

FIRST RECORD OF THE GENUS *HYOTHERIUM* (MAMMALIA: SUIDAE) FROM JAPAN

Mitsuharu OSHIMA¹, Yukimitsu TOMIDA², Tetsuji ARAKI³
and Yoichi AZUMA⁴

¹ Kanagawa Prefectural Museum of Natural History, 499 Iryuda, Odawara, Kanagawa 250-0031, Japan

² National Museum of Nature and Science, 3-23-1 Hyakunin-cho, Shinjuku-ku, Tokyo 169-0073, Japan

³ Fukui Municipal Ago Elementary School, 4-12 Hondou-cho, Fukui, Fukui 918-8076, Japan

⁴ Fukui Prefectural Dinosaur Museum, 51-11 Terao, Muroko, Katsuyama, Fukui 911-8601, Japan

ABSTRACT

Suid fossil discovered from the early Middle Miocene Aratani Formation of Fukui Prefecture is the best-preserved specimen among those from the Miocene of Japan. The specimen consists of left and right dentary fragments with left c1, p4 fragment, m2–3, right p3, and m1–3. It shows primitive characters within Suidae and is identified as *Hyotherium shanwangense*, known from the late Early Miocene of central China. This is the first record of the genus in Japan, indicating a close paleobio-geographic relationship between Japan and China. The material from Fukui slightly differs in morphology from the type of *H. shanwangense*, and the differences could be interpreted as an evolutionary change during the period of about 2 Ma, between the present specimen (ca. 16 Ma) and the type specimen (ca. 18 Ma), although no direct evidence is present.

Key words: *Hyotherium*, Suidae, Miocene, Aratani Formation, Fukui, Japan, MN 5

大島光春・富田幸光・荒木哲治・東 洋一 (2008) *Hyotherium* 属 (Mammalia: Suidae) 化石の日本初記録. 福井県立恐竜博物館紀要 7: 25–32.

福井県の丹生山地に分布する中期中新世前期の海成層、荒谷層からイノシシ類の化石が発見された。この標本は日本の中新統から見つかっているイノシシ類の中でもっとも保存状態が良く、c と p4 の破片、m2–3 を伴う左下顎骨と、p3 と m1–3 を伴う右下顎骨からなる。この標本は原始的なイノシシ類の特徴を示し、中国の前期中新世後期から知られている *Hyotherium shanwangense* に同定された。これは日本における *Hyotherium* 属の初記録であり、日本と中国が古生物地理学的に近かったことを示唆している。福井県で発見された標本は *H. shanwangense* のタイプ標本とは、わずかではあるが形態的な差異を生じている。直接的な証拠はないが、このことは福井県で発見された標本（約 16 Ma）とタイプ標本（約 18 Ma）との 200 万年の間に生じた進化を示すと解釈することができる。

INTRODUCTION

Fossil records of the family Suidae (Mammalia: Artiodactyla) in the Miocene of Japan are very rare with only four fossil records known so far. The first record is a right lower jaw fragment with two molars, which was described as a new species *Palaeochoerus japonicus* by Takai (1950, 1954), found in the Mimasaka coal-bearing beds in current Mimasaka City, Okayama Prefecture. The original specimen was stored in the Museum of Geology and Paleontology, Tohoku University (Takai, 1954), but it is currently missing. The second specimen was mentioned in Shikama (1975, p. 456) as “suid tooth (or teeth?)” was found from the Miocene of Toki County, Gifu Prefecture”, but the original specimen is missing. The third is an

upper molar fragment of Suinae found in the Oiso Formation of the Upper Miocene in Oiso Town, Kanagawa Prefecture (Oshima, 2007).

The fourth record is the specimen described in this paper. Azuma and Araki found the specimen from an exposure near Takasu-machi, Fukui City (Fig. 1) in 1979 during their survey of the geology of the Neogene deposits. It was just mentioned as *Palaeochoerus?* sp. with no other words in Azuma (1985), and further study was not conducted. This specimen is identified as *Hyotherium shanwangense* in this paper. This is the first record of the genus in Japan.

Dental terminology: For the terminology of the tooth morphology, we follow Pickford (1988) in this paper, and it is shown in figure 2. The term “talonid” usually means the structure posterior to the trigonid, including the talonid basin and surrounding cusps of entoconid, hypoconid, and hypoconulid. But, we follow the practice of previous papers (Fig. 2; e.g., Pickford, 1988; Liu et al., 2002).

Received March 27, 2008. Accepted September 3, 2008.

Corresponding author—Mitsuharu OSHIMA

E-mail: oshima@nh.kanagawa-museum.jp

(*を半角@に変えてご入力ください)



FIGURE 1. Map showing the locality (x mark) of *Hyotherium shanwangense* from Japan (after 1:25,000 topographic map "Ayukawa" published by Geographical Survey Institute of Japan).

GEOLOGIC OUTLINE

The present specimen came from the middle part of the Aratani Formation of Kano et al. (2007) (= Middle Member of the Kunimi Formation in Azuma, 1985), which is exposed near Takasu-machi in Fukui City, Fukui Prefecture, central Japan (Fig. 1).

The Aratani Formation consists mainly of tuffaceous sandstones and siltstones, and includes andesite pyroclastic rocks in the base and middle part of the formation (Kano et al., 2007). The Aratani Formation yields abundant molluscan fossil assemblages characteristic to the lower part of the sublittoral zone or deeper, and those characteristic to the middle-upper part of the sublittoral zone (Nakagawa and Tahara, 1991; Kano et al., 2007). This formation produced large foraminifer fossils correlative with the *Operculina-Miogyopsina* Zone (Matsumaru et al., 1979), and also has yielded planktonic foraminifers correlative with the upper part of Blow's (1969) N8 Zone (Nakagawa and Tahara, 1991). N8 ranges from ca. 17.0 Ma to ca. 14.8 Ma (Lourens et al., 2004).

A K-Ar date of 15.7 ± 0.5 Ma has been obtained from the whole rock sample of andesite lava that is a part of the Aratani Formation (Nakajima et al., 1990). However, according to Kano et al. (2007), this date is actually obtained from a sill that intruded into the basaltic andesite pyroclastic rocks of the formation, and therefore, the geologic age of the Aratani Formation is thought to be the same as this date or slightly older than that. This radiometric date is correlated with the MN 5 Zone of European land mammal zones (Steining, 1999).

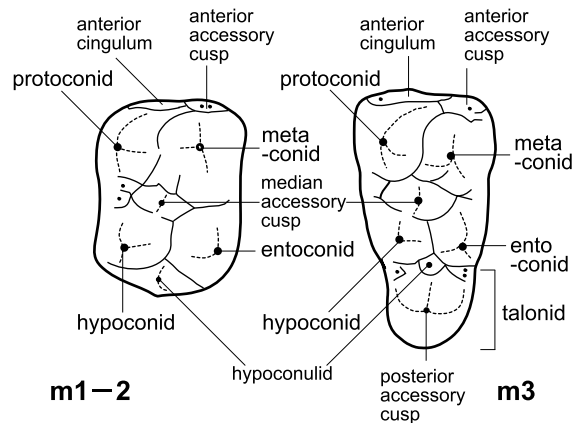


FIGURE 2. Terminology of lower molars of the Suidae.

SYSTEMATIC PALEONTOLOGY

Class MAMMALIA Linnaeus, 1758
Order ARTIODACTYLA Owen, 1848
Suborder SUIFORMES Jaekel, 1911
Family SUIDAE Gray, 1821

Subfamily Incertae sedis

HYOTHERIUM von Meyer, 1834

HYOTHERIUM SHANWANGENSE Liu et al., 2002

Type specimen.—Anterior part of a male skull (IVPP, V11942.1) and a right lower jaw (IVPP, V11942.2).

Synonym.—*Paleochoerus?* sp., Azuma (1985, p. 10)

Material.—Fukui Prefectural Dinosaur Museum (abbreviated as FPDM) specimen number FPDM-V8272: Left lower canine, anterior part of left mandible, middle part of left mandible with p4 fragment, posterior part of left mandible with m2–3, right p3 with a fragment of the mandible, middle part of right mandible with m1–2, and posterior part of right mandible with m3; all of them are considered to belong to a single individual. It is referred to as FPDM-V8272 in the following description, comparison, and discussion sections.

Locality.—Takasu-machi, Fukui City, Fukui Prefecture, central part of Japan (36°06' 50" N, 136°06' 13" E) (Fig. 1).

Horizon and age.—Middle part of the Aratani Formation (Kano et al., 2007). Early Middle Miocene (ca. 16Ma).

Description.—Mandible: The left mandible is broken into three pieces antero-posteriorly (Fig. 3-2a–4a, 2b–4b, 3c), all of which are fragmentary. In the most anterior piece, dorsal half is broken and a large groove (ventral part of canine alveolus) is observable. This large groove accepts the canine, which somewhat splays outside. In the middle piece the lingual surface is depressed, forming irregularly concave surface. Distal part of the posterior root of p3, p4 (see below for detail), and an enamel fragment of possibly m1 are preserved. The enamel fragment of the possible m1 is not located on the original position but in postero-lingual to p4, which indicates the enamel is a fragment of broken tooth. The posterior piece preserves the horizontal ramus from the point beneath the anterior end of m2 to the point beneath the posterior end of m3 and a small portion of ascending ramus just posterior to m3. Buccal surface in all

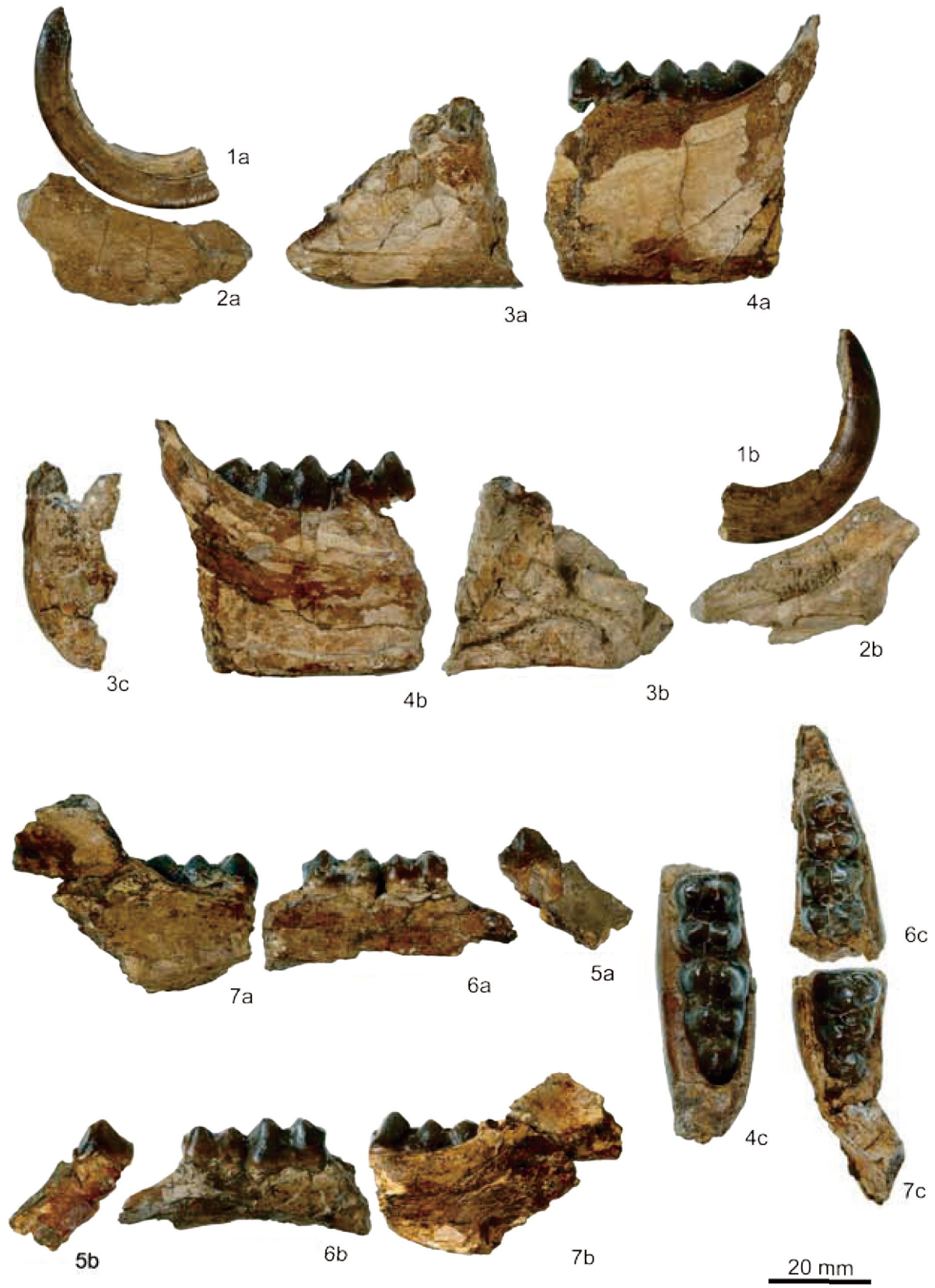


FIGURE 3. *Hyotherium shanwangense* (FPDM-V8272) from Fukui, Japan. 1, left lower canine; 2, anterior part of left mandible; 3, middle part of left mandible with p4 fragment; 4, posterior part of left mandible with m2–3; 5, right p3 with a fragment of right mandible; 6, middle part of right mandible with m1–2; and 7, posterior part of right mandible with m3. 1a–7a, buccal views; 1b–7b, lingual views; 3c, cross section in posterior view; and 4c, 6c, 7c, occlusal views.

TABLE 1. Measurements of the dentition of FPDM-V8272 (in millimeters).

Abbreviations: L = left, R = right, length = length of crown, width 1 = anterior width of crown, width 2 = posterior width of crown, width 3 = width of talonid, and a measurement in parentheses indicates the crown is partially broken.

elements	L/R	length	width 1	width 2	width 3
p3	R	12.27	5.69		
m1	R	12.68	9.71	10.46	
m2	L	16.20	12.84	(12.40)	
m2	R	15.59	12.58	12.66	
m3	L	24.12	13.76	11.61	7.89
m3	R	23.20	14.48	12.04	8.40

pieces are preserved naturally (Fig. 3-2a, 3a, 4a), and it is rather flat, indicating somewhat thin horizontal ramus. Height of the dentary between m2 and m3 is 32.4 mm, while the width is 19.5 mm. The dorsal part of lingual surface is natural, but the ventral part is depressed, forming concave surface (Fig. 3-4b). This depression is deeper anteriorly. The ascending ramus departs from the horizontal ramus near the posterior end of m3; the dorsal surface of mandible lingual to m3 is clearly higher (but not much) than that of buccal, and therefore, the m3 is not hidden by the ascending ramus in buccal view (Fig. 3-4a), while it is slightly hidden in lingual view (Fig. 3-4b).

Right mandible is also broken into three pieces antero-posteriorly, all of which are fragmentary. The anterior piece is a small fragment (Fig. 3-5a, 5b), and shows no distinct character. The middle piece preserves approximately dorsal half of the horizontal ramus, and the buccal surface is somewhat expanded buccally, while lingual surface is nearly vertical (Fig. 3-6b). Posterior piece fits the middle one, but they are not aliened in the original positions, indicating that they might have been broken in the process of diagenesis. Because this part of the mandible is basically same as the left one, no additional character can be observed.

c: Canine is a rootless tooth and is curved dorso-buccally. Its cross section is typical “scrofic type”; the posterior surface with no enamel is wider than buccal surface, and both of them are much narrower than the lingual surface. Shallow groove is present at posterior side of the buccal surface (Fig. 3-1a). A sharp ridge between the posterior and buccal surfaces is more highlighted by that groove. There is a wear facet near and at the apex of the posterior surface (Fig. 3-1b), the length of which is ca. 14 mm.

p3: The lateral view of p3 is approximately an isosceles triangle in outline (Fig. 3-5a, 5b). Two small facets are present lingual to the anterior edge, and two smaller facets are also present on the posterior edge (Fig. 4-a). The postero-buccal corner of the tooth is widened buccally (Fig. 4-a, b). A weak posterior cingulum is present postero-lingually (Fig. 4-a), and a weak anterior cingulum is present along the anterior edge of the tooth. The cervical line is convex coronally on both lateral and lingual views (Fig. 3-5a, 5b).

p4: Only left talonid is preserved (Fig. 5-a, b). Antero-buccal part of the trigonid and the majority of the crown are missing. The talonid is composed of a medium sized cusp

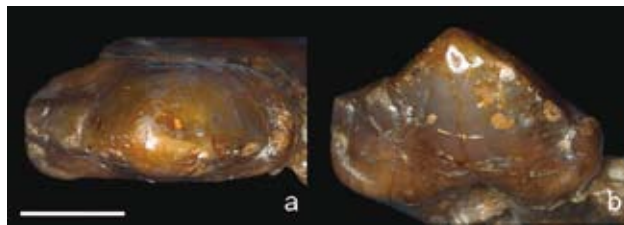


FIGURE 4. Right p3 of *Hyotherium shanwangense* (FPDM-V8272) from Fukui, Japan. a, occlusal view; b, bucco-occlusal view. Scale bar equals 5 mm.

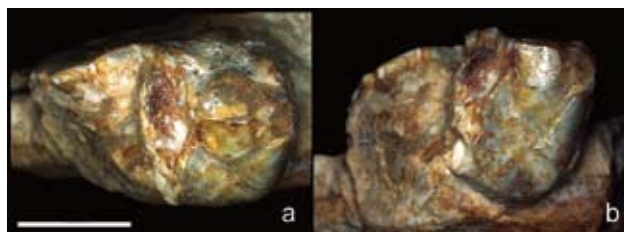


FIGURE 5. Left p4 of *Hyotherium shanwangense* (FPDM-V8272) from Fukui, Japan. a, occlusal view; b, bucco-occlusal view. Scale bar equals 5 mm.

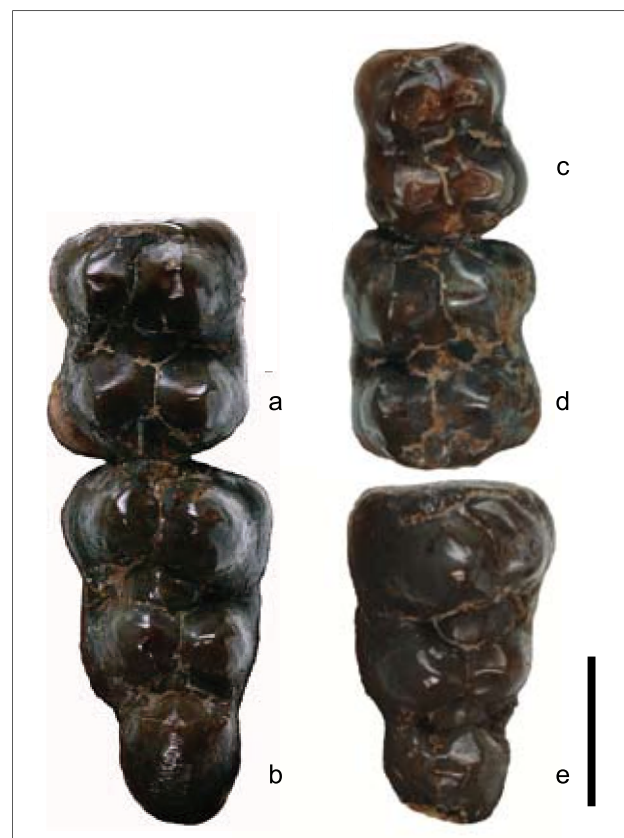


FIGURE 6. Occlusal views of lower molars of *Hyotherium shanwangense* (FPDM-V8272) from Fukui, Japan. Scale bar equals 10 mm.

TABLE 2. Data matrix of FPDM-V8272 and selected genera, showing differences and similarities of characters in lower dentition among those genera. Data are extracted from Liu (2003) and Harris and Liu (2007) except for FPDM-V8272 (this study). "?" indicates unknown.

character no.	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
FPDM-V8272	2	1	?	1	1	0	0	2	?	1	2	2	1	1	1	2	0	1	2	1	0
<i>Sinapriculus</i>	?	?	0	0	1	0	0	2	1	1	2	2	1	1	1	2	0	1	1	1	0
<i>Palaeochoerus</i>	1	1	0	1	0	0	0	2	1	1	2	2	1	1	0	1	0	0	1	1	0
<i>Miochoerus</i>	1	?	0	1	2	0	0	3	1	1	2	2	1	1	1	2	0	1	2	2	0
<i>Hyotherium</i>	2	1	0	1	1	0	0	2	1	1	2	2	1	1	1	2	0	1	2	1	0

which has two wear facets on lingual and buccal sides. A weak posterior cingulum can be observed on the postero-lingual and postero-buccal edges (Fig. 5-a, b). There is a V-shaped, shallow depression (or pit) on the base of the buccal side of the hypoconid (Fig. 5-b). The cervical line is convex coronally on both buccal and lingual views as in p3.

m1: In occlusal view, it is somewhat trapezoidal in out line, slightly wider posteriorly (Fig. 3-6c; Fig. 6-c). Two lingual cusps (metaconid and entoconid) of the four main cusps are slightly higher than buccal cusps. The metaconid is the highest cusp; and its occluding surface is the largest among the four main cusps (Fig. 3-6a, 6c; Fig. 6-c). Anterior accessory cusp is present but very small. Median accessory cusp is relatively large, and a pillar is present, at the buccal end of the median valley (Fig. 6-c). The hypoconulid is represented by small dentine window, and is smaller than median accessory cusp (Fig. 6-c). The anterior cingulum and posterior cingulum are both weak but present (Fig. 3-6a, 6b, 6c; Fig. 6-c).

m2: m2 is similar to, but larger than m1. In the occlusal view, m2 is rectangular shape in outline (Fig. 3-4c, 6c; Fig. 6-a, d). The metaconid is highest, and the area of occluded surface is the largest among the four cusps as in m1. A pillar is present at the buccal end of the median valley (Fig. 6-a, d) and is antero-posteriorly longer than that of m1. A weak ridge runs from the protoconid antero-lingually (see m3 section below). Other characteristics are the same as those of m1.

m3: In occlusal view, m3 is trapezoidal in outline with much narrower posterior end, or narrow triangle in outline (Fig. 3-4c, 7c; Fig. 6-b, e). Among the main cusps, the metaconid is the highest, and the entoconid is the lowest. Anterior accessory cusp is present but small (Fig. 6-b, e). Median accessory cusp is clearly present at the center of the four main cusps, and is larger than that of m2, and a pillar is present at the buccal end of the median valley (Fig. 6-b, e). The 2/3 cusplet of Pickford (1988, fig. 5) is absent. The hypoconulid is present but smaller than in m2 (Fig. 6-b, e). The posterior accessory cusp is present and is as large as main cusps. The talonid is simple and narrow, and is represented by the large posterior accessory cusp (Fig. 6-b, e). Other minor cusps of the talonid are represented by lingual and buccal narrow ridges which are connected to the posterior accessory cusp (Fig. 6-b, e). A distinct ridge runs from the protoconid antero-lingually, and it is probably because the groove 4 of Pickford (1988, fig. 5) is absent.

COMPARISON

In terms of the classification of the Suoidea, we follow Harris and Liu (2007), and the FPDM-V8272 will be compared with

TABLE 3. Characters of the lower dentition and their states used in Table 2 (after Liu, 2003).

32	Lower male canine: (0) oval; (1) verrucose section; (2) scrofic section.
33	Lower male canine: (0) rooted; (1) rootless.
34	p1: (0) present; (1) absent.
35	p3 longer than m1: (0) yes; (1) no.
36	The talonid cusp on p3: (0) absent; (1) incipient single cusplet; (2) distinct single cusplet, (3) two cusplets; (4) distinct and very high (hypoconulid almost to the height of main cusp).
37	Hypertrophy of p3 and p4: (0) absent; (1) weakly present; (2) strong present.
38	Entoconid in p4: (0) absent; (1) present.
39	p4 hypoconid: (0) absent; (1) present but small; (2) distinct but low (below the half of main cusp's height); (3) distinct and very high (over half of the main cusp's height); (4) almost to the level of
40	p4 metaconid: (0) absent; (1) present but fused with protoconid; (2) separated from protoconid; (3) well separated from protoconid by deep groove.
41	Entoconid on lower molar: (0) small; (1) normal size as other main cusps.
42	Paraconid on lower molar: (0) distinct; (1) close to metaconid; (2) fused to metaconid.
43	Paracristid: high(0) high; (1) low; (2) very low and weak.
44	Cristid obliqua: (0) present; (1) absent.
45	Hypoconid and entoconid: (0) connected by hypopholid; (1) without hypoconid connection; (2) cusp with tendency to lophodonty (3) cusp sublophodont; (4) cusp lophodont.
46	Protoconid and metaconid: (0) with protocristid connection; (1) without protocristid connection; (2) cusp with tendency of lophodonty.
47	Hypoconulid in lower molar: (0) none; (1) incipient; (2) distinct.
48	m3 hypoconid: (0) present; (1) reduced.
49	m3 elongation: (0) third lobe single cusp; (1) third lobe with a hypoconulid between it and the rear cusp pair; (2) with elongate hypoconulid; (3) third lobe double cusps; (4) forth lobe double cusps.
50	Lower molar central accessory cusps: (0) none; (1) incipient; (2) distinct.
51	Lower molar anterior lobe higher than posterior: (0) strongly present; (1) weakly present; (2)
52	Transverse valley on molar: (0) narrow valley and shallow floor; (1) narrow valley and deep floor; (2) wide valley deep floor.

their taxa. As described above, FPDM-V8272 is characterized in short as follows: (1) relatively small size; (2) the lower canine scrofic type; (3) p3–p4 simple in morphology, narrow in width, and without wrinkled enamel surface; (4) typically bunodont molars and m3 with relatively small talonid; (5) relative size increase from m1 to m3 moderate; (6) lower molars with the main cusps uneven size and uneven height; (7) ascending ramus not hiding the rear portion of m3 in side view. The combinations of these characters exclude the possibility of FPDM-V8272 to be identified as any of the followings: Tayassuidae, Sanitheriidae, other suoid genera, and all the subfamilies of Suidae listed in Harris and Liu (2007).

Harris and Liu (2007) listed eight genera in Suidae without subfamily assignment. Among them, *Pecarichoerus*, *Albanohyus*, and *Aureliachoerus* can be distinguished from FPDM-V8272 also by the characters listed above. Other five genera, namely *Eocenchoerus*, *Hyotherium*, *Sinapriculus*, *Paleochoerus*, and *Miochoerus* are included in Liu (2003), in which she introduced the cladistic analysis on the systematic study of Chinese suoid fossils. She included 25 genera of Suoidea as ingroups and three genera of non-suoids as outgroups. Although she counted 81 characters, the comparisons with FPDM-V8272 are possible only on the characters of lower dentition, character numbers from 32 to 52 (except for 34 and 40, which are missing on FPDM-V8272) of Liu (2003). Although the lower dentition of *Eocenchoerus* is unknown, it is known from the Late Eocene and is very primitive form, and therefore it can be separated from FPDM-V8272. Table 2 is compiled after Liu (2003), Harris and Liu (2007), and our observation on FPDM-V8272. Most of the characters are synapomorphies that are not reflected in Liu's phylogenetic analysis (Liu, 2003, fig. 2), but they are useful to show the differences and similarities among those genera. FPDM-V8272 can be distinguished from *Sinapriculus*, *Palaeochoerus*, and *Miochoerus* based on her data matrix. *Palaeochoerus* differs from FPDM-V8272 on the character numbers 32, 36, 46, 47, 49, and 50, while *Miochoerus* differs from the latter on 32, 36, 39, and 51 (Table 2); thus, both

genera differ from FPDm-V8272. The character number 32 of *Miochoerus* is “?” in Liu (2003), but Harris and Liu (2007) show that it is “1” = verrucose canine. *Sinapriculus* differs from FPDm-V8272 on the character numbers 35 and 50. Although character number 32 (male lower canine) of *Sinapriculus* is “?” (unknown) because the holotype is female, it is more likely “1” = verrucose. *Hyotherium* agrees with FPDm-V8272 on all character numbers except for 34 and 40, which are unknown on the latter (Table 2).

Although several named species have been known in the genus *Hyotherium*, we follow Liu et al. (2002) for the classification of species within the genus, and they recognize three valid species: *H. meissneri*, *H. soemmeringi*, and *H. shanwangense*. Although Liu et al. (2002) compared three species in size of cheek teeth, in dental proportions, and in non-metric morphological characters, FPDm-V8272 can be compared directly only with the size, and it is closest to *H. shanwangense*. None of the morphological characters that Liu et al. (2002, table 3) listed is applicable to FPDm-V8272, but *H. soemmeringi* can be distinguished from FPDm-V8272 by the presence of developed hypoconid on p4, and *H. meissneri* is also distinguished from FPDm-V8272 by the presence of somewhat better developed hypoconids on p3 and p4 (Hellmund, 1991). Liu (2003) listed in her cladistic analysis that (1) the talonid cusp on p3 is incipient single cusplet (character number 36) and (2) p4 hypoconid is distinct but low (below the half of main cusp's height) (character number 39), as common characters among the species of the genus *Hyotherium*. These characters, however, vary among the species: both characters are more distinct in *H. meissneri* than *H. shanwangense* and the p4 character is most distinct in *H. soemmeringi*. And thus, FPDm-V8272 is almost identical with *H. shanwangense*. The slight difference is the relative size increase from m1 to m3; that is, in the holotype of *H. shanwangense*, m1 is larger but m3 is smaller than FPDm-V8272, while m2 is about the same size in both specimens. This difference may be interpreted as intra-specific evolution during the time period between the Shanwang bed and Aratani Formation, because there is a general tendency that later forms within a same genus have larger m3 in the family Suidae (e.g., Made (1989) for *Conohyus* lineage; Harris and White (1979) for *Nyanzachoerus*–*Notochoerus* lineage). In addition, FPDm-V8272 differs from the holotype in (1) small anterior and posterior cingulum of p3 is somewhat better developed in the latter; (2) number of pillars on the buccal end of median valley in m1 is one in FPDm-V8272 and four in the holotype; (3) the maximum width in m1 and m2 appears slightly above the cervical line in FPDm-V8272, while it appears at about the cervical line. These differences can be observed among a population of living Japanese wild boar (*Sus scrofa leucomystax*), and thus can be interpreted as variation within a species.

Although Takai (1954) gave a new name, *Palaeochoerus japonicus*, to a suid jaw fragment from the Miocene Mimasaka coal-bearing beds in Okayama Prefecture of Japan, he (1) gave no specific characters to identify the specimen as the genus *Palaeochoerus*, other than “dental characteristics and stratigraphic viewpoints” (p. 332), (2) mentioned “its reference to the genus *Palaeochoerus* is tentative” (p. 334), and (3) gave no specific diagnosis other than “much blunt cusps and still bigger size” relative to *P. aurelianusensis* (p. 334) among 11 species he listed. Thus, *P. japonicus* is obviously nomen dubium

or may be nomen nudum. Because the Mimasaka specimen is currently missing, the comparison is made with the photos and descriptions of Takai (1954). Among the characters used by Liu (2003), character numbers 41 to 47 are those of m1 and m2 (Table 2). The Mimasaka specimen shows that the protoconid and metaconid have no connection with the protocristid (= there is no protocristid; 1 in character number 46), and the hypoconulid is distinct (2 in character number 47), while the former has the connection with the protocristid (0 in character number 46), and the latter is incipient (1 in character number 47) in the genus *Palaeochoerus* (Table 2). Both characters are obvious in *Palaeochoerus* types (e.g., Hellmund, 1992). Therefore, the Mimasaka specimen does not belong to the genus *Palaeochoerus* in current taxonomy. However, *Sinapriculus*, *Miochoerus*, and *Hyotherium* share the same characters in the character numbers 41 to 47 with the Mimasaka specimen (*Kubanochoerus* is also the same, but can be distinguished by its much larger size), in addition to the similar size to each other, it is impossible to identify the Mimasaka specimen at generic level, without finding additional characters.

Based on the description by Takai (1954) and his photos, the Mimasaka specimen and FPDm-V8272 share the following characters: in m1 (1) talonid width is wider than trigonid width (= trapezoidal in outline), (2) four main cusps are not equal in size (Takai described as equal in size, but actually they differ from each other based on the photos), (3) protocristid is not present, and (4) hypoconulid is distinct, in addition to the following differences (1) two median accessory cusps (although one is very small) are present in the former, while only one in the latter, and (2) length of m2 relative to its width is longer in the former while it is shorter in the latter (L/W = 1.37 vs 1.23). The first two shared characters are those that are common in a number of other genera in the family, and the last two shared characters are common within the genera *Sinapriculus*, *Miochoerus*, and *Hyotherium* (Liu, 2003). Two differences mentioned above alone are not useful in taxonomic identification. Therefore, the Mimasaka specimen does not show any useful characters to compare with FPDm-V8272 in taxonomic identification.

DISCUSSION

Geologic age of FPDm-V8272 is estimated as 15.7 ± 0.5 Ma or slightly older, which is correlated with the MN 5 in European land mammal zones (Steininger, 1999). The type locality of *H. shanwangense* is the type of Shanwangian age and is correlated with the time slightly younger than 18 Ma and MN 4 of European land mammal zones (Deng, 2006). Therefore, there is a time gap of about 2 million years between the holotype of *H. shanwangense* and FPDm-V8272. The total of evolution before and after arriving Japan for about 2 million years (although there is no evidence when it reached Japan) may explain the slight differences between the holotype and FPDm-V8272, especially the relative size increase from m1 to m3. This difference is consistent with the general tendency in Suidae, in which later forms within a single lineage have larger m3 than the earlier forms (e.g., Made (1989) for *Conohyus* lineage; Harris and White (1979) for *Nyanzachoerus*–*Notochoerus* lineage).

ACKNOWLEDGMENTS

We thank L.-P. Liu of Institute of Vertebrate Paleontology and Paleoanthropology, Beijing for providing plaster casts of the holotype of *H. shanwangense*. Reviews of the submitted manuscript were provided by K. Miyata of Fukui Prefectural Dinosaur Museum and an anonymous referee. Financial supports for MO and YT have derived from the Sasagawa Scientific Research Grant in 2003 (15-341G), and a grant of National Museum of Nature and Science in 2007 (entitled “Studies on the Geography and Evolution of Biodiversity in Japan”), respectively.

REFERENCES

- Azuma, Y. 1985. The Miocene stratigraphy in the northwestern part of the Niu Mountains, Fukui Prefecture: with special reference to a newly found unconformity of the Middle Miocene. *Bulletin of Fukui Prefectural Museum* 1: 1–17.**
- Blow, W. H. 1969. Late Middle Eocene to Recent planktonic foraminiferal biostratigraphy. *Proceeding of 1st International Conference Planktonic Microfossils*, E. J. Brill, Leiden 1: 199–422.
- Deng, T. 2006. Chinese Neogene mammal biochronology. *Vertebrata Palasiatica* 44(2): 143–163.
- Gray, J. E. 1821. On the natural arrangement of vertebrate animals. *London Medical Repository* 15: 296–310.
- Harris, J. M., and L. Liu. 2007. Superfamily Suidae; pp.130–150 in D. R. Prothero and S. E. Foss (eds.), *The Evolution of Artiodactyls*. Johns Hopkins University Press, Baltimore.
- Harris, J. M., and T. D. White. 1979. Evolution of the Plio-Pleistocene African Suidae. *Transactions of the American Philosophical Society* 69 (2): 1–128.
- Hellmund, M. 1991. Schweinartige (Suina, Artiodactyla, Mammalia) aus oligo-miozänen Fundstellen Deutschlands, der Schweiz und Frankreichs. I. *Hyotherium meissneri* (Suidae) aus dem Unter-miozän von Ulm-Westtangente (Baden-Württemberg). *Stuttugarter Beiträge zur Naturkunde Serie B* 176: 1–69.
- Hellmund, M. 1992. Schweineartige (Suina, Artiodactyla, Mammalia) aus oligo-miozänen Fundstellen Deutschlands, der Schweiz und Frankreichs. II. Revision von *Palaeochoerus* Pomel 1847 und *Propalaeochoerus* Stehline 1899 (Tayassuidae). *Stuttugarter Beiträge zur Naturkunde Serie B* 189: 1–75.
- Jaeckel, O. 1911. Die Wirbeltiere. Eine Übersicht über die fossilen und lebenden Formen Berlin, viii + 1–252.
- Kano, K., H. Yamamoto and T. Nakagawa. 2007. Geology of the Fukui district. With geological sheet map 1:50,000, Fukui, Geological Survey of Japan, AIST, 68 p.**
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Vol. 1: Regnum animale. Editio decimal, reformata. Laurentii Salvii, Stockholm
- Liu, L. 2003. Chinese fossil Suidae: Systematics, Evolution, and Paleoeology. University of Helsinki Printing House 40 pp.
- Liu, L., M. Fortelius and M. Pickford. 2002. New fossil Suidae from Shanwang, Shandong, China. *Journal of Vertebrate Paleontology* 22 (1): 152–163.
- Lourens, L., F. Hilgen, N. J. Shackleton, J. Laskar and D. Wilson. 2004. The Neogene Period; pp. 409–440 in F. M. Gradstein, J. G. Ogg and A. G. Smith (eds.), *A Geologic Time Scale 2004*. Cambridge University Press, Cambridge.
- Made, J. Van der. 1989. A *Conohyus* - Lineage (Suidae, Artiodactyla) from the Miocene of Europe. *Revista Española de Paleontología* 4: 19–28.
- Matsumaru, K., Y. Azuma and K. Takeyama. 1979. Discovery of *Miogypsina* and *Operculina* from the Miocene sediments of Niu Mountains, Fukui Prefecture and its significance. *Journal of Geological Society, Japan* 85 (12): 771–774.*
- Meyer, H. v. 1834. Die fossilen Zähne und Knochen und ihre Ablagerung in der Gegend von Georgensgmünd in Bayern. J. D. Verlag Sauerländer Frankfurt. pp. i–viii + 126 pp., 14 pls.
- Nakagawa, T., and N. Tahara. 1991. The Miocene Lithostratigraphy in the northern part of Niu Mountains, Fukui Prefecture, Central Japan. Professor S. Miura Memorial Volume 11–27.**
- Nakajima, T., Y. Sawada, T. Nakagawa, A. Hayashi and T. Itaya. 1990. Paleomagnetic results and K-Ar dating on Miocene rocks in the northern part of Fukui Prefecture, Central Japan—with reference to the rotation of Southwest Japan—. *Journal of Mineralogy, Petrology and Economic Geology* 85: 45–59.
- Oshima, M. 2007. On a molar teeth of Upper Jaw of Suidae from the Miocene Oiso Formation, Kanagawa Prefecture, Japan. *Bulletin of Kanagawa Prefectural Museum (Natural Science)* (36): 29–32.**
- Owen, R., 1848. Description of teeth and portions of jaw of two extinct anthracotheriid quadrupeds (*Hyopotamus vectianus* and *Hyop. bobinus*) discovered by the Marchioness of Hastings in the Eocene deposits on the N. W. coast of the Isle of Wight: with an attempt to develop Cuvier’s idea of classification of pachyderms by the number of their toes. *Quaternary Journal of the Geological Society, London* 4: 103–141.
- Pickford, M. 1988. Revision of the Miocene Suidae of the Indian subcontinent. *Münchener Geowissenschaftliche Abhandlungen Reihe A Geologie und Paläontologie, München* 12: 1–91.
- Shikama, T. (ed.) 1975. *Paleontology III* (new version). Asakura Publishing Co., Ltd., Tokyo iv+527 pp.*
- Steininger, F. F. 1999. Chronostratigraphy, Geochronology and Biochronology of the Miocene “European Land Mammal Mega-Zones” (ELMMZ) and the Miocene “Mammal-Zones (MN-Zone)”; pp. 9–24 in G. E. Rössner and K. Heissig (eds.), *The Miocene Land Mammals in Europe*. Verlag Dr. Friedrich, München.
- Takai, F. 1950. About the Fossil wild boar from Tsuyama Basin. *Journal of Geological Society, Japan* 56: 278–279.*
- Takai, F. 1954. An addition to the Mammalian fauna of the Japanese Miocene. *Journal of Faculty of Science, University of Tokyo, Section of Geology*, 9: 331–335.

* : in Japanese

** : in Japanese with English abstract

< 地名・地層名 >

Aratani Formation 荒谷層
 Fukui Prefecture..... 福井県
 Mimasaka coal-bearing beds
美作夾炭層

Mimasaka City.....美作市
 Toki County.....土岐郡
 Oiso Formation 大磯層

Oiso Town大磯町
 Takasu-machi高須町
 Kunimi Formation 国見層