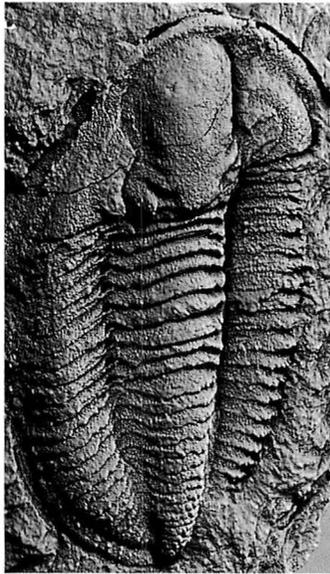


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The fossil on the cover is *Phillipsia ohmorensis* Okubo, an Early Carboniferous trilobite from the Hikoroichi Formation in the Higuchizawa valley, Ofunato City, Iwate Prefecture, northeast Japan (Collected by A. Haga, PA 5766, $\times 3.0$; after Kobayashi and Hamada, 1980, pl. 6, fig. 4).

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880. NEW TAXA IN THE LATE TRIASSIC DAEDONG FLORA, SOUTH KOREA. PART 2*

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Abstract. Continued from our previous issue (Part 1), this paper deals with the description of the following newly recognized taxa in the Daedong Flora: *Pterophyllum cheondaeriense*, sp. nov., *Anthrophyopsis decurrens*, sp. nov., *Drepanozamites* sp. A, *Podzamites* ex gr. *schenki* Heer, *P.* sp. A, *Cycadocarpidium* sp. cf. *C. asaense* Kon'no, *C.* sp. cf. *C. nagatoense* Kon'no, *C.* sp. A, *Taeniopteris cheondaeriensis*, sp. nov. and *T. mungyeongensis*, sp. nov.

Key words. Daedong flora, Korea, Late Triassic.

Systematic description

Specimens described in this paper are kept in the National Science Museum of Korea, Daejeon City.

Bennettitales (continued from our
previous paper)

Genus *Pterophyllum* Brongniart, 1828

Pterophyllum cheondaeriense

Kimura et Kim, sp. nov.

Figures 10a-f

Material: Holotype; Reg. no. T-0126A (Cheondaeri). Paratypes; Reg. nos. T-0109, 0110 0127 (Cheondari). Examined specimens: Reg. nos. T-0032, 35, 38, 57, 64, 74, 107, 113, 121, 122 and 126B-C. *Stratum*

*Received July 9, 1987: revised manuscript accepted July 30, 1989.

typicum: Amisan Formation at Cheondaeri. *Locus typicus*: Cheondaeri Coal-Mine, Cheondaeri, Janggog-myeon, Hongseong-gun, Chungcheongnam-do (see Kimura and Kim, 1988, p. 604). *Derivatio nominis*: After the locality.

Diagnosis: Leaf more than 15 cm long, oblanceolate in outline, 8.4 cm wide at the widest portion; rachis marked with three longitudinal striations, up to 2 mm wide below. Pinnae borne closely at an angle of 65-90 degrees, long and narrow, and nearly parallel-sided for the most part; the longest 4.7 cm long and 4-5 mm wide above, but shorter, elongate-triangular in form below. Pinnae not expanding distally, but slightly expanded at base. Pinna apex mostly acutely or sometimes obtusely pointed. Veins weak, arising from the lateral sides of rachis, 9-12 in number (10-12 per cm) at the base of each pinna, mostly simple, but one of them

once forked at or near the base, parallel, ending at the distal margin.

Distribution and occurrence: *Pterophyllum cheondaeriense* is locally common, the broken leaves being often thickly massed, but is only known from the Amisan Formation at the Cheondaeri area.

Discussion and comparison: In our leaves examined, cuticle is not preserved. The petiole and reproductive organs are not known.

This new species is characterized by its long and narrow pinnae above and elongate-triangular ones below, both having an acutely or obtusely pointed apex and mostly simple veins, 10–12 per cm in density.

There are many *Pterophyllum* species similar in form and size to ours as listed below, but they are all distinguished from *P. cheondaeriense* on account of various features as briefly mentioned below:

Pterophyllum astartense Harris: Harris, 1932b, Rhaetian of Greenland: Adjacent pinnae sometimes separated. Basal pinnae variable in form, with rounded or truncated apex. Veins mostly forked at all levels.

P. ctenoides Oishi: Oishi, 1932a, Upper Triassic Nariwa Group: Rachis thick, nearly 1 cm wide at the base. Pinnae more than 10 cm long. Veins 8 in number in each pinna, basiscopic veins decurrent.

P. jaegeri Brongniart: Brongniart, 1828 and others, e.g. Leuthardt, 1903. Mainly from the Upper Triassic of Europe: Rachis thick. Pinna apex truncated.

P. longifolium Brongniart (non Jaeger): Brongniart, 1828 and others. Mainly from the Upper Triassic of Europe:

Pinnae expanded distally, with truncated apex. Veins 4–5 in number in each pinna.

P. subaequale Hartz: Hartz, 1896, Liassic of Greenland; Johansson, 1922 (identified as *P. andraeanum*): Rachis always transversely wrinkled. Basal pinnae with rounded or truncated apex.

P. thomasi Harris: Harris, 1952, 1969, Middle Jurassic of Yorkshire: Rachis thick, up to 8 mm wide. Veins 4 in number in each pinna.

P. tietzei Schenk: Schenk, 1887; Zeiller, 1902–1903 and others, Upper Triassic of Iran, North Viet Nam, China and elsewhere: Pinna apex rounded. Veins 15–22 in number at the middle of each pinna.

P. xiphopterum Harris: Harris, 1932b, Rhaetian of Greenland: Rachis thick. Pinnae attached to the upper sides of rachis. Basal pinnae with truncated apex. Veins forked at all levels, 50 per cm in distal half of pinna.

Under the circumstances, we propose *Pterophyllum cheondaeriense* as a new species herein.

Cycadales

Genus *Anthrophyopsis* Nathorst, 1878

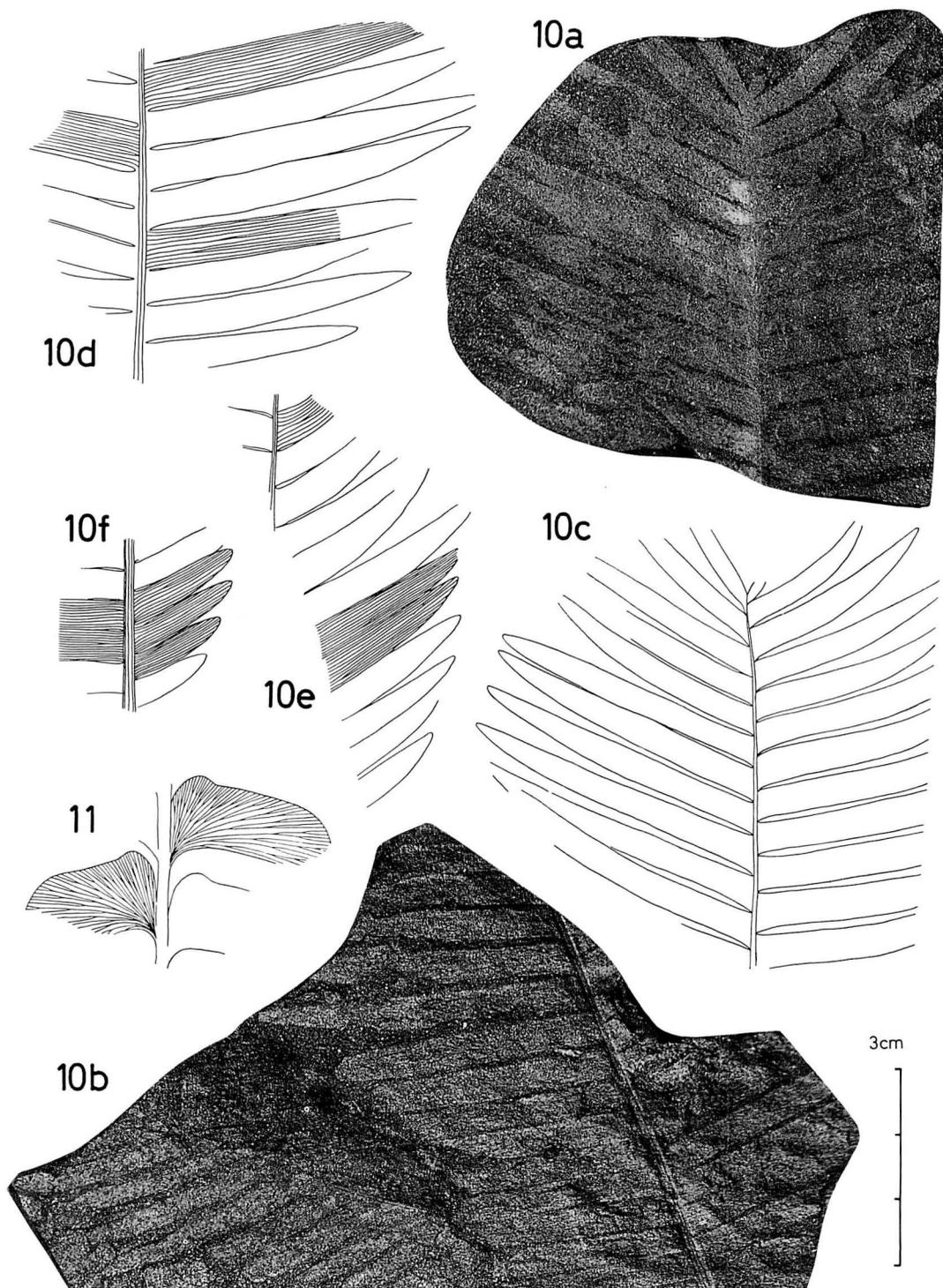
Anthrophyopsis decurrens

Kimura et Kim, sp. nov.

Figures 12a–b

Material: Holotype; Reg. no. 81-023T (Cheondaeri). Paratype; Reg. no. 81-038T (Cheondaeri). *Stratum typicum*: Amisan Formation. *Locus typicus*: Cheondaeri Coal-Mine, Cheondaeri, Janggog-myeon,

→ **Figures 10 (a–f)—11.** All natural size. **10.** *Pterophyllum cheondaeriense* Kimura et Kim, sp. nov.: All from Cheondaeri (Cheondaeri Coal-Mine). **10a.** Apical portion of a leaf (Reg. no. T-0126A, Holotype). **10b.** Showing the occurrence. Broken leaves are thickly massed (Reg. no. T-122). **10c.** Drawn from Figure 10a. **10d.** Middle portion of a leaf (Reg. no. T-0127, Paratype). **10e.** Basal portion of leaf (Reg. no. T-0127C, Paratype). **10f.** Proximal part of a leaf, with detailed venation (Reg. no. T-126B). **11.** *Drepanozamites* sp. A: A part of a leaf, showing the mode of attachment of pinnae and venation (Reg. no. T-0196). Loc. Cheondaeri



Hongseong-gun, Chungcheongnam-do (see Kimura and Kim, 1988, p. 604). *Derivatio nominis*: From markedly decurrent lateral veins.

Diagnosis: Leaf elongate-obovate in outline, more than 14.6 cm long and 6 cm wide at the widest portion. Margins entire. Rachis thick, 1.05 cm wide below and 0.25 cm above, longitudinally striated on its surface, giving

off lateral veins at an angle of 40 degrees below and 50-60 degrees middle to above, and at intervals of 1.5 mm (6.7 per cm in density). Lateral veins parallel, markedly decurrent near their origin, forming elongate-reticulate meshes. Meshes varied in length according to their position, typically 7-8 mm long and 1-1.5 mm wide.

Distribution and occurrence: Two leaves

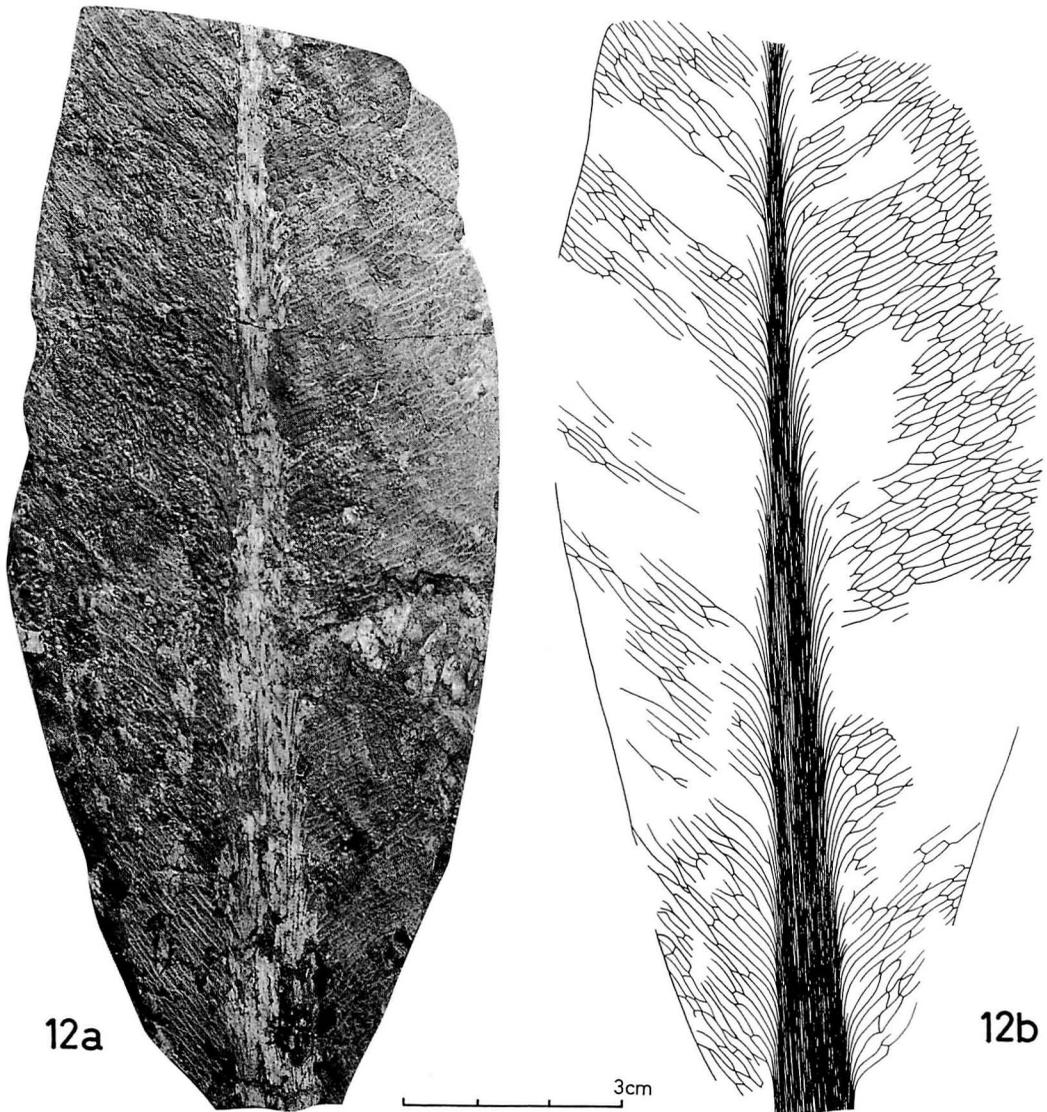


Figure 12. *Anthrophyopsis decurrens* Kimura et Kim, sp. nov.: Natural size. **12a.** Holotype (Reg. no. 81-023T). Loc. Cheondaeri. **12b.** Drawn from Figure 12a.

were obtained from the Amisan Formation at the Cheondaeri area.

Discussion and comparison: The present leaves, though their both ends are missing, resemble those of *Anthrophyopsis*, *Ctenis* and *Glossopteris* because of their networked venation. We prefer to assign our leaves to *Anthrophyopsis*, because *Ctenis* leaves are usually not entire but segmented and *Glossopteris* leaves have been known mostly from the Permian plant-beds in the Gondwana Floristic Province. However, resemblance between our leaves and some *Glossopteris* leaves is quite remarkable. We are of the opinion that *Anthrophyopsis decurrens* is a spurious imitation of some *Glossopteris* leaves.

Anthrophyopsis decurrens is distinguished from the following hitherto known *Anthrophyopsis* species by its markedly decurrent lateral veins:

Anthrophyopsis crassinervis Nathorst: Upper Triassic of Sweden (Nathorst, 1878a, 1886); Greenland (Harris, 1926, 1932a); Western Pamir (Vladimirovich, 1958); South China (Sze and Hsü, 1954; Sze *et al.*, 1963; Feng *et al.*, 1977; Chen *et al.*, 1978; Zhou, 1978).

A. leeiana (Sze) Florin: Upper Triassic of South China (Sze, 1931; Sze and Hsü, 1954; Sze *et al.*, 1963; Li, 1964).

A. miassica Vladimirovich: Upper Triassic of Eastern Ural (Vladimirovich, 1958).

A. naruensis Doludenko et Svanidze: Lower Jurassic? of Georgia (Doludenko and Svanidze, 1970).

A. tuberculata Chow et Yao and *A. venulosa* Chow et Yao: Upper Triassic of South China (in Feng *et al.*, 1977; Chen *et al.*, 1978; He *et al.*, 1979).

Sagenopteris glossopteroides originally described by Hsü *et al.* (1974) from the Upper Triassic Daqiaode Formation Yunnan, China has leaflets similar in form and venation to our leaves, but it is distinguished from ours by its palmately compound leaf.

In our leaves cuticle is not preserved.

Unclassified Cycadopsida
Genus *Drepanozamites* Harris, 1932b
Drepanozamites sp. A

Figure 11

Material: Reg. no. T-0196 (Cheondaeri).

Description: Obtained specimen is a single leaf-fragment, more than 8 cm long with 5 pairs of subopposite pinnae borne on the lateral sides of the slender rachis (2 mm wide). The pinnae are 2.4 cm long and 0.9 cm wide at the middle portion, broadest at the base, with more or less auriculated acroscopic base, attached by a somewhat decurrent basicopic basal corner, and tapering to a rounded apex usually pointing backwards; margins are entire. The veins are slender, diverging from the point of attachment of pinna, mostly forked thrice freely, 14-15 in number per cm at the middle of pinna. Cuticle is not preserved.

Distribution and occurrence: Very rare. Known only from the Amisan Formation at the Cheondaeri area.

Remarks: Judging from its slender rachis, the present specimen appears to represent the middle or upper part of a leaf, because in Harris' type species, *Drepanozamites nilssoni*, basal rachis is fairly thick, being 3-4 mm wide. If our specimen is indeed that part of a leaf, our pinnae differ in size from those of *Drepanozamites nilssoni*, because in the type-species the pinnae on the middle to upper parts of a leaf are more elongated and about twice as large as ours.

Drepanozamites p'ani originally described by Sze (1956b) from the Upper Triassic Yanchang Formation, North China is distinguished from ours by its thick rachis (5 mm wide) and by the presence of a vaguely defined midrib in its pinnae.

According to Sze (1956b), *Rhacopteris* (?) *gothani* originally described by Sze (1933b) from the Upper Triassic Anyuan Formation in Jiangxi, which was later referred by Harris

(1937) to *Drepanozamites nilssoni*, is different from the type species despite the margin of pinnae being more or less dissected distally, crenated and occasionally even lobed. Therefore, Sze (1956b) proposed to refer those leaves to *Drepanozamites gothani* in his discussion. In their later monograph (Sze *et al.*, 1963), however, they regarded those leaves as *Drepanozamites nilssoni* together with additional specimens from the Upper Triassic Xujiahe Formation in Sichuan.

Our leaf is somewhat different from these Chinese leaves in having less elongated pinnae which point backwards. *Drepanozamites* ? sp. indet. from the Upper Triassic Nariwa Group (Oishi and Huzioka, 1938) differs from ours in its trapezoid pinna with a small number of veins.

Coniferales

Genus *Podozamites* Braun in Münster, 1843
Podozamites ex gr. *schenki* Heer

Figures 13a—c

Podozamites schenki Heer: Kawasaki, 1925, p. 55, pl. 41, figs. 112–113; pl. 45, fig. 120.

Material: Reg. no. 81–123 (Hanaeri) and many other leaf-fragments.

Description: Figure 13a shows a broken leafy shoot, 8 cm long. The axis is slender, 0.8 mm wide, traversed longitudinally by a few ridges and furrows, and sends off spirally

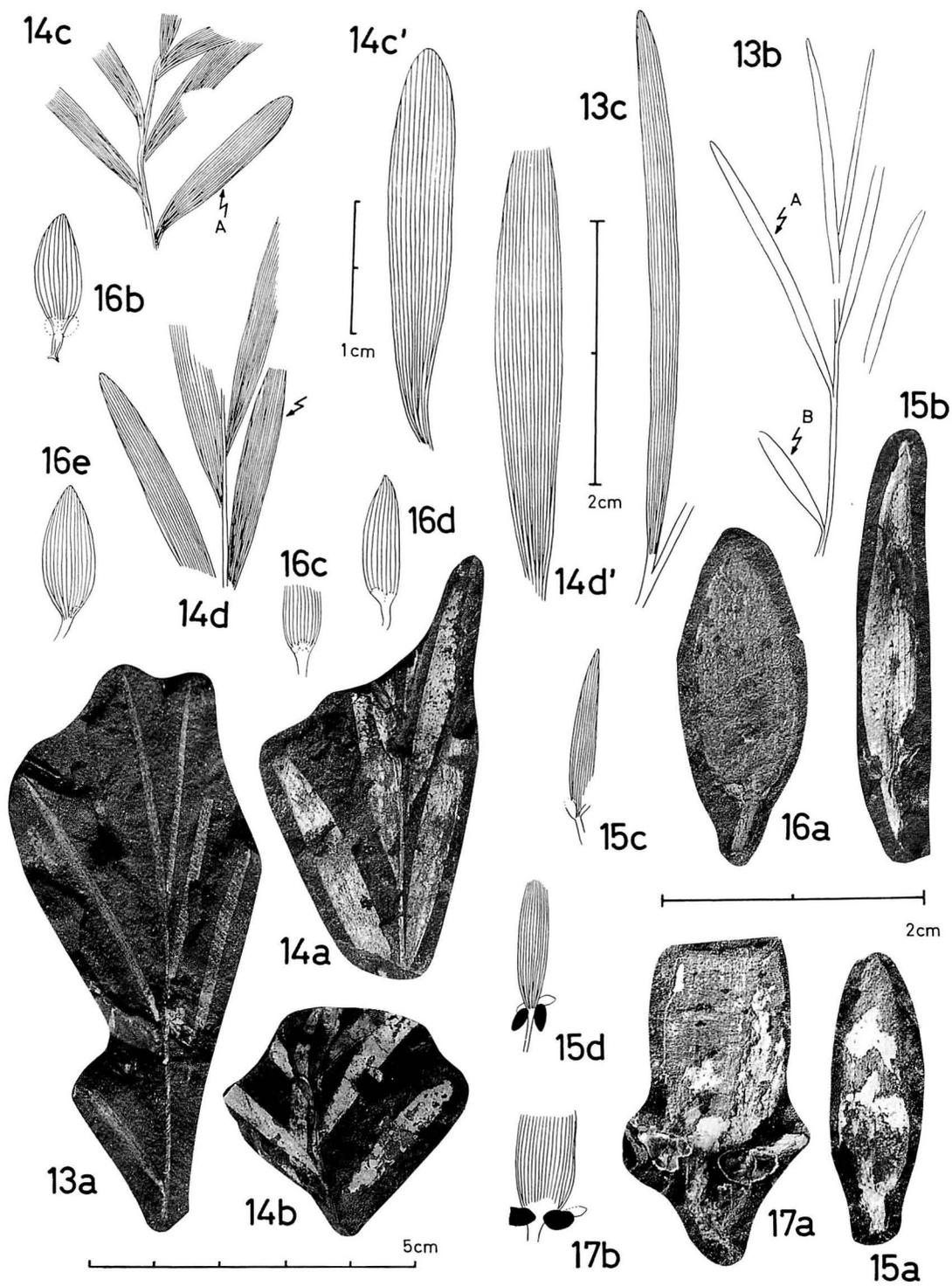
arranged leaves which lack petiole. The leaves are mostly long and slender, nearly parallel-sided for the most part but narrowed gradually towards both ends, being 4.3 cm long and 2 mm wide (a leaf indicated by the arrow-A in Figure 13b); the apex is obtusely pointed. A leaf shown by the arrow-B (Figure 13b) is elongate-oval in outline, 1.8 cm long and 2.5 mm wide; its apex is rounded and base is markedly decurrent and appressed to the axis; the ratio (L/W) of our leaves ranges from 7.2 to 31.3, typical number being 21.5. The veins are dichotomously forked near the base, parallel to each other, not converging at apex, typical numbers being 7–8 (40–47 per cm) in each leaf; in a leaf indicated by the arrow-B (Figure 13b), the veins number 11 but the vein-density is normal (44 per cm). Cuticle is not preserved.

Distribution and occurrence: *Podozamites* ex gr. *schenki* is locally common in the Gimpo, Nampo and Bansong Groups.

Remarks: Our specimens are closely referable macroscopically to those of *Podozamites schenki* known widely from the older Mesozoic plant-beds. At present we regard them as *Podozamites* ex gr. *schenki*, because our leafy shoots occasionally bear such elongate-oval leaves as shown in Figure 13a (an arrow-B in Figure 13b) which have not been recorded from other localities.

The leafy shoots described by Kawasaki (1925) from the Gimpo and Nampo Groups as *Podozamites schenki* are indistinguishable

→ **Figures 13 (a–c)—17 (a–b)**. Natural size, unless otherwise indicated. **13**. *Podozamites* ex gr. *schenki* Heer: **13a**. A typical leafy shoot (Reg. no. 81-123). **13b**. Drawn from Figure 13a. **13c**. Drawn from a leaf indicated by an arrow-A in Figure 13b, showing the venation. Loc. Hanaeri. **14**. *Podozamites* sp. A: **14a**. A broken leafy shoot with elongate leaves (Reg. no. 81-053). Loc. Hanaeri. **14b**. A broken leafy shoot with 6 spirally arranged leaves (Reg. no. 81-031T). Loc. Cheonndaeri. **14c**. Drawn from Figure 14b. **14c'**. Enlarged from a leaf indicated by an arrow-A in Figure 14c, showing the detailed venation. **14d**. Drawn from Figure 14a. **14d'**. Enlarged from a leaf indicated by an arrow in Figure 14d, showing the detailed venation. **15**. *Cycadocarpidium* sp. cf. *C. asaense* Kon'no: **15a–b**. Enlarged bracts with biovuliferous scale-scars (Reg. no. 81-002T). Loc. Cheonndaeri. **15c**. Drawn from Figure 15b. **15d**. A bract with digitate and biovuliferous scales (Reg. no. 81-002T). Loc. Cheonndaeri. **16**. *Cycadocarpidium* sp. cf. *C. nagatoense* Kon'no: **16a**. Enlarged bract; ovuliferous scales are missing (Reg. no. 81-003T). **16b, d**. Bracts with two scars of seeds (the other one is invisible) (Reg. no. 81-008T). **16c**. A bract with three scars of seeds (Reg. no. 82P-B). **16e**. Drawn from Figure 16a (16a, b, d; from Cheonndaeri, 16c; from Hanaeri). **17**. *Cycadocarpidium* sp. A: **17a**. An enlarged bract with two large-sized scale-lobes and ovules. Loc. Cheonndaeri. **17b**. Drawn from Figure 17a.



from ours.

In Japan, it is noted that *Podozamites* leafy shoots bearing such long and narrow leaves are restricted to the Late Triassic floras. Our *Podozamites* ex gr. *schrenki* resembles externally *P. gramineus* originally described by Heer (1876) from Ust-Balei. Heer's original specimen (*P. gramineus*) is a single detached leaf and is distinguished from ours by its more elongated leaf with four veins. However, leafy shoots regarded as *Podozamites gramineus* by many authors (e.g. Vakhrameev, 1958; Vassilevskaja and Pavlov, 1963; Prosviryakova, 1966) are externally indistinguishable from ours except for the elongate-oval-shaped leaf.

Podozamites agardhianus (Brongniart) Nathorst known from the Upper Triassic of Sweden resembles in leaf-form *P. ex gr. schrenki*, but it is distinguished by its leaves being rather expanded near the base as shown by Nathorst (1878c, pl. 3, fig. 14).

Podozamites sp. A

Figures 14a—d'

Material: Reg. nos. 81-031T (Cheondaeri), 81-020, 046, 053 (Hanaeri) and many other broken leafy-shoots and detached leaves.

Description: Many incomplete leafy-shoots were obtained. The axis is slender, 0.9 mm wide below and 0.7 mm above and gives off spirally arranged leaves. The leaves are sessile and varied in size and form. The leaves on the distal part of a shoot are generally longer than those on the proximal part of the same shoot. The longer leaves are typically elongate-oval in form, up to 4 cm long and at most 0.5 cm wide, with obtusely pointed or rounded apex, and they are attached to the axis at a narrow angle as shown in Figure 14d. The leaves on the proximal part of a shoot are typically oblanceolate in form, and measure up to 3 cm long and at most 0.45 cm wide, with rounded apex and they are

attached to the axis at a wide angle as shown in Figure 14c. The veins are dichotomously forked at or near the base, then running parallel to each other, ending at distal and lateral margins, and not converging at apex, and their numbers range from 13 to 15 in each leaf. Cuticle is not preserved.

Distribution and occurrence: *Podozamites* sp. A is locally common in the Mungyeong and Chungnam Coal-Fields, especially so at the Cheondaeri and Hanaeri localities.

Remarks: *Podozamites* sp. A is characterized by its small-sized leafy-shoots, and it is distinguished from *P. ex gr. distans* (Presl) Braun and *P. ex gr. schrenki* Heer (both are common elements in the Daedong Flora) by its small-sized leaves and its leaf-form, respectively. Our *Podozamites* sp. A resembles somewhat some detached leaves described as *P. lanceolatus* var. (or forma) *eichwaldi* Heer from China by Schenk (1883, pl. 50, figs. 2?, 3; pl. 51, fig. 3; pl. 52, fig. 8), Krasser (1905, pl. 4, fig. 4), Sze (1933b, pl. 8, fig. 7), Sze *et al.* (1963, pl. 99, fig. 5 = Krasser's specimen) in leaf-form and venation.

Podozamites sp. A also resembles in its leaf-size *P. agardhianus* (Brongniart) Nathorst var. *acuminatus* proposed by Kon'no (1961) from the Carnian Momonoki Formation, but *P. sp. A* is distinguished by having leaves whose apex is obtusely pointed or rounded instead of being acuminate, and by possessing 13–15 veins in each leaf compared with 8–10 in the latter.

The leaves of *Podozamites agardhianus* known from the Upper Triassic of Sweden (Nathorst, 1878c) are longer, twice as long as those of *P. sp. A* and bear smaller number of veins (9 at middle).

Seed-bearing fructifications

Genus *Cycadocarpidium* Nathorst, 1886

Cycadocarpidium organs are rather abundant in Upper Triassic formations of Yamaguchi Prefecture, Japan. They were described by Kon'no (1961) together with *Pod-*

ozamites leafy-shoots. In his paper, Kon'no distinguished seven *Cycadocarpidium* species or forms and four *Podozamites* species or varieties. However, until now no *Cycadocarpidium* species has been described from Korea in spite of its common occurrence from the Amisan Formation at Cheondaeri and the Bongmyeongri Formation at Hanaeri. Thus, we made here the first record of this genus and distinguished four forms, including a questionably identified one (*C.* ? sp. B).

Florin (1951, 1953) stated that the cone-scale was not a compound carpellary leaf carrying ovuliferous pinnae at its base but one composed of a bract with an axillary fertile shoot or seed-scale complex. In this study, we could not confirm this statement by Florin.

Key to the species or forms (excluding *C.* ? sp. B)

1. Bract narrowly lanceolate, veins 10 in number.....*C.* sp. cf. *C. asaense*
2. Bract ovate or elongate-ovate, veins 7-12*C.* sp. cf. *C. nagatoense*
3. Bract possibly elongated, veins 16*C.* sp. A

Cycadocarpidium sp.
cf. *C. asaense* Kon'no

Figures 15a-d

Compared: *Cycadocarpidium asaense* Kon'no: Kon'no, 1961, p. 202, pl. 24, figs. 2-4.

Material: Reg. nos. 81-002T, 011T, 030T (Cheondaeri), 82-PA, 81-127G (Hanaeri) and many other bract-fragments.

Description: Cone-scale consists of bract and ovuliferous scales. The bract is lanceolate in outline, being 2.6 cm long and 0.35 cm wide (Figure 15b) and more than 2 cm long and 0.45 cm wide (Figure 15a), and has an acutely pointed apex. The veins fork dichotomously near the base or simply, run parallel to each other and to the lateral

margins of bract. They number 10 at the middle and are not converging at apex. The ovuliferous scale is bidigitate and biovuliferous; the lobe of ovuliferous scale is nearly triangular or oblong, measures 0.35 cm long and 1.5 mm wide and bears a pointed apex. The ovule is ovate in form, 3.5 mm long and 2 mm wide, and directed downwards. The pedicel of cone-scale is well defined, more than 7.5 mm long, and up to 0.8 mm wide. Cuticle is not preserved.

Distribution and occurrence: Common in the Amisan Formation at Cheondaeri and in the Bongmyeongri Formation at Hanaeri. Associated *Podozamites* species include *P.* ex gr. *distans* and *P.* sp. A at Cheondaeri, and *P.* ex gr. *schenki* and *P.* sp. A at Hanaeri.

Remarks: The present specimens are identifiable, in their form and venation of bract and biovuliferous scale, with *Cycadocarpidium asaense* originally described by Kon'no (1961) from the Ladino-Carnian Hiramatsu Formation. In our specimens, however, the ovules are shorter (3.5 mm) than those of the original specimens (6 mm) and the bracts are slender (3.5-4.5 mm wide) than those of original ones (6.5-7 mm wide). Thus, we herein refrain from making a full identity of our specimens with Kon'no's species.

Cycadocarpidium sp. cf. *C. asaense* is clearly distinguishable from *C.* sp. cf. *C. nagatoense* and *C.* sp. A both of which are described together because of its slender habit of bract.

Some specimens of *Cycadocarpidium swabii* illustrated by Harris (1935) are similar in form and size of cone-scale to ours, but they are distinguished in having smaller numbers of veins converging at apex and indistinct ovuliferous lobes. *Cycadocarpidium swabii* described by Oishi (1932c) from the Momonoki Formation is similar in form of bract, but it is distinct in its veins converging at apex and possessing longer ovules (6 cm long and 2 mm wide).

Biovuliferous *Cycadocarpidium issykkul-*

ense, *C. insignis* and *C. dzerganense* all described by Genkina (1963, 1966) from the Upper Triassic Issyk-Kul Basin are distinguished from ours by their large-sized bracts and in the last mentioned species by its small-sized circular ovules (1 mm in diameter).

Cycadocarpidium erdmanni Nathorst (sensu lato) is also similar to ours in form of bract and ovuliferous scale and size of ovule, but it is clearly distinguishable by its small number of veins (4-6).

Kon'no (1961) mentioned that *Cycadocarpidium asaense* was associated with *Podozamites* sp. cf. *P. astartensis* Harris which bears large-sized and oblong-ovate leaves. In Korea, there found are no such large-sized *Podozamites* leaves as those referable to *P.* sp. cf. *P. astartensis*, except for *P.* ex gr. *distans*.

Cycadocarpidium sp.
cf. *C. nagatoense* Kon'no

Figures 16a—e

Compared: *Cycadocarpidium nagatoense* Kon'no: Kon'no, 1961, p. 203, pl. 23, figs. 7-8.

Material: Reg. nos. 81-003T, 008T (Cheondaeri), 81-092, 82-PB (Hanaeri) and many other fragments of sterile bracts.

Description: Among the collection, there are three complete bracts; their dimensions excluding short pedicel are 1.85 cm long and 7.5 mm wide, 2 cm long and 6 mm wide, and 2 cm long and 8 mm wide. The pedicel is 3-4 mm long and 1 mm wide, but it expands abruptly at its upper end into the broad base of bract. The bract is ovate or elongate-ovate in outline, with an obtusely pointed or rounded apex. The veins fork dichotomously once or twice near the base, then running parallel to each other and to the margins, and do not converge at apex; they number 7-12 at the middle of bract. No interstitial vein has been observed. The ovules shed to leave their scars; the largest ovule is 3.5 mm long

and 2.5 mm wide. The ovules are three in number (triovuliferous) (Figure 16c). No trace of ovuliferous lobe has been recognized. Cuticle is not preserved.

Distribution and occurrence: Common in the Amisan Formation at Cheondaeri and in the Bongmyeongri Formation at Hanaeri. Associated *Podozamites* species are *P.* ex gr. *distans* and *P.* sp. A at Cheondaeri, and *P.* ex gr. *schrenki* and *P.* sp. A at Hanaeri.

Remarks: The present specimens are, in form of bract, venation and size of ovules, most close to *Cycadocarpidium nagatoense* originally described by Kon'no (1961) from the Carnian Momonoki Formation. However, we were unable to identify fully our specimens to Kon'no's species because of the indistinctness of our ovuliferous scales.

Harris (1935) showed the form-variation of cone-scales of *Cycadocarpidium swabii* Nathorst (sensu lato). *Cycadocarpidium swabii* differs from *C. nagatoense* in its biovuliferous scale. Some of Harris' specimens agree with ours in form of bract but our bracts are further distinguished from those of *Cycadocarpidium swabii* by the veins not converging at apex.

Cycadocarpidium swabii described by Oishi (1932c) from the Momonoki Formation is not triovuliferous but apparently biovuliferous, and differs from the present specimens in its veins converging at apex.

Cycadocarpidium swabii described by Sun (1979) from the Upper Triassic Malugou Formation, Jilin, Northeast China is comparable with ours in venation, but it is distinguished from ours by its biovuliferous habit and its obovate or elongate-oval bracts.

Some specimens regarded as *Cycadocarpidium tricarpum* Prynada by Stanislavsky (1976) from the Upper Triassic of the Donetz Basin are similar in form of bract to the present specimens, but they are distinguished by a small number of veins (4-8 in each bract).

Kon'no (1961) mentioned that *Cycadocarpidium nagatoense* and *Podozamites distans*

var. *nagatoensis* Kon'no bearing small-sized ovate leaves might belong to the same plant. However, no such small-sized *Podozamites* leaves have been found in association with the present *C.* sp. cf. *C. nagatoense* in Korea.

Cycadocarpidium sp. A

Figures 17a—b

Material : Reg. no. 81-031T (Cheondaeri).

Description : There obtained was a single broken cone-scale characterized by its multinerved bract, bidigitate and biovuliferous scales and large-sized ovules. The bract is 9 mm wide but its whole shape is not ascertained. Pedicel is thick, being 2 mm wide. The veins fork dichotomously once or twice near the base, then run parallel to each other, number 16 at the middle, and possibly do not converge at apex, judging by the right one ending the lateral margin of bract as shown in Figure 17b. The ovuliferous lobe is possibly triangular in form and is 6 mm long. The still-preserved ovule is oval in form, 5 mm long and 3 mm wide, and arranged perpendicularly to the pedicel.

Distribution and occurrence : Only a single specimen was obtained at Cheondaeri in close association with *Podozamites* sp. A.

Remarks : *Cycadocarpidium* sp. A is comparable with *C. giganteum* originally described by Sun (1979) from the Upper Triassic Malugou Formation, Jilin, Northeast China in its large-sized and multi-nerved bract and also large-sized ovules. According to Sun (1979), his biovuliferous *Cycadocarpidium giganteum* is characterized by a broadly lanceolate bract, typically 5.5–6 cm long (the largest 8 cm) and 1.3–1.4 cm wide, 14–17 veins traversing the middle of bract, and large-sized oval ovules which are 6–7 mm long and 4–5.5 mm wide. Thus *Cycadocarpidium* sp. A resembles closely *C. giganteum*, but we at present reserve to make its specific identity later, because of our cone-scale being represented only by a single broken one.

Unclassified plants

Form-genus *Taeniopteris* Brongniart, 1828

Taeniopteris cheondaeriensis

Kimura et Kim, sp. nov.

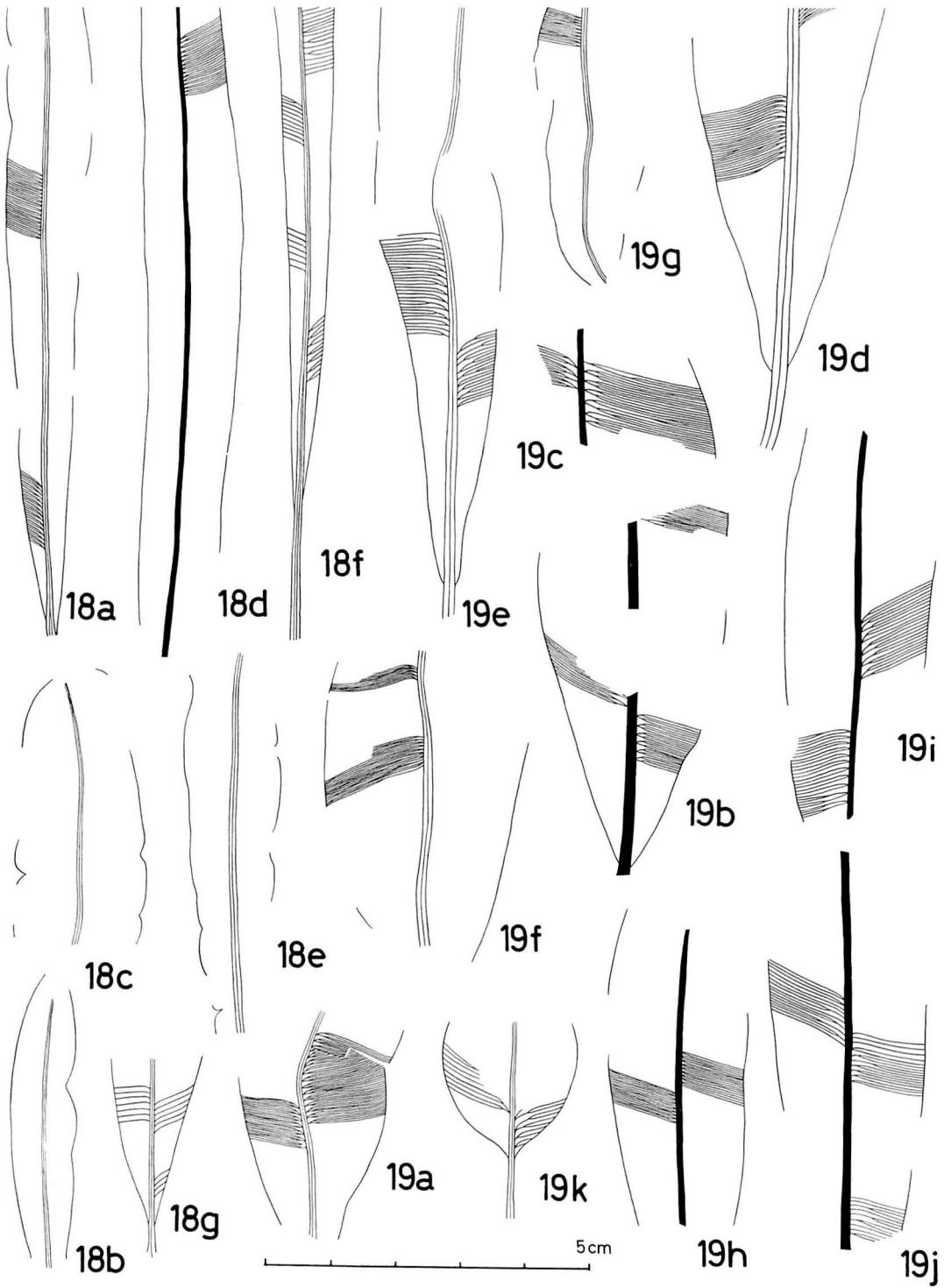
Figures 18a—g

Material : Holotype ; Reg. no. 81-007TA (Cheondaeri). Paratypes ; Reg. nos. 81-007TB-E (Cheondaeri). Examined specimens ; Reg. nos. T-0082, 81-003T-035T (Cheondaeri), 81-113A, 127D, 240A (Hanaeri). *Stratum typicum* : Amisan Formation at Cheondaeri. *Locus typicus* : Cheondae Coal-Mine, Cheondaeri, Janggog-myeon, Hongseong-gun, Chungcheongnam-do (see Kimura and Kim, 1988, p. 604). *Derivatio nominis* : From the locality.

Diagnosis : Taeniopteroid leaves variable in form and size, shortly petioled, typically elongate-oblancoelate to elongate-oblong in outline. The longest one more than 11 cm, width variable depending on leaves, ranging from 1 cm to 2.2 cm at the widest portion. Lamina attached to the lateral sides of slender rachis up to 1 mm wide, gradually narrowed to the well-defined petiole. Margins entire or broadly wavy. Lateral veins originating from rachis at an angle of 75 degrees ; angle reduced towards the base of lamina ; usually forked once at their origin ; density 20–33 per cm, but in those unusually elongated laminae veins sometimes simple and sparse.

Distribution and occurrence : The present new species is common in the Amisan Formation at Cheondaeri and in the Bongmyeongri Formation at Hanaeri.

Discussion and comparison : The present new species is characterized by its elongated leaves usually with veins forked once at their origin. In some unusually elongated laminae (e.g. Figure 18f), however, they show unusual venation, either simple or forked once and rather sparsely distributed. Figure 18g also shows a cuneate base of lamina which unusually has simple and sparse veins. Unfortunately, in our specimens cuticle is not preserved.



ved and their apices are all missing.

The following species are similar in size and form to our *Taeniopteris cheondaeriensis*, but they are distinguished from ours by those features which are briefly mentioned below :

Taeniopteris maclellandi (Oldham et Morris) Feistmantel, 1876, p. 36; Zeiller, 1902-1903, p. 61, pl. 9, figs. 3-5: Larger in size with stout rachis. Kawasaki's specimens (1925, p. 34, pl. 20, figs. 62-63), regarded by him as *T. maclellandi*, are referable to *T. richthofeni* as mentioned by Oishi (1940, p. 141, 149).

T. minensis Oishi (Oishi, 1932c, p. 60, pl. 2, figs. 1-5): Lateral veins are simple or forked once at variable distance from their origin; the veins are somewhat coarser (20-25 per cm) than ours.

T. shitakensis Oishi (Oishi, 1932b, p. 10, pl. 3, fig. 8): This species was defined on the basis of a single leaf with stout rachis. Lateral veins are simple or forked once near their origin, and are somewhat coarser (25-30 per cm) than ours.

T. stenophylla Kryshstofovich (Kryshstofovich, 1910, p. 11, pl. 2 fig. 1): Lateral veins are forked once or twice at variable distances from their origin, and are coarser (20-25 per cm) than ours.

T. tenuinervis Brauns (Nathorst, 1878b, p. 47, pl. 7, fig. 6; pl. 8, figs. 8, 11-12, 14-16; pl. 10, figs. 2-5; 1879, p. 59, pl. 11, fig. 9): Lateral veins are mostly simple.

Taeniopteris mungyeongensis

Kimura et Kim, sp. nov.

Figures 19a—k

Material: Holotype; Reg. no. 81-163B (Hanaeri). Paratypes; Reg. nos. 81-163A, C, D (Hanaeri). Examined specimens: Reg. nos. 81-052, 063, 073, 101A, B, C, 113, 127, 151, 0240 (Hanaeri). *Stratum typicum*: Bongmyeongri Formation, Bansong Group. *Locus typicus*: Hanaeri (East side), Maseong-myeon, Mungyeong-gun, Gyeong-sangbuk-do (see Kimura and Kim, 1988, p. 604). *Derivatio nominis*: From the name of Mungyeong Coal-Field.

Diagnosis: Leaf oblanceolate-obovate in outline, shortly petioled, apex broadly rounded, lamina attached to the upper sides of rachis, with markedly cuneate or rarely rounded base, more than 15 cm long, width variable according to leaves, up to 3 cm at the widest portion. Rachis rather slender, 1.2 mm wide at base, giving off numerous veins at a wide angle. Margins entire or irregularly undulated. On the most part of lamina, veins usually forked twice, the first forked at the base, the second near the base; density 20-42 per cm at the margin; often bending downwards near the base. On the cuneate part of lamina, a half of veins forked twice and the rest once, the first forked at the base, the second on the midway; density 21 per cm at the margin. In some of the leaves, veins either simple or forked once irregularly.

Distribution and occurrence: The present

← **Figures 18 (a-g)—19 (a-k)**. All natural size. **18**. *Taeniopteris cheondaeriensis* Kimura et Kim, sp. nov.: **18a**. (Reg. no. 81-007TA, Holotype). **18b**. One of paratypes (Reg. no. 81-007TB). **18c**. The widest leaf (2 cm wide) with rounded apex (Reg. no. 81-035T). **18d**. The longest leaf (more than 11 cm); vein-density 28 per cm (Reg. no. 81-240A). **18e**. A leaf with waved margins; vein-density 20 per cm (Reg. no. T-0082). **18f**. An unusually cuneate leaf-base with disordered veins (Reg. no. 81-127D). **18g**. A cuneate base with simple and sparse veins (Reg. no. 81-003T). Loc. Cheondaeri (18a-c, e, g) and Hanaeri (18d, f). **19**. *Taeniopteris mungyeongensis* Kimura et Kim, sp. nov.: **19a**. Holotype (Reg. no. 81-163B). **19b**. A slightly distorted leaf; vein-density 35 per cm (Reg. no. 81-127B). **19c**. A distorted leaf; vein-density 30 per cm (Reg. no. 81-127A). **19d-e**. Cuneate bases with distorted veins (Reg. nos. 81-240B, 81-101A). **19f, g, h, i**. Leaves with once or twice forked veins (19f; vein-density 42 per cm, 19g; 40 per cm). Reg. nos. 81-073B (19f, g), 81-127C (19h, i). **19j**. An unusual leaf with disordered veins (Reg. no. 81-151). **19k**. An unusually small-sized leaf with oblong lamina (Reg. no. 81-0240C). Loc. Hanaeri.

new species is common but only known from the Bongmyeongri Formation at Hanaeri.

Discussion and comparison: The present new species is characterized by its oblanceolate-obovate leaves with regularly twice forked veins except for the basal cuneate part, and it differs in venation from any known Mesozoic taeniopteroid species from East Asia. According to our present knowledge, Mesozoic taeniopteroid leaves with twice forked veins are rather rare.

A leaf shown in Figure 19k displays unusual venation, either simple or forked once irregularly. However, we consider it to be rare example and it indeed belongs to this species, because that leaf occurred among other normal leaves of *Taeniopteris mungyeongensis*.

Taeniopteris mungyeongensis, sp. nov. resembles *T. nabaensis*, a little known species first described by Oishi (1932a) from the Norian Nariwa Group in its leaf-size and venation, but in Oishi's species, the second vein-forking occurs in their mid-course of extent unlike ours with forking regularly occurring close to their origin.

Taeniopteris lanceolata also first described by Oishi (1932a) from the Nariwa Group has once or twice forked veins. However, their forking occurs at variable distances from the base.

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韓国大同累層群産後期三疊紀植物化石の新種ほか: 韓半島の大同, 金浦, 漣川, 忠南, 聞慶および丹陽炭田地域に露出する非海成の大同累層群の植物化石は, かつて矢部長克, 川崎繁太郎, 大石三郎, 小島信夫らによって研究されたが, 1945年以来その研究は途絶えていた。筆者らは1973年以来, この地域の炭田の開発にともない, おもに忠南および聞慶炭田地域の新産地から多くの植物化石を入手することに成功し, 現在までに, 38属79種を識別し, またこれらの中には, 従来知られていなかった分類群, 1新属および10新種を加え20属33種を含む。本論文は以上の新種を含むこの植物群の特徴種14属19種を記載した。大同累層群の植物群の時代は, かつて, ジュラ紀初~中期と考えられたが, 少なくとも金浦, 忠南, 聞慶炭田地域から得られた化石植物群集に関する限り, その組成は, 日本, 沿海州南部および中国東北の東南部, および中国南部の三疊紀後期植物群と完全に一致し, これら地域のジュラ紀初~中期植物群とは著しく異なる。 木村達明・金 鳳均

881. AN EARLY MIDDLE PLEISTOCENE MURID RODENT MOLAR FROM THE KOBIWAKO GROUP, JAPAN*

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Abstract. A murid M¹ obtained from the Hiraen Clay Member of the Kobiwako Group is the oldest record of the family in the Japanese Islands. The molar is assigned to the small Japanese field mouse, *Apodemus argenteus*, an endemic species living in the islands today. It indicates that this species originated by the early Middle Pleistocene (0.65-0.7 Ma). Moreover, the molar contributes to reconstructing the Quaternary mammalian faunal succession in Japan, because the faunal content of mammalian biozone QM3 (0.5 to 0.73 Ma) is poorly known.

Key words. Murid, *Apodemus argenteus*, early Middle Pleistocene, Kobiwako Group, central Japan.

Introduction

Until recently, murid remains from the Japanese Islands were known only from sediments younger than the early Middle Pleistocene. They were mostly obtained from cave and fissures, and their ages were ambiguous. A murid molar described here was collected from a lacustrine clay bed of the Kobiwako Group, which is dated with confidence as the early Middle Pleistocene. Therefore this find is very important from biostratigraphic view, and is now regarded as the oldest record of murids in the islands.

Mammalian remains of the early Middle Pleistocene are extremely rare in Japan (Kamei *et al.*, 1988). Only a few forms of large mammals are known. Therefore the

present specimen provides the important information on micro-mammals of this period.

The main purpose of this paper is to present a detailed systematic description of the specimen. Furthermore, we briefly describe the stratigraphic sequence of the Kobiwako Group around the fossil locality, and discuss the biostratigraphic problems.

Geological setting

The Kisen River is a small stream that runs from west to east through the northern part of the Katata Hills into Lake Biwa (Figure 1). A branch of the river flowing down from the southern outskirts of Kurihara cuts a small gorge. The murid molar was found by one of us (Iida) in a clay block lying on the riverbed of the branch in October 1986. The block had undoubtedly fallen down from a

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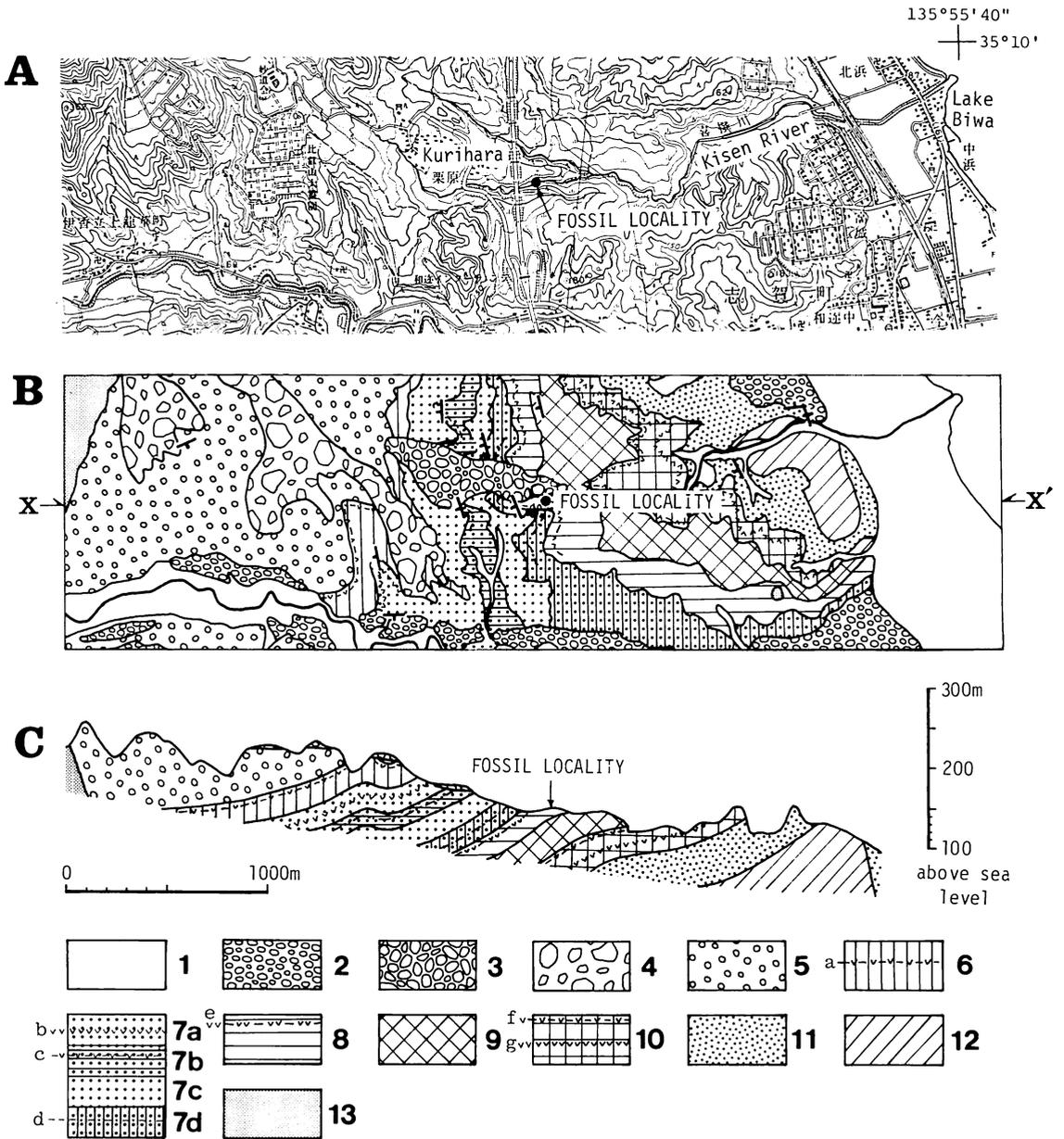


Figure 1. Map showing the location of the fossil locality (A), geological map of the same area (B) and section along X-X' (C). 1-13: lithologic units (5-12: members of the Kobiwako Group). 1: alluvium. 2: lower terrace deposits. 3: middle terrace deposits. 4: higher terrace deposits. 5: Ryuge Sand and Gravel. 6: Sakawa Clay. 7: Kurihara Alternation of Sand and Clay (7a: upper part, 7b: middle part, 7c: lower part, 7d: lowest part). 8: Hiraen Clay. 9: Takashiro Alternation of Sand and Clay. 10: Kisen Clay. 11: Kitahama Sand. 12: Nijigaoka Clay. 13: basement rocks (Pre-Tertiary). a-g: volcanic ash layers. a: Sakawa II. b: Kurihara III. c: Kurihara II. d: Kurihara I. e: Biotite II. f: Biotite I. g: Kisen.

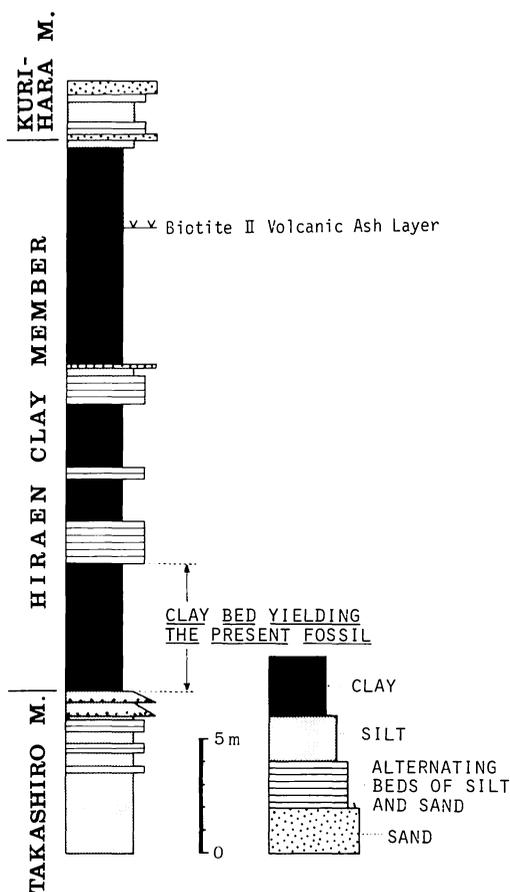


Figure 2. Columnar section of the Kobiwako Group observed along the gorge wall of the fossil locality.

clay bed exposed on the northern wall of the gorge. This bed is 5.6 m in thickness, and consists of bluish gray massive clay with remains of plants and freshwater shells (Figure 2). Teeth and bones of freshwater fishes are also contained but rare. They show the same state of preservation as that of the murid molar.

After finding the molar, 161 kg of sediment were collected from the clay bed, and washed through screen (0.5 mm mesh). Although remains of freshwater fishes and shells were obtained, no other mammalian fossils were found.

On the basis of the stratigraphy of the gorge

wall, the clay bed is assigned to the lowest part of the Hiraen Clay Member. This member is the fifth lithologic unit of the Katata Formation, Kobiwako Group (Hayashi, 1974; Figure 3). Around the fossil locality, westward dipping beds allow the ascending stratigraphy of the formation to be observed from east to west (Figure 1).

Iida (1988, MS) inferred from the sedimentological analyses that the Hiraen Clay Member was deposited in a shallow lake. On the other hand, the Research Group for Natural History of Lake Biwa (1986) studied green algae, diatoms, protozoans, molluscs and insects from the lower part of the Katata Formation including the Hiraen Clay, and considered that it was deposited in the littoral zone of a shallow lake.

Eighteen volcanic ash layers intercalated in the Katata Formation play an important role as marker beds (Figure 3). Among them, the Kisen and B Volcanic Ash Layers in the Kisen Clay Member, and the E Volcanic Ash Layer in the Ryuge Sand and Gravel Member are correlated with the Azuki, Sayama and Kasuri Volcanic Ash Layers in the Osaka Group, respectively (Ishida and Yokoyama, 1969; Hayashi, 1974; Yoshikawa, 1983). The Azuki and Kasuri Volcanic Ash Layers were dated at 0.87 ± 0.07 Ma and 0.37 ± 0.04 (or 0.38 ± 0.03) Ma, respectively by fission track (Nishimura and Sasajima, 1970). On the other hand, Suzuki (1988) determined the ages of the Sayama and Kasuri Volcanic Ash Layers as 0.77 ± 0.31 Ma and 0.42 ± 0.08 Ma, respectively by the same method. Additionally, a fission track age of 0.7 ± 0.14 Ma was obtained from the Biotite I Volcanic Ash Layer in the Kisen Clay Member by Nishimura and Yokoyama (1975). On the other hand, Hayashida *et al.* (1976) designated the Brunhes-Matuyama geomagnetic boundary to the horizon about 10 m above the Biotite I Volcanic Ash Layer in the section of the Kisen River. On the basis of these chronological data, the horizon of the murid molar is estimated as about 0.65 to 0.7 Ma in age.

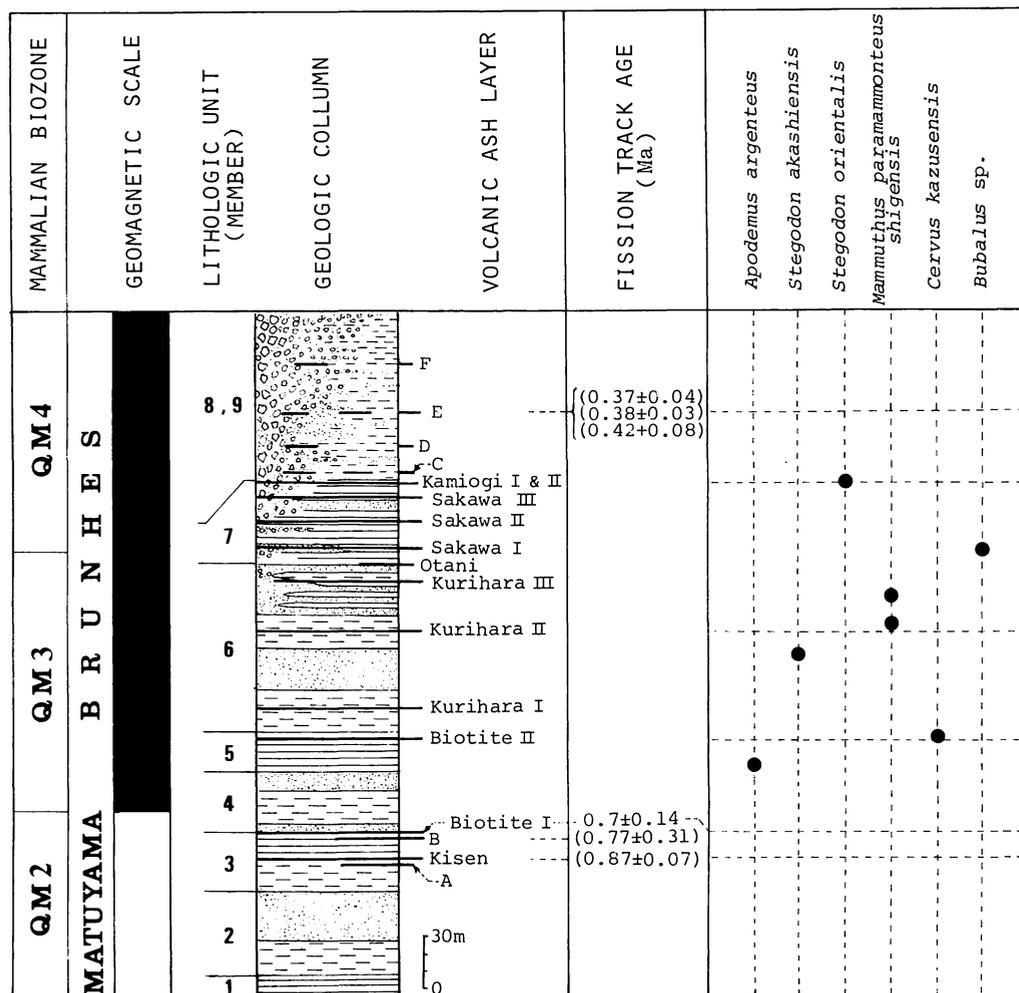


Figure 3. Generalized sequence of the Katata Formation and stratigraphic distribution of fossil mammals. The fission track ages in parentheses indicate those of the correlative volcanic ash layers in the Osaka Group. 1: Nijigaoka Clay Member. 2: Kitahama Sand Member. 3: Kisen Clay Member. 4: Takashiro Alternation Member. 5: Hiraen Clay Member. 6: Kurihara Alternation Member. 7: Sakawa Clay Member. 8, 9: Ryuge Sand and Gravel Member, and Yamashita Alternation Member.

Biostratigraphic consideration

Proboscideans and artiodactyls are reported from the Katata Formation in the Katata Hills (Naumann, 1881; Hiki, 1915; Matsumoto and Ozaki, 1959; Ikebe *et al.*, 1966; Kamei, 1966; Okazaki and Matsuoka, 1979; Tamura *et al.*, 1982; Taruno *et al.*, 1983; Kamei, 1984 *etc.*). The murid specimen is the first record of micro-mammal in the formation. The stratigraphic position of these

mammalian remains is summarized in Figure 3. The murid specimen occurs at the lowest horizon among them.

Kamei *et al.* (1988) proposed a mammalian biozonation of the Late Neogene and Quaternary sediments in the Japanese Islands. They divided the Middle Pleistocene into three biozones, QM3 (0.73 to 0.5 Ma), QM4 (0.5 to 0.3 Ma) and QM5 (0.3 to 0.12 Ma). The faunal contents of QM4 and QM5 are abundant, but that of QM3 is almost un-

known. Only two forms, *Mammuthus* cf. *armeniacus* and *Bison* sp., were reported from QM3. Accordingly the present specimen is an important addition to the mammalian fauna of this biozone.

Systematic description

Descriptive terminology and method of measurements are given in Figure 4. The specimen described here is stored in the Department of Geology and Mineralogy, Faculty of Science, Kyoto University.

Order Rodentia Bowdich, 1821

Family Muridae Gray, 1821

Genus *Apodemus* Kaup, 1829

Apodemus argenteus (Temminck, 1844)

Figure 5

Mus argenteus Temminck, 1844, p. 51, pl. 15, fig. 1.
Other synonyms are given in Kawamura (1989).

Material.— 1 isolated left M¹ (KUJC 100718).

Locality.— Kurihara, Shiga-cho, Shiga-gun, Shiga Prefecture (135°54'13"E; 35°9'37"N).

Horizon.— Hiraen Clay Member, Katata Formation, Kobiwako Group.

Age.— Early Middle Pleistocene (ca. 0.65 to 0.7 Ma).

Description.— The crown is as high as those of the living species of *Apodemus*, but somewhat higher than those of *Micromys* (B and C of Figure 5). In occlusal view, it has an oval outline, and comprises three chevron-shaped cusp rows (anterior, middle and posterior chevrons), which are the basic pattern of murid M¹. The buccal cusps (labial anterocone, paracone, metacone and posterior cingulum) and central cusps (lingual anterocone, protocone and hypocone) are inclined to the front, while the lingual cusps (anterostyle, enterostyle and posterostyle) are almost erect. The central cusps are larger than other cusps.

The dentine fields of the three cusps of the

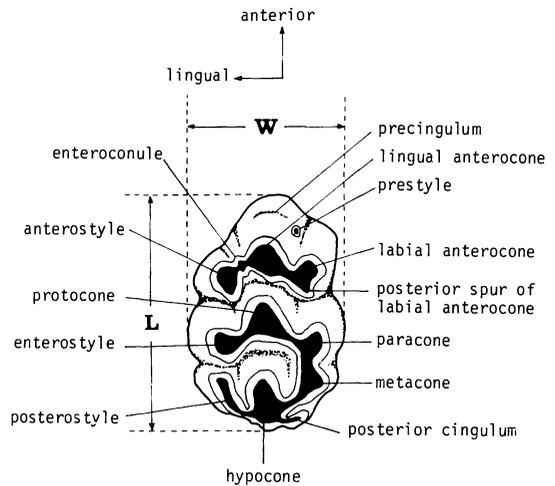


Figure 4. Terminology and method of measurements of murid M¹. The terminology is based mainly on Jacobs (1978).

anterior chevron are well confluent with each other. Neither precingulum nor prestyle are recognized. The occlusal surface of the labial anterocone is considerably anterior to that of the anterostyle. The posterior spur of the former cusp is well defined, while that of the latter cusp is indistinct. The anterior chevron is clearly separated from the middle chevron by a deep transverse valley. No accessory cusps are observed at the lingual or buccal entrance of the valley.

The dentine fields of the three cusps of the middle chevron are also confluent. Moreover, that of the paracone is continuous with that of the metacone in the posterior chevron. The occlusal surfaces of the paracone and enterostyle are approximately set in the same transverse line. The transverse valley between the middle and posterior chevrons is deep, but opens only lingually.

The dentine fields of the four cusps of the posterior chevron are confluent with each other. The morphology of this chevron is of the "argenteus type" as discussed by Kawamura (1989). Namely, the posterior cingulum is well developed and strongly connected to the metacone and hypocone. Furthermore, the hypocone is directly connected to

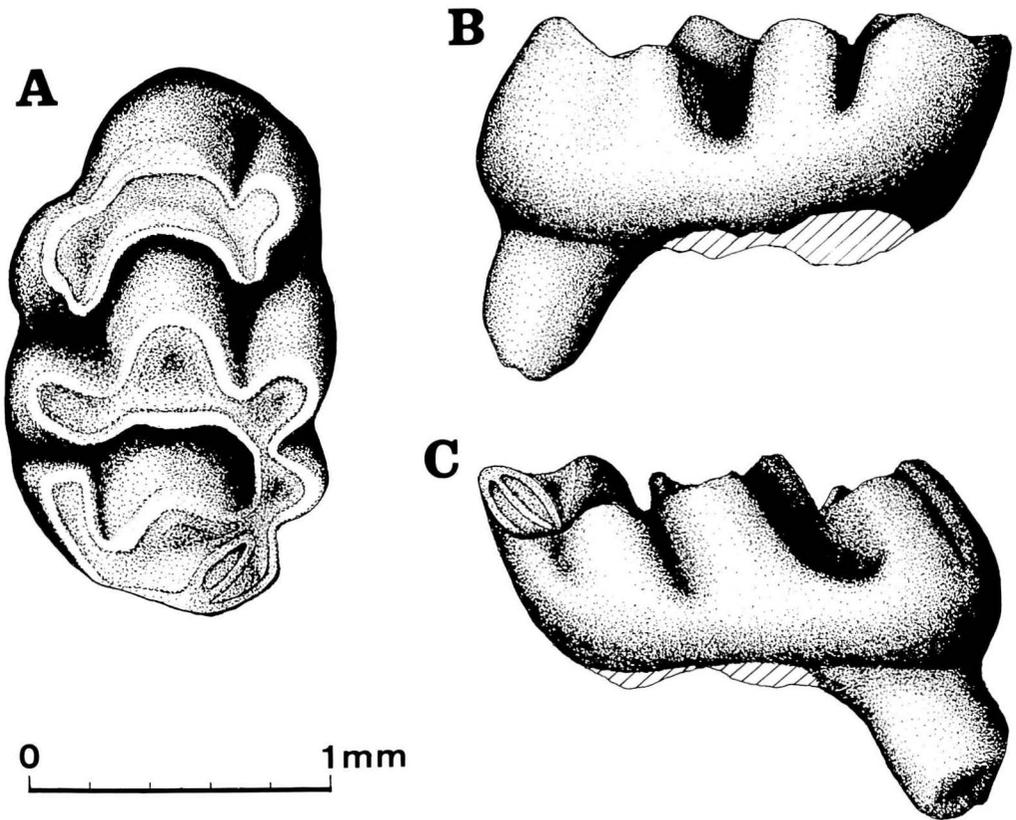


Figure 5. *Apodemus argenteus* (Temminck, 1844). Left M¹ from the Hiraen Clay Member (KUJC100718). A: occlusal view. B: lingual view. C: buccal view.

the metacone. The valley between the hypocone and posterior cingulum is distinct, but becomes a slender closed pit. The posterostyle is well developed and elongate antero-posteriorly.

A root below the lingual anterocone is preserved. It extends antero-superiorly. It is thick and has an antero-posteriorly elliptical cross section.

Measurement.—The specimen was measured by a profile projector (Nikon V-12) with an electric digital counter (Nikon CM-65). The measurements of the comparative living materials (Figure 6) were also obtained by the same instrument.

Length of crown (L).....1.77 mm

Width of crown (W).....1.08 mm

Comparison and discussion.—The present

specimen was compared with the actual molars of six living murid genera known from Japan (*Apodemus*, *Diplothrix*, *Micromys*, *Mus*, *Rattus* and *Tokudaia*), and with the descriptions and illustrations of the molars of 46 living murid genera (*Abditomys*, *Anonymomys*, *Archboldomys*, *Bandicota*, *Batomys*, *Berylmys*, *Bullimus*, *Bunomys*, *Carpomys*, *Celaenomys*, *Chiromyscus*, *Chirodomys*, *Chrotomys*, *Crateromys*, *Cremnomys*, *Crunomys*, *Dacnomys*, *Diomys*, *Echiothrix*, *Eropeplus*, *Golunda*, *Hadromys*, *Haeromys*, *Hapalomys*, *Kadarsanomys*, *Lenomys*, *Lenothrix*, *Leopoldamys*, *Limnomys*, *Margartamys*, *Maxomys*, *Melasmothrix*, *Millardia*, *Nesokia*, *Niviventer*, *Palawanomys*, *Paruromys*, *Phloeomys*, *Pithecheir*, *Rhynchomys*, *Srilankamys*, *Sun-*

damys, *Taeromys*, *Tateomys*, *Tryphomys*, *Vandeleuria*) given by Misonne (1969), Musser (1981, 1982a, b), and Musser and Newcomb (1983). Additional comparisons were carried out on the basis of the descriptions and illustrations of the molars of 15 fossil murid genera (*Antemus*, *Anthracomys*, *Castillomys*, *Chardinomys*, *Karnimata*, *Occitanomys*, *Orientalomys*, *Paraethomys*, *Parapelomys*, *Parapodemus*, *Progonomys*, *Rhagamys*, *Rhagapodemus*, *Stephanomys*, *Valerymys*) given by Schaub (1938), Michaux (1969), Bruijn and Meulen (1975), Weerd (1976), Jacobs (1978), and Jacobs and Li (1982).

As the result, it is strongly suggested that the morphological characters of the specimen are best coincident with those of *Apodemus*, to which the specimen is undoubtedly assigned.

The genus *Apodemus* comprises many living and fossil species. The following species are representatives of the genus:

A. mystacinus (Danford et Alston)
A. jeanteti Michaux
A. flavicollis (Melchior)
A. sylvaticus (Linnaeus)
A. dominans Kretzoi
A. microps Kratochvil et Rosicky
A. argenteus (Temminck)
A. speciosus (Temminck)
A. peninsulae (Thomas)
A. giliacus (Thomas)
A. draco (Barrett-Hamilton)
A. latronum Thomas
A. semotus Thomas
A. agrarius (Pallas)

Kawamura (1989) distinguished three morphotypes in the posterior chevrons of M¹ and M² of *Apodemus*. In the "speciosus type", the posterior cingulum is absent, or forms a weak projection of the hypocone. In the latter case, it is never connected to the metacone, but the hypocone is connected to the metacone by a strong ridge, which is separated from the posterior cingulum. In the

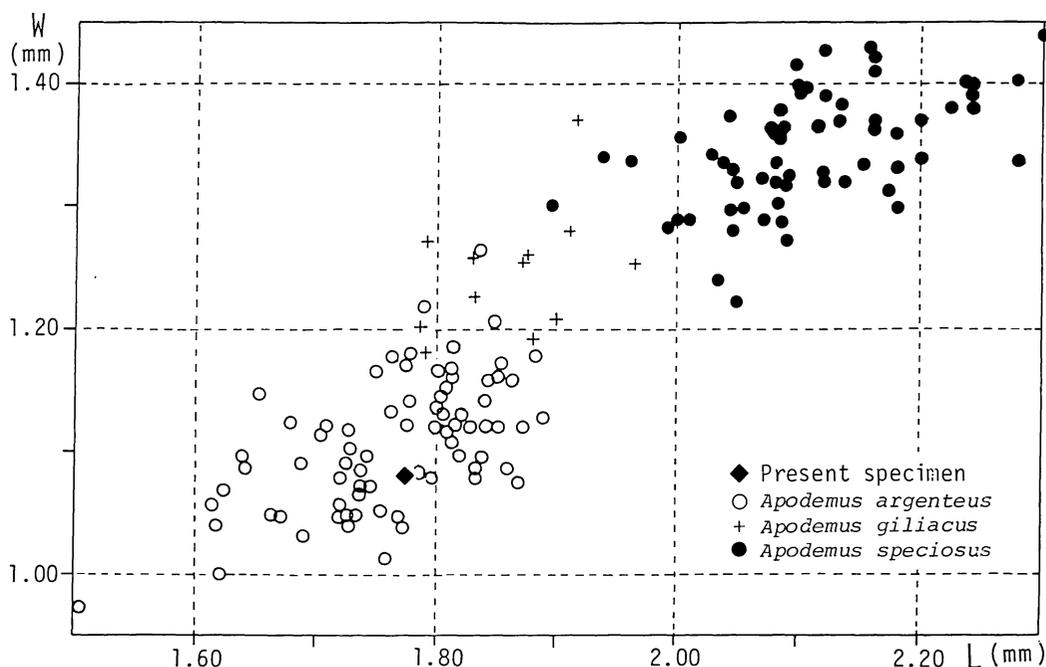


Figure 6. Scatter diagram showing the relationship between the length and width of crown for the present specimen and M¹ of the Japanese living *Apodemus*.

"*giliacus* type", the posterior cingulum is situated on the ridge between the metacone and hypocone. The "*argenteus* type" is characterized by a well-developed posterior cingulum which is connected to the hypocone and metacone, but separated from the ridge between the last two cusps.

Among the above-listed species, *A. mystacinus*, *A. jeanteti*, *A. flavicollis*, *A. sylvaticus*, *A. dominans*, *A. microps*, *A. speciosus*, *A. peninsulae*, *A. giliacus*, *A. semotus* and *A. agratius* are different from the present specimen in having M¹ with the posterior chevron of the *speciosus* or *giliacus* type. Moreover, M¹ of these species except *A. microps* are larger than the present specimen. Although available information on the dental morphology of *A. draco* and *A. latronum* is poor, M¹ of these two species seem to be larger than the specimen.

M¹ of the remaining species, *A. argenteus*, strongly resembles the specimen in outline and height of crown, arrangement and morphology of each cusp (especially the posterior chevron with the pattern of the *argenteus* type) and size. As shown in Figure 6, the length and width of the specimen plot in the center of the cluster of the living *A. argenteus*. Because no significant differences are found between the specimen and M¹ of *A. argenteus*, the specimen can be referred to *A. argenteus*.

Kawamura (1989) described many specimens of *A. argenteus* from middle Middle Pleistocene to Holocene localities in the Japanese Islands. These are very similar to the present specimen in the morphology of crown and size. He also pointed out that *A. argenteus* remained almost unchanged in these characters from the middle Middle Pleistocene to Holocene. The present specimen indicates that such an unchanged condition can be traced back to the early Middle Pleistocene. Therefore, it is inferred that *A. argenteus* originated from its ancestral species in or prior to the Early Pleistocene.

The Early Pleistocene fossil records of

Apodemus in China are very important for considering the ancestry of *A. argenteus*. Unfortunately, they are very few. *A. cf. sylvaticus* from Huaiyu (Teilhard, 1940) is the only comparable form. However, this form is considerably different from *A. argenteus* (Kawamura, 1989). Furthermore, as mentioned above, the Early Pleistocene and Pliocene fossil species from Europe such as *A. jeanteti* and *A. dominans* also differ from *A. argenteus*. Consequently, the ancestry of *A. argenteus* remains unknown. As pointed out by Kawamura (1989), this species seems to have evolved along an independent lineage from the other known species of *Apodemus*.

Conclusion

The murid molar found in the Hiraen Clay Member of the Kobiwako Group is undoubtedly referred to M¹ of *Apodemus*. The comparisons with many species of the genus show that the morphology and size of the molar are best compared with those of *A. argenteus*, an endemic species of the present Japanese Islands. Because the geological age of the molar is estimated to be 0.65 to 0.7 Ma, it is concluded that the biostratigraphic range of *A. argenteus* extends back to QM3, and this species already inhabited in the islands in the early Middle Pleistocene. The occurrence of the molar strongly supports the opinion of Kawamura (1989) that *A. argenteus* arose from its ancestral species in or prior to the Early Pleistocene.

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Hiraen 比良園, Huaiyu 灰峪, Kamiogi 上仰木, Katata 堅田, Kisen 喜撰, Kitahama 北浜, Kobiwako 古琵琶湖, Kurihara 栗原, Nijigaoka 虹ヶ丘, Otani 大谷, Ryuge 龍華, Sakawa 佐川, Sayama 狭山, Shiga-cho 志賀町, Shiga-gun 滋賀郡, Takashiro 高城, Yamashita 山下.

古琵琶湖層群から産出した中期更新世前期の齧歯目ネズミ科の臼歯化石: 古琵琶湖層群の比良園粘土層から産出した齧歯類の上顎第1大臼歯は、ネズミ科の化石としては日本列島最古のものである。この化石は、現在の日本列島の固有種であるヒメネズミ *Apodemus argenteus* に同定される。このことは、本種が中期更新世前期の 0.65-0.7 Ma までに種分化していたことを示している。さらに日本では、中期更新世前期に相当する哺乳動物化石帯の QM3 帯 (0.5 Ma から 0.73 Ma) の動物相の内容が現在ほとんど知られていないことから、今回の化石は日本列島の哺乳動物相の変遷史を考える上で重要である。

河村善也・飯田和明

**882. DENTICULOPSIS PRAEHYALINA, SP. NOV. :
AN EARLY MIDDLE MIOCENE PENNATE DIATOM FROM
DOGO, OKI ISLANDS, SOUTHWEST JAPAN***

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Abstract. A new pennate diatom, *Denticulopsis praehyalina*, from the early Middle Miocene diatomite of the Oki Islands is described. This species has many affinities to *Denticulopsis hyalina* but differs from it by having areolation on valve face. The new species combines morphological features of two *Denticulopsis* species, *D. hyalina* and *D. lauta*. A predominance or acme of *D. praehyalina* is restricted to the uppermost part of Middle Miocene *D. hyalina* Zone in the Northwest Pacific, and it is a good maker for the horizon.

Key words. *Denticulopsis*, diatom, Middle Miocene, Oki Islands.

Introduction

Early Middle Miocene diatomite collected from Dogo, Oki Islands contains a new *Denticulopsis* species which has morphological characteristics similar to those reported for *Denticulopsis hyalina* (Schrader) Simonsen (Schrader, 1973a; Simonsen, 1979).

Denticulopsis hyalina is characterized by the double-layered perforation of mantle and hyaline valve surface. The new species also has the same mantle structure. Distinct areolation, however, is found on valve face of the new species.

This paper will present a description of the new species, and its biostratigraphical and evolutionary implication.

Geological notes

The Neogene in Dogo, Oki Islands crops out around the basement complex, gneisses

and granitic rocks, exposed in the central part of the island. It is divided into the Tokibariyama, Kori, Kumi, Tsuma and Yui Formations in ascending order, with unconformities separating each of the formations (Tomita, 1936; Okubo, 1984; Yamazaki, 1984). The Tokibariyama and Kori Formations consist mostly of acidic to intermediate lava and pyroclastic rocks, but contain some intercalated conglomerate, sandstone and mudstone. The Kumi Formation, from the base upward, is composed of sandstone, shale and thick massive diatomite (Yamazaki, 1984). The formation ranges from a few meters to about 200 meters in thickness. The Tsuma Formation is mainly composed of sandstone and sandy mudstone. The Yui Formation is characterized by basic lava and pyroclastic rocks with some intercalated clastic rocks.

The massive diatomite of the Kumi Formation is early Middle Miocene in age on the basis of diatom-based correlations (Yokota, 1984; Okubo and Yokota, 1984).

All the samples for this study were collected from the diatomite bed of the Kumi

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Formation.

Outcrops and material

Thirty-six samples were collected for this study from three outcrops of the Kumi Formation (Figures 1, 2). The Iinoyama outcrop is a working diatomite mine located on the south side of Saigo-wan. This outcrop, from the base upward, contains dark gray stratified siliceous shale and yellowish white massive diatomite. The siliceous shale grades upward into diatomite which is unconformably overlain by a thick stratified carbonaceous sandstone of the Tsuma Formation. The thickness of the diatomite reaches more than 40 meters at the thickest part. The uppermost part of the diatomite is tuffaceous with large quantity of glauconitic minerals and sponge spicules. Fourteen samples were collected from the stratigraphic section of the mine at one to ten meters intervals.

At Minoura, the formation consists of dark

gray siliceous shale and yellowish white massive diatomite, as in the Iinoyama outcrop, but it contains some intercalated pale orange fine-grained sandstone in the lowermost part. The diatomite is estimated to be 26 meters thick. Nodules of opaline cristallite, 10 to 30 centimeters thick, is commonly found in the diatomite. Three layers of glauconitic minerals are also found in the upper part.

The Tsuma outcrop is composed of three small roadside cliffs. The formation contains dark gray siliceous shale and yellowish white massive diatomite about 13 meters thick. Twenty-two samples were collected from the Minoura and Tsuma outcrops at one to five meters stratigraphic intervals.

Methods

Twenty-five samples were selected for this study. A preparation of slide was done as follows; about one gram of dried sample was placed in a 200 ml beaker with a boiled solution of hydrogen peroxide (H_2O_2 , 15%) for disaggregation of rocks. After boiling for about 20 minutes, the beaker was filled with distilled water, and kept at room temperature for about 7 hours. Then fine material in

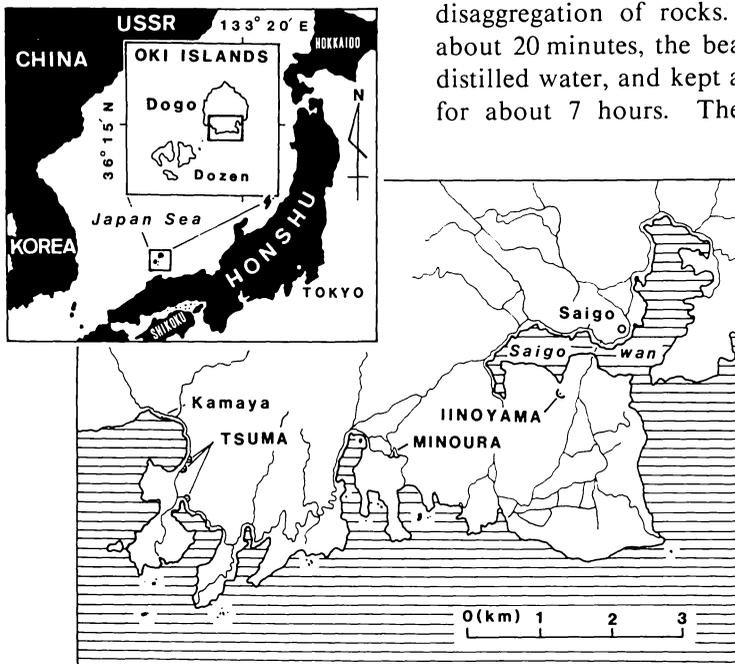


Figure 1. Location of outcrops.

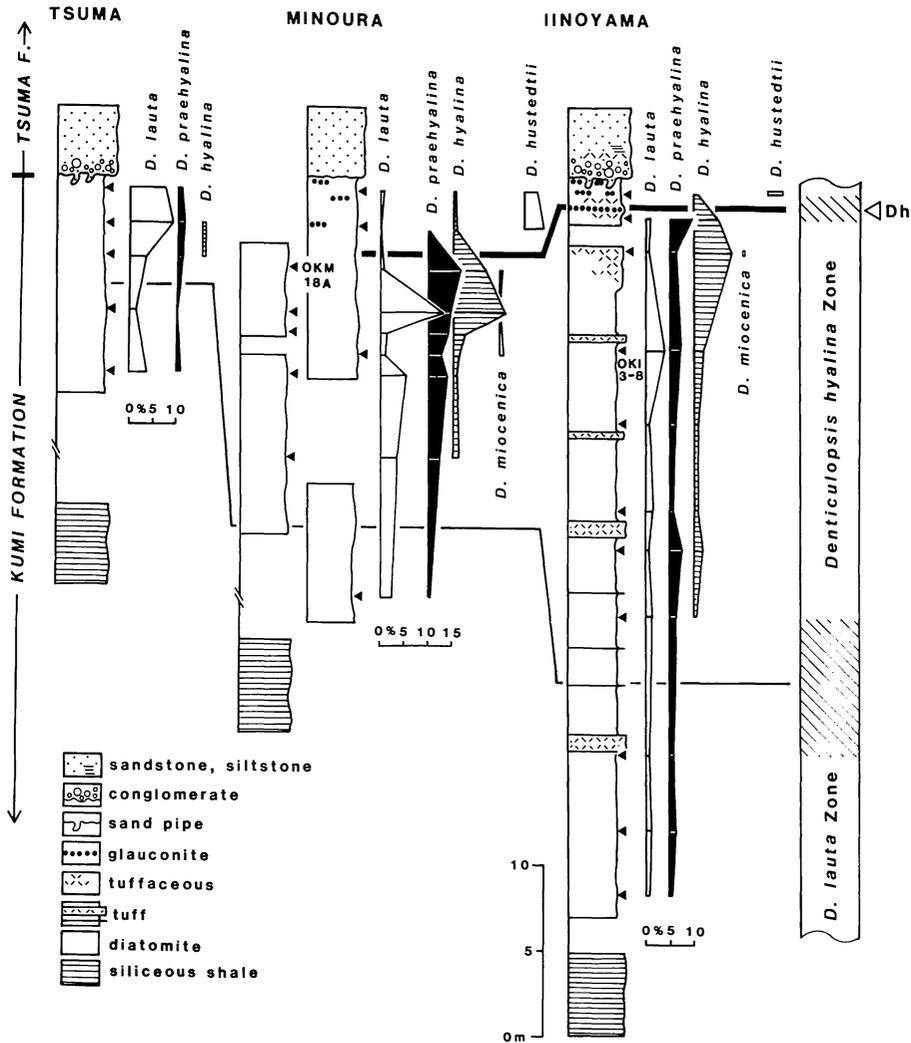


Figure 2. Stratigraphic occurrences of *Denticulopsis* species in the upper part of the Kumi Formation. Dh; first common occurrence of *Denticulopsis hustedtii*.

suspension was carefully removed by decantation, and the beaker was filled again with distilled water. This procedure was repeated at three times. A 0.1 to 0.5 ml of the final residue was diluted by distilled water to obtain a suspension of proper density. For slide preparation, 0.5 ml of the suspension was taken with an automatic micropipette with disposable plastic tips, and was placed on a square cover glass, 18×18 mm in size. After drying, it was mounted on slide glass with Pleurux.

Observation and identification of diatoms were made at ×1,250 magnification with direct transmitted light and Nomarskii differential interference contrast. For scanning electron microscopic observation, diatom valves were collected by filtration of the suspension within 0.8 μm milipore filter.

Relative abundance of each *Denticulopsis* species in a flora was estimated by counting over 200 valves while traversing a slide under a LM.

Observations

Denticulopsis praehyalina Tanimura, sp. nov.

Figures 3-1-9; 4-1-7

Synonym: *Denticulopsis lauta* (Bailey) Simonsen; Schrader, 1973a, pl. 2, figs. 21-22; Schrader, 1973b, pl. 1, fig. 20.

Description.— Valves heavily silicified, elliptical to linear-elliptical with bluntly rounded ends, 10–40 μm long, 5–9 μm wide. Valve face slightly convex or almost flat. Primary pseudosepta about 3 in 10 μm . Marginal ribs short and thick. Secondary pseudosepta absent, but one or two apical pseudosepta present at each apex of most specimens. Apical pseudosepta usually oblique to transapical axis. The punctae arrangement on valve face is fairly variable. Valve face sporadically or densely punctated, 12–24 punctae in 10 μm . Transapical striae of densely punctated specimens about 15–20 in 10 μm ; punctae more or less decussate arrangement. In some sporadically punctated specimens, only one or two lines of transapical striae found near each pseudosepta. In many sporadically punctated specimens, clusters of puncta are arranged in a line along the raphe-bearing valve margin. Under a LM observation, each cluster looks like a rounded triangle to hexagonal large pore, about 0.5–0.7 μm wide, 6–8 in 10 μm . Round large depression, about 1.5 μm in diameter, present in two apically arranged rows. Small spinule form a line along the both sides of valve face edges, about 10–13 in 10 μm . Raphe situated on the upper part of valve mantle. Mantle is high and perforated. The pore of mantle consists of an outer fine perforation, 32–38 in 10 μm , and an inner round to hexagonal large pore, 7–10 in 10

μm . Foramen of septum oval to elliptical, about 3 in 10 μm . Thickening between each two foramens 2–4 μm long, about 0.5–1.5 μm wide.

Holotype.— MPC (Micropaleontology collection, National Science Museum, Tokyo) slide 04231 (sample OKI 3-8), illustrated in Figures 3-2a, b.

Paratype.— MPC slide 04232 (sample OKM 18A), illustrated in Figures 3-3a, b.

Type locality.— Minoura outcrop, Dogo, Oki Islands, Shimane Prefecture.

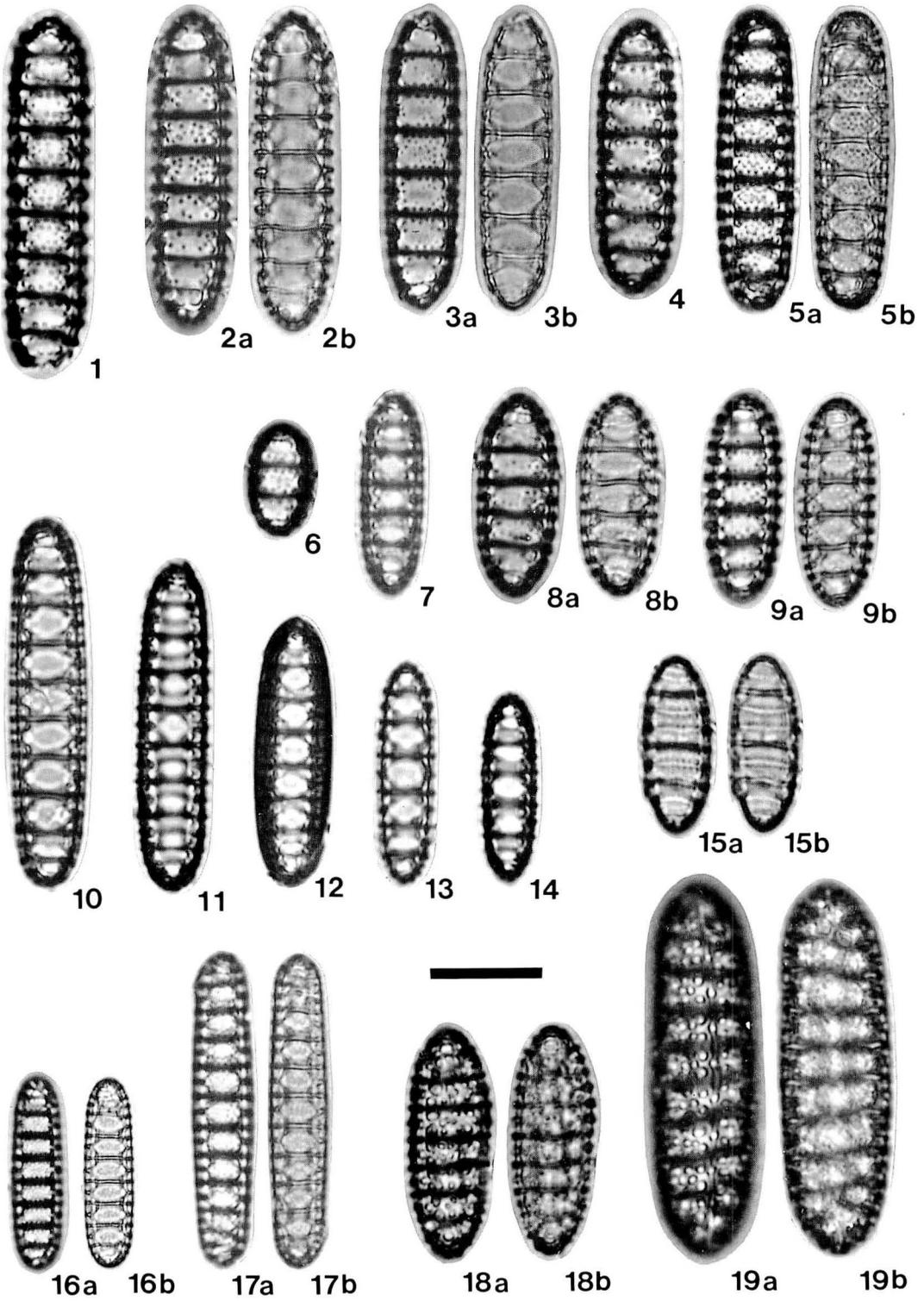
Stratigraphic range.— Rare to common in early Middle Miocene.

Remarks.— This new species is close to *Denticulopsis hyalina* and *D. miocenica* (Schrader) Simonsen (Schrader, 1973a; Simonsen, 1979). The most striking feature of the new species is the double-layered areolation of mantle (Figures 4-3, 4). This characteristic structure is also found in *D. hyalina* and *D. miocenica*. A definite difference between *D. hyalina* and this species is the absence of valve face punctae of the former. This species also differs from *D. miocenica* by the rhombic valve shape, well-developed broad septum deck and small round septum foramen of the latter.

Some densely punctated specimens (Figures 3-5; 4-4) of this species closely resemble *Denticulopsis lauta* (Bailey) Simonsen, (Simonsen et Kanaya, 1961; Simonsen, 1979) in valve view under a LM observation. In the specimens from the Kumi Formation, however, they can be distinguished from the latter by their broad valve shape and coarse punctae of valve face. In addition, the mantle structure is an easily discernible diagnostic structure under a SEM observation.

Three forms described and illustrated by Schrader (Schrader, 1973a, pl. 2, figs. 21–22; 1973b, pl. 1, fig. 20) as *Denticula lauta* are

→ **Figure 3. 1–9.** *Denticulopsis praehyalina*, n. sp.; 2–4, 6–9, Sporadically punctated specimen; 1, 5, Densely punctated specimen; 2a, 2b, Holotype; 3a, 3b, Paratype. 10–14, *Denticulopsis hyalina*, Kumi Formation. 15, *Denticulopsis hustedtii* (Simonsen et Kanaya) Simonsen, Kumi Formation. 16–17, *Denticulopsis lauta* (Bailey) Simonsen, Kumi Formation. 18, 19, *Denticulopsis miocenica* (Schrader) Simonsen, Kumi Formation. (Scale bar = 10 μm)



identical with the new species. These show the common features in heavily silicified valves, sporadically arranged puncta and the line of rounded triangle to hexagonal large pores on valve face.

Okuno (1964) described the two varieties of *Denticula* (= *Denticulopsis*) *lauta* from the diatomite of the Kumi Formation, Minoura outcrop; *D. lauta* var. *punctata* Okuno (Okuno, 1964, pl. 504, fig. b) and *D. lauta* var. *valida* (Pedicino) Okuno (Okuno, 1964, pl. 505, bottom figs.). Some sporadically punctated types of the new species (Figures 3-1; 4-1) are possibly identical with *D. lauta* var. *punctata*. Definite identification, however, are difficult. Because, the mantle structure, the most distinctive feature of the new species, is not shown in Okuno's description and illustration of the variety. In addition, the repository of type material is uncertain, so the re-examination of the type slides is impossible (Okuno, per. com., 1988).

The figured specimens of *D. lauta* var. *valida* (Okuno, 1964, pl. 505) consist of two different forms. Secondary pseudosepta are present in the top figures and absent in the bottom. The former is assignable to be *Denticulopsis hustedtii* (Simonsen et Kanaya) Simonsen (Simonsen and Kanaya, 1961; Simonsen, 1979) or its allied species, and the latter corresponds to his description (Okuno, 1965) about the variety.

Denticula elegans var. *valida* Pedicino which was described from the hot springs of Ischia Island, the Gulf of Napoli (Pedicino, 1867), was raised to the specific rank, *D. valida*, by Grunow (van Heurck, 1881). *Denticula valida* is recombined with *D. lauta* as its variety, *D. lauta* var. *valida*, by Okuno

(1964). *Denticula lauta* var. *valida* is not the same form as *D. elegans* var. *valida* or *D. valida*. The valve outline of *D. elegans* var. *valida* (Pedicino, 1867, pl. 1, figs. 42-45) and *D. valida* (van Heurck, 1881, pl. 49, fig. 5; Hustedt, 1928, pl. 3, figs. 6, 8) are more lanceolate with elongated apices, while the poles of *D. lauta* var. *valida* (Okuno, 1964, pl. 505, bottom left fig.; Okuno, 1965, pl. 2, fig. h) are broadly rounded and the valve sides are more or less linear. Therefore, it is highly probable that Okuno's recombination is not appropriate.

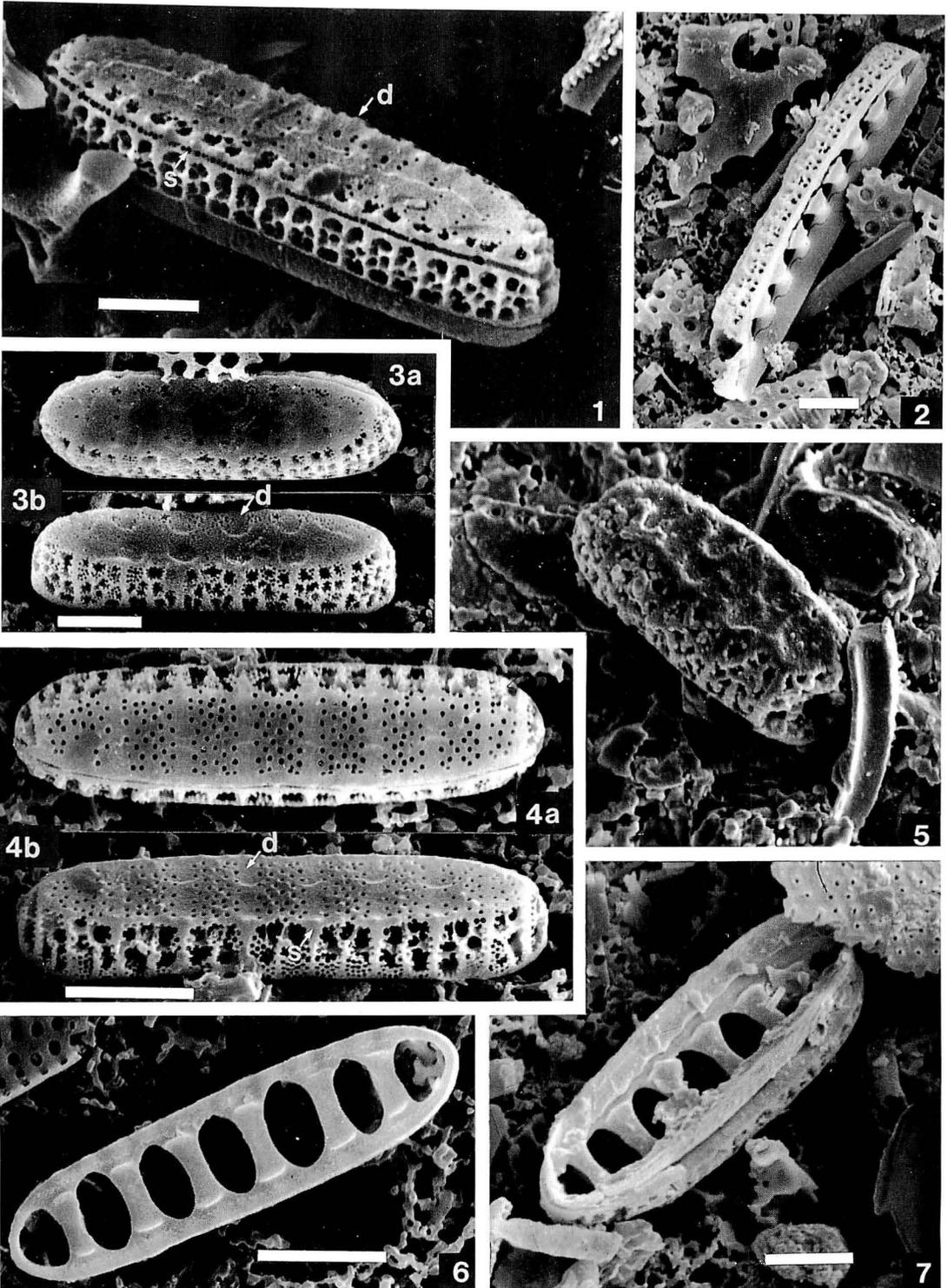
The bottom left figure of plate 505 (Okuno, 1964) resembles some morphological types (Figures 3-5; 4-4) of the new species. These show the common features in heavily silicified valves and densely arranged puncta, so the specimen (Okuno, 1964, pl. 505, bottom left fig.; not Okuno, 1964, pl. 505, reconstruction diagram and Okuno, 1965, pl. 2, figs. f, g) probably is a densely punctated type of the new species.

Stratigraphic distribution

Figure 2 shows the stratigraphic distribution of *Denticulopsis* species in the three outcrops investigated. At the Iinoyama and Minoura outcrops, *D. praehyalina* is sparse in the lower part of the diatomite sections. The species occupies 0.5 to 2.5% of the flora. An increase in abundance appears in the upper or uppermost part of the sections. Here, *D. praehyalina* accounts for more than 3% (up to 7%) of the flora. Abundant to common specimens of *D. lauta* are also found at and around the same horizons.

Denticulopsis hyalina is present in the

→ **Figure 4. 1-7.** *Denticulopsis praehyalina*, n. sp. **1**, Sporadically punctated specimen, oblique exterior view of valve; Arrows with letter symbols d and s indicate large depression and small spinule, respectively; Outer fine perforation of mantle is dissolved; **2**, Oblique girdle view of broken valve; **3**, Sporadically punctated specimen; **a**) Valve exterior, note clusters of punctae along valve margin; **b**) Oblique girdle view showing double-layered perforation of mantle; **4**, Densely punctated specimen, **a**) Valve exterior, **b**) Oblique girdle view showing double-layered perforation of mantle; Arrows with letter symbols d and s indicate large depression and small spinule, respectively; **5**, Sporadically punctated specimen, oblique view of valve exterior; Valve is thickened by silica overgrowth; **6**, Sporadically punctated specimen, valve interior, note apical pseudosepta; **7**, Oblique internal view of valve. (Scale bar = 5 μ m)



middle to upper part of the diatomite sections. In the middle part it comprises 0.5–2.5% of the flora, and increases upward. In the uppermost part of the sections, there is a sudden drop in abundance of *D. hyalina*, and it is followed by the first common occurrence of *D. hustedtii* (open triangle with letter symbol *Dh*). The characteristic distributions of these species are not found in the section of the Tsuma outcrop, for the reason that the diatomite section of the Tsuma outcrop represents only the lower to middle part of the whole diatomite bed of the Kumi Formation.

These biostratigraphical data show that the occurrence of *D. praehyalina* ranges from the upper part of the *D. lauta* Zone (Koizumi, 1973) to the horizon just above the *D. hyalina* Zone (Maruyama, 1984).

The stratigraphic occurrence of *D. hyalina* and *D. hustedtii* have been documented in several localities of Japanese Islands and adjacent seas, for example Matsushima, Northeast Honshu (Akiba *et al.*, 1982), Pacific side sections of Honshu (Maruyama, 1984) and DSDP Hole 438A (Maruyama, 1984). In these localities the predominance or acme of *D. hyalina* is reported to be in the uppermost part of the *D. hyalina* Zone, and to be just below the first common occurrence of *D. hustedtii*. The absolute age of the horizon of this predominance or acme was estimated to be 15–14 Ma on the basis of radioisotopic dating- and paleomagnetic stratigraphy-based correlations (Koizumi, 1985). An abundant occurrence of *D. praehyalina* at and around the same horizon is also a good marker of the horizon.

Notes on evolutionary trends

In as much as *Denticulopsis praehyalina*, *D. hyalina* and *D. miocenica* share a double-layered perforation of mantle, the most characteristic morphological feature of these species, it may be inferred that these three species are on the same evolutionary line. The fact that intermediate forms occur fairly

commonly among these three species supports this inference.

The stratigraphic occurrence of *Denticulopsis* species have been well documented in many localities of North Pacific (Simonsen and Kanaya, 1961; Schrader, 1973a, b; Barron, 1980; Koizumi, 1985; Akiba and Yanagisawa, 1986). In these works, it has been generally accepted that *D. hyalina* evolves from *D. lauta*. Two abrupt morphological changes, however, were involved in the evolution; a formation of double-layered perforation of valve mantle and complete reduction of areolae on valve face. By the introduction of *D. praehyalina*, the gradual evolution from *D. lauta* to *D. hyalina* can be understood easily.

Denticulopsis praehyalina occurs in the lowermost part of diatomite bed of the Kumi Formation. The species probably evolves from *D. lauta* or its variety. *Denticulopsis hyalina* is a descendant of the species. This group shows tendency to create hyaline surface structure. This evolutionary line seems to go on into *Denticulopsis katayamae* Maruyama (Maruyama, 1984) which possesses secondary pseudosepta, shallower valve mantle and valve face edge punctae. The double-layered mantle pore are also found in *D. katayamae* valve by SEM observation (Akiba and Yanagisawa, 1985, p. 489, pl. 20, figs. 4, 5, 7).

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I am grateful to Drs. Itaru Koizumi of Hokkaido University, John A. Barron of the U.S. Geological Survey (Menlo Park), Fumio Akiba of Japan Petroleum Exploration Company and Kazuhiko Uemura of National Science Museum for kindly reviewing the manuscript and for many valuable suggestions. I also thank Drs. Haruo Okuno of Professor Emeritus of Kyoto Institute of Technology, Yasuji Saito of National Science Museum, Yukio Yanagisawa of Geological Survey of Japan and Toshiaki Maruyama of

Tohoku University for their helpful advice.

Four samples marked Mu were collected by Dr. Yasuji Saito and Mr. Takashi Mitsuoka of the same Museum.

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Iinoyama 飯山, Kamaya 釜谷, Kori 郡, Kumi 久見, Minoura 箕浦, Saigo 西郷, Tokibariyama 時張山, Tsuma 都万, Yui 油井.

Denticulopsis praehyalina, 隠岐島後産中期中新世初期羽状目珪藻の一新種: 隠岐諸島, 島後に発達する中期中新世海成珪藻土より産する一新種 *Denticulopsis praehyalina* を記載・報告する。同種は *Denticulopsis hyalina* と形態上多くの共通点を有する。しかし、殻面に点紋を有することで明確に区別される。*D. praehyalina* は *D. lauta* と *D. hyalina* の形態上の特徴をあわせもち、進化上両種の間中に位置づけられるものと考えられる。また同新種は、中期中新世の珪藻化石帯 *D. hyalina* Zone の最上部で多産し、この層準を識別するよい示準となる。谷村好洋

883. CENOMANIAN (CRETACEOUS) INOCERAMIDS (BIVALVIA) FROM HOKKAIDO AND SAKHALIN — I

Birostrina nipponica (Nagao et Matsumoto)*

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Abstract. In this paper *Birostrina nipponica* (Nagao et Matsumoto, 1939) is redefined and fully described. It is markedly inequivalve, with very small or scarcely discernible posterior wing; left valve is very convex, with much incurved umbo; ornament is fine and weak. This species is very variable and includes at least three forms, viz. (α) slender form with a strongly projected left umbo, (β) form with subrounded main part of valve which shows a uniform convexity and (γ) narrowly convex form with a summit along the growth-axis. The three forms seem to intergrade. None of them is identical to any of the variable forms of Albian *B. concentrica* (Parkinson) nor to Middle Cenomanian *B. tamurai* which has a posterior radial groove and develops irregular ribs in late growth-stage.

Some of the specimens hitherto called *Inoceramus concentricus* var. *nipponicus* are transferred to certain other species. For instance, those from the Zone of *Mantelliceras japonicum* (Lower Cenomanian) should be mostly referred to *I. tenuis* Mantell; a few are to be referred to a Turonian species allied to *I. inaequalis* Schlüter. *B. nipponica* in a revised sense occurs so far from the high Middle to low Upper Cenomanian of Hokkaido and Sakhalin. A form represented by several specimens is allied to but different from this species and described tentatively under *B. aff. nipponica*.

Key words. *Birostrina*, *Inoceramus*, Albian, Cenomanian, Hokkaido, Sakhalin.

Introduction

Twelve species of the Inoceramidae which occur in the Cenomanian of Japan have been recently described in five successive papers (I to V) (Matsumoto and Noda, 1986; Matsumoto *et al.*, 1987, 1988; Matsumoto and Tanaka, 1988; Matsumoto, 1989).

There are still more specimens to be described and illustrated. As the major title shows, we now include the older collections

from South Sakhalin (mainly the Naibuchi and northeasterly adjacent Aikawa areas) in addition to those from selected areas of Hokkaido. The results are to be published in a series of numbered papers, which may be written by a variety of different authors.

In this paper (Part I) we give a revised description of *Birostrina nipponica* (Nagao et Matsumoto, 1939), and clarify both its taxonomic status and geological age. The material for the restudy of *B. nipponica* consists primarily of the specimens obtained by one of us (Matsumoto, 1942-43), sometimes with a

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coworker (Matsumoto and Okada, 1973), and those recently acquired by the other (A.A.) through field works in the Ashibetsu and Obirashibe (simply called Obira) areas. The syntypes of Nagao and Matsumoto (1939) and hypotypes of Ikegami and Omori (1957), with prefix OM, have been examined, so far as they are accessible.

The repositories of the described and/or discussed specimens are as follows, with abbreviations in parentheses:

- British Museum (Natural History), London (BM)
- Geological Collections, Kyushu University (GK)
- Collections of Geology and Mineralogy, Hokkaido University, Sapporo (GMH)
- Institute of Geology and Palaeontology, Tohoku University, Sendai (IGPS)
- School of Education, Waseda University, Tokyo (WE)
- Sedgwick Museum, University of Cambridge (SM)
- University Museum, University of Tokyo (UMUT)

As to the technical terms and their abbreviations, we follow those defined and used in the aforementioned five papers, especially Matsumoto and Noda (1986, p. 410–411) and Matsumoto *et al.* (1987, p. 147). In addition to them we propose to measure the length of the curved line along the axis of growth, which is abbreviated to G. In a highly convex valve, with a much incurved umbo, the ratio G/H is a useful parameter. A curvimeter is used for the measurement of G.

For the locality records and stratigraphy readers may refer to Matsumoto (1942–1943), Ikegami and Omori (1957), Matsumoto and Okada (1973) and Sekine *et al.* (1985). Asai is preparing a paper on the Upper Cretaceous stratigraphy of the Ashibetsu area.

Palaeontological description

Family Inoceramidae Zittel, 1881
Genus *Birostrina* J. Sowerby, 1821

Birostrina nipponica
(Nagao et Matsumoto, 1939)

Figures 1–28, 32

- 1939. *Inoceramus concentricus* Parkinson var. *nipponicus* Nagao et Matsumoto, p. 267, pl. 25 (3) figs. 1, 3, 6 (*non* pl. 24 (2), fig. 2; pl. 25 (3), figs. 2, 4, 5).
- 1957. *Inoceramus concentricus* var. *nipponicus* Nagao et Matsumoto; Ikegami and Omori, pl. 5, fig. 1; pl. 6, figs. 1, 2.
- 1966. *Inoceramus nipponicus* (Nagao et Matsumoto); Pergament, p. 32, pl. 2, figs. 1–4.
- 1976. *Inoceramus concentricus nipponicus* Nagao et Matsumoto; Noda and Matsumoto, pl. Cr-31, fig. 1 (*non* fig. 2).

Lectotype.—IGPS specimen (BV) figured by Nagao and Matsumoto (1939, pl. 25, fig. 1), from the Ugui-zawa (sometimes called Ugoi-zawa), a tributary to the River Naibuchi (=Naibuti or Naibu), South Sakhalin, designated by Pergament (1966, p. 32).

Material.—Fairly well preserved specimens in our collections, *i.e.* (1) GK. H440 (BV, comp. int. m. with inner shell layer partly preserved and outer shell layer on the umbonal part of LV) (Figure 1) collected by T.M. from loc. Y216p, in the Shiyubari area, northeast of Oyubari; (2–6) GK. H8262 (BV) (Figure 2), H8263 (BV) (Figure 3), H8264 (Figure 4), H8265 (LV) and H8266 (juvenile LV) (Figure 5) comp. int. m. with altered inner shell layer partly preserved, and also ext. m. of LV of H8262, all in one and the same nodule collected by H. Okada and T.M. with assistance of T. Nishida, from loc. R101, about 900 m west of Kiritachi Pass on Highway 239 between Soueushinai and Kotanbetsu.

(7–33) Numerous specimens from one and the same nodule collected by T.M. from loc. N67–68p of the Birin-zawa, a branch of the

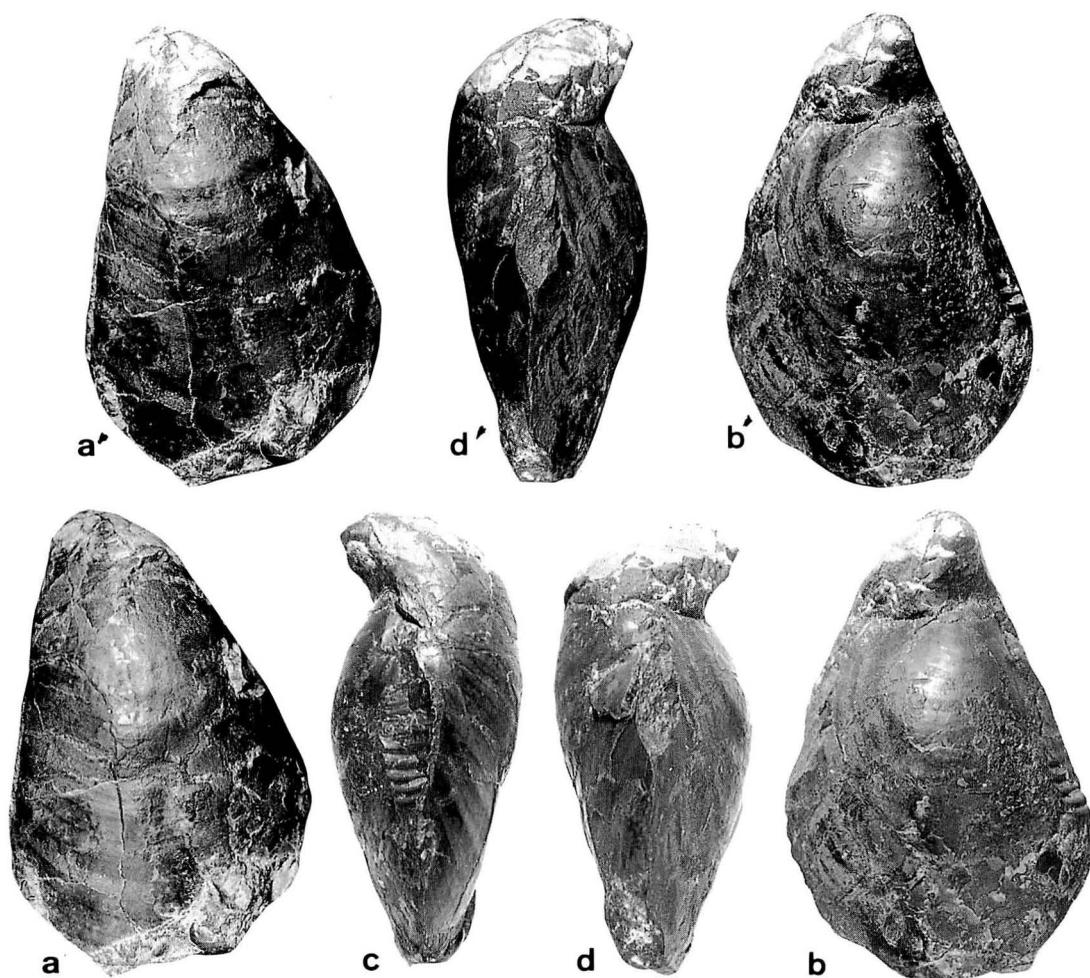


Figure 1. *Birostrina nipponica* (Nagao et Matsumoto). GK. H440 (BV) (form α) from loc. Y216p, Shiyubari area (T. M. Coll.). Left (a) and right (b) lateral, anterior (c) and posterior (d) views, $\times 1$. Duplicate figures (a' b' d') in dissimilar lights are complementary to show minor details of the ornamentation. The very apex of the beak in LV is destroyed. A tiny juvenile crops out from the rock matrix on the ventral margin of LV. Photos (Figures 1–20) by M. Noda and S. Toshimitsu.

River Naibuchi, derived from the sandy siltstone of the fossiliferous uppermost part of the Kawakita Group (marked as Mh-Kz), of which the numbered specimens are GK. H244A (LV) and B (RV); GK. H245A, B (both LV) (Figures 7, 8), C (LV) (Figure 6) and D (LV); GK. H246A (Figure 9), B, C, D, and E (all LV); GK. H247A and B (both BV) (Figures 14–16), C (RV) and D (LV) (Figure 17), E and F (both RV) (Figures 18,

19); GK. H248A (LV) (Figure 20), B (LV), C (RV), D-G (LV) and H (BV); GK. H249A (RV) (Figure 13), B (LV) and C (RV); GK. H250A (LV) (Figure 10), B (RV) (Figure 11), C (RV) (Figure 12) and D (LV); GK. H251A (BV). These are mostly composite internal moulds, with inner shell layer partly attached. There is an external mould (B') for H250B.

In the WE Collections the following speci-

mens are selected: (34–36) WE. P025A (LV and displaced RV with incomplete umbonal part) (Figure 21), WE P026A (LV) (Figure 22) and WE. P027A (BV) (Figure 23) — these three internal moulds, with a prominent altered, dark green inner shell layer are from loc. As 1065, the Poroko-ashibetsu, a tributary to the upper reaches of the River Ashibetsu, central Hokkaido (A. Asai Coll.); (37–39) WE. P028T (LV) (Figure 24), WE P030T (LV) (Figure 25) and WE. P031T (RV) (Figure 26) — these three composite internal moulds, with inner shell layers adhered to some portions, are from loc. T6082a86, Member Mh on the River Obirashibe, north-western Hokkaido (A. Asai Coll.); (40–41) WE. P041A (LV) (Figure 27) and WE P042A (LV) (Figure 28), both comp. int. m., with an altered, dark green inner shell layer adhered to a considerable area, from a drifted boulder on the Tsukimi-zawa, a western tributary to the River Ashibetsu, central Hokkaido (A. Asai Coll.).

(42) GMH. 7167 (LV) (Nagao and Matsumoto, 1939, pl. 25, fig. 6), from Hakkin-zawa, Oyubari area; (43) GMH. 7163 (LV) (*Ditto*, pl. 25, fig. 3), from the Naibuchi area, South Sakhalin (now missing); (44–46) OM. II-476 (BV) (Ikegami and Omori, 1957, pl. 5, fig. 1), comp. int. m., covered with inner shell layer for the major part, from loc. IK B-6 (Coll. Yoshimi Yamaguchi), OM. II-478 (LV) (*Ditto*, pl. 6, fig. 1), comp. int. m. with inner shell layer partly adhered, from loc. IK B-5 (Coll. Satosi Ikuno) and OM. II-479 (BV) (*Ditto*, pl. 6, fig. 2) comp. int. m. from loc. IK R-19 (Coll. T. Omori) (read anterior view for posterior view in their explanation of pl. 6), the above three from the lower part of Member Iic (=Mk2 of Ikegami and Omori), Mikasa Formation of the Ikushumbets Valley, central Hokkaido. They were obtained during the construction of the water way tunnel from the Katsura-zawa dam to the electric power station.

Diagnosis.— Shell small, highly inequivalve. Left valve very convex and much

elongated along the axis of growth; its umbonal part prominent, exceeding greatly the hinge line, and curving markedly inward to somewhat prosocline beak. Right valve less convex than the left, with simple prosocline beak.

Outline of shell inequilateral and considerably variable. The umbonal part of left valve more or less narrow; the main disk oblong to suboval or rather subround, with the axis of growth nearly straight or gently concave forward. Hinge line short; anterior margin nearly straight and somewhat concave below the umbonal part; ventral margin more or less narrowly rounded and somewhat asymmetric, passing to a long, arcuate posterior margin. Posterior wing very narrow or scarcely discernible.

Surface of shell typically nearly smooth, only with fine concentric lirae at juvenile stage which develop to concentric rings later; in addition to them, concentric subcostae and/or major concentric undulations or weak ribs may sometimes occur, with or without somewhat deeper interspaces, at middle to late growth-stages.

Dimensions.— See Table 1.

Observation.— This species is so variable that at least three forms are distinguished as follows:

(α) — The slender, oval form, represented by GMH. 7167 (one of the syntypes of Nagao and Matsumoto, 1939, pl. 25, fig. 6) and GK. H440 (Figure 1) from the Oyubari-Shiyubari area, OM. II-476 (Ikegami and Omori, 1957, pl. 5, fig. 1) (Figure 32 in this paper) from the Ikushumbets area, WE. P041A (Figure 27) and WE. P042A (Figure 28) from the Ashibetsu area. The left valve is slender and greatly elongated along the growth-axis. Its narrow umbilical part broadens gradually to the suboval main part of the disk. The outline of the right valve is subtrapezoid-oblong. The shell is ornamented with fine concentric lirae on the surface or rings on some parts and later faint concentric undulation may appear, with subcostae on

Table 1. Measurements of *Birostrina nipponica* on selected specimens.

Specimens	V	form	H	L	L/H	G	G/H	G/L	b	b/H	s	s/L	α	γ	δ
Lectotype	LV	$\alpha(\beta)$	~50	~34	.68	~70	1.40	2.06	~17	.34					
GK. H440	LV	α	64.0	41.2	.64	~92	1.44	2.23	20.5	.32			$\beta=58^\circ$		
"	RV	α	54.4	41.2	.76	~62	1.14	1.50	~12	.22	16.0	.39	100°	115°	65-70°
WE. P041A	LV	α	56.6	36.1	.64	~90	1.59	2.49	~21	.37			$\beta\sim 60^\circ$		
GK. H8262	LV	β	33.8	23.8	.70	~53	1.57	2.23	13.3	.39					
"	RV	β	29.3	23.8	.81	~34	1.16	1.43	7.8	.27	10.2	.43	105°		65-75°
GK. H8263	LV	β	32.8	24.0	.73	~52	1.58	2.17	12.5	.38			$\beta\sim 63^\circ$		
"	RV	β	27.5	23.7	.86	~33	1.20	1.39	8.6	.31	10.6	.45	105°	~100°	63°
WE. P026A	LV	$\beta(\alpha)$	30.2	21.2	.70	~42	1.39	1.98	11.5	.38					
WE. P028T	LV	$\beta(\alpha)$	41.8	~28	.67	~64	1.53	2.29	15.8	.38					
GK. H247B	LV	γ	37.0	20.0	.54	~55	1.49	2.75	16.3	.44					
" A	RV	γ	29.7	16.6	.56	~37	1.25	2.23	9.3	.31	~7.8	.47	~90°	127°	68°
WE. P025A	LV	γ	33.0	~17	.52	~52	1.58	3.06	15.0	.45					
WE. P030T	LV	γ	34.0	18.4	.54	~60	1.76	3.26	17.0	.50					

some of their summits.

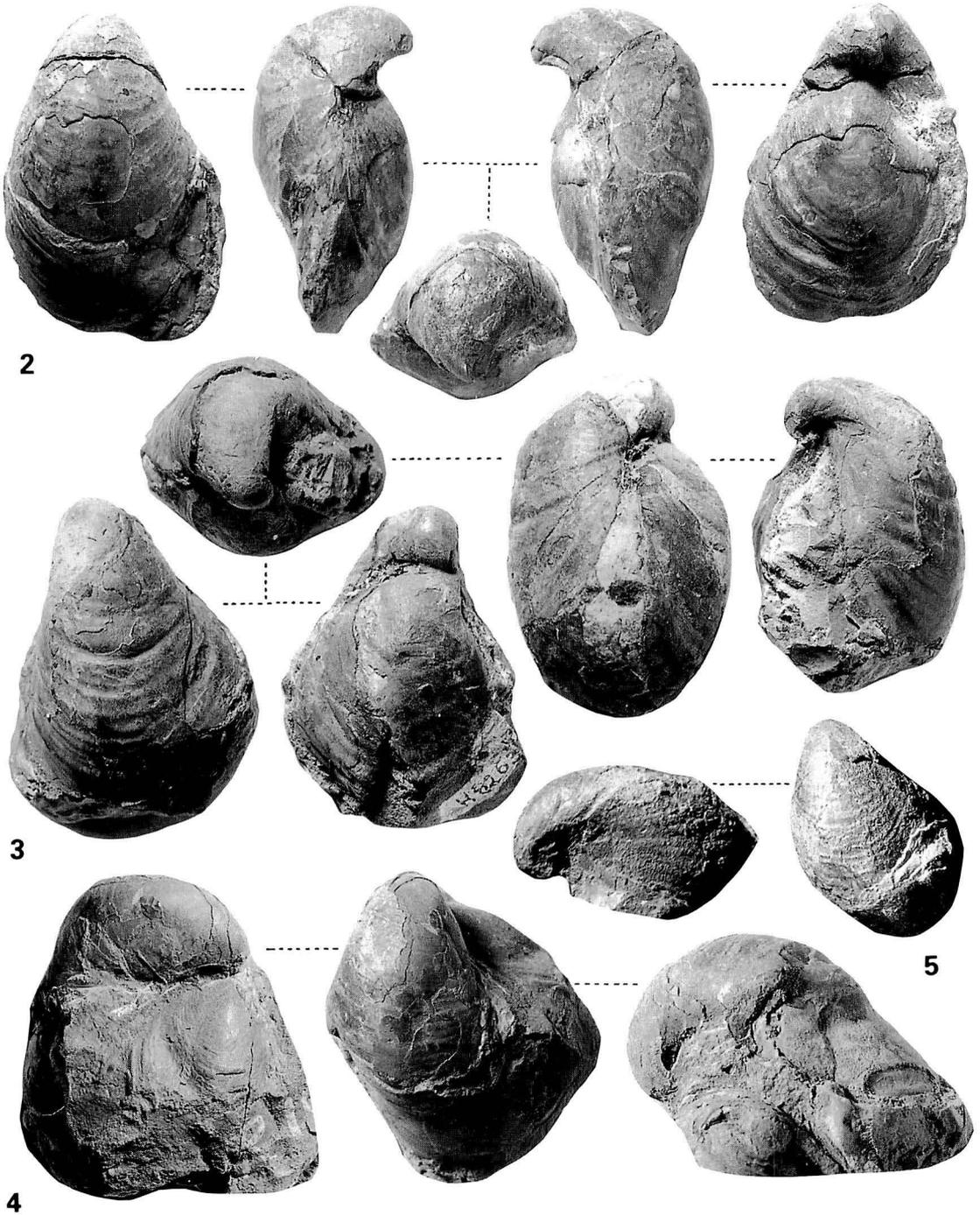
The lectotype is referable to this α form, with respect to its nearly smooth shell with faint undulations at late stage; however its shell form is not so slender as WE. P041A, being intermediate between α and β forms. As it had no register number, it is not traced with certainty at IGPS, but we cannot state that it is lost. It may be deposited in the old building of the IGPS at Katahira-cho. Pergament designated it as the lectotype without inspecting the actual specimen.

(β) — The tumid, suboval form, represented by GK. H8262 (Figure 2) and GK. H8263 (Figure 3) from loc. R101, Kotanbetsu route. This is smaller, less high and broader, with larger L/H, and more inflated than the form α ; however G/H or G/L is not very different between the two forms. It shows rather uniform convexity on the main part of the valve. The umbonal part of its left valve is not so narrow as that of the form α and gradually

broadens to the main part. The ventral margin is well rounded, though somewhat asymmetrical. The fine concentric lirae on the shell or fine rings on the composite internal mould are as characteristic as those in the form α . They may be better shown on the otherwise smooth young part (see Figure 5). Concentric subcostae or narrow ribs develop at the middle to late stages. Some of them are accompanied by constriction-like deeper interspaces.

WE. P026A (Figure 22), from the Porokoashibets, and WE. P028T (Figure 24), from the Obirashibe, are referable to form β with respect to the shell-form, but their subcostae are weaker and the constriction is almost undeveloped as in the form α . Incidentally, the very apex of the beak is missing in these two specimens. S. Toshimitsu (personal communication) has suggested that the incurved apical portion of the beak must have been in a hollow state, while the main part of the

→ **Figures 2–5.** *Birostrina nipponica* (Nagao et Matsumoto). Four specimens, representing the form β , all from loc. R101 on Highway 239 (Kotanbetsu-Soeushinai) (Coll. T. M. and H. Okada, assisted by T. Nishida). **2:** GK. H8262; **3:** GK. H8263; **4:** GK. H8264; **5:** GK. H8266 (juvenile). Different views of the same specimen are connected by dotted lines. The views (left lateral, right lateral, anterior, posterior and dorsal) are self-explanatory and not repeated. The same way of illustration is kept also for Figures 6–32. Magnification for **2–4:** $\times 1.5$, **5:** $\times 2$.



valve was filled with mud. In one example (WE. P026A) there is a trace of later calcification in the hollowed apical portion.

(γ)—The oblong form, with highly convex left valve, is represented by GK H247A, B (Figures 14–16) and many others (Figures 6–10) in the population of the Birin-zawa, Naibuchi area. WE. P025A (Figure 21), which came from the same locality as the aforementioned, WE. P026A, is also an example of the form γ .

This form is small, being less than 35 mm in H of LV. Its left valve is highly convex not only from the beak to the ventral margin but also from the anterior margin to the posterior, forming a summit along the major part of the growth-axis, which itself is nearly straight. Thus, the left valve is narrow, erect, highly convex and very oblong. The right valve is also erect, less convex and more or less oblong (elongate-subelliptical), showing an asymmetric curvature of the ventral to posterior margin. The surface of the shell is mainly smooth, with only fine concentric lirae and rings. At more or less late growth-stages, a few narrow ribs or subcostae appear on both valves, normally with associated deep interspaces or narrow constrictions.

Smaller examples, e.g. GK. H245C (Figure 6) and WE. P027A (Figure 23), which do not show the distinct ribs or constrictions, as mentioned above are probably juveniles of this form. GK. H245A (Figures 7, 8), GK. H246A (Figure 9) and GK. H250A (Figure 10), which are slightly larger than the above two show a constriction with or without associated riblet at or near the preserved ventral margin. WE. P030T (Figure 25) (internal mould of LV) is certainly assigned to the form γ in view of its diagnostic shell-

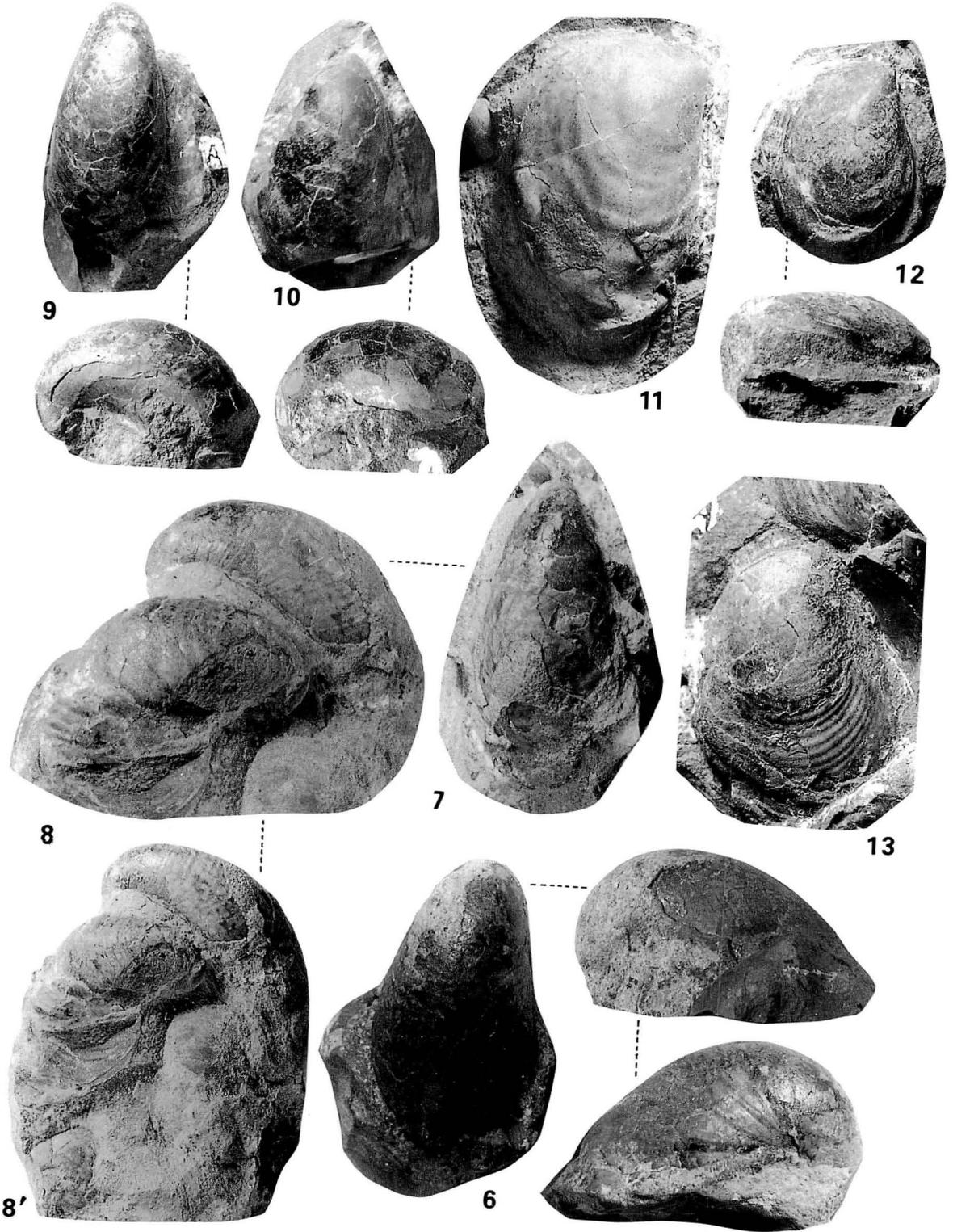
form, but its ornament is very weak as compared with GK. H247A and B of nearly equal size. It shows faint concentric undulations and weak, partial subcostae, like those of the form α . It should be noted further that this specimen was obtained at the same locality as WE. P031T (RV of rather α type) (Figure 26) and WE. P028T (LV of rather β type) (Figure 24) mentioned above.

On the other hand, GK. H248A (Figure 20) and GK. H247C and D (Figure 17) and probably H247E and F (Figures 18, 19) are intermediated between the forms β and γ . Incidentally GK. H247A, B and some others from the same locality show a particular posture of embedding (see Figures 14, 15), which may be taphonomically explained (S. Toshimitsu, pers. comm.).

To sum up, the three forms, which we designate α , β and γ for convenience, do not deserve to be ranked as subspecies, because they occur sometimes in the same place or in the same fossiliferous zone and because we see occasionally intermediate or transitional forms and also forms with mixed characters.

Comparison and discussion.—*Inoceramus concentricus* Parkinson var. *nipponicus* Nagao et Matsumoto, 1939 (p. 267) was evidently a mixture of several species. *Birostrina nipponica* (Nagao et Matsumoto) in a revised definition is described above and some of the syntypes described and illustrated 40 years ago should be excluded from this species. For example, GMH. 5965 and GMH. 5971, figured by Nagao and Matsumoto (1939, pl. 25, figs. 2, 5), were collected by the late Dr. Kenichiro Otatume from Nutapomanai of Kami-hobetsu in the upper reaches of the River Hobetsu. By courtesy of Professor T. Kato, one of us (T.M.) had an

→ **Figures 6–13.** *Birostrina nipponica* (Nagao et Matsumoto). All the specimens from a large nodule at loc. N67-68p, Birin-zawa, a branch of the River Naibuchi, derived from the fossiliferous Zone Mh-Kz, South Sakhalin (T.M. Coll.), mostly representing the form γ unless otherwise stated. All $\times 1.5$, except 6: $\times 2$ and 8: $\times 1$. 6: GK. H245C (LV); 7: GK. H245A (LV); 8: GK. H245A (above) and GK. H245B (LV) (below); 8': same as 8 with some other incompletely exposed specimens; 9: GK. H246A (LV); 10: GK. H250A (LV); 11: GK. H250B (RV); 12: GK. H250C (RV); 13: GK. H249 (RV), one of the abundantly assembled specimens.



opportunity to read Otatume's unpublished thesis in the Institute of GMH to compare his route map with a result of T.M.'s field work (Matsumoto, 1981, fig. 2). It is now evident that the above two specimens came from the Turonian part of the section. They have a triangular postero-dorsal wing or ear, which is well demarcated from the inflated umbonal part of the left valve, being clearly shown by the actual specimen of GMH. 5971 and partly concealed by the rock matrix in GMH. 5965. Nagao and Matsumoto failed to show the wing in the illustration. This form is allied to, if not identical with, *Inoceramus inaequivalvis* Schlüter (1877, p. 265) (= *I. striatus* of Goldfuss, 1836, pl. 112, fig. 2; *non* Mantell, 1822).

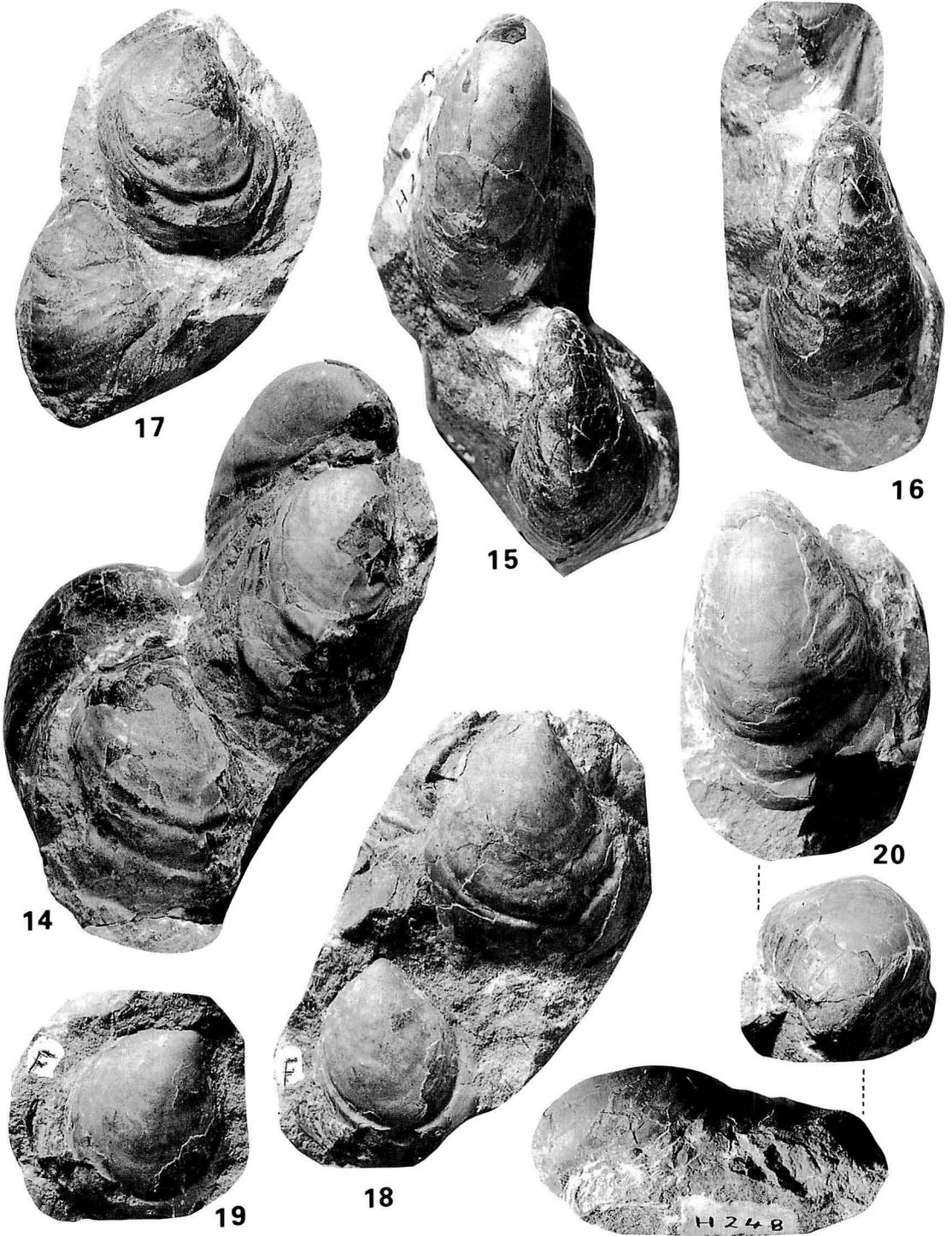
Another example which should now be excluded from *B. nipponica* is UMUT. MM6478 (=Tk. I-687), a syntype of Nagao and Matsumoto (1939, pl. 24, fig. 2). It was collected in 1901 by the late Professor Hisakatsu Yabe, when he was a graduate student. Its locality on the label by Yabe's handwriting is "the middle course of the River Obirashibets" (now shortend to Obirashibe or Obira), but its provenance is not exactly known. As small ammonites referable to *Desmoceras (Pseudouhligella)* cf. *japonicum* Yabe are in the rock matrix, a Cenomanian age may be suggested. The left valve has a flat postero-dorsal wing; the inflated umbonal part inclines abruptly and steeply to the flat wing but the fine concentric rings continue from the main part of the disk to the wing. The umbo is somewhat (but not strongly) incurved and the apex of the beak is acutely pointed. The ornament on the composite internal mould consists of numerous, fine and even, concentric rings which are at

middle to late growth-stages combined with regular, weak to moderate concentric ribs. The hinge line is nearly a half of the shell length and the valve is moderately (not strongly) convex. This specimen is referable to *Inoceramus pictus minus* Matsumoto (1989, p. 19) (see also Kauffman, 1977, p. 174).

Birostrina nipponica of the Cenomanian age is certainly similar to *B. concentrica* (Parkinson) of the Albian, but how these two species are related has yet to be worked out. Kauffman (1978a, p. iv•2-iv•3) wrote his preliminary observation on the British material, expecting successive change with stratigraphic sequence from the upper Lower Albian to the highest Upper Albian. The earliest form which he called *B. concentrica*, n. subsp. A, from the upper part of the Zone of *Douvilleiceras mammillatum* (uppermost Lower Albian) is described as "a small, highly convex, narrow and very elongated along the height axis (nearly tear-drop shaped)" and seems to be similar to the form α of *B. nipponica* in shell-form. According to Kauffman, it has "an anterior sulcus and a few coarse, widely and unevenly spaced, concentric rugae". Therefore, it seems to be quite dissimilar to our form α with respect to the ornamentation. Anyhow, it is difficult to fully understand the subspecies A, B, C, D and subsp. *brasiliensis* (White) from England, without full descriptions and adequate illustrations.

Pending the issue of Kauffman's monograph, we should compare *B. nipponica* with the typical form of *B. concentrica*, that is *B. concentrica concentrica* in the sense of Kauffman (1978a, p. iv•3). Although Parkinson's (1819, p. 59, pl. 1, fig. 5) holotype

→ **Figures 14–20.** *Birostrina nipponica* (Nagao et Matsumoto). Some other specimens from a large nodule at loc. N67-68p, Birin-zawa of Naibuchi area, Zone Mh-Kz, South Sakhalin (T. M. Coll.) (continued from Figs. 6–13), all $\times 1.5$. **14:** GK. H247A (BV) (above) and B (BV) (below), showing the lateral view of RV and posterior view of LV; **15:** *Ditto*, lateral view of LV of H247A and dorso-lateral view of LV of H247B; **16:** GK.H247B, normal lateral view; **17:** GK. H247C (RV) (above) and D (LV) (below), both somewhat distorted secondarily; **18:** GK.H247E(RV) (above) and F (RV) (below), the latter somewhat inclined to the posterior; **19:** GK.H247F, normal lateral view; **20:** GK: H248A (LV), intermediate form between β and γ .



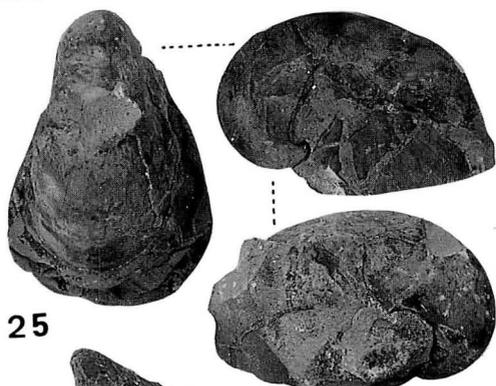
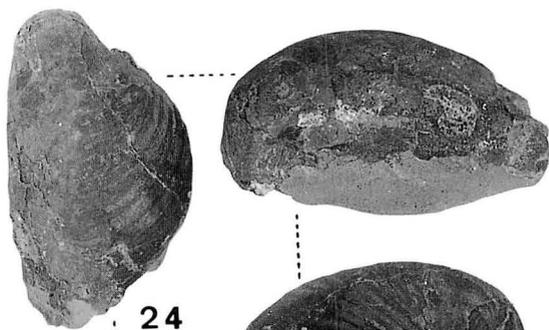
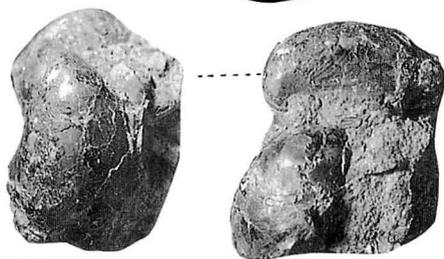
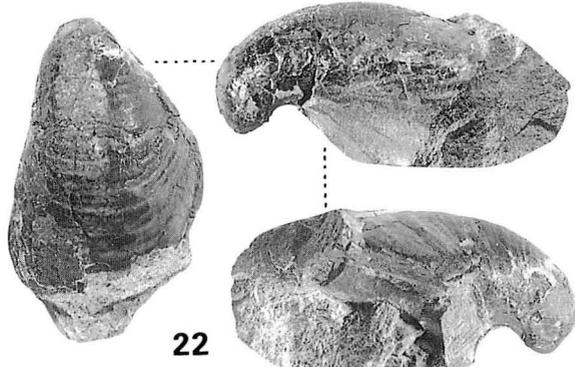
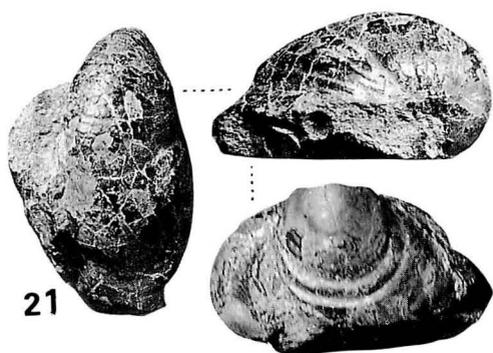
cannot be traced (Woods, 1911, p. 267), the specimens from the Gault at Folkestone illustrated by Woods (1911, pl. 46, figs. 1-7) are regarded as representing the typical form of *B. concentrica*, which is said to range from the upper half of Middle Albian to the basal Upper Albian (*cristatum* nodule bed) (Kauffman, 1978a, p. iv•3). One of us (T. M.) once looked at these specimens of Woods at Sedgwick Museum and British Museum (Natural History). This typical form of *B. concentrica* has a rather evenly convex and rounded main part of the valves, and is somewhat similar to the form β of *B. nipponica*, but there are some differences. In the left valve of the former the umbonal part is narrow and broadens abruptly to the main part, whereas in that of the latter the umbonal part gradually broadens to the main flank. Generally the former is more oblique than the latter. In both forms the young part is nearly smooth, showing only fine and dense concentric rings. On the middle to late part, weak subcostae may appear occasionally and irregularly in the former, whereas subcostae develop more frequently in the latter, some of which are raised to narrow ribs and accompanied by constrictions of deep interspaces. The forms α and γ of *B. nipponica* are undoubtedly different from the typical form of *B. concentrica*.

Pergament (1966, p. 32, pl. 2, figs. 1-4) described some examples of *B. nipponica* from the Cenomanian of the Koryak-Kamchatka region, Far East of the USSR. They seem to

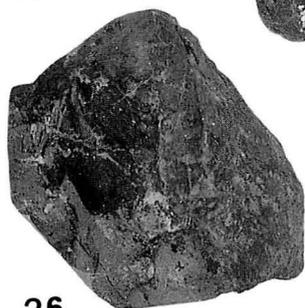
be generally referable to the form β in this paper, although some inclination towards the form α is shown by those with weak ornamentation (pl. 2, figs. 1, 2) and that towards the form γ by another (pl. 2, fig. 3). However, without inspecting the actual specimens, we cannot confirm these identifications. The same remarks are applied to the incompletely preserved specimens from the Cenomanian of the Naibu (Naibuchi) area of Sakhalin, which Pergament (1966, p. 30, pl. 1, figs. 1-4) described under "*Inoceramus* cf. *concentricus*".

On numerous but often incompletely preserved specimens from the Albian of the Antarctic Peninsula region, Crame (1980, 1985) has fully described *Birostrina concentrica*. The outline of the left valve is so variable that he distinguished at least three main types. The first of these (represented by figs. 5, 6 in Crame, 1985, pl. 59) may be similar to the slender form (α) of *B. nipponica*, but the former is more oblique and has an expanded, postero-dorsal, wing-like flat area. The second, pear-shaped type (Crame, 1985, pl. 59, figs. 1, 7, 8) may be somewhat similar to the form β of *B. nipponica* in the convex, subrounded main part of the valve, but the left umbonal part of the latter is not so narrow as that of the former, showing gradual broadening (*i.e.* increase of L/H) toward the main part. The third, squatter type of Crame (1985, pl. 59, fig. 10) has no counterpart in *B. nipponica*, but some variety of our form β could be similar to it, at least superficially.

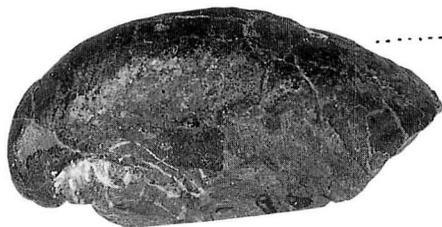
→ **Figures 21–28.** *Birostrina nipponica* (Nagao et Matsumoto). Examples of various forms in the WE Collections. **21:** WE. P025A (form γ) (LV; with a deficient RV attached in perpendicular to LV), from loc. As 1065 of the Poroko-ashibetsu, tributary on the west side of the Ashibetsu Valley (A. A. Coll.), $\times 1.2$. **22:** WE. P026A (LV) (form β with some inclination to α), from the same locality as above (A. A. Coll.), $\times 1.2$. Note that the apex of the incurved beak was destroyed away. **23:** WE. P027A (BV) (juvenile, probably intermediate form between β and γ), from the same locality as above (A.A. Coll.), $\times 1.2$. **24:** WE. P028T (LV) (from β somewhat inclined to α) from loc. T6082a86, left bank of the upper main course of the River Obirashibe (A.A. Coll.), $\times 1$. The figure on the left side above is in normal lateral view, that on the left side below in dorsal-lateral view. The apex of the beak was again destroyed away. **25:** WE. P030T (LV) (form γ), from the same locality as above (A.A. Coll.), $\times 1$. **26:** WE. P031T (RV) (form α or β), from the same locality as above, $\times 1$. **27:** WE. P041A (LV) (form α), from a boulder at loc. As3028 on the Tsukimi-zawa, Ashibetsu Valley (A.A. Coll.), $\times 1$. **28:** WE. P042A (LV) (juvenile of form α), from the same locality as above (A.A. Coll.), $\times 0.9$. Photos (21–23) by M. Noda; others by A. Asai.



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There is no example in the specimens illustrated by Crame which is comparable with the form γ of *B. nipponica*, although an example of the right valve (Crame, 1985, pl. 59, fig. 13) seems to be somewhat similar to, but not quite identical with, some right valves (e.g. RV of GK. H247A, Figure 14 above; GK. H250A, Figure 12 of this paper) of the form γ .

According to Crame (1985, p. 508) "no rigid morphologic or stratigraphic divisions can be placed between the three types and it is almost certain that they intergrade". The same statement can be applied to the three forms in our material. There is, however, no identical forms between the populations of the Antarctic Albian and those of the Japanese Cenomanian (precisely speaking Middle to Upper Cenomanian). Likewise, there are no similarities between the populations of the British Albian and those of the Japanese Cenomanian.

Birostrina concentrica itself is long ranging. According to Dhondt and Dieni (1988, p. 24), that species ranges from the *Douvilleiceras mamillatum* Zone (upper Lower Albian) to the Upper Albian (*Hysterocheras varicosum* Subzone included) and shows world-wide distribution.

Taking all the characters into consideration, as well as the separation in geological occurrences, we are inclined to distinguish *B. nipponica* as a species independent of *B. concentrica*, although the phylogenetic relationship between the two species has yet to be worked out.

Birostrina tamurai Matsumoto et Noda (1986, p. 411, pl. 81, figs. 1-6; pl. 82, figs. 1-3; pl. 83, figs. 1-3; pl. 85, figs. 4-5), from the Middle Cenomanian of Kyushu and Hokkaido, is similar to *B. nipponica* in shell-form but distinguished in having a radial sulcus on the posterior part and stronger but often irregular ribs at more less late growth-stages. On the average *B. nipponica* is less oblique than *B. tamurai*, although the variations of the two species in this regard may overlap to

some extent and the secondarily deformed specimens should be excluded from this comparison.

Inoceramus concentricus var. *costatus* Nagao et Matsumoto (1939, p. 270) needs careful restudy. Its lectotype was designated by Tamura and Matsumura (1974, p. 49) as UMUT. MM6480 (=Tk. I-690) (Nagao and Matsumoto, pl. 24, fig. 1). It was obtained in 1935 by T.M. at loc. Ik12 (precisely 12-12, southern one of the two points at 12 on the route map of fig. 1 in Nagao *et al.*, 1938), from the middle part of Member IId, *i.e.* the upper part of the tripartite Mikasa Formation on the eastern wing of the Ikushumbetsu anticline. The bed at Ik 12-2 is one of the sandstone beds with intercalated layers of conglomerate rich in *Glycymeris* and slightly below the zone characterized by *Inoceramus hobetsensis* Nagao et Matsumoto. It is somewhat above the predominant tuffite, a key marker of the Lower Turonian Zone of *Mytiloides mytiloides* in central Hokkaido. Therefore, the type locality (Ik-12) is evidently assigned to the Turonian, probably rather low in the Middle Turonian.

The lectotype of var. *costatus* itself is somewhat inequivalve, but its left umbo is not so prominent and not so strongly incurved as that of *B. nipponica* and its right valve is moderately convex. It is ornamented with concentric rings and subcostae which are clearly coarser than those of *B. nipponica*. Thus it represents, together with similar specimens from various areas of Hokkaido, a distinct species, *Inoceramus costatus* Nagao et Matsumoto, which is independent of *B. nipponica* and *B. concentrica*. A faint posterior radial depression is discernible on the left valve of the lectotype, although it is not so distinct as that of *B. tamurai*. The left umbo of *I. costatus* is not so prominent and incurved as that of *B. tamurai* and the subcostae of *I. costatus* is more uniform and not so irregularly strong as those on the late part of *B. tamurai*. One of us (T.M.) presumes that *I. mametensis* Pergament (1971, p. 44, pl.

4, figs. 2, 3; pl. 5, figs. 2-5; pl. 7, figs. 2, 3) could be a junior synonym or a subspecies of *I. costatus*. More precise description of *I. costatus* based on a large number of specimens from Japan is now in preparation by M. Noda.

Matsumoto (1977, fig. 1,; also fig. 1 in Takayanagi and Matsumoto, 1981) once set the Zone of *Inoceramus nipponicus* in the upper Lower Cenomanian in parallel with the Zone of *Mentelliceras japonicum*, but this was a mistake. It is now evident that *I. nipponicus* in those charts is mostly *I. tenuis* Mantell, which has a less prominent and much less incurved left umbo and less narrowly rounded ventral margin than *B. nipponica* (see Matsumoto *et al.*, 1987).

Occurrence.— The lectotype was collected from the Ugui-zawa, a tributary to the River Naibuchi. This stream runs mainly along Zone Mh2 (*i.e.* the Turonian Zone of *Inoceramus hobetsensis*; see geological map by Matsumoto, 1942, pl. 5), but several small branches come from the ridge formed by sandstones of the upper part of the Kawakita Group across the Cenomanian fossiliferous zones of Kz-Mh and Mho. As this specimen belongs to the old collections of IGPS, its exact provenance is hardly decided, but the label indicates No. II Group, which is the late Dr. Shimizu's (1935, p. 169) division and Cenomanian on the evidence of ammonites. From the position in the stratigraphic section, Mho is probably referable to the upper Cenomanian and Kz-Mh the lower Upper or upper Middle Cenomanian.

GMH. 7167, an example of the form α which was called the typical form by Nagao and Matsumoto (1939), came from the upper reaches of the Hakkin-zawa, where Cenomanian strata are extensively exposed, but what part of the Cenomanian is not precisely recorded.

OM. II-476, figured by Ikegami and Omori (1957), is one of the best specimens of the form α . This and two other specimens were collected from the lower part of Member IIC

of the Mikasa Formation in the Ikushumbetsu valley, *i.e.* the lower Upper Cenomanian on the evidence of *Eucalycoceras pentagonum* (Jukes-Browne) described by Matsumoto (1975).

WE. P041A and WE. P042A (both form α) were in a drifted nodule at loc. As 3029 in the Tsukimi-zawa of the Ashibetsu valley. From the lithological character and the location of As 3029, their provenance is inferred as the middle part (silty fine-grained sandstone to sandy siltstone) of the Mikasa Formation, *i.e.* upper part of the Cenomanian (For the stratigraphic section across the western wing of the Ashibetsu syncline, see Matsumoto and Okada, 1973, fig. 10, although it is along the Hachigatsu-zawa, north of the Tsukimi-zawa.). The loc. As 3029 is stratigraphically about 50 m higher than the loc. As 3211 of Tsukimi-zawa, where several specimens of *Calycoceras* (*Newboldiceras*) sp. were obtained along with *Desmoceras* (*Pseudouhligella*) *japonicum*.

GK. H8262-H8266, which represent the form β , were in a nodule from the mudstone of loc. R101. on highway 239 (between Kotanbetsu and Soeushinai), which is stratigraphically somewhat (about 60 m) higher than the loc. R100, where *Calycoceras* (*Newboldiceras*) sp. was found, and is assigned tentatively to the lower part of the Upper Cenomanian (see Matsumoto and Okada, 1973, fig. 8).

Loc. As. 1065 of the Poroko-ashibetsu in the Ashibetsu valley, where WE. P025A, P027A (both γ -form) and WE. P026A (rather β -form) were obtained, is referable to somewhere in the middle to upper part of the Cenomanian, for it is slightly higher than the layer where *Desmoceras* (*Pseudouhligella*) *japonicum* occurs commonly and considerably below the layer with *Mytiloides mytiloides* (Mantell), although the minor geologic structures are somewhat complicated in the outcrops along this stream.

Loc. T6082a86, where WE. P028T (form β with some inclination to α), WE. P030T

(form γ) and WE. P031T (RV of form α ?) were obtained, is a cliff on the left side of the meandering main course of the River Obirashibe, 100 m west of loc. MH390 of Tanaka (1963, map II), mudstone of the Member Mh, Upper Cenomanian.

Loc. N67-68p, a large nodule in the Birinzawa, a branch of the River Naibuchi (South Sakhalin), in which numerous specimens of the form γ and some of form β were contained, must have been derived from the fossiliferous, silty sandstone, marked Mh-Kz (Matsumoto, 1942) at the top of the Kawakita Group. This is either the upper part of the Middle Cenomanian or lower part of the Upper Cenomanian, from its stratigraphic position (no acanthoceratid ammonite has been found there).

To sum up, *B. nipponica* is early Late Cenomanian and possibly also late Middle Cenomanian in age, on the evidence of the representative specimens described in this paper. To know the true range, further material from more sections in various areas should be investigated.

The three forms, called α , β and γ , occur predominantly in particular lithofacies of different places, although there may be intermingling to a minor degree. This fact suggests that each of them may have adapted to a particular type of environment (S. Toshimitsu, personal discussion with T.M.). To confirm this idea satisfactorily, further analyses will be necessary.

Birostrina aff. *nipponica*
(Nagao et Matsumoto, 1939)

Figures 29—31

Material.— GK. H221 (Figure 29) (LV with shell adhering to major part) from loc. N309h, left bank of the River Naibuchi immediately south of the entrance to the Yunosawa, Zone Mho of Matsumoto (1942) (T. M. Coll.); GK. H8276A, B (Figure 30) (LV) and C (BV but half concealed by rock matrix)

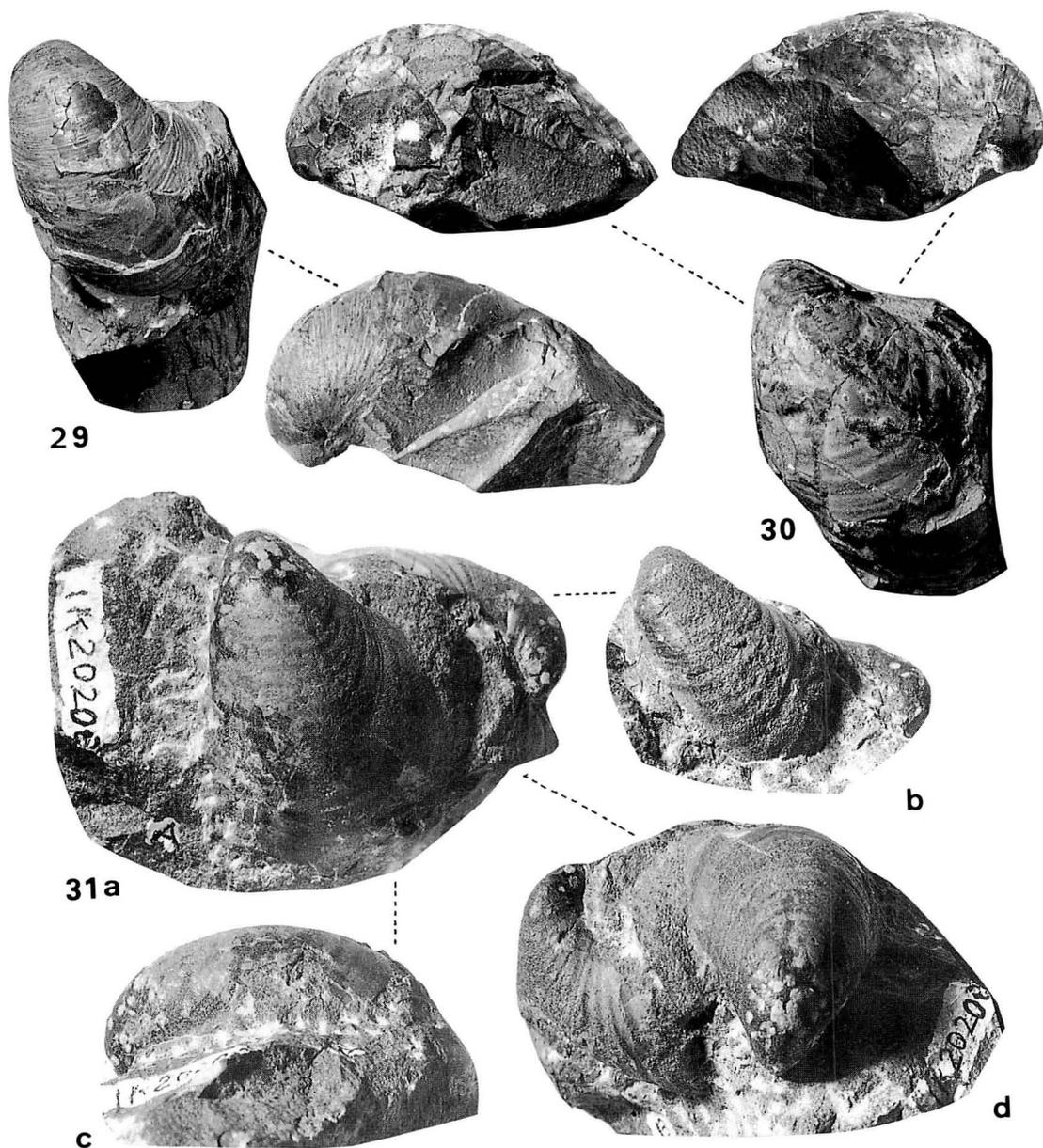
(comp. int. m., with inner shell layer adhering to some portions), from loc. Ik2020e, gorge of the River Pombets a tributary to the River Ikushumbets, central Hokkaido (T.M. Coll.); WE. P029T (Figure 31) (LV, comp. int. m., with inner shell layer adhering partly), from loc. T6054a84, right side of the River Obirashibe (see Sekine *et al.*, 1985, fig. 3•2), north-western Hokkaido (Coll. by Y. Tanaka, S. Ago and A. Matsuzawa).

Description.— Shell small and inequivalve. Left valve highly convex, with much incurved and prosocline umbo and beak; axis of growth sigmoidal, with forward convex curvature on the main or late part of the valve; outline obliquely suboval, with somewhat expanded postero-ventral part which tends to be flattened; anterior margin slightly concave below the beak and very broadly convex in the main part, passing to the asymmetrically rounded ventral margin; postero-dorsal margin gently concave, forming an obtuse angle with the postero-ventral margin. Right valve less convex than the left and subtrapezoid-suboval in outline.

Surface of the shell marked by fine concentric striae. The internal mould at first smooth and then ornamented with concentric rings which correspond to the interspaces of the striae on the shell surface. Concentric subcostae or narrow and weak ribs may develop at more or less late growth-stage. A very faint radial depression may be discernible in some specimens (GK. H8276 A and C).

Comparison.— Although *B. nipponica* is considerably variable and includes several forms as described above, we exclude this particular form from that species. It is indeed somewhat similar to the form β of *B. nipponica*, but clearly distinguished by its sinuous growth-axis which curves obliquely to the posterior with growth, forming anteriorly convex curvature on the main part of the valve.

This form looks somewhat similar to *B. concentrica brasiliensis* (White) (1887, p. 56,



Figures 29–31. *Birostrina* aff. *nipponica* (Nagao et Matsumoto). **29:** GK. H221 (LV), from loc. N309h, Zone Mho, Naibuchi valley (T.M. Coll.), $\times 1.3$. **30:** WE. P029T (LV), from loc. T6054a84, Member Mh, Obirashibe valley (collected by Y. Tanaka, S. Ago and A. Matsuzawa), $\times 1.5$. **31:** GK. H8276A and B (both LV), from loc. IK2020e, Pombets Gorge, lower part of Mikasa Formation, Ikushunbets valley (T.M. Coll.), $\times 1.2$. a: lateral view of H8276A and posterior view of H8276B; b: lateral view of partly concealed H8276B, with a postero-dorsal portion of H8276A at the right corner; c: anterior view of H8276A; d: anterior view of H8276B on the left and dorsal-lateral view of H8276A. Photos (21–23) by M. Noda.

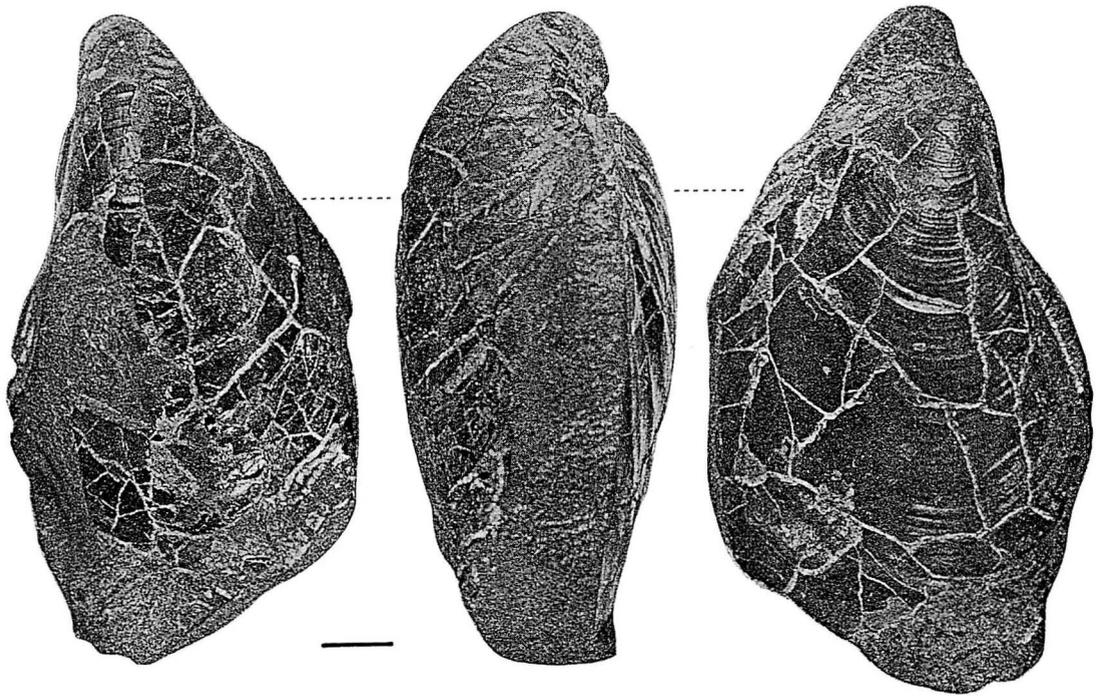


Figure 32. *Birostrina nipponica* (Nagao et Matsumoto). OM. II-476 (BV) (form α), collected by Yoshimi Yamaguchi from loc. IK B-6 of the water-way tunnel from the Katsura-zawa dam to the station of the electric power, Ikushumbets valley (reproduced from Ikegami and Omori, 1957, by permission). Scale bar : 10 mm.

Table 2. Measurements of *Birostrina* aff. *nipponica* on selected specimens.

Specimens	V	H	L	L/H	G	G/H	G/L	b	b/H
GK. H221	LV	32.0	24.0	.75	52.0	1.63	2.2	13.4	.42
GK. H8276A	LV	36.0	25.6	.71	53.0	1.47	2.1	16.0	.44
WE. P029T	LV	36.5	~26	.71	55.0	1.51	2.1	16.5	.45

pl. 3, figs. 11, 12; Maury, 1937, pl. 8, figs. 9, 10, 13; Kauffman, 1978b, pl. 1, figs. 11, 16), from the Middle Albian of Brazil, South Africa and elsewhere, but its left beak is not so strongly prosogyrous as in that subspecies and its occurrence is much separated in geological age. Therefore, the similarity may be due to a homeomorphy.

Dimensions.— See Table 2.

Occurrence.— Loc. N309h, Zone Mho, sandy siltstone in the lower part of the Miho Group, upper part of the Cenomanian.

Loc. Ik2020e, calcareous nodule in the greenish grey fine to medium-grained sand-

stone in the lower part of the Mikasa Formation on the western wing of the Ikushumbets anticline. It is slightly above the layer in which fragmentary pieces of *Calycoceras* (*Newboldiceras*) sp. are intermingled with abundant trigonian shells, probably upper part of the Middle Cenomanian.

Loc. T6054a84, mudstone of the Member Mh (Tanaka, 1963) of the Obirashibe valley, upper part of the Cenomanian.

The stratigraphic range of this form has yet to be worked out by the study of more material from various sections.

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We wish to thank Professor Hiromichi Hirano for his pertinent supervision to one of us (A.A.) and for generous help in various ways to both of us; also Drs. Masayuki Noda and Seiichi Toshimitsu for fruitful discussions and for kind help in taking photographs of the GK and some of WE specimens.

We owe much to the persons who assisted us in the field works. Their names are indicated in the item *Material*. Thanks are extended to Dr. J.A. Crame who has kindly read our first draft, giving valuable suggestion and information, and also to the late Dr. J.B. Reeside, Jr. and Dr. Peter Bengtson who supplied to one of us (T.M.) with Brazilian papers which were inaccessible in Fukuoka. Miss Saiko Nitani assisted us in preparing the typescript.

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- (J): in Japanese with English abstract or brief explanation. (R): in Russian.

Aikawa 相川, Ashibetsu 芦別, Birin-zawa 備林沢, Hachigatsu-zawa 八月沢, Hakkin-zawa 白金沢, Hobetsu 穂別, Ikushumbets (Ikushunbetsu) 幾春別, Kami-hobetsu 上穂別, Katahira 片平, Katsura-zawa 桂沢, Kawakita 川北, Kiritachi 霧立, Kotanbetsu 古丹別, Miho 美保, Mikasa 三笠, Naibuchi (=Naibuti or Naibu) 内淵, Nutapomanai ヌタポマナイ, Obira 小平, Obirashibe (Obirashibetsu) 小平薬, Oyubari 大夕張, Pom-bets (Ponbetsu) 奔別, Poroko-ashibetsu 幌子芦別, Sakhalin サハリン, Shiyubari シュウバリ (主夕張), Soeushinai 添牛内, Tsukimi-zawa 月見沢, Ugui-zawa (Ugoi-zawa) うぐい沢, Yu-no-sawa 湯の沢.

北海道・サハリン産白亜紀セノマニアン期のイノセラムス類 — I. *Birostrina nipponica* (Nagao et Matsumoto): *Inoceramus concentricus* var. *nipponicus* Nagao et Matsumoto, 1939 は定義が不明確で、その地質時代の記録にも誤があった。今回新資料も加えて再検討した。改正種は *Birostrina* に属するが、アルビアンの *B. concentrica* (Parkinson), 本階中部の *B. tamurai* Matsumoto et Noda とは識別される。変異が著しく、便宜上 3 型 (α , β , γ) に分けて各々の形質を記した。しかし 3 者は密接で漸移する。レクトタイプは α 型だが β 型に移行の傾向を示す。検討した標本は上部セノマニアンの下部の多いが、一部同階中部の上部にわたる可能性がある。3 型の産出時代に差はないが、生息環境に若干の差があったのかもしれない。従来の中 *I. concentricus nipponicus* 中には *I. tenuis* Mantell, *I. pictus minus* Matsumoto, *B. aff. nipponica* (本文末尾に記述), さらにチューロニアンの *I. inaequivalvis* Schlüter に近縁のものさえ含まれていた。松本達郎・浅井明人

884. DINOFLAGELLATE CYST ANALYSIS OF HOLOCENE SEDIMENTS FROM LAKE HAMANA IN CENTRAL JAPAN*

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Abstract. Dinoflagellate cysts occur in the Holocene sediments of Lake Hamana, Central Japan. The cyst assemblages are dominated by *Brigantidium* spp., *Selenopemphix quanta* and *Seleno. hamanaensis* of the Peridinioid Lineage, and *Polykrikos schwartzii*, *Poly. kofoidii* and *Pheopolykrikos hartmannii* of the Gymnodinioid Lineage. A few cysts of the Gonyaulacoid and Tuberculodinioid Lineages are also present in the samples. Six dinoflagellate cyst assemblage zones are established based on differences of species composition. From the cores of central Lake Hamana, environmental changes from stable inner bay to brackish-water lake and then to freshwater lake and finally to brackish-water lake were recorded in the cyst composition. One new species, *Selenopemphix hamanaensis*, and four cysts are described.

Key words. Dinoflagellate cyst, Holocene, paleoenvironment, Lake Hamana.

Introduction

Studies of Quaternary dinoflagellate cysts have been carried out mainly in the North Atlantic region since the 1960's. Initially, the majority of these studies were descriptive works (e.g., Rossignol, 1961, 1962); later studies focused on comparisons of the Quaternary assemblages with modern cyst distributions (e.g., Harland, 1977; Reid and Harland, 1977). More recently, dinoflagellate cysts have been useful in paleoenvironmental studies (e.g., Dale 1985; Long *et al.*, 1986) and Harland (1988) suggested the possibility of paleoclimatic analysis using such cysts.

In Japan, there have been only a few works on Quaternary cysts. Matsuoka (1976) described palynomorphs including dinoflagellate cysts from the Pleistocene Osaka Group. Harada (1984) carried out a paleoenvironmental study based on dinoflagellates in the samples obtained from

the New Kansai International Airport in Osaka Bay. There has been only one work on cysts in Holocene sediments. Matsuoka (1987a) discussed the Holocene paleoenvironment based on dinoflagellate cyst assemblages in core samples from Kawasaki City.

This paper describes the Holocene dinoflagellate cyst assemblage and discusses paleoenvironmental changes in Lake Hamana.

Samples

Samples were collected from two locations as shown in Figure 1. These core samples were taken to investigate environmental changes by a research team from Shizuoka University (Representative: N. Ikeya). These samples were taken with a thin-walled sampler and triple-tube sampler.

85H-1 (Location: 34°45'59"N, 137°35'31"E)

This site is situated in the northern part of Lake Hamana and has the deepest water (about -12 m) (Figure 1). The core samples

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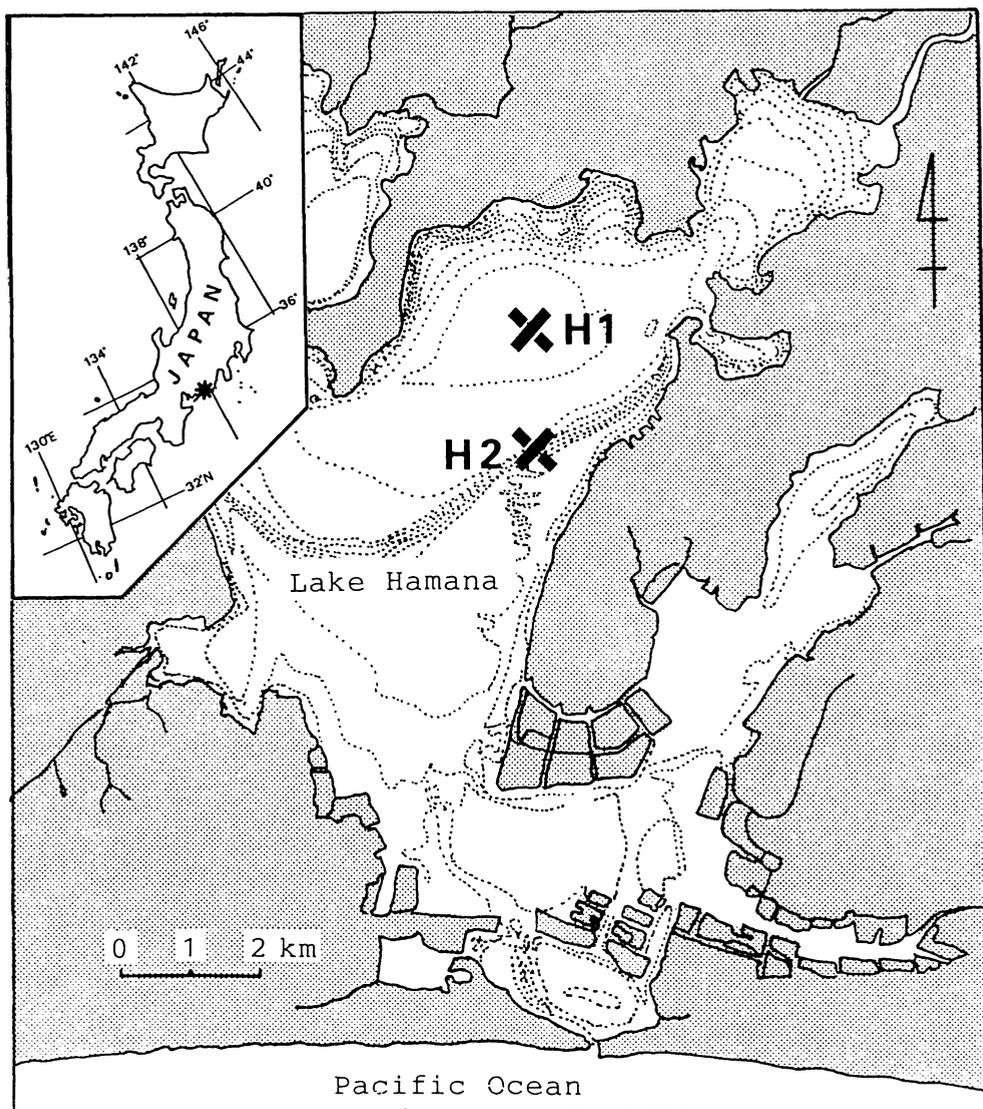


Figure 1. Location of coring sites, 85H-1 and 85H-2.

were obtained from a depth of 1.45~16.75 m from the bottom of the lake.

The sediments in this core mainly consist of homogeneous gray silt and the geologic ages were confirmed by tephra intercalated at three horizons (Figure 2). These tephra were Osa-wa scoria (-6.49~-6.55 m, ca. 3,000 y.B.P.), Kawagodaira pumice (-6.56~-6.58 m, ca. 3,000 y.B.P.) and Kikai-Akahoya tephra (-14.18~-14.32 m, ca. 6300 y.B.P.) in descend-

ing order (Ikeya *et al.*, 1987). The sedimentation rate at this site is calculated to be approximately 0.22 cm/year based on these ages.

85H-1B (Location: about 1 m north of 85H-1)

These samples correspond to the loss in the upper part of core 85H-1. The supplementary core ranges -0.32~-1.22 m from the bottom of the lake. They consist mainly of

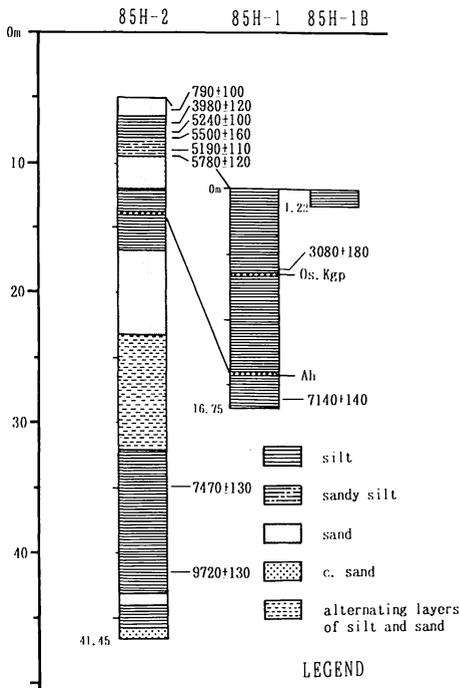


Figure 2. Columnar section of the sampling sites. Os: Osawa scoria, Kgp: Kawagodaira pumice, Ah: Kikai-Akahoya tephra (adapted from Ikeya *et al.* 1987).

dark greenish-gray silt laminated with black and light gray silt. They contain shell fragments and give off a hydrogen sulfide (Ikeya *et al.*, 1987).

85H-2 (Location: 34°45'03"N, 137°35'31"E)

This site is situated at the edge of a trough in the lake (Figure 1). The water depth is approximately 5 m. The recovered core material ranges in depth from 0 to -41.64 m and is composed of alternating beds of silt and sand. The sediments are more sandy than those of 85H-1 and the sedimentary facies changes frequently.

The ^{14}C ages measured for eight horizons (Figure 2) are as follows (Ikeya *et al.*, 1987):

Depth (m)	Age (y.B.P.)	Sample
0.86	790±100	Gastropoda
1.90	3980±120	Gastropoda
2.80	5240±100	Gastropoda

3.09	5500±160	Gastropoda
4.12	5190±110	Gastropoda
4.38	5780±120	Phytoclast
29.84	7470±130	Gastropoda
36.61	9720±130	Pelecypoda

Only one tephra bed was recognized as Kikai-Akahoya tephra (-8.98 m, ca. 6,300 y. B.P.) in this core (Ikeya *et al.*, 1987).

Methods

All the samples were processed using palynological preparation techniques (Shimazaki, 1979). However, they were not treated with in order to avoid damaging the cysts (Matsuoka, 1984b). An outline of the process used follows:

- (1) An approximately 10% solution of hydrochloric acid is added to the sample (1 cc) to dissolve the calcium carbonate particles.
- (2) The remains are treated with an approximately 50% solution of hydrofluoric acid to remove silicate particles.
- (3) The organic remnants are sieved through a 150-mesh screen to exclude large grains.
- (4) The residue is sieved through a 635-mesh screen to trap cysts, and the refined material is examined microscopically.

The refined samples (with water) mixed with a solution of polyvinyl alcohol are spread over cover glasses (18 mm×24 mm) and dried on a hot plate at about 40°C. Each cover glass with the specimen is mounted in polyester resin.

Forty three samples of 85H-1 and 85H-1B, and forty-six samples of 85H-2 were examined by palynological analysis. The absolute number of cysts per three slides was calculated for 85H-1 and 85H-1B, and the absolute number of cysts per 0.1 cc of refined sample was counted for 85H-2.

Dinoflagellates often have two scientific names, one for the vegetative stage, and the other for the resting cyst stage. Some cysts with no cyst-based name are referred to by

This zone is characterized by an abundance of *Polykrikos* cysts. *Poly. schwarztii* makes up 40~92% of samples 85H-1, [1] and [3]. *Poly. kofoidii* increases suddenly at the top of this zone, sample 85H-1, [1]. *Pseudoschizaea rubina*, with unidentified microfossils, occurs in this zone.

Assemblage zone B (85H-1, [4]~[15]; 85H-2, [2]?)

There are a few cysts in this zone. *Poly. schwarztii* is very abundant in sample 85H-1, [11]. Gonyaulacoid cysts are recorded in samples 85H-1, [7] and [13]. Peridinioid cysts are found in samples 85H-1, [10] and

Table 1. Continued.

(19)	(20)	(21)	(22)	(23)	(24)	(25)	(26)	(27)	(28)	(29)	(30)	(31)	(32)	(33)	(34)	(35)	(36)	(37)	(38)	(39)	(40)	(41)	(42)	(43)
7.80-7.81	8.25-8.26	8.60-8.61	9.05-9.06	9.40-9.41	9.80-9.81	10.20-10.21	10.60-10.61	11.00-11.01	11.40-11.41	11.80-11.81	12.00-12.01	12.20-12.21	12.55-12.56	13.00-13.01	13.20-13.21	13.60-13.61	13.80-13.81	14.00-14.01	14.20-14.21	14.35-14.36	14.60-14.61	14.80-14.81	15.00-15.01	15.60-15.61
			1														1				1			
		2	1	1		1	1							1										
3		1	1	1		1	1						1	2	1	2	1				1		2	
		1	1		3					2	1		1	2	3	2	2				1			
					1	1					1		1	1	3	1		3	1		3			2
							1																	
3	1			2				3			1			1			2							
								3		5	1							1			4			
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		5		1										1					1	2	1			
7	10	46	49	60	49	11	21	16	9	21	50	34	22	23	74	71	38	44	16	21	74	14	4	25
			3								1											1		1
								1														2		1
	2	4		1						2	1			1	4	2	1	1	2		2	7	1	1
26		33	18	65	58	12	27	31	6	19	49	17	33	31	27	58	38	68	17	17	29	6	2	16
8	5	7	8	12	21	54	73	18	7		19	109	84	13	16	8	49	59	26		3			
		1															1							
		2		9	6	10	3	4	2	4	3	4	2	3		5	18	3	5	2	1			3
		1	4	1			1				1	1	1	1			1				1	2		
		1	2	4	11	1	9	35	5	10	9	2	2	8		5	53	5	2	1	15	2		11
																		1						
						8	1			1		4	5	16			1		2	4				6
								3									1							
			1					2		1				2		1								
1			8	1		1	2	3	4	1	2	3	2	4	2	6	5	1		2	1			5
3	3	9	1	6	1	5	3	11						1		10					1			1
40	17	14	13	18	31	13	30	67	3	1	5	17	5	5	1	3	5	3		4		1	1	
2		29	24	10	13	95	24	2		3	9	13	46	20	63	10	20	8	170	153	50	6	4	12
9		3	8	3	6	1		1			3		1	3	1	1	4				1	2	1	1
102	37	159	138	200	200	214	201	200	36	70	145	206	205	153	200	198	249	200	244	216	200	34	14	89

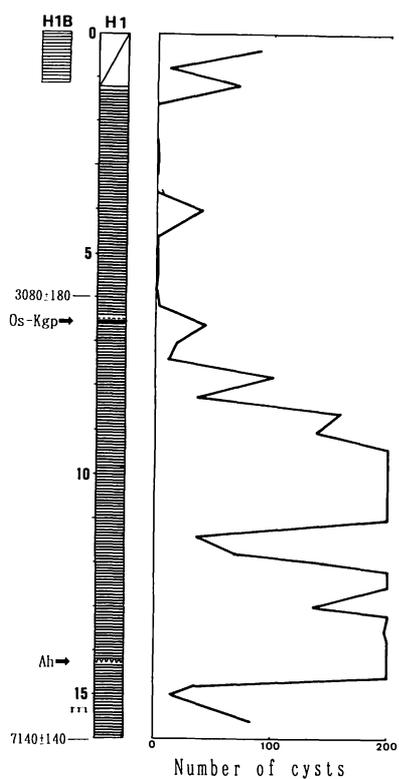


Figure 3. Vertical distributions of dinoflagellate cysts in core 85H-1.

[15]. The samples in this zone include fresh-water planktonic algae, *Pediastrum* and *Staurastrum*.

Assemblage zone C (85H-1, [16]~[27]; 85H-2, [3]~[38]?)

Brigantedinium spp., *Selenopemphix hamanaensis*, *Poly. kofoidii*, *Poly. schwartzii* and *Pheopolykrikos hartmannii* are continu-

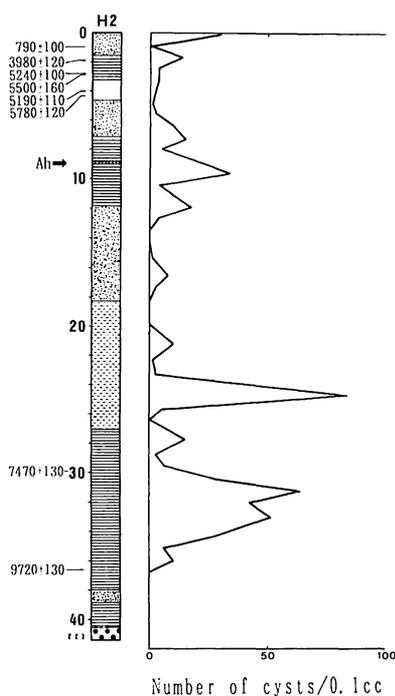


Figure 4. Vertical distributions of dinoflagellate cysts in core 85H-2.

ous throughout this zone. Gonyaulacoid cysts are present at less than 3%. *Brigantedinium* spp. are observed abundantly from sample 85H-1, [21] to [24]. *Seleno. hamanaensis* is found plentifully in the upper part of this zone. *Polykrikos* cysts are found evenly throughout these samples. *Votadinium carvum* and *Lejeunecysta concreta* are restricted to the samples from the middle to upper parts and their occurrence corresponds with cyst abundance. The number of cysts

Table 3. Dinoflagellate cyst assemblage zone for cores 85H-1 and 85H-2.

Assemblage zone	Age (y.B.P.)	Sample No.	Depth (m)	Sample No.	Depth (m)
A	168~536	85H-1-[1]~[3]	0.37~1.18	85H-2-[1]	0.05~0.06
B	727~2800	[4]~[15]	1.60~6.16		
C	3000~5005	[16]~[27]	6.60~11.01	[3]	1.65~
D	5182~5368	[28]~[29]	11.40~11.81	↓	
E	5455~6641	[30]~[40]	12.00~14.61	↓	
F	6727~7095	[41]~[43]	14.80~15.61	[38]	~34.30
				[39]~[40]?	35.10~36.01

decreases higher in the zone.

Assemblage zone D (85H-1, [28]~[29]; 85H-2, [3]~[38]?)

This zone is distinct in 85H-1 but indistinct in core 85H-2. The number of cysts, especially Gymnodinioid cysts, decreases in this zone. *Brigantedinium* spp. and *Seleno. quanta* are frequent and *Lejeunecysta concreta* is found in constant numbers, but *Seleno. hamanaensis* is rarely found.

Assemblage zone E (85H-1, [30]~[40]; 85H-2, [3]~[38]?)

This zone is marked by the cyst dominance. *Brigantedinium* spp., *Seleno. quanta* and *Pheo. hartmannii* are also recorded throughout the samples, and *Seleno. hamanaensis* is also present except sample 85H-1, [39]. These four cysts make up a high percentage in the assemblage. *Tuberculodinium vancampoeae* also occurs throughout the samples, but is not as abundant. Gonyaulacoid cysts are concentrated around the middle part of this zone. Samples 85H-1, [38] and [39] are characterized by a dominance of *Pheo. hartmannii*. These two samples may correspond to 85H-2, [13] and [28] which also have a high percentage of *Pheo. hartmannii*.

Assemblage zone F (85H-1, [41]~[43]; 85H-2, [39]~[40]?)

The samples in this zone are characterized by a continuous occurrence of *Brigantedinium* spp., *Seleno. quanta* and *Pheo. hartmannii*, and the amounts of cysts decrease higher in the zone. The assemblage zone for the samples of 85H-2, [39] and [40] is unclear because there are a few cysts.

Paleoenvironment

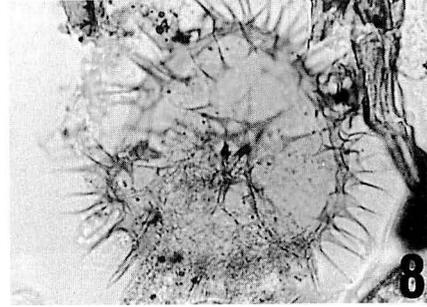
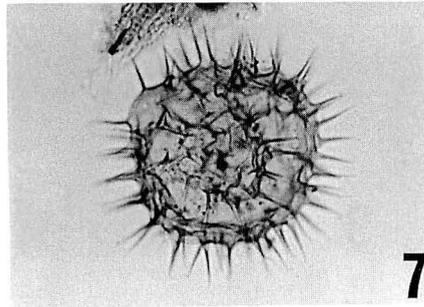
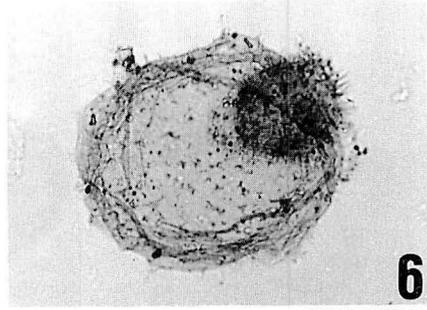
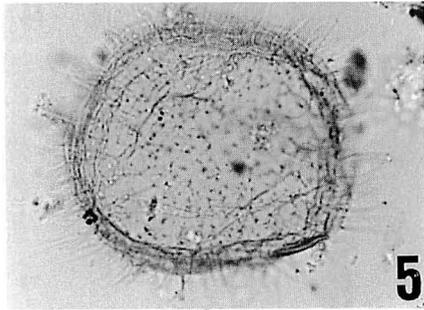
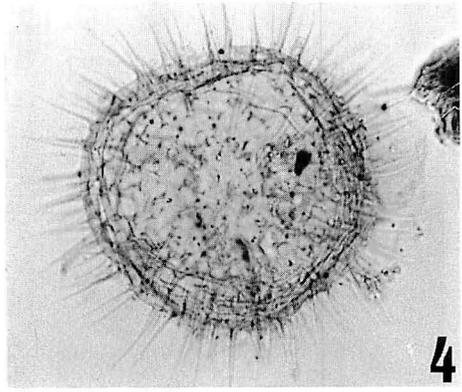
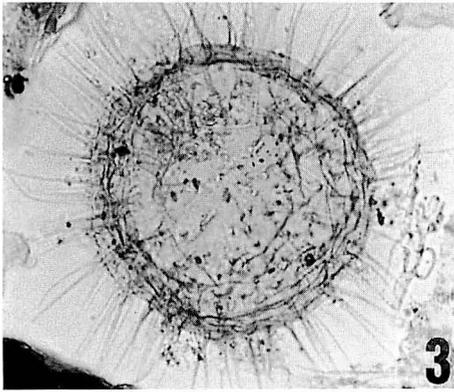
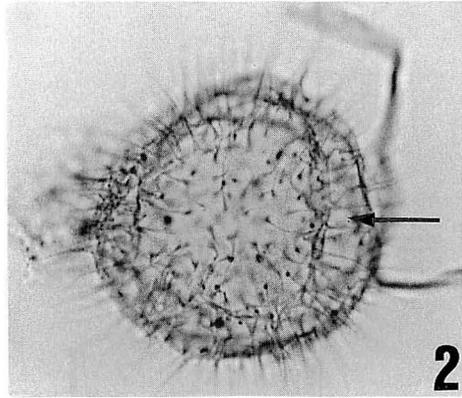
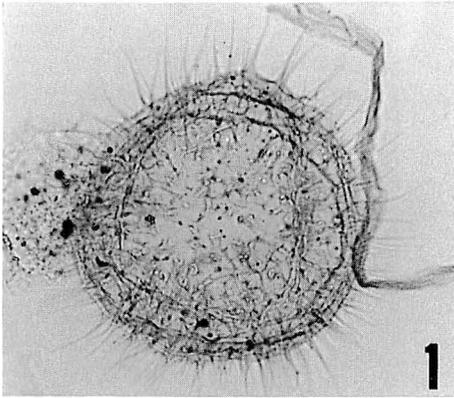
Using cyst assemblages, geographical distribution data on modern dinoflagellate cysts provide important information for environmental analysis. A relationship between environmental inclinations and cyst distribution in surface sediments has been recognized since William's report (1971a, b).

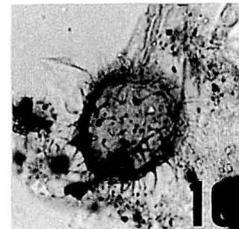
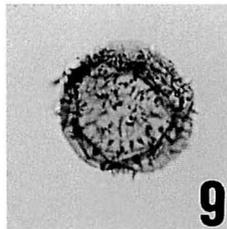
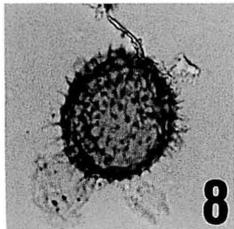
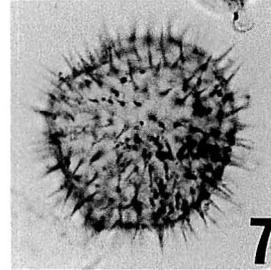
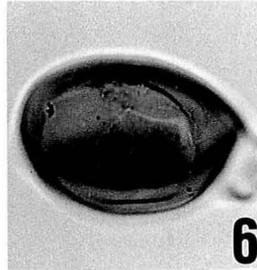
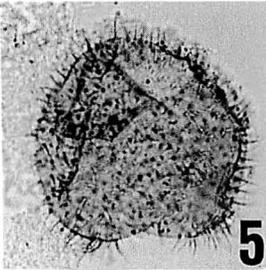
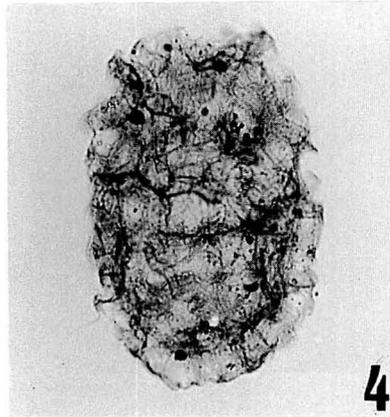
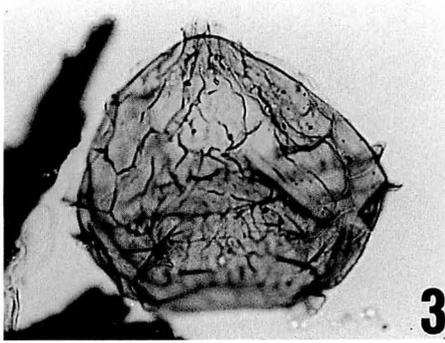
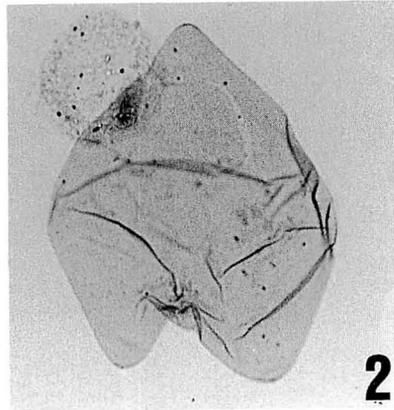
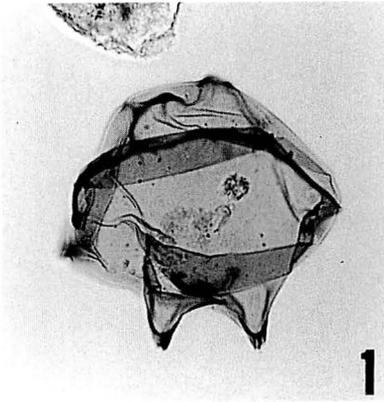
Wall *et al.* (1977) and Harland (1983) described modern cyst distribution in the North Atlantic Ocean. The former authors examined the relationship between cyst assemblage types and their oceanographic environments. Similar investigations have been carried out since the 1970's (*e.g.*, Williams 1971a, b; Davey and Rogers, 1975), although there are still insufficient data on the environmental information derived from cysts. Harland (1983) compiled the data as accumulated results and they have since proved valuable, although more detailed information on cyst distribution is needed.

Paleoenvironmental research in Japan is mainly based on local information on cyst distribution (Harada, 1974; Kobayashi *et al.*, 1986; Matsuoka, 1976, 1982, 1985a, b, 1987b) and the use of cyst studies for paleoenvironmental analysis data (Harada, 1984; Matsuoka, 1987a). Dinoflagellate cyst distribution shows distinct provincialism.

In Nagasaki Bay southwestern Japan, the percentage of cyst species of the Peridinioid group is 40.3% in the outer part of the bay and the average number of species is 7.5. The corresponding values for the inner area of the bay are 32.3% and 5.7, respectively. The species number of the Peridinioid group,

→ **Figure 5.** All photographs $\times 600$. **1, 2.** *Selenopemphix hamanaensis*, sp. nov. **1**; holotype, polar view. **2**; holotype, polar view showing archeopyle (arrow), slide 85H-1 10.60~10.61 m ① (97.1/33.2 L). **3.** *Selenopemphix hamanaensis*, sp. nov., paratype, polar view, slide 85H-1 10.60~10.61 m ② (99.9/36.0 L). **4.** *Selenopemphix hamanaensis*, sp. nov., paratype, polar view, slide 85H-1 10.60~10.61 m ② (100.2/38.6 L). **5.** *Selenopemphix hamanaensis*, sp. nov., polar view, slide 85H-1 13.80~13.81 m ② (99.0/23.2 L). **6.** ? *Selenopemphix hamanaensis*, polar view, short-spined type?, slide 85H-2 31.20~31.21 m ② (101.0/38.2 L). **7.** *Selenopemphix quanta* (Bradford) Matsuoka, polar view, slide 85H-1 10.60~10.61 m ② (89.0/22.3 L). **8.** *Selenopemphix quanta* (Bradford) Matsuoka, polar view, slide 85H-1 14.20~14.21 m ① (99.5/40.2 L).





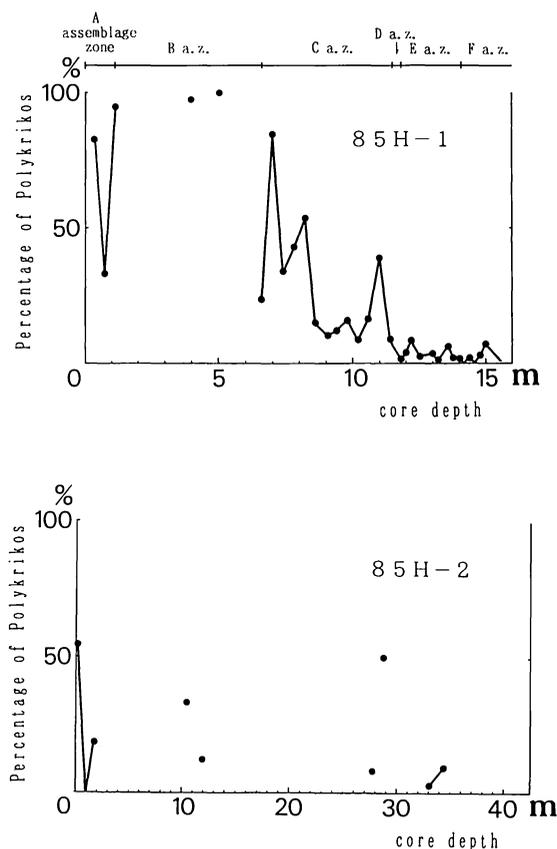


Figure 7. *Polykrikos* cyst percentages in the cores 85H-1 and 85H-2.

therefore, generally decreases toward the inner bay (Matsuoka, 1985a).

Akkeshi Bay and Lake Saroma are situated in eastern Hokkaido, which is in northern Japan. In Akkeshi Bay, which is open to the inflow of oceanic water, the percentage of cyst species of the Peridinioid group is 53% and the average number of species is 10.8. On the other hand, Lake Saroma, which has a narrow lake mouth, has corresponding values of

34.7% and 5.2, respectively. The average rate and species number are smaller than those in Akkeshi Bay (Matsuoka, 1987a). The number of cyst species of the Peridinioid group tends to decrease in the presence of fresh water.

The decrease in the number of cyst species of the Peridinioid group in Lake Hamana at approximately 5,000 y.B.P. indicates the presence of oceanic water until that time. The cysts of the genus *Polykrikos* are distributed in inner bay areas around Japan (Matsuoka, 1985b). The period, ca. 4,000 y.B.P.~ca. 3,000 y.B.P., of this species coincides with the period of freshwater diatoms (Kashima, 1987) and the occurrence of planktonic algae living in fresh to brackish water. The high ratio in the occurrence of *Polykrikos* cysts indicates a period of desalination of the environment of a decrease in the amount of oceanic water. Figure 7 illustrates these environmental oscillations. The relative ratio of *Polykrikos* cyst in 85H-1 clearly shows the environmental history at this site. Especially, obvious environmental changes appear to have occurred at the -8 m and -11 m horizons. The same standardized graph of 85H-2 is discontinuous because of the unstable sedimentary conditions at this site. The upper part of this core shows a high percentage of *Polykrikos* and this is in accord with the trend in 85H-1.

The changing aspects of the assemblages and data on an absolute age scale obtained by radiocarbon dating, tephra and sedimentation rate revealed the paleoenvironmental history in the northern and central area of Lake Hamana.

Ca. 9,700 y.B.P.~ca. 7,500 y.B.P. (85H-2, [34]~[38]: 85H-1, not observed): Many

← Figure 6. All photographs $\times 600$. 1. *Lejeunecysta concreta* (Reid) Matsuoka, dorso-ventral view, slide 85H-1 13.80~13.81 m ② (95.2/39.4L). 2. Cyst of *Protoperidinium oblongum*, dorsal view, slide 85H-1 10.60~10.61 m ②. 3. Cyst of *Protoperidinium* sp., ventral view, slide 85H-1 13.80~13.81 m ① (95.7/25.3L). 4. *Polykrikos schwartzii* Bütschli, dorso-ventral view, slide 85H-1 11.00~11.01 m ① (93.3/45.6 L). 5. *Votadinium spinosum* Reid, dorso-ventral view, slide 85H-1 11.00~11.01 m ① (87.5/36.7 L). 6. *Brigantedinium simplex* (Wall) Reid, slide 85H-1 9.40~9.41 m ③ (94.1/29.9 L). 7. *Pheopolykrikos hartmannii* (Zimmermann) Matsuoka and Fukuyo, slide 85H-1 10.60~10.61 m ①. 8. Dinoflagellate cyst ? type E, slide 85H-2 32.00~32.01 m ① (100.2/27.8 L). 9. Dinoflagellate cyst ? type A, slide 85H-1 7.60~7.61 m ① (98.5/29.3 L). 10. Dinoflagellate cyst ? type D, slide 85H-2 29.50~29.51 m ① (91.0/43.8).

cyst species are found and *Tuberculodinium vancampoae* occurs throughout this interval. This species has been observed in bay areas around Japan (Matsuoka 1985b). This evidence may indicate inner bay conditions during this period.

Ca. 7,500 y.B.P. ~ ca. 6,400 y.B.P. (assemblage zone F): There are a few species. This condition indicates lake obstruction or inflow of marine water.

Ca. 6,400 y.B.P. ~ ca. 5,400 y.B.P. (assemblage zone E): Many species occur through this interval. A large number of cysts is also observed. The ratio of *Polykrikos* decreases in comparison in the upper part of this core and the occurrence of *Operculodinium centrocarpum* is frequent. Species of Gonyaulacoid cysts increases in the middle part of this interval. The distribution of *Polykrikos* cysts is known to be inner bay areas and *O. centrocarpum* increases from the inner bay to the bay mouth (Matsuoka, 1985a, Kobayashi *et al.*, 1986). These observations indicate that oceanic water invaded the bay in large quantities.

Ca. 5,400 y.B.P. ~ ca. 5,200 y.B.P. (assemblage zone D): An abrupt reduction of cyst number suggests closing of the bay mouth.

Ca. 5,200 y.B.P. ~ ca. 3,000 y.B.P. (assemblage zone C): Cysts increase again, but the ratio of *Polykrikos* rises to more than the level in the period before ca. 5,400 y.B.P. The environment returned to a stable inner bay, but obstruction to sea water is greater than before. This is reflected in a decreased number of Peridinioid cysts. These conditions indicate that the flow of marine water is blocked. Thereafter, the number of cyst gradually decreased and the relative ratio of *Polykrikos* increased further. At this time, planktonic freshwater algae occurred and brackish water diatoms increased (Kashima, 1987). These data suggest that desalination of the lake progressed slowly.

Ca. 3,000 y.B.P. ~ ca. 536 y.B.P. (assemblage zone B): Occurrence of cysts is scarce, but a lot of *Polykrikos* cysts are regularly found

during this period. The lake was almost completely filled with fresh water but was periodically invaded with marine water.

Ca. 536 y.B.P. ~ present (assemblage zone A): This interval yields a stable number of cysts again. The cyst assemblage resembles that of surface sediments (Kojima, unpublished data). Therefore the conditions of this lake became similar to the present conditions which were formed by a tsunami in 1498 (Nonaka 1977).

This paper describes paleoenvironment based on the distribution of cysts, but this type of research has just started in Japan.

Taxonomy

There are two systems used for the classification of dinoflagellate cysts and motile forms, but at the present the two systems have not yet been unified. Because the relationship between motile and cyst forms is not well understood and some dinoflagellates do not produce cysts. Furthermore, we cannot estimate motile forms of fossil species. Although the systems have been improved, in this paper the criterion set forth by Matsuoka (1985a, 1987b) are followed.

All specimens are stored in the Laboratory of Paleobotany at Osaka City University (OCU).

Class Dinophyceae Fritsch, 1929

Family Peridiniaceae Ehrenberg, 1832

Cyst-genus *Selenopemphix* Benedek, 1972
emend. Bujak 1980

Type species; *Selenopemphix nephroides* Benedek, 1972

Selenopemphix hamanaensis, sp. nov.

Figures 5-1-6

Derivation of name: From its occurrence in Lake Hamana.

Holotype: Core 85H-1, interval 10.60~10.61 m, slide 85H-1 10.60~10.61 m ① (97.1/33.2 L) (OCU-1). Holocene, Lake Hamana, Shizuoka Pref., Central Japan.

Diagnosis: *Intermedia pentagonia* cysta brunneola in coloris compressaque in directionis polaris. Murus cum lubrica pagina ornatus flexibilis angustis aciculatis spinis, aequaliter distributis supra testam. Archeopyle intercalata 2a.

Diagnosis: The intermediate pentagonal cyst is compressed in the polar direction and is pale brown in color. The wall has a smooth surface and is ornamented with flexible slender acicular spines uniformly distributed on the test. Archeopyle intercalary 2a.

Descriptions: The test is peridinioid from the equatorial view and nearly circular from the polar view. The cyst wall consists of an autophragm only. The epicyst has dome-like or conical structure and the hypocyst may have a slightly antapical lobe. The paracingulum is confirmed by faint ridges but each adcingular border may be marked by rows of spines. The parasulcus is occasionally recognized by a slight indentation.

Dimensions: Width 74~54 μm , Thickness 72~48 μm , Length of spine 4~24 μm (20 specimens measured).

Remarks: *Seleno. hamanaensis* is similar to *Seleno. armata* and *Seleno. quanta*, but the former differs from the latter in being more completely circular from the polar view and having more slender spines. This species has a relatively constant width but the spines show various lengths, ranging from 4 μm to 24 μm . The cyst is mostly observed from the polar view because the morphological characteristics cause the cyst to be oriented in the same direction. No motile form of this cyst is known, but it probably belongs to *Protoperidinium*.

Genus *Protoperidinium* Bergh, 1882

Cyst of *Protoperidinium* sp.

Figure 6-3

Description: A medium-sized, brown cyst made up of two layers. The periphragm forms a membranous structure. The external form from the dorso-ventral view is pentagonal. The epicyst is conical to dome-like in shape, and the hypocyst is trapezoidal from the equatorial view. Both the apical and antapical parts have no prominent projections. The paracingulum is obviously distinguished by a membranous ridge. The parasulcus is obscure. Archeopyle intercalary, formed by the loss of plate 2a (?).

Dimensions: Length 50~60 μm , Breadth 58 μm , Breadth of cingulum 6~7 μm (2 specimens measured) (OCU-2).

Incertae sedis

Dinoflagellate cyst ? type A

Figure 6-9

Description: This small spherical cyst is dark brown in color. The test is covered with spines but there are not many. The spines are short (about 1 μm) and conical in shape. The shell is approximately 30 μm in diameter except for the spines. The archeopyle is chasmic.

Occurrence: 85H-2, -9.60~ -9.61 m. (OCU-3)

Dinoflagellate cyst ? type D

Figure 6-10

Descriptive remarks: Type D is small, spherical and pale brown. Its test is covered by spines but there are only a few. Spines are each about 4 μm in length. The central body is approximately 30 μm in diameter. This acritarchous cyst is similar to "Dinoflagellate cyst ? type A", but differs in having longer processes and a lighter-colored wall.

Occurrence: 85H-2, -6.40~ -6.41 m, -

8.80~ -8.81 m, -12.60~ -12.61 m, -24.70
~ -24.71 m, -29.50~ -29.51 m.(OCU-4)

Dinoflagellate cyst ? type E

Figure 6-8

Descriptive remarks : Like type A, type E is small spherical and dark brown. Its test is overlaid by spines, but the spine density is higher than in types A and D. Spines are each 1~3 μm in length. The test is 20~30 μm in diameter, except for the spines.

Occurrence : 85H-2, -31.20~ -31.21 m, -32.00~ -32.01 m, -34.30~ -34.31 m. (OCU-5)

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浜名湖の完新統から産出する渦鞭毛藻シストの分析: 浜名湖の完新統コア試料から渦鞭毛藻シストが産出した。産出したシスト群集は主にペリディニウムグループに属する *Brigantidium* spp., *Selenopemphix quanta*, *Seleno. hamanaensis*, ギムノディニウムグループに属する *Polykrikos schwartzii*, *Poly. kofoidii*, *Pheopolykrikos hartmannii* からなり、ゴニオラックスグループ、テュバクロディニウムグループに属するシストも少量産出した。これらのシストは6つの群集帯にわかれ、構成種の変化より安定内湾域から汽水湖、さらに淡水湖をへて再び汽水湖という環境変化が推定された。なお、1新種 (*Selenopemphix hamanaensis*) を含む5種を記載した。小島夏彦

**885. FOORDICERAS AND DOMATOCERAS (NAUTILOID
CEPHALOPODS) FROM THE UPPER PERMIAN
TOYOMA FORMATION, SOUTHERN KITAKAMI
MASSIF, NORTHEAST JAPAN***

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Abstract. Two specimens of nautiloids, identified as *Foordiceras* cf. *F. wynnei* and *Domatoceras ogatsuense*, n. sp., are described from the Lower Toyoman Series (Upper Permian, Dzhulfian) in the Southern Kitakami Massif. The genus *Foordiceras* is first described from the Dzhulfian in Japan, and the genus *Domatoceras* is also first recorded from Japan in this paper. These nautiloids are closely related to those from the Dzhulfian beds of the Central Tethys.

Key words. *Foordiceras*, *Domatoceras*, nautiloid, Permian, Southern Kitakami, Northeast Japan.

Introduction

During his geological studies in the Ogatsu district, Southern Kitakami Massif, one of the authors (F.T.) collected two specimens of nautiloids, referable to *Foordiceras* and *Domatoceras*, from the Upper Permian (Dzhulfian) Toyoma Formation. They warrant description because the occurrence of cephalopods is quite limited in the younger Paleozoic formations of Japan. Additionally, the present specimen of *Domatoceras* represents a new species.

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manuscript.

Geological and paleontological note

The specimens described here as *Foordiceras* cf. *F. wynnei* (Waagen) and *Domatoceras ogatsuense*, n. sp., were discovered in 1985 and in 1987, respectively, from sandy shale of the basal part of the Toyoma Formation exposed on a river-bed, about 500 m northeast of Myojin, Ogatsu-cho, Monoo-gun, Miyagi Prefecture (Figure 1). The Permian of the Ogatsu district is composed of the Oyakejima Formation and the overlying Toyoma Formation. The latter is unconformably overlain by the Triassic (Upper Scythian) Hiraiso Formation. Some cephalopods, such as *Stacheoceras* sp. and *Timorites intermedium* have been reported from the Oyakejima For-

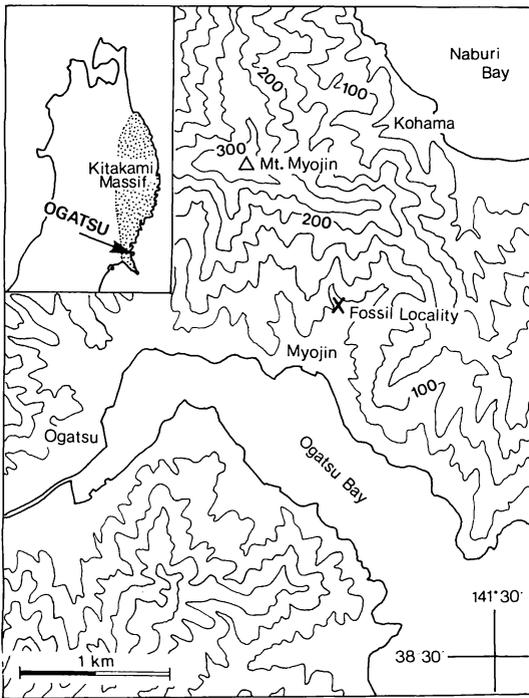


Figure 1. Map showing the fossil locality.

mation (Hayasaka, 1940; Ehiro *et al.*, 1986), and *Cycloceras* nov. sp. (= *Protocycloceras* cf. *P. cyclophorum*), *Stacheoceras otomoi* and *S.* sp. from the Toyoma Formation (Hayasaka, 1924; Shimizu and Obata, 1936; Ehiro *et al.*, 1986). Murata and Shimoyama (1979) divided the Toyoman Series into three zones based on molluscan fossils and they recognized the lower two zones in the Ogatsu district. The present specimens were obtained from the lowest zone *i.e.* Lower Toyoman Series. The Lower-Middle Toyoman Series corresponds to the *Araxoceras* Zone of Ehiro (1987) and is correlated to the Dzhulfian of Transcaucasia and Iran, and to the Wujapingian of South China (Ehiro and Bando, 1985; Ehiro, 1987).

Species of *Foordiceras* have already been reported in the Japanese Islands from the formations slightly older than the Toyoma Formation, *i.e.*, the Kanokura Formation (Guadalupian-Abadehian) or its correlatives. They are *Foordiceras wynneiforme* from the

Oguradani beds of Central Japan (Hayasaka and Ozaki, 1955) and from the Kanokuran Series in the Southern Kitakami Massif (Kozumi, 1975), *F. gregarium* from the Kashiwadaira Formation in the Abukuma Massif, Northeast Japan (Yanagisawa, 1967), and *F. akiyamai* and *F. ?* sp. from the Kanokuran Series in the Southern Kitakami Massif (Hayasaka, 1960, 1962). The present study is the first description of *Domatoceras* from Japan.

The species *Foordiceras wynnei*, to which the Ogatsu specimen is compared, is only known as a single specimen collected from the Upper *Productus* Limestone (Chhidru Formation) in the Salt Range of Pakistan (Waagen, 1879). The Chhidru Formation is now correlated to the Upper Dzhulfian, based on paleontological evidence (Pakistani-Japanese Research Group, 1985). *Domatoceras ogatsuense*, n. sp., is closely related to *D. hunicum*, originally described by Diener (1903) from a limestone of Chitichun in the Tibetan Himalayas in association with ammonoids such as *Cyclolobus walkeri* Diener and *Xenodiscus carbonarius* Waagen. It is also known from the Dzhulfian *Araxoceras* beds of Soviet Dzhulfa (Ruzhentsev and Sarycheva, 1965) and those of Iranian Julfa (Teichert and Kummel, 1973).

Systematic description

Family Tainoceratidae Hyatt, 1883

Genus *Foordiceras* Hyatt, 1893

Type species: — *Nautilus goliatus*
Waagen, 1879

Foordiceras cf. *F. wynnei* (Waagen)

Figures 2-1a, 1b

cf. *Nautilus wynnei* Waagen, 1879, p. 55, pl. 3, figs. 1a-b.

Material: — A single internal mold, obtained by F. Takizawa in 1985, from Myo-

jin, Ogatsu. GSJ. (Geol. Surv. Japan) F. 12866.

Description: — The specimen is deformed into an ellipse and only its right side is preserved. It is fairly large, thickly discoidal, evolute, with a wide umbilicus. Measurements at the preserved end, in the deformed state, are as follows (in mm):

Diameter (D)	116
Umbilical diameter (U)	44 (U/D 0.38)
Height (H)	38 (H/D 0.33)

The whorl section is rectangular to trap-ezoidal, with an apparently broadly arched venter, and flat side that converge dorsally. Ventral shoulders are narrowly rounded, and umbilical shoulders more broadly rounded. Prominent transverse ribs extend from the ventral shoulders to the umbilical shoulders. They are nodose on the ventral margin and diminish gradually toward the umbilical shoulder. The number of ribs is estimated to be nineteen on the last whorl. Suture is unknown.

Comparison: — With respect to the general shell-form and shell ornamentation, the Ogatsu specimen is comparable with *Foordiceras wynnei* (Waagen, 1879), from the Upper *Productus* Limestone of the Salt Range, Pakistan. Our specimen has less sinuous ribs, however, than those of the latter.

The present specimen somewhat resembles another Salt Range species *Nautilus flemingianus* Koninck (Waagen, 1879, p. 48, pl. 3, figs. 2a, b) in the general shell form, but it is distinguished from the latter in having prominent nodes at the ventro-lateral shoulders. The Japanese species *Foordiceras wynneiforme* Hayasaka and Ozaki (1955, p. 183, pl. 1, fig. 1) is closely allied to *F. wynnei* and consequently to the present specimen. However, the former differs from the last two in its less conspicuous nodes (Hayasaka and Ozaki, 1955, p. 184).

Occurrence: — Dark gray sandy shale of the basal part of the Toyoma Formation, NE of Myojin, Ogatsu-cho, Monoo-gun, Miyagi Prefecture, Northeast Japan.

Family Grypoceratidae Hyatt,
in Zittel, 1900

Genus *Domatoceras* Hyatt, 1891

Type species: — *Domatoceras umbilicatum*
Hyatt, 1891

Domatoceras ogatsuense Ehiro and
Takizawa, n. sp.

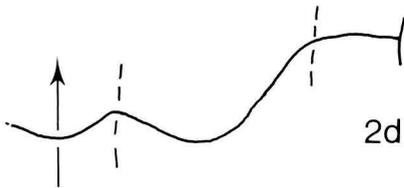
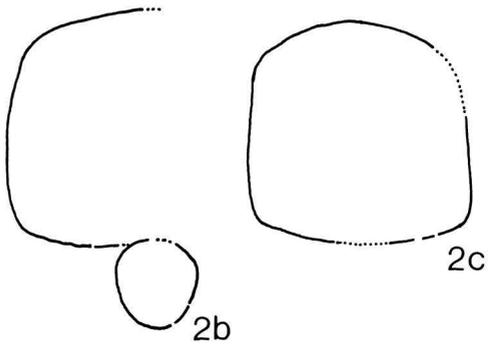
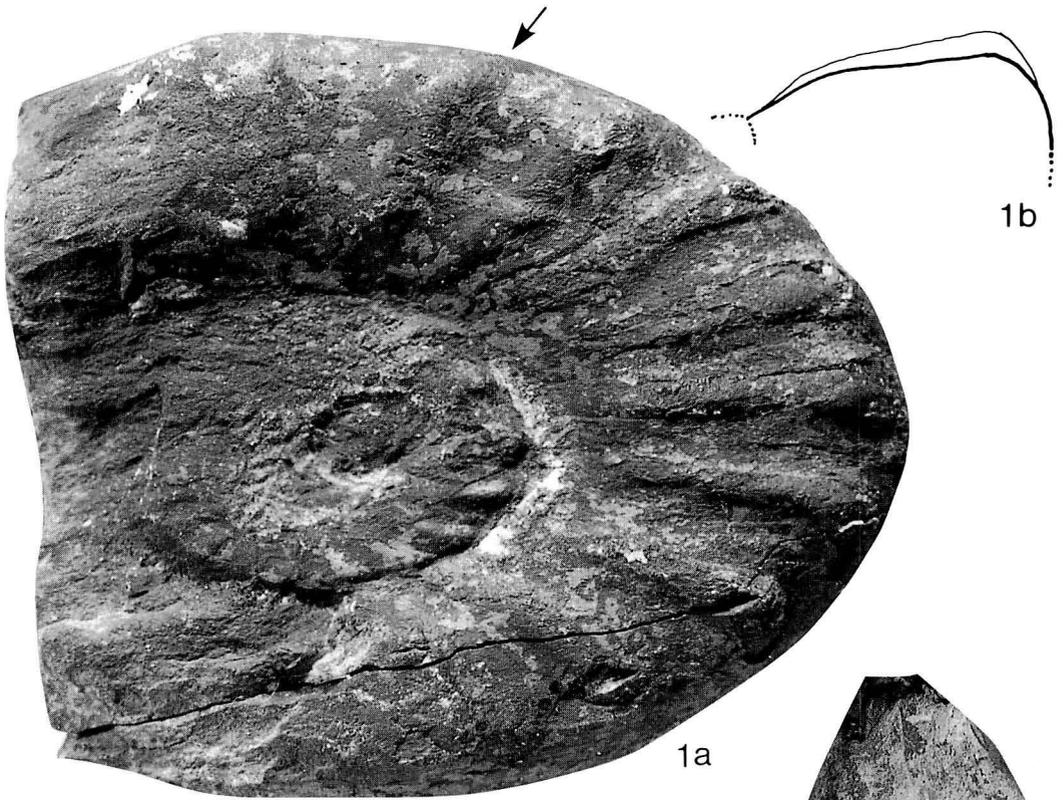
Figures 2-2a—2d

Material: — A single fragmental internal mold, obtained by F. Takizawa, in 1987, from Myojin, Ogatsu. Holotype, GSJ. F. 12867.

Diagnosis: — *Domatoceras* with nodose ribs on the lateral zone and a subcircular cross section in early stage; at maturity, the flanks are smooth and the cross section subquadrate.

Description: — The specimen is elliptically deformed, with parts of two volutions. The conch is fairly large, thickly discoidal, evolute, with a wide and deep umbilicus. Fine biconvex growth lines are preserved on the umbilical wall and on a part of the lateral zone of the inner whorl. The outer whorl is of subquadrate section, with smooth surface. The venter is slightly convex and the flanks are flat, converging slightly toward the venter. The whorl height near the adapical end of the outer volution is about 35 mm, and the corresponding greatest width, near the umbilical shoulder, measures about 35 mm. The ventrolateral and umbilical shoulder, measures about 35 mm. The ventrolateral and umbilical shoulders are rounded. The inner whorl is of subcircular section, with prominent ribs on the lateral zone. They are

→ **Figure 2.** **1a—1b**, *Foordiceras* cf. *F. wynnei* (Waagen), GSJ. F. 12866, **1a**, lateral view; **1b**, cross section, thin line shows the cross section through rib, $\times 0.8$. **2**, *Domatoceras ogatsuense*, n. sp., Holotype, GSJ. F. 12867, **2a**, lateral view; **2b**, **2c**, cross sections; **2d**, suture line $\times 0.8$. Arrows (b, c) mark the position of the cross sections.



nodose at the ventrolateral margin and diminish toward the umbilical shoulder. Height and width at the adoral end of the inner whorl are 16 and 15 mm, respectively, in the deformed state.

The suture (Figure 2-2d) has a ventral lobe that occupies most of the venter and a moderately deep lateral lobe that occupies nearly all of the flank.

Comparison: —In the general shape of the whorl section and in the form of the suture, the present new species is comparable to *Domatoceras hunicum* (Diener, 1903, p. 5, pl. 1, figs. 1a-c; Shimansky, in Ruzhentsev and Sarycheva, 1965, p. 41, pl. 15, figs. 12a-b; Teichert and Kummel, 1973, p. 421, pl. 1, figs. 7-8, pl. 2, figs. 3-4), but it differs from the latter in having convex venter in the outer whorl, deeper umbilicus and prominent ribs in the inner whorl.

Upper Permian species, *Domatoceras parallelum* (Abich, 1878, p. 17, pl. 3, fig. 2; Arthaber, 1900, p. 213, pl. 18, figs. 2a-2c; Shimansky, in Ruzhentsev and Sarycheva, 1965, p. 41, pl. 15, fig. 10; Teichert and Kummel, 1973, p. 421, pl. 2, figs. 1-2, 9-10) and *D. gracile* Shimansky (Shimansky, in Ruzhentsev and Sarycheva, 1965, p. 160, pl. 16, fig. 1), are clearly distinguished from the present specimen in the compressed whorl section.

Occurrence: —Dark gray sandy shale of the basal part of the Toyoma Formation, NE of Myojin, Ogatsu-cho, Monoo-gun, Miyagi Prefecture, Northeast Japan.

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Hiraiso 平磯, Kanokura 叶倉, Kashiwadaira 柏平, Monoo-gun 桃生郡, Myojin 明神, Ogatsu 雄勝, Oguradani 小椋谷, Oyakejima 大八景島, Toyoma 登米,

南部北上山地の上部ベルム系登米層産ノーチロイド *Foordiceras* および *Domatoceras*: 南部北上山地の下部登米統 (上部ベルム系ズルファー階) 産の 1 新種を含むノーチロイド 2 種, *Foordiceras* cf. *F. wynnei* および *Domatoceras ogatsuense*, n. sp. を記載した。*Foordiceras* はわが国のズルファー階から, *Domatoceras* はわが国からはじめて報告された。これらはそれぞれ中部テキサス地域のズルファー階から産するものに近縁である。

永広昌之・滝沢文教

886. TAXONOMY AND MORPHOLOGIC DIVERSITY OF *MANDARINA* (PULMONATA) IN THE BONIN ISLANDS*

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Abstract. Fifteen fossil and extant species including seven new species of the Pleistocene. Recent land snail genus *Mandarina* (Pulmonata; Camaenidae) of the Bonin Islands are described, and their morphologic and possible interspecific relationships are considered. *Mandarina* has undergone remarkable adaptive radiation in this small, isolated archipelago. The diversified shell morphology of these snails is characterized by complex allometric trends generated by the interplay of juvenile shell form and later shell growth patterns. Morphologic features in the juvenile stage are little influenced by habitat conditions, and the classification of species based on juvenile shells matches well with that based on genitalia. In contrast, adult shell characters are strongly influenced by environmental conditions, suggesting that they are useful to consider habitats of fossil species. Phylogenetic relationships of these species were preliminarily reconstructed from quantitative analysis of juvenile shell and penial morphology. It is assumed that not only distinct diversification of shell morphology in the same stock but also convergence of adult shell features between the two species of different stocks has been occurred.

Key words. *Mandarina*, adaptive radiation, island biogeography, Bonin Islands.

Introduction

Mandarina, a peculiar land snail genus belonging to the pulmonata Camaenidae, has undergone adaptive radiation in the Bonin Islands in northwestern Pacific, as Darwin finches have done in Galapagos. Indeed, the Bonin Islands have been entirely isolated from other regions, and most animals and plants are indigenous.

The biota in small isolated islands has attracted many biologists' attention, and their works have much contributed to establish theories on biogeography and evolution. "In the science of biogeography, the island is the first unit that the mind can pick out and begin to comprehend. By studying clusters of islands, biologists view a simpler micro-

cosm of the seemingly infinite complexity of continental and oceanic biogeography" (MacArthur and Wilson, 1967, p. 3). I regard that land snails are one of the best materials to study the island life from the viewpoint of evolution because of their low dispersal ability and diverse life habits as well as their rich fossil records. Indeed, Gould (1969a) recognized in his study on Bermudian land snails that extinction and speciation as well as very rapid morphological change frequently occurred during the Pleistocene. Similar events can be expected well in the fossil record of *Mandarina* in Bonin, and this is the main reason why I treat the land snail in this study. The final object is to understand the tempo and mode of evolution from various paleontological and neontological viewpoints. But there are two problems to be conquered. First, the taxonomy of *Man-*

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darina has not yet been studied sufficiently. Two Holocene fossil species *M. luhuana* (Sowerby, 1839), and *M. pallasiana* (Pfeiffer, 1850), which were formerly regarded as Pleistocene fossil species (Iwasaki and Aoshima, 1970, Habe, 1973), and six living species. *M. mandarina* (Sowerby, 1839), *M. hirasei* Pilsbry, 1902, *M. hahajimana* Pilsbry, 1902, *M. ponderosa* Pilsbry, 1901, *M. exoptata* Pilsbry, 1902, and *M. suenoae* Minato, 1978, were hitherto described (Sowerby 1839, Pfeiffer 1850; Pilsbry 1901, 1902a, b, c, d; Minato 1978). The descriptions of these species by previous authors are mostly too insufficient to realize the exact taxonomic relationship because they are based on the external morphology of adult shells and genitalia in small samples. Second, no paleontological description was made on *Mandarina* except for the Holocene species, and abundant occurrence of fossil from the Pleistocene deposits has never been recorded in the Bonin Islands before this work. Thus the main purpose of this paper is (1) to revise the previous descriptions, (2) to describe fossil forms, and (3) even if preliminarily, to reconstruct the phylogenetic relationships of these living and fossil species.

The genus *Mandarina* was proposed by Pilsbry (1894), designating *M. mandarina* as the type species. Pilsbry (1894, 1928) regarded the genus as indigenous to Bonin. Subsequently, Emura (1943) and Minato (1978) supported Pilsbry's view from the observation of genitalia.

Mandarina is strikingly diversified in the Bonin Islands, occupying various habitats such as tree, ground, mountain forest and coastal bush. This is probably because no other large land snails could reach this archipelago. The adaptive radiation produced unusually wide inter- and intraspecific variation in adult shell size and form (e.g., apertural shape, presence or absence of umbilicus and keel) and shell coloration. For this reason, it is difficult to classify *Mandarina* species simply only from adult shell charac-

ters. In this paper I evaluate taxonomic significance of various morphologic characters of the shell and genitalia in living samples, and the results are applied to the classification of fossil samples.

Material

The present study is based on 43 living samples belonging to 10 species and 27 fossil samples belonging to 11 species (6 extant and 5 extinct species). The symbol, number of individuals and age of each samples are indicated in Table 1, and the exact locality is shown in Figure 1. Though the number of individuals is not always sufficiently large for statistical treatment, these living samples seem to represent local populations. Fossils were collected from the Holocene dunes and Pleistocene cave or fissure deposits. All of the specimens are deposited in the University Museum, University of Tokyo (UMUT).

Because the cave and fissure deposits are commonly poorly stratified, it is often difficult to recognize fossil populations on the basis of these samples. They may represent some mixtures of allochronic living populations. Therefore, I determined the absolute age of selected individuals of fossil specimens by electron spin resonance (ESR) method. As shown in Table 2, the result of ESR dating suggests considerably long time spans for such fossil samples. For instance, the ESR age for a sample from the fissure deposit of Minamizaki (Loc. 14) ranges from 16,000 yr B.P. to 53,500 yr B.P., suggesting a mixture of allochronic individuals. The result, however, is coincident with the ^{14}C age ($32,400 \pm 700$ yr B.P.) which was obtained about a bulk of 50 gram individuals. Because the present results of ESR and ^{14}C datings must be further cross-checked by other method, they are applied in this paper only to the preliminary estimation and discrimination of sample ages.

Table 1. Sample list of *Mandarina*. L : Living, H : Holocene, P : Pleistocene.

Species (forma)	Sample	Loc.	N	Age	Species (forma)	Sample	Loc.	N	Age	
<i>M. aureola</i>	A18	18	25	L	<i>M. hayamii</i>	Y14(P)	14	14	P	
	A18(P)	18	24	P		<i>M. sp.</i>	F1	1	2	L
	A24	24	20	L	<i>M. mandarina</i>		M3	3	19	L
	A24(H)	24	7	H			M4	4	12	L
	A25	25	30	L			M5	5	10	L
	A26	26	25	L			M6	6	10	L
	A27	27	25	L	M8		8	18	L	
	A27(H)	27	10	H	<i>M. nola</i>	N14(P)	14	12	P	
A28(H)	28	11	H	<i>M. chichijimana</i> (A)		Ca3	3	30	L	
<i>M. polita</i>	O17	17	4		L	Ca14(P)	14	52	P	
	O20	20	15	L	<i>M. chichijimana</i> (B)	Cb7	7	8	L	
	O21	21	6	L		Cb8	8	7	L	
	O22	22	19	L		Cb9	9	7	L	
	O23	23	23	L		Cb10(H)	10	18	H	
	O23(P)	23	25	P		Cb11	11	2	L	
<i>M. ponderosa</i> (A)	Pa26	26	16	L		Cb12	12	17	L	
	Pa27	27	25	L		Cb13	13	24	L	
	Pa27(H)	27	14	H		Cb14	14	25	L	
	Pa28(H)	28	1	H	Cb14(H)	14	32	H		
	Pa29	29	9	L	Cb15(H)	15	30	H		
	Pa30	30	7	L	Cb14(P)	14	16	P		
<i>M. ponderosa</i> (B)	Pb18	18	4	L	<i>M. chichijimana</i> (C)	Cc2	2	14	L	
	Pb18(P)	18	12	P		<i>M. hirasei</i>	H2	2	4	L
	Pb19	19	24	L	H5		5	18	L	
	Pb20	20	9	L	H10(H)		10	10	H	
<i>M. ponderosa</i> (C)	Pc23(P)	23	4	P	H13		13	4	L	
<i>M. hahajimana</i>	J18	18	4	L	H14(H)		14	22	H	
	J19	19	10	L	H15(H)		15	10	H	
	J20	20	10	L	<i>M. io</i>	I14(P)	14	16	P	
	J23	23	8	L		<i>M. luhuana</i> (A)	La14(H)	14	30	H
	J26	26	1	L	La15(H)		15	30	H	
	J27	27	6	L	<i>M. luhuana</i> (B)	Lb14(P)	14	30	P	
<i>M. exoptata</i>	E20	20	10	L		<i>M. luhuana</i> (C)	Lc10(H)	10	8	H
<i>M. suenoae</i>	S6	6	3	L	<i>M. luhuana</i> (D)		Ld10(H)	10	1	H
	S8	8	10	L		<i>M. titan</i>	T15(P)	15	4	P

Methods

Genital apparatus: Genital morphology, which seems to be important for the systematics of *Mandarina*, has previously been examined only to a little extent (Emura 1943;

Minato 1978). In the present study, not only the external but also the internal morphology of penis was examined under an optical microscope about five to ten specimens for each living species.

Shell form: I examined various shell char-

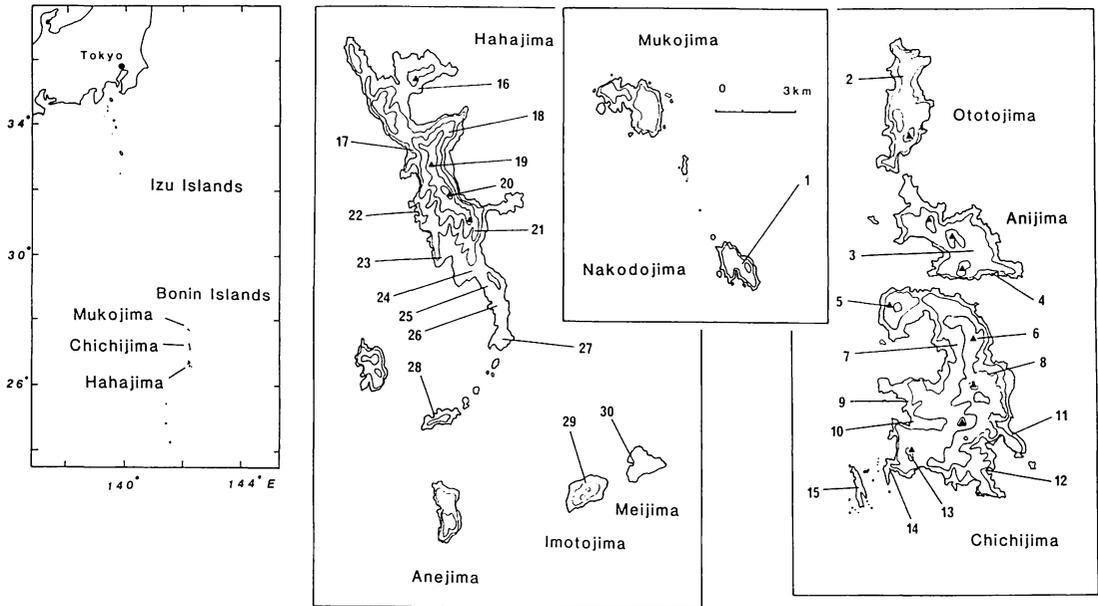


Figure 1. Sample localities of fossil and living population of *Mandarina*.

1: Byobuyama, 2: Hironeyama, 3: Anijima (Central part of plateau area), 4: Mansakuhama, 5: Mikazukiyama, 6: Yoakeyama, 7: Sakaiura, 8: Hatsuneyama, 9: Kohiyama, 10: Kominato, 11: Higashikaigan, 12: Nishikaigan, 13: Takayama, 14: Minamizaki (John Beach), 15: Minamijima, 16: Higashiyama, 17: Nagahama, 18: Sekimon, 19: Sakaigatake, 20: Chibusayama, 21: Kensakiyama, 22: Nishiura, 23: Okimura, 24: Nankinhama, 25: Nakanodaira, 26: Houraine, 27: Minamizaki, 28: Hirashima, 29: Imotojima, 30: Meijima. Contour interval: 100 m.

Table 2. Cross check between ^{14}C and ESR ages of fossil samples.

Locality	Facies	Data y.BP	
		Carbon 14	ESR
Chichijima			
Minamijima (Loc. 15)	Dune	960 ± 50	—
Minamizaki (Loc. 14)	Red soil	1550 ± 60	1500—2500
Minamijima (Loc. 15)	Brown soil	—	5000—13000
Minamizaki (Loc. 14)	Fissure deposits	32400 ± 700	16800—53500
Hahajima			
Minamizaki (Loc. 27)	Red soil	1990 ± 60	—
Sekimon (Loc. 18)	Cave deposits	9140 ± 110	—
Okimura (Loc. 23)	Cave deposits	13300 ± 130	—

acters at different growth stages. For this purpose, each shell was cut along the coiling axis and various portions were measured with an aid of a digital micrometer (accuracy, 1 μm) attached to a profile projector (Nikon, V16D). Basic morphology and measure-

ments of a *Mandarina* specimen in cross section are diagrammatically shown in Figure 2. Geometric parameters explaining the shape of spire and aperture analyzed are listed in Table 3. Adult shell can be easily recognized by their thickened and reflected outer

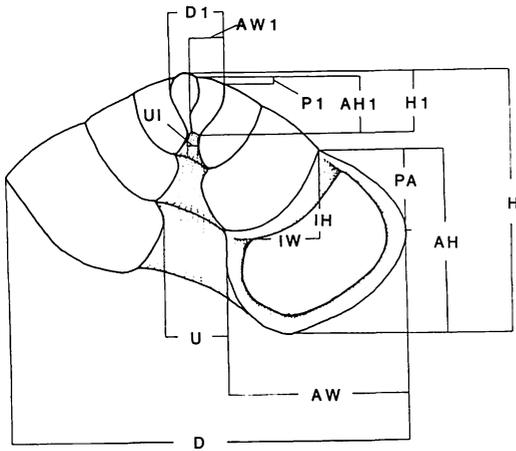


Figure 2. Linear measurements on a cross section of shell. For abbreviation of measurements see Table 3.

lip.

Color pattern: Longitudinal reddish bands are visible on the shells of some *Mandarina* species. Although the number and state of development of color bands are considerably variable even in a single population sample, their position on the whorls is invariable in many species: two bands appear on the upper part of whorls and one band on the lower part. In addition, the umbilical portion is sometimes tinged with reddish color.

I adopted a coding method to describe the color banding patterns in the samples examined; 1 for the uppermost band, 2 for the band just below the periphery, 3 for the band between periphery and umbilicus, and 4 for the band near the umbilicus (Figure 3). In the case of a very narrow band compared with the light colored ground, the code is described as "n". If a band is perfectly absent, the code is described as 0. In the case of fused bands, the code number is enclosed by parentheses.

Classification: Discrimination of living species is based on the following criteria.

1. If the specimens from a given locality or area can be classified into two groups on the basis of disjunct difference of genital

Table 3. Linear measurements and indices used in this paper. Peripheral angularity was provided at the 1/2 whorl before the adult aperture by the rank from 0 (rounded periphery) to 5 (periphery with distinctly sharp keel). IPA was measured at the 1/2 whorl before the adult aperture. Juvenile umbilicus was measured at the second whorl.

WH	: number of whorls
H	: shell height
H1	: shell height of the first whorl
D	: shell diameter
D1	: shell diameter of the first whorl
AH	: apertural height
AH1	: apertural height of the first whorl
AW	: apertural width
AW1	: apertural width of the first whorl
IH	: height of inner lip
IW	: width of inner lip
PA	: length of aperture from top to periphery
IPA	: index of peripheral position (PA/AH)
P1	: value of PA in the first whorl
U	: width of umbilicus
UM	: relative width of umbilicus (U/D)
UI	: juvenile umbilicus width
UJ	: relative width of juvenile umbilicus
KE	: index of peripheral angularity

morphology (especially penial internal ornamentation), the two groups are regarded as different species.

2. If the two samples from the two geographically separated areas are conchologically differentiated but have the same or only slightly different genital morphology, they are judged as belonging to different subspecies here treated as formae of the same species.

3. If the two samples with similar genital morphology occur at the same locality but inhabit different habitats, they are judged as different species.

By use of these criteria, more objective and biological classification was attempted. However, it is not easy to apply rigid biological species concept. For instance, a complex hybridization may occur between popula-

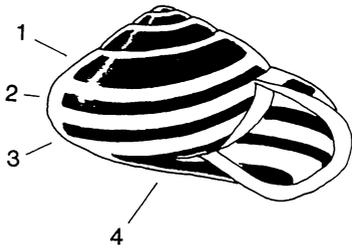


Figure 3. The coding system for banding patterns. Uppermost band: 1, band above the lower periphery: 2, subperipheral band: 3, band around umbilicus: 4.

tions. Populations having similar genital morphology may be sometimes reproductively isolated from one another, as reviewed by Emberton (1988). In the case of fossil samples, species discrimination is based mainly on the disjunct difference of shell morphology in the early growth stage and its comparison with intrapopulational variation of shell morphology in living species.

Comparative morphology

Genital apparatus: External and internal penial morphology in *Mandarina* is diagram-

matically shown in Figure 4. The penial tube is long in every species, extremely narrow at the middle portion in some species (*M. aureola*, *M. ponderosa*, *M. polita*). The basal penis is thick in these three species. A collar-like muscular sheath attaches to the basal penis. External morphology of penis in each species is illustrated in Figure 5. The internal ornamentation of penis consists basically of several columns of equal-sized pilasters. In some species they show markedly longitudinal outgrowth. They vary both in size and shape among species. At the uppermost portion of penis, conical shaped or relatively flat verge is present surrounding the ejaculatory pore. Its shape, sculpture and size are different among species. Internal wall of basal penis is smooth without pilasters. It has longitudinally arranged smooth regular folds. Atrium, which is the portion between the genital pore and vaginal opening, has a smooth wall covering randomly arranged folds.

Seasonal variation in the size and shape of hermaphroditic duct, albumen gland and vagina are significant. Also, variation of

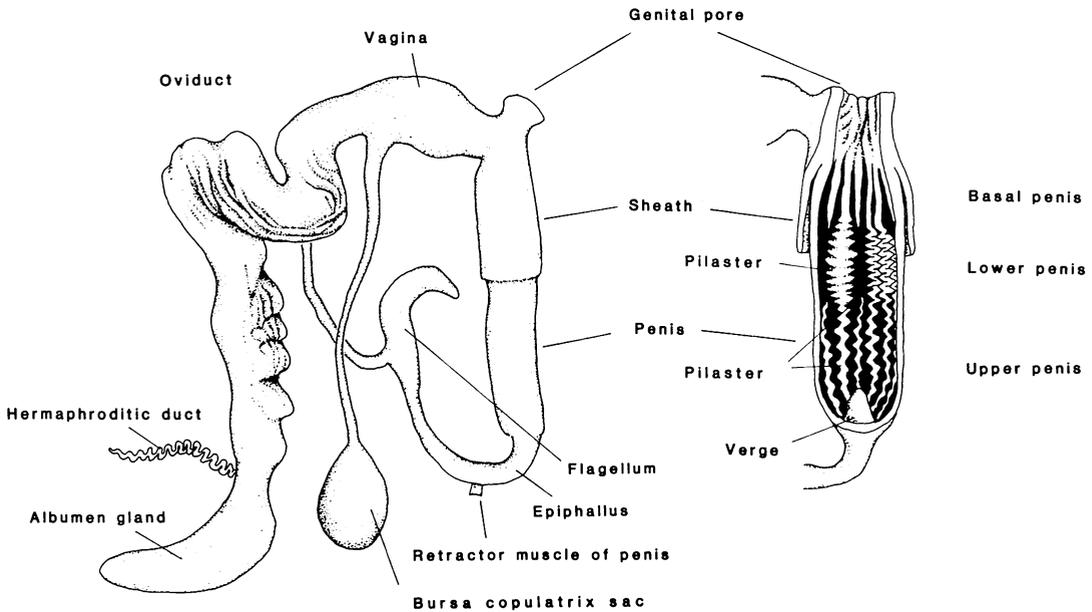
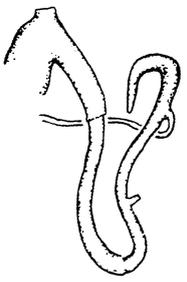
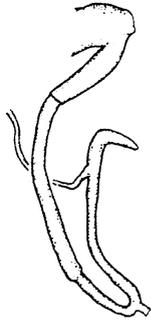


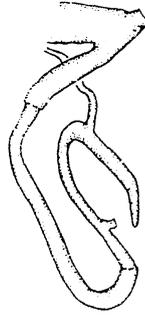
Figure 4. Diagrammatic genital morphology and terminology of *Mandarina*.



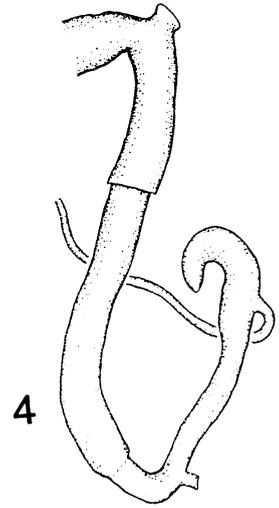
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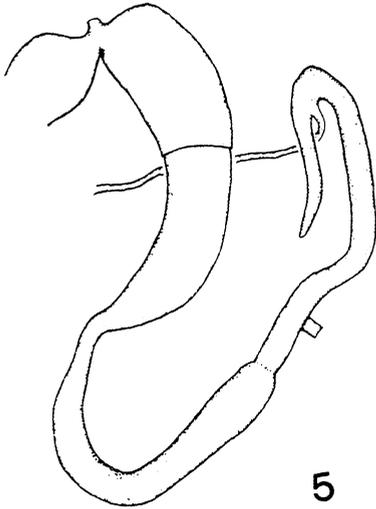
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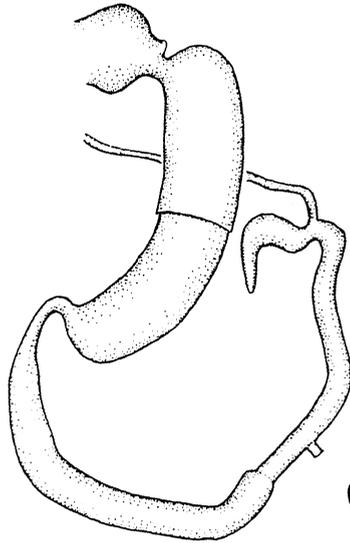
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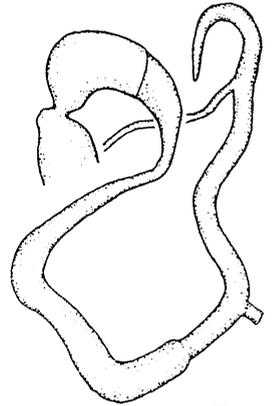
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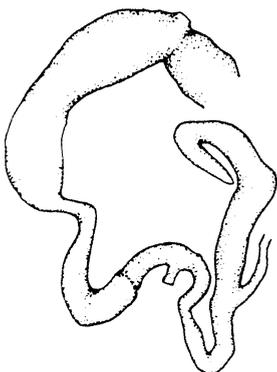
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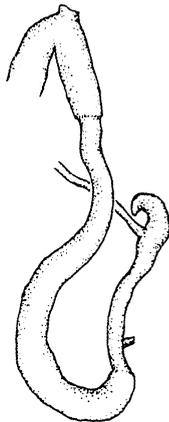
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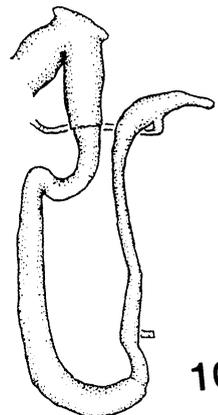
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9



10



penis length, sheath length, retractor-muscle length, and shape of folds in the basal penis within a given population is wide because of the difference of the contractile condition of the organ. The use of these characters for systematics therefore should be cautious. On the other hand, intra- and inter-population variation of sculptural details within a species is insignificant. For example, the internal penial morphology of two populations of *M. chichijimana* is essentially similar, though they can be apparently discriminated by shell features as forma A and forma B (Figures 6a-1, 6a-2). Because of the genital mor-

phological stability, each species seems to be defined adequately by the penial sculpture.

Shell morphology and color pattern: The shell shape of *Mandarinina* changes remarkably with growth. The ontogenetic change is explained by plotting the ratio of height to shell diameter versus whorl number for a typical specimen of each species (Figure 7). Some species having mutually similar shape in the juvenile stage show extremely different shape in the adult stage. On the other hand some other species having mutually different shape in the juvenile stage show similar shape in the adult stage. In addition, color pattern

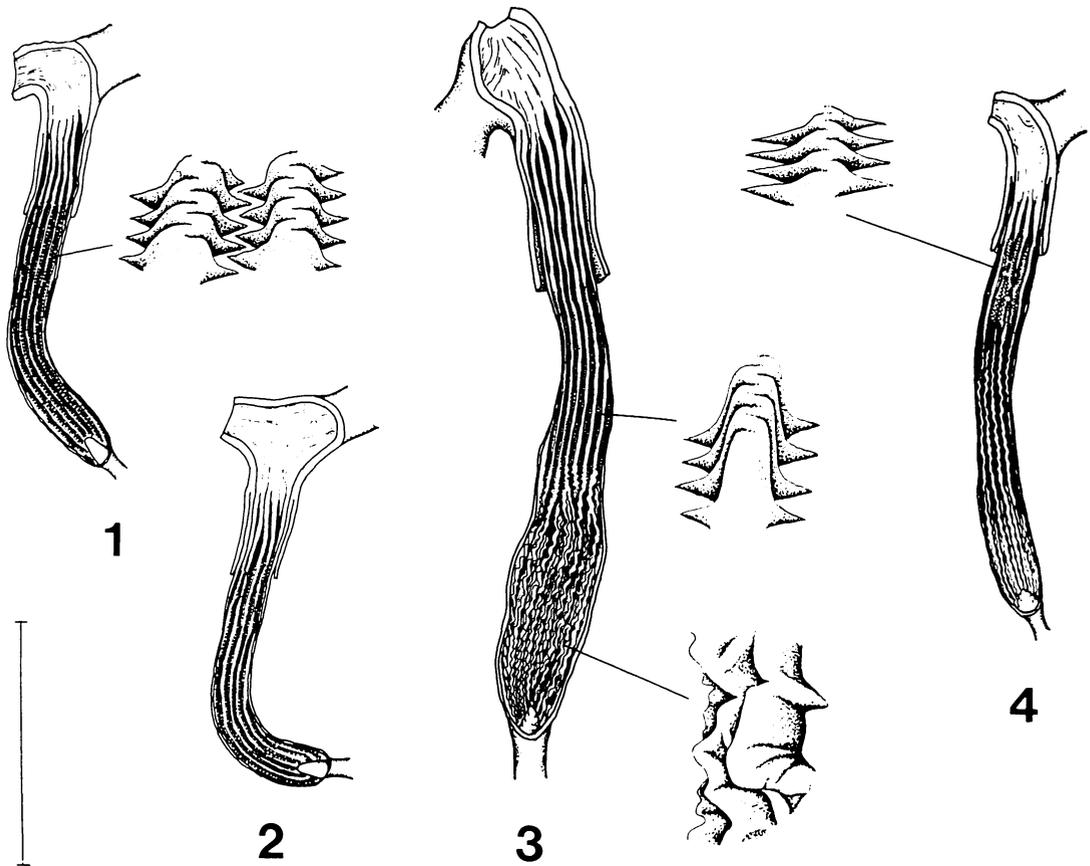
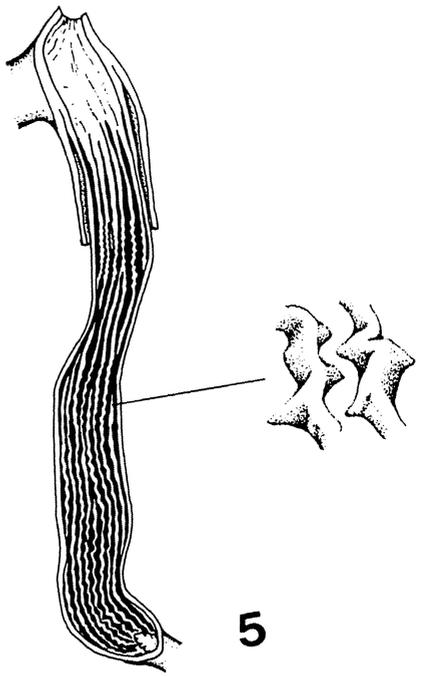
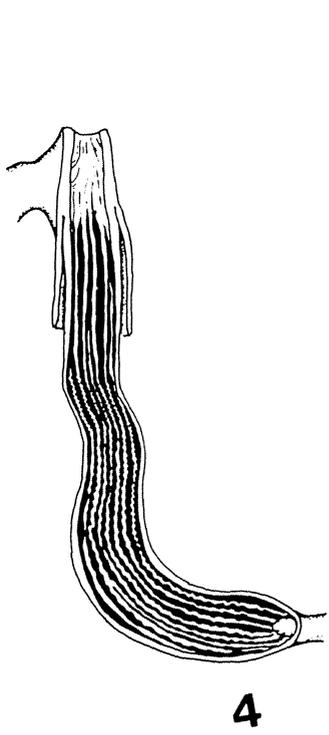
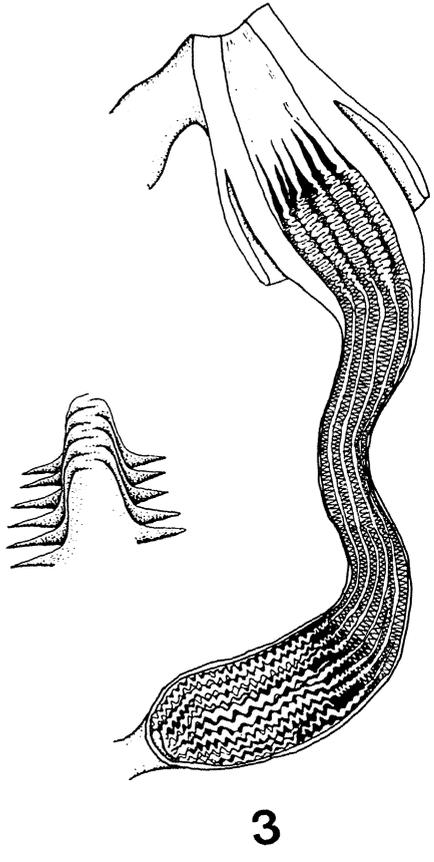
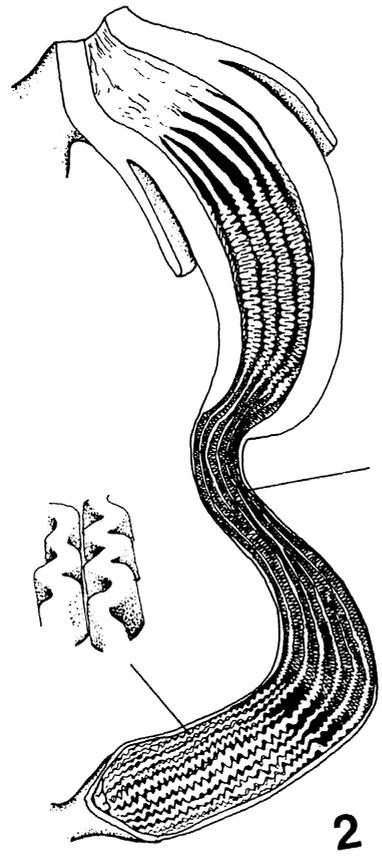
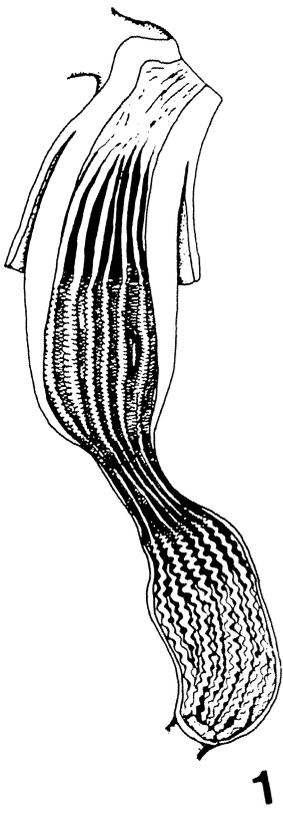


Figure 6a. Internal penial morphology in *Mandarinina* species: 1: *M. chichijimana* (B), Cb14; 2: *M. chichijimana* (A), Ca3; 3: *M. mandarina*, M3; 4: *M. hirasei*, H5. Scale bar indicates 1 cm.

← **Figure 5.** External penial morphology in *Mandarinina* species: 1: *M. chichijimana* (B), Cb14; 2: *M. chichijimana* (A), Ca3; 3: *M. hirasei*, H5; 4: *M. mandarina*, M3; 5: *M. aureola*, A18; 6: *M. aureola*, A25; 7: *M. polita*, O22; 8: *M. ponderosa* (A), Pa27; 9: *M. hahajimana*, J20; 10: *M. suenoae*, S8. Each scale bar represents 1 cm.

Satoshi Chiba



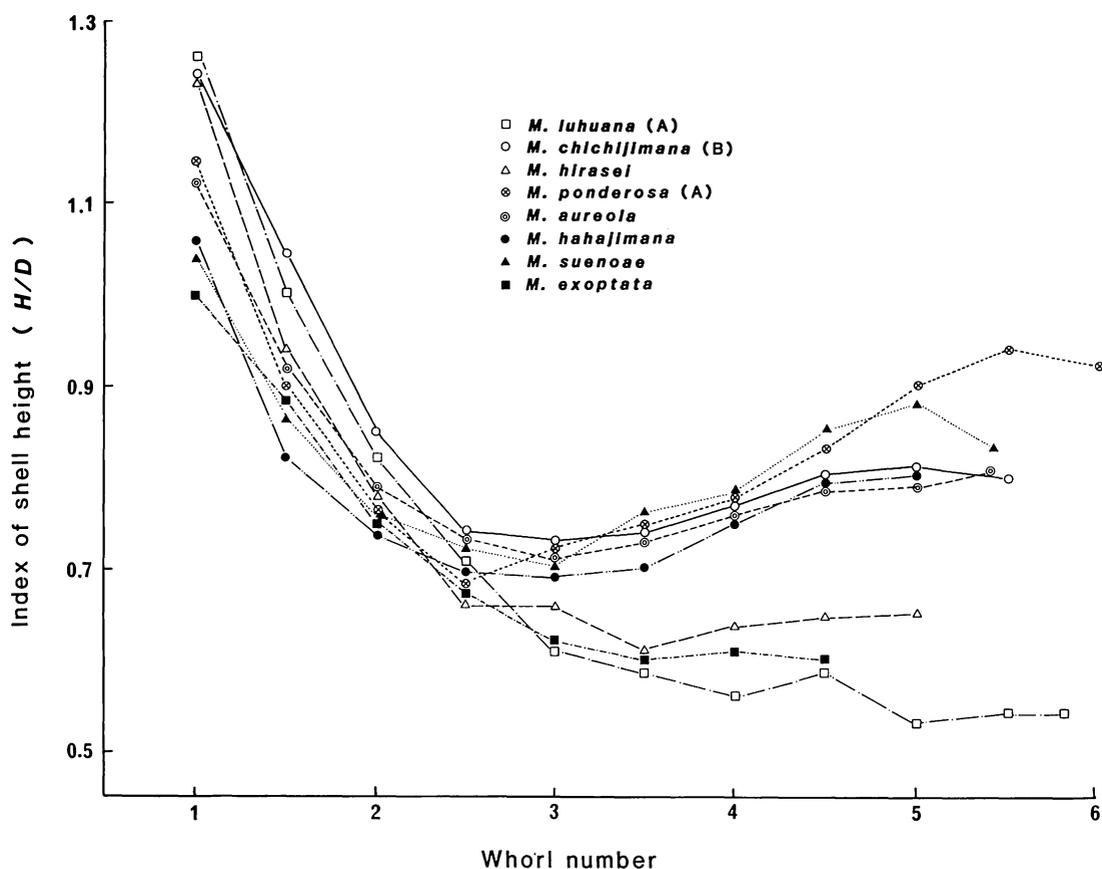


Figure 7. Ontogenetical change of shell height index versus whorl number in typical specimens of eight species of *Mandarina*. This indicates that the characters of juvenile shell in *Mandarina* species are overcome by the later shell growth pattern.

is often different between juvenile and adult stage. The variation of adult shell morphology in living and fossil species are summarized in Table 4. The variation of juvenile shell morphology among species are presented in Table 5.

Systematic description

Order Stylommatophora
 Family Camaenidae
 Genus *Mandarina* Pilsbry, 1894

1894. *Mandarina* Pilsbry, *Man. of Conch.*, (2), 9: 214

1901. *Boninia* Pilsbry, *Ann. Mag. Natural History*, 7, 8: 4

Type species: *Helix mandarina* Sowerby, 1839 by original designation.

Diagnosis. Shell solid, quite variable in shape. Shell diameter from 20 mm to 72 mm. Spire from high to low. Some species with umbilicus or sharp peripheral angle. Coloration variable within each species, but commonly with 2–4 reddish brown bands

Table 4. Linear measurements in mm, ratios and indices of adult shells. \bar{x} : mean, s : standard deviation. Sample sizes are given in Table 1.

Samples	WH	D	H	H/D	AH/AW	IW/AW	IH/AH	IPA	UM		KE	
	\bar{x} (s)	Min.	Max.									
M3	5.67(.16)	25.6(1.2)	20.1(1.0)	.788(.027)	.940(.030)	.628(.030)	.542(.057)	.434(.033)	—	—	0	0
M4	5.54(.14)	22.5(1.3)	18.2(1.1)	.808(.013)	.941(.025)	.616(.008)	.564(.027)	.431(.025)	—	—	0	0
M6	5.66(.14)	27.3(1.1)	21.7(1.7)	.794(.051)	.935(.043)	.578(.027)	.580(.053)	.428(.039)	—	—	0	0
M8	5.86(.17)	26.6(1.2)	21.7(1.3)	.814(.026)	.943(.032)	.595(.040)	.520(.034)	.454(.040)	—	—	0	0
N14(P)	5.10(.08)	22.0(.69)	17.7(.43)	.805(.031)	1.10(.027)	.508(.065)	.476(.024)	.431(.025)	.092(.101)	—	0	0
Ca3	5.15(.17)	23.8(1.2)	18.0(1.2)	.756(.029)	.956(.031)	.529(.046)	.465(.029)	.462(.030)	.078(.014)	—	0	1
Ca14(P)	4.80(.18)	29.4(1.6)	19.8(1.0)	.674(.037)	.961(.039)	.458(.037)	.469(.032)	.395(.034)	.103(.010)	—	0	4
Cb7	5.80(.22)	25.6(.46)	21.5(1.1)	.840(.037)	.933(.024)	.587(.029)	.531(.038)	.449(.043)	—	—	0	0
Cb8	5.85(.09)	26.0(.77)	21.0(.65)	.810(.010)	.960(.050)	.581(.047)	.563(.043)	.439(.024)	—	—	0	0
Cb10	5.80(.21)	25.3(1.5)	21.3(1.2)	.852(.042)	.978(.038)	.591(.034)	.554(.041)	.441(.029)	—	—	0	0
Cb12	5.73(.12)	24.6(1.2)	21.3(.70)	.865(.032)	.964(.026)	.564(.035)	.537(.034)	.443(.032)	—	—	0	0
Cb13	5.72(.15)	24.0(.75)	20.1(.83)	.835(.038)	.959(.019)	.611(.043)	.532(.033)	.425(.033)	—	—	0	0
Cb14	5.61(.16)	23.9(1.1)	19.2(.98)	.805(.035)	.964(.029)	.600(.038)	.533(.027)	.440(.020)	—	—	0	0
Cb14(H)	5.61(.16)	23.7(.98)	18.4(.85)	.777(.029)	.993(.057)	.594(.051)	.520(.025)	.437(.027)	—	—	0	0
Cb14(H)	5.52(.13)	23.8(.75)	19.1(.72)	.803(.025)	.973(.040)	.604(.050)	.484(.020)	.466(.033)	—	—	0	0
Cb14(P)	5.83(.16)	28.3(1.0)	22.9(1.5)	.806(.035)	.976(.052)	.607(.029)	.508(.024)	.427(.039)	—	—	0	0
Cc2	5.51(.08)	25.4(1.1)	20.7(.94)	.816(.033)	.933(.032)	.497(.021)	.480(.010)	.471(.039)	—	—	0	0
H2	5.03(.045)	22.9(.64)	15.4(.34)	.674(.021)	.930(.090)	.440(.031)	.449(.026)	.427(.015)	.100(.010)	—	0	1
H5	4.78(.16)	21.9(.90)	14.5(.89)	.662(.030)	.952(.041)	.432(.048)	.418(.048)	.425(.030)	.110(.014)	—	0	2
H10(H)	4.63(.10)	20.0(.95)	12.5(.73)	.626(.029)	.939(.043)	.458(.038)	.476(.019)	.431(.023)	.104(.008)	—	0	1
H14(H)	4.84(.18)	21.7(1.1)	13.3(.90)	.614(.026)	.943(.018)	.442(.035)	.420(.043)	.419(.032)	.092(.009)	—	0	1
I14(P)	4.96(.14)	29.2(1.2)	20.0(1.0)	.686(.030)	.957(.022)	.486(.035)	.452(.026)	.423(.030)	—	—	0	0
La14(H)	5.94(.19)	42.0(1.6)	21.7(1.5)	.516(.035)	.975(.042)	.276(.026)	.520(.023)	.231(.032)	.208(.015)	—	0	2
La15(H)	5.95(.12)	42.7(2.0)	23.2(.76)	.545(.024)	.968(.045)	.323(.044)	.497(.029)	.213(.029)	.210(.017)	—	0	2
Lb14(P)	5.76(.19)	47.3(2.4)	25.0(1.5)	.528(.025)	1.02(.042)	.416(.038)	.538(.052)	.214(.056)	.140(.009)	—	3	5
Lc10(H)	5.70(.15)	40.6(2.4)	24.5(1.1)	.603(.017)	.900(.014)	.532(.029)	.496(.034)	.371(.017)	.127(.007)	—	3	5
Ld10(H)	5.50(—)	42.0(—)	21.2(—)	.505(—)	.837(—)	.420(—)	.519(—)	.392(—)	.129(—)	—	0	0
T15(P)	6.10(—)	72.0(—)	33.1(—)	.520(—)	.862(—)	.386(—)	.416(—)	.337(—)	.192(—)	—	1	1
A18	5.56(.15)	26.5(1.3)	19.9(1.3)	.752(.030)	.974(.030)	.550(.028)	.491(.024)	.426(.003)	—	—	0	0
A18(P)	5.41(.21)	29.2(1.2)	21.1(1.3)	.723(.041)	.958(.031)	.580(.039)	.509(.024)	.426(.024)	—	—	0	0
A24	5.67(.16)	24.7(1.2)	19.8(.81)	.800(.029)	.955(.024)	.601(.022)	.501(.024)	.448(.028)	—	—	0	0
A25	5.65(.19)	24.4(.97)	20.0(.94)	.823(.039)	.990(.046)	.577(.050)	.489(.033)	.465(.034)	—	—	0	0
A27	5.58(.19)	23.7(1.1)	18.4(.86)	.777(.024)	.986(.034)	.569(.034)	.483(.045)	.444(.018)	—	—	0	0
A28(H)	5.81(.21)	22.3(.75)	19.0(.99)	.851(.034)	.977(.038)	.590(.034)	.511(.025)	.465(.024)	—	—	0	0
O17	5.75(.05)	22.3(.56)	18.5(.41)	.831(.006)	.960(.041)	.608(.033)	.488(.003)	.451(.025)	—	—	0	0
O20	5.32(.18)	23.3(.76)	17.6(.75)	.755(.024)	.954(.041)	.553(.026)	.516(.032)	.456(.031)	—	—	0	0
O22	5.50(.19)	23.8(1.2)	18.4(1.7)	.776(.074)	.990(.057)	.589(.036)	.494(.036)	.459(.036)	—	—	0	0
O23	5.51(.16)	21.4(.68)	18.4(1.1)	.862(.041)	.990(.050)	.600(.038)	.489(.024)	.474(.035)	—	—	0	0
O23(P)	5.24(.18)	27.2(.86)	18.9(.98)	.728(.029)	.980(.023)	.596(.038)	.511(.027)	.438(.025)	—	—	0	1
Pa27	5.85(.16)	22.1(.72)	21.0(.87)	.947(.046)	1.00(.041)	.570(.024)	.488(.035)	.490(.041)	—	—	0	2
Pa27(H)	6.10(.11)	24.2(1.2)	22.6(.42)	.939(.054)	.985(.041)	.587(.044)	.472(.026)	.497(.022)	—	—	0	0
Pa29	6.00(.25)	21.1(1.5)	20.1(1.7)	.952(.051)	1.01(.027)	.580(.029)	.530(.021)	.507(.030)	—	—	0	0
Pa30	6.13(.19)	21.0(1.0)	19.4(1.2)	.922(.023)	.980(.037)	.592(.027)	.491(.008)	.500(.020)	—	—	3	5
Pb18(P)	5.89(.12)	26.5(.49)	21.4(.92)	.809(.038)	.940(.025)	.587(.054)	.518(.039)	.446(.022)	—	—	2	5
Pb19	5.64(.15)	23.8(.57)	18.7(.85)	.788(.030)	.944(.025)	.610(.031)	.495(.030)	.417(.014)	—	—	3	4
Pc23(P)	5.93(.03)	26.4(.40)	20.5(.29)	.775(.025)	.990(.050)	.610(.031)	.518(.034)	.465(.017)	—	—	0	0
J19	4.86(.19)	19.5(1.0)	15.0(1.1)	.769(.048)	.934(.057)	.570(.041)	.479(.036)	.497(.030)	—	—	0	0
J20	4.93(.23)	20.2(.74)	15.7(.63)	.779(.039)	.894(.013)	.587(.023)	.462(.028)	.514(.008)	.068(.016)	—	0	1
J23	4.60(.12)	19.9(.64)	13.0(.90)	.650(.6030)	.936(.028)	.448(.056)	.468(.016)	.446(.016)	.104(.003)	—	0	0
J27	4.90(.17)	21.5(.94)	15.8(2.1)	.738(.035)	.946(.037)	.561(.037)	.512(.066)	.452(.043)	.065(.038)	—	0	1
E20	4.51(.08)	21.2(1.6)	12.9(1.1)	.609(.022)	.895(.032)	.514(.026)	.418(.043)	.420(.015)	.107(.007)	—	4	5
S8	5.52(.23)	19.5(1.1)	17.0(1.0)	.878(.062)	.937(.027)	.565(.038)	.474(.028)	.527(.029)	.035(.037)	—	1	2
Y14(P)	4.88(.14)	27.4(1.4)	17.8(1.0)	.652(.033)	.894(.029)	.559(.032)	.487(.029)	.472(.031)	—	—	4	5
F1	6.10(—)	20.5(—)	18.8(—)	.917(—)	1.01(—)	.597(—)	.477(—)	.424(—)	—	—	0	0

Table 5. Linear measurements (in mm) and ratios of juvenile shell. \bar{x} : mean, s: standard deviation.

Samples	N	D1	H1	H1/D1	AH1/AW1	P1/H1	UJ
		\bar{x} (s)					
M3	10	2.14(.18)	2.69(.22)	1.26(.041)	2.02(.11)	.099(.018)	.096(.010)
M8	14	2.00(.12)	2.55(.13)	1.27(.049)	2.00(.11)	.103(.020)	.080(.010)
N14(P)	5	2.61(.04)	3.13(.12)	1.20(.030)	1.91(.11)	.103(.012)	.107(.014)
Ca3	10	2.18(.17)	2.72(.18)	1.25(.076)	2.12(.18)	.090(.021)	.120(.009)
Ca14(P)	25	2.43(.18)	3.11(.16)	1.28(.071)	2.09(.14)	.084(.019)	.170(.020)
Cb13	13	1.98(.14)	2.50(.20)	1.26(.064)	2.01(.14)	.098(.011)	.100(.011)
Cb14	17	2.02(.14)	2.60(.17)	1.28(.057)	2.06(.17)	0.94(.018)	.113(.029)
Cb14(P)	9	2.16(.11)	2.63(.16)	1.23(.073)	2.02(.18)	.085(.024)	.113(.021)
H5	10	1.92(.22)	2.35(.09)	1.24(.130)	1.94(.10)	.110(.020)	.149(.010)
H14(H)	14	1.85(.21)	2.31(.13)	1.26(.110)	1.99(.10)	.120(.015)	.137(.013)
I14(p)	12	2.14(.16)	2.67(.11)	1.26(.070)	2.05(.14)	.072(.020)	.164(.025)
La14(H)	15	2.33(.14)	2.96(.21)	1.28(.086)	2.02(.12)	.082(.018)	.214(.031)
La14(P)	15	2.49(.18)	2.98(.17)	1.19(.050)	1.95(.12)	.076(.017)	.176(.022)
A18	12	1.95(.15)	2.16(.11)	1.12(.079)	1.80(.14)	.121(.022)	.094(.017)
A27	14	2.02(.10)	2.36(.29)	1.14(.046)	1.86(.12)	.146(.020)	.093(.010)
A28(H)	5	2.13(.09)	2.47(.06)	1.16(.046)	1.81(.10)	.132(.016)	.107(.011)
O20	3	1.89(.11)	2.08(.11)	1.12(.031)	1.78(.09)	.112(.014)	.040(.012)
O23	15	2.05(.14)	2.27(.11)	1.11(.050)	1.81(.10)	.150(.020)	.054(.010)
O23(P)	8	1.98(.14)	2.26(.21)	1.13(.038)	1.76(.09)	.102(.015)	.043(.014)
Pa27	12	2.08(.10)	2.45(.14)	1.15(.100)	1.82(.11)	.119(.023)	.119(.011)
Pb19	12	1.84(.20)	2.19(.17)	1.19(.060)	1.77(.11)	.106(.017)	.116(.016)
J20	7	1.85(.17)	2.00(.17)	1.08(.017)	1.66(.13)	.153(.018)	.108(.016)
J27	11	1.97(.15)	2.19(.14)	1.10(.040)	1.71(.08)	.147(.021)	.118(.015)
E20	6	1.83(.28)	1.87(.19)	1.03(.060)	1.56(.12)	.158(.025)	.112(.005)
S8	6	1.78(.24)	1.94(.16)	1.10(.066)	1.61(.12)	.220(.020)	.077(.015)
Y14(P)	6	2.15(.22)	2.34(.15)	1.05(.041)	1.55(.18)	.185(.019)	.088(.014)

or without color bands. Penis cylindrical in shape, with thick sheath and without penial appendix. Internal part of uppermost penis with verge. Internal penial wall ornamented with some numbers of strongly or weakly folding pilasters.

Mandarina mandarina (Sowerby, 1839)

Figures 5-4, 6a-3, 8-1, 15-1

1839. *Helix mandarina* Gray, MS.; Sowerby, in Richardson *et al.* p. 143, pl. 34, fig. 2; pl. 38, fig. 3.
 1894. *Helix mandarina* Gray; Pilsbry, p. 124-125,

pl. 31, fig. 32.

1930. *Mandarina mandarina* (Sowerby); Kuroda, p. 206-207, pl. 14, fig. 1.
 1978. *Mandarina mandarina* (Sowerby); Minato, p. 38, 39, 48, 49, pl. 3 fig. 4.

Material. RM18400 (N=19, sample M3), RM18401 (N=12, sample M4), RM18402 (N=10, sample M5), RM18403 (N=4, sample M6), RM18404 (N=18, sample M8).

Diagnosis. Medium-sized species of *Mandarina* characterized by color pattern 1(23)0 in both juvenile and adult stages and upper penis sculptured by columns of weakly,

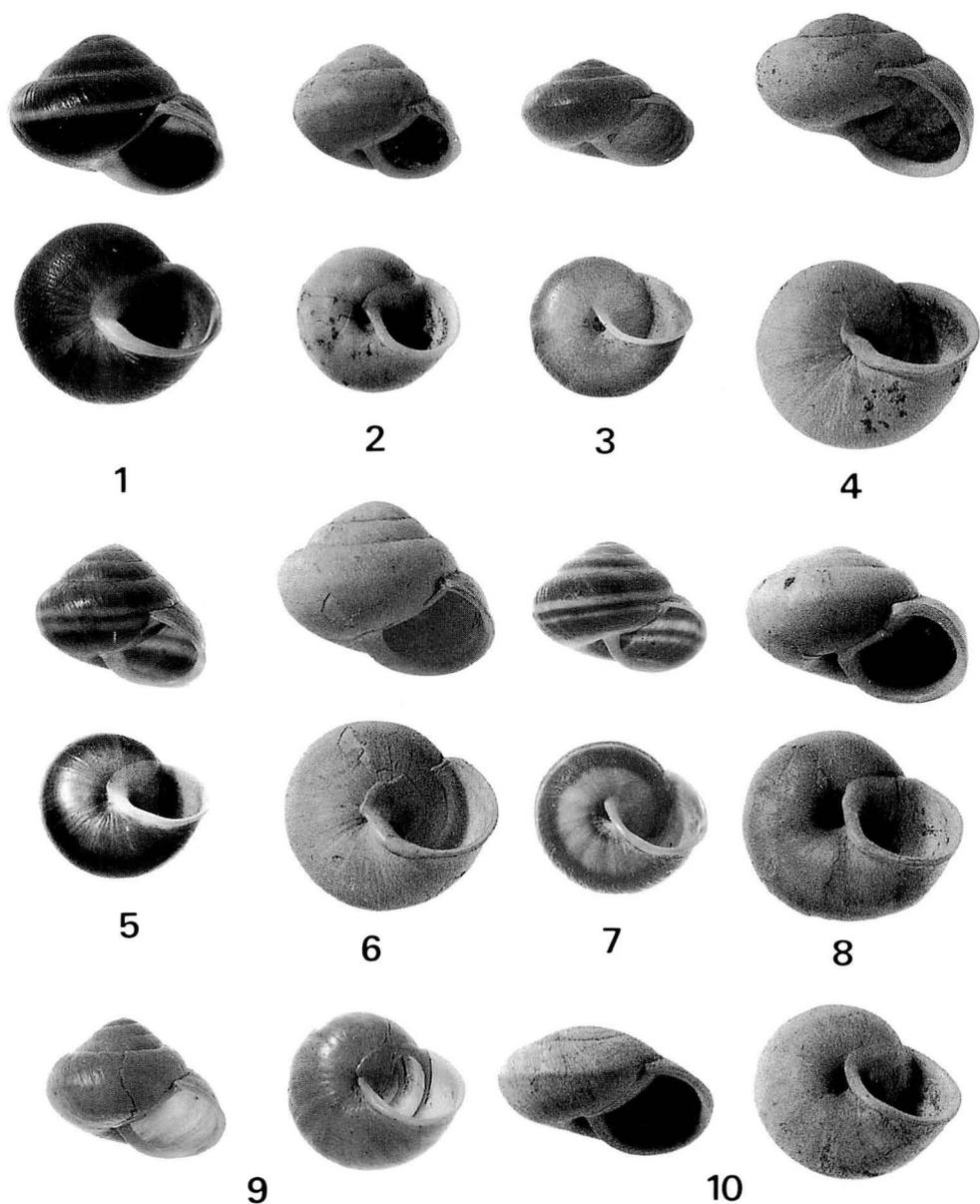


Figure 8. 1: *M. mandarina*, RM18403-a from Loc. 6; 2: *M. nola*, CM18405-a (holotype) from Loc. 14 (Pleistocene); 3: *M. hirasei*, RM18421-a from Loc. 5; 4: *M. io*, CM18426-a (holotype) from Loc. 14 (Pleistocene); 5: *M. chichijimana* (B), RM18415-a (holotype) from Loc. 14; 6: *M. chichijimana* (B), CM18418-a from Loc. 14 (Pleistocene); 7: *M. chichijimana*(A) RM18406-a from Loc. 3; 8: *M. chichijimana* (A), CM18407-a from Loc. 14 (Pleistocene); 9: *M. chichijimana* (C), RM18419 from Loc. 2; 10: *M. chichijimana* (A), CM18407-b from Loc. 14 (Pleistocene). All in natural size.

irregularly folded, merged pilasters.

Description.

Genital morphology: Externally, flagellum uniformly slender with a sharp and slender

tip. Epiphallus invariably thick. Penis uniformly thick and covered by sheath at the basal portion. The thickness of penis almost the same as that of vagina. Internally, lower

penis covered with 7–8 columns of regularly and equilaterally folded, unmerging, equal-sized pilasters. Center of the column slightly ridged. Upper penis covered with many randomly complex merging column of irregularly and weekly folded pilasters. Verge large, longer than wide, with a ventrally subterminal pore and sculptured with slightly folded cords continued from upper penial wall.

Shell morphology: Shell medium in size for the genus and solid. Spire rather high and domed. Body whorl inflated. Umbilicus closed. Base circular and convex. Aperture rather oblique, semicircular in shape. Peristome slightly thickened, expanded and reflected. Whorls 5.3–6.0 in number.

Measurements (mm).

Specimen	WH	D	H	AH	AW	IPA
RM18400-a:	5.6	26.8	21.5	14.2	15.6	0.45

Observation and comparison. Some geographical variation in shell size can be found; specimens from coastal area of Anijima (Loc. 4) have smaller shell than that from other areas, and specimens from mountain area of Chichijima (Loc. 6) have very large shell. However, geographical variation in shell shape is insignificant for the genus.

Several specimens from Sakaiura samples (Loc. 6) have intermediate features between *M. mandarina* and *M. chichijimana*. These intermediates are assumed to be hybrids between the two species.

Distribution. The distribution area of *M. mandarina* is restricted to Anijima and the northeastern part of Chichijima (Locs. 3, 4, 5, 6, 8).

Mandarina nola, n. sp.

Figures 8-2, 15-2

Material. Holotype: CM18405-a selected from sample N14 (P). Paratypes: CM18405 [N=11, sample N14 (P)].

Diagnosis. Small sized species of *Mandarina*. Shell with distinctly high aperture

and clear umbilicus. Color pattern 1 (23) in both adult stage and juvenile stage.

Description. Shell solid and conical in shape. Umbilicus clear and deep. Spire high and strongly domed. The number of whorls in adult shell from 5.0 to 5.2. Aperture oblique in shape and high for the genus. Base circular and convex. Peristome thickened and reflected.

Measurements (mm).

Specimen	WH	D	H	AH	AW	IPA	U
Holotype (CM18405-a):	5.1	23.2	17.5	13.1	12.4	0.41	2.1

Observation and comparison. This species has similar color pattern to *M. mandarina*. However, the new species is distinguished from *M. mandarina* in having distinctly higher aperture, smaller shell, narrower color bands and clear umbilicus.

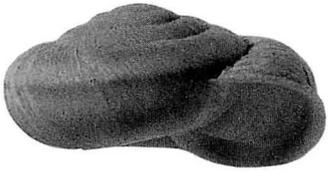
Distribution. This species occurs in the John beach fissure deposits (Loc. 14) of before 33,000 yr B.P.

Mandarina chichijimana, n. sp.

Figures 5-1–2, 6a-1–2, 8-5–10, 15-3–5

1969. *Mandarina mandarina* (Sowerby); Habe, p. 21, pl. 2, figs. 5-7.
 1973. *Mandarina mandarina* (Sowerby); Habe, p. 51, pl. 4, figs. 6-8.
 1978. *Mandarina mandarina* (Sowerby); Minato, p. 38, 41, 49, figs. 1, 6-7.

Material. Holotype (forma A): RM 18415-a selected from sample Cb14. Paratypes: RM18406 (N=30, sample Ca3) CM18407 [N=52, sample Ca14 (P)], RM18408 (N=8, sample Cb7), RM18409 (N=7, sample Cb8), RM18410 (N=7, sample Cb9), RM18411 [N=18, sample Cb10 (H)], RM18412 (N=2, sample Cb11), RM18413 (N=17, sample Cb12), RM18414 (N=24, sample Cb13), RM18415 (N=24, sample Cb14), CM18416 [N=32, sample Cb14 (H)], CM18417 [N=30, sample Cb15(H)], CM18418 [N=16, sample Cb14 (P)], RM18419 (N=14, sample Cc2).



1

3

4



2

5

Diagnosis. Medium-sized species of *Mandarina* characterized by color pattern 1n34, nnn4, 0n04, 0000 in adult shell, 0n04 or 0000 in juvenile shell, and internal penial wall uniformly sculptured by longitudinal columns with regularly, equilaterally folded pilasters.

Description.

Genital morphology: Externally, flagellum slender with a sharp and slender tip. Epiphallus uniformly thin. Penis uniformly thin and covered by sheath at the basal portion. Usually, penis far thinner than vagina. Internally, middle and upper penial wall uniformly covered with 7–8 rows of columns of regularly, equilaterally folded, unmerging, equal-sized pilasters. Verge large, longer than wide, sculptured with longitudinal and lateral regular cords.

Shell morphology: Three forms, formae A, B and C, are distinguishable in this species. The holotype belongs to forma B.

Forma A: Shell of medium-size for the genus and solid. Spire low or medium in height. Umbilicus clearly open. Body whorl rounded or with weak to strong peripheral angle. Aperture circular in shape. Peristome moderately thick and slightly reflected. Base rounded and convex. Whorls 4.6–5.5 in number. Color pattern 1n34, nnn4 (band 1, 3, 4 sometimes incomplete and flamed) 0n04, 0000 in adult shell, and 0n04, 0000 in juvenile shell.

Forma B: Shell medium-sized for the genus and solid. Spire rather high and strongly domed. Body whorl inflated. Umbilicus closed. Base rounded, convex. Aperture rather oblique, semicircular in shape. Peristome slightly thickened, expanded and reflected. Whorls 5.2–6.1 in number. Color pattern 1n34 band sometimes incomplete and flamed in adult shell, and 0n04 in juvenile shell.

Forma C: Shell morphology almost the same as forma B except for having shorter inner-lip. Color pattern 1n34 (band sometimes incomplete and flamed) in adult shell, and 0n04 in juvenile shell.

Measurements. (mm)

Specimens	WH	D	H	AH	AW	IPA	U
Holotype (RM18415-a):	5.6	24.0	19.5	13.0	13.6	0.43	—
Paratype (CM18418-a):	5.6	27.0	21.6	14.5	14.5	0.43	—
Paratype (CM18407-a):	4.6	28.9	18.7	14.3	15.2	0.38	2.9
Paratype (RM18406-a):	5.1	23.8	17.2	12.2	13.1	0.47	2.0

Observation and comparison. Forma A and forma B are apparently different in shell shape but the difference of genital morphology is almost negligible. They are regarded as subspecific status. Though the genitalia of forma C could not be examined in this study, it may be regarded as another subspecies of *M. chichijimana*, because of its similarity in color patterns and shell shape with forma B.

Forma A shows a significant change of shell morphology in the fossil record; most specimens before 40,000 yr B.P. and some specimens of 25,000–30,000 yr B.P. both have a sharp peripheral angle on the last whorl and a shallow suture on the spire. However, specimens of 30,000–40,000 yr B.P. and living specimens both show no or only a weak peripheral angulation on the whorl and have a deep suture on the spire. In addition, fossil specimens are generally larger and wider than living specimens.

Remarks. Previous authors (Pilsbry 1894; Habe 1969, 1973; Minato 1978) regarded this species as belonging to *M. mandarina*. For instance, Minato (1978) attributed the difference between *M. chichijimana* and *M. mandarina* to the geographic variation within the same species. The former, how-

← **Figure 9.** 1: *M. luhuana* (A), CM18428-a from Loc. 15 (Holocene); 2: *M. luhuana* (B), CM18429-a from Loc. 15 (Pleistocene); 3: *M. luhuana* (C), CM18430-a from Loc. 10 (Holocene); 4: *M. luhuana* (D) CM18431 from Loc. 10 (Holocene); 5: *M. titan*, CM18432-a (holotype) from Loc. 15 (Pleistocene). All in natural size.

ever, can be distinguished from the latter because of the difference of sculpture on upper penial wall and existence of the two species at the same locality.

Distribution. In the deposits before 25,000 yr B.P., forma A is abundant. About 25,000 yr B.P., however, forma A seems to have been replaced by forma B in the southern part of Chichijima. Now, forma B is distributed in the southern part of Chichijima (Locs. 7-15). Forma A already became extinct in Chichijima, and its distribution area is now restricted to Anijima (Loc. 3). Forma C is now distributed in Ototojima (Loc. 2), and its fossil occurrence has not yet been confirmed.

Mandarina hirasei Pilsbry, 1902

Figures 5-3, 6a-4, 8-3, 15-6

1902. *Mandarina hirasei* Pilsbry, p. 141.
 1973. *Mandarina hirasei*; Pilsbry; Habe, p. 52, pl. 4, figs. 9-11.
 1978. *Mandarina hirasei* Pilsbry; Minato, p. 41, 42, 48, 49, fig. 4, pl. 4, figs. 1, 2.

Material. RM18420 (N=4, sample H2),

RM18421 (N=18, sample H5), CM18422 [N=10, sample H10 (H)], RM18423 (N=4, sample H13), CM18424 [N=22, sample H14 (H)], RM18425 [N=10, sample H15 (H)].

Diagnosis. Small-sized species of *Mandarina* characterized by low spire, smooth surface without color bands, clear umbilicus and thin shell. Penial wall covered by columns of regularly, equilaterally folded, equal-sized pilasters.

Description.

Genital morphology: Externally, flagellum long with a slender tip. Epiphallus regularly slender. Penis uniformly narrow and covered by sheath at the position of basal penis. Internally, lower penial walls uniformly covered with 5-7 columns of regularly, equilaterally folded pilasters. Middle penial wall covered with 6-7 columns of straight or slightly meandering pilasters. Upper penial wall covered with 10-13 numbers of slightly meandering pilasters. Verge large and longer than wide.

Shell morphology: Shell small, flat and thin for the genus. Umbilicus wide. Surface smooth. Aperture relatively large and oval in shape. Body whorl inflated with

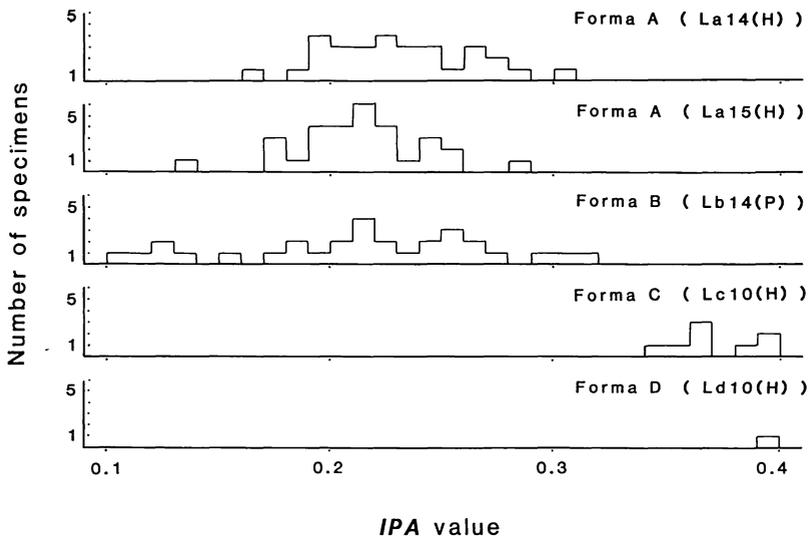


Figure 10. Histograms of index of peripheral position (IPA) in five samples of *M. luhuana*. This indicates that the present species can be divided into two groups; one is forma A and forma B and the other is forma C and forma D.

obtuse peripheral angle. Peristome slightly colored, thickened and reflected. Color pattern usually 0000, but sometimes 1030 or 0200.

Measurements. (mm)

Specimen	WH	D	H	AH	AW	IPA	U
RM18421-a	5.0	21.1	13.4	11.0	11.5	0.49	1.9

Distribution. This species is usually found in the basal portion of the leaves of *Livistona* and *Pandanus*.

Living and Holocene specimens can be found in coastal area of Chichijima (Locs. 5, 10, 13, 14, 15) and Ototojima (Loc. 2). The occurrence of *M. hirasei* was recorded also in Nakodojima (Loc. 1) (Habe 1969). This species is abundant in Holocene dunes, although there is no fossil record in the deposits older than 5,000 yr. B.P.

Mandarina io, n. sp.

Figures 8-4, 15-7

Material. Holotype: CM18426-a selected from sample I14(P). Paratype: CM18426 [N=14, sample I14 (P)].

Diagnosis. Medium-sized species of *Mandarina*. Shell thin. Spire flat. Body whorl markedly inflated. Color pattern 0000.

Description. Shell thin and medium-sized for the genus. Body whorl remarkably inflated and periphery rounded. Umbilicus wide in juvenile shells but closed in adult shells. Surface smooth. Most specimens lack color band. Spire flat and weakly doming. Aperture oblique and semicircular in shape. Peristome thickened and reflected. Base rounded and convex. Suture distinctly deep. Whorls 4.5-5.0 in number. Color pattern 0000.

Measurements. (mm)

Specimens	WH	D	H	AH	AW	IPA
Holotype (CM18426-a)	4.9	29.1	18.1	15.5	16.4	0.41
Paratype (CM18426-b)	4.7	29.9	19.9	16.9	17.5	0.43

Observation and comparison. This species is similar to *M. chichijimana* forma A of 30,000-40,000 yr. B.P. in having a deep suture and a round periphery on the body whorl. The former however differs from the latter in having thinner shell, smoother surface, relatively larger and more inflated body whorl, oblique shape of aperture, and closed umbilicus in adult stage.

Distribution. This species occurs in the John beach fissure deposits (Loc. 14) of about 22,000-32,000 yr. B.P.

Mandarina luhuana (Sowerby, 1839)

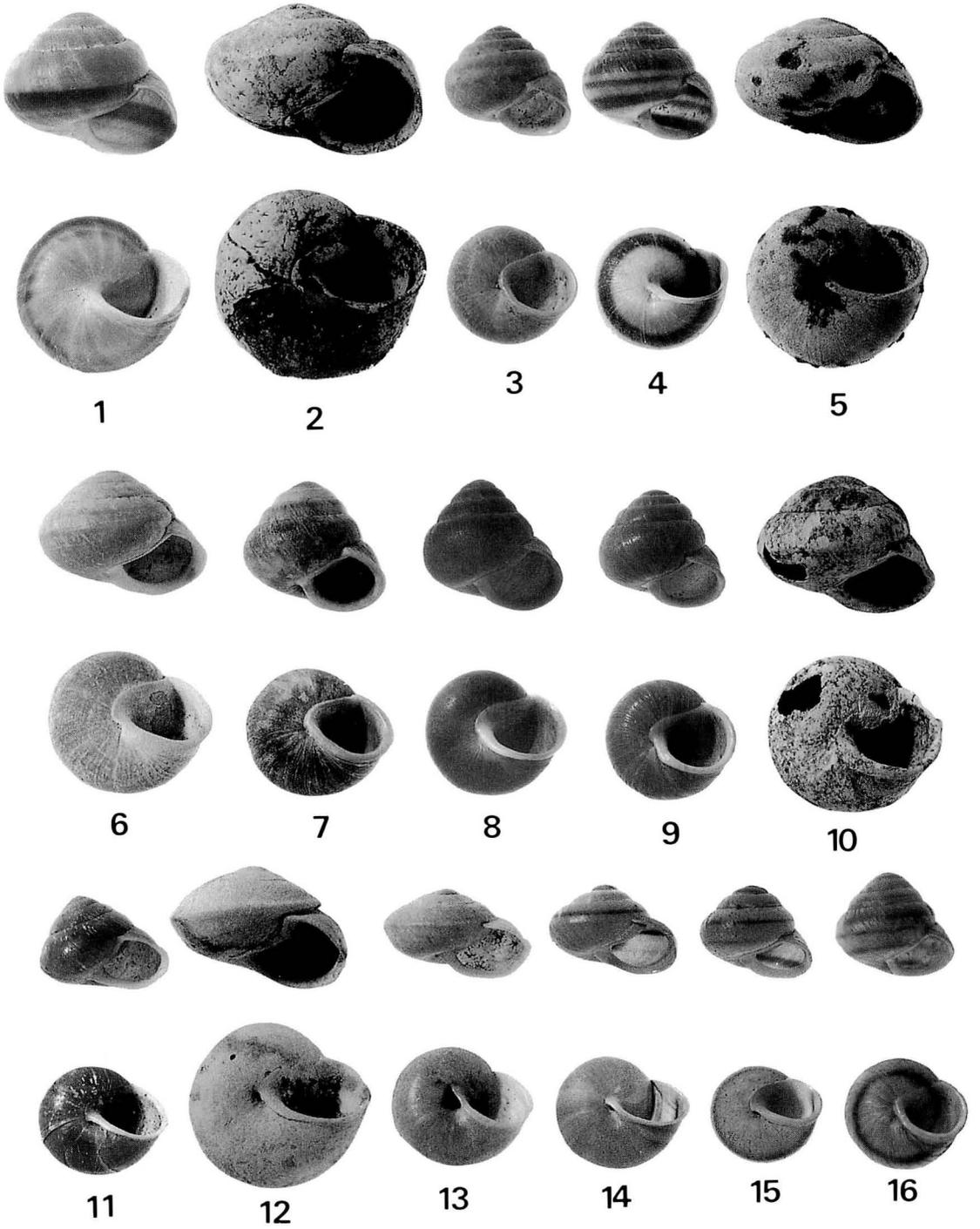
Figures 9-1-4, 15-8-9

1839. *Helix luhuana* Sowerby, p. 143. pl. 35, fig. 4.
 1850. *Helix pallasiana* Pfeiffer, p. 67.
 1886. *Helix pallasiana* Pfeiffer; Tryon, p. 131, pl. 44, figs. 49, 50.
 1890. *Euhadra luhuana* Sowerby; Pilsbry, p. 305.
 1890. *Nanina ruschenbergeri* Pilsbry, p. 186, text-fig. 3.
 1902. *Mandarina ruschenbergeri* Pilsbry; Pilsbry, p. 141.
 1930. *Mandarina luhuana* (Sowerby); Kuroda, p. 206, pl. 14, figs. 3, 4.
 1930. *Mandarina pallasiana* (Pfeiffer); Kuroda, p. 206, pl. 14, fig. 2.
 1969. *Mandarina luhuana* (Sowerby); Habe, p. 19, 23, pl. 1, figs. 3, 4.
 1969. *Mandarina pallasiana* (Pfeiffer); Habe, p. 19, 23, pl. 1, figs. 1, 2.
 1973. *Mandarina luhuana* (Sowerby); Habe, p. 51, pl. 4, figs. 1-3.
 1973. *Mandarina pallasiana* (Pfeiffer); Habe, p. 51, pl. 4, fig. 4.
 1978. *Mandarina luhuana* (Sowerby); Minato, p. 43, 50, pl. 4, figs. 7, 8.
 1978. *Mandarina pallasiana* (Pfeiffer); Minato, p. 44, 50, pl. 4, figs. 9, 10.

Material. CM18427 [N=30, sample La14 (H)], CM18428 [N=30, sample La15 (H)], CM18429 [N=30, Lb14 (P)], CM18430 [N=4, Lc10 (H)], CM18431 [N=1, Ld10 (H)].

Diagnosis. Large species of *Mandarina* characterized by flat spire and wide umbilicus.

Description. Four forms, *i.e.* formae A, B,



C and D are distinguishable in this species.

Forma A: Shell large, solid, heavy for the genus. Spire very low but domed. Suture deep. Umbilicus distinctly wide. Body whorl with obtuse peripheral angle. Aperture oblique in shape. Base rounded and convex. Perioistome reflected and thickened. Whorls 5.6–6.5 in number. Color pattern of juvenile shell On04. The basic color pattern of adult shell 1n34, On04, 0(23)4, 1(23)4 or (123)4, but sometimes the band incomplete and flamed.

Forma B: Shell large, solid, heavy for the genus. Spire very low and slightly domed. Suture shallow. Umbilicus wide for the genus, but narrower than that of forma A. Surface sculptured by many numbers of spiral lines. Body whorl with sharp peripheral angle. Aperture oblique in shape and higher than forma A. Perioistome thinner and more weakly reflected than that of forma A. Whorls 5.4–6.0 in number. The color pattern of juvenile shell On04. Basic color pattern of adult shell (123)4. The band sometimes incomplete and flamed.

Forma C: The basic features of forma C is similar to forma B. But forma C has lower peripheral position than forma B (Figure 10).

Forma D: The basic features of forma D is similar to forma A. But forma D has lower peripheral angle and narrower umbilicus than forma A (Figure 10). Forma B and forma C are easily discriminated from forma D in having sharply angulated periphery.

Measurements (mm).

Specimens	WH	D	H	AH	AW	IPA	U	KE
CM18428-a	5.8	42.0	19.0	18.0	19.5	0.22	9.90	1
CM18429-a	5.8	51.0	27.3	25.0	25.5	0.21	7.21	5

CM18430-a	5.7	38.0	23.1	17.9	19.5	0.38	4.90	4
CM18431-a	5.5	42.0	21.2	18.5	22.1	0.39	5.46	0

Remarks. All the specimens described as *M. luhuana* by previous authors belong to forma A. Forma C was described as *M. pallasiana* (Pfeiffer, 1850) but is regarded here as one of the formae of *M. luhuana*. No intermediate specimen between pairs of these four formae could be found in the Holocene specimens. However, in Pleistocene sample [Lb14(P)], a few intermediate specimens between forma A and forma B, and forma B and forma C can be found.

Distribution. The occurrence of *M. luhuana* is limited to the southern part of Chichijima. Forma A mainly occurs in the Holocene dune deposits at Minamizaki (Loc. 14) and Minamijima (Loc. 15). Forma B and a few intermediate specimens between forma A and forma B occur from the Pleistocene fissure deposits at John beach (Loc. 14). Forma C occurs in the Holocene dune deposits of Kominato (Loc. 10). Forma D also occurs in the Holocene dune deposits of Kominato (Loc. 10).

Mandarina titan, n. sp.

Figures 9–5, 15–10

Material. Holotype: CM18432-a selected from sample T15 (P). Paratypes: CM18432 [N=3, sample T15(P)].

Diagnosis. Remarkably large species of *Mandarina* characterized by low spire, thick and reflected perioistome, and wide umbilicus.

Description. Shell remarkably large, solid, heavy, exceeding 70 mm in diameter. Spire very low and weakly domed. Aperture

← **Figure 11.** 1: *M. aureola*, RM18448-a from Loc. 25 (holotype); 2: *M. aureola*, CM18445 from Loc. 18 (Pleistocene); 3: *M. aureola*, CM18452-a from Loc. 28 (Holocene); 4: *M. polita*, RM18457-a (holotype) from Loc. 23; 5: *M. polita*, CM18458-a from Loc. 23 (Pleistocene); 6: *M. ponderosa* (B), RM18439-a from Loc. 19; 7: *M. ponderosa* (A), RM18434-a from Loc. 27; 8: *M. ponderosa* (A), RM18437-a from Loc. 29; 9: *M. ponderosa* (A), RM18438-a from Loc. 30; 10: *M. ponderosa* (C), CM18443-a from Loc. 23 (Pleistocene); 11: *M. suenoae*, RM18467-a from Loc. 8; 12: *M. hayamii*, CM18468-a (holotype) from Loc. 14 (Pleistocene); 13: *M. exoptata*, RM18465-a from Loc. 20; 14: *M. hahajimana*, RM18461-a from Loc. 20; 15: *M. hahajimana*, RM18460-a from Loc. 19, 16: *M. sp.*, RM18469-a from Loc. 1. All in natural size.

oblique, semicircular in shape. Peristome thickened, markedly expanded and reflected. Base rounded and convex. Body whorl with weakly angular periphery. Whorls about 6 in number. Color pattern (123)4.

Measurements. (mm)

Specimen	WH	D	H	AH	AW	IPA	U	KE
Holotype	6.1	72.0	33.1	33.2	37.2	0.34	13.8	1
(CM18432-a)								

Observation and comparison. *M. titan* is the largest species of *Mandarina*. It is morphologically distinct from *M. luhuana* in the much larger shell size, low spire and markedly expanded, reflected peristome.

Distribution. The present species occurs from the fissure deposits of Minamijima (Loc. 15). It appeared about 13,000 yr. B.P. and possibly became extinct before 8,000 yr B.P.

Mandarina ponderosa Pilsbry, 1901

Figures 5-8, 6b-1, 11-6-10, 15-13-14

1901. *Mandarina mandarina* var. *ponderosa* Pilsbry, p. 402-403.
 1902. *Mandarina mandarina* var. *conus* Pilsbry, p. 6.
 1969. *Mandarina ponderosa* Pilsbry; Habe, p. 21, pl. 2, fig. 8.
 1969. *Mandarina conus* Pilsbry; Habe, p. 21, pl. 2, fig. 1.
 1978. *Mandarina ponderosa* Pilsbry; Minato, p. 39, 49, pl. 3, figs. 8, 9.
 1978. *Mandarina mandarina* (Sowerby); Minato, p. 49, pl. 3, fig. 3.
 1987. *Mandarina ponderosa* Pilsbry; Maeda *et al.*, p. 68, pl. 20, figs. 288a-c.
 1987. *Mandarina mandarina* (Sowerby); Maeda *et al.*, p. 68, pl. 20, fig. 283.

Material. RM18433 (N=16, sample Pa26), RM18434 (N=25, sample Pa27), CM18435 [N=14, sample Pa27 (H)], CM18436 [N=1, sample Pa28 (H)], RM18437 (N=4, sample Pa29), RM18438 (N=6, sample Pa30), RM18439 (N=4, sample Pb18), CM18440 [N=12, sample Pb18 (P)], RM18441 (N=19, sample Pb19), RM18442 (N=9, sample Pb20), CM18443 [N=4, sample Pc23 (P)].

Diagnosis. Medium-sized species of *Mandarina* characterized by upper penial wall sculptured with columns of slightly meandering zig-zag fold and lower penial wall sculptured with tightly folded pustules. Color pattern n(23)0 in juvenile shell, and 1(23)0 or (123)0 in adult shells.

Description.

Genital morphology: Externally, flagellum distinctly large, occupying one-third of total penial portion in length, and curved near the tip. Epiphallus short and uniformly thick. Penis relatively thick at the uppermost portion, distinctly narrowed at the middle portion. Penis distinctly thickened, cylindrical in shape in the middle to basal region and covered with sheath at the basal portion. Internally, upper penial wall sculptured with columns of irregularly meandering fold. Middle and upper basal portions the wall sculptured with 7 or 8 columns of tightly, equilaterally folded pilasters. The center of each column ridged.

Shell morphology: Three forms (formae A, B and C) are distinguishable in this species, although they are all moderate in size.

Forma A: Shell conical in shape. Spire high and domed. Body whorl rounded or barely angulated at the periphery. Umbilicus closed in the adult stage. Aperture rounded and high. Peristome markedly thickened and slightly reflected. Base rounded, convex. Whorls 5.3 to 6.2 in number. Color pattern n(23)0 in juvenile shells, and 1(23)0 or (123)0 in adult shells. The bands sometimes flamed. Usually, ground color dark, but the specimens from Meijima reveal light ground color with flamed bands.

Forma B: Spire from low to high and weakly or strongly domed. Suture shallow. Surface rough with clear spiral lines. Body whorl with a strong peripheral angle. Aperture rounded in shape and relatively wide. Peristome markedly thickened and reflected. Base flattened. Whorls 5.4 to 6.0 in number. Color pattern n(23)0 in juvenile shell; 1 (23) 0 or (123)0 in adult shells. Ground color

sometimes dark as well as color bands.

Forma C: Shell distinctly domed. Suture shallow. Body whorl with angular periphery. Aperture round and high. Peristome markedly thickened. Whorls about 6 in number. Color pattern 1(23)0.

Measurements (mm).

Specimens	WH	D	H	AH	AW	IPA	KE
RM18434-a	5.7	22.5	20.9	13.0	13.1	0.50	0
RM18441-a	5.7	23.8	18.0	12.5	13.0	0.41	4
CM18443-a	5.9	26.8	20.1	15.2	15.0	0.45	4

Remarks. The type specimen of *M. ponderosa* seems to belong to forma B. Some specimens of forma A were described as *M. mandarina conus* by Pilsbry (1902). Minato (1978) regarded forma A as a variant of *M. mandarina*. The present species is, however, distinguishable from *M. mandarina* by the difference of external and internal morphology of penis and color pattern in juvenile shells.

Distribution. Living populations of forma A are distributed in the coastal area of the southern part of Hahajima (Locs. 26, 27), Meijima (Loc. 30), and Imotojima (Loc. 29). Forma B is found in mountain area of Hahajima (Locs. 18–20). Pleistocene fossils belonging to forma A occur in the cave deposits of Sekimon (Loc. 18). Forma C occurs in the Pleistocene deposits of Okimura cave (Loc. 23). Specimens of forma A were also obtained from the Holocene dune deposits of Minamizaki (Loc. 27) and Hirasima (Loc. 28), and their shell morphology is quite similar to that of living specimens of the same forma.

Mandarina aureola, n. sp.

Figures 5-5—6, 6b-2, 11-1—3, 15-11

1978. *Mandarina mandarina* (Sowerby); Minato, p. 41, fig. 2.
 1987. *Mandarina mandarina* (Sowerby); Maeda *et al.*, p. 68, pl. 20, fig. 287b.

Material. Holotype: RM18448-a from

sample A25). Paratypes: RM18444 (N=25, sample A 18), CM18445 [N=24, sample A18 (P)], RM18446 (N=20, sample A24), CM18447 [N=7, A24 (H)], RM18448 (N=29, sample A25), RM18449 (N=25, sample A26), RM18450 (N=25, sample A27), CM18451 [N=10, sample A27 (H)], CM18452 [N=11, sample A28 (H)].

Diagnosis. Medium-sized species of *Mandarina* characterized by pilastral pustules of lower penis and lower penial wall sculptured by columns of regularly and tightly folding large pilasters, and upper penial wall sculptured by columns of regularly meandering zig-zag pilasters.

Description.

Genital morphology: Externally, flagellum short with a sharp tip. Epiphallus uniformly long and narrow. Penis relatively thick at the upper part, but distinctly narrow at the middle part. Middle and base penis distinctly thickened and the shape cylindrical, slightly bent. Basal penis covered with sheath. Internally, upper penis sculptured with columns of irregularly folding pilasters. Middle and upper basal portions of the penis sculptured with 5–8 numbers of columns of tightly, equilaterally folded pilasters. The pilasters are remarkably developed at the upper half. Verge small and wider than long.

Shell morphology: Shell medium-sized for the genus. Spire moderate in height. Suture deep. Body whorl inflated with rounded periphery. Umbilicus closed in adult shells. Base rounded and convex. Aperture rounded. Peristome thickened and reflected. Whorls 5.1–6.1 in number. Color pattern 0200, 1n30 in juvenile stage; basically 1230, (band 1 and band 3 sometimes narrowed, fused or lacked) and sometimes 1n30, 1030, (123)0 in adult stage.

Measurements (mm).

Specimens	WH	D	H	AH	AW	IPA
Holotype (RM18448-a)	5.8	25.8	21.0	14.8	14.4	0.49
Paratype (CM18445-a)	5.4	30.8	22.6	16.8	17.8	0.46

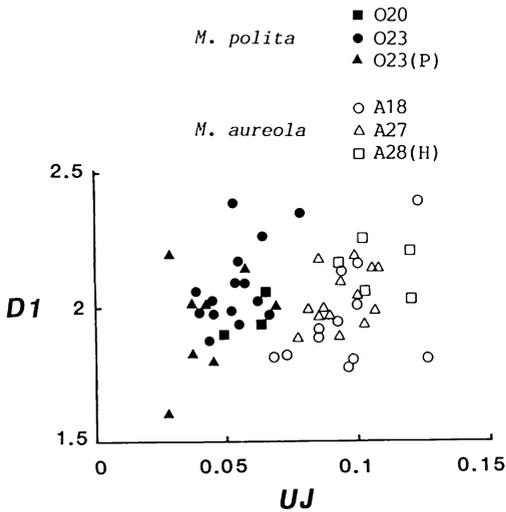


Figure 12. Scatter diagram showing the relationship between the diameter of the first whorl ($D1$) and juvenile umbilicus width (UJ) for samples of *M. polita* and *M. aureola*. The two species is clearly distinguished by the difference of UJ .

Paratype (RM18452-a) 6.1 22.1 19.9 12.5 12.3 0.47

Observation and comparison. This species shows slight geographic variation in the penial morphology. For instance, the specimens from Sekimon (Loc. 18) and Nankinhama (Loc. 24) both have the similar features as those from Minamizaki (Loc. 27), although the former have longer flagellum than the latter. The shape of flagellum of the Sekimon and Nankinhama specimens are similar to that of *M. polita*. Conchologically, geographic variation is conspicuous; Sekimon specimens (Loc. 18) have relatively large, flat, reddish colored shells, while Nakanodaira specimens (Loc. 25) have relatively small, high, yellowish colored shells. Furthermore, Minamizaki (Loc. 27) specimens have relatively wide, light colored shell. Hirasima specimens (Loc. 28) are small with a high spire.

The Pleistocene fossil specimens (about 10,000 yr B.P.) occur from the deposits of Sekimon cave. These specimens have flatter and larger shell than living specimens. The Holocene fossil specimens (about 2,000 yr B.

P.) occurs at Minamizaki. Basic features of them are the same as living specimens.

Remarks. The present Hahajima species was regarded as inclusive in the geographic variation of *M. mandarina* by previous authors (Habe 1969; Minato 1978). However, the new species is distinguished from *M. mandarina* from Chichijima in having distinctly thicker basal penis, narrower middle penis and the larger pilaster. The discrepancy of penial morphology between *M. mandarina* and this species is more significant than the difference between *M. mandarina* and *M. chichijimana*. Conchologically, this species is somewhat similar to *M. chichijimana*, but differs from the latter in the lower shell, wider aperture and absence of band 4 in the juvenile stage.

Distribution. This species is distributed only in Hahajima islands. Living populations are found in Sekimon (Loc. 18) and Minamizaki-Nankinhama (Locs. 24–28) areas of Hahajima, Imotojima and Meijima. Holocene fossils occur in dune deposits of Nankinhama (Loc. 24), Minamizaki (Loc. 27) and Hirasima (Loc. 28).

Mandarina polita, n. sp.

Figures 5-7, 6b-3, 11-4—5, 15-12

Material. Holotype: RM18457-a selected from sample O23. Paratypes: RM18453 (N=6, sample 017), RM18454 (N=15, sample O20), RM 18455 (N=6, sample O21), RM18456 (N=19, sample O22), RM18457 (N=22, sample O23), CM18458 [N=25, sample O23 (P)].

Diagnosis. Medium-sized species characterized by markedly thick basal penis and small umbilicus in juvenile shell.

Description.

Genital morphology: Flagellum long and slender. Epiphallus uniformly long. Penis narrowed at the middle position. Basal penis covered with sheath and distinctly thickened, knob-like in shape. Internally,

uppermost penial wall sculptured with irregularly folding pilasters. Middle and upper penial walls ornamented with 5 to 7 columns of tightly, equilaterally folding pilasters. Middle and lower penial walls sculptured with about 5 columns of tightly folding and distinctly developed pilasters. Verge small and wider than long.

Shell morphology: Shell medium in size, usually not exceeding 30 mm in diameter, solid for the genus. Spire domed. Last whorl with rounded periphery. Umbilicus almost closed in juvenile stage and never open in adult stage. Aperture rounded. Periostracum thickened and reflected. Base rounded and convex. Whorls 5.0–5.8 in number. Color pattern basically 1n30, but it is sometimes variable among specimens from the same locality. Ground color usually reddish.

Measurements (mm).

Specimens	WH	D	H	AH	AW	IPA
Holotype (RM18457-a)	5.8	21.5	19.3	12.2	12.5	0.48
Paratype (CM18458-a)	5.4	27.9	20.7	15.8	16.8	0.44

Observation and comparison. In the genital features *M. polita* is similar to *M. aureola* and *M. chichijimana*. *M. aureola* differs from this species in having wider umbilicus in the juvenile stage and with yellowish ground color (Figure 13) and apparently different shape of penis. *M. chichijimana* is distinguished from this species in having higher aperture in juvenile stage and the presence of band 4.

The present species shows a significant geographic variation in shell shape, size and coloration. For instance, color pattern in both living and fossil samples from Locs. 17, 21, 22 and 23 is invariably 1n30, but such patterns as 12n0, 1nn0, 1020, 1n30 are found in the sample from Loc. 20. Specimens from Loc. 20 possess a very low spire (mean value of H/D is 0.755), while those from Loc. 23 mostly have a remarkably high spire (mean value of H/D is 0.862). The Pleistocene fossil sample from Loc. 23 consists of unusu-

ally large shells (mean value of diameter is 27.2 mm) with a relatively low spire (mean value of H/D is 0.775).

Remarks. *M. polita* was previously regarded as inclusive in the geographic variation of *M. mandarina* by Habe (1969) and Minato (1978). However, the former differs from the latter in having thicker basal penis and narrower middle penis. The discrepancy of penial morphology between *M. mandarina* and this species is more significant than that between *M. mandarina* and *M. chichijimana*.

Distribution. Living populations are distributed in the central and northern parts of Hahajima (Locs. 16, 17, 20, 21, 22, 23). The Pleistocene fossil specimens occur in the cave deposits at Okimura (Loc. 23).

Mandarina hahajimana Pilsbry, 1902

Figures 5-9, 6b-4, 11-14—15, 15-15

1902. *Mandarina mandarina* var. *hahajimana* Pilsbry, p. 29.
 1969. *Mandarina hahajimana* Pilsbry; Habe, p. 21, pl. 2, fig. 4.
 1978. *Mandarina hahajimana* Pilsbry; Minato, p. 40, 41, 50, pl. 4, figs. 3, 4.
 1987. *Mandarina hahajimana* Pilsbry; Maeda *et al.*, p. 68, pl. 20, figs. 285a, b.

Material. RM18459 (N=4, sample J18), RM18460 (N=10, sample J19), RM18461 (N=10, sample J20), RM18462 (N=8, sample J23), RM18463 (N=1, sample J26), RM18464 (N=6, sample J27).

Diagnosis. Small-sized species of *Mandarina* characterized by upper penial wall ornamented with separate columns of irregularly and slightly folded pilasters.

Description.

Genital morphology: Flagellum short with a sharp tip. Epiphallus of uniform thickness and relatively short. Penis uniformly long and covered with sheath near the basal penis. Middle penial wall ornamented with 7 or 8 columns of zig-zag, fold-like pilasters. Up-

per penial wall ornamented with 10 or 11 columns of slightly meandering, fold-like pilasters. Vorge conical in shape and longer than wide.

Shell morphology: Shell small, thin with smooth surface. Spire weakly domed. Last whorl with rounded or barely angulated periphery. Umbilicus closed or open. Aperture oblique in shape, wider than high and narrowed at the basal position. Periostracum rather thick and slightly reflected. Base rounded and convex. Whorls 4.5–5.2 in number. Color pattern 1030, n0n0, nnn0, 0000.

Measurements (mm).

Specimens	WH	D	H	AH	AW	IPA	U	KE
RM18461-a	5.1	22.5	16.0	12.0	13.0	0.458	—	
RM18464-a	5.0	21.3	15.9	12.1	13.1	0.389	1.9	

Observation and comparison. All individuals of the sample collected from Loc. 19 have a relatively high spire and a closed umbilicus. In contrast, a clear umbilicus can be seen in some specimens from Loc. 20 and Loc. 27. The sample from Loc. 23 consists of specimens with a low spire and a clear and wide umbilicus.

Distribution. This species is found on leaves or trunks of trees in Hahajima (Locs. 17, 18, 19, 20, 23, 25, 26, 27). Fossils are unknown.

Mandarina exoptata Pilsbry, 1902

Figures 11–13, 15–16

1902. *Mandarina exoptata* Pilsbry, p. 117.

1969. *Mandarina exoptata* Pilsbry; Habe, p. 21, pl. 2, fig. 3.

1978. *Mandarina exoptata* Pilsbry; Minato, p. 43, 49, pl. 3, figs. 1, 2.

1987. *Mandarina exoptata* Pilsbry; Maeda *et al.*, p. 68, pl. 20, fig. 284.

Material. RM18465 (N = 10, sample E20).

Diagnosis. Small-sized species of *Mandarina* characterized by angular periphery and clear umbilicus.

Description. Shell small for the genus. Spire low and weakly domed. Suture shallow.

Body whorl relatively large with strong peripheral angle. Umbilicus widely open. Aperture oblique in shape. Periostracum slightly thickened and reflected. Whorls about 4.5 in number. Color pattern 0000.

Measurements (mm).

Specimen	WH	D	H	AH	AW	IPA	U	KE
RM18465-a	4.5	21.5	13.0	10.8	12.5	0.43	2.3	4

Distribution. Central mountain area of Hahajima (Locs. 19, 20). Fossils are unknown.

Mandarina suenoae Minato, 1978

Figures 5–10, 6b–5, 11–11, 15–17

1978. *Mandarina suenoae* Minato, p. 40, 41, 50, pl. 3, figs. 5, 6.

Material. RM18466 (N = 3, sample S6), RM18467 (N = 10, sample S8).

Diagnosis. Small-sized species of *Mandarina* characterized by upper penial wall ornamented with separate columns of weakly folded pilasters.

Description.

Genital morphology: Flagellum short with a sharp tip. Epiphallus slender and relatively long. Penis uniformly long, covered with sheath at the basal position. Upper penial wall ornamented with 10 or 11 separate columns of weakly meandering, fold-like pilasters. Middle penial wall ornamented with straight columns of pilasters. Verve longer than wide.

Shell morphology: Shell small, thin, olive in color and conical in shape with a pointed apex. Spire high but weakly domed. Surface smooth. Suture shallow. Last whorl with an obtuse peripheral angle. Umbilicus closed or small but sometimes clearly open. Aperture oblique in shape. Periostracum thickened and reflected. Whorls 5.2–5.8 in number. Color pattern usually 0000 and sometimes 1020.

Measurements (mm).

Specimen	WH	D	H	AH	AW	IPA	KE
RM18467-a	5.6	21.5	17.1	11.6	12.6	0.53	1

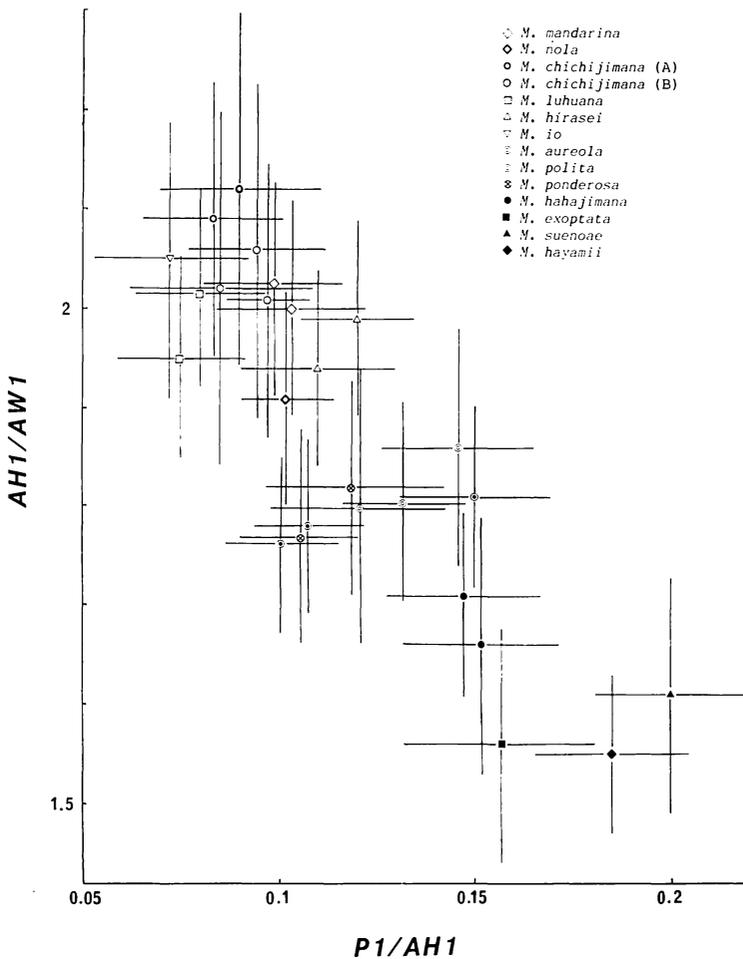


Figure 13. Scatter diagram showing the relation between the apertural height-breadth ratio ($AH1/AW1$) and the flank height-whorl height ratio ($P1/AH1$) of the first whorl in thirteen of *Mandarina* species. Horizontal and vertical bars indicate the range of one standard deviation for each species. Samples used in this figure are indicated in Table 5.

Observation and comparison. This species is similar to *M. hahajimana* in genital morphology. However, the former differs from the latter in having more tightly meandering, fold-like pilasters on upper and middle penial walls and in having longer epiphallus.

Distribution. This species is found on leaves of trees in central mountain area of Chichijima (Locs. 6, 7, 8).

Mandarina hayamii, n. sp.

Figures 11-12, 15-18

Material. Holotype: CM18468-a selected from sample Y14 (P). Paratype: CM18468 [N = 13, sample Y14(P)].

Diagnosis. Medium-sized species of *Mandarina* characterized by sharp peripheral angle, closed or very small umbilicus and sharply pointed apex.

Description. Shell medium in size, thin and triangular in shape. Apex pointed

(mean PI/HI value is 0.185). Spire weakly domed and relatively low. Suture shallow. Last whorl inflated with a strong peripheral angle. Umbilicus closed or very small. Whorls 4.7–5.0 in number. Color pattern 0000.

Measurements (mm).

Specimens	WH	D	H	AH	AW	IPA	KE
Holotype (CM18468-a)	4.9	27.2	17.9	13.5	16.0	0.47	5
Paratype (CM18468-b)	4.9	25.9	17.8	13.4	14.2	0.49	5

Observation and comparison. This species resembles *M. exoptata* in the general morphology of shell. However, the former differs from the latter in having apparently larger shell and sharper apex, almost or perfectly closed umbilicus and lower position of peripheral angle (mean of IPA : 0.472 (*M. hayamii*), 0.420 (*M. exoptata*)).

Distribution. All the specimens were collected from the Pleistocene fissure deposits at Loc. 14 in Chichijima.

Mandarina sp.

Figure 11-16

1903. *Mandarina mandarina* var. *trifasciata* Pilsbry, p. 137, fig. 7.
 1978. *Mandarina mandarina*: Minato, p. 49, pl. 3, fig. 5. (non Sowerby, 1839).

Material. RM18469 (N=2, sample F1)

Description. Shell medium-sized for the genus. Spire rather high and domed. Suture deep. Last whorl with rounded periphery. Aperture rounded in shape. Base rounded and convex. Periostome thickened and reflected. Whorls 5.5 in number. Color pattern 1n30.

Measurements (mm).

Specimen	WH	D	H	AH	AW	IPA
RM18469-a	6.1	20.5	18.8	12.0	11.9	0.42

Observation and comparison. The present species is regarded as *M. mandarina trifasciata* Pilsbry, 1903 described from Nakodjima on account of the color pattern (nnn0)

and general shell shape. This species is similar to *M. chichijimana* in shell form and color pattern. However, it is at present difficult to determine whether this is conspecific with *M. chichijimana* or not, because genital morphology and juvenile shell features have not yet been realized.

Distribution. Nakodjima (Mukojima Islands) at present.

Discussion

Classification of Mandarina species.

All the extant *Mandarina* species have their own characteristics in the external and internal penial features and juvenile shell morphology. On this basis, I here consider the probable phylogenetic relationship of *Mandarina* including fossil species.

Penial morphology in the extant species can be classified into three types: A, B and C, as summarized below.

Type A. Basal penis slender, upper and middle penis uniformly thickened. Middle penial wall ornamented with columns of tightly, regularly, equilaterally folded pilasters (Figure 5). Verge large, longer than wide. *M. mandarina*, *M. chichijimana* and *M. hirasei* possess the penis of this type.

Type B. Basal penis distinctly thick, middle penis narrow. Middle and upper basal penial walls sculptured with columns of regularly, tightly, equilaterally folded pilasters. The pilasters distinctly outgrowth (Figure 5). Verge small, wider than long. The penis of this type is observed in *M. aureola*, *M. polita* and *M. ponderosa*.

Type C. Basal penis slender, upper penis slightly thick. Middle and upper penial walls uniformly sculptured with separate columns of slightly meandering, fold-like pilasters. Verge large, longer than wide. *M. suenoae* and *M. hahajimana* have the penis of this type.

In most species geographic variation of juvenile shell characters is much smaller than that of adult shell characters. In *M. chichi-*

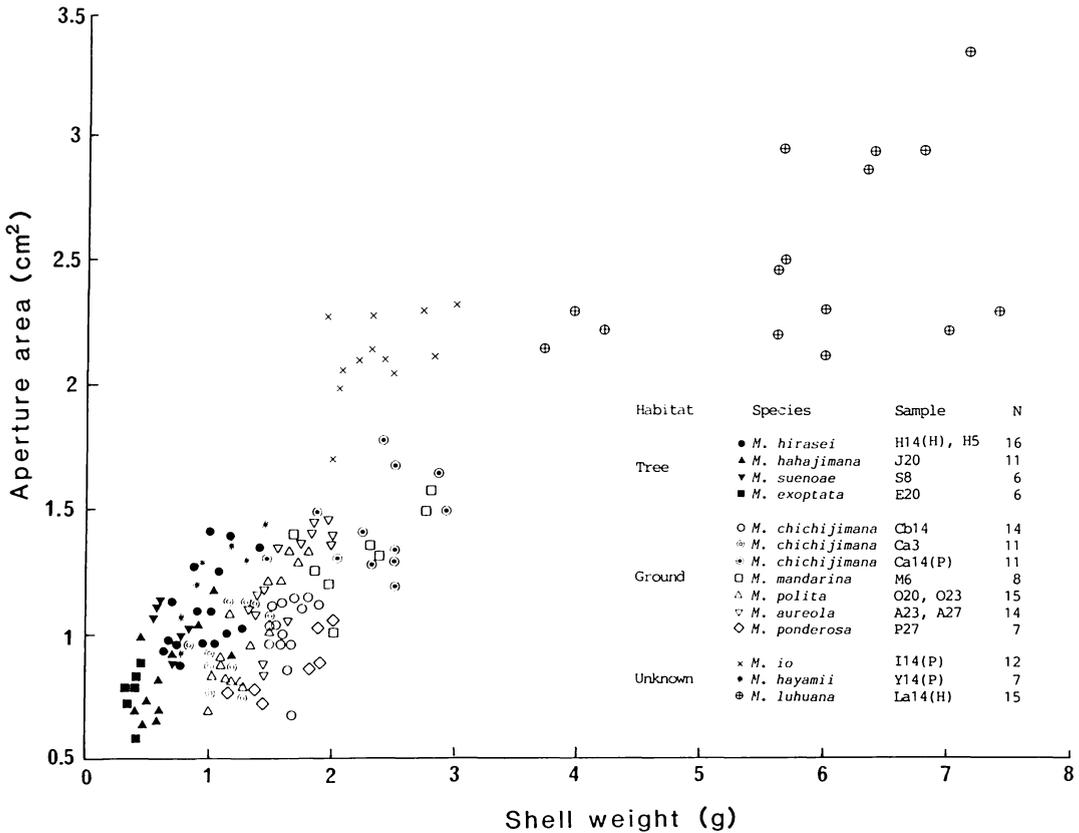


Figure 14. Scatter plots of shell weight vs. apertural area for 14 samples of 12 *Mandarina* species. This figure shows that tree snails and ground snails can be clearly classified into two clusters by the two characters.

jimana, for example, the range of variation of the mean value of the character H/D (see Table 4) is from 0.674 to 0.865, while that of the character $H1/D1$ (see Table 5) is from 1.23 to 1.28. Based on the statistical data listed in Table 5, juvenile shell features of extant and extinct *Mandarina* species are grouped in the following three morphotypes.

Morphotype 1. Juvenile shells with a high spire (mean $H1/D1=1.19-1.28$) and a long aperture (mean $AH1/AW1=1.94-2.12$) with a high position of periphery (mean $P1/H1=0.072-0.120$). This form is shared by *M. mandarina*, *M. nola*, *M. chichijimana*, *M. hirasei*, *M. luhuana*, *M. titan* and *M. io*.

Morphotype 2. This type is characterized by a moderately high spire (mean $H1/D1=$

1.11- 1.19) and rounded aperture (mean $AH1/AW1=1.76-1.86$) with a moderately high position of periphery (mean $P1/H1=0.102-0.150$). *M. aureola*, *M. polita* and *M. ponderosa* possess the juvenile shells of this type.

Morphotype 3. Juvenile shell having a low spire (mean $H1/D1=1.03-1.10$) and a wide aperture (mean $AH1/AW1=1.55-1.71$) with a low position of periphery (mean $P1/H1=0.147-0.200$). *M. hahajimana*, *M. exoptata*, *M. suenoae* and *M. hayamii* share the juvenile shell morphology of this type.

At least in extant species, the classification of *Mandarina* based on penial morphology matches well with that based on juvenile shell morphology. This fact strongly suggests that

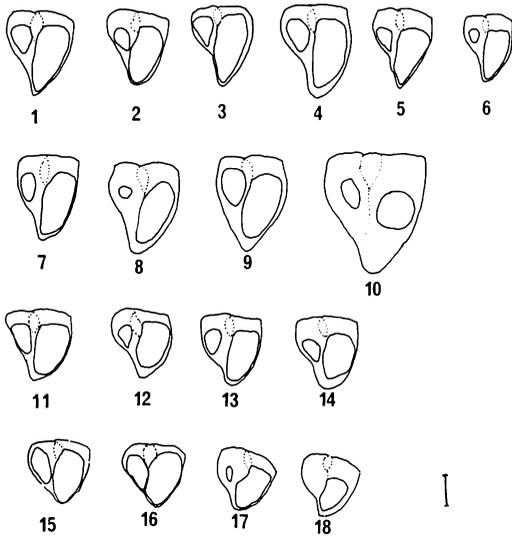


Figure 15. Juvenile shell morphology of 14 species of *Mandarinina* (cross section) **1:** *M. mandarina*, M8; **2:** *M. nola*, N14(P); **3:** *M. chichijimana* (A), Ca3; **4:** *M. chichijimana* (A), Ca14(P); **5:** *M. chichijimana* (B), Cb14; **6:** *M. hirasei*, H14(H); **7:** *M. io*, I14(P); **8:** *M. luhuana* (A), La14(H); **9:** *M. luhuana* (B), Lb14(P); **10:** *M. titan*, T15(P); **11:** *M. aureola*, A25; **12:** *M. polita*, P23; **13:** *M. ponderosa*(A), Pa27; **14:** *M. ponderosa* (B), Pb19; **15:** *M. hahajimana*, J20; **16:** *M. exoptata*, E20; **17:** *M. suenoae*, S8; **18:** *M. hayamii*, Y14(P). Scale bar indicates 1 mm.

juvenile shell characters are useful for reconstructing phylogenetic relationships of *Mandarinina* species. Based on juvenile shell features, extinct species could be classified as well as living species.

I treat the species with Type A, Type B and Type C penis as constituting Stock I, Stock II and Stock III, respectively. I tentatively include extinct species belonging to Morphotype 1 in Stock I, Morphotype 2 in Stock II and Morphotype 3 in Stock III.

Among the species belonging to Stock III, *M. exoptata* and *M. hahajimana* are now restricted in distribution to Hahajima Island, while *M. suenoae* and *M. hayamii* are found in Chichijima Island. The former two species share more pointed apex and narrower juvenile umbilicus than the latter two species.

Judging from the overall shell morphologies, *M. exoptata* and *M. hahajimana* are respectively regarded as allopatric sister taxa of *M. suenoae* and *M. hayamii*. It seems certain that the former two and the latter two species have evolved independently in Hahajima and Chichijima, forming two substocks.

Species forming Stock I (*M. mandarina*, *M. nola*, *M. chichijimana*, *M. hirasei*, *M. io*, *M. luhuana* and *M. titan*) are all distributed in Chichijima Islands. Adult shell morphologies of *M. luhuana* and *M. titan* are distinct from those of other *Mandarinina* species in having markedly large and flat shells.

However, these two species are phylogenetically close to *M. mandarina* or *M. chichijimana*, which have similar adult shells to *M. aureola* or *M. polita* belonging to Stock II. It suggests that remarkable radiation of adult shell morphology has occurred in Chichijima Islands. Extant species of Stock I occurring in Chichijima include both tree species (*M. hirasei*) and ground species (*M. mandarina* and *M. chichijimana*). This fact suggests that the adaptation of *M. hirasei* to the trees occurred in Chichijima Islands at different times from that of other tree species (*M. suenoae*, *M. exoptata* and *M. hahajimana*).

Species forming Stock II (*M. aureola*, *M. polita* and *M. ponderosa*) are all ground snails and indigenous to Hahajima Islands, though their adult morphology is often superficially similar to that of some species of Stock I of Chichijima Islands. This fact indicates speciation occurred independently in Chichijima and Hahajima Islands.

Adaptive significance of adult shell form. Classification of *Mandarinina* species based on adult shell characters is little correlated with that relying on penial anatomy. However, adult shell form is useful to assume the habitats of fossil species. The plots of shell weight versus apertural area in adult shells (Figure 14) show that tree snails (*M. hirasei*, *M. hahajimana*, *M. exoptata* and

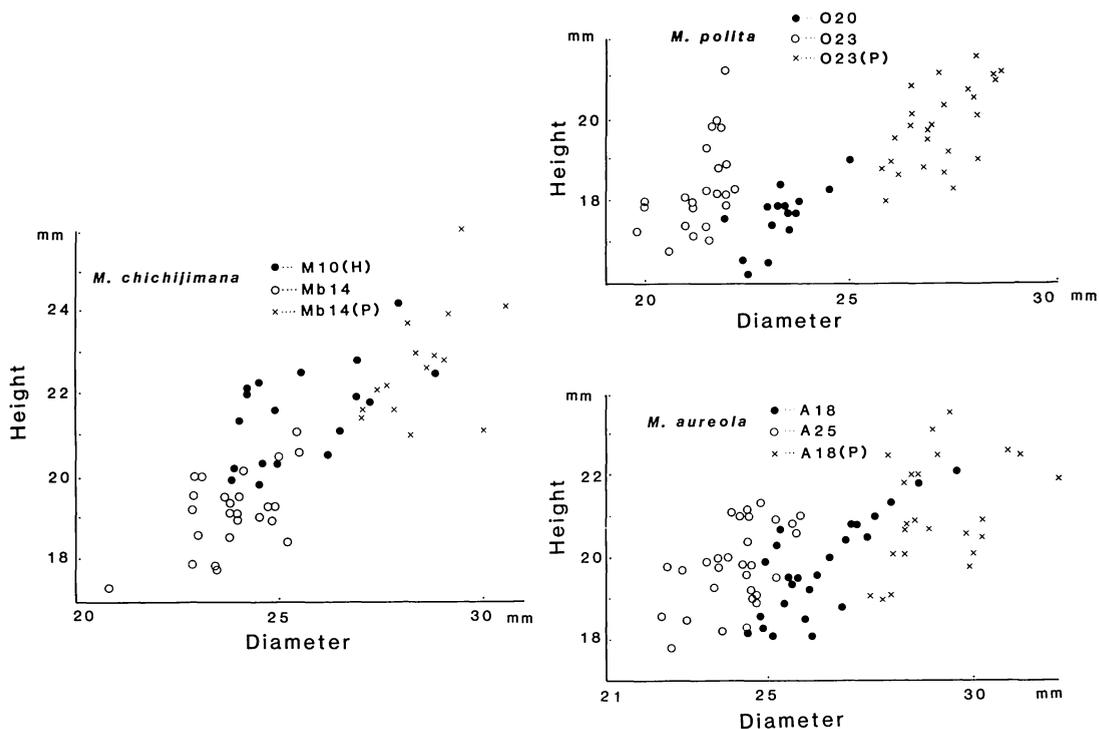


Figure 16. Scatter plots of height vs. diameter in adult shell of the 3 *Mandarina* species, showing the wide shell size variation among samples from different habitats.

M. suenoae) have a relatively lighter shell and a larger apertural area than ground snails, which enables climbing life. Tree snails have usually a wide aperture (smaller AH/AW) with a relatively shorter innerlip (smaller IW/AW or IH/AH). In *Mandarina*, tree snails show pale coloration. For instance, *M. hirasei*, *M. suenoae* and *M. exoptata* lack any dark coloration, and *M. hahajimana* has no or narrow color bands. These tree snails undoubtedly share (1) a light shell, (2) a large and wide aperture with a short innerlip, and (3) pale coloration. By using these criteria, habitat of each fossil species can be assumed. *M. io* and *M. hayamii* were probably tree snails, while other fossil species are regarded as ground snails (Figure 14).

It is difficult to recognize the adaptive significance of shell morphology in the tree snails. Large aperture and thin shell may be advantageous for tree snails to adhere to

trunks or leaves. However, there is an alternative interpretation for the above morphologic characteristics. For instance, it is probable that tree snails cannot obtain sufficient calcium carbonate to construct a thick shell. The peculiar shell features of these tree snails may have resulted both from adaptational and environmental factors. The mutually similar features of tree snails, especially *M. hirasei* and *M. hahajimana*, are interpreted as due to convergence.

Adult shell features in ground species of *Mandarina* also seem to indicate their habitats. Scatter diagram of shell height versus shell width in some samples of three selected species (Figure 16) shows that samples from mountain or relatively wet habitats (Locs. 10, 18, 20) and Pleistocene fossil samples have larger shell size than samples from coastal localities (Locs. 14, 23, 25). In *M. polita* and *M. aureola*, mountain and Pleistocene samples share a relatively low shell. The same

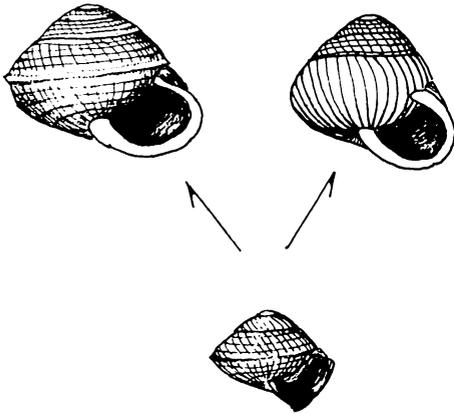


Figure 17. The set of non-paedomorph, forma A (left) and paedomorph, forma B (right) and their juvenile of *M. ponderosa*.

relationship can be seen in other ground species of *Mandarina*. This suggests that mountain environment prevailed over coastal environment during the Pleistocene when sea stood lower level. On the contrary, mountain environment had been replaced by coastal condition as the sea-level ascended. The reason of these relationships between the size or flatness of shell and the environment is poorly known. However, in the Bermudian land snail *Poecilozonites* larger shell is produced under wet climate (Gould 1969a).

Also, Gould (1969b) suggested that in another land snail *Cerion* the larger shell size of Pleistocene samples than living samples was probably due to the rich vegetation of the Pleistocene time. Gould's idea can be applied to the case of *Mandarina* judging from the similar historical change of adult shell size in many species. Emberton (1988) mentioned that increase of flatness is an adaptive feature for crevice-dwelling life habit in the Triodopsinae land snails. However, such morphologic feature cannot be well documented in *M. chichijimana* and *M. polita*. For instance, *M. polita* commonly occurs in limestone crevices (e.g. sample 023), but the crevice specimens have rather higher spire than the animals living under fallen leaves. Vermeij (1980) suggested that in many land snails high spire is produced under severe environment (for instance, dry climate or deficient foods) owing to the slow down of growth rate. Higher spire of coastal and living samples than mountain and the Pleistocene samples in *M. aureola* and *M. polita* may be attributable to dry and less favorable condition.

Deep coloration of adult shell is a common feature in the Pleistocene and extant mountain *Mandarina* species. For instance, speci-

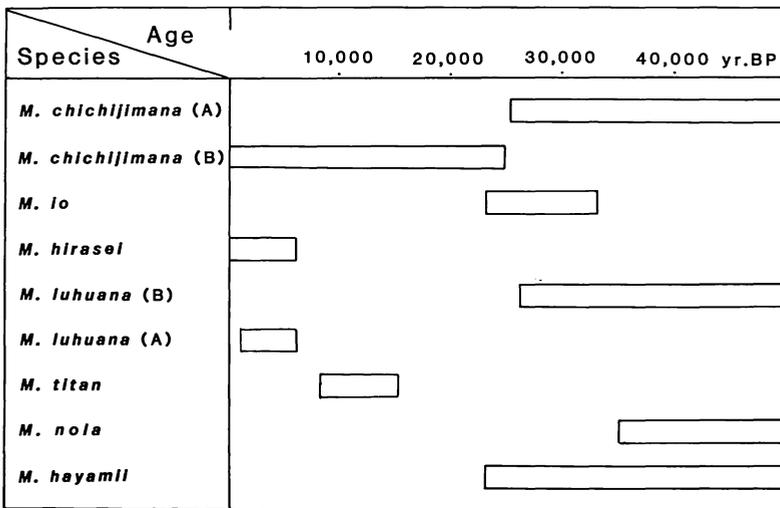


Figure 18. Chronologic ranges of fossil species, indicated by ESR and ¹⁴C datings.

mens in mountain samples of *M. aureola* have a wider color band than those in coastal samples (some specimens with color pattern (123)0 in coastal samples are assumed to be hybrids with *M. ponderosa*). And in the Pleistocene samples of *M. aureola* the color band is markedly wide to merge with other band, suggesting their mountainous habitat. The Pleistocene form of *M. luhuana* has color pattern (123)0, but this color pattern is rare in the Holocene form.

Evolutionary history of Mandarina.

Gould (1969a) documented that in Bermudian *Poecilozonites* that a paedomorph subspecies branched from a non-paedomorph subspecies in the glacial period. Paedomorph and non-paedomorph combination like Bermudian land snails can be found in *Mandarina*. In *Mandarina*, angular periphery, thinner shell and clear striation on the shell surface are all considered to be produced by paedomorphosis. Based on these criteria, forma B and forma C of *M. luhuana* are regarded as paedomorphs of forma A and forma D of the same species. The paedomorph forma B is an extinct form, occurring only in the Pleistocene deposits. The other paedomorph forma C occurs in non-limestone area, and non-paedomorph forma A are known from the Holocene deposits of limestone area. The three formae of *M. ponderosa* also show a paedomorphic relationship (Figure 17). In the last glacial period (ca, 13,300 yr B.P.) a paedomorph, forma C, was distributed in Okimura area, Hahajima Island. It became extinct in the Holocene period in this area. Another paedomorph, forma B is restricted to the mountain area, while forma A, a non-paedomorph of forma B, never occur in the mountain area. Such a paedomorph is thought to be adaptive to mountainous (cool and wet) condition and lime-poor environment. The reason of local extinction of paedomorphs in limestone area can be explained as follows; in glacial period wet

climate produced thick humus soil and it was favorable to paedomorphs. In Holocene the present coastal area became dry, and limestone was exposed. In short frequent extinction event of paedomorphs may have resulted from the above climatic change since the last glacial period.

M. chichijimana has an interesting morphotype set; one morphotype possesses a clear umbilicus and narrow color bands, and another a closed umbilicus and wide and dark color bands. The former is forma A, and the latter is formae B and C. Living animals of forma A are distributed in Anijima, but fossil forma A occurs in the southern part of Chichijima. Forma B, now living in the southern part of Chichijima, appeared in 25,000 yr. B.P., when the sea probably stood at the lowest level, and at that time forma A was disappeared in that area. Living forma A is distributed on plateau where is moderately dry environment covered with scrubby sclerophyllous evergreen forest, and never occurs surrounding the plateau. On the other hand, forma B occurs from both areas of plateau and valleys. Such a plateau area is widely distributed in Anijima but occupies small area in Chichijima, and this is the reason why forma A is not distributed in Chichijima now. However, it is assumed that suitable condition for forma A prevailed widely at that time also in Chichijima, because such a wide plateau as that of Anijima is thought to have covered Chichijima formerly (Asami 1970). The erosion of the plateau is thought to be progressed especially in the main glacial period because of the effect of the lower sea level. The substitution of these two formae is thought to have been rapidly accomplished in view of their fossil records and the result of ESR dating (Figure 18). The following two possibilities can be presumed about the process of substitution.

1. Forma B evolved from forma A about 25,000 yr B.P. in the southern part of Chichijima.

2. Forma B migrated to the area where forma A became extinct.

The possibility of the case 2 is rather unlikely, because forma B of *M. chichijimana* can live both on the dry plateau and in the wet valley. Judging from the later appearance of fossil record and the distribution of forma B, I regard that forma B evolved from forma A about 25,000 yr. B.P. in the valley area newly developed in southern Chichijima. Owing to the low mobility, the distribution area of the two formae have been unchanged since that time.

Forma C of *M. chichijimana* is now distributed in Ototojima. Though there is no fossil record of forma C, the mutual resemblance in shell form between forma B and forma C indicates that the latter branched from forma A in the similar manner with the appearance of the former. The above phenotypic level evolution in *M. chichijimana* had occurred in Chichijima and Ototojima independently.

The presence of morphologically dissimilar populations within the same species or among species of the same stock strongly suggests that the adult shell morphology is remarkably flexible and strongly influenced by the local environment.

Conclusion

The endemic land snail genus *Mandarina* in the Bonin Islands seems to be an interesting organism for considering the tempo and mode of evolution from the viewpoint of historical biology. Analyses of genitalia anatomy and shell morphology on many living and fossil samples have lead me to the following conclusions.

1. Classification of *Mandarina* based on the early shell characters matches well with that based on genitalia. In every species juvenile shell morphology is little influenced by habitat conditions, and it can be used for phylogenetic reconstruction.

2. *Mandarina* species can be classified

into three stocks, Stock I, Stock II and Stock III. Stock I consists of seven species containing two tree species, Stock II three ground species and Stock III four tree species. Species belonging Stock III are distributed in both Chichijima and Hahajima Islands and have counterparts in both islands. However, Stock I and Stock II are restricted to Chichijima and Hahajima, respectively. Speciation in Stock I and Stock II, and in each counterpart in Stock III occurred distinctly in Chichijima and Hahajima Islands at several times, often followed by surprisingly rapid and remarkable morphological change and by radiation to tree and ground habitats. Mutual resemblance of shell features among *M. hirasei*, *M. hahajimana* and *M. exoptata* belonging to different stocks is interpreted as convergence owing to their leave- or trunk-adhering life habit.

3. In many species adult shell features are strongly influenced by habitat or environmental conditions. By analyzing these characters quantitatively, we can presume the life habits and habitat conditions of fossil species.

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Mukojima 婿島, Ototojima 弟島, Anijima 兄島, Chichijima 父島, Minamijima 南島, Hahajima 母島, Hirasima 平島, Imotojima 妹島, Meijima 姪島.

小笠原諸島における陸貝, *Mandarina* の分類と形態変異: 小笠原諸島に固有分布する陸貝, *Mandarina* 属について 7 新種を含む 15 種を記載するとともに, その形態変異と系統関係について考察した。*Mandarina* は, 小笠原諸島において著しい適応放散を行ない, その殻形態は, 種間のみならず同種内においても極めて変異に富む。ただし, 成長初期の殻の特徴は生息様式や環境の影響をあまり受けておらず, これに基づく分類は生殖器に基づく分類とよく一致する。一方, 成貝の殻形態は, 生活様式や環境の影響を強く受けており, これを用いて化石種の生活様式を推測することができる。これらの種群の系統関係は, 主として初期殻の量的形質と雄性生殖器の特徴を用いて推測され, その結果, 異なる系統間における殻形態の取れんや, 同一系統内における殻形態の急速な分化が予想された。

千葉 聡

PROCEEDINGS OF THE PALAEOONTOLOGICAL
SOCIETY OF JAPAN

日本古生物学会第 138 回例会

日本古生物学会第 138 回例会が 1989 年 6 月 24 日-25 日に長崎大学教養部で開催された (参加者 140 人).

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夜間小集会

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 ……………世話人 高柳洋吉・鎮西清高・小西健二

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日本古生物学会特別号編集委員会
(代表者 柳田 壽一)

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- ◎講演申込は共著を含めて一人2題までとし、講演時間は討論を含め15分です。一題目ずつ葉書で期日までに下記宛申し込んで下さい。
- ◎1990年137回例会は6月30日・7月1日に瑞浪市化石博物館で開催される予定です。準備が進められています。詳細は追ってお知らせいたします。

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