphological analyses indicating that, contrary to *Siamotherium*, *Progenitohyus* and *Pakkokuhyus* are non-hippopotamoid cetartiodactyls.

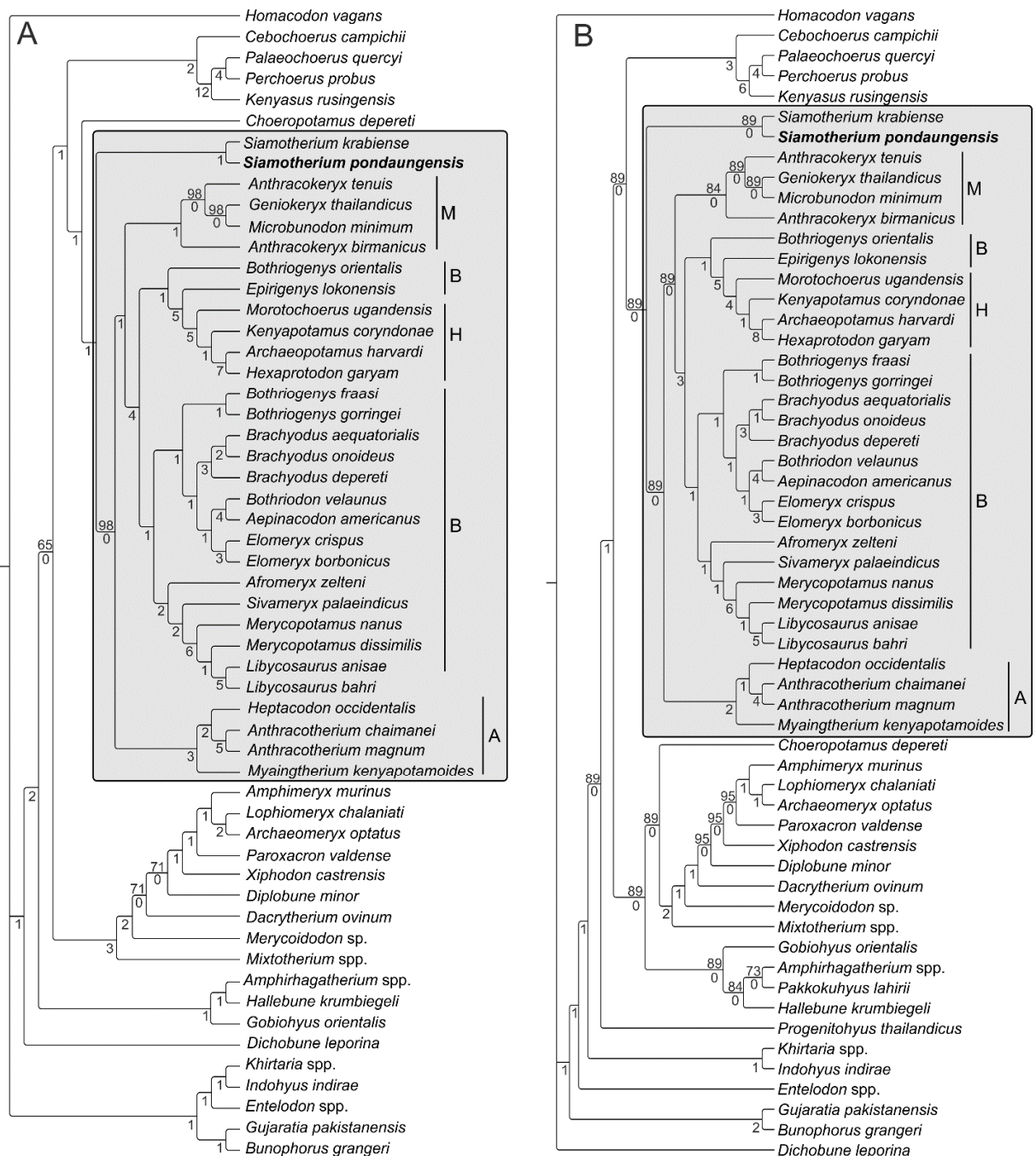


FIGURE 4. A – 50% majority-rule consensus tree of the 43 most parsimonious trees (1002 steps, CI = 0.219, RI = 0.609) obtained in the first analysis (55 taxa). **B** – 50% majority-rule consensus tree of the 37 most parsimonious trees (1009 steps, CI = 0.217, RI = 0.608) obtained in the second analysis (57 taxa). Values below the branches are Bremer support indices. Values above the branches are the frequencies among the most parsimonious trees of the resolved clades in the majority-rule consensus tree (frequencies of resolved clades with unspecified values = 100%) Abbreviations: A, Anthracotheriinae; B, Bothriodontinae; H, Hippopotamidae; M, Microbunodontinae.

5. Conclusions

Even after a century, the late middle Eocene deposits of the Pondaung Formation regularly yield new fossil material that can either be attributed to new taxa or that improves the knowledge of poorly known species. Among them, *Siamotherium pondaungensis* is a much less common taxon in Pondaung than other anthracotheres and it has long been known only by fragmentary dental remains for which the taxonomic affinities have been debated. This small anthracothere is now documented by its almost complete dentition that confirms its attribution to the family, its close relationships with *S. krabiense* from the late Eocene of Thailand and its basal phylogenetic position within hippopotamoids. The lower dentition of *S. pondaungensis* being more primitive than that of *S. krabiense* in several aspects reinforces the Pondaung species as the most plesiomorphic anthracothere known so far. *Siamotherium pondaungensis* further represents, together with *Anthracokeryx tenuis*, one of the best known taxon in the rich Pondaung anthracothere assemblage, and as such is a crucial species to investigate the origins and early differentiation of Hippopotamoidea in southern Asia.

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