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Reassessment of the Middle Pleistocene Japanese rhinoceroses (Mammalia, Rhinocerotidae) and paleobiogeographic implications

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Abstract. A rhinocerotid fossil (NMNS-PV9600) from the lower part of the Isa Formation (Middle Pleistocene), Isa area, Mine City, Western Japan, is described. Previously, this specimen had been identified as *Dicerorhinus nipponicus*. However, the specimen shares the following features with the genus *Stephanorhinus*: molarised premolars; absence of P1; absence of metacone fold on P3 and P4; presence of crochet on the premolars and molars; presence of a crista on the molars; absence of medifossette on both premolars and molars; triangular-shaped M3. In this study, NMNS-PV9600 is redescribed as *Stephanorhinus kirchbergensis* based on morphological and metric comparisons with other Eurasian Pleistocene rhinocerotids. NMNS-PV9600 is close to *S. kirchbergensis* from Choukoutien, suggesting *S. kirchbergensis* could have reached the Japanese archipelago during the middle Pleistocene (before or around 0.43 Ma). NMNS-PV9600 was an adult individual around 25 years in age when it died, based on the tooth eruption and wear stage. The cheek teeth morphology suggests that *S. kirchbergensis* from Japan was probably a browser as the species has before been considered in occurrences from other countries.

Key words: paleobiogeography, Pleistocene, Rhinocerotidae, *Stephanorhinus*, Western Japan, Yamaguchi Prefecture

Introduction

In Japan, abundant land mammal fossils have been discovered from Pleistocene deposits (e.g. Kawamura, 1991). Of these, rhinocerotid fossils were discovered from Central and Western Japan (Figure 1). Some specimens were identified as belonging to the genus *Dicerorhinus* or *Rhinoceros*. Shikama *et al*. (1967) described a skull of a rhinocerotid from Isa in Mine City, Yamaguchi Prefecture, as a new species *Dicerorhinus nipponicus* based on comparison with Chinese Pleistocene species of *Dicerorhinus*. *Dicerorhinus* cf. *nipponicus* and *Dicerorhinus* sp. were reported from Matsugae in Fukuoka Prefecture by Okazaki (2007) and Ogino *et al*. (2009), respectively. Shikama (1967) reported *Rhinoceros* aff. *sinensis* from Aira in Kagoshima Prefecture. Nagasawa (1961) described *Rhinoceros* sp. from Kuzuu in Tochigi Prefecture, although Shikama *et al*. (1967) noted that this specimen possibly belongs to *D. nipponicus*. In contrast, the precise taxonomic position of the other rhinocerotid fossils from Yage, Bisan-Seto and Tsukumi area, is uncertain (e.g. Handa, 2015).

In the last decades, taxonomic revisions of European and Northern Asian Plio-Pleistocene rhinoceroses have been conducted by many researchers and the fossil species usually referred to the genus *Dicerorhinus* have been reassigned to *Stephanorhinus* (Groves, 1983; Fortelius *et al*., 1993; Cerdeño, 1995; Lacombat, 2005; Tong and Wu, 2010; Tong, 2012; Pandolfi, 2013; Pandolfi and Marra, 2015; Pandolfi and Tagliacozzo, 2015). In Japan, several researchers also pointed out that *D. nipponicus* was comparable to the Eurasian species of *Stephanorhinus* (e.g. Ogino *et al*., 2009). However, a thorough taxonomic revision of *D. nipponicus* has not been undertaken since its first descriptions. Here, we reexamine the holotype of *D. nipponicus* described by Shikama *et al*. (1967) and discuss its taxonomic affinities and paleobiogeographic implications.

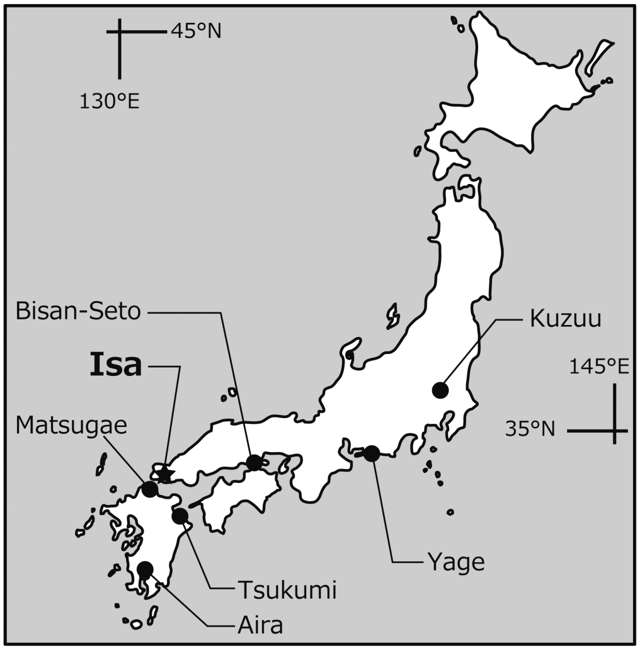

Figure 1. Map showing the localities of the Pleistocene rhinocerotid fossils from Japan (modified from Handa, 2015).

Materials and methods

The studied specimen is stored in the National Museum of Nature and Science, Tsukuba, Japan. The specimen was morphologically compared with several Pleistocene remains referred to *Coelodonta antiquitatis* (Blumenbach, 1799), *Stephanorhinus kirchbergensis* (Jäger, 1839), *S. hemitoechus* (Falconer, 1859), *S. etruscus* (Falconer, 1868), *S. hundsheimensis* (Toula, 1902), *S. yunchuchenensis* (Chow, 1963a), *S. lantianensis* (Hu and Qi, 1978) and with the extant *Rhinoceros unicornis* Linnaeus, 1758, *Dicerorhinus sumatrensis* (Fischer, 1814) and *R. sondaicus* Desmarest, 1822. These specimens were collected from a number of Eurasian localities and are currently housed in different institutions and museums. Tooth terminology follows that introduced by Guérin (1980) and revised by Antoine (2002). The metric methodology is based on the work of Guérin (1980).

Institutional abbreviations.—IGF = Museo di Storia Naturale, sezione di Geologia e Paleontologia, Florence, Italy, IQW = Institute für Quartärpaläontologie, Weimar, Germany, IVPP = Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China, MCP = Museo della Certosa di Calci, Pisa, Italy, MfN = Museum für Naturkunde, Berlin, Germany, MNCN = Museo Nacional de Ciencias Naturales, Madrid, Spain, MNHN = Musèum National d’Histoire Naturelle, Paris, France, MPI = Museo Paleontologico di Isernia La Pineta, Isernia, Italy, MPUR = Museo Paleontologico dell’Università Sapienza di Roma, Rome, Italy, MVC = Museo Paleontologico e Archeologico “Virginio Caccia”, San Colombano al Lambro, Italy, NHML = Natural History Museum, London, United Kingdom, NHMW = Naturhistorisches Museum, Wien, Austria, NMB = Naturhistorisches Museum, Basel, Switzerland, NMNS = National Museum of Nature and Science, Tsukuba, Japan, SMNS = Staatliches Museum für Naturkunde, Stuttgart, Germany.

Systematic paleontology

Family Rhinocerotidae Gray, 1821
Subfamily Rhinocerotinae Gray, 1821
Tribe Rhinocerotini Gray, 1821
Genus ***Stephanorhinus*** Kretzoi, 1942a

Type species.—*Stephanorhinus etruscus* (Falconer, 1868).

Included species.—*Stephanorhinus kirchbergensis* (Jäger, 1839), *Stephanorhinus hemitoechus* (Falconer, 1859), *Stephanorhinus hundsheimensis* (Toula, 1902), *Stephanorhinus yunchuchenensis* (Chow, 1963a), *Stephanorhinus jeanvireti* (Guérin, 1972), *Stephanorhinus lantianensis* (Hu and Qi, 1978), maybe *“Stephanorhinus” miguelcrusafonti* (Guérin and Santafé-Llopis, 1978) and with uncertainty *Stephanorhinus*? *africanus* (Arambourg, 1970).

Occurrence.—From the lower Pliocene to the uppermost Pleistocene in Eurasia and during the Upper Pleistocene in Africa. The genus was reported from the lower-middle Pliocene of Tunisia with uncertainly (*Stephanorhinus*? *africanus*) and was also recorded at about 3–3.5 Ma in Chad (Geraads, 2010).

Diagnosis.—Large to medium size two-horned rhinoceroses. Presence of a rostrally ossified nasal septum which connected the intermaxilla with the nasal bones, molarised premolars, absence of functional incisors, P1 normally absent, metacone fold absent or weakly developed on the upper premolars, crochet rarely absent, M3 triangular shaped in occlusal view, and brachydont to semi-hypsodont cheek teeth (see Tong and Wu, 2010; Tong, 2012; Pandolfi and Tagliacozzo, 2015). The diagnosis of the genus *Stephanorhinus* also reflects that of the subgenus *Brandtorhinus* given by Guérin (1980, 2004).

Remarks.—Recently, Pandolfi and Tagliacozzo (2015) agreed with the considerations reported by Guérin (1980, 2004) on works published by Kretzoi (1942a, b) which established the genus *Stephanorhinus*. Nevertheless, Pandolfi and Tagliacozzo (2015) also noticed that *Stephanorhinus* appears to be a valid name according to the International Commission on Zoological Nomenclature

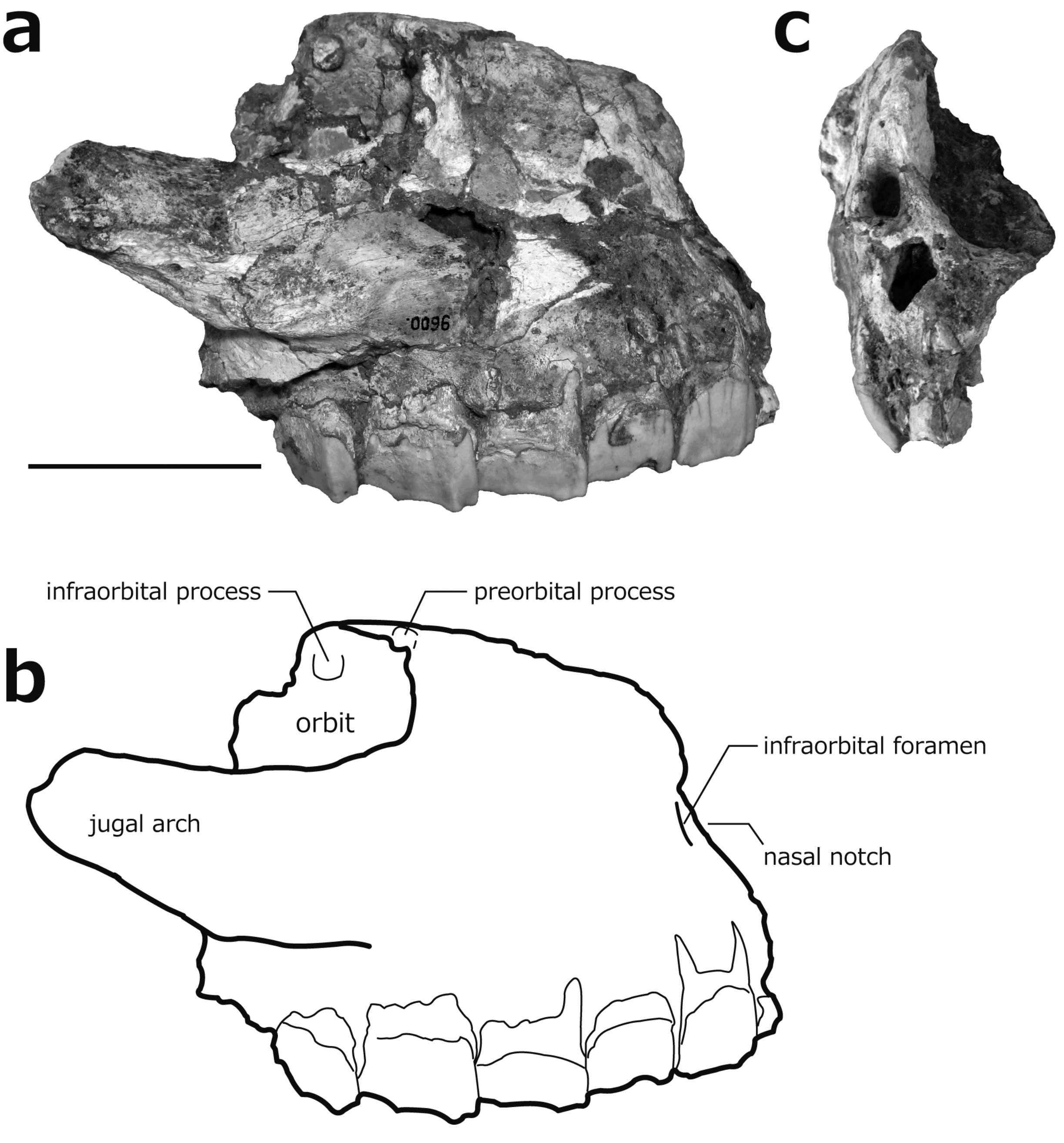

Figure 2. *Stephanorhinus kirchbergensis* from Isa area, Mine City, Yamaguchi Prefecture, Western Japan (NMNS-PV9600). **a**, lateral view; **b**, schematic drawing of lateral view; **c**, anterior view. Scale bar = 10 cm.

(2000; ICZN) rules. In fact, the works of Kretzoi (1942a, b) satisfies the Articles 8, 11.8, 13.1, 13.3, 42 in ICZN.

Stephanorhinus kirchbergensis (Jäger, 1839)

Figures 2, 3a, b

Rhinoceros kirchbergense Jäger, 1839, p. 180, pl. 16, figs. 31–33.

Rhinoceros mercki Kaup, 1841. von Meyer, 1864, p. 235, pls. 35–38, pl. 39, fig. 4; Brandt, 1877, p. 1, pl. 1, pl. 2, figs. 1–3, pl. 3, pl. 7, figs. 14–16, pl. 11; Wüst, 1911, p. 133, pl. 10, figs. 4–6; Schroeder, 1930, p. 5, pl. 1, figs. 4–9, pls. 2–9, pl. 10, figs. 45, 49–50, pl. 11, figs. 53–54, pls. 12–13, 16–21, 24–26.

Dicerorhinus choukoutiensis Wang, 1931, p. 69–76, pls. I–IV; Chow, 1963a, p. 62, pl. I.

Stephanorhinus kirchbergensis (Jäger, 1839). Kretzoi, 1942a, p. 312;

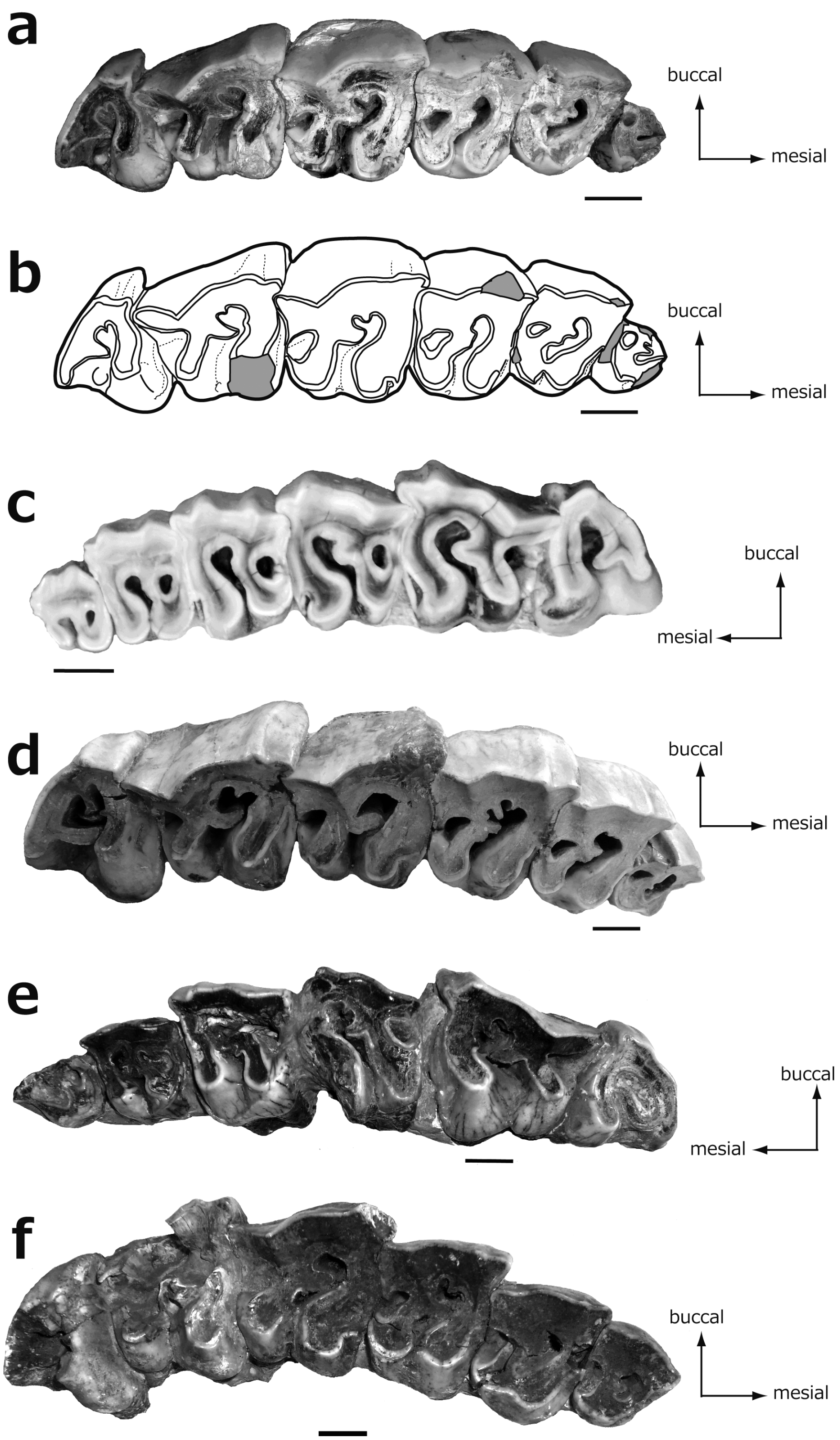

Figure 3. Upper cheek tooth series of NMNS-PV9600 and selected compared specimens. **a**, occlusal view of the upper tooth series of NMNS-PV9600; **b**, schematic drawing of the upper tooth series; **c**, left upper cheek tooth series of *Dicerorhinus sumatrensis* (NMB105129); **d**, right upper cheek tooth series of *Stephanorhinus kirchbergensis* (NHML22020); **e**, left upper cheek tooth series of *S. kirchbergensis* (MPUR1498); **f**, right upper cheek tooth series of *S. kirchbergensis* (MPUR1519). e and f are modified from Pandolfi and Marra (2015). Gray shading indicates a damaged portion. Scale bar = 2 cm.

Kretzoi, 1942b, p. 348; Fortelius *et al.*, 1993, p. 66, pl. 1, fig. 3, pl. 2, fig. 3, pl. 4, fig. 4, pl. 5, figs. 3, 7, pl. 8, figs. 4, 8, 11, pl. 9, fig. 4, pl. 11, fig. 5, pl. 12, fig. 4, pl. 13, fig. 4, pl. 15, figs. 4, 8, pl. 16, figs. 4, 8, 11, 15, 19.

Dicerorhinus nipponicus Shikama *et al.*, 1967, pls. 1, 2.

Dicerorhinus mercki (Kaup, 1841). Borsuk-Bialynicka and Jakubowski, 1972, p. 188, figs. 1A, 2, pls. 1–4; Guérin, 1980, p. 623.

Dicerorhinus kirchbergensis (Jäger, 1939). Xu, 1986, p. 229, pl. I, figs. 3, 4.

Brandtorhinus mercki (Kaup, 1841). Guérin, 1989, p. 9.

Diagnosis.—Considering *D. mercki* as a junior synonym of *S. kirchbergensis*, an exhaustive diagnosis can be deduced from Guérin (1980: p. 1040). A revised diagnosis of the species was also reported by Tong and Wu (2010) and Tong (2012).

Referred Material.—The studied specimen (NMNS-PV9600) is composed of a partial skull and two left mandibular fragments with roots of cheek teeth, that was described by Shikama *et al*. (1967).

Locality and Horizon.—The present specimen was found from Isa quarry of the Ube Kosan Company in Isa area, Mine City, Yamaguchi Prefecture, Japan (Figure 1). According to Shikama *et al*. (1967), the present specimen was collected from the red clay of the lower part of the Isa Formation, which has yielded large mammal fossils such as *Stegodon orientalis*, *Panthera youngi*, *Ursus arctos* and *Sinomegaceros yabei* (e.g. Shikama and Okafuji, 1958; Okafuji and Otsuka, 1977). The age of the formation is estimated as Middle Pleistocene based on the mammal fossils (Kamei *et al*., 1988).

Description

The studied specimen is a right half of a skull (Figure 2). The anterior and neurocranial parts of the skull are missing. In lateral view, the nasal notch is located at half of P2 (Figure 2a, b). The infraorbital foramen is located at the anterior half of P3. The anterior margin of the orbit is situated at the anterior part of M2. On the anterior margin of the orbit, the preorbital process projects laterally. The short infraorbital process projects postero-ventrally. In lateral view, the partial jugal arch is gently oriented postero-dorsally (Figure 2a, b).

Right P2 to M3 are preserved (Figure 3a, b). The teeth are moderately worn. The occlusal surface of the teeth is concave. There is no coronal cement on the teeth.

The buccal and mesio-lingual parts of P2 are broken (Figure 3a, b). The protoloph and metaloph are connected at this wear stage. The crochet and crista project toward the mesial. These do not connect to each other. The postfossette is small and oval in shape. There is the trace of a lingual cingulum.

The ectoloph of P3 is slightly undulated (Figure 3a, b). The protoloph and metaloph bend disto-lingually. These lophs are connected at this wear stage (Figure 3a, b). The parastyle is short. The paracone fold is weak. The crochet is bifid. The postfossette is small. There is a mesial cingulum. The trace of a short lingual cingulum is preserved. There is no buccal cingulum.

The ectoloph of P4 is partially broken and slightly undulated as in P3 (Figure 3a, b). The protoloph and metaloph bend disto-lingually. The parastyle and metastyle are short. The crochet projects mesially. There are no crista and antecrochet. A mesial-lingual cingulum occurs on the corner of the protocone. There is a short lingual cingulum at the entrance of the medisinus. The buccal cingulum is not developed.

M1 is almost completely preserved (Figure 3a, b). The ectoloph is slightly undulated. The protoloph and metaloph are almost oriented lingually. The anterior protocone groove is weak. The paracone fold is slightly developed. There are crochet and crista, which do not contact each other. A short mesio-lingual cingulum occurs on the mesio-lingual margin of the protocone. A trace of the lingual cingulum is located at the entrance of the medisinus. There is no buccal cingulum.

The morphology of M2 is similar to that of M1 (Figure 3a, b). The lingual part of the protocone is broken. The posterior part of the ectoloph is concave. The protoloph and metaloph are disto-lingually oriented. The paracone fold is developed and it disappears at the base of the crown. The parastyle is short. The metastyle is relatively long at this wear stage. Crochet and crista are present. The mesial cingulum is low and located along the protoloph. The distal cingulum is also low. The buccal cingulum is not developed. A short lingual cingulum is preserved.

M3 is well preserved (Figure 3a, b). The protoloph is lingually oriented. The ectometaloph extends disto-lingually. The anterior protocone groove is weak. The paracone fold and the parastyle are developed. Crochet and crista are present. The mesial cingulum is located along the protoloph and it is characterized by the presence of several small tubercles on it. The distal cingulum is knob-like. There is a pillar-like lingual cingulum at the entrance of the medisinus.

Morphological comparison

Comparison with Pleistocene–Holocene Asian species

NMNS-PV9600 differs from *Rhinoceros unicornis* in having less marked paracone and metacone folds on the premolars, a developed mesostyle on P2 and P3, a usually not constricted metaloph on the premolars, no medifossette on the premolars and a rounded lingual wall of the protocone on M3. Moreover, the lingual cingulum is not present on the premolars of *R. unicornis*.

NMNS-PV9600 differs from *Rhinoceros sondaicus* in showing the following characters: the crista is present on both premolars and molars, the crochet is present on the premolars, the mesostyle is present on the premolars, the hypocone is slightly smaller than the protocone on P2 and the paracone fold is less marked on the molars.

Cranial material of *Rhinoceros sivalensis* is poorly known, being represented by only a few specimens collected from the Siwalik Hills (Pandolfi and Maiorino, 2016). This species has been also considered as synonym of *R. unicornis* (Antoine, 2012). The taxonomic status of *R. sinensis* is still debated (Antoine, 2012 and references therein; Pandolfi, 2015; Pandolfi and Maiorino, 2016) because the species was established only on fragmented and isolated teeth by Owen (1870). Chinese material assigned as *R. sinensis* has been recently referred to *Dicerorhinus sumatrensis* and *S. kirchbergensis* (Tong and Wu, 2010; Tong, 2012). A careful revision of the Asian material referred to *R. sinensis* is therefore needed.

On the upper teeth of *Dicerorhinus sumatrensis* (Figure 3c), the metacone fold is present and developed on the premolars, the crista is absent on the premolars and it has been reported only once time on the molars (Guérin, 1980), the crochet is absent or very weak on the premolars, the metacone is larger than the protocone on the premolars, protocone and hypocone are separated on P2 and P3 and the paracone fold is marked on the molars.

Comparison with *Coelodonta*

NMNS-PV9600 differs from the Middle and Late Pleistocene *Coelodonta* by having a smooth enamel without cement, no hypsodont teeth, absence of a medifossette on the upper teeth, slightly undulated ectoloph, a lingually directed protoloph and a metaloph on M1 and M2, a lingually directed protoloph on M3, and a triangular M3 in occlusal view.

Comparison with *Stephanorhinus*

The crista is usually absent on the upper teeth of *Stephanorhinus etruscus*; this structure has been only observed on the M3s of two maxillae from Senezè (lower Pleistocene, France) and Upper Valdarno (lower Pleistocene, Italy) (NMB Se187; Va453). The ectoloph profile is quite flattened or slightly convex on the premolars of *S. etruscus* and the mesostyle is not evident on P3 and P4; the lingual cingulum, when present, is more developed on P3 and P4 of *S. etruscus* than on NMNS-PV9600.

The upper teeth of *Stephanorhinus yunchuchenensis* (IVPP V2879: lower Pleistocene of China; Chow, 1963a) are much worn, the crista is present on M1 and M2 but on M1s and on the right M2 it is rather close to the crochet bearing a medifossette. The ectoloph profile on M2 is rather oblique and the mesial side of this tooth appears more developed transversally than the distal side.

The upper teeth of *Stephanorhinus lantianensis* (IVPP V5413: lower Pleistocene of China; Hu and Qi, 1978) are much worn and useful morphological characters are not evident. According to Tong (2012) the protoloph and the metaloph are parallel and vertical to the long axis of the tooth series on P3-M2 and a metacone fold occurs on M3. These features are not present on NMNS-PV9600.

On *Stephanorhinus hundsheimensis*, the lingual cingulum is evident on the upper premolars, the mesostyle is absent on P3 and P4 and the ectoloph profile is less wavy on these two premolars than in those of NMNS-PV9600. The crista is present on both premolars and molars of *S. hundsheimensis*. The molars in NMNS-PV9600 do not differ as well from those of *S. hundsheimensis*. A small crista can be observed on the upper molars of the specimen IQW 1964-680 from Süssenborn (Middle Pleistocene, Germany). In the latter specimen, however, the ectoloph profile of the premolars is slightly convex and the lingual cingulum on the premolars is developed and continuous as well as on the specimen from Hundsheim (NHMW A5591-312/G3/3: Middle Pleistocene, Austria) and Isernia La Pineta (MPI 33084: Middle Pleistocene, Italy). In the specimen from Isernia La Pineta the M1 also displays a reduced lingual cingulum at the entrance of the medisinus; the specimen, however, differs from NMNS-PV9600 by having several accessory folds on the premolars, a relatively convex profile of the ectoloph on P3 and P4, and protocone and hypocone slightly joined lingually. These characters are also evident on the specimen NHML 18705 from Pakefield (Middle Pleistocene, England). A small crista is also present on M1 and M2 of *S. hundsheimensis* from Mosbach (MNHN PW1977-13: Middle Pleistocene, Germany); however, the premolars of the specimens collected from this locality display several folds in the medisinus (e.g. double crista), sometimes a medifossette, an evident lingual cingulum and lack of the mesostyle.

The upper teeth of the *Stephanorhinus hemitoechus* skull from Ilford (Middle Pleistocene, England) are much worn (NHML 45205, 40939, 40946). The mesostyle appears absent on P3 and P4 which display a weak metacone fold. M2 and M3 have a small crista as in NMNS-PV9600. The ectometaloph profile on M3 of NHML 45205 is convex whereas it appears flattened in NMNS-PV9600. The specimen NHML 40939 resembles NHML 45205. The crista is absent on the molars of the specimen NHML 40946 but it is present on P4 only; P3 and P4 of NHML 40946 display a weak metacone fold. A reduced lingual cingulum occurs at the entrance of the medisinus on P3 and P4, as in NMNS-PV9600. The folds on the M2 ectoloph appear more marked than in NMNS-PV9600. The M3 in NHML 40946 displays a slightly convex profile of the ectometaloph. The upper tooth series from Montesacro (MPUR 1497 and 1497a: Middle Pleistocene, Italy) display a crista on M1 and M2, but they differ from NMNS-PV9600 by having a convex profile of the ectometaloph on M3, marked ectoloph folds on M2 and by lacking the mesostyle on P3 and P4; the latter tooth also has a long parastyle. Marked ectoloph folds on M2 also occur on the upper tooth series from Cueva Millan (MNCN 61743: Upper Pleistocene, Spain) which also has separate protocone and hypocone, a crista, a weak metacone fold and a long parastyle on P4. On erupting P3 of the tooth series from Maspino (IGF 11641: Middle Pleistocene, Italy), the mesostyle is absent and the parastyle is long, the crista is absent on M1 and M2 which display marked ectoloph folds. Other specimens (housed at IGF and MCP: Azzaroli, 1962) from Maspino and neighboring localities have a convex ectometaloph profile on M3, the crista is rarely observed on the molars (in particular it occurs only on M2) and the mesostyle is absent on the premolars. On the upper tooth series of the specimen from San Colombano (MVC: Upper Pleistocene, Italy) the crista is absent on the molars, the ectometaloph on M3 is convex, the crochet is double on P3 and M2, the mesostyle is absent on P3 and P4; and the latter tooth also displays a long parastyle.

The presence of the crista on the molars, of a reduced lingual cingulum on the premolars and of a wavy ectoloph on P3 and P4 can be observed on the specimens assigned to *Stephanorhinus kirchbergensis*. However, the M2 of *S. kirchbergensis* from Kirchberg (NMB no code: Middle Pleistocene, Germany) differs from NMNS-PV9600 by having a more wavy profile of the ectoloph and bulbously lingual cones, whereas the M3 from the same locality lacks the crista and has a less curved protoloph than in NMNS-PV9600. A fragment of maxilla with P2-M1 (MfN MbMa42546) of *S. kirchbergensis* from Taubach (Upper Pleistocene, Germany) differs from NMNS-PV9600 by having a more wavy profile of the ectoloph on M1, a small crista on P4, separated protocone and hypocone on P3, a long parastyle and metastyle on P3 and P4. The M3s from Taubach and Rixdorf (MfN: Upper Pleistocene, Germany) resemble the M3 of NMNS-PV9600 but their protocone is wider at the base than in the studied specimen. The upper tooth series from Grays (NHML 22020: middle Pleistocene, England) (Figure 3d) differs from NMNS-PV9600 by having a long parastyle on P3 and P4, a small antecrochet on M3 and a small crista on P4. The ectoloph profiles of the teeth from Grays resemble those of NMNS-PV9600, including the presence of a slight mesostyle on P3 and P4. The differences and similarities between NMNS-PV9600 and NHML 22020 can be also recognized on several isolated teeth of *S. kirchbergensis* from Grays which show certain variability in the presence and development of the internal folds. The morphologies of NMNS-PV9600 resemble the upper tooth series from the suburban area of Rome (MPUR). The composite specimen MPUR 1498 (Figure 3e) displays a crista on M1 and M2, a wavy ectoloph on premolars and molars, a slight mesostyle on P4, a reduced lingual cingulum on the premolars, and a double crochet on P4. The specimen differs from NMNS-PV9600 by having a medifossette on M3, a small antecrochet on M2, a multiple crochet on P3, a slight metacone fold on P3, and a well evident lingual cingulum on P4. On the specimen MPUR 1518, the lingual cingulum is absent on the premolars (but a weak cingulum is present on MPUR 1519 (Figure 3f) belonging to the same individual of MPUR 1518), the crista is absent on M1 whereas it is present on P4, the ectoloph is slightly wavy on the premolars, and the metacone fold appears absent whereas the mesostyle is shallow. The Chinese specimen IVPP V4569 is rather worn, it displays the following common features with NMNS-PV9600: a crista on M2 and M3, a wavy profile of the ectoloph on M2 with shallow folds, a reduced lingual cingulum at the entrance of the medisinus on P4, weak crochet on P3 and P4, a weak mesostyle on P4.

The upper tooth series of *Stephanorhinus kirchbergensis* from Rhino Cave (Upper Pleistocene, China: Tong and Wu, 2010; fig. 2A, B) morphologically resemble NMNS-PV9600 but differ from it by having a strong protocone constriction on M1 and M2, a posterior groove on M3 and by lacking a crista on M1.

The upper premolars from Migong Cave (Upper Pleistocene, China) figured by Chen *et al.* (2012; fig. 3B, C) differ from NMNS-PV9600 by having a strong lingual cingulum, several internal folds (i.e., complex crochet, crista) and a rather convex ectoloph profile on P4. The M1 and M2 from the same locality display a strong protocone constriction and also a metaloph constriction (on M1 and M3), the crista is absent and the ectoloph profile is less wavy. The two M3 from Migong Cave are morphologically rather close to that of NMNS-PV9600 but one of them doesn't display a crista, whereas the other one has two cristae.

The isolated upper premolars from Choukoutien (upper lower Pleistocene, China) figured by Wang (1931: pl. II) differs from NMNS-PV9600 by having a small crista on P3, a wide postfossette on P4, an S-shaped metaloph on P4 in occlusal view and a less wavy ectoloph on P3 and P4. The isolated upper molars from Choukoutien (Wang, 1931: pl. I) differ from NMNS-PV9600 by lacking the crista, by having a marked protocone constriction on M1 and by a convex ectometaloph profile on M3.

On the upper tooth series of the *Dicerorhinus choukoutienensis* skull (Chow, 1963b: pl. I, fig. 3), a weak

Table 1. Measurements (in mm) of upper cheek teeth row comparing NMNS-PV9600 with *Stephanorhinus* species. $L_{\text{max, P-M}}$, maximal length of the tooth series; $L_{\text{max, P}}$, maximal length of the premolar row; $L_{\text{max, M}}$, maximal length of the molar row. 1, data from Guérin (1980); 2, data from Chow (1963b); 3, data from Lacombat (2005); 4, data from Kahlke (1977).

	NMNS-PV9600	*S. etruscus*[1]	*S. hundsheimensis*[1]	*S. hemitoechus*[1]	*S. kirchbergensis*[1]	*S. yunchuchenensis*[2]	*D. choukoutienensis*[2]	*S. hundsheimensis*[3]	*S. etruscus*[3]	*S. hemitoechus*[3]	*S. kirchbergensis*[4]
$L_{\text{max, P-M}}$	238+	220–245	226–263.5	243–267	266–289.5	259	300	241–244	223–232	–	–
$L_{\text{max, P}}$	102.8+	100–135	96–119.5	101–125	111–133	110	130	104.5–116.6	94.9–101.66	–	131.2
$L_{\text{max, M}}$	145.4	126–145	128–159.5	133–168	159–176	–	167	137.6–147.07	133.92–135.16	151.26	168.8

Table 2. Measurements (in mm) of the upper cheek teeth comparison of NMNS-PV9600 with other species of *Stephanorhinus*. 1, data from Guérin (1980); 2, data from Chow (1963b). Abbreviations: *L*, length; *W*, width; min., minimal value; max., maximal value; mean, mean value.

		NMNS-PV9600	*S. etruscus*[1]			*S. hundsheimensis*[1]			*S. hemitoechus*[1]			*S. yunchuchenensis*[2]
			min.	max.	mean	min.	max.	mean	min.	max.	mean	
P2	*L*	22.8	29	35	32	28.5	37.5	34.5	31	34.5	32.71	33
	W	26.8+	32	42.5	38.11	33	44	38.59	34	39	36.46	38
P3	*L*	39.7	35	41	38.35	35	46	40.93	38	43.5	40.73	37
	W	53.4	42	54	48.66	45	57.5	50.03	44	53	49.07	–
P4	*L*	42.9	37	42.5	39.89	39	48.5	43.09	38	48	43.73	42
	W	56.1	45	63	54.69	50	59	54.69	47	62	55.44	58
M1	*L*	53.3	41	50.5	48	44	57.5	49.9	43.5	57.5	53.2	47
	W	60.6	48	60.5	55.61	51	63	57.44	53	68	61.09	64
M2	*L*	55.8	45.5	57	49.89	47	63	53.88	46.5	65	59.25	56
	W	60.8	48	65.5	57.25	52	67	59.42	56	72	64.22	–
M3	*L*	50.2	47	59	53.2	50.5	66	55.71	50	77	65.41	–
	W	55.5	46	56.5	51.91	46	60	53.07	52	65	59.54	–

crista is present on M1 and P4, the crochet is shallow on the premolars, the lingual cingulum is reduced and occurs at the entrance of the medisinus on premolars, M1 and M2. The ectoloph profiles of P3 and P4 of Choukoutien resemble those of NMNS-PV9600 as well as the ectoloph profiles of M1 and M2. The Chinese specimen and the Japanese one also display similar features in the morphology of the protoloph and metaloph of premolars and molars, in the presence of a shallow protocone constriction on M1 and in the morphology of the ectolometaloph and protoloph of M3. According to Shikama *et al.* (1967) *D. nipponicus* is nearest to *D. choukoutienensis*, but differs by having a higher orbit and maxilla. In fact, the preserved zygomatic arch on NMNS-PV9600 appears high and with an oblique lower border of the jugal in respect to the tooth series, whereas on the skull from Choukoutien it is low and with a parallel lower border of the jugal in respect to the tooth series. However, the studied specimen appears damaged on the lower margin of the preserved zygomatic arch and the morphology of the upper border of the latter, as well as the position of the anterior border of the orbital cavity and of the infraorbital foramen, doesn't differ from those of several *Stephanorhinus kirchbergensis* skulls (e.g. SMNS 6616.2.11.89.13).

Metric comparison

The measurements of NMNS-PV9600 and compared specimens are shown in Tables 1–3. The maximal length of the upper tooth series of NMNS-PV9600 falls within the dimensional ranges of *Dicerorhinus etruscus etruscus* (= *Stephanorhinus etruscus*) and *D. etruscus brachycephalus* (= *S. hundsheimensis*, but excluding the type

Table 3. Measurements (in mm) of upper cheek teeth of NMNS-PV9600 compared with *Stephanorhinus kirchbergensis*. 1, data from Chen *et al*. (2012); 2, data from Tong and Wu (2010); 3, data from Xu (1986); 4, data from Chow (1979); 5, data from Guérin (1980). Abbreviations: *L*, length; *W*, width; min., minimal value; max., maximal value; mean, mean value.

		NMNS-PV9600	Migong Cave[1]		Rhino Cave[2]			Anping[3]		Choukoutien[4]			Western Europe[5]		
			min.	max.	min.	max.	mean	min.	max.	min.	max.	mean	min.	max.	mean
P2	*L*	22.8	–	–	–	–	–	32.5	36.8	30	36	33.8	36.5	41	38.25
	W	26.8+	–	–	–	–	–	40.1	41.8	39	43	41.6	41	44.5	42.67
P3	*L*	39.7	45.6	51.8	–	–	–	38.2	43.2	38	39	38.6	45.5	49	47.13
	W	53.4	60.6	61.3	–	–	–	55.9	60.2	57	61	59.3	50	63	57.3
P4	*L*	42.9	54.7	–	48.3	–	–	44.2	51	44	50	46.3	50	53	51.88
	W	56.1	63.7	–	67.1	–	–	60.8	66.3	64	69	66.7	56	69.5	63.6
M1	*L*	53.3	60.1	–	56.9	–	–	47.2	54.7	52	56	54.3	52	63.5	58.3
	W	60.6	69.7	–	71.6	–	–	61.2	67.2	60	74	69.5	60	71.5	67.2
M2	*L*	55.8	61.2	61.7	68.9	69.6	69.3	53.4	62.7	50	60	55	61.5	67	64.8
	W	60.8	65.4	71.8	69.4	77.1	73.3	66	70.9	64	71	67.1	62	72.5	67.6
M3	*L*	50.2	60.3	61.7	63	70	66.9	60.5	67.2	60	67	63.2	63	65	63.9
	W	55.5	55.1	55.4	52.1	66.6	57.4	60.2	63.5	59	67	62.4	59.5	68.5	63.4

specimen) given by Guérin (1980) and of *S. etruscus* given by Lacombat (2005). The length of the premolar series falls within the dimensional ranges of *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus* given by Guérin (1980), whereas the length of the molar series falls within the range of *S. hundsheimensis* and *S. hemitoechus* given by Guérin (1980) and of *S. hundsheimensis* given by Lacombat (2005). The length of the tooth series is considerably smaller than those of *S. yunchuchenensis*, *D. choukoutienensis* (= *S. kirchbergensis*) and *S. kirchbergensis* (= *D. mercki* in Guérin, 1980) (Table 1).

The P2 dimensions of NMNS-PV9600 are smaller than those of middle Pleistocene Eurasian rhinoceroses (Table 2). The lengths of P3, M2 and M3 fall within the range of *Stephanorhinus etruscus*, *S. hundsheimensis* and *S. hemitoechus* given by Guérin (1980). The length of P2 is slightly larger than that of *S. etruscus*. The length of M1 falls within the range of *S. hundsheimensis* and *S. hemitoechus* given by Guérin (1980) whereas the values of *S. etruscus* are smaller (Figure 4a). The width of P3 falls within the range of *S. etruscus* and *S. hundsheimensis*, whereas the widths of P4 and M2 fall within the range values of *S. etruscus*, *S. hundsheimensis* and *S. hemitoechus* given by Guérin (1980). The width of M1 is close to that of *S. etruscus* (Figure 4b). Finally, the lengths of P3, P4 and M2 are close to those of *S. yunchuchenensis* (Table 2).

The dimensional values of NMNS-PV9600 teeth are generally smaller than those of *Stephanorhinus kirchbergensis* from Western Europe and from China (including *Dicerorhinus choukoutienensis*) with the following exceptions: The length of M2 falls within the range values of the specimens from Anping and Choukoutien; The length of P3 falls within the range values of the specimens from Anping, and is slightly larger than that of the specimens from Choukoutien; The length of P4 is close to the minimal values of *S. kirchbergensis* from Anping and Choukoutien; The length of M1 falls within the dimensional range of *S. kirchbergensis* from Western Europe, Anping and Choukoutien (Table 3).

Discussion and conclusion

The studied specimen NMNS-PV9600 has fully erupted permanent teeth. The premolars are well worn down and all the molars, especially M3, are moderately worn. This tooth eruption and occlusal pattern are compared to the wear class XIII (age 20–28) of *Ceratotherium simum* in Hillman-Smith *et al*. (1986). Goddard (1970) also investigated the age class of *Diceros bicornis* based on the tooth eruption and wear pattern. Compared to his study, the present specimen is similar to the age class XIII (mean age 25). Anders *et al*. (2011) proposed six "individual dental age stages (IDAS)" based on the tooth eruption and wear of the cheek teeth of many ter-

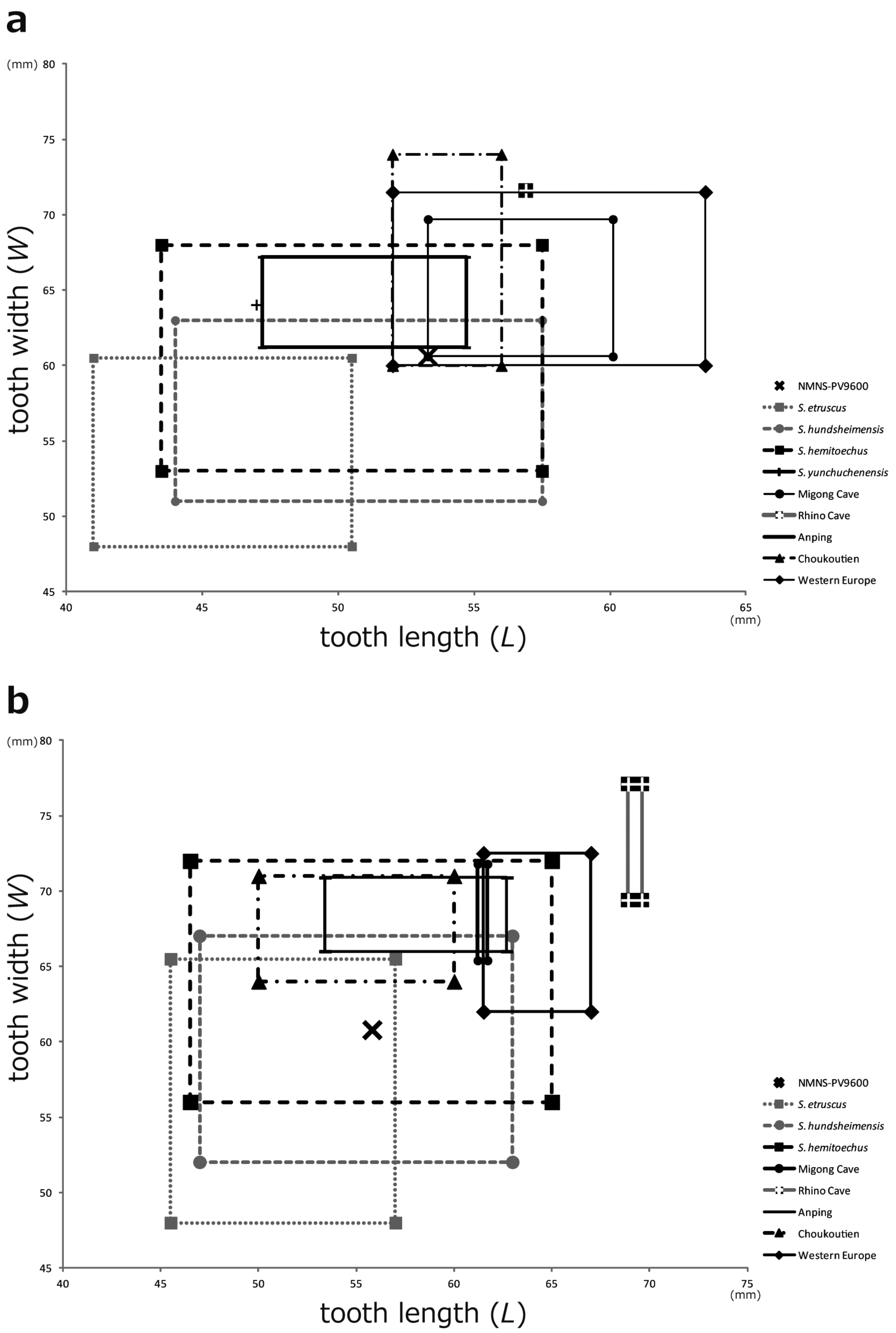

Figure 4. Metric comparison of M1 **(a)** and M2 **(b)** of NMNS-PV9600 and those of *Stephanorhinus etruscus*, *S. hundsheimensis* and *S. hemitoechus* from Western Europe, *S. yunchuchenensis* from China and *S. kirchbergensis* from China (Migong Cave, Rhino Cave, Anping and Choukoutien) and Western Europe (source data are reported in Tables 2 and 3).

restrial mammals. According to this study, the present specimen is compared to IDAS 3 (adult). These results suggest that the present specimen was an adult individual around 25 years old when it died.

Morphological characters enable us to assign NMNS-PV9600 to the Eurasian genus *Stephanorhinus*. In fact, the studied specimen shares the following common features with this genus: molarised premolars, absence of P1, absence of metacone fold on P3 and P4, presence of crochet on premolars and molars, presence of a crista on the molars, absence of medifossette on both premolars and molars, triangular-shaped M3.

Morphologically, the studied specimen is closer to *Stephanorhinus kirchbergensis*, in particular to the specimens from Choukoutien, than to other Eurasian Pleistocene rhinoceroses. The presence of a small crista on the upper molars seems to be a peculiar feature of NMNS-PV9600, but this structure show a high variability within the *Stephanorhinus* species and, as reported by Guérin (1980), the crista is "une formation relativement labile" (Guérin, 1980, p. 58).

The metric comparison reveals that NMNS-PV9600 is generally smaller than *Stephanorhinus kirchbergensis* from Western Europe, and a few measurements, in particular the lengths, fall within the range values of *S. kirchbergensis* from Anping (upper Middle Pleistocene: Xu, 1986) and Choukoutien (upper lower Pleistocene: Wang, 1931; Chow, 1963b) (Tables 2, 3). Moreover, we noticed that the Chinese material is slightly smaller in length than the Western European material (Table 2). These differences could reflect a subspecific differentiation within the species such as that reported for extant rhinoceroses like *Diceros bicornis* or *Dicerorhinus sumatrensis* (Groves, 1967; Guérin, 1980; Strien *et al*., 2008; Emslie, 2012) and supposed for fossil European species (Pandolfi and Petronio, 2011; Pandolfi and Tagliacozzo, 2015). A few morphological differences seem to be also present between the Western European and the East Asian material referred as *S. kirchbergensis*, in particular in the wave of the ectoloph and the presence of enlarged lingual cones on the molars. A careful analysis of the whole Eurasian material will be useful to test the presence of different *S. kirchbergensis* subspecies.

A relationship between *Stephanorhinus kirchbergensis* from China and the Japanese rhino could suggest that *S. kirchbergensis* reached the Japanese archipelago, together with several other Asian taxa (e.g. *Macaca*, *Sus*, *Cervus*), during the middle Pleistocene and slightly decreased in size due to "island effect". The immigration of continental Asian taxa in Japan occurred twice during the middle Pleistocene according to Kawamura (1991, 1998) and Konishi and Yoshikawa (1999): around 0.63 Ma, with the entrance of Southern Chinese taxa, and around 0.43 Ma, with the entrance of Northern Chinese taxa. According to Ogino *et al*. (2009), the taxa belonging to the second immigration event (*Palaeoloxodon* stage) and collected from the Matsugae limestone cave deposits (Tokunaga, 1931; Saito, 1939; Naora, 1944; Ogino and Otsuka, 2005, 2008; Ogino *et al*., 2009) are comparable to the Middle Pleistocene Northern Chinese Locality 1 of the Choukoutien fauna. The Matsugae fauna, recently correlated with the QM4 (0.3 to 0.5 Ma, Quaternary mammal zones in the Japanese Islands: Kamei *et al*., 1988) by Ogino *et al*. (2009), includes *Panthera* and *Stegodon orientalis*, which also occurs in the red clay of the Lower Isa Formation, Yamaguchi Prefecture, where the rhinoceros specimen under examination was collected (Shikama *et al*., 1967). In Japan, almost all the Pleistocene rhinoceroses seem to be present only during the QM4 (Ogino *et al*., 2009), which represents an important time span for immigration of continental taxa into the Japanese archipelago *via* the Korean Peninsula. One exception is *Rhinoceros* aff. *sinensis* from possibly lower Pleistocene deposit in Aira, Kagoshima (Shikama, 1967). The morphological affinities between NMNS-PV9600 and the Chinese material support the hypothesis of a dispersal of Northern Chinese taxa towards Japan during the middle Pleistocene. Indeed, *S. kirchbergensis* is a common taxon within Northern Chinese faunas that are middle Pleistocene in age (Tong, 2002, 2012) and its southernmost occurrence in China is from the Upper Pleistocene locality of Rhino Cave, in Shennongjia (Tong and Wu, 2010).

The fragment of M2 collected from the Matsugae deposits (Tokunaga, 1931; Ogino *et al*., 2009) also resembles several M2s of *Stephanorhinus kirchbergensis* by having crista, crochet, antecrochet and a relatively large lingual cone. This specimen was assigned to *Rhinoceros shindoi* by Tokunaga (1931) and was reported as *Dicerorhinus* sp. by Ogino *et al*. (2009). If the presence of different subspecies is confirmed by further material, the Japanese rhino should be named *S. kirchbergensis shindoi* because of the priority of Tokunaga's name over *Dicerorhinus nipponicus* proposed by Shikama *et al*. (1967). The Western European *S. kirchbergensis* would become the nominal subspecies *S. kirchbergensis kirchbergensis* (Jäger, 1839), whereas the Chinese one should be called *S. kirchbergensis choukoutienensis* (Wang, 1931). We should assert that these names are not being introduced here as official names.

The teeth of NMNS-PV9600 show the following dental features: concaved occlusal surface, unequal enamel thickness, inclined buccal and lingual wall, sawtooth wear profile of the ectoloph and triangular-shaped M3. These features are found in brachydont teeth of rhinoceroses (Fortelius, 1982), suggesting that the present species was probably a browser. The feeding habits of *S. kirchbergensis* from Europe have been evaluated as that of a browser based on the following characters: relatively low crowned cheek teeth, long limbs, high head posture (e.g. Fortelius *et al*., 1993; Made, 2010). In contrast, the other species of *Stephanorhinus*, *S. hemitoechus*, from Europe, has short legs and more hypsodont cheek teeth with abundant coronal cement, suggesting that this species was adapted to grazing (e.g. Fortelius *et al*., 1993; Made, 2010). Additionally, mesowear analysis of *S. kirchbergensis* and *S. hemitoechus* suggests that *S. kirchbergensis* was a browser, whereas the diet of *S. hemitoechus* consisted of more abrasive material (Hernesniemi *et al*., 2011). Nevertheless, van Asperen and Kahlke (2015) recently suggested that despite these two species having a preferred optimal diet, they had a considerable dietary flexibility and adapted their diet according to what was available in their environment (van Asperen and Kahlke, 2015). Therefore, *S. kirchbergensis* from Japan would have a similar ecology to that of *S. kirchbergensis* from Europe, although more materials are needed to discuss this hypothesis.

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References

Anders, U., Koenigswald, W. von, Ruf, I. and Smith, B. H., 2011: Generalized individual dental age stages for fossil and extant placental mammals. *Paläontologisches Zeitschrift*, vol. 85, p. 321–339.

Antoine, P.-O., 2002: Phylogenie et evolution des Elasmotheriina (Mammalia, Rhinocerotidae). *Mémoires du Muséum National d'Histoire Naturelle*, vol. 188, p. 1−359.

Antoine, P.-O., 2012: Pleistocene and Holocene rhinocerotids (Mammalia, Perissodactyla) from the Indochinese Peninsula. *Comptes Rendus Palevol*, vol. 11, p. 159–168.

Arambourg, C., 1970: Les vertébrés du Pléistocène de l'Afrique du Nord. *Archives du Muséum d'Histoire Naturelle*, *Paris*, vol. 7, p. 1–126.

Asperen, E. N. van and Kahlke, R.-D., 2015: Dietary variation and overlap in Central and Northwest European *Stephanorhinus kirchbergensis* and *S. hemitoechus* (Rhinocerotidae, Mammalia) influenced by habitat diversity. *Quaternary Science Reviews*, vol. 107, p. 47–61.

Azzaroli, A., 1962: Validità della specie *Rhinoceros hemitoechus* Falconer. *Paleontographia Italica*, vol. 57, p. 21–34.

Blumenbach, J. F., 1799: *Handbuch der Naturgeschichte. Sechste Ausgabe. 6th Edition*, p. 1–703. Johan Christian Dieterich, Göttingen.

Borsuk-Bialynicka, M. and Jakubowski, G., 1972: The skull of *Dicerorhinus mercki* (Jäger) from Warsaw. *Prace Muzeum Ziemi*, vol. 20, p. 187–199.

Brandt, J. F., 1877: Versuch einer Monographie der Tichorhinen Nashorner nebst Bemerkungen über *Rhinoceros leptorhinus* Cuvier. *Mémoires de l'Académie Impériale des Sciences de St. Pétersbourg*, *Série 7*, vol. 24, p. 1–135.

Cerdeño, E., 1995: Cladistic analysis of the family Rhinocerotidae (Perissodactyla). *American Museum Novitates*, no. 3143, p. 1–25.

Chen, S.-K., Huang, W.-B., Pei, J., He, C.-D., Qin, L., Wei, G.-B. and Leng, J., 2012: The latest Pleistocene *Stephanorhinus kirchbergensis* from the Three Gorges area and re-evaluation of Pleistocene rhinos in Southern China. *Acta Anthropologica Sinica*, vol. 31, p. 381–394.

Chow, B.-S., 1963a: A new species of *Dicerorhinus* from Yushe, Shansi, China [*D. yunchuchenensis*]. *Vertebrata PalAsiatica*, vol. 12, p. 325–329.

Chow, B.-S., 1963b: On the skull of *Dicerorhinus choukoutienensis* Wang from Choukoutien locality 20. *Vertebrata PalAsiatica*, vol. 7, p. 62–70.

Chow, B.-S., 1979: The fossil rhinocerotides of locality 1 Choukoutien. *Vertebrata PalAsiatica*, vol. 17, p. 236–258.

Desmarest, A. G., 1822: *Mammalogie, ou Description des Espèces des Mammiferes. Seconde partie*, p. 277–555. Veuve Agasse, Paris.

Emslie, R., 2012: *Diceros bicornis. The IUCN Red List of Threatened Species*. Version 2014. 2 [online]. [Cited 22 July 2015]. Available from http://www.iucnredlist.org.

Falconer, H., 1859: Modifications apportés par Mr. Falconer à la faune du Val d'Arno. *Bulletin de la Société Vaudoise des Sciences Naturelles*, vol. 6, p. 130–131.

Falconer, H., 1868: On the European Pliocene and Post-Pliocene species of the genus *Rhinoceros*. *In*, Murchison, C. and Hardwicke, R. *eds*., *Palaeontological Memoirs and Notes of the late Hugh Falconer*, *Vol. II. Mastodon*, *Elephant*, *Rhinoceros*, *Ossiferous Caves*, *Primeval Man and His Contemporaries*, p. 309–403. Robert Hardwicke, London.

Fischer, W. G. von, 1814: *Zoognosia. Tabulis Synopticis Illustrata, in Usum Praelectionum Academiae Imperialis Medico-chirurgicae Mosquensis - Volumen Tertium. Quadrupedum Reliquorum*, *Cetorum et Monotrymatum Descriptionem Continens*, 734 p. Nicolai Sergeidis Vsevolozsky, Mosquae (Moscow).

Fortelius, M., 1982: Ecological aspects of dental functional morphology in the Plio-Pleistocene rhinoceroses of Europe. *In*, Kurten, B. *ed*., *Teeth: Form*, *Function*, *and Evolution*, p. 163−181. Columbia University Press, New York.

Fortelius, M., Mazza, P. and Sala, B., 1993: *Stephanorhinus* (Mammalia: Rhinocerotidae) of the Western European Pleistocene, with a revision of *S. etruscus* (Falconer, 1868). *Palaeontographia Italica*, vol. 80, p. 63–155.

Geraads, D., 2010: Rhinocerotidae. *In*, Werdelin, L. and Sanders, W. J. *eds*., *Cenozoic Mammals of Africa*, p. 669–683. University of California Press, Berkeley.

Goddard, A., 1970: Age criteria and vital statistics of a black rhinoceros population. *East African Wildlife Journal*, vol. 8, p. 105–121.

Gray, J. E., 1821: On the natural arrangement of vertebrose animals. *London Medical Repository*, vol. 15, p. 297–310.

Groves, C. P., 1967: On the rhinoceroses of South-East Asia. *Säugetierkundliche Mitteilungen*, vol. 15, p. 221–237.

Groves, C. P., 1983: Phylogeny of the living species of rhinoceros. *Zeitschrift für Zoologische Systematik und Evolutionsforschung*, vol. 21, p. 293–313.

Guérin, C., 1972: Une nouvelle espèce de Rhinocéros (Mammalia, Perissodactyla) à Vialette (Haute-Loire, France) et dans d'autres gisements du Villafranchien Inférieur Européen: *Dicerorhinus jeanvireti* n. sp. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon*, vol. 49, p. 53–161.

Guérin, C., 1980: Les rhinocéros (Mammalia, Perissodactyla) du Miocene terminal au Pléistocène supérieur en Europe occidentale, comparaison avec les espèces actuelles. *Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon*, vol. 79, p. 3–1183.

Guérin, C., 1989: La famille des Rhinocerotidae (Mammalia, Perissodactyla): systématique, histoire, évolution, paléoécologie. *Cranium*, vol. 6, p. 3–14.

Guérin, C., 2004: Les rhinocéros (Mammalia, Perissodactyla) du gisement villafranchien moyen de Saint-Vallier (Drôme). *Geobios*, vol. 37, p. 259–278.

Guérin, C. and Santafé-Llopis, J. V., 1978: *Dicerorhinus miguelcrusafonti* nov sp, une nouvelle espèce de rhinocéros (Mammalia, Perissodactyla) du gisement Pliocène supérieur de Layna (Soria, Espagne) et de la formation Pliocène de Perpignan (Pyrenées-Orientales, France). *Geobios*, vol. 11, p. 457–491.

Handa, N., 2015: A Pleistocene rhinocerotid (Mammalia, Perissodactyla) from Yage, Shizuoka Prefecture, central Japan. *Paleontological Research*, vol. 19, p. 139–142.

Hernesniemi, E., Blomstedt, K. and Fortelius, M., 2011: Multi-view stereo 3D reconstruction of lower molars of recent and Pleistocene rhinoceroses for mesowear analysis. *Palaeontologia Electronica*, vol. 14, p. 1–15.

Hillman-Smith, K., Owen-Smith, R. N., Anderson, J. L., Hall-Martin, A. J. and Selaladi, J. P., 1986: Age estimation of the white rhinoceros (*Ceratotherium simum*). *Journal of Zoology (London)*, vol. 210, p. 355–379.

Hu, C. K. and Qi, T., 1978: Gongwangling Pleistocene mammalian fauna of Lan-tian, Shaanxi. *Palaeontologia Sinica*, *New Series C*, no. 21, p. 1–64.

International Commission on Zoological Nomenclature, 2000: International Code of Zoological Nomenclature, fourth edition. *The International Trust for Zoological Nomenclature* [online]. [Cited 28 July 2015]. Available from http://iczn.org/iczn/index.jsp.

Jäger, G. F., 1839: *Über die Fossilen Säugetiere Welche in Württemberg in Verschiedenen Formationen Aufgefunden Worden Sind*, *nebst Geognotischen Bemerkungen über Diese Formationen*, 214 p. C. Erhard Verlag, Stuttgart.

Kahlke, H. D., 1977: Die Rhinocerotidenreste aus den Travertinen von Taubach. *Quart Ärpaläontologie*, vol. 2, p. 305–359.

Kamei, T., Kawamura, Y. and Taruno, H., 1988: Mammalian stratigraphy of the Late Neogene and Quaternary in the Japanese Islands. *Journal of the Geological Society of Japan (Chishitsugakuronshu)*, vol. 30, p. 181–204. (*in Japanese with English abstract*)

Kaup, J. J., 1841: *Akten der Urwelt oder Osteologie der Urweltlichen Säugethiere und Amphibien*, x + 54 p. The author, Darmstadt.

Kawamura, Y., 1991: Quaternary mammalian faunas in the Japanese Islands. *The Quaternary Research*, vol. 30, p. 213–220.

Kawamura, Y., 1998: Immigration of mammals into the Japanese Islands during the Quaternary. *The Quaternary Research*, vol. 37, p. 251–257. (*in Japanese with English abstract*)

Konishi, S. and Yoshikawa, S., 1999: Immigration times of the two proboscidean species, *Stegodon orientalis* and *Palaeoloxodon naumanni*, into the Japanese Islands and the formation of land bridge. *Earth Science (Chikyu Kagaku)*, vol. 53, p. 125–134. (*in Japanese with English abstract*)

Kretzoi, M., 1942a: Bemerkungen zur System der Nachmiozänen Nashorn-Gattungen. *Földtani Közlöny*, vol. 72, p. 309–318.

Kretzoi, M., 1942b: Präokkupierte und durch ältere zu ersetzende Säugetiernamen. *Földtani Közlöny*, vol. 72, p. 345–349.

Lacombat, F., 2005: Les Rhinocéros fossiles des sites prehistoriques de l'Europe Mediterranéenne et du Massif Central—Paléontologie et implications biochronologiques. *British Archeological Reports*, vol. 1419, p. 1–175.

Linnaeus, C., 1758: *Systema Naturae*, *per Regna Tria Naturae*, *Secundum Classes*, *Ordines*, *Genera*, *Species*, *cum Characteribus*, *Differentiis*, *Synonymis*, *Locis. Editio Decima*, *Reformata. Tomus I*, iv + 823 p. Laurentii Salvii, Holmiae (Stockholm).

Made, J. van der, 2010: The rhinos from the middle Pleistocene of Neumark-Nord (Saxony-Anhalt). *Veröffentlichungen des Landesamtes für Archäologie*, vol. 62, p. 432–527.

Meyer, H. von, 1864: Die diluvialen Rhinoceros-Arten. *Palaeontographica*, Band 11, p. 233–283.

Nagasawa, J., 1961: A fossil rhinoceros from Kuzuu, Tochigi Prefecture, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan*, *New Series*, no. 42, p. 63–67.

Naora, N., 1944: *The History of Japanese Mammals*, 265 p. Yotokusha, Nara. (*in Japanese; original title translated*)

Ogino, S. and Otsuka, H., 2005: Morphological study of fossil *Macaca* cf. *fuscata* detected in the Middle Pleistocene Matsugae Fauna excavated from the cave deposits in northern Kyushu, Japan. *Primate Research*, vol. 21, p. 1–9. (*in Japanese with English abstract*)

Ogino, S. and Otsuka, H., 2008: New middle Pleistocene Galictini (Mustelidae, Carnivora) from the Matsugae cave deposits, northern Kyushu, West Japan. *Paleontological Research*, vol. 12, p. 159–166.

Ogino, S., Otsuka, H. and Harunari, H., 2009: The Pleistocene Matsugae fauna, northern Kyushu, West Japan. *Paleontological Research*, vol. 13, p. 367–384.

Okafuji, G. and Otsuka, H., 1977: Discovery of *Sinomegaceros* from Isa-machi, Yamaguchi Prefecture. *Journal of the Geological Society of Japan*, vol. 83, p. 143–144. (*in Japanese*)

Okazaki, Y., 2007: Several fossils of Pleistocene rhinocerotid from the "Matsugae Cave", Kitakyushu City, Japan. *Jubilee Publication in Commemoration of Prof. Kamei Tadao's 80th Birthday*, p. 135–140. Commemorative Association of Prof. Kamei Tadao's 80th Birthday, Tokyo. (*in Japanese with English abstract*)

Owen, R., 1870: On the fossil remains of mammals found in China. *Quarterly Journal of the Geological Society of London*, vol. 26, p. 417–434.

Pandolfi, L., 2013: Rhinocerotidae (Mammalia, Perissodactyla) from the Middle Pleistocene site of Ponte Milvio, Central Italy. *Bollettino della Società Paleontologica Italiana*, vol. 52, p. 219–229.

Pandolfi, L., 2015: *Sistematica e Filogenesi dei Rhinocerotini (Mammalia*, *Rhinocerotidae)—Systematics and Phylogeny of Rhinocerotini (Mammalia*, *Rhinocerotidae).* Tesi di Dottorato, Università degli Studi di Roma Tre, Roma, ciclo XXVII, p. 1–319.

Pandolfi, L. and Maiorino, L., 2016: Reassessment of the largest Pleistocene rhinocerotin *Rhinoceros platyrhinus* (Mammalia, Rhinocerotidae) from the Upper Siwaliks (Siwalik Hills, India). *Journal of Vertebrate Paleontology*, vol. 36, e1071266.

Pandolfi, L. and Marra, F., 2015: Rhinocerotidae (Mammalia, Perissodactyla) from the chrono-stratigraphically constrained Pleistocene deposits of the urban area of Rome (Central Italy). *Geobios*, vol. 48, p. 147–167.

Pandolfi, L. and Petronio, C., 2011: The small sized rhinoceros from the late Pleistocene of Apulia (Southern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, vol. 117, p. 509–520.

Pandolfi, L. and Tagliacozzo, A., 2015: *Stephanorhinus hemitoechus* (Mammalia, Rhinocerotidae) from the late Pleistocene of Valle Radice (Sora, Central Italy) and re-evaluation of the morphometric variability of the species in Europe. *Geobios*, vol. 48, p. 169–191.

Saito, H., 1939: On Canidae fossils from Ku-Hshiang-Tung, Manchuria, and from Japan. *Report of the First Scientific Expedition to Manchoukuo, Section 2*, *Part 4*, p. 1–18. (*in Japanese with English abstract*)

Schroeder, H., 1930: Über *Rhinoceros mercki* und seine nord- und mitteldeutschen Fundstellen. *Abhandlungen der Königlich Preussischen Geologischen Landesanstalt*, *Neue Folge*, vol. 124, p. 1–114.

Shikama, T., 1967: Note on the occurrence of fossil rhinoceros from Kagoshima Prefecture, southern Japan. *In*, Committee for the Commemoration of Prof. Ichiro Hayasaka's 76th Birthday *ed*., *Contributions to Celebrate Prof. Ichiro Hayasaka's 76th Birthday*, p. 117–119. Hashimotokabundo, Kanazawa.

Shikama, T., Hasegawa, Y. and Okafuji, G., 1967: On a rhinocerotid skull from Isa (Yamaguchi Prefecture, Japan). *Bulletin of the National Science Museum (Tokyo)*, vol. 10, p. 455–462.

Shikama, T. and Okafuji, G., 1958: Quaternary cave and fissure deposits and their fossils in Akiyosi District, Yamaguchi Prefecture. *Science Reports of Yokohama National University*, *Section II*, *Biology and Geology*, vol. 7, p. 43–103.

Strien, N. J. van, Manullang, B., Sectionov, Isnan, W., Khan, M. K. M., Sumardja, E., Ellis, S., Han, K. H., Boeadi, P. J. and Bradley, M. E., 2008: *Dicerorhinus sumatrensis*. *The IUCN Red List of Threatened Species*. Version 2014. 2. [online]. [Cited 22 July 2015]. Available from http://www.iucnredlist.org

Tokunaga, S., 1931: Remains of the Pleistocene den dwellers in Honshu, Kyushu and Chosen. *Nippon Gakujyutsu Hokoku*, vol. 6, p. 175–178. (*in Japanese*)

Tong, H., 2002: Fossil materials of rhinos (*Dicerorhinus mercki*) from the middle Pleistocene Nanjing *Homo erectus* site. *In*, Rukang, W. U. *ed*., *Home erectus from Nanjing*, p. 111–120. Science and Technology Publishing House, Jiangsu.

Tong, H., 2012: Evolution of the non-*Coelodonta* dicerorhine lineage in China. *Comptes Rendus Palevol*, vol. 11, p. 555–562.

Tong, H. and Wu, X. Z., 2010: *Stephanorhinus kirchbergensis* (Rhinocerotidae, Mammalia) from the Rhino Cave in Shennongjia, Hubei. *Chinese Science Bulletin*, vol. 55, p. 1157–1168.

Toula, F., 1902: Das Nashorn von Hundsheim: *Rhinoceros* (*Ceratorhinus* Osborn) *hundsheimensis* nov. form.: mit Ausführungen uber die Verhältnisse von elf Schadeln von *Rhinoceros* (*Ceratorhinus*) *sumatrensis*. *Abhandlungen der Geologischen Reichsanstalt*, vol. 19, p. 1–92.

Wang, K. M., 1931: Die fossilen Rhinocerotiden von Chou-kou-tien. *Contributions from the National Research Institute of Geology*, *Academia Sinica*, *Nanking*, vol. 1, p. 69–84.

Wüst, E., 1911: Zwei bemerkenswerte Rhinoceros-Schädel aus dem Pliozän Thüringens. *Palaeontographica*, vol. 58, p. 133–138.

Xu, X., 1986: *Dicerorhinus kirchbergensis* (Jäger, 1839) from the late Middle Pleistocene mammalian fauna of Anping, Liaoning. *Vertebrata PalAsiatica*, vol. 24, p. 229–241.