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Cover: Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto, 1988).

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Fossil red deer *Cervus elaphus* from the sea-floor of the East China Sea off Amakusa-shimoshima Island, southwestern Kyushu, Japan

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Abstract. A skull of a fossil deer dredged from the sea-floor of the East China Sea off Ushibuka City, Kumamoto Prefecture, southwestern Kyushu, Japan is identified by the size and shape of its pedicles as the red deer *Cervus elaphus*, presently living on the Eurasian and North American continents. This is the first well-documented fossil record of red deer from Japan, although less reliable and doubtful fossil occurrences of the species have previously been reported from the Pleistocene of central Japan. A ^{14}C date of 19,780±190 yr BP was obtained for collagen fractions extracted from the fossil skull of *C. elaphus* using a Tandetron accelerator mass spectrometer. The geologic age of the fossil agrees with the accepted ^{14}C age of the Last Glacial maximum. The present finding of the fossil red deer strongly indicates that during the Last Glacial maximum the Asian continent and Kyushu were connected by a land bridge in the northern part of East China Sea.

Key words: *Cervus elaphus*, glacial period, Japan, land bridge, late Pleistocene, skull

Introduction

In 1990, a well-preserved partial skull of a fossil deer was dredged by a fisherman from a depth of about 160 m in the East China Sea off Ushibuka City, Kumamoto Prefecture, southwestern Kyushu, Japan (Figure 1). Several other fossil remains including an elephant tusk have been recovered from the sea-bottom of this area, and a number of fossil mammals such as *Palaeoloxodon naumanni* and *Elaphurus mayai* have also been dredged from other area in the East China Sea (Otsuka, 1982 ; Otsuka, 1987). The fossil deer was loaned to us for study through the courtesy of Tetsuro Tateshi in Ushibuka City. Our comparative morphological study has confirmed that the fossil specimen is referable to the red deer *Cervus elaphus* Linnaeus, presently living in Eurasia and North America (Figure 2). In East Asia, occurrences of fossil red deer are very rare, being known from the middle Pleistocene of Tingtsun in China and Tologoy in Russia (Pei *et al*., 1958 ; Vangengeim and Sher, 1971) and from the upper Pleistocene of Sjara-osso-gol, Choukoutien (Upper Cave) and Ku-hsiang-tung in China (Boule *et al*., 1928 ; Pei, 1940 ; Tokunaga and Naora, 1939). In Japan, poorly-preserved fragments of a mandible and an antler referred to the red deer have been reported from the Upper Kobiwako Group of middle Pleistocene age (Shikama, 1941) and the upper Kuzuü Formation (Shikama, 1949) of late Pleistocene age, respectively. However, these fossils are too incomplete to unequivocally identify them as *Cervus elaphus*. This paper confirms for the first time that red deer once lived in Japan and adds information about the dispersal area of *Cervus elaphus* in the Pleistocene of Eurasia.

Systematic description

Order Artiodactyla Owen, 1848
Family Cervidae Gray, 1821
Subfamily Cervinae Gray, 1821
Genus ***Cervus*** Linnaeus, 1758

Cervus elaphus Linnaeus, 1758

Figures 3, 4

Cervus canadensis Erxleben. Matsumoto, 1926, p. 35-37, pl. 12 (1), figs. 7-10 ; Boule *et al*., 1928, p. 55-57, pl. 12, figs. 2-4, pl. 13, fig. 5 ; Pei, 1940, p. 68-71, text-figs. 34-36, pl. 8, figs. 3, 4 ; Pei *et al*., 1958, p. 34-36, text-fig. 9, pl. 2, fig. 2.

Cervus elaphus Linnaeus. Tokunaga and Naora, 1934, p. 64, pl. 17, figs. 3, 5 ; Tokunaga and Naora, 1939, p. 45, 46, text-fig.

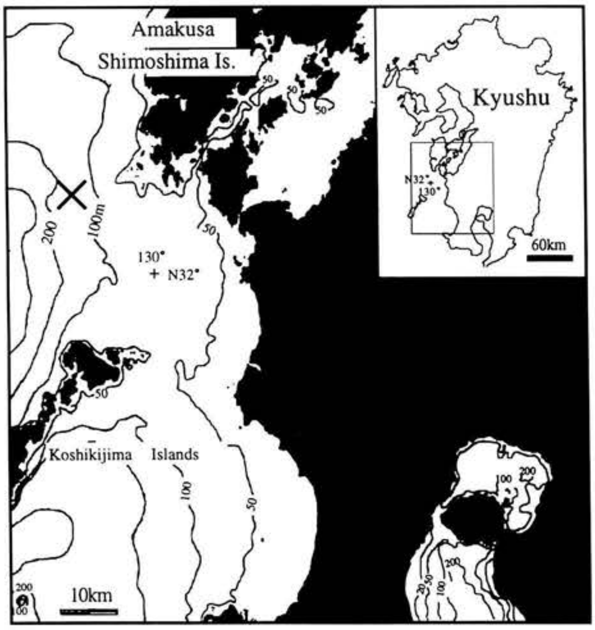


Figure 1. Map showing the collecting locality (X) of the fossil red deer skull in the East China Sea off Amakusa-shimoshima Island, southwestern Kyushu, Japan.

12, pl. 1, fig. 16, pl. 3, fig. 9.
(Synonymy includes only citations of fossil remains recovered in East Asia.)

Material studied.—A fragment of an adult male skull including the neurocranium and part of the frontals with pedicles (Ushibuka City Kaisaikan Museum, UCKM-V-1) (Figure 3); collected from the sea-floor of the East China Sea off Ushibuka City, Kumamoto Prefecture, Japan. ^{14}C date: 19,780±190 yr BP (Laboratory code number NUTA-5266)

Description.—The neurocranium is large and wide, measuring 83.6 mm in width and 73.1 mm in height. In lateral view, the angle between the parietal and frontal is 113.5°. The minimum width of the frontals is 108.5 mm. The dorsal surface of the parietal joins the posterior surface of the occipital almost perpendicularly. The interfrontal suture is somewhat protruding and notched. The sagittal suture is partly fused and is recognized as a zigzag line between the parietal bones. The supraorbital foramina are ellipsoidal in shape and located at central part of the frontals. The maximum width between the supraorbital foramina is 67.0 mm. The sulci above them are not very deep and extend obliquely and slightly upward.

The pedicles are very stout especially at their bases. They are short and in lateral view do not protrude and overhang the parietal surface. The antero-posterior diameters of the pedicles (36.5 mm on the right and 37.9 mm on the left) are a little smaller than their transverse diameters (40.0 mm on the right and 41.0 mm on the left). The angle of pedicle diversion is 66°. The minimum distance between the pedicles measures 78.1 mm. In lateral view the pedicles are slightly inclined backwards. The surface of the pedicles is marked by a number of thin vertical sulci.

The roof of the neurocranium is well developed. In dorsal view it appears clearly depressed in front of the occipital and at the level of the temporal bone. In lateral view the occipital condyles are quite convex, although the surface of the occipital is slightly convex. In posterior view the occipital condyles have blunt outlines except for their lower ends, so that each of their lateral margin becomes gradually narrower ventrally. The medial margins of the occipital condyles are parallel with each other. The dorsal margin of the foramen magnum curves downward on either side of the midline. The dorsal margin of the occipital shield is gently convex.

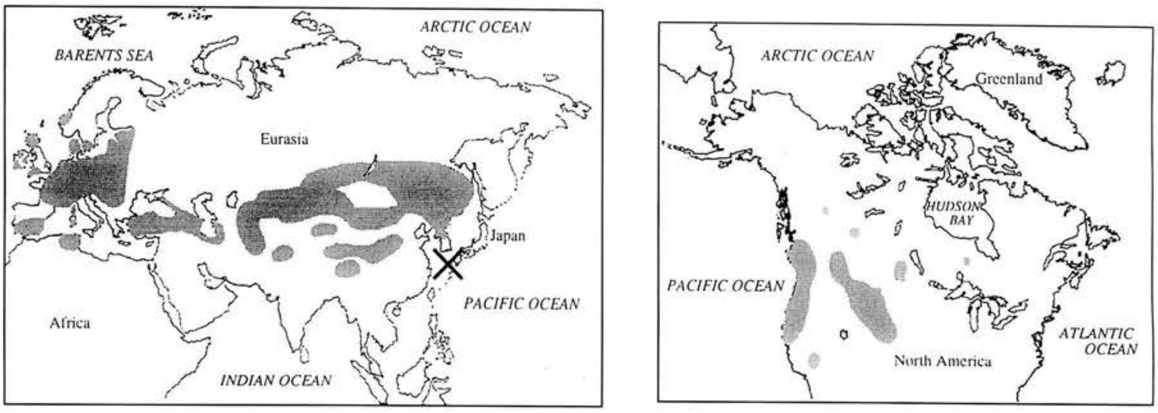
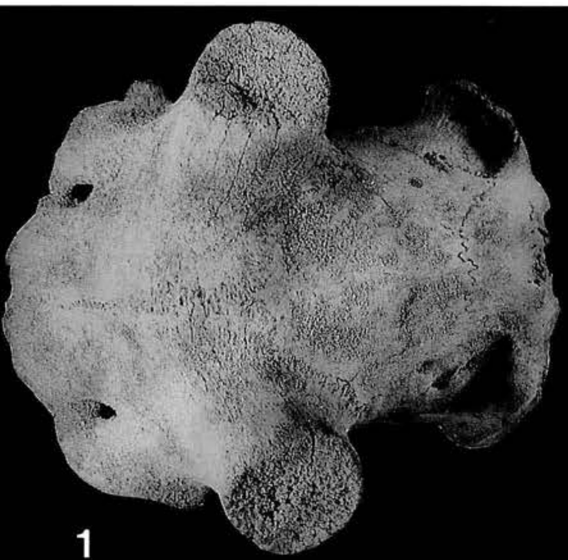


Figure 2. Map showing the distribution of the fossil and living red deer. Dotted area: the distribution of living red deer (after Whitehead, 1972). X: the locality of fossil red deer studied in this paper.

Figure 3. *Cervus elaphus* Linnaeus. Partial adult male skull consisting of the neurocranium and part of the frontals with pedicles (UCKM-V-1) from the sea-floor of the East China Sea off Ushibuka, Kyushu. **1**: Dorsal view, **2**: Ventral view, **3**: Left lateral view, **4**: Right lateral view, **5**: Frontal view, **6**: Posterior view. Scale bar equals 4 cm.



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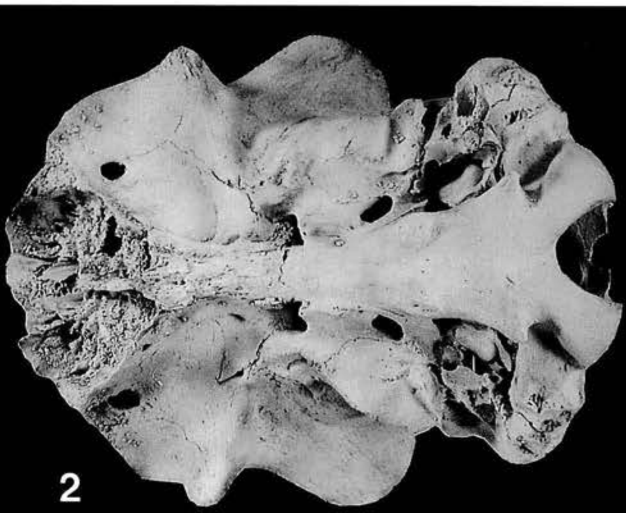

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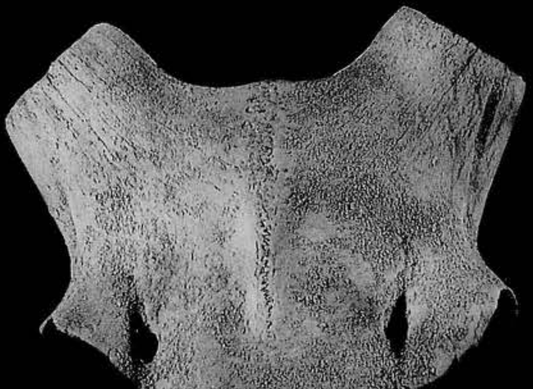

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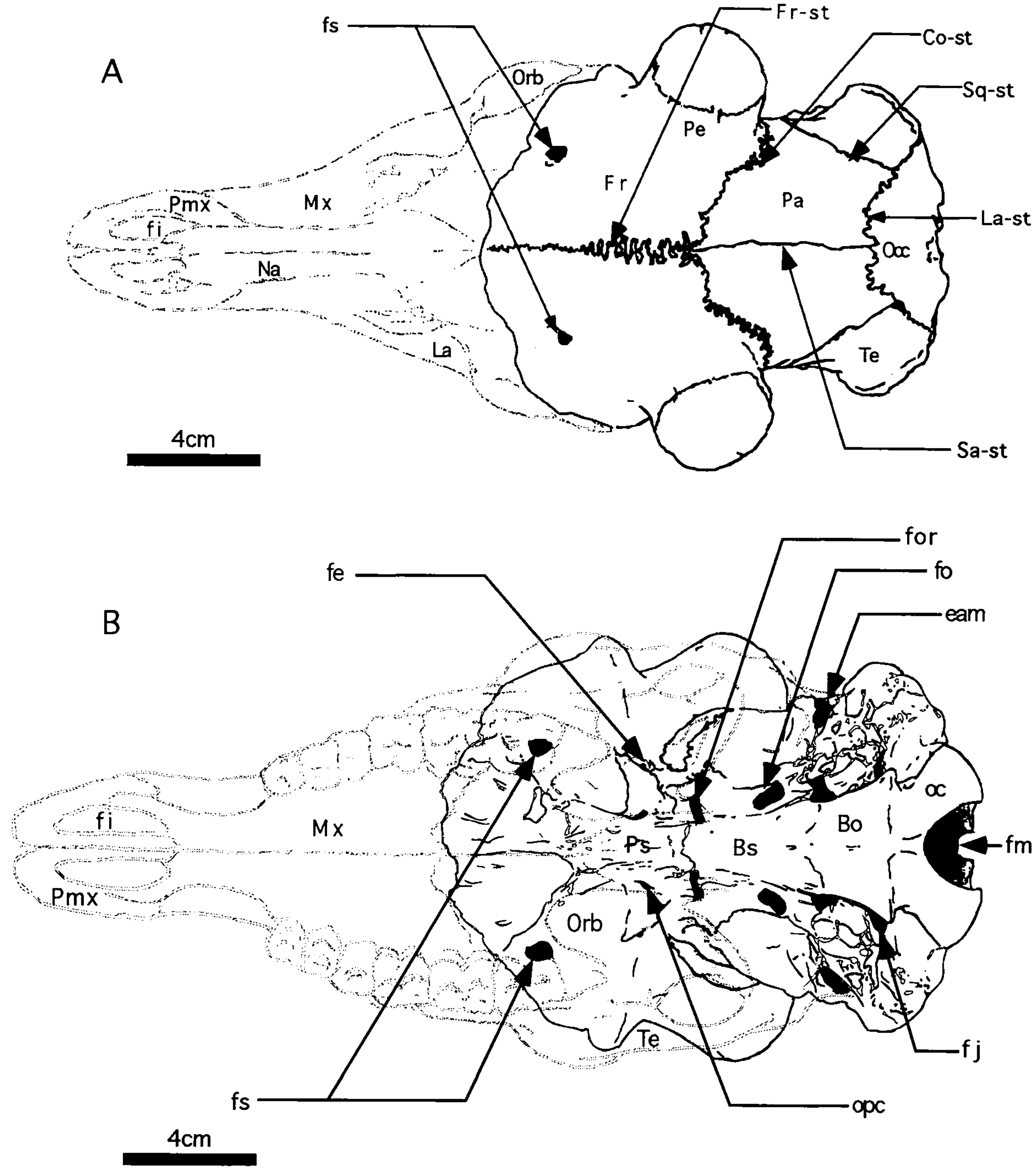

In ventral view the occipital condyles are bluntly rounded. The occipital condyles and the basioccipital are bounded by a well-developed constriction. The tubercles for the muscular insertions are well inflated. The oval foramina are elongate, ellipsoidal in shape and their anterior margins are inclined inwards.

Measurements.—Basic morphology and measurements adopted in this paper are presented in Figure 5 and Table 1.

Comparisons.—Comparisons have been made with the living and fossil Cervidae including 14 species and 24 subspecies among 5 genera. To avoid the effect of sex and age difference, we only used male adult skulls except for a female individual of *Cervus* (*Axis*) *axis* Erxleben from India housed in the Nagoya Higashiyama Zoo, Japan. Some scientists considered that the European red deer is specifically distinguishable from the Asian and North American red deer on the basis of external morphology (Whitehead, 1972; Putman, 1988). Lowe and Gardiner (1989), however, consid-

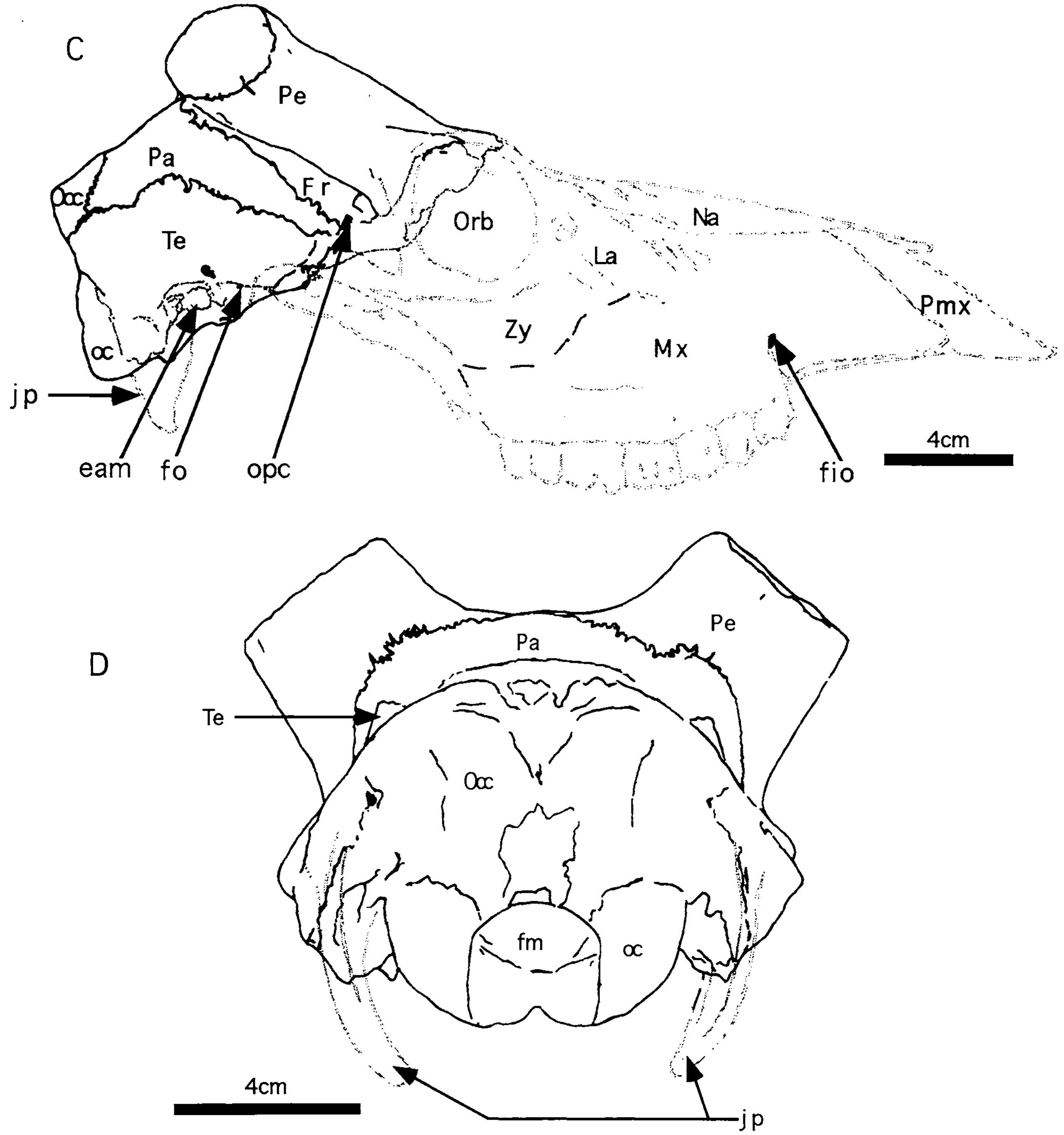

Figure 4. Restoration of the fossil skull of *Cervus elaphus*. **A** : dorsal view, **B** : ventral view, **C** : right lateral view, **D** : posterior view. Solid line : a part of skull preserved as the fossil specimen, Dotted line : broken parts. Bo = basioccipital, Bs = basisphenoid, Co-st = coronal suture, eam = external acoustic meatus, fe = ethmoidal foramen, fi = incisive foramen, fio = infraorbital foramen, fj = jugular foramen, fm = foramen magnum, fo = oval foramen, for = orbital round foramen, Fr = frontal, Fr-st = frontal suture, fs = supraorbital foramen, jp = jugular process, La = lacrimal, La-st = lambdoid suture, Mx = maxilla, Na = nasal, oc = occipital condyle, Occ = occipital, opc = optic canal, Orb = orbital, Pa = parietal, Pe = pedicle, Pmx = premaxilla, Ps = presphenoid, Sa-st = sagittal suture, Sq-st = squamosal suture, Te = temporal, Zy = zygomatic.

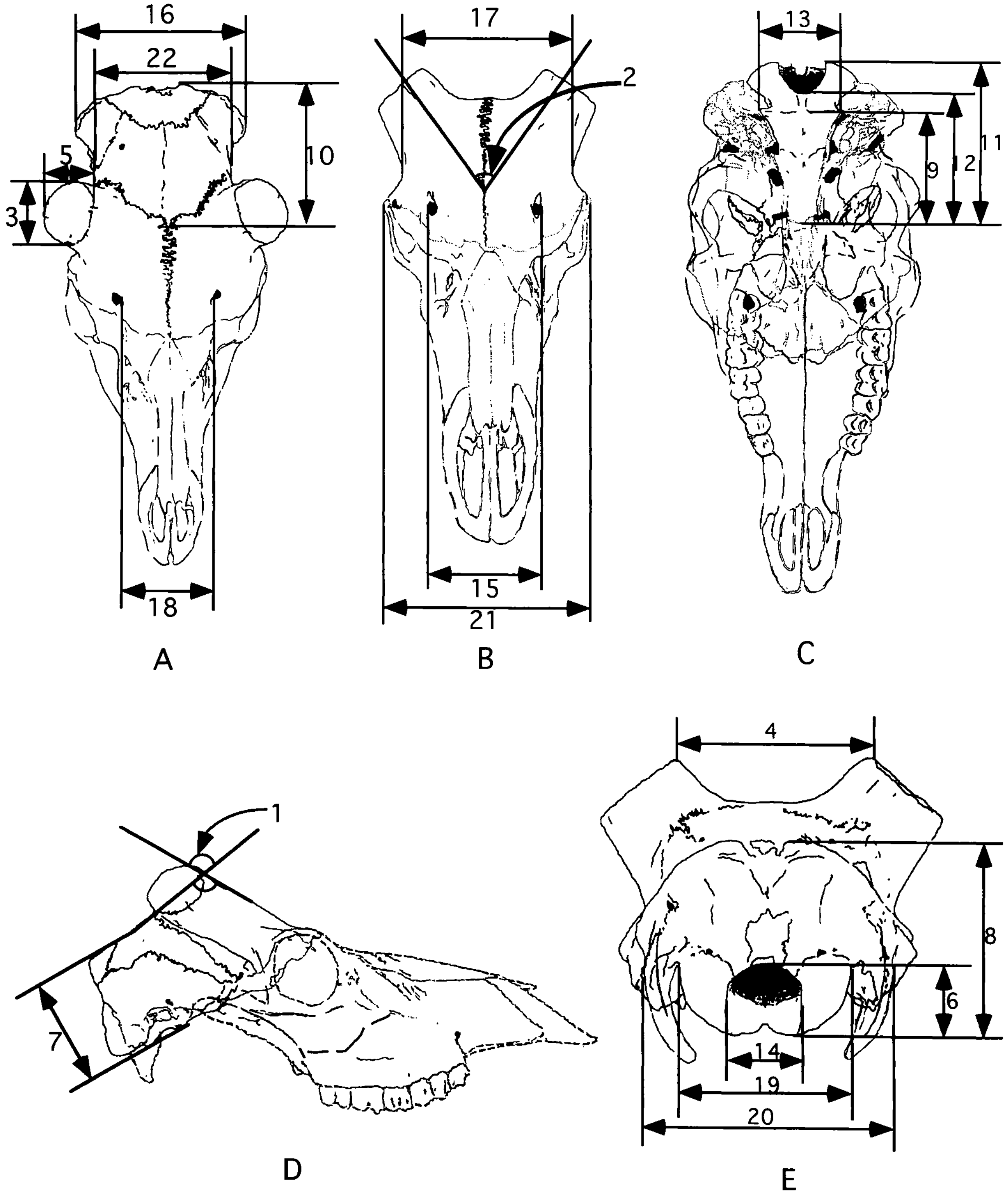

Figure 5. Location of measurements taken of the fossil skull of *Cervus elaphus*. **A**: dorsal view, **B**: frontal view, **C**: ventral view, **D**: right lateral view, **E**: posterior view. See Table 1 for explanation of the measured parts.

Table 1. Measurements of the skull of fossil red deer following Dreisch (1976). For measured parts see Figure 5. (1) ang fr-par: angle between frontal and parietal plane, (2) ang ped: angle of pedicle diversion, (3) dap ped: antero-posterior diameter of the pedicles, (4) dis ped: minimum distance between pedicles, (5) dt ped: transverse diameter of the pedicles, (6) h fm: height of the foramen magnum, (7) h neu: neurocranium height, (8) h occ: occipital height, (9) l bas: basioccipital length, (10) l i-br: inion-bregma length, (11) l max sph-occ: maximum length of sphenoid-occipital, (12) l min sph-occ: minimum length of sphenoid-occipital (=basicranial axis), (13) w bas occ: basioccipital width, (14) w fm: width of the foramen magnum, (15) w max fs: maximum width between supraorbital foramina, (16) w max neu: maximum neurocranium width, (17) w min fr: minimum frontal width, (18) w min fs: minimum width between supraorbital foramina, (19) w oc: external width of the occipital condyles, (20) w occ: occipital width, (21) w orb: skull width at the orbital level, (22) w par: neurocranium width (=parietals width).

Measured parts	in mm/degree	Proportion	Ratio
1) ang fr-par	113.5		
2) ang ped	66.0		
3) dap ped (right)	36.5	dap ped (r)/w occ	0.41
3) dap ped (left)	37.9	dap ped (l)/w occ	0.43
4) dis ped	78.1	dis ped/w occ	0.88
5) dt ped (right)	40.0	dt ped (r)/w occ	0.45
5) dt ped (left)	41.0	dt ped (l)/w occ	0.46
6) h fm	25.0	h fm/w occ	0.28
7) h neu	73.1	h neu/w occ	0.82
8) h occ	71.6	h occ/w occ	0.81
9) l bas	61.7	l bas/w occ	0.70
10) l i-br	85.9	l i-br/w occ	0.97
11) l max sph-occ	86.0	l max sph-occ/w occ	0.97
12) l min sph-occ	69.8	l min sph-occ/w occ	0.79
13) w bas occ	43.7	w bas occ/w occ	0.49
14) w fm	25.5	w fm/w occ	0.29
15) w max fs	67.0	w max fs/w occ	0.76
16) w max neu	108.2	w max neu/w occ	1.22
17) w min fr	108.5	w min fr/w occ	1.22
18) w min fs	58.0	w min fs/w occ	0.65
19) w oc	61.0	w oc/w occ	0.69
20) w occ	88.6		
21) w orb	125.2	w orb/w occ	1.41
22) w par	83.6	w par/w occ	0.94

ered that it is impossible to distinguish both groups clearly at the species level based on the skull morphology. In this study we have treated both groups of the red deer as the same species *Cervus* (*Cervus*) *elaphus* following the opinion of Lowe and Gardiner (1989).

The fossil skull UCKM-V-1 clearly preserves characters typical of the subfamily Cervinae, especially the genus *Cervus*. The shape of the basioccipital and occipital condyles closely resemble those of species of the genus *Cervus*. The ratios of external width of the occipital condyles/occipital width (0.69), occipital height/occipital width (0.81) and minimum length of sphenoid-occipital/occipital width (0.78) of the specimen fall within the known range of species of *Cervus* (0.65-0.77, 0.71-0.87, 0.70-0.84, respectively). The fossil skull is much larger than living and fossil sika deer from Japan and roe deer from Korea such as *Cervus* (*Sika*) *nippon nippon* Temminck from Kirishima of mainland Kyushu, *C.* (*S.*) *n. centralis* Kishida from Chichibu, *C.* (*S.*) *grayi katokiyomasai* Shikama and Hasegawa from the sea-floor of Bisan-seto housed in Kagoshima University, *C.* (*S.*) *pulchellus* Imaizumi from Tsushima Island, *C.* (*S.*) *n. mageshimae* Kuroda et Okada from Tanegashima Island, *C.* (*S.*) *n. yakushimae* Kuroda et Okada from Yakushima Island after Matsumoto *et al.* (1984) and *Capreolus capreolus bedfordi* Thomas from the Korean peninsula housed in the National Science Museum, Tokyo (Reg. no. M 11126), and is almost the same size as *Cervus* (*C.*) *elaphus siciliae* Pohlig from Sicily, Italy after Gliozzi *et al.* (1993) (Figure 6). However, the skull is small in comparison to the Japanese megacerid *Sinomegaceros yabei* (Shikama) from the Seto Inland Sea off Matsuyama, Japan housed in Kagoshima University, *Elaphurus davidianus* Milne-Edwards housed in the National Science Museum, Tokyo (Reg. no. M 13066) and the European red deer such as *C.* (*C.*) *e. hippelaphus* Erxleben and *C.* (*C.*) *e. acoronatus*

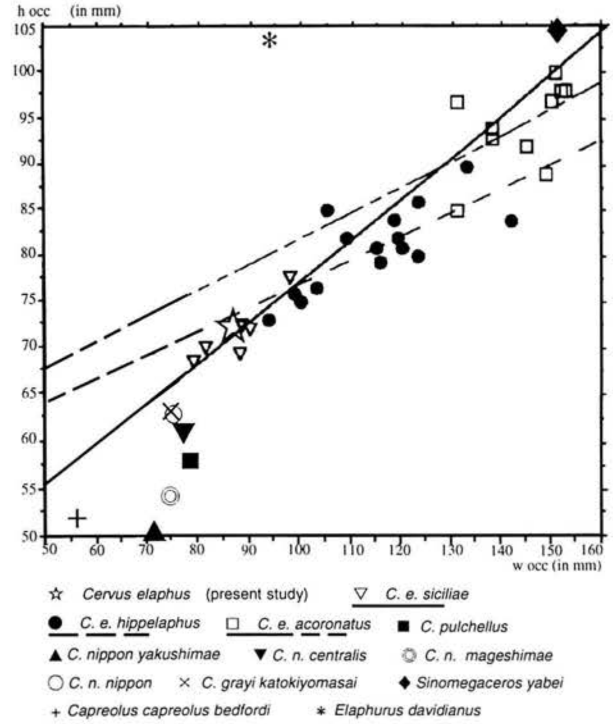

Figure 6. Scatter diagram and regression lines showing the relationship between (w occ) and (h occ) of the occipitals in *Cervus* (*Cervus*) *elaphus* studied in this paper, *C.* (*C.*) *e. siciliae*, *C.* (*C.*) *e. acoronatus*, *C.* (*C.*) *e. hippelaphus* (data after Gliozzi *et al.*, 1993), *C.* (*Sika*) *pulchellus*, *C.* (*S.*) *nippon mageshimae*, *C.* (*S.*) *n. yakushimae* (data after Matsumoto *et al.*, 1984), *C.* (*S.*) *n. nippon* from Kirishima, Japan, *C.* (*S.*) *grayi katokiyomasai* from the sea-floor of the Bisan-seto, Japan, *C.* (*S.*) *n. centralis* from Chichibu, Japan, *Sinomegaceros yabei* from the Seto Inland Sea, Japan housed in Kagoshima University, *Elaphurus davidianus* and *Capreolus capreolus bedfordi* from the Korean peninsula, Korea housed in the National Science Museum, Tokyo (Reg. no. M 13066 and M 11126, respectively).

Beninde after Gliozzi *et al.* (1993) based on the statistical data of Gliozzi *et al.* (1993) that summarize the relationships between occipital height and width (Figure 6).

The neurocranium proportion, with a width/height ratio of 1.14, seems close to those of *C.* (*C.*) *elaphus* subspecies such as *C.* (*C.*) *e. siciliae* (1.12-1.21), *C.* (*C.*) *e. acoronatus* (1.15) and *C.* (*C.*) *e. priscus* Kaup (1.12-1.20) from Mauer, Germany after Stefano and Petronio (1992). They are also comparable to *C.* (*S.*) *g. katokiyomasai* (1.06) and *C.* (*S.*) *nippon* subspecies such as *C.* (*S.*) *n. nippon* (1.23) and *C.* (*S.*) *n. centralis* (1.12), but they are quite different from other Cervinae species such as *E. davidianus* (0.97), *C.* (*Rusa*) *unicolor* Bechstein (0.97) housed in the National Science Museum, Tokyo (Reg. no. M 8932), *C.* (*A.*) *axis* (1.27), *C.* (*Nipponicervus*) *praenipponicus* Shikama (1.24-1.33) after Fossil Deer Research Group of Ichihara (1994) and *C.* (*Przewalskium*) *albirostris* Prezewalski (1.45) after Flerov (1952). In lateral view, the angle between the parietal and frontal bones (113.6°) is almost identical to *C.* (*C.*) *elaphus* subspecies like *C.* (*C.*) *e. siciliae* (111-123°), *C.* (*C.*) *e. priscus* (112-125°) and *C.* (*C.*) *e. acoronatus* (117°). It is also comparable to *C.* (*P.*) *albirostris* (107°), *C.* (*S.*) *g. katokiyomasai* (122°), *E. davidianus* (113°) and *C.* (*S.*) *nippon* subspecies such as *C.* (*S.*) *n. nippon* (110°) and *C.* (*S.*) *n. centralis* (128°), but it is definitely smaller than *C.* (*R.*) *unicolor* (142°), *Dama dama* Smith (136°) after Flerov (1952) and *C.* (*C.*) *e. canadensis* Erxleben (135°) from Canada housed in the National Science Museum (Reg. no. M 1094). The ratio of minimum width of frontal/occipital height (1.52) of the fossil skull is nearly identical to that of *C.* (*C.*) *e. siciliae* (1.50-1.52), but differs from those of *C.* (*P.*) *albirostris* (1.38), *C.* (*R.*) *unicolor* (1.30), *E. davidianus* (1.28), *C.* (*A.*) *axis* (1.29), *Capreolus capreolus bedfordi* (1.22) and *C.* (*S.*) *n. yesoensis* (Heude) (1.32-1.36) from Ashoro, Japan after Fossil Deer Research Group of Ichihara (1994) (Figure 7).

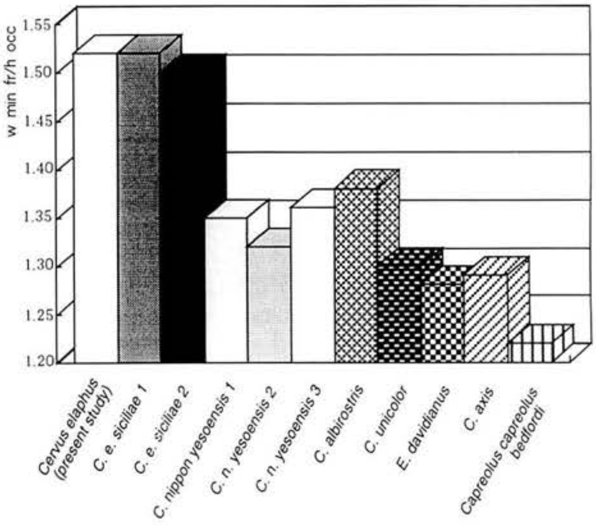

Figure 7. Bar graph showing the minimum frontal width/occipital height in *Cervus* (*Cervus*) *elaphus* (present study), *C.* (*C.*) *e. siciliae* (data after Gliozzi *et al.*, 1993), *C.* (*Sika*) *nippon yesoensis* from Ashoro, Japan (data after Fossil Deer Research Group of Ichihara, 1994), *C.* (*Rusa*) *unicolor, Elaphurus davidianus, Capreolus capreolus bedfordi* from the Korean peninsula, Korea housed in the National Science Meseum, Tokyo (Reg. nos. M 8932, M 13066 and M 11126, respectively), *Cervus* (*Przewalskium*) *albirostris* (data after Flerov, 1952) and *C.* (*Axis*) *axis* from India housed in the Nagoya Higashiyama Zoo, Japan. The ratio for fossil red deer (present study) is nearly identical with the values of *C.* (*C.*) *e. siciliae*.

The protruding of the frontal suture is not so marked as in *C.* (*C.*) *e. canadensis*. In dorsal view the posterior margin of the roof does not curve posteriorly as much as that of *E. davidianus*. In the fossil, the ratio of maximum width between supraorbital foramina/occipital width is 0.76. This value is close to the known range (0.65-0.72) of several Cervinae species except for *C.* (*R.*) *unicolor* (0.49) and *C.* (*A.*) *axis* (0.47). UCKM-V-1 differs from skulls of large-sized Cervinae like *C.* (*C.*) *e. canadensis, E. davidianus* and *C.* (*R.*) *unicolor* in lacking additional nerve foramina above each supraorbital foramen. In posterior view the occipital is subcircular in shape like *C.* (*N.*) *praenipponicus* and subspecies of *C.* (*C.*) *elaphus* and *C.* (*S.*) *nippon* while that of *C.*

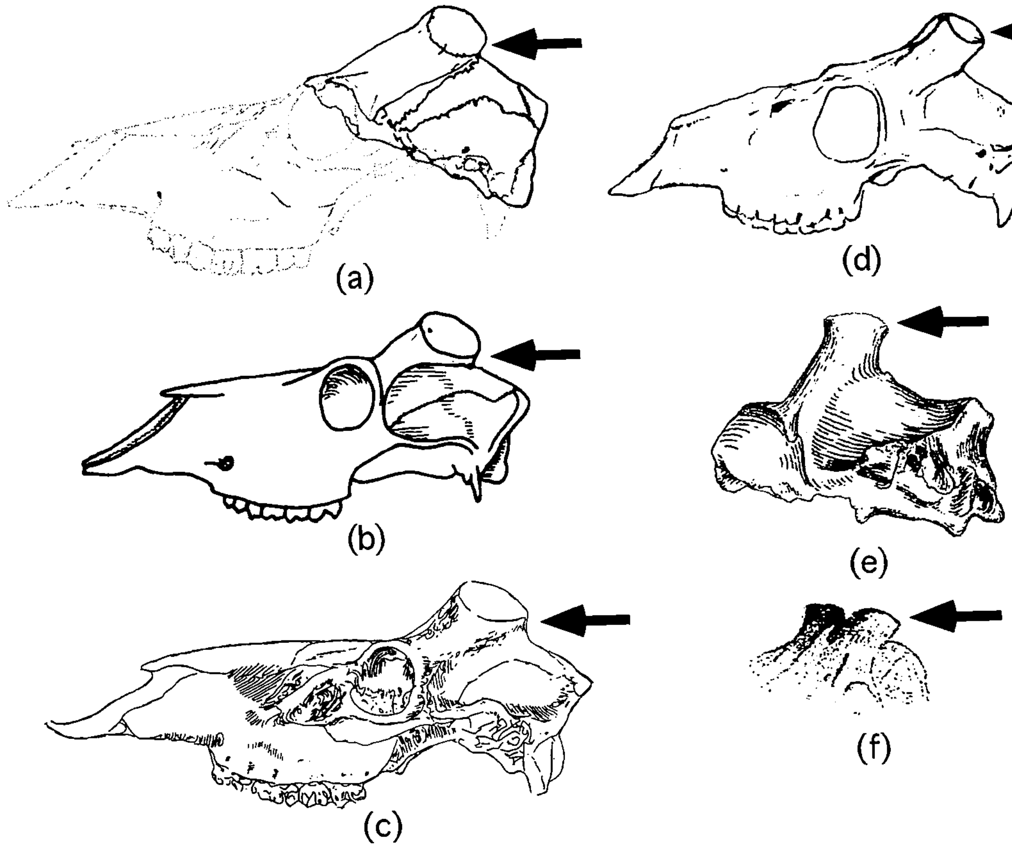

Figure 8. Diagram showing the different features of pedicles in the skulls of (**a**) *Cervus* (*Cervus*) *elaphus* studied in this paper, (**b**) *C.* (*C.*) *e. siciliae* (data after Gliozzi *et al.*, 1993), (**c**) *C.* (*C.*) *e. canadensis* (data after Flerov, 1952), (**d**) general *C.* (*Sika*) *nippon*, (**e**) *C.* (*S.*) *grayi* (data after Pei *et al.*, 1958) and (**f**) *C.* (*Rucervus*) *eldi* (data after Lydekker, 1898). Notice that *C.* (*S.*) *nippon*, *C.* (*S.*) *grayi* and *C.* (*R.*) *eldi* have pedicles that overhang the surface of the parietal.

(*S.*) *g. katokiyomasai* is trapezoidal in shape. In lateral view, the surface of the occipital is not so convex as in *D. dama*, *C.* (*S.*) *g. katokiyomasai* and *Capreolus capreolus bedfordi*. In ventral view the occipital condyles and the basioccipital are bounded by well-developed constriction unlike *Cervus* (*N.*) *praenipponicus*.

The angle of pedicle diversion (66°) is comparable to subspecies of *C.* (*C.*) *elaphus* like *C.* (*C.*) *e. siciliae* (61-78°), *C.* (*C.*) *e. yarkandensis* Blanford (60°), *C.* (*C.*) *e. affinis* Hogdson (62-70°) after Gliozzi *et al.* (1993) and *C.* (*C.*) *e. canadensis* (64°). It is also close to those of *C.* (*P.*) *albirostris* (68°), *C.* (*S.*) *g. katokiyomasai* (62°), *D. dama* (71°) and *C.* (*S.*) *nippon* subspecies such as *C.* (*S.*) *n. nippon* (63°) and *C. n. centralis* (73°). But it is greater than *C. unicolor* (48°) and *Capreolus capreolus bedfordi* (51°), and less than *E. davidianus* (78°). The ratio of minimum distance between pedicles/occipital width (0.88) is nearly identical to that of *Cervus* (*C.*) *elaphus siciliae* (0.89-0.90), but is different from other Cervidae species such as *C.* (*C.*) *e. canadensis* (0.61), *C.* (*P.*) *albirotris* (0.52), *C.* (*S.*) *g. katokiyomasai* (0.80), *C.* (*R.*) *unicolor* (0.73), *E. davidianus* (1.03) and *Capreolus capreolus bedfordi* (0.54). The pedicles are not flat transversely as seen in *Cervus* (*N.*) *praenipponicus* collected from the Osaka Group. In lateral view the pedicles on the fossil skull are not inclined backwards as much as they are in *C.* (*S.*) *n. centralis*, *C.* (*N.*) *praenipponicus* and *C.* (*R.*) *unicolor*. In addition, they are considerably shorter and stouter like *C.* (*C.*) *e. siciliae* and *C.* (*C.*) *e. canadensis* after Flerov (1952), and do not overhang the parietal surface as seen in *C.* (*Rucervus*) *eldi* Beevan after Lydekker (1898), *C.* (*S.*) *grayi* Zdansky from Tingtsun, China after Pei *et al.* (1958) and subspecies of *C.* (*S.*) *nippon* (Figure 8).

Based on these comparisons, we conclude that the fossil skull most closely resembles the red deer *Cervus* (*Cervus*) *elaphus* Linnaeus and therefore we assign it to that species.

Remarks.—The small size of the fossil specimen may justify recognition of a new subspecies endemic to Japan in the same way that the fossil deer *Cervus elaphus siciliae* Pohlig has been distinguished from Pleistocene deposits in the Mediterranean Sea (Gliozzi *et al.*, 1993). The proposal of a new subspecies is, however, postponed until additional well-preserved specimens are discovered. The fossil specimen has undergone some degree of alteration and is dark brown in color. The surface of the fossil is coated with well-rounded and well-sorted quartz grains of sand dune origin. We can infer from its good state of preservation that this fossil was not transported by a river system from the Asian continent, but was probably buried near the site of the animal's death.

Discussion

Recent paleoceanographic researches suggested that Japan had lost its connection with Asia, except for the land bridge between Hokkaido and Sakhalin, in the last glacial period (Oba *et al.*, 1984 ; Oba, 1984). From a paleobiogeographic point of view, it is also suggested that land mammals could not migrate from the Korean peninsula to Japan via the Tsushima Strait in the late Pleistocene, although they could have migrated to Honshu via Hokkaido from Sakhalin (Kamei, Kawamura and Taruno, 1988 ; Kamei, Taruno and Kawamura, 1988 ; Kawamura, 1982 ; Kawamura *et al.*, 1989, etc.).

In order to estimate the geologic age of the fossil red deer, we have conducted ^{14}C dating, with a Tandetron accelerator mass spectrometer (AMS) at Nagoya University, on carbon from collagen fractions extracted from a part of fossil skull of *C. elaphus*. The ^{14}C age of 19,780±190 yr BP was obtained for the fossil red deer from the sea-floor of the East China Sea. The geologic age of the fossil agrees with the accepted ^{14}C age (around 18,000 yr BP) of the Last Glacial maximum. The present finding of the fossil red deer strongly indicates that during the Last Glacial maximum the Asian continent and Kyushu were connected by a land bridge in the northern part of East China Sea.

The red deer *Cervus elaphus* first appeared in the early Middle Pleistocene of Europe (Kurtén, 1968). During the Middle to Late Pleistocene it dispersed throughout the mid-latitudinal zone of the Eurasian continent (Geist, 1971). The fossil occurrence of red deer from the East China Sea off Ushibuka City, western Kyushu, indicates the migration of this species to Japan at the Last Glacial period. During the Pleistocene, this widespread species evolved into a number of subspecies that today exhibit an adaptive response to regional environmental conditions on both the Eurasian and North American continents (Putman, 1988).

It has been shown that the living red deer *Cervus elaphus* and the sika deer *Cervus nippon* can hybridize in the natural state in the sympatric zones of the eastern Asian continent despite their differences in body size (Mirol'ubov, 1949, etc.). A sika-like deer first appeared in the early Pleistocene of the Asian continent and seems to have been ancestral to *Cervus elaphus* (Geist, 1971). Though dispersal and speciation processes of these species remain unsolved, future molecular, morphologic and palaeontologic studies will clarify the phylogenetic relationship between the red deer and sika deer.

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References cited

Boule, M., Breuil, H., Licent, E. and Teilhard de Chardin, P., 1928 : Le Paléolithique de la Chine. *Archives de l' Institut de paléontologie humaine : Mémoire*, vol. 4, p. 1-138. (*in French*)

Driesch, A., 1976 : A guide to the measurement of animal bones from archaeological sites. *Peabody Museum of Harvard University, Massachusetts*, p. 27-57.

Flerov, C.C., 1952 : *Musk deer and deer, Fauna of U.S.S.R.*, vol. 1, no. 2, 257 p. Academic Science of U.S.S.R. (English translation U.S. Dept of Commerce), Washington, D.C.

Fossil Deer Research Group of Ichihara, 1994 : Morphological study on *Cervus* (*Nipponicervus*) *praenipponicus* Shikama from the Upper Pleistocene in the northern part of Boso Peninsula. *Earth Science*, vol. 48, no. 3, p. 181-207. (*in Japanese*)

Geist, V., 1971 : The relation of social evolution and dispersal in ungulates during the Pleistocene, with emphasis on the Old World deer and the genus *Bison*. *Quaternary Research*, vol. 1, p. 283-315.

Gliozzi, E., Malatesta, A. and Scalone, E., 1993 : Revision of *Cervus elaphus siciliae* Pohlig, 1893, late Pleistocene endemic deer of the Siculo-Maltese District. *Geologica Romana*, vol. 29, p. 307-353.

Kamei, T., Kawamura, Y. and Taruno, H., 1988 : Mammalian stratigraphy of the late Neogene and Quaternary in the Japanese Island. *Memoirs of the Geological Society of Japan*, vol. 30, p. 181-204. (*in Japanese*)

Kamei, T., Taruno, H. and Kawamura, Y., 1988 : Implication of mammal fauna for the Quaternary geohistory of the Japanese Islands. *Quaternary Research*, vol. 26, p. 293-303. (*in Japanese*)

Kawamura, Y., 1982 : Biogeographical aspects of the Quaternary mammals of Japan. *Mammalian Science*, vol. 43/44, p. 99-130. (*in Japanese*)

Kawamura, Y., Kamei, T. and Taruno, H., 1989 : Middle and late Pleistocene mammalian faunas in Japan. *Quaternary Research*, vol. 28, p. 317-326. (*in Japanese*)

Kurtén, B., 1968 : *Pleistocene Mammals of Europe*, 317 p. Weidenfeld and Nicolson, London.

Lowe, V.P.W. and Gardiner, A.S., 1989 : Are the new and old world wapitis (*Cervus canadensis*) cospecific with red deer (*Cervus elaphus*) ? *Journal of Zoology, Society of London*, vol. 218, p. 51-58.

Lydekker, R., 1898 : *The deer of all lands*, 329 p. Rowland Ward, London.

Matsumoto, H., 1926: On some fossil cervids from Shantung, China. *Science Reports of the Tohoku University. 2nd Series*, vol. 10, no. 2, p. 27-37, pls. 12-15.

Matsumoto, M., Nishinakagawa, H. and Otsuka, J., 1984: Morphometrical study on the skull of *Cervus pulchellus, Cervus nippon mageshimae* and *Cervus nippon yakushimae*. *Journal of the Mammalogical Society of Japan*, vol. 10, no. 1, p. 41-53. (*In Japanese*)

Mirol'ubov, I.I., 1949: Gibridizacija pjatnistogo olenja s izjubrom [The hybridization between sika and iz'ubra red deer]. *Karakulevodstvo i zverovodstvo*, p. 74-75. (*in Russian*)

Oba, T., 1984: The oxygen and carbon isotopes. *Earth Monthly*, vol. 6, p. 558-566. (*in Japanese*)

Oba, T., Omura, A., Kato, M., Kitazato, H., Koizumi, I., Sakai, T., Takayama, T. and Mizota, T., 1984: The palaeoenvironmental change. *Earth Monthly*, vol. 6, p. 571-575. (*in Japanese*)

Otsuka, H., 1982: The Cenozoic vertebrate fauna of Kyushu and the Ryukyu Islands, West Japan, viewed from the faunal relation to those of the Asiatic Continent. *Proceeding of Memorial Symposium on the 100th Meeting of the Nishinihon Branch, Geological Society of Japan*, p. 109-116. (*in Japanese*)

Otsuka, H., 1987: Middle- and Late Pleistocene mammalian faunae in the Japanese Islands with special reference to the mammalian fauna of the Nishiyagi Formation in Akashi District. *Bulletin of the National Museum of Japanese History*, vol. 13, sec. 6, p. 275-287. (*in Japanese with English abstract*)

Pei, W.C., 1940: The upper cave fauna of Choukoutien. *Palaeontologia Sinica, New Series C*, vol. 10, p. 1-84.

Pei, W.C., Woo, J.K., Chia, L.P., Chou, M.Z., Liu, H.T. and Wang, C.Y., 1958: Report on excavation of Palaeolithic sites at Tingtsun, Hsiangtenhsien, Shansi Province, China. *Institute of Vertebrate Palaeontology, Academy of Sinica, Series 1, Monograph*, no. 2, p. 1-111, 46 pls. (*in Chinese*)

Putman, R., 1988: *The natural history of deer*, 191 p. Christopher Helm, London.

Shikama, T., 1941: Fossil deer in Japan. *Jubilee Publication in the Commemoration of Professor H. Yabe's 60th Birthday*, vol. 2, p. 1125-1170.

Shikama, T., 1949: The Kuzuü Ossuaries. Geological and palaeontological studies of the limestone fissure deposits in Kuzuü, Totigi Prefecture. *Science Reports of the Tohoku University, 2nd Series*, vol. 23, p. 1-209.

Stefano, G.D. and Petronio, C., 1992: New data on *Cervus elaphus acoronatus* Beninde on the European Pleistocene. *Bollettino della Societa Paleontologica Italiana*, vol. 31, no. 3, p. 295-315. (*in Italian*)

Tokunaga, S. and Naora, N., 1934: Report of diggings at Ho-Chia-Kou, Ku-Hsiang-Tung, Kirin, Manchoukuo. *Report of the First Scientific Expedition to Manchoukuo*, sec. 2, pt. 1, p. 1-119. (*in Japanese*)

Tokunaga, S. and Naora, N., 1939: Fossil remains excavated at Ku-Hsiang-Tung near Harbin, Manchoukuo. *Report of the First Scientific Expedition to Manchoukuo*, sec. 2, pt. 4, p. 1-229. (*in Japanese*)

Vangengeim, E.A. and Sher, A.V., 1971: Siberian equivalents of the Tiraspol faunal complex. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 8, p. 197-207.

Whitehead, G.K., 1972: *Deer of the world*, 194 p. Constable, London.

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Miocene mollusks from the Kumano Group of the Ukui area, southeastern part of the Kii Peninsula, southwestern Honshu, Japan

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Abstract. The Shimosato Formation comprises the lower part of the Kumano Group of the southeastern Kii Peninsula, southwestern Honshu. It yields such mollusks as *Saccella miensis* (Araki), *Cyclocardia siogamensis* (Nomura), *Macoma* (*Macoma*) *izurensis* (Yokoyama), *Cultellus izumoensis* Yokoyama, *Dosinia* (*Phacosoma*) *nomurai* (Otuka), *Periploma* (*Aelga*) *mitsuganoense* Araki, *Thracia watanabei* Itoigawa and Shibata, *Turritella* (*Hataiella*) *sagai* Kotaka, and *Fulgoraria* (*Musashia*) *yanagidaniensis* Araki. The *Periploma-Saccella-Cyclocardia* and *Turritella-Dosinia* assemblages of the Shimosato Formation are inferred to represent lower sublittoral to bathyal and sublittoral environments, respectively.

The fauna of the Shimosato Formation is comparable with the subtropical Akeyo Fauna of late Early Miocene age, based on the occurrence of diagnostic species such as *Dosinia* (*Phacosoma*) *kawagensis* Araki, *Thracia watanabei* Itoigawa and Shibata, *Turritella sagai*, and *Fulgoraria yanagidaniensis*. The assemblages of the middle part of the Shikiya Formation and the lower part of the Mitsuno Formation are comparable with those of the tropical Kurosedani (subtropical Kadonosawa) Fauna of latest Early to earliest Middle Miocene age.

Key words : Assemblages, fauna, Kumano Group, Miocene, mollusks, systematic description

Introduction

The Miocene Kumano and Owase Groups of the Nankai Geologic Province are exposed in the southeastern part of the Kii Peninsula, southwestern Honshu (Figure 1). The Kumano Group rests upon the Shimanto Supergroup with clino-unconformity or is faulted against it and is intruded by the Kumano Acidic Rocks. The age of the Kumano Acidic Rocks is between 14 and 15 Ma (Chijiwa, 1988). The Kumano Group consists largely of mudstone and sandstone from 1,500 to 4,000 m thick and is divided into three lithologic units, in ascending order: the Shimosato (Onuma), Shikiya (Koguchi) and Mitsuno Formations (Hisatomi, 1984) (Figure 2).

The contemporaneous Setouchi Miocene Series (upper Lower to lower Middle Miocene) of the Setouchi Geologic Province is extensively distributed in central and western Honshu, to the north of the Kii Peninsula (Figure 1). The molluscan paleontology of the Setouchi strata has been studied in detail (*vide* Itoigawa and Shibata, 1992). For example, Itoigawa (1987, 1988) named and defined the subtropical Akeyo Fauna (late Early Miocene ; ca. 18 to 16 Ma) based on mollusks of the Akeyo Formation of the Mizunami Group. Similar fauna has also been recorded from: the Ichishi, Ayugawa and Tsuzuki Groups of the Eastern Setouchi Miocene Series in southwestern Honshu ; the Kurami Group in central Honshu ; the upper part of the Kunugidaira Formation, and the Nakayama and Yotsuyaku Formations in northeastern Honshu (Ozawa *et al*., 1995 ; Matsubara, 1995a).

On the other hand, the tropical Kurosedani Fauna (Tsuda, 1960) has been recorded from southwestern Japan, and the contemporaneous subtropical Kadonosawa Fauna has been recorded from northeastern Honshu and southern Hokkaido, northern Japan (Itoigawa, 1988). Both faunas are restricted within the N. 8 zone of Blow (1969) of latest Early to earliest Middle Miocene age (Ogasawara and Noda, 1996). The Akeyo Fauna differs from the Kurosedani Fauna by lacking the tropical mollusks of the latter (Itoigawa, 1988). It also differs from the Kadonosawa Fauna by lacking the characteristic species of the latter : *Anadara* (*Hataiarca*) *kakehataensis* Hatai and Nisiyama, *Vasticardium ogurai* (Otuka), *Glycydonta itoigawae* (Tsuda), *Tateiwaia tateiwai* (Makiyama), *T. yamanarii* (Makiyama), and *Zeuxis minoensis* (Itoigawa) (Itoigawa, 1988).

A Miocene fauna has been reported from several places in the Kii Peninsula (Mizuno, 1953, 1957 ; Tanai and Mizuno, 1954 ; Katto and Masuda, 1978 ; Katto *et al*., 1976, 1980 ; Ujihara and Shibata, 1982 ; Chijiwa and Tomita, 1985 ;

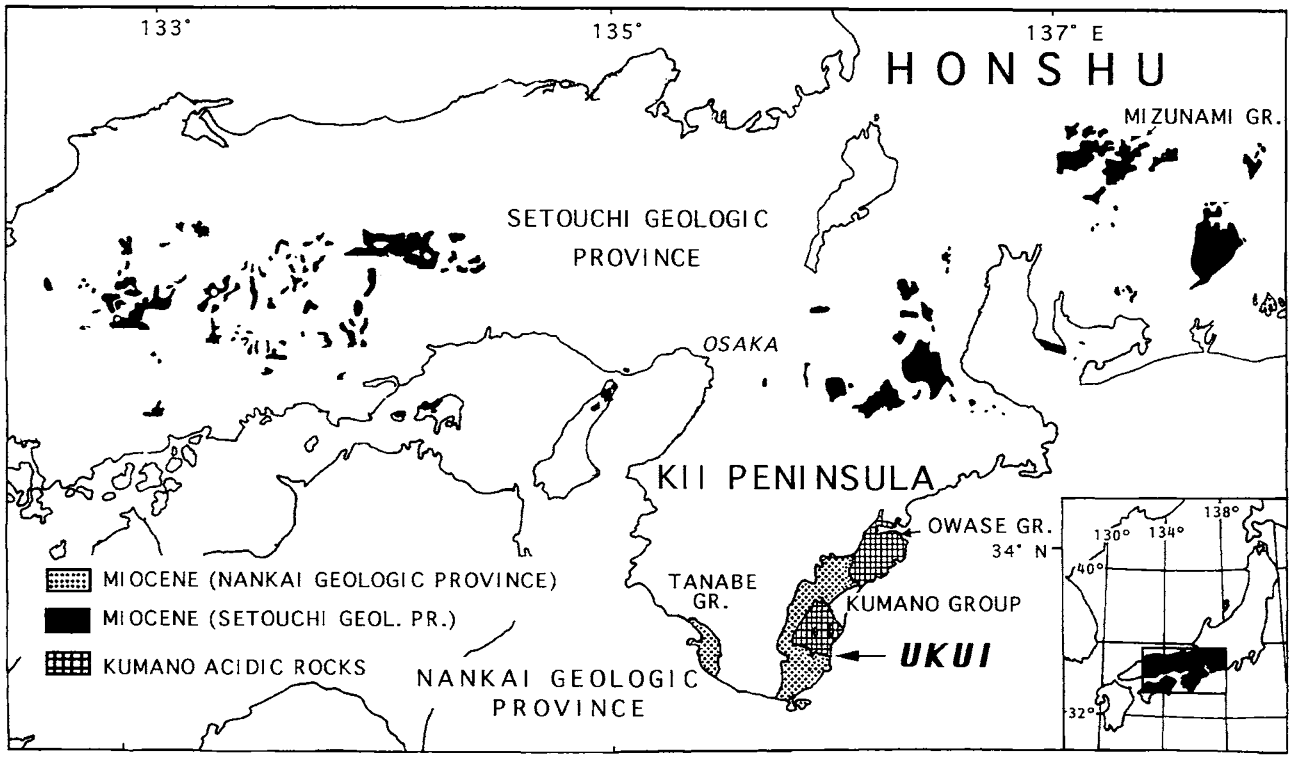


Figure 1. Distribution of the Miocene strata of the Nankai and Setouchi Geologic Provinces, central and southwestern Honshu (*redrawn from*: Itoigawa and Shibata, 1992; Editorial Committee of KINKI, *ed*., Part 6 of Regional Geology of Japan, 1987).

Honda, 1992). However, much data are required to reconstruct the Miocene paleoenvironments in the Nankai Geologic Province.

In 1976 and 1977, one of us (SU) collected several hundred fossil mollusks from a construction site at Ukui Junior High School (Loc. 2; Figures 3, 4), as well as several tens of specimens from an outcrop on a wave-cut terrace at Loc. 7 on Kitsune-jima (Figure 3). Recently, one of us (YH) obtained more specimens from additional localities in the Ukui area. All of these localities are assigned to the Shimosato Formation and together they contain mollusks such as *Saccella miensis* (Araki), *Cyclocardia siogamensis* (Nomura), *Macoma* (*Macoma*) *izurensis* (*Yokoyama*), *Cultellus izumoensis* Yokoyama, *Dosinia* (*Phacosoma*) *nomurai* (Otuka), *Periploma* (*Aelga*) *mitsuganoense* Araki, *Thracia watanabei* Itoigawa and Shibata, *Turritella* (*Hataiella*) *sagai* Kotaka, and *Fulgoraria* (*Musashia*) *yanagidaniensis* Araki (Table 1).

The purpose of this study is to record the molluscan assemblages of the Shimosato Formation, and to describe their characteristic species, including those representative of the Akeyo Fauna. We also wish to clarify the molluscan faunal succession of the Kumano Group of the Nankai Geologic Province of southwestern Japan.

Outline of geology and molluscan fauna

The upper Muro Group (Upper Oligocene to Lower Miocene) of the Shimanto Supergroup and the Shimosato Formation of the Kumano Group are exposed in the Ukui area. The Muro Group consists largely of interbedded gray sandstone and black shale. The Shimosato Formation, on the other hand, is made up of massive, gray, fine- or very fine-grained sandstone, and sandy siltstone. In a wave-cut platform on Kitsune-jima (Loc. 7 in Figure 3), the Shimosato Formation is made up of well-sorted, well-jointed, pale gray, tuffaceous, fine-grained sandstone. The fine-grained sandstone at this locality frequently contains sand-pipes. The Shimosato Formation strikes about N50°E and dips about 10° to 20°SE, and is approximately 200 m thick. Conglomerate of the lowermost Shimosato Formation, which attains a thickness of 30 to 80 cm, rests upon black shale of the uppermost Muro Group with clino-unconformity.

The Kumano Acidic Rocks also crop out in this area. They consist largely of granite porphyry, and intrude into the upper Muro and Kumano Groups. A vertical pyroclastic dike, which is closely related to the Kumano Acidic Rocks (Suzuki, 1976), is exposed in two small cuts at Ukui Junior High School. This dike intrudes into very fine-grained sandstone of the Shimosato Formation, varies in width from approximately 0.5 to 5 m, and trends about N80°E. Figure 3 is a map showing the location of fossil localities in the Shimosato Formation, and Figure 4 shows fossil localities in columnar sections.

Mollusks reported previously from the Shimosato Formation by Ujihara and Shibata (1982) include *Neilonella* cf. *N. isensis* Shibata, *Saccella miensis*, *Portlandia* (*Portlandella*)

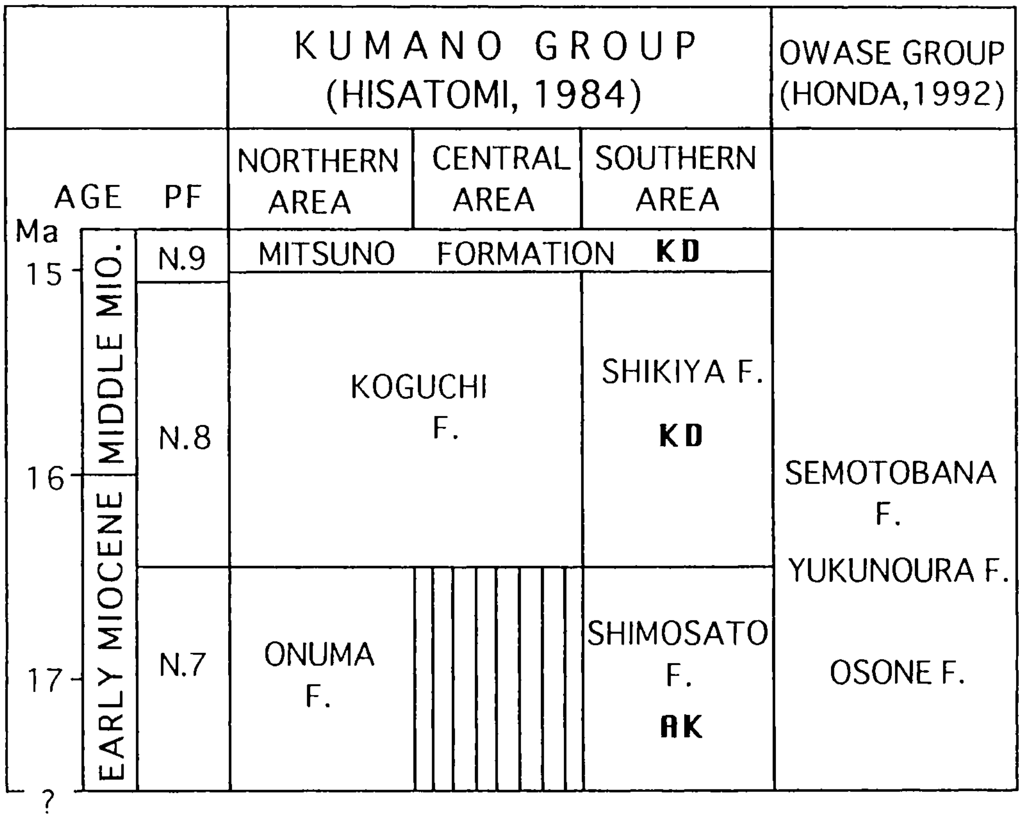


Figure 2. Stratigraphic classification of the Kumano and Owase Groups, southeastern Kii Peninsula. **AK**, occurrence of the molluscan fauna comparable with the Akeyo Fauna; **KD**, occurrences of the assemblages comparable with those of the Kurosedani (Kadonosawa) Fauna. PF, zonation by planktonic foraminifera (Blow, 1969).

watasei (Kanehara), *Yoldia* (*Cnesterium*) sp., *Lucinoma* sp., *Macoma* (*Macoma*) *optiva* (Yokoyama), *Turcicula* (*Turcicula*) *osawanoensis* (Tsuda), *Turritella* (*Turritella*) *kiiensis* (Yokoyama), *Orectospira* sp., and *Euspira mitsuganoensis* Shibata.

Mizuno (1957) reported mollusks in the Shimosato Formation of the Ukui area (Loc. 7 in Figure 3), including *Dosinia* (*Phacosoma*) *nomurai* Otuka and *Turritella* (*Idaella*) *tanaguraensis* Kotaka. Chijiwa and Tomita (1985) noted the following mollusks in the Onuma Formation: *Saccella miensis, Portlandia watasei, Cyclocardia siogamensis, Macoma optiva, M. izurensis, Cultellus izumoensis* Yokoyama, and *Periploma* cf. *P. mitsuganoense*.

The Shikiya Formation contains mollusks such as *Acharax tokunagai* (Yokoyama), *Acilana tokunagai* (Yokoyama), *Conchocele bisecta* (Conrad), *Lucinoma kamenooensis* (Otuka), *Macoma optiva, Turritella sagai*, and *T.* (*Hataiella*) *kadonosawaensis* Otuka (Mizuno, 1953; Tanai and Mizuno, 1954). Katto *et al.* (1976) proposed the Uematsu Formation for the middle part of the Shikiya Formation (Hisatomi and Miyake, 1981), which crops out in the southernmost part of the Kii Peninsula. The Uematsu Formation yields many warm-water mollusks such as *Cucullaea toyamaensis* Tsuda, *Crassatellites pauxillus* (Yokoyama), *Mikadotrochus* sp., and *Conus* (*Chelyconus*) *tokunagai* Otuka (Katto *et al.*, 1976; Katto and Masuda, 1978), in association with larger foraminifers such as *Lepidocyclina* (*Nephrolepidina*) *japonica* (Yabe) and *Miogypsina* sp. (Nishimura and Miyake, 1973).

The lower part of the Mitsuno Formation also contains many warm-water mollusks such as *Glycymeris* (*Veletuceta*) *cisshuensis* Makiyama, *Anadara* (*Anadara*) *kiiensis* Mizuno, *Crassatellites nanus* (Adams and Reeve), and *Conus tokunagai* (Mizuno, 1953; Tanai and Mizuno, 1954). Katto *et al.* (1980) also studied mollusks from the lower part of the Mitsuno Formation (*vide* Saeki and Koto, 1972) and noted the presence of warm-water mollusks such as *Anadara* cf. *A.* (*Anadara*) *ogawai* (Makiyama), *Veremolpa minoensis* (Itoigawa), *Vasticardium ogurai*, and *Paphia hataii* Masuda and Noda.

Honda (1992) studied molluscan fossils of the Owase Group, which crops out on the southeastern margin of the Kii Peninsula to the north of the Kumano Group. The Yukunoura Formation of the Owase Group contains mollusks such as *Acila* sp., *Portlandia* sp., *Cyclocardia siogamensis, Lucinoma* sp., *Macoma optiva, Cultellus otukai* Ogasawara and Tanai, *Periploma* sp., and *Turritella sagai* (Honda, 1992). The assemblages of the Yukunoura Formation resemble those of the Shimosato, Shikiya, and Onuma Formations within the lower and middle parts of the Kumano Group; and those of the Eastern Setouchi Miocene Series in central and

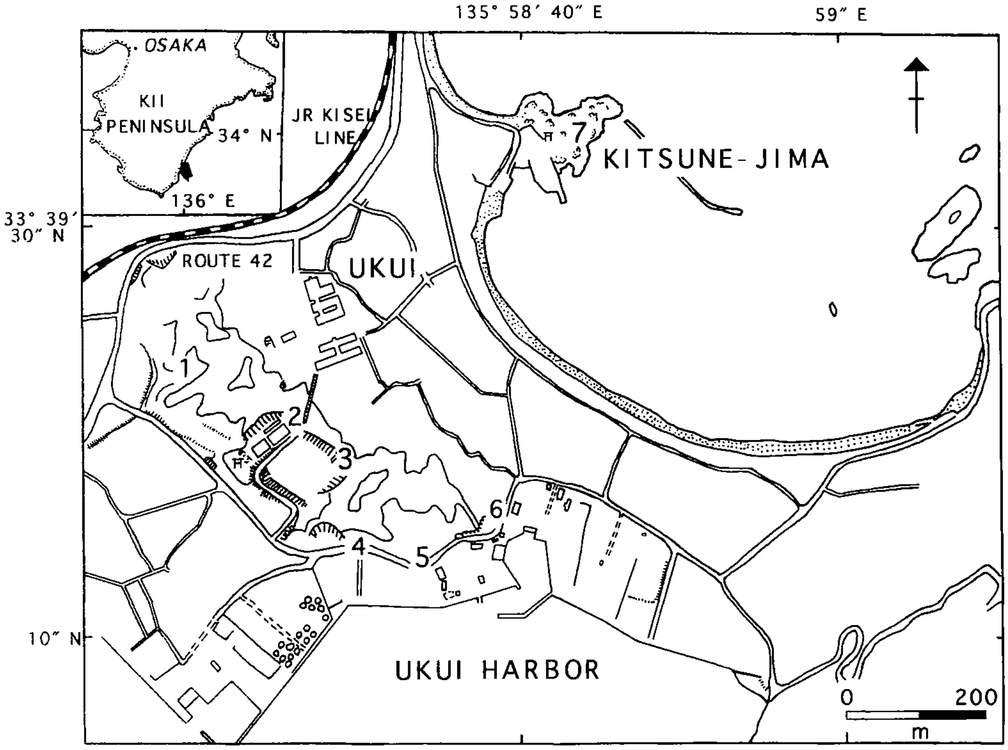


Figure 3. Map showing fossil localities in the Shimosato Formation. 1-7, fossil localities.

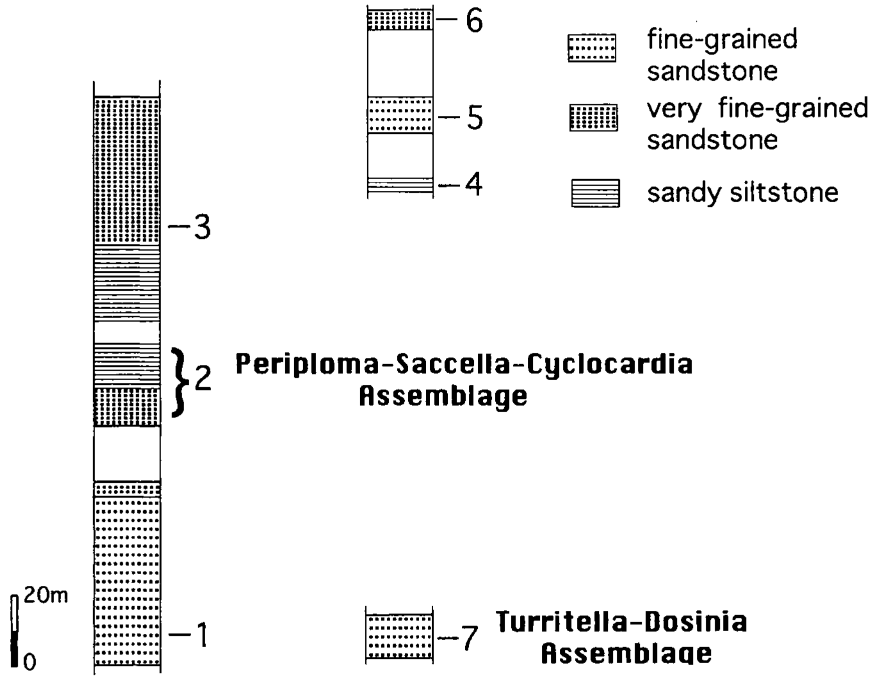


Figure 4. Columnar sections of the Shimosato Formation. 1-7, fossil localities.

Table 1. Occurrences of fossil mollusks in the Shimosato Formation. VA, very abundant (20 or more individuals); A, abundant (10 to 19 individuals); C, common (5 to 9 individuals); F, few (2-4 individuals); R, rare (one individual). One individual is defined herein as consisting of more than half of a separated valve or an articulated pair of bivalves, and more than half of a gastropod specimen. See also Figure 5 and Tables 2, 3.

SPECIES	LOCALITY						
	1	2	3	4	5	6	7
Bivalves:							
Acila cf. *A.* (*Acila*) *submirabilis* Makiyama							R
Acila sp.					R	F	
Ennucula sp.		A					
Saccella miensis (Araki)		VA				R	
Solamen sp.		F					
Septifer ? sp.		F					
Chlamys cf. *C. iwamurensis* Itoigawa		R					
Cycladicama sp.		R					
Cyclocardia siogamensis (Nomura)		VA					C
Cyclocardia sp.		C					
Lucinoma sp.		F	R				
Mactra sp.		R					
Macoma (*Macoma*) *izurensis* (Yokoyama)		A					
Angulus cf. *A. kagayamensis* Ogasawara and Tanai		F					
Nitidotellina sp.		R					
Cultellus izumoensis Yokoyama		A					
Disinia (*Phacosoma*) *kawagensis* Araki							F
Dosinia (*Phacosoma*) *nomurai* (Otuka)		R					A
Dosinia sp.		R					C
Paphia sp.		R					
Glauconome sp.		F					
Mya sp.		A					
Anisocorbula sp.		R					
"*Teredo*" sp.			C				
Periploma (*Aelga*) *mitsuganoense* Araki		VA		R			
Periploma (*Aelga*) sp.		VA					
Thracia watanabei Itoigawa and Shibata		F				R	
Thracia sp.					R		
Gastropods:							
Turritella (*Hataiella*) *sagai* Kotaka		A					A
Turritella sp.		R					F
Bittium sp.	F	A					
Euspira sp.		R					
Ancistrolepis sp.		A					
Fulgoraria (*Musashia*) *yanagidaniensis* Araki		C					
Eocylichna sp.		C					

southwestern Honshu.

Molluscan assemblages and environments

Approximately 400 specimens were collected from 7 localities in the Shimosato Formation. These specimens comprise 22 genera and 28 species of bivalves and 6 genera and 7 species of gastropods (Table 1). Mollusks occur sporadically in the fine- and very fine-grained sandstone and sandy siltstone of the Shimosato Formation. Almost all specimens are complete or nearly so, but all except those from Locality 7 lack original shell material. Two molluscan assemblages are recognized herein: the *Periploma-Saccella-Cyclocardia* (Loc. 2) and *Turritella-Dosinia* assemblages (Loc. 7). Mollusks from Localities 1 and 3-6 are not used for recognition of assemblages, because each yielded fewer than 10 specimens. Table 2 summarizes the molluscan assemblages and characteristic and associated species.

The *Periploma-Saccella-Cyclocardia* assemblage

This assemblage occurs in beds of sandy siltstone and overlying very fine-grained sandstone at Locality 2. Both beds are up to about 10 m thick. The assemblage is characterized by the dominant occurrence of *Periploma* (*P.*

Table 2. Molluscan assemblages of the Shimosato Formation. vfs : very fine sandstone ; sdy slt : sandy siltstone ; fs : fine sandstone.

MOLLUSCAN ASSEMBLAGE	CHARACTERISTIC SPECIES	ASSOCIATED SPECIES	LITHOLOGY	LOC.
Periploma-Saccella-Cyclocardia Ass.	*Periploma mitsuganoense* *Saccella miensis* *Cyclocardia siogamensis*	*Ancistrolepis* sp. *Bittium* sp. *Ennucula* sp. *Mya* sp. *Cultellus izumoensis* *T. sagai* *Macoma izurensis*	vfs sdy slt	2
Turritella-Dosinia Assemblage	*Turritella sagai* *Dosinia nomurai* *D. kawagensis*	*C. siogamensis* *Acila* cf. *A. submilabilis*	fs	7

mitsuganoense : Figures 5-12, 5-13, and *P.* sp. : Figure 5-8), *Saccella miensis* (Figure 5-1), and *Cyclocardia* (*C. siogamensis* : Figure 5-14, and *C.* sp.), but also contains *Ancistrolepis* sp., *Bittium* sp., *Ennucula* sp. (Figure 5-2), *Mya* sp. (Figure 5-10), *Cultellus izumoensis* (Figure 5-11), *Turritella sagai* (Figure 5-9), and *Macoma izurensis* (Figure 5-7 ; Table 2). This assemblage typically contains many extant genera that live in upper sublittoral to bathyal depths (N_1-B) off Japan and neighboring countries, including *Saccella, Cyclocardia* and *Turritella* (Table 3). However, it also includes *Periploma, Ancistrolepis* and *Musashia*, which live in lower sublittoral to bathyal depths (N_3-B, Table 3). Consequently, the *Periploma-Saccella-Cyclocardia* assemblage is inferred to represent a lower sublittoral to bathyal environment.

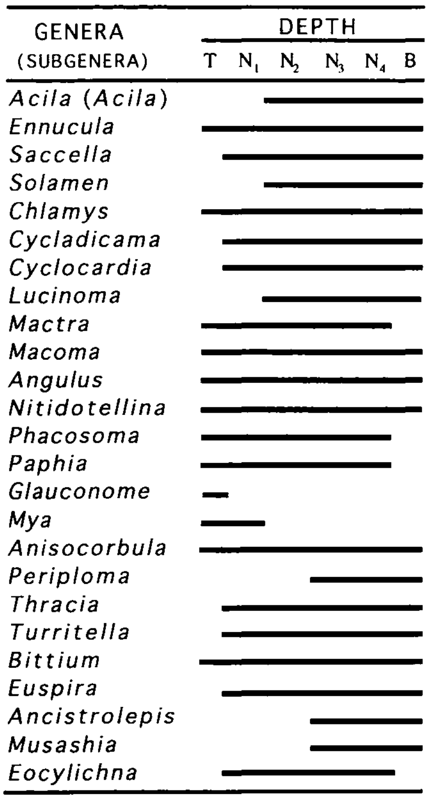
Comparison : The Onuma Formation of the Kumano Group contains a number of species known from this assemblage, including *Saccella miensis, Cyclocardia siogamensis, Macoma izurensis*, and *Cultellus izumoensis* (Chijiwa and Tomita, 1985). This assemblage is therefore correlative with those of the Onuma Formation, which represent lower sublittoral environments (Chijiwa and Tomita, 1985).

In addition, the *Periploma-Saccella-Cyclocardia* assemblage contains many species in common with the *Periploma-Acila* and *Macoma-Lucinoma* assemblages in the Eastern Setouchi Miocene Series of central and southwestern Honshu, including *Saccella miensis, Periploma* sp., *M. izurensis, Cultellus izumoensis*, and *Cyclocardia siogamensis* (Shibata, 1978). This assemblage is therefore also correlative with the *Periploma-Acila* and *Macoma-Lucinoma* assemblages, which represent upper sublittoral and sublittoral environments, respectively (Shibata, 1978).

The *Turritella-Dosinia* assemblage

This assemblage occurs in gray, fine-grained sandstone at Locality 7 and is characterized by the dominant occurrence of *Turritella* (*T. sagai* : Figure 5-9, and *T.* sp.) and *Dosinia* (*D. nomurai* : Figures 5-15, 5-19, *D. kawagensis* : Figure 5-16, and *D.* sp.) (Table 2). *Cyclocardia siogamensis* and *Acila* cf. *A. submirabilis* (Figure 5-6) are also present in this assemblage (Table 2). The presence of many intact specimens in this assemblage implies that there was little or no post-mortem transportation. Modern *Turritella, Cyclocardia* and *Acila* species live in upper sublittoral to bathyal depths (N_1 (N_2)-B), and *Dosinia* (*Phacosoma*) dwells in the tidal to lower sublittoral zone (T-N_4) (Table 3). The *Turritella-Dosinia* assemblage is therefore inferred to represent a sublittoral environment.

Table 3. Modern bathymetric distribution of extant northwestern Pacific bivalves and gastropods in the Shimosato molluscan fauna (Higo and Goto, 1993). Depth ; T, tidal zone ; N_1, low-water line to 30 m ; N_2, 30-60 m ; N_3, 60-120 m ; N_4, 120-200 m ; B, over 200 m deep (Taki and Oyama, 1954, *partly revised*).



Comparison : This assemblage contains *Turritella sagai*


1


2


3


4a


4b


5a


5b


6


7

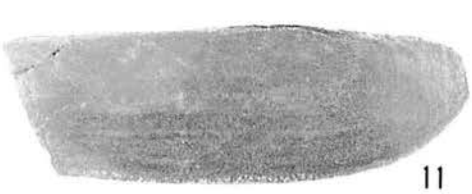

8


9


10a


10b

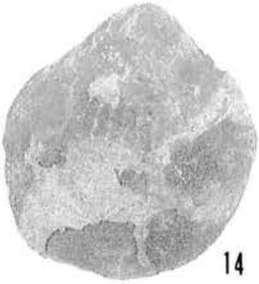

10c


11


12a


12b


13


14


15


16


17


18


19

and *Dosinia nomurai* in common with the *Turritella-Lucinoma* assemblage of the Tomikusa Group (upper Lower Miocene) in the Eastern Setouchi Miocene Series of central Honshu (Shibata, 1978). This assemblage is therefore correlative with the *Turritella-Lucinoma* assemblage, which represents an upper sublittoral environment (Shibata, 1978).

Discussion

Honda (1992) noted that two types of molluscan assemblage are present in the Kumano and Owase Groups. The first type has been recorded from the Shimosato, Shikiya, and Onuma Formations within the lower and middle parts of the Kumano Group (Mizuno, 1953 ; Tanai and Mizuno, 1954 ; Ujihara and Shibata, 1982 ; Chijiwa and Tomita, 1985) ; and the Yukunoura Formation of the Owase Group (Honda, 1992). The type is characterized by *Portlandia watasei, Cyclocardia siogamensis, Lucinoma* sp., *Macoma optiva* (*M. izurensis*), *Cultellus izumoensis*, and *Turritella sagai* (*T. kadonosawaensis, T. shataii, T. kiiensis*).

The *Periploma-Saccella-Cyclocardia* and *Turritella-Dosinia* assemblages of the Shimosato Formation contain many species in common with those of the first type, including *Cyclocardia siogamensis, Macoma izurensis, Cultellus izumoensis*, and *Turritella sagai* (Table 2). Both assemblages therefore belong to the first type. In addition, the Shimosato Formation contains *Dosinia kawagensis, Thracia watanabei, Turritella sagai*, and *Fulgoraria yanagidaniensis* (Table 1), which characterize the fauna of the Akeyo Formation. The fauna of the Shimosato Formation is therefore comparable with the Akeyo Fauna of late Early Miocene age (ca. 18 to 16 Ma ; Itoigawa, 1987, 1988) (Figure 2).

On the other hand, the second type of molluscan assemblage has been reported from the middle part of the Shikiya and the lower part of the Mitsuno Formation within the middle and upper parts of the Kumano Group (Mizuno, 1953 ; Tanai and Mizuno, 1954 ; Katto and Masuda, 1978 ; Katto *et al.*, 1980). The type is characterized by many warm-water mollusks such as *Anadara* cf. *A. ogawai, Cucullaea toyamaensis, Crassatellites pauxillus, C. nanus, Vasticardium ogurai, Mikadotrochus* sp., and *Conus tokunagai*.

Among these species, *Cucullaea toyamaensis* and *Conus tokunagai* characterize the Kurosedani Fauna of southwestern Japan. *Conus tokunagai* is also characteristic in the Kadonosawa Fauna of northern Japan. The middle part of the Shikiya Formation yields *Cucullaea toyamaensis* and *Conus tokunagai* (Katto and Masuda, 1978), in association with larger foraminifers such as *Lepidocyclina japonica* and *Miogypsina* sp. (Nishimura and Miyake, 1973). In addition, *Conus tokunagai* has been reported from the lower part of the Mitsuno Formation (Mizuno, 1953 ; Tanai and Mizuno, 1954 ; Katto *et al.*, 1980).

Accordingly, the assemblages of the middle part of the Shikiya Formation and the lower part of the Mitsuno Formation are comparable with those of the Kurosedani (Kadonosawa) Fauna (Figure 2). The occurrence of the Kurosedani (Kadonosawa) Fauna corresponds to the warm marine climatic episode during the latest Early to earliest Middle Miocene period (ca. 16-15 Ma) (Chinzei, 1986).

Such a different stratigraphic occurrence of the molluscan assemblages suggests a warming of climate and not merely a change in the sedimentary environment. The warming of climate is also recognized in the transition from the subtropical Akeyo to tropical Kurosedani Fauna in the Mizunami Group of the Eastern Setouchi Miocene Series (Itoigawa, 1988, 1989).

A similar scenario has also been proposed for another taxonomic group in the Kumano Group. For instance, Nishimura and Miyake (1973) reported larger foraminifers such as *Lepidocyclina japonica* and *Miogypsina* sp. from the middle part of the Shikiya Formation. Using planktonic foraminifers, Ibaraki (1990) assigned the *Lepidocyclina-Miogypsina-bearing* horizon to the N8.b zone of Blow (1969). From the occurrence of *Orbulina universa* d'Orbigny (Ikebe *et al.*, 1975), the uppermost part of the Shikiya Formation and the Mitsuno Formation correlate with the N.9 zone of Blow (1969) (Hisatomi, 1987) (Figure 2).

As was discussed in the aforementioned lines, the molluscan assemblages of the lower part of the Mitsuno Formation (Mizuno, 1953 ; Tanai and Mizuno, 1954 ; Katto *et al.*, 1980) are comparable with those of the Kurosedani (Kadonosawa) Fauna. The fauna, however, is restricted within the N. 8 zone of Blow (1969) of latest Early to earliest Middle Miocene age (Ogasawara and Noda, 1996). Further studies are needed to clarify the molluscan faunal succession of the Kumano Group of the Nankai Geologic Province of southwestern Japan.

Summary of faunal discussion

1) The *Periploma-Saccella-Cyclocardia* and *Turritella-Dosinia* assemblages of the Shimosato Formation are inferred to represent lower sublittoral to bathyal and sublittoral environments, respectively.

2) The fauna of the Shimosato Formation is comparable with the subtropical Akeyo Fauna of late Early Miocene age,

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Figure 5. **1.** *Saccella miensis* (Araki). Loc. 2, MES* 1015. **2.** *Ennucula* sp. x2, Loc. 2, MES 1016. **3, 5a-b.** *Thracia watanabei* Itoigawa and Shibata. 3 ; Loc. 2, MES 1017. 5a-b ; Loc. 6, MES 1018. **4a-b.** *Glauconome* sp. Loc. 2, MES 1019. **6.** *Acila* cf. *A.* (*Acila*) *submirabilis* Makiyama. x1.5, Loc. 7, MES 1020. **7.** *Macoma* (*Macoma*) *izurensis* (Yokoyama). Loc. 2, MES 1021. **8.** *Periploma* (*Aelga*) sp. Loc. 2, MES 1022. **9.** *Turritella* (*Hataiella*) *sagai* Kotaka. Loc. 7, MES 1023. **10a-c.** *Mya* sp. Loc. 2, MES 1024. **11.** *Cultellus izumoensis* Yokoyama. Loc. 2, MES 1025. **12a-b, 13.** *Periploma* (*Aelga*) *mitsuganoense* Araki. 12a-b. Loc. 2, MES 1026. 13 ; Loc. 2, MES 1027. **14.** *Cyclocardia siogamensis* (Nomura). x1.5, Loc. 2, MES 1028. **15, 19.** *Dosinia* (*Phacosoma*) *nomurai* (Otuka). 15 ; Loc. 2, MES 1029. 19 ; Loc. 7, MES 1030. **16.** *Dosinia* (*Phacosoma*) *kawagensis* Araki. Loc. 7, MES 1031. **17.** *Fulgoraria* (*Musashia*) *yanagidaniensis* Araki. Loc. 2, MES 1032. **18.** *Chlamys* cf. *C. iwamurensis* Itoigawa. Loc. 2, MES 1033. All figures natural size unless otherwise stated. *Abbreviation for the Department of Earth Sciences, Faculty of Education, Mie University.

based on the occurrence of diagnostic species such as *Dosinia kawagensis, Thracia watanabei, Turritella sagai*, and *Fulgoraria yanagidaniensis*.

3) The assemblages of the middle part of the Shikiya Formation and the lower part of the Mitsuno Formation are comparable with those of the tropical Kurosedani (subtropical Kadonosawa) Fauna of latest Early to earliest Middle Miocene age.

Systematic notes on some important species

Phylum Mollusca
Class Bivalvia
Family Veneridae
Subfamily Dosiniinae
Genus ***Dosinia*** Scopoli, 1777
Subgenus ***Phacosoma*** Jukes-Browne, 1912

Dosinia (***Phacosoma***) ***kawagensis*** Araki, 1960

Figure 5-16

Dosinia nomurai Otuka ; Itoigawa, 1956, pl. 2, fig. 3 (*non* Otuka, 1934).
Dosinia japonica kawagensis Araki, 1960, p. 95, pl. 7, fig. 3.
Dosinia (*Phacosoma*) *kawagensis* Araki ; Masuda, 1963, p. 22, pl. 4, figs. 1-8 (fig. 1, reproduced from Araki, 1960) ; Yoon, 1979, p. 15, pl. 2, figs. 7, 9, 10 ; Matsubara, 1995b, p. 330, pl. 4, figs. 9-11.
Dosinia kawagensis Araki ; Hayashi and Miura, 1973, pl. 2, fig. 12 ; Hayashi, 1973, pl. 1, figs. 2, 3 ; Ishida *et al*., 1980, pl. 3, fig. 12.
Dosinorbis kawagensis (Araki) ; Itoigawa *in* Itoigawa *et al*., 1974, p. 87, pl. 23, figs. 1-6.
Phacosoma kawagensis (Araki) ; Itoigawa *et al*., 1981 (1982, p. 80), pl. 14, figs. 6a-b ; Shibata and Ina, 1983, p. 48, pl. 5, fig. 12 ; Itoigawa and Shibata, 1986, pl. 16, fig. 13 ; Muramatsu, 1992, pl. 49, fig. 10.
Dosinia (*Phacosoma*) *chikuzenensis nomurai* Otuka ; Hayashi, 1988, p. 5, pl. 1, figs. 2, 3 (reproduced from illustration of *Dosinia kawagensis* in Hayashi (1973)).

Remarks.—Two incomplete closed valves were obtained from fine-grained sandstone of the Shimosato Formation. The present species was originally described by Araki (1960) (as *D. japonica kawagensis*) from the Kaisekizan Formation (upper Lower Miocene ; *vide* Yoshida, 1991 ; Shibata, 1967) of the Ichishi Group, Mie Prefecture, southwestern Honshu. Itoigawa (1956) had earlier cited "*D. nomurai*" from the Tsuzuki Group (upper Lower Miocene) of Kyoto Prefecture, but Masuda (1963) later assigned this occurrence to *D. kawagensis*.

The present species resembles *D.* (*Phacosoma*) *nomurai* Otuka, 1934, which was originally described from the Kadonosawa Formation (uppermost Lower to lowermost Middle Miocene ; Irizuki and Matsubara, 1994) of Iwate Prefecture, northeastern Honshu. However, *D.* (*P.*) *kawagensis* differs by having a more anteriorly expanded anterodorsal margin. The present species also resembles *D.* (*P.*) *japonica* (Reeve), which is living in Japan, but differs from the latter by having a smaller and somewhat more inequilateral shell.

The present species has also been recorded from the upper Lower to lowermost Middle Miocene formations of Honshu and Korea. These include the Akeyo Formation of the Mizunami Group, and other strata of the Eastern Setouchi Miocene Series in central and southwestern Honshu (Itoigawa *et al*., 1981) ; the Shiode, Ajiri, and Yotsuyaku Formations of northeastern Honshu (Masuda, 1963 ; Matsubara, 1995b) ; and the Sinhyeon Formation of Korea (Yoon, 1979).

Occurrence.—As characteristic species of *Turritella-Dosinia* ass. at Locality 7.

Family Periplomatidae
Genus ***Periploma*** Schumacher, 1817
Subgenus ***Aelga*** Slodkewitsch, 1935

Periploma (***Aelga***) ***mitsuganoense*** Araki, 1959

Figures 5-12a-b, 13

Periploma mitsuganoense Araki, 1959, p. 163, pl. 18, figs. 2a-b ; Araki, 1960, p. 85, pl. 5, figs. 13a-b (reproduced from Araki, 1959) ; Shibata in Itoigawa *et al*., 1974, p. 108, pl. 34, figs. 12-17 ; Ishida *et al*., 1980, pl. 4, fig. 21 ; Itoigawa *et al*., 1981 (1982, p. 115), pl. 22, figs. 14a-b ; Itoigawa and Shibata, 1986, pl. 17, fig. 13 ; *non* Hayashi, 1973, pl. 5, fig. 1.

Remarks.—Approximately 80 slightly deformed specimens were collected from sandy siltstone of the Shimosato Formation. Araki (1959) based this species on specimens from the Kaisekizan Formation (upper Lower Miocene) of the Ichishi Group, Mie Prefecture, southwestern Honshu. It closely resembles *Periploma* (*Aelga*) *besshoense* (Yokoyama, 1924), which was originally described from the Asagai Formation (Lower Oligocene) of the Joban coal field, northeastern Honshu, but is distinguished from the latter in having a more inequilateral shell. *Periploma owasense* Suzuki (1934, p. 348, text-fig. 4), described from the Owase Group (upper Lower to lowermost Middle Miocene) of Mie Prefecture, southeastern Kii Peninsula, is allocated here to *Periploma* sp. indet., owing to the poor preservation of the specimen. *Periploma mitsuganoense* has also been recorded from the Akeyo Formation of the Mizunami Group, and other strata of the Eastern Setouchi Miocene Series (Itoigawa *et al*., 1981).

Occurrence.—As characteristic species of *Periploma-Saccella-Cyclocardia* ass. at Locality 2 and also from Loc. 4.

Family Thraciidae
Genus ***Thracia*** Leach, 1824

Thracia watanabei Itoigawa and Shibata, 1975

Figures 5-3, 5a-b

Thracia sp. (n. sp.) ; Itoigawa *in* Itoigawa *et al*., 1974, p. 108, pl. 34, figs. 10-11.
Thracia watanabei Itoigawa and Shibata, 1975, p. 31, pl. 8, figs. 21-24 ; Itoigawa *et al*., 1981 (1982, p. 116), pl. 22, fig. 16.

Remarks.—Only four specimens were obtained from gray, very fine-grained sandstone at two localities in the Shimosato Formation. The present species was proposed by Itoigawa and Shibata (1975) from the Yamanouchi Member of the Akeyo Formation of the Mizunami Group. *Thracia watanabei* has also been recorded from the Tomikusa, Iwamura and Ayugawa Groups of the Eastern Setouchi Miocene Series in central and southwestern Honshu (Itoigawa *et al.*, 1981).

Occurrence.—Localities 2, 6.

Class Gastropoda
Family Turritellidae
Genus *Turritella* Lamarck, 1799
Subgenus *Hataiella* Kotaka, 1959

Turritella* (*Hataiella*) *sagai Kotaka, 1951

Figure 5-9

Turritella s-hataii sagai Kotaka, 1951, p. 87, pl. 12, figs. 13-17.

Turritella (*Hataiella*) *sagai* Kotaka ; Kotaka, 1959, p. 89, pl. 9, figs. 6-8, 10, 12, 18 ; Yoon, 1979, p. 21, pl. 5, fig. 11 ; Marincovich and Kase, 1986, p. 61, pl. 2, figs. F-H (in part) ; Honda, 1992, pl. 58, fig. 8.

Non Turritella (*Hataiella*) *sagai* Kotaka ; Marincovich and Kase, 1986, pl. 2, figs. A-E (in part) ; Marincovich, 1988, p. 15, pl. 3, figs. 3, 5-9 (3, 5-7, 9 ; reproduced from Marincovich and Kase, 1986, p. 61, pl. 2, figs. A-E) ; Zhidkova and Sal'nikov, *eds.*, 1992, p. 248, pl. 46, figs. 3a-b.

Turritella sagai Kotaka ; Shibata *in* Itoigawa *et al.*, 1974, p. 132, pl. 40, figs. 11, 12 ; Ishida *et al.*, 1980, pl. 5, figs. 10, 11 ; Itoigawa *et al.*, 1981 (1982, p. 164), pl. 28, figs. 13-14 ; Itoigawa and Shibata, 1986, pl. 17, fig. 2 ; Muramatsu, 1992, pl. 50, fig. 9.

Remarks.—A total of 26 specimens are to hand. The present species was originally described by Kotaka (1951, p. 87, pl. 12, figs. 13-17) from the Togari Member of the Akeyo Formation of the Mizunami Group. As noted by Kotaka (1951), *T.* (*Hataiella*) *sagai* resembles *T.* (*H.*) *shataii* Nomura, originally described from the "Shiogama" Formation (Lower Miocene ; Ishii *et al.*, 1982, p. 14, 20) of Miyagi Prefecture, northeastern Honshu. The present species also resembles *T.* (*H.*) *belogolovaensis* Ilyina, originally described from the Kuluven Formation (Lower Miocene) of western Kamchatka (*vide* Titova, 1994, p. 7), but it differs from the latter in having a more slender shell.

Marincovich and Kase (1986, p. 61, pl. 2, figs. A-H) cited *Turritella sagai* from the Bear Lake Formation (lowermost Middle Miocene, in part) of southwestern Alaska (figs. A-E), and the Akebihara Sandstone of the Ayugawa Group (upper Lower Miocene) of southwestern Honshu (figs. F-H). Specimens from the Bear Lake Formation are assigned here to *T. belogolovaensis*, as was done by Titova (1994). Zhidkova and Sal'nikov, *eds.* (1992, p. 248, pl. 46, figs. 3a-b) cited *T.* (*H.*) *sagai* from the Neveliskaya Formation (Lower Miocene) of southern Sakhalin, and this occurrence is also assigned here to *T. belogolovaensis*.

Turritella sagai has been recorded from the Akeyo Formation of the Mizunami Group and other strata of the Eastern Setouchi Miocene Series (Itoigawa *et al.*, 1981), and the Hwabongri Formation (lower Middle Miocene) of Korea (Yoon, 1979).

Occurrence.—As characteristic species of *Turritella-Dosinia* ass. at Loc. 7, and as associated species of *Periploma-Saccella-Cyclocardia* ass. at Loc. 2.

Family Volutidae
Subfamily Fulgorariinae
Genus *Fulgoraria* Schumacher, 1817
Subgenus *Musashia* Hayashi, 1960

Fulgoraria* (*Musashia*) *yanagidaniensis Araki, 1959

Figure 5-17

Fulgoraria hirasei yanagidaniensis Araki, 1959, p. 165, pl. 18, fig. 6 ; Araki, 1960, p. 104, pl. 8, fig. 5 (reproduced from Araki, 1959).

Musashia (*Neopsephaea* ?) *yanagidaniensis* (Araki) ; Shikama, 1967, p. 115, text-fig. 20, pl. 13, figs. 5-8.

Musashia (*Neopsephaea*) *yanagidaniensis* (Araki) ; Shikama, 1967, pl. 14, fig. 1 (same specimen as Shikama, 1967, pl. 13, fig. 8).

Musashia yanagidaniensis (Araki) ; Hayashi, 1973, pl. 3, fig. 8 ; Shibata and Ina, 1983, p. 62, pl. 9, fig. 6.

Psephaea ? *yanagidaniensis* (Araki) ; Shibata *in* Itoigawa *et al.*, 1974, p. 167, pl. 51, figs. 1-3, pl. 52, figs. 1, 2, pl. 53, figs. 1-3, pl. 54, figs. 5a-c.

Fulgoraria yanagidaniensis (Araki) ; Ishida *et al.*, 1980, pl. 6, figs. 34a-b.

Musashia (s. s.) *yanagidaniensis* (Araki) ; Itoigawa *et al.*, 1981.

Musashia ? *yanagidaniensis* (Araki) ; Itoigawa *et al.*, 1982, p. 239, pl. 40, figs. 1-2.

Fulgoraria (*Psephaea* ?) cf. *ashiyaensis* Shikama ; Hayashi, 1988, p. 7, pl. 3, fig. 8 (reproduced from *Musashia yanagidaniensis* ; Hayashi, 1973).

Remarks.—Seven specimens were collected from gray, very fine-grained sandstone at one locality in the Shimosato Formation. Araki (1959) proposed the present species under the name of *Fulgoraria hirasei yanagidaniensis* from the Kaisekizan Formation (upper Lower Miocene) of the Ichishi Group. The present species has also been recorded from the Akeyo Formation of the Mizunami Group and other strata of the Eastern Setouchi Miocene Series (Itoigawa *et al.*, 1981).

Occurrence.—Locality 2.

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References

Araki, Y., 1959 : On some Miocene Mollusca from Mie

Prefecture, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 36, p. 161-167, pl. 18.

Araki, Y., 1960: Geology, paleontology and sedimentary structures (including problematica) of the Tertiary formations developed in the environs of Tsu City, Mie Prefecture, Japan. *Bulletin of the Liberal Arts Department, Mie University, Special Volume*, no. 1, p. 1-118, pls. 1-11.

Blow, W.H., 1969: Late Middle Eocene to Recent planktonic foraminiferal biostratigraphy. *In*, Brönnimann, P. and Renz, H.H. *eds., Proceedings of the First International Conference on Planktonic Microfossils, Geneva, 1967*, Vol. 1, p. 119-422, pls. 1-54, E.J. Brill, Leiden, The Nederlands.

Chijiwa, K., 1988: Post-Shimanto sedimentation and organic metamorphism: an example of the Miocene Kumano Group, Kii Peninsula. *Modern Geology*, vol. 12, p. 363-387.

Chijiwa, K. and Tomita, S., 1985: On the Onuma Formation of the Kumano Group (A study of the Tertiary formations of the Kumano coal-field in the Kii Peninsula, Southwest Japan, Part 3). *Memoirs of the Faculty of Science, Kyushu University, Ser. D, Geology*, vol. 25, no. 3, p. 319-336, pl. 41.

Chinzei, K., 1986: Faunal succession and geographic distribution of Neogene molluscan faunas in Japan. *Palaeontological Society of Japan, Special Papers*, no. 29, p. 17-32.

Editorial Committee of KINKI, *ed.*, 1987: *Regional Geology of Japan Part 6 KINKI*, 297 p. Kyoritsu Shuppan Co., Tokyo. (*in Japanese*)

Hayashi, T., 1973: Fossils from the environs of Horaijisan. *Bulletin of the Horaijisan Natural Science Museum*, p. 10-17, incl. pls. 1-6. (*in Japanese*)

Hayashi, T., 1988: Reexamination of fossils from the environs of Horaijisan. *Bulletin of the Horaijisan Natural Science Museum*, no. 18, p. 3-14, incl. pls. 1-6. (*in Japanese*)

Hayashi, T. and Miura, Y., 1973: The Cenozoic sediments in the southern part of Okazaki City, central Japan. *The Bulletin of Aichi University of Education*, vol. 22, *Natural Science*, p. 133-149, incl. pls. 1-2. (*in Japanese with English abstract*)

Higo, S. and Goto, Y., 1993: *A Systematic List of Molluscan Shells from the Japanese Is. and the Adjacent Area*, 879 p. Elle Scientific Publications, Yao, Osaka. (*in Japanese*)

Hisatomi, K., 1984: Sedimentary environment and basin analysis of the Miocene Kumano Group in the Kii Peninsula, Southwest Japan. *Memoirs of the Faculty of Science, Kyoto University, Series of Geology and Mineralogy*, vol. 50, nos. 1-2, p. 1-65, pls. 1-4.

Hisatomi, K., 1987: The Kumano Group. *In*, Editorial Committee of KINKI *ed., Regional Geology of Japan Part 6 KINKI*, p. 128-131. Kyoritsu Shuppan Co., Tokyo. (*in Japanese*)

Hisatomi, K. and Miyake, Y., 1981: Upheaval movement and igneous activity in the Shionomisaki area, Kii Peninsula, Southwest Japan. *The Journal of the Geological Society of Japan*, vol. 87, no. 10, p. 629-639. (*in Japanese with English abstract*)

Honda, Y., 1992: A Miocene molluscan fauna from the Owase Group, Kii Peninsula, Southwest Honshu. *Bulletin of the Mizunami Fossil Museum*, no. 19, p. 413-425, pl. 58.

Ibaraki, M., 1990: Geologic ages of *Lepidocyclina* in Japan with implications in the northward drift of the Izu Peninsula. *In*, Tsuchi, R. *ed., Pacific Neogene Events, Their Timing, Nature and Interrelationship*, p. 137-149. University of Tokyo Press.

Ikebe, N., Chiji, M. and Morozumi, Y., 1975: *Lepidocyclina* horizon in the Miocene Kumano Group in reference to planktonic foraminiferal biostratigraphy. *Bulletin of the Osaka Museum of Natural History*, no. 29,, p. 81-89, pls. 20-21. (*in Japanese with English abstract*)

Irizuki, T. and Matsubara, T., 1994: Vertical changes of depositional environments of the Lower to Middle Miocene Kadonosawa Formation based on analysis of fossil ostracode faunas. *The Journal of the Geological Society of Japan*, vol. 100, no. 2, p. 136-149. (*in Japanese with English abstract*)

Ishida, S., Okamura, Y. and Matsuoka, C., 1980: Stratigraphy and fossils of the Ayugawa Group. *In*, Branch of Geomorphology and Geology, Nature Study Society of Shiga Prefecture *ed., Land and Life in Shiga, Separate Volume for Geomorphology and Geology and Geological Map of Shiga Prefecture 1 : 100,000 in Scale*, p. 251-299, incl. pls. 1-6. Foundation of Nature Conservation in Shiga Prefecture. (*in Japanese with English summary*)

Ishii, T., Yanagisawa, Y., Yamaguchi, S., Sangawa, A. and Matsuno, K., 1982: *Geology of the Matsushima District. Quadrangle Series, Scale 1 : 50,000*, 121 p. Geological Survey of Japan. (*in Japanese with English abstract*)

Itoigawa, J., 1956: Molluscan fauna of the Tsuzuki Group in Kyoto Prefecture, Japan. *Memoirs of the College of Science, University of Kyoto, Ser. B (Geology and Mineralogy)*, vol. 23, no. 2, p. 179-192, pls. 1-3.

Itoigawa, J., 1987: Early to Middle Miocene molluscan faunas in Southwest Japan and Korea. *Geological Reports of Shimane University*, no. 6, p. 29-38. (*in Japanese with English abstract*)

Itoigawa, J., 1988: The Miocene Kadonosawa fauna of Japan. *In*, Grant-Mackie, J.A., Masuda, K. and Ogasawara, K. *eds., Professor Tamio Kotaka Commemorative Volume on Molluscan Paleontology, Special Publication, Saito Ho-on Kai Museum of Natural History*, no. 2, p. 397-403.

Itoigawa, J., 1989: Tropical spike in early Middle Miocene (ca. 16 MA) of Southwest Japan. *In*, Gengwu, L., Tsuchi, R. and Qibin, L. *eds., Proceedings of International Symposium of Pacific Neogene Continental and Marine Events*, p. 19-26. National Working Group of China for IGCP-246, Nanjing University Press, Nanjing.

Itoigawa, J. and Shibata, H., 1975: New Miocene pelecypods from the Mizunami Group, Mizunami City, central Japan. *Bulletin of the Mizunami Fossil Museum*, no. 2, p. 15-34, pls. 6-8.

Itoigawa, J. and Shibata, H., 1986: Molluscan fauna of the Setouchi Miocene Series, Southwest Japan. *Palaeontological Society of Japan, Special Papers*, no. 29, p. 149-159, pls. 16-17.

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

Itoigawa, J., Shibata, H. and Nishimoto, H., 1974: Molluscan fossils from the Mizunami Group. *Bulletin of the Mizunami Fossil Museum*, no. 1, p. 43-203, pls. 1-63. (*in Japanese*)

Itoigawa, J., Shibata, H., Nishimoto, H., and Okumura, K., 1981: Miocene fossils of the Mizunami Group, central Japan. 2. Molluscs. *Monograph of the Mizunami Fossil Museum*, no. 3-A, p. 1-53, pls. 1-52. (*in Japanese*)

Itoigawa, J., Shibata, H., Nishimoto, H., and Okumura, K., 1982: Miocene fossils of the Mizunami Group, central Japan. 2. Molluscs (Continued). *Monograph of the Mizunami Fossil Museum*, no. 3-B, p. 1-330. (*in Japanese*)

Katto, J. and Masuda, K., 1978: Tertiary Mollusca from the southern part of Kii Peninsula, Wakayama Prefecture, Southwest Japan. *Research Reports of the Kochi University*, vol. 27, *Natural Science*, p. 97-111, pls. 1-5.

Katto, J., Masuda, K. and Sako, Y., 1976: A note on the so-called Upper Muro Group, Wakayama Prefecture. *Research Reports of the Kochi University*, vol. 24, *Natural Science*, no. 15, p. 1-10, pls. 1-4. (*in Japanese with English abstract*)

Katto, J., Masuda, K., Taira, A., and Sako, Y., 1980: On the molluscan fauna and lithofacies of the Kumano Group at the Komugi area, Nachikatsuura Town, Wakayama Prefecture. *In*, Taira, A. and Tashiro, M. *eds., Selected Papers in Honor of Prof. Jiro Katto, Geology and Paleontology of the Shimanto Belt*, p. 101-108, pls. 14-15. Rinyakosaikai Press, Kochi. (*in Japanese with English abstract*)

Kotaka, T., 1951: Recent *Turritella* of Japan. *Short Papers from the Institute of Geology and Paleontology, Tohoku University*, no. 3, p. 70-90, pls. 11-12.

Kotaka, T., 1959: The Cenozoic Turritellidae of Japan. *The Science Reports of the Tohoku University, Second Series* (*Geology*), vol. 31, no. 2, p. 1-135, pls. 1-15.

Marincovich, L., Jr., 1988: Recognition of an earliest Middle Miocene warm-water event in a southwestern Alaskan molluscan fauna. *In*, Grant-Mackie, J.A., Masuda, K. and Ogasawara, K. *eds., Professor Tamio Kotaka Commemorative Volume on Molluscan Paleontology, Special Publication, Saito Ho-on Kai Museum of Natural History*, no. 2, p. 1-24, pls. 1-3.

Marincovich, L., Jr. and Kase, T., 1986: An occurrence of *Turritella* (*Hataiella*) *sagai* in Alaska: implications for the age of the Bear Lake Formation. *Bulletin of the National Science Museum, Tokyo, Ser. C*, vol. 12, no. 2, p. 61-66.

Masuda, K., 1963: Three Miocene *Dosinia* from near Sendai City, Miyagi Prefecture, Northeast Honshu, Japan, with reference to some Miocene *Dosinia*. *Saito Ho-on Kai Museum of Natural History, Research Bulletin*, no. 32, p. 18-29, incl. pls. 3-4.

Matsubara, T., 1995a: Fossil Mollusca of the Lower Miocene Yotsuyaku Formation in the Ninohe district, Iwate Prefecture, Northeast Japan. Part 1. General consideration of the fauna. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 180, p. 303-320.

Matsubara, T., 1995b: Fossil Mollusca of the Lower Miocene Yotsuyaku Formation in the Ninohe district, Iwate Prefecture, Northeast Japan. Part 2 (1). Bivalvia and Scaphopoda. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 180, p. 321-335.

Mizuno, A., 1953: Notes on the Miocene molluscs from the Kumano Group in the south-eastern Kii Peninsula, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 9, p. 9-18.

Mizuno, A., 1957: *Explanatory text of the geological map of Japan. Scale 1: 50,000, Nachi*, 40 p. Geological Survey of Japan. (*in Japanese with English abstract*)

Muramatsu, K., 1992: Geology and molluscan assemblages of the Ayugawa Group, Shiga Prefecture, Japan. *Bulletin of the Mizunami Fossil Museum*, no. 19, p. 301-317, pls. 48-50. (*in Japanese with English abstract*)

Nishimura, A. and Miyake, Y., 1973: Occurrences of *Lepidocyclina* and *Miogypsina* from the Kumano Group. *Collected Papers from Symposium on the Shimanto Geosyncline*, p. 37-38. Published by Wakayama University, Wakayama. (*in Japanese*)

Ogasawara, K. and Noda, H., 1996: Miocene *Hataiarca* (Mollusca, Bivalvia) invasion event in the Japanese Islands from a viewpoint of Indo-Pacific connection. *In*, Noda, H. and Sashida, K. *eds., Professor Hisayoshi Igo Commemorative Volume on Geology and Paleontology of Japan and Southeast Asia*, p. 133-139.

Otuka, Y., 1934: Tertiary structures of the northwestern end of the Kitakami mountainland, Iwate Prefecture, Japan. *Bulletin of the Earthquake Research Institute*, vol. 12, part 3, p. 566-638, pls. 44-51.

Otuka, Y., 1939: Tertiary crustal deformations in Japan (with short remarks on Tertiary paleogeography). *Jubilee Publication in the Commemoration of Prof. H. Yabe, M.I.A. Sixtieth Birthday*, vol. 1, p. 481-519.

Ozawa, T., Inoue, K., Tomita, S., Tanaka, T., and Nobuhara, T., 1995: An outline of the Neogene warm-water molluscan faunas in Japan. *Fossils*, no. 58, p. 20-27. (*in Japanese with English abstract*)

Saeki, H. and Koto, J., 1972: Geology and ore deposits of the central Kie Peninsula. *Mining Geology*, vol. 22, no. 7, p. 437-447. (*in Japanese with English abstract*)

Shibata, H., 1967: Geology of the Miocene Ichishi Group. *The Journal of the Geological Society of Japan*, vol. 73, no. 7, p. 337-346. (*in Japanese with English abstract*)

Shibata, H., 1978: Molluscan paleoecology of the Miocene First Setouchi Series in the eastern part of the Setouchi geologic province, Japan. *Bulletin of the Mizunami Fossil Museum*, no. 5, p. 23-110.

Shibata, H. and Ina, H., 1983: Mollusks and plants from the Shidara Group (Miocene), central Japan. *Monograph of the Mizunami Fossil Museum*, no. 4, p. 1-89, pls. 1-24. (*in Japanese*)

Shikama, T., 1967: System and evolution of Japanese fulgorarid Gastropoda. *Science Reports of the Yokohama National University, Sec. 2, Biological and Geological Sciences*, no. 13, p. 23-132, pls. 1-17.

Suzuki, H., 1976: The Muro Group and the Kumano Group of the Ukui district in the Kii Peninsula, Southwest Japan. *The Science and Engineering Review of Doshisha University*, vol. 17, no. 2, p. 126-137. (*in Japanese with English abstract*)

Suzuki, K., 1934: On the geological age of the Miyai Coal-bearing Tertiary in the southeastern Kii Peninsula. *Chikyu* (*The Globe*), vol. 21, no. 5, p. 329-364. (*in

Japanese)

Taki, I. and Oyama, K., 1954: Matajiro Yokoyama's the Pliocene and later faunas from the Kwanto region in Japan. *Palaeontological Society of Japan, Special Papers*, no. 2, p. 1-68, pls. 1-49.

Tanai, T. and Mizuno, A., 1954: Geological structure in the vicinity of the Kumano coal field in southeastern Kii Peninsula. *The Journal of the Geological Society of Japan*, vol. 60, no. 700, p. 28-39. (*in Japanese with English abstract*)

Titova, L.V., 1994: Revision of the Neogene Turritellidae (Mollusca: Gastropoda) from Kamchatka. *Ruthenica*, vol. 4, no. 1, p. 1-20.

Tsuda, K., 1960: Paleo-ecology of the Kurosedani fauna. *Journal of the Faculty of Science, Niigata University, Ser. 2*, vol. 3, no. 4, p. 171-203.

Ujihara, A. and Shibata, H., 1982: Molluscs and elasmobranchs from the Miocene Kumano Group in the southern part of the Kii Peninsula, Japan. *Bulletin of the Mizunami Fossil Museum*, no. 9, p. 25-33, pls. 5-6. (*in Japanese with English abstract*)

Yokoyama, M., 1924: Molluscan remains from the lowest part of the Jôban coal-field. *Journal of the College of Science, Tokyo Imperial University*, vol. 45, p. 1-22, pls. 1-5.

Yoon, S., 1979: The Tertiary deposits of the Ulsan Basin. No. 2. Molluscan Fossils. *The Journal of the Geological Society of Korea*, vol. 15, no. 1, p. 1-36, incl. pls. 1-5.

Yoshida, F., 1991: Planktonic foraminifera from the Ichishi, Fujiwara, and Morozaki groups in the Eastern Setouchi Geologic Province, central Japan. *Bulletin of the Mizunami Fossil Museum*, no. 18, p. 19-31, pls. 1-2.

Zhidkova, L., S. and Sal'nikov, B.A. *eds*., 1992: *Reference section of Paleogene-Neogene deposits of south-east Sakhalin* (*Makarov Section*), 357 p., 68 pls. All-Russia Petroleum Scientific-Research Geological-Exploration Institute (VNIGRI), St.-Petersburg. (*in Russian*)

Ajiri 網尻，Akebihara 山女原，Akeyo 明世，Asagai 浅貝，Ayugawa 鮎川，Ichishi 一志，Iwamura 岩村，Kadonosawa 門ノ沢，Kaisekizan 貝石山，Kitsune-jima キツネ島，Kurosedani 黒瀬谷，Koguchi 小口，Kumano 熊野，Kunugidaira 椚平，Kurami 倉真，Mitsuno 三津野，Muro 牟婁，Nachikatsuura 那智勝浦，Nakayama 中山，Nankai 南海，Onuma 大沼，Osone 大曽根，Owase 尾鷲，Semotobana 瀬元鼻，Setouchi 瀬戸内，Shikiya 敷屋，Shimosato 下里，Shiode 塩手，Shiogama 塩釜，Tanabe 田辺，Togari 戸狩，Tomikusa 富草，Tsuzuki 綴喜，Uematsu 植松，Ukui 宇久井，Yamanouchi 山野内，Yotsuyaku 四ツ役，Yukunoura 行野浦

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A new species of *Nemestheria* (Crustacea, Conchostraca) from the Aioi Group (Cretaceous) of Okayama, Japan

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Abstract. *Nemestheria aidaensis* sp. nov. represents the first appearance in Japan of this genus, which is considered as the leading form of conchostracan fossils in nonmarine Cenomanian deposits and has a wide distribution. This new species is very similar to *Nemestheria lineata* Chang and Chen and *Nemestheria robusta* Zhang and Chen collected from the Qingshankou Formation of NE China. The results of both palaeontological researching and Fission-Track dating have shown that the Tsurukame Upper Formation of the Aioi Group might be Cenomanian in age.

Key words : Aioi Group, Cenomanian, conchostracans, Okayama

Introduction

The genus *Nemestheria* was established within the family Bairdestheriidae Novojilov by Chang and Chen (1964) based on the type species *N. lineata* Chang and Chen from the Cenomanian Qingshankou Formation of NE China. It has been also found in the Red Branch Member of the Woodbine Formation of Northern Texas (Stephenson, 1952 ; Zhang *et al*., 1976) ; the Matoushan Formation of Central Yunnan of China (Chen, 1977) ; the Chaochuan Formation of Zhejiang, the Hekou Formation of Fujian and the Huizhou Formation of southern Anhui Provinces of southern China (Chen and Shen, 1982) ; the Kukebai Formation of Kashgal, Xinjiang Ugur Automonous Region, northern China (Li and Chen, 1992).

This paper reports a new species of *Nemestheria* from a black shale of the Kagami Member of the Tsurukame Upper Formation, Cretaceous Aioi Group (Igi and Wadatsumi, 1980) near Nakaiso of Aida Town, Okayama Prefecture, Southwest Japan (Figures. 1 and 2). The conchostracans-bearing volcano-sedimentary series of Hyogo Prefecture has been referred to as the Sasayama Group, correlated generally to the Inkstone Group of the Hiroshima or Okayama area, or the Kanmon Group of Kitakyushu area, as early Cretaceous rocks (Matsuura and Yoshikawa, 1992). According to the carapace and ornamentation of growth bands, the conchostracan fossils collected from Sasayama Town, Taki County, Hyogo of Japan (Kusumi, 1960) are similar to those from the Inakura Formation near Yamaji village of Ibara City, Okayama, and probably belong to the yanjiestherids (Chen, 1996, pl. 1, figs. 1-8 ; pl. 2, figs. 1-2). The specimens described in the present paper, however, differ from them in having a smaller carapace, strong and stout growth lines with a median groove, and both long and short radial lirae in the growth bands. All of them show the characteristics of *Nemestheria*. The occurrence of *Nemestheria* indicates that the Kagami Member of the Tsurukame Upper Formation might probably be Cenomanian in age. This estimation of the age of the member seems to be conformable to the age of the Takitani Member overlying the Kagami Member by fission-track dating (Masumoto and Wadatsumi, 1983).

Systematic description

Family Jilinestheriidae Zhang and Chen, 1976

Remarks.—Carapace valve elliptic, rectangular, oval or subcircular in outline ; growth lines stout and strong ; intervals (growth bands) broad and few in number, ornamented with various complex striae and lattice-work all developing from the simple radial striae ; these complex sculptures of lineal arrangement in the posterior or postero-vental part of valve.

It includes.—*Nemestheria* Chang and Chen, 1964, *Jilinestheria* Zhang and Chen, 1976, *Pletestheria* Zhang and Chen, 1976 and *Dictyestheria* Chang and Chen, 1964.

Geologic age.—Cretaceous.

Genus **Nemestheria** Chang and Chen, 1964

Type species.—*Nemestheria lineata* Chang and Chen, 1964 from Cenomanian Qingshankou Formation at Huaide of Jilin Province, NE China.

Diagnosis.—Carapace valve of small to moderate size ; oval, elongately elliptic, circular or subquadrate in outline ; umbo anterior or subcentral ; long and radial striae intercalated with short lirae in the growth bands ; the short lirae only in the lower half of each interval, missing near the umbo (Chang and Chen, 1964).

Distribution.—East Asia and Northern America ; Cenomanian.

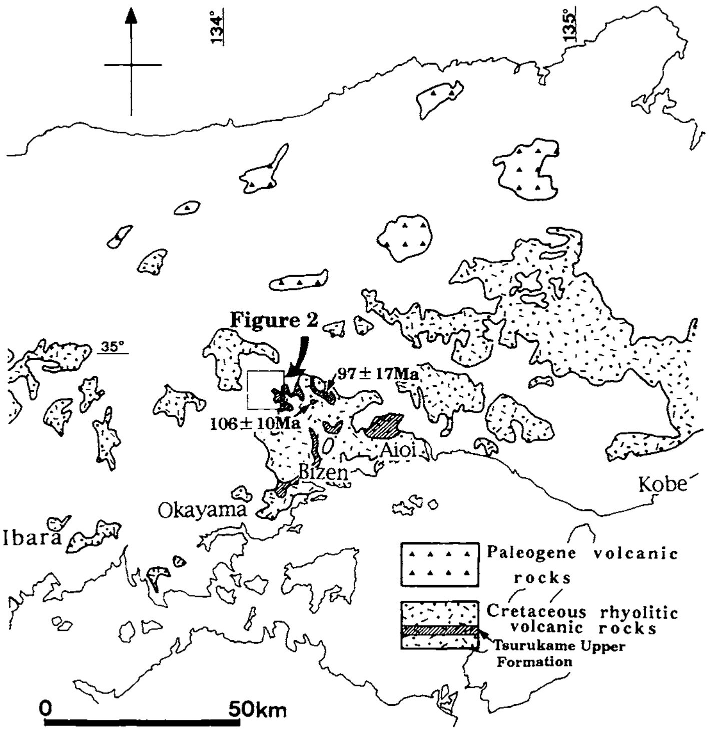

Figure 1. Distribution of the Cretaceous to Paleogene rhyolitic to dacitic volcanic rocks in Inner Southwest Japan. Locality of Figure 2 and the place and data of the fission-track dating (Masumoto and Wadatsumi, 1983) are also shown.

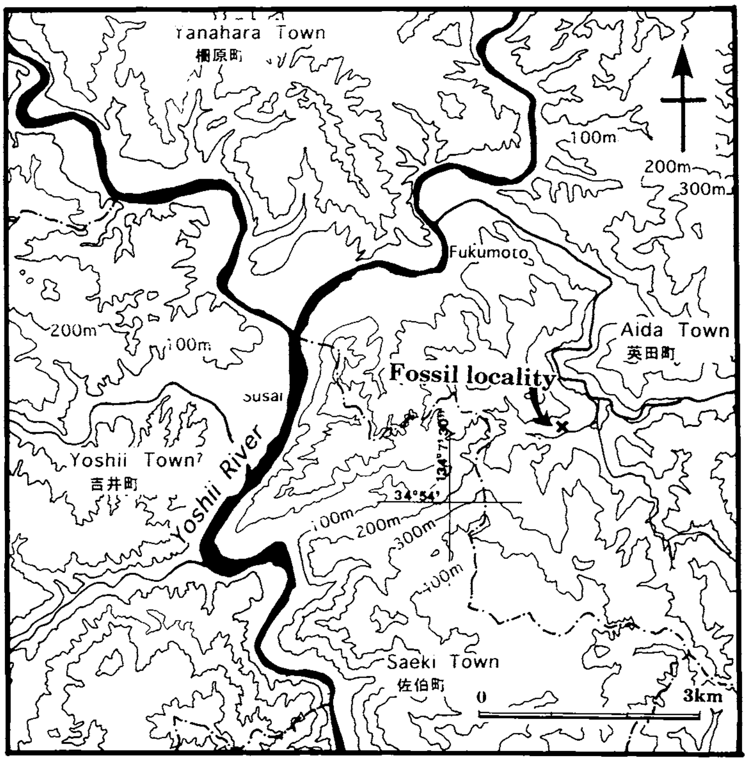

Figure 2. Map of the Aida area, Okayama Prefecture, showing the fossil locality.

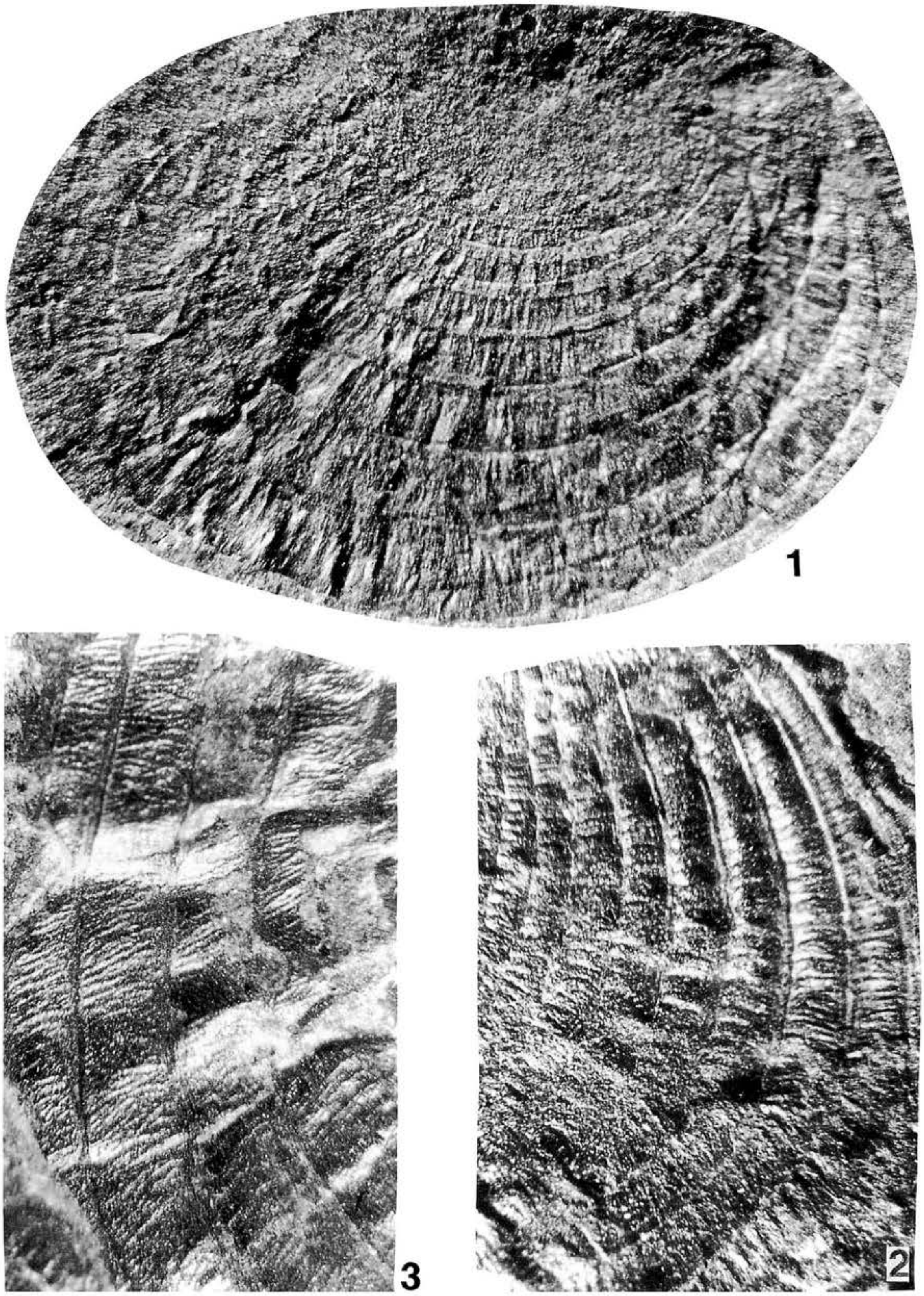

Figure 3. *Nemestheria aidaensis* Chen and Suzuki sp. nov. **1.** external mould of left valve, ×40, A10A.T.; cat. no. 128937. **2.** frangment of right valve, ×40, A10A.T.; cat. no. 128938. **3.** sculpture of growth bands near the postero-ventral margin of the holotype, ×40, A10A.T.; cat. no. 128939.

Nemestheria aidaensis sp. nov.

Figures 3-1—3 ; 4-1—5

Diagnosis.—A *Nemestheria* species having shorter elliptic outline of carapase valve and broadly curved ventral margin.

Materials.—Only one sample with about 70 carapace valves. It was collected from a black shale of the Kagami Member of the Tsurukame Upper Formation, the Aioi Group in southwestern Aida Town of Okayama Prefecture, Southwest Japan. Holotype : right valve cat. no. 128939. All specimens utilized here are housed in the Nanjing Institute of Geology and Palaeontology.

Description.—Carapace small to medium in size, elliptical to subcircular in outline, 3.5-8.0 mm long, 2.1-5.4 mm high. Dorsal margin broken with umbo between its center and anterior end. Anterior and posterior margins rounded, ventral margin broadly curved downward. 13-20 stout growth lines with median grooves. Long and radial striae intercalated with 1-2 short lirae in growth bands ; the short lirae only in the lower half of each interval, missing near umbo (Figures 3-1—2 ; Figures 4-5) or expanding as long as radial striae near ventral margin (Figures 3-3).

Remarks.—The new species closely resembles *N. lineata* Chang and Chen and *N. robusta* Zhang and Chen from the Qingshankou Formation of the Songliao Basin in NE China, but it differs from the former in having shorter elliptic outline of the carapace valve and from the latter in having a broadly curved ventral margin.

Locality and horizon.—Southwestern Aida Town of Okayama Prefecture, Southwest Japan ; Kagami Member of the Tsurukame Upper Formation (Cenomanian age), Cretaceous Aioi Group.

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Reference cited

Chang, W.T. and Chen, P.C., 1964 : New Cretaceous Conchostraca from Jilin and Heilongjiang. *Acta Palaeontologica Sinica*, vol. 12, no. 1, p. 1-25, pls. 1-5. (*in Chinese with English abstract*)

Chen, P.J. 1977 : Mesozoic and Cenozoic conchostracans from Yunnan, China. *Mesozoic fossils of Yunnan*, no. 2, p. 331-372, pls. 1-26, Science Press, Beijing. (*in Chinese*)

Chen, P.J. 1996 : Lower Cretaceous conchostracans of SW Japan. *Bulletin of the Kitakyushu Museum of Natural History*, no. 15, p. 1-12, pls. 1-4.

Chen, P.J. and Shen, Y.B., 1982 : Late Mesozoic conchostracans from Zhejiang, Anhui and Jiangsu provinces. *Palaeontologia Sinica, New Series B*, no. 17, 117 p., 47 pls. (*in Chinese with English abstract*)

Igi, S. and Wadatsumi, K., 1980 : *Geology of the Kamigori district*, 74 p. Quadrangle Series, Scale 1 : 50,000, Geological Survey of Japan. (*in Japanese with English abstract*)

Kusumi, H. 1960 : On the occurrence of Cretaceous estherids in North Kyushu. *Journal of Science, Hiroshima University, Series C*, vol. 3, no. 1, p. 15-24, pls. 1-4.

Li, W.B. and Chen, J.H., 1992 : Cretaceous of Tarim. *In*, Zhou, Z.Y. and Chen, P.J. *eds., Biostratigraphy and Geological Evolution of Tarim*, p. 315-336, Science Press, Beijing.

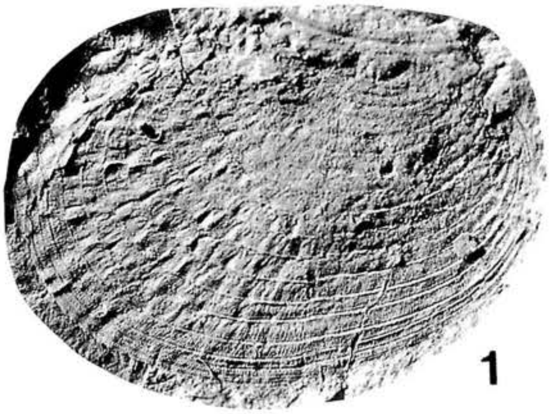
Masumoto, S. and Wadatsumi, K., 1983 : Paleogene dike swarms in the Yanahara area—Dike method for analysis of regional and local stress field. *Journal of the Geological Society of Japan*, vol. 89. no. 2, p. 87-97. (*in Japanese with English abstract*)

Matsuura, H. and Yoshikawa, T., 1992 : Radiometric ages of the Early Cretaceous Sasayama Group, Hyogo Prefecture, Southwest Japan. *Journal of the Geological Society of Japan*, vol. 98, no. 7, p. 635-643. (*in Japanese with English abstract*)

Stephenson, L.W. 1952 : Larger Invertebrate fossils of the Woodbine Formation (Cenomanian) of Texas. *U. S. Geological Survey, Professional Paper*, no. 242, p. 1-226, pls. 8-59.

Zhang, W.T., Chen, P.J. and Shen, Y.B., 1976 : *Fossil Conchostraca of China*. 325 p., 138 pls., Science Press, Beijing. (*in Chinese*)

Figure 4. *Nemestheria aidaensis* Chen and Suzuki sp. nov. **1.** holotype, right valve, ×8.5, A10A.T. ; cat. no. 128939. **2.** broken right valve, ×8.5, A10A.T. ; cat. no. 128940. **3.** sculpture of growth bands in upper half of valve, ×40, A10A.T. ; cat. no. 128940. **4.** opening two valves, ×8.5, A10A.T. ; cat. no. 128941. **5.** sculpture of growth bands, ×40, A10A.T. ; cat. no. 128941.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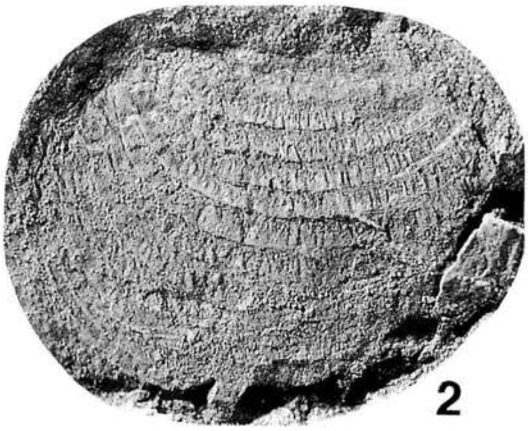
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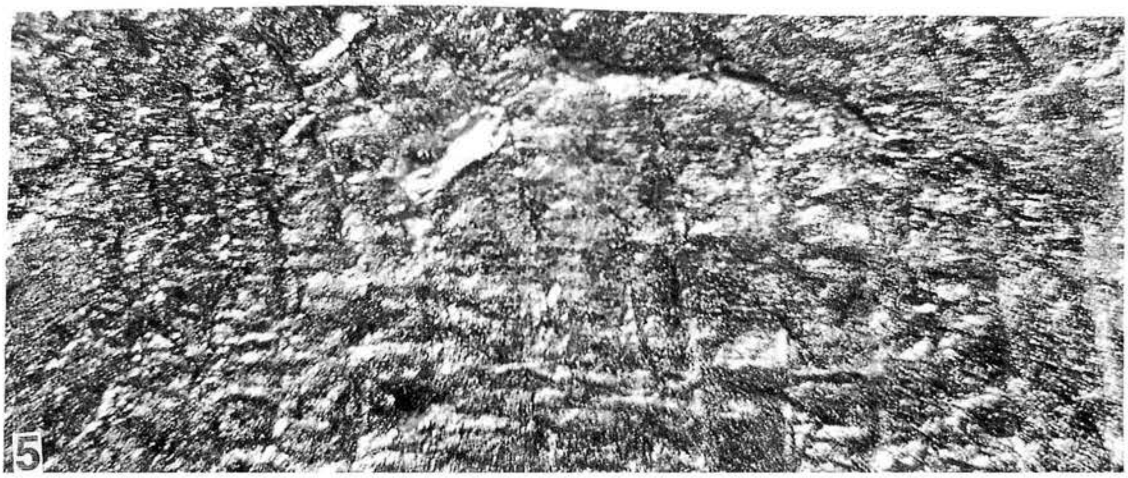
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Ostracode faunal changes after the mid-Neogene climatic optimum elucidated in the Middle Miocene Kobana Formation, Central Japan

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Abstract. One hundred and forty-nine ostracode species are identified among 42 samples from the lower to middle part of the Middle Miocene Kobana Formation, Arakawa Group, distributed in Tochigi Prefecture, Central Japan. Dominant throughout the formation are such species living around Japan as *Schizocythere kishinouyei* (Kajiyama), *Paracytheridea neolongicaudata* Ishizaki, *Cornucoquimba moniwensis* (Ishizaki), *Cornucoquimba saitoi* (Ishizaki) and *Cythere omotenipponica* Hanai. Tropical to warm-temperate species living off Southwest Japan are abundant, but circumpolar and cryophilic species are also present (less than 10%) in most samples. Q-mode cluster and principal components analyses disclose the following sequence of ostracode faunas : 1) The lowest part is dominated by nearshore and subtropical species and contains about 5-13% of circumpolar and cryophilic species ; 2) The lower middle part is dominated by lower sublittoral to upper bathyal muddy dwellers, suggesting a rapid increase of water depth. The horizon characterized by the increase of deep cool-water species is recognized ; 3) The middle to upper part, characterized by lower to middle sublittoral subtropical to warm-temperate water species mixed with intertidal to upper sublittoral ones ; 4) The upper part containing many *Laperousecythere* species, suggesting a cooler climate. Analyses of ostracode faunas indicate that after the mid-Neogene climatic optimum, benthic environments underwent fluctuations of water temperatures, with no rapid decrease, in the Karasuyama area.

Key words : Central Japan, Kobana Formation, Middle Miocene, Miocene isotope, Ostracoda

Introduction

Based on oxygen isotope data at DSDP Site 588 and vertical changes in diatom frequencies at Site 572, three periods of significant climatic warming were noted by Barron and Baldauf (1990) during the Miocene in the North Pacific region. One of these climatic optima, which lasted from ca. 16.5 to 15 Ma, has been referred to as the "mid-Neogene climatic optimum" of Tsuchi (1986), "tropical spike" of Itoigawa (1989), or "climatic optimum 1" of Barron and Baldauf (1990). This interval is characterized by relatively low oxygen-isotope values for benthic foraminifers from deep seas of the equatorial Pacific Ocean (e.g., Savin *et al.*, 1981 ; Woodruff *et al.*, 1981 ; Woodruff and Savin, 1989 ; Kennett, 1986). During this interval, the tropical to subtropical shallow-water Kurosedani-Kadonosawa molluscan fauna spread up to southern Hokkaido in Japan (e.g., Oyama, 1950 ; Chinzei, 1986 ; Tsuchi, 1986 ; Itoigawa, 1989 ; Itoigawa and Yamanoi, 1990). Mangrove swamps also developed were especially on the proto-Japan Sea side at that time (Oyama, 1950 ; Yamanoi *et al.*, 1980 ; Itoigawa and Yamanoi, 1990). After that, major middle Miocene cooling began 14.9 Ma and continued to 12.4 Ma, particularly at high latitudes (Savin *et al.*, 1981 ; Woodruff *et al.*, 1981). During this interval, oxygen isotope values for benthic foraminifers increased by more than 1.0‰ (Savin *et al.*, 1981 ; Woodruff *et al.*, 1981 ; Woodruff and Savin, 1989) and the cool-temperate water Shiobara-Yama molluscan fauna dominated in northeastern Japan (Chinzei and Iwasaki, 1967 ; Iwasaki, 1970). Such marine climatic cooling was caused globally by the formation of the East Antarctic ice sheet (Woodruff *et al.*, 1981 ; Kennett, 1986) and locally by collision of Southwest Japan and the

Izu-Bonin Arc (Nishimura, 1994). Recently Miller *et al.* (1991), Wright and Miller (1992) and Wright *et al.* (1992) proposed global Oligocene-Miocene oxygen isotope zones. Their syntheses suggest that glacial episodes have repeatedly punctuated post-Eocene climatic history.

Many workers have studied the relationships between ostracode faunas and Plio-Pleistocene climatic fluctuations in Japan (e.g., Ishizaki *et al.*, 1993; Cronin *et al.*, 1994, Ozawa, 1996). However, Miocene ostracode faunas have been studied only locally in Japan (Ishizaki, 1963, 1966; Nohara, 1987; Yajima, 1988, 1992; Irizuki, 1994; Irizuki and Matsubara, 1994, 1995; Ishizaki *et al.*, 1996), and only a few attempts have so far been made at revealing faunal sequences in relation to Early to Middle Miocene marine climatic history. Irizuki and Matsubara (1994, 1995) analyzed in detail vertical changes of ostracode faunas from the Lower to Middle Miocene Kadonosawa and Middle Miocene Suenomatsuyama Formations in the Ninohe area, northeastern Japan. They recognized that circumpolar and cryophilic species first appeared at the base of the *Denticulopsis praelauta* Zone (the middle part of the Kadonosawa Formation). In addition, they mentioned that circumpolar and cryophilic ostracodes commonly continued to occur up to the lower part of the Suenomatsuyama Formation (the upper part of the *Denticulopsis praelauta* Zone) and warm-water species in turn increased upward in the section. The interval represented by the dominance of circumpolar and cryophilic ostracodes (ca. 25-60%) in the Ninohe area is chronologically correlative with the Miocene isotope 2 event, which is defined as located between chronozones C5Cn and C5Br (ca. 16 Ma) (Miller *et al.*, 1991). The Miocene isotope 2 event is recorded not only by benthic δ^{18}O at worldwide ODP and DSDP sites but also by planktonic δ^{18}O in the western equatorial Indian Ocean (e.g., Woodruff *et al.*, 1981; Woodruff and Savin, 1989; Vincent *et al.*, 1985; Kennett, 1986). Thus circumpolar and cryophilic ostracodes possibly spread south during the intervals of Miocene isotope events.

Continuous marine Middle to Upper Miocene sedimentary sequences composing the Arakawa Group are distributed in the Karasuyama area. Many workers are involved in investigations of various groups of microfossils from the same samples, and radioactive dating of intercalated tuff layers and sedimentology of the Arakawa Group. The Kobana Formation, composing the lowest part of the Arakawa Group, yields well-preserved calcareous fossils in abundance, including ostracodes which provided material for our studies. The purpose of this paper is to discuss quantitatively ostracode faunal sequences in the lower to middle part of the Kobana Formation for the first time, with reference to global marine climatic cooling (Miocene isotope events) after the mid-Neogene climatic optimum.

Geologic outline of the Karasuyama area

The Karasuyama area lies about 25 km northeast of Utsunomiya City, Tochigi Prefecture, Central Japan and is on the west side of the Yamizo Mountains of the Jurassic accretionary complex (Figure 1). The geology of this district has been investigated by Kawada (1948, 1949, 1953) and Sakai (1986). The Miocene distributed around the Karasuyama area comprises two groups: the Nakagawa and Arakawa (Figure 2). The Nakagawa Group consists mainly of pyroclastic rocks and comprises four formations: the Ichiba (conglomerate), the Motokozawa (conglomerate, sandstone, siltstone, tuff and lignite seam), the Yamanouchi (basaltic to andesitic volcaniclastic deposits and lava) and the Motegi (sandstone, siltstone, pumice tuff and andesitic to dacitic lava) in ascending order (Kawada, 1953; Takahashi and Hoshi, 1995; Hoshi and Takahashi, 1996a). The Motegi and Motokozawa Formations are dated at 16.7 ± 0.9 Ma and 18.6 ± 1.3 Ma by the fission track method, respectively (Takahashi and Hoshi, 1995, 1996; Hoshi and Takahashi, 1996b). The Arakawa Group unconformably overlies the Nakagawa Group. It consists of marine clastic rocks with many intercalated felsic tuff layers and comprises four formations: the Kobana (basal conglomerate, calcareous sandstone, siltstone and tuff), the Ogane (sandstone, siltstone and hard shale), the Tanokura (diatomaceous mudstone), and the Irieno (muddy sandstone) in ascending order (Figure 2). Both groups are covered unconformably with the Quaternary Kawasaki Group (gravel, sand and mud). Reported from the Arakawa Group have been various groups of marine fossils: molluscs by Kanno (1961) and Hirayama (1954, 1967, 1981); radiolarians by Sakai (1986) and Sugie (1993); diatoms by Sakai (1986); planktonic foraminifers by Sakai (1986) and

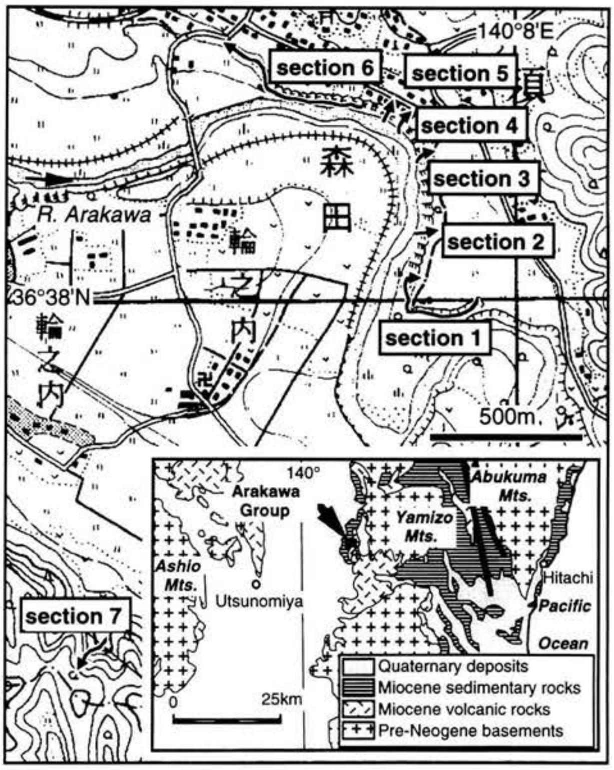

Figure 1. Geologic sketch map with the study area and topographic map showing locations of sections of the Kobana Formation measured along or near the Arakawa River (a part of topographic map "Karasuyama", 1:25,000 scale, Geographical Survey Institute of Japan).

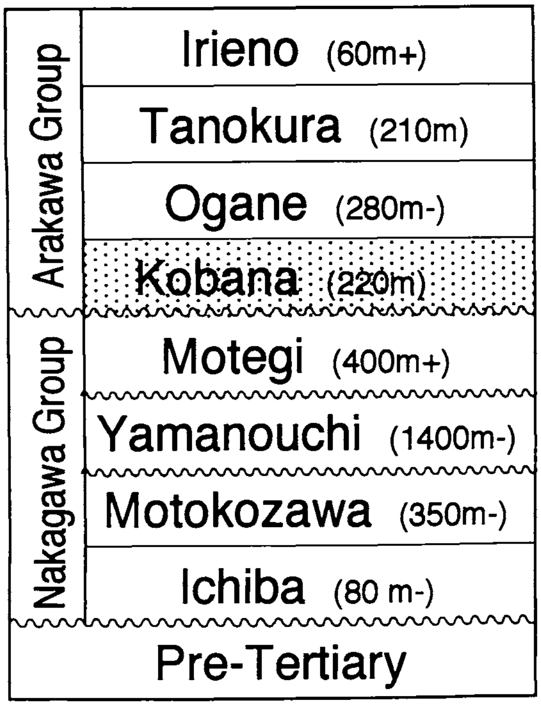

Figure 2. Stratigraphic division of the Neogene sequence of the Motegi and Karasuyama areas modified from Takahashi and Hoshi (1996).

Usami *et al.* (1995, 1996). The lower to middle part of the Kobana Formation is composed of basal conglomerate, very coarse- to medium-grained calcareous sandstone including large quantities of molluscan fossils, fine-grained sandstone, sandy siltstone, mudstone, and silty sandstone, in ascending order (Figure 3). The middle to upper part is composed mainly of sandy siltstone to silty sandstone with many intercalated felsic tuff layers (Kb 10 to Kb 30 of Sakai, 1986) and is conformably overlain by sandy siltstone of the Ogane Formation. Hirayama (1954, 1967, 1981) reported such subtropical molluscan fossils as *Chlamys arakawai* (Nomura), *Nipponopecten akihoensis* (Matsumoto) and *Siratoria siratoriensis* (Otuka) from the Kobana Formation. Some of them are constituents of the Kadonosawa Fauna, which represents the Early to Middle Miocene tropical to subtropical molluscan fauna. Recently, Tanaka and Takahashi (1997) determined the last occurrence horizon of *Sphenolithus heteromorphus* Deflandre between Kb 2 and Kb 3 tuff layers in the lower part of the Kobana Formation and that of *Cyclicargolithus floridanus* (Roth and Hay) Bukry in the lowermost part of the overlying Ogane Formation. Thus the Kobana Formation ranges over the calcareous nannofossil Zones CN4 to CN5a of Okada and Bukry (1980). Kb 1 and Kb 23 tuff layers are dated at 14.27±0.33 Ma or 14.28±0.33 Ma and 12.40±0.28 Ma or 12.37±0.28 Ma by the K-Ar method, respectively (Takahashi unpub. data). A sedimentation rate estimated by the chronologic controls implies that the studied interval ranges in age from about 13 to 14.5 Ma (Figure 4).

Materials and laboratory procedures

For studies of several kinds of microfossil groups, about 120 samples were collected from the Kobana Formation in ten measured sections exposed along or around the Arakawa River in Minaminasu-machi (Figure 1). A total of 42 samples obtained from the lower to middle part of the Kobana Formation were selected for examining vertical changes of ostracode faunas (Figure 3). The upper part of the Kobana Formation (tuffaceous silty sandstone with many intercalated tuff layers) contains too few fossil ostracodes to perform quantitative analyses. One hundred and sixty grams of dried sediment were treated with a saturated sodium sulfate solution and naphtha for rock maceration (Maiya and Inoue, 1973), washed through a 200 mesh sieve screen (75 μm), and dried again. These procedures were repeated until the whole sediment sample disintegrated. Samples containing abundant ostracode specimens were divided by a sample splitter into workable aliquot parts, each with around 200 specimens. The ostracode number refers to the minimum number of individuals as determined by adding larger numbers of either of the valves to the carapaces, picked from fractions coarser than 125 μm (115 mesh).

Analyses of ostracode faunas

One hundred and forty-nine species were identified from 42 samples obtained from the lower to middle part of the Kobana Formation. Figures 5 and 6 illustrate selected species from the Kobana Formation.

Only those species which were represented by three or more individuals in one or more samples were selected for further multivariate examination (Appendix I). To reveal faunal sequences of ostracodes quantitatively, the data on stratigraphic distributions of the selected 76 species by 42 samples were subjected to two kinds of multivariate analyses: Q-mode cluster and principal components analyses. The number of species, species diversity, equitability and individual number per 10 g sediment of ostracodes were selected to represent their faunal structure.

Q-mode cluster analysis

Q-mode cluster analysis using the weighted pair group arithmetic average method was carried out based on the overlap index of Horn (1966) to recognize biotopes of fossil ostracodes. This procedure grouped 42 samples into five clusters (biotopes) (A to E) (Figure 7). Table 1 summarizes dominant and subordinate ostracodes characterizing each biotope. Biotopes A to E are positioned upward in the sequence, with biotope D recurring in the uppermost part

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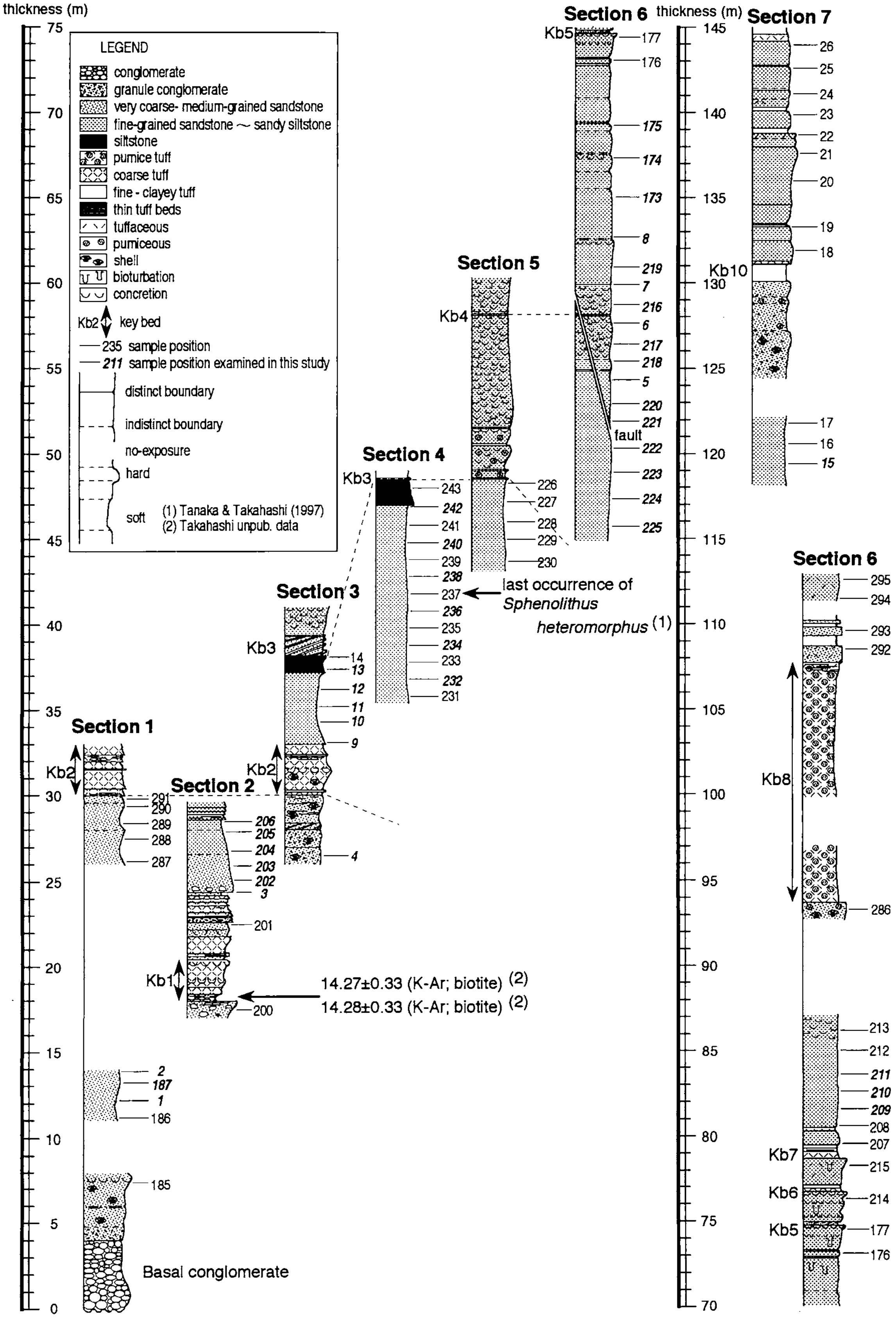
Figure 3. Columnar sections of the Kobana Formation in the Karasuyama area. Bold and italic numbers show samples used in this study.


thickness (m)
LEGEND
conglomerate
granule conglomerate
very coarse- medium-grained sandstone
fine-grained sandstone ~ sandy siltstone
siltstone
pumice tuff
coarse tuff
fine - clayey tuff
thin tuff beds
tuffaceous
pumiceous
shell
bioturbation
concretion
Kb2 key bed
235 sample position
211 sample position examined in this study
distinct boundary
indistinct boundary
no-exposure
hard
soft
(1) Tanaka & Takahashi (1997)
(2) Takahashi unpub. data
Section 1
Section 2
Section 3
Section 4
Section 5
Section 6
Section 7
Kb1
Kb2
Kb3
Kb4
Kb5
Kb6
Kb7
Kb8
Kb10
fault
last occurrence of Sphenolithus heteromorphus (1)
14.27±0.33 (K-Ar; biotite) (2)
14.28±0.33 (K-Ar; biotite) (2)
Basal conglomerate

(sample no. 15) of the sequence. It is notable that these biotopes are separated by major tuff beds. Figure 8 shows the stratigraphic position of the five biotopes and percentages of 19 taxa dominating each biotope.

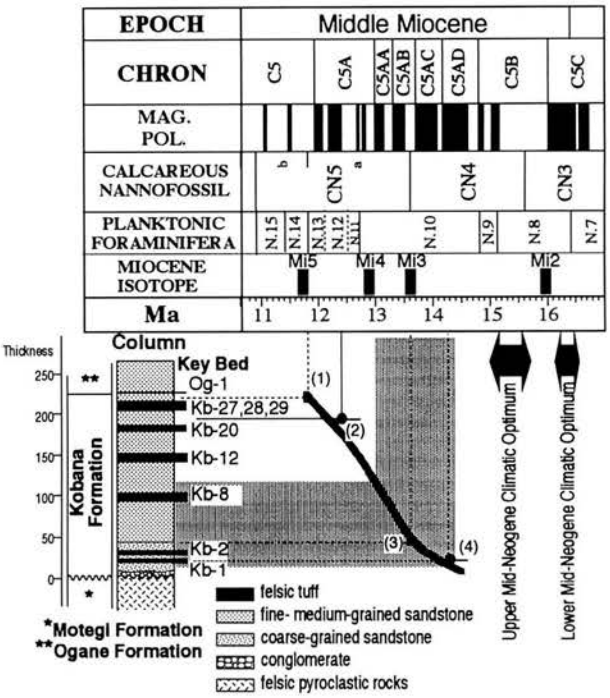


Figure 4. Geologic age and sedimentation rate of the Kobana Formation. The chronology and Miocene isotope events are based on Berggren *et al*. (1995) and Miller *et al*. (1991), respectively. (1) and (3) show the CN5a/CN5b and CN4/CN5a boundaries of calcareous nannofossil zones of Okada and Bukry (1980) as determined by Tanaka and Takahashi (1997). (2) and (4) mean K-Ar ages by Takahashi (unpub. data). Shaded area shows the studied interval. The so-called mid-Neogene climatic optimum may be subdivided into two intervals (lower and upper) by the Miocene isotope 2 event.

Faunal structure

The faunal structure of ostracode assemblages is determined by the following four indices: the number of species, species diversity ($H(S)$), equitability ($Eq.$) and individual number per 10 g sediment. Species diversity can be expressed by the Shannon-Wiener formula which is independent of sample size: Diversity $(H(S)) = -\Sigma p_i \ln p_i$, where p_i is the proportion of the i-th species in a sample. This index has been often used in paleoecological studies. Equitability was also calculated by using the equation of Buzas and Gibson (1969): Equitability $(Eq.) = e^{H(S)}/S$, S means the number of species. Maximum and minimum values of the number of species, species diversity and equitability are 61 (sample no. 5) and 22 (sample no. 232), 3.557 (sample no. 221) and 2.628 (sample no. 211), and 0.756 (sample no. 12) and 0.416 (sample no. 211), respectively. Species diversity is generally high in biotope D (average no. = 3.347), moderate in biotopes A (2.857), B (2.945) and C (3.029), and low in biotope E (2.772), depending on the number of species rather than equitability values (Figure 9).

Sample nos. 2, 3, and 216 contain more than 200 individuals per 10 g sediment. Sample no. 232 contains the fewest, 7.3 per 10 g. Average numbers are lowest in biotope C (ca. 16.2) and highest in biotope D (ca. 106) (Figure 9).

Q-mode principal components analysis

Q-mode principal components analysis was carried out to obtain clues to the intersample relationships and identify end members (samples having extreme properties). The correlation coefficient, however, may be considered inappropriate as a measure of similarity between samples (Davis, 1986) because our data set (percentage expression) will not be normally distributed. Thus the proportional similarity ($\cos\theta$) was used in this study: $\cos\theta_{ij} = \Sigma_{k=1}^{m} X_{ik} X_{jk} / (\Sigma_{k=1}^{m} X_{ik}^2 \Sigma_{k=1}^{m} X_{jk}^2)^{1/2}$, where x_{ik} and x_{jk} are the proportions of the k-th species in samples x_i and x_j. Calculated eigenvalues show that the first four components explain about 83% of the total variance (Table 2). Subsequently component scores were calculated to figure out the degree to which individual ostracode species contribute to each of the first four components (Appendix I). Figure 9 shows the stratigraphic distribution of factor loadings (correlation coefficients between initial data and components) in relation to the first four components.

The first component.—This component explains 59.5% of the total variance. *Schizocythere kishinouyei* (Kajiyama) (score = +64.13), *Paracytheridea neolongicaudata* Ishizaki (score = +56.50), *Cornucoquimba moniwensis* (Ishizaki) (score = +55.46), *Cornucoquimba saitoi* (Ishizaki) (score = +34.26) and *Neonesidea* cf. *elegans* (Brady) (score = +29.94) contribute greatly to this component. They are

Figure 5. Selected ostracode species from the Kobana Formation (part 1). All micrographs are of adult specimens. RV = right valve; LV = left valve; RC = right lateral view of carapace. **1**: *Neonesidea* cf. *elegans* (Brady), female RV, Loc. no. 7, ×43.7. **2**: *Argilloecia hanaii* Ishizaki, RV, Loc. no. 8, ×58.5. **3**: *Krithe antisawanensis* Ishizaki, RC, Loc. no. 217, ×58.5. **4**: *Callistocythere kotorai* Ishizaki, RV, Loc. no. 4, ×90. **5**: *Callistocythere subsetanensis* Ishizaki, RV, Loc. no. 1, ×90. **6**: *Cythere omotenipponica* Hanai, female RV, Loc. no. 7, ×90. **7**: *Schizocythere kishinouyei* (Kajiyama), female RV, Loc. no. 219, ×90. **8**: *Palmenella limicola* (Norman), RV, Loc. no. 5, ×90. **9**: *Hemicythere kitanipponica* (Tabuki), female RV, Loc. no. 223, ×58.5. **10**: *Hemicythere ochotensis* Schornikov, female LV, Loc. no. 3, ×58.5. **11**: *Aurila* sp., male RV, Loc. no. 219, ×58.5. **12**: *Pseudoaurila okumurai* (Yajima), male RV, Loc. no. 219, ×58.5. **13**: *Pseudoaurila* sp., RV, Loc. no. 218, ×58.5. **14**: *Finmarchinella hanaii* Okada, female LV, Loc. no. 2, ×90. **15**: *Finmarchinella japonica* (Ishizaki), female RV, Loc. no. 221, ×90. **16**: *Laperousecythere* aff. *robusta* (Tabuki), female RV, Loc. no. 211, ×58.5. **17**: *Laperousecythere sendaiensis* (Ishizaki, Fujiwara and Irizuki), female RV, Loc. no. 15, ×58.5. **18**: *Laperousecythere* sp., female RV, Loc. no. 219, ×58.5.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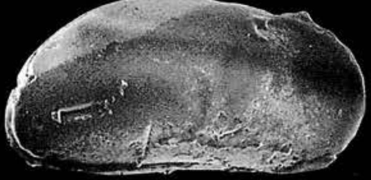
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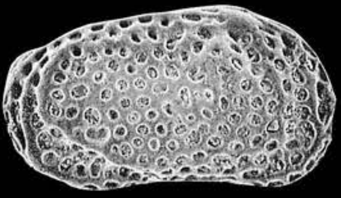
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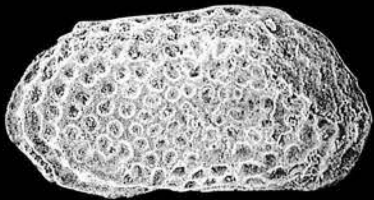
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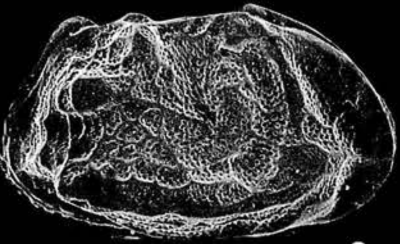
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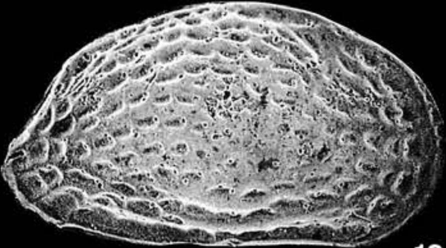
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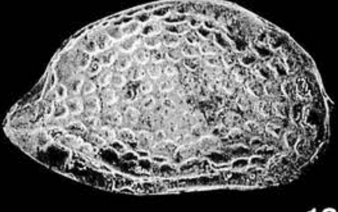
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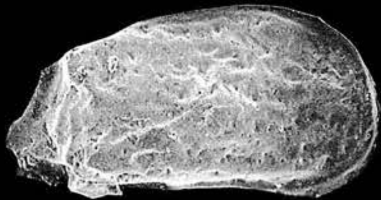
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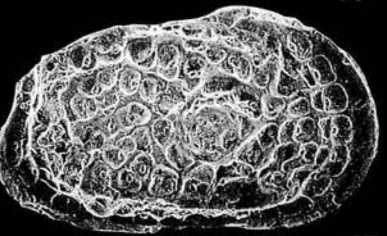
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contained in abundance in most of the samples examined. The first component scores are related to the abundance of ostracode species. Most of those ostracodes are intertidal to upper sublittoral species and live predominantly in subtropical to warm-temperate areas around Japan, influenced by the Kuroshio Warm Current (e.g., Hanai *et al.*, 1977 ; Tsukagoshi and Ikeya, 1987 ; Ikeya and Cronin, 1993 ; Zhou, 1995). They also have often been recorded from Neogene deposits around Japan, Korea and Formosa (e.g., Hanai *et al.*, 1977 ; Hu, 1984, 1986 ; Huh and Paik, 1992a, b, 1993 ; Huh, 1994). Vertical fluctuations of the first factor loading are concordant with those of the number of species and species diversity. The second to fourth components can be interpreted by not only values of corresponding component scores but also by the ratio of scores with regard to the first to each of the remaining components.

The second component.—This component explains 9.87% of the total variance. *Laperousecythere* sp. (score= +16.452), *Krithe antisawanensis* (score= +16.114), *Laperousecythere sendaiensis* (Ishizaki, Fujiwara and Irizuki) (score= +15.849), *Palmenella limicola* (Norman) (score= +13.106), *Falsobuntonia taiwanica* Malz (score= +12.743) and *Hirsutocythere*? sp. 1 (score= +11.657) have high positive scores of the second component and also high ratios of the first to second component scores. *Neonesidea* cf. *elegans* (score= −23.714), *P. neolongicaudata* (score= −21.933), *C. saitoi* (score= −17.868) and *Cythere omotenipponica* Hanai (score= −11.830) have high negative scores of the second component. *Loxoconcha* sp. (c1 : c2 ratio= −1.779), *Schizocythere* sp. (ratio= −1.663), *Finmarchinella* spp. (ratio= −1.098– −1.201) and *Hemicytherura* cf. *clathrata* (Sars) (ratio= −1.611), have high negative ratios of the first to second component scores. *Krithe antisawanensis, P. limicola* and *F. taiwanica* are extant and live predominantly in the lower sublittoral to upper bathyal around Japan (more than 150 m in depth) (Ishizaki, 1977, 1981 ; Ikeya and Suzuki, 1992 ; Zhou and Ikeya, 1992 ; Zhou, 1995) and were reported from black mudstone of the Lower to Middle Miocene Kadonosawa Formation (Irizuki and Matsubara, 1994). On the other hand, species with high negative component scores and ratios are abundant in intertidal to upper sublittoral areas (e.g., Hanai *et al.*, 1977 ; Ikeya and Itoh, 1991 ; Zhou, 1995). Moreover, vertical fluctuations of the second factor loading are in inverse relation with those of individual numbers of ostracodes in 10 g sediment. Ostracodes are generally more abundant in the sublittoral than in the bathyal. Thus the second component is interpreted as a relative water depth (positive=deep ; negative=shallow).

The third component.—This component explains 8.51% of the total variance. *Laperousecythere sendaiensis* (score= +39.021), *Laperousecythere* sp. (score= +20.645), *Aurila* sp. (score= +18.051) have high positive scores. *Laperousecythere* aff. *robusta* (Tabuki) (c1 : c3 ratio= +2.181), *Munseyella hokkaidoana* Hanai (ratio= +1.433) and *Acanthocythereis munechikai* Ishizaki (ratio= +1.193) have high positive ratios of the first to third component scores. *Schizocythere kishinouyei* (score= −17.546), *P. neolongicaudata* (score= −15.317) have high negative scores. *Hirsutocythere* ? sp. 1 (c1 : c3 ratio= −0.876), *Semicytherura* sp. 1 (ratio= −0.779), *Palmoconcha* sp. (ratio= −0.758) and *Hemicytherura* cf. *clathrata* (ratio= −0.727) have high negative ratios of the first to third component scores. It is rather difficult to interpret the significance of this component since *L. sendaiensis, Laperousecythere* sp. and *Aurila* sp. are extinct species. However, other species having high positive values seem to have lived in offshore open shelf environments. On the other hand, species having high negative values dominate nearshore sandy facies. *Hirsutocythere* ? sp. 1 and *Palmoconcha* sp. were reported from the biotope B in the lower part of the Kadonosawa Formation, suggesting an enclosed muddy bay facies (Irizuki and Matsubara, 1994). Hence this component probably suggests relatively nearshore (negative) versus offshore open-shelf (positive) environments.

The fourth component.—This component explains 6.81% of the total variance. *Aurila* sp. (score= +17.92), *Neonesidea* cf. *elegans* (score= +6.223) and *C. moniwensis* (score= +6.111) have high positive scores. *Trachyleberis* cf. *mizunamiensis* Yajima (c1 : c4 ratio= +1.087), *Krithe japonica* Ishizaki (ratio= +1.058) have high positive ratios of the first to fourth component scores. *Laperousecythere sendaiensis* (score= −30.375), *P. neolongicaudata* (score= −18.066), *S. kishinouyei* (score= −14.52) have high negative scores. *Laperousecythere* aff. *robusta* (c1 : c4 ratio= −2.061), *L. sendaiensis* (ratio= −1.863), *M. hokkaidoana* (ratio= −1.313), *Hemicytherura* cf. *clathrata* (ratio= −1.205) and *Finmarchinella* spp. (ratio= −0.767– −0.993) have high negative ratios of the first to fourth component scores. *Neonesidea* cf. *elegans* is comparable to *N. elegans* reported from continental shelves off eastern and southeastern China (Whatley and Zhao, 1988). *Trachyleberis mizunamiensis* was reported from the "Shukunohora Sandstone" of the Akeyo Formation

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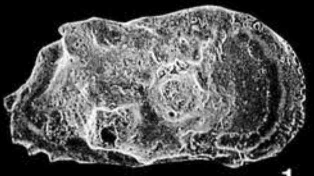
Figure 6. Selected ostracode species from the Kobana Formation (part 2). All micrographs are of adult specimens. **1** : *Cornucoquimba moniwensis* (Ishizaki), female RV, Loc. no. 219, ×58.5. **2** : *Cornucoquimba saitoi* (Ishizaki), male ? RV, Loc. no. 8, ×90. **3** : *Cornucoquimba kagitoriensis* Ishizaki, Fujiwara and Irizuki, female RV, Loc. no. 219, ×58.5. **4** : *Hermanites* ? *posterocostatus* Ishizaki, male RC, Loc. no. 8, ×58.5. **5** : *Coquimba* sp. 1, RV, Loc. no. 1, ×58.5. **6** : *Acanthocythereis munechikai* Ishizaki, female RC, Loc. no. 210, ×58.5. **7** : *Hirsutocythere* ? *hanaii* Ishizaki, female RV, Loc. no. 173, ×43.7. **8** : *Abrocythereis* cf. *guangdongensis* Gou, female RV, Loc. no. 216, ×58.5. **9** : *Falsobuntonia taiwanica* Malz, female ? RV, Loc. no. 220, ×58.5. **10** : *Hemicytherura* cf. *clathrata* (Sars), female RV, Loc. no. 187, ×120. **11** : *Kangarina yamaguchii* Tabuki, RV, Loc. no. 5, ×120. **12** : *Cytheropteron miurense* Hanai, RV, Loc. no. 3, ×90. **13** : *Cytheropteron postornatum* Zhao, RV, Loc. no. 234, ×90. **14** : *Cytheropteron sendaiense* Ishizaki, female RV, Loc. no. 218, ×90. **15** : *Cytheropteron* cf. *smithi* Nohara, RV, Loc. no. 5, ×120. **16** : *Cytheropteron uchioi* Hanai, female RV, Loc. no. 223, ×90. **17** : *Metacytheropteron* sp. ; RV, Loc. no. 173, ×58.5. **18** : *Paracytheridea neolongicaudata* Ishizaki, RV, Loc. no. 218, ×58.5.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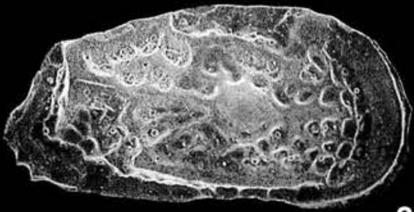
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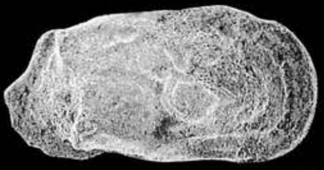
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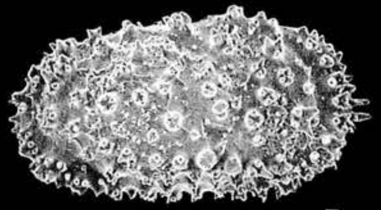
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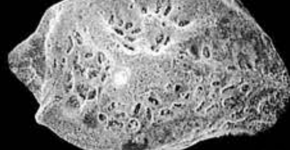
8


9


10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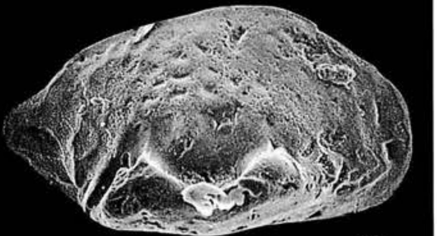
12


13


14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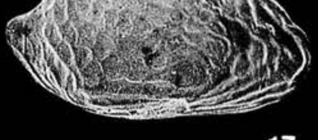
16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18

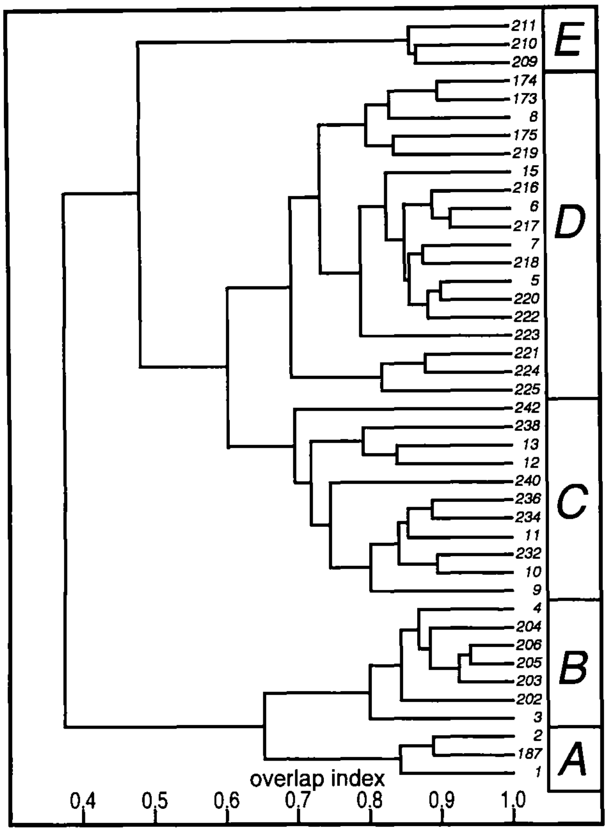


Figure 7. Dendrogram resulting from Q-mode cluster analysis based on the index of Horn's (1966) overlap. Groups A to E refer to biotopes.

which contains tropical molluscs, larger foraminifers and mangrove plants (Yajima, 1988, 1992). On the other hand *Laperousecythere* species have been reported in abundance from the lower part of the Suenomatsuyama Formation deposited during the interval of Miocene isotope 2 event (Irizuki and Matsubara, 1995) and the Upper Miocene Tsunaki Formation (ca. 8 Ma) (Ishizaki *et al.*, 1996). Both formations yield the cool-water Shiobara molluscan fauna. Only two species (*L. robusta* and *L. yahtsensis* Brouwers) are extant and living in middle sublittoral open seas of subarctic to cool-temperate zones around northern Hokkaido, northern Japan, (Itoh, 1996) and Alaska Bay (Brouwers, 1993). Other ostracodes having high negative ratios of the first to fourth component scores are equated with modern species inhabiting subarctic to mild-temperate shallow water areas or species reported from Plio-Pleistocene deposits yielding the cool-water Omma-Manganji molluscan fauna (Cronin and Ikeya, 1987). Moreover, vertical fluctuations of the fourth factor loading are inversely accordant with those of the percentage of shallow circumpolar and cryophilic species (Figure 9). Among those species are *Finmarchinella hanaii* Okada, *F. japonica* (Ishizaki), *F. nealei* Okada, *Hemicythere kitanipponica* (Tabuki), *H. ochotensis* Schornikov, *Hemicytherura* cf. *clathrata* and *Laperousecythere* aff. *robusta*. Thus the fourth component suggests water temperatures (positive = dominance of warm; negative = presence of cool shallow-water species).

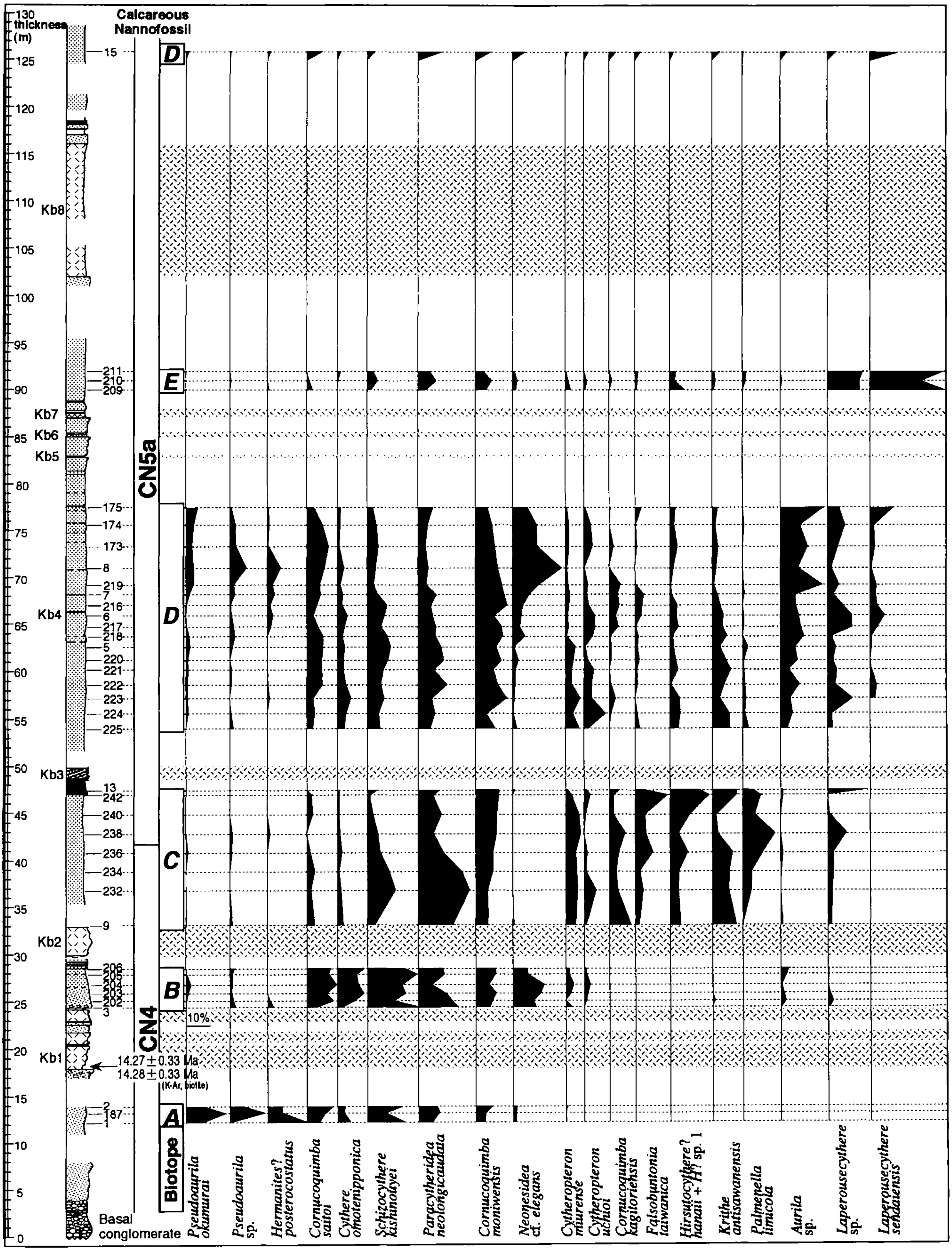
Temporal changes of paleoenvironments

Quantitative analyses of faunal composition and structure of ostracodes demonstrate temporal changes of paleoenvironments after the mid-Neogene climatic optimum in the Kobana Formation.

Table 1. Summary of Q-mode cluster analysis.

Biotope	Sample	Dominant Taxa	Subordinate Taxa
A	1, 187, 2	*Pseudoaurila* spp. *Paracytheridea neolongicaudata* *Hermanites* ? *posterocostatus*	*Cornucoquimba saitoi* *Schizocythere kishinouyei* *Coquimba* sp. 1
B	3, 4, 202-206	*Paracytheridea neolongicaudata* *Neonesidea* cf. *elegans* *Schizocythere kishinouyei*	*Cornucoquimba saitoi* *Cythere omotenipponica* *Cornucoquimba moniwensis*
C	9-13, 232-242	*Schizocythere kishinouyei* *Cornucoquimba moniwensis* *Hirsutocythere* ? spp.	*Krithe antisawanensis* *Paracytheridea neolongicaudata* *Palmenella limicola*
D	5-8, 15, 216-225, 173-175	*Cornucoquimba moniwensis* *Aurila* sp. *Schizocythere kishinouyei*	*Paracytheridea neolongicaudata* *Neonesidea* cf. *elegans* *Cornucoquimba saitoi*
E	209-211	*Laperousecythere sendaiensis* *Laperousecythere* sp. *Schizocythere kishinouyei*	*Cornucoquimba moniwensis* *Laperousecythere* aff. *robusta* *Cytheropteron* sp. 2

Figure 8. Diagram showing stratigraphic positioning of biotopes and percentages of each of the 19 taxa. A to E stand for biotopes. CN 4 and CN5a are calcareous nannofossil zones of Okada and Bukry (1980) as determined by Tanaka and Takahashi (1997). For explanation of columnar section see Figure 3.


thickness (m)
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
85
90
95
100
105
110
115
120
125
130
Kb1
Kb2
Kb3
Kb4
Kb5
Kb6
Kb7
Kb8
Basal conglomerate
1
2
87
3
202
203
204
205
206
9
232
234
236
238
240
242
13
225
224
223
222
221
220
5
218
217
6
216
7
219
8
173
174
175
209
210
211
15
14.27±0.33 Ma
14.28±0.33 Ma
(K-Ar, biotite)
Calcareous Nannofossil
CN4
CN5a
Biotope
A
B
C
D
E
D
10%
Pseudoaurila okumurai
Pseudoaurila sp.
Hermanites? posterocostatus
Cornucoquimba saitoi
Cythere omotenipponica
Schizocythere kishinouyei
Paracytheridea neolongicaudata
Cornucoquimba moniwensis
Neonesidea cf. elegans
Cytheropteron miurense
Cytheropteron uchioi
Cornucoquimba kagitoriensis
Falsobuntonia taiwanica
Hirsutocythere? hanaii + H? sp. 1
Krithe antisawanensis
Palmenella limicola
Aurila sp.
Laperousecythere sp.
Laperousecythere sendaiensis

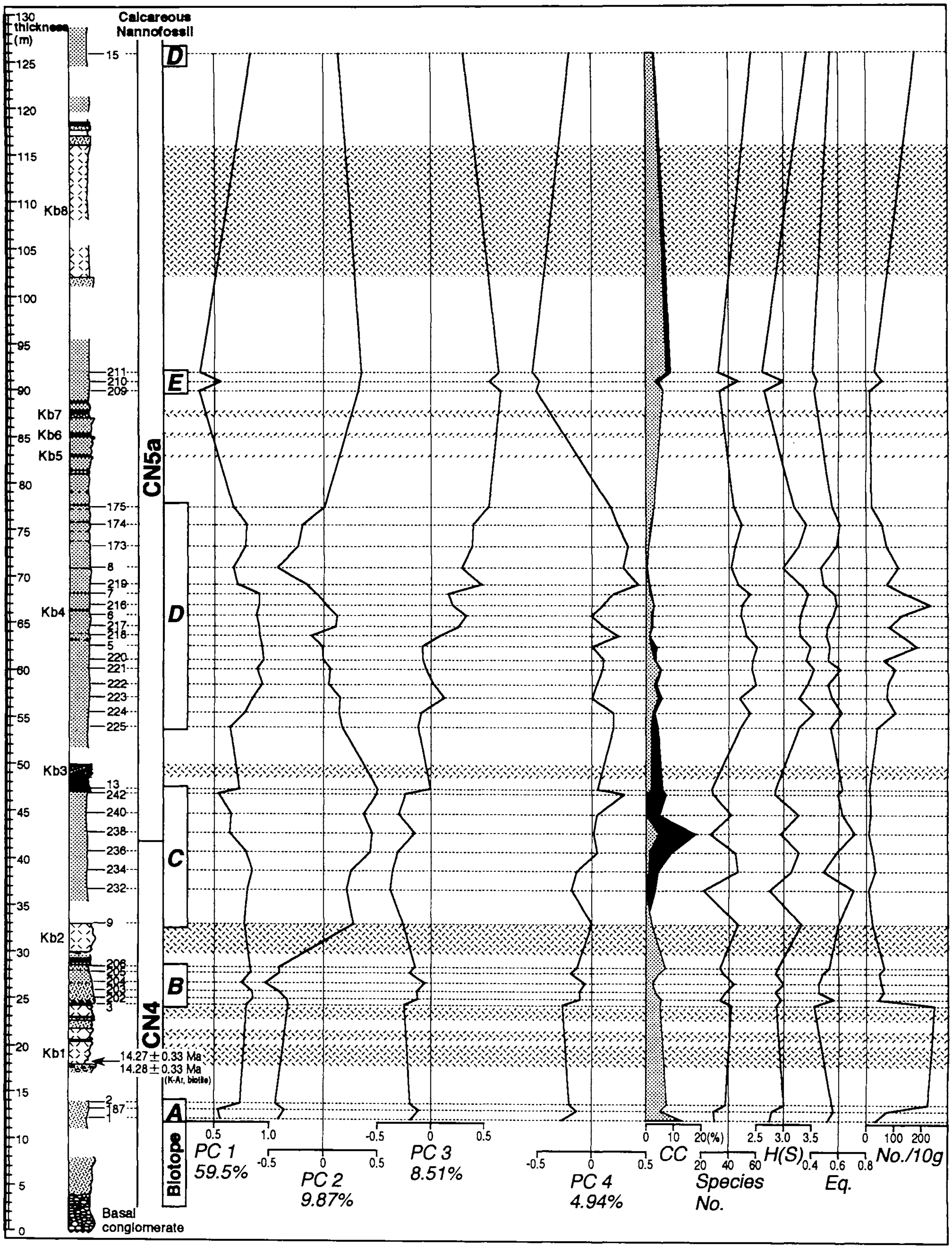

130
thickness (m)
125
120
115
110
105
100
95
90
85
80
75
70
65
60
55
50
45
40
35
30
25
20
15
10
5
0
Calcareous Nannofossil
CN5a
CN4
Kb8
Kb7
Kb6
Kb5
Kb4
Kb3
Kb2
Kb1
15
211
210
209
175
174
173
8
219
7
216
6
217
218
5
220
221
222
223
224
225
13
242
240
238
236
234
232
9
206
205
204
203
202
3
2
187
1
14.27±0.33 Ma
14.28±0.33 Ma
(K-Ar, biotite)
Basal conglomerate
D
E
D
C
B
A
Biotope
PC 1 59.5%
PC 2 9.87%
PC 3 8.51%
PC 4 4.94%
CC
20(%)
Species No.
H(S)
Eq.
No./10g
0.5
1.0
-0.5
0
0.5
0
10
20
40
60
2.5
3.0
3.5
0.4
0.6
0.8
100
200

Table 2. Summary of Q-mode principal components analysis.

	Eigenvalue	Percentage	Cumulative Per.
PC 1	24.991	59.503	59.503
PC 2	4.145	9.870	69.373
PC 3	3.573	8.508	77.881
PC 4	2.073	4.937	82.818

The general pattern of ostracode faunas is shown by vertical changes in factor loadings with respect to the first component. Subtropical to warm-temperate open sublittoral ostracodes are abundant throughout the Middle Miocene Kobana Formation except for samples from the upper half of biotope C (upper bathyal species are dominant) and biotope E (cool-water ostracodes endemic to northern Japan are dominant).

Water depth

Samples in the lower part (biotopes A and B) have high negative loadings of the second component (shallow waters) and high negative third factor loadings (nearshore environments). Samples in the middle and upper parts (biotope C, the lower part of biotope D and biotope E) have high positive second factor loadings (deep waters). Such lower sublittoral to upper bathyal species as *P. limicola*, *K. antisawanensis*, *Hirsutocythere* ? spp., *F. taiwanica* and *C. kagitoriensis* begin to occur in biotope C and linger on to the uppermost sample. The lowest values of individual numbers of ostracodes per 10 g in biotopes C and E are in good agreement with high positive factor loadings with respect to the second component, suggesting the prevalence of the greatest water depth during deposition of these biotopes (Figure 9). Samples in the upper part of biotope D have high negative second factor loading, and yielded large quantities of shallow-water ostracodes. However, they also commonly contain lower sublittoral to upper bathyal species (Figure 8). The third component shows that the upper part of biotope D was deposited on an open shelf. In modern offshore southwestern Japan, many intertidal and upper sublittoral species are transported downslope and are found at a depth of several hundred meters (Zhou, 1995). Thus shallow-water specimens contained in the upper part of biotope D are considered to have been displaced, resulting in large numbers of specimens and species diversity.

In this way, the second and third factor loadings show vertical changes in paleodepth during deposition of the Kobana Formation: 1) The Kobana Formation was deposited in shallow littoral to sublittoral, relatively nearshore environments during deposition of biotopes A and B; 2) Water depth rapidly increased and upper bathyal ostracodes dominated biotope C; 3) After that, water depth gradually began to decrease, leading to mixing of upper sublittoral and lower sublittoral species in biotope D; 4) Finally middle to lower sublittoral open-water species dominated biotope E.

Water temperature

Biotope A contains abundant *Pseudoaurila okumurai* (Yajima), *Pseudoaurila* sp., *Paracytheridea neolongicaudata*, *Hermanites*? *posterocostatus* Ishizaki, *Callistocythere subsetanensis* Ishizaki and *Coquimba* sp. 1. These species are all extinct except *P. neolongicaudata*. This fauna is very similar to the tropical to subtropical shallow-water fauna reported from Lower to Middle Miocene deposits which yield the Akeyo, Kurosedani and Kadonosawa molluscan faunas (Ishizaki, 1966; Yajima, 1988, 1992; Huh and Paik, 1992b). However, such cryophilic and circumpolar species as *Finmarchinella hanaii*, *F. nealei*, *Hemicythere kitanipponica* and *Hemicytherura* cf. *clathrata* are also included in biotope A in amounts of 5-13% (Figure 9) whereas tropical *Bairdoppilata* is absent. These species have high negative ratios of the first to fourth component scores and are included neither in Middle Miocene deposits distributed in southwestern Japan (Ishizaki, 1963, Yajima, 1988, 1992) nor in the lower part of the mid-Neogene climatic optimum (e.g., the lower part of the Kadonosawa Formation) (Irizuki and Matsubara, 1994). On the contrary, cryophilic and circumpolar species are recognized in the upper part of the mid-Neogene climatic optimum of northeastern Japan (Irizuki and Matsubara, 1994, 1995). It might be possible that Miocene counterparts of modern circumpolar-cryophilic species never experienced cold-water environments, unlike Recent ones. However, in reality, they have not been recorded from deposits in southwestern Japan during the interval of the mid-Neogene climatic optimum. They are, therefore, expected to have lived in slightly colder water, if at all, than other species in the Miocene. Thus the lower part of the Kobana Formation (biotope A) is treated as a deposit in warm shallow water, influenced by cooler coastal currents from northern areas.

In species composition biotope B is similar to the Sunakosaka and Moniwa Formations (Ishizaki, 1963, 1966), which were also deposited in the mid-Neogene climatic optimum. Biotope B also includes cryophilic and circumpolar species in abundances of 2-7%.

It is difficult to discuss bottom paleotemperature in shallow areas during deposition of biotope C because biotope C and the lower part of biotope D contain large quantities of lower sublittoral to upper bathyal ostracodes. Sample nos. 13, 238 and 242 include, however, *P. limicola*, *Laperousecythere* sp. and *C. kagitoriensis* in abundance (Figure 8). *Palmenella limicola* lives in the middle sublittoral in high-latitude areas of the Northern Hemisphere (Brouwers, 1993) in contrast to upper bathyal zones around Japan (e.g., Ikeya and Suzuki, 1992). Ishizaki *et al*. (1996) described *C. kagitoriensis* from the Upper Miocene Tsunaki Formation, northeastern Japan and suggested that this species increased in number with

Figure 9. Diagram showing vertical fluctuations of factor loadings with respect to the first four components, percentage of circumpolar and cryophilic species (*CC*), the number of species, species diversity (*H(S)*), equitability (*Eq.*), and individual number per 10 g sediment (*No./10 g*). ■ and ▨ in *CC* stand for percentages of shallow circumpolar and cryophilic species and *Palmenella limicola*, respectively.

decreasing water temperatures. The boundary between the calcareous nannoplankton Zones CN4 and CN5a is placed above sample no. 237 (between sample nos. 236 and 238) (Tanaka and Takahashi, 1997) and is chronologically correlative with the period of the Miocene isotope 3 event (Miller *et al.*, 1991). Thus the increase of those species possibly reflects decreased bottom-water temperatures in lower sublittoral to upper bathyal zones during the interval of the Miocene isotope 3 event. Faunas, including circumpolar *P. limicola*, in these biotopes do not contain such upper bathyal circumpolar species as *Acanthocythereis dunelmensis* (Sars) s.l., *Elofsonella* cf. *concinna* (Jones) or *Normanicythere* sp., reported from the Middle Miocene Kadonosawa and Suenomatsuyama Formations, located 500 km north of the present studied area (Irizuki and Matsubara, 1994, 1995), but do contain *Hirsutocythere* ? *hanaii, Argilloecia hanaii* Ishizaki and *K. antisawanensis*, all of which live predominantly in lower sublittoral to upper bathyal zones of subtropical to warm-temperate areas around Japan. Thus bottom-water temperature during deposition of both biotopes C and D of the Kobana Formation was warmer than that of the upper part of the Kadonosawa and the lower part of the Suenomatsuyama Formation. It is noteworthy that *Laperousecythere sendaiensis* first occurred in the lower part of biotope D (Figure 8).

The upper part of biotope D has high negative values of the fourth factor loading (relatively warm). Most samples in the upper part of biotope D contain relatively high ratios of shallow warm-water species (*Pseudoaurila* spp., *Hermanites* ? *posterocostatus* and *Neonesidea* cf. *elegans*) and such tropical to subtropical open-shelf forms as *Abrocythereis* cf. *guangdongensis* Gou, *Acanthocythereis munechikai* Ishizaki, *Cytheropteron postornatum* Zhao, *Cytheropteron uchioi* Hanai, *Kangarina yamaguchii* Tabuki, *Metacytheropteron* sp., *Pacambocythere* spp., *Saida* spp. and *Typhlocythere* spp., which live now in the East and South China Seas (Ishizaki, 1977, 1981; Malz and Tabuki, 1988; Zhao, 1988; Zhao and Wang, 1988 ; Zhou, 1995). Hence bottom-water temperatures may have increased again during deposition of the upper part of biotope D.

Biotope E has the highest negative loading of the fourth factor, with the dominance of *Laperousecythere* spp. and the decrease of subtropical to warm-temperate water ostracodes mentioned above. *Laperousecythere sendaiensis* is a principal constituent of this biotope. It is clear that this biotope includes cooler-water species than the other biotopes. The third component reveals that biotope E was deposited in open-shelf environments (Figure 9). Hence it is suggested that some climatic cooling occurred even in the open shelf around the time when the boundary between biotopes D and E was settled. This water temperature decrease appears to have been minor because cryophilic and circumpolar species amount only to less than 10% in biotope E (Figure 8).

Bottom water temperatures fluctuated during deposition of biotopes C to E.

Conclusions

The following four major results were obtained from the study of faunal changes of ostracodes from the lower to middle part of the Kobana Formation.

1. One hundred and forty nine species of ostracodes were discriminated in the Middle Miocene Kobana Formation. Among the dominant species are some living now in subtropical to warm-temperate sublittoral areas.
2. Q-mode cluster analysis grouped 42 samples into five clusters (biotopes) (A to E)
3. The second principal component shows vertical changes of water depth as follows: intertidal to middle sublittoral in the lower part; a rapid increase of water depth (upper bathyal) in the lower middle part; a gradual decrease of water depth (lower to middle sublittoral) from the middle to upper part.
4. Vertical changes of bottom-water temperature during deposition of the Kobana Formation were suggested by the fourth principal component as follows: a) The lower part was influenced predominantly by subtropical shallow water, with inflowing cooler waters; b) Fluctuations of bottom water temperature were recognized in the middle to upper part; c) Two intervals of climatic deterioration were recognized: the first is at the horizon around the upper part of biotope C (the boundary between calcareous nannoplankton CN4 and CN5a assigned to the Miocene isotope 3 event) and the second is in the depositional interval of biotope E (the upper part of the studied section).

After the mid-Neogene climatic optimum, water temperatures fluctuated, with no rapid decrease in the Karasuyama area.

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References cited

Barron, J.A. and Baldauf, J.G., 1990: Development of biosiliceous sedimentation in the North Pacific during the Miocene and Early Pliocene. *In*, Tsuchi, R. *ed., Pacific Neogene Events, their Timing, Nature and Interrelationship*, p. 43-63. University of Tokyo Press.

Berggren, W.A., Kent, D.V., Swisher, C.C. and Aubry, M.-P., 1995: A revised Cenozoic geochronology and chronostratigraphy. *In*, Berggren, W.A., Kent, D.V., Aubry, M.-P. and Hardenbol, J. *eds., Geochronology, time scales and global stratigraphic correlation*, Special Publication, no. 54, p. 129-212. SEPM.

Brouwers, E.M., 1993: Systematic paleontology of Alaska. Part 2: Families Trachyleberididae, Hemicytheridae, Loxoconchidae, Paracytherideidae. *U.S. Geological Survey, Professional Paper*, no. 1531, p. 1-47.

Buzas, M.A. and Gibson, T.G., 1969: Species diversity: benthic foraminifera in western North Atlantic. *Science*, no. 163, p. 72-75.

Chinzei, K., 1986: Faunal succession and geographic distribution of Neogene molluscan faunas in Japan. *Palaeontological Society of Japan, Special Paper*, no. 29, p. 17-32.

Chinzei, K. and Iwasaki, Y., 1967: Paleoecology of shallow sea molluscan faunae in the Neogene deposits of Northeast Honshu, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 67, p. 93-113.

Cronin, T.M. and Ikeya, N., 1987: The Omma-Manganji ostracod fauna (Plio-Pleistocene) of Japan and the zoogeography of circumpolar species. *Journal of Micropalaeontology*, vol. 6, no. 2, p. 65-88.

Cronin, T.M., Kitamura, A., Ikeya, N., Watanabe, M. and Kamiya, T., 1994: Late Pliocene climatic change 3.4-2. 3 Ma: paleoceanographic record from the Yabuta Formation, Sea of Japan. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 108, p. 437-455.

Davis, J.C., 1986: *Statistics and Data Analysis in Geology, Second Edition*. 646 p. John Wiley and Sons. New York.

Hanai, T., Ikeya, N., Ishizaki, K., Sekiguchi, Y. and Yajima, M., 1977: *Checklist of Ostracoda from Japan and its Adjacent Seas*. 119 p. University of Tokyo Press.

Hirayama, K., 1954: Miocene Mollusca from the Arakawa Group, Tochigi Prefecture, Japan (Part I). *Science Reports of Tokyo Kyoiku Daigaku, Series C*, vol. 3, p. 43-76.

Hirayama, K., 1967: Miocene Mollusca from the Arakawa Group, Tochigi Prefecture, Japan (Part II). *Professor H. Shibata Memorial Volume*, p. 389-395.

Hirayama, K., 1981: Remarks on the Tertiary molluscan fauna from the marginal regions of the Kwanto Plain, Japan. *In*, Habe, T. and Omori, M. *eds., Study of Molluscan Paleobiology (Professor M. Omori Memorial Volume)*, p. 251-258. (*in Japanese with English abstract*)

Horn, H.S., 1966: Measurement of "overlap" in comparative ecological studies. *The American Naturalist*, vol. 100, no. 914, p. 419-424.

Hoshi, H. and Takahashi, M., 1996a: Stratigraphy and geologic structure of the Lower Miocene in the Motegi area: The relationship between N-S trending fault activity and tectonics in Miocene Northeast Japan. *Journal of the Geological Society of Japan*, vol. 102, no. 1, p. 25-39. (*in Japanese with English abstract*)

Hoshi, H. and Takahashi, M., 1996b: Magnetostratigraphy of the Early to Middle Miocene volcanic sequence in the Motegi area, Northeast Japan, and the time of volcanic activity. *Journal of the Geological Society of Japan*, vol. 102, no. 7, p. 573-590. (*in Japanese with English abstract*)

Hu, C.-H., 1984: New fossil ostracod faunas from Hengchun Peninsula, southern Taiwan. *Journal of Taiwan Museum*, vol. 37, no. 1, p. 65-129.

Hu, C.-H., 1986: The ostracodes from the Tungshiao Formation (Pleistocene), west coast of Miaoli District, Taiwan. *Journal of Taiwan Museum*, vol. 39, no. 1, p. 99-173.

Huh, M., 1994: Miocene Ostracoda and paleoenvironments of the Doumsan and Ododong areas, Pohang basin, Korea. *Korean Journal of Petrology and Geology*, vol. 2, no. 1, p. 1-7.

Huh, M. and Paik, K.-H., 1992a: Miocene Ostracoda from the Seojeongri Area, Pohang Basin, Korea. *Journal of the Geological Society of Korea*, vol. 28, no. 3, p. 273-283.

Huh, M. and Paik, K.-H., 1992b: Miocene Ostracoda from the Pohang Basin, Korea. *Paleontological Society of Korea, Special Publication*, no. 1, p. 101-119.

Huh, M. and Paik, K.-H., 1993: A paleoenvironmental study on Ostracoda from the Miocene Chunbuk Conglomerate and Hakrim Formations in the Doumsan area, Pohang basin, Korea. *Journal of the Korean Earth Science Society*, vol. 14, no. 4, p. 500-509. (*in Korean with English abstract*)

Ikeya, N. and Cronin, T.M., 1993: Quantitative analysis of Ostracoda and water masses around Japan: Application to Pliocene and Pleistocene paleoceanography. *Micropaleontology*, vol. 39, no. 3, p. 263-281.

Ikeya, N. and Itoh, H., 1991: Recent Ostracoda from the Sendai Bay region, Pacific coast of northeastern Japan. *Reports of Faculty of Science, Shizuoka University*, vol. 25, p. 93-145.

Ikeya, N. and Suzuki, C., 1992: Distributional patterns of modern ostracodes off Shimane Peninsula, southwestern Japan Sea. *Reports of the Faculty of Science, Shizuoka University*, vol. 26, p. 91-137.

Irizuki, T., 1994: Late Miocene ostracods from the Fujikotogawa Formation, northern Japan-with reference to cold water species involved with trans-Arctic interchange-. *Journal of Micropalaeontology*, vol. 13, part 1, p. 3-15.

Irizuki, T. and Matsubara, T., 1994: Vertical changes of depositional environments in the Lower to Middle Miocene Kadonosawa Formation based on analyses of fossil ostracode faunas. *Journal of the Geological Society of Japan*, vol. 100, no. 2, p. 136-149. (*in Japanese with English abstract*)

Irizuki, T. and Matsubara, T., 1995: Early Middle Miocene ostracodes from the Suenomatsuyama Formation, Ninohe City, Northeast Japan and their paleoenvironmental significance. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 177, p. 65-78.

Ishizaki, K., 1963: Japanese Miocene ostracodes from the Sunakosaka Member of the Yatsuo Formation, east of Kanazawa City, Ishikawa Prefecture. *Japanese Journal of the Geology and Geography*, vol. 34, no. 1, p. 19-34.

Ishizaki, K., 1966: Miocene and Pliocene ostracodes from the Sendai Area, Japan. *Science Reports of the Tohoku University, Second Series* (*Geology*), vol. 37, no. 2, p. 131-163.

Ishizaki, K., 1977: Distribution of Ostracoda in the East China Sea -a justification for the existence of the Paleo-Kuroshio Current in the Late Cenozoic. *In*, Löffler, H. and Danielopol, D. *eds., Aspects of Ecology and Zoogeography of Recent and Fossil Ostracoda*, p. 425-440. Dr. W. Junk b. v. Publishers, The Hague.

Ishizaki, K., 1981: Ostracoda from the East China Sea. *Science Reports of the Tohoku University, Second Series* (*Geology*), vol. 51, nos. 1-2, p. 37-45.

Ishizaki, K., Fujiwara, O. and Irizuki, T., 1996: Ostracod faunas from the Upper Miocene Tsunaki Formation near the southern border of Sendai City, Northeast Japan. *Proceedings of the 2nd European Ostracodologists*

Meeting, p. 113-120. British Micropalaeontological Society, London.

Ishizaki, K., Irizuki, T. and Sasaki, O., 1993: Cobb Mountain spike of the Kuroshio Current detected by Ostracoda in the lower Omma Formation (Early Pleistocene), Kanazawa City, central Japan: analysis of depositional environments. *In*, McKenzie, K.G. and Jones, P.J., *eds., Ostracoda in the Earth and Life Sciences*, p. 315-334. A.A. Balkema, Rotterdam.

Itoh, H., 1996: Ostracode fauna off Rebunto Island and Abashiri, northern Hokkaido. *Abstracts of the 1996 Annual Meeting of the Palaeontological Society of Japan*, p. 142. (*in Japanese, title translated*)

Itoigawa, J., 1989: Tropical spike in early Middle Miocene (ca. 16 Ma) of Southwest Japan. *In*, Liu G., Tsuchi, R. and Lin Q. *eds., Proceeding of International Symposium on Pacific Neogene Continental and Marine Events*, p. 19-26. Nanjing.

Itoigawa, J. and Yamanoi, T., 1990: Climatic optimum in the mid-Neogene of the Japanese Islands. *In*, Tsuchi, R. *ed., Pacific Neogene Events, their Timing, Nature and Interrelationship*, p. 3-14.

Iwasaki, Y., 1970: The Shiobara-type molluscan fauna. An ecological analysis of fossil molluscs. *Journal of the Faculty of Science, University of Tokyo, Section 2*, vol. 17, part 3, p. 351-444.

Kanno, S., 1961: Miocene *"Pleurotomaria"* and its associated fauna from Tochigi Prefecture, Japan. *Japanese Journal of Geology and Geography*, vol. 32, no. 1, p. 111-118.

Kawada, K., 1948: On the Tertiary distributed around the Washinoko Massif, Tochigi Prefecture. *Journal of the Geological Society of Japan*, vol. 53, no. 622, p. 92. (*in Japanese, title translated*)

Kawada, K., 1949: Geological structure of the Tertiary around the Washinoko Massif, Tochigi Prefecture. *Journal of the Geological Society of Japan*, vol. 54, no. 639, p. 170. (*in Japanese, title translated*)

Kawada, K., 1953: Geological Studies on the Yamizo, Torinoko and Toriashi mountain blocks and their neighbourhood in the northeastern Kwanto district. *Science Reports of Tokyo Bunrika Daigaku, Section C*, vol. 2, p. 217-307.

Kennett, J.P., 1986: Miocene to early Pliocene oxygen and carbon isotope stratigraphy in the southwest Pacific, Deep Sea Drilling Project Leg 90. *In*, Kennett, J.P., von der Borch, C.C. *et al. eds., Initial Reports of the Deep Sea Drilling Projects*, vol. 90, p. 1383-1411. U.S. Govt. Printing Office, Washington, D.C.

Maiya, S. and Inoue, Y., 1973: On the effective treatment of rocks for microfossil analysis. *Fossils* (*Palaeontological Society of Japan*), nos. 25/26, p. 87-96. (*in Japanese with English abstract*)

Malz, H. and Tabuki, R., 1988: The ostracod genus *Abrocythereis* (Miocene to Recent) from the Indopacific. *Geologica et Palaeontologica*, vol. 22, p. 157-173.

Miller, K.G., Wright, J.D. and Fairbanks, R.G., 1991: Unlocking the Ice House: Oligocene-Miocene oxygen isotopes, eustacy, and margin erosion. *Journal of Geophysical Research*, vol. 96, no. B4, p. 6829-6848.

Nishimura, S., 1994: Tectonics of Southeast Asia and climate changes of the arc of Japan. *Chikyu Monthly*, vol. 16, no. 3, p. 147-149. (*in Japanese, title translated*)

Nohara, T., 1987: Cenozoic ostracodes of Okinawa-Jima. *Bulletin of College of Education, University of the Ryukyus*, no. 30, part 3, p. 1-105.

Okada, H. and Bukry, D., 1980: Supplementary modification and introduction of code numbers to the low latitude coccolith biostratigraphic zonation (Bukry, 1973; 1975). *Marine Micropaleontology*, vol. 5, p. 321-325.

Oyama, K., 1950: Studies on fossil molluscan biocoenosis, no. 1, biological studies of the mangrove swamps, with description of new species from Yatsuo Group. *Report, Geological Survey of Japan*, no. 132, p. 1-16.

Ozawa, H., 1996: Ostracode fossils from the Late Pliocene to Early Pleistocene Omma Formation in the Hokuriku district, central Japan. *Science Reports of Kanazawa University*, vol. 41, no. 2, p. 77-115.

Sakai, T., 1986: Lithostratigraphy of Neogene Arakawa Group at the Type Section (Tochigi Prefecture, Japan). *Bulletin of the Faculty of General Education, Utsunomiya University*, no. 19, Sec. 2, p. 49-70. (*in Japanese with English abstract*)

Savin, S.M., Douglas, R.G., Keller, G., Killingley, J.S., Shaughnessy, L., Sommer, M.A., Vincent, E. and Woodruff, F., 1981: Miocene benthic foraminiferal isotope records: a synthesis. *Marine Micropaleontology*, vol. 6, p. 423-450.

Sugie, H., 1993: Analysis of paleoenvironment by radiolarians in the Late Miocene Arakawa Group (Tochigi Prefecture, Japan). *News of Osaka Micropaleontology, Special Volume*, no. 9, p. 313-335. (*in Japanese with English abstract*)

Takahashi, M. and Hoshi, H., 1995: Radiometric ages of the Early Miocene volcanic rocks in the Motegi area, Tochigi Prefecture, central Japan. *Journal of the Geological Society of Japan*, vol. 101, no. 10, p. 821-824. (*in Japanese*)

Takahashi, M. and Hoshi, H., 1996: Geologic age of the Nakagawa Group in the Motegi area, Tochigi Prefecture: Tectonic significance. *Bulletin of the Geological Survey of Japan*, vol. 47, no. 6, p. 317-333. (*in Japanese with English abstract*)

Tanaka, Y. and Takahashi, M., 1997: Calcareous nannofossil biostratigraphy of the lower part of the Miocene Arakawa Group in the Karasuyama area, Tochigi Prefecture, central Japan. *Abstracts of the 104th Annual Meeting of the Geological Society of Japan*, p. 114. (*in Japanese*)

Tsuchi, R., 1986: Mid-Neogene migration of Tethyan tropical Mollusca and larger foraminifera into northern Japan. *In*, McKenzie, K.G. *ed., Shallow Tethys 2*, p. 455-459. A.A. Balkema, Rotterdam.

Tsukagoshi, A. and Ikeya, N., 1987: The ostracod genus *Cythere* O.F. Müller, 1785 and its species. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series,* no. 148, p. 197-222.

Usami, M.; Oda, M. and Takahashi, M., 1995: Planktonic foraminiferal biostratigraphy of Arakawa Group Kobana Formation, Tochigi Prefecture. *Abstracts of the 102nd Annual Meeting of the Geological Society of Japan*, p. 137. (*in Japanese*)

Usami, M., Oda, M. and Takahashi, M., 1996: Planktonic foraminiferal biostratigraphy of the Kobana Formation, Arakawa Group. *Abstracts of the 103rd Annual Meeting of the Geological Society of Japan*, p. 144. (*in*

Japanese)

Vincent, E., Kilingley, J.S. and Berger, W.H., 1985 : Miocene oxygen and carbon isotope stratigraphy of the tropical Indian Ocean. *Geological Society of America, Memoir*, no. 163, p. 103-130.

Whatley, R. and Zhao, Q., 1988 : A revision of Brady's 1869 study of the Ostracoda of Hong Kong. *Journal of Micropalaeontology*, vol. 7, no. 1, p. 21-29.

Woodruff, F. and Savin, S.M., 1989 : Miocene deepwater oceanography. *Paleoceanography*, vol. 4, no. 1, p. 87-140.

Woodruff, F., Savin, S.M. and Douglas, R.G., 1981 : Miocene stable isotope record : a detailed deep Pacific Ocean study and its paleoclimatic implications. *Science*, vol. 212, p. 665-668.

Wright, J.D. and Miller, K.G., 1992 : Miocene stable isotope stratigraphy, Site 747, Kerguelen Plateu. *In*, Wise, S.W. Jr., Schlich, R. *et al. eds., Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 120, p. 855-866. College Station, TX (Ocean Drilling Program).

Wright, J.D., Miller, K.G. and Fairbanks, R.G., 1992 : Early and Middle Miocene stable isotopes : implications for deepwater circulation and climate. *Paleoceanography*, vol. 7, no. 3, p. 357-389.

Yajima, M., 1988 : Preliminary notes on the Japanese Miocene Ostracoda. *In*, Hanai, T., Ikeya, N. and Ishizaki, K. *eds., Evolutionary Biology of Ostracoda-its Fundamentals and Applications*, p. 1073-1085. Kodansha, Tokyo.

Yajima, M., 1992 : Early Miocene Ostracoda from Mizunami, central Japan. *Bulletin of the Mizunami Fossil Museum*, no. 19, p. 247-268.

Yamanoi, T., Tsuda, K., Itoigawa, J., Okamoto, K. and Taguchi, E., 1980 : On the mangrove community discovered from the Middle Miocene formations in Southwest Japan. *Journal of the Geological Society of Japan*, vol. 86, p. 636-638. (*in Japanese*)

Zhao, Q., 1988 : Chapter V : Ostracoda. *Foraminifera and Ostracoda in Bottom Sediments of the East China Sea*, p. 181-280. China Ocean Press, Beijing. (*in Chinese with English abstract*)

Zhao, Q. and Wang, P., 1988 : Distribution of modern Ostracoda in the shelf seas off China. *In*, Hanai, T., Ikeya, N. and Ishizaki, K. *eds., Evolutionary Biology of Ostracoda-its Fundamentals and Applications*, p. 805-821. Kodansha, Tokyo.

Zhou, B.C., 1995 : Recent ostracode fauna in the Pacific off Southwest Japan. *Memoirs of the Faculty of Science, Kyoto University, Series of Geology and Mineralogy*, vol. 57, no. 2, p. 21-98.

Zhou, B.C. and Ikeya, N., 1992 : Three species of *Krithe* (Crustacea : Ostracoda) from Suruga Bay, central Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 166, p. 1097-1115.

Appendix I. Scores with respect to the first four principal components and ratios of scores with regard to the first to each of the remaining components for 76 species selected for both Q-mode principal components and cluster analyses.

Kobana Formation	PC1	PC2	PC2/PC1	PC3	PC3/PC1	PC4	PC4/PC1
Abrocythereis cf. *guangdongensis*	1.930	0.945	0.490	−0.228	−0.118	0.476	0.247
Acanthocythereis munechikai	1.830	2.136	1.167	2.184	1.193	−2.026	−1.107
Argilloecia hanaii	7.805	2.162	0.277	−0.073	−0.009	2.627	0.337
Argilloecia toyamensis	1.815	0.565	0.311	−0.199	−0.110	0.571	0.315
Argilloecia sp. 1	1.580	−0.312	−0.198	0.237	0.150	0.949	0.600
Aurila sp.	27.201	−4.382	−0.161	18.051	0.664	17.917	0.659
Callistocythere kotorai	5.008	−2.916	−0.582	−1.588	−0.317	−1.656	−0.331
Callistocythere subsetanensis	1.392	−0.844	−0.606	−0.685	−0.492	−0.793	−0.570
Callistocythere sp.	1.084	−0.383	−0.354	−0.562	−0.519	−0.534	−0.493
Coquimba sp. 1	4.973	−4.132	−0.831	−0.986	−0.198	−1.093	−0.220
Cornucoquimba kagitoriensis	12.357	7.964	0.645	−1.444	−0.117	1.846	0.149
Cornucoquimba moniwensis	55.459	4.574	0.082	3.646	0.066	6.111	0.110
Cornucoquimba saitoi	34.260	−17.868	−0.522	1.018	0.030	−0.372	−0.011
Cornucoquimba sp.	5.209	1.239	0.238	4.073	0.782	−0.334	−0.064
Cythere omotenipponica	22.746	−11.830	−0.520	−3.388	−0.149	−4.249	−0.187
Cythere uranipponica	4.178	−1.005	−0.240	−0.908	−0.217	−0.789	−0.189
Cytheropteron miurense	17.553	6.553	0.373	−4.929	−0.281	−0.091	−0.005
Cytheropteron postornatum	1.816	1.434	0.790	−0.706	−0.389	−0.552	−0.304
Cytheropteron sendaiense	6.981	−0.179	−0.026	2.157	0.309	0.714	0.102
Cytheropteron cf. *smithi*	1.783	0.986	0.553	−1.087	−0.610	0.185	0.104

Cytheropteron uchioi	13.089	1.640	0.125	1.964	0.150	3.814	0.291
Cytheropteron sp. 1	14.939	8.304	0.556	−1.846	−0.124	−0.937	−0.063
Cytheropteron sp. 2	3.929	2.077	0.529	5.680	1.446	−3.628	−0.924
Cytheropteron sp. 3	3.894	−1.097	−0.282	−0.972	−0.250	−0.449	−0.115
Cytheropteron sp. 4	2.730	0.032	0.012	2.108	0.772	0.576	0.211
Cytheropteron sp. 5	1.695	0.073	0.043	0.063	0.037	0.759	0.448
Cytheropteron sp. 6	0.931	0.451	0.484	0.566	0.608	−0.260	−0.280
Eucythere sp. 1	0.924	0.334	0.361	0.836	0.905	−0.320	−0.346
Falsobuntonia taiwanica	12.544	12.743	1.016	−3.492	−0.278	4.548	0.363
Finmarchinella hanaii	1.372	−1.507	−1.098	−0.744	−0.543	−1.052	−0.767
Finmarchinella japonica	5.304	−0.001	0.000	−0.666	−0.126	0.213	0.040
Finmarchinella nealei	0.274	−0.329	−1.201	−0.178	−0.651	−0.272	−0.993
Hemicythere kitanipponica	7.123	−5.565	−0.781	−1.556	−0.218	−3.644	−0.512
Hemicythere ochotensis	2.403	−0.448	−0.187	−0.311	−0.129	−0.299	−0.125
Hemicytherura cf. *clathrata*	0.565	−0.910	−1.611	−0.411	−0.727	−0.681	−1.205
Hemicytherura cuneata	1.919	−0.137	−0.072	0.059	0.031	−0.030	−0.015
Hermanites ? *posterocostatus*	8.049	−7.689	−0.955	0.257	0.032	−3.235	−0.402
Hirsutocythere ? *hanaii*	14.705	9.097	0.619	1.218	0.083	−1.958	−0.133
Hirsutocythere ? sp. 1	6.563	11.657	1.776	−5.746	−0.876	4.850	0.739
Kangarina yamaguchii	1.225	0.106	0.086	−0.807	−0.659	−0.287	−0.234
Kotoracythere cf. *abnorma*	0.676	0.210	0.310	0.375	0.555	−0.195	−0.288
Krithe antisawanensis	25.462	16.114	0.633	−6.628	−0.260	5.534	0.217
Krithe japonica	5.059	3.329	0.658	−1.775	−0.351	5.350	1.058
Laperousecythere cf. *robusta*	2.828	2.932	1.037	6.166	2.181	−5.828	−2.061
Laperousecythere sendaiensis	16.307	15.849	0.972	39.021	2.393	−30.375	−1.863
Laperousecythere sp.	26.191	16.452	0.628	20.645	0.788	−9.314	−0.356
Loxoconcha nozokiensis	5.494	−2.295	−0.418	0.281	0.051	1.481	0.270
Loxoconcha pulchra	1.486	−1.099	−0.740	−0.523	−0.352	−0.338	−0.228
Loxoconcha sp.	0.285	−0.507	−1.779	−0.097	−0.339	−0.171	−0.601
Macrocypris cf. *decora*	1.955	−0.188	−0.096	−0.305	−0.156	0.031	0.016
Metacytheropteron sp.	1.098	0.248	0.225	0.965	0.879	−0.093	−0.085
Munseyella hokkaidoana	0.883	0.847	0.959	1.265	1.433	−1.159	−1.313
Munseyella japonica	1.940	−0.730	−0.376	−0.001	0.000	−0.139	−0.072
Neomonoceratina japonica	4.437	2.951	0.665	0.184	0.041	0.466	0.105
Neonesidea cf. *elegans*	29.937	−23.714	−0.792	12.147	0.406	6.223	0.208
Neonesidea sp. 1	0.510	−0.775	−1.519	0.108	0.212	0.053	0.104
Pacambocythere sp.	1.981	0.500	0.253	−0.040	−0.020	0.544	0.275
Palmenella limicola	10.957	13.106	1.196	−6.983	−0.637	1.076	0.098
Palmoconcha sp.	7.106	7.293	1.026	−5.386	−0.758	0.238	0.033
Paracypris sp. 1	0.973	−0.377	−0.388	0.999	1.027	0.744	0.765
Paracytheridea neolongicaudata	56.504	−21.933	−0.388	−15.317	−0.271	−18.066	−0.320
Pectocythere sp.	0.709	−0.729	−1.029	0.141	0.199	−0.015	−0.021
Pseudoaurila okumurai	10.638	−9.456	−0.889	1.136	0.107	−0.721	−0.068
Pseudoaurila sp.	9.398	−8.142	−0.866	0.721	0.077	0.473	0.050
Rotundracythere ? sp.	6.922	5.826	0.842	−3.467	−0.501	−0.660	−0.095
Saida sp.	0.940	0.605	0.644	0.497	0.528	−0.154	−0.164
Schizocythere kishinouyei	64.125	6.252	0.098	−17.546	−0.274	−14.520	−0.226
Schizocythere sp.	0.739	−1.229	−1.663	−0.527	−0.713	−0.904	−1.223
Sclerochilus sp. 1	2.238	−0.543	−0.243	0.578	0.258	1.479	0.661
Semicytherura henryhowei	7.822	−4.253	−0.544	−2.385	−0.305	−3.008	−0.385
Semicytherura miurensis	0.942	−1.021	−1.083	−0.341	−0.361	−0.408	−0.433
Semicytherura sp. 1	0.866	−1.067	−1.231	−0.675	−0.779	−0.986	−1.138
Trachyleberis cf. *mizunamiensis*	0.667	−0.289	−0.433	0.641	0.961	0.725	1.087
Xestoleberis hanaii	3.075	−1.877	−0.610	0.252	0.082	0.056	0.018
Xestoleberis cf. *setouchiensis*	2.644	−0.043	−0.016	−1.121	−0.424	−0.717	−0.271
Gen. et sp. indet. 1	2.310	0.487	0.211	0.001	0.000	1.215	0.526

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Preliminary results of a taphonomic study of a vertebrate accumulation from the Tetori Group (Lower Cretaceous) of Japan

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Abstract. A predominantly microvertebrate assemblage from the Tetori Group (Lower Cretaceous) of central Honshu is described. The fauna consists of many hundreds of vertebrate fossils which represent a diverse terrestrial/non-marine fauna. Taxa present include fish, reptiles, amphibians and birds. The preservation of the fossils is generally good, although there are few articulated and associated remains.

Key words : Japan, Lower Cretaceous, Tetori Group, Vertebrates

Introduction

Neocomian vertebrate fossils have been described from a variety of localities in central Honshu, Japan. The first of these sites to be described, Kasekiheki, Shiramine Village, Ishikawa Prefecture, yielded a carnosaur tooth and dinosaur footprints (Manabe *et al*., 1989). More recent fieldwork has increased the numbers and taxonomic range of fossils from the Tetori Group, for example, iguanodontid teeth from Shiramine (Hasegawa *et al*., 1995), a hypsilophodontid tooth from Gifu Prefecture (Hasegawa *et al*., 1990), an incomplete pterosaur wing phalange from Shokawa, Gifu Prefecture (Unwin *et al*., 1996), and crocodile remains from Katsuyama, Fukui Prefecture (Manabe *et al*., 1989).

Over recent years a series of excavations at a stream section in Gifu Prefecture has produced many hundreds of vertebrate fossils, representing fish, turtles, dinosaurs, frogs, choristoderes, salamanders and birds.

Geological setting and locality

The Tetori Group outcrops in central Honshu (Figure 1). It ranges in age from Middle Jurassic to Early Cretaceous (Maeda, 1961). The outcrops are generally of limited extent, due to the lush vegetation, and are often found in stream sections or road cuttings. The Tetori Group sediments (conglomerate, sandstone and mudstone) form part of the Hida Terrane. The terrane is mainly composed of igneous and metamorphic rocks (Maeda, 1961).

The Tetori Group is subdivided into the Kuzuryu, Itoshiro and Akaiwa Subgroups (Maeda, 1952). The oldest, Kuzuryu Subgroup ranges from Bajocian to Oxfordian in age and is composed mainly of conglomerate, shales and sandstones. The Itoshiro Subgroup is Kimmeridgian to Berriasian in age and is also composed predominantly of conglomerates, sandstones and shales. The youngest Akaiwa Subgroup is Valanginian to Albian in age. It comprises conglomerates, arkosic sandstones, shales and occasional tuffs (Maeda, 1961).

The vertebrate materials described here come from site KO-2 (36°03′N, 136°53′E) close to Shokawa Village, Gifu Prefecture (Figure 1). The dominant lithologies are alternating fine- and coarse-grained sandstones and mudstones. These sediments form part of the lowest section of the Okurodani Formation (upper part of the Itoshiro Subgroup) and are of Lower Cretaceous age (Manabe and Hasegawa, 1995 ; Hasegawa *et al*., 1995) ; and were stratigraphically placed by non-marine fossils (Maeda, 1961) and dated at 140-120 Ma by fission track analysis (Gifu-Ken Dinosaur Research Committee, 1993).

Vertebrate fauna

To date some 800 specimens have been recovered, prepared and described from Shokawa site KO-2. A variety of taxa has been identified.

The most common elements of the fauna are fish (Figure 2). Most of these fossils are preserved as isolated scales, vertebrae and bone fragments. Turtle remains are also common, mostly preserved as isolated dermal material and bones, although some associated and articulated specimens have been discovered. Less common taxa include choristoderes, lizards, frogs, salamanders, dinosaurs and birds. The choristodere is the earliest record from Asia east of Inner Mongolia (Manabe and Hasegawa, 1995).

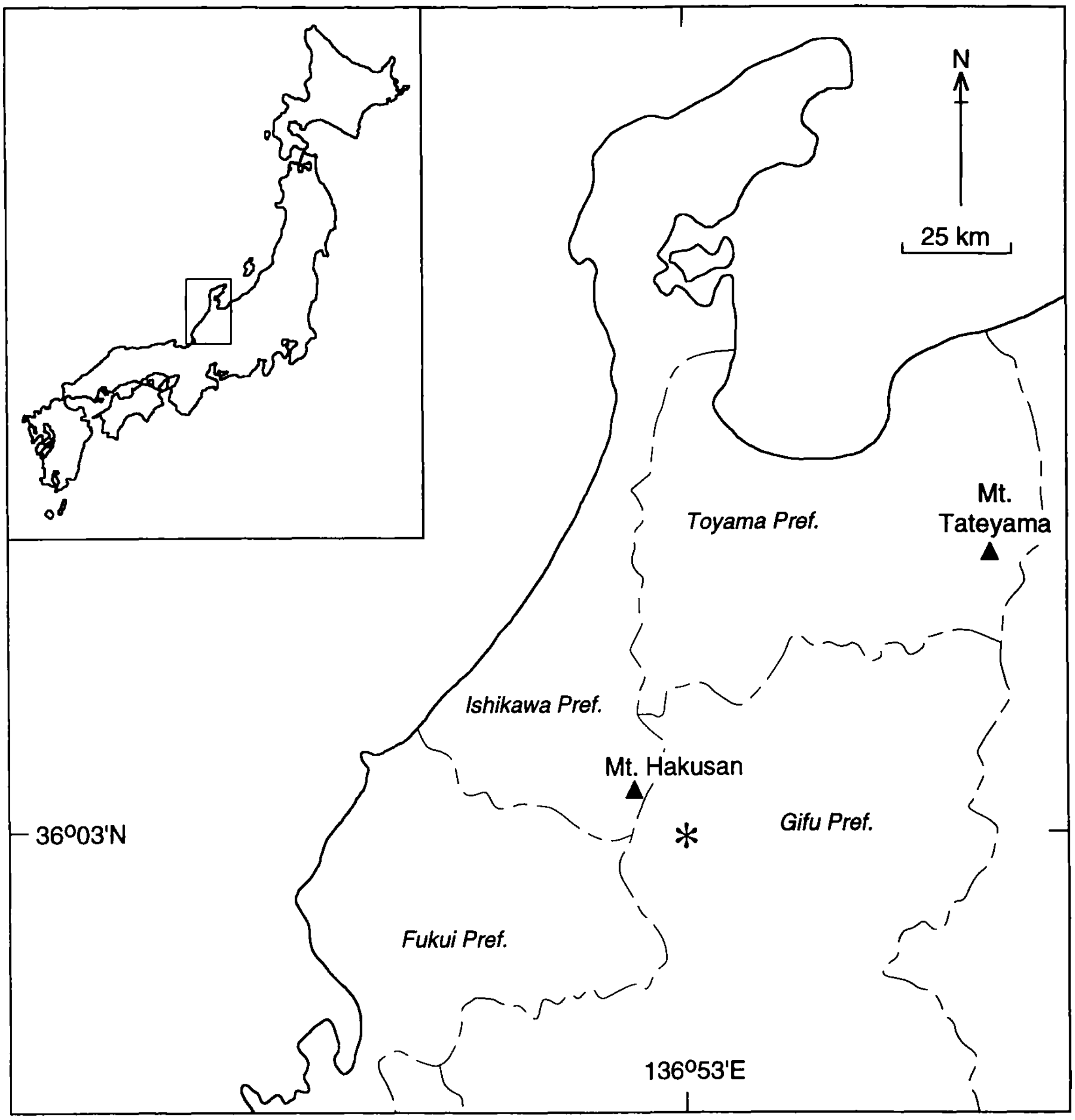

Figure 1. Location of Shokawa Village site KO-2 (Lower Cretaceous), Gifu Prefecture, marked with*.

Vertebrate taphonomy

The vertebrate debris comes from a layer no more than 200 mm thick, located in a thick sequence of siltstones, sandstones and occasional volcanic tuffs. The bone bed is a dark grey silty sandstone. Fossils are not evenly distributed through this horizon; rather they occur in well-defined layers (Figure 3).

The bottom of the bed is marked by large plant fossils. This is overlain by a concentration of shell debris (including fresh water unionid bivalves and viviparid gastropods) and bones. Generally, the scales and bone fragments occur in the lower parts of this concentration. The better preserved and associated materials (e.g., turtles and choristodere fossils) occur towards the top. A few tens of millimetres of barren sediment separates this bone concentration from a layer containing dinosaur teeth at the very top of the bed. The discrete layers of fossils probably represent a combination of taxonomic and hydrodynamic sorting. This is the only evidence of sedimentary structures found in the bone-bed horizon.

A series of taphonomic characters were described for the KO-2 fossil collections. Each bone or tooth fragment was described according to its state of abrasion and weathering; and the degree of fragmentation and nature of fractures present.

Fiorillo (1988) formulated a descriptive classification scheme for vertebrate materials:

Stage 0-Very angular: the bone (or tooth) is fresh and unabraded. Processes and bone edges are sharp and well-

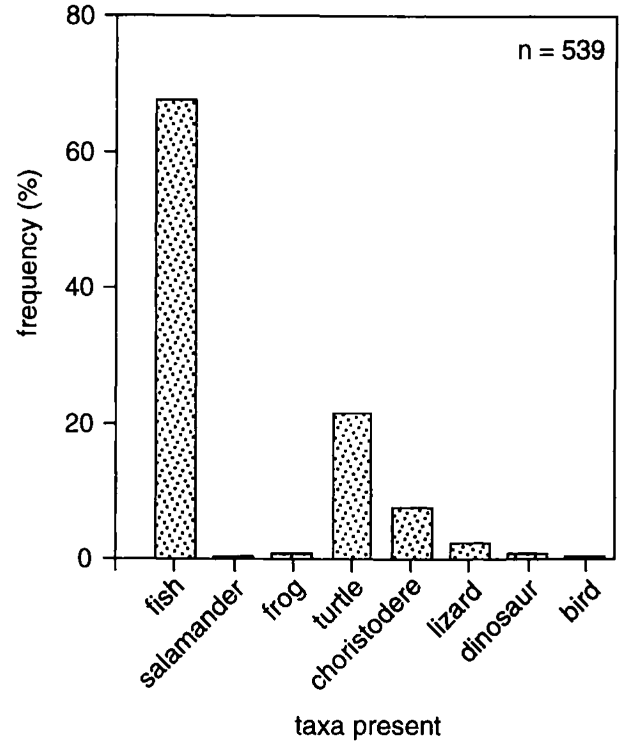

Figure 2. Relative proportions of identifiable fossils from site KO-2. 229 unidentifiable bone fragments were recorded.

defined.

Stage 1-Subangular: the bone processes and edges are slightly abraded and polished.

Stage 2-Subrounded: the bone edges are well rounded, processes are still recognisable. This stage is characteristic of moderate abrasion.

Stage 3-Rounded: edges show a high degree of rounding, processes are generally remnant.

It is necessary to include a final stage:

Stage 4-Extreme rounding, often spherical (Cook, 1995).

This scheme is discontinuous; abrasion characteristics are continuous, therefore intermediate stages are included (Cook, 1995).

Classically, the abrasion state relates to the distance a bone fragment has travelled in a fluvial system. However, it is more realistic to consider that the rounding is produced by a combination of physical processes (transport in rivers and the effects of trampling by animals) and reworking.

The material from KO-2 covers the full spectrum of possible abrasion stages (Figure 4). The majority of the materials range from stage 0-1 to stage 1-2, characteristic of slight abrasion. The range of abrasion stages indicates that the fossil assemblage is attritional rather than catastrophic in origin.

Changes in temperature and relative humidity modify bones as they lie on the ground prior to burial. These modifications take the form of cracks, initially on the outer layers of tissue, then working inwards until the bone breaks into a series of indeterminate fragments (Behrensmeyer, 1978; Fiorillo, 1988). The KO-2 specimens were examined and no evidence of *in situ* weathering modification was found.

Many of the KO-2 fossils are incomplete, that is they have been broken at some point between death and description. In most cases it was not possible to determine the relative timing of these fractures. Most of the identifiable fractures appear to be post-mineralisation; although pre-mineralization fractures and breakages caused during preparation are also present.

The fractures expose internal structures of the bones, often revealing cavities that have been infilled with white, cream or yellowish minerals. The nature of these mineral infills has yet to be determined.

Although the bulk of the collection comprises isolated skeletal elements, some associated and articulated fossils have been discovered. For example, an almost complete articulated (but crushed) turtle carapace and plastron, and an associated partial skeleton of a choristodere.

Discussion

The vertebrate fossils from the Tetori Group KO-2 site are generally characterised by a lack of modification caused by *in situ* weathering, slight abrasion, disarticulation and fragmentation. The absence of evidence for *in situ* weathering suggests that the bones were either buried rapidly, or quickly transported into rivers, where the sediment and water afforded protection from fluctuating environmental conditions. The full range of abrasion states indicates that the bone assemblage accumulated over an extended period of time, rather than during a catastrophic event. The generally low levels of rounding (abrasion) suggest that any transport affecting the bones was minimal. Few confirmed pre-mineralization fractures support this.

The majority of specimens recovered so far occur as isolated skeletal elements. Disarticulation results from a variety of processes, for example scavenging and fluvial transportation. It is likely that a combination of physical and biological processes resulted in the disarticulation state of the KO-2 fossil. Articulated and associated remains are restricted to turtle and choristodere fossils, perhaps explained by their semiaquatic lifestyles. If these creatures died in water, it is possible that they were rapidly covered by a protective layer of sediment. Fish dying in fluvial systems generally disarticulate, so scales and isolated bones are preserved (Wilson, 1996; Cook, 1997).

All of the above ties in well with our current understanding of the palaeoenvironments represented by the lithological and palaeontological records of the Tetori Group, and specifically site KO-2. The environment of deposition was terrestrial with a predominance of fluvial channels. In many respects it is comparable with the classic Lower Cretaceous Wealden sediments of southern England (Allen, 1981, 1990). However, major differences exist between the KO-2 fauna and that of the Wealden beds. Namely, the absence of crocodiles and mammals at KO-2. The lack of crocodile remains is unusual for a wetland environment, and is possibly explained by a taphonomic bias, or that the fossils haven't

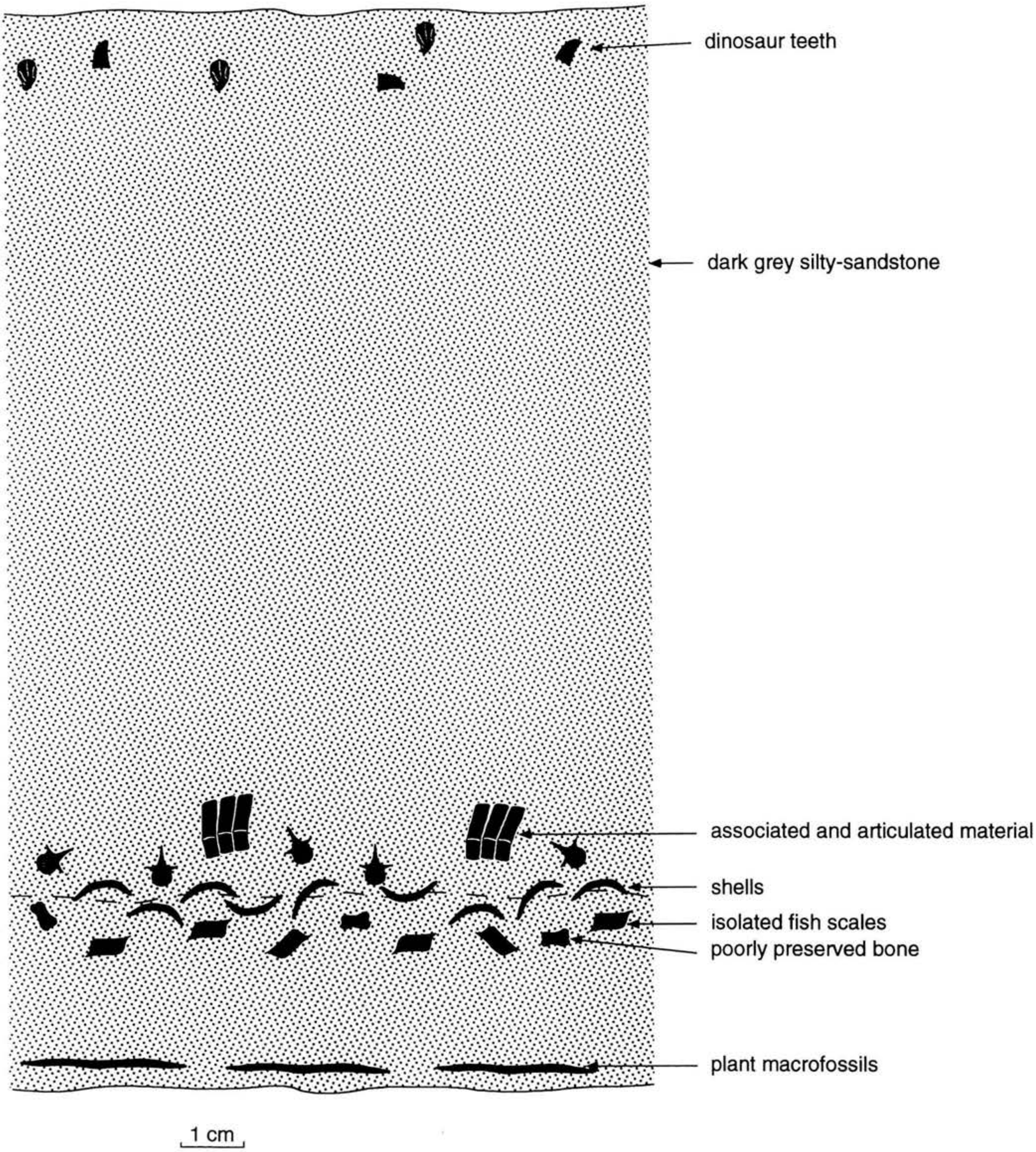

Figure 3. Schematic cross section of the bone-bearing horizon at Shokawa site KO-2, clearly showing the discrete levels of plant and vertebrate fossil materials.

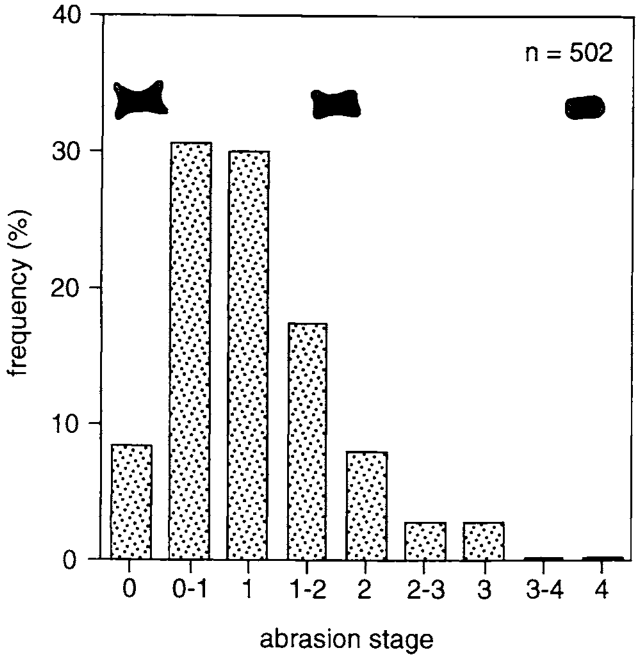

Figure 4. Abrasion states of the Shokawa site KO-2 vertebrate fossils. Classification scheme based on Fiorillo (1988) and Cook (1995).

been found yet, or a real absence of crocodiles in this part of Japan during the early Cretaceous. Perhaps choristoderes filled the 'crocodile-type' ecological niches. In contrast, the early Cretaceous environment of southern England supported several crocodile species (Buffetaut and Ford, 1979 ; Buffetaut and Hutt, 1980 ; Buffetaut, 1983 ; Cook and Ross, 1996). The absence of mammals is less strange ; mammal fossils are very rare in the Wealden sediments (Clemens and Lees, 1971).

Conclusions

The vertebrate fossils from the Tetori Group, locality KO-2, give a valuable insight into the palaeoecology of Japan during the early Cretaceous. The site is also significant in that it has produced the oldest dinosaur fauna from Japan, and the earliest record of a choristodere for eastern Asia (Manabe and Hasegawa, 1995).

The taphonomic characteristics of the fossils suggest a post mortem history of limited transport and reworking, rapid burial in fluvial sediments before diagenetic alteration and mineral infill.

Acknowledgements

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References

Allen, P., 1981 : Pursuit of Wealden models. *Journal of the Geological Society,* vol. 138, p. 375-405.

Allen, P., 1990 : Wealden research-ways ahead. *Proceedings of the Geologists' Association,* vol. 100, p. 529-564.

Behrensmeyer, A.K., 1978 : Taphonomic and ecological information from bone weathering. *Paleobiology,* vol. 4, p. 150-162.

Buffetaut, E., 1983 : The crocodilian *Theriosuchus* Owen, 1879 in the Wealden of England. *Bulletin on the British Museum (Natural History),* vol. 37, p. 93-97.

Buffetaut, E. and Ford, R.L.E., 1979 : The crocodilian *Bernissartia* in the Wealden of the Isle of Wight. *Palaeontology,* vol. 22, p. 905-912.

Buffetaut, E. and Hutt, S., 1980 : *Vectisuchus leptognathus,* n. g. n. sp., a slender-snouted goniopholid crocodilian from the Wealden of the Isle of Wight. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte,* vol. 7, p. 385-390.

Clemens, W.A. and Lees, P.M., 1971 : A review of English early Cretaceous mammals. *In,* Kermack, D.M. and Kermack K.A., *eds., Early Mammals,* p. 117-130. Linnean Society, Academic Press, London.

Cook, E., 1995 : Taphonomy of two non-marine Lower Cretaceous bone accumulations from southeastern England. *Palaeogeography, Palaeoclimatology, Palaeoecology,* vol. 116, p. 263-270.

Cook, E., 1997 : Sedimentology and vertebrate taphonomy of bone-bearing facies from the Clockhouse Rock Store (Weald Clay, late Hauterivian), Capel, Surrey, UK. *Proceedings of the Geologists' Association,* vol. 108, p. 49-56.

Cook, E. and Ross, A.J., 1996 : The stratigraphy, sedimentology and palaeontology of the Lower Weald Clay (Hauterivian) at Keymer Tileworks, West Sussex, southern England. *Proceedings of the Geologists' Association,* vol. 107, p. 231-239.

Fiorillo, A.R., 1988 : Taphonomy of Hazard Homestead Quarry (Ongalla Group), Hitchcock County, Nebraska. *Contributions to Geology, University of Wyoming,* vol. 26, p. 57-97.

Gifu-Ken Dinosaur Research Committee, 1993 : *Report on the dinosaur fossil excavation in Gifu Prefecture, Japan,* 46 p. Gifu Prefectural Museum, Gifu. (*In Japanese*)

Hasegawa, Y., Ohikura, M. and Manabe, M., 1990 : Smaller dinosaur, *Hypsilophodon* tooth from Gifu Prefecture. *Abstracts of the 139th Regular Meeting of the Palaeontological Society of Japan* : vol. 36. (*In Japanese*)

Hasegawa, Y., Manabe, M., Isaji, S., Ohkura, M., Shibata, I. and Yamaguchi, I., 1995 : Terminally resorbed iguanodontid teeth from the Neocomian Tetori Group, Ishikawa and Gifu Prefecture, Japan. *Bulletin of the National Science Museum, Tokyo, Series C,* vol. 21, nos. 1/2, p. 35-49.

Maeda, S., 1952 : A stratigraphical study on the Tetori series in the upper Shokawa district in Gifu Prefecture. *Journal of the Geological Society of Japan,* vol. 58, p. 145-153.

Maeda, S., 1961 : On the geological history of the Mesozoic Tetori Group in Japan, *Japanese Journal of Geology and Geography,* vol. 32, p. 375-396.

Manabe, M. and Hasegawa, Y., 1995 : Diapsid fauna and its palaeobiologeographical implications ; the Neocomian section of the Tetori Group, Japan. *In,* Sun, A. and Wang, Y. *eds., Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, short papers,* p. 179. China Ocean Press, Beijing.

Manabe, M., Hasegawa, Y. and Azuma, Y., 1989 : Two new dinosaur footprints from the early Cretaceous Tetori Group of Japan. *In,* Gillette, D.D. and Lockley, M.G. *eds., Dinosaur Tracks and Traces,* p. 309-312. Cambridge University Press, New York.

Unwin, D.M., Manabe, M., Shimizu, K. and Hasegawa, Y., 1996 : First record of pterosaurs from the early Cretaceous Tetori Group : a wing-phalange from the Amagodani Formation in Shokawa, Gifu Prefecture, Japan. *Bulletin of the National Science Museum, Tokyo, Series C,* vol. 22, nos. 1/2, p. 37-46.

Wilson, M.V.H., 1996 : Taphonomy of a mass-death layer of fishes in the Paleocene Paskapoo Formation at Joffre Bridge, Alberta, Canada. *Canadian Journal of Earth Science,* vol. 33, p. 1487-1498.

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A new tillodont from the early Middle Eocene of Japan and its implication to the subfamily Trogosinae (Tillodontia: Mammalia)

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Abstract. A new large tillodont, represented by a fragmentary right mandible with M/2-3, was found in the upper part of the Akasaki Formation, the early Middle Eocene of Japan. It is the first record of the order Tillodontia in Japan, and is described as a new genus and species, ***Higotherium hypsodon***, of the subfamily Trogosinae. It resembles the North American forms ***Trogosus*** and ***Tillodon*** in size; however it apparently differs from those and ***Kuanchuanius*** from China in having more hypsodont molars with well developed cusps. In detailed comparison with other trogosine molars, this new tillodont is one of the most derived taxa of the order, and morphologically situated in between the above three genera and the genus ***Chungchienia*** known from China, which was recently reassigned to the order. Morphological differences among these genera, including ***Higotherium hypsodon***, indicate that the new taxon shows a closer relationship with ***Chungchienia*** than with North American genera, and that the rapid evolutionary diversification of the Trogosinae occurred before and during the Middle Eocene.

Key words: Akasaki Formation, early Middle Eocene, ***Higotherium***, phylogenetic relationships, Tillodontia, Trogosinae

Introduction

Tillodonts are extinct herbivorous mammals having elongated I2/2, and are known from the Paleocene to Eocene strata in North America, Europe, and Asia. The order Tillodontia Marsh, 1875, which was systematically revised by Gazin (1953), includes a single family Esthonychidae Cope, 1883, that is divided into two subfamilies: Esthonychinae and Trogosinae, based mainly on the morphology of I2/2. Although various authors have discussed tillodont origins and phylogenetic relationships with the mammalian orders Pantodonta (e.g., Chow and Wang, 1979; Muizon and Marshall, 1992; Lucas, 1993) and Anagalida (Ting and Zheng, 1989), the oldest and most primitive tillodonts are known only from the early to middle Paleocene of China (Ting and Zheng, 1989). The occurrences of the earliest tillodonts in China suggest that their ancestor originated in Asia, and that tillodonts then migrated into North America and Europe via Beringia during the Late Paleocene to Middle Eocene (Gingerich and Gunnell, 1979; Stucky and Krishtalka, 1983; Krause and Maas, 1990; Baudry, 1992; Chow *et al*., 1996).

The subfamily Trogosinae hitherto included four genera: *Trogosus* Leidy, 1871 and *Tillodon* Gazin, 1953 from North America, and *Kuanchuanius* Chow, 1963a and *Chungchienia* Chow, 1963b from China (see Chow *et al*., 1996). The first three genera are known from the late Early to early Middle Eocene, based on recent chronological and biostratigraphical studies (Krishtalka *et al*., 1987; Tong, 1989; Prothero, 1995). Chow *et al*. (1996) systematically revised the taxonomic position of *Chungchienia*, known from the middle Eocene, and concluded that it is the most derived genus of Trogosinae. The subfamily Trogosinae, established by Gazin (1953), is characterized by having many derived characters: elongated rootless I2/2 with labial enamel band, more hypsodont molars than those of esthonychines, massive skull, and deep mandible with well developed symphysis. Although tillodont material is never plentiful, several phylogenetic hypotheses regarding the Tillodontia have recently been proposed by Stucky and Krishtalka (1983), Baudry (1992), Lucas (1993), and Chow *et al*. (1996). Their cladograms suggest that the trogosine tillodonts are phylogenetically situated in the most derived monophyletic group within the order, whereas the Esthonychinae are no longer a monophyletic group.

Eocene mammals have seldom been found in Japan, and the new tillodont described below is the oldest known mammalian fossil from the Tertiary of Japan. Although remains of the new tillodont do not include the diagnostic incisors, it certainly belongs to the subfamily Trogosinae based on the cusp patterns of hypsodont molars and its large size. This paper adds a new taxon from Japan to Trogosinae, and focuses on the phylogenetic position and affinities between North American and Asian trogosines.

The following institutional abbreviations are used in this paper: **AMNH**, American Museum of Natural History, New York, New York; **ANSP**, Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, People's Republic of China; **NMC**, Canadian Museum of Nature, Ottawa, Canada (formerly the National Museums of Canada); **NSM**, Department of Geology, National Science Museum, Shinjuku, Tokyo, Japan; **USNM**, National Museum of Natural History, Washington, D. C.; **YPM**, Peabody Museum of Natural History, Yale University, New Haven, Connecticut.

Geological setting and the age of Akasaki Formation

The locality of the tillodont specimen described below is located on the coast at Akasemachi, Uto Peninsula, about 15 km west of Uto City, Kumamoto Prefecture, Japan (Figure 1). The specimen was found in the gray-blue siltstone belonging to the upper part of the Akasaki Formation. The Akasaki Formation belongs to the Miroku Group of Nagao (1926) or the Akasaki Group of Matsushita (1949); it is the basal unit of the Paleogene strata distributed in the western part of Uto Peninsula and Amakusa area. The Paleogene strata are widely distributed in the area and unconformably overlie the Upper Cretaceous Himenoura Group. The Paleogene stratigraphy was established by Nagao (1926), who divided it into three Groups: the Miroku, Hondo, and Sakasegawa Groups in ascending order (Figure 1). After his work, several stratigraphic nomenclature revisions of the Paleogene strata have been proposed by other authors, and their stratigraphic schemes and detailed stratigraphy are summarized by Miki (1972, 1975).

The Akasaki Formation is composed of nonmarine fluvial sediments; it consists largely of red siltstone, gray-blue siltstone, and conglomerate. This formation is approximately 400m in thickness at Uto Peninsula, but unrecognized in

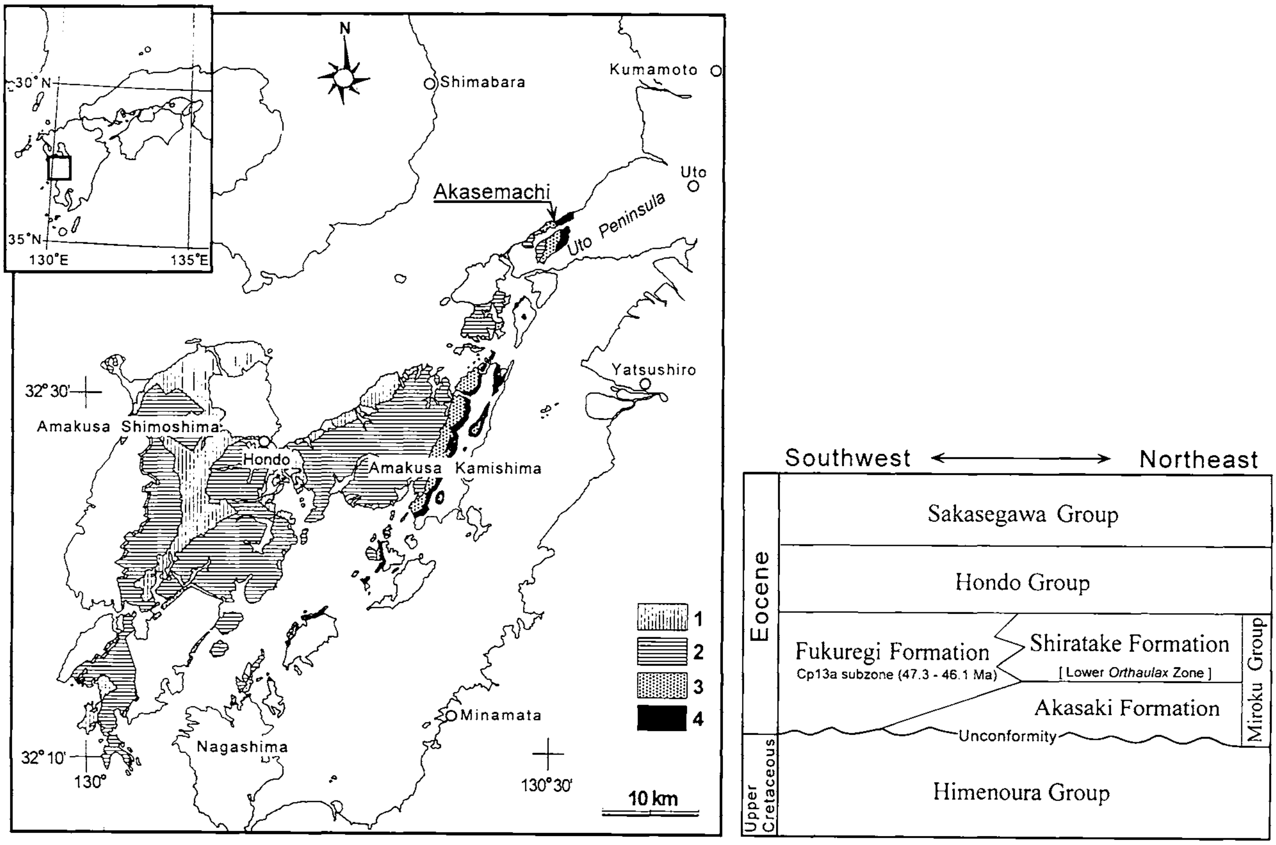

Figure 1. Left, Geological sketch map showing the fossil locality (Akasemachi), Amakusa area and Uto Peninsula, western part of Kyushu, Japan (modified from Miki, 1975). **1**: Sakasegawa Group, **2**: Hondo Group, **3**: Shiratake and Fukuregi Formations, **4**: Akasaki Formation. Right, stratigraphic relationships of the Paleogene strata distributed in the area.

the Amakusa Shimoshima, and has hitherto been unfossiliferous. Because no reliable fossil evidence has been found in the Akasaki Formation, the geologic age of the Akasaki Formation has been discussed by various authors (e.g., Miki, 1975; Takai and Satoh, 1982; Miki and Matsueda, 1985) based mainly on stratigraphic correlation with the conformably overlying strata: the Fukuregi and Shiratake Formations (see also Figure 1) which include marine invertebrate fossils. The Shiratake Formation, distributed in the eastern part of Amakusa area and Uto Peninsula, consists mainly of shallow marine sediments and yields abundant molluscan fossils near the basal part. The molluscan fossiliferous horizon was named "Lower *Orthaulax* Zone" by Nagao (1926), and is widely traceable in the area. The Shiratake Formation is generally correlated with the Fukuregi Formation based on the lithofacies and similar molluscan fauna (Miki, 1972, 1975). The Fukuregi Formation, which is another basal unit of the Paleogene strata distributed in the Amakusa Shimoshima, bears larger foraminifera such as *Nummulites* and *Discocyclina* in addition to the molluscan fossils. The *Nummulites*-bearing rocks of the Fukuregi Formation and the Lower *Orthaulax* Zone of the Shiratake Formation are regarded as the same fossiliferous horizon, and both were previously considered Ypresian (Early Eocene) in age on the basis of the *Nummulites* and molluscan fossils (Hanzawa and Urata, 1964; Miki, 1975). Consequently, Miki and Matsueda (1985) referred to the previous interpretation of the Paleogene stratigraphy, and estimated the geological time range of the Akasaki Formation as Middle Paleocene to Early Eocene based on their preliminary work on the magnetostratigraphy of this formation.

However, the previous biostratigraphic interpretation from the molluscan fauna and *Nummulites* is not supported by data from the nannoflora from the Fukuregi Formation (Tashiro *et al.*, 1980). Recently, Okada (1992) reported on the nannofossil zones of the Paleogene distributed in the western part of Kyushu, and reassigned the nannoflora of the Fukuregi Formation to the Cp13a subzone (approximately 47.3-46.1 Ma, Berggren *et al.*, 1995, p. 194), the early Middle Eocene. Therefore, the geologic age of the Lower *Orthaulax* Zone, previously assigned to the Early Eocene as mentioned above, is also more likely placed in the early Middle Eocene on the basis of Okada's (1992) conclusion. The horizon of the new tillodont is situated at about 18 m below the Lower *Orthaulax* Zone. Although the geologic age of the lower limit of the Akasaki Formation has not been resolved, the gray-blue siltstone that yielded the tillodont fossil is probably the same age, early Middle Eocene, without any great time gap.

Systematic paleontology

Order Tillodontia Marsh, 1875
Family Esthonychidae Cope, 1883
Subfamily Trogosinae Gazin, 1953
Genus ***Higotherium*** gen. nov.

Type species.—*Higotherium hypsodon* sp. nov.

Diagnosis.—Size similar to those of *Tillodon* and *Trogosus*, but smaller than that of *Chungchienia*, and much larger than that of *Kuanchuanius*. Lower molars much more hypsodont than those of *Tillodon, Trogosus*, and *Kuanchuanius*, with well developed cusps. The buccal crowns not so distinctly tapering upward as in *Tillodon*, and not so markedly convex in transverse section as in *Trogosus*. M/3 has an elongated large metaconid and anteroposteriorly shortened third lobe which displays a deep, enclosed basin; M/3 also has two additional small cusps, namely a mesoconid on the cristid obliqua and a cusp on the paracristid.

Etymology.—From Higo, an ancient name of present Kumamoto Prefecture, plus therium (Gr.), beast.

Higotherium hypsodon sp. nov.

Figures 2-4

Holotype.—A right mandible fragment with M/2 and M/3, NSM-PV 20118.

Type locality.—Coast at Akasemachi, Uto City, Kumamoto Pref., Japan (Figure 1).

Horizon.—The upper part of the Akasaki Formation (approximately 18m below the Lower *Orthaulax* Zone).

Age.—Most likely early Middle Eocene.

Etymology.—From hypsos (Gr.), high, plus odon (Gr.), tooth, referring to its hypsodont molars.

Diagnosis.—Same as for the genus until other species may be found.

Description

Terminology of molar structures mostly follows that of Bown and Kraus (1979), and extra terms are indicated in Figure 3A.

Mandible: The anterior portion of mandible (anterior to M/2) and the distal ends of the coronoid, condyle, and angular processes are missing. In addition, the mandibular ramus is weakly laterally compressed. However, the remaining portion of mandible is well-preserved, and the outline of the missing portion is faintly preserved as a weak impression on the matrix. The length of the complete mandible is estimated to have been approximately 30 cm, judging from the impression and the size of the remaining portion. The mandible is massive and deepest in the area between M/2 and M/3. The masseteric fossa, extending between coronoid and condyle processes, is deeply concave at the anterior portion of mandibular ramus. The anterior margin of the mandibular ramus is subvertical relative to the occlusal surface of the tooth row (the angle of about 80°), and rises behind the M/3 talonid (Figure 2).

Lower molars: The lower molars are extremely hypsodont on the buccal side in contrast to the appearance of the lingual side, as in other tillodonts. The buccal wall is columnar with a narrow and deep hypoflexid between the trigonid and talonid, while the lingual wall is almost flattened (Figure 3B). The cristid obliqua is very strong and links to the posterolingual wall of the protocristid near the base of the metaconid as in other trogosines. The enamel surface on the buccal side is entirely rugose with longitudinal, weak

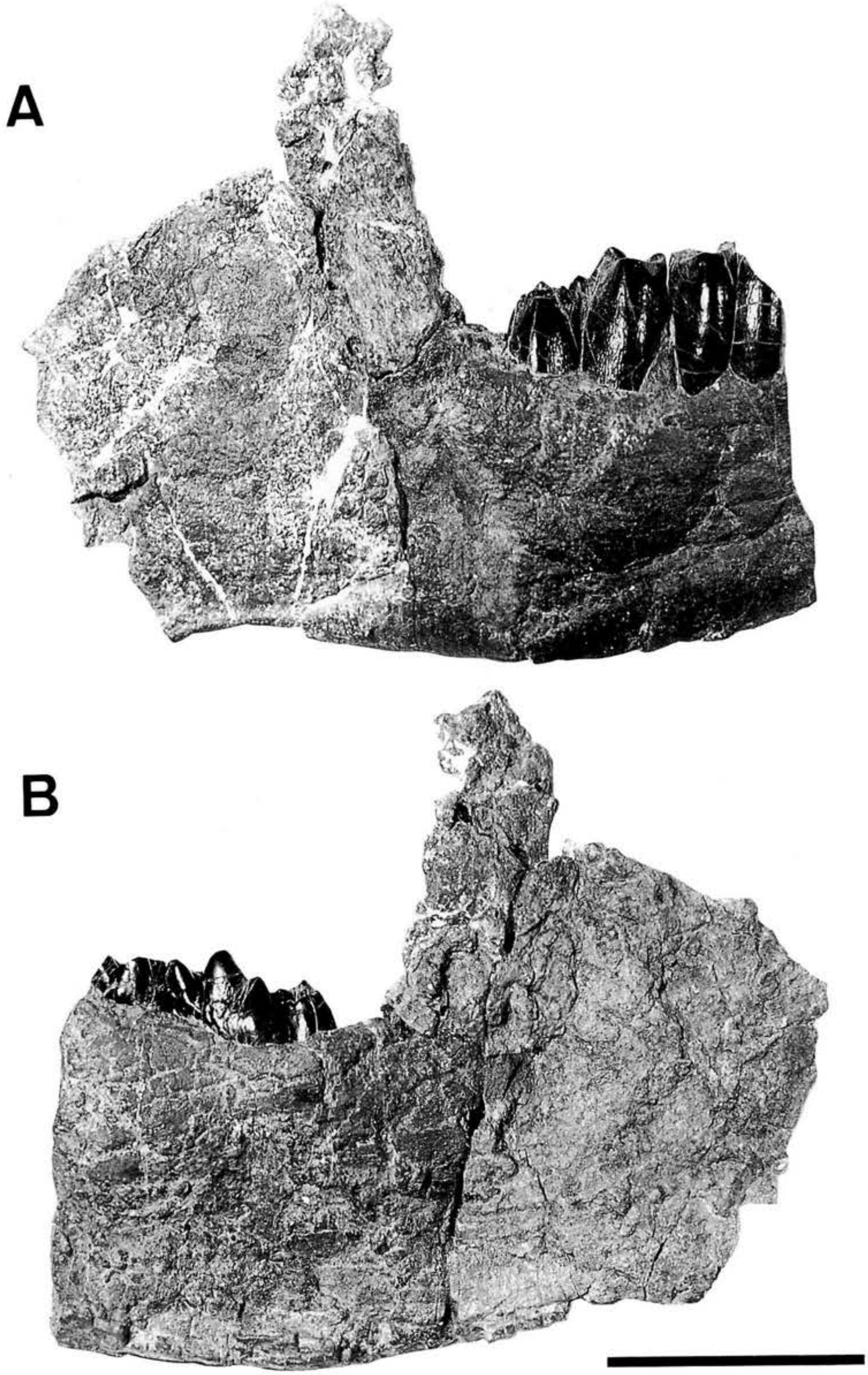

Figure 2. *Higotherium hypsodon* gen. et sp. nov. Holotype : NSM-PV 20118, right fragmentary mandible with M/2 and M/3. **A** : buccal view, **B** : lingual view. Scale bar equals 5 cm.

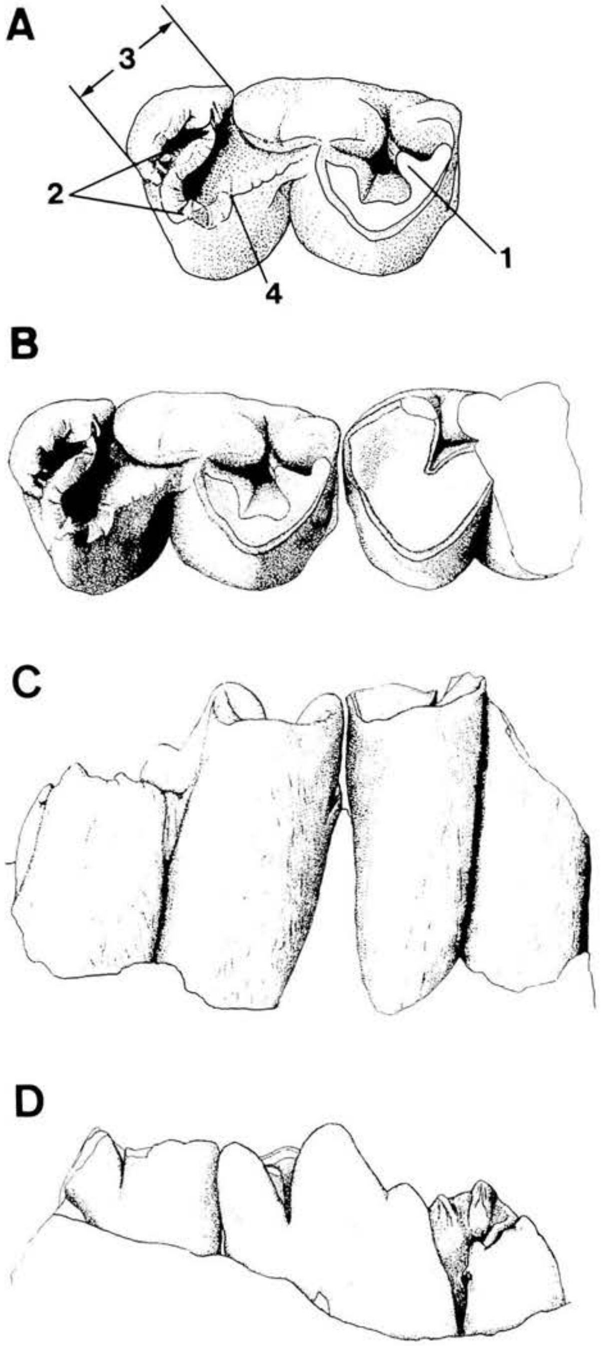

Figure 3. Right M/2 and M/3 of *Higotherium hypsodon* gen. et sp. nov. Holotype: NSM-PV 20118. **A**: positions of extra cusps and ridges on the M/3 discussed in the text, 1: an additional cusp on the paracristid, 2: posthypocristid, 3: third lobe, 4: mesoconid. **B**: occlusal view, **C**: buccal view, **D**: lingual view. Scale bar equals 1 cm.

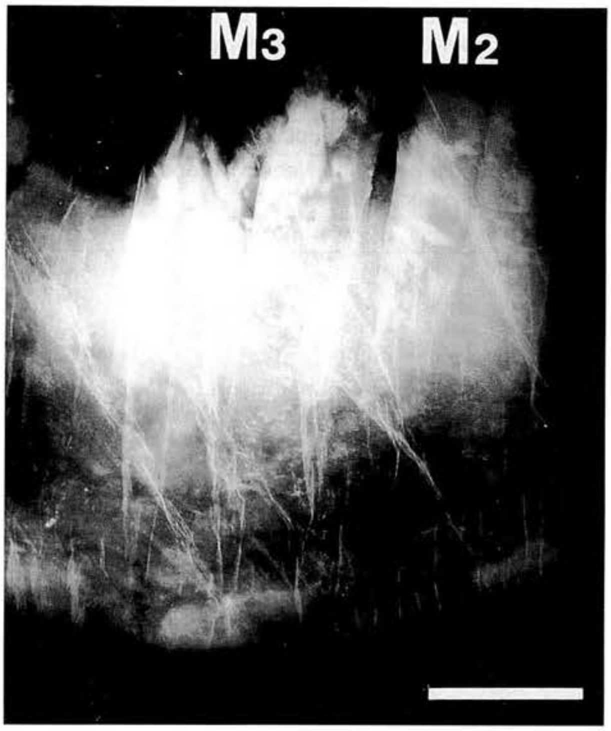

Figure 4. Lingual radiograph of right M/2 and M/3 of *Higotherium hypsodon* gen. et sp. nov. Holotype: NSM-PV 20118. Scale bar equals 2 cm.

lines, that are absent on the lingual side (Figures 3C and D). The cervical line is unexposed above the dentary in both molars (Figure 3C). Although soft X-ray photographs of NSM-PV 20118 were taken in order to examine the development of the molar roots, it could not be determined whether the roots were formed or not. However, it is clear that both molars extend deep in the dentary (Figure 4), and thus they are quite hypsodont.

M/2: Most of the M/2 trigonid was missing when collected, hence cusps of the trigonid are unknown. Width of the trigonid is almost equal to that of the talonid (Table 1), and the trigonid is slightly shorter anteroposteriorly than that of M/3, judged by the remaining part of the crown. The buccal wall of the talonid is slightly bowed toward the occlusal surface in posterior view, and the buccal margin of the talonid exhibits a swollen V-shape in horizontal cross section. The posterior portion of the metaconid is distinctly elongated, but detailed structure of the metastylid is mostly unknown since its apex is not preserved. The entoconid, hypoconulid, and hypoconid have lost much of their details by heavy wear. Two ridges extend from the hypoconid: the cristid obliqua anterolingually and a ridge joining to the hypoconulid posterolingually; and the hypoconulid is further connected with the entoconid by another ridge (i.e., postcristid). All three ridges are very strong and broad. The talonid notch between the entoconid and metastylid is narrow and deep. The cristid obliqua becomes narrower anteriorly and is separated from the metastylid by a narrow notch. This narrow notch steeply descends posteriorly and joins with the

Table 1. Measurements (in mm) of mandible and lower molars of NSM-PV 20118, holotype of *Higotherium hypsodon* gen. et sp. nov. Asterisk (*) indicates measurement of damaged tooth.

Mandible	
Internal maximum depth, between M/2 and M/3	67.8
Maximum thickness, under M/2	25.3
Lower molars	
M/2 Length	20.8*
Width of trigonid	17.5
Width of talonid	18.1
M/3 Length	35.4
Width of trigonid	20.5
Width of talonid	19.5
Width of third lobe	10.5

talonid notch.

M/3: M/3 is an almost unworn tooth in contrast to the heavily worn M/2 (Figure 3B). Width of the trigonid and talonid are nearly equal to those of M/2 (Table 1). In horizontal cross section, the outlines of the buccal margin of both trigonid and talonid are swollen V-shape as in M/2. The buccal wall of the talonid slightly tapers upward. The trigonid basin notch between the paraconid and metaconid is deep and narrow lingually; its bottom is situated slightly lower than that of the M/2 talonid notch at the eruptional stage. The paraconid is sloping and swollen posteriorly; it is slightly constricted at the base of the lingual side. The metaconid is the highest and largest cusp, with the apex slightly curved posteriorly. The posterior arm of the metaconid markedly protrudes from the posterior wall of the protocristid (Figures 3B and C). A prominent metastylid is located on the posterior slope of the metaconid. The paracristid and protocristid extend to the apices of the paraconid and metaconid, respectively. An additional small cusp exists on the paracristid close to the paraconid; it displays a distinct protuberance into the trigonid basin by wear (1 in Figure 3A). A narrow but sharp precingulid is present on the anterior wall of the trigonid (Figures 3B and C).

The M/3 talonid is highly specialized. The talonid basin notch which separates the metastylid from the entoconid displays a lingually opened fissure (Figure 3D). The hypoconid and entoconid are united by a strong ridge (i.e., posthypocristid, 2 in Figure 3A), which separates the primary talonid basin anteriorly and third lobe basin posteriorly, as in *Trogosus grangeri* (see also comparisons section). The third lobe (3 in Figure 3A) is anteroposteriorly shortened, and slightly inclined anteriorly; it shows an oval shape parallel to the cristid obliqua in horizontal cross section. The third lobe also displays a deep enclosed basin which is surrounded by the entoconid, posthypocristid, and a ridge with unidentified cuspules (Figure 3B). The posterobuccal wall of the entoconid swells into the third lobe basin. The cristid obliqua becomes narrower dorsally and is separated from the metastylid by a narrow notch that joins the talonid notch as in M/2. A minute but distinct mesoconid exists on the cristid obliqua (4 in Figure 3A); lingual walls of both hypoconid and mesoconid swell into the talonid basin.

Comparisons

Gazin (1953) divided the Esthonychidae into two subfamilies, Esthonychinae and Trogosinae, based principally on the morphology of I2/2. Although the I2/2 are absent in NSM-PV 20118, *Higotherium hypsodon* certainly belongs to the Trogosinae based on the following characters: much larger size, particularly deep mandible, more hypsodont molars with cristid obliqua close to metaconid, and developed M/3 third lobe basin with a posthypocristid. *Higotherium* is sufficiently distinguished from all other trogosines by many characters as mentioned below. The main comparative measurements and characters discussed in the text are shown in Tables 2 and 3, respectively; and the comparisons were made with original specimens, plus illustrations and descriptions in the literature (Gazin, 1953; Robinson, 1966; Chow, 1963a, b; Chow *et al.*, 1996). Detailed comparisons with North American trogosines that focus on cusps are difficult because the cheek teeth are heavily worn in almost all specimens. Thus, comparisons are based primarily on the specimens having best-preserved crowns among known specimens as shown in Figures 5 and 6.

***Trogosus* Leidy, 1871**: Gazin (1953) recognized five species in the genus *Trogosus*: *T. castoridens* (type species), *T. hyracoides, T. grangeri, T. hillsii*, and *T. latidens*. The last species was previously questionable and was defined only by its very large size, but was later regarded as a valid species (Stucky and Krishtalka, 1983; Gunnell *et al.*, 1992). Gazin also recognized two structural types among these species: the "long-faced" species (*T. grangeri* and *T. hyracoides*) and "short-faced" species (*T. hillsii* and *T. castoridens*), which probably indicated sexual dimorphism: *T. grangeri* and *T. hyracoides* are related to *T. hillsii* and *T. castoridens*, respectively (Gazin, 1953, p. 40). Although the sexual dimorphic relationships have never been demonstrated, Robinson (1966) believes that *T. hillsii* is probably synonymous with *T. grangeri*.

The mandible of NSM-PV 20118 differs from those of the holotypes of *T. castoridens* (ANSP 10337, AMNH 15590: cast of holotype) and *T. hillsii* (USNM 17157) in having greater depth, a more vertical ascending ramus, and a posteriorly extending masseteric fossa (Table 3). The mandible of NSM-PV 20118 is slightly deeper than those of the holotype of *T. grangeri* (AMNH 17008) and of the specimen (USNM 17886) referred to *T. hyracoides* by Gazin (1953). The M/2-3 of NSM-PV 20118 are slightly larger than those of almost all specimens of *Trogosus* (Tables 1 and 2), and are nearly equal to those of the largest specimen of *T. grangeri* (YPM 16449, examined by Robinson, 1966). Lower molars of *Trogosus* are rather hypsodont, but much less than those of *Higotherium hypsodon*. In fact, the height of the M/2 crown exceeds twice the height of YPM 16449 despite being at nearly the same wear stage (Figures 3C and 5B), and the trigonid and talonid notches, particularly in M/3, are much deeper and narrower in *H. hypsodon*. Gazin (1953, p. 35) noted as a diagnostic feature of *Trogosus* that the buccal walls of lower molars are distinctly convex in transverse

Table 2. Measurements (in mm) of the lower molars of trogosine tillodonts discussed in the text. Asterisks (*) indicate measurements of damaged tooth. The measurements of NMC 8709 and IVPP V 10805 are from Gazin (1953) and Chow *et al.* (1996), respectively.

Species and catalogue no.	M/1L	M/1W	M/2L	M/2W	M/3L	M/3W
Trogosus grangeri :						
AMNH 17008 (holotype)	14.8	13.8	18.6	15.8	28.8	15.8
AMNH 17009	16.0	13.8	20.0	15.5	31.2	15.5
AMNH 17495A	20.1	15.6*	25.3*	18.2	38.8*	15.0
YPM 16449	20.3	16.4*	21.9	17.5	38.6	18.4
Trogosus hyracoides :						
AMNH 18982	18.0	15.3	20.6	17.2	31.3	15.3
USNM 17886	15.5	14.3	19.8	17.1	27.2	17.6
Trogosus castoridens :						
AMNH 15590 (cast of ANSP 10337 : holotype)	13.5	13.2	19.6	18.0	25.7	12.4
Trogosus cf. *castoridens* :						
USNM 18165					29.2	16.3*
Trogosus hillsii :						
USNM 17157 (holotype)	15.7	13.4	19.3	14.5	29.8	15.6
Trogosus latidens :						
NMC 8709	20.5		26.3			
Tillodon fodiens :						
YPM 11087 (holotype)	17.2	15.5*	20.9	21.1	35.4	19.4
USNM 18164	16.0	16.6	21.7	19.7*	37.4	19.1
Kuanchuanius shantunensis :						
IVPP V 2764 (holotype)			19.4	14.9	26.5*	13.3
Chungchienia lushia :						
IVPP V 10805 (holotype)	24	24	28	26	43	22

section, whereas the buccal walls of NSM-PV 20118 are columnar, only slightly convex. All individual cusps of *Trogosus* molars, especially the M/3 metaconid, are less developed than those of *H. hypsodon*. Detailed features of the M/2 entoconid and hypoconulid are also unknown in both YPM 16449 and NSM-PV 20118, but in the latter the postcristid is stronger and wider (Figures 3B and 6B). Moreover, in *Trogosus* the M/3 entoconid is apparently separated from the hypoconulid by a small notch at the unworn stage, whereas in NSM-PV 20118 the M/3 hypoconulid portion is specialized and more strongly connects with the entoconid. In addition, precingulids are apparently reduced or lost in all specimens of *Trogosus* including YPM 16449. Although the presence on M/3 of a mesoconid and an additional cusp on the paracristid cannot be easily assessed in almost all *Trogosus* specimens, the latter accessory cusp is probably absent in *Trogosus* based on our examination of YPM 16449.

In general, the M/3 third lobe of *Trogosus* is elongated posteriorly as in YPM 16449 (Table 2), whereas in NSM-PV 20118 the lobe is much shortened anteroposteriorly and located much more lingually. However, except for the differences of the molar elongation and cusp position, *H. hypsodon* is similar to YPM 16449 in having the same structure on M/3 : the talonid is divided into two basins by a strong posthypocristid (Figures 3B and 6B). According to Gazin (1953, p. 44), the divided M/3 talonid basin is a distinctive character of the "Huerfano specimens" of *Trogosus* (*T. grangeri* and *T. hillsii*) from the Huerfano Formation, Colorado. Robinson (1966) also recognized the peculiar character of M/3 of the Huerfano *Trogosus*. As Gazin (1953, p. 38) mentioned, in *T. hyracoides* the M/3 talonid basin is little divided or undivided ; actually the entoconid and hypoconid are not directly united to each other by a posthypocristid on the left M/3 of AMNH 18982 (Figure 6A, examined by Gazin, 1953), but these two cusps on the right M/3 are slightly connected by a low and narrow posthypocristid based on our careful reexamination. Moreover, a distinct protuberance is present on the buccal side of the left M/3 third lobe in AMNH 18982 (Figures 5A and 6A), but this condition is rarely observed in other *Trogosus* specimens.

***Tillodon* Gazin, 1953** : *Tillodon* is a monotypic genus including *Tillodon fodiens* (Marsh, 1875). *T. fodiens* was previously regarded as the most derived tillodont ; it possesses an enlarged skull with somewhat broad and long rostrum, deepened mandible with well developed angular process, a long diastema between P/2 and P/3, loss of I/1 and I/3, less molariform P/4, and a narrower and shorter M3/ than M2/. The known specimens referred to this species are very few : YPM 11087 (holotype), USNM 18164, and USNM 17158 (hypotypes examined by Gazin, 1953).

Higotherium hypsodon is comparable to *Tillodon fodiens* in size (Table 2), and the depth of mandible of NSM-PV 20118 is almost equal to that of YPM 11087 and USNM 18164. However, in *Tillodon* the deepest part of the mandible is not clear, since the ventral edge of the mandible is really parallel

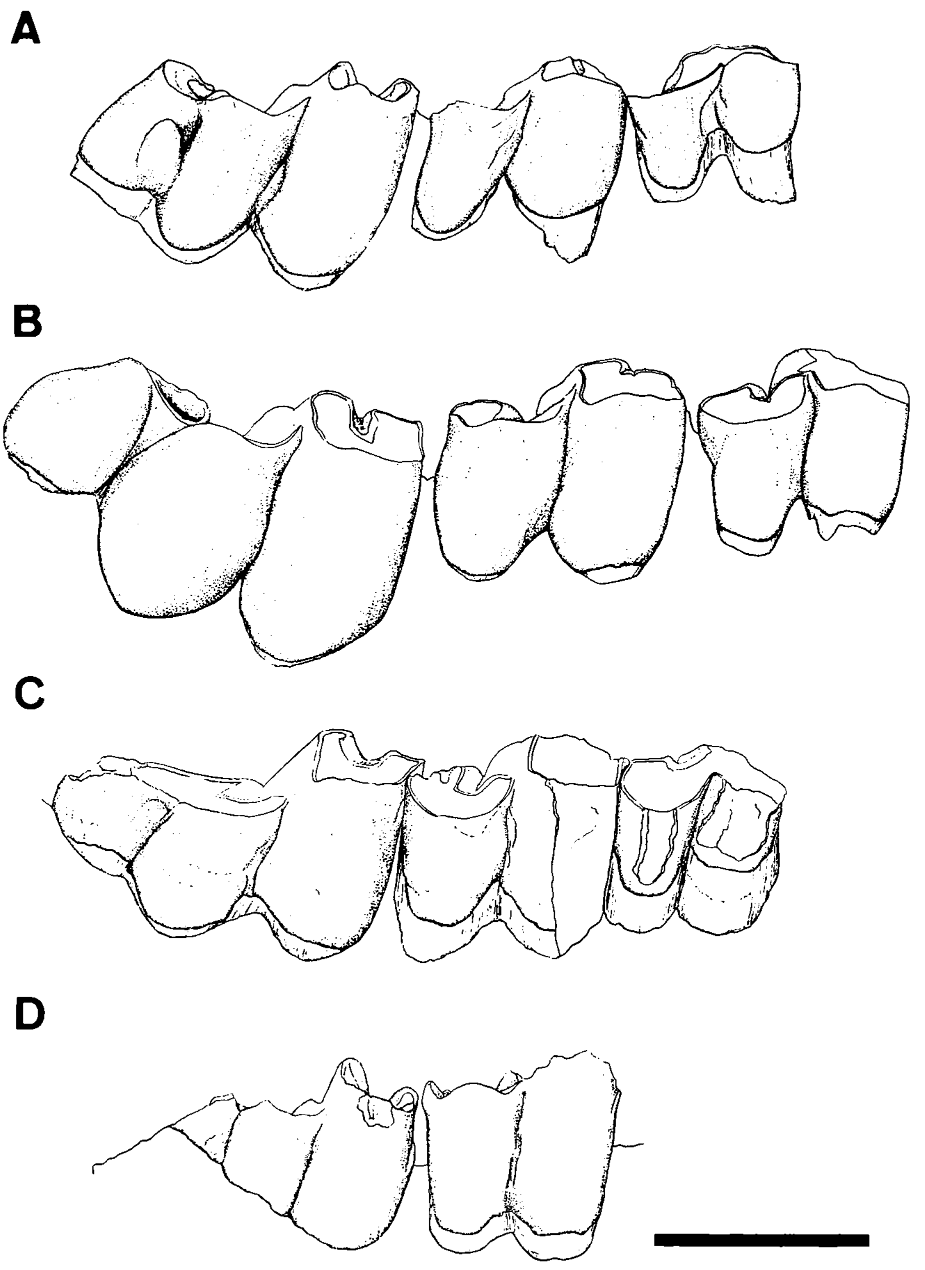

Figure 5. Sketches of well preserved lower molars of trogosines in buccal view. **A** : *Trogosus hyracoides* (AMNH 18982, reversed), **B** : *Trogosus grangeri* (YPM 16449), **C** : *Tillodon fodiens* (USNM 18164), **D** : *Kuanchuanius shantunensis* (holotype : IVPP V 2764). Scale bar equals 2 cm.

to the tooth row. The lower molars of NSM-PV 20118 are much more hypsodont than those of *T. fodiens*, which is distinguished from other trogosines by having brachydont molars despite its large body size (Table 2 and Figure 5C). As Gazin (1953, p. 49) pointed out, in *Tillodon* the buccal walls of the lower molars distinctly taper upward and are externally convex at the base (Figure 5C). Moreover in the lower cheek tooth row of *Tillodon*, the tooth size apparently increases posteriorly (Table 2) ; the lower molars are tightly arrayed to each other with no space between the teeth ; and the transverse width in M/3 decreases posteriorly (Figure 6C). These features are unlike those of *H. hypsodon*. On the basis of our examination of USNM 18164, all individual cusps on the molars are bulbous in *Tillodon*. The M/3 metaconid of USNM 18164 is relatively low ; its posterior slope never protrudes posteriorly from the posterior wall of the protocristid as in NSM-PV 20118 (Figures 3B and 6C). A marked difference is loss of the M/3 metastylid in USNM 18164. A precingulid and a cusp on the paracristid are also absent in the M/3 of *Tillodon*, but these conditions are

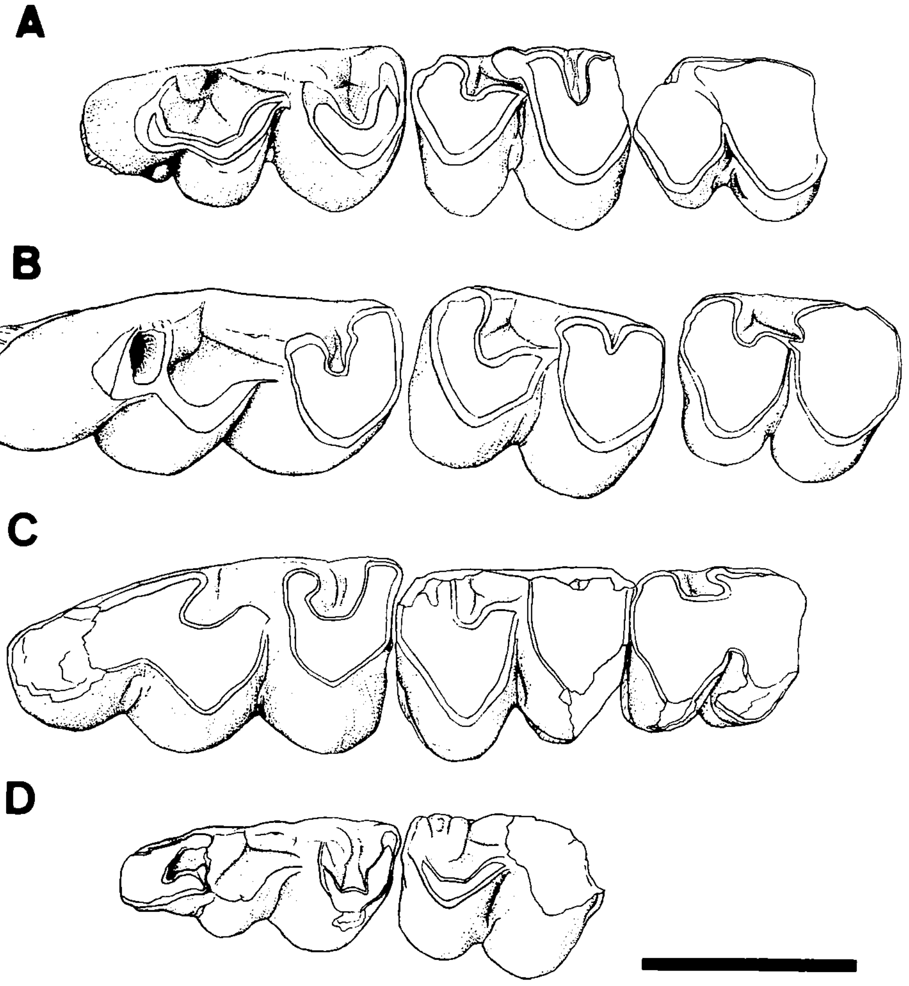

Figure 6. Sketches of well preserved lower molars of trogosines in occlusal view. **A** : *Trogosus hyracoides* (AMNH 18982, reversed), **B** : *Trogosus grangeri* (YPM 16449), **C** : *Tillodon fodiens* (USNM 18164), **D** : *Kuanchuanius shantunensis* (holotype : IVPP V 2764). Scale bar equals 2 cm.

unfortunately indeterminate in the holotype (YPM 11087) because of heavy wear. The presence of a mesoconid on M/3 is also not observable on either YPM 11087 and USNM 18164, owing to wear. However, the M/3 third lobe of NSM-PV 20118 obviously differs from that of USNM 18164 ; USNM 18164 has a broad occlusal area of the M/3 talonid with a much elongated entocristid anteroposteriorly (Figure 6C).

***Kuanchuanius* Chow, 1963** : *Kuanchuanius* includes two species : *K. shantunensis* Chow, 1963a (type species) and a questionable species, *K.* ? *danjiangensis* Cheng and Ma, 1990. The former is known by fragmentary mandibles with right and left I/2, right M/2 and M/3 (IVPP V 2764, holotype), and the latter only by an isolated left M/1. Although Chow (1963a) never specified that this Chinese genus belongs to the subfamily Trogosinae, various authors have recognized the morphological similarities between *Kuanchuanius* and *Trogosus* (Rose, 1972 ; Stucky and Krishtalka, 1983 ; Lucas 1993).

Higotherium hypsodon is much larger than *K. shantunensis* ; the mandible of IVPP V 2764 is about 40 percent shallower than that of NSM-PV 20118 when compared with the greatest depth. The mandible of IVPP V 2764 is considerably more slender and shorter among known trogosine specimens, and is similar to the holotypes of *T. castoridens* (ANSP 10337) and of *T. hillsii* (USNM 17157) in having shallow depth, a short diastema between P/2 and P/3, anteriorly extending masseteric fossa, and lower angle of the ascending ramus (Table 3). The M/2-3 of *K. shantunensis* are much less hypsodont than those of *H. hypsodon* and are narrower in width relative to other trogosine specimens (Table 2). The two molars of IVPP V 2764 show features clearly because they are almost unworn in spite of their eruption, although a part of the M/2 trigonid and a posterior portion of the M/3 third lobe are broken off. In IVPP V 2764, the M/2 trigonid is much wider than the talonid ; M/3 becomes narrower posteriorly ; the hypoflexid on M/2-3 is relatively wide ; the M/3 third lobe is posteriorly elongated ; and the M/2 buccal wall is distinctly convex, as in *Trogosus*,

Table 3. Comparative table of mandibular and lower dental characters among trogosines discussed in the text. **1** : *T. hyracoides* and *T. grangeri* (long-faced species), **2** : *T. castoridens* and *T. hillsii* (short-faced species), **3** : *T. grangeri*, **4** : *T. hyracoides*. Question marks (?) indicate not observable.

Mandibular characters

	Trogosus	*Tillodon*	*Kuanchuanius*	*Higotherium*	*Chungchienia*
Depth of mandible	Deep (**1**) or shallow (**2**)	Deep	Shallow	Deep	Extremely deep
Posterior extension of symphysis	P/4 talonid or M/1	P/4 talonid or M/1 talonid	Anterior margin of M/1	?	?
Anterior extension of masseteric fossa	Behind (**1**) or under M/3 talonid (**2**)	Behind M/3 talonid	Under M/3 talonid	Behind M/3 talonid	?
Angle of ascending ramus for tooth row	ca. 70° (**1**) or 60-50° (**2**)	ca. 80-70°	ca. 50°	ca. 80°	?

Lower dental characters

	Trogosus	*Tillodon*	*Kuanchuanius*	*Higotherium*	*Chungchienia*
I/1 and I/3	Retained	Lost	Retained	?	?
Longitudinal groove on I/2 labial surface	No	No	Yes	?	No
Space between cheek teeth	Loose (**1**) or crowded (**2**)	Much crowded	Loose	Loose	?
Diastema before P/3	Relatively long (**1**) or short (**2**)	Long	Short	?	Extremely long
P/4	Submolariform	Less molariform	?	?	Talonid reduced or lost
Crown of molars	High	Low	High	Much high	Extremely high, rootless
Buccal enamel surface of molars rugose	No	No	No	Yes	Yes, distinct
M/3 metaconid	Somewhat elongated	Less elongated	Slender	Much elongated	?
M/3 metastylid	Prominent	Weak or lost	Prominent	Prominent	?
M/3 talonid basin apparently divided	Yes (**3**) or no (**4**)	?	Yes	Yes	?
Presence of M/3 mesoconid	?	?	No	Yes	?
Additional cusp on M/3 paracristid	No	No	No	Yes	?
M/3 precingulid	Reduced or lost	Reduced or lost	Distinct	Distinct	?

whereas the M/3 buccal wall is much less so or not convex (Figures 5D and 6D). These features are unshared with *H. hypsodon*. In addition, in IVPP V 2764 all cusps on the molars are less developed; especially the M/3 metaconid is more slender; all ridges are narrower; and on M/3 a mesoconid is never recognized. However, *K. shantunensis* possesses a few similar accessory cusps on the molars; the broken M/3 third lobe has a hint of forming a small enclosed basin with a low posthypocristid as in *T. grangeri*; and a sharp precingulid obviously exists in both M/2 and M/3 (Figure 5D).

***Chungchienia* Chow, 1963**: Chow *et al*. (1996) recently reexamined the systematic position of *Chungchienia* Chow, 1963b, and concluded that it is the most derived and gigantic genus of tillodonts, with an extremely deeper mandible and highly specialized teeth. All known lower cheek teeth of *Chungchienia* are rootless with enamel covering restricted to the buccal side (Chow *et al*., 1996). This Chinese genus includes two species: *C. sichuanica* Chow, 1963b (type species) and *C. lushia* Chow *et al*., 1996. As Chow *et al*. (1996) mentioned, *Chungchienia* was previously believed to be an edentate or taeniodont until a new huge species, *C. lushia*, was described.

Higotherium differs from *Chungchienia* in having a shallower mandible, less hypsodont cheek teeth with lingual enamel covering, and an anteroposteriorly shortened M/3 third lobe (Tables 1 and 2). The extremely hypsodont teeth of *Chungchienia* suggest that the mandible of *Chungchienia* was much deeper than that of *Higotherium*. The depth of the mandible is over 60 mm in *C. sichuanica* (IVPP V 2767; Chow, 1963b), and the depth is estimated to have been over 80 mm in *C. lushia* (IVPP V 10805), although the mandible of *C. lushia* has never been found. Individual cusps of the lower molars of IVPP V 10805 are not observed because of the heavy wear; the presence of precingulids of the molars is also unknown in *Chungchienia*. However, in *Chungchienia* the buccal enamel surfaces of the cheek teeth are markedly rugose with longitudinal fine lines (see also Chow *et al*., 1996 and Chow, 1963b). The lower molars of *Higotherium* also possess a similar rugose enamel surface on the buccal side.

Discussion

Dental characters of *Higotherium*: Compared with *Kuanchuanius, Trogosus*, and *Tillodon, Higotherium* apparently possesses much more hypsodont molars with additional accessory cusps, but it is not so highly specialized as *Chungchienia*. In the first three genera, cervical lines are observed on lower molars above the dentary; in *Higotherium* the cervical lines are unexposed in spite of the fully erupted (M/2) and considerably erupted (M/3) crowns; this enamel extension into the dentary in *Higotherium* indicates a higher degree of hypsodonty. Moreover, the eruptional stages and wear patterns of *Higotherium* apparently differ from those of *Kuanchuanius, Trogosus*, and *Tillodon*: the M/3 eruption is much later than that of M/2 in *Higotherium*, and the M/3 talonid never sufficiently erupted to chew in this stage. The higher degree of hypsodonty and the delayed eruption of M/3 relative to M/2 are both among evolutionary patterns related to the elongation of the tooth wear as seen on various other mammals. In addition, the presence of an additional small cusp on the M/3 paracristid is unknown in previously described tillodonts. The high-crowned M/3 third lobe of NSM-PV 20118 forms a complete, enclosed basin, but it is anteroposteriorly shortened. The short M/3 third lobe is extraordinary in Trogosinae. The lack of elongation of the M/3 third lobe may be interpreted as a pathologic feature, although Gazin (1953, p. 68) noted the variability of development of a third lobe in M/3 of *Trogosus*; however, we do not have sufficient evidence to consider this as a pathologic feature. On the other hand, presence of precingulids in *Kuanchuanius* and *Higotherium* can be interpreted as a vestigial feature for trogosines since the more primitive taxa (e.g., *Esthonyx* Cope, 1874, *Plesiesthonyx* Lemoine, 1891, and *Franchaius* Baudry, 1992) also have sharp precingulids on their lower molars, whereas in *Trogosus* and *Tillodon* precingulids are almost completely reduced or lost, as mentioned in the previous section.

Trogosine monophyly and phylogenetic position of *Higotherium*: Previously proposed phylogenetic hypotheses among Tillodontia (e.g., Stucky and Krishtalka, 1983; Baudry, 1992; Lucas, 1993) verify the monophyly of Trogosinae, but raise a few arguments and problems. As for trogosine monophyly, it is difficult to assess the precise phylogenetic relationships within trogosines because of the incompleteness of Asian material (Lucas, 1993). Therefore, the comparative characters which support the interrelationships are based mostly on the mandible and lower dentition, and the upper dental character states suggested by nodes 9 and 10 of Lucas (1993) should be viewed as provisional, until other characters become established in Asian trogosines.

We believe the subfamily Trogosinae is a monophyletic group composed of five valid genera: *Trogosus, Tillodon, Kuanchuanius, Higotherium*, and *Chungchienia* (see also Figure 7). Based on our reexamination, these five genera share the following synapomorphies: elongated rootless I2/2 (*), much deepened mandible with posteriorly extending symphysis at least under P/4 talonid (*), distinctly hypsodont lower cheek teeth with developed cusps and ridges, and basin-shaped M/3 third lobe (node 1 in Figure 7), although definitive data on characters with asterisks (*) are absent for *Higotherium*. Some of these are modified from the previous hypotheses (i.e., node 7 of Stucky and Krishtalka, 1983; node 9 of Lucas, 1993), but all character states support trogosine monophyly. However, single-rooted P/2 represented by Stucky and Krishtalka (1983) is no longer a synapomorphy of Trogosinae, since this character occurs in some other tillodonts: *Esthonyx spatularius* Cope, 1880, *Azygonyx gunnelli* Gingerich, 1989, *Megalesthonyx hopsoni* Rose, 1972, and probably *Basalina basalensis* Dehm and Oettingen-Spielberg, 1958 (Gingerich and Gunnell, 1979; Lucas and Schoch, 1981). Moreover, reduction of C, P/2, and talonids on P/3-4 are plesiomorphic for trogosines because these characters also occur in *Megalesthonyx hopsoni*.

Lucas (1993) proposed a broader conception of Trogosinae which include *Megalesthonyx* Rose, 1972 and

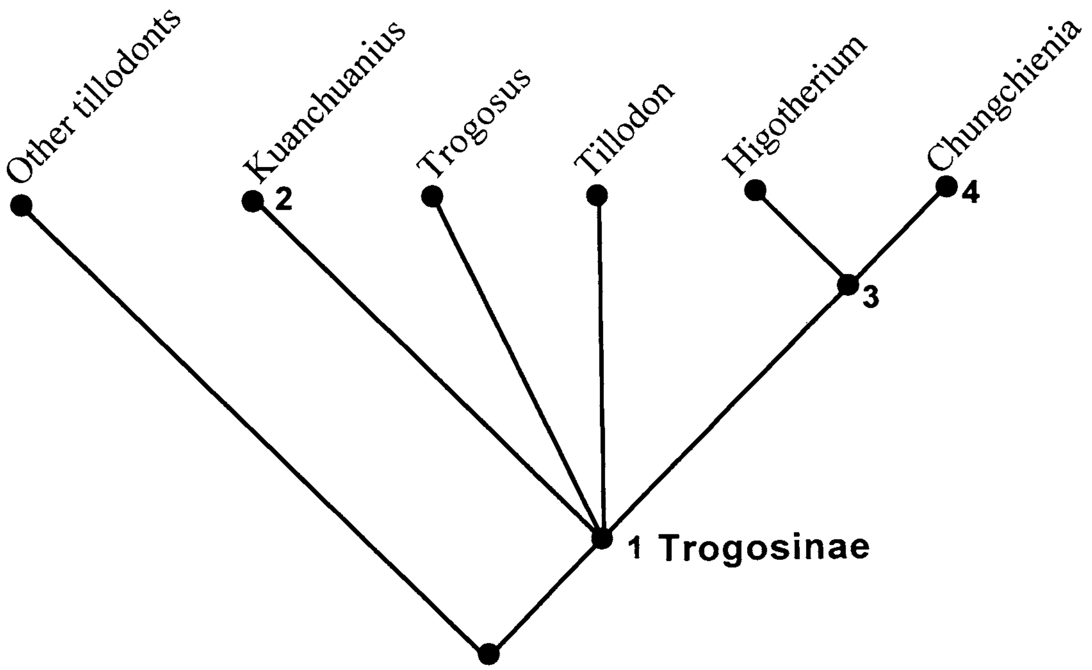

Figure 7. A phylogenetic hypothesis among Trogosinae. **Node 1**: elongated rootless I2/2, much deepened mandible with posteriorly extending symphysis at least under P/4 talonid, distinctly hypsodont lower cheek teeth with developed cusps and ridges, basin-shaped M/3 third lobe; **node 2**: presence of a longitudinal groove on labial surface of I/2; **node 3**: much more hypsodont molars with expanded enamel extending into dentary; **node 4**: gigantic body size, extremely deeper mandible, further reduction or loss of talonids on P/3 and/or P/4, elongated rootless cheek teeth without lingual enamel layer.

Adapidium Young, 1937, using criteria other than I2/2 morphology (Chow *et al.*, 1996). Although these two taxa possess a few derived trogosine dental characters (e.g., cristid obliqua close to metaconid; see nodes 6 and 7 of Lucas, 1993), it is questionable whether *Megalesthonyx* and *Adapidium* should be included in Trogosinae since synapomorphies of the traditional classification of Gazin (1953) and Rose (1972) are absent or unestablished. We do not readily accept Lucas's taxonomic suggestion since these two taxa possess none of the synapomorphies we list above.

As the tetrachotomy in Figure 7 shows, it is difficult to resolve the phylogenetic relationships among *Kuanchuanius, Trogosus*, and *Tillodon* at present. Lucas (1993) reassigned *Kuanchuanius* as a junior synonym of *Trogosus*, and other authors (Stucky and Krishtalka, 1983; Baudry, 1992; Chow *et al.*, 1996) suggested that *Kuanchuanius* may be a questionable taxon among the trogosine monophyletic group. Actually, *K. shantunensis* is similar to the "short-faced" *Trogosus* species (*T. castoridens* and *T. hillsii*) in its mandibular size and morphology. The slender cusps, sharpened ridges on the molars, and short diastema between P/2 and P/3 may also indicate that *Kuanchuanius* is morphologically primitive, close to a common ancestor of all other trogosines, as Stucky and Krishtalka (1983, p. 389) mentioned. However, *Kuanchuanius* also possesses peculiar I/2 characters which were already pointed out by Chow (1963a): the I/2 is oval in cross section, and a shallow but marked groove runs longitudinally on the labial enamel surface (node 2 in Figure 7). The former condition may be interpreted as primitive among trogosines, but the latter condition is probably an autapomorphy based on our reexamination.

Tillodon possesses many derived characters (e.g., somewhat broad and long rostrum, long diastema between P/2 and P/3, loss of I/1 and I/3, less molariform P/4, and smaller M3/ than M2/) in comparison with *Trogosus* and *Kuanchuanius*. However, we can not identify what are its own autapomorphies and synapomorphies shared with other genera among these character states. Chow *et al.* (1996) concluded that *Chungchienia* is more similar to *Tillodon* than *Trogosus* and *Kuanchuanius* in having the following three aspects: a greatly elongate rostrum suggested by the large second incisor, much longer diastema before P/3, a narrow M3/ reflected by the narrow M/3. These derived similarities seem reasonable to infer close relationships between these two genera, but it is disputable to regard these as synapomorphies shared only with *Tillodon* and *Chungchienia*. For example, *Trogosus grangeri* also possesses a relatively long diastema between P/2 and P/3; and another example, if the posteriorly narrower M/3 undoubtedly reflects that M3/ is narrower (smaller) than M2/, *Kuanchuanius* also shares this feature. Furthermore, the lower cheek teeth of *Tillodon* are relatively brachydont with bulbous cusps in spite of its large body size, and this conflicting character dose not support close relationship with *Chungchienia*. The dental morphological gap between *Chungchienia* and the other previously described genera is very broad.

Higotherium is more derived than *Kuanchuanius, Trogosus*, and *Tillodon* in having much more hypsodont molars. The possession of expanded enamel extending into the dentary (=higher degree of hypsodonty) indicate that *Higotherium* is phylogenetically and morphologically closer to *Chungchienia* than to the three other genera (node 3 in Figure 7). However, the two additional M/3 accessory cusps in *Higotherium* cannot be demonstrated to be its own autapomorphies until the detailed features of cusp patterns in other genera are better established. In any case, *Chungchienia* is the most derived trogosine in having the following autapomorphies (node 4 in Figure 7): extremely deeper mandible due to its gigantic body size, further reduction or loss of talonids on P/3 and/or P/4, and elongated rootless cheek teeth without lingual enamel layer (Chow *et al*., 1996).

Our hypothesis of phylogenetic relationships among the trogosines leaves room for a variety of interpretations; for example, it is possible that almost all generic diversification within Trogosinae occurred in Asia, and North American trogosines were immigrants or descendants of immigrants from Asia as Stucky and Krishtalka (1983) pointed out. According to Stucky and Krishtalka (1983) and Krishtalka *et al*. (1987), *Trogosus* has been known only from the Bridgerian (late Early to early Middle Eocene; Prothero, 1995) of North America. Its first appearance, together with certain other taxa such as *Palaeosyops* and *Hyrachyus*, identifies the beginning of the Bridgerian (Krishtalka *et al*., 1987; Gunnell *et al*., 1992). *Tillodon* is also recorded from the Bridgerian (Krishtalka *et al*., 1987: 88), although known occurrences of *Tillodon* are very rare. In China, *Kuanchuanius shantunensis* and *K*.? *danjiangensis* are known from the Guanzhuang Formation, Xintai Basin, and the lower part of Dacangfang Formation, Liguanqiao Basin, respectively. These two formations of China are correlated with the Bridgerian land mammal age of North America based on the mammal fauna (Tong, 1989). *Chungchienia* is known from Middle Eocene strata of China (Chow, 1963b; Chow *et al*., 1996): the Hetaoyuan Formation in Liguanqiao (=Xichuan) Basin (*C. sichuanica*) and Lushi Formation in Lushi Basin (*C. lushia*); these two formations are slightly younger than the Guanzhuang Formation according to Tong (1989). These occurrences, in addition to the occurrence of *Higotherium*, indicate that the rapid generic diversification of trogosines occurred slightly before and during the Middle Eocene. It is most likely that Early Eocene tillodonts from Asia are very important keys for trogosine origins although to date none have been found.

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References cited

Baudry, M., 1992: Les Tillodontes (Mammalia) de l'Éocène inférieur de France. *Bulletin Museum National d'Histoire Naturelle Paris, 4^e sér., 14, section C*, no. 2, p. 205-243, pls. 1-3.

Berggren, W.A., Kent, D.V., Swisher, C.C., III. and Aubry, M.-P., 1995: A revised Cenozoic geochronology and chronostratigraphy. *In*, Berggren, W.A., *et al. eds., Geochronology, time scales and global stratigraphic correlation*, Special publication, no. 54, p. 129-212. SEPM.

Bown, T.M. and Kraus, M.J., 1979: Origin of the tribosphenic molar and metatherian and eutherian dental formulae. *In*, Lillegraven, J.A., Kielan-Jaworowska, Z. and Clemens, W.A. *eds., Mesozoic mammals: the first two-thirds of mammalian history*, p. 172-181. University of California Press, Berkeley.

Cheng, J. and Ma, A., 1990: The new mammalian materials from the Eocene of Liguanqiao Basin. *Vertebrata PalAsiatica*, vol. 28, no. 3, p. 228-244, pls. 1-2. (*in Chinese with English summary*)

Chow, M., 1963a: Tillodont materials from Eocene of Shantung and Honan. *Vertebrata PalAsiatica*, vol. 7, no. 2, p. 97-104, pl. 1. (*in Chinese with English summary*)

Chow, M., 1963b: A xenarthran-like mammal from the Eocene of Honan. *Scientia Sinica*, vol. 12, no. 12, p. 1889-1893, pl. 1.

Chow, M. and Wang, B., 1979: Relationship between the pantodonts and tillodonts and classification of the order Pantodonta. *Vertebrata PalAsiatica*, vol. 17, no. 1, p. 37-48. (*in Chinese with English abstract*)

Chow, M., Wang, J. and Meng, J., 1996: A new species of *Chungchienia* (Tillodontia, Mammalia) from the Eocene of Lushi, China. *American Museum Novitates*, no. 3171, p. 1-10.

Cope, E.D., 1874: Report upon vertebrate fossils discovered in New Mexico, with descriptions of new species. Extract from *Appendix FF of the Annual Report of the Chief of Engineers, 1874, U.S. Government Printing Office*, p. 589-606.

Cope, E.D., 1880: The northern Wasatch fauna. *American Naturalist*, vol. 14, p. 908-909.

Cope, E.D., 1883: On the mutual relations of the bunotherian Mammalia. *Proceedings of the Academy of Natural Sciences of Philadelphia*, p. 77-83.

Dehm, R. and Oettingen-Spielberg, T., 1958: Paläontologische und geologische Untersuchungen im Tertiär von Pakistan. 2. Die mitteleocänen Säugetiere von Ganda Kas bei Basal in Nordwest-Pakistan. *Bayerische Akademie der Wissenschaften Mathematisch-Naturwissenschaftliche Klasse, Abhandlungen*, Neue Folge, no. 91, p. 1-54, pls. 1-3.

Gazin, C.L., 1953: The Tillodontia: an early Tertiary order of mammals. *Smithsonian Miscellaneous Collections*, vol. 121, no. 10, p. 1-110, pls. 1-16.

Gingerich, P.D., 1989 : New earliest Wasatchian mammalian fauna from the Eocene of northwestern Wyoming : composition and diversity in a rarely sampled high-floodplain assemblage. *University of Michigan Papers on Paleontology*, no. 28, p. 1-97.

Gingerich, P.D. and Gunnell, G.F., 1979 : Systematics and evolution of the genus *Esthonyx* (Mammalia, Tillodontia) in the early Eocene of North America. *Contributions from the Museum of Paleontology, the University of Michigan*, vol. 25, no. 7, p. 125-153, pls. 1-3.

Gunnell, G.F., Bartels, W.S., Gingerich, P.D. and Torres, V., 1992 : Wapiti Valley faunas : Early and Middle Eocene fossil vertebrates from the North Fork of the Shoshone River, Park County, Wyoming. *Contributions from the Museum of Paleontology, the University of Michigan*, vol. 28, no. 11, p. 247-287.

Hanzawa, S. and Urata, H., 1964 : Supplementary note to the nummulitic rocks of Amakusa, Kyushu, Japan. *Reports on Earth Science, Department of General Education, Kyushu University*, vol. 11, p. 1-12, pls. 1-6.

Krause, D.W. and Maas, M.C., 1990 : The biogeographic origins of late Paleocene-early Eocene mammalian immigrants to the Western Interior of North America. *In*, Bown, T.M. and Rose, K.D. *eds., Dawn of the age of mammals in the northern part of the Rocky Mountain interior, North America*, Special paper, no. 243, p. 71-105. Geological Society of America.

Krishtalka, L., Stucky, R.K., West, R.M., Mckenna, M.C., Black, C.C., Bown, T.M., Dawson, M.R., Golz, D.J., Flynn, J.J., Lillegraven, J.A. and Turnbull, W.D., 1987 : Eocene (Wasatchian through Duchesnean) biochronology of North America. *In*, Woodburne, M.O. *ed., Cenozoic mammals of North America : geochronology and biostratigraphy*, p. 77-117. University of California Press, Berkeley.

Leidy, J., 1871 : Remarks on fossil vertebrates from Wyoming. *Proceedings of the Academy of Natural Sciences of Philadelphia*, vol. 23, no. 2, p. 228-229.

Lemoine, V., 1891 : Etude d'ensemble sur les dents des mammifères fossiles des environs de Reims. *Bulletin de la Société géologique de France, Paris*, *3^{e} sér.*, vol. 19, p. 263-290, pls. 10-11.

Lucas, S. G., 1993 : Pantodonts, tillodonts, uintatheres, and pyrotheres are not ungulates. *In*, Szalay, F.S., Novacek, M.J. and McKenna, M.C. *eds., Mammal phylogeny : placentals*, p. 182-194. Springer-Verlag, New York.

Lucas, S.G. and Schoch, R.M., 1981 : *Basalina*, a tillodont from the Eocene of Pakistan. *Bayerische Staatssammlung für Paläontologie und Historische Geologie, Mitteilungen*, no. 21, p. 89-95, pl. 15.

Marsh, O.C., 1875 : New order of Eocene mammals. *American Journal of Science and Arts*, vol. 9, p. 221.

Matsushita, H., 1949 : Geology of the coal fields in northern Kyushu. *Science Reports of the Faculty of Science, Kyushu University, Geology*, vol. 3, no. 1, p. 1-57. (*in Japanese*)

Miki, T., 1972 : Cretaceous-Tertiary unconformity in the western part of Amakusa-Shimoshima. *Memoirs of the Faculty of Science, Kyushu University, Series D, Geology*, vol. 21, no. 2, p. 217-237, pls. 34-35.

Miki, T., 1975 : Formation and development of sedimentary basins during the Paleogene in Amakusa and its adjacent areas, Western Kyushu. *Memoirs of the Faculty of Science, Kyushu University, Series D, Geology*, vol. 23, no. 2, p. 165-209, pls. 27-31.

Miki, T. and Matsueda, H., 1985 : Genesis of the Paleogene purple-red beds in Western Kyushu, Japan. *Memoirs of the Faculty of Science, Kyushu University, Series D, Geology*, vol. 25, no. 3, p. 399-415.

Muizon, C. de and Marshall, L.G., 1992 : *Alcidedorbignya inopinata* (Mammalia : Pantodonta) from the Early Paleocene of Bolivia : phylogenetic and paleobiogeographic implications. *Journal of Paleontology*, vol. 66, no. 3, p. 499-520.

Nagao, T., 1926 : The Palaeogene stratigraphy of Kyushu. *Journal of Geography, Tokyo geographical Society, Japan*, vol. 38, no. 445, p. 115-130. (*in Japanese*)

Okada, H., 1992 : Calcareous nannofossils and biostratigraphy of the Paleogene sequences of the northern Kyushu, Japan. *Journal of the Geological Society of Japan*, vol. 98, no. 6, p. 509-528, pls. 1-2.

Prothero, D.R., 1995 : Geochronology and magnetostratigraphy of Paleogene North American land mammal "ages" : an update. *In*, Berggren, W.A., *et al. eds., Geochronology, time scales and global stratigraphic correlation*, Special publication, no. 54, p. 305-315. SEPM.

Robinson, P., 1966 : Fossil Mammalia of the Huerfano Formation, Eocene, of Colorado. *Peabody Museum of Natural History, Yale University, Bulletin*, no. 21, p. 1-95, pls. 1-10.

Rose, K.D., 1972 : A new tillodont from the Eocene upper Willwood Formation of Wyoming. *Peabody Museum of Natural History, Yale University, Postilla*, no. 155, p. 1-13.

Stucky, R.K. and Krishtalka, L., 1983 : Revision of the Wind River faunas, early Eocene of central Wyoming. Part 4. the Tillodontia. *Annals of Carnegie Museum*, vol. 52, article 17, p. 375-391.

Takai, Y. and Satoh, H., 1982 : Geology of the Onikizaki and Ushibuka district (including a part of the Akune district). *Quadrangle Series, scale 1 : 50,000, Geological Survey of Japan*, 87 p., pls. 1-4. (*in Japanese with English abstract*)

Tashiro, M., Taira, A. and Matsumoto, T., 1980 : Biostratigraphy and depositional facies of the Cretaceous-Tertiary boundary strata in Amakusa-Shimojima, Kyushu, Western Japan. *Cretaceous Research*, vol. 1, p. 13-26.

Ting, S. and Zheng, J., 1989 : The affinities of *Interogale* and *Anchilestes* and the origin of Tillodontia. *Vertebrata PalAsiatica*, vol. 27, no. 2, p. 77-86, pl. 1. (*in Chinese with English summary*)

Tong, Y., 1989 : A review of Middle and Late Eocene mammalian faunas from China. *Acta Palaeontologica Sinica*, vol. 28, no. 5, p. 663-682. (*in Chinese with English summary*)

Young, C.C., 1937 : An early Tertiary vertebrate fauna from Yuanchü. *Bulletin of the Geological Society of China*, vol. 17, nos. 3-4, p. 413-438.

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SHORT NOTES

Survival of crinoid stalk fragments and its taphonomic implications

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Abstract. Paleontological evidence indicates that crinoids (sea lilies : Echinodermata) were a major constituent of Paleozoic and Mesozoic shallow-marine communities (Meyer and Macurda, 1977 ; Cain, 1968). In the fossil record crinoid stalks usually occur in much greater abundance than other body parts such as arms and calyces. This difference has been attributed to selective preservation, the result of post-mortem process of fossilization or taphonomy (Baumiller and Ausich, 1992 ; Moore and Jeffords, 1968). Our observation of living crinoids in aquaria demonstrates that stalk fragments detached and isolated from a living crinoid survive more than one year, whereas other body parts tend to disarticulate rapidly. Such long survival of stalk fragments of crinoids firstly explains the dominance of crinoid stalks over other body parts in the fossil record, and secondly, and more importantly, it strongly suggests that such detached fossil stalks, as well as stalk pieces observed on today's sea floor, continued living for a long time, and were not dead body parts as previously considered.

Key words : Crinoid, taphonomy

Introduction

It is well known that among crinoid skeletal parts stalk (or stem) fragments predominate in shallow-marine deposits, whereas other skeletal parts, such as arms and calyces are rarely found (Moore and Jeffords, 1968). Given the original proportions of skeletal elements in crinoids, it is a mystery that stalk fragments are so predominant whereas other parts of disarticulated crinoid skeletons are rare.

Recent observations by submersibles and underwater cameras have demonstrated that detached stalk fragments of modern stalked crinoids are often found in association with entire crinoids (Conan *et al*., 1981 ; Fujita *et al*., 1987 ; Messing *et al*., 1988). Such stalks without crowns sometimes stand erect off the substrate, grasping gravels and other hard objects by the appendages called cirri, as if they still held their crowns. During growth, new stalk plates are formed at the top of the stalk just below the crown (Breimer, 1978), and the distal (old) part of the stalk is repeatedly detached from the main stalk and left on the sea floor (Rasmussen, 1977). Fossil stalks are abundant in Paleozoic and Mesozoic shallow-water deposits. Such fossil stalk fragments were thought to be selectively preserved after death whereas the other body parts were disarticulated and lost (Baumiller and Ausich, 1992 ; Moore and Jeffords, 1968). However, other than experiments on the post-mortem disintegration of the isocrinid stalks (Baumiller and Ausich, 1992), there has been no information about the "fate" of such isolated stalk fragments. The purpose of the present study is to test if these autotomized and isolated stalk fragments remain alive for a long time, and also to consider the implications of the results for the taphonomy of crinoid skeletons.

Material and methods

We have collected adult specimens of the modern stalked crinoid *Metacrinus rotundus* Carpenter from the depths of 135-150 m in NE Suruga Bay, central Japan. Specimens were transferred to a large, temperature-controlled aquarium (13°C) at the Misaki Marine Biological Station, University of Tokyo, within several hours after capture. They were kept alive for over one year (Amemiya and Oji, 1992). During this period, most specimens autotomized their distal stalks as well as their crowns, and the isolated stalk fragments were left on the bottom of the aquarium.

For comparison with the autotomized and isolated fragments of stalk, the distal stalks with two to three nodals were dissected at an articulation below a nodal by a razor blade, and they were also kept on the bottom of the aquarium. We have also examined the nucleus and ligament using histochemical and fluorescent dye staining to see if a stalk left for ten months and another stalk dissected and left for 13 months in the aquarium were living. Stalk fragments were fixed and decalcified with Bouin solution, and subsequently embedded in paraffin and stained with a fluorescent dye, Hechst 33258, or with hematoxylin-eosin after sectioning.

As a control, another distal stalk fragment, which was dissected directly from an intact specimen with arms and a calyx, was immediately fixed and processed as above for comparison.

Results

The autotomized fragments usually range from 8 to 17 cm long, with four to eight nodal plates. They were apparently detached at almost flat articulations below a nodal plate, which is believed to be a specialized articulation for stalk autotomy (Emson and Wilkie, 1980). One specimen of *Metacrinus rotundus* collected on Oct. 7, 1989 detached its distal stalk within several days of capture. The detached stalks have held the same postures and some remained attached to pebbles by the cirri for approximately one year (Figure 1).

The stalks dissected by a razor blade below a nodal plate, also remained fully articulated for 10 to 13 months, indicating that ligamentary fibers connecting each plate of the stalks and cirri had not disintegrated or degraded during this period.

By the histochemical and fluorescent dye staining, the nuclei in the autotomized stalk fragments were all well preserved and stained clearly with both stains (Figure 2a, c) and they were similar to the control (Figure 2d), indicating that the cells were living. The collagen-like fibers composing the stalk ligament in the autotomized stalk fragments left in the aquaria (Figure 2b) were also well preserved, supporting the idea that the fragments were still viable. Dissected stalk fragments which were left in the aquarium for about a year showed similar characteristics in the stained thin sections.

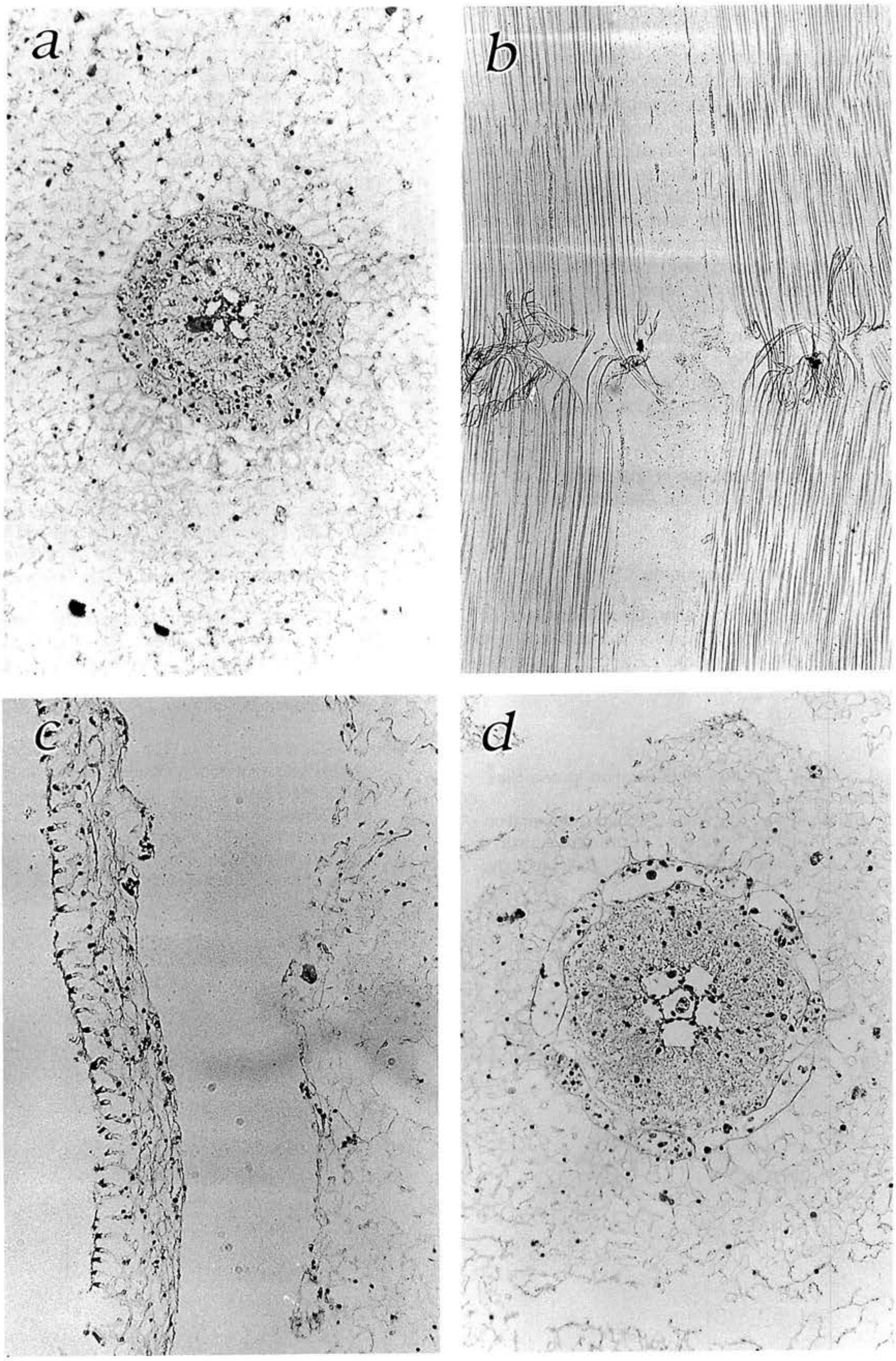
Discussion

Our findings strongly suggest that fragmented stalks can live for more than one year in the natural environment. Also it suggests that similar isolated isocrinid stalks observed in the crinoid habitat by submersibles (Conan *et al*., 1981 ; Messing *et al*., 1988) and underwater photographs (Fujita *et al*., 1987) were also living.

In contrast to the strong regeneration power in the arms and visceral mass (Emson and Wilkie, 1980 ; Meyer, 1985 ; Amemiya and Oji, 1992) of crinoids, there has been no record of apparent stalk regeneration in Recent stalked crinoids. At least as regards isocrinid crinoids, the isolated stalk fragments were presumably living passively, without regenerating or growing. However, an Ordovician stalk with an

Figure. 1. One of the specimens collected on Oct. 7, 1989 autotomized its distal stalk as well as its crown several days after capture (Left). The autotomized stalk fragments (right and center) were derived not only from the specimen on the left side, but also from other specimens. They retained almost the same posture and some remained attached to pebbles by cirri for approximately one year. Arrows indicate such autotomized stalks. Photo taken on Oct. 23, 1990. The width of the picture is approximately 60 cm.

Figure. 2. Micrographs of the stalk of *Metacrinus rotundus*. Magnification x 108 in a, b and d ; x 44 in c. **a** : Cross section of axial area of stalk which autotomized from the main body and was left in the aquarium for approximately one year. Note well-stained nuclei in and around the axial canal. **b** : Longitudinal section of the different stalk fragment with two stalk plates, which was also autotomized and left in the aquarium for approximately one year. Through-going ligaments still attach two stalk plates (above and below) tightly. **c** : Epithelium and outer area of the cross section of the stalk. The same stalk fragment as in b. **d** : Cross section of axial area of stalk which was not autotomized and directly cut from an intact specimen. No significant difference is observed between this section and the autotomized one (a).


a
b
c
d

anomalous form was recently reinterpreted as a regenerated stalk (Ausich and Baumiller, 1993).

Fossil stalks are often abundant in Paleozoic and Mesozoic strata. Many of these occurrences represent crinoid banks formed in a shallow-water environment (Meyer and Macurda, 1977). Most of the stalk fragments consist of a series of articulated stalk plates, indicating that ligamentary fibers united these plates before their burial in the sediment. The present results, as well as the Ordovician anomalous fossil stalk, suggest that at least some of these stalk fragments have/had the ability to remain alive for a long time on the sea floor, despite lacking any food-gathering organ. The presence of stalks and the absence of calyces and arms in fossil deposits do not suggest that these stalks were dead prior to fossilization. Instead, the successful preservation of crinoid stalks may reflect their longer survival and later time of death than their crowns. Arms tend to be disarticulated rapidly into small skeletal grains, and thus have a smaller chance to be preserved intact, whereas stalk fragments with at least several columnal plates remain integrated for a long time, possibly resulting in contrasting chance of preservation between arm and stalk elements in the fossil record.

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References

Amemiya, S. and Oji, T., 1992: Regeneration in sea lilies. *Nature*, vol. 357, p. 546-547.

Ausich, W.I. and Baumiller, T.K., 1993: Column regeneration in an Ordovician crinoid (Echinodermata): paleobiologic implications. *Journal of Paleontology*, vol. 67, p. 1068-1069.

Baumiller, T.K. and Ausich, W.I., 1992: The "Broken stick" model as a null hypothesis for crinoid stalk taphonomy and as a guide to the distribution of connective tissue in fossils. *Paleobiology*, vol. 18, p. 288-298.

Breimer, A., 1978: General morphology, Recent crinoids. *In*, Moore, R.C. and Teichert, C. *eds., "Treatise on Invertebrate Paleontology", pt. T*, p. T9-T58. Geological Society of America and University of Kansas, Boulder, Colorado.

Cain, J.D.B., 1968: Aspects of the depositional environment and palaeoecology of crinoidal limestones. *Scottish Journal of Geology*, vol. 4, p. 191-208.

Conan, G., Roux, M. and Sibuet, M., 1981: A photographic survey of a population of a stalked crinoid *Diplocrinus* (*Annacrinus*) *wyvillethomsoni* (Echinodermata) from the bathyal slope of the Bay of Viscay. *Deep-Sea Research*, vol. 28A, p. 441-453.

Emson, R.H. and Wilkie, I.C., 1980: Fission and autotomy in echinoderms. *Oceanography and Marine Biology, Annual Review*, vol. 18, p. 155-250.

Fujita, T., Ohta, S. and Oji, T., 1987: Photographic observations of the stalked crinoid *Metacrinus rotundus* Carpenter in Suruga Bay, central Japan. *Journal of the Oceanographical Society of Japan*, vol. 43, p. 333-343.

Messing, C.G., RoseSmyth, M.C., Mailer, S.R. and Miller, J.E., 1988: Relocation movement in a stalked crinoid (Echinodermata). *Bulletin of Marine Science*, vol. 42, p. 480-487.

Meyer, D.L., 1985: Evolutionary implications of predation on Recent comatulid crinoids. *Paleobiology*, vol. 11, p. 154-164.

Meyer D.L. and Macurda, D.B., Jr., 1977: Adaptive radiation of the comatulid crinoids. *Paleobiology*, vol. 3, p. 74-82.

Moore, R.C. and Jeffords, R.M., 1968: Classification and nomenclature of fossil crinoids based on studies of dissociated parts of their columns. *University of Kansas Paleontological Contribution*, vol. 46, Art. 9, p. 1-86.

Rasmussen, H.W., 1977: Function and attachment of the stem in Isocrinidae and Pentacrinitidae: review and interpretation. *Lethaia*, vol. 10, p. 51-57.

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Ager, D.V., 1963: *Principles of Paleoecology,* 371 p. McGraw-Hill Co., New York.

Barron, J.A., 1983: Latest Oligocene through early Middle Miocene diatom biostratigraphy of the eastern tropical Pacific. *Marine Micropaleontology,* vol. 7, p. 487-515.

Barron, J.A., 1989: Lower Miocene to Quaternary diatom biostratigraphy of Leg 57, off northeastern Japan, Deep Sea Drilling Project. *In*, Scientific Party, *Initial Reports of the Deep Sea Drilling Project*, vols. 56 and 57, p. 641-685. U.S. Govt. Printing Office, Washington, D.C.

Burckle, L.H., 1978: Marine diatoms. *In*, Haq, B.U. and Boersma, A. *eds., Introduction to Marine Micropaleontology*, p. 245-266. Elsevier, New York.

Fenner, J. and Mikkelsen, N., 1990: Eocene-Oligocene diatoms in the western Indian Ocean: Taxonomy, stratigraphy, and paleoecology. *In,* Duncan, R.A., Backman, J., Peterson, L.C., *et al., Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 115, p. 433-463. College Station, TX (Ocean Drilling Program).

Koizumi, I., 1972: Marine diatom flora of the Pliocene Tatsunokuchi Formation in Fukushima Prefecture. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series,* no. 86, p. 340-359.

Kuramoto, S., 1996: Geophysical investigation for methane hydrates and the significance of BSR. *Journal of the Geological Society of Japan,* vol. 11, p. 951-958. (*in Japanese with English abstract*)

Palaeontological Society of Japan (JSP) Standing Committee Actions

During its meeting on January 24, the JSP Standing Committee enacted the following changes to its membership.

New members elected;
Kengo Ieda, Toshie Igawa, Yoko Kakegawa,
Yusuke Nakano, Hajime Naruse, Yota Sakai,
Kenji Shiga, Kazuaki Ueda, Muhammad Yousaf Warraich.

Subscribing member elected;
Alexander I. Kafanov.

Resigned members;
Yasuo Hasegawa, Tetsuya Kawabe, Asako Konosu,
Kunio Makishima, Kennosuke Ogawa, Jun'ichi Sato.

Deceased member;
Manjiro Nakamura.

Palaeontological Society of Japan (JSP) Council Actions

During its meeting on January 29, the JSP Council enacted the following changes to its membership.

New fellow members;
Masatoshi Goto, Chikara Hiramatsu, Nobuyuki Honda,
Ken Ikehara, Akitoshi Inoma, Masahito Kadota,
Kazuo Kaneko, Satoru Kojima, Arata Momohara,
Hiromi Nagai, Nagayuki Nemoto, Isao Niikawa,
Akinobu Nikaido, Haruo Saegusa, Osamu Sasaki,
Koji Seto, Tetsuro Suekane, Mikihiro Sugimoto,
Eiji Taguchi, Masanaru Takai, Katsumi Takayasu,
Shigeru Takizawa, Keiko Yamaguchi.

行事予定

◎第147回例会は1998年6月27日（土）〜6月28日（日）に，北海道大学で開催されます。一般講演の申し込み締切は5月11日です。シンポジウムとして6月27日に「復元の科学（その2）：海洋古環境復元における古生物学とその境界領域，世話人：岡田尚武，小泉　格，大野照文）が行われます。

◎1999年年会は1999年1月29日（金）〜1月31日（日）に，東北大学で開催されます。一般講演の申し込み締切は12月3日です。シンポジウム等の企画をお持ちの方は5月28日までに行事係までお申し込み下さい。

◎1999年年会以降の行事予定としては，第149例会に「兵庫県立人と自然の博物館」から，また2000年年会・総会に「早稲田大学」から開催の申し込みがありました。

◎現在，常務委員会は2001年からの学会行事の変更を検討しております。2001年からは，従来とは異なった時期や開催形式で年会，例会，総会が開催される可能性があります。従いまして，第150回例会（2000年6月末に開催予定）までは，従来通り開催の申し込みを受け付けますが，2001年以降の開催申し込みは，しばらくの間見あわさせて頂きます。

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