Journal of Asian Earth Sciences 37 (2010) 154–165

Contents lists available at ScienceDirect

Journal of Asian Earth Sciences

journal homepage: www.elsevier.com/locate/jseaes

A review of fossil rhinoceroses from the Neogene of Myanmar with description of new specimens from the Irrawaddy Sediments

Zin-Maung-Maung-Thein [a,d,*], Masanaru Takai [a], Takehisa Tsubamoto [b], Naoko Egi [a], Thaung-Htike [c], Takeshi Nishimura [a], Maung-Maung [d], Zaw-Win [e]

[a] Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, Japan
[b] Center for Paleobiological Research, Hayashibara Biochemical Laboratories, Inc., Okayama 700-0907, Japan
[c] Shwebo Degree College, Shwebo, Myanmar
[d] Mandalay University, Mandalay, Myanmar
[e] Monywa University, Monywa, Myanmar

ARTICLE INFO

Article history:
Received 20 January 2009
Received in revised form 16 May 2009
Accepted 5 August 2009

Keywords:
Indian Subcontinent
Irrawaddy sediments
Myanmar
Neogene
Paleobiogeography
Rhinocerotidae
Southeast Asia

ABSTRACT

Four genera and one indeterminate genus (total eight species) of fossil rhinoceroses (Mammalia; Perissodactyla; Rhinocerotidae) are recognized from the Neogene of central Myanmar. In the early Miocene, most area of central Myanmar were under the shallow marine condition, and no rhinocerotid remain has been documented yet. During the middle to late Miocene, the rhinocerotid remains are commonly found and are represented by "*Diceratherium*" *naricum*, *Brachypotherium perimense*, *Brachypotherium fatehjangense* and an indeterminate rhinocerotid. In the latest Miocene, these archaic rhinoceroses became extinct. In the late Neogene, the extant genera, *Rhinoceros* (late Miocene to Pleistocene) and *Dicerorhinus* (Plio-Pleistocene) first appeared in Myanmar. They appear to have dispersed to the Island Southeast Asia from the continental Asia during the early Pleistocene to middle Pleistocene when the eustatic sea level became low remarkably.

1. Introduction

Rhinoceroses, the family Rhinocerotidae, currently inhabit in Africa and South and Southeast Asia, represented by four genera and five species (Nowak, 1999). In the fossil record, the family was widely distributed in Eurasia, North America and Africa. The rhinocerotids were well diversified in the late Eocene to the early Oligocene of North America, although they were still poorly documented in contemporaneous Eurasia (Prothero and Schoch, 2002; Antoine et al., 2003a). In the late Oligocene, they began to diverge into major subfamilies and became common land mammals in the Neogene fauna of Europe, Africa, North America and Asia (Carrol, 1988). During the Neogene, they were widely spread in Eurasia, North America and Africa, showing high taxonomic diversity in the fossil records (Prothero et al., 1989; Prothero and Schoch, 2002). In the Pliocene, they were extinct in North America, but some rhinoceroses survived the Pleistocene in Eurasia (Prothero and Schoch, 2002; Prothero, 2005).

Fossil remains of rhinoceroses are common in the Neogene of central Myanmar and several species have been recognized (Pilgrim, 1910a; Colbert, 1938, 1943; Cotter, 1938; Chavasseau et al., 2006; Zin-Maung-Maung-Thein et al., 2006, 2008). However, most of the descriptions on these specimens have been provisional due to the fragmentary nature of materials. Furthermore, there has been no revision on the Neogene fossil rhinoceroses of Myanmar since Colbert (1938). In this work, we review the fossil rhinoceroses from the Neogene of Myanmar, describing several new specimens recovered from the Irrawaddy sediments.

2. Geological setting

The terrestrial Neogene sediments are widely distributed along Irrawaddy (=Ayeyarwaddy) and Chindwin Rivers in the central part of Myanmar (Fig. 1). These sediments are mainly composed of fluviatile sediments and are characterized by the abundance of silicified fossil woods. They interfinger with the marine deposits of the Oligocene to Miocene Pegu Group (between 20° and 22° N) in the northern part of central Myanmar. The interfingering was caused by the marine transgression and regression during the Miocene and later periods (Stamp, 1922). The terrestrial Neogene sediments of Myanmar yield remains of many terrestrial and aquatic vertebrates. The geological ages of these sediments have been esti-

* Corresponding author. Tel.: +81 568 63 0536.
E-mail address: zinmaung@pri.kyoto-u.ac.jp (Zin-Maung-Maung-Thein).

1367-9120/$ - see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jseaes.2009.08.009

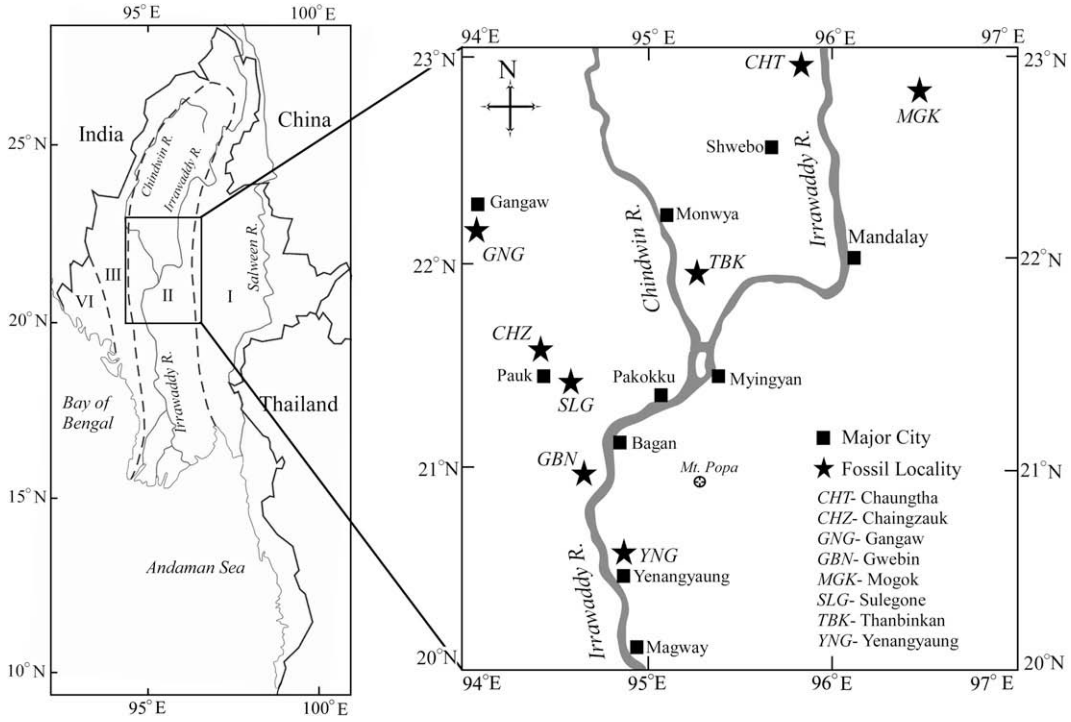

Fig. 1. Map of Myanmar, showing four major geological regions (left) and the fossil localities of rhinoceros in central Myanmar (right). I. Sino-Burman Ranges, II. Central Cenozoic Belt, III. Indo-Burman Ranges, IV. Arakan Coastal Plain.

mated on the basis of the correlation of vertebrate faunas to those of the Indian Subcontinent and China. However, at present, most of the mammalian fossils recovered from the terrestrial Neogene of Myanmar are fragmentary and the exact geological ages of these sediments have not been fully understood with confidence.

The terrestrial Neogene of Myanmar can be divided into three major units: in ascending order, the Freshwater Pegu Beds, Irrawaddy sediments and River Terrace Deposits (Fig. 2). Most of the fossil mammals from the Freshwater Pegu Beds show resemblances to those from the Kamlial and Chinji Formations of the Siwalik Group, suggesting an early to middle Miocene age (Takai et al., 2006). On the other hand, Colbert (1938) suggested an age of Oligocene through the late Miocene for Freshwater Pegu Beds on the basis of occurrence of the amynodont *Cadurcotherium*, the anthracothere *Telmatodon* sp., and the tragulid *Dorcatherium*. The Irrawaddy sediments are traditionally subdivided into upper and lower parts (Colbert, 1935; Bender, 1983). The Lower Irrawaddy sediments have been correlated to the Dhok Pathan Formation of the Siwalik Group, suggesting an age of the late Miocene to early Pliocene. However, the base of the Lower Irrawaddy sediments probably extends to the late middle Miocene because some taxa from the Lower Irrawaddy sediments, such as *Hemimeryx blanfordi*, *Brachypotheium fatehjangense*, *Siamotragulus* sp., and *Conohyus thailandicus* also occur in the Chinji Fauna of Indian Subcontinent (Bender, 1983; Chavasseau et al., 2006). The Upper Irrawaddy sediments have been conventionally referred to the early Pleistocene (Colbert, 1938, 1943; Bender, 1983). However, the Upper Irrawaddy fauna shows close resemblances to the Tatrot and Pinjor

Ma	Geological age		Myanmar		Indian Subcontinent	East Asia	Europe
	Pleistocene		River Terrace Deposits		Boulder conglomerate	Nihewanian	Biharian
	Pliocene	L	Irrawaddy sediments	Upper Irrawaddy	Pinjor		Villafranchian
		E			Tatrot	Yushean	Ruscinian
5	Miocene	L		Lower Irrawaddy	Dhok Pathan	Baodean/ Lufengian	Turolian
10					Nagri		Vallesian
		M			Chinji	Tunggurian	Astaracian
15			Freshwater Pegu Beds		Kamlial	Shanwangian	Orleanian
20		E			Dera Bugti	Xiejian	Agenian

Fig. 2. Stratigraphy of Neogene sediments in central Myanmar and their correlations to stratigraphy of the Indian Subcontinent and land mammal ages of East Asia and Europe.

faunas of the Indian Subcontinent, suggesting a late Pliocene to early Pleistocene correlation for the Upper Irrawaddy sediments. The River Terrace Deposits conformably overlie the Upper Irrawaddy sediments and probably correspond to the middle Pleistocene to Holocene (De Terra, 1943; Colbert, 1943). The fauna of the River Terrace Deposits contains many extant genera, but it includes some rewashed fossils from the Upper Irrawaddy sediments (Colbert, 1943).

3. Materials and methods

The specimens described here are housed in the National Museum of Myanmar, Department of Archaeology (South Branch), and Yangon University, all of which are located in Yangon, Myanmar. The taxonomy used in this paper follows that of Prothero and Schoch (1989). The terminology of anatomical designations and corresponding measurements generally follow the convention by Guérin (1980) (Fig. 3). *Institutional abbreviations*. NMMP–KU–IR = National Museum of Myanmar Paleontology–Kyoto University (Japan)–Irrawaddy; DA–MC = Department of Archaeology–Ministry of Culture, Yangon, Myanmar. *Anatomical abbreviations*. I1/, first upper incisor; P1/, first upper premolar; M1/, first upper molar; I/1, first lower incisor; P/1, first lower premolar; M/1, first lower molar.

4. Systematic paleontology

Order Perissodactyla Owen, 1848
Family Rhinocerotidae Owen, 1845
Rhinocerotidae indet. Chavasseau et al., 2006

Comment: Chavasseau et al. (2006) described two dento-gnathic specimens of an indeterminate juvenile rhinocerotid from the middle Miocene Chaungtha locality in northern part of central Myanmar (Fig. 1). The referred specimens are distinguished from the contemporaneous species at Chaungtha, *B. fatehjangense* in the presence of a well-developed paraconid in P/2 and comparatively small teeth size. In the middle Miocene of South and Southeast Asia, there are several rhinoceros genera that will be available for comparison and taxonomic assignment for these specimens. However, the dental characteristics brought by the deciduous teeth do not provide much information for a reliable taxonomic assignment (e.g. Antoine, 2002b) and we thus prefer to treat these specimens as an indeterminate rhinocerotid.

Subfamily Diceratheriinae Dollo, 1885
Genus "*Diceratherium*" Marsh, 1875
"*Diceratherium*" *naricum* Pilgrim, 1912

Discussion: In Myanmar, "*Diceratherium*" *naricum* has been reported from the middle Miocene Maw Beds (equivalent to Freshwater Pegu Beds) in Gangaw of Magway Division (Fig. 1) by Cotter (1938). *Diceratherium* was distributed in the late Oligocene to the middle Miocene of North America (Prothero, 2005), from the middle to late Miocene of China (Tong, 2001), from the late Oligocene to early Miocene of western Europe (Heissig, 1999) and from the early Miocene portion of Bugti Hills of Pakistan (Welcomme et al., 2001). However, it has been suggested that Asian diceratheriines are different from North American *Diceratherium* and the formerly described specimens of this genus from northern China may correspond to the aceratheriine rhinoceroses (Bohlin, 1937; Qiu and Yan, 1982). Moreover, *Diceratherium naricum* from the early Miocene portion of Bugti Hills has been referred as *Plesiaceratherium naricum* (Welcomme et al., 2001; Métais et al., 2009). Therefore, there is a possibility that the reported specimens of "*Diceratherium*" *naricum* from the Maw Beds of Myanmar also belong to the Aceratheriinae and the phylogenetic status of Myanmar *Diceratherium* should be revised here. However, Cotter (1938) provided neither systematic description nor relevant figure, and did not mention the depository of the referred specimens. Consequently, it is difficult to assess the validity of "*Diceratherium*" *naricum* and we tentatively list this genus and species in the Myanmar fauna with double quotation marks.

Subfamily Aceratheriinae Dollo, 1885
Tribe Teleoceratini Hay, 1902
Genus *Brachypotherium* Roger, 1904

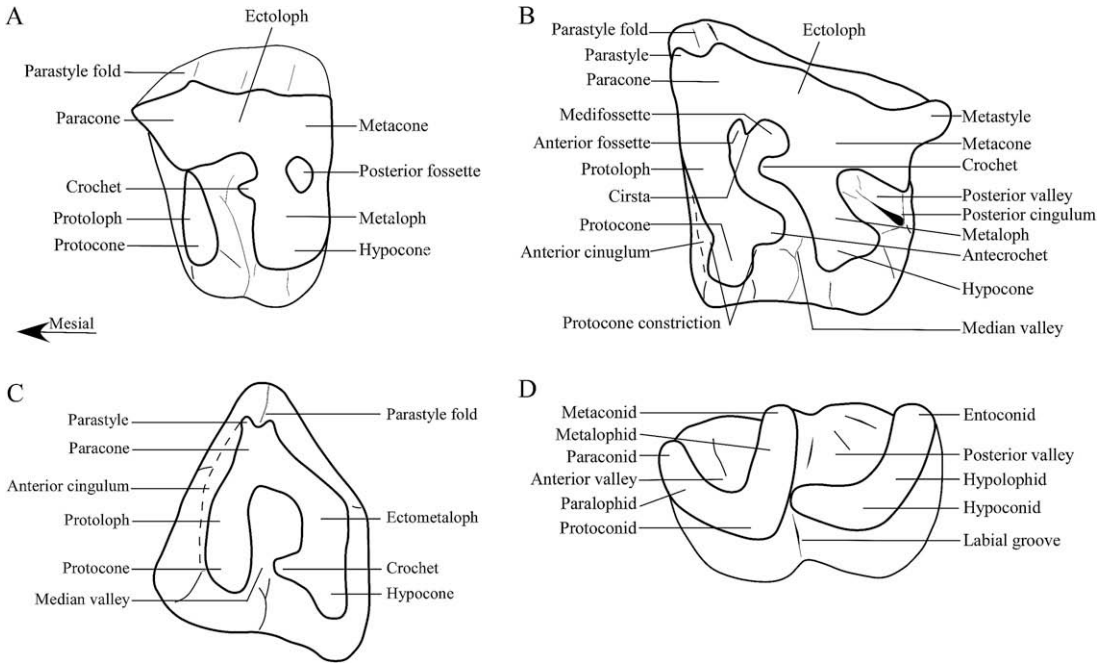

Fig. 3. Terminology of rhinoceros cheek teeth (modified after Guérin, 1980). A, left P3/; B, left M1/; C, left M3/; D, right M/1.

Brachypotherium perimense (Falconer and Cautley, 1847) Heissig, 1972

Syn. *Rhinoceros iravaticus* Lydekker, 1876, pp. 36–41, pl. 5, Figs. 1–4

Aceratherium perimense (Falconer and Cautley, 1847) Lydekker, 1881, p. 10

Rhinoceros perimensis Lydekker, 1886, pp. 155–156, Fig. 19

Brachypotherium sp. Takai et al., 2006, pp. 147–149, Fig. 4, Table 1

Discussion: We here consider the previous description of *Aceratherium* from the Irrawaddy sediments as an invalid taxon, and will refer them to *Brachypotherium perimense*. Lydekker (1876) first described the fossil rhinoceros from the Lower Irrawaddy sediments at Yenangyaung area as *Rhinoceros irravaticus*, and later assigned it to *Aceratherium perimense*, comparing it with the rhinoceros specimens from the middle Siwalik of the Indian Subcontinent (Lydekker, 1881). Pilgrim (1910b) described *Aceratherium lydekkeri* from Yenangyaung (Fig. 1), suggesting the correlation of the Irrawaddy sediments at Yenangyaung area to the middle Siwalik. This species was synonymized with *A. perimense* by Matthew (1929). In the late 20th century, the phylogenetic status of several Siwalik rhinoceros has been revised, and *Aceratherium perimense* from the Siwalik Group has been assigned to the genus *Brachypotherium perimense* by Heissig, 1972. Similarly, the specimens previously described as *Aceratherium* from the Irrawaddy sediments (Lydekker, 1876, pl. 5, Figs. 1–4, 1886, Fig. 19) possibly belong to *B. perimense* in having the following characteristics: a weak protocone constriction, moderately or weakly developed crochet, indistinct antecrochet and absence of lingual cingulum in the lingual side of protocone and hypocone, and the dental size of Myanmar specimen closely match with those of Siwalik *B. perimense* (Colbert, 1935; Heissig, 1972).

Recently, Takai et al. (2006) reported *Brachypotherium* sp. from the middle Miocene sediments at Thanbinkan area (Fig. 1) based on a right mandibular fragment with M/2–M/3. The referred specimen has relatively large teeth dimension (M/2: mesiodistal length = 58.1 mm; greatest buccolingual width = 38.6 mm; M/3: *L* = 54.3 mm; *W* = 35.2 mm) (Fig. 4). On the lower molars, the labial groove is shallow and wide, the hypolophid is long, and the lingual cingulid is absent, but labial cingulid is represented by an array of small tubercles. These characteristics show close resemblance to *B. perimense* from the Chinji Formation of Siwalik Group (Heissig, 1972, pl. 10, Figs. 1–2, pl. 11, Figs. 1–3) and consequently, we refer this specimen to *B. perimense*.

Brachypotherium fatehjangense (Pilgrim, 1910a) Heissig, 1972

Comment: Chavasseau et al. (2006) described *Brachypotherium fatehjangense* from another middle Miocene locality, Chaungtha in the northern part of central Myanmar (Fig. 1). They compared the referred specimens to *B. fatehjangense* from the early Miocene to the late Miocene of South Asia. However, the taxonomic name, "*Aprotodon*" *fatehjangense*, was used instead of *B. fatehjangense* in their citations (Heissig, 1972, pp. 73–79, Table 34; Antoine and Welcomme, 2000, p. 786; Welcomme et al., 2001, Fig. 4). We assume that they synonymize *B. fatehjangense* with "*A*". *fatehjangense* without any relevant comments.

Subfamily Rhinocerotinae Owen, 1845

Tribe Rhinocerotini Hay, 1902

Subtribe Rhinocerotina Owen, 1845

Genus *Rhinoceros* Linnaeus, 1758

Rhinoceros sondaicus Desmarest, 1822

New material: DA-ME 0001, a fragment of skull with left P2/–M2/ and right M1/–M2/ (Figs. 5 and 6). The zygomatic arch, nasal and occipital portion are broken.

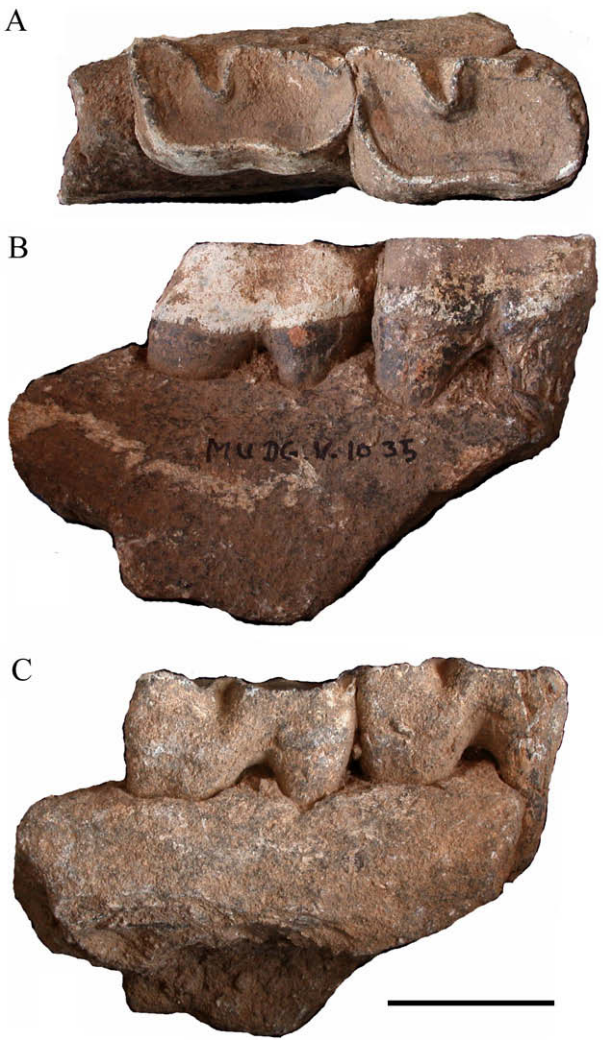

Fig. 4. *Brachypotherium perimense*, MUDG-V 1035, a right mandibular fragment with P/2–M/3 from the Freshwater Pegu Beds, Thanbinkan: A, occlusal view; B, buccal view; C, lingual view. Scale bar is 50 mm. Remark: Takai et al., 2006 described only the buccal view of the specimen.

Locality: Magway Division, central Myanmar. DA-ME 0001 was collected by local villagers many years ago and has been kept at the Department of Archaeology (Yangon) for a long time. Thus, the exact locality and geological horizon of the specimen are unconfirmed.

Horizon and Age: The teeth crown pattern of the specimen is identical to those of extant *R. sondaicus* (Javan rhinoceros); thus, the specimen probably came from the younger horizon such as the Plio-Pleistocene Irrawaddy sediments widely exposed along Irrawaddy River in central Myanmar rather than the Miocene deposits.

Diagnosis: Rhinoceros with a single nasal horn; occipital plane inclined anteriorly; anterior margin of the orbit at the level of P4/; molar crochet moderately developed; crista absent; antecrochet absent; both parastyle and parastyle fold distinct; ectoloph wall sinuous behind the parastyle fold; anterior valley deeper than the posterior one in premolars, and vice versa in molars (Pocock, 1943; Groves, 1983; Laurie et al., 1983; Cerdeño, 1995; Antoine, 2002a,b; Antoine et al., 2003b).

Description: The skull is broken in the nasal and occipital parts. The right side of the skull is damaged and covered with hard matrix. There is no rugose area or horn boss on the frontal bone.

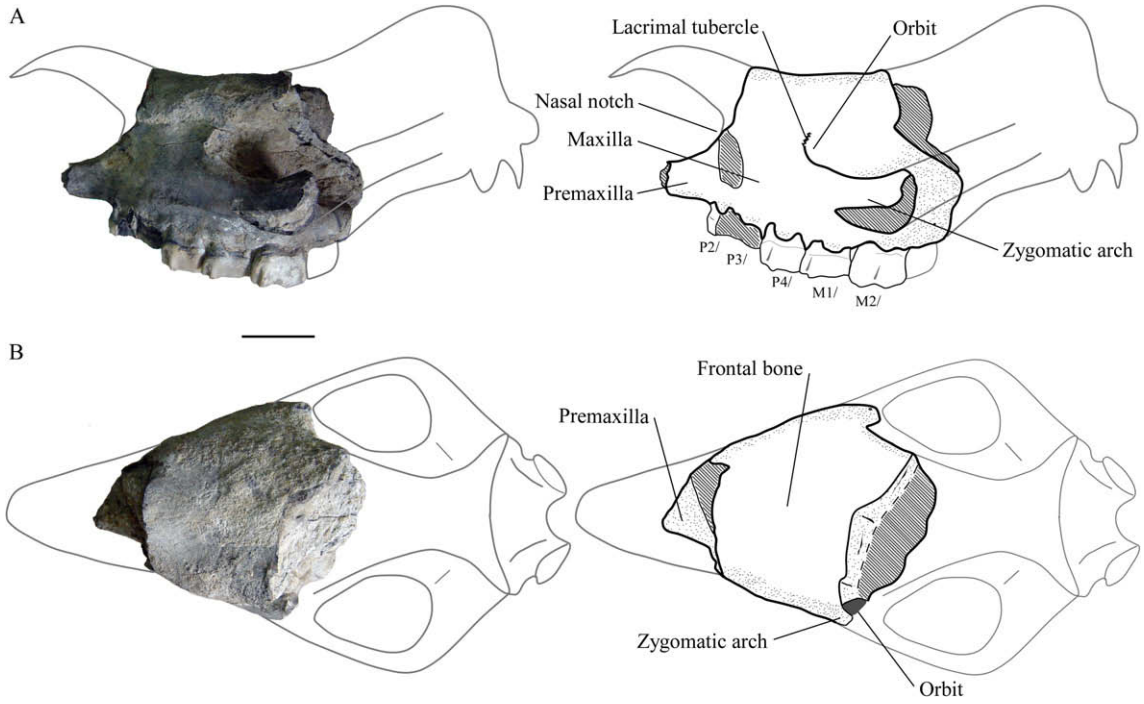

Fig. 5. *Rhinoceros sondaicus*, DA-MC 0001 from the Irrawaddy sediments: (A) lateral view of the left side of the skull with a schematic drawing; (B) dorsal view of the skull with a schematic drawing. Scale bar is 100 mm.

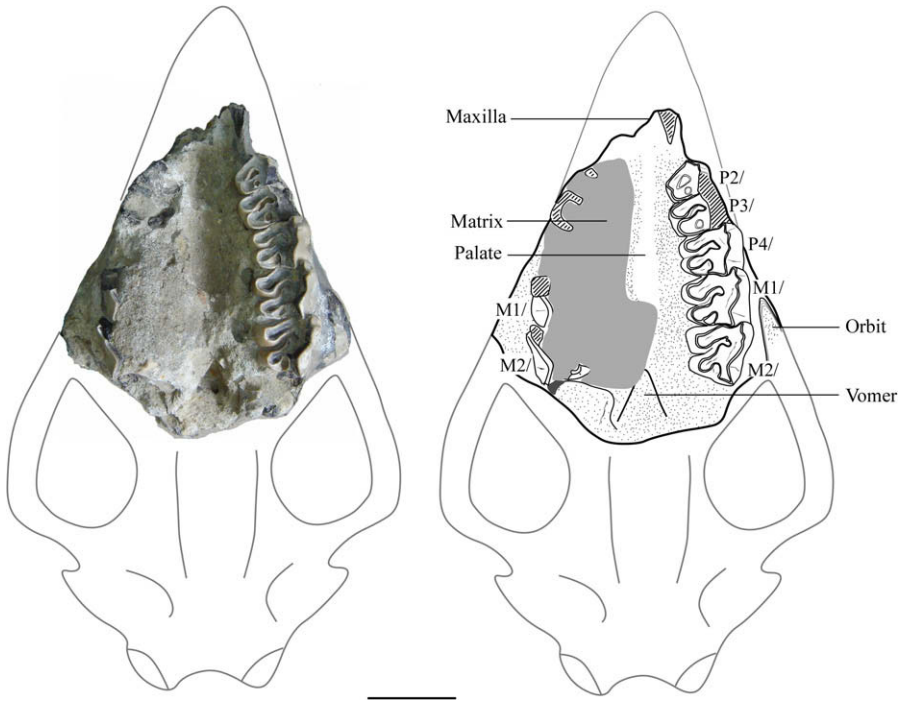

Fig. 6. Ventral view of the skull of *Rhinoceros sondaicus*, DA-MC 0001 from the Irrawaddy sediments with a schematic drawing. Scale bar is 100 mm.

The anterior part of the premaxilla is not preserved. The nasal notch is situated at the level of P3/. The mental foramen is not preserved because the region close to the nasal notch is superficially damaged/covered with matrices on both sides. The rounded anterior border of the orbit is located at the level of P4/ and connects laterally with the base of the zygomatic arch. The lacrimal tubercles are small and are observed at the upper anterior corner of the orbit. Although the zygomatic arch is broken on both sides, the anterior end of the arch is preserved on the left side, indicating its anterior position at the level of M1/ (Fig. 5).

On the ventral view, the palate is partly covered with the matrix and ends at the level of M2/. The upper dentition is moderately worn, and especially M1/ is worn down to the level of the posterior cingulum. The enamel is thick at the lingual part of the protoloph and metaloph (2.6–3.0 mm) and is thin at the ectoloph and the median valley (0.8–1.6 mm). Neither protocone constriction nor

antecrochet is observed. There is no lingual cingulum or tubercle at the entrance to the median valley. The premolars are molarized. On the right side, only M1/ and M2/ are preserved, but they are covered with matrix. On the left side, P2/ to M2/ are preserved (Fig. 6).

On the premolars, the anterior valleys are markedly deeper than the posterior one; however, these two valleys show similar depth on the molars. On P2/, the distal portion of the ectoloph is broken; both the parastyle and paracone fold are observed; the median valley is closed due to the connection between the protocone and hypocone; there is neither crochet nor crista in the median valley; and the posterior fossette is oval-shaped. On P3/, the ectoloph is lost; the small crochet is visible in the median valley but the crista is absent; the protoloph and metaloph are in contact with each other at the entrance to the median valley; the posterior valley is closed to form the oval-shaped postfossette; the anterior cingulum is small and terminates at the mesial end of the protoloph. On P4/, the parastyle is strong; the parastyle fold is distinct; the metacone fold is absent although the ectoloph wall is somewhat bulged in the position of the metacone; the crochet is weakly developed; the crista is absent; the ectoloph is higher than the protoloph and metaloph, showing the saw-tooth profile on the labial view; the median valley open narrowly.

On M1/, the parastyle and parastyle fold are pronounced as on P4/; the protoloph bulges distally at the protocone due to the advanced wear stage and nearly block the median valley; the ectoloph wall is nearly flat; the crochet is not well developed; the anterior cingulum is restricted at the mesial end of the protoloph. On M2/, the parastyle and parastyle fold are distinct; the ectoloph is concave lingually behind the parastyle fold; the crochet is somewhat strong; the median valley is wide mesiodistally and open lingually; the crista is small; the anterior cingulum is terminated at the mesial end of the protoloph; the posterior cingulum is dissected by the distally open posterior valley.

Comparison and discussion: DE-MC 0001 is assigned to the genus *Rhinoceros* based on the following preserved cranial and dental characteristics: the frontal horn boss is absent; the anterior border of the orbit is located at the level of P4/; the protocone is not constricted off; the antecrochet and lingual cingulum are absent and the anterior valleys are deeper than the posterior ones in premolar, and vice versa or nearly same depth in molars (Groves, 1983; Laurie et al., 1983). This specimen is referred to *R. sondaicus* in the presence of the distinct parastyle fold and moderately developed molar crochet, the lingually concave profile of the ectoloph, and in the absence of the crista and protocone fold in the upper molars (Pocock, 1943; Hooijer, 1946; Guérin, 1980).

DE-MC 0001 is distinct from *R. unicornis* in absence of the strong molar crochet and crista which contact each other to form the medifossette in the median valley (Groves, 1983). *R. sinensis* from the Pleistocene of China is distinct from DE-MC 0001 in having hypsodont molars, a well developed molar crochet and a small crista or small enamel projection into the medifossette (Colbert and Hooijer, 1953, pls. 20–21). *R. sivalensis* from the Plio-Pleistocene of the Indian Subcontinent (Falconer and Cautley, 1847, pl. 14, Figs. 1–2) is distinguished from DE-MC 0001 in having more

Table 1
Measurements (in mm) of the skull of *Rhinoceros sondaicus* from Plio-Pleistocene Irrawaddy sediments (DA-MC 0001) and comparisons with those of extant *Rhinoceros* species (*, estimate).

	Measurements	*R. sondaicus* (DA-MC 0001)	[a]*R. sondaicus*	[a]*R. unicornis*
9	Distance between the nasal notch and orbit	75.0	96.0–126.0	107.0–129.0
19	Width between the supraorbital tuberosities	200.0	166.5–220.0	192.0–244.0
20	Width between the lacrimal tubercle	230.0*	176.5–231.0	201.5–254.0
25	Height of skull anterior to P2/	175.0	142.0–195.0	177.0–258.0
26	Height of skull anterior to M1/	185.0	140.0–186.0	179.0–246.0
27	Height of skull anterior to M3/	190.0*	146.0–204.0	186.0–241.0
28	Width of palate anterior to P2/	42.0	60.5–83.5	72.5–103.0
29	Width of palate anterior to M1/	65.0	79.0–107.5	88.0–120.0
30	Width of palate anterior to M3/	78.0*	77.0–107.0	88.0–108.0

[a] Guérin (1980).

Table 2
Measurements (in mm) of the upper cheek teeth of *Rhinoceros sondaicus* from Plio-Pleistocene Irrawaddy sediments (DA-MC 0001) and comparisons with other *Rhinoceros* species (*, estimate).

Taxa	P3/			P4/			M1/			M2/			M3/	
	L	W1	W2	*L*	W1	W2	*L*	W1	W2	*L*	W1	W2	*L*	W1
R. sondaicus (DG-MC 0001)	34.0*	35.7	39.9	37.1*	44.0	43.0	45.3*	51.6	45.8	49.6	54.2	46.3		
[a]*R. sondaicus* (NMMP-KU-IR 0404)	–	–	–	–	–	–	53.1*	61.3	59.3	52.3	68.8	59.4	54.4*	45.7
[a]*R. sondaicus* (NMMP-KU-IR 0408)	–	–	–	–	–	–	46.6	62.0	57.8	53.3	62.6	46.6	52.8	55.5
[b]*R. sondaicus* (Dub. 1983)	47.0	57.0	53.0	42.0*	62.0	59.0	44.0*	65.0	56.0	47.0*	62.0	53.0	62.0	56.0
[c]*R. sinensis*	36.8	56.1	52.9	39.6	63.2	62.2	47.7	68.7	63.7	52.8	72.4		61.6	62.8
[d]*R. sivalensis*	40.6	58.4		38.1	66.0		44.6	66.0		50.8	66.0		63.5	58.4
[e]*R. unicornis*	47.8	58.3		46.0	64.0		53.3	65.7		57.6	68.6		63.0	61.8
[e]*R. sondaicus*	41.3	49.6		43.8	54.9		46.0	52.5		44.5	53.0		51.8	50.4

Remark: average teeth size for [b]*R. sinensis*, [d]*R. sondaicus*, [d]*R. unicornis*. Abbreviations: *L* = ectoloph length, W1 = protoloph length, W2 = metaloph length. Remark: for M3/, *L* = Ectometaloph.
[a] Zin-Maung-Maung-Thein et al. (2006).
[b] Hooijer (1946).
[c] Colbert and Hooijer (1953).
[d] Falconer (1867).
[e] Guérin (1980).

developed molar crochet, which may unite with the protoloph to form a medifossette and in being larger tooth size. DE-MC 0001 is distinguished from *Dicerorhinus*, of which anterior margin of the orbit is located at the level of M1/ or M2/, and of which rugose area or horn boss is present on the frontal bone (Groves and Kurt, 1972; Groves, 1983). The skull and tooth size of DE-MC 0001 closely match with those of the extant *R. sondaicus*, and it is smaller than *R. unicornis* and extinct species of *Rhinoceros* (Tables 1 and 2).

Zin-Maung-Maung-Thein et al. (2006) also reported an occurrence of early Pleistocene *R. sondaicus* from the Irrawaddy sediments at the Pauk area (Fig. 1) based on the two maxillary fragments with the associated molars. Dental characteristics of these specimens resemble those of DE-MC 0001 in the presence of lingually concave profile of the ectoloph, strong parastyle fold and moderately developed crochet, and in the absence of protococone constriction, crista and antecrochet (Figs. 6 and 7).

Rhinoceros sp.

Material: MMP-KU-IR 0984, a left mandibular fragment with P/4–M/3 (Fig. 8).

Locality: Chaingzauk (21°31′45″N; 94°31′37″E), Pauk Township, Magway Division, central Myanmar (Fig. 1).

Horizon and Age: Lower Irrawaddy Sediments; latest Miocene to early Pliocene. The Irrawaddy sediments at Chaingzauk locality yield many mammalian remains such as, *Agriotherium* sp., *Propotamochoerus hysudricus*, *Sivachoerus prior*, *Hexaprotodon irravaticus*, *Merycopotamus* sp., cf. *Brachyodus* sp., *Tragoportax* sp. and *Selenoportax* sp. *Rhinoceros* sp., *Stegodon* sp. and *Sinomastodon* sp. This faunal assemblage is correlated with the Dhok Pathan Formation of the Siwalik Group, suggesting the latest Miocene to the early Pliocene age for the Irrawaddy sediments at Chaingzauk area.

Description: The mandible, NMMP-KU-IR 0984, is broken at the middle of M/1. All cheek teeth but P/2 are preserved. The mandibular symphysis and ascending ramus are broken. The height of mandible is 60 mm at the level of P/4 and 75 mm at the level of M/3. The lower margin of the mandible is slightly convex ventrally. The parasagittal lingual groove is present on the posterior half of the mandible. Although P/2 is broken, the mandibular fragment under P/2 is preserved including posterior half of the mental foramen.

The cheek teeth are heavily worn. The teeth show a rectangular shape. The labial groove is deep and reveals V-shape in occlusal view. The cingulum is totally absent. On P/3, the protolophid is broken lingually; a small tubercle is observed in the labial groove; the posterior valley has disappeared due to the advanced wear stage. On P/4, the labial groove is broken; the anterior valley has disappeared; the posterior valley is represented by a V-shaped notch in the occlusal view. The fourth lower premolar (P/4) is much larger than P/3. The first lower molar (M/1) is heavily worn and enamel is broken buccally, and so its dental morphology is hardly visible. On M/2, the anterior valley is V-shaped and shallower than the posterior one, whereas the posterior one is U-shaped in the occlusal view; the trigonid is acute or in a right angle while the talonid is obtuse. On M/3, the anterior and posterior valleys show V-shaped outline; the hypolophid is broken distally; the anterior and posterior valleys are nearly the same in depth.

Comparison and discussion: Previously described rhinocerotid materials from the late Neogene sediments of Myanmar have been provisionally referred to the large extinct species, *R. sivalensis* from the Indian subcontinent (Colbert, 1938). However, the descriptions of Myanmar specimens are based on the fragmentary dento-gnathic materials, and they are relatively smaller than those from the Upper Siwalik Group, suggesting the taxonomic assignment is dubious (Colbert, 1938, 1943). Therefore, the previously reported *R. sivalensis* from Myanmar (Colbert, 1938, pp. 417–418; Colbert, 1943, pp. 406–407, Fig. 80) is here referred as *Rhinoceros* sp. Colbert (1943) also described *Rhinoceros* sp. from the middle Pleistocene cave deposits of Mogok (p. 420, pl. 31, figs. 1–3) (Fig. 1)

NMMP-KU-IR 0984 shares morphological characteristics with *Rhinoceros* in having the deep labial groove, acute trigonid, oblique hypolophid, and in the absence of the labial and lingual cingulids (Cerdeño, 1995; Antoine, 2002a,b; Antoine et al., 2003b). The parasagittal lingual groove is still retained in the posterior half of the mandible. Although this characteristic is generally present in juvenile *Rhinoceros* (Antoine, 2002b), NMMP-KU-IR 0984 is a specimen of an old adult because its teeth are heavily worn. The position of the mental foramen under the level of P/2 suggests its affinity with *Rhinoceros* rather than with *Dicerorhinus* (Antoine, 2002b). On the other hand, the dental size of the present specimen is closely

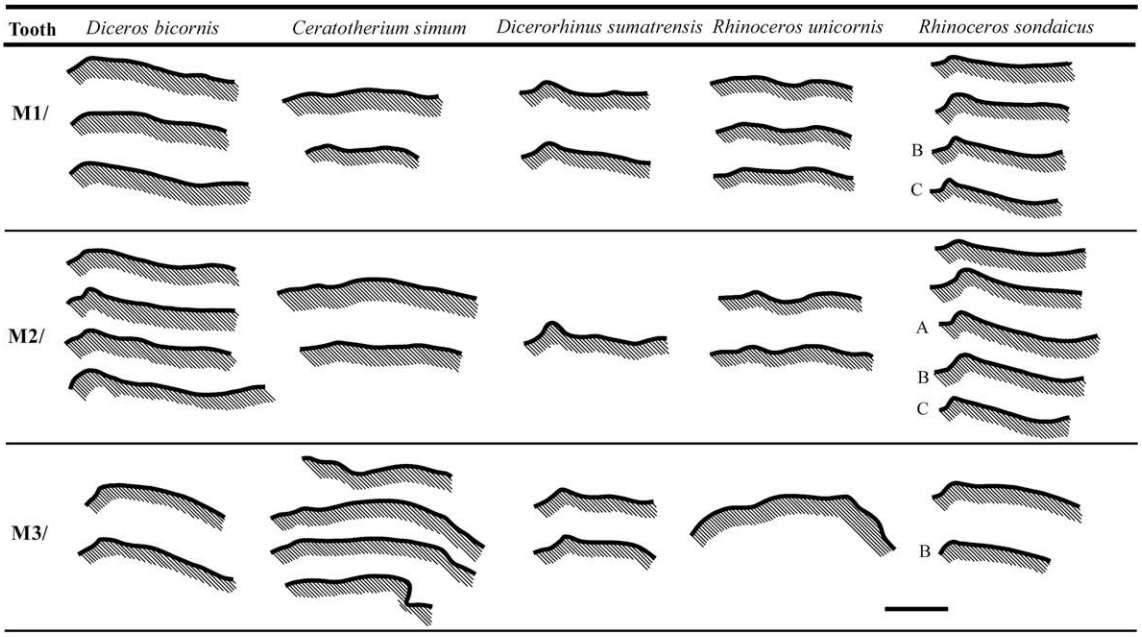

Fig. 7. Comparison of the ectoloph profile of *R. sondaicus* from the Plio-Pleistocene of Myanmar with those of extant rhinoceroses. (A) NMMP-KU-IR 0404; (B) NMMP-KU-IR 0408; (C) DA-MC 0001. Ectoloph profiles of extant rhinoceros are redrawn from Guérin (1980) and those of NMMP-KU-IR 0404 and 0408 are drawn from Zin-Maung-Maung-Thein et al. 2006. Scale bar is 20 mm.

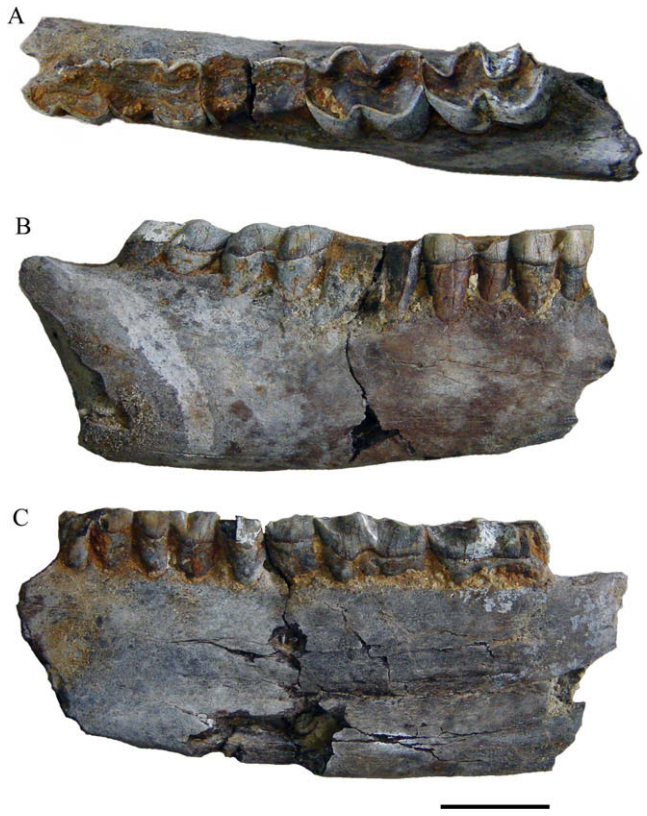

Fig. 8. *Rhinoceros* sp., NMMP-KU-IR 0984, a left mandibular fragment with P/2–M/3 from Irrawaddy sediments, Chaingzauk: (A) occlusal view; (B) buccal view; (C) lingual view. Scale bar is 50 mm.

similar to that of *R. sivalensis* and *R. sondaicus* and smaller than that of other species of *Rhinoceros* (Table 3). The lower mandibular fragment or teeth of the rhinocerotids do not give much information for making a reliable generic assignment, and even the position of the isolated lower cheek teeth can not be determined with confidence as pointed out by Hooijer (1946). Consequently, we attribute the present specimen to the genus *Rhinoceros* which is common in the late Neogene deposits of the Oriental region.

Subtribe Dicerorhinina Ringström, 1924
Genus *Dicerorhinus* Gloger, 1841
Dicerorhinus sp. cf. *D. sumatrensis* Fischer, 1814

Material: NMMP-KU-IR 0358/0359, associated left mandibular fragments with P/2–M/3 (P/4 and M/1 are broken) (Fig. 9).

Locality: Sulegone locality (21°20′19″N; 94°40′03″E), Pauk Township, Magway Division, central Myanmar. The present specimen was recovered from the Irrawaddy sediments at Sulegone locality on west bank of Irrawaddy River (Fig. 1).

Horizon and age: Upper Irrawaddy sediments; Plio-Pleistocene. The sediments at Sulegone yield several mammalian fossils represented by Bovidae indet., *Sivachoerus prior*, *Merycopotamus* sp., *Rhinoceros* sp., and *Stegodon* sp. This mammalian assemblage suggests an age of the Plio-Pleistocene.

Diagnosis of Dicerorhinus sumatrensis: Rhinoceros with nasal and front horns; dolichocephalic skull; anterior border of the orbit located at the level of M1/; occipital plane backwardly inclined or nearly vertical; brachydont to subhypsodont cheek teeth; molar crochet moderately developed; molar antecrochet absent; crista absent; median valley deeper than posterior one in molars; I/1 absent; I/2 large and tusk-like (Groves and Kurt, 1972; Groves, 1983; Cerdeño, 1995; Antoine, 2002a,b; Antoine et al., 2003b).

Description: The mandible is broken into two pieces at the level of M/1, and can not be fixed together because the parts between P/4 and M/2 is lost. It retains the left part of the mandibular symphysis, ascending ramus, and coronoid process. The ascending ramus is slightly inclined backwardly. The posterior border of the symphysis terminates at the level of P/2. A large mental foramen is present and is situated at the middle position of the mandibular depth and in front of P/2. The other two small mental foramina are also observed in front of the large mental foramen. Although the mandibular condyle is broken, the mandibular foramen is preserved at the level of the alveolar margin. The ventral margin of the mandible is slightly concave dorsally, and curves upwards at symphyseal region. The first lower incisor (I/1) is absent. The second lower incisor (I/2) is broken, but a large circular-shaped alveolus is observed.

All cheek teeth are heavily worn. The enamel is thicker in molars (3.0–8.5 mm) than in premolars (2.6–1.5 mm). The teeth show the rectangular shape, and deep V-shaped labial grooves are visible in the occlusal view. No cingulid is present on all teeth. On P/2, the protocone is broken; the anterior valley has disappeared; the posterior valley shows small rectangular outline. On P/4, the anterior and posterior valleys show V-shaped in occlusal view, and the latter is much deeper than the former. On M/2, the anterior valley is disappeared; the posterior valley is wide and open lingually. On M/3, the entoconid is broken; the posterior valley is extended labially and is nearly in contact with the labial groove.

Comparison and discussion: On NMMP-KU-IR 0358/0359, neither I/1 nor alveolus is present whereas the large alveolus of I/2 is preserved; the mental foramen is located in front of P/2; neither labial nor lingual cingulum is present. These features suggest its close affinity with *Dicerorhinus* (Groves, 1983; Cerdeño, 1995; Antoine, 2002a,b; Antoine et al., 2003b). The species of *Dicerorhinus* clade have been assigned mainly based on cranial materials. Therefore, it is difficult to assign the present specimen to a specific species based on the morphology of its preserved dental and gnathic materials. On the other hand, the dimension of mandible and tooth of the present specimen are generally similar to the average size of those of *D. sumatrensis* (extant Sumatran rhinoceros). *D. gwebinen-*

Table 3
Measurements (in mm) of lower cheek teeth of *Rhinoceros* from the late Miocene to early Pleistocene Irrawaddy Sediments at Chaingzauk (MMP-KU-IR 0984) and comparisons with other *Rhinoceros* species (*, estimate).

Taxa	P/3		P/4		M/1		M/2		M/3	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
Rhinoceros sp. (NMMP-KU-IR 0984)	34.7	20.3	38.5	26.2	39.5	29.0*	45.2	30.2	48.4	29.1
[a]*R. sinensis*	39.3	26.0	45.3	30.0	51.7	33.1	55.4	33.0	54.0	32.0
[b]*R. sivalensis*	35.5	21.6	41.9	27.9	37.1	26.7	50.8	30.5	–	–
[c]*R. unicornis*	40.3	29.1	43.8	30.1	46.7	30.1	54.1	32.5	57.5	30.9
[c]*R. sondiacus*	36.0	24.5	39.1	26.9	43.6	28.8	46.2	29.4	47.7	27.2

Remark: average teeth size for *R. sodaicus*, *R. unicornis* and *R. sinensis*. Abbreviation: *L* = mesiodistal length, *W* = greatest buccolingual width.
[a] Colbert and Hooijer (1953).
[b] Lydekker (1881).
[c] Guérin (1980).

Fig. 9. *Dicerorhinus* sp. cf. *D. sumatrensis*, NMMP-KU-IR 0358/0359, associated left mandibular fragments with P/2–M/3 (P/4 and M/1 broken) from the Irrawaddy Sediments, Sulegone: (A) occlusal view; (B) buccal view; (C) lingual view; (D) mesial view. Scale bar is 50 mm.

sis from the Plio-Pleistocene of Myanmar also show similar tooth sizes and dimensions as in the present specimen, but it possesses much smaller P/2 than the latter. Consequently, we refer this specimen to *Dicerorhinus* sp. cf. *D. sumatrensis* (Tables 4 and 5).

Dicerorhinus gwebinensis Zin-Maung-Maung-Thein, Takai M., Tsubamoto T., Thaung-Htike, Egi N. and Maung-Maung, 2008

Comments: This species was discovered from the Plio-Pleistocene deposits of Irrawaddy sediments at the Gwebin area in central Myanmar (Fig. 1). It is morphologically distinct from the extant species *D. sumatrensis* in having the comparatively shorter nasal, the more concave dorsal profile of the skull, the more elevated occiput and presence of molar crista on M3/ (Zin-Maung-Maung-Thein et al., 2008). However, the specimen of *D. gwebinensis* does not preserve the premaxillary bone and basioccipital portion. Therefore, it is difficult to evaluate the phylogenetic relationship with the Sumatran rhinoceros and Plio-Pleistocene European *Dicerorhinus* (=*Stephanorhinus*: Kretzoi, 1942; Groves, 1983).

5. Neogene rhinoceroses and their temporal change in Myanmar

In this study, we recognized five genera and eight species of fossil rhinoceroses from the Neogene of Myanmar: Rhinocerotidae indet., "*Diceratherium*" *naricum*, *Brachypotherium perimense*, *Brachypotherium fatehjangense*, *Rhinoceros sondaicus*, *Rhinoceros* sp., *Dicerorhinus* sp. cf. *D. sumatrensis* and *Dicerorhinus gwebinensis* (Fig. 10; Table 6). An existence of the genus *Diceratherium* in Myanmar is uncertain.

Table 4
Measurements (in mm) of the mandible of cf. *Dicerorhinus sumatrensis* from the Plio-Pleistocene Irrawaddy Sediments at Sulegone (NMMP-KU-IR 0358/0359) and comparisons with other *Dicerorhinus* species (*, estimate).

	Measurements	*D.* cf. *sumatrensis*	[a]*D. gwebinensis*	[b]*D. sumatrensis*
		NMMP-KU-IR 0358/0359	NMMP-KU-IR 0469-2	
1	Length of mandible	470.0*	465.0*	408.0–460.0
3	Height of the horizontal ramus anterior to P/3	70.0	70.0	49.5–65.0
4	Height of the horizontal ramus anterior to P/4	75.0	75.0	54.0–68.5
5	Height of the horizontal ramus anterior to M/1	67.0	78.0	55.0–72.0
6	Height of the horizontal ramus anterior to M/2	70.0	80.0	61.0–80.0
7	Height of the horizontal ramus anterior to M/3	80.0	85.0	59.0–81.0
8	Height of the horizontal ramus posterior to M/3	90.0	85.0	64.0–79.0
16	Height of the coronoid process	200.0*	–	171.0–213.0

[a] Zin-Maung-Maung-Thein et al. (2008).
[b] Guérin (1980).

Table 5
Measurements (in mm) of the teeth of cf. *Dicerorhinus sumatrensis* from the Plio-Pleistocene Irrawaddy Sediments at Sulegone (NMMP-KU-IR 0358/0359) and comparisons with other *Dicerorhinus* species (*, estimate).

Taxa	P/2		P/3		M/2		M/3	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*
D. cf. sumatrensis (NMMP-KU-IR 0358/0359)	32.9*	24.6	42.4	28.8	46.3	30.1	45.5*	28.5
[a]*D. gwebinensis*	20.0	12.0	31.0	19.0	40.0*	28.0*	–	–
[b]*D. sumatrensis*	30.4	20.4	33.8	23.0	43.3	26.1	45.1	24.8

Abbreviations: *L* = mesiodistal length, *W* = greatest buccolingual width. Remark: average teeth size for extant *D. sumatrensis*.
[a] Zin-Maung-Maung-Thein et al. (2008).
[b] Guérin (1980).

In the early Miocene, most areas of central Myanmar were under the shallow marine condition (Bender, 1983; Wandrey, 2006), leaving only few mammalian fossils and no rhinocerotid remain has been discovered yet.

The middle Miocene of Myanmar is characterized by the presence of Rhinocerotidae indet., "*Diceratherium*" *naricum*, *Brachypotherium perimense*, and "*Brachypotherium*" *fatehjangense*, and its rhinoceros fauna corresponds to the lower and middle Siwalik fauna of the Indian Subcontinent (Colbert, 1935; Heissig, 1972). The co-occurrence of several mammalian taxa, such as *Conohyus*, *Tetraconodon*, *Conohyus*, *Brachypotherium*, *Prodeinotherium*, *Choerolophodon* and trilophodont gomphothere in both faunas supports that the Indian Subcontinent and Southeast Asia were in the same biogeographic province since the middle Miocene as suggested by Ducrocq (1994).

These archaic rhinoceroses declined in the late Miocene of Myanmar, and seem to have disappeared at the Miocene/Pliocene boundary in Myanmar as in the other regions (Cerdeño, 1998; Deng, 2002). This is contemporaneous with the global episode of cooling and increasing aridity (Zachos et al., 2001).

In the late Miocene to early Pleistocene, the extant Asiatic genera, *Rhinoceros* (late Miocene to Pleistocene) and *Dicerorhinus* (Plio-Pleistocene) first appeared. The coexistence of *R. sondaicus* and *Dicerorhinus* in the pre-Pleistocene or early Pleistocene of Myanmar suggests these taxa originated in the Continental Asia as early as the early Pleistocene and migrated to the Island Southeast Asia in the late early Pleistocene. This coincides with the occurrence of remarkable sea level lowering in these regions (Vrba et al., 1989).

Table 6
List of Neogene fossil rhinoceroses in Myanmar.

Family Rhinocerotidae
  Gen. et sp. indet. (middle Miocene)
  Subfamily Dicertheriinae
    Genus "*Diceratherium*"
"*Diceratherium*" *naricum* (middle Miocene)
  Subfamily Aceratheriinae
    Tribe Teleoceratini
      Genus *Brachypotherium*
        Brachypotherium perimense (middle Miocene)
        Brachypotherium fatehjangense (middle Miocene)
  Subfamily Rhinocerotinae
    Tribe Rhinocerotini
      Subtribe Rhinocerotina
        Genus *Rhinoceros*
          Rhinoceros sondaicus (Plio-Pleistocene)
          Rhinoceros sp. (late Miocene to Pleistocene)
      Subtribe Dicerorhinina
        Genus *Dicerorhinus*
          Dicerorhinus sp. cf. *D. sumatrensis* (Plio-Pleistocene)
          Dicerorhinus gwebinensis (Plio-Pleistocene)

Neogene rhinoceros of Myanmar are also commonly known in the Indian Subcontinent, indicating the possible faunal exchanges between these regions. However, presence of some faunal elements such as *Sinomastodon* (Gomphotheriidae) and *Propotamochoerus* (Suidae) in the Pliocene or later period suggests a possible faunal exchange with East Asia (Takai et al., 2006). Similarly, *Dicerorhinus* probably migrated to the Southeast Asia via East Asia

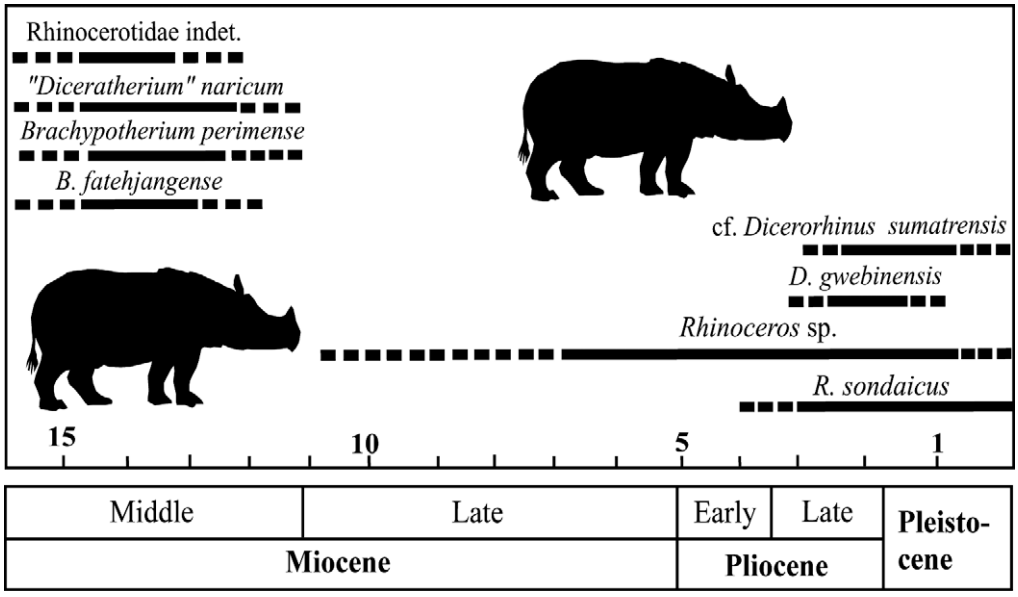

Fig. 10. Temporal distribution of Neogene rhinoceroses in Myanmar.

(Sino-Malayan Route) rather than via South Asia (Zin-Maung-Maung-Thein et al., 2008). The scarcity or absence of this clade in the Neogene mammalian fauna of South Asia seems to support this hypothesis.

Acknowledgements

We gratefully thank to the personnel from the Ministry of Education and the Ministry of Culture of the Union of Myanmar for giving permissions for the field works in Myanmar. We are also indebted to Prof. Nobuo Shigehara for his supports to our field works. Special thanks are due to all members of Myanmar-Japan Joint Palaeontological Research Team and to the curators from the National Museum of Myanmar for their help and for access to the specimens. Hideo Nakaya (Kagoshima University, Kagoshima, Japan), Akira Fukuchi (Okayama University, Okayama, Japan), Shintaro Ogino (Kyoto University, Inuyama, Japan) and Chit Sein (Hinthada University, Hinthada, Myanmar) gave us critical discussion and helped in collecting literature. Naoki Kohno (National Museum of Nature and Science, Tokyo, Japan), Yoshikazu Ueno (Higashiyama Zoo, Nagoya, Japan), Yoshikazu Hasegawa and Tomoko Anezaki (Gunma Prefectural Museum, Tomioka, Japan), and Yohoko Okumura (Kuzuu Museum, Sano, Japan) provided access to the rhinoceros specimens for the comparative work. We also wish to express our thanks to the ambassadors and staffs of the Myanmar Embassy in Tokyo and the Japan Embassy in Yangon for providing necessary assistances. Financial supports were provided by the MEXT Grants-in-Aid for Scientific Research (Overseas Academic Research) to M. T. (Nos. 16405018 and 20405015) and by the MEXT Global COE Program (A06 to Kyoto University). Research by T. Tsubamoto was partly supported by the Hayashibara Museum of Natural Sciences, Okayama, Japan.

References

Antoine, P.-O., 2002a. Middle Miocene Elasmotheriine Rhinocerotidae from China and Mongolia: taxonomic revision and phylogenetic relationships. Zoologica Scripta 32, 95–118.

Antoine, P.-O., 2002b. Phylogénie et évolution des Elasmotheriina (Mammalia, Rhinocerotidae). Mémoires du Muséum national d'Histoire naturelle 188, 1–359.

Antoine, P.-O., Welcomme, J.-L., 2000. A new rhinoceros from the lower Miocene of the Bugti hills, Baluchistan, Pakistan: the earliest Elasmotheriine. Palaeontology 43 (5), 795–816.

Antoine, P.-O., Ducrocq, S., Marivaux, L., Chaimanee, Y., Crochet, J.-V., Jaeger, J.-J., Welcomme, J.-L., 2003a. Early Rhinocerotids (Mammalia: Perissodactyla) from South Asia and a review of the Holarctic Paleogene rhinocerotid record. Canadian Journal of Earth Science 40, 365–374.

Antoine, P.-O., Duranthon, F., Welcomme, J.-L., 2003b. *Alicornops* (Mammalia, Rhinocerotidae) dans le Miocène supérieur des collines Bugti (Balouchistan, Pakistan): implications phylogénétiques. Geodiversitas 25 (3), 575–603.

Bender, F., 1983. Geology of Burma. Gebruder Bortrager, Berlin. pp. 1–293.

Bohlin, B., 1937. Eine tertiäre Säugetier-Fauna aus Tsaidam (Reports from the Scientific Expedition to the NW Provinces of China under leadership of Dr. Sven Heden. VI, Vertebrate Palaeontology). Palaeontologia Sinica 4 (1), 60–98.

Carrol, R.L., 1988. Vertebrate Paleontology and Evolution. Freeman, New York. pp. 1–698.

Cerdeño, E., 1995. Cladistic analysis of the Family Rhinocerotidae (Perissodactyla). American Museum Novitates 3143, 1–25.

Cerdeño, E., 1998. Diversity and evolutionary trends of the Family Rhinocerotidae (Perissodactyla). Palaeogeography, Palaeoclimatology, Palaeoecology 141, 13–34.

Chavasseau, O., Chaimanee, Y., Tun, Soe Thura, Soe, Aung Naing, Barry, C.J., Marandt, B., Suder, J., Marivaux, L., Ducrocq, S., Jaeger, J.J., 2006. Chaungtha, a new middle Miocene mammal locality from the Irrawaddy Formation, Myanmar. Journal of Asian Earth Sciences 28, 354–362.

Colbert, E.H., 1935. Siwalik mammals in the American Museum of Natural History. Transactions of the American Philosophical Society New Series 26, 1–401.

Colbert, E.H., 1938. Fossil mammals from Burma in the American Museum of Natural History. Bulletin of the American Museum of Natural History 74 (6), 255–436.

Colbert, E.H., 1943. Pleistocene vertebrates collected in Burma by the American Southeast Asiatic Expedition. Transactions of the American Philosophical Society New Series 32, 395–429.

Colbert, E.H., Hooijer, D.A., 1953. Pleistocene mammals from the limestone fissures of Szechwan, China. Bulletin of the American Museum of Natural History 102, 1–134.

Cotter, G.P., 1938. The geology of parts of the Minbu, Myingyan, Pakokku, and lower Chindwin Districts, Burma. Memoris of the Geological Survey of India 72 (1), 1–136.

Desmarest, A.G., 1822. Mammalogie ou description des espèces de mammfères. Encyclopèdie Mèthodique. Agasse, Paris. pp. 1–555.

Deng, T., 2002. Evolution of Chinese Neogene Rhinocerotidae and its response to climatic variations. Acta Geologica Sinica 76 (2), 139–145.

De Terra, H., 1943. The Pleistocene of Burma. Transactions of the American Philosophical Society new series 32, 271–392.

Dollo, L., 1885. Rhinocéros vivants et fossils. Revue des Questions Scientifiques 17. pp. 293–299.

Ducrocq, S., 1994. Ages and paleoenviroment of Miocene mammalian faunas from Thailand. Palaeogeoraphy, Palaeoclimatology, Palaeoecology 108, 149–163.

Falconer, H., 1867. Description of the Plates of the Fauna Antiqua Sivalensis from Notes and Memoranda. Robert Hardwicke, London. pp. 1–136.

Falconer, H., Cautley, P.T., 1847. Fauna Antiqua Sivalensis. Atlas, Smith, Elder and Co., London. pp. 1–90.

Fischer, G., 1814. Zoognosia: tabulis synopticis illustrate. N.S. Vsevolozsky, Moscow. pp. 1–732.

Gloger, C.W.L., 1841. Gemeinnütziges Hand- und Hilfbuch der Naturgeschichte. Aug. Schutz and Comp., Breslau. pp. 1–495.

Groves, C.P., Kurt, F., 1972. Dicerorhinus sumatrensis. Mammalian Species 21, 1–6.

Groves, C.P., 1983. Phylogeny of the living species of rhinoceros. Zeitschrift fur zoologische Systematik und Evolutionforschung 21 (4), 293–313.

Guérin, C., 1980. Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale: comparaison avec les espèces actuelles. Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon 79, 1–1182.

Hay, O.P., 1902. Bibliography and catalogue of fossil Vertebrata of North America. United States Geological Survey Bulletin 179, 1–868.

Heissig, K., 1972. Heissig, K., 1972: Paläontologische und geologische Untersuchungen im Tertiär von Pakistan 5. Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-Schichten. Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Neue Folge 152, pp. 1–112.

Heissig, K., 1999. Family Rhinocerotidae. In: Rössner, G.E., Heissig, K. (Eds.), The Miocene Land Mammals of Europe. Pfeil, München, pp. 175–188.

Hooijer, D.A., 1946. Prehistoric and fossil rhinoceros from the Malay Archipelago and India. Zoologische Mededeelingen 26, 1–138.

Kretzoi, M., 1942. Bemerkungen zum system der nächmiozänen Nashorn-Gattungen. Földtani Közlöny 72, 309–318.

Laurie, W.A., Lang, E.M., Groves, C.P., 1983. Rhinoceros unicornis. Mammalian Species 211, 1–16.

Linnaeus, C., 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera,species cum characteribus, differentiis, synonymis, locis*, Editio decimal reformata. Stockholm. Laurentii Salvii 1, pp. 1–824.

Lydekker, R., 1876. Molar teeth and other remains of mammalia. Palaeontologia Indica 10 (1), 19–87.

Lydekker, R., 1881. Siwalik Rhinocerotidae. Palaeontologia Indica 10 (2), 1–62.

Lydekker, R., 1886. Catalogue of the fossil mammalian in the British Museum (part 3). Taylor and Francis, London. pp. 1–186.

Marsh, O.C., 1875. Notice of new Tertiary mammals. American Journal of Sciences and Arts 109 (51), 239–250.

Matthew, W.D., 1929. Critical observation upon Siwalik mammals. Bulletin of American Museum of Natural History 56 (7), 437–560.

Métais, G., Antoine, P.-O., Baqri, S.R.H., Crochet, J.-Y., Franceschi, D.E., Marivaux, L., Welcomme, J.-P., 2009. Lithofacies, depositional environments, regional biostratigraphy and age of the Chitarwata Formation in the Bugti Hills, Balochistan, Pakistan. Journal of Asian Earth Sciences 34, 154–167.

Nowak, R.M., 1999. Walker's Mammals of the World, sixth ed., 1936 pp.

Owen, R., 1845. Odontography. Hippolyte Baillière, London. pp. 1–655.

Owen, R., 1848. On the Archetype and Homologies of the Vertebrate Skeleton. J. van Voorst, London. pp. 1–1560.

Pilgrim, G.E., 1910a. Notices of new mammalian genera and species from the Tertiaries of India. Records of the Geological Survey of India 40, 63–71.

Pilgrim, G.E., 1910b. Preliminary note on a revised classification of the Tertiary freshwater deposits of India. Records of the Geological Survey of India 40, 185–205.

Pilgrim, G.E., 1912. The vertebrate fauna of the Gaj Series in the Bugti Hills and the Punjab. Paleontologia Indica 4, 1–82.

Pocock, R.I., 1943. Some cranial and dental characteristics of the existing species of Asiatic rhinoceros. Proceeding of the Zoological Society of London 114, 437–450.

Prothero, D.R., Guérin, C., Manning, E., 1989. The history of the Rhinocerotoidea. In: Prothero, D.R., Schoch, R.M. (Eds.), The Evolution of Perissodactyls. Oxford University Press, New York, pp. 321–340.

Prothero, D.R., Schoch, R.M., 1989. Classification of the Perissodactyla. In: Prothero, D.R., Schoch, R.M. (Eds.), The Evolution of Perissodactyls. Oxford University Press, New York, pp. 530–537.

Prothero, D.R., Schoch, M.R., 2002. Horn, Tusk and Flippers. Johns Hopkins University Press, Baltimore and London. pp. 1–311.

Prothero, D.R., 2005. The Evolution of North American Rhinoceroses. Cambridge University Press, Cambridge. pp. 1–218.
Qiu, Z., Yan, D., 1982. A horned *Chilotherium* skull from Yushe, Shansi. Vertebrata Palasiatica 20 (2), 122–132.
Ringström, T., 1924. Nashörner der Hipparion-Fauna Nord-Chinas. Palaeontologica Sinica, Series C 1 (4), 1–159.
Roger, O., 1904. Wirbelthierreste aus dem Obermiocan der baryerisch-schwabischen Hochebene. Bericht des naturwissenschaftliches Vereines für Schwaben und neuburg 36, 1–22.
Stamp, L.D., 1922. An outline of Tertiary geology of Burma. Geological Magazine 59, 481–501.
Takai, M., Saegusa, H., Thaung-Htike, Zin-Maung-Maung-Thein, 2006. Neogene mammalian fauna in Myanmar. Asian Paleoprimatology 4, 143–172.
Tong, H., 2001. Rhinocerotids in China – systematics and material analysis. Geobios 41, 585–591.
Vrba, E.S., Denton, G.H., Prentice, M.L., 1989. Climatic influences on early hominid behavior. Ossa 14, 127–156.
Wandrey, C.J., 2006. Eocene to Miocene composite total petroleum system, Irrawaddy-Andaman and north Burma Geologic Provinces, Myanmar, Chapter E. In: Wandrey, C.J. (Ed.), Petroleum Systems and Related Geologic Studies in Region 8, South Asia: U.S. Geological Survey Bulletin 2208-E. U.S. Geological Survey, Virginia, pp. 1–26.
Welcomme, J.-W., Benammi, M., Crochet, J.-V., Marivaux, L., Métais, G., Antoine, P.-O., Baloch, I., 2001. Himalayan Forelands: Palaeontological evidence for Oligocene detrital deposits in the Bugti Hills (Balochistan, Pakistan). Geological Magazine 138, 397–405.
Zachos, J., Pagani, M., Sloan, L., Thomas, E., Billups, K., 2001. Trends, rhythms, aberrations in Global Climate 65 Ma to Present. Science 292, 686–693.
Zin-Maung-Maung-Thein, Thaung-Htike, Tsubamoto, T., Takai, M., Egi, N., Maung-Maung, 2006. Early Pleistocene Javan rhinoceros from the Irrawaddy Formation, Myanmar. Asian Paleoprimatology 4, 197–204.
Zin-Maung-Maung-Thein, Masanaru, T., Tsubamoto, T., Thaung-Htike, Egi, N., Maung-Maung, 2008. A new species of *Dicerorhinus* (Rhinocerotidae) from the Plio-Pleistocene of Myanmar. Palaeontology 51 (6), 1419–1433.