

THE EARLIEST KNOWN PIG FROM THE UPPER EOCENE OF THAILAND

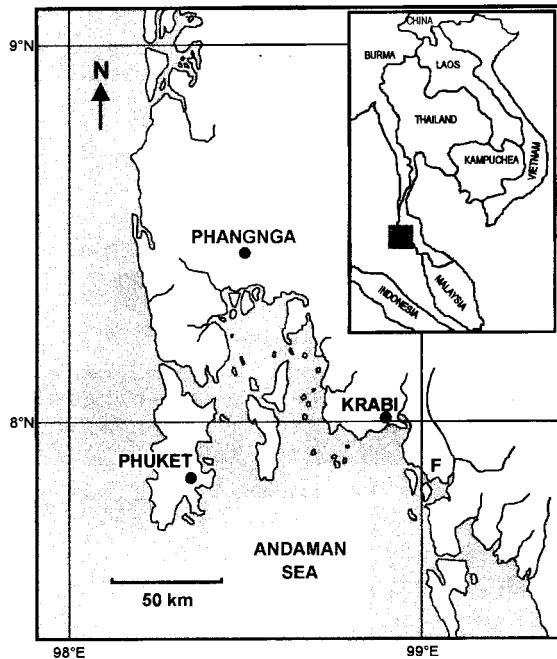
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ABSTRACT. Several dental remains of a new suid, *Siamochoerus banmarkensis* gen. et sp. nov., have been collected in the Late Eocene Krabi basin in southern Thailand. This species is morphologically close to but more primitive than *Dubiotherium waterhousi* (formerly *Palaeochoerus waterhousi*), and represents one of the oldest known suids. The date of origination of suids can therefore be placed back to the Late Eocene or even earlier, and the early evolution and diversification of the family might have occurred largely in the Oligocene of Asia.

PIGS are artiodactyls belonging to the family Suidae, characterized by their ubiquity and ability to radiate rapidly in new territories. For these reasons, suids are considered to be useful for intercontinental as well as local and regional biostratigraphy. The palaeontological history of the family Suidae is well documented in the Miocene and afterwards (Pickford 1988, 1993), but the fossil record and the evolutionary history of suids and their close relatives the tayassuids is almost unknown during the Paleogene of the Old and New worlds. According to the recent work of Pickford (1993), only two tayassuids (the peccaries *Palaeochoerus* and *Doliochoerus*) and one suid (*Hyotherium*) occur in Paleogene deposits of the Old World. The earliest known true suid is *Hyotherium* from the Upper Oligocene of Europe (Pickford 1993). *Hyotherium* belongs to the subfamily Hyotheriinae which is considered to be the ancestral group that gave rise to further subfamilies of pigs. However, the major evolution and diversification of suids occurred during the Neogene in the Old World, with over 30 genera recognized. Suidae evolved in a rather different way than Tayassuidae and are distinguished by limb structure (four toes on both front and hind limbs and unfused third and fourth metatarsals) and dentition (for example, suids possess outwardly and upwardly curved upper canines; see for example Nowak and Paradiso 1984).

The Late Eocene Krabi Basin in southern Thailand (Text-fig. 1) has yielded a rich and diverse mammalian fauna including a dermopteran, a megabat, primates, carnivores, rodents, a tayassuid, anthracotheres, ruminants, a tapir and a rhino (Ducrocq *et al.* 1995, 1996; Chaimanee *et al.* 1997). Holroyd and Ciochon (1994) have dated the Krabi basin as late Mid Eocene, and of similar age to the locality of Pondaung, Burma, because of similarities between the anthracothere associations at both sites. However, they based their work on information from Ducrocq *et al.* (1992) that has since been updated. The anthracotheres from Krabi are somewhat more derived than those from Pondaung, and morphologically closer to forms described from the basal Oligocene of Europe (Monteviale, Italy) and China (Ducrocq 1993, 1994a). In addition, the recently described anthropoid primate *Siamopithecus eoceanus* Chaimanee, Jaeger, Suteethorn and Ducrocq, 1997, displays strong similarities to *Pondaungia cotteri* from Pondaung, but shows somewhat more derived dental features compared to those of the Burmese species. We therefore conclude that the Krabi fauna is more probably Late Eocene in age rather than older.

Dental remains of a small artiodactyl have been collected from the Late Eocene Bang Mark pit at the Krabi mine in southern Thailand. The morphology and structure of these fossils allow them to be attributed to a suid and they are placed in a new genus and species. This new form from Thailand further illustrates the early differentiation of Suidae in South-east Asia.



TEXT-FIG. 1. Map of Thailand showing location of the Krabi Basin fossil site. The mine that yielded the specimens of *S. banmarkensis* reported here, is represented by the letter F.

SYSTEMATIC PALAEOLOGY

Order ARTIODACTYLA Owen, 1848

Family SUIDAE Gray, 1821

Genus SIAMOCHOERUS gen. nov.

Derivation of name. From *Siam* (former name of Thailand), and from 'choerus', the Greek for pig.

Type species. *Siamochoerus banmarkensis* sp. nov.

Diagnosis. As for species.

Siamochoerus banmarkensis gen. et sp. nov.

Text-figures 2-4

Derivation of name. From Bang Ban Mark, the type locality.

Holotype. A left lower jaw with P_4 - M_3 ; Specimen No. TF 2905 (Text-figs 2-3), Collections of the Department of Mineral Resources, Bangkok.

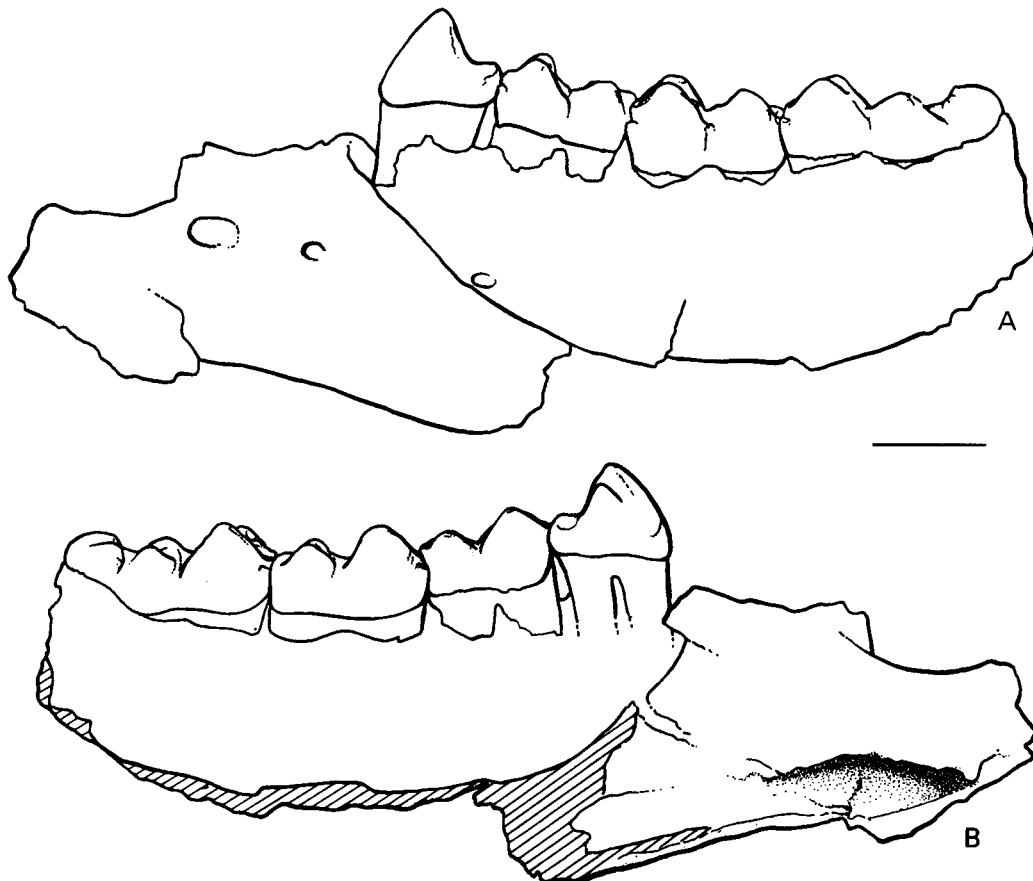
Additional material. All from Bang Ban Mark: isolated left P_3 (TF 2963; Text-fig. 4A-B); isolated left M_3 (TF 2906); and fragmentary left maxillary with damaged M^1 - M^3 (TF 2907; Text-fig. 4C).

Type locality. Lignite mine, Bang Ban Mark pit, Krabi basin, southern Thailand (latitude: between $7^{\circ} 54' 49''$ N and $8^{\circ} 12' 16''$ N; longitude: between $98^{\circ} 11' 35''$ E and $99^{\circ} 8' 35''$ E).

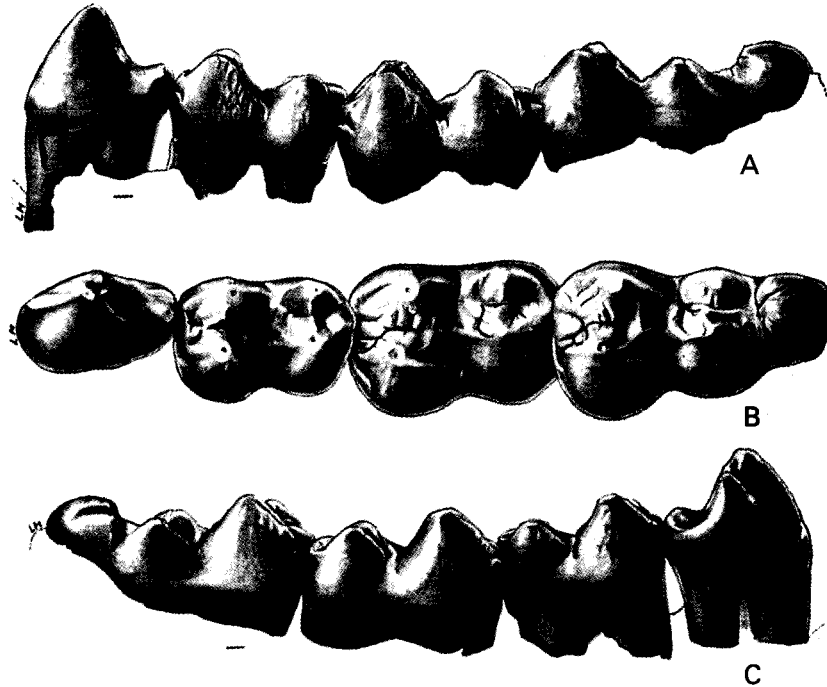
Horizon. Upper level of the main lignite seam of Bang Ban Mark pit (Formation B2, see Bristow 1991). The mammalian fauna associated with the suid remains is identical to that from Wai Lek pit (which yielded most of the taxa known in Krabi) and Bang Mark pit, and faunal evidence indicates a Late Eocene age (see above and Ducrocq *et al.* 1995).

TABLE 1. Dental dimensions of *Siamochoerus banmarkensis* gen. et sp. nov. (in mm).

		Length	Width (trig.)	Width (tal.)
TF 2963	Left P ₃	10.3	5.3	—
TF 2905	Left P ₄	9.4	6.4	—
	Left M ₁	10.9	7.9	7.6
	Left M ₂	13.8	10.2	9.4
	Left M ₃	18.7	10.5	8.4
TF 2907	Left M ₃	18.6	9.8	8.3
TF 2907	Left M ₂	12.5	—	—
	Left M ₃	13.7	14.6	—

TEXT-FIG. 2. *Siamochoerus banmarkensis* gen. et sp. nov.; TF 2905; left lower jaw preserving P₄-M₃; Bang Ban Mark, south Thailand. A, labial, and B, lingual views. Scale bar represents 10 mm.

Diagnosis. Primitive suid, close to *Propalaeochoerus pusillus* in size. P₃ simple lacking a metaconid, P₄ with small metaconid and hypoconid and lacking a paraconid. Lower molars show a marked increase in size from front to back, with the mesial lobe wider than distal lobe, a small hypoconulid and extremely weak accessory cusps. M₃ elongated with two-cusped hypoconulid. Upper molars



TEXT-FIG. 3. *Siamochoerus banmarkensis* gen. et sp. nov.; holotype, TF 2905; left lower dental row (P_4 - M_3); Bang Ban Mark, south Thailand; Late Eocene A, labial, B, occlusal, and C, lingual views. Scale bars represent 1 mm.

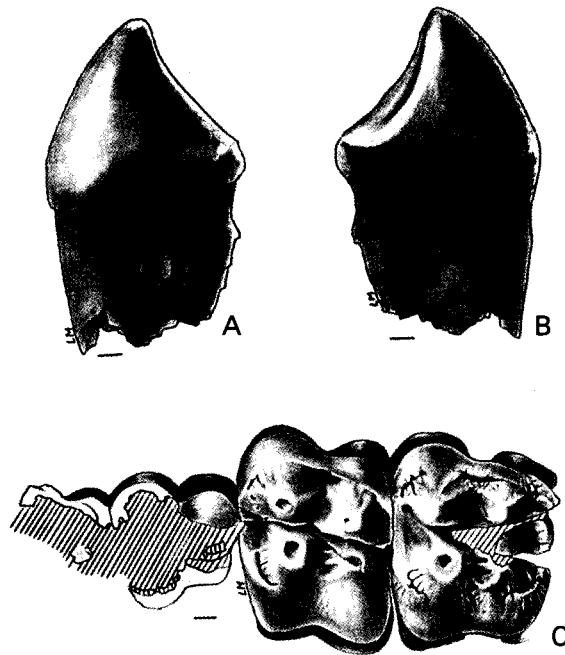
simple, lacking accessory cusps. M^3 without distally salient talon. Enamel very finely wrinkled. Measurements given in Table 1.

Description. The lower jaw is laterally crushed, so that it is not possible to know with certainty if the horizontal ramus was wide, as is generally the case in suids. However, the base of the mandible is broken and it can be supposed that it was relatively deep (Text-fig. 2). Three dental foramina occur on the mandible: one under the posterior root of P_2 , one under the posterior root of P_3 and a third, which is also the smallest, under the anterior root of M_1 . On the lingual face of the mandible, the posterior end of the symphysis reaches P_2 .

The isolated P_3 and the fragmentary lower jaw very probably belong to the same individual on the basis of their state of preservation. P_3 displays a sharp triangular shape, and is more distally curved than P_4 . There is no accessory cusp, and only a small depression runs lingually from the apex of the cusp to the base of the crown. The talonid is made of a weak elongation of the distal part of the tooth. A weak crest is present on the mesial and distal edges of the tooth (Text-fig. 4A-B).

The morphology of P_4 is typical of the ancestral condition in suids. It is triangular, somewhat posteriorly curved. It displays a main cusp (protoconid) and a very small lingual cusp (metaconid or 'Innenhügel' according to Stehlin [1899, 1900]) situated on the distolingual edge of the main cusp, but slightly lower than it. The apices of these two cusps are joined by a very weak crest. A talonid is well developed and consists of a single labial cusp (hypoconid) connected with the apex of the protoconid by a straight crest. A very slight cingular spur of enamel occurs on the mesial side of the crown and might be interpreted as an incipient paraconid. A very weak crest runs up the mesial face of the premolar. The enamel is smooth and there is no cingulid (Text-fig. 3).

TEXT-FIG. 4. *Siamochoerus banmarkensis* gen. et sp. nov. A-B, TF 2963; isolated left P_3 . A, labial and B, lingual views. C, TF 2907; left maxilla with crushed M^{1-3} , occlusal view. Scale bars represent 1 mm.



The M_1 is an elongated tooth with four main cusps (protoconid, metaconid, hypoconid and entoconid), the mesial cusps being slightly higher than the distal ones. A small hypoconulid occurs on the distal side in a median position, and there are slight swellings of the enamel in the transverse valley and in the trigonid basin that might correspond to incipient accessory cusps. Weak transverse crests join the metaconid to the protoconid and the entoconid to the hypoconid. The middle of the lingual and labial faces of the molar is waisted, so that the anterior and posterior lobes are clearly distinct. A tiny cingulid only occurs on the mesial edge of M_1 , and the anterior lobe is slightly wider than the posterior lobe. M_2 is similar to M_1 except in its larger size (Text-fig. 3).

M_3 displays the same structure as M_1 and M_2 , but its width decreases from front to rear. This tooth also possesses a hypoconulid consisting of a large posterolabial cusp associated with a smaller lingual one. The third lobe is joined to the middle of the second lobe by a very low longitudinal crest. The two cusps that form the hypoconulid are separated by a shallow groove. The isolated left M_3 does not differ from the M_3 of the holotype. On all molars the trigonid is somewhat higher than the talonid part, and the system of grooves or 'Furchenplan' of von Hünemann (1968) is well expressed. The enamel of all the molars is very finely wrinkled, especially on the apices of cusps and on M_3 (Text-fig. 3).

Although they are badly crushed, the upper molars display a rather simple structure with four main cusps (paracone, metacone, protocone and hypocone) and no well-defined accessory cusps. The 'Furchenplan' is poorly expressed. The crests that join the different cusps are weak and low, and a cingulum occurs on the mesial and distal faces and between the paracone and the metacone on the labial face. The enamel is finely wrinkled and the roots of the molars are unfused (Text-fig. 4C).

COMPARISONS

Dental and mandibular features of suids include the transversely thick horizontal ramus of the mandible; a dental row that crosses over the body of the mandible from anterolabial to posterolingual; a tendency for the lower canine to splay out laterally; lingual and labial flaring of

the molars; molars with four main cusps and anterior, median and posterior accessory cusps; scoring of the main cusps of the molars by three distinct grooves (= 'Furchenplan' of von Hünemann (1968); anterior and posterior cingula on the upper molars; strong elongation of M_3 with a complex and polybunous talonid; and unfused molar roots. Other cranial features that characterize suids, although lacking in the Thai fossil material, are a basicranium in which the convex glenoid cavity is higher than the level of the occlusal plane of the cheek teeth, but lacking a postglenoid 'stop' and thus allowing lateral movement of the jaws (Pickford 1993).

Several dental features allow us to suggest that *Siamochoerus* belongs not in Tayassuidae but in Suidae. *Siamochoerus* displays the association of laterally flared lower and upper molars, with incipient accessory cusps and a distinct 'Furchenplan', an elongated M_3 , with a complicated talonid part, and unfused molar roots. Moreover, although it displays a protoconid and a tiny metaconid the P_4 trigonid of the Thai specimen is not fully developed and the two trigonid cusps are dissimilar in size. In addition, the P_3 is about the same size as the P_4 (whereas it is generally smaller in Tayassuidae), and is the simpler of the two, indicating that the anterior lower premolars (P_1 and P_2) were probably even less molarized. It is not possible to know whether the horizontal ramus of the mandible was thick laterally, because the bone was crushed during fossilization; however, the unfused molar roots together with the lateral flare of the molars suggest that the mandible was thick.

A major difficulty in the familial attribution of this specimen is that the classification of Suidae differs from one author to another. Pickford (1988, 1993), for example, considered the genus *Palaeochoerus* to belong in Suidae, whilst Hellmund (1992) attributed it to Tayassuidae. Moreover, several taxa formerly referred to Tayassuidae have, after revisions, been shifted into Suidae. This is the case, for example, for *Palaeochoerus waterhousii*, now considered by Hellmund (1992) as a suid (= *Dubiotherium waterhousii*) and for *Odoichoerus uniconus* from the Lower Oligocene of China (Tong and Zhao 1986) which Ducrocq (1994b) referred to Suidae. As these points of view are not shared by different authors, we think it is better to begin by comparing *Siamochoerus* with different early suoid taxa, including members of Tayassuidae and Suidae.

Tayassuidae

As the basic topological morphology of the molars is rather constant throughout the family Suidae (Pickford 1988), the lower premolars of *Siamochoerus* are a valuable element that allow the Thai species to be compared with other known suoid taxa. The fourth premolar of *Siamochoerus* differs markedly from that of members of the Doliochoerinae (a tayassuid subfamily), described by Ginsburg (1974, p. 60), in its distolingually situated with respect to the main cusp (protoconid), accessory cusp or 'Innenhügel' (metaconid), its labially displaced and unique posterior cusp (hypoconid), its much less developed paraconid, and in its lower crest connecting the hypoconid and the protoconid. Also, the P_3 of *Siamochoerus* displays a posterior crest running from the protoconid down to the distal base of the crown which, unlike the condition in tayassuids, is not divided into small cusplets.

The oldest known European suoids are the genera *Propalaeochoerus* and *Doliochoerus* from the Lower Oligocene of Europe (Ginsburg 1974; Hellmund 1992). Both these genera differ from *Siamochoerus* in that P_3 has a higher and better developed distal crest, P_4 is much more molarized and the upper and lower molars have better developed accessory cusps and crests. *Doliochoerus quercyi* differs from *Siamochoerus* further in its shorter and more massive M_3 , better developed cingula on the upper molars and stronger talon on M^3 . *Palaeochoerus* (a tayassuid known from the beginning of the Oligocene, according to Ginsburg (1974) and Pickford (1993), but considered as a suid by Hellmund (1992)) also differs from the Thai species in its distolingually to mesiolingually elongated upper molars, its much stronger cingula, its better developed preprotocrista, and its less bulbous lower molars and more molarized P_4 .

Odoichoerus uniconus was described as a tayassuid from the Lower Oligocene of China by Tong and Zhao (1986). Recently, Ducrocq (1994b), suggested that, on the basis of its dental morphology,

this Chinese species probably belongs to Suidae rather than to Tayassuidae. Therefore, it seems that *Odoichoerus* might be one of the earliest known representatives of the family Suidae. This genus differs from *Siamochoerus* in its smaller size, its shallower mandibular ramus, a much smaller hypoconulid on M_3 and sharper and simpler P_4 without accessory cusps, but with a higher distal crest. Tong and Zhao (1986) further compared *Odoichoerus* to the tayassuids *Taucanamo* and *Albanohyus* (the latter being considered a synonym of *Taucanamo* by Pickford (1993)) in which P_4 is simpler than in other tayassuid taxa. *Taucanamo* is known from the Miocene of Europe (Thenius 1956) and Turkey (Pickford 1979, 1993). The P_4 of *Siamochoerus* is similar to that figured by Pickford (1979, fig. 6) and attributed to cf. *Taucanamo* from Turkey. However, the Turkish premolar differs from that of the Thai species in its larger size, the greater lingual development of the metaconid, which is more mesially situated, and in its better developed mesial and distal cingulids. In addition, the lower molars associated with cf. *Taucanamo* are less elongated, less waisted labially and more massive than those of *Siamochoerus*. The latter is about the size of *T. sansaniense*, but differs from it in its more elongated M_3 , its smaller hypoconulid and in its weaker accessory cusps. *Siamochoerus* is also distinguished from *T. pygmaeum* by its shorter P_3 without cingulid, M_1 is much smaller than M_2 , the system of grooves ('Furchenplan') is poorly expressed and the upper molars are squared, not elongate, and have very weak accessory cusps.

The tayassuid *Egatochoerus jaegeri* from the Krabi Basin, south Thailand (Ducrocq 1994b) is very different from *Siamochoerus*. Both taxa differ in their size and in their upper and lower premolar and molar structure and morphology. Given their distinct tooth morphology, Tayassuidae and Suidae seem therefore to have diverged before the Late Eocene.

Suidae

In his revision of the Oligocene suoids from western Europe, Hellmund (1992) erected the new genus *Dubiotherium* for the Late Oligocene *Palaeochoerus waterhousi*, and placed it in Suidae. *Dubiotherium* and *Siamochoerus* are similar in overall morphology, but can be distinguished by several features: *Siamochoerus* is somewhat smaller; the mesial face of its P_3 is convex; its P_4 exhibits a more reduced metaconid and a shallower and weaker crest connecting the protoconid and the hypoconid; the lower molars lack the enamel cuspules on their distal cingulid, and the M_3 is more slender distally.

According to Pickford (1993, p. 242), it is not clear whether early suid-like fossils from Asia attributed to the genus *Propalaeochoerus* are suids or tayassuids. Pickford (1993) further argued that the European forms of this genus, considered to belong in Hyotheriinae, might be the ancestral group for other subfamilies of pigs. The only hyotheriid known in the Paleogene (Upper Oligocene in Europe and the Indian subcontinent) is *Hyotherium*. However, *Siamochoerus* differs markedly from *Hyotherium* in its narrower P_{3-4} with much less developed trigonid and talonid, without mesial and distal cingulid, its slender lower molars that lack well developed accessory cusps and labial cingulid, its shorter upper molars with a stronger increase in size from front to back, the absence of mesial and medial distinct accessory cusps, and the absence of a distal expansion of the M^3 talon.

Other Eurasian suid genera (e.g. the Miocene *Aureliachoerus* and *Listriodon*) are too specialized to be related, at least from a morphological point of view, to the Thai species. They differ from *Siamochoerus* in the same features that distinguish *Hyotherium*, and *Listriodon* also exhibits lophodont cheek teeth.

Among other primitive artiodactyls, the genus *Cebochoerus* from the Middle–Upper Eocene of western Europe has previously been suggested as a possible ancestor to the Suidae (Pearson 1927). This hypothesis is now abandoned (Hellmund 1992). The lower molars of the European genus display few similarities to those of *Siamochoerus* (bunodont cusps, bulbous labial tooth walls, and faint mesial cingulid). However, *Cebochoerus* differs from *Siamochoerus* in its more elongated and massive lower premolars with better developed mesial and distal cusps, its shorter, lower M_3 with more simple third lobe, and in details of the upper molars which have external cusps joined by a crest and more selenodont internal cusps.

DISCUSSION

In its overall morphology, the dental material of *Siamochoerus banmarkensis* is more similar to that of *Dubiotherium* than to other European species, although the Thai species is obviously more primitive. The structurally simple lower molars and the elongated M_3 with relatively simple hypoconulid are found in both European and Thai genera. Indeed, the lower molars of the suid *Dubiotherium waterhousi* (from the MP 26 European level (= late Early Oligocene)) are similar to those of *Siamochoerus* in the relative height of the mesial and distal cusps, the lack of well defined accessory cuspules, the salient distal hypoconulid on M_{1-2} (called the enamel knob or 'Schmelzknospe' by Hellmund (1992, p. 25)), and the absence of an accessory cusp between the second and third lobe on M_3 , which also has a two-cusped hypoconulid lobe. In addition, P_4 in *Dubiotherium* and *Siamochoerus* has a crest that connects the apex of the protoconid and the mesiolingual corner of the tooth, and lacks a distinct paraconid and entoconid. P_3 is also very simple in both genera, with a very short talonid and lacks the incipient metaconid. No upper molars are attributed to *Dubiotherium*; thus a comparison of these teeth is not possible. However, the posterior lower premolars are more derived in *Dubiotherium*, reflecting the separation of Tayassuidae and Suidae before these families invaded Europe.

The Thai species might be related to the previously described *Odoichoerus uniconus* from the Lower Oligocene of China (Tong and Zhao 1986). Indeed, the Early Oligocene age attributed to the Chinese species does not contradict such an hypothesis since it has recently been suggested that most Chinese fossiliferous localities might be older than currently considered (Ducrocq 1993). In addition, the sparse mammal fauna associated with *Odoichoerus* (cf. *Anthracoeryx* sp., *Heothema* sp., cf. *Indomeryx* sp., and *Guixia?* sp.) seems to indicate a Late Eocene rather than an Early Oligocene age (it should also be noted that the genus *Heothema* is synonymized with *Anthrotherium* by Ducrocq 1992, in press). *Odoichoerus* displays lower molars with four main cusps and slight swellings of the enamel in the transverse valleys which might be regarded as incipient accessory cusps. These structures are better developed in *Siamochoerus* and *Dubiotherium*, and fully developed in *Hyotherium*. In addition, the M_3 hypoconulid lobe of *Odoichoerus* is very small, but exhibits three distinct cusplets that might foreshadow further complexity of this structure, as seen in *Siamochoerus* and *Dubiotherium*. The labial flare of the lower molars observed in *Siamochoerus* also occurs in *Odoichoerus*, and M_1 is markedly smaller than M_2 (M_1 is 20–26 per cent. shorter than M_2) in both these taxa and *Dubiotherium*. In addition, the P_4 of *Odoichoerus* does not display the lingual cusp (metaconid) as in *Siamochoerus*, but exhibits a sharp and high crest that runs from the apex of the protoconid down to the distal end of the crown. The distal half of the crest shows two weak cusplets reminiscent of the P_4 of *Hyotherium* rather than that of *Siamochoerus*. Nevertheless, *Odoichoerus* might represent an ancestor to *Siamochoerus* because of its smaller size and the more primitive morphology of P_4 and the lower molars. These observations and the known fossil record suggest that suids had appeared by the Late Eocene in Asia and then colonized Europe in the Early Oligocene. This is contrary to the opinion of Pickford (1993) who suggested that the earliest known suids are from the Upper Oligocene of Europe. Moreover, if suids originated from Tayassuidae, as Pickford suggested (1993, p. 242), the splitting probably occurred during the Late Eocene or even earlier, because the oldest known tayassuid (*Egatochoerus jaegeri*) so far described was found in the Upper Eocene of Thailand (Ducrocq 1994). This species already displays characteristic tayassuid features, such as the vertical lower canine without labial symphyseal splaying, the strongly developed trigonid of P_4 and the poorly expressed 'Furchenplan' on the molars, and thus suggests that the tayassuid pattern was achieved by the early or mid Late Eocene.

The difficulty of distinguishing between early tayassuid and suid dental morphologies, together with the poorly documented fossil record of Asian Oligocene mammal localities, has long obscured our knowledge of the earliest representatives of suoids. In addition, our incomplete understanding of suoid systematics renders their use for biostratigraphical purposes and stratigraphical inferences somewhat doubtful. These apparent deficiencies in the fossil record and related biostratigraphy clearly demand further investigation of the Paleogene mammal localities of Asia.

CONCLUSIONS

At present, the Krabi mammal fauna contains the most primitive known Eurasian tayassuid (*Egatochoerus jaegeri* Ducrocq, 1994), but, it must be stressed that, because of the well-differentiated structure of its teeth, this form cannot represent the stem-taxon of both tayassuids and suids. In the same way, *Siamochoerus banmarkensis* gen. et sp. nov. from the Upper Eocene of Thailand is a true suid that displays affinities with European *Dubiotherium* and the Chinese *Odoichoerus*. These new finds suggest that the origin of suoids might have occurred earlier than previously thought: obviously by the Late Eocene and perhaps even earlier. The as yet unknown common ancestor of Suidae and Tayassuidae probably emerged in southern Asia, and should be searched for in deposits older than those that yielded *Egatochoerus* and *Siamochoerus*.

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