Paleontological Research, vol. 15, no. 4, pp. 247–257, December 31, 2011

doi:10.2517/1342-8144-15.4.247

Revision of fossil rhinoceroses from the Miocene Mizunami Group, Japan

AKIRA FUKUCHI[1] AND KOUJI KAWAI[2]

[1] *Hanshin Consultants Co., Ltd., 1765-3 Katahirayama, Gumizaki, Satsumasendai City, Kagoshima 895-0132, Japan (e-mail: afkc@goo.jp)*
[2] *Koyo Junior High School, 1306 Mitake, Mitake Town, Kani City, Gifu 505-0116, Japan (e-mail: kouji8@d8.dion.ne.jp)*

Received May 11, 2009; Revised manuscript accepted July 31, 2011

Abstract. A reinvestigation of *Chilotherium* from the Mizunami Group revealed that they do not belong to the genus and comprise two species, *Brachypotherium*? *pugnator* and *Plesiaceratherium* sp. It was found that *B.*? *pugnator* is more closely related to the Early Miocene Asian *Brachypotherium* (*B. fatehjangense* and *B. shanwangensis*) than to other species; this is inferred on the basis of the dental characteristics of strongly constricted protocones and prominent antecrochets in upper molars. *Plesiaceratherium* sp. resembles *Pl. gracile* rather than other European species in terms of the weak rugosities on the labial walls of the P_{2-3}. The assemblage of rhinoceros fossils of the Mizunami Group is very similar to that of the Early Miocene Shanwang Fauna in China.

Key words: *Brachypotherium*, Japan, late Early Miocene, Mizunami Group, *Plesiaceratherium*, Rhinocerotidae

Introduction

The Miocene Mizunami Group, which fills the Kani and Toki basins in central Japan (Figure 1), is one of the most fossiliferous formations in Japan (Itoigawa, 1980). It has yielded mammalian fossils, including gomphotheres, tapirs, rhinoceroses, horses, artiodactyls, and rodents (Matsumoto, 1921; Tokunaga, 1933; Takai, 1939, 1949; Kamei and Okazaki, 1974; Okumura *et al.*, 1977; Okazaki, 1980; Tomida and Goda, 1995). About one-third of the fossil specimens from this group are rhinoceros fossils (Okumura *et al.*, 1977).

The study of rhinoceros fossils from the Mizunami Group began with the work of Matsumoto (1921), who discovered a new species, *Teleoceras (Brachypotherium) pugnator*, in the Kani Basin. Tokunaga (1926) noted another two new species, *T.* (?) *kaniensis* and *T.* (?) *tokiensis* in the group. However, Takai (1939) stated that these two species are junior synonyms of *T. pugnator* and proposed a new combination, *Chilotherium pugnator*, following the work of Ringström (1924). Takai (1949) later found a specimen of *C. pugnator* in the Kani Basin. Kamei and Okazaki (1974) found additional specimens in the Kani and Toki basins and recognized two species: *C. pugnator* and the lesser species referred to as Rhinocerotidae gen. et sp. indet. Okumura *et al.* (1977) examined 11 additional specimens from the Kani Basin and also reported two rhinoceroses: *C. pugnator* for the larger of the two species, and *Chilotherium*? sp. for the smaller one. These works focused mainly on dental material, while Okazaki (1980) studied the postcranial bones and also recognized two species. Hence, two species of *Chilotherium* have been recognized in the Mizunami Group.

In our opinion, the Japanese *Chilotherium* species has been incorrectly defined because of the following reasons. First, most rhinoceros fossils from the Mizunami Group are so fragmentary that they cannot provide us with the diagnostic characteristics required for identification of the species and genus. Second, *C. pugnator* has been found to have morphologically different characteristics in previous studies: one study revealed a curved hypolophid in the lower cheek teeth, whereas another revealed an angular hypolophid (Okumura *et al.*, 1977: pl. IV-3, fig. 1, pl. IV-4, fig. 1, pl. IV-5, fig. 1; Okazaki, 1977: pl. 5, fig. 2, pl. 6, fig. 1). Finally, Japanese *Chilotherium* occurs much earlier than other species of the genus. Since *Subchilotherium* has been raised up to genus level by Heissig (1989), the earliest and the most primitive member of *Chilotherium* is thought to be *C. primigenius* from the early Late Miocene in China (Deng, 2006a). Deng (2006a) also noted that the origin of *Chilotherium* could date back to the Middle Miocene (*ca.* 16.0–11.6 Ma), whereas the earliest occurrence of the Japanese *Chilotherium* is dated as 19.6–18.4 Ma (Shikano, 2003).

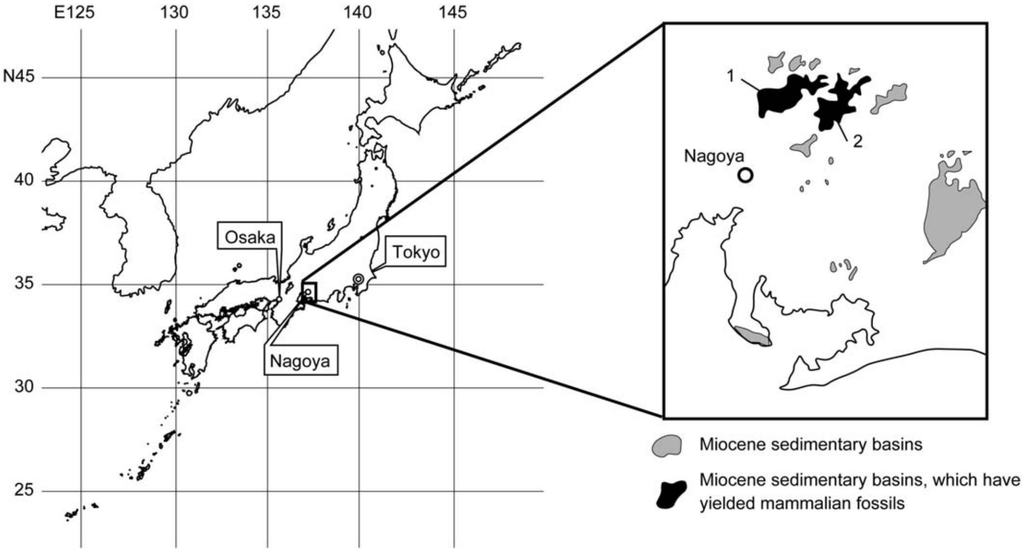

Figure 1. Miocene sedimentary basins in central Japan. The figure is modified from that of Itoigawa and Shibata (1992). 1: Kani Basin; 2: Toki (Mizunami) Basin.

There has been no systematic study of rhinoceros fossils from the Mizunami Group since the work of Takai (1939). However, the phylogeny and classification of Rhinocerotidae have been revised since the 1970s by several authors (e.g., Heissig, 1973; Guérin, 1980, 1989; Groves, 1983; Prothero *et al.*, 1986; Geraads, 1988; Fortelius and Heissig, 1989). Computer-based cladistic analysis has also been attempted since the 1990s (Cerdeño, 1995; Antoine, 2002; Antoine *et al.*, 2003). The phylogenetic relationships and suprageneric classification of the family are still controversial; nevertheless, in this paper we adopt the systematic works proposed by Heissig (1973, 1989) and Guérin (1989) because they are widely accepted among researchers.

Unfortunately, most rhinoceros fossils from the Mizunami Group are too fragmentary for us to consider the problem, as noted above. Accordingly, we focused on two relatively well preserved specimens in the available materials.

Materials and methods

The specimens presented in this paper are stored in the Board of Education at the Kani City and Mizunami Fossil Museum, Mizunami City. The materials from the Siwaliks referred to in the comparisons were examined in the American Museum of Natural History, New York. Other materials shown in the comparisons were not directly examined; for those, we used published data. The dental terminology and measurement follow the work of Peter (2002). Measurements of the specimens examined were taken using calipers.

Abbreviations: AMNH: American Museum of Natural History, New York; BEK: Board of Education, Kani, Japan; MFM: Mizunami Fossil Museum, Mizunami, Japan; L, mesiodistal length; W, labiolingual width.

Systematic paleontology

Family Rhinocerotidae Owen, 1845
Subfamily Aceratheriinae Dollo, 1885
Tribe Teleoceratini Hay, 1902
Genus ***Brachypotherium*** Roger, 1904

Diagnosis.—Brachyodont to subhypsodont cheek teeth with developed secondary enamel fold. A detailed diagnosis was given in Heissig (1972).

Brachypotherium? ***pugnator*** Matsumoto, 1921

Figure 2.1

Teleoceras (Brachypotherium) pugnator Matsumoto, 1921, p. 6, pl. 2
Rhinoceros (Chilotherium) pugnator (Matsumoto): Takai, 1939, p. 192–193.
Chilotherium pugnator (Matsumoto): Okumura *et al.*, 1977, p. 31, pl. 4–14, fig. 2, p. 33, pl. 4–2, fig. 2.
Chilotherium pugnator (Matsumoto): Okazaki, 1977, p. 16, pl. 5, fig. 2.

Holotype.—a palate with right and left P^2–M^3 (private collection), Matsumoto 1921, pl. 2.

Material.—Fragment of a right maxilla with P^4–M^1, BEK 1107.

Locality.—Sugekari, Kani City, Gifu Prefecture.

Horizon.—Nakamura Formation (lower Miocene) of the Mizunami Group.

Emended diagnosis.—Large *Brachypotherium* with a strongly constricted protocone in upper molars. Prominent antecrochet in upper molars.

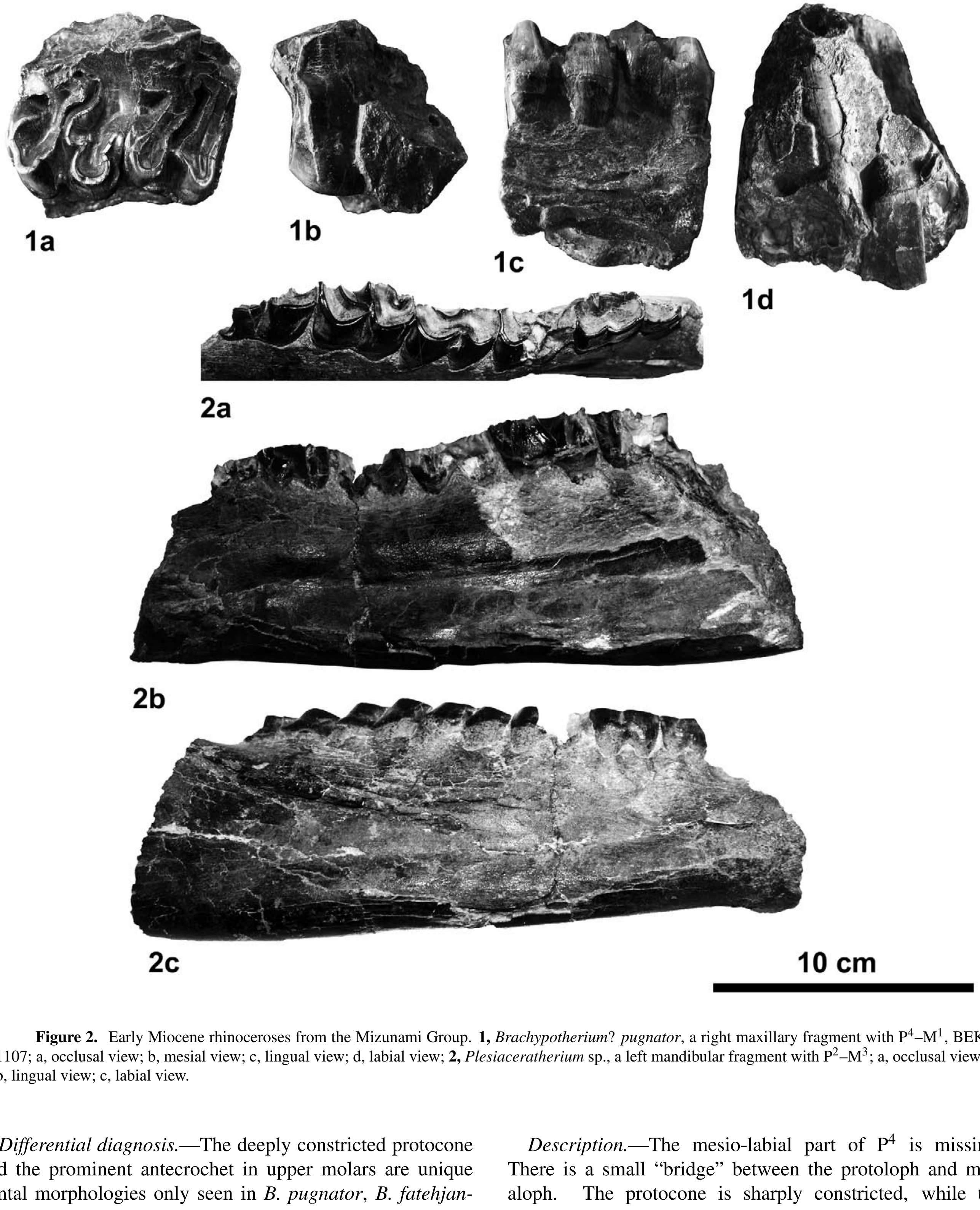

Figure 2. Early Miocene rhinoceroses from the Mizunami Group. **1,** *Brachypotherium*? *pugnator*, a right maxillary fragment with P^4–M^1, BEK 1107; a, occlusal view; b, mesial view; c, lingual view; d, labial view; **2,** *Plesiaceratherium* sp., a left mandibular fragment with P_2–M_3; a, occlusal view; b, lingual view; c, labial view.

Differential diagnosis.—The deeply constricted protocone and the prominent antecrochet in upper molars are unique dental morphologies only seen in *B. pugnator*, *B. fatehjangense*, and *B. shanwangensis* in *Brachypotherium*. The first species is clearly discriminated from the latter two by its larger size and low-crowned cheek teeth.

Description.—The mesio-labial part of P^4 is missing. There is a small "bridge" between the protoloph and metaloph. The protocone is sharply constricted, while the hypocone is not constricted. The lingual ends of the lingual cusps are rounded. The protoloph is roughly an S-shape. The metaloph is nearly straight and oblique to the ectoloph. The

Table 1. Measurements of the upper cheek teeth of Teleoceratini and *Plesiaceratherium* in millimeters.

		P^3		P^4		M^1		M^2		M^3		Reference
		L	W	L	W	L	W	L	W	L	W	
B. pugnator	BEK1107			>39.0	>59.3	>44.7	>65.4					This paper
	mean	41.5	61.5	47.5	70.0	59.0	75.0	65.0	76.0	62.0	69.5	Matsumoto (1921)
	min.	41.0	61.0	47.0				65.0	76.0	60.0	69.0	
	max.	42.0	62.0	48.0				65.0	76.0	64.0	70.0	
B. shanwangensis	mean	39.7	52.3	43.0	61.0					59.5	58.0	Wang (1965)
	min.	37.0	51.0							56.0		
	max.	42.0	54.0							63.0		
B. fatehjangense	mean	39.3	49.9	44.8	55.8*	51.8	63.1*	63.1	66.8	57.0	60.7	AMNH-FM19408
	min.			44.0		51.5		62.4				
	max.			45.5		52.0		63.7				
B. perimense	mean	42.0	54.3	51.9	71.9	64.8	73.6	71.9	78.4	59.5	64.4	AMNH-FM19410,
	min.	39.1	47.6	51.6		62.0		71.2		58.0	62.9	19470, 19692,
	max.	46.0	61.5	52.1		67.6		72.5		60.9	66.0	93300
B. brachypus	mean	40.9	53.7	45.7	61.5	57.9	64.1	60.9	65.4	55.4	63.9	Cerdeño (1993)
	min.	35.5	47.8	44.3	60.9	48.7	61.7	57.3	56.4	49.5	59.5	
	max.	43.7	60.0	47.7	67.8	63.4	67.4	62.4	73.0	60.0	71.3	
B. snowi	mean	40.3	60.3	44.0	70.0	54.5	71.0	61.5	77.0	61.0	—	Hamilton (1973)
	min.	40.0	60.0					61.0	75.0			
	max.	41.0	61.0					62.0	79.0			
B. heinzelini	mean	36.0	54.0	48.5	63.3			63.0	77.0	55.0	65.0	Hooijer (1966)
	min.			48.0	62.0							
	max.			49.0	66.0							
B. lewisi	mean	46.1	72.5	50.8	87.3	64.4	92.1	74.5	89.7	69.5	75.2	Harris and Leakey (2003)
	min.	42.2	71.9	44.7	85.9	63.6	91.8	63.6	88.6	61.6	70.3	
	max.	50.0	73.1	57.0	88.6	65.3	92.5	80.6	90.3	73.6	79.2	
A. aralensis	mean	31.5	45.0	36.0	53.5	43.0	58.5	51.0	62.0			Borissiak (1954) cited in Wang (1965)
	min.	31.0	42.0		53.0	41.0	58.0	50.0	61.0			
	max.	32.0	48.0		54.0	45.0	59.0	52.0	63.0			
A. lanzhouensis	mean	31.3	43.7	35.2	49.4	43.0	50.0	51.0	53.0			Qiu and Xie (1997)
P. germanicus	mean	28.6	34.8	31.6	41.2	36.2	40.7					Cerdeño (1996)
	min.	26.2	33.0	28.0	39.3	31.0	37.0					
	max.	30.5	40.8	35.4	45.6	39.3	45.6					
P. douvillei	mean	31.7	39.9	36.5	46.1	41.7	45.4					Cerdeño (1996)
	min.	25.4	34.2	33.0	40.6	36.1	41.1					
	max.	37.4	47.8	41.7	54.5	46.2	49.9					
D. aurelianense	mean	35.2	45.7	40.5	53.9	47.8	56.1	56.6	57.5	47.7	53.2	Cerdeño (1993)
	min.	32.8	42.9	36.9	51.6	46.1	52.8	51.0	54.0	44.3	50.8	
	max.	39.7	48.4	44.3	58.3	54.4	62.3	63.6	60.8	51.0	55.8	
T. americanus	mean	34.0	49.0	37.0	56.0	46.0	60.0	51.0	61.0	53.0	56.0	Prothero (2005)
T. meridianum	mean					46.0	61.0	49.0	68.0	47.0	51.0	Prothero (2005)
T. medicornutum	mean	32.0	48.0	36.0	58.0	41.0	61.0	50.0	64.0	50.0	61.0	Prothero (2005)
T. brachyrhinum	mean	39.0	58.0	41.0	66.0	51.0	68.0	57.0	68.0	52.0	63.0	Prothero (2005)
T. major	mean	34.0	46.0	41.0	59.0	48.0	63.0	53.0	63.0	47.0	57.0	Prothero (2005)
T. fossiger	mean	47.0	59.0	50.0	63.0	65.0	71.0	62.0	76.0	54.0	71.0	Prothero (2005)
T. proterum	mean	39.0	43.0	41.0	49.0	47.0	55.0	54.0	56.0	49.0	42.0	Prothero (2005)
T. hicksi	mean	33.0	47.0	43.0	67.0	45.0	73.0	53.0	71.0	52.0	60.0	Prothero (2005)
T. guymonense	mean	36.0	53.0	44.0	56.0	45.0	64.0	53.0	65.0	50.0	62.0	Prothero (2005)

Table 1. Continued.

		P^3		P^4		M^1		M^2		M^3		Reference
		L	W	L	W	L	W	L	W	L	W	
Pl. gracile	min.	34.0	41.0	37.0	43.0	46.0	48.0	48.0	50.0	45.0	46.0	Yan and Heissig (1986)
	max.	37.0	42.0	38.0	48.0	48.0		50.0	51.0	46.0	47.0	
Pl. fahlbuschi	min.	29.0	39.0	32.0	42.0	32.0	44.0	36.0	45.0	39.0	42.0	Yan and Heissig (1986)
	max.	33.0	41.0	35.0	44.0	40.0	45.0	44.0	41.0	39.0	44.0	
Pl. mirallesi	min.	35.0	44.0	37.0	48.0	41.0	47.0	45.0	51.0	41.0	45.0	Yan and Heissig (1986)
	max.	35.0	45.0	39.0	49.0	43.0	47.0	46.0	51.0	43.0	45.0	
Pl. platyodon	min.	28.0	43.0	34.0	45.0	35.0	43.0	38.0	45.0	36.0	42.0	Yan and Heissig (1986)
	max.	31.0			47.0	36.0	43.0	43.0	47.0	45.0	48.0	
Pl. lumiarense	min.	34.7	44.0	35.7	48.8	41.3	49.1	45.4	49.5	38.0	48.8	Antunes and Ginsburg (1983)
	max.	40.2	48.1	40.0	53.5	44.6	49.2					

antecrochet is strongly developed. The crochet is also clearly developed with a single enamel fold. The crista is long, but does not connect to the metaloph. Judging from the clear metacone rib, the labial wall may have been undulated. The cingula cover the lingual end of the tooth, except for the lingual cusps. The labial cingulum is absent on the disto-labial wall. The inclinations of the lingual and labial walls indicate that this tooth is low-crowned.

The ectoloph is totally missing in M^1. The protocone is strongly constricted by the anterior and posterior grooves. These grooves are deeper than those of P^4. The anterior hypocone groove is also sharp. The lingual end of the protocone is mesiodistally flat, whereas that of the hypocone is rounded. The robust antecrochet extends distally, and its lingual margin is mesiodistally flat. If this tooth was worn more heavily, the antecrochet would connect to the metaloph. The crochet is slightly smaller than the antecrochet. The crista is faintly developed. The oval-shaped postfossette is deeper than the medisinus. There is a tubercle-like cingulum at the lingual opening of the medisinus.

Remarks.—This material was first reported as a tapir fossil, *Paleotapirus*, by Yoshida (1957). Later, Okumura *et al.* (1977) and Okazaki (1977) stated that it is a right maxillary fragment with M^1–M^2 of *C. pugnator*. However, the distal tooth is apparently worn more heavily than the mesial tooth is (the height of the grinding surface of the protocone is 14.8 mm in the former and 20.2 mm in the latter; Figure 2). This wearing condition suggests that this maxillary fragment retains the last premolar and first molar.

The dental morphologies of the specimen described here are in accordance with those of *C. pugnator*: the molarized premolar, the deeply constricted protocone in the molar, the sharp anterior hypocone groove in the first and second molars, and the strongly developed antecrochet. Although the measurements of BEK1107 cannot be directly compared with those of *C. pugnator*, this specimen seems to be smaller than the holotype of the species (Matsumoto, 1921, pl. 2). Compared with the dental size variations of living species (Guérin, 1980), this size difference between the two specimens can be considered as intraspecific variability. Therefore, BEK1107 must belong to *C. pugnator*.

Generic assignment.—BEK1107 provides us the dental characteristics, which cannot be observed in the heavily worn material presented in the work of Matsumoto (1921). In the following discussion, the dental features and measurements of *C. pugnator* presented by Matsumoto (1921) are used to compensate for the lack of information from BEK1107.

It is not appropriate to discuss the generic assignment only based on the upper cheek teeth, but its large size (W of M^1 excesses 70 mm, Table 1) is a key character for identification. In addition to the large size, the species shows a strongly constricted protocone in the upper cheek teeth. These features are observed in *Brachypotherium*, *Teleoceras*, *Elasmotherium*, *Sinotherium* and *Parelasmotherium*.

C. pugnator is easily discriminated from *Elasmotherium*, *Sinotherium* and *Parelasmotherium* by the simple enamel folding, the absence of cristella in the upper cheek teeth, and the absence of coronal cement (Antoine, 2002).

The size distribution of upper cheek teeth of *C. pugnator* is within the range of *Brachypotherium* or *Teleoceras*, and similar to *B. perimense* or *T. fossiger* (Figure 3).

Chavasseau *et al.* (2006) allocated *Aprotodon fatehjangense* to *Brachypotherium* based on the reduced paraconid in P_2, which is an autapomorph of *Brachypotherium* in the cladistic analysis shown in Antoine (2002). Consequently, there is no difference between *Aprotodon* and *Brachypotherium* in the morphology of the upper cheek teeth. *C. pugnator* cannot be classified into either genus only by the upper dental morphology. However, the upper cheek teeth of *Brachypotherium* are clearly larger than those of *Aprotodon*, except for the width of M^2 which shows the overlap between *B. brachypus* and *A. aralensis* (Figure 3). The size distribution of the upper cheek teeth is useful for discriminating these genera: the upper cheek teeth of *C. pugantor* are clearly

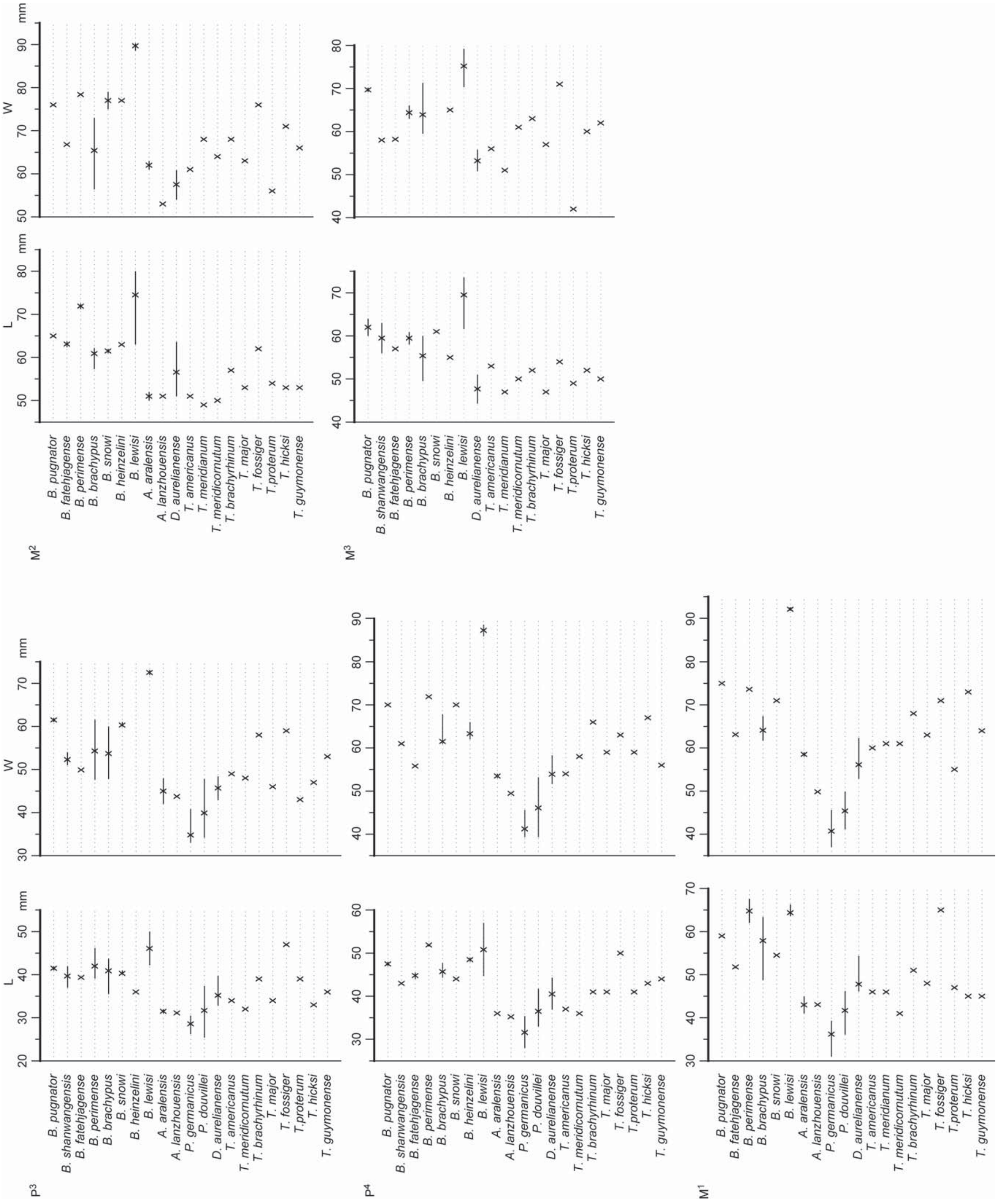

Figure 3. Dental size variation of Teleoceratini. X indicates the mean value. Data are taken from Table 1.

larger than those of *Aprotodon* (Figure 3).

C. pugnator is similar to *B. fatehjangense* in having the strongly constricted protocone in upper molars and the small bridge between protoloph and metaloph in upper premolars. However, the former species differs from the latter by the absence of the constriction of the distal side of the hypocone in M^{1-2} and the low-crowned cheek teeth.

C. pugnator is discriminated from *T. fossiger* by the continuous lingual cingulum in P^{2-4} (Antoine, 2002; Antoine *et al.*, 2003). *Teleoceras* generally differs from *C. pugnator* by having high-crowned cheek teeth and thick coronal cement (Prothero, 2005). However, within the genus *T. americanus* has lower-crowned teeth (Prothero, 2005) and significant differences between *C. pugnator* and *T. americanus* in the upper dental morphology are not found. Prothero (2005) showed that the *Teleoceras* lineage indicates an increase in the hypsodonty and two patterns of body size change: a dwarfing pattern (the dwarfed *T. meridianum* and *T. guymonense* for *T. brachyrhinum*) and an increase in size (from *T. americanum* to *T. meridicornutum*, *T. major*, *T. fossiger*, and *T. hicksi*, which shows a slight size reduction). *C. pugnator* is similar in size to *T. fossiger*, the most derived and the largest species in the genus. If the former species were included in *Teleoceras*, it should have high-crowned teeth with coronal cement like *T. fossiger*. However, it is impossible to deny the possibility that *C. pugnator* is a conservative species of *Teleoceras* and an exception to the general evolutionary trend of this genus.

The above comparisons suggest that *C. pugnator* is accordant with *Brachypotherium* in the dental features and dimensions. Here, we propose *Brachypotherium*? *pugnator* against *C. pugnatori*, as originally described by Matsumoto (1921).

Phyletic position in the genus.—B.? *pugnator* shows a peculiar dental morphology among *Brachypotherium*. Such features are only seen in *B. fatehjangense* in the genus. The Early Miocene Chinese rhinoceros also shows a strong protocone constriction in the upper cheek teeth like this species. However, the classification of this Chinese species, like that of the Japanese rhinoceros, is controversial.

This Chinese species was first described as *Plesiaceratherium shanwangensis* by Wang (1965) with an emphasis on the similarities in the dental morphology between *Pl. shanwangensis* and *B.*? *pugnator*. The latter species is also included in *Plesiaceratherium* (Wang, 1965). Later, Yan *et al.*, (1983) introduced the new combination *Brachypotherium shanwangensis* for the species without any explanations. Yan and Heissig (1986) made a revision of *Plesiaceratherium*, but *Pl. shanwangensis* was not included in the genus.

The generic assignment of *Pl. shanwangensis* must be examined because of the similarities in the dental features between it and cf. *B. pugnator*. The combination *Pl. shanwangensis* is doubtful because the comparison was made with *Diaceratherium* and the wrong specimens of *Plesiaceratherium* according to the literature cited in Wang (1965). The type specimen of *Pl. gracile* in Young (1937) contains the upper premolar series of *Brachypotherium* sp. (Yan and Heissig, 1986). Yan and Heissig (1986) also stated that other dental specimens for *Pl. gracile* figured by Young (1937) belong to the species of Aceratherini, not to *Pl. gracile*.

Pl. shanwangensis is characterized by the semimolariform premolar (*sensu* Heissig, 1989), the continuous lingual cingulum in the upper premolar, and the strongly constricted protocone in upper molars. These dental features are also observed in *Chilotherium andersoni* (Antoine, 2002; Antoine *et al.*, 2003). Antoine *et al.* (2003) coded "0: weak" for the character "116: M^{1-2}, protocone constriction" of *Aprotodon fatehjangense* (= *Brachypotherium fatehjangense*, see above), but the protocone constriction is confidently strong in upper molars of this species (AMNH 19408) like those of *Teleoceras* and *Chilotherium* (personal observation by AF).

In *Chilotherium*, the protocone is also strongly constricted in upper molars among *C. habereri*, *C. samium*, *C. schlosseri*, *C. kowalevskii*, *C. xizangensis*, *C. persiae*, *C. kiliasi*, and *C. andersoni* (Deng, 2006a). These species differ from *Pl. shanwangensis* by the high crown of the cheek teeth (Deng, 2006a).

The upper cheek teeth of *Pl. shanwangensis* are larger than those of *T. americanum*, the most primitive species of *Teleoceras*, and fall within the size distribution of *T. major*, *T. hicksi*, *T. guymonense*, and *T. brachyrhinum* (Figure 3). The crown of the cheek teeth of *Pl. shanwangensis* is lower than that of *T. major*, *T. hicksi*, and *T. guymonense* (Prothero, 2005). Prothero (2005) noted that the crown of the cheek teeth of *T. brachyrhinum* is not as high as that of *T. major*. The relatively high crown of the cheek teeth of *Pl. shanwangensis* is not significantly different from that of *T. brachyrhinum*. However, the absence of coronal cement in the upper cheek teeth of *Pl. shanwangensis* is inconsistent with the derived species of *Teleoceras*, including *T. major*, *T. hicksi*, *T. guymonense*, *T. brachyrhinum*, *T. medicornutum*, *T. meridianum*, and *T. fossiger* (Cerdeño, 1995; Prothero, 2005). In view of the general evolutionary trend of *Teleoceras*, the dental feature of *Pl. shanwangensis* is inconsistent with that of the derived species of *Teleoceras*.

The above comparisons suggest that *Pl. shanwangensis* is inconsistent in its dental features with *Chilotherium* and *Teleoceras*. In addition to the similarities of the dental features between *Pl. shanwangensis* and *B.*? *pugnator*, the size distribution of the former species is within the range of *Brachypotherium* (Figure 3). We support in this paper the combination *Brachypotherium shanwangensis* suggested by Yan *et al.* (1983).

It is interesting that the Early Miocene Asian *Brachypotherium* species (*B.*? *pugnator*, *B. shanwangesis*, and *B. fatehjangense*) show the unique dental features that are not

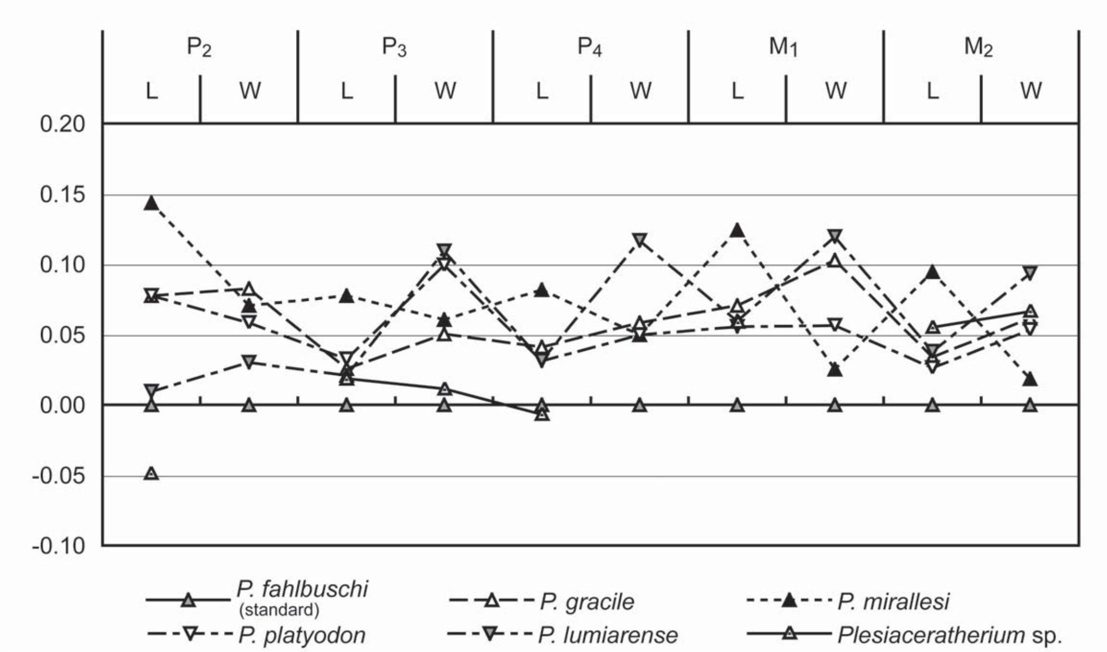

Figure 4. Log ratio diagram of the lower dentition of MFM18153 (*Plesiaceratherium* sp.), *Pl. gracile*, *Pl. mirallesi*, *Pl. platyodon*, and *Pl. lumiarense* versus that of *Pl. fahlbuschi*. Data are taken from Table 2.

observed in other species of this genus. Here, we suggest a *B.*? *pugnator*–*B. shanwangensis*–*B. fatehjangense* group on the basis of unique dental features.

The trend of increasing crown height is found in most rhinoceros lineages, and it is also known that the increase in hypsodonty in rhinocerotids can be related to a change in their diet (Heissig, 1989). The low-crowned cheek teeth of cf. *B. pugnator* suggest that this species could be more primitive than *B. shanwangensis* and *B. fatehjangense*, which have subhypsodont cheek teeth (Wang, 1965; Heissig, 1972).

Tribe Aceratherini Dollo, 1885
Genus *Plesiaceratherium* Young, 1937

Diagnosis.—Rugosities on the labial wall in P_{2-3}. A detailed diagnosis was given in Yan and Heissig (1986).

Plesiaceratherium sp.

Material.—Figure 2.2, a right mandibular fragment with P_2–M_3, MFM18153.

Locality.—Kawai, Minokamo City, Gifu Prefecture.

Horizon.—The lower member of the Nakamura Formation.

Description.—The ventral border of the mandibular body rises rostrally upwards near the symphysis. The mental foramen is at the level of the contact between P_1 and P_2.

P_2 is worn down and appears triangular in shape from an occlusal view. The labial cingulum runs continuously behind the protoconid to the hypoconid. The shallow but sharp outer groove originates from the cingulum. Rugosities are weakly developed on the whole labial wall. P_3 is nearly complete. There is a shallow but sharp vertical groove between the paraconid and protoconid. The labial walls are nearly straight with a shallow outer groove, originating from the labial cingulum. The cingulum is also developed in the lingual wall. The labial wall of the metalophid is rounded, while that of the hypolophid is mesiodistally straight. The weak rugosities are restricted to the labial wall of the trigonid. P_4 is poorly preserved. The trigonid is heavily damaged and the labial groove is missing. The lingual cingulum is observed at the base of the lingual wall of the talonid. The labial wall of the hypolophid is rounded in contrast to that of P_3. The mesiolingual side of M_1 is damaged. The trigonid is worn down, but the talonid is retained. The metalophid is mesiodistally shorter than the hypolophid. The labial walls are rounded with a deep outer groove. There is a tubercle-like cingulum at the base of the outer groove. The M_2 is very similar to the M_3 in morphology. The former tooth lacks a lingual side and the latter preserves only the mesio-labial side. The labial side of the metalophid is mesiodistally flat, while that of the hypolophid is rounded. There is a deep outer groove. No cingula are found in the labial wall.

Generic assignment.—This material was identified as *Chilotherium*? sp. by Okumura *et al.* (1977), but the dental features in the lower premolars of the material do not accord

Table 2. Measurements of the lower cheek teeth of *Plesiaceratherium* in millimeters.

	P_2		P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W	L	W
Plesiaceratherium sp.												
MFM18153	20.6	12.3*	31.0	19.2	31.8	—	37.0	—	42.0	26.8	—	—
Pl. gracile												
mean^1	27.5	18.5	31.5	21.0	35.5	25.5	38.0	27.5	40.0	26.5	43.5	26.5
Pl. fahlbuschi												
mean^1	23.0	15.3	29.7	18.7	32.3	22.3	32.3	21.7	37.0	23.0	40.5	23.0
Pl. mirallesi												
mean^1	32.0	18.0	35.5	21.5	39.0	25.0	43.0	23.0	46.0	24.0	45.5	26.0
Pl. platyodon												
mean^1	27.5	17.5	32.0	23.5	34.7	25.0	36.7	24.7	39.3	26.0	40.0	24.0
Pl. lumiarense												
mean^2	23.5	16.4	31.2	24.1	34.7	29.2	37.1	28.6	40.4	28.5	42.0	26.4

*: deformed.

1, calculated from data in Yan and Heissig (1986); 2, calculated from data in Antunes and Ginsburg (1983).

with those of *Chilotherium*. The rugosities on the labial wall in P_{2-3} are observed in *Plesiaceratherium mirallesi*, *Pleuroceros pleuroceros*, and *Hoploaceratherium tetradactylum* in Antoine (2002) and Antoine *et al.* (2003). This material is inconsistent with *Pl. pleuroceros* in the following points: the smooth outer groove in the lower cheek teeth, the rounded labial wall of the trigonid in the lower cheek teeth, the presence of the lingual cingulum in the lower premolars (Antoine *et al.*, 2003). This material is also different from *H. tetradactylum* by the presence of the lingual cingulum in the lower premolars (Antoine *et al.*, 2003). Accordingly, MFM18153 is included to *Plesiaceratherium*.

Comparison.—Yan and Heissig (1986) noted that *Plesiaceratherium gracile* shows rugosities on the labial wall in the lower premolars only in some specimens. It is not clear that the weak rugosities on the labial wall in the P_{2-3} of MFM18153 is a key feature for distinguishing this material from *Pl. gracile*. However, the weak external rugosities in the P_{2-3} of MFM18153 indicate that this material does not belong to the European species (*Pl. fahlbuschi*, *Pl. mirallesi*, *Pl. platyodon*, and *Pl. lumiarense*), which strongly show the rugosities on the labial wall of the lower premolars. The weakness of the rugosities on the labial wall in the P_{2-3} of MFM18153 suggests that it is more closely related to *Pl. gracile* than to other species.

Figure 4 shows the log ratio diagrams of the lower dentition of *Plesiaceratherium* species. In comparison with *Pl. fahlbuschi*, the premolars of MFM18153 are smaller than those in *Pl. gracile*, *Pl. platyodon*, *Pl. mirallesi*, and *Pl. lumiarense*. On the other hand, the molars of the present specimen are roughly similar in terms of dimensions to those of the above four species. In the present specimen, P_3 appears to have a rather slender form like that of *Pl. mirallesi*, whereas M_2 is relatively widened buccolingually like those of *Pl. gracile*, *Pl. platyodon*, and *Pl. lumiarense* and in contrast to the slender M_2 in *Pl. mirallesi*.

Biogeographical discussion

B. pugnator has been reported from the Nakamura and Hiramaki formations in the Miocene Mizunami Group, Central Japan. The ages of both formations are estimated as *ca.* 19.6–18.4 Ma and 18.4–17.0 Ma by fission track dating (Shikano, 2003). These formations have yielded fossil mammals, including *Brachypotherium*? *pugnator* (this paper), *Plesiacertherium* sp. (this paper), *Anchitherium* aff. *A. gobiensis*, *Plesiotapirus yagii*, *Gomphotherium annectens*, *Amphitragulus minoensis*, *Plesiosorex* sp., *Amphilagus*? sp., *Youngofiber sinensis*, *Eucastor*? sp., and *Megapeomys* sp. (Matsumoto, 1921; Kamei and Okazaki, 1974; Okazaki, 1977; Okumura *et al.*, 1977; Tomida, 2000; Miyata and Tomida, 2010; and cited therein). Of these fossil mammals, *Y. sinensis* and *P. yagii* are common to the Early Miocene mammalian faunas (Sihong and Shanwang) of China (Qiu and Qiu, 1995; Deng, 2006b). Saegusa (2008) correlated *G. annectens*-bearing Miocene formations in Japan with Chron C5E. In addition to this correlation, the rhinoceros fossil assemblages from the Nakamura and Hiramaki formations can be correlated rather to the Shanwang fauna than to the Sihong fauna (Qiu and Qiu, 1995; Deng, 2006b).

It is interesting that primitive forms of large mammals, including *B.*? *pugnator* and *G. annectens*, have been reported from Japan, while they have not been found in China. It is also notable that *B.*? *pugnator*, the primitive species of *Brachypotherium*, persists in Japan, but is represented by the more derived species *B. shanwangensis* in the contemporary Shanwang fauna in China (Qiu and Qiu, 1995; Deng, 2006b).

This biogeographic difference would have been caused by a barrier between Japan and the Asian mainland. Shuto *et al.* (2006) reported that the geochemical features of the volcanic rocks (22–20 Ma) from the Niigata region, NE Japan, are almost identical to those from the continental rift zone such as the Rio Grande rift. This shows that NE Japan could have been rifted in the earliest Early Miocene. We suggest a possibility that rifting before the opening of the Sea of Japan (*ca.* 16 Ma: Kano *et al.*, 2002; Shuto *et al.*, 2006) partially formed a barrier between Japan and the Asian mainland before the deposition of the Nakamura Formation.

Conclusion

The revision of the rhinoceros fossils from the Mizunami Group revealed that the previously reported *Chilotherium pugnator* and *Chilotherium*? sp. should be assigned to *Brachypotherium*? *pugnator* and *Plesiaceratherium* sp., respectively.

On the basis of dental features and size distribution of the upper cheek teeth, *B.*? *pugnator* is a valid species in the genus and has similarities in dental morphology with the Early Miocene Asian *Brachypotherium*: *B. fatehjangense* and *B. shanwangensis*. *B.*? *pugnator* is easily distinguished from *B. fatehjangense* and *B. shanwangensis* by its comparatively larger size and low-crowned cheek teeth. The latter trait may indicate that *B.*? *pugnator* is the most primitive member of a *B.*? *pugnator*–*B. shanwangensis*–*B. fatehjangense* group.

Another species is assigned to *Plesiaceratherium* sp. on the basis of the dental morphology of the lower cheek teeth. The weak rugosities on the labial walls in P_{2-3} suggest that this species is more closely related to *Pl. gracile* from the lower Miocene of China than to other species. However, this species differs from *Pl. gracile* in having slender lower premolars and slender P_3. We do not establish a new species on the basis of the present material because the very small number of specimens from the Mizunami Group cannot indicate whether this is a matter of interspecific or intraspecific variability.

The fact that the primitive forms (*B.*? *pugnator* and *G. annectens*) persisted in the Lower Miocene Nakamura Formation of Japan suggests the possibility that a barrier between Japan and the Asian mainland was formed before the deposition of the Nakamura Formation.

Acknowledgments

We would like to express our sincere thanks to Masao Katsuno, Mizunami Fossil Museum, and the Board of Education of Kani City for permitting us access to the rhinoceros fossil collection. Both authors are also indebted to Atsushi Matsuda for the assistance provided. We also thank Jin Meng and Chris Norris and the staff of the American Museum of Natural History for assistance at the Museum. Haruo Saegusa and Hideo Nakaya are thanked for their constructive and critical reviews of the manuscript.

References

Antoine, P. O., 2002: Phylogénie et evolution des Elasmotheriina (Mammalia, Rhinocerotidae). *Mémoires du Muséum National d'Histoire Naturelle*, no. 188, p. 1–359.

Antoine, P. O., Duranthon, F. and Welcome, J. L., 2003: *Alicornops* (Mammalia, Rhinocerotidae) dans le Miocène supérieur des Collines Bugti (Balouchistan, Pakistan): implications phylogénétiques. *Geodiversitas*, vol. 25. p. 575–603.

Antunes, M. T. and Ginsburg, L., 1983: Les rhinocérotidés du Miocène de Lisbonne—systématique, écologie, paleobiogéographie, valeur stratigraphique. *Ciências de Terra*, no. 7, p. 17–98.

Cerdeño, E., 1993: Étude sur *Diaceratherium aurelaianense* et *Brachypotherium brachypus* (Rhinocerotidae, Mammalia) du Miocène moyen de France. *Bulletin du Museum National d'Histoire Naturelle, Série 4*, vol. 15, p. 25–77.

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

Cerdeño, E., 1996: *Prosantorhinus*, the small teleoceratine rhinocerotid from the Miocene of Western Europe. *Geobios*, vol. 29, p. 111–124.

Chavasseau, O., Chaimanee, Y., Tun, S. T., Soe, A. N., Barry, J. C., Marandat, B., Sudre, J., Marivaux, L., Ducrocq, S. and Jaeger, J. J., 2006: Chaungtha, a new Middle Miocene mammal locality from the Irrawaddy Formation, Myanmar. *Journal of Asian Earth Sciences*, vol. 28, p. 354–362.

Deng, T., 2006a: A primitive species of *Chilotherium* (Perissodactyla, Rhinocerotidae) from the Late Miocene of the Linxia Basin (Gansu, China). *Cainozoic Research*, vol. 5, p. 93–102.

Deng, T., 2006b: Chinese Neogene mammalian biochronology. *Vertebrata PalAsiatica*, vol. 44, p. 143–163.

Dollo, L., 1885: Rhinocèros vivants et fossils. *Revue des Questions Scientifiques*, vol. 17, p. 293–300.

Fortelius, M. and Heissig, K., 1989: The phylogenetic relationships of the Elasmotherini (Rhinocerotidae, Mamm.). *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie*, vol. 29, p. 227–233.

Geraads, D., 1988: Révision des Rhinocerotinae (Mammalia) du Turolien de Pikermi. Comparaison avec les formes voisines. *Annales de Paléontologie (Vert.-Invert.)*, vol. 74, p. 13–41.

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

Guérin, C., 1980: Les rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pléistocène supérieur en Europe occidentale. Comparaison avec les especes actuelles. *Documentes des Laboratoires de Géologie de l'Université de Lyon, Sciences de la Terre*, vol. 79, p. 1–1184.

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

Hamilton, W. R., 1973: North African Lower Miocene rhinoceroses. *Bulletin of the British Museum (Natural History) Geology*, vol. 24, p. 351–395.

Harris, J. M. and Leakey, M. G., 2003: Lothagam Rhinocerotidae. *In*, Leakey, M. G. and Harris, J. M. *eds.*, *Lothagam: the Dawn of Humanity in Eastern Africa*, p. 371–387. Columbia University Press, New York.

Hay, O. P., 1902: Bibliography and catalogue of fossil Vertebrata of North America. *United States Geological Survey Bulletin*, vol. 179, p. 1–868.

Heissig, K., 1972: Paläontologische und geologische Untersuchungen im Tertiär von Pakistan 5. Rhinocerotidae (Mamm.) aus den unteren und mittleren Siwalik-Schichten. *Bayerische Akademie der Wissenschaften, Mathematische-Naturwissenschaftliche Klasse, Abhandlungen, Neue Folge*, 152, p. 7–112.

Heissig, K., 1973: Die Unterfamilien und Tribus der rezenten ud fossilen

Rhinocerotidae (Mammalia). *Säugetierkundliche Mitteilungen*, 21, p. 25–30.

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

Hooijer, D. A., 1966: Fossil mammals of Africa No.21 Miocene rhinoceroses of East Africa. *The Bulletin of the British Museum (Natural History), Geology*, vol. 13, p. 119–190.

Itoigawa, J., 1980: Geology of the Mizunami district, central Japan. *Monograph of the Mizunami Fossil Museum*, no. 1, p. 1–50. (*in Japanese with English abstract*)

Itoigawa, J. and Shibata, H., 1992: Miocene paleogeography of the Setouchi geological province, Japan, a revision. *Monograph of the Mizunami Fossil Museum*, no. 19, p. 1–12. (*in Japanese with English abstract*)

Kamei, T. and Okazaki, Y., 1974: The mammalian fossils of the Mizunami Group, Central Japan. *Bulletin of the Mizunami Fossil Museum*, no. 1, p. 263–291. (*in Japanese*)

Kano, K., Yoshikawa, T., Yanagisawa, Y., Ogasawara, K. and Danhara, T., 2002: An unconformity in the early Miocene syn-rifting succession, northern Noto Peninsula, Japan: Evidence for short-term uplifting precedent to the rapid opening of the Japan Sea. *The Island Arc*, vol. 11, p. 170–184.

Matsumoto, H., 1921: Descriptions of some new fossil mammals from Kani District, Province of Mino, with revisions of some Asiatic fossil rhinocerotids. *The Science Reports of the Tohoku Imperial University, Second Series (Geology)*, vol. 5, p. 75–91.

Miyata, K. and Tomida, Y., 2010: *Anchitherium* (Mammalia, Perissodactyla, Equidae) from the Early Miocene Hiramaki Formation, Gifu Prefecture, Japan, and its implication for the early diversification of Asian *Anchitherium*. *Journal of Paleontology*, vol. 84, p. 763–773.

Okazaki, Y., 1977: Mammalian fossils from the Mizunami Group, Central Japan. *Monograph of the Mizunami Fossil Museum*, no. 4, p. 9–24. (*in Japanese with English abstract*)

Okazaki, Y., 1980: The limb bone fossils from Kani District, Central Japan. *Bulletin of the Gifu Prefectural Museum*, no. 1, p. 1–12. (*in Japanese*)

Okumura, K., Okazaki, Y., Yoshida, S. and Hasegawa, Y., 1977: The mammalian fossils from Kani Town, Central Japan. *Geology and Paleontology of Kani Town, Central Japan*, p. 21–44. (*in Japanese*)

Owen, R., 1845: *Odontography*, 655 p. Hippolyte Baillière, London.

Peter, K., 2002: Odontologie der Nashornverwandten (Rhinocerotidae) aus dem Miozän (MN5) von Sandelzhausen (Bayern). *Zitteliana*, vol. 22, p. 3–168.

Prothero, D. R., 2005: *The Evolution of North American Rhinoceroses*, 218 p. Cambridge University Press, Cambridge.

Prothero, D. R., Manning, E. M. and Hanson, C. B., 1986: The phylogeny of the Rhinocerotoidea (Mammalia, Perissodactyla). *Zoological Journal of the Linnean Society*, vol. 87, p. 341–366.

Qiu, Z. and Qiu, Z., 1995: Chronological sequence and subdivision of Chinese Neogene mammalian faunas. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 116, p. 41–70.

Qiu, Z. and Xie, J., 1997: A new species of *Aprotodon* (Perissodactyla, Rhinocerotidae) from Lanzhou Basin, Gansu, China. *Vertebrate PalAsiatica*, vol. 35, p. 250–267.

Ringström, T., 1924: Nashörner der Hipparion-Fauna Nord-Chinas. *Palaeontologia Sinica*, vol. 1, p. 1–156.

Roger, O., 1904: Wirbeltierreste aus dem Obermiocän der bayerisch-schwäbischen Hochebene. *Bericht des Naturwissenschaftlichen Vereines für Schwaben und Neuburg*, vol. 36, p. 1–22.

Saegusa, H., 2008: Dwarf *Stegolophodon* from the Miocene of Japan: Passengers on sinking boats. *Quaternary International*, vol. 182, p. 49–62.

Shikano, K., 2003: The fission track ages of the lower Miocene Mizunami Group in the Mionokamo Basin, Gifu Prefecture, Japan. *Memoirs of the Minokamo City Museum*, no. 2, p. 1–8. (*in Japanese*)

Shuto, K., Ishimoto, H., Hirahara, Y., Sato, M., Matsui, K., Fujibayashi, N., Takazawa, E., Yabuki, K., Sekine, M., Kato, M. and Rezanov, A. I., 2006: Geochemical secular variation of magma source during Early to Middle Miocene time in the Niigata area, NE Japan: back-arc basin opening. *Lithos*, vol. 86, p. 1–33.

Takai, F., 1939: The mammalian faunas of the Hiramakian and Togarian stages in the Japanese Miocene. *In*, Yabe Hisakatsu Kyôju Kanreki Kinen-Kai [Commemorative Association of Professor Hisakatsu Yabe's Sixtieth Birthday] *ed.*, *Jubilee Publication in Commemoration of Professor Hisakatsu Yabe, M.I.A., Sixtieth Birthday, Vol. 1*, p. 189–203. Yabe Hisakatsu Kyôju Kanreki Kinen-Kai, Sendai.

Takai, F., 1949: Fossil mammals from Katabira-mura, Kani-gun, Gifu Prefecture, Japan. *Japanese Journal of Geology and Geography*, vol. 21, p. 285–290.

Tokunaga, S., 1926: Fossils of Rhinocerotidae found in Japan. *Proceedings of the Imperial Academy*, vol. 2, p. 289–291.

Tokunaga, S., 1933: A list of the fossil land mammals of Japan and Korea with descriptions of new Eocene forms from Korea. *American Museum Novitates*, no. 627, p. 1–7.

Tomida, Y., 2000: New taxa of small mammals from the early Miocene of Japan and the origin of *Keramidomys* (Eomyidae). *Journal of Vertebrate Paleontology*, vol, 20, supplementary, 74A.

Tomida, Y. and Goda, M., 1995: Dota local fauna: the first small mammal fauna from the Japanese Tertiary. *Journal of Vertebrate Paleontology*, vol. 15, supplementary, 57A.

Wang, B. Y., 1965: A new Miocene aceratherine rhinoceros of Shanwang, Shantung. *Vertebrata PalAsiatica*, vol. 9, p. 109–113. (*in Chinese with English summary*)

Yan, D. and Heissig, K., 1986: Revision and autopodial morphology of the Chinese–European rhinocerotid genus *Plesiaceratherium* Young 1937. *Zitteliana*, vol. 14, p. 81–109.

Yan, D., Qiu, Z. and Meng, Z., 1983: Miocene stratigraphy and mammals of Shanwang, Shandong. *Vertebrate PalAsiatica*, vol. 21, p. 211–222. (*in Chinese with English summary*)

Yoshida, S., 1957: Tertiary deposits of Katabira, Gifu Prefecture, Japan. *Bulletin of the Aichi Gakugei University*, vol. 6, p. 77–84. (*in Japanese*)

Young, C. C., 1937: On a Miocene mammalian fauna from Shantung. *Bulletin of the Geological Society of China*, vol. 15, p.171–187.