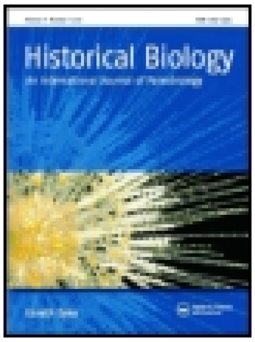

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ARTICLE

Reappraisal of a middle Pleistocene rhinocerotid (Mammalia, Perissodactyla) from the Matsugae Cave, Fukuoka Prefecture, southwestern Japan

Naoto Handa[a], Naoki Kohno[b] and Yuichiro Kudo[c]

[a]Museum of Osaka University, Toyonaka, Japan; [b]Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba, Japan; [c]National Museum of Japanese History, Sakura City, Japan

ABSTRACT

Here we describe a few cheek teeth and mandibular remains of a Pleistocene rhinocerotid from the Matsugae Cave in Kitakyushu City, Fukuoka Prefecture, western Japan. Previously, these remains had been identified as *Dicerorhinus* cf. *nipponicus* or *Dicerorhinus* sp. The present study redescribes and identifies them as belonging to *Stephanorhinus* sp. indet., like several other Japanese middle Pleistocene rhinocerotid remains. The present and other studies suggest that this genus reached Far East Asia during the middle Pleistocene. *Stephanorhinus* sp. from the Matsugae Cave would have migrated from northern China in 0.43 Ma as a member of the group of terrestrial mammals found in the cave.

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Japan; the Matsugae Cave; middle Pleistocene; Paleobiogeography; Rhinocerotidae; *Stephanorhinus*

Introduction

In Japan, Pleistocene fluvio-lacustrine and marine sediments or cave deposits have yielded various terrestrial mammal fossils. These are important for the discussion of mammal biostratigraphy and migratory patterns between the Asian Continent and the Islands of Japan during the Pleistocene (e.g. Kamei et al. 1988; Kawamura 1998). Proboscidean fossils, in particular, have contributed to such discussions (e.g. Konishi and Yoshikawa 1999; Takahashi and Namatsu 2000; Yoshikawa et al. 2007; Taruno 2010). Among other large mammals, the family Rhinocerotidae, a group of the order Perissodactyla, has been found in the Pleistocene deposits in Japan (Figure 1). Previously, several Japanese rhinocerotid remains were identified as an endemic species, *Dicerorhinus nipponicus* or an Asian species *Rhinoceros* aff. *sinensis* (e.g. Shikama 1967; Shikama et al. 1967).

Recently, taxonomic reexaminations of Eurasian Pleistocene rhinocerotids have been conducted by many scholars (e.g. Lacombat 2005; Van der Made 2010; Tong 2012; Handa and Pandolfi 2016; Pandolfi and Maiorino 2016; Kirillova et al. 2017; Pandolfi et al. 2017; Kosintsev et al. 2018). A few Japanese remains have also been redescribed as belonging to the genus *Stephanorhinus* or as being of indeterminate genus of Rhinocerotidae (Handa 2015, 2019; Handa and Pandolfi 2016; Handa and Takechi 2017). However, the taxonomies of several remains have not been revised.

Abundant middle Pleistocene mammal remains were collected from the Matsugae Cave in Kitakyushu City, Fukuoka Prefecture. Okazaki (2007) described two upper deciduous teeth and two juvenile mandibles as *Dicerorhinus* cf. *nipponicus*. Ogino et al. (2009) also reviewed the Matsugae fauna adding new rhinocerotid material such as a skull fragment with a deciduous tooth, a molar fragment, and an isolated lower deciduous tooth. Although they identified them as *Dicerorhinus* sp., they empathized that the reassessment and comprehensive revision of *Dicerorhinus* sp. from the Japanese Islands including specimens from the Matsugae Cave were necessary.

Handa and Pandolfi (2016) implied that the Matsugae remains described by Ogino et al. (2009) resemble a Eurasian species, *Stephanorhinus kirchbergensis*, but the detailed comparison was not conducted. In other words, there is no detailed taxonomic discussion of Matsugae materials since the initial description of Okazaki (2007) and Ogino et al. (2009).

In the present study, we redescribe rhinocerotid remains from the Matsugae Cave as the genus *Stephanorhinus*. In addition, the paleobiogeographical implications for the middle Pleistocene Japan are discussed.

Material and methods

A left maxillary fragment with DP4 (A-636-1-1-35-1), a fragment of left M1 or M2 (A-636-1-1-35-3), a left lower deciduous molar (A-636-1-1-35-2), and a McIII? fragment (A-636-1-1-35-4) are stored at the National Museum of Japanese History in Chiba Prefecture. Of these, the maxillary fragment and isolated upper and lower cheek teeth were described as *Dicerorhinus* sp. by Ogino et al. (2009). A right DP2 and DP3 (KMNH VP 099,999) are stored in the Kitakyushu Museum of Natural History and Human History in Fukuoka Prefecture. A right mandibular fragment with dp2 to dp4 (KUM-F58-1) and a left mandibular fragment with dp2 and dp3 (KUM-F58-2) are stored in Kyushu University Museum in Fukuoka Prefecture. Of these, the remains stored at National Museum of Japanese History is

CONTACT Naoto Handa k1552325@kadai.jp

part of the Nobuo Naora Collections and the remain stored at Kitakyushu Museum of Natural History and Human History is a deposited specimen of Kyushu Institute of Technology, Fukuoka Prefecture. These specimens were reported as *Dicerorhinus* cf. *nipponicus* by Okazaki (2007).

The classification of the Rhinocerotidae has been a matter of debate (Heissig 1973, 1989; Prothero and Schoch 1989; Cerdeño 1995; McKenna and Bell 1997; Antoine 2002; Antoine et al. 2010; Becker et al. 2013). In particular, the treatment of the tribes is complicated. In this study, two Pleistocene rhinoceroses (Rhinocerotini and Elasmotheriini) in Eurasia are compared with the studied specimens, namely rhinocerotine (*Rhinoceros, Dicerorhinus, Stephanorhinus, Coleodonta*) and elasmotheriine (*Elasmotherium*). The rhinocerotine and elasmotheriine are included the tribe Rhinocerotini and Elasmotheriini, respectively (e.g. Antoine 2002; Deng et al. 2011; Pandolfi and Tagliacozzo 2015). This study follows them. The dental terminology (Figure 2) and the measurement method follow Antoine et al. (2010).

The taxonomy of the Pleistocene rhinocerotids from Eurasia is also a subject of some debate. Tandem horned rhinoceroses that were previously identified as belonging to the genus *Dicerorhinus* have been reassigned to *Stephanorhinus*, except for *D. sumatrensis* (Sumatran rhino) (e.g. Groves 1983; Fortelius et al. 1993; Zin-Maung-Maung-Thein et al. 2008; Tong and Wu 2010; Van der Made 2010; Tong 2012; Pandolfi and Tagliacozzo 2015; Handa and Pandolfi 2016).

With regard to the genus *Rhinoceros*, numerous species had been described from Asian fossil localities (e.g. Antoine 2012 and their references herein). Antoine (2012) reviewed Pleistocene and Holocene rhinocerotids from the Indochinese Peninsula and pointed out that extinct species of *Rhinoceros* are junior synonyms of *R. unicornis* (Indian rhino) or *R. sondaicus* (Java rhino). Tong (2012) reviewed Pleistocene rhinocerotids from China and reidentified several materials of an extinct species, *Rhinoceros sinensis*, as two species of *Stephanorhinus*. Besides those studies, Yan et al. (2014) described a new species of *Rhinoceros, R. fusuiensis*, and treated *R. sinensis* and *R. sivalensis* as valid species. Pandolfi and Maiorino (2016) redescribed *Rhinoceros platyrhinus* on the basis of a skull from the Upper Siwalik in India. They also recognised the validity of *R. sinensis* and *R. sivalensis*. In our study, these species of *Rhinoceros* (*R. unicornis, R. sondaicus, R. sivalensis, R. sinensis, R. fusuiensis* and *R. platyrhinus*) are treated as distinctive taxa for comparison.

Abbreviations

KMNH, Kitakyushu Museum of Natural History and Human History; KUM, the Kyushu University Museum; NMJH, National Museum of Japanese History; MIS, Marine isotope stages; DP, upper deciduous tooth; dp, lower deciduous tooth; M, upper molar.

Geological setting

The studied specimens were collected from the Matsugae Cave that is situated in a limestone quarry in Moji-ku, Kitakyushu City, Fukuoka Prefecture, western Japan (Figure 1). The Matsugae cave is in Permian limestone, which is a part of the accretionary complex at southeastern Japan. The length of the cave is 100 to 120 m, and Pleistocene deposits in the cave are divided into first and second layers (Ogino et al. 2009). The first layer (bone bed) overlays the second layer (reddish brown coloured chert conglomerates sediment). The rhinocerotid specimens described by Ogino et al. (2009) were collected from the

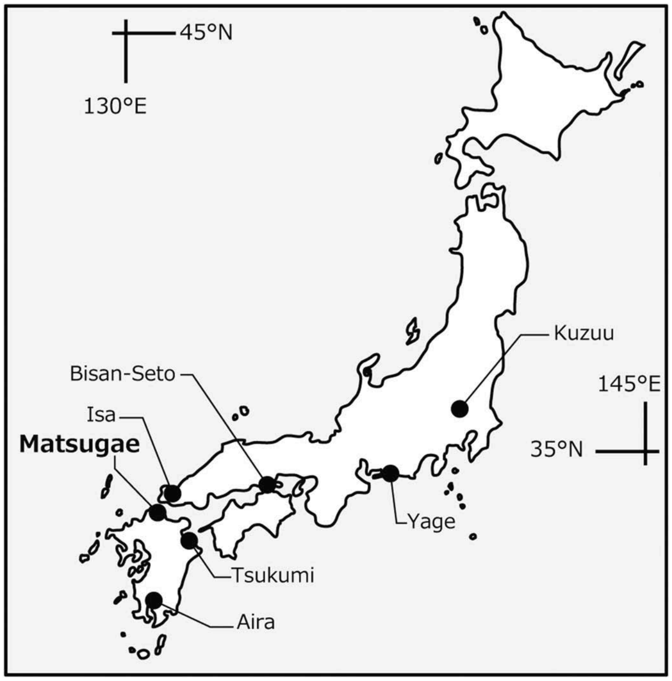

Figure 1. Map showing the localities of the Pleistocene rhinocerotids in Japan (modified after Handa and Pandolfi 2016).

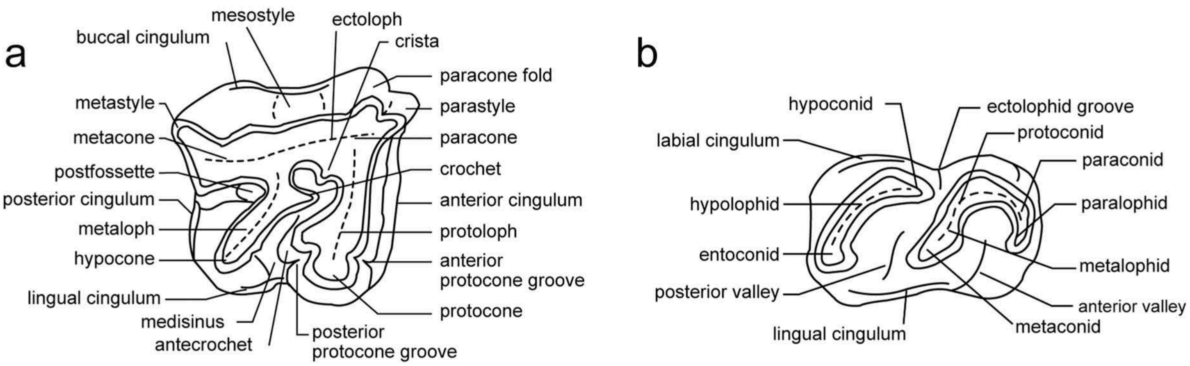

Figure 2. Terminology of the cheek teeth of Rhinocerotidae (Terminology follows Antoine et al. 2010. Illustrations are modified after Fukuchi 2003).

first layer. In contrast, data on the stratigraphic position of other rhinocerotid remains studies here is unclear.

In addition to rhinocerotid remains, various terrestrial mammal remains were also found from the cave; i.e., those of Rodentia (*Apodemus speciosus, A. argenteus, Microtus epiratticepoides*), Lagomorpha (*Lepus* sp.), Carnivora (*Cuon* sp., *Oriensictis nipponica, Meles* sp., *Musutela itatsi, Panthera* sp.), Cetartiodactyla (*Ceruvus* sp., *Sus scrofa*), and Primates (*Macaca* cf. *fuscata*) (Ogino and Otsuka 2005; Ogino et al. 2009). Two Proboscidean species, *Stegodon* sp. and *Palaeoloxodon naumanni*, were purported to be collected from the cave, but these remains have been lost (Ogino et al. 2009) and their exact localities and coexistences are also uncertain (Harunari 2017).

The age of the Matsugae fauna is estimated as middle part of the middle Pleistocene (0.5 to 0.3 Ma) based on the correlation with Pleistocene mammal faunas of other Japanese other sites, and of Choukoutien locality 1 in China (Ogino et al. 2009).

Systematic paleontology

Order PERISSODACTYLA Owen, 1845
Family RHINOCEROTIDAE Gray, 1821
Subfamily RHINOCEROTINAE Gray, 1821
Tribe RHINOCEROTINI Gray, 1821
Genus *Stephanorhinus* Kretzoi, 1942

Emended diagnosis

Large to medium-sized two-horned rhinoceros; the presence of a rostrally ossified nasal septum that connected the intermaxilla with the nasal bones; Molarised premolars; Absence of functional incisors; Brachydont to semi-hypsodont cheek teeth (Pandolfi and Tagliacozzo 2015). In addition, DP2 with weak parastyle and mesostyle; DP3 with the presence of a crista and a weak metacone fold; DP4 with the presence of a crista, a developed paracone fold, and a reduced cingulum.

Stephanorhinus sp.
(Figures 3–4, Tables 1–2)

Dicerorhinus sp. cf. *nipponicus*: Okazaki, 2007, p. 137, figures 1-2, p. 138, figure 3 *Dicerorhinus* sp.: Ogino et al. 2009, p. 379, figure 19A–M

Locality

The Matsugae Cave, Moji-ku, Kitakyushu City, Fukuoka Prefecture, western Japan (Okazaki 2007; Ogino et al. 2009).

Description

A left maxillary fragment (Figure 3a) is poorly preserved. Therefore, the characteristics of the maxillary part are unclear. The crown of DP3 is broken. DP4 is unworn. The ectoloph inclines disto-lingually. The ectoloph profile is slightly wavy. Both proto- and metalophs are slightly oriented to distolingual. The anterior protocone groove is well marked at the base. The posterior protocone groove is faint at the base. There is a shallow hypocone groove. The simple crochet extends mesially. A short crista is present at the base of the medisinus and is not in contact with the crochet. The paracone fold and parastyle are strongly developed. The mesostyle

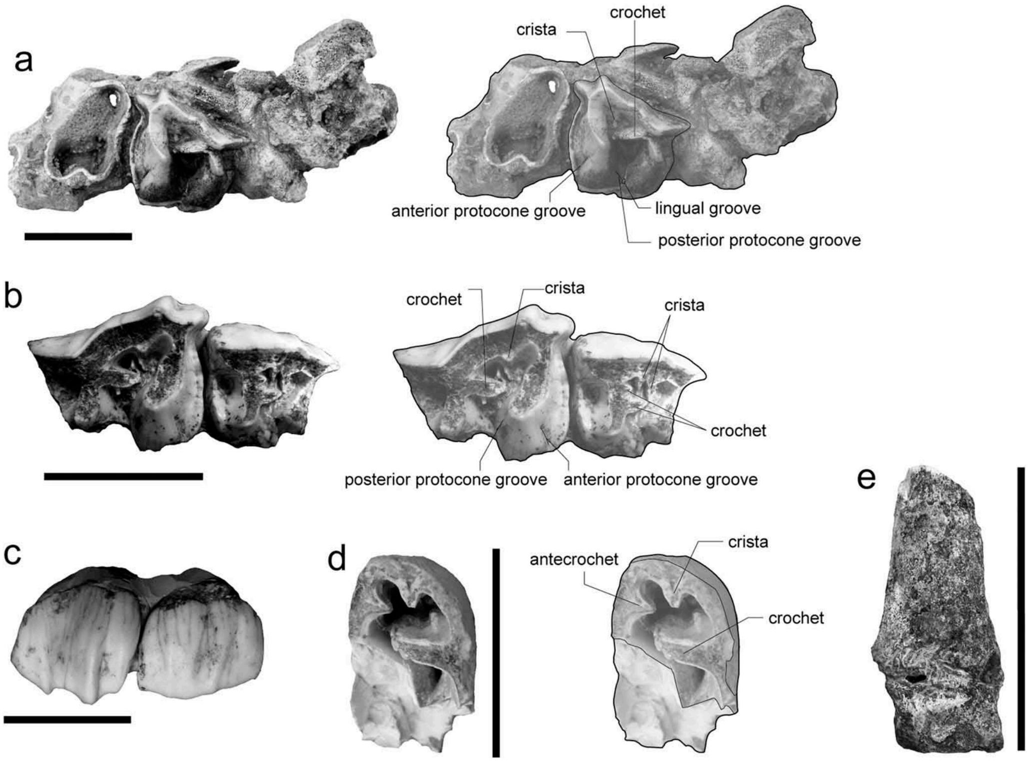

Figure 3. *Stephanorhinus* sp. indet. from the Matsugae Cave, western Japan. a; NMJH-A-636-1-1-35-1, a left maxilla with DP4, b-c; KMNH VP 099,999, right DP2 and DP3, b; occlusal view, c; buccal view, d; A-636-1-1-35-3, left upper M1 or M2 fragment, e; A-636-1-1-35-4, McIII? fragment, Scale bar: a-d; 5 cm, e; 10 cm.

is weak. The metastyle is long. The medisinus is open at the lingual side. The postfossette is small and narrow at this wear stage. The anterior cingulum is low and continuous from the parastyle to protocone. The posterior cingulum is short and low. There is a small knob-like cingulum on the lingual side of the tooth. The cement is absent.

Right DP2 and DP3 (Figure 3(b)–(c)) are partially damaged. The protoloph on DP2 lacks the lingual portion of the protocone and the DP3 lacks the lingual portion of the hypocone. There is no cement on these teeth. In DP2, the protoloph connects to the ectoloph. The metaloph extends lingually. The ectoloph profile of the DP2 is slightly convex buccally. The presence of the protocone constriction is unclear because that part is lacking. The double crochet projects mesially. The double crista is projected from the ectoloph. The longer crista slightly contacts the tips of the crochet at this wear stage. The parastyle projects well. The mesostyle is little developed in the occlusal view and is weak toward the tooth neck in buccal view. The metacone fold is weak. The medisinus and medifossette are deep. The postfossette is deep and wide bucco-lingually. There is no buccal cingulum. The posterior cingulum is low and continuous. The anterior and lingual cingula are not preserved.

In DP3, the protoloph slightly bends disto-lingually. The metaloph is oriented bucco-lingually. The ectoloph profile is wavy beyond the paracone fold. A shallow anterior protocone groove is present at the base of the protocone. The faint posterior protocone groove is present at the base on the distal side of the protocone. The lingual side of the protocone is rounded. The simple crochet is long. There is no antecrochet. A few short additional folds are located near the crista. The paracone fold is developed. The parastyle extends mesially. The metacone fold is weak. The metastyle is long. There is no buccal cingulum. The anterior cingulum is low and continuous. The posterior and lingual cingula are lacking on the preserved portion of the tooth.

A fragment of left M1 or M2 (Figure 3(d)) has a simple crochet that extends mesially, and does not reach the protoloph. There are also a short antecrochet and a crista. There is no cement in the medisinus.

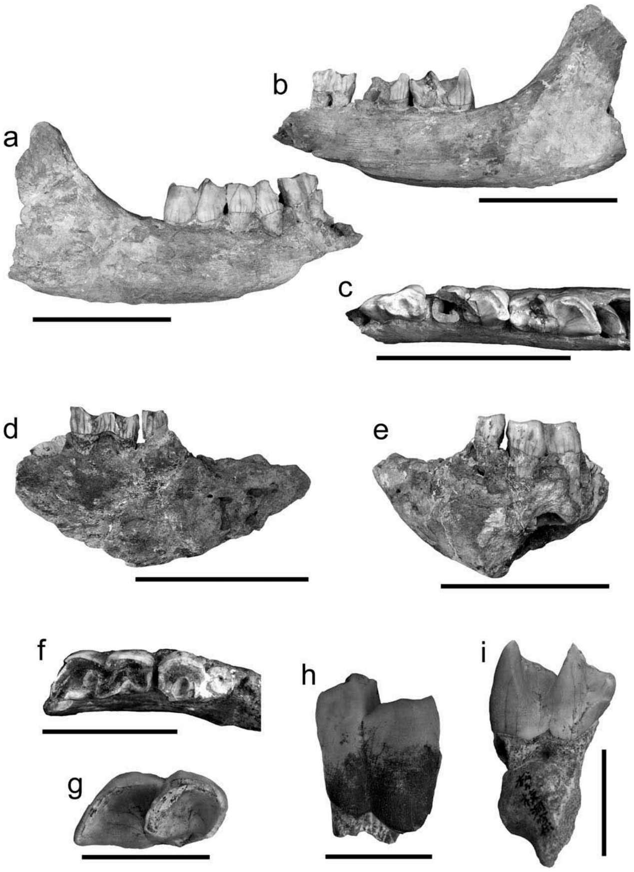

Figure 4. *Stephanorhinus* sp. indet. from the Matsugae Cave, western Japan. a-c; KUM-F58-1, right mandible with dp2, dp3, and dp4, d-f; KUM-F58-2, left mandible with dp2 and dp3, a and e; buccal view, b and d; lingual view, c and f; occlusal view. g-i; A-636-1-1-35-2, isolated deciduous lower premolar, g; occlusal view, h; buccal view, i; lingual view, Scale bar: a-e; 10 cm, g-i; 5 cm.

A right mandibular fragment with dp2, dp3, and dp4 (Figure 4(a)–(c)), is lacking symphysis and vertical ramus. The presence of mental foramina cannot be verified. There is no lingual groove on the lingual surface of the mandibular body. The ventral margin of the preserved mandibular body is convex. The mandibular foramen is below the tooth neck. The mesial half and mesiolingual part are broken on dp3 and dp4, respectively. The m1 has not erupted. The dp2 and dp3 are moderately worn, while dp4 is less worn than the first two deciduous ones. The enamel surface of the teeth is smooth. There is no cement on each tooth. The dp2 is relatively well-preserved. The ectolophid is weak. The anterior groove of the ectolophid is absent. The paralophid is simple. The posterior valley is open lingually at this wear stage. The dp3 and dp4 have a similar morphology in the preserved portions. The ectolophid groove of dp3 and dp4 is developed and continuous until the neck. The buccal wall of the metalophid and hypolophid of the dp3 is rounded and that of dp4 is almost flat. Metaconid is lacking on both teeth. The entoconid on dp3 and dp4 is not constricted. The anterior valley of the dp4 is U-shaped in lingual view and wide in occlusal view. The posterior valley of the dp4 is wide V-shaped in lingual view and wide in occlusal view. There are no buccal and lingual cingula on dp3 and dp4. There is a short mesiolingual cingulum on dp4. There is no lingual groove on the entoconid of dp3.

A left mandibular fragment with dp2 and dp3 (Figure 4(d)–(f)) is a part of the horizontal ramus with two teeth. The surface of the mandibular body is poorly preserved. The mesial half and disto-lingual parts of dp2 are lost. The enamel surface of each tooth is smooth. Cement is absent on both the preserved teeth. In dp2, the posterior valley is lingually closed and its shape is oval in occlusal view, at this wear stage. The buccal wall of the protoconid on dp2 is rounded. There are no buccal, lingual, or distal cingula on dp2. The dp3 is well-preserved. The ectolophid groove is deep and reaches until the neck. The buccal wall of the hypolophid is flat. At this stage of wear, the anterior and posterior valleys are V-shaped and U-shaped in lingual view, respectively. The posterior valley is wider than the anterior valley is in occlusal view. There is no ectolophid fold. The paralophid is double, but the mesial tip is lacking. Metaconid and entoconid are not constricted. The lingual groove of the entoconid is absent. There are no cingula on the tooth.

Table 1. Measurements of upper deciduous teeth of *Stephanorhinus* sp. indet. from the Matsugae Cave, western Japan, and other species of *Stephanorhinus* in Eurasia. *: greatest length and width. Abbreviations: L, length; Wa, mesial width, Wp, distal width; H, height.

	DP2				DP3				DP4					
Taxa	L	Wa	Wp	H	L	Wa	Wp	H	L	Wa	Wp	H	Locality	Reference
Stephanorhinus sp.	29.5	>36.7	>37.3	28.4	>41.9	>43.9	>32.6	35.1					Matsugae	Present study (KMNH VP 099,999)
Stephanorhinus sp.									>48.16	45.29	>37.54	-	Matsugae	Present study (A-636-1-1-35-1)
Stephanorhinus jeanvireti	34.5	33	-	-	39.5–46	38.5–46	-	-	45	40–42	-	-	Western Europe	Guérin (1980)
Stephanorhinus etruscus	35–40	35.5–37	-	-	36–46	36–46	-	-	43–48.5	42–47	-	35.5–36	Western Europe	Guérin (1980)
Stephanorhinus etruscus	35.02	-	31.5–31.66	-	40.8	40.49	32.9	17.43–21.6	47.9–48.72	46.83	38.57–39.73		Sanéze	Lacombat (2005)
Stephanorhinus etruscus	36.35–38.05	32.5–36.8	33.51–36.73	23.06–26.48	40.45–44.3	40.55–43.53	35.28–40.23	17.28–34.16	48.19–48.88	44.05	-		Upper Valdarno	Lacombat (2005)
Stephanorhinus hemitoechus	33–38	30–38.5	-	27.5–29	39–48	39–44.5	-	31–36.5	44–51.5	41–56	-	33.5–43	Western Europe	Guérin (1980)
Stephanorhinus hemitoechus	31.72–37.63	-	-	-	31.59–48.1	-	-	-	44.44–46.52	-	-	-	Arago	Lacombat (2005)
Stephanorhinus hemitoechus	36.23	-	-	29.42	-	-	-			-	-	-	Orgnac 3	Lacombat (2005)
Stephanorhinus hundseimensis	34–41	32.5–39	-	-	36–46.5	33.5–46.5	-	40	44–58	43.5–56.5	-	45–47.5	Western Europe	Guérin (1980)
Stephanorhinus hundseimensis	33.18–37.03	30.72–33.19	34.93–36.1	-	34.63–44.33	33.2–44.91	36.15–41.88		41.41–50.57	43.06–49.95	39.2–43.09		Vallonnet	Lacombat (2005)
Stephanorhinus kirchbergensis	34–39.5	31–43	-	25	41.5–50.5	42.0–54.5	-	36.5	48–57	51–57.5	-	42	Western Europe	Guérin (1980)
Stephanorhinus kirchbergensis	37.92	16.38	35.18	20.55									Aldène	Lacombat (2005)
Stephanorhinus kirchbergensis									48.53	-	-	35.25	Grotte du Prince	Lacombat (2005)
Stephanorhinus kirchbergensis	34.2–37.1	36.8–39.6		-	41.5–43.2	47.8		-	50.8	52.3		-	Taubach	Kahlke (1977)*
Stephanorhinus kirchbergensis					49.3	51.1	45.3	>21.4	59.1	54.2	49.6	>40.8	Migon Cave	Chen et al. (2012)
Stephanorhinus kirchbergensis					50.6–55.8	48.2–52							Rhino Cave	Chen et al. (2012)
Stephanorhinus kirchbergensis					43.5	49	49	-	48.5–53.5	47–49.5	47–49.5		Northern China	Chen et al. (2012)

Table 2. Measurements of lower deciduous teeth of *Stephanorhinus* sp. indet. from the Matsugae Cave, western Japan, and other species of *Stephanorhinus* in Eurasia. Abbreviations: L, length; W width; H, height.

	dp2			dp3			dp4				
Taxa	L	W	H	L	W	H	L	W	H	Locality	Reference
Stephanorhinus sp.	29.1	17.65	16.26	-	22.18	20.33	42.07	24.5	25.23	Matsugae	Present study (KUM-F58-1)
Stephanorhinus sp.	-	16.92	20.64	>37.42	21.83	15.01				Matsugae	Present study (KUM-F58-2)
Stephanorhinus jeanvireti	-	-	-	40–47	23–26.5	28.5	41	26	-	Western Europe	Guérin (1980)
Stephanorhinus etruscus	27–31.5	16–19	-	38–42	19–22.5	20.5–28	39–43	22.5–25	28.5–32	Western Europe	Guérin (1980)
Stephanorhinus etruscus	29.28–30.55	15.1–16.62	14.33–17.33	38.53	-	15.9–17.33	39.5–41.84	-	-	Senèze	Lacombat (2005)
Stephanorhinus etruscus	37.9–39	21.66	20.23–23.4	37.82–39.11	22.7	25.69–28.16	37.82–39.11	22.7	25.69–28.16	Upper Valdarno	Lacombat (2005)
Stephanorhinus hemitoechus	28.5–35	15–18.5	20–25	37.5–45.5	20–23.5	27.5–35	37–50.5	22–27.5	28–37.5	Western Europe	Guérin (1980)
Stephanorhinus hemitoechus	27.17–30.67	14.19–16.06	8.24–24.51	37.09–43.02	19.24–21.47	14.26–37.4	40.23–46.84	20.03–25.47	11.7–42	Arago	Lacombat (2005)
Stephanorhinus hemitoechus	25.7	13.8	16.4							Orgnac 3	Lacombat (2005)
Stephanorhinus hemitoechus	33.36	21	23.58							Mars	Lacombat (2005)
Stephanorhinus hemitoechus	29.37	14.74	25.23							Grotte de l'Observatoire	Lacombat (2005)
Stephanorhinus hundseimensis	27.5–34	17.5–20	-	30–47	18–28.5	28–31.5	36–47	22.5–31	28.5–39	Western Europe	Guérin (1980)
Stephanorhinus hundseimensis	28.5–32.87	15.46–18.95	-	38.15–41.7	19.2–21.41	-	38.1–41.99	23.42–25.46	19.2–35.7	Vallonnet	Lacombat (2005)
Stephanorhinus hundseimensis							40–42.39	24.5	23.41–29.6	Isernia	Lacombat (2005)
Stephanorhinus kirchbergensis	28–38	16.5–21.5	-	38–44.5	21–28.5	28.5	42–51	21–31	30–35.5	Western Europe	Guérin (1980)
Stephanorhinus kirchbergensis	28.67	16.17	17.09	37.73–38.88	21.12–22.4	18.53–38.23	41.74	24.53	28.34	Grotte du Prince	Lacombat (2005)
Stephanorhinus kirchbergensis	30	15.83	23.22	41.17	22.23	25.68	44.15	25.26	34.18	Grotte des Enfants	Lacombat (2005)
Stephanorhinus kirchbergensis	31.1–32.1	19.2–19.3	-	41.5–44.0	23.4–26.1	-	45.3–46.5	25.0–30.1	-	Taubach	Kahlke (1977)
Stephanorhinus kirchbergensis	30.5–38.8	16.7–20	-	49.2	25.1	-	49.5–52	27.1–27.4	-	Rhino Cave	Tong and Wu (2010)
	L	W	H								
Stephanorhinus sp. (isolated tooth)	49.17	>30.28	>61.23								Present study (A-636-1-1-35-2)

An isolated left lower deciduous tooth (Figure 4(g)–(h)) is unworn. The enamel surface is smooth. The morphology of the tooth is similar to that of dp4 of KUM-F58. The anterior valley is wide and U-shaped in both buccal and lingual views, respectively. The posterior valley is also wide in occlusal view, and wide V-shaped in lingual view. The buccal wall of the protoconid is angular. The hypolophid bends disto-lingually. The simple paralophid extends lingually. The metaconid and entoconid are not constricted. There is no lingual groove on the entoconid. The ectolophid groove is deep and developed up to the tooth neck. There is no buccal cingulum. The short lingual cingulum is on the mesiolingual side of the anterior valley. The posterior cingulum is also small.

A McIII? fragment (Figure 3(e)) is preserved but only the dorso-distal surface part. The transverse width of the shaft increases toward distally. The distal margin of the articular facet for the phalanx is transversely almost straight in dorsal view.

Comparisons

Two Rhinocerotidae tribes survived in Eurasia during the Pleistocene (e.g. Heissig 1989), namely the Rhinocerotini (including *Rhinoceros, Dicerorhinus, Stephanorhinus*, and *Coelodonta*) and the Elasmotheriini that includes only *Elasmotherium* (e.g. Guérin 1980; Fortelius et al. 1993; Tong and Moigne 2000; Lacombat 2005; Takai et al. 2008, 2010; Tong 2012; Yan et al. 2014; Pandolfi and Maiorino 2016).

The present specimens are clearly distinct from *Elasmotherium* and *Coelodonta*. The cheek teeth of the genus *Elasmotherium* have a corrugated enamel surface, abundant cement on the upper and lower cheek teeth; distally elongated proto- and metalophs, a strongly constricted protocone, and a long crista on the upper cheek teeth. (e.g. Antoine 2002; Tong et al. 2014; Schvyreva 2015). Those characteristics are not present in the studies specimens.

The present specimens are also distinguished from the genus *Coelodonta* in having upper and lower cheek teeth with a smooth enamel surface, no cement on the teeth, upper cheek teeth with lingually elongated proto- and metalophs, absence of the medifossette, no developed mesostyle (e.g. Qiu et al. 2004; Tong and Wang 2014).

Comparisons with Dicerorhinus *species*

The present specimens are different from the upper cheek teeth of *D. sumatrensis* (GMNH-VM-562; Hooijer 1946; Guérin 1980; Tong and Guérin 2009) in lacking the metacone fold on DP3 and DP4, and having much deeper anterior protocone constriction on DP3, the presence of a crista on DP4, and a long crochet, presence of crista and antecrochet on the upper molar. The studied lower deciduous cheek teeth differ in that of *D. sumatrensis* found from the early Pleistocene locality of Liucheng *Gigantopithecus* Cave in South China (Tong and Guérin 2009), in having dp2 with a shallower extolophid groove, simple paralophid, and the more rounded buccal wall of the hypolophid; dp4 without anteroposterior singula.

The present molar also differs from that of *D. gwebinensis* from the Irrawaddy sediments (Plio-Pleistocene) in Myanmar (Zin-Maung-Maung-Thein et al. 2008) in having a long crochet, a crista, and antecrochet. Comparison of the lower cheek teeth is impossible because the deciduous tooth of *D. gwebinensis* are not found. A mandible with permanent lower teeth of *D. gwebinensis* was described, but those dental characters are hardly visible due to extremely worn down.

Comparisons with Rhinoceros *species*

The studied specimens are distinguished from *R. unicornis* (KPM-NF1002747; KPM-NF1003651; Guérin 1980) in having a less developed metacone fold on DP3, a more developed paracone fold on DP4, no closed medifossette on DP3 and the molar, the presence of antecrochet on the molar, and no cement on the teeth.

The studied specimens differ from *R. sondaicus* from South to Southeastern Asia (Hooijer 1946; Guérin 1980; Groves and Leslie 2011) in having a weak wavy buccal wall of the ectoloph on DP3, the presence of the crista on DP3 and DP4, and a developed crista and antecrochet on M2.

The external groove of the studied lower deciduous teeth is continued to the neck but relatively shallow which differs in that of extant species of *Rhinoceros* (Guerin, 1980). The studied lower deciduous teeth have more V-shaped valleys in lingual view than that of *R. unicornis* (KPM-NF1003651).

The present specimens are different from *R. sinensis* from the Pleistocene deposits in China (Matthew and Granger 1923; Colbert and Hooijer 1953; Yan et al. 2014) in having less developed para- and metacone folds on DP2, a knob-like lingual cingulum on DP4, and a more developed crista and antecrochet on the molar. The present lower deciduous teeth differ in that of *R. sinensis* by Colbert and Hooijer (1953) in having shallower ectolophid groove.

The present molar differs from that of *R. sivalensis* from Asia (Falconer and Cautrey 1847; Colbert 1935) in having the crista and antecrochet on the molars. Unfortunately, the differences in the deciduous cheek teeth are uncertain because of the absence of a description of that of *R. sivalensis*.

The present specimens are different from *R. fusuiensis* from Yanliang Cave, Fusui, South China (Yan et al. 2014) in having a less developed mesostyle on DP2, a DP3 with a weak mesostyle, no posterior protocone groove, and the presence of a crista, and an M2 with an antecrochet and crista. Yan et al. (2014) did not describe lower deciduous teeth, thus a comparison between the present lower deciduous teeth with those of *R. fusuiensis* is impossible.

The present molar is different from that of a skull with teeth of *R. platyrhinus* from Upper Siwalik in India (Pandolfi and Maiorino 2016) in having no closed medifossette and in the presence of the antecrochet. Comparisons of lower deciduous teeth are difficult due to no description of the corresponding teeth for *R. platyrhinus*.

Comparison with Stephanorhinus

The present specimens show the following dental characteristics of the genus *Stephanorhinus*: DP2 with weak parastyle and mesostyle; DP3 with the presence of a crista and weak metacone fold; DP4 with the presence of a crista, developed paracone fold, and reduced cingulum.

In Europe, several species of *Stephanorhinus* (*S. jeanvireti, S. etruscus, S. hemitoechus, S. hundsheimensis*, and *S. kirchbergensis*) have been described (e.g. Guérin 1980; Fortelius et al. 1993; Lacombat 2005; Made 2010; Ballatore and Breda 2016; Tsoukala and Guérin 2016). Among them, *S. kirchbergensis* has also been found in Asia (e.g. Billia 2008; Tong 2012; Handa and Pandolfi 2016; Kirillova et al. 2017). Other Asian species of *Stephanorhinus, S. lantianensis* and *S. yunchuchenensis*, are known from China (Tong 2012 and references therein).

Comparison with S. jeanvireti

The present specimens are similar to the upper deciduous teeth of *S. jeanvireti* (in Guérin 1972, 1980; Guérin and Tsoukala 2013; Tsoukala and Guérin 2016; see also Ballatore and Breda 2016: *S. elatus*) from Europe, in having a crista and lacking the cingulum on DP2 and DP3, a weak convex buccal wall with mesostyle and the presence of the medifossette on DP2, a strong paracone fold on DP3, and a strong paracone fold, presence of a weak crista, and no antecrochet on DP4. However, the present specimens are different from the upper deciduous teeth of *S. jeanvireti* in having DP2 without antecrochet. The present molar is similar to M2 of *S. jeanvireti* in having a simple crochet and a crista (Guérin and Tsoukala 2013).

Comparison with S. etruscus

The present specimens are similar to that of *S. etruscus* (=*D. etruscus etruscus* in Guérin 1980) from western Europe in having a DP2 with a double crista, DP3 with a developed paracone fold, weak metacone fold, the presence of a crochet and crista, and the absence of an antecrochet, and a DP4 with a crista and crochet. The antecrochet and crista are rare in the upper molar of *S. etruscus* (Guérin 1980), but it is similar to the present specimens in having this folds.

Comparison with S. hemitoechus

The present specimens are similar to *S. hemitoechus* (=*D. hemitoechus* in Guérin 1980) from Europe (e.g. Guérin 1980; Pandolfi 2013; Pandolfi and Marra 2015; Tsoukala and Guérin 2016) in having a crochet and crista, as well as a closed medifossette on DP2; the presence of a crochet and crista on DP3; a mesostyle, a simple crochet and crista, a deep anterior protocone groove, a developed paracone fold and parastyle, a reduced lingual cingulum, and a hypocone groove on DP4; the presence of simple crochet and crista on the molar. However, they differ from *S. hemitoechus* in having a less undulated ectoloph on DP2 and DP3 (Figure 5). In addition, the cheek teeth of *S. hemitoechus* have a rough enamel surface and cement (Fortelius et al. 1993), which are not seen in the teeth of the present specimens.

Comparison with S. hundsheimensis

The present specimens are similar to *S. hundsheimensis* (=*D. etruscus brachycephalus* in partim in Guérin 1980; see also Fortelius et al. 1993; Lacombat 2005) from western Europe, in having a DP2 with a multiple crochet and crista,

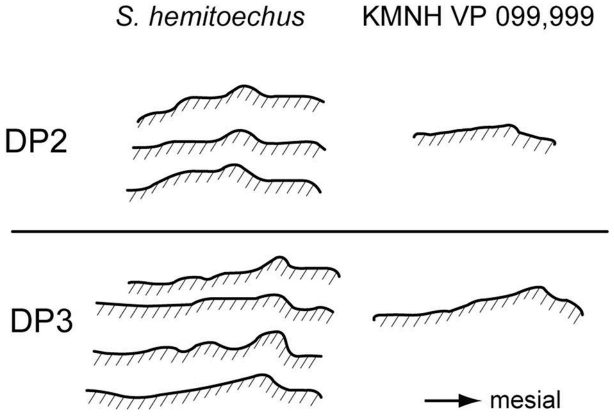

Figure 5. Comparison of the ectoloph profile of DP2 and DP3 in the Matsugae specimen (KMNH VP 099,999) and *Stephanorhinus hemitoechus* (after Guérin 1980; the figures are reflected).

and no antecrochet; a DP3 with the presence of a crochet and crista; a DP4 with a mesostyle, weak crista, and a developed paracone fold; and an M1 or M2 with a simple crochet and crista and a weak antecrochet. Several characteristics of the present specimens are different from *S. hundsheimensis* (Guérin 1980; Lacombat 2005) such as weak protocone constriction on DP3 and the molars, more developed secondary folds on the molar, and presence of the crista on DP4.

Comparison with S. kirchbergensis *from Europe*

Numerous remains of *S. kirchbergensis* (=*Diceorhinus mercki* in Guérin 1980) have been found from Europe (e.g. Kahlke 1977; Guérin 1980; Pandolfi and Marra 2015; Persico et al. 2015). The present specimens are similar to those from Europe in having a DP2 with a crochet, crista, a weak convex ectoloph profile, a developed paracone fold and parastyle, and absence of a buccal cingulum and closed medifossette; a DP3 with a developed paracone fold, crochet, crista, shallow anterior protocone groove and opened medifossette; and a DP4 with a developed paracone fold, weak mesostyle, crista, crochet, no antecrochet, and opened medifossette. The M1 and M2 of *S. kirchbergensis* show a crochet and crista that are similar to those of the present molar.

Comparison with S. kirchbergensis *from Asia*

Several remains of *S. kirchbergensis* have also been known from Asia. The present specimens are similar to that of *S. kirchbergensis* from the late Pleistocene site of Rhino Cave in Shennongjia, Hubei, in China (Tong and Wu 2010) in having a developed crochet and crista forming the medifossette, a long parastyle, and a slightly waved buccal wall on DP2, DP3, and DP4, with a developed crochet and paracone fold. However, the present DP3 and DP4 differ from that of the Rhino Cave specimen in having weaker posterior protocone constriction on the upper molars.

The present specimens are different from *S. kirchbergensis* from Migong Cave in the late Pleistocene site of China in having, the absence of a hypocone groove, no antecrochet, and a well-developed paracone fold on DP3 and DP4, as well as the presence of a crochet and antecrochet on the molar (Chen et al. 2012).

The present molar differs in that of *S. kirchbergensis* (=*D. choukoutienensis*) from the Locality 20 in Choukoutien, in China (Chow 1963a) in having more developed crista and antecrochet.

In Japan, *S. kirchbergensis* was found in a middle Pleistocene deposit exposed in a quarry at the Isa area in Yamaguchi Prefecture (Shikama et al. 1967; Handa and Pandolfi 2016). The present upper molar is similar to NMNS-PV9600 (=the holotype of *D. nipponicus* in Shikama et al. 1967) in having no cement on the teeth, a long simple crochet, and a crista. However, these are more developed than those of the Isa specimen and there is a long antecrochet on the present molar, which is absent on those of NMNS-PV 9600.

Kirillova et al. (2017) described a skull with upper cheek teeth of *S. kirchbergensis* from northern part of the Primorskaya (Yano-Indigirskaya) lowland, Arctic Russia. The present molar differs in that of the Russian specimen in having crista and cristella.

Comparisons with other species of Stephanorhinus *from Asia*

The dental characteristic of *S. lantianensis* is unclear because of the heavily worn-out condition of the molars (Tong 2012). Another species, *S. yunchuchenensis*, is known from Yuncu in Yushe in Shanxi, China (Chow 1963b). The present molar differs from that of *S. yunchuchenensis* in having no medifossette and longer antecrochet.

Morphological variation of the internal fold of Stephanorhinus

The characteristics of secondary folds (crochet, crista, and antecrochet) are used for taxonomic identification. However, these often show morphological change by stage of wear or intraspecific variation (Guérin 1980; Fortelius et al. 1993; Lacombat 2005).

According to previous studies, the characteristics of the internal folds of those species are polymorphic (Table 3). The crochet on DP2 is normally simple but is double or multiple on the tooth of *S. hundsheimensis* (Guérin 1980; Lacombat 2005). The present DP2 is also a double crochet. The present DP2 is similar to that of *S. hundsheimensis, S. etruscus* in having a double shaped crista (Guérin 1980; Lacombat 2005) and that of *S. hemitoechus* (Guérin 1980). The present DP2 has a closed medifossette, which is also seen in that of *S. jeanvireti, S. hundsheimensis, S. etruscus*, and *S. kirchbergensis* (Guérin 1980; Lacombat 2005). According to Lacombat (2005), the crochet on DP3 is single or double in *S. hundsheimensis* and *S. etruscus*. The crista on DP3 is rather present in that of *S. hemitoechus*, but it is indifferently present or absent in *S. etruscus* and *S. hundsheimensis* (Lacombat 2005). The characteristics of the present DP4 are similar to those of *S. kirchbergensis* rather than those of other species in having a crista, a simple crochet, and no antecrochet (Guérin 1980; Lacombat 2005).

The crochet on the M1 and M2 of the species of *S. kirchbergensis* is simple (Lacombat 2005) and/or multiple (Guérin 1980). The crochet on the M1 of *S. hemitoechus* is simple and/or double (Guérin 1980; Lacombat 2005), and that

Table 3. Comparisons of the secondary folds of DP and molar in tKMNH VP099,999 and species of *Stephanorhinus* (after Kahlke 1977; Guérin 1980; Lacombat 2005; Guérin and Tsoukala 2013).

Tooth	Characters	Matsugae specimen	*S. kirchbergensis*	*S. hemitoechus*	*S. hundseimensis*	*S. etruscus*	*S. jeanvireti*
DP2	crochet	double	simple or multiple	simple or multiple	simple or multiple	simple or multiple	simple or multiple
	crista	double	simple	simple	double	simple or multiple	simple or multiple
	antecrochet	absent	absent	absent	present or absent	present	present
DP3	crochet	simple	simple	simple	simple or double	simple	present
	crista	simple	simple	simple	simple or double	simple	present
	antecrochet	absent	absent	absent	present or absent	absent	absent
DP4	crochet	simple	simple	simple	simple	simple	present
	crista	simple	simple	simple	simple	simple	present
	antecrochet	absent	absent	absent	absent	absent	absent
Molar	crochet	simple	simple	simple	simple or double	simple	simple
	crista	simple	simple	simple or double	simple or double	simple or double	simple
	antecrochet	present	present	present	present	absent	absent

on the M2 of *S. hundsheimensis* is rarely double (Guérin 1980; Lacombat 2005). The crista on the M1 is variable (presence or absence) in the species of *Stephanorhinus* (Guérin 1980; Lacombat 2005). The crista on the M2 is mostly absent in *S. jeanvireti, S. hundsheimensis* and *S. etruscus* (Guérin 1980; Lacombat 2005), whereas that on the other species is simple or double (Guérin 1980; Lacombat 2005).

Comparisons of lower deciduous cheek teeth of Stephanorhinus

The present lower deciduous teeth are also similar to those of *Stephanorhinus* in having a dp3 without buccal and lingual cingula and a dp4 with a mesial cingulum but no buccal, lingual, or distal cingula (Kahlke 1977; Lacombat 2005). The ectolophid groove of the deciduous teeth is open in the occlusal view, as in those of European species (Kahlke 1977; Lacombat 2005).

On the other hand, the interspecific variability of characteristics of the lower deciduous cheek teeth often overlaps. The present dp2 has a V-shaped posterior valley as in the *S. etruscus* reported by Guérin (1980), *S. hundsmeiensis* and *S. hemitoechus* described by Lacombat (2005), and *S. kirchbergensis* described by Kahlke (1977). The present dp2 is also similar to those of *S. kirchbergensis* and *S. hemitoechus* reported by Guérin (1980) in having a closed posterior valley.

The present dp3 is similar to that of *S. etruscus, S. hemitoechus*, and *S. hundsmeiensis* described reported by Guérin (1980) and Lacombat (2005), as well as *S. kirchbergensis* described by Kahlke (1977), in having a V-shaped anterior valley. It is also similar to that of *S. etruscus, S. hundsmeiensis*, and *S. kirchbergensis* in having a wide V-shaped posterior valley, respectively (Guérin 1980; Lacombat 2005). The difference in the height of both valleys of the present dp3 is small, as it is in that of *S. etruscus* and *S. hundsheimensis* (Lacombat 2005).

The present dp4 is similar to that of *S. hundseimensis* and *S. kirchbergensis* in having a U-shaped anterior valley (Kahlke 1977; Guérin 1980), and is similar to that of *S. etruscus, S. hundseimensis*, and *S. kirchbergensis* in having a wide V-shaped posterior valley in lingual view (Kahlke 1977; Guérin 1980; Lacombat 2005). The differences in height between the bases of the valleys of the present dp4 are high, as they are in *S. kirchbergensis* (Lacombat 2005).

In conclusion, the comparisons with Pleistocene Rhinocerotini and Elasmotheriini reveal that the present specimens are similar to those of genus *Stephanorhinus* in having DP2 with weak parastyle and mesostyle; DP3 with the presence of a crista and a weak metacone fold; DP4 with the presence of a crista, a developed paracone fold, and a reduced cingulum. However, the main diagnostic characteristics of the species of *Stephanorhinus* are based on skull and permanent cheek teeth (e.g., Kahlke 1977; Guérin 1980; Lacombat 2005; Made 2010). In fact, both the upper and lower deciduous teeth show polymorphic characteristics and these often overlap among the species. These results mean that it is difficult to determine the specific identify of the present specimens. Metrically, the size range of the present upper cheek teeth fall within the dimensions of the various comparative specimens (Table 1–2), suggesting that it is also difficult to identify the species for the present specimens on the basis the dental dimensions. Therefore, the present specimens described here are identified as *Stephanorhinus* sp.

Discussion

As mentioned above, several Japanese Pleistocene rhinocerotid remains have been redescribed by recent studies (Handa 2015; Handa and Pandolfi 2016; Handa and Takechi 2017; Handa 2019). Of these, the remains from the middle Pleistocene localities in the Isa area and Bisan-Seto sea bottom (Figure 1) were reidentified as *S. kirchbergensis* and *Stephanorhinus* sp., respectively (Handa and Pandolfi 2016; Handa and Takechi 2017), suggesting that this genus reached Far East Asia during the middle Pleistocene.

The present result will also contribute to the migratory hypothesis of Rhinocerotidae between the Asian Continent and Japanese Islands during the Pleistocene. Only three remains of Rhinocerotidae have been found in mid-Pliocene localities (around 3.5 Ma) (Hasegawa et al. 1991; Kato 2001; Murakami and Tsubamoto 2018). Of these, Murakami and Tsubamoto (2018) described an isolated lunar as Rhinocerotini gen. et sp. indet., suggesting that this tribe already lived in Japan during the mid-Pliocene. Handa (2019) described a few upper cheek teeth from the early to middle Pleistocene (1.0 to 0.5 Ma) Kokubu Group in Aira, Kagoshima Prefecture, as Rhinocerotidae gen. et sp. indet. He also reviewed rhinocerotid fossils from the early part of the Pleistocene in Japan (including footprints) and noted that Pleistocene rhinocerotids have been present in Japan since the earliest Pleistocene (ca. 2.58 Ma). However, the taxonomic relationships between the Pliocene and

Pleistocene rhinocerotids in Japan are uncertain due to the incompleteness of the fossil remains.

Migration of the Pleistocene terrestrial mammals between Asian Continent and Japanese Islands has been discussed on the basis of a comparison of the Proboscidean fossil occurrences, and marine isotope stages, and composition of terrestrial mammals between Japan and China (Kawamura 1998; Konishi and Yoshikawa 1999; Takahashi and Namatsu 2000; Yoshikawa et al. 2007; Taruno 2010). Based on those studies, land connections between the Asian Continent and Japanese Islands with migrations of terrestrial mammals were thought to be twice during the middle Pleistocene. The first is estimated to be around 0.63 Ma (MIS16), with Oriental elements (southern Chinese *Stegodon* fauna). The second was around 0.43 Ma (MIS12) with Palearctic elements (northern Chinese *Palaeoloxodon* fauna) (e.g., Yoshikawa et al. 2007).

Ogino et al. (2009) discussed the age of the Matsugae fauna on the basis of comparison with other Japanese Pleistocene terrestrial mammal fauna. The Matsugae fauna was correlated with the mammal fauna of the middle part of the middle Pleistocene such as Lower Kuzuu, Ikumo, and Bisan-Seto faunas (Ogino et al. 2009). These faunas are correlated with the Quaternary Mammal Zone 4 of the Japanese Islands (QM4, 0.5 to 0.3 Ma, Kamei et al. 1988). Ogino et al. (2009) have also correlative of the Matsugae fauna with Asian continent fauna, suggesting that the Matsugae fauna was comparable to the middle Pleistocene northern Chinese Locality 1 of Choukoutien fauna. *Stephanorhinus kirchbergensis* has been found mainly in northern China (e.g., Chow 1963a; Tong 2012). Therefore, *Stephanorhinus* sp. from the Matsugae Cave would have migrated from northern China around 0.43 Ma as a part of the Matsugae fauna. Handa and Pandolfi (2016) also noted that *S. kirchbergensis* from the Isa area also migrated from the northern China around 0.43 Ma. These studies suggest that the Japanese Pleistocene *Stephanorhinus* would be an immigrant of the northern Chinese fauna that migrated during the middle part of the middle Pleistocene. Handa and Pandolfi (2016) briefly noted the possibility of the presence of different subspecies of *S. kirchbergensis* between European and Asian remains. However, further Asian remains are needed to discuss this hypothesis as they noted.

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