

Fossil deer *Cervus (Nipponicervus) praenipponicus* from the Upper Pleistocene of Shinsaku, Kawasaki City, Central Japan: Skull restoration and comparative osteology of *C. (N.) praenipponicus*

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Key words: *Cervus (Nipponicervus) praenipponicus*, Japanese endemic fossil deer, comparative osteology, restoration of skull, Shinsaku, Upper Pleistocene Shimosueyoshi Formation

I. Introduction

A fossil deer was found in the Upper Pleistocene Shimosueyoshi Formation at Shinsaku, Takatsu-ku, Kawasaki City, Kanagawa Prefecture, Central Japan, during road construction in 1960 (Fig.1). The fossil specimen consists of many skeletal parts such as the skull, upper teeth, antlers, lumber vertebrae and metatarsus of an adult male individual. The specimen is referable to *Cervus (Nipponicervus) praenipponicus*, based on its antler morphology, as described in this study. Several finds of *C. (N.) praenipponicus*, including a mandible (Geological Survey of Japan, 1960) and previously unreported antlers, have been made in the Shimosueyoshi Formation in this area. Antlers of this species have also been found in the same formation at Shimosueyoshi, Tsurumi-ku, Yokohama City, Kanagawa Prefecture (Hasegawa, 1969).

Many morphological studies have been done on *C. (N.) praenipponicus*, which is a Pleistocene species endemic to the Japanese Islands (Shikama, 1936a, 1941, 1949; Shikama and Okafuji, 1958; Otsuka and Shikama, 1977; Nonaka *et al.*, 1986; Otsuka, 1988a, 1989; Fossil Deer Research Group of Ichihara, 1994 etc.). However, most of these studies have been based on antlers alone, since they occur commonly in the Pleistocene sediments. No studies have been made of the skull and post-cranium of the species except for Shikama (1949), Shikama and Okafuji (1958) and the Fossil Deer Research Group of Ichihara (1994). In particular, no studies of the palatine parts of the male skull have previously been done.

Shikama (1941) inferred that the extinct deer *C. (N.) praenipponicus* diverged from the common ancestor *Cervoceros novorossiae* with the congeneric living deer *C. (Rusa) unicolor*, based on similar antler morphology. Recent molecular phylogenetic studies, however, indicate that antler morphology is not always consistent with cervid phylogeny (Miyamoto *et al.*, 1990; Kuwayama and Ozawa, 2000). Further, it is generally considered that the osteologic characters of the skull and teeth are more reflective of mammalian phylogeny.

Fig. 1

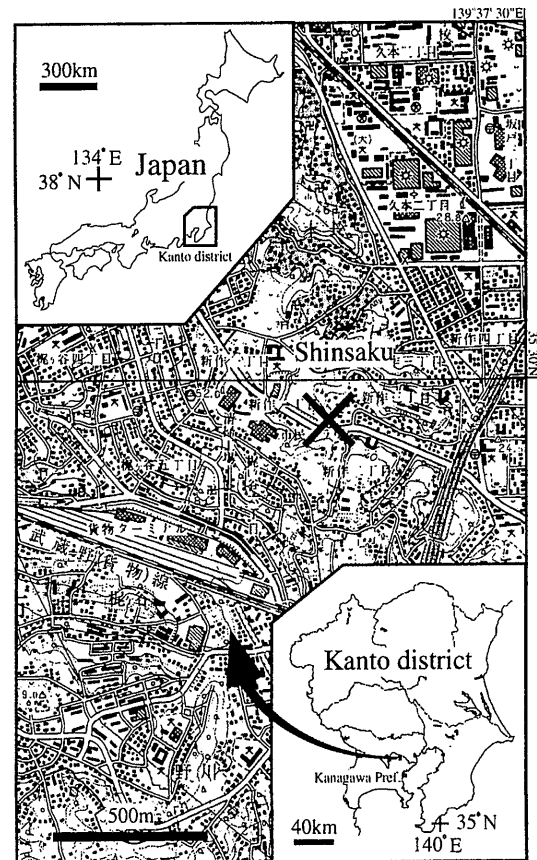


Fig.1 Map showing the collecting locality (X) of *Cervus (Nipponicervus) praenipponicus* in Shinsaku, Takatsu-ku, Kawasaki City, Kanagawa Prefecture, Central Japan (Mizonokuchi and Eda quadrangles, 1:25,000 scale; Geographical Survey Institute of Japan).

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The specimen of *C. (N.) praenipponicus* discussed here preserves the palatine parts of the skull and several post-cranial bones, which are fully described and measured in this paper. The male skull of this species was restored for the first time in the course of the present study. A comparative osteological investigation was performed between *C. (N.) praenipponicus* and *C. (R.) unicolor* with special reference to the skull and upper teeth.

II. Systematic description

Order Artiodactyla Owen, 1848

Family Cervidae Gray, 1821

Subfamily Cervinae Gray, 1821

Genus *Cervus* Linnaeus, 1758

Subgenus *Nipponicervus* Krezoi, 1941

Cervus (Nipponicervus) praenipponicus Shikama, 1936
Figs. 2, 3

Cervus (cfr. *Anoglochis*) *praenipponicus* Shikama, 1936a, p. 170-174, pl. 9, figs. 1-5.

Cervus (Depéretia) naorai Shikama, 1936b, p. 252-254, text-figs. 1, 2; Shikama, 1941, p. 1150, text-fig. 3, no. 4.

Cervus (Depéretia) praenipponicus Shikama, 1941, p. 1147-1148, text-fig. 2, nos. 7, 8, text-fig. 3, no. 1; Shikama, 1949, p. 85-99, pl. 7, figs. 2-6, pl. 8, figs. 1, 3, 4, pl. 9, figs. 1-4, pl. 10, figs. 1-6, pl. 11, figs. 2-16, pl. 12, figs. 1-11, pl. 13, figs. 1-8, pl. 14, figs. 1-9, pl. 15, figs. 1-10, pl. 16, figs. 1-11, pl. 17, fig. 14; Shikama and Okafuji, 1958, p. 75-78, pl. 5, figs. 5-26, pl. 6, figs. 1-17.

Cervus (Nipponicervus) praenipponicus Otsuka and Shikama, 1977, p. 28-31, text-figs. 7, 8, pl. 4, figs. 1-5, pl. 5, figs. 1-7; Otsuka, 1988a, p. 80-83, pl. 160, figs. 1-13, pl. 161, figs. 1-17, pl. 162, figs. 1-14, pl. 163, figs. 1-8; Otsuka, 1989, p. 75-76, pl. 4, figs. 1-5; Fossil Deer Research Group of Ichihara, 1994, p. 183-193, text-fig. 4, pl. 1, figs. 1-5, pl. 2, figs. 1-7, pl. 3, figs. 1-6, pl. 4, figs. 1-14, pl. 5, figs. 1-13.

1. Material studied

Several parts of an adult male skeleton, including the skull, upper teeth, antlers, mandible, lower teeth, vertebrae, rib, pelvises, and hind limbs (Kawasaki Municipal Science Museum for Youth, KMSY-2034Ma) (Table 1). These bones are thought to be from one individual, because of their sympatric occurrence, the presence of just one example of any one bone,

and the sizes of the bones. The bones were collected from the Upper Pleistocene Shimosueyoshi Formation in Shinsaku, Takatsu-ku, Kawasaki City, Kanagawa Prefecture, Central Japan (Fig.1). This formation is assigned to oxygen isotope stage 5e (ca. 130,000 yr BP) (Machida and Arai, 1992).

Table 1 Preserved parts of the fossil specimen (KMSY-2034Ma) from Shinsaku, Takatsu-ku, Kawasaki City, Kanagawa Prefecture, Central Japan.

Preserved part	Reg. No.
Skull	
left nasal	KMSY-2034Ma-7
right nasal	KMSY-2034Ma-7
left lachrymal	KMSY-2034Ma-7
right lachrymal	KMSY-2034Ma-3, 22
left zygomatic	KMSY-2034Ma-4
left maxilla	KMSY-2034Ma-4
right maxilla	KMSY-2034Ma-3, 26
left premaxilla	KMSY-2034Ma-25
right premaxilla	KMSY-2034Ma-24
left frontal	KMSY-2034Ma-7, 9
right frontal	KMSY-2034Ma-8, 20
right parietal	KMSY-2034Ma-8
left presphenoid	KMSY-2034Ma-23
Upper teeth	
left 2nd premolar	KMSY-2034Ma-4
left 3rd premolar	KMSY-2034Ma-4
right 3rd premolar	KMSY-2034Ma-6
left 4th premolar	KMSY-2034Ma-4
left 1st molar	KMSY-2034Ma-4
right 1st molar	KMSY-2034Ma-3
left 2nd molar	KMSY-2034Ma-5
right 2nd molar	KMSY-2034Ma-3
Antler	
left antler	KMSY-2034Ma-9
right antler	KMSY-2034Ma-8
antler	KMSY-2034Ma-19
Mandible	
left mandible	KMSY-2034Ma-2
Lower teeth	
left 2nd molar	KMSY-2034Ma-2
left 3rd molar	KMSY-2034Ma-2
Vertebrae	
2nd lumbar vertebra	KMSY-2034Ma-16-1
3rd lumbar vertebra	KMSY-2034Ma-16-2
4th lumbar vertebra	KMSY-2034Ma-16-3
6th lumbar vertebra	KMSY-2034Ma-15
sacral vertebra	KMSY-2034Ma-15
1st caudal vertebra	KMSY-2034Ma-27
Rib	
left rib	KMSY-2034Ma-13
Pelvis	
left pelvis	KMSY-2034Ma-12
right pelvis	KMSY-2034Ma-18
Hind limbs	
right astragalus	KMSY-2034Ma-10
right cubo-navicular	KMSY-2034Ma-11
right metatarsus	KMSY-2034Ma-14

Fig. 2

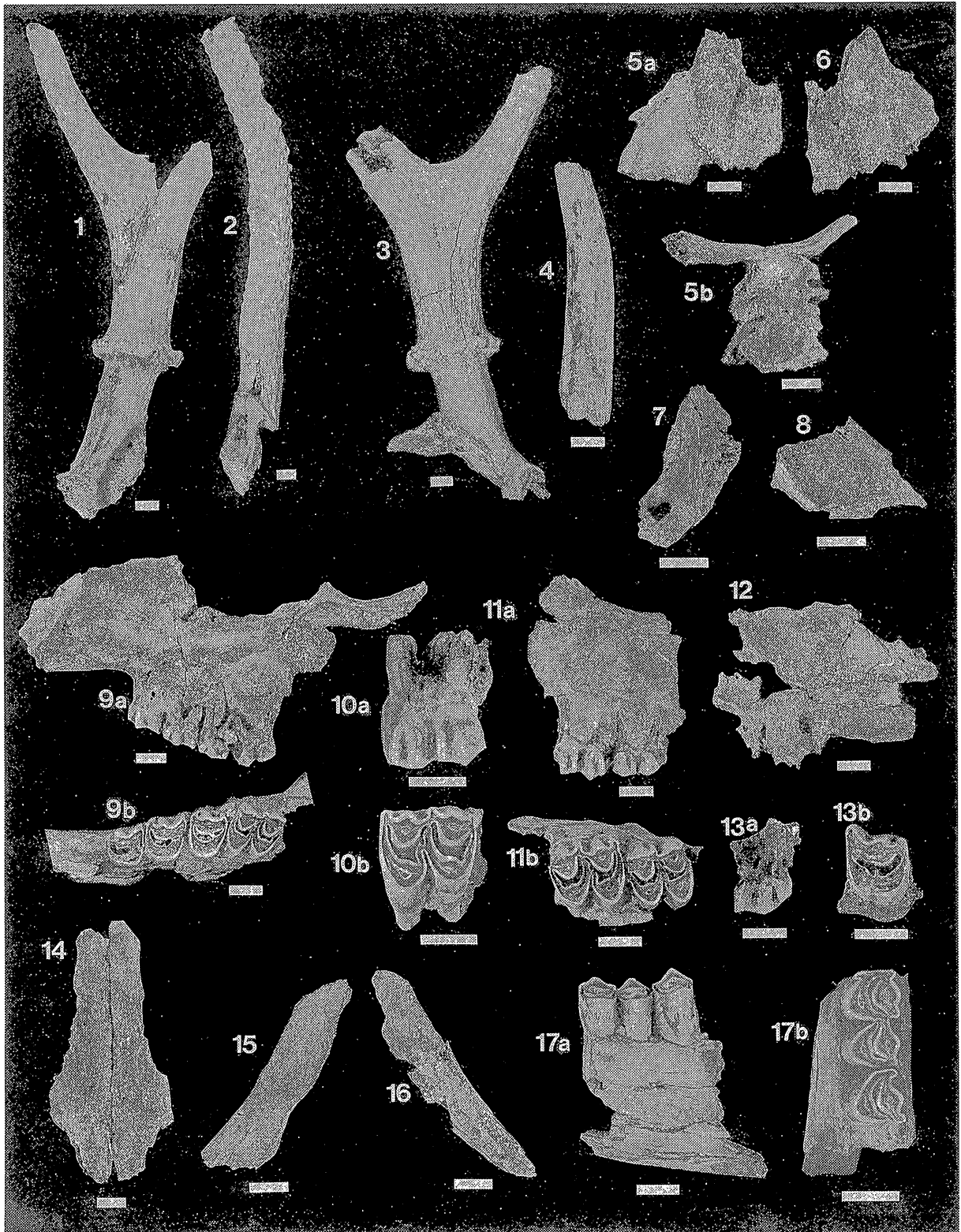


Fig. 2 *Cervus (Nipponicervus) praenipponicus* Shikama, 1936. Antler, skull, upper teeth, mandible and lower teeth (KMSY-2034Ma). 1. Left antler with pedicle (KMSY-2034Ma-9), in lateral view. 2. Left antler (KMSY-2034Ma-9), in lateral view. 3. Right antler with pedicle and parietal (KMSY-2034Ma-8), in lateral view. 4. Antler fragment of unknown position (KMSY-2034Ma-19). 5a-b. Left frontal with lachrymal (KMSY-2034Ma-7), 5a: dorsal view, 5b: lateral view. 6. Right frontal (KMSY-2034Ma-20), in dorsal view. 7. Left presphenoid (KMSY-2034Ma-23), in lateral view. 8. Right lachrymal (KMSY-2034Ma-22), in lateral view. 9a-b. Left maxilla with zygomatic and cheek teeth (KMSY-2034Ma-4), 9a: lateral (buccal) view, 9b: ventral (occlusal) view. 10a-b. Left upper 2nd molar with partial maxilla (KMSY-2034Ma-5), 10a: buccal view, 10b: occlusal view. 11a-b. Right maxilla with zygomatic, lachrymal and molars (KMSY-2034Ma-3), 11a: lateral (buccal) view, 11b: ventral (occlusal) view. 12. Right maxilla (KMSY-2034Ma-26), in lateral view. 13a-b. Right upper 3rd premolar with part of maxilla (KMSY-2034Ma-6), 13a: buccal view, 13b: occlusal view. 14. Right and left nasals (KMSY-2034Ma-7), in dorsal view. 15. Left premaxilla (KMSY-2034Ma-25), in lateral view. 16. Right premaxilla (KMSY-2034Ma-24), in lateral view. 17a-b. Left mandible with molars (KMSY-2034Ma-2), 17a: lateral (buccal) view, 17b: dorsal (occlusal) view. Scale bars equal 1 cm.

Fig. 3



Fig. 3 *Cervus (Nipponicervus) praenipponicus* Shikama, 1936. Vertebrae, rib, pelvis and hind limbs (KMSY-2034Ma). 1a-b. Second lumbar vertebra (KMSY-2034Ma-16-1), 1a: caudal view, 1b: dorsal view. 2a-b. Third lumbar vertebra (KMSY-2034Ma-16-2), 2a: caudal view, 2b: dorsal view. 3a-b. Fourth lumbar vertebra (KMSY-2034Ma-16-3), 3a: caudal view, 3b: dorsal view. 4a-b. Sixth lumbar and sacral vertebrae (KMSY-2034Ma-15), 4a: dorsal view, 4b: ventral view. 5. First caudal vertebra (KMSY-2034Ma-27), in dorsal view. 6. Left rib (KMSY-2034Ma-13), in caudal view. 7. Left pelvis (KMSY-2034Ma-12), in ventro-lateral view. 8. Right pelvis (KMSY-2034Ma-18), in ventro-lateral view. 9. Left and right pelvis (KMSY-2034Ma-12 and KMSY-2034Ma-18), in dorsal view. 10. Right astragalus (KMSY-2034Ma-10), in dorsal view. 11. Right cubo-navicular (KMSY-2034Ma-11), in proximal view. 12. Right metatarsus (KMSY-2034Ma-14), in dorsal view. Scale bars equal 1 cm.

2. Description

1) Skull

Both nasals are almost perfectly preserved (Fig. 2-14). They agglutinate with each other at the internasal suture, and protrude dorsally around the suture. The nasals measure 92.60 mm in maximum length and 43.00 mm in maximum width.

The left lachrymal consists of the posterior part including the lachrymal fossae (Fig. 2-5), and the right lachrymal consists of the middle and ventral parts (Fig. 2-8, 11). It is inferred from the incomplete bones that the lachrymals are deeply concave medially at the middle and ventral parts.

The left zygomatic consists of the ventral part of the lower margin of the left orbit (Fig. 2-9), and the anterior part of the right zygomatic is partially preserved (Fig. 2-11). The facial crest on the left zygomatic is well developed. The dorsal surfaces of both zygomatics sutured with the lachrymals are nearly horizontal.

The left maxilla is almost perfectly preserved except for the posterior part (Fig. 2-9), while the right maxilla is fragmentary (Fig. 2-11, 12). The alveolus for the left upper canine is preserved at the anterior end of the left maxilla, and measures about 8 mm in antero-posterior length. Both infraorbital foramina are preserved about 10 mm dorsal to the cervical lines of the upper 2nd premolars. The turbinate and palatine process of the left maxilla are fragmentarily preserved on the medial part of the left maxilla. The heights of the maxillae are 41.15 mm on the left and 40.75 mm on the right, measured from the anterior ends of the facial crests on the zygomatics. Both facial tubercles are well developed. In lateral view, the mesial margin of the left upper 2nd premolar makes an acute angle with the ventral margin of the anterior part of the left maxilla.

Both premaxillae are missing small portions of their anterior parts (Fig. 2-15, 16), and their remaining lengths are 59.25 mm for the left and 66.20 mm for the right.

Both frontals consist of the anterior parts (Fig. 2-5, 6) and the posterior parts including the pedicles and surrounding parts (Fig. 2-1, 3). Although both frontals around the pedicles are separated from each other, the frontal suture (about 14 mm long) is preserved in front of the bregma in both sides.

The transverse diameters of the pedicles (27.15 mm on the left and 26.75 mm on the right) are slightly larger than their antero-posterior diameters (25.25 mm on the left and 24.50 mm on the right). In lateral view, the antero-posterior lengths of the pedicles become narrower toward the bases.

The remaining part of the fragmentary right parietal (Fig. 2-3) is 40.75 mm in maximum length. It agglutinates with the posterior margin of the right frontal, and the agglutinating coronal suture is approximately 35 mm in length.

The remaining part of the fragmentary left presphenoid (Fig. 2-7) is 34.00 mm in maximum length. The optic canal is perfectly preserved and ellipsoidal in shape, measuring 5.10 mm along its major axis.

2) Upper teeth

The almost perfectly-preserved upper cheek teeth consist of the left 2nd-4th premolars (Fig. 2-9), the right 3rd premolar (Fig. 2-13), the left 1st-2nd molars (Fig. 2-9, 10) and the right 1st-2nd molars (Fig. 2-11). The enamel on the crowns and grinding surfaces is generally gray in color, but partly brown around the cervical lines and along the styles. The crown surfaces are marked by small reticulate sulci. The dentins on the grinding surfaces and the cementums on the root surfaces are dark brown in color. The grinding surfaces are well worn.

The left 2nd premolar is 12.45 mm in length and 11.15 mm in width. In occlusal view, the middle part of the lingual margin slightly curves lingually. The distal margin joins the lingual margin almost perpendicularly.

The lengths of the 3rd premolars are 11.55 mm on the left and 11.35 mm on the right. Their widths are 12.80 mm and 13.20 mm, respectively. In occlusal view, the middle parts of their lingual margins slightly curve lingually, and the mesial margins nearly parallel the distal margins. The metastyles are well developed.

The length of the left 4th premolar, at 11.15 mm, is the smallest among the premolars. The width of the premolar is 12.80 mm. In occlusal view, the middle part of the lingual margin does not curve lingually.

The lengths of the 1st molars are 14.95 mm on the left and 14.85 mm on the right, and their

widths are 13.95 mm and 14.70 mm, respectively. Their accessory columns are slightly developed. The lengths and the widths of the 1st lobes are almost the same as those of the 2nd lobes. The buccal margins of the protocones and the metaconules are nearly straight antero-posteriorly, and fold distally and a little lingually at their distal ends.

The lengths of the 2nd molars are 17.25 mm on the left and 17.20 mm on the right, and their widths are 15.20 mm and 15.15 mm, respectively. Their lengths and the widths are larger than those of the 1st molars, and their accessory columns are slightly developed as seen in the 1st molars. The lengths and the widths of the 1st lobes are nearly the same as those of the 2nd lobes. The buccal margins of the protocones and the metaconules are nearly straight antero-posteriorly, and fold distally and slightly lingually at their distal ends.

3) Antler

The left antler is missing the portion above the middle of the beam above the 1st fork (Fig. 2-1, 2); the beam above the 1st fork is broken around the upper margin of the 1st fork. The maximum remaining length of the left antler is 316.15 mm from the lower margin of the burr to the middle part of the beam above the 1st fork. The right antler is missing the point of the 1st tine and the part above the upper margin of the 1st fork (Fig. 2-3). The maximum remaining length of the right antler is 142.95 mm from the lower margin of the burr to the broken end of the 1st tine. In addition to these fragments, a fragmental antler of unknown position is preserved (Fig. 2-4), measuring 76.60 mm in maximum length.

The cross sections of the burrs are nearly round in shape. The beams below the 1st forks stand almost vertical to the horizontal plains of the burrs, and their surfaces are marked by a number of vertical sulci. The heights of the 1st forks are 60.60 mm on the left and 60.25 mm on the right. The heights of the upper margins of the 1st forks are 100.55 mm on the left and 94.25 mm on the right. The angles of the 1st forks are 66 degrees on the left and 74 degrees on the right. Both the left and right 1st tines extend antero-dorsally and laterally, and gently curve dorsally. The left beam above the 1st fork extends postero-dorsally and laterally, and changes the extending direction slightly dorsally at a point

about 150 mm above the upper margin of the 1st fork. Many small protrusions are present on the surfaces of the 1st tines and on the left beam above the 1st fork. One antler surface of unknown position is very smooth.

4) Mandible

The middle part of the left body is preserved along with the 2nd molar and the 1st lobe of the 3rd molar (Fig. 2-17). The remaining mandible lacks the middle of the medial portion antero-posteriorly. The minimum heights of the mandible are 30.70 mm on the lateral side and 34.40 mm on the medial side from the distal end of the cervical line of the 2nd molar. The maximum remaining length is 44.60 mm. The maximum width is 16.60 mm below the distal margin of the 1st lobe of the 3rd molar.

5) Lower teeth

The lower cheek teeth consist of the left 2nd molar and the 1st lobe of the left 3rd molar (Fig. 2-17). Their overall appearance is very similar to that of the upper cheek teeth.

The left 2nd molar is 16.75 mm in length and 10.20 mm in width. The mesial cingulum is developed as well as the parastylid. The 1st lobe is slightly larger than the 2nd lobe. The buccal column is developed.

The 1st lobe of the left 3rd molar is 9.45 mm in length and 9.45 mm in width. The mesial cingulum is not as developed as in the 2nd molar. The buccal column is recognizable.

6) Lumbar vertebrae

The 2nd lumbar vertebra is lacking the head and both transverse processes (Fig. 3-1), and this incomplete specimen measures 70.65 mm in height and 37.35 mm in body length. In lateral view, the cranial margin of the spinous process curves cranially. In cranial view, the mammillary articular processes are distinctly constricted at the bases of the lateral sides.

The 3rd lumbar vertebra is lacking the left and the tip of the right transverse processes (Fig. 3-2), and measures 69.80 mm in height and 40.25 mm in body length. In lateral view, the caudal margin of the spinous process extends straight dorsally. In cranial view, the mammillary articular processes are constricted well at the bases of the lateral sides.

The 4th lumbar vertebra is lacking the right body and both transverse processes (Fig. 3-3), and it measures 70.20 mm in height and 39.90 mm in body length. In lateral view, the caudal margin of the spinous process is nearly straight and inclines cranially. In cranial view, the mammillary articular processes are constricted at the bases of the lateral sides.

The 6th lumbar vertebra is lacking the left and the tip of the right transverse processes (Fig. 3-4), and it agglutinates with the sacral vertebra. It measures 66.20 mm in height and 37.05 mm in body length. In cranial view, the mammillary articular processes are constricted well at the bases of the lateral sides.

7) Sacral vertebra

The sacral vertebra is lacking the left wing and the anterior part of the spinous process (Fig. 3-4), and measures 43.00 mm in height and 95.40 mm in length. In lateral view, the spinous process thickens in its dorsal part. The dorsal sacral foramina are not recognized, except for the first foramina. In lateral view, the caudal margins of the auricular surfaces extend crano-ventrally.

8) Caudal vertebra

The 1st caudal vertebra is missing the spinous process and the right transverse process (Fig. 3-5). It measures 26.25 mm in remaining body length and 24.60 mm in the remaining width of the caudal articular processes. The cranial articular processes protrude well proximally. The medial margins of the cranial articular processes slightly protrude medially along their middle portions.

9) Rib

The proximal part of the left rib is fragmentarily preserved (Fig. 3-6), measuring 82.35 mm in maximum remaining length. The maximum width is 16.40 mm at the proximal end and 13.85 mm at the distal end. The costal angle is well-developed, and the costal groove is deep. The transverse section of the body is nearly rhombic in shape. The remaining rib is inferred to be the 4th or 5th rib, based on the size and morphology.

10) Pelvis

The left pelvis is missing the caudal part of the ischium and the crano-dorsal part of the ilium wing (Fig. 3-7, 9). The right pelvis lacks the caudal part of the ischium and the cranial part of the ilium

wing (Fig. 3-8, 9).

The maximum remaining lengths are 213.80 mm on the left and 219.75 mm on the right. In dorsal view, the ischium spines curve laterally. The left obturator foramen is perfectly preserved and ellipsoidal in shape. The foramen measures 59.45 mm along its major axis and 31.60 mm along its minor axis. The acetabular fossae are separated into medial and lateral parts, and the former is much smaller than the latter.

11) Astragalus

The right astragalus is nearly perfectly preserved (Fig. 3-10), and measures 38.15 mm in maximum length of the lateral half and 25.15 mm in width at the distal end. In plantar view, the proximal margin of the articular surface with the cubo-navicular goes around the center of the body.

12) Cubo-navicular

The right cubo-navicular is almost perfectly preserved (Fig. 3-11), measuring 23.50 mm in length and 32.05 mm in width. In dorsal view, the proximal part of the medial margin is nearly straight.

13) Metatarsus

The right metatarsus lacks the medial part of the distal end (Fig. 3-12). It measures 218.00 mm in maximum length and 17.85 mm in minimum width at the middle of the body. In plantar view, the medial end of the proximal margin protrudes medially, and the medial end of the cubo-navicular facet protrudes proximally.

3. Measurements

Basic osteology and the location of measurements adopted in this paper are shown in Fig. 4. Measurements of the bones of the specimen KMSY-2034Ma are presented in Appendixes 1-8. For bilateral bones, left and right values are shown on the left and right sides of the slash marks (/) in the appendixes, respectively. An asterisk (*) means that measurements were impossible, owing to breakage.

Fig. 4

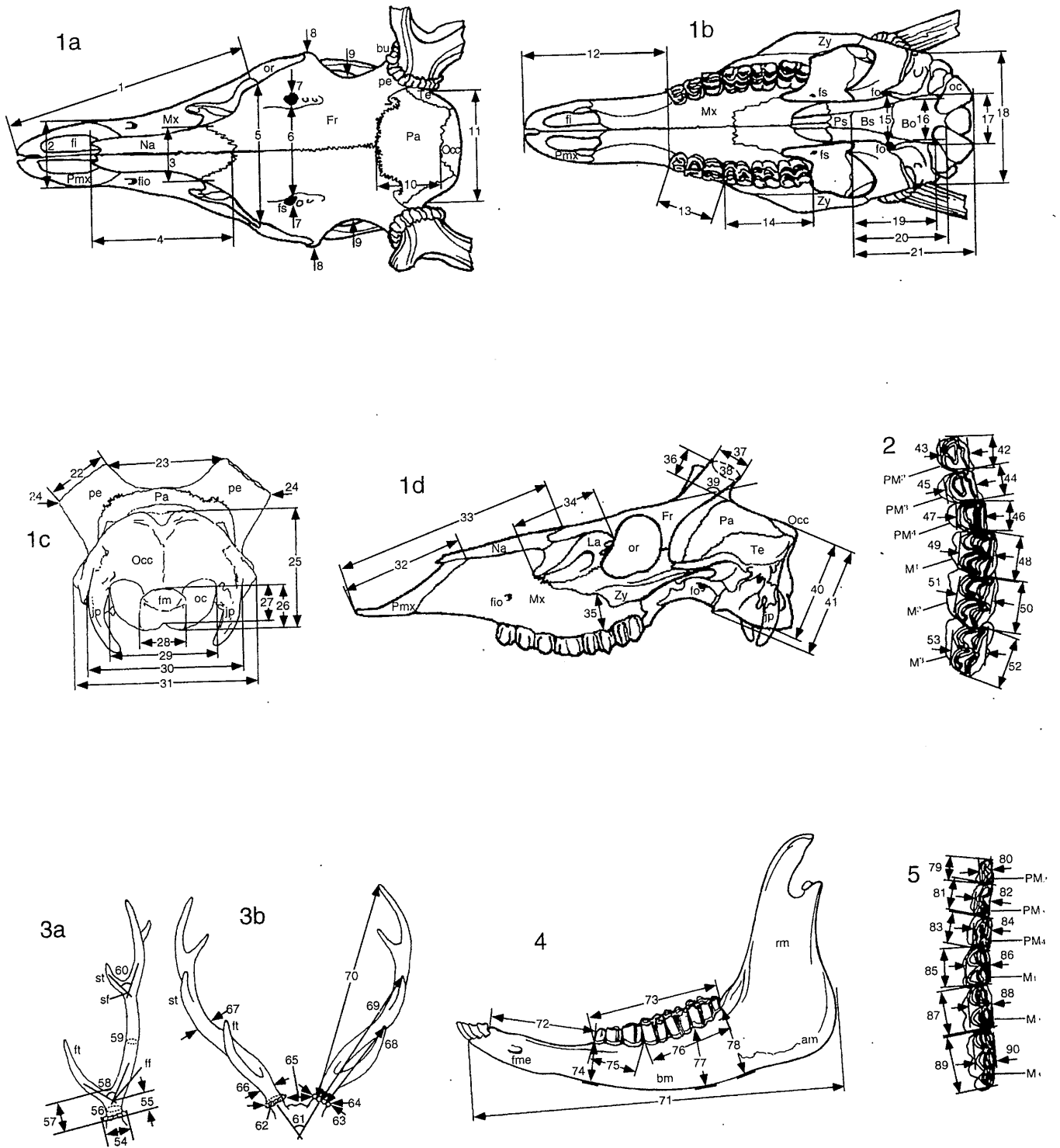


Fig. 4 (Continued)

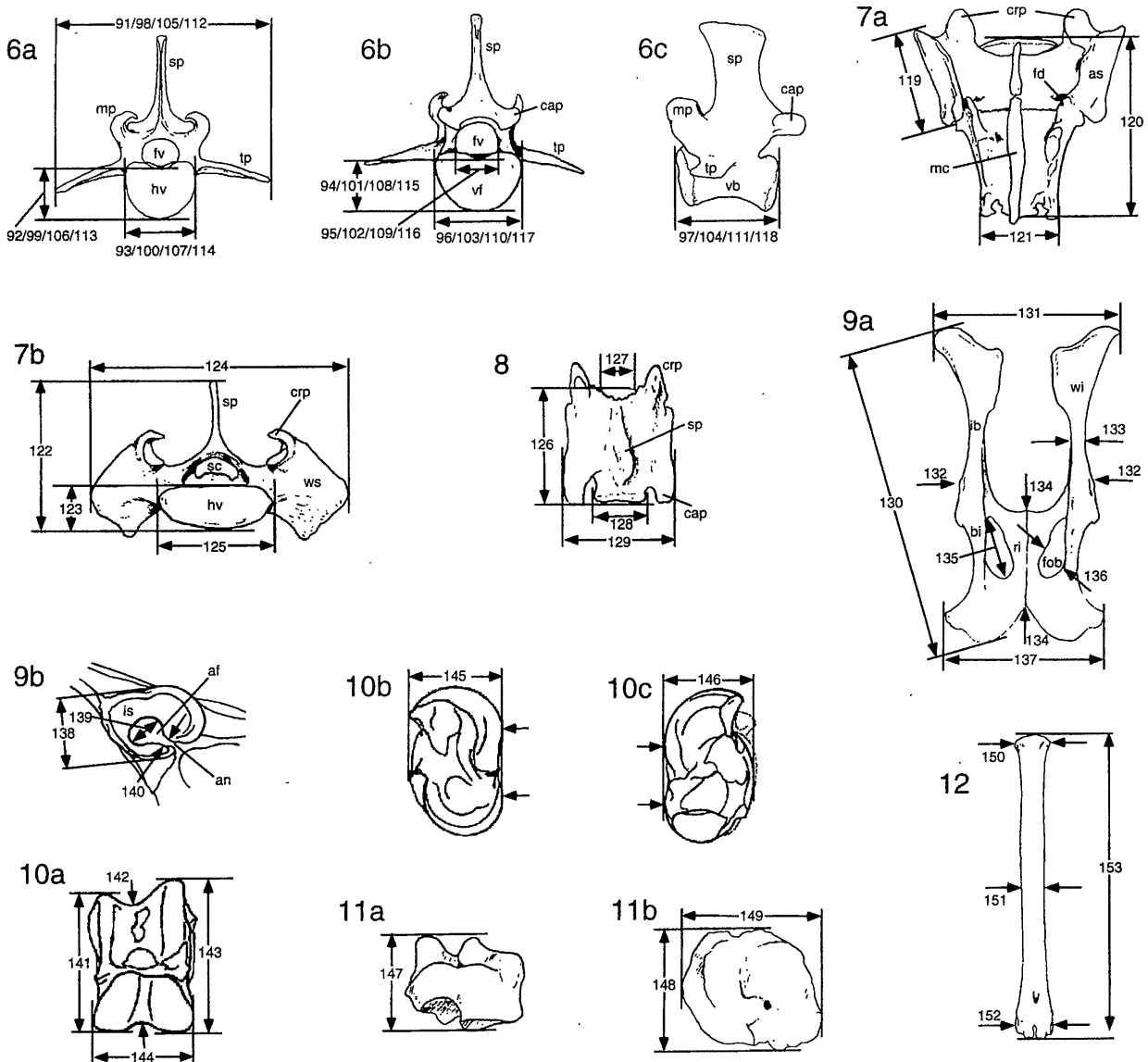


Fig. 4 Basic osteology and location of measurements for skeletal specimens of fossil and living deer (modified after Driesch, 1976; Otsuka, 1988b). 1a-d. Skull, 1a: dorsal view, 1b: ventral view, 1c: posterior view, 1d: left lateral view. 2. Upper cheek teeth, in occlusal view. 3a-b. Antler, 3a: left antler, in lateral view, 3b: both antlers, in anterior view. 4. Left mandible, in lateral view. 5. Lower cheek teeth, in occlusal view. 6a-c. Lumbar vertebra, 6a: cranial view, 6b: caudal view, 6c: left lateral view. 7a-b. Sacral vertebra, 7a: dorsal view, 7b: cranial view. 8. First caudal vertebra, in dorsal view. 9a-b. Pelvis, 9a: dorsal view, 9b: left acetabular, in ventro-lateral view. 10a-c. Left astragalus, 10a: dorsal view, 10b: medial view, 10c: lateral view. 11a-b. Left cubo-navicular, 11a: dorsal view, 11b: proximal view. 12. Left metatarsus, in dorsal view. af=acetabular fossa, am=angle of mandible, an=acetabular notch, as=auricular surface, bi=body of ischium, bm=body of mandible, Bo=basioccipital, Bs=basisphenoid, bu=burr, cap=caudal articular process, crp=cranial articular process, fd=dorsal sacral foramen, ff=1st fork, fi=incisive foramen, fio=infraorbital foramen, fm=foramen magnum, fme=mental foramen, fo=oval foramen, fob=obturator foramen, Fr=frontal, fs=supraorbital foramen, ft=1st tine, fv=vertebral foramen, hv=head of vertebra, ib=iliac body, jp=jugular process, La=lachrymal, ls=lunate surface, M¹=upper 1st molar, M₁=lower 1st molar, M²=upper 2nd molar, M₂=lower 2nd molar, M³=upper 3rd molar, M₃=lower 3rd molar, mc=median sacral crest, mp=mammillary articular process, Mx=maxilla, Na=nasal, oc=occipital condyle, Occ=occipital, or=orbit, Pa=parietal, pe=pedicle, PM²=upper 2nd premolar, PM₂=lower 2nd premolar, PM³=upper 3rd premolar, PM₃=lower 3rd premolar, PM⁴=upper 4th premolar, PM₄=lower 4th premolar, Pmx=premaxilla, Ps=presphenoid, ri=ramus of ischium, rm=ramus of mandible, sc=sacral canal, sf=2nd fork, sp=spinous process, st=2nd tine, Te=temporal, tp=transverse process, vb=vertebral body, vf=vertebral fossa, wi=wing of ilium, ws=wing of sacrum, Zy=zygomatic. For explanation of the measured parts see Appendixes 1-8.

4. Comparison

The height of the antler's 1st fork is very high on the specimen KMSY-2034Ma, measuring 60.60 mm on the left and 60.25 mm on the right. Otsuka and Shikama (1977) drew a scatter diagram showing relationships between height and the angle of the 1st fork of the antler in several fossil species of *Cervus*. In the present study, those values for the specimen (KMSY-2034Ma) were plotted on the same diagram, and fall among the values for *C. (N.) praenipponicus* (Fig. 5). The left beam above the 1st fork extends straight in the specimen KMSY-2034Ma, and this morphologic character is also identical to that in *C. (N.) praenipponicus* (Shikama, 1949). Based on these comparisons, the specimen KMSY-2034Ma is referred to *C. (N.) praenipponicus*.

Fig. 5

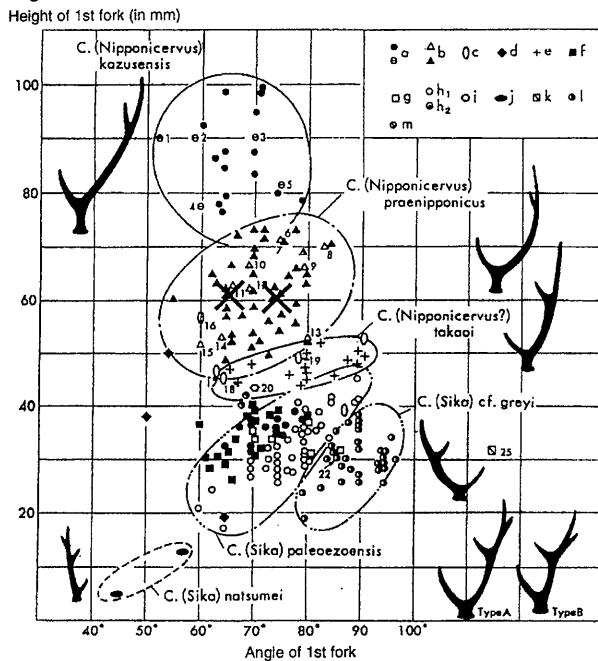


Fig. 5 Scatter diagram showing relationship between height and angle of 1st fork of antler from the fossil deer studied in this paper (X) and several fossil species of *Cervus* in Japan (after Otsuka and Shikama, 1977). For explanation of the marks see Otsuka and Shikama (1977).

5. Remarks

Ohtaishi (1980) showed age estimation methods for the modern deer *C. (Sika) nippon*, based on the cervical line condition, the wear index and the molar ratio of each lower molar. The present fossil specimen (KMSY-2034Ma) is inferred to have been 4.5-5.5 years old, by the use of the age estimation methods (Ohtaishi, 1980).

The lachrymal of the specimen (KMSY-2034Ma) is very large, and is deeply concave medially on the middle and lower parts. Furthermore, the dorsal surfaces of both zygomatics sutured with the lachrymals are nearly horizontal. Based on those characters, *C. (N.) praenipponicus* is thought to have scented frequently with well-developed infraorbital glands.

III. Skull restoration

One male neurocranium of *C. (N.) praenipponicus* has been found in the Upper Pleistocene Kioroshi Formation in Hikita, Ichihara City, Chiba Prefecture, Central Japan (Fossil Deer Research Group of Ichihara, 1994), and several skulls have been found in the Upper Pleistocene Kuzuu Formation in Kuzuu, Tochigi Prefecture, Central Japan (Shikama, 1949). No records, however, have ever been reported on the palatine parts of the male skull.

It is inferred that the skull size of the specimen KMSY-2034Ma is nearly identical to that of the neurocranium specimen from Hikita, Chiba Prefecture, reported by the Fossil Deer Research Group of Ichihara (1994), based on the sizes of the antlers and pedicles of both specimens. The relative ages of both specimens are estimated to have been nearly equal, by the use of the pedicle index that is shown by Otsuka (1988b) to estimate the age of the living deer *C. (S.) nippon*. In this study, the male skull of *C. (N.) praenipponicus* is restored for the first time, based on the well-preserved palatine parts of the specimen (KMSY-2034Ma) and the neurocranium specimen from Hikita, Chiba Prefecture (Fossil Deer Research Group of Ichihara, 1994) (Fig. 6).

The morphologic characters of the skull restored are given as follows: The skull measures 243.10 mm in maximum length, and 93.60 mm in maximum height anterior to the orbit. In left lateral view (Fig. 6a), the anterior end of the left orbit is dorsal from the posterior margin of the upper 2nd molar. The left orbit is nearly ellipsoidal in shape. The left lachrymal is 60.15 mm in maximum length. The row of left upper cheek teeth curves dorsally. In dorsal view (Fig. 6b), the posterior ends of the nasals are located around the center of the anterior ends of both orbits. The zygomatics well expand posteriorly. For detailed morphology of the neurocranium, see the Fossil Deer Research Group of Ichihara (1994).

Fig. 6

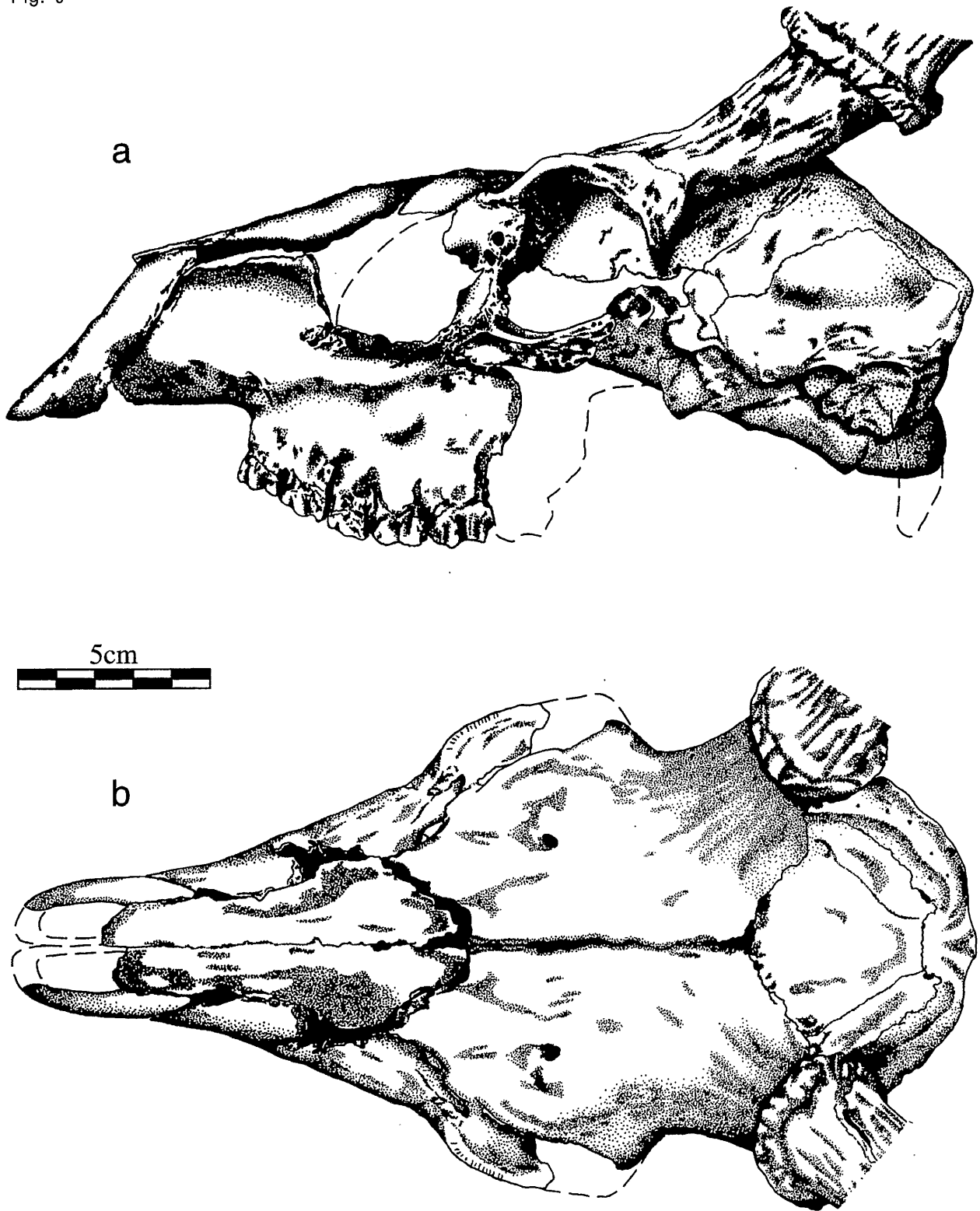


Fig. 6 Restoration of the male skull of *Cervus (Nipponicervus) praenipponicus*. Anterior parts of frontals, nasals, lacrymals, zygomatics, maxillae, premaxillae and cheek teeth are based on the present specimen (KMSY-2034Ma), and posterior parts of frontals, parietals, temporals, occipital, basioccipital, basisphenoid, and presphenoid are based on a specimen reported by the Fossil Deer Research Group of Ichihara (1994). Broken lines show missing parts. a: left lateral view, b: dorsal view.

IV. Comparative osteology

1. Materials compared

A comparative osteological investigation, with special reference to the skull and upper teeth, was performed between *C. (N.) praenipponicus* and *C. (R.) unicolor*, a modern deer that has been considered to be its closest living relative (Shikama, 1941). Table 2 shows the skeletal specimens of both species examined in this study. The specimen KMSY-131Ma is a replica of the original specimen (GSJ-F3992) that is housed in the Geological Survey of Japan. The specimens of *C. (N.) praenipponicus* include a female and individuals of unknown sex, as it is rather difficult to distinguish sex by skeletal parts other than antlers or the skull with pedicle. In the present

study, skeletal specimens of the congeneric living deer *C. (S.) nippon* were also studied in order to evaluate osteologic similarities and differences between *C. (N.) praenipponicus* and *C. (R.) unicolor* (Table 2).

In the following comparisons, the registration number (or numbers) and the number of individual elements (n) are shown following the species name for *C. (N.) praenipponicus* and for *C. (R.) unicolor* and *C. (S.) nippon*, respectively. The fossil specimen reported by the Fossil Deer Research Group of Ichihara (1994) has not yet been registered, so its provisional name of Hikita specimen is used here. Right-side measurements are adopted in the comparisons for all species, unless the right-side bones are broken or missing.

Table 2 Skeletal specimens of *C. (N.) praenipponicus*, *C. (R.) unicolor*, and *C. (S.) nippon* examined in the present study.

Species	Reg. No.	Preserved part	Sex	Collecting locality	Keeping	Notes
<i>C. (N.) praenipponicus</i>	IGPS-58804	skull with antler, mandible with teeth	male	Kuzuu, Tochigi Pref.	Tohoku University Museum	Shikama (1936a), Shikama (1949); Holotype
	IGPS-58805	antler with pedicle	male	Kuzuu, Tochigi Pref.	Tohoku University Museum	Shikama (1936a), Shikama (1949); Paratype
	IGPS-61693	antler with pedicle	male	Kuzuu, Tochigi Pref.	Tohoku University Museum	Shikama (1949)
	IGPS-61695	skull	female	Kuzuu, Tochigi Pref.	Tohoku University Museum	Shikama (1949)
	IGPS-61697	skull	unknown	Kuzuu, Tochigi Pref.	Tohoku University Museum	Shikama (1949)
	IGPS-65505	mandible with teeth	unknown	Kuzuu, Tochigi Pref.	Tohoku University Museum	Shikama (1949)
	IGPS-65510	upper teeth	unknown	Kuzuu, Tochigi Pref.	Tohoku University Museum	
	IGPS-65524	sacral vertebra	unknown	Kuzuu, Tochigi Pref.	Tohoku University Museum	Shikama (1949)
	IGPS-65525	lumbar and sacral vertebrae	unknown	Kuzuu, Tochigi Pref.	Tohoku University Museum	
	IGPS-65537	pelvis	unknown	Kuzuu, Tochigi Pref.	Tohoku University Museum	Shikama (1949)
	IGPS-65546	astragalus	unknown	Kuzuu, Tochigi Pref.	Tohoku University Museum	Shikama (1949); 4 specimens
	IGPS-65547	cubo-navicular	unknown	Kuzuu, Tochigi Pref.	Tohoku University Museum	Shikama (1949); 2 specimens
	IGPS-65550	metatarsus	unknown	Kuzuu, Tochigi Pref.	Tohoku University Museum	Shikama (1949)
	IGPS-77077	mandible with teeth, upper teeth	unknown	Kuzuu, Tochigi Pref.	Tohoku University Museum	
	KMSY-131Ma	mandible with teeth	unknown	Shinsaku, Kawasaki City, Kanagawa Pref.	Kawasaki Municipal Science Museum for Youth	Geological Survey of Japan (1960); replica
	KMSY-2034Ma	skull with antler, mandible etc.	male	Shinsaku, Kawasaki City, Kanagawa Pref.	Kawasaki Municipal Science Museum for Youth	this study
	unregistered	skull with antler	male	Hikita, Ichihara City, Chiba Pref.	Sodegaura high school, Chiba Pref.	Fossil Deer Research Group of Ichihara (1994)
<i>C. (R.) unicolor</i>	IGPS-6327	skull with antler	male	unknown	Tohoku University Museum	
	NSM-1146	skull with antler	male	India	National Science Museum, Tokyo	
	NSM-8932	skull with antler	male	unknown	National Science Museum, Tokyo	
	NSM-8947	skull with antler	male	unknown	National Science Museum, Tokyo	
	NSM-8950	skull with antler	male	unknown	National Science Museum, Tokyo	
	NSM-9624	skull with antler	male	unknown	National Science Museum, Tokyo	
	NSM-26698	skull with antler	male	Philippine	National Science Museum, Tokyo	semi-adult
<i>C. (S.) nippon</i>	NSM-31214	skeleton	male	unknown	National Science Museum, Tokyo	
	GMNH-VM-133	skeleton	male	Hokkaido	Gunma Museum of Natural History	
	TFM-OS-027	skull, mandible	male	Minami-shinano, Nagano Pref.	Togakushi Fossil Museum	
	TFM-OS-079	skull	male	Takegi, Nagano Pref.	Togakushi Fossil Museum	
	TFM-OS-087	skeleton	male	Kita-mimaki, Nagano Pref.	Togakushi Fossil Museum	semi-adult
	TPM-053	skeleton	male	Ashio, Tochigi Pref.	Tochigi Prefectural Museum	
	TPM-171	skeleton	male	Nikko City, Tochigi Pref.	Tochigi Prefectural Museum	
	TPM-216	skeleton	male	Urahoro, Hokkaido	Tochigi Prefectural Museum	
	TPM-222	skeleton	male	Urahoro, Hokkaido	Tochigi Prefectural Museum	
	TPM-226	skeleton	male	Urahoro, Hokkaido	Tochigi Prefectural Museum	
	TPM-228	skeleton	male	Urahoro, Hokkaido	Tochigi Prefectural Museum	
	TPM-230	skeleton	male	Urahoro, Hokkaido	Tochigi Prefectural Museum	
	TPM-324	skeleton	male	Nikko City, Tochigi Pref.	Tochigi Prefectural Museum	

elements (n) are shown following the species name for *C. (N.) praenipponicus* and for *C. (R.) unicolor* and *C. (S.) nippon*, respectively. The fossil specimen reported by the Fossil Deer Research Group of

2. Comparisons

1) Skulls

The nasals are relatively wide in *C. (N.) praenipponicus* (KMSY-2034Ma) and *C. (R.) unicolor* (n=5)(Fig. 7). The ratios of nasal width/length in both species are similar to each other and are higher than in *C. (S.) nippon* (n=11)(Fig. 8). In dorsal view, the posterior ends of the nasals of *C. (N.) praenipponicus* (KMSY-2034Ma) and *C. (S.) nippon* (n=12) are located around the centers of the anterior ends of both orbits, while the posterior ends of the nasals of *C. (R.) unicolor* (n=8) are located anterior to the centers.

In lateral view, the lacrymals of *C. (N.) praenipponicus* (KMSY-2034Ma) and *C. (R.) unicolor* (n=8) are deeply concave medially at the middle and ventral portions (Fig. 9A-B). However, the lacrymal of *C. (S.) nippon* (n=12) is slightly concave medially at its middle (Fig. 9C). The ratio of maximum length of lacrymal/upper premolar length closely resemble between *C. (N.) praenipponicus* (KMSY-2034Ma) and *C. (R.) unicolor* (n=7), and the values of both species are higher than those of *C. (S.) nippon* (n=12) (Fig. 10).

The facial crest on the zygomatic is more developed in *C. (N.) praenipponicus* (KMSY-2034Ma) and *C. (R.) unicolor* (n=8) than in *C. (S.) nippon* (n=12). The dorsal surface of the zygomatic sutured with the lacrymal is nearly horizontal in *C. (N.) praenipponicus* (KMSY-2034Ma) and *C. (R.) unicolor* (n=8), while this surface in *C. (S.) nippon* (n=12) inclines laterally.

The orbits of *C. (N.) praenipponicus* (KMSY-2034Ma) and *C. (R.) unicolor* (n=8) are nearly ellipsoidal in shape, but the orbit of *C. (S.) nippon* (n=12) is almost round.

The height of the maxilla in *C. (N.) praenipponicus* (KMSY-2034Ma) is high measured from the anterior ends of the facial crests on the zygomatics, and the ratio of height of maxilla/length of the upper premolar row is 1.12. On the other hand, the heights of *C. (R.) unicolor* (n=7) and *C. (S.) nippon* (n=12) are relatively low, with ratios of 0.73-1.00 (avg. 0.88 ± 0.11) and 0.77-1.10 (avg. 0.97 ± 0.09), respectively.

The pedicle of *C. (N.) praenipponicus* (KMSY-2034Ma, IGPS-58804, IGPS-61693, Hikita specimen) is slightly flat transversely, and the ratio of transverse diameter/antero-posterior diameter of the pedicle in *C. (N.) praenipponicus* is 1.04-1.09 (avg. 1.07 ± 0.03). On the other hand, the pedicles of *C. (R.) unicolor* (n=7) and *C. (S.) nippon* (n=11)

tend to be slightly flat antero-posteriorly, with ratios of 0.93-1.01 (avg. 0.98 ± 0.03) and 0.83-1.04 (avg. 0.95 ± 0.06), respectively. In lateral view, the antero-posterior length of the pedicle becomes narrower antero-ventrally in *C. (N.) praenipponicus* (KMSY-2034Ma, IGPS-58804, IGPS-58805, IGPS-61693, Hikita specimen) and *C. (S.) nippon* (n=12), but the pedicle length of *C. (R.) unicolor* (n=8) scarcely narrows antero-ventrally.

In ventral view, the posterior margin of the basioccipital does not bend posteriorly in *C. (N.) praenipponicus* (IGPS-58804, IGPS-61695, IGPS-61697, Hikita specimen), as described by the Fossil Deer Research Group of Ichihara (1994). This character is also present in *C. (R.) unicolor* (n=4), while the margin of *C. (S.) nippon* (n=12) tends to bend posteriorly.

Fig. 7

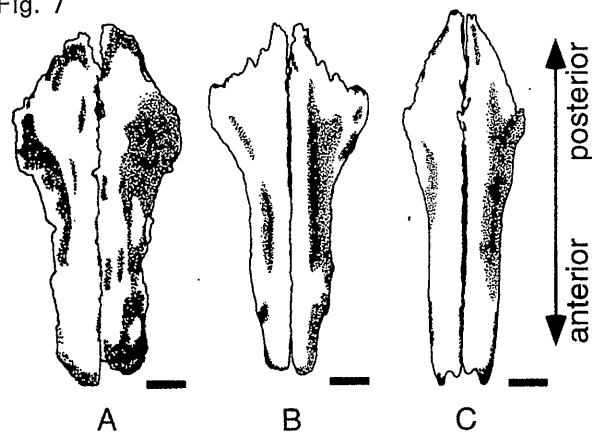


Fig. 7 Osteological characters of nasals, in dorsal view. A. *C. (N.) praenipponicus* (KMSY-2034Ma). B. *C. (R.) unicolor* (IGPS-6327). C. *C. (S.) nippon* (TPM-216). Scale bars equal 1 cm.

Fig. 8

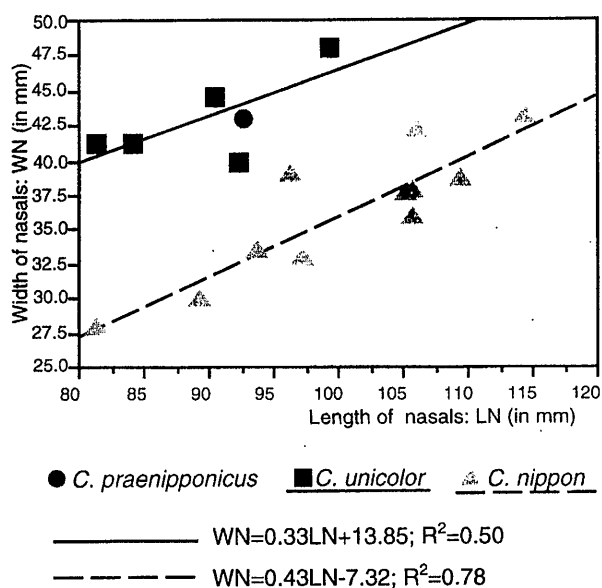


Fig. 8 Scatter diagram and regression lines showing relationship between length and width of nasals in *C. (N.) praenipponicus* (KMSY-2034Ma), *C. (R.) unicolor*, and *C. (S.) nippon*.

Fig. 9

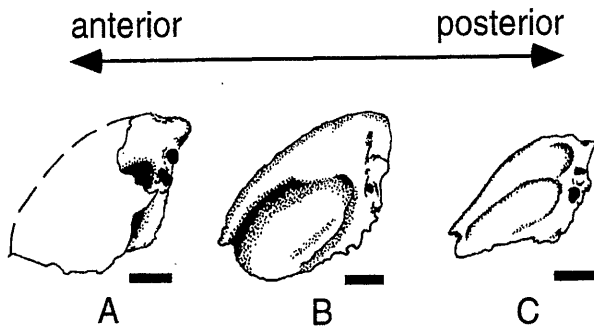


Fig. 9 Osteological characters of left lachrymals, in lateral view. A. *C. (N.) praenipponicus* (KMSY-2034Ma). B. *C. (R.) unicolor* (NSM-8947). C. *C. (S.) nippon* (TPM-216). Scale bars equal 1 cm.

Fig. 10

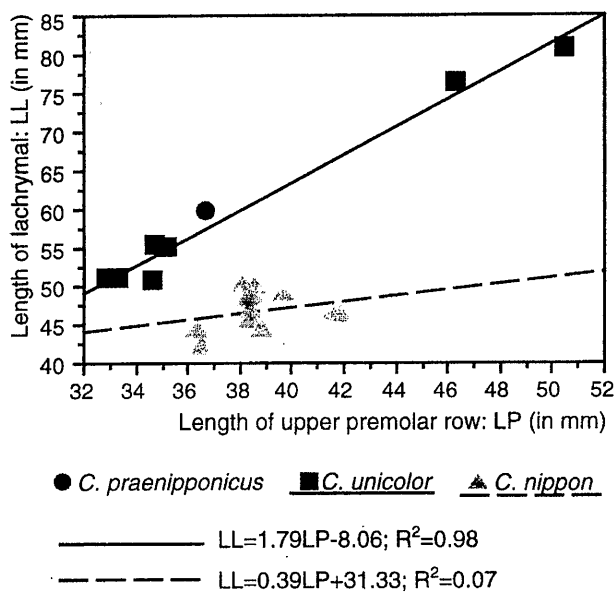


Fig. 10 Scatter diagram and regression lines showing relationship between lengths of lachrymal and upper premolar row in *C. (N.) praenipponicus* (KMSY-2034Ma), *C. (R.) unicolor*, and *C. (S.) nippon*.

2) Upper teeth

The distal margin of the 2nd premolar joins the lingual margin nearly perpendicularly in *C. (N.) praenipponicus* (KMSY-2034Ma, IGPS-65510, IGPS-77077) and *C. (R.) unicolor* (n=4), while the distal margin of *C. (S.) nippon* (n=10) joins the lingual margin obtusely (Fig. 11). The distal margin of the 2nd premolar and the mesial margin of the 3rd premolar are nearly parallel in *C. (N.) praenipponicus*

(KMSY-2034Ma, IGPS-77077) and *C. (R.) unicolor* (n=4), but both margins widen lingually in *C. (S.) nippon* (n=10).

The mesial margin of the 3rd premolar is nearly parallel to the distal margin in *C. (N.) praenipponicus* (KMSY-2034Ma, IGPS-77077). This tendency is also recognized in *C. (R.) unicolor* (n=4), but both margins of *C. (S.) nippon* (n=10) distinctly widen buccally. The middle part of the lingual margin of the 3rd premolar slightly curves lingually in *C. (N.) praenipponicus* (KMSY-2034Ma, IGPS-77077) and *C. (S.) nippon* (n=10), while the middle part more strongly curves lingually in several specimens of *C. (R.) unicolor* (n=4).

The middle part of the lingual margin of the 4th premolar does not curve lingually in *C. (N.) praenipponicus* (KMSY-2034Ma, IGPS-65510, IGPS-77077) and *C. (S.) nippon* (n=11), whereas its middle part slightly curves lingually in several specimens of *C. (R.) unicolor* (n=5).

The buccal margins of protocones and metaconules of the 1st and 2nd molars are folding distolingually in *C. (N.) praenipponicus* (KMSY-2034Ma, IGPS 65510, IGPS-77077) at the distal ends. This tendency is also recognized in *C. (R.) unicolor* (n=6), but not in several specimens of *C. (S.) nippon* (n=12).

Fig. 11

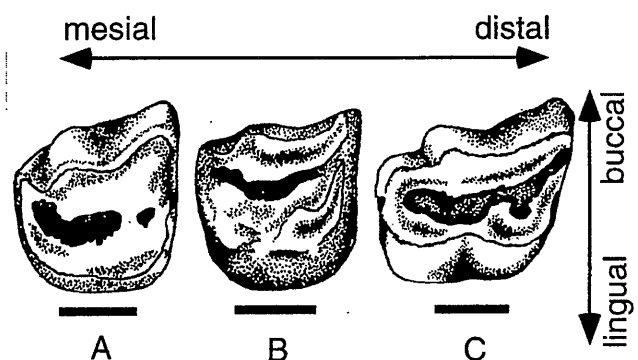


Fig. 11 Osteological characters of left upper 2nd premolars, in occlusal view. A. *C. (N.) praenipponicus* (KMSY-2034Ma). B. *C. (R.) unicolor* (NSM-8950). C. *C. (S.) nippon* (TFM-OS-027). Scale bars equal 1 cm.

3) Antlers

The height of the 1st fork of the antler is very great in *C. (N.) praenipponicus* (KMSY-2034Ma, IGPS-58804, IGPS-58805, IGPS-61693, Hikita specimen), measuring 60.25-75.70 mm (avg. 66.19 ± 6.80 mm), except for IGPS-61693 (38.10 mm). However,

the height is relatively low in *C. (R.) unicolor* (n=6) and *C. (S.) nippon* (n=9), measuring 14.85-65.05 mm (avg. 35.89 ± 16.15 mm) and 17.50-46.65 mm (avg. 28.64 ± 10.08 mm), respectively.

The angle of the 1st fork of the antler is 70-82 degrees (avg. 75.80 ± 5.40 degrees) in *C. (N.) praenipponicus* (KMSY-2034Ma, IGPS-58804, IGPS-58805, IGPS-61693, Hikita specimen) and 59-99 degrees (avg. 78.00 ± 10.74 degrees) in *C. (S.) nippon* (n=9). The angle in *C. (R.) unicolor* (n=6) is slightly smaller than those in *C. (N.) praenipponicus* and *C. (S.) nippon*, at 54-88 degrees (avg. 66.17 ± 11.18 degrees).

4) Mandibles

The minimum mandible height in *C. (N.) praenipponicus* (KMSY-131Ma, KMSY-2034Ma, IGPS-65505, IGPS-77077) is 29.95-33.90 mm (avg. 31.84 ± 1.83 mm) on the buccal side from the distal margin of the cervical line of the 2nd molar. The heights of *C. (R.) unicolor* (n=1) and *C. (S.) nippon* (n=11) are nearly identical to those of *C. (N.) praenipponicus*, measuring 33.46 mm and 29.60-37.10 mm (avg. 33.12 ± 2.37 mm), respectively.

5) Lower teeth

The buccal columns of the 2nd and 3rd molars in *C. (R.) unicolor* (n=1) are more developed than in *C. (N.) praenipponicus* (KMSY-131Ma, KMSY-2034Ma, IGPS-65505, IGPS-77077) and *C. (S.) nippon* (n=11). Overall, the characters of the lower teeth closely resemble each other in *C. (N.) praenipponicus*, *C. (R.) unicolor*, and *C. (S.) nippon*.

6) Vertebrae

In lateral view, the cranial margin of the spinous process of the 2nd lumbar vertebra curves cranially in *C. (N.) praenipponicus* (KMSY-2034Ma) and *C. (S.) nippon* (n=8), but scarcely curves cranially in *C. (R.) unicolor* (n=1). In cranial view, the lateral sides of the mammillary articular processes are well-constricted at the bases in *C. (N.) praenipponicus* (KMSY-2034Ma) and *C. (S.) nippon* (n=8), but are not constricted in *C. (R.) unicolor* (n=1). The width of the 2nd vertebral foramen is wide in *C. (N.) praenipponicus* (KMSY-2034Ma) and *C. (R.) unicolor* (n=1), and the ratio of the width of 2nd vertebral foramen/width of 2nd vertebral fossa is 0.61 in *C. (N.) praenipponicus* and 0.65 in *C. (R.) unicolor*. On the other hand, the width of the 2nd vertebral foramen in *C. (S.) nippon* (n=8) is relatively narrow, with a ratio of 0.45-0.53 (avg. 0.48 ± 0.03).

In lateral view, the caudal margin of the spinous process of the 3rd lumbar vertebra extends straight dorsally in *C. (N.) praenipponicus* (KMSY-2034Ma),

while the caudal margins of *C. (R.) unicolor* (n=1) and *C. (S.) nippon* (n=9) protrude caudally on the dorsal portions. In cranial view, the lateral sides of the mammillary articular processes are well-constricted at their bases in *C. (N.) praenipponicus* (KMSY-2034Ma) and *C. (S.) nippon* (n=9), but not in *C. (R.) unicolor* (n=1). The width of the 3rd vertebral foramen is great in *C. (N.) praenipponicus* (KMSY-2034Ma) and *C. (R.) unicolor* (n=1), and the ratio of the width of the 3rd vertebral foramen/width of the 3rd vertebral fossa is 0.69 in *C. (N.) praenipponicus* and 0.64 in *C. (R.) unicolor*. The width of the 3rd vertebral foramen in *C. (S.) nippon* (n=9) is relatively narrow, with the ratio of 0.45-0.51 (avg. 0.49 ± 0.02).

In lateral view, the caudal margin of the spinous process of the 4th lumbar vertebra is nearly straight and inclines cranially in *C. (N.) praenipponicus* (KMSY-2034Ma), whereas the dorsal part of the caudal margin protrudes caudally in *C. (R.) unicolor* (n=1) and *C. (S.) nippon* (n=9). In cranial view, the lateral sides of the mammillary articular processes are constricted at the bases in *C. (N.) praenipponicus* (KMSY-2034Ma) and *C. (S.) nippon* (n=9), but not in *C. (R.) unicolor* (n=1).

In lateral view, the dorsal part of the spinous process of the sacral vertebra is thicker in *C. (N.) praenipponicus* (KMSY-2034Ma) than in *C. (R.) unicolor* (n=1) and *C. (S.) nippon* (n=9).

7) Pelvises

The width of the acetabular notch is great in *C. (N.) praenipponicus* (KMSY-2034Ma), and the ratio of the width of acetabular notch/width of acetabular is 0.19. On the other hand, the width is relatively slight in *C. (R.) unicolor* (n=1) and *C. (S.) nippon* (n=9), with ratios of 0.09 and 0.07-0.15 (avg. 0.12 ± 0.02), respectively. The acetabular fossa of *C. (N.) praenipponicus* (KMSY 2034Ma) is separated into medial and lateral parts, but this character is scarcely present in *C. (R.) unicolor* (n=1) and *C. (S.) nippon* (n=9).

8) Metatarsi

The minimum width at the middle of metatarsus is great in *C. (N.) praenipponicus* (KMSY 2034Ma, IGPS-65550) and *C. (R.) unicolor* (n=1), and the ratio of the minimum width at the middle of the metatarsus/maximum length of metatarsus is 0.082-0.086 (avg. 0.084 ± 0.003) in *C. (N.) praenipponicus* and 0.083 in *C. (R.) unicolor*. However, the width in *C. (S.) nippon* (n=7) is relatively slight, with a ratio of 0.067-0.078 (avg. 0.073 ± 0.004).

3. Measurements

Appendixes 1-8 show the bone measurements of *C. (N.) praenipponicus*, *C. (R.) unicolor*, and *C. (S.) nippon* examined in this study. In these appendixes, an asterisk (*) means that measurements were impossible, owing to breakage of *C. (N.) praenipponicus* bones. For measurements of bilateral bones of *C. (N.) praenipponicus*, left and right values are presented on the left and right sides of the slash marks (/), respectively. Right-side measurements are shown for *C. (R.) unicolor* and *C. (S.) nippon*, unless the right-side bones are broken or missing.

V. Discussion

It was found that *C. (N.) praenipponicus* shares the following eight characters with *C. (R.) unicolor*, as a result of comparative osteologic examinations with special reference to the skull and upper teeth (Table 3): 1) ratio of nasal width/length is high; 2) lachrymal is deeply concave medially at the middle and ventral portions; 3) ratio of maximum lachrymal length/upper premolar length is high; 4) facial crest on zygomatic is developed; 5) dorsal surface of zygomatic sutured with lachrymal is nearly horizontal; 6) orbit is nearly ellipsoidal in shape; 7) distal margin of 2nd premolar joins its lingual margin nearly perpendicularly; and 8) distal margin of 2nd premolar is nearly parallel to mesial margin of 3rd premolar. These findings are in concordance with previous phylogenetic inference (Shikama, 1941) about *C. (N.) praenipponicus* that was based on antler morphology, and suggest a close sister group relationship between *C. (N.) praenipponicus* and *C. (R.) unicolor*.

On the other hand, *C. (N.) praenipponicus* is distinguishable from *C. (R.) unicolor* in the following three characters (Table 3): 1) the posterior ends of the nasals of *C. (N.) praenipponicus* are located around the centers of the anterior ends of both orbits, while the posterior ends of the nasals of *C. (R.) unicolor* are located anterior to the centers; 2) the ratio of minimum height of maxilla/upper premolar length is higher in *C. (N.) praenipponicus* than in *C. (R.) unicolor*; and 3) the antero-posterior length of the pedicle becomes narrower antero-ventrally in *C. (N.) praenipponicus*, but the pedicle length of *C. (R.) unicolor* scarcely narrows antero-ventrally. Based on these characteristic differences between both species, *C. (N.) praenipponicus* is referable to be a distinct species from *C. (R.) unicolor*.

The early fossil records of the subgenus *Nipponicervus* have been reported in the Lower Pleistocene deposits of Yushe, Shanhsi, South China (Teilhard de Chardin and Trassaert, 1937; Shikama, 1941) and of West Japan (Matsumoto, 1926; Shikama, 1936c; Otsuka, 1967; Otsuka *et al.*, 1995) (Fig. 12). During the Early Pleistocene in East Asia including the Japanese Islands, the subgenus *Rusa* was the dominant group in *Cervus*, and was distributed south of about latitude 40°N (Teilhard de Chardin and Piveteau, 1930; Otsuka, 1966; Hu and Qi, 1978; Ji and Li, 1979 etc.) (Fig. 12). The distributions of both subgenera were partly overlapped around the north bounds of the distribution of the subgenus *Rusa* at that time (Fig. 12). Based on these fossil records and on comparative osteological data, it is considered that the subgenus *Nipponicervus* diverged from the lineage of the subgenus *Rusa* by the Early Pleistocene in East Asia.

Table 3 Distribution of skull and upper teeth characters in *C. (N.) praenipponicus*, *C. (R.) unicolor* and *C. (S.) nippon*. 1: ratio of nasal width/length, 2: lachrymal concavity at the middle and ventral portions, 3: ratio of maximum lachrymal length/upper premolar length, 4: facial crest on zygomatic, 5: dorsal surface of zygomatic sutured with lachrymal, 6: shape of orbit, 7: angle between distal and lingual margins of upper 2nd premolar, 8: distal margin of 2nd premolar and mesial margin of 3rd premolar, 9: location of posterior ends of nasals, 10: ratio of minimum height of maxilla/upper premolar length, 11: antero-posterior length of pedicle at the anterior part. Shaded portions denote the distribution of characters in *C. (N.) praenipponicus* and the same distribution as in this species.

	<i>C. (N.) praenipponicus</i>	<i>C. (R.) unicolor</i>	<i>C. (S.) nippon</i>
1	high	high	low
2	deep	deep	shallow
3	high	high	low
4	developed	developed	undeveloped
5	horizontal	horizontal	incline laterally
6	ellipsoidal	ellipsoidal	round
7	perpendicular	perpendicular	obtuse
8	parallel	parallel	widen lingually
9	center of anterior ends of both orbits	anterior to both orbits	center of anterior ends of both orbits
10	high	low	low
11	narrow	wide	narrow

Fig. 12

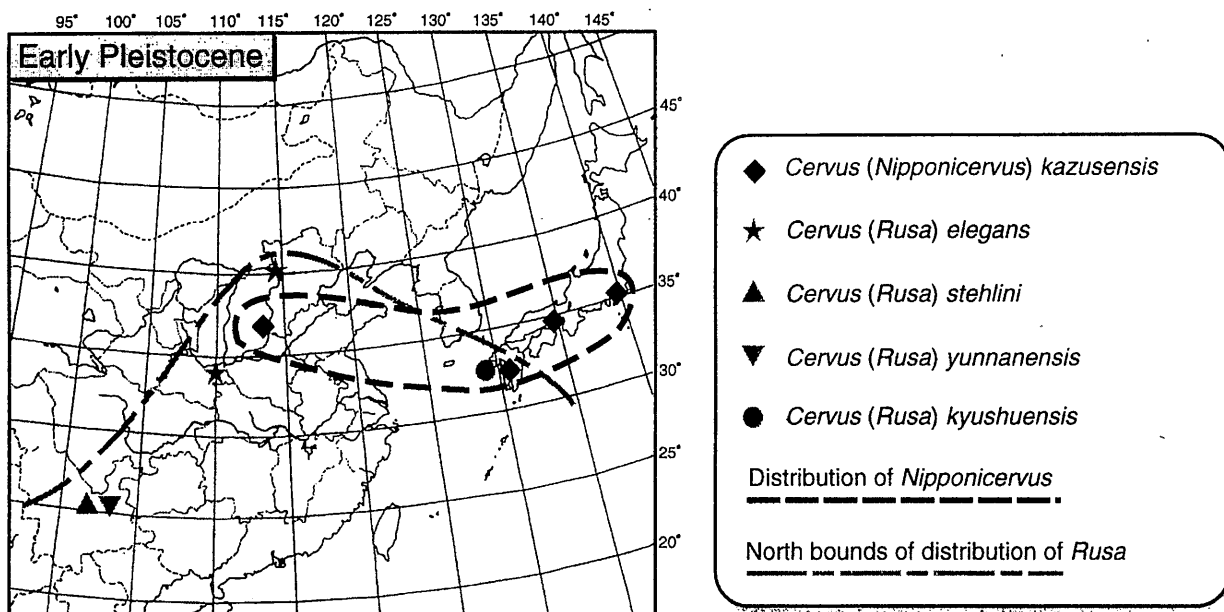


Fig. 12 Map showing distributions of *Nipponicervus* and *Rusa* in East Asia including the Japanese Islands during the Early Pleistocene (modified after Kawamura, 1982).

Summary

A new fossil occurrence of the deer *Cervus (Nipponicervus) praenipponicus* is reported from the Upper Pleistocene Shimosueyoshi Formation in Shinsaku, Kawasaki City, Central Japan. The specimen treated herein consists of numerous skeletal elements, including the skull, upper teeth, antlers, mandible, lower teeth and several post-cranial bones of an adult male individual.

Basic osteologic data for *C. (N.) praenipponicus* are presented, along with a detailed description and measurements of the specimen. The male skull of this species is restored for the first time based mainly on the present specimen. The osteologic characters of *C. (N.) praenipponicus* is compared with those of its closest living relative, *C. (Rusa) unicolor*, with special reference to the skull and upper teeth. Consequently, it becomes clear that a number of osteological characters, including the lachrymal and nasal bones, closely resemble between the two species. These osteologic data support previous phylogenetic inference about *C. (N.) praenipponicus* that was based solely on antler morphology.

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Appendix 1

Skull measurements of *C. (N.) praenipponicus*, *C. (R.) unicolor*, and *C. (S.) nippon* (in mm or degrees). For measured parts see Fig. 4. 1: length from prosthion to anterior end of orbit, 2: maximum width across premaxillae, 3: maximum width of nasals, 4: maximum length of nasals, 5: minimum width between orbits, 6: minimum width between supraorbital foramina, 7: maximum width between supraorbital foramina, 8: maximum frontal width, 9: minimum frontal width, 10: lambda-bregma length, 11: parietals width, 12: premolare-prosthion length, 13: length of upper premolar row, 14: length of upper molar row, 15: minimum width between oval foramina, 16: minimum width of occipital condyles, 17: basioccipital width, 18: maximum mastoid width, 19: length from synsphenion to posterior margin of basioccipital, 20: basion-synsphenion length, 21: length from synsphenion to posterior ends of occipital condyles, 22: transverse diameter of pedicle, 23: minimum distance between pedicles, 24: maximum distance between pedicles, 25: occipital height, 26: height of foramen magnum, 27: height from bregma to dorsal end of foramen magnum, 28: maximum width of foramen magnum, 29: external width of occipital condyles, 30: occipital width, 31: maximum neurocranium width, 32: lateral length of premaxilla, 33: nasion prosthion length, 34: lachrymal length, 35: height of maxilla from anterior end of facial crest, 36: pedicle length, 37: antero-posterior diameter of pedicle, 38: circumference of distal end of pedicle, 39: angle between frontal and parietal planes, 40: akrokranium-basion height, 41: neurocranium height.

	<i>C. (N.) praenipponicus</i>						<i>C. (R.) unicolor</i>			<i>C. (S.) nippon</i>			
	KMSY-2034Ma	IGPS-58804	IGPS-61693	IGPS-61695	IGPS-61697	Hikita specimen	n	Mean	S.D.	n	Mean	S.D.	
1	111.25/ *	*	*	*	*	*	7	169.91	35.22	11	159.00	8.85	
2	43.90	*	*	*	*	*	7	46.19	9.64	11	45.03	3.07	
3	43.00	*	*	*	*	*	5	45.06	4.73	12	36.58	4.84	
4	92.60	*	*	*	*	*	6	100.05	26.64	11	100.39	9.75	
5	107.10	*	*	*	*	*	8	80.14	20.10	12	88.75	6.62	
6	*	*	*	*	*	*	50.80	7	48.87	10.51	12	55.61	2.65
7	*	*	*	*	*	*	57.70	7	58.58	12.31	12	67.65	4.24
8	110.25+	119.20+	127.40	*	*	*	8	125.98	20.48	12	131.35	7.55	
9	101.70	104.35	106.65	*	*	*	103.45	8	99.12	15.17	12	98.87	6.11
10	*	54.45	*	49.65	58.15	*	50.00	8	57.95	4.70	12	59.32	3.76
11	*	78.15	*	70.35	*	*	74.75	8	80.33	12.85	12	79.87	3.70
12	59.50+	*	*	*	*	*	6	81.43	13.00	11	81.00	4.81	
13	36.65/ *	*	*	*	*	*	7	37.99	5.80	12	38.72	1.77	
14	* / 31.45+	*	*	*	*	*	7	53.15	8.69	12	52.70	4.71	
15	*	22.45	*	*	*	*	24.50	5	23.63	3.39	12	23.64	1.35
16	*	33.10	*	30.00	31.90	*	30.80	3	33.80	1.67	12	32.06	1.55
17	*	36.95	*	33.30	39.30	*	35.25	4	41.77	4.70	12	40.71	2.08
18	*	90.70+	*	76.35+	*	*	103.70+	6	108.65	17.31	12	100.06	6.86
19	*	60.90	*	*	*	*	55.30	4	60.06	4.40	12	66.15	7.83
20	*	67.40	*	*	*	*	59.60	4	65.14	6.39	12	69.34	6.74
21	*	83.50	*	*	*	*	75.25	4	84.50	7.98	12	87.60	6.61
22	27.15 / 26.75	31.00 / 29.50	33.10 / 33.55	*	*	29.20	28.90	7	38.48	7.86	11	32.12	5.93
23	74.90	88.65	82.80	*	*	*	86.00	7	71.16	7.98	11	75.96	6.34
24	131.35	137.10	143.20	*	*	*	125.15	8	138.88	14.04	11	132.01	10.24
25	*	63.50	*	60.60	67.45	*	59.40	5	73.39	8.19	12	69.08	3.93
26	*	21.50	*	22.60	27.40	*	23.40	5	25.27	5.86	12	22.50	2.65
27	*	20.85	*	21.35	25.10	*	20.00	4	23.70	6.16	12	18.13	4.62
28	*	20.35	*	21.60	*	*	23.25	5	26.67	3.06	12	26.52	1.66
29	*	53.25	*	47.35	*	*	50.45	4	70.55	8.47	12	59.90	4.40
30	*	80.10	*	68.50	*	*	80.05	5	96.96	17.21	12	84.33	5.49
31	*	103.45	*	84.55	*	*	98.80	5	114.15	21.64	12	103.45	7.35
32	59.25+ / 66.20+	*	*	*	*	*	7	77.34	22.73	11	76.72	5.79	
33	128.40+	*	*	*	*	*	7	142.59	39.59	11	149.85	12.26	
34	60.15/ *	*	*	*	*	*	8	58.75	12.55	12	46.61	2.49	
35	41.15 / 40.75	*	*	*	*	*	7	34.10	8.89	12	37.14	2.57	
36	21.40 / 19.40	19.45 / 20.35	17.45 / 18.65	*	*	24.00 / 22.10	7	22.66	5.02	11	29.29	4.10	
37	25.25 / 24.50	29.55 / 28.20	29.65 / 30.85	*	*	27.80 / 27.75	7	39.12	7.35	11	33.62	5.18	
38	84.0 / 85.0	94.0 / 92.0	93.5 / 94.5	*	*	91.0 / 92.0	7	149.93	43.57	11	103.86	20.32	
39	*	121	*	*	*	*	122	8	124.38	5.10	12	121.00	3.30
40	*	61.40	*	56.60	65.75	*	54.65	4	67.95	5.92	12	68.14	4.06
41	*	77.10	*	73.15	*	*	70.20	4	76.66	5.88	12	75.80	4.28

Appendix 2

Upper teeth measurements of *C. (N.) praenipponicus*, *C. (R.) unicolor*, and *C. (S.) nippon* (in mm). The measurements for IGPS-61700 and IGPS-65504 are taken from Shikama (1949). For measured parts see Fig. 4. 42: length of upper 2nd premolar, 43: width of upper 2nd premolar, 44: length of upper 3rd premolar, 45: width of upper 3rd premolar, 46: length of upper 4th premolar, 47: width of upper 4th premolar, 48: length of upper 1st molar, 49: width of upper 1st molar, 50: length of upper 2nd molar, 51: width of upper 2nd molar, 52: length of upper 3rd molar, 53: width of upper 3rd premolar.

	<i>C. (N.) praenipponicus</i>						<i>C. (R.) unicolor</i>			<i>C. (S.) nippon</i>		
	KMSY-2034Ma	IGPS-61700	IGPS-65504	IGPS-65510	IGPS-77077	n	Mean	S.D.	n	Mean	S.D.	
42	12.45 / *	*	13.4	11.15 / *	*/12.00	5	11.93	2.18	11	13.00	0.60	
43	11.15 / *	*	12.4	9.75 / *	*/9.80	5	9.67	2.43	11	10.73	1.69	
44	11.55 / 11.35	13.0	12.4	*	*/11.65	5	12.48	2.10	11	13.01	0.73	
45	12.80 / 13.20	14.8	12.7	*	*/11.50	5	10.41	2.72	11	12.07	1.76	
46	11.15 / *	12.0	11.4	12.40 / *	11.25 / 11.50	6	12.33	1.94	12	12.67	1.29	
47	12.80 / *	15.0	13.8	16.65 / *	10.45 / 11.10	6	10.23	2.38	12	11.59	1.62	
48	14.95 / 14.85	16.0	15.4	15.80 / *	17.90 / 18.05	6	15.88	1.64	12	16.70	2.00	
49	13.95 / 14.70	18.0	16.3	16.60 / *	13.65 / 13.70	6	12.48	2.85	12	13.59	1.40	
50	17.25 / 17.20	19.0	17.9	18.65 / *	20.00 / 19.90	6	19.13	2.03	12	19.22	1.48	
51	15.20 / 15.15	18.5	17.8	16.55 / *	12.45 / 12.50	6	13.39	2.70	12	13.85	1.98	
52	*	18.5	19.0	19.40 / 19.40	17.80 / 17.45	6	18.03	2.24	12	19.16	1.44	
53	*	18.5	17.4	15.10 / 15.10	11.40 / 10.75	6	12.16	2.88	12	13.02	1.92	

Appendix 3

Antler measurements of *C. (N.) praenipponicus*, *C. (R.) unicolor*, and *C. (S.) nippon* (in mm or degrees). For measured parts see Fig. 4. 54: antero-posterior diameter of burr, 55: height of 1st fork, 56: minimum circumference of beam below 1st fork, 57: height of upper margin of 1st fork, 58: angle of 1st fork, 59: minimum circumference of beam above 1st fork, 60: angle of 2nd fork, 61: angle of pedicle diversion, 62: circumference of burr, 63: transverse diameter of burr, 64: maximum distance between burrs, 65: minimum distance between burrs, 66: minimum diameter of beam below 1st fork, 67: minimum diameter of beam above 1st fork, 68: distance between lower margin of burr and point of 1st tine, 69: distance between lower margin of burr and point of 2nd tine, 70: maximum length of antler.

	<i>C. (N.) praenipponicus</i>					<i>C. (R.) unicolor</i>			<i>C. (S.) nippon</i>		
	KMSY-2034Ma	IGPS-58804	IGPS-58805	IGPS-61693	Hikita specimen	n	Mean	S.D.	n	Mean	S.D.
54	41.75 / 43.25	45.40 / 44.05	39.65 / *	45.50 / 46.15	41.95 / 42.30	6	56.93	7.46	9	55.05	4.15
55	60.60 / 60.25	70.60 / 66.20	62.60 / *	37.40 / 38.10	78.60 / 75.70	6	35.89	16.15	9	28.64	10.08
56	88.5 / 91.0	96.0 / 94.5	90.5 / *	101.5 / 102.5	89.0 / 86.5	6	141.83	26.24	9	124.06	13.64
57	100.55 / 94.25	100.10 / 96.05	101.45 / *	73.90 / 73.05	108.40 / 100.95	6	73.79	22.31	9	67.48	14.20
58	66 / 74	80 / 81	70 / *	76 / 82	*/72	6	66.17	11.18	9	78.00	10.74
59	81.0 / *	85.0 / *	90.0 / *	84.0 / 83.0	78.0 / 80.5	6	97.17	24.19	9	88.22	12.37
60	*	67 / *	*	*	78 / 82	6	65.83	14.48	9	71.33	8.67
61	70	84	*	*	78	8	58.38	12.85	12	53.17	13.81
62	134.0 / 131.0+	146.5 / 142.0	122.0+ / *	149.5 / 153.0	131.0 / 131.0	6	176.33	23.21	9	167.40	11.10
63	42.20 / 41.05	46.10 / 45.40	*	48.30 / 49.30	40.95 / 41.95	6	54.93	7.60	9	51.23	3.66
64	145.25	154.60	*	159.20	142.40	6	155.40	9.52	9	155.73	8.62
65	67.05	84.65	*	73.45	70.15	6	55.76	6.75	9	63.06	8.21
66	23.05 / 23.50	25.15 / 25.25	25.95 / *	26.45 / 24.65	24.55 / 25.60	6	36.48	10.93	9	32.67	5.60
67	22.70 / *	26.55 / *	24.55 / *	24.60 / 24.20	24.15 / 24.45	6	29.28	7.90	9	26.51	4.20
68	165.00+ / 142.45+	199.15+ / *	103.00+ / *	137.80+ / 208.45	*/221.40	6	193.62	41.91	9	209.36	27.78
69	*	414.70+ / *	*	*	358.95 / 372.40	6	286.32	79.05	9	341.29	52.99
70	*	559.0+ / *	*269.50+ / 422.90+	474.00 / 451.60+		6	338.66	76.83	9	549.26	79.79

Appendix 4

Mandible measurements of *C. (N.) praenipponicus*, *C. (R.) unicolor*, and *C. (S.) nippon* (in mm). For measured parts see Fig. 4. 71: length from posterior end of angle to anterior end of mandible, 72: length from anterior end of alveolus of lower 2nd premolar to posterior end of alveolus of 4th incisor, 73: length of cheek teeth row, 74: height of mandible in front of lower 2nd premolar, 75: length of lower premolar row, 76: length of lower molar row, 77: height of mandible behind lower 2nd molar, 78: height of mandible behind lower 3rd molar.

	<i>C. (N.) praenipponicus</i>					<i>C. (R.) unicolor</i>			<i>C. (S.) nippon</i>		
	KMSY-2034Ma	KMSY-131Ma	IGPS-58804	IGPS-65505	IGPS-77077	n	Mean	S.D.	n	Mean	S.D.
71	*	*	130.60+ / *	* / 110.60+	165.90+ / 112.20+	1	285.85	0	11	225.00	13.69
72	*	*	54.45 / *	*	53.55 / *	1	73.80	0	11	57.86	4.57
73	*	*	*	*	99.35 / *	1	121.45	0	11	99.45	6.13
74	*	*	22.80 / *	*	23.05 / *	1	29.45	0	11	22.33	2.06
75	*	*	37.40 / *	*	39.95 / *	1	48.45	0	11	39.05	3.09
76	*	56.10 / *	*	* / 65.05	62.15 / *	1	71.50	0	11	60.88	4.41
77	30.70 / *	29.95 / *	*	* / 33.90	33.80 / 32.80	1	33.46	0	11	33.12	2.37
78	*	*	*	* / 37.35	* / 35.65	1	39.55	0	11	36.57	2.70

Appendix 5

Lower teeth measurements of *C. (N.) praenipponicus*, *C. (R.) unicolor*, and *C. (S.) nippon* (in mm). For measured parts see Fig. 4. 79: length of lower 2nd premolar, 80: width of lower 2nd premolar, 81: length of lower 3rd premolar, 82: width of lower 3rd premolar, 83: length of lower 4th premolar, 84: width of lower 4th premolar, 85: length of lower 1st molar, 86: width of lower 1st molar, 87: length of lower 2nd molar, 88: width of lower 2nd molar, 89: length of lower 3rd molar, 90: width of lower 3rd premolar.

	<i>C. (N.) praenipponicus</i>					<i>C. (R.) unicolor</i>			<i>C. (S.) nippon</i>		
	KMSY-2034Ma	KMSY-131Ma	IGPS-58804	IGPS-65505	IGPS-77077	n	Mean	S.D.	n	Mean	S.D.
79	*	*	8.30 / *	*	6.50 / *	1	6.22	0	11	7.25	0.41
80	*	*	5.70 / *	*	4.20 / *	1	6.30	0	11	4.97	0.53
81	*	*	13.30 / *	*	13.85 / *	1	18.15	0	11	13.85	0.90
82	*	*	12.00 / *	*	5.95 / *	1	8.15	0	11	6.78	0.53
83	*	12.90 / *	14.45 / *	*	15.65 / *	1	20.15	0	11	15.06	1.39
84	*	7.65 / *	9.20 / *	*	7.70 / *	1	9.90	0	11	8.07	0.78
85	*	14.45 / *	14.70 / *	* / 15.90	16.85 / *	1	19.60	0	11	16.93	1.50
86	*	9.25 / *	10.30 / *	* / 11.00	9.05 / *	1	12.20	0	11	9.26	0.99
87	16.75 / *	18.40 / *	*	* / 19.90	20.70 / *	1	22.35	0	11	19.85	1.63
88	10.20 / *	9.10 / *	*	* / 11.85	8.80 / *	1	12.90	0	11	9.43	1.43
89	9.45+ / *	22.60 / *	*	* / 26.35	22.70 / 23.30	1	29.10	0	11	25.17	2.05
90	9.45+ / *	9.45 / *	*	* / 11.55	7.60 / 7.70	1	11.95	0	11	8.84	1.64

Appendix 6

Vertebrae and pelvis measurements of *C. (N.) praenipponicus*, *C. (R.) unicolor*, and *C. (S.) nippon* (in mm). For measured parts see Fig. 4. 91: maximum width of 2nd lumbar vertebra, 92: height of head of 2nd lumbar vertebra, 93: width of head of 2nd lumbar vertebra, 94: height of 2nd lumbar vertebral fossa, 95: width of 2nd lumbar vertebral foramen, 96: width of 2nd lumbar vertebral fossa, 97: length of 2nd lumbar vertebral body, 98: maximum width of 3rd lumbar vertebra, 99: height of head of 3rd lumbar vertebra, 100: width of head of 3rd lumbar vertebra, 101: height of 3rd lumbar vertebral fossa, 102: width of 3rd lumbar vertebral foramen, 103: width of 3rd lumbar vertebral fossa, 104: length of 3rd lumbar vertebral body, 105: maximum width of 4th lumbar vertebra, 106: height of head of 4th lumbar vertebra, 107: width of head of 4th lumbar vertebra, 108: height of 4th lumbar vertebral fossa, 109: width of 4th lumbar vertebral foramen, 110: width of 4th lumbar vertebral fossa, 111: length of 4th lumbar vertebral body, 112: maximum width of 6th lumbar vertebra, 113: height of head of 6th lumbar vertebra, 114: width of head of 6th lumbar vertebra, 115: height of 6th lumbar vertebral fossa, 116: width of 6th lumbar vertebral foramen, 117: width of 6th lumbar vertebral fossa, 118: length of 6th lumbar vertebral body, 119: length of auricular surface, 120: sacral vertebral length from cranial end of head to caudal margin of apex, 121: sacral vertebral width at caudal end, 122: maximum height of sacral vertebra, 123: height of head of sacral vertebra, 124: maximum width of sacral vertebra, 125: width of head of sacral vertebra, 126: length of 1st caudal vertebral body, 127: width of head of 1st caudal vertebra, 128: width of 1st caudal vertebral fossa, 129: maximum width of 1st caudal vertebra, 130: maximum length of one half, 131: maximum width across lateral angle, 132: maximum width across acetabular, 133: minimum width of iliac body, 134: length of pelvic symphysis, 135: major axis of obturator foramen, 136: minor axis of obturator foramen, 137: maximum width across ischial tuberosity, 138: acetabular width, 139: maximum inner length of acetabular fossa, 140: width of acetabular notch.

	<i>C. (N.) praenipponicus</i>				<i>C. (R.) unicolor</i>			<i>C. (S.) nippon</i>		
	KMSY-2034Ma	IGPS-65524	IGPS-65525	IGPS-65537	n	Mean	S.D.	n	Mean	S.D.
91	34.65+	*	*	*	* 1	168.00	0 8	120.74	10.19	
92	*	*	*	*	* 1	27.60	0 8	21.58	1.71	
93	23.35+	*	*	*	* 1	29.45	0 8	27.90	1.52	
94	18.55	*	*	*	* 1	26.35	0 8	21.68	1.99	
95	16.80	*	*	*	* 1	21.90	0 8	15.40	1.80	
96	27.75	*	*	*	* 1	33.60	0 8	32.21	2.57	
97	37.35+	*	*	*	* 1	48.35	0 8	42.11	3.70	
98	60.75+	*	*	*	* 1	185.00	0 9	131.26	10.41	
99	18.75	*	*	*	* 1	28.90	0 9	22.72	1.59	
100	24.20	*	*	*	* 1	30.25	0 9	27.92	1.57	
101	18.05	*	*	*	* 1	25.50	0 9	21.16	2.04	
102	19.90	*	*	*	* 1	17.85	0 9	15.94	1.67	
103	28.90	*	*	*	* 1	25.70	0 9	32.23	2.33	
104	40.25	*	*	*	* 1	47.60	0 9	40.90	4.42	
105	40.80+	*	*	*	* 1	191.85	0 9	139.94	12.10	
106	19.90	*	*	*	* 1	28.00	0 9	22.51	1.84	
107	26.30	*	*	*	* 1	31.55	0 9	28.30	1.64	
108	18.45	*	*	*	* 1	25.50	0 8	20.19	1.82	
109	*	*	*	*	* 1	27.15	0 8	17.88	2.11	
110	28.90+	*	*	*	* 1	38.75	0 9	34.39	2.61	
111	39.90	*	*	*	* 1	49.05	0 9	41.98	4.54	
112	64.25+	*	50.50+	*	* 1	160.90	0 9	131.43	9.72	
113	19.65	*	17.75	*	* 1	23.30	0 9	20.21	1.59	
114	28.95	*	30.80	*	* 1	39.65	0 10	34.27	1.83	
115	*	*	17.45	*	* 1	21.25	0 10	19.43	1.57	
116	*	*	24.10	*	* 1	34.40	0 10	24.29	2.44	
117	36.80	*	37.55	*	* 1	49.45	0 10	46.11	3.02	
118	37.05	*	37.75	*	* 1	44.40	0 10	38.43	3.51	
119	* / 43.80	38.55 / 37.40	* / 44.00	*	* 1	56.75	0 9	48.61	3.94	
120	95.40	39.35+	29.90+	*	* 1	141.70	0 9	109.74	19.60	
121	27.30+	*	*	*	* 1	41.50	0 9	34.28	4.69	
122	43.00+	25.05+	*	*	* 1	73.25	0 9	58.85	10.23	
123	*	15.85	15.70	*	* 1	18.25	0 9	17.64	1.48	
124	75.65+	90.10+	62.65+	*	* 1	129.45	0 9	99.53	7.59	
125	36.15	37.25	30.45+	*	* 1	45.95	0 9	43.63	5.27	
126	26.25+	*	*	*	* 1	35.90	0 9	29.96	3.89	
127	16.25	*	*	*	* 1	15.50	0 9	16.42	3.07	
128	*	*	*	*	* 1	18.95	0 9	13.66	1.83	
129	24.60+	*	*	*	* 1	45.30	0 9	34.31	4.88	
130	189.00+ / 193.00+	*	*	204.90+ / *	* 1	351.25	0 9	279.39	23.30	
131	133.00+	*	*	*	* 1	233.65	0 9	181.69	15.65	
132	117.95	*	*	*	* 1	154.25	0 9	125.84	7.74	
133	12.35 / 12.05	*	*	10.15 / *	* 1	14.10	0 9	12.26	1.53	
134	72.70	*	*	*	* 1	132.85	0 9	93.47	4.83	
135	59.45 / *	*	*	*	* 1	85.80	0 9	57.03	7.18	
136	31.60 / 31.90	*	*	*	* 1	48.35	0 9	32.34	3.58	
137	*	*	*	*	* 1	131.70	0 9	130.01	14.33	
138	36.00 / 35.40	*	*	25.70+ / *	* 1	41.35	0 9	36.18	2.01	
139	14.50 / 14.35	*	*	*	* 1	20.15	0 9	17.12	2.16	
140	7.35 / 6.85	*	*	*	* 1	3.60	0 9	4.42	0.94	

Appendix 7

Astragalus measurements of *C. (N.) praenipponicus*, *C. (R.) unicolor*, and *C. (S.) nippon* (in mm). For measured parts see Fig. 4. 141: maximum length of medial half, 142: minimum length of astragalus, 143: maximum length of lateral half, 144: width at distal end, 145: maximum depth of medial half, 146: maximum depth of lateral half.

	<i>C. (N.) praenipponicus</i>					<i>C. (R.) unicolor</i>			<i>C. (S.) nippon</i>		
	KMSY-2034Ma	IGPS-65546-1	IGPS-65546-2	IGPS-65546-3	IGPS-65546-4	n	Mean	S.D.	n	Mean	S.D.
141	*/36.40	*/40.05	40.60/*	*/39.90	39.35/*	1	53.25	0	8	42.43	3.07
142	*/30.35	*/34.00	34.85/*	*/33.35	33.70/*	1	45.80	0	8	35.66	2.47
143	*/38.15	*/42.40	44.40/*	*/43.00	42.05/*	1	55.10	0	8	46.02	2.99
144	*/25.15	*/26.95	26.30/*	*/27.55	25.90/*	1	34.25	0	8	28.88	2.10
145	*/22.40	*/24.95	25.10/*	*/25.45	23.60/*	1	31.85	0	8	28.57	4.72
146	*/20.45	*/21.75	24.50/*	*/23.95	22.70/*	1	29.70	0	8	24.67	1.29

Appendix 8

Cubo-navicular and metatarsus measurements of *C. (N.) praenipponicus*, *C. (R.) unicolor*, and *C. (S.) nippon* (in mm). For measured parts see Fig. 4. 147: maximum length of cubo-navicular, 148: maximum depth of cubo-navicular, 149: maximum width of cubo-navicular, 150: maximum width of metatarsus at proximal end, 151: minimum width of metatarsus at middle portion, 152: maximum width of metatarsus at distal end, 153: maximum length of metatarsus.

	<i>C. (N.) praenipponicus</i>				<i>C. (R.) unicolor</i>			<i>C. (S.) nippon</i>		
	KMSY-2034Ma	IGPS-65547-1	IGPS-65547-2	IGPS-65550	n	Mean	S.D.	n	Mean	S.D.
147	*/23.50	24.20/*	23.95/*	*	1	32.25	0	7	27.15	1.43
148	*/27.95	28.45/*	31.05/*	*	1	37.75	0	7	33.49	1.98
149	*/32.05	32.35/*	33.75/*	*	1	43.20	0	7	36.93	2.42
150	*/27.20	*	*	26.90/*	1	40.40	0	7	30.77	1.94
151	*/17.85	*	*	18.40/*	1	21.40	0	7	18.63	1.09
152	*/16.25+	*	*	32.35/*	1	39.90	0	7	34.28	2.61
153	*/218.00	*	*	213.80/*	1	258.95	0	7	256.79	16.35