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ミャンマーの新第三紀サイ科の化石

Rhinocerotidae (Mammalia, Perissodactyla) from the Neogene of Myanmar

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修士論文

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by

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CONTENTS

Abstract

In this paper, new fossil materials of Rhinocerotidae from the Neogene Sediments of Myanmar are described. The phylogeny, paleoecology and migration of the Neogene rhinocerose into Myanmar and Southeast Asian region are also discussed. So far, 4 species of rhinoceros, *Dicerathrium naricum*, *Aceratherium perimense*, *A. lydekkeri* and *Rhinoceros sivalensis* are reported from the Neogene Sediments, and I first report cranial and dental materials of four species, cf. *Gaindartherium*, *Brachyopotherim perimense*, *Dicerorhinus* sp. and *Rhinoceros sondaicus*.

The two species, *Gaindartherium* sp. and *B. perimense* are recovered from the middle Miocene Freshwater Pegu Beds .The dental characteristics and size of the rhinoceros specimens from middle Miocene of Myanmar show close resemblances with those known from the early Miocene to the late Miocene from Indian subcontinent. It supports the idea that South-East Asia and India-Pakistan were part of the same biogeographic province since the middle Miocene.

Rhinoceros recovered from the late Miocene to the early Pleistocene Irrawaddy Group belong to the same genera as the living Asian rhinoceros, *Dicerorhinus* and *Rhinoceros*. The fossil material of *Dicerorhinus* from the Pliocene-Pleistocene of Myanmar shares the *D. sumatresis* from the middle Pleistocene to Recent of Southeast Asia in the presence of nearly vertical occiput, anterior part of the orbit above M^2, nasal incision above P^3, and convex and wide nasal bone. The present specimen also shows similar dental characteristics with extant species in presence of molar crista, protocone fold, and absence of protocone constriction and molar crochet. The discovery of *Dicerorhinus* from the Neogene sediments of Myanmar fills the chronological and geographical gap of this lineage in Southeast Asia. It also suggests an affinity with the Eastern Asian *Dicerorhinus* due to the lack of valid fossil record from the Southern Asia in the Neogene.

Two species of *Rhinoceros*, *R. sivalensis* and *R. sondaicus* from the Irrwaddy Group share the similar dental characteristics with its counterpart from the Neogene of Southern Asia and Southeast Asia. Discovery of *R. sondaicus* from the early Pleistocene of Myanmar suggests the origin of this species in continental Asia, and its possible migration into island Asia during the late early Pleistocene and later ages.

1. Introduction

The family Rhinocerotidae first arose in the Eocene as one clade of the super family Rhinocerotoidae together with Hyracodontidae and Amynodontidae. This family is now in the danger of extinction, and its distribution is limited to Africa and Asian Region (Martin *et al*, 2001). However, it was diversified into many genera and species, and was widely distributed throughout North America, Asia, Europe and Africa in the geological past (Prothero *et al*. 1989).

In contrast with the extant rhinoceros, most of the early rhinoceros were hornless or paired horns on the nose. They first occurred in the late middle Eocene of North America and Asia (Hanson, 1989). Although the fossil records of early rhinocerotids are poorly documented in the late Eocene to the early Oligocene of Eurasia, they were well diversified in North America (Prothero, 1989). The late Eocene Eurasian rhinocerotids was recorded based on scarce dental remains from few localities such as “Far East Province of Russia”, Guangxi and Yunan Provinces of China, southern Mongolia, Krabi (Thailand) and Pondaung (Myanmar) (You, 1977; Hanson, 1989; Antoine, 2002; Holyord, 2006). By the late Oligocene, rhinoceros begin to diverge into major subfamilies. During the Neogene, rhinoceroses become a dominant land mammal, and their fossil materials have been recovered from various localities in Asia, Europe, Africa and North America.

In Myanmar, fossil materials of Rhinocerotids have been frequently recovered from the fresh water Neogene deposits exposed in central Myanmar. According to the previous workers, four species of *Rhinoceros, A. perimense, A. lydekkeri*, *Diceratherium naricum* and *R. sivalensis* were recorded respectively (Stamp, 1922; Colbert, 1938; Cotter, 1938). But most of the specimens are fragmentary, and some descriptions on these specimens are provisional (Colbert, 1938, 1943). So it is now needed to revise the generic status of previously described Neogene rhinoceros from Myanmar.

Previous researchers have reported *Aceratherium* from Bugti sediments, Siwalik sediments, and Neogene sediments from Myanmar (eg., Pilgrim, 1910b; Stamp, 1922; Cotter, 1938). Two species of *Aceratherium, A. perimens* and *A. lydekkeri* are likely to be synonyms (Matthew, 1929; Colbert, 1938). On the other hand, Hessig (1972) assigned the *Aceratherium* from the lower and middle Siwalik Group as separate taxa, *Brachypotherium*. There is also no citation of this genus in recent works of Bugti Hills and Siwalik (eg., Welcomme, 2001; Basu, 2004). Moreover, it is now difficult to identify the original specimens from Myanmar, and I prefer to use “*Aceratherium*” tentatively for the previously described specimens. Similarly, the middle Miocene Asian Diceratheriinae is likely to be different from North American *Diceratherium,* and correspond to the Aceratheriinae, *Acerorhinus* (Hessig, 1975; Qiu et al., 1982). Former description of *Diceratherium* from Myanmar may correspond to Aceratheriinae. However, I refer the “*Diceratherium*” in this work due to the unavailability of the original specimens. The fossil materials of *Rhinoceros sivalensis* belong to the same genus as the extant Asian one-horned rhinoceros had been recorded from the early Pleistocene upper Irrawaddy Group (Colbert, 1938, 1943). This genus was widely distributed in the Plio-Pleistocene deposits of Indo-Pakistan, China and South East Asian region, and still survives in the Indian subcontinent and South East Asia.

In this work, *Brachypotherium perimense*, *Dicerorhinus* sp., *Rhinoceros sondicus* are reported from the Neogene of Myanmar for the first time, and the new dental materials of *R. sivalensis* are described. I provide the comparison of Neogene rhinoceroses of Myanmar with the contemporaneous fauna from the neighbouring regions, and discuss the migration of rhinoceros into Southeast Asian region. Finally, paleoecology of the rhinoceros in Neogene of Myanmar is provided.

2. History of Investigations on Neogene Rhinocerotidae of Myanmar

Lydekker (1876) first described the fossil rhinoceroses from Myanmar under the name of *Rhinoceros irrvaiticus*. He then assigned this species to *Aceratherium perimense* (Lydekker, 1881). Pilgrim (1910b) described *Acerathrium lydekkeri* (possible synonym with *A. perimense*) from the lower Irrawaddy Group. In the same publication, he also recorded the *Rhinoceros sivalensis* from the early Pleistocene upper Irrawaddy Group. Stamp (1922) cited *Aceratherium* from lower Irrawaddy Group and suggested pre Pliocene age for thelower Irrawaddy in correlation with Dhok Pathan Horizon. Colbert (1938) referred to the works of above authors, and describes the new specimens of rhinocerotids, a mandibular symphysis with incisor alveoli, from the upper part of the Irrawaddy Group. He provisionally assigned this specimen to *Rhinoceros sivalensis*. Subsequently, Colbert (1943) described isolated teeth of rhinoceros from the upper part of the Irrawaddy Group. Although the specimens from Myanmar are smaller than *R. sivalensis* from Siwalik Group, he pointed out similar dental characteristics with Siwalik specimens and suggested Pleistocene extension of this species into Myanmar. He also described the rhinoceros teeth from the middle Pleistocene Mogoke cave deposits, and referred to *Rhinoceros* in the same volume. Cotter (1938) also recorded *Diceratherium naricum* and *Aceratherim perimense* from Maw Gravel (correspond to fresh water Pegu Sediments) from the western part of central Myanmar without relevant description on these specimens.

3. Geological Setting

Myanmar can be divided into four north-south trending geotectonic regions: Eastern Highlands (=Sino-Burman Ranges); Central Cenozoic Belt (=Central Myanmar Tertiary Basin);Western Ranges (=Indo-Burman Ranges); Rakhine Coastal Plain (=Arakan Coastal Area) (Stamp, 1922; Chhibber, 1934; Maung Thein, 1973; Bender, 1983; Kyi Khin and Myitta, 1999). Neogene freshwater sediments mainly derived from the Eastern Highlands (Shan Plateau), Eastern Himalayas and Western Ranges are mainly exposed in central Myanmar, and consits of two sedimentary units: Fresh Water Pegu Beds (middle Miocene) and Irrawaddy group (late Miocene to the early Pleistocene). These units are constituted as Neogene continental sediments of Myanmar yielding remains of terrestrial and aquatic vertebrates (Figure 1)

The Pegu Group (Oligocene to middle Miocene) is mainly composed of the marine sediments in the lower part in the south and continental in the upper part in the north, where transition boundary occur in the area between 20˙N and 22˙N latitudes (Stamp, 1922; Aung Khin and Kyaw Win, 1969; Bender, 1983) (Fig. 2). This is due to the fact that gulf was existed in the region between Western Ranges and Eastern Highland during the Oligo-Miocene time (Krishnan, 2005). Sediments gradually filled up this gulf as the sea was receding southward. Many authors described the various name for these sediments (eg. The fresh water Pegu Beds: Stamp, 1922; Colbert, 1938: Fresh water Formation of Pegu Group: Aung Khin and Kyaw Win), and the term “Fresh water Pegu Beds” of Stamp (1922) is used in this work. Colbert (1938) suggested the late Oligocene through the late Miocene age for this fluvatile beds based on the few scattered mammalian fossil like *Cadurcotherium*, *Telmatodon* and *Dorcatherium*. Cotter (1938) also reported *Aceratheium, Tetrabelodon, Hemimeryx, Antharcotherium* and *Deinotherium* from the Maw gravels (equivalent with fresh water Pegu Beds) and suggests its correlation with the lower Siwalik Group (Kamlial Formation). Recently, fossil materials of hippo like rhinoceros, *Brachypotherium*, have been recovered together with the proboscidean fossil, *Prodeinotherium*, *Choerolophodon* and *Gomphotherium* at Thanbingan in central Myanmar. These fauna also indicate its correlation with the lower Siwalik Group, and suggest the middle Miocene age for the Fresh Water Pegu Beds.

On the other hand, Irrawaddy Group (Fossil Wood Group: Theobald, 1869; Irrawaddian Series: Noetling, 1900; Irrawaddy Formation: Aung Khin and Kyaw Win, 1969; Irrawaddy Group: Bender, 1983) can be correlated with the middle and upper Siwalik Group in faunal similarities. Traditionally, Irrawaddy Group is divided into two parts, lower and upper parts based on the lithological and paleontological criteria. Although the stratigraphic position of this formation has not been fully understood due to the lack of geological age calibrated from radioisotope, and paleomagnetism, some age estimates has been done using correlation of the vertebrate faunas. It has been suggested that the lower part of the formation is the late Miocene to Pliocene, and that the upper part is early Pleistocene (Colbert, 1943; Bender, 1983).

According to Chibber (1934), approximately 43 percent of the species found in Myanmar are common to the Siwaliks of the Salt Range and the sub-Himalayan Region. To date, 4 orders (Carnivora, Perissodactyla, Artiodactyla, and Proboscidea), 15 families, and 40 genera of mammals have been reported from the Neogene deposits. Judging by the percentage of specimens discovered, Proboscideans and Bovids were dominant fauna. Preliminary analysis of faunal composition suggests greater similarity of the Myanmar fauna to the South Asian Fauna (i.e. Siwalik fauna) than East Asia fauna until the Pliocene (Takai *et al.* 2006).

4. Abbreviations

All fossil materials used in this work are deposited in National Museum and Geological Museum of Yangon University, Yangon and Geological Museum of Mandalay University, Mandalay in Myanmar.

NMMP-KU-IR, National Museum - Myanmar - Paleontology - Kyoto University - Irrawaddy (stored in the National Museum, Yangon, Myanmar, and in the Geological Museum, Yangon University, Yangon, Myanmar).

MUDG-V, Mandalay University - Department of Geology - Vertebrate (stored in the Geological Museum, Mandalay University, Mandalay, Myanmar)

5. Taxonomic System

The systematic relationship of the rhinocerotids was discussed by Prothero (1989), and four subfamilies, Dicerathriinae, Menoceratheriinae, Aceratheriinae and Rhinocerotinae are recognized. Cladastics analysis of Cerdeno (1995) suggests only two subfamailies, Rhinocerotinae and Aceratheriinae. Two subfamilies, Diceratheriinae and Menoceratinae of Prothero (1986), and Prothero and Schoch (1989) are supposed to be paraphyletic groups. However, more extended phylogenetic analysis based on 282 cranial, dental and postcranial characters of 36 taxa supports the monophyly of these two subfamilies within the Rhinocerotidae, and suggest the new subfamily, Elasmotheriinae together with subfamily Rhinocerotinae (Antoine, 2002).

6. Methods

I generally follow the terminologies of Guèrin (1980) (Figure 3). Dental measurements are taken at the base of the crown corroding to Hooijer (1948). Taxonomic system is mainly based on the Prothero and Schoch (1989).

7. Systematic Paleontology

Order PERISSODACTYLA Owen, 1848

Family RHINOCEROTIDAE Owen, 1845

Subfamily RHINOCEROTINAE Owen 1845

Tribe TELEOCERATINI Hay, 1902

Genus *Brachypotherium* Roger, 1904

Brachypotherium perimense Falconer & Cautley, 1847

Plate 1 and 2

Locality.— Middle Miocene fresh water Pegu Beds, Thanbingan, central Myanmar

Geographical distribution.—Africa, Western Europe, India, China, Myanmar, Thailand

Materials.— MUDG-V 1046, right maxilla fragment with P^{3-4}; MUDG-V 1128, right M^3; MUDG-V 1131, Left M^3; MUDG-V 1132, Right M^3; MUDG-V 1134; left M^3; MUDG-V 1040, right M_3; MUDG-V 1035, right mandibular fragment with M_{2-3}

Diagnosis.— Short nasal; horn absent; large-size rhinoceroses; large upper incisor and brachyodont cheek teeth; upper premolar molariform; ectoloph flattened behind parastyle fold; moderate antecrochet; slight protocone constricton; lower canines present, Ectolophid groove in lower molar usually flattend out. Trigonoid is rounded, apparently U-shape. Lingual cingulum mostly absent.

Description.— In MUDG- V 1046, premolars are worn and show molariform. Both buccal and lingual cingula are absent. Sligth protocone constriction is observed on P^4. There is neither crochet nor antecrochet. Parastyle and parastyle fold are observed on these teeth.

In MUDG-V- 1128, posterior portion of ectometaloph is lost, and is moderately worn. Molar crochet and molar crista are present on both teeth, and there is no molar antecrochet. Trace of constriction can be observed at the base of protoloph. Median valley is wide, and there are no tubercles at the entrance.

MUDG- V 1134 shows similar characteristics with MUDG-V 1128. Trace of poster cingulum is visible, and posterior end of the ectometaloph is pointed in this specimen. Metacone bulge can be observed on both specimens.

In MUDG- V 1131, teeth are worn down, and paracone is lost. Crochet can be observed, and trace of antecrochet is also visible. Molar crista is absent in this specimen. There is a slight protocone constriction. Anterior cingulum is present, and tubercle is present at the entrance to the media valley. There is also a trace of posterior cingulum.

In MUDG- V 1132, the protocone portion of the teeth is already lost. The crochet is double, and crista can be observed. Antecrochet is also developed. The protocone constriction is slight. Although the lingual cingulum is absent, anterior cingulum and trace of posterior cingulum can be observed.

MUDG-V 1040 is isolated M_3, and it is unworn. Trigonid is rounded in occlusal view. Anterior valley is shallow. Hypolophid is long and posterior valley is relatively wide. Ectolophid groove is shallow and rounded. Cingulid is not observed on this tooth.

In MUDG-V 1035, teeth are so worn to show characteristics of trigonoid and talonid basin. However, rounded outline of both trigonid and talonid basins are visible in occlusal view. Ectolophid grooves are shallow and rounded Hypolophid. This specimen does not show trace of cingulid.

Comparison and Discussion

Brachypotherium is the common rhinoceroses in the Miocene of the Old World with several species, and survive until late Pliocene in East Africa (Hessig, 1989). In Asia, fossil materials of this genus have been recovered from the early to middle Miocene deposits of Indo-Pakistan, Nepal, China, Myanmar and Thailand (Hessig, 1972; West *et al*. 1978; Tong, 2001). This genus can be distinguished from the other middle Miocene rhinoceros by its greater size. Most of the specimens referred to this genus from the middle Miocene fresh water Pegu Beds are isolated teeth. The present specimens from Myanmar generally show the similar teeth size with *B. perimense* from the lower Siwalik (Figure 4).

Two isolated M^3 from the Myanmar, MUDG- V 1128 and V 1134 share the teleoceratines, *Aprotodon* of the middle Miocene of Siwalik in presence of crista although Myanmar specimens are larger in size. Other isolated teeth also show slightly different dental characteristics such as difference in degree of protocone constriction and presence or absence of antecrochet. These variations suggest that there are at least two species of rhinoceros are present in the middle Miocene of Myanmar. However, Forster-Cooper (1934) pointed out that strongly constricted protocone, a large antecrochet, a cingulum, etc., are features too widely spread to afford any safe guide to generic distinction. So, differences in dental characteristics are likely to be individual variation, and it is reasonable to assign these referred specimens to Teleoceratini, *B. premense* at present.

The dental characteristics of lower molars are consistent with the *B. perimense* from the middle Miocene Chinji Formation of Pakistan in long hypolophid and shallow lingual groove although M_2 of the Myanmar specimen are larger in size. The presence of *Brachyopotherium* in Myanmar suggests the Southeast Asia and India and Pakistan are in the same biogeographic province since the middle Miocene.

Order PERISSODACTYLA Owen, 1848

Family RHINOCEROTIDAE Owen, 1845

Subfamily RHINOCEROTINAE Owen, 1845

Tribe RHINOCEROTINII Owen, 1845

Genus *Gaindartherim* Colbert, 1934

cf. *Gaindartherium* Cobert, 1934

Plate 4

Diagnosis.— Single nasal horned, medium size rhinoceros; brachyodont, simple molar teeth without antecrochet and crista; the crochet slighthly developed; the vertical occiput; the postglenoid and posttympanic are fused.

Locality.— Middle Miocene fresh water Pegu Beds in central Myanmar

Geographical distribution.— Indian subcontinent, China, Thailand, Myanmar

Material.— MUDG-V 1130, right mandibular fragement with M_2 and M_3

Description.— The mandible is cracked, and anterior part of trigonid of M_2 and hypolophid of M_3 is crushed. In M_2, the crown is worn out, and anterior and posterior valleys are invisible. Ectolophid groove is deep and show V-shape in occlusal view. M3 also show V shape ectolophid groove in occlusal view. Cingulid are absent on the teeth.

Discussion.— The rhinocerotid materials attributed *Gaindartherium* have been reported from the middle Miocene Chinji Formation of Indo-Pakistan, Thailand and China (Cobert, 1935; Hessig, 1972; Ducrocq, 1994, Tong, 2001).

Colbert (1934) suggested that *Gaindartherium* is the direct ancestor of the *Rhinoceros*. Howerver, Hessig (1972) argued that it is likely to be forebear of the *R. unicornis*, and "*Eurhinoceros" sondaicus* (=*R. sondaicus*) have already separated from this lineage. Moreover, absence of I_1 in *Gaindartherium* hamper its affinity with the *Rhinoceros* (Groves, 1983). According to the cladistics analysis of Cerdeno (1990), it is closer to *Dicerorhinus* (*Latetotherium*) than *Rhinoceros*.

The present specimen is similar to Siwalik specimens in having deep ectolophid groove, and relatively broad transverse width compared with anteroposterior length. However, the present specimen is provisionally assigned to *Gaindarthrium* due to the poor preservation and fragmentary material.

Order PERISSODACTYLA Owen, 1848

Family RHINOCEROTIDAE Owen, 1845

Subfamily RHINOCEROTINIAE Owen, 1845

Tribe RHINOCEROTINI Owen, 1845

Subtribe DICERORHINA Ringstrom, 1924

Genus *Dicerorhinus* Gloger, 1841

Dicerorhinus sp. Gloger 1841

Plate 5

Material.—NMMP-KU-IR 0469. A skull

Locality.—Early Pleistocene upper Irrawaddy Group at Seikphyu, central Myanmar

Geographic distribution.— Middle-Miocene to Pleistocen deposits of Europe, Africa and Asia

Diagnosis.— Rhinoceros with nasal and frontal horns; dolichocephalic skull; elongated occipital plane incline backward or nearly vertical; brachyodont–subhyposodont teeth; weak crochet and absence of antecrochet and crista; protocone fold present on upper molars. Metacone bulge on M^3

Description.— Occiput is covered with matrix. Cranium is curshed and is filled with small pebble and sands. Some part of the palate is also covered with matrix. Distortion of the skull is visible on the ventral view. The profile of the skull is long and concave, and occipital plane is nearly vertical. The nasal bone is convex and rugose, and indicates presence of horn. Frontal bone is lost, and it is impossible to confirm the presence of second horn. Nasal incision is above P^3 and ossification of nasal septum is apparently absence. Anterior margin of the orbit is situated between M^1 and M^2. Zygomatic arches are also broken, and anterior end of the zygomatic arches is apparently above M2. Both of premaxillaries are lost. All cheek teeth are nearly worn out indicating the skull of an old adult. Moreover, ectoloph are totally or partly lost in all teeth. On all upper cheek teeth, the lingual cingula are absent; protocone constrictions are absent; and medifossette are visible. All premolars are nearly worn out to show other characteristics. Similarly, molars are worn out, but some characteristics are still visible. Protocone folds are present on M^2, and crochets are observed on left M^2 and M^3. Small molar crochet is visible on the Left M^3. On the right molars, M^3 is already lost. M^1 is deeply worn out to show any characteristics. In M^2, prtocone bulge and postfossette are observed.

Comparison and Discussion

The skull from the Myanmar shows nearly vertical occipt, long and concave view in dorsal profile, and simple cheek teeth. Although the presence of second frontal horn is doubtful, the above characteristics clearly show its closed affinity with *Dicerorhinus*. The presence of horn and absence of protocone constriction on cheek teeth exclude this skull from the affinity with Aceratherinii rhinoceros. In this specimen, the skull is doliocephalic, and anterior margin of the orbit is approximately located at the middle part of the skull. The length of the occiput to the anterior part of the orbit is nearly equal to that of the tip of nasal to the anterior part of the orbit. This characteristic clearly distinguishes it from the *Rhinoceros* in which the skull is brachycephalic; the occiput incline forward; and the length of occiput to the anterior part of the orbit is longer. It shares some characteristic with *Gaindartherium* in long saddle shape and nearly vertical or slightly inclined forward occiput, but the former possess larger skull proportion than latter.

Although most of the teeth are nearly worn out, crochet and protocone fold are observed at left M^2 and M^3. Lingual cingulum is absent, and backward extension of protoloph is observed in molars. Postfossette retain on all teeth. These dental characteristics are observed both on *Rhinocerose* and *Dicerorhinus*. However, the skull characteristics clearly indicate its affinity with *Dicerorhinus.*

The extant species, *D. sumatrensis* is still living in the rain forest of Southeast Asian region. *Dicerorhinus* was first recorded from the early Miocene of France. It was a dominant genus in Europe, Africa and Eastern Asia with several species, and survived until the Middle to late Pleistocene. However, most of the extinct species are placed in the genus, *Dicerorhinus*, and this genus becomes wastebasket taxon.

In Asia, *D. abeli* from the middle Miocene Chinji Formation of Siwalik Group, *D. ringstroemi* and *D. orientalis* from the Vallesian and Turolian of China were recorded respectively (Prothero, 1989). During the Plio-Pleistocene period, this genus had undergone many changes like loss of incisor, acquisition of nasal septum, and increased hyposodonty with complex enamel patterns. Severe climate condition brought the steppe-adapted species, *D. hemitoecus* and the larger *D. kircbergensis* in Europe, and *D. choukotiensis* and *D. yunchuchensis in* China (Hessig, 1989).

Kretzoi (1942) assigned the temperate zone *Dicerorhinus* to a new genus, *Stephanorhinus,* steppe rhinoceros. Grooves and Kurt (1972) divided this genus into primitive group and specialized group. The extant species is included in the primitive form as it retains low, forwardly inclined occipit and anterior dentition, and it is closely related to *D. sansaniensis* and other Miocene species. The specialized group shows long upwardly or backwardly inclined occipital crest, and reduce or absence of anterior dentition. This group consist of large steppe adapted rhinoceroses of Pleistocene, and it is closely related to wooly rhinocerose, *Coelodonta*. Groves (1983) pointed out that temperate-zone Plio-Pleistocene *Dicerorhinus* is closer to *Rhinocerose* in the firm fusion of postglenoid and post-tympanic, the great mastoid inflation, and the strong molarization of premolars, and supported assignment of new genus *Stephanorhinus.*

The fossil record of this genus is rather poor in Southeast Asian region except the sub fossil teeth from the Padaung caves of Sumatra, late Pleistocene and early Holocene remains from Sarawak of Malaysia and Thailand (Hooijer, 1946; Medway, 1966; Tougard, 2000). The discovery of this species in the early Pleistocene deposits fills the chronological and geological gap of this lineage in the Southeast Asia.

The present specimen is smaller than Pleistocene "*Dicerorhinus*" (=*Stephenorhinus*) from Europe and Eastern Asia in skull proportion. However, the occiput is higher than *D. mercki* from Europe and Eastern Asia. The length of the occipital crest to tip of the nasal of the present specimen is shorter than that of extant *Dicerorhinus* in maximum length. However, Myanmar specimen shows the higher occipital crest than the extant one. The width of the nasal bone is smaller than the minimum size of the extant one, indicating the presence of small nasal hornn. This fact also suggests it is likely to be a female. Measurerments of *Dicerorhinus* skull from Myanmar and other regions are given in Table 2.

In Southern Asia, the record of *Dicerorhinus* in the Plio-Pleistocene period is absent, and the generic status of *D. abeli* from middle Miocene Chinji Formation is questionable. Moreover, the present specimen is different from *D. abeli* in dental characteristics such as absence of antecrochet and weak cingulm. In contrast, there are several species of *Dicerorhinus* from the Plio-Pleistocene of the Eastern Asia, and some show similar characteristics with steppe rhinoceros in absence of incisor and in the fusion of postglenoid and post-tympanic process (eg. *D. choukoutienensis*). The specimen from Myanmar retains generally vertical occiput, and it suggests an affinity with a specialized group of Groves and Kurt (1972). However, the extant species also generally have vertical occiput. It also shares the other cranial characteristics with extant species in the presence of the anterior part of the orbit above M^2, nasal incision above P^3, and convex and rugose nasal bone. Although the presence of anterior dentition is questionable, dental characteristics of present specimen closely resemble the extant *Dicerorhinus sumatrensis* in the presence of simple enamel pattern on molars.

Due to the lack of the valid fossil record from the Southern Asia, it can be generally assumed that *Dicerorhinus* from the Plio-Pleistocene of Myanmar and extant species is likely to have an affinity with the primitive group of Eastern Asian *Dicerorhinus*. It also suggests that *Dicerorhinus* migrated into mainland Southeast Asia in the Pliocene or early Pleistocene from the eastern Asia, and dispersed into island Southeast Asia during the middle Pleistocene. However, the phylogenetic position of the Eastern Aisan *Dicerorhinus* is not well understood yet, and it is now difficult to evaluate the phylogenetic relationships of the extant species and Eastern Asian *Dicerorhinus*.

Order PERISSODACTYLA Owen, 1848

Family RHINOCEROTIDAE Owen, 1845

Subfamily RHINOCEROTINI Owen, 1845

Tribe RHINOCEROTINI Owen, 1845

Subtribe RHINOCEROTINA Owen, 1845

Genus *Rhinoceros* Linnaeus, 1758

Rhinoceros sivalensis Falconer and Cautley, 1847

Plate 6

Materials.— NMMP-KU-IR 0407, Right maxilla with P3-M2 (Jugual), Mgw-0002, right mandible with M1 to M2 and M3 in erupting stage

Locality.— Early Pleistocene upper Irrawaddy Group, Pauk, central Myanmar

Geographical distribution.— Miocene- Plesitocene deposits of Indian Subcontinet, China and Myanmar

Diagnosis.— Large species of a single nasal horned Rhinoceros; high occipial crest inclined forward; Molars with parastylefold; distinct crochet which unite with may unite with the protoloph to form medifossette; absence of crista and lingual cingulum; protocone fold presence.

Description.— In IR 0407, anterior part of the zygomatic arch is still retained, and anterior end of arch is situated above M^1. All teeth are relatively worn out, but show hypsodonty. In P^3, parastyle fold is broken. Only trace of crochet is observed in the median valley. Anterior and posterior cingula are present. Posterior valley is closed, and postfossette is observed. In P^4, there is a strong parastyle, and parastyle fold goes down at the base of the teeth. Posterior part of the Ectoloph is straight, and metastyle folds are absent on all molars. Weak crochet occurs at the median valley. Small tubercles are present at the entrance of median valley. The posterior valley is still open but apparently tends to occur posstfossette. In M^1, parastyle is weak compared to P^3 and P^4, and parastyle fold is terminated above the base of the crown. The median valley is wide, and small tubercles are observed at the entrance to the valley. Double crochet tends to occur on the metaloph. Trace of protocone folds is observed on both M^1 and M^2. In M^2, part of ectoloph and metaloph are lost, but presence of crochet can be visisble. There are weak backward extensions of protocone on all teeth.

Comaparison and Discussion

R. sivalensis is the common fossils in the Neogene sediments of Indian subcontinent. It share the cranial and dental morphology with the Indian rhinoceroses, *R. unicornis* in the the large horn boss, the deep saddle shape cranial profile, rather flat ectoloph, and prsence of parastyle and parastyle fold and it is likely to be direct ancestor of *R. unicornis* (Colbert, 1942). However this species was first recorded in the lower Miocene deposits of Western Sind (Blanford, 1876), it is common in Plio-Pleistocene deposits of Indian subcontinent, Myanmar and China.

Dental characteristics of present specimen are closely related to genus *Rhinoceros* in presence of strong parastyle fold; backward extension of protoloph; presence of crochet, absence crista and antecrochet. Absence of protocone constriction omits its affinity with large hornless aceratherinii rhinoceros. The present specimen differs from the *R. sinensis* of China by larger in size; absence of strong crochet and crista or small enamel projection into meidfossette, and in having hyposodont molars.

Rhinoceros sondaicus is distinct from present specimen in having smaller in size; presence of sinuous ectoloph and presence of moderately developed crista. This specimen shares the Plio-Pleistocene *Rhinoceros sivalensis* from Indo-Pakistan in large molar size among genus *Rhinoceros*; presence of parastyle and parastyle fold and in having straight ectoloph behind parastyle fold. However, Myanmar specimen shows weak molar crochet。 These differences are within the limit of individual variation, and Plio-Pleistocene extension of this gigantic rhinoceros, *Rhinoceros sivalensis*, into Myanmar is undoubtful.

Order PERISSODACTYLA Owen, 1848

Family RHINOCEROTIDAE Owen, 1845

Subfamily RHINOCEROTINAE Owen, 1845

Tribe RHINOCEROTINI Owen, 1845

Subtribe RHINOCEROTINA Owen, 1845

Genus *Rhinoceros* Linnaeus, 1758

Rhinoceros sondaicus Desmarest, 1822

Plate 7 and 8

Locality.— Early Pleistocene Upper Irrawaddy Group, Pauk, central Myanmar.

Geographical distribution.— ?Late Miocene to recent of Indo-Pakistan, Nepal, China and Southeast Asia

Diagnosis.— Small single horned Asian Rhinoceroses. Occipial crest inclined forward; Molars with parastylefold; Distinct crochet which seldom unite protoloph ; absence of crista and lingual cingulum; Sinuous ectoloph behind the parastyle.

Materials.—NMMP-KU-IR 0404, a right maxilla with M^1-M^3; and NMMP-KU-IR 0408, a left maxilla with M^1-M^3

Description.—In NMMP-KU-IR 0404, the teeth are subhyposodont, and the crowns are moderately worn. The parastyle of M^1 and crown portion of M^3 are lost. M^1 and M^2 are roughly quadrate although M^3 is triangular in occlusal view. The crochet is moderately developed, and molar crista and antecrochet are absent. The parastyle fold is strong. On M^1, the protocone shows backward extension. On M^2, there is a wide median valley without protocone bulge and deeper mdian valley than posterior valley. The corchet of M^2 is stronger than that of M1 though there is no tendency to form medifossette. The anterior and posterior congula are well developed on all the molars although there is no lingual cingulum. The posterior cingulum is divided by a V-shaped incision, and shows crenulation. The ectoloph is concave in posterior part showing sinuosity.

In NMMP-KU-IR 0408, the teeth are roughly quadrate in occlusal view, and the crowns are moderately worn. M^3 has a triangular shaped outline, and a small antecrochet is observed. There is a moderately developed crochet on each molar, and these teeth lack crista and antecrochet. A small tubercle is present in posterior valley of M^1. The protocone bulge is absent, showing a wide and deep median valley. Tubercles are totally absent on all teeth. There is no protocone constriction as well as protocone fold. Ectoloph show convexity on posterior part of the ectoloph. The metastyle is relatively strong on M^1 and M^2, and there is no metacone bulge on all teeth.

Comparison and Discussion

Dental characteristics of these rhinocerotid materials from Myanmar are identical to those of *Rhinoceros sondaicus,* which has been reported from the middle Pleistocene to Recent of Java and Sumatra. They share the following dental characteristics: presence of the strong parastyle fold, concavity of the posterior part of the ectoloph showing sinuosity, absence of the crista and antecrochet, and presence of the moderately developed crochet (Hooijer, 1946; Pocock, 1945).

The present specimens are also similar to *Rhinoceros sinensis* from the Pleistocene of China in having the following characteristics: a backward extension on the protoloph, presence of the parastyle fold, and sinuosity of the ectoloph. However, *R. sinensis* differs from the Myanmar specimens in showing generally larger size, and in having more hypsodont molars, a stronger molar crochet, and crista or small enamel projection into medifossette (Colbert, 1942). *Rhinoceros sivalensis* from the Plio-Pleistocene of Indo-Pakistan is distinct from the fossil rhinoceros of Myanmar in having a disticnt crochet which may unite with the protoloph to enclose a fossette and in being larger in size (Colbert, 1942). Fossil and sub-fossil specimens of *Rhinoceros* show larger in molar size than recent ones (eg., the width of M^1 of an extinct R. sivalensis is about 80 mm; Colbert, 1935) (Figure. 5). The specimens from Myanmar also show the larger molar size than extant *R. sondaicus*, suggesting that body size dwarfing in this lineage occurred probably in the late Pleistocene or Holocene.

Rhinoceros unicornis from the middle Pleistocene to Recent of Java and India differs from the present specimens in presence of a flattened molar ectoloph and of a well-developed molar crista, which unites with crochet to form medifossette (Laurie *et al*., 1983). The fossil rhinoceros from Myanmar shares some primitive characteristics with the late Miocene genus *Gaindatherium* from the Siwaliks of Indo-Pakistan, such as sinuosity of the ectoloph and the prominent parastyle fold. However, it is larger in size than *Gaindatherium* (Colbert, 1934; 1938).

Colbert (1942) compared the cranial and dental characteristics of *Rhinoceros sondaicus* with *Gaindatherium*, and suggested that *R. sondaicus* is morphologically primitive among extinct and extant *Rhinoceros* although its remains have been recovered from the middle and late Pleistocene of Asia. He assumed that *Gaindartherium* is a direct ancestor of Asian one-honrned Rhinoceros. However Groves (1983) pointing out an autapomorphic character, lost of I_1, in Gaindartherium and ruled out Colbert`s hypothesis. The cladistics analysis of Cerdeno (1995) revealed that *Gaindartherium* has closer affanity with *Latertotherium* (=*Dicerorhinus sansaniensis*) from the early

Miocene of Europe. On the other hand, Hessig (1972; 1973; 1981) recognized dental materials of *R. sondaicus* together with the other two Asian genera in the Lower Siwalik deposits (middle to late Miocene), and suggests *Gaindaertherium* is a forebear of the restricted genus *Rhinoceros unicornis* and its relatives. He used the term of Gray (1867) "*Eurhinoceros*" for *R. sondaicus*, and assumed that Javan Rhinoceros was evolved in parallel with *R. unicornis* from a common ancestor. His identification of *R. sondaicus* form the lower Siwalik group is based upon the isolated teeth, and there is no citation of the occurrence of this species in late Miocene or older deposits in his later work (1989).

At present, undisputable fossil remains of *R. sondaicus* have been recorded from the middle Pleistocene Djetis Bed and Trinil Bed of Java (Hooijer, 1957), and the middle to lat Pleistocene deposits of China and South east Asian region (Tougard, 2001). Therefore, the discovery of *Rhinoceros sondaicus* from the early Pleistocene of Myanmar suggests this species originated as early as the early Pleistocene in continental Asia, and its possible migration to island Southeast Asia during the late early Pleistocene and later ages. If Hessig`s indentification of *R. sondaicus* from the lower Siwalik is true, this species might originated in continental Asia in the middle or late Miocene.

8. Paleoecology

8 species of rhinoceroses are recorded from the Neogene of Myanmar. The species from the middle Miocene generally show simple, brachyodont cheek teeth, and suggest the habitat of the rain forest. *Brachypotherim* is a conservative genus in teeth and limbs shortening. Its cheek teeth are broad and brachydont suggesting a diet of soft plants (Hessig, 1999). However, dental wear analysis suggest mixed feeder (Fortelius, 1990; Fortelius and Solounias, 2000). In Myanmar, this genus has been found together with *Prodeinotherium* and gomphothere which have the preference for the forest habitat. This co-occurence suggests an intermediate environment between the rain forests and steppe for this genus (Hessig, 1996). *Gaindartherium* is a medium size rhinoceros and possess simple brachyodont cheek teeth, and is likely to be browser. *Aceratherium* also possess brachyodont cheek teeth, indicating that the genus browsed mainly upon shrub leaves, and was adapted to shrubby wood land (Qiu et., al 1982). Generally, it can be assumed that woodland or forested environment for the middle Miocene rhinoceros.

From the late Miocene onwards, the rhinoceros belonging to same genera with extant one appeared, and the ecology of the extant rhinoceros is a good indicator for paleoenviroment of their extinct counterpart. *R. sivalensis* is a large size rhinoceros, and its upper cheek teeth show a rather flat extoclph surface like the extant *R. unicornis* which prefers swampy floodplains and, is mainly grazer (Prothero and Schoch, 2002). In contrast, *R. sondaicus* lives in dense tropical jungles where it feeds on a variety of leaves and shrubs. Its upper cheek teeth shows saw-toothed ectoloph wear profile and it also suggests the habitant of forest (Fortelius, 1982). The extant *Dicerorhinus* inhabits in the tropical rain forest and, it is believed that its extinct counterparts prefer same environment. Its upper cheek teeth also show saw-toothed ectoloph wear profile and it is also considered to be a woodland dweller. So it can be considered that the forest associated flood plain environment for the rhinoceros from the late Miocene to Pleistocene.

9. Conclusion

6 genera and 8 species of fossil Rhinocerotidae are recorded from the Neogene sediments of Myanmar. The generic status of two genera, *Diceratherium* and *Aceratherium* are uncertain due to unavailability of the fossil materials of previous researchers, and lack of the new specimens in present study.

Fossil materials of *Brachypotherum* and cf. *Gaindartherium* are recovered from the middle Miocene fresh water Pegu Beds. These specimens show close resemblance with those known from the Indian Subcontinent in dental characteristics and size. It supports that South East Asia and Southern Asia were part of the same biogeographic province since the middle Miocene.

Rhinoceros and *Dicerorhinus* which belong to the same genera with the extant Asiastic rhinoceros are discovered from the late Miocene to the early Pleistocene Irrawaddy Group. The fossil materials of extinct species, *R. sivalensis* are common fossil in the Neogene of Indian subcontinent and, this species likely migrated into Myanmar as early as the late Miocene. In contrast with the *R. sivlaensis,* the fossil materials of *R. sondaicus* are scarce, and the earliest fossil record is from the middle Pleistocene of Indonesia. The discovery of this species from the early Pleistocene deposit of suggests the Pliocene or early Pleistocene origin of this lineage in continental Asia, and its possible migration into island Southeast Asia during the late early Pleistocene and later ages.

Dicerorhinus from the early Pleistocene of Myanmar shows similar cranial and dental characteristcs to extanct species, *D. sumatrensis*. Although *Dicerorhinu*s was widely distributed in the Africa and Europe and Eastern Asia from the early Miocene until Pleistocene, the valid fossil record of this lineage from the Neogene sediments of Southern Asia is absent. In the Southeast Asia, earliest fossil record is from the middle to late Pleistocene deposits. The discovery of Dicerorhinus from the early Pleistocene of Myanmar fills the chronological and geological gap of this lineage in Southeast Asia and suggests an affinity with the Eastern Asian Dicerorhinus. It can also be assumed that *Dicerorhinus* migrated into mainland Southeast Asia in the Pliocene or early Pleistocene, and dispersed into island Southeast Asia during the middle Pleistocene.

Generally, Neogene rhinoceros from Myanmar inhabited in the rain forest or woodland associated with flood plain environments like their extant counterparts.

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Plates

Plate 1. *Brachypothrium perimense*. MUDG-V 1046, right maxillary fragement with P^{3-4}

(a) occlusal view; (b) buccal view; (c) lingual view

Plate 1

(a)

(b)

(c)

50 mm

Plate 2. *Brachypotherium perimense*. A: MUDG-V 1128, right M^3. B: MUDG-V 1131, left M^3. C: MUDG-V 1132, Right M^3. D: MUDG-V 1134, right M^3. E: MUDG-V 1040, Right M_3 (a) occlusal view; (b) buccal view; (c) lingual view

Plate 2

A.

B.

C.

D.

E.

(a) (b) (c)

20 mm

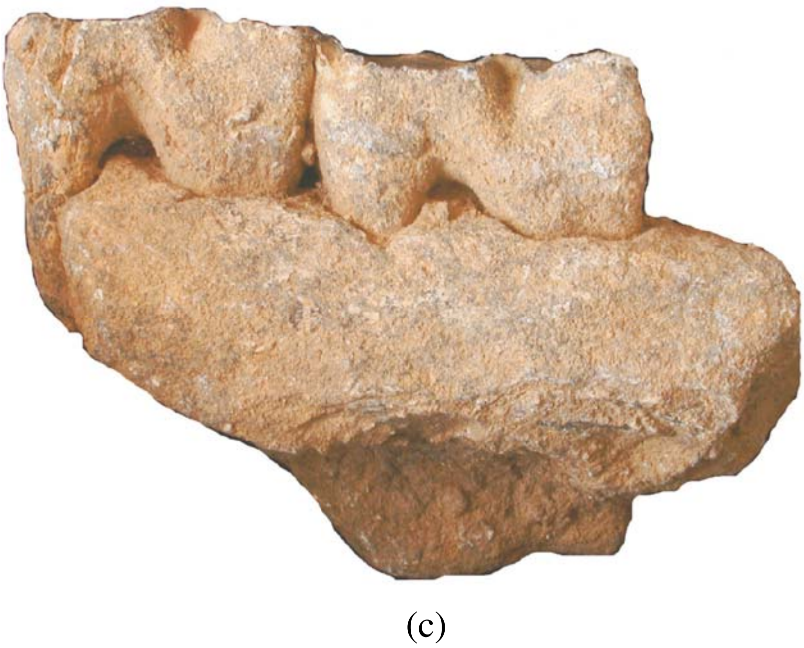
Plate 3. *Brachypotherim perimense*. MUDG-V 1035, right mandibular fragement with M_{2-3}

(a) occlusal view; (b) buccal view; (c) lingual view

Plate 3

(a)

(b)



(c)

40 mm

Plate 4. cf. *Gaindartherium*. MUDG-V 1130, right mandibular fragement with M_{2-3}

(a) occlusal view; (b) buccal view; (c) lingual view

Plate 4

(a)

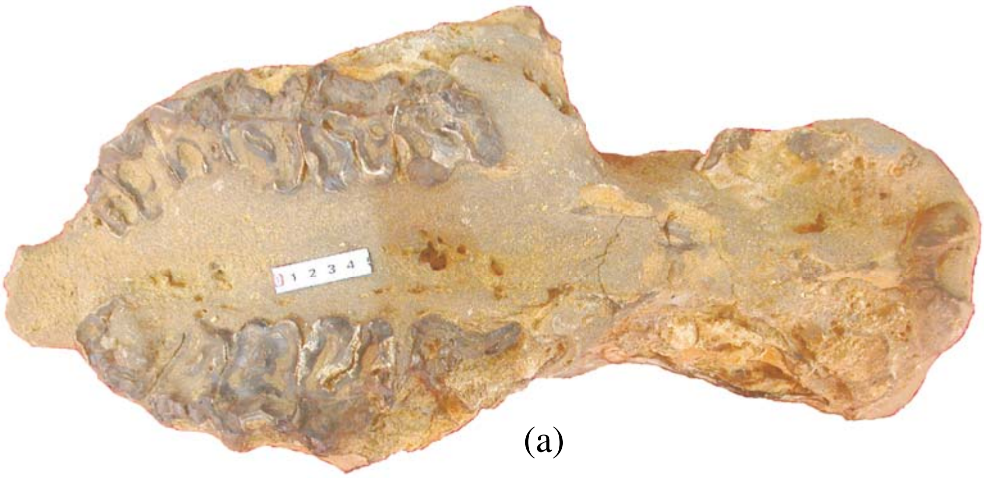
(b)

(c)

50 mm

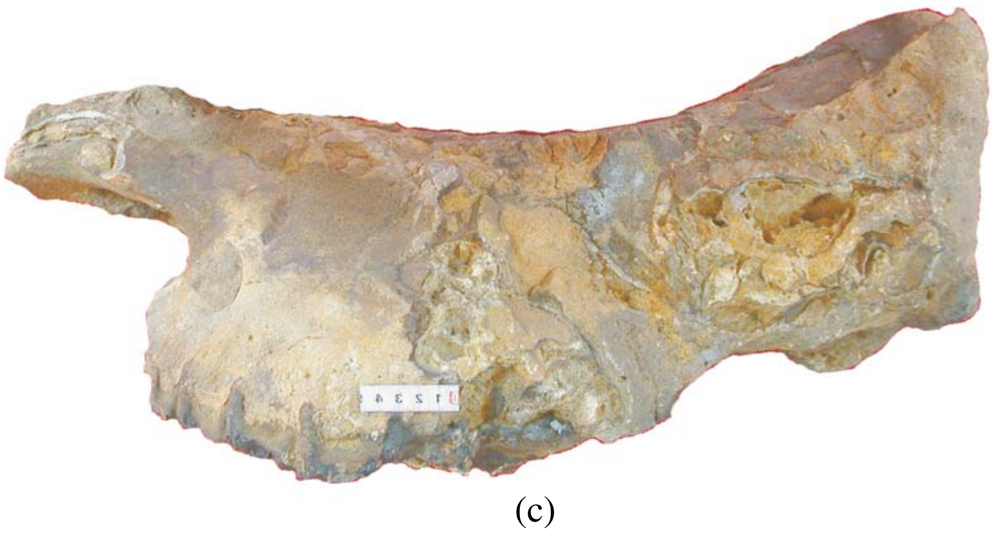
Plate 5. *Dicerorhinus*. NMMP-KU-IR 0469, a skull (a) ventral view (b) dorsal view (c) lateral view

Plate 5



(a)

(b)



(c)

50 mm

Plate 6. *Rhinoceros sivalensis*. NMMP-KU-IR 0407

(a) occlusal view; (b) buccal view; (c) lingual view

Plate 6

(a)

(b)

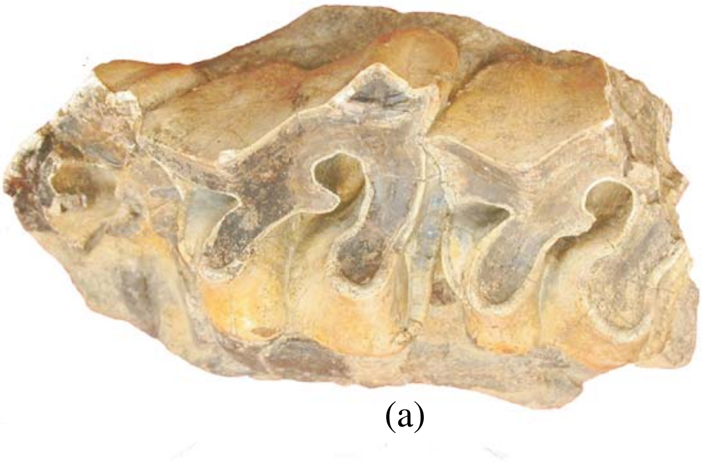
(c)

30 mm

Plate 7. *Rhinoceros sondaicus*. NMMP-KU-IR 0404, a right maxillary fragement with M^{1-3}

(a) occlusal view; (b) buccal view; (c) lingual view

Plate 7



(a)

(b)

(c)

40 mm

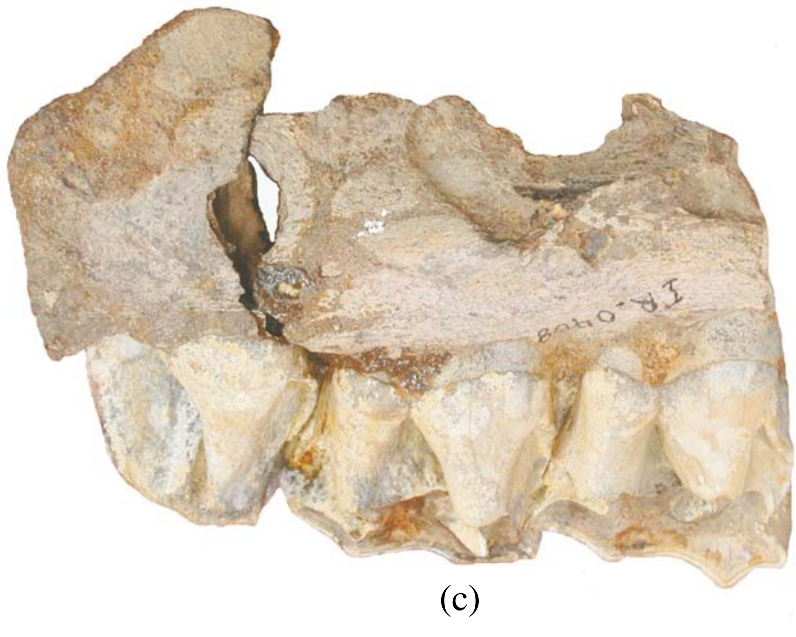
Plate 8. *Rhinoceros sondaicus*. NMMP-KU-IR 0408, a left maxillary fragement with M^{1-3}

(a) occlusal view; (b) buccal view; (c) lingual view

Plate 8

(a)

(b)



(c)

40 mm

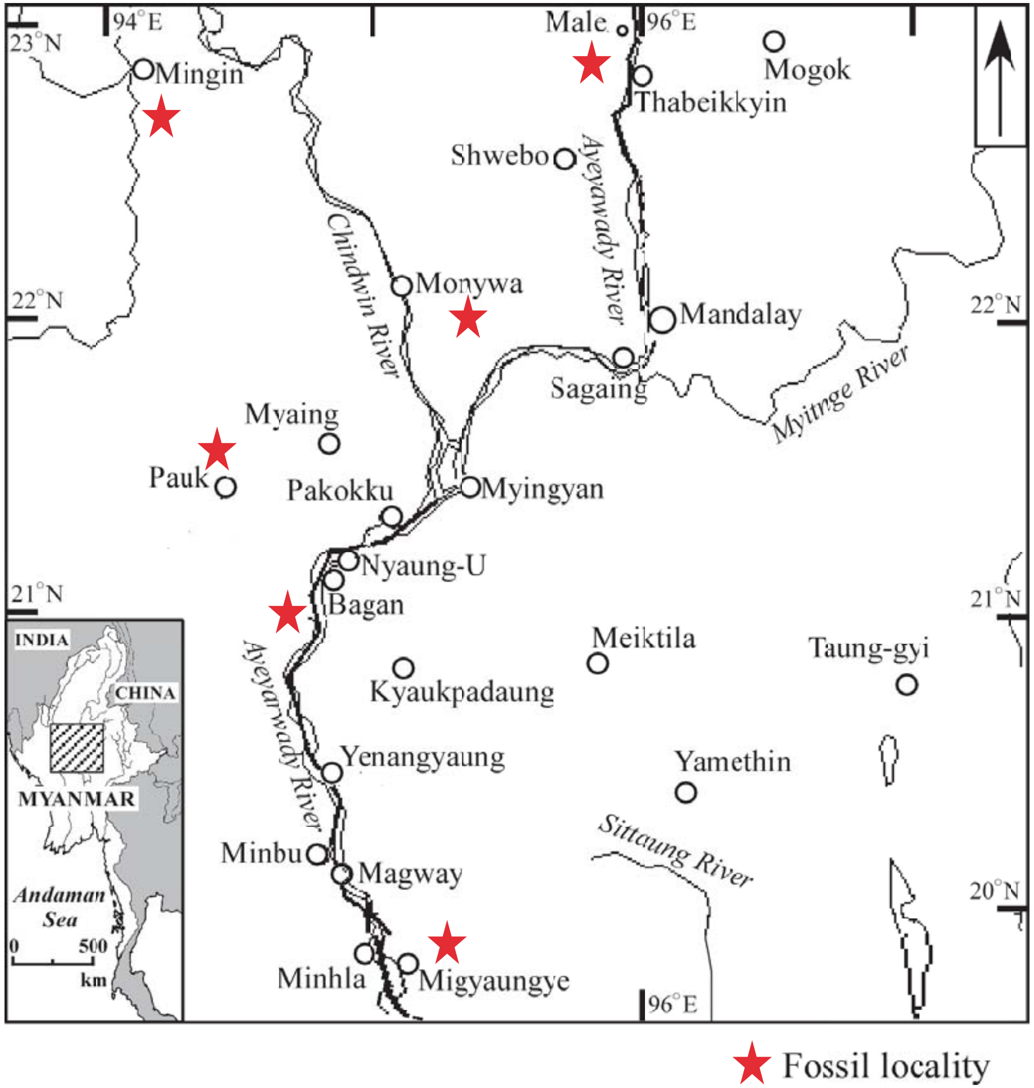


Figure 1. Map of Myanmar showing the Neogene fossil localities in central Myanmar

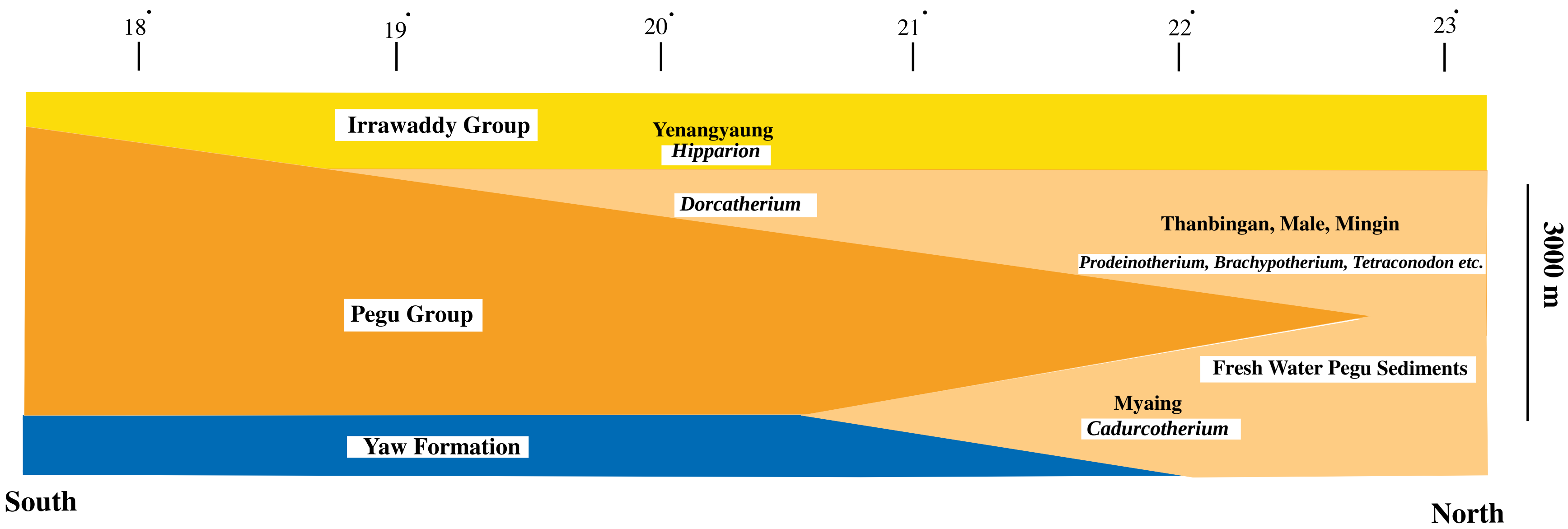


Figure 2. Generalized diagram of the stratigraphy of the Neogene deposits in Central Myanmar showing the relationship of the marine Pegu Group in the South and fresh water Pegu Sediments in the North. (modified after Stamp, 1922)

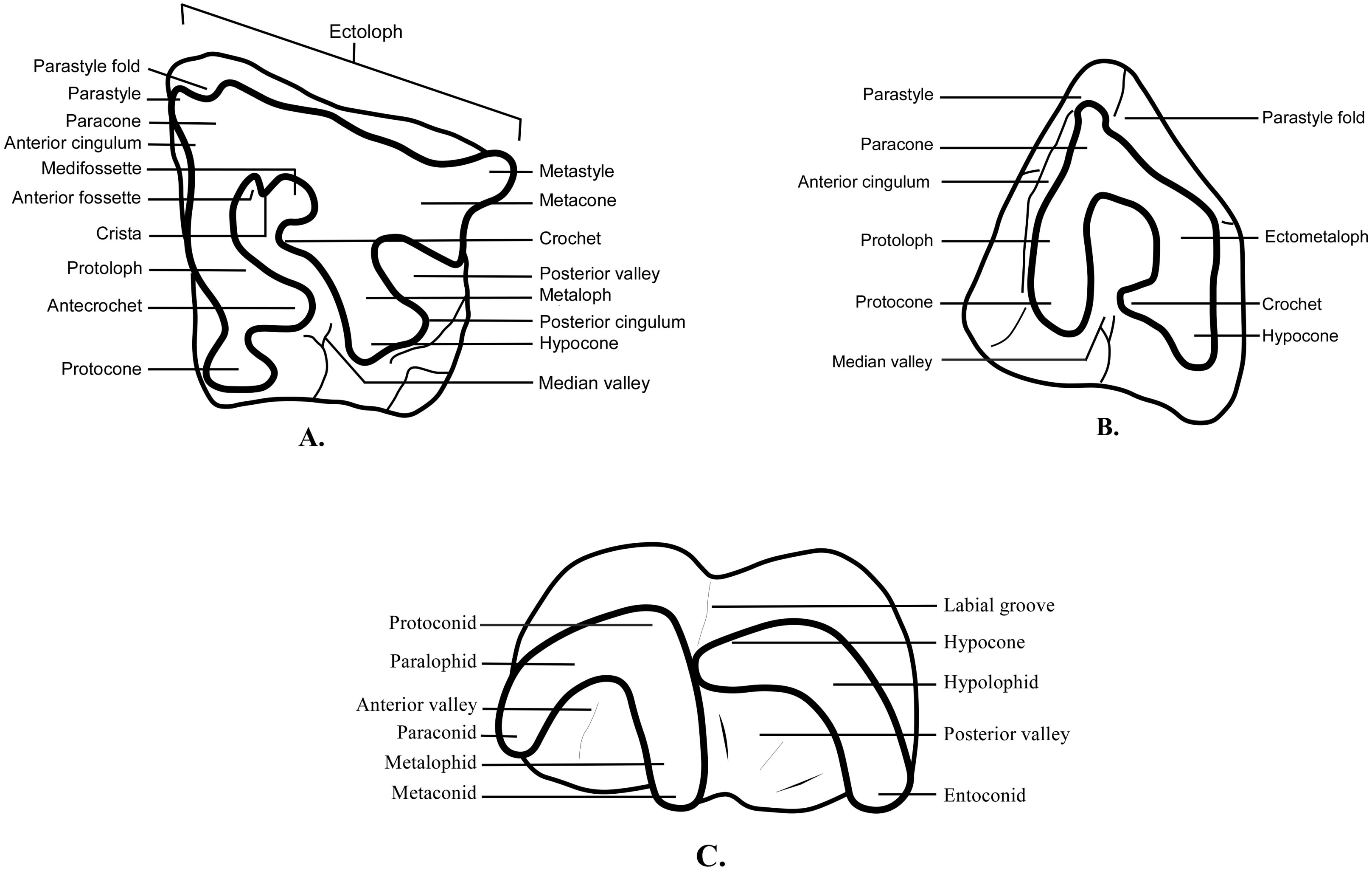


Figure 3. Dental terminology of the rhinoceros teeth, A. Right M^1; B. Right M^3; C. Right M_1 (After Guerin, 1980)

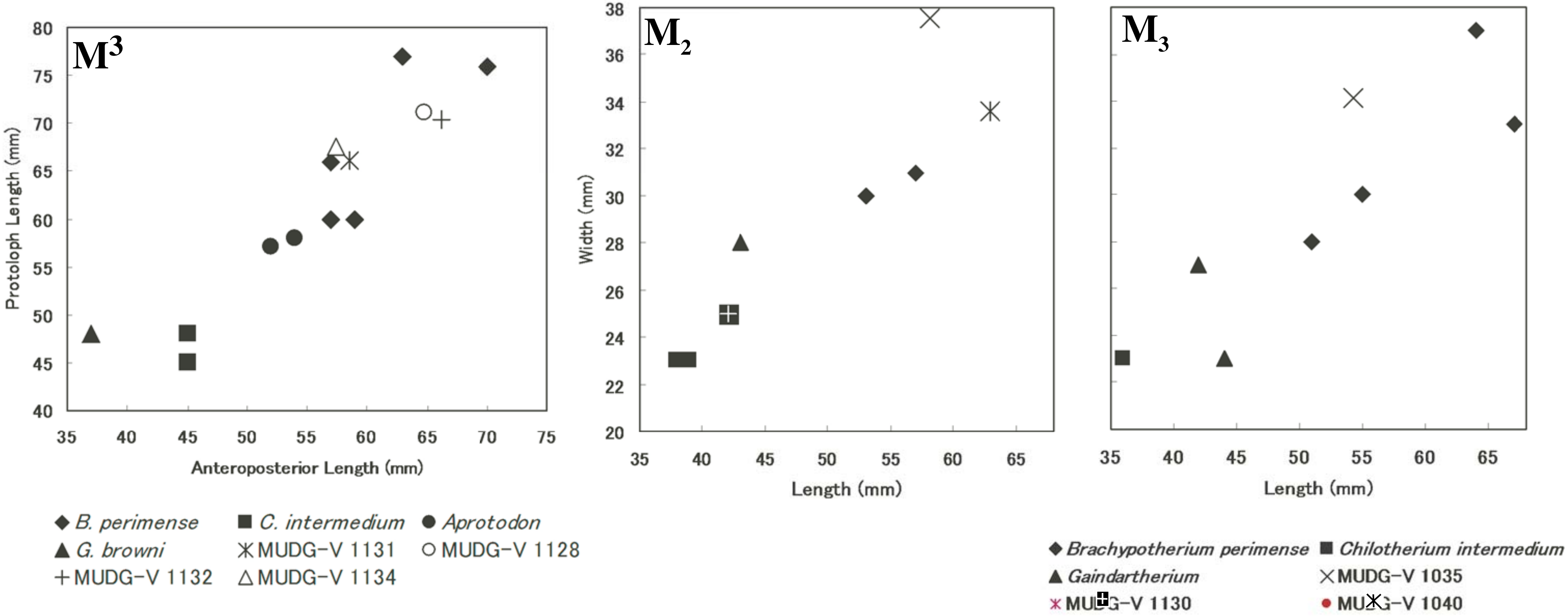


Figure 4. Molar size comparisons of the middle Miocene rhinoceros from Myanmar and Indian subcontinent.
(Measurements from Hessig, 1972)

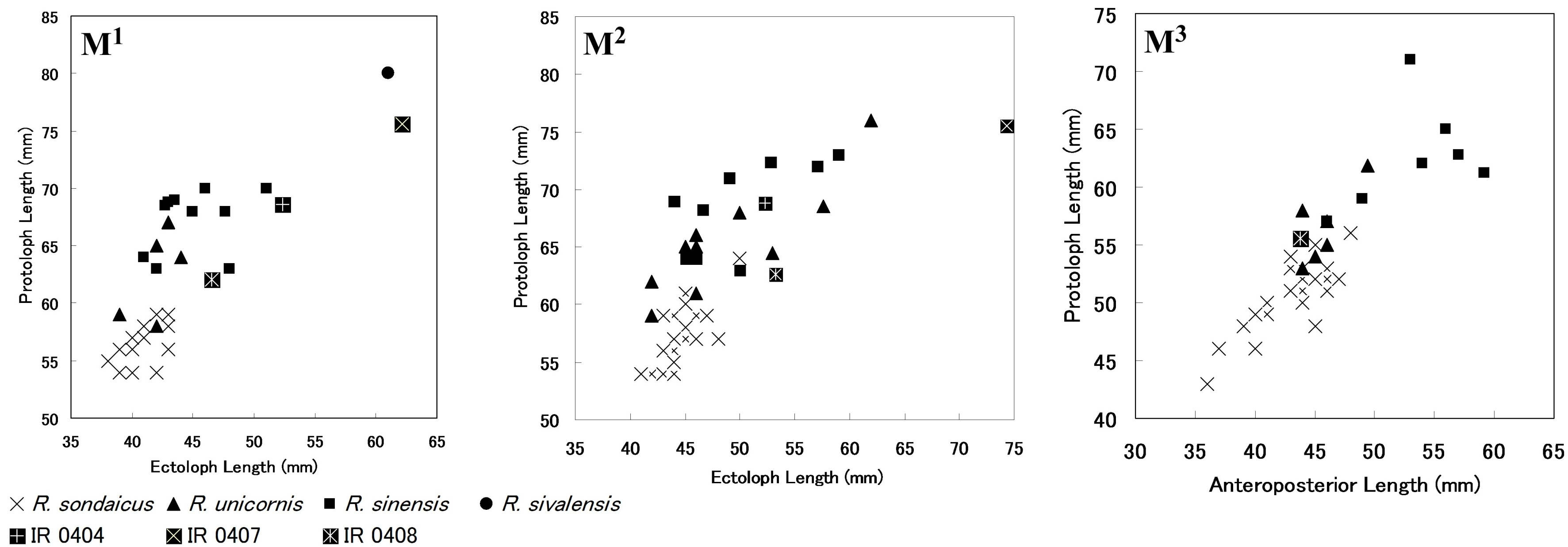


Figure 5. Molar size comparison between extinct and extant *Rhinoceros*.
(Measurements from Colbert,1935; Colbert& Hooijer, 1953 and Hooijer, 1946)

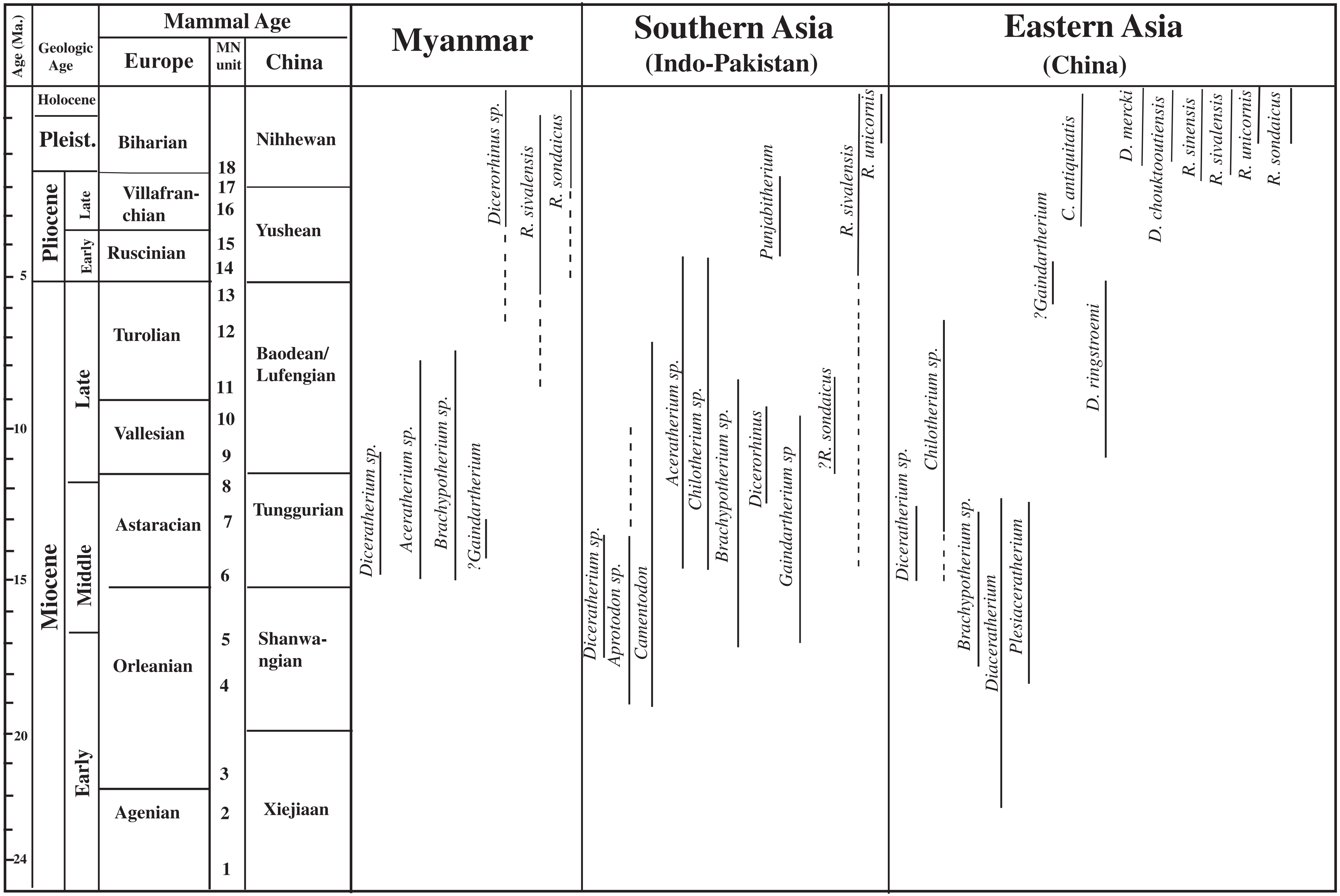


Table 1. Chronological distribution of the Neogene Rhinocerotidae in Myanmar and neighbouring regions

	Dicerorhinus. (IR 0469)	*D. sumatrensis* (Mean)	*D. sumatrensis* (Minimum)	*D. sumatrensis* (Maximum)	*D. mercki*	*D. sansaniensis*
Length, occipital condyle to nasal	570	539.82	490	581	708	
Length, occiput crest to tip of nasal	560	524.5	440	588	735	484*
Length, occiput to anterior part of orbit	300*	288.33	239	320	402	270
Length, anterior part of the orbit to notch of nasal	120*	113.63	98.5	247	112.5	95
Length, occipital condyle to M^3	220	224.31	182	247	320	220
Length, anterior part of the orbit to tip of nasal	280	263.84	225	296	362.5	226*
width of nasal	80	111.73	95	121.5	152.5	106.5
Height of the occiput	170	123.05	111	139	162.25	167
Height of the cranial above P^2	150	153.97	131	173	233	161
Height of the cranial above M^1	180	155.64	127	175	231	166
Height of the cranial above M^3	110	164.47	137	188	194	
Width of palate between P^2	32*	60.47	53.5	69		59.5
Width of the palate between M^1	60*	82.44	73.5	95	70	76.75
Width of the palate between M^3	65	80.16	68	94	82	69.5
Diameter of foramen magnum	30	42.03	33	51	55.83	44.5

Table 2. Cranial Measurements of *Dicerorhinus* from Myanmar and other regions (Measurements from Guerin, 1980). *= estimated measurements