

# First discovery of Helohyidae (Artiodactyla, Mammalia) in the Late Eocene of Thailand: a possible transitional form for Anthracotheriidae

## *Première découverte d'un artiodactyle helohyidé (Mammalia) dans l'Éocène supérieur de Thaïlande : une forme de transition possible pour les anthracothères*

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### ABSTRACT

Dental remains of the earliest known helohyid artiodactyl are described from the Late Eocene of Krabi in South Thailand. This new form, *Progenitohyus thailandicus* n.g. n.sp., is distinct from *Gobiohyus*, a specialized genus from the Middle Eocene of Mongolia, and it displays strong affinities with the primitive anthracotheriid *Siamotherium krabiense* from Krabi. Both Thai species certainly testify to an ancestor–descendant relationship, but an even earlier differentiation of Helohyidae and Anthracotheriidae should be searched for in the Middle Eocene or even earlier.

**Keywords:** Late Eocene, South Asia, Thailand, Burma, Anthracotheriidae, Helohyidae, Artiodactyls

### RÉSUMÉ

Le bassin Éocène supérieur de Krabi (Thaïlande péninsulaire) a livré les premiers restes fossiles attribués à un artiodactyle helohyidé. La nouvelle forme décrite, *Progenitohyus thailandicus* n.g. n.sp., se distingue de *Gobiohyus*, un genre déjà spécialisé de l'Éocène moyen de Mongolie, et montre des affinités marquées avec le petit anthracothère primitif de Krabi *Siamotherium krabiense*. Les deux espèces de Thaïlande témoignent certainement de relations d'ancêtre à descendant. Cependant, une différenciation encore plus ancienne des Helohyidae et des Anthracotheriidae devrait être recherchée dans les terrains d'âge Éocène moyen ou encore plus anciens.

**Mots clés :** Éocène supérieur, Asie du Sud, Thaïlande, Birmanie, Anthracotheriidae, Helohyidae, Artiodactyles

### VERSION ABRÉGÉE

#### Introduction

Le bassin de Krabi, dans le sud de la Thaïlande (figure 1), a livré une des faunes de mammifères les plus riches et les plus diversifiées d'Asie du Sud. Une trentaine d'espèces distinctes

de mammifères et six genres de reptiles (Ducrocq 1994a ; Ducrocq et al., 1992a, 1992b, 1993, 1995a, 1995b, 1996 ; Chaimanee et al., 1997) ont été reconnus dans trois mines de lignites contemporaines. L'ensemble de ces formes, très impor-

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tantes d'un point de vue phylogénétique et paléobiogéographique, se caractérise par l'abondance des artiodactyles représentés par sept familles distinctes. Parmi celles-ci, un nouvel Helohyidae, *Progenitohyus thailandicus* n.g. n.sp., est décrit ici (figure 2) et semble témoigner de relations phylogéniques directes entre les Helohyidae et les Anthracotheriidae, suivant en cela l'hypothèse proposée par Coombs et Coombs (1977).

## Discussion

Bien qu'elle soit morphologiquement proche des petits anthracothères primitifs (Suteethorn et al., 1988), cette nouvelle forme s'en distingue, de même que des Raoellidae (Sahni et al., 1981) et des autres Helohyidae connus (*Gobiohyus* en Mongolie, *Heloyus* en Amérique du Nord et *Pakkokubyus* en Birmanie, voir Holroyd et Ciochon, 1995, Pilgrim, 1928) principalement par ses dimensions, sa bunodontie, la position de son paraconide et l'extension de son hypoconulide sur la M<sub>3</sub> (figure 3). Cependant, la structure de ses molaires inférieures semble traduire, pour *Progenitohyus*, des affinités avec les anthracothères primitifs et les helohyidés, en particulier le genre *Pakkokubyus* de Pondaung, qui apparaît comme étant une forme bien moins spécialisée que les espèces de Mongolie et d'Amérique du Nord. Coombs et Coombs (1977) avaient admis des relations de groupes-frères entre Anthracotheriidae et Helohyidae. Ducrocq (1994b) a discuté cette hypothèse, en insistant sur le fait que les Helohyidae alors connus (*Gobiohyus* et *Heloyus*) possédaient une morphologie dentaire trop spécialisée pour pouvoir représenter le groupe souche des Anthracotheriidae. Cependant, le nouvel helohyidé décrit par Holroyd et Ciochon (1995) et la découverte de *Progenitohyus* en Thaïlande ne vont pas à l'encontre de l'hypothèse proposée

## Introduction

The Late Eocene mammalian fauna from Krabi (figure 1) in southern Thailand is one of the richest and most diversified mammal communities of Southeast Asia. About 30 different species of mammals have so far been recovered, together with six genera of reptiles (Ducrocq et al., 1992a, 1995a; Chaimanee et al., 1997) in three distinct but contemporaneous pits (Bang Ban Mark, Wai Lek and Bang Pu Dam). The peculiar aspect of the Tertiary mammals from Krabi has allowed the description of several new taxa, whose importance at a phylogenetic and paleobiogeographic level can be considered as a reference for paleomammalogy (Ducrocq, 1994; Ducrocq et al., 1992b, 1993, 1995b, 1996). Most of the taxa represent new forms that can nevertheless be related to known Late Eocene and/or Early Oligocene forms from Europe, Asia, or even North America. One of the most diversified mammal groups in Krabi is represented by artiodactyls, with at least seven distinct families (Tayassuidae, Suidae, Entelodontidae, Anthracotheriidae, Lophiomerycidae, and possibly Tragulidae) and 11 genera (Ducrocq et al., 1995a, 1996). We report here the occurrence of an additional artiodactyl family in the Late Eocene of Thailand, represented by a

par Coombs et Coombs (1977), mais suggèrent plutôt qu'un groupe moins spécialisé d'helohyidés aurait pu conduire aux anthracothères. Les Dichobunidae (artiodactyles hypoconifères) peuvent être exclus de l'ascendance des Anthracotheriidae, principalement à cause de la présence, sur leurs molaires supérieures, d'un hypocône (le tubercule correspondant chez les Anthracotheriidae étant un métaconule). Si l'on considère *Progenitohyus* comme un ancêtre potentiel de *Siamotherium krabiense*, alors le scénario de Coombs et Coombs (1977) peut toujours être retenu, puisque les Helohyidae pourraient être issus des Dichobunoidea *sensu lato*, un groupe qui rassemble les Dichobunidae et les Helohyidae. Ainsi, certaines formes asiatiques (*Pakkokubyus*, *Progenitohyus*) auraient pu développer une morphologie dentaire de type anthracothère, alors que d'autres (*Gobiohyus*) auraient conduit à des formes plus spécialisées.

## Conclusion

Des relations phylogéniques directes entre *Pakkokubyus* de l'Éocène moyen de Birmanie et *Progenitohyus* de l'Éocène supérieur de Krabi sont peu probables, étant donné les différences structurelles et morphologiques qui caractérisent les dentures des deux espèces. Quoi qu'il en soit, bien qu'une divergence Helohyidae-Anthracotheriidae ait pu se produire au cours de l'Éocène moyen, peut-être en Asie du Sud, étant donné la présence d'Anthracotheriidae dans l'Éocène moyen de Birmanie (Colbert, 1938; Holroyd et Ciochon, 1991), *Progenitohyus* pourrait être considéré comme un proche parent de *Siamotherium*. Il représenterait alors une forme de transition entre les deux familles qui aurait persisté pendant l'Éocène supérieur en Asie du Sud-Est.

new genus and species of the family Helohyidae. This group is so far restricted to the three Middle Eocene genera *Helohyus* Marsh, 1872 from North America, *Gobiohyus* Matthew and Granger, 1925 from Mongolia and *Pakkokubyus* (Pilgrim, 1928) from Burma. The new form reported here represents the most southerly occurrence of helohyids, and it clearly shows morphological similarities to the primitive anthracotheres known in Thailand. It also suggests possible direct phylogenetic relationships between Helohyidae and Anthracotheriidae, in accord with the hypothesis previously proposed by Coombs and Coombs (1977).

## Systematic paleontology

*Progenitohyus* n.g. (figure 2)

*Type-species: Progenitohyus thailandicus* n.sp.

*Diagnosis:* That of the type-species.

*Horizon and locality:* Main lignite seam, Bang Pu Dam pit, Krabi Basin, South Thailand (figure 1). The mammalian fauna associated with helohyid remains is identical in Bang Pu Dam, Wai Lek and Bang Ban Mark pits, and faunal evidence indicates a Late Eocene age (Ducrocq et al., 1995a).

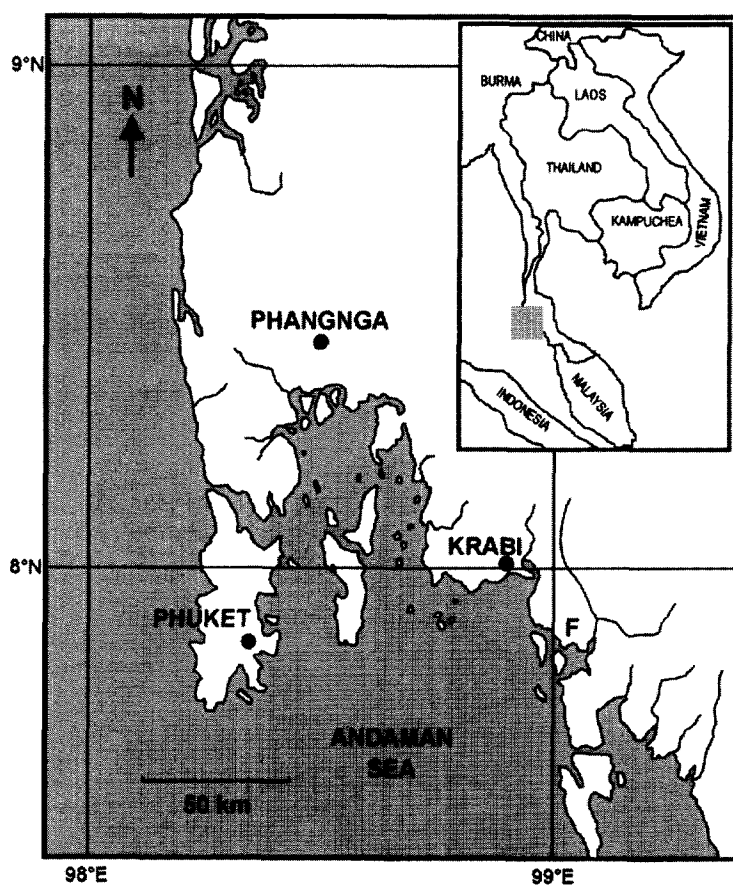


Figure 1. Location map of Krabi basin showing the fossil site. The mine that yielded the specimen of *Progenitohyus thailandicus* reported here, is represented by the letter F.

Carte de localisation du bassin de Krabi. La mine de lignite ayant livré *Progenitohyus thailandicus* est représentée par la lettre F.

*Progenitohyus thailandicus* n.sp. (figure 2)

**Holotype:** Fragmentary left lower jaw preserving  $M_1$ – $M_3$ , TF 2668, DMR, Bangkok (figure 2).

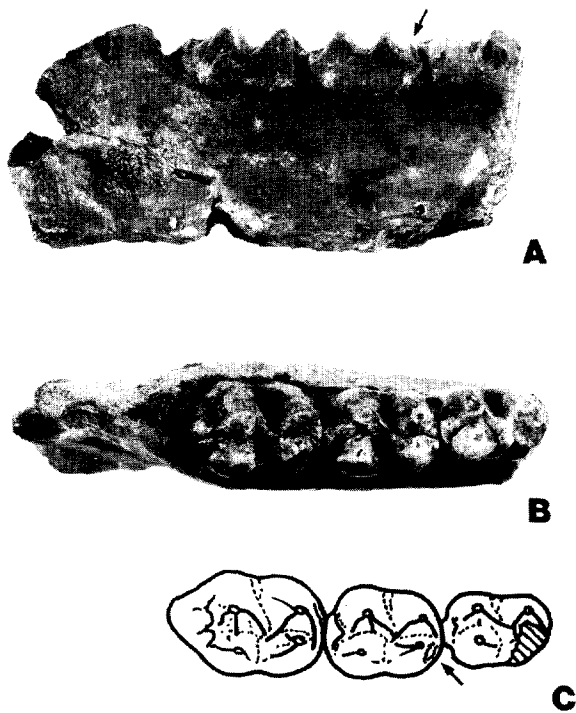
**Derivatio-nominis:** Refers to "Progenitor", Latin word for direct ancestor, and "hyus", Greek name for pig. Species name refers to the country of discovery.

**Diagnosis:** Medium-sized artiodactyl with lower molars characterized by a regular increase in size from front to back, a vestigial paraconid at least on  $M_2$ , a weak and straight hypolophid, a reduced hypoconulid lobe on  $M_3$ , and by the absence of labial cingulid. The horizontal ramus of the mandible is shallow and wide. Differs from the primitive anthracotheriid *Siamotherium* in its smaller size, its  $M_3$  with a reduced hypoconulid, its straighter hypolophid, and in having a vestigial paraconid on  $M_2$ . Differs from the Burmese *Pakkokuhyus* in being larger, in having a small paraconid on  $M_2$  and a more reduced hypoconulid on  $M_3$ , and in lacking a labial cingulid. Differs from *Gobiohyus* and *Helohyus* in lacking a labial cingulid and in having a reduced paraconid, in its larger hypoconulid on  $M_{1-3}$  (*Gobiohyus*) and in its less bunodont lower molars with reduced  $M_3$  hypoconulid (*Helohyus*).

## Description

The molars are basically quadritubercular (figure 2) and increase in size from front to back. The cusps are bunodont and of medium height. The bases of the crowns are

inflated, especially on  $M_3$ , and the labial face of the teeth gently slopes medially. The protoconid and metaconid are slightly higher than the talonid cusps on  $M_1$ – $M_2$ , and are situated close together. The protoconid is slightly more mesially situated than the metaconid on  $M_3$ . A weak crest runs down from the apex of the protoconid and extends along the anterior face of the trigonid toward the mesial face of the metaconid. This crest stops in front of the metaconid and seems to join the mesial cingulid on  $M_3$ , but it connects with a very small enamel knob on the mesial face of the metaconid on  $M_2$ . This knob is separated from the mesial face of the metaconid by a furrow, and may be homologous to a vestigial paraconid. This structure is absent on  $M_3$ , and it is not possible to know if it occurred on  $M_1$ , the mesiolingual part of the latter being broken away. A weak and low crest joins the two trigonid cusps. The talonids of  $M_1$ – $M_2$  are somewhat wider than the trigonids. The entoconid is slightly more mesial than the hypoconid on  $M_2$ – $M_3$ , and on all molars the two cusps are connected by a small hypolophid. The low cristid obliqua is mesiolingually directed and meets the posterior trigonid wall at the midline of the tooth. The hypoconulid is connected to the hypoconid by a weak crest on all molars. The hypoconulid is comparatively smaller on  $M_2$  than on  $M_1$ , but this cusp is very reduced on  $M_3$  where it is much smaller than the trigonid and talonid cusps. No labial cingulum occurs on the lower molars, but the anterior one is weakly developed.



**Figure 2.** *Progenitohyus thailandicus* n.g. n.sp. Holotype, TF 2668 (Collections of the Department of Mineral Resources, Bangkok); left lower jaw with  $M_1$ – $M_3$ ; Ban Pu Dam, southern Thailand; Late Eocene. A. Lingual view. B. Occlusal view. C. Interpretative drawing of TF 2668. Scale bar = 10 mm. Arrow indicates the vestigial paraconid on the mesial face of the metaconid.

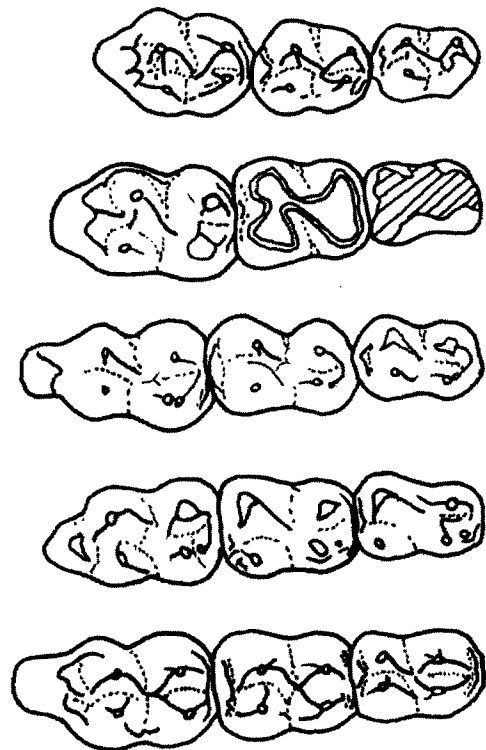
*Progenitohyus thailandicus* n.g. n.sp. Holotype, TF 2668 (collections du DMR, Bangkok) ; mandibule gauche préservant  $M_1$ – $M_3$  ; Ban Pu Dam, Thaïlande du Sud ; Éocène supérieur. A. Vue linguale. B. Vue occlusale. C. Dessin interprétatif du spécimen. Échelle = 10 mm. La flèche indique le paraconide vestigial sur la face mésiale du métaconide.

The mandible is robust, shallow, and rather wide under  $M_2$ – $M_3$ . However, a radiograph examination of TF 2668 revealed that the  $M_1$ – $M_3$  described here correspond to permanent teeth. The posterior part of the lower jaw is broken, but the angular process projects slightly ventrally, and there is no retromolar space behind  $M_3$  (figure 2A). Measurements (in mm):  $M_1$ : length = 10.5, width = 6.8;  $M_2$ : length = 11.2, width = 7.5;  $M_3$ : length = 13.6, width = 8.5. Height of horizontal ramus under  $M_3$  = 22.5.

## Comparisons

The Thai species combines a set of original characters that makes it unique among all described forms of helohyids. Although it displays an overall morphological similarity to the small anthracotheriid *Siamotherium krabiense*, Suteethorn et al., 1988, *Progenitohyus* can be distinguished from it by its smaller size, its shallower horizontal ramus, its shorter lower molars with closely appressed metaconid and protoconid, its  $M_2$  with a vestigial paraconid, its  $M_3$  with very reduced hypoconulid and more medially

slanted labial wall, and by its distinct and straight hypolophid (figure 3). Also, the Thai specimen cannot be attributed to the Dichobunidae mainly because of its pyramidal entoconid, its well-developed transverse cristid between the entoconid and the hypoconid, and its curved posthypocristid. However, the association of several dental features in *Progenitohyus* suggests that it might be included in the family Helohyidae. These features are the occurrence of a vestigial paraconid on  $M_2$  (probably more developed on  $M_1$ , but lost on  $M_3$ ), closely appressed trigonid cusps, the absence of a mesiolabially directed premetacristid, the short and straight hypolophid, the very reduced hypoconulid on  $M_3$ , a slight basal inflation of lower molars, and the apparently shallow horizontal ramus.



**Figure 3.** Interpretative drawings of the lower molars of several artiodactyls. From top to bottom: left  $M_1$ – $M_3$  of *Progenitohyus thailandicus* (TF 2668), right  $M_1$ – $M_3$  of *Pakkokuhyus lahirii* (GSI B-766, reversed), right  $M_1$ – $M_3$  of *Gobiohyus orientalis* (AM 20250, reversed), left  $M_1$ – $M_3$  of *Helohyus plicodon* (AMNH 12148), and left  $M_1$ – $M_3$  of *Siamotherium krabiense* (TF 2333.2). All specimens at same scale.

Dessins interprétatifs des molaires inférieures de plusieurs artiodactyles. De haut en bas :  $M_1$ – $M_3$  gauches de *P. thailandicus* (TF 2668),  $M_1$ – $M_3$  droites de *Pakkokuhyus lahirii* (GSI B-766, inversé),  $M_1$ – $M_3$  gauches de *Helohyus plicodon* (AMNH 12148) et  $M_1$ – $M_3$  gauches de *Siamotherium krabiense* (TF 2333.2). Tous les spécimens sont à la même échelle.

A helohyid artiodactyl has been recently described from the Pondaung fauna in Burma by Holroyd and Ciochon (1995) who recognized *Anthracokeryx? lahirii* (previously described as an anthracotheriid) as a new genus of the family Helohyidae, *Pakkokuhyus lahirii* (Pilgrim, 1928). This species mainly differs from *Progenitohyus* by its

smaller size, in lacking a paraconid, its lower molars with a labial cingulid, with lingual cusps distal to the buccal ones, and in its more developed  $M_3$  hypoconulid. *Progenitohyus* differs from the helohyid genus *Gobiohyus* from the Mongolian Middle Eocene in lacking a paraconid on  $M_3$  and a labial cingulid on lower molars, in having a very reduced  $M_2$  paraconid, a straighter paracristid, a somewhat larger  $M_{1-2}$  hypoconulid, a larger  $M_3$  hypoconulid, and a weaker mesial cingulid. The Thai species differs from *Helohyus* from the early Middle Eocene (Bridgerian) of North America in being less bunodont, in having a much reduced  $M_2$  paraconid,  $M_3$  lacking a paraconid and with a more reduced hypoconulid, and in lacking labial cingulid.

Although they display some resemblance with *Progenitohyus*, genera included in the Raoellidae (*Indohyus*, *Khirtharia*, *Bunodentus*, *Metkatus*, and possibly *Haqueina*), an Asian artiodactyl family created by Sahni *et al.* (1981), can be distinguished from the Thai species by their lower molars lacking a paraconid and a hypoconulid, especially on  $M_1$ – $M_2$ . Also, *Progenitohyus* differs from the possible raoellid *Haqueina* in its larger size, its more robust  $M_3$  with a weaker hypoconulid, and in lacking a postcristid. Asian diacodexids appear to be distinct from *Progenitohyus* mainly in being smaller, in lacking a hypolophid on lower molars, and in having a labial cingulid and a stronger hypoconulid on  $M_3$ . European Haplobunodontidae mainly differ from *Progenitohyus* in their more selonodont labial cusps, their more developed  $M_3$  hypoconulid, and in the presence of a premetacristid on lower molars.

## Discussion

*Progenitohyus* cannot clearly be referred to the family Anthracotheriidae because it displays evidence of a paraconid in its lower molars, an unknown condition in anthracotheres. It must be stressed that one of the characters listed by Holroyd and Ciochon (1995, p. 181) to distinguish bunodont Asian anthracotheriids from *Pakkokuhyus* (common occurrence of a double hypoconulid on  $M_3$ ) cannot be used as a diagnostic feature. Indeed, the common double hypoconulid on  $M_3$  is unknown in primitive Anthracotheriidae, such as *Siamotherium* or *Anthracokeryx* (Colbert, 1938; Suteethorn *et al.*, 1988), and rather begins to appear in larger species like *Anthracotherium*.

However, *Progenitohyus* shows affinities with the Helohyidae, in being otherwise also morphologically similar to primitive anthracotheres. It might therefore be seen as a transitional form that would link Asian helohyids and anthracotheriids. Indeed, Coombs and Coombs (1977) supported the hypothesis that Helohyidae were the sister-group of Anthracotheriidae on the basis of several shared derived features (squared upper molars, small or absent hypocone, hypertrophied metaconule shifted posterolingually, regular size increase from  $M_1$  through  $M_3$ , and enlarged  $M_3$  hypoconulid). Ducrocq (1994b) questioned this hypothesis because new primitive anthracotheriid

species had since been described (*Siamotherium krabiense* from Thailand), and because several dental characters shared by helohyids and anthracotheriids were considered convergent. In addition, the two genera then attributed to the Helohyidae (*Helohyus* and *Gobiohyus*) were too specialized to be regarded as close relatives of Anthracotheriidae. However, the description of *Pakkokuhyus* by Holroyd and Ciochon (1995) and the discovery of *Progenitohyus* no longer challenge the hypothesis proposed by Coombs and Coombs (1977), but rather suggest that less specialized representatives of the family Helohyidae might have led to anthracotheres. *Progenitohyus* can not at present be positioned close to any known species of Helohyidae, and therefore needs to be referred to a new genus. Helohyidae now appear to have included genera characterized by a specialized dental morphology (*Helohyus* and *Gobiohyus*) together with forms that display a more primitive condition (*Pakkokuhyus* and *Progenitohyus*). As stressed by Ducrocq (1994b), the Dichobunidae (artiodactyls with hypocones on upper molars) can be excluded from the stem-group of Anthracotheriidae, mainly on the basis of a distinct hypocone on their upper molars (the corresponding cusp being an enlarged metaconule in Anthracotheriidae). Also, the Raoellidae have evolved in an independent way from Anthracotheriidae, since they are characterized by bilophodont upper molars. If *Progenitohyus* really belongs to the Helohyidae, and can be considered a suitable ancestor for *Siamotherium krabiense*, then the hypothesis proposed by Coombs and Coombs (1977), according to which Helohyidae and Anthracotheriidae are sister-groups, can be retained. This line of evidence does not contradict the arguments of Ducrocq (1994b) because the Helohyidae might have issued from the Dichobunoidea *sensu lato*, a group that included Dichobunidae and Helohyidae. Also, some Asian forms (*Progenitohyus*, *Pakkokuhyus*) might have evolved to develop an anthracotheriid dental morphology, whereas others (*Gobiohyus*) might have continued to evolve in a more specialized direction.

*Pakkokuhyus* is late Middle Eocene in age according to Holroyd and Ciochon (1995), and *Progenitohyus* is Late Eocene in age. In addition, a direct relationship between the two forms is unlikely, because of the major features that distinguish them (major difference in size, absence of a paraconid, lower molars with a labial cingulid and larger  $M_3$  hypoconulid in *Pakkokuhyus*). However, although the divergence between helohyids and anthracotheriids might have occurred during the Middle Eocene, *Progenitohyus* may be allied with primitive anthracotheriids such as *Siamotherium*. In that case, it might represent a late transitional form between Helohyidae and Anthracotheriidae that survived during the Late Eocene in Southeast Asia.

## Conclusions

*Progenitohyus* is the first helohyid artiodactyl described from Thailand, and therefore documents the most southern record of the family in Asia. It also displays a

morphology that testifies to its probable relationships with primitive anthracotheriids rather than with other helohyids. Helohyidae might have given rise to two distinct lineages, one leading to specialized forms such as the Mongolian *Gobiohyus*, and the second one resulting in the Anthracotheriidae. However, the occurrence of an-

thracothers in the Middle Eocene of Burma (Holroyd and Ciochon, 1991) suggests that the differentiation between Helohyidae and Anthracotheriidae probably occurred during the Middle Eocene or even earlier, and other early Asian transitional forms should be searched for in such levels.

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