AN EOCENE PECCARY FROM THAILAND AND THE BIOGEOGRAPHICAL ORIGINS OF THE ARTIODACTYL FAMILY TAYASSUIDAE

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ABSTRACT. Recent field work in the upper Eocene Krabi Basin (south Thailand) has yielded several dental and postcranial remains of a new genus and species, *Egatochoerus jaegeri*, of a tayassuid morphologically very close to the upper Eocene North American genus *Perchoerus*. According to the somewhat more primitive morphology of the Thai species, the family Tayassuidae seems to have originated in South East Asia, and then migrated into the New World as early as late Eocene. The familial status of the alleged tayassuid *Odoichoerus uniconus* from the lower Oligocene of China is also reconsidered, and this species should be referred to the Suidae on the basis of its dental and mandibular morphology.

PECCARIES are pig-like ungulates belonging to the family Tayassuidae (including the genera *Tayassu* and *Dicotyles*) and are now confined to North and South America, where they occupy an ecological niche resembling that of the Suidae. Peccaries differ from the pigs mainly in their somewhat smaller size, their downwardly directed upper canines (in suids, they curve more or less outward and upward), in their fused third and fourth metatarsals, and in having four toes on the front feed and three on the hind feed (Nowak and Paradiso 1984).

Unambiguous Tayassuidae appeared in Europe during the early Oligocene with the genus *Propalaeochoerus* Stehlin, 1899 (Hellmund 1992), and during the middle Oligocene with *Doliochoerus quercyi* Filhol, 1882 (Ginsburg 1974). The family appeared in North America in the late Eocene (middle Chadronian; see Stucky 1992) with the genera *Perchoerus* Leidy, 1869 (up to the middle Oligocene = Whitneyan) and *Tinohyus* Marsh, 1875 (sometimes considered as a synonym of *Perchoerus*) in the early Oligocene (Orellan).

Only a few tayassuids are known from the Palaeogene of Asia. The most ancient possible representatives of this group come from the upper Eocene of northern China (a new genus cited from the Naduo Formation, *in* Russell and Zhai 1987). An indeterminate tayassuid has also been reported from southern China (Gongkang Formation, Bose and Yongle basins) at the Eocene-Oligocene boundary by Xu (1982), and then attributed to a new genus, '*Eopecarihyus*', but never published. Finally, the species *Odoichoerus uniconus* Tong and Zhao, 1986 was created for a fragmentary lower jaw, probably from the same locality (Tong and Zhao, 1986).

The Tayassuidae diversified considerably over the entire northern hemisphere (in North America from the late Eocene to Recent, in Asia from the late Eocene to the late Miocene, and in Europe from the early Oligocene to the late Miocene), and in a large part of the southern hemisphere (in Africa from the early Oligocene to the early Pliocene and in South America from the lower Pliocene to Recent).

Dental and postcranial remains have been collected from the upper Eocene localities of Wai Lek and Bang Pu Dam (Krabi Basin, see Ducrocq *et al.* 1992) in Thailand (which also yielded numerous remains of anthracotheres, see further), and are attributed to a new genus and species of Tayassuidae. These elements do not display significant size and structural differences from one locality to another, and are assumed to represent a single species.

TEXT-FIG. 1. *Egatochoerus jaegeri* gen. et sp. nov. Bang Pu Dam, Thailand; upper Eocene. A, TF 2672; right maxilla with M1/-M2/, occlusal view, stereo pair; scale bar = 10 mm. B, interpretative drawing of the same specimen. Scale bar = 10 mm.

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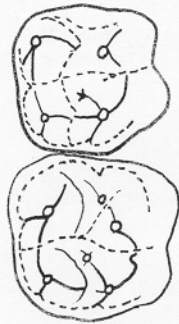
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SYSTEMATIC PALAEONTOLOGY

Order ARTIODACTYLA Owen, 1848
Family TAYASSUIDAE Palmer, 1897
Genus EGATOCHOERUS gen. nov.

Type species. Egatochoerus jaegeri sp. nov.

Derivation of name. From EGAT (Electricity Generating Authority of Thailand), the company which mines the lignite in Krabi and which has allowed us to work in the lignite mines for several years.

Diagnosis. As for species.

*Egatochoerus jaegeri* sp. nov.

Derivation of name. In honour of Professor J.-J. Jaeger, the discoverer of the holotype.

Holotype. A right lower jaw with C and P/2-M/3; Specimen No. TF 2681, Collections of the Department of Mineral Resources, Bangkok.

Type locality. Lignite mine, Bang Pu Dam, Krabi Basin, southern Thailand (latitude, about 8° N; longitude, about 99°E).

Horizon. Thin lignite seam 10 metres below the base of the main lignite seam (Formation B2, see Bristow 1991); Krabi Tertiary Basin, upper Eocene (see Ducrocq *et al.* 1991, 1992 for discussion about the age).

TEXT-FIG. 2. *Egatochoerus jaegeri* gen. et sp. nov. Bang Pu Dam, Thailand; upper Eocene. A, TF 2826; right upper DP4/, occlusal view, stereo pair. B, interpretative drawing of the same specimen; scale bar = 10 mm. TF 2681. C–E, interpretative drawings of right lower P/4; C, lingual view; D, mesial view; E, distal view. Scale bar = 10 mm.
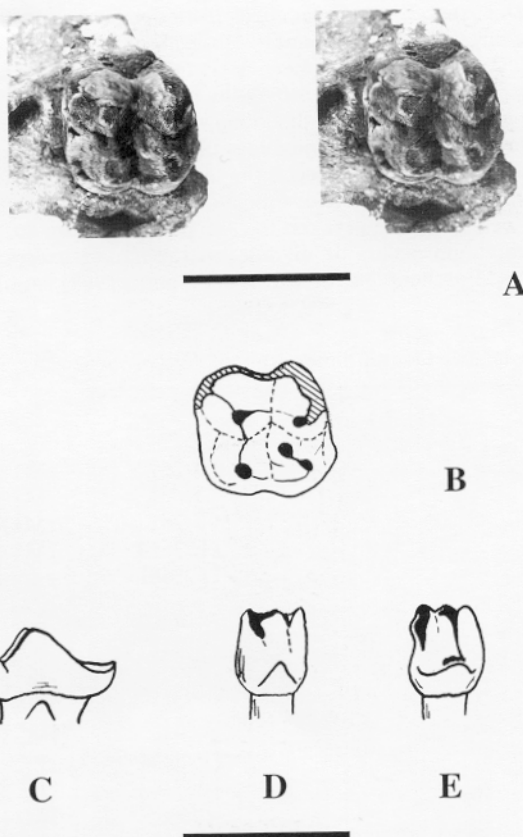
Other material. Fragmentary left lower jaw with P/3-M/3 (TF 2825, Bang Pu Dam), fragmentary right maxillary with P4/-M1/ (TF 2674, Wai Lek), fragmentary right maxillary with M1/-M2/ (TF 2672, Wai Lek), fragmentary left maxillary with DP4/(TF 2826, Wai Lek), left M2/ (TF 2827, Wai Lek), right M1(?)/(TF 2673, Bang Pu Dam), isolated left I/2 (TF 2967, Bang Pu Dam), isolated right I/3 (TF 2968, Bang Pu Dam), isolated right I1/ (TF 2969, Bang Pu Dam), right astragalus (TF 2813, Bang Pu Dam) associated with a right calcaneum (TF 2814, Bang Pu Dam), right astragalus (TF 2812, Bang Pu Dam).

Diagnosis. Tayassuid close to *Perchoerus* in its dental morphology. Size similar to that of *Odoichoerus uniconus.* Mandible deep, becoming shallower anteriorly, with a well developed angular process, and unfused symphysis. Vertical lower canine with triangular cross-section, premolars increasing in size distally, diastema between C and P/2, P/1 lost, P/4 with two main cusps (protoconid and metaconid), lower molars with a deep waist between the two lobes and M/3 with strong hypoconulid. Upper molars with four main cusps and two (mesial and distal) lingually situated accessory cusps, fused internal roots, system of grooves ('Furchenplan' of von Hünermann) poorly expressed. Astragalus morphologically close to that of *Tayassu.*

Distinguished from *Perchoerus* by loss of P/1, an M/3 with more massive hypoconulid, a more simple P4/ and by upper molars with less developed accessory cusps and weaker cingula. Differs from *Doliochoerus* in its smaller size, more rectilinear and more massive lower canine, deeper mandible, lower premolars with a greater size differential from front to rear and in having upper molars with weaker crests. *Egatochoerus* is smaller than *Palaeochoerus* and it further differs from it by having a more massive mandible and by its upper molars with weaker crests, stronger accessory cusps and no lingual cingula. *Egatochoerus* differs from *Propalaeochoerus* in its deeper lower jaw, squared molars and more simple P/4.

Description. The upper cheek teeth display an easily recognizable structure. On TF 2674, P4/ displays a lingual conical cusp (protocone) with a mesial crest well developed and directed towards the labial cusp, which is lacking on this specimen. A slightly crenulated cingulum occurs mesially and distally as a tiny shelf.

All upper molars display the same pattern (Text-figs 1, 2A–B). They consist of four main cusps, more or less pyramidal in shape, the labial ones laterally more compressed and slightly more mesial in position than the lingual ones. The paracone is the highest cusp. Two mesial and distal enamel swellings, scarcely differentiated as accessory cusps, recall the upper molars of the North American genus *Perchoerus* Leidy, 1869. The mesial swelling occurs between the two anterior main cusps and is close to the labial face of the protocone. The distal swelling occurs between the two posterior main cusps and is close to the mesiolabial face of the hypocone. The cingulum occurs on all sides of the molars except the lingual side. The typical system of grooves in suoids (= 'Furchenplan' of von Hünermann, 1968) is only weakly expressed (tooth dimensions in Table 1).

TABLE 1. Dental dimensions of *Egatochoerus jaegeri* gen. et sp. nov. (all measurements are in mm).

		Length	Width
TF 2672	rM1/	9·5	9·3
	rM2/	10·5	11·3
TF 2673	rM1/?	10·1	–
TF 2674	rM1/	9·9	–
TF 2681	r Canine	15·7	7·5
	rP/2	5·5	2·9
	rP/3	7·0	3·8
	rP/4	8·0	5·0
	rM/1	9·0	7·0
	rM/2	10·1	7·8
	rM/3	13·4	8·1
TF 2825	lP/3	6·7	4·1
	lP/4	8·4	5·9
	lM/1	9·0	6·7
	lM/2	9·5	8·2
	lM/3	13·8	8·7
TF 2827	lM2/	10·6	10·5
TF 2826	lDP4/	8·5	7·9
TF 2967	lI/2	5·8	5·5
TF 2968	rI/3	2·7	4·2
TF 2969	rI1/	4·4	7·1

The mandible is deep and massive (Text-fig. 3), but its depth decreases from P/3 anteriorly. The symphysis is low and extends distally as far as the mesial side of P/3. The angular process is strong, and salient downwards behind M/3, but not as downwardly salient as in *Perchoerus*. The ascending ramus is almost vertical and rises just behind M/3. There is no retromolar space.

The lower canine is triangular in section (Text-fig. 4) and of *verrucosa* type (labial and lingual face about the same length and forming an acute angle of about 45°, according to the nomenclature proposed by Stehlin 1899–1900, p. 229). It is high, massive and vertical, and its insertion in the lower jaw is not marked by an outwards splaying of the bone, as is the case in many Suidae (Pickford 1988). Based on the reduced size of P/2, the P/1 is probably lost, which is confirmed by the absence of visible roots and alveoli in the radiographs of the specimen (Text-fig. 3c). However, the bony regions between the canine and P/2 are crushed, and it is difficult to be certain. The size of lower premolars increases from P/2 to P/4. The P/2 is damaged, and only parts of dentine and enamel are visible; but this tooth is small, with one root, and separated from the canine by a short diastema (about 8 mm). P/3 and P/4 are double-rooted and they display a well developed talonid. The P/4 is broad, with two main cusps (protoconid and metaconid) and displays a small mediolingual paraconid linked to the protoconid by a weak crest. The protoconid is slightly mesial to the metaconid, and a well developed hypoconid occurs on the labial side of the talonid (Text-fig. 2c–E; dimensions Table 1).
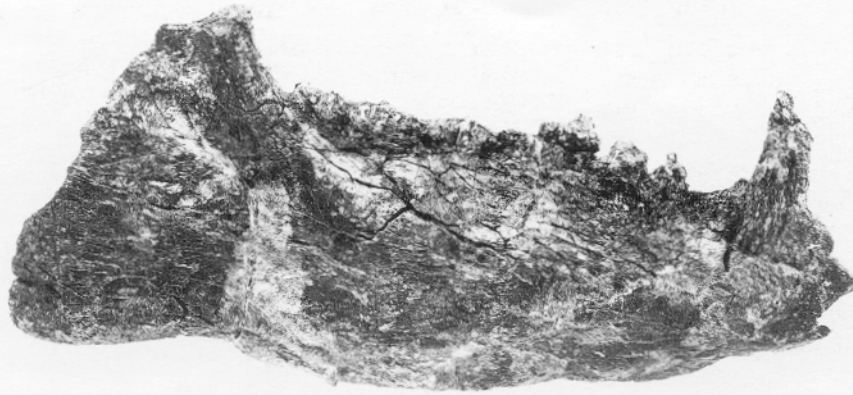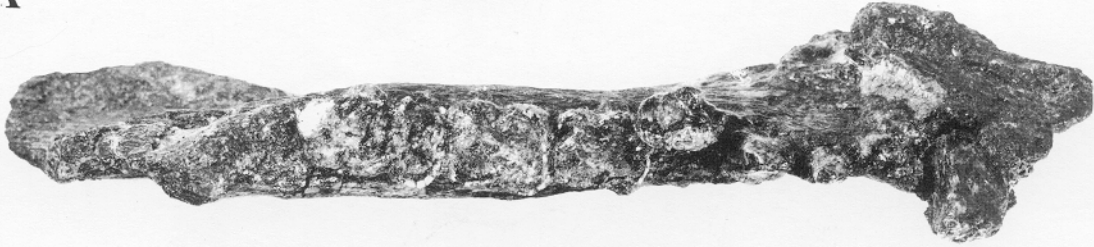
TEXT-FIG. 3. *Egatochoerus jaegeri* gen. et sp. nov. TF 2681; right lower jaw with canine and P/2-M/3; Bang Pu Dam, Thailand; upper Eocene. A, labial view; B, lingual view; C, lingual radiograph. Scale bar = 10 mm.
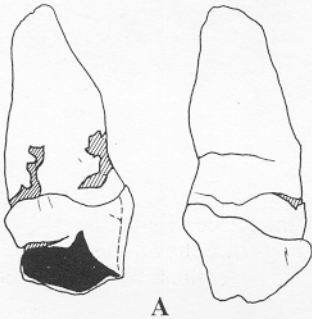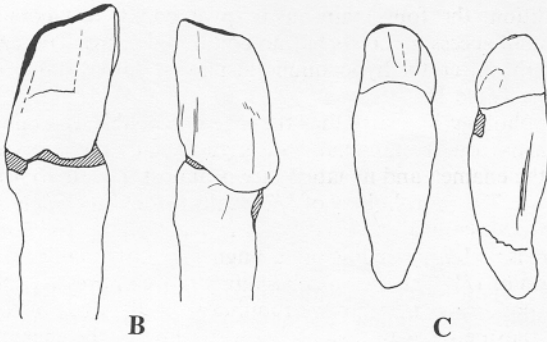
A

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TEXT-FIG. 4. *Egatochoerus jaegeri* gen. et sp. nov. Bang Pu Dam, Thailand; upper Eocene. A, TF 2681; right lower jaw with canine and P/2-M/3, occlusal view. B, interpretative drawing of the same specimen. Scale bar = 10 mm.
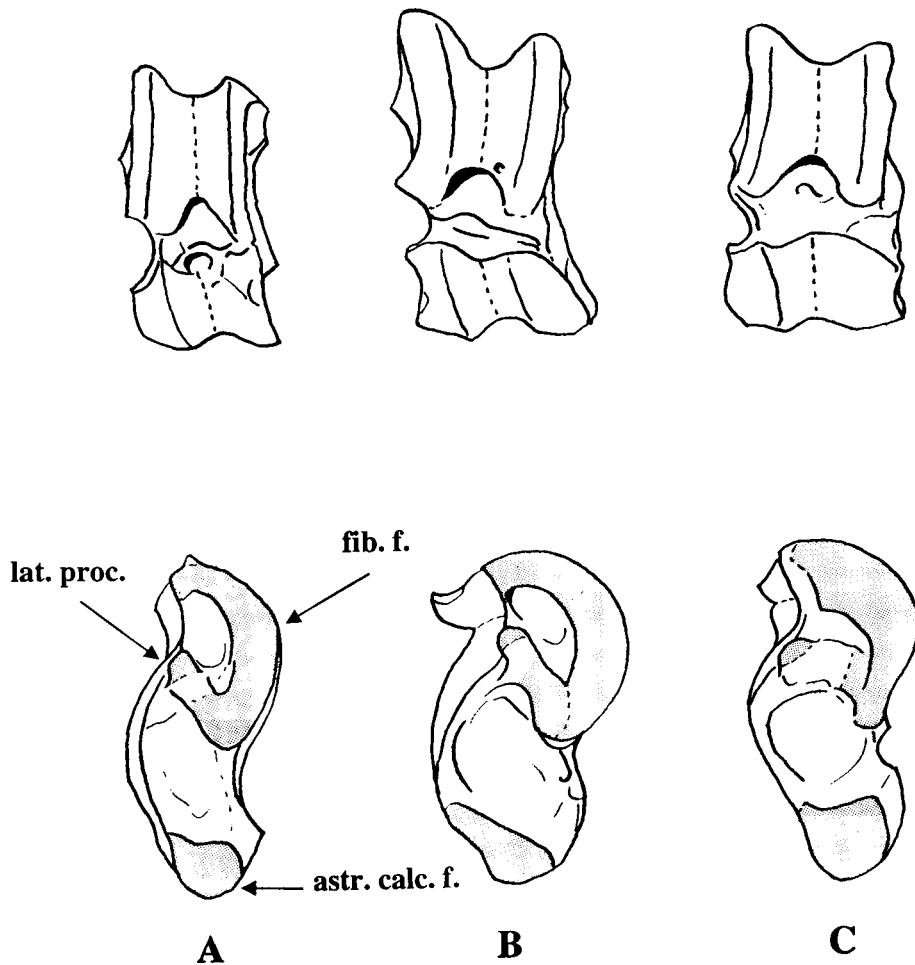
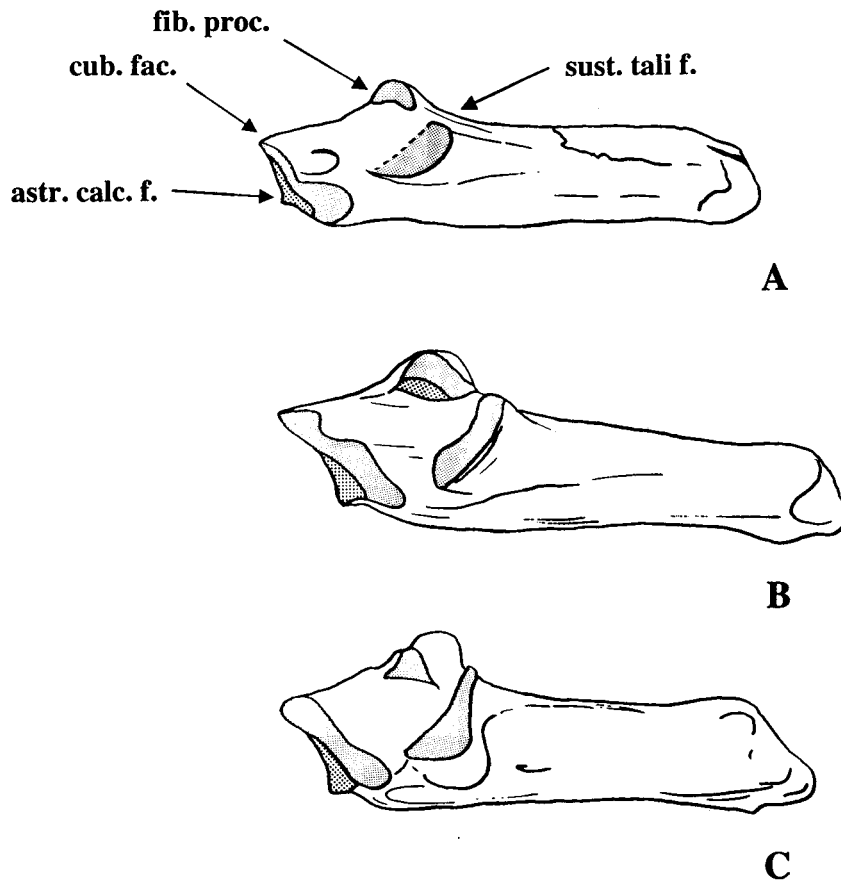

TEXT-FIG. 5. *Egatochoerus jaegeri* gen. et sp. nov. Bang Pu Dam, Thailand; upper Eocene. A, TF 2969; right I1/ in lingual (left) and labial (right) views. B, TF 2967; left I/2 in lingual (left) and labial (right) views. C, TF 2968; right I/3 in lingual (left) and labial (right) views. Scale bar = 10 mm.

TEXT-FIG. 6. Comparison of astragali of A, *Egatochoerus jaegeri* gen. et sp. nov. (TF 2812); B, *Doliochoerus quercyi*, inversed (GAR 480, Collections of the Laboratoire de Paléontologie de Montpellier II); and C, extant *Tayassu*. Upper line shows dorsal views, lower line lateral views. The bones are shown at about the same scale. Abbreviations: lat. proc. = lateral process on the dorsolateral side of the bone; fib. f. = fibular facet; astr. calc. f. = astragalo-calcaneal facet.

The lower molars are strongly worn, but on the lingual side of the teeth it is possible to distinguish two mesial and distal lobes separated by a deep groove. In addition, the four main cusps (protoconid, metaconid, hypoconid and entoconid) seem to be associated with small accessory crests but no additional cusps. The size of the lower molars increases from M/1 to M/3, and on the latter, the hypoconulid displays a third distal lobe narrower than the anterior ones (Text-fig. 4; dimensions Table 1).

The lower incisors are relatively small and their morphology indicates that they were probably emerging almost horizontally from the mandible. I/2 displays a narrow, rectangular and linguolabially compressed crown. Its lingual face shows a slight basal swelling of the enamel, and its labial face is almost flat. Its root is rectilinear and is about three times the length of the crown. The morphology of I/2 recalls those of *Perchoerus* and *Tayassu* (Text-fig. 5B). I/3 is reduced, as in *Perchoerus*, conical, and its crown is slightly linguolabially compressed. Its labial face is somewhat convex, and there is no basal swelling on its lingual face. Its root is very short (Text-fig. 5C). I1/ is obliquely worn by the abrasion of I/1. The crown is labiolingually compressed and the root is short but broad. The lingual face is slightly concave with a groove running from the apex of the crown to its base. Mesially, this groove is limited by a sharp edge with a small basal swelling of the enamel.

TEXT-FIG. 7. Comparison of internal view of calcanei of A, *Egatochoerus jaegeri* gen. et sp. nov. (TF 2814); B, *Doliochoerus quercyi* (GAR 459, Collections of the Laboratoire de Paléontologie de Montpellier II); and C, extant *Tayassu*. The bones are shown at about the same scale. Abbreviations: fib. proc. = fibular process; astr. calc. f. = astragalo-calcaneal facet; cub. fac. = cuboid facet; sust. tali f. = facet for the *sustentaculum tali*.

The labial face is very slightly concave, and the crown does not have serrate cutting edges, as in *Perchoerus* (Text-fig. 5A; dimensions Table 1).

Among the postcranial material found in association with the dental remains, two astragali and a calcaneum can be attributed to *Egatochoerus*.

The astragalus of *Egatochoerus* is slender, with the proximal trochlea wider and longer than the distal one. The distal trochlea is rotated medially with respect to the proximal trochlea. The sagittal ridge on the distal trochlea is sharp. The sustentacular facet is mediolaterally convex and occupies the whole width of the plantar face. A very slight ridge occurs on the medial side of the sustentacular facet. In lateral view, an articular facet corresponding to the fibula runs along the whole anterior part of the proximal trochlea. The facet joins a small lateral process on the dorsolateral side of the bone that articulates with the fibular process of the calcaneum. Distally, a large facet occurs and articulates with the anteromedial part of the calcaneum (Text-fig. 6).

The calcaneum is slender with a laterally compressed *processus calcanei*. On its distal end, it inflates as a bilobed process (*tuber calcanei*) that is divided by a slight groove (*flexor digitalis pedis superficialis*). Medially, the *sustentaculum tali* is massive and displays a somewhat circular articular facet for the sustentacular facet of the astragalus. On the dorsal face of the calcaneum, the fibular process is short and it displays on its anterior edge a flat articular surface for the fibula. On its medial side, a kidney-shape facet corresponds to the small lateral process of the lateral face of the astragalus. On the anterior side of the calcaneum, a narrow elongated facet articulates with the cuboid. This facet displays an angle of about 50° with the *processus calcanei*. An

TABLE 2. Dimensions of postcranial elements of *Egatochoerus jaegeri* gen. et sp. nov. LH = lateral height; TDDT = transverse diameter of the distal trochlea; TDPT = transversal diameter of the proximal trochlea; TH = total height; TDPC = transverse diameter of the *processus calcanei*; TDST = transverse diameter of the *sustentaculum tali*; HFP = height of the fibular process (all measurements are in mm).

Astragalus	LH	TDDT	TDPT	
TF 2812	23·3	10·5	10·5	
TF 2813	23·6	10·6	10·8	
Calcaneum	TH	TDPC	TDST	HFP
TF 2814	41·9	6·0	9·8	4·4

anteromedial facet articulates with the lateral part of the distal trochlea of the astragalus. The ventral side of the calcaneum somewhat inflates under the *sustentaculum tali* and the fibular process (Text-fig. 7).

COMPARISONS

In the present work, *Egatochoerus* will be compared with the European genera *Propalaeochoerus*, *Palaeochoerus*, *Doliochoerus*, the North American genus *Perchoerus* and the Chinese genus *Odoichoerus* because these Palaeogene suoids display morphologies close to that of the form described here. In addition, postcranial material will also be compared with that of *Doliochoerus* and of extant *Tayassu*. The main characters of the principal genera discussed in the text are shown in Table 3.

Propalaeochoerus. The mandible of *Propalaeochoerus* is much shallower than that of *Egatochoerus*, with a fused symphysis and a very weak angular process. In addition, *Egatochoerus* differs from *Propalaeochoerus* and *Palaeochoerus* in its P/4 with weaker hypoconid and entoconid, less well developed paraconid, protoconid less mesial to the metaconid and talonid slightly narrower than trigonid. In *Egatochoerus*, the lower molars are more square in occlusal view, and the waist between the two lobes is much deeper. The upper molars of *Egatochoerus* are slightly more square with narrower mesial and distal cingulum.

Palaeochoerus. The European species of *Palaeochoerus* differ from *Egatochoerus* in their larger size, their upper molars with stronger labial cingula and with lingual cingula (in *P. typus* Pomel, 1847 for example), with a more reduced metaconule, indistinct mesial and distal accessory cusps, less bulbous cusps and in their more slender mandible.

Doliochoerus. According to Ginsburg (1974, p. 60), *Doliochoerus quercyi* possessed a P/4 recalling the lower carnassial tooth of a carnivore, with its reduced metaconid, and the protoconid linked by a crest to a lingual and well expressed paraconid. This structure is also observed in *Egatochoerus*. However, it must be stressed that the lower canine in *Egatochoerus* is less curved, and that its internal and external faces form a more open angle than in *Doliochoerus quercyi*. In addition, the increasing size of lower premolars is more pronounced in *Egatochoerus*, its mandible is deeper, and the depth of its horizontal ramus increases backwards. The upper molars of *Doliochoerus* are also more bulbous, the accessory cusps are smaller and hidden in crests, and its P4/ is better developed. Finally, the two species of the European genus are larger than *Egatochoerus*.

Despite these differences, several derived characters are shared between *Doliochoerus* and *Egatochoerus*: general structure of the molars, P/4 with bifid apex and distinct paraconid and talonid, occurrence of a small talonid on P/3 and symphysis reaching P/3. However, *Egatochoerus* also displays a more conservative condition than *Doliochoerus* by its less developed P/4, its upper molars with weaker crests, its less molarized P4/ and by its smaller size.

Perchoerus. The North American *Perchoerus* is known from the middle Chadronian (upper Eocene, see Stucky 1992) to the Whitneyan (middle Oligocene). This genus differs mainly from

TABLE 3. Comparative table of the main characters of the principal genera discussed in the text.

	Egatochoerus	Doliochoerus	Perchoerus	Propalaeochoerus	Palaeochoerus	Tayassu
Mandible Deepness of mandible	Deep Yes	Shallow No	Deep Yes	Shallow No	Shallow No	Deep Yes
Angular process downwardly salient	Yes	No	Yes	No	No	Yes
Lower canine vertical	Yes	No	Yes	Yes	Yes	Yes
P/1	Lost	Retained	Retained	Retained	Retained	Lost
P/4 talonid	Weakly developed	Strong	Strong	Strong	Strong	Strong
Position of paraconid on P/4	Low	High	Low	High	High	High
P/4 talonid narrower than trigonid	Yes	Same width	Yes	Talonid wider than trigonid	Same width	Same width
Size reduction of premolars anteriorly	Strong	Weak	Strong	Weak	Weak	Strong
Sulcus between lobes of lower molars	Deep	Weak	Deep	Weak	Weak	Weak
Width of first and second lobes of M/3	1st = 2nd	1st > 2nd	1st > 2nd	1st > 2nd	1st > 2nd	1st > 2nd
Lingual cingulum on P4/	No	Yes (weak)	Yes (weak)	Yes (strong)	Yes (weak)	No
Occlusal outline of upper molars	As long as wide	Wider than long	Wider than long	Wider than long	Wider than long	As long as wide
Labial cingulum of upper molars	Weak	Strong	Strong	Strong	Strong	Strong
Accessory cusps on upper molars	Two, distinct	Fused in crests	Three, distinct	Fused in crests	Fused in crests	Fused in crests
Lingual roots of upper molars	Fused	Fused	?	Fused	Distinct or fused (1)	Distinct

Egatochoerus in its larger size, the retention of P/1, and by the slightly longer talonids of its P/3 and P/4. The common features shared by *Egatochoerus* and *Perchoerus* (molar and premolar structure, morphology of the mandible) suggest a close relationship between the two taxa. However, *Egatochoerus* is more primitive than *Perchoerus* in having a slightly less molarized P/4 and by the less developed diastema in the lower premolar row. On the other hand, the loss of P/1 in *Egatochoerus* indicates a more advanced condition for the Asian form.

The systematic position of Odoichoerus uniconus *Tong and Zhao, 1986*

The fragmentary mandible attributed to *Odoichoerus uniconus* from the lower Oligocene of China (Tong and Zhao 1986) differs strongly from *Egatochoerus* in its much shallower horizontal ramus, its narrower lower molars with better developed talonid, yet with extremely reduced hypoconulid on M/3 and mainly by the structure of its P/4, which is a very simple, triangular and sharp tooth. The Chinese species, as suggested by Tong and Zhao (1986), appears to be closer to Neogene forms such as *Taucanamo* and *Albanohyus* by the very primitive morphology of its P/4. However, *Taucanamo* is larger, its lower molars are much more complex, and its P/4 is sharp and made up of only one main cusp. The latter character suggests a position for *Odoichoerus* outside the family Tayassuidae which is characterized, among other features, by the presence of a more molarized P/4. The dental and mandibular morphologies of the Chinese species warrant an attribution to the family Suidae.

Postcranial skeleton

The postcranial elements of *Egatochoerus* permit comparisons with the genera *Doliochoerus* and *Tayassu*, the astragalus of *Perchoerus* being unknown.

The astragalus of *Egatochoerus* is slender, with the proximal trochlea wider and better developed than the distal trochlea, whereas the latter is about the same width as the proximal trochlea in the other two genera (Text-fig. 6). The astragali of *Egatochoerus* and *Tayassu* are about the same height, but in *Tayassu* this bone is wider and more massive. The axes of the proximal and distal trochleae are in a slightly more open angle in *Tayassu* than in *Egatochoerus* and *Doliochoerus*. On the other hand, the gulley of the proximal trochlea is wider in *Tayassu* and *Egatochoerus* than in *Doliochoerus*. In these three taxa, the articular facet for the cuboid is reduced and narrower than that for the navicular. Moreover, the groove between these two facets is much more marked in *Tayassu* and *Egatochoerus* than in *Doliochoerus* in which this surface is rather flat. The astragalus of *Egatochoerus* thus displays a morphology slightly closer to that of *Tayassu* (dimensions Table 2).

The proportions of the calcanei are similar in the three forms. The major difference is the occurrence of a posteroventral extension of the *sustentaculum tali* in *Tayassu*, which is absent in the fossil taxa (Text-fig. 7). This structure also displays an almost circular articular facet in all three genera (dimensions Table 2). One can also observe that the orientation of the facet for the *sustentaculum tali* becomes more vertical from *Egatochoerus* to *Tayassu*. This can be correlated with the articulation between the astragalus and the calcaneum and thus with the position of the hind limb which displays a more acute angle between the tibia and the metapodials in *Egatochoerus* and a more open angle between these two elements in *Tayassu*. The hind limb of *Egatochoerus* was probably less erected than that of *Tayassu*. In addition, it must be stressed that the fibular process is better developed from *Egatochoerus* to *Tayassu*, suggesting that the posterior limb of *Tayassu* is more limited in its lateral motions than that of *Doliochoerus* and *Egatochoerus*.

Among the tarsal bones, both the astragali and the calcanei display diagnostic characters discriminating the different genera. The structure of these bones varied considerably during evolution according to the constraints linked to body weight, the motions of the posterior limb and thus to adaptations for different displacements of these bones.

DISCUSSION

Dental characters in Tayassuidae

It must be stressed that the distinction between the two families Tayassuidae and Suidae is unclear. The genus *Palaeochoerus*, the familial status of which has been diversely interpreted, is a typical example of this, as Pickford (1988) has recently pointed out. Indeed, Viret (1961) classified this genus among the Suidae, Ginsburg (1974) included it in Tayassuidae, while Pickford (1988) returned it to the Suidae and created the subfamily Palaeochoerinae. Finally, Hellmund (1992) referred the genera *Palaeochoerus* and *Propalaeochoerus* to the Tayassuidae. According to Pickford, the subfamily Palaeochoerinae is the most ancient among the Suidae, and closely related to the Tayassuidae, based on retention of numerous primitive characters in this group. As Pickford claimed, the systematic position of *Palaeochoerus* depends on the choice of characters. In addition, he made the Tayassuidae the stem-group of the Suoidea in his proposed cladogram (1988, p. 10).

Most of the dental characters proposed by Pickford (1988) to define the Palaeochoerinae are primitive and can also apply to the Tayassuidae. In addition, Pickford gave a list of characters of the base of the skull; these unfortunately are impossible to compare with the Thai form. However, *Egatochoerus jaegeri* can be distinguished dentally from representatives of the subfamily by the presence of a marked diastema between the canine and P/2 and by the absence of a partial overlapping of the talonid of M/3 by the base of the ascending ramus.

Pickford and Morales (1989) compiled a list of dental and cranial characters that they considered typical of the family Tayassuidae and differentiating it from the Suidae: lower canine vertical and close to the lower premolars in the dental row, absence of symphyseal splaying of the lower jaw in the canine area (as is the case in Suidae), lower premolars in a closed series, strongly developed trigonid on P/4, gradual increase in size and complexity of the lower premolar crown morphology from front to rear, lower and upper molars lingually and labially poorly salient, system of grooves (= 'Furchenplan' of von Hünermann 1968) poorly expressed and rather thin enamel. It is possible to add two characters that Pickford and Morales did not give (but later cited by Pickford 1988, pp. 12, 13), namely the lower dental row which is not oblique in comparison with the longitudinal axis of the horizontal ramus (in Suidae, the dental row crosses over the body of the mandible from antero-labial to postero-lingual) and the weak linguo-labial thickness of the horizontal ramus (in Suidae, lower molars display very divergent roots, and the linguo-labial thickness of the horizontal ramus is important). These features also occur in *Egatochoerus*, *Perchoerus* and the extant *Tayassu*, in addition to a downward and backward salient angular process of the mandible, the anteriorly shallowness of the horizontal ramus, the shallow symphysis and the absence of a retromolar space behind M/3. This suggests an immediate phylogenetic relationship between the Asiatic form and *Perchoerus*. Indeed, *Egatochoerus* seems to have more affinities with the North American genus than with any other known taxon from the Old World. *Egatochoerus* is more primitive than *Perchoerus* and is characterized by numerous conservative features (morphology of the angular process and of the P/4, P4/ without lingual cingulum, upper molars with poorly defined accessory cusps and without lingual cingulum,...), which indicate that the origin of the Suoidea, and probably the Suidae, is rooted among the Tayassuidae. On the other hand, the difficulties encountered in establishing a set of derived characters for the Tayassuidae that allows us to distinguish them from the Suidae illustrate the close relationships that exist between the two families. Among these characters, one can cite the early molarization of P/4, and later that of P/3. This molarization began as early as the late Eocene, as displayed by the lower jaw of *Egatochoerus*, and possibly earlier in Tayassuidae, because Suidae are characterized by an increasing chewing surface on molars. A process of reversion in the molarization of the lower premolars in Suidae that occurred from the Miocene can thus be envisaged.

The tayassuid–hippopotamid relationships

Pickford (1989) suggested that hippopotamids could have originated from an Old World peccary stock. As part of this theory, he proposed that if the lineage of hippopotamids could be traced back to the Oligocene tayassuid *Doliochoerus*, the unknown ancestor of *Doliochoerus* might be found among the Cebochoeridae (an Artiodactyl family known exclusively from the Eocene of Europe), as suggested by Pearson (1927). Observation of the dental morphology of the Cebochoeridae indicates that there is probably no relationship between them and *Doliochoerus*. Indeed, the Cebochoeridae differ from the Suidae and Tayassuidae in their upper molars with labial cusps linked by a crest and with lingual cusps that tend to be selenodont, a two-rooted upper canine, lower molars with crescentiform labial cusps, a caniniform P/1 and in their incisiform lower canine. The similarities that may have occurred between the two groups can be considered only as convergences, and the hypothesis proposed by Pickford (1989) is therefore less likely. It is more logical to derive *Doliochoerus* from less specialized forms such as the Chinese *Odoichoerus* which displays a primitive suid morphology.

Biogeographical hypothesis of the family Tayassuidae during the Palaeogene

It is not yet possible to demonstrate that the Krabi mammal fauna is certainly older than the North American localities that have yielded the oldest remains of *Perchoerus*, but several lines of evidence argue for such a conclusion. The first occurrence of *Perchoerus* in North America is estimated to be at about 36–35 Ma (middle Chadronian according to Stucky 1992). However, an age comprised between 40 and 35 Ma (late Eocene) has been proposed for Krabi (Ducrocq *et al.* 1991). In addition, the anthracotheres associated with *Egatochoerus* in Krabi display a dental morphology intermediate between that of the upper Eocene taxa from Pondaung in Burma and that of the anthracotheres from the basal Oligocene of Monteviale in Italia (Ducrocq *et al.* 1992; Ducrocq 1994). The dental morphology of the anthracotheres from Central Europe, radiometrically dated from about 37 Ma (Fejfar 1987), is nearly identical with that of the forms from Thailand and suggests that a similar age could be envisaged for the Krabi fauna (Ducrocq 1994). In addition, the occurrence of the most primitive known anthracothere *Siamotherium krabiense* in Krabi (Suteethorn *et al.* 1988, Ducrocq *et al.* 1992) strongly argues for an early late Eocene age for the mammalian association from Thailand. Finally, given the evolutive degree of both *Egatochoerus* and *Perchoerus*, it is possible to suppose that the Asian form is slightly older than the North American taxon.

The earliest known representative of the family Tayassuidae (*Egatochoerus jaegeri*) appeared in the late Eocene of South East Asia (South Thailand). This form migrated into North America during the late Eocene and gave rise to *Perchoerus* which locally radiated up to the middle Oligocene (Whitneyan). The Oligocene evolution of North American tayassuids took place, apparently without influence from the Old World taxa, and the North American peccaries never left the New World after their first arrival there. On the basis of the present fossil record, *Egatochoerus* cannot be related directly to other Asian suoids, and it could be suggested that the Thai species became extinct in Asia without leaving descendants. Another migration occurred from Asia into Europe during the late Eocene or the early Oligocene, but it cannot yet be determined if *Egatochoerus* was at the origin of this migration, given the poor fossil record of Palaeogene tayassuids. The Oligocene genera *Doliochoerus*, *Propalaeochoerus* and *Palaeochoerus* 'suddenly' appeared in western Europe without known direct ancestors. The tayassuids evolved in Europe and Asia up to the late Miocene. On the basis of their dental and mandible morphologies, it is unlikely that the European Palaeogene tayassuids derived from an ancestor such as *Egatochoerus*. The direct ancestry of the European taxa should be investigated among conservative forms resembling the Chinese *Odoichoerus*.

CONCLUSIONS

Egatochoerus jaegeri from the upper Eocene of Thailand is the oldest known member of the Tayassuidae, and its affinities with the North American genus *Perchoerus* confirm that faunal exchanges were possible in Asia and North America at least during the late Eocene. The migration probably occurred from Asia to the North American landmass given the more archaic condition of the Thai specimen with respect to the New World form, and a South East Asian origin for the tayassuids seems actually well established. The ancestor of the European tayassuids *Doliochoerus*, *Propalaeochoerus* and *Palaeochoerus* is unknown at present but it could be sought in a form more conservative than *Egatochoerus*. In addition, the Chinese species *Odoichoerus uniconus* is tentatively removed from the Tayassuidae mainly on the basis of its P/4 morphology, and is referred to the Suidae.

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