

A NEW SPECIES OF *DICERORHINUS* (RHINOCEROTIDAE) FROM THE PLIO-PLEISTOCENE OF MYANMAR

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Abstract: A skull and mandible of the new species *Dicerorhinus gwebinensis* sp. nov. of Rhinocerotidae (Mammalia, Perissodactyla) is described. The material is collected from the upper part of the Irrawaddy sediments (Plio-Pleistocene) in central Myanmar. *D. gwebinensis* sp. nov. is morphologically more similar to the extant species *D. sumatrensis* (Sumatran rhinoceros) than to other species of the genus but differs from *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 in M3/. This is the first discovery of *Dicero-*

rhinus in the upper Miocene to lower Pleistocene of the Indian subcontinent and Mainland Southeast Asia, and fills the chronological and geographical gap of this lineage in Asia. The *Dicerorhinus* clade probably migrated into Southeast Asia from East Asia by the Pliocene or early Pleistocene. This hypothesis is supported by the scarcity or absence of this clade in the Neogene mammalian fauna of the Indian Subcontinent.

Key words: Irrawaddy sediments, Myanmar, *Dicerorhinus gwebinensis* sp. nov., Rhinocerotidae, Plio-Pleistocene.

DICERORHINUS is one of the extant genera of the Rhinocerotidae (Mammalia, Perissodactyla), and currently inhabits in the rain forests of Malay peninsular, Sumatra and Borneo and was formerly distributed in the Himalayan foothills of Bhutan, eastern India, Myanmar, Thailand, Vietnam to Yunnan Province of southern China (Peacock 1931; Groves and Kurt 1972; Nowak 1991; Corbert and Hill 1992). The earliest fossil records of *Dicerorhinus* clade have been documented from the late Oligocene or the early Miocene of the western Europe, East Africa and South Asia (Hooijer 1966; Hessig 1999; Welcomme *et al.* 1997, 2001; Antoine and Welcomme 2000). The molecular analysis also suggests a split at 25.9 ± 1.9 Ma between *Dicerorhinus* and *Rhinoceros*, and this is generally concordant with the palaeontological evidences (Tougaard *et al.* 2001).

The *Dicerorhinus* clade comprises at least 14 extinct species ranging from the early Miocene to Pleistocene in Europe and Africa and from the early Miocene to Holocene in Asia (Hooijer 1966; Groves and Kurt 1972). At present, the phylogenetic relationships between the extant Sumatran rhinoceros (*Dicerorhinus sumatrensis*) and the extinct species of this clade are controversial. Several spe-

cies of this clade have been assigned to separate genera, such as *Larterotherium*, *Stephanorhinus*, *Dihoplus*, *Procerorhinus*, and *Brandtorhinus* (Kretzoi 1942; Ginsburg 1974; Guérin 1980; Groves 1983; Cerdeño 1995; Mckenna and Bell 1997). On the other hand, several researchers prefer to use *Dicerorhinus* for most of the species of this clade (e.g. Tong 2001; Orlando *et al.* 2003; Guérin 1982, 1989, 2004). Here, we also use the collective genus *Dicerorhinus* for all the species of this clade because there has been no specific consensus among researchers.

In this article, we describe the skull remains including cranial, dental and gnathic materials of *Dicerorhinus* discovered from the Irrawaddy sediments of central Myanmar. This is also the first discovery of this genus from the upper Miocene to lower Pleistocene of the Indian Subcontinent and Mainland Southeast Asia. These specimens are assigned to a new species of the genus.

MATERIALS AND METHODS

The present specimens described here are housed in the National Museum, Yangon, Myanmar. The measurements

were made with a digital caliper for teeth, and a measuring tape for the skull and the mandible length. All the measurements are given in mm. The taxonomy used in this paper follows Prothero and Schoch (1989). The terminology for anatomical designations and the corresponding measurements follow conventions of Guérin (1980).

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

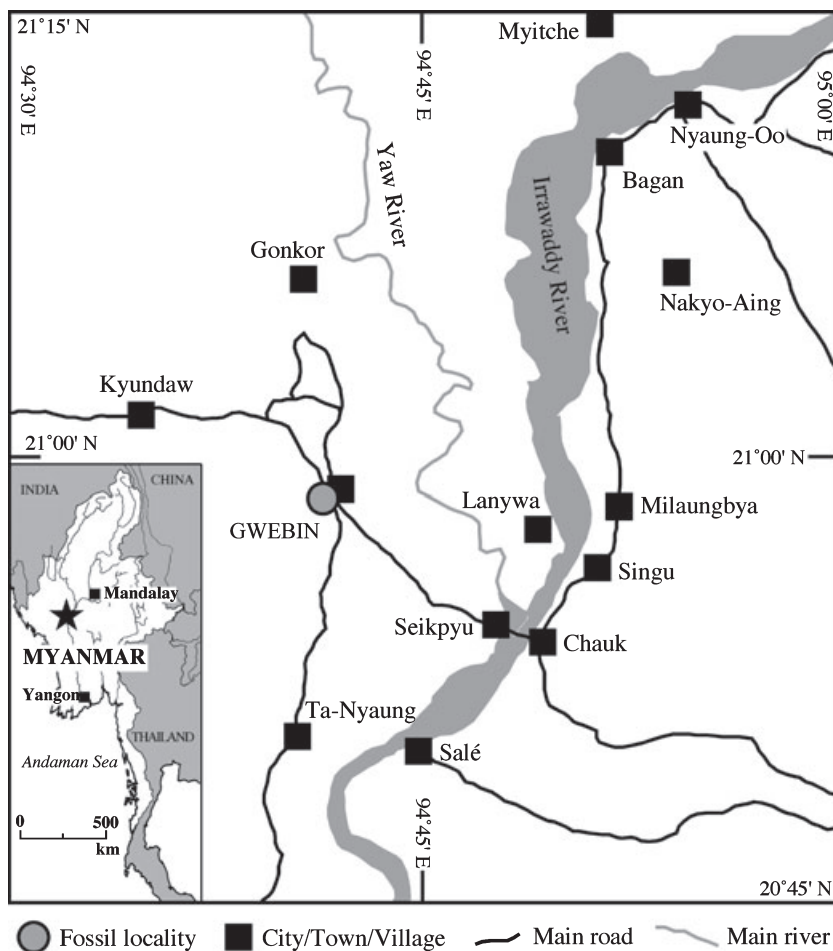
Anatomical abbreviations. I1/, first upper incisor; P1/, first upper premolar; M1/, first upper molar; I/1, first lower incisor; P/1, first lower premolar; M/1, first lower molar.

GEOLOGICAL SETTING

The Neogene Irrawaddy sediments (= Fossil wood Group: Theobald 1869; = Irrawaddian Series: Noetling 1900; = Irrawaddy Formation: Aung Khin and Kyaw Win 1969; = Irrawaddy Group: Bender 1983) are widely distributed along the Irrawaddy River (= Ayeyarwady River) in cen-

tral Myanmar (Text-fig. 1). They are mainly composed of the fluvial sediments derived from the Indo-Burman Ranges, Eastern Himalayas and Shan Plateau, and its thickness has been estimated to be 2000–3000 m (Bender 1983; Wandrey 2006). These sediments unconformably overlie the predominantly marine deposits of the Oligocene to Miocene Pegu Group, and are overlain by the middle Pleistocene to Holocene Terrace Deposits (Text-fig. 2). However, the Irrawaddy sediments partly interfinger with the upper part of the Pegu Group (= non marine Fresh water Pegu Beds: Stamp 1922) in the northern part of central Myanmar (20–22°N) due to the marine transgression and regression in the Miocene and later period (Stamp 1922; Aung Khin and Kyaw Win 1969; Bender 1983).

The Irrawaddy sediments are traditionally subdivided into the 'Lower Irrawaddy' and 'Upper Irrawaddy' based on the lithological and palaeontological criteria (Stamp 1922; Colbert 1938; Bender 1983). The Lower Irrawaddy consists of cross-bedded sandstones, gravels and pebbly red soil layers with carbonate and iron concretions. The Upper Irrawaddy consists of abundant gravels and poorly consolidated sandstones with few red soil layers. However,



TEXT-FIG. 1. Map of Myanmar showing the fossil locality in central Myanmar.

Age (Ma)	Geological age	Mammal Age		Stratigraphy	Mammalian fossils		
		Europe	MN unit			China	
5	Pleistocene	Biharian	18 17	Nihewanian	River Terrace Deposits	<i>Hystrix</i> sp., <i>Sus scrofa</i> , <i>Cervus</i> sp., <i>Bos</i> sp., <i>Hemibos triquetricornis</i> , <i>Equus</i> sp., <i>Rhinoceros</i> sp., <i>Stegodon orientalis</i> , <i>Elephas namadicus</i> , <i>E. Hysudricus</i>	
							Irrawaddy sediments
	Early	Ruscinian	Lower Irrawaddy				
	Miocene	Late	Turolian	Baodean/ Lufengian			
			Vallesian				
			Astaracian				
		Middle	6	Tunggurian			
			Early	5	Shanwan- ngian		
				4			
	3	Xiejian	Fresh water Pegu Beds	Cf. <i>Conohyus</i> sp., <i>Tetraconodon malensis</i> , <i>Tetraconodon</i> sp., <i>Listriodon</i> sp., <i>Hemimeryx</i> sp., <i>Telmatodon</i> sp., <i>Dorcatherium</i> sp., " <i>Aceratherium</i> " <i>perimense</i> , " <i>Diceratherium</i> " <i>narium</i> , <i>Brachypotherium perimense</i> , <i>Cadurcotherium</i> sp., <i>Prodeinotherium</i> sp., <i>Choerolophodon corrugatus</i> , Gomphotheriidae indent.			

TEXT-FIG. 2. Schematic stratigraphy of the continental Neogene deposits in Central Myanmar (Colbert 1938, 1943; Moe Nyunt 1987; Chavasseau *et al.* 2006; Chit Sein 2006; Takai *et al.* 2006).

it is difficult to differentiate lithologically between the Upper and the Lower Irrawaddy units in the field without palaeontological evidence.

The Irrawaddy sediments yield abundant silicified fossil woods, mollusca fossils, and terrestrial and aquatic vertebrates. To date, four orders (Carnivora, Perissodactyla, Artiodactyla, and Proboscidea), 14 families, and 31 genera of mammals have been reported from these sediments (Colbert 1938; Takai *et al.* 2006; Chit Sein 2006). Judging from the number of samples in the collected fossils, proboscideans and bovids are the dominant elements in the mammalian fauna. The gigantic land tortoise (*Colossochelys*), fresh water tortoises (*Trionyx* and *Emys*), alligators (*Gharialesis*), and shark (*Carcharodon*) have also been documented (Chibber 1934).

At present, most of the mammalian fossils recovered from the Neogene terrestrial sediments of Myanmar are fragmentary and stratigraphic position of these sediments has not been fully understood yet due to the lack of geological age calibrated from the radioisotope or palaeomagnetism. Therefore, the geological age of these sediments has been estimated by using the correlation of the vertebrate faunas from Indian Subcontinent and China. Most of the mammals from the Fresh water Pegu Beds show resemblance to those from the Kamlial and Chinji Formations of Siwalik Group, suggesting early to middle Mio-

cene age. On the other hand, Colbert (1938) suggested the Oligocene to Miocene age for Fresh water Pegu Beds due to the occurrence of archaic Oligocene forms such as *Cadurcotherim*. The Lower Irrawaddy has been correlated to the Dhok Pathan Formation of Siwalik Group, suggesting late Miocene to early Pliocene age. However, the base of the Lower Irrawaddy probably extends to the middle Miocene due to the occurrence of the fossil taxa of the Chinji Fauna (Cotter 1938; Bender 1983; Chavasseau *et al.* 2006; Chit Sein, 2006). The Upper Irrawaddy has conventionally been referred as the early Pleistocene (Colbert 1938, 1943; Bender 1983). The Upper Irrawaddy fauna show close resemblance to the Tatrot and Pinjor fauna of Indian subcontinent, suggesting the extension of its geological age to the late Pliocene. The River Terrace Deposits are continuation of the Upper Irrawaddy and probably correspond to the middle Pleistocene to Holocene (Colbert 1943). The River Terrace fauna mostly contains extant genera and some are probably reworked from the Upper Irrawaddy (Text-fig. 2).

The fossil records of small mammals in the Neogene sediments of Myanmar are rare probably due to the collection bias as well as preservation bias. On the other hand, the gradual uprising of Indo-Burman Ranges probably induces the rain shadow effect in the late Neogene leading to the occurrence of the arid condition in the central Myanmar

(Chibber 1934). This uprising may also have affected on the migration and dispersion of mammals, especially on the small mammals, into the central Myanmar.

The present specimens come from the Upper Irrawaddy at Gwebin area, situated in the western part of central Myanmar (Text-fig. 1). The deposits at Gwebin area yields many mammalian remains such as, *Stegodon insignis birmanicus*, *Stegodon elephantoides*, *Rhinoceros* sp., cf. *Nestoritherium* sp., *Dorcabune* sp., *Propotamochoerus* sp., *Hexaprotodon* sp., *Merycopotamus* sp., *Bos* sp., and *Capricornis* sp. (Colbert 1943; Moe Nyunt 1987; Tsubamoto *et al.* 2006; Thaug-Htike *et al.* 2006). This faunal assemblage has been correlated with the Tatrot and Pinjor Formations of the Siwalik Group of the Indian Subcontinent and with the Ma Kai valley deposits of southern China, suggesting an early Pleistocene age for the deposits at Gwebin area (Text-fig. 2). However, *Propotamochoerus* is a common suid from the Dhok Pathan Formation of Siwalik Group and the tragulid *Dorcabune* is also represented in the lower and middle Siwalik Group. The Gwebin locality therefore probably belongs to older geological age such as Pliocene.

SYSTEMATIC PALAEOLOGY

Order PERISSODACTYLA Owen, 1848

Family RHINOCEROTIDAE Owen, 1845

Subfamily RHINOCEROTINAE Owen, 1845

Tribe RHINOCEROTINI Owen, 1845

Genus DICERORHINUS Gloger, 1841

Type species. *Dicerorhinus sumatrensis* (Fischer, 1814).

Other included species. *Dicerorhinus schleiermacheri* Kaup, 1832; *Dicerorhinus megarhinus* De Christol, 1834; *Dicerorhinus merckii* Jäeger, 1839; *Dicerorhinus hemitoechus* Jäeger, 1839; *Dicerorhinus steinheimensis* Jäeger, 1839; *Dicerorhinus sansaniensis* Lartet, 1851; *Dicerorhinus etruscus* Falconer, 1859; *Dicerorhinus orientalis* Schlosser, 1921; *Dicerorhinus choukoutienensis* Wang, 1931; *Dicerorhinus abeli* Forster-Cooper, 1934; *Dicerorhinus ringstroemi* Arambourg, 1959; *Dicerorhinus yunchuchenensis* Chow, 1963b; *Dicerorhinus nipponicus* Shikama *et al.* 1967; *Dicerorhinus leakeyi* Hooijer, 1966; *Dicerorhinus jeanvireti*, Guérin, 1972; *Dicerorhinus gwebinensis* sp. nov.

Dicerorhinus gwebinensis sp. nov.

Text-figs 3–8

Derivation of name. From Gwebin, the name of the fossil locality.

Holotype. NMMP-KU-IR 0469-1, an adult skull with right P2/–M2/ and left P2/–M3/.

Referred material. NMMP-KU-IR 0469-2, a mandible with broken teeth possibly belongs to the same individual with the holotype.

Type horizon, locality, and age. Upper part of the Irrawaddy sediments; Gwebin village, Seikphyu Township, central Myanmar; Pliocene to early Pleistocene.

Diagnosis. *Dicerorhinus* with the nasal and frontal horns?; dolichocephalic form; nasal comparatively short; occipital plane high and nearly vertical; dorsally concave skull profile: nasal notch located at the level of P2/; infraorbital foramen at the level of P3/; anterior margin of the orbit at the level of M2/; molar crochet moderately developed; molar antecrochet absent; molar protocone constriction absent; crista absent except M3/; protoloph backwardly extended; molar protocone fold exists; median valley deeper than the posterior one in molars; tubercles absent at the entrance to the median valley. Dental formula: ?/1, 0/0, 3/3, 3/3.

Measurements. Shown in Tables 1–4. The teeth are almost worn down and broken. Therefore, it is difficult to get the precise measurements of teeth.

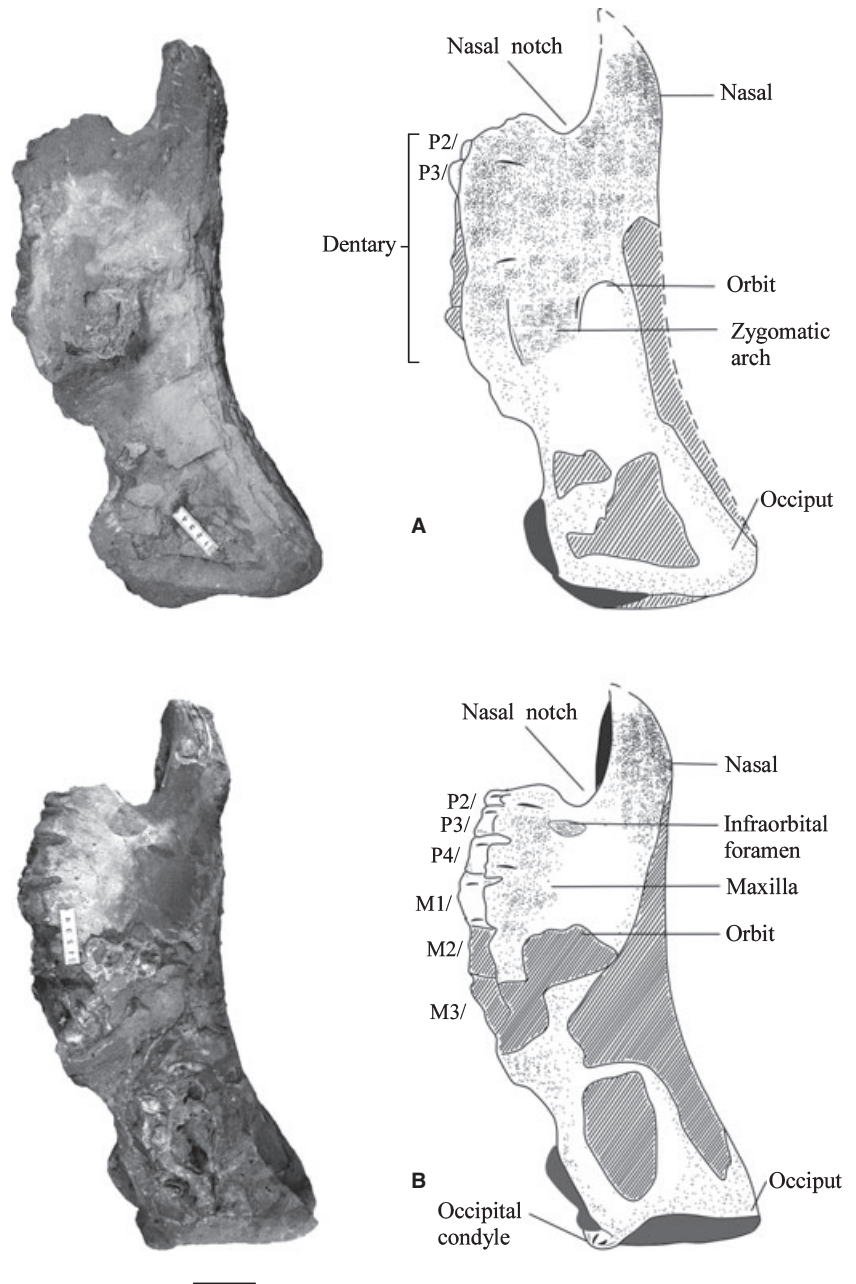
Description

Skull. The skull is relatively long and dorsally concave though it is slightly distorted in ventral view. The occipital plane is nearly vertical, though its surface is covered with sand matrix. The parietal and temporal parts are crushed in both sides, and they are filled with pebbles and sands (Text-fig. 3).

The tip of the nasal is rounded in dorsal view, though it is slightly broken. The nasal notch is situated at the level of P2/, and nasal septum is assumed to be absent. The nasal is convex and rugose indicating the presence of the first nasal horn, although the presence of second frontal horn is unconfirmed due to the poor preservation of the frontal. The width of the nasal is relatively small, indicating that the first horn is small. In the extant Asian rhinoceros, the sexual dimorphism is usually observed on the size of the horn (Pocock 1945). This fact indicates that NMMP-KU-IR 0469-1 likely belongs to a female (Text-fig. 4).

The maxilla is covered with matrix, but the infraorbital foramen is visible at the level of P3/ on the right side. The anterior margin of the orbit is situated at the level of M2/. The palate is covered with matrix. The width of the palate is decreased due to a laterally shifting of the left tooth row during preservation. The foramen magnum is sub-triangular in the outline. The frontal and parietal ridges are not preserved. Although the zygomatic arch is broken on both sides, the anterior root of the arch is persevered on the left side, indicating its anterior position at the level of M2/ and M3/. The posterior end of the left zygomatic process is also visible on the ventral view. The premaxilla and postorbital processes are not preserved. The basioccipital is poorly preserved. A wide notch exists at the occipital crest. The occipital condyle shows oval shape, but it is broken on the right side (Text-fig. 5).

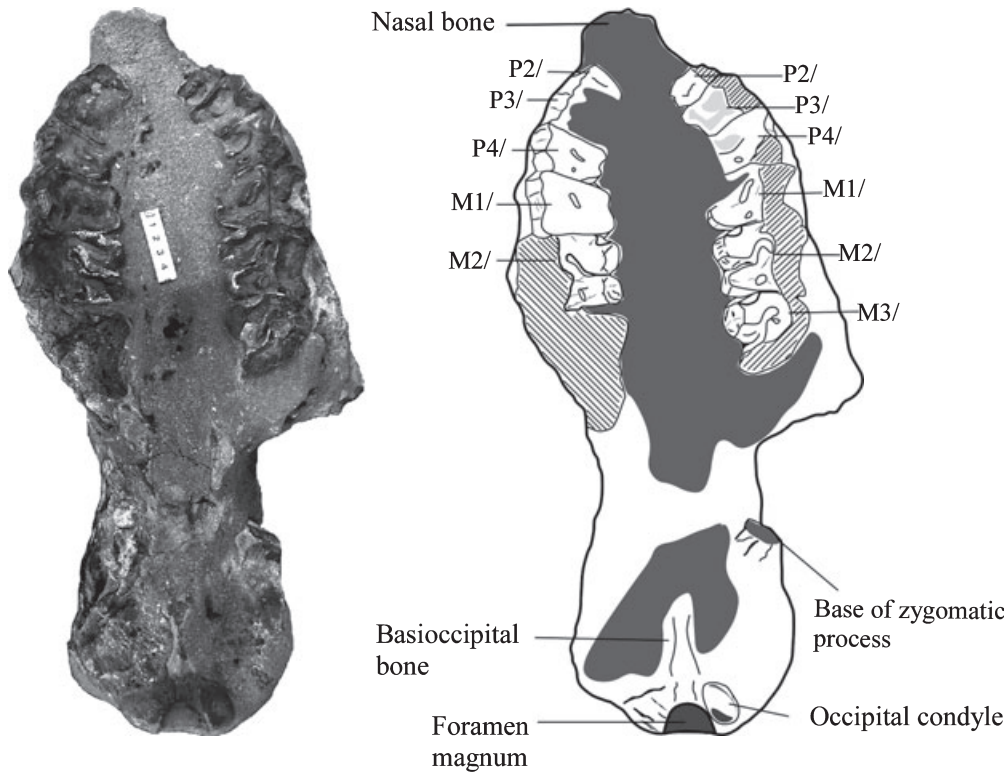
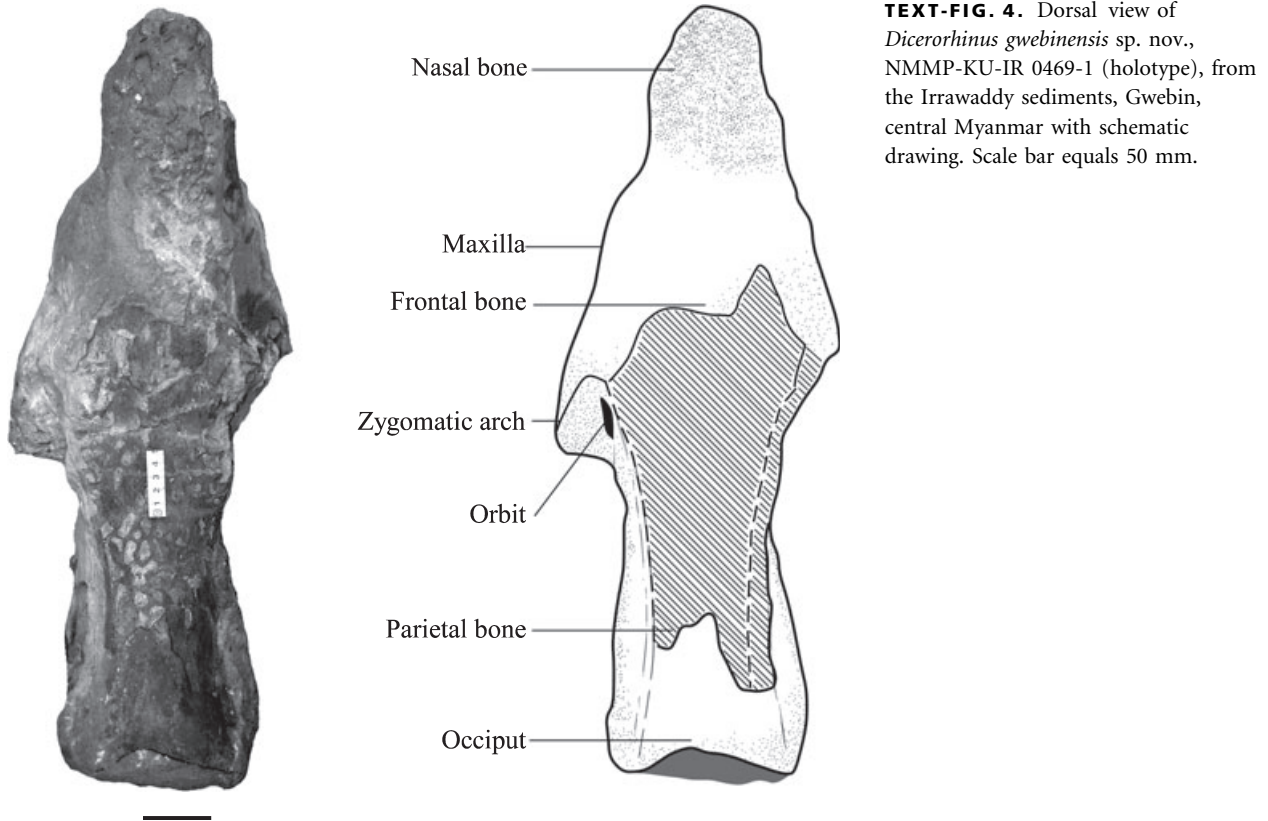
TEXT-FIG. 3. *Dicerorhinus gwebinensis* sp. nov., NMMP-KU-IR 0469-1 (holotype), from the Irrawaddy sediments, Gwebin, central Myanmar. A, left lateral view of the skull with a schematic drawing. B, right lateral view of the skull with schematic drawing (reversed). Scale bar equals 50 mm.



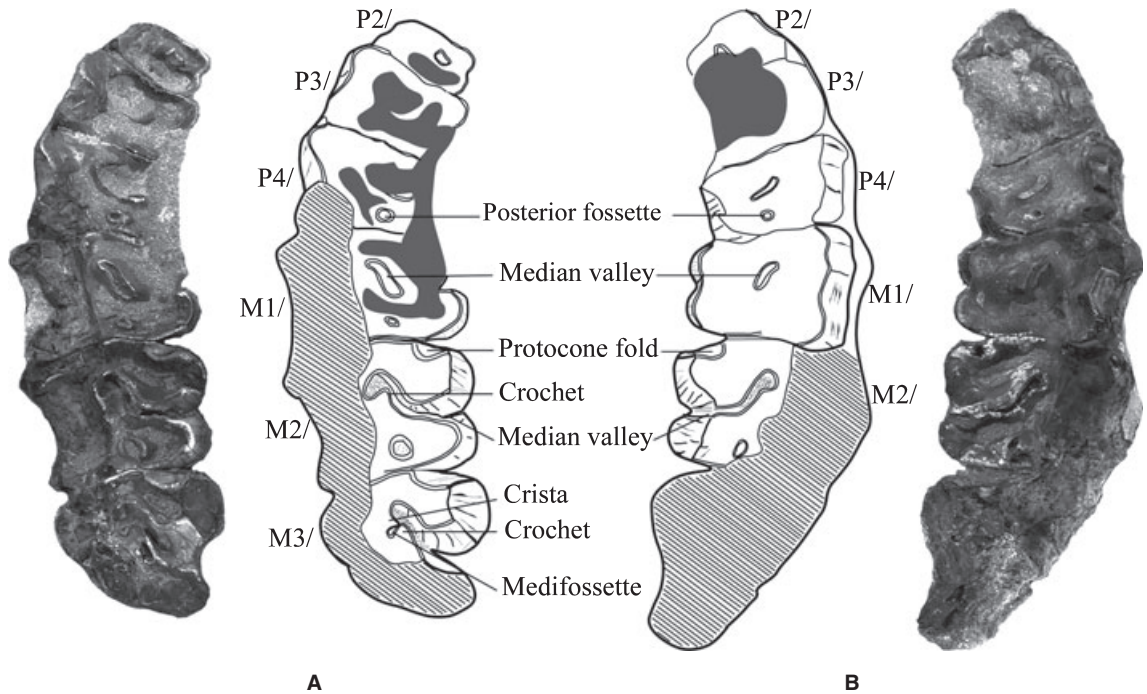
Upper dentition. The premolars are heavily worn and few dental characteristics are visible. In all premolars, the proto-loph is connected to the metaloph, and the median valley has almost disappeared forming a small rectangular-shape mark. On left P2/, the ectoloph is broken whereas it is preserved on right P2/, and a small median valley is observed. On left P3/, the ectoloph is preserved, though the proto-loph and metaloph are covered with matrix; and on right P3/, it is worn down and is covered with matrix. On left P4/, the anterior part of the ectoloph, median valley, and posterior fossette are preserved; and on right P4/, the ectoloph, median valley, and circular-shaped posterior fossettes are preserved, though its enamel of the ectoloph is broken (Text-fig. 6).

On left M1/, the ectoloph is broken; the proto-loph is covered with matrix; the proto-loph are connected to the metaloph; the median valley is represented by a small semi-rectangular shape marking; the posterior valley is also closed to form the circular-shaped posterior fossette. On right M1/, the ectoloph with saw-tooth profile is preserved; the proto-loph is connected with the metaloph due to heavy wear; the median valley is represented by a small marking; the posterior valley is disappeared due to heavy wear.

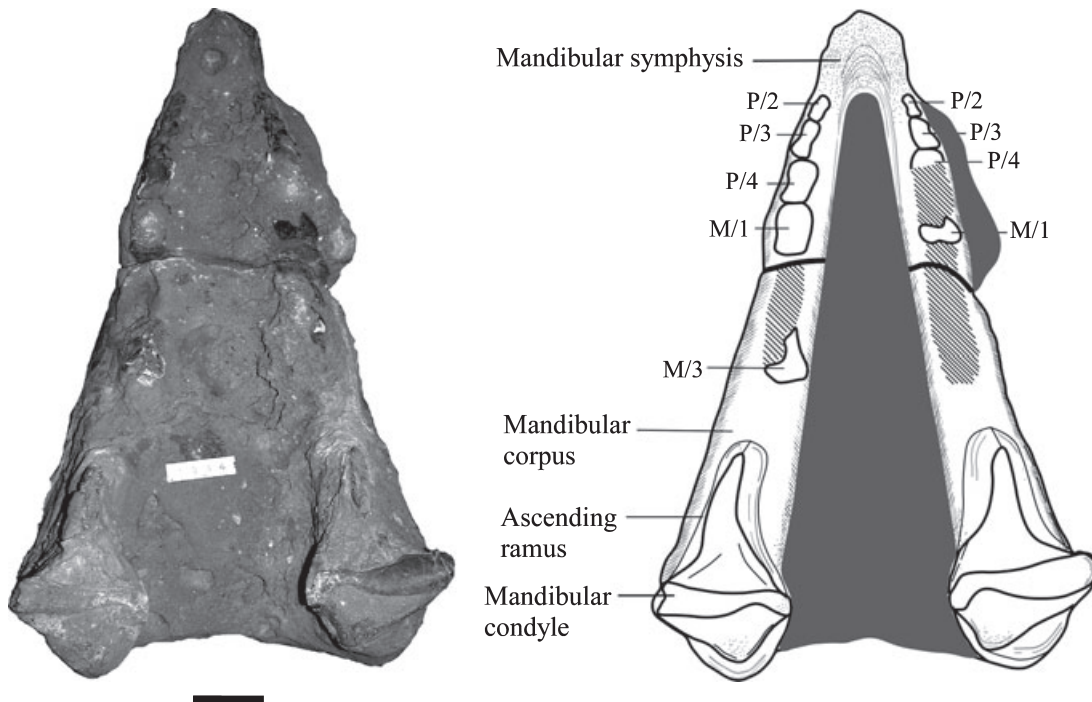
On left M2/, the ectolophs is broken; the proto-loph extends backward; the median valley becomes narrow; the crochet is moderately developed; the crista is absent; the protocone fold is observed although the proto-loph is slightly broken in its anterior



TEXT-FIG. 5. Ventral view of *Dicerorhinus gwebinensis* sp. nov., NMMP-KU-IR 0469-1 (holotype), from the Irrawaddy sediments, Gwebin, central Myanmar with a schematic drawing. Scale bar equals 50 mm.



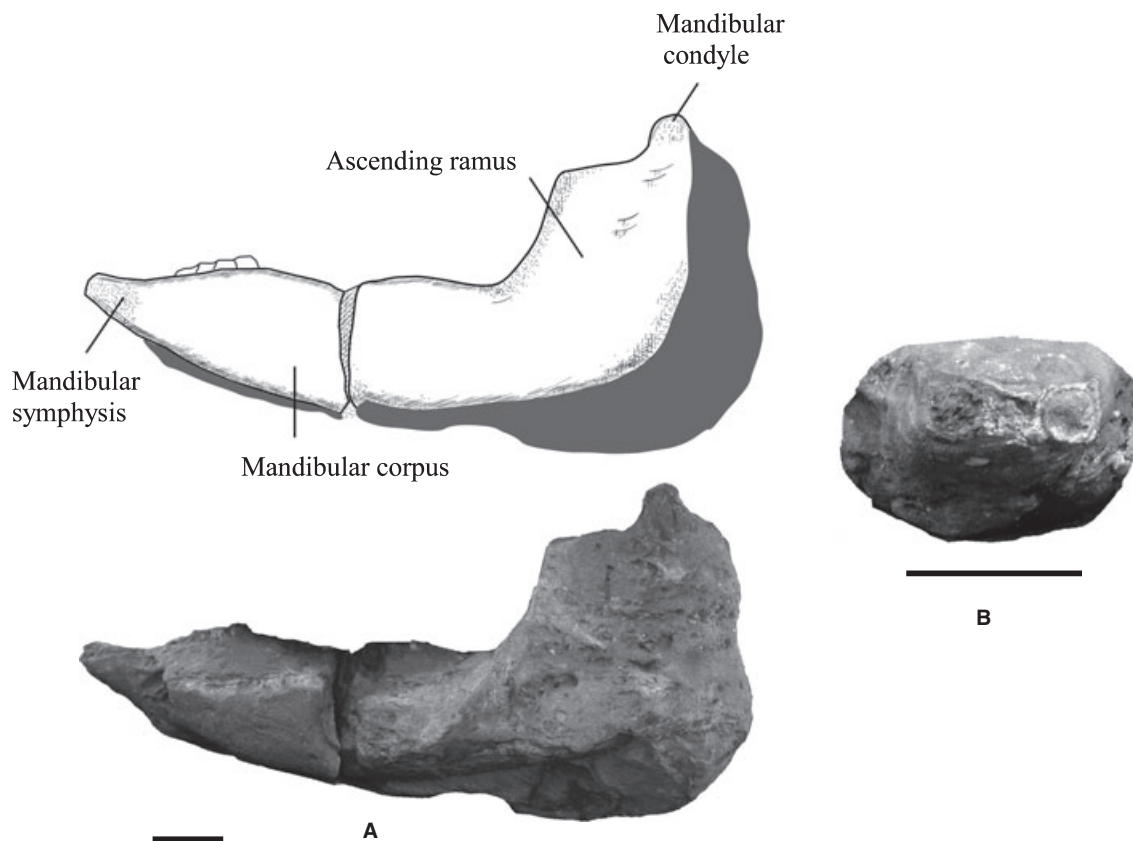
TEXT-FIG. 6. Upper teeth of *Dicerorhinus gwebinensis* sp. nov., NMMP-KU-IR 0469-1 (holotype), from the Irrawaddy sediments, Gwebin, central Myanmar. A, occlusal view of the left upper teeth with a schematic drawing. B, occlusal view of the right upper teeth with a schematic drawing. Scale bar equals 50 mm.



TEXT-FIG. 7. Occlusal view of the mandible of *Dicerorhinus gwebinensis* sp. nov., NMMP-KU-IR 0469-2, from the Irrawaddy sediments, Gwebin, central Myanmar with schematic drawing. Scale bar equals 50 mm.

part; the lingual cingulum is absent; the tubercle is absent at the entrance to the median valley; the posterior valley is closed and becomes postfossette. On right M2/, the ectoloph is lost; the

anterior parts of the protocone and hypocone are slightly broken; the median valley is narrow due to the backward extension of the protoloph; the protocone fold is observed; the crochet is



TEXT-FIG. 8. Mandible of *Dicerorhinus gwebinensis* sp. nov., NMMP-KU-IR 0469-2, from the Irrawaddy sediments, Gwebin, central Myanmar. A, lateral view with a schematic drawing. B, anterior view. Scale bar equals 50 mm.

indistinct because the enamel is broken; the crista is absent; the posterior fossette is semicircular-shaped in the occlusal view.

Left M3/ preserves the protoloph and the lingual part of the ectometaloph. The outline is triangular in shape. The protoloph extends backward though the anterior part is broken. The crochet and crista are contact to each other to form the medifossette. There are no tubercles at the entrance to the median valley. Right M3/ is broken (Text-fig. 6).

Mandible. The mandible (NMMP-KU-IR 0469-2) is embedded in hard-sandstone matrix. It preserves the mandibular corpus, ascending ramus, and condyles; but the coronoid process is broken. The ascending mandibular ramus is nearly vertical. The mandibular symphysis is narrow and is covered with the layer of matrix. The lower margin of the mandible is slightly concave dorsally, and curves upwards at symphyseal region (Text-fig. 7).

Lower dentition. Most of the lower teeth are worn out and/or broken, and the dental characteristics are hardly visible. I/1s are absent. The anterior parts of I/2s are broken on both sides, although its roots are visible in the circular-shaped alveoli. Shapes of the lower cheek teeth are rectangular, and the shallow labial grooves are visible in the left premolars. In the left mandible, P/2–M/1 are preserved although they are heavily worn; and M/2 and the paralophid of M/3 are lost. In the right mandible,

the premolars are also heavily worn, and the molars are partly broken or totally lost (Text-figs 7–8).

COMPARISONS

The Myanmar specimens can be assigned to the genus *Dicerorhinus* based on its preserved cranial, dental and gnathic characteristics (Groves 1983; Cerdeño 1995). The cranial material from Myanmar is morphologically more similar to the extant Sumatran rhinoceros, *D. sumatrensis*, than to other species of this genus, suggesting a close relationship to *D. sumatrensis*. They share the following characteristics: the skull is dolichocephalic form; the cranial dorsal profile is concave; the occipital plane is nearly vertical; nasal incision is located at the level of P2/; the anterior margin of the orbit is located at the level of M2/; the protocone constriction and antecrochet are absent in molars; the protocone folds is present and the median valleys are deeper than the posterior ones in molars (Hooijer 1946; Groves and Kurt 1972; Groves 1983; Guérin 1980; Cerdeño 1995; Antoine 2002). However, the present specimen differs from *D. sumatrensis* in

TABLE 1. Measurements (in mm) and comparisons of the skull of *Dicerorhinus gwebinensis* sp. nov. from the Irrawaddy sediments of Myanmar.

Measurements	<i>D. gwebinensis</i> NMMP-KU-IR 0469-1	^a <i>D. sumatrensis</i>	^a <i>D. sansaniensis</i>	^b <i>D. choukoutienensis</i>	^c <i>D. yunchuchenensis</i>	^d <i>D. leakeyi</i>
2 Distance between occipital condyle and nasal tip	575*	490–581	476	750	717	–
3 Distance between nasal tip and occipital crest	565*	440–588	484	741	–	630*
4 Distance between nasal tip and bottom of the nasal notch	150*	128–182.5	130	232	263	160–180
5 Minimal width of braincase	100*	89.5–128.5	85	–	–	–
6 Distance between occipital crest and postorbital process	–	178–258	220	–	–	–
7 Distance between occipital crests and supraorbital tuberosity	–	222–292	250	–	–	–
8 Distance between occipital crests and lacrimal tubercle	300*	239–320	270	428	–	–
9 Distance between nasal notch and orbit	125	98.5–134	95	140	120	135*
13 Distance between occipital condyle and M3/	220	182–247	220	–	–	–
14 Distance between nasal tip and orbit	280*	225–296	226	366	375	–
15 Width of occipital crest	140	105–149	154	267	223	–
16 Width between mastoid process	160*	160.5–231	179	–	–	–
20 Width between lacrimal tubercle	230*	162–215	195	237	234	–
21 Maximal width between zygomatic process	–	244–305	210	335	380	–
22 Width of nasal base	100	95–121.5	106.5	147	145	–
23 Height of occipital surface	170	111–139	152–182	226*	165	–
25 Cranial height in front of P2/	175	131–173	161	–	–	–
26 Cranial height in front of M1/	180*	127–175	166	–	–	160*
27 Cranial height in front of M3/	170*	137–188	–	–	–	–
28 Palatal width in front of P2/	32	53.5–69	30	140	130	–
29 Palatal width in front of M1/	52	73.5–95	76.75	234	203	–
30 Palatal width in front of M3/	65	68–94	50	–	–	–
31 Width of foramen magnum	30	33–51	44.5	53	57	–
32 Width between exterior borders of occipital condyle	83*	90.5–119.5	113	145	138	–

* , estimate.
^aGuérin (1980).
^bChow (1963a).
^cChow (1963b).
^dHooijer (1966).

TABLE 2. Measurements (in mm) and comparisons of the upper teeth of *Dicerorhinus gwebinensis* sp. nov.

	<i>D. gwebinensis</i> (NMMP-KU-IR 0469-1)	^a <i>D. sumatrensis</i>	^b <i>D. choukouti-enensis</i>	^c <i>D. yunchuchen-ensis</i>	<i>D. nipponicus</i> (Museum No. 9600)
P2/					
Length	24*	27–32	34	33	27*
Width	36*	27–36.5	42	38	31*
P3/					
Length	34*	33.5–37.5	46	37	39.4
Width	48*	37–47	63	–	47.7
P4/					
Length	41*	36–39	46	42	42.6
Width	49*	42.5–51.5	68	58	47.6
M1/					
Length	45*	46–51.5	51	47	55
Width	60*	46.5–54	69	64	56.9
M2/					
Length	46*	47.5–55	62	56	54.7
Width	48*	48–57	77	–	53.3
M3/					
Length	51*	47.5–56	68	–	50.7
Width	44*	44.5–47.5	51	–	40

*, estimate.

^aGuérin (1980).^bChow (1963a).^cChow (1963b).**TABLE 3.** Measurements (in mm) and comparisons of the mandible of *Dicerorhinus gwebinensis*.

	Measurements	<i>D. gwebinensis</i> NMMP-KU-IR 0469-2	^a <i>D. sumatrensis</i>
1	Length of mandible	465*	408–460
3	Height of the horizontal ramus anterior to P/3	70	49.5–65
4	Height of the horizontal ramus anterior to P/4	75	54–68.5
5	Height of the horizontal ramus anterior to M/1	78	55–72
6	Height of the horizontal ramus anterior to M/2	80	61–80
7	Height of the horizontal ramus anterior to M/3	85	59–81
8	Height of the horizontal ramus posterior to M/3	85	64–79
9	Distance between the horizontal rami anterior to M/1	60*	32–42
10	Distance between the horizontal rami anterior to M/3	75*	37.5–45
13	Anteroposterior diameter of the ascending ramus	152*	112–135
14	Transverse diameter of the mandibular condyles	100	77–93
15	Height of the condyle	210*	171–213

*, estimate.

^aGuérin (1980).

having a comparatively shorter nasal, the more concave dorsal profile, the higher position of occipital crest, and the presence of molar crista connecting with the crochet that tends to form the medifossette in M3/ (Text-fig. 9; Table 1). These facts lead us to consider this specimen as the new species of *Dicerorhinus*, *D. gwebinensis* (Text-fig. 9; Table 1). The convex and rugose nasal bone indicates the presence of nasal horn, while the presence of

second frontal horn is unconfirmed due to the poor preservation of the frontal bone.

The estimated measurements of the upper teeth of *D. gwebinensis* are similar to the average size of *D. sumatrensis* (Table 2). The skull length of *D. gwebinensis* is slightly shorter than the maximum length of *D. sumatrensis* (the occipital crest to tip of the nasal: 588 mm; Guérin 1980), although it is longer than the average skull length

TABLE 4. Measurements (in mm) and comparisons of the lower teeth of *Dicerorhinus gwebinensis*.

	<i>D. gwebinensis</i> NMMP-KU-IR 0469-2	^a <i>D. sumatrensis</i>
P/2		
Length	20	24–27
Width	11	14–16.5
P/3		
Length	31	27–33.5
Width	16	18.5–22.5
P/4		
Length	32	32–38
Width	23	21.5–25
M/1		
Length	40*	31–40.5
Width	26*	23–27.5

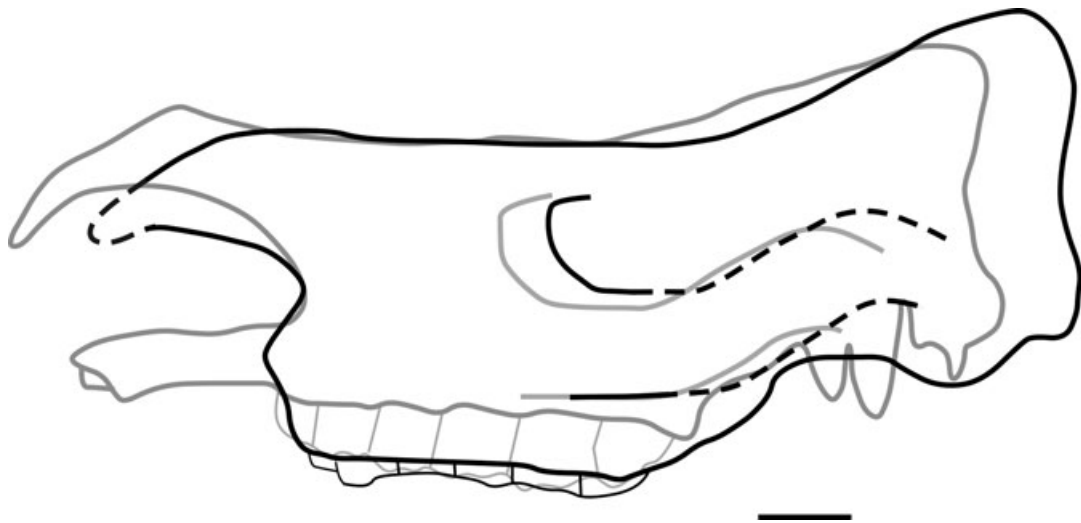
*, estimate.

^aGuérin (1980).

of *D. sumatrensis*. The occipital elevation of *D. gwebinensis* is higher than that of *D. sumatrensis*. *D. gwebinensis* has a nasal shorter than *D. sumatrensis*: this probably indicates the absence of partly developed nasal septum in *D. gwebinensis* (Text-fig. 8).

The mandible of *D. gwebinensis* is also similar to *D. sumatrensis* in lacking I/1: I/1 is present in the primitive species such as *D. leakyi* and *D. sansaniensis* (Hooijer 1966; Groves 1983). However, the mandible of *D. gwebinensis* is slightly larger than that of *D. sumatrensis* (Table 3). P/2 of *D. gwebinensis* is smaller than that of *D. sumatrensis*, although the sizes of other teeth of the former are similar to the average size of the latter (Table 4).

D. gwebinensis is distinguished from primitive species of this genus from Europe and East Africa. It differs from *D. sansaniensis* of the early Miocene of western Europe (Lartet 1851; Guérin 1980, pls 5–6) in having a comparatively longer skull, moderately developed crochet and crista in molars and in absence of protocone constriction and antecrochet in molars. However, they share with respect to nearly vertical occipital plane, similar height of the occipital surface, anterior margin of the orbit at the level of M2/, and position of the nasal notch at the level of P2/. *D. gwebinensis* is distinguished from *D. leakyi* of the early Miocene of Africa (Hooijer 1966, pls 1–3), in that the skull is larger, the nasal is long and the nasal horn boss is strong, the antecrochet present and the crochets and crista are weak or absent in molars. On the other hand, they are similar in having anterior border of the orbit at the level of M2/ and nearly vertical occipital plane. *D. gwebinensis* has an upwardly curved lower border of the mandible in symphyseal region, whereas *D. sansaniensis* and *D. leakyi* have a nearly straight lower border of the mandible. *D. gwebinensis* is distinct from *D. steinheimensis* (Jaeger, 1839; Guérin 1980, pl. 8, figs A–E, pl. 9, figs A–E) of the middle Miocene of Europe in having larger teeth size (M1/ Length: 32.25–34, M1/ Width: 37–41 in *D. steinheimensis*; Guérin 1980), the moderately developed crochet and crista in molars and in absence of protocone constriction in molars. *D. gwebinensis* is different from *D. schleiermachi* (Kaup, 1832; Guérin 1980, pl. 8, fig. D, pl. 9, fig. E) and *D. orientalis* (Gaudry 1862–67, pl. 32, fig. 1; Schlosser 1921) from the late Miocene of Europe. In *D. schleiermachi*, the skull size is markedly large, the base of the nasal horn is strong, the anterior margin of the orbit is located posteriorly (at the level of

**TEXT-FIG. 9.** Comparison of the outline of *Dicerorhinus gwebinensis* sp. nov. (black line) with that of extant *D. sumatrensis* (grey line). Scale bar equals 50 mm.

the middle of M2/), and antecrochet and protocone constriction are present on molars. In *D. orientalis*, the skull size is larger, the occiput is more elevated (210 mm; Hooijer 1966), the anterior margin of the orbit is located at the level of the Middle of M2, the crochet is well developed and antecrochet is present in molars. These Miocene species from Europe and Africa have been referred as separate genus, *Lartetotherium* due to the presence of autapomorphic characteristics (Ginsburg 1974; Groves 1983). The cladistics analysis of Cerdeño (1995) also supports the validity of the genus, *Lartetotherium*. However, fossil materials of small *D. steinheimensis* are incomplete for valid allocation (Groves 1983; Cerdeño 1995).

D. gwebinensis differs from *D. abeli* from the early Miocene Bugti of Pakistan (Forster-Cooper, 1934, fig. 11, fig. 12B, pls 65–66). In *D. abeli*, the skull is broad distally, the infraorbital foramen is located at the level of P4/ indicating the recession of nasal notch (probably at the level of P4/ or M1/), lingual cingula are present in upper premolars and molars and protocone constrictions weakly developed in molars.

D. gwebinensis is distinct from *D. ringstromi* of the late Miocene of East Asia (Ringström 1924, figs 1–2; Arambourg 1959; Deng 2006, fig. 1). In *D. ringstromi*, the skull size is markedly larger, the nasal is longer and wider, the nasal notch is located at the level of P3/–P4/, and the anterior margin of the orbit is located at the level of the middle of M2/, the crochet is well developed, and the wide and short antecrochet present.

D. gwebinensis is distinguished from *D. megarhinus* (De Christol, 1834; Guérin 1980, pl. 8), *D. hemitoechus* (Jaeger, 1839; Falconer 1868b, pls 15–17; Guérin 1980, pl. 16, figs D–E), *D. merckii* (Jaeger, 1839; Guérin 1980, pl. 16, figs B–C, pl. 17, figs A–B), *D. etruscus* (Falconer, 1859; Falconer 1868b, pls 26–28; Guérin 1980, pl. 16, fig. A), and *Dicerorhinus jeanvireti* (Guérin, 1972, pl. 1, 1980, pl. 12, fig. C) of the Plio-Pleistocene of Europe, northwestern Asia and East Asia, of which the skulls are markedly large, the nasals are long (the distances between tip of the nasal to bottom of the nasal notch: 220–297 mm; Guérin 1980) and sometimes co-ossified with the premaxilla and maxilla tending to form nasal septum and the nasal notches are recessed, locating at the level of P4/ and M1. These Plio-Pleistocene *Dicerorhinus* species show autapomorphic characteristics such as elongated nasal bone, deep nasal notch, presence of nasal septum, posteriorly located orbit, total loss of incisor and have been referred as a separate genus, *Stephanorhinus* (Kretzoi 1942; Groves 1983; Cerdeño 1995).

D. gwebinensis is distinguished from the Pleistocene Chinese species, *D. choukoutienensis* (Wang, 1931; Chow 1963a, pl. 1, figs 1–3) and *D. yunchuchenensis* (Chow 1963b, pl. 1, figs 1–3). In *D. choukoutienensis*, the skull and teeth size is much larger, the nasal is comparatively

longer and the tip of the nasal is broad and rounded, the nasal septum is partly ossified with the premaxilla, the crochets are strong on molars, and the crista is absent in M3/. However, *D. gwebinensis* and *D. choukoutienensis* share with respect to the position of the anterior margin of the orbit above the level of M2/, the presence of protocone folds on upper molars, and nearly vertical occipital plane. *D. yunchuchenensis* differs from *D. gwebinensis* in having comparatively longer skull, large and plow-like nasal, partly ossified nasal septum, and posteriorly located orbit (above the level of M2/ and M3/). The occipital height of *D. yunchuchenensis* (165 mm; Chow, 1963a) is lower than that of *D. choukoutienensis* (226 mm; Chow 1963b), and is similar to that of *D. gwebinensis* (170 mm).

D. gwebinensis is distinct from *D. nipponicus* from the middle Pleistocene of Japan (Shikama *et al.* 1967, pls 1–2). In *D. nipponicus*, the anterior margin of the orbit is located at the level of M2/ and M3/, the crochets are well developed and contact with the protoloph, and the cristae present in the molars. In M3/, two small cristae are observed, and a distinct tubercle is present at the entrance to the median valley.

D. gwebinensis is distinguished from *Rhinoceros sivalensis* (Falconer and Cautley, 1847; Falconer 1868a, pl. 14, figs 1–2), *R. unicornis* (Linnaeus, 1758) and *R. sondaicus* (Desmarest, 1822) from the late Miocene to Holocene of the Oriental region (Indian Subcontinent, Southeast Asia and southern China). In *Rhinoceros* species, the skull shows a brachycephalic form, the occipital plane inclines forward, and the anterior margin of the orbit is located at the level of P4/ (Groves and Kurt 1972; Groves 1983).

DISCUSSION

The fossil record of the *Dicerorhinus* clade from the Neogene of Oriental region is rare; and its pre-Holocene distribution in this region is still not clearly known. The only known fossil record of this clade from Southeast Asia was the fossils of the extant species *D. sumatrensis* from the middle Pleistocene to Holocene deposits of the Indonesian islands, Vietnam, Thailand and Laos (Hooijer 1946; Tougaard 2000). In the Indian Subcontinent, *D. abeli* (= *Aceratherium abeli*; Forster-Cooper 1934) and *D. shahbazi* from the early Miocene deposits of Dera Bugti had been documented (Hessig 1972; Antoine and Welcomme 2000; Welcomme *et al.* 2001). These two rhinoceros are respectively comparable to *D. steinheimensis* from the middle Miocene of Europe and to *D. leakeyi* from the East Africa (Hessig 1989; Antoine and Welcomme 2000). Hessig (1972) also recorded *D. abeli* and *D. sumatrensis* from the early to middle Miocene Chinji Formation of the Siwalik Group. However, his identification of

D. sumatrensis is based upon the isolated teeth, and there are no citations of this species in his later works (Hessig 1989, 1999). Moreover, the fossil materials of this genus from southern China is scanty and fragmentary (Jiang et al. 1989).

Therefore, *D. gwebinensis* from the Irrawaddy Formation of Myanmar is the only known skull of this lineage from the late Miocene to the early Pleistocene deposits of Oriental region. The discovery of *Dicerorhinus* from Myanmar fills the chronological and geographical gap of this clade in Asia.

Although many genera of mammals from the Irrawaddy Formation are shared with those of the Siwalik Group of the Indian subcontinent (Chibber 1934; Takai et al. 2006), *Dicerorhinus* is absent in the upper Miocene to Pleistocene of the Siwalik Group. On the other hand, *Dicerorhinus* of the Indian subcontinent, the early Miocene *D. abeli*, is morphologically distantly related to the Plio-Pleistocene *Dicerorhinus* from Asia including the extant *D. sumatrensis* and *D. gwebinensis*. Therefore, *Dicerorhinus* lineage probably migrated from East Asia into Mainland Southeast Asia in the Pliocene or early Pleistocene, and dispersed into Island Southeast Asia during the late early to middle Pleistocene. The scarcity or absence of this clade from the Neogene sediments of Indian Subcontinent seems to support this hypothesis. However, the East Asian *Dicerorhinus* species (*D. choukoutienensis* and *D. yunchuchenensis*) show close affinity with the Plio-Pleistocene European species in having the large skull size and similar autapomorphic characteristics such as acquisition of nasal septum, absence of incisor, and fusion of postglenoid and posttympanic processes. Unfortunately, *D. gwebinensis* does not preserve the premaxillary bone and basioccipital portion, so it is difficult to evaluate the phylogenetic relationship with these East Asian species.

At present, phylogenetic relationship between extant *D. sumatrensis* and extinct species are still controversial, and some species of this clade have been referred as separate genera (Groves 1983; Cerdeño 1995). Moreover, the evolutionary trend from the Miocene forms to the Plio-Pleistocene *Dicerorhinus* and extant Sumatran rhinoceros is not well understood. On the other hand, *D. sumatrensis* is considered as the most primitive rhinoceros among the five extant species, and it retains the primitive cranial and dental characteristics seen in *D. sansanensis* of the early Miocene of western Europe (Hooijer 1966; Groves 1983). However, the extant species also possesses somewhat specialized characteristics such as the long nasal bone, partly ossified nasal septum, and loss of I/1 in the mandible. This fact suggests that *Dicerorhinus* clade has undergone its later evolutionary process in Southeast Asia. More discoveries of *Dicerorhinus* fossils from the Oriental region would enhance this hypothesis.

CONCLUSION

The rhinocerotid skull and lower jaw described in this paper are assigned to a new species of *Dicerorhinus*, *Dicerorhinus gwebinensis*. This is the first record of the *Dicerorhinus* in the upper Miocene to lower Pleistocene of the Indian Subcontinent and mainland Southeast Asia. The discovery of this genus from Myanmar fills the chronological and geological gap of this lineage in Asia. It also suggests migration of this genus from East Asia into Mainland Southeast Asia in the Pliocene or early Pleistocene, and dispersion into Island Southeast Asia during the late early to middle Pleistocene.

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