# First Record of a Chalicothere from the Miocene of Myanmar

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# First record of a chalicothere from the Miocene of Myanmar

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Here we describe the first record of a chalicothere from the Miocene of Myanmar. The chalicothere, documented by a partial mandible, was unearthed from the lower portion of the Irrawaddy Formation in the region of Magway, Central Myanmar. The Burmese material belongs to an early late Miocene fauna which recently yielded hominoid remains attributed to *Khoratpithecus*. The specimen, which is attributed to a chalicotheriine, does not reliably match with any described Miocene Eurasian species of this subfamily, suggesting the possibility it belongs to a new taxon. The discovery of a chalicotheriine in the surroundings of Magway contributes to the hypothesis that closed habitats were an important component of the paleoenvironment of *Khoratpithecus*.

Key words: Mammalia, Perissodactyla, Chalicotheriidae, Chalicotheriinae, *Khoratpithecus*, paleoenvironment, Miocene, Myanmar.

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## Introduction

Chalicotheriidae is a family of clawed perissodactyls known from the Oligocene to the Pleistocene whose peculiar anatomy has long drawn the attention of vertebrate paleontologists. Unfortunately, this family is poorly documented in the fossil record, which renders its evolutionary history difficult to reconstruct. The Chalicotheriidae are classically divided into two subfamilies, the Chalicotheriinae and the Schizotheriinae, which evolved simultaneously during most of the Neogene (Coombs 1989). The relatively rich chalicothere record of western and southern Europe has played a central role in the knowledge of the family's diversity, systematics and evolution for the whole of the Miocene of Eurasia (e.g., Bonis et al. 1995; Geraads et al. 2001; Anquetin et al. 2007). The discovery of cranial and mandibular remains in the Miocene of northern China has also contributed to the understanding of the phylogeny of the family (Colbert 1934; Xue and Coombs 1985; Wang and Wang 2001). In Southern Asia, however, the fossil record of chalicotheres is much poorer. Except for brief reports from the middle Miocene of northern Thailand (Thomas et al. 1990; Ducrocq et al. 1994) and the Pleistocene of Myanmar (Takai et al. 2006), the richest chalicothere material is that of *Chalicotherium salinum* Forster-Cooper, 1922 from the middle and late Miocene of the Siwaliks of Pakistan. This species represents the only well documented Miocene chalicothere from this region.

Since the end of the 19th century, the Neogene continental Irrawaddy Formation, which crops out throughout the Myanmar Central Basin, has yielded terrestrial mammalian faunas (e.g., Noetling 1895, 1897; Pilgrim 1927; Colbert 1938). However, few of the fossils have been formally de-
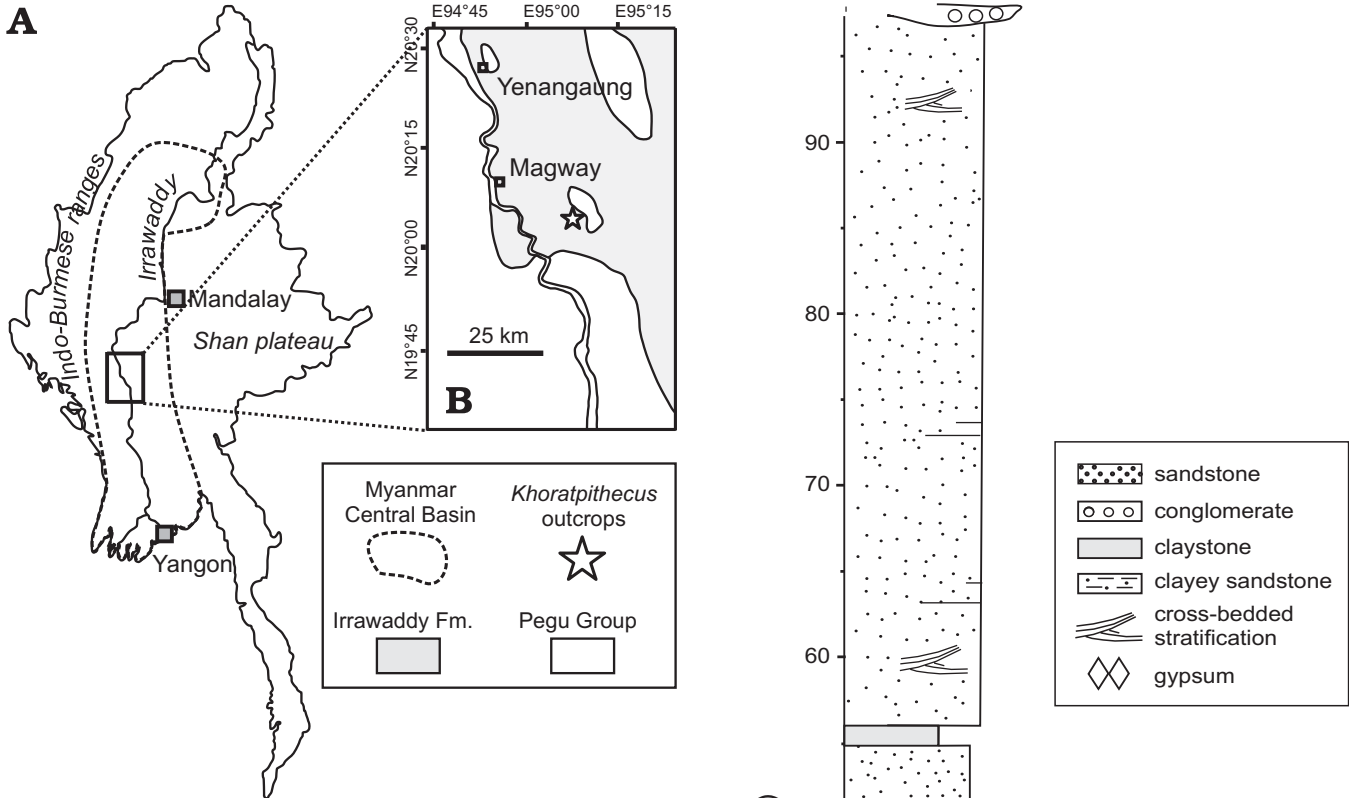
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Fig. 1. **A**. Map of Myanmar showing the area of study within the Myanmar Central Basin. **B**. Detailed map of the Magway region positioning the outcrops that yielded the chalicothere mandible MFI-105.

scribed while most of the reports have mentioned geographically and stratigraphically imprecise spots, impeding the paleontological potential of the formation, which is supposed to range from the middle Miocene to the Pleistocene (e.g., Bender 1983; Chavasseau et al. 2006).

First in 2002, then yearly since 2006, the French-Myanmar paleontological team surveyed the outcrops of the Irrawaddy Formation with the aim of improving the comprehension of the evolution of the Neogene faunas of Southeast Asia. These efforts led to the discovery 20 km southeast of Magway (Fig. 1) of an early late Miocene mammalian fauna comprising the remains of the hominoid *Khoratpithecus* (JJJ, unpublished data). All the fossils of this fauna were discovered in a 100 m thick section showing rapid lateral variation of facies, and mostly composed of cross-bedded coarse yellowish sands interstratified with sandy clays, thin clay layers, and numerous thin ferruginous conglomerate layers (Fig. 2). In December 2007, a partial mandible of a chalicothere was unearthed near the village of Ondwe from a ferruginous layer located stratigraphically approximately 15 meters above the *Khoratpithecus*-bearing level (Fig. 2). This discovery is of interest given the scarcity of chalicotheres in the fossil record of Southeast Asia, especially when taking into consideration that no Miocene remains of this family have yet been described from Myanmar. This paper aims, by describing this new specimen, to contribute both to the knowledge of the Miocene faunas of Southeast Asia and to that of the chalicothere evolution
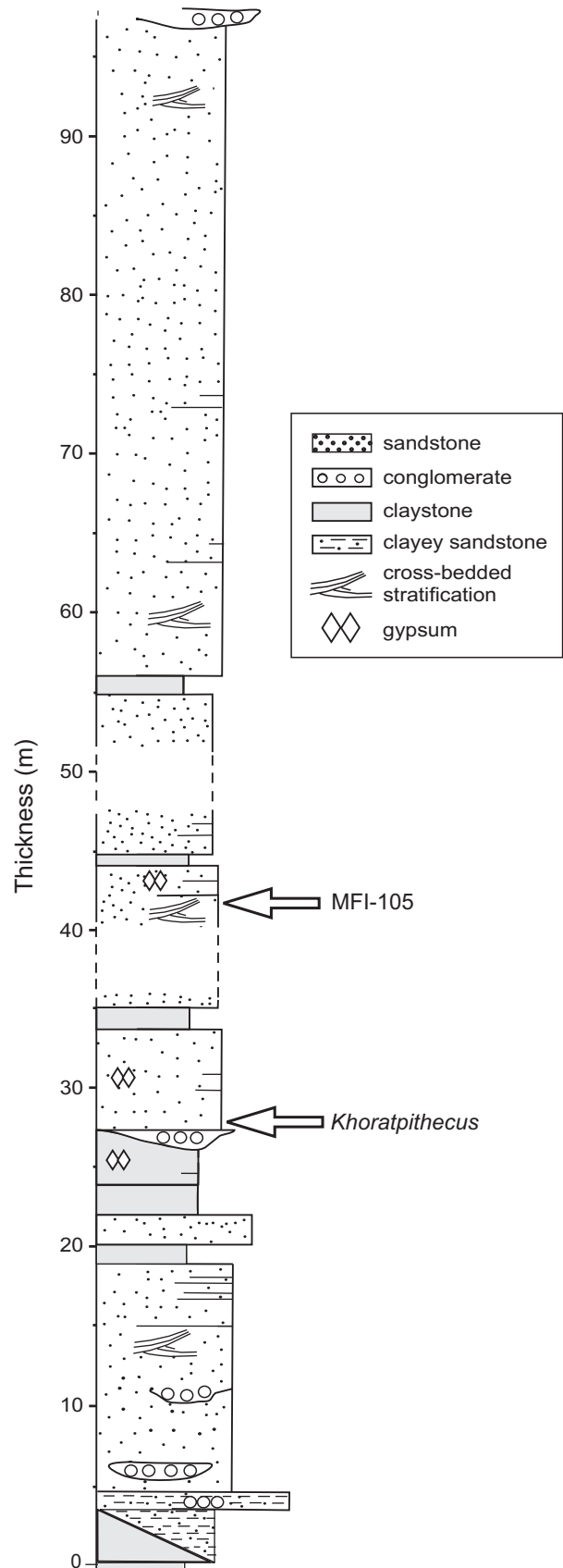


Fig. 2. Synthethic lithology of the Irrawaddy Formation *Khoratpithecus*-bearing outcrops 20 km southeast of Magway positioning the hominoid fossil and the chalicothere specimen MFI-105.
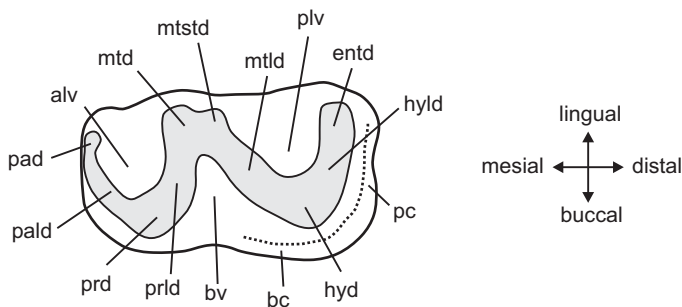
Fig. 3. Lower teeth nomenclature adopted in this article displayed on a composite m1 of *Chalicotherium salinum* (drawn from a mirror image of GSP 23046 with the exception of the "metastylid" pattern which was drawn from GSP 9665). After Coombs (1978). Abbreviations: alv, anterior lingual valley; bc, buccal cingulum; bv, buccal valley; entd, entoconid; hyd, hypoconid; hyld, hypolophid; mtd, metaconid; mtld, metalophid; mtstd, "metastylid"; pad, paraconid; pald, paralophid; pc, posterior cingulum; plv, posterior lingual valley; prd, protoconid; prld, protolophid.

in this region. The nomenclature adopted hereafter for lower cheek teeth is displayed in Fig. 3.

*Institutional abbreviations.*—AMNH, American Museum of Natural History, New York, USA; ANR, Agence nationale de la recherche, France; CNRS, Centre national de la recherche scientifique, France; GSP, Geological Survey of Pakistan, Quetta, Pakistan; IPHEP, Institut International de Paléoprimatologie et de Paléontologie Humaine: Evolution et Paléoenvironnements, Université de Poitiers, Poitiers, France; MFI, Myanmar-French Irrawaddy Mission Collection deposited at Department of Archaeology, Ministry of Culture, Mandalay, Myanmar; MNHN, Muséum national d'Histoire naturelle, Paris, France; TRF, Thailand Research Fund, Thailand.

# Systematic paleontology

Order Perissodactyla Gray, 1848

Family Chalicotheriidae Gill, 1872

Subfamily Chalicotheriinae Gill, 1872

Gen. et sp. indet.

Figs. 4, 5.

*Locality and age*: MFI-105 was discovered in early late Miocene *Khoratpithecus*-bearing outcrops at N20°06'30.56'' E95°07'28.25'', near the village of Ondwe which is situated 20 km southeast of Magway (Fig. 1).

*Material.*—MFI-105, left hemimandible corpus belonging to an adult individual and preserving a long portion of the diastema, the root of the p2, p3–m1 crowns and the partial anterior alveolus of the m2. This fossil is conserved at the Department of Archaeology of the National Museum and Library of Mandalay under the authority of the Ministry of Culture of the Union of Myanmar.

*Description.*—MFI-105 specimen preserves the central portion of the corpus, which is slender and straight. The anterior part of the specimen displays a very slightly outwardly curved partial diastema whose minimum length is 26 mm. The depth of the corpus is extremely shallow at the anteriormost portion of the diastema (18 mm) and increases sharply until the p2 (mean angle of 25° relative to the alveolar plane, Fig. 5). Below the teeth, the depth of the corpus becomes almost uniform. A mental foramen is noticeable slightly posterior to the anterior edge of the symphyseal break. As visible on the lingual side of the specimen, the posterior extremity of the symphysis reaches the level of the p2.

The p2, the crown of which was not preserved, is double-rooted. The posterior root presents a subcircular section of moderate size (5.2 × 4.6 mm). Mesially, small dentine fragments and a damaged alveolus, remnants of the anterior root, are distinguishable.

The p3 is also double-rooted. Its crown is only slightly worn and built of two lobes of equal breadth, which renders it rectangular in occlusal view. The trigonid is dominated by a bulbous and high protoconid. A nearly mesio-distal and spur-like paralophid starts from the mesial border of the
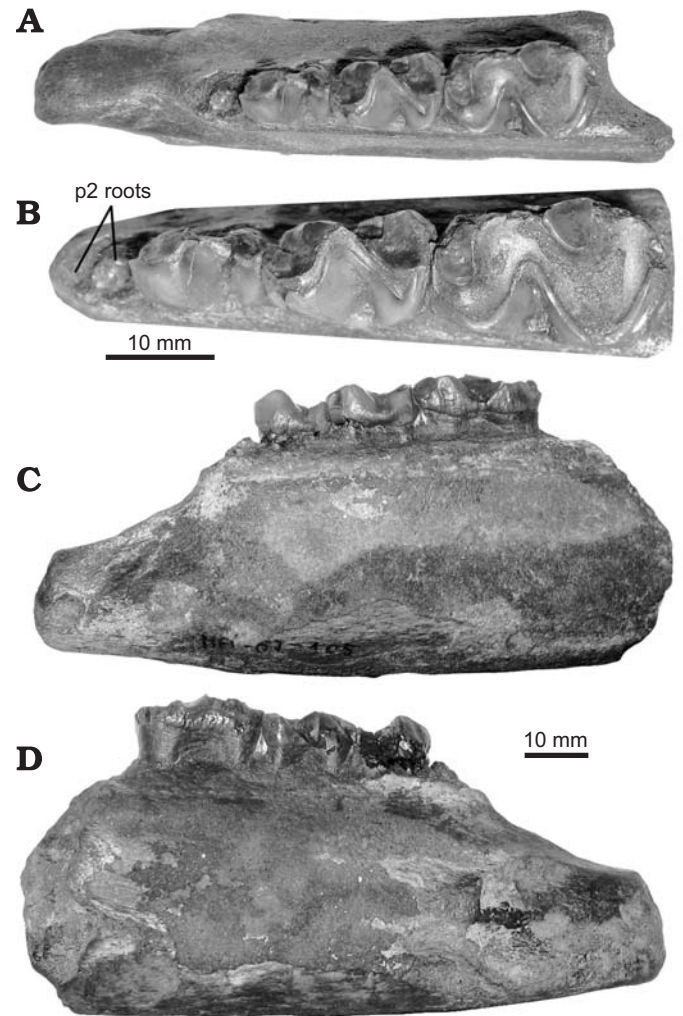


Fig. 4. Chalicotheriine mandible MFI-105 from the early late Miocene of Ondwe (Magway province, Myanmar) in occlusal view (**A**), enlarged occlusal view of the teeth (**B**), buccal view (**C**), and lingual view (**D**).
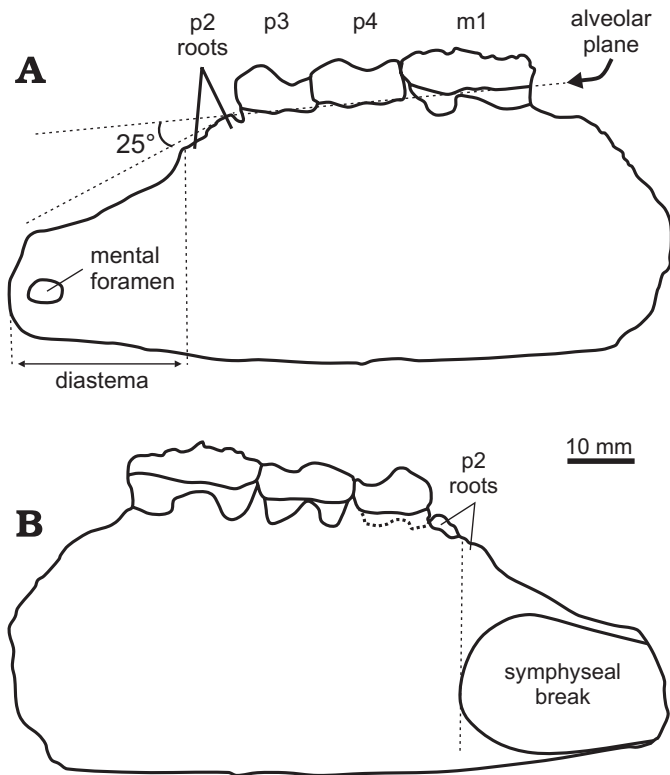
Fig. 5. Interpretive drawings of MFI-105 from the early late Miocene of Ondwe (Magway province, Myanmar) in buccal (**A**) and lingual (**B**) views.

tooth and joins the summit of the protoconid. There is no distinct paraconid at the origin of this paralophid. A short and mostly mesio-distally oriented protolophid starts from the apex of the protoconid and descends linguo-distally, but there is no distinct metaconid. The talonid, whose lingual wall is damaged, is as long as the trigonid. It displays a disto-buccally directed metalophid, which is connected mesially to the protolophid and distally to the hypoconid. The orientation of the metalophid shows only a weak bucco-lingual component. The height of the hypoconid is approximately half that of the protoconid. Buccally, a weakly expressed valley closed by a low cingulum separates the protoconid from the hypoconid. The features of the disto-lingual part of the tooth (e.g., possible presence of an entoconid) are not accessible because of damage.

The p4, displaying a paraconid, a metaconid and an entoconid, is more molarized than the p3. Its outline is subrectangular with a trigonid equal in length to the talonid but distinctly narrower than the latter (Table 1). The stage of wear of this tooth is faintly more advanced than that of the p3. The crest patterns are similar to those of the p3, except that they possess more oblique orientations. The mesio-lingual valley is U-shaped. Its opening is wide because the paralophid does not extend to the lingual half of the crown. Contrary to the condition displayed by the p3, the hypoconid is nearly as high as the protoconid. The buccal valley is deeper and wider than on the p3 but remains closed by a low cingulum. A distinct entoconid is discernible disto-lingually.

This cusp is bucco-lingually elongated, lower and less worn than the other cusps, and connected to the hypoconid by a weak hypolophid.

The m1 is strongly worn and exhibits an outline close to that of the p4, except for a greater length (Table 1). The trigonid is shorter than the talonid. The paralophid is more transverse and more lingually extended than those of the premolars. Combined with the advanced stage of wear, this renders the anterior lingual valley narrow and U-shaped in occlusal view. The region of the metaconid is too worn to determine whether a "metastylid" was present or not. The appearance of the wear outline indicates that this tooth most probably possessed a fully developed entoconid and a hypolophid. As observed on the p3 and the p4, a thin cingulum closes the opening of the buccal valley. A weak and low cingulum is also present at the opening of the posterior lingual valley while a thicker cingulum surrounds the posterior wall.

# Discussion

## Subfamilial attribution of the Burmese mandible

Among chalicotheres, the lower jaws of the Chalicotheriinae are distinguishable from those of the Schizotheriinae by a more robust corpus, and shorter and lower crowned molars (e.g., Coombs 1989; Bonis et al. 1995; Anquetin et al. 2007; Coombs 2009).

The corpus of MFI-105 displays only a slight increase in depth between the p2 and the m1. The Chalicotheriinae, contrary to the Schizotheriinae, show frequently an increase in mandibular depth towards the distal side (Anquetin et al. 2007). Nevertheless, this feature cannot distinguish unambiguously these subfamilies so that the uniform depth of the corpus of MFI-105 does not necessarily imply schizotheriine affinities. For instance, a chalicotheriine discovered at Titov Veles (Macedonia) has a constant mandibular depth (Garevski and Zapfe 1983) while some Schizotheriinae (e.g., *Metaschizotherium bavaricum* von Koenigswald, 1932 from the middle Miocene of Germany) exhibit deeper corpora distally (Coombs 2009). Moreover, the increase in jaw depth is generally mostly concentrated posterior to the first molar in chalicotheriines (see Zapfe 1979; Bonis et al. 1995; Wang and Wang 2001; Anquetin et al. 2007), a region not preserved on MFI-105.

The corpus of MFI-105 possesses a thickness-depth ratio of 0.61 at the level of the m1. In comparison, a mandible of the schizotheriine *Schizotherium* cf. *S. avitum* Matthew and Granger, 1923, AMNH 103336, shows a ratio of 0.44 (estimated from Coombs 1978: fig. 3) while a mandible of the chalicotheriine *Chalicotherium salinum*, GSP 6006, displays a value of 0.51 for a similar ratio. The corpora of *Metaschizotherium bavaricum* (Coombs 2009: figs. 1, 3) appear also notably more slender than that of MFI-05 at only slightly younger ages.

Table 1. Mandibular and dental measurements and indices of MFI-105 and other Eurasian chalicotheriines. Distances are expressed in millimeters. Trigonid breadth index = (trigonid breadth)/(talonid breadth)*100. Breadth index = (maximum breadth)/length*100. Data: *Anisodon grande*, range of Neudorf an der March (Devínska Nová Ves, Slovakia) specimens from Zapfe (1979) and Zapfe (1989); *Anisodon macedonicus*, average values of left and right hemimandibles DKO 234 (Dytiko, Greece) from Bonis et al. (1995); *Chalicotherium goldfussi*, range of specimens of Rheinhessen and Höwenegg (Germany) from Zapfe (1989); *Chalicotherium salinum*, Colbert (1935) and direct measurements at Harvard Peabody Museum. GSP 23046 and 9665 come from the Chinji Formation (14–11.2 Ma according to Barry et al. 2002). *measured from roots.

| | Length | Breadth (trigonid talonid) | Height | Trigonid breadth index | Breadth index |
|---|---|---|---|---|---|
| **MFI-105** | | | | | |
| p2 | >7.9* | 5.2* | – | – | – |
| p3 | 12.07 | 7.79 | 7.44 | – | 64.5 |
| p4 | 15.18 | 9.26 10.61 | – | 87.3 | 61.0 |
| m1 | 21.99 | 11.36 13.22 | – | 85.9 | 60.1 |
| Corpus depth under m1 | – | – | 40 | – | – |
| Corpus thickness at m1 | – | 24.5 | – | – | – |
| Maximum corpus thickness | – | 26 | – | – | – |
| Diastema length | >26 | – | – | – | – |
| Total length | 101 | – | – | – | – |
| *Anisodon grande* | | | | | |
| p4 | 21.0–24.8 | 14.5–16.1 15.4–18.1 | – | 84.0–96.0 | – |
| m1 | 28.1–33.2 | 15.7–20.3 16.8–21.6 | – | 89.7–96.1 | – |
| *Anisodon macedonicus* | | | | | |
| p2 DKO 234 | 10.80 | – 8.35 | – | – | 77.3 |
| p3 DKO 234 | 14.40 | – 11.15 | – | – | 77.4 |
| p4 DKO 234 | 20.00 | – 14.85 | – | – | 74.3 |
| m1 DKO 234 | 26.75 | – 17.15 | – | – | 64.1 |
| *Chalicotherium goldfussi* | | | – | | |
| p4 | 25–31.5 | 16.5–19.5 17.2–19.5 | – | 94.2–103.0 | – |
| m1 | 35.4–39.0 | 20.5–23.0 20.0–23.5 | – | 91.4–105.0 | – |
| *Chalicotheriun salinum* | | | | | |
| p2 (right) GSP 6006 | 12.20 | 10.00 – | 9.40 | – | 82.0 |
| p3 (right) GSP 6006 | 10.76* | 8.09* | – | – | – |
| p4 (right) GSP 6006 | 14.39* | 10.94* | – | – | – |
| m1 GSP 6006 | 24.79 | 12.83 14.19 | – | 90.4 | 57.2 |
| m1 GSP 9665 | 19.05 | 10.65 ~10.31 | – | 103.3 | 54.1 |
| m1 GSP 23046 | 17.42 | 9.56 10.40 | – | 91.9 | 59.7 |
| m1 AMNH 19577 | 27 | 17 | 14 | – | 63.0 |

Table 2. Morphological comparison of MFI-105 with other Eurasian Miocene chalicotheriines. Data from Anquetin et al. (2007) (*Chalicotherium goldfussi* and *Anisodon grande*), Zapfe (1979) and Zapfe (1989) (*Chalicotherium goldfussi* and *Anisodon grande*), Bonis et al. (1995) (*A. macedonicus*), Wang and Wang (2001) ("*Chalicotherium*" cf. *C. brevirostris*), Colbert (1935) and personal observations in the collections of the Harvard-Geological Survey of Pakistan project (*C. salinum*). The choice of the characters mostly relies on the work of Bonis et al. (1995) and Anquetin et al. (2007). * the diastema is short in the juvenile individual AMNH 19577 (Colbert 1935: figs. 73, 74).

| Feature\Taxon | MFI-105 | *Chalicotherium goldfussi* | *Chalicotherium salinum* | *Anisodon grande* | "*Chalicotherium*" cf. *brevirostris* | *Anisodon macedonicus* |
|---|---|---|---|---|---|---|
| Posterior extent of the symphysis | p2 | ? | p2 | p2 | p4 | p3–p4 |
| Mandibular depth decrease anteriorly to p2 | marked | marked? | ? | unmarked | unmarked | unmarked |
| Diastema length | long | long | short?* | long | short | long |
| Number of roots of p2 | 2 | ? | 1 | 1/2 | 1? | 2 |
| p4 entoconid | distinct | distinct | ? | weak | distinct | distinct |
| p3 outline | rectangular | ? | rectangular | ? | rounded | rectangular |
| "Metastlylid" on molars | ? | strong | weak/strong | weak | weak | strong |
| m1 trigonid | markedly narrower than talonid | slightly narrower than talonid | slightly narrower than talonid | markedly narrower than talonid | slightly narrower than talonid | slightly narrower than talonid |

With a width-length index of 60 (Table 1), the m1 of MFI-105 is proportionally less elongated than those of *Metaschizotherium bavaricum*, *M. fraasi* von Koenigswald, 1932 and the schizotheriine material from the French locality of La Grive [respectively 50–56 (N = 8), 56 (N = 1) and 52–53 (N = 3). Data from Coombs 2009: table 2] but falls within the range showed by the species of *Schizotherium* (55–65; calculated from Coombs 1978: table 1) and is close to m1s of *Phyllotillon naricus* Pilgrim, 1910 and *Ancylotherium pentelicum* Gaudry and Lartet, 1856 (56 and 64 for the first, and 60 for the second; data from Coombs 2009: table 2). On the other hand, the width-length ratio of the m1 of MFI-105 falls as well within the bracket of various chalicotheriines (Table 1). Thus, the measurements of the first molar of MFI-105 cannot be used to allocate the Burmese specimen either to the Schizotheriinae or to the Chalicotheriinae, the characteristic molar elongation of the Schizotheriinae seeming more accentuated on m2 and m3 than on m1.

Finally, the combination of low crowns, m1 not elongated mesio-distally relative to its breadth and robust corpus displayed by MFI-105 exclude it from the Schizotheriinae and justify its allocation to the subfamily Chalicotheriinae.

## Comparisons with other known chalicotheriines

Anquetin et al. (2007) recently published a discussion on chalicotheriine systematics and phylogeny. This work, which combines a new study of the material of the classical European species and a cladistic analysis based on a large set of cranial and dental features, will serve here as a reference for the systematics of the subfamily. The most important results of these authors from the perspective of our study can be summarized as follows:

*Anisodon* Lartet, 1851 is a valid genus name and applies to several taxa of the Old World formerly attributed to *Chalicotherium*, *Macrotherium*, and *Nestoritherium*.

*Macrotherium* is not a valid name. These two points had already been proposed by Geraads et al. (2001).

The chalicotheriines are divided into two principal clades, the *Anisodon* clade and the *Chalicotherium* clade. The *Anisodon* clade is formed of *Anisodon grande* Blainville, 1849, type-species of *Anisodon*, *A. macedonicus* Bonis, Bouvrain, Koufos, and Tassy, 1995, *A sivalense* Falconer and Cautley, 1843, *A. wuduensis* Xue and Coombs, 1985, and the material from Titov Veles (Macedonia) and Vathylakkos (Greece). The *Chalicotherium* clade comprises *Chalicotherium goldfussi* Kaup, 1833, the type-species of *Chalicotherium*, and *C. brevirostris* Colbert, 1934.

The next sections propose comparisons between MFI-105 and the main Eurasian chalicotheriines, beginning with the taxa analyzed by Anquetin et al. (2007) and subsequently extending to Asian chalicotheriine material unconsidered by these authors. Table 2 displays a summary of the main features of MFI-105 as compared with other Eurasian chalicotheriines.

**Comparison with *Butleria*.**—This genus is known by a single species, *Butleria rusingensis* Butler, 1965, from the early Miocene of Kenya (Butler 1965). *B. rusingensis* is considered as a basal chalicotheriine and the sister-group of all known post-early Miocene representatives of this subfamily (Bonis et al. 1995; Anquetin et al. 2007). This African species differs from MFI-105 by an increase in corpus depth distally. The strong "metastylid" on the molars of *B. rusingensis* cannot be compared with MFI-105 on which this trait is not accessible. *B. rusingensis* and MFI-105 share the retention of a p2, the posterior extent of the symphysis at the level of the p2, a distinct entoconid on the p4 and V-shaped trigonids on molars. However, these features are all primitive in the present taxonomical context. Hence, there are no exclusively shared synapomorphies between the Burmese mandible and *B. rusingensis*, which are presumably not closely related.

**Comparison with the *Anisodon* clade.**—According to Anquetin et al. (2007), the *Anisodon* clade members are charac-

terized on the mandible by a strong ventral expansion of the angular area and a reduction of the "metastylid" on lower molars. Both features are unfortunately inaccessible on the Burmese mandible. Nevertheless, MFI-105 can easily be distinguished from all the taxa of the *Anisodon* clade with the exception of *Anisodon grande* by retention of the primitive state regarding the distal extension of the symphysis (ending at the level of the p2). In addition, MFI-105 clearly differs from these species by its smaller size, a clearly greater decrease in depth of the mandibular corpus in front of the p2, and a greater development of the entoconid on the p4. Hence, MFI-105 does not match with any of the *Anisodon* clade taxa.

As the Burmese mandible shares with *A. grande* a primitive symphyseal character, it also displays two other common features with this species. First, MFI-105 possesses a double rooted p2 like the *A. grande* specimen of Sansan MNHN Sa 15671 (Anquetin et al. 2007). However, intraspecific variation in the number of roots is common among mammals (Kovacs 1971). Indeed, Zapfe (1979: fig. 14) figured a single-rooted p2 from Devínska Nová Ves, implying a possible intraspecific variation of this feature in *A. grande*. Moreover, the double-rooted p2 is most probably another primitive trait, since that a similar character state is observable in the primitive chalicotheroid *Eomoropus* (Obsorn 1913) and in the schizotheriines *Schizotherium* and *Moropus* (Coombs 1978; Coombs et al. 2001). Second, MFI-105 exhibits narrow trigonids on its p4 and m1 and resembles in this respect the *A. grande* sample from Devínska Nová Ves (Table 1; Zapfe 1979, 1989) and the *Anisodon* from Titov Veles (Garevski and Zapfe 1983). While the tendency of front to rear breadth enlargement is common on lower cheek teeth of chalicotheriines, the p4 and m1 trigonids of MFI-105, *A. grande* and the *Anisodon* from Titov Veles are the narrowest (relative to the talonid) among the chalicotheriines (Table 2; Garevski and Zapfe 1983). Note that the narrowness of the first lobe is greater on the m1 of MFI-105 than on the corresponding tooth of *A. grande* at Devínska Nová Ves, the trigonid breadth index of the Burmese mandible being lower than the minimum value of the European sample. This character state is difficult to interpret from an evolutionary perspective. If derived, it might only illustrate a lineage-restricted allometry rather than a synapomorphy. Hence, no derived feature on MFI-105 clearly testifies for affinities with *A. grande* and the *Anisodon* from Titov Veles and more generally with the *Anisodon* clade.

**Comparison with the *Chalicotherium* clade**.—None of the two unambiguous synapomorphies of the *Chalicotherium* clade of Anquetin et al. (2007) can be checked on MFI-105 since these features concern the upper dentition and skull morphology.

*Chalicotherium brevirostris*.—This species is known from the middle Miocene Tunggur Formation in northern China (Colbert 1934). Unfortunately, it is now impossible to perform a direct comparison between MFI-105 and this species

because no mandibular specimens are undoubtedly referable to it (but see further comments below).

*Chalicotherium goldfussi*.—This European species is much larger than MFI-105 (Zapfe 1989). Its molars have U-shaped trigonids (Anquetin et al. 2007) that are generally as broad as the talonid (Zapfe 1989; Table 2), as opposed to the narrow and V-shaped trigonid of the m1 for the Burmese mandible. Moreover, the p4 of *C. goldfussi*, unlike that of MFI-105, is quadrate in shape with a trigonid as broad as the talonid (Zapfe 1989; Table 2). This tooth also possesses a less oblique metalophid and a thicker and more complete buccal cingulum in *C. goldfussi* (Zapfe 1989). Thus, MFI-105 is distinct from the type-species of *Chalicotherium*. *Chalicotherium goldfussi* and MFI-105 share a long diastema mesial to the premolars but this feature is presumably primitive for chalicotheriines since it is displayed by the primitive Eocene chalicotheroid *Eomoropus* (Osborn 1913), in the schizotheriine *Moropus* (Coombs et al. 2001) and by at least four chalicotheriine lineages (Table 2).

**Other Asian chalicotheriines**.—Although the analysis of Anquetin et al. (2007) is comprehensive regarding the European chalicotheriine fossil record, its sampling is not exhaustive for the Miocene Asian chalicotheriines. The geographical provenience of MFI-105 invites comparisons with these taxa.

*Chalicotherium* cf. *C. brevirostris*.—In northern China, two mandibular specimens have been considered as putatively corresponding to *C. brevirostris*. The first is a virtually complete mandible from Hebei province reported by Hu (1959) and assigned to *Chalicotherium* cf. *C. brevirostris* on the basis of the short anterior region of the symphysis displayed by the fossil. Interesting features of this specimen, accessible through the illustrations of Wang and Wang (2001), are: posterior extent of the symphysis at the level of the p4, ventrally expanded angular region, V-shaped trigonid, sub-rectangular outline, lack of distinct "metastylid" and low paralophid on lower molars, probably single rooted p2, p3–p4 with short lengths, great posterior breadth, very reduced talonid on the p3, distinct entoconid on the p4, retromolar gap, extremely shortened anterior region of the mandible.

The second is a jaw fragment with m2–m3 discovered in the late middle Miocene deposits of the Lower Youshashan Fm. in Qinghai province and assigned to the same taxon as the Hebei province mandible because of their similar size and molar morphology (Wang and Wang 2001).

MFI-105, with its narrow trigonid on the m1, its symphysis reaching the level of the p2, its double-rooted p2, its elongated p3 talonid and its much smaller size is obviously different from these Chinese fossils. Note that the latter fossils display a combination of features that match the diagnosis of *Anisodon* sensu Anquetin et al. (2007): all known species of *Anisodon* have reduced "metastylids" on lower molars and a ventrally expanded angular area; all species of *Anisodon* except *A. grande* have the posterior extent of the symphysis at the level of p3–p4. Consequently, unless a par-

allelism, the lower jaws described by Hu (1959) and Wang and Wang (2001) are unlikely to represent *Chalicotherium* following the criteria of Anquetin et al. (2007).

*Chalicotherium salinum*.—In the Siwaliks of Pakistan, chalicotheriine specimens discovered in the middle Miocene Chinji Formation and early late Miocene Nagri Formation were allocated to the species *Chalicotherium salinum* Forster-Cooper, 1922 (Forster-Cooper 1922; Colbert 1935; Pickford 1982). The Siwalik material consists mostly of isolated dental and postcranial elements. The holotype of the species is a left M3 collected in the Chinji Formation (Forster-Cooper 1922). The most complete specimen attributed to *C. salinum*, and consequently the key fossil for comparisons, is GSP 6006. This fossil was collected in the Nagri Formation and has an age of 9.6 Ma (John Barry, personal communication 2008). It consists of a left hemi-mandible with m2–m3, the angular region and a part of the ascending ramus and a right hemi-mandible with p2, m1, m3 erupting and the coronoid process. The dental material of *C. salinum*, while scarce, presents an important range of size between the smaller middle Miocene specimens and the larger late Miocene ones (Table 1). Morphological variation on the "metastylid" is also noticeable. This cusp is distinct in some of the specimens from the Chinji Formation and absent from the younger GSP 6006. These observations bring into question the monospecific status of the chalicotheriine material from the Chinji and Nagri formations proposed by Pickford (1982), but the lack of material impedes further analysis (Coombs 1989).

The teeth of MFI-105 teeth are intermediate in size between the middle Miocene specimens and GSP 6006 (Table 1). The Burmese specimen shares with GSP 6006 a posterior extent of the symphysis at the level of the p2 and a very modest increase in depth of the mandible between the p2 and the m1. Nevertheless, several morphological discrepancies indicate that MFI-105 most probably does not belong to the same species as GSP 6006. The p2 of GSP 6006 is large and built of a single large root of circular section whereas the p2 has two roots on MFI-105. The molars of GSP 6006 display wider trigonids (Table 1), a greater lingual extension of the paralophid, and more complete and thicker buccal and distal cingula than the m1 of MFI-105. The m1 of the juvenile mandible AMNH 19577 (Colbert 1935: figs. 73, 74) seems close to that of GSP 6006 in terms of extension of the paralophid, cingula development and breadth of the trigonid while the m2 AMNH 19437 (Colbert 1935: fig. 75) also displays a lingually extended paralophid and a trigonid close in breadth to the talonid. Finally, the specimens from the Chinji Fm., which possess weaker cingula, have also broader trigonids (Table 1) and a more lingually extended paralophid than the m1 of MFI-105. Hence, conspecific or not, the fossils regrouped under the binomen *C. salinum* do not match satisfyingly MFI-105.

*Chalicotherium* from Thailand.—In South Asia, *Chalicotherium* was reported from the Thai middle Miocene locality of Huai Siew (Thomas et al. 1990) and identified as *Chalico-*

*therium* cf. *brevirostris* (Ducrocq et al. 1994). Unfortunately, this material has never been described or figured and cannot be compared with the Burmese mandible.

Chalicotheriines from southern China.—Some of the *Lufengpithecus*-bearing localities of Yunnan province have yielded putative chalicotheriine remains. In the Yuanmou basin, a chalicothere baptized "*Macrotherium*" *yuanmouensis* is listed in the associated fauna of *Lufengpithecus hudienensis* (e.g., Qi et al. 2006). Another chalicothere has been identified in the hominoid locality of Lufeng as the chalicotheriine from the Miocene of the Siwaliks of Pakistan ("*Macrotherium*" *salinum*; e.g., Li et al. 1984). Unfortunately, no formal descriptions of these chalicotheres have been published to our knowledge.

# Conclusions

**Taxonomic status of the Burmese mandible**.—The above comparisons reveal that the Burmese specimen cannot be satisfyingly assigned to any of the formerly described chalicotheriine taxa. The retention in MFI-105 of primitive traits such as posterior extent of the symphysis at the level of the p2 and a slender mandible (for a chalicotheriine), renders more probable its belonging to the *Chalicotherium* clade since *Anisodon* species are commonly derived in these respects (Coombs 1989; Anquetin et al. 2007). Nevertheless, no unambiguous derived feature can link the mandible to either the *Anisodon* or *Chalicotherium* clades. Some features displayed by the Burmese mandible might even be autapomorphic. This is the case for the very narrow trigonid on its p4 and m1 and for the sharp decrease of the mandibular depth at the level of the diastema which differs from all other Eurasian chalicotheriines. It should be noted that *Chalicotherium goldfussi* possesses a dorso-ventrally thinned symphysis (Anquetin et al. 2007) and may therefore be suspected of having an abrupt mandibular corpus decrease at the beginning of the diastema. The ratio between the symphyseal thickness taken at the level of the mental foramen and the corpus depth under the m1 is approximately 0.65 according to the illustrations of Anquetin et al. (2007; though newly described, no measurements of this material are included in this work). The same ratio is 0.45 for MFI-105, suggesting a rostrally more sharply tapering corpus than in *C. goldfussi*. Although the two potential autapomorphies of MFI-105 might indicate its belonging to a new taxon, these features are too poorly known to justify the erection of a new name. Thus MFI-105 is treated as an indeterminate genus and species of Chalicotheriinae until further material is discovered.

**Paleoenvironmental implications**.—Chalicotheriines are considered as forest-dwelling browsers (e.g., Coombs 1989; Bonis et al. 1999) even though some isotopic data suggest that they might have moved to slightly more open habitats to take water (Nelson 2007). The presence of a chalicotheriine

in the *Khoratpithecus* fauna of Magway points reasonably to a significant wooded component in this ape's environment. Such an assertion is reinforced by the presence in the fauna of a giraffe and three suids including a species of *Tetraconodon* (JJJ, unpublished data), a genus whose representative in the Siwaliks of Pakistan seems distinctly associated with wooded habitats (Nelson 2003). The evidence for closed habitats in Central Myanmar by the early late Miocene is further fortified by preliminary stable isotope analyses performed on "*Hipparion*" teeth of the *Khoratpithecus* fauna. These specimens yielded highly depleted $\delta^{18}$O and $\delta^{13}$C values suggesting closed and humid habitat for these equids (JJJ, unpublished data). Present environmental conditions in Central Myanmar are characterized in a large portion of Magway and Mandalay provinces by a subtropical semi-arid climate (e.g., Terra 1943; Gulliver and Latham 2005). The vegetation of this region is dominated by open shrublands and grasslands. Thus, the chalicothere contributes to the recognition that the early late Miocene paleoenvironment of the Magway area was drastically different from the present day conditions in Central Myanmar.

**Future research**.—Recently, a tooth was reported of the chalicotheriine genus *Nestoritherium* (referred by Anquetin et al. 2007 to *Anisodon*) in the Pleistocene beds of the Irrawaddy Formation of Myanmar (Takai et al. 2006). Hence, the fossil record of Southeast Asian chalicotheres spans through the Neogene and into the Pleistocene. The Irrawaddy Formation, whose continental series encompass middle Miocene to Pleistocene ages (e.g, Bender 1983; Chavasseau et al. 2006; Takai et al. 2006), has thus an interesting potential to further document the still poorly understood regional evolution of these perissodactyls.

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