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General palaeontology, systematics and evolution (Vertebrate palaeontology)

Evolution of the non-*Coelodonta* dicerorhine lineage in China

Évolution des Dicérorhinés (autres que Coelodonta) de Chine

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ARTICLE INFO

Article history:

Received 1st February 2012
Accepted after revision 1st June 2012
Available online 28 July 2012

Presented by Philippe Taquet

Keywords:

Dicerorhines
Dicerorhinus
Stephanorhinus
Evolution
China

Mots clés :

Dicérorhinés
Dicerorhinus
Stephanorhinus
Évolution
Chine

ABSTRACT

In China, the non-*Coelodonta* dicerorhines are too diverse to be placed entirely in the genus *Dicerorhinus*. Most of the Pleistocene species should be transferred to the European genus *Stephanorhinus* because they differ from the *Dicerorhinus* species. Those differences include a much larger body size, a dolicocephalic skull, the absence of incisors, a partially ossified nasal septum, a closed subaural channel, a more anteriorly positioned infraorbital foramen, and a robust postglenoid process combined with a less developed paroccipital process. However, the cranium once referred to *Rhinoceros sinensis* from the Yunxian Man Site should be transferred to *Dicerorhinus* because of the presence of smaller incisors, an open subaural channel, a high and nearly vertical occipital face, and the more anterior position of the anterior root of the zygomatic arch. In China, the interspecific differences among the *Stephanorhinus* species are more striking than among those of Europe. The evolution of the non-*Coelodonta* dicerorhines in China was punctuated around the Plio/Pleistocene transition, and it seems difficult to link the diverse Pleistocene dicerorhines with the indigenous Neogene ones. The generic attributions of the Neogene dicerorhines require further study.

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RÉSUMÉ

En Chine, les Dicérorhinés fossiles, autres que ceux appartenant au genre *Coelodonta*, présentent une diversité trop importante pour qu'ils soient tous classés dans le genre *Dicerorhinus*. La plupart des formes du Pléistocène devraient être classées dans le genre *Stephanorhinus* créé pour des fossiles européens. En effet, ces formes se distinguent de *Dicerorhinus* dans les domaines suivants : corps beaucoup plus grand, crâne dolichocéphale, absence d'incisives, cloison nasale partiellement ossifiée, pseudo-méat auditif externe est fermé vers le bas, foramen infra-orbitaire situé davantage en avant, apophyse post-glénoïde robuste, apophyse paroccipitale moins développée. Les fossiles du Site d'Homme Yunxian, déterminés en *Rhinoceros sinensis*, devraient être attribués au genre *Dicerorhinus* à cause des caractéristiques suivantes : présence de petites incisives, pseudo-méat auditif externe ouvert vers le bas, face occipitale haute et presque verticale. Les différences interspécifiques observables parmi les espèces de *Stephanorhinus* de Chine sont plus importantes que pour les formes européennes. La diversification des Dicérorhinés (autres que *Coelodonta*) s'est produite en Chine autour de la transition Plio/Pléistocène et il semble difficile de relier ce groupe qui a prospéré durant le Pléistocène avec les formes du Néogène. Les attributions génériques des Dicérorhinés du Néogène restent des questions ouvertes.

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1. Introduction

The taxonomic affinities of the non-*Coelodonta* dicerorhines in China remain unclear, and that is the result of the scarcity of fossil material and the discontinuity of their fossil records. In the past century, all the non-*Coelodonta* dicerorhines, even including the earliest representatives of Miocene age in China, were placed in the single genus *Dicerorhinus* (whose type species *Dicerorhinus sumatrensis* is extant in South-east Asia). Placing all the different extinct forms in the recent genus does not appear to be the most reasonable solution. In North China, the Quaternary rhinoceros fauna is dominated by the dicerorhines and *Coelodonta*. The non-*Coelodonta* dicerorhines is the more problematic group.

The extinct dicerorhines are fairly different from the extant one, and even they are quite different from one another. I re-evaluated the extinct species once included in the genus *Dicerorhinus*, because the current concept of *Dicerorhinus* borders on being a paraphyletic “wastebasket” taxon (Prothero et al., 1989). In particular, I discuss possibly placing the Chinese Pleistocene dicerorhines in *Stephanorhinus*, a genus that has been used for many of the European species (Groves, 1983; Heissig, 1989; Cerdeño, 1998; Fortelius et al., 1993; van der Made, 2010). Additionally, I propose a taxonomic revision of the cranium once referred to *Rhinoceros sinensis* from the Yunxian Man site in Hubei Province.

2. Abbreviations

- **CKT**: Chou-kou-tien (= Zhoukoudian).
- **HMV**: Hezheng Paleozoological Museum in Gansu Province.
- **IVPP**: Institute of Vertebrate Paleontology and Paleoanthropology.
- **LGC**: Liucheng *Gigantopithecus* Cave.
- **Loc**: Locality.

3. Systematics (supra-subfamilial systematics after Guérin, 1980)

Class: MAMMALIA Linnaeus, 1758
 Order: PERISSODACTYLA Owen, 1848
 Family: RHINOCEROTIDAE Owen, 1840
 Subfamily: DICERORHININAE Simpson, 1945

***Dihoplus* Brandt, 1878**

Dihoplus ringstroemi (Arambourg, 1959)

***Dicerorhinus* Gloger, 1841**

Dicerorhinus cixianensis Chen and Wu, 1976

Dicerorhinus sumatrensis (Fischer, 1814)

***Stephanorhinus* Kretzoi, 1942**

Stephanorhinus yunchuchenensis (Chow, 1963)

Stephanorhinus lantianensis (Hu and Qi, 1978)

Stephanorhinus kirchbergensis (Jäger, 1839)

3.1. *Dihoplus ringstroemi* (Arambourg, 1959)

1924. *Dicerorhinus orientalis* Ringström, p. 5–25, figs. 1–8, pls. I.

1959. *Dicerorhinus orientalis* var. *ringstroemi* Arambourg, p. 73.

1978. *Dicerorhinus orientalis* (Ringström, 1959) - Liu et al., p. 176.

1978. *Dicerorhinus ringstroemi* (Arambourg, 1959) - Yan, p. 31, pl. I-1.

2004. *Dicerorhinus ringstroemi* (Arambourg, 1959) - Deng and Wang, p. 222–225, fig. 4.

2006b. *Dicerorhinus ringstroemi* (Arambourg, 1959) - Deng, p. 51–52, fig. 3.

2011. *Dihoplus ringstroemi* (Arambourg, 1959) - Deng et al., p. 1287, fig. 2.

Diagnosis: Larger than *Dicerorhinus orientalis*; skull is long; nasal bone is long and wide and has a domed horn boss; nasal notch above P3/P4; anterior border of orbit above M2; frontal horn boss small; sagittal crest absent; subaural channel closed; I2 and i1 absent, I1 and i2 reduced; P1 lost; molars with developed crochet (Geraads, 1988; Deng, 2006b).

Specimens: Complete toothrows and almost complete crania (Figs. 1-E, 2-E and 3-E), mandibles, forefoot bones, tibia, metacarpals and talus.

Localities: Xin'an, Henan; Baode, Shanxi; Lantian, Shaanxi; Jingmen, Hubei; Qaidam, Qinghai; Linxia, Gansu.

Horizon: From late Miocene to Early Pliocene, corresponding to NMU 9 to NMU 12 (Deng and Downs, 2002).

Remarks: The specimens allocated to this species were referred to *Dicerorhinus orientalis* before the 1960s. In 1959, Arambourg established the new variety, *Dicerorhinus orientalis* var. *ringstroemi*, for the Neogene dicerorhines from China. The reason was that the Chinese specimens are much more robust than *Dicerorhinus orientalis*. However, Arambourg did not designate a type, and later, that variety was raised to species rank (Yan, 1978).

Although this species has been reported from several localities, fossils of it are fairly scarce. Except for one nearly complete cranium and some deciduous tooth rows, most of the specimens are fragmentary and isolated. This species is not well known.

Concerning its phylogenetic relationships, it differs from the extant *D. sumatrensis* not only in its larger size, but also in the following aspects: deeply saddled in the fronto-parietal part of the cranium; lacking upper incisors; a closed subaural channel and a very well developed nasal bone. I propose that the generic attribution of the Neogene dicerorhines should be reconsidered. In Europe, the Miocene dicerorhines were allocated either to *Dihoplus* Brandt, 1872 or to *Lartetotherium* Ginsburg, 1974 (Heissig, 1999). In that taxonomic scenario, the genus *Dicerorhinus* only encompasses the living species *D. sumatrensis* according to Groves (1983). Under such a situation, it is better to move the species *D. ringstroemi* to the genus *Dihoplus* as proposed by Deng et al. (2011). The phylogenetic position of the species *D. ringstroemi* is still uncertain.

3.2. *Dicerorhinus cixianensis* Chen and Wu, 1976

Diagnosis: Small size; naso-frontal part flat, nasal tip bends downward; nasal notch reaches the level anterior to

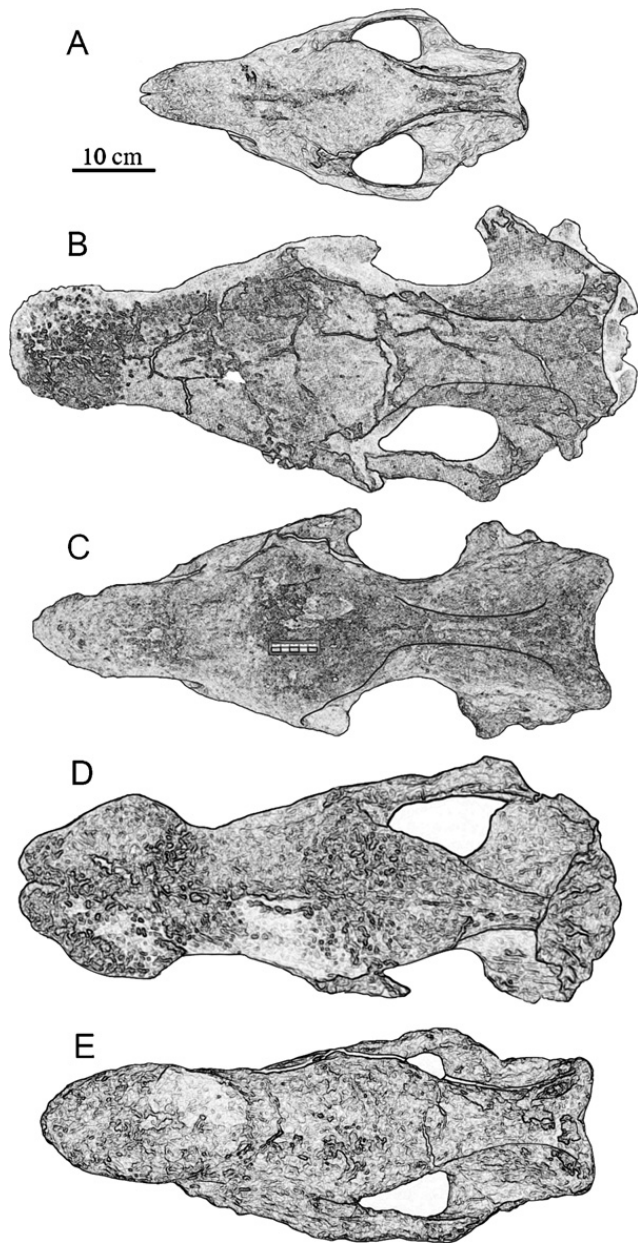


Fig. 1. Crania of fossil dicerorhinines in dorsal views, compared with the extant one. A. *Dicerorhinus sumatrensis* (IVPPC/O. 34), Recent. B. *Stephanorhinus kirchbergensis* (IVPPV 2682), modified from [Chow \(1963a\)](#), Middle Pleistocene. C. *Dicerorhinus lantianensis* (IVPPV 5413), Early Pleistocene. D. *Stephanorhinus yunchuchenensis* (IVPPV 2879), modified from [Chow \(1963b\)](#), Early Pleistocene. E. *Dihoplos ringstroemi* (HMV 1115), modified from [Deng \(2006b\)](#), Late Miocene.

Fig. 1. Crânes de Dicérorhinés fossiles en vues dorsales, comparés à une forme actuelle. A. *Dicerorhinus sumatrensis* (IVPPC/O. 34), actuel. B. *Stephanorhinus kirchbergensis* (IVPPV 2682), modifié de [Chow \(1963a\)](#), Pléistocène moyen. C. *Dicerorhinus lantianensis* (IVPPV 5413), Pléistocène inférieur. D. *Stephanorhinus yunchuchenensis* (IVPPV 2879), modifié de [Chow \(1963b\)](#), Pléistocène inférieur. E. *Dihoplos ringstroemi* (HMV 1115), modifié de [Deng \(2006b\)](#), Miocène supérieur.

DP1; infraorbital foramen is at the level of the posterior border of DP1; premaxilla very thin and extends downward; mandible gracile; inferior border of mandibular corpus slightly convex, and rises in the symphysis part; symphysis is narrow and long; angular part extends backward;

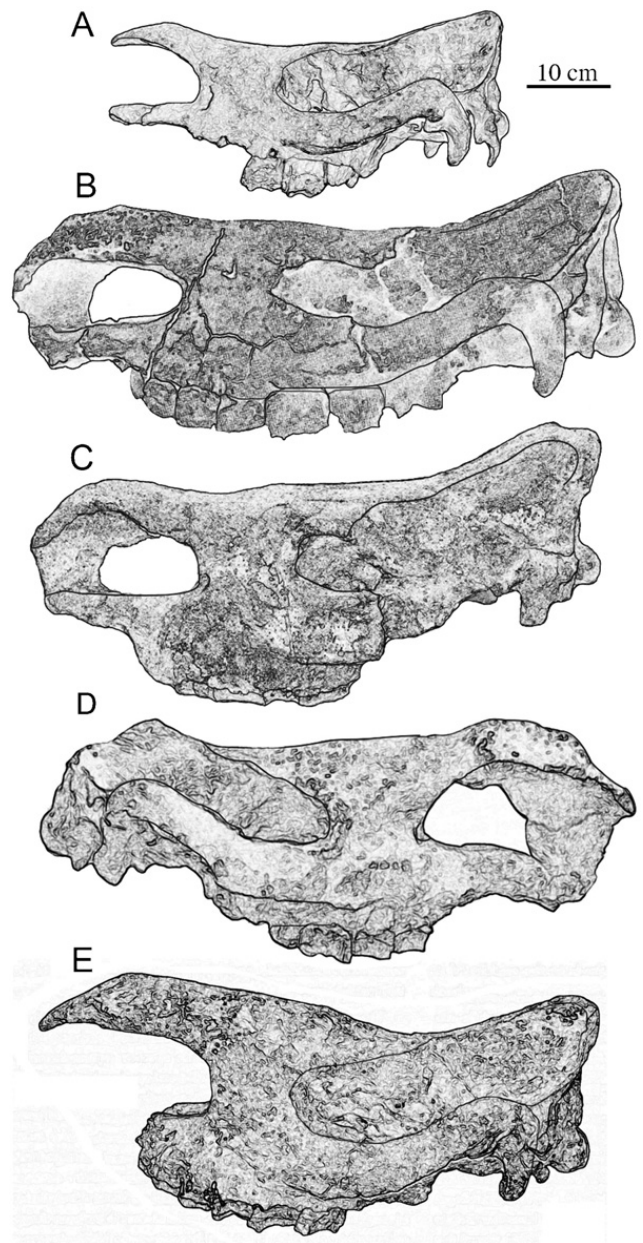


Fig. 2. Crania of fossil dicerorhinines in lateral views, compared with the extant one. A. *Dicerorhinus sumatrensis*. B. *Stephanorhinus kirchbergensis*. C. *Dicerorhinus lantianensis*. D. *Stephanorhinus yunchuchenensis*. E. *Dihoplos ringstroemi*.

Fig. 2. Crânes de Dicérorhinés fossiles vues latérales, comparés à une forme actuelle. A. *Dicerorhinus sumatrensis*. B. *Stephanorhinus kirchbergensis*. C. *Dicerorhinus lantianensis*. D. *Stephanorhinus yunchuchenensis*. E. *Dihoplos ringstroemi*.

cheek teeth small and brachyodont; upper molars block-shaped, parastyle rib developed; protocone constriction weak; without anticrochet and crista; no lingual cingulum; two pairs of lower deciduous incisors, di1 bean-shaped, di2 caniniform, i2 moderately developed (in alveolus); dp2 smaller than usual (partially modified from [Chen and Wu, 1976](#)).

Holotype: Broken cranium with mandible of a juvenile individual (IVPP V4833).

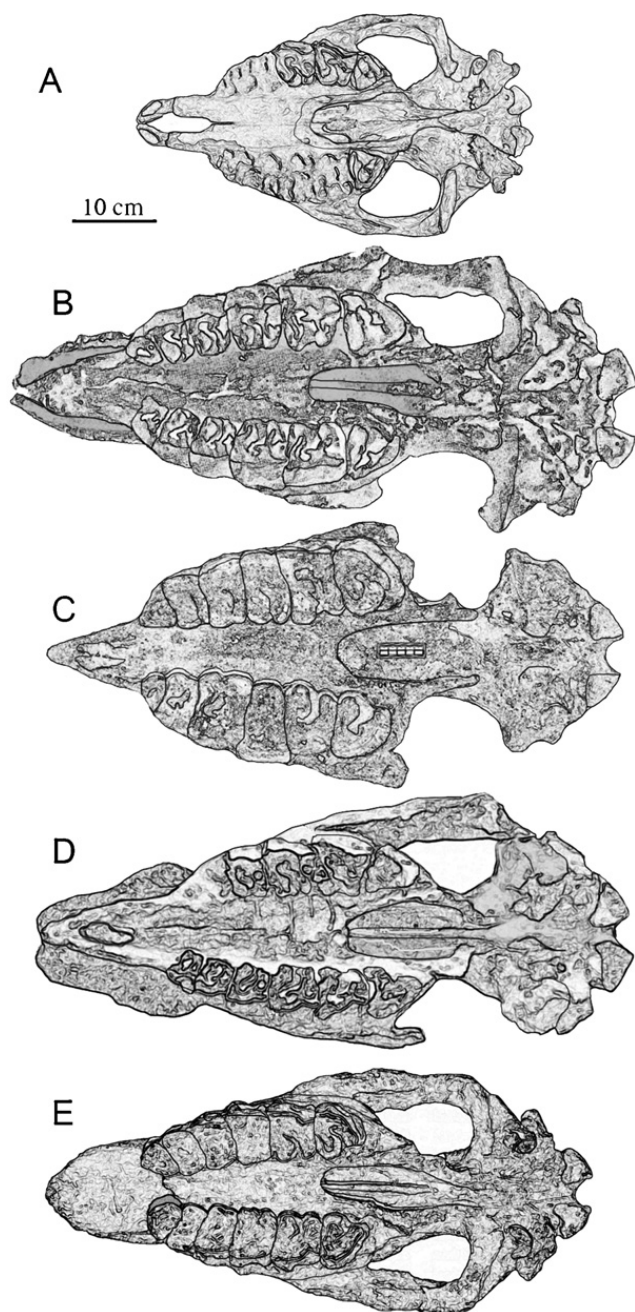


Fig. 3. Crania of fossil dicerorhinines in ventral views, compared with the extant one. A. *Dicerorhinus sumatrensis*. B. *Stephanorhinus kirchbergensis*. C. *Dicerorhinus lantianensis*. D. *Stephanorhinus yunchuchenensis*. E. *Dihoplus ringstroemi*.

Fig. 3. Crânes de Dicerorhinés fossiles en vues ventrales, comparés à une forme actuelle. A. *Dicerorhinus sumatrensis*. B. *Stephanorhinus kirchbergensis*. C. *Dicerorhinus lantianensis*. D. *Stephanorhinus yunchuchenensis*. E. *Dihoplus ringstroemi*.

Type locality: This species is known from a single locality, Jiulongkou, Cixian County, Hebei Province (Chen and Wu, 1976).

Horizon: Mid-Middle Miocene, correlated with MN Zone 6 (Deng, 2006a).

Remarks: The following characters make it reasonable to refer these specimens to the genus *Dicerorhinus* rather than to the tribe Aceratheriini: nasal bone developed but not straight, relatively advanced DP1 and dp1, narrowed

mandibular symphysis with moderately developed i2 (in alveolus). In contrast, *D. cixianensis* is much smaller than the Quaternary two-horned or tandem-horned rhinoceros, and even smaller than the extant species. The DP1–4 length is only 119 mm and the dp1–4 length is 110 mm, which is much smaller than the only available data (DP1–4 length is 130 mm) measured from the Neolithic *D. sumatrensis* from Hemudu (the measurement was taken from the drawings by Wei et al., 1989). It is very probable that *D. cixianensis* represents the smallest species in the tribe Rhinocerotini, but this only can be verified when an adult skull is found.

3.3. *Dicerorhinus sumatrensis* (Fischer, 1814)

2001. *Rhinoceros sinensis* (Owen, 1870) - Li and Feng, p. 35, pl. 6.

2008. *Rhinoceros sinensis* (Owen, 1870) (partim) - Echassoux et al., pp. 294–306, figs. 25–26.

Diagnosis: Large zygomatic width relative to cranial length; small size; two horns; occasionally with bony nasal septum; nasal notch and anterior border of orbit moved backward; postglenoid not fused with post-tympanic; sagittal crest absent; occipital plane sub-vertical, occipital outline trapezoidal; orbitonasal length surpassing orbitoaural length; occipitonasal and condylo-nasal lengths are subequal; I² and I₁ absent, I¹ and I₂ reduced; P¹ absent; molars with crochet (Figs. 1–A, 2–A, 3–A and 4) (Geraads, 1988; Groves, 1967; Loose, 1975; Pocock, 1945; Tong and Guérin, 2009).

Referred specimens: Broken cranium, mandibles, isolated teeth and few postcranial bones.

Localities: Liucheng *Gigantopithecus* Cave, Guangxi (Tong and Guérin, 2009); Xiawanggang, Henan (Chia and Chang, 1977); Yuyao, Zhejiang (Wei et al., 1989) and Yunxian, Hubei.

Horizon: Early Pleistocene to Holocene.

Remarks: The earliest record of *D. sumatrensis* is from the Early Pleistocene Liucheng *Gigantopithecus* Cave, Guangxi; the fossil material mainly includes isolated teeth and one nearly complete mandible with all the cheek teeth in situ. Another broken cranium without provenance was also referred to this species (Tong and Guérin, 2009). There is a gap between the earliest occurrence in the Pleistocene and Holocene records. The cranium (Fig. 4) once referred to *Rhinoceros sinensis* from the Yunxian Man Site (Echassoux et al., 2008; Li and Feng, 2001) should be transferred to *Dicerorhinus* because of the presence of the following features: smaller incisors, an open subaural channel, a high and nearly vertical occipital face, a cranial dorsal profile with slight rather than great occipital elevation, and a zygomatic process of the maxilla arising from the same vertical level as the orbital rim rather than obviously posterior to it (as in *Rhinoceros*). However, the fossil cranium is slightly larger than the maximum dimensions of the extant *D. sumatrensis* provided by Guérin (1980).

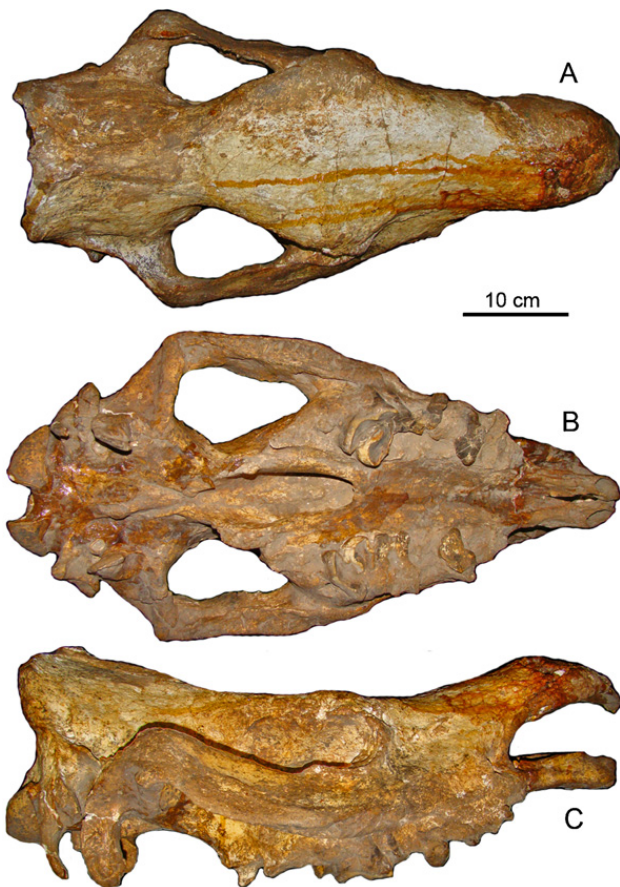


Fig. 4. Cranium of *Dicerorhinus* cf. *sumatrensis* (EV8-2002) from the Yunxian Man site, Hubei Province. A. Dorsal view. B. Ventral view. C. Lateral view.

Fig. 4. Crâne de *Dicerorhinus* cf. *sumatrensis* (EV8-2002) du site de l'Homme de Yunxian, Province de Hubei. A. Vue dorsale. B. Vue ventrale. C. Vue latérale.

3.4. *Stephanorhinus yunchuchenensis* (Chow, 1963)

1963b. *Dicerorhinus yunchuchenensis* Chow, p. 325–329, pl. I.

Diagnosis: A relatively large dicerorhine with massive and broad cranium. Nasals plow-like in outline, expanding at the nasal horn boss; tip of the nasals tapered and bifid, with a vertical groove at the middle; nasal septum partially ossified, and nasal opening very high. Upper incisors absent; cheek teeth brachyodont; entrance to medisinus wide and shallow on molars (modified from Chow, 1963b). The mandibular characters are not known because of the lack of fossil material.

Holotype: An almost complete cranium with left P2–M2 and right P4–M2 in situ (IVPP V2879) (Fig. 1-D, 2-D and 3-D).

Type locality: Yuncu, Yushe County, Shanxi Province (Chow, 1963b); but the exact location is uncertain.

Horizon: The exact provenance of the material is uncertain (Chow, 1963b). The regional geological information shows that the fossils must have been recovered from Early Pleistocene deposits.

Remarks: This species is known from only a single locality. From the rough horn bosses, it seems that this animal had very strong nasal and frontal horns. Its extraordinarily expanded nasal bone distinguishes it from other species.

3.5. *Stephanorhinus lantianensis* (Hu and Qi, 1978)

1978. *Dicerorhinus lantianensis* Hu and Qi, p. 38–39, pl. XI.

Diagnosis: Smaller than *S. kirchbergensis* and *S. yunchuchenensis*; tip of the nasal bone is sharply tapered; teeth are large (P2–M3 length is 250 mm); the protoloph and metaloph are parallel and are vertical to the long axis of the toothrow on P3–M2; the outer wall of the ectoloph is smooth; M3 has a metacone rib.

Holotype: An almost complete cranium of an old individual (IVPP V5413) (Figs 1-C, 2-C and 3-C).

Type locality: Gongwangling, Lantian County, Shaanxi Province (Hu and Qi, 1978).

Horizon: Late Early Pleistocene, about 1.15 Ma.

Remarks: This species is known from only a single locality. Its sharply tapered nasal bone makes it very different from other known *Stephanorhinus* species.

3.6. *Stephanorhinus kirchbergensis* (Jäger, 1839)

1931. *Dicerorhinus choukoutiensis* Wang, p. 69–76, pls. I–IV.

1941. *Rhinoceros mercki* (Jäger, 1939) - Teilhard de Chardin and Pei, p. 62–65, figs. 50–52b.

1942. *Rhinoceros choukoutiensis* (Wang, 1931) - Teilhard de Chardin and Leroy, p. 64.

1963a. *Dicerorhinus choukoutienensis* (Wang, 1931) - Chow, p. 62–70, pl. I.

1976. *Dicerorhinus kirchbergensis* (Jäger, 1939) - Ji, p. 62, pl. I.

1976. *Dicerorhinus mercki* (Jäger, 1939) - Jinniushan, p. 120–127, pl. I.

1979. *Dicerorhinus choukoutienensis* (Wang, 1931) - Chow, p. 236–258, pls. I–II.

1980. *Dicerorhinus mercki* (Jäger, Kaup, 1939, 1841) - Guérin, p. 623.

1986. *Dicerorhinus kirchbergensis* (Jäger, 1939) - Xu, 229–241, pl. I, figs. 3–4.

1996. *Dicerorhinus mercki* (Jäger, 1939) - Huang, p. 183–188, pls. XXX–XXXI.

1998. *Rhinoceros sinensis* (Owen, 1870) - Wu, p. 121–136, pl. I.

2002. *Dicerorhinus mercki* (Jäger, 1939) - Tong, p. 111–120, pls. 11–12, figs. 3.6–3.7.

Diagnosis: Very large in size (Guérin, 1980); high head; with nasal and frontal horns; nasal horn long; nasal septum partially ossified; nasal notch moved backward; anterior border of orbit and the posterior edge of palatine posteriorly positioned; plane of the occipital surface subvertical; subaural channel closed; mastoid inflated, the widest part of the occipital is at the level of the mastoid; mastoid not fused with the paroccipital process; the

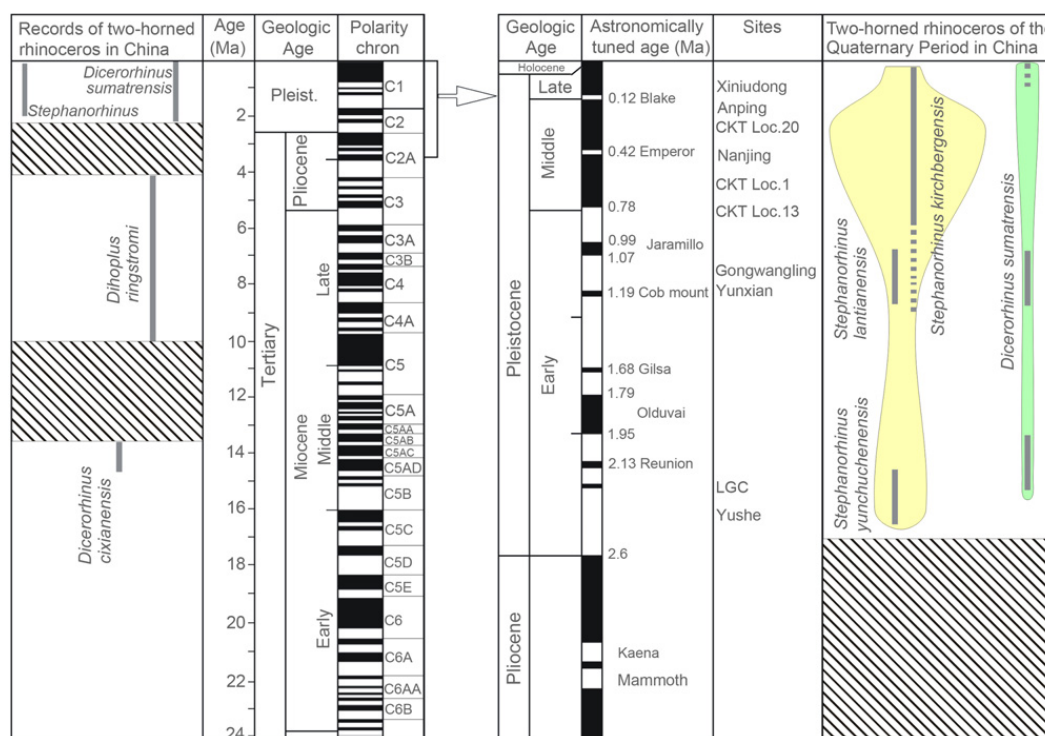


Fig. 5. Temporal ranges of the non-*Coelodonta* dicerorhines in China. The hatched area represents the gap or bottleneck in the evolution of the dicerorhines in China.

Fig. 5. Positions chronologiques des Dicérorhinés (autres que *Coelodonta*) de Chine. Les zones hachurées représentent une lacune ou un goulot d'étranglement.

angle γ (between opisthion + basion and palate) is less than 110° ; upper and lower incisors absent; cheek teeth big and with smooth enamel surface; anticrochet and metastyle on upper cheek teeth absent; upper premolar highly molarized and quite hypsodont; molars subhypsodont; upper teeth much higher buccally than lingually, and thus extremely ectolophodont; ascending ramus slopes backward; long limbs and strongly concave limb joints indicate a graviportal locomotion (Fortelius et al., 1993; Groves, 1983; Loose, 1975).

Referred specimens: The best material is an almost complete cranium with all the teeth *in situ* (IVPP V2682) from CKT Loc. 20 (Chow, 1963a) (Figs 1-B, 2-B and 3-B); quite a number of broken crania and mandibles, isolated teeth as well as postcranial bones were also reported from CKT Loc. 1 (Wang, 1931; Chow, 1979) and CKT Loc. 13 (Teilhard de Chardin and Pei, 1941) as well as from Anping, Liaoning Province (Xu, 1986); few specimens come from the Nanjing *Homo erectus* site (Huang, 1996; Tong, 2002). The most typical and richest specimens of this species were recovered in the Rhino Cave (named “Xiniudong” in Chinese) in Shennongjia, Hubei Province (Tong and Wu, 2010; Wu, 1998).

Localities: At present, nearly 30 localities in China have been reported with fossils of *S. kirchbergensis* (Tong, 2002).

Horizons: From the Early to Late Pleistocene, but concentrated in the Middle Pleistocene (Fig. 5). The earliest occurrence is CKT Loc. 13 and the youngest record is the site at Harbin (20 ka). The most reliable youngest occurrence of this species in China is from the Rhino Cave in Hubei Province, a site of Early Late Pleistocene age that is

rich in *S. kirchbergensis* fossils (Wu, 1998; Tong and Wu, 2010).

Remarks: *S. kirchbergensis* is the most geographically and temporally widespread species of dicerorhines recovered in China. The taxonomy of this species has been in a state of confusion over the past few decades because the majority of the Quaternary non-*Coelodonta* rhinoceroses in North China were allocated to this species. Unfortunately, most of the fossil specimens are very poorly preserved. Recently, this species was placed in *Dihoplus* by Deng et al. (2011) without any discussion.

4. On the evolution of the non-*Coelodonta* dicerorhines in China

In Pliocene Europe, the dicerorhines replaced the Neogene aceratherine lineage (i.e., the hornless rhinoceros). The Plio/Pleistocene in Europe is characterized by *Stephanorhinus* (Cerdeño, 1992, 1998; Guérin, 1980). It appears to have been a gradual transition between the two groups through time.

By contrast, there appears to be a bottleneck, or a punctuation, in rhinoceros evolution around the Plio/Pleistocene transition in China (Deng and Downs, 2002; Tong, 2001; Tong and Moigne, 2000). Biostratigraphic work conducted in recent decades demonstrates that the major Aceratheriini fossil-bearing strata in China are Miocene, not Pliocene in age (Qiu and Qiu, 1990). The two major groups of Neogene rhinoceros (Teleoceratini and Aceratheriini) became extinct prior to or during the Pliocene in China. The Elasmotheriini has a long gap during

Pliocene (Antoine, 2002), and reappeared in early Pleistocene in North China. Pliocene rhinoceros records in China are really very rare, and even the lowermost Pleistocene strata bear few rhinoceros fossils.

The Pleistocene rhino fauna in China diversified very quickly after 2Ma. The rhino fauna in South China that belongs to the Oriental Region was dominated by *Rhinoceros sinensis* and *D. sumatrensis*. The rhino fauna in North China that belongs to the Palearctic Region was dominated by dicerorhines, including *Stephanorhinus* and *Coelodonta*; the former usually represents an interglacial period, and the latter indicates cold climate. However, in a few localities, fossils of these two genera were found together (Tong, 2004). It is difficult to determine the origin of the Chinese Quaternary rhino fauna. It is very probable that the non-*Coelodonta* dicerorhines came from Europe.

5. Conclusions

In China, the fossil dicerorhines are too diverse to remain classified under *Dicerorhinus*. The attributions of the Neogene dicerorhines to the *Dicerorhinus* should be reconsidered because they are much larger than the extant species of *Dicerorhinus*, the nasal bone is too big, and the subaural channel is closed. In my opinion, most of the Pleistocene dicerorhine species should be transferred to the genus *Stephanorhinus*. The Pleistocene dicerorhine species differ from the *Dicerorhinus* species in the following aspects: much larger, incisorless, nasal septum partially ossified, subaural channel closed, infraorbital foramen more anteriorly positioned (almost invisible in lateral view), and with a robust postglenoid process but less developed paroccipital process. Few Pleistocene non-*Coelodonta* dicerorhines in China can be attributed either to *Dihoplus* or to *Dicerorhinus*.

The cranium once referred to *Rhinoceros sinensis* from the Yunxian Man Site should be transferred to *Dicerorhinus* because of the following features: small incisors, subaural channel open, high and nearly vertical occipital face, and the anterior root of the zygomatic arch arises from a more anterior position.

In China, the interspecific differences among the *Stephanorhinus* species are more striking than among those in Europe. The evolution of the non-*Coelodonta* dicerorhines in China was punctuated, and it seems difficult to link the Pleistocene dicerorhines with the local Neogene ones. Most likely the Pleistocene dicerorhines in China came from Europe, where the same group flourished from the Miocene to the end of the Pleistocene.

Acknowledgments

I thank Mr. Lu C.Q. for allowing access to the collections in the Hubei Provincial Museum, Profs Qiu Z.X. and Deng T. for fruitful discussions, and Drs. J. van der Made and L.W. van den Hoek Ostende, as well as Dr. P.E. Mollé for constructive suggestions and corrections of the English to French translations of the abstract, respectively. Sincere appreciation is expressed to Drs. Thomas Stidham and Corwin Sullivan for checking the grammar of the English text. This work was supported by the Special Basic Research

Project (Grant No: 2007FY110200) of MST of China and the IVPP Project (Grant No: KA209508) as well as the special fund for fossil excavation and preparation of the Chinese Academy of Sciences.

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