Paleontological Research

Palaeontological Society of Japan

日本古生物学会

Papers in Press

Humblet, M. and Iryu, Y. 2014: Pleistocene coral assemblages on Irabu-jima, South Ryukyu Islands, Japan. *Paleontological Research*, doi: 10.2517/2014PR020.

doi:10.2517/2018PR009

Reassessment of a Pleistocene rhinocerotid (Mammalia, Perissodactyla) from Aira, Kagoshima, southwestern Japan

Naoto Handa

Museum of Osaka University, 1-20 Machikaneyama-cho, Toyonaka, Osaka 560-0043, Japan. e-mail: k1552325@kadai.jp

Abstract. This study describes right upper postcanaine teeth of a single individual of Pleistocene rhinocerotid (Mammalia, Perissodactyla) from the lower to lower middle Pleistocene Kamo Formation of the Kokubu Group in Aira City, Kagoshima Prefecture, southwestern Japan. These teeth are heavily worn and are identified as P2–M2 with missing M1. They are identified as an indeterminate genus and species of the Rhinocerotidae, although they were previously named as *Rhinoceros* aff. *sinensis*. These dental fossil specimens and the rhinocerotid footprints from the lower to lower middle Pleistocene of Japan indicate that

rhinocerotid certainly existed in Japan during the early to early middle Pleistocene.

Key words: Japan, Pleistocene, Quaternary, Rhinocerotidae, tooth

Introduction

The Pleistocene deposits in Japan yields many fossils of large terrestrial mammals. For example, abundant proboscidean fossils were discovered in the Pleistocene of Japan, and their paleobiogeography and migration timing between Japan and the Asian Continent have been discussed in several contributions (e.g. Kawamura, 1998; Konishi and Yoshikawa, 1999; Takahashi and Namatsu, 2000; Yoshikawa *et al*., 2007), although the proboscidean do not inhabit in Japan now. Similarly, although rhinocerotids do not in habit in Japan now, their fossils have been found in the Miocene to Pleistocene of Japan (Tomida *et al*., 2013; Nakagawa *et al*., 2013). The Pleistocene fossil records of the rhinocerotids in Japan are fewer than those of the proboscideans. Most rhinocerotid fossils from the Pleistocene in Japan are known from the middle middle Pleistocene (ca. 0.5−0.4 Ma) (e.g., Handa and Pandolfi, 2016 and references therein). In contrast, early to early middle Pleistocene rhinocerotid remains from Japan are scarce.

The Pleistocene rhinocerotid specimens from Japan have been previously considered to belong to *Dicerorhinus*, *Rhinoceros* or indeterminate species (e.g. Shikama, 1967; Shikama *et al*., 1967; Kawamura *et al*., 1977; Taruno, 1988, 2000; Okazaki, 2007; Ogino *et al*., 2009). In the last decade, however, taxonomic revisions of the Pleistocene rhinoceroses of northern Eurasia and China have been conducted by many scholars (e.g. Groves, 1983; Fortelius *et al*., 1993; Cerdeño, 1995; Lacombat, 2005; Tong and Wu, 2010; Antoine, 2012; Tong, 2012; Yan *et al*., 2014; Pandolfi and Marra, 2015). Also, a few Japanese specimens have been taxonomically reappraised recently (Handa, 2015; Handa and Pandolfi, 2016; Handa and Takechi, 2017).

In the present work, I reappraise and describe upper postcanine teeth of a single individual of a rhinocerotid collected from the uppermost to lower middle Pleistocene locality in Aira City, Kagoshima, Japan. These specimens were originally named as *Rhinoceros* aff. *sinensis* based on the brief comparison with Chinese Pleistocene rhinocerotids by Shikama (1967). However, they have not been reappraised after the recent taxonomic revisions of the Pleistocene Eurasian taxa of the Rhinocerotidae.

Material and methods

The specimens described here were discovered in Aira City, Kagoshima Prefecture, southwestern Japan (Figure 1) and stored in Kagoshima Prefectural Museum, Kagoshima City. The taxonomy of the suprageneric classification of the family Rhinocerotidae used in this study follows Antoine *et al*. (2010). The dental terminology (Figure 2) follows Guérin (1980), Fukuchi (2003) and Antoine *et al*. (2010). Metrical methodology uses the standard measurement method by Guérin (1980).

In this study, the present specimen are compared with Pleistocene Asian taxa of the Rhinocerotidae, that is, the subtribe Rhinocerotina (= the tribe Rhinocerotini in Heissig, 1973) and subtribe Elasmotheriina (= the tribe Elasmotheriini in Heissig, 1973) from Asia such as *Dicerorhinus, Rhinoceros, Dihoplus, Stephanorhinus*, *Coelodonta*, and *Elasmotherium*. Note that several extinct species of *Dicerorhinus* have been treated as *Stephanorhinus* or *Dihoplus* by several researchers (e.g. Tong and Wu, 2010; Tong, 2012; Handa and Pandolfi, 2016). This study follows those opinions.

The taxonomic status of *Rhinoceros* from Asia is still debatable. Two extinct species of *Rhinoceros* have been reported from Asia such as *Rhinoceros sinensis* and *R.*

sivalensis. Antoine (2012) noted that these extinct species are treated as synonyms for *R. unicornis*. He also noted that other extinct species of *Rhinoceros* (*R. oweni*, *R. plicidens*, *R. simplicidens*, *R. chiai*, *R. palaeindicus*, *R. deccanensis*, *R. sinhaleyus*, *R. kagavena*) are also synonyms for *R. unicornis*. Tong (2012) assigned several materials of *R. sinensis* to two species of *Stephanorhinus*. On the contrary, Yan *et al*. (2014) established *R. sinensis* and *R. sivalensis* as well as a new species of *Rhinoceros*, *R. fusuiensis*. Pandolfi and Maiorino (2016) also reported *R. sinensis* and *R. sivalensis* as valid species considering type and selected materials. Additionally, they redescribed a well-preserved skull from the Upper Siwalik in India as *Rhinoceros platyrhinus*. In this study, these species of *Rhinoceros* (*R. unicornis, R. sivalensis, R. sinensis, R. fusuiensis* and *R. platyrhinus*) are treated as distinctive taxa for comparison.

Abbreviations.—P, upper premolar; M, upper molar; GMNH, Gunma Museum of Natural History, Gunma Prefecture, Japan; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; KPM, Kanagawa Prefectural Museum of Natural History, Odawara, Japan; NMMP, National Museum of Myanmar (Yangon, Myanmar), Paleontology; NMNS, National Museum of Nature and Science, Tsukuba, Japan; MIS, Marine isotope stages.

Systematic paleontology

Family Rhinocerotidae Gray, 1821

gen. et sp. indet.

Figure 3

Rhinoceros aff. *sinensis* Owen, 1870. Shikama, 1967, pl. 4 (1), figs. 1−4.

Material.—Specimen number F00000554, right P3−M2 (M1 is missing now), which belong to the same single individual. These teeth were originally described as right P2 to M1 by Shikama (1967). Generally, P2 of the rhinocerotids has a trapezoidal shape in occlusal view and is smaller than that of P3 (Guérin, 1980). However, "P2" described by Shikama (1967) has relatively rectangle shaped outline (Figure 3) and its size is similar to that of the "P3" described by Shikama (1967) (Table 1). Therefore, the tooth formula of "P2 to M1" described by Shikama (1967) is revised to P3 to M2 in this study. Originally, M1 ("P4" in Shikama, 1967) was collected together with other teeth at that time, but it is currently lost.

Dental measurements.—Shown in Table 1.

Locality and horizon.—Around Nishihinabe area in Kajiki town, Aira City, Kagoshima Prefecture, southwestern Japan (Figure 1); the Kamo Formation of the Kokubu Group (Figure 5); possibly latest early to early middle Peistocene (> 0.5 Ma), as explained below.

According to Shikama (1967), the present teeth (F00000554) were collected from the lower Pleistocene “Yoshida clay bed” in Aira City. Later, Otsuka and Nishiinoue (1980) reinvestigated the detail fossil locality based on the lithology of the matrix of the studied specimen and pollen fossil assemblage in the matrix, suggesting that the specimens would be derived from the Kamo Formation of the Kokubu Group around Nishihinabe area in Kajiki town, Aira City.

The Kokubu Group is the lower to middle Pleistocene deposits (ca. 1 Ma to 0.5 Ma) which distributed in the northern part of Kagoshima Prefecture (Uchimura *et al*., 2014). The Kokubu Group is subdivided into Kajiki, Nabekura, Kamo, Obama, Asahi, Oda, Hayato, and Fumoto formations in ascending order (Kagawa and Otsuka, 2000). Whole-rock K–Ar dating provided ages of 0.87±0.50 Ma for the Yuwandake andesite which intrudes into the Nabekura Formation (Kagawa and Otsuka, 2000; Uchimura *et al*., 2014). The age of the Kobayashi pyroclastic flow deposits overlying the Kokubu Group is estimated to be ca. 0.52 Ma (Uchimura *et al*., 2014). The Kuwanomaru pyroclastic flow deposit in the Kamo Formation is correlated with the Shimokado pyroclastic flow deposits (0.57±0.03 Ma) in the northwestern part of Kagoshima Prefecture (Uchimura *et al*., 2014 and reference therein). In conclusion, the age of the Kamo Formation is probably the latest early to early middle Pleistocene (> 0.5 Ma).

Description.—The teeth are heavily worn down and their occlusal surfaces are almost flat in mesio-distal view. M2 is almost broken except around medisinus. The medisinus of the all teeth are deeper than the postfossette. The all teeth have no dental cement. M1 would be lost as mentioned above, thus the morphological characteristics of M1 are based on the description and figures by Shikama (1967) (Figure 3c).

P3 is relatively well preserved but heavily worn. It is wider than long. The marginal profile of the ectoloph is unclear because this portion is covered with plaster. Based on the figure of Shikama (1967), no trace of the paracone fold and the parastyle can be observed (Figure 3c). The protoloph and metaloph are connected each other at this stage of wear. Thus, the medisinus is closed and is sub-triangular in occlusal view. The postfossette is not preserved at this wear stage. The presence of the crochet and crista is uncertain. There are no buccal and lingual cingula. The trace of the anterior cingulum is located on the mesio-lingual corner of the protocone. The posterior cingulum is not preserved. The preserved enamel surface is smooth.

P4 is relatively well preserved as in P3. The buccal and disto-buccal corners are covered with plaster. At the stage of wear, the morphology of the tooth is similar to that of P3, namely, a connection of the protoloph with the metaloph, absence of the cingula, a closed mediofossette, and a smooth enamel surface. The mediofossette is narrow. The posterior fossette is oval. The presence of the paracone fold and parastyle cannot be observed due to the heavy wear.

Based on the description and figures by Shikama (1967), the buccal side of M1 (“P4” in Shikama, 1967) is broken (Figure 3c). The mediofossette is narrow and oval-shaped and is relatively larger than that of P4. A small postfossette is preserved. It is uncertain whether the lingual cingulum is present or not.

M2 consists only of a small portion of the tooth. The middle part of the tooth is covered by plaster. The medisinus is narrow and mesially curved. The protoloph and metaloph are not connected with each other. Secondary folds such as crochet, antecrochet, and crista are not visible at this stage of wear. The oval-shaped postfossette is preserved and located posterior to the medisinus.

Comparisons

The present specimens are lophodont cheek teeth which composed of the protoloph, metaloph, and ectoloph. These morphologies are typical characteristics of family rhinocerotids (Heissig, 1999). In Eurasia, five tribes of the Rhinocerotidae (Aceratheriini, Teleoceratini, Elasmotheriini, Rhinocerotini, and Dicerotini: *sense* Heissig, 1973) were distributed during the Miocene to early Pliocene. After the late Pliocene, however, only two subtribes of the Rhinocerotini survived in Eurasia (e.g. Heissig, 1989), namely Rhinocerotina (*Rhinoceros*, *Dicerorhinus*, *Stephanorhinus*, *Dihoplus*, and *Coelodonta*) and Elasmotheriina (*Elasmotherium*) (e.g. Guérin, 1980; Lacombat, 2005; Zin-Maung-Maung-Thein *et al*., 2008, 2010; Tong and Moigne, 2000; Tong, 2012; Yan *et al*., 2014; Pandolfi and Maiorino, 2016).

The specimen described here is distinguished from *Coelodonta* and *Elasmotherium*. The upper cheek teeth of *Coelodonta* have the following dental features, which the present specimen lacks: a rugose enamel surface, upper molars longer than wide, and distally elongated proto- and metalophs (Qiu *et al*., 2004; Tong and Wang, 2014). The upper cheek teeth of *Elasmotherium* also differ from the present specimen in having a corrugated enamel layer (e.g., Antoine, 2002; Schvyreva, 2015).

The developments of the secondary fold (including crochet, crista and antecrochet) and ectoloph profile in the Rhinocerotidae are often used for taxonomic identification in the family (Guérin, 1980; Zin-Maung-Maung-Thein *et al*., 2010; Yan *et al*., 2014;

Handa and Pandolfi, 2016). Shikama (1967) noted that several molars of *Rhinoceros sinensis* described by Colbert and Hooijer (1953) have an obsolete crochet and that this character is similar to the Aira specimens. However, the present specimens are heavily worn, so that the development of the secondary fold of the present specimens cannot be evaluated for comparison.

Shikama (1967) noted that the “P3” (= P4 in the present study) length is similar in size to that of *Rhinoceros sinensis* from the “*Stegodon* bed” at Szechwan in China (P3 length is 32–42 mm: Colbert and Hooijer, 1953). Compared with the several species of the Rhinocerotidae from Asia, the P3 and P4 dimensions of the present specimens are much smaller than those of *Stephanorhinus* and *Dihoplus* from Asia (Table 1). *Rhinoceros platyrhinus* from the Upper Siwalik of India is also distinguished from the present specimens in having its larger dental dimensions (Table 1). The dimensions of the present specimens resemble to the minimum size of the range of teeth of *R. sinensis* from Longgudong in China, and the teeth of *D. sumatrensis* of the GMNH specimen (living individual, cast specimen) (Table 1). Based on the dental size similarity, therefore, the present specimens are comparable to *R. sinensis* or *D. sumatrensis*. However, the dental features that can be observed in the present specimens do not display any tribal diagnosis. Additionally, the present specimens are heavily worn, so that the dental size can be also influenced by the wear. Therefore, the tribal or more precise taxonomic identification of the present specimens is impossible.

Discussion

Among the Plio-Pleistocene rhinocerotid fossils from Japan, most of them were from the middle middle Pleistocene (ca. 0.5–0.4 Ma) (e.g., Handa and Pandolfi, 2016 and references therein). The Japanese rhinocerotid records in the Pliocene and lower to lower middle Pleistocene are scarce.

Only three rhinocerotid fossil records have so far been found in Japan, and all of them from the mid-Pliocene (around 3.6 to 3.5 Ma) localities in Japan (e.g. Nakagawa *et al*., 2013). A uniciform were found from the Kanzawa Formation in Kanagawa Prefecture (Hasegawa *et al*., 1991). Isolated lower cheek teeth were described from the Tsubusagawa Formation in Oita Prefecture (Kato, 2001). A lunar was reported from the Ueno Formation of the Kobiwako Group in Mie Prefecture (Yamamoto, 2006).

Although there is no dental or skeletal fossil (body fossil) from the lower Pleistocene in Japan so far except for the present dental specimen (from the lower or lower middle Pleistocene), a number of rhinocerotid footprints (trace fossil) were documented from the lower Pleistocene of Japan (Okamura *et al*., 2011, 2016; Okamura, 2016: Figure 5). The Gamo and Kusatsu formations of the Kobiwako Group around Lake Biwa, central Japan have yielded chronologically continuous rhinocerotid footprints (Okamura *et al*., 2011, 2016; Okamura, 2016). Several rhinocerotid footprints have also been known from the Kameyama Formation of the Tokai Group in Suzuka City, Mie Prefecture, central Japan (Okamura, 2016 and their reference therein). Additionally, a rhinocerotid footprint has also been known from the upper Pliocene to lower Pleistocene Gunchu Formation (Ikeda *et al*., 2017) in Iyo City, Ehime Prefecture, although its detailed footprint fossil bearing horizon is uncertain (Okamura, 2016).

The age of the present specimens is the early Pleistocene to early middle Pleistocene, so that the present specimens fill the gap of the Japanese record of rhinocerotid dental/skeletal fossils between the mid-Pliocene and the middle middle Pleistocene (Figure 4). Furthermore, rhinocerotid footprints were discovered in the early middle Pleistocene (ca. 0.55 Ma) of the Katada Formation of the Kobiwako Group in Otsu City, Shiga Prefecture, central Japan by Okamura (2011) (Figures 1, 4). The presence of the present dental specimens in Aira with the presences of rhinocerotid footprints in the lower to lower middle Pleistocene in Japan indicates that the rhinocerotids had certainly existed in central/western Japan through the mid-Pliocene to middle

Pleistocene (Figures 1, 4, 5).

Several taxa of the Pleistocene terrestrial mammalian fauna in Japan are considered to have migrated from the Asian Continent into Japan through land bridges between them. Twice migration timings of the terrestrial mammal fauna into Japan have been estimated based on the fossil occurrences of the two proboscidean species between Japan and China (Kawamura, 1998; Konishi and Yoshikawa, 1999; Yoshikawa *et al*., 2007). The timing of first migration is around 0.63 Ma (MIS 16), with *Stegodon orientalis* and other several taxa of the southern Chinese fauna. The timing of second migration is around 0.43 Ma (MIS 12), with *Palaeoloxodon naumanni* and some other taxa of the northern Chinese fauna (Figure 4). Handa and Pandolfi (2016) have noted that *Stephanorhinus kirchbergensis* from the middle Pleistocene in Isa, Yamaguchi Prefecture, western Japan (Figure 1), likely have migrated during the second migration timing based on the composition of the Isa mammal fauna. Furthermore, the Matsugae mammalian fauna (including the Rhinocerotidae) from Matsugae in Fukuoka Prefecture, western Japan (Figure 1), was correlated with the Quaternary Mammal Zones 4 (QM4: middle middle Pleistocene) of Japanese Islands (Figure 4: Kamei *et al*., 1988), and was also considered to be the migrant of second migration timing based on the similarity with the Northern Chinese Locality 1 of the Choukoutien fauna (Ogino *et* *al*., 2009) (Figure 4). However, the relationship between the first migration event (ca. 0.63 Ma) and the Japanese Pliocene to early middle Pleistocene rhinocerotids is still unclear due to the scarcity of the fossil records.

Acknowledgements

The author would like to thank Takushima, T. (Kagoshima Prefectural Museum, Kagoshima, Japan) for research permission. The author also thanks to Deng, T., Sun, D.-H., and Jiangzuo, Q. (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China) for providing access to specimens for the comparative works. The author wish to thanks Shigeta, Y. (Editor in Chief), Tsubamoto, T. (associated editor), Tong, H.-W. (a reviewer), and an anonymous reviewer, whose comment and suggestions improved the original manuscript. This study was supported in part by grants from the Fujiwara Natural History Foundation (award in 2016).

References

Antoine, P.-O., 2002: Phylogénie et évolution des Elasmotheriina (Mammalia, Rhinocerotidae). *Memoire du Muséum National d'Histoire Naturelle*, vol. 188, 1–359.

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

Antoine, P.-O., Downing, K. F., Crochet, J.-Y., Duranthon, F., Flynn, L. J., Marivaux, L., Métais, G., Rajapar, A. R. and Roohi, G., 2010 : A revision of *Aceratherium blanfordi* Lydekker, 1884 (Mammalia: Rhinocerotidae) from the Early Miocene of Pakistan: postcranials as a key. *Zoological Journal of the Linnean Society*, vol. 160, p. 139–194.

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

Colbert, E. H. and Hooijer, D. A., 1953: Pleistocene mammals from the limestone fissures of Szechwan, China. *Bulletin of the American Museum of Natural History*, vol. 102, p. 7–134.

Deng, T., 2002: The earliest known wooly rhino discovered in the Linxia basin, Gansu Province, China. *Geological Bulletin of China*, vol. 21, p. 604–608. (*in Chinese with English abstract*)

Deng, T., 2006: Neogene rhinoceroses of the Linxia Basin (Gansu, China). *Courier Forschungsinstitut Senckenberg*, vol. 256, p. 43–56.

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

Fukuchi, A., 2003: A note on dental nomenclature in the Rhinocerotidae. *Okayama University Earth Science Report*, vol. 10, p. 33–37 (*in Japanese*).

Garutt, N.V., 1994: Dental ontogeny of the wooly rhinoceros *Coelodonta antiquitatis* (Blumenbach, 1799). *Cranium*, vol. 11, p. 37–48.

Gray, J. E., 1821: On the natural arrangement of vertebrate animals. *London Medical Repository*, vol. 15, p. 296–310.

Groves, C. P., 1983: Phylogeny of the living species of rhinoceros. *Journal of Zoological Systematics and Evolutionary Research*, vol. 21, p. 293–313.

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

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

Handa, N. and Pandolfi, L., 2016: Reassessment of the Middle Pleistocene Japanese rhinoceroses (Mammalia, Rhinocerotidae) and paleobiogeographic implications. *Paleontological Research*, vol. 20, p. 247–260.

Handa N. and Takechi, Y., 2017: A Pleistocene rhinocerotid (Mammalia, Perissodactyla) from the Bisan-Seto area, western Japan. *Journal of the Geological Society of Japan*, vol. 123, p. 433–441.

Hasegawa, Y., Koizumi, A., Matsushima, Y., Imanaga, I. and Hirata, D. 1991: Fossil remains from the Nakatsu Group. *Research Report of the Kanagawa Prefectural Museum Natural History*, no. 6, 1–98. (*in Japanese*)

Heissig, K., 1973: Die Unterfamilien und Tribus der rezenten und fossilen Rhinocerotidae (Mammalia). *Säugetierkundliche Mitteilungen*, vol. 21, p. 25–30. (*in German*)

Heissig, K., 1989: The Rhinocerotidae. *In*, Prothero, D. R., Schoch, R. M. eds., *The evolution of Perissodactyls*, p. 399–417. Oxford University Press, New York.

Heissig, K., 1999: Family Rhinocerotidae. *In*, Rössner, G. E., Heissig, K. eds., The Miocene Mammals of Europe. P. 175–188. Verlag Dr. Friedrich Pfeil, München.

Ikeda, M., Goto, H., Tsutsumi, H., 2017: Tectonic landform and geology of the Median

Tectonic Line Fault Zone in western Shikoku, southwest Japan. *Journal of the Geological Society of Japan*, vol. 123, p. 445–470. (*in Japanese with English abstract*)

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

Kagawa, A., Otsuka, H., 2000: Stratigraphic sequence and volcano-tectonic event deposits of the middle Pleistocene Kokubu Group on the coastal area of the north Kagoshima Bay, South Kyusyu, Japan. *Journal of the Geological Society of Japan*, vol. 106, p. 762–782 (*in Japanese with English abstract*).

Kato, T., 2001: Discovery of the Pliocene Rhinocerotidae (Perissodactyla) from the Tsubusagawa Formation, Oita Prefecture. *Research Report of the Lake Biwa Museum*, no. 18, p. 164−168. (*in Japanese with English abstract*)

Kawamura, Y., 1998: Immigration of Mammals into the Japanese Islands during the Quaternary. *The Quaternary Research (Daiyonki-Kenkyu)*, vol. 37, p. 251–157. (*in Japanese with English abstract*)

Kawamura, Y., Ogawa, N. and Inoue, Y., 1977 : The occurrence of a rhinocerotid fossil from Tsukumi, Oita Prefecture. *Journal of the Geological Society of Japan*, vol. 83,

p. 59–61. (*in Japanese with English abstract*)

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

Lacombat, F., 2005: Les Rhinocéros fossiles des sites prehistoriques de l'Europe Mediterranéenne et du Massif Central—Paléontologie et implications biochronologiques. *British Archaeological Reports*, no. 1419, p. 1–175.

Nagasawa, J., 1961: A fossil rhinoceros from Kuzuu, Tochigi Prefecture, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan*, *New Series*, vol. 42, p. 63–67.

Nakagawa, R., Kawamura, Y. and Taruno, H., 2013: Pliocene Land mammals of Japan. *In*, Wang, X., Flynn, L. and Fortelius, M. *eds*., *Fossil Mammals of Asia, Neogene Biostratigraphy and Chronology*, p. 334–350. Columbia University Press, New York.

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

Okamura, Y. 2016: The Cenozoic fossil footprints in Japan. *Research Report of the*

Lake Biwa Museum, no. 29, p. 1–111. (*in Japanese*)

Okamura, Y., Takahashi, K., Satoguchi, Y., Ishida, S., Hattori, N., Hirao, F. and Mitsuya, N., 2011: The first discovery of rhinocerotid footprint fossils from the Plio-Pleistocene Kobiwako Group, central Japan. *Journal of Fossil Research*, vol. 44, p. 11–19. (*in Japanese with English abstract*)

Okamura, Y., Takahashi, K. and Satoguchi, Y., 2016: Newly discovered rhinocerotid fossil footprints from the Plio-Pleistocene Kobiwako Group. *Journal of Fossil Research*, vol. 48, p. 26–38. (*in Japanese with English abstract*)

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

Otsuka, H. and Nishiinoue, T., 1980: Quaternary geology of the coastal area of Kagoshima Bay, south Kyushu, *Japan. Reports of the Faculty of Science, Kagoshima University (Earth Science, Biology)*, vol. 13, p. 35–76. (*in Japanese with English abstract*)

Owen, R., 1870: On the fossil remains of mammals found in China. *Quaternary*

Journal of the Geological Society of London, vol. 26, 417–434.

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

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

Qiu, Z.-X., Deng, T. and Wang, B.-Y., 2004: Early Pleistocene mammalian fauna from Longdan, Dongxiang, Gansu, China. *Palaeontologia Sinica, New Series C.*, vol. 27, p. 1–198. (*in Chinese, 1–156, in English, 157–198*)

Satoguchi, Y. 2017: Consideration of paleo-water system changes based on geological history around paleo-lake Biwa basin, central Japan. *Journal of Fossil Research*, vol. 50, p. 60–70. (*in Japanese with English abstract*)

Schvyreva, A. K., 2015: On the importance of the representatives of the genus *Elasmotherium* (Rhinocerotidae, Mammalia) in the biochronology of the Pleistocene of Eastern Europe. *Quaternary International*, vol. 379, p. 128−134.

Shackleton, N. J., 1995: New data on the evolution of Pliocene climatic variability. *In*, Vrba, E. S., Denton, D. H., Partridge, T. C. and Burkle, L. H. *eds*., *Paleoclimate and Evolution with Emphasis on Human Origins*, p. 242−248. Yale University, New Haven.

Shikama, T., 1949: The Kuzuü ossuaries. *The science reports of the Tohoku University, 2 (Geology)*, vol. 23, p. 1−209.

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

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

Takahashi, K. and Namatsu, K., 2000: Origin of the Japanese Proboscidea in the Plio-Pleistocene. *Earth Science (Chikyu Kagaku)*, vol. 54, p. 257−267.

Taruno, H., 1988. Vertebrate fossils from the Bisan Seto, part 1, Proboscidea etc. *In*, Kurashiki Museum of Natural History. *ed*., *Vertebrate Fossils from the Sea Bottom of Bisan-Seto, West Japan. Report of Researches on the Yamamoto Collection I*, p. 11–61. Kurashiki Museum of Natural History, Kurashiki. (*in Japanese*)

Taruno, H., 2000: Proboscidea etc. *In*, Kurashiki Museum of Natural History. *ed.*, *Vertebrate Fossils from Bisan-Seto Sea, preserved in the Kurashiki Museum of Natural History –Research report of Yamamoto Collection (Part II) –. Catalogue of the Materials in the Kurashiki Museum of Natural History No. 9*, p. 1–31. Kurashiki Museum of Natural History, Kurashiki.

Tomida, Y., Nakaya, H., Saegusa, H., Miyata, K. and Fukuchi, A. 2013: Miocene land mammals and stratigraphy of Japan. *In*, Wang, X., Flynn, L., and Fortelius M. *eds.*, *Fossil Mammals of Asia, Neogene Biostratigraphy and Chronology*, p. 314–333, Columbia University Press, New York.

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

Tong, H.-W. and Guérin, C., 2009: Early Pleistocene *Dicerorhinus sumatrensis* remains from the Liucheng *Gigantopithecus* Cave, Guanxi, China. *Geobios*, vol. 42, p. 525−539.

Tong, H. and Moigne, A.-M., 2000: Quaternary Rhinoceros of China. *Acta Anthropologica Sinica Supplement*, vol. 19, p. 257−263.

Tong, H.-W. and Wang, X.-M., 2014: Juvenile skulls and other postcranial bones of *Coelodonta nihowanensis* from Shanshenmiaozui, Nihewan Basin, China. *Journal* *of Vertebrate Paleontology*, vol. 34, p. 710–724.

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

Tong, H.-W., Wang, F., Zheng, M. and Chen, X., 2014: New fossils of *Stephanorhinus kirchbergensis* and *Elasmotherium peii* from the Nihewan Basin. *Acta Anthropologica Sinica*, vol. 33, p. 369–388.

Uchimura, K., Kano, K. and Oki, K., 2014: Quaternary deposits in Kagoshima Rift. *Journal of the Geological Society of Japan*, vol. 120 (supplement), p. 127−153. (*in Japanese with English abstract*)

Yamamoto, K., 2006: A rhinocerotid fossil from the Ueno Formation of the Kobiwako Group. *Konseki*, vol. 29, p. 19−21. (*in Japanese*)

Yan, Y., Wang, Y., Jin, C. and Mead, J. I., 2014: New remains of *Rhinoceros* (Rhinocerotidae, Perissodactyla) associated with *Gigantopithecus blacki* from the Early Pleistocene Yanliang Cave, Fusui, South China. *Quaternary International*, vol. 354, p. 110−121.

Yoshikawa, S., Kawamura, Y. and Taruno, H., 2007: Land bridge formation and proboscidean immigration into the Japanese Islands during the Quaternary. *Journal* *of Geoscience, Osaka City University*, vol. 50, p. 1–6.

Zin-Maung-Maung-Thein, Takai, M., Tsubamoto, Thaung-Htike, T., Egi, N. and Maung-Maung, 2008: A new species of *Dicerorhinus* (Rhinocerotidae) from the Plio-Pleistocene of Myanmar. *Palaeontology*, vol. 51, p. 1419–1433.

Zin-Maung-Maung-Thein, Takai, M., Tsubamoto, T., Egi, N., Thaung-Htike, Nishimura, T., Maung-Maung and Zaw-Win, 2010: A review of fossil rhinoceroses from the Neogene of Myanmar with description of new specimens from the Irrawaddy Sediments. *Journal of Asian Earth Sciences*, vol. 37, p. 154−165.

Captions for figure and table

Figure 1. Map showing the localities of Pleistocene rhinocerotid fossil records in Japan (after Handa and Takechi, 2017). References: Shikama (1949) and Nagasawa (1961) for the Kuzuu locality, Tochigi Prefecture; Shikama (1967) and present study for the Aira locality, Kagoshima Prefecture; Shikama *et al*. (1967) and Handa and Pandolfi (2016) for the Isa locality, Yamaguchi Prefecture; Kawamura *et al*. (1977) for the Tsukumi locality, Oita Prefecture; Okazaki (2007) and Ogino *et al*. (2009) for the Matsugae locality, Fukuoka Prefecture; Handa (2015) for the Yage locality, Shizuoka Prefecture; Taruno (1988, 2000) and Handa and Takechi (2017) for the Bisan-Seto locality, Okayama Prefecture; Okamura *et al*. (2011, 2016) and Okamura (2016) for the Otsu, Koban, Iga, and Kousa localities (the Kobiwako Group) of central Japan and for Suzuka locality (around the Ise Bay) of Mie Prefecture.

Figure 2. Terminology of the upper cheek teeth (Terminology follows Guérin, 1980; Fukuchi, 2003; Antoine *et al*., 2010. Illustration is after Fukuchi, 2003).

Figure 3. Rhinocerotidae gen. et sp. indet. (F00000554) from the Pleistocene Kamo

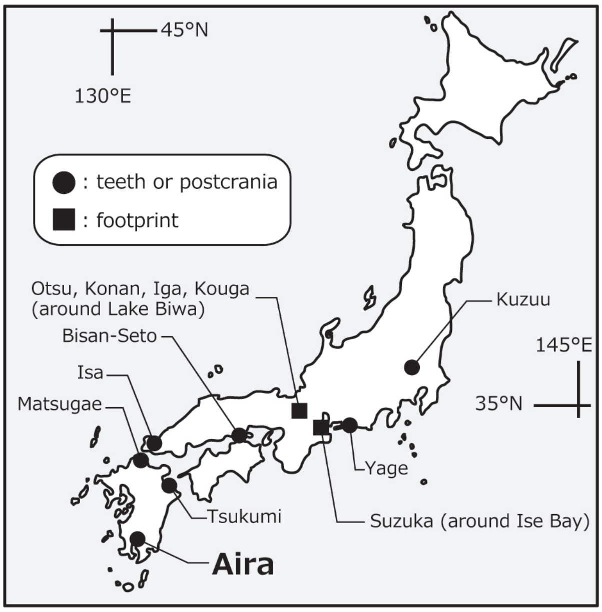
Formation of Japan. **a,** occlusal view; **b**, schematic drawing; **c**, schematic redrawing of F00000554 based on the figure of Shikama (1967).

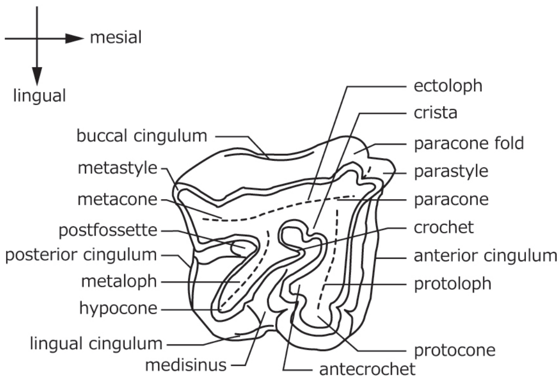
Figure 4. Chronology and stratigraphy of selected Japanese Pleistocene rhinocerotid, and immigration events of the Proboscidea in Japan (after Ogino *et al*., 2009; Okamura *et al*., 2011). Abbreviations: Pn, *Palaeoloxodon naumanni*; So, *Stegodon orientalis*; Rs, rhinocerotid; Fm., formation; QM, Quaternary Mammal zones of Japanese Islands (Kamei *et al*., 1988).

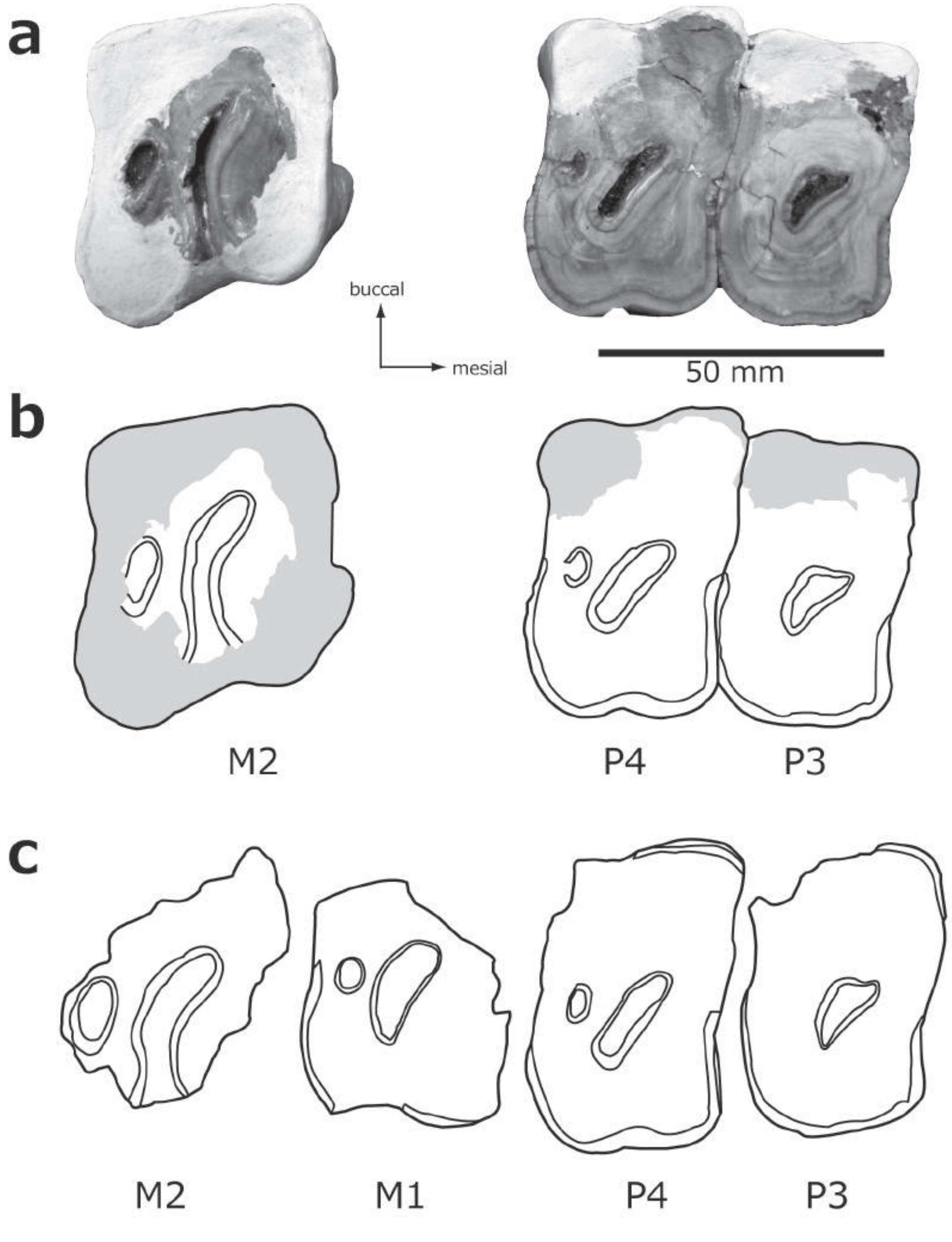
Figure 5. Stratigraphic distribution of major rhinocerotid footprint fossils from the Pleistocene around the Lake Biwa and Ise Bay of central Japan, and the stratigraphic range and rhinocerotid horizon of the Aira Formation of the Kagoshima Prefecture. The tephro- and magnetostratigraphy are after Satoguchi (2017). The localities of footprint fossils (Okamura *et al*., 2011, 2016; Okamura, 2016) are as follows: (1) Ikadachimukouzaichi Town, Otsu City, Shiga Prefecture, (2) Yamakami Town, Higashioumi City, Shiga Prefecture, (3) Mashita, Hino Town, Gamou District, Shiga Prefecture, (4) Nakayama, Hino Town, Gamou District, Shiga Prefecture, (5) Mizuguchi Town, Kouga City, Shiga Prefecture, (6) Yoshinaga, Konan City, Shiga

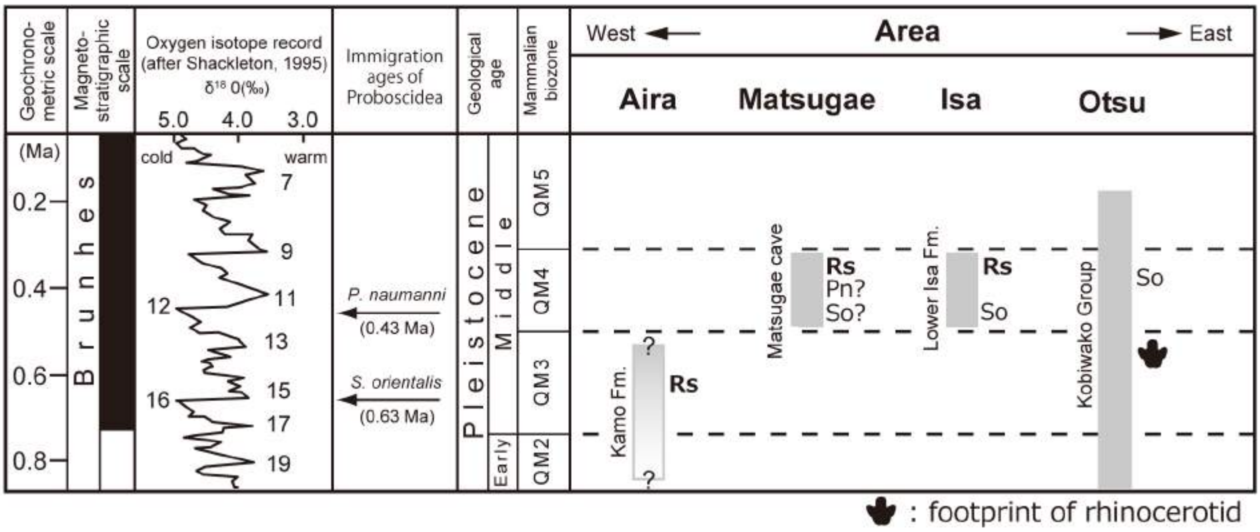
Prefecture, (7) Ifuna Town, Suzuka City, Mie Prefecture, (8) Higashishounai Town, Suzuka City, Mie Prefecture.

Table 1. P3 and P4 measurements of Rhinocerotidae gen. et sp. indet. (F00000554) from the Pleistocene Kamo Formation of Japan and the compared specimens (in mm). Abbreviations: *L*, length; *W*, width; *H*, height.

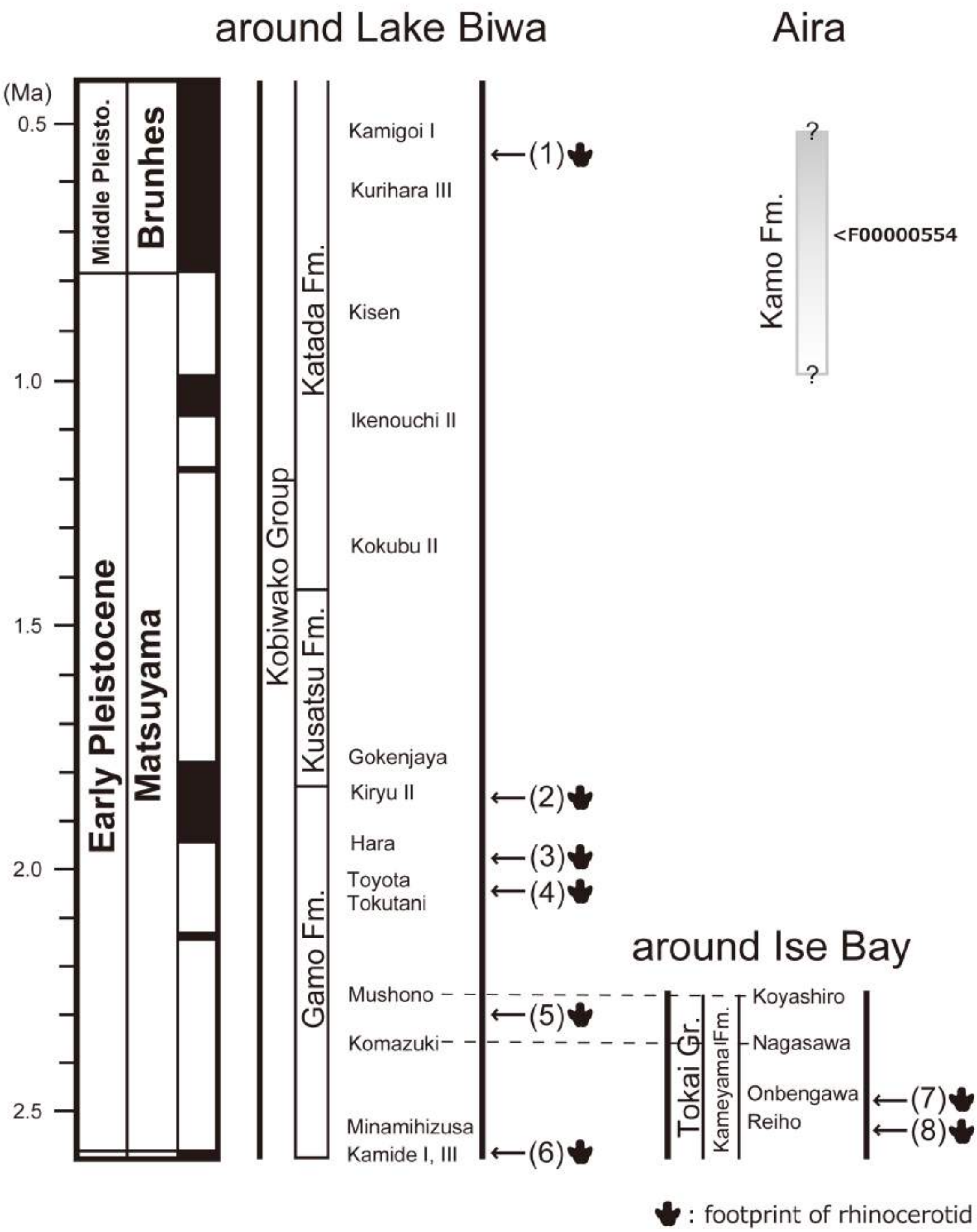

45°N
130°E
: teeth or postcrania
: footprint
Otsu, Konan, Iga, Kouga
(around Lake Biwa)
Bisan-Seto
Isa
Matsugae
Tsukumi
Aira
Kuzuu
145°E
35°N
Yage
Suzuka (around Ise Bay)


mesial
lingual
buccal cingulum
metastyle
metacone
postfossette
posterior cingulum
metaloph
hypocone
lingual cingulum
medisinus
ectoloph
crista
paracone fold
parastyle
paracone
crochet
anterior cingulum
protoloph
protocone
antecrochet


a
buccal
mesial
50 mm
b
M2
P4
P3
c
M2
M1
P4
P3



Geochronometric scale
Magneto-stratigraphic scale
Oxygen isotope record (after Shackleton, 1995)
δ18 O(‰)
5.0 4.0 3.0
cold
warm
Immigration ages of Proboscidea
Geological age
Mammalian biozone
West
Area
East
Aira
Matsugae
Isa
Otsu
(Ma)
0.2
0.4
0.6
0.8
Brunhes
7
9
11
12
13
15
16
17
19
P. naumanni
(0.43 Ma)
S. orientalis
(0.63 Ma)
Pleistocene
Middle
Early
QM5
QM4
QM3
QM2
Kamo Fm.
Rs
Matsugae cave
Rs
Pn?
So?
Lower Isa Fm.
Rs
So
Kobiwako Group
So
: footprint of rhinocerotid



around Lake Biwa
Aira
(Ma)
0.5
1.0
1.5
2.0
2.5
Middle Pleisto.
Brunhes
Early Pleistocene
Matsuyama
Kobiwako Group
Katada Fm.
Kusatsu Fm.
Gamo Fm.
Kamigoi I
Kurihara III
Kisen
Ikenouchi II
Kokubu II
Gokenjaya
Kiryu II
Hara
Toyota
Tokutani
Mushono
Komazuki
Minamihizusa
Kamide I, III
(1)
(2)
(3)
(4)
(5)
(6)
Kamo Fm.
?
<F00000554
?
around Ise Bay
Tokai Gr.
Kameyama Fm.
Koyashiro
Nagasawa
Onbengawa
Reiho
(7)
(8)
: footprint of rhinocerotid

	P3			P4				
Taxa	*L*	*W*	*H*	*L*	*W*	*H*	Reference	Remarks
Rhinocerotidae gen. et sp. indet.	30.12	>43.65	18.90	32.69	>51.80	15.26	present study	F00000554
Rhinoceros fusuiensis	34.2–38.8	43.9–50	-	34.8–43.9	45.3–53.8	-	Yan *et al* . (2014)	Yanliang Cave (China) materials
Rhinoceros sinensis	32–42	51–63	-	35–48	57–70	-	Yan *et al* . (2014)	Yanjinggou (China) materials
Rhinoceros sinensis	31.3–37.8	46–55.5	-	34–47	49.9–60	-	Yan *et al* . (2014)	Longgudong (China) materials
Rhinoceros sivalensis	40.6	58.4	-	38.1	66	-	Zin-Maung-Maung-Thein *et al* . (2010)	
Rhinoceros unicornis	42.4	60.85	46.73	43.35	65.79	52.22	direct observation	KPM-NF1002747 (extant)
Rhinoceros unicornis	42.86	57.85	45.08	45.15	67.19	53.72	direct observation	KPM-NF1002747 (extant)
Rhinoceros unicornis	43–50	55.5–60.5	-	42–51	59–69.5	-	Yan *et al* . (2014)	
Rhinoceros sondaicus	36.5-50	42-55	-	41-47.5	52-59	-	Yan *et al* . (2014)	
Rhinoceros sondaicus	34	35.7	-	37.1	44	-	Zin-Maung-Maung-Thein *et al* . (2010)	DG-MC 0001
Rhinoceros sondaicus	47	57	-	42	62	-	Zin-Maung-Maung-Thein *et al* . (2010)	Dub. 1983
Rhinoceros platyrhinus	69.79	78.47	-	72.47	95.49	-	Pandolfi and Mariorino (2016)	estimated based on Figure 4F in Pandolfi and Mariorino (20
Dicerorhinus gwebinensis	34	48	-	41	49	-	Zin-Maung-Maung-Thein *et al* . (2008)	NMMP-KU-IR 0469-1
Dicerorhinus sumatrensis	35.68	44.43	>14.08	38.47	50.83	12.36	Tong and Guerin (2009)	IVPP-V2877
Dicerorhinus sumatrensis	33.5–37.5	37–47	-	36–39	42.5–51.5	-	Yan *et al* . (2014)	
Dicerorhinus sumatrensis	29	38.6	26.9	32.4	45.3	33.2	direct observation	GMNH-VM-562 (extant, cast)
Dicerorhinus sumatrensis	28.7	39.1	27.7	29.5	45	34.2	direct observation	GMNH-VM-562 (extant, cast)
Stephanorhinus kirchbergensis	39.7	53.4	44.2	42.9	56.1	38.3	Handa and Pandolfi (2016)	NMNS-PV9600: Japanese material
Stephanorhinus kirchbergensis	45.6–51.8	60.6–61.3	-	54.7	63.7	-	Handa and Pandolfi (2016)	Migong Cave (China) materials
Stephanorhinus kirchbergensis	-	-	-	48.3	67.1	-	Handa and Pandolfi (2016)	Rhino Cave (China) material
Stephanorhinus kirchbergensis	38.2–43.2	55.9–60.2	-	44.2–51	60.8–66.3	-	Handa and Pandolfi (2016)	Anping (China) materials
Stephanorhinus kirchbergensis	38–39	57–61	-	44–50	64–69	-	Handa and Pandolfi (2016)	Choukoutien (China) materials
Stephanorhinus yunchuchenensis	37	-	-	42	58	-	Handa and Pandolfi (2016)	Yonch (China) material
Coelodonta nihowanensis	40.5	50	39	42	55.5	46.5	Deng (2002)	Linxia basin (China) material
Coelodonta antiquitatis	33–43	35–47.5	44–68	37–51.5	44–55.5	53.5–69	Guérin (1980)	
Dihoplus ringstroemi	44	69	-	50	69	-	Deng (2006)	estimated based on Figure 3 in Deng (2006)
Elasmotherium peii				47	57	-	Tong *et al* . (2014)	
Elasmotherium caucasicum	45–46	45–47	-	40–62	50–57	-	Tong *et al* . (2014)	
Elasmotherium sibiricum				41–49.5	39.8–50		Tong *et al* . (2014)	

16)