
Article

A partial skeleton of *Paleoparadoxia* from San-yama, Ogano-cho, Saitama Prefecture, central Japan

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Abstract

A partial skeleton of *Paleoparadoxia* sp. from the Lower Miocene of the Chichibu Basin, central Japan (SMNH VeF-61) is described. Though rather incomplete compared with other superb skeletons found so far from Japanese Miocene, detailed description of the present specimen sufficiently illuminates the problems in current specific level taxonomy and dental morphology of the genus *Paleoparadoxia*.

Key words: cheek tooth, Desmostylia, Japan, Miocene, postcrania.

Introduction

The Tertiary of the Chichibu Basin, central Japan, is important in the study of peculiar marine ungulates, desmostylians, since it has borne six specimens of this rare animal including two nearly complete skeletons (Arai, 1953; Fujimoto and Sakamoto, 1978; Tsunoda et al., 1978; Sakamoto, 1983; Yoshida, 1984). However, none of those specimens have been described adequately, including SMNH VeF-61 (= Chichibu Ogano specimen of Inuzuka, 1984b and Yoshida, 1984), which is described here. Though its occurrence was reported earlier (Tsunoda et al., 1978) and has been referred to as one of the oldest *Paleoparadoxia* from the Japanese Islands (Chinzei, 1984), the specimen has remained to be described for two decades. During those two decades, desmostylian taxonomy and functional morphology have advanced greatly (e.g. Inuzuka et al., 1995; Inuzuka, 2000a,b). Superb skeletal specimens of desmostylians found from both sides of Northern Pacific provided the basis for this advancement. However, among them, only one skeleton, UHR no.18466, has been fully described (Ijiri and Kamei, 1961; Shikama, 1966, 1968; Inuzuka, 1980, 1981, 1982, 1984a). All the others have been described partially or left totally

undescribed. Paucity of detailed descriptions of those materials causes difficulties in communication among those interested in desmostylian taxonomy, since only formal descriptions of specimens provides a common basis for discussion. Under the present conditions, the description of the present specimen still may have some significance, although it is rather fragmental and less informative compared with other superb skeletons. Thus, the primary purpose of this paper is to add to the available information on the dental and skeletal anatomy of Desmostylia, in order to facilitate future discussions on desmostylian taxonomy and paleobiology.

Museum abbreviations used in the text are FM: Fukushima Museum (Aizuwakamatsu, Japan); FMI: The Folk Museum of Itsukaichi (Itsukaichi, Tokyo, Japan); IPM: Iwate Prefectural Museum (Morioka, Japan); NSMT: National Science Museum (Tokyo, Japan); SMNH: Saitama Museum of Natural History (Nagatoro, Chichibu, Saitama, Japan); UCMP: University of California, Museum of Paleontology (Berkeley, California, U.S.A.).

Mode of occurrence and geological setting

SMNH VeF-61, which is here described, was

found on the riverbed of the Akahira River at Koganezawa, San-yama, Oganomachi, Chichibu County, Saitama Prefecture, Japan by Messrs. Tatsuya Sasaki and Naokazu Kuroda in 1978 (Tsunoda et al., 1978). SMNH VeF-61 consists of four postcranial elements (scapula, humerus, femur, and lumbar vertebra), one molar and several rib fragments. First upper molar, condyle of humerus, neural spine and arch of the lumbar vertebra and cranial half of the left scapula were found exposed and eroded on the riverbed. The skeletal elements were found completely disarticulated in the siltstone, but to be concentrated in an area of approximately 100 x 50 cm. Significantly, no skeletal elements other than those mentioned above were found. The association suggests the presence of a single individual (however, see further below). Numerous molluscan fossils were found together with fossil bones and a tooth. Irregular pits are found on the surface of the distal extremity of femur, costal surface of scapula, deltoid tuberosity of humerus and the body of the lumbar vertebra. Obviously, these pits were formed before burial because they are seen on the surface of the bones that had been covered with the matrix before the preparation. They may have been formed by some benthonic animals or algae during the exposure of the disarticulated bones on the sea floor. Distal ends of a femur, a humerus, right scapula, and the body of a lumbar vertebra were

encased in hard calcareous concretion. Minute faults run transversally on the proximal end of the femur and the distal end of the left scapula, but there appears to be no compressional deformation on the bones.

The Tertiary strata of the Chichibu Basin have been variously subdivided and named (e.g. Hayakawa, 1930; Ijiri et al., 1950; Watanabe et al., 1950; Arai and Kanno, 1960; Takahashi, 1992; see Takahashi, 1992, fig.2). Among them, Arai and Kanno (1960) provide the most concise and thorough description of the Tertiary of the Chichibu Basin. Because of this, their work has been referred to most frequently by later authors including those who mentioned the occurrences and stratigraphic distribution of desmostylians in the Tertiary of the Chichibu Basin (Tsunoda et al., 1978; Fujimoto and Sakamoto, 1978; Sakamoto, 1983; Yoshida, 1984). In order to maintain continuity to the previous description of the occurrences and stratigraphic distribution of desmostylians in the Tertiary of the Chichibu Basin, here, I adopt the stratigraphy proposed by Arai and Kanno (1960).

According to Arai and Kanno (1960), the Tertiary in the Chichibu Basin is divided into the Hikokubo Group composed of the Ushikubitoge Formation and the Nenokami Sandstone, the Oganomachi Group consisting of the Miyato, Yoshida and Sakurai Formations and the Chichibumachi Group made of

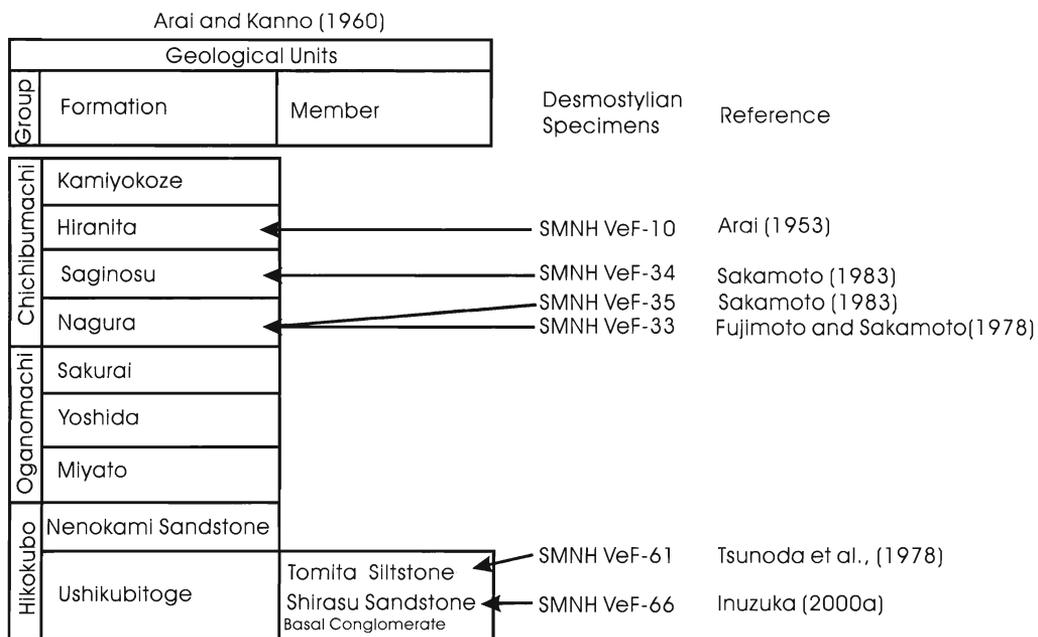


Fig.1. Stratigraphic positions of the Desmostylia from the Chichibu Basin. Stratigraphy after that of Arai and Kanno (1960). Note that the members of the Miyato and the upper formations are omitted.

the Nagura, Saginosu, Hiranita and Kamiyokoze Formations, in ascending order (Fig.1). The SMNH VeF-61 was yielded by the Tomita Siltstone Member of the Ushikubitoge Formation.

Besides the present specimen (Tsunoda et al., 1978), five specimens of desmostylians are said to be found from the Chichibu Basin (Arai, 1953; Fujimoto and Sakamoto, 1978; Sakamoto, 1983; Inuzuka, 2000 a). Their finding horizons can be classified into five horizons (Fig.1). The lowest horizon, the Shirasu Sandstone Member of the Ushikubitoge Formation represents the lowest desmostylian horizon, which bears a desmostylian metatarsal (SMNH VeF-66) (Inuzuka, 2000a). The Tomita Siltstone Member of the Ushikubitoge Formation, which overlies the former member, bears the present specimen. The next horizon, in which two desmostylian skeletons (SMNH VeF-35 and SMNH VeF-33) were found, is the Nagura Formation of the Chichibumachi Group (Fujimoto and Sakamoto, 1978; Sakamoto, 1983). SMNH VeF-34 (Sakamoto, 1983) has been found in the overlying Saginosu Formation, and SMNH VeF-10 (Arai, 1953) is from the Hiranita Formation of the same group. The latter record is the uppermost desmostylian horizon in this basin. Thus from the Tertiary succession of the Chichibu Basin, desmostylians have been known from the basal part to the upper most part, except for the Oganomachi Group in the middle of the succession.

The geologic age of the Tertiary in the Chichibu Basin has been discussed on the basis of the mollusks (e.g. Arai and Kanno, 1960; Ogasawara, 2000), planktonic foraminifers (Ujiie and Iijima, 1959; Saito, 1963; Matsumaru, 1980; Ibaraki, 1981; Matsumaru et al., 1982; Takahashi, 1992), calcareous nannofossils (Takahashi et al., 1989), magnetic polarity (Hyodo, 1986; Hyodo and Niitsuma, 1986) and fission-track age (Adachi et al., 1998), and the age estimations involve several discrepancies especially in both of the lower and upper limits. Ujiie and Iijima (1959) placed the Akahira Group nearly corresponding to the Hikokubo Group and lowest part of the Oganomachi Group as early Miocene age based on the benthic and planktonic foraminifer assemblages. They reported *Catapsydrax dissimilis* from the Nenokami Sandstone, which is an index species of the upper limit of the planktonic foraminifer zone N6 of Blow (1969). Arai and Kanno (1960) considered the Tertiary of the Chichibu Basin is composed of a fairly long sequence ranging from the Oligocene (Hikokubo Group) to

lower Miocene (Oganomachi and Chichibumachi Groups) by means of the mollusks. Saito (1963) examined planktonic foraminifers from the Miyato, Hiranita and Saginosu Formations and reported assemblages assignable to the upper part of N8.

Matsumaru (1980) preliminarily reported *Globorotalia peripheroacuta* from the Kamiyokoze Formation, the uppermost constituent of the Chichibu Group. This species is the index of the lower limit of N10. Ibaraki (1981) examined planktonic foraminifers from the Miyato, Saginosu and Kamiyokoze Formations, and concluded that these formations are assigned to the upper part of N8 and the lowest part of N9. Matsumaru et al. (1982) correlated the Saginosu Formation with the upper part of N8 and the Hiranita and Kamiyokoze Formations with the lowest part of N10.

Based on the above planktonic foraminifer data, Tsuchi and IGCP-114 National Working Group of Japan (1981) concluded that the Tertiary of the Chichibu Basin is correlated with N6 to N10. Thus, a desmostylian from the Tomita Siltstone Member of the Ushikubitoge Formation has been considered to be the geochronologically oldest record of *Paleoparadoxia* from Japan (Chinzei, 1984; Yoshida, 1984).

On the other hand, some authors suggested a shorter range of the geological age than previously assumed. Hyodo (1986) and Hyodo and Niitsuma (1986) correlated normal polarity in the Chichibumachi Group with Chron 5B. Takahashi et al. (1989) assigned the Tomita Siltstone Member of the Ushikubitoge Formation and the Miyato Formation to NN4 or NN5 of Martini (1971) or CN 3 or CN 4 of Okada and Bukry (1980). These zones range from late Early to early Middle Miocene age. Takahashi (1992) concluded that the Tertiary of the Chichibu Basin was deposited during N8 of Blow (1969) based on the planktonic foraminifers obtained from the Miyato and upper formations and magnetostratigraphic result of Hyodo (1986). Adachi et al. (1998) reported a fission-track age of 15.6 ± 0.8 Ma (error: 1σ) from a tuff bed in the Nenokami Sandstone. They doubted the occurrence of *Catapsydrax dissimilis* reported by Ujiie and Iijima (1959) because no additional finding of this species has been known from the Tertiary of the Chichibu Basin.

Recently Ogasawara (2000) argued that the occurrence of *Mytilus tichanovitchi* from the

Nenokami Sandstone (Majima et al., 1996) could be used for the correlation with the lower Miocene Goyasu Formation in the Joban area, Fukushima Prefecture, northeast Japan. According to this correlation, the geological age of the Ushikubitoge Formation can be estimated as between 19 and 18.5 Ma.

Previous complications concerning the geological age of the Ushikubitoge Formation appear to be derived in part from the integrated Neogene planktonic microfossil time scale of Oda (1986) (Takahashi et al., 1989). According to Ujiie and Iijima (1959) and Takahashi et al. (1989), *Catapsydrax dissimilis* and *Sphenolithus heteromorphus* co-occurred in the Ushikubitoge Formation and such co-occurrence is in conflict with the time scale of Oda (1986). In the latest time scale (Berggren et al., 1995), however, such discrepancies are dispelled. According to Berggren et al. (1995) the co-occurrence of above two species in the Ushikubitoge Formation (Ujiie and Iijima, 1959; Takahashi et al., 1989) is not discrepant and indicates an overlapped interval between CN3 and N6 or late Early Miocene age (18.2-17.3 Ma). This age estimation is rather younger than the age estimated by Ogasawara (2000).

Recently, the geologic age of the desmostylian-bearing formations in southwest Japan has been revised by means of diatom fossils, and several formations were found to be of older age than that previously estimated. The Yamanouchi Member of the Akeyo Formation in the Mizunami Basin, which has borne the neotype of *Paleoparadoxia tabatai* (NSMT P-5601), had been placed in Blow (1969)'s zone N8 (e.g. Tsuchi and IGCP-114 National Working Group of Japan, 1981; Chinzei, 1984). On the other hand, Gladenkov (1998) noted that this member can be placed within *Crucidenticula sawamurae* zone (18.4-16.9 Ma: Yanagisawa and Akiba, 1998). In addition, Ito et al. (1999) indicated the Awano Formation, the uppermost constituent formation of the Tomikusa Group, is also correlated with same diatom zone. The Tomikusa Group is also known to have yielded *Paleoparadoxia* sp. (Tanaka and Kamei, 1977) from the Oshimojo Formation occupying the middle part of this group. Thus, *Paleoparadoxia* from these two formations can be regarded as old as the specimens from the Ushikubitoge Formation.

Systematic Paleontology

Class Mammalia Linnaeus, 1758
 Order Desmostylia Reinhart, 1953
 Family Paleoparadoxiidae Reinhart, 1959
 Genus *Paleoparadoxia* Reinhart, 1959

Revised Diagnosis

Premolar bunodont, Molars brachyodont and styloidont with extremely long roots; cingulum varies from subtle swelling to distinct shelf-like structure; mandibular symphysis, incisors, and canines horizontally oriented; diastema between p2 and p3 large; centrum of the lumbar vertebra high dorso-ventrally and short cranio-caudally; tuberculum majus of humerus higher than the head; thin and wide humeral trochlea; lessor trochanter of femur small and projecting; strong median inclination of tuber calcanei

Paleoparadoxia sp.

Material

SMNH-VeF-61 consists of following elements. An isolated upper cheek tooth, lumbar vertebra, left and rights scapulae, left humerus, left femur, and several rib fragments. SMNH-VeF-61 is housed at the Saitama Museum of Natural History. As mentioned above, the mode of occurrence of SMNH VeF-61 strongly suggests that all the elements belonging to SMNH VeF-61 come from a single individual. However, there remains some possibility that they are from more than one individual (see further below). Thus, in the following, I give remarks on each element separately just after the description of the each element

Description

Upper Cheek Tooth (Fig.2, Pl.1, figs.1-4): The crown of the tooth is completely preserved while its root is broken 22 mm below the base of the crown. The cross section of the root shows buccolingually oblong outline and there is neither trace of pulp cavity nor bifurcation of the root at its broken end. Thus, the root may have been single and columnar. There are four main cusps on the crown and their dentine is exposed at the center of these cusps. Mesial two cusps, protocone and paracone, are larger than the distal two, metacone and hypocone. Hypocone is the smallest cusp on the crown. Protocone and hypocone are

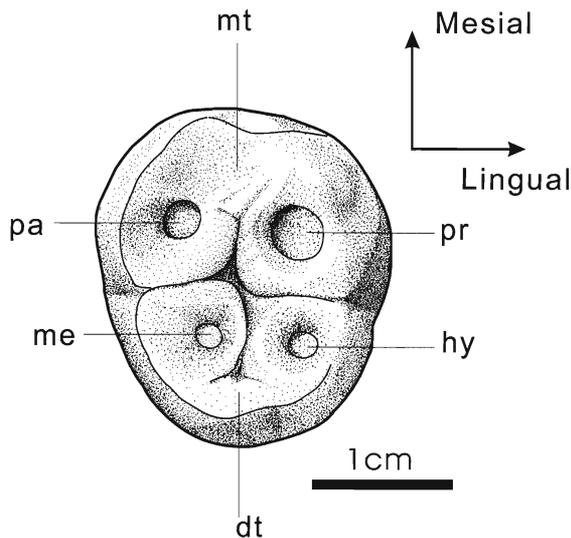


Fig.2. Cheek tooth of SMNH VeF-61.

View: occlusal surface.

Key: dt, distal tubercle; hy, hypocone; me, metacone; mt, mesial tubercle; pa, paracone; pr, protocone.

slightly displaced distally against paracone and metacone, respectively. Tubercles are seen at both the mesial and distal end of the crown. They do not expose dentine. A mesial tubercle is located at the mesial median portion of the crown and separated from paracone and protocone by rudimentary furrows that derived from median deep furrow running between protocone and paracone. Though mesial tubercle does not show dentine exposure, it is only slightly smaller than the hypocone and should be a homologue of paraconule (= mesial talon of Inuzuka, 1987). Compared with the mesial tubercle, the distal one is much smaller and more rudimentary. This tubercle is located at median and distal part of the crown and separated from metacone and hypocone by extremely faint and short furrow extending from the distinct furrow separating hypocone and metacone.

Of the worn surface, the mesiobuccal corner of paracone is the highest. The worn surface of the crown is separated from the buccal surface of the crown by a sharp edge. This ridge runs from the buccal corner of the mesial tubercle (= anterior cone) to the lingual corner of the distal tubercle, via highest point of the worn surface of the crown at the mesiobuccal corner of paracone. On the other hand, lingual margin of the worn surface is largely obliterated, especially at the lingual margin of the worn surface of the protocone, where worn surface of the occlusal surface of the crown is continuous, almost without interruption, to the unworn lingual surface of the crown. The interdental facet is in the

middle of the mesial surface of the crown.

Besides the mesial and distal tubercles, neither cingulum nor tubercle is seen on the crown. As has been much worn, it is not clear, whether cingulum was present before the heavy wear or not. However, judging from the fact that the transverse furrow, which separates the two mesial cusps from the distal ones, reaches both the buccal and lingual surfaces of the crown, there may have been no cingulum. Fine wrinkles are seen on the unworn enamel surface of the cervix. Similar wrinkles are commonly present in other specimens of *Paleoparadoxia*, both with and without distinct cingulum.

Measurements—

Buccolingual width of the crown: 21.6 mm

Mesiodistal length of the crown: 24.1 mm

Remarks—

The following morphological features that identify SMNH VeF-61 as pertaining to *Paleoparadoxia*: its brachydonty, bunodonty, stylodonty and supposed presence of elongated and columnar root. The combination of these features leaves no doubt that the SMNH VeF-61 represents an individual of *Paleoparadoxia*. However, there remains some problem concerning the absence of cingulum in SMNH VeF-61.

Distinct cingulum is a characteristic feature of *Paleoparadoxia*, according to Inuzuka (2000a, b). However, the molar cingulum of *Paleoparadoxia* appears to be variable, being distinct shelf-like structure in some specimen, but subtle swelling in other specimens.

Absence or poor development of cingulum has been reported in several *Paleoparadoxia* specimens. Poor development of the cingulum is observed in molars of *Paleoparadoxia* from the Tokigawa Group (Shimada and Inuzuka, 1994). An upper first molar (KZD 07) has several small tubercles but no cingulum. A worn lower third molar (KZD 10) also does not have cingulum. Because of this, Shimada and Inuzuka (1994) identified those two teeth as *Paleoparadoxia? tabatai*.

Cheek teeth of SMNH VeF-10 from the Chichibumachi Group also show poor development of cingulum (Arai, 1953). In a cheek tooth identified as an upper fourth premolar by Arai (1953), distinct cingulum is observed at the buccal side of the crown. On the other hand, in a cheek tooth that was identified as a upper fourth premolar or first molar by Arai (1953), no distinct cingulum is seen at either side

of the crown, except for subtle swelling at the cervix.

Molars of FM-N8600706 may also represent a variation whose cingulum is very weak or absent. They have never been described in detail, but their pictures in Hasegawa and Taketani (1999, pls.13-14) clearly show that unworn third molars have very weak cingulum whereas no swelling or cingulum is seen on the cervix of worn first and second molars. Absence of cingulum in the latter two molars can be explained by the wear because cingulum on the third molar is so weak that it can be lost by moderate wear. Thus development of the cingulum varies from distinct shelf-like structure to subtle swelling, at least in *Paleoparadoxia tabatai*. On the other hand, the fine wrinkle on the unworn cervix is commonly seen feature in molars of *Paleoparadoxia*, including SMNH VeF-61. Thus the poor development or absence of cingulum in the present specimen does not refute the identification that the present specimen is placed in the genus *Paleoparadoxia*.

The present specimen is undoubtedly a cheek tooth of the genus *Paleoparadoxia*, but there remain several problems in the identification of its tooth class. Most concrete identification of tooth class of teeth must be made by the comparison with those found on a skull. Five skulls of *Paleoparadoxia* (NSMT P-5601, SMNH VeF-33, FMI A-1737, FM-N8600706 and UCMP114285) have been known to be accompanied by cheek teeth (Ijiri and Kamei, 1961; Fujimoto and Sakamoto, 1978; Clark, 1991;

Hasegawa and Taketani, 1999; Hasegawa et al., 1995). Among them, upper cheek teeth of NSMT P-5601, FM-N8600706, SMNH VeF-33 and UCMP 114285 are described or figured and thus available for present comparison. The upper first molars are preserved in NSMT P-5601 and FM-N8600706, but their crown morphology is not known because of heavy wear of the crown. The upper second and third molars of NSMT P-5601, SMNH VeF-33 and FM-N 8600706 differ from that of SMNH VeF-61 by its greater development of paraconule, accessory tubercle and cingulum. Concerning *P. weltoni*, the mesial half of the upper second molar is missing in UCMP114285 (the one and only known skull of this species), and thus it is not clear whether paraconule is also developed like *P. tabatai* or not. The upper third molar of the same skull differs from present specimen in strong development of paraconule. Thus, no upper second or third molars accompanied with skulls known to date can compare best with a cheek tooth of SMNH VeF-61. However, the upper fourth premolars of FM-N8600706 figured by Hasegawa and Taketani (1999) show similarity to SMNH VeF-61. The description of the upper fourth premolars of FM-N 8600706 is not detailed but in their figure, two small cusps are seen on the crown in addition to the three main cusps. Those two small cusps are obviously homologous with the two tubercles located on both sides of the protocone in the upper fourth premolar of the NSMT P-5601. The cheek tooth of SMNH VeF

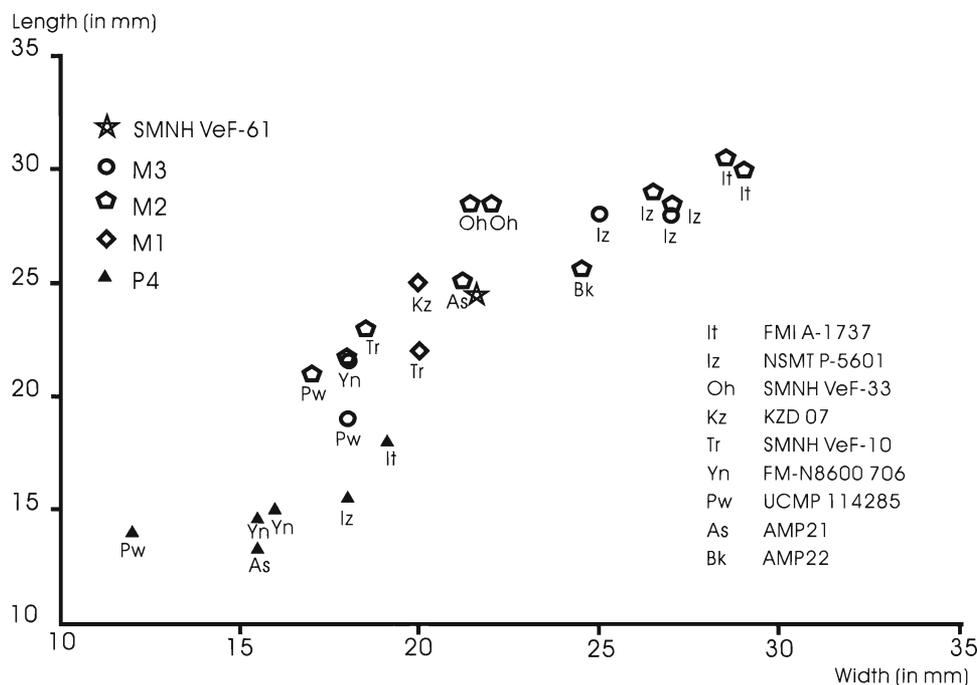


Fig.3. Scatter diagram of length and with of upper cheek teeth of *Paleoparadoxia* shown in Table 1.

Table 1. Dental measurements of specimens of *Paleoparadoxia*.

Specimen#	Species	tooth class	width	length	reference
SMNH VeF-61	<i>Paleoparadoxia</i> sp.	M1 or M2	21.6	24.5	present paper
FM-N8600 706	<i>P. tabatai</i>	P4	15.5	14.6	Hasegawa and Taketani, 1999
ditto	ditto	P4	16	15	ditto
ditto	ditto	M2	18	21.8	ditto
ditto	ditto	M2	18	21.7	ditto
ditto	ditto	M3	18	21.8	ditto
ditto	ditto	p4	13	16.5	ditto
ditto	ditto	m1?	15.4	15	ditto
ditto	ditto	m2	16.7	22.6	ditto
ditto	ditto	m2	16.2	23	ditto
NSMT P-5601	ditto	P4	18	15.5	Ijiri and Kamei, 1961
ditto	ditto	M2	26.5	29	ditto
ditto	ditto	M2	27	28.5	ditto
ditto	ditto	p4	15.5	20	ditto
ditto	ditto	m2	25	28.5	ditto
ditto	ditto	m2	24	28	ditto
SMNH VeF-33	ditto	M2	22	28.5	Hasegawa <i>et al.</i> , 1995
ditto	ditto	M2	21.4	28.5	ditto
FMI A-1737	ditto	P4	19.1	18	ditto
ditto	ditto	M2	29	30	ditto
ditto	ditto	M2	28.5	30.5	ditto
UCMP114285	<i>P. weltoni</i>	P4	12	14	Clark, 1991
ditto	ditto	M2	17	21	ditto
ditto	ditto	M3	18	19	ditto
ditto	ditto	p4	12	17	ditto
ditto	ditto	p4	12	18	ditto
ditto	ditto	m2	16	22	ditto
ditto	ditto	m2	16	21	ditto
KZD07	<i>Paleoparadoxia</i> sp.	M1?	20	25	Shimada and Inuzuka, 1994
AMP22	<i>Behemotops katsui</i>	M2	24.5	25.6	Inuzuka, 2000b
AMP21	<i>Ashoroa laticosita</i>	P4	15.5	13.3	ditto
ditto	ditto	M2	21.2	25.1	ditto
SMNH VeF-10	<i>Paleoparadoxia</i> sp.	M1	20	22	Arai, 1953
ditto	ditto	M2	18.5	23	ditto
ditto	ditto	m1	18.5	23.7	ditto

-61 has only four cusps, but mesial tubercle of it can be considered as insufficiently developed paracone. Thus, the cheek tooth of SMNH VeF-61 is not so different from that of upper fourth premolars of FM-N 8600706 in the number of cusps. However, upper fourth premolar of FM-N8600706 is far smaller than the present specimen (Table 1, Fig.3). Furthermore, a cheek tooth of the present specimen is larger than the fourth premolar of FMI A-1737 (Hasegawa *et al.*, 1995) that is the largest fourth premolar of *Paleoparadoxia* reported so far. Thus, the cheek tooth of the present specimen can not be a premolar unless it belongs to a gigantic *Paleoparadoxia* sp. nov. of Inuzuka (2000b). The latter possibility can not be examined further since the latter species have never been described and no morphological details of the species are available for the present comparison.

Some isolated upper molars reported so far are similar to SMNH VeF-61 in both shape and size. KZD 07 from Kuzubukuo, Saitama Prefecture is the only the specimen of *Paleoparadoxia* which have been described in detail as an isolated upper first molar (Shimada and Inuzuka, 1994). According to them, KZD 07 has five cusps and compares well with heavily worn upper first molar of NSMT P-5601 in its dimensions. In KZD 07, protocone and hypocone are displaced strongly against paracone and metacone and this brought about mesiobuccal projection of the outline of the crown in occlusal view. Though heavily worn, the upper first molar of the NSMT P-5601 also shows this mesiobuccal projection. This similarity to KZD 07 suggests that when unworn, cusp arrangement of NSMT P-5601 was similar to that of KZD 07. Thus, KZD 07 can be identified as upper first molar (Shimada and Inuzuka, 1994).

The following two cheek teeth are similar to KZD 07 and could be upper first molars of *Paleoparadoxia* as well: UCMP45274 reported by Mitchell and Repening (1963), and a cheek tooth (SMNH VeF-10) from Terao, Chichibu Basin described by Arai (1953, figs.11-15). UCMP45274 was figured but not described by Mitchell and Repening (1963). Shimada and Inuzuka (1994) later identified UCMP45274 as an upper first molar. A cheek tooth of SMNH VeF-10 was identified and figured as an upper fourth premolar by Arai (1953), but my observation on the original specimen revealed that the specimen is an upper first molar (see Appendix).

Besides the upper first molar mentioned above, Arai (1953) described another upper cheek tooth of SMNH VeF-10 as an upper fourth premolar or first molar. Except for its earlier wearing stage, this tooth is quite similar to the upper first molar of SMNH VeF-10 and is obviously a second molar of the same individual (see Appendix).

The above four upper molars (KZD 07, UCMP 45274 and SMNH VeF-10) show close similarity to the present specimen in both cusp arrangement and dimensions (Table 1, Fig.3). Those four molars and SMNH VeF-61 have a mesial cuspsule in addition to four cusps. The mesial cuspsule of them is closely appressed to the protocone and paracone and thus can be considered as an insufficiently developed paraconule. However, in the extent of distal displacement of lingual cusps against buccal cusps, a cheek tooth of SMNH VeF-61 is different from the above four molars. In latter four, protocone and hypocone are displaced strongly against paracone and metacone and this brought about mesiobuccal projection of the outline of the crown in occlusal view. On the other hand, this displacement is very weak and thus there is no marked projection of mesiobuccal corner of the crown in SMNH VeF-61. Besides this difference, the cheek tooth of SMNH VeF-61 is very similar to above four molars (KZD07, UCMP45274 and SMNH VeF-10).

In the development of the tubercle, slight differences are seen among them. In KZD 07, there is one tubercle mesial and two tubercles distal to the metacone (Shimada and Inuzuka, 1994). In the upper second molar of SMNH VeF-10, a tiny mesial

tubercle is situated buccal to the mesial cuspsule. UCMP45274 has no tubercle. The upper first molar of SMNH VeF-10 and the cheek tooth of SMNH VeF-61 have single tiny distal tubercle. Thus, the cheek tooth of SMNH VeF-61 compares best with the upper first molar of SMNH VeF-10 in the development of the tubercle. However, such differences in the tubercle seem to be merely individual variations and thus do not verify particular identification of tooth class.

In conclusion, all of the above four molars (KZD 07, UCMP45274 and SMNH VeF-10) can be equally well compared with the cheek tooth of the present specimen.

Lumbar vertebra (Fig.4, Pl.1, Figs.6-11): Right lamina of the neural arch, spine, entire right and two-thirds of left caudal articular process are missing. Epiphysis lines are completely closed. Body is

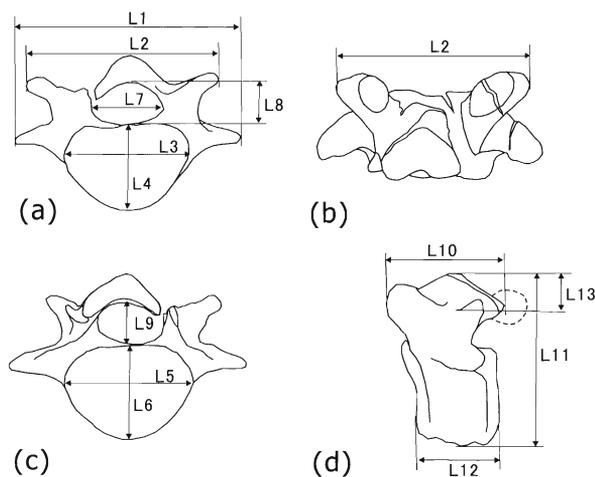


Fig.4. Measurements taken on the lumbar vertebra of SMNH VeF-61.

Views: (a) cranial; (b) dorsal; (c) caudal; (d) lateral.

Key: L1, distance across both transverse processes; L2, maximal width of the anterior articular process; L3, transverse diameter of the cranial surface of the body; L4, height of the cranial surface of the body; L5, transverse diameter of the caudal surface of the body; L6, height of the caudal surface of the body; L7, transverse diameter of the vertebral foramen; L8, height of the vertebral foramen at the cranial end; L9, height of the vertebral foramen at the caudal end; L10, Maximum antero-posterior length of the preserved portion of the vertebra; L11, height of the preserved portion of the lumbar; L12, cranio-caudal length of the body; L13, maximal thickness of the lamina.

Table 2. Measurements of lumbar vertebra See Fig.4 for abbreviations.

	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	L12	L13
mm	134	106.7	71.8	47.5	73.5	48.9	39	29	29.3	63	91	39.4	21

parallelogrammic-shaped and lower to the back in lateral view and dorso-ventrally depressed heart-shaped in cranial and caudal view. Vertebral foramen is low with triangular outline. Pedicles are wide and slightly tilted medially. Lamina is rather wide transversely, anterior margin with wide parabolic notch reaching the posterior margin of the articular surface. Anterior notch is small, while posterior notch deep. Groove for spinal nerve running backward but slightly downward. Spinous process is missing. Transverse processes originate at level of inferior margin of vertebral foramen, project horizontally, swing posteriorly, and are short and tapering towards tip. Cranial articular processes protrude strongly, and their articular surfaces face medio-dorsally, but not rolled up. The articular surface of cranial articular process gently inclines medially at an angle of 30 to 35 degrees to a plane perpendicular to the sagittal plane of the lumbar vertebra. The cranial articular process protrudes more anteriorly to the anterior surface of the body. Mammillary processes project upward and cranio-laterally with a crest extending mediocaudally from the process. There is no marked groove separating articular surface of the cranial articular process from the basal part of mammillary process. There is no median keel on the ventral surface of the body. Accessory process is absent, as is usual with ungulates.

Judging from the depressed heart-shaped outline of the body in cranial and caudal view, from the gentle inclination of the articular surface of cranial articular process, and from posterior swing of transverse processes, this specimen is anterior lumbar. This lumbar vertebra might be the first or second one, because posterior swing of transverse processes is seen only in those two anterior lumbar vertebrae in NSMT P-5601 (Shikama, 1966, textfig.7). If this identification is correct, transverse process of SMNH VeF-61 is shorter than that of NSMT P-5601.

Remarks—

Unlike cheek teeth, materials available for the comparison are limited in postcranial elements because of the paucity of the published materials on them. Thus, following remarks on postcranial elements are heavily dependent on the taxonomic notes of Inuzuka (1989, 2000a, b).

According to Inuzuka (1984a), the lumbar vertebrae of *Desmostylus* are unique in showing a parallelogrammic outline of the body with its posteroventral corner pointed in lateral aspect, and the

cranial articular process protrudes more anteriorly to the anterior surface of the body. Those characters are also seen in the present specimen and appear to be common features of the Order Desmostylia.

Inuzuka (1989, 2000a, b) mentioned that desmostylian genera can be distinguished from each other by the shape of centrum, transverse process, laminar and articular process of lumbar vertebrae. In SMNH VeF-61, the latter two parts of lumbar vertebrae can not be compared with those of other specimens with confidence, because of their poor preservation. However, former two parts of the present specimen exhibit the shape described as characteristic of *Paleoparadoxia*, by Inuzuka (1989, 2000a, b).

According to Inuzuka (1989, 2000a), the body of the lumbar vertebra is lower and wider in *Desmostylus* than in *Paleoparadoxia* and *Behemotops*. As the centrum of the present specimen is depressed in heart shape in cranial and caudal view, it is obviously higher and narrower than that of *Desmostylus* and compares well with *Paleoparadoxia* (Fig.4, Table 2).

Inuzuka (1989) noted the following generic differences in transverse process: in *Behemotops*, transverse process is longer than that of *Desmostylus* and *Paleoparadoxia*. Transverse process tapers at its tip in *Paleoparadoxia*, is wide at its tip in *Behemotops*, and its anterior and posterior border are parallel to each other in *Desmostylus*. As transverse process of the present specimen is short and tapers at its tip, the present specimen is of *Paleoparadoxia* type, according to Inuzuka's description.

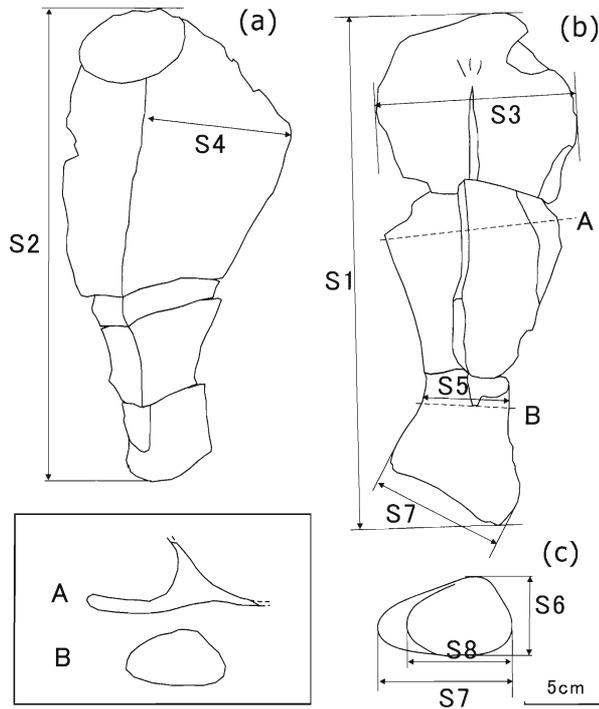
As the shape of centrum and the transverse process is similar to that of *Paleoparadoxia*, the lumbar vertebra of the present specimen can be identified as that of *Paleoparadoxia*.

Scapula (Fig.5, Pl.2, figs.1-6): Left and right scapulae are found. Both of them have not been subjected to compressional deformation, but broken at following parts.

In left scapula, cranial half of the spine and entire supraspinous fossa were lost by erosion. The posterior border of the scapula is fairly well preserved, except for its dorsal end. The portion distal to the neck, including the ventral angle of the scapula, is missing. Three small faults run anteroposteriorly on the ventral half of the scapula. Each of blocks bounded by these small faults is slightly displaced caudally relative to the proximal adjacent block.

Table 3. Measurements of scapulae. See Fig.5 for abbreviations.

	S1	S2	S3	S4	S5	S6	S7	S8
mm	323	297	130	99	54	52.8	89.3	62.5

**Fig.5.** Measurements and cross-sections taken on the scapula of SMNH VeF-61.

Views: (a) lateral view of left scapula; (b) lateral view of right scapula; (c) ventral view of ventral angle of the right scapula. Broken lines indicate the positions where cross-sections are taken. Cross-sections are shown in the box.

Key: S1 and S2, maximal dorso-ventral length of preserved portion; S3, maximal width of the blade; S4, maximal width of preserved portion of infraspinatus fossa; S5, minimal antero-posterior width of the neck; S6, maximal medio-lateral width of the ventral angle; S7, maximal antero-posterior width of the ventral angle; S8, maximal antero-posterior width of glenoid cavity.

Surface of the bone is irregularly pitted and very rough so that the original texture of bony surface, such as rugosity of muscular attachment, can not be identified. The dorsal border is poorly preserved. A fragment of anterior rib is attached on the costal surface.

In right scapula, surface of the bone is irregularly pitted and original texture of bony surface is obliterated, except for the neck. Neck and ventral angle are preserved. Free lateral margin of the spine, acromion, the dorsal half of the posterior border, and entire dorsal and anterior borders are missing. Glenoid surface is slightly worn, exposing cancerous

inner texture of the bone.

Overall, outline of the scapula is an elongated triangle. Neck bends inward and spine leans backward. Costal surface is concave as a whole, except dorsal part. The scapula is thick mediolaterally at the posterior border. The cranial half of the blade is thin. Judging from the preserved width of the supraspinous fossa, it is large and the spine is located at the half way between anterior and posterior border. The dorsal border of scapula is badly preserved in both scapulae but may have run straight sagittally.

Ventral one-fourth of the anterior border is preserved in right scapula and is anteriorly and inwardly concave.

Though the posterior border is better preserved in left scapula than in right, dorsal 5 cm or more of posterior border seems to be lost in left scapula. In the preserved portion, the posterior border is linear in dorsal half and concave backward in ventral half. Thickness of the scapula varies from 10 to 13 mm at the posterior border.

Lateral lip branches off medially from posterior border at a point 53 mm ventral to the preserved dorsal end of the border and ascends in parallel with the border to dorsal broken end of the border. The narrow flat region between the posterior border and the lip measures 18 mm wide. This region may represent the insertion site of teres major muscle. Similar configuration is present in UHR no.18466 (Inuzuka, 1981). However, UHR no.18466 differs from the present specimen in its greater length and the presence of slightly concave surface ventral to the flat region. Posterior border slightly decreases in thickness ventrally, and thickens again in its ventral end at the infraglenoid tubercle (tuberculum infraglenoidale).

In various ungulates (e.g. *Sus*, *Equus*, *Bos*, *Cervus* and so on), a blunt but distinct ridge runs dorso-ventrally along the posterior border on the costal surface, while on the dorsal surface, shallow elongate depression runs dorso-ventrally along the posterior border. Such configurations, however, are not seen on either costal or dorsal surface of SMNH VeF-61 and UHR no.18466. This might be one of the characteristic features of *Desmostylia*.

The costal surface (facies costalis) is concave

medially in caudal view and the extent of this concaveness is greater than in other ungulates. Costal surface is hollowed by subscapular fossa (Fossa subscapularis) in the middle, reflecting presence of spine on lateral surface. Cranio- and caudo-dorsal corners of the costal surface are slightly elevated. They may have been the insertion sites of serratus ventralis muscle. However, this is difficult to judge because of the poor state of preservation.

The spine is better preserved in the right scapula than in the left. The base of the spine is stocky, and slightly convex anteriorly in lateral view. The spine leans caudally and slightly overhangs fossa infraspinatus (Fig.5). Unfortunately, the free edge of the spine is badly damaged. Acromion may have been present a few cm dorsal to the neck, judging from the location of thickest part (about 13 mm) of the spine. Dorsal end of the spine, including its free edge, is preserved in right scapula, and it gradually decreases in height towards vertebral border, forming a fan-shaped gentle slope. This fan-shaped slope at the dorsal end of the spine is very similar to that of UHR no.18466.

The shape of supraspinatous fossa in lateral view is not clear because of the heavy damage to the anterior border. Infraspinous area is a dorsoventrally long triangle. The neck is moderately long and flattened laterally. Its cross-section is triangular with shortest line cranial, intermediate latero-caudal and longest base medial (Fig.5). Epiphyses are completely fused with diaphysis.

Glenoid cavity is oval, long cranio-caudally, and faintly depressed in center. The center of the cavity is slightly anterior to the ventral end of the spine in ventral view. The cavity is large in proportion to overall size of the scapula.

Glenoid surface of SMNH VeF-61 is flat. This flatness of glenoid in SMNH VeF-61 is partly due to erosion of the surface, but the erosion of this surface seems to be not so great because the rim around the glenoid cavity is preserved. Glenoid cavity inclines forward at about 60 degrees to the trend of the base of the spine. This steep inclination of the glenoid surface is not an artifact but an original morphological characteristic because the extent of erosion of the glenoid is not so great.

The supraglenoid tubercle is situated anterior to the glenoid cavity, and massive but with no marked anterior or ventral projection. The infraglenoid tubercle is broken, but judging from the preserved

portion, it is small, situated dorsocaudal to the glenoid cavity, and making the ventral end of the posterior border.

Remarks—

According to Inuzuka (1981, 1984a), the scapula of *Desmostylus* is characterized by the elongated triangular outline, broad supraspinatus fossa, large glenoid and that the acromion terminates above the neck. Those characteristics can be found not only in UHR no.18466 but also in the present specimen and suggest desmostylian affinities of the scapula in the present specimen.

Scapulae of *Paleoparadoxia* have been known in at least five skeletons (NSMT P-5601, IPMM32669, UCMP114285, UCMP81302 and GMNH-PV-097), besides the present specimen (Shikama, 1966; Oishi et al., 1990; Clark, 1991; Hasegawa et al., 2000). However, they have never been described in detail nor compared with that of *Desmostylus*, except for short comment made by Clark (1991) and Inuzuka (2000a, b). They argued that generic distinction could be made with the shape of the anterior border. In *Paleoparadoxia*, anterior border of the scapula projects anteriorly, while in *Desmostylus* it is rather straight (Clark, 1991). In other words, the scapular notch is distinct in *Paleoparadoxia*, while it is not in *Desmostylus* (Inuzuka, 2000a, b). Unfortunately, the anterior border is heavily damaged in both scapulae of the present specimen so that its shape can not be compared with other specimens with confidence.

Besides the above character of scapula, Inuzuka (2000a, b) suggested that following characters of scapula can be used in generic distinction: shape of spine, depth of subscapular fossa, and teres major muscle surface. The former two characters can not be examined with confidence in present specimen because of poor preservation. On the other hand, teres major muscle facet of the present specimen is fairly well preserved. Inuzuka (2000b) noted that teres major muscle surface of the scapula is convex in *Paleoparadoxia tabatai* and his undescribed *P. sp. nov.* As scapulae of the previous specimens of *Paleoparadoxia* have never been described, it can not be concluded that teres major muscle surface of present specimen is of *Paleoparadoxia* type, which defined by Inuzuka (2000b).

Humerus (Fig.6, Pl.1, fig.12, Pl.3, fig.1-4): The specimen is judged as being the left humerus, based on the lateral deltoid tuberosity, greater and lesser

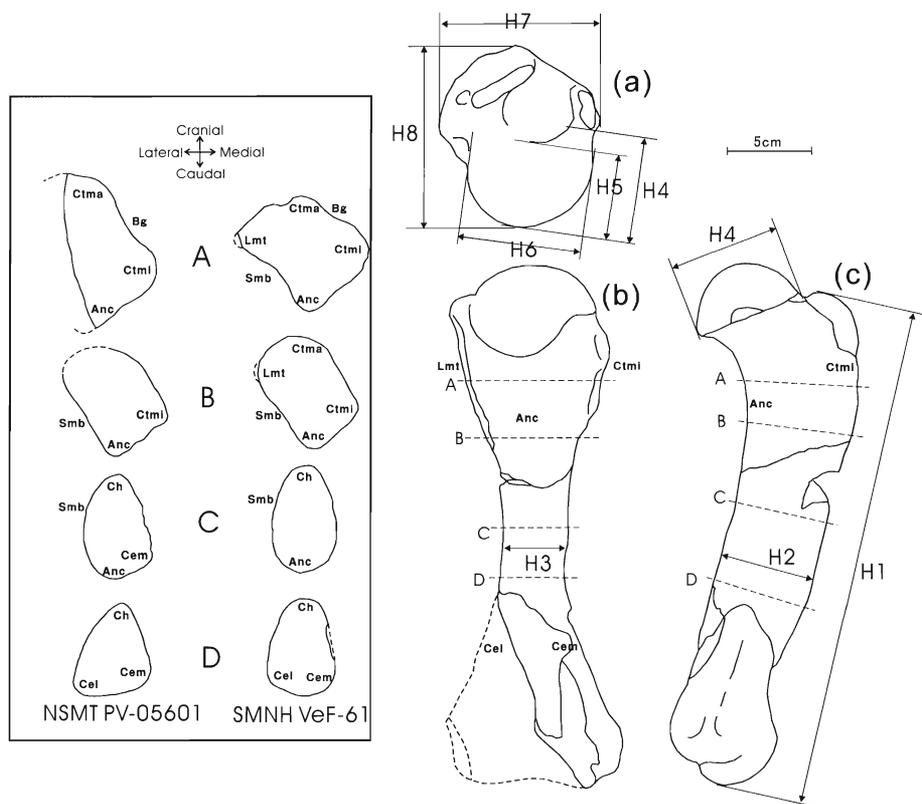


Fig.6. Measurements and cross-sections taken on the humerus.

Views: (a) proximal; (b) caudal; (c) medial. Broken lines indicate the positions where cross-sections are taken. Cross-sections are shown in the box.

Key: H1, distance between greater tubercle and the distal extremity; H2, antero-posterior width of the shaft measured at the H3; H3, minimal transverse width of the shaft; H4, distance between lesser tubercle and the distal end of the head; H5, antero-posterior diameter of the head; H6, transverse diameter of the head; H7, maximal transverse diameter of the proximal extremity; H8, maximal anteroposterior diameter of the proximal extremity; Anc, anonymous crest; Bg, bicipital groove; Cem, crista epicondylis medialis; Cel, crista epicondylis lateralis; Ch, crista humeri; Ctma, crista tuberculi majoris; Ctmi, crista tuberculi minoris; Lmt, linea m. tricipitus; Smb, sulcus m. brachialis.

Table 4. Measurements of humerus. See Fig.6 for abbreviations.

	H1	H2	H3	H4	H5	H6	H7	H8
mm	307	58	38	64	56	70	94	98

tubercles. The lateral half of the distal end, proximal surface of greater and lesser tubercles, proximal half of lateral border of the humerus and the surface of deltoid tuberosity are broken. There is no compressional deformation.

Proximal and distal ends of the humerus are robust. The shaft of the bone is flattened mediolaterally (Fig.6). Head is large, projecting caudally and slightly proximally. Epiphyses are completely fused with diaphysis.

The head of the humerus is sub-spherical but wider transversely than in sagittal diameter (Table 4). In proximal view, the head is reniform with its depressed part facing cranially. In caudal view, head

is egg shaped, with its long axis extending mediolaterally. The distoposterior circumference of head curves more strongly than the proximal surface in posterior view. In lateral and medial view, curvature of head is a little larger than in proximal view. Head projects caudad and is located posterior to the plane extending from the posterior surface of the humerus.

Greater tubercle lies anterolateral to head. The proximal tip of the tubercle is damaged but its original shape can be assumed from the preserved portion. Judging from the preserved portion, the greater tubercle is of moderate size, slightly projects above the head of the humerus, and making a ridge

running in anteromedial to posterolateral direction. The lesser tubercle is situated anteromedial to head, making a short ridge running in anterolateral to posteromedial direction. The tip of the tubercle is broken. Judging from the preserved portion, it is of moderate size, and projects cranial but is lower than the head.

Anterior to the head, there is a shallow depression perforated by several vascular foramina. This depression is comparable with the rugose flat surface situated anterior to the head in various ungulates such as equids, ruminants, and suids. Between this depression and the bicipital groove, there is a low and short ridge running transversally between the greater and lesser tubercles. In NSMT P-5601, such a ridge is not present. A bicipital groove is shallow, wide transversally, facing anteromedially and becomes indistinct at a point 30% from the proximal end of the humerus.

Surface for the insertion of infraspinatus, teres minor and deltoideus muscles can not be identified with confidence because of the distortion of the bony surface. The cranial and lateral aspects of the humeral shaft exhibit distinct but low deltoid (= anconeal or tricipital line) and pectoral (= the crest of the greater tubercle) crests that merge distally on the anterior surface of the shaft. The area, between deltoid and pectoral crest, exhibits irregularly pitted, anterolaterally faced surface. Its distal half possibly represents deltoid tuberosity. At a point about 40% from the proximal end of the humerus, the deltoid crest joins the pectoral crest, and the humeral crest (crista humeri) rises. Proximal part of the humeral crest runs parallel to the longitudinal axis of the humerus. Distal part of the humeral crest continues the remaining distance to the medial rim of the trochlea and runs distally and slightly medially. In NSMT P-5601, marked rugosity occurs on the humeral crest, but it is not recognized in SMNH VeF-61 because of the poor preservation of bony surface.

Medially, the crest of lesser tubercle (crista tuberculi minoris) runs distally and then fades out at a point about 40% from the proximal end of the humerus. In NSMT P-5601, however, this crest continues distally as posteromedial border of the humerus (= crista epicondylis medialis).

Shape in cross section is parallelogrammic just under the head, and is rectangular in proximal one-third, and elliptical with long axis running anteroposteriorly in the distal one third of the shaft

(Fig.6).

In posterior view, an unnamed crest runs distally from the point just below the head, and becomes quite obtuse at the point about 40% from the proximal end of the humerus. Proximal to this point, posterior surface of the humerus is divided into posterolateral and posteromedial surfaces by this unnamed crest. In NSMT P-5601, this crest extends further and remains distinct until it reaches the crista epicondylis lateralis. However, in SMNH VeF-61, the crest fades out and transversally rounded surface is developed below this point (Fig.6).

The lateral half of the distal end of the humerus is lost due to erosion. The preserved part of the epicondylus medialis faces medially and slightly anteriorly, and protrudes as strongly as in NSMT P-5601.

Remarks—

Inuzuka (1989, 2000a, b) noted distinction between *Behemotops*, *Paleoparadoxia* and *Desmostylus* in distal end of the humerus. Unfortunately, lateral half of distal extremity of the humerus of present specimen is missing so that above generic criterion suggested by him can not be used in SMNH VeF-61.

As noted above, tuberculum majus of present specimen is damaged but judging from the preserved part, it was of moderate size and higher than the head. Distal end of the present specimen is also damaged but judging from the remaining part, epicondylus medialis of present specimen is as large as NSMT P-5601. Thus, in tuberculum majus and epicondylus medialis, present specimen shares same characteristic features with NSMT P-5601.

Femur (Fig.7, Pl.1, fig.13, Pl.3, figs.5-8): The specimen is judged as being the left femur, based on the condyles on the posterior surface and head on the medial. The femur is short and stocky with large proximal and distal ends (Fig.7, Table 5). As a whole, the width of the femur is large for its length and cranio-caudal diameter is small. Epiphyses are completely fused with diaphysis.

Proximal top of greater trochanter is damaged and exposing cancerous bone tissue. Four small faults run transversally at the greater trochanter, head and proximal part of shaft. Displacement caused by those faults measures a few millimeters. The original shape of the bone can be restored without difficulty by setting back this displacement. The surface of the distal epiphysis is irregularly pitted by postmortem

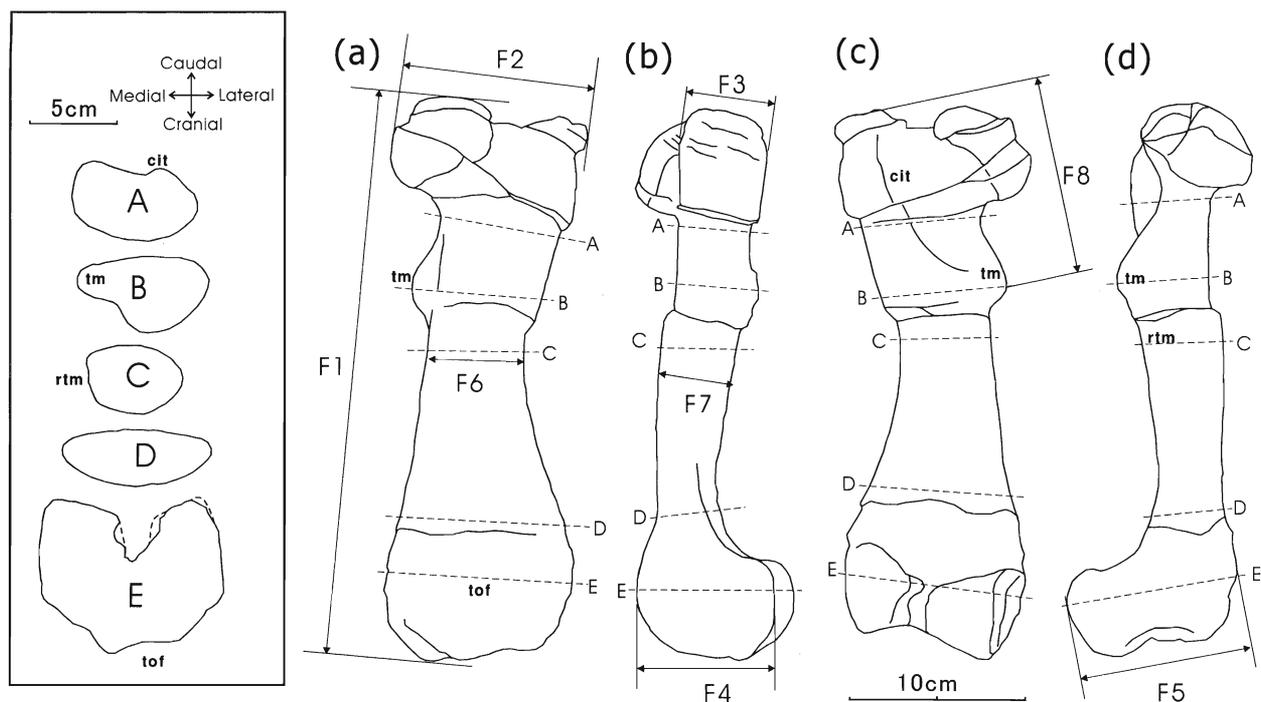


Fig.7. Measurements and cross-sections taken on the femur.

Views: (a) cranial; (b) lateral; (c) caudal; (d) medial. Broken lines indicate the positions where cross-sections are taken. Cross-sections are shown in the box.

Key: F1, distance between proximal and distal extremities measured along the axis of the shaft; F2, transverse width of the proximal extremity; F3, maximal thickness of greater trochanter; F4, antero-posterior diameter of the lateral condyle; F5, antero-posterior diameter of the medial condyle; F6, minimal transverse width of the shaft; F7, antero-posterior width of the shaft measured at F6; F8, distance between greater and lesser trochanters measured along the axis of the shaft; cit, crista intertrochanterica; rtm, rugosity located distal to trochanter minor; tm, trochanter minor; tof, trochlea ossis femoris.

Table 5. Measurements of femur. See Fig.7 for abbreviations.

	F1	F2	F3	F4	F5	F6	F7	F8
mm	322	122	46.5	84	88	55.9	42.2	108

distortion, except for the lateral two-thirds and medial three-fourths of the lateral and medial condyles respectively.

In proximal view, the femur exhibits hourglass-shape. Head is semispherical in shape, and measures 63 mm in diameter. Its direction is nearly equal to that of the neck. It makes an angle of 45 degrees medial to the shaft, 20 degrees cranial in medial view. It is twisted at 10 degrees cranial to transverse axis in proximal view. Surface smooth and fovea capitis femoris indistinct.

The neck (collum femoris) is short but is distinctly constricted in all directions, with minimum diameter of 56 mm in anterior view, minimal cranio-caudal diameter of 35 mm in medial.

The preserved portion of greater trochanter is slightly lower than the head, but may have been as

high as the head. It projects backwards and forwards from neck in proximal view, is rectangular in lateral view, and measures 46.5 mm in antero-posterior diameter. Anterior corner of the trochanter appears to be damaged by pre-burial distortion.

The trochanteric fossa is a reversed triangle in outline, lying in proximal one quarter of shaft. Its maximum width is about one half of that of proximal part of shaft. Depth of the fossa corresponds to expansion of the trochanter major in anterior surface. Two small depressions are present on the bottom of the deepest part of the fossa.

The lesser trochanter is triangular in anterior view, flattened antero-posteriorly, and is situated approximately 35% of the distance from the proximal end of the humerus. On the anterior surface of the shaft, a shallow groove runs proximo-distally along the base

of the lesser trochanter (Fig.7). Rough surfaced area lies along the medial margin in half of the shaft below trochanter minor. It measures 25 mm in maximum width and 32 mm in length. The area is flat, long ellipsoid in outline as a whole, and facing medially. An intertrochanteric crest overhanging on trochanteric fossa runs obliquely at an angle of about 25 degrees to longitudinal axis of shaft from proximolateral to distal.

The shaft of the femur is compressed antero-posteriorly with fusiform cross section (Fig.7), straight proximo-distally and moderately narrowed at the midshaft. In anterior view, the medial margin runs distomedially, and is straight, except for the area occupied by trochanter minor. On the other hand, the lateral margin curves gently in anterior view. Inuzuka (1982, 1984a) described a small rough area on the lateral margin of femoral shaft of UHR no.18466, but no such rough area is present on the femur of SMNH VeF-61.

Smooth posterior surface is flatter than anterior surface, with no rough surface in middle and distal. The posterior surface of the shaft is comparable with the facies aspera of other mammals and the lateral margin can be homologized with labium laterale and medial margin with labium mediale of the other mammals, respectively. In NSMT P-5601, lateral edge (homologue of labium laterale of other mammals), which rises just distal to the greater trochanter, is expressed as a sharp crest (Inuzuka and Karasawa, 1986). However, the lateral edge of the SMNH VeF-61 is not as sharp as other previously described femurs of *Paleoparadoxia* (Fig.7). Apart from this difference, the shaft of the SMNH VeF-61 is very similar to NSMT P-5601 in the extent of cranio-caudal compression and the curvature of the lateral edge.

The trochlea is damaged except for a small area at the middle of the surface. Judging from the preserved portion, it may have been smoothly convex in lateral view, not concave in transverse direction, and its height and width are nearly equal. When the femur stands on both condyles, longitudinal axis of the shaft tilts laterally at about 15 degrees.

Medial condyle is larger than lateral condyle. Medial margin of the lateral condyle and lateral margin of medial condyle are irregularly pitted and heavily damaged. The bottom of the intercondyloid fossa is well preserved. Judging from the preserved portion, intercondyloid fossa may have been very

narrow, and runs in proximomedial to distolateral direction at an angle of 18 degrees to longitudinal axis in posterior view. Numerous vascular foramina perforate the bottom of intercondyloid fossa. Medial and lateral epicondyles are obliterated by distortion.

Remarks—

Inuzuka and Karasawa (1986) mentioned that the lateral margin of the femoral shaft curves gently in anterior view in *Paleoparadoxia*, while in *Desmostylus*, its curvature becomes stronger distally. However, recently figured femora of IPMM32669 (Oishi et al., 1990) and FM-N8600706 (Hasegawa and Taketani, 1999, plate 29) show close similarity to UHR no.18466 in the curvature of lateral margin of the femoral shaft. As those two specimens belong to *Paleoparadoxia* (Hasegawa and Taketani, 1999; Inuzuka, 2000a), generic distinction in femoral shaft noted by Inuzuka and Karasawa (1986) can no longer be considered valid (Inuzuka, personal communication, Dec., 2001).

Besides the above character, two femoral characters, morphologies of the neck and lesser trochanter can be used for the generic distinctions according to Inuzuka (2000a). Concerning the femoral neck, distortion of this part is so heavy that it can not be compared with other specimens with confidence. On the other hand, lesser trochanter of SMNH VeF-61 is preserved without distortion and clearly shows close similarity to those of other *Paleoparadoxia* specimens. In *Paleoparadoxia*, the lesser trochanter is small and projecting while in *Desmostylus*, it extends distally (Inuzuka, 2000a, p.21, fig.9). In *Behemotops katuiei*, the projection of lesser trochanter is not distinct (Inuzuka, 1989). The lesser trochanter of SMNH VeF-61 is small and projecting and thus most similar to those of other *Paleoparadoxia* specimens.

Taxonomic remarks on SMNH VeF-61

The combination of the characters obtained from more than one element will make more precise taxonomic identification possible than that from any single element. Thus, the question of whether all the elements in question certainly come from a single individual is crucial in the taxonomic discussion. As mentioned above, the mode of occurrence of SMNH VeF-61 strongly suggests that all the elements of SMNH VeF-61 come from a single individual. However, there remains some possibility that they are

from more than one individual.

The isolated cheek tooth of SMNH VeF-61 has been reported as M1 (Tsunoda et al., 1978; Inuzuka, 1984b). As discussed above, isolated cheek tooth of SMNH VeF-61 is similar to a M1 of SMNH VeF-10, in the size and the number of cusps and tubercles. However, if cheek tooth of SMNH VeF-61 is M1, the individual age suggested by its wear stage contradicts with that suggested by the postcrania of present specimen. Complete fusion of epiphyses with diaphysis suggests that SMNH VeF-61 is an aged animal, older than NSMT P-5601 and FM-N8600706 in which epiphysal lines are not closed. The cheek tooth of SMNH VeF-61 still retains much of its crown and if it is an upper first molar, this specimen is younger than NSMT P-5601 and FM-N8600706 in which the upper first molar has lost much of its crown due to heavy wear. Therefore, if the cheek tooth of SMNH VeF-61 is an upper first molar, there will be a strong discrepancy between individual ages suggested by two lines of evidence and some possibility that the tooth and bones are in fact not from a single individual. Thus there are two possibilities: 1) the tooth of SMNH VeF-61 is a M1 and it was associated with bones of another individual in the sediment by chance, 2) they are from a single individual but the cheek tooth is not M1.

Both hypotheses have their strong points and shortcomings and thus they are equally likely. In the first case, it is not necessary to assume that M2 or M3 of some individual of *Paleoparadoxia* has simple crown morphology as seen in SMNH VeF-61, but rather a complex history of the burial of the tooth and postcrania. On the other hand, in the second case, it is not necessary to assume complex burial process, but that simple crown morphology is present also in M2 or M3 of some individual of *Paleoparadoxia*. Though undamaged original upper second molars of UCMP114285 may have had simple crown morphology comparable to the present specimen, no well preserved M2 and M3 on skulls known to date show such morphology of the crown. As the above two possibilities are equally likely, there would be two equally possible taxonomic allocations of SMNH VeF-6. In the following, I examine those two taxonomic allocations in order.

If the tooth and the bones do not come from single individual, their taxonomic status must be examined separately. I examined that of the cheek tooth first. The cheek tooth of SMNH VeF-61 can be M1

without problem, if the bones accompanying it belong to another individuals. As mentioned above, the combination of features seen in the cheek tooth of the SMNH VeF-61 leaves no doubt that the tooth represents an individual of *Paleoparadoxia*. However, it is very hard to make specific identification of SMNH VeF-61 because the same crown morphology is not found in the upper first molars on skulls known to date, but only among isolated molars such as the upper first molar of SMNH VeF-10.

Two described species of *Paleoparadoxia* (*P. tabatai* and *P. weltoni*) can be distinguished from each other by several dental and cranial characters (Clark, 1991; Hasegawa et al., 1995), but not in the characters common to three tooth classes of upper molars. Formerly, small dimension of the molars of *P. weltoni* has been considered to be a distinguishing character of this species and *P. weltoni* was said to be the smallest species of *Paleoparadoxia* (Clark, 1991; Inuzuka et al., 1994). However, the small body size of the only known specimen of this species (UCMP 114285) could not be a specific character, because comparable small body size is now known in a female of *P. tabatai* (Hasegawa et al., 1995; Hasegawa and Taketani, 1999). Thus the dimension of the molar cannot be used for the distinction between two species.

Hasegawa et al. (1995, p.518) noted that in *P. weltoni* the roots of P3 and M2 are bifurcated while they are not in *P. tabatai*. If they are correct, bifurcation of the roots of upper molars could be a differential diagnosis of *P. weltoni*. However, according to Clark(1991), "the single root is smaller in diameter" in P3, "the condition of the roots is not apparent" in M2 and "the roots are not exposed" in M3. Unfortunately, Hasegawa et al. (1995, p.518) did not mention the source of the description of the root of upper cheek teeth of *P. weltoni*. Therefore it is not clear that whether they have observed the root of cheek teeth of UCMP114285 firsthand or they inferred morphology of the root from the Figure 5 of Clark (1991), in which the root of the M3 looks bifurcated. Since the source is not clear, the shape of the root of the molar mentioned by Hasegawa et al. (1995, p.518) can not be used for the distinction between two species. In conclusion, characters that can be used for the specific identification are not found in the upper cheek tooth of SMNH VeF-61, if it is an upper first molar.

Next, the taxonomic assignment of the postcrania

of SMNH VeF-61 is examined. Though there are several minor differences, all of the postcranial elements of SMNH VeF-61 can be considered those of *Paleoparadoxia*, except for scapulae. As noted above, lumbar vertebra of the present specimen is similar to that of *Paleoparadoxia* (Inuzuka, 1989, 2000a, b) in narrow and high centrum and short and tapering transverse process. The humerus is very similar to that of NSMT P-5601 especially in well-developed medial epicondyle and greater tubercle. Femur shares small but distinctly protruding lesser trochanter with other *Paleoparadoxia* specimens. Thus, except for scapulae, all of the postcranial elements of SMNH VeF-61 suggest that they belong to *Paleoparadoxia*.

Characters that can be used for the specific identification are not found in the postcrania of SMNH VeF-61 either. Among preserved portion, only the morphology of teres major muscle facet is expected to provide specific distinctions between *P. weltoni* and *P. tabatai*. But as detailed description of the specimens of *Desmostylia* is not available for present comparison, it is not safe to say that the teres major muscle surface of SMNH VeF-61 is definitely of *Paleoparadoxia* type, which was defined by Inuzuka (2000b).

As mentioned above, if the individual age suggested by postcranial element is reliable and the postcranial elements and cheek tooth certainly come from a single individual, the degree of wear in the cheek tooth of SMNH VeF-61 is too small for a first upper molar of an old individual. This suggests that the cheek tooth of SMNH VeF-61 cannot be an upper first molar but either an upper fourth premolar, upper second molar or upper third molar, if the tooth and the postcrania come from a single individual.

As suggested by Inuzuka (1987), increase of the number of cusps in cheek teeth of *desmostylians* is accomplished by the enlargement of former tubercles and this tendency seems to be present not only among the molars but also in premolars. Thus, the enlargement of tubercles can bring about the moralization of premolars and this may result that in some cases, the fourth premolar of an individual of a larger species can be indistinguishable from the first molar of an individual of a smaller species in the number and arrangement of cusps. In such cases, distinction between the fourth premolar of a larger species and the first molar of a smaller species can be made only when other elements are available

for the estimation of individual age and body size of those animals. In case of the cheek tooth of SMNH VeF-61, the tooth is not likely to be P4 because of its size. If the postcranial elements and cheek tooth certainly come from a single individual, the cheek tooth is that of smaller species of *Paleoparadoxia*, such as *P. weltoni* and *P. tabatai*, but not gigantic *Paleoparadoxia* sp. nov. of Inuzuka (2000b), because postcrania accompanying the teeth are of a moderate-sized animal. As noted above, the cheek tooth of SMNH VeF-61 is larger than the largest P4 of *P. weltoni* and *P. tabatai* ever known (Table 1).

Contrarily, the size of the cheek tooth of SMNH VeF-61 is within the observed range of M2 and M3 of smaller species of *Paleoparadoxia*. As noted earlier, no skull known to date has M2 and M3 comparable to the cheek tooth of SMNH VeF-61. On the other hand, three isolated molars (KZD07, UCMP 45274 and SMNH-VeF-10) can be equally compared with the cheek tooth of the present specimen. A cheek tooth of SMNH-VeF-10 can be an upper second molar (see Appendix) that shows fairly simple crown morphology comparable to the present specimen. Thus, it seems that M2 of some individual of some species of *Paleoparadoxia* represented by isolated molars exhibit simple crown morphology that has never been recognized in M2 associated with skulls known to date. In addition to this, KZD 07 and UCMP45274 could be M2 (see Appendix), though they have been identified as M1 (Shimada and Inuzuka, 1994). Therefore, several individuals of some species of *Paleoparadoxia* seem to have M2 showing fairly simple crown morphology comparable to the present specimen. If the cheek tooth and postcrania of present specimen come from a single individual, the present specimen represents one of such individuals. The question is whether such simple crown morphology of M2 shared by those individuals warrants specific distinctions between those individuals and previously known species or is a mere individual variation commonly seen in known species of *Paleoparadoxia*. Unfortunately, we still do not have enough material to provide any definite answer to this problem. Under present circumstances, associated postcrania, for instance scapulae, do not provide the reliable basis for the specific identification of the present specimen either, as noted earlier.

In sum, specific identification of SMNH VeF-61 is still difficult in both of the above two cases. In addition to the continuous efforts to find new fossils,

further investigation, especially detailed description of reported skeletons and cheek teeth of *Desmostylia*, must be prerequisite for the further specific identification of the present specimen. Until such works have been carried out, the present specimen should be identified as *Paleoparadoxia* sp.

Conclusion

SMNH VeF-61 is described and identified as *Paleoparadoxia* sp. There remain some problems concerning individual variation of the *Paleoparadoxia* in skeletal and dental characters. Because of this, specific identification of the present specimen is still difficult and for its solution, detailed description of other superb specimens of desmostylians is necessary.

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Appendix

Identification of the tooth class of SMNH VeF-10

Arai (1953) identified three cheek teeth of SMNH VeF-10 as follows: a fairly worn upper cheek tooth (Arai, 1953, figs.11-15, here after TERA0-1) as P4; a slightly worn upper cheek tooth (Arai, 1953, figs.16-20, here after TERA0-2) as P4 or M1; a fairly worn lower cheek tooth (Arai, 1953, figs.11-10, here after TERA0-3) as p4. According to him, those teeth were found together with skeletal fragments in a narrow area and this occurrence strongly suggests that all the elements of SMNH VeF-10 come from a single individual.

However, tooth class identification done by Arai (1953) contradicts with the idea that they come from a single individual. First of all, TERA0-1 and 2 can not be the same tooth class, P4, because of the great difference in wear stage: TERA0-1 is worn greatly and exposing dentine widely at the center of the cusp, while TERA0-2 is still in very early stage of wear. The remaining combination suggested by Arai (1953) is that TERA0-1 and TERA0-2 are P4 and M1 respectively, but in this case, eruption sequence of cheek teeth deduced from their wear stage contradicts with that of ordinal mammals. Rejecting the identification made by Arai (1953), only the following combinations of tooth class identification can be considered:

- 1) TERA0-1 and TERA0-2 are P4 and M2, respectively;
- 2) TERA0-1 and TERA0-2 are Dp3 and Dp4, respectively;
- 3) TERA0-1 and TERA0-2 are Dp4 and M1, respectively;
- 4) TERA0-1 and TERA0-2 are M1 and M2, respectively;
- 5) TERA0-1 and TERA0-2 are M2 and M3, respectively.

First and third combinations are not plausible because greater size difference between TERA0-1 and TERA0-2 would be expected in those combinations than actually observed in SMNH VeF-10 (Table 1, Fig.3). Second combination is not likely because this combination suggests that SMNH VeF-10 would be juvenile but this contradicts with the individual age assumed from an accompanying mandible fragment. The head of the mandible of SMNH VeF-10 is not fully ossified but the mandible of this specimen appears to be only slightly smaller

than that of NSMT P-5601. In NSMT P-5601, height of corpus mandibulae at m1 is 86 mm (Ijiri and Kamei, 1961), while estimated height of that in SMNH VeF-10 is about 80 mm (Arai, 1953). Thus, SMNH VeF-1 is not juvenile but subadult or older.

Last two combinations are most plausible but were excluded from the consideration by Arai (1953), because of small dimension of the teeth. Actually, TERA0-1 and TERA0-2 are indeed smaller than the molars of NSMT P-5601, which was the only known complete skeleton at that time. However, according to a recent study on sexual dimorphism in *Paleoparadoxia* (Hasegawa et al.,1995), molars of this genus can be as small as TERA0-1 and 2 in case of female. Thus, on the size basis alone, both of last two combinations are plausible. However, the fifth combination of tooth class identification is not concordant with the young individual age suggested by the ossification stage of the mandible. Thus, only the fourth identification, that TERA0-1 and TERA0-2 are M1 and M2 respectively, is possible.

Some questions about previous identification of some isolated molars arises from above revised identification of SMNH VeF-10. KZD 07 and UCMP 45274 have been identified as M1 (Shimada and Inuzuka, 1994). However, their identification of tooth class is no longer valid because their identification is solely based on the comparison between the molars of NSMT P-5601 and KZD 07. As shown in the first and second molars of SMNH VeF-10, the shape of upper molars varies far more greatly than had been expected from the NSMT P-5601. Thus, both KZD 07 and UCMP45274 can be also M2 or M3.

Arai (1953) described a fairly worn lower cheek tooth (TERA0-3) as p4, but NSMT P-5601, which gave the basis for his identification, was still insufficiently prepared at that time. As TERA0-3 shows strong wear, only TERA0-1 or missing P4 of SMNH VeF-10 can be the counter part of TERA0-3. Thus, TERA0-3 must be p4 or m1 and should be compared with other cheek teeth of those two tooth classes.

TERA0-3 has four large cuspids of equal size and a small cuspule distally, while p4 of NSMT P-5601 has only four cuspids and smaller than TERA0-3. The lower first molar of NSMT P-5601 is not informative because its crown is not preserved. Incidentally, lower second molar of NSMT P-5601 is much larger and shows more complex cuspid arrangement than TERA0-3. Therefore, no cheek

tooth showing the same morphology as TERA0-3 can be found in NSMT P-5601.

The lower fourth premolar of *P. weltoni* (UCMP 114285) is the same as TERA0-3 in number and arrangement of cusps, but somewhat smaller than TERA0-3. Lower second molar of UCMP114285 has 5 cusps as well and its dimensions are close to those of TERA0-3 (Table1). However this does not mean that TERA0-3 is most similar to m2 of *P. weltoni* or allied animals, because TERA0-3 might not be m2, as mentioned above.

The lower fourth premolar of FM-N8600706 is figured but not described in detail. Judging from the picture of this tooth in Hasegawa and Taketani (1999), p4 of this specimen has five cusps. However, the tooth is much smaller than TERA0-3. Thus, TERA0-3 should be m1, the crown morphology of which has never been known in other specimens. Specific identification of SMNH VeF-10 is still very difficult since comparable crown morphology is not known in any known skull of *Paleoparadoxia*.

Plate I

All figures in the plates are of the specimens (SMNH-VeF-61) from San-yama, Ogano-cho, Chichibu Basin, Central Japan.

Figs.1-5. Right upper cheek tooth

1. occlusal view. 2. mesial view. 3. distal view. 4. lingual view. 5. buccal view.

Figs.6-11. Lumbar vertebra

6. cranial view. 7. caudal view. 8. right lateral view. 9. dorsal view. 10. ventral view. 11. left lateral view.

Fig.12. Left humerus, proximal view.

Fig.13. Left femur, proximal view.

Scale bars 2cm for Fig.1-5 and 5 cm for Figs.6-13, respectively.

Plate II

All figures in the plates are of the specimens (SMNH-VeF-61) from San-yama, Ogano-cho, Chichibu Basin, Central Japan. Scale bar 5 cm long.

Figs.1-3. Right scapula

1. caudal view. 2. lateral view. 3. medial view.

Figs.4-5. Left scapula

1. medial view. 2. lateral view. 3. caudal view.

Plate III

All figures in the plates are of the specimens (SMNH-VeF-61) from San-yama, Ogano-cho, Chichibu Basin, Central Japan. Scale bar 5cm long.

Figs.1-4. Left humerus

1. lateral view. 2. caudal view. 3. medial view. 4. cranial view.

Figs.5-8. Left femur

5. medial view. 6. cranial view. 7. lateral view. 8. caudal view.

Plate I

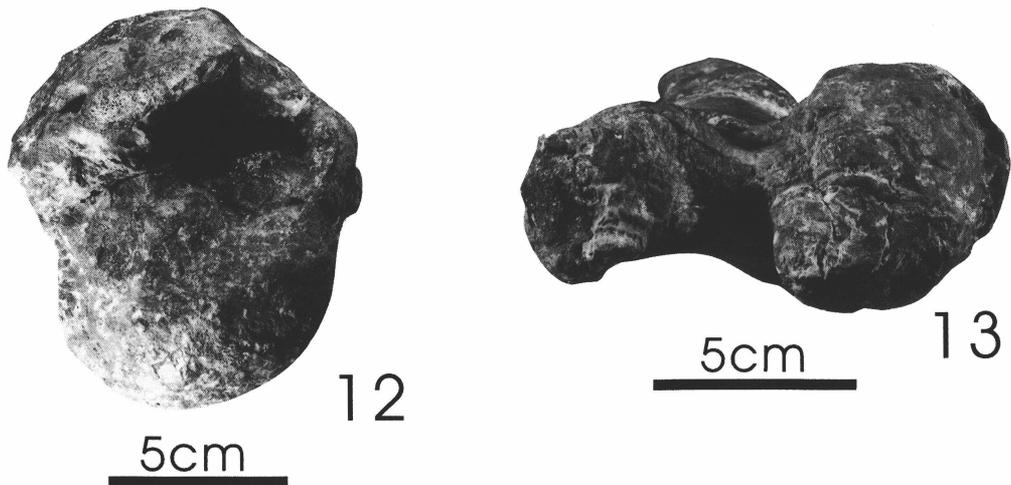
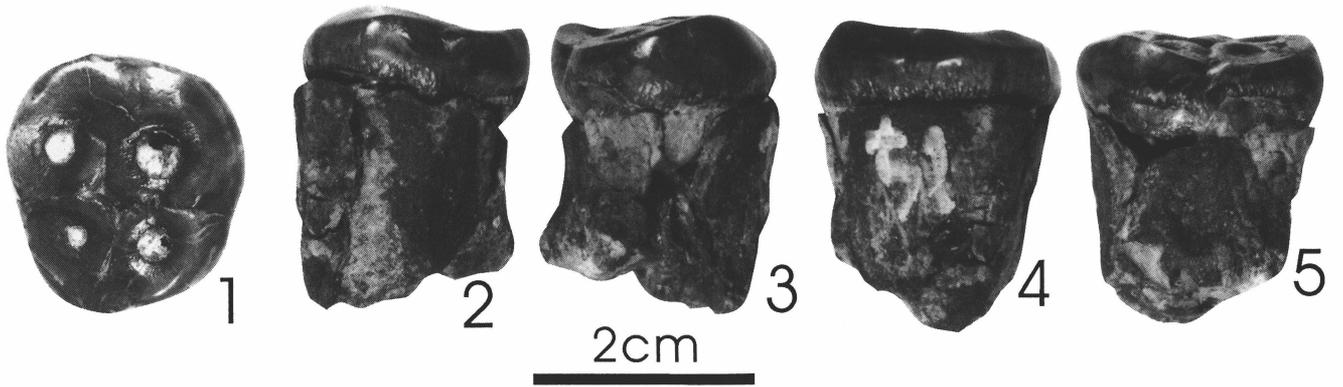
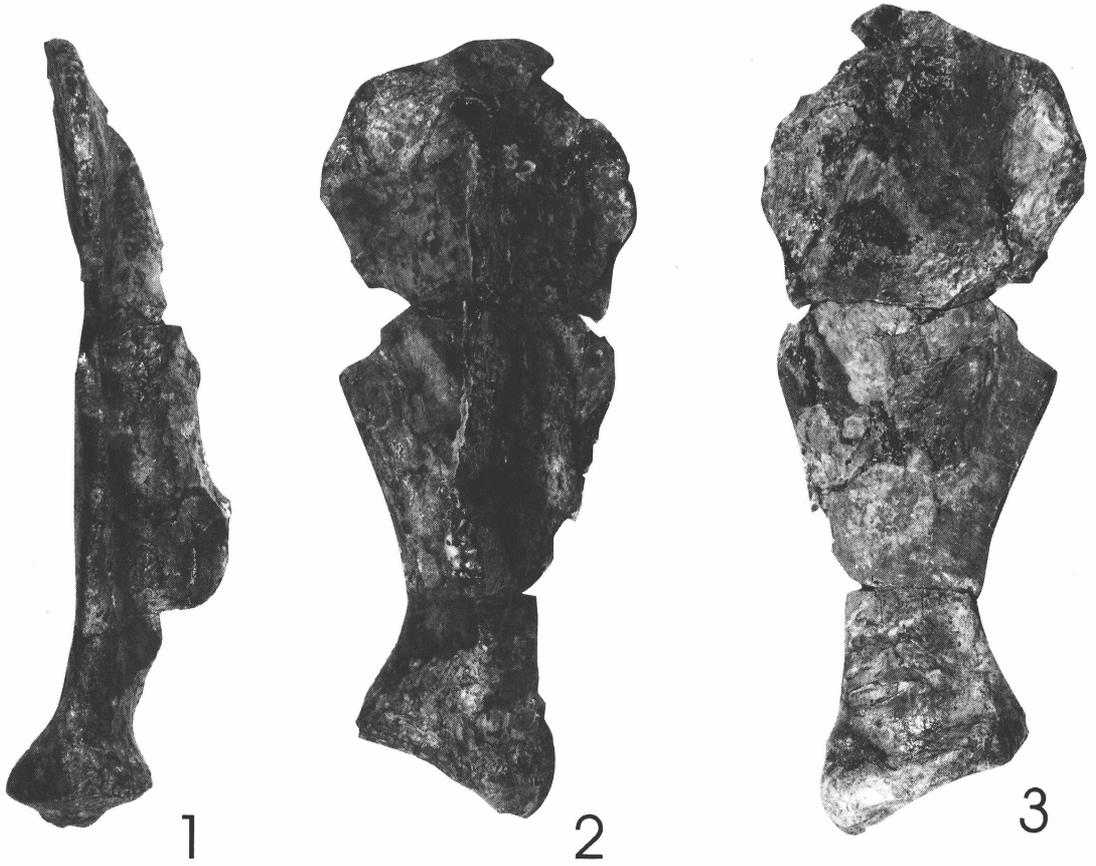


Plate II



5cm

Plate III



5cm

