Early rhinocerotids (Mammalia: Perissodactyla) from South Asia and a review of the Holarctic Paleogene rhinocerotid record[1]

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Abstract: The earliest rhinocerotids from South Asia are identified on the basis of few dental remains originating from the Late Eocene of Thailand (Wai Lek mine, Krabi Basin) and the Early Oligocene of Pakistan (Paali nala C2, Bugti Hills). Once synthesized, the Holarctic Paleogene rhinocerotid record points out a westward diachronism of rhinocerotid First Appearance Data, from North America to Europe via Asia, throughout mid-Cenozoic times. The faunal similarity among mammal localities from the Late Eocene and Early Oligocene of peninsular Thailand, southern China, and Pakistan suggests the existence of a single South Asian paleoprovince during this interval and the persistence of a tropical–subtropical climate. Substantial faunal changes recorded in eastern Balochistan reveal a significant climatic deterioration from the middle part of the Oligocene. Neither provinciality nor endemism is noticeable for rhinocerotoid taxa recognized in the Oligocene of the Indian subcontinent: neither the Himalayas nor the Tibet Plateau was a paleogeographic barrier for large mammals during this interval.

Résumé : Les plus anciens rhinocérotidés d'Asie du Sud sont identifiés grâce à quelques restes dentaires provenant de l'Eocène supérieur de Thaïlande (Mine de Wai Lek, Bassin de Krabi) et de l'Oligocène inférieur du Pakistan (Paali nala C2, Collines Bugti). La synthèse du registre fossile paléogène holarctique des rhinocérotidés révèle un net diachronisme des premières apparitions de rhinocérotidés depuis l'est (Amérique du Nord) vers l'ouest (Asie, puis Europe) au cours du Cénozoïque moyen. La similarité des communautés de mammifères entre les localités de l'Eocène supérieur et de l'Oligocène inférieur de Thaïlande péninsulaire, de Chine du Sud et du Pakistan, suggère l'existence d'une seule Paléoprovince sud-asiatique pendant la période considérée, sous un climat tropical à subtropical. Les changements fauniques enregistrés au Balouchistan oriental révèlent une détérioration climatique significative à partir du milieu de l'Oligocène. Aucun indice de provincialisme ou d'endémisme n'est relevé pour les rhinocérotoïdes oligocènes du Sous-continent indien : ni les Himalayas ni le Plateau du Tibet ne constituaient à l'époque une barrière paléogéographique pour les grands mammifères.

Introduction

Although represented by only five endangered living species, rhinocerotids were the most flourishing perissodactyl mammals during Tertiary times (Prothero and Schoch 1989). They first occur in the late Middle Eocene of North America, with *Penetrigonias* (Duchesnean; Prothero 1998), and Asia, with *Teletaceras* (Beliajeva 1959; Russell and Zhai 1987; Hanson 1989). Early rhinocerotids are well diversified in North America (Prothero 1998), but they are still poorly documented throughout the Late Eocene and Early Oligocene in Eurasia (Fig. 4). The Late Eocene Old World rhinocerotid record is so far restricted to scarce dental remains from very few localities of East Asia (Fig. 4): "Far East Province" of Russia (Beliajeva 1959; Hanson 1989); southern China (Guangxi and Yunnan provinces; You 1977; Wang and Zhang 1983); eastern China (Henan Province; Wang and Zhou 1982), and southern Mongolia (Ergilin Dzo; Beliajeva 1954; Dashzeveg 1991).

This article reports the earliest rhinocerotid occurrences

Received 28 June 2002. Accepted 15 November 2002. Published on the NRC Research Press Web site at http://cjes.nrc.ca on 14 March 2003.

Paper handled by Associate Editor H.-D. Sues.

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[1] Mission Paléontologique Française au Balouchistan Publication n° 20; Institut des Sciences de l'Evolution de Montpellier Publication n° 2002-056.
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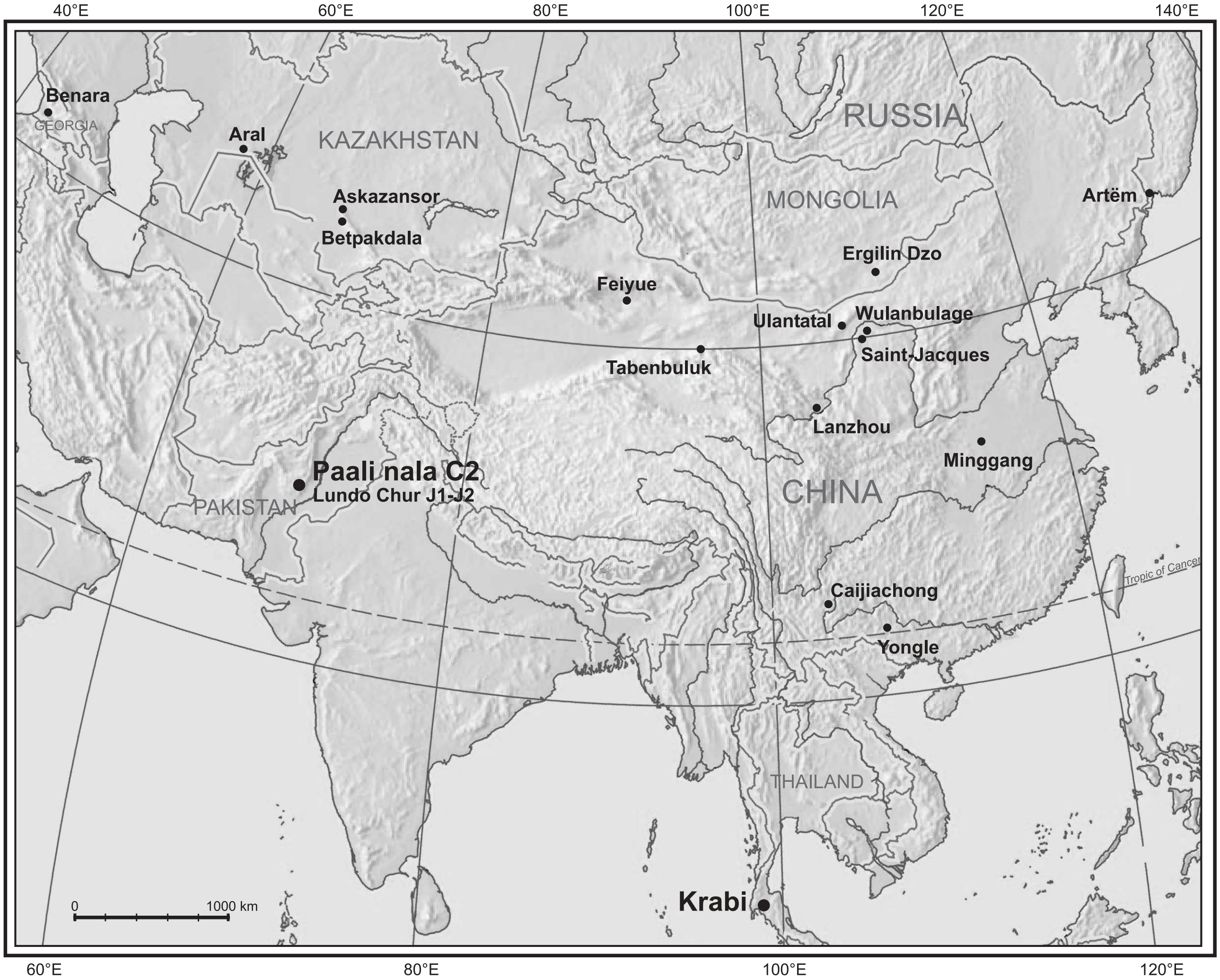
doi: 10.1139/E02-101

Fig. 1. Map of Eurasian Paleogene localities yielding rhinocerotid perissodactyls, referred to in this work (main text and Fig. 4).



from Thailand and the Indian subcontinent in a taxonomic, biostratigraphic, paleogeographic, and paleoenvironmental framework. The specimens come from the Late Eocene of peninsular Thailand (Wai Lek mine, Krabi Basin; Fig. 1) (Ducrocq et al. 1995, 1997) and the Early Oligocene of eastern Balochistan, Pakistan (Paali nala C2, Bugti Hills; Fig. 1) (Welcomme et al. 2001).

Material and methods

We have compared the new studied specimens with well-known non-rhinocerotid Rhinocerotoidea, such as the early *Hyrachyus eximius* Leidy, 1871, the hyracodontine *Hyracodon nebraskensis* Leidy, 1850, the indricotheriine *Indricotherium transouralicum* Pavlova, 1922, and the amynodontid *Metamynodon planifrons* Scott and Osborn, 1887, to ensure their taxonomic identification. Among Rhinocerotidae, the comparison has been made with the following rhinocerotid genera and species from the Eocene and the Early Oligocene of Eurasia and North America (Fig. 4): *Teletaceras* Hanson, 1989 (*Teletaceras radinskyi* Hanson, 1989: upper cheek teeth (UCT), lower cheek teeth (LCT), and milk teeth (MT)); *Guixia* You, 1977 (*Guixia simplex* You, 1977: UCT and LCT; *Guixia youjiangensis* You, 1977: UCT); *Penetrigonias* Tanner and Martin, 1976 (*Penetrigonias hudsoni* Tanner and Martin, 1976: UCT; *Penetrigonias sagittatus* (Russell, 1982) = “*Subhyracodon*” *sagittatus*: UCT); *Trigonias* Lucas, 1900 (*Trigonias osborni* Lucas, 1900: UCT, LCT, and MT; *Trigonias wellsi* Wood, 1927: UCT); *Amphicaenopus* Wood, 1927 (*Amphicaenopus platycephalus* (Osborn and Wortman, 1894): UCT and LCT); *Subhyracodon* Brandt, 1878 (*Subhyracodon occidentalis* (Leidy, 1851): UCT, LCT, and MT; *Subhyracodon mitis* (Cope, 1873): UCT); *Diceratherium* Marsh, 1875 (*Diceratherium armatum* Marsh, 1875: UCT, LCT, and MT; *Diceratherium tridactylum* (Osborn, 1893): UCT); *Epiaceratherium* Abel, 1910 (*Epiaceratherium bolcense* Abel, 1910: UCT and LCT; *Epiaceratherium magnum* Uhlig, 1999: UCT, LCT, and MT); *Ronzotherium* Aymard, 1854 (*Ronzotherium velaunum* Aymard, 1854: UCT and LCT; *Ronzotherium filholi* Osborn, 1900: UCT, LCT, and MT; *Ronzotherium romani* Kretzoï, 1940: UCT, LCT, and MT; *Ronzotherium brevirostre* (Beliajeva, 1954) = “*Symphysorrachis*” *brevirostre* = *Ronzotherium orientale*

Dashzeveg, 1991: UCT and LCT); and *Protaceratherium* Abel, 1910 (*Protaceratherium albigense* (Roman, 1912): UCT and LCT).

The dental terminology used is after Heissig (1969, pp. 9, 10), Uhlig (1999, p. 15), and Antoine (2002, fig. 72). Upper case letters are used to indicate upper teeth (D, P, and M), and lower case letters to indicate lower teeth (d, p, and m). All dimensions are in millimetres, except where indicated.

Systematic paleontology

Perissodactyla Owen, 1848
Ceratomorpha Wood, 1937
Rhinocerotidae Gray, 1821
incertae sedis
Epiaceratherium Abel, 1910
Epiaceratherium cf. *magnum* Uhlig, 1999

REFERRED MATERIAL: DBC2-RHI-1, right D1 (length 21.6; anterior width 14.8; posterior width 18.5; height of the crown 10.2); DBC2-RHI-2, left D2 without ectoloph (length > 24.0); DBC2-RHI-3, left M3 without ectoloph; DBC2-RHI-4, protoloph of a right M3. Specimens were collected in the locality of Paali nala C2 in 2000 and 2002 by the Mission Paléontologique Française au Balouchistan (MPFB) and temporarily housed in the Laboratory of Paleontology of the Université de Montpellier II (UM2), Montpellier, France.

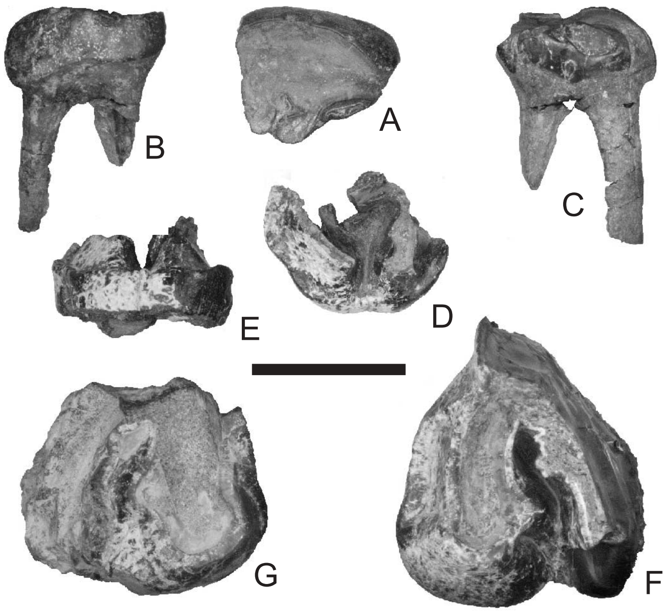
HORIZON AND LOCALITY: Deltaic sands of the Paali nala C2 locality (DBC2: Dera Bugti locus C2), 20 km south of Dera Bugti, southern Sulaiman Range, eastern Balochistan, Pakistan (Fig. 1). Lower part of the Bugti Member, Chitarwata Formation (Raza and Meyer 1984). Early Oligocene (Rupelian) after Marivaux et al. (1999) and Welcomme et al. (2001).

DESCRIPTION: The teeth are middle-sized. There are no enamel foldings. Some coronary cement is preserved in the central valley of one M3 (DBC2-RHI-4; Fig. 2G); a thin layer of cement is partly covering the valleys of P1 (Fig. 2C). The crowns are low and conical. The enamel is thin on both D1 and D2 (approximately 0.6 mm), thick on M3 (up to 2.5 mm), and always thinly wrinkled vertically.

DBC2-RHI-1 has a very thin enamel (approximately 0.6 mm), which allows us to identify it as a D1 rather than a P1. Being much worn, it might have been persistent; many details have vanished due to wear (Fig. 2A). The two roots are thin, long, and straight. The occlusal outline is a rounded isosceles triangle, higher than wide. The ectoloph is very thick due to wear. Its anterior part is curved inward. There is no labial cingulum. The lingual cingulum is sharp and sigmoid in lingual view. It vanishes in the anterior side of the protocone. P1 is molariform, with a thin but complete protoloph, obliquely joining the thick paracone and the small protocone. The metaloph, totally worn, was probably transverse. A small and triangular medisinus is preserved between the lophs. It is open lingually. Yet, no trace of postfossette is preserved.

The D2 (DBC2-RHI-2) is partly broken: the labial part, including the entire ectoloph, is lacking (Fig. 2D). The occlusal outline was probably trapezoid, with a lingual length much weaker than the labial one. A horizontal cingulum surrounds the whole preserved part of the tooth, 5–7 mm above the neck. The anterior cingulum is thick and sharp, with an almond-shaped wear facet in its labial third. A small vertical enamel ridge lies in front of the protoloph, from the neck to the top of the anterior cingulum. The cingulum is thin along the lingual side of the protocone (Fig. 2E). It is also interrupted on the whole lingual side of the hypocone: the lingual cingulum is restricted to three small enamel tubercles that partly close the lingual entrance of the deep and narrow median valley. The posterior cingulum is thick and high, yet the preserved part of it slopes down labially, following the shape of the postfossette. The tooth is molariform, with complete protoloph and metaloph. A small prefossette might have occurred on D2 due to the labial inflexion of the protoloph. The protoloph is curved backward, short of any constriction or antecrochet. Its anterior and posterior sides converge strongly. The metaloph is straight and oblique, with the hypocone anterior to the metacone. There are two close minute ridges on the anterior side of the metaloph, located in the median part of it and restricted to the top of the crown. They most probably correspond to a crochet. The postfossette is very wide because of the orientation and the straight shape of the metaloph. The lingual side of the ectoloph is strongly curved (a crista?), which partly closes the median valley. Thus, the latter has a Y-shaped bottom in occlusal view.

Fig. 2. *Epiaceratherium* cf. *magnum* Uhlig, 1999, Early Oligocene (Rupelian), Paali nala C2, Bugti Hills, Balochistan, Pakistan. (A, B, C) DBC2-RHI-1, right D1 in occlusal, labial, and lingual views. (D, E) DBC2-RHI-2, left broken D2 in occlusal and lingual views. (F) DBC2-RHI-3, left broken M3 in occlusal view. (G) DBC2-RHI-4, right broken M3 in occlusal view. All in natural size. Scale bar = 20 mm.



Both M3 show identical morphology and dimensions. Because DBC2-RHI-4 is more worn than DBC2-RHI-3, one can deduce that they represent two distinct individuals. The external side is lacking in both specimens (Figs. 2F, 2G), and thus measurements cannot be provided. The enamel is thick on the protoloph (2.5 mm) and thinner on the lingual side of the ectometaloph (0.9 mm). The anterior roots were entirely independent, whereas the lingual ones could have been slightly connected (DBC2-RHI-4). The antecrochet is strong on both specimens. The anterior constriction of the protocone, marked on the base of the crown, shallows to the top and ends before it. The multiple crochet is restricted to the top of the crown on DBC2-RHI-3, whereas it forms only a smooth convexity on the more worn DBC2-RHI-4. There is no crista nor medifossette. The anterior cingulum is strong and thick. The lingual cingulum is restricted to small and low tubercles in the entrance of the median valley: there is no trace of a lingual cingulum on the lingual side of the protocone. The median valley is deeper in its anterolabial tip. According to the orientation of the metaloph, the ectoloph and the metaloph were most likely fused into an ectometaloph. The protoloph is transverse and slightly curved backward. The protocone is elongated sagittally and flattened lingually.

DISCUSSION: The dimensions and morphologic features of the teeth from Paali nala C2 are homogeneous enough to document a single taxon. The rhinocerotid from Paali nala C2 exhibits several plesiomorphic features, shared with the main primitive rhinocerotids and hyracodontids (Antoine 2002): the enamel is wrinkled; cheek teeth (M3) are low-crowned; D1 is bilophodont; D2 lacks a lingual wall, a mesoloph (sensu Antoine 2002), and secondary folds. Nonetheless, such a morphology sets the Paali nala C2 rhinocerotid apart from *Diceratherium* (Osborn 1898; Antoine 2002); D2 is bilophodont, with a thick and curved protoloph and a straight metaloph. Though few and (or) fragmentary, these specimens bear several synapomorphies of Rhinocerotidae, such as a reduced D1 and the fusion of the ectoloph and the metaloph into an ectometaloph on M3 (Prothero et al. 1989). These features are independently present in some giant hyracodontids (Forster-Cooper 1934; Gromova 1959; Prothero et al. 1989), whose teeth are much larger, however, than those of the specimens from Paali nala C2. In addition, the M3 are neither elongated sagittally nor hypsodont, as they are in amynodontids. The crochet (multiple), the antecrochet, and the sinuous protoloph on M3 further point to rhinocerotid affinities.

The D1, D2, and M3 from Paali nala C2 have a reduced lingual cingulum, and D1 lacks a labial cingulum, as in *Epiaceratherium* (Dal Piaz 1930; Uhlig 1999) and *T. radinskyi* (Hanson 1989), contrary to most early rhinocerotids: *Ronzotherium* (Brunet 1979), *Penetrigonias*, *Trigonias* (Gregory and Cook 1928; Russell 1982), *Subhyracodon*, *Diceratherium* (Osborn 1898; Scott 1941), and *P. albigense* (Roman 1912) have well-developed cingula. The presence of coronary cement has rarely been reported for Paleogene rhinocerotids (including *Epiaceratherium*). Nevertheless, some cement is present in *D. armatum* (Antoine 2002), and Hanson (1989, p. 388) mentions “patches of cement on the surface of the ectoloph, in the median valley, and in the postfossette” on the upper cheek teeth of the early rhinocerotid, *T. radinskyi* from the Late Eocene of North America.

On M3, the crochet is present, like in *E. magnum* (Uhlig 1999), *Guixia* (You 1977), *Penetrigonias* (Tanner and Martin 1976), and *Diceratherium*. Its shape, i.e., multiple, dentate, and restricted to the top of the crown, is only observed in *E. magnum*, *G. youjiangensis*, and *Diceratherium*. Interestingly, the Paali nala C2 rhinocerotid was formerly identified as “cf. *Diceratherium* sp.” (Welcomme et al. 2001, p. 398), only on the basis of the fragmentary M3. Additional comparison, however, provided morphological evidence against this preliminary assumption: the combination of a strong antecrochet, a weak anterior constriction protocone, and a lingually flattened protocone appear as exclusive of *E. magnum* (Uhlig 1999), in the sense that *E. bolcense* and *P. albigense* show rounded protocones (Roman 1912; Dal Piaz 1930), and *Diceratherium* displays a weak antecrochet.

A bilophodont D1, with cross-lophs as in Paali nala C2, is a plesiomorphic condition in rhinocerotoids, since it is observed in hyracodontids, amynodontids, and in most early rhinocerotids, particularly from North America: *Penetrigonias*, *Trigonias*, *Amphicaenopus*, *Subhyracodon* (Osborn 1898; Scott 1941), *Ronzotherium* (Heissig 1969; Brunet 1979), and, to a lesser degree, *T. radinsyi* (Hanson 1989). In *E. magnum* (Uhlig 1999) and *P. albigense* (Roman 1912), the median valley is open rostrally and closed lingually, and the metaloph is consequently disconnected from the ectoloph. The proportions of DBC2-RHI-1 are similar to those of most rhinocerotids, except for *G. youjiangensis* (You 1977, pl. 1, fig. 1) and *S. occidentalis* (Osborn 1898, pl. 13, fig. 7), which display widened D1.

Concerning D2, the strong development of the “crista,” leading to a median valley with a “Y-shaped” bottom (Fig. 2D), is only observed in *E. magnum*, *Ronzotherium* (Brunet 1979; Uhlig and Böhme 2001), and *Subhyracodon* (Osborn 1898). The orientation of the metaloph in DBC2-RHI-2 (hypocone anterior to metacone) is still more discriminative, since it is only shared with *E. magnum*: the usual rhinocerotid dental pattern is a transverse metaloph (*R. filholi*, *Penetrigonias*, *Subhyracodon*) or a hypocone posterior to the metacone (*Ronzotherium* sp. sensu Uhlig and Böhme 2001; *Diceratherium*). Besides, the development of a “crochet” on D2 is strongly similar to that of *E. magnum* (Uhlig 1999, p. 39, fig. 16).

In other words, both D2 and M3 from Paali nala C2 show the greatest affinities (including dimensions and proportions) with those of the European *E. magnum*, as widely described and abundantly figured by Uhlig (1999). The only differences concern D1 (bilophodonty and absence of external ribs in Paali nala C2). As it is widely admitted that the first jugal tooth is the most variable one in Paleogene rhinocerotids (e.g., Brunet 1979), we propose to assign the Paali nala C2 rhinocerotid to *E.* cf. *magnum*.

Guixia You 1977
? *Guixia* sp. cf. *G. simplex* You, 1977

REFERRED MATERIAL: TF 2657, left m2 (length 23.9; anterior width ~17.8; posterior width 18.2; height 11.4); TF 2658, left m3 from the same individual (length 29.1; anterior width 18.0; posterior width 17.0; height 11.1). Specimens collected in the Wai Lek mine, Krabi Basin (Thailand), in 1990 and temporarily deposited in the collections of the Université de Montpellier II.

HORIZON AND LOCALITY: Wai Lek mine, Krabi Basin, peninsular Thailand (Fig. 1). Latest Eocene after Benammi et al. (2001).

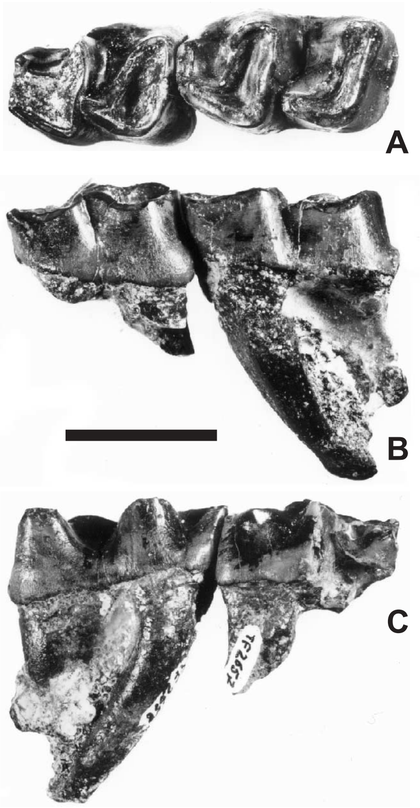
DESCRIPTION: The lower molars from Wai Lek are small, with a rectangular occlusal outline. Their pattern is similar, consisting of two crescents open lingually (Fig. 3A). TF

2658, moderately worn, is free of any posterior wear due to contact with a following tooth. This allows us to identify it as an m3, and TF 2657 as an m2. Both specimens have the same width, but m2 is much shorter than m3 (23.9 mm versus 29.1 mm). The teeth are brachydont; the crown is more prismatic on m3. No trace of coronary cement is preserved. The enamel is thick (1.7 mm) with respect to the size of the teeth. It is thinly wrinkled vertically on the whole crowns. Teeth are two-rooted: the roots are long, thin, inclined, and curved backwardly (Figs. 3B, 3C). There is neither lingual nor labial cingulum. Nonetheless, the anterior cingulum extends posterolabially on m2 and forms a short and oblique ridge. The posterior cingulum is wide and low on m2. It is much narrower on m3, where it only forms a smooth median triangular spur. The ectolophid groove, though marked on the top of the crown, ends before the neck. It is oblique and orientated frontward, similarly to the crowns (Fig. 3B). The slightly worn paralophid is wide and transversely oriented on m3, and it is crushed on m2. The angulous trigonid forms an acute angle in occlusal view, whereas the talonid is more rounded. The metalophid is directed transversely on both teeth. There is no protoconid fold on m3. The metaconid is slightly constricted on m3. The entoconid is short of any anterior or lingual constriction on both m2 and m3. The U-shaped posterior valley is widely open lingually, and much deeper than the anterior one. The hypolophid is slightly oblique, but nearly transverse in occlusal view.

DISCUSSION: The m2 and m3 from Wai Lek follow the general rhinocerotoid pattern, with two contiguous crescents open lingually. Although usually considered as particularly monotonous among Rhinocerotoidea, the lower molars exhibit several diagnostic features of the Rhinocerotidae (Antoine 2002): the metalophid is transverse, instead of oblique in both hyracodontids and amynodontids. In addition, these molars are not elongated like in amynodontids. Accordingly, the lower molars from Wai Lek can be unambiguously referred to a rhinocerotid, as initially suggested by Ducrocq (1992).

These molars bear several symplesiomorphic traits for rhinocerotids, such as a pronounced ectolophid groove vanishing before the neck, an angulous and acute trigonid, and a transverse hypolophid (Antoine 2002). These features are not discriminating, since they occur in all Paleogene rhinocerotids compared in this work (*Teletaceras*, *Guixia*, *Ronzotherium*, *Penetrigonias*, *Trigonias*, *Amphicaenopus*, *Sybhyracodon*, *Diceratherium*, *Epiaceratherium*, and *Protaceratherium*; Fig. 4). The reduction of the posterior cingulum (spur-like) on the m3 from Wai Lek is only observed in *G. simplex* from the Naduo Formation of south China (Guangxi Province; You 1977), *E. bolcense* (Dal Piaz 1930), *D. tridactylum* (Osborn 1898), and *P. albigense* (Roman 1912). The molars from Wai Lek lack labial and lingual cingula. Such a morphology, shared by *G. simplex*, *Epiaceratherium*, and *T. radinskyi* (Hanson 1989), excludes *Diceratherium* (Osborn 1898; Scott 1941) and *P. albigense*. The combined absence of constricted entoconid and metaconid sets the Wai Lek rhinocerotid apart from *Teletaceras* (Hanson 1989) and *Epiaceratherium* (Dal Piaz 1930; Uhlig 1999). The U-shaped posterior valley on m2–m3 was so far exclusive of *G. simplex* (You 1977) and *Ronzotherium*, whereas the usual morphology (i.e., shared by other taxa) is a V-shaped valley. Furthermore, the m2 is short and widened with respect to the m3, which is only observed in the rhinocerotid from Wai Lek and in *G. simplex*.

Fig. 3. ? *Guixia* sp. cf. *G. simplex* You, 1977, Late Eocene (late Bartonian), Wai Lek mine, Krabi Basin, Thailand. (A, B, C) TF 2657, left m2, and TF 2658, left m3, from the same individual in occlusal, labial, and lingual views. All in natural size. Scale bar = 20 mm.

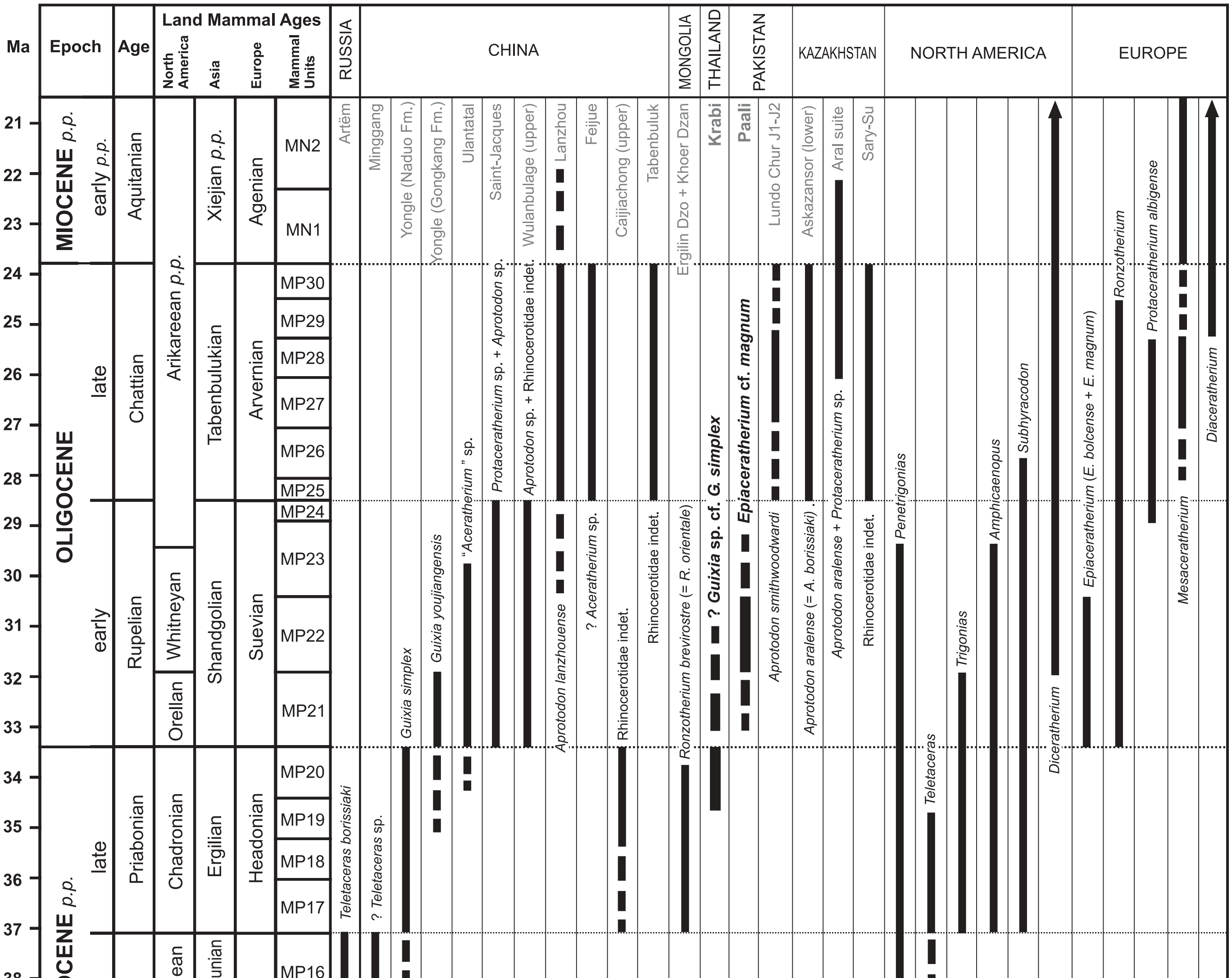


To sum up, the closest of relationships can be assumed between the specimens from Wai Lek and *G. simplex* from south China, whose dimensions are strongly comparable, following You (1977, pl. 1, fig. 2). It is impossible to establish a direct comparison between the rhinocerotid material currently available from Wai Lek and *G. youjiangensis*, since the latter is only known by upper cheek teeth (You 1977). Nonetheless, *G. youjiangensis* displays much larger dimensions than *G. simplex*. Accordingly, we can exclude it from the discussion. Further material (i.e., upper cheek teeth) would be necessary for strengthening the specific identification of the Wai Lek rhinocerotid. Consequently, we provisionally refer the material from Wai Lek to ? *Guixia* sp. cf. *G. simplex*.

Paleogene rhinocerotids from Thailand and Pakistan

The recognition of ? *Guixia* sp. cf. *G. simplex* in the Late Eocene of the Krabi Basin widely predates the former first appearance datum (FAD) for Rhinocerotidae in Thailand: thus far, rhinocerotids were recorded only in Neogene localities, from the early Miocene up to recent times (Ginsburg 1985; Mein and Ginsburg 1997; Tougard 2001). *Guixia* was confined to the Late Eocene Naduo and Gongkang formations in south China (Yongle Basin, Guangxi Province; You 1977; Fig. 1).

Fig. 4. Updated Holarctic Paleogene rhinocerotid record. From left to right, the columns are organized in the following order: Asian occurrences (localities from Russia, China, Mongolia, Thailand, Pakistan, and Kazakhstan), North American genera, and European genera and (or) species. Rhinocerotid-bearing localities and (or) formations appear in grey letters. Stratigraphic and biochronologic ranges revised after Abel (1910), Roman (1912), Teilhard de Chardin (1926), Dal Piaz (1930), Borissiak (1944), Beliajeva (1954, 1959), Heissig (1969), Bonis (1973), You (1977), Zhai (1978), Brunet (1979), Wang et al. (1981), Huang (1982), Wang and Zhou (1982), Wang and Zhang (1983), Russell and Zhai (1987), Hanson (1989), Heissig (1989), Prothero and Schoch (1989), Dashzeveg (1991), Stucky (1992), Wang (1992), Berggren et al. (1995), Bonis et al. (1997), Daxner-Höck et al. (1997), McKenna and Bell (1997), Qiu and Xie (1997), Vislobokova (1997), Emry et al. (1998), Lucas et al. (1998), Meng and McKenna (1998), Prothero (1998), Qi and Beard (1998), Uhlig (1999), Welcomme et al. (2001), Benammi et al. (2001), and Marivaux et al. (2001, 2002). *p.p.*, pro parte.



The mammal fauna of Krabi is strongly similar to that of the Gongkang Formation, on the basis of anthracotheres and primates (Ducrocq et al. 1995, 1997; Qi and Beard 1998; Ducrocq 1999; Benammi et al. 2001). Even though continental Oligocene deposits are still undocumented in Thailand (Ducrocq et al. 1997), the persistence of rhinocerotids throughout the Oligocene in northern and (or) peninsular Thailand might be expected anyway, according to the wide expansion of the Oligocene rhinocerotids elsewhere in Eurasia (Fig. 4; see later in the paper).

Similarly, the presence–absence of continental Oligocene deposits in the Indian subcontinent, especially in Pakistan, has been debated for decades (e.g., Pickford 1988; Downing et al. 1993). For instance, the Bugti Member, defined as the lower part of the Chitarwata Formation in the Sulaiman geological province, was originally attributed to the Early Miocene (Raza and Meyer 1984). Recently, the fieldwork led by the MPFB in the Bugti Hills (1995–2002) has demonstrated that the Bugti Member was entirely Oligocene in age (fig. 1 in Welcomme et al. 2001), with five successive fossiliferous levels recognized from the Early to the Late Oligocene. Rhinocerotoids occur from the lowermost level, with the amynodontid *Cadurcotherium indicum* Pilgrim, 1910 and the hyracodontid *Paraceratherium bugtiense* (Pilgrim, 1908); both species persist throughout the Bugti Member (Welcomme et al. 2001). The following fossiliferous level is Paali nala C2, the lowest level that yields rhinocerotid remains (*E.* cf. *magnum*). *Epiaceratherium magnum* is confined thus far to the earliest Oligocene of Europe (Italy, Germany, Czech Republic, Switzerland, France; Uhlig 1999; mammal units MP21 and MP22 in Fig. 4). The occurrence of *Epiaceratherium* in Paali nala C2 is consistent with the Early Oligocene age previously assumed for this locality on the basis of rodents and artiodactyls (Marivaux et al. 1999; Welcomme et al. 2001). From the same locality, Marivaux et al. (2001, 2002) have also reported the first primate assemblage in the Oligocene of Asia (i.e., posterior to the European “*Grande Coupure*”; Stehlin 1909), including anthropoids (L. Marivaux, unpublished data), adapiforms (sivaladapids), and lemuriforms (cheirogaleid-like). Other rhinocerotid remains have been collected by the MPFB in the Bugti Member, but always in higher levels, i.e., Late Oligocene in age (Lundo Chur J1 and J2; Welcomme et al. 2001). They are referred to *Aprotodon smithwoodwardi* Forster-Cooper, 1915, originally described from the same locality (i.e., “Chur Lando” following Forster-Cooper 1915, 1934). *Aprotodon smithwoodwardi* is the type species of the genus *Aprotodon*, widely distributed in Asia and recognized in the Oligocene of China and Kazakhstan (Figs. 1, 4; Borissiak 1944; Beliajeva 1954; Qiu and Xie 1997). This further pleads for the Oligocene age of Lundo Chur J1 and J2.

Holarctic Paleogene rhinocerotid record

Figure 4 illustrates an updated synthesis of the Holarctic Paleogene rhinocerotid record, with a special emphasis on the Asian record. The middle Late Eocene corresponds to the FAD of Rhinocerotidae, with *Teletaceras* on the western side of “Beringia” (Fig. 1; Beliajeva 1959; Hanson 1989) and *Penetrigonias* in North America (Prothero 1998). Besides, Wang and Zhou (1982) mention the presence of “Rhinocerotidae indet.” in the late Middle Eocene of Minggang (Pingchangguan Basin, China) on the basis of a “d3/4.” Nonetheless, this specimen (Wang and Zhou 1982, pl. 1, fig. 3) shows morphologic features and dimensions which closely match with those of the m1–m2 of *T. radinskyi* (Hanson 1989, p. 389, fig. 20.6). Therefore, we propose to refer this lower tooth to ? *Teletaceras* sp. In any case, *Teletaceras* is only recognized near the Pacific Ocean, in mid-latitudes (30°–45°N): western Oregon and California in North America (Hanson 1989), Maritime Province in Russia, and questionably Henan Province in China (Fig. 1). The climate was warm in the whole area (estimated average annual temperature about 25°C; Leopold et al. 1992, fig. 20.1).

Rhinocerotids widely diversified in the Late Eocene of North America, with five genera (Prothero 1998; S.G. Lucas, personal communication, 2002). In Eurasia, the record is restricted to East Asia, with the northern *Ronzotherium* from Mongolia (Fig. 1; Beliajeva 1954; Dashzeveg 1991) and the southern *Guixia* from south China and Thailand (Fig. 1). *Ronzotherium* displays North American affinities (e.g., with *Trigonias* and *Penetrigonias*: thick lingual cingula on cheek teeth, middle to large size), and *Guixia* seems to be closely related to *Teletaceras* (weak cingula, smaller size).

The Early Oligocene marks the FAD of Rhinocerotidae in Europe, with Asian-like *Ronzotherium* and *Epiaceratherium* (Fig. 4). This period documents the earliest multispecific rhinocerotid assemblages in Asia (e.g., *Protaceratherium* sp. + *Aprotodon* sp. in Saint-Jacques, Inner Mongolia; revised after Teilhard de Chardin 1926) and Europe (e.g., *R. filholi* + *E. magnum* in Villebramar, France; Brunet 1979; Uhlig 1999). Meanwhile, no renewal is noticeable in North America: *Diceratherium* is the only genus to emerge throughout the Oligocene, and Late Eocene genera became extinct (Heissig 1989; Prothero 1998).

Although well represented in Eurasian mid-latitudes (China, Kazakhstan, Georgia, and Europe; Figs. 1, 4), the Late Oligocene is still poorly known south of 30°N, especially in the Indian subcontinent (Métais et al. in press): as a consequence, Lundo Chur J1 and J2 are the only rhinocerotid-bearing localities in South Asia. Both loci yield *A. smithwoodwardi* (Welcomme et al. 2001), type species of the most widespread Oligocene rhinocerotid genus of Asia (Fig. 4).

Later, Early Neogene times correspond to a major turnover for Holarctic Rhinocerotidae, with a significant renewal ratio (Prothero et al. 1989), and the subsequent dispersal toward Africa (Heissig 1989; Antoine 2002).

Paleogeography and paleoenvironments

Rhinocerotids were supposed to have spread into the Indian subcontinent from “continental” Asia during the Early Miocene (e.g., Made 1999). The recognition of *Epiaceratherium* cf. *magnum* in the Early Oligocene and the occurrence of *Aprotodon* in the Late Oligocene of central Balochistan preclude such a hypothesis. On the contrary, the role of the Tibet Plateau and the Himalayas as physical barriers to the dispersal of large mammals between Asia and the Indian subcontinent throughout the Oligocene can be minimized, as argued by Qiu and Xie (1997). Rhinocerotoids provide abundant evidence: the rhinocerotid *Aprotodon* (Fig. 4; Pakistan, Kazakhstan, China; Qiu and Xie 1997) and the giant hyracodontid *Paraceratherium* (Pakistan, Kazakhstan, China, Mongolia, Balkans; Lucas and Sobus 1989) occur contemporaneously on both sides of the Himalayas and the Tibet Plateau, while the rhinocerotid *Epiaceratherium* (Fig. 4) and the amynodontid *Cadurcotherium* (Welcomme et al. 2001) are documented in both western Europe and Pakistan.

The Late Eocene and the Early Oligocene are classically characterized by a global cooling (e.g., Berggren and Prothero 1992). Such a climatic deterioration is not recorded in the studied area (Fig. 1), since the mammalian communities from the Krabi Basin and the Bugti Hills (Paali nala C2) are characteristic of dense forested environments under a tropical to subtropical climate (Marivaux et al. 2000, 2001, 2002;

Welcomme et al. 2001). In fact, the paleolatitude of the Bugti Hills ca. 31 Ma was ~14° farther south than in recent times (i.e., ~15°N) due to the northward drift of the Indian Plate (Mattauer et al. 1999), which might explain these unexpected environmental conditions. Besides, the strong faunal similarity among southern China, peninsular Thailand, and central Pakistan mammal localities (Ducrocq et al. 1995; Qi and Beard 1998; Marivaux et al. 2000, 2002) further supports the existence of a single and wide South Asian faunal province during mid-Cenozoic times.

By contrast, the Late Oligocene faunal assemblage from the Bugti Hills (Lundo Chur J1 and J2; Welcomme et al. 2001) is closely comparable to coeval assemblages from Asian (China, Mongolia, Kazakhstan, Georgia; Fig. 1) and (or) European mid-latitudes. Such mammal communities portray drier and more open environments (i.e., open deciduous woodlands) under a temperate climate (Leopold et al. 1992). This implicit climatic deterioration, particularly noticeable throughout the mammal faunas of the Bugti Member, seems to be related to both the formation of orogenic highlands and the retreat of the epicontinental Paratethys Sea, as a direct consequence of the India–Eurasia collision (Ramstein et al. 1997; Fluteau et al. 1999).

Acknowledgments

The authors are very grateful to Nawab Mohammad Akbar Khan Bugti, Lord of the Bugti Tribes, and Zulficar and Bramdan Khan Bugti for their invitation and useful help. Many thanks to Dr. Grégoire Métais for his critical reading of a former version of the manuscript. The Associate Editor Hans-Dieter Sues and the referees Spencer G. Lucas and Donald R. Prothero greatly improved the manuscript. The fieldwork projects in both Thailand and Pakistan benefitted from financial support from the Centre National de la Recherche Scientifique (ECLIPSE, Environnements et climats du passé: histoire et evolution program). This work has received grants from the Fondation de France, and the Bleustein-Blanchet, Fyssen, Leakey, Singer-Polignac, and Wenner Gren foundations.

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