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Original article

A new basal tapiromorph (Perissodactyla, Mammalia) from the middle Eocene of Myanmar

Un nouveau tapiromorphe basal (Perissodactyla, Mammalia) de l'Eocène moyen du Myanmar

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Abstract

A new genus and species of tapiromorph, *Skopaiolophus burmese* nov. gen., nov. sp., is described from the middle Eocene Pondaung Formation in central Myanmar. This small form displays a striking selenolophodont morphology associated with a mixture of primitive "condylarthran" dental characters and derived tapiromorph features. *Skopaiolophus* is here tentatively referred to a group of Asian tapiromorphs unknown so far. The occurrence of such a form in Pondaung suggests that primitive tapiromorphs might have persisted in southeast Asia until the late middle Eocene while they became extinct elsewhere in both Eurasia and North America.

Résumé

Un nouveau genre et une nouvelle espèce de tapiromorphe, *Skopaiolophus burmese* nov. gen. nov. sp., sont décrits dans la Formation de Pondaung d'âge fini-éocène moyen, au Myanmar. Cette forme de petite taille présente une morphologie lophosélénodonte remarquable associée à une mosaïque de caractères dentaires primitifs de type condylarthre et de traits dérivés tapiromorphes. *Skopaiolophus* est ici attribué provisoirement à un groupe de tapiromorphes asiatiques encore inconnu. La présence d'un tel taxon à Pondaung suggère que les tapiromorphes primitifs auraient pu persister en Asie du Sud-Est jusqu'à la fin de l'Eocène moyen alors qu'ils avaient disparu en Eurasie et en Amérique du Nord.

Keywords: Perissodactyls; Tapiromorphs; *Skopaiolophus burmese* nov. gen., nov. sp.; Late middle Eocene; Pondaung; Myanmar

Mots clés : Périssodactyles ; Tapiromorphes ; *Skopaiolophus burmese* nov. gen., nov. sp. ; Eocène moyen terminal ; Pondaung ; Myanmar

1. Introduction

Several middle and late Eocene faunas display a wide variety of tapiroids in Asia mainly in Mongolia, Central Asia and China, whereas they are less common in South Asia (Russell and Zhai, 1987). Tapiromorphs underwent an important radiation in the Eocene of North America and Asia (Schoch, 1989) but their specific diversity decreased throughout the Oligocene and the Neogene and today they are only represented by the monogeneric family Tapiridae (Janis, 1984). Froehlich (1999, 2002) and Holbrook (1999, 2001) have recently provided a comprehensive phylogenetic analysis of Paleogene perissodactyls highlighting the problematic familial assignment of most basal tapiromorphs (sensu Froehlich, 1999) which are usually

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included in the paraphyletic family Isectolophidae (Froehlich, 1999). Isectolophids are represented by early to middle Eocene small-sized forms with a Holarctic distribution and they exhibit relatively generalized adaptations (Schoch, 1989). The history of classificatory schemes of the different families included within the tapiroids is summarized in Schoch (1989). Radinsky (1963) diagnosed the tapiroids in a dental point of view as such: brachyodont teeth with complete cross lophs on upper and lower molars, but ectoloph short and metalophid incomplete or absent.

We report here a new genus and species of a basal tapiromorph discovered in the late middle Eocene deposits of the Pondaung Formation, central Myanmar (Fig. 1). Previous studies on tapiroids from Pondaung have reported only two forms: the isectolophid *Indolophus guptai* (see McKenna and Bell, 1997) and the deperetellid *Deperetella birmanica* (Pilgrim, 1925; Colbert, 1938). Recently, Tsubamoto et al. (2000) reassessed the genus *Deperetella* on the basis of scanty material and they established faunal correlations between the Pondaung fauna and Mongolian localities where tapiroids are taxonomically more diversified (Radinsky, 1965). The new form described here is associated with a rich and diversified mammal fauna that includes rhinocerotoids, brontotheres, ruminants, anthracotheres, carnivores, rodents, and primates (Pilgrim and Cotter, 1916; Pilgrim, 1925, 1928; Jaeger et al., 1998, 1999, 2004; Ducrocq et al., 2000; Holroyd and Ciochon, 2000; Métais et al., 2000; Takai et al., 2001; Dawson et al., 2003; Marivaux et al., 2003, 2005). The study of the Pondaung fauna led to the proposal of a late middle Eocene age for this community on the basis of faunal comparisons with Chinese and Thai localities of similar ages (Ducrocq et al., 2000). In addition, new geochronological evidence has established more precisely the age of the fossiliferous deposits of Pondaung. Indeed, the palaeomagnetic study of the Bahin section performed by Benammi et al. (2002) supports a late middle Eocene age (around 37 Ma). Independently, Tsubamoto et al. (2002) published a fission-track analysis on zircon grains from a tuff bed in the Paukkaung section that advocates an age of 37.2 ± 1.3 Ma. These results confirm the biochronological assumptions and make the Pondaung fauna the most reliably dated Eocene fauna in south Asia.

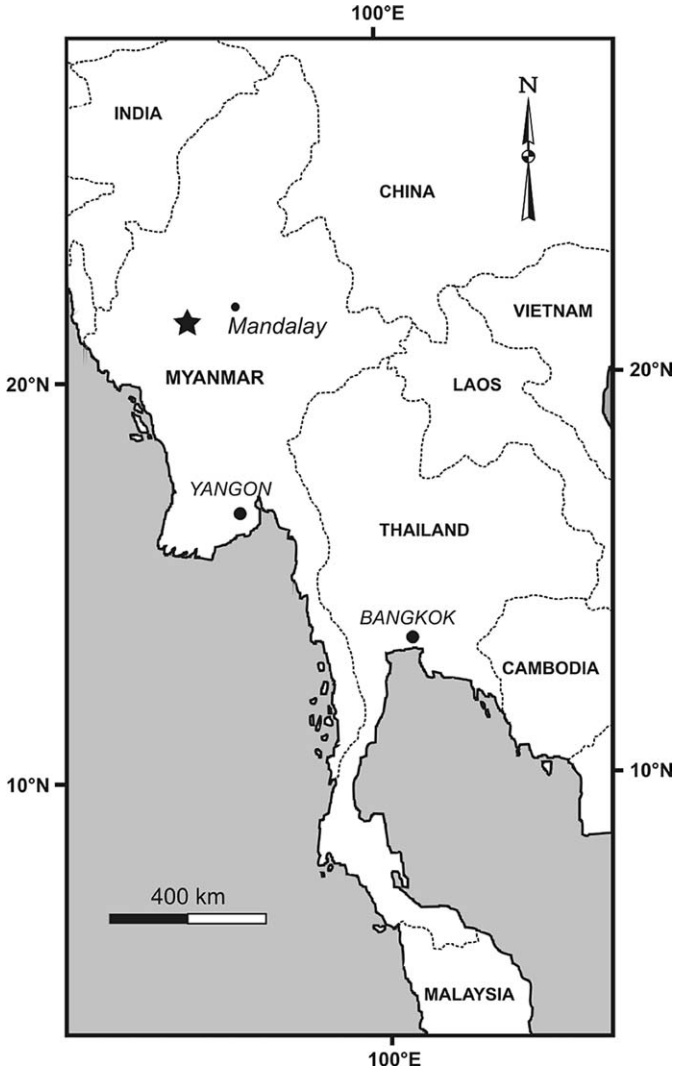

Fig. 1. Location map of Sabapontaung (Pondaung Formation), central Myanmar. The star indicates the fossiliferous locality.
Fig. 1. Localisation de Sabapontaung (Formation de Pondaung), Myanmar central. L'étoile indique la localité fossilifère.

Dental terminology follows Hooker (1994: Fig. 2). The abbreviations used in the text are L = molar length; W = molar width.

2. Systematic paleontology

MAMMALIA Linnaeus, 1758
PERISSODACTYLA Owen, 1848
TAPIROMORPHA Haeckel, 1866
Family indeterminate
Genus ***Skopaiolophus*** nov. gen.

Type species: *Skopaiolophus burmese* nov. sp.

Diagnosis: small tapiromorph close in size to the living ruminant *Tragulus* and characterized by its selenolophodont and high-crowned lower molars, its lingual cusps distally displaced (especially the metaconid), its trigonid widely open lingually, the presence of a reduced twinned metaconid, a vestigial paraconid and a tiny cingular bulge on the postcristid on M_2. Differs from artiodactyls in having developed transverse crests and by the distally situated lingual cusps with respect to the labial ones. Differs from primitive perissodactyls in its selenolophodont pattern, the retention of a paraconid on lower molars and in the medial orientation of the cristid obliqua which tends to extend longitudinally in early tapiromorphs. Differs from early hippomorphs by the lack of a true M_2 hypoconulid and developed cingulids. Differs from selenolophodont "condylarths" such as *Pleuraspidotherium*, *Meniscotherium*, *Ectocion* and *Hilalia* in having a narrower hypoconulid on M_3, a tiny distal cingular bulge on M_2 and in the retention of a minute paraconid.

Etymology: from the Greek *skopaios* (dwarf), and *lophos* (crest).

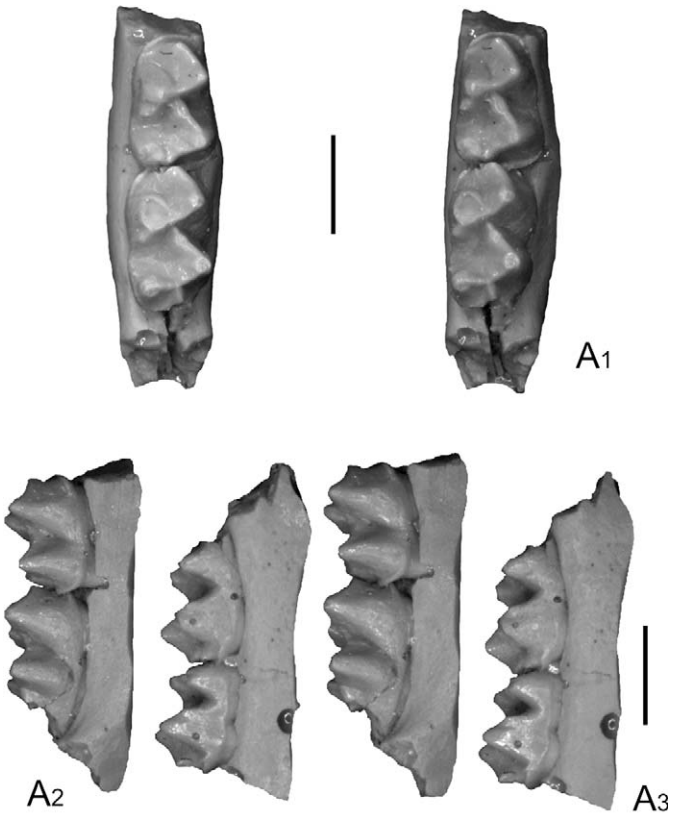

Fig. 2. *Skopaiolophus burmese* gen. nov, sp. nov.; holotype specimen SPG-3 (cast); late Middle Eocene; Sabapontaung, Pondaung Formation, central Myanmar. **A**, occlusal view; **B**, labial view; **C**, lingual view. All views are stereopairs. Scale bar = 5 mm.

Fig. 2. *Skopaiolophus burmese* gen. nov, sp. nov. ; spécimen holotype SPG-3 (moulage) ; fin de l'Eocène moyen ; Sabapontaung, Formation de Pondaung, Myanmar central. **A**, vue occlusale ; **B**, vue labiale ; **C**, vue linguale. Toutes les photos sont en stéréo. Échelle = 5 mm.

Skopaiolophus burmese nov. sp.

Fig. 2

Material: holotype specimen SPG-3 (fragmentary right mandible preserving M_2-M_3) housed in the National Museum of Myanmar, Yangon.

Geological setting: Sabapontaung, North West of Bahin village, Myaing Township, Central Myanmar (Fig. 1); Pondaung Formation, late middle Eocene (Ducrocq et al., 2000; Benammi et al., 2002; Tsubamoto et al., 2002).

Etymology: after the former name of Myanmar (Burma).

Diagnosis: that of the genus.

3. Description

The molars of *Skopaiolophus* are high-crowned and they display a selenolophodont pattern. Both molars described here are narrow with the lingual and labial cusps of similar height. The lower molars have a rectangular occlusal outline and the trigonid is almost as wide as the talonid. The lingual cusps are somewhat posteriorly displaced with respect to the labial cusps, giving a W-shape to the ectolophid.

On M_2 ($L = 6.6$ mm; $W = 3.9$ mm), the protoconid and the metaconid are conical and the protoconid is slightly larger and higher than the metaconid. Both cusps are joined by a sharp, transverse and slightly notched protolophid. The metaconid is twinned but the second cusp is smaller than the metaconid. A low paracristid extends down mesiolingually from the protoconid and then runs lingually into a tiny bulge that might be interpreted as a reduced paraconid. Consequently, the trigonid is widely open lingually. A thick cingulid occurs along the mesial side of the tooth and grows thinner along the labial side of the protoconid before it disappears on the labial side of the hypoconid. A distal cingulid is present along the posterior side of the tooth. There is no lingual cingulum. The cristid obliqua runs mesiolingually down from the hypoconid to the base of the protolophid wall midway between the protoconid and the metaconid. The hypoconid and the entoconid are similar in size and somewhat lower than the mesial cusps. A posthypocristid extends distolingually from the hypoconid and joins the short and transversely oriented postentocristid. As a result, the hypolophid forms a widely and mesially open V in occlusal view and it is medially weakly notched in posterior view. A tiny enamel swelling occurs between the hypoconid tip and the medial notch on the posthypocristid. There is no distinct hypoconulid at the junction between the postentocristid and the posthypocristid but rather a tiny cingular bulge.

The third molar (estimate $L = 8.2$ mm; $W = 3.8$ mm) is morphologically similar to M_2 but it is slightly narrower. The apex of the metaconid is broken away but the second posterior cusp is distinct. The hypoconulid lobe is also broken but it was probably rather wide according to the width of its remaining connection with the crown.

4. Comparisons

The lower molars of *Skopaiolophus* are structurally similar to those of some artiodactyls, perissodactyls and selenolophodont "condylarths". The crescentic labial cusps, the orientation of the cristid obliqua and the large lingual opening of the trigonid are derived features shared with lophiomerycid ruminants for which a trends towards lophodonty has already been pointed out by Janis (1987). However, the development of the transverse crests and the distal displacement of the lingual cusps with respect to the labial ones rule out the inclusion of SPG-3 in artiodactyls.

4.1. "Condylarthra"

Most primitive ungulates are usually included in the paraphyletic order "Condylarthra" (e.g. Archibald, 1998). Few "condylarths" have been described so far in Asia and they are often geographically restricted. Quettacyonidae (arctocyonid-like forms) known from the Eocene of Pakistan (Gingerich et al., 1997, 1999) display bunodont lower molars with a protoconid and a metaconid in line transversely and twinned entoconid and hypoconid that set apart quettacyonids from SPG-3. On the other hand, the Burmese form can be distinguished

from the Chinese phenacolophids such as *Conolophus* and *Yuelophus* (Zhang, 1978) by its smaller size, the greater development of its crests, the presence of a twinned metaconid and by the weakness of its cingulids. Moreover, phenacolophids and phenacodontids have generally relatively long, curved paralophids whereas this crest is short, straight and mesio-lingually oriented in *Skopaiolophus*. The enigmatic "condylarth" *Hilalia* from the middle Eocene of Turkey recently described by Maas et al. (2001) mainly resembles *Skopaiolophus* in its selenolophodont lower molars. However, *Hilalia* displays a strong and transversely oriented paracristid that tends to close the trigonid lingually and its cristid obliqua reaches the distal wall of the metaconid instead of connecting the protocristid midway between the two mesial cusps as in *Skopaiolophus*.

The Phenacodontidae have long been considered closely related to the basal perissodactyls (e.g. Radinsky, 1966, 1969) with a special reference to *Radinskya* from the late Paleocene of China (McKenna et al., 1989) that is often considered as the sister taxon of all perissodactyls (e.g. Prothero and Schoch, 1989; Beard, 1998). The molars of *Skopaiolophus* resemble those of North American phenacodontids *Ectocion* and *Meniscotherium* (Hooker, 1989; Williamson and Lucas, 1992) in their selenolophodont pattern with a medially oriented cristid obliqua, the general structure of their trigonid and in their metaconid which is distally situated with respect to their protoconid. However, both North American genera display a prominent hypoconulid on M_2 unlike *Skopaiolophus*. *Ectocion* further displays a M_3 hypoconulid wide and twinned with the entoconid whereas it is likely narrower and distinct from the entoconid in *Skopaiolophus*. *Meniscotherium* from the late Paleocene-middle Eocene of North America (Williamson and Lucas, 1992) resembles *Skopaiolophus* in its selenodont lower molars and in the loss of the hypoconulid on its M_2. However, its more lophodont teeth, its cristid obliqua that joins the metaconid lingually and its metastylid (Archibald, 1998) rule out close relationships between SPG-3 and *Meniscotherium*. Similarly, the lower molars of the European phenacodontid *Pleuraspidotherium* (McKenna and Bell, 1997) shares several features with SPG-3 like the general structure of the transverse crests and the orientation of both paracristid and cristid obliqua. The shape of the trigonid is very similar in both genera but the paraconid is slightly more reduced in the Burmese form. However, the talonid structure of *Skopaiolophus* slightly differs from that of *Pleuraspidotherium* in having a more conical entoconid lacking a transverse crest and a posthypocristid extending farther lingually. According to Archibald (1998), selenolophodont "archaic ungulates" are generally considered as derived with respect to other bunodont "condylarths", and their stratigraphical range rarely extends farther than the middle Eocene in North America whereas they became extinct in the latest Paleocene of Europe. All dental similarities that can be observed between *Skopaiolophus* and North American and European selenolophodont "condylarths" might be interpreted as convergences and more complete material for *Skopaiolophus* would help to better interpret the dental pattern of the Burmese species.

4.2. Perissodactyls

Dentally, *Skopaiolophus* presents greater similarities with basal perissodactyls known from the early to middle Eocene of Eurasia and North America than with any other Eocene ungulate. The main derived features that relate *Skopaiolophus* to early perissodactyls are the trend towards the formation of transverse crests on lower molars and the orientation of the cristid obliqua. However, these characters likely arose several times within ungulates and are far from being exclusive to perissodactyls (e.g. Jernvall et al., 1996). Moreover, the marked selenolophodont structure of the lower molars and the retention of a paraconid are unusual in perissodactyls. Froehlich (1999, 2002) has recently provided a comprehensive phylogenetic analysis of Paleogene perissodactyls including a large spectrum of characters sampled in most Paleogene taxa. The scarcity of the Burmese material does not allow *Skopaiolophus* to be included in such a broad analysis, but the high number of characters listed permitted adequate comparisons with most basal perissodactyls. *Skopaiolophus* strongly differs from large amynodonts from Pondaung by its size and general tooth morphology. It also can be distinguished from the tapiroid *Indolophus guptai* (Tsubamoto et al., 2003) by its smaller size, the lingual orientation of its paracristid and by its metaconid which is markedly shifted distally. The lower molars of the deperetellid *Deperetella birmanica* from Pondaung (Pilgrim, 1925) further differs from *Skopaiolophus* in its complete bilophodont lower molars and in its larger size.

4.3. Brontotheres and chalicotheres

Like *Skopaiolophus*, Eomoropids, a family of primitive chalicotheres, retain the hypoconulid lobe on M_3. However, their cristid obliqua that ends lingually to a metastylid and their lingual and labial cusps in line rule out any relationship between *Skopaiolophus* and eomoropids. The lower molars of brontotheres are characterized by their generally larger size and in having a peculiar symmetrical W-shape (Lucas and Schoch, 1989), two features that are very different from those exhibited by lower teeth of *Skopaiolophus*. Furthermore, the cristid obliqua of small brontotheres such as *Nanotitanops* (Qi and Beard, 1998) always reaches the lingual border of the tooth at the level of the metaconid, giving a typical shape of the lower molars very different from that of *Skopaiolophus*.

4.4. Early Hippomorpha

Most authors have long considered *Hyracotherium* either as the first offshoot of equoids (e.g. Stirton, 1940) or as the primitive morphotype for all perissodactyls. Froehlich (2002) has split the North American "*Hyracotherium*" into several new genera (*Minippus*, *Sifrhippus*, *Arenahippus*), all of them being placed at the base of the equoid radiation. The European *Hyracotherium leporinum* is usually set close to the ancestry of European palaeotheriids (Hooker, 1994) and it represents the morphotype of European equoids. None of those early hippo-

morphs displays a marked selenolophodont dental pattern like the Burmese form does. *Hyracotherium*, *Minippus*, *Sifrhippus* and *Arenahippus* (Gingerich, 1989, 1991; Hooker, 1994; Froehlich, 2002) differ from *Skopaiolophus* in their more bunodont molars with strong cingula, their closed trigonid, their relatively large hypoconulid on M_2 connected with the distolingual margin of the hypoconid by a strong postcristid and by their possibly larger M_3 hypoconulid (according to what can be judged from the remaining connection between the broken away hypoconulid lobe and the crown on the M_3 of *Skopaiolophus*). On the other hand, *Skopaiolophus* shares dental similarities with small representatives of European palaeotheriids such as *Lophiotherium* or *Anchilophus* (see, for example, Hooker and Weidmann, 2000), including the distal position of entoconid and metaconid, a conical entoconid (*Anchilophus*) and the presence of a twinned metaconid (although this character seems to be highly variable in palaeotherids). However, *Lophiotherium* displays a better developed labial cingulid, a distinct hypoconulid on its M_2 and a more lingual cristid obliqua that tends to connect with the metaconid. *Anchilophus* exhibits a complete and straight hypolophid. The basal palaeotheriid *Propachynolophus* (Savage et al., 1965) shares the similar arrangement of crests on the talonid with *Skopaiolophus*, but it differs from it by its distinct hypoconulid on M_2, its strong labial cingulid on lower molars, the orientation of its paralophid and by its more mesial metaconid. Given the numerous similarities shared by palaeotheriids and the Burmese form we cannot completely rule out close phylogenetic relationships between early hippomorphs and *Skopaiolophus*.

4.5. Middle and late Eocene Asian tapiromorphs

Skopaiolophus shows few resemblances with the Asian Helaletidae and Deperetellidae (Radinsky, 1965) which display bilophodont lower molars with a reduced cristid obliqua, but deperetellids exhibit a very reduced hypoconulid on M_3 and their paralophid is reduced without any trace of paraconid. Like *Skopaiolophus*, the lophialetid *Breviodon* from the late middle Eocene of Shara Murun (Mongolia) shows a short paralophid but no paraconid, its trigonid is widely open and its metaconid is slightly displaced distally. However, *Breviodon* retains a minute hypoconulid on its M_2 and a straight and complete hypolophid.

4.6. Early tapiromorphs (Isectolophidae sensu Froehlich, 1999)

Most basal tapiromorphs (*Sastrilophus*, *Orientolophus*, *Cymbalophus*, *Systemodon*, *Karagalax*, *Kalakotia*, *Cardiolophus*, *Homogalax*, *Isectolophus*) are included in the Isectolophidae known from the early Eocene of Eurasia and North America, although *Cymbalophus* might be an equoid and *Karagalax* a ceratomorph according to Hooker and Dashzeveg (2003). *Skopaiolophus* differs from all isectolophids by its more lingual and straighter paracristid and it can be distinguished from other early tapiromorphs in lacking a labial cingulid and a large hypoconulid lobe on M_3. *Skopaiolophus* and *Orientolophus* from the earliest Eocene of China retain a twinned metaconid on their lower molars (Ting, 1993; Froehlich, 2002), but the Chinese genus is more bunodont and it displays a cristid obliqua more labially situated and deeply notched protolophid and hypolophid. *Isectolophus* (middle Eocene of North America and Asia, see Lucas et al., 2003), *Cardiolophus* and *Homogalax* (early Eocene of North America) differ from *Skopaiolophus* in having notched protolophid and hypolophid (*Isectolophus* and *Homogalax*), a less lingually open trigonid and in lacking a twinned metaconid (except *Cardiolophus*). Likewise, *Cymbalophus* can be distinguished from *Skopaiolophus* by its more bunodont lower molars with a hypoconulid on M_2 and by the more labially orientated cristid obliqua (Hooker, 1989, 1994).

The lower molars of *Skopaiolophus* display some features seen in basal tapiromorphs such as the transverse development of a high and slightly notched protolophid, a reduced hypoconulid on M_2, a probably narrow and small hypoconulid lobe on M_3, a twinned metaconid (*Orientolophus*, *Cymbalophus*, *Systemodon*) and a straight and strong hypolophid. Although none of these characters is strictly exclusive to basal tapiromorphs their association in *Skopaiolophus* lead us to favour its affinities with a specialized branch of tapiromorphs.

5. Discussion

Although *Skopaiolophus* shares several resemblances with "condylarths", we favour affinities with perissodactyls because all dental features displayed by the Burmese specimen can be found separately in basal perissodactyls. The likely short and narrow hypoconulid lobe of M_3 connected by a crest to the posthypocristid in *Skopaiolophus* is an unusual configuration in selenolophodont condylarths where the three cusps forming the talonid are joined by a crest surrounding the posterior border of the tooth. Furthermore, most phenacodontids have completely lost the third lobe on M_3 and none of the selenolophodont forms displays lower molars as transversely compressed as in the Burmese species. The twinned metaconid is variably present in early tapiromorphs (*Orientolophus, Cymbalophus, Systemodon*) and primitive hippomorphs display this structure. All other early perissodactyls do not show this feature which seems to appear iteratively in ungulates. The development of lophs is characteristic of early perissodactyls, although it is associated with a selenodont pattern in *Skopaiolophus*. The configuration of the talonid on its M_3 evokes the primitive condition of lophialetids but more material (especially upper molars) would be necessary to confirm this hypothesis. Our current knowledge of the dental material of *Skopaiolophus* thus supports its inclusion in perissodactyls, although its unusual selenolophodont pattern might indicate a highly specialized diet.

However, three characters observed in the Burmese specimen are unusual among perissodactyls: the retention of a paraconid, the marked distal displacement of the lingual cusps with respect to the labial ones and the minute distal cingular bulge on M_2. The first feature is supposed to have been lost early in

the evolution of perissodactyls and in their putative sister group (phenacodontids and phenacolophids). However, a paraconid can be observed on some specimens of *Hyracotherium* (although it is never fully developed). The distal shift of the lingual cusps is never as marked as in *Skopaiolophus* but some palaeotheriids (*Lophiotherium* and *Anchilophus*) tend to have a distally displaced entoconid and, to a lesser degree, metaconid. The hypoconulid is always present in selenolophodont condylarths and basal perissodactyls and is therefore a critical apomorphic character in regard to most plesiomorphic character states in *Skopaiolophus*. In addition, the M_2 hypoconulid is completely lost in ceratomorphs (Froehlich, 2002), it tends to be reduced in basal tapiromorphs and it is usually strong in all equoids. Consequently, *Skopaiolophus* is derived among basal tapiromorphs whereas the retention of a tiny paraconid is unambiguously a plesiomorphic character among ungulates. Given the mosaic of primitive (retention of a paraconid) and derived features (loss of M_2 hypoconulid and of cingulids) retained in *Skopaiolophus*, it is difficult to assess its tapiromorph or hippomorph affinities with certainty on the basis of lower molars only. However, the structure of its protolophid and the likely shape of its M_3 hypoconulid lead us to favour affinities with basal tapiromorphs (sensu Froehlich, 1999, 2002).

6. Conclusions

Skopaiolophus burmese displays a mosaic of derived (transversely developed molars, absence of well marked notchs on lophids and absence of both well-developed hypoconulid on M_2 and cingulid) and primitive characters (small size, retention of a paraconid) unknown in perissodactyls. The selenolophodont pattern of *Skopaiolophus* lower molars can be interpreted as an apomorphic condition related to the marked distal displacement of the lingual cusps with respect to the labial ones. Although we favour possible relationships between *Skopaiolophus* and tapiromorph perissodactyls, it is difficult to be precise about its phylogenetic position within tapiromorphs because of the scarce material currently available and the absence of diagnostic upper teeth. Froehlich (1999, 2002) has recently provided an inclusive phylogenetic analysis of early Paleogene perissodactyls but the material described here does not allow *Skopaiolophus* to be included in this matrix of characters, since missing data for this taxon would weaken the significance of results. *Skopaiolophus* might likely be nested within tapiroids and it might represent a dwarf and dentally specialized lineage of perissodactyls. For now, the earliest evolution of Asian ungulates still depends on new fossil discoveries and further material would be necessary in order to better understand the phylogenetic relationships of *Skopaiolophus* with other basal tapiromorphs.

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