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Journal of Geosciences, Osaka City University
Vol. 43, Art. 4, p. 57-95, March, 2000

Middle Pleistocene wild boar remains from NT Cave, Niimi, Okayama Prefecture, west Japan

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Abstract

Wild boar remains of Pleistocene age are generally scarce in the mainland of Japan. Recent excavations of NT Cave produced abundant wild boar remains from the cave sediments of Middle Pleistocene age. These remains are described in detail in order to elucidate the morphological characters of the Middle Pleistocene wild boar of Japan, and their taxonomic position is determined on the basis of the recent suid taxonomy. The morphological characters of the remains indicate that they belong to the subfamily Suinae among the six suid subfamilies designated by Pickford (1988). Furthermore, the characters coincide with those of the genus *Sus* among many suine genera, and thereby the remains are assigned to the genus *Sus*. The specific allocation of the remains is determined by comparison with a number of living and fossil species, which results in allocating the remains to *S. scrofa*.

Pleistocene *Sus* remains so far recorded from the mainland of Japan are revised on the basis of the data obtained by us as well as the recent taxonomy of the living *Sus* species. In our opinion, they are mostly assigned to *S. scrofa* as the case of the remains from NT Cave, and thus *S. scrofa* inhabited the mainland of Japan in the Middle and Late Pleistocene as well as in the Holocene, although *S. scrofa* of the Middle Pleistocene was generally larger than those of the other periods, and *S. scrofa* was scarce in the Late Pleistocene. A revision is required on the phylogenetic relationships among the *Sus* species of Japan, China, Indonesia and the Indian Subcontinent so far proposed.

Key words : *Sus scrofa*, NT Cave, Japan, Middle Pleistocene, systematics

1. Introduction

In contrast to elephants and deer, wild boars of Pleistocene age are relatively scarce in the mainland of Japan, although they are known in abundance from archaeological sites of Holocene age in the same area. The first description of Pleistocene wild boars in Japan was published by Matsumoto (1915a). He described a skull and a mandible from the Late Pleistocene of Tsukinoki in Akita Prefecture and referred them to a new species, *Sus nipponicus*. The Pleistocene wild boar remains assigned to *S*. cf. *lydekkeri*, were subsequently described by Shikama (1949) from the Lower Kuzuü Formation (Middle Pleistocene) in Tochigi Prefecture. Additionally, a few remains of wild boar have been recorded from the Middle Pleistocene of Matsugae Cave in Fukuoka Prefecture (Naora, 1954), from the Middle Pleistocene of Locality 1 of Ube Kosan Quarry in Yamaguchi Prefecture (Kawamura,1988) and from the Late Pleistocene of the Kannondo cave site in Hiroshima Prefecture (Kawamura, 1992 etc.). On the other hand, Shikama (1936), Shikama and Okafuji (1958), and Shikama and Hasegawa (1965) also described wild boar remains, but they are uncertain in geological age.

Middle Pleistocene fossiliferous cave sediments were recently recovered from NT Cave in the limestone quarry of the Nittetsu Kogyo Co. at Tarumi, Niimi City. The stratigraphy, chronology and faunal composition of the sediments are briefly given in Inada *et al*. (1998). The sediments contain many wild boar remains in association with a large number of other vertebrate remains. The wild boar remains are probably more abundant than those in other mammalian fossil localities dated certainly as the Pleistocene. The de-

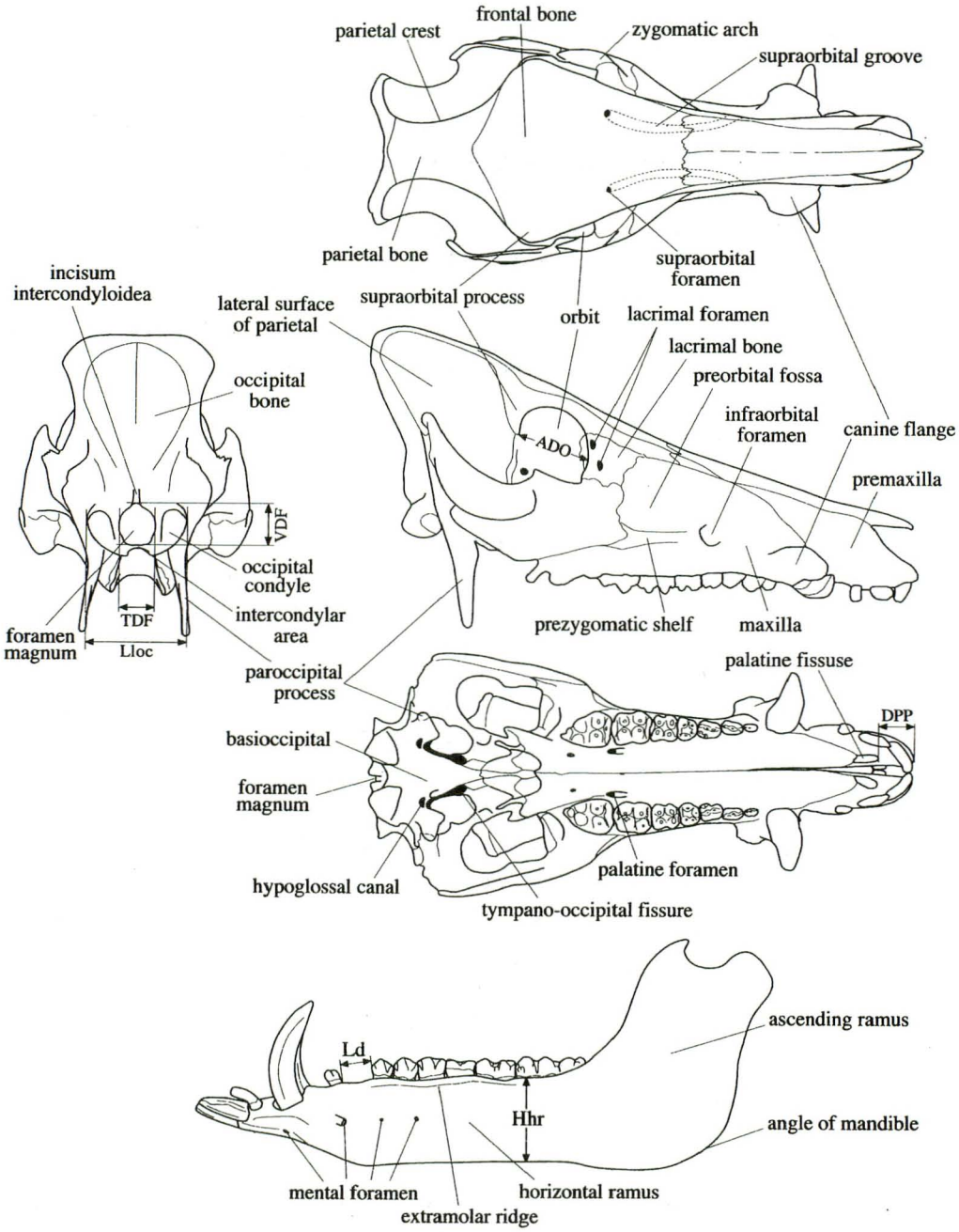

Fig.1. Terminology and measuring method for a suid skull and mandible. For the abbreviations see text.

scription of the remains is therefore important for elucidating the morphological characters of Pleistocene wild boars of Japan. In this paper, we describe them in detail, and discuss their systematic position and paleontological significance with a revision of the Pleistocene wild boars in the mainland of Japan.

2. Terminology and measuring method with abbreviations

For the terminology of the skull, we mainly follow Sisson and Grossman (1953), Wilkinson (1976), Evans and Cristensen (1979), Groves (1981) and Pickford (1988). For the teeth, we mainly follow the terminology of Made (1996). The terminology and measuring method used here are collectively shown in Figs.1-4. The abbreviations relating to the terminology and measuring method are also listed below.

Skull and mandible ——

ADO : Antero-posterior diameter of the orbit.

DPP : Distance between the anterior tip of the premaxilla and that of the palatine fissure.

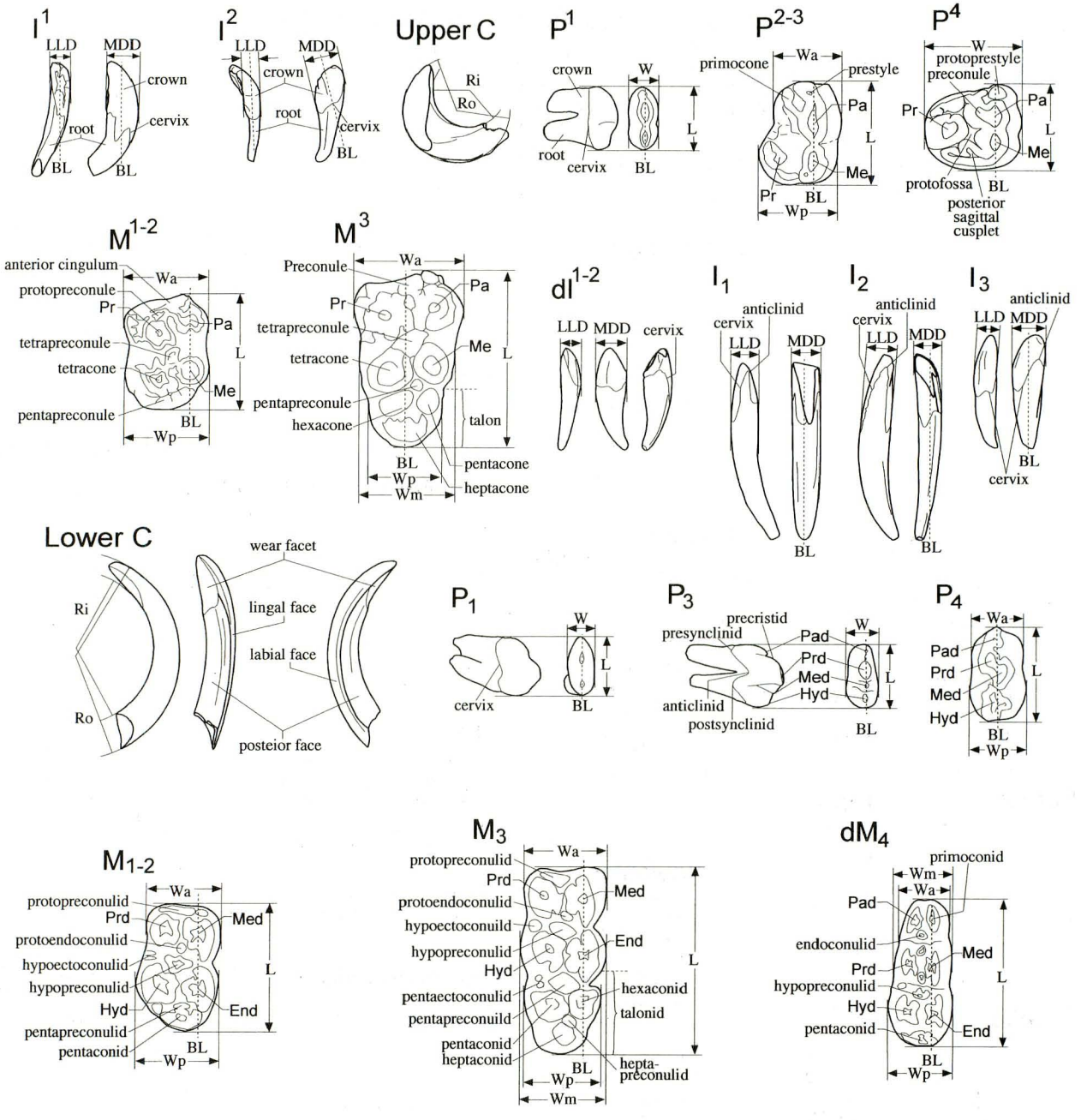

Fig.2. Terminology and measuring method for suid teeth. For the abbreviations see text.

Hhr : Height of the horizontal ramus of the mandible below the anterior part of M_3, measured along the buccal side.

Ld : Length of the diastema between P_1 and P_2.

Lloc : Length between the lateral borders of the left and right occipital condyles.

TDF : Transverse diameter of the foramen magnum.

VDF : Vertical diameter of the foramen magnum.

Tooth (terminology) ——

End : entoconid

Hyd : hypoconid

Me : metacone

Med : metaconid

Pa : paracone

Pad : paraconid

Pr : protocone

Prd : protoconid

Tooth (measuring method) ——

BL : Base line for measurement. The tooth measurements are mostly taken parallel to or at right angles to the base line.

L : Length of the crown.

LLD : Labio-lingual diameter of the tooth measured at right angles to the base line.

MDD : Mesio-distal diameter of the tooth measured at right

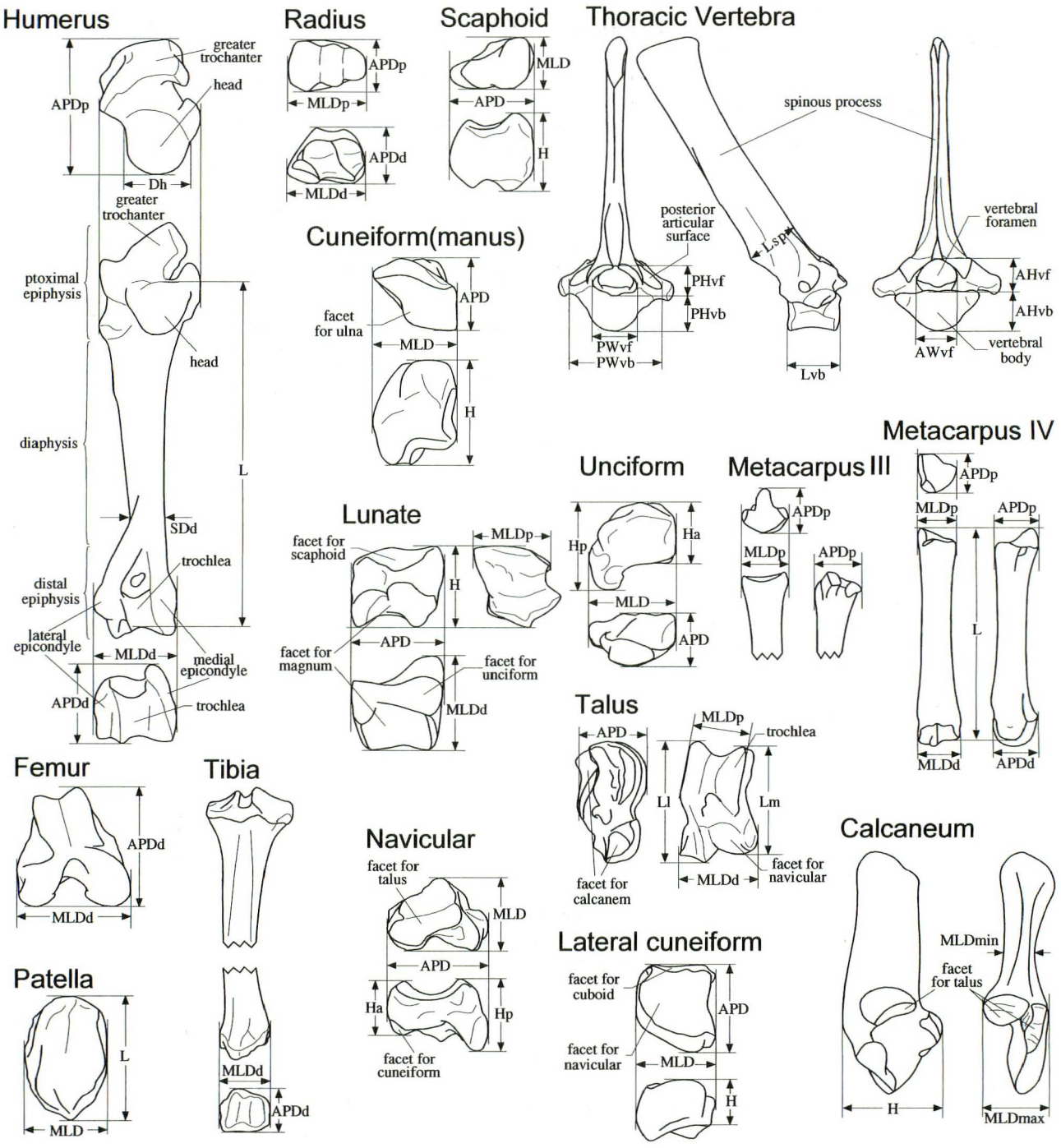

Fig. 3. Measuring method for suid postcranial bones. For the abbreviations see text.

angles to the base line.

Ri : Radius of curvature of the canine measured from the inner side.

Ro : Radius of curvature of the canine measured from the outer side.

W : Width of the crown.

Wa : Anterior width of the crown.

Wm : Middle width of the crown.

Wp : Posterior width of the crown.

Thoracic vertebra ——

AHvb : Anterior height of the vertebral body.

AHvf : Anterior height of the vertebral foramen.

AWvf : Anterior width of the vertebral foramen.

Lsp : Length of the spinous process.

Lvb : Length of the vertebral body.

PHvb : Posterior height of the vertebral body.

PHvf : Posterior height of the vertebral foramen.

PWvb : Posterior width of the vertebral body between the

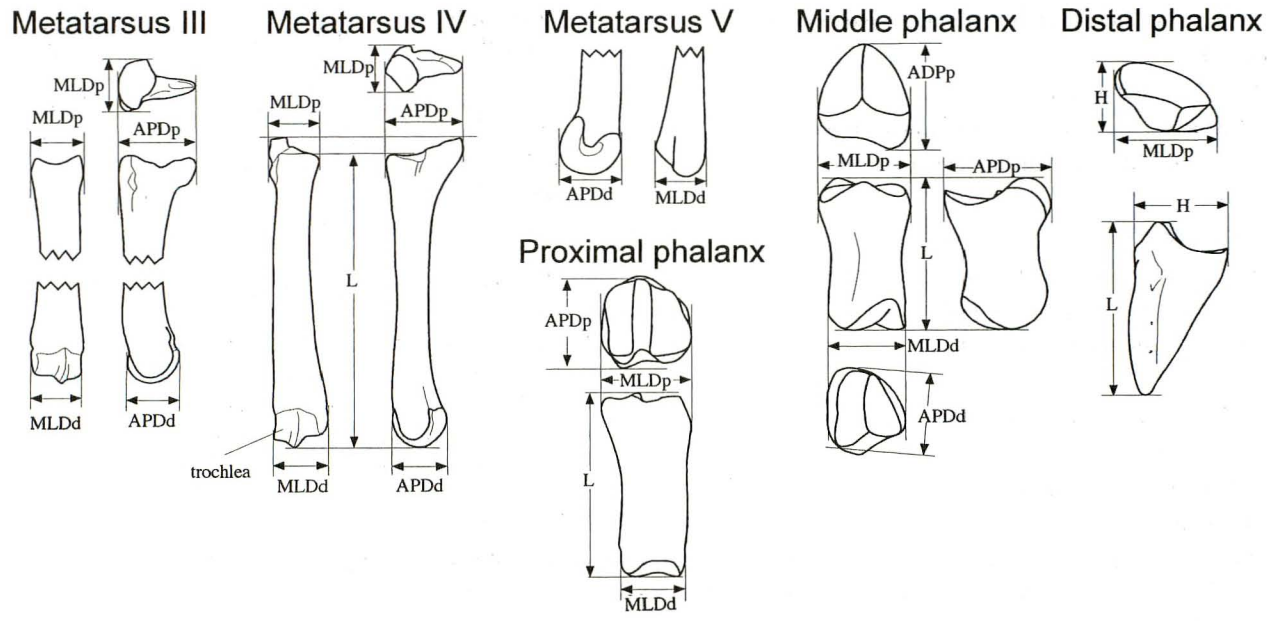

Fig. 4. Measuring method for suid postcranial bones. For the abbreviations see text.

lateral margins of the posterior articular surfaces.

PWvf : Posterior width of the vertebral foramen.

Humerus ——

APDd : Antero-posterior diameter of the distal epiphysis measured from the anterior border of the trochlea to the posterior border of the medial epicondyle.

APDp : Antero-posterior diameter of the proximal epiphysis measured from the anterior border of the greater trochanter to the posterior border of the head.

Dh : Diameter of the head.

L : Length from the most proximal point of the head to the uppermost point of the lower border of the trochlea.

MLDd : Medio-lateral diameter of the distal epiphysis measured from the medial border of the medial epicondyle to the lateral border of the lateral epicondyle.

SDd : Smallest diameter of the diaphysis.

Radius ——

APDd : Antero-posterior diameter of the distal epiphysis.

APDp : Antero-posterior diameter of the proximal epipysis.

MLDd : Medio-lateral diameter of the distal epiphysis.

MLDp : Medio-lateral diameter of the proximal epiphysis.

Scaphoid ——

APD : Antero-posterior diameter.

H : Height.

MLD : Medio-lateral diameter.

Lunate ——

APD : Antero-posterior diameter.

H : Height.

MLDd : Medio-lateral diameter in its distal part.

MLDp : Medio-lateral diameter in its proximal part.

Cuneiform (manus) ——

APD : Antero-posterior diameter.

H : Height.

MLD : Medio-lateral diameter.

Unciform ——

APD : Antero-posterior diameter.

Ha : Height in its anterior part.

Hp : Height in its posterior part.

MLD : Medio-lateral diameter.

Metacarpus ——

APDd : Antero-posterior diameter of the distal epiphysis.

APDp : Antero-posterior diameter of the proximal epiphysis.

L : Length from the proximal end to the distal border of the lateral part of the distal articular facet.

MLDd : Medio-lateral diameter of the distal epiphysis.

MLDp : Medio-lateral diameter of the proximal epiphysis.

Femur ——

APDd : Antero-posterior diameter of the distal epihysis.

MLDd : Medio-lateral diameter of the distal epiphysis.

Patella ——

L : Length measured proximo-distally.

MLD : Medio-lateral diameter.

Tibia ——

APDd : Antero-posterior diameter of the distal epiphysis.

MLDd : Medio-lateral diameter of the distal epiphysis.

Talus ——

APD : Antero-posterior diameter from the anterior border of the trochlea to the posterior border of the facet for calcaneum.

Ll : Length of the lateral part.

Lm : Length of the medial part.

MLDd : Medio-lateral diameter of the distal part.

MLDp : Medio-lateral diameter of the proximal part.

Calcaneum ——

H : Maximum height.

MLDmax : Maximum medio-lateral diameter.

MLDmin : Minimum medio-lateral diameter.

Navicular ——

APD : Antero-posterior diameter.

Ha : Height of the anterior part.

Hp : Height of the posterior part.

MLD : Medio-lateral diameter.

Lateral cuneiform ——

APD : Antero-posterior diameter.

H : Height.

MLD : Medio-lateral diameter.

Metatarsus and Phalanx ——

APDd : Antero-posterior diameter of the distal epiphysis.

APDp : Antero-posterior diameter of the proximal epiphysis.

H : Height (distal phalanx only).

L : Length from the lowest point of the anterior margin of the proximal articular facet to the distal end of the trochlea in the fourth metatarsus, and length from the most proximal point to the most distal point in the phalanges.

MLDd : Medio-lateral diameter of the distal epiphysis.

MLDp : Medio-lateral diameter of the proximal epiphysis.

Among the bones and teeth, the morphology of the male lower canine has been regarded as being important for suid taxonomy (Stehlin, 1899-1900 ; Wilkinson, 1976 ; Groves, 1981 etc.). Two types are traditionally recognized in the canines, namely, the verrucosic and scrofic types, which are easily distinguishable in their cross sections (Fig. 5). In the verrucosic type, the labial face is nearly as broad as the lingual face, and is much broader than the posterior face. Additionally, the posterior face is almost horizontal. In the scrofic type, however, the labial face is narrower than the posterior face, and is much narrower than the lingual face. The posterior face is steeply inclined labio-inferiorly. In addition to these two types, we here propose an intermediate type, because some suids which we observed have the canines intermediate between the typically verrucosic and typically scrofic types (Fig.5). The intermediate type is characterized by the posterior face being nearly as broad as the labial face, but narrower than the lingual face. In this type, the posterior face is inclined more gently than in the scrofic type.

3. Abbreviations for institutions

Besides institutions in Japan, two of us (Fujita and Kawamura) visited two institutions in China in 1996 and 1997, and Kawamura also visited many institutions in the United States and Europe in 1998, in order to observe living and fossil specimens of wild boars comparable with the remains from NT Cave. The institutions related to the present study are abbreviated as follows :

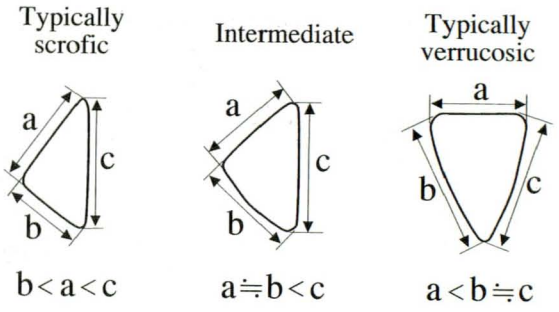

Fig. 5. Schematic cross sections of suid male lower canines, showing the difference among the scrofic type, verrucosic type and their intermediate type. a : width of the posterior face, b : width of the labial face, c : width of the lingual face.

AMNH : American Museum of Natural History (New York)

AUE : Department of Earth Sciences, Aichi University of Education (Kariya)

BMNH : British Museum of Natural History (London)

BQ : Bereich Quartärpaläontologie, Institut für Geowissenschaften, Friedrich-Schiller-Universität Jena (Weimar)

FS : Forschungsinstitut Senckenberg (Frankfurt am Main)

HLD : Hessisches Landesmuseum Darmstadt (Darmstadt)

IZ : Institute of Zoology, Academia Sinica (Beijing)

IVPP : Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica (Beijing)

MCZ : Museum of Comparative Zoology, Harvard University (Cambridge)

MNHN : Museum National d'Histoire Naturelle (Paris)

NMB : Naturhistorisches Museum Basel (Basel)

NMM : Naturhistorisches Museum Mainz (Mainz)

OCU : Department of Anatomy, Osaka City University (Osaka)

OUA : Department of Archaeology, Okayama University (Okayama)

SMNS : Staatliches Museum für Naturkunde Stuttgart (Stuttgart)

TU : Natural History Museum, Tohoku University (Sendai)

UF : Museo di Geologia e Paleontologia, Universita degli Studi di Firenze (Florence)

4. Systematic description

Order Artiodactyla Owen, 1848

Family Suidae Gray, 1821

Subfamily Suinae Zittel, 1893

Genus ***Sus*** Linnaeus, 1758

Sus scrofa Linnaeus, 1758

(Figs.6-8 ; Pls.1-7)

Sus scrofa, Linnaeus 1758, *Systema Naturae* (10th ed.), **1**, 49.

Synonym (*confined to Pleistocene fossil forms from the mainland of Japan*) ——

Sus nipponicus, Matsumoto 1915 ; *Sci. Rep. Tohoku Imp. Univ.*, 2nd. Ser., **3**, 41-46, pls. 17-19 ; from Tsukinoki, Showa, Akita Prefecture (Late Pleistocene).

Sus leucomystax Temminck ; Shikama 1936, *Jour. Geol. Soc. Japan*, **43**, 647-659, pl.36 ; from the estuary of the Murasakigawa River, Kokura (currently Kokurakita-ku), Kitakyushu, Fukuoka Prefecture (geological age uncertain ; possibly Pleistocene)

Sus cf. *lydekkeri* Zdansky ; Shikama 1949, *Sci. Rep. Tohoku Imp. Univ.*, 2nd Ser., **23**, 76-82, pl.5 ; from the third fissure of Yoshizawa Quarry, Ogano, Kuzuü, Tochigi Prefecture (Lower Kuzuü Formation ; Middle Pleistocene)

Sus cf. *lydekkeri* Zdansky ; Shikama and Hasegawa 1965, *Sci. Rep. Yokohama Nat. Univ.*, Sect. 2, (12), 37-43, pls.2-3 ; from Kurihama, Yokosuka, Kanagawa Prefecture (geological age uncertain ; possibly Pleistocene)

Referred specimens ——

All the specimens are stored in OUA. Their specimen numbers are given in parenthesis, and are prefixed by OUA-NT.

2 skull fragments (00001, 00002) ; 1 premaxillary fragment with I^1 and I^2 (00007) ; 1 maxilla with P^1 to M^3 (00012) ; 1 maxilla with P^3 to M^3 (00016) ; 1 maxillary fragment with M^1 to M^3 (00021) ; 1 maxillary fragment with P^4 (00018) ; 1 maxillary fragment with M^1 (00022) ; 2 maxillary fragments with dM^4 (00058, 00059) ; 4 I^1 (00003-00006) ; 1 I^2 (00008) ; 2 upper canines (00009, 00010) ; 1 P^1 (00011) ; 1 P^2 (00013) ; 2 P^3 (00014, 00015) ; 1 P^4 (00017) ; 2 M^1 (00019, 00020) ; 2 M^2 (00023, 00024) ; 2 dI^1 (00051, 00052) ; 1 dI^2 (00053) ; 2 dM^2 (00054, 00055) ; 2 dM^3 (00056, 00057) ; 1 dM^4 (00060) ; 1 mandible with M_1 fragment, M_2 and M_3 (00048) ; 1 mandibular fragment with C and P_1 to P_4 (00034) ; 1 mandibular fragment with P_3 to M_1 (00050) ; 1 mandibular fragment with M_1 to M_3 (00044) ; 1 mandibular fragment with M_2 (00047) ; 1 mandibular fragment with M_3 (00049) ; 1 I_1 (00025) ; 3 I_2 (00026-00028) ; 4 I_3 (00029-00032) ; 1 lower canine (00033) ; 1 P_1 (00035) ; 3 P_2 (00036-00038) ; 1 P_3 (00039) ; 4 M_1 (00040-00043) ; 2 M_2 (00045, 00046) ; 3 dI_1 (00061-00063) ; 3 dI_2 (00064-00066) ; 3 dM_4 (00067-00069) ; 2 cheek tooth fragments (00070).

3 thoracic vertebrae (00071-00073) ; 4 humeri (00074-00077) ; 2 radii (00078, 00079) ; 2 scaphoids (00080, 00081) ; 1 lunate (00082) ; 1 cuneiform of manus (00083) ; 1 unciform (00084) ; 2 third metacarpi (00085, 00086) ; 1 fourth metacarpus (00087) ; 1 femur (00088) ; 1 patella (00089) ; 2 tibiae (00090, 00091) ; 1 talus (00092) ; 2 calcanea (00093, 00094) ; 1 navicular (00095) ; 1 lateral cuneiform (00096) ; 2 third metatarsi (00097, 00098) ; 3 fourth metatarsi (00099-00101) ; 1 fifth metatarsus (00102) ; 3 proximal phalanges (00103-00105) ; 7 middle phalanges (00106-00112) ; 3 distal phalanges (00113-00115).

Detailed specimen data are given in the appendix.

Description

Skull ——

OUA-NT 00007 preserves the anterior part of the premaxilla. This bone is thick and stout in comparison with average individuals of the living *Sus scrofa leucomystax*. The distance between its anterior tip and the anterior margin of the alveolus of I^1 is longer than in the average individuals, and measures 7.1 mm along the median line. The distance between the anterior tip of the premaxilla and that of the palatine fissure (DPP in Fig. 1) is also longer, and measures 29.9 mm. The anterior tip of the fissure is situated slightly posterior to that of the alveolus of I^2. The lateral wall of the premaxilla preserved is slightly concave. The diastema between I^1 and I^2 and that between I^2 and I^3 measure 6.5 mm and 5.5 mm respectively.

The maxilla is preserved in OUA-NT 00012, 00016, 00018, 00021, 00022, 00058 and 00059. Of the specimens, OUA-NT 00012 preserves the lateral face of the rostrum (Pl.2, fig.3a). This face is weakly concave antero-posteriorly, and seems not to have a developed prezygomatic shelf or preorbital fossa. The canine flange is as weak as those of average male individuals of the living *S. scrofa leucomystax*, but weaker than in male individuals of such fossil species as *S. minor, S. strozzii, S. falconeri, S. brachygnathus* and *S. macrognathus*, as compared below. Its posterior border leaves the lateral face of the rostrum above the posterior part of P^2, and extends antero-laterally (Pl. 2, fig. 3b). A small foramen penetrates the anterior margin of the infraorbital foramen, which lies above the posterior border of P^4. The palatine foramen opens medially to the anterior lobe of M^3 in OUA-NT 00012 and to the posterior lobe of M^2 in OUA-NT 00016.

The frontal, parietal and lacrimal bones are preserved in OUA-NT 00001. The dorsal surface of the skull above the orbit is smooth (Pl.1, fig.1a). In lateral view, it curves slightly upward, as in the living *S. scrofa leucomystax* (Pl. 1, fig. 1b). The supraorbital foramen opens above the anterior margin of the orbit. It is broadly elliptic, and measures 5.1 mm and 4.0 mm in antero-posterior and transverse diameters respectively. From this foramen, the supraorbital groove extends anteriorly. This groove is, however, shallow and indistinct. The lacrimal bone is penetrated by two lacrimal foramina, which lie more anteriorly than in the living *S. scrofa leucomystax*. They are elliptic and have the maxi-

mum diameters of about 3 mm. Of the foramina, the superior one opens about 9 mm anterior to the anterior margin of the orbit, while the inferior one lies about 14 mm antero-inferiorly to the superior one. The orbit is circular, and measures 43.1 mm in antero-posterior diameter (ADO in Fig.1). The supraorbital process is weak, and its posterior margin, forming the anterior end of the parietal crest, is blunt, and does not form a sharp edge. The lateral surface of the parietal is inflated laterally.

The occipital bone is preserved in OUA-NT 00002. The foramen magnum is circular, and measures 21.5 mm and 20.9 mm in transverse and vertical diameters respectively (TDF and VDF in Fig. 1). The incisum intercondyloidea is a short groove with a width of 3-4 mm and a length of about 9-12 mm, which extends vertically from the upper margin of the foramen magnum. The occipital bone above the foramen magnum forms a smooth, convex surface. The occipital condyle is rounded triangular in posterior view. It extends antero-laterally to the side of the posterior part of the paroccipital process (Pl.1, fig.2b). The length between the lateral borders of the left and right occipital condyles measures 65.0 mm. The intercondylar area is thick and measures 7.6 mm in vertical thickness. The basioccipital with a fine median ridge is slightly concave on both sides of the ridge. It is penetrated by a number of small foramina. Of the foramina, the hypoglossal canal is the largest. It opens just medially to the paroccipital process and about 15 mm laterally to the median ridge. This canal is elliptic, and has the maximum diameter of 4.5 mm. The posterior end of the tympano-occipital fissure, showing a foramen-like shape, is situated just anterior to the hypoglossal canal.

I^1 ——

I^1 is preserved in five specimens (OUA-NT 00003 to 00007). This tooth with a stout root shows a canine-like form with curved upper and lower margins in lateral view. An unworn crown surface is observable in OUA-NT 00006, in which a small cusp lies at the mesial tip of the crown. This cusp is followed distally by a sharp ridge with many cusplets, which runs along the labial margin of the crown. The cusp and ridge are divided by a fine furrow which extends from the labial face to the lingual face of the crown. The measurements of I^1 are given in Table 1.

Table 1. Measurements of I^1 of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 2 and p.59-60 .

	OUA-NT00003	OUA-NT00004	OUA-NT00005	OUA-NT00007
MDD	13.8	11.5	16.1	14.0
LLD	7.0	6.3	8.5	7.5

I^2 ——

I^2 is preserved only in OUA-NT 00007 and 00008, in which their crowns are severely worn up to near the cervices, so that the morphology of the crowns is almost unknown. The wear facet is flat, and has a narrowly elliptic outline in ventral view (Pl. 2, fig.1b). The cervix is almost straight on the lingual face, while it is undulated on the labial face (Pl. 2, fig.1a). The root is stout, and has a triangular shape in lingual or labial view, which gradually tapers from the cervix to the apex.

The mesio-distal and labio-lingual diameters measure 16.2 mm and 5.6 mm respectively in OUA-NT 00007, and 15.5 mm and 5.9 mm respectively in OUA-NT 00008.

Upper canine ——

The male upper canine is represented by OUA-NT 00009 and 00010, but no female upper canines are known.

The canine is a large open-rooted tooth which curves dorsally. In dorsal and ventral views, the tooth is almost constant in width from the basal part to the apical part. In the apical part, however, it is cut diagonally by a vertical wear facet, which is elliptic in apical view (Pl. 4, fig. 4a). In anterior and posterior views, the tooth slightly broadens apically. The cross section of the tooth is broadly elliptic with indentation mainly on the ventral face (Fig. 6).

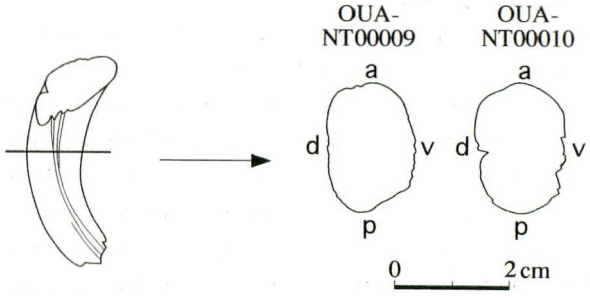

Fig. 6. Cross sections of the male upper canines of *Sus scrofa* from NT Cave. Left figure (anterior view) not in scale. a : anterior face, d : dorsal face, p : posterior face, v : ventral face.

The ventral and anterior faces of the tooth are covered by an enamel layer. Futhermore the layer is coated by cementum on the anterior face and on the anterior part of the ventral face. The surface of the enamel has many longitudinal fine furrows. The dentine is exposed on the dorsal face of the tooth. Weak and fine longitudinal striation is seen on the dentine surface. In addition to the striation, there is a fine but deep longitudinal furrow on the center of the dorsal face in OUA-NT 00010. The dentine is also exposed on the postrior face in OUA-NT 00009, but the face is coated by cementum in OUA-NT 00010. In the former specimen, a short and slender enamel band covers the apical part of the edge between the posterior and dorsal faces of the tooth.

The antero-posterior and dorso-ventral diameters at the posterior end of the wear facet measure 21.5 mm and 16.7 mm respectively in OUA-NT 00009, and 23.1 mm and 17.7 mm respectively in OUA-NT 00010. The radius of curvature measured from the inner side (Ri in Fig. 2) and that measured from the outer side (Ro in Fig. 2) are 38 mm and 49 mm respectively in OUA-NT 00009, and 29 mm and 39 mm respectively in OUA-NT 00010.

P^1 ——

P^1 is preserved only in OUA-NT 00011 and 00012. In the latter specimen, this tooth is crowded out laterally from the cheek tooth row on the maxilla, so that the long axis of the crown becomes oblique to those of the other cheek teeth in palatal view (Pl. 2, fig. 3b). The crown has a narrowly elliptic occlusal outline with a slight constriction at the central part, and is composed of three cusps which are set in a single line and connected with each other by high ridges. Of the cusps, the central one is the largest and highest, and the posterior one is somewhat smaller than the central one. The anterior one is, however, much smaller than the posterior one. The length and width of the crown measure 10.9 mm and 4.8 mm respectively in OUA-NT 00011, and 11.6 mm and 5.1 mm respectively in OUA-NT 00012.

This tooth has two thick roots.

P^2 ——

P^2 is preserved only in OUA-NT 00012 and 00013. The crown has an ovate outline in occlusal view. The paracone, the largest and highest cusp in the crown, is situated in the central part of the crown. The prestyle is attached on the anterior face of the paracone, and is lower and much smaller than the paracone. In OUA-NT 00013, the metacone is a large cusp connected posteriorly to the paracone. In OUA-NT 00012, however, it seems to be indistinct and to form a posterior ridge of the paracone.

The paracone, prestyle and metacone comprise the main part of the crown, which annexes accessory cusps on its lingual face. Of the accessory cusps, two are observed on the lingual side of the prestyle in OUA-NT 00012, but they are very small and much lower than the prestyle. A shallow, small depression is formed between the accessory cusps and prestyle in this specimen. In OUA-NT 00013, however, the accessory cusps are absent, and a short, steep valley is observed there.

Other accessory cusps are observed on the lingual side of the metacone. They are smaller and lower than the metacone, and form a ridge extending along the lingual margin of the crown. A shallow furrow runs antero-posteriorly between the ridge and the metacone. In OUA-NT 00012, these accessory cusps are three, of which the anterior one is indistinct. In OUA-NT 00013, the anterior one is absent, and thus they are only two.

The length and width of the crown measure 13.1 mm and 9.0 mm respectively in OUA-NT 00012, and 13.7 mm and 8.8 mm in OUA-NT 00013 (the width corresponds to Wp in $P^{2\text{-}3}$ of Fig. 2).

P^3 ——

P^3 is observable in four specimens (OUA-NT 00012, 00014 to 00016). The occlusal outline of the crown is a rounded trapezoid elongating antero-postriorly. The basic structure of the crown is the same as that of P^2, but some of the lingual accessory cusps are better developed. The paracone and metacone form a high cutting edge extending antero-posteriorly in the buccal part of the crown. These cusps are almost indistinguishable from each other except in the unworn specimen (OUA-NT 00015). The prestyle constitutes the anterior end of the cutting edge, but is much lower than the paracone. The primocone is observed at the antero-lingual corner of the crown. It is connected with the prestyle and the antero-lingual face of the paracone, so that a shallow closed depression is formed among these cusps. The protocone is much larger than the primocone, but much lower than the cutting edge. This cusp is connected to the metacone by a low ridge extending along the posterior margin of the crown. A shallow groove is formed between the protocone and cutting edge. Small accessory cusps are observed on the lingual face of the paracone. The number of the cusps is one in OUA-NT 00012 and 00014, two in OUA-NT 00016 and three in OUA-NT 00015.

Three roots are present. Of these, the anterior one is the largest, and has a longitudinal broad groove on its posterior face. The postero-buccal one is the smallest, and has an elliptical cross section.

The measurements of the crown are given in Table 2.

Table 2. Measurements of P^3 of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 2 and p. 59-60.

	OUA-NT00012	OUA-NT00014	OUA-NT00015	OUA-NT00016
L	14.3	14.4	14.5	16.9
Wa	8.8	9.1	10.6	11.2
Wp	12.5	11.4	11.8	13.5

P^4 ——

P^4 is preserved in four specimens (OUA-NT 00012, 00016 to 00018). The occlusal outline of the crown is roughly a square with a rounded lingual margin.

The three main cusps (paracone, metacone and protocone) are larger and higher than the accessory cusps, including the protoprestyle and preconule. This feature is clearly observed in the unworn specimen (OUA-NT 00017).

The paracone and metacone are large conical cusps aligned along the buccal margin of the crown. These cusps are separated by a fine transverse furrow branching from the protofossa. This furrow easily disappears on the occlusal surface by attrition.

The preconule is attached on the lingual face of the paracone, so that the wear facets of the two cusps are easily coalescent with each other by attrition. A ridge extends anteriorly from the preconule to the anterior margin of the crown, where it meets another ridge running from the protocone along the anterior margin of the crown. The latter ridge is formed by the coalescence of small accessory cusps, and is separated from the protoprestyle by a fine furrow extending antero-posteriorly. This furrow becomes a small closed pit by attrition. The protoprestyle, a small accessary cusp, is observed at the antero-buccal corner of the crown.

The protocone is a large conical cusp in the lingual part of the crown. Its apex is situated on the same line as the transverse furrow separating the paracone from the metacone. The ridge along the posterior margin of the crown runs from the posterior face of the metacone to that of the protocone. It is also formed by the coalescene of small accessory cusps. Of the cusps, the central one (posterior sagittal cusplet) is the largest.

The protofossa is a deep and fine groove somewhat meandering on the central part of the crown. It has many branches, and opens lingually behind the protocone.

The measurements of the crown are given in Table 3.

Table 3. Measurements of P^4 of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 2 and p.59-60.

	OUA-NT00012	OUA-NT00016	OUA-NT00017	OUA-NT00018
L	13.6	14.5	14.5	13.7
W	15.0	16.7	15.7	13.8

M^1 ——

M^1 is observable in six specimens (OUA-NT 00012, 00016, 00019 to 00022). The crown has a broadly oblong occlusal outline with rounded corners and central constriction. The crown comprises four main cusps (protocone, paracone, metacone and tetracone), an intermediate cusp (tetrapreconule), and marginal accessory cusps and cingula, including the protopreconule and pentapreconule. Of the four main cusps, the buccal two are somewhat higher than the lingual two, but all of them are approximately equal in size. The main cusps are conical, and are complicated in appearance by fine vertical furrows radiating from their apical parts. The intermediate cusp is somewhat lower, but considerably smaller than the main cusps. This cusp also has fine vertical furrows, and is oval or round in occlusal view.

The marginal accessory cusps and cingula are lower than the main cusps and intermediate cusp. The anterior cingulum forms the anterior margin of the crown, and extends from the antero-buccal corner to the antero-lingual corner of the crown. Its lingual end is slightly elevated to be cusp-like. The protopreconule is a small cusplet which is interposed among the anterior cingulum, protocone and paracone.

Two small accessory cusps are observed at the lingual entrance of the transverse valley between the protocone and tetracone in OUA-NT 00019, 00020, 00021 and 00022. In the transverse valley between the paracone and metacone, there are two or three small accessory cusps in OUA-NT 00019, 00020 and 00022, but no accessory cusps in OUA-NT 00016.

A cingulum is observed along the posterior margin of the crown. This cingulum is formed by several small accessory cusps, and is somewhat shorter than the anterior cingulum. Of the accessory cusps, the pentapreconule is the largest, and is situated behind the tetracone.

The cervix is almost straight or slightly undulates on both lingual and buccal faces of the tooth. Four roots are present above the cervix.

The measurements of the crown are given in Table 4.

Table 4. Measurements of M^1 of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 2 and p.59-60.

	OUA-NT 00012	OUA-NT 00016	OUA-NT 00019	OUA-NT 00020	OUA-NT 00021	OUA-NT 00022
L	18.2	19.2	20.2	19.6	17.5	18.4
Wa	15.8	17.1	16.2	16.0	—	—
Wp	15.7	17.1	15.8	16.0	15.2	15.7

M^2 ——

M^2 is represented by five specimens (OUA-NT 00012, 00016, 00021, 00023, 00024). This tooth is only a large version of M^1, and thus the occlusal outline, the patterns of the cusps and cingula, and the morphology of the cervix are almost coincident with those of M^1.

In the transverse valley between the protocone and tetracone, there are one to three small accessory cusps in all the specimens. In the transverse valley between the paracone and metacone, there are one or two small accessory cusps in OUA-NT 00012, 00016, 00023 and 00024, but no accessory cusps in OUA-NT 00021.

This tooth is four-rooted as in M^1. The measurements of the crown are given in Table 5.

Table 5. Measurements of M^2 of *Sus scrofa* from NT Cave, in mm. For the measuring method see Fig. 2 and p. 59-60.

	OUA-NT 00012	OUA-NT 00016	OUA-NT 00021	OUA-NT 00023	OUA-NT 00024
L	24.8	25.3	21.9	25.1	24.7
Wa	19.7	22.2	19.9	20.1	20.3
Wp	20.0	21.4	18.7	20.2	19.1

M^3 ——

M^3 is preserved in three specimens (OUA-NT 00012, 00016, 00021). The occlusal outline of the crown is an obovate with transverse constriction in two parts. The structure of the crown anterior to the pentapreconule is the same as those of M^1 and M^2.

The pentapreconule is smaller and lower than the tetrapreconule, and is divided into two cusplets in OUA-NT 00012 and 00021. The hexacone is a large cusp which rivals the tetracone in size, but is somewhat lower than the latter cusp. One or two fine vertical furrows are observed in its antero-lingual part. The pentacone lies on the buccal side of the hexacone, and is smaller and lower than the hexacone. A tiny accessory cusp is attached on the postero-buccal face of the hexacone in OUA-NT 00012 and 00016. The pentacone has no vertical furrows, and is variable in the degree of development. It is considerably large in OUA-NT 00021, while it is as small as marginal accessory cusps in OUA-NT 00016. In OUA-NT 00012, it is intermediate in size (*vide* Pl. 2, figs. 2 and 3 ; Pl. 3, fig. 1). One or two small accessory cusps are observed in the valley between the tetracone and hexacone, and in the valley between the metacone and pentacone. In OUA-NT 00021, the heptacone is well developed, and is nearly as large as the hexacone. Its lingual and buccal parts are weakly separated from the central part to be two accessory cusps. In OUA-NT 00012, the heptacone is a small and low but distinct cusp attached on the posterior face of the hexacone. In OUA-NT 00016, however, it is completely absent.

The cervix is weakly undulated or nearly straight on both lingual and buccal sides of the tooth. This tooth seems to be five-rooted.

The measurements of the crown are given in Table 6.

Table 6. Measurements of M^3 of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 2 and p.59-60.

	OUA-NT00012	OUA-NT00016	OUA-NT00021
L	39.5	39.4	39.9
Wa	21.5	24.6	21.7
Wm	19.2	22.3	17.9
Wp	15.2	15.3	15.5

dI^1 ——

dI^1 is represented by OUA-NT 00051 and 00052. The overall morphology is similar to that of I^1, but this tooth is smaller, and thinner labio-ligually. The main cusp lies at the mesial corner of the crown, from which the main cutting edge steeply slopes toward the distal corner of the crown. On the lingual face of the crown, a subsidiary low ridge formed by a few cusplets runs from the lingual rib of the main cusp to the distal corner of the crown. A shallow furrow is formed between the ridge and the main cutting edge. The labial face of the crown is smooth. The cervix remarkably descends below the main cusp on the lingual face, but it gently undulates on the labial face. This tooth has a stout root with an elliptic section elongated mesio-distally. It remarkably curves posteriorly, and gradually tapers toward its apex.

The mesio-distal and labio-lingual diameters of the tooth measure 7.8 mm and 4.2 mm respectively in OUA-NT 00051, and 9.4 mm and 4.5 mm respectively in OUA-NT 00052.

dI^2——

dI^2 is observed only in OUA-NT 00053. Its morphology is generally similar to that of I^2, but this tooth is smaller. Both labial and lingual faces of the crown are smooth. The main cusp is situated somewhat distal to the mesial tip of the crown. An indistinct, small accessory cusp is located at the mesial tip. Another small accessory cusp is observed somewhat distal to the main cusp. These three cusps form a straight cutting edge extending mesio-distally in the center of the crown in occlusal view. This ridge gently slopes mesially from the main cusp, but steeply slopes distally from the same cusp. The cervix on the labial face undulates gently, but the cervix on the lingual face descends mesially from the distal end of the crown. A thick root is observed above the cervix. It has an elliptic section near the cervix, and extends straight postero-dorsally.

The mesio-distal and labio-lingual diameters of the tooth measure 7.5 mm and 4.9 mm respectively.

dM^2 ——

dM^2 is preserved in OUA-NT 00054 and 00055. The crown has a subovate occlusal outline with central constriction. The structure of the crown is similar to that of P^3.

The crown comprises the central crest, forming a high, sharp cutting edge, and two low lingual heels. The crest extends straight antero-posteriorly in occlusal view, and is highest in the center of the crown in buccal or lingual view. The crest has a weak indentation which is easily worn away. Of the heels, the anterior one is much smaller than the posterior one, and comprises two or three cusplets. The posterior heel is composed of a ridge along the lingual margin of the crown and a longitudinal furrow between the ridge and

the central crest. A cusplet is recognizable in the ridge, and is larger than the cusplets of the anterior heel. The cervix lowers centrally on both lingual and buccal faces of the tooth, and ascends anteriorly and posteriorly toward the bases of the roots.

The tooth is three-rooted. The anteior root has an elliptic cross section elongated linguo-buccally, and has a vertical groove on its posterior face. The postero-lingual and postero-buccal roots are united with each other in more than half of their total length, and then divided in their apical part. In the united part, a vertical groove is observed both on the lingual and buccal faces. In the apical part, the roots have broadly elliptic cross sections, elongated antero-posteriorly.

The length and width of the crown measure 11.4 mm and 7.0 mm respectively in OUA-NT 00054, and 12.1 mm and 7.8 mm respectively in OUA-NT 00055.

dM^3 ——

dM^3 is preserved in OUA-NT 00056 and 00057. The crown has an ovate occlusal outline, and is more cuspidate than in dM^2.

The crown is composed of four conical cusps (prestyle, paracone, metacone and protocone). Of the cusps, the prestyle is the smallest, and lies at the anterior tip of the crown. It is lower than the paracone, and distinctly separated from the cusp by a transverse valley. The paracone, the largest cusp, lies posterior to the prestyle. From the apex of the paracone, a weak ridge extends anteriorly toward the prestyle, and two other weak rigdes runs posteriorly and postero-lingually. The latter two rigdes are interrupted by the transverse valley which separates the paracone from the metacone and protocone. The latter two cusps lie in the postero-buccal and postero-lingual parts of the crown respectively. These cusps are approximately equal in size, and each of them has an indistinct ridge extending anteriorly.

A distinct cingulum, formed by the coalescene of many tiny cusplets, runs from the lingual side of the prestyle to the antero-lingual face of the protocone along the lingual margin of the crown. Another cingulum is observed along the posterior margin of the crown. The cervix is weakly undulated or almost straight both on the lingual and buccal sides of the tooth.

dM^3 has three roots. Of the roots, the anterior one is elongated linguo-buccally, and has a broad vertical groove on its posterior face, so that the cross section of the root is crescentic. The postero-lingual root approximates the anterior root in size. The postero-buccal root is separated from the postero-lingual root even near the cervix.

The length and width of the crown measure 13.8 mm and 9.9 mm respectively in OUA-NT 00056, and 13.8 mm and 9.1 mm respectively in OUA-NT 00057.

dM^4 ——

dM^4 is preserved in three specimens (OUA-NT 00058 to 00060). The crown has an oblong occlusal outline with round corners and central constriction. Its anterior margin is almost straight, and extends somewhat obliquely to the transverse axis of the crown in occlusal view. The basic structure of the crown is almost the same as that of M^1, but the size is much smaller.

The four main cusps are conical, and have nearly the same size. They have wrinkled surfaces as in the permanent molars. Of the cusps, the buccal two are somewhat higher than the lingual two. The tetrapreconule is much smaller and lower than the main cusps. The anterior cingulum is also much lower than the main cusps, and is longer than the posterior cingulum. The protopreconule is not recognized. A tiny accessory cusp is observed at the lingual entrance of the central transverse valley, and one or two tiny accessory cusps are also observed at the buccal entrance of the same valley. The pentapreconule is recognizable as one or two low cusplets in the posterior part of the longitudinal valley between the metacone and tetracone. The posterior cingulum is formed behind the pentapreconule, and is lower than the cusplet.

The cervix is slightly undulated both on the buccal and lingual faces of the tooth, and is almost straight on the anterior and posterior faces. This tooth has four roots, which are present above the four main cusps.

The length, anterior width and posterior width measure 16.0 mm, 13.3 mm and 13.0 mm respectively in OUA-NT 00058, 16.1 mm, 12.3 mm and 12.1 mm respectively in OUA-NT 00059, and 16.5 mm, 13.4 mm and 13.6 mm respectively in OUA-NT 00060.

Mandible ——

The mandible is observable in six specimens (OUA-NT 00034, 00044, 00047 to 00050), but most of them are very fragmental. In OUA-NT 00034, two of mental foramina are observed on the buccal face of the horizontal ramus. One lies below the anterior margin of the canine, and another lies below P_4. The diastema between P_1 and P_2 measures 7.5 mm in the same specimen. The horizontal ramus below the molars and the basal part of the ascending ramus preserved in OUA-NT 00048 are morphologically similar to those of the living *S. scrofa leucomystax* (Pl. 3, fig. 2). In lateral view, the lower border of the horizontal ramus is nearly straight but descends slightly towards the angle of the mandible. No extramolar ridge is seen along the alveoli of the molars. In dorsal view, the horizontal ramus is not so thick, and a slight depression is observed postero-buccally to M_3. The mandibular foramen opens at the level of the alveolar border of the molars.

The height and thickness of the horizontal ramus below the anterior part of M_3 measure 47.4 mm and 31.7 mm respectively.

I_1 ——

I_1 is observable only in OUA-NT 00025. This tooth is peg-like, and is compressed mesio-distally. It is symmetrical in lingual or labial view, and its mesial and distal margins are almost parallel to each other. The crown is considerably worn and the wear facet expands from the anterior face to all the lingual face. The anterior border of the wear facet slightly inclines distally. The labial face of the crown is smooth. The root is stout and has nearly the same height and width as the crown. It is a narrowly ovate in cross section. The cervix projects anteriorly to form the anticlinid on the mesial and distal faces.

The mesio-distal and labio-lingual diameters of the tooth measure 7.2 mm and 11.2 mm respectively.

I_2 ——

I_2 is observable in three specimens (OUA-NT 00026 to 00028). This tooth is also peg-like. It is asymmetrical, because its distal margin gently curves in lingual or labial view. The anterior border of the crown remarkably slopes distally. On the lingual face of the crown, there is a marked central rib extending from the tip of the crown to the cervix. It is somewhat biassed distally. Along the distal margin of the crown, there is a distal rib, which is narrower and lower than the central rib. A shallow but distinct groove is formed between the central and distal ribs. This groove is traceable on the linguo-distal face of the root.

Furthermore, a mesial rib is observed along the mesial margin of the crown. This rib is shorter than the distal rib. A shallow groove between this rib and the central rib is also shorter than the distral groove. The labial face of the crown is smooth.

The root is also stout, and has nearly the same height and width as the crown near the cervix, but gradually tapers toward its apex. The root has an ovate cross section compressed mesio-distally. The anticlinid projects much more anteriorly on the mesial face than on the distal face.

The mesio-distal and labio-lingual diameters of the crown measure 7.8 mm and 10.8 mm respectively in OUA-NT 00026, 8.3 mm and 11.3 mm respectively in OUA-NT 00027, and 8.1 mm and 11.7 mm respectively in OUA-NT 00028.

I_3 ——

I_3 is observed in four specimens (OUA-NT 00029 to 00032). It is also peg-like, but much smaller and shorter than I_1 and I_2. This tooth is asymmetrical in lingual and labial views. The cutting edge has weak or no indentation, and steeply slopes down distally. The lingual face of the crown is somewhat inflated, and is almost smooth. On this face, however, there is an indistinct furrow along the distal margin of the crown. The labial face of the crown is smooth with neither furrows nor striations. The root is also stout, and gradually tapers towards its apex. It also has an oval cross section compressed mesio-distally. No groove is observed on the surface of the root. The anticlinid of the mesial face projects much more anteriorly than that of the distal face as in I_2.

The measurements of I_3 are given in Table 7.

Table 7. Measurements of I_3 of *Sus scrofa* from NT Cave, in mm. For measuring method and abbreviations see Fig. 2 and p.59-60.

	OUA-NT00029	OUA-NT00030	OUA-NT00031	OUA-NT00032
MDD	8.2	7.7	8.4	7.9
LLD	7.1	6.2	5.5	5.0

Lower canine ——

The male lower canine is represented by OUA-NT 00033 and 00034, but no female canine is known. The canine is a huge open-rooted tooth splayed labially from the mandible (Pl. 4, fig. 1a). Its overall mophology is very similar to that of the living *S. scrofa leucomystax*. The wear facet appears to be rounded triangular, although its apical part is broken in OUA-NT 00033 (Pl. 4, fig. 5b). Its postero-lingual corner projects posteriorly.

The lingual and labial faces of the canine are covered by enamel, but the posterior face is enamel-free. The lingual face is the largest among the three, while the labial face is the smallest. It is also observed in cross section (Fig. 7), where the triangular section shows the longest lingual, intermediate posterior and shortest labial faces. Thus, the canine is of the typically scrofic type (*vide* Fig. 5).

The lingual face is smooth, but the posterior face has a low, longitudinal rib biassed labially. A shallow longitudi-

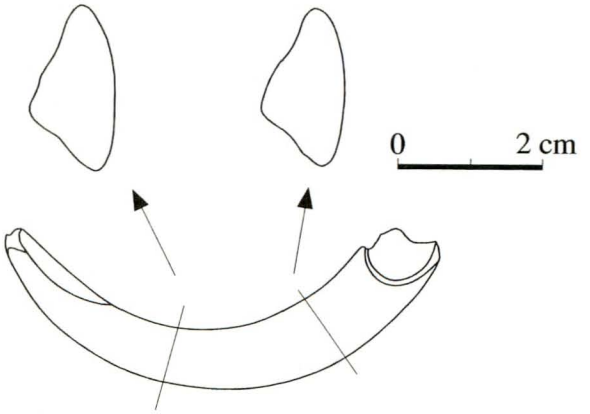

Fig. 7. Cross sections of the male lower canine of *Sus scrofa* from NT Cave (OUA-NT 00033). Lower figure (lingual view) not in scale.

nal furrow is observed along the rib. On the labial face, there is also a shallow longitudinal furrow. In OUA-NT 00033, the widths of the lingual, posterior and labial faces at the posterior end of the wear facet measure 21.5 mm, 16.3 mm and 12.9 mm respectively. In the same specimen, these at the central part (30 mm behind the posterior end of the wear facet) also measure 21.8 mm, 16.7 mm and 13.0 mm respectively. Additionally, the radius of curvature measured from the inner side (Ri in Fig. 2), and that measured from the outer side (Ro in Fig. 2) are 46 mm and 62 mm respectively.

P_1 ——

P_1 is preserved only in two specimens (OUA-NT 00034, 00035). The crown has an elliptic occlusal outline, and comprises two cusps, the anterior main cusp and posterior accessory cusp, which are aligned to form a sharp cutting edge. The former cusp is much higher than the latter. No cingulum is observed. The cervix is straight on the lingual face, while it is somewhat raised centrally on the buccal face. This tooth is two-rooted, but the roots are merged to be a single stout root near the cervix. The length and width of the crown measure 8.3 mm and 4.5 mm respectively in OUA-NT 00034, and 9.8 mm and 4.0 mm respectively in OUA-NT 00035.

P_2 ——

P_2 is represented by four specimens (OUA-NT 00034, 00036 to 00038). The occlusal outline of the crown is narrowly ovate, sometimes with a central constriction. The crown comprises three cusps, namely, the central main cusp and the anterior and posterior accessory cusps. The first cusp is much larger and higher than the others. These cusps are arranged in a single antero-posterior line, and form a sharp cutting edge. The cutting edge between the main cusp and posterior accessory cusp is slightly indented. A small and low additional accessory cusp is attached on the lingual face of the posterior accessory cusp in OUA-NT 00036 and 00038, but it is absent in the other specimens. No cingulum is present. On the buccal and lingual faces of the tooth, the cervix is raised below the main cusp, while it is lowered above the roots.

P_2 has two stout roots, whose cross sections are elliptical or round. They are well separated just below the cervix.

The measurements of the crown are given in Table 8.

Table 8. Measurements of P_2 of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 2 and p.59-60

	OUA-NT 00026	OUA-NT 00036	OUA-NT 00037	OUA-NT 00038
L	13.6	11.3	11.0	11.2
W	6.0	5.4	4.7	6.4

P_3 ——

P_3 is observed in OUA-NT 00034, 00039 and 00050. The crown possesses an oval outline in occlusal view, and comprises four cusps (paraconid, protoconid, metaconid and hypoconid ; *vide* Fig.2). These cusps are aligned antero-posteriorly to form a high, sharp cutting edge. Of the cusps, the protoconid is the highest, which is followed by the metaconid. The paraconid and hypoconid are the lowest, and approximate in height to each other. The precristid is steeply inclined anteriorly. No cingulum is observed. On both lingual and buccal faces, the cervix is raised below the protoconid to form the anticlinid, and is lowered above the roots to form the presynclinid and postsynclinid, as in P_2.

This tooth also has two stout roots, which are separated just below the cervix. The anterior root possesses a round cross section, while the posterior one possesses an elliptical section elongated bucco-lingually.

The length and width of the crown measure 14.3 mm and 7.8 mm respectively in OUA-NT 00034, 14.0 mm and 6.9 mm respectively in OUA-NT 00039, and 14.9 mm and 8.4 mm respectively in OUA-NT 00050.

P_4 ——

P_4 is observed only in OUA-NT 00034 and 00050. The crown has an oval occlusal outline, which is broader than that of P_3. As in P_3, the four cusps constitute most of the cutting edge, but the precristid is replaced by a small accessory cusp which approximates in height to the metaconid. The protoconid is higher than these two cusps, which exceed the paraconid and hypoconid with an approximate height to each other as in P_3. In occlusal view, these cusps are arranged almost in a single antero-posterior line, but the metaconid is slightly shifted lingually from the line, and the hypoconid is slightly shifted buccally. The protoconid is placed somewhat anterior to the center of the crown. Short and steep valleys are observed on both lingual and buccal sides of the metaconid. No cingulum is seen.

On the buccal face of the tooth, the cervix undulates as in P_3. On the lingual face, however, the anticlinid and postsynclinid are indistinct. P_4 seems to have three roots.

The length, anterior width and posterior width measure 16.4 mm, 9.0 mm and 10.3 mm respectively in OUA-NT 00034. They measure 16.7 mm, 8.8 mm and 10.5 mm respectively in OUA-NT 00050.

M_1 ——

M_1 is observed in seven specimens (OUA-NT 00040 to 00044, 00048 and 00050). The occlusal outline of the crown is an oblong with rounded corners and a slight central constriction. The crown comprises four main cusps (protoconid, metaconid, hypoconid and entoconid), two additional cusps attached to the protoconid or metaconid (protopreconulid and protoendoconulid), and three subsidiary

cusps (hypopreconulid, pentapreconulid and pentaconid). The main cusps are larger than the other cusps, of which the subsidiary cusps are much lower. Fine but deep furrows radiate from the apical parts of the main cusps. They make the cusp pattern of the tooth more complicated. Of the main cusps, the lingual ones are somewhat higher than the buccal ones.

On the anterior margin of the crown, there is a narrow cingulum. The hypopreconulid has a transversely narrowly elliptic outline in occlusal view. On the buccal side of this cusp, the hypoectoconulid is observed, and it is divided into two tiny cusplets, which are very low. The pentaconid and pentapreconulid are close to each other, and are divided by a fine transverse furrow.

Along the posterior margin of the crown, a low ridge extends from the pentaconid to the posterior base of the entoconid, and another low ridge extends from the same cusp to the posterior base of the hypoconid in OUA-NT 00040. In OUA-NT 00041 and 00042, these ridges are more cuspidate, and each of them is divided into two or three cusplets.

The cervix is nearly straight, or weakly undulates on both lingual and buccal sides. This tooth is four-rooted.

The measurements of the crown are given in Table 9.

Table 9. Measurements of M_1 of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 2 and p.59-60.

	OUA-NT 00040	OUA-NT 00041	OUA-NT 00042	OUA-NT 00043	OUA-NT 00044	OUA-NT 00050
L	18.8	20.0	19.0	–	18.8	18.4
Wa	11.1	11.9	10.8	–	12.7	–
Wp	11.4	12.3	11.0	12.1	13.5	–

M_2 ——

M_2 is represented by five specimens (OUA-NT 00044 to 00048). This tooth is considerably larger than M_1, but the occlusal outline of the crown, the cusp and ridge patterns, and the morphology of the cervix and roots are almost the same as those of M_1.

The measurements of M_2 are given in Table 10.

Table 10. Measurements of M_2 of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 2 and p.59-60.

	OUA-NT 00044	OUA-NT 00045	OUA-NT 00046	OUA-NT 00047	OUA-NT 00048
L	24.4	24.2	24.5	23.6	20.7
Wa	16.4	16.1	16.0	15.1	–
Wp	17.2	15.6	16.0	16.2±	15.5

M_3 ——

M_3 is represented by three specimens (OUA-NT 00044, 00048, 00049). The occlusal outline of the crown is a narrowly oblong with rounded anterior corners and a round posterior margin. The morphology of the crown anterior to the pentapreconulid is equivalent to those of M_1 and M_2, while the talonid is greatly elongated posteriorly.

The pentapreconulid is a large cusp with broadly elliptic or rhombic occlusal outline. This cusp is lower than the hypoconid and entoconid, and has radiating fine grooves in OUA-NT 00048, but such gooves are absent in OUA-NT 00044. The pentaectoconulid is observed on the buccal side of the pentapreconulid, and is lower than the latter cusp. In OUA-NT 00049, the pentaectoconulid is divided into two cusplets. On the other hand, three low accessory cusps are present on the lingual side of the pentapreconulid in OUA-NT 00048 and 00049.

The pentaconid is a large cusp which rivals the entoconid in size and height, and is larger and higher than the hexaconid which is separated from the pentaconid by a fine but deep longitudinal furrow. The antero-buccal part of the pentaconid tends to be an independent cusplet which lies just posterior to the pentaectoconulid. The heptaconid is also a large cusp which forms the posterior margin of the crown. In OUA-NT 00044, it is as high as the pentaconid, and two longitudinal fine furrows divide its lingual and buccal parts into cusplets. In OUA-NT 00049, the cusp pattern of this part is more complicated. In this specimen, the heptapreconulid is formed between the pentaconid—hexaconid and heptaconid. This cusp is as high as the heptaconid. An accessory cusp is observed on the lingual face of the heptapreconulid, and on that of the heptaconid. These accessory cusps are much lower than the heptapreconulid and heptaconid. An indistinct cusplet is attached to the buccal face of the heptaconid.

The cervix slightly undulates on both lingual and buccal sides of the tooth. The tooth has five roots. Of the roots, the anterior pair lies below the protoconid and metaconid, and extends almost vertically. The middle pair lies below the hypoconid and entoconid, and extends vertically but somewhat posteriorly. The posterior one is the largest, and is elongated antero-posteriorly. This root supports all the talonid, and extends infero-buccally.

The measurements of M_3 are given in Table 11.

Table 11. Measurements of M_3 of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 2 and p.59-60.

	OUA-NT00044	OUA-NT00048	OUA-NT00049
L	45.3	41.2	43.7
Wa	19.5	16.7	17.2
Wm	18.7	16.6	16.9
Wp	17.7	14.7	14.0

dI_1 ——

dI_1 is observed in three specimens (OUA-NT 00061 to 00063). This tooth is peg-like, and its overall morphology is equivalent to that of I_1. In this tooth, however, the size is much smaller, and the distal half of the lingual face of the crown is longitudinally elevated to form a marked broad rib. Along the mesial side of the rib, there is a shallow furrow.

The mesio-distal and labio-lingual diameters of the tooth measure 4.6 mm and 5.7 mm respectively in OUA-NT 00061, 4.4 mm and 5.7 mm respectively in OUA-NT 00062, and 4.4 mm and 6.5 mm respectively in OUA-NT 00063.

dI_2 ——

dI_2 is observed also in three specimens (OUA-NT 00064 to 00066). This tooth is also peg-like, and strikingly resembles I_2 in the morphology of the crown and cervix. But it is much smaller than I_2. The root is mostly lost in the three specimens, and thus its morphology is almost unknown. The mesio-distal and labio-lingual diameters of the tooth measure 4.8 mm and 6.0 mm respectively in OUA-NT 00065, and 4.7 mm and 5.9 mm respectively in OUA-NT 00066.

dM_4 ——

dM_4 is represented by three specimens (OUA-NT 00067 to 00069). The occlusal outline is narrowly oblong with round corners.

The crown comprises three pairs of the main cusps (paraconid and primoconid; protoconid and metaconid; hypoconid and entoconid), two intermediate cusps (endoconulid and hypopreconulid), and marginal accessory cusps and a posterior cingulum. The main cusps are much higher and larger than the other cusps and cingulum. The surfaces of the main cusps are finely wrinkled. The lingual main cusps are somewhat higher than the buccal ones.

As regards the anterior pair, the paraconid lies close to the primoconid, and is separated from the latter cusp by a fine and shallow longitudinal furrow. These cusps are elongated antero-posteriorly. The endoconulid is a tiny cusp attached on the postero-lingual face of the paraconid. It is divided into two cusplets in OUA-NT 00068. A broad and deep transverse valley separates the anterior pair from the middle pair. A tiny accessory cusplet is observed at the buccal entrance of this valley only in OUA-NT 00069.

In the middle pair, the protoconid is separated from the metaconid by a shallow longitudinal furrow, which is broader than that of the anterior pair. This pair is also set apart from the posterior pair by a broad and deep transverse valley. One or two tiny low cusplets are present at the buccal entrance of the valley. In the posterior pair, the hypoconid is well separated from the entoconid. The hypopreconulid is attached on the antero-lingual face of the hypoconid. The posterior cingulum runs from the postero-lingual base of the entoconid to the postero-buccal base of the hypoconid along the posterior margin of the crown. The central part of the cingulum is remarkably inflated anteriorly and somewhat elevated to form the pentaconid.

This tooth has six roots which are present below the six main cusps. Of the roots, the antero-lingual one seems to be united with the antero-buccal one in their basal parts.

The measurements of the crown are given in Table 12.

Table 12. Measurements of dM_4 of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 2 and p.59-60.

	OUA-NT00067	OUA-NT00068	OUA-NT00069
L	20.6	20.6	21.7
Wa	7.2	6.9	7.5
Wm	8.4	8.6	–
Wp	9.3	9.4	10.0

Thoracic vertebra ——

The thoracic vertebrae are represented by three specimens (OUA-NT 00071 to 00073). The morphological differences among the specimens reflect their positional difference in the thoracic vertebral series. OUA-NT 00071 is probably assigned to the second thoracic vertebra. In comparison with the living specimens of *S. scrofa leucomystax*, no basic morphological difference is recognized between them, but the fossil specimens are considerably larger than the living specimens.

The measurements of the thoracic vertebrae are given in Table 13.

Table 13. Measurements of the thoracic vertebrae of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 3 and p.60-61.

	OUA-NT00071	OUA-NT00072	OUA-NT00073
AHvb	19.4	20.9	–
AHvf	12.9	11.3	12.5
AWvf	16.1	13.1	15.7
Lvb	29.2	28.8	27.7
Lsp	30.7	–	–
PWvb	41.0	–	–
PWvf	17.4	17.0	18.3
PHvb	ca.18.8	22.7	–
PHvf	12.4	12.2	13.9

Forelimb bones other than phalanges ——

The humerus and radius are represented by four specimens (OUA-NT 00074 to 00077) and two specimens (OUA-NT 00078, 00079) respectively. Any significant differences are not observed in the morphology of these bones between the fossil specimens and the living specimens of *S. scrofa*

leucomystax compared. The fossil specimens are, however, decidedly larger than the living specimens. The measurements of the humerus are given in Table 14. As regards the radius, the antero-posterior and medio-lateral diameters of the proximal ephiphysis measure 20.0 mm and 31.6 mm respectively in OUA-NT 00078, while the antero-posterior and medio-lateral diameters of the distal epiphysis measure 28.2 mm and 37.3 mm respectively in OUA-NT 00079.

Table 14. Measurements of the humerus of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig.3 and p.61.

	OUA-NT 00074	OUA-NT 00075	OUA-NT 00076	OUA-NT 00077
APDd	–	43.6±	–	49.9±
APDp	74.7	–	–	84.9±
Dh	37.1	–	–	39.6
L	–	–	–	222
MLDd	–	–	44.2±	53.9
SDd	–	–	–	23.2

The scaphoid and lunate are represented by two specimens (OUA-NT 00080, 00081) and one specimen (OUA-NT 00082) respectively. The cuneiform and unciform are represented by one specimen each (OUA-NT 00083, 00084). The morphology of these bones is variable in each individual of the living *S. scrofa leucomystax* observed. The fossil specimens can be accommodated in the morphological variation of these bones of the living *S. scrofa leucomystax*, but their sizes are considerably larger than those of the living specimens. The measurements of the fossil specimens are given in Table 15.

Table 15. Measurements of the scaphoid, lunate, cuneiform and unciform of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 3 and p.61.

	Scaphoid		Lunate	Cuneiform	Unciform
	OUA-NT 00080	OUA-NT 00081	OUA-NT 00082	OUA-NT 00083	OUA-NT 00084
APD	26.9	26.3	23.1	24.8	16.5
H	23.4	22.5	21.2	27.5	–
Ha	–	–	–	–	17.9
Hp	–	–	–	–	23.9
MLD	14.9	14.8	–	17.8	30.0
MLDp	–	–	13.8±	–	–

The third and fourth metacarpi are represented by two specimens (OUA-NT 00085, 00086) and by one specimen (OUA-NT 00087) respectively. The morphology of these bones is well coincident with that of the living specimens of *S. scrofa leucomystax*, but the size is considerably larger

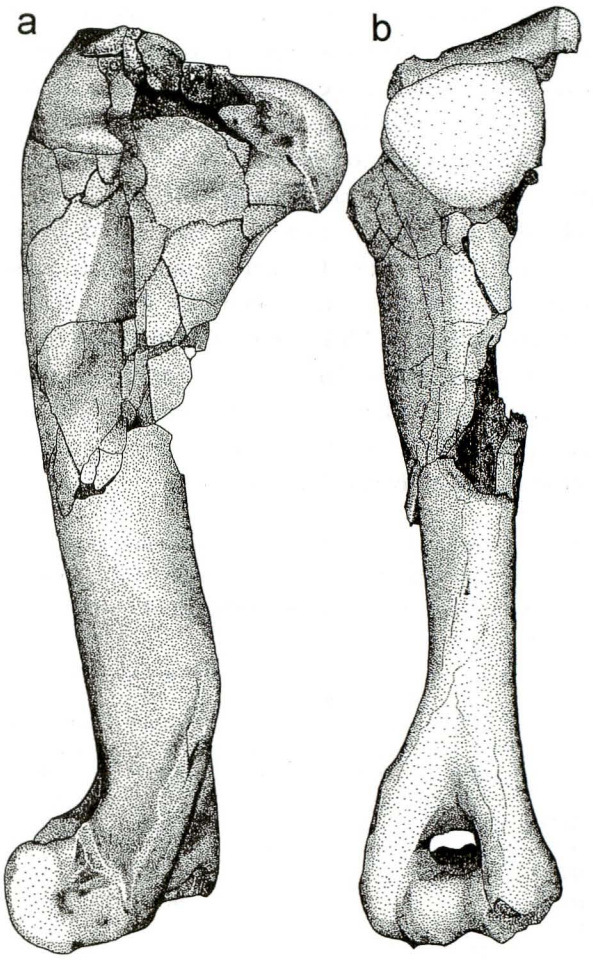

Fig. 8. Left humerus of *Sus scrofa* from NT Cave (OUA-NT 00077). a : lateral view, b : posterior view. One half natural size.

than that of the living specimens. The antero-posterior diameter of the proximal epiphysis (APDp) and medio-lateral diameter of the same epiphysis (MLDp) of the third metacarpus measure 23.0 mm and 25.9 mm respectively in OUA-NT 00086. As regards the fourth metacarpus, APDp, MLDp, the length (L), antero-posterior diameter of the distal epiphysis (APDd) and medio-lateral diameter of the distal epiphysis (MLDd) measure 18.8 mm, 19.2 mm, 84.7 mm, 18.4 mm and 17.3 mm respectively.

Hindlimb bones other than phalanges ——

The femur, patella and tibia are represented by one specimen (OUA-NT 00088), one specimen (OUA-NT 00089) and two specimens (OUA-NT 00090, 00091) respectively. The tarsal bones comprise one talus (OUA-NT 00092), two calcanea (OUA-NT 00093, 00094), one navicular (OUA-NT 00095) and one lateral cuneiform (OUA-NT 00096). The third, forth and fifth metatarsi are preserved in two specimens (OUA-NT 00097, 00098), three specimens (OUA-NT 00099 to 00101) and one specimen (OUA-NT 00102) respectively. No significant differences are observed between these fossil bones and the cor-

responding bones of the living *S. scrofa leucomystax* compared. The sizes of the fossil specimens are, however, considerably larger than those of the living *S. scrofa leucomystax*, as in the other bones and teeth.

The antero-posterior diameter of the distal epiphysis (APDd) and medio-lateral diameter (MLDd) of the same epiphysis of the femur measure 64.5 mm and 55.2 mm respectively. The length (L) and medio-lateral diameter (MLD) of the patella measure 45.6 mm and 31.2 mm respectively. APDd and MLDd of the tibia measure 33.1 mm and 37.8 mm respectively in OUA-NT 00090. Additionally, the measurements of the talus, calcaneum, navicular and lateral cuneiform are given in Table 16, and those of the metatarsi are also given in Table 17.

Table 16. Measurements of the talus, calcaneum, navicular and lateral cuneiform of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 3 and p.61-62.

	Talus	Calcaneum		Navicular	Lat.Cuneif.
	OUA-NT 00092	OUA-NT 00093	OUA-NT 00094	OUA-NT 00095	OUA-NT 00096
APD	25.2	–	–	34.3	17.9
H	–	–	37.2	–	12.8
Ha	–	–	–	18.7	–
Hp	–	–	–	26.3	–
Ll	47.3	–	–	–	–
Lm	42.9	–	–	–	–
MLD	–	–		26.4	16.0
MLDd	27.2	–	–	–	–
MLDp	23.6	–	–	–	–
MLDmax	–	25.3	–	–	–
MLDmin	–	12.9	12.5	–	–

Table 17. Measurements of the metatarsi of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 4 and p.62.

	3rd metatarsus		4th metatarsus			5th mt.
	OUA-NT 00097	OUA-NT 00098	OUA-NT 00099	OUA-NT 00100	OUA-NT 00101	OUA-NT 00102
APDd	–	21.7	18.0	19.9	–	18.6
APDp	–	–	28.6	–	–	–
L	–	–	90.8	95.8	–	–
MLDd	–	22.4	19.5	–	23.4	12.2
MLDp	23.2	–	19.1	21.7	–	–

Phalanx——

The proximal, middle and distal phalanges are represented by three specimens (OUA-NT 00103 to 00105), seven specimens (OUA-NT 00106 to 00112) and three specimens (OUA-NT 00113 to 00115) respectively. The morphology of these bones is similar to that of the living specimens of *S. scrofa leucomystax* compared, but the size is considerably larger than that of the living specimens. The measurements of the phalanges are given in Table 18.

Table 18. Measurements of the phalanges of *Sus scrofa* from NT Cave, in mm. For the measuring method and abbreviations see Fig. 4 and p.62. The detailed positional data of each phalanx are also given in the appendix.

	Proximal phalanx			Middle phalanx		
	OUA-NT 00103	OUA-NT 00104	OUA-NT 00105	OUA-NT 00106	OUA-NT 00107	OUA-NT 00108
APDd	8.2	12.9	10.9	–	8.4	15.1±
APDp	11.9	20.0	14.2	18.8	11.0	–
H	–	–	–	–	–	–
L	21.0	37.7	31.2	27.5	13.5	25.1
MLDd	8.8	16.9	11.3	14.0	–	–
MLDp	10.7	19.5	14.7	17.8	9.2	–

	Middle phalanx				Distal phalanx		
	OUA-NT 00109	OUA-NT 00110	OUA-NT 00111	OUA-NT 00112	OUA-NT 00113	OUA-NT 00114	OUA-NT 00115
APDd	15.5	12.7	–	14.5	–	–	–
APDp	19.3	15.5	20.2±	19.1	–	–	–
H	–	–	–	–	17.7	11.1	9.4
L	27.7	23.5	29.2	27.5	–	20.3	–
MLDd	14.4	12.9	15.8	14.2	–	–	–
MLDp	18.2	14.9	–	18.2	23.8	13.7	11.1

Subfamilar and generic taxonomy

The specimens described above possess suid characters in cranial, dental and postcranial morphology, and thus, undoubtedly belong to the family Suidae. Many suid genera have been recorded from the Neogene and Quaternary of Africa and the Indian Subcontinent, but their taxonomy had been considerably confused until recently. Recent revisions of the Miocene suids from those continents by Pickford (1986, 1988) have greatly contributed to the suid taxonomy. Pickford (1988) provided the subfamiliar classification of the family, in which he recognized the following six subfamilies : Palaeochoerinae, Listriodontinae, Kubanochoerinae, Tetraconodontinae, Hyotheriinae and Suinae. He also gave cranial and dental characteristics of each subfamily, and phylogenetic relationship among them, which was illustrated in a cladogram. We here use Pickford's classification to allocate the present specimens to one of the subfamilies, although Made (1994) and Made (1998) transferred Palaeochoerinae from Suidae to the different families, Tayasuidae and Palaeochoeridae, respectively. In the pres-ent allocation, we refer to the descriptions and illustrations of Lydekker (1884), Stehlin (1899-1900), Pilgrim (1926), Colbert (1935), Godina *et al*. (1962), Hünermann (1968) and

Schmidt-Kittler (1971), in addition to those of Pickford (1986, 1988).

Palaeochoerinae is distinct from the present specimens in having primitive small canines elongating vertically from the jaws, no canine flanges, and simpler and more primitive structures of the cheek teeth. Listriodontinae is also distinct from the specimens in having much longer diastema, no canine flanges, broader and spatulate I^1, rudimentary or no P^1_1, an oblique main cusp ridge in P^2 and P^3, lophodont P^4_4 and molars in various degree, and a simpler talon and talonid in M^3_3.

Kubanochoerinae is easily distinguishable from the present specimens in having no distinct canine flanges, relatively large I^3 and P^1, an oblique main cusp ridge in P^2 and P^3, a distinct lingual cingulum in P^4, a distinct buccal cingulum in each upper molar, cuspidate P_4 without a blade-like ridge, and simpler upper and lower molars with the main cusps being the same height above the cervix.

Tetraconodontinae possesses the following peculiar characters which easily distinguish it from the present specimens. The canine flanges are not developed. The teeth have very thick enamel, and the furrows on each cusp ("Furchen" of Hünermann, 1968) are indistinct. P^3_3 and P^4_4 are very large. Their cusps are inflated and wrinkled on the surfaces. The cusps of the molars are also inflated and show relatively simple patterns. The talon of M^3 is also simple.

Hyotheriinae differs from the present specimens in having a rooted male upper canine with a round cross section ; relatively larger P_1 and P_2 ; a distinct anterior cingulum in P_3 and P_4 ; and no anterior sagittal cusplet (preconule in Made, 1996) and no posterior sagittal cusplet, in the sagittal valley (protofossa in Made, 1996) of P^4. Pickford (1988) considered the last character as apomorphic to distinguish Hyotheriinae from Suinae. On the other hand, the characters of Suinae given by Pickford (1988) are well coincident with those of the present specimens. Thus, the specimens are safely allocated to the subfamily Suinae.

Pickford (1988) listed the following 14 genera as the components of this subfamily : *Propotamochoerus, Hippohyus, Sivahyus, Hippopotamodon, Sus, Potamochoerus, Phacochoerus, Babyrousa, Stylochoerus, Microstonyx, Hylochoerus, Mesochoerus, Metridiochoerus* and *Notochoerus*. Of these, seven are Eurasian genera (*Propotamochoerus, Hippohyus, Sivahyus, Hippopotamodon, Sus, Babyrousa* and *Microstonyx*), while the others are exclusively known from Africa. We therefore compare the present specimens with the Eurasian genera.

Pickford (1988) gave the generic diagnoses of *Propotamochoerus, Hippohyus, Sivahyus and Hippotamodon* as well as their illustrations. In addition to them, we refer to the descriptions and illustrations of Falconer and Cautley (1846), Falconer (1868), Lydekker (1884), Pilgrim (1926) and Wilkinson (1976).

Propotamochoerus is different from the present specimens in having a robust zygomatic arch which branches laterally above M^1, a strong prezygomatic shelf which forms a depression just in front of the orbit, a more robust and thicker horizontal ramus of the mandible, a more cuspidate and more lingually positioned metaconid ("Innenhügel" of Stehlin, 1899-1900) in P_4, thicker enamel and shallower cusp furrows in each molar, a simpler talon in M^3 and a simpler talonid in M_3.

Hippohyus is distinct from the present specimens in having a stronger prezygomatic shelf, the lower border of the maxilla curved downward between P^3 and M^3 in lateral view, more hypsodont cheek teeth, very deep furrows on each cusp of the cheek teeth, horse-like occlusal patterns of the molars, P^3 with two buccal main cusps and two transverse ridges, P^4 with more prominent sagittal cusplets, and more cuspidate P_4.

Sivahyus is also distinguished from the present specimens in its smaller size, and in having more hypsodont cheek teeth with occlusal patterns similar to *Hippohyus* which are formed by deep furrows on each cusp, and in having more cuspidate P_4, and much shorter and simpler M^3_3.

Hippopotamodon is different from the present specimens in having broader I^2 with a lingual cingulum, a broader occlusal outline of P^3, larger and inflated paracone of P^3, a much larger posterior sagittal cusplet of P^4, broader P_3 and P_4 in occlutsal view, a more cuspidate pattern of P_4, and more prominent metaconid situated lingually to the protoconid in P_4.

Babyrousa is a peculiar suid genus with upward extending spiral upper canines. Judging from the figures and descriptions given by Lydekker (1884), Stehlin (1899-1900) and Groves (1980), *Babyrousa* is easily distinguishable from the present specimens in morphology of the male upper canines, and in having a longer diastema, a round occlusal outline of P^2, a simpler occlusal pattern of P^3, a lingual cingulum in P_4, simpler patterns of the molars and shorter M^3_3.

The illustrations and descriptions of *Microstonyx* are given in Stehlin (1899-1900), Pearson (1928), Godina *et al*. (1962), Hünermann (1968), Thenius (1970), Made and Moyà-Solà (1989) and Made *et al*. (1992). Judging from them, *Microstonyx* differs from the present specimens in having frontal bones steeply elevated above the orbit, a strong prezygomatic shelf extending laterally above M^1 or M^2, a longer diastema, much weaker canines, more cuspidate P_4, lingually positioned metaconid in P_4, a more distinct anterior cingulum in P_3 and P_4, and shorter M_3.

Among the seven Eurasian genera, *Sus*, the remaining

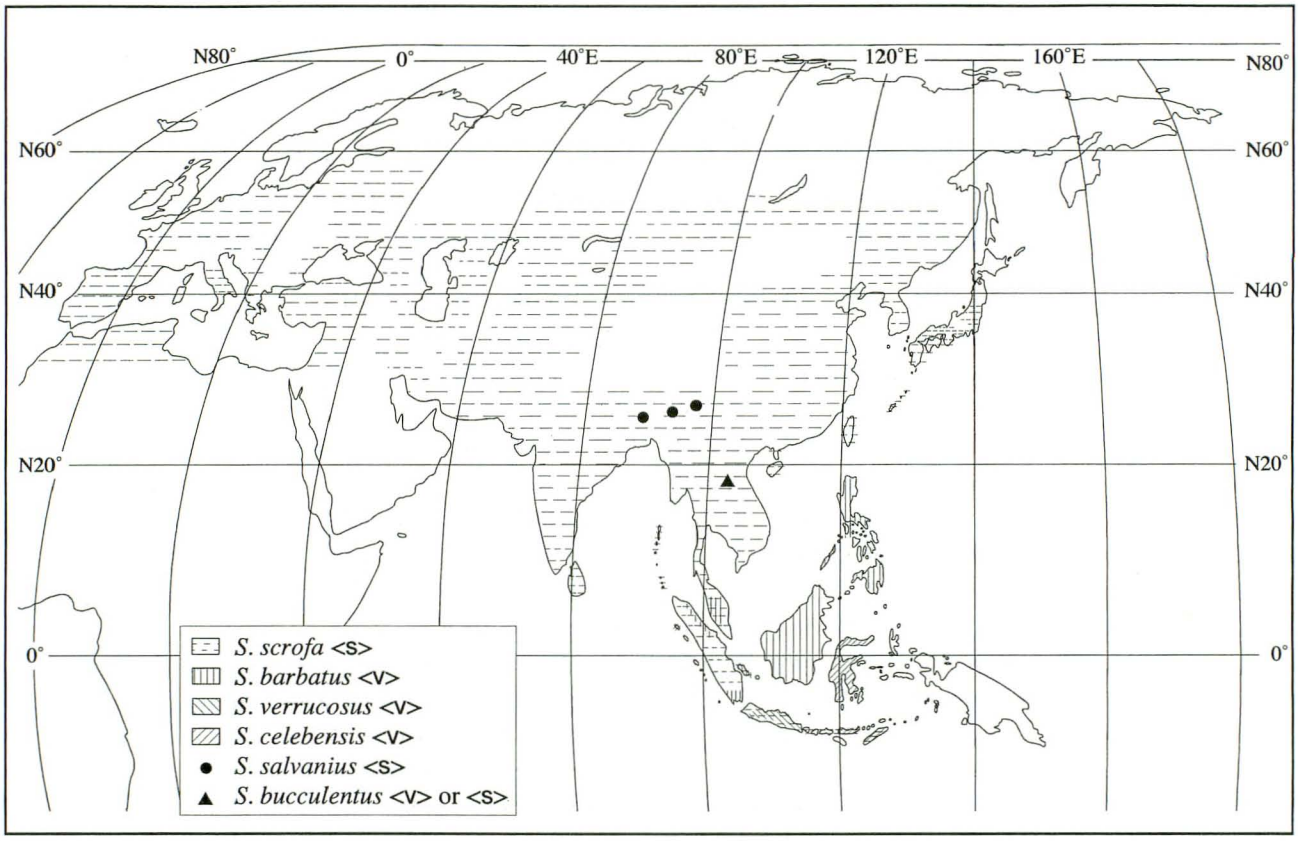

Fig. 9. Distribution of the living species of *Sus*, based on Corbet (1978), Groves (1981), Corbet and Hill (1992) and Groves *et al*. (1997). <s> : species with scrofic male lower canine, <v> : species with verrucosic male lower canine. As regards *S. bucculentus*, Groves *et al*. (1997) noted that its canine is not like *S. verrucosus* as claimed in the original description.

genus for comparison, shows a number of osteological and dental characters well coincident with those of the present specimens. Thus the specimens are referable to *Sus*.

Specific taxonomy

The taxonomy of the living species of *Sus* was recently revised by Groves (1981), who recognized the following five species (their distributions are given in parenthesis ; *vide* Fig. 9) :

Sus scrofa Linnaeus (most part of Eurasia excluding the boreal cold areas, but including North Africa opposite to Europe, Sri Lanka, East Indies, Taiwan and Japan)

S. salvanius Hodgson (Assam)

S. verrucosus Müller (Java and its adjacent islands)

S. barbatus Müller (Malaya, Sumatra, Borneo, Luzon, Mindanao, and their adjacent islands)

S. celebensis Müller (Sulawesi and its adjacent islands)

This classification was followed by Corbet and Hill (1992), although Hardjasasmita (1987) recognized two additional Indonesian species, *S. heuneri* sp. nov. and *S. timorensis* Müller et Schlegel.

Of the species listed above, *S. verrucosus, S. barbatus* and *S. celebensis* possess verrucosic male lower canines. This character distinguishes them from the present specimens which have a typically scrofic male lower canine (Fig. 7). According to Hardjasasmita (1987), *S. heuneri* and *S. timorensis* also have verrucosic male lower canines, and thus these species are distinguishable from the present specimens. On the other hand, *S. salvanius* possesses scrofic male lower canines, but this species is much smaller than the present specimens.

In addition to the living species listed above, Groves *et al*. (1997) recently rediscovered the specimens of *Sus bucculentus* Heude which indicated its specific difference from *S. scrofa* and *S. verrucosus* (*vide* Fig. 9). In spite of the scarcity of the information on its morphology, *S. bucculentus* seems to differ from the present specimens in having a deeper preorbital fossa, a straight dorsal margin of the braincase in lateral view and longer premolars compared to the molars.

The remaining living species, *S. scrofa*, shows a wide range of morphological and size variation in relation to its vast geographical range (Fig. 9). The morphological characters of the present specimens described in the preceding chapter indicate that the specimens are accommodated in the range of *S. scrofa*, and are indistinguishable from *S. scrofa*.

Many fossil species of the genus *Sus* have been described from the Pliocene and Pleistocene of Eurasia. Miocene species have been also recorded from the Indian Subcontinent (*S. praecox, S. comes, S. peregrinus, S. advena* and *S. adolescens*). Pickford (1988), however, regarded the allocation of these Miocene species to *Sus* as incorrect. Thus we compare the present specimens with the representative Eurasian Pliocene and Pleistocene fossil species listed below, whose recorded areas and geological ages are also given in parenthesis (*vide* Fig. 10) :

Sus minor Depéret (Europe, western Asia, North Africa and China ; Pliocene)

Sus nanus Made (Corsica ; Pliocene)

Sus strozzii Meneghini (Europe ; Late Pliocene to Early Pleistocene)

Sus falconeri Lydekker (Indian Subcontinent ; Pliocene)

Sus cautleyi Pilgrim (Indian Subcontinent ; Pliocene)

Sus bakeri Pilgrim (Indian Subcontinent ; Pliocene)

Sus gomphotherioides Sarwar (Indian Subcontinent ; Pliocene)

Sus choprai Gaur (Indian Subcontinent ; Early Pleistocene)

Sus namadicus Pilgrim (Indian Subcontinent ; Pleistocene)

Sus karnuliensis Lydekker (Indian Subcontinent ; Pleistocene)

Sus stremmi Koenigswald (Indonesia ; ?Late Pliocene)

Sus brachygnathus Dubois (Indonesia ; Early to Late Pleistocene)

Sus macrognathus Dubois (Indonesia ; Middle to Late Pleistocene)

Sus sangiranensis Koenigswald (Indonesia ; ?Middle Pleistocene)

Sus subtriquetra Xue (North China ; Late Pliocene or Early Pleistocene)

Sus lydekkeri Zdansky (North China ; Early to Middle Pleistocene)

Sus xiaozhu Han *et al*. (South China ; Early Pleistocene)

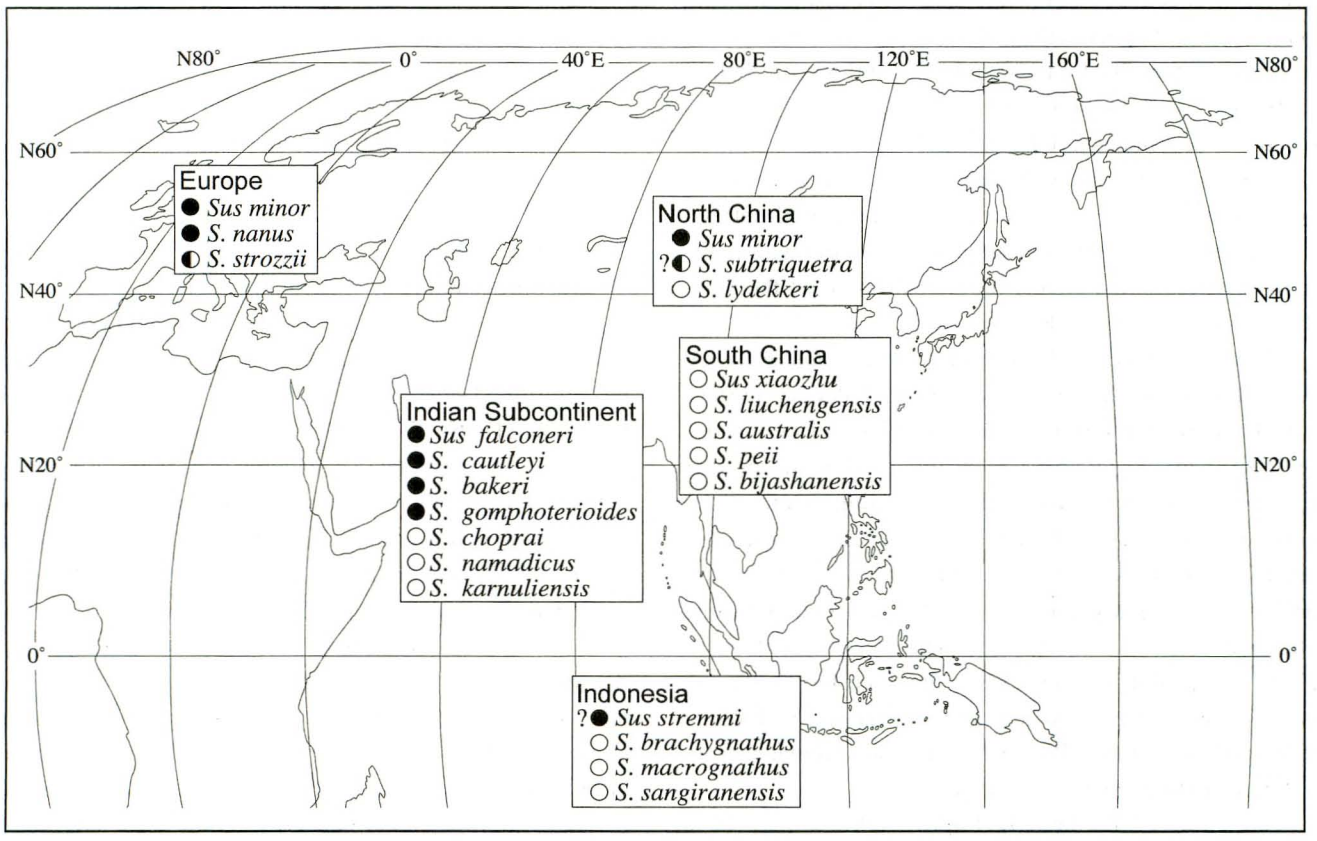

Fig. 10. Representative fossil species of *Sus* in Eurasia. ●Pliocene species, ◐Late Pliocene to Early Pleistocene species, ○Pleistocene species.

Sus liuchengensis Han (South China ; Early Pleistocene)

Sus australis Han (South China ; Early Pleistocene)

Sus peii Han (South China ; Early Pleistocene)

Sus bijiashanensis Han *et al*. (South China ; Early Pleistocene)

As regards *Sus minor*, *S. arvernensis* described from the European Pliocene is considered to be a "nomen dubium" and possibly to be synonymous with this species (Azzaroli, 1975), although Made and Moyà-Solà (1989) used the name "*S. arvernensis*". The illustrations and descriptions provided by Azzaroli (1952, 1975), Hünermann (1971) and Berdondini (1992) suggest that *S. minor* is different from the present specimens in its smaller size, better developed canine flange, thicker horizontal ramus of the mandible especially at M_2, simpler and shorter M^3, and in having a verrucosic male lower canine.

Sus nanus is a dwarf insular species described by Made (1988). This species is still smaller than *S. minor*, and has simpler molar patterns, especially in M^3 (Made, 1988 ; Made and Moyà-Solà, 1989). These characters distinguish *S. nanus* from the present specimens.

On the other hand, *Sus strozzii* is a very large species which rivals the present specimens in size, and has similar patterns of cheek teeth. But this species is distinguishable from the present specimens in the following characters, on the basis of the illustrations and descriptions of Stehlin (1899-1900) and Azzaroli (1952, 1975), and the observations of the specimens in UF and NMB.

Sus strozzii is somewhat larger, and has a better developed canine flange, more posteriorly positioned infraorbital foramen, a larger and thicker male upper canine with a different cross section, a thicker horizontal ramus of the mandible and a verrucosic male lower canine.

The descriptions and illustrations of *Sus falconeri* are given in Falconer and Cautley (1846), Falconer (1868), Lydekker (1884), Pilgrim (1926) and Colbert (1935). Judging from them, *S. falconeri* is different from the present specimens in having an oval orbit elongating antero-posteriorly in lateral view, a longer and better developed male canine flange terminating posteriorly above the anterior part of M^1, a proportionately longer M^3, more complicated patterns in M^3, and a verrucosic male lower canine. Colbert (1935) considered *S. falconeri* as the ancestor of *Phacochoerus* now living in Africa, although Harris and White (1979) recognized that *Phacochoerus* had originated from an African extinct genus, *Metridiochoerus*.

Sus cautleyi, defined by Pilgrim (1926), may be a large variant of *S. falconeri* (Colbert, 1935). *S. cautleyi* is distinguishable from the present specimens in its much larger size and more complicated patterns of M^2 and M^3.

Sus bakeri was also established by Pilgrim (1926) on the basis of the mandible numbered 15373 of BMNH. According to Lydekker (1885), this specimen is figured as Fig. 10 of Plate 71 in Falconer and Cautley (1846). *S. bakeri* differs from the present specimens in its smaller size and in having simpler cusps of the molars with less folded enamel, and a simpler talonid of M_3.

Sus gomphotherioides was recently proposed by Sarwar (1988) on the basis of fragmental materials. This species seems to be differnt from the present specimens in having an occlusal outline of M_3 tapering posteriorly, and a simpler pattern of M_3.

Sus choprai was also proposed by Gaur (1987) on the basis of a left mandible. Judging from Gaur's description and illustrations, this species differs from the present specimens in having a thicker horizontal ramus of the mandible, proportionately smaller premolars, and longer and more complicated M_3.

Sus namadicus, described by Pilgrim (1926), is based mainly on the mandible numbered 36843 of BMNH, which had been also illustrated and described by Falconer and Cautley (1846), Falconer (1868) and Lydekker (1884). Judging from these references, *S. namadicus* is similar to the present specimens, in dental and mandibular morphology, and in the length of M_3, but M_3 is considerably broader, and has a cusp behind the heptaconid. An additional material, questionably assigned to *S. namadicus* by Pilgrim (1926 ; Pl. 20, Fig.16), has a scrofic male lower canine, which corresponds with that of the present specimens. Lydekker (1884, 1885) suggested that *S. namadicus* (his *Sus* sp.) closely resembled the living *S. cristatus* which is generally regarded as a subspecies of *S. scrofa* (Groves, 1981 ; Corbet and Hill, 1992 etc.).

Sus karnuliensis was first described by Lydekker (1886), and additional comments to this species were given by Pilgrim (1926). On the basis of the illustrations of Lydekker (1886), *S. karnuliensis* is larger and has somewhat more complicated M^3 patterns than those of the present specimens, which are nearer to *S. cristatus* (=*S. scrofa cristatus*) illustrated in the same paper. But the morphology of the male lower canine of *S. karnuliensis* is not described in the papers.

Sus stremmi, described by Koenigswald (1933), is represented by few materials from an unknown stratigraphic level (Hardjasasmita, 1987). The only M^3 of this species shows the shape of M_3 as pointed out by Hardjasasmita (1987), and differs from M^3 of the present specimens in having a more squarish occlusal outline and better developed talon. Owing to the poor materials and stratigraphic data, Hardjasasmita (1987) mentioned that *S. stremmi* must be considered a "nomen dubium".

Sus brachygnathus and *S. macrognathus* were briefly described by Dubois (1908), and their detailed description with several illustrations was recently published by Hardjasasmita (1987). On the basis of the latter descripition, *S. bachygnathus* is different from the present specimens in its smaller size, and in having a better developed canine flange, a thicker horizontal ramus of the mandible, a remarkable extramolar ridge on the ramus (*vide* p.14-15 of Hardjasasmita, 1987), and a verrucosic male lower canine. *Sus macrognathus*, including *S. terhaari* Koenigswald as its subspecies, has about the same size as the present specimens, but differs from them in having a verrucosic male lower canine and a proportionately broader P_4, and a more complicated pattern of the posterior part of the talonid of M_3.

The descriptions of *Sus sangiranensis* given by Koenigswald (1963) and Hardjasasmita (1987) indicate that this species is distinct from the present specimens in its much smaller size and simpler M^3 pattern.

Sus subtriquetra, described by Xue (1981), is an aberrant form represented only by a few fragmental materials. This species seems to be different from the present specimens in its smaller size and in having a roundly triangular section of the lower canine whose posterior surface is convex.

Sus lydekkeri, a large species comparable to the present specimens in size, was first described by Zdansky (1928), and its detailed description on the basis of rich materials was subsequently published by Young (1932). We observed the specimens identified as *S. lydekkeri* mainly from Zhoukoudian (=Choukoutien), from which Zdansky's and Young's materials were obtained, in IVPP. On the basis of our observation and the descriptions of Zdansky (1928) and Young (1932), *S. lydekkeri* is similar to the present specimens in the curvature of the dorsal margin of the skull above the orbit in lateral view ; the outline and size of the orbit ; the position and shape of the supraorbital foramen, supraorbital groove, infraorbital foramen and palatine foramen ; the position of the posterior border of the canine flange ; the morphology of the mandible ; and the patterns of the cheek teeth.

On the other hand, *S. lydekkeri* differs from the present specimens in the morphology of the male lower canine which is not typically scrofic (Fig. 11). Zdansky (1928) also showed that the cross section was of intermediate type in his Figure 6. The molars of *S. lydekkeri* are, generally, somewhat broader in proportion to their length than those of the present specimens (Fig. 12).

Additionally, some minor differences are also observed between *S. lydekkeri* and the present specimens. In *S. lydekkeri*, the lacrimal foramina are positioned more posteriorly ; the supraorbital process is stronger ; a short diastema is observed between P^1 and P^2 ; the diastema between the lower canine and P_1, and that between P_1 and P_2

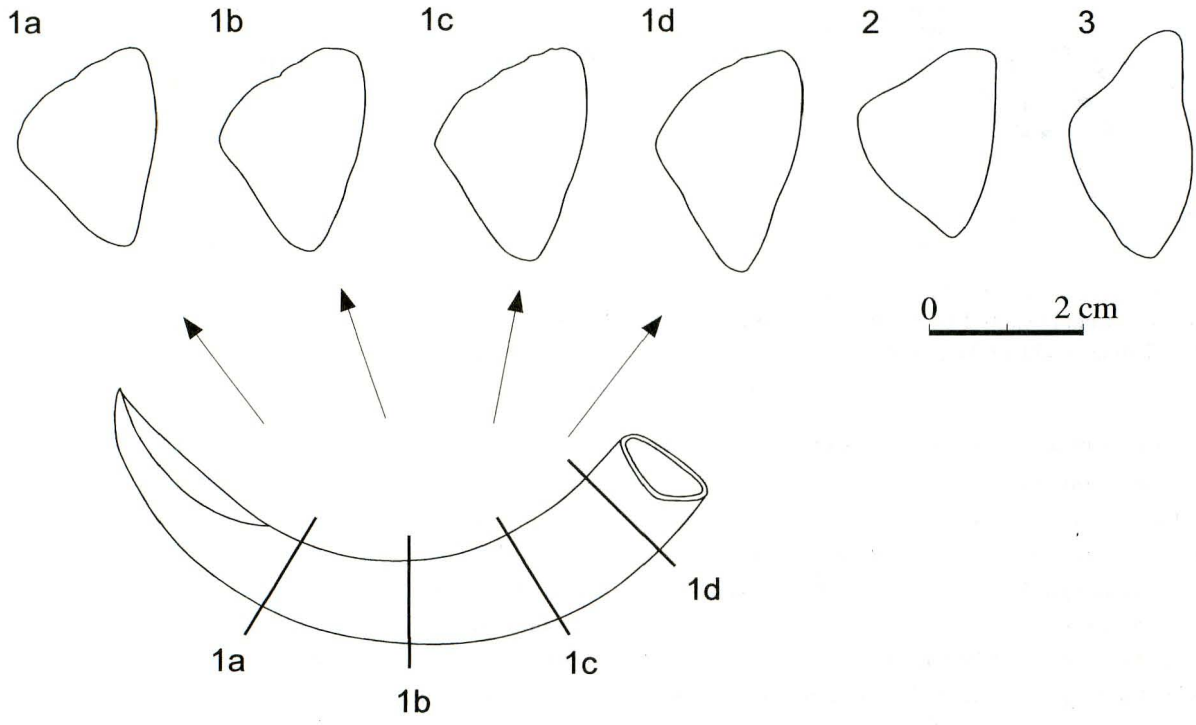

Fig. 11. Cross sections of the male lower canines of *Sus lydekkeri* (=*S. scrofa lydekkeri* in the present treatment) from Locality 1 of Zhoukoudian. 1 : L.31.G.2 51.46. stored in IVPP (a-d : cross sections in various positions), 2 : RV.32001.1. stored in IVPP (cross section in the same position as 1a), 3 : cross section redrawn from Zdansky (1928). Lower figure not in scale.

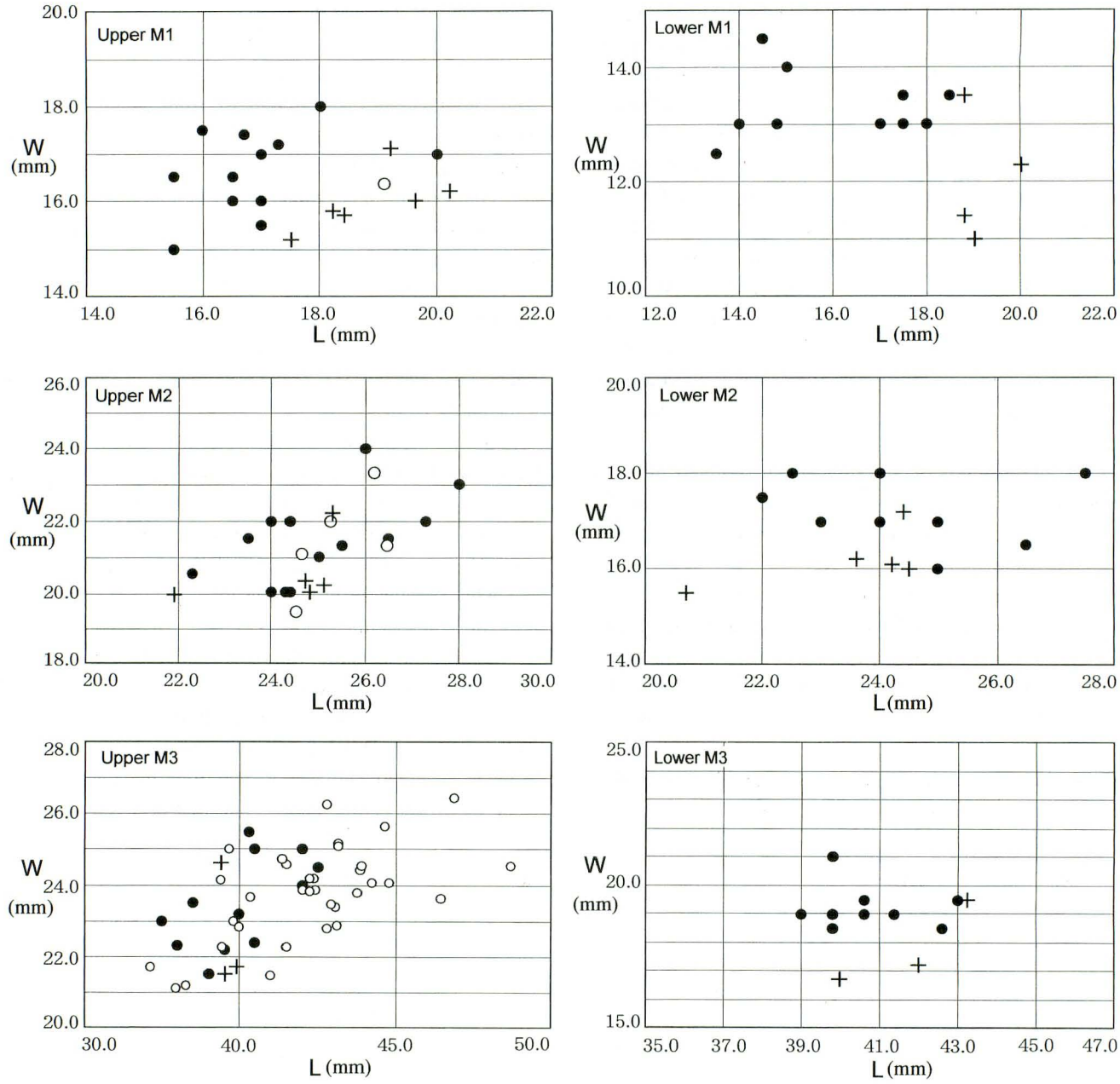

Fig. 12. Scatter diagram comparing the molar sizes of the specimens from NT Cave (+) with those of *S. lydekkeri* (= *S. scrofa lydekkeri*) from Locality 1 of Zhoukoudian (● data by Young, 1932 ; ○ our measurements in IVPP). L : length of the crown, W : maximum width of the crown (the largest width among Wa, Wm and Wp).

are longer. These minor differences, however, seem to be less valuable in taxonomy.

Thus the difference between *S. lydekkeri* and the present specimens is rather slight. As discussed in the next chapter, we herein regard *S. lydekkeri* as a large-sized fossil subspecies of *S. scrofa*.

Sus xiaozhu was described by Han *et al*. (1975) and Han (1987). Judging from their descriptions and illustrations, this species is distinguishable from the present specimens in its much smaller size, and in having simpler patterns of the molars, a square occlusal outline of M^2, a small and simple talon of M^3, and a short talonid of M_3 consisting mainly of a single large cusp (pentaconid).

Sus liuchengensis, *S. australis* and *S. peii* were described by Han (1987). On the basis of Han's descriptions and illustrations, the three species are distinguished from the present specimens by the following characters : *S. liuchengensis* is considerably smaller, and has a more lingually positioned tetrapreconule of M^3 which is connected with the tetracone, and has no heptaconid in the talonid of M_3, although there are two cusps (pentaconid and hexaconid) in the same part. *S. australis* is somewhat smaller in

general, and has less folded enamel on each cusp, less developed cingula and accessory cusps in the molars, a round occlusal outline of P^3, and proportionately broader M_3, although the basic patterns of the molars are similar to those of the present specimens. *S. peii*, the largest species of the three, has a better developed canine flange whose posterior end reaches above the position between P^3 and P^4. In M^3 of this species, the enamel fold of each cusp is weaker, and the tetrapreconule, pentapreconule, pentacone and accessory cusps are less developed. In the male lower canine, the posterior face is narrower than the buccal face (Fig. 3 and p.167 of Han, 1987). Thus the canine is of verrucosic type. The talonid of M_3 possesses one or two cusps (pentaconid and hexaconid), but lacks heptaconid.

Sus bijiashanensis, described by Han *et al*. (1975), is different from the present specimens in its smaller size, and in having proportionately shorter M^3 which results from strong reduction of the talon, in having a roundly triangular cross section of the male lower canine whose posterior side is convex (*vide* Fig. 3 of Han 1987), and in having no heptaconid in M_3.

In conclusion, the present specimens are distinguishable from the above listed fossil species except *S. namadicus* and *S. lydekkeri* which are more similar to the specimens. As mentioned above, *S. namadicus* seems to be near to the subspecies of *S. scrofa* (*S. scrofa cristatus*), and *S. lydekkeri* is also considered to be a subspecies of *S. scrofa* herein. These suggest that the present specimens are morphologically near to *S. scrofa*, and are probably accommodated in the range of *S. scrofa*, including the fossil forms.

On the other hand, the comparison with the living species mentioned above indicates that the specimens are discriminated from the species other than *S. scrofa*, but indistinguishable from *S. scrofa*. The present specimens are, therefore, assignable to *S. scrofa*.

Discussion

In the Japanese Islands, *Sus* remains of Pleistocene age have been mostly identified as *S. nipponicus*, *S.* cf. *lydekkeri, S. leucomystax* and *S. scrofa*. A revision of the identification is required in the light of the recent taxonomic advance of *Sus* and the abundant comparative data on fossil and living specimens of *Sus* obtained by us in many institutions, when we consider the paleontological significance of the *Sus* remains from NT Cave.

According to Matsumoto (1915a), *S. nipponicus* has scrofic male lower canines, and therefore, he included it in his *scrofa*-group. He adopted excessively splitting taxonomy of living *Sus* at that time, and treated *S. leucomystax* of Japan, *S. taivanus* of Taiwan and *S. cristatus* of India as independent species, although all of them are regarded as subspecies of *S. scrofa* in the recent taxonomy (for example Corbet, 1978 ; Groves, 1981 ; Corbet and Hill, 1992). Furthermore, Matsumoto divided the *scrofa*-group into the *scrofa*-series represented by *Sus scrofa* with short last molars, and the *leucomystax*-series represented by *S. leucomystax, S. taivanus* and *S. cristatus* with very long last molars which exceed the united length of the first and second molars. He mentioned that *S. nipponicus* had the characters of the *leucomystax*-series, but differed from *S. leucomystax* and *S. taivanus* in its larger skull, mandible and teeth, and differed from *S. cristatus* in its shorter and wider skull, higher and wider rostrum, wider mandible, stouter lower canines, and shorter and narrower molars. He also considered that *S. nipponicus* was intermediate between *S. cristatus* and *S. leucomystax* — *S. taivanus*.

In spite of Matsumoto's discussion, the differences are not specific on the basis of the recent taxonomy as well as our observation of living specimens stored in many institutions (AMNH, AUE, BMNH, IZ, MCZ, MNHN and OCU) ; therefore, the differences between these four (*S. scrofa, S. leucomystax, S. taivanus* and *S. cristatus* in his sense) and *S. nipponicus* are too slight to distinguish them specifically. It is concluded that *S. nipponicus* is synonymous with *S. scrofa* in species level, as briefly stated by Hayashi (1983) that *S. nipponicus* and *S. scrofa leucomystax* were transitional, and belonged to a single species. Furthermore, the specimens from NT Cave are larger than *S. nipponicus* measured by Matsumoto (1915a ; 1930a, b, c, d), and we could not recognize any morphological differences significant for specific distinction between the specimens and the holotype of *S. nipponicus*, when we observed it in TU. The specimens from NT Cave are identified as *S. scrofa* as mentioned above, and thereby *S. nipponicus* is naturally included in the range of *S. scrofa*. The taxonomic problems on *S. nipponicus* will be discussed in a separate paper on the basis of the abundant data obtained, because they are not the main theme of the present paper.

As regards *S. lydekkeri*, a revision of the Zhoukoudian materials is required on the basis of the descriptions of Zdansky (1928) and Young (1932) and our observation in IVPP, before discussing the Japanese *Sus* remains identified as *S.* cf. *lydekkeri*. The diagnostic characters of *S. lydekkeri* are summarized by Young (1932) as (1) the larger size, (2) long, broad and flat nose, (3) simple and cutting shape of the lower premolars, and (4) extraordinary thickness of the paroccipital process (post-glenoidal process). As regards the character (1), Young (1932) stated that the teeth of *S. lydekkeri* did not differ, except in their larger size, from the common type met in the living *Sus* of Europe and N. Asia. The size of *S. lydekkeri*, however, can be accommodated in the larger part of the size range of the living *Sus*

scrofa in the sense of the recent taxonomy. Among the subspecies of *S. scrofa, S. scrofa ussuricus* Heude (including *S. gigas* Heude as its synonym ; *vide* Groves, 1981) is as large as or sometimes larger than *S. lydekkeri* from Zhoukoudian, on the basis of our measurements in AMNH, BMNH and MCZ. The characters (2), (3) and (4) are also obscure for specific distinction, when we compare *S. lydekkeri* from Zhoukoudian with many living specimens of *S. scrofa* (in the sense of the recent taxonomy) obtained from various parts of Eurasia.

Thus, we conclude that *S. lydekkeri* is indistinguishable from some variants of *S. scrofa*, and is included in the species. As already mentioned, the male lower canine is of intermediate type in *S. lydekkeri*, while it is typically scrofic in many living subspecies of *S. scrofa*. Taking this difference and the older geological age into consideration, we here treat *S. lydekkeri* as a chronological subspecies of *S. scrofa*, namely *S. scrofa lydekkeri*. We tentatively define *S. scrofa lydekkeri* as a large Pleistocene subspecies of *S. scrofa* with the male lower canine of the intermediate type. The taxonomic problems of this subspecies will be discussed in detail on the basis of abundant data in a separate paper, as in the case of *S. nipponicus*.

In Europe, Middle Pleistocene *Sus* remains are sometimes assigned to *S. scrofa priscus* De Serres, which is larger than the living *S. scrofa* of Europe (Kurtén, 1968). Judging from the figures of Stehlin (1899-1900 ; Pl. 7, fig. 5), *S. scrofa priscus* has a male lower canine of the intermediate type. The relationship between *S. scrofa priscus* and the living *S. scrofa* of Europe seems to correspond to that between *S. scrofa lydekkeri* and the living *S. scrofa* of East Asia.

The remains assigned to *S.* cf. *lydekkeri* from the Lower Kuzuü Formation of Middle Pleistocene age consist of only three specimens, which are a fragmental skull with mandibular fragments, and two skull fragments (Shikama, 1949). On the basis of the descriptions of Young (1932), Miller (1912) and Koenigswald (1933), Shikama compared the remains with *S. lydekkeri*, *S. scrofa* (equivalent to the European subspecies, *S. scrofa scrofa*) and *S. macrognathus*. He mentioned that *S. lydekkeri* corresponded to the remains from the Lower Kuzuü Formation in the size of the teeth and in the ratio of their length and width, and it was difficult to decide whether *S. scrofa* and *S. macrognathus* were near to them. In conclusion, he assigned them to *S.* cf. *lydekkeri*, because there were no records of *S. scrofa* and *S. macrognathus* in East Asia at that time, and because *S. lydekkeri* occurred from the Middle Pleistocene localities geographically near Japan. Hence this taxonomic conclusion was not deduced from a morphological viewpoint.

On the basis of Shikama's description (1949) and our observation of the specimens described by him and stored in TU, no significant differences can be found in size and morphology between the specimens from the Lower Kuzuü Formation and those from NT Cave. In our opinion, both of the specimens belong to a single species, *S. scrofa* in the sense of the present paper, although the former specimens lack male lower canines.

A well-preserved female skull and a fragmental pelvic bone of *Sus* from Kurihama were assigned to *S.* cf. *lydekkeri* (Shikama and Hasegawa, 1965). They were found one meter below sea bottom under the construction of the steam power plant, and thus their stratigraphic position is quite obscure. Judging from the description and figures of Shikama and Hasegawa (1965), the skull characters are generally coincident with those of *S. scrofa* in the sense of the recent taxonomy, but are distinct from those of the *Sus* species with verrucosic canines, including *S. strozzii, S. verrucosus, S. barbatus* and *S. celebensis*, which have the zygomatic arches more expanded laterally. Furthermore, the size of the specimens from Kurihama approximates those of the specimens from NT Cave and the Lower Kuzuü Formation, and thus it is considered that all of them belong to a single species, *S. scrofa*.

Sus remains from Kokura were identified as *S. leucomystax* by Shikama (1936), and represented by only two poorly preserved specimens (a maxillary fragment with cheek teeth and a mandibular fragment with molars). The specimens were obtained by dredging for the construction of the embankment, and thus their stratigraphic position was unknown. As stated by Shikama, these specimens are almost indistinguishable from *S. scrofa leucomystax*. They are also similar to the specimens from NT Cave in dental morphology, although they are smaller. On the basis of the recent taxonomy, the specimens from Kokura should be treated as *S. scrofa*, as those from NT Cave.

Shikama (1936, 1949) illustrated the phylogenetic relationship among the fossil and living *Sus* species known from Japan, China, Indonesia and the Indian Subcontinent at that time. He considered that *S. nipponicus* from Tsukinoki was derived from *S.* cf. *lydekkeri* from the Lower Kuzuü Formation which was a descendant of *S. falconeri* of the Indian Subcontinent ; that *S. leucomystax* from Kokura, a direct ancestor of the living *S. leucomystax*, was evolved from *S. comes* of the subcontinent ; and that these two lineages were independent since the Pliocene. His scenario cannot be accepted from our opinion and the viewpoint of the recent taxonomy, because *S. falconeri* is the ancestor of *Phacochoerus*, but not of *Sus* as pointed out by Colbert (1935) ; because *S. comes* does not belong to *Sus*, but to *Propotamochoerus hysudricus* (Pickford, 1988) ;

and because *S. nipponicus* from Tsukinoki, *S.* cf. *lydekkeri* from the Lower Kuzuü Formation, and *S. leucomystax* from Kokura are allocated to a single species, *S. scrofa*, as discussed above.

Additionally, the remains assigned to *S. scrofa* were reported from the Middle Pleistocene of Locality 1 of Ube Kosan Quarry (Kawamura, 1988), and from the Late Pleistocene of the Kannondo cave site (Kawamura, 1980, 1992, 1995). They are scarce in number and fragmental, and are indistinguishable from *S. scrofa* in the sense of the present paper, as far as the preserved parts are concerned. But their allocation to *S. scrofa* should be pending owing to their poor preservation. We assign them to *S.* cf. *scrofa* herein.

The remains assigned to *S. leucomystax* were also reported from the caves in the Akiyoshi District, Yamaguchi Prefecture (Shikama and Okafuji, 1958). Of these remains, Shikama and Okafuji considered the geological age of the remains from the "Husen-ana bed" and "Akiyosi brown clay bed" of Husen-ana Cave as Late Pleistocene. According to their description, those from the "Husen-ana bed" were not collected in the sediments, but from the surface of the cave floor. Thus, we believe that there are no reasons for allocating the remains to the Late Pleistocene. Moreover, Shikama and Okafuji's opinion regarding the "Akiyosi brown clay bed" as Late Pleistocene are doubtful judging from its faunal composition, artifacts, ^{14}C age and fluorine content of fossil bones as pointed out by Kawamura and Tamiya (1980), Kawamura (1988) and Kawamura *et al*. (1996). In our opinion, it is more likely that the bed is of Holocene age, and there are no *Sus* remains in Shikama and Okafuji's material whose geological age is assigned to the Pleistocene with confidence.

Among *Sus* remains so far recorded from the mainland of Japan, those of Pleistocene age are almost restricted to the remains from NT Cave, Tsukinoki, the Lower Kuzuü Formation, Locality 1 of Ube Kosan Quarry and the Kannondo cave site. The remains from these localities are exclusively assigned to *S. scrofa* or *S.* cf *scrofa* here. The remains from Kurihama and Kokura seem to be of Pleistocene age, if we adopt the age estimation of their original descriptions. These remains are also assignable to *S. scrofa* as discussed above. The allocation of all the Pleistocene remains to *S. scrofa* or *S.* cf. *scrofa* suggests that this species inhabited the mainland of Japan during the Middle and Late Pleistocene, although *S. scrofa* seems to have been extremely scarce in the Late Pleistocene and to have been confined to its later part, as stated by Kawamura (1980, 1992) and Kawamura *et al*. (1990). In spite of the phylogeny and origin of the Japanese wild boars postulated by Matsumoto (1915a, b) and Shikama (1936, 1949), we can provide a different scenario on the history of wild boars in and around Japan.

In the Middle Pleistocene, *Sus scrofa* was already distributed not only in the mainland of Japan but also in China, as in the present day. Its size was relatively large in Japan and in North China (*S. scrofa lydekkeri* type), but was smaller in South China as described by Colbert and Hooijer (1953). From the late Middle Pleistocene to early Late Pleistocene, it remarkably decreased or became extinct in the mainland of Japan, but it flourished during this time in China. The reappearance of *S. scrofa* or *S.* cf. *scrofa* in the fossil records of the late Late Pleistocene indicates the revival of *S.scrofa* in mainland Japan. *S. scrofa* became a dominant element of the megafauna in the Holocene there, after the mammalian extinction event between 20,000 and 10,000 yrs.B.P. (Kawamura, 1994).

5. Conclusion

On the basis of the morphological characters, the wild boar remains from the Middle Pleistocene of NT Cave are assigned to the subfamily Suinae among the six suid subfamilies designated by Pickford (1988), and to the genus *Sus* among the seven Eurasian genera of the Suinae. The recent taxonomic revisions by Groves (1981), Corbet and Hill (1992) and Groves *et al*. (1997) recognize six living species in the genus *Sus* (*S. scrofa, S. salvanius, S. verrucosus, S. barbatus, S. celebensis* and *S. bucculentus*). Among them, the remains are most similar to *S. scrofa*. The comparisons with the representative fossil species of *Sus* so far described from the Pliocene to Pleistocene of Eurasia indicate that the remains resemble *S. namadicus* and *S. lydekkeri*, which seem to be conspecific with *S. scrofa*, while the remains are distinguishable from the other fossil species. The remains from NT Cave are, therefore, allocated to *S. scrofa*.

In the mainland of Japan, *Sus* remains of Pleistocene age were mostly identified as *S. nipponicus*, *S.* cf. *lydekkeri*, *S. leucomystax* and *S. scrofa*. They are dated as the Middle Pleistocene and the later part of the Late Pleistocene. Our revision indicates that the remains assigned to *S. nipponicus*, *S.* cf. *lydekkeri* and *S. leucomystax* are included in the range of *S. scrofa*, and thus can be allocated to *S. scrofa*. This allocation and the abundant occurrence of *S. scrofa* in the Holocene also indicate that *S. scrofa* has inhabited the mainland of Japan since the Middle Pleistocene, except in the early part of the Late Pleistocene. A revision is required on the phylogenetic relationship between the *Sus* species of Japan and those of China, Indonesia and the Indian Subcontinent so far proposed, because our conclusion on the taxonomy and Quaternary history of *Sus* in the mainland of Japan is considerably different from those of previous authors.

Acknowledgments

We wish to thank Prof. T. Inada of OUA, the leader of the NT Cave excavations, for permitting us to study the wild boar remains from the cave and giving us full facilities for the present study. We also thank Prof. H. Kumai of Osaka City University for providing us valuable suggestions and encouragement.

The following colleagues and staff members assisted us in studying the collections in their institutions and gave us facilities, assistance and advice : Dr. Jin C. Z. and Mr. Wei G. B. (IVPP) ; Prof. Feng Z. J. and Ms. M. Luo (IZ) ; Dr. L. J. Flynn (Peabody Museum, Harvard University) ; Prof. R. H. Tedford, Dr. X. M. Wang and Ms. F. Brady (AMNH) ; Dr. B. Engesser and Ms. M. Sutermeister (NMB) ; Dr. P. Tassy, Mr. F. Renoult, and Prof. J. Cuisin (MNHN) ; Dr. E. Cioppi and Prof. A. Azzaroli (UF) ; Dr. R.-D.Kahlke and Dr. L. Maul (BQ) ; Dr. G. Storch, Ms. C. Seiffert, Mr. O. Lütt, Ms. J. Oelkers-Schaefer (FS) ; Dr. F. O. Neuffer and Mr. T. Engel (NMM) ; Ms. M. Blume (HLD) ; Dr. R. Ziegler (SMNS) ; Dr. J. Hooker, Mr. A. P. Currant and Dr. P. D. Jenkins (BMNH) ; Mr. J. Nemoto and Prof. K. Mori (TU) ; Dr. M. Abe (OCU). Many other staffs of the institutions listed in p.62 also gave us facilities and help. We would like to express our gratitude to these persons.

Thanks are also due to Prof. W. v. Koenigswald (Universität Bonn) and Prof. N. Schmidt-Kittler and Dr. C. Mödden (Johannes-Gutenberg-Universität) who provided us with useful information and advice on the German institutions, and to Dr. J. van der Made (Museo Nacional de Ciencias Naturales), Dr. M. Pickford (Collège de France) and Dr. C. Groves (Australian National University), who provided us with useful references. Furthermore, we wish to extend our thanks to many students of OUA who participated the field work of the excavations of NT Cave, to the employees concerned of Nittetsu Kogyo Co., who gave us permission and facilities during the excavations, and to Ms. A. Wakamatsu (AUE), who assisted us in preparing the fossil specimens and drafts of this paper.

This study was partly supported by Grants-in-Aid for Scientific Research from the Ministry of Education, Science, Sports and Culture of Japan (project numbers : 07459015 and 09208101).

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Manuscript received September 2, 1999.
Revised manuscript accepted March 6, 2000.

Plate 1

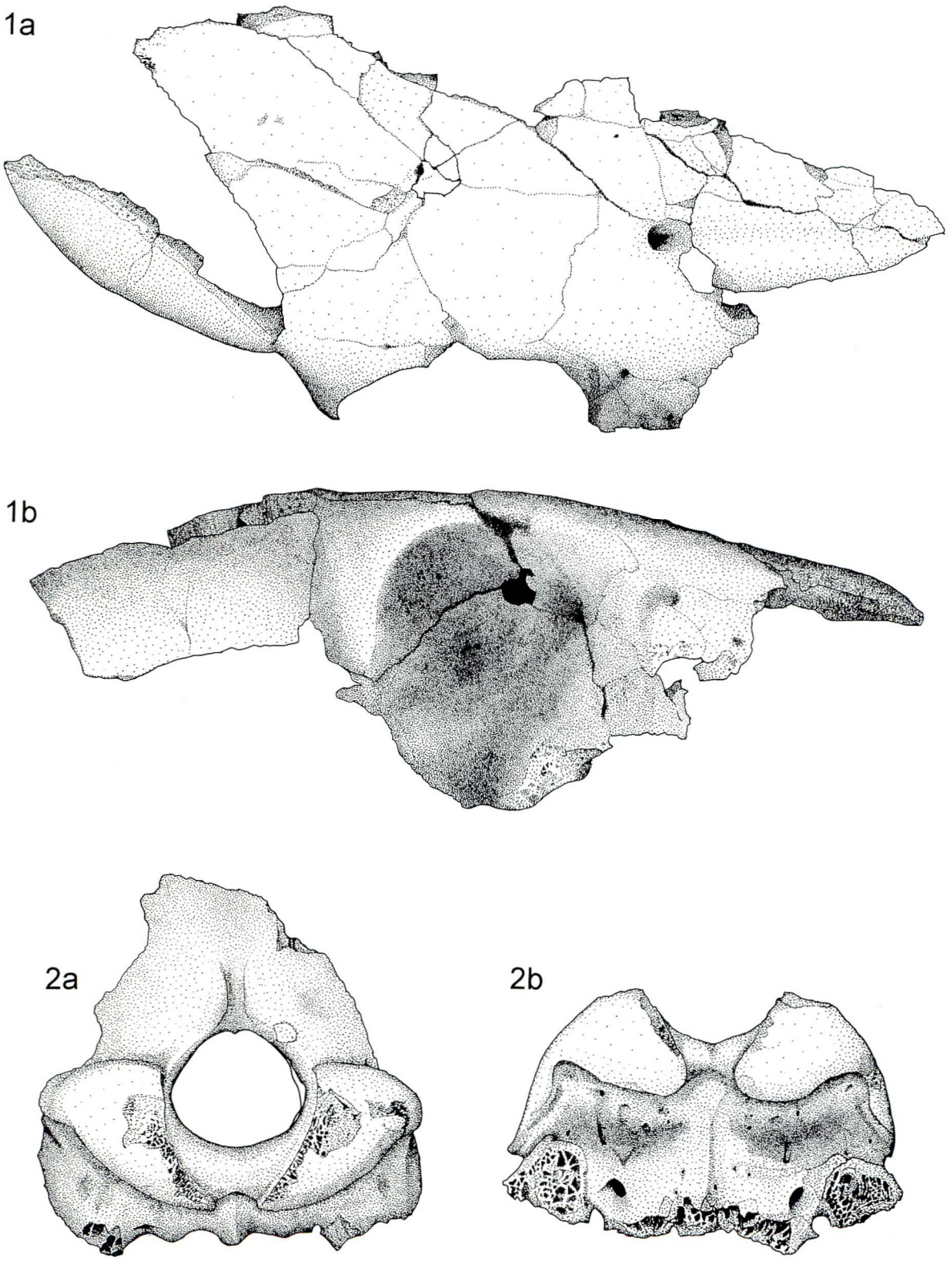

Plate 1. *Sus scrofa* from NT Cave. 1 : Skull fragment numbered OUA-NT 00001 (1a : dorsal view, 1b : right lateral view). 2 : Occipital bone numbered OUA-NT 00002 (2a : posterior view, 2b : ventral view). All figures natural size.

Plate 2

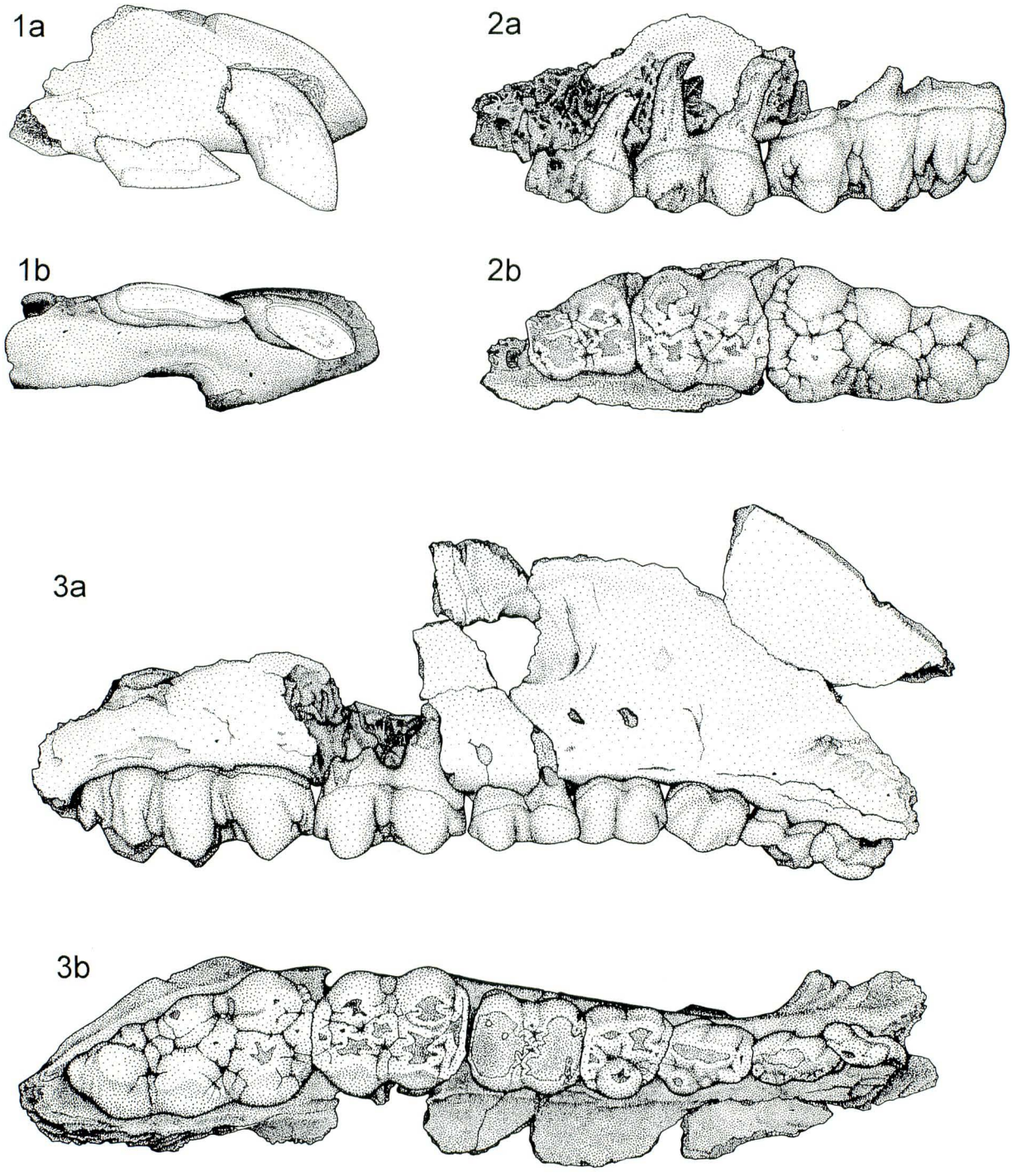

Plate 2. *Sus scrofa* from NT Cave. 1 : Right premaxilla with I^1 and I^2 numbered OUA-NT 00007 (1a : labial view, 1b : palatal view). 2 : Left maxillary fragment with M^1 to M^3 numbered OUA-NT 00021 (2a : buccal view, 2b : palatal view). 3 : Right maxilla with P^1 to M^3 numbered OUA-NT 00012 (3a : buccal view, 3b : palatal view). All figures natural size.

Plate 3

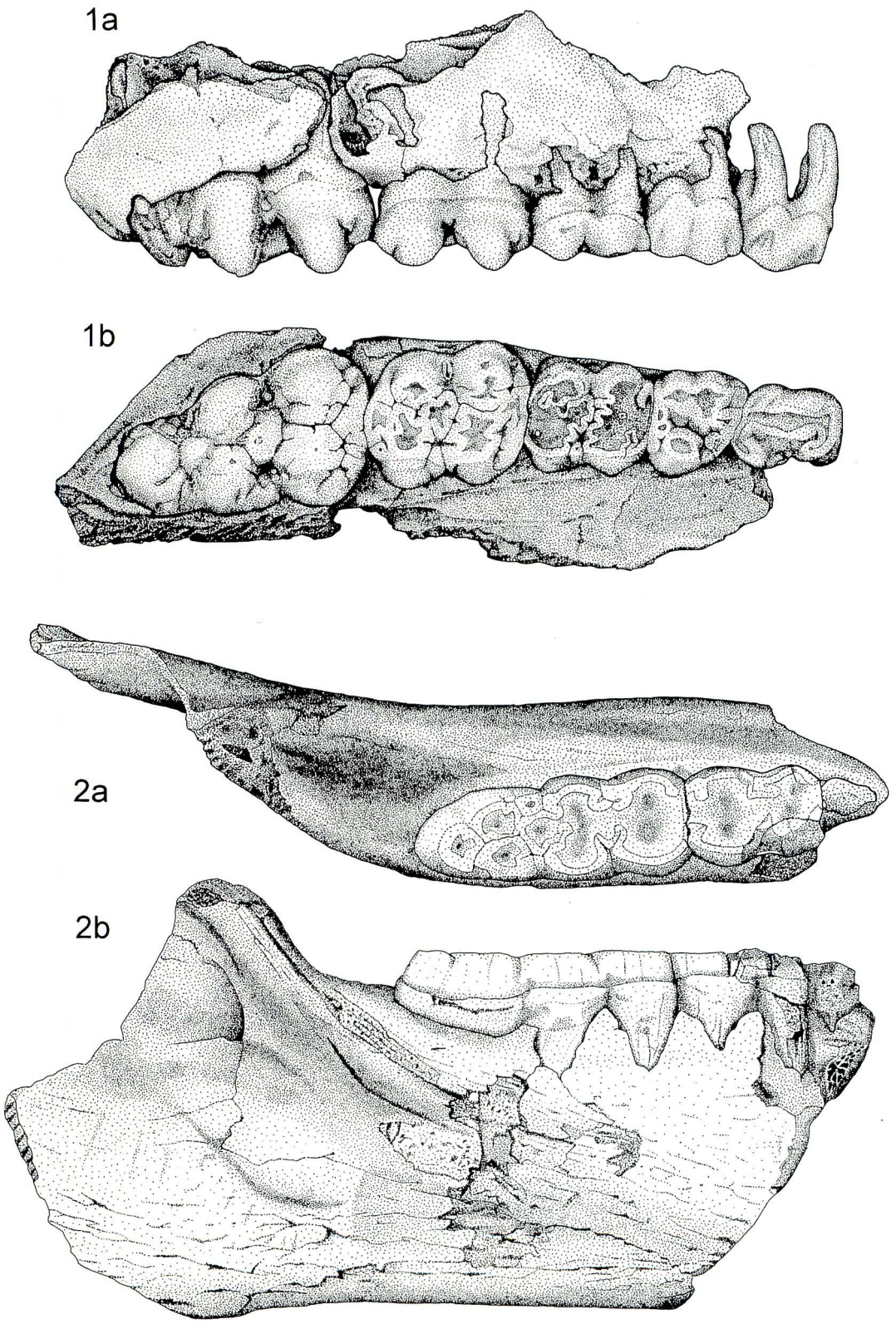

Plate 3. *Sus scrofa* from NT Cave. 1 : Right maxilla with P^3 to M^3 numbered OUA-NT 00016 (1a : buccal view, 1b : palatal view). 2 : Left mandible with M_1 fragment, M_2 and M_3 numbered OUA-NT 00048 (2a : occlusal view, 2b : lingual view). All figures natural size.

Plate 4

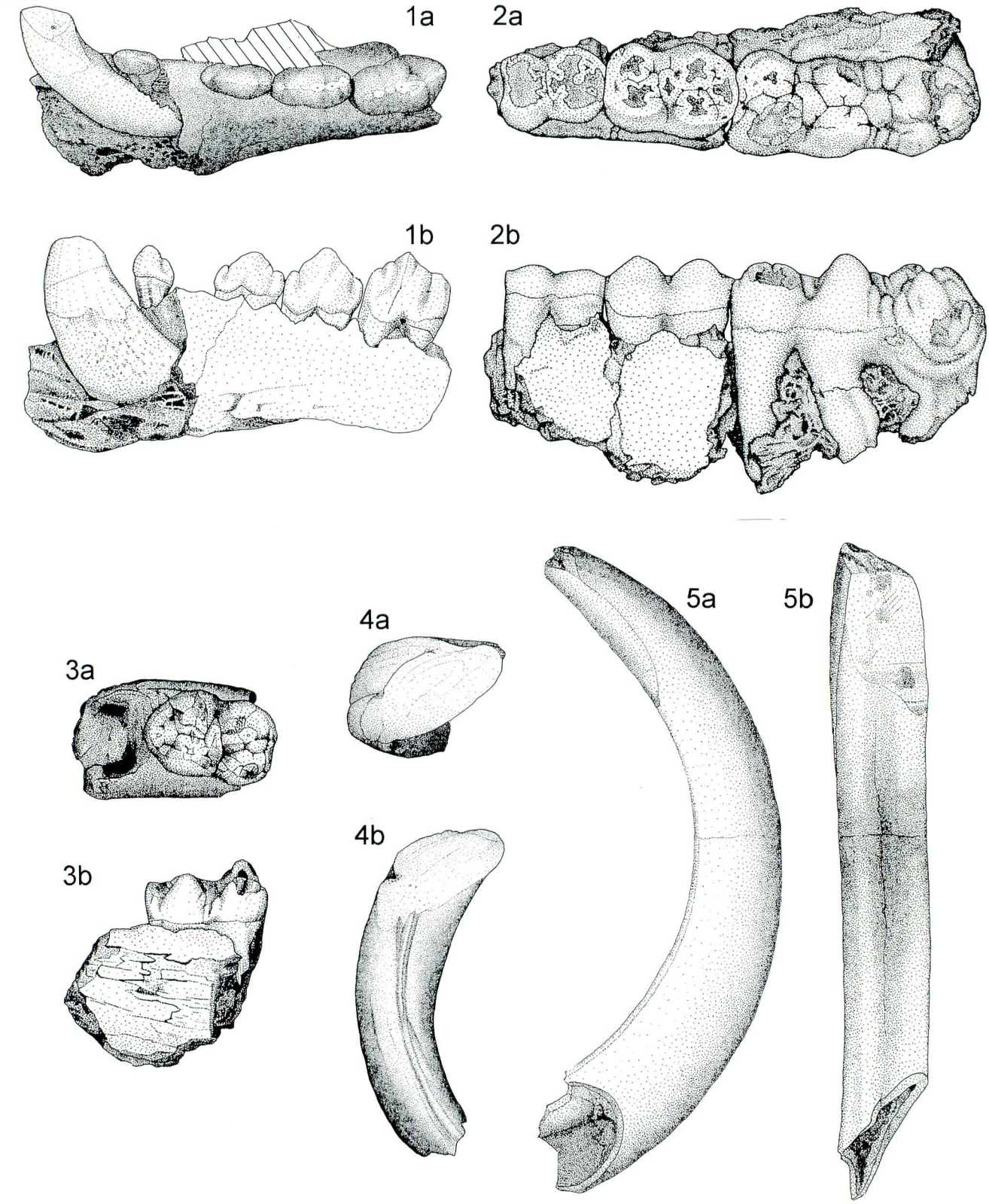

Plate 4. *Sus scrofa* from NT Cave. 1 : Right mandibular fragment with a canine and P_1 to P_4 numbered OUA-NT 00034 (1a : occlusal view, 1b : lingual view). 2 : Right mandibular fragment with M_1 to M_3 numbered OUA-NT 00044 (2a : occlusal view, 2b : lingual view). 3 : Right mandibular fragment with M_2 numbered OUA-NT 00047 (3a : occlusal view, 3b : buccal view). 4 : Right male upper canine numbered OUA-NT 00009 (4a : antero-buccal view, 4b : anterior view). 5 : Left male lower canine numbered OUA-NT 00033 (5a : lingual view, 5b : posterior view). All figures natural size.

Plate 5

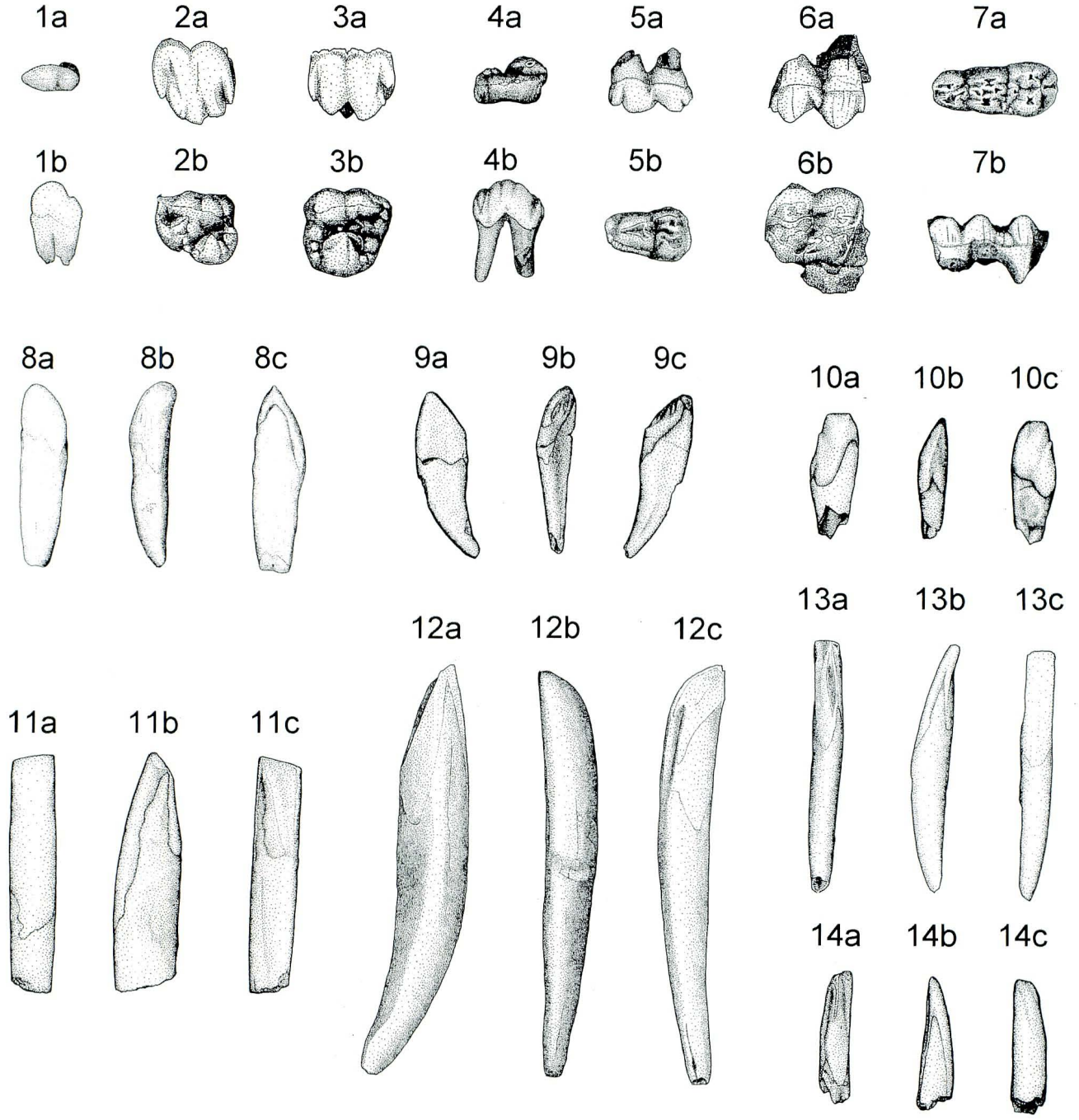

Plate 5. *Sus scrofa* from NT Cave. 1 : Left P_1 numbered OUA-NT 00035 (1a : occlusal view, 1b : buccal view). 2 : Left P^3 numbered OUA-NT 00015 (2a : buccal view, 2b : occlusal view). 3 : Right P^4 numbered OUA-NT 00017 (3a : buccal view, 3b : occlusal view). 4 : Right dM^2 numbered OUA-NT 00055 (4a : occlusal view, 4b : buccal view). 5 : Left dM^3 numbered OUA-NT 00057 (5a : buccal view, 5b : occlusal view). 6 : Right maxillary fragment with dM^4 numbered OUA-NT 00058 (6a : buccal view, 6b : occlusal view). 7 : Left dM_4 numbered OUA-NT 00067 (7a : occlusal view, 7b : buccal view). 8 : Left I_3 numbered OUA-NT 00030 (8a : labial view, 8b : lingual view, 8c : mesial view). 9 : Right dI^1 numbered OUA-NT 00051 (9a : labial view, 9b : mesial view, 9c : lingual view). 10 : Right dI^2 numbered OUA-NT 00053 (10a : lingual view, 10b : mesial view, 10c : labial view). 11 : Right I_1 numbered OUA-NT 00025 (11a : labial view, 11b : mesial view, 11c : lingual view). 12 : Left I_2 numbered OUA-NT 00027 (12a : mesial view, 12b : labial view, 12c : lingual view). 13 : Right dI_1 numbered OUA-NT 00061 (13a : lingual view, 13b : mesial view, 13c : labial view). 14 : Left dI_2 numbered OUA-NT 00065 (14a : lingual view, 14b : mesial view, 14c : labial view). All figures natural size.

Plate 6

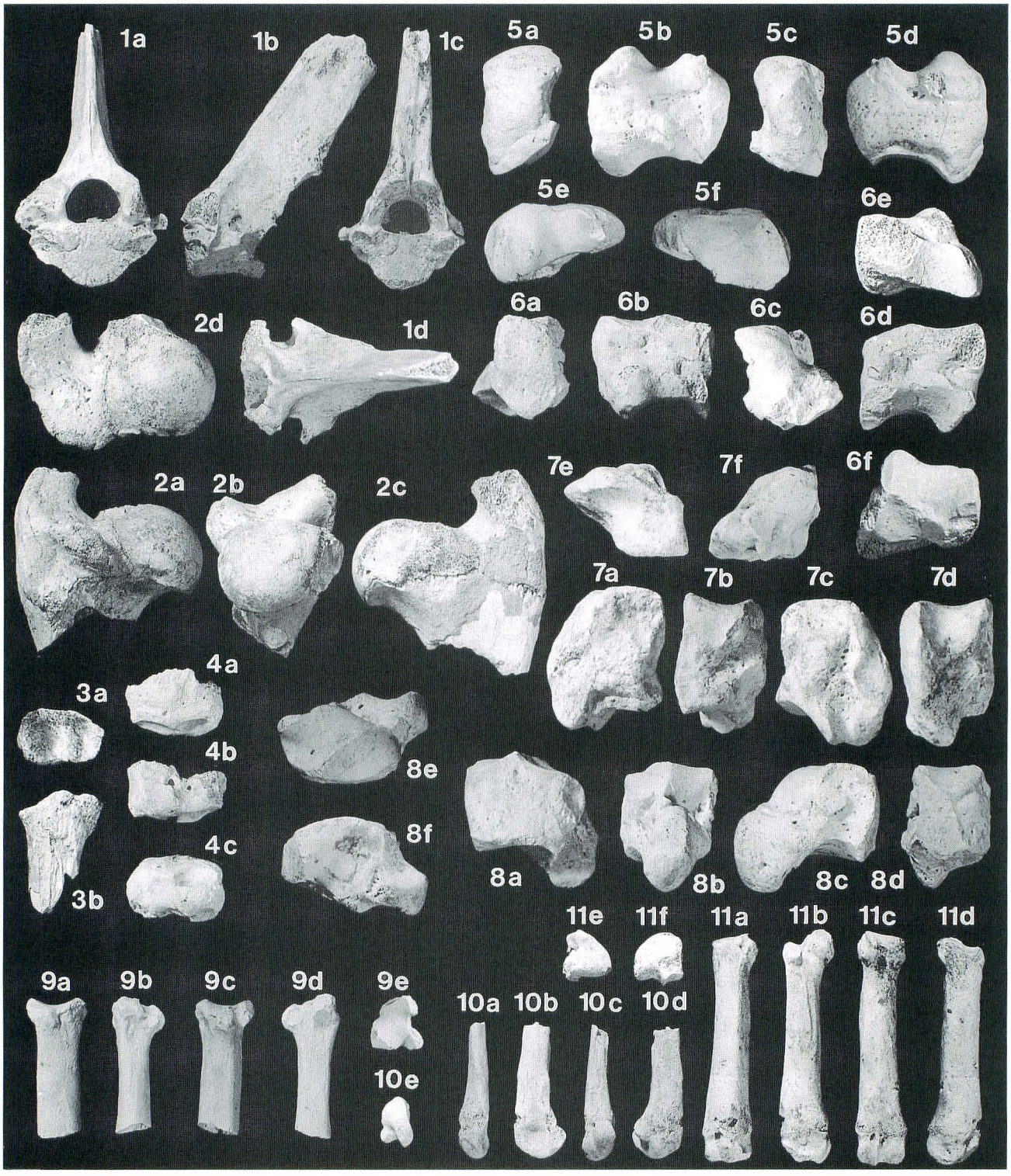

Plate 6. *Sus scrofa* from NT Cave. 1a-d : Thoracic vertebra (OUA-NT 00071). 2a-d : Left humerus (OUA-NT 00074). 3a-b : Left radius (OUA-NT 00078). 4a-c : Right radius (OUA-NT 00079). 5a-f : Left scaphoid (OUA-NT 00080). 6a-f : Right lunate (OUA-NT 00082). 7a-f : Right cuneiform of manus (OUA-NT 00083). 8a-f : Left unciform (OUA-NT 00084). 9a-e : Right third metacarpus (OUA-NT 00086). 10a-f : Right fourth metacarpus (OUA-NT 00087). 11a-f : Right fifth metatarsus (OUA-NT 00102). 1a, 3b, 4a, 5a, 6a, 7a, 8a, 9a, 10a, 11a : anterior view. 1c, 2b, 4b, 5c, 6c, 7c, 8c, 9c, 10c, 11c : posterior view. 2d, 3a, 5e, 6e, 7f, 8e, 9e, 11e : proximal view. 4c, 5f, 6f, 7e, 8f, 10e, 11f : distal view. 2c, 5d, 6b, 7b, 8d, 9b, 10b, 11 b : medial view. 1b, 2a, 5b, 6d, 7d, 8b, 9d, 10d, 11d : lateral view. 1d : superior view.
5a-f, 6a-f, 7a-f, 8a-f natural size ; the other figures one half natural size.

Plate 7

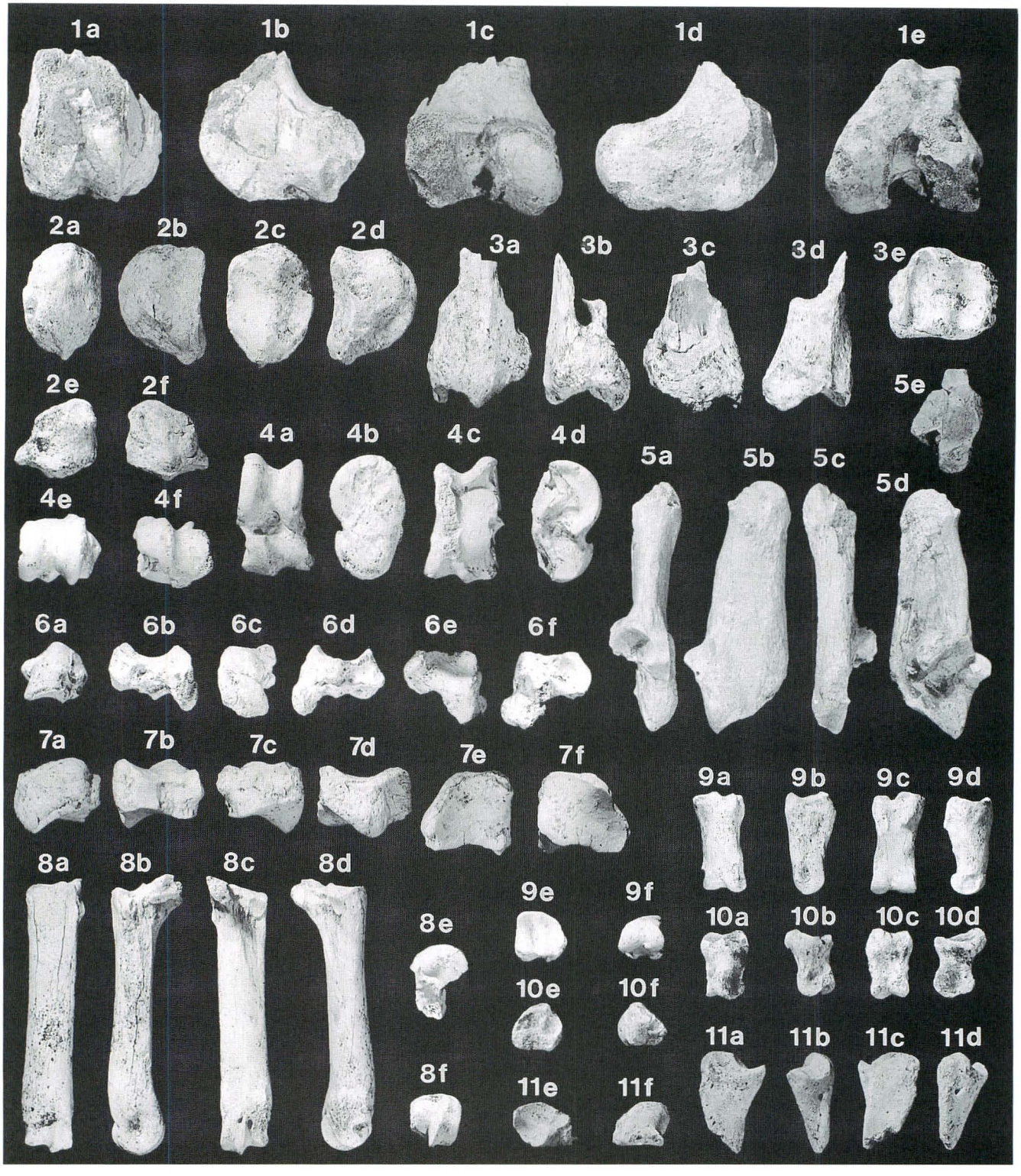

Plate 7. *Sus scrofa* from NT Cave. 1a-e : Left femur (OUA-NT 00088). 2a-f : Left patella (OUA-NT 00089). 3a-e : Right tibia (OUA-NT 00090). 4a-f : Right talus (OUA-NT 00092). 5a-e : Left calcaneum (OUA-NT 00094). 6a-f : Left navicular (OUA-NT 00095). 7a-f : Left lateral cuneiform (OUA-NT 00096). 8a-f : Right fourth metatarsus (OUA-NT 00100). 9a-f : Proximal phalanx (OUA-NT 00104). 10a-f : Middle phalanx (OUA-NT 00109). 11a-f : Distal phalanx (OUA-NT 00113).

1a, 2a, 3c, 4a, 5a, 6a, 7a, 8a, 9a, 10a, 11a : anterior view. 1c, 2c, 3a, 4c, 5c, 6c, 7c, 8c, 9c, 10c, 11c : posterior view. 2e, 4e, 5e, 6e, 7f, 8e, 9e, 10e, 11e : proximal view. 1e, 2f, 3e, 4f, 6f, 7e, 8f, 9f, 10f, 11f : distal view. 1d, 2d, 3d, 4b, 5d, 6d, 7d, 8b : medial view. 1b, 2b, 3b, 4d, 5b, 6b, 7b, 8d : lateral view. 9b, 9d, 10b, 10d, 11b, 11d : medial or lateral view. 7a-f, 11a-f natural size ; the other figures one half natural size.

Appendix

The specimen data of the remains of *Sus scrofa* from NT Cave are tabulated herein. The data are composed of the registration numbers, the part and side of each specimen, and the excavation grid and horizon from which each specimen was collected. For further information on the excavation grid and horizon, see Inada *et al*. (1998).

Registration number	Part	Side	Excavation grid	Horizon (depth in cm)
OUA-NT00001	skull fragment (frontal, parietal and lacrimal)		1-1	-49
OUA-NT00002	skull fragment (occipital)		1-2	-48
OUA-NT00003	upper I1	L	1-1	-40
OUA-NT00004	upper I1	L	1-2	-240～-260
OUA-NT00005	upper I1	L	4	-260～-280
OUA-NT00006	upper I1	R	2-3	-280～-300
OUA-NT00007	premaxilla with I1 and I2	R	1-1	-40
OUA-NT00008	upper I2	L	1-1	-40～-60
OUA-NT00009	upper C (male)	R	1-1	-40
OUA-NT00010	upper C (male)	R	1-1	-70
OUA-NT00011	upper P1	R	1-1	-40～-60
OUA-NT00012	maxilla with P1-M3	R	1-1	-48
OUA-NT00013	upper P2	L	1-2	-220～-240
OUA-NT00014	upper P3	L	1-1	-40～-60
OUA-NT00015	upper P3	L	2-3	-280～-300
OUA-NT00016	maxilla with P3-M3	R	1-1	-37
OUA-NT00017	upper P4	R	2-3	-280～-300
OUA-NT00018	maxillary fragment with P4	R	4	surface
OUA-NT00019	upper M1	R	2-3	-300～-320
OUA-NT00020	upper M1	L	2-3	-300～-320
OUA-NT00021	maxillary fragment with M1-M3	L	1-2	-172.3
OUA-NT00022	maxillary fragment with M1	L	1-1	-40～-60
OUA-NT00023	upper M2	L	1-2	-165.8
OUA-NT00024	upper M2	R	2-3	-280～-300
OUA-NT00025	lower I1	R	1-1	-40～-50
OUA-NT00026	lower I2	R	1-1	-80～-100
OUA-NT00027	lower I2	L	1-1	-40
OUA-NT00028	lower I2	R	1-1	-40
OUA-NT00029	lower I3	R	1-1	-40
OUA-NT00030	lower I3	L	1-1	-20～-40
OUA-NT00031	lower I3	L	2-3	-260～-280
OUA-NT00032	lower I3	R	2-3	-260～-280
OUA-NT00033	lower C (male)	L	1-1	-38
OUA-NT00034	mandibular fragment with C, P1-P4 (male)	R	1-1	-90
OUA-NT00035	lower P1	L	1-1	-20～-40
OUA-NT00036	lower P2	R	2-3	-320～-340
OUA-NT00037	lower P2	L	2-3	-340～-360
OUA-NT00038	lower P2	L	2-3	-340～-360
OUA-NT00039	lower P3	L	1-1	-40～-60
OUA-NT00040	lower M1	L	2-3	-300～-320
OUA-NT00041	lower M1	R	2-3	-320～-340
OUA-NT00042	lower M1	R	2-3	-320～-340
OUA-NT00043	lower M1	R	4	surface
OUA-NT00044	mandibular fragment with M1-M3	R	1-2	-200.6
OUA-NT00045	lower M2	L	2-3	-300～-320
OUA-NT00046	lower M2	R	2-3	-320～-340
OUA-NT00047	mandibular fragment with M2	R	1-1	-90
OUA-NT00048	mandible with M1 fragment, M2, M3	L	2-3	-240
OUA-NT00049	mandibular fragment with M3	R	2-3	-255
OUA-NT00050	mandibular fragment with P3-M1	L	1-2	-239
OUA-NT00051	upper dI1	R	2-3	-340～-360
OUA-NT00052	upper dI1	R	2-3	-340～-360
OUA-NT00053	upper dI2	R	2-3	-260～-280
OUA-NT00054	upper dM2	R	2-3	-240～-260
OUA-NT00055	upper dM2	R	2-3	-340～-360
OUA-NT00056	upper dM3	L	2-3	-300～-320

Registration number	Part	Side	Excavation grid	Horizon (depth in cm)
OUA-NT00057	upper dM3	L	2-3	-300～-320
OUA-NT00058	maxillary fragment with dM4	R	2-3	-240～-260
OUA-NT00059	maxillary fragment with dM4	L	2-3	-300～-320
OUA-NT00060	upper dM4	R	2-3	-300～-320
OUA-NT00061	lower dI1	R	2-3	-280～-300
OUA-NT00062	lower dI1	R	2-3	-320～-340
OUA-NT00063	lower dI1	L	2-3	-300～-320
OUA-NT00064	lower dI2	R	2-3	-280～-300
OUA-NT00065	lower dI2	L	2-3	-320～-340
OUA-NT00066	lower dI2	R	2-3	-320～-340
OUA-NT00067	lower dM4	L	2-3	-300～-320
OUA-NT00068	lower dM4	R	2-3	-320～-340
OUA-NT00069	lower dM4	L	2-3	-320～-340
OUA-NT00070	2 cheek tooth fragments		1-1	-40～-60
OUA-NT00071	thoracic vertebra (2nd)		4	surface
OUA-NT00072	thoracic vertebra		1-1	-49
OUA-NT00073	thoracic vertebra		2-3	-245
OUA-NT00074	humerus	L	1-1	-70
OUA-NT00075	humerus	R	1-2	-231.8
OUA-NT00076	humerus	R	2-3	-245
OUA-NT00077	humerus	L	2-3	-340～-360
OUA-NT00078	radius	L	1-2	-20～-30
OUA-NT00079	radius	R		-300～-320
OUA-NT00080	scaphoid	L	1-2	-220～-240
OUA-NT00081	scaphoid	R	4	surface
OUA-NT00082	lunate	R	2-3	-400～-420
OUA-NT00083	cuneiform (manus)	R	4	surface
OUA-NT00084	unciform	L	2-3	-240～-260
OUA-NT00085	3rd metacarpus	R	2-3	-300～-320
OUA-NT00086	3rd metacarpus	R	1-2	-40～-50
OUA-NT00087	4th metacarpus	R	1-2	-30～-40
OUA-NT00088	femur	L	2-3	-380～-400
OUA-NT00089	patella	L	2-3	-240～-260
OUA-NT00090	tibia	R	1-1	-38
OUA-NT00091	tibia	L	4	-259
OUA-NT00092	talus	R	1-2	-200～-220
OUA-NT00093	calcaneum	R	1-2	-154.6
OUA-NT00094	calcaneum	L	4	-400～-420
OUA-NT00095	navicular	L	1-2	-220～-240
OUA-NT00096	lateral cuneiform	L	1-2	-220～-240
OUA-NT00097	3rd metatarsus	R	2-3	-240～-260
OUA-NT00098	3rd metatarsus	L	2-3	-320～-340
OUA-NT00099	4th metatarsus	R	1-1	-27
OUA-NT00100	4th metatarsus	R	2-3	-265
OUA-NT00101	4th metatarsus	R	1-2	-220～-240
OUA-NT00102	5th metatarsus	R	4	surface
OUA-NT00103	left 2nd or right 5th proximal phalanx		1-2	-170～-190
OUA-NT00104	left 3rd or right 4th proximal phalanx		1-3	-100～-120
OUA-NT00105	left 4th or right 3rd proximal phalanx		1-2	-220～-240
OUA-NT00106	left 3rd or right 4th middle phalanx		2-3	-320～-340
OUA-NT00107	left 2nd or right 5th middle phalanx		4	-400～-420
OUA-NT00108	left 3rd or right 4th middle phalanx		1-2	-140～-180
OUA-NT00109	left 4th or right 3rd middle phalanx			-400～-420
OUA-NT00110	left 4th or right 3rd middle phalanx			-280～-300
OUA-NT00111	left 4th or right 3rd middle phalanx		1-2	-240～-260
OUA-NT00112	left 4th or right 3rd middle phalanx		2-3	-280～-300
OUA-NT00113	left 3rd or right 4th distal phalanx		1-3	-120～-140
OUA-NT00114	left 3rd or right 4th distal phalanx		4	surface
OUA-NT00115	left 5th or right 2nd distal phalanx		4	-400～-420