

Original article

# Early Pleistocene *Dicerorhinus sumatrensis* remains from the Liucheng *Gigantopithecus* Cave, Guangxi, China<sup>☆</sup>

*Les restes des Dicerorhinus sumatrensis du Pléistocène inférieur de la grotte à Gigantopithecus de Liucheng, Guangxi, Chine*

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## Abstract

The Liucheng *Gigantopithecus* Cave is very famous for its rich mammalian fauna and *Gigantopithecus* fossils. The *Gigantopithecus* Cave Fauna has been regarded as the typical Early Pleistocene fauna in South China. The majority of the fossils unearthed has been studied and published during the past decades. The only group remaining unpublished is the rhinoceros, which is studied in this paper. The rhino materials available today are only mandibles and lower cheek teeth. The dimensions of the tooth rows and the isolated teeth fall well within the range of the recent *Dicerorhinus sumatrensis*. Therefore, the rhino fossils from the Liucheng *Gigantopithecus* Cave can be referred to this living species. The reduced lower incisors and the U-shaped lingual contour of the mandible also support this taxonomic determination. The rhino materials from the Liucheng *Gigantopithecus* Cave represent the earliest known record of this species and the smallest Pleistocene rhinocerotid in China.

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**Keywords:** *Dicerorhinus sumatrensis*; Rhinocerotidae; Liucheng *Gigantopithecus* Cave; South China; Early Pleistocene

## Résumé

La Grotte à *Gigantopithecus* de Liucheng est bien connue pour sa richesse en mammifères fossiles, dont des restes de *Gigantopithecus*. Sa faune est considérée comme typique du Pléistocène inférieur de Chine du sud. À l'exception des Périssodactyles, elle a été étudiée et publiée au cours des dernières décennies. Les restes de *Rhinocerotidae* qui subsistent, essentiellement des rangées dentaires et des dents inférieures isolées, sont décrits dans le présent travail. Les dimensions des dents et des rangées dentaires se placent dans l'intervalle de variation du *Dicerorhinus sumatrensis* actuel ; le contour lingual en V de la mandibule ainsi que la réduction des incisives confirment cette détermination. Les restes de rhinocéros de la Grotte à *Gigantopithecus* de Liucheng représentent donc le plus ancien témoignage de la présence de *D. sumatrensis* en Chine. C'est aussi le plus petit rhinocérotyde du Pléistocène en Chine.

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**Mots clés :** *Dicerorhinus sumatrensis* ; Rhinocerotidae ; Grotte à *Gigantopithecus* ; Liucheng ; Chine du sud ; Pléistocène inférieur

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## 1. Abbreviations

IVPP	Institute of Vertebrate Paleontology and Paleoanthropology (Beijing, China)
L	length
LGC	Liucheng <i>Gigantopithecus</i> Cave

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MNHN Muséum National d'Histoire Naturelle (Paris, France)  
 W width  
 Wa/Wp anterior width/posterior width

## 2. Introduction

In 1956, a major project to study the paleontology and paleoanthropology of Guangxi, a Province in South China, was undertaken by IVPP. The field excavation, which took place from 1957 to 1963, recovered a large number of fossils. The most important finds of the missions are *Gigantopithecus* and related fauna from the Liucheng *Gigantopithecus* Cave (LGC, 24° 40' N, 109° 15' E; Fig. 1). Most of the material has been studied and the results published after completion of the fieldwork (Pei, 1965, 1987; Han, 1987). The Perissodactyls are the only group which remains to be investigated. In 1979, at a conference, Prof. Li Youheng presented a communication outlining the preliminary study on the Perissodactyls from LGC. He proposed three new specific names for some of these specimens, i.e. *Nestoritherium praesinense* for a chalicothere, *Tapirus peii* for a tapir, and finally *Rhinoceros chaii* for a rhinoceros. Fortunately, the majority of the fossil materials

survived, and the *Hesperotherium sinense* (chalicothere) and part of the *T. peii* (tapir) materials have been restudied and published recently (Tong, 2005, 2006). However, the rhinoceros material is fragmentary and remained to be investigated. In order to record the complete composition of the LGC Fauna, especially considering that the LGC Fauna has long been regarded as the most important fauna of Early Pleistocene age in South China, it is necessary to study and to publish the rhinoceros materials.

This paper presents the results of our study of the rhino materials from LGC. Although the samples are incomplete, which possibly may result in biased conclusions, the available material is important enough to present a detailed description.

Because of the lack of good materials, in the past century, even today, almost all of the rhino materials of Pleistocene age from South China were exclusively put into the fossil species *Rhinoceros sinensis*, a species occupying a more or less intermediate position between *Rhinoceros unicornis* and *Rhinoceros sondaicus* both in size and characters (Colbert and Hooijer, 1953). But most of the identification works of the isolated rhino finds are provisional and superficial.

Concerning the rhino materials from LGC, they look quite different from the materials of *R. sinensis* from the type locality, at least they are remarkably smaller in size. In many aspects, the

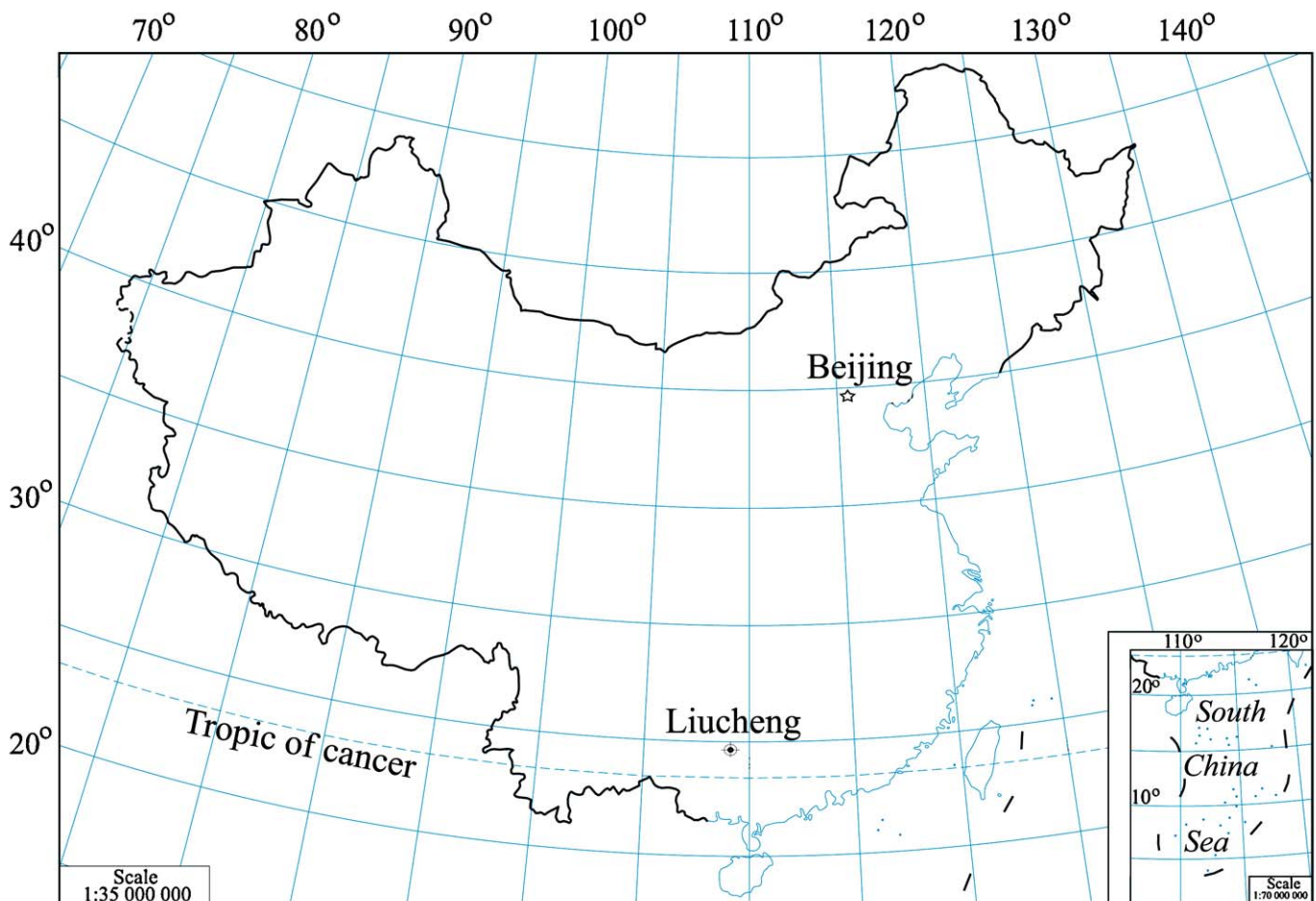


Fig. 1. Sketch map showing the location of the Early Pleistocene Liucheng *Gigantopithecus* Cave, Guangxi, China.  
 Carte de localisation de la Grotte à *Gigantopithecus* de Liucheng (Pléistocène inférieur).

LGC rhino materials resemble the living species *Dicerorhinus sumatrensis*. At present, there is no report about the existence of *D. sumatrensis* of pre-Holocene age in China. The origination of this species is still unknown up to now because of the scarcity of fossil materials. Based on such an incomplete fossil sample like the LGC rhinos, it is difficult to go much further into the study of the evolutionary history of this peculiar species.

### 3. Methods and terminology

The teeth were measured following Guérin (1980). The data were expressed as minimum, maximum, and mean values, respectively; standard deviation and coefficient of variation were calculated. Scatter diagrams were used to show the distribution of the dimensions of each individual tooth. X-ray method was employed in the detection of the lower incisor alveolus of the compared materials.

Concerning the terminology, two different scenarios exist (Fig. 2). The difference of the two scenarios essentially affects the nomenclature for the lophids: the first scenario only recognizes three lophids in the lower cheek teeth (paralophid, metalophid and hypolophid), while the second scenario recognizes four lophids (paralophid, protolophid, metalophid and hypolophid). In the two scenarios, the “protolophid” and the “metalophid” refer to different parts (Fig. 2).

When Osborn (1907: p. 73) established the nomenclature system for the rhinoceros molars, he wrote “in the lower molars (the paraconid is disappearing), the union of the metaconid and protoconid forms the anterior crest or metalophid, while the hypoconid and entoconid unite to form the hypolophid”. The present paper will follow the first scenario of Fig. 2, which originated mainly from Osborn’s system. In the present paper, the cuspids include paraconid, protoconid, metaconid, hypoconid and entoconid; the lophids include paralophid, metalophid and hypolophid.

### 4. Systematic paleontology

Class MAMMALIA Linnaeus, 1875  
Order PERISSODACTYLA Owen, 1848  
Family RHINOCEROTIDAE Owen, 1840  
Subfamily RHINOCEROTINAE Owen, 1845

Tribe RHINOCEROTINI Owen, 1845  
Genus *Dicerorhinus* Gloger, 1841  
*Dicerorhinus sumatrensis* (Fischer, 1814)

**Diagnosis (emended; Pocock, 1945a, 1945b; Groves, 1967; Loose, 1975; Geraads, 1988; Antoine, 2002):** small in size; nasal notch and anterior border of orbit moved backward; post-glenoid not fused with post-tympanic; sagittal crest absent; occipital plane subvertical, occipital outline trapezoidal; orbitonasal length surpassing orbitoaural length; occipitonasal and condylonasal lengths are subequal;  $I^2$  and  $I_1$  absent,  $I^1$  and  $I_2$  reduced.

**Referred material:** the available samples only include mandibles and lower teeth; it is definitely biased by collection management during the past half century.

Mandibles: almost complete in the left horizontal branch with the whole left tooth row and right  $P_2$ - $M_1$  (IVPP V 5779.103); broken mandible with right  $P_4$ - $M_1$  (V 5779.104); mandible fragment with left  $M_{1-3}$  (V 5779.105-1); mandible fragment with right  $M_{1-3}$  (V 5779.105-2).

DP<sub>1</sub>: V 5779.264, V 5779.265.

DP<sub>2</sub>: V 5779.262, V 5779.263, V 5779.266, V 5779.267, V 5779.270, V 5779.269.

DP<sub>3</sub>: V 5779.245, V 5779.247, V 5779.248, V 5779.249, V 5779.250, V 5779.252, V 5779.253, V 5779.254, V 5779.256, V 5779.257, V 5779.258, V 5779.259, V 5779.260, V 5779.261.

DP<sub>4</sub>: V 5779.157, V 5779.162, V 5779.169, V 5779.171, V 5779.177, V 5779.182, V 5779.198, V 5779.204, V 5779.208, V 5779.251, V 5779.180.

P<sub>2</sub>: V 5779.165, V 5779.168, V 5779.223, V 5779.224, V 5779.226, V 5779.228, V 5779.227, V 5779.229, V 5779.230, V 5779.231, V 5779.232, V 5779.233, V 5779.234, V 5779.235, V 5779.236, V 5779.237, V 5779.238, V 5779.239, V 5779.240, V 5779.241, V 5779.242, V 5779.244, V 5779.268.

P<sub>3</sub>: V 5779.154, V 5779.156, V 5779.158, V 5779.159, V 5779.160, V 5779.161, V 5779.163, V 5779.164, V 5779.166, V 5779.167, V 5779.170, V 5779.172, V 5779.173, V 5779.176, V 5779.178, V 5779.179.

P<sub>4</sub>: V 5779.152, V 5779.155, V 5779.175, V 5779.185, V 5779.186, V 5779.187, V 5779.189, V 5779.191, V 5779.196, V 5779.197, V 5779.199, V 5779.202, V 5779.203, V 5779.205, V 5779.206, V 5779.207.

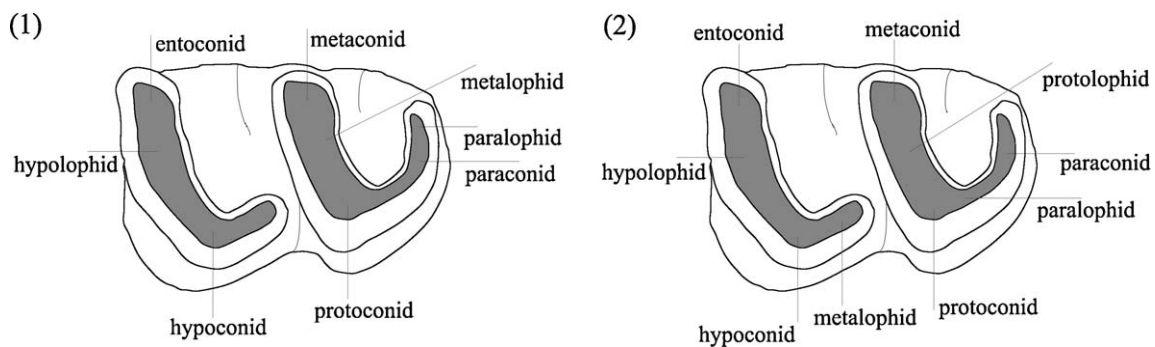


Fig. 2. Terminology of the lower tooth structure of rhinocerotids: (1) after Guérin (1980); (2) Niethammer et al. (1989). (1) and (2) are drawn based on a  $M_2$  of *Dicerorhinus sumatrensis* (IVPP V 5779.152).

Terminologie employée dans la description des dents jugales inférieures de Rhinocerotidae.



M<sub>1</sub>: V 5779.84, V 5779.122, V 5779.123, V 5779.124, V 5779.125, V 5779.128, V 5779.129, V 5779.130, V 5779.144, V 5779.148, V 5779.150, V 5779.151, V 5779.183, V 5779.184, V 5779.190, V 5779.192, V 5779.193, V 5779.194, V 5779.195, V 5779.201, V 5779.212, V 5779.218, V 5779.219, V 5779.220, V 5779.221.

M<sub>2</sub>: V 5779.85, V 5779.86, V 5779.95, V 5779.96, V 5779.97, V 5779.98, V 5779.99, V 5779.108, V 5779.210, V 5779.114, V 5779.115, V 5779.119, V 5779.127, V 5779.139, V 5779.141, V 5779.143, V 5779.147, V 5779.211, V 5779.216, s-1, s-2, s-3, s-4, V 5779.113, V 5779.109, V 5779.174.

M<sub>3</sub>: V 5779.80, V 5779.81, V 5779.82, V 5779.83, V 5779.88, V 5779.89, V 5779.90, V 5779.91, V 5779.92, V 5779.93, V 5779.101, V 5779.102, V 5779.107, V 5779.110, V 5779.111, V 5779.112, V 5779.116, V 5779.117, V 5779.120, V 5779.126, V 5779.133, V 5779.135, V 5779.136, V 5779.138, V 5779.139,

V 5779.140, V 5779.142, V 5779.146, V 5779.153, V 5779.180, V 5779.214, V 5779.215, V 5779.222.

**Repository:** Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Beijing, China.

**Locality and horizon:** Liucheng *Gigantopithecus* Cave, Guangxi, China; Early Pleistocene.

**Description:**

Mandible: mandibles are very poorly represented in the sample. The mandibular body can only be observed on two broken mandibles. The body depth is low relative to that of *R. sondaicus*. The mental foramen located below P<sub>2</sub>-P<sub>3</sub> is very small. The posterior edge of the mandibular symphysis is close to the anterior part of the P<sub>3</sub>. From the ventral view, the lingual mandibular contour is U-shaped (Fig. 3). No trace of the incisor alveolus can be detected in front of P<sub>2</sub>, indicating that the lower incisor should be either reduced or

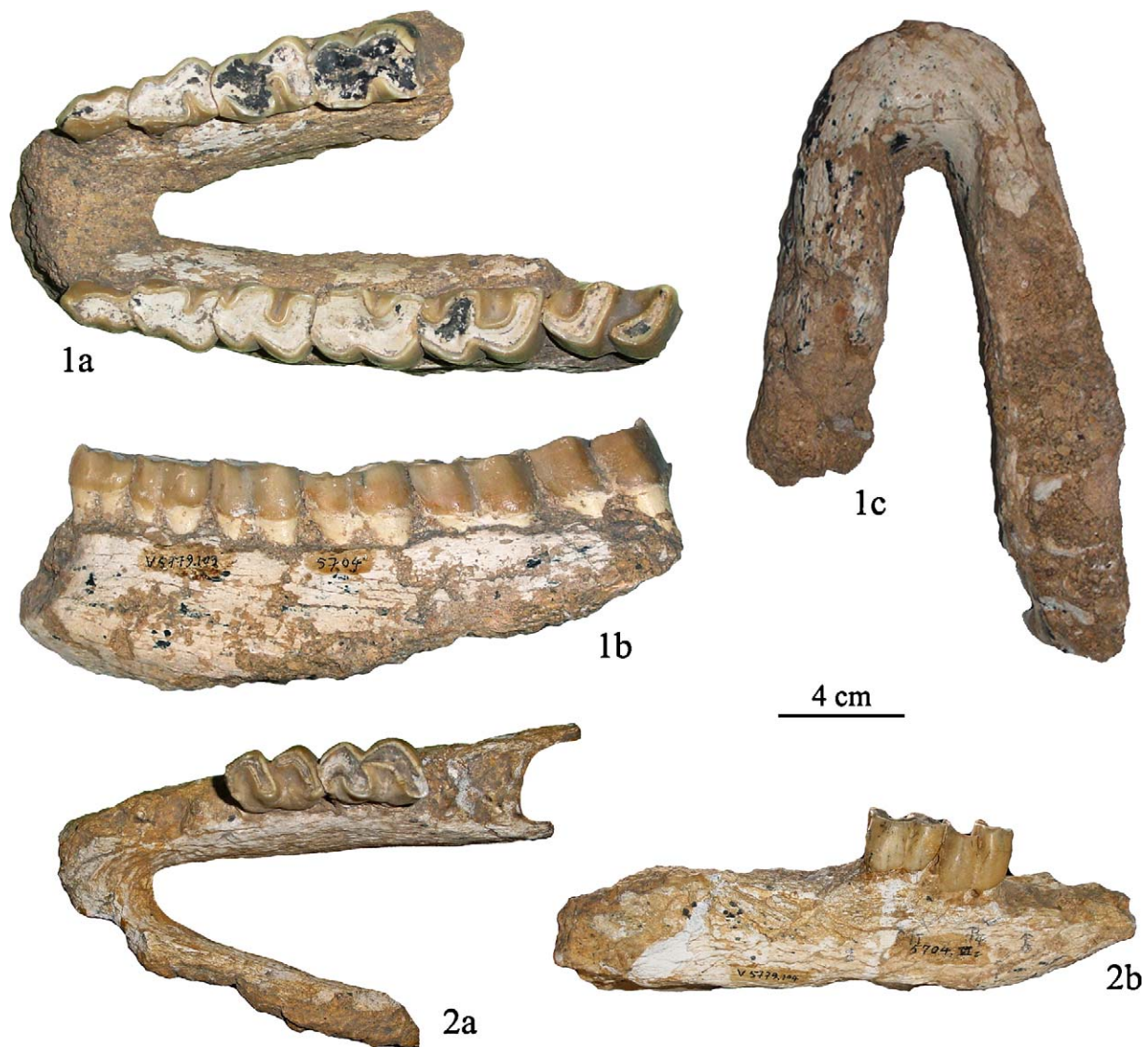


Fig. 3. Mandibles of *Dicerorhinus sumatrensis* from LGC, Guangxi, China (Early Pleistocene). 1: mandible with left P<sub>2</sub>-M<sub>3</sub> and right P<sub>2</sub>-M<sub>1</sub> (V 5779.103); 2: mandible with right P<sub>4</sub>-M<sub>1</sub> (V 5779.104). 1a, 2a: crown views; 1b, 2b: buccal views; 1c: ventral view.

*Mandibules de Dicerorhinus sumatrensis de LGC.*

Table 1

Cheek tooth dimensions (in mm) of *Dicerorhinus sumatrensis* from Liucheng, Guangxi, China (Early Pleistocene).  
*Dimensions (en mm) des dents jugales du Dicerorhinus sumatrensis de Liucheng.*

Tooth	Number of samples	Dimensions	Minimum value	Maximum value	Mean	Standard deviation	Coefficient of variation (%)
DP <sub>1</sub>	2	L	14.5	19.4	–	–	–
		W	9.8	10.4	–	–	–
DP <sub>2</sub>	5	L	23.2	29.1	25.8	2.59	10.05
		W	13.0	14.0	13.4	0.38	2.3
DP <sub>3</sub>	15	L	32.8	49.2	38.5	4.18	10.87
		W	17.5	24.0	20.0	1.95	9.75
DP <sub>4</sub>	10	L	36.0	42.1	37.9	2.07	5.45
		W	18.7	24.0	21.0	1.49	7.07
P <sub>2</sub>	22	L	20.8	28.4	25.0	2.20	8.78
		W	13.7	20.4	16.2	1.44	8.87
P <sub>3</sub>	16	L	26.1	34.8	29.6	2.66	8.99
		W	17.2	24.7	20.3	2.19	10.8
P <sub>4</sub>	16	L	32.3	43.9	36.4	2.85	7.83
		W	20.7	27.1	24.2	1.91	7.88
M <sub>1</sub>	25	L	34.6	45.0	40.0	2.57	6
		W	22.7	31.1	25.2	1.97	7.79
M <sub>2</sub>	25	L	41.4	52.7	45.9	2.69	5.85
		W	25.4	34.2	28.8	2.74	9.53
M <sub>3</sub>	32	L	43.5	52.3	46.5	2.01	4.33
		W	24.0	29.2	26.2	1.31	4.99
P <sub>2</sub> –P <sub>4</sub>	1	L	79.6	–	–	–	–
M <sub>1</sub> –M <sub>3</sub>	3	L	112.8	119.0	115.3	–	–
P <sub>2</sub> –M <sub>3</sub>	1	L	198.0	–	–	–	–

lost. The front part of the symphysis and the ascending rami are broken off.

Teeth: teeth are the most abundant material from the LGC, but most of them are isolated. Only a few broken mandibles survived, either with complete cheek tooth row or with complete molar series.

The values of the measurements (Table 1) of the tooth row are very small, falling completely within the range of *D. sumatrensis*.

DP<sub>1</sub>: only two DP<sub>1</sub>s were recognized among the specimens, and both of them quite well preserved. Morphologically, the first one is very small and simply constructed; it has one lobe, and the valley is not prominent. The second DP<sub>1</sub> is almost unworn; it has two lobes, the metalophid and the hypolophid, but the latter is much smaller than the former; both the anterior and the posterior valleys are shallow and open. The ectoflexid is almost indistinct. The enamel layer is very thin. There are two roots (Figs. 4(1, 2)). The diversified form of DP<sub>1</sub> is supposed to be related to sexual dimorphism or more widely intraspecific variability.

DP<sub>2</sub>: morphologically, two kinds of DP<sub>2</sub> can be recognized. One of them has the posterior valley closed on the lingual side by an enamel wall that is formed by the metaconid and the entoconid (V 5779.270); but most of them are open. The axis of the posterior valley is oblique instead of perpendicular to the long axis of the tooth. The anterior valley is very narrow and V-shaped, and there is no prominent gulf in the anterior lobe. The protoconid fold is thick and well separated from the paraconid and metaconid by remarkable grooves. The ectoflexid is becoming eminent in some individuals. The average Wa and Wp are 12.2 mm and 13.4 mm, respectively (Figs. 4(3–5)). The

DP<sub>2</sub>s are similar to P<sub>2</sub>s in size, but differ in having the anterior contact facet in 5/6 specimens of DP<sub>2</sub> (in 23 samples of P<sub>2</sub>s, no anterior contact facet was detected). Additionally, DP<sub>2</sub>s usually are relatively longer than P<sub>2</sub>s, and show more folds.

DP<sub>3</sub>: relative to DP<sub>2</sub>, the most remarkable difference of DP<sub>3</sub> is its larger size and the development of a parastylid and the anterior and posterior valleys. Some of the DP<sub>3</sub>s are even bigger than DP<sub>4</sub>s. The paralophid is very developed and sometimes is furcated. On the lingual side of the parastylid, a small gulf exists, sometimes with a faint cingulum. The anterior and the posterior lobes are almost equal. The ectoflexid is very deep. The average Wa and Wp are 17.3 mm and 20 mm, respectively.

DP<sub>4</sub>: among the lower deciduous teeth, DP<sub>4</sub> is characterized by its high degree of molarization and the very open valleys, both anterior and posterior. There are anterior and posterior cingula. The average Wa and Wp are 19 mm and 21 mm, respectively.

The dimensions of the deciduous teeth are very well clustered (Fig. 5). However, DP<sub>3</sub> and DP<sub>4</sub> are mixed to some extent.

The P<sub>2</sub> is a small and simple-structured tooth, whose anterior lobe is tipped at the anterior portion. Most of the valleys are V-shaped, but the variation is also remarkable (Fig. 6), because most of the anterior valleys and some of the posterior valleys are not well developed; and some of the posterior valleys are closed on the lingual side. The length of DP<sub>2</sub> and P<sub>2</sub> is very similar, but the difference lies in the latter has higher tooth crown and thicker enamel layer as well as larger W/L ratio. The average Wa and Wp are 14.2 mm and 16.2 mm, respectively. The P<sub>2</sub>s are much smaller than that of *R. sinensis* (Colbert and Hooijer, 1953).



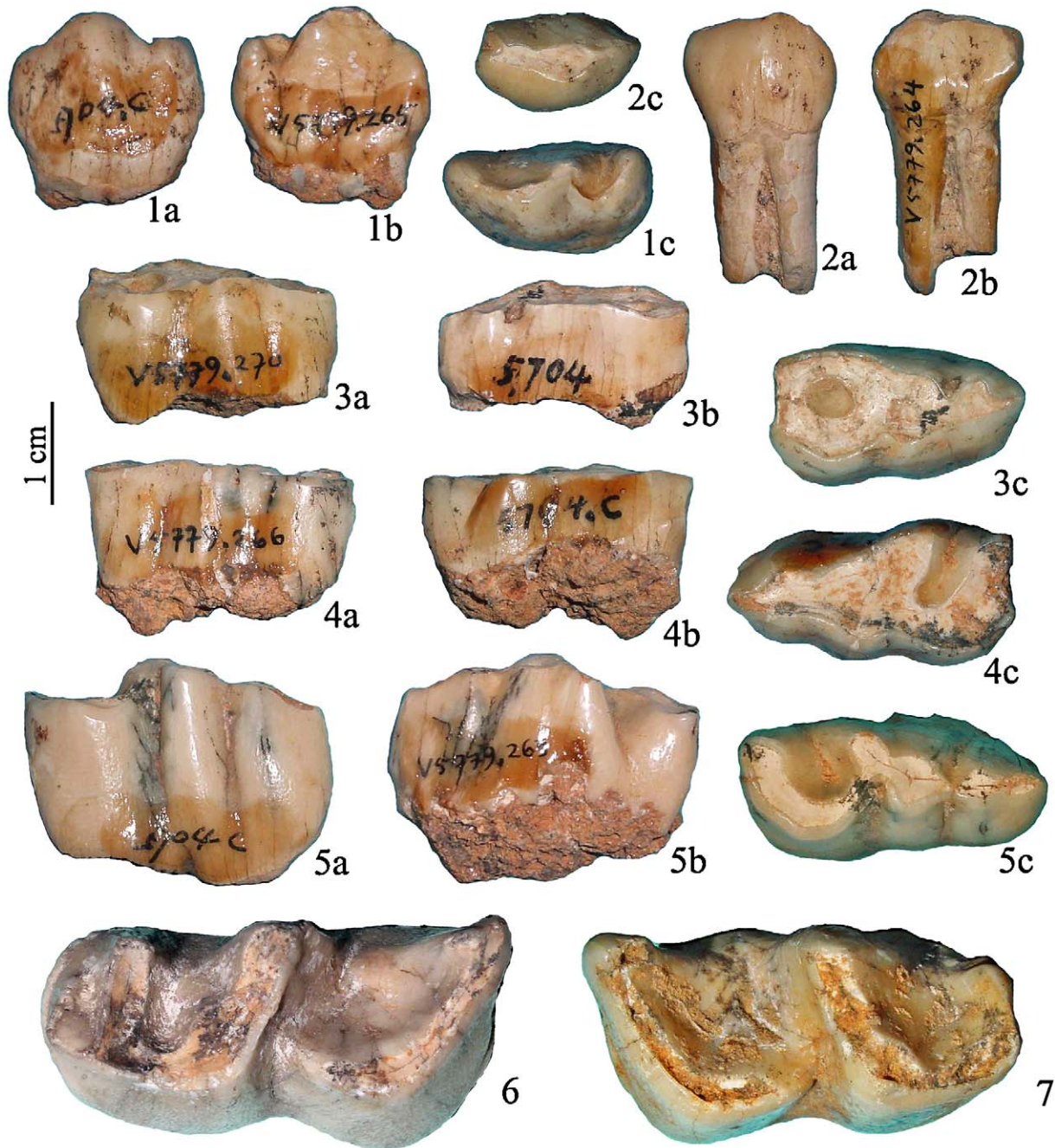


Fig. 4. Deciduous teeth of *Dicerorhinus sumatrensis* from LGC, Guangxi, China (Early Pleistocene). 1: left DP<sub>1</sub> (V 5779.265); 2: right DP<sub>1</sub> (V 5779.264); 3: right DP<sub>2</sub> (V 5779.270); 4: left DP<sub>2</sub> (V 5779.266); 5: right DP<sub>2</sub> (V 5779.263); 6: left DP<sub>3</sub> (V 5779.245); 7: right DP<sub>4</sub> (V 5779.169). 1a to 5a: buccal views; 1b to 5b: lingual views; 1c to 5c, 6 and 7: occlusal views.

*Dents de lait de Dicerorhinus sumatrensis de LGC.*

P<sub>3</sub> is remarkable by its short length and a strongly reduced Wa/Wp ratio. The anterior valley is narrow. The paralophid is not developed. The posterior valley is situated more backward than in P<sub>4</sub> and molars. The anterior width is much smaller than that of the posterior one. The average Wa and Wp are 17.6 mm and 20.3 mm, respectively.

P<sub>4</sub> is larger than P<sub>3</sub> and smaller than M<sub>1</sub>. The paralophid is relatively more developed than in P<sub>3</sub>, but not so much as in the molars. At the antero-external corner, a faint cingulum exists.

There exists a narrow groove at the bottom of the posterior valley. The Wa/Wp ratio is obviously larger than that of P<sub>3</sub>, but the posterior width is still obviously larger than that of the anterior one. The average Wa and Wp are 22.4 mm and 24.2 mm, respectively.

M<sub>1</sub> has almost anterior and posterior widths identical. There exists a narrow groove at the bottom of the posterior valley. The Wa is very close to Wp. The average Wa and Wp are 24.2 mm and 25.2 mm, respectively.

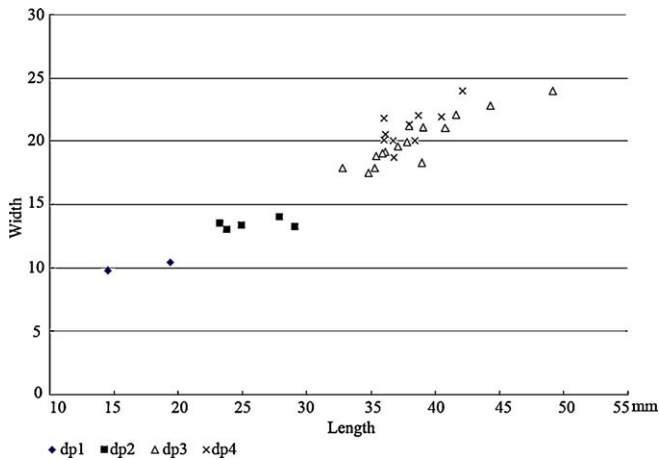


Fig. 5. Scatter diagram of lower deciduous teeth of *Dicerorhinus sumatrensis* from LGC, Guangxi, China (Early Pleistocene).  
 Diagramme de dispersion longueur-largeur des molaires de lait inférieures de *Dicerorhinus sumatrensis* de LGC.

M<sub>2</sub> has an almost equal width of both the anterior and the posterior lobes. There exists a narrow groove at the bottom of the posterior valley. The average Wa and Wp are 27.8 mm and 28.8 mm, respectively. The M<sub>2</sub>s can be distinguished from M<sub>3</sub>s in having both the anterior and posterior contact facets. For the unworn teeth, M<sub>2</sub> is determined mainly according to the Wa/Wp ratio.

M<sub>3</sub> has a high Wa/Wp ratio, with a posterior cingulum. The anterior width is a little larger than the posterior one. The anterior and posterior valleys are largely open. The average Wa and Wp are 26.3 mm and 26.2 mm, respectively: M<sub>3</sub> is the only tooth that has the anterior width slightly larger than the posterior width.

The dimensions of the lower permanent molars are not so well clustered as DP<sub>1</sub> and DP<sub>2</sub> as well as the premolars, but the M<sub>1</sub>s are distinctly separated from the M<sub>2</sub>s and the M<sub>3</sub>s (Fig. 7). Many M<sub>2</sub>s and M<sub>3</sub>s overlap in the scatter diagram (Fig. 8). It means that premolars are easier to be distinguished from one another, but the size difference among the molars is very slight, especially between M<sub>2</sub> and M<sub>3</sub>; in the scatter diagram, these two sorts of tooth are almost mixed.

Although some parts of the horizontal ramus of the mandible have been preserved, very limited features about the mandibular body can be recognized. We have to employ the evidence from the dimensions of the teeth to discover some useful traits.

A total of 177 isolated teeth were measured, nine of which are broken and were not taken into account in the statistical analysis in Table 1. From the values of the coefficient of variation, it can be seen that the lengths of DP<sub>2</sub> and DP<sub>3</sub> as well as the width of P<sub>3</sub> are among the most variable dimensions. The least variable tooth is M<sub>3</sub>.

In the scatter diagram, P<sub>2</sub>, P<sub>3</sub> and P<sub>4</sub> are distinctly separated, only very small overlap exists between P<sub>2</sub> and P<sub>3</sub> (Fig. 7). Although the molars are not so well separated from one another, the M<sub>1</sub>s' ranges are distinctly defined.

5. Comparisons and discussions

5.1. Comparisons in morphological characters of mandible and teeth

The characters of *D. sumatrensis* are fairly well defined as follows: channel beneath the auditory orifice in the skull open, but very narrow inferiorly in some old skulls; occipitonasal and

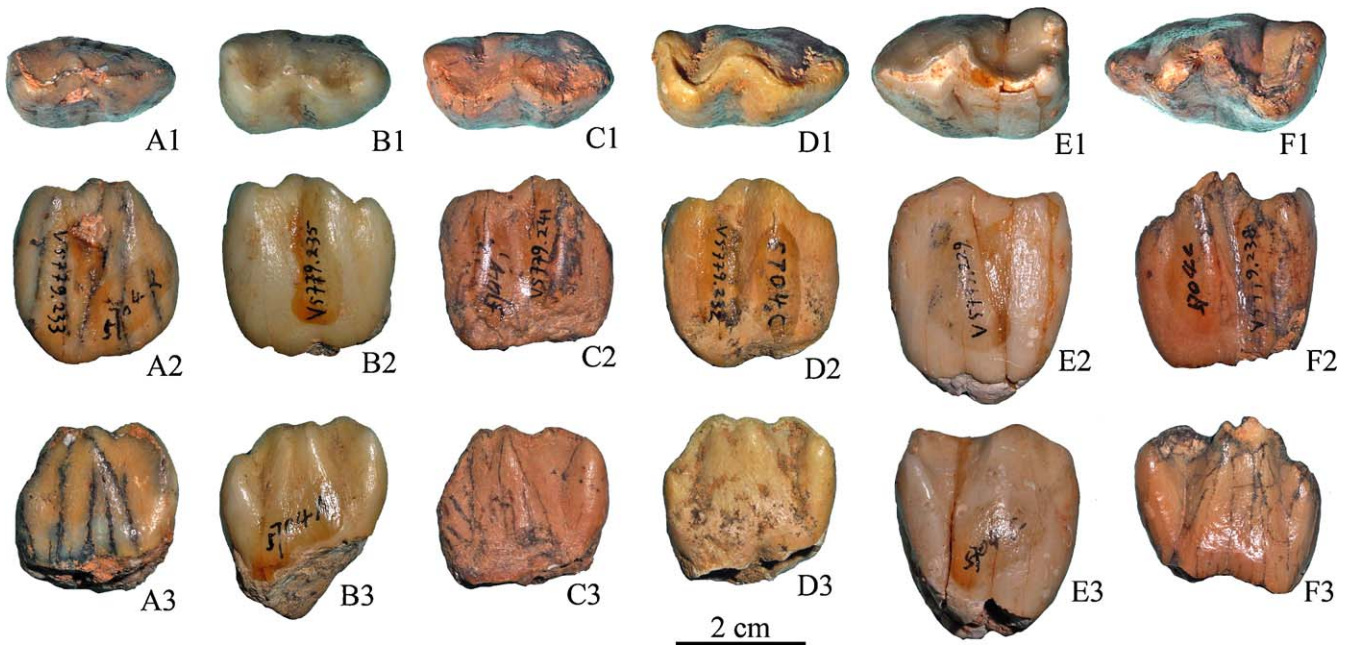


Fig. 6. Morphological variations of P<sub>2</sub> of *Dicerorhinus sumatrensis* from LGC, Guangxi, China (Early Pleistocene). A1–F1. Occlusal views. A2–F2. Buccal views. A3–F3. Lingual views.  
 Variation morphologique des P<sub>2</sub> de *Dicerorhinus sumatrensis* de LGC.



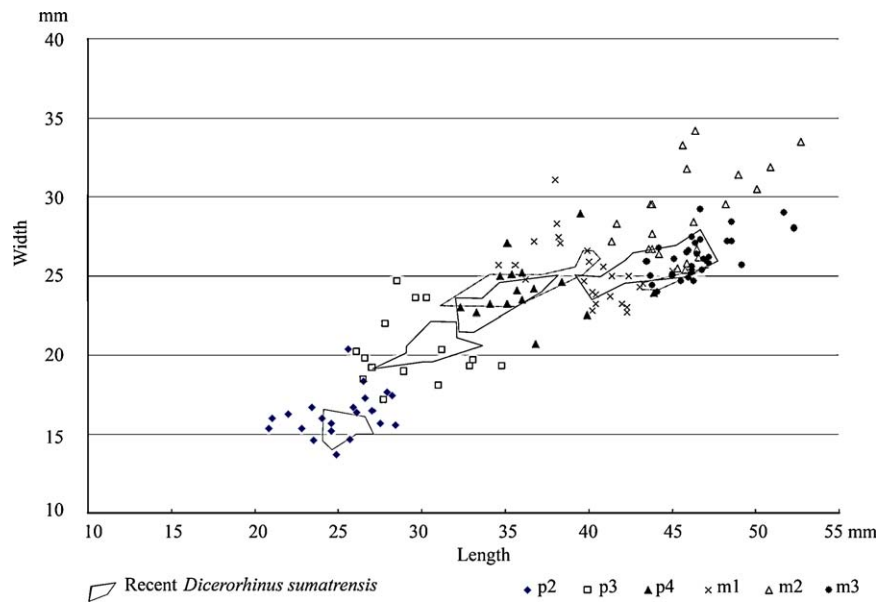


Fig. 7. Scatter diagram of lower cheek teeth of *Dicerorhinus sumatrensis* from LGC, Guangxi, China (Early Pleistocene). The outlines represent the ranges of the corresponding teeth of the living *D. sumatrensis*; it shows the weak overlapping of the ranges of  $M_1$  and  $M_2$  between the fossil and the living specimens. *Diagramme de dispersion longueur-largeur des dents jugales inférieures de Dicerorhinus sumatrensis de LGC.*

condylo-nasal lengths subequal; orbitonasal length surpassing the orbitoaural length; two horns, etc (Pocock, 1945b). But nothing is mentioned about the mandible and lower teeth in Pocock's paper.

Groves (1983) selected 42 characters to compare the living rhino species, 15 of which being associated with *D. sumatrensis*, with only one autapomorphy, i.e. the loss of the lower first (or central) incisor (Fig. 9). Groves gave the following conclusion about the characters of *Dicerorhinus*: "Mandibular symphysis abbreviated, with loss of lateral

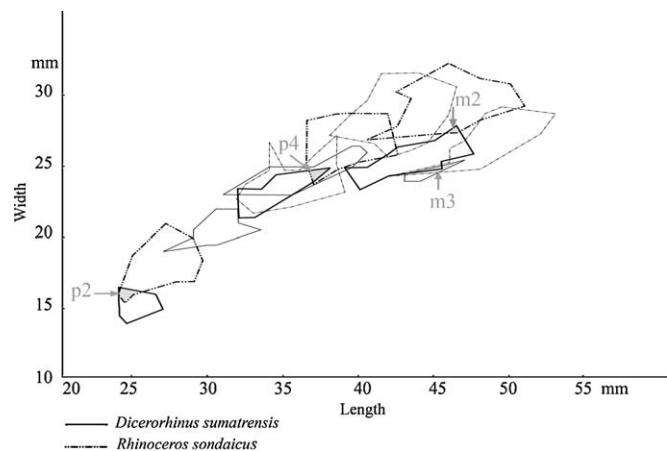


Fig. 8. Comparison of the recent *Dicerorhinus sumatrensis* and *Rhinoceros sondaicus* in scatter diagram of the lower cheek teeth. It shows that there exists very little overlap (shaded areas) between the counterpart teeth of these two species. The outlines of the ranges were defined by connecting the outermost points of each cluster.

*Diagramme de dispersion longueur-largeur des dents jugales inférieures de Dicerorhinus sumatrensis et Rhinoceros sondaicus actuels.*

diastema ridges; inferior border of mandible convex, angle reduced; ascending ramus slopes backward; upper and lower incisors very reduced, peg-like, or more usually absent; foreleg longer than hindleg". Additionally, the mandibular foramen is under the level of alveoli (Guérin, 1980).

From a morphological point of view, *D. sumatrensis* is commonly considered to retain a large number of primitive characters, which explains why it is so difficult to classify with respect to the other rhinoceros species (Groves, 1983). *D. sumatrensis* is also the most primitive member of its genus (Groves, 1967). In the cladistic analysis of Cerdeño (1995, 1996), *Dicerorhinus* is characterized by at least five reversals to plesiomorphic states (cranial dorsal profile flattened, vertical occipital face, protocone on upper premolars and upper molars not constricted, high and narrow astragalus); it is grouped with *Rhinoceros* and *Punjabitherium*.

In the cladogram proposed by Antoine (2002), *D. sumatrensis* is at the node between *Coelodonta* and the Asian extant *Rhinoceros*, and its cladistic diagnosis is proposed.

In regard to the mandible of *D. sumatrensis*, some features can be used to identify the materials from LGC, such as the reduced lower incisor and the small mental foramen. The mandible from LGC has a very tiny mental foramen, which is much smaller than that of *R. unicornis*. In the species of *Dicerorhinus*, and *Coelodonta*, the small mental foramen is very typical.

Concerning the identification of the isolated teeth, Hooijer (1946) presented comments on previous studies and made some comparisons of the upper molars, concluding that the mandibular teeth did not furnish any specific characters. It is even impossible to determine the serial position of the loose lower molars, although Bacon et al. (2004) made an attempt to distinguish the isolated teeth of *R. sondaicus* from those of



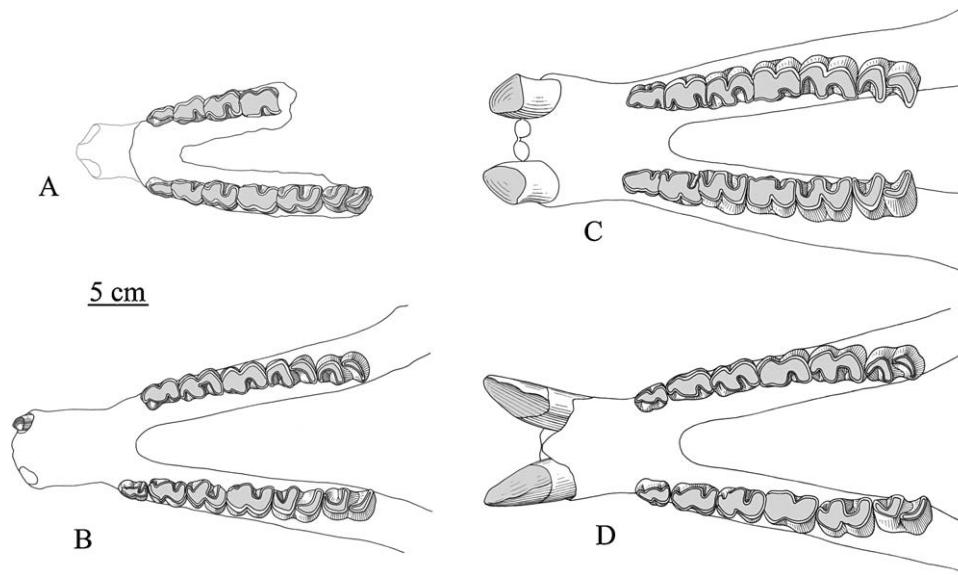


Fig. 9. The mandible of *Dicerorhinus sumatrensis* from LGC, Guangxi, China (Early Pleistocene), compared with the extant Asiatic rhino species. **A.** *D. sumatrensis*, fossil from LGC (V 5779.103). **B.** *D. sumatrensis*, recent (MNHN A7965). **C.** *Rhinoceros unicornis* (MNHN A7971). **D.** *Rhinoceros sondaicus* (MNHN 1960.59). All in crown views.

*Mandibule de Dicerorhinus sumatrensis de LGC, comparée avec des spécimens actuels de D. sumatrensis, Rhinoceros unicornis et Rhinoceros sondaicus.*

*D. sumatrensis*. The ectolophid groove is deep and acute down to the neck in the lower molars of *R. sondaicus*.

It may be concluded that it is quite possible to distinguish rhinoceros skulls of different species, whereas the determinations for poorly preserved mandibles and isolated lower teeth are really not easy. Indeed, the inter-specific similarity and the intra-specific variation make it more difficult to determine the isolated teeth of rhinos to the specific level. The only practical solution is to make some comparisons of dimensions and W/L ratios for the isolated teeth.

### 5.2. Comparisons of teeth and tooth row dimensions

Considering the wide variation in tooth morphology, we have to search for other solutions to distinguish the isolated teeth. There is a difference in size between the corresponding molars and premolars of recent *D. sumatrensis* and recent *R. sondaicus*, the dimensions in the former being as a rule smaller than in the latter (Hooijer, 1946; Tables 2 and 3; Fig. 8). Additionally, the W/L ratios of the teeth of *D. sumatrensis* are always larger than that of *R. sondaicus* (Fig. 8). Compared with the two extant rhino species in Southeast Asia (Tables 2 and 3),

it seems that the rhino material from the Liucheng *Gigantopithecus* Cave is much more similar to *D. sumatrensis* than to *R. sondaicus* in tooth row and P<sub>2</sub> dimensions.

In the monograph on the Yanjinggou (Yenchingkou) Fauna by Colbert and Hooijer (1953), some mandibles of *R. sinensis* with complete lower cheek tooth row were mentioned in the material list, but without detailed descriptions nor measurements. Fortunately, the authors provided some measurements of two other mandibles with P<sub>2</sub>-M<sub>2</sub>. The lengths of P<sub>2</sub>-M<sub>2</sub> are 220 mm (A.M.N.H. No. 18780) and 224 mm (A.M.N.H. No. 18628), respectively (calculated from Colbert and Hooijer's data in Table 37). In the living form of *D. sumatrensis* (C/034) in the IVPP collection, the lower cheek tooth row length is 212 mm (P<sub>2</sub> and P<sub>3</sub> are not in position). Groves (1967) measured the tooth row lengths of *R. sondaicus* and *D. sumatrensis*, the range of the former being 227–240 mm (Table 2), and of the latter 191–220 mm (Table 3); but the values are not specified to upper or lower rows. Guérin (1980) also measured the lower cheek tooth row length: the range for *D. sumatrensis* is 175–222 mm (sample size is 13); the range for *R. sondaicus* is 211.5–257 mm (sample size is 24; Table 4). These dimensions shows that there is almost

Table 2

Comparison of LGC specimens with the tooth row and P<sub>2</sub> length of recent adult *Rhinoceros sondaicus* measured by Groves (1967). Numbers in parenthesis: sample size.

*Comparaison des dimensions des rangées dentaires et des P<sub>2</sub> de Rhinoceros sondaicus actuel (d'après Groves, 1967) et des spécimens de LGC. Entre parenthèses : nombre de spécimens.*

	LGC	Java	Sumatra	Malaya	Vietnam	Bengal
Tooth row length	198	227.1 ± 8.1 (14)	232.5 ± 4.9 (6)	225.5 ± 7.8 (2)	230.0 ± 2.8 (2)	240.0 ± 5.0 (4)
P <sub>2</sub> length	25.1 (22)	27.5 ± 2.5 (7)	26.9 ± 1.7 (5)	28.6 ± 2.7 (3)	23.8 ± 2.4 (2)	27.1 ± 2.7 (3)

Table 3  
Comparison of LGC specimens with the tooth row and P<sub>2</sub> length of recent adult *Dicerorhinus sumatrensis* measured by Groves (1967). Numbers in parenthesis: sample size.

*Dimensions des rangées dentaires et de P<sub>2</sub> de Dicerorhinus sumatrensis actuel (d'après Groves, 1967). Entre parenthèses : nombre de spécimens.*

	LGC	Borneo	Sumatra	Malaya	Pegu	Burma
Tooth row length	198	190.7 ± 10.6	201.3 ± 14.4	193.8 ± 12.3	208	219.7 ± 2.4
P <sub>2</sub> length	25.1 (22)	22.8 ± 2.0 (7)	24.5 ± 1.8 (10)	24.8 ± 1.8 (8)	–	28.0 ± 0.3 (2)

Table 4  
Tooth row dimensions (in mm) of *Dicerorhinus sumatrensis*, compared with other species of both living and fossil forms.  
*Dimensions (en mm) comparées des rangées dentaires.*

Taxa	Geologic time	Upper tooth row length	Lower tooth row length	M <sub>1–3</sub> length	Sources
<i>Dicerorhinus sumatrensis</i>	Recent	180.5–232	175–222	103–133.5	Guérin, 1980
<i>Rhinoceros sondaicus</i>	Recent	219–264	211.5–257	126.5–147	Guérin, 1980
<i>Diceros bicornis</i>	Recent	222–316	222–308	123.5–178	Guérin, 1980; unpublished data
<i>Ceratotherium simum</i>	Recent	245.5–314	236.5–304	138–175	Guérin, 1980; unpublished data
<i>Rhinoceros unicornis</i>	Recent	248–288	242–276	147.5–161	Guérin, 1980
<i>Dicerorhinus sumatrensis</i>	Holocene	208	–	123.5–147	Wei et al., 1989; Guérin, unpublished data
<i>Dicerorhinus choukoutienensis</i>	Middle Pleistocene	300	292	–	Chow, 1963a, 1979; Wang, 1931
<i>Rhinoceros sinensis</i>	Middle Pleistocene	225–259	–	–	Colbert and Hooijer, 1953
	Middle Pleistocene	290	–	–	Matthew and Granger, 1923
<i>Dicerorhinus sumatrensis</i>	Early Pleistocene	–	198	112.8–119	This paper
<i>Dicerorhinus yunchuensis</i>	Early Pleistocene	259	–	–	Chow, 1963b
<i>Rhinoceros sinensis</i>	Early Pleistocene	267 (DP <sup>1</sup> -M <sup>3</sup> ) 255 (P <sup>2</sup> -M <sup>3</sup> )	–	–	You et al., 1978
<i>Chilotherium gracile</i>	Pliocene	244 (DP <sup>1</sup> -M <sup>3</sup> )	219	–	Qiu, 1979
<i>Chilotherium fenhoense</i>	Pliocene	236–251 (DP <sup>1</sup> -M <sup>3</sup> )	212–233	–	Tong et al., 1975
<i>Chilotherium cornutum</i>	Late Miocene	250 (DP <sup>1</sup> -M <sup>3</sup> )	–	–	Qiu and Yan, 1982

no overlap between the ranges of *D. sumatrensis* and *R. sondaicus*. The tooth row length of the LGC mandible is 198 mm, which falls well within the range of *D. sumatrensis* (Fig. 10). However, the tooth length ranges of the individual teeth show that the overlap between *D. sumatrensis* and *R. sondaicus* is quite common (Fig. 11).

Compared with the dominant taxa of fossil rhinocerotids recovered in China, the *D. sumatrensis* specimens from LGC are the smallest both in tooth row length and in isolated teeth dimensions (Table 4 and Fig. 10). Although the LGC has only given a few good specimens, they could provide enough evidence to show that they are different from *R. sinensis*, especially in tooth dimensions (Fig. 11).

### 5.3. Incisor alveolus

The reduced incisor provides positive evidence in identifying *D. sumatrensis*. The x-ray scanning of a recent specimen shows that the alveoli of the lower incisors of *D. sumatrensis* do not extend very far backward inside the mandibular symphysis. On the contrary, the alveoli of the lower incisors of *R. unicornis* can reach as far back as to the lingual side of P<sub>2</sub> (Fig. 12). In the fossil materials, only two mandibles have the symphysis part preserved (V 5779.103 and V 5779.104), but neither of them shows the trace of the lower incisor alveoli. It means that the alveoli of the lower incisors do not reach very far backward, which coincides with the character of the living *D. sumatrensis*.

## 6. On the geological age of Liucheng Gigantopithecus Cave Fauna

The representative elements of the LGC fauna include the following taxa:

- *Gigantopithecus blacki*;
- *Ailuropoda micrata*;
- *Sinicuon dubius*;
- *Pachycrocuta licenti*;
- *Arctonyx minor*;
- *Sivapanthera pleistocaenicus*;
- *Felis teilhardi*;
- *Sinomastodon intermedius*;
- *Stegodon preorientalis*;
- *Tapirus peii*;
- *Hesperotherium sinense*;
- *Dicoryphochoerus ultimus*;
- *Potamochoerus nodosarius*;
- *Dorcabune liuchengense*;
- *Muntiacus lacustris*;
- *Cervus fenqii*;
- *Megalovis guangxiensis*.

This assemblage is typical of the Early Pleistocene of South China, making the *D. sumatrensis* specimens described herein the earliest occurrence of this species in China.

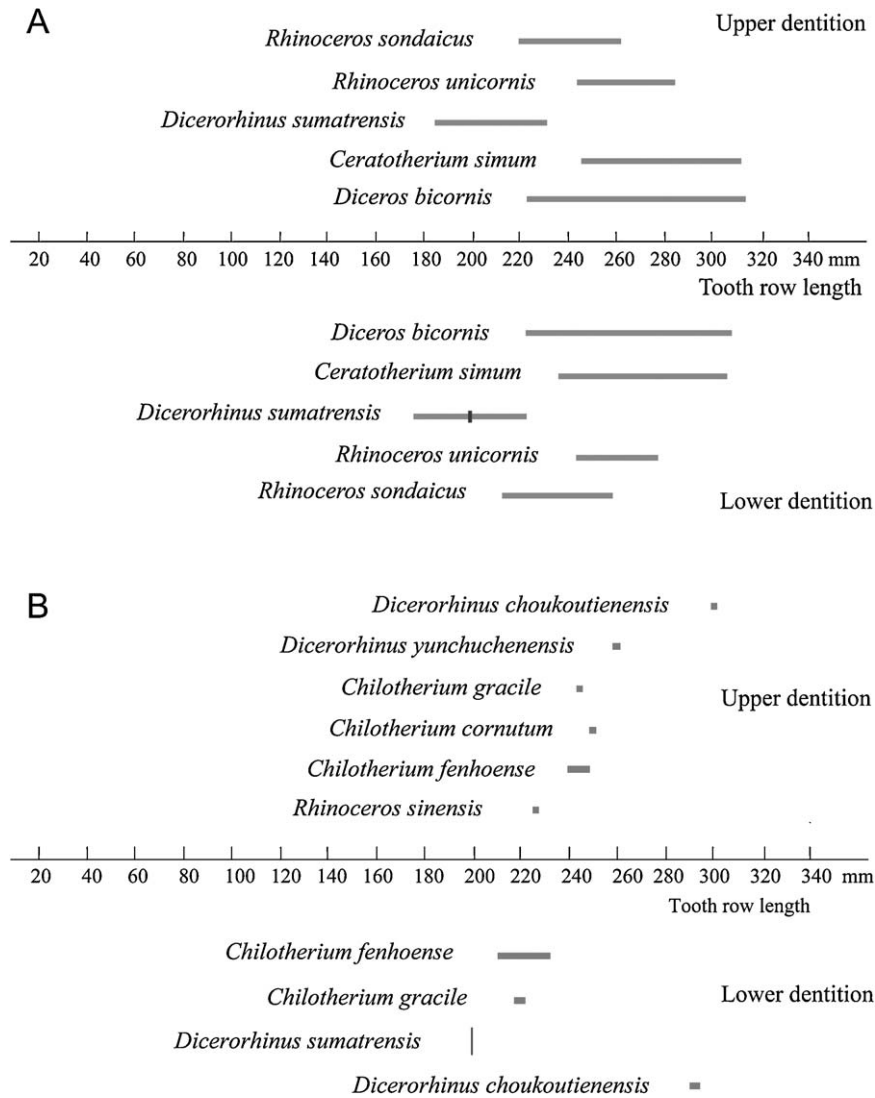


Fig. 10. Tooth row length comparisons. **A.** With the five extant rhino species (data from Guérin, 1980). **B.** With other fossil and subfossil rhinocerotids (data sources: see Table 4). The vertical bar represents the LGC material.

Comparaison de la longueur des rangées dentaires des rhinocéros actuels et fossiles (pour les sources voir le Tableau 4).

Table 5

Fossil and sub-fossil records of *Dicerorhinus sumatrensis* ever reported.

Gisements à *Dicerorhinus sumatrensis* fossiles et subfossiles.

Locality	Age	Materials	Sources
Hemudu (China)	6570–6950	4 pieces	Wu, 1983; Wei et al., 1989
Lida Ayer, Sumatra (Indonesia)	80,000 yrs	22 pieces	Hooijer, 1946; Vos, 1983 Long et al., 1996
Punung, Java (Indonesia)	80,000 yrs	37 pieces	Badoux, 1959; Vos, 1983 Long et al., 1996
Niah Cave, Borneo (Malaysia)	40,000 yrs	–	Medway, 1966
Borneo (Malaysia)	Late Pleistocene-Holocene	DP3, dp4, M1, 2 × M2, M3, p3, p4, m1, m1/m2, m3, 3 × radius, 3 × Mc III, 3 × Mc IV, 2 × calcaneum, talus, humerus, tibia, patella, cuboid, scaphoid, unciform, magnum, vertebrae, scapula, MtII, 3rd phalanx	Cranbrook, 1986
Sibrambang, Sumatra (Indonesia)	Late Pleistocene	–	Vos, 1983
Lang Trang (Vietnam)	Late Pleistocene	190 pieces	Long et al., 1996
Cave II, breccia 5			
Duoi U’Oi (Vietnam)	Late Pleistocene	m2, m3	Bacon et al., 2008
Tam Hang (Cambodge)	M-L Pleistocene	Cheek teeth	Beden et al., 1972
Sosianwali, Siwaliks (Pakistan)	Middle Miocene	P <sup>2</sup> ( <i>Didermocerus</i> aff. <i>sumatrensis</i> )	Heissig, 1972



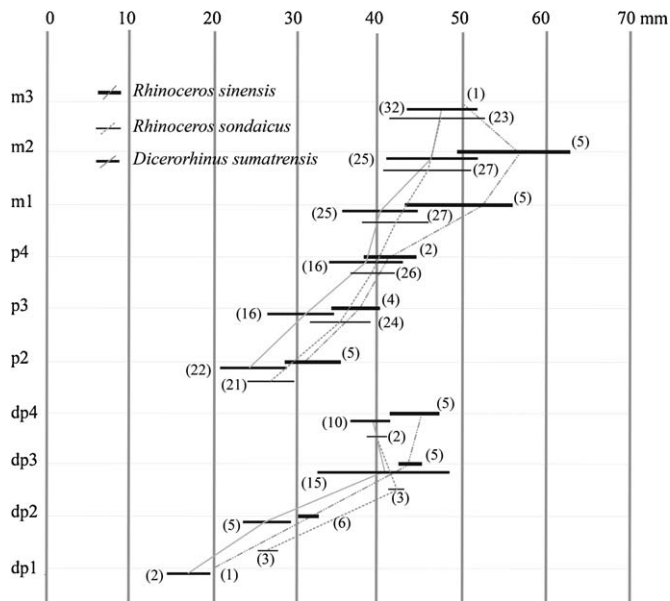


Fig. 11. Ranges of tooth length of *Dicerorhinus sumatrensis* from LGC, Guangxi, China (Early Pleistocene), compared with that of *Rhinoceros sinensis* from Yanjinggou and the recent *Rhinoceros sondaicus*. Very few overlaps exist in ranges between *Dicerorhinus sumatrensis* and *R. sinensis*, but overlaps between *Dicerorhinus sumatrensis* and *R. sondaicus* are quite common. Numbers in parenthesis: sample size; data for *R. sinensis* after Colbert and Hooijer, 1953; data for recent *R. sondaicus* provided by Guérin.

*Dimensions comparées des dents de Dicerorhinus sumatrensis de LGC avec les Rhinoceros sondaicus actuels et les Rhinoceros sinensis fossiles. Entre parenthèses : nombre de spécimens.*

The earliest representative of this species was traced back to Middle Miocene (Heissig, 1972), but the material is too poor to support this assumption. Up to now, the knowledge about the fossil records of *D. sumatrensis* is still very limited (Table 5), just like Groves and Kurt (1972) said: “the pre-Holocene distribution of *D. sumatrensis* is a complete mystery”. Cerdeño (1998) once mentioned that *D. sumatrensis* has a geological distribution since the Early Pleistocene, but no further details are available.

In China, most of the fossil materials once referred to the genus *Dicerorhinus* have nothing to do with the species *D. sumatrensis*, because they show characters such as big size, partially ossified nasal septum, more molarized premolars, fusion of postglenoid and posttympanic, great mastoid inflation, incisor loss, etc, which are absent in *Dicerorhinus* but exist in *Stephanorhinus*.

Concerning the possible ancestors of *D. sumatrensis*, the second author of this paper proposes that two other species, *Dicerorhinus sansaniensis* (Lartet, 1851) in Europe and *Dicerorhinus leakeyi* Hooijer, 1966 in Africa, should be taken into consideration as nearby relatives. The position is far from clear, however, because even the arguments about the phylogenetic position of the living form of this species are still ongoing. A recently published paper (Zin-Maung-Maung-Thein et al., 2008) established a new species, *Dicerorhinus gwebinensis*, which is more similar in morphology to the extant species *D. sumatrensis*. The materials of this new species were recovered in the Plio-Pleistocene Irrawaddy sediments in central Myanmar, which can throw some new light on the study of this kind of rhinos.

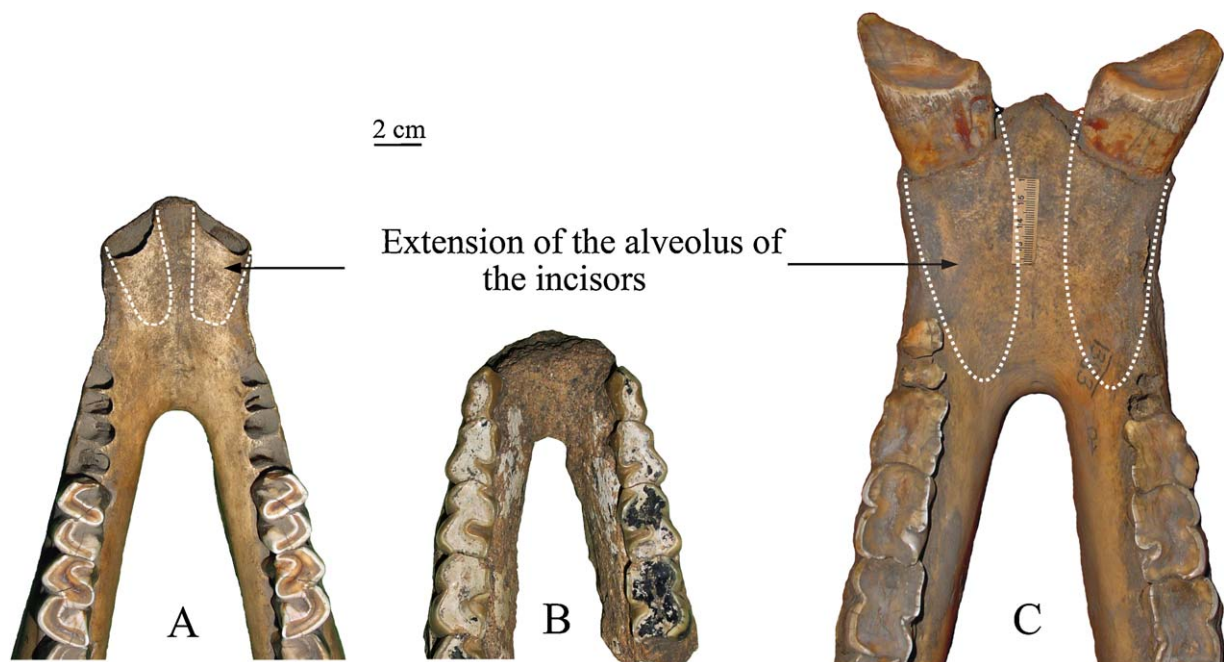


Fig. 12. Comparison of incisor alveolus of selected rhinocerotids. The extension of the incisor alveolus was defined based on the x-ray radiography. A. *Dicerorhinus sumatrensis*, recent (IVPP C/O.34). B. *D. sumatrensis*, fossil from LGC (V5779.103). C. *Rhinoceros unicornis*, recent (IVPP OV 1383). The incisor alveoli of living and fossil *D. sumatrensis*, are not extended so far backward as that of *R. unicornis*.

*Comparaison de la taille des alvéoles des incisives entre Dicerorhinus sumatrensis et Rhinoceros unicornis.*

## 7. Conclusion

The fossil specimens from the Liucheng *Gigantopithecus* Cave can be referred to *D. sumatrensis* according to the following characters: small size, undeveloped incisors, small mental foramen and U-shaped lingual mandibular contour. This material represents the earliest known record of *D. sumatrensis* in China, being of Early Pleistocene age. It is also the smallest rhinocerotid of Pleistocene age ever discovered in China.

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## Postscript

In the collection of IVPP, there is a broken skull (V2877) of a rhinocerotid, which has the following parts preserved: complete nasal, left side of maxilla and zygomatic arch, premaxilla, left cheek tooth row ( $M^3$  not *in situ*) and right  $P^2$ . Unfortunately, we were unable to find any information about the origin (location and horizon) of this specimen. However, it seems that the material is Pleistocene in age, based on its degree of fossilization.

This specimen is valuable for taxonomic studies, because it is the only relatively complete skull of *D. sumatrensis* of

probable Pleistocene age recognized in China up to now. This skull is described below.

Systematic paleontology (Suprageneric system as the foregoing text)

Genus *Dicerorhinus* Gloger, 1841

*Dicerorhinus sumatrensis* (Fischer, 1814)

## Description:

Nasal: the nasal bone is robust, but terminates anteriorly in a point and bends downward; the ventral surface of the nasal bone is spoon-like; quite deep nasal opening.

Frontal: part of the frontal is preserved. The cranial profile is quite flat relative to that of the saddle-shaped *R. sondaicus*.

Horn bosses: a slight rugosity of nasal horn boss can be detected on the middle of the nasal bone, in the center of the boss, there exists a sharp tiny elongated tubercle; the frontal horn boss is represented by a less pronounced boss which is located just in front of the level of the orbit.

Left side of the skull: the left anterior part of the skull is almost completely preserved. But the sutures around maxilla, nasal, frontal and lacrimal are undetectable; infraorbital foramen is large; there exists a prominent infraorbital depression; on the lacrimal bone, there occurs a moderately developed lacrimal tubercle; the root of the zygomatic arch begins from the same level as the anterior border of the orbit.

Premaxilla: the premaxilla is almost completely preserved, with the alveoli of  $I^1$ s, but the incisors detached. The two sides of the premaxillae are not fused together.

Premolars: the premolars are simply structured and deeply worn; premolars without crochet, which is typical of *Dicerorhinus*; premolars are also completely molarized. No trace of  $DP^1$  can be detected, which means that, unlike the species of the genus *Rhinoceros*,  $DP^1$  is not retained into adult life in *Dicerorhinus*.

Molars: only  $M^1$  and  $M^2$  preserved *in situ*, both of which are seriously worn; molars are also simply structured, no crochet can be detected either.

Table 6

Measurements (in mm) of the provenance-lacking skull of *Dicerorhinus sumatrensis* (IVPP-V2877).

*Dimensions (en mm) du crâne de Dicerorhinus sumatrensis sans provenance (IVPP-V2877).*

Measurements	V2877	<i>Dicerorhinus sumatrensis</i>	<i>Dicerorhinus sumatrensis</i>	<i>Rhinoceros sondaicus</i>
		Guérin (1980)	IVPP C/O.34	Guérin (1980)
Nasal breadth	111	95–121.5	97.2	102–133
Length of the narial notch	159	128–182.5	138	133–177
Distance between nasal notch and orbit	144.8	98.5–134	102.8	96–126
Distance between nasal tip and orbit	300	225–296	230	226–274
Cranial height in front of $P^2$	137.6	131–173	105	142–195
Cranial height in front of $M^1$	170.6	127–175	114.4	140–186
Cranial height in front of $M^3$	173.7	137–188	125.7	146–204
Palatal width in front of $P^2$	54.7	53.5–69	55.6	60.5–83.5
Length of $I^1$ (measured by alveolus)	25.9	–	33	–
Breadth of $I^1$ (measured by alveolus)	10.6	–	14	–
Outer premolar tooth row length	102	–	–	–
Inner premolar tooth row length	83.5	–	–	–



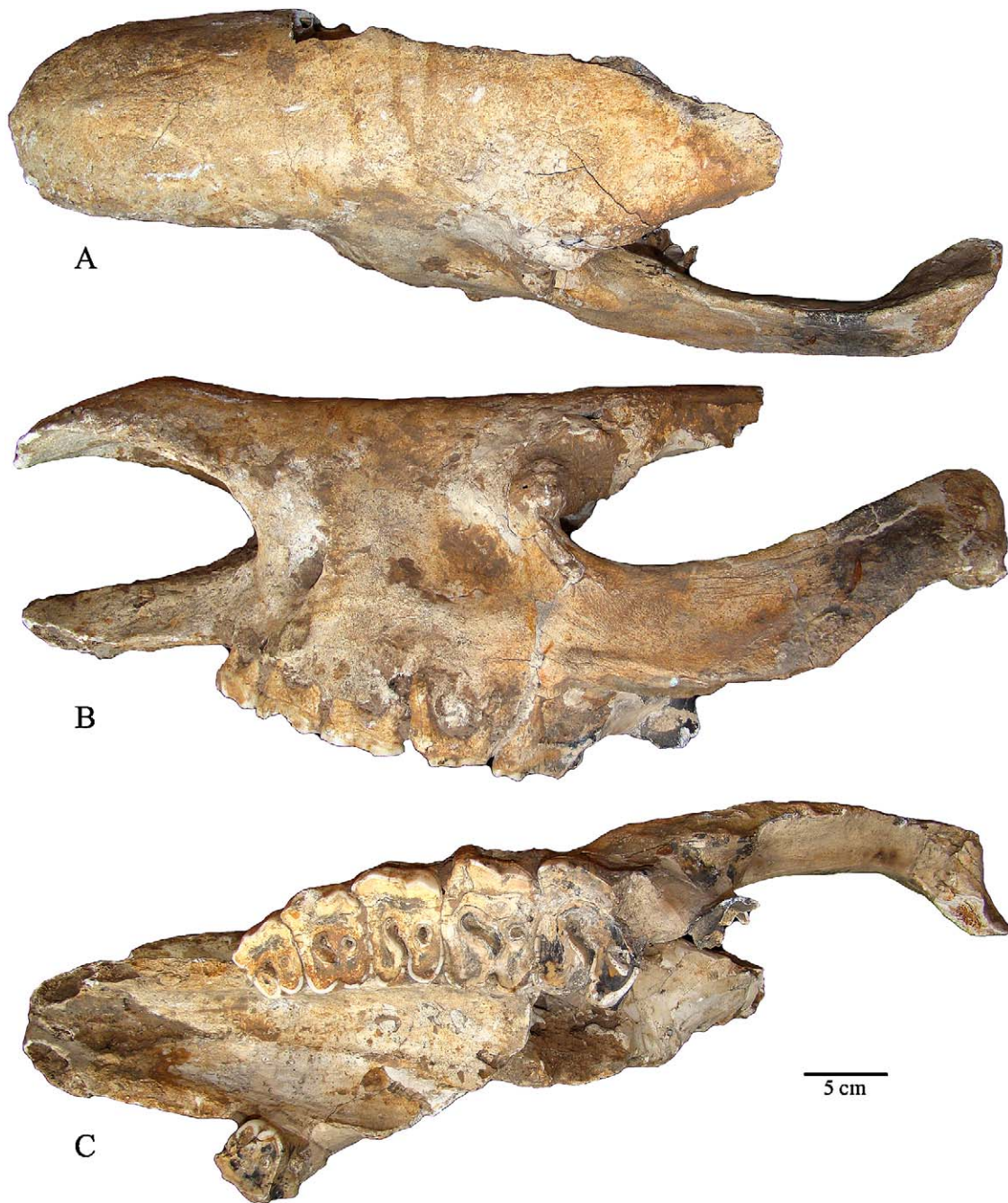


Fig. 13. *Dicerorhinus sumatrensis*, skull (V2877). A. Dorsal view. B. Lateral view. C. Ventral view.  
*Dicerorhinus sumatrensis*, crâne (V2877). A. Vue dorsale. B. Vue latérale gauche. C. Vue inférieure.

The total length of P<sup>2</sup>-M<sup>2</sup> is 153 mm on the lingual side and 184.2 mm on the buccal side.

The characters mentioned above fit well with that of the species *D. sumatrensis*. Additionally, almost all the values of the dimensions fall within the range of Guérin's (1980), database, except the distance between nasal notch and orbit, which is remarkably larger than that of the extant form. On the other hand, it is different from the other Pleistocene two-horned rhinos of China in its much smaller size, unossified nasal septum and by retaining the upper I<sup>1</sup> (Table 6 and Fig. 13).

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