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The fossil on the cover is *Vicarya yokoyamai* Takeyama, an Early Middle Miocene gastropod from the Kurosedani Formation at Kakehata, Yatsuo-cho, Nei-gun, Toyama Prefecture, central Japan (Collected by T. Kotaka and K. Ogasawara, IGPS No. 99075, photo by S. Ohtomo and Y. Kikuchi, x0.9).

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832. CRETACEOUS *EOMIODON* AND *COSTOCYRENA* (BIVALVIA) FROM SOUTHWEST JAPAN

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Abstract. In this paper 4 species of *Eomiodon* and 8 species and 2 subspecies of *Costocyrena* (including *Costocyrena ohnishii*, sp. nov., *Costocyrena hojiensis*, sp. nov. and *Costocyrena otsukai obsoleta*, subsp. nov.) belonging to the Family Neomiodontidae are described from the Cretaceous at various localities in southwest Japan.

Geographic distribution of *Eomiodon* and *Costocyrena* species seems to change through the Cretaceous time in southwest Japan. In the Lower Cretaceous, *Eomiodon* species restrictedly occur from the southern side of Kurosegawa Tectonic Belt, while all *Costocyrena* species are known from the northern side of that belt, Northern Chichibu Belt. In the Upper Cretaceous, the geographic distribution of the two genera becomes overlap, and they occur together even at the same localities especially in central Kyushu. This may not mean habitat change of these bivalves, but seems to support the hypothesis of the Early Cretaceous movement of a large lateral fault in the Chichibu Belt.

Introduction

Many species of *Eomiodon* and *Costocyrena* belonging to the Family Neomiodontidae widely thrived during the Cretaceous times in Japan. They occur abundantly from the various stratigraphic horizones characterized by the so-called brackish water facies, ranging from Hauterivian to Cenomanian, at many localities in Southwest Japan.

Eomiodon and *Costocyrena* species described in this paper seem to be important for the correlation of the Cretaceous strata in Japan. Changing of the geographic distribution of *Eomiodon* and *Costocyrena* species through the Cretaceous times also involve interesting problems both on palaeoecology and tectonic developments of eastern Asia.

I wish to express my sincere thanks to Miss Takako Ohnishi of Kagawa Pref., Mr. Hideyuki Yanagisawa of Fukui Pref. and Mr. Seiji Matsuda of Kochi Pref. for their supply of material.

The studied specimens (KSG) are kept in the Faculty of Science, Kochi University.

Systematic descritpion

Family Neomiodontidae Casey, 1955

Subfamily Eomiodontinae Hayami, 1965

Genus *Eomiodon* Cox, 1935

Eomiodon sakawanus (Kobayashi et Suzuki)

Figures 1-7–12

1939. *Astarte sakawana* Kobayashi et Suzuki, *Japan. Jour. Geol. Geogr.*, vol. 13, nos. 3–4, p. 219, pl. 13, fig. 11 (non pl. 13, figs. 12 and 13).

1973. *Eomiodon sakawanus* (Kobayashi et Suzuki); Ohta, *Bull. Fukuoka Univ. Educ.*, vol. 22, no. 3, p. 250, pl. 1, figs. 1–11.

1975. *Eomiodon sakawanus* (Kobayashi et Suzuki); Hayami, *Univ. Mus., Univ. Tokyo, Bull.*, 10, p. 138.

1976. *Eomiodon sakawanus* (Kobayashi et Suzuki); Ohta, *Atlas of Japanese fossils*, vol. 44, Mesozoic bivalves (3), figs. 7–9.

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*Received September 16, 1986; revised manuscript accepted July 6, 1987; read June 15, 1985 at Osaka City University.

Materials:—KSG 3803 and KSG 3804, external moulds of right valves, from Uchiyama of Aioi, Tokushima Prefecture. KSG 3805 and KSG 3806, external moulds of right and left valves, from Yonenomoto of Ittku, Kochi City.

Measurements:—(in mm.)

Specimens	Length	Height	Thickness
KSG 3803, r. ext. mol.	13.0	11.0	2.5
KSG 3804, r. ext. mol.	10.0	9.0	1.5
KSG 3805, r. ext. mol.	14.1	11.5	2.5
KSG 3806, l. ext. mol.	18.0	15.0	2.0

Remarks:—The holotype was occurred from the Kaisekiyama Formation of Kamo, Sakawa in Kochi Prefecture. Two species, treated in this study (Figures 5-1, 11 and 12), preserved in the Fossil Museum of Sakawa (not registered), were also collected from the type locality.

This species is characterized by more broadly spaced concentric ribs on the disk and less inflated valve than other Japanese *Eomiodon* species. About 5 concentric ribs are countable on the adult stage. They are narrower than their interspaces and roof-shaped on the top.

Occurrence and geological age:—Fine-grained sandstone of the Nakaizu Formation at Uchiyama of Aioi, Naka-gun in Tokushima Prefecture; Aptian. Very fine-grained sandstone of the Funadani Formation at Ittku of Kochi City, Kochi Prefecture; Aptian. Sandy mudstone of the Kaisekiyama Formation at Kaisekiyama of Sakawa, Kochi Prefecture. This species is also known from the upper part of the Yamabu Formation at Yamabu, Minami-Amabe-gun in Oita Prefecture; Aptian(?).

Eomiodon matsumotoi Ohta

Figures 1-1–6

1973. *Eomiodon matsumotoi* Ohta, *Bull. Fukuoka Univ. Educ.*, vol. 22, no. 3, p. 245, pl. 2, figs. 1–13.

1975. *Eomiodon matsumotoi* Ohta; Hayami, *Univ. Mus., Univ. Tokyo, Bull.*, 10, p. 139.

1976. *Eomiodon matsumotoi* Ohta; Ohta, *Atlas of Japanese fossils*, vol. 44, Mesozoic bivalves (3), figs. 10–15.

1979. *Eomiodon matsumotoi* Ohta; Katto and Tashiro, *Res. Rep., Kochi Univ.*, vol. 27, *Nat. Sci.*, pl. 2, figs. 1–7.

1981. *Eomiodon matsumotoi* Ohta; Ohta, *Bull. Fukuoka Univ. Educ.*, vol. 31, no. 3, p. 103, pl. 7, figs. 1–8.

Materials:—KSG 3807–KSG 3810, external moulds of left valves; KSG 3811, external mould of right valve; all from Ohta of Tanoura, Ashikita-gun in Kumamoto Prefecture. KSG 3812 – KSG 3813, external moulds of left valves, from Uchiyama of Aioi, Naka-gun in Tokushima Prefecture.

Measurements:—(in mm.)

Specimens	Length	Height	Thickness
KSG 3807, l. ext. mol.	29.5	23.0	4.0
KSG 3809, l. ext. mol.	10.5	88.0	2.0
KSG 3811, r. ext. mol.	22.0	16.0	3.0

Remarks:—This species is characterized by the very fine concentric striae which are developed on the interspaces of the concentric ribs on the disk. Although this species resembles *Eomiodon sakawanus* (Kobayashi et Suzuki) in its roundly subtrigonal outline of the valve and distinct concentric ribs on the disk, it difers from *E. sakawanus* in its more inflated valve, numerous and more or less irregularly spaced concentric ribs, and fine concentric striae on their interspaces.

Occurrence and geological age:—Gray siltstone of the Kawaguchi Formation at Ohta of Tanoura, Ashikita-gun, Kumamoto Prefecture; Hauterivian. Fine-grained sandstone of the Shobu Formation at Uchiyama of Aioi, Naka-gun in Tokushima Prefecture; Hauterivian. This species had been reported from the lower member of Doganaro Formation of the Shimanto Belt in Kochi Prefecture (Katto and Tashiro, 1979) and from the lower part of Yamabu Formation of the Chichibu Belt in Ohita Prefecture (Tashiro, 1985a), both in the Hauterivian in age. This is also known from the Uminoura Formation in central Kyushu (Ohta and Monji, 1976). The geological age of the Uminoura Formation is probably the earliest Cretaceous.

Eomiodon matsubasensis Tamura

Figures 1-13–25

1977. *Eomiodon matsubasensis* Tamura, *Mem. Fac. Educ. Kumamoto Univ.*, no. 26, *Nat. Sci.*, p. 107, pl. 6, figs. 9–19.
1982. *Eomiodon matsubasensis* Tamura; Tashiro and Matsuda, *Trans. Proc. Palaeont. Soc. Japan, N.S.*, no. 127, p. 410, pl. 65, figs. 14–15.
1985. *Eomiodon matsubasensis* Tamura; Matsuda, *Fossils*, no. 39, pl. 2, figs. 9–10.

Materials:—KSG 3814–KSG 3815, external moulds of left and right valves, from Higashimachi (Shishijima island) in Kagoshima Prefecture. KSG 3816–KSG 3818, external moulds of left and right valves, from Karakizaki (Goshonoura island) in Kumamoto Prefecture. KSG 3819 – KSG 3810, external moulds of left and right valves, from Chikaraishi, Kami-mashiki-gun in Kumamoto Prefecture, KSG 3821–KSG 3830, external moulds of left and right valves, from Furuyashiki (Goshonoura island) in Kumamoto Prefecture.

Measurements: - (in mm.)

Specimens	Length	Height	Thickness
KSG 3816, r. ext. mol.	15.0	14.0	4.0
KSG 3818, r. ext. mol.	9.0	8.0	2.0
KSG 3814, l. ext. mol.	13.0	11.5	3.0
KSG 3823, l. ext. mol.	11.0	8.0	2.0
KSG 3819, l. ext. mol.	4.0	3.5	1.0
KSG 3825, l. ext. mol.	6.5	6.5	2.0

Remarks:—Numerous specimens are undoubtedly conspecific with *Eomiodon matsubasensis* Tamura (1977) are collected from the Mifune Group in central Kyushu.

Occurrence and geological age:—Dark gray to greenish gray mudstone of the lower member of Mifune Group at Chikaraishi, Mashiki-machi of Shimo-mashiki-gun in Kumamoto Prefecture; Middle Cenomanian. Very fine-grained sandstone of the S-II Formation of Goshonoura Group at Tateishi, Higashimachi (Shishijima island) of Izumi-gun in Kagoshima Prefecture; Lower Cenomanian. Greenish gray mudstone of the Upper (III) Formation of Goshonoura Group at Karakizaki, Goshonoura-machi (Goshonoura island) of Amakusa-gun in Kumamoto Prefecture; Lower Cenomanian. This species is common in the lower member of the Mifune Group at Magano, Subayashi and Katashida areas of Shimo-mashiki-gun in Kumamoto Prefecture. This is also known from the Fukigoshi Formation of the Sotoizumi Group at Nagase of Odochi, Monobe-mura of Kami-gun in Kochi Prefecture (Lower Cenomanian) (Tashiro and Matsuda, 1982).

Eomiodon? *kumamotoensis* Tamura

1959. *Eomiodon kumamotoensis* Tamura, *Trans. Proc. Palaeont. Soc. Japan, N.S.*, no. 33, p. 115, pl. 12, figs. 17–18.
1960. *Eomiodon kumamotoensis* Tamura; Tamura, *Mem. Fac. Educ. Kumamoto Univ.*, vol. 8, *Nat. Sci.*, p. 240.
1975. *Astarte*? *kumamotoensis* (Tamura); Hayami, *Univ. Mus., Univ. Tokyo, Bull.*, 10, p. 128.
1986. *Eomiodon kumamotoensis* Tamura; Tashiro and Katto, *Res. Rep., Kochi Univ.*, vol. 34, *Nat. Sci.*, pl. 1, figs. 15–17.

Material:—KSG 3931, conjoined valves, from Tainokawa of Obama, Susaki City in Kochi Prefecture.

Remarks:—The typical specimen of this species was described from the Upper Jurassic Sakamoto Formation of the Torinosu Group at Sakamoto in Kumamoto Prefecture, by Tamura (1959).

Occurrence and geological age:—Dark greenish gray mudstone of the basal part of Doganaro Formation of the Shimanto Belt at about 350 m west of Tainokawa of Obama, Susaki City in Kochi Prefecture; Uppermost Jurassic or lowest Cretaceous.

Genus *Costocyrena* Hayami, 1965

Costocyrena radiatostriata (Yabe et Nagao)

Figures 2-13–22

1926. *Cyrena radiatostriate* Yabe et Nago, in Yabe, Nagao and Shimizu, *Sci. Rep., Tohoku Imp. Univ., Ser. 2*, vol. 9, no. 2, p. 51, pl. 12, figs. 29–35.
1965. *Costocyrena radiatostriata* (Yabe et Nagao); Hayami, *Mem. Fac. Sci., Kyushu Univ., Ser. D, Geol.*, vol. 17, no. 2, p. 73, pl. 19, figs. 1–7.
1975. *Costocyrena radiatostriata* (Yabe et Nagao); Hayami, *Univ. Mus., Univ. Tokyo, Bull.*, 10, p. 140.
1976. *Costocyrena radiatostriata* (Yabe et Nagao);


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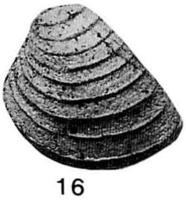
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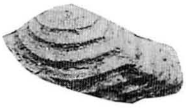
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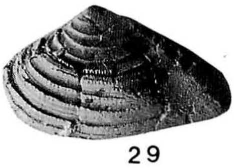
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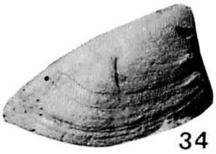
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Ohta, *Atlas of Japanese fossils,* vol. 44, no. 3, figs. 22–26.
1977. *Costocyrena radiatostriata* (Yabe et Nagao); Matsukawa, *Jour. Geol. Soc. Japan,* vol. 83, no. 2, pl. 1, fig. 8.
1979. *Costocyrena radiatostriata* (Yabe et Nagao); Matsukawa, *Ibid.,* vol. 85, no. 1, pl. 1, figs. 3, 4 and 9.
1979. *Costocyrena* sp. B aff. *C. radiatostriata* (Yabe et Nagao); Matsukawa, *Ibid.,* vol. 85, no. 1, pl. 1, figs. 1–2.
1980. *Costocyrena radiatostriata* (Yabe et Nagao); Tashiro *et al.,* in Taira and Tashiro *eds. Geology and paleontology of the Shimanto Belt,* pl. 10, fig. 18.

Materials:—KSG 3831–KSG 3835, right valves: KSG 3836–KSG 3840, left valves; all from Todoronotaki of Hibihara, Monobe-mura, Kami-gun in Kochi Prefecture.

Measurements:—(in mm.)

Specimens	Length	Height	Thickness
KSG 3836, r. v.	9.5	7.0	2.5
KSG 3837, r. v.	9.5	7.5	1.0
KSG 3838, r. v.	14.5	13.5	3.6
KSG 3834, l. v.	10.5	9.0	4.5
KSG 3839, r. v.	16.5	12.5	2.0

Remarks:—This species was described originally from the Sebayashi Formation of Sanchu in central Japan. Hayami (1965) referred this species to *Costocyrena.* The present species undoubtedly belongs to *Costocyrena radiatostriata* (Yabe et Nagao) by the diagnostic characters of which were well defined by Hayamai (1965).

Occurrence and geological age:—Dark-gray mudstone of the lower member of Yunoki Formation of the Monobegawa Group at Todoronotaki of Hibihara (Monobe area), Kami-gun in Kochi Prefecture; Upper Barremian.

Costocyrena matsumotoi Hayami

Figures 5-1–13

1965. *Costocyrena matsumotoi* Hayami, *Mem. Fac. Sci., Kyushu Univ., Ser. D, Geol.,* vol. 17, no. 2, p. 133, pl. 18, figs. 2–12.
1975. *Costocyrena matsumotoi* Hayami; Hayami, *Univ. Mus., Univ. Tokyo, Bull.,* 10, p. 140, pl. 7, figs. 10–11.
1976. *Costocyrena matsumotoi* Hayami; Ohta, *Atlas of Japanese fossils,* vol. 44, Mesozoic bivalves, no. 3, Cr. 26.
1981. *Costocyrena matsumotoi* Hayami; Ohta, *Bull. Fukuoka Univ. Educ.,* vol. 31, no. 3, p. 103, pl. 8, figs. 8–12.

Materials:—KSG 3841–KSG 3843, external moulds of right valves; KSG 3844–KSG 3853, external moulds of left valves; all from Jhoguzan

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← **Figures 1-1–6.** *Eomiodon matsumotoi* Ohta, x1

1, KSG 3807; 2, KSG 3811; 3, KSG 3808; 4, KSG 3809; 5, KSG 3810; Loc. Ohta of Tanoura, Ashikita-gun, Kumamoto Pref., 6, KSG 3812; Loc. Mamidani of Nakaizu, Kami-katsu-gun, Tokushima Pref.

7–12. *Eomiodon sakawanus* (Kobayashi et Suzuki)

7, KSG 3803; 8, KSG 3804; x1.5, Loc. Uchiyama of Aioi, Naka-gun, Tokushima Pref., 9, KSG 3805; 10, KSG 3806; x1, Loc. about 200 m south of Yonenomoto, Kochi City, Kochi Pref., 11 and 12, x1.5, Loc. Kaisekiyama of Kamo, Sakawa, Takaoka-gun, Kochi Pref.

13–25. *Eomiodon matsubasensis* Tamura, x2

13, KSG 3816; 14, KSG 3817; 15, KSG 3818; Loc. Karakizaki, Goshonoura-jima, Amakusa-gun, Kumamoto Pref., 16, KSG 3814, Loc. Higashimachi, Shishijima, Izumi-gun, Kagoshima Pref., 17, KSG 3821; 18, KSG 3822; 19, KSG 3823; 21, KSG 3824; 22, KSG 3825; 23, KSG 3826; 24, KSG 3829; 25, KSG 3830; Loc. Furuyashiki of Hongo, Goshonoura-jima, Amakusa-gun, Kumamoto Pref., 20, KSG 3819, Loc. Chikaraishi of Miyanomoto, Kamimashiki-gun, Kumamoto Pref.

26–30. *Costocyrena otsukai otsukai* (Yabe et Nagao), x2

26, KSG 3910, Loc. Tatsukawa of Katsuura, Kamikatsu-gun, Tokushima Pref., 27, KSG 3907, Loc. Yonenomoto of Ittku, Kochi City, Kochi Pref., 28, KSG 3912; 30, KSG 3905; Loc. Kaganoi of Kuma, Kochi City, Kochi Pref., 29, KSG 3913, Loc. Kami-Koshigoe, Minami-Amabe-gun, Ohita Pref.

31–37. *Costocyrena otsukai obsoleta,* subsp. nov., x2

31, KSG 3896, holotype; 32, KSG 3899, paratype; 33, KSG 3900, paratype; 34, KSG 3901, paratype; 35, KSG 3897, paratype; 36, KSG 3902, paratype; 37, KSG 3898, paratype; Loc. Idaira of Inasa, Shizuoka Pref.

All the specimens are gum cast of the external moulds, except for 11 and 12.

of Miyaji (type locality of this species by Hayami, 1965), Yatsushiro City in Kumamoto Prefecture.

Measurements:—(in mm.)

Specimens	Length	Height	Thickness
KSG 3841, r. ext. mol.	20.0	16.5	4.5
KSG 3842, r. ext. mol.	11.0	8.5	2.3
KSG 3843, r. ext. mol.	10.0	9.0	2.0
KSG 3845, l. ext. mol.	14.5	11.5	3.5
KSG 3850, l. ext. mol.	21.0	18.0	4.5
KSG 3852, l. ext. mol.	15.0	11.0	4.0

Remarks:—Many external and internal moulds of this species are at hand. This specis resembles *Costocyrena radiatostriata* (Yabe et Nagao), in its subtrigonal outline, but it differs clearly from the latter by its less numerous and distinct concentric ribs on the disk, and less numerous and stronger radial striae on the disk.

Occurrence and geological age:—Dark gray mudstone of the Yatsushiro Formation at Jhoguzan of Miyaji, Yatsushiro City in Kumamoto Prefecture; upper part of the Lower Albian by Matsumoto *et al.* (1981).

Costocyrena minor Ohta

Figures 2-29–33

1981. *Costocyrena minor* Ohta, *Bull. Fukuoka Univ. Educ.*, vol. 31, no. 3, p. 103, pl. 8, figs. 19–36.

Materials:—KSG 3854–KSG 3856, external moulds of right valves; KSG 3857–KSG 3859, external moulds of left valves; both from Doiban of Yunoki (Monobe area), Kami-gun, Kochi Prefecture. KSG 3860–KSG 3862, external moulds of left and right valves, from Imaizumi of Yatsushiro City in Kumamoto Prefecture.

Measurements:—(in mm.)

Specimens	Length	Height	Thickness
KSG 3857, l. ext. mol.	5.0	4.5	1.0
KSG 3858, l. ext. mol.	6.0	5.5	1.0
KSG 3854, r. ext. mol.	5.5	5.0	1.0
KSG 3859, l. ext. mol.	6.5	5.5	1.4
KSG 3860, r. ext. mol.	6.0	4.8	1.0
KSG 3862, r. ext. mol.	5.0+	5.0	1.2

Remarks:—The specimens from the Monobe area in Kochi Prefecture, are somewhat larger than the specimens from the Yatsushiro area in Kumamoto Prefecture. Other features between the specimens from the two areas, are entirely identical in each others. This species is discriminated from *Costocyrena radiatostriata* (Yabe et Nagao), in its very smaller valve, and more distinct concentric ribs on the disk.

Occurrence and geological age:—Dark greenish gray mudstone of the basal part of Hibihara Formation at Yunoki of Odochi, Kami-gun in Kochi Prefecture (Monobe area); Aptian. Dark gray mudstone of the Miyaji Formation at Imaizumi Yatsushiro City in Kumamoto Prefecture (Yatsushiro area); Aptian(?). This species is also

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→ **Figures 2-1–12.** *Costocyrena ohnishii*, sp. nov., x2

1, KSG 3884, paratype; 2, KSG 3881, paratype; 3. KSG 3882, paratype; 4, KSG 3885, paratype; 5, KSG 3880, holotype; 6, KSG 3883, paratype; Loc. Tatsukawa of Katsuura, Kamikatsu-gun, Tokushima Pref., 7, KSG 3887, paratype; 8, KSG 3892, paratype; 9, KSG 3893, paratype; 10, KSG 3891, paratype; 11, KSG 3886, paratype; 12, KSG 3888, paratype; Loc. Idaira of Inasa, Shizuoka Pref.

13–22. *Costocyrena radiatostriata* (Yabe et Nagao), x2

13, KSG 3831; 14, KSG 3836; 15, KSG 3837; 16, KSG 3838; 17, KSG 3839; 18, KSG 3840; 19, KSG 3832; 20, KSG 3833; 21, KSG 3834; 22, KSG 3835; Loc. Todoronotaki of Yunoki, Odochi area, Kami-gun, Kochi Pref.

23–28. *Costocyrena mifunensis* Tamura, x2

23, KSG 3864; 24, KSG 3865; 26, KSG 3866; 27, KSG 3867; 28, KSG 3863; Loc. Karakizaki of Goshonoura-jima, Amakusa-gun, Kumamoto Pref., 25, KSG 3868; Loc. Higashimachi of Shishijima, Izumi-gun, Kagoshima Pref.

29–33. *Costocyrena minor* Ohta, x2

29, KSG 3857; 30, KSG 3858; 31, KSG 3854; 32, KSG 3859; 33, KSG 3855; Loc. Doiban of Yunoki, Odochi area, Kami-gun, Kochi Pref.

All the specimens are gum casts of the external moulds.


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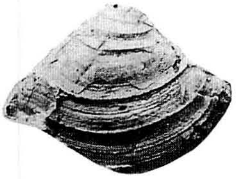
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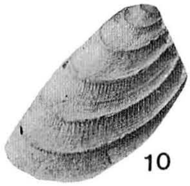
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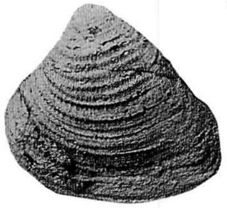
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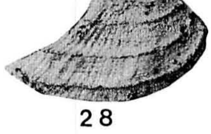
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known from the basal part of the Hinagu Formation (Aptian) at Koda of Yatsushiro City in Kumamoto Prefecture.

Costocyrena mifunensis Tamura

Figures 2-23–28

1977. *Costocyrena mifunensis* Tamura, *Mem. Fac. Educ. Kumamoto Univ.*, no. 26, *Nat. Sci.*, p. 107, pl. 12, figs. 12–20.

1985. *Costocyrena mifunensis* Tamura; Matsuda, *Fossils*, no. 39, pl. 2, fig. 8.

Materials:–KSG 3863–KSG 3867, external moulds of right and left valves, from Furuyashiki of Hongo, Goshonoura island in Kumamoto Prefecture. KSG 3868, right external mould, from Higashi-machi, Shishijima island in Kagoshima Prefecture.

Measurements:–(in mm.)

Specimens	Length	Height	Thickness
KSG 3863, r. ext. mol.	15.0	10.0	2.0
KSG 3864, r. ext. mol.	11.5	7.0	3.0
KSG 3865, l. ext. mol.	19.0	13.0	4.0
KSG 3866, r. ext. mol.	16.0	8.0	3.0
KSG 3867, l. ext. mol.	11.0	8.0	2.0
KSG 3868, r. ext. mol.	16.0	9.5	2.0

Remarks:–Although the specimens from the Goshonoura Group, treated in this paper, are deformed, they are undoubtedly identified with *Costocyrena mifunensis* Tamura, from the Mifune Group in central Kyushu, by its strongly elevated concentric ribs on the disk and broadened area behind the posterior carina. This species is easily discriminated from other species of *Costocyrena, e.g., C. radiatostriata* (Yabe et Nagao), *C. minor* Ohta or *C. otsukai* (Yabe et Nagao), in its very strong concentric ribs, less numerous but strong radial striae, and broadened posterior slope (area) behind the posterior carina.

Occurrence and geological age:–Dark gray mudstone of the upper formation (III) of Goshonoura Group at Furuyashiki of Hongo, Goshonoura-machi (Goshonoura island), Amakusa-gun in Kumamoto Prefecture; Lower Cenomanian. Fine-grained sandstone of the S-II (Katasoba) Formation of the Goshonoura Group at Higashi-machi (Shishijima island), Izumi-gun in Kagoshima Prefecture; Lower Cenomanian. The type specimen (KE2669) by Tamura (1977), was recorded from the Lower Formation of Mifune Group (Middle Cenomanian), in central Kyushu.

Costocyrena hojiensis, sp. nov.

Figures 3, 5-28–37

Materials:–Holotype, KSG 3869, left external mould; paratypes, KSG 3870–KSG 3871, right external moulds; paratypes, KSG 3872–KSG 3875, left external moulds; KSG 3877–KSG 3879, internal moulds of left and right valves; all from Tatsukawa of Katsuura-machi, Tokushima Prefecture.

Diagnosis:–Shell trigonally ovate; umbo strongly prosogyrous, located at about one fourth or less from front of valve; surface with numerous concentric ribs; posterior carina weak.

Description:–Shell moderate in size, trigonally ovate or roundly subtrigonal in outline, weakly inflated, longer than high; umbo small, a little prominent, strongly prosogyrate for the genus, located at about one fourth or one fifth from front of valve; anterior dorsal margin short, weakly concave; anterior margin nearly straight, forming a blunt angle about 110° with broadly arched ventral margin; posterior margin weakly convex; posterior dorsal margin long, slightly convex; posterior carina weak; escutcheon narrow but elongated; lunule very narrow, distinctly

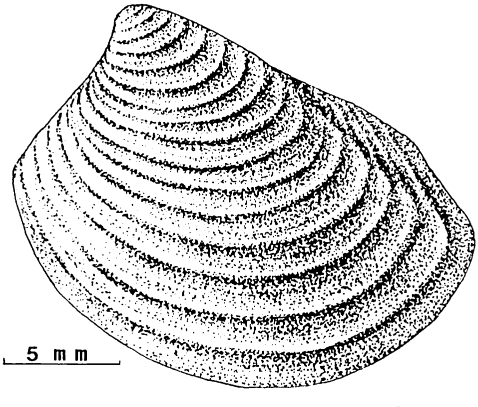

Figure 3. Sketch of the holotype, *Costocyrena hojiensis*, sp. nov.

depressed from the disk; surface ornamented with crowded concentric ribs; ribs roof-shaped, narrower than their interspaces, number about 20 on adult specimens; hinge of lucinoid, cardinal 2 and 3b large, oblique; cardinal 3a small, subvertical; inner margin smooth.

Measurements:—(in mm.)

Specimens	Length	Height	Thickness
KSG 3872, l. ext. mol.	12.0	10.0	2.0
KSG 3873, l. ext. mol.	15.0	11.0	2.0
KSG 3869, l. ext. mol.	13.0	9.0	3.0
KSG 3874, l. ext. mol.	13.0	9.5	2.0
KSG 3870, r. ext. mol.	16.0	13.0	3.5
KSG 3875, l. ext. mol.	16.5	12.0	3.5
KSG 3871, r. ext. mol.	17.5	13.0	5.0

Observation:—On some specimens of this species very fine and numerous radial striae appear subinternally on the interspaces of the concentric ribs on the disk. The posterior carina is very weak except for umbonal region.

Comparison:—The immature forms of this species are closely similar to the mature forms of *Costocyrena minor* Ohta, in having its subtrigonal outline of the valve and remarkable concentric ribs on the disk. This species is probably related to *Costocyrena minor.*

Occurrence and geological age:—Fine-grained sandstone of the basal part of the Hoji Formation of the Monobegawa Group at Tatsukawa of Katsuura-machi, Kami-katsu-gun in Tokushima Prefecture; Aptian.

Costocyrena ohnishii, sp. nov.

Figures 2-1–12, 4

Materials:—Holotype, KSG 3880, external mould of left valve; paratypes, KSG 3881–KSG 3883, external moulds of right valves; KSG 3884–KSG 3885, external moulds of left valves; all from Tatsukawa of Katsuura, Tokushima Prefecture. Paratypes, KSG 3886–KSG 3888, external moulds of left valves; KSG 3889–KSG 3895, external moulds of right valves; both from Idaira of Inasa, Shizuoka Prefecture.

Diagnosis:—Shell trigonally ovate; umbo strongly prosogyrate, located at about one fourth to two fifths from front of valve; surface ornamented by strongly prominent and crenulated concentric ribs which are very widely spaced; posterior carina distinctly angulated.

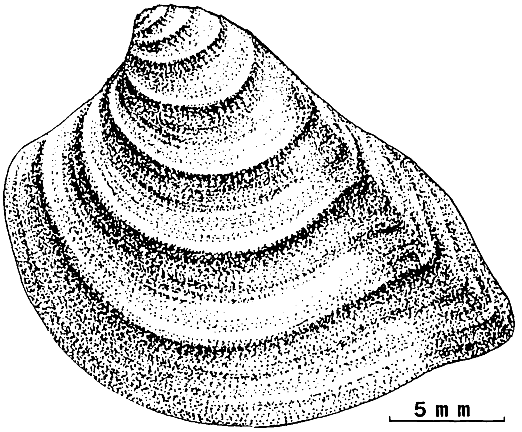

Figure 4. Sketch of the holotype, *Costocyrena ohnishii,* sp. nov.

Description:—Shell moderate in size, trigonally ovate or elliptically subtrigonal in outline, more or less inflated, slightly longer than high; umbo prominent, strongly prosogyrous for the genus, located anteriorly at one fourth to two fifths in shell length; anterior dorsal margin weakly concave; anterior margin very short, nearly straight, forming nearly a right angle with broadly arcuated ventral margin; posterior margin short, subvertical, very weakly convex; posterior dorsal margin very long, nearly straight or very weakly arched; posterior carina strongly angulated, extended nearly straight from umbo to postero-ventral corner; lunule distinctly separated from the disk, deeply depressed; escutcheon very narrow but elongated; surface ornamented with about 7 strong concentric ribs which are narrower than their interspaces and very finely crenulated; hinge with typical Lucinoid; inner margin smooth.

Measurements:—(in mm.)

Specimens	Length	Height	Thickness
KSG 3884, l. ext. mol.	13.5	10.0	2.0
KSG 3881, r. ext. mol.	15.0	9.5	2.0
KSG 3882, r. ext. mol.	16.0	15.0	4.0
KSG 3885, l. ext. mol.	15.0	14.0	4.0

KSG 3880, l. ext. mol.	13.0	11.0	2.0
KSG 3889, r. ext. mol.	11.0	8.5	2.0
KSG 3890, r. ext. mol.	11.5	9.0	3.0
KSG 3891, r. ext. mol.	14.5	11.5	3.0
KSG 3886, l. ext. mol.	10.5	7.0	3.0
KSG 3892, r. ext. mol.	15.0	9.0	3.0

Observation:—The concentric ribs on the disk are somewhat variable in strength but are rather uniform in number. On some specimens, very fine radial striae which are concerned with the crenulations on the concentric ribs, appear on the outsklits of the ribs (see Figure 2-10).

Comparison:—This species resembles *Costocyrena otsukai* (Yabe et Nagao in Yabe, Nagao and Shimizu, 1926), from the Shiroi Formation of the Sanchu area in central Japan, in its less developed radial striae on the disk, but the former differs from the latter in its strong and less numerous concentric ribs and more or less prominent umbo.

Occurrence and geological age:—Dark gray mudstone of the Tatsukawa Formation at Tatsukawa, Katsuura-gun in Tokushima Prefecture; Upper Hauterivian. Dark gray shale of the Idaira Formation at Inasa, Inasa-gun in Shizuoka Prefecture; Barremian(?) or Upper Hauterivian.

Costocyrena otsukai otsukai (Yabe et Nagao)

Figures 1-26–30

1926. *Cyrena otsukai* Yabe et Nagao, in Yabe, Nagao and Shimizu, *Sci. Rep. Tohoku Imp. Univ., Ser. 2*, vol. 9, no. 2, p. 50, pl. 2, figs. 20–24.
1973. *Costocyrena otsukai* (Yabe et Nagao); Ohta, *Bull. Fukuoka Univ. Educ.*, vol. 22, no. 3, p. 256, pl. 3, figs. 1–11.
1973. *Costocyrena crenatus* Ohta, *Ibid.*, vol. 22, no. 3, p. 258, pl. 3, fig. 12.
1975. *Costocyrena otsukai* (Yabe et Nagao); Hayami, *Univ. Mus., Univ. Tokyo, Bull.*, 10, p. 139.
1976. *Costocyrena otsukai* (Yabe et Nagao); Ohta, *Atlas of Japanese fossils*, vol. 44, Mesozoic bivalves, no. 3, Cr. 26, figs. 16–20.
1977. *Costocrena otsukai* (Yabe et Nagao); Matsukawa, *Jour. Geol. Soc. Japan*, vol. 83, no. 2, pl. 1, figs. 7, 10 and 11.
1979. *Costocyrena otsukai* (Yabe et Nagao); Matsukawa, *Ibid.*, vol. 85, no. 1, pl. 1, figs. 5–6.
1981. *Costocyrena otsukai* (Yabe et Nago); Ohta, *Bull. Fukuoka Univ. Educ.*, vol. 31, no. 3, p. 103, pl. 7, figs. 13–34.

Materials:—KSG 3903–KSG 3904, external moulds of left and right valves, from Yonenomoto of Ittku, Kochi City in Kochi Prefecture. KSG 3905–KSG 3908, external moulds of left and right valves, from Kaganoi of Higashi-kuma, Kochi City. KSG 3909–KSG 3912, external moulds of right and left valves, from Tatsukawa of Katsuura, Katsuura-gun in Tokushima Prefecture. KSG 3913–KSG 3916, external moulds of right valves, from Kami-koshigoe, Minami-Amabe-gun in Ohita Prefecture.

Measurements:—(in mm.)

Specimens	Length	Height	Thickness
KSG 3906, l. ext. mol.	16.0	12.5	2.5
KSG 3907, r. ext. mol.	17.0	11.5	3.5
KSG 3909, l. ext. mol.	14.0	9.5	2.5
KSG 3910, r. ext. mol.	16.0	11.5	2.0
KSG 3911, r. ext. mol.	18.0	11.0	2.0
KSG 3913, l. ext. mol.	15.5	9.0	2.5
KSG 3912, l. ext. mol.	18.0	13.5	3.0

→ **Figures 5-1–13.** *Costocyrena matsumotoi* Hayami, x2

1. KSG 3844; 2, KSG 3845; 3, KSG 3841; 4, KSG 3846; 5, KSG 3842; 6, KSG 3847; 7, KSG 3848; 8, KSG 3843; 9, KSG 3849; 10, KSG 3850; 11, KSG 3851; 12, KSG 3852; 13, KSG 3853; Loc. Jhogusan of Miyaji, Yatsushiro City, Kumamoto Pref.

14–27. *Costocyrena* sp. cf *C. peikangensis* Hayami, x2

14, KSG 3917; 15, KSG 3920; 18, KSG 3918; 20, KSG 3922; 21, KSG 3923; 22, KSG 3924; 26, KSG 3919; 27, KSG 3921; Loc. Kasanokawa of Okho, Ryoseki area, Nangoku City, Kochi Pref., 16, KSG 3929; 25, KSG 3928; 17, KSG 3930; 19, KSG 3927; Loc. Todai of Hase, Kami-ina-gun, Nagano Pref., 23, KSG 3926; Loc. Idaira of Inasa, Inasa-gun, Shizuoka Pref., 24, x3, showing surface ornamentation, Loc. Kasanokawa.

28–37. *Costocyrena hojiensis*, sp. nov., x2

28, KSG 3876; 29, KSG 3872, paratype; 30, KSG 3871, paratype; 31, KSG 3870, paratype; 32, KSG 3875, paratype; 33, KSG 3873, paratype; 34, KSG 3869, holotype; 35, KSG 3877, paratype; 36, KSG 3879, paratype; 37, KSG 3878, paratype; Loc. Kawanishi of Kami-katsu-gun, Tokushima Pref.

All the specimens are gum casts of the internal and external moulds.


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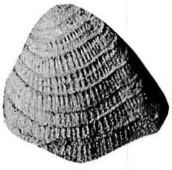
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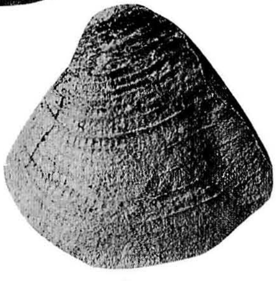
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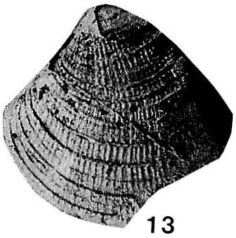
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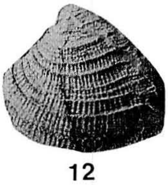
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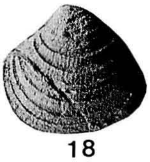
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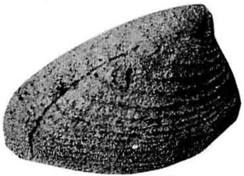
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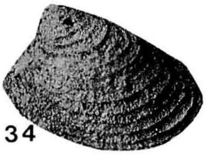
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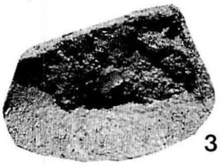
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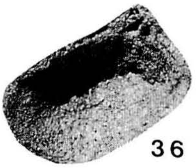
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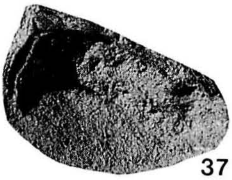
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Remarks:—This subspecies is one of the well known Early Cretaceous bivalves, representative of the so-called Ryoseki Fauna in southwest Japan. The concentric ribs on the disk are variable from 8 to 15 in number. Very fine radial striae or crenulations are often observable on the top or outsklits of the concentric ribs.

The crenulations on the concentric ribs are described as the subspecific characters which were discriminated *Costocyrena otsukai crenatus* Ohta from *C. otsukai otsukai* by Ohta (1973). In so far as I can see the distinctions between them are one of the varieties of *C. otsukai otsukai.*

Occurrence and geological age:—Fine-grained sandstone or silty mudstone of the upper member of Ryoseki Formation of the Monobegawa Group, at Yonenomoto of Ittku and Kaganoi of Higashikuma, both in Kochi City; Hauterivian. Dark greenish gray mudstone of the upper member of the Ryoseki Formation at about 1600 m north of Suita, Kami-gun in Kochi Prefecture; Hauterivian. Greenish gray sandy mudstone of the Tatsukawa Formation of the Monobegawa Group at Tatsukawa of Katsuura, Katsuura-gun in Tokushima Prefecture; Hauterivian. Dark gray mudstone of the upper member of Koshigoe Formation (Haidate II Formation by Tashiro *et al.,* 1983) at Kami-koshigoe of Honjho, Minami-Amabe-gun in Ohita Prefecture; Hauterivian. Dark gray mudstone of the Kawaguchi Formation at Kami-tanoura of Tanoura-machi, Ashikita-gun in Kumamoto Prefecture. The holotype was recorded from the Shiroi Formation of the Sanchu area in central Japan. This species is also known from the Yuasa Formation at Yuasa in Wakayama Prefecture.

Costocyrena otsukai obsoleta, subsp. nov.

Figures 1-31–37, 6

Materials:—Holotype, KSG 3896, external mould of left valve; paratypes, KSG 3897 – KSG 3898, external moulds of left valves; KSG 3899 – KSG 3902, external moulds of right valves; all from Idaira of Inasa, Inasa-gun in Shizuoka Prefecture.

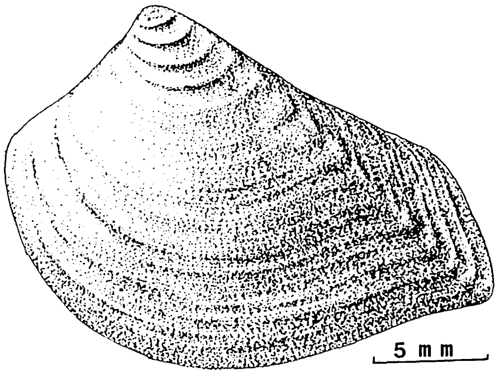

Figure 6. Sketch of the holotype, *Costocyrena otsukai obsoleta,* subsp. nov.

Diagnosis:—Shell trigonal ovate; umbo prosogyrate, weakly prominent; surface nearly smooth except for several weak concentric ribs near umbo; posterior carina distinctly angulated.

Description:—Shell medium in size, trigonally ovate, longer than high, moderately inflated; umbo small, weakly prosogyrate, a little prominent, pointed at two fifths from front of valve; anterior dorsal margin nearly straight; anterior margin well rounded; ventral margin broadly arched; posterior margin short, nearly straight or very weakly convex; posterior dorsal margin elongated with about twice length of the anterior dorsal margin, weakly convex; surface nearly smooth except for several weak concentric ribs which are very narrower than their interspaces, occupied near the umbonal region; postero-ventral corner obtusely angulated with nearly right angle; posterior carina distinctly angulated, extended from umbo to postero-ventral corner; escutcheon very narrow but elongated; lunule very narrow and short; posterior area or slope rather broad for the genus; hinge identical with that of *Costocyrena otsukai otsukai* (Yabe et Nagao); inner margin smooth; adductor scars very weakly impressed.

Measurements.—(in mm.)

Specimens	Length	Height	Thickness
KSG 3896, l. ext. mol.	16.0	11.0	4.0
KSG 3897, l. ext. mol.	13.0	11.0	3.5
KSG 3898, l. ext. mol.	11.0	6.5	2.0
KSG 3899, r. ext. mol.	18.0	12.5	3.0
KSG 3900, r. ext. mol.	15.5	10.0	3.5

KSG 3901, r. ext. mol.	15.0	10.5	3.0
KSG 3902, r. ext. mol.	17.0	9.5	3.5

Observation:—In this new subspecies, the umbonal concentric ribs are variable in number and strength, and usually occupied about one third from the umbo in the shell height. The hinge structure and internal features of the valve are entirely identical with those of *Costocyrena otsukai otsukai* (Yabe et Nagao), from the Lower Cretaceous of southwest Japan (Yabe, Nagao and Shimizu, 1926; Hayami, 1965; Ohta, 1973, 1981).

Comparison:—This new subspecies differs from *Costocyrena otsukai otsukai* (Yabe et Nagao), in its nearly smooth external surface at their adult stage. In their younger stages this subspecies is, however, difficult to discriminate from *C. otsukai otsukai* in the same diagnostic features. Although this subspecies resembles *Costocyrena ohnishii*, sp. nov. in its subtrigonal outline, the former differs from the latter by its smooth surface.

Occurrence and geological age:—Dark gray mudstone of the Idaira Formation at Idaira of Inasa, Inasa-gun in Shizuoka Prefecture; Barremian or Hauterivian.

Costocyrena sp. cf. *C. peikangensis* Hayami

Figures 5-14–27

Compared with:—

1965. *Costocyrena peikangensis* Hayami, in Matsumoto, Hayami and Hashimoto, *Petrol. Geol. Taiwan*, no. 4, p. 12, pl. 2, figs. 5–6.

1975. *Costocyrena peikangensis* Hayami; Hayami, *Univ. Mus., Univ. Tokyo, Bull.*, 10, p. 140.

Materials:—KSG 3917–KSG 3921, external moulds of left valves; KSG 3922–KSG 3925, external moulds of right valves; both from Kasanokawa of Okho, Nangoku City in Kochi Prefecture. KSG 3927–KSG 3930, external moulds of right and left valves, from Todai of Hase, Nagano Prefecture. KSG 3926, external mould of right valve, from Idaira of Inasa, Inasa-gun in Shizuoka Prefecture.

Description:—Shell small, roundly ovate in outline, slightly longer than high, weakly inflated; umbo small, prosogyrous, weakly prominent, located at about one third from front of valve; anterior dorsal margin short, weakly concave; anterior margin narrowly rounded; ventral margin broadly arched and gradually changing into subvertical posterior margin; posterior dorsal margin long, very weakly convex; surface ornamented with regularly spaced concentric ribs and very fine numerous radial striae; posterior carina weak for the genus; escutcheon narrow and lanceolate; lunule very narrow and short, distinctly separated from the disk by angulated ridge.

Measurements:—(in mm.)

Specimens	Length	Height	Thickness
KSG 3917, l. ext. mol.	10.0	8.0	2.0
KSG 3918, l. ext. mol.	13.0	10.0	3.5
KSG 3920, l. ext. mol.	8.0	6.0	1.0
KSG 3922, r. ext. mol.	9.0	8.5	1.5
KSG 3923, r. ext. mol.	10.0	9.0	2.0
KSG 3930, l. ext. mol.	8.5	7.0	1.5

Observation:—Abundant specimens, mostly external and internal moulds, of this species are at hand. This species is characterized by rounded outline of the valve, and weak posterior carina for the genus *Costocyrena*. The concentric ribs are somewhat variable in number, but countable to about 15 in some specimens. They are very narrower than their interspaces and roof-shaped on the top. About 5 on umbonal ones are densely crowded but the other ones are widely spaced. The radial striae on the disk generally appear on the interspaces of the concentric ribs and its number is about 4 in the breadth of 1 mm.

Comparison:—This species is very similar to *Costocyrena peikangensis* Hayami (1965) from the Lower Cretaceous of Taipei in Taiwan, in its nearly identical features of the valve. The umbonal concentric ribs are somewhat more crowded in this species than in *C. peikangensis*. This resembles *Costocyrena minor* Ohta (1981) from the Miyaji Formation of central Kyushu in its small valve and very fine radial striae on the disk, but the former differs from the latter in the rounded outline and weak posterior carina.

Occurrence and geological age:—Very fine-grained sandstone of the upper part of Monobe

Formation of the Monobegawa Group at Hokuryo of Kasanokawa, Ryoseki area, Nangoku City in Kochi Prefecture. Dark gray siltstone of the Ogurogawa Formation at Todai of Hase, Kamiina-gun in Nagano Prefecture. Dark gray siltstone or very fine-grained sandstone of the Idaira Formation at Idaira of Inasa, Inasa-gun in Shizuoka Prefecture; Lower Barremian and Hauterivian(?).

Distribution of *Eomiodon* and *Costocyrena*

I. *Eomiodon*

The stratigraphical and geographical distributions of all species of *Eomiodon* from the Cretaceous of Japan are summarized as follows.

* *Eomiodon? kumamotoensis* Tamura (Uppermost Jurassic or Lowest Cretaceous), Sakamoto Formation (Kumamoto) of the Torinosu Group in Kyushu; basal part of the A Member of Doganaro Formation (Kochi) of the Shimanto Terrain in Shikoku.

* *Eomiodon matsumotoi* Ohta (Lower Hauterivian to Barremian), "Kawaguchi" Formation (Kumamoto) of the Nankai Group(?), lower part of the Yamabu Formation (Ohita), Uminoura Formation (Kumamoto) in Kyushu; Shobu Formation (Tokushima) of the Nankai Group in Shikoku; sandstone of the "Torinosu Group" at south of Birafu (Kochi) in Shikoku; middle part of the A Member of Doganaro Formation (Kochi) of the Shimanto Terrain in Shikoku.

* *Eomiodon nipponicus* Ohta ("Neocomian": not treated in this paper), Yoshimo Formation (Yamaguchi) of the Toyonishi Group in west Honshu.

* *Eomiodon hayamii* Ohta ("Neocomian": not treated in this paper), Yoshimo Formation (Yamaguchi) of the Toyonishi Group in west Honshu.

* *Eomiodon sakawanus* (Kobayashi et Suzuki) (Aptian), upper part of the Yamabu Formation (Ohita) in Kyushu; Kaisekiyama Formation (Kochi), Funadani Formation (Kochi) and basal part of the Nakaizu Formation (Tokushima) of the Nankai Group in Shikoku.

* *Eomiodon matsubasensis* Tamura (Lower Cenomanian to Middle Cenomanian), Fukigoshi Formation (Kochi) of the Sotoizumi Group in Shikoku; Mifune Group (Kumamoto) and Goshonoura Group (Kumamoto), in central Kyushu.

II. *Costocyrena*

The stratigraphical and geographical distributions of all species of *Costocyrena* in the Cretaceous of Japan are summarized as follows.

* *Costocyrena ominensis* (Nakazawa et Murata, 1966) ("Neocomian": not treated in this paper), Ohshima Formation (Miyagi) of the Kamihei Group in north Honshu.

* *Costocyrena otsukai otsukai* (Yabe et Nagao) (Hauterivian) Ryoseki Formation (Kochi) and Tatsukawa Formation (Tokushima) of the Monobegawa Group in Shikoku; Kawaguchi Formation (Kumamoto) and Koshigoe Formation (Ohita) of the Monobegawa Group in Kyushu; Yuasa Formation (Wakayama), Ogurogawa Formation (Nagano) and Shiroi Formation (Nagano) in central Honshu.

* *Costocyrena otsukai obsoleta* Tashiro (Lower(?) Barremian), Idaira Formation (Shizuoka) of the Monobegawa Group(?) in central Honshu.

* *Costocyrena ohnishii* Tashiro (Hauterivian), Idaira Formation (Shizuoka) of the Monobegawa Group(?) in central Honshu, Tatsukawa Formation (Tokushima) of the Monobegawa Group in Shikoku.

* *Costocyrena* sp. cf. *C. peikangensis* Hayami (Hauterivian(?) to Lower Barremian), Ogurogawa Formation (Nagano) and Todai Formation (Shizuoka) in central Honshu; Monobe Formation (Kochi) of the Monobegawa Group in Shikoku.

→ **Figure 7.** Map showing the distribution of *Eomiodon* and *Costocyrena* during Hauterivian to Cenomanian in southwest Japan. C: *Costocyrena*, E: *Eomiodon*, $\overset{\circ}{\text{E}}$: Uppermost Jurassic or lowest Cretaceous *Eomiodon*? from the Torinosu and Shimantogawa Groups. Dotted line: Northern border line of the Kurosegawa Tectonic Belt.

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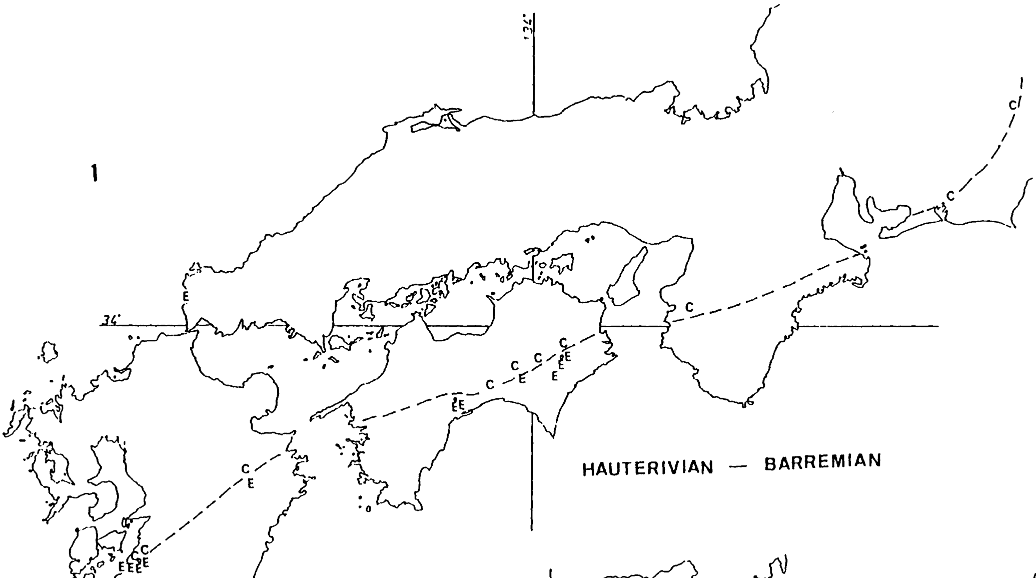

HAUTERIVIAN — BARREMIAN

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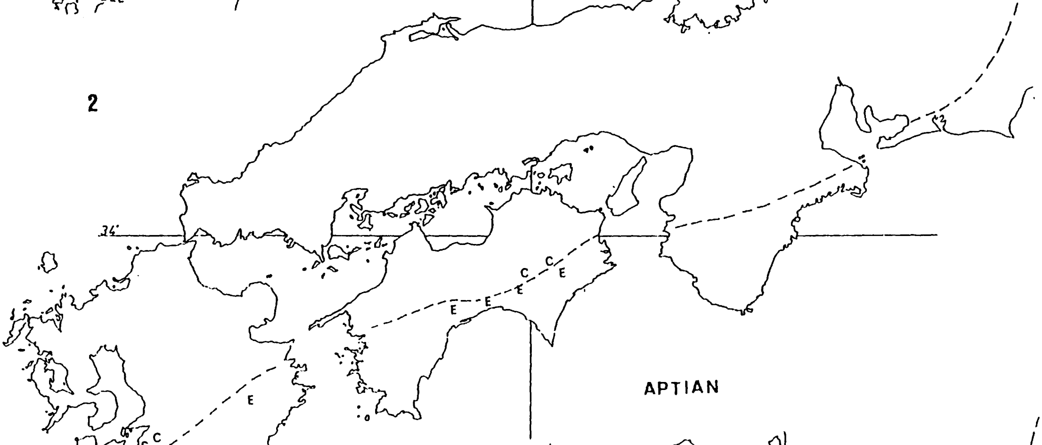

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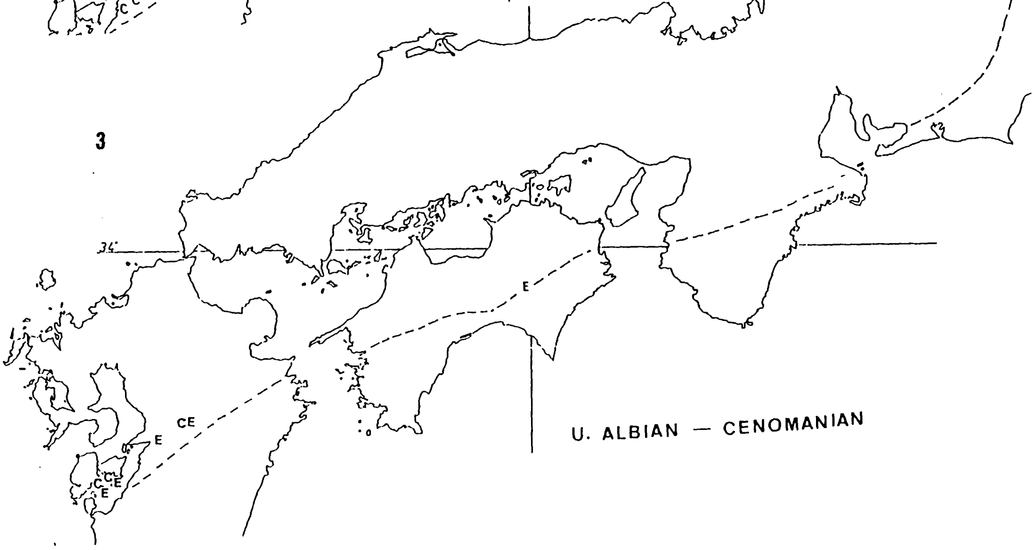

U. ALBIAN — CENOMANIAN

- * *Costocyrena radiatostriata* (Yabe et Nagao) (Upper Barremian), Yunoki Formation (Kochi) of the Monobegawa Group in Shikoku; Sebayashi Formation (Nagano) of central Honshu.
- * *Costocyrena minor* Ohta (Aptian), Miyaji Formation (Kumamoto), basal part of the Hinagu Formation (Kumamoto) in Kyushu; basal member of the Hibihara Formation (Kochi) of the Monobegawa Group in Shikoku.
- * *Costocyrena hojiensis* Tashiro (Aptian), Hoji Formation (Tokushima) of the Monobegawa Group in Shikoku.
- * *Costocyrena matsumotoi* Hayami (Albian?), Yatsushiro Formation of the Monobegawa(?) Group in Kyushu.
- * *Costocyrena mifunensis* Tamura (Lower Cenomanian to Middle Cenomanian), Mifune Group (Kumamoto) and Goshonoura Group (Kumamoto) of central Kyushu.

III. Concluding remarks

In the Lower Cretaceous of Japan, the species of *Eomiodon* occur from the uppermost part of Torinosu Group, Nankai and Shimantogawa Groups in Southwest Japan (all of which are located in the southern side of Kurosegawa Tectonic Belt), and Toyonishi Group in western Honshu. On the contrary, *Costocyrena* species distribute in the Monobegawa Group which seems to be located in the northern side of the Kurosegawa Tectonic Belt, in southwest Japan, and Shiroi and Sebayashi Formations of Sanchu area in central Japan, and Kamihei Group in northeast Japan. Geographic distribution of *Eomiodon* species is in a sharp contrast to that of *Costocyrena* species, separated by the Kurosegawa Tectonic Belt, particularly in the Lower Cretaceous strata of southwest Japan, except for the Toyonishi Group which is located at northern side of the Median Tectonic Line.

The Upper Cretaceous species of *Eomiodon* and *Costocyrena* occur together at some localities in central Kyushu: *i.e.*, the Goshonoura and Mifune Groups. In these areas, *Eomiodon* is more predominant than *Costocyrena*. In the Fukigoshi Formation of the Sotoizumi Group in Shikoku, *Eomiodon matsubasensis* occurs characteristically but *Costocyrena* species are entirely lacking.

Temporal change of geographic distributions of two genera, *Eomiodon* and *Costocyrena*, during the Cretaceous time seem to be one of the important clues to testify the presence of the Early Cretaceous lateral fault movement of the Kurosegawa Tectonic Belt in the Chichibu Terrain of Southwest Japan (Tashiro, 1985, 1986).

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西南日本白亜紀二枚貝 *Eomiodon* と *Costocyrena*：西南日本の白亜紀に多産する“汽水生二枚貝” *Eomiodon* と *Costocyrena* を検討した結果，4 種の *Eomiodon* と 8 種 2 亜種の *Costocyrena* を識別した。その中には *Costocyrena ohnishii*, sp. nov., *Costocyrena hojiensis*, sp. nov., *Costocyrena otsukai obsoleta*, subsp. nov. の 2 新種 1 新亜種が含まれる。

下部白亜系では *Eomiodon* の種は黒瀬川構造帯より南側に産し，*Costocyrena* はその北側（秩父帯北側）から知られる。上部白亜系では、両者は御所浦・御船層群にみられるごとく，同一層準から産し，しばしば同一岩体にも見出される。この事実は，おそらく前期白亜紀を中心に起った秩父帯の横ずれ断層の動きと密接な関係があると思われ，その運動を支持する材料の 1 つでもある。 田代正之

Trans. Proc. Palaeont. Soc. Japan, N. S., No. 147, pp. 109–116, 3 Figs., October 30, 1987

833. THE THIRD ADDITION TO THE SILURIAN TRILOBITE FAUNA OF YOKOKURA-YAMA, SHIKOKU, JAPAN

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Abstract. Seven species of trilobites including two new genera and three new species are here described from Mt. Yokokura. *Metaleiolichas* and *Paraleiolichas* are two new genera, each represented by a new species. A new species of *Japonoscutellum* is added to them. Two pygidia are new to the two known species and one pygidium is so well preserved that it is capable of emending the existing description. Finally, a free cheek is a new find of a species for its locality. Thus the previous knowledge of the Yokokura-yama fauna is well advanced with all of these specimens.

A new collection of trilobites from Mt. Yokokura contains 7 species in 7 genera and 5 families, *i.e.* the Scutelluidae, Illaenidae, Cheiruridae, Encrinuridae and Lichidae as follows:

1: *Japonscutellum tunidum*, sp. nov.
2. *Bumastus glomerosus* Kobayashi and Hamada, 1974
3. *Cerauroides orientalis* Kobayashi and Hamada, 1973
4. *Encrinurus subtrigonalis* Kobayashi and Hamada, 1985
5. *Metaleiolichas tuberculatus*, gen. et sp. nov.
6. *Paraleiolichas globulus*, gen. et. sp. nov.
7. *Dicranopeltis tricornis* Kobayashi and Hamada, 1986

Thus the collection contains three new species and two new genera, namely, *Metaleiolichas* and *Paraleiolichas* of the Lichidae. Among the known species pygidia have been unknown of *Cerauroides orientalis* and *Dicranopeltis tricornis.* Of *Bumastus glomerosus* the associate pygidium to the cephalon has been imperfect. Therefore its description is here emended with a better specimen.

All specimens of the collection were derived from Gomi limestone quarry except for the free cheek of *Encrinurus subtrigonalis* from Sugihara. This new occurrence confirms the contention that the Gomi and Sugihara trilobites horizons are inseparable.

The authors record here their best thanks to Dr. Jiro Katto, Professor Emeritus of Kochi University for presentation of the new collection.

Family Scutelluidae R. and E. Richter, 1955

Genus *Japonoscutellum* Přibyl and Vaněk, 1971

Japonoscutellum tumidum, sp. nov.

Figures 3-3a–c

Description:—Pygidium semiparabolic in outline and distinctly vaulted with the top at about one-fourth from anterior margin and depressed near periphery; axial lobe subtrigonal, one-fifth

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as broad as anterior margin; its median part distinctly elevated above lateral parts; median rib similar to seven lateral ones on each side in breadth and prominence in anterior, but more broadened and bifurcate in posterior; all ribs crossed by concentric lirae; pleural furrows narrower than ribs near axial lobe, but becoming much wider near postero-lateral margin.

Comparison:—This pygidium is tentatively referred to *Japonoscutellum*, because it resembles *Japonoscutellum japonicum* and *J. geniculatum* in outline and some other aspects. The pygidium is slanting at about one-third from the posterior periphery in *J. geniculatum* Kobayashi and Hamada, 1985. Incidentally, the median rib is bifurcate in this specimen as well as *J. japonicum* as seen in the pygidia in fig. 5, pl. 4 and fig. 15, pl. 5 (Kobayashi and Hamada, 1974).

Occurrence:—Limestone, Gomi Quarry, Kochi.

Family Illaenidae Hawle and Corda, 1849

Genus *Bumastus* Murchison, 1839

Bumastus glomerosus Kobayashi and Hamada

Figures 1-A, 2-1a–d

1974. *Bumastus glomerosus* Kobayashi and Hamada, *Palaeont. Soc. Japan, Spec. Pap.*, no. 18, p. 47, pl. 1, figs. 3–8, text-fig. 2A.

Pygidium more or less elliptical, but more well rounded on posterior side than the other, its ratio of length to breadth being 11 to 25; maximum breadth through near one-third of length from anterior margin where it is most convex; convexity there corresponding to about a half of pygidial length; axial lobe limited by distinct depressions on its lateral sides half as wide as pygidium.

The pygidium here described is better preserved than the two above cited (1974). The anterior margin is broadly arcuate, instead of straight as previously restored in text-fig. 2A. This pygidium is simply convex without flattened marginal border as in the previous description. Only very fine striae are discernible near the margin. Otherwise the test is smooth.

Occurrence:—Limestone, Gomi Quarry.

Family Cheiruridae Hawle and Corda, 1847

Genus *Cerauroides* Prantl and Přibyl, 1946

Cerauroides orientalis Kobayashi and Hamada

Figures 1-C, 2-3

1973. *Cerauroides orientalis* Kobayashi and Hamada, *Proc. Japan Acad.*, v. 47, no. 8, p. 547, text-figs. 1–5.

1974. *Cerauroides orientalis* Kobayashi and Hamada, *Palaeont. Soc. Japan, Spec. Pap.*, no. 18, p. 84, pl. 6, figs., 1–4, text-fig. 6A.

The pygidium is composed of four segments; axial lobe a little broader than one-third of pygidium, but its relative breadth reducing posteiorly; first pleura very large and produced back into a long spine; second pleura of moderate size terminating at a minute spine; succeeding two pleurae fused and embracing posterior part of axis; two large posterior spines only a little divergent backwards; test smooth.

Compared to *Cerauroides lunshanensis* (Grabau, 1924) the first pair of pleural spines are not so widely divergent and the second pair of spines rudimentary in this species. Otherwise both of them have the construction very similar to each other. In the slight divergence of the posterior spines it is nearer to the pygidium of *Ceraurinium intermedium* (Kielan, 1955) from the Ashgillian of Poland, but the spines are straight and the posterior margin of the pygidium is entire in that species.

This pygidium belongs probably to either *Cerauroides orientalis* or *C. elongatus* both of which occur at Gomi quarry where the pygidium was collected. It is provisionally located in the former species simply because, it is more common and better known than the latter species. It is noted here that the hypostoma of *Cerauroides orientalis* is closely allied to that of *Ceraurinium intermedium*, although the posterior margin is sinuated in *C. orientalis.*

Occurrence:—Limestone, Gomi Quarry.

Family Encrinuridae Angelin, 1854

Genus *Encrinurus* Emmrich, 1844

Encrinurus subtrigonalis Kobayashi and Hamada

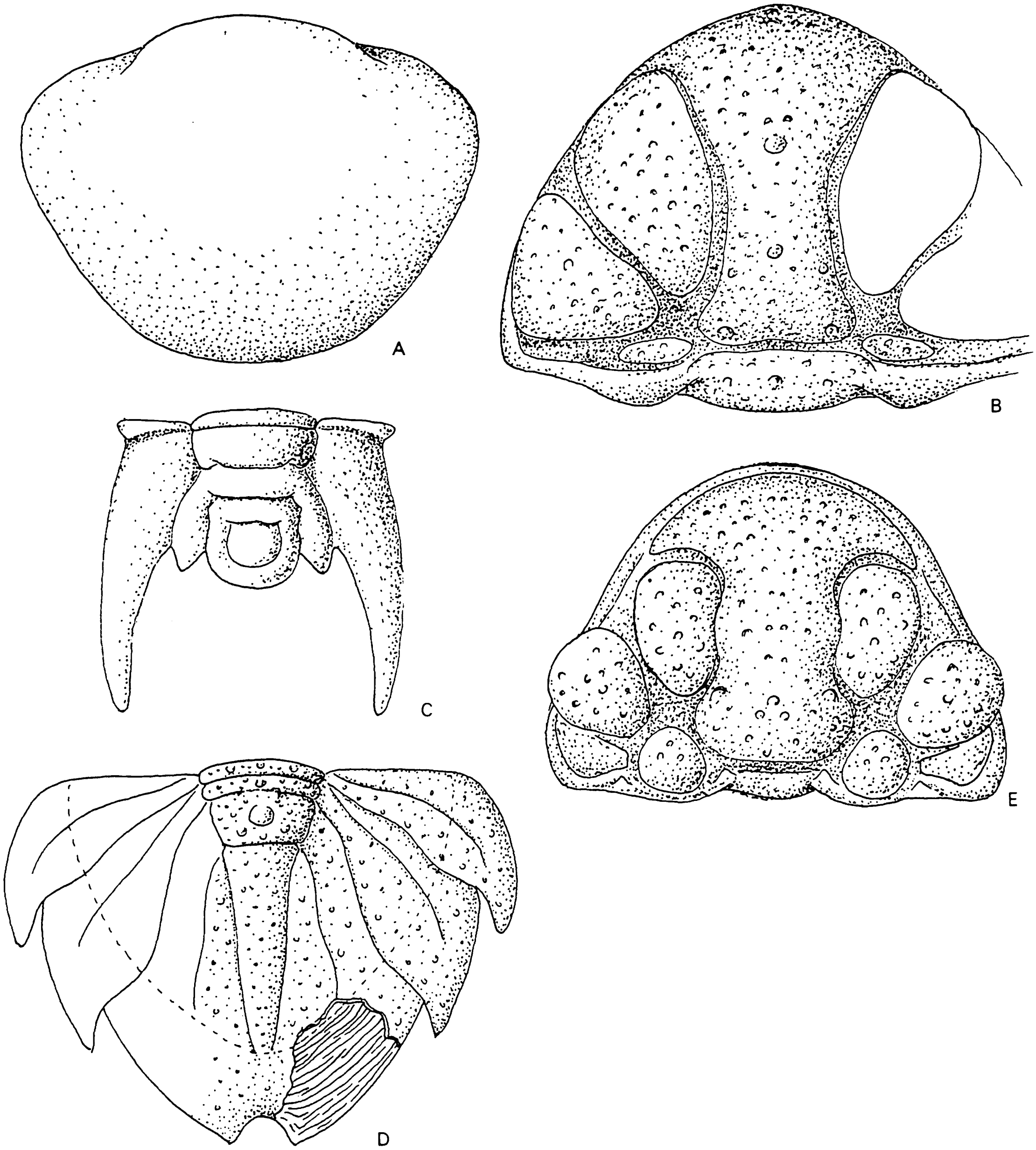
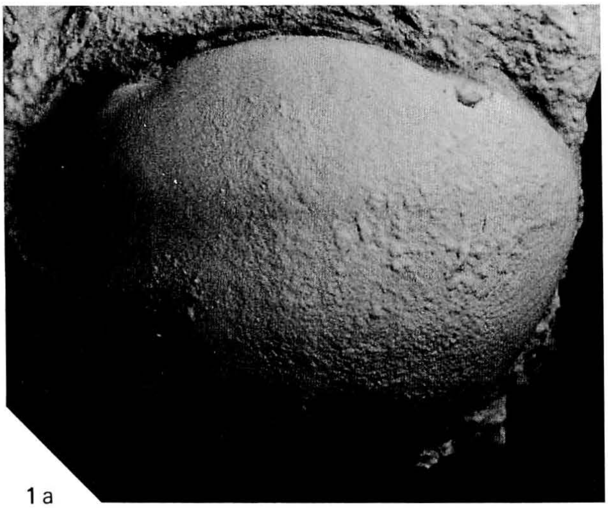


Figure 1. Reconstruction of five trilobite species from Yokokura-yama.
A. *Bumastus glomerosus* Kobayashi and Hamada, 1974, x6; B. *Metaleioleichas tuberculatus*, gen. et sp. nov., x5; C. *Cerauroides orientalis* Kobayashi and Hamada, 1973, x3; D. *Dicranopeltis tricornis* Kobayashi and Hamada, 1986, x3; E. *Paraleiolichas globulus*, gen. et ep. nov., x8.

Figures 3-2a, b

1985. *Encrinurus subtrigonalis* Kobayashi and Hamada, *Trans. Proc. Palaeont. Soc. Japan, N. S.*, no. 139, p. 210, pl. 28, figs. 4a–c, pl. 29, figs. 2a–d.

A right free cheek of *Encrinurus* has an eye of medium size from which the proparian facial suture extends to the lateral margin of the cephalon. It is densely granulate and most granules;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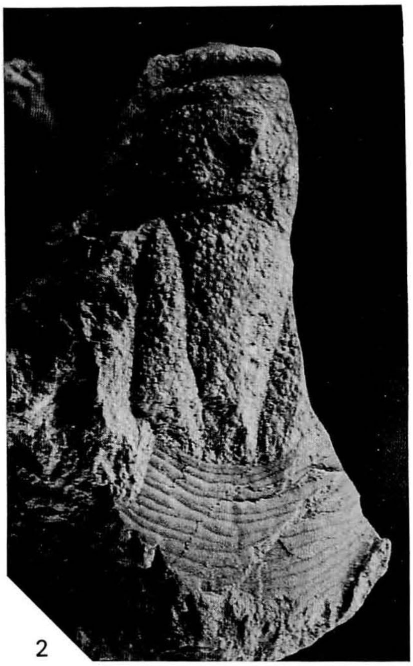
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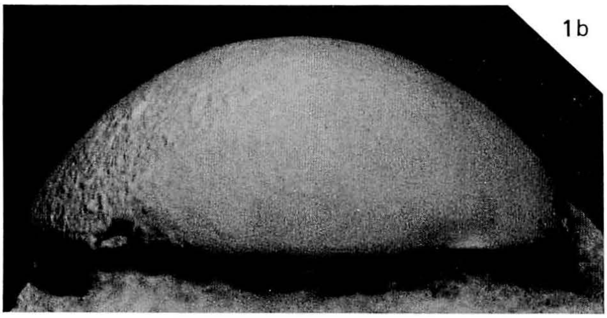
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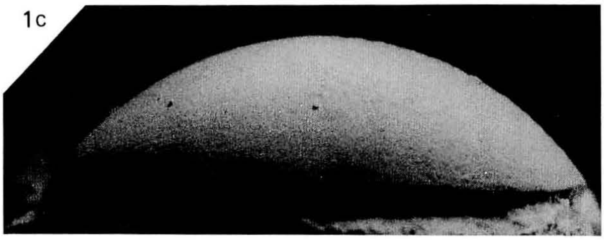
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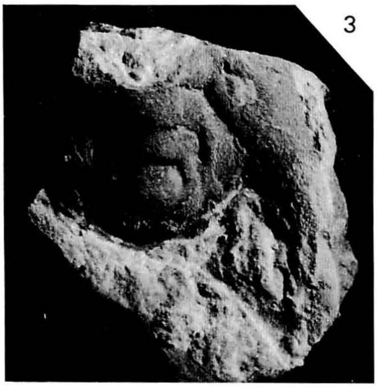
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have a central pit. This is the characteristic texture of the cephalon of *Encrinurus subtrigonalis.* Therefore this is the new find of this species at Sugihara.

Occurrence:—Tuffaceous sandy shale; Sugihara.

Family Lichinae Hawle and Corda, 1874

The group of *Leiolichas* Schmidt, 1885 in the Lichidae was represented only by *Lichas illaenoides* Nierzkowsky, 1857 which occurs in the Upper Ordovician in East Baltic region and also in North Germany in Ordovician boulders. Its shield is quite smooth and the furrows are weak, although they are distinct in casts. Later Warburg (1939) described *Leiolichas illaenoides* from the Macrourus limestone of Oland found in boulders.

The two genera, *Metaleiolichas* and *Paraleiolichas,* proposed here best agree with *Leiolichas* in the fundamental configuration of the cranidium, but they are different from that genus in the median lobe much larger, the median, bicomposite and basal lobes each forming a swell, their boundary furrows all strongly excavated in their whole length and the surface densely granulate. In *Leiolichas,* on the contrary, the test is smooth, the median lobe relatively narrow, this lobe constitutes the same dome with lateral and basal lobes and the longitudinal furrows become obsolete near the occipital ring.

These two new genera differ from each other in the general outline of the cranidum and the mode of its division into lobes, as detailed later. An additional distinction is found in the periphery of the cephalon. It is represented by non-tuberculate rim and strong marginal furrow in *Metaleiolichas* and by a depressed and tuberculate band on the outer side and the linear furrow in the inner side in *Paraleiolichas.*

Genus *Metaleiolichas,* gen. nov.

Generic characteristics are included in the description of the monotypic species.

Metaleiolichas tuberculatus, sp. nov.

Figures 1-B, 3-4a–c

An imperfect cranidium having median lobe, a narrow bicomposite left lobe and a small left basal lobe which are all outlined clearly by persistent furrows; median lobe strongly convex, broad and much more expanded in anterior than posterior; bicomposite lobe narrowing backward, strongly convex, but its top near longitudinal furrow a little below median lobe; basal lobe fusiform, elongated laterally. Axial furrow, posterior marginal furrow and terminus of occipital furrow are all preserved. Surface ornamented with tubercles of different sizes except for frontal rim and furrows.

This cranidium agrees with *Leiolichas* in the fundamental configuration, but the median lobe is incomparably developed, longitudinal furrow persistent in its whole length and the test densely tuberculate.

Occurrence:—Limestone, Gomi Quarry.

Genus *Paraleiolichas,* gen. nov.

Paraleiolichas globulus, sp. nov.

Figures 1-E, 2-4, 3-1a–b

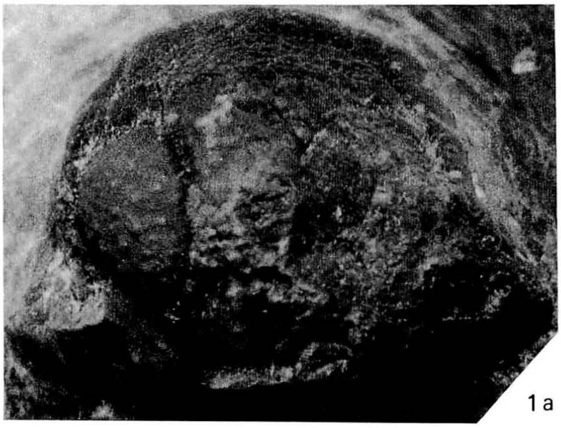
Cranidium globular; median lobe subcylindrical in middle part, but a little expanded in posterior and remarkably flaring in anterior; bicomposite lobe semiglobular and medium sized;

← **Figures 2-1a–d.** *Bumastus glomerosus* Kobayashi and Hamada, 1974, dorsal, anterior, posterior and left lateral views of a well-preserved pygidium. x6.5 PA18089.

2. *Dicranopeltis tricornis* Kobayashi and Hamada, 1986, a dorsal view of an incomplete pygidium. x3.4 PA 18092.

3. *Cerauroides orientalis* Kobayashi and Hamada, 1973, a dorsal view of an incomplete pygidium. x3.5 PA 18090.

4. *Paraleiolichas globulus,* gen. et sp. nov., a posterior view of the holotype caranidium. x6.5 PA 18094. (vide Figures 3-1a, b)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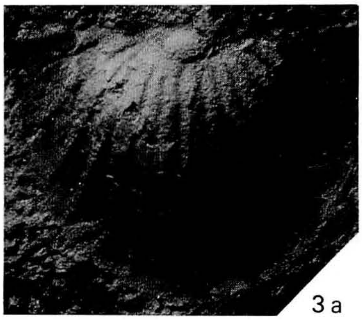
2 b


1 b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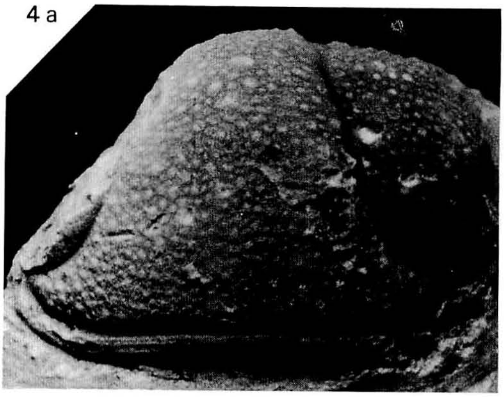
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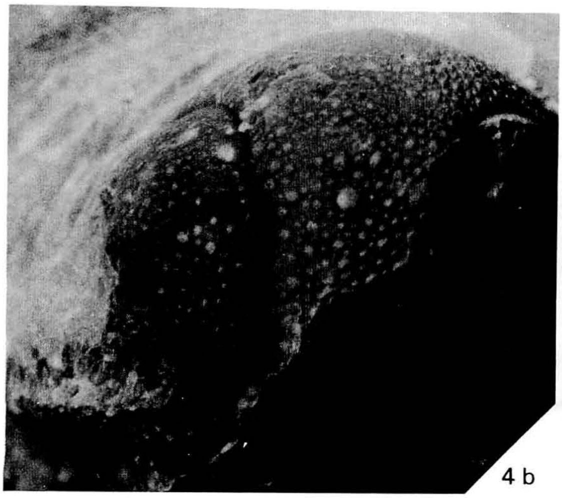
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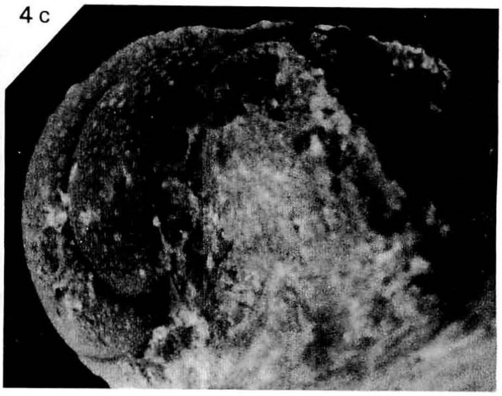
4 c

basal lobe relatively large and trigonally ovoid; these glabellar lobes and fixed cheek all granulate and completely separated from one another by deep furrows; frontal border flat, depressed, granulate and limited inside by linear furrow.

Compared to *Metaliolichas* this cranidium is longer in outline, its basal lobe much larger in comparison with the bicomposite lobe. Nevertheless, they have same pattern and quite distinct from *Leiolichas* in the development of the median lobe, persistent glabellar furrrows and dense granulation or tuberculation.

Occurrence:—Limestone, Gomi Quarry.

Genus *Dicranopeltis* Hawle and Cords, 1974

Dicranopeltis tricornis Kobayashi and Hamada

Figures 1-D, 2-2

1986. *Dicranopeltis tricornis* Kobayashi and Hamada, *Trans. Proc. Pal. Soc. Japan, N. S.*, no. 143, p. 458, pl. 92, figs. 1a–g, text-figs. C1–3.

This species was instituted with a cephalon resembling *Dicranopeltis scabra,* but having a median spine issuing from the top of the glabella besides a pair of long genal spines. The pygidium now at hand is such a fragmentary specimen in which only the axial part is preserved. It is, however, astonishing that it coincided with the pygidium of *D. scabra* so nicely as shown in text-fig. 4.

The axial lobe of this pygidium consists of two axial rings which are very short (sag.) and well defined by deep ring furrows, the third axial ring which is so large that two rings can be fused and the long terminal piece which is gradually tapering back without any lateral expansion as seen in *D. scabra.* The third pleura is divided into two bands by an interpleural furrow as seen on the left side of the terminal piece. On the other side, there is the posterior band of the third pleura. All of them are, however, exfoliated in posterior where the doublure of similar breadth as that of *D. scabra* is exposed. In tracing terrace lines it is recognizable that the third pleura is ending at a short spine. The most important distinction of this pygidium from *D. scabra* lies in the possession of a stout spine as shown by its scar on the third axial ring. Like the cephalon of this species fine granules are distributed densely on the surface.

Occurrence:—Limestone, Gomi Quarry.

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← **Figures 3-1a, b.** *Paraleiolichas globulus,* gen. et sp. nov., dorsal and frontal views of the holotype cranidium. x6.5 PA 18094. (vide Figure 2–4).

2a, b. *Encrinurus subtrigonalis* Kobayashi and Hamada, 1985, a free cheek (inner mould). x3.5 PA 18091.

3a–c. *Japonoscutellum tunidum,* sp. nov., dorsal, left lateral and posterior views of hte holotype pygidium. x3.3 PA 18088.

4a–c. *Metaleiolichas tuberculatus,* gen. et sp. nov., frontal, dorsal and left lateral views of the holotype cranidium. x6.6 PA 18093.

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四国横倉山の志留紀三葉虫群への第3追加：本論文には5科7属に属する7種が記載してある。そのうちに2新属*Metaleiolichas, Paraleiolichas*があり，共に新種に基づいている。その他に1新種がある。残余の4種中には尾板が新たに判ったもの2種，尾板の保存良好なために既知の記載を補正するもの，そして産地として新しいものなどがあり，何れもが新知見を付加している。

小林貞一，浜田隆士

Trans. Proc. Palaeont. Soc. Japan, N. S., No. 147, pp. 117–130, 5 Figs., October 30, 1987

834. EARLY CARBONIFEROUS *EOSTAFFELLA* (PRIMITIVE FUSULINACEA) FROM THE ICHINOTANI FORMATION, FUKUJI DISTRICT, CENTRAL JAPAN*

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Abstract. The lower part of the Ichinotani Formation at Fukuji, Gifu Prefecture, central Japan contains a very rich assemblage of foraminifers. *Eostaffella* (primitive fusulinacea) is described here to provide a basis for the precise biostratigraphic subdivision and age-determination of the lower Ichinotani Formation. The eostaffelloids consist of eight species including three new species, *i.e., Eostaffella excavata, E. igoi* and *E. subulba.* This assemblage permits recognition of Igo's *Eostaffella kanmerai* zone ranging from latest Viséan to early Serpukhovian (Namurian A) in age.

Introduction

Eight species of eostaffelloid fusulinaceans are described in this paper from the lower part of the Ichinotani Formation in the Fukuji district, Gifu Prefecture, central Japan. The Ichinotani Formation is exposed mainly in the Ichinotani Valley, Mizuboradani Valley and lower course of the Mizuyagadani Valley in a series of NEE-SWW trending small faulted blocks, and comprises about 350 m thick of predominatingly carbonate rocks of late Early Carboniferous to Early Permian in age.

Material for systematic study was collected from two localities as listed below and shown in Figure 1.

Locality A: Middle course of the Ichinotani Valley.

Locality B: On the mountain slope facing south of the same valley.

The continuous outcrops at the locality A allow to measure a complete columnar section and to determine the occurrence-boundary of many fossils, although in the locality B outcrops are

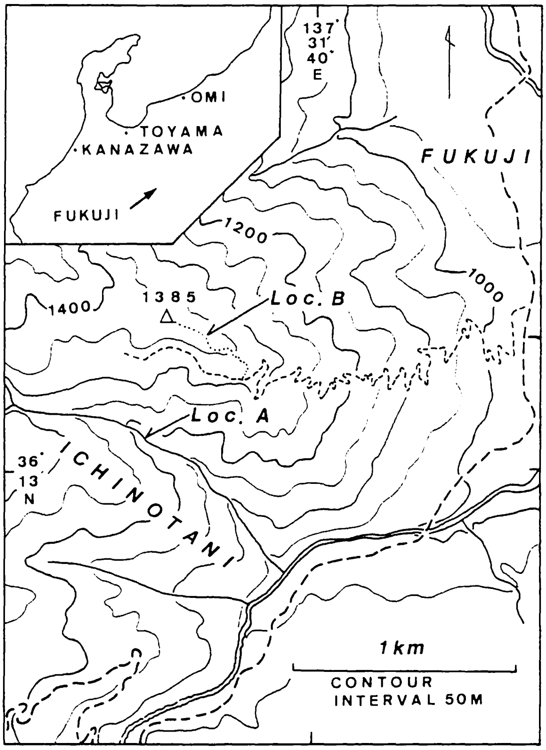

Figure 1. Map showing the fossil localities.

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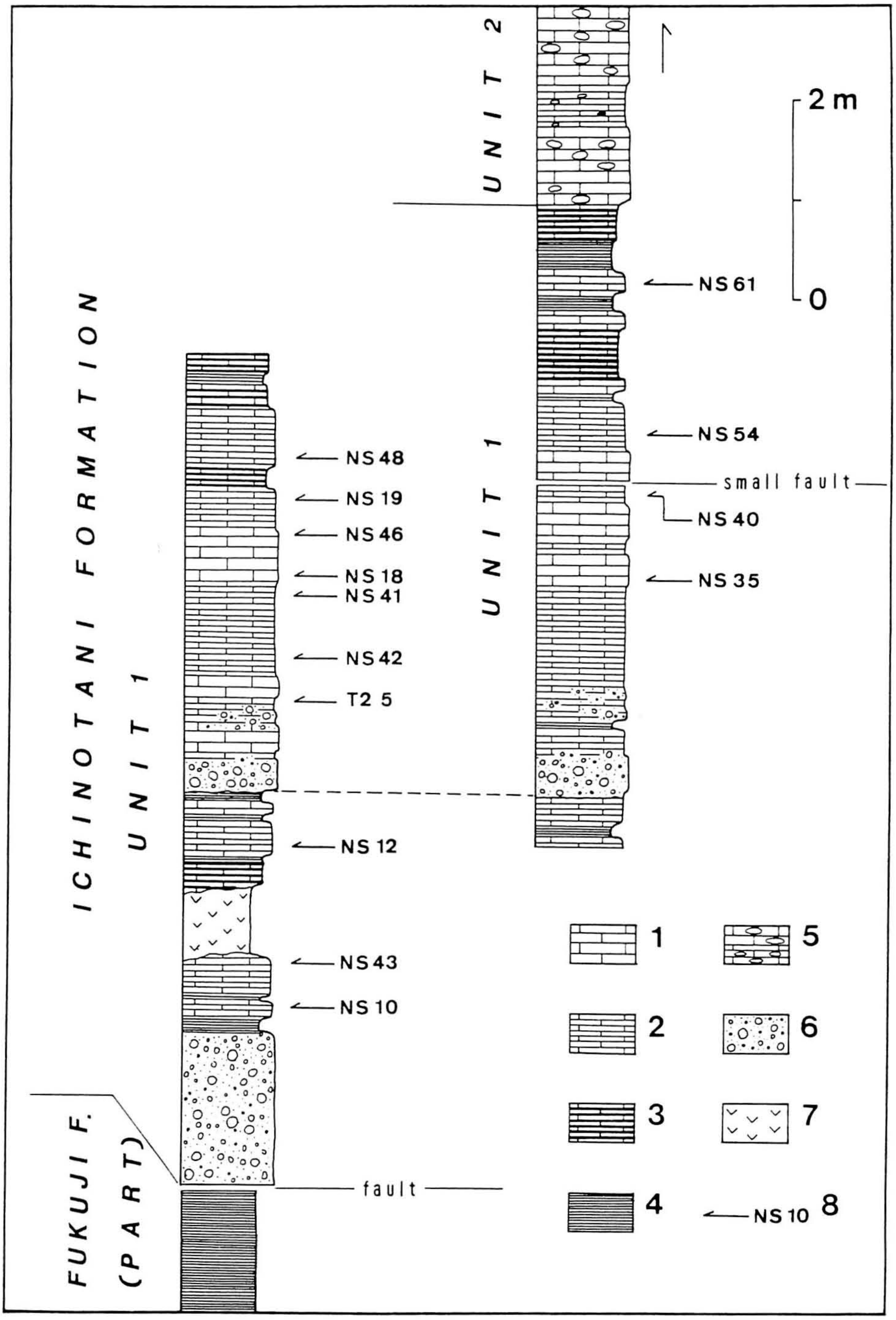


Figure 2. Columnar sections showing the lithology and stratigraphic positions of samples at locality A, the middle course of the Ichinotani Valley. 1: thick-bedded limestone; 2: thin-bedded limestone; 3: thin alternating beds of limestone and shale; 4: shale; 5: limestone with chert concretions; 6: conglomerate; 7: dyke rock; 8: sample number and location.

poor due to thick vegetation. The other purpose of this article is to analyze stratigraphic distribution of foraminifera for a basis of biostratigraphic subdivision and precise correlation with the faunal successions in the standard areas of Upper and Lower Carboniferous boundary in West Europe and U.S.S.R.

Accounts of the foraminiferal successions of this formation have been presented by Igo (1956, 1957), Niikawa (1978, 1980), Igo and Adachi (1981a), Igo, Adachi and Igo (1984), Adachi (1985) and Niko (1985, 1986). Further, lithostratigraphically, Igo and Adachi (1981a) and Adachi (1985) divided the Ichinotani Formation into three members, 61 Unit-beds. The primitive fusulinacean assemblage of the present study is related with the lowest Unit 1 of Igo and Adachi's scheme, and thus it falls within the lowermost fusulinacean zone of *Eostaffella kanmerai* zone, which probably ranges from latest Viséan to early Serpukhovian (Namurian A) in age (Niko, 1986).

At the type section (locality A) Unit 1 of this formation is 9.5 m thick, and is composed of a (basal?) conglomerate bed of 1.5 m thick being succeeded by a thin bedded black to dark-gray limestone (6.3 m) and further by an alternation of limestone and thin shale (1.7 m). The (basal?) conglomerate is characterized by the predominance of ill-sorted and subangular volcanic fragments of acidic composition (Niko *et al.*, 1984). Most of the carbonates of Unit 1 is made up of skeletal grains, peloids, and with extraclast (acidic volcanic fragments), and are predominatingly packstone and wackestone with minor amounts of grainstone and lime mudstone.

Besides the rich assemblage of foraminifers, these limestones contain many corals including *Kueichouphyllum, Dibunophyllum, Heterocaninia, Neokoninckophyllum, Siphonodendron* and others (Kato, 1959; Igo and Adachi, 1981b *etc.*), and such other fossils as productid brachiopods (Tazawa and Kato, 1986), bryozoans (Sakagami, 1960), trilobites, crinoids and ostracods.

Specimens used in this study are stored in the following institutions:

IGUT Institute of Geoscience, The University of Tsukuba.
UMUT University Museum, The University of Tokyo.

Systematic paleontology

Family Eostaffellidae Mamet in Mamet, Mikhailov and Mortelmans, 1970

Genus *Eostaffella* Rauzer-Chernousova, 1948

Table 1. Occurrences of *Eostaffella* in the Ichinotani Formation. The stratigraphic positions of samples are shown in Figure 2, except for samples from "float blocks" (*) of limestone.

Sample No. / Taxon	Locality A																				Locality B		
	NS 10	NS 43	NS 12	T2 5	NS 42	NS 41	NS 18	NS 35	NS 46	NS 19	NS 40	NS 48	NS 54	NS 61	T7 7*	NSR 1*	NSR 5*	NSR 6*	BAR 6*	BAR 15*	DC 10*	DC 11*	DC 19*
Eostaffella excavata	x	x	x	x	x	x		x	x	x	x	x					x			x			
E. igoi				x																	x	x	
E. kanmerai							x					x	x										
E. mosquensis															x		x		x				x
E. cf. *postmosquensis*						x											x						
E. subulba	?													x				x					
E. tenebrosa				x							x												
E. sp.																x							

Type species:–*Staffella* (*Eostaffella*) *parastruvei* Rauzer-Chernousova, 1948.

Eostaffella excavata Niko, sp. nov.

Figures 3-A–H

Material studied:–Holotype, UMUT PF 18013 (sample NS 40, Figure 3-A); paratypes UMUT PF 18014 (sample NS 40, Figure 3-B), 18015 (sample NS 42, Figure 3-F), 18016 (sample T2 5, Figure 3-C), 18017 (sample T2 5, Figure 3-E), 18018 (sample T2 5, Figure 3-D), 18019 (sample NS 41, Figure 3-H), 18020 (sample T2 5, Figure 3-G). In addition to the holotype and paratypes, some other specimens were studied. All the specimens were obtained from loc. A.

Diagnosis:–Small *Eostaffella* with discoidal test, broadly umbilicate on both sides, and rounded periphery in the last volution. Coiling plectogyroid in juvenarium, becoming planispiral in outer volutions. Septa long, slightly curved.

Description:–Test is small, discoidal, with broadly umbilicate on both sides. Periphery is bluntly pointed in the inner volutions but the last volution of the mature specimens has a rounded periphery. The holotype (Figure 3-A) contains 5 volutions that is 0.195 mm in length and 0.46 mm in width; form ratio is 0.42. Radius vectors of the third to fifth volutions of the holotype are 0.08, 0.15, and 0.26 mm, respectively. The initial 1 to 1 1/2 volutions are skew at nearly 90 degrees to the remaining essentially planispiral whorls. The last volution is partially evolute. Proloculus is nearly constant in size in the examined specimens, being 0.017 to 0.019 mm in its inside diameter. Wall, approximately 0.008 mm thick in the outer volutions, consists of a tectum, and lower and upper tectoria. Septa are long, slightly curved, and inclined forward. Septal counts of the second to forth volutions of a paratype (Figure 3-H) are 9, 11, and 12, respectively. Tunnel is low and narrow. Asym-

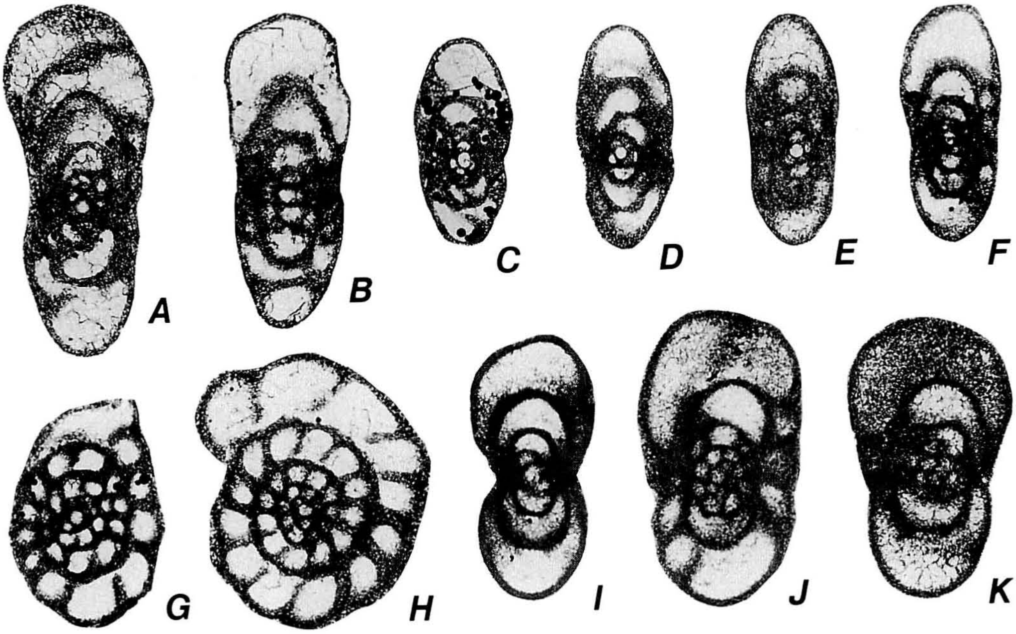


Figure 3. A–H, *Eostaffella excavata*, sp. nov. A, axial section of the holotype, UMUT PF 18013. B, tangential section of a paratype, UMUT PF 18014. C, axial section of a paratype, UMUT PF 18016. D, axial section of a paratype, UMUT PF 18018. E, axial section of a paratype, UMUT PF 18017. F, axial section of a paratype, UMUT PF 18015. G, neary sagittal section of a paratype, UMUT PF 18020. H, sagittal section of a paratype, UMUT PF 18035. I–K, *Eostaffella* cf. *postmosquensis* Kireeva. I, axial section, UMUT PF 18035. J, slightly diagonal section, UMUT PF 18036. K, axial section, UMUT PF 18037. All specimens X100.

metrical chomata are present in the outer volutions. Aperture is low and basal.

Remarks:—This new species belongs to *Eostaffella* of the group *E. pseudostruvei* that consists of the following species:

pseudostruvei (Rauzer-Chernousova and Beljaev, 1936)
p. var. *angusta* Kireeva, 1951
p. var. *chomatifera* Kireeva, 1951
p. var. *elegantissima* Manukalova, Il'ina and Serezhikova, 1969
p. var. *losovskensis* Manukalova, Il'ina and Serezhikova, 1969
excavata Niko (this report)

Eostaffella excavata is most closely allied to *E. pseudostruvei* var. *angusta* Kireeva from the lower Bashkirian of the Donetz Basin and Russian Platform of U.S.S.R. in essential features, but the former is different from the latter in having smaller proloculus. The present species somewhat resembles *E. pseudostruvei* var. *chomatifera* Kireeva, but *E. excavata* differs in its smaller size and by its weaker chomata, and more rounded periphery in the last volution.

Evolute coiling of the last volution suggests an assignment of this species to other genera, especially *Millerella* and *Zellerina*. However, this form differs from *Millerella* by its plectogyroid coiling in juvenarium and less numerous septal counts; and from *Zellerina* by its bluntly pointed periphery in the inner volutions and well differentiated spirotheca.

Eostaffella igoi Niko, sp. nov.

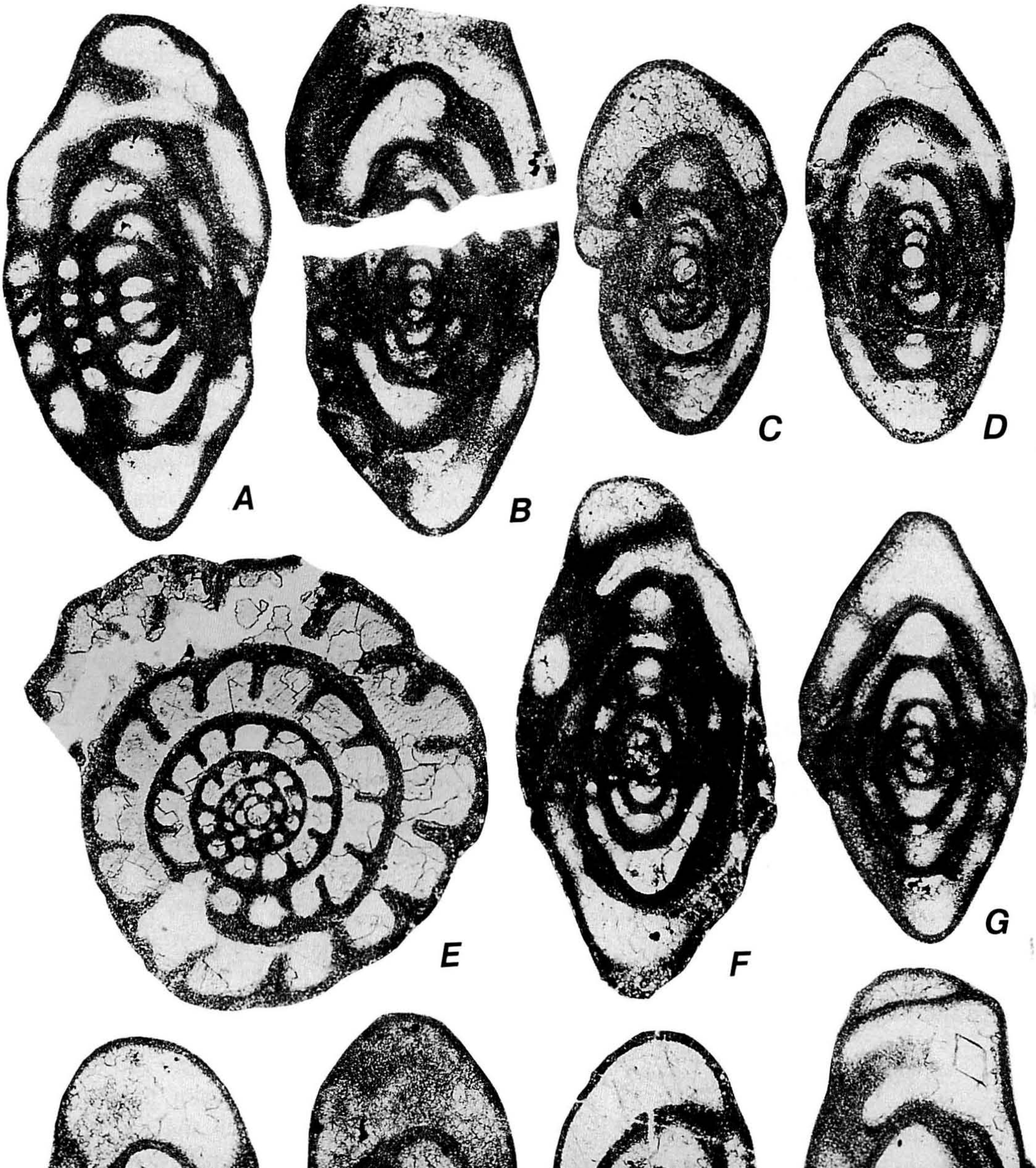
Figures 4-A–E

Material studied:—Holotype, UMUT PF 18021 (sample T2 5, Figure 4-b); paratypes, UMUT PF 18022 (sample T2 5, Figure 4-A), 18023 (sample T2 5, Figure 4-D), 18024 (sample T2 5, Figure 4-C), 18025 (sample T2 5, Figure 4-E). In addition to the holotype and paratypes, some other specimens were studied. All specimens from loc. A except for two ill-oriented specimens that were obtained from loc. B.

Diagnosis:—Large *Eostaffella* with discoidal to lenticular test, pointed periphery and nearly straight to slightly concave lateral slopes. Coiling more or less planispiral. Spirotheca relatively thick. Septa short and straight. Chomata well-developed.

Description:—Test of *Eostaffella igoi*, sp. nov. is larger for the genus, and discoidal to lenticular shape with umbilicate on both sides. Umbilicus is relatively well-developed in the last volution. Periphery is pointed in axial section and lateral slopes are nearly straight to slightly concave. Mature specimens of 5 1/2 volutions are 0.36 to 0.38 mm in length and 0.65 to approximately 0.73 mm in width, giving form ratios of approximately 0.52. Radius vectors of the first to fifth volutions of the holotype (Figure 4-C) are 0.04, 0.08, 0.12, 0.20, and 0.32, respectively. Proloculus is approximately 0.030 mm in inside diameter. Coiling is more or less planispiral. Septa are short, straight and usually inclined forward. Septal sutures are slightly depressed in the outer volutions. Septal counts of the first to fifth volutions of a paratype (Figure 4-E) are 5, 9, 10, 13, and 14, respectively. Wall is calcareous, microgranular and approximately 0.010 to 0.013 mm thick in the outer volutions. It is differentiated into thin tectum, and lower and upper tectoria. Supplemental deposits, in form of an asymmetrical chomata, are well-developed in the outer volutions. Tunnel is relatively high and narrow. Aperture is low, basal and simple.

Remarks:—*Eostaffella igoi* somewhat resembles *E. kanmerai* (Igo) from the Ichinotani Formation and *E. oregonensis* Sada and Danner from the Late Mississippian (Chesterian) Coffee Creek Formation of central Oregon. *E. kanmerai*, however, has a smaller shell and lower form ratio, and its coiling is somewhat irregular. *E. oregonensis* has a lower form ratio, weaker chomata, and deeper umbilical depression. In the general shape of *E. columbiana* Sada and Danner from British Columbia somewhat resembles examined specimens which nevertheless have smaller numbers of shorter septa. Illustrated specimens of *E. columbiana* suggest the presence of diaphanotheca. There would be some possibility that this species might belong to a genus *Pseudoendothyra.*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Eostaffella kanmerai (Igo)

Figures 4-H–J

Millerella kanmerai Igo, 1957, p. 175–177, pl. 1, figs. 20–26, pl. 2, fig. 14.

Eostaffella kanmerai (Igo): Sada, 1964, p. 230–231, pl. 21, figs. 8, 16–17; Sada, 1967, p. 144–145, pl. 12, figs. 1–10; Sada, 1969, p. 120–121, pl. 12, figs. 1–12, 13?, pl. 13, figs. 1–2; Reitlinger, 1973, p. 62, pl. 10, figs. 18–19, pl. 11, figs. 5–6; Sada and Danner, 1974, p. 259–261, pl. 37, figs. 1–3, 5, 18–19; Sada, 1975, p. 35–36, pl. 8, figs. 1–5; Niikawa, 1978, p. 538, pl. 1, figs. 11–12; Sada, 1980, p. 68–69, pl. 1, figs. 1–5, 11–13; Rich, 1980, p. 40–41, pl. 18, figs. 6, 8–12, 14?; Sada, Nomura and Oho, 1984, p. 390–391, pl. 75, figs. 1–8.

Eostaffella cf. *kanmerai* (Igo): Massa and Vachard, 1979, pl. 6, fig. 5.

Material studied:—Four specimens (UMUT PF 18026, sample NS 18, Figure 4-H; 18027, sample NS 54, Figure 4-J; and two unfigured specimens) are referred to this species.

Remarks:—Here no description of this species is given, because none of the well-oriented and complete materials were recovered during the present study even they came from the type locality.

The combination of morphological features of this species suggest a relationship to the following species; *Eostaffella igoi* Niko (this report), *E. infulaeformis* Ganelina, *E. oregonensis* Sada and Danner, *E. pseudostruvei* (Rauzer-Chernousova and Beljaev), *E. toriyamai* Ozawa, but *E. kanmerai* is recognized by its somewhat irregular coiling of volutions and weak chomata.

Igo's holotype (1957, pl. 1, fig. 20) is reillustrated in this report in order to show its complete morphology.

Eostaffella mosquensis Vissarionova, 1948

Figures 5-D, F, G, H?

Eostaffella mosquensis Vissarionova, 1948, p. 222, pl. 14, figs. 4–6; Ganelina, 1951, p. 188–189, pl. 2, figs. 1–2; Brazhnikova *et al.*, 1956, pl. 15, figs. 9–11; Golubtsov, 1957, p. 165–166, pl. 9, figs. 20–21; Durkina, 1959, p. 196–197, pl. 20, fig. 10; Bogush and Iuferev, 1962, p. 172, pl. 6, fig. 26; Rozovskaia, 1963, p. 93–94, pl. 16, figs. 16–17, pl. 17, figs. 1–5; Manukalova-Grebeniuk, Il'ina and Serezhnikova, 1969, p. 25, pl. 9, figs. 9–12; Malakhova, 1972, p. 40, pl. 7, figs. 1–3; Ivanova, 1973a, pl. 7, fig. 6; Wu, Chang and Ching, 1974, pl. 4, fig. 10; Ozawa, 1976, p. 121–122, pl. 22, figs. 1–15, 16?, 17–19; Niikawa, 1978, p. 538, pl. 1, figs. 5–7, 15; Rich, 1980, p. 41, pl. 18, figs. 13, 15–16, 20, 25; Matsusue, 1986, pl. 6, figs. 1–2.

Eostaffella mosquensis mosquensis Vissarionova: Vachard, 1977, pl. 5, fig. 23.

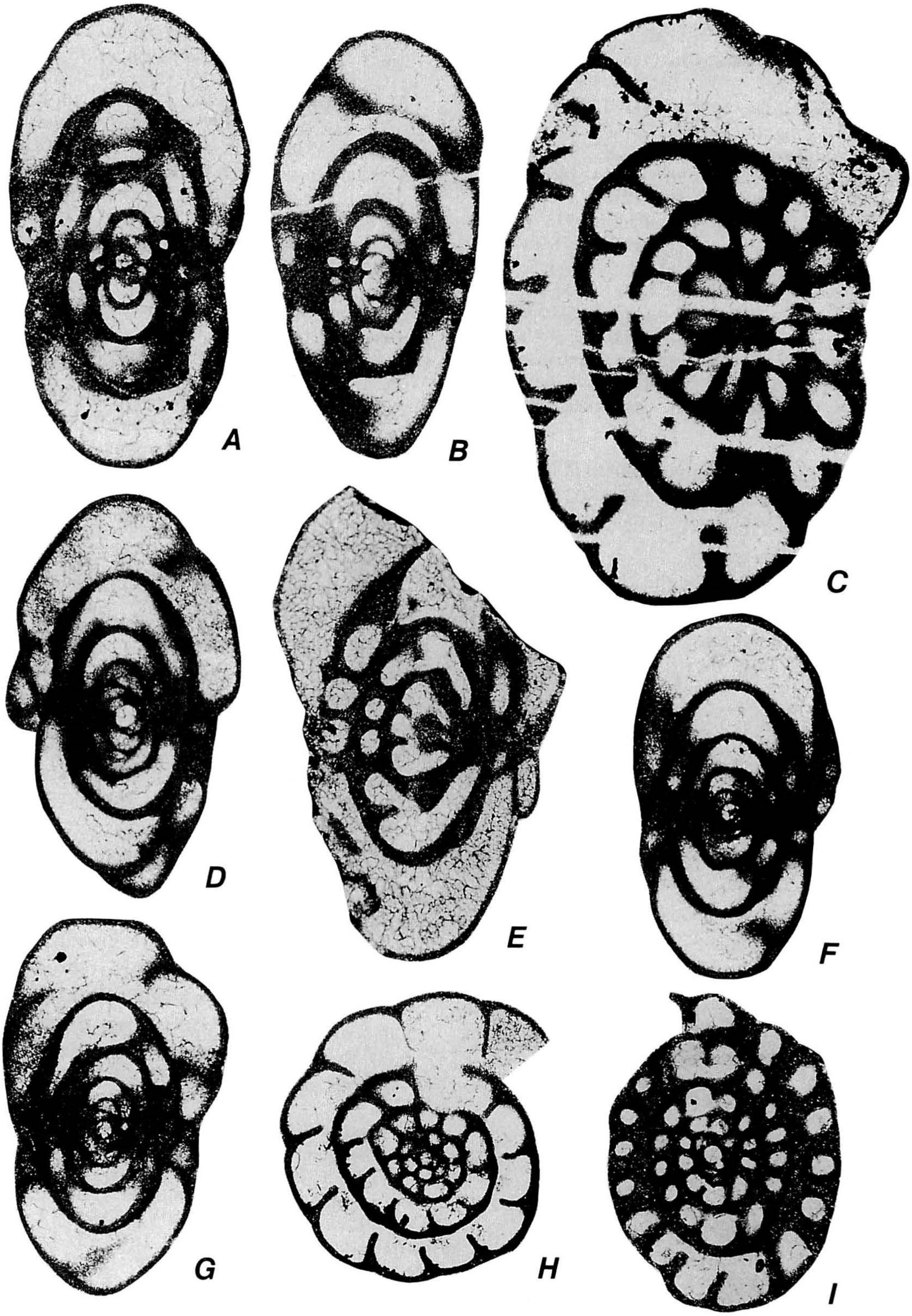
Eostaffella mosquensis acuta Rauzer-Chernousova, 1948, p. 236–237, pl. 14, fig. 5; Ganelina, 1951, p. 190–191, pl. 2, figs. 3–4; Brazhnikova *et al.*, 1956, pl. 15, figs. 5–7; Golubtsov, 1957, p. 166–167, pl. 9, figs. 22–25; Vachard, 1977, pl. 5, fig. 22.

Eostaffella acuta Rauzer-Chernousova: Armstrong and Mamet, 1977, p. 85.

Material studied:—Specimens including four axial sections (UMUT PF 18032, sample NSR 5, Figure 5-G; 18033, sample DC 19, Figure 5-D; 18034, sample NSR 5, Figure 5-F; and one unfigured specimen), one tangential section, and one sagittal section (UMUT PF 18070, sample NSR 5, Figure 5-H) of questionable assignment to this species were examined. All specimens were obtained from loc. A except for UMUT PF 18033 from loc. B.

Description:—Test is moderately large for the genus, involute, and umbilicate on both sides. Periphery is rounded to bluntly pointed in axial section, and lateral slopes are broadly convex. Mature specimens contain 5 1/2 volutions that are 0.32 to 0.37 mm in length and 0.56 to 0.62 mm in width. Form ratio ranges from 0.58 to 0.60. Radius vectors of the first to sixth (5 1/2) volutions of the typical specimen (Figure 5-G)

← **Figure 4.** A–E, *Eostaffella igoi*, sp. nov. A, diagonal section of a paratype, UMUT PF 18022. B, incomplete axial section of the holotype, UMUT PF 18021. C, axial section of a paratype (immature), UMUT PF 18024. D, axial section of a paratype (immature), UMUT PF 18023. E, sagittal section of a paratype, UMUT PF 18025. F, G, *Eostaffella tenebrosa* Vissarionova. F, axial (slightly tangential) section, UMUT PF 18040. G, axial section, UMUT PF 18038. H–J, *Eostaffella kanmerai* (Igo). H, diagonal section, UMUT PF 18026. I, axial (slightly tangential) section of the holotype, IGUT 20369 (reillustration of Igo, 1957, pl. 1, fig. 20). J, incomplete tangential section, UMUT PF 18027. K, *Eostaffella* sp., axial section, UMUT PF 18041. All specimens X100.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are 0.02(?), 0.06, 0.10, 0.16, 0.25, and 0.32, respectively. The initial 1 to 1 1/2 volutions are skew at approximately 40 degrees to the remaining essentially planispiral volutions. Proloculus is 0.024 to 0.033 mm in inside diameter. Chamber increases in height uniformly throughout the growth. Wall consists of a thin tectum, and lower and upper tectoria; it is 0.010 to 0.014 mm thick in the final volution. Tunnel is low and narrow except for the ultimate volution which is wider than the penultimate one. Weak, slightly asymmetrical chomata are present in the outer 2 or 3 volutions, its both (tunnel side and poleward side) sides are relatively gentle, occasionally extending to poles.

Remarks:—This species has considerably wide variation in the shape of periphery in the outer volutions. However, in the immature stage the size and skewness of coiling of examined specimens are nearly equal. Specimen having pointed periphery (Figure 5-D) could be classified as *Eostaffella mosquensis acuta* Rauzer-Chernousova, but Rozovskaia (1963) has shown that *E. mosquensis acuta* is synonymous with *E. mosquensis*. Her classification is followed in this paper.

This species has been recorded from the Upper Viséan (Alexinsky to Michailovsky horizons) of the Russian Platform and Urals, from the Lower Serpukhovian (C_1^5) of the Donetz Basin, from the Upper Viséan (V_3b-V_3c) of West Europe, and from the Upper Chesterian (Zone 18) of North America.

Eostaffella cf. *postmosquensis* Kireeva, 1951

Figures 3-I–K

Compare:—

Eostaffella postmosquensis Kireeva, 1951, p. 48–49, pl. 1, figs. 1–2; Bogush and Iuferev, 1962, p. 178–179, pl. 7, fig. 3; Brazhinikova *et al.*, 1967, pl. 21, fig. 7; Manukalova-Grebeniuk, Il'ina and Serezhikova, 1969, p. 25–26, pl. 6, figs. 9–11; Watanabe, 1973, p. 377–378, pl. 51, figs. 9–14; Ivanova, 1973a, pl. 2, figs. 5–7, pl. 4, figs. 11–12; Reitlinger, 1973, p. 62, pl. 10, figs. 1–2; Matsusue, 1986, pl. 6, fig. 8.

E. postmosquensis postmosquensis Kireeva: Grozdilova and Lebedeva, 1954, p. 114–115, pl. 14, fig. 9.

E. ex. gr. *postmosquensis* Kireeva: Ivanova, 1973a, pl. 30, fig. 17.

Material studied:—Description is based on two axial sections (UMUT PF 18035, sample NS 31, Figure 3-I; 18037, sample NSR 5, Figure 3-K) and one slightly diagonal section (UMUT PF 18036, sample NSR 5, Figure 3-J). All specimens were obtained from loc. A.

Description:—Test is small for the genus, deeply umbilicate on both sides. Periphery is rounded in axial section through all growth stage of the shell. Lateral slopes are broadly convex. Mature specimens contain 4 1/2 volutions that are 0.17 to 0.22 mm in length and 0.35 to 0.37 mm in width. Form ratio ranges from 0.50 to 0.59. The initial 1 to 2 volutions are skew to the remaining essentially planispiral volutions. The last volution is partially evolute. Proloculus is approximately 0.020 mm in inside diameter. Wall in the earlier volutions appears three layered because of an upper tectorium produced by secondary deposits on the chamber floors. Chomata are weak and sometimes absent. Tunnel is very low and narrow.

Remarks:—*Eostaffella postmosquensis* was originally described by Kireeva in Rauzer-Chernousova *et al.* (1951) from the Vereisky and Kashirsky horizons (Lower Moscovian) of the Russian Platform and later this species was identified from the Upper Serpukhovian (Zapaltubinsky horizon) of the Donetz Basin. The Kireeva's types generally have much smaller shell at corresponding volutions. However, so far as the general shell shape (rounded periphery, deep

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← **Figure 5.** A–C, E?, *Eostaffella subulba*, sp. nov. A, tangential section of the holotype, UMUT PF 18028. B, tangential section of a paratype, UMUT PF 18029. C, oblique section of a paratype, UMUT PF 18030. E, incomplete diagonal section of questionably assignment to this species, UMUT PF 18031. D, F, G, H?, *Eostaffella mosquensis* Vissarionova. D, axial section, UMUT PF 18033. F, axial section, UMUT PF 18034. G, axial section, UMUT PF 18032. H, sagittal section of questionably assignment to this species, UMUT PF 18070. I, *Eostaffella tenebrosa* Vissarionova, sagittal (slightly diagonal) section, UMUT PF 18039. All specimens X100.

umbilication on both sides) and weaker chomata are concerned examined specimens well agree with the type specimens.

This species resembles *Eostaffella cooperi* (Zeller) from the Kinkaid Limestone of Illinois, but it differs in having smaller proloculus and well-developed umbilical depressions.

The internal morphology of this species exemplifies very close relationship to *Eostaffella* and *Zellerina,* but I have assigned the materials to *Eostaffella* because they have well-differentiated spirotheca.

Eostaffella subulba Niko, sp. nov.

Figures 5-A–C, E?

Material studied:–Holotype, UMUT PF 18028 (sample NS 61, Figure 5-A); paratypes, UMUT PF 18029 (sample NSR 6, Figure 5-B), 18030 (sample NS 61, Figure 5-C), and a specimen of questionable assignment to this species 18031 (sample NS 10, Figure 5-E) were examined. All specimens were obtained from loc. A.

Diagnosis.–Large *Eostaffella* with discoidal to elliptical test, rounded periphery and rapid expansion of the last volution. Septa short and straight. Chomata well-developed.

Description:–Test is large for the genus, discoidal to elliptical and umbilicate on both sides. Periphery is rounded in axial section and lateral slopes are broadly convex. The holotype (Figure 5-A) contains at leat 5 volutions that is 0.38 mm in length and 0.71 mm in width. Form ratios of the outer 4 volutions of the holotype are approximately 0.53, 0.56, 0.54, and 0.54, respectively. A paratype (Figure 5-B) contains at least 4 volutions is 0.33 mm in length and 0.65 mm in width, giving form ratio 0.51. The largest specimen (Figure 5-C) attains to 0.90 mm in width. Septa are short and straight except for the last three ones, which are relatively long and faintly curved. Septal counts of the last two volutions of a paratype (Figure 5-C) are 14 and 13. Wall appears three layered because of an upper tectorium produced by the secondary deposits on the chamber floors; in the last volution the wall consists of tectum and lower tectorium. Thickness of spirotheca of the last volution of the holotype is approximately 0.015 mm. Asymmetrical chomata are well-developed in the outer volutions. Tunnel is low and narrow, but in the last volution it becomes wider rapidly than in the penultimate volution. Aperture is very low, basal and slit like.

Remarks:–*Eostaffella subulba* somewhat resembles *E. hohsienica* Chang from the Hochow Limestone of Anhui Province, China, but this new species differs from the latter in having loosely coiled shell, weaker chomata and fewer septa at corresponding volutions. *E. endothyroidea* described by Chang (1962) from the Hochow Limestone and *E. mosquensis* have smaller shell than *E. subulba.*

Unfortunately, it is impossible to determine the proloculus size and characters of the juvenarium volutions of this form owing to ill-orientation.

Eostaffella tenebrosa Vissarionova

Figures 4-F, G, 5-I

Eostaffella ikensis tenebrosa Vissarionova, 1948, p. 220–221, pl. 13, figs. 11–13; Ganelina, 1951, p. 182–183, pl. 1, figs. 2–3; Grozdilova and Lebedeva, 1954, p. 124, pl. 13, fig. 18; Brazhnikova *et al.,* 1956, pl. 16, fig. 6; Durkina, 1959, p. 199–200, pl. 20, figs. 21–22; Rozovskaia, 1963, p. 98, pl. 18, figs. 1–2; Manukalova-Greboniuk, Il'ina and Serezhnikova, 1969, p. 32–33, pl. 9, figs. 13–14; Malakhova, 1973, pl. 6, fig. 5; Ivanova, 1973a, pl. 17, fig. 2, pl. 24, figs. 1–3, pl. 30, fig. 14; Sosnina and Nikitina, 1976, pl. 9, fig. 29.

Eostaffella cf. *ikensis tenebrosa* Vissarionova: Chang, 1962, p. 437–438, pl. 1, figs. 14–15.

Eostaffella tenebrosa Vissarionova: Bogush and Iuferev, 1962, p. 174, pl. 11, fig. 29.

Material studied:–Specimens including two axial sections (UMUT PF 18038, sample T2 5, Figure 4-G; 18040, sample NS 40, Figure 4-F), three oblique sections, and one sagittal section (UMUT PF 18039, sample T2 5, Figure 5-I) were studied. All sepcimens were obtained from loc. A.

Description:–Test is lenticular to rhomboidal with arched poles. Outer periphery is pointed in axial section, and lateral slopes are nearly straight to slightly concave. Mature specimens contain 5 1/2 to 6 volutions that are 0.31 to 0.36 mm in length, and 0.57 to 0.77 mm in width. Form ratio ranges from 0.52 to 0.55. In a typical specimen (Figure 4-F) radius vectors of the second to six volutions are 0.04, 0.08, 0.15, 0.25, and 0.37 mm, respectively. Proloculus is approximately 0.021 to 0.025 mm in inside diameter. The initial 1 to 1 1/2 volutions are plectogyrally coiled, but the rest are planispiral. Septa are short, straight and slightly inclined forward. Septal counts of the third to fifth volutions of a specimen (Figure 5-I) are 10, 14, and 16, respectively. Outer periphery of septal sutures is smooth. Wall is calcareous, microgranular and 0.008 to 0.009 mm thick in the penultimate volution; it is differentiated into a thin tectum and tectoria. Tunnel is low and narrow in the inner five volutions, but rather broad in the last volution. Asymmetrical chomata are well-developed through shell except for the juvenarium. Tunnel sides of chomata are steep, but poleward slopes are very gentle and extending to poles.

Remarks:—*Eostaffella tenebrosa* was originally described by Vissarionova as a variety of *E. ikensis*, and was reported from the Michailovsky (Late Viséan) to Steshevsky horizons (Middle Serpukhovian) of the Donetz Basin, Russian Platform, Urals, and Sikhote Alin. The Vissarionova's original types have a more pointed periphery and tightly coiled than examined specimens. However, it is identical in the general shell shape, and short and straight septa.

Eostaffella tenebrosa has about the same dimensions with *E. ikensis* and *E. enormis*. But *E. ikensis* has a more rounded periphery in the outer volutions, and *E. enormis* has a larger shell and well-developed chomata.

Eostaffella sp.

Figure 4-K

Material studied:—Description is based on only one specimen (UMUT PF 18041, sample NSR 1) from loc. A.

Descriptive remarks:—This differs from other specimens of the genus in its rapid expansion of the last volution, hence this may represent a new species. Test is moderately large for the genus, involute with slightly umbilicate on both sides. Periphery is pointed in the outer three volutions and more or less rounded in the last volution. The specimen contains 5 volutions that is 0.33 mm in length and 0.66 mm in width, giving form ratio 0.50. The initial volution is skewed at angle of about 48 degrees to the remaining essentially planispiral volutions. The last volution inflates more rapidly than the inner volutions. Proloculus is approximately 0.025 mm in inside diameter. Wall consists of a tectum, and lower and upper tectoria. Low asymmetrical chomta occur in the outer volutions. Tunnel is relatively high and wide in the last volution.

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Ichinotani 一ノ谷，Fukuji 福地，Mizuboradani 水洞谷，Mizuyagadani 水屋ヶ谷，Hochow 和州，Anhui 安徽。

福地地域一ノ谷層からの石炭紀前期*Eostaffella*（原始的フズリナ類）：岐阜県吉城郡上宝村福地地域の一ノ谷層下部からは豊富な有孔虫化石群を産出する。今回，3新種（*Eostaffella excavata, E. igoi, E. subulba*）を含む8種の原始的フズリナ類（*Eostaffella*）を生層序学的分帯のための基礎的データとして記載した。このフズリナ化石群は，Igo (1956) による *Eostaffella kanmerai* zone に含められ，その時代はビゼアン最後期からセルプークホービアン前期であると考えられる。
児子修司

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835. ON THE SILURIAN TRILOBITE FAUNULE OF HITOEGANE NEAR FUKUJI IN THE HIDA PLATEAU, JAPAN*

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Abstract. A new collection from Hitoegane adjacently north of Fukuji, Gifu Prefecture contains more than nine species of trilobites in the Scutelluidae, Illaenidae (?), Proetidae, Cheiruridae and Encrinuridae, including four new species, namely *Kosovopeltis hidensis, Proetus (Coniproetus) tenuiceps, P. (Coniproetus?) subconicus* and *Cheirurus hitoeganensis.* This faunule is late or middle Ludlovian in age and shows affinities to the East Australian fauna through the Yokokura-yama, Shikoku and the Bohemian fauna through the trilobites of the Mongolian geosyncline. *Encrinurus* cf. *similis* found at Hakubado, Fukui Prefecture is about the same age.

The *Favosites* fauna of Ichinotani at Fukuji, Kamitakara Village, Yoshiki County, Gifu Prefecture which has once been considered Silurian (Kamei, 1949) was later transferred to the Devonian (Kobayashi and Igo, 1956) and still later the Fukuji Formation was determined to be within the range from Gedinnian to Eifelian (Igo *et al.*, 1975; Kobayashi and Hamada, 1977; Igo and Adachi, 1981). Prior to this a few pygidia were found in limestone boulders at Hitoegane hill about 1500 m to the north-northeast of Fukuji. They were found to be a new species of *Encrinurus* as denominated *Encrinurus fimbriatus* by the authors (1974). Thus the Silurian limestone was proven to exist at Hitoegane in the Fukuji area.

Ohno, Okazaki and Hirano (1977) on the other hand discovered *Encrinurus* at Hakubado, Izumi Village, Ohno County, Fukui Prefecture. The authors are of opinion that it is *Encrinurus* cf. *similis.* Hitoegane and Hakubado are two Silurian fossil localities in the Hida plateau which are located respectively in the eastern and western parts of the plateau with a distance of about 90 km between them. The geology of these localities are so highly complicated that the relation of these Silurian rocks to the older and younger Paleozoic formations is not yet clarified.

A new trilobite collection of Hitoegane contained mostly in limestones, but *Encrinurus* cf. *kitakamiensis* whose mother rock is green tuffaceous shale casts a question on the age of *Scutellum* (?) sp. indet. The authors reported it as a Silurian trilobite (1965), but later a Devonian one (1977). Now it becomes more probably a Silurina trilobite in looking the similarity of its mother rock with that of *Encrinurus* cf. *kitakamiensis.* As the result of restudy on this specimen it is called here *Decoroscutellum* (?) sp. indet.

The Hitoegane trilobites in the new collection are the following forms in the Scutel-

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luidae, Illaenidae (?), Proetidae, Cheiruridae and Encrinuridae.

Kosovopeltis hidensis, sp. nov.
Kosovopeltis hidensis f. *striatus*, forma. nov.
Illaenid (?) gen. et. sp. indet.
Proetus (*Coniproetus*) *tenuiceps*, sp. nov.
Proetus (*Coniproetus*?) *subconicus*, sp. nov.
Cheirurus hitoeganensis, sp. nov.
Cheirurid, gen. et sp. indet. (Hypostoma)
Sphaerexochus sp. indet.
Encrinurus fimbriatus Kobayashi and Hamada
Encrinurus cf. *kitakamiensis* Sugiyama

All of these trilobites are contained in limestone except for *Encrinurus* cf. *kitakamiensis*. In the Kitakami mountains, North Japan *E. kitakamiensis* horizon lies immediately above the middle Ludlovian limestone containing *Schedohalysites kitakamiensis* (Hamada, 1961). Therefore the superadjacent trilobite horizon must be late Ludlovian, if not Pridolian in age. *Decoroscutellum* as a genus ranges from Wenlockian to Lower Devonian, although it thrived in the Ludlovian. The generic reference of the pygidium in question is provisional. Therefore the exact age of *Decoroscutellum* (?) sp. indet. in schalstein is indeterminable.

Among the trilobites in the limestone of Hitoegane there is none spcifically identifiable with any species from Yokokura-yama or other locality in Japan. *Kosovopeltis, Proetus, Sphaerexochus* and *Encrinurus* are common genera between the Hitoegane and Yokokura-yama faunas, but *Proetus* (*Coniproetus*) is unknown from Yokokura-yama. *Kosovopeltis* Šnajdr, 1958 is a Silurian scutelluid genus flourished in the Ludlovian (Kopanina to Lochkov beds) in Bohemia (Emsian) and a species is known from the Urals (Šnajdr, 1960). Among the Japanese trilobites *K. hidensis* is allied to *K. angusticostatus* of the Yokokura-yama fauna. *Proetus* (*Coniproetus*) as a genus is distributed in Europe and North Africa in the range from Silurian (lower Budnanian) to Devonian (Emsian) (Alberti, 1969). *Cheirurus hitoeganensis* is closely allied to *Cheirurus insignis* Beyrich from the upper Wenlockian (Liten high) in Bohemia (Horný and Bastl, 1970). *Encrinurus fimbriatus* was primarily founded on some pygidia from Hitoegane. The new collection contains not only pygidia but also cranidia. This species is allied to not only *E. subtrigonalis* and *E. yokokurensis* from Mt. Yokokura in Japan but also *E. sinicus* Kuo from near Kirin, Northeast China (Kuo, 1962). Judging from these facts the Hitoegane limestone faunule is Ludlovian and probably middle or late Ludlovian in age.

Thus there are three trilobite horizons in the Hitoegane area. The tuffaceous shale containing *Encrinurus* cf. *kitakamiensis* is probably upper Ludlovian. Judging from the lithological similarity the *Decoroscutellum* (?) bearing schalstein may be about the same age. The trilobite faunule in the limestone of Hitoegane is judged to be lower-middle Ludolovian. The Hitoegane trilobites as a whole suggest the faunal connection to the fauna of eastern Australia through the Yokokura-yama fauna on one side and on the other side to the Central European fauna through the Urals. This biogeographic suggestion is in support of the trilobite pygidia from Hakubado, as they look very similar to *Encrinurus similis* from Gomi quarry on Mt. Yokokura.

Description of trilobites of the Hitoegane Faunule

Beside some known species and indeterminable forms four new dpecies are here included as follows:

Kosovopeltis hidensis, sp. nov.
Kosovopeltis hidensis forma *striatus*, forma nov.
Proetus (*Coniproetus*) *tenuiceps*, sp. nov.
Proetus (*Coniproetus*?) *subconicus*, sp. nov.
Cheirurus hitoeganensis, sp. nov.

The hypostoma is known of *Encrinurus fimbriatus*. On this occasion *Encrinurus* cf. *similis* from Hakubado is also described. Some notes are supplemented on the Genus *Proetus*, Subgenus *Proetus* (*Coniproetus*) and Genus *Encrinurus*.

Family Scutelluidae R. and E. Richter, 1955

Genus *Kosovopeltis* Šnajdr, 1945

Kosovopeltis hidensis Kobayashi and Hamada, sp. nov.

Figures 1-1a–c, 2, 3-7

Description:—Cranidium broad and gently inflated. Glabella expanded in anterior more than twice its breadth in posterior, somewhat contracted at posterior lateral furrows and slightly depressed behind frontal rim; anterior and middle lateral furrows transversal, disconnected from lateral margin and the latter half as wide as the former; posterior lateral furrow shown by roundly subquadrate depression incised from lateral margin; median smooth zone as wide as posterior lateral furrow; middle lateral lobe narrow (sag.); anterior lateral lobe a little wider than two others; occipital furrow transversal; neck ring narrowing laterally; its posterior margin arcuate; axial furrow deep. Fixed cheek depressed, moderate in breadth; eyes large, opposed at posterior lateral furrows and expanded postero-laterally; eye-ridge present; alae small, semicircular, opposed at galbellar constriction. Frontal rim separated from glabella by narrow furrow, broadly arcuate, distinctly elevated and extending beyond eyes; frontal marginal furrow becoming deeper on lateral sides; anterior facial sutures widely divergent from eyes, but bent back at marginal rim. Doublure vertical. Very fine transversal striae densely distributed nearly whole cranidium.

Observation:—An associated pygidium is nearly flat except for the axial lobe whose outline is triangular and a little elevated above the level of the pleural field. This lobe is simply flat-topped, non-trilobate and decorated with fine transversal striae. The axial furrow is nearly straight and shallow but fairly wide. The post-axial rib is somewhat broadened in posterior. Seven pleural ribs on its lateral side look more or less convex antero-laterally. All of these ribs are crossed by sharp ridges on the top. The pleural furrows are narrow and profound.

Comparison:—Though the pygidium is imperfect, its outline may be semi-elliptical. It agrees with the above cranidium in the low convexity and the mode of striation on the axial lobe. Its obsolete trilobation is very distinctive among scutelluids. It is somewhat similar to *Kosovopeltis angusticostatus* from Mt. Yokokura, but the ribs are narrower than furrows and ornamented with fine crenulation.

In *Kosovopeltis nebula* Campbell, 1967 from Oklahoma the trilobation of the axial lobe is obsolete in anterior, but a pair of longitudinal furrows are distinct in posteiror.

Finally, *Bronteus partschi* Barrande by Weber, 1951 in fig. 13, pl. 2 is a similar pygidium in obsolete trilobation of the axial lobe and in fine crenulation of the ribs and the pleural furrows stronger in the Kazakhstan form. The pygidium is probably longer and the axial lobe relatively smaller in that species.

Occurrence:—Limestone, Hitoegane. An imperfect thoracic segment having lirae like the cephalon is contained in the collection.

Kosovopteris hidensis forma *striatum* Kobayashi and Hamada, forma nov.

Figure 1-3

This cranidium agrees best with *Kosovopeltis hidensis* in most aspects, but the test is more strongly striated and the striation becomes very irregular in posterior. The frontal marginal furrow is rudimentary, the anterior outline more convex forward and the middle lateral furrow indicated by a very small but deep pit. The fixed cheek is much more convex in this form, if compared with the preceding.

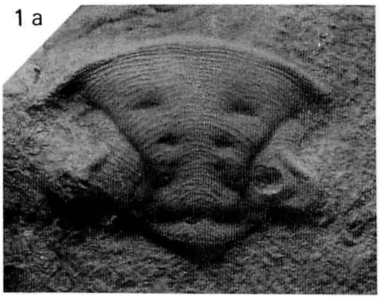
Occurrence:—Limestone, Hitoegane.

Genus *Decoroscutellum* Šnajdr, 1958

Decoroscutellum (?) sp. indet.

1965. *Scutellum* (?) sp. indet. Kobayashi and Hamada, *Trans. Proc. Pal. Soc. Japan, N. S.*, no. 58, p. 78, pl. 7, figs. 4a–b, text-fig. 2

1977. *Scutellum* (?) sp. indet. Kobayashi and Hamada, *Palaeont. Soc. Japan, Spec. Pap.*, no. 20, p. 80, pl. 1, figs. 4a–b.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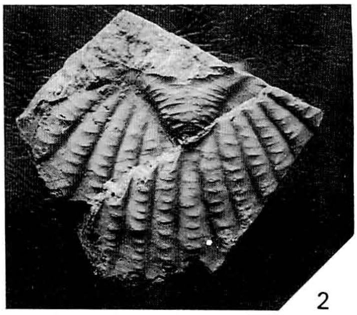
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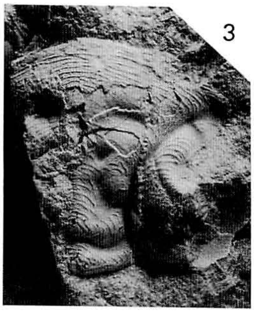
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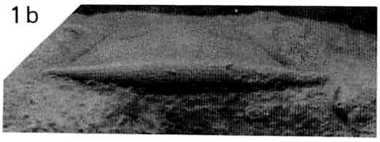
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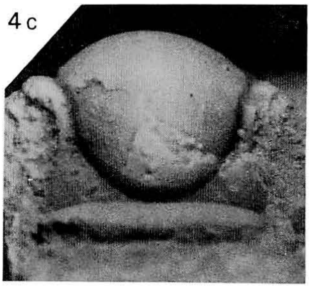
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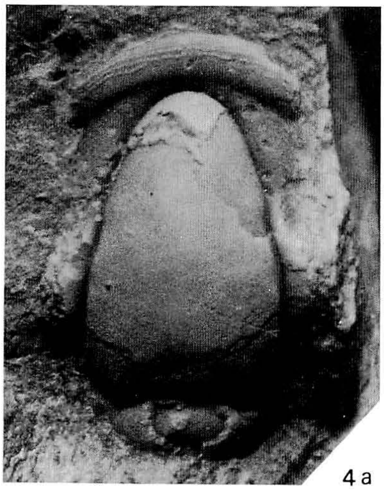
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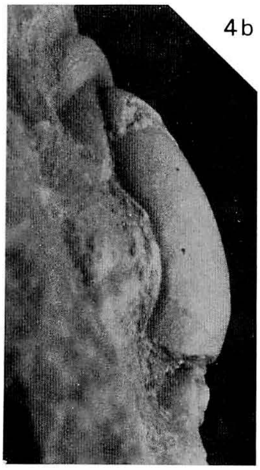
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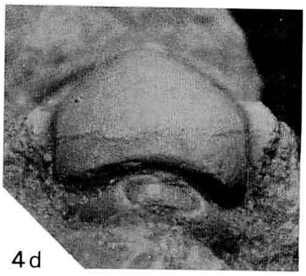
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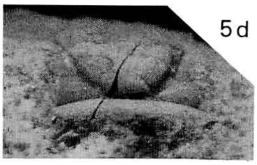
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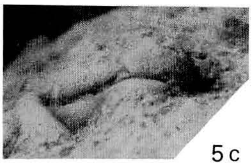
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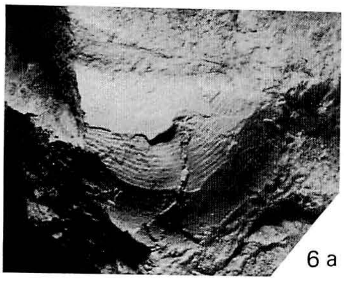
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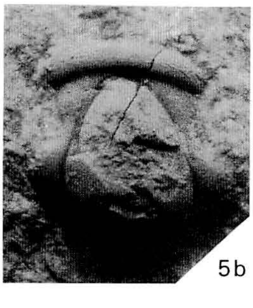
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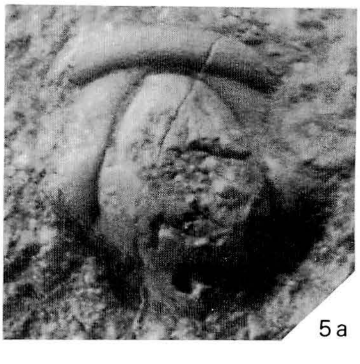
5 a

An imperfect pygidium of a scutelluid whose anterior margin is broad and straight. Its triangular axial lobe is trilobate and the median lobe swelling upward in posterior, possibly forming a median tubercle. The post-axial median rib is much broader than lateral ribs in anterior, somewhat narrowing back and then broadened backward. Whether it is bifurcate or not is indeterminable. Among seven pairs of lateral ribs the second and third ones are distinctly bent with convexity on the antero-lateral side. The fourth and sixth ribs are somewhat arcuate toward the opposite side in the distal half. Thus the lateral ribs are more or less sigmoidal. All ribs are flat and separated from one another by much narrower furrows. The lateral posterior margins are unknown, but it is known that the doublure extends about an outer half of the pleural field.

The pygidium is presumably subpentagonal in outline. In the distinct trilobation of the axial lobe, the posterior tubercle (?) of its median lobe and the more or less sigmoidal pleural ribs, this pygidium agrees with *Decoroscutellum* (*Decoroscutellum*) *haidingeri* (Barrande) from the Kopanina beds in figs. 1–3, pl. 6 in Šnajdr (1960). In this pygidium, however, the pleural furrows are considerably narrower than in Barrande's species. The furrows are, however, very narrow in *D.* (*Decoroscutellum*) *lepidum lepidum* Bouček) from the Lochkov beds in fig. 4, pl. 7, Šnajdr (1960). The median rib is well bifurcate in Bouček's species, whereas the bifurcation occurs only in the terminal part in Barrande's species. Thus it is probable that this pygidium belongs to an unknown species of *Decoroscutellum*.

Occurrence:—The specimen is contained in schalstein of Hitoegane. It was once considered a Devonian *Scutellum*, but its age would be late Silurian, judging from the other Hitoegane trilobites.

Family Proetidae Salter, 1864

Subfamily Proetinae Salter, 1864

Genus *Proetus* Steininger, 1831

As stated already in 1977 (pp. 132, 180), the classification of the Proetidae and Proetacea is a subject of most discussion. Many questions are also attached to the subgeneric division of genus *Proetus*. *Proetus* (*Coniproetus*) is, however, acceptable as a good subgenus, although a question still remains as to the synonymy of *Bohemiproetus* with *Coniproetus*.

Subgenus *Coniproetus* Alberti, 1966

Diagnosis:—Glabella coniform; lateral glabellar furrows not incised; short (sag.) preglabellar field commonly developed; lateral occipital lobes well defined; eye platform typically absent; long genal spines in most species; pygidial border well-developed; band of parallel terrace lines around pygidial margin; exoskeleton smooth, or with granular sculpture.

Type-species:—*Proetus glandiferus* Novák, 1890

Remarks:—This subgenus was primarily founded on *Proetus condensus* Přibyl, 1965. According to Owens (1973), however, its type-species must be *Proetus gladiferus* Novák, 1890, because both of them belong to an identical

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← **Figures 1-1a–c, 2.** *Kosovopeltis hidensis* Kobayashi and Hamada, sp. nov. A dorsal (a), frontal (b) and right lateral (c) views of the holotype cranidum. x4.2, PA 18095. 2. A dorsal view of an incomplete pygidium. x1.6, PA 18096.

3. *Kosovopeltis hidensis* forma *striatum* Kobayashi and Hamada, forma nov. A dorsal view of an incomplete cranidium. x1.7, PA 18097.

4a–d. *Proetus* (*Coniproetus*) *tenuiceps* Kobayashi and Hamada, sp. nov. A dorsal (a), left lateral (b), frontal (c) and posterior (d) views of the holotype cranidium. x5.3, PA 18098. (Vide Figures 2-1a, b also).

5a–d. *Proetus* (*Coniproetus*?) *subconicus* Kobayashi and Hamada, sp. nov. Dorsal (a, b), left lateral (c) and frontal (d) views of an incomplete cranidium. a: x8.2, b, c, d: x7.1, PA 18099.

6a, b. Illaenid (?) gen. et sp. indet. A dorsal (a) and posterior (b) views of an ill-preserved pygidium showing the slanting margin which is covered by striation on the undersurface of doublure. x3.7, PA 18113.

species. Furthermore *Proetus* (*Bohemiproetus*) Pillet, 1969 is synonymous with *Proetus* (*Coniproetus*) because *Proetus bohemicus* Hawle and Corda, the type-species of the former, is not so different from *P. glandiferus* as they can be separated subgenerically. Thus the above quoted diagnosis was given by Owens.

Distribution:—According to Alberti (1969) this subgenus is distributed from Silurian (lower Budnanian) to Devonian (Emsian) in Europe-Africa. As noted by the authors (1974, 1977), its trans-Eurasiatic distribution through the Mongolian geosyncline is shown by the occurrences of *Proetus bohemicus* in the Lower Devonian of Turkestan (Weber, 1932) as well as *Proetus* (*Coniproetus*) *fukujiensis* from the Lower-Middle Devonian of Fukuji, Japan. *Preoetus* (*Coniproetus*) *subconicus* here described proves further that such an extensive distribution of the subgenus was started already in the late Silurian age.

Proetus (*Coniproetus*) *tenuiceps* Kobayashi and Hamada, sp. nov.

Figures 1-4a–d, 3-1a–b

Description:—Glabella longiconic, well convex, almost straight laterally and abruptly rounded in front; lateral furrows obsolete; occipital furrow profound and transversal; occipital ring very short sagittaly, well arcuate on posterior side, depressed below glabella, provided with a median tubercle and a pair of small lateral lobes indicated by a pair of notches; palpebral lobe fairly long and located far posteiorly; fixed cheek narrow; frontal border convex, well developed, separated from glabella by marginal furrow; preglabellar field almost nullified between frontal and dorsal furrows; facial sutures slightly divergent from eyes as far as parallels through lateral eye-limits and then curved inward; test smooth.

Observation:—The median tubercle is seen on the exfoliate part of the test. The occipital lobes are indicated by short oblique notches from the occipital furrow into the occipital ring. The dorsal furrow is separated from the narrow frontal marginal furrow by a space *i.e.* the preglabellar field, narrower than these furrows. Some parallel striae are seen on the frontal border.

Comparison:—This species can be distinguished from not only *Proetus* (*Coniproetus*) *glandiferus* Novák, but also the Devonian species from North Africa (Alberti, 1969) and the Armorican massif, France (Pillet, 1972) in the longiconic glabella. In the general aspect of the cranidium it resembles *Proetus* (*Longiproetus*) *pseudotenuis* (Pillet), an Armorican species closely, but the median tubercles absent on the neck ring and the marginal border is flat or concave in *Proetus* (*Longiproetus*). Ludlovian *Proetus obconicus* Lindström which Owens (1973) referred to *Proetus* (*Lacunoproetus*) Yolkin, 1966 and also Wenlockian *P.* (*L.*) *confusus* Owens, 1973 have the cranidium and glabella similar to this species in outline and convexity, but the lateral furrows are completely effaced on the glabella and the eyes larger and located more posteriorly in this species. *Proetus* (*Bohemicus*) *magnicerviculus* from Mt. Yokokura agrees with this species nicely, but the glabellar outline is quite different. Judging the essential characteristics of the cranidium this form is considered best to place in *Proetus* (*Coniproetus*).

Occurrence:—Limestone, Hitoegane.

→ **Figures 2-1a, b.** *Sphaerexochus* sp. indet. A dorsal (a) and right lateral (b) views of an ill-preserved cranidium showing a distinct basal lobe and a neck ring. x1.8, PA 18103.

2a, b. Cheirurid, gen. et sp. indet. (hypostome). A ventral (a) and left lateral (b) views of an incomplete hypostoma showing the general outline. x1.9, PA 18102.

3a–c. *Cheirurus hitoeganensis* Kobayashi and Hamada, sp. nov. A dorsal (a), left lateral (b) and posterior (c) views of an incomplete pygidum. x3.4, PA 18101.

4a–c, 5a–d. *Encrinurus fimbriatus* Kobayashi and Hamada, 1974. A dorsal (a), frontal (b) and left lateral (c) views of a cranidium showing hte general outline with rounded genal angle. x1.8, PA 18104. 5a–d. Another specimen of cranidum. x1.7, PA 18105.


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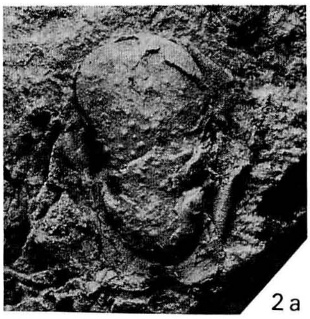
2 b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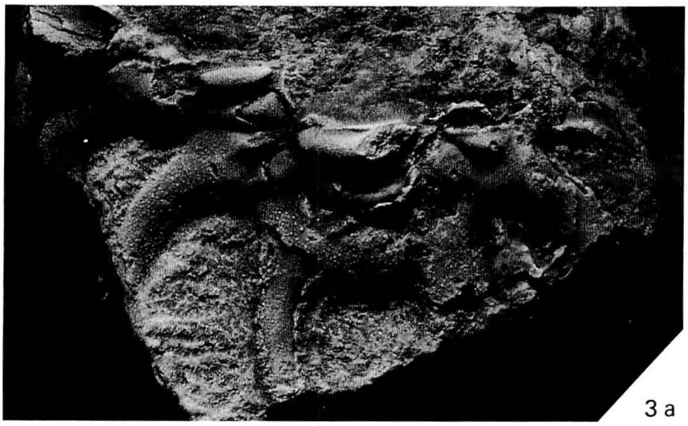
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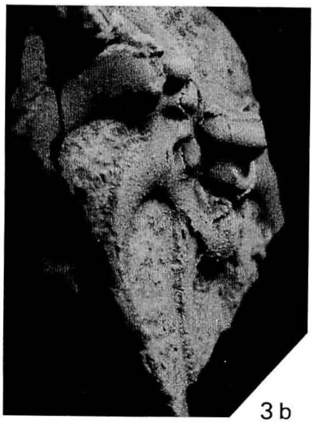
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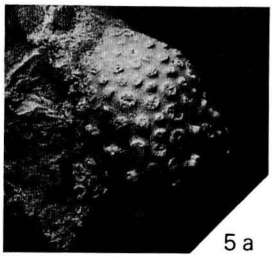
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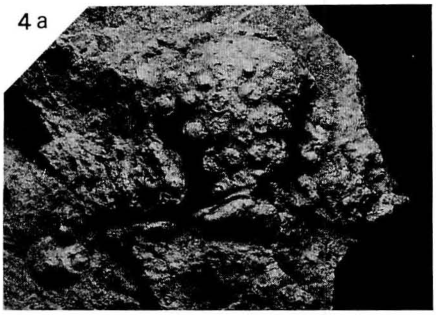
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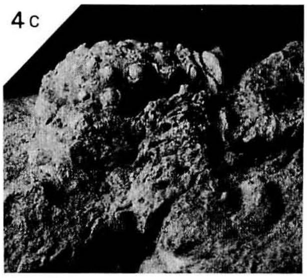
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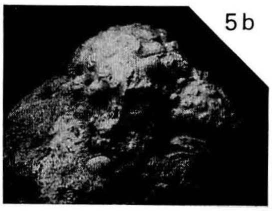
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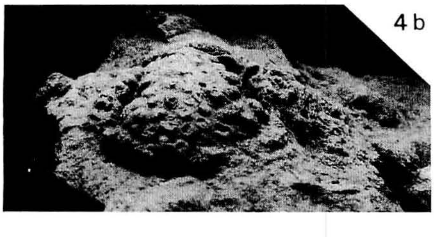
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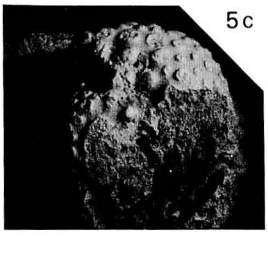
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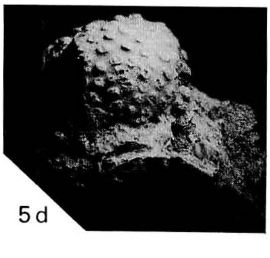
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Proetus (*Coniproetus*?) *subconicus* Kobayashi and Hamada, sp. nov.

Figures 1-5a–d

Description:—Cranidium nearly as long as broad and moderately inflated. Glabella conical, rounded in front, gently rising toward its center; occipital ring well developed and provided with a pair of lateral lobes; occipital and dorsal furrows profound. Fixed cheek narrow; palpebral lobe large, semicircular, provided with narrow eye-band and opposed in posterior of glabella. Frontal border well convex, thick and separated from glabella by narrow marginal furrow; anterior fixed cheek expanded laterally, as long as frontal border and divided into two parts by a weak crest. Facial sutures running forward diagonally from two sides of eyes. Test smooth.

Observation and Comparison:—An imperfect cheek having a low crest parallel to the cheek margin and distinct depression along its inner side belongs probably to this species. The cephalon of this species resembles *Proetus* (*Coniproetus*) *tenuiceps* in the conical glabella and absence of the preglabellar field, although the glabellar outline tapers more slowly and broadly rounded in front in that species. The low crest on the cheek is the most important distinction from *Proetus* (*Coniproetus*).

Occurrence:—Limestone; Hitoegane.

Family Cheiruridae, Salter, 1864

Genus Cheirurus Beyrich, 1845

Cheirurus hitoeganensis Kobayashi and Hamada, sp. nov.

Figures 2-3a–c

Description:—Pygidium exclusive of spines subtriangular; axial lobe composed of three rings and a terminal piece; pleural part of anterior two segments divided into two short ridges by diagonal interpleural furrow for a short distance till lateral spine issues; third segment also bisected but into narrower ridges; three pairs of equally long spines extending laterally and posteriorly with convexity on antero-lateral side; terminal pieces ill-developed; posterior margin between third spines simply convex backward. Test apparently smooth.

Comparison:—This pygidium best agrees with *Cheirurus insignis* Beyrich, but the terminal piece of the axial lobe is ill-defined and the posterior margin not produced as in *C. insignis*. *Dideropanon* has three pairs of lateral spines on the pygidium, but only the anterior two pairs are elongated. In *Cheirurus* on the other hand has three pairs of spines all long like in this species. The axial lobe consists of three rings and a terminal piece which the last is protruded behind in the typical species of *Cheirurus*. The pygidium of *Contracheirurus errator* Lane, 1984 is similar to this pygidium in possession of three pairs of long lateral spines and the entire post-axial margin. The terminal piece of the axial lobe is, however, clearly defined and the lateral spines become shorter posteriorly in that species.

→ **Figures 3-1a, b.** *Proetus* (*Coniproetus*) *tenuiceps* Kobayashi and Hamada, sp. nov. A dorsal (a) and lateral (b) views of an incomplete free cheek. x6.0, PA 18098.

2a–c, 3a–c, 4a–d. *Encrinurus fimbriatus* Kobayashi and Hamada, 1974. 2a–c. A dorsal (a), right lateral (b) and posterior (c) views of a large pygidium. x1.9, PA 18106. 3a–c. A dorsal (a), posterior (b) and right lateral views of another pygidium. x2.1, PA 18107. 4a–d. A dorsal (a), posterior (b), right (c) and left lateral views of another small pygidium. x2.1, PA 18108.

5. Trilobita, gen. et sp. indet. A fragmentary free cheek showing a long genal spine and the surface tuberculation. x3.6, PA 18114.

6. *Encrinurus* cf. *kitakamiensis* Sugiyama, 1941. A dorsal view of somewhat flattened pygidum preserved in shale. x3.1, PA 18111.

7. *Kosovopeltis hidensis* Kobayashi and Hamada? A dorsal view of a fragmentary thoracic segment. x1.9, PA 18115.

8a–d. *Encrinurus* cf. *similis* Kobayashi and Hamada, 1974. A dorsal (a), left lateral (b) and posterior (c) views of an imperfect pygidum (a latex replica) obtained from a small exposure nearby the Hakubado, Fukui Prefecture. x2.1, PA 18112.


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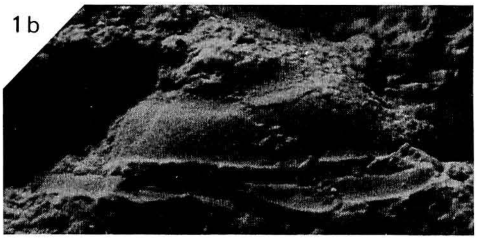
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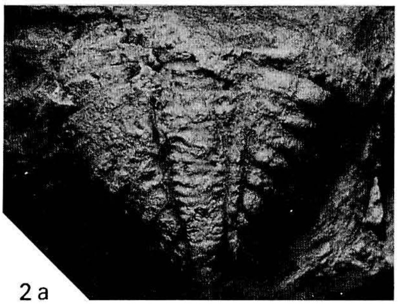
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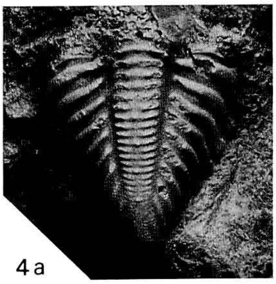
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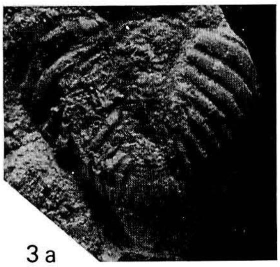
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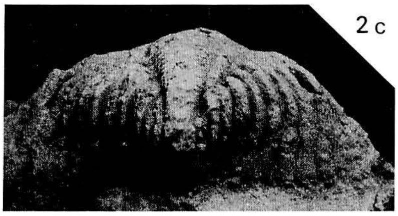
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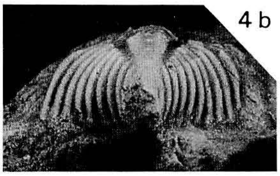
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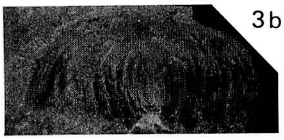
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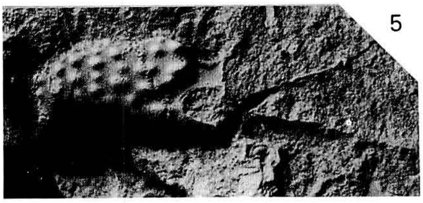
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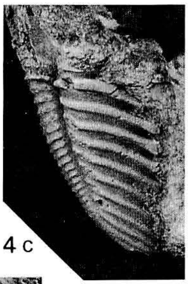
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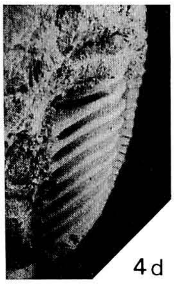
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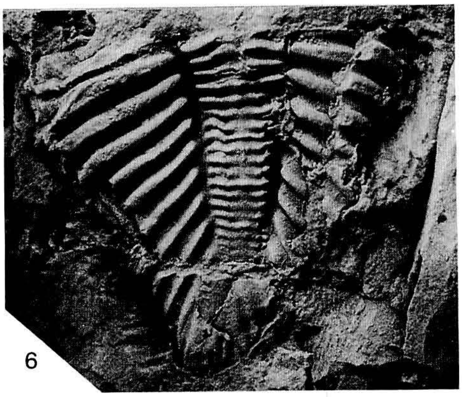
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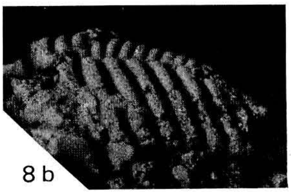
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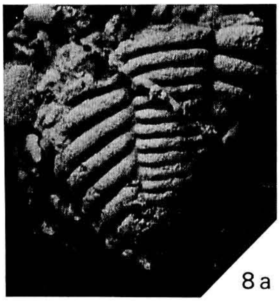
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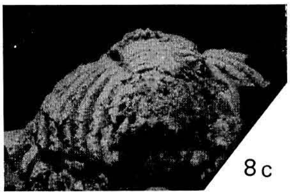
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Occurrence:—Limestone; Hitoegane.

Cheirurid, gen. et sp. indet., Hypostoma

Figures 2-2a–b

A fairly large hypostoma, much longer than broad, well rounded and auriculate in anterior; lateral margins gradually tapering back behind small anterior wings and truncated by transversal posterior margin; main body long, oval and separated from posteior part by deep, short and oblique depressions on lateral parts; lateral border moderate in breadth and depressed. Test with fine granules.

This hypostoma measures 17 mm in length and 8.6 mm in breadth. It is not so well preserved that its outline is traceable exactly. Its general aspect, however, suggests its reference to the Cheiruridae (Prantl and Přibyl, 1947, Lane, 1971, Ramsköld, 1982). It looks similar to the hypostoma of *Cheirurus insignis* Beyrich, 1840. Compared to the cranidium and pygidium it is considerably larger. Its reference to that species is hesitated by its coarse granulation.

Occurrence:—Limestone, Hitoegane.

Subfamily Sphaerexochinae Oepik, 1937

Genus *Sphaerexochus* Beyrich, 1985

Sphaerexochus sp. indet.

Figures 2-1a–b

An imperfect cranidium of *Sphaerexochus* whose occipital and pre-occipital furrows are very broad and fairly deep. They are confluent to each other to isolate the basal lobe. The two other lateral furrows are unpreserved or completely effaced in front of the pre-occipital furrow. The basal lobe of moderate size looks roundly subquadrate. The cheeks and all other parts are unknown. Therefore its comparison with *Sphaerexochus hiratai* or any other species cannot be made.

Occurrence:—Limestone, Hitoegane.

Family Encrinuridae Angelin, 1854

Genus *Encrinurus* Emmerich, 1844

Encrinurus is well represented in Japan by various pygidia from many localities among which ten species can be distinguished with reference to the segmentation, relative breadth of the axial lobe, presence or absence of the smooth median band or/and median tubercles on the lobe and so forth. Cephala are not so common, but three kinds were found in Mt. Yokokura collection. Because they are detached, their combination is inevitably a play of presumption.

Hitoegane collection contains not only two pygidia but also a cephalon of *Encrinurus fimbriatus* all in the same kind of limestone, beside a pygidium of *Encrinurus* aff. *kitakamiensis* in a shaly rock. *Encrinurus* cf. *similis* occurs at Hakubado in limestone.

Encrinurus fimbriatus Kobayashi and Hamada, 1974

Figures 2-4a–c, 5a–d, 3-2a–c, 3a–c, 4a–d,
4-1a–e, 2a–e, 5.

1974. *Encrinurus fimbriatus* Kobayashi and Hamada, *Pal. Soc. Japan, Spec. Pap.*, no. 18, p. 107, pl. 11, figs. 10–11, text-fig. 7H.

This species was primarily founded on pygidia which are subtriangular, but its anterior margin is well arcuate near lateral extremities, and strongly convex, arching down on the lateral and posterior sides, but the adaxial pleural part is nearly flat; axial lobe narrow, long, conical, regularly tapering back, gently convex, a little elevated above the pleural lobes and abruptly bent down near posterior end, terminating at blunt end inside the posterior margin for a short distance, and divided into numerous rings. Pleural

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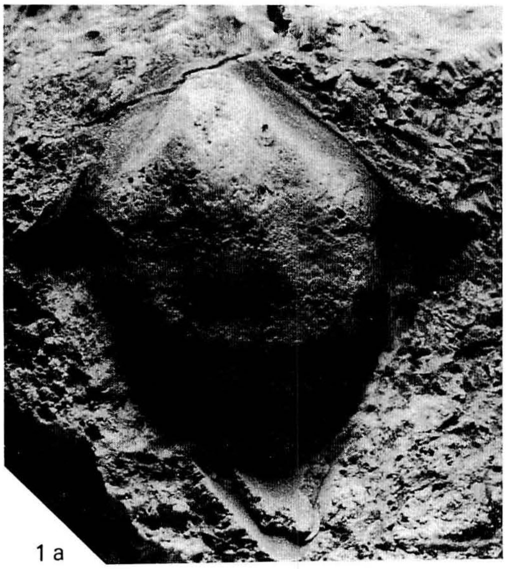
→ **Figures 4-1a–e, 2a–e.** *Encrinurus fimbriatus* Kobayashi and Hamada, 1974. Two casts of hypostomata showing the general outline and the rough musclature. 1a–e, x5.0, PA 18109, 18110. This specimen was found in association with a pygidium of *Encrinurus fimbriatus* that is shown in Figures 3-4a–d, 2a–e, x5.7, PA 18108.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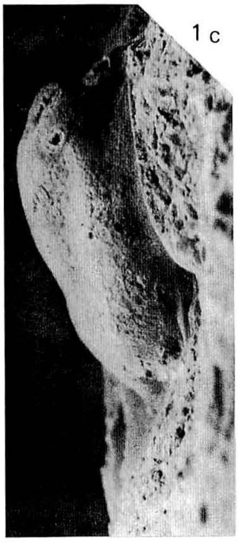
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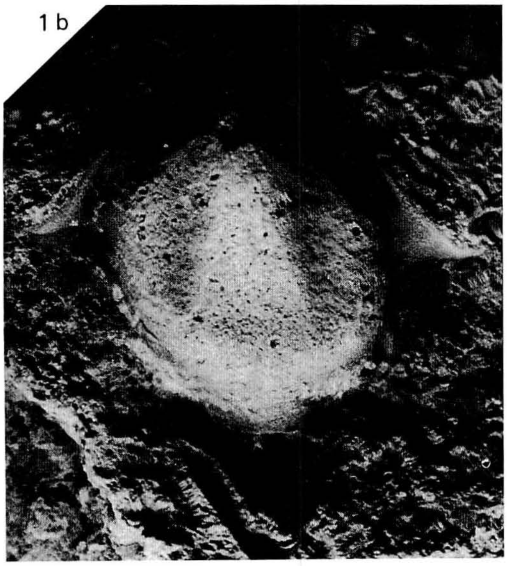
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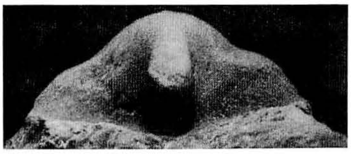
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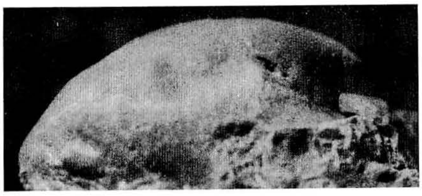
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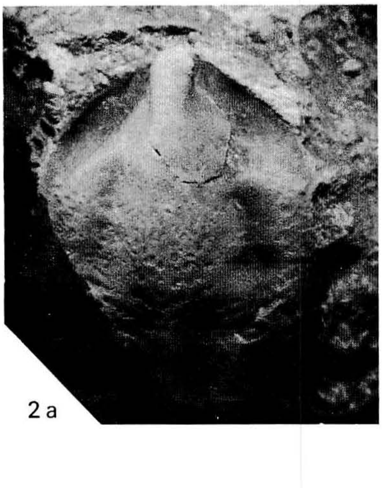
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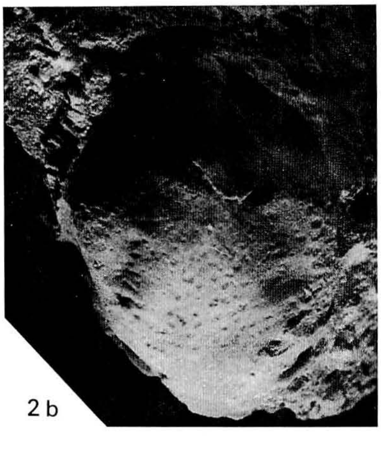
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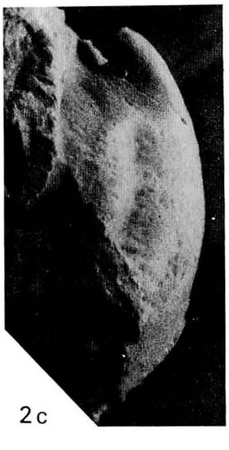
2 c

lobes are divided into 10 to 11 ribs by profound pleural furrows, the most anterior one of which is very narrow.

The axial lobe is about one-fourth as wide as the pygidium. Some 20 axial rings are countable on its main part. In adding incountable posterior ones on the terminal bent part, they probably attain 30 in total. The median smooth band is absent, but some rings are depressed mesially. Median tubercles are very sparse. The pleural ribs are somewhat expanded at their lateral termini.

The new collection contains four pygidia. A small one which is better preserved than the others shows the mode of segmentation clearly. The details of the axial rings, pleural ribs and furrows are better shown in this than the holotype pygidium. The small specimen in Figures 2-4a–c is 15 mm long, 14 mm wide, and 5.3 mm high and its axial lobe is 5 mm wide at the anterior end. The respective dimensions are 21.7 mm, 17.3 mm, 9 mm and 8.3 mm in a large pygidium. The proportional differences between the two pygidia chiefly depend upon the convexity. The former pygidium is compressed laterally, whereas the latter is depressed longitudinally so much that the posterior bent becomes vertical.

This species resembles *Encrinurus subtrigonalis* and *E. similis* in the subtriangular outline and strong convexity of the pygidium. These Yokokura-yama pygidia, however, have much broader axial lobes and pleural ribs in smaller number. They are 9 to 10 in this species but 7 to 8 in that species. The tuberculation is well developed on the pleural ribs, particularly in *Encrinurus subtrigonalis*, but the ribs are non-tuberculate in this species.

Encrinurus sinicus Kuo, 1960, from Northeast China has 25 axial rings some of which bear median tubercles. His fig. 5, pl. 1 and fig. 7, pl. 2 show that the axial rings are interrupted by a median smooth band. Pleural ribs are said eight in number, but the pygidium in his fig. 6, pl. 1 has 9 or possibly 10 ribs. The axial lobe is as. narrow as one-fifth the pygidium. The lobe is evidently much narrower than in this species.

Two imperfect cephala from Hitoegane which are roundly subtriangular in outline and strongly convex are considered to belong probably to this species. The glabella is well inflated, arching down in anterior and densely tuberculate. Five pairs of tubercles are aligned along the lateral margins, middle three of which are more prominent than two others; smaller tubercles irregularly distributed in the inner part. The occipital margin is unpreserved. Axial furrows are well developed. Cheeks are largely destroyed. The right cheek is a little displaced from the glabella in a cranidium in Figure 5. The eye-scar of moderate size is seen on its posterior part. The genal angle is rounded; genal spine absent.

Among the three kinds of *Encrinurus*-cephala so far known from Japan it is most similar to *E. yokokurensis* from which, however, it differs in the mode of tuberculation. It agrees better with *Encrinurus sinicus*, from Northeast China in possession of five pairs of tubercles on the glabella along axial furrows, middle three of which are more developed than two others. In this species two rows of tubercles counted from the posterior side are composed of four tubercles as in *E. sinicus*. The tuberculation in further anterior is complicate and their arrangement disagrees with *E. sinicus*. In that species the occipital lobe is much wider than the glabellar base. Of *E. sinicus* it is said that "genal angles incomplete apparently terminating in spines."

This cephalon resembles alos *Encrinurus kongshaensis* Reed, 1906, from Burma, but "the fifth (basal) pair (of tubercles) is smaller and its members are connected together by a weak ridge across the glabella." This aspect is quite distinctive for this Burmese species from this species, other Japanese species and also *E. sinicus*.

Hypostoma of *Encrinurus fimbriatus*: The hypostoma of this species is rhomboidal, a little longer than broad and more or less protruded laterally as well as posteriorly. The central body is suboval, but its posterior outline is expanded backward in the median part. In the middle part of the body there are some five pairs of depressions on the two sides of the axial elevation which in turn is pitted and forms a beak-like projection as far as the antero-median extremity of the hypostoma.

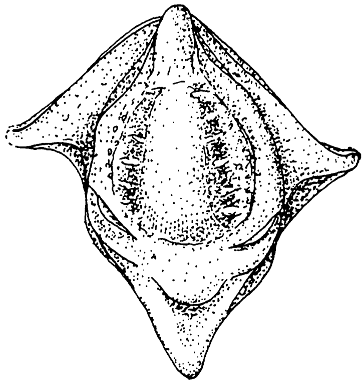

Figure 5. Reconstruction of hypostoma of *Encrinurus fimbriatus.* x4.

Observation:—The Hitoegane collection contains two hypostomata one of which (a) in Figure 4-1 is found with a pygidium of this species in Figures 3-4a—b. It agrees with the other hypostoma (b) in essential characteristics of *Encrinurus* and there is no other species of the genus in the limestone of Hitoegane. Therefore, it is certain that the hypostoma (a) belongs to *Encrinurus fimbriatus.* Its difference from the other (b) may be no more than subspecific value and in part a matter of preservation.

The hypostoma (a) shows the general outline and convexity better than the other except for the anterior part which is broken. The latter hypostoma (b) reveals unusual lateral depressions in about five pairs in the middle part, but they are obsolete in the former.

Comparison:—It is certain that this hypostoma belongs to the same group with those of *Encrinurus* and *Bolizoma.* Truncated by the transvers frontal margin it is pentagonal in *Coronocephalus* and *Senticulus* of the Coronocephalinae Zhang, 1983. In its general outline and the anterior projection of the axial part of the central body, particularly it resembles the hypostoma of *Bolizoma variolaris* (Brongniart) (Tripp *et al.*, 1977). In this species, however, the projection takes a narrow beak-shape and the axial fold is provided with lateral depressions on its two sides in the main part of the central loby. In these characteristics this hypostoma is quite distinct from all others.

Occurrence:—Limestone; Hitoegane. Two granulate free cheeks with long genal spines in the collection which may belong to this species as there is no other granulate cranidium.

Encrinurus cf. *kitakamiensis* Sugiyama, 1941

Figures 3-6

1941. cf. *Encrinurus* (*Coronocephalus*) *kitakamiensis* Sugiyama, *Proc. Imp. Acad.*, v. 17, p. 108–109, figs. 1–2.
1959. cf. *Coronocephalus kitakamiensis;* Hamada, *Japan. J. Geol. Geogr.*, v. 30, p. 84–85, pl. 6, figs. 19–20.
1974. cf. *Encrinurus Kitakamiensis;* Kobayashi and Hamada, *Pal. Soc. Japan, Spec. Pap.*, no. 18, p. 105–106, pl. 19, figs. 19–20, pl. 11, fig. 12, text-fig. 7F.

This pygidium is subtrigonal in outline with somewhat arcuate anterior margin; axial lobe about one-fourth as wide as pygidium and divided into about 27 rings; median tubercles present on a few anterior rings, but median smooth band is absent. Pleural ribs 10 to 11 in number; axial and pleural furrows well developed; interpleural furrows present on some anterior ribs.

In *E. fimbriatus* median tubercles are more developed, axial rings depressed in median part, although they do not form a median longitudinal smooth band, and interpleural furrows are absent.

This pygidium is closely allied to *Encrinurus kitakamiensis* in the outlines of the pygidium and axial lobe, numerous axial rings, number of pleural ribs and the presence of interpleural furrows. They were obscure in Sugiyama's paper (1941), but later they were clearly shown with his holotype specimen by Hamada (1959) and Kobayashi, and Hamada (1974). It has neither median tubercles nor a median smooth band. Interpleural furrows are on the other hand distinct in some anterior pleural ribs in that species as in this pygidium. The axial lobe looks, however, somewhat narrower in that species.

Occurrence:—Shaly rock, Hitoegane.

Encrinurus cf. *similis* Kobayashi and Hamada, 1985

Figures 3-8a–d

1977. *Encrinurus* sp. Ono, Okazaki and Hirao, *Chigaku-kenkyu*, v. 28, nos. 4–6, p. 188–190.

The pygidium in the above cited paper is quite distinct from all pygidia from Hitoegane in the broader axial lobe with the distinct median band. It is subtrigonal and moderately inflated. The axial lobe is almost one-third as wide as pygidium and divided into more than 20 rings, and in the middle-posterior part they are interrupted by the median smooth band. A few median tubercles are present. The pleural lobe is divided into about 10 non-tuberculate ribs by deep and wide pleural furrows, both bent back near lateral margin.

This pygidium is most similar to *Encrinurus similis* but less inflated and possesses a few more pleural ribs. *Encrinurus ishii* is another similar species which differs from it by minute tuberculation of the pleural ribs. In *E. tosensis* the median band is well developed, but median tubercles are absent.

A pygidium in Figure 3-8 which was collected from the same locality has also a broad axial lobe and median tubercles on some axial rings. These two pygidia belong to an identical species of *Encrinurus* closely allied to *Encrinurus similis* from the Yokokura limestone, but distinct from the two species of Hitoegane. Therefore it is probable that the ages of the Hitoegane and Hakubado faunas are different, although time displacement may be not large.

Occurrence:–Limestone, Hakubado, Fukui.

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飛驒高原の福地近傍一重ヶ根産の志留紀三葉虫群：岐阜県吉城郡上宝村福地地方の一重ヶ根産の三葉虫中にScutelluidae, Illaenidae, Proetidae, Cheiruridae, Encrinuridaeに属する8種以上の種属が含まれていて，そのなかに *Kosovopeltis hidensis, Proetus* (*Coniproetus*) *tenuiceps, P.* (*Coniproetus ?*) *subconicus, Cheirurus hitoeganensis* の4新種が含まれていて，*Encrinurus fimbriatus* hypostomata もある。このフォーナーはLudlovianでその石灰岩中のものはその中後期である。また，凝灰質頁岩産の *Encrinurus* cf. *kitakamiensis* は同後期或はPridolianで，輝緑凝灰岩産の *Decoroscutellum* (?) sp. indet. も之と近い時代のものであろう。そして一重ヶ根三葉虫群は全体として一方では横倉山三葉虫群を通じて豪州東部ものと，他方では蒙古地向斜を通じてボヘミアのものとのつながりが認められる。福井県大野郡和泉村の九頭竜湖北岸白馬洞産の *Encrinurus* cf. *similis* もこれとほぼ同時代のものである。

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836. SOME INOCERAMIDS (BIVALVIA) FROM THE CENOMANIAN (CRETACEOUS) OF JAPAN – II

THREE SPECIES FROM HOKKAIDO, WELL KNOWN ABROAD BUT HITHERTO UNDESCRIBED IN JAPAN

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Abstract. In our recent acquisitions from the Obira and northerly adjoining Kotanbetsu areas and also from the Oyubari area of Hokkaido there are following three species, which are well known abroad but hitherto undescribed in Japan: (1) *Inoceramus tenuis* Mantell; This is fairly common in the lower and middle parts of the Cenomanian in the Obira and adjacent areas. Our forms are mostly smaller than but otherwise similar to the holotype from England. (2) *Inoceramus gradilis* Pergament; A fine example, with both valves preserved, was obtained from the Middle Cenomanian bed with *Calycoceras* sp. of *newboldi* group in the Kotanbetsu area. Ten other specimens came from Member Mh (upper part of the Cenomanian) of the Obira area. This species was originally reported from the Koryak Range of the USSR and its distribution is now extended to Hokkaido. (3) *Inoceramus virgatus* Schlüter; This species is so variable that we include in it "*I. scalprum* Böhm" as a synonym, giving a revised diagnosis. Examples from Hokkaido occur in the middle to uppermost part of Member Mf of the Obira area, probably referable to the lower Middle Cenomanian; also in the Lower Cenomanian of the Oyubari area.

Introduction

The main purpose of this series of papers was written at the beginning of Part I (Matsumoto and Noda, 1986). Succeeding to the four species described in Part I, three species from the Cenomanian of Hokkaido are described in Part II. They are mainly based on the recent acquisitions by the Waseda University team of the students conducted by Hirano through field works in the southern part of the Oyubari area, central Hokkaido, and the northeastern part of the Obira area, northwestern Hokkaido.

The results of these field works have been reported preliminarily in Japanese by Hirano *et al.* (1981) and by Sekine *et al.* (1985) respectively, showing fossil localities in route maps. The official geological maps of the scale 1:50,000 are available for the two areas: *i.e.*, Nagao *et al.* (1954) for the Oyubari quadrangle, Tsushima *et al.* (1958) for the Tappu (pronounced Tap) and Igi *et al.* (1958) for the Horokanai quadrangles,

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the latter two of which cover the main part of the Obira area. The Cretaceous stratigraphy of the Obira area was described in detail by Tanaka (1963), whose lithostratigraphic subdivision is still available and cited in this paper. There is another work by Tanabe *et al.* (1977), with whom Matsumoto and Hirano cooperated.

Meanwhile, one of us (T.M.) was invited to Waseda University to study some of the collections there. Furthermore, selected specimens which T.M. examined at Kyushu University and Hokkaido University have been added to the material of this study. Their localities are in the Obira and Oyubari areas and also in the eastern part of the Kotanbetsu (Kotambets) area, *i.e.*, in the official geological map of the Soeushinai quadrangle (Hashimoto *et al.*, 1958) northerly adjacent to the Obira area. The fossil localities of the Kotambets area are precisely shown in a route map and stratigraphic column by Matsumoto and Okada (1973, text-figs. 7, 8).

While the Cretaceous researches are continued in Japan, one of us (A.A.) follows the predecessors in the palaeontology and biostratigraphy of the inoceramids. Some of Asai's collections from the northeastern part of the Obira area are added to the material of this study. Also selected specimens of K. Tanaka's collections from the Obira area have been examined by one of us (T.M.).

The repositories of the described or mentioned specimens are as follows with abbreviation in parentheses:

British Museum (Natural History) London (BM)
Geological Collections, Kyushu University, Fukuoka (GK)
Geological and Mineralogical Collections, Hokkaido University, Sapporo (GMH)
Geological Museum, Geological Survey of Japan, Tsukuba (GSJ)
Sedgwick Museum, Cambridge (SM)
Palaeontological Collections, School of Education, Waseda University, Tokyo (WE)

The locality numbers have the prefix Y for the Oyubari area, succeeding to those in Matsumoto (1942), Hirano *et al.* (1977) *etc*.; the prefix T (derived from Tappu) for the Obira area in the field works of Waseda University and the prefix R (derived from Rumoi district) for the Obira and adjacent areas in the field works conducted by Matsumoto. The prefix T has been used by Matsumoto since 1942 for the localities of the Saku-Abeshinai and contiguous areas in the northern Teshio Mountains. These T-numbers of Matsumoto appeared in Part I but are not cited in this part. Therefore there would be no confusion with the T-numbers of Waseda University. K. Tanaka's (1963) localities in the Obira area have prefix NH.

As to the subdivision of the Cenomanian Stage, we follow Kennedy (1986 *in* Reyment and Bengtson) for the definition of the Lower, Middle and Upper Cenomanian. The three substages have been defined on the ammonite zones in the type area (Sarthe in the Paris Basin) and can be extended to southern England and also to southeastern France. In certain sequences in Japan the correlatives of these substages are well recognized and in such cases the terms Lower, Middle and Upper Cenomanian are used in this paper. When the correlation is not so definitive, these terms are avoided and we may write, for instance, the lower part of the Cenomanian and so on. Even in the former cases, it is difficult to set precisely the positions of the stage or substage boundaries in our sequences. Although some species of the Inoceramidae may be useful for that problem, we do not intend to discuss the boundaries in this paper.

As to the abbreviated letters or symbols in the measurements, we follow those used in Part I. To avoid confusion we write in this paper BV, LV and RV for both valves, left valve and right valve. For brevity we may write int.m., ext.m., comp.int.m., *etc*. for the internal mould, external mould, composite internal mould and so on. The symbol $\sim$ at the beginning of the measured value means approximate or restored.

Systematic descriptions

Genus *Inoceramus* Sowerby, 1814

Type species:–*Inoceramus cuvierii* Sowerby, 1814.

Remarks:—Genus *Inoceramus* has been used in a broad sense, but currently *Mytiloides* Brongniart, 1822, *Sphenoceramus* Böhm, 1915 and *Birostrina* J. Sowerby, 1821 are excluded from it as independent genera. There are still a number of subgenera which are affiliated to the genus *Inoceramus* and how to treat them may be a problem. Such species as *I. lamarcki* Parkinson, *I. hobetsensis* Nagao et Matsumoto, *I. iburiensis* Nagao et Matsumoto and *I. teshioensis* Nagao et Matsumoto, all of Turonian age, are examples of *I.* (*Inoceramus*) in a strict sense.

For the Cenomanian species, however, little has been accomplished as to their taxonomy at generic or subgeneric level, aside from the nomenclatorially invalid or doubtful ones proposed by Heinz (1932, *etc.*). For instance, *I. crippsi* Mantell is a celebrated Cenomanian species, but according to Kauffman (personal communication to T.M. in a field excursion to a Cenomanian locality in England, 1981) this species may represent a genus independent of *Inoceramus*.

As we have not comprehensively studied numerous species from the Cenomanian of Europe and other oversea regions, we have to use *Inoceramus* in a fairly broad sense for the descriptions of species in this paper.

Inoceramus tenuis Mantell, 1822

Figures 1 – 3

1822. *Inoceramus tenuis* Mantell, p. 132.
1911. *Inoceramus tenuis* Mantell; Woods, p. 271, text-figs. 31–32 (non pl. 48, fig. 1).
1928. *Inoceramus tenuis* Mantell; Heinz, p. 60, pl. 4, fig. 2.
1959. *Inoceramus tenuis* Mantell; Dietze, p. 858, pl. 1, figs. 3–4.
1966. *Inoceramus tenuis* Mantell; Pergament, p. 44, pl. 23, figs. 3–4; pl. 24, figs. 1–4.
1967. *Inoceramus tenuis* Mantell; Tröger, p. 33, pl. 1, fig. 8.
1982. *Inoceramus tenuis* Mantell; Keller, p. 59, pl. 2, fig. 2.

Holotype:—BM. No. 5890 (figured by Woods, 1911, text-figs. 31–32), from the Chalk Marl of Hamsey, which one of us (T.M.) once examined at British Museum (Nat. Hist.).

Material:—WE. P014T (Figs. 1-1a–e) (int.m. of BV, with inner shell layer partly preserved) collected by A. Takagi, H. Sekine, K. Hattori and H. Hirano at loc. T5201a83, the Kanajiri-zawa; WE. P011T (comp. int.m. of LV: Figs. 1-2a–c, and comp. int.m. of deficient RV: Fig. 1-3) and WE. P012T (Figs. 1-4a–b) (int.m. of LV, partly with inner shell layer) collected by A. Asai at loc. T6238b84 of the Jiro-zawa; all Member Mf (defined by Tanaka, 1963) of the Obira area. WE. P019T (Figs. 2-3a–c) (int.m. of BV) and five others (1BV, 3LV and 1RV) collected by A. Asai at loc. T5222b84 of the Kanajiri-zawa, Member Me (or possibly Md), Obira area. One of us (T.M.) examined also K. Tanaka's Collections from the Obira area, now kept in the Museum of the Geological Survey of Japan, with register numbers GSJ.F8215 (LV) from loc. NH210 and GSJ.F8216 (BV, int. and ext.m.) from loc. NH617, upper reaches of the River Obirashibe; GSJ.F8217 (LV and immature RV) from loc. NH419, Kaba-no-sawa and GSJ.F8218 (3LV, immature BV and RV) from loc. NH554 all in nodules of limonitic tint, upper part of Member Mf which contains *Calycoceras orientale* Matsumoto, Saito et Fukada.

GK.H10083 (Figs. 2-1a–c) (comp. int.m. of

→ **Figure 1.** *Inoceramus tenuis* Mantell Page 148

1a–e: WE. P014T (BV) from loc. T5201a83, upper part of Member Mf, Obira area (Coll. A. Takagi and others); right lateral (a), left lateral (b, c), anterior (d), and umbonal (e) views; 1c x2, others x1.5. Scale bar = 10 mm.

2a–c: WE. P011T (LV) from loc. T6238b84, Member Mf, Obira area (Coll. A. Asai); lateral (a), anterior (b) and posterior (c) views; x1.

3: WE. P011T (RV, deficient int.m. of the same individual as above LV) from loc. T6238b84 (Coll. A. Asai); x0.9. Scale bar = 10 mm.

4a–b: WE. P012T (LV) from loc. T6238b84 (Coll. A. Asai); lateral (a) and anterior (b) views; x1.

5: WE. P013Y (LV, with damaged apex of beak) from loc. 2YC7045a79, Member M2, Oyubari area (Coll. R. Morita); lateral view; x1.

Photos by courtesy of Dr. M. Noda, except 1c, 2c by A. Asai.


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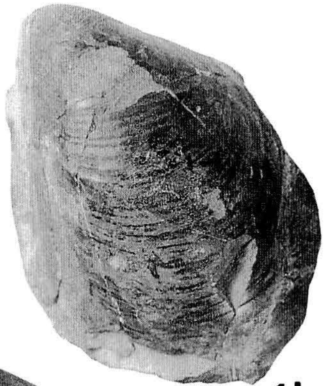
1d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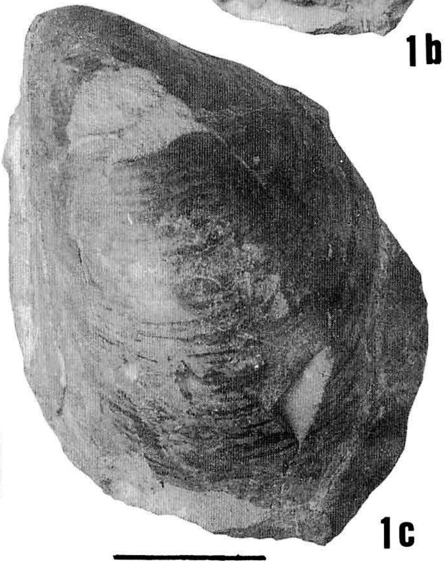
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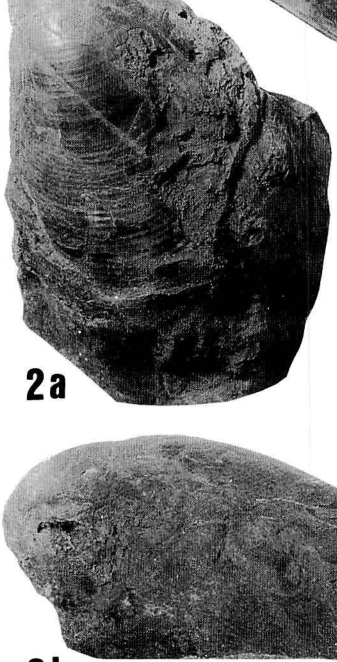
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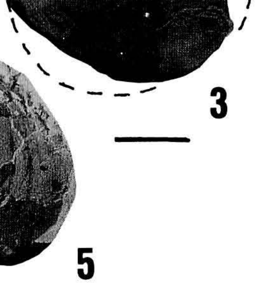
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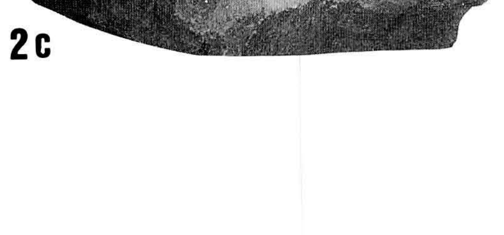
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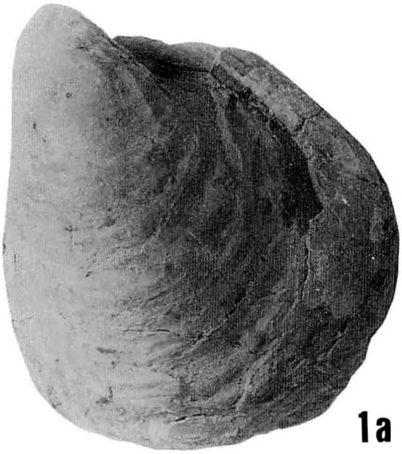

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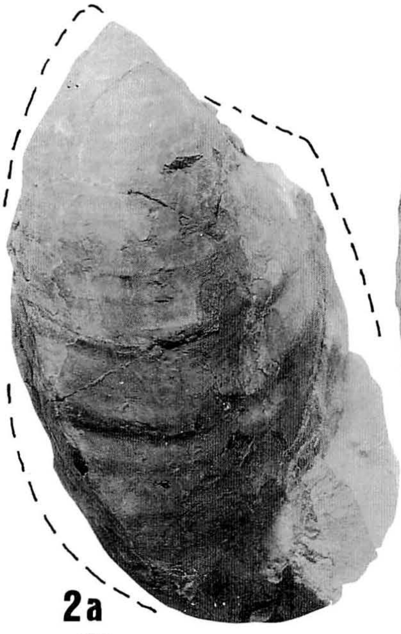

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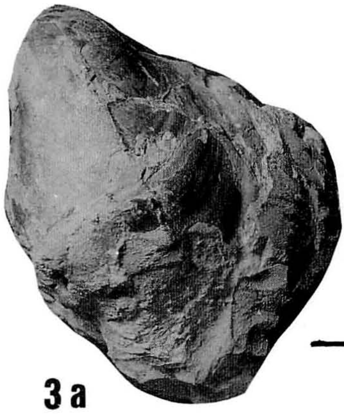

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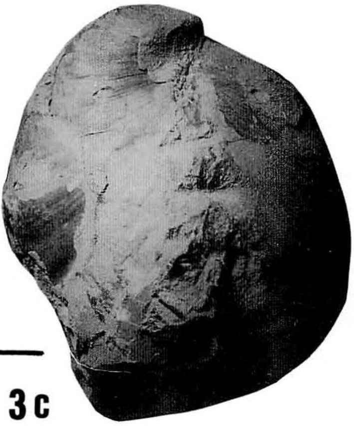

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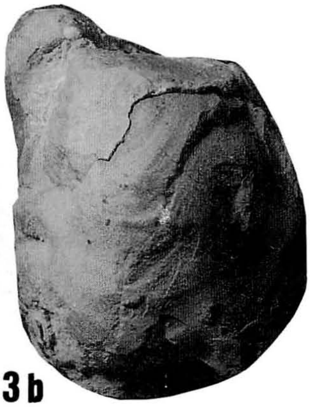


3b

LV) and GK.H10165 (Figs. 2-2a–c) (BV, comp. int.m.) collected by T. Matsumoto and H. Okada at loc. R100, 800 m west of the Kiritachi Pass (see Matsumoto and Okada, 1973), from nodules of limonitic tint in a mudstone member which contains *Calycoceras* of the *newboldi* group.

WE.P013Y (Fig. 1-5) (LV, lacking the apex of beak, int.m. partly with test) collected by R. Morita at loc. 2YC7045a79, Kaneo-betsu, Member M2 of the Oyubari area (see Hirano *et al.*, 1981).

Diagnosis:—Shell rather small, inequivalve and obliquely suboval in outline, with the axis of growth nearly straight or gently concave forward.

Left valve moderately convex, with prominent and incurved umbo; right valve gently convex. Postero-dorsal part compressed. H larger than L, as examplified by the holotype in which L/H = 0.69 (LV) and 0.72 (RV); hinge line varied in length from 1/2 to 2/3 in s/L.

Anterior marginal part straight and nearly perpendicular to the plane of valve, but antero-dorsal part somewhat excavated; ventral margin asymmetrically rounded, becoming more convex with growth; posterior margin gently arcuate in passing from the ventral margin and then becoming nearly straight, forming an obtuse angle with the hinge-line.

Surface ornamented with fine concentric lirae or rings, but incipient major concentric undulations may appear in some individuals.

Measurements:—See Table 1.

Observation:—The holotype from the Chalk Marl of Hamsey, a classic locality in Sussex, England (see Wright and Kennedy, 1984, p. 9), is well preserved and the description by Woods (1911, p. 271) is clear. Its dimensions, which were omitted by Woods and measured by one of us (T.M.), are shown in this paper (Table 1). The length of the hinge line in the holotype is actually shorter than what Woods mentioned: "about two-thirds of the height of the shell". The hinge line in some specimens from Hokkaido is nearly two-thirds of the length of the shell. The ratio s/l seems to vary with growth as well as between individuals.

SM.B42106 from the "Red Limestone" near Louth, England, which was illustrated by Woods (1911, pl. 18, fig. 1) under *I. tenuis*, is not in our opinion the named species, because it has a subrounded–subquadrate outline, more evenly rounded ventral margin, longer hinge line and

Table 1. Measurements of selected specimens of *I. tenuis*.

Specimen	Val.	h	l	l/h	H	L	L/H	b	b/h	s	s/l	s/L	α	β	γ	δ
Holotype	LV	97.0	76.0	.78	103.0	71.0	.69	34.0	.35	–	–	–	–	60°		
	RV	87.5	76.0	.87	99.0	71.0	.72	25.0	.29	35.0	.46	.49	100°	–	140°	54°
WE.P011T	LV	–	–	–	~61.5	~41	.67	~17	–	–	–	–	~90°	54°		
	RV	~50	~37	.74	~51.5	~35	.68	~12	.24	~19	.51	.54	~90°	–	~140°	55°
WE.P013Y	LV	33.0	25.5	.77	39.0	28.0	.72	~11	.33	~18	.71	.64				
WE.P014T	LV	36.0	26.7	.74	42.0	28.0	.67	12.0	.33	17.2	.64	.67	–	60°	130°	54°
	RV	29.3	24.5	.83	38.0	26.0	.68	9.3	.32	16.5	.67	.67	90°	–	130°	54°
GK.H10083	LV	57.0	44.0	.77	62.5	43.0	.69	27.3	.48	28.2	.69	.63	–	57°	130°	57°
GK.H10165	LV	–	–	–	~86	~58	.67	~30								

← **Figure 2.** *Inoceramus tenuis* Mantell Page 148

1a–c: GK. H10083 (LV, comp. int.m.) from loc. R100, 800 m west of the Kiritachi Pass on Highway 239 from Soeushinai to Kotanbetsu (Coll. T. Matsumoto and H. Okada); lateral (a), anterior (b) and dorsal (c) views; x1.

2a–c: GK. H10165 (BV, int.m. with deficient apex of beak) from loc. R100 (same as above); left (a) and right (b) lateral and posterior (c) views; x1.

3a–c: WE. P019T (BV, int.m.) from loc. T5222b84, Kanajiri-zawa, Member Me (possibly Md), Obira area (Coll. A. Asai); x1.2. Scale bar = 10 mm.

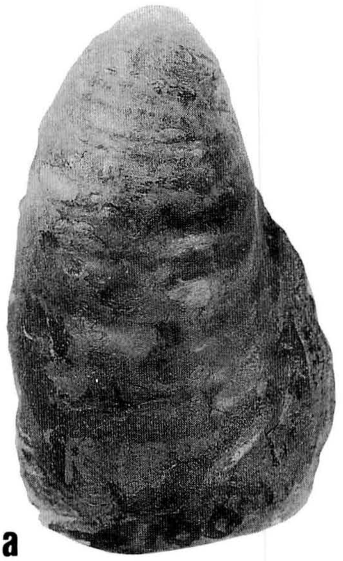
Photos by courtesy of Dr. M. Noda.

denser lirae on the shell surface as compared with the holotype and other examples.

The specimens from Hokkaido are mostly smaller than the holotype and their concentric rings are proportionally finer. Those from Germany (Tröger, 1967; Keller, 1982) and the Pacific side of the USSR (Pergament, 1966) are also more or less smaller than the holotype. In other words, the holotype from England may represent a specially well grown individual. GH.H10165 (Fig. 2-2) in our material is exceptionally large, being closer in size to the holotype. Its concentric lirae or rings are as coarse as those of the holotype, and moreover it has incipient concentric major undulations. One of the specimens illustrated by Pergament (1966, pl. 24, fig. 3) is similar to GK.H10165 in these respects.

Figure 3. *Inoceramus tenuis* Mantell Page 148
A number of specimens embedded in a nodule from the upper part of Member Mf at loc. T5201a83 (Coll. A. Takagi and others) (see also Fig. 1-1). Scale bar = 10 mm. Photo by courtesy of Dr. M. Noda.

→ **Figure 4.** *Inoceramus gradilis* Pergament Page 155
1a–d: GK. H10163 from loc. R100 on Highway 239 (Coll. T. Matsumoto and H. Okada); left (a) and right (b) lateral, posterior (c) and anterior (d) views of BV.
2a, b: WE. P008T from loc. T5017e83, Kanajiri-zawa (Coll. A. Takagi and others); LV, RV and another RV(?) embedded with overlapping, in two views (a, b).
3a–c: WE. P016T from loc. T6051h84, on the main course of the River Obirashibe (Coll. S. Ago and others); two lateral (a, b) and anterior (c) views of LV. 1, 2 are natural size; 3 slightly enlarged. Scale bar = 10 mm. Photos by courtesy of Dr. M. Noda, without whitening.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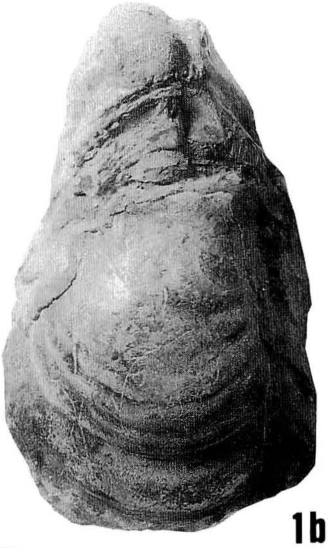
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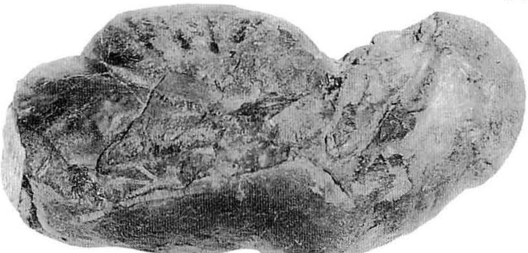
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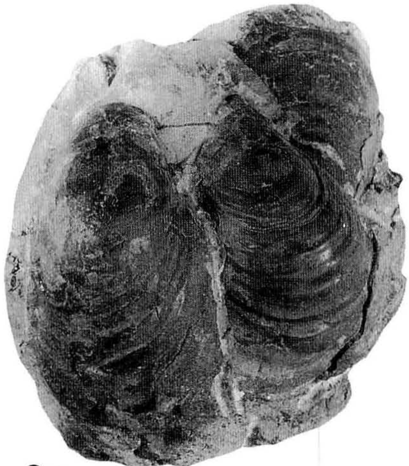
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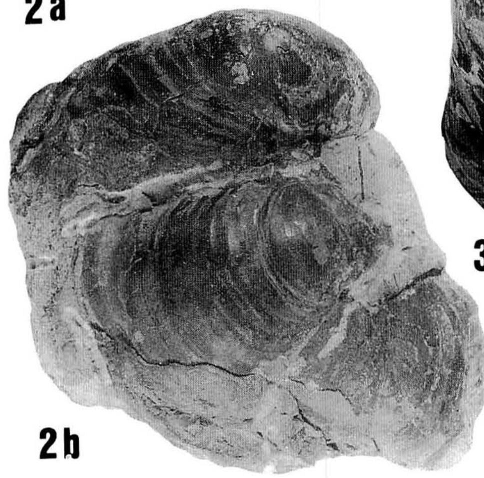
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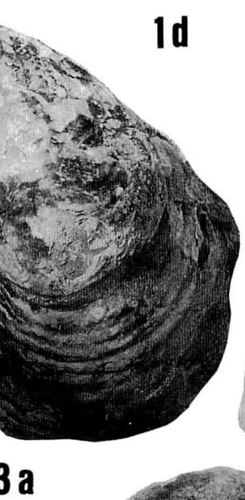
3a


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3c


1b


1a


2b


3b

3a


2a


4a


4b


4c


4d

Comparison:—As Woods (1911, P. 272) has already stated, this species resembles *Birostrina concentrica* (Perkinson) but has less prominent umbo of the left valve, higher value of l/h or L/H and less prominent concentric rings. Kauffman (1978, p. iv-4) foretells briefly that there are transitional forms between *I. tenuis* and "the *Birostrina concentrica* lineage", but places *I. tenuis* in the subgenus *I.* (*Inoceramus*) instead of *Birostrina*. *I.* (*Inoceramus*) should have less incurved and less prominent umbo of the left valve, longer hinge line with broader postero-dorsal flattened wing-like area and more distinctly developed major ribs, as compared with *Birostrina*. In these respects this species is not a typical member of *I.* (*Inoceramus*). It may be situated at a transitional position between *Birostrina* and *Inoceramus*, or it may be rather closer to typical species of *Birostrina* than to that of *I.* (*Inoceramus*).

For the time being, we follow Kauffman to refer this species to *Inoceramus*, awaiting the issue of the Kauffman's descriptions of the Cenomanian inoceramid species from England in further details.

Birostrina nipponica (Nagao et Matsumoto, 1939) in a revised sense (see Pergament, 1966, p. 32) has a narrower and more incurved umbo of the left valve than the left umbo of *I. tenuis*. It has a smaller value of L/H and shorter hinge line than those of the latter. Its axis of growth is somewhat sinuous. In some of previously published papers *I. tenuis* and certain other species were misidentified with *I. nipponicus* and a restudy of the so-called *I. nipponicus* is necessary.

Occurrence:—According to Kauffman (1978), who studied the British inoceramids with the framework of the ammonite zonation by Kennedy (1971), *I. tenuis* occurs characteristically in the Zone of *Neostringoceras carcitanense* (lower part of the Lower Cenomanian) and ranges upward to the Zone of *Turrilites acutus* (middle part of the Middle Cenomanian). Keller (1982) records the range of *I. tenuis* as Lower Cenomanian to lower Middle Cenomanian in the sequence of Germany.

On the basis of the specimens examined by us, the range of *I. tenuis* is from Member Me (or possibly upper Md) to Member Mf (of Tanaka, 1963) in the sequence of the Obira area. This is in harmony with the range in England and Germany, but the most characteristic occurrence is in the upper part of Mf. The GK specimens of loc. R100 on the Soeushinai – Kotanbetsu route (Highway 239) came from the fossiliferous zone with *Calycoceras* of *newboldi* group, which is somewhat higher than upper Mf of the Obira area. This zone may be referred to upper part of the Middle Cenomanian, whereas *N. carcitanense* was obtained at loc. R81 of the same route well below loc. R100 (see Matsumoto and Okada, 1973, figs. 7, 8).

The material from the Oyubari area is insufficient to tell the range and abundance of this species. A single available specimen came from Member M2 (Hirano *et al.*, 1981), which is probably referred to the lower part of Cenomanian.

Inoceramus gradilis Pergament, 1966

Figures 4, 5

1940. *Inoceramus corpulentus* McLearn var. a; Warren and Stelck, p. 148, pl. 4, figs. 4–6.
1966. *Inoceramus gradilis* Pergament, p. 49, pl. 29, figs. 2–5; pl. 31, figs. 1–2; pl. 32, fig. 1.

Holotype:—The specimen designated by Pergament (1966, p. 49, pl. 32, fig. 1) (no. 8-3580-74 in the text and no. 8-3580-75 in the explanation

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← **Figure 5.** *Inoceramus gradilis* Pergament Page 155
1a, b: WE. P015T (LV) from loc. T5017e83, Kanajiri-zawa (Coll. A. Takagi and others); lateral (a) and posterior (b) views.
2a, b: WE. P007T (LV) from loc. T5016a83 (Coll. A. Takagi and others); lateral (a) and anterior (b) views, x1.2.
3a, b: WE. P017T (BV) from loc. T5017e83 (Coll. A. Takagi and others); left (a) and right (b) lateral views.
4a–d: WE. P018T (BV) from loc. T5019m83 (Coll. A. Takagi and others); left (a) and right (b) lateral, anterior (c) and umbonal (d) views.
All figures natural size, except 2a, b. Scale bar = 10 mm. Photos by courtesy of Dr. M. Noda.

of plate, of which the latter may be misprinted), from the Cenomanian on the bay of Ugol'naya at the north end of the Koryak Mountains.

Material:—At least twelve specimens from Hokkaido, some of which consist of slightly displaced left and right valves of the same individual. GK. H10163 (Fig. 4-1) (BV, int.m., with test remaining in the hinge and antero-dorsal part, of which RV somewhat displaced towards the venter and its last portion is not preserved) collected by T. M. with H. Okada in 1967 from loc. R100, 800 m west of the Kiritachi Pass on Highway 239 between Soeushinai and Kotanbetsu; WE. P007T (Fig. 5-2) (LV, int.m., with test remaining in the anterior marginal part) from loc. T5016a83; WE. P008Ta, b, c (Fig. 4-2) (LV and two RV, int.m., with weathered test attaching on the umbonal part of a and b, and anterior part of a and antero-vental portion of b); WE. P015T (Fig. 5-1) (LV, int.m., with weathered test on the umbonal and anterior marginal parts); WE. P017T (Fig. 5-3) (LV, int.m., somewhat damaged at the beak and in the antero-ventral part; also young part of RV, int.m., with test on the umbonal part) from loc. T5017e83; WE. P018T (Fig. 5-4) (LV, int.m., with test on a portion of the umbonal part and RV of the same individual, int.m., with test on the postero-dorsal portion) from loc. T5019m83; all of the above seven collected by a field-work team of A. Takagi, H. Sekine, K. Hattori and H. Hirano from the outcrops of Member Mh on the Kanajiri-zawa, a tributary to the River Obirashibe, Obira area (Tappu quadrangle); WE. P016T (Fig. 4-3) (LV, with inner shell layer remaining on the major part) collected by S. Ago, Y. Tanaka and A. Matsuzawa at loc. T6051h84 from the outcrop of Member Mh on the main course of the River Obirashibe, Tappu quadrangle, Obira area.

Diagnosis (translated from Pergament, 1966 with some revision):—Shell small to medium-sized, markedly inequivalve, inequilateral and higher than long (H > L); left valve highly convex with incurved umbo, showing stepwise changes of convexity from the beak to the ventral margin with accompanied constrictions; right valve less convex than the left but constricted at periodic intervals.

Fine concentric lirae or rings on the young part up to the first constriction; fairly crowded concentric subcostae and/or ribs in the middle stage; major concentric ribs develop in the late growth-stage; sometimes ribs may be bifurcated or intercalated, giving rise to somewhat irregular aspect in ribbing.

Measurements:—See Table 2.

Observation:—The specimens from Hokkaido listed above (in *Material*) show clearly the diag-

Table 2. Measurements of selected specimens of *I. gradilis*.

Specimen	Val.	H1	L1	H2	L2	b1	b2	s1	s2	L1/H1	L2/H2	b1/L1	b2/L2	s2/L2
GK.H10163	LV	~24	22.0	45.0	30.3	15.5	~22	–	23.0	.91	.69	.70	.73	.75
	RV	23.6	20.4	39.7	34.2	–	–	–	–	.86	.86	(sec. comp.)		
WE.P008Ta	LV	–	–	50.5	28.0	12.5	17.5							
b	RV	–	–	41.0	27.5	–	~12							
WE.P015T	LV	22.8	16.0	37.4	24.5	~11	–	–	–	.70	.65	.69		
WE.P016T	LV	31.0	21.0	49.0	≥33.5	14.0	~20	–	–	.68	>.68	.67	≥.60	
													$\beta = 50°$	
WE.P017T	LV	33.2	25.0	~75	~35	19.5	–	–	–	.75	.47	.70		
(sec. def.)	RV	23.0	16.0	–	–	–	–	~10	13.6	–	–	–	–	.52
				h=33.4		l=26.0				l/h=.78			$\alpha = \sim 90°$	
WE.P018T	LV	22.6	17.0	47.0	37.4	~12	–	–	–	.75	.79	.70		
	RV	21.8	17.0	37.5	30.5	–	–	–	–	.78	.81			

H1, L1, b1, s1 : measured at the first constriction
H2, etc. : measured at the second constriction

nostic characters of *I. gradilis.* GK. H10163 (Figs. 4-1a–d) is very good in showing the left and right valves of one and the same individual and also a part of the hinge plate and thus supplements the holotype from the Koryak.

Our specimens are small or medium-sized like the holotype and certain other examples illustrated by Pergament (1966, pl. 28, figs. 2-5; pl. 32, fig. 1) but we have not yet obtained somewhat larger forms like those of Pergament (1966, pl. 31, figs. 1-2)

The axis of growth extends obliquely to the postero-ventral extremity in reference to the hinge line, which is often concealed in the left valve by the inflated and incurved umbonal part but can be seen inside the left valve of GK. H10163 as well as on the dorsal margin of right valve.

The abrupt change in the convexity from the beak to the ventral margin with accompanied constriction occurs in the left valve at least twice during the growth. We can recognize the corresponding constrictions on the right valve, although sometimes they may not be so well marked as those on the left valve. The dimensions at the 1st and 2nd constrictions are shown with H1, L1 etc. and H2, L2 *etc*. (see Table 2). Because of the umbonal convexity or inflation, the ratio b1/L1 is fairly large (0.65–0.70).

Comparison:–*Inoceramus corpulentus* McLearn (1926, p. 123, pl. 21, figs. 5–7) from the Smoky River Formation of Alberta, Canada is higher than long and much convex along the axis of growth, and has nearly vertical, high anterior marginal part. The plaster cast of its holotype, kindly sent by Dr. J. A. Jeletzky from the Geological Survey of Canada to Kyushu University (GK. H9624), shows that it is evenly convex and does not show such abrupt changes as those in *I. gradilis.* It is ornamented with fine concentric lirae (nearly smooth on the int.m.) in the young stage, then weak concentric subcostae and weak to moderate concentric ribs combined with concentric rings in the late stage. Despite its small size there is a postero-dorsal flattened area. It is described as nearly equivalve. We agree with McLearn in regarding *I. corpulentus* as allied to *I. apicalis* Woods, 1912. These two species are Turonian in age.

Taking all the above facts into consideration, we regard the similarity of *I. gradilis* to *I. corpulentus* as superficial. There is no phylogenetic affinity between them.

The form described under *I. corpulentus* var. a by Warren and Stelck (1940, p. 148, pl. 4, figs. 5-6; 4?) from the Dunvegan Formation (Cenomanian) of Alberta, Canada looks very similar to the left valve of *I. gradilis*, although it is smaller than any of the specimens as described above.

Occurrence:–A well preserved (BV) example of this species was obtained from the outcrop of mudstone at loc. R100 immediately after the construction of Highway 239. At the same locality *I. tenuis* and *Calycoceras* aff. *C. asiaticum*, i.e. *C.* of the *newboldi* group, were obtained among others. Hence the age of this mudstone is Middle Cenomanian.

This species has been obtained not infrequently at the four localities in the Obira area, *i.e.* locs. T5016a83, T5017e83, T5019m83 and T6051h84 of Sekine *et al.* (1985), from the mudstone of Member Mh of Tanaka (1963), which is probably referred to the upper part of the Cenomanian. The occurrence of both valves, with only slight displacement is noteworthy.

Inoceramus virgatus Schlüter, 1877

Figures 6–8

1836. *Inoceramus lamarcki* Sowerby; Goldfuss, p. 114, pl. 111, fig. 2.
1842. *Inoceramus laevigatus* Leymerie, p. 9, pl. 10, fig. 4.
1877. *Inoceramus virgatus* Schlüter, p. 257.
1911. *Inoceramus etheridgei* Woods, p. 278, pl. 49, figs. 2–4.
1914. *Inoceramus scalprum* Böhm, p. 599.
1959. *Inoceramus scalprum* Böhm, Moskvin, p. 142, pl. 1, fig. 4.
1966. *Inoceramus scalprum* Böhn, Pergament, p. 46, pl. 25, figs. 1–4.
1967. *Inoceramus virgatus* Schlüter; Tröger, p. 29, pl. 1, figs. 1–7.
1978. *Inoceramus virgatus* Schlüter; Sornay, p. 510, pl. 2, fig. 4.
1978. *Inoceramus virgatus scalprum* Böhm; Sornay, p. 509, pl. 2, figs. 2, 5.

1982. *Inoceramus virgatus virgatus* Schlüter; Keller, p. 51, pl. 1, fig. 1.

1982. *Inoceramus virgatus scalprum* Böhm; Keller, p. 54, pl. 1, fig. 2.

1985. *Inoceramus virgatus virgatus* Schlüter; Kaplan, Keller and Wiedmann, pl. 8, figs. 3, 4.

Types:—The holotype of *I. virgatus* Schlüter, 1877 is the specimen illustrated by Goldfuss (1836, pl. 111, fig. 2) from Lower Saxony of Germany. None of us has examined the original specimen and we depend on a photograph by Sornay (1978, pl. 2, fig. 4). The holotype of *I. scalprum* Böhm, 1914 is one of the syntypes of *I. etheridgei* Woods (1911, p. 278, pl. 49, fig. 3) (SM. B297) from the Totternhoe Stone (Zone of *Holaster subglobosus*) of Burwell, England. It is a left valve, whereas the topotype (another syntype) illustrated by Woods (1911, pl. 49, fig. 4) is a right valve. One of us (T. M.) once studied them at Sedgwick Museum, Cambridge.

Material:—WE. P005T (Fig. 6) (comp.int.m. of BV, with test attached in a portion) and WE. P006T (Fig. 7-2) (int.m. of RV, with test remaining in the postero-dorsal part) from Member Mf at loc. T5112e83, the Korinto (Corinth)-zawa, a branch of the Kanajiri-zawa; WE. P003T (Fig. 8-1) (comp. int.m. of RV) from the uppermost part of Member Mf at loc. T5051a83 and WE.

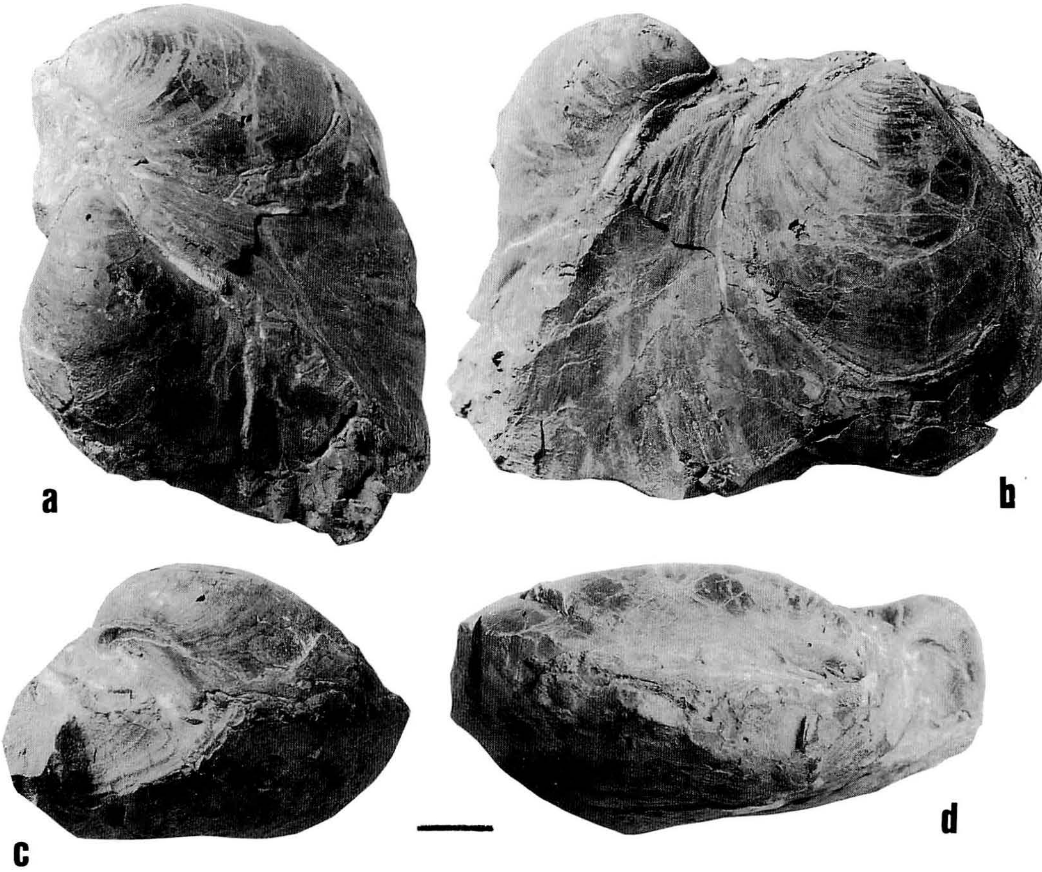

Figure 6. *Inoceramus virgatus* Schlüter Page 157

a–d: WE. P005T (BV) from loc. T5112e83, Korinto-zawa, the uppermost part of Member Mf, Obira area (Coll. A. Takagi and others); lateral view of deficient LV (a) with oblique view of RV, lateral view of RV (b), anterior view of LV (c), anterior view of RV (d) with umbonal part of LV; All figures natural size. Scale bar = 10 mm. Photos by courtesy of Dr. M. Noda.

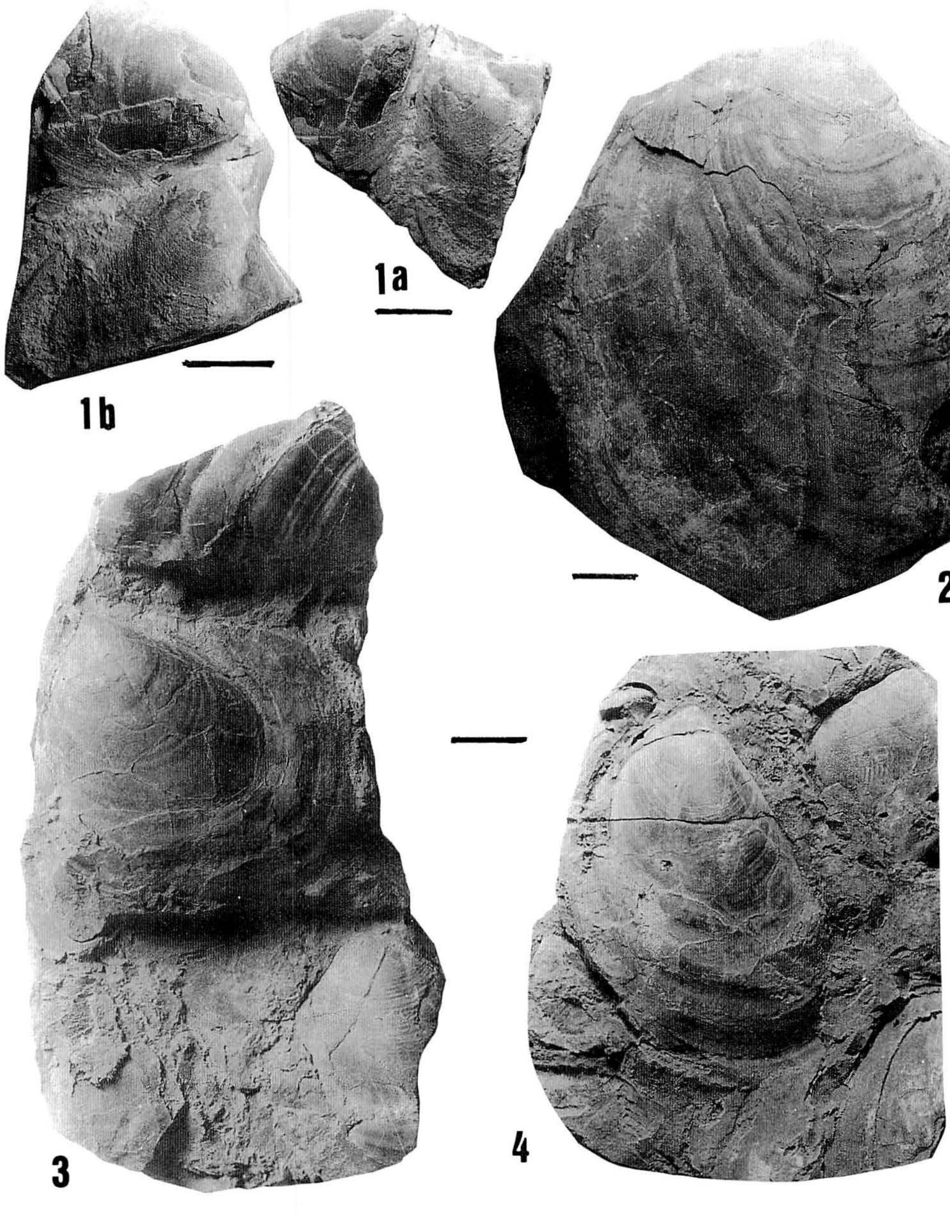

Figure 7. *Inoceramus virgatus* Schlüter Page 157
1a–b: WE. P004T (BV) from loc. T5051c83, the uppermost part of Member Mf, Kanajiri-zawa, Obira area (Coll. A. Takagi and others); a × 1, b × 1.2.
2: WE. P006T (RV) from loc. T5112e83, Korinto-zawa, the uppermost part of Member Mf, Obira area (Coll. A. Takagi and others); ×0.8.
3: WE. P010T (LV) and 4: WE. P009T (RV), both from loc. T6238b84, Jiro-zawa, Member Mf, Obira area (Coll. A. Asai); ×1.
Scale bar = 10 mm. Photos by courtesy of Dr. M. Noda.

P004T (Fig. 7-1) (comp. int.m. of RV, with inner shell layer partly attached) from the same horizon at loc. T5051c83; all the four collected by A. Takagi, H. Sekine, K. Hattori and H. Hirano. WE. P009T (Fig. 7-4) (comp.int.m. of RV) and WE. P010T (Fig. 7-3) (comp. int.m. of LV) collected by A. Asai at loc. T6238b84, the Jiro-zawa, a branch of the River Obirashibe. All the above occurred in the Obira area. GMH. 7247 (Fig. 8-2) (LV, comp.int.m., with test on anterior marginal part) from near the contact with serpentine in the upper reaches of the Hakkin-zawa, Oyubari area.

Diagnosis:—Shell slightly inequivalve, somewhat inequilateral, gently to moderately convex in the main part of the valve and compressed in the postero-dorsal part; the left valve slightly more convex than the right; umbones terminal, and the left umbo slightly curved inward and forward.

Outline of shell broadly suboval or subcircular; height being somewhat greater or nearly as great as length. Hinge line of moderate length on the average, forming an angle of 55° to 65° with the axis of growth, which is nearly straight in the young stage or throughout growth but may sometimes be curved gradually forward or backward in the late stage. Antero-dorsal part nearly perpendicular to the plane of the valves, sometimes concave near the umbo; anterior margin nearly straight; ventral margin fairly convex or nearly semi-circular, passing to gently arcuate posterior margin which forms an obtuse angle with the hinge line.

Surface of shell ornamented with very fine and dense concentric lirae and faintly perceptible major concentric undulations, sometimes with subcostae or weak ribs on the summits of the undulations. Delicate radial lines or striae often discernible on the internal mould, being probably impressions of the internal structure.

Measurements:—See Table 3.

Observation:—This species is fairly variable and we agree with Sornay (1978) who has pointed out that *I. scalprum* Böhm, 1914 (= *I. etheridgei* Woods, 1911) is not separable from *I. virgatus* Schlüter as an independent species. Sornay interpreted them as geographical subspecies, because the former is dominant in England and France and the latter is so in Germany. Keller (1982) followed Sornay in the subspecific nomenclature, *I. virgatus virgatus* and *I. virgatus scalprum*, but examples of the two forms occur abundantly in the same area of Germany. According to him the two "subspecies" are worldwide in the Lower Cenomanian and lower part of the Middle Cenomanian. The coexistence of the two subspecies in the same age of the same province with similar abundance is biologically peculiar. Should the two forms show constantly the differences as tabulated by Keller (1982, p. 57, table 1), it would be better to separate them as distinct species.

We have examined the specimens from Hokkaido and also illustrations of the specimens from oversea areas, with the result that this

Table 3. Measurements of selected specimens of *I. virgatus*.

Specimen	Val.	h	l	l/h	H	L	L/H	b	b/h	s	s/l	s/L	α	β	γ	δ
WE.P003T	RV	~48	~42	.88	~54	~41	.76	–	–	~28	.67	.68	~90°	–	130°	60°
WE.P004T	LV	~26	~22	.85	~28	~24	.86	10.0	.38	~17	.77	.71	–	65°	123°	55°
	RV	~26	~24	.92	~30.5	~26	.85	5.0	.19	~17.5	.73	.67	~90°	–	123°	55°
WE.P005T	LV	33.0	28.5	.86	40.0	28.4	.71	14.0	–	21.0	.74	.74				
	RV	54.8	43.2	.79	56.5	43.4	.77	13.5	.25	23.7	.55	.55	105°	–	140°	65°
	RV	92.0	77.0	.84	99.0	78.0	.79	–	–	37.0	.48	.47	105°	–	130°	63°
WE.P006T	RV	(distorted)			~96	~80	.83	–	–	38.0	–	.47				
WE.P009T	RV	(distorted)			~50	~32	.64	–	–	23.5	–	.73				
WE.P010T	LV	(distorted)			~44	~41.5	.94	–	–	27.5	–	.66	~100°	77°		
GMH.7247	LV	75.0	70.0	.93	87.0	72.0	.83	–	–	50.0	.71	.69	105°	–	120°	55°
SM.B297	LV	58.2	51.4	.88	59.0	55.0	.93	~17	.29	~27	.53	.49	110°	90°	≥130°	~70°

species is so variable that it is not always subdivided into two forms. In other words, "*I. virgatus scalprum*" is merely one of varieties. For example, WE. P009T is higher than long (H > L) but its axis of growth is concave to the anterior. WE. P010T, among many others, from the same locality as WE. P009T, is as high as long (H = L) but its axis of growth is somewhat convex to the anterior. As Sornay has stated, the mode of preservation, such as the presence or absence of the test or the effect of secondary deformation, may give apparently different aspects. Therefore, we should continue to examine more examples. In this paper we call this species *I. virgatus* in a comprehensive concept.

The examined specimens from Hokkaido and

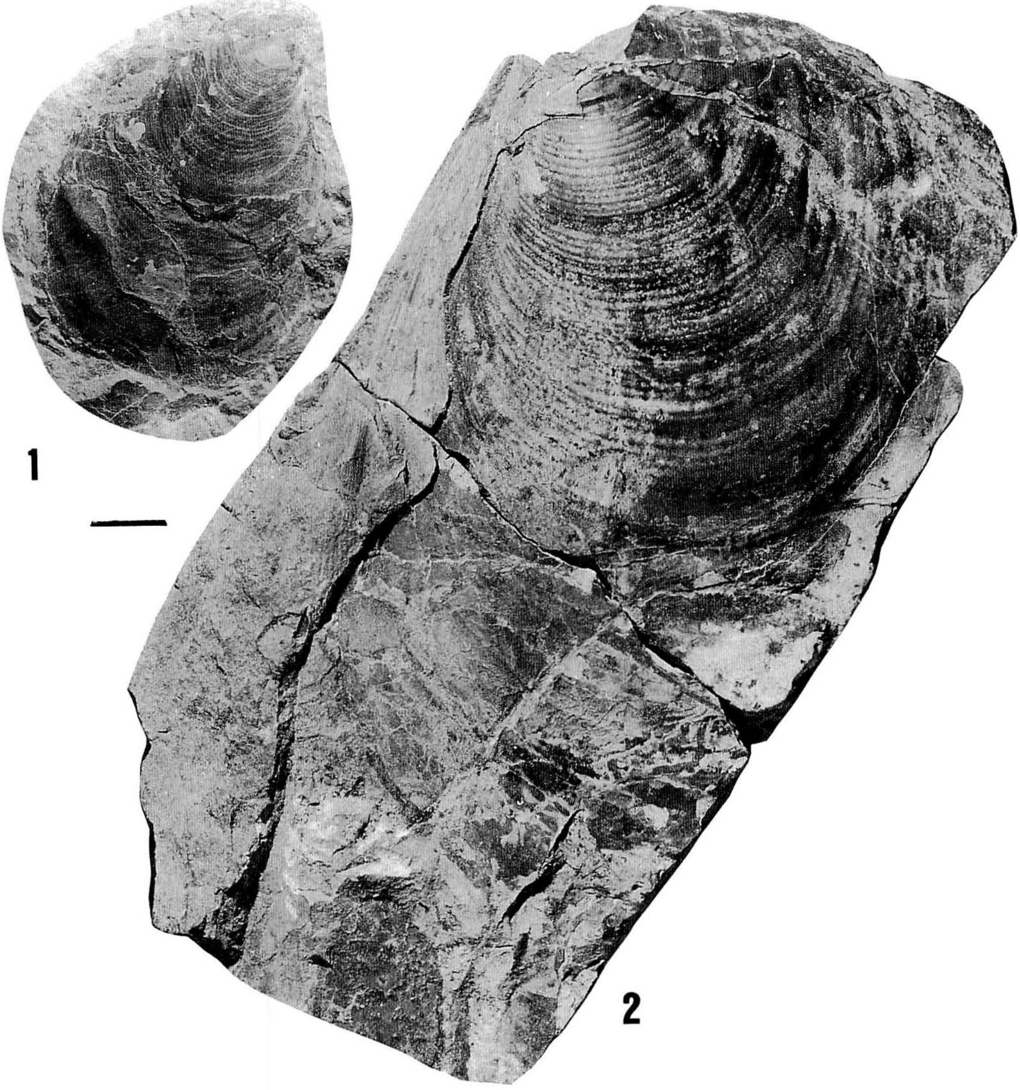

Figure 8. *Inoceramus virgatus* Schlüter

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1: WE. P003T (RV) from loc. T5051a83, same as for Fig. 7-1; × 1.
2: GMH. 7247 from the Hakkin-zawa near the contact with serpentinite, Oyubari area; × 1. Scale bar = 10 mm.
Photos by courtesy of Dr. M. Noda.

the hitherto illustrated ones from Europe, Central Asia and the Pacific province of the USSR are mostly medium sized. GMH. 7247 from the Oyubari area is much larger than them, but essentially similar to them in other characters. It is provisionally included in this species, but we reserve a possibility that it could be an allied but different species.

Comparison:—The affinity of this species is problematic. In the outline and gentle convexity of the valve, this species is somewhat similar to *I. atlanticus* (Heinz, 1936), but the latter has regular concentric ribs in addition to the dense and fine lirae, as seen in the lectotype, BM. L1038 (= *I. crippsi* var. *reachensis* Woods, 1911, pl. 49, fig. 1), and also Gueranger's specimen (Sornay, 1978, pl. 1, fig. 4). *I. anglicus* Woods, 1911 (p. 264, pl. 45, figs. 8–10, text-fig. 29) from the Upper Albian and basal Cenomanian of England, Germany and various regions of the world, is also similar to *I. atlanticus* and *I. virgatus* in shell-form, but has fairly crowded, narrow but distinct and regular concentric ribs. Only on the shell surface of its young stage the dense and fine lirae are discernible.

The group represented by these species (and probably also *I. crippsi* Mantell, 1822) is not the subgenus *I.* (*Inoceramus*) of the strict sense. In this paper it is provisionally referred to *Inoceramus* of a broad sense. The shell and hinge structure have yet to be investigated carefully.

Occurrence:—According to Keller (1982), this species ranges from the upper Lower Cenomanian to the middle of Middle Cenomanian and is distributed world-wide.

In Hokkaido the examined specimens from the Obira area range stratigraphically from the middle to the uppermost part of Member Mf of Tanaka (1963). This is probably within the range concluded by Keller, because *Turrilites acutus* Passy occurs in the overlying Member Mg. The large specimen from the Hakkin-zawa of the Oyubari area may have come somewhere in the sequence from the Lower Cenomanian *Sharpeiceras* bearing bed to the Middle Cenomanian bed with *Cunningtoniceras* sp.

Summary

As a summary the species described in this paper are listed below with indication of their known age and area in Japan.

Inoceramus tenuis Mantell, common in the Middle Cenomanian of the Obira and adjacent areas and begin to appear in the Lower Cenomanian of the Obira and Oyubari areas.

Inoceramus gradilis Pergament, not infrequent in the Middle and Upper Cenomanian of the Obira and adjacent areas.

Inoceramus virgatus Schlüter, not infrequent in a zone from the Middle to uppermost part of Member Mf in the sequence of the Obira area. This is lower than the *Turrilites acutus* bearing Member Mg and probably referable to the lower Middle Cenomanian; also doubtfully in the Lower or Middle Cenomanian of the Oyubari area.

These three species have been well known world-widely, but this is the first described record in Japan. We would expect more examples to be obtained from various areas in Japan, so that their systematic positions and stratigraphic occurrences may be made clearer.

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本邦白亜系セノマニアン階産イノセラムス—Ⅱ．海外でよく知られ本邦では未記載であった3種：北海道産の標本に基づき次の3種を記述・図示した。但し属名には広義*Inoceramus*を暫定的に使う。

(1) *Inoceramus tenuis* Mantell.左右不等殻，斜めに延びた小型の準卵形，同心円状細肋があるだけで平滑に近いが，成長後期に同心円状起伏が弱く発達することがある。

*Birostrina concentrica*に似るが，左殻頂部が短く，内方屈曲が弱く，鉸線がやや長く後背部が明確に平坦化する。小平，古丹別地域と大夕張地域のセノマニアン下部～中部に産し，海外での層序的産出と調和する。

(2) *I. gradilis* Pergament.小～中型，左右著しく不等殻；左殻は高く盛り上って成長軸に沿い段階的に急変し，そこにくびれがある。右殻は盛り上りが低いが対応したくびれはある。殻の装飾は段階的に(i)殆んど平滑，(ii)同心円状の弱小肋，(iii)明確な肋の発達と変化し，分岐・挿入がありやや不規則である。右殻は*I. reduncus* Pergamentとかなり似ている。古丹別と小平の中部・上部セノマニアンに産する。

(3) *I. virgatus* Schlüter.従来別種又は亜種とされていた*I. scalprum* Böhmを同一種内の1変異とし，改正定義した。左右準等殻で，殻は平坦に近いが，左殻はやや高まり，殻頂も鉸線を少し越えている。準円形か太めの準卵形で，HとLはほぼ等長か，いくらかH＞L；鉸線は長く，成長軸はこれを55°～65°で直線状に走り，後期に前又は後方に凹のゆるい曲線をなすこともある。殻表面に同心円状の細密な条線とゆるい起伏（肋の前兆程度）がある。この起伏がもっと強くなれば*I. atlanticus* Heinzに近くなる。殻内面に放射状の条線が時おり認められる。小平地域Mfの中部～最上部に産し，大夕張にも若干の資料があり，海外でのセノマニアン下部～中部の産出と調和する。

松本達郎・浅井明人・平野弘道

Trans. Proc. Palaeont. Soc. Japan, N. S., No. 147, pp. 165–179, 8 Figs., October 30, 1987

837. ONTOGENETIC SHELL VARIATION AND STREAMLINING OF SOME CRETACEOUS AMMONITES*

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Abstract. Comparative shell shape analysis of some Cretaceous ammonites has provided significant differences in the ontogenetic pattern and variation of geometric coiling parameters. The differences are especially conspicuous in the distance of venter from coiling axis (D), relative whorl thickness (S) and flank position (F), all of which are key factors for considering hydrodynamic efficiency of the shells. In every species, the ranges of variation of the geometric parameters tend to decrease with age. At the same growth stage, intraspecific variation of parameters S and D is largest in the heavily ornamented morphotypes (Acanthocerataceae) and heteromorphs (Scaphitaceae), intermediate in fine-ribbed platycones (Lytocerataceae), and smallest in the weakly ribbed, highly streamlined involute-compressed morphotypes (*Hypophylloceras, Placenticeras* and most Desmocerataceae). This evidence strongly suggests a wide variety of adaptive designs of the shells related to the mode of life of ammonites.

Introduction

The paleoecology of ammonites has long been discussed from various viewpoints. Although opinions on life habits are still divided as to whether ammonites were bottom dwelling or nektoplanktonic, many authors have accepted the idea that most normally coiled ammonites had a certain degree of swimming ability. This interpretation is largely based upon indirect paleontologic evidence such as comparative anatomy (Mutvei, 1964; Mutvei and Reyment, 1973; Jordan, 1968; Stürmer, 1970; Lehmann, 1976) and similarity in fundamental shell morphology to living *Nautilus* (Trueman, 1941). Quantification of hydrodynamic properties of ectocochiliate cephalopod shells has been made experimentally using actual specimens (Schmidt, 1930; Kummel and Lloyd, 1955) and scale models (Chamberlain, 1976, 1981; Chamberlain and Westermann, 1976). The experiments demonstrated that the variation in shell geometry caused significant variation in drag coefficients. Hydrodynamic efficiency of shell shape in fossil ectocochiliates has recently been discussed by Ward (1980) and Chamberlain (1981). These papers rely on generic level analysis of certain simple shell shape parameters over various taxonomic groups. Intra- and interspecific variation of shell shape has also been examined extensively in the Upper Paleozoic Agoniatitida and Goniatitida (Kullmann and Kant, 1970, 1972; Kant, 1977; Kant and Scheuch, 1973, 1980; Saunders and Swan, 1984) and Mesozoic Ammonitida (Westermann, 1966; Bayer and McGhee, 1984; Ward, 1980, 1986), but the ontogenetic variation of shell geometry has little investigated in the Cretaceous ammonites. This paper presents quantitative data on the ontogenetic change and variation of shell shape in some late Cretaceous ammonite species, and discusses their adaptive significance for streamlining.

Material and methods

Material—Twenty Cretaceous ammonite species listed in Table 1 were treated in this study. Most species are represented by several individuals which were preserved in single calcareous

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Table 1. List of material. Samples with prefix R are from the Cenomanian-Santonian of the Obira area, northwestern Hokkaido (see Tanabe *et al.*, 1977, figs. 4–11 for localities and ages). The localities and ages of the remaining samples are as follows. M135 and PM3007: Upper Turonian of the Manji area, central Hokkaido (see Tanabe *et al.*, 1978, fig. 1 for localities), S2211p and S3006: Lower Campanian at Matsumoto's (1942, pl. 12) loc. T281, middle course of Abeshinai River, Saku area, northern central Hokkaido, Hb-10: from river gravel in the upper course of Nakafutamata River, Haboro area, northwestern Hokkaido (derived from the Coniacian).

Major taxonomy	Species	Sample & locality
Phylloceratina		
Phyllocerataceae	*Hypophylloceras subramosum* (Spath)	R4018 (N= 5), Obira
Lytoceratina		
Lytoceratacea	*Tetragonites glabrus* (Jimbo)	R4020 (N= 6), Obira
	Tetragonites popetensis Yabe	S3006 (N=17), Saku
	Gaudryceras denseplicatum (Jimbo)	R4020 (N= 5), Obira
Ancyloceratina		
Scaphitaceae	*Scaphites planus* (Yabe)	R2110 (N= 4), Obira
	Otoscaphites puerculus (Jimbo)	R2110 (N= 7), Obira
Ammonitina		
Desmocerataceae	*Desmoceras japonicum* (Yabe)	R3013 (N=11), Obira
	Tragodesmoceroides subcostatus Matsumoto	R4001 (N=18), Obira
	Damesites ainuanus Matsumoto	R4582 (N=12), Obira
	Damesites damesi (Jimbo)	R4701p(N=11), Obira
	Damesites semicostatus Matsumoto	R2672 (N=17), Obira
	Damesites sugata (Forbes)	Hb-10 (N= 8), Haboro
	Desmophyllites diphylloides (Forbes)	S2211p(N= 6), Saku
	Neopuzosia ishikawai (Jimbo)	R101p (N= 6), Obira
Acanthocerataceae	*Subprionocyclus bravaisianus* (d'Orbigny)	R4017 (N= 6), Obira
	Subprionocyclus neptuni (Geinitz)	PM3007(N=14), Manji
	Reesidites minimus (Hayasaka & Fukada)	M135 (N=13), Manji
	Yubariceras yubarense Matsumoto, Saito & Fukada	R6020 (N= 1), Obira
	Yubariceras japonicum Matsumoto, Saito & Fukada	R4020 (N= 1), Obira
Hoplitaceae	*Placenticeras intercalare* Meek	USGS loc. no.8036 (N= 1), Montana
Nautilida		
Nautilaceae	*Nautilus pompilius* Linné	Off Suva, Fiji Is. (N= 9)

nodules embedded in the Upper Cretaceous deposits of Hokkaido, Japan. The localities and ages of the samples examined are summarized in the explanation of Table 1. Specimens of *Scaphites planus* and *Otoscaphites puerculus* were studied biometrically by Tanabe (1977), and measurements by him are cited in this paper.

In addition to these ammonites, single mature shells of *Placenticeras intercalare, Yubariceras yubarense, Y. japonicum* (see Table 1 for locality records), and nine *Nautilus pompilius* Linné (captured from the Suva area of Fiji; Tanabe, 1985) were used for morphologic comparison. Specimens of the two scaphitids and *N. pompilius* are stored at Kyushu and Kagoshima Universities respectively. All other specimens are kept at University Museum, University of Tokyo with registered numbers beginning UMUT.

Methods—Most specimens were cut and polished along the median plane, and then cut perpendicular along the maximum diameter of the protoconch (X-Y plane in Figure 1). The cross sections were etched with 1% acetic acid for ten minutes, and acetate peels were prepared by pressing a sheet of triacetylcellulose film (25 μm in thickness) onto the section flooded with acetone. Shell diameter, radius vector of venter, radius vector of umbilicus, whorl height, whorl breadth and inner whorl height were measured at intervals of one half whorl on the peeled cross section using a profile projector (NIKON V16) attached to a digital micrometer (accuracy 1 μm) (Figure 1). The measurement data were transferred directly to a personal computer through an interface, and the four geometric parameters developed by Raup (1966, 1967) and Chamberlain (1976); *i.e.* the whorl expansion rate (*W*), the distance of venter from coiling axis (*D*), the relative whorl thickness (*S*), and the flank position (*F*) were calculated at intervals of one half whorl for each specimen (Figure 1). Other important aspects of shell morphology, such as the "strength" and density of external sculpture (ribs, tubercles and a keel) were not analyzed quantitatively, but considered in the morphotypic classification.

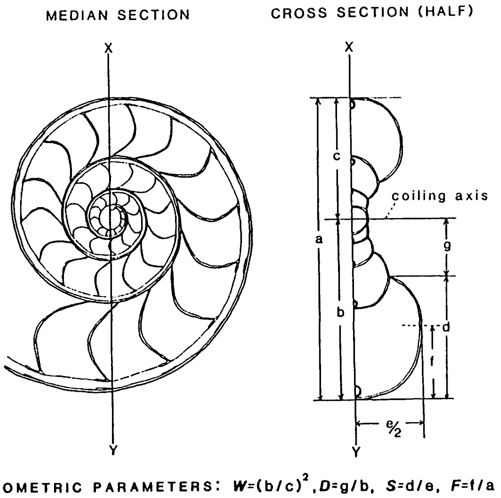


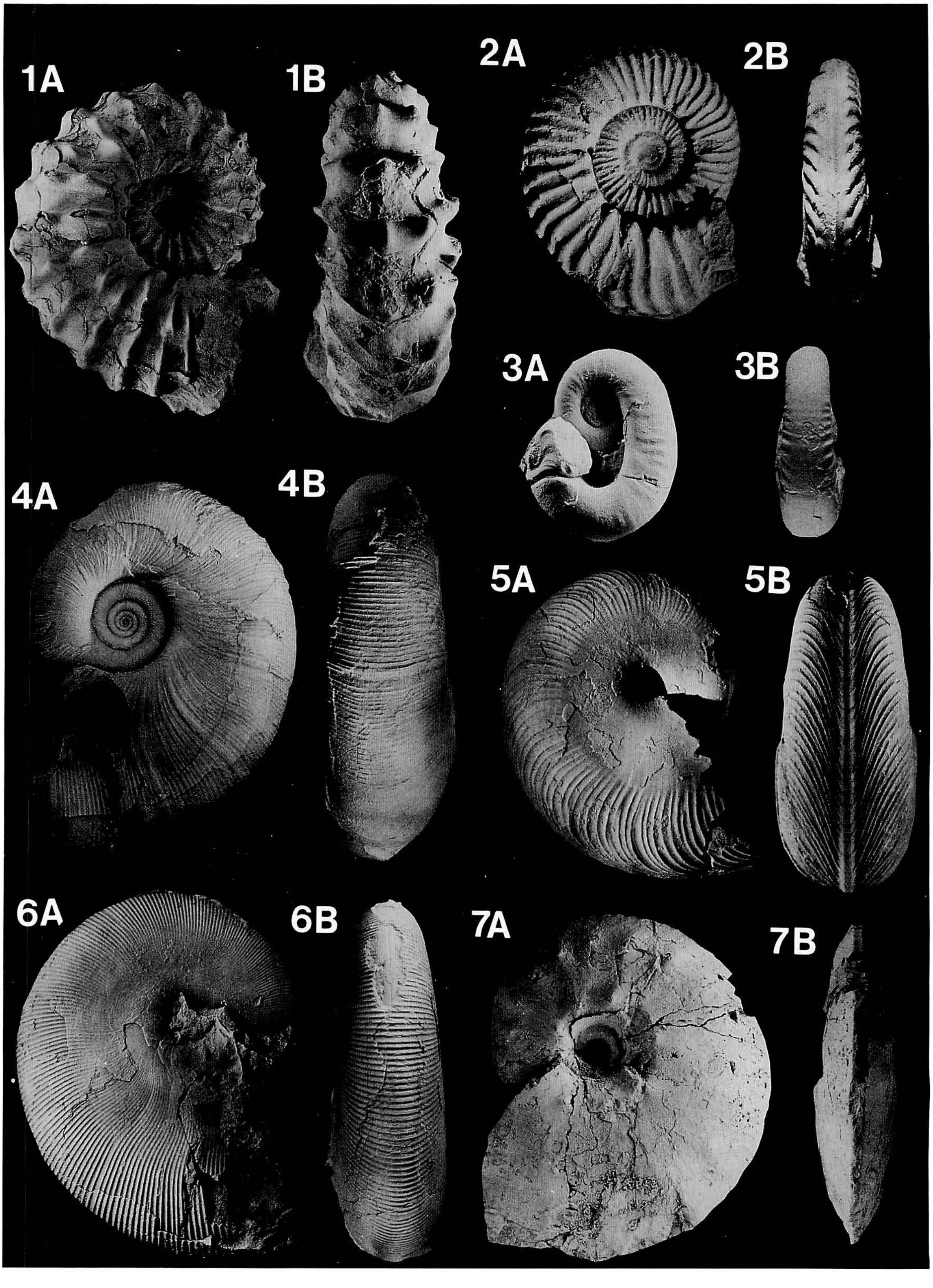
Figure 1. Basic morphology and measurements of an ammonite shell in median and cross sections. a, shell diameter; b & c, radius vector of venter; d, whorl height; e, whorl breadth; g, radius vector of umbilicus; f, inner whorl height. Based on these measurements, four geometric parameters, *W* (whorl expansion rate), *D* (distance of venter from coiling axis), *S* (relative whorl thickness), and *F* (flank position) were calculated at intervals of half whorl. Read S = e/d for S = d/e.

Morphotypic variation

Although the Cretaceous ammonites examined vary in coiling, whorl shape, and surface ornament, they possess characteristic features of shell morphology. They are roughly classified into the following morphotypes: (1) narrowly umblicate and compressed with fine ribs (*Hypophylloceras, Desmoceras, Tragodesmoceroides, Desmophyllites, Placenticeras*) or with fine ribs and a prominent keel (*Damesites*), (2) moderately umbilicate platycone with dense fine ribs (*Tetragonites* and *Gaudryceras*), (3) widely umblicate and compressed with strong ribs, tubercles (*Yubariceras*) and also with a keel (*Subprionocyclus* and *Reesidites*), and (4) planispirally coiled heteromorph (*Scaphites* and *Otoscaphites*). Selected examples of these ammonites are shown in Figure 2.

Geometric analysis

Ontogenetic variation—Ontogenetic changes of geometric parameters were examined in seventeen Cretaceous ammonite species. Changes of sample means of parameters *W, D, S* and *F* versus whorl number for each species are shown in Figures 3–6 respectively. In every species, parameter *W* regularly fluctuates between 1.5 and 2.5 at intervals of one whorl in the first three whorls. This is largely due to the abrupt change in allometric growth of whorl radius at the primary constriction near the end of the first whorl. After the third whorl most species have *W* parameters of about 2.0, but in the scaphitids *W* exceeds 3.5 in the loosely coiled adult stage (Figure 3). *D* parameters of *Hypophylloceras subramosum* and most desmoceratids decrease with age in the first three whorls, and after the third whorl remain almost constant (*ca.* 0.1) (Figure 4). In *Neopuzosia ishikawai* (Desmocerataceae) *D* is also small in the second and third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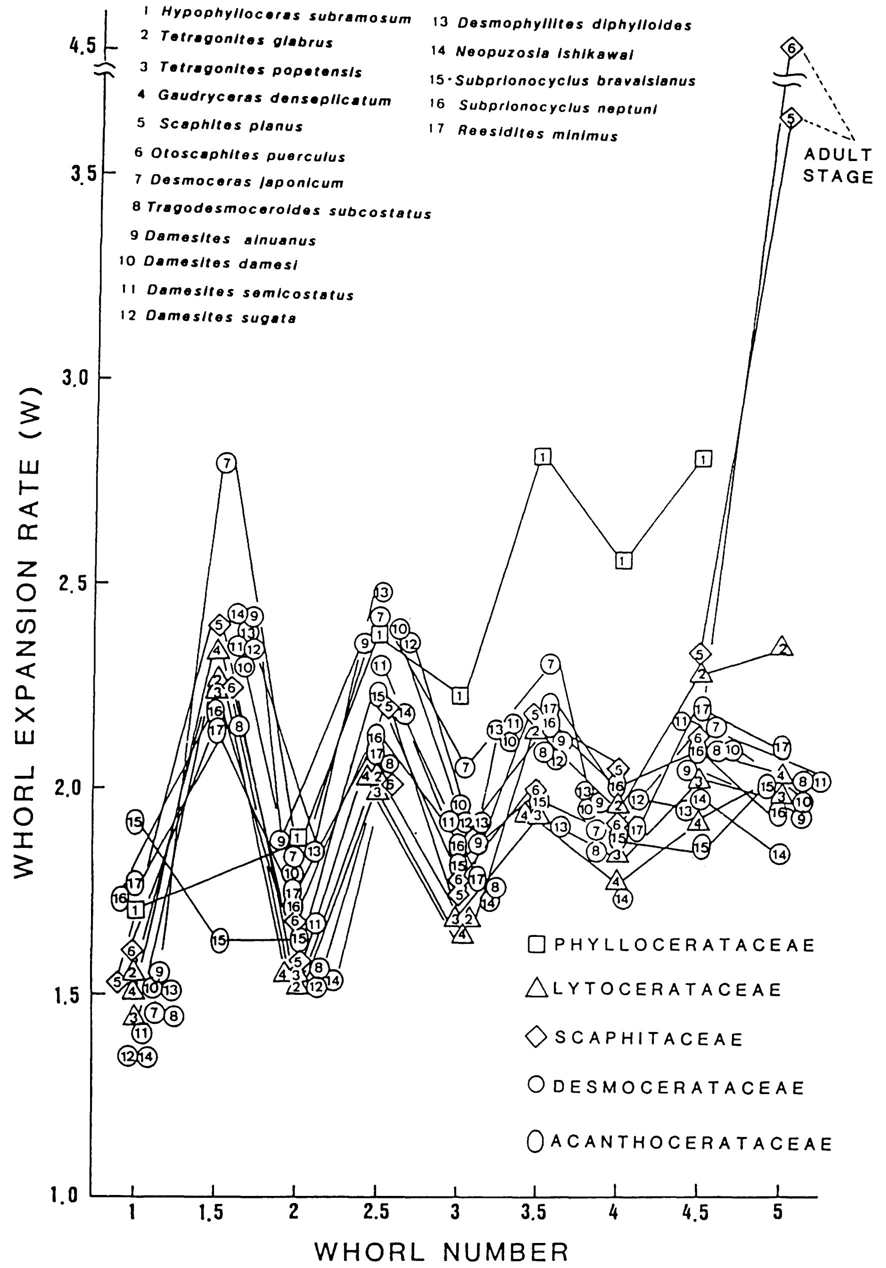

Figure 3. Ontogenetic change of the parameter W in relation to whorl number for seventeen ammonite species. Sample mean at each stage is plotted for every species. The regular fluctuation of W parameters in the first two whorls is due to the abrupt change in growth of whorl diameter at the primary constriction.

← Figure 2. Wide variation of shell shape and surface ornament observed in selected Cretaceous ammonites. Lateral (A) and ventral (B) views are shown for each species. For locations see Table 1. 1A–B. *Yubariceras japonicum* Matsumoto, Saito & Fukada (UMUT MM 18213; X0.2). 2A–B. *Subprionocyclus bravaisianus* (d'Orbigny) (UMUT MM 18209; X0.8). 3A–B. *Otoscaphites puerculus* (Jimbo) (Kyushu Univ. specimen, GK. H 5753; X1.6). 4A–B. *Gaudryceras denseplicatum* (Jimbo) (UMUT MM 18200; X0.3). 5A–B. *Damesites semicostatus* Matsumoto (UMUT MM 18205; X0.8). 6A–B. *Hypophylloceras subramosum* (Spath) (UMUT MM 18197; X0.8). 7A–B. *Placenticeras intercalare* Meek (UMUT MM 18214; X0.26).

whorls but then increases abruptly. *D* parameters of other species are almost constant throughout growth (*ca.* 0.3–0.5) and larger than in *Hypophylloceras* and most desmoceratids at the same growth stage. Two scaphitids possess extremely large *D* parameters in the adult stage. In every species examined, parameter *S* tends to decrease with age (Figure 5). At the same stage, it is

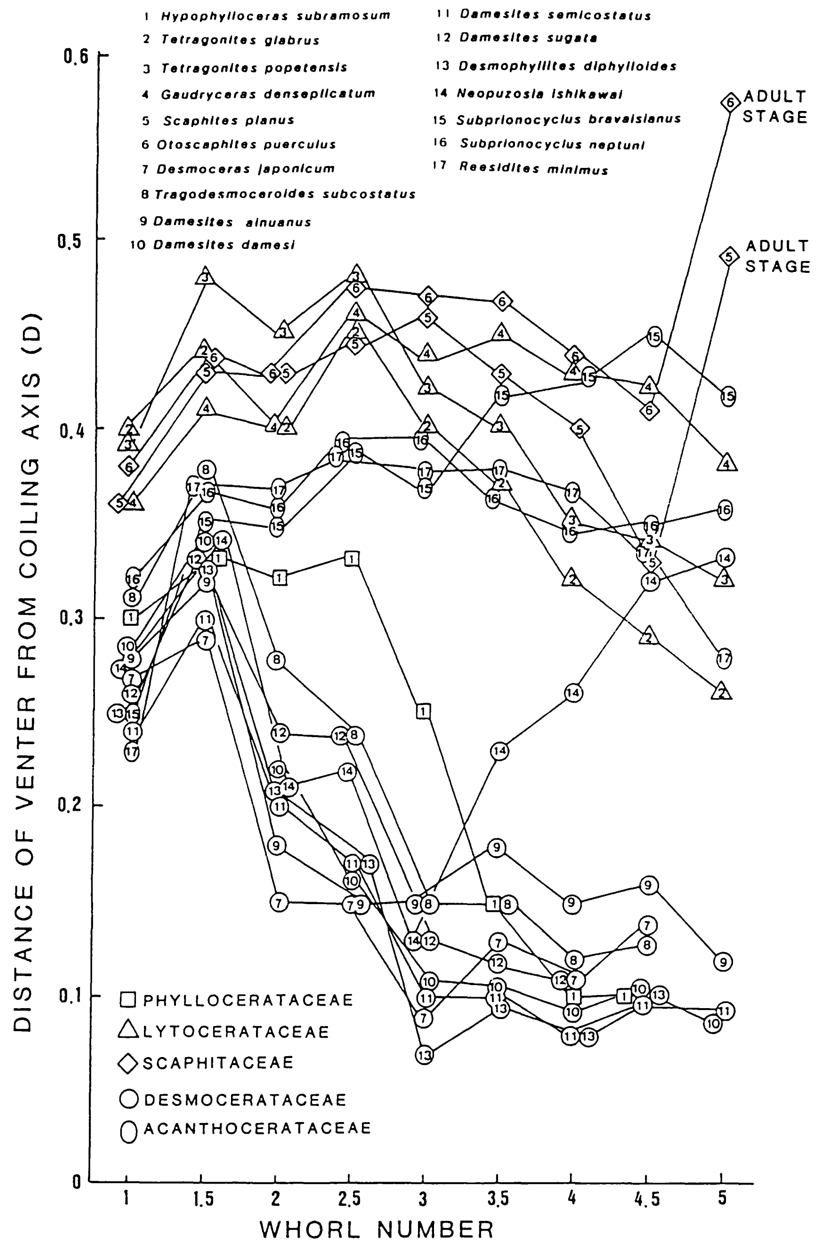

Figure 4. Ontogenetic change of the parameter *D* in relation to whorl number for seventeen ammonite species. Sample mean at each stage is plotted for every species. In the third to fifth whorls, *D* parameters of the Phyllocerataceae and most Desmoceratacea are much smaller than those of other superfamilies.

smallest in the species of the Phylloceratateae and the Acanthocerataceae, intermediate in the Desmocerataceae, and largest in the Lytocerataceae and the Scaphitaceae. Ontogenetic change of parameter F also varies greatly among the species examined (Figure 6). It increases rapidly with age in *Hypophylloceras* or slowly in *Tetragonites, Gaudryceras* and *Reesidites*. F parameters of most desmoceratids are relatively large (*ca.* 0.30) and remain almost constant during onto-

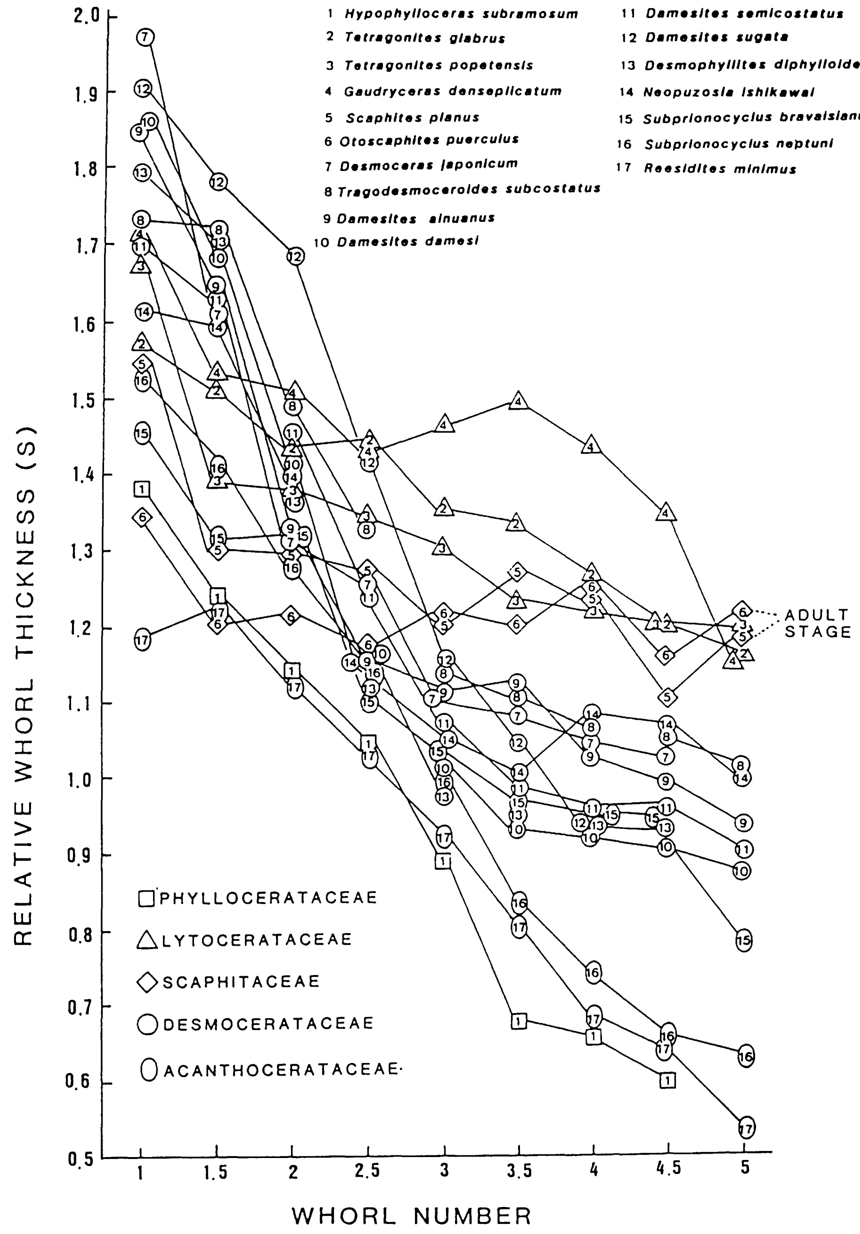

Figure 5. Ontogenetic change of the parameter S in relation to whorl number for seventeen ammonite species. Sample mean at each stage is plotted for every species. In every species S decreases with age, but the interspecific variation at the same whorl stage is fairly large.

geny. The only exception is *Neopuzosia ishikawai* with *F* gradually decreasing.

Intra- and interspecific variation—Shell shape variation in the species examined is summarized in two sets of *S-D* and *W-F* diagrams at different growth stages (Figures 7–8). In every species, intraspecific variation of geometric parameters is larger in the early stage than in the later stage.

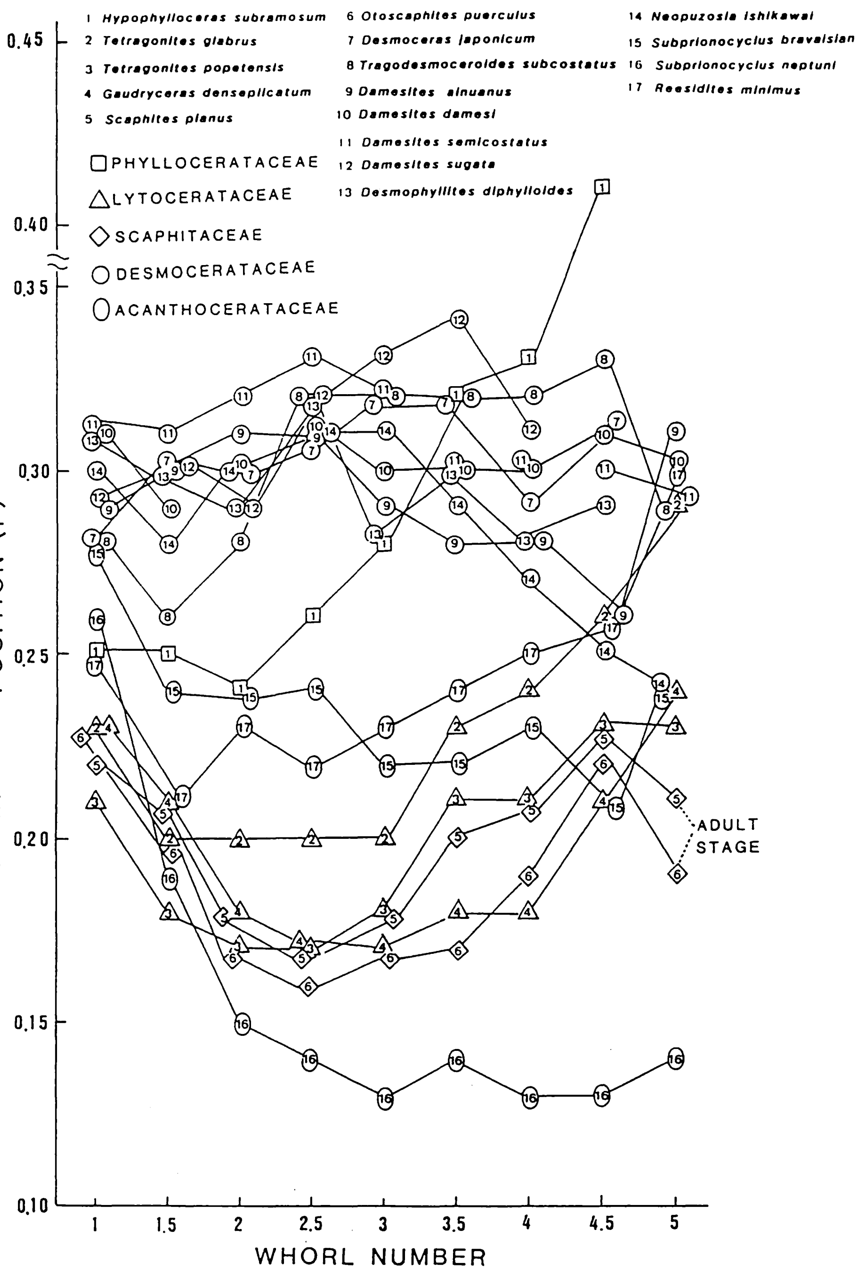

Figure 6. Ontogenetic change of the parameter *F* in relation to whorl number for seventeen ammonite species. Sample mean at each stage is plotted for every species. Wide interspecific variation can be observed among the species examined at the same whorl stage.

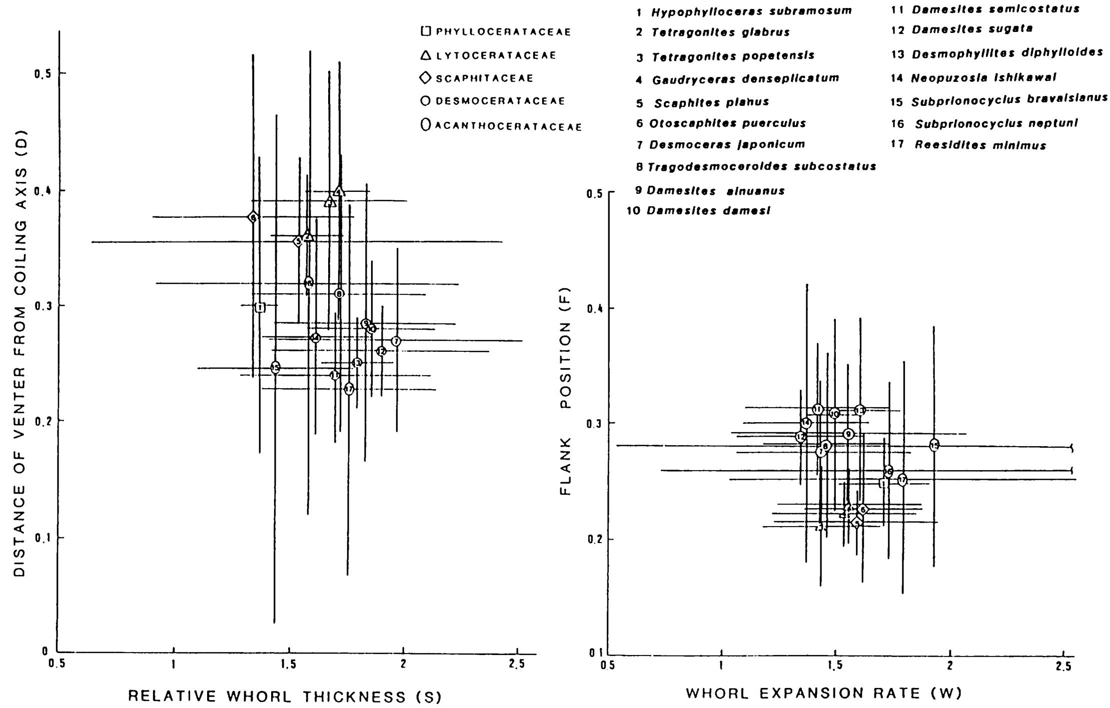

Figure 7. Variation of the geometric parameters at the end of the first whorl in seventeen ammonite species. Sample mean and two standard deviations (horizontal and vertical lines) are indicated for each species. The two figures indicate similarity in juvenile shell morphology among the Cretaceous ammonites.

The species examined do not show significant differences in juvenile shell morphology (Figure 7). In contrast, they show a large interspecific variation in the later growth stage (Figure 8). The coefficients of variation of parameters S and D at the fourth whorl stage are usually largest in the Acanthocerataceae and Scaphitaceae, intermediate in the Lytocerataceae, and smallest in the Phyllocerataceae and Desmocerataceae, at least for the samples examined (Table 2). Geometric parameters of adult *Placenticeras intercalare* and *Hypophylloceras subramosum* are very similar to those of *Nautilus pompilius* (Figure 8).

Discussion

This study demonstrates that the shells of Cretaceous ammonite species examined differ in coiling at all ontogenetic stages. Coefficients of variation of parameters at a given growth stage also vary greatly among these species (Table 2). Interspecific difference in the sample mean is especially conspicuous for parameters S, D and F. Based on these observations we consider the morphologic adaptations of the high variation in shell geometry. Truly remarkable intraspecific variability has been recognized in many near-shore-type Acanthocerataceae and Hoplitaceae, such as in species of *Acanthoceras* (Kennedy and Hancock, 1970), *Collignoniceras* (Kennedy *et al.*, 1980), *Pseudotissotia* and *Wrightoceras* (Hirano, 1983), and *Neogastroplites* (Reeside and Cobban, 1960). In contrast, shell shape variation is much smaller in the offshore-type ammonites investigated such as *Gaudryceras* (Hirano, 1975, 1978) and *Tetragonites* (Y. Shigeta's unpublished data). Two major adaptive strategies have been considered for the function of ammonite external shell morphology: (1) protective (defensive) in thick-shelled whorls with spines or prominent ribs preventing shell breakage by predators

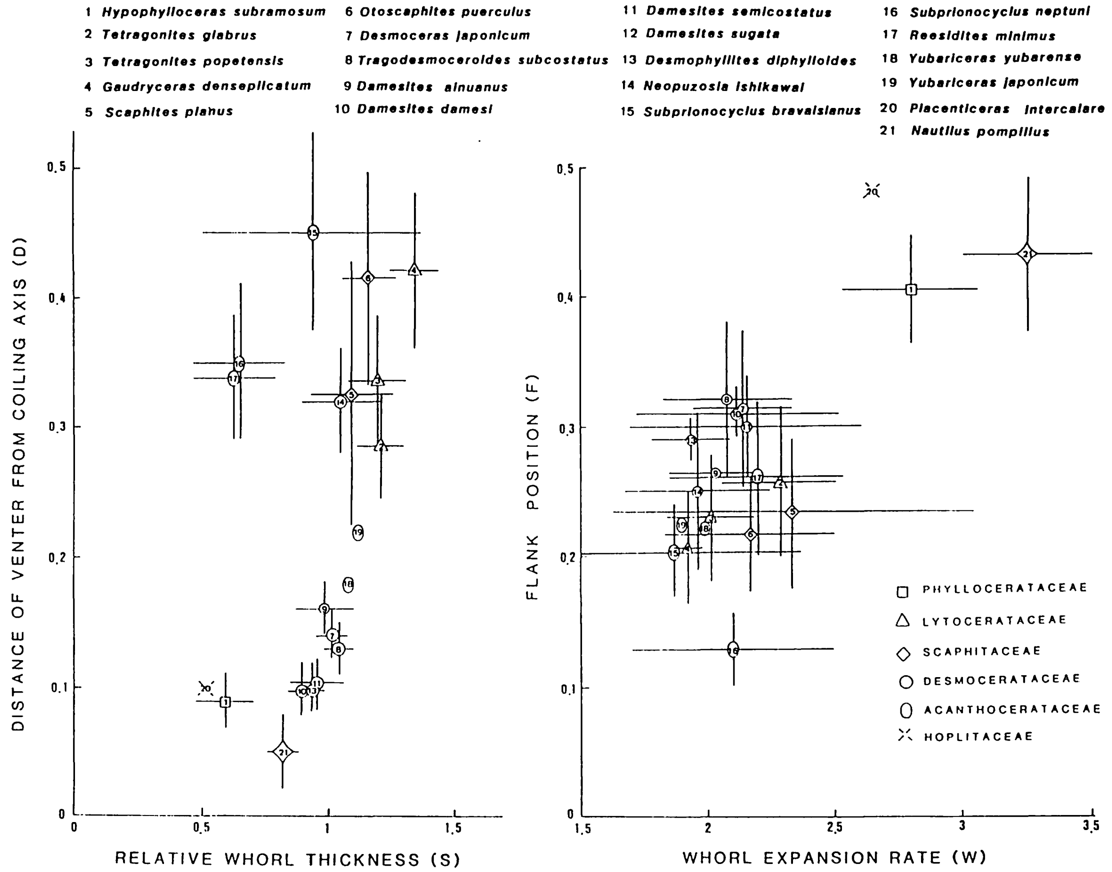

Figure 8. Variation of the geometric parameters at the middle of the fifth whorl in seventeen ammonite species. Data of adult shells of three ammonite species (nos. 18–20) and *Nautilus pompilius* are also indicated for comparison. Sample mean and two standard deviations (horizontal and vertical lines) are indicated for each species. Intraspecific variation of parameters S and D is especially small in the Phylloceratacea and the Desmoceratacea. *Hypophylloceras* (no. 1), *Placenticeras* (no. 20) and modern *Nautilus* (no. 21) possess similar geometric parameters.

(Westermann, 1971; Ward, 1980) and (2) hydromechanical for increasing swimming ability (Chamberlain, 1976, 1981; Chamberlain and Westermann, 1976). These two strategies are largely exclusive because hydromecanical efficiency decreases as the external ornament becomes more prominent (Kummel and Lloyd, 1955; Chamberlain and Westermann, 1976; Chamberlain, 1981). Quantitative analysis of the relations between shell geometry and drag coefficients in the ectocochiliate cephalopod shells has been done by Chamberlain (1976, 1981). He used cephalopod scale models with round-whorl sections ($S = 1$) and smooth surfaces, and measured drag coefficients acting on the shells at various water velocities. For aquatic animals the drag force acting on a swimming body can be approximated by the following equation.

$$D_F = 1/2\rho\, V^2 A\, C_D,$$

where D_F is drag force, ρ is fluid density, V is swimming velocity, A is equivalent to a body size (shell size in this case), and C_D is the drag coef-

Table 2. Coefficients of variation of the geometric parameters at the middle of fifth whorl in the seventeen ammonites and *Nautilus pompilius.*

Species	Geometric parameters			
	W	*S*	*D*	*F*
Phylloceratacea				
Hypophylloceras subramosum	4.79	5.00	7.44	5.19
Lytoceratacea				
Tetragonites glabrus	5.04	4.17	7.10	6.17
Tetragonites popetensis	4.48	5.00	7.37	5.13
Gaudryceras denseplicatum	1.53	3.73	7.33	5.98
Scaphitaceae				
Scaphites planus	15.34	8.18	15.59	12.45
Otoscaphites puerculus	8.03	4.31	9.88	10.14
Desmocerataceae				
Desmoceras japonicum	4.57	2.45	8.21	9.89
Tragodesmoceroides subcostatus	6.20	3.05	7.76	8.68
Damesites ainuanus	4.18	5.98	8.67	8.45
Damesites damesi	9.36	3.57	5.72	4.28
Damesites semicostatus	5.73	3.37	7.18	7.55
Damesites sugata	7.53	6.95	7.62	3.33
Desmophyllites diphylloides	3.65	3.12	4.38	5.94
Neopuzosia ishikawai	3.36	5.42	9.99	6.60
Acanthocerataceae				
Subprionocyclus bravaisianus	13.66	23.40	8.33	8.78
Subprionocyclus neptuni	9.56	13.85	8.68	10.85
Reesidites minimus	7.97	12.31	7.12	11.58
Nautilaceae				
Nautilus pompilius	4.01	3.87	18.62*	6.91

* Umblicus is covered by callus.

ficient (Chamberlain, 1976). If we consider that the fluid density of seawater and shell size are constant, the above equation is rewritten as follows.

$$V = \sqrt{2D_F/C_D}$$

Assuming that D_F is constant, V increases as C_D decreases. Thus, C_D is an index of a shell's hydrodynamic efficiency (Chamberlain, 1976).

Chamberlain (1976, 1981) has demonstrated experimentally that at the same shell size C_D varies greatly with geometry. C_D decreases as either W, D or S decrease. S causes the most pronounced changes in C_D, and the degree of shell compression should be a key factor in cephalopod adaptive design. The effect of F on C_D was not demonstrated, but Chamberlain (1980) suggested that within a suite of low S shells, lower drag coefficients will occur when W and D are low, and F is high.

Hydromechanically efficient cephalopod shells are high-shouldered, involute shells (Chamberlain, 1981). Our adult shells of *Hypophylloceras subramosum* ($W = 2.8$, $S = 0.6$, $D = 0.1$, $F = 0.4$; Figures 2-6A–B) and *Placenticeras intercalare* ($W = 2.7$, $S = 0.5$, $D = 0.1$, $F = 0.5$; Figures 2-7A–B) are closely allied to this morphotype. The shell shape rather resembles that of *N. pompilius*, whose drag coefficient (in 30° attitude) is 0.48 (Chamberlain, 1976), and a similar or smaller drag coefficient is indicated for the adult stage.

Seven desmoceratines also have relatively low D and high F, but their S parameters are large (*ca.* 1.0), at least for the fourth and fifth whorls. In the adult stage (six whorls; 100 mm shell diameter) the whorls of *Damesites semicostatus* are narrowly umblicate and strongly compressed (low S) with a prominent keel (see Figures 2-5A–B). This implies that the shell of this species tends to be well streamlined. Shells of the three lytocerataceans (Figures 2-4A–B) may be compared with the model no. 26 of Chamberlain (1976, table 1). The shells of the three collignoniceratids, *Subprionocyclus bravaisianus*, *S. neptuni* and *Reesidites minimus*, are fairly compressed (S = 0.6–0.7 at fourth to fifth whorls), but D is large. These Turonian collignoniceratids are very closely interrelated, and possibly belong to a single clade (Matsumoto, 1965; Reyment, 1975, 1982; Obata *et al.*, 1979). The oldest species, the middle Turonian *Subprionocyclus bravaisianus* (Figures 2-2A–B), has larger D and S than the latest, the late Turonian *R. minimus.* The middle to late Turonian *S. neptuni* has intermediate values. In correspondence to this, surface ornament (tubercles and ribs) tends to weaken from *S. bravaisianus* to *R. minimus*. As Obata *et al.* (1979) have briefly mentioned, these trends of shell form and ornamentation can be interpreted as adaptation to increasing hydromechanical efficiency. Two species of *Yubariceras* possess robust depressed shells, with a pair of five rows of tubercles (Figures 2-1A–B). The large S (*ca.* 1.1) and small F (*ca.* 0.2) parameters and the coarse ornamentation suggest that both species were poor swimmers. The coiling parameters in the immature stage of scaphitids are similar to those of normally coiled species, but possess extremely large parameters W (*ca.* 4.0) and D (*ca.* 0.5) at maturity (Figures 2-3A–B). Their shell type corresponds to Chamberlain's (1976, Table 1) model no. 29, whose drag coefficient is 0.81. These lines of evidence suggest that the scaphitids changed their way of life during ontogeny. In all probability, they abandoned an active mode of life at maturity (Tanabe, 1977).

In conclusion, the results of this study indicate a wide variety of hydromechanical adaptations among Cretaceous ammonites confirming the conclusion of previous authors (*e.g.* Raup and Chamberlain, 1967; Ward, 1980, 1983; Chamberlain, 1981; Saunders and Swan, 1984) based on *W-D* analysis of many ammonites and nautiloids. According to Chamberlain's *W-D* contour maps (1981, figs. 18–19), the range of the morphologic variation of the Ammonoidea is much wider than that of the Nautiloidea. Furthermore, the range of geometric variation in the Mesozoic Ammonoidea is wider than in the Paleozoic, and the main adaptive peak shifts larger D values. In our material, the W and D values of the seven desmoceratines, *Hypophylloceras subramosum*, and the well-streamlined *Placenticeras intercalare* all plot near the adaptive peaks of the post-Jurassic Nautilida and the Paleozoic Ammonoidea in the diagrams of Chamberlain (1981, figs. 18–19). W and D data of the other species resemble those of the common Jurassic-Cretaceous ammonites (Ward, 1980, figs. 3–4; Chamberlain, 1981, fig. 19). Coarsely ornamented planispiral ammonites with robust ribs, spines and tubercles became very common in the early Cretaceous, and during the middle to late Cretaceous the number of heteromorph and strongly ornate species comprised more than 50% of the total species (Ward, 1981, 1983, 1986). Most of these morphotypes had larger D and S parameters than streamlined shells (Figure 2; Ward, 1980). Ward (1981) speculated that the increase of coarsely ornamented species in the Cretaceous was a defensive adaptation against shell-crushing predators. In the Upper Cretaceous of Hokkaido, occurrences of coarsely ornated ammonites such as acanthoceratids and collignoniceratids are restricted to the nearshore, coarse-grained lithofacies (Tanabe, 1979). Complete preservation of the aperture and clustered occurrences at a single locality supports the autochthonous origin of these fossil assemblages (Tanabe *et al.*, 1978; Tanabe, 1979). This supports the predation interpretation. We believe that most heavily ornamented ammonites were poor swimmers, and that their possible mode of life was mobile benthic or nektobenthic. Concerning the paleoecology of heteromorphs, opinions remain divided; some believe that they were planktonic (Trueman, 1941; Ward, 1976, 1979; Ward and Westermann, 1977), other that they were benthic (Scott, 1940; Ziegler, 1967; Tanabe *et al.*, 1981). The former interpretation is based mainly on the hydrostatic properties of the shells, and the latter on field occurrence. The mode of coilings and ornamentation in the Cretaceous heteromorphs are, however, quite variable, and a single mode of life may not have applied to all groups. Heteromorphs with weakly ornamented and straight shells (*e.g. Baculites*) probably could swim, while the presence of different coiling modes during ontogeny in some nostoceratids (*e.g. Eubostrychoceras* and *Madagascarites*) suggest the loss of swimming ability, even if they were neutrally buoyant (personal communication with T. Okamoto). Further data on comparative morphology, anatomy and field occurrence are needed to clarify the above problem.

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白亜紀アンモナイト数種の成長に伴う殻形変異と流線効果：北海道産の後期白亜紀アンモナイト17種の集団標本を用いて，成長に伴う殻形パラメータの変化を比較検討した。検討したパラメータは，Raupによって提唱された螺環拡張率（W），螺環被覆率（D），螺環の高さに対する幅の比（S），側面の相対的位置（F）の4つである。これらのうち，D, SおよびFは，幼期には種間で大差ないが，成長に伴って大きく異なるようになる。成年期には，表面装飾の乏しいフィロセラス超科やデスモセラス超科の種ではSやDは小さく，かつそれらの種内変異量も小さい。逆に，表面装飾の著しいアカントセラス超科や異常巻のスカフィテス科の種では，S, Dは大きく，それらの種内変異量は大きい。従来の流体実験の結果では，S, Dは流線効果に大きく関与し，それらの小さい平滑型の類は小さい抗力係数を持つことがわかっている。一方強い刺や肋は，流線効果にはマイナスでも捕食者に対する防御として効果的であったと考えられる。以上のことから，白亜紀アンモナイト類に認められる殻形の大きな変異は，多様な生活様式と対応した適応形態を反映していると推察される。

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838. LIFE HABIT AND RELATIVE GROWTH OF SOME LAQUEID BRACHIOPODS FROM JAPAN

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Abstract. Japanese Cenozoic laqueid brachiopods generally show two allometric trends. One is the ontogenetic increase in valve convexity versus valve length, and the other is the ontogenetic decrease in valve width versus valve length. To examine the causation of these morphologic changes, the general morphology, life habit, and allometric relationships of some metric characters were investigated in the Recent samples of *Laqueus rubellus* (Sowerby). The following are three explanations for the relative increase of shell convexity: 1) efficient secretion of shell material, 2) strengthening the shells, and 3) providing larger space for adult gonad. Among them, the third explanation seems most appropriate at least in *L. rubellus*, because of a diphasic allometric relationship between valve convexity and valve length: while valve convexity is positively allometric to valve length in adults, they are isometrically related in juveniles.

Introduction

In many cases, post-Paleozoic brachiopods have simple elliptical outlines and show allometric growth during ontogeny. Brachiopod shells often show significant deviation from ideal logarithmic spirals (Rudwick, 1959; McGhee, 1980). McGhee (1980) examined 324 genera of four orders of articulate brachiopods, and showed that well over a half of them changes their whorl expansion rates during ontogeny. An overwhelming trend is the relative increase of valve convexity with growth.

Brachiopods change the form of the commissure during ontogeny as well as their general shape. For example, Raup and Stanley (1978) cited relative growth in a Carboniferous brachiopod, *Ectochorisites wattsi*, which alters the commissure form ontogenetically from the shape that is wider than long to the shape that is longer than wide.

Causation of the allometry in the brachiopods is not decisive, but some interpretations were hitherto proposed. Raup and Stanley (1978) suggested that the allometry in *E. wattsi* may be size-related, though how size relates to the change of the shape was not mentioned. McGhee (1980) interpreted the ontogenetic increase in valve convexity in many biconvex brachiopods as obtaining maximum internal volume by minimum shell surface area. Maximum internal shell volume is favorable to house intricated lophophore, whereas minimum shell surface area is advantageous because it costs least metabolic energy to secrete shells.

Here, I propose several explanations for the allometric changes observed in the living brachiopod, *L. rubellus*. I suggest that these explanations may also apply to some cases of allometric growth in fossil brachiopods.

The following abbreviations are used in this study for the metric characters and the statistical values. L: length of the ventral valve, W: width of the shell, T: thickness of the articulated valves, F: diameter of the foramen, Wt: shell weight, Lm: length of the median septum, Sl: surface area of the lophophore, A: surface area of the shell, V: inner volume of the shell, α: regression

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coefficient, slope of allometry, K: statistical value for discrimination of allometry (Hayami and Matsukuma, 1971).

General morphology of laqueid species

The articulate superfamily Terebratellacea, characterized by having long-looped brachidium, are classified into several families by different mode of development of the loop. Hatai (1965) defined Laqueidae, one of the terebratellacean families, as possessing loops with interconnecting bands which unite ascending and decending branches. Laqueidae was redefined by Richardson (1975) as "Loop passing through axial, annular, and haptoid phases to a bilacunar loop pattern; bilacunar pattern may be the adult loop pattern or be followed either by bilateral and laterovertical phases or by trabecular and teloform phases."

Adult morphology of *Laqueus rubellus*

Figures 1-1–3 show an adult shell of *L. rubellus*. Figure 2 shows gross morphology, measurements, and internal morphology of the dorsal valve of adult *L. rubellus*. The shell is so thin (less than 0.5 mm) and translucent except for the cardinalia that the gonad can be seen through the shell. The shell is mostly yellowish red, with deeper tinges at concentric lines. The intervals of the growth lines become denser near the margin. An adult *L. rubellus* has a bilateral brachidium (Figure 2).

The gonad sticks on the inner surface of both ventral and dorsal valves, being lapped in membranes. The males and females can be easily distinguished by binocular observation of the gonads. Two types of texture are observed, one is the aggregated small particles, the other is a lump of smooth appearance. SEM observation of gonads confirms that the former and the latter are of females and males respectively (Figure 3). The egg is about 70 μm in diameter, whereas the head of the sperm is about 1 μm in diameter. Sexual dimorphism was not observed at least for the gross morphology and size of the shells.

Juvenile morphology of *Laqueus rubellus*

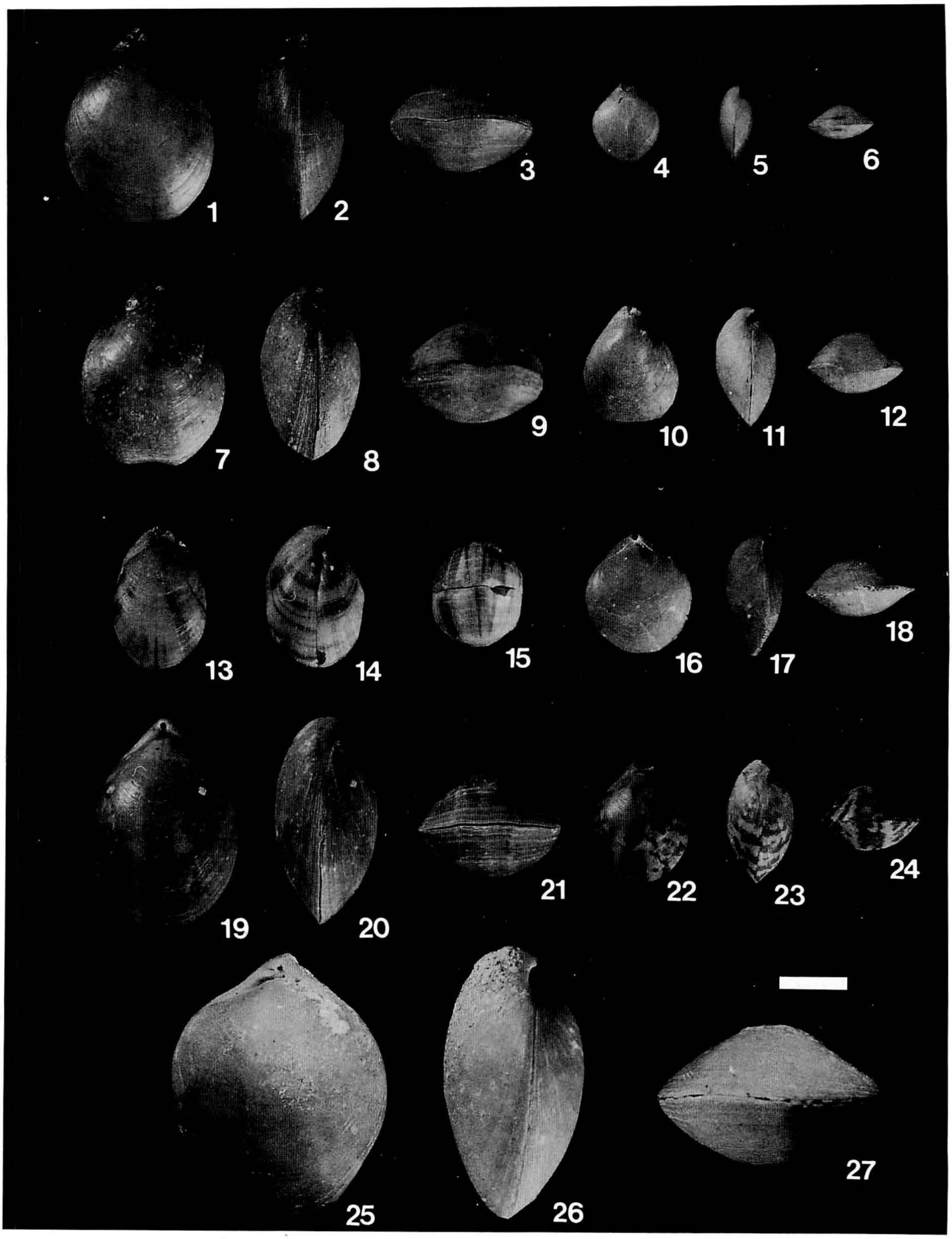
The juvenile shell is distinguished from the adult shell by the poorly developed gonad and smaller size. The figured specimen (Figures 1-4–6, L = 11.95 mm) is certainly juvenile because it has no gonads.

The shell morphology of the juveniles is different from that of the adults. Lateral sides and anterior margin in dorsal view are broadly rounded and forming almost circular outline. The valves are nearly equally convex, but both valves are compressed or less convex compared to that of the adults. Although the absolute foramen size is smaller than that of the adults, relative foramen size to the shell length is larger than that of the adults. The shell is always fresh and it is so thin that the lophophore and other soft parts are seen through from the exterior.

The loop pattern in the specimens of *ca.* 10 mm in shell length is already bilateral. The earlier loop development phase, namely bilacunar, is observed in the specimens of 7 mm long. The still earlier phase, namely haptoid, is observed in the specimens less than 4 mm in length. The phase in lophophore pattern of the figured specimen (UMUT RB18186b) is already plectolophous. In the specimens with a bilacunar loop pattern, the lophophore is plectolophous, while it is zygolophous in the specimens with a haptoid loop pattern.

Morphologic features of other species

Eight laqueid species treated here show rather similar biconvex form of smooth shell surface (Figure 1). Every species, except for *Laqueus blanfordi* and *L. quadratus*, thicken the posterior part of the shell during growth. The adult individual of *L. blanfordi* has a pedicle as long as the length of the shell. However, in *Pictothyris picta* and *P.* sp., the pedicle is so short that in most case the shell is attached directly to the substrate. The foramen of *Kikaithyris hanzawai* is so minute that the pedicle may have been atrophied in the adult phase (Table 1).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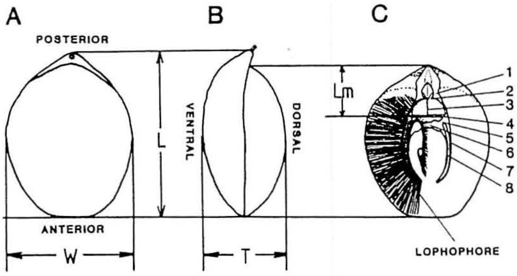

Figure 2. Gross morphology, measurements and internal morphology of the dorsal valve of *Laqueus rubellus*. A: dorsal view; B: right lateral view; C: internal view of the dorsal valve showing the bilateral loop and the configuration of the lophophore (half ommitted). *L*: length of the ventral valve; *W*: width of the ventral or the dorsal valve; *T*: thickness of the articulated valves; *Lm*: length of the median septum; 1: crura; 2: crural process; 3: median septum; 4: connecting band; 5: interconnecting band; 6: transverse band; 7: descending branch; 8: ascending branch.

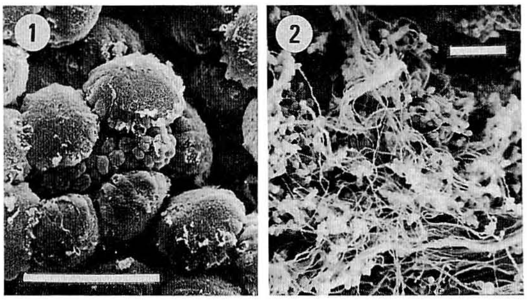

Figure 3. SEM photographs of the gonad of *L. rubellus* [Sample *Rk* (104), April 8, 1986]. 1, Ova, UMUT RB18186c, scale bar indicates 100 μm; 2, Sperm, UMUT RB18186d, scale bar indicates 10 μm.

Life habit of laqueid species

Ecology of *Laqueus rubellus*

Hatai (1940) compiled the data on the Recent brachiopods collected by the cruises of R/V

Table 1. Some adult morphologic characters in eight laqueid species examined.

SPECIES	SAMPLE	LOOP PATTERN	WEIGH DOWN	PEDICLE	MINUTE FORAMEN	MAX. L (mm)
Laqueus rubellus	Jz(L), Rk	bilateral	●	medium		29.55
L. blanfordi	Ot			long		28.35
L. quadratus	Na, Hi			medium		21.75
L. sp.1	Ts(L)		●	medium		21.45
L. sp.2	Sw		●	–		21.10
Pictothyris picta	Jz(P), Rk(P)	latero-vertical	●	short		31.75
P. sp.	Ts(P)		●	short		18.40
Kikaithyris hanzawai	Wa		●	–	●	40.20

← **Figure 1.** Overall shell morphology of eight laqueid brachiopods. (All figures × 1, scale bar indicates 1 cm.) 1-3, *Laqueus rubellus* (Sowerby), adult specimen, off Jyogashima, Sagami Bay, Sample *Rk* (82), UMUT RB18186a; 4-6, *L. rubellus*, juvenile specimen, off Jyogashima, Sagami Bay, Sample *Rk* (17), UMUT RB18186b; 7-9, *L. blanfordi* (Dunker), Otsuchi Bay, Sample *Ot* (2), UMUT RB18188a; 10-12, *L. quadratus* Yabe and Hatai, off Hinomisaki, Kii Channel, Sample *Hi*, UMUT RB18190a; 13-15, *L.* sp. 1, off Tsukumi, Bungo Channel, Sample *Ts* (L), UMUT RB18191a; 16-18, *L.* sp. 2, Sawane Formation, Sado Island, Sample *Sw*, UMUT CB18192a; 19-21, *Pictothyris picta* (Dillwyn), off Jyogashima, Sagami Bay, Sample *Rk* (P), UMUT RB18194a; 22-24, *P.* sp., off Tsukumi, Bungo Channel, Sample *Ts* (P), UMUT RB18195a; 25-27, *Kikaithyris hanzawai* (Yabe), Wan Formation, Kikai Island, Sample *Wa*, UMUT CB18196a.

Soyo I. His collections from 81 stations show that *Laqueus rubellus* is found from 30 m water depth to depths in excess of 499 meters. Most specimens were collected on sand or gravel bottoms and bottom temperatures range from 2.0°C to 23°C ($\overline{X}$ = 15–20°C). Though Hatai (1940) failed to describe whether the individuals were living or not, the major habitats of *L. rubellus* became clear: sandy or coarser substrata on the continental shelves and the uppermost part of slope under the influence of warm ocean currents.

Living specimens of *L. rubellus* and *Pictothyris picta* were repeatedly dredged by R/V Rinkai of the Misaki Marine Biological Station of the University of Tokyo in various seasons at the depths of 85–90 m from sandy bottoms near the edge of the continental shelf of eastern Sagami Bay, about 2 km west of the western end of Jyogashima-Islet. A total of 780 individuals of *L. rubellus* were collected and 35 of *P. picta* in 17 samples.

Most of the living individuals of *L. rubellus* were dredged with the pedicle attached to pebbles or shell fragments. Some rock fragments were incrusted both by individuals of *L. rubellus* and *P. picta*. The diameter of the substrate particles falls in the range of 5–15 mm. During growth the substrate for these brachiopods becomes relatively small, and it would be insufficient to support the whole shell. In addition, the shell weight shows an allometric increase during growth mainly due to the thickening of the posterior part of the shell (Figure 4). Therefore, the adult individuals of *L. rubellus* from Sagami Bay must be free-lying on the sea bottom.

Many brachiopods are known to reorient to water currents (LaBarbera, 1977, 1978; Richardson, 1981b). Juvenile form of *L. rubellus* may have the ability to reorient to water current because of the relatively stable attachment, while the adults may not have this ability because of their relatively small-sized substrates.

The feeding and the excretion of faeces occur through filtering system of the lophophore (Rudwick, 1970). Adult individuals of *L. rubellus* from Sagami Bay were kept in aquaria with continuous circulation of fresh seawater for two

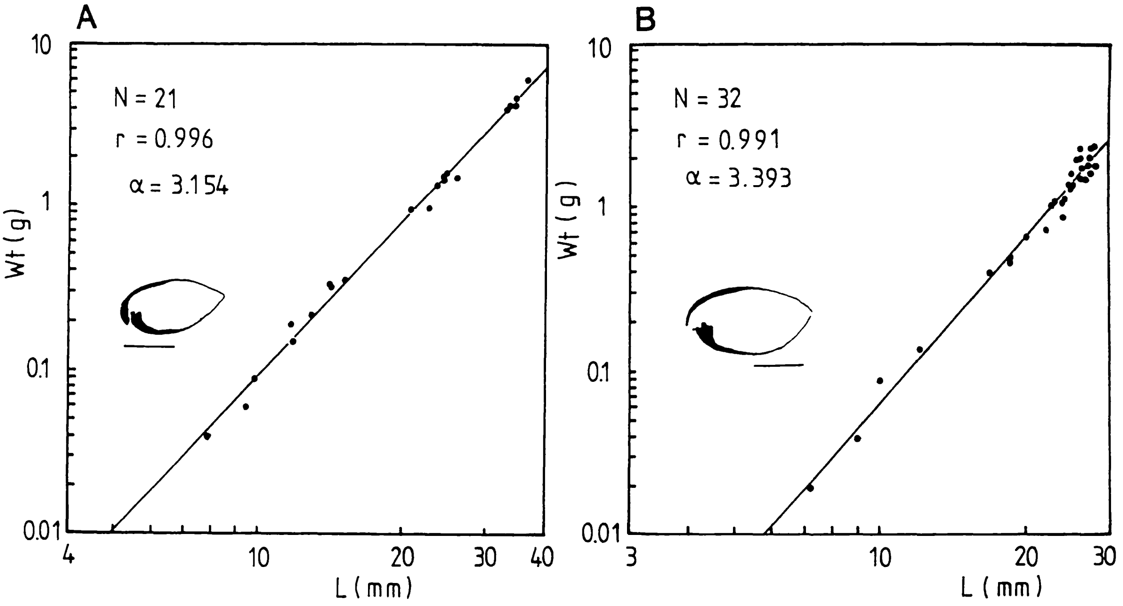

Figure 4. Double logarithmic plots and regression line with the reduced major axis of shell length (*L*) vs. shell weight (*Wt*). A: *Kikaithyris hanzawai* (Sample *Wa*); B: *Laqueus rubellus* [Sample *Rk* (80)]. Shell section along the plane of symmetry is also shown in each figure. Scale bar indicates 1 cm. This figure shows positive allometry of *Wt* to *L* owing to the differential thickening of the posterior part of the shell.

days. All the individuals gaped slightly (the angle of gape is about 5–10°), and fully extend the filaments of the lophophore, which trembled weakly. They quickly closed the valves periodically without any stimulation at intervals of several minutes, and after a while, they gradually opened the valves. When touched, they quickly closed the valves.

To observe the filtering system more in detail, the valves of *L. rubellus* were separated after two days' rearing in aquaria. The individuals were still alive after the separation of two valves. The observed movement of the filaments was contrary to expectations. Each filament of the lophophore moved somewhat individually and flexibly, though the movement of one filament accompanies the movement of the neighboring filament. The mode of movement resembles the motion of the tentacles of a sea anemone. The expected conformation of filaments, that the filaments fully extended with the tips of them along the commissure, was also observed, but this state did not last for more than one minute. When stimulated by a needle, all the filaments were observed to recoil. These unexpected motions may be partly due to the separation of the valves, but it suggests the ability of the filaments to move flexibly. Similar movements of the filaments in separated valves in other terebratellacean species were reported by Thayer (1986) who suggested that the movements are a mechanism of rejecting nonfood particles.

As listed below, numerous living individuals of *L. rubellus* were collected in various seasons from almost same station: (1) May 25 and 26, 1978, (2) October 4 and 5, 1979, (3) March 11, 1982, (4) July 27, 1982, (5) Aug. 3, 1983, (6) July 10, 1985, (7) April 8, 1986, and (8) April 28 and 30, 1987.

Every sample includes adult specimens with both moderately and poorly developed gonads. There is no seasonality of maximum gonad development, so the time of reproduction is still unknown.

Mode of life of other species

Laqueus rubellus possesses a secondarily free-lying life habit. Individuals of *Pictothyris picta* from the same stations of Sagami Bay [Sample *Rk* (P)] also attached themselves to small unstable particles. Such free-lying mode of life has not been described in extant articulate brachiopods except for Richardson (1981a). Permanent attachment to hard stable substrate seems more common in extant articulate brachiopods.

Individuals of *Pictothyris* sp. [Sample *Ts* (P)] attach themselves to pebbles of moderate size ranging three to five times as large as the adult shells. This relative size of adhering material suggests an intermediate mode of life between free-lying and permanently attached. Specimens of *Laqueus blanfordi* (Sample *Ot*) were collected in a fishing net with the individuals attached to a tangled rope of about 1.5 cm in diameter. From this mode of occurrence, an attached life is strongly suggested for this species, although the type of substrate may be very different in different samples.

Kikaithyris hanzawai (Sample *Wa*), a Plio-Pleistocene fossil species from Ryukyu Islands and Formosa, shows the characteristic shell morphology suggesting a reclining mode of life. The shell of *K. hanzawai* is fairly large. The dorsal view is shouldered in comparison with *L.*

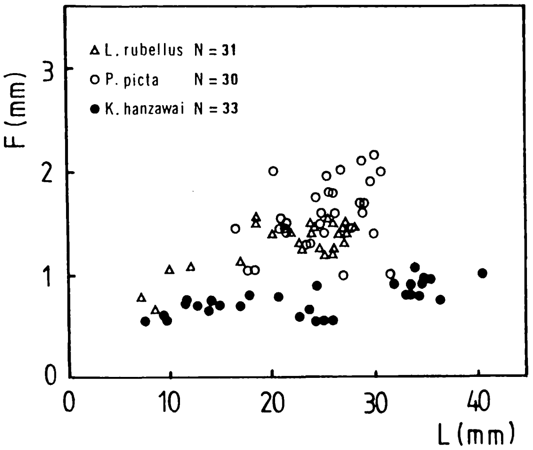

Figure 5. Scatter plots of F versus L in *L. rubellus* [Sample *Rk* (80)], *Pictothyris picta* [Sample *Rk* (P)], and *Kikaithyris hanzawai* (Sample *Wa*). The margin of the foramen of *L. rubellus* and *P. picta* is resorbed and the diameter becomes large with growth. However, in *K. hanzawai*, the margin of the foramen is scarcely resorbed.

rubellus (Figure 1-25). It has a strongly incurved beak (Figure 1-26) and a foramen which is unusually minute for its large shell (Figure 5, Figure 1-25). The shell is thin (less than 0.5 mm) except for the thick posterior part of the shell. The weight of the shell is positively allometric to the cube of length owing to the differential thickening of the shell in posterior region (Figure 4). These morphologic features indicate a free-lying mode of life in this species; the pedicle of *K. hanzawai* must have been degenerated with growth, because the size of the foramen determines the diameter of the pedicle. Moreover, the incurved beak is unfavorable to hold a pedicle because it points to the dorsal valve (Figure 1-26). Judging from the similar outline to *L. rubellus* in the early stage, *K. hanzawai* probably changes the mode of life from an attached life habit to a completely free-lying one without a functioning pedicle during ontogeny. In modern seas only one species, *Neothyris lenticularis*, is certainly free-lying without pedicle attachment (Rudwick, 1970; Richardson, 1981a).

Laqueus quadratus (Sample *Hi*) does not possess thickening of the posterior part of the shell. In a strong bottom current, a free-lying state of such light shells would be unstable and disadvantageous. Therefore, attached mode of life is suggested for this species as in *L. blanfordi*. Individuals of *Laqueus* sp.1 [Sample *Ts* (L)] and *Laqueus* sp.2 (Sample *Sw*) thicken their posterior part of the shells. This character, however, does not necessarily mean a free-lying mode of life because the equivocal species *Pictothyris* sp. [Sample *Ts* (P)] exhibits similar features.

Relative growth

The shell form of *Laqueus rubellus* changes during ontogeny from a circular outline in dorsal view to an elongate oval. The shell also becomes more strongly convex in the adult stage. In order to quantify this allometric change, bivariate analyses of *L* and *W* as well as *L* and *T* were performed.

The bivariate analysis assumes a simple power function between *L* and *W*, and *L* and *T*. The regression line was calculated using the reduced major axis method (Imbrie, 1956), in which the slope (α) of allometry in a log-log plot (regression coefficient) is given as:

$$\alpha = \frac{S_y}{S_x},$$

where S_x and S_y are the standard deviations of x and y, respectively. The regression coefficients are tested against the null hypothesis,

$$H_0 : \alpha = 1, \; K = \frac{\alpha - 1}{S_\alpha} \quad \text{(Hayami and Matsukuma, 1971),}$$

where K has a normal distribution, and S_α is the standard error of the regression coefficient.

Discrimination between isometry and allometry is arbitrarily defined at the confidence level of 95% (Hayami and Matsukuma, 1971): The value of K over 1.96 means the y-variable is positively allometric to the x-variable; and negatively allometric when $K < -1.96$; if the value of K is between 1.96 and -1.96, the null hypothesis (isometry) cannot be rejected.

Figure 6 shows an example of bivariate analysis on the *L-W* relation and the *L-T* relation. The reduced major axes on double logarithmic scatter diagrams indicate that *W* is negatively allometric to *L*, and that *T* is positively allometric to *L*.

Figure 7 shows another example of bivariate analysis on the *L-W* and *L-T* relationships. In this sample, the males and the females are analyzed separately. In both males and females, *W* grows significantly negative allometric to *L*, and *T* grows positive allometric to *L*. The difference of regression coefficients is not significant between the males and the females at 95% confidence level.

Table 2 lists the results of the average relative growth analyses of *T* vs. *L* and of *W* vs. *L* on 8 samples of 7 species. Double logarithmic scatter diagrams for *P. picta* and *K. hanzawai* are shown in Figure 8 and Figure 9 respectively.

In all species examined, *T* shows a more or less positive allometry to *L*. Except for *L.*

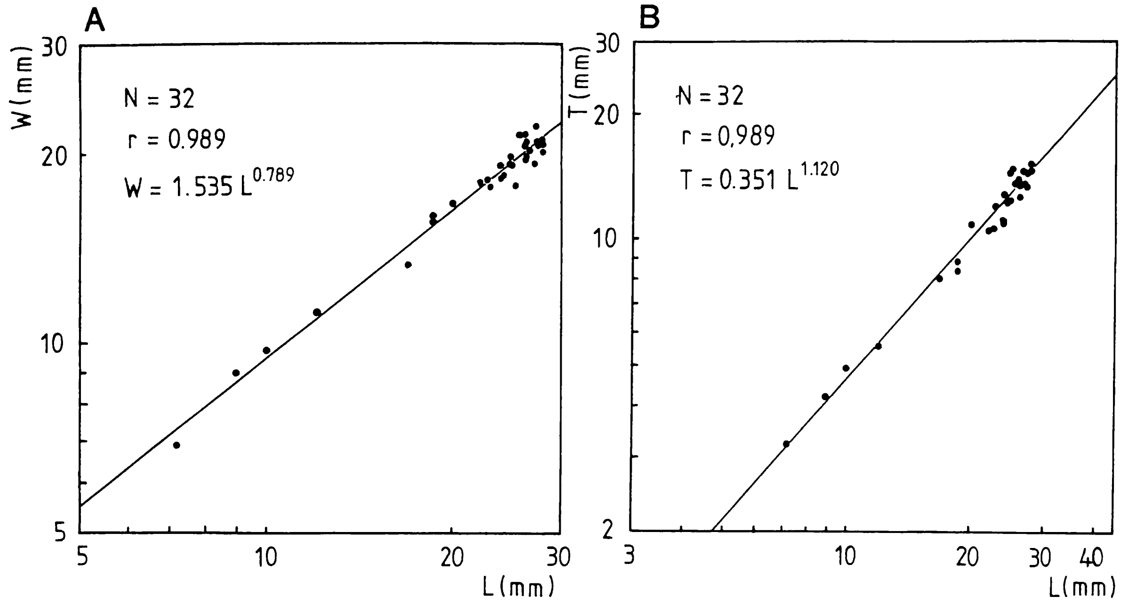

Figure 6. Double logarithmic allometric relationship between L and W (A) and between L and T (B) in *L. rubellus* [Sample *Rk* (80)]. Regression line with the reduced major axis is indicated in the this figure.

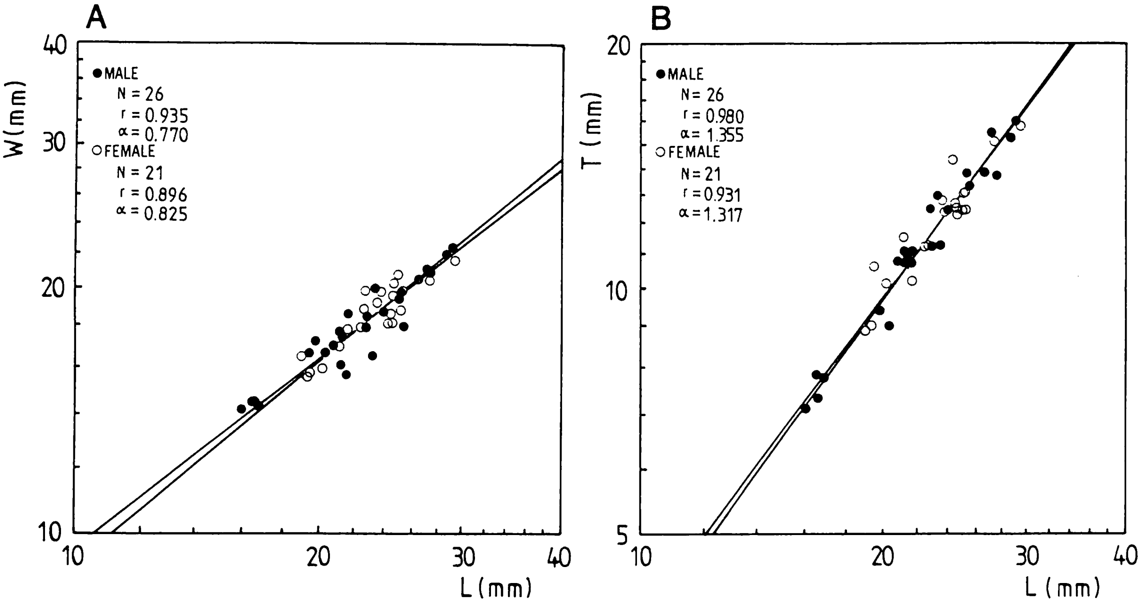

Figure 7. Double logarithmic allometric relationship between L and W (A) and between L and T (B) in *L. rubellus* [Sample *Rk* (13)]. Males and females are separately treated. Regression line with the reduced major axis is indicated in this figure.

Table 2. Allometric relationship between L and W and between L and T in eight samples of seven species. N: number of individuals; α: regression coefficient, slope of reduced major axis in the double logarithmic scatter diagram; σ: standard error of α; r: correlation coefficient; K: statistical value for discrimination of allometry (Hayami and Matsukuma, 1971).

species	sample	N	L - W				L - T			
			α	σ	r	K	α	σ	r	K
Laqueus rubellus	Rk(13)	47	0.786	0.043	0.926	- 4.96	1.345	0.049	0.968	7.04
L. rubellus	Rk(80)	32	0.789	0.021	0.989	-10.18	1.120	0.030	0.988	4.02
L. blanfordi	Ot(1,2)	27	1.004	0.014	0.997	0.30	1.206	0.015	0.998	13.76
L. sp. 1	Ts(L)	46	0.801	0.059	0.864	- 3.34	1.496	0.102	0.887	4.86
L. sp. 2	Sw	44	0.923	0.025	0.984	- 2.87	1.176	0.036	0.979	4.84
Pictothyris picta	Rk(P)	36	0.824	0.033	0.971	- 5.34	1.229	0.047	0.973	4.85
P. sp.	Ts(P)	43	0.867	0.024	0.983	- 5.44	1.178	0.033	0.983	5.39
Kikaithyris hanzawai	Wa	33	0.940	0.013	0.997	- 7.05	1.091	0.014	0.996	5.51

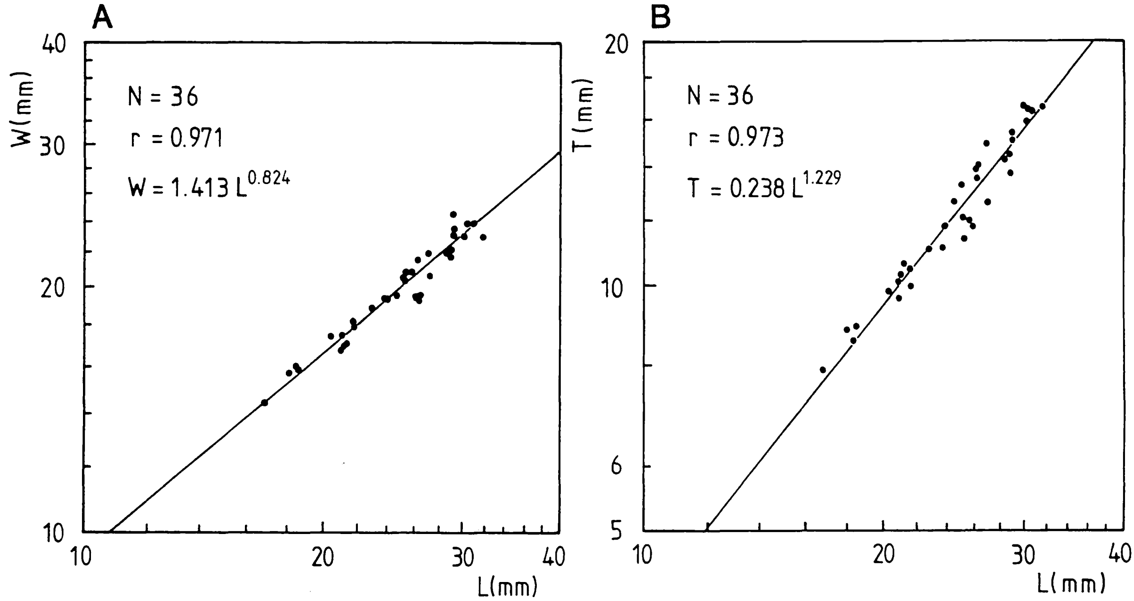

Figure 8. Double logarithmic allometric relationship between L and W (A) and between L and T (B) in *Pictothyris picta* [Sample *Rk* (P)]. Regression line with the reduced major axis is indicated in this figure.

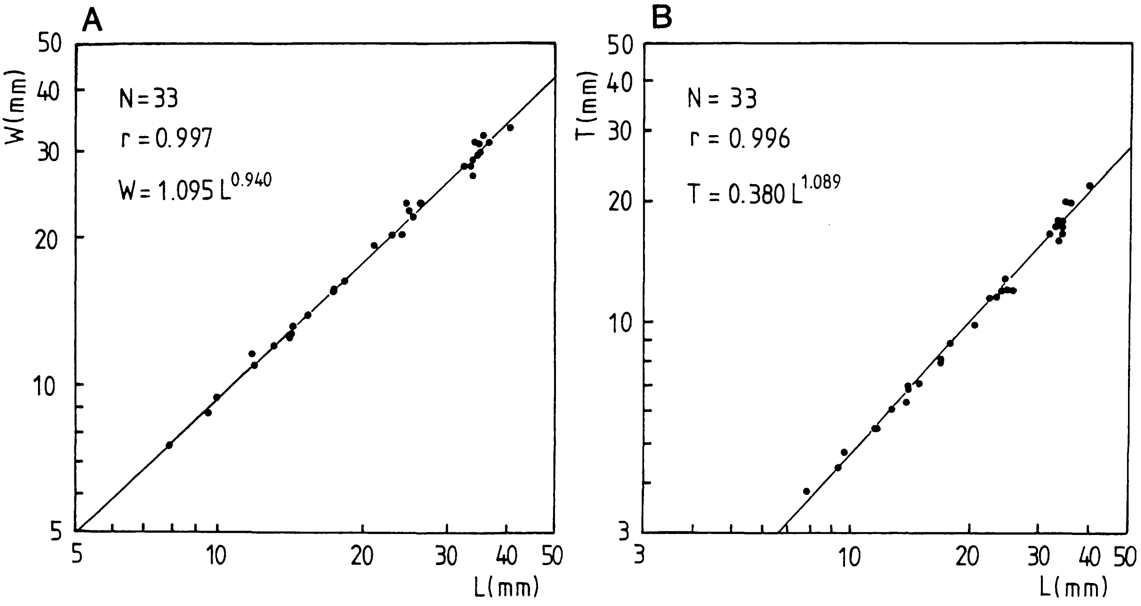

Figure 9. Double logarithmic allometric relationship between L and W (A) and between L and T (B) in *Kikaithyris hanzawai* (Sample *Wa*). Regression line with the reduced major axis is indicated in this figure.

blanfordi, the slope of allometry for W vs. L is negatively allometric, and this indicates the decrease in the ratio W/L with growth.

Interpretation of ontogenetic increase in valve convexity

Raup and Stanley (1978) stated that "ontogenetic change in shape accompanies two other sorts of change; *i.e.* change in mode of life and change in size." The change of shell shape with the change in mode of life is examined as the cause of ontogenetic increase in valve convexity. The mode of life in many living articulate brachiopods has been assumed to be rather monotonous; except for the larval stage, they permanently attached to hard substrate, feeding on the suspension matter through the lophophore.

In such an attached species, significant change in mode of life may not occur. However, some instances of secondary free-lying mode of life are observed in modern articulate species by Richardson (1981a, 1981b). Free-lying species sometimes retain attached nature to fragments of shells and pebbles, all of which are smaller in size than the animal, as is the case with *L. rubellus* from Sagami Bay.

In such free-lying species, the post-larval juveniles must attach themselves to some objects. The attached object may become unnecessary as living animals grow larger. It is at present unclear how the above change in mode of life relates tc the change in valve convexity or in commissure form. One possible explanation is hydrodynamic stability of the shell. Possibly, free-lying brachiopods are selected for hydrodynamic stability. Allometric increase in valve weight, as already stated, may have a role for this purpose. However, Alexander (1984) finds that hydrodynamic stability is highest in dorsal-ventrally compressed and concavo-convex species. Thus, allometric growth in laqueid brachiopods may not be produced by selection for hydrodynamic stability.

Ontogenetic increase in valve convexity was observed in all laqueid species from Japan including both the attached and free-lying species. For example, *L. blanfordi* attached rope shows positive allometry of T relative to L. The shift from the attached to the free-lying does not explain the change in shell form.

I believe that most allometric growth can be explained by size increase. McGhee (1980) assumed that the metabolic requirement of a brachiopod is a function of volume of the soft tissues and that the capacity of the lophophore to meet these requirements is a function of its filamental area, as expressed by the relative increase in the surface area of the lophophore. Therefore, the inner volume of the shell increases in ontogeny to house the allometrically growing lophophore. The economics of shell secretion dictates that a spherical surface is most efficient to attain the greatest inner volume. Because of the accretionary growth of two coiling tubes in articulation, truely spherical form is not attainable. Therefore, brachiopods grow allometrically to increase shell convexity during ontogeny by decreasing the whorl expansion rate.

Surface area of the lophophore (*S1*), the inner volume of the shell (*V*), and the surface area of the shell (*A*) were measured to analyze the area-volume relationship discussed by McGhee (1980). All measurements were made on the sample *Rk* (80) of *L. rubellus*.

The surface area of the lophophore was calculated through the following procedure. The excised lophophore was cut into pieces and photographed at fixed magnification. The printed fragments were cut out along the margins, and the cut pieces of the printing paper were weighed. Lastly the weight was converted into the area. The inner volume was estimated by filling both valves with #800 carborundum and the weight of the carborundum was converted into inner volume. The surface area of the shell was calculated on an assumption that an ellipsoid approximates the outline of *L. rubellus*.

Because the length of the median septum (*Lm*, see Figure 2) roughly represents a linear dimension of the soft tissues and because the soft tissues occupy the space between the anterior and posterior edges of the median septum near the hinge line, these three measurements (*S1, A, V*) were compared to *Lm*. *Lm* was measured under the profile projector with a digital micrometer.

Table 3 shows the results of regression analyses on the relationship among *S1, A, V* and *Lm*. *S1* does not increase as the cube of *Lm* (α = 0.748), but it is positively allometric to the square of *Lm* at 95% confidence level. As is expected, the approximate surface area of the shell decreases with growth, relative to a linear dimension of the soft tissues (Figure 10). Since the surface area of the shell is two dimensional, the level of isometry in the relation between Lm^2 and A is at $\alpha = 1$. The actual growth of A to Lm^2 indicates negative allometry (α = 0.935). In spite of the ontogenetic change in the shell form, V increases isometrically

Table 3. Results of bivariate analyses on *S1, A, V* and *Lm*. [Sample *Rk* (80)]. For abbreviations see explanation in Table 2.

x y	N	α	r	K
Lm^2– Sl	32	1.123	0.962	2.26
Lm^3– Sl	32	0.748	0.962	-6.97
Lm^2– A	32	0.935	0.985	-2.27
Lm^3– V	24	0.986	0.982	-0.36

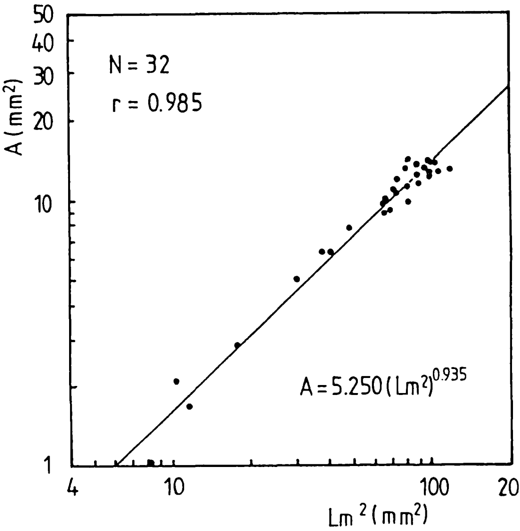

Figure 10. Double logarithmic allometric relationship between the square of *Lm* and *A* in *L. rubellus* [Sample *Rk* (80)]. Regression line with the reduced major axis is indicated in this figure.

relative to Lm^3. The plot of Lm^3 against V shows a regression coefficient of 0.986 and indicates near isometry.

The results obtained seem to consistent with the hypothesis of McGhee (1980) as a whole. The surface area of the lophophore ontogenetically increases over the square of the length, while the surface area of the shell ontogenetically decreases below it. However, contrary to expectations, the surface area of the lophophore does not increase as much as the cube of the length of the body. The inner volume of the shell increases nearly isometrically versus the cube of the length of the soft part. These facts indicate that the capacity to meet the metabolic requirement may not be a function of the filamental area of the lophophore, but a function of the inner volume of the shell, which the lophophore effectively occupies.

Another possible size-related explanation is that brachiopods become more convex to increase mechanical strength of the valves. The test of adult laqueid brachiopods is thin except for the cardinalial (posterior) part. The test thickness does not increase as the shell grows. This indicates the gradual decrease of the relative strength of the shell with growth, and, therefore, the reinforcement by shell form is considered to be required. The predator of the brachiopods is unknown, but non-fatal injuries in some specimens of *L. rubellus* from Sagami Bay suggest crabs are possible predators. The inflated form may be advantageous for avoiding shell crushing crabs.

The highly allometric growth of brachiopod valve inflation may also be explained by enlargement of the gonad during growth. As to *L. rubellus*, the gonad develops in the individuals whose shell length is larger than about 15 mm (the smallest adult individual ever measured is 14.75 mm and the largest juvenile is 21.30 mm in shell length). The weight of the gonad in an adult individual of *L. rubellus* attains more than 25% of the whole soft tissue weight (Table 4). In order to test this hypothesis, the allometric growth of gonad vs. shell size in juveniles and the adults of *L. rubellus* was analyzed separately using specimens in the three samples *Rk* (13), *Rk* (17), and *Rk* (80).

Table 4. Dried weight of each soft tissue in three specimens of *L. rubellus* [Sample *Rk* (100)].

SPECIMEN / BODY PARTS	1		2		3	
	WT.	%	WT.	%	WT.	%
GONAD	11.94	25.9	16.68	33.1	13.50	30.2
MANTLE & PERIOSTRACUM	9.11	19.8	14.08	28.0	8.19	18.3
PEDICLE & MUSCLE	10.08	21.9	8.17	16.2	11.64	26.0
DIGESTIVE SYSTEM	7.03	15.3	3.89	7.7	3.40	7.6
LOPHOPHORE	7.87	17.1	7.53	15.0	7.97	17.8
TOTAL	46.03	100.0	50.35	100.0	44.70	99.9

$\times 10^{-3}$g

Figure 11-A indicates that *T* and *L* are positively allometric in adults, but are isometrically related in juveniles. The regression coefficient of the adults is 1.342, the K-value against the null hypothesis of $\alpha = 1$ is 11.29. On the other hand, in the juveniles the regression coefficient value is 0.987 ($K = -0.53$).

The K-value against the null hypothesis of homogeneity of regression coefficients between juveniles and the adults is -9.09. The regression coefficients between mature and immature samples are different at the 95% level, and the relationship between *L* and *T* is considered to be diphasic allometry. *T* increases isometrically to *L* during the early growth stage, and *T* increases positively allometrically to *L* after initiation of gonad development. The co-ordinates of the turning (or "critical") point are calculated as $L = 17.9$ and $T = 8.3$ in mm. The close agreement between these measurements and the size at which gonad development begins strongly supports my suggestion that shell convexity increases to house the enlarged gonad. As to the *L-W* relation, no significant difference in regression coefficient between the juvenile and the adult was detected (Figure 11-B).

Conclusion

A common allometric trend is detected among examined laqueid brachiopods. The trend is two-

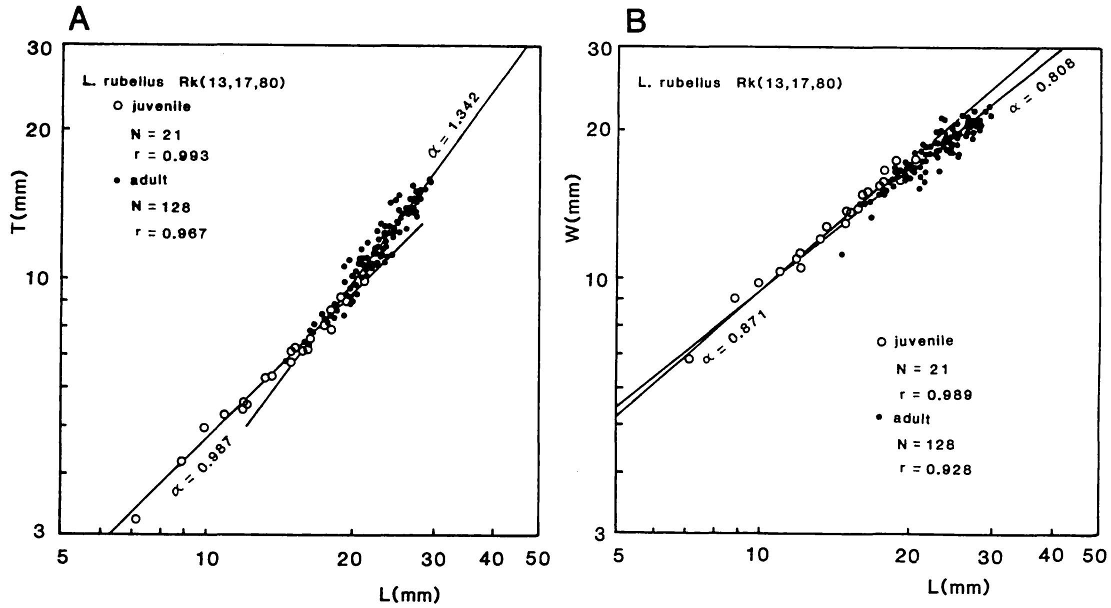

Figure 11. "Diphasic allometry" in the relationship between L and T (A), and "monophasic allometry" in the relationship between L and W (B). Sample *Rk* (13, 17, 80) of *L. rubellus*.

fold; one is relative increase of valve convexity to the length of the shell (L-T relation), and the other is relative decrease of valve width to the length of the shell (L-W relation).

Four different explanations may be possible about the L-T relation:

(1) to obtain hydrodynamic stability in the free-lying stage of life,
(2) to economize the secretion of shell material,
(3) to strengthen valves, and
(4) to host the well developed gonad.

Of these explanations, (1) is invalid because it does not explain the allometry in some permanently attached species, and because compressed shells are inferred to be more stable to the water current. Among the remaining three explanations, (4) is most convincing at least in the case of *L. rubellus* because of the apparent "diphasic" allometric relation between L and T. No plausible explanation for the L-W relation is still obtained. It requires a further study.

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Appendix

The following samples belonging to eight species of three genera were examined in this study. Their localities are roughly shown in Figure 12. All specimens utilized are stored at the University Museum of the University of Tokyo with registered numbers with prefix UMUT.

1. *Laqueus rubellus* (Sowerby) Figures 1-1–6
    - Fossil sample *Jz* (L) [N = 2] [UMUT CB18185]
        - Locality: Yamadakubo, Ichihara City, Chiba Prefecture (loc. 3).
        - Lithology and horizon: muddy medium grained sand of the Jizodo Formation of the Shimosa Group.
        - Age: Late Pleistocene.
        - Collector: Y. Kondo.
        - Remarks: Same locality as loc. no. 132 of Tokuhashi and Endo (1984).
    - Recent sample *Rk* (13, 17, 80, 82, 100, 104) [N = 184] [UMUT RB18186].
        - Locality: eastern part of Sagami Bay, about 2 km west of the Jogashima Islet (loc. 7) (35°7.9'N, 139°35.1'E, 80–90 m).
        - Status: living.
        - Bottom substrates: coarse grained sand with

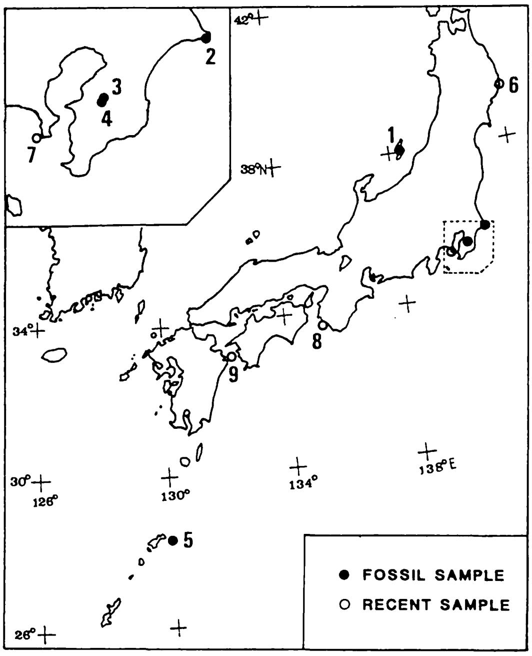

Figure 12. Map showing the localities of fossil and Recent samples studied in this paper. Fossil localities; 1: Sawane Formation at Sawada Town; 2: Na-arai Formation at Nagasakibana; 3: Jizodo Formation at Yamadakubo; 4: Jizodo Formation at Atebi; 5: Wan Formation at Kamikatetsu. Localities of Recent samples; 6: Mouth of Otsuchi Bay; 7: Off Jyogashima Islet; 8: Off Hinomisaki; 9: Off Tsukumi.

pebbles and shell fragments.
Collector: I. Hayami *et al.* (R/V Rinkai).

2. *Laqueus blanfordi* (Dunker) Figures 1-7–9
   Recent sample *Ot* (1) [N = 18] [UMUT RB18187].
   Locality: Mouth of Otsuchi Bay (loc. 6).
   Status: living.
   Collector: K. Endo.
   Recent sample *Ot* (2) [N = 9] [UMUT RB18188].
   Locality: Mouth of Otsuchi Bay (loc. 6).
   Status: dead.
   Collector: E. Tsuchida.
3. *Laqueus quadratus* Yabe and Hatai Figures 1-10–12
   Fossil sample *Na* [N = 16] [UMUT CB18189].
   Locality: eastern coast of Nagasakibana, Tokawa, Choshi City, Chiba Prefecture (loc. 2).
   Lithology and Horizon: tuffaceous matrix of conglomerate of the Na-arai Formation of the Inubo Group.
   Age: Pliocene.
   Collector: K. Endo.
   Recent sample *Hi* [N = 13] [UMUT RB18190].
   Locality: off Hinomisaki (loc. 8) (248 m), off Etsuzaki (165–240 m, 215–297 m), off Mugi (248 m), off Tanabe (264 m), Kii Channel.
   Status: dead.
   Collector: E. Tsuchida.
4. *Laqueus* sp. 1 Figures 1-13–15
   Recent sample *Ts* (L) [N = 46] [UMUT RB18191].
   Locality: off Tsukumi, Bungo Channel (loc. 9) (33°2.2'N, 132°5.4'E, 72–76 m).
   Status: living and dead.
   Bottom substrates: coarse grained sand with pebbles.
   Collector: I. Hayami *et al.* (R/V Tansei).
   Remarks: st. 31 of the cruise KT-84-12.
5. *Laqueus* sp. 2 Figures 1-16–18
   Fossil sample *Sw* [N = 44] [UMUT CB18192].
   Locality: Kaitate, Sawada Town, Sado Island, Niigata Prefecture (loc. 1).
   Lithology and Horizon: coarse grained sand of the lower Sawane Formation.
   Age: Pleistocene.
   Collector: K. Endo.
   Remarks: Precise locality is loc. no. 2 of Endo (1986).
6. *Pictothyris picta* (Dillwyn) Figures 1-19–21
   Fossil sample *Jz* (P) [N = 10] [UMUT CB18193].
   Locality: Atebi, Kisarazu City, Chiba Prefecture (loc. 4).
   Lithology and Horizon: medium grained sand of the Jizodo Formation of the Shimosa Group.
   Age: Late Pleistocene.
   Collector: K. Endo.
   Recent sample *Rk* (P) [N = 36] [UMUT RB18194].
   Locality: eastern part of Sagami Bay, about 2 km west of the Jogashima Islet (loc. 7) (35°7.9'N, 139°35.1'E, 80–90 m).
   Status: living.
   Bottom substrates: coarse grained sand with pebbles and shell fragments.
   Collector: I. Hayami *et al.* (R/V Rinkai).
7. *Pictothyris* sp. Figures 1-22–24
   Recent sample *Ts* (P) [N = 43] [UMUT RB18195].
   Locality: off Tsukumi, Bungo Channel (loc. 9) (33°2.2'N, 132°5.4'E, 72–76 m).
   Status: living.
   Bottom substrates: coarse grained sand with pebbles.
   Collector: I. Hayami *et al.* (R/V Tansei).
   Remarks: st. 31 of the cruise KT-84-12.
8. *Kikaithyris hanzawai* (Yabe) Figures 1-25–27
   Fossil sample *Wa* [N = 33] [UMUT CB18196].
   Locality: road-cut about 500 m north of Kamikatetsu, Kikai Island, Kagoshima Prefecture (loc. 5).
   Lithology and Horizon: coral sand of the Wan Formation of the Ryukyu Group.
   Age: Late Pleistocene.
   Collector: I. Hayami.

日本産ラクエウス科腕足動物の生態と相対成長：日本産新生代ラクエウス科腕足動物は，個体発生において相対成長に2つの傾向を示す。殻長に対する殻のふくらみの相対的増加と殻長に対する殻幅の相対的減少である。これらの異成長の原因を知るために現生 *Laqueus rubellus* (Sowerby) を主に用いて，形態，生態および殻の成長に関連するいくつかの変量の相対成長を調べた。殻のふくらみの相対的増大の理由として，(1)殻物質の経済的沈着，(2)殻強度の増大，及び(3)生殖巣収納スペースの確保の3つの説明が考えられる。*L. rubellus* に関しては，成体において殻のふくらみが殻長に対して優成長を示すのに対し，生殖巣をもたない幼体においては，殻のふくらみと殻長の関係は等成長を示すことから，これらのうち(3)の説明が最も適切である。

遠藤一佳

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