

New remains of primitive ruminants from Thailand: evidence of the early evolution of the Ruminantia in Asia

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A new tragulid, *Archaeotragulus krabiensis*, gen. n. et sp. n., is described from the late Eocene Krabi Basin (south Thailand). It represents the oldest occurrence of the family which was previously unknown prior to the Miocene. *Archaeotragulus* displays a mixture of primitive and derived characters, together with the M structure on the trigonid, which appears to be the main dental autapomorphy of the family. We also report the occurrence at Krabi of a new Lophiomerycid, *Krabimeryx primitivus*, gen. n. et sp. n., which displays affinities with Chinese representatives of the family, particularly *Lophiomeryx*. The familial status of *Iberomeryx* is discussed and a set of characters is proposed to define both Tragulidae and Lophiomerycidae. Results of phylogenetic analysis show that tragulids are monophyletic and appear nested within the lophiomerycids. The occurrence of Tragulidae and Lophiomerycidae in the upper Eocene of south-east Asia enhances the hypothesis that ruminants originated in Asia, but it also challenges the taxonomic status of traguloids within the Ruminantia.

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Introduction

Ruminant artiodactyls are the most geographically and ecologically successful living group of large mammals. The suborder Ruminantia is traditionally defined as artiodactyls possessing a cuboid fused with the navicular and incisiform lower canines. The former character is ambiguous because of its occurrence in the late Eocene ruminant-like genus *Amphimeryx* from Western Europe (Sudre 1977), whereas the second feature is rarely preserved in fossils of primitive ruminants. The latter are classically divided into two main groups whose content is discussed. Pecora (horned ruminants) and Tragulina-Pecora are nowadays the most diversified ruminants, and fossils are well known during the Neogene in Eurasia, North America and Africa. Globally, the phylogenetic relationships between early ruminants are misunderstood, mainly because of the scarcity of remains of Eocene Asian ruminants. *Archaeomeryx*, the earliest known ruminant from Shara Murun (late–middle Eocene, Mongolia), is sometimes

considered as the oldest of the Pecora group (Matthew & Granger 1925a; Colbert 1941).

Tragulina are believed to be of primitive grade among ruminants (e.g. Janis 1987). This group includes both North American and Eurasian forms, and may be considered as a paraphyletic group of primitive non-pecoran ruminants (Scott & Janis 1993), although no consensus is established concerning the first unambiguous Pecora. During the late Palaeogene, tragulines was diversified and one classically comprised by Eocene North American traguloids and some ambiguous Eurasian forms whose affinities are discussed below. Among North American Palaeogene traguloids, hypertragulids are the most primitive forms. This is mainly based on their cranial and postcranial characters. Recently, however, Vislobokova (1998) pointed out the presence of a new hypertragulid ruminant from the late Eocene of Khoer-Dzan (Mongolia), extending the geographical range of hypertragulids to Asia during the Palaeogene. Leptomerycids

are mainly known from the late Eocene of North America onwards, but some unclear and poorly documented Asian forms are related to leptomerycids (e.g. McKenna & Bell 1997). Their cranial and postcranial features indicate a more derived state in comparison with hypertragulids (Webb & Taylor 1980; Janis 1987), and Geraads *et al.* (1987) considered leptomerycids as being close to Old World tragulids.

Tragulids are traditionally considered as the most primitive living ruminants (e.g. Janis 1984), and they still survive as tropical relicts: the water chevrotains (*Hyemoschus*) of Africa and the mouse deer or Asiatic chevrotain (*Tragulus*) of south-east Asia. They are characterized by their skeletal and dental features which are primitive within ruminants, and their general shape, digestive system and ethology which are reminiscent to those of pigs (Dubost 1965). The family Tragulidae is the only surviving family from the assumed paraphyletic Tragulina (Janis 1984). Therefore, the evolutionary history of tragulids remains unknown before the Eurasian and African Miocene *Dorcatherium*, although the potential Eocene occurrence of Tragulidae has been previously expected by both morphological (e.g. Webb & Taylor 1980) and molecular (e.g. Miyamoto *et al.* 1993) data. Sudre (1984) considered the Oligocene genus *Cryptomeryx* (since put in synonymy with *Iberomeryx* by Bouvain *et al.* 1986) from the Oligocene of Quercy (France), Benara (Georgia) and north India (Gabounia 1964; Sudre 1984; Nanda & Sahni 1990) as the oldest Tragulidae. However, Janis (1987) suggested that this problematic genus should be included in the new family Lophiomerycidae, mainly because of the presence of an anterior cingulid and of the figure eight shape trigonid on lower molars. While the first version of this paper was in review, Guo *et al.* (2000) published the description of the lophiomerycid *Zbailimeryx* from the late-middle Eocene of central China, thus confirming the antiquity of the Lophiomerycidae in Asia.

The Tertiary Krabi Basin, located in Peninsular Thailand (Fig. 1), has yielded more than 30 mammalian species, most of which are typical of swampy environments (Ducrocq 1994). The study of the Krabi fauna has led to a late Eocene age being proposed for this community, on the basis of faunal comparisons (Ducrocq *et al.* 1997; Ducrocq 1999) and magnetostratigraphic investigations (Benammi *et al.* 2001). The purpose of this paper is to describe new tragulid and lophiomerycid dental remains from the late Eocene of Thailand, and to discuss the origin and early diversification of the ruminants in south-east Asia.

In this work, we followed the nomenclature from Gentry & Hooker (1988) and Moya-Sola (1988) for the upper and lower teeth. The term 'M structure', first used by Mottl (1961), is the same as the 'Σ structure', sometimes used by later authors (e.g. Qiu & Gu 1991), and the cristid obliqua is equivalent to the prehypocristid. According to Janis (1987),

the *Dorcatherium* fold refers to the fold occurring on the posterior side of the metaconid on the lower molars of some primitive ruminants and extant tragulids (see 'Discussion' section). The 'entoconidian groove' refers to the two parallel folds (thus forming a groove) occurring on the mesial side of the entoconid. This structure was first pointed out by Pilgrim (1928) in *Indomeryx arenae*, and may be considered as equivalent to the *Zbailimeryx* fold (Guo *et al.* 2000). Finally, the *Tragulus* fold (Geraads *et al.* 1987) more specifically designates the fold situated on the posterior side of the protoconid and basally linked to the prehypocristid (Fig. 3, see later).

We used the following abbreviations: TF, Thai fossil at the Department of Mineral Resources, Bangkok, Thailand; WIF/A 415, specimen housed in the Museum Repository of Wadia, Institute of Himalayan Geology, Dehra Dun, India.

Systematics

Order ARTIODACTYLA Owen, 1848

Suborder RUMINANTIA Scopoli, 1777

Family TRAGULIDAE Milne-Edwards, 1864

Genus *Archaeotragulus*, gen. n.

Type species. *Archaeotragulus krabiensis*, sp. n. (Fig. 2A–D) only known species of genus.

Locality. Wai Lek lignite pit, Krabi Basin, southern Thailand.

Horizon and age. Upper level of the main lignite seam of Wai Lek pit (Formation B2, see Bristow 1991), late Eocene (see Ducrocq *et al.* 1995).

Etymology. From the Greek 'archaeos' that refers to the archaic dental morphology of the Thai specimen; 'meryx', Greek for ruminant. The species name refers to the Krabi Basin where the material was found.

Holotype. Fragmentary mandible with P₂–M₂ (TF 2997).

Paratype. Fragmentary lower jaw with M₁–M₃ (TF 2989). All specimens are housed in the Department of Mineral Resources (DMR) of Bangkok, Thailand.

Diagnosis. Small primitive ruminant with lower molars resembling those of *Dorcatherium* by the presence of a typical tragulid M structure at the rear of the trigonid (Fig. 4) and the derived pattern of its lower premolars, including the lack of a metaconid and the presence of a longitudinal groove on the posterior half of P₄. Differs from *Dorcatherium* by its smaller size, its cusps more labio-lingually compressed, the lack of an ectostylid, the presence of a well-marked 'entoconidian groove' opening forwards, the presence of a rudimentary hypoconulid on M₂₋₃ and by the transversely compressed hypoconulid on M₃. Differs from *Iberomeryx* by its larger size,

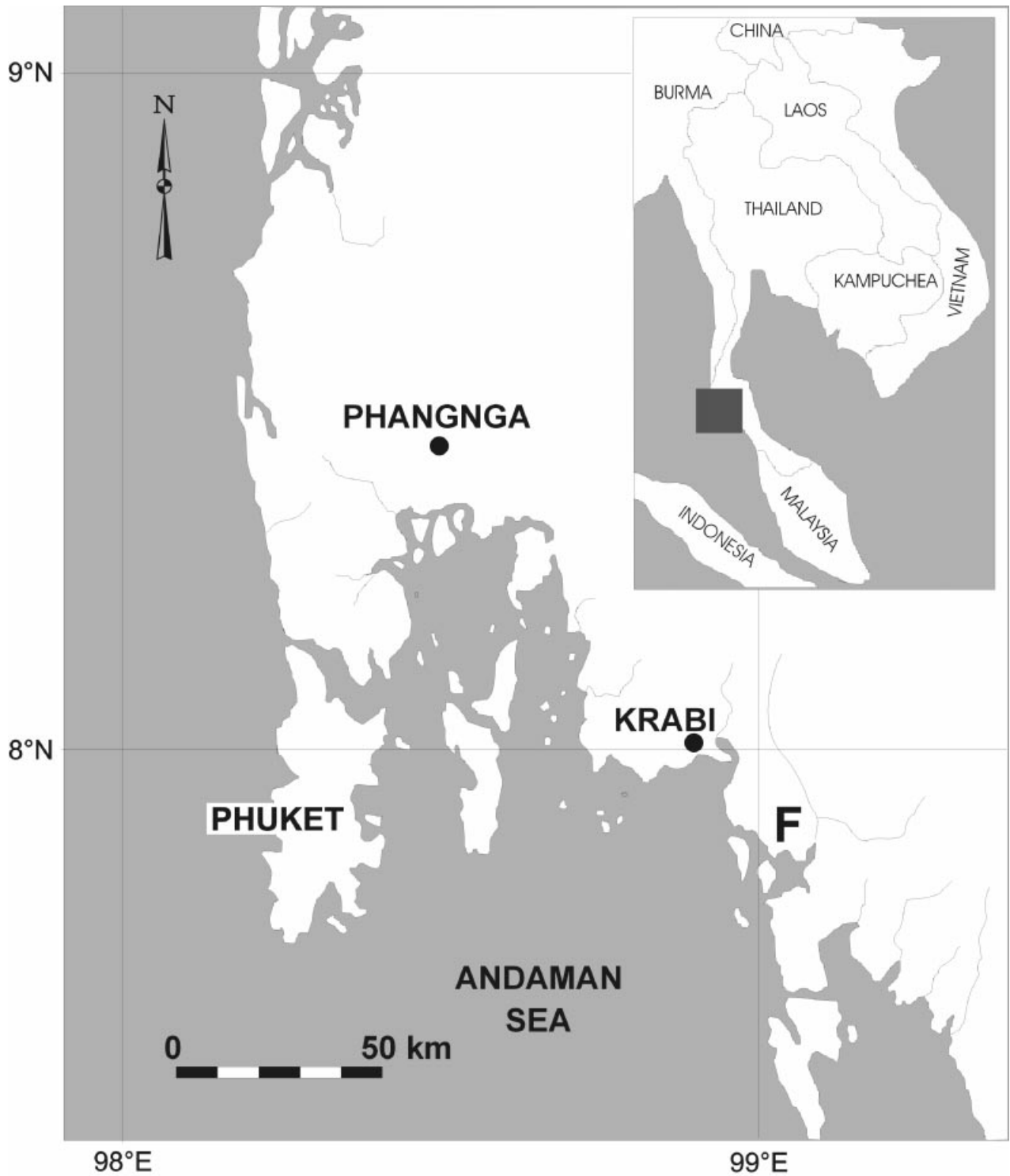


Fig. 1 Map of Thailand showing the location of the Krabi Basin where the fossils described here were found. The Wai Lek mine that yielded the specimens reported here is represented by the letter 'F'.

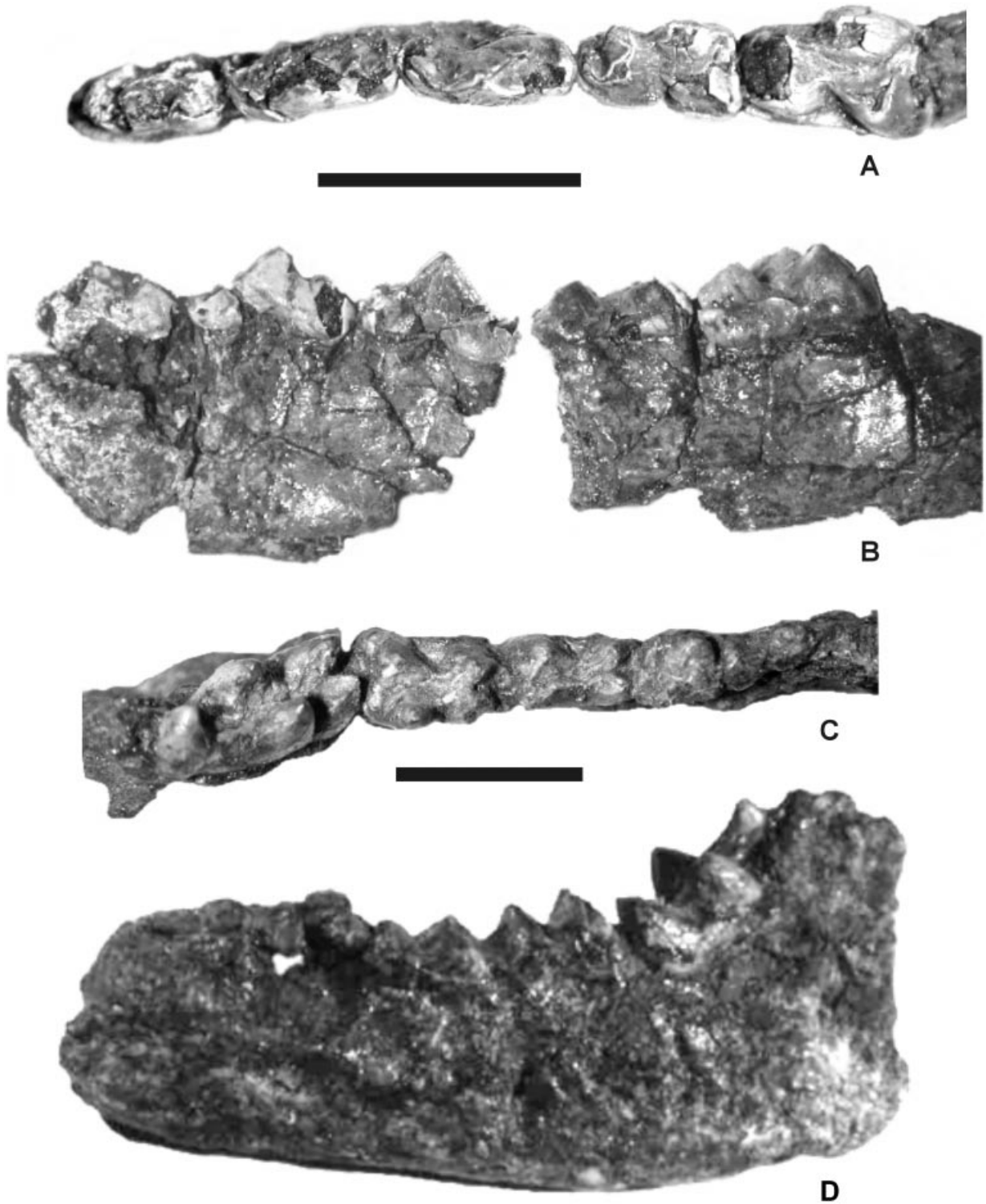


Fig. 2 A–D. *Archaeotrragulus krabiensis*, gen. n. et sp. n. (TF 2997 type). —A, B. Fragmentary left lower jaw with P₂–M₂ in occlusal (A) and labial (B) views. —C, D. Fragmentary left lower jaw with M₁–M₃ (TF 2989) in occlusal (C) and labial (D) views. Scale bar = 10 mm.

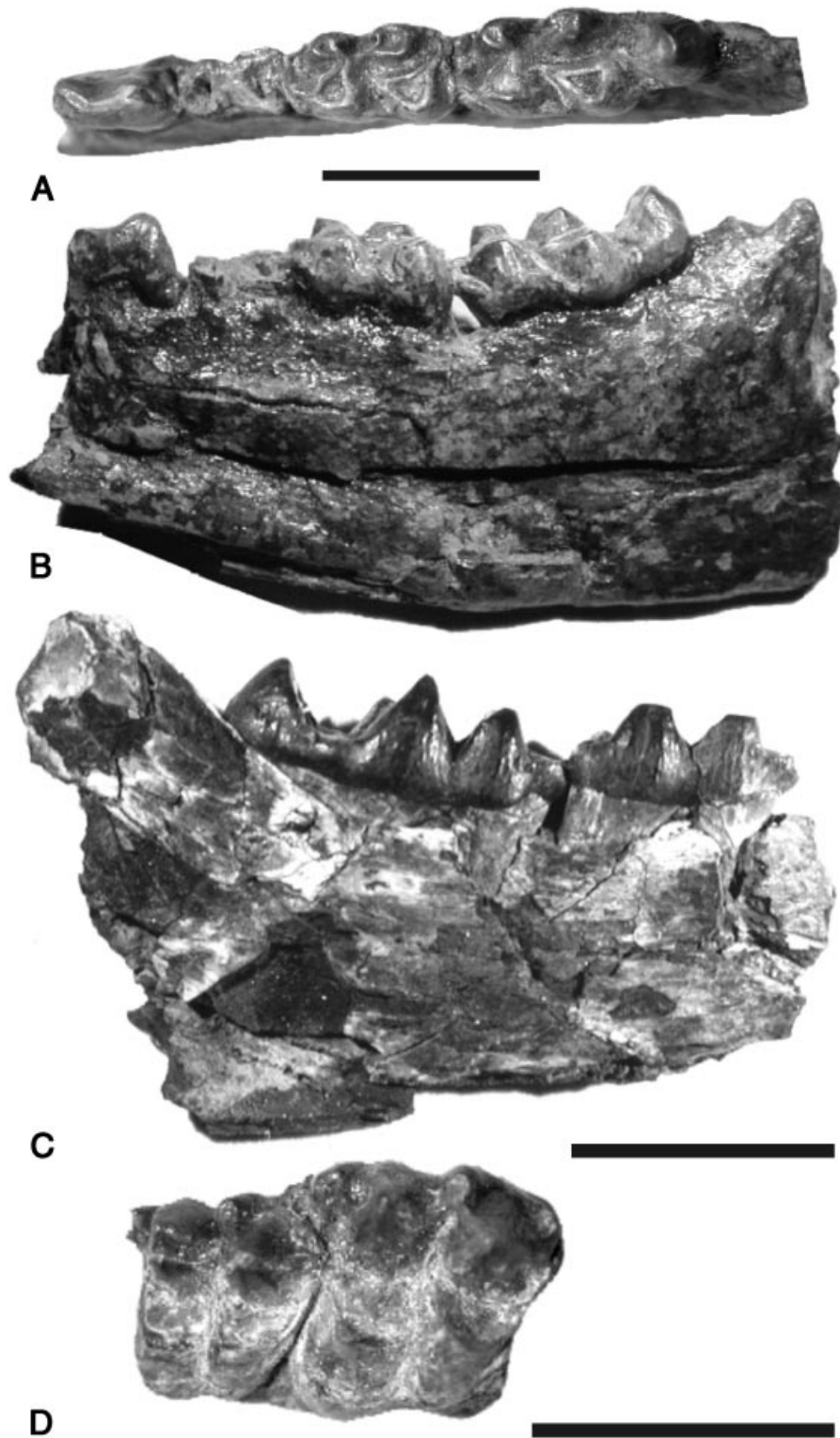


Fig. 3 A–D. *Krabimeryx primitivus*, gen. n. et sp. n. (TF 2676 type). —A, B. Fragmentary left lower jaw with P₄–M₃ in occlusal (A) and labial (B) views. —C. Fragmentary left lower jaw with M₂–M₃ (TF 2677) in labial view. —D. Fragmentary maxillary with M₁–M₂ (TF 2993) in occlusal view. Scale bar = 10 mm.

Table 1 Dental measurements (mm) of *Archaeotragulus krabiensis*, gen. n. et sp. n. and *Krabimeryx primitivus*, gen. n. et sp. n. from Krabi. Asterisks indicate estimated values. The letters ‘p’ and ‘m’ indicate, respectively, a lower premolar and a lower molar, both followed by the rank of the tooth. The capital letter ‘M’ indicates an upper molar.

| | | | | Width | |
|------------------------|---------|--------|-------|----------|---------|
| | | Length | | Trigonid | Talonid |
| <i>Archaeotragulus</i> | TF 2989 | m1 | 7.2 | 3.53 | 3.95 |
| | | m2 | 7.45 | 4.56 | 4.85 |
| | | m3 | 10.48 | 4.65 | 4.95 |
| | TF 2997 | p2 | 5.55 | 2.57 | 2.57 |
| | | p3 | 7.16 | 3.49 | 3.49 |
| | | p4 | 7.04 | 3.93 | 3.93 |
| | | m1 | 6.83 | 3.17 | 3.97 |
| | m2 | 7.28 | 4.19 | 5.05 | |
| <i>Krabimeryx</i> | TF 2988 | p4 | 6.82 | 2.51 | 2.76 |
| | | m1 | 9.1 | 3.23 | 3.94 |
| | | m2 | ? | 4.42* | ? |
| | | m3 | 13.55 | ? | 5.8* |
| | TF 2676 | p4 | 5.7 | 2.28 | 2.8 |
| | | m1* | 4.85? | ? | ? |
| | | m2 | 7.75 | 4.12 | 4.43 |
| | | m3 | 11.6 | 4.53 | 4.81 |
| | TF 2987 | m3 | 12.9 | 5.61 | 6.2 |
| | TF 2677 | m2 | 8.91 | 4.9 | 5.48 |
| | | m3 | ? | 5.44* | 5.52* |
| | TF 2998 | m2 | 8.55 | 3.95 | 4.45 |
| | | m3 | 11.61 | 4.35 | 5.04 |
| TF 2993 | M1 | 7.18 | 6.56 | | |
| | M2 | 8.55 | 8.2 | | |

its cristid obliqua more lingually orientated, a well-marked M structure on the posterior side of the trigonid, the absence of an ectostylid and by its transversely compressed and pinched hypoconulid on M_3 . *Archaeotragulus* further differs from *Zhailimeryx* by its M structure, the lack of rudimentary paraconid on the lower molar and by its P_4 lacking both distinct metaconid and entoconid.

Description. Close in size to the Miocene tragulid *Siamotragulus* (Thomas *et al.* 1990). The base of the mandible relatively deep; longitudinal groove extending from front to back on the base of the lingual face of the mandible; no retromolar space occurring on the type.

Premolars (Table 1) are triangular in lateral view and increase in length from front to back; P_2 is the smallest premolar; P_3 slightly more elongated than P_4 ; P_2 and P_3 displaying almost the same configuration with a strong protoconid linked by a straight longitudinal crest to a small, mesio-lingually situated paraconid. The latter crest is slightly curved lingually, and joins the more lingually situated paraconid. Conical hypoconid weaker and lower than the protoconid, located behind a strong protoconid at the rear of the tooth. Posterior side of hypoconid forming a slight but

well-marked transverse spur on P_3 , where it delimits a small, lingually open rounded basin; talonid basin absent on P_2 , with more lingually situated hypoconid.

P_4 with paraconid well developed and more lingually situated; preprotocristid joining the paraconid and slightly lingually bent; two parallel crests extend from the apex of the strong protoconid to the posterior border of the tooth, forming a triangular and narrow basined talonid; tiny hypoconid extending along the posterior border of the tooth; groove delimited by both parallel crests opened postero-lingually which lingual crest without trace of metaconid probably fused in the postero-lingual crest or with the protoconid.

Lower molars (Table 1) bunoselenodont, rectangular in shape and transversely compressed, increasing in size from M_1 to M_3 ; trigonid always narrower than the talonid because of the great size of the hypoconid; lingual cusp transversely compressed; rear labial cusp crescentic in shape; paralophid extending mesio-lingually; front side of the metaconid rounded without any crest; trigonid largely open with strong and mesio-lingually orientated paralophid forming a thick anterior cingulum and a prominent anterior border of molar; anterior cingulum extending on the labial side of the protoconid where it becomes thinner; posterior side of the protoconid displaying a deep groove with the outer flank linked to the cristid obliqua (not homologous to the cervoid *Palaeomeryx* fold); inner flank of the protoconid connected with the outer flank of the well-marked *Dorcatherium* groove at the rear of the metaconid and open at the lingual base of the metaconid on worn tooth; fusion of both crests into a single edge joining the preentocristid, involving an ‘M’ shape on the posterior side of the trigonid; entoconid rounded posteriorly and situated forward with respect to the hypoconid; metaconid at the same level as the protoconid; entoconid displaying a deep groove well developed on the unworn M_3 (TF 2989), but attenuated on M_1 and M_2 ; posthypocristid extends disto-lingually reaching the postero-lingual corner of the tooth and displaying an enamel swelling at its distal end; the latter might be interpreted as the remains of a hypoconulid, as Sudre (1984) described for *Iberomeryx*; hypoconulid of M_3 labially twisted and transversely compressed; two parallel crests extending forward from the apex of the hypoconulid to reach the rear of the second lobe without any accessory small cusp; no distinct ectostylid, but a weak labial cingulid extends between the hypoconid and hypoconulid. Enamel slightly wrinkled.

Family LOPHIOMERYCIDAE Janis, 1987

Genus *Krabimeryx*, gen. n.

Type species. *Krabimeryx primitivus*, sp. n. (Fig. 4A–D) only known species of the genus.

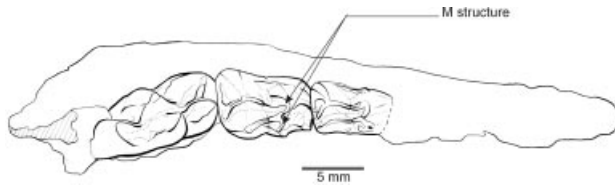


Fig. 4 Drawing of the lower jaw of *Archaeotragulus krabiensis*, gen. n. et sp. n. (TF 2989) showing the M structure on the distal side of the trigonid of the lower molars (see text for explanations). Scale bar = 5 mm.

Locality. Wai Lek lignite pit, Krabi Basin, southern Thailand.

Horizon and age. Upper level of the main lignite seam of Wai Lek pit (Formation B2, see Bristow 1991), late Eocene (see Ducrocq *et al.* 1995)

Etymology. From Krabi Basin, where the fossils were found, and from ‘meryx’, the Greek suffix for ruminant.

Holotype. Fragmentary mandible with left P_4 – M_3 (TF 2676).

Paratype. Fragmentary lower jaw with right M_2 – M_3 (TF 2677, Bang Pu Dam).

Other material. Fragmentary lower jaw with left M_2 – M_3 (TF 2998, Wai Lek), fragmentary lower jaw with left P_4 – M_3 (TF 2988, Bang Pu Dam), right M_3 (TF 2987, Wai Lek), fragmentary maxillary with left M_1 – M_2 (TF 2993, Wai Lek). All specimens are housed in the Department of Mineral Resources (DMR) of Bangkok, Thailand.

Diagnosis. Small primitive ruminant with lower molars morphologically close to those of *Zhailimeryx*. Differs from *Zhailimeryx* in its lingual cusps on lower molar more labiolingually compressed, its entoconid displaced forward with respect to the hypoconid, the lack of both rudimentary paraconid and hypoconulid on M_{1-2} and in its P_4 with a metaconid more distally situated and without distinct entoconid. Further differs from *Lophiomeryx* by its smaller size, its labial cusps less selenodont on lower molars, the remains of a *Dorcatherium* fold and by a distinct groove on the anterior side of the entoconid. *Krabimeryx* further differs from *Lophiomeryx* by its P_4 with a metaconid more distally situated and less individualized. *Krabimeryx* is larger than *Iberomeryx*, and it may be distinguished from it in having a well-marked ‘entoconidian groove’, a more transversely compressed hypoconulid and in lacking an ectostylid.

Description. Mandible deep and slender with depth decreasing frontwards; angular process rising just behind M_3 (although broken on the type); no retromolar space. P_4 longer than M_1 , triangular in lateral view, slightly wider at the level of the heel, displaying a main central cusp (protoconid) and a small lingual cusp (paraconid) situated at the end of the mesio-lingual edge of the main cusp, but lower than it; single crest

extending backwards from the protoconid for less than half of the length of the talonid where it bifurcates; short transversely orientated crest joins a tiny metaconid; crest extending along the labial and posterior border of the tooth, and delimiting a rounded, basined and postero-lingually open talonid.

Lower molars bunoselenodont, rectangular in shape with four cusps (except for M_3 that displays a hypoconulid), increasing in size from M_1 to M_3 , the latter being twice as long as M_1 ; lingual cusps slightly transversely compressed and higher than the labial ones; paralophid low and extending mesio-lingually and then transversely forming a distinct pre-fossid; anterior side of the metaconid rounded with a distinct *Dorcatherium* fold on its posterior side, the trigonid opening lingually and mesially; thick anterior cingulum extending just below the paralophid; no trace of labial cingulum, except between the protoconid and the hypoconid, nor ectostylid; posterior side of protoconid without any fold linked to the cristid obliqua as in the tragulids; lingual and labial parts of the protocrisid transversely orientated and fusing to form a single low crest that joins to the labial flank of the entoconidian groove on the mesial side of the entoconid; entoconid shifted forwards with respect to the hypoconid, with its posterior side rounded and lacking any fold; prehypocrisid (= cristid obliqua) mesio-lingually orientated without any connection, as in *Lophiomeryx*, although a very slight remnant of a *Tragulus* fold obviously occurs on TF 2676; posthypocrisid extending postero-lingually until the postero-lingual corner of the tooth; slight postcingulum on M_1 and M_2 ; hypoconulid of M_3 labially curved and transversely slightly compressed; third lobe of M_3 with two crests directed forwards and delimiting a shallow valley without any accessory cusp; weak labial cingulum between hypoconid and hypoconulid; enamel slightly wrinkled.

Upper molars brachyodont, bunoselenodont and quadrutubercular, with M_2 larger than M_1 ; paracone displaying a strong labial rib very excavated on the mesial side, whereas the labial wall of the metacone is almost flat with only a very weak rib; parastyle strong and excavated; mesostyle strong; no trace of metastyle; protocone wider and less seleniform than the slightly antero-posteriorly compressed metaconule; postprotocrisid posteriorly orientated and ending against the mesial side of the metaconule; thick cingulum surrounding the protocone and the mesial half of the metaconule, but no entostyle occurring. Enamel slightly wrinkled.

Comparisons

The specimens attributed to *Archaeotragulus* show striking affinities with representatives of the family Tragulidae. The presence of the M structure on the posterior wall of the trigonid, the talonid wider than the trigonid and the morphology of the premolars (close to those of *Dorcatherium*) fully corroborate the tragulid status of the Thai fossils.

However, the time interval that separates the Thai tragulid and the much younger ones does not allow precise relationships to be inferred between them. The fossil record of Palaeogene tragulids is very scarce and, in the present work, *Archaeotragulus* will be compared with the ambiguous Oligocene Eurasian genus *Iberomeryx* and the Neogene tragulids. Comparisons with Lophiomerycidae and some of the poorly known Eocene genera from south Asia (*Gobiomeryx*, *Indomeryx*, *Notomeryx*), all belonging to primitive pro-dremotheriids (Guo *et al.* 1999), will also be made.

Iberomeryx is known from the early Oligocene (MP 22) to the mid-Oligocene (MP 25) of Quercy (France) in Western Europe. The genus also occurs in the late Oligocene of Benara (Georgia) and Kargil (India). *Iberomeryx* mainly differs from *Archaeotragulus* by its smaller size, its weaker fold on the posterior side of the protoconid, the presence of a remaining paraconid (see 'Discussion' section), a strong and bulbous ectostylid and by the absence of a thick labial and anterior cingulid surrounding the protoconid on the lower molars as in TF 2997 (less marked on TF 2989). Moreover, the cusps of *Iberomeryx* are more bulbous and less transversely compressed, and its molar prehypocristid is more lingually orientated than in *Archaeotragulus*, in which this crest is almost longitudinal and always linked to the *Tragulus* fold (*sensu* Geraads *et al.* 1987; see 'Discussion' section). The hypoconulid of M_3 is also more transversely compressed and more elongated in *Archaeotragulus*, while it is stronger, rounded and wide in *Iberomeryx*. The latter also displays a strong anterior crest that runs down from the apex of the hypoconulid. *Iberomeryx* exhibits a P_3 similar to that of the Thai form, with a smaller paraconid. In addition, contrary to the Thai form, the P_4 of *Iberomeryx* is shorter than M_1 with a stronger and more conical paraconid. Both genera also share a distinct metaconid extended backwards, but the posterior depression of P_4 is posteriorly closed in *Iberomeryx* and it is lingually open in *Archaeotragulus*. The latter further differs from *Iberomeryx* by a slight lingual incision at the point where the groove is open and the posterior border of the tooth rises up to form a distinct spur. The lower molars of *Iberomeryx* also resemble those of the Thai form, but they differ by the strong and very bulbous lingual flank of the *Dorcatherium* fold, that tends to develop an incipient metastylid in the more recent *I. parvus* from Benara. Moreover, the lower molars of *Iberomeryx* do not display a labial cingulid as in TF 2997.

The first undoubted fossil tragulid is the early Miocene genus *Dorcatherium* from Africa and Eurasia. The numerous species referred to *Dorcatherium* mainly differ by their size (West 1980). However, the smallest species, known only by isolated upper molars (*D. minimus* from the Chinji Formation, Lower Siwaliks, Pakistan), is smaller than *Archaeotragulus*. The Thai form consistently appears to be more primitive in several characters, although the polarity of some dental

features is difficult to determine. *Archaeotragulus* can be distinguished from *Dorcatherium* by its more transversely compressed cusps, the absence of a premetacristid and of an ectostylid, the shape of the hypoconulid of M_3 , which is strong and rounded in *Dorcatherium*, and by its smooth enamel. However, *Archaeotragulus* shows marked similarities with *Dorcatherium*, such as the distinct M structure on the posterior side of the trigonid, with a cristid obliqua always linked to the *Tragulus* fold, the presence of a weak groove on the mesial side of the entoconid, the P_4 without distinct metaconid, the two parallel crests extending backwards from the protoconid and the narrow basin lingually open.

Another tragulid known in the Miocene and Pliocene of the Siwaliks is the large genus *Dorcabune*. Pilgrim (1915) suggested that *Dorcabune* was morphologically close to *Dorcatherium*, although more primitive than the latter. *Dorcabune* combines a set of original characters that makes it unique among all described tragulids. *Dorcabune* is characterized by its very bunodont molars with thick and wrinkled enamel and the presence of the 'double fold' (Pilgrim 1915: 226) on the protocone of the upper molars. Pilgrim (1915) also pointed out a well-developed cingulum, a premetacristid closing the trigonid anteriorly and a well-pronounced M structure with a double fold on the posterior side of the protoconid on the lower molars. According to Qiu & Gu (1991), some of the European species of *Dorcatherium* might be assignable to *Dorcabune*. Although Colbert (1935) considered its unquestionable tragulid affinities, Gentry (1978) claimed that *Dorcabune* might be a primitive anthracothere. With the exception of the M structure and the presence of a weak entoconid groove, *Dorcabune* does not display other apomorphies with *Archaeotragulus*. The former differs from the Thai form by its larger size and by its molars more bunodont and less transversely compressed. It is therefore clear that no close relationship exists between the two taxa, and according to Gentry (1978) the tragulid status of *Dorcabune* can be questioned.

Siamotragulus from the middle Miocene of the Pong Basin (north Thailand; Thomas *et al.* 1990) and *Yunnanotherium* from the late Miocene of Lufeng (China; Han 1986) display a peculiar derived morphology close to that of the extant genus *Tragulus*: their molars are more selenodont and hypsodont, their premetacristid is well developed and closes the anterior side of the trigonid, and they display a strong ectostylid. Although *Archaeotragulus* is known only from dental material, it appears to be more primitive by the shape of its molars with an open trigonid, and by the less derived morphology of its premolars. According to Thomas *et al.* (1990), the premolars of *S. sanyathanai* are very trenchant, and its P_4 presents a simple postero-lingual extension of the metaconid as in all other tragulids. Moreover, Han (1986) pointed out, in *Yunnanotherium*, the long, narrow and transversely

compressed premolars and the talonid of P₄, which displays two short edges with a notch on the lingual side of the tooth as in the Thai form. The premolar pattern seems thus to be constant in tragulids and corroborates the tragulid status of *Archaeotragulus*.

Guo *et al.* (2000) have recently described *Zhailimeryx* from the late–middle Eocene Heti Formation (Shanxi Province, China). *Zhailimeryx* now appears to be the oldest lophiomerycid in Asia. *Archaeotragulus* may be distinguished from *Zhailimeryx* by its premolar pattern (without conical metaconid situated next to the protoconid) and by the presence of the ‘M structure’ on the lower molars. Moreover, Guo *et al.* (2000) pointed out the presence of both rudimentary paraconid and hypoconulid in *Zhailimeryx*. The specimens referred to *Archaeotragulus* do not display any trace of a paraconid, but the presence of a tiny hypoconulid is assumed, despite the poorly preserved lower molars on the holotype. The tragulid from Krabi is nearly the same size as the Chinese species of *Lophiomeryx*, although narrowed. The European species of *Lophiomeryx* differ from *Archaeotragulus* by their larger size, the morphology of their P₄, which displays a strong conical metaconid without posterior extension to form a lingual wall, their lower molars lacking the M structure (although *L. shinaoensis* from the late Eocene of China appears to possess a *Dorcatherium* fold; see ‘Discussion’ section) and by their cristid obliqua more lingually orientated that joins the connection between the preentocristid and postmetacristid. However, *Lophiomeryx* exhibits a lingually open trigonid as in other Palaeogene traguloid ruminants. The dental characters of *Lophiomeryx* appear to be more derived than those of Tragulidae, notably in the premolar morphology with a distinct and conical metaconid on P₄.

Trofimov (1957) previously referred *Gobiomeryx* from the early Oligocene of Erguil Obo (Mongolia) and from the middle Oligocene of Kazakhstan (Musakulova 1963, 1971) to the Tragulidae. This genus is now included in the pecoran family Proremotheriidae (Guo *et al.* 1999). The molars of *Gobiomeryx* are transversely strongly compressed and they display a metastylid and a premetacristid that close the trigonid lingually. No fold is observed either on the posterior side of the trigonid or on the mesial side of the entoconid, and the third lobe of M₃ possesses a lingual accessory small cusp. All these features suggest that close relationships are unlikely between *Gobiomeryx* and *Archaeotragulus*. Finally, the Thai form can be distinguished from *Indomeryx* from the Eocene Pondaung fauna (Myanmar) and from the Baise Basin (Guangxi, China) by its lingually open trigonid, the lack of metastylid (although the latter feature seems to be variable in *Indomeryx*) and by the presence of an ‘M structure’ on the posterior wall of the trigonid. However, the morphology of P₄ with two parallel crests extending backwards from the protoconid resembles that of *Archaeotragulus*. The entoconid groove is well

marked in *Indomeryx*, although this character is known to vary with the tooth state of wear (Métais *et al.* 2000). Thus, this character might have appeared in parallel in different lineages of primitive ruminants. Finally, the Chinese genus *Notomeryx*, now included in the Proremotheriidae, is distinguished by its larger size, the robustness of the mandible, its lower molars with outer cusps more seleniform in shape, the closed trigonid and the postero-labial side of the entoconid displaying a double-ridge (Guo *et al.* 1999).

Among all Palaeogene traguloid ruminants from Eurasia, *Krabimeryx* is most strikingly similar to the oldest lophiomerycid *Zhailimeryx* from the late–middle Eocene of China (Guo *et al.* 2000), although because of the retention of both minute paraconid and hypoconid, the Chinese form appears as the most primitive lophiomerycid in our phylogenetic analysis (see below). The main shared characters between both genera are the presence of a *Dorcatherium* fold and of an entoconid groove (*Zhailimeryx* fold for Guo *et al.* 2000). However, *Zhailimeryx* differs from the Thai genus by the structure of its P₄, which displays a conical metaconid situated at the level of the protoconid, and a distinct entoconid. Among lophiomerycids, *Lophiomeryx* is a well-known (Brunet & Sudre 1987) and geographically widespread genus from the late Eocene and Oligocene of Eurasia. The south-eastern Asian species seems to be most similar to *Krabimeryx*. Miao (1982) described two new species of *Lophiomeryx* from the late Eocene or early Oligocene of the Shinao Basin (Guizhou Province, China). The smallest species (*L. gracilis*) is close to *L. shinaoensis*, which is characterized by its lower molars with the shortened hypolophid and the lengthened paralophid, and its smaller size in comparison with European species. Moreover, Miao (1982) pointed out the occurrence of a ‘metaconid posteriorly extending into a spur on an unworn specimen’, and Janis (1987) claimed that the lower molars of *L. shinaoensis* possess a *Dorcatherium* fold and a distinct ectostylid as is the case in *Iberomeryx*. In addition, it seems that its P₄ with a backwards projecting metaconid is similar to those of tragulids, although Miao (1982) focused on the widely opened P₄ on its lingual side as in the large Oligocene European form *L. chalaniati*. Therefore, except for the ectostylid, the Chinese species of *Lophiomeryx* are closer to *Krabimeryx*, despite the tragulid morphology of P₄. *Krabimeryx* further resembles *Lophiomeryx* in its P₄ with a talonid open lingually and an incipient metaconid, although the latter is well developed in European species of *Lophiomeryx*. The metaconid is more posteriorly situated from the protoconid in *Krabimeryx*, involving a shortened and rounded talonid. This feature might be the primitive state for P₄ in lophiomerycids, although *Iberomeryx* displays a rather *Bachitherium*-like pattern of P₄. However, both a strong metaconid and a posteriorly rounded talonid, as in the Thai form, have been observed on some specimens of *L. chalaniati* from the Oligocene

of Quercy (France). Another striking feature is the well-developed postcingulid on M_{1-2} which is often connected to a bulge occurring in the postero-lingual corner of the tooth, at the extremity of the hypolophid. This structure occurs in *L. turgaicus* from the Oligocene of Chelkar Teniz (Kazakhstan) and in both *L. mouchelini* and *L. chalaniati* from Western Europe. This cingulid decreases in thickness from the summit of the lingual side of the crown to the base of the postero-labial side of the tooth. This character also occurs in *Krabimeryx*, but is much weaker in *Archaeotragulus*. Although Janis (1987) considered the presence of the anterior cingulid on the lower molars as a synapomorphy for all ruminants, except the more primitive leptomerycids, hypertragulids and tragulids, there is a weak anterior cingulid in both Eocene North American ruminants and in *Archaeotragulus*. However, *Krabimeryx* can be distinguished from *Lophimeryx* by its more bunodont cusps, the presence of a distinct groove on the mesial side of the entoconid and of a *Dorcatberium* fold (the latter seems to occur in Chinese species of *Lophimeryx*) and by the wider hypoconulid of M_3 . Lophimerycids lack a well-marked M structure on the posterior side of the trigonid, although a weak remnant of this structure occurs in *Iberomeryx* and *Krabimeryx*.

The upper molars attributed to *Krabimeryx* also seem to be similar to *L. shinaoensis* in terms of their weak rib on the labial side of the metacone, the occurrence of a thick inner cingulum and by their well-developed metaconule higher than the protocone on unworn molars, with the anterior crest joining the mesostyle. However, the upper molars of *Krabimeryx* have less salient styles, involving the absence of an excavated metacone, in comparison with *L. chalaniati*. Moreover, the rib on the labial wall of the paracone is very strong in the Thai form, whereas this feature tends to disappear from M_3 to M_1 in *L. chalaniati*. Furthermore, some molars of the latter display an incipient entostyle, although this character does not seem to be constant. Thus, the lower dentition of *Krabimeryx* is close to that of *Lophimeryx*, but in the upper molars it significantly differs from that of the Thai form.

Krabimeryx primitivus is also morphologically close to the lophimerycid *Iberomeryx*. Both genera share a well-marked *Dorcatberium* fold, a distinct postcingulid and a wide hypoconulid on M_3 . However, the upper molars display the most striking similarities: a strong parastyle and mesostyle; a prominent labial rib on the paracone and a weak one on the metacone, which is not excavated as in *Lophimeryx*; the occurrence of a lingual cingulum, although the latter is very faint in *Iberomeryx*. The Thai form can, however, be distinguished from *Iberomeryx minus* by its slightly larger size, the P_4 lacking a deep groove extending from the protoconid to the rear of the tooth as in the pecoran(?) genus *Bachitherium*, the metaconid of P_4 weaker and more postero-lingually situated, the labial cusps of the molars less selenodont, the

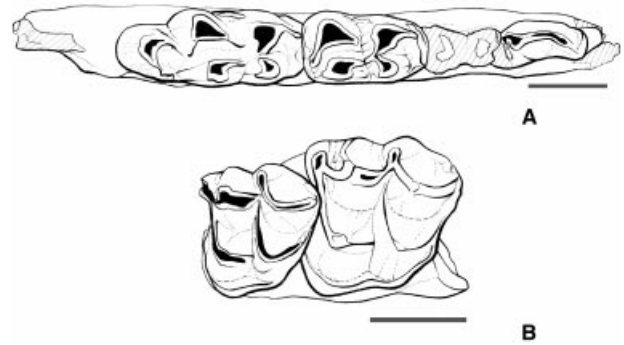


Fig. 5 Drawing of the fragmentary lower jaw of *Krabimeryx primitivus*, gen. n. et sp. n. (TF 2676 type) in occlusal view (A), and the upper molars (TF 2993) in occlusal view (B). Scale bar = 5 mm.

presence of a well-marked groove on the mesial side of the entoconid and by the lack of an ectostylid on lower molars. Furthermore, the premetaconule-crista is bifurcated at the base of the paracone in *Iberomeryx*, whereas this crest is single and orientated towards the mesostyle in *Krabimeryx*. Sudre (1984) considered that the bulge occurring at the extremity of the hypolophid on M_1 and M_2 of *Iberomeryx* might be an hypoconulid. We have not observed this tiny hypoconulid in any specimen but, in agreement with Sudre (1984), a remnant of the hypoconulid may be present on the lower molars of *Iberomeryx*.

Krabimeryx can be distinguished from *Archaeotragulus* by its P_4 which shows a tiny but distinct metaconid, the lack of an M structure at the rear of the trigonid and the posterior cingulid on the lower molars and by its wider hypoconulid on M_3 (Fig. 5). Therefore, although both Thai forms described here are morphologically close, the structure of the P_4 and the lack of M structure on the posterior side of the trigonid led us to consider *Krabimeryx* as the most primitive representative of lophimerycids. The retention of features such as the *Dorcatberium* fold and the entoconidian groove in both *Archaeotragulus* and *Krabimeryx* supports a common origin of both lophimerycids and tragulids.

Finally, the lophimerycid from Krabi shares some features with some prodremotheriid Pecora. As previously emphasized, the entoconidian groove is present in both ruminants from Krabi, but it also occurs in *Indomeryx*. However, the configuration of the trigonid on the lower molars makes close relationships between these taxa unlikely.

Discussion

Significance of the M structure

In its overall morphology, *Archaeotragulus krabiensis* is more similar to *Dorcatberium*, although it shares several dental features with the supposed lophimerycid genus *Iberomeryx*. However, the presence of a well-marked M structure on the

posterior face of the trigonid on the lower molars seems to be a valuable dental feature that allows the Thai form to be included in the Tragulidae.

It must be pointed out that the distinction between the families Tragulidae and Lophiomerycidae is unclear. The genus *Iberomeryx* is a typical example of this ambiguous status and of the difficulty in characterizing the early representatives of both families. Sudre (1984) classified this genus among the Tragulidae on the basis of the well-defined *Dorcatherium* fold on its lower molars, whereas Janis (1987) included it together with *Lophiomeryx* in the Lophiomerycidae because of the occurrence of the figure eight on the trigonid and of the mesial cingulum on the lower molars. However, according to Brunet & Sudre (1987), the homogeneity of the genus *Lophiomeryx* is doubtful, and Vislobokova (1998) recently assigned *Lophiomeryx gobiae* from the late Eocene of Khoer-Dzan (eastern Mongolia) to the new hypertragulid genus *Praetragulus*. Moreover, the generic status of *L. shinaoensis* and *L. gracilis* from the early Oligocene of Shinao in China (Miao 1982) remains ambiguous. Indeed, these species display a molar morphology similar to that of *Iberomeryx*, and they exhibit a distinct *Dorcatherium* fold on their lower molars. The latter feature is also observed on *Lophiomeryx* from the early Oligocene of Dètàn (Fejfar 1987), although we noticed an incipient metastylid rather than a true *Dorcatherium* fold on the specimen. The *Lophiomeryx* species from the Oligocene of Montalban in Spain (Moya-Sola 1988) also displays a weak *Dorcatherium* fold, but this structure is always inconstant/variable in European lophiomerycids. Contrary to the complete M structure which characterizes the tragulids, the *Dorcatherium* fold seems to appear in parallel in early traguloids as stressed by Janis & Scott (1987). In *Lophiomeryx*, the labial and lingual protocristid are short and transversely orientated, and they fuse at their extremities to form a single ridge extending backwards towards the entoconid, as described by Moya-Sola (1988). The labial protocristid (or metacristid) extends backwards to form the labial flank of the *Dorcatherium* groove in *Iberomeryx*, contrary to *Lophiomeryx* in which this crest is almost transversely orientated. Moreover, it must be pointed out that a few specimens of *Indomeryx* from Pondaung also possess a very weak *Dorcatherium* fold, even if the overall dental morphology of *Indomeryx* is obviously greatly different from that of traguloids (Métais *et al.* 2000). This feature is considered by Janis (1987) as an apomorphic character for ruminants which appears in parallel in different lineages. Indeed, a similar homologous(?) structure occurs in some specimens of *Bachitherium* and *Gelocus* from Eurasia, and in North American *Leptomeryx*. Consequently, the strict homology of the various structures observed on the posterior side of the metaconid in several lineages of primitive ruminants may be questioned.

Classically, the term '*Dorcatherium* fold' has been defined by Mottl (1961) as a pair of folds occurring on the distal side of the trigonid. Janis (1987) restricted the *Dorcatherium* fold to the lingual crest extending posteriorly from the tip of the metaconid to its base. The length of this crest seems to be variable with respect to the wear of the tooth, as stressed in the present description of *Archaeotragulus*. The shortened *Dorcatherium* fold might recall an incipient metastylid, even if the strict homology between these structures is not yet well demonstrated. Thus the *Dorcatherium* fold and the labial protocristid develop a groove at the posterior face of the metaconid. It would be consequently more accurate to use the term '*Dorcatherium* groove' for the structure on the posterior face of the metaconid in *Archaeotragulus*, *Iberomeryx*, *Krabimeryx*, *Zhailimeryx* and the Neogene tragulids.

The posterior face of the protoconid also possesses a single fold linked to the cristid obliqua and usually called the '*Palaeomeryx* fold' after Mottl (1961). However, this fold rather characterizes cervoid taxa, in which it is more labially orientated and is not linked with the cristid obliqua as in the tragulids. Geraads *et al.* (1987) have proposed the term '*Tragulus* fold' when this crest is linked to the cristid obliqua. As the '*Palaeomeryx* fold' and the '*Tragulus* fold' are probably not homologous, it is more suitable to designate them by a distinct name. Nevertheless, the extant *Tragulus* does not exhibit a fold on the posterior side of its protoconid, and the cristid obliqua is not linked to the rear of the protoconid. Although *Tragulus* is derived in comparison with Palaeogene tragulids and has obviously lost this primitive dental structure characterizing the early representatives of the family, it would be suitable to avoid the term '*Tragulus* fold' for fossils of tragulid lower molars. According to us, the 'M structure' is more appropriate to designate such a dental character which comprises both '*Tragulus* fold' and *Dorcatherium* fold (*sensu* Janis 1987). It seems that many features appeared in parallel in several lineages of ruminants, and the apparent homology is sometimes deceptive. In this way, Janis (1987) claimed that all specimens of *Bachitherium* display a *Dorcatherium* fold. The lower molars of *Bachitherium* share a short lingual protocristid with a very attenuated groove on its lingual side. As pointed out by Sudre (1995), the *Dorcatherium* fold is very attenuated in *Bachitherium* and more lingually situated. In our opinion, this pseudo-*Dorcatherium* groove is linked to the transverse orientation of the labial protocristid in relation to the advanced selenodont state of the labial cusps in *Bachitherium*. The presence of a *Dorcatherium* fold is always determined by the shape of the protoconid on the lower molars. Owing to the lengthening of the lingual protocristid, which extends between metaconid and entoconid in fully selenodont forms (North American Leptomerycids, hypertragulids and the European *Bachitherium*), the *Dorcatherium* fold does not occur.

However, most of the bunoselenodont Eocene and early Oligocene ruminants from Eurasia, such as *Lophiomeryx*, *Iberomeryx* and *Krabimeryx*, display this structure, probably linked to the forward orientated paracristid as suggested by Moya-Sola (1988).

The functional meaning of the M structure is unclear, but it may be related to the more efficient chewing mechanism. The increasing crested surface on the posterior face of the trigonid might form an additional shearing surface linked to a change of diet. As emphasized by Scott & Janis (1993), the complete loss of this feature might be a consequence of an increasing selenodonty, although it can be occasionally observed on the bovid genus *Cephalophus*. During occlusion, the *Dorcatherium* fold area occludes with the mesial side of the protocone. However, the dental pattern of the upper molars is so constant among primitive ruminants that it may be difficult to differentiate certain taxa. Besides, no peculiar shearing surface on the upper molar occluding area may be observed in traguloids for which upper molars are known. Jernvall *et al.* (1996) have shown that the upper molar crown type diversity greatly increases during the Eocene with a maximum in the late Eocene (well marked in Asia), paralleling the taxonomic diversity among ungulates. Moreover, the growth of crests in molars of some lineages of artiodactyls is probably related to a shift of feeding towards a more folivorous diet (Webb 1977; Collinson & Hooker 1991). The studies of late Lutetian flora from Europe testify to a blunt cooling with the appearance of a drier climate (Collinson *et al.* 1981). With the vegetation becoming more fibrous, the growth of wear surfaces associated with the appearance of new crests probably improved the chewing process (Hunter & Jernvall 1995). These structures on the lower molars seem to be related to the apparent synchronic development of a selenodont grade in Asia, Europe and North America (Sudre & Lecomte 2000). However, only 'traguloids' from Asia that dispersed to Europe at the beginning of the Oligocene seem to have developed these structures. Thus, we consider that the M structure has not only adaptive meaning, but also phylogenetic significance.

Another striking feature occurring in *Archaeotragulus*, *Krabimeryx* and *Zbailimeryx* is the groove on the mesial side of the entoconid. This character is also present in some specimens of *Indomeryx*, *Dorcatherium* and in the doubtful tragulid *Dorcabune*. It is absent in *Archaeomeryx* and North American ruminants. This groove is well marked on the fresh teeth (M_3) of *Archaeotragulus*, but it tends to be attenuated on the M_1 of the type (TF 2997). It seems to be more persistent in *Krabimeryx* in which it is related to the mesial extension of the preentocristid towards the trigonid. This groove then disappeared in later more selenodont ruminants, and it can be considered as a symplesiomorphy among Asian primitive ruminants (Métais *et al.* 2000).

The likely Asian origin for ruminants

Among the Palaeogene ruminants from Eurasia, the case of the lophiomerycid *Iberomeryx* is very interesting. This genus is known from the Oligocene of Europe, and was previously mentioned in the literature as *Cryptomeryx gaudryi* (see Sudre 1995 for summary). Gabounia (1964) described a new ruminant from Benara (Georgia) which was represented by a single species, *I. parvus*. Sudre (1984) revised the genus *Cryptomeryx* initially erected by Schlosser (1886) for *Lophiomeryx gaudryi* Filhol 1877 from the oldest Quercy collections. Bouvrain *et al.* (1986) put *Cryptomeryx* in synonymy with *Lophiomeryx*. However, the fossils other than the Filhol type, attributed by Schlosser to *C. gaudryi*, are in fact conspecific with '*Bachitherium*' *minor* Filhol (1882), which is itself congeneric with *Iberomeryx* Gabounia (1964). The single *Iberomeryx* species known in Western Europe is *I. minus* which mainly characterizes the MP 23 Mammal level (Sudre & Blondel 1996). Its P_4 resembles that of *Bachitherium* because of its triangular basined talonid formed by two parallel ridges. However, this feature seems to appear convergently in several lineages of primitive ruminants. A slight concavity occurs just behind the metaconid on the lingual wall by which the postero-lingual side of the tooth is closed, contrary to the P_4 of *Archaeotragulus* and *Dorcatherium*. Furthermore, the orientation of the cristid obliqua is variable on the lower molars of *Iberomeryx*. Some specimens display an attenuate M structure on well-worn M_1 , whereas the unworn M_3 does not possess this structure. The prehypocristid is sometimes connected to the base of the posterior side of the trigonid, but it can also join the labial part of the protocristid together with the lingual protocristid and preentocristid, as in *Lophiomeryx chalaniati* from the middle Oligocene (MP 25) of Western Europe. The familial status of *Iberomeryx* thus remains ambiguous, its dental characters being intermediate between those of lophiomerycids and tragulids. Consequently, *Iberomeryx* might testify to the common origin of both families as suggested by several authors (Brunet & Sudre 1987; Blondel 1997).

The most eastern locality for *Iberomeryx* is from the north of India where it has been reported by Nanda & Sahni (1990). The P_4 of *I. savagei* from the late Oligocene of the Kargil Basin (India) displays a slightly different shape from that of the European representatives of the genus. According to Nanda & Sahni (1990: 3), the posterior depression at the back of P_4 is circular rather than groove-like, as in *I. minus* and other species from Quercy. This morphology of P_4 is reminiscent of that of *Krabimeryx primitivus* from Krabi, suggesting strong affinities between the two genera. Further material would probably show that the Indian form belongs to another traguloid genus distinct from *Iberomeryx*. Moreover, the upper molars (holotype: WIF/A 415) of *I. savagei* display a prominent lingual cingulum which is unknown in

other species of *Iberomeryx* from Western Europe or Benara (Georgia). Although both M_3 referred to *I. savagei* by Nanda & Sahni (1990) are worn, the styles seem to be very salient in comparison with those of the upper molars of the European species of *Iberomeryx*. This upper molar morphology of *I. savagei* strongly recalls some specimens from the Oligocene of the Bugti Hills (in preparation) and further challenges the inclusion of the material referred to *Iberomeryx* from the Kargil Basin to this genus. In fact, it might be necessary to attribute the Indian species to a different genus when this form becomes better known.

Another striking feature seen in *Iberomeryx minus* lower molars is the large and elongated prefossid lingually open by the forward extended paracristid. As pointed out by D. E. Savage *et al.* (unpublished work 1985), this lingual extension of the paracristid is unique among artiodactyls and recalls the lingual extension of the paralophid in several Eocene perissodactyls. At the end of the latter crest of *I. minus*, we observed a distinct bulge which could correspond to a remnant of the paraconid not completely integrated into the paracristid. This remnant of the paraconid rather suggests that the acquisition of tetratuberculy on the lower molars (except for M_3) has been achieved by anterior fusion of the reduced paraconid with the paracristid. As emphasized by Moya-Sola (1988), the configuration of the trigonid of *Archaeomeryx* and *Indomeryx* strongly differs from that of traguloid ruminants. The study of the late-middle Eocene ruminant *Indomeryx* from Pondaung by one of us (Métais *et al.* 2000) shows that the remnant of a paraconid not completely fused with the metaconid occurs in the large species *I. pilgrimi*. These two possible modes of disappearance of the paraconid challenge a unique ancestry for Ruminantia, although this observation has not yet been confirmed in other primitive traguloid ruminants.

As stressed by several authors, the stem group of ruminants is still unknown and their geographical origin has long been a matter of debate. Although it is known only by dental remains, *Archaeotragulus krabiensis* can be regarded as the most primitive hitherto known tragulid, and it leads us to reconsider the origins of the family and probably of the suborder Ruminantia. With the exception of the well-known *Archaeomeryx*, few Eocene ruminants are described in Asia, and the occurrence of tragulid and lophiomerycid remains in south-east Asia allows us to propose an Asian origin for both families. Several authors (Geraads *et al.* 1987; Moya-Sola 1988; Blondel 1997) have stressed that lophiomerycids were the most primitive ruminants, while Janis (1987) considered their dental characters as derived related to incomplete selenodonty. Additionally, she suggested that *Lophiomeryx* might form the sister taxon to the Pecora. *Lophiomeryx* appeared in Europe during the lower Oligocene (MP 22) with *L. mouche- lini*, in which the posterior lobe of M_3 is strongly reduced as emphasized by Brunet & Sudre (1987). This reduction of the

Table 2 Dental characters used in the construction of the data matrix for the phylogenetic analysis in this paper.

| | |
|------------------------|---|
| <i>Lower premolars</i> | |
| 1 | Mesio-distally elongated (0), shortened (1) |
| <i>Fourth premolar</i> | |
| 2 | Metaconid present (0), absent (1) |
| 3 | Metaconid conical (0), backwards elongated (1) |
| 4 | Metaconid at the level of the protoconid (0), or more distally situated (1) |
| 5 | Posterior groove present (0), absent (1) |
| 6 | Entoconid distinct (0), indistinct (1) |
| <i>Lower molars</i> | |
| 7 | Paraconid well developed (0), rudimentary (1), absent (2) |
| 8 | Trigonid lingually open (0), closed (1) |
| 9 | Premetacristid absent (0), weak (1) |
| 10 | <i>Dorcatherium</i> fold present (0), absent (1) |
| 11 | M structure present (0), absent (1) |
| 12 | Entoconidian groove present (0), absent (1) |
| 13 | Entoconid labio-lingually compressed present (0), absent (1) |
| 14 | Postentocristid absent (0), weak (1) |
| 15 | Posthypocristid reaching the postero-lingual corner of the M_{1-2} (0), ending before (1) |
| 16 | Hypoconulid well developed (0), rudimentary (1), absent (2) |
| <i>Upper premolars</i> | |
| 17 | Protocone on P_2 absent (0), incipient (1), well developed (2) |
| <i>Upper molars</i> | |
| 18 | Lingual cingulum well developed (0), weak (1), absent (2) |
| 19 | Labial rib on metacone strong (0), weak (1), absent (2) |

metaconule (also observed in *L. angarae* from the Oligocene of Mongolia) results in a triangular shape of this tooth, and this configuration is obviously a plesiomorphic character of the family, although the structure and shape of M_3 is unknown in *Krabimeryx*.

Phylogenetic analysis and results

Although the new taxa described above are poorly represented, they provide new insight into the polarity of character states that affect the phylogeny of the entire group Ruminantia. In order to propose a preliminary assessment of their relationships with other traguloid ruminants, a data matrix comprising 19 dental characters across 11 taxa was established (Tables 2 and 3), and the analysis of the data set was run using the heuristic search with PAUP version 3.1.1 (Swofford 1993). The North American genus *Homacodon* and *Diacodexis pakistanensis* from the early-middle Eocene Kuldana Formation in Pakistan were selected for outgroup comparisons. All characters were equally weighted and unordered, except for characters 7 and 16 which are considered ordered by the fact that the reappearance of both paraconid (character 7) and hypoconid (character 16) on the lower molars seems highly unlikely. The analysis yielded one most parsimonious tree (tree length = 42 steps, CI = 0.55, RI = 0.62). *Archaeotragulus* appears as the earliest offshoot within the monophyletic

Table 3 Matrix of characters.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
|------------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|
| <i>Homacodon</i> | 0 | 1 | — | — | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| <i>Diacodexis</i> | 0 | 1 | — | — | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 |
| <i>Lophiomeryx</i> | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 2 | 1 | 1 | 2 |
| <i>Zhailimeryx</i> | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 |
| <i>Krabimeryx</i> | 0 | 0 | 0 | 1 | 1 | ? | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | ? | 0 | 2 |
| <i>Iberomeryx</i> | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 2 | 2 |
| <i>Archaeotragulus</i> | 0 | 1 | — | — | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | ? | ? | ? |
| <i>Dorcatherium</i> | 0 | 1 | — | — | 0 | 1 | 2 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 0 |
| <i>Archaeomeryx</i> | 1 | 0 | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 1 |
| <i>Gelocus</i> | 0 | 0 | 0 | 0 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 2 | 1 |
| <i>Siamotragulus</i> | 0 | 1 | — | — | 0 | 1 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 1 | 0 |

tragulid clade comprising the Miocene genera *Dorcatherium* and *Siamotragulus*. Both the M structure on the lower molars and the lack of metaconid on the lower premolars represent the main dental characters supporting the monophyly of the Tragulidae. Tragulids are nested within the paraphyletic lophiomerycids, in which *Zhailimeryx* appears to be the earliest offshoot of the family (Fig. 6). These preliminary results indicate a basal dichotomy within Ruminantia distinguishing traguloids and ‘Protopecora’, which are represented here by *Archaeomeryx* and *Gelocus*. However, an increase in taxa and character (notably postcranial features) sampling is now necessary to substantiate these assumptions.

The earliest ruminants are known from the middle Eocene of Mongolia with the critical genus *Archaeomeryx* from the Irdin Manha fauna (Matthew & Granger 1925c; Russell & Zhai 1987). *Archaeomeryx* persisted into the later Shara Murun Formation where it is known by a complete skeleton (Matthew & Granger 1925b; Webb & Taylor 1980). In its overall morphology, *Archaeomeryx* appears as the most primitive ruminant (Colbert 1941), although Webb & Taylor (1980) suggested its inclusion within leptomerycids on the basis of more derived characters than in tragulids and hypertragulids. Except for *Archaeomeryx*, the fossil record of Eocene Asian bunoselenodont artiodactyls is very poor and mainly consists of dental remains from central and eastern Asia. Consequently, given the difficulties in understanding the polarity of cranial and postcranial characters (see, for example, Norris 1999), the fossil record of Asian primitive ruminants is so far inadequate to assess the phylogenetic relationships between the early ruminants, even if — for several authors (e.g. Pilgrim 1940) — Asia is supposed to have played a major role in the early differentiation of ruminants. However, several authors have supported a North American origin for ruminants on the basis of the well-documented and diversified fossils of selenodont artiodactyls which suddenly appeared in the early Uintan (middle Eocene) of North America (Stucky 1998). Among them, hypertragulids and leptomerycids had an adaptive radiation at the middle–late

Eocene boundary continuing into the Oligocene (Webb 1998). As stressed by Emry (1978), the earlier hypertragulid *Simimeryx* displays several primitive dental features in comparison with other hypertragulids, and its inclusion in the family may be questioned. Indeed, except for *Simimeryx*, the molars of hypertragulids display a fully selenodont dental pattern in comparison with that of contemporaneous Asian ruminants, such as *Archaeomeryx*, *Indomeryx* or *Lophiomeryx*. However, the occurrence of the hypertragulid *Praetragulus* in the late Eocene of Khoer-Dzan (Mongolia) led Vislobokova (1998) to infer an Asian origin for the hypertragulids, and hence of the ruminants. Gazin (1955) proposed that the North American homacodontid genus *Mesomeryx* might be closely related to *Simimeryx*, involving the first offshoot of the ruminants in North America. More recently, Stucky (1998: 359) reaffirmed that ‘the homacodonts probably include the basal members of both tylopods and ruminants’. Additionally, Joeckel & Stavas (1996: fig. 1) rehabilitated the previous ideas proposed by Scott (1899) about the supposed close relationships between protoceratids (formerly included within Tylopoda) and ruminants on the basis of basicranial anatomy. Moreover, a study of the Uintan (late–middle Eocene) most plesiomorphic protoceratid *Leptotragulus*, which occurred together with the first appearance of North American ruminants in the fossil record, led Norris (2000) to suggest that North American hypertragulids and leptomerycids might be closely related to leptotragulines. Likewise, the fusion of the cuboid and the navicular in the European genus *Amphimeryx* from Escamps (MP 19; Sudre 1977) led several authors (e.g. Geraads *et al.* 1987) to include the amphimerycids among ruminants, thus involving a possible European origin for ruminants. Nonetheless, Sudre (1984) demonstrated that amphimerycids cannot be related to both Asian and North American ruminants because of their dental features. Sudre (1984) rather proposed an autochthonous origin for amphimerycids from primitive early Eocene dichobunids, such as *Hyperdichobune*. Finally, Moya-Sola (1988) excluded both North American archaic ruminants and the amphimerycids

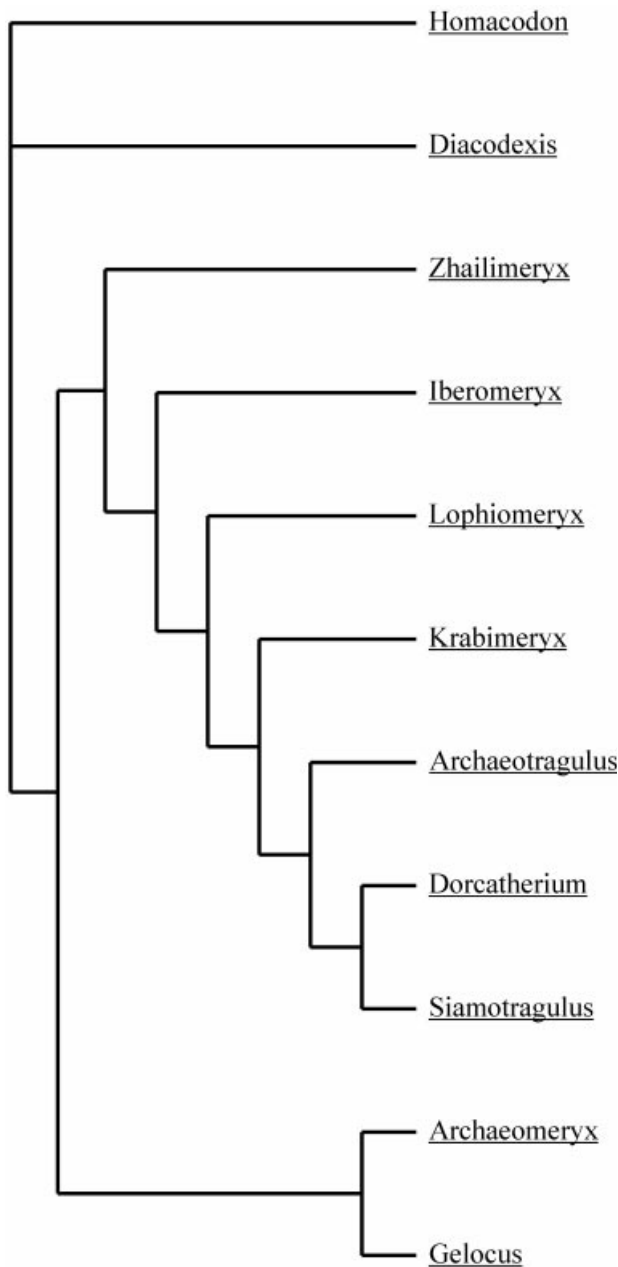


Fig. 6 Phylogenetic relationships of *Archaeotragulus*, gen. n. and *Krabimeryx*, gen. n. within Ruminantia (tree length = 42 steps, CI = 0.55, RI = 0.62), based on the analysis of the data set shown in Tables 2 and 3 (see text for explanations).

from the Ruminantia, and he even questioned the inclusion of *Indomeryx* and *Archaeomeryx* within that suborder.

Sudre (1984) considered *Iberomeryx* to be close to the ruminant archetype because of the reduced metaconule on its upper molars. This led him to suggest an origin of ruminants from primitive dichobunids with triangular upper molars. If the evolution of the dental pattern of the upper molars is

usually reliable to infer phylogenetic relationships between taxa, this does not seem to be the case for the ruminants. Indeed, the tetratubercular pattern of the molars of ruminants was probably acquired rapidly during the middle Eocene, because that structure appeared simultaneously in both Europe and North America. Nevertheless, the morphology of the lower molars seems so far more informative concerning the systematic and phylogenetic relationships between Asian ruminants. The open trigonid with a mesio-lingually orientated paracristid, characterizing both lophiomerycids and tragulids, is unknown among artiodactyls, although the Eocene fossil record of Asian artiodactyls is unfortunately very poor in comparison with those of North America or Europe. Until now, no non-ruminant Eocene artiodactyl groups have displayed a tendency towards an opening of the trigonid as in traguloids. However, contrary to the European or North American species of *Diacodexis*, the oldest artiodactyls from Asia, *Diacodexis pakistanensis* from the late–early Eocene Kuldana Formation (north-west Pakistan), possess a reduced paraconid with a rather mesio-lingually orientated paracristid. The subcontemporaneous dichobunid genus *Chorlakkia* has already lost its paraconid, although Thewissen *et al.* (1983) note a possible minute paraconid on unworn teeth. *Pakibume* from the late–early Eocene of Chorlakkia (Kuldana Formation, Pakistan) displays a labially situated paraconid which distinguishes it from other dichobunids from south Asia (Thewissen *et al.* 1987). Its paracristid is lingually bent and the cusps do not display a tendency towards selenodonty, and consequently cannot be related to the hypothetical ancestral morphotype of Asian selenodont artiodactyls. With the exception of *Aksyiria*, known by a single upper molar (Gabunia 1977), very few middle Eocene dichobunids were described from central Asia, and the paucity of artiodactyl remains from east Asia does not allow further discussion of the likely stem group for ruminants.

Among other Eocene Asian artiodactyls, the Raoellidae is an endemic family of the late–early Eocene of India and Pakistan and has been variously defined since its erection by Sahni *et al.* (1981). However, in raoellids, the paracristid is reduced and the paraconid has totally disappeared, and some of their representatives display a tendency towards bunolophodonty. Thewissen *et al.* (1987) inferred close relationships between raoellids and the European genus *Tapirulus*, although resemblances very likely correspond to parallelism (Sudre & Lecomte 2000). Pilgrim (1940) linked Tragulina with the Helohyidae, a family known in the middle Eocene of Asia and North America (Coombs & Coombs 1977). Helohyids exhibit bunoselenodont lower molars strikingly reminiscent to those of primitive anthracotheres. However, Ducrocq (1999) has demonstrated that helohyids are dentally too specialized to be closely related to anthracotheriids. In the same way, it is unlikely that ruminants emerged from helohyids

because of the enclosed trigonid, their well-developed metaconid on P₄ and the bunodonty of their upper molars surrounded by a thick cingulum and displaying a straight centrocrista. The appearance of selenodont molars in Europe from the bunoselenodont dacrytheriid *Dacrytherium* (Sudre & Lecomte 2000) might be transposed for Asia, although few intermediate 'euartiodactyl' (*sensu* Stehlin 1910) forms are known between the oldest (early Eocene) artiodactyls and the better known already fully selenodont artiodactyls from the late Eocene. In this context, we propose to link '*faute de mieux*' the Asian ruminants to the Asian diacodexeiids as previously proposed by Vislobokova (1998). However, and according to our current knowledge about the emergence of selenodont artiodactyls, the derivation of ruminants from North American homacodontids, such as *Mesomeryx* (e.g. Stucky 1998), cannot be completely ruled out. As emphasized by several authors (e.g. Gazin 1955; Sudre 1984; Sudre & Lecomte 2000), the evolution of selenodont artiodactyls occurred convergently in Europe, North America and probably in Asia during the late–middle Eocene. The lack of middle Eocene bunoselenodont Asian euartiodactyls does not allow pertinent inferences to be made of an origin of ruminants from other forms than the primitive Asian diacodexeiids. Likewise, recent discoveries of ruminants in the middle Eocene of both China (Qi *et al.* 1996; Guo *et al.* 2000) and Myanmar (Métais *et al.* 2000, in preparation) corroborate the antiquity of ruminants and their probable origin in Asia.

Conclusions

The traguloid ruminants from Krabi testify to the presence of a diversification of ruminants in south-east Asia during the late Eocene. *Archaeotragulus krabiensis* is the oldest known member of the Tragulidae, and it notably extends backwards the stratigraphic range for the tragulids, hitherto restricted to the Oligo-Miocene, including the still questionable genus *Iberomeryx*. The ruminants from Krabi thus support the predicted antiquity of the tragulids, and the assumption, deduced from biogeography, of their south Asian centre of dispersion. In the same way, *Krabimeryx primitivus* confirms the occurrence of lophiomerycids and provides evidence for a common origin of both lophiomerycids and tragulids in south-east Asia. The hypothesis of south-east Asia as an important evolutionary centre for ruminants is strongly supported by these new finds. Although our current limited knowledge of *Archaeotragulus* prevents further precision about the early evolution of tragulids, it reinforces the diagnostic dental character for the family and confirms the polarity of some features. We show here that tragulids are already dentally well differentiated from the late Eocene onwards. These new finds suggest that the origin of the family might have occurred earlier than previously thought. The fossil record of artiodactyls in Asia is still inadequate to propose a stem group

for ruminants. However, further discoveries of artiodactyls in the early and middle Eocene of Asia would probably shed new light on the early radiation of ruminants in Asia.

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