

A NEW CERATOMORPH (PERISSODACTYLA, MAMMALIA) FROM THE LATE EOCENE OF SOUTHEAST ASIA

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The infraorder Ceratomorpha (see Hooker, 2005; Colbert, 2005) is today represented by only two families (Tapiridae and Rhinocerotidae), but it underwent an important radiation in the Holarctic region during the Eocene (Colbert and Schoch, 1998). Ceratomorphs flourished in Asia, where about ten families occurred, including small to large forms (Hooker, 2005). Although ceratomorphs represent an important component of the middle-late Eocene mammal communities in Mongolia, China, and Central Asia, they remain poorly known in Southeast Asia, represented only by some specimens from the late middle Eocene Pondaung Formation in Myanmar (Pilgrim, 1925; Colbert, 1938; Tsubamoto et al., 2003).

We report a new ceratomorph from the late Eocene deposits of the Krabi basin, southern Thailand (Fig. 1). This form is associated with a diverse mammal fauna that includes more than 30 species (Ducrocq et al., 1992; 1993; 1995a, 1996, 1998; Ducrocq, 1994, 1999; Chaimanee et al., 1997; Marivaux et al., 2000; Peigné et al., 2000; Métais et al., 2001; Antoine et al., 2003). The composition of the fauna, together with a magnetostratigraphic analysis, indicates a late Eocene age (Ducrocq et al., 1995b; Benammi et al., 2001) for the Krabi mammal assemblage. Perissodactyls are usually an important component of Asian Paleogene mammal faunas (Russell and Zhai, 1987), but the Krabi fauna is dominated by artiodactyls (about 15 different species), with only two perissodactyls reported so far (including the form described herein). No satisfactory hypothesis has been suggested to explain this distribution. The low diversity could reflect an incompleteness of the Paleogene fossil record in south Asia, but a collecting bias seems unlikely in this case because the lignite deposits in Krabi have been thoroughly prospected and screen-washed in the past 15 years. The greater diversity of dental patterns for artiodactyls in Krabi (ruminants, anthracotheres, suoids) seems to be analogous with that of perissodactyls from most other Paleogene Asian localities (Russell and Zhai, 1987).

The material reported here was recovered in the Wai Lek pit, from the main lignite seam that has yielded almost all mammal remains known from Krabi. It consists of a right maxilla preserving three molars whose morphology is typical of that of ceratomorphs. The classification of perissodactyls and particularly that of ceratomorphs has gone through several substantial changes over the past years (e.g., Radinsky, 1963; Prothero and Schoch, 1989; Schoch, 1989; McKenna and Bell, 1997; Dashzeveg and Hooker, 1997; Colbert and Schoch, 1998; Froehlich, 1999; Holbrook, 1999; Colbert, 2005; Hooker, 2005), and we will adopt here the scheme proposed by Hooker (2005).

Dental terminology follows Dashzeveg and Hooker (1997:fig. 24) and abbreviations used in the text are L = molar length and W = molar width.

SYSTEMATIC PALEONTOLOGY

Order PERISSODACTYLA Owen, 1848
Infraorder CERATOMORPHA Wood, 1937
Superfamily RHINOCEROTOIDEA Gray, 1821
SIAMOLOPHUS KRABIENSE, gen. et sp. nov.
(Fig. 2)

Holotype—TF 2645, fragmentary right maxilla preserving M1-M3, housed in the Department of Mineral Resources, Bangkok.

Type Locality—Main lignite seam (Formation B2) (see Bristow 1991); Wai Lek pit, Krabi Basin, peninsular Thailand (N 07° 58' 13", E 99° 03' 38"; Fig. 1).

Distribution—Late Eocene (Benammi et al., 2001; Ducrocq et al., 1995b).

Diagnosis—Small-sized rhinocerotoid with upper molars transversely elongated, lacking conules and mesostyle. Metacone tilted lingually and labially flattened and reduced on M3, paracone conical and labially convex, metaloph joins ectoloph slightly anteriorly to the metacone, parastyle mesially salient and postmetacrista obliquely oriented. Differs from most Tapiroidea by its upper molar metaloph that joins ectoloph slightly in front of metacone. Differs from Hyracodontidae and Rhinocerotidae by its shorter metacone wall on M1–2 and by its longer M3 metastyle and metacone not inflected lingually. Differs from Amynodontidae by its antero-posteriorly shorter M3 with a longer metaloph. Differs from Rhodopagidae by its less lingually tilted metacone. Differs from 'Hyrachyidae' by its metacone more tilted lingually and by the retention of a cingulum labial to the metacone.

Etymology—*Siamo*, from Siam the former name of Thailand; *-lophus*, a common suffix for lophodont mammals. The species name refers to the type locality.

Description—The first two molars are very similar in morphology: they are transversely developed (LM1 = 8.0 mm; WM1 = 8.9 mm; LM2 = 8.6 mm; WM2 = 9.3 mm) with the lingual cusps as high as the labial ones. The lingual cusps are anteroposteriorly compressed so that the protoloph and the metaloph are sharp. The short paracone is labially convex and the somewhat longer metacone is transversely compressed with its labial wall slanting lingually so that it is more lingually situated than the paracone. The upper molars lack both a paraconule and a metaconule. The metaloph joins the ectoloph slightly anteriorly to the apex of the metacone, and the protoloph connects to the preparacrista between the parastyle and the paracone. The parastyle is moderately developed, rounded and mesiolabially salient. The distal end of the ectoloph develops a slight distolabial spur that connects to the distal cingulum. The transverse valley between the protoloph and the metaloph is narrow and shallow, and it is lingually closed by a very short and low crest connecting the lingual cusps. The ectoloph is notched between the paracone and the metacone, and no mesostyle occurs on the centrocrista. A distinct but narrow cingular shelf occurs labially to the metacone, and mesial and distal narrow cingula extend on most of the width of the teeth. There is no continuous lingual cingulum except for a weak cingular rim between the hypocone and the protocone that is better developed on M3.

The M3 is somewhat smaller than the anterior molars (LM3 = 7.6 mm; WM3 = 8.1 mm) and it displays a sub-triangular occlusal outline. The metacone is reduced to a small spur on the distal part of the ectoloph and it is more lingually displaced than on the preceding teeth, so that the paracone is the largest cusp on the labial wall and the metaloph is shorter than the protoloph. The protoloph and the metaloph are more transversely oriented than on M1 and M2. The parastyle is weaker than on the preceding teeth and the mesial and distal cingula are narrow but well developed along the width of the tooth. A short ridge occurs distally at the junction between the ectoloph and the metaloph and it connects to the distal cingulum. The labial side of the metacone lacks the cingular shelf as on M1-M2.

DISCUSSION AND CONCLUSIONS

TF 2645 displays a set of dental characters (molars transversely elongated with well-defined protoloph and metaloph, absence of conules and

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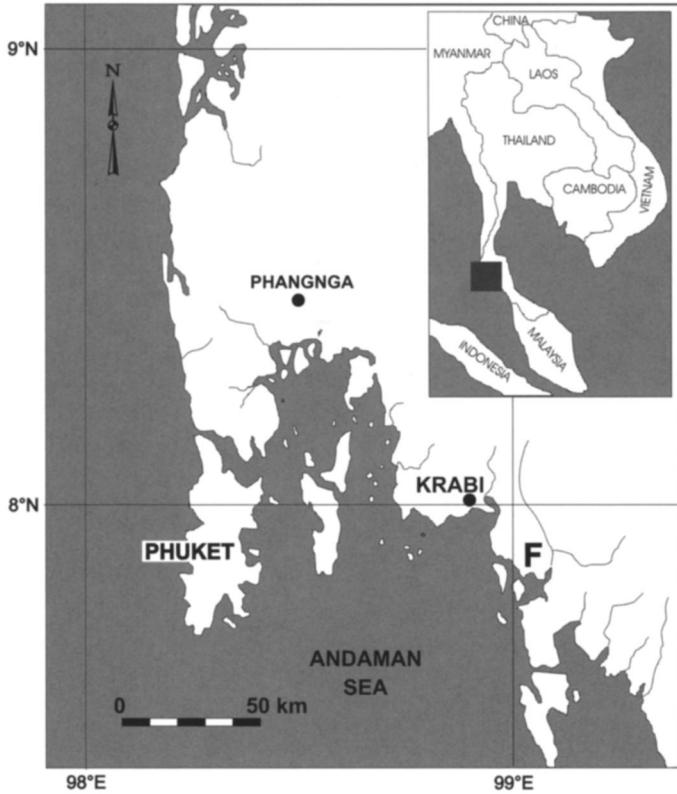


FIGURE 1. Location map of the Krabi Basin in southern Thailand. 'F' indicates the fossiliferous locality.

of a mesostyle, metacone labially flattened and reduced on M3, paracone conical and labially convex, metaloph joining the ectoloph slightly anteriorly to the metacone, mesially salient parastyle, notched centrocrista) that makes its molar structure unique among the Eocene ceratomorphs. Indeed, the endemic Asian Eocene Lophialetidae differ from *Siamolophus* by their metaloph attached much more mesially to the ectoloph, their shorter metacone and by their more oblique meta- and protoloph. The Asian Deperetellidae can be typically distinguished from TF 2645 by their larger size, their upper molars with straighter proto- and metaloph forming an inverted U, smaller metacone on M1-M2 and by the metacone very reduced or even absent on M3. Similarly, the Tapiridae possess



FIGURE 2. *Siamolophus krabiense*, gen. et sp. nov., TF 2645 (cast), right M1-M3 in occlusal view. Note the peculiar outline of M3. Scale bar equals 5 mm.

upper molars with more convex and labially placed metacones and straighter transverse lophs. In a general way, the Rhinocerotoida have their metaloph that distinctly joins the ectoloph mesially to the metacone on the upper molars, as seen on *Siamolophus*. Furthermore, the Asian Eocene Rhodopagidae exhibit a metacone much more lingually tilted than in the Thai specimen, while Amyndodontidae have an anteroposteriorly elongated M3 with a strong metastyle and they tend to reduce their metaloph, especially on M3—a feature that is shared with Hyracodontidae. The latter, and Rhinocerotidae, display reduced parastyles, metacone wall lengthened on M1-2, and a M3 metastyle and metacone shortened and curved lingually (Prothero, 1998a, b; Wall, 1998).

However, *Siamolophus* is morphologically closer to *Heleletes* and *Hyrachyus*, two taxa that are traditionally included in paraphyletic groups ('Helaletidae' and 'Hyrachyidae' respectively). The Thai specimen shares with both genera the general morphology of upper molars with the slightly anterior attachment of the metaloph to the ectoloph, and the M1-2 metacone not reduced, labially flattened and lingually deflected. The flatness of the labial face of the metacone in *Siamolophus* is more similar to that of *Hyrachyus*, but the latter differs from the Thai form in having a stronger parastyle, no cingulum labial to the metacone, and the lingual part of upper molars mesiodistally longer (M1-3). Other taxa referred to uncertain tapiroid families (*Heleletes*, *Heptodon*, *Desmatotherium*, *Dilophodon*, *Selenaletes*, *Plesiocolopirus*, *Colodon* and *Jhagirilophus*) can be distinguished from *Siamolophus* by their upper molars with a metacone less lingually placed, a paracone less salient labially (*Heptodon*), straighter transverse lophs (*Dilophodon*, *Plesiocolopirus*, *Colodon*), stronger parastyle, and M3 less reduced. The Krabi specimen exhibits derived ceratomorph features (upper molar metacone labially flat and markedly tilted lingually, metaloph that joins the ectoloph slightly in front of the metacone, postmetacrista obliquely orientated), but in the absence of further diagnostic dental material (especially premolars) the family cannot be identified with certainty.

As an attempt to establish more precise relationships between *Siamolophus* and ceratomorphs, we performed a phylogenetic analysis using PAUP 4.0 (Swofford, 2002) in which we coded the specimen from Krabi in the data matrix of Dashzeveg and Hooker (1997). We selected the same options as those chosen by these authors (see Appendix 1). The resulting strict consensus tree (from 9 trees of 57 steps with a consistency index of 0.578, see Fig. 3) displays the same topology as that of Dashzeveg and Hooker (1997: fig. 25), with the Thai form being a sister taxon to

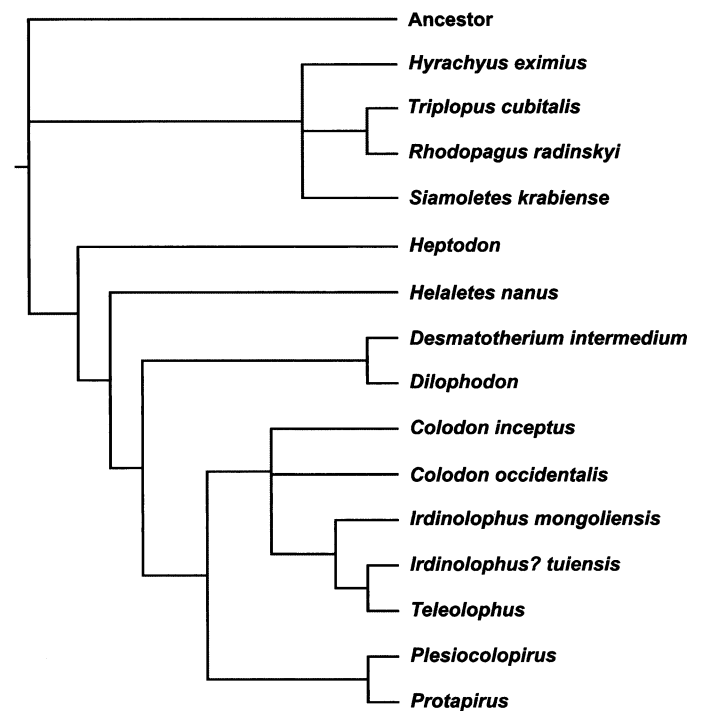


FIGURE 3. Strict consensus cladogram from PAUP 4.0 analysis of the data matrix (Appendix 1) modified from Dashzeveg and Hooker (1997).

the group including *Rhodopagus*, *Triplopus* and *Hyrachyus*. The *Rhodopagus-Siamolophus* group is defined by the upper molar metacone strongly tilted lingually, but rhodopagids differ from the Thai species in having a metacone clearly more tilted lingually that is confluent with the metaloph. In addition, *Hyrachyus*, *Rhodopagus*, *Triplopus* and *Siamolophus* share the metaloph that connects slightly in front of the metacone, although this configuration is sometimes seen in tapiroids (Dashzeveg and Hooker, 1997). The lack of more diagnostic dental material for the Thai specimen that could be included into the data matrix might explain its ambiguous position within ceratomorphs. However, the analysis suggests that *Siamolophus* might be more closely related to the Rhinocerotoida than to the Tapiroidea, implying that the new Thai species might be close to the ancestry of the Rhinocerotoida or part of a basal radiation of rhinocerotoids. Another rhinocerotid has been recently described from Krabi (Antoine et al., 2003) but it is represented by two large lower molars, which precludes comparisons between both Thai specimens. However, the occurrence of two rhinocerotoids in the late Eocene of southern Thailand suggests that ecological conditions then were not favourable to the radiation of tapiroids.

In conclusion, *Siamolophus krabiense* displays a combination of features unknown in any other ceratomorph. Whether, as suspected, it played an important role in the basal radiation of rhinocerotoids must await the discovery of more complete material. From a biogeographic point of view, the discovery of a second rhinocerotoid in the late Eocene of peninsular Thailand substantially extends the geographic range of the group far into southeast Asia. Additional material from this area would certainly improve our understanding of the evolutionary history of ceratomorphs and more especially the phylogenetic relationships between Asian and North American forms.

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APPENDIX 1. Data matrix from Dashzeveg and Hooker (1997) with characters coded for *Siamolophus krabiense*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26		
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
<i>Hyrachyus eximius</i>	0	0	0	0	A	0	0	0	A	0	0	0	1	0	0	C	1	0	0	1	0	1	0	0	0	0	1	
<i>Heptodon</i>	0	0	0	1	0	0	0	0	B	0	0	0	1	0	A	A	0	0	0	0	0	1	0	0	0	0	1	
<i>Helalates nanus</i>	A	0	0	0	B	0	0	0	B	0	0	0	1	0	A	A	0	0	0	0	0	1	0	0	0	0	1	
<i>Desmatotherium intermedium</i>	?	?	?	0	B	0	1	0	B	0	0	0	1	0	A	C	0	0	1	0	0	1	0	1	0	0	1	
<i>Dilophodon</i>	?	?	?	0	B	0	1	0	B	0	0	0	0	0	A	C	1	0	1	0	0	1	0	1	0	0	1	
<i>Colodon occidentalis</i>	B	1	1	1	B	0	1	1	B	0	0	0	1	0	B	A	1	1	0	0	1	1	0	1	0	0	1	
<i>Colodon inceptus</i>	B	?	?	1	B	0	1	0	B	0	0	0	1	0	B	B	1	1	0	0	1	1	0	1	0	0	1	
<i>Plesiocolopirus</i>	B	1	?	0	A	0	1	0	B	0	0	0	1	0	B	A	0	1	0	0	?	?	0	1	0	0	1	
<i>Protapirus</i>	B	1	0	0	0	0	1	0	B	0	0	0	1	0	B	C	0	1	0	0	1	1	0	1	0	0	1	
<i>Irdinolophus mongoliensis</i>	B	?	?	1	B	1	1	0	B	0	A	0	1	0	B	A	?	0	0	0	0	1	1	1	0	0	1	
<i>Irdinolophus? tuiensis</i>	?	?	?	1	B	1	1	0	B	1	B	1	1	1	B	?	?	?	?	0	?	?	?	?	?	?	1	?
<i>Teleolophus</i>	B	?	1	1	B	1	1	1	B	1	B	1	0	1	B	C	1	0	0	0	0	1	1	1	1	1	1	
<i>Rhodopagus radinskyi</i>	0	0	?	1	B	0	0	0	A	0	0	0	1	0	0	C	0	0	0	1	0	0	0	0	0	0	1	
<i>Triplopus cubitalis</i>	0	0	1	0	A	0	1	0	A	0	0	0	1	0	0	C	0	0	0	1	0	1	0	0	1	1	1	
<i>Siamolophus krabiense</i>	?	?	?	1	B	0	0	0	A	0	0	0	1	0	0	?	?	?	?	?	?	?	?	?	?	0	?	

For symbols and other details, see Dashzeveg and Hooker (1997).