



Review Article

A review of the taxonomy, biostratigraphy and paleobiogeography of Plio-Pleistocene rhinoceroses in Japan

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ABSTRACT

The Rhinocerotidae were distributed in Eurasia and Africa during the late Neogene. In particular, the subtribe Rhinocerotina which includes the living species, diversified during the Plio-Pleistocene in Eurasia. Japan, which is situated in Far East Asia, has also yielded Plio-Pleistocene rhinocerotids, but their taxonomic position has not been revised since their first descriptions. Considering recent taxonomic revisions of many Eurasian Rhinocerotidae, it is necessary to also revise the Japanese remains. Here, taxonomy and fossil records of the Plio-Pleistocene Japanese rhinocerotids are reviewed. A total of 16 bones and teeth remains have been found from the mid-Pliocene to the middle Middle Pleistocene. Three Pliocene rhinocerotids are identified as *Rhinocerotina* gen. et sp. indet. In the earliest Pliocene, the close relative of the Japanese Pliocene rhinocerotid migrated from continental Asia. *Stephanorhinus kirchbergensis* was distributed in central to southwestern Japan during the middle Middle Pleistocene. In addition, indeterminate species were also present in the Early to Middle Pleistocene. The Late Pleistocene fossil record is uncertain due to the lack of stratigraphic and chronological data. Japanese *S. kirchbergensis* immigrated from the continental Asia (middle part of China) at ca. 0.65 Ma with a species of *Stegodon* together.

1. Introduction

The family Rhinocerotidae is contained in the Order Perissodactyla. In Asia, the living species of Rhinocerotidae inhabits mainly the rainforests, montane moss forests or riverine grasslands under a tropical to sub-tropical climate in South/Southeastern Asia (Antoine, 2012; Rookmaaker and Antoine, 2012; Ellis and Talukdar, 2019, 2020a, b; Pant et al., 2021). Many species of Rhinocerotidae, however, had been distributed in Eurasia and Africa during the late Neogene. In particular, the subtribe Rhinocerotina which includes the living species, diversified during the Middle Miocene to Plio-Pleistocene in Eurasia (e.g., Pandolfi, 2018; Liu et al., 2021). Recently, considerable literatures have grown up around the theme of their diversity and distribution based on abundant fossil records from Europe and China (Tong, 2012; Pandolfi, 2018). Japan, which is situated in Far East Asia, has also yielded Plio-Pleistocene rhinocerotids (Fig. 1). However, their taxonomic position has not been revised since their first descriptions. Recently, taxonomic revisions of some Eurasian Rhinocerotidae have been carried out, including Plio-Pleistocene Chinese rhinocerotid specimens (Tong, 2012). These developments have heightened the need for revisions of

the Japanese specimens.

During the Middle Pleistocene the sea-levels was declined because of the cooling of global temperatures, resulting in a connection between proto-Japan and the Asian continent. These conditions allowed for an exchange of land mammals between both areas, forming the basis the present Japanese mammal fauna (Kawamura et al., 1989; Takahashi and Izuho, 2012). The Plio-Pleistocene marine strata or volcanoclastic deposits, which are useful key beds for stratigraphic correlations, are interbedded in the terrestrial sediments in Japan. Based on that stratigraphy, the timing of migration of land mammals and the Japanese mammal faunal composition have been estimated (Kawamura, 2007; Hasegawa, 2012; Takahashi and Izuho, 2012). For example, extensive research has provided information on the biostratigraphy, evolution, habitats and migration timing of Japanese proboscideans (Takahashi and Namatsu, 2000; Saegusa et al., 2005; Takahashi et al., 2006; Konishi et al., 2007; Taruno and Kawamura, 2007; Aiba et al., 2010; Taruno, 2010; Nakagawa et al., 2013; Yamakawa, 2017). In contrast, few studies have systematically investigated the migration time of the Rhinocerotidae. This issue would contribute to the discussion of the formative process of the Japanese land mammal fauna in Far East Asia during the

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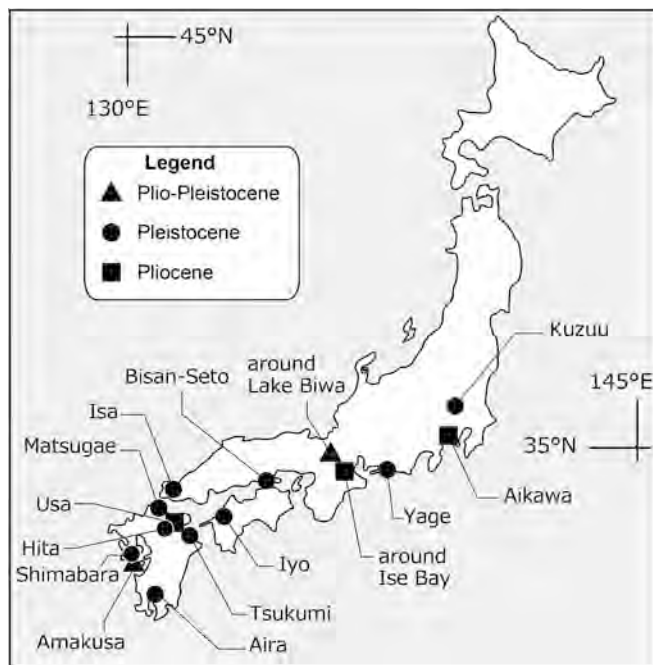


Fig. 1. Map showing the fossil localities of Plio-Pleistocene rhinocerotid fossils in Japan (modified after Handa and Kato, 2020).

Plio-Pleistocene. Here, we review the taxonomy and fossil records of Plio-Pleistocene Japanese rhinocerotids, together with a description of some undescribed remains and discuss their paleobiogeography.

2. Materials and methods

The review covers as many the Plio-Pleistocene Japanese rhinocerotid fossils as possible, but there are several specimens in private collections, as well as specimens that have not yet been published, or that have been lost. Consequently, we focus on the specimens that have already been published and/or examined directly. All specimens described in this study are listed in Table 1. Taxonomy in this study follows Antoine et al. (2010) and Pandolfi (2018) (Table 2). Standard measurements follow the method of Guérin (1980). Dental terminology follows Antoine et al. (2010).

Anatomical abbreviations. DP, upper deciduous premolar; dp, lower deciduous premolar; i, lower incisor; P, upper premolar; p, lower premolar; M, upper molar; m, lower molar; Mc, metacarpal.

Institutional abbreviations. KMNH: Kitakyushu Museum of Natural History and Human History; KUM: the Kyushu University Museum; KPM: Kanagawa Prefectural Museum of Natural History, Odawara, Kanagawa Prefecture, Japan; LBM: Lake Biwa Museum, Kusatsu, Shiga Prefecture, Japan; NMJH: the National Museum of Japanese History, Sakura, Chiba Prefecture, Japan; NMNS: National Museum of Nature and Science, Tsukuba, Ibaraki Prefecture, Japan; OMNH: Osaka Museum of Natural History; SFM: Shinshushinmachi Fossil Museum, Nagano Prefecture, Japan; YM: Mammal fossil of Yamamoto collection in the Kurashiki Museum of Natural History, Kurashiki, Japan.

3. A review of Pliocene rhinoceroses in Japan

Family Rhinocerotidae GRAY, 1821.
Subfamily Rhinocerotinae GRAY, 1821.
Tribe Rhinocerotini GRAY, 1821.
Subtribe Rhinocerotina GRAY, 1821.
Rhinocerotina gen. et sp. indet.

3.1. Referred specimens

LBM 142,001,248 (a right mandible) (Fig. 2B), LBM 0142001230 (a left p4 fragment), LBM 0142001231 (a left m1) and LBM 0142001232 (a left m2) from Ajimu, Usa City, Oita Prefecture (Fig. 2A); OMNH-TV-0342 (a right lunate) from the Hattori River, Iga City, Mie Prefecture (Fig. 2C).

3.2. Remarks

Kato (2001) reported a few lower cheek teeth (LBM 0142001230, LBM 0142001231, LBM 0142001232) from the Tsubusagawa Formation as Rhinocerotidae gen. et sp. indet. (Fig. 2A). Handa and Kato (2020) redescribed these specimens and compared them with Late Miocene to Pleistocene Asian species. They show several characteristics of the Rhinocerotina such as a deep ectolophid groove, acute trigonid, no buccal and lingual cingula, U-shaped posterior valley, lack of constricted meta- and entoconids, oblique hypolophid, and absence of the lingual groove on the entoconid, resulting in an identification as Rhinocerotina gen. et sp. indet.

Handa et al. (2023) also described a rhinocerotid mandible (LBM 142001248) from the Tsubusagawa Formation in the Ajimu area (Fig. 2B). This specimen was compared with the Late Miocene to Pleistocene species from Eurasia, resulting in the conclusion that specimen LBM 142001248 is similar to the mandibles of two species of the Rhinocerotina, *Dihoplus ringstroemi* and *Pliorhinus megarhinus*. Owing to the lack of generic diagnostic characters, LBM142001248 was identified as Rhinocerotina gen. et sp. indet.

OMNH-TV-0342 was found in the mid-Pliocene Ueno Formation of the Kobiwako Group. The specimen was originally reported as an indeterminate species of rhinocerotid (Yamamoto, 2006) (Fig. 2C). Murakami and Tsubamoto (2018) redescribed the specimen and identified it as Rhinocerotini gen. et sp. indet. (=Rhinocerotina by Pandolfi, 2018) based on a third scaphoid facet and a caudal prolongation of the pyramidal facet. They noted that OMNH-TV-0342 is morphologically similar to that of *Stephanorhinus*.

Rhinocerotidae gen. et sp. indet.

3.3. Referred specimen

KPM-NN 5208 (a left unciform of the carpal bone) from Aikawa town, Aikou district, Kanagawa Prefecture (Fig. 2D).

3.4. Remarks

Hasegawa et al. (1991) reported KPM-NN 5208 as Rhinocerotidae gen. et sp. indet. This specimen is currently being studied by T. Murakami at the Saga Prefectural Museum in Japan. Murakami et al. (2019) pointed out in a conference paper, without a detailed that KPM-NN 5208 shows a close resemblance to the Rhinocerotina.

4. A review of Pleistocene rhinoceros in Japan

Family Rhinocerotidae GRAY, 1821.
Subfamily Rhinocerotinae GRAY, 1821.
Tribe Rhinocerotini GRAY, 1821.
Subtribe Rhinocerotina GRAY, 1821.
Genus *Stephanorhinus* KRETZOI, 1942.
Stephanorhinus kirchbergensis (JAGER, 1839).
Synonymy.
Dicerorhinus nipponicus Shikama et al., 1967, pls. 1, 2.
Dicerorhinus nipponicus Shikama, 1970, plt. 68, Fig. 12.
Dicerorhinus nipponicus Kamei, 1981, p. 167.

Table 1
The studied materials of Plio-Pleistocene rhinocerotids in Japan.

Age	Locality	Tribe	Subtribe	Geus and species	Identification of previous study	Specimen number	Element	Remarks
Pliocene	Hattori River, Iga	Rhinocerotini	Rhinocerotina	gen. et sp. indet.	Rhinocerotini gen. et sp. indet.	OMNH-TV-0342	lunate	Murakami and Tsubamoto (2018)
Pliocene	Ajimu, Usa	Rhinocerotini	Rhinocerotina	gen. et sp. indet.	Rhinocerotidae gen. et sp. indet.	LBM 0142001230, LBM 0142001231, LBM 0142001232	lower cheek teeth	Kato (2001); Handa and Kato (2020)
Pliocene	Ajimu, Usa	Rhinocerotini	Rhinocerotina	gen. et sp. indet.	—	LBM 142,001,248	mandible	Handa et al. (2023)
Pliocene	Aikawa, Aikou	indet.	indet.	gen. et sp. indet.	Rhinocerotidae gen. et sp. indet.	KPM-NN 5208	magnum	Hasegawa et al. (1991); Murakami et al. (2019)
Pleistocene	Isa Cement Quarry, Isa	Rhinocerotini	Rhinocerotina	<i>Stephanorhinus kirchbergensis</i>	<i>Dicerorhinus nipponicus</i>	NMNS-PV 9600	maxilla with cheek teeth, mandibular fragment and vertebra fragment	Shikama et al. (1967); Handa and Pandolfi (2016)
Pleistocene	Ogano, Kuzuu	Rhinocerotini	Rhinocerotina	<i>Stephanorhinus kirchbergensis</i>	<i>Rhinoceros</i> sp.	no. 94347861	maxilla fragment with cheek teeth	Naora (1954); Nagasawa (1961)
Pleistocene	Isa Cement Quarry, Isa	Rhinocerotini	Rhinocerotina	<i>Stephanorhinus kirchbergensis</i>	—	no. 255, no. 256	upper and lower cheek teeth	present study
Pleistocene	Bisan-Seto area	Rhinocerotini	Rhinocerotina	<i>Stephanorhinus</i> sp.	Rhinocerotidae gen. et sp. indet.	YM-059, YM-1048	femur and tibia	Taruno (1988, 2000); Handa and Takechi (2017)
Pleistocene	Matsugae Cave	Rhinocerotini	Rhinocerotina	<i>Stephanorhinus</i> sp.	<i>Dicerorhinus</i> cfr. <i>nipponicus</i>	KMNH VP 099,999, KUM-F58-1, KUM-F58-2	lower mandibles	Okazaki (2007); Handa et al. (2019)
Pleistocene	Matsugae Cave	Rhinocerotini	Rhinocerotina	<i>Stephanorhinus</i> sp.	<i>Dicerorhinus</i> sp.	A-636-1-1-35-1, A-636-1-1-35-2, A-636-1-1-35-3, A-636-1-1-35-4	upper and lower cheek teeth and a metapodial fragment	Ogino et al. (2009); Handa et al. (2019)
Pleistocene	Kuzuu	Rhinocerotini	Rhinocerotina	<i>Stephanorhinus</i> sp.	<i>Rhinoceros sinensis</i>	N/A	DP2	Morishita (1977)
Pleistocene	Yage, Hamamatsu	Rhinocerotini	Rhinocerotina	gen. et sp. indet.	Rhinocerotinae gen. et sp. indet.	SFM 04-11306	i2	Handa (2015)
Pleistocene	Ogano, Kuzuu	indet.	indet.	gen. et sp. indet.	<i>Dicerorhinus</i> (?) sp.	N/A	a lower cheek tooth	Shikama (1949)
Pleistocene	Aira	indet.	indet.	gen. et sp. indet.	<i>Rhinoceros</i> aff. <i>sinensis</i>	F00000554	upper cheek teeth	Shikama (1967); Handa (2019)
Pleistocene	Suisho-zan, Tsukumi	indet.	indet.	gen. et sp. indet.	Rhinocerotidae gen. et sp. indet.	N/A	mandibles with cheek teeth	Kawamura et al. (1977)
Pleistocene	Bisan-Seto area	indet.	indet.	gen. et sp. indet.	Rhinocerotidae gen. et sp. indet.	YM-455	radius fragment	Taruno (1988)

Table 2
The classification of the subtribe Rhinocerotina based on the taxonomic frame works of Antoine et al. (2010) and Pandolfi (2018). *: extinct genera.

Perissodactyla
Rhinocerotidae
Elasmotheriinae
Rhinocerotinae
<i>incertae sedis</i> (<i>Acerateres sensu lato</i>)
Aceratheriini (<i>Aceratheres sensu stricto</i>)
Rhinocerotini
Teleoceratina
Rhinocerotina
<i>Ceratotherium</i>
<i>Coelodonta</i> *
<i>Dicerorhinus</i>
<i>Diceros</i>
<i>Dihoplus</i> *
<i>Gaindatherium</i> *
<i>Lartetotherium</i> *
<i>Nesorhinus</i> *
<i>Paradiceros</i> *
<i>Pliorhinus</i> *
<i>Rhinoceros</i>
<i>Rusingaceros</i> *
<i>Stephanorhinus</i> *

4.1. Referred material

NMNS-PV 9600 (a right partial skull with P2-M3, two mandibular fragments and a cervical vertebra) from Isa Cement Quarry, Isa, Yamaguchi Prefecture (Fig. 3A).

4.2. Remarks

Shikama et al. (1967) originally described NMNS-PV 9600 as a new species *Dicerorhinus nipponicus*, based on the comparison with a Pleistocene Chinese species, *Dicerorhinus choukoutiensis*. Later, *D. choukoutiensis* was compared with a Pleistocene northern Eurasian species, *S. kirchbergensis* (Tong, 2012; Pandolfi, 2018). Handa and Pandolfi (2016) redescribed NMNS-PV 9600 and identified it as *S. kirchbergensis* based on the characteristics such as the presence of the crista on the molars, a reduced lingual cingulum on the premolars, and a wavy ectoloph on P3 and P4. They noted that NMNS-PV 9600 resembles a Chinese specimen of *S. kirchbergensis* (= *Dicerorhinus choukoutiensis*) described by Chow (1963).

Shikama (1970) identified an upper molar as *Dicerorhinus nipponicus*, although its detailed occurrence data is unclear. This material resembles the features of *S. kirchbergensis* such as no constriction of the proto- and hypocones, simple crochet, absence of antecrochet and crista, and no cement. Thus, this material is considered as *S. kirchbergensis* in this

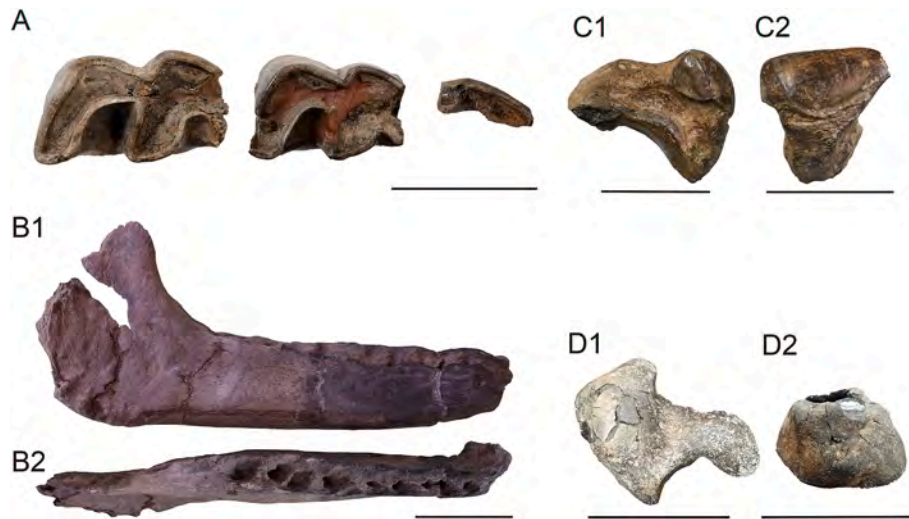


Fig. 2. Japanese Pliocene rhinocerotid fossils. A, Rhinocerotina gen. et sp. indet. from the Tsubusagawa Formation, left p4 (LBM 0142001230); left m1 (LBM 0142001231); left m2 (LBM 0142001232). B, Rhinocerotina gen. et sp. indet. from the Tsubusagawa Formation, right mandible (LBM 142001248). B1, lateral view. B2, dorsal view. C, Rhinocerotina gen. et sp. indet. from the Ueno Formation, right lunate (OMNH-TV-0342). C1, lateral view. C2, cranial view. D, Rhinocerotidae gen. et sp. indet. from the Kanzawa Formation, left unciform (KPM-NN 5208). D1, dorsal view. D2, cranial view. Scale bar = 5 cm for A, C, D; 10 cm for B.

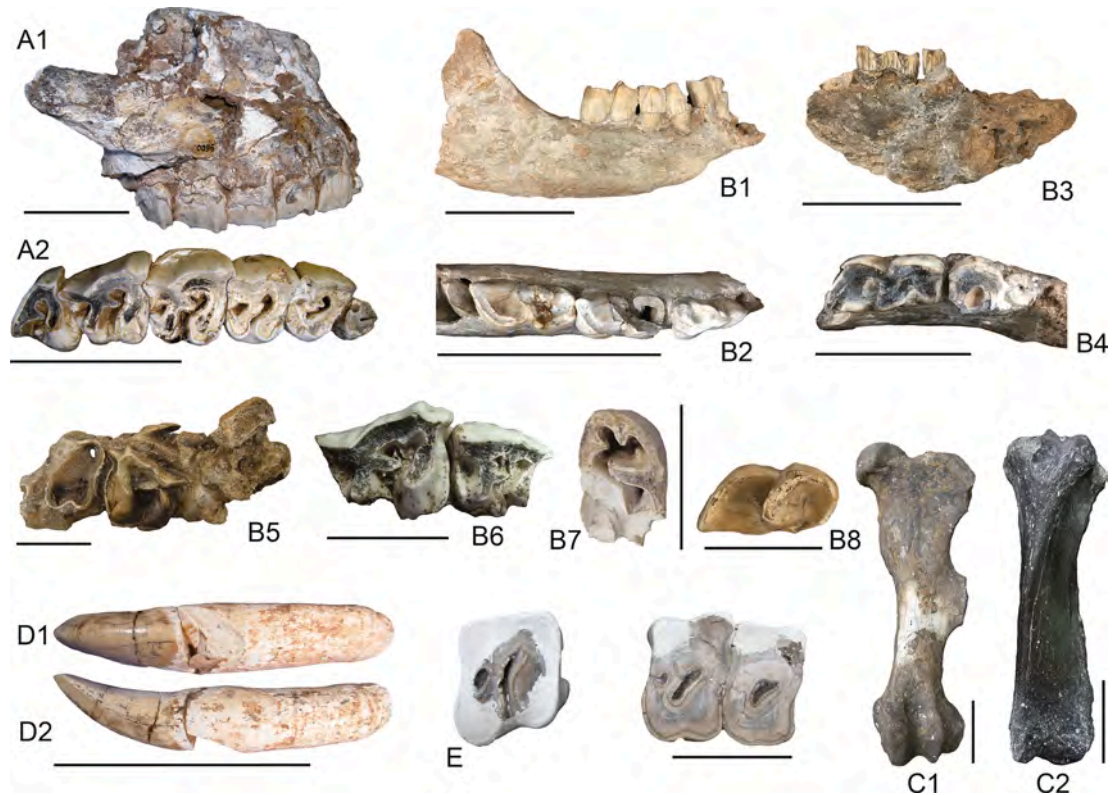


Fig. 3. Japanese Pleistocene rhinocerotid fossils. A, *Stephanorhinus kirchbergensis* from Isa Quarry, right maxilla, (NMNS-PV 9600). A1, lateral view. A2, tooth row of NMNS-PV 9600. B, *Stephanorhinus* sp. from Matsugae Cave. B1, right mandible (KUM-F58-2; lateral view). B2, tooth row of KUM-F58-2. B3, left mandibular fragment (KUM-F58-1; lateral view). B4, tooth row of KUM-F58-1. B5, left upper maxilla with deciduous teeth (A-636-1-1-35-1). B6, right upper deciduous molars (KMNH VP 099,999). B7, left upper molar fragment (A-636-1-1-35-3). B8, left lower molar (A-636-1-1-35-2). C, *Stephanorhinus* sp. from the Bisan-Seto sea area. C1, left femur (YM-1048). C2, left tibia (YM-059). D, Rhinocerotina gen. et sp. indet. from the Yage Formation, left i2 (SFM04-11306). D1, lateral view. D2, distal view. E, Rhinocerotidae gen. et sp. indet. from the Kamo Formation, right upper cheek teeth (F00000554). Scale bars = 10 cm for A, B1, B2, B3, C, D; 5 cm for B4, B5, B6, B7, B8, E.

study.

Stephanorhinus sp.

Synonymy.

Rhinoceros shindoi Naora, 1954, Fig. 19.

Rhinoceros sinensis Morishita, 1977, plt. 48, Fig. 9.

Rhinoceros shindoi Kamei, 1981, p. 167.

Dicerorhinus sp. cfr. *nipponicus* Okazaki, 2007, Figs. 1, 2, 3.

Dicerorhinus sp. Ogino et al., 2009, fig. 20.

4.3. Referred materials

A-636-1-1-35-1 (A left maxillary fragment with DP4: Fig. 3B5), A-636-1-1-35-3 (a left M1 or M2 fragment: Fig. 3B7), KMNH VP 099,999 (DP2 and DP3: Fig. 3B6), A-636-1-1-35-2 (a left lower deciduous molar: Fig. 3B8), KUM-F58-1 and KUM-F58-2 (two mandibles: Fig. 3B1-4), A-636-1-1-35-4 (a MIII? fragment) from Matsugae Cave in Fukuoka Prefecture; YM-1048 (a left femur) and YM-059 (a left tibia) from the seabed in the Bisan-Seto sea area between Okayama and Kagawa prefectures (Fig. 3C1, 2).

4.4. Remarks

Several rhinocerotid remains have been found from the fissure deposits in the Matsugae Cave in Fukuoka Prefecture (Naora, 1944). Tokunaga (1930) listed the Matsugae specimens as “*Rhinoceros shindoi*”, “*Rhinoceros* α sp.” and “*Rhinoceros* β sp.” without any descriptions, figures and type specimen designations. Kamei (1981) listed *R. shindoi* as a member of the Japanese Middle Pleistocene fauna. Okazaki (2007) described two upper deciduous teeth (KMNH VP 099,999) and two juvenile mandibles (KUM-F58-1 and KUM-F58-2) from the Matsugae Cave as *Dicerorhinus* cf. *nipponicus*. Ogino et al. (2009) also described a few Matsugae specimens (A-636-1-1-35-1, A-636-1-1-35-3, A-636-1-1-35-2) as *Dicerorhinus* sp. Later, Handa et al. (2021) redescribed the specimens described by Okazaki (2007) and Ogino et al. (2009), together with an undescribed metacarpal fragment (A-636-1-1-35-4). The Matsugae specimens show the characteristics of DPs of *Stephanorhinus* such as a weak parastyle and a mesostyle on DP2, the presence of a crista and a weak metacone fold on DP3, DP4 with the presence of a crista, a developed paracone fold, and a reduced cingulum, resulting in that the Matsugae remains were reidentified as *Stephanorhinus* sp. (Handa et al. 2021).

Taruno (1988, 2000) tentatively reported a few limb bones collected from the seabed in the Bisan-Seto area, although the precise taxonomy was not discussed. Of these, a femur (YM-1048) and a tibia (YM-059) were redescribed as *Stephanorhinus* sp. (Handa and Takechi, 2017) based on the characteristics of a relatively slender femur with a weakly developed lesser trochanter, and the tibia with a slender shaft, a low and rounded posterior apophysis and a low medial malleolus.

Morishita (1977) figured a DP2 (no catalog number) of a Pleistocene rhinocerotid from Kuzuu as *Rhinoceros sinensis*. This tooth is similar to the DP2 of *Stephanorhinus* sp. from Matsugae (Handa et al., 2021) in having the protoloph connecting to the ectoloph, slightly convex ectoloph, double crochet, the crista which contacts the crochet, slightly developed mesostyle, and a weak paracone fold. Thus, this specimen is considered *Stephanorhinus* sp. in this study.

Subtribe Rhinocerotina GRAY, 1821.

Rhinocerotina gen. et sp. indet.

4.5. Referred material

SFM04-11306 (a left i2) from the middle or upper Pleistocene Yage Formation in Yage, Hamamatsu City, Shizuoka Prefecture (Fig. 3D).

4.6. Remarks

Nishizawa (1972) briefly introduced SFM04-11306 as a “canine” of a rhinocerotid. Handa (2015) described SFM04-11306 as an i2 of Rhinocerotinae gen. et sp. indet. based on the tusk-like shape, the labial side enamel, and teardrop-shaped oval cross-sections at both the tooth crown and the root sides. SFM04-11306 is comparable to the i2 of *Rhinoceros unicornis* in terms of its large size, massive tooth crown, and tusk-like shape. However, the specimen lacks any diagnostic features that would allow for a specific identification. Consequently, this incisor is classified as an indeterminate species of Rhinocerotina in this study.

Rhinocerotidae gen. et sp. indet.

4.7. Referred materials

F00000554 (P3, P4 and M2) from the Kokubu Group in Aira, Kagoshima Prefecture Otsuka and Nishiinoue (1980) (Fig. 3E); unnumbered specimen (a left lower molar) from the Kuzuu Formation in Ogano Quarry at Kuzuu, Tochigi Prefecture; unnumbered specimen (two mandibular fragments with deciduous teeth) from Suisyo-zan in Tsukumi City, Oita Prefecture; YM-455 (a radius fragment) from the seabed of the Bisan-Seto area between Okayama and Kagawa prefectures.

4.8. Remarks

Shikama (1967) described a few upper cheek teeth (F00000554) derived from the Kokubu Group in Aira, Kagoshima Prefecture. He compared these specimens with Chinese Pleistocene species of *Rhinoceros* and identified them as *Rhinoceros* aff. *sinensis*. However, F00000554 are severely worn, making it difficult to ascertain diagnostic characteristics. Consequently, Handa (2019) redescribed and identified them as Rhinocerotidae gen. et sp. indet.

An isolated lower molar (no catalog number) from the Kuzuu Formation in the Kuzuu area was reported as “*Dicerorhinus* (?) sp.” (Shikama, 1949, Pl. V, Fig. 3a-c). As illustrated in Shikama (1949), the Kuzuu lower molar exhibits characteristics typical of the lower cheek tooth of rhinocerotids, including a deep ectolophid groove, a lingually directed metalophid and hypolophid, a bifid paralophid, rounded buccal walls of the trigonid and talonid, no lingual groove on the entoconid, no constriction of the metaconid and entoconid, absence of the buccal and lingual cingulids, V-shaped anterior valleys in the buccal and lingual views, and a U-shaped and wide V-shaped posterior valley in buccal and lingual views, respectively. Unfortunately, this specimen is lost so we could not directly examine it. Therefore, we currently classify this specimen as an indeterminate species at present.

Kawamura et al. (1977) briefly reported right and left side mandibular fragments with deciduous cheek teeth (dp2 to dp4 and dp3 and dp4 on the left and right side respectively) of an individual rhinocerotid (no catalog number) from mud sediments (probably Pleistocene) in a limestone quarry of Suisho-zan at Tsukumi City in Oita Prefecture, without including a detailed comparison. According to the description and figures of Kawamura et al. (1977), all dp's are not worn. The anterior and posterior valleys are wide U-shaped in occlusal view. There is no buccal cingulids. The ectolophid groove is relatively deep and continues near the tooth neck. The buccal wall on dp3 and dp4 is almost flat. The paralophid on dp2 is oriented mesially. The metalophid and hypolophid extend lingually on dp3 and dp4. The paralophid on dp3 is bifid. Kawamura et al. (1977) pointed out that these remains resemble the mandible of *Rhinoceros sinensis* by Colbert and Hooijer (1953). A detailed description and comparison are needed to identify these remains, but it is uncertain where the specimens were deposited. Thus, the specimens from Tsukumi are tentatively considered as Rhinocerotidae gen. et sp. indet. in this study.

A radius shaft of a rhinocerotid (YM-455) was reported from the seabed in the Bisan-Seto area (Taruno, 1988). YM-455 was identified as the middle part of the radius, but is too fragmentary to identify, resulting in its detailed taxonomic position being unclear as noted by Taruno (1988).

5. Description of additional Pleistocene rhinocerotids from Japan

Family Rhinocerotidae GRAY, 1821.

Subfamily Rhinocerotinae GRAY, 1821.

Tribe Rhinocerotini GRAY, 1821.

Subtribe Rhinocerotina GRAY, 1821.

Genus *Stephanorhinus* KRETZOI, 1942.

Stephanorhinus kirchbergensis (JAGER, 1839).

Figs. 4, 5.

Synonymy.

Rhinoceros sp. Naora 1954, fig. 18.

Rhinoceros sp. Nagasawa 1961, text-Figs. 1, 2, 3.

5.1. Specimens

No. 94347861 (a right maxilla fragment with P2 and P3) from the Yoshizawa Quarry in Ogano, Kuzuu, Tochigi Prefecture (Fig. 4), which is stored in the Edo-Tokyo Open Air Architectural Museum, Koganei City, Tokyo; no. 255 (isolated left P3, left M1, right M2 and left lower molar), and no. 256 (an isolated right upper premolar) from the Isa Cement Quarry in Isa City, Yamaguchi Prefecture, which are stored in the Mine Fossil Museum and the Mine City Museum of History and Folklore, Mine City, Yamaguchi Prefecture (Fig. 5). Table 3 presents the tooth measurements.

Naora (1954) observed an isolated P2 of a rhinocerotid from the Yoshizawa Cement Quarry in Ogano, Tochigi Prefecture. Naora (1954) identified it as *Rhinoceros* sp. Subsequently, Nagasawa (1961) described a skull with upper cheek teeth and a P2 (no. 94347861), which was initially reported by Naora (1954). Additionally, he observed that the P2 and the skull belonged to the same individual. Shikama et al. (1967) noted that no. 94347861 was a synonym of *D. nipponicus* at the time. Unfortunately, no. 94347861 is lacking the main part of the maxilla. However, the anterior part of the skull, with P2 and P3 is stored in the museum (Fig. 4). The teeth specimens from Isa (no. 255 and no. 256) were exhibited at the Mine Fossil Museum and the Mine City Museum of History and Folklore.

5.2. Description

No. 94,347,861 lacks most of the maxilla (Fig. 4). The buccal part of the P3 is broken. The enamel surface of the teeth is smooth. There is no coronal cement. The ectoloph of P2 is convex buccally. The paracone fold is weak. The protocone is isolated from the ectoloph and connects to

the hypocone. The postfossette is oval at this wear stage. The crochet is bifid, and is lacking tips. There is no buccal cingulum, whereas a low lingual cingulum is on the mesio-lingual side. The protoloph of P3 extends disto-lingually. The protocone of P3 is not constricted. There is no hypocone groove. The lingual wall of the proto- and hypocone is rounded. The crochet is bifid as in P2. The postfossette is tiny at this wear stage. The crista and cristella are not seen at this stage. The anterior cingulum is low. There is no lingual cingulum.

The isolated cheek teeth (no. 255 and 256) have no coronal cement. The enamel surface is smooth. The upper premolar fragment (no. 256: Fig. 5A) is molariform and lacks a lingual side. The crown height is relatively high. The buccal wall is almost flat. There is a trace of the paracone fold. The parastyle is weak. The crochet projects mesially and its tip bends lingually. The protoloph and metaloph are connected on the lingual side at this wear stage. The posterior protocone groove and anterochet are absent.

P3 (no. 256: Fig. 5B) is also molariform and its buccal side is broken. The tooth is well worn down. The occlusal surface is almost flat in mesio-lingual view. The protoloph and metaloph are directed lingually. The protocone is not constricted. The crochet and anterochet are absent. The hypocone is also not constricted. The lingual side of the protocone and hypocone is rounded. A short and low anterior cingulum is preserved. The trace of the lingual cingulum is on the lingual side. The postfossette is oval shaped at this wear stage.

M1 (no. 255; Fig. 5C) is well preserved and moderately worn. The paracone fold is weak at this wear stage. The parastyle projects mesially. The mesostyle is very weak. The protoloph and metaloph extend lingually. The protocone and hypocone are not constricted. The lingual wall of the protocone and hypocone are rounded. There is no lingual protocone groove. The crochet is only developed as an internal fold. The postfossette is a small teardrop outline at this wear stage. The buccal and lingual cingula are absent. There is a faint anterior cingulum at this wear stage. The occlusal surface is concave in mesiodistal view.

M2 (no. 255; Fig. 5D) is less worn than the M1. The buccal wall is

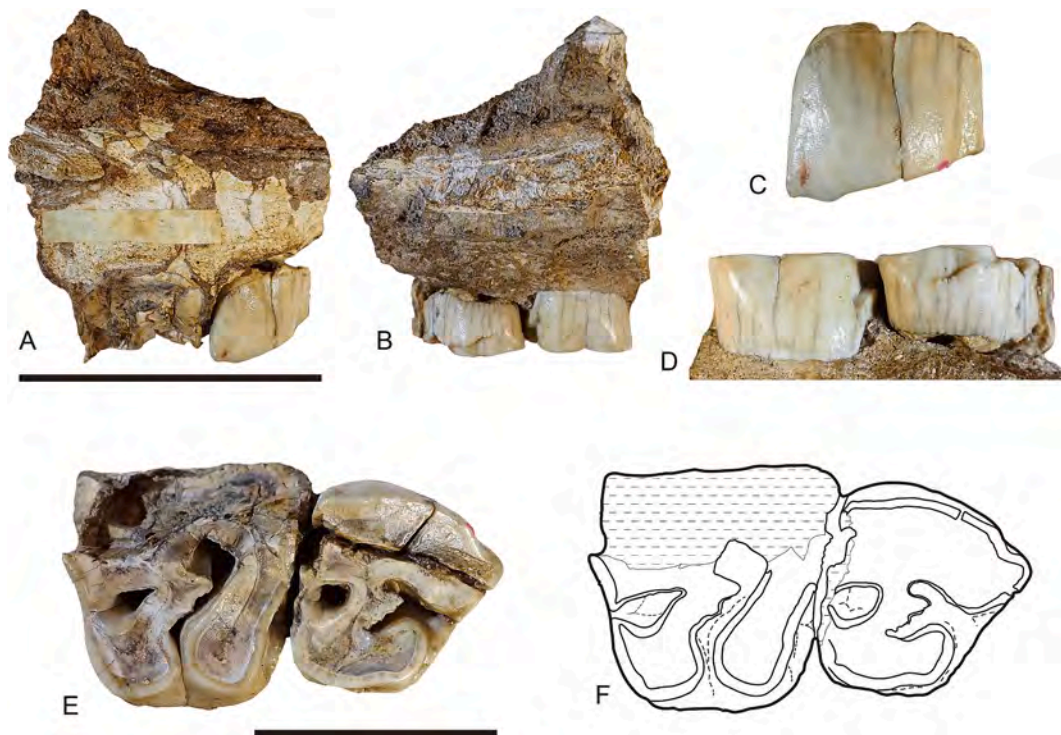


Fig. 4. *Stephanorhinus kirchbergensis* from the Yoshizawa Quarry in Ogano, Tochigi Prefecture (no. 94347861). A, buccal view of the skull fragment. B, lingual view of the skull fragment. C, buccal view of the P2. D, lingual view of the P2 and P3. E, occlusal view of the P2 and P3. F, schematic drawing of the occlusal view of the cheek teeth. Scale bar = 10 cm for A and B, 5 cm for C-F.

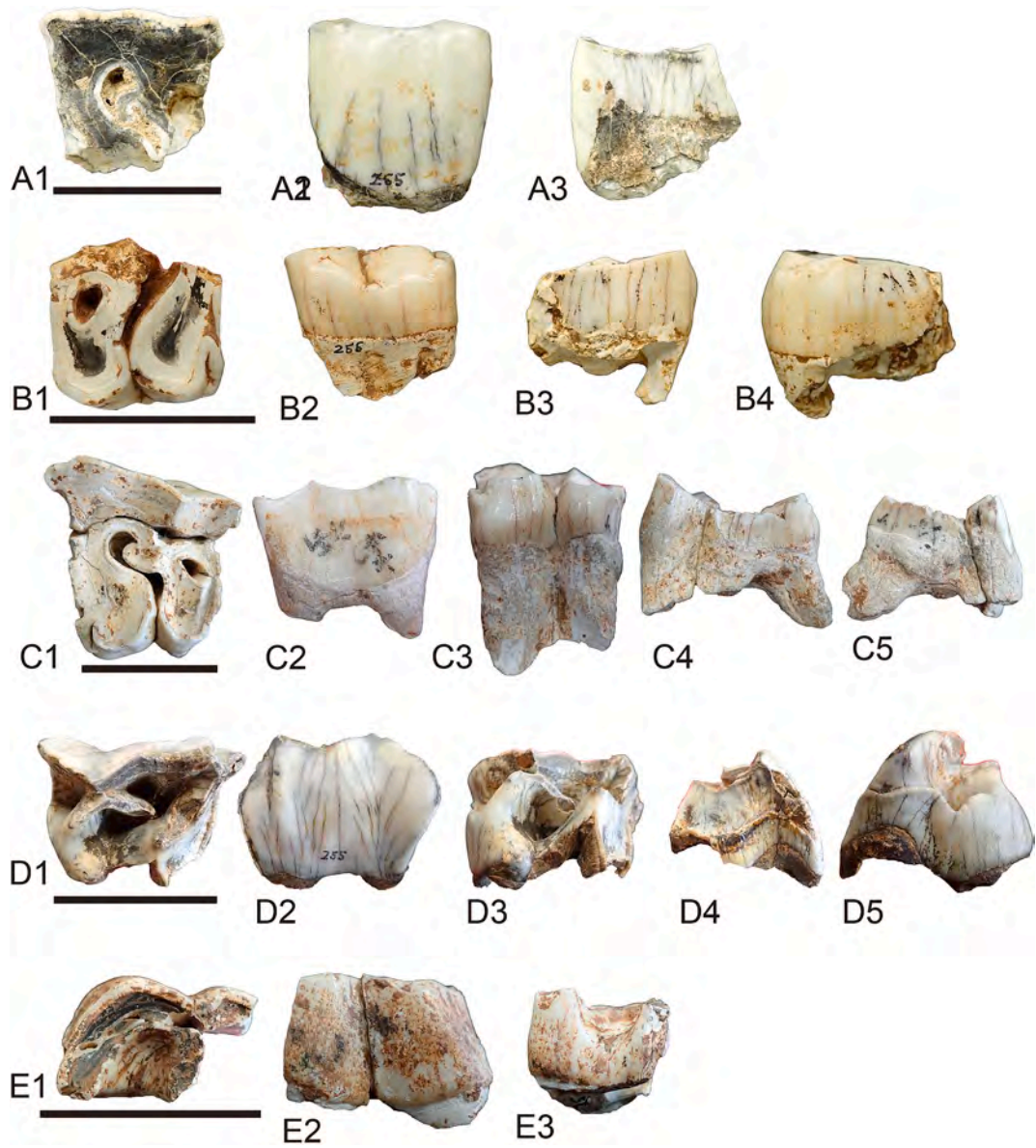


Fig. 5. *Stephanorhinus kirchbergensis* from Isa Quarry in Isa City, Yamaguchi Prefecture (no. 255, no. 256). A, left P3 (no. 255). B, right upper molar (no. 256). C, left M1 (no. 255). D, right M2 (no. 255). E, left lower molar. A1, B1, C1, D1, E1 = occlusal views. A2, C2, D2, E2 = buccal views. B2, C3, D3, E3 = lingual views. A3, B3, C4, D4 = mesial views. B4, C5, D5 = distal views. Scale bar = 5 cm.

Table 3

Tooth measurements of *Stephanorhinus kirchbergensis* from Yoshizawa Quarry in Ogano, Tochigi Prefecture (no. 94347861) and from Isa Quarry in Isa City, Yamaguchi Prefecture (no. 255, no. 256). Abbreviations. L, mesiodistal length. Wa, buccolingual width (anterior side). Wp, buccolingual width (posterior side). H, crown height.

Specimen number	tooth	L	Wa	Wp	H
no. 94347861	P2	35.72	34.53	38.25	28.83
	P3	38.79	>51.01	48.05	—
no. 255	P3	40.16	>41.61	>41.93	37.84
no. 256	M1	56.59	63.49	58.19	34.4
	M2	56.81	>47.10	44.91	42.73

wavy at this wear stage. The paracone fold and parastyle project distinctly. The mesostyle is weak, as in M1. The protoloph and metaloph bend distolingually. The crochet is long. The crista is weak and is not worn at this wear stage. The protocone and hypocone are not constricted. The lingual protocone groove is absent. The anterior and

posterior cingula are low. The medisinus is wide and deep. The buccal wall is absent, as in M1.

The isolated lower premolar (no. 255: Fig. 5E) lacks a mesiolingual part. The ectolophid groove is deep and continues to the neckline. The posterior valley is wide and deep, U-shaped in buccal and lingual views. The buccal wall of the protocone and trigonid is acute. The hypolophid bends distolingually. The entoconid is not constricted. There is no entoconid groove. There is no cingulids on the tooth.

5.3. Comparison

All specimens described here are different from the cheek teeth of *Coelodonta antiquitatis* in lacking the coronal cement and the mediofossette (Qiu et al., 2004). They are lacking the developed enamel folding on the cheek teeth, suggesting that these teeth are not of the genus *Elasmotherium* (Schvyreva, 2015). They also differ from the cheek teeth of *Dicerorhinus sumatrensis* lacking developed paracone- and metacone folds (GMNH-VM-562, cast of the modern specimen). They are also

distinguished from the cheek teeth of the species of the genus *Rhinoceros* in having the weak parastyle, paracone- and metacone folds (Colbert and Hooijer, 1953; Guérin, 1980; Yan et al., 2014).

No. 94347861 resembles the teeth of *S. kirchbergensis* from Isa (NMNS-PV 9600) in having a smooth enamel surface on the premolars, P2 with bifid crochet, absence of the coronal cement on the teeth, the protocone connected to the hypocone, oval-shaped postfossette, a low lingual cingulum, and P3 with the bifid crochet, the absence of the protocone constriction, and without the lingual cingulum. Therefore, we identified no. 94347861 as *S. kirchbergensis*.

Two isolated cheek teeth (no. 255 and no. 256) are similar to the upper cheek tooth row of *S. kirchbergensis* (NMNS-PV 9600) in having the premolar with molariform, almost flat ectoloph, weak paracone fold, absence of the crista, faint lingual cingulum, no buccal cingulum, and no protocone constriction; the molars have a weak paracone fold and parastyle, faint mesostyle, long metastyle, simple crochet, weak crista, no constriction of the protocone and hypocone, absence of the buccal cingulum, absence of the lingual protocone groove, and no coronal cement. Therefore, no. 255 and no. 256 are identified as *S. kirchbergensis*.

6. Footprint fossils of Plio-Pleistocene Rhinocerotidae

The rhinocerotid footprint fossils have been found mainly in three areas, namely Ajimu, around Ise Bay, and around Lake Biwa (Figs. 1, 6). The Kobiwako Group around Lake Biwa has yielded abundant footprint fossils dated at 4.1 Ma to 1.8 Ma and 1.0 Ma to 0.5 Ma. The Kameyama and Oizumi formations of the Tokai Group (3.5 Ma to 2.9 Ma, 2.6 Ma to 2.3 Ma, 1.8 Ma and 1.6 Ma to 1.4 Ma) have also yielded abundant footprint fossils (Okamura, 2016 and references therein; Okamura et al., 2017; Okamura and Kitada, 2021). Several Plio-Pleistocene footprint fossil localities are known in Oita Prefecture beside Ajimu, although detailed horizons and ages are unclear (Okamura, 2001, 2018; Okamura et al. 1997).

A few rhinocerotid footprints were reported from the Plio-Pleistocene Saitsu Formation in Amakusa associated with cervid and bird footprints (Okamura et al., 2017). Several possible rhinocerotid footprints have been reported from the Middle Pleistocene Oyama Formation in Hita City, Oita Prefecture with other footprints of ruminants, reptiles (crocodilian or lizard), and a large salamander (Okamura, 2018). The Pleistocene Gunchu Formation in Iyo, and the Early Pleistocene Kazusa Formation of the Kuchi-notsu Group in Shimabara (Fig. 1) have both yielded possible rhinocerotid fossil footprints, (Okamura, 2016; Okamura and Kitabayashi, 2022). The details of these fossil bearing-horizons and ages, however, are unclear. Rhinocerotid footprints have often been described as ichnospecies (Guérin and Demathieu, 1993; Costeur et al., 2009; Herrero et al., 2022), but no Japanese ichnotaxa have been identified have so far.

7. Discussion

7.1. Plio-Pleistocene faunal zonation in Japan

Kamei et al. (1988) proposed eight mammal faunal zones for the Japanese Plio-Pleistocene (PM1 to PM2 for the “Pliocene” and QM1 to QM6 for the “Pleistocene,” where the Plio-Pleistocene boundary was defined as 1.8 Ma). Takahashi and Izuho (2012) also proposed four periods (The First, Second, Third and Fourth periods) for the Plio-Pleistocene Japanese mammal fauna. In this study, we adopt both proposed systems to discuss the migration time of the Japanese Rhinocerotidae.

7.2. Pliocene rhinoceroses in Japan

7.2.1. Fossil records

Pliocene rhinocerotids appeared by 4.1 Ma in central Japan (around

Ise Bay and around Lake Biwa) based on the fossil footprints from the Kobiwako and Tokai groups (Fig. 6). OMNH-TV-0342 was discovered in the horizon near the Hattorigawa I tephra bed in the Ueno Formation (Murakami and Tsubamoto, 2018), suggesting that the chronological age of this specimen is approximately 3.6 Ma.

In the Second period, the Late Pliocene rhinocerotid records of both body and footprint fossils increase. Rhinocerotina gen. et sp. indet. from Ajimu were found from the lower part of the Tsubusagawa Formation, which is estimated to be between 3.5 to 3.4 Ma (Handa and Kato, 2020; Handa et al., 2023). Although the precise horizon of KPM-NN 5208 is unclear, the Kanzawa Formation in Aikawa is correlated with the middle Late Pliocene, based on the magnetostratigraphy (Ueki et al., 2013). Hase et al. (2017) calculated the fission track age of the Saitsu Formation that yielded the footprint fossils, suggesting that this formation is dated as 2.6 ± 0.4 Ma. These results suggest that rhinocerotids were distributed in the central to southwestern parts of Japan during the Late Pliocene (Fig. 6). In particular, the subtribe Rhinocerotina was in central to southeastern parts of Japan at that time (Murakami and Tsubamoto, 2018; Handa and Kato, 2020; Handa et al., 2023). In China, the species of the Rhinocerotina have been reported from Pliocene sediments (Deng and Downs 2002; Deng and Qiu 2007; Tong 2012; Pandolfi 2018; Fig. 7). The Japanese Pliocene rhinocerotid occurrences exhibit a comparable trend to the Chinese fossil records.

7.2.2. Paleobiogeography

In the First period, proto-Japan was connected with continental Asia, but was disconnected a few time during the Pliocene part of the Second period (ca. 3.2 Ma, 2.9 Ma, and 2.4 Ma: Kitamura and Kimoto, 2006; Takahashi and Izuho, 2012; Fig. 6). Unfortunately, the detailed taxonomy of the rhinocerotid fossil records in this period is unclear due to fragmentary specimens or footprints. Therefore, it is debatable whether the rhinocerotids in this period were descendants of the Japanese Miocene species (“Teleoceratinae” gen. et sp. indet. reported by Yoshida et al., 1989) or newcomers from continental Asia in the Late Pliocene. Handa and Kato (2020) and Handa et al. (2023) proposed two hypotheses on the migration time of Japanese Pliocene rhinocerotids. One hypothesis is that the ancestor of the Japanese Pliocene taxa migrated from continental Asia during the earliest Pliocene. In Japan, proboscideans are well-represented by various fossils from the Neogene, which have contributed to discussions about the migration times. *Stegodon miensis*, a Japanese endemic Proboscidean, is present in the Pliocene (Fig. 6). The oldest record of Japanese *Stegodon*, which has similar molar morphology of *Stegodon zdanskyi*, is from the Tatsunokuchi Formation (5.32 Ma) in Sendai, northern Japan (Saegusa et al., 2005; Taruno, 2010). *Stegodon zdanskyi* has been widely distributed in the latest Miocene or earliest Pliocene localities of northern China (Chen, 2011). Consequently, this species may have migrated to proto-Japan during the latest Miocene or earliest Pliocene and was evolved to *S. miensis* (Takahashi and Namatsu, 2000; Saegusa et al., 2005; Taruno, 2010). *Stegodon miensis* has been found from Ajimu (Takahashi and Kitabayashi, 2001).

Several species of Rhinocerotina have also been found from the upper Miocene to lower Pliocene in northern China, such as in Shanxi, Shaanxi, and Gansu (Geraads et al., 2021 and references therein). Handa et al. (2023) considered that there was the possibility for a migration route from northern China because the mandibular specimen of the Rhinocerotina gen. et sp. indet. from Ajimu resembles those of *Dihoplus ringstroemi* or *Priorhinus megarhinus*, which were found from the northern Chinese late Mio-Pliocene localities. Therefore, the ancestor of Japanese Pliocene Rhinocerotina might have migrated at the same times as in the case of the ancestor of *S. miensis*.

The Ajimu fauna in Usa was correlated with a tropical to subtropical fauna in South China and Southeast Asia. This suggests that the Ajimu fauna may represent animals from the Oriental Realm that expanded their northern range during the warm period of the first half of the Pliocene. This allowed them to migrate to proto-Japan, after which they

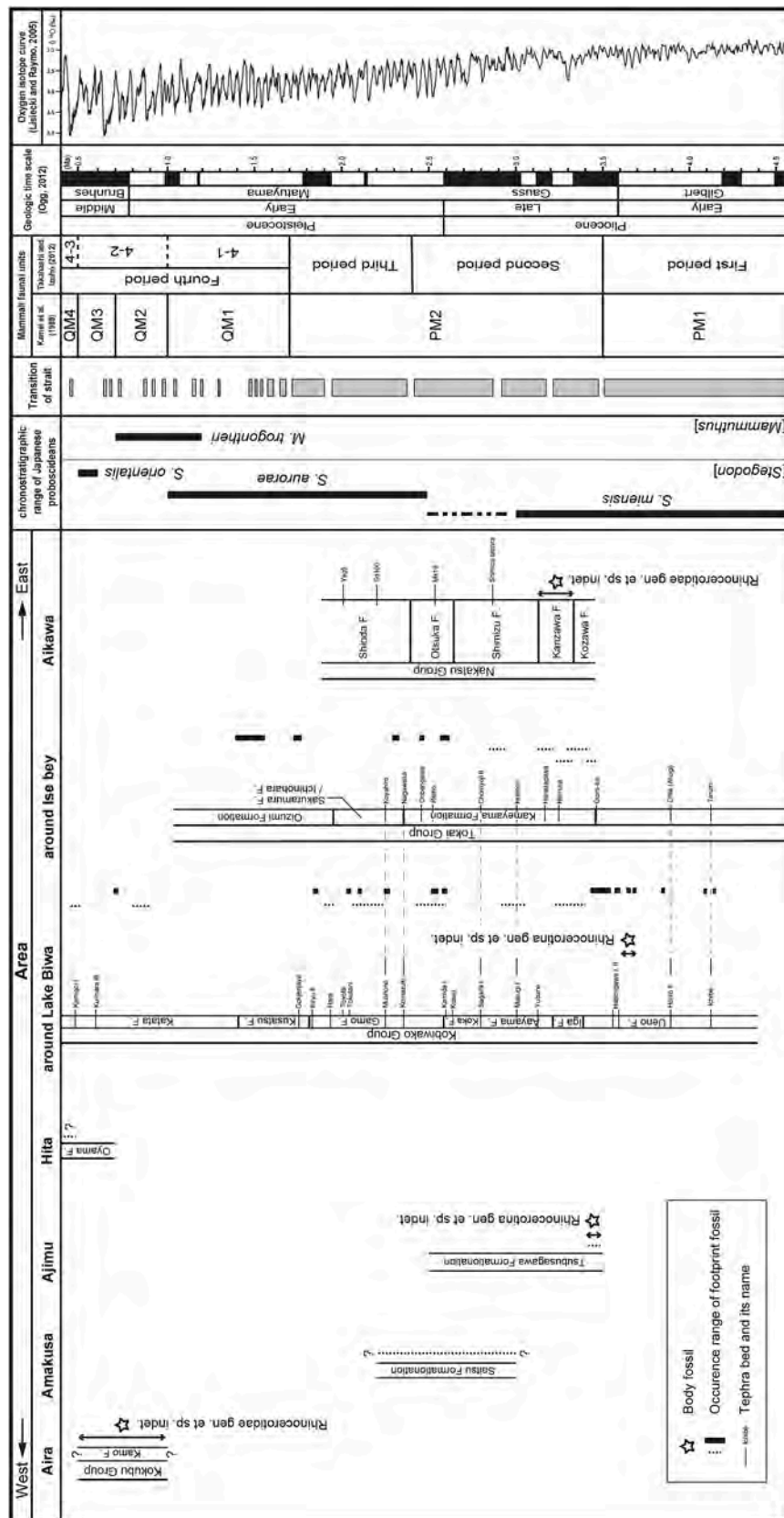


Fig. 6. The stratigraphic range of the Pliocene to Middle Pleistocene Japanese rhinocerotid fossils. Stratigraphic units are after [Satoguchi and Nagahashi \(2012\)](#), [Hase et al. \(2017, 2019\)](#), [Hita City Museum \(2018\)](#), [Handa \(2019\)](#), [Okamura and Kitada \(2021\)](#), [Lisiecki and Raymo \(2005\)](#), and [Ueki et al. \(2013\)](#). Chronostratigraphic ranges of Japanese Proboscidean follow [Takahashi \(2013\)](#). Transition of strait is after [Takahashi and Izuho \(2012\)](#); Gray colored bars indicate land connections between Japan and the continental Asia. The solid line of the footprint fossils indicate the occurrence durations. The dashed lines of the footprint fossils indicate the estimated occurrence duration.

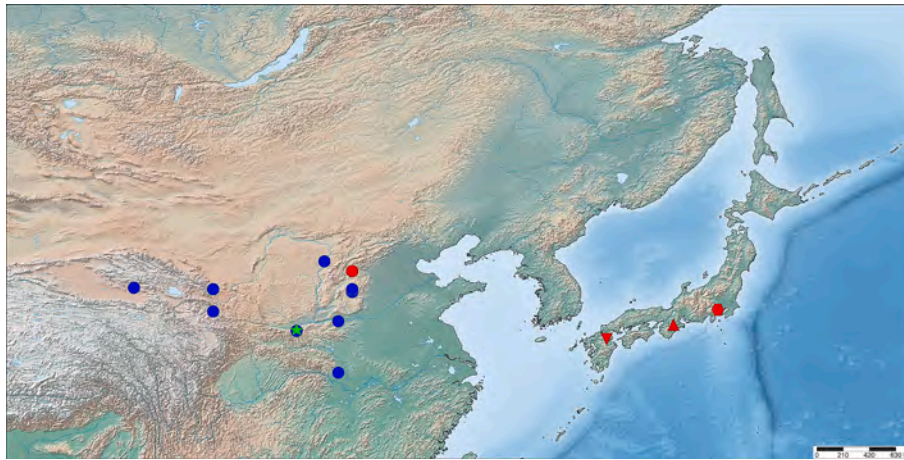


Fig. 7. Map showing the fossil localities of Late Miocene to Pliocene Rhinocerotina from China and Japan. The fossil records are by Geraads et al. (2020) and the present study. The map was created using Simplemappr (Shorthouse, 2010). Abbreviations: blue circle = *Dihoplus ringstroemi* (Late Miocene), red circle = *Dihoplus ringstroemi* (Early Pliocene), star = *Dicerops gansuensis* (Late Miocene), red triangle = Rhinocerotina gen. et sp. indet. from Iga, around Lake Biwa, red inverse triangle = Rhinocerotina gen. et sp. indet. from Ajimu, red hexagonal = Rhinocerotidae gen. et sp. indet. from Aikawa. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

survived as the climate cooled. Takahashi (2001) and Takahashi and Izuho (2012) proposed that the subtropical fauna in south China and Southeast Asia expanded from continental Asia to proto-Japan. As mentioned above, *S. miensis* is likely a descendant of *S. zdanskyi* from northern Chinese taxa. Kato and Kitabayashi (2018) also reported a possible Palearctic element rodent, *Micromys* sp., from the Ajimu fauna, which may have originated in the Palearctic realm. They proposed that this group migrated to the southern Japan when the climate cooled. Consequently, the Ajimu fauna encompasses both southern and northern elements, including those from the Oriental and Palearctic realms. It is noteworthy that the flora associated with the Ajimu fauna is comparable to that of deciduous broad-leaved forests in the present climate zone (Iwauchi and Hase, 1986; Yamakawa, 2001).

Considering these fossil records and the phylogenetic hypothesis, we propose the following hypothesis. Before ca. 3.5 Ma, both northern and southern China were under warm temperature climates (Li et al., 2011, 2014). Based on the Japanese and Chinese fossil records, a rhinocerotid and *Stegodon*, migrated to proto-Japan, reaching northern Japan (Sendai) during this period. After 3.5 Ma, the paleoclimate of northern China and proto-Japan became cooler (Yamakawa, 2001; Liu et al., 2002; Li et al., 2011). This resulted in the Japanese Pliocene fauna living under a temperature climate in central and southwest areas, as noted by Takahashi and Izuho (2012).

Another hypothesis is that the Pliocene Japanese rhinocerotids are descendants of the Late Miocene species (Handa and Kato, 2020). In the early Late Miocene, the southwestern part of the proto-Japan was connected with continental Asia (Noda and Goto, 2004). A few species of Rhinocerotina, such as *Dihoplus megarhinus* (= *Dihoplus ringstroemi*) and *Dicerops gansuensis* were present in China during the Late Miocene (Deng and Qiu 2007; Tong 2012; Pandolfi et al. 2015; Pandolfi et al. 2021b; Shi et al. 2023) (Fig. 7). Thus, a taxon of the Rhinocerotina might have migrated to proto-Japan. However, the Late Miocene Japanese rhinocerotid fossils are scarce (Tomida et al., 2013). This hypothesis must await further fossil discoveries from the Late Miocene fossil record in Japan.

7.3. Pleistocene rhinoceroses in Japan

7.3.1. Fossil records

Rhinoceros sinensis is listed as part of the Middle Pleistocene terrestrial fauna from Ikumo Quarry in Yamaguchi Prefecture (Hasegawa, 1966; Kawamura et al., 1989). However, its detailed descriptions and figures are lacking. In addition, this record has not been cited by recent

studies on the Japanese mammalian fauna (Hasegawa, 2012). Therefore, the record of *R. sinensis* from Ikumo Quarry is excluded from this study.

A mandibular fragment of rhinocerotid identified as *Dicerorhinus* cf. *nipponicus* was discovered in the Middle Pleistocene Mandano Formation of the Kazusa Group in Chiba Prefecture (Database of the Chiba Prefectural Museum, 2022). However, the availability of detailed descriptions, figures, and geological information is insufficient. Consequently, this specimen is also excluded from our discussion.

The Third period is correlated with the early part of the Early Pleistocene (Takahashi and Izuho, 2012; Fig. 6). In this period, proto-Japan and continental Asia were disconnected at ca. 2.4 Ma and ca. 1.9 Ma (Kitamura and Kimoto 2006). During this period, there are no obvious rhinocerotid body fossils reported from Japan, but footprint fossils have been found from the earliest Pleistocene localities.

The Fourth period is correlated with the later part of the Early Pleistocene to the present, and is divided into four sub-periods (4-1 to 4-4). During the 4-1 to 4-2 sub-periods, there are few rhinocerotid fossil records (Figs. 6, 8). The Kamo Formation of the Kokubu Group in Aira, which yielded Rhinocerotidae gen. et sp. indet. is correlated with ca. 1.0 to 0.5 Ma, although its precise chronostratigraphic range is unclear (Handa, 2019). The fission track ages of the lower and upper pyroclastic flow deposits in the Oyama Formation are 0.5 ± 0.2 Ma and 0.36 ± 0.09 Ma, respectively (Iwauchi and Hase, 1989; Hase et al., 2018, 2019) (Figs. 6, 8).

The 4-3 sub-period is correlated with the middle Middle Pleistocene. As in the remains from Kuzuu and Yage (Shikama, 1949; Handa, 2015), *S. kirchbergensis* (NMNS-PV 9600) was also collected from fissure deposits (the Lower Isa Formation) at the Isa Limestone Quarry. Unfortunately, its exact geological age is unclear. In Japan, two proboscideans, *Stegodon orientalis* and *Palaeoloxodon naumanni* are considered to have migrated from the Asian continent approximately 0.63 and 0.43 Ma respectively (Konishi and Yoshikawa, 1999; Yoshikawa et al. 2007). Later, Takahashi (2023) suggested that *P. naumanni* migrated during MIS 10 (0.36–0.34 Ma) based on the fossil record of this species and the oxygen isotope ratio was calculated using planktonic foraminifera shells from a core in the Sea of Japan. The faunas that include *S. orientalis* and *P. naumanni* are correlated with QM3 (4-2 sub-period) and QM4 (4-3 sub-period), respectively (Kamei et al., 1988; Takahashi and Izuho, 2012). Shikama et al. (1967) noted that *S. kirchbergensis* from Isa would have been found in the same bed that yielded *S. orientalis*. These results suggests that the geological age of the Lower Isa Formation that yielded *S. kirchbergensis* is correlated with 4-2 sub-period/QM3 (Fig. 8).

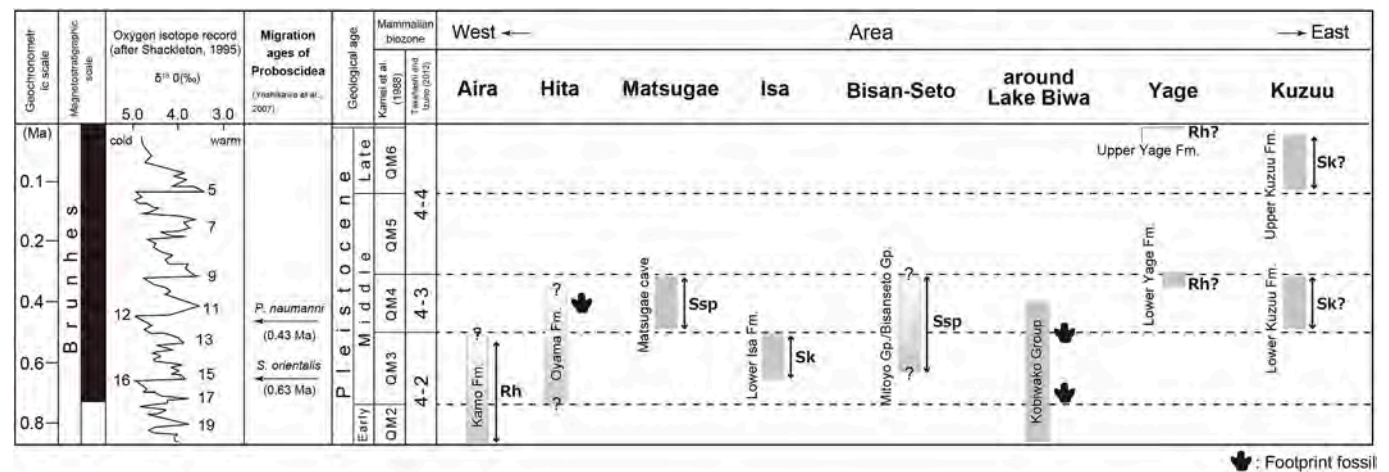


Fig. 8. The stratigraphic range of the Pleistocene Japanese rhinocerotid fossils (modified after Ogino et al., 2009). The stratigraphic ranges are after Kawamura and Matsuhashi (1989), Ogino et al. (2009), Matsuhashi (2012), Kawamura et al. (2014), Nojima et al. (2014), Hase et al. (2018), Handa (2019). Abbreviations: Rh, Rhinocerotiina gen. et sp. indet. Sk, *Stephanorhinus kirchbergensis*, Ssp, *Stephanorhinus* sp.

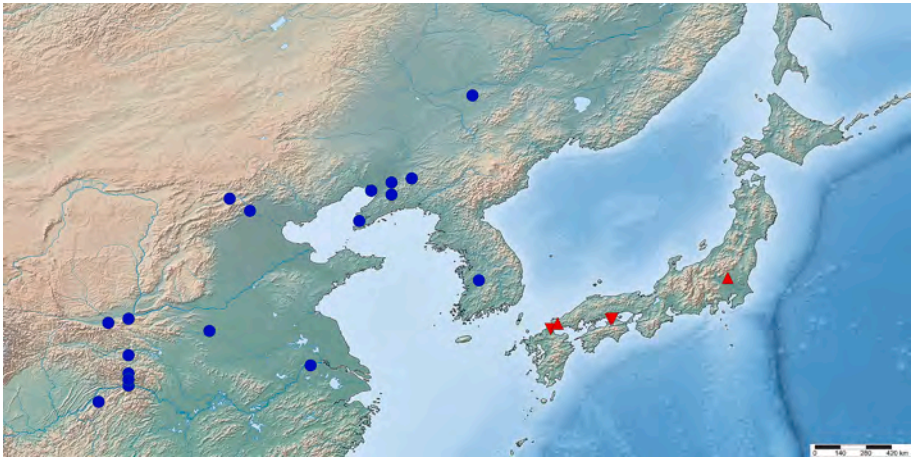


Fig. 9. Map showing the selected fossil localities of *Stephanorhinus kirchbergensis* (includes *S. cf. kirchbergensis* and *Stephanorhinus* sp.) from China, South Korea and Japan. The fossil records are by Lee (2001), Chen et al. (2012), Geraads et al. (2020); Sun et al. (2022) and the present study. The map was created using Simplemappr (Shorthouse, 2010). Abbreviations: blue circle, *Stephanorhinus kirchbergensis* and *S. cf. kirchbergensis* in Asian continent. red triangle, *Stephanorhinus kirchbergensis* from Japan. inverse triangle, *Stephanorhinus* sp. from Japan.

The geological age of the Matsugae Fauna, which includes *Stephanorhinus* sp., was estimated based on the correlation with the Pleistocene terrestrial mammal fauna in Japan by Ogino et al. (2009). The faunal composition of the Matsugae Fauna was correlated with those of middle Middle Pleistocene faunas, such as Bisan-Seto, Ikumo and Kuzuu, indicating that the Matsugae fauna compared with QM4 (Ogino et al., 2009) (Fig. 8).

Stephanorhinus sp. was found in the Mitoyo Group or the Ozuchijima Formation of the Bisan-Seto Group of the Bisan-Seto seabed, and its ages were estimated by tephra chronology and the terrestrial mammal fauna. There are abundant sea basins in the Bisan-Seto sea area. The Ozuchijima and Bannosu formations of the Bisan-Seto Group are distributed in the sea basins M and P, which include the rhinocerotid fossil localities (Taruno, 1988, 2000). These sea basins have yielded *S. orientalis* and *P. naumannii* (Taruno, 1988). Although, the precise horizon of the *Stephanorhinus* sp. is uncertain. Based on these proboscidean fossils, the age of the formation in the sea basins called “M” and “P” are correlated to the middle Middle Pleistocene to late Middle Pleistocene (QM3 to QM5) based on these proboscidean fossils. In contrast, Kawamura (2014) reexamined the stratigraphy of the Bisan-Seto Group based on the tephrochronology, resulting in an age estimate of ca. 0.62–0.61 Ma to

older than 0.53 Ma for the Ozuchijima Formation. Thus, there is a contradiction between the estimated age of the fossil occurrences and the tephrochronology. This discussion is far beyond the scope of the current work; the ages of the *Stephanorhinus* sp. fossils from the Bisan-Seto seabed are considered to be the middle Middle Pleistocene to the late Middle Pleistocene (QM3 to QM4) in this study (Fig. 8).

Late Pleistocene rhinocerotid records are poorly known in Japan. Two rhinocerotid specimens have been reported probably from the Late Pleistocene age (Fig. 8). One is SFM04-11306 from the Yage Formation. The Yage Formation is subdivided into the lower and upper parts. The lower part is considered the Middle Pleistocene lacustrine deposit. The upper part is a fissure deposit that corresponds to the Late Pleistocene, based on the mammal fossils (Nojima, 2002; Nojima et al., 2014). If SFM04-11306 was derived from the upper Yage Formation, this specimen is from the Late Pleistocene. However, it is uncertain which parts of the formation yielded SFM04-11306. Kohno et al. (2023) carried out radiocarbon dating for East Asian Pleistocene mammal fossils, including SFM04-11306, but could not obtain an estimated age for this specimen.

Another possibility of a Late Pleistocene record is the specimens from the Kuzuu Formation in Ogano Quarry, in the Kuzuu area. As previously mentioned, a DP2 of a species belonging to the genus *Stephanorhinus* has

been identified from a locality in the Ogano Quarry, which is believed to be of late Pleistocene age (Morishita, 1977). According to Shikama (1949), a lower cheek tooth (number unavailable) was also collected from the upper Pleistocene “*Palaeoloxodon*-bed” in the same area. Kamei (1981) also listed *Dicerorhinus* (?) sp. as a member of the Japanese Late Pleistocene fauna, likely based on the record from Ogano Quarry by Shikama (1949).

Middle and Late Pleistocene deposits have been recognized in the Ogano quarry based on the mammal fauna (Shikama, 1949). Unfortunately, there are no detailed descriptions of the occurrence information about the specimens from this quarry, such as the age index, fossil-bearing horizon, and other associated fossils. Furthermore, these specimens are currently missing. The partial maxilla specimen of *S. kirchbergensis* (no. 94347861) from Kuzuu also lacks a detailed chronostratigraphic age (Nagasawa, 1967). Consequently, it is not possible to ascertain whether the Kuzuu specimens are of the Late Pleistocene or not. Many rhinocerotid specimens that include a well-preserved skeleton have been reported from the fissure deposits of several quarries in the Kuzuu area (Shimizu, 1992). Further investigations into the Kuzuu remains are needed to discuss this issue based on these materials.

7.3.2. Paleobiogeography

In the Third period, the land connection between the proto-Japan and the Asian continent was generally presented, while the Fourth period, the proto-Japan and the continental Asia were generally disconnected, and a land bridge was only formed in the southwestern part of proto-Japan during low sea-level periods due to glacial sea-level changes (Tada and Irino, 1994; Kitamura et al., 2001; Kitamura and Kimoto, 2006) (Fig. 6). The paleoclimate in the Fourth period became cooler compared to the former period. Similarly, a cold temperature fauna was distributed in the northern and middle parts of China at that time and the close relatives of this fauna would have migrated to Japan, including *Cervus* (*Nipponicervus*) *kazusensis*, *Elaphurus* *shikamai* and *Axis japonicus* (Takahashi and Izuho, 2012; Takahashi and Tomida, 2021).

Fossil footprint records are recognized discontinuously in the Kobiwako and Tokai groups during the Third and Fourth periods (Fig. 6). It is possible that close relatives of Japanese Pleistocene taxa may have existed in proto-Japan during the Early Pleistocene. However, the detailed taxa in Japan are uncertain due to the paucity of fossil records. Rhinocerotidae gen. et sp. indet. from the lower (or middle) Pleistocene in Aira is similar in size to that of the Sumatran rhino (*Dicerorhinus sumatrensis*) and *R. sinensis*. However, the relationship between the Aira specimen and these taxa is uncertain due to a lack of cheek teeth characteristics (Handa, 2019). Consequently, it is currently challenging to elucidate the migration event of the Early Pleistocene rhinocerotids between the Asian continent and Japan.

Several specimens of *Stephanorhinus* were found in the Middle Pleistocene fauna in Japan (Fig. 8). *Stephanorhinus kirchbergensis* has been widely found at the late Early to Late Pleistocene localities in northern Eurasia (Tong and Moigne, 2000; Tong, 2002, 2012; Pandolfi et al. 2021a). In China, *S. kirchbergensis* has been found mainly from the Middle Pleistocene, although several remains of this species have been found in a late Early Pleistocene localities (Tong, 2012; Tong et al., 2014) and possibly the early Early Pleistocene locality (see Dong et al., 2021). In addition, this species has been found from the probably Middle Pleistocene fauna in the Turubong Cave complex, South Korea (Lee, 2001). According to Takai (1959), *Rhinoceros shindoi* (= *S. kirchbergensis*) was found from the Pleistocene in Korea, although precise description and locality information are lacking. The distribution of *S. kirchbergensis* in Asia was mainly in the northern part of China, but several remains of this species have been found in more southern regions, such as the Middle Pleistocene (ca. 0.5 Ma) Nanjing Man Site, Nanjing (Tong, 2001, 2002, 2012) and Bailongdong in Yunxi, Hubei (Tong et al., 2019) (Fig. 9). As noted above, *S. kirchbergensis* from Isa was found from the bed that yielded *S. orientalis*. Therefore, it can be postulated that *Stephanorhinus* migrated from middle part of China to Japan, as was the

case with *S. orientalis* (Fig. 8), when the global sea level dropped and connected Japan to continental Asia (ca. 0.65 Ma) (Konishi and Yoshikawa, 1999; Konishi et al., 2007). Besides large mammals, Lee et al. (2014) investigated that the morphological similarity between Pleistocene Korean *Macaca* with Chinese and Japanese ones, suggesting that ancestral group of this taxon would have invaded from the continent to Japan during the Middle Pleistocene. This result confirms our hypothesis as immigration from the continental Asia to proto-Japan.

Another hypothesis is that *S. kirchbergensis* migrated from northern China in the late Early Pleistocene. Taruno and Kawamura (2007) reviewed the evolution and paleobiogeography of mammoths of East Asia, and they noted that *Mammuthus trogontherii* would have migrated from northern China at ca. 1.2 Ma via the land bridge between the Korean peninsula/Yellow Sea and Japan. In China, *S. kirchbergensis* has been found from the Early Pleistocene locality in Nihewan Basin, northern China (Tong et al., 2014). *Mammuthus trogontherii* has also been found from the several localities in Nihewan Basin (Cai et al., 2013). Therefore, it is possible that *S. kirchbergensis* migrated from northern China at the same time as *M. trogontherii* during the late Early Pleistocene. However, Japanese Early Pleistocene records of *S. kirchbergensis* are unknown so far. Thus, more Early Pleistocene specimens are required for the discussion of the possibility of a migration timing of *S. kirchbergensis* during the Early Pleistocene.

8. Conclusion

In this study, the taxonomy of Japanese Plio-Pleistocene rhinocerotids was revised. In addition, the paleobiogeography is discussed.

Pliocene: A few indeterminate species of the Rhinocerotina lived in central-southwestern Japan in the mid-Pliocene. The ancestral stock of the Japanese Pliocene rhinocerotids would have migrated to proto-Japan during the Early Pliocene together with the ancestor of *S. miensis*. Another hypothesis is that the ancestor of the Japanese Pliocene rhinocerotids might have migrated in the Late Miocene, but the Japanese Late Miocene fossil records are poorly known. Therefore, further records are needed to discuss this hypothesis.

Pleistocene: A few rhinocerotids (*Stephanorhinus kirchbergensis*, *Stephanorhinus* sp. and Rhinocerotina gen. et sp. indet.) were distributed in the Early to Middle Pleistocene in Japan. The existence of a Late Pleistocene rhinocerotid cannot be discussed in this study because there are no fossil records with precise geological ages available. The genus *Rhinoceros* has not been found from the Pleistocene in Japan so far as in the case of the Pliocene. Two indeterminate rhinocerotids (Rhinocerotidae gen. et sp. indet. and Rhinocerotina gen. et sp. indet.) were in central to southwestern Japan (Aira and Yage areas) possibly Early to Middle Pleistocene. *Stephanorhinus kirchbergensis* was distributed in central to southwestern Japan in the middle Middle Pleistocene. This species would have migrated from continental Asia ca. 0.65 Ma with a species of *Stegodon* from the middle part of China at that time. As another hypothesis, considering the fossil records of *S. kirchbergensis* in China and the migration timing of the steppe mammoth (*Mammuthus trogontherii*) to Japan, *S. kirchbergensis* might have migrated to Japan during the Early Pleistocene (ca. 1.2 Ma). However, as no fossils of *S. kirchbergensis* have been found from the Early Pleistocene localities in Japan, we cannot discuss this hypothesis so far. The discovery of more Pleistocene rhinocerotid fossils could solve this problem.

CRediT authorship contribution statement

Naoto Handa: Writing – review & editing, Writing – original draft, Investigation. **Keiichi Takahashi:** Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence

the work reported in this paper.

Data availability

No data was used for the research described in the article.

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