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RESEARCH PAPER

A Pliocene rhinocerotid (Mammalia, Perissodactyla) from Ajimu, Oita Prefecture, southwestern Japan, with comments on the Japanese Pliocene rhinocerotid fossil records

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Abstract

A few lower cheek teeth of rhinocerotid, probably belonging to the same individual, from the upper Pliocene Tsubusagawa Formation in Ajimu, Oita Prefecture, southwestern Japan, are described. Morphologically, the Ajimu specimen is obviously distinguished from the subtribe Teleoceratina (*Brachypotherium*), Elasmotheriina (*Elasmotherium*) and a species of subtribe Rhinocerotina, *Coelodonta*, but it is similar to the Late Miocene species of tribe Aceratheriini and Miocene to Pleistocene species of Rhinocerotina. The Ajimu specimen is metrically similar to the lower cheek teeth of several species of Rhinocerotina, such as species of genus *Diceros*, *Dicerorhinus*, *Dihoplus*, *Rhinoceros* and *Stephanorhinus*. Therefore, the Ajimu specimen is identified as Rhinocerotina gen. et sp. indet. The previous works and present result reveal that this group was presented in Japan during mid-Pliocene. We also briefly summarize fossil records of the Japanese Pliocene rhinocerotid including footprints, suggesting that Pliocene rhinocerotid distributed in Japan through about 4.2 Ma to the end of the Pliocene. Japanese Pliocene rhinocerotids would be migrated from the Asian continent during the Early Pliocene or early Late Miocene when the proto-Japan connected with the Asian continent. However, more Japanese Pliocene specimens and detailed comparison with Asian species are needed to discuss this issue.

Keywords East Asia · Japan · Late Pliocene · Paleobiogeography · Rhinocerotina

Introduction

In Japan, chronologically informative key strata such as tuff and marine beds intercalate in the Pliocene fossil-bearing sediments, and detailed magnetostratigraphic studies have been investigated for those strata. These chronostratigraphic studies contribute for paleobiogeography of the terrestrial vertebrates. As a good example, the dispersal timing and phylogenetic relationship on the Pliocene Proboscidean between Japan and Asian continent have been carried out based on the fossil records and chronostratigraphic works (e.g., Takahashi and Namatsu 2000; Saegusa et al. 2005; Taruno 2010; Takahashi and Izuho 2012).

As another large terrestrial mammal, Rhinocerotidae, a group of Perissodactyla, has been known from the Pliocene sediments in Japan (e.g., Hasegawa et al. 1991; Nakagawa et al. 2013; Murakami and Tsubamoto 2018). Recently, abundant footprints of rhinocerotid have also been discovered from the Pliocene localities in Japan (Okamura 2001, 2016, 2018). In China, few rhinocerotid fossil records have been known from the Pliocene localities. Actually, several Pliocene mammalian localities and rhinocerotid fossils were discovered in China, such as *Shansirhinus ringstromi* from the Linxia Basin, Gansu and *Coelodonta thibetana* from the Zanda Basin Tibet (e.g., Deng 2005; Deng et al. 2011). Therefore, Japanese Pliocene fossil records provide the detail distribution of Pliocene rhinocerotid in East Asia, especially in the eastern coastal margin of the continent. However, few

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discussion of detailed dispersal timing of Japanese Pliocene rhinocerotid is carried out so far.

The Pliocene Tsubusagawa Formation in Ajimu Town, Usa City, Oita Prefecture has yielded various vertebrate fossils. Those are called Ajimu Fauna (Takahashi 2001) and are known as a representative Japanese Pliocene fauna. The fauna includes fishes (Cyprinidae, Bagridae and Cobitidae), anuran (Ranidae and Rhacophoridae), a salamander (Cryptobranchidae), a snake (Colubridae), turtles (Platysternidae, Trionychidae and Bataguridae), crocodylians (Alligatoridae and Crocodylidae), birds (Pelecaniformes, Falconiformes, Anseriformes and Gruiformes), rodents (Muridae and Cricetidae), a proboscidean (Stegodontidae), a cervid (Cervidae), a ursid (Ursidae) and a rhinocerotid (Nakajima and Kitabayashi 2001; Watanabe and Kitabayashi 2001; Matsui et al. 2001; Hirayama 2001; Aoki 2001; Matsuoka 2001; Takahashi and Kitabayashi 2001; Kato 2001; Iijima et al. 2016; Nakajima et al. 2018; Ikeda et al. 2018; Aoki 2018; Kato and Kitabayashi 2018; Takahashi 2018).

The rhinocerotid fossil in Ajimu fauna was briefly identified as Rhinocerotidae gen. et sp. indet. (Kato 2001). The Ajimu specimen is the only tooth remains among the Japanese Pliocene rhinocerotid fossil. Thus, this specimen can provide which group presented in the Pliocene Japan to identify its detailed taxonomy. In this study, we redescribe a few lower cheek teeth of rhinocerotid from the Tsubusagawa Formation. Additionally, we briefly summarize the fossil record of Japanese Pliocene rhinocerotid. Then, these occurrence ranges are briefly summarized. We also proposed the possibility of two immigration timing of Pliocene rhinocerotid into the proto-Japan.

Geological setting

The studied specimen was found from the Pliocene Tsubusagawa Formation that is distributed in the southern area of Usa City, Oita Prefecture, northern Kyushu (Iwauchi and Hase 1986; Hase et al. 2001; Fig. 1). This formation is composed mainly of fluvio-lacustrine deposits and is subdivided into lower, middle and upper parts in ascending order (Iwauchi and Hase 1986). The formation in Ajimu overlies the Usa Formation unconformably and is underlined the Higashishiiya Formation (Hase et al. 2001). The K–Ar ages of the lava in the Usa and Higashishiiya formations are 4.8 ± 0.4 and 2.4 ± 0.5 Ma, respectively (Kamata and Muraoka 1984). Therefore, the geological age of the Tsubusagawa Formation is included in these time span. Hase et al. (2001) and Satoguchi (2001) calculated the fission-track ages of several tephras intercalated the lower part of the Tsubusagawa Formation, suggesting that the ages were estimated 4.9–3.1 Ma. Satoguchi (2016) investigated the petrographic property and chemical composition of the tephra beds in the lower part of the Tsubusagawa Formation. He suggested that tephra beds, named Mori 1 and Tanokuchi beds, in the Tsubusagawa Formation are correlated with the NKT-2 and NKT-13 tephra beds (3.5–3.4 Ma) in the Miyazaki Group in southern Kyushu, respectively, suggesting that the deposition age of the lowermost part of the Tsubusagawa Formation is estimated to 3.5 Ma.

The studied specimen was collected from Tanokuchi area in Ajimu Town, Usa City, Oita Prefecture (Fig. 1; Kato 2001). The outcrop that yielded the studied specimen is composed of the mudstone, sandstone and tuff beds, with a few lignite layers (Kato 2001). This outcrop is correlated with the lower part of the Tsubusagawa Formation (Iwauchi and Hase 1986). The mudstone in the lower part of the

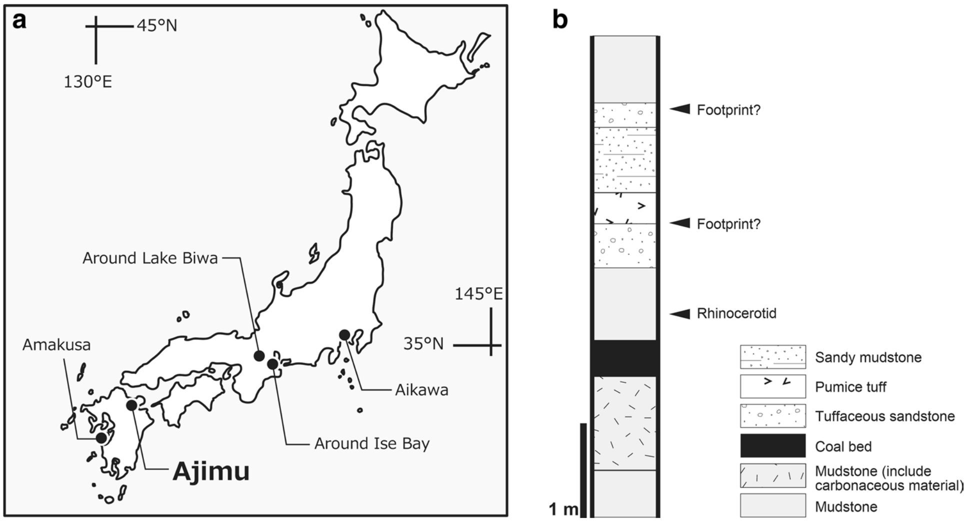

Fig. 1 **a** Map showing the localities of the Pliocene rhinocerotids (modified after Handa 2019); **b** columnar section of the locality at Tanokuchi (modified after Kato 2001). Data from the fossil records follow: Hasegawa et al. (1991) for Aikawa; Kato (2001) for Ajimu; Murakami and Tsubamoto (2018) and Okamura (2016) for around Lake Biwa; Okamura (2016) for around Ise Bay; Okamura et al. (2017) for Amakusa

outcrop includes abundant diatom and plant fragment fossils, suggesting that the sediments in this outcrop deposited in a pond. Besides the rhinocerotid, a few footprints of proboscidean and deer, and a partial skeleton of trionychid turtle have been recovered from the outcrop (Okamura et al. 1997). The studied specimen was collected from the horizon that is under a few meters of the Tanokuchi tephra. Therefore, the geological age of the fossil-bearing horizon is the Late Pliocene (3.5–3.4 Ma).

Materials and methods

The studied specimen is stored in Lake Biwa Museum, Kusatsu City, Shiga Prefecture, Japan. The anatomical terminology used in the present study follows Antoine et al. (2010) (Fig. 2) and the measurements follow Guérin (1980). Although the taxonomy of the species of the Rhinocerotidae is debatable (e.g., Heissig 1972, 1989; Prothero and Schoch 1989; Cerdeño 1995; Antoine 2002; Antoine et al. 2010), the present study follows opinions of Antoine (2002), Antoine et al. (2010), Pandolfi (2016, 2018) and Pandolfi et al. (2015). The studied specimens were compared with Late Miocene to Pleistocene rhinocerotids from Asia such as species of *Diceros*, *Rhinoceros*, *Dicerorhinus*, *Dihoplus*, *Stephanorhinus*, *Coelodonta*, *Acerorhinus*, *Chilotherium*, *Shansirhinus*, *Brachypotherium* and *Elasmotherium*. Two Late Miocene Japanese rhinocerotids were also compared with the studied specimen (Online Appendix).

Anatomical abbreviations. m—lower molar; p—lower premolar.

Metrical abbreviations. L—mesiodistal length of the tooth; Wa—buccoligual width of the anterior part of the tooth; Wp—buccoligual width of the posterior part of the tooth; H—tooth height.

Institutional abbreviations. GMNH—Gunma Museum of Natural History, Tomioka, Japan; HMV—vertebrate fossil specimens of Hezheng Paleozoological Museum in Gansu, China; IVPP—Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences Beijing, China; LBM—Lake Biwa Museum, Kusatsu, Japan.

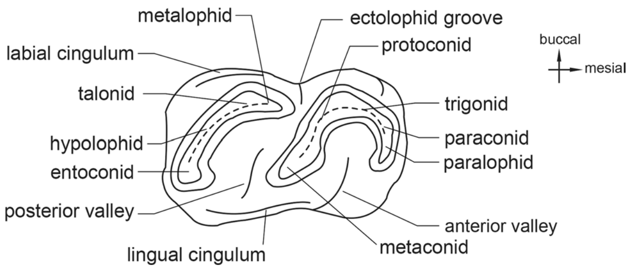

Fig. 2 Nomenclature of lower cheek tooth (Terminology follows Antoine et al. 2010. Illustration is modified after Fukuchi 2003)

Systematic paleontology

Family **Rhinocerotidae** Gray, 1821
Subfamily **Rhinocerotinae** Gray, 1821
Tribe **Rhinocerotini** Gray, 1821
Subtribe **Rhinocerotina** Gray, 1821

gen. et sp. indet.
Figure 3

Synonym. Rhinocerotidae gen. et sp. indet. Kato 2001: fig. 1.

Material. Left p4 fragment (LBM0142001230), m1 (LBM0142001231) and m2 (LBM0142001232).

Locality and horizon. The lower part of the Tsubusagawa Formation (the Late Pliocene; 3.5–3.4 Ma), Tanokuchi, Ajimu Town, Usa City, Oita Prefecture (Kato 2001).

Description. All teeth belong to the same individual. There is no coronal cement on the teeth. The enamel surface is smooth on all teeth. The p4 fragment (LBM0142001230) is a fragment around trigonid. The trigonid is rounded. The preserved ectolophid groove is deep and continued until the neck. A short mesial cingulum is preserved. There is no buccal cingulum on the preserved part.

The m1 (LBM0142001231) and m2 (LBM0142001232) are moderately worn down. The mesial tip on both teeth and the talonid on m2 are damaged. The tooth roots of the teeth are missing. The buccal wall of both teeth inclines buccally in mesiodistal view. Narrow occlusal facet is on the buccal margin of both teeth. The m1 and m2 are similar morphology as follows: no enamel folding, deep ectolophid groove that continued until the neck, acute trigonid, wide posterior valley, U-shaped posterior valley in occlusal view, not constricted metaconid and entoconid, no buccal and lingual cingula, short mesial cingulum on the mesiobuccal side, faint distal cingulum, oblique hypolophid, absence of the lingual groove on the entoconid, and a facet for the adjacent tooth on the distal surface.

Comparison. In Asia, a species of the subtribe Teleoceratina, *Brachypotherium* has been found during the Miocene (e.g., Heissig 1972; Fukuchi and Kawai 2011). The Ajimu specimen differs from the lower cheek teeth of *Brachypotherium*

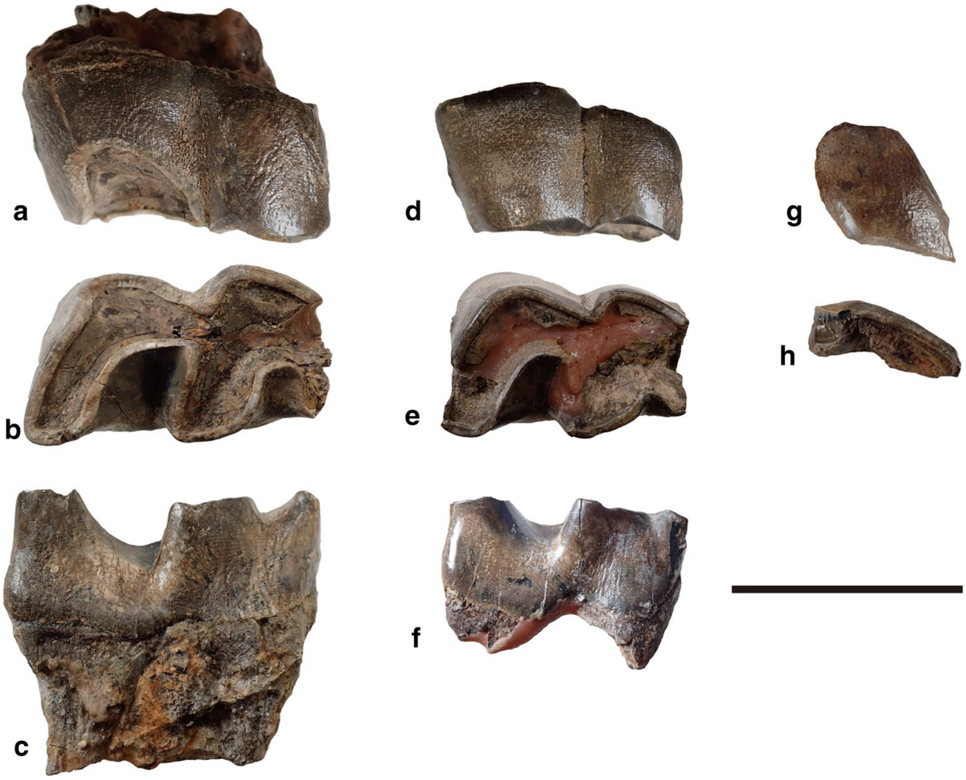

Fig. 3 Rhinocerotina gen. et sp. indet. from the Tsubusagawa Formation in Ajimu, Usa City, Oita prefecture. **a–c** m2 (LBM0142001232); **d–f** m1 (LBM0142001231); **g–h** p4 (LBM0142001230); **a, d, g** buccal view; **b, e, h** occlusal view; **c, f** lingual view. Scale bar equals 5 cm

(Heissig 1972; Cerdeño 1993), in having deep ectolophid groove and acute trigonid.

The Ajimu specimen is also different from the lower cheek teeth of the subtribe Elasmotheriina. The Late Miocene taxa of this subtribe such as *Sinotherium* and *Iranotherium*, and the Pleistocene ones, *Elasmotherium*, show abundant coronal cement, corrugated enamel fold, a constricted entoconid, and high tooth crown (e.g., Ringström 1924; Antoine 2002; Deng 2005; Tong et al. 2014; Schvyreva 2015). These characteristics are not evident in the Ajimu specimen.

The Ajimu specimen differs in the teeth of the most derived species of *Chilotherium*, *C. licenti* from the Late Miocene locality in Gansu in China (Sun et al. 2018), in having a V-shaped posterior valley on the molars and a rounded trigonid on m2.

Concerning the subtribe Rhinocerotina, the cheek teeth of Plio-Pleistocene species of *Coelodonta* is different from the Ajimu specimen. The lower cheek teeth of *Coelodonta* show hypsodont teeth, abundant coronal cement, a constricted entoconid, and rugose enamel surface (Antoine 2002; Qiu et al. 2004). In contrast, the Ajimu specimen is brachydont, no coronal cement is present, no constricted entoconid, and displays smooth enamel surface.

Two rhinocerotid remains have been reported from the early Late Miocene (around 9 Ma) localities in Japan. Yoshida et al. (1989) described a skull fragment and a mandible with teeth from the Upper Miocene Yagii Formation in Kawamoto, Saitama Prefecture. Asano (1996) described an isolated m1 that is derived from the Upper Miocene Aoso Formation in Taiwa, Miyagi Prefecture. Both studies preliminarily identified these remains as “Teleoceratinae” gen. et sp. indet. The Ajimu specimen is similar to both remains in having the following dental characteristics; absence of enamel folding, deep ectolophid groove, acute trigonid, U-shaped posterior valley in occlusal view, no constricted meta- and entoconids, no buccolingual cingula, oblique hypolophid.

The Ajimu specimen is also morphologically similar to the lower molars of compared species of Rhinocerotina (*Diceros gansuensis*, *Stephanorhinus kirchbergensis*, *Stephanorhinus jeanvireti*, “*Stephanorhinus*” *miguelcrusafonti*, *Dihoplus megarhinus*, *Shansirhinus ringstromi*, *Dicerorhinus sumatrensis*, *Rhinoceros fusuiensis*, *Rhinoceros* sp.) and of Aceratheriini (*Acerorhinus yuanmouensis*, *Chilotherium wimani*) in lacking coronal cement and enamel folding, and in having the molars with no coronal cement and enamel folding, deep ectolophid groove, acute trigonid, no buccal and lingual cingula, U-shaped posterior valley in occlusal view, no constricted metaconid and entoconid, oblique hypolophid, and absence of the lingual groove on the entoconid. These morphological similarities between the Ajimu specimen and compared specimens are difficult to explain generic and specific identify for it. Indeed, the morphology of the lower teeth is quite conservative in Late Miocene–Pliocene Rhinocerotina (Pandolfi et al. 2015).

The metrical comparison reveals that the measurements of the Ajimu specimen are similar to those of the Asian species of Rhinocerotina (Table 1). Especially, the dimensions of the Ajimu specimen are included within the range of *R. sinensis* from the Pleistocene locality of Yanjinggou in China. The Ajimu specimen has almost the same size as that of *S. kirchbergensis* from the Pleistocene in China and *Dih. megarhinus* (=*Dih. ringstromi*) from China and western Europe. The dimension of the Japanese rhinocerotid specimen ("Teleoceratinae" gen. et sp. indet.) from Kawamoto is also relatively similar in size with that of the Ajimu specimen. In contrast, the Ajimu specimen is larger than that of other compared Late Miocene species of Aceratheriini from Asia (Table 1).

In sum up, the Ajimu specimen is obviously distinguished from the Teleoceratina (*Brachypotherium*), Elasmotheriini (*Elasmotherium*) and a species of Rhinocerotina, *Coelodonta*. Compared with Late Miocene to Pleistocene Asian rhinocerotid, it is difficult to distinguish the Ajimu specimen with the compared taxa due to the high similarity of the morphological characteristics. Based on the dental dimensions, the size of the Ajimu specimen resembles that of Late Miocene or Pleistocene taxa of Rhinocerotina; whereas, it differs from that of the taxa of Aceratheriini. Therefore, the Ajimu specimen is identified as Rhinocerotina gen. et sp. indet. in this study.

Discussion

Japanese Pliocene rhinocerotid fossils and those ages

An isolated unciform has been found from the Late Pliocene Kanzawa Formation of the Nakatsu Group in Aikawa, Kanagawa Prefecture (Hasegawa et al. 1991). Ueki et al. (2013) investigated tephro- and chronostratigraphy in the Nakatsu Group, resulting in that the ages of the Kanzawa Formation were correlated with Late Pliocene (around 3.2 Ma). This specimen is currently under study by Murakami at Ehime University.

An isolated lunate of rhinocerotid is found from the mid-Pliocene Ueno Formation in the Kobiwako Group in Mie Prefecture (Yamamoto 2006). The lunate has been collected from the siltstone horizon a few under the Hattorigawa I tuff bed in the Ueno Formation (Murakami and Tsubamoto 2018). The Hattorigawa I bed was correlated with the tuff beds in the neighbor regions, suggesting that the age of the Hattorigawa I tuff bed was estimated between 3.6 and 3.5 Ma (Satoguchi 2015). Therefore, the lunate from the Ueno Formation would be in age around 3.6 Ma. Recently, Murakami and Tsubamoto (2018) described this remains as an indeterminate species of Rhinocerotini (sensu Heissig 1999 = Rhinocerotina in Pandolfi 2018) and noted that this lunate resembles those of *S. kirchbergensis*, *S. jeanvireti* or *S. etruscus*. These fossil records and the present study indicate the presence of rhinocerotid, especially subtribe Rhinocerotina, in Japan during the mid- to late Pliocene (Fig. 4).

Besides the teeth remains, a few rhinocerotid footprints have been found from the Tsubusagawa Formation in the riverbed of the Fukami River at Mori area in Ajimu, Oita Prefecture (Okamura 2001). In addition, several rhinocerotid footprints have been found from the Pliocene Harutagawa and Kuroboshi formations in Oita Prefecture, although precise horizon and age span are unknown (Okamura 2001, 2016, 2018).

Beside Oita Prefecture, the Plio-Pleistocene Kobiwako and Tokai groups around Lake Biwa and Ise Bay have yielded abundant footprint fossils (Okamura 2016 and references therein). Several rhinocerotid footprints have also been found from the Saitsu Formation in Amakusa area, Kumamoto Prefecture (Okamura et al. 2017). Hase et al. (2017) investigated the fission-track age of the Goryo pyroclastic flow layer in the Saitsu Formation, suggesting that the age of the layer was estimated as 2.6 ± 0.4 Ma (Late Pliocene to Early Pleistocene). These fossil records indicate the continuous presence of rhinocerotid in Japan, since the Early Pliocene (ca. 4.2 Ma) to the end of the Pliocene (Fig. 4).

The possibility of immigration timing of the Pliocene rhinocerotid of Japan

There are no fossil records of Rhinocerotina from the Miocene in Japan so far (Tomida et al. 2013). In contrast, several remains of Rhinocerotina, such as *S. kirchbergensis*, have been found from the Pleistocene deposits in Japan (e.g., Handa and Pandolfi 2016). In China, the species of Rhinocerotina have been known from the Late Miocene and Pliocene localities such as *Dic. gansuensis* and *Dih. megarhinus* (=*Dih. ringstroemi*) from the Upper Miocene, and species of *Dih. megarhinus* from the Pliocene (e.g., Deng and Downs 2002; Deng and Qiu 2007; Tong 2012; Pandolfi 2018). Therefore, it expects that Rhinocerotina in Asian continent would have migrated in Japan, and might be an ancestor of the Pliocene Japanese Rhinocerotina.

Here, we propose the possibility of two immigration timing of Pliocene rhinocerotid into the proto-Japan. One hypothesis is that the rhinocerotid immigration into Japan

Table 1 Tooth measurements (in mm) of Rhinocerotina gen. et sp. indet. from the Tsubusagawa Formation in Ajimu, Usa City, Oita Prefecture with compared specimens

	Species	m1				m2				References	Remarks
		L	Wa	Wp	H	L	Wa	Wp	H		
Rhinocerotina	Rhinocerotina gen. et sp. indet.	54.06	34.16	39.14	32.37	57.66	35.75	37.97	31.23	Present study	Ajimu, Oita, Japan
	Stephanorhinus kirchbergensis	42.3	31.1	33.8	> 28.2	51.9	32.5	34.7	> 29.4	Chen et al. (2012)	Three Gorges, China
	Stephanorhinus kirchbergensis	41.8–47.9	33.1–37			51.8–56.5	34.6–36.3			Chen et al. (2012)	Rhinoceros Cave, China
	Stephanorhinus kirchbergensis	40–51.1	29–37.1			38–54.7	29–36.3			Chen et al. (2012)	Northern China
	Stephanorhinus kirchbergensis	43–43.3	31.5–31.9			48–48.7	30.9–31.8			Tong et al. (2014)	Nihewan Basin, China
	Stephanorhinus kirchbergensis	40–45	29–33			38–53	29–34			Tong et al. (2014)	Choukoutien Loc. 1, China
	Stephanorhinus kirchbergensis	42	32			43	31			Tong et al. (2014)	Choukoutien Loc. 9, China
	Stephanorhinus jeanvireti	40–47	25–33			43–53.5	27–34.5			Guérin (1972)	Vialette, France
	Stephanorhinus jeanvireti	40–47	25–32			47.5–53.5	29–34.5			Guérin (1980)	Western Europe
	“*Stephanorhinus*” *miguelcrusafonti*	41	33.5			47.5	32.5			Guérin and Santafé-Llopis (1978)	Layna, Spain
	Shansirhinus ringstromi	42.5	29.5			41.5	27			Deng (2005)	Yinchuan, Linxia, China
	Rhinoceros fusuiensis	40–46.6	22.1–28.0			37.1–48.9	24.5–26.9			Yan et al. (2014)	Yanliang Cave, Fusui, China
	Rhinoceros sinensis	36.5–52.3	26–31.8			43–51.5	25.8–35.5			Yan et al. (2014)	Longgudong, China
	Rhinoceros sinensis	48–55	31–36			49–61	29–37			Colbert and Hooijer (1953)	Yanjinggou, China
	Rhinoceros sondaicus	40–43	26–31			42–48	26–31			Colbert and Hooijer (1953)	
	Rhinoceros unicornis	36–51	26–31			47–56	27–30			Colbert and Hooijer (1953)	
	Rhinoceros sp.	39.5	*29			45.2	36.2			Zin-Maung Maung-Thein et al. (2010)	Chaingzauk, Myanmar
	Dicerorhinus gwebinensis					*40	*28			Zin-Maung Maung-Thein et al. (2010)	Gwebin, Myanmar
	Dicerorhinus sumatrensis	35.7	25.5			36.9	24.9			GMNH-VM-562 (cast)	Living specimen
	Dicerorhinus sumatrensis	34.6–45	22.7–31.1			41.4–52.7	25.4–34.2			Tong and Guérin (2009)	Liucheng, Guangxi, China
	Dicerorhinus cf. *sumatrensis*					46.3	30.1			Zin-Maung Maung-Thein et al. (2010)	Sulegone, Myanmar
	Dihoplus megarhinus	45–53	28.5–34			47–57	31–37.5			Guérin (1980)	Western Europe
	Dihoplus megarhinus	53	34		32.5					Deng and Wang (2004)	Qaidam Basin, China (IVPP-V13798)
	Dihoplus megarhinus	51	–			53	36			Deng and Wang (2004)	Qaidam Basin, China (IVPP-V13799)
	Diceros gansuensis	54.2	38.5		43.7	60.4	39		50.5	Deng and Qiu (2007)	Linxia basin, Gansu, China (HMV 1421)
	Diceros gansuensis	42	39.6		16.2	52	41.6		23	Deng and Qiu (2007)	Linxia basin, Gansu, China (HMV 1422)
	Diceros gansuensis	53	39		42	59.5	40		40	Deng and Qiu (2007)	Linxia basin, Gansu, China (HMV 1428)

Table 1 (continued)

	Species	m1				m2				References	Remarks
		L	Wa	Wp	H	L	Wa	Wp	H		
Aceratheriini	*Acerorhinus yuanmouensis*	40	30			42	30			Lu et al. (2014)	Yuanmou Basin, Yunnan, China
	Aceratherium incisivum	41	28			45	29			Lu et al. (2014)	
	Chilotherium anderssoni	32.5	25.5			43.1	30			Ringström (1924)	
	Chilotherium wimani	38.3–43	24–31		14–23	42–49.5	26.5–30.3		21–33	Deng (2001)	Fugu, Shaanxi, China
	Chilotherium licenti	33.5	26.3			36.6	26.9			Sun et al. (2018)	Qingyang, Gansu, China
Uncertain	”Teleoceratinae” gen. et sp. indet.	48.3	29.3	23.9	23.8					Yoshida et al. (1989)	Kawamoto, Saitama, Japan
	”Teleoceratinae” gen. et sp. indet.	51.2	33.42	32.65						Asano (1996)	Taiwa, Miyagi, Japan

Asterisk mark indicates estimated size

would have occurred in the Early Pliocene. The proto-Japan island connected the Asian continent from 5 to 3.5 Ma, and there was a land bridge between the Korean Peninsula and southeast Japan (Kitamura and Kimoto 2006; Takahashi and Izuho 2012). Takahashi (2001) and Takahashi and Izuho (2012) noted that the Ajimu fauna includes sub-tropical elements in South Asian or Southeastern Asia such as the salamander, crocodiles, turtles, cervid and rhinocerotid. Therefore, the southern Chinese or southeastern Asian faunas in those habitats immigrated to Japan, and later, that fauna would be the Ajimu fauna (Takahashi 2001; Takahashi and Izuho 2012). In contrast, Kato and Kitabayashi (2018) described two rodents from the Tsubusagawa Formation, namely *Micromys* sp. and Arvicolinae gen. et sp. indet. Those are historically a Palearctic distribution. A Japanese Pliocene proboscidean, *Stegodon miensis* has been found from the Tsubusagawa Formation (Takahashi 2018). The ancestor of this species would be migrated from North China during the Early Pliocene (Takahashi and Namatsu 2000; Saegusa et al. 2005; Taruno 2010). It is unclear that which areas (North China, South China or Southeastern Asia) are plausible as the origin for the ancestor of the Japanese Pliocene rhinocerotid because of the insufficiency of the specimens. Nevertheless, the Pliocene rhinocerotid would have immigrated into Japan the same timing with other vertebrates mentioned above.

Another hypothesis is that ancestral stock of Japanese Pliocene rhinocerotid migrated from China during the late Miocene, although there are no Japanese fossil records in this period. The proto-Japan was archipelago and separated by the seaway from the Asian continent during the late Early to late Middle Miocene (e.g., Noda and Goto 2004). Later, during the early Late Miocene (ca. 10 Ma), the proto-Japan was reconnected Asian continent (Tada 1994; Noda and Goto 2004; Matsuzaki et al. 2018 and references therein). In the early Late Miocene, species of Rhinocerotina, *Dic. gansuensis* and *Dih. megarhinus* presented in China (Deng and Qiu 2007; Tong 2012). Thus, the close relatives of these taxa might be immigrated in Japan at this timing, although Chinese Late Miocene ones have much smaller teeth size than the Ajimu specimen. Iijima et al. (2016) also noted that the ancestor of *Alligator sinensis* found from Ajimu would have migrated from Asia at around 10 Ma as one possibility. If so, that opinion confirms the present hypothesis.

Unfortunately, the detailed relationship between the Mio-Pliocene Asian rhinoceroses and Japanese ones could not be discussed due to few fossil records from Japan. Further materials of Miocene to Pliocene rhinocerotids in Japan and detailed comparison with Asian ones are needed to discuss the subject.

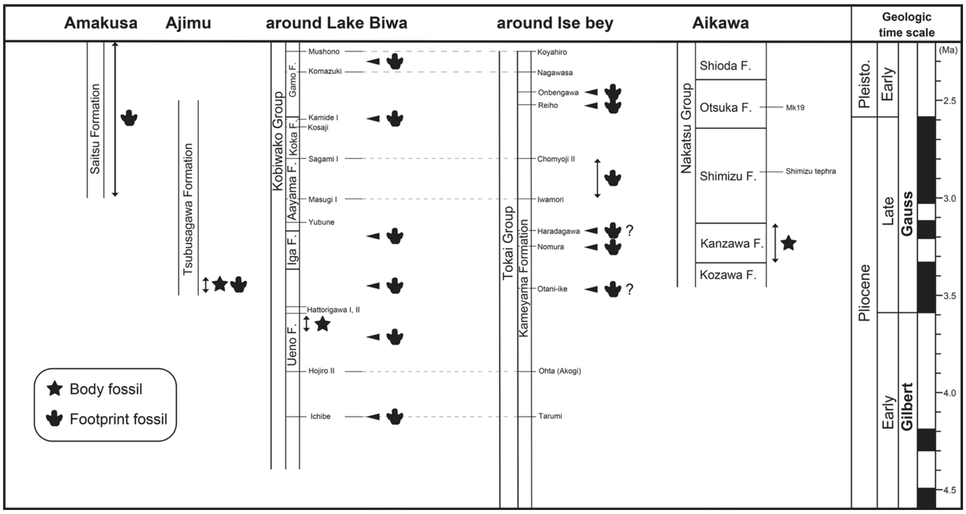

Fig. 4 Chronostratigraphic range of the Pliocene to earliest Pleistocene rhinocerotid from Japan (including footprints) (modified after Satoguchi 2017). The geological data are as follows: Hasegawa et al. (1991) and Ueki et al. (2013) for Aikawa; Kato (2001), Okamura (2001) and Satoguchi (2016) for Ajimu; Murakami and Tsubamoto (2018) and Okamura (2016) for around Lake Biwa; Okamura (2016) for around Ise Bay; Hase et al. (2017) and Okamura et al. (2017) for Amakusa

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