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New fossil remains of Rhinocerotidae (Perissodactyla) from the early Late Miocene Tebingan area, central Myanmar

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ABSTRACT

New fossil remains of Rhinocerotidae, dated from the early Late Miocene, were discovered from the lowermost part of the Irrawaddy Formation in the Tebingan area, Magway Region, central Myanmar. The Tebingan rhinoceros fossils, consisting of isolated teeth, maxillae, and mandibles, are assigned to three taxa: *Brachypotherium perimense* defined by a constricted protocone, a well-developed parastyle and broad upper teeth, to '*Brachypotherium*' *fatehjangense* with a flat ectoloph, crochet, and the absence of tubercle at the entrance of the median valley. Other specimens were assigned to *Rhinoceros* sp. due to having a developed parastyle, crochet and a strong anterior cingulum and the absence of a constricted protocone and ante-crochet. The evolutionary history of Rhinocerotidae is poorly known in Southeast Asia, and few rhinoceros' species have been identified from the Irrawaddy Formation. The newly identified *Rhinoceros* specimens from the early Late Miocene Tebingan area are the oldest fossil records for *Rhinoceros* in Southeast Asia. The Tebingan mammal fauna is similar to the Nagri and Dhok Pathan faunas of the lower/middle Siwaliks of the Indian subcontinent, indicating the faunal exchange between these two regions in the late Neogene.

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Introduction

The rhinoceros family, Rhinocerotidae, is represented by four genera and five species known in Africa, South and Southeast Asia (Nowak 1991). In the fossil record, the family is widely distributed in Eurasia, Africa and North America. They are well diversified from the late Eocene to the Miocene in North America and from the early Oligocene in Europe and Africa (Prothero and Schoch 1989; Prothero 1998; Antoine et al. 2003). At the beginning of the Neogene, they became common land mammals in Europe, North America, Asia and Africa with a great diversity of taxa belonging to different genera and tribes (Prothero et al. 1989; Prothero 1993; Heissig 1999; Antoine 2002; Prothero and Schoch 2002; Pandolfi et al. 2021; Sanisidro and Cantalapeira 2022; Lu et al. 2023). They became extinct in North America after the Pliocene, while other rhinoceroses remained during the Quaternary in Eurasia and Africa and up to the present day (Prothero 2005).

Rhinocerotid fossil remains are common in the Neogene of Southeast Asia, and several species belong to two tribes: the Rhinocerotini including *Rhinoceros, Dicerorhinus, Nesorhinus* and *Gaindatherium* and Teleoceratini including the genus, *Brachypotherium* (Chavasseau et al. 2006; Zin-Maung-Maung-Thein et al. 2006, 2008; Khan et al. 2014; Pandolfi and Maiorino 2016; Pandolfi 2018; Geraads et al. 2021; Antoine et al. 2022). But the evolutionary history of Rhinocerotidae, as *Rhinoceros*, in Southeast Asia is still poorly known.

Brachypotherium was distributed from the late Early to the early Late Miocene in Europe (Antoine et al. 2000), while it survived until the latest Miocene at Lothagam in Africa (Guérin 2008; Geraads 2010) and in the latest Miocene of Sahabi (Libya) with by *B. lewisi* (Pandolfi and Rook 2019). In Asia, *Brachypotherium* occurred in the late Middle Miocene in the Chinji Formation of Siwaliks (Pakistan), in the lowermost part of the Irrawaddy sediments (Myanmar), and in Nakhon Ratchasima (Thailand) (Chavasseau et al. 2006; Takai et al. 2006; Khan et al. 2012; Antoine et al. 2013; Thein and Maung 2017; Handa et al. 2020) including two species, *B. perimense* reported in Southeast Asia during the Miocene (Takai et al. 2006; Handa et al. 2020) and '*B*'. *fatehjangense* in Myanmar and Pakistan (Chinji and Nagri Formation) (Chavasseau et al. 2006; Khan et al. 2010; Zin-Maung-Maung-Thein et al. 2010).

Rhinoceros is known from the Late Miocene to the Pleistocene of Pakistan, Myanmar, Thailand, Indonesia and China (McNeely and Cronin 1972; Van den Bergh et al. 2001; Khan 2009; Zin-Maung-Maung-Thein et al. 2010 ; Antoine 2012). Two is known to survive, *R. unicornis* and *R. sondaicus* in the Himalayan foothills excluding the Indochina region and at the western end of Java, respectively (Laurie et al. 1983; Murphy 2004; Groves and Leslie 2011; Antoine 2012).

In the present work, we describe several new rhinocerotid fossils discovered from the lowermost part of the Irrawaddy Formation of the Tebingan area in Magway Region, central Myanmar. These fossils consist of mandibles, maxillary fragments and mostly isolated teeth. This is the first extensive systematic description of the early Late Miocene rhinocerotids from Myanmar and will shed light on the evolutionary history and palaeobiogeography of Rhinocerotidae in the Neogene of Southeast Asia.

Geological settings

The Irrawaddy Formation, dated from the Late Miocene to the Early Pleistocene, consists of non-marine sediments widely exposed along the Ayeyarwaddy (=Irrawaddy) and Chindwin rivers (Figure 1). It has been subdivided into lower and upper parts based on palaeontological and lithological criteria (Stamp 1922). The mammalian fauna from the lower part of Irrawaddy Formation

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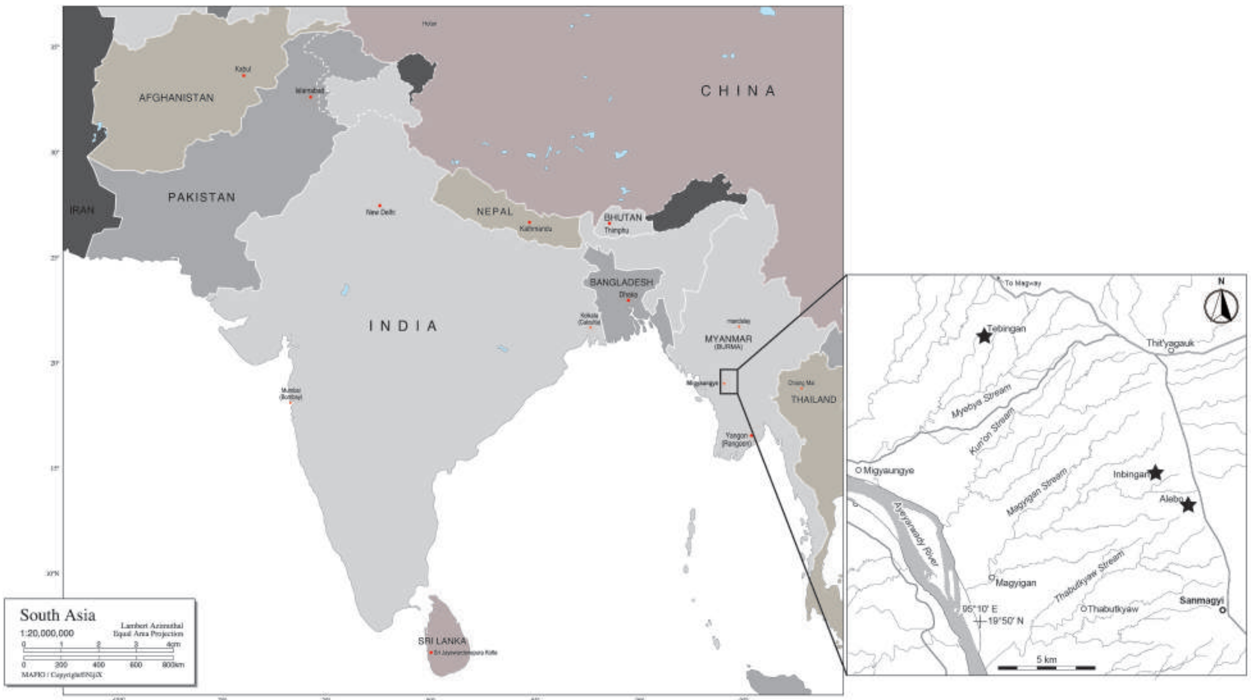

Figure 1. Index map of the study area indicating the villages of Tebingan, Alebo, Inbingan and Sanmagyi.

is comparable to the Nagri (11.5 Ma to 9 Ma) and Dhok Pathan (9.8 to ca. 3.5 Ma) Formations in the middle Siwalik, corresponding with the latest middle Miocene to the early Pliocene (Zin-Maung-Maung-Thein et al. 2011; Takai et al. 2015), while the upper Irrawaddy fauna is comparable to the upper Siwalik, dated from the late Pliocene to the early Pleistocene (Colbert 1943; Bender 1983).

In the Tebingan area, the fluvial Irrawaddy Formation conformably overlies the shallow marine Obogon Formation (middle Miocene) of the Pegu Group (Takai et al. 2021). Most Tebingan vertebrate fossils are collected from the lowermost part of the Irrawaddy Formation or the upper parts of the Obogon-Irrawaddy transition zone (Figure 2). The geological age of the Irrawaddy Formation in Tebingan is estimated from the combination of several mammals' genera with a well-established chronological distribution in the Siwalik deposits (Northern Pakistan) suggesting an early Late Miocene age (9–8Ma) (Barry et al. 2002; Takai et al. 2021). Although the Tebingan mammalian fauna is represented by Primate, Carnivora, Proboscidea, Artiodactyla and Perissodactyla (Sein and Thein 2013; Egi et al. 2018; Chit Sein 2020; Takai et al. 2021), and Perissodactyla are still very poorly documented, represented by *Anisodon* (Chalicotheridae), *Hipparion* (Equidae), and *Brachypotherium* and *Rhinoceros* (Rhinocerotidae) (Takai et al. 2021).

Materials and methods

Fossil specimens described in the present paper were collected by villagers during farm work between 2017 and 2022 in the Tebingan area (19°58′N:95°10′E), about 50 km south-east of Magway city, including several villages, such as Tebingan, Inbingan, Alebo and Sanmagyi (Figure 1). In Myanmar, it is forbidden to lend fossils outside the country, so epoxy casts of the important fossils were made through silicon moulds taken in Myanmar. The fossils specimens, consisting of upper cheek teeth, mandibles and maxillae, were measured at a 0.1 mm scale using digital calipers.

Institutional abbreviations. MZKB-K, Zaykabar Museum, Yangon, Myanmar. NMMP-KU-IR, National Museum of Myanmar Palaeontology, Kyoto-University, Irrawaddy.

Anatomical abbreviations. L, mesiodistal length; P2, second upper premolar; P3, third upper premolar; p4, fourth lower premolar; P4, fourth upper premolar; m1, first lower molar; M1, first upper molar; m2, second lower molar; M2, second upper molar; m3, third lower molar; M3, third upper molar; Wa, anterior width; Wp, posterior width.

Systematic palaeontology

Order Perissodactyla Owen, 1848
Family Rhinocerotidae Gray, 1821
Subfamily Rhinocerotinae Gray, 1821
Tribe Rhinocerotini Gray, 1821
Subtribe Teleoceratina Hay, 1902
Genus *Brachypotherium* Roger, 1904

Diagnosis

Largest taxon of Teleoceratina. Massive skull and short nasals. Brachyodont and large molars with strong cingula. Moderately developed crochet, a reduced antecrochet, a possible rudimentary crista and a constricted protocone (Heissig 1972).

Geographic and stratigraphic ranges

Lower Miocene to the Pliocene deposits in Eurasia and Africa.

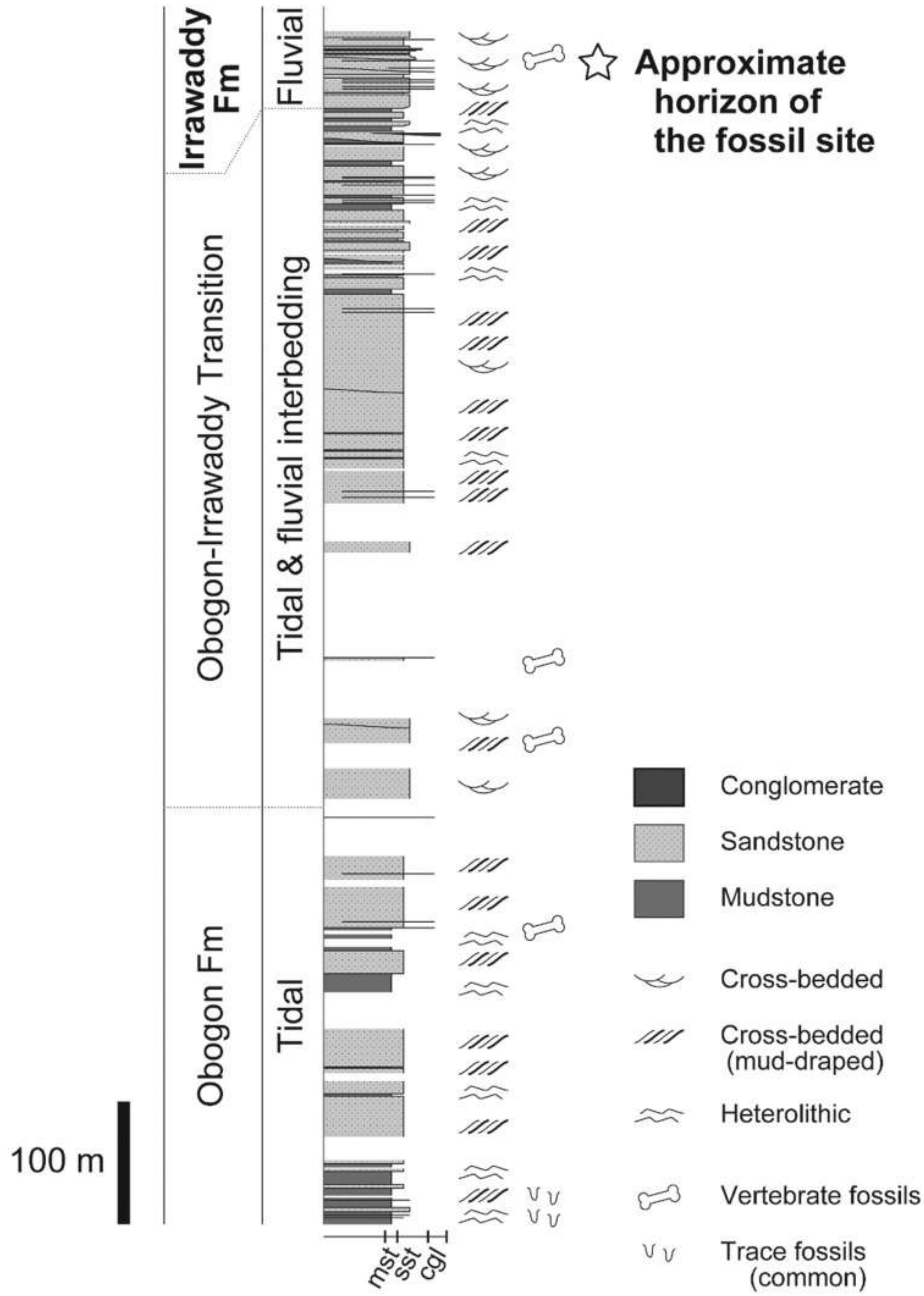

Figure 2. Stratigraphy of Neogene sediments in central Myanmar and correlations with stratigraphy of Indian subcontinent, East Asia and Europe.

Brachypotherium perimense Falconer and Cautley, 1847

Diagnosis

Largest species of *Brachypotherium*. Molariform upper premolars with a convex outer wall. Upper molars usually with reduced cingula, developed crochet, weaker ante-crochet and a rudimentary crista. Protocone slightly constricted. Narrow lower molars without ectolophid groove (Heissig 1972).

Geographic and stratigraphic ranges

Southeast Asia during the Miocene.

Materials

NMMP-KU-IR-5218 and 5632, right M2; NMMP-KU-IR-5024, 5630, 5642 and MZKB-K-667, left M2; NMMP-KU-IR-5626 and MZKB-K-668, left M3; NMMP-KU-IR-6478, right M3.

Locality and age

The Tebingan area, Magway Region, Myanmar, the early late Miocene.

Description

Upper molars: M2: NMMP-KU-IR-5218 and 5632 are large, right M2 (Figure 3A and B). Both teeth are large (Table 1) and have

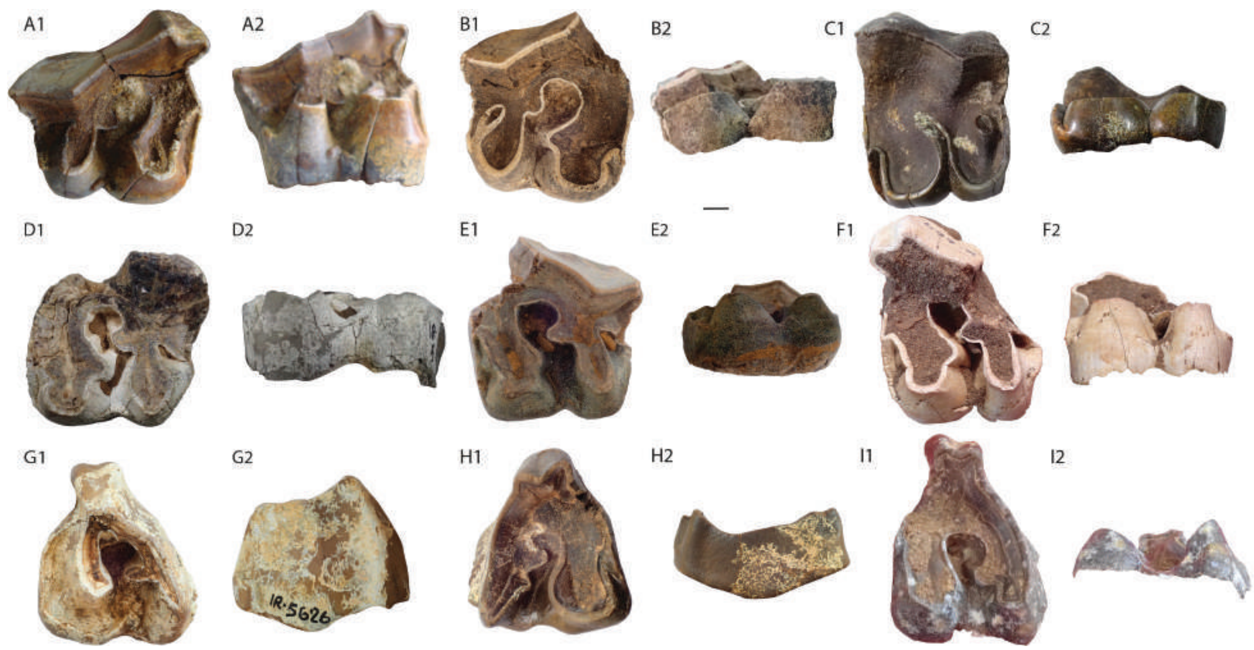

Figure 3. Upper molars of *Brachypotherium perimense* of the Tebingan Area in occlusal (A1-J1), lingual (A2-F2, J2), and labial (G2, H2) views. A, right M2 (NMMP-KU-IR -5218); B, right M2 (NMMP-KU-IR-5632); C, left M2 (NMMP-KU-IR-5024); D, left M2 (NMMP-KU-IR-5630); E, left M2 (NMMP-KU-IR-5642); F, left M2 (MZKB-K-667); G, left M3 (NMMP-KU-IR-5626); H, right M3 (NMMP-KU-IR-6478); I, left M3 (MZKB-K-668). Scale bar=10mm.

a lingually directed ectoloph, the crochet and ante-crochet are present and the median valley is narrow. The protocone is constricted in NMMP-KU-IR-5632 but less marked in IR-5218 (Figure 3A). Tubercles are present at the entrance to the median valley, the anterior cingulum is small and the posterior cingulum is present in NMMP-KU-IR-5218 (Figure 3A) but absent in IR-5632 (Figure 3B). The parastyle and paracone folds are strongly developed in NMMP-KU-IR-5218 (Figure 3A).

NMMP-KU-IR-5024, 5630, 5642 and MZKB-K-667 (Figure 3C, D, E, F) are moderately worn left M2. NMMP-KU-IR-5630, 5642 and MZKB-K-667 have a constricted protocone, an ante-crochet and a crochet moderately developed (Figure 3D, E, F). The median valley is narrow in each tooth, and there is a small tubercle at the entrance of the median valley. NMMP-KU-IR-5024 (Figure 3C) is different from the other teeth, the crochet and ante-crochet are absent and the median valley is narrow. Those differences can be explained by the extreme wear of the tooth, in lingual view, the tooth is very thin (Fig. 3C2). The postfossette is close by a hypoconal flange fused with the metacone, whereas the postfossette is enclosed by a posterior cingulum in NMMP-KU-IR-5630 and 5642. Furthermore, the anterior cingulum is present.

M3: NMMP-KU-IR-5626 and MZKB-K-668 are left M3 (Figure 3G and I). MZKB-K-668 is more worn than NMMP-KU-IR-5626. The parastyle and the paracone fold are very developed, the crochet is present, the protoloph and the ectometaloph are convex. In addition, the anterior cingulum is weakly marked and the posterior cingulum is absent. The lingual cingulum is present at the level of the protocone in NMMP-KU-IR-5626. The median valley is narrow.

Additionally, NMMP-KU-IR-6478 is a right M3 (Figure 3H). This tooth has the same features as the teeth described above, except that the constriction of the protocone is moderately marked on this tooth, and it has a double crochet.

Table 1. Measurements (in mm) of the upper cheek teeth of fossils specimens in comparison with the dental size of the two Asian species of *Brachypotherium*.

	M1			M2			M3		
	L	Wa	Wp	L	Wa	Wp	L	Wa	Wp
« B. » fatehjangense	52	64	-	50.3	67.4	-	53	57.5	-
B. perimense	50.3	68.5	56	64.4	78	-	59.8	68.2	-
NMMP-KU-IR-5024	55.6	72.5	62.3	-	-	-	-	-	-
NMMP-KU-IR-5218	-	-	-	71.6	73.3	60.4	-	-	-
NMMP-KU-IR-5642	-	-	-	49.2	69.8*	58.7	-	-	-
NMMP-KU-IR-5632	-	-	-	60.1	73*	61.6	-	-	-
NMMP-KU-IR-5630	-	-	-	64.6	-	-	-	-	-
MZKB-K-667	-	-	-	-	85.3	-	-	-	-
NMMP-KU-IR-5626	-	-	-	-	-	-	48	54.9	68.1
NMMP-KU-IR-6478	-	-	-	-	-	-	50.6	60.5	58.5
MZKB-K-668	-	-	-	-	-	-	59.2	74.8	74.2
NMMP-KU-IR-5025	-	-	-	-	-	-	45.5	59	56.7
NMMP-KU-IR-5221	-	-	-	-	-	-	40.4	48.9	47.1
NMMP-KU-IR-5223	-	-	-	-	-	-	-	52.8	53.3

Remarks: Range and sample size for '*B*'. *fatehjangense* and *B. perimense* (Colbert 1935; Hooijer and Patterson 1972; Rafeh et al. 2020). *Abbreviations*: *: Estimated size; L: ectoloph length; Wa: protoloph length; Wp: metaloph length and for the M^3; Wp: ectometaloph length.

Comparisons and discussion

In Southeast Asia, several genera of Rhinocerotidae have been identified: *Alicornops* and *Gaindatherium* in Pakistan, *Chilotherium* in China and Pakistan, *Aceratherium* in Thailand, *Iranotherium* from South China, and *Brachypotherium, Dicerorhinus* and *Rhinoceros* found in several Southeast Asian countries. (Deng 2005; Khan 2009; Tong and Guérin 2009; Deng et al. 2013). The Tebingan specimens cannot be assigned to one of these genera: *Alicornops* has a strong anterior cingulum, a median valley widely open lingually, absence of ante-crochet and a small crochet (Khan et al. 2012), *Gaindatherium* has very simple teeth, absence of ante-crochet or crista, the crochet is poorly developed (Khan 2009), *Chilotherium* from the south of China has a parastyle fold indistinct or absent and teeth are smaller than the Tebingan specimens (Khan 2009). Furthermore, *Aceratherium* does not have constriction of the protocone, and the paracone is moderately developed on M2 and M3 and Tebingan specimens do not belong to *Iranotherium*, the entrance to the median valley is closed on every molar in *Iranotherium*. Furthermore, the crochet is absent on the M1 and M2, a strong anterior cingulum on M3 and the labial wall is flat (Deng 2005; Deng et al. 2013). The Tebingan species are too large to belong to *Dicerorhinus* or *Rhinoceros*. Furthermore, these genera do not have constricted protocone (Khan 2009; Tong and Guérin 2009) (Figure 4).

The Tebingan specimens can be related to *Brachypotherium*, a hornless rhinoceros, considered to have lived in forest or wooded habitats and possibly in semi-aquatic habitats (Handa et al. 2018; Rafeh et al. 2020). It includes three Asian species, including *B. gajense*, which is not yet described in the literature (Antoine et al. 2013), '*B*'. *fatehjangense*, and *B. perimense*; two European species including *B. goldfussi* and *B. brachypus*, and four African species including *B. snowi, B. lewisi, B. minor* and *B. heinzelini* (Hooijer 1963; Hooijer and Patterson 1972; Cerdeño 1993; Geraads and Miller 2013; Koufos and Kostopoulos 2013). *Brachypotherium* can be differentiated from other rhinoceros by its large size and hippo-like body proportion (Antoine 2002). The Tebingan specimens do not match with any African species of *Brachypotherium: B. minor* found in Kenya, has a flat ectoloph, a short ante-crochet and a small crochet on their upper molars (Geraads and Miller 2013). *B. heinzelini* from the early Miocene of East and South Africa (Hooijer 1963, 1966, 1973), is different from the Tebingan specimens due to having a hollow ectoloph and a simple crochet on M1 and M2 and, on M3, a weak ante-crochet and crochet and, a straight ectometaloph (Guérin 2008). Finally, *B. lewisi* from Pliocene of Kenya and Libya, has a flat ectoloph on their upper molars and lophs are straight and parallel on M1 and M2. Furthermore, M3 has a posterior cingulum with knobs, and there is a constricted protocone (Hooijer and Patterson 1972; Pandolfi and Rook 2019). The Tebingan fossils cannot be assigned to European species either. *B. brachypus* has a straight ectoloph with an external cingulum and a broad hypocone on M1 and M2, a crista, a forked crochet and a well-developed ante-crochet (Cerdeño 1993; Koufos and Kostopoulos 2013). A forked crochet can be observed on NMMP-KU-IR-6478, but it can be considered as a variation.

The Tebingan specimens can be compared to the Asian *Brachypotherium* species but can be differentiated from '*B*'. *fatehjangense* of Siwalik, which has a rather thick and short crochet, a straight ectoloph, and a protocone without constriction on M1 and M2. The crochet seems absent on M3, only the ante-crochet and a constricted protocone are developed on M3 (Khan et al. 2010; Rafeh et al. 2020) (Fig. 4B). Furthermore, the dental size of '*B*'. *fatehjangense* is smaller than that of *B. perimense*, and so then of our specimens (Table 1). As for *B. perimense*, it is defined by a constricted protocone, well-developed parastyle and metastyle on upper molars; a convex ectometaloph on M3 (Fig. 4A). The anterior and posterior cingulum are present. M1 and M2 have a crochet and ante-crochet but not on M3, which retains only the crochet and a rudimentary crista (Rafeh et al. 2020; Handa et al. 2020). NMMP-KU-IR-5024 is slightly different from the other specimens identified here due to having neither tubercle at the entrance of the median valley, a crochet nor ante-crochet, this difference can be due to the worn condition of the teeth. But, it can still be related to *B. perimense* by the presence of a well-marked groove on the anterior part of the protocone, also a lingually inclined and slightly wavy ectoloph. All these dental characters and dental sizes allow to assign NMMP-KU-IR-5024 to *B. perimense* (Table 1).

'Brachypotherium' fatehjangense Pilgrim, 1912

Diagnosis

Hypsodont teeth smaller than *B. perimense*. Molariforms premolars with a strong paracone fold. Upper molars with a flat ectoloph. The protocone constriction is absent on M1 and M2. Short and thick crochet, the crista is absent and the ante-crochet is developed. Well-developed paracone fold and parastyle (Heissig 1972).

Geographic and stratigraphic ranges

Myanmar and Pakistan (Chinji and Nagri Formation) during the Miocene.

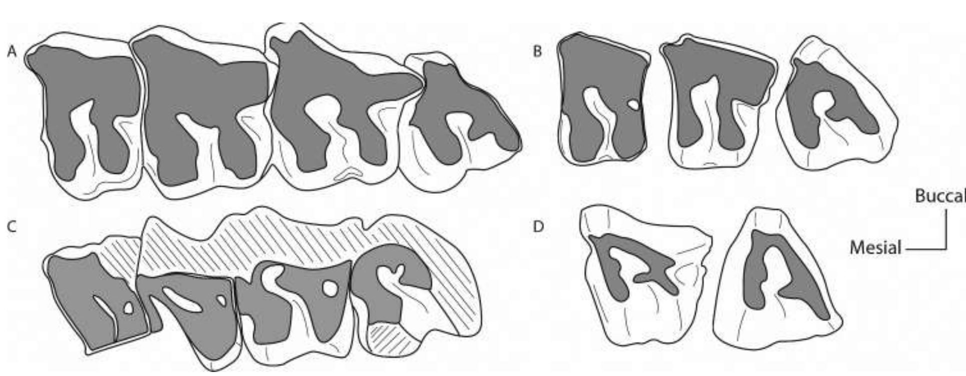

Figure 4. Upper cheek tooth of selected compared specimens in occlusal view. A) *B. perimense* (P4-M3) (Handa et al. 2020); B) *B. fatehjangense* (P4, M2-M3) (Rafeh et al. 2020); C) *D. gwebinensis* (P4-M3) (Zin-Maung-Maung-Thein et al. 2008); D) *Rhinoceros* sp. (M2-M3) (Zin-Maung-Maung-Thein et al. 2010).

Materials

NMMP-KU-IR-5025, 5221 and 5223, left M3.

Locality and age

Inbingan village, Magway Region, central Myanmar, early late Miocene.

Description

Upper molars: NMMP-KU-IR-5025, 5221 and 5223 are left M3 (Fig. 5A-C), and have a well-developed parastyle and paracone fold. The ectometaloph is flat, and the protoloph is slightly convex in NMMP-KU-IR-5221 compared to IR-5025 (Fig. 5A and B). The crochet is short and thick in these three specimens. NMMP-KU-IR -5025 has a well-developed anterior cingulum, while the anterior cingulum is smaller in both NMMP-KU-IR-5221 and IR-5223. Furthermore, the posterior and lingual cingulum are represented by a tubercle at the level of the hypocone and also at the entrance to the median valley. However, NMMP-KU-IR-5221 does not have a tubercle at the entrance of the median valley.

Comparisons and discussion

As mentioned above, the Tebingan specimens cannot be related to *Alicornops, Aceratherium, Chilotherium, Gaindatherium, Iranotherium, Dicerorhinus* or *Rhinoceros*. They can be assigned to *Brachypotherium*. The Tebingan specimens do not belong to any African species of *Brachypotherium. B. minor* is characterised by a weak crochet and a weakly marked parastyle groove (Geraads and Miller 2013). *B. heinzelini* is different due to having a marked protocone constriction and a rudimentary crista (Hooijer 1966; Guérin 2008). *B. lewisi* has a slightly convex ectometaloph, and as in *B. heinzelini*, the protocone constriction is well marked (Hooijer and Patterson 1972). They also differ from *B. brachypus,* which has a well-constricted protocone and an ante-crochet (Koufos and Kostopoulos 2013).

The Tebingan specimens can be compared to the Asian species of *Brachypotherium*. However, NMMP-KU-IR-5027, 5221 and 5223 can be differentiated from *B. perimense* from the middle Miocene of the Siwalik (Pakistan). In the latter, the ectometaloph is longer than the protoloph, the ante-crochet is present, the ectometaloph is convex and has a tubercle at the entrance to the median valley (Fig. 4A). In addition, the size of the teeth of *B. perimense* is larger than our specimens (Rafeh et al. 2020). They share more common characters with '*B*'. *fatehjangense* of Siwalik and Fatehjang from the middle Miocene (Heissig 1972; Rafeh et al. 2020) than *B. perimense* due to having a well-marked parastyle and a flat outer wall on the ectometaloph. Furthermore, the size of the two lophes are the same. There is a slight constriction at the base of the protoloph but not observed on the surface. Only short and thick crochet is present on upper molars (Heissig 1972; Rafeh et al. 2020) (Fig. 4B). Therefore, all teeth NMMP-KU-IR-5027, 5221 and 5223, can be assigned to '*B*'. *fatehjangense*. Furthermore, the size of the teeth of our specimens coincides with the dental size of '*B*'. *fatehjangense* (Table 1).

'*B*'. *fatehjangense* is less well-represented in the Miocene deposits compared to *B. perimense*. '*B*.' *fatehjangense* is still debatable: some authors have assigned this species to *Aprotodon fatehjangense*, to *Chilotherium* (*C. fatehjangense* and *C. blanfordi*) or *Diaceratherium* (Heissig 1972, 1975; Deng 2006; Saña 2008). Saña (2008) showed that "*B*". *fatehjangense* may be phylogenetically isolated from the genus *Brachypotherium* but closer to *Diaceratherium*, and renamed "*B*". *fatehjangense* as *D. fatehjangense*. Recent study also cites "*B*". *fatehjangense* as *D. fatehjangens*" (Hullot et al. 2023). The new assignment of "*B*". *fatehjangense* to *D. fatehjangense* was made by a phylogenetic analysis performed by Saña (2008), but no morphological descriptions have been done yet, and other analyses need to be realised to confirm this new assignment. In recent literature, "*B*". *fatehjangense* is still assigned to *Brachypotherium* (Rafeh et al. 2020; Handa et al. 2020; Samiullah et al. 2021), so we will use "*B*". *fatehjangense* with quotation marks due to its debated assignment.

Subtribe Rhinocerotina Owen, 1845

Genus *Rhinoceros* Linnaeus, 1758

Diagnosis

Hypsodont teeth with a wavy external wall on upper molars. A strong parasty'e 'uttress and a distinct crochet and no crista. Strong anterior cingulum . Lack of protocone constriction and lingual cingulum. The median valley is deeper than the posterior valley in the upper premolars and, the opposite in the upper molars. Deep labial groove and neither the labial nor lingual cingulid on lower molars (Colbert 1943; Heissig 1972).

Geographic and stratigraphic ranges

Southeast Asia since the early Late Miocene.

Rhinoceros sp.

Materials

NMMP-KU-IR-5627 and 5471, left P4; NMMP-KU-IR-5026, 5625, 6474 and 6475, right P4; NMMP-KU-IR-5219, 5220, right M1; NMMP-KU-IR-5117, left and right M2, respectively; MZKB-K-075, left M3; NMMP-KU-IR-5472, right maxilla preserving M1-M2; MZKB-K-899, right maxilla preserving P2-M1; MZKB-K-840 and 842, left mandibles preserving m2-m3; NMMP-KU-IR-5466, left mandible preserving p4-m3.

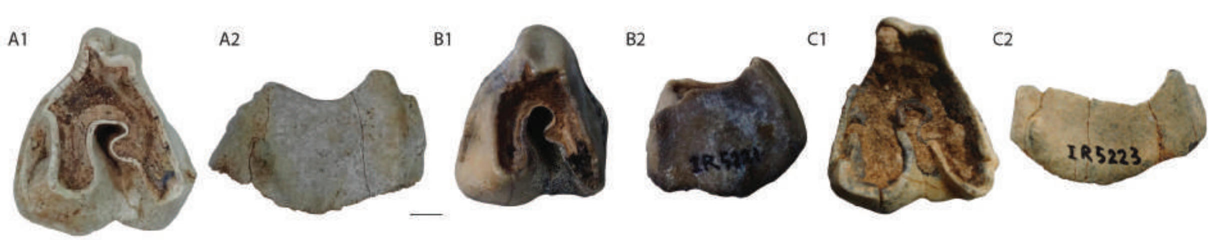

Figure 5. Upper third molars of '*Brachypotherium*' *fatehjangense* of the Tebingan area in occlusal (A1-C1) and labial (A2-C2) views. A, left M3 (NMMP-KU-IR-5025); B, left M3 (NMMP-KU-IR-5221); C, left M3 (NMMP-KU-IR-5223). Scale bar=10mm.

Locality and age

The Tebingan area, Magway Region, Myanmar, the early late Miocene.

Description

Upper premolars: NMMP-KU-IR-6475, 6474, 5625 and 5026 are right P4 (Figure 6 A, B, D and E) and NMMP-KU-IR-5471 and 5627 are left P4 (Figure 6C and F). They share some features such as a developed parastyle and paracone fold, a strong anterior cingulum and a postfossette closed by a posterior cingulum, with the exception of NMMP-KU-IR-5627, where the postfossette is closed by a hypoconal flange (Figure 6F). The ectoloph is slightly wavy. The protoloph on NMMP-KU-IR-5471 (Figure 6C) is not connected to the paracone; on the other hand, NMMP-KU-IR-6475 has a constriction at the same location (Figure 6A). NMMP-KU-IR -6474 and 5471 have several small crochets. NMMP-KU-IR-5625 (Figure 6D) has the same features as the teeth described above except that it is slightly smaller and the entrance to the median valley is blocked by the contact between the protocone and hypocone.

NMMP-KU-IR-5026 is a heavily worn right P4 (Fig. 6E). The bulge of the protocone has merged with the hypocone, closing the median valley on the lingual part. The paracone and the metacone are prominents. The parastyle is very weak. On the distal part of the tooth, the postfossette is slightly visible, and it is closed by a hypocone flange. The crochet is present but very small, and the crista and the ante-crochet are absent. The median valley is very shallow due to the advanced wear of the tooth.

Upper molars: M1: NMMP-KU-IR-5219 and 5220 (Figure 6G and H) are right M1, and they share common features. The parastyle and paracone folds are well-developed. Behind the paracone fold, the ectoloph is slightly convex and then becomes concave due to the slightly raised metastyle. The crochet is well developed, and the crista is present in NMMP-KU-IR-5219 but absent in IR-5220. The ante-crochet, on the other hand, is absent. There is a small protocone fold on the anterior part of the protoloph. The anterior and posterior cingula are present, the posterior cingulum encloses the postfossette. The latter appears to be as deep as the median valley. The cingulum or tubercle are absent.

M2: NMMP-KU-IR-5117 is a left M2 and has a slightly undulating ectoloph behind the paracone fold with a raised metastyle (Fig. 6I). The parastyle and paracone fold are moderately developed. There appears to be a protocone fold on the anterior and posterior part of the protoloph, but no constriction of the protocone is observed in the occlusal view. The ante-crochet is present but weak. The crochet is broken on its distal part and bifurcated towards the ectoloph. Multiple cristae are present. The anterior cingulum is present and low on the crown. A V-shaped posterior cingulum encloses a small postfossette, which is shallower than the median valley. The latter is rather narrow and deep without a lingual cingulum or tubercle at its entrance.

M3: MZKB-K-075 is a well-preserved left M3 (Figure 6J). The M3 has a triangular shape, typical pattern of rhinoceros, with a straight ectometaloph and a slightly convex protoloph, anterior cingulum and a thin crochet. There is no lingual cingulum.

Maxillae: NMMP-KU-IR-5472 is a right maxilla preserving M1 and M2 (Figure 6K). On the M1, the postfossette is closed by a small posterior cingulum. The postfossette is smaller and shallower than the median valley. The crochet is well-developed. On M2, the parastyle and paracone folds are developed. The anterior cingulum is present and lies on the half of the protoloph to its mesio-lingual part. The crochet is well-

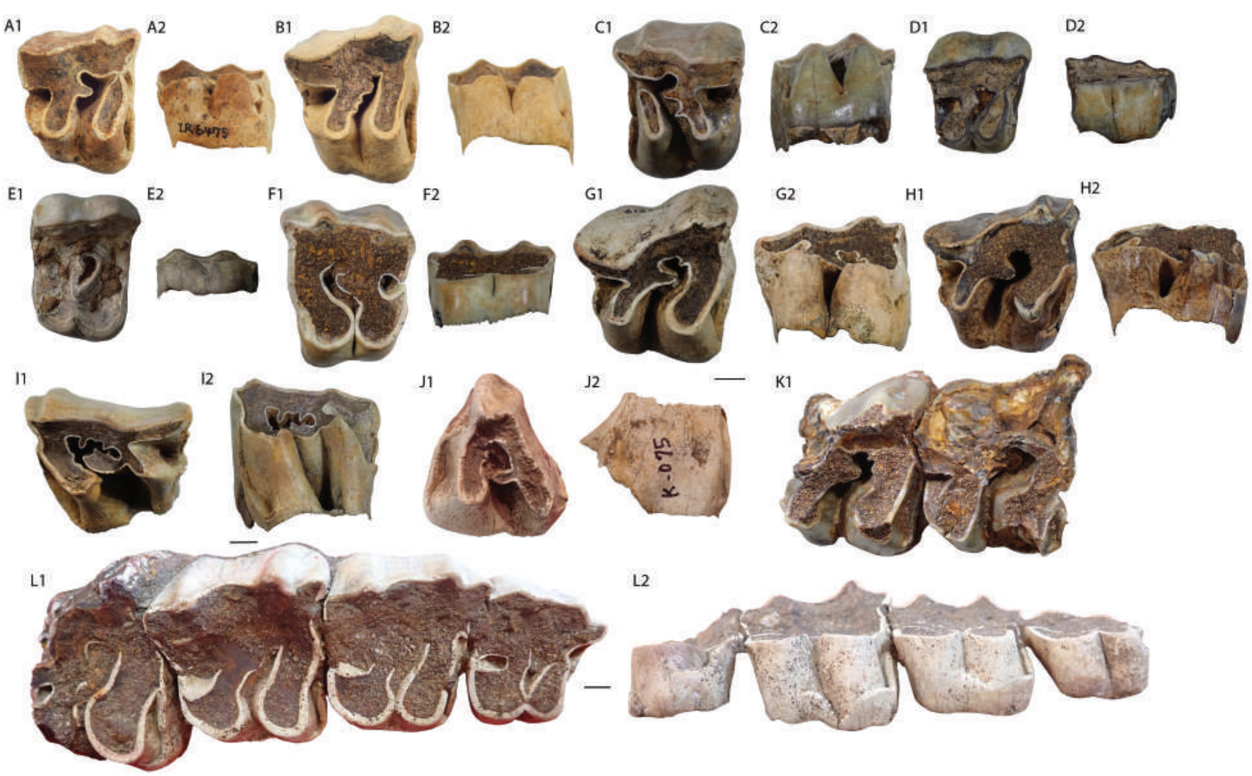

Figure 6. Upper premolars and molars of *Rhinoceros* sp. of the Tebingan Area in occlusal (A1-L1) and lingual (A2-L2) views. A, right P4 (NMMP-KU-IR-6475); B, right P4 (NMMP-KU-IR-6474); C, left P4 (NMMP-KU-IR-5471); D, right P4 (NMMP-KU-IR-5625); E, right P4 (NMMP-KU-IR-5026); F, left P4 (NMMP-KU-IR-5627); G, right M1 (NMMP-KU-IR-5219); H, right M1 (NMMP-KU-IR-5220); I, right M2 (NMMP-KU-IR-5117), J, left M3 (MZKB-K-075); K, right maxillary with M1 and M2 (NMMP-KU-IR-5472); L, right maxillary with P2-M1 (MZKB-K-899). Scale bar=10mm.

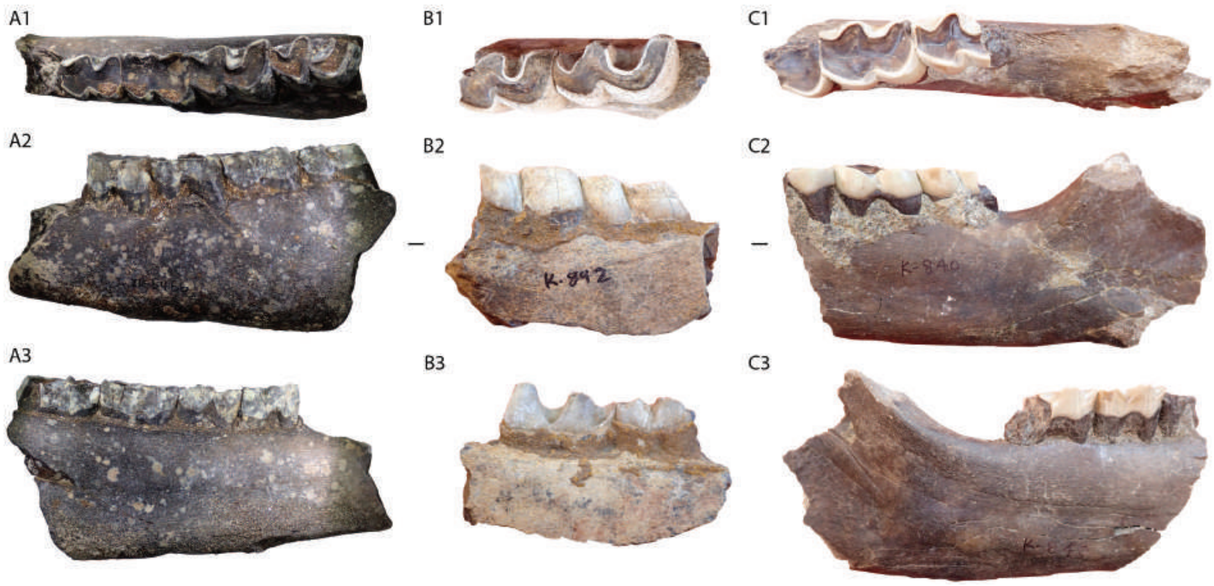

Figure 7. Left mandibles of *Rhinoceros* sp. from the Tebingan Area in occlusal (A1-C1), labial (A2-C2), and lingual (A3-C3) views. A, NMMP-KU-IR-5466 with p4 – m3; B, MZKB-K-842 and C, MZKB-K-840 with m2-m3. Scale bar=10mm.

developed, and a rudimentary crista is present. There is neither a lingual cingulum nor tubercle at the entrance to the median valley.

MZKB-K-899 is a right maxilla preserving P2-M1 (Figure 6L). Only the anterior part of the M1 is preserved. All the teeth in the row are similar, P2 being the smallest. The parastyle and paracone folds are developed, the hypoconal flange encloses the postfossette, the median valley is narrow, and the anterior cingulum is present. There is no lingual cingulum.

Mandibles: The NMMP-KU-IR-5466 is a left mandible preserving p4-m3 (Figure 7A) and MZKB-K-842 and 840 are mandibular fragments with m2 and m3 (Figure 7B and C). All teeth have the same features, such as the deep labial groove, the V-shaped anterior valley and the U-shaped posterior valley. There is neither labial nor lingual cingulum. The angle of the trigonid is acute contrary to the talonid on m3.

Comparisons and discussion

The Tebingan teeth cannot be assigned to *Chilotherium* from Nagri Formation (Pakistan). Indeed, *Chilotherium* has an indistinct or absent parastyle fold, a constricted protocone, and a crochet absent on the premolars and the ectometaloph is convex on the M3 (Khan 2009). They cannot be assigned to *Aceratherium* from Dhok Pathan Formation (Pakistan) due to the strongly constricted protocone on M1 and M2, a long labial wall with a flat margin on the molars and the nearly flat ectoloph (Khan 2009). The teeth of *Gaindatherium* from the Chinji Formation are very simple: only a small crochet is present, the ectometaloph of the M3 is convex and there is cement on the M1 (Khan et al. 2014). The Tebingan specimen differs from *Alicornops*. This genus has an ante-crochet and a lingual cingulum on upper molars. Furthermore, lower molars have an angular trigonid and acute dihedral at the talonid (Antoine et al. 2003).

The Tebingan teeth differ from the genus *Brachypotherium*. The dental size of *Brachypotherium* is large, a constricted protocone is present and the parastyle is strongly developed (Rafeh et al. 2020). They cannot be assigned to *Dicerorhinus* because their premolars do not have a crochet, which is typical of this genus. Furthermore, the ectoloph of the upper molars is almost flat (Tong and Guérin 2009).

Therefore, all Tebingan specimens can be assigned to the genus *Rhinoceros* based on the following preserved dental characteristics: a developed parastyle and crochet, a strong anterior cingulum, absence of a constricted protocone, absence of the ante-crochet, and the lingual cingulum; the anterior valley is deeper than the posterior ones in premolars, but the same depth on upper molars (Colbert 1943; Laurie et al. 1983; Groves and Leslie 2011). Also, Tebingan specimens can be assigned to *Rhinoceros*. This genus has a deep labial groove, oblique hypolophid, absence of the labial and lingual cingulids and an acute trigonid (Figure 8) (Antoine 2002; Antoine et al. 2003). As suggested by Hooijer (1946), a lower mandibular fragment does not give much information on the attribution of specimens to a species, even isolated lower teeth cannot be identified with certainty. Therefore, mandibles NMMP-KU-IR -5466, MZKB-K-842 and 840 can be assigned to *Rhinoceros* sp. (Table 3).

The evolutionary history of *Rhinoceros* from Southeast Asia, and even India, is still poorly understood and disputed. The species *R. sivalensis* Falconer and Cautley 1847, from the Upper Siwaliks of Pakistan and India, is considered as valid species, as are *R. platyrhinus, R. sinensis* (in addition to the two living species *R. sondaicus* and *R. unicornis*) (Pandolfi and Maiorino 2016; Antoine et al. 2022). However, their phylogenetics and systematics of this genus are not resolved. The validity of several species of *Rhinoceros* is still debatable. Indeed, *R. kendengindicus* Dubois 1908 from Java and *R. sivalensis* from Pakistan may be synonymous with *R. unicornis* (Antoine 2012). However, *R. sivalensis* is unquestionably arepresentative of the genus *Rhinoceros* but its hypodigms of *R. sivalensis* is probably one of a chimera, which shows that some fossils assigned to *R. sivalensis*, may possibly belong to another genus or another species of *Rhinoceros*. This species would need a revision on its own (Antoine pers. comm.). Colbert (1938) identified *R. sivalensis*, which was discovered from the Pleistocene sediments of Myanmar, but this attribution is dubious because the recovered fragments were smaller than those from Siwalik (Pakistan). They were renamed as *Rhinoceros* sp. by Zin-Maung-Maung-Thein et al. (2010). More recently, Yan et al. (2014)

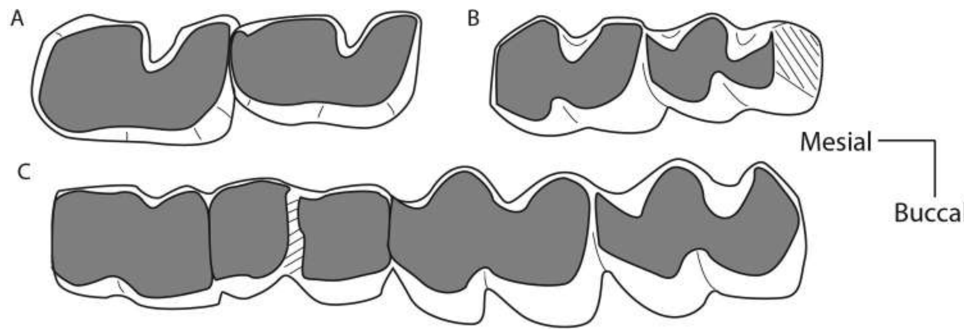

Figure 8. Lower cheek teeth of selected compared specimens in occlusal view. A) *B. perimense* (m2-m3); B) *Dicerorhinus* sp. (m2-m3) and C) *Rhinoceros* sp. (p4-m3). Based on Zin-Maung-Maung-Thein et al. 2010.

identified a new species, *R. fusuiensis*, from Guanxi Province, southern China, but it was subsequently renamed by Antoine et al. (2022) as *Dicerorhinus fusuiensis*. These results demonstrate that our taxonomic understanding of this genus is far from clear, and we consider six species possibly valid, as discussed above.

The Tebingan specimens are distinct from *R. unicornis* by the absence of a medifossette formed by a crista and a crochet in the median valley on upper premolars and molars, a completely formed protoloph and a flat ectoloph on the upper premolars (Suraprasit et al. 2016; Filoux and Suteethorn 2018). These fossils cannot be assigned to *R. sinensis* due to the presence of a medifossette on the upper teeth, the absence of ribs on the ectoloph on premolars, the separation of the protocone and hypocone and the large upper cheek teeth (Table 2) (Colbert and Hooijer 1953; Zheng 2004) (Fig. 4E). NMMP-KU-IR-5117 shares a dental character with *R. sinensis*, multiple cristae on the upper molars (Colbert and Hooijer 1953). However, this single common feature is not sufficient to conclude that NMMP-KU-IR-5117 is related to *R. sinensis*. As for *R. sivalensis*, this species is different from our fossils as noted by the presence of a medifossette on the premolars and molars, a flat ectoloph, and a strong, constricted protocone. Furthermore, on the premolars, the postfossette is open distally on P3-P4, and there is a strong lingual cingulum on P2-P4 (Khan 2009). *R. platyrhinus* also has a medifossette on the upper teeth, a constricted hypocone and a small and narrow crochet on the premolars (Pandolfi and Maiorino 2016). *R. kendengindicus* is distinct from our specimens due to having a postfossette closed and

Table 2. Measurements (in mm) of upper cheek teeth of *Rhinoceros* sp. from Tebingan Area and comparisons with other *Rhinoceros* species.

	P4			M1			M2			M3		
	L	Wa	Wp	L	Wa	Wp	L	Wa	Wp	L	Wa	Wp
R. unicornis[a]	46.0	64.0	-	53.2	65.6	-	57.6	68.6	-	-	-	-
R. sinensis[b]	39.6	63.2	62.2	47.7	68.7	63.7	52.8	72.4	63.6	-	-	-
R. platyrhinus[c]	-	-	-	51	78	-	61	74	-	-	-	-
R. sivalensis[d]	38.1	66.0	-	44.6	66.0	-	50.8	66	-	-	-	-
R. sondaicus[e]	43.8	54.9	-	48.9	55.8	-	50.5	57.5	-	-	-	-
R. kendengindicus[f]	Ca.39	63	60	Ca.44	65	56	47	66	55	-	-	-
NMMP-KU-IR-5026	37.7	52.4	47.9	-	-	-	-	-	-	-	-	-
NMMP-KU-IR-5625	38.5	44.7	41.8	-	-	-	-	-	-	-	-	-
NMMP-KU-IR-5627	43.1	56.2	53.5	-	-	-	-	-	-	-	-	-
NMMP-KU-IR-5471	43.6	54.2	49.2	-	-	-	-	-	-	-	-	-
NMMP-KU-IR-6475	42.5	53.1	47.4	-	-	-	-	-	-			
NMMP-KU-IR-6474	48.5	60.5	54.9	-	-	-	-	-	-			
NMMP-KU-IR-5219	-	-	-	54.6	58.7	47.5	-	-	-	-	-	-
NMMP-KU-IR-5220	-	-	-	51.3	55.1	49.7	-	-	-	-	-	-
NMMP-KU-IR-5472	-	-	-	43.9*	59.9*	53.9	-	57.7	46.1	-	-	-
NMMP-KU-IR-5117	-	-	-	-	-	-	55.7	48.5	33.9	-	-	-
MZKB-K-074	-	-	-	-	-	-	50.1	54.7	48.3	-	-	-
MZKB-K-899	47.1	56.9	53.4	-	61.9	-	-	-	-	-	-	-
MZKB-K-075	-	-	-	-	-	-	-	-	-	50.1	54.7	48.3

Remarks: Range and sample size for *R. unicornis, R. sondaicus* and *R sinensis. Abbreviations*: L: ectoloph length; Wa: protoloph length; Wp: metaloph length. *a*: Guérin 1980; b: Colbert and Hooijer 1953; *c*: Colbert 1935; *d*: Falconer and Cautrey 1867; *e*: Thomas et al. 1980; *f*: Hooijer 1946.

Table 3 Measurements (in mm) of lower cheek teeth of *Rhinoceros* sp. from Tebingan Area and comparisons with other *Rhinoceros* species.

	p4		m1		m2		m3	
	L	W	L	W	L	W	L	W
R. sondaicus[a]	39.1	27	43.5	28.8	46.1	29.4	47.7	27.2
R. unicornis[b]	43.8	31	46.7	30.1	54.1	32.4	57.4	30.8
R. sinensis[c]	45.3	29.6	51.7	33.1	55.4	33	54.6	32
R. sivalensis[d]	41.9	27.9	37.1	26.7	50.8	30.5	-	-
NMMP-KU-IR-5466	35.2	28.4	38.8	35.9	43.3	34.8	54.7	30.4
MZKB-K-840	-	-	-	-	57.4	32.0	-	31.3
MZKB-K-842	-	-	-	-	46.1	30.5	54.6	29.8

Remarks: Range and sample size for *R. unicornis, R. sondaicus* and *R sinensis. Abbreviations*: L: ectoloph length; Wa: protoloph length; Wp: metaloph length. *a*: Guérin 1980; *b*: Colbert and Hooijer 1953; *c*: Colbert 1935; *d*: Falconer and Cautley 1867.

compressed laterally on the premolars and molars. The crochet is thick and pointed, and a crista is present on the premolars. In addition, the protocone is strongly directed backwards, the medifossette is closed on the upper molars (Hooijer 1946). Finally, the Tebingan fossils are different from *R. sondaicus* from the Plio-Pleistocene Irrawaddy sediments, which has no protocone fold and a strong sinuosity of the ectoloph on upper molars and premolars. And the lophes are separated and parallel on upper premolars (Zin-Maung-Maung-Thein et al. 2010; Khan 2009). The postfossette is deeper than the median valley, and the crochet can be bifurcated on the premolars (Hooijer 1946; Khan 2009). Some important characters for the identification of specimen NMMP-KU-IR-5472 are missing. Indeed, the ectoloph is missing on both molars, the parastyle and paracone folds are missing on M1. The left mandible of *Rhinoceros* sp. has also been described from the latest Miocene to the early Pliocene Chaingzauk area in central Myanmar (Zin-Maung-Maung-Thein et al. 2010). This specimen is comparable to the Tebingan *Rhinoceros* sp. due to having a deep labial groove, acute trigonid, oblique hypolophid and no labial and lingual cingulids.

Discussion

Fossil records and palaeobiogeography of *Brachypotherium*

Brachypotherium is found from the Miocene deposits in Eurasia and Africa. *B. perimense* has been described from the early Miocene to the late Miocene in Pakistan, India, Nepal, Myanmar, Thailand and also in Iraq (Geraads 2010; Zin-Maung-Maung-Thein et al. 2010; Khan et al. 2012; Nishioka et al. 2018; Rafeh et al. 2020; Handa et al. 2020) (Figure 9). The Iraq specimen was described as *B.* cf. *perimense* by Thomas et al. (1980). As for '*B*'. *fatehjangense*, it is only known from the early Miocene to the late Miocene localities in Pakistan and Myanmar (Chavasseau et al. 2006; Khan et al. 2010; Zin-Maung-Maung-Thein et al. 2010). According to the palaeogeographic distribution of *Brachypotherium* in South and Southeast Asia, the genus would have dispersed from the Indian subcontinent to Southeast Asia during the middle Miocene (Figure 10). In Europe, *B. brachypus* and *B. goldfussi* have been identified from the middle to late Miocene deposits in central and western Europe and also in the eastern part of the Mediterranean region (Antoine

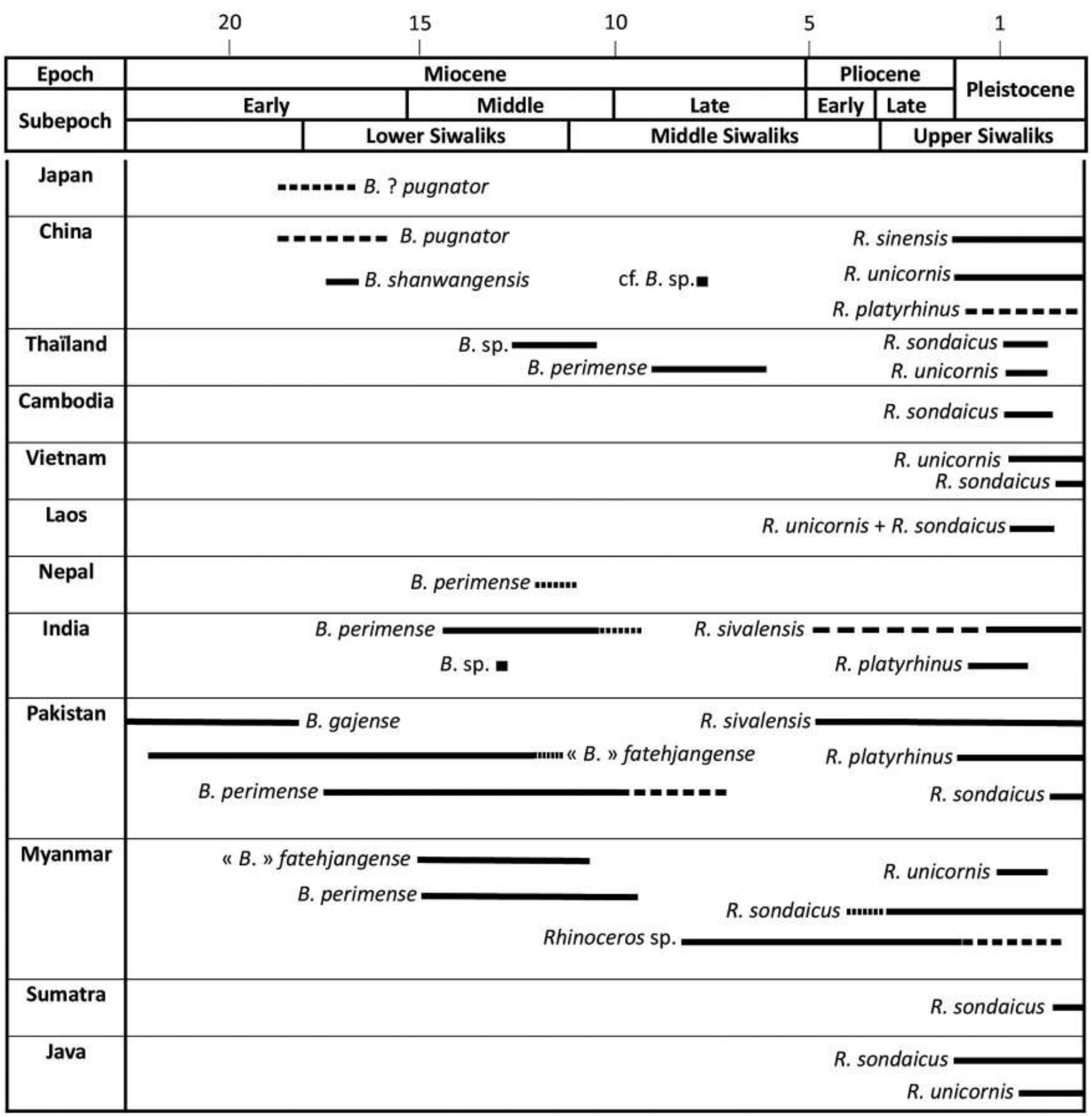

Figure 9. Chronology of *Brachypotherium* and *Rhinoceros* in South and Southeast Asia. Fossil record and locality age according to: Zin-Maung-Maung-Thein et al. 2009; Antoine 2012; Antoine et al. 2013; Zhang et al. 2013; Handa et al. 2020.

et al. 2000). *Brachypotherium* sp. has been identified from the late Miocene in Bulgaria, considered one of the last representatives of the genus (Geraads and Spassov 2009), and few specimens belonging to *B. brachypus* of the Miocene of Spain (Cerdeño 1992). However, Antoine (2012) described that their assignment remains doubtful, and *B. goldfussi* may be synonymous with *B. brachypus*. African *Brachypotherium* species (*B. snowi, B. lewisi, B. minor* and *B. heinzelini*) are found from the early Miocene in Sub-Saharan, Egypt and Libya until the early Pliocene with *B. lewisi* (Geraads and Miller 2013; Handa et al. 2018).

The fossil record of *Brachypotherium* in East Asia is very scarce and debatable. *B. pugnator* and *Brachypotherium* sp. were found from the Mizunami Group (Gifu prefecture) and Oiso Formation of the Kanagawa Prefecture, eastern of Japan, and *B. shanwangensis* from China (Zin-Maung-Maung-Thein et al. 2009; Fukuchi and Kawai 2011). *B. pugnator* and *B. shanwangensis* are thought to be close to '*B*'. *fatehjangense* from South and Southeast Asia (Pakistan and Myanmar) (Chavasseau et al. 2006; Khan et al. 2010; Zin-Maung-Maung-Thein et al.) (Figure 9). Furthermore, Zhang et al. (2013) assigned rhino specimens from the late Miocene Bahe Formation of Shaanxi Province, China, to *Brachypotherium* sp. without a detailed description. If '*B*'. *fatehjangense* and *B. shanwangensis* would belong to *Aprotodon fatehjangense* (or another genus) and *Plesiaceratherium gracile*, respectively, *Brachypotherium* would not have extended to East Asia (Handa et al. 2020). The taxonomic status of the genus in this area is not well known.

This archaic rhinoceros began to decline during the late Miocene and disappeared at the Miocene-Pliocene boundary possibly due to a more arid climate, giving way to modern Asian *Rhinoceros* (late Miocene to Pleistocene) and *Dicerorhinus* (Pliocene to Pleistocene) (Barry et al. 2002; Deng 2002). The presence of both genera at Tebingan shows that *Brachypotherium* and *Rhinoceros* must have coexisted during the late Miocene before *Rhinoceros* became dominant from that period.

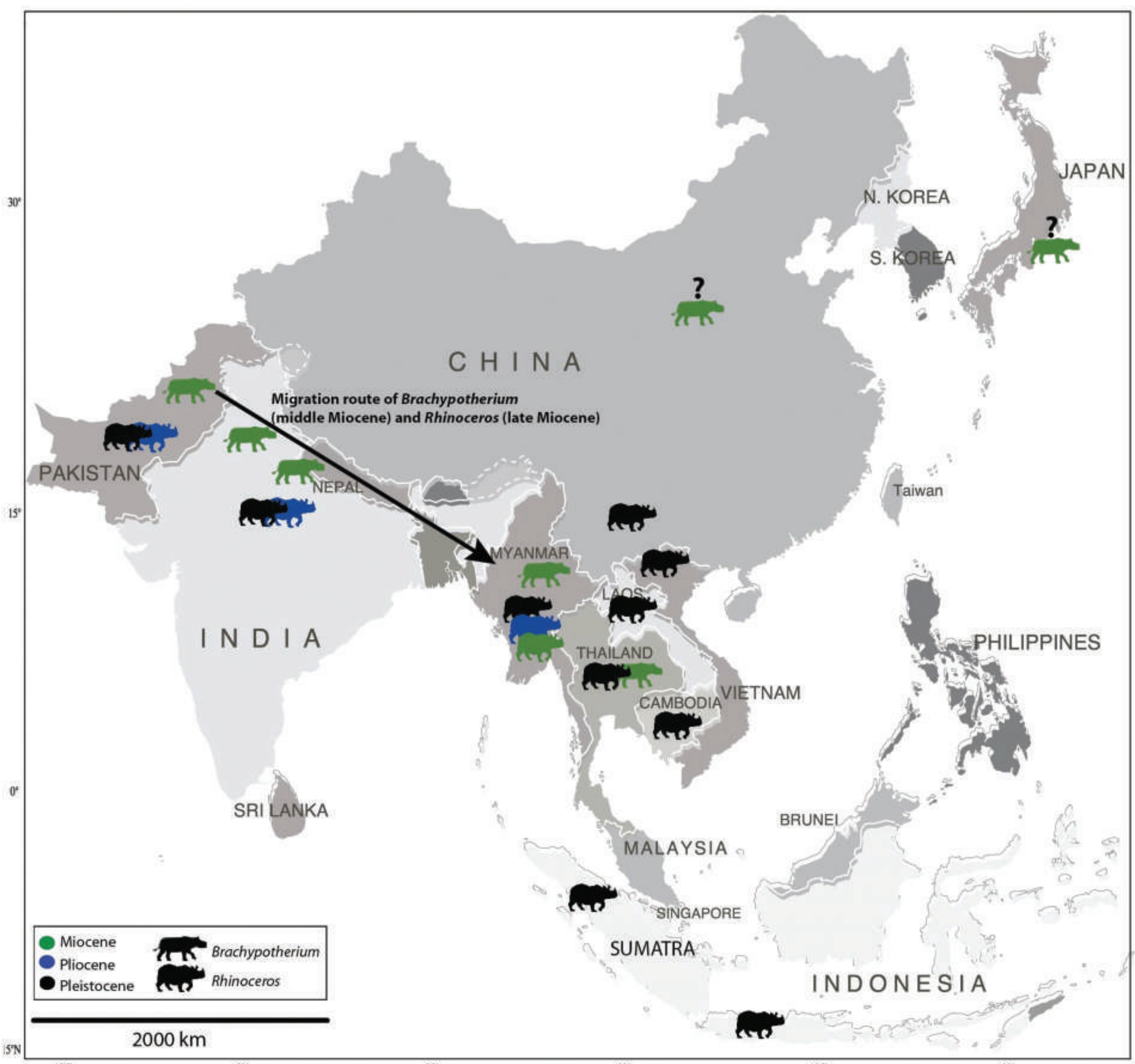

Figure 10. Geographical distribution of *Brachypotherium* and *Rhinoceros* in South and Southeast Asia during the Neogene and Pleistocene. Based on Zin-Maung-Maung-Thein et al. 2009; Antoine 2012; Antoine et al. 2013; Zhang et al. 2013; Handa et al. 2020.

Table 4. Biogeographic and biochronologic distribution of the different species of *Rhinoceros* (Based on data from Colbert and Hooijer 1953, Hooijer 1966, Khan 2009, Zin-Maung-Maung-Thein et al. 2010, Antoine 2012, Zin-Maung-Maung-Thein et al. 2014, Pandolfi and Maiorino 2016, Siddiq et al. 2016).

Species	Age	Area
Rhinoceros sondaicus	late Pliocene-Holocene	South and Southeast Asia, Indonesia
Rhinoceros unicornis	Pleistocene-Holocene	South and Southeast Asia, Indonesia
Rhinoceros sivalensis	Miocene-Pleistocene	Indian subcontinent, China
Rhinoceros sinensis	Pleistocene	China
Rhinoceros platyrhinus	late Pleistocene-early Middle Pleistocene	Indo-Malayan
Rhinoceros kendengindicus	Pleistocene	Indonesia
Rhinoceros sp.	late Pliocene-Pleistocene	Indian subcontinent
Rhinoceros sp. (described here)	early late Miocene	Myanmar

Fossil records and palaeobiogeography of *Rhinoceros*

Rhinoceros is known since the latest Miocene/early Pliocene in Myanmar and Indian subcontinent (Zin-Maung-Maung-Thein et al. 2011; Antoine et al. 2013). The genus diversified during the Pleistocene with many specimens found in the Indian Subcontinent (Antoine et al. 2013; Pandolfi 2018), southern China (Antoine 2012), Thailand (Filoux and Suteethorn 2018; Handa et al. 2020), Cambodia, Vietnam, Laos, Sumatra and Java (Bacon et al. 2008; Antoine 2012) (Figure 10). The Dhok Pathan fauna, middle Siwaliks (India/Pakistan), demonstrates a significant diversity of Rhinocerotidae fossils, such as the genera *Chilotherium, Aceratherium, Rhinoceros, Brachypotherium* and *Alicornops* (Barry et al. 2002; Khan 2009; ; Khan et al. 2013; Siddiq et al. 2016). However, the representatives of *Rhinoceros* were not well diverse in the Dhok Pathan fauna, only *R. sondaicus* and *R. sivalensis* have been reported, as in Myanmar (Zin-Maung-Maung-Thein et al. 2008, 2010; Khan 2009). *Rhinoceros* survived until today with only two species: *R. unicornis* (the Indian rhinoceros) and *R. sondaicus* (the Java rhinoceros) (Laurie et al. 1983; Groves and Leslie 2011).

Fossil specimens of the genus *Rhinoceros* are known in central Myanmar since the latest Miocene with *Rhinoceros* sp., *R. sivalensis* and *R. sondaicus* (Zin Maung Maung Thein et al. 2010; Antoine 2012), but *R. sivalensis* is now considered as the synonym of *R. unicornis* (Antoine 2012) (Figure 9). Our recent description allows us to show that the genus was present around 9 to 8 Ma in central Myanmar, where it is, for the moment, represented by *Rhinoceros* sp., the oldest known *Rhinoceros* fossils in Southeast Asia (Table 4). Discovered fossils consist mainly of isolated teeth with varying degrees of wear, some have good occlusal shape preserved but for some, the advanced wear of the tooth makes the identification of diagnostic characters difficult. Especially for the lower teeth, which provide little information for species identification and therefore, the assignment is done only at the genus level. Other specimens from Myanmar and Pakistan could be assigned to *R. sivalensis* or *R. sondaicus* only (Zin-Maung-Maung-Thein et al. 2008, 2010; Antoine 2012).

During the Miocene, shallow marine conditions prevailed in most areas of central Myanmar, with the paleoshoreline probably lying between 18 ° to 20 ° N. (Zin-Maung-Maung-Thein et al. 2011, 2021). At the end of the Miocene, the coastline started to retreat towards the south of the country, giving way to new terrestrial environments such as forests or woodland. At this time, the climate of central Myanmar would have been more humid than today. Such environmental conditions may have helped the occurrence of *Rhinoceros* in Myanmar, which lives mainly in humid forests and woodland. According to the stable isotopes analysis of tooth enamel of mammals from the Irrawaddy Formation, during the late Miocene, the climate changes became more pronounced, leading to arid conditions with seasonality (Zin-Maung-Maung-Thein et al. 2011; Habinger et al. 2022). At this time, the archaic genera of rhinoceros, such as *Brachypotherium*, may have disappeared, replaced by modern genera, such as *Rhinoceros* (Barry et al. 2002). The first fossil record of *Rhinoceros* (*Rhinoceros* (*Rhinoceros*) aff. *sivalensis*) from the Dhok Pathan Formation (Heissig 1972) and the new identifications of *Rhinoceros* sp. from the Tebingan Area suggest that *Rhinoceros* occurred at least in the early late Miocene in Southeast Asia or Southern Asia.

Conclusion

The rhinoceros fossils from the lowermost part of the Irrawaddy Formation at the Tebingan area in central Myanmar include *B. perimense*, '*B*'. *fatehjangense* and *Rhinoceros* sp., endemic to the Neogene of South and Southeast Asia. Among them, Tebingan *Rhinoceros* sp. is the oldest fossil record for this genus in Southeast Asia. Several species of *Brachypotherium* were documented from the Miocene of Eurasia and Africa. At the end of Miocene, the archaic rhinoceros began to decline due to the fragmentation of forests, likely giving way to modern species of rhinoceros, such as *Rhinoceros* and *Dicerorhinus*.

Fossil remains of *Rhinoceros* have been found from the Late Miocene of the Indian subcontinent through the Pleistocene of China to Southeast Asia. According to the fossil records of *Rhinoceros* sp. in South and Southeast Asia, this clade would have dispersed from the Indian subcontinent to Southeast Asia during the late Miocene. The retreat of the coastline southward in central Myanmar, giving way to a seasonal climate and new terrestrial environments such as forests and woodlands, would have favoured the arrival of *Rhinoceros* in that period. Further detailed analysis of more complete tooth material and postcranial material could provide a better understanding of the evolutionary history of Rhinocerotidae during the Neogene not only in Myanmar but also in Southeast Asia.

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