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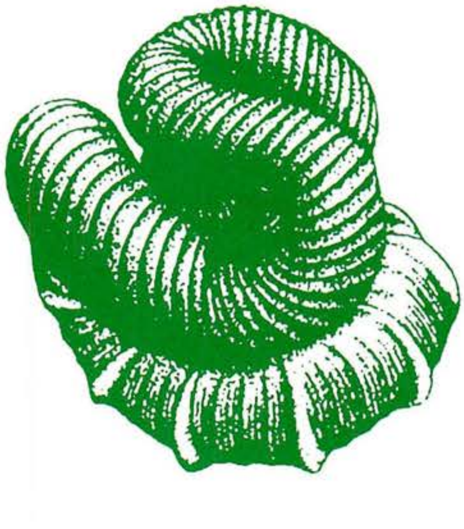

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Cover : Idealized sketch of *Nipponites mirabilis* Yabe, a Late Cretaceous (Turonian) nostoceratid ammonite. Various reconstructions of the mode of life of this species have been proposed, because of its curiously meandering shell form (after T. Okamoto,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

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Permian bivalves from West Spitsbergen, Svalbard Islands, Norway

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Abstract. The bivalve fossils collected by Japanese-Norwegian research groups from the Kapp Starostin Formation in west Spitsbergen are described. They comprise fourteen species belonging to the Pterioida and two species of the Arcoida. Among them, six species, including two that are indeterminate, are newly described. They are *Grammatodon* (*Cosmetodon*)? *suzukii, G.* (*C.*)? sp. ind., *Streblochondria winsnesi, Vorkutopecten svalbardensis, Deltopecten* sp. ind., and *Palaeolima nakamurai*. The fauna belongs to the Boreal bioprovince, but a single species, *Cassianoides sexcostatus* (Stuckenberg) has also been reported from the Central Rocky Mountains of the United States. The bivalve fauna suggests an Artinskian-Kungurian age for the Kapp Starostin Formation. This is somewhat earlier than the age deduced from brachiopods and bryozoans, but it is not decisive because the materials are poor. The Kapp Starostin Formation is conformably overlain by the *Otoceras*-bearing, earliest Triassic Vardebukta Formation, so a time-gap corresponding at least to the Dorashamian and Dzhulfian (= Tatarian) is inferred between the two formations.

Key words: Kapp Starostin Formation, Permian bivalves, Spitsbergen

Introduction

The study materials were collected by Nakamura *et al.* in 1984 and 1990, and by Nakazawa *et al.* in 1986 from the Permian Kapp Starostin Formation of west Spitsbergen, in the Svalbard Islands, Norway. Brachiopods and bryozoans are most abundant among the macrofossils. Many species of brachiopods have been described by various authors, notably, Frebold (1937) and Gobbet (1963). Bivalves are found rather rarely and the descriptive studies are few. Toula (1873, 1875a, b) first described the following species, collected from "Carboniferous-Permian" strata on Sørkapp Island off the southerntip of Spitsbergen, and Axel Island in Bellsund and on Hornsund, on the west coast of Spitsbergen :

Pecten (*Aviculopecten*) *bouei* Verneuil, *Pecten* (*Aviculopecten*) *kokscharofi* Verneuil, *Pecten* (*Aviculopecten*) cf. *ellipticus* Phillips, *Pecten* (*Aviculopecten*) cf. *dissimilis* Fleming, *Pecten* (*Aviculopecten*) *wilczeki* Toula, *Gervillia* cf. *antiqua* Münster, *Aviculopecten draschei* Toula and *Gervillia* sp.

Frebold (1937) described the following species, mostly from the upper part of the Kapp Starostin Formation in the Festningen section, located on the southern coast of Spitsbergen at the entrance to Isfjorden and from Sørkapp Island :

Aviculopecten (*Deltopecten*) cf. *mutabilis* Licharew and *A.* (*D.*) cf. *hiemalis* Salter, *Aviculopecten*? sp. indet., *Pecten* (*Aequipecten*)? *keyserlingiformis* Licharew, *Pecten* (*Aequipecten*) *keyserlingi* Stuckenberg, *Pecten* (*Pseudamusium*) cf. *ufaensis* Tschernyschew, *Pecten* (*Pseudamusium*) ex aff. *sericeus* Verneuil, *Parallelodon* sp. ind., genus [=*Parallelodon*?] et sp. ind., *Clidophorus*? sp. ind., *Pecten wilczeki* Toula, and *Leda* sp. ind.

Among the species described by Toula, *Aviculopecten bouei* was referred to *Aviculopecten* (*Deltopecten*) *mutabilis* by Licharew (1927). *Pecten* cf. *ellipticus* was identified as *Pecten* (*Pseudamusium*) ex aff. *sericeus* Verneuil, and *Pecten* (*Aviculopecten*) cf. *dissimilis* was compared to *Aviculopecten netschajewi* Licharew and reported as *Aviculopecten*? sp. ind. by Frebold (1937). *Aviculopecten kokscharofi* reported by Toula (1873) is probably identical with *Aviculopecten* cf. *hiemalis* illustrated by Licharew (1927, especially pl. 5, fig. 20), and is referred to *Etheripecten* cf. *mutabilis* Licharew in the present paper.

Among the species reported by Frebold, *Aequipecten keyserlingi* was considered to belong to the genus *Morrispecten* Muromtseva and Guskov by Muromtseva (1984, p. 75). *Morrispecten* is, however, a junior synonym of *Undopecten* Waterhouse, 1982 (Newell and Boyd, 1995). *Pecten* (*Aequipecten*)? *keyserlingiformis* and *Aviculopecten* (*Deltopecten*) cf. *mutabilis* and *A.* (*D.*) cf. *hiemalis* of Frebold are referred to *Etheripecten keyserlingiformis* and *E.* cf. *mutabilis*?, respectively. *Pseudamusium* cf. *ufaensis* and *Parallelodon* sp. ind. are identified as *Streblochondria winsnesi* sp. nov. and *Grammatodon* (*Cosmetodon*)? *suzukii* sp.

nov., respectively, in the present paper. Sixteen species including four new species and two indeterminable ones are described. All the materials are kept at the Department of Geology and Mineralogy, Faculty of Science, Kyoto University.

Stratigraphy

The fossils were collected at four localities in west Spitsbergen, namely, the Festningen section along the southern coast of the entrance to Isfjorden, the Skansbukta section at Billfjorden, and the Reinodden and Ahlstrandodden sections along the southern coast near the entrance of Van Keulenfjorden, in Bellsund (Figure 1). Faunas from the first and second localities were collected on Nakamura's expedition in 1984 and in 1990. The stratigraphy of these sections was published by Nakamura *et al.* in 1990 and, in more detail, by the Japanese-Norwegian Research Group (1992). The other two localities were examined by Nakazawa's party in 1986 and the results were published by Nakazawa *et al.* (1990). All the materials are from the Permian Kapp Starostin Formation which was defined by Cutbill and Challinor (1965). The formation corresponds to the Brachiopod Cherts (including the *Spirifer* Limestone at the base) of previous authors (e.g., Gee *et al.*, 1953). At the type locality, Festningen, the formation is divided into three members, the Vøringen, Svenskeegga, and Hovtinden Members in ascending order (Cutbill and Challinor, 1965).

(1) *Festningen section* (Figure 2A)

At Festningen the Kapp Starostin Formation is 385 m in thickness and divided into twelve units (Nakamura *et al.*, 1990; Japanese-Norwegian Research Group, 1992). Unit 1, about 20 m thick, is represented by brachiopod-rich, bioclastic limestone beds corresponding to the Vøringen Member. Units 2 to 5, about 140 m thick, constitute the Svenskeegga Member, each represented mainly by siliceous shale, spicularite, spicularite and shale, and bioclastic limestone, respectively.

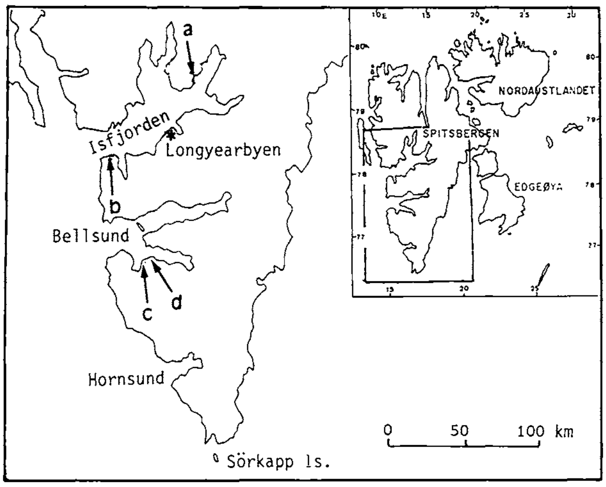

Figure 1. Map of southern Spitsbergen showing fossil localities. a: Skansbukta, b: Festningen, c: Reinodden, d: Ahlstrandodden.

The Hovtinden Member, about 225 m thick, consists of seven units, 6 to 12, each composed mainly of spicularite, alternation of spicularite and spicularitic shale, bioclastic limestone, spicularite, bioclastic limestone (partly silicified), alternation of siltstone and paper shales, and quartzose sandy shale or siltstone, respectively, in ascending order. Bivalve fossils have been obtained from Units 5, 7, 8, 9 and 11.

(2) *Reinodden section* (Figure 2B)

At Reinodden the formation reaches more than 300 m in thickness. It is classified into eight units, A to H, in ascending order (Nakazawa *et al.*, 1990). Unit A, less than 5 m thick, is the Vøringen Member consisting of fossiliferous bioclastic limestone. Units B and C are referred to the Svenskeegga Member. Unit B, about 40 m thick, is subdivided into three beds or subunits, 2 to 4. Beds 2 and 4 are represented by nodular or irregularly bedded, alternating spicularitic chert and thin mudstone. Bed 3 consists of black laminated shale and siltstone. Unit C, about 80 m thick, includes bedded black shale (Bed 5), and alternations of calcareous sandstone and limestone (Beds 6 and 7).

The Hovtinden Member (Units D to H), about 180 m thick, is characterized by coarse-grained sandstone and spicularite. It is subdivided into fourteen beds, Beds 8 to 21, as shown in Figure 2B. Glauconite is commonly found in the sandstones. Macrofossils have been collected from ten horizons (RP 1∼10) in the Kapp Starostin Formation, among which RP 3, 7 and 9 contain bivalve fossils.

(3) *Ahlstrandodden section* (Figure 2C)

At Ahlstrandodden the formation is about 250 m thick. It is divided into eight units, 1 to 8 (Nakazawa *et al.*, 1990). Unit 1, 7.6 m thick, consists of brachiopod-rich bioclastic wackestone of the Vøringen Member. Units 2 and 3, which are 40 m and 58 m thick, respectively, are correlated to the Svenskeegga Member. Units 4 to 8, about 140 m thick altogether, correspond to the Hovtinden Member. They are composed mainly of spicularitic chert or spicularite, siliceous shale and a minor amount of limestone. Glauconite grains are commonly found in siliceous sandstones throughout the Hovtinden Member.

Among nine fossiliferous horizons (AP 1∼9) within the formation, five horizons, AP 1, 2, 6, 7 and 8, yield bivalve shells. The fossiliferous horizons AP 8 and 9 of the upper part of the Hovtinden Member can be correlated with horizons RP 9 and 10 in the Reinodden section. They are considered to correspond to horizon F 8 of the Festningen section.

Fossil occurrence and age assignment

Sixteen species in nine genera are identified from three sections mentioned above, plus one species, *Acanthopecten licharewi* (Fredericks), from Skansbukta (SA 7), as shown in Figures 3. The localities and stratigraphic horizons are shown in Figure 2.

Nakamura *et al.* (1987, 1992) distinguished five brachiopod assemblage zones in the Kapp Starostin Formation of the Isfjorden area. They compared these faunas to those of Russia, Arctic Canada, Greenland, and Alaska, all belonging

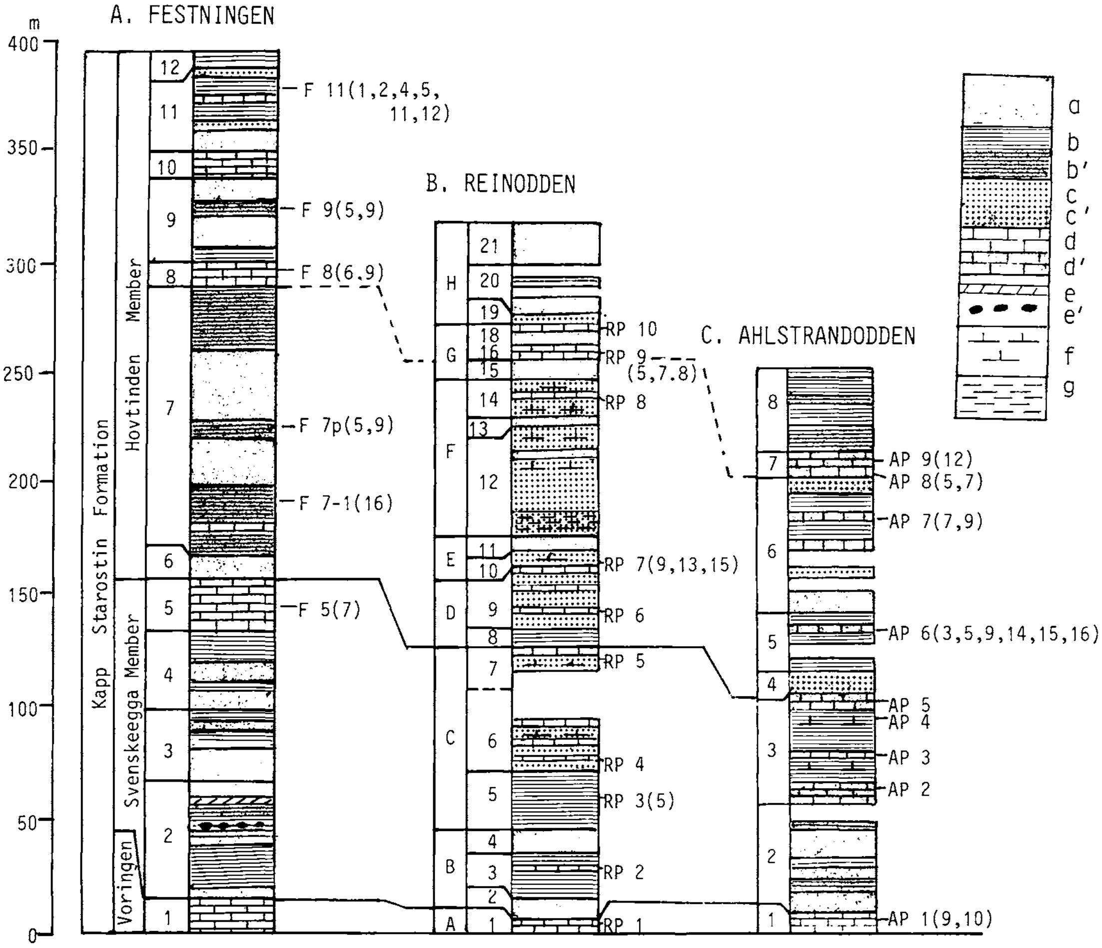

Figure 2. Geological columnar sections of the Kapp Starostin Formation at three localities showing horizons of macrofossils. a : chert or spicularite, b : shale or mudstone, b′ : siliceous or spicularitic, c : sandstone, c′ : siliceous, d : limestone, d′ : siliceous, e : dolostone, e′ : dolostone nodule, f : calcareous, g : muddy. Numbers in parentheses correspond to those of bivalve species in Figure 3. A : simplified from Japanese-Norwegian Research Group (1992, fig. 2), B and C : from Nakazawa *et al.* (1990, fig. 2).

to the Boreal bioprovince. From the correlation of these faunas, they concluded that the Kapp Starostin Formation ranges in age from Kungurian up to Midian or early Dzhulfian (Tatarian). Sakagami (1992) studied the bryozoans and pointed out the similarity of the fauna from the Vøringen Member with the Kungurian fauna in the Timan-Pechora region. Faunas of the Svenskeegga and Hovtinden Members resemble Ufimian faunas of Arctic Canada and the Russian Far East, the Kazanian fauna of the southern Urals, and the Late Permian fauna of British Columbia. These comparisons are consistent with the age range inferred from the brachiopods, except that there is no positive evidence, from the bryozoans, of the presence of Dzhulfian strata. These observations support previous views on the age of the Kapp Starostin Formation, for example, Forbes *et al.* (1958) and Flood *et al.* (1971).

The ranges of the bivalve species are shown in Figure 3. Only two species, *Vorkutopecten svalbardensis* and *V.* aff. *svalbardensis* have been found in the Vøringen Member. The overlying Svenskeegga Member is also poor in bivalves. Five species have been collected there, namely, *Etheripecten* cf. *mutabilis*, *Etheripecten wilczeki*, *Vorkutopecten svalbardensis*, *Acanthopecten licharewi*, and *Deltopecten* sp. All infrequently occur and their ranges extend up into the Hovtinden Member. Accordingly, the fauna is not essentially different from that of the Hovtinden Member.

Eight and ten species could be identified from the lower and upper parts of the Hovtinden Member, respectively. In addition to species ranging up from the Svenskeegga Member, *Streblopteria* cf. *eichwaldi*, *Streblopteria* ? sp. and *Palaeolima nakamurai* appear from the lower part, but they have not been found from the upper part. The upper part is relatively rich in bivalve fossils. *Grammatodon* (*Cosmetodon*) ? *suzukii*, *G.* (*C.*) ? sp., *Etheripecten keyserlingiformis*, *E.* aff. *sichuanensis*, *E.*? *alatus*, *Streblochondria winsnesi* and *Cassianoides sexcostatus* appear here.

The intimate relationship of the Spitsbergen fauna with that of the Russian Arctic region (Ural, Pechora, Russian Platform, Verkhoyansk) is shown by the occurrence of the following species :

	Vøringen	Svenkeegga Member	Hovtinden Member	
			Lower	Upper
1. *Grammatodon* (*Cosmetodon*)? *suzukii* sp. nov.				*
2. *Grammatodon* (*Cosmetodon*)? sp. ind.				*
3. *Acanthopecten licharewi* (Fredericks)		X	★	*
4. *Etheripecten keyserlingiformis* (Licharew)				*
5. *Etheripecten* cf. *mutabilis* (Licharew)		☆	★*	★*☆
6. *Etheripecten* aff. *sichuanensis* (Chen et al.)				*
7. *Etheripecten wilczeki* (Toula)		*		★☆
8. *Etheripecten*? cf. *alatus* (Lyutkevich and Lobanova)				
9. *Vorkutopecten svalbardensis* sp. nov.	★	★	★*☆	★*
10. *Vorkutopecten* aff. *svalbardensis* sp. nov.	★			
11. *Cassianoides sexcostatus* (Stuckenberg)				*
12. *Streblochondria winsnesi* sp. nov.				★ *
13. *Deltopecten* sp. ind.		★	☆	
14. *Streblopteria* cf. *eichwaldi* (Stuckenberg)			★	
15. *Streblopteria*? sp. ind.			★	
16. *Palaeolima nakamurai* sp. nov.			*	

Figure 3. Compiled range-chart of bivalve fossils. * : Festningen, ☆ : Reinodden, ★ : Ahlstrandodden, × : Skansbukta.

Acanthopecten licharewi (Asselian-Artinskian of the Urals, Kungurian of Pechora, Lower Permian of Verkhoyansk), *Etheripecten keyserlingiformis* (Upper Carboniferous ?-Lower Permian of the Urals and Pechora), *E.* cf. *mutabilis* (Upper Carboniferous-Lower Permian of the Urals, Timan, Siberia), *E.? alatus* (Lower Permian of Pai Khoi in Siberia), *Streblopteria* cf. *eichwaldi* (Artinskian of the Urals and Russian Platform), and *Cassianoides sexcostatus* (Artinskian of the Urals and Russian Platform). *Cassianoides sexcostatus* is also reported from the Guadalupian of the United States (Branson, 1930; Ciriacks, 1963) and *Etheripecten sichuanensis* occurs in the Upper Permian of South China (Cheng *et al.*, 1974).

The stratigraphic occurrences of these species suggest that the Kapp Starostin Formation ranges in age from Artinskian to Kungurian. This is somewhat earlier than the age range inferred from the brachiopods and bryozoans, but the materials are poor and the conclusion is not definitive.

The Kapp Starostin Formation is conformably overlain by the Lower Triassic Vardebukta Formation of the Sassendalen Group (Nakazawa *et al.*, 1990; Nakamura *et al.*, 1990). The earliest Triassic age of the basal part of this formation is indicated by the occurrence of *Otoceras boreale* Spath together with *Claraia stachei* (Bittner) (Kortshinskaya, 1986; Nakazawa *et al.*, 1987). Hence, a time-gap corresponding at least to Dzhulfian-Dorashamian ages is indicated between the Permian and the Triassic beds.

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Systematic description

Order Arcoida Stoliczka, 1871
Family Parallelodontidae Dall, 1890
Subfamily Grammatodontinae Branson, 1942
Genus **Grammatodon** Meek and Hayden, 1861
Subgenus **Cosmetodon** Branson, 1942

***Grammatodon* (*Cosmetodon*)? *suzukii* sp. nov.**

Figures 4-1a, b

Parallelodon sp. ind. Frebold, 1937, p. 55, pl. 1, figs. 8, 9.

Materials.—A pair of left and right external molds.

Holotype, Reg. no. HP 100050.

Etymology.—Dedicated to Dr. Hiroyuki Suzuki of Doshisha University, who worked in the field with the author.

Diagnosis.—Permian *Grammatodon* characterized by well developed, fine radial ribs and a little arcuate ventral margin.

Description.—Shell moderate in size, a little inflated, elongated subquadrate with subparallel dorsal and ventral margins, rounded anterior and truncated posterior margins; ventral margin slightly arcuate; 41 mm long and 19 mm high; umbo broad and low, raised above the hinge margin, situated at anterior one-fifth of shell length; bluntly rounded umbonal ridge running from the umbo to the posteroventral extremity; surface covered by numerous, weak radial striae, wider than the interstices, approximately fifteen per centimetre width on the medial surface of the shell, one centimetre from the umbo; densely spaced concentric growth lines form cancellate sculpture with the radials (Figure 4-1b); hinge and internal characters not observable.

Comparison.—Two incomplete specimens illustrated by Frebold (1937) from near the same horizon at Festung (= Festningen) are identical with the present species. Based on Permian material from Malaysia, Yancey (1985) pointed out the possibility that most of the Paleozoic species described as *Parallelodon* should be referred to *Grammatodon* (*Cosmetodon*). Although the present species does not show its hinge characters, it is identified with that genus on the basis of its external shape and ornament. It is similar to the Guadalupian *Cosmetodon multistriatus* (Girty, 1908, p. 423, pl. 31, figs. 13, 14) in its shape and weak radial ornament, but it differs from that species in having less numerous radial striae, a little arcuate ventral margin and a larger size.

Occurrence.—Rare in black shale of the uppermost fossil horizon, in the Hovtinden Member (F11) at Festningen.

***Grammatodon* (*Cosmetodon*)? sp. ind.**

Figures 4-2a, b

Genus (*Parallelodon*)? et sp. ind. Frebold, 1937, p. 56, pl. 2, fig. 4.

Material.—One incomplete, right external cast. Reg. no. HP 100051.

Description.—Posterodorsal marginal part is missing. Preserved part of the specimen is 30 mm long and 18.5 mm high. It is twice as long as high judging from the growth line. Surface is covered by numerous, close-set radial striae and growth lines which are very weak, but visible under the magnifying glass. The radials reach about forty per centimetre width on the medial part of the shell, one centimetre from the umbo (Figure 4-2b).

Discussion.—The present material most probably belongs to the species doubtfully referred to *Parallelodon* by Frebold (1937) from Festningen. It is similar to *G.* (*C.*)? *suzukii* in shape, but differs from it in more densely spaced and more irregular radial ornament. In its numerous radial striae it is similar to *Grammatodon multistriatus* (Girty), but it has a different shape with a more convex ventral margin than the latter species. Evidence is not adequate to support a new species for this specimen.

Occurrence.—Locality and horizon are identical with those for the preceding species.

Order Pterioida Newell, 1965
Superfamily Pectinacea Rafinesque, 1815
Family Aviculopectinidae Meek and Hayden, 1864
Subfamily Aviculopectininae Meek and Hayden, 1864
Genus ***Acanthopecten*** Girty, 1903

Acanthopecten licharewi (Fredericks, 1915)

Figures 4-3—5

Pterinopecten Licharewi Fredericks, 1915, p. 28, pl. 1, fig. 14.
Aviculopecten (*Acanthopecten* ?) *licharewi* (Fredericks). Licharew, 1927, p. 91, pl. 6, fig. 24.
Acanthopecten licharewi (Fredericks). Muromtseva, 1984, p. 66, pl. 25, fig. 26; pl. 28, figs. 7, 8, 11, 12.

Materials.—One nearly complete and one incomplete external cast of left valves, an incomplete external mold of a left ? valve, and an incomplete external mold of a right valve. Reg. nos. HP 100052~55.

Description.—All the specimens are incomplete internal molds or somewhat abraded external casts, and the details of the ornament are imperfectly preserved.

Shell small, subequivalve, subcircular in shape; left valve a little inflated; right valve nearly flat; anterior auricle of left valve trigonal and sharply defined; posterior auricle relatively large, flat, alate and protruding posterodorsally, but not sharply defined from the disc. Shape variable, probably due to secondary deformation; one left valve of nearly equal height and length, with an apical angle of 100° (Figure 4-3) and another left valve more elongate (L/H ratio of 1.34) with

Table 1. Measurements of *Acanthopecten licharewi* (Fredericks). Abbreviations and notation of Tables 1-8. L: length, H: height, U: distance of umbo from the anterior end of the shell, l: hinge length, r: total number of radial ribs, $r_{1,2}$: number of primary and secondary radials, respectively, $r_{2\sim4}$: number of secondary to fourth-order radials between primary radials, r_{3+4}: number of third- and fourth-order radials between primary and secondary radials, c: number of comarginal lamellae or costae, a: apical angle (in degrees), V: valve (R: right, L: left), *: estimated value, linear dimensions in mm, Hor.: horizon.

Reg.	no.	L	H	H/L	a	r	c	V	Hor.
HP	100052	23.0	19.5*	0.85	100	13	11	L	AP 6
HP	100055	20.5_+	—	—	120	17	9_+	R	AP 6
HP	100054	28.5	22_+	—	—	14_+	6_+	R	AP 6
HP	100053	14_+	14.8	—	—	8_+	7	L	SA 7

1a

2a

3

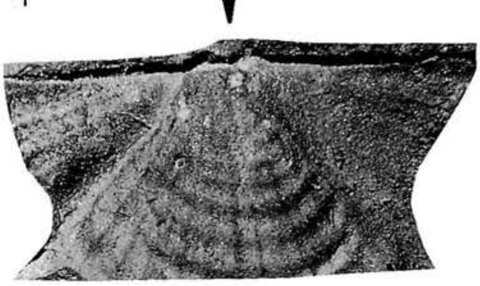
2b

1b

5

4

6

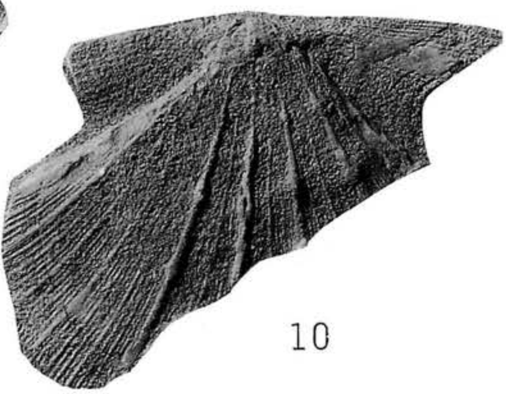


7b

7a

8

11



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12

a larger apical angle, 120°; radial ribs narrow and widely spaced varying in number from 13 to 17; interspaces between radials slightly concave or nearly flat; lamellose comarginal sculpture widely disposed, becoming wider later in growth stage with distally oriented spines in the middle of the interspaces of the radial ribs (Figure 4-5).

Discussion.—This species is similar to the Lower Permian *Acanthopecten licharewi* (Fredericks, 1915) from the Urals, Pechora and Verkhoyansk, and to the Upper Carboniferous *Acanthopecten carbonarius* (Stevens) reported from the United States (e.g., Newell, 1938), China (Chao, 1927), and the Donetz Basin (Jakowlew, 1903) in its small size and relatively small number of radial ribs. According to Muromtseva (1984), *A. licharewi* is distinguished from *A. carbonarius* in having less numerous radial ribs and completely flat interspaces between the radials. In these respects, the present material is identical with *A. licharewi*.

Occurrence.—Rare in calcareous shale or muddy siliceous limestone of Unit 5 (lower part of Hovtinden Member) at Ahlstrandodden (AP 6), and in black shale of Unit 7 (upper part of Svenskeegga Member) at Skansbukta (SA 7). According to Thore S. Winsnes (personal communication, 1995) it also occurs in Permian strata in the valley north of Stensiöfjellet, inner Sassendalen.

Subfamily Etheripectininae Waterhouse, 1982

Genus **Etheripecten** Waterhouse, 1963

Discussion.—This genus was introduced by Waterhouse (1963) based on *Etheripecten striatura* Waterhouse from the Upper Permian of New Zealand. The ornament of the left valve resembles that of "*Aviculopecten*" with radial ribs increasing in number by insertion and differentiated into more than two orders. The radial ribs of the right valve of this species also increase in number by insertion, but are usually weaker and less differentiated than those of the left valve. In "*Aviculopecten*", the number of radial ribs of the right valve increases by bifurcation or ramification. In this respect, *Etheripecten* is similar to *Limipecten*, but according to Waterhouse (1969) the concentric lamellae between radial ribs of *Etheripecten* point dorsally, while those of *Limipecten* point ventrally as in the case of *Aviculopecten planoradiatus* M'Coy, the type species. Recently, Newell and Boyd (1995) reexamined the Late Paleozoic pectinoids. They defined *Aviculopecten* and Aviculopectinidae as bivalves with equiconvex shells, provided with simple plicae in both valves. On the other hand, the family Etheripectinidae is characterized by inequiconvex and paradiscordant shells, with multicostate ornament. Newell and Boyd stressed the variability of multiplicated ribbing and concentric sculpture in this family, treating the genera *Aviculopecten* and *Deltopecten* of authors, *Etheripecten* Waterhouse, *Paradoxipecten* Zhang, *Corrugopecten* Waterhouse, *Fletcheripecten* Waterhouse and *Squamuliferipecten* Waterhouse as synonyms of *Heteropecten* Kegel and Costa. In this case, *Heteropecten* contains a vast number of species with various kinds of ornamentation. In this paper, *Etheripecten* is treated as a distinct genus from *Heteropecten*, the type species of which, *Aviculopecten catharinae* Reed, has broad and bifurcated radial ribs in the right valve. *Fletcheripecten* and *Paradoxipecten* are here considered to be synonyms of *Etheripecten*.

Etheripecten keyserlingiformis (Licharew, 1927)

Figures 4-6, 7a, b

Pecten (*Aequipecten*)? *keyserlingiformis* Licharew, 1927, p. 33, pl. 3, figs. 1-3; Frebold, 1937, p. 52, pl. 7, fig. 7.

Aviculopecten keyserlingiformis (Licharew). Muromtseva, 1984, p. 60, pl. 28, fig. 10.

Materials.—One nearly complete, left semiexternal cast (HP 100056) and one incomplete, left internal mold (HP 100057).

Description.—Shell medium in size, pectiniform, a little inflated, prosocline, extended posteroventrally; disc fan-like in shape with slightly arcuate anterodorsal, nearly straight posterodorsal, and rounded ventral margins; anterior auricle trigonal with slightly convex anterior margin; posterior auricle a little larger than anterior one, sinuated posteriorly; hinge margin straight, shorter than shelllength; ligament area narrow, nearly smooth, provided with a trigonal alivincular ligament pit beneath the umbo (Figure 4-7b); umbo not prominent, slightly salient above the hinge margin, situated at about anterior two-fifths of shell length; surface ornamented with nine or ten slender primary radial ribs alternating with secondaries, some of which become as strong as the primaries; two or three radial riblets of third and fourth order inserted in each interspace; strong concentric folds developed over the whole surface of the disc, more widely spaced in later growth stage; three radial ribs observable on anterior auricle, and obsolete ones on posterior auricle.

Discussion.—These specimens are identical with *Pecten* (*Aequipecten*) *keyserlingiformis* reported by Licharew (1927) and Frebold (1937), in its characteristic ornamentation. Probably due to secondary deformation, one specimen (Fig-

Figure 4. **1a, b.** *Grammatodon* (*Cosmetodon*) ? *suzukii* sp. nov., 1a: a pair of external molds of left and right valves, holotype (HP 100050), 1b: enlarged figure showing details of sculpture, ×2.5. **2a, b.** *Grammatodon* (*Cosmetodon*) ? sp., 2a: right external cast (HP 100051), 2b: enlarged figure showing details of sculpture, ×4. **3-5.** *Acanthopecten licharewi* (Fredericks), 3, 4: left semiexternal casts (HP 100052 and 53), ×2 and ×1.5, 5: right external mold (HP 100054), ×1.5. **6, 7a, b.** *Etheripecten keyserlingiformis* (Licharew), 6: left semiexternal cast (HP 100056), 7a: left semiexternal cast (HP 100057), 7b: enlarged figure showing alivincular ligament pit (arrow), ×2.5. **8, 9.** *Etheripecten wilczeki* (Toula), 8: gypsum cast of left external mold (HP 100058), ×1.5, 9: left external mold (HP 100059), ×2. **10.** *Etheripecten* sp. aff. *E. sichuanensis* (Chen *et al.*), gypsum cast of left external mold (HP 100060). **11, 12.** *Etheripecten* sp. cf. *E. mutabilis* (Licharew), 11: gypsum cast of left external mold (HP 100062), 12: left semiexternal cast (HP 100071). All are in natural size unless otherwise indicated.

Table 2. Measurements of *Etheripecten keyserlingiformis* (Licharew).

Reg.	no.	L	H	H/L	r_{1+2}	r_{3+4}	a	c	Hor.
HP	100056	45.5	40.0	0.89	18	3	115	15	F 11
HP	100057	–	17.6	–	15_+	$1\sim2$	90	11	F 11

ure 4-6) is extended posteroventrally and has a more elongated shape than the previously described species, but another (Figure 4-7a) has a shape and ornamentation similar to the type specimen. Although the right valve of this species has not been reported, the shape and ornamentation of its left valve are very similar to those of *Etheripecten striatura* Waterhouse, the type species of the genus, so the species is here included in *Etheripecten*.

Occurrence.—Rare in black shale of the uppermost fossil horizon of the Hovtinden Member at Festningen (F11).

Etheripecten wilczeki (Toula, 1875)

Figures 4-8, 9

Pecten (*Aviculopecten*) *Wilczeki* Toula, 1875a, p. 152, pl. 1, fig. 12.
Pecten wilczeki Toula. Frebold, 1937, p. 54.

Materials.—One nearly complete, left external mold and several fragmental molds of left valves. Reg. nos. HP 100058, 59.

Description.—Shell relatively small, pectiniform, a little inflated; fan-like in shape, with nearly straight anterodorsal, slightly dorsally arcuate posterodorsal, and rounded ventral margins; prosocline, extended posteroventrally; umbo not prominent, slightly salient above the hinge margin, lying at about anterior two-fifths of shell length; apical angle 95-110°; anterior auricle small, trigonal; posterior auricle a little larger than the posterior one, alate with arcuate posterior margin; both auricles sharply distinct from disc; surface of the shell ornamented with nine primary radial ribs; wide, nearly flat interspaces are sculptured by 8-12 weak, radial threads, some a little stronger than the rest referred to as secondary ribs, but not alternating with the primaries; umbonal part of the shell, to 16 mm, ornamented with concentric wrinkles, which later fade away; two or three radial striae discernible on both auricles; ligament unknown.

Comparison.—The type specimen described by Toula has seven strong, slender radial ribs, and smooth interspaces without finer radial ribs. *Pecten* (*Aequipecten*) ? *wilczekiformis* Licharew (1927, p. 35, pl. 3, figs. 4, 6, 7) is distinguished from *E. wilczeki* in its development of interstitial radial riblets.

According to Frebold (1937) the type specimen of *E. wilczeki* is not well preserved. He recognized the presence of finer radial ribs in the marginal area of his specimen, where the shell is preserved, and regarded the two species as being conspecific. However, the finer interstitial radial ribs of the specimen described here are very weak, numerous and subequal in strength, whereas those of *P.*(*A.*) ? *wilczekiformis* are differentiated into second, third or even fourth orders. Both species are considered to belong to *Etheripecten*. *E. wilczekiformis* is more closely allied to *E. keyserlingiformis* than to *E. wilczeki*. *E. wilczeki* is most similar to *Euchondria cancellata* Gu and Liu (1976, p. 171, pl. 12, figs. 17, 18), from the Lower Permian Kufeng Series of South China, in shape and ornament. It differs only a little from the latter species in its lesser development of concentric folds and greater height relative to length. The genus *Euchondria* is characterized by a costate left valve, a nearly smooth right valve, and a series of ligament pits perpendicular to the hinge margin, in addition to a large, central ligament pit. In *E. cancellata* only left valves are known and the hinge character is unknown. Therefore, its generic position is uncertain.

Occurrence.—Rare in calcareous shale of the uppermost horizon of the Svenskeegga Member at Festningen (F5); rare in muddy limestone of the upper part of the Hovtinden Member at Ahlstrandodden (AP 7, 8) and Reinodden (RP 9).

Etheripecten sp. aff. ***E. sichuanensis***
Chen, Zhang and Xu, 1974

Figures 4-10

Resembles.—
Etheripecten sichuanensis Chen, Zhang and Xu, 1974, p. 302, pl. 158, figs. 14, 17; Fang, 1987, p. 373, pl. 2, figs. 1-6.
? *Etheripecten sichuanensis* Liu, 1976, p. 179, pl. 13, figs. 10-13; Gan and Yin, 1978, p. 336, pl. 14, figs. 17, 20.
Etheripecten hunanensis Zhang, 1981, p. 261, pl. 2, figs. 6-8.

Material.—One incomplete left external mold obtained by dissolving away shell material. Reg. no. HP 100060.

Description.—Shell relatively large, a little inflated, longer than high, estimated to be 65 mm long and 58 mm high; disc fan-like in shape with straight antero- and posterodorsal margins and a broadly rounded ventral margin; hinge margin straight, a little shorter than shell length; anterior auricle small, subtrigonal, a little inlated, clearly separated from the disc by a sulcus; posterior auricle large, flat, sinuated posteriorly, protruding posterodorsally; umbo subdued, slightly salient above hinge margin; apical angle 110°; surface ornamented with radial ribs of three orders; primaries seven in number, strong and round-topped, alternating with weaker secondaries; five to six, thread-like rdial riblets of third order inserted in each interspace; auricles with radial and concentric sculpture making a lattice ornament; hinge not preserved.

Discussion.—The external shape and the ornamentation indicate a close relationship of this species with *Etheripecten sichuanensis* Chen, Zhang and Xu (1974) and *E. hunanensis* Zhang (1981), both from the Upper Permian Luntang Series in South China. The former species was later illustrated as ? *E. sichuanensis* sp. nov. by Liu (1976) based on the same specimens. Zhang distinguished *E. hunanensis* from *E. sichuanensis* by the presence of striations and spinose projections on the primary ribs. According to Fang (1987), however, these differences represent infraspecific variation.

The specimen described here differs from *sichuanensis* in its more elongate shape with larger apical angle and larger size.

Occurrence.—Arenaceous limestone of the upper part of the Hovtinden Member at Festningen (F8).

Etheripecten sp. cf. *E. mutabilis* (Licharew, 1927)

Figures 4-11, 12; Figures 5-1—4

Pecten (*Aequipecten*) *Kokscharofi* Toula (non Verneuil), 1873, p. 20, pl. 5, fig. 6.

Aviculopecten cf. *hiemalis* Salter. Licharew, 1927, p. 76, pl. 5, figs. 18-21; pl. 6, fig. 1.

? *Aviculopecten* (*Deltopecten*) cf. *mutabilis* Licharew and *A.* cf. *hiemalis* Salter. Frebold, 1937, p. 51, pl. 1, figs. 2, 3.

Compared with.—

Pecten (*Aequipecten*) *Bouei* Toula, 1873, p. 19, pl. 5, fig. 8.

Aviculopecten mutabilis Licharew, 1927, p. 72, pl. 5, figs. 7-10, 12, 14-17.

Aviculopecten (*Deltopecten*)? *mutabilis* Licharew. Lyutkevich and Lobanova, 1960, p. 102, pl. 15, figs. 1-6.

Material.—Eight incomplete left valves, one complete and two incomplete right valves. Reg. nos. HP 100061～68, 100070, 71.

Description.—Shell moderate in size, inequivalve, inequilateral, prosocline, nearly as long as high, apical angle 90-100°. Left valve moderately inflated; umbo not prominent, a little salient above the hinge margin; beak situated at about anterior one-third of shell length; disc fan-like in shape with slightly concave anterodorsal, nearly straight posterodorsal, and well rounded ventral margins; anterior auricle subtrigonal, with a rounded anterior margin, demarcated from the disc by a sulcus; posterior auricle only partly preserved; surface covered with many radial ribs differentiated into three or four orders; primary ribs 7 to 9 in number, strong, round-topped, a little projected at ventral margin; second- and third- order radials alternating regularly with lower-order radials; some tertiary radials as strong as secondaries; fourth-order radials very weak, sporadically inserted near the margin; growth lines close-set, curving ventrally on radial ribs and dorsally on interspaces, showing scaly or spinose projections on the primary ribs (Figures 5-1b, 2). Right valve nearly flat; anterior auricle deeply incised below; posterior auricle subtrigonal, nearly equal in length to the anterior auricle, a little sinuated posteriorly; numerous radial ribs increasing in number by insertion; first- and second-order radials becoming subequal in strength; a small number of third-order radials, very weak and thread-like; total number of radials, 34; close-set, weak concentric sculpture, making a lattice ornament with the radials; alivincular ligament pit partly seen in one left internal mold.

Remarks and comparison.—In this material, the number of radial ribs increases by insertion in both the left and right valves. The comarginal sculpture curves ventrally on the radial ribs and dorsally on the interspaces. Therefore, these specimens are referred to *Etheripecten* Waterhosue (1969). In their well differentiated radial ornament and robust primary radial ribs, these shells are identical with *Pecten* (*Aequipecten*) *kokscharofi* as described by Toula (1873), *Aviculopecten* cf. *hiemalis* Licharew (1927), and probably *Aviculopecten* (*Deltopecten*) cf. *mutabilis* and *A.* (*D.*) cf. *hiemalis* Frebold (1937). They are very similar to *Aviculopecten mutabilis* Licharew (1927). According to Licharew (1927) the latter species is distinguished from *Aviculopecten* cf. *hiemalis* by its more pointed posterior auricle, the sharper restriction of auricles from the disc, the weaker bend of antero- and posterodorsal margins of the disc, and less regularity in the appearence of ribs. These differences, though, are not distinctive, as noted by Licharew himself. *A.* cf. *hiemalis* of Licharew has generally more robust primary radials than *A. mutabilis*. It is clearly distinguished from the original *A. hiemalis* reported from the Himalayas (cf. Diener, 1897, p. 9, pl. 5, figs. 10a, b, 11) in taller shape and smaller posterior auricle and is more closely related to *A. mutabilis*. Lyutkevich and Lobanova (1960) illustrated the right valve of *A. mutabilis* (pl. 15, figs. 2, 5), which shows inserted radial ribs. Therefore, *A. mutabilis* is considered to belong to the genus *Etheripecten*. The right valve of *Etheripecten mutabilis* has less uniform radial ornament than the present species.

Occurrence.—Common in the Hovtinden Member at Festningen, Reinodden, and Ahlstrandodden; rare in Svenskeegga Member at Reinodden.

Etheripecten? sp. cf. *E. alatus*
(Lyutkevich and Lobanova, 1960)

Figures 5-5

Compared with.—

Pseudomonotis alata Lyutkevich and Lobanova, 1960, p. 116, pl. 17, fig. 9.

Description.—Only one incomplete, semiexternal cast of a

Table 3. Measurements of *Etheripecten* sp. cf. *E. mutabilis* (Licharew). ☆: Total number of primary and secondary radial ribs, #: total number of radial ribs.

Reg.	no.	L	H	H/L	U	U/L	r_1	$r_{2\sim4}$	a	V	Hor.
HP	100060	60_+	58_+	—	—	—	7_+	4～6	100	L	F 9
HP	100062	21.5	22.8	1.06	—	—	7	3	85	L	RP 3
HP	100063	22.3	21.5	0.96	8.0	0.36	26☆		90	R	F 11
HP	100064	30_+	32_+	—	—	—	6_+	3～4	—	L	F 9
HP	100065	33.5	35.0	1.04	12.5	0.37	9	3～5	90	L	F 11
HP	100066	21.0	—	—	—	—	24#		85	R	F 11
HP	100067	25.0	25.0	1.00	7.5	0.30	8	3～4	90	L	F 11
HP	100071	25.3	25.7	1.02	10.5	0.42	7	3	90	L	F 7p

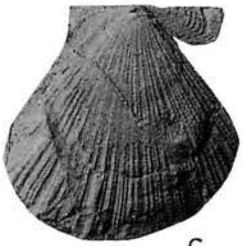

1a


1b


3


4


2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11


12

left ? valve is available (Reg. no. HP 100069). More than posterior one-third of the shell is not preserved. Shell 38 mm high and more than 30 mm long, nearly flat; disc inferred to be fan-like in shape ; anterodorsal margin straight ; anterior auricle trigonal, flat, clearly marked off from the disc ; surface ornamented with six strong, round-topped primary radial ribs ; broad, flat or slightly concave interspaces with weak secondary and tertiary radials five to eight in number ; close-set weak concentric striae partly preserved.

Discussion.—The present material is quite similar in shape and sculpture to *Pseudomonotis alata*, described on the basis of a right valve by Lyutkevich and Lobanova (1960) from the Lower Permian at Pai Khoi of the northern coast of Siberia. It differs slightly from that species in taller outline. The well differentiated, straight radial ornament of these Siberian and Spitsbergen species suggests that they belong to *Etheripecten* rather than to *Pseudomonotis*.

Occurrence.—Dark grey calcareous shale of Unit G of the Hovtinden Member at Reinodden (RP 9).

Family Streblochondriidae Newell, 1938

Genus **Streblochondria** Newell, 1938

Streblochondria winsnesi sp. nov.

Figures 6-2a, b—4

Pecten (*Pseudamusium*) cf. *ufaensis* Tschernyschew. Frebold, 1937, p. 53, pl. 1, fig. 3-5.

Material.—One complete right valve (external and internal molds, holotype, Reg. no. HP 100094a, b) and a nearly complete right valve (internal and external molds, Reg. no. HP100095a, b). Holotype specimen occurs in black shale of Unit 11 of the Hovtinden Member at Festningen.

Etymology.—Dedicated to Thore S. Winsnes for his contribution to the geological understanding of West Spitsbergen.

Diagnosis.—Permian *Streblochondria* characterized by a broad shape and very fine cancellate ornament composed of numerous radial and concentric striae.

Description.—Shell medium in size, a little inflated, and subcircular in shape, with well rounded ventral, slightly convex posterodorsal, and slightly concave anterodorsal margins ; as long as high ; opisthocline ; umbo subdued, not salient above the hinge margin ; apical angle varying from 90° to 110° ; posterior auricle very small, obtuse-triangular, truncated posteriorly ; anterior auricle relatively large, rounded trigonal, and marked below by deep slit-like byssal notch ; surface covered with numerous, uniform radial striae increasing in number by insertion, 70 per cm in the medial area 1 cm away from the umbo ; dense concentric fila making a cancellate ornament with the radials, slightly raised scales on the radials ; anterior auricle ornamented with five distinct radial ribs and growth lines ; hinge characters unknown.

Table 4. Measurements of *Streblochondria winsnesi* sp. nov.

Reg.	no.	L	H	H/L	I	a	Hor.
HP	100094	33.5	ca33	0.99	9.5	90~110	F 11
HP	100095	20.0	20.0	1.00	–	90~110	AP 9

Discussion.—Frebold (1937) illustrated three right valves identified as *Pecten* (*Pseudamusium*) cf. *ufaensis* Tschernyschew from the upper part of the Kapp Starostin Formation at Festningen. One of them shows a distinct sculpture, very similar to that described here, so it is considered to be conspecific with this species. It is similar to *Streblochondria sculptilis* (Muller), the type of the genus, from the Carboniferous of the United States (cf. Newell, 1938, p. 38, pl. 16, figs. 5a-c, 7, 9a, b). However, the present new species has a larger apical angle, a lower outline, and finer ornament than that species. It is more closely allied to *S. ufaensis* (Tschernyschew) (Licharew, 1927, p. 30, pl. 2, figs. 7, 8 ; Lyutkevich and Lobanova, 1960, p. 131, pl. 21, fig. 1), but differs from that species in the finer radial sculpture as noticed by Frebold and, furthermore, in its longer outline.

Occurrence.—Rare in siliceous limestone of the upper part of the Hovtinden Member at Ahlstrandodden (AP 9), and the uppermost horizon of the Hovtinden Member at Festningen (F11).

Genus **Streblopteria** M'Coy, 1851

Streblopteria sp. cf. ***S. eichwaldi*** (Stuckenberg, 1898)

Figures 6-6, 7a, b, c

Pecten (*Aviculopecten*) cf. *ellipticus* Toula, 1873, p. 20, pl. 5, fig. 1.
Pecten (*Pseudamusium*) sp. ind. ex aff. *sericeus* Frebold, 1937, p. 54.
Compared with.—
Pecten Eichwaldianus Stuckenberg, 1898, p. 203, pl. 1, figs. 25a, b.

Materials.—A pair of valves, two internal molds, and two incomplete external molds. Reg. nos. HP 100087~90.

Description.—Shell small, nearly equivalve, subcircular in shape, opisthocline, a little extended anteriorly ; left valve gently inflated ; right valve slightly less convex than left ; anterodorsal margin of the disc a little concave, ventral and posterior margins well rounded ; umbo lying a little posterior to the middle of the shell, not salient above the hinge

Figure 5. **1-4.** *Etheripecten* sp. cf. *E. mutabilis* (Licharew), 1a : gypsum cast of left external mold (HP 100061), 1b : enlarged figure showing details of sculpture, ×3, 2 : gypsum cast of left external mold (HP 100064), 3 : silicon rubber cast of right external mold (HP 100066), 4 : gypsum cast of right external mold (HP 100063). **5.** *Etheripecten* ? sp. cf. *E. alatus* (Lyutkevich and Lobanova), left ? semiexternal cast (HP 100069). **6-10.** *Vorkutopecten svalbardensis* sp. nov., 6 : gypsum cast of right external mold, holotype (HP 100072), 7 : semiinternal mold of left valve, paratype (HP 100076), 8 : gypsum cast of right external mold (HP 100075) ×1.2, 9 : gypsum cast of right external mold (HP 100077), 10 : gypsum cast of right external mold (HP 100078), ×1.4. **11, 12.** *Deltopecten* sp., 11 : semiexternal cast of left valve (HP 100085), ×1.1. 12 : silicon rubber cast of external mold of right valve (HP 100086). All are natural size unless otherwise indicated.

2a

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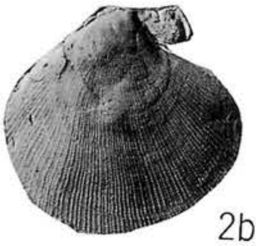

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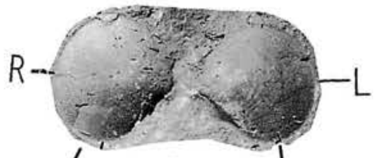

7a

6

7b

7c

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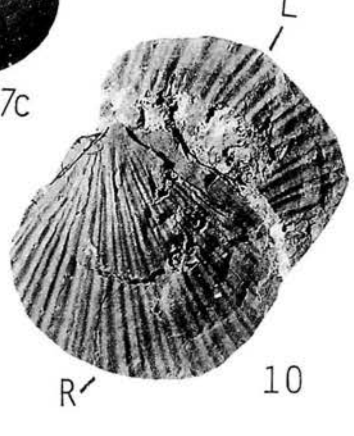

10

margin; apical angle 90° in umbonal portion and 110-120° in later growth stages; posterior auricle small, obtuse-triangular; anterior auricle larger, obtuse-triangular in left valve, and deeply incised below in the right valve; surface almost smooth, weak concentric sculpture discernible in the internal mold and partly preserved external cast; no radial ornament observed.

Discussion and comparison.—The genus *Streblopteria* was established by McCoy (1851). The Carboniferous *Meleagrina laevigata* McCoy from Ireland was designated as type species by Meek and Worthen (1866). The genus is characterized by smooth shells of acline to opisthocline pectinoid form, and is distinguished from *Streblochondria* Newell (1938) which has cancellate sculptures. The posterior auricle of the type species is much larger than the anterior auricle, poorly distinguished from the disc. However, the forms with a small, obtuse-triangular, more or less clearly defined posterior auricle are also included in *Streblopteria* or referred to *Pseudamusium* Verrill by many authors.

According to Cox *et al*. (1969) *Pseudamusium* is a junior synonym of the Cenozoic genus, *Palliolum* Monterosato. Several small *Pseudamusium* species, such as *P. eichwaldi* (Stuckenberg), *P. pusillus* (Schlotheim), and *P. ellipticum* (Phillips), have very weak radial ribs or cancellate ornament on a limited part of the shell. They were doubtfully assigned to *Streblochondria* by Newell (1938). However, they have a longer shape than *Streblochondria* and are more similar to smooth forms of *Streblopteria* or "*Pseudamusium*". This hardly warrants recognition as a different genus. In this paper, all these species are treated as *Streblopteria*, although they differ somewhat from the type species. The species described here is most similar to *S. eichwaldi* (Stuckenberg, 1898) in shape, but the surface ornament is insufficiently known for specific identification. *Pecten* cf. *ellipticus* reported by Toula (1873) from the south point of Spitsbergen was referred to *Pecten* (*Pseudamusium*) aff. *sericeus* Verneuil by Frebold (1937). However, *P. sericeus* has a more opisthocline shell that is extended more anteriorly. It is probably identical with the present species.

Occurrence.—Siliceous limestone of the lower part of the Hovtinden Member at Ahlstrandodden (AP 6).

Streblopteria ? sp. ind.

Figures 6-8

Discussion.—One incomplete right internal mold (Reg. no. HP 100092), estimated at 24 mm long and a little more than 24 mm high, is at hand. The shell is subcircular in outline and provided with a concave anterodorsal margin. The surface is covered by a weak concentric sculpture. The auricular part of the shell is not preserved. It probably belongs to *Streblopteria*, but is too imperfectly preserved to be certain.

Occurrence.—Siliceous shale of the lower part of the Hovtinden Member at Ahlstrandodden (AP 6).

Family Deltopectinidae Dickins, 1957
Genus **Vorkutopecten** Guskov, 1984

Vorkutopecten svalbardensis sp. nov.

Figures 5-6—10

Material.—Eight right external and internal molds and three left external and internal molds. Reg. nos. HP 100072~83 (holotype HP 100072). Holotype from Unit 9 of the Hovtinden Member at Festningen.

Etymology.—Derived from Svalbard Islands, where the species occurs.

Diagnosis.—Shell is higher than long; ornamentation of both left and right valves consists of numerous radial ribs differentiated into three orders, increasing in number by insertion. Concentric costae arch ventrally in the interspaces of radial ribs.

Description.—Shell inequivalve, inequilateral, suborbicular in shape, a little higher than long; right valve moderately to weakly inflated; left valve more inflated than right; umbo situated a little anterior to the middle of shell, nearly acline and slightly salient above the hinge margin in the left valve, but not in the right valve; apical angle about 90°; anterior and posterior auricles nearly equal in length; posterior one trigonal and sinuated posteriorly; right anterior auricle deeply incised below; surface of disc covered with numerous, slender radial ribs narrower than interstices, increasing in

Table 5. Measurements of *Streblopteria* sp. cf. *S. eichwaldi* (Stuckenberg).

Reg.	no.	L	H	H/L	l	l/L	U	U/L	a	V	Hor.
HP	100087a	8.0	7.5	0.94	4.0	0.50	4.0	0.50	~110	L	AP 6
HP	100087b	8.0	7.8	0.98	3.7*	0.46	4.5	0.56	90~120	R	AP 6
HP	100088	12.7	11.6	0.91	5.7	0.45	7.2	0.56	90~120	R	AP 6
HP	100089	13.0*	12.5	0.96	–	–	7.5	0.57	~120	R	AP 6

Figure 6. 1. *Vorkutopecten* sp. aff. *V. svalbardensis* sp. nov., gypsum cast of right external mold (HP100084). **2-4**. *Streblochondria winsnesi* sp. nov., 2a: right external mold, holotype (HP 100094), ×1.4, 2b: gypsum cast, 3: right internal mold of the same, 4: right external mold (HP 100095). **5**. *Cassianoides sexcostatus* (Stuckenberg), left external mold (HP 100093), ×2.4. **6, 7a-c**. *Streblopteria* sp. cf. *S. eichwaldi* (Stuckenberg), 6: right internal mold (HP 100088), ×1.5, 7a: a pair of internal molds of left (L) and right (R) valves (HP 100087), ×2, 7b-c: enlarged figures of right (b) and left (c) valves, ×3. **8**. *Streblopteria* ? sp., right external cast (HP 100092). **9, 10**. *Palaeolima nakamurai* sp. nov., 9: right external cast, paratype (HP 100097), ×1.5, 10: right external cast (R), holotype (HP 100096) and a part of left valve (L), ×1.2. All are natural size unless otherwise indicated.

number by insertion; primary radial ribs varying in number from 12 to 17, with two or three radials of second and third orders in each interspace between the primaries; total number of radials 35 to 50 or more; secondary radials of right valve become as strong as primaries; lamellose concentric sculpture developed on the whole surface, curving dorsally on radial ribs and ventrally in interstices; both auricles sculptured by radial ribs and concentric costae; a small, trigonal ligament pit partly preserved in one left internal mold.

Remarks and comparison.—The radial ribs of both left and right valves increase in number by insertion, as in *Etheripecten, Limipecten*, and *Vorkutopecten*. The concentric sculpture swings ventrally between radial ribs as in *Limipecten*, not *Etheripecten*. The shell length of *Limipecten* is usually equal to or larger than the height, and the radial ribs of the right valve are finer and more numerous than those of the left valve. Furthermore, the right valve is nearly flat. The present species has a greater height than length. The ornamentaion is similar in both valves, although secondary ribs of the right valve grow as strong as the primaries. The right valve is more or less inflated. In these respects, it can be identified with *Vorkutopecten* established by Guskov (in Muromtseva, 1984), based on *Aviculopecten giganteus talis* Lyutkevich and Lobanova (1960, p. 108, pl. 16, fig. 10; pl. 17, fig. 1). Guskov included two species in the genus in addition to the type species, namely, *Aviculopecten subclathratus* (Keyserling) and *A. netschajewi* Licharew. However, the type specimen of the latter species has branching radial ribs in the right valve and is excluded from *Vorkutopecten*. On the other hand, materials described as *Vorkutopecten netschajewi* by Guskov (Muromutseva, 1984, pl. 29, fig. 8) have inserted radial ribs and cannot be identified with this species, which is more similar to *A. subclathratus*. The Spitsbergen species is similar to *A. subclathratus* and *A. netschajewi* of Guskov, but differs in its more numerous primary radial ribs and larger posterior auricle. *Vorkutopecten*, characterized by broad, alivincular ligament pit and a grooved ligament area, is included in Family Deltopectinidae. The present species has a relatively small ligament pit.

Occurrence.—Common in siliceous limestones of the Hovtinden Member at Festningen (F 7p, F 8 and 9), rare in limestone of the Vøringen Member (AP 1), common in siliceous limestone of the Svenskeegga (AP 2) and the Hovtinden Member (AP 6, 7) at Ahlstrandodden, rare in calcareous sandstone of the Hovtinden Member at Reinodden (RP 7).

Vorkutopecten sp. aff. ***V. svalbardensis*** sp. nov.

Figures 6-1

Discussion.—The species is represented by a single, large external mold of a right valve (Reg. no. HP 100084). It is 86 mm long and 91 mm high and has an apical angle of 100°. The shell is gently convex and sculptured with as many as 60 radial ribs. The radials are differentiated into three orders, but due to poor preservation distinction between primary and secondary ribs is difficult. This species is very similar to the preceding new species in shape and ornamentation, but its size is much larger and its apical angle is a little greater.

Occurrence.—Arenaceous limestone of Unit 1 (Vøringen Member) at Ahlstrandodden (AP 1).

Genus ***Deltopecten*** Etheridge, Jr., 1892

Deltopecten sp. ind.

Figures 5-11, 12

Material.—One incomplete left semiexternal cast, and one incomplete right valve represented by external and internal molds. Reg. nos. HP 100085, 86.

Description.—Shell moderate in size, subcircular in shape, nearly equiconvex and subequilateral; umbo not prominent, located subcentrally; apical angle 100-110°; anterior auricle triangular, with slightly concave anterior margin in the left valve and byssate in the right valve; left posterior auricle not preserved; right posterior one partly preserved, obtuse-triangular and probably smaller than the anterior one; surface of the left valve sculptured by relatively slender, rounded primary ribs, 18 in number, separated by wide interspaces and alternating with very weak, secondary radials; right valve ornamented with flat-topped primary radial ribs; intervening flat interspaces of a width nearly equal to that of the radial ribs, with weak secondary radials inserted in the medial part of the shell; surface of both valves covered with close-set concentric fila swinging slightly ventrally, in the interspaces; ligament not preserved.

Discussion.—Although the ligament cannot be observed, the present species can be referred to *Deltopecten* judging from the nearly equiconvex shell and relatively simple, flat-topped radial ribs. This species is somewhat similar to

Table 6. Measurements of *Vorkutopecten svalbardensis* sp. nov.

Reg.	no.	L	H	H/L	l	U/L	a	r_1	r	V	Hor.
HP	100072	31.0*	30.5*	0.98	19_+	0.48	88	16	54	R	F 9
HP	100074	29.0	31.5	1.09	20.0	0.38	90	11?	47	R	F 7p
HP	100075	35.0	38.0	1.09	35.0	0.46	88	17	46_+	R	F 9
HP	100076	24.0*	27.0	1.13	—	0.46	85	14	30_+	L	AP 1
HP	100077	20.0*	22.0	1.10	—	0.50	90	12	42	R	F 7p
HP	100078	27.0*	28.7	1.06	22.0	0.50	90	12	40	L	AP 1
HP	100080	34.3*	35.8	1.04	26.0	0.43	90	12	37	R	AP 2
HP	100081	26.0*	30.3	1.17	13.0	0.49	90	?	35	R	AP 7

Table 7. Measurements of *Deltopecten* sp. ind.

Reg.	no.	L	H	H/L	U	U/L	a	r_1	V	Hor.
HP	100085	35.5	33.5	0.94	16.7	0.47	105	18	L	RP 7
HP	100086	30+	35.0	–	17.5	0.50	110	15?	R	AP 2

Deltopecten lyonsensis Dickins (1957, p. 41, pl. 7, figs. 1-5 and 9 ; pl. 8, figs. 11-13 ; pl. 9, fig. 12 ; pl. 10, figs. 3-4) from West Australia, but differs from that species in its less numerous primary radial ribs and the development of secondary radials in the left valve.

Occurrence.—Rare in calcareous sandstone of Unit E of the Hovtinden Member at Reinodden (RP 7) and in siliceous limestone of Unit 3 of the Svenskeegga Member at Ahlstrandodden (AP 2).

Family Cassianoididae Newell and Boyd, 1995
Genus **Cassianoides** Newell and Boyd, 1995

Discussion.—The present family and genus were established by Newell and Boyd (1995) on the basis of a single species, *Cassianoides kingorum* Newell and Boyd of the Middle to Late Permian of West Texas. The genus is characterized by small, strongly inequivalve shells ; the left valve is strongly convex, ornamented with a few widely spaced, strong primary costae and a few comarginal, tubular hyote spines on the radial ribs ; the right valve is flat, sculptured by spineless, subdued radial ribs. *Cyrtorostra sexradiata* Branson (1930, p. 45, pl. 11, figs. 13-15) from the Upper Permian Park City Formation was later shifted to the genus *Cassianella* of the Family Cassianellidae by Ciriacks (1963). This species was considered to be a junior synonym of *Pseudomonotis sexcostatus* Stuckenberg (1898, p. 207, pl. 1, fig. 40) from the Permian of Russia and to belong to *Aviculopecten* by Muromtseva (1984). The species is very similar to *Cassianoides kingorum*, not only in shell form but also in the characteristic ornamentation of both the left and right valves. It undoubtedly belongs to *Cassianoides*.

Aviculopecten crassispinosus Chronic, reported by Newell *et al.* (1953, p. 155, pl. 33, figs. 10-13) from the Lower Permian of Peru, is also referred to as a member of this genus. *Cassianella rara* described by Waterhouse (1987, p. 145, pl 3, figs. 1, 7, 10) from the Middle Permian of East Australia is another example. Waterhouse noticed the close relation of this species to *C. sexradiata* and *C. crassispinosus*. His figs. 1 and 7, illustrated as a right valve, are quite similar to the left valve of *A. crassispinosus* (especially fig. 13a of Newell *et al.*, 1953), and are believed to be a left valve. The genus *Crassinoides* is now known from the Permian of the United States, Peru, Australia, Russia, and Spitsbergen.

Cassianoides sexcostatus (Stuckenberg, 1898)

Figure 6-5

Pseudomonotis sexcostatus Stuckenberg, 1898, p. 207, pl. 1, fig. 40.

Cyrtorostra sexradiata Branson, 1930, p. 45, pl. 2, figs. 13-15.

Cassianella sexradiata (Branson). Ciriacks, 1963, p. 45, pl. 5, figs. 5-7.

Aviculopecten sexcostatus (Stuckenberg). Muromtseva, 1984, p. 61, pl. 27, fig. 6 ; pl. 33, figs. 10-13.

Material.—Only one external mold of a left valve. Reg. no. HP 100093.

Description.—Shell small, 14 mm long and 14 mm high, strongly inflated ; umbo narrow, orthogyrate, salient above the hinge margin and curving down over the hinge ; anterior auricle rounded-trigonal, a little inflated and marked off from the disc by a deep and wide sulcus ; posterior auricle imperfectly preserved, relatively small, obtuse-triangular, with its posterior margin weakly sinuated and set off from the disc by a strong, posterior, radial marginal rib ; surface ornamented with nine slender but sharply raised radial ribs, projecting ventrally at ventral margin ; interspaces between radials wide, slightly concave ; distinct, regular concentric fila, closely spaced, curving dorsally in the interspaces, and with comarginal spinose projections on the radials ; hinge margin straight, shorter than shell length ; hinge not preserved.

Remarks.—The present specimen differs from the type in its more numerous radial ribs, but this is considered to be due to infraspecific variation. *Crassianoides sexcostatus* can be distinguished from *C. crassispinosus* (Chronic) by its weaker radial ribs and less spinose concentric sculpture, and from *C. rara* (Waterhouse) by the absence of secondary radial riblets.

Occurrence.—Black siliceous shale of the uppermost fossil horizon of the Hovtinden Member at Festningen (F11).

Superfamily Limacea Rafinesque, 1815
Family Limidae Rafinesque, 1815
Genus **Palaeolima** Hind, 1903

Palaeolima nakamurai sp. nov.

Figures 6-9, 10

Materials.—External casts and molds of a complete right valve and an incomplete left valve, and a nearly complete external cast of a right valve. Reg. nos. HP 100096 (holotype) and 100097. Holotype specimen occurs in shale of Unit 7 of the Hovtinden Member at Festningen.

Diagnosis.—Broadly rounded *Palaeolima* ornamented with wide, rounded, branching radial ribs intercalated with narrow furrows.

Etymology.—Dedicated to Dr. K. Nakamura, who surveyed West Spitsbergen several times as a leader of the Japanese Expedition.

Description.—Shell equivalve, inequilateral, a little inflated, broad and oblique-oval in shape, opisthocline, extended anteroventrally ; umbo not prominent, a little salient above the hinge margin ; apical angle about 110° ; umbonal angle about 80°, no umbonal ridge ; umbo situated near the middle of the straight hinge margin ; height slightly less than the length ; both auricles obtuse-triangular, anterior one

Table 8. Measurements of *Palaeolima nakamurai* sp. nov. A : umbonal angle (angle between hinge line and longest axis of the shell)

Reg.	no.	L	H	H/L	U	U/L	a	A	r	r_1	V	Hor.
HP	100096	31.0	29.7	0.96	18.8	1.65	80	110	33	15	R	F 7-1
HP	100097	24_+	24.5	–	–	–	80	110	30	16	R	AP 6

depressed, obscurely defined from the main body ; posterior one marked off anteriorly by a steep umbonal slope ; surface ornamented with 15-16 broadly rounded, primary radial ribs wider than interstitials, increasing in number by bifurcation, reaching 30 or more in total ; growth lines weak ; anterior auricle nearly smooth ; posterior one sculptured by weak radial costae ; hinge not preserved.

Comparison.—The species is similar in ornament to *Palaeolima simplex* Hind (1903, p. 39, pl. 39, figs. 24-27) from the Carboniferous of England, *P. petaline* Zhang (1981, p. 213, pl. 11, figs. 17) and *P. fasciculicostata* Liu (1976, p. 236, pl. 17, figs. 22, 24, 25), both from the lower Upper Permian of South China. It is distinguished from them by its larger size and more circular outline. *Palaeolima krotowi* (Stuckenberg, 1898, p. 336, pl. 1, fig. 29) from the Upper Carboniferous of Russia has radial ribs narrower than its interstitial furrows and is easily distinguished from the present species. Specimens referred to *P. krotowi* by Licharew (1927, p. 37, pl. 3, figs. 8-12, 14) and Muromtseva (1984, p. 79, pl. 33, fig. 11), from the Lower Permian of the Urals and Pechora, have broader radials than interstices, so the specific identification is doubtful. These shells are more similar to the present new species than to *P. krotowi*, but they differ from it being more anteroventrally extended and more oblique in shape.

Occurrence.—Rare in black shale of the lower part of the Hovtinden Member at Festningen (F 7-1) and at Ahlstrandodden (AP 6).

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An early Late Cretaceous mammal from Japan, with reconsideration of the evolution of tribosphenic molars

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Abstract. The morphology of a mandibular fragment with a left lower molar discovered in the "Upper Formation" (upper Cenomanian-lower Turonian) of the Mifune Group in central Kyushu, southwestern Japan, suggests that this fossil should be assigned to a new species of Late Cretaceous mammal, *Sorlestes mifunensis* sp. nov. (Infraclass Eutheria; Order Proteutheria; Family Zhelestidae). *S. mifunensis* is the oldest zhelestid yet recorded. Some workers suggest that the Zhelestidae have a close affinity with ungulates. A detailed comparison between the lower molar of the new species and those of ungulates supports this suggestion. The comparison also suggests that the Zhelestidae have a closer affinity with ungulates than the Zalambdalestidae and other contemporary mammals, and that *S. mifunensis* has a relatively primitive character within the Zhelestidae. This comparison leads us to revise the diagnoses of the family Zhelestidae and of the genus *Sorlestes*. The unique character of the entoconid-hypoconulid twinning seen in the Zhelestidae was probably caused by the movement of the hypoconid (the presumed first single talonid cusp seen in the first therian *Kuehneotherium*) to the buccal side, far away from the other talonid cusps. This twinning pattern is distinct from the twinning pattern seen in marsupials.

Key words: Japan, Late Cretaceous, Mesozoic mammal, Mifune Group, *Sorlestes*, tribosphenic molar

Introduction

It is generally believed that tribosphenic mammals first appeared around the Jurassic-Cretaceous boundary (Bown and Kraus, 1979; Kielan-Jaworowska *et al.*, 1979b; Sigogneau-Russell, 1991). They are ancestors of the eutherian and metatherian mammals which probably differentiated during the Neocomian (Early Cretaceous) (Kielan-Jaworowska *et al.*, 1979a; Cifelli, 1993; Eaton, 1993; Wang *et al.*, 1995). The eutherian orders radiated widely at the beginning of the Tertiary. However, recent fossil finds suggest that the eutherian orders may have originated and differentiated in the Late Cretaceous (Fox and Youzwyshyn, 1994; Archibald, 1996; Gheerbrant *et al.*, 1996).

Until 20 years ago there were only very few reports of tribosphenic mammals from the early Late Cretaceous (Cenomanian-Santonian). This situation has, however, changed and many such fossils are now known from this period (Cifelli and Eaton, 1987; Cifelli, 1993; Eaton, 1993; Nessov *et al.*, 1994; Nessov *et al.*, 1998). In particular, Nessov *et al.* (1994) report many early Late Cretaceous tribosphenic mammals from Middle Asia (Uzbekistan, Kazakhstan and Tajikistan).

In the present study, we document a mammal fossil specimen, which was first reported by Setoguchi (1992), from the "Upper Formation" (upper Cenomanian-lower Turonian; lower Upper Cretaceous) of the Mifune Group in central Kyushu, southwestern Japan. The specimen is a small mandibular fragment with a tribosphenic lower molar. The new find is significant because it is the only known example of a mammal fossil from the Late Cretaceous eastern coastal lowlands of the Asian Continent. The other Asian Late Cretaceous mammal fossils, in contrast, come from either inland deposits or deposits along the Tethys sea and the

Turgai Strait of that time (Clemens *et al.*, 1979 ; Nessov *et al.*, 1994).

The tooth nomenclature used in this contribution is that of Bown and Kraus (1979) and Nessov *et al.* (1998).

Geological setting

The present fossil material was discovered in the "Upper Formation" of the Mifune Group, which is distributed in the Mifune Town area of Kumamoto Prefecture, central Kyushu, southwestern Japan (Figure 1). The Mifune Group unconformably overlies green schist associated with serpentinite in the northern area, and the Upper Permian Mizukoshi Formation in the southern area (Matsumoto, 1939). The Mifune Group is, in turn, unconformably overlain by the Upper Cretaceous Gankaizan Formation (Tamura and Tashiro, 1966). The Mifune Group is considered to be early Late Cretaceous in age (see below), and to have formed in a sedimentary basin situated on the east coastal margin of the Late Cretaceous Asian Continent.

The Mifune Group has a total thickness of about 1,500 m and consists of "Basal", "Lower" and "Upper" formations (Matsumoto, 1939). The lowermost or "Basal Formation" is dominated by conglomerate and very coarse-grained sandstone (Matsumoto, 1939), yielding fresh-water bivalves, such as *Trigonioides*, (Tamura, 1979 ; Matsumoto *et al.*, 1982). The middle or "Lower Formation" is dominated by sandstone and sandy mudstone (Matsumoto, 1939), yielding brackish-water and shallow-marine molluscan fossils, such as *Inoceramus concentricus costatus* and *Eucalycoceras* sp. cf. *E. spathi* of middle Cenomanian age (Tamura and Matsumura, 1974 ; Tamura, 1979 ; Matsumoto *et al.*, 1982). The uppermost or "Upper Formation" is dominated by red mudstone (Matsumoto, 1939), yielding non-marine bivalves (Tamura, 1979) and several vertebrate fossils, such as dinosaurs, pterosaur, and the present specimen (Tamura *et al.*, 1991 ; Setoguchi, 1992 ; Okazaki and Kitamura, 1996).

The Gankaizan Formation, which unconformably overlies the Mifune Group, consists of conglomerate, coarse-grained sandstone and red mudstone (Tamura and Tashiro, 1966 ; Matsumoto *et al.*, 1982), yielding *Inoceramus* (*Platyceramus*) *amakusensis*, of lower Santonian age, in its upper part (Tamura and Tashiro, 1966 ; Matsumoto *et al.*, 1982).

The present fossil material comes from the upper part of the "Upper Formation" near the Amagimi Dam, Mifune Town (Figure 1). The stratum where the fossil was discovered

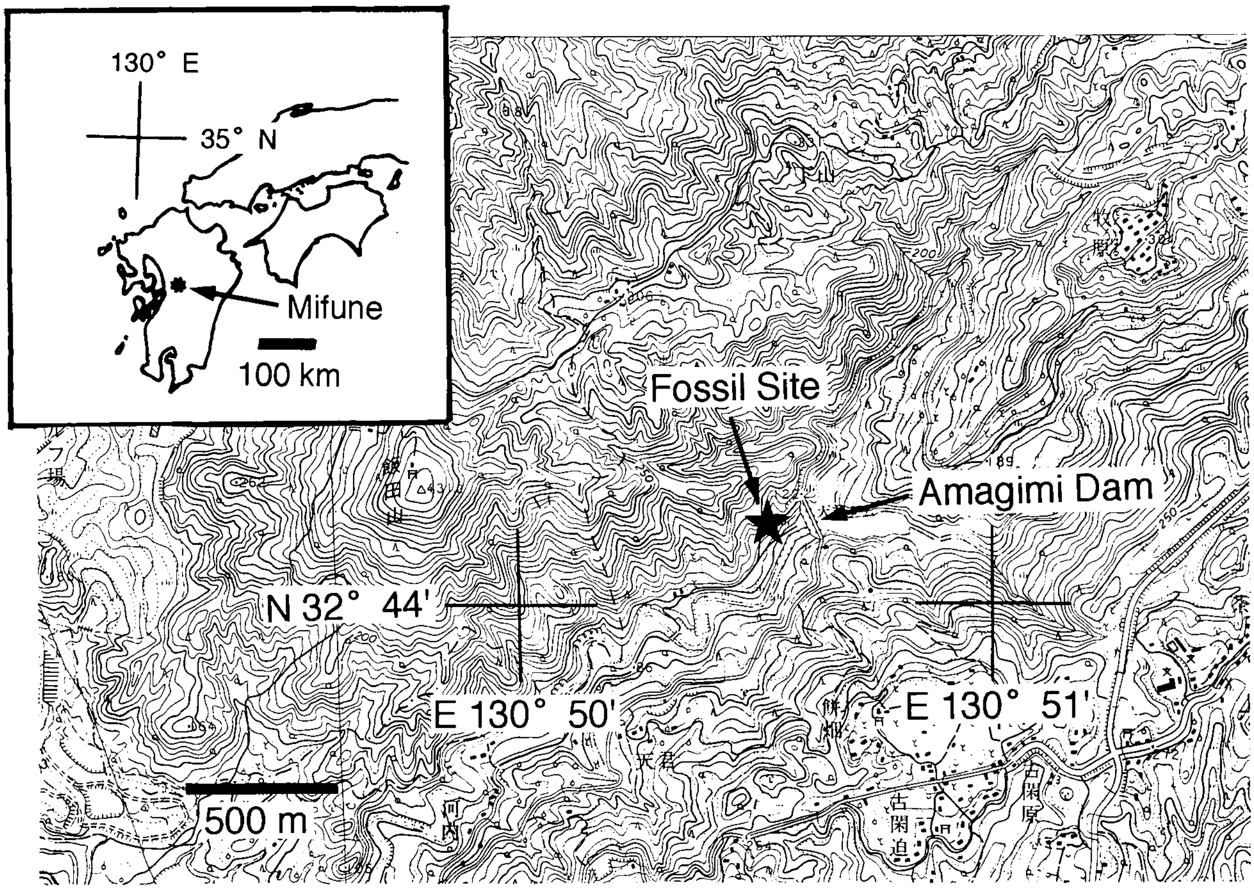

Figure 1. Topographic map showing the fossil locality, near the Amagimi Dam, Mifune Town, Kumamoto Prefecture, Kyushu, southwestern Japan (a part of topographic map "Mifune", 1 : 25,000 scale, Geographical Survey Institute of Japan).

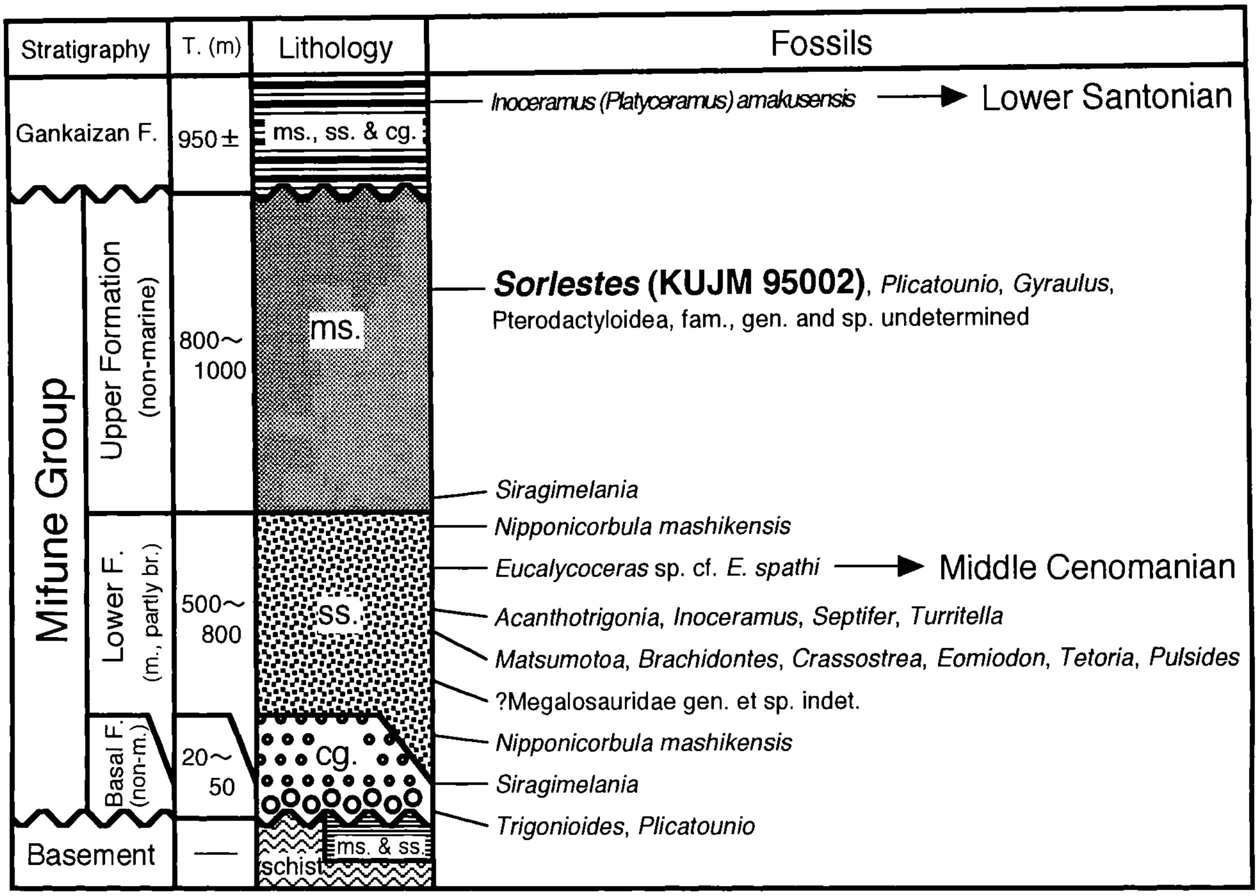

Figure 2. Stratigraphy of the Cretaceous deposits in the south of Kumamoto City, Kyushu, Japan (modified from Matsumoto, 1939 ; Tamura and Tashiro, 1966 ; Matsumoto *et al.*, 1982 ; Tamura *et al.*, 1991 ; Hasegawa *et al.*, 1992 ; Okazaki and Kitamura, 1996). Abbreviations : m., marine ; br., brackish ; T., thickness ; ms., mudstone ; ss., sandstone ; cg., conglomerate.

consists of coarse-grained sandstone. The age of the "Upper Formation" is considered to be late Cenomanian to early Turonian on the basis of the ages of the Lower Formation and the Gankaizan Formation. A synthetic scheme of the stratigraphy of the Mifune Group is shown in Figure 2.

Systematic paleontology

Class Mammalia Linnaeus, 1758
Infraclass Eutheria Gill, 1872
Order Proteutheria (Romer, 1966) Butler, 1972
Family Zhelestidae (Nessov, 1985) Nessov, 1990

Revised diagnosis.—The upper and lower molars are typical tribosphenic types. The protocone is large and mesiodistally expanded. The stylar shelf is relatively narrow, but the parastylar region is wide and expanded mesially bearing two cusps. A small paraconid is displaced relatively lingually and relatively close to the metaconid. Compared with other proteutherians, the trigonid height is lower relative to talonid height. The talonid is about as wide as the trigonid and mesiodistally longer and lower than the trigonid. The talonid basin is deep and open lingually, so that the deepest part of the talonid basin is situated at its lingual margin. The entoconid and hypoconulid are markedly close to one another, and are quite clearly separated from the hypoconid.

The upper and lower last premolars are premolariform (*sensu* Krishtalka, 1976), but the upper one has a incipient metacone. In occlusal view, the upper one is somewhat mesiodistally constricted between the paracone and the protocone.

Genus ***Sorlestes*** Nessov, 1985

Type species.—*Sorlestes budan* Nessov, 1985.

Included species.—*S. budan* Nessov, 1985 ; *S. kara* Nessov, 1993 ; *S. mifunensis* sp. nov.

Revised diagnosis.—The paraconid is not strongly appressed to the metaconid. The protoconid is larger than in *Aspanlestes* (Zhelestidae). The entoconid is very markedly close to the hypoconulid (entoconid-hypoconulid twinning), and both are located at the distolingual corner of the talonid, opposite the hypoconid which is located at the distobuccal corner. The cristid obliqua extends just below the notch of the protocristid between the protoconid and the metaconid.

Sorlestes mifunensis sp. nov.

Figure 3

Holotype.—KUJM 95002, a left mandibular fragment with a molar. (KUJM means Kyoto University, Japan, Mesozoic)

Hypodigm.—The type specimen only.

Etymology.—Named after Mifune Town, where the type specimen was discovered.

Repository.—Department of Geology and Mineralogy, Division of Earth and Planetary Sciences, Graduate School of Science, Kyoto University, Japan.

Locality.—Lat. 32°44′09″ N ; Long. 130°50′32″ E : Loc. 1 of Tamura *et al*. (1991, fig. 1 ; Figure 1), near the Amagimi Dam, Mifune Town, Kumamoto Prefecture, Kyushu, southwestern Japan.

Horizon.—Upper part of the "Upper Formation", Mifune Group (Figure 2).

Age.—Late Cenomanian to early Turonian ; Late Cretaceous.

Diagnosis.—The lower molar of *S. mifunensis* is almost as large as *S. budan*, and larger than *S. kara*. Compared to *S. budan*, the paraconid is less appressed to the metaconid, and the entoconid and hypoconulid are closer together.

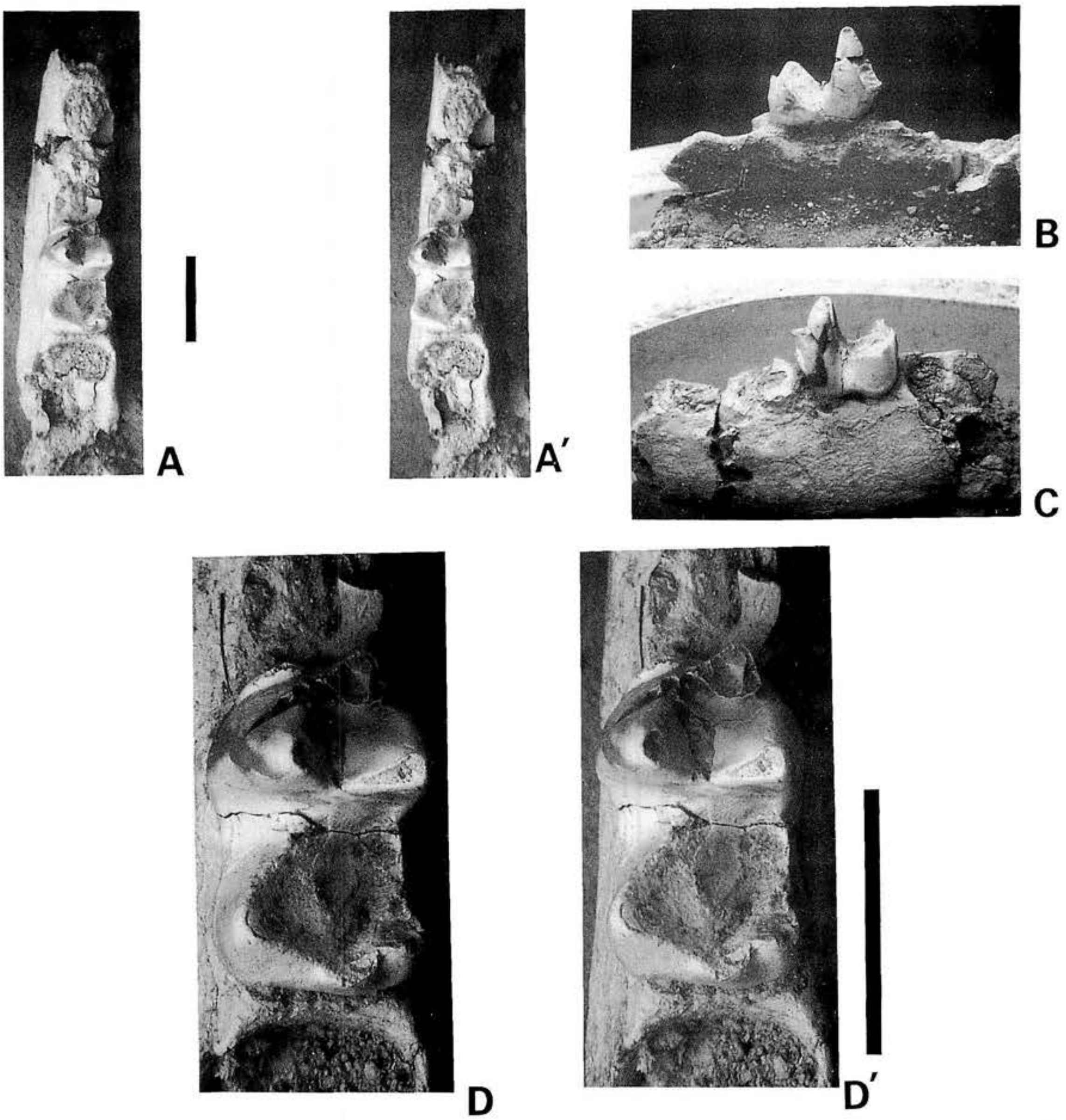

Figure 3. *Sorlestes mifunensis* sp. nov., KUJM 95002, holotype. **A, A′**, occlusal view (stereophotographic pair). **B**, lingual view. **C**, buccal view. **D, D′**, occlusal view of the preserved molar (stereophotographic pair). Scale bars = 2 mm (left scale corresponds to A, A′, B, C, right scale corresponds to D, D′).

Description.—The type specimen (KUJM 95002) is a fragmentary left mandible with a molar. The preserved part of the mandibular ramus is about 8 mm in length, and about 4 mm in height and about 2 mm in width below the preserved molar. Immediately mesial to the molar, there is a broken root, which is circular and not compressed anteroposteriorly in occlusal view (Figures 3-A, A'). Immediately distal to the molar, there is a broken alveolus. Mental foramen could not be identified in KUJM 95002.

The protoconid of the preserved molar is much larger and higher than the metaconid, and leans somewhat lingually. The metaconid is situated just lingual to the protoconid. Although badly broken at the base, it is clear that the paraconid is near the anteroposterior midline, and less anteriorly appressed than in *S. budan*. There is no crest joining the paraconid with the metaconid. A distinct precingulid runs downward from the mesiobuccal base of the paracristid notch, disappearing at the buccal base of the protoconid. The posterior trigonid wall is almost vertical, and nearly perpendicular to the mandibular extension.

The talonid is longer than wide. It is longer than, as wide as, and roughly half as tall as the trigonid. The hypoconid and entoconid are almost the same height, and somewhat higher than the hypoconulid. The hypoconulid is only very slightly projected posteriorly. The entoconid and hypoconulid are closer together than in *S. budan*, and are located at the distolingual corner of the talonid. A very weak postcingulid runs down buccally from the hypoconulid, disappearing at the buccal base of the hypoconid. The deepest part of the talonid basin is situated at its lingual margin, so that the deep talonid basin is open lingually, and inclined lingually as a whole. The cristid obliqua originates directly below the notch between the protoconid and the metaconid, and is much higher than the entocristid. The hypoflexid is well-formed and deep.

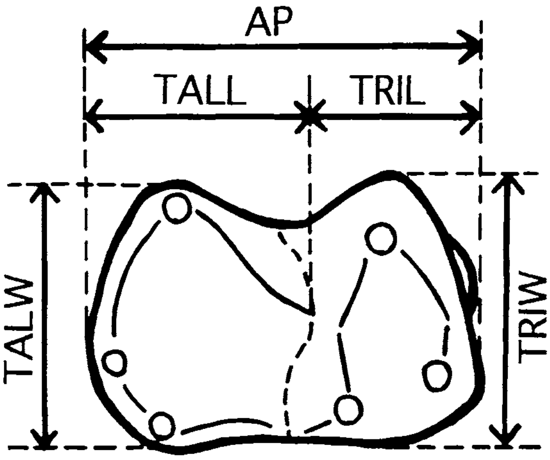

Figure 4. Orientations of the measurements of lower molars (modified from Nessov *et al*., 1994). Buccal to top of page; anterior to right. Abbreviations are shown in Table 1.

Wear facets can be observed from the tip of the protoconid to the tip of the metaconid through the protocristid. The tips of the hypoconid, hypoconulid and entoconid are slightly worn. The talonid basin is also worn (although the effects of secondary erosion are difficult to assess), which forms a U-shaped "wear facet".

Dental measurements are given in Table 1 and Figure 4.

Discussion

Identification of the present lower molar

The tooth class of the molar preserved in KUJM 95002 can be identified as M_2, because the trigonid is as wide as the talonid which is the same as on M_2 of *S. budan*. The possibility that it should be identified as M_1 cannot, however, be immediately excluded. As Lillegraven (1976) pointed out, it is a usual therian condition that the paraconid is most buccally set on M_1 and becomes progressively more lingual on M_2-M_3. Furthermore, Cretaceous eutherians characteristically have a protoconid that leans somewhat more lingually on M_1 than that on M_2, so the distance between the tip of the protoconid and that of the metaconid in occlusal view is shorter on M_1 than that on M_2. These characters are also observed in the zhelestid *Aspanlestes* (Nessov *et al*., 1994, pl. 4, fig. 1). KUJM 95002 shows a combination of these M_1 characters.

In either case, KUJM 95002 and *S. budan* clearly have distinct lower molar structures (see diagnosis of *S. mifunensis*). *S. kara*, another species of *Sorlestes*, has much smaller molar size than KUJM 95002. We, therefore, consider KUJM 95002 to be a new species of *Sorlestes*.

Phyletic position of *Sorlestes mifunensis*

Phylogenetic relationships of the Zhelestidae have been discussed by various workers (Figure 5). Lillegraven (1976) described *Gallolestes*, which was subsequently classified as belonging to the Zhelestidae by Nessov *et al*. (1994), based on the lower molar morphology. Lillegraven (1976) favors eutherian affinities for *Gallolestes*, and points out the similarities between *Gallolestes* and hyopsodontid condylarths. Butler (1977), however, points out that *Gallolestes* shares some derived characters of the lower molars with *Zalambdalestes* (Proteutheria; Zalambdalestidae) and with *Purgatorius* (Primatomorpha), and he doesn't exclude the possi-

Table 1. Measurements (in mm) of the preserved molars of the type specimens of *Sorlestes mifunensis* sp. nov. The measurements are oriented as shown in Nessov *et al.* (1994, fig. 1; see Figure 4). Abbreviations: AP, anteroposterior length; TRIL, trigonid length; TALL, talonid length; TRIW, trigonid width; TALW, talonid width.

[mm]	AP	TRIL	TALL	TRIW	TALW
KUJM 95002 (*S. mifunensis*) left lower molar (M_1 or M_2)	2.60	1.15	1.45	1.75	1.70

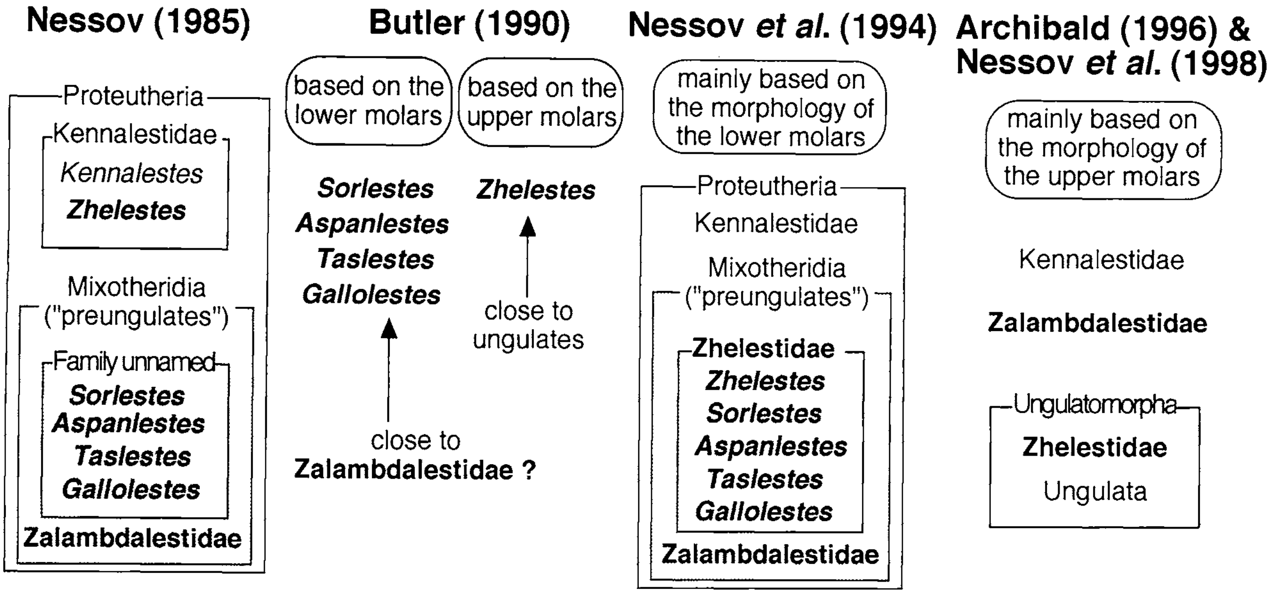

Figure 5. The classifications and phylogenetic relationships used in recent studies for the Zhelestidae.

bility of a relationship between *Gallolestes* and *Protungulatum* (Condylarthra). Clemens (1980) concludes that *Gallolestes* is possibly a representative of another lineage of metatherian-eutherian grade of dental evolution that cannot be assigned to either the Eutheria and Metatheria.

Based on the lower molar morphology, Nessov (1985) suggests that *Taslestes, Aspanlestes, Sorlestes* and *Gallolestes* should be combined in the same taxonomic group, a group which was subsequently classified as belonging to the Zhelestidae in Nessov *et al.* (1994). Nessov (1985) proposed a new suborder Mixotheridia (Proteutheria) including both the above genera and the Zalambdalestidae, and suggested that this suborder was related to condylarths. In the same paper, he described a new genus *Zhelestes*, based on the upper dentition. He classified it into the new subfamily Zhelestinae (Proteutheria; Kennalestidae), and at this time didn't include it in the Mixotheridia. Later, he raised this subfamily to the family level (Nessov, 1990). Butler (1990) points out that the zalambdalestids differ from *Aspanlestes, Sorlestes* and *Gallolestes* in some molar features, suggesting that relationships of these genera to zalambdalestids is not impossible, but it needs to be substantiated. He also considers that *Zhelestes* might be an earlier representative of condylarths. According to Nessov *et al.* (1994), the Zhelestidae include *Gallolestes, Taslestes, Aspanlestes* and *Sorlestes*, and these are all included in the suborder Mixotheridia along with the Zalambdalestidae. They consider the Mixotheridia (both the Zhelestidae and the Zalambdalestidae) to be "preungulates". In contrast, based mainly on the upper molar's morphology, Archibald (1996) and Nessov *et al.* (1998) consider that the Zhelestidae are sister groups of ungulates, and the Zalambdalestidae are only distantly related to them.

In this paper, we follow the suggestions of Archibald (1996) and Nessov *et al.* (1998). The reasons for our preference are briefly summarized below.

On the basis of the lower molar structure, Nessov *et al.* (1994) claimed that both the Zhelestidae and the Zalambdalestidae are closely related to ungulates. However, the two families show the following differences: (1) The Zhelestidae have more low-crowned lower molars with a trigonid that is less elevated to the talonid (Butler, 1990). (2) The paraconid and metaconid in the Zhelestidae are less closely appressed than in the Zalambdalestidae. (3) The Zhelestidae have a lingually open talonid, whereas the talonid is lingually closed in the Zalambdalestidae (see Kielan-Jaworowska, 1984, pl. 14, 15). In these features, the Zhelestidae are morphologically more similar to early ungulates than to the Zalambdalestidae. Most early ungulates (for instance, *Protungulatum, Diacodexis*, and so on) share the diagnostic characteristics of zhelestids, that is, the high, large, wide and lingually open talonid with the hypoconulid situated markedly close to the entoconid, and the rather lingually displaced paraconid with some appression to the metaconid (see McKenna, 1960, figs. 52, 53, 56, 57; Archibald, 1982, figs. 56, 60; Estravis and Russell, 1989, pl. 1; Rose, 1996, fig. 1). This combination of characteristics is not seen in any other contemporary mammal. For example, in *Purgatorius*, an early primatomorphan, the talonid is large, wide and high, but is closed lingually with the hypoconulid situated centrally (see Clemens, 1974, fig. 2; Buckley, 1997, fig. 1). In *Gypsonictops*, a Late Cretaceous insectivore, the talonid is large, wide and somewhat lingually open. However, the hypoconulid is centrally situated, and the paraconid is situated rather centrally than lingually (see Clemens, 1973, figs. 1, 4; Cifelli, 1990, fig. 2).

Based mainly on an analysis of upper molar morphology, Archibald (1996) and Nessov *et al.* (1998) suggest that the Zalambdalestidae does not have a close affinity with ungulates. Similarly, a study of lower molar morphology indicates that the Zhelestidae most closely resemble early ungulates. The lingually closed talonid in the Zalambdalestidae, which is shared by many other eutherians, may be an apomorphic character which zhelestids and early ungulates do not posses (see below). This would imply that the Zalambdalestidae should be excluded from a very close relationship with ungulates. In support of this idea, some workers (Van Valen, 1964; McKenna, 1975; Stucky and McKenna, 1993; Archibald, 1996) consider the Zalambdalestidae to be more closely related to *Anagale* and rabbits.

Compared with the Zhelestidae, early ungulates have a relatively high talonid with robust cusps on the lower molars. Compared to the other representatives of the Zhelestidae, *Sorlestes mifunensis* shows a primitive characteristic in that the paraconid is less appressed to the metaconid.

Nessov (1993) created a new family Kulbeckiidae (consisting of a single new genus *Kulbeckia*) within the Mixotheridia. In the Kulbeckiidae, the hypoconulid is markedly close to the entoconid, and the paraconid is lingually situated with appression to the metaconid, similar to the Zhelestidae. Unfortunately, it is not clear whether the talonid is open or not in the Kulbeckiidae, so it is difficult to discuss any possible relationship between the Zhelestidae, Kulbeckiidae and other mammals.

Evolution of tribosphenic molars

The most characteristic feature of *Sorlestes mifunensis* is the lower molar with the hypoconulid situated markedly close to the entoconid, quite clearly opposed to the hypoconid. This twinning pattern is rarely seen in other Cretaceous eutherians, in which the hypoconulid is centrally-located between the hypoconid and the entoconid. The recognition of this character prompted us to reconsider the evolution of the talonid cusps. It seems that the talonid cusps developed along with the occluding upper tooth and the adjacent lower tooth.

1. First cusp formed in the talonid of *Kuehneotherium*, the first therian mammal: The earliest therian mammal, *Kuehneotherium*, had already appeared by the Norian (Late Triassic) (Fraser *et al.*, 1985). In the lower molars of Kuehneotherium, the tallest and largest cusp can be recognized as homologous with the protoconid of the later tribosphenic molars. The other two cusps, which are situated mesiolingually and distolingually from the protoconid, can likewise be identified as equivalents of the paraconid and metaconid, respectively (Kermack *et al.*, 1968). These homologies of the trigonid cusps are now not really in debate (Slaughter, 1971).

In the lower molars of *Kuehneotherium*, there is, however, a unicuspid distal heel or talonid, posterior to the trigonid (Kermack *et al.*, 1968, fig. 3). The homology of this cusp has been discussed by several workers (Slaughter, 1971; Clemens and Lillegraven, 1986), and the two main opinions are that it corresponds to either the hypoconid or hypoconulid.

Mills (1967) used the occlusal relationship between the upper and lower molars to propose that the single talonid cusp of Jurassic pantotheres corresponds to the hypoconid on the basis of the occlusal relationship between the upper and lower molars. The same conclusion was also reached by Freeman (1979) and Prothero (1981). In contrast, Kermack (1967) interpreted the single talonid cusp in Welsh pantothere (*Kuehneotherium*) as the hypoconulid on the basis of the relationship between the talonid and its following tooth. Crompton (1971), Slaughter (1971) and Butler (1978) also correlated this cusp with the hypoconulid, although the latter didn't completely exclude the possibility that it could represent the hypoconid.

The next stage in evolution toward the tribosphenic molar is seen in *Amphitherium* or *Palaeoxonodon*, whose talonid extends distobuccally from the base of the metaconid and bears a large single cusp at its distobuccal margin (Simpson, 1928, fig. 38; Freeman, 1979, pls. 16, 17). In *Palaeoxonodon*, there is a small cuspule at the approximate median point of the oblique crest which links the metaconid and a large single talonid cusp (Freeman, 1979). Further development is seen in *Peramus*. In this genus the talonid bears two or three cusps, identified as the hypoconid, hypoconulid and entoconid of the tribosphenic molar (Clemens and Mills, 1971; Clemens and Lillegraven, 1986). The talonid basin is not fully basined and is open lingually (Clemens and Mills, 1971, pl. 3).

By comparing the molar morphology of the animal mentioned above with later tribosphenic mammals, we consider that the single talonid cusp seen in *Kuehneotherium* corresponds to the hypoconid, as proposed by Mills (1967). This suggestion is also supported by the following arguments. (1) We would like to stress the occlusal relationship between the upper main cusp (paracone) and the first talonid cusp. The paracone is the largest cusp in the upper molar and is functionally very important for masticating foods. We, therefore, propose that the occlusal relationship between the paracone and the single talonid cusp, as well as between the paracone and the protoconid, is likely to be maintained in the therians. (2) In *Amphitherium* or *Palaeoxonodon*, the talonid extends distobuccally from the base of the metaconid and bears a large single cusp at its distobuccal margin, where the hypoconid of the tribosphenic molar is situated. (3) We propose, furthermore, that the groove separating the hypoconid and the hypoconulid in tribosphenic molars is also significant. This groove is deeper and stronger than the groove separating the hypoconulid and the entoconid, so the hypoconulid and entoconid are likely to be related more closely to each other than to the hypoconid. (4) Freeman (1979) stated that in certain specimens of *Palaeoxonodon* there is an incipient development of the entoconid and hypoconulid in addition to the large talonid cusp situated distobuccally.

We, therefore, propose the following sequential development. The first talonid cusp seen in *Kuehneotherium* corresponds to the hypoconid, and the entoconid and hypoconulid appeared at some later stage, being more closely related to each other than to the hypoconid.

2. Entoconid-hypoconulid twinning: The primitive talonid for a tribosphenic molar envisaged by most workers is basined and lingually opened with a relatively large hypoconid, smaller hypoconulid and in some cases also an entoconid (Clemens and Lillegraven, 1986; Szalay, 1994). Examination of Early Cretaceous tribosphenic mammals suggests that the roughly centrally-placed hypoconulid between the hypoconid and the entoconid may also be a primitive characteristic.

In Late Cretaceous mammals, the lower molars of many eutherians have a centrally-placed hypoconulid. In contrast, the molars of contemporary marsupials have a hypoconulid twinned with an entoconid. In this respect the molars of the eutherian Zhelestidae resemble those of marsupials. However, the twinning in the Zhelestidae is clearly distinct from that in marsupials (Figure 6).

In marsupials, the hypoconulid is distolingually displaced compared to the Zhelestidae. The twinning pattern seen in the Zhelestidae is associated with a primitive-type talonid as seen in the tribosphenic pattern. This association suggests that the twinning seen in the Zhelestidae is more primitive than in marsupials. The twinning pattern seen in the Zhelestidae is likely to have been caused by the movement of the hypoconid to the buccal side far away from the other talonid cusps, corresponding to the expansion of the protocone of the upper molars (Archibald, 1996 ; Nessov *et al.*, 1998). The twinning pattern seen in marsupials is more likely to be a secondary feature (Cifelli, 1993), and could be functionally related to the early trend of the enlargement of the metacone and reduction of the paracone in this group (Clemens and Lillegraven, 1986).

The entoconid-hypoconulid twinning is also related to the position of the paraconid of the posterior molar. This is because the paraconid fits into the groove between the hypoconulid and the entoconid of the anterior tooth. In many eutherians, the paraconid is situated centrally, because the hypoconulid of the anterior tooth is centrally-placed between the hypoconid and the entoconid, and the groove between the hypoconulid and the entoconid is situated more buccally. In the Zhelestidae, the paraconid is situated more lingually than centrally, because the hypoconulid is situated lingually and twinned with the entoconid, and the groove between the two cusps is situated more lingually than centrally. In marsupials, the paraconid is situated more mesiolingually than in eutherians (include the Zhelestidae), because the hypoconulid of the anterior tooth is situated more distolingually and twinned with the entoconid, and the groove between the two cusps is situated far more distolingually.

As mentioned above, the lingually open talonid with a hypoconulid markedly close to the entoconid as seen in the Zhelestidae is probably a reflection of the primitive state. This condition is also seen in early eutherian like *Prokennalestes* (Kielan-Jaworowska and Dashzeveg, 1989, figs. 26, 27), but not seen in early metatherian, *Kokopellia* (Cifelli, 1993, fig. 1).

Co-evolution of mammals and plants

The age from the Albian to the Cenomanian was a very important period for the mammalian evolution. At this time the flora underwent a change from one dominated by ferns and gymnosperms to one with abundant angiosperms. Flowering angiosperms appeared at the beginning of the Cretaceous, and very rapidly became a major plant group (Crane, 1987 ; Collinson, 1990). Angiosperms have leaves,

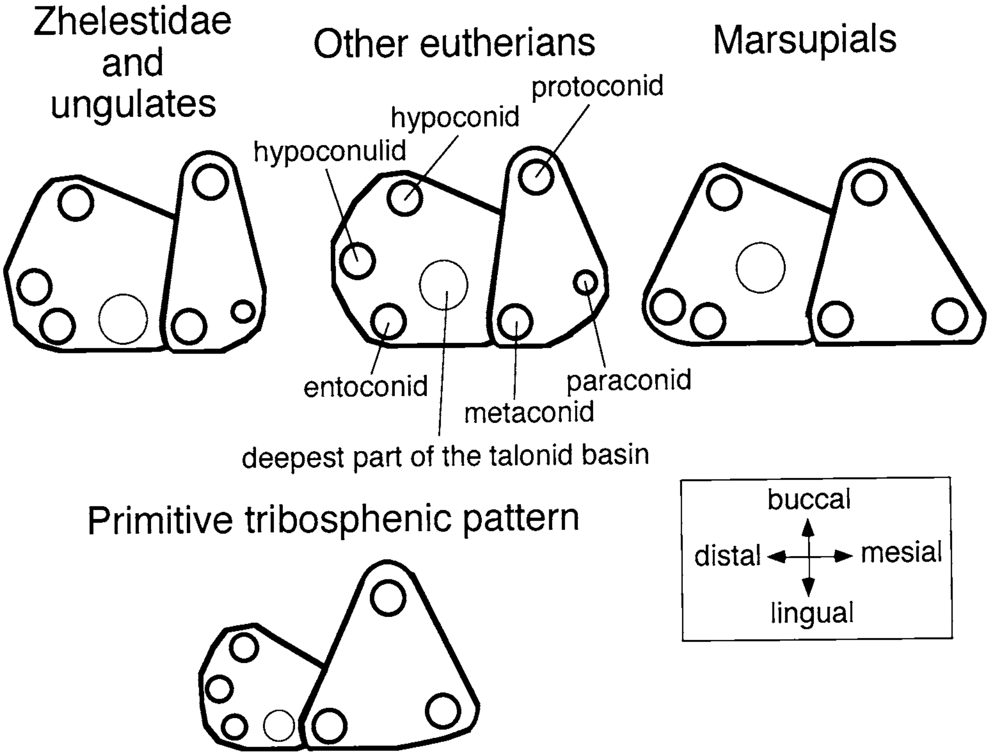

Figure 6. Comparisons of the lower molar patterns of tribosphenic mammals (occlusal view of the left lower molars).

flowers, fruit, pollen and honey. In other words, these plants have foods with high nutritive value. It was for this reason that insects began to evolve explosively at this time. It follows, therefore, that insectivorous mammals, whose staple foods were insects and/or larvae of insects, also began to increase in numbers and diversity. The mammals who began to diversify and radiate in this way are the Cretaceous tribosphenic mammals. The period when the Mifune Group was deposited is the very period when angiosperms had become a major plant group, and when insectivorous mammals like *Sorlestes* evolved rapidly.

Conclusions

Morphological studies of the mammalian remain discovered from the lower Upper Cretaceous Mifune Group in central Kyushu, southwestern Japan suggest that it should be assigned to a new species of the genus *Sorlestes* (Order Proteutheria; Family Zhelestidae), and is here named *S. mifunensis*.

The lower molars of the Zhelestidae exhibit a series of ungulate-like characteristics. It suggests that the Zhelestidae and early ungulates are far more closely related to each other than to the Zalambdalestidae and other mammals. The twinning pattern of the hypoconulid and entoconid in the Zhelestidae, including *Sorlestes mifunensis*, shows a more primitive state than that of metatherians and most of the other eutherians.

Sorlestes mifunensis is the oldest known zhelestid yet recorded, and suggests that the origin of ungulates perhaps goes back even further to the early Late Cretaceous, or at least, that mammals having ungulate-like characters had already been differentiated by the late Cenomanian to early Turonian. The find of *Sorlestes mifunensis* also indicates that zhelestid existed not only in western Asia but also on the coastal plain of eastern Asia.

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A new cheirolepidiaceous conifer from the Lower Cretaceous (Albian) of Hokkaido, Japan

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Abstract. A new fossil conifer, *Pseudofrenelopsis glabra* sp. nov., (Cheirolepidiaceae) is described based on a single specimen obtained from the Lower Cretaceous Yezo Group (Albian) of Hokkaido, Japan. The new species is characterized by cuticle possessing thin periclinal walls, a well-developed hypodermis, and absence of trichomes on internode and outer leaf surface. Recently, the author described *Frenelopsis pombetsuensis* from the Lower Cretaceous Yezo Group (Albian) of Hokkaido. The family Cheirolepidiaceae is a diagnostic taxon of the Ryoseki-type element that is reported only from the Ryoseki- and the Mixed-type floras. Thus *Pseudofrenelopsis glabra*is the second evidence of the Ryoseki-type element from Hokkaido.

Key words: Albian, conifer, Hokkaido, Middle Yezo Group, *Pseudofrenelopsis glabra*, Ryoseki-type floras.

Introduction

Jurassic and Early Cretaceous floras in eastern Eurasia have been classified by Kimura (1980, 1987) and Ohana and Kimura (1995) into three characteristic floras, the Ryoseki- and the Tetori-type floras, and the Mixed-type floras comprising elements of both the Ryoseki- and the Tetori-type floras. According to these authors, the Ryoseki-type floras grew under tropical to subtropical conditions with an annual long arid season, while the Tetori-type floras grew under temperate and moderately humid conditions.

The genus *Pseudofrenelopsis* belongs to the extinct conifer family Cheirolepidiaceae. Although this family is a dominant group of Mesozoic conifers, its closer affinity remain equivocal. The members of the family have various kinds of shoot morphology ranging from *Brachyphyllum-Pagiophyllum*-type shoots bearing scale leaves to *Frenelopsis-Pseudofrenelopsis*-type cylindrical segmented shoots bearing minute leaves. The single most reliable character of this family is possession of the pollen of the genus *Classopollis* Pflug (Watson, 1988). Although the plants yielding fossil remains attributed to the genus *Pseudofrenelopsis* were widely distributed during the Early Cretaceous (Berriasian-Albian) of North America, Europe, North Africa and Asia, they were apparently restricted to the Cretaceous (Table 1).

The frenelopsids, which include the genus *Pseudofrenelopsis* and the closely related genus *Frenelopsis*, have been used as indicator taxa of tropical to subtropical arid climate (Alvin, 1982). In east Asia the occurrence of the frenelopsids in fossil floras is restricted to the Ryoseki- and the Mixed-type floras. Although *Frenelopsis* is known from the Ryoseki-type floras of the Upper Jurassic to Lower Cretaceous in Japan, fossil remains assigned to *Pseudofrenelopsis* have not been reported yet. In the present paper, the remains of shoot and associated cuticular features of *Pseudofrenelopsis* from Japan are described.

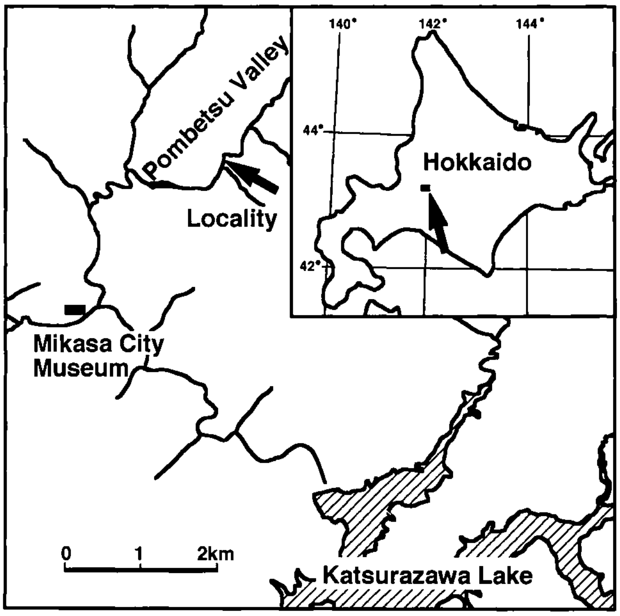
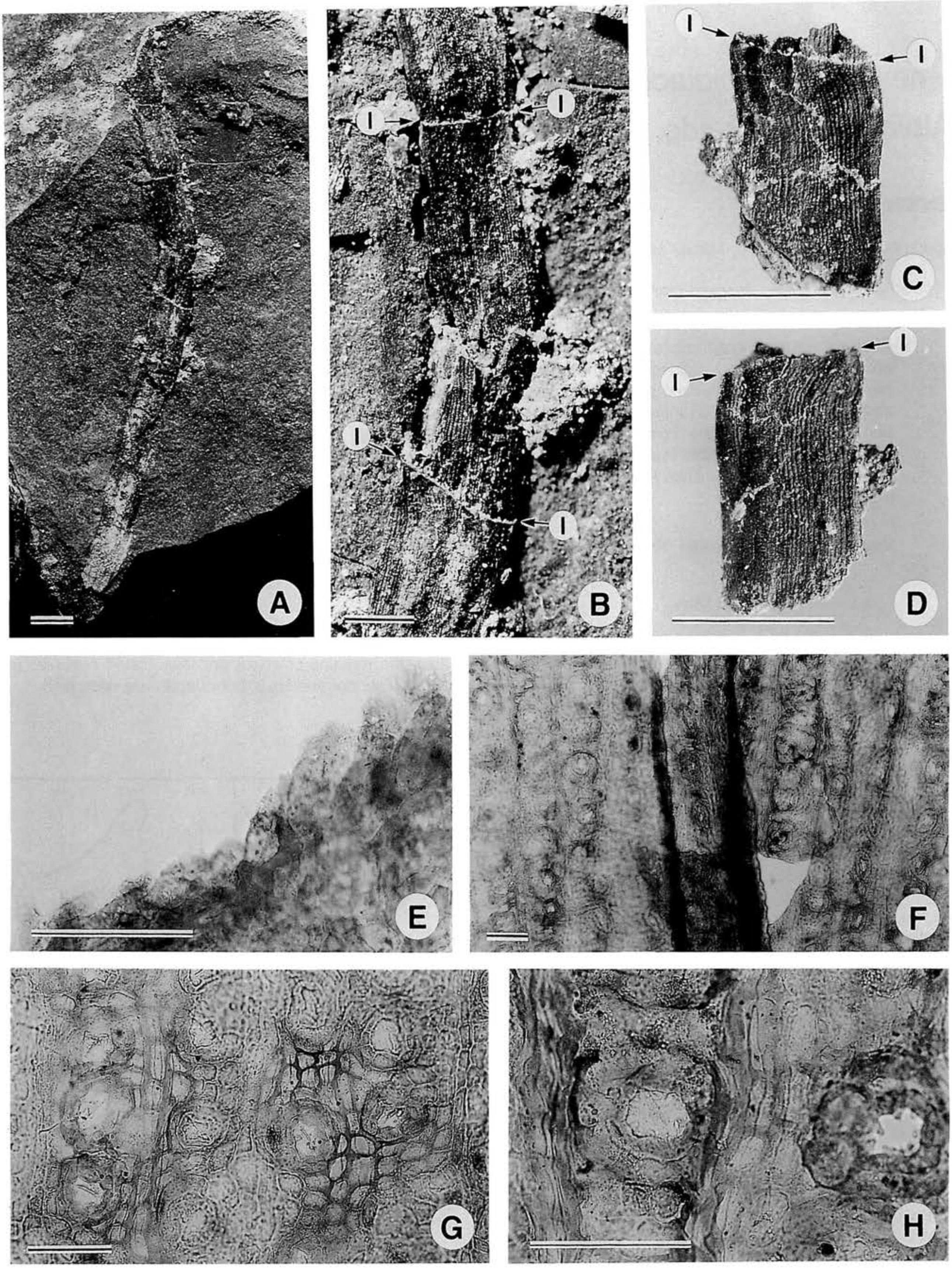


Figure 1. Map of Hokkaido, Japan showing the location of the Pombetsu Valley.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Material and Methods

Material.—A compressed conifer shoot was found in the Pombetsu Valley about 60 km northeast of Sapporo (Figure 1). The specimen was obtained from the mudstone bed of the so-called "Main part of Middle Yezo Group". The locality is situated between Matsumoto's outcrops Ik 2025 and 2031, from where the Albian ammonite *Ammonoceratites yezoensis* Yabe has been reported (Matsumoto, 1965, fig. 3).

Methods.—Fossil remains were immersed in Schulze's solution followed by diluted NaOH. The cuticle was mounted in Eukitt for light microscopy. For SEM observation, cuticles were coated with Pt-Pd in a Hitachi E-1030 ion sputter and photographed with Hitachi S-800.

All specimens used in this study are deposited in the Mikasa City Museum (MCM), Ikushumbets-nishikicho, Mikasa, Hokkaido.

Systematic description

Order Coniferales
Family Cheirolepidiaceae Takhtajan, 1963
Genus ***Pseudofrenelopsis*** Nathorst, 1893

Remarks of the genus.—The diagnosis originally based only on the type species was emended by Watson (1977) after studying specimens of *Frenelopsis varians* Fontaine, which is now placed in this genus. Recently, Srinivasan (1995) emended the diagnosis of *Pseudofrenelopsis* based on new morphological characters of Puddledock material. Srinivasan's concept is followed here.

Pseudofrenelopsis glabra sp. nov.

Figures 2A-H, 3A-I

Material.—Holotype, MCM-P030

Horizon.—Main part of the Middle Yezo Group (Albian).

Type locality.—Pombetsu Valley, Mikasa, Hokkaido (Figure 1; ca. 43°16′31″N, 141°59′20″E). The locality is about 80 m south of Matsumoto's (1965) outcrop Ik 2031.

Diagnosis.—Segmented shoot bears a simple spiral of leaves, each leaf encircling the stem. Leaf margin having hairs; outer surface of both abaxial and adaxial leaf cuticle smooth, without trichomes. Internode cuticle well developed. Outer surface of cuticle smooth, nonpapillate. Stomata arranged in longitudinal rows. Stomatal complex consisting of a pair of guard cells and 7-9 subsidiary cells. Guard cells sunken below a ring of subsidiary cells with irregularly oriented apertures. Stomatal pit rounded in surface view. Outer surface of subsidiary cells forming a raised rim bounded by a deep groove around stomatal pit. A well-developed cutinized hypodermis of thin-walled cells covering most of the internal surface of the cuticle.

Description.—A single compressed shoot was obtained (Figures 2A, B). The shoot is segmented, bearing a simple spiral of leaves. Each of the leaves encircles the stem. The internode is 6-9 mm long and 4 mm wide (Figures 2A, B). Triangular part of the leaf is up to 1.5 mm high at a node (Figures 2B, C; 3A). The leaf margin has hairs up to 40 μm long (Figures 2E; 3B, C). Outer surface of both abaxial and adaxial leaf cuticle is smooth, without trichomes (Figures 3B-D).

The internode cuticle is well developed, about 8 μm in total thickness. The cuticle consists of outer periclinal epidermal wall about 3 μm thick, anticlinal wall and thinly cutinized hypodermis (Figure 3E). No dorsiventrality is observed (Figure 2F). Stomata are about the same optical density as the rest of cuticle and are arranged in well marked longitudinal rows in 7-9 rows per mm. Each row of stomata is a single stoma wide. 70-100 per mm^2 in density. (Figures 2F, G; 3F, G). The bands of epidermal cells between the rows of stomata are 20-70 μm (1-3 cells) wide, consist of longitudinally arranged epidermal cells. The epidermal cells are elongated rectangular to polygonal in shape, 25-50 μm long and 10-25 μm wide (Figures 2F, G; 3G). Outer surface of the cuticle is smooth, nonpapillate (Figure 3F).

The stomatal complex is 80-120 μm in diameter, consists of a pair of guard cells and 7-9 subsidiary cells (Figure 3G). The guard cells are 40-70 μm long and 10 μm wide and are sunken below a ring of subsidiary cells. The aperture of the stoma is irregularly oriented (Figure 3G). The stomatal pit is about 30 μm in diameter and is rounded in surface view (Figures 3F, H). Outer surface of the subsidiary cells forms a raised rim bounded by a deep groove around stomatal pit. Each of the subsidiary cells has a single papilla projecting into the stomatal pit (Figures 2H; 3F, H, I).

A well developed cutinized hypodermis of thin-walled cells cover most of the internal surface of the cuticle except for the region immediately beneath each stomatal apparatus. The hypodermal cells are rectangular or polygonal under the stomatal zone and are axially elongate rectangular under the nonstomatal zone (Figures 3E, G).

Discussion.—Due to the fragmentary nature of the fossil specimen the arrangement of the branch system of *Pseudofrenelopsis glabra* is uncertain. External and cuticular observations of the specimen clearly indicate the absence of a groove or suture separating the basal cushions, as seen in living species of the Cupressaceae.

Although the epidermal cells are clearly visible with light microscopy (Figure 2G), SEM microscopy of the inner surface of cuticle shows only hypodermis and stomatal complexes,

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Figure 2. *Pseudofrenelopsis glabra* sp. nov. (MCM-P030). **A**: Holotype (MCM-P030). **B**: Middle region of the holotype showing leaf margins (l). **C, D**: Opposite sides of the same shoot fragment showing the margin of a single leaf (l). **E**: Light microscope image of the leaf margin showing short hairs. **F**: Light microscope image of cuticle from internodal region showing fold represented by central dark line, and cuticles of both sides of the compressed specimen. Arrangement of stomata and epidermal cells show no siginificant difference on both sides of the cuticles. **G**: Light microscope image of cuticle from the internodal region showing longitudinally arranged stomata, light microscope. **H**: Light microscope image of stomata, focused through the stomatal pit showing the papillae. Scale bars = 5 mm in A-D; 100 μm in E-H.

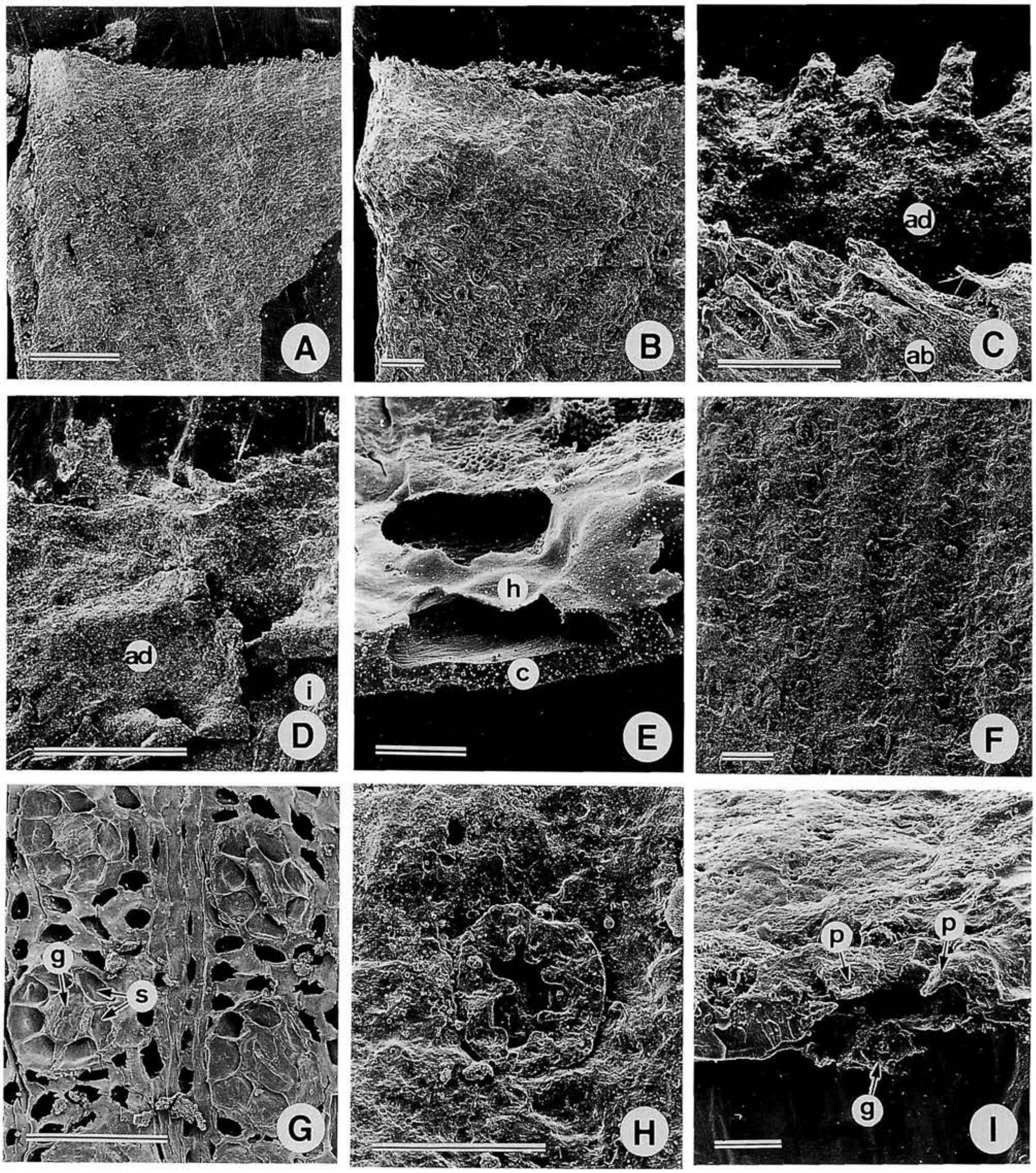

Figure 3. SEM micrographs of *Pseudofrenelopsis glabra* sp. nov. cuticle (MCM-P030). **A**: Triangular free part of leaf. **B**: Edge of a leaf, showing marginal hairs and outer surface of abaxial leaf cuticle. **C**: Enlarged photo of 3B showing the short marginal hairs and smooth outer surface of the abaxial (ab) and adaxial (ad) leaf cuticle. **D**: Surface view of adaxial leaf cuticle (ad) and inner view of cuticle from the internodal region (i). **E**: Section of cuticle showing cutinized epidermis (c) and hypodermis (h). **F**: Outer view of cuticle from the internodal region showing mouth of stomatal pit. **G**: Cuticle from the internodal region showing longitudinally arranged stomatal complexes. Inner view of stomatal complexes showing the guard cells (g), and subsidiary cells (s). **H**: Outer view of a stoma showing the rounded mouth of the stomatal pit with papillae. **I**: Section of stoma showing guard cells (g), and papillae in throat of stoma (p). Scale bars = 500 μm in A, B; 50 μm in C, D, F-H; 10 μm in E, I.

Table 1 Comparative morphometices of *Pseudofrenelopsis glabra* sp. nov. and related species.

Characters/Species	***P. varians***	***P. parceramosa***	***P. papillosa***	***P. dalatzensis***	***P. heishanensis***	***P. nathorstiana***	***P. glabra*** **sp. nov.**
Internode length	1.5-17 mm	1-11 mm	5-11 mm	5.5-10 mm	5-6 mm	1.0-2.9 mm	6-8 mm
Internode width	3-7 mm	1 mm<	3-7.5 mm	3-6.5 mm	2.5-4 mm	1.0-2.0 mm	4 mm
Presence of suture or gap	none	in some 'open' form	none	none	none	yes	none
Maximum length of free leaf	1.5 mm	2 mm	1.5 mm	2 mm	2 mm	1.0 mm	1.5 mm
Leaf margin	hairs up to 60 μm	hairs up to 80 μm	hairs up to 80 μm	without hairs	without hairs	hairs up to 145.0 μm	hairs up to 40 μm
Trichomes or hairs on adaxial surface of leaf	hairs present	hairs present	hairs present	normally without hairs	without hairs	trichomes	without hairs
Internode cuticle thickness	50-110 μm	30 μm	5-7.5 μm	(5-)7.5-10(-25)μm	3-5 μm	10.0 μm	3 μm
Trichomes or hairs on epidermal cells	up to 80 μm	none to very long hairs	usually present	with large papillae	none	up to 200 μm	none
Cutinized hypodermis	in "open" leaf-base cushions	well cutinized	none	none	none	none	well cutinized
Stomatal arrangement	scatterred in "closed" form, rows in "open" form	well defined rows	longitudinal rows with scattered stomata	well defined rows	well defined rows	mostly ill defined rows	well defined rows
Density of stomatal rows	8-10 per mm	6-10 per mm	(4-)6-7(-9) per mm	(6-)7-8(-10) per mm	8-9(-10) per mm	11-12 per mm	7-9 per mm
Diameter of stomatal apparatus	70-100 μm	50-80 μm	40-92.5 μm	55-95 μm	62.5-100 μm	50-73×54-62 μm rarely 103.0 μm	80-120 μm
Number of subsidiary cells	(4-)5-8(-9)	(4-)5-6(-7)	(4-)5-6(-8)	5-6	5-6(-7)	(4-)5-6(-7)	6-8
Rim of stomatal pit	round: -with papillae	round: -with or without papillae	round: -with papillae	stellate	stellate	elliptical to round : -with papillae	round: -with papillae
Stratigraphic range	Aptian-Albian	Berriasian-Albian	Lower Cretaceous	Lower Cretaceous	Aptian-Albian	lower-mid-Albian	Albian
Distribution	North America	North America, Europe	China	China	China	China	Japan
References	Watson, 1977	Alvin, 1977 Alvin *et al.* 1978 Watson, 1977	Chow and Tsao, 1977 Zhou and Cao, 1979 Zhou, 1995	Chow and Tsao, 1977 Zhou, 1995	Zhou, 1995	Srinivasan, 1995	

because the epidermal cells are covered by cutinized hypodermis (Figure 3G).

Comparison.—Although the present specimen is fragmentary, both external and cuticular features of the specimen correspond well with the diagnosis of *Pseudofrenelopsis* Nathorst emended by Srinivasan (1995) in its segmented shoot bearing a simple spiral of leaves, smooth cylindrical internode, and guard cells sunken below ring of subsidiary cells.

Among the species of *Pseudofrenelopsis* previously described, the European *P. varians* (Fontaine) Watson and American *P. parceramosa* (Fontaine) Watson differ from *P. glabra* in possessing an extremely thick cuticle and having trichomes on the adaxial surface of the leaf cuticle (Watson, 1977).

Although various species of *Pseudofrenelopsis* have been reported from China, most are provided with brief descriptions (Zhou, 1995). Recently, Zhou (1995) reexamined and combined the Chinese *Pseudofrenelopsis* into the following three species : *P. papillosa* (Chow et Tsao) Zhou, *P. dalatzensis* (Chow et Tsao) Zhou, and *P. heishanensis* Zhou (Table 1). *Pseudofrenelopsis glabra* is similar to these Chinese species in possessing a thinner internode cuticle than the European and American species. *Pseudofrenelopsis dalatzensis* and *P. heishanensis* can be distinguished from *P. glabra* by the stellate rim of the stomatal pit and absence of hairs on their leaf margins.

The shape of the cells, smooth periclinal walls, and thin anticlinal walls of the hypodermis of *Pseudofrenelopsis glabra* (Figures 3G, E) are very similar to the "epidermal cells" of *Pseudofrenelopsis heishanensis* described by Zhou (1995). However, detailed light and SEM microscopy of *P. heishanensis* is required prior to meaningful comparison of *P. heishanensis* and *P. glabra*.

Pseudofrenelopsis papillosa, redescribed in detail by Zhou (1995), possesses the most similar cuticle to that of *P. glabra* in having hairs on the margin of the leaf, round stomatal pits, and a thin cuticle. These resemblances may indicate a close phylogenetic relationship between these two species. *Pseudofrenelopsis glabra* is however, clearly distinguished from *P. papillosa* by a smaller number of subsidiary cells and absence of trichomes on the outer surface of the leaf adaxial cuticle.

Paleophytogeography.—Since Kimura (1961, 1975) has divided the Late Jurassic-Early Cretaceous floras of Japan and its adjacent areas into the Ryoseki-type and the Tetori-type floras, this paleophytogeographical distinction has been extended to East Asia with some modification, and the Mixed-type flora that consist predominantly of the Ryoseki-type element and subordinate Tetori-type element was added (Kimura, 1980, 1987 ; Kimura and Ohana, 1992 ; Cao, 1994 ; Ohana and Kimura, 1995).

Although the Mesozoic flora of Hokkaido is famous for its well preserved permineralized materials, the stratigraphic range of these materials is restricted to the Upper Cretaceous (Nishida, 1991). So far, the absence of Jurassic and Lower Cretaceous fossil plants from Hokkaido had prevented comparison of the Early Cretaceous flora of Hokkaido with the Ryoseki- and the Tetori-type floras. Recently, Saiki (1997) described *Frenelopsis pombetsuensis*, from the Lower Cretaceous Yezo Group (Albian) of Hokkaido. The family Cheirolepidiaceae is a diagnostic taxon of the Ryoseki-type element reported only from the Ryoseki- and the Mixed-type floras (Ohana and Kimura, 1995). Thus, *Pseudofrenelopsis glabra* is the second evidence of the presence of Ryoseki-type element from Hokkaido.

Ohana and Kimura (1995) estimated that the Ryoseki-type floras flourished under tropical or subtropical conditions with an annual long arid season. Their idea is consistent with the thermophilous nature of frenelopsids proposed by Alvin (1982) based on the distribution of frenelopsids of the world and their possession of a thick cuticle. However, the two frenelopsids species from Hokkaido lack two of the xeromorphic features observed in many other frenelopsids, namely, a thick cuticle and trichomes on the internode surface. The cuticle thickness of eight species listed in Alvin (1982) are 8-110 μm thick in their periclinal wall rather than 3 μm and 3-4 μm thick as in *Frenelopsis pombetsuensis* and *Pseudofrenelopsis glabra* respectively. The cuticular features of *Frenelopsis pombetsuensis* and *Pseudofrenelopsis glabra* may reflect the rather humid condition inferred for the Albian of Pombetsu, rather than the xeric conditions from other regions of the world where frenelopsids were distributed (Alvin, 1982). This assumption is consistent with recent palynological data indicating that the group inhabited a variety of ecological niches (Watson, 1988).

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Paleontological Research, vol. 3, no. 1, pp. 36-40, 3 Figs., April 30, 1999

The first record of *Mesoturrilites* (Ammonoidea) from Hokkaido

(Studies of the Cretaceous ammonites from Hokkaido and Sakhalin — LXXXIII)

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Abstract. **Several small specimens collected years ago by A.I. from a locality in the Soeushinai area of Hokkaido are now identified as *Mesoturrilites boerssumensis* (Schlüter, 1876). The species has been reported from the Lower Cenomanian of western and central Europe and western Asia. Our material is also referred to the Lower Cenomanian on the biostratigraphic evidence. This may be the first record of *Mesoturrilites* in the northern Pacific region.**

Key words : Cenomanian, geographic distribution, Hokkaido, *Mesoturrilites*, Pacific region, Turrilitidae

Introduction

A number of species belonging to *Mariella, Pseudhelicoceras, Ostlingoceras, Neostlingoceras, Turrilites* and *Hypoturrilites* of the family Turrilitidae [Ammonoidea] show worldwide distribution. Some of them occur fairly commonly in the Upper Albian and Cenomanian strata in Japan, although many of them are waiting for complete descriptions. In this paper a species of *Mesoturrilites* from Hokkaido is described.

Stratigraphic setting

The area concerned, called "Soeushinai", was geologically mapped by Hashimoto *et al.* (1965) and has been recently reinvestigated by Nishida *et al.* (1996, 1997, 1998a, b). According to these authors, a thick series of strata called the Middle Yezo Subgroup of late Albian through Turonian age, is extensively exposed in this area. The subgroup is subdivided into Members My1 to My8 in a revised scheme of Nishida *et al.* (1996, fig. 10). The specimens described below were contained in a transported nodule obtained by A.I. in 1959. That nodule was collected in the upper reaches of the Sanjussen-zawa, a tributary of the River Uryu. The nodule is interpreted as a derivative from Member My3. This member consists primarily of mudstones which have sometimes fine-grained sands or sandy laminae and contain commonly calcareous nodules. Ammonoids occur fairly abundantly in Member My3 together with inoceramids and other mollusks. Some of them were described by Matsumoto and Inoma (1975, 1991) and Inoma (1980) and also amply listed by Nishida *et al.* (1996, 1997). The fauna forms the Assemblage Zone of *Graysonites adkinsi*, indicating the lower part of the Lower Cenomanian.

The overlying Member My4 is composed of ill-sorted conglomerates in some parts and predominant sandstones with some mudstones and conglomerates in other parts. It is poor in fossils. The succeeding Member My5 consists mainly of mudstones which contain numerous inoceramids with some associated ammonoids, representing the rest of the Cenomanian.

The Inoma's locality, numbered AI-72803, is concisely indicated in a map by Matsumoto and Inoma (1975, fig. 2) and more precisely in Figure 1. A fossiliferous nodule contains small specimens of *Algericeras proratum* (Coquand) and *Euhystrichoceras* cf. *nicaisei* (Coquand) besides those of *Mesoturrilites* described herein. At another locality, R7239p, about 70m NEE of AI-72803, Y. Kawashita and N. Egashira obtained another ammonite which is identified by T.M. with *Gabbioceras yezoense* Shigeta. The three ammonite species indicate an early Cenomanian age and the mudstones around the above localities are referable to Member My3. Incidentally, as a result of Y. Inoue's examination of foraminifera, the strata exposed in the source area of the Sanjussen-zawa, including localities R7238, R7231, R7232, R7233 and R7234, have proved to be Member My5 (middle to upper part of the Cenomanian) (for details see Nishida *et al.*, 1998a). The two members My3 and My5 are probably in fault contact (Figure 1).

Repository

The specimens described below have numbers with the prefix TKD, which is the abbreviation of "Tokyo Kyoiku Daigaku [Tokyo University of Education]", where A.I. was a student. Since this university was closed, A.I.'s collection of ammonoids from the Soeushinai area under TKD numbers has been temporarily stored in the Department of Geology,

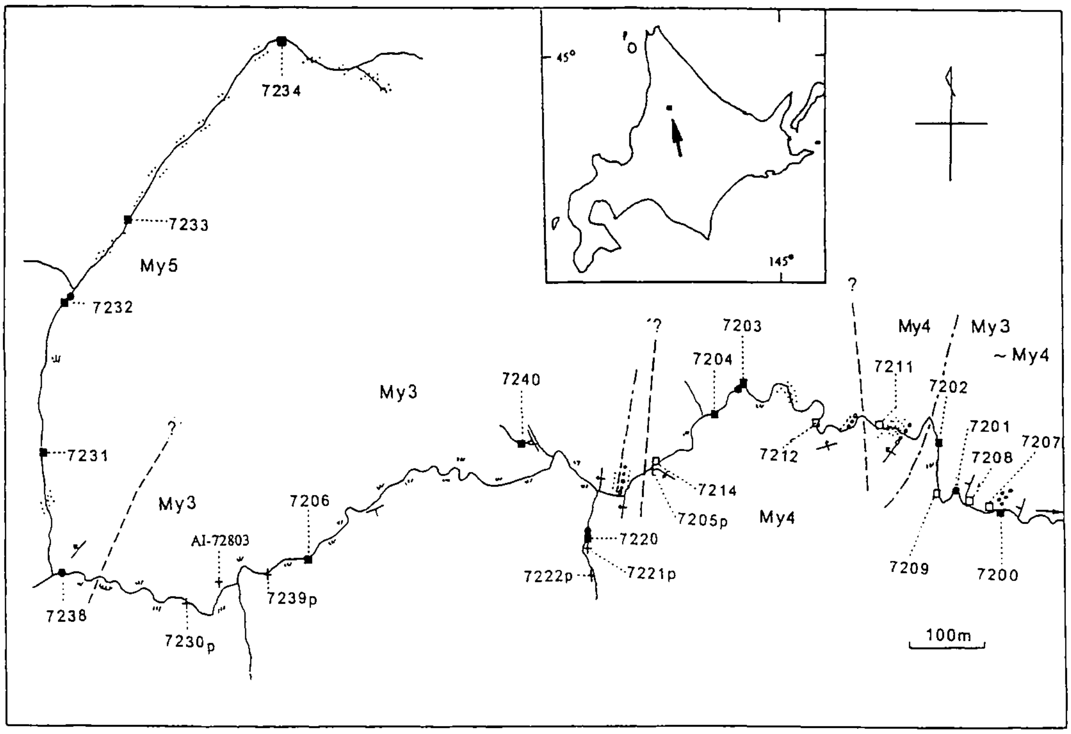

Figure 1. Route map along the upper course of the Sanjussen-zawa, cited from Nishida *et al.*, 1998a by permission. Inset is a map of Hokkaido in which the Soeushinai area is indicated by an arrow. Small solid circle : megafossil (in situ), cross : ditto (trantported nodule), solid square : microfossil sample, empty square : rock sample, tiny empty circle : conglomerate, dots : sandstone, grass : no outcrop, blank along the route : mudstone, broken line : fault (inferred), chain : boundary of lithostratigraphic units (members). All the locality numbers should have prefix R, except for AI-72803.

Kyushu University in Fukuoka, but they should be eventually returned to the Deparrtment of Geosciences, Tsukuba University, Tsukuba, 305-0006 Japan, which is the new guise of the TKD.

Morphological terms

For the morphological terms used to describe the turrilitid ammonoids, we follow those of Wright and Kennedy (1996). Setting the apex of the turrical shell at the top, the terms upper and lower or adapical and adapertural [=adoral] are defined and the rows of tubercles or ribs on the face of each whorl are described in descending order as the first, the second and so on.

Palaeontological description

Order Ammonoidea Zittel, 1884
Suborder Ancyloceratina, Wiedmann, 1966
Family Turrilitidae Gill, 1871
Genus ***Mesoturrilites*** Breistroffer, 1953

Type species.—Turrilites aumalensis Coquand (1862, p. 323, pl. 35, fig. 5), by original designation of Breistroffer (1953, p. 1351).

Diagnosis.—Turrilitid ammonoid with four rows of tubercles or ribs ; the upper row made up of ribs or rounded tubercles, the second and the third rows spirally elongated tubercles on semicontinuous, narrow ridges separated by a groove ; the fourth row of weak tubercles at the outer edge of the lower whorl surface ; faint ribs may be elongated from the fourth row of tubercles toward a narrow umbilicus.

Remarks.—The lectotype and paralectotypes of the type species have been photographically illustrated by Wright and Kennedy (1996, text-fig. 146A-G).

At present five species are known in *Mesoturrilites*. The distinction between species is based on the size of the apical angle, mode of ribbing and/or tuberculation, whorl shape etc. Atabekian (1985, p. 75) referred *Turrilites colcanapi* Boule, Lemoine and Thévenin, 1907 to *Mesoturrilites*. However, we agree with Spath (1937, p. 523) and also Wright and Kennedy (1996, p. 323) on their assignment of *T. colcanapi* to *Ostlingoceras*.

The phylogenetic origin of *Mesoturrilites* is uncertain, but it can likely be sought in some form of *Mariella*. A sulcate variety of *Mariella oehlerti* (Pervinquière) may be a candidate, as Pervinquière (1910, p. 55, pl. 5, fig. 17) has already mentioned its affinity to *Mesoturrilites aumalensis*. Wright and Kennedy (1996, p. 346) have suggested *Mariella bicarinata* (Kner) as another allied form.

The type species and some other species of *Mesoturrilites* have been recorded from the Lower Cenomanian of both the

Tethys and Boreal provinces.

Mesoturrilites boerssumensis (Schlüter, 1876)

Figures 2 and 3

Turrilites börssumensis Schlüter, 1876, p. 129, pl. 38, figs, 6, 7.
Turrilites (*Mesoturrilites*) *boerssumensis* Schlüter. Immel, 1979, p. 636, pl. 4, fig. 4 ; Hiss, 1982, p. 190, pl. 7, figs. 11, 12 ; Atabekian, 1985, p. 75, pl. 27, figs. 3, 4.
Mesoturrilites boerssumensis (Schlüter). Wright and Kennedy, 1996, p. 347, pl. 105, figs. 4, 20 (with full synonymy) ; Lehmann, 1998, p. 36, pl. 5, fig. 5.

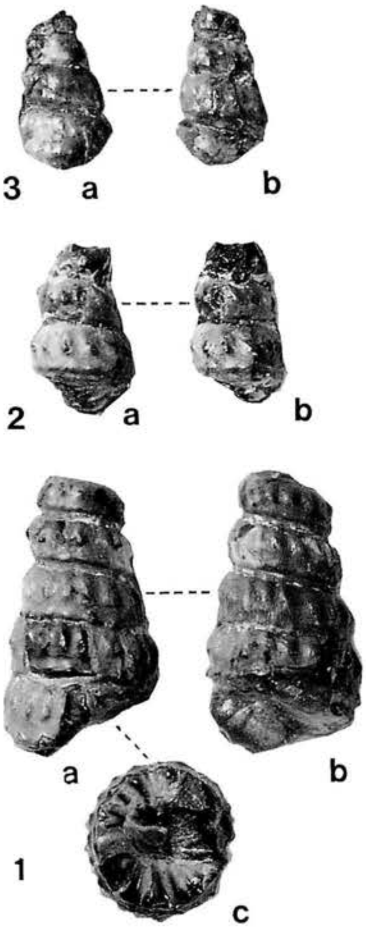

Figure 2. *Mesoturrilites boerssumensis* (Schlüter). **1.** TKD30089A, two lateral (a, b) and basal (c) views. **2.** TKD30089B, two lateral (a, b) views. **3.** TKD30089C, two lateral (a, b) views. All × 2.

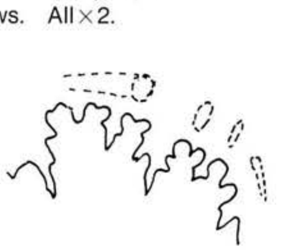

Figure 3. *Mesoturrilites boerssumensis* (Schlüter). Suture of TKD30089C, showing relative position of the ribs and tubercles by dotted lines. Approximately × 8.

Lectotype.—The original of Schlüter, 1876, pl. 38, figs. 6, 7, from the Cenomanian Pläner near Börssum, Germany, by subsequent designation of Juignet and Kennedy (1976, p. 67).

Material.—Four specimens, TKD30089A (Figure 2-1), TKD30089B (Figure 2-2), TKD30089C (Figure 2-3 ; Figure 3) and TKD30089D (unillustrated). They were removed by A.I. from a transported nodule at locality AI-72803 in the upper reaches of the Sanjussen-zawa of the Soeushinai area, northwestern Hokkaido (Figure 1).

Description.—TKD30089A consists of four whorls with estimated tower height 23.3 mm, apical angle about 19°, height and diameter of the preserved last whorl 5.4 mm and 11.2 mm respectively. Other three are smaller than the above and incomplete, representing younger stages.

The main part of the exposed whorl face is flattened or slightly convex and the interwhorl junction is feebly impressed. The ornament is typical for *Mesoturrilites*. On the upper half of the exposed whorl face there are slightly prorsiradiate ribs of moderate breadth and density (Figure 2-1). They number 21 per whorl at diameter of 11 mm in TKD30089A and 16 or 15 at diameter 7 or 6 mm in TKD30089B or TKD30089C. At about the middle of the whorl face the ribs terminate at tubercles of the first row. These tubercles are subrounded at the base and pointed at the top, as far as the test is well preserved. The tubercles of the second row are narrowly clavate and rest on a blunt spiral ridge. They correspond in number to the tubercles of the first row but are displaced adaperturally. The space between the first and the second rows of tubercles forms a smooth band and may appear to be slightly concave on the internal mould. The tubercles of the third row are narrowly clavate and aligned along the narrow ridge along the lower seam of the whorl. The narrow interspace between the second and the third rows of clavi is distinctly sulcate. As is shown by TKD30089A, the spiral groove between the second and third rows of semi-continuous ridges is immediately above the interwhorl junction in early growth stages, but later it is covered by the shell layer of the succeeding whorl (Figure 2-1). The tubercles of the fourth row are close to those of the third row, but they are aligned on the outer margin of the lower whorl face. Weak ribs run from them toward a narrow umbilicus, showing slightly rursiradiate curvature (Figure 2-1c).

A septal suture of a young stage is exposed on the whorl face of TKD30089C. As is shown in Figure 3, the saddle E/L is much broader than L/U. The relative disposition of the tubercles with respect to the sutural elements in shown is the same figure.

Discussion.—The specimens described above are undoubtedly identified with *Mesoturrilites boerssumensis* (Schlüter, 1876), redefined by Wright and Kennedy (1996, p. 347). In view of the variation of the rib density with growth and between individuals, the 17 ribs to a whorl specified in Schlüter's (1876, p. 636) description may not be incorrect. Hiss (1982, p. 190) counted 20 ribs on an example from Westphalia. Wright and Kennedy (1996, p. 347) estimated as many as 24-26 ribs per whorl in a specimen from England, but 9 or 10 ribs are shown on its illustrated face of slightly less than half a whorl (*op. cit.*, pl. 105, fig. 4) as in our TKD30089A (Figure 2-1).

Hitherto described specimens, comprising those from Hokkaido, are more or less small, with diameters of the preserved last whorl less than 25 mm. The small size may be, therefore, a diagnostic character of this species. However, further investigation is required to search out a completely preserved specimen with a rostrate peristome and also to examine the problem of dimorphism.

Occurrence.—As for material. *M. boerssumensis* has been reported from the Lower Cenomanian of Germany (Westphalia and Bavaria), England, Poland and southern Turkmenistan (see synonymy list). Now its distribution is extended to Hokkaido. This may be the first record of *Mesoturrilites* from the northern Pacific region.

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Hokkaido 北海道, Sanjussen-zawa 三十線沢, Shumarinai 朱鞠内, Soeushinai 添牛内, Uryu 雨竜, Yezo 蝦夷

Paleontological Research, vol. 3, no. 1, pp. 41-48, 5 Figs., April 30, 1999

Early Silurian actinocerid and orthocerid cephalopods from the Kerman area, East-Central Iran

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Abstract. Six species of uncoiled cephalopod, including the actinocerids Actinoceratidae, gen. and sp. indet., *Armenoceras banestanense* sp. nov., *A.* sp., *Elrodoceras* sp. and *Huroniella iranica* sp. nov., and an orthocerid Proteoceratidae ?, gen. and sp. indet., are present in collections made recently from an unnamed formation near Banestan village in the Kerman area of southern East-Central Iran. The cephalopod fauna contains forms closely related with those from Laurentia, and is considered to be of Early Silurian age. This discovery reveals that the geologic age of these cephalopod-bearing horizons should be revised from a vague late Ordovician or early Silurian one. These horizons are correlative with the Niur Formation in the Shirgesht area of northern East-Central Iran.

Key words: Actinocerida, cephalopods, Early Silurian, Iran, Orthocerida

Introduction and geologic setting

During the course of field work in February, 1996, several uncoiled cephalopods were discovered by two of us (Y.K. and D.W.) at three localities near Banestan village in the Kerman area of southern East-Central Iran (Figure 1). The purpose of this paper is to document the fauna and to discuss its implications. The specimens are deposited in the University Museum of the University of Tokyo (UMUT).

Until its separation and northward drifting at or near the Permian-Triassic boundary, the Iran terrane belonged to the Gondwana continent, and the Kerman area was part of a carbonate platform around the margin of Gondwana (e.g., Lensch *et al.*, 1984). The geology of the Kerman area has been described by Huckriede *et al.* (1962), Zohrenbakhsh and Vahdati Daneshmand (1992) and Richards *et al.* (1994). These investigatiors discerned three units in the Lower to Middle Paleozoic strata: Upper Cambrian to Lower Ordovician carbonates of the Mila Formation, the Arenig (upper Lower Ordovician) graptolite shale of the Katkoyeh Formation, and an unnamed formation probably ranging from Upper Ordovician to Middle Devonian that mainly consists of clastics with subordinate carbonates. The cephalopods described herein occur in argillaceous and/or bioclastic limestone of the unnamed formation (Figure 2). The cephalopod-bearing horizons have been described as "orthoceras limestone" by Huckriede *et al.* (1962), and regarded as being of late Ordovician or early Silurian age. However, the exact biostratigraphic range of the cephalopod-bearing horizons has so far been a matter of debate.

Detailed analysis of morphologic features of the present cephalopods resulted in the identification of five Early Silurian actinocerid and one orthocerid species that provide insights into the precise age and paleobiogeographic affinities of the fauna. This is the first modern taxonomic treatment of Silurian cephalopods from the Iran terrane.

Systematic paleontology

Subclass Actinoceratoidea Teichert, 1933
Order Actinocerida Teichert, 1933
Family Actinoceratidae Saemann, 1853

Genus and species indeterminate

Figures 3-7, 5-5, 6

Discussion.—A single incomplete specimen of a gently cyrtoconic (?) phragmocone is assigned to the Actinoceratidae, genus and species indeterminate, based on its relatively long and normal cyrtochoanitic septal necks and the high ratio (at least 3.2) of maximum diameter/length of its siphuncular segments.

The restricted development of the annulosiphonate

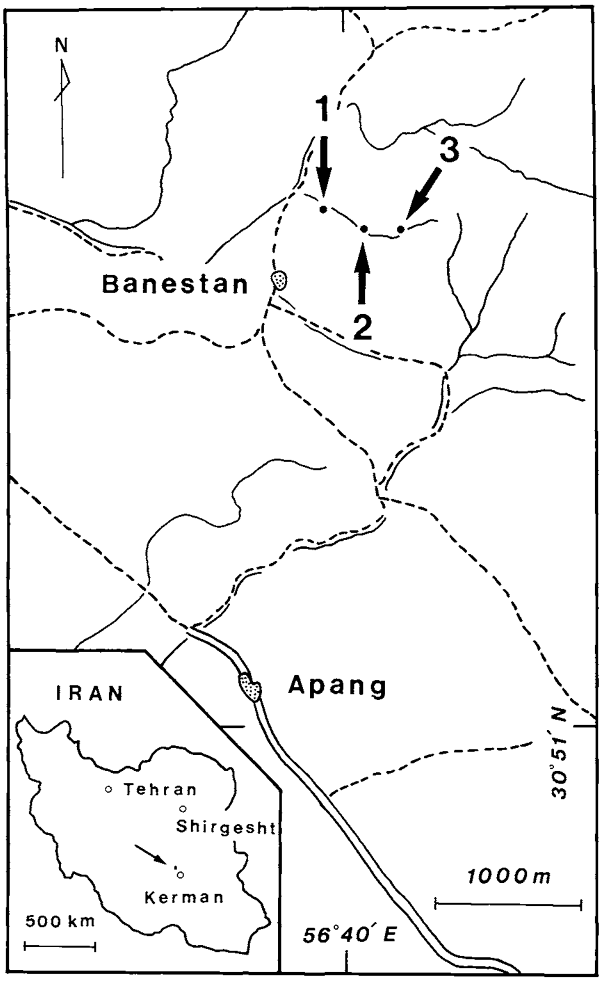

Figure 1. Index map of fossil localities (1-3) in the Kerman area (small arrow in inset), southern East-Central Iran.

deposits on the ventral siphuncular wall and the straight radial canals projecting to the vicinity of brims are an unusual diagnosis for the family and indicate a possibility that the species represents a new genus. Unfortunately the ventral shell is not preserved in the only specimen available. Until additional material is found, the present material is considered too poor to justify naming it to the generic level.

Material and occurrence.—UMUT PM 27332, 72 mm in length, from locality 3.

Family Armenoceratidae Troedsson, 1926
Genus *Armenoceras* Foerste, 1924a

Type species.—*Actinoceras hearsti* Parks, 1913.

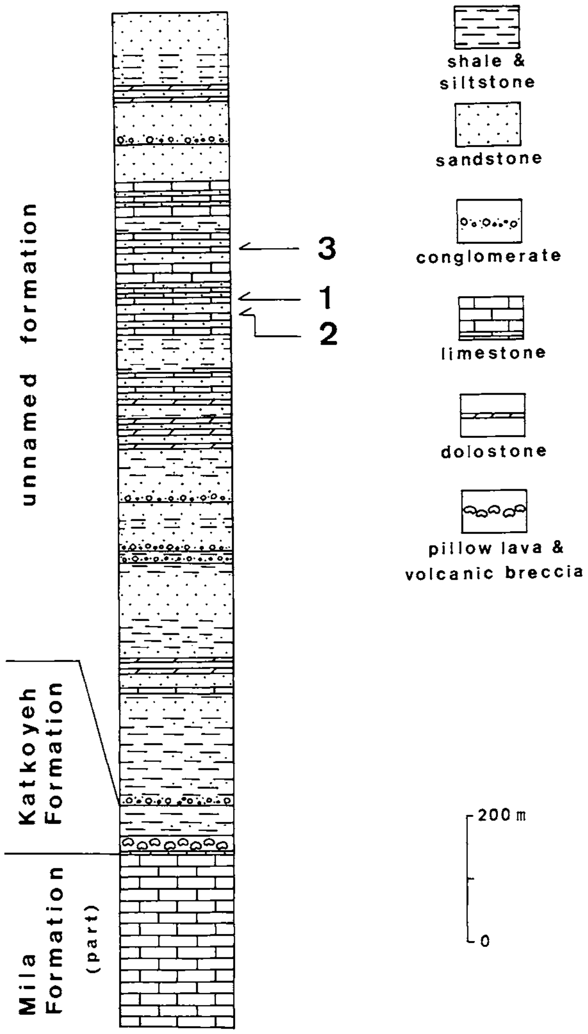

Figure 2. Generalized stratigraphic section of the Lower to Middle Paleozoic rocks near Banestan village in the Kerman area. Stratigraphic horizons of each locality are indicated.

Armenoceras banestanense sp. nov.

Figures 3-1—6

Diagnosis.—*Armenoceras* with smaller ratio of maximum siphuncular diameter to shell diameter (approximately 0.3-0.4), very narrow adnation areas in dorsal siphuncular wall; cameral deposits well developed; central canal situated on dorsal margin.

Description.—Orthoconic shells with circular cross sections, moderate shell expansion for the genus, lacking

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Figure 3. **1-6.** *Armenoceras banestanense* sp. nov., 1-4, 6: holotype, UMUT PM 27328, 1, dorsoventral thin section, venter on left, ×2, 2, dorsoventral thin section, showing details of ventral wall of siphuncle, ×14, 3, dorsoventral thin section, showing details of dorsal wall of siphuncle, note very narrow adnation area, ×14, 4, dorsoventral thin section, showing details of ventral shell, ×5, 6, transverse thin section of adoral end, venter down, ×2, 5: paratype, UMUT PM 27327, weathered surface of dorsal side, coated with ammonium chloride, ×2. **7.** Actinoceratidae, gen. and sp. indet., UMUT PM 27332, dorsoventral thin section, venter on right, ×2.


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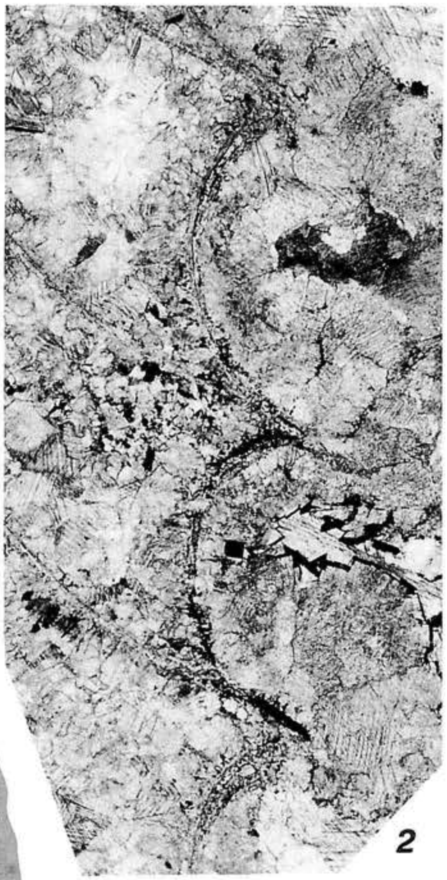
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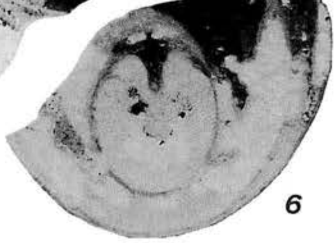
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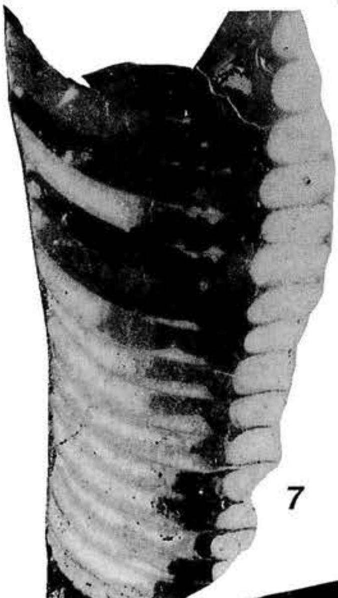
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conspicuous surface ornamentation; adoral end of imperfect phragmocone of holotype attains approximately 25 mm (slightly deformed) in diameter. Septa closely spaced, moderately shallow; siphuncle large, ratio of maximum siphuncular diameter to shell diameter is small for genus, approximately 0.3-0.4, submarginal in position; septal necks very short, 0.15-0.21 mm in length, strongly recurved cyrtochoanitic; brims short for genus, 0.44 mm in well preserved dorsal brim of holotype, in contact with apical surface of septa; diameter of septal foramen 5.9-8.9 mm in holotype; connecting rings broadly expanded; adnation areas moderate to relatively narrow (their length in dorsoventral section approximately 0.9 mm) in ventral siphuncular wall, and very narrow (*do*. approximately 0.3 mm) in dorsal siphuncular wall; maximum diameter/length ratio of siphuncular segments 3.5-4.0. Cameral deposits well developed, episeptal-mural and forming circumsiphuncular ridges, additional hyposeptal deposits recognized in ventral side of camerae; ventral endosiphuncular deposits fusing to form thick lining on siphuncular wall, differentiated into outer annuli and inner lining deposits; profile of outer annuli laterally elongated elliptical in longitudinal section; development of endosiphuncular deposits on dorsal siphuncular wall weak, separated annuli with semicircular profile in longitudinal section. Central canal situated on dorsal margin, branching off narrow radial canals, of which distal parts are curved adorally; perispatia small, situated near adoral end of each connecting ring.

Discussion.—*Armenoceras banestanense* sp. nov. is most similar to *A. hearsti* (Parks, 1913; 1915, pl. 6, fig. 5; Foerste, 1924a, pl. 13, fig. 4) which has a siphuncular position and a form ratio of the siphuncular segments like the new species. *Armenoceras hearsti* was reported from "Limestone Rapids" on the Severn River, Ontario, Canada, and derived from the Ekwan River or Attawapiskat Formation of late Llandovery (Early Silurian) age (Jin *et al*., 1993). However the former is distinguishable from the latter by its smaller siphuncle (ratio of maximum siphuncular diameter to shell diameter approximately 0.45 in *A. hearsti* versus 0.3-0.4 in *A. banestanense*), its somewhat weaker inflation of the connecting rings with the narrower adnation area, and the marginal position of its central canal.

The brims of *Armenoceras banestanense* and the cooccurring *A*. sp. (this report) are frequently missing or obscured by diagenesis, thus they are apt to be incorrectly described as "achoanitic".

Material and occurrence.—Holotype, UMUT PM 27328, an incomplete phragmocone, 51 mm in length; paratype, UMUT PM 27327, an incomplete phragmocone, 42 mm in length. Both from locality 3.

Etymology.—The specific name is derived from the village named Banestan near the type locality.

Armenoceras sp.

Figures 4-5, 7, 8

Description.—Orthoconic shells with gradual shell expansion, shell diameter reaches 20 mm at adoral end of largest specimen (UMUT PM 27329). Siphuncle subcentral in position, consisting of strongly recurved cyrtochoanitic septal necks and expanded connecting rings with relatively wide adnation area; brims in contact with septa; maximum diameter/length ratio of siphuncular segments approximately 2.5. Cameral deposits episeptal-mural and hyposeptal; endosiphuncular deposits of annuli have elliptical profile in longitudinal section. Nearly straight radial canals connect with prespatia in apical shell.

Discussion.—This species is easily distinguished from *Armenoceras banestanense* sp. nov. by its subcentral siphuncular position and the smaller form ratio of the siphuncular segments.

Material and occurrence.—Two incomplete phragmocones, UMUT PM 27329, 62 mm in length, and 27330, 61 mm in length, from locality 3.

Genus ***Elrodoceras*** Foerste, 1924b

Type species.—*Cyrtoceras indianense* Miller, 1892.

Elrodoceras sp.

Figures 5-1—3

Description.—Siphuncle gently curved (?) and large, attains at least 15.5 mm in maximum diameter, with relatively low ratio of maximum diameter/length in siphuncular segment for armenoceratids, at approximately 2.5-2.7; siphuncular position submarginal (?). Septal necks bend adapically, thus septal foramen is funnel-shaped; brims strongly recurved cyrtochoanitic, in contact with septa; connecting rings form very wide adnation area and moderately inflated free parts. Cameral deposits episeptal-mural and hyposeptal; endosiphuncular deposits well developed, annulosiphonate. Central canal surrounded by lining deposits that are darker in color than annulosiphonate deposits; radial canal arched with branches.

Discussion.—Except for the deposit-filled siphuncle, the shell of this only known specimen is broken and weathered on the dorsum, thus accurate shell shape and siphuncular position can not be determined in the present material. Nevertheless, this species appears most similar to *Elrodoceras* in its siphuncular morphology such as the funnel-shaped

Figure 4. 1-4, 6. *Huroniella iranica* sp. nov., holotype, UMUT PM 27326, isolated siphuncle, 1, dorsoventral thin section, venter on left, ×2, 2, transverse thin section of apical end, venter down, ×2, 3, dorsoventral thin section, showing details of ventral wall of siphuncle, ×5, 4, dorsoventral thin section, showing details of dorsal wall of siphuncle, ×5, 6, dorsoventral thin section, showing details of septal neck and radial canal in ventral wall of siphuncle, note contact layer and depression on apical surface of septum, ×14. **5, 7, 8.** *Armenoceras* sp., 5, 7: UMUT PM 27330, 5, dorsoventral thin section, venter on right, ×2, 7, dorsoventral thin section, showing details of ventral wall of siphuncle, ×14, 8: UMUT PM 27329, weathered surface of ventral side, coated with ammonium chloride, ×2.


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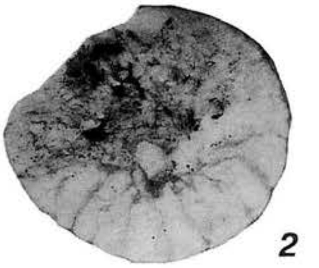
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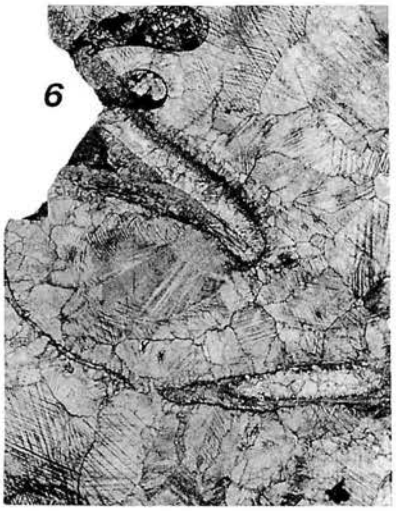
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septal foramen, arched radial canals and relatively low form ratio of the siphuncular segments.

Material and occurrence.—UMUT PM 27331, 55 mm in length, from locality 3.

Family Huroniidae Foerste and Teichert, 1930
Genus ***Huroniella*** Foerste, 1924a

Type species.—*Huronia inflecta* Parks, 1915.

Huroniella iranica sp. nov.

Figures 4-1—4, 6

Diagnosis.—*Huroniella* with asymmetrical connecting rings; siphuncular segments short; adoral bending of septa lacking; width of septal foramen/distance of neighboring septal necks 2.3-3.0; perispatia wide, attain distal end of brim.

Description.—Large straight siphuncle, 20.5 mm in lateral diameter of apical end of holotype; septal necks short, approximately 0.5 mm in length, strongly recurved cyrtochoanitic; brims 0.63-0.68 mm in length, in contact with apical surface of septa; diameter of septal foramen 12.5-14.0 mm; shape of connecting rings asymmetrical in dorsoventral section, ventral connecting rings strongly inflated, bluntly pointed arcs with obliquely adoral direction in longitudinal section; adnation area in adoral surface of septa very wide, forming contact layer by thickening of connecting ring; in contrast to adoral surface of septa, relatively narrow in apical surface, contact layer also recognized where septa are weakly depressed; dorsal connecting rings semicircular with narrow adnation area lacking evident contact layer; siphuncular segments short for huroniids, width of septal foramen/distance of neighboring septal necks 2.3-3.0. Endosiphuncular deposits of annuli well developed leaving large central canal in a position slightly shifted from axis; radial canals curving adapically and branching, to join wide perispatia, which attain distal end of brim.

Discussion.—*Huroniella iranica* sp. nov. appears to be most like *H. persiphonata* (Billings, 1857; Foerste, 1927, pl. 44, fig. 1; Teichert, 1933, figs. 4, 20) from the upper Llandovery Jupiter Formation of Anticosti Island, Canada. The Laurentian species shares the asymmetrical profile of its connecting rings with the present new species. The most obvious difference between these species is the septal morphology, i.e., a strong adoral bending of the septum is recognized in *Huroniella persiphonata*, but only a weak depression on the adoral septal surface is representative of *H. iranica.* In addition, the width of septal foramen/distance of neighboring septal necks ratio (approximately 2 in *H. persiphonata* versus 2.3-3.0 in *H. iranica*) is also a diagnostic feature.

Huroniella inflecta (Parks, 1915, pl. 6, fig. 4; Foerste, 1924a, pl. 16, figs. 2a, b; Teichert, 1933, fig. 12), known from the "Limestone Rapids" in Ontario, is distinguished from the present species by having more strongly inflated dorsal connecting rings with a nearly symmetrical profile in dorsoventral section.

Material and occurrence.—Holotype, UMUT PM 27326, an isolated and incomplete siphuncle 65 mm in length, from locality 1.

Etymology.—The specific name in derived from Iran.

Subclass Nautiloidea Agassiz, 1847
Order Orthocerida Kuhn, 1940
Superfamily Pseudorthoceratacеae Flower and Caster, 1935
? Family Proteoceratidae Flower, 1962

Genus and species indeterminate

Figures 5-4, 7

Discussion.—The poorly preserved specimen consists of a gradually expanding orthoconic shell with relatively short camerae, subcentral siphuncle consisting of short cyrtochoanitic septal necks and inflated connecting rings. Its maximum diameter/length ratio of siphuncular segments is approximately 1.5, and cameral deposits are episeptal.

This species probably belongs to the Proteoceratidae, and its large siphuncular segment ratio for an orthocerid suggests a possible relationship with *Ephippiorthoceras*, although the material is insufficiently preserved to identify any further.

Material and occurrence.—Single incomplete phragmocone, UMUT PM 27333, 74 mm in length, from locality 2.

Stratigraphic and paleobiogeographic implications

The cephalopod species recognized at each locality are as follows: locality 1, *Huroniella iranica* sp. nov.; locality 2, Proteoceratidae?, gen. and sp. indet.; and locality 3, Actinoceratidae, gen. and sp. indet., *Armenoceras banestanense* sp. nov., *A.* sp., and *Elrodoceras* sp. The most useful taxon for correlation is *Huroniella*, whose range is known with certainty from late Llandovery to early Wenlock strata in Laurentia and Baltica. Species similar to *Huroniella iranica* are found in the Anticosti Island and Hudson Bay areas and are of late Llandovery age. *Elrodoceras* is the only Silurian cephalopod previously known from Laurentia, Avalonia, Baltica and Siberia. *Armenoceras banestanense* sp. nov. is related to the late Llandovery species *A. hearsti* from the Hudson Bay area, and the genus is cosmopolitan

Figure 5. **1-3.** *Elrodoceras* sp., UMUT PM 27331, 1, dorsoventral thin section, venter on right, ×2, 2, dorsoventral thin section, showing details of ventral wall of siphuncle, ×5, 3, dorsoventral thin section, showing details of septal necks, radial canal and connecting ring in ventral wall of siphuncle, note adapical bending of septal necks, ×14. **4, 7.** Proteoceratidae?, gen. and sp. indet., UMUT PM 27333, 4, longitudinal thin section, ×2, 7, longitudinal thin section, showing details of siphuncle, ×8. **5, 6.** Actinoceratidae, gen. and sp. indet., UMUT PM 27332, 5, dorsoventral thin section, showing details of ventral wall of siphuncle, arrows indicate septal necks, ×14, 6, dorsoventral thin section, showing details of dorsal wall of siphuncle, ×14.


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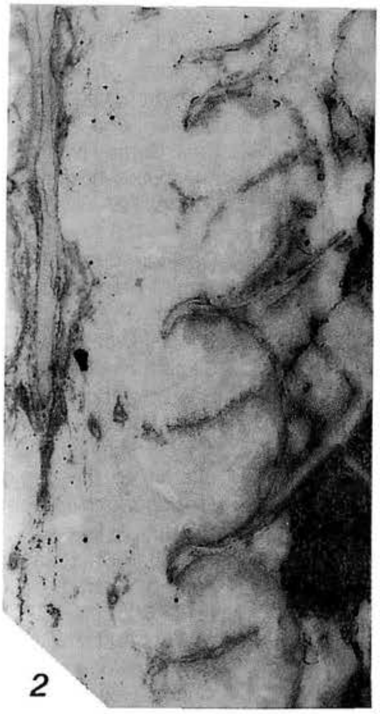
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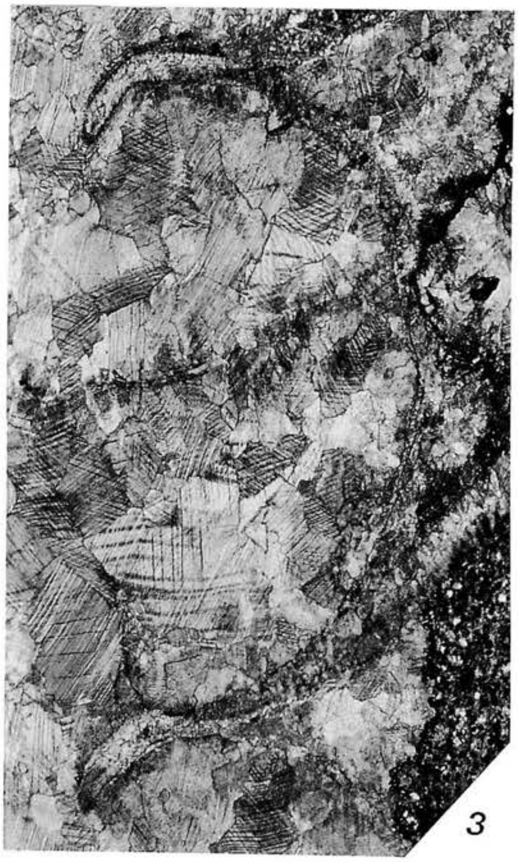
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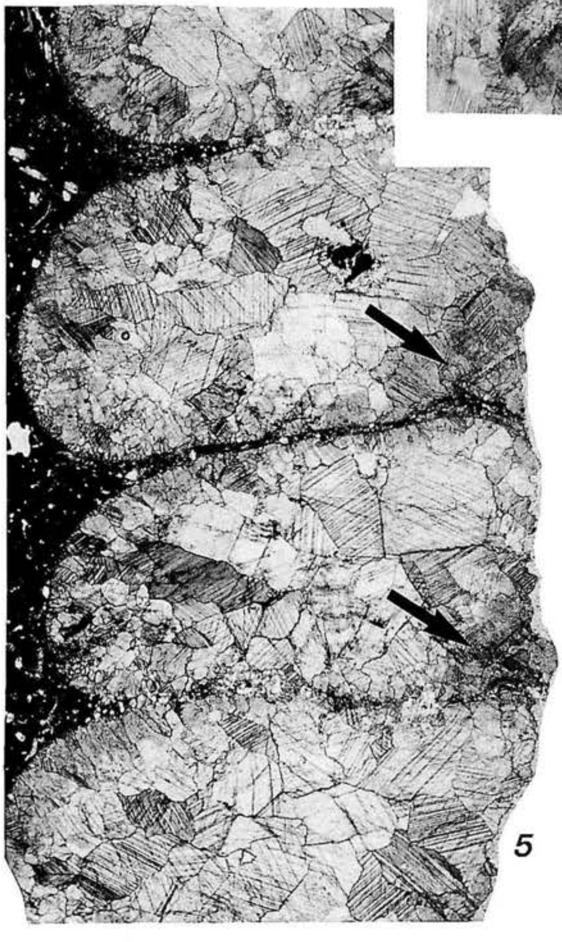
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and ranges from Middle Ordovician to Late Silurian in age. Besides cephalopods, the Wenlockian bryozoan species *Trematopora beikhemensis* is identified by S. Sakagami (personal communication) from locality 1. Although locality 2 lacks a clear age indicator, lithologically the three horizons may belong to a stratigraphic unit without notable breaks. On the basis of this evidence, we infer that at least the cephalopod-bearing horizons in the unnamed formation indicate a late Llandovery (or early Wenlock) age, and are lithologically and chronostratigraphically correlative with the Niur Formation (Ruttner *et al.*, 1968) in the Shirgesht area of northern East-Central Iran. On the other hand, the affinity of the cephalopod fauna is apparently with northeastern Laurentia. This new material suggests a faunal connection between Gondwana and Laurentia during Early Silurian times.

Acknowledgments

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Occurrence of Carboniferous corals from the Geumcheon Formation of Danyang area, Korea

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Abstract. Two species of Carboniferous coral, *Arachnastraea manchurica* and *Diphyphyllum delicatum*, are described for the first time from the upper part of the Geumcheon Formation of the Danyang area, Korea. They were previously reported as Devonian corals, *Disphyllum* sp. and *Phillipsastraea* sp. Associated fossils are fusulinids, including *Beedeina schellwieni, B. siviniensis, B. samarica, B.* sp., *Fusulina cylindrica, F.* sp., *Fusulinella mosquensis, Fusulinella provecta, Neostaffella sphaeroidea*, and *Ozawainella turgida*. Occurrence of these corals and fusulinids suggests that the upper part of the Geumcheon Formation is middle Moscovian in age.

Key words: Carboniferous, coral, Danyang area, Korea

Introduction

Yabe and Suzuki (1955) first reported specimens of corals from a limestone bed in Danyang area, Korea. They assigned them in open nomenclature to colonial corals of Devonian type as *Disphyllum* sp. and *Phillipsastraea* sp. and suggested that Devonian deposits existed in Danyang area. Unfortunately, their specimens were lost. Furthermore, they figured only one weathered surface and one polished-slab figure of *Disphyllum* sp. and offered no systematic descriptions.

On the basis of a second discovery of coral specimens of *Phacellophyllum* sp.? (*Disphyllum* sp.) associated with fusulinids including *Fusulina* sp., *Fusulinella* sp., and *Neostaffella* sp. from nearly the same horizon as that of Yabe and Suzuki (1955), Cheong (1972) saw a problem in the Danyang area, with a Devonian dating. He mentioned that the limestone containing the coral is not Devonian but Moscovian (Late Carboniferous) in age and surmised that this coral, which had been known as a Devonian type, probably survived into the Carboniferous.

Several months after Cheong's report, Kato (1972) reexamined the figures of Yabe and Suzuki (1955) and briefly documented that *Disphyllum* sp. and *Phillipsastraea* sp. reported from the Danyang area by Yabe and Suzuki (1955) are *Diphyphyllum* sp. and *Arachnastraea* sp. respectively.

Recently well preserved coral specimens, which are closely associated with abundant fusulinids, were discovered from a limestone bed of the Geumcheon Formation by the present authors. The purpose of this paper is to report an additional occurrence of Carboniferous coral specimens, which are described here as *Diphyphyllum delicatum* and *Arachnastraea manchurica*, and to compare these with the Devonian corals *Disphyllum* sp. and *Phillipsastraea* sp. illustrated by Yabe and Suzuki (1955).

Geologic setting and fossil locality

General geological studies in the Danyang area have previously been carried out by many investigators (Kobatake, 1942; Brill, 1957; Lee and Kim, 1966; Son *et al.*, 1967; Park and Cheong, 1975; Park *et al.*, 1975; Kim, 1981). Kim (1971) studied the Paleozoic and Mesozoic paleocurrents of the Danyang Coalfield on the basis of sedimentary structures. Structural analysis and tectonic studies of the Danyang area have been recently carried out by Cho *et al.* (1986), Kim and Koh (1992), Kim *et al.* (1992a), Kim *et al.* (1992b), and Kim *et al.* (1994).

The Permo-Carboniferous sedimentary strata, the Pyeongan Supergroup, in southern Korea are widely distributed in the Danyang, Taebaeg, Yeongweol, Jeongseon, and Gangneung areas. The sediments are shallow marine to fluvial in origin and consist predominantly of sandstone and shale with small amounts of carbonate.

Cheong (1973) subdivided the Pyeongan Supergroup into the Carboniferous Manhang and Geumcheon formations, the Permian Bamchi, Jangseong, Hambaegsan, Dosagok and Kohan formations, and Triassic Donggo Formation in ascending order.

In Danyang area, the Carboniferous strata disconformably cover the Ordovician strata and are divided into two formations, namely, the Manhang and Geumcheon formations (Cheong, 1971) and are inturn unconformably overlain by the Jurassic deposits (Figure 1). Cheong (1971) firstly carried out biostratigraphic research on fusulinids in the Danyang area and described 37 fusulinid species belonging to 11 genera.

The Carboniferous Manhang Formation unconformably overlies the Ordovician strata. The formation, about 175 m thick, is characterized by red to purple shale and greenish coarse sandstone, with the intercalation of nine white and

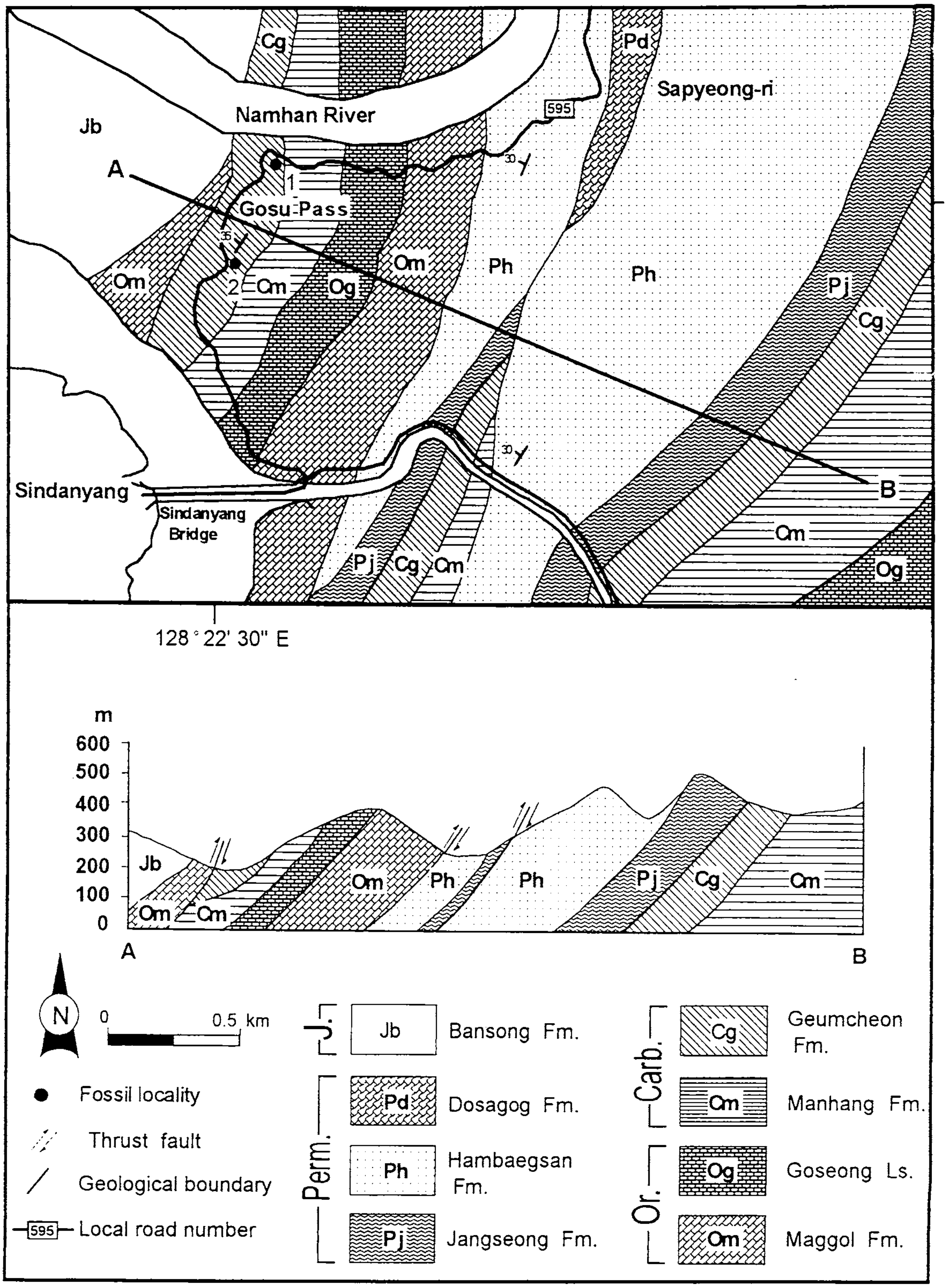


Figure 1. Geological map and fossil localities of study area. (After Son *et al.*, 1967 ; Lee and Kim, 1995)

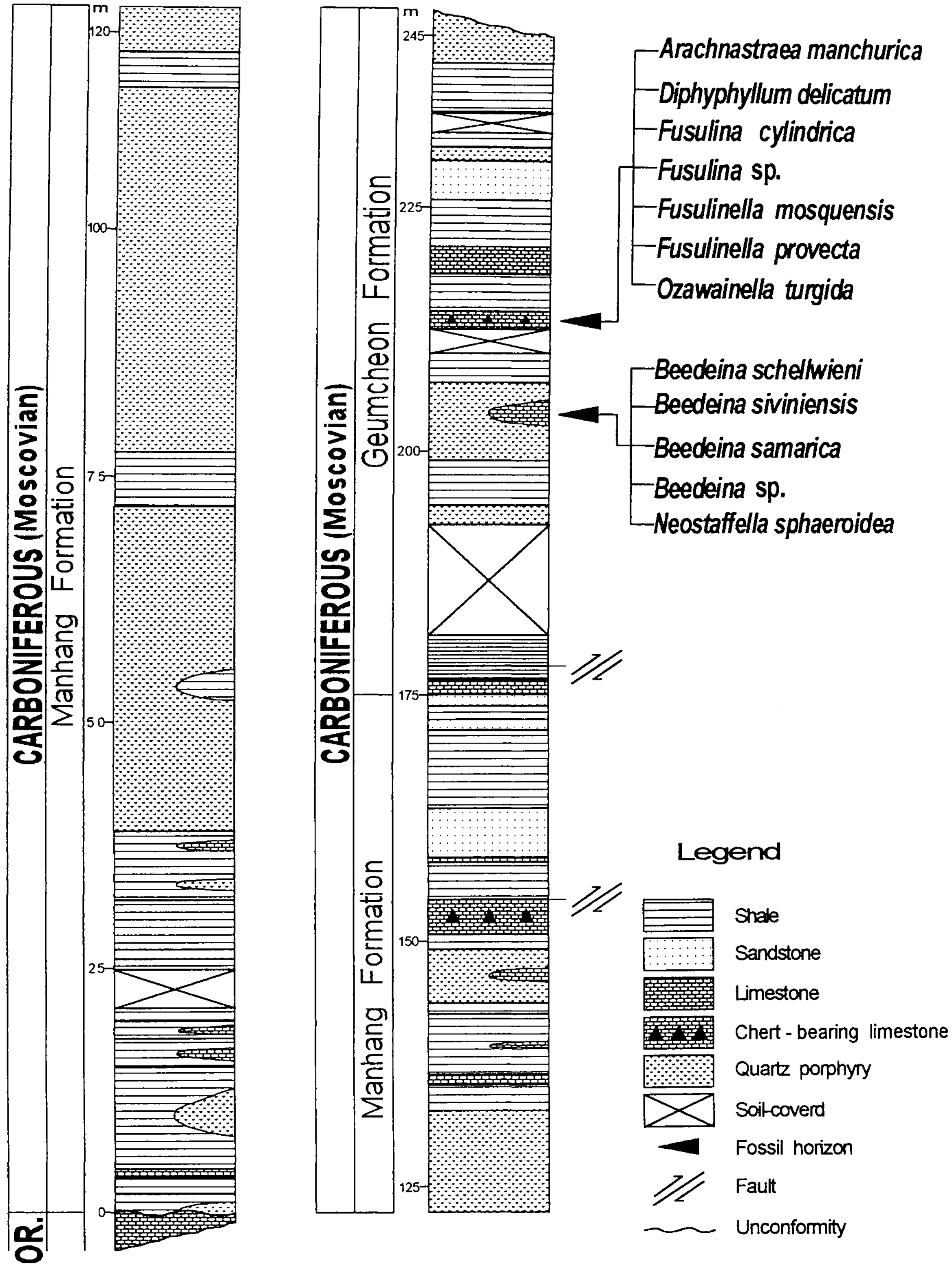
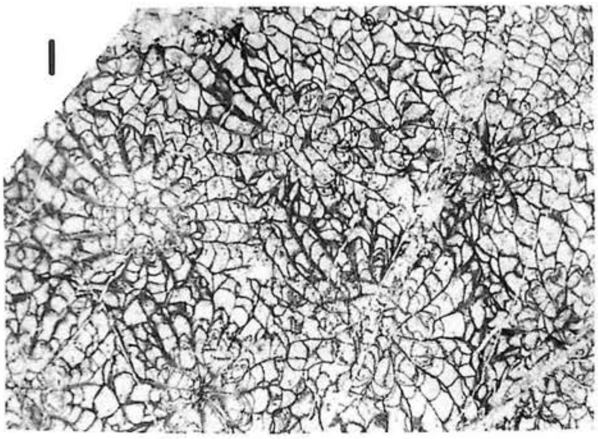


Figure 2. Measured stratigraphic section of study area.

light gray limestone beds or lenses in the measured section (Figure 2). In the upper part, the formation contains gray to bluish-gray limestone which bears white chert.

The Geumcheon Formation from which the coral specimens were collected is about 70 m thick and comformably covers the Manhang Formation. The formation comprises a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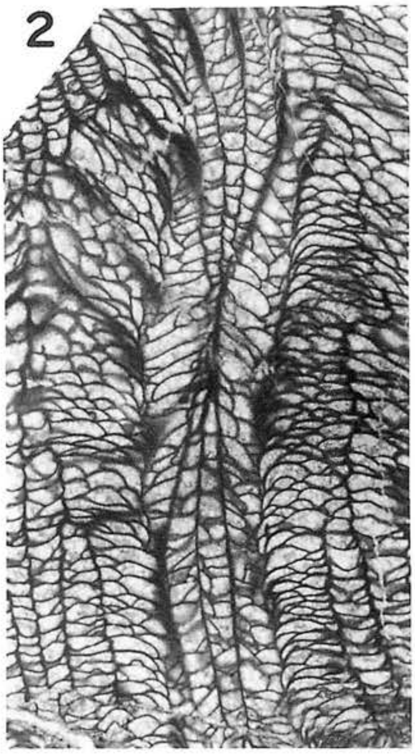
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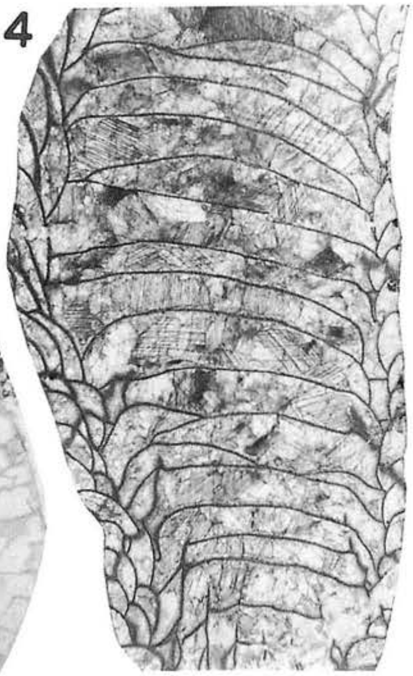
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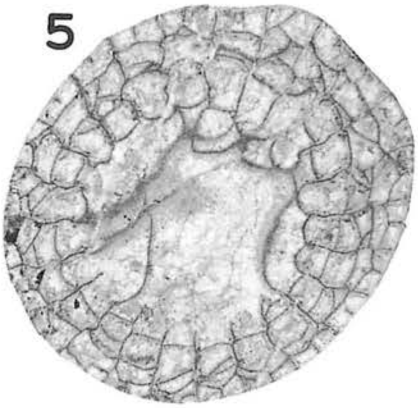
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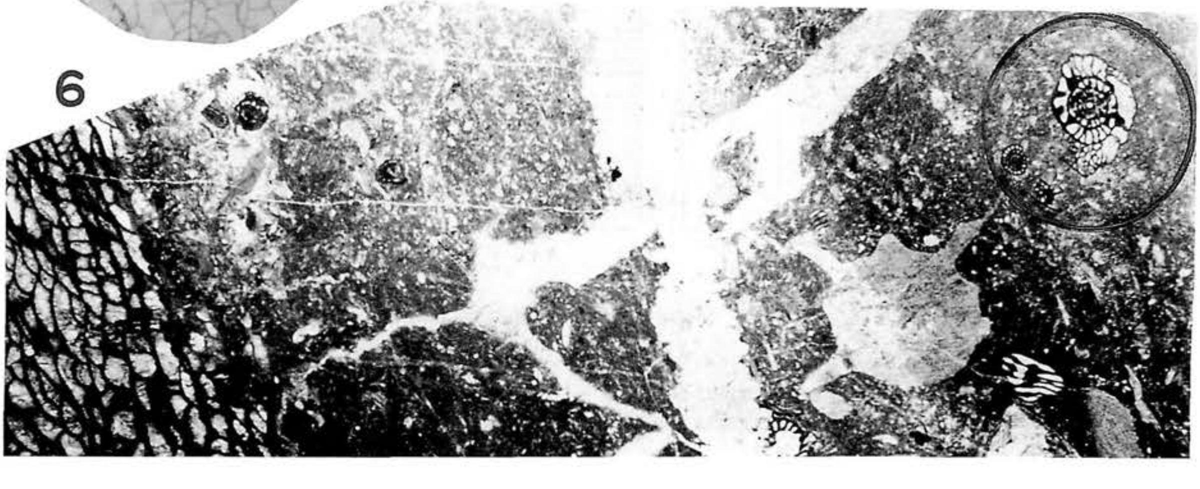
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variety of terrigenous sediments intercalated with dark gray limestone lenses (Figure 2). The upper part of the formation is characterized by black shale and greenish sandstone. Abundant and diverse corals and fusulinids were only recorded from the limestone units in the formation. Lee and Kim (1995) also described *Beedeina schellwieni, Fusulina* sp., *Neostaffella sphaeroidea*, and *Ozawainella turgida* from the Geumcheon Formation near Gosu Pass in the Danyang area.

All of the specimens considered here were collected from a measured section of the Geumcheon Formation exposed in Gosu Pass along the local road 595, Danyang area (Figure 1). The fossil locality 1 is exposed near the top of Gosu Pass, about 1.2 km north of the Sindanyang Bridge. The limestone bed of locality 1, which is 2 m in thickness, is composed of abundant fusulinids and coral fragments which can not be used in the description. Many kinds of bioclasts, foraminifera, conodonts, brachiopods, and crinoids, were also found from the limestone bed.

The fossil locality 2 is about 800 m northwest from the Sindanyang Bridge. Fossil specimens were collected from a 5 m thick chert-bearing limestone bed which is stratigraphically nearly 40 m above the base of the Geumcheon Formation. The limestone is characterized by gray to dark gray color (Figure 2). Abundant corals together with fusulinids, brachiopods, bryozoa, and crinoid stems are cleary shown on the weathered surface of limestone bed.

Systematic description

The conventional treatment has been followed in the taxonomic hierarchy above the species level. The morphologic terminology used for systematic description followed is that of Hill (1935, 1956, 1981), the terminology of microstructural elements is that of Kato (1963, 1968). Specimens collected for the present study and described herein are housed in the Department of Earth Science Education, Korea National University of Education.

Phylum Cnidaria Hatschek, 1888
Class Anthozoa Ehrenberg, 1834
Order Rugosa Milne-Edwards and Haime, 1850
Suborder Streptelasmatina Wedekind, 1927
Family Lithostrotionidae d'Orbigny, 1851
Genus ***Arachnastraea*** Yabe and Hayasaka, 1916

Arachnastraea Yabe and Hayasaka, 1916, p. 69.

Type species.—Arachnastraea manchurica Yabe and Hayasaka, 1916, from the Lower Permian of South Manchuria.

Diagnosis.—Corallum compound, massive, typically cerioid or astraeoid. Septa numerous, of two orders. Septa thin, usually extending across tabularium to columella but partly discontinuous in dissepimentarium. Both major and minor septa are well developed. Tabulae conical, complete or incomplete, regular dissepimentarium (slightly modified after Hill, 1956).

Remarks.—In the typical species of the Devonian *Phillipsastraea* d'Orbigny, the septa never extend to the center of the corallites with horse-shoe dissepiments. The septa are dilated, especially at inner margin of dissepimentarium, and there is always a conspicuous inner wall formed by the abrupt thickening of all the septa. These characteristic features are not visible in *Arachnastraea* (Yabe and Hayasaka, 1916). Kato (1972) concluded that Yabe and Sugiyama (1940) misdescribed *Arachnastraea* as *Phillipsastraea* in an occurrence from Cheonseongri, Suncheongun, Pyeongannamdo, Northwest Korea.

Arachnastraea manchurica Yabe and Hayasaka, 1916

Figures 3-1 ; 3-2

Arachnastraea manchurica Yabe and Hayasaka, 1916, p. 69.

Material.—KNUE 96201-96216 (KNUEDY Locality 2). Four specimens for this study were collected by the present authors from the measured stratigraphic section (see Figure 2).

Description.—Transverse section description : Corallum is astraeoid and composed of nearly equal-sized polygonal corallites which are 4.1-6.6 mm in diameter and have 9-11 major septa. Septa are thin, straight, alternately long and short, and fibronormal in terms of microstructure. Major septa reach the center of the corallite. Corallite walls are almost indistinguishable from septa and dissepiments. In most corallites, the major septa are 2.0-3.5 mm long and minor septa are 0.8-2.4 mm long. Minor septa typically extend about 2/3 length of major septa to tabularium wall. Dissepimentarium is formed by 3-5 rows and is 0.3-2.7 mm. Tabularium has a diameter of on average 2.3 mm.

Longitudinal section description : Dissepiments are well developed in the peripheral part, elongate in form and not much inclined. Dissepimentarium rather wide, occupying about 2/3 of the diameter of the corallites and consisting of 3-5 rows of dissepiments which are an average of 2 mm long. Axial tabellae and periaxial tabellae are similarly inclined. Diameter of the tabularium varies around the average of 2.2 mm, from 1.8 to 3.0 mm. In the tabularium, the tabulae adjacent to the dissepimentarium have a slope of 25°-40°.

Remarks.—One of the so-called 'Devonian type corals' from Cheonseongri described by Yabe and Sugiyama (1940) was reidentified by Kato (1972) as *Arachnastraea kaipingensis* (Grabau). It was the first record of occurrence of *Arachnastraea* in Korea. *Arachnastraea manchurica* differs from *Arachnastraea kaipingensis* in corallite walls, columella and

Figure 3. 1, 2. *Arachnastraea manchurica* Yabe and Hayasaka ; 1, transverse section (×7, KNUE 96201), 2, Longitudinal section (×7.5, KNUE 96215). **3-5.** *Diphyphyllum delicatum* Minato and Kato ; 3, transverse section showing both the early and mature stages (×8, KNUE 96219), 4, slightly obliquely cut logitudinal section (×7, KNUE 96229), 5, slightly obliquely cut transverse section (×7, KNUE 96217). **6.** association of *Arachnastraea manchurica* and *Fusulinella* sp. (×10, KNUE 96199).

dissepimentarium. In the latter the corallum is cerioid-astraeoid and corallite walls are well developed, sharply zigzag and partially depressed. The dissepimentarium of the latter consists of 3-4 rows of regular dissepiments.

Family Lithostrotionidae d'Orbigny, 1851
Subfamily Diphyphyllininae Dybowski, 1873
Genus ***Diphyphyllum*** Lonsdale, 1845

Diphyphyllum Lonsdale, Hill, 1956, p. 283; Hill, 1981, p. 383.

Type species.—Diphyphyllum concinnum Lonsdale, 1845.

Diagnosis.—Fasiculate corallum, typically without columella. Septa short, continuous in dissepimentarium and amplexoid in tabularium. Columella absent or impersistent. Tabulae convex or flat, with downturned edges. Dissepimentarium narrow, composed of one or more rows of small dissepiments (slightly modified after Hill, 1956).

Remarks.—The species of *Diphyphyllum* may have a wide range of variability in terms of the structure, shape and mode of the tabulae. This genus has inner tabulae which are strongly arched, and each arch rests upon the arch below. In addition, Sando and Bamber (1985) mentioned that this genus is very similar to *Siphonodendron,* from which it differs by having flat or convex tabulae and by lacking a columella or having a thin, vertically discontinuous one.

Armstrong (1970) regarded a smaller group of species, such as *Diphyphyllum venosum*, *Diphyphyllum nasorakensis* and *Diphyphyllum klawockensis*, as having complete tabulae with broad flat tops and downturned edges that extend to the dissepimentarium without touching the lower tabulae.

The majority of the descibed species of *Diphyphyllum* indicated a late Early Carboniferous age (Minato and Kato, 1975). This genus is common in North America and is found exclusively in the shallow-water carbonate lithofacies (Sando and Bamber, 1985).

Diphyphyllum delicatum Minato and Kato, 1957

Figures 3-3—3-5

Diphyphyllum delicatum Minato and Kato, 1957, p. 137, text-figs. A-C; Minato and Kato, 1974, p. 56-60.

Material.—KNUE 96217-96245 (KNUEDY Locality 2). Only two specimens for this study were collected by the present authors from the measured stratigraphic section (see Figure 2).

Description.—Transverse section description: Corallum is compound, fasciculate and dendritic rather than phaceloid. Corallites are circular to subcircular. Corallites are closely adjacent, and are often in contact. Mature corallites range from about 6.7 to 11.4 mm in diameter and possess 18 to 25 major septa. Both major and minor septa are thin, fibronormal in terms of microstructure. Major septa are 1.5-2.2 mm in length, protruding 0.2-0.9 mm in tabularium, except for some major septa which are 0.9-1.1 mm in length. Minor septa are usually confined to adaxial first row of dissepiments, rarely protruding into second row of dissepiments, and are 0.25 to 0.38 mm in length. Dissepimentarium ranges from 1.1 to 2.2 mm in width and consists of one to three rows of regular dissepiments. Tabularium varies from 4.1 to 6.4 mm in width and is open without any axial structure.

Longitudinal section description: Corallites are cylindrical and rather closely disposed. Dissepimentarium is 0.5 to 1.9 mm wide and consists of one to three rows of *inclined*, inflated to globose dissepiments. Tabulae are mostly complete, slightly concave in central part of the corallite, 4 to 9 in a vertical distance of 5 mm. However, they turn downward at an average angle of 32° before joining the dissepiments.

Remarks.—Our specimens differ slightly from Minato and Kato's (1975, pl. 9, figs. 2-6, pl. 10, figs. 1-4) species *Diphyphyllum delicatum*, which was described from the Upper Carboniferous Nagaiwa Series of northeast Japan, by having more numerous major septa, a wider dissepimentarium, and a more strongly developed row of dissepiments. Igo and Kobayashi (1980) described a new subspecies, *Diphyphyllum delicatum nishitamensis*, from the Itsukaichi District, Tokyo, Japan, which is similar to, but not conspecific with *Diphyphyllum delicatum* illustrated by Minato and Kato (1975). Igo and Kobayashi (1980) noted that *Diphyphyllum delicatum* and *Diphyphyllum delicatum nishitamensis* differ noticeably in the length of major and minor septa. The former is characterized by short major and minor septa, while the subspecies has longer septa compared with the size of the corallite.

As Minato and Kato (1957) mentioned, *Diphyphyllum* has a long stratigraphic range from the Lower Carboniferous to Permian, but this particular species is confined to the upper part of the Upper Carboniferous Geumcheon Formation in the Danyang area.

Discussion

One of the purposes of this study is to reexamine the Devonian corals mentioned by Yabe and Suzuki (1955). According to Kato (1972), Suzuki earlier collected several coral specimens in Gosuri, Danyang in 1944, but these materials are lost. Yabe and Suzuki (1955) reported the occurrence of the Devonian corals *Disphyllum* sp. and *Phillipsastraea* sp. Their figures 1 and 2 are index maps of the fossil locality, while figures 3 and 4 show the corals on the weathered surface of the limestone near Gosu Pass in Danyang area. The figures are not clear, but colony type and internal structure of corals were, however, distinguished.

On the basis of their figure 3, several clues to identification of the corals were found by the present authors. First of all, the corallites in figure 3 are compound, fasciculate and dendritic rather than phaceloid. Although Yabe and Suzuki (1955) identified them as *Disphyllum* sp., the branches of their coral specimens are too irregular to be those of *Disphyllum*. The second is that the septa are very short and the dissepimentarium are very narrow with one or two rows of small dissepiments. In longitudinal view, the tabulae are convex with downturned edges without columella. These are typical characters of *Diphyphyllum.* It is considered that the coral specimens described by Yabe and Suzuki (1955) are not of the Devonian genus *Disphyllum*, but the Carboniferous *Diphyphyllum*. *Disphyllum* sp. is illustrated only in figure 3 of

Yabe and Suzuki (1955), but they did not provide any illustrations of *Phillipsastraea* sp.

Furthermore, fusulinids and conodonts occur abundantly from the Geumcheon Formation. A number of fusulinids are observed together with corals in the same thin sections (Figure 3-6). Because the Carboniferous corals have long ranges, both fusulinids and conodonts may provide a useful criteria for understanding the paleoecology and determining the geologic age of the Geumcheon Formation.

Conclusion

Two species of rugose corals from the Geumcheon Formation in the Danyang area, Korea are described as *Arachnastraea manchurica* and *Diphyphyllum delicatum*. The corals indicate that the age of the Geumcheon Formation is middle Moscovian, Late Carboniferous.

Coral specimens from the Danyang area once illustrated as the Devonian corals *Disphyllum* sp. and *Phillipsastraea* sp. (Yabe and Suzuki, 1955), are considered Carboniferous corals, *Diphyphyllum* sp. and *Arachnastraea* sp. respectively.

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Relation of growth rings to reproductive cycle in *Cryptopecten vesiculosus*, a dimorphic pectinid bivalve

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Abstract. The relation between growth rings and reproductive cycle in a dimorphic pectinid bivalve, *Cryptopecten vesiculosus* (Dunker, 1877) was examined histologically on the basis of semi-regularly collected samples from Sagami Bay. This pectinid is hermaphroditic. Male and female gonads ripen between June and September, and spawning occurs during July to November. A strong growth ring is formed just before spawning, and the first ring indicates that the specimens has reached the stage of sexual maturity. This means that growth rings are formed once a year after the individual reaches sexual maturity. No visual difference was detected in the gonad development between the two phenotypes ; their gonadal weight indices are statistically identical throughout the year. Therefore the previous interpretation that the dimorphism represents discontinous intrapopulational variation is upheld. The results of this study are applicable to life history analysis in extant and fossil populations.

Key words : Dimorphism, growth rings, life history, pectinid bivalve, reproductive cycle

Introduction

The pectinid bivalve, *Cryptopecten vesiculosus* (Dunker, 1877) is characterized by a few prominent commarginal growth rings, which consist of periodic changes in the convexity of the disc surface. It has been judged that the growth rings are caused by a growth pause during the reproductive season. Furthermore, *C. vesiculosus* has been considered a dimorphic species, because two discrete phenotypes exist in every population. One phenotype has highly elevated and generally quadrate radial ribs, while the other has low and generally rounded radial ribs. They have been called "Phenotype Q" and "Phenotype R", respectively. These two phenotypes are strictly sympatric, and their allozyme patterns show no statistical difference. Consequently it has been believed that the dimorphism is due to discontinous intrapopulational variation (Hayami, 1984 ; Sarashina, 1995).

Histological observations on the development of gonads through the year is vital to prove the assumptions mentioned above, as well as to trace a clear relation between growth rings and the reproductive cycle. The relation, if clarified, would become fundamental to analyses of life history (especially, age, lifespan, growth rate and mortality rate) not only in extant but also in fossil populations.

Material and method

Cryptopecten vesiculosus (Dunker, 1877) is distributed from the central part of Japan to the East and South China Sea. It is a lower sublittoral species, living commonly on sandy bottoms at the depth of 50-200 m (Hayami, 1984). Fossils of this species are also found abundantly in Early Pliocene and later marine deposits of Japan. Living individuals of *C. vesiculosus* were collected monthly to bimonthly between March 1997 and February 1998 almost at one and the same station, about 2 km west of the western end of Jôgashima Islet in the eastern part of Sagami Bay [35°08′N, 139°35′E, 80-85 m]. Table 1 shows the dates of dredging and the number of collected living individuals. The integrated relative frequency of the two phenotypes is almost identical with the ratio indicated by Hayami (1984) in samples Jg (1-26) collected during 1974-1983 at nearby stations in Sagami Bay, and statistically there is no significant difference.

To clarify the reproductive cycle and the shell size at sexual maturity, I observed the process of gametogenesis and determined the gonad developmental phase for many individuals in each phenotype. Collected specimens were anesthetized with 0.01% 2-phenoxyethanol methylene glycol diluted with sea water, and then fixed for 48 hours in a solution of 10% formaldehyde. The dissected gonadal tissue of each specimen was excised and weighed after rinsing in water. It was dehydrated through a graded series of ethanol and benzol, and then embedded in paraffin (melting

Table 1. Collecting dates and the number of individuals of *Cryptopecten vesiculosus*.

Date	N_Q	N_R	N	P	σ_P
Mar. 25, 1997	9	14	23	0.61	0.10
May 1, 1997	42	30	72	0.42	0.06
Jun 4, 1997	26	25	51	0.49	0.07
Jul. 29, 1997	54	30	84	0.36	0.05
Sep. 30, 1997	79	67	146	0.46	0.04
Nov. 19, 1997	35	28	63	0.44	0.06
Dec. 18, 1997	44	31	75	0.41	0.06
Feb. 16, 1998	36	36	72	0.50	0.06
Total	325	261	586	0.45	0.02

N : Total number of individuals ; N_Q : Number of individuals belonging to Phenotype Q ; N_R : Number of individuals belonging to Phenotype R ; $P=N_R/N$; σ_P : Standard error.

point : 56~58°C). Thin transverse sections of the gonadal tissue were prepared at intervals of 8 μm and stained with Lillie-Mayer's hematoxylin-eosin. The stained thin sections were observed and photographed using an Olympus model BX50 optical microscope. Based on histological examination of the thin-sectioned gonadal tissue, each specimen was assigned to a specific gonad developmental phase : early active phase (EA), late active phase (LA), ripe phase (R), partially spawned phase (PS), or spent phase (S). Further, the mean gonad index [(gonad weight×100)/soft body weight] was calculated for sexually mature individuals to analyze the annual reproductive cycle of the population.

The results were analysed to determine whether or not growth rings can be used as an index of age. Shell height from the umbo to each growth ring, normal to the hinge line, was measured in all the samples with a digimatic caliper (accuracy±0.02 mm). In addition, the numbers of growth rings was counted, and the mean shell height at each growth ring was calculated for individuals with more than three growth rings. The fit of these mean values to von Bertalanffy, Gompertz and logistic curves was examined. These curves are expressed by the following formulae :

$$H(B)=K(1-\exp(a-Rt)) \qquad \text{(von Bertalanffy curve)}$$

$$H(G)=K\exp(-a\exp Rt) \qquad \text{(Gompertz curve)}$$

$$H(l)=K/(1+\exp(a-Rt)) \qquad \text{(logistic curve)}$$

where H is the size of the animal (shell height in this case) at age t, K is the upper limit of the curve, R is the specific growth rate, and a is a constant defined by the initial size ($=H_0$) at $t=0$.

Results

1. The reproductive cycle of *Cryptopecten vesiculosus*

Spermatozoa were observed in the milky white proximal part of the crescentic gonad and oocytes in the orange distal part. In consequence, it was confirmed that *Cryptopecten vesiculosus* is hermaphroditic and that the shell dimorphism is never sexual. Histological examination of gonadal tissue revealed that gametogenesis in *C. vesiculosus* is essentially similar to that in the commercial scallop *Azumapecten farreri nipponensis*, which was analyzed by Kanno and Tanita (1961), though that species is dioecious. Following the general classification of gametogenetic phases in bivalves proposed by Ropes (1968) and Sato (1995), the reproductive cycle of *C. vesiculosus* is described below.

Early active phase (Figure 1A, B)

In the male gonad of this phase, many spermatogoniums about 8 μm in diameter, each of which consists of a nucleus and thin nucleoplasm, appear along the inner periphery of the alveolar walls. Further, spermatocytes about 5 μm in diameter proliferate towards the lumina from the alveolar walls. Oogoniums and oocytes which protrude inside the alveolar walls are seen in the female gonad. The oogoniums range from 15 to 20 μm and the oocytes range from 20 to 30 μm in diameter. Each oocyte has a nucleus about 15-20 μm, which contains a nucleolus approximately 4 μm in diameter.

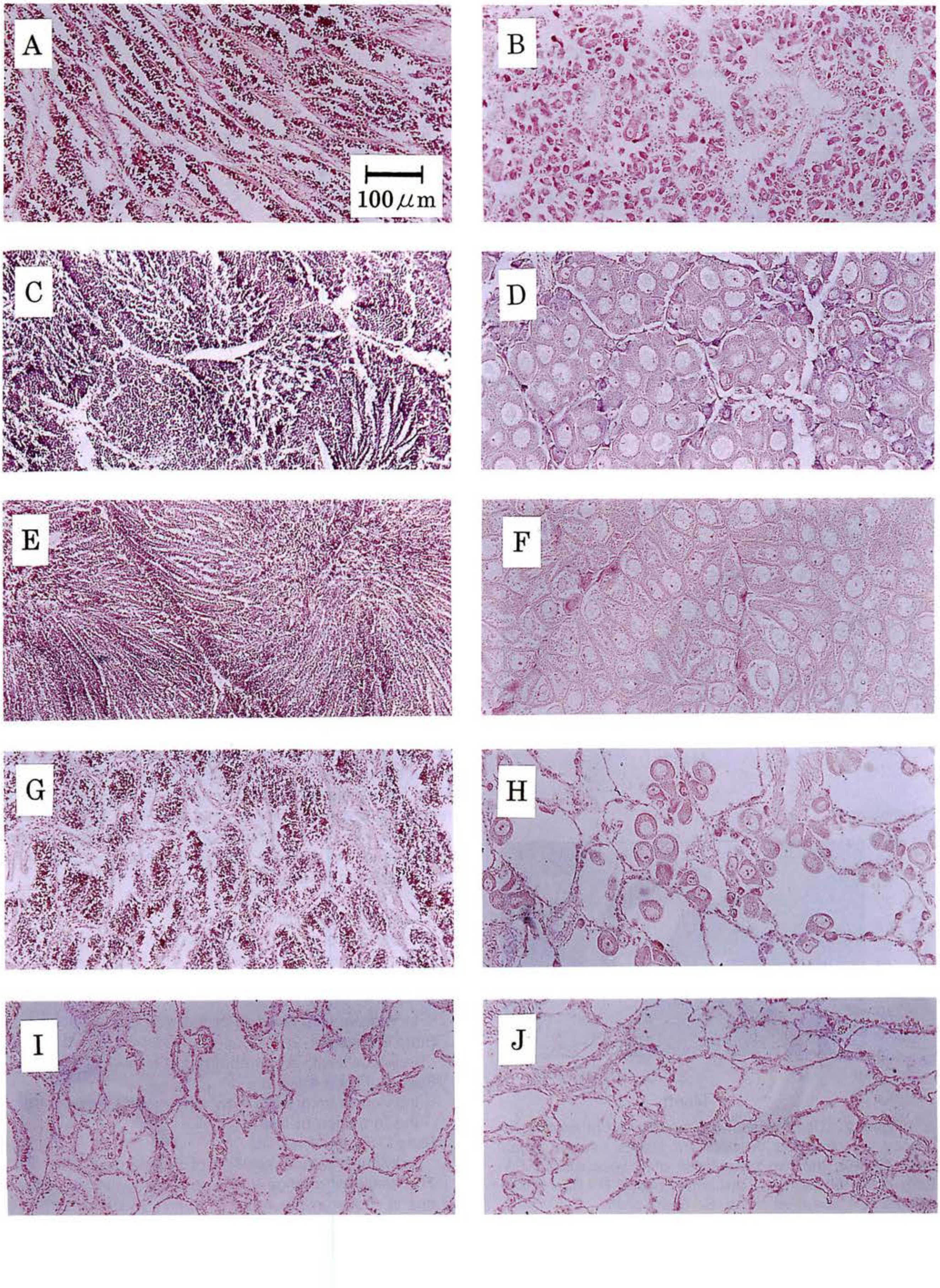
Late active phase (Figure 1C, D)

Many spermatocytes are seen in the male gonad of this phase. Spermatids about 4.5 μm in diameter also are seen, and they form dense masses near the center of the alveoli. A transformation of the spermatids results in the appearance of sperm. They form weak columns toward the center of the alveoli. Oocytes in the late active phase are mostly rounded and larger than in the early active phase. Some oocytes are attached to the basement membrane of the alveoli, but most are free in the lumina. In this phase oogoniums and ripe oocytes coexist within one and the same female gonad.

Ripe phase (Figure 1E, F)

In this phase, spermatozoa or free oocytes occupy the major space in the gonadal tissue. The head of each sperm is corn-shaped and about 2 μm in length. Oocytes are free in the lumina of the alveoli. Each oocyte about 60 μm in diameter contains a round or oval nucleus ranging from 30 to 35 μm, and each nucleus possesses one small opaque basophilic nucleolus about 5 μm in diameter. Ripe gonads typically have a dense appearance because the alveoli are crowded together and are filled with large oocytes or numer-

Figure 1. Optical photomicrographs of sections of male and female gonadal tissues in *Cryptopecten vesiculosus* in each phase of the reproductive cycle. The scale bar in A pertains as well to B-J. All specimens were collected from Sagami Bay. **A** : Early active phase of a male collected on 16 February 1998. **B** : Early active phase of a female collected on 16 February 1998. **C** : Late active phase of a male collected on 25 March 1997. **D** : Late active phase of a female collected on 25 March 1997. **E** : Ripe phase of a male collected on 29 July 1997. **F** : Ripe phase of a female collected on 29 July 1997. **G** : Partially spawned phase of a male collected on 19 November 1997. **H** : Partially spawned phase of a female collected on 19 November 1997. **I** : Spent phase of a male collected on 18 December 1997. **J** : Spent phase of a female collected on 18 December 1997.


A
100 μm
B
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J

ous spermatozoa.

Partially spawned phase (Figure 1G, H)

In the male gonad of this phase, spermatozoa are still present near the center of alveoli, but they are substantially less numerous than in the ripe phase. A few large ripe oocytes remain free in the lumina of some alveoli of the female gonad.

Spent phase (Figure 1I, J)

In this phase the alveoli of male and female gonads contain few or no spermatozoa or oocytes. Their lumina characteristically are open.

Seasonal change in the relative frequency of the five gametogenetic phases in the samples of *Cryptopecten vesiculosus* from Sagami Bay in 1997-1998 is shown in Figure 2. Individuals belonging to the late active phase amount to than 80% of the population between March and May, while ripe-phase individuals become dominant between June and September. Some individuals begin to spawn in July, and almost all individuals reach the spent phase in December. After that, the proportion of individuals in the early active phase increases gradually. The mean gonad index increases from March to June, scarcely changes from June to September, and decreases significantly after September (Figure 3). Therefore, the reproductive season of *C. vesiculosus* is considered to be a relatively long period between early June and late September. Neither visual nor statistical difference was detected between the two phenotypes in their reproductive cycles and seasonal changes of gonad indices.

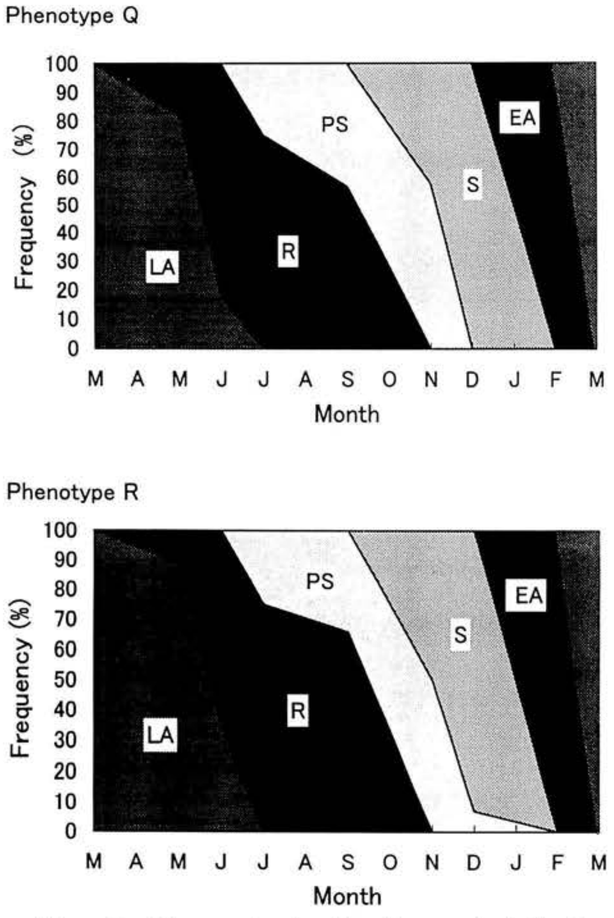

Figure 2. Diagram showing the change of relative frequency (%) of gonad development stages through a year (1997-1998) in the two phenotypes of *C. vesiculosus*. EA: Early active phase, LA: Late active phase, R: Ripe phase, PS: Partially spawned phase, S: Spent phase.

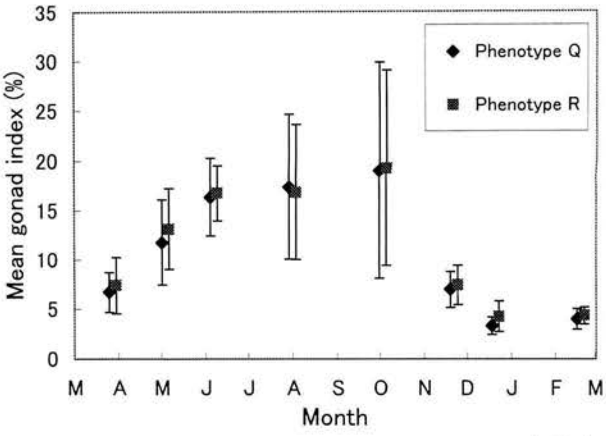

Figure 3. Seasonal changes in mean gonad index [(gonad weight × 100)/soft body weight]. The mean and the range of one standard deviation (vertical bar) are indicated. No statistical difference was detected between the two phenotypes.

2. The size at sexual maturity

Table 2 indicates the frequencies of juvenile, semimature and mature specimens and their relation to shell height in the samples collected during the reproductive season. Reproductive cells were not observed at all in individuals smaller than 10 mm in shell height, and gonadal tissue, if present, was so small that they are regarded as juvenile. Individuals larger than 14 mm in shell height can be regarded as mature. Most individuals between 10 and 14 mm possess only a few reproductive cells. They are regarded here as semimature, and spawn like mature individuals. It is, therefore, considered that individuals of *C. vesiculosus* reach sexual maturity at about 10 mm in shell height.

3. Formation of growth rings

The position of growth rings was observed, and the following four states are discriminated by the relation between the last growth ring and the ventral margin (Figure 4).

State A (Figure 4-1a, 1b)
Individuals with swelling of the marginal area
State B (Figure 4-2a, 2b)
Individuals with a growth ring just on the ventral margin
State C (Figure 4-3a, 3b)
Individuals with slight new shell growth (<5 mm) after the formation of last ring
State D (Figure 4-4a, 4b)
Individuals without swelling of the marginal area

The seasonal change in the relative frequency of these states is shown in Figure 5. In spring, many individuals in

Table 2. Distribution of the stages of sexual maturation in relation to shell height in the samples of *Cryptopecten vesiculosus* collected from Sagami Bay during the reproductive season.

Shell height (mm)	Sampling date May 1			June 4			July 29			Sept. 30			Nov. 19		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
6-8							1								
8-10	1						1						1		
10-12				1			1	9			4	1		6	1
12-14		1			2			12	3		3	4		2	3
14-16						1			8		1	7		2	9
16-18			6			3			4			14			4
18-20			9			16			5			28			4
20-22			11			9			6			25			12
22-24			2			6			3			15			7
24-26			1			1			1			4			
26-28									1						

A : Juveniles, B : Semimature individuals, C : Mature individuals

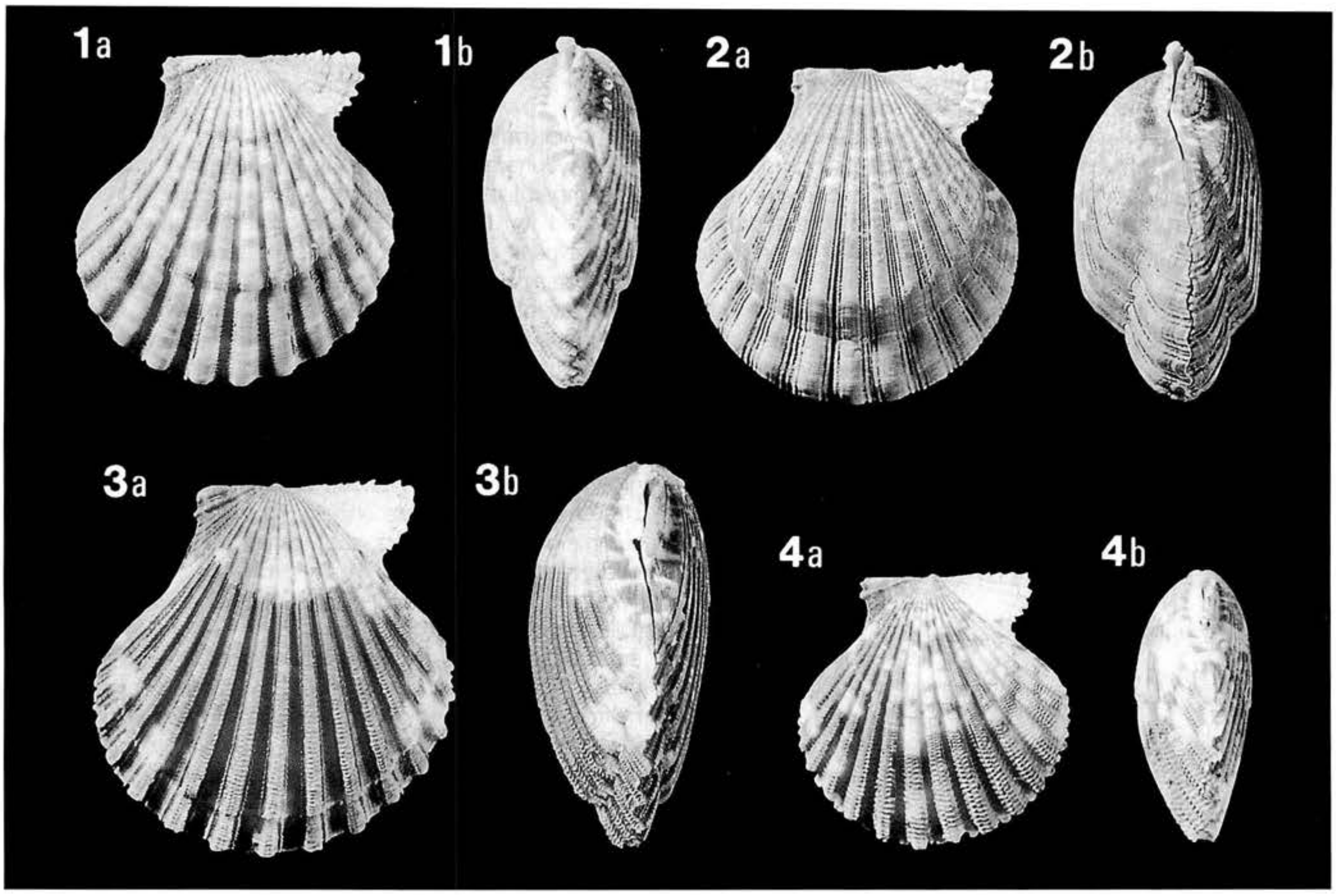

Figure 4. Extant sample of *Cryptopecten vesiculosus* collected from Sagami Bay. **1** : Individual of Phenotype Q with swelling of marginal area (State A) collected on 1 May 1997, (a) right view, (b) anterior view ; **2** : Individual of Phenotype R with a growth ring just on ventral margin (State B) collected on 30 September 1997, (a) right view, (b) anterior view ; **3** : Individual of Phenotype Q with slight new growth (<5 mm) after the formation of the last growth ring (State C) collected on 16 February 1997, (a) right view, (b) anterior view ; **4** : Individual of Phenotype Q without swelling of marginal area (State D) collected on 25 March 1997, (a) right view, (b) anterior view. All figures magnified about 1.9 times.

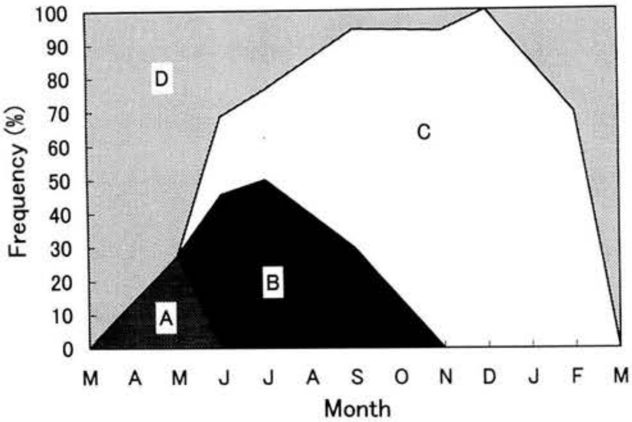

Figure 5. Diagram showing the relative frequency (%) of four states of shell growth. State A : Individuals with a swelling of the marginal area, State B : Individuals with a growth ring just on the ventral margin, State C : Individuals with slight new growth (<5 mm) after the formation of the last growth ring, State D : Individuals without swelling of the marginal area.

state A appear simultaneously with the early development of the gonads. Individuals in state B become most abundant in July. This produces a temporary cessation of shell growth. On the other hand, the proportion of individuals in state C gradually increases from June and becomes almost 100% in November. The result indicates that the growth rings are formed once a year and can be used as an index of age.

The shell height at each growth ring was measured in all individuals (Figure 6). The first growth ring is formed at a height of 9-11 mm in most individuals. Using individuals with more than three growth rings, I calculated the mean shell height at each growth ring. I then examined how the data adapt to the von Bertalanffy, Gompertz and logistic growth curves. The results of computation show that the shell growth of this species fits well to all of the three curves, especially to the Gompertz curve (Table 3).

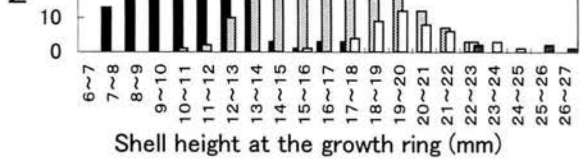

Figure 6. Frequency distribution of shell height at each growth ring in the samples of *Cryptopecten vesiculosus* collected during March 1997-February 1998.

Table 3. Mean shell height at each growth ring and its adaptability to three theoretical growth curves of the extant sample of *Cryptopecten vesiculosus* collected from Sagami Bay.

Age (years)	1	2	3	4
Mean shell height (mm)	10.20	17.45	21.91	24.33
Standard deviation	1.472	2.295	1.824	1.634
Number of individuals	337	176	47	5
Calculated values (mm)				
von Bertalanffy curve	10.20	17.50	21.80	24.35
Gompertz curve	10.20	17.43	21.98	24.30
logistic curve	10.20	17.41	22.16	24.16
Calculated formula curve				
von Bertalanffy curve				
$H(B)=28.02\,(1-\exp(-0.453-0.527t))$				$r=0.999$
Gompertz curve				
$H(G)=26.24\,\exp(-2.180\,\exp\,0.837t)$				$r=1.000$
logistic curve				
$H(l)=25.16/(1+\exp(1.574-1.192t)$				$r=0.998$

Discussion

The spawning season of *Cryptopecten vesiculosus* begins in early June and extends to late September, continuing for a comparatively long period. No visual difference was detected in the gonad development between the two phenotypes ; seasonal changes of weight indices of the gonads show very similar patterns (Figure 3). Therefore, the previous interpretation that the dimorphism is due to discontinous intrapopulational variation is upheld.

Growth rings are formed clearly on the shell surface in many bivalves and are often useful in determining the age of individuals and their growth rate. Kennish (1980) called the strong internal growth lines of bivalves growth breaks. The growth breaks reflect various enviromental or physiological stresses such as freeze shocks (in winter), heat shocks (in summer), thermal shocks, shell-margin abrasions, spawning, neap tides, and storms. There is often a direct relationship between internal growth breaks and external growth rings (Dillon and Clark, 1980). Therefore, growth rings are considered to be formed by the same factors as internal growth breaks. Among various bivalves, growth rings are produced by freeze-shock breaks (e.g., *Pecten maximus*, Mason, 1957 ; *Tivela stultorum*, Hall *et al*., 1974 ; *Modiolus modiolus*, Seed and Brown, 1978 ; *Aequipecten opercularis*, Broom and Mason, 1978 ; *Mya arenaria*, Goshima, 1982 ; *Phacosoma japonicum*, Tanabe, 1988) or heat-shock breaks (e.g., *Mercenaria campechiensis*, Jones *et al*., 1990 ; *Chamelea gallina*, Ramón and Richardson, 1992). Spawning breaks are also used to assess annual growth increment in some species (e. g., *Spisula solidisima*, Jones *et al*., 1978 ; *Arctica islandica*, Thompson *et al*., 1980).

Generally, a growth ring is formed by an interruption of the shell growth. Because various states of the ventral margin are observed within each simultaneous sample of *C. vesiculosus*, it is unlikely that growth cessation due to thermal stress or any other such instantaneous events.

The cause of ring formation may be better understood, if gametogensis and spawning are taken into consideration. Some individuals of *C. vesiculosus* begin to spawn in July, but the spawning season extends until the end of September (Figure 2). Moreover, the number of individuals with newly grown shell after the formation of the last growth ring gradually increases from June on (Figure 5). Consequently, it is obvious that a growth ring is formed just before spawning, when the gonad is still filled with sperm and free oocytes. On the other hand, the gonad index becomes much smaller in individuals with newly grown shell. Reproduction is one of the most energy-consuming physiological activities; it is therefore likely that gametogenesis exerts a great influence on shell formation.

In this connection Gutsell (1930) discussed the formation of growth rings in *Argopecten irradians*. He believed that a decline of metabolic activity, which is related to the development of eggs and sperm rather than spawning, must be responsible for the growth cessation. It is considered that the growth ring of *C. vesiculosus* is also formed by growth cessation in relation to energy consumed in gametogenesis. The surface swelling before the formation of a growth ring may be caused by the retardation of shell growth. The growth rings of *C. vesiculosus* must be produced just before spawning. The present interpretation is in agreement with the trade-off relationship between somatic and reproductive cells.

Since mature reproductive cells were observed in the individuals larger than 10 mm in shell height, sexual maturity may be attained at this size. The first growth ring is comparatively weak and is formed at 9-11 mm in shell height in most individuals (Figure 6). This is consistent with the sexual maturity size. Therefore, the growth rings of *C. vesiculosus* are considered to be formed once a year after the individual has reached sexual maturity. The growth rings are thus useful for determining the age of extant specimens and can presumably be applied to fossils as well. The shell growth pattern fits well with the von Bertalanffy, Gompertz and logistic curves. The shell height indicates a decrease in specific growth rate as the shell size approaches its upper limit of 26-28 mm. The number of growth rings indicates that the maximum lifespan of *C. vesiculosus* is four or five years.

The absolute growth pattern, however, may change geographically and chronologically within one and the same species. In fact, the growth rate and ultimate size in the samples from Sagami Bay are significantly smaller than those of some other extant and fossil samples, as shown by Hayami (1984, fig. 7). The exact age distribution and mortality rate are difficult to obtain from the present samples, because juvenile individuals smaller than 10 mm in height are not present in most samples and may have passed through the mesh of the dredging gear. It is also not clear whether the first ring is formed during the first year. However, the relation between growth rings and the reproductive cycle has been made very clearer through the present study.

Such prominent growth rings occur in some other pectinids; e.g. *Swiftopecten swiftii, Chlamys cosibensis* (a fossil species), and *Decatopecten striatus*. Although more detailed study is necessary for each species, the mode and periodicity of growth rings are very similar in these species to those of *C. vesiculosus*. It is likely that gametogenesis is related to the formation of growth rings in those species also. It is expected that applying the knowledge about growth rings will clarify the life history of fossil populations and their evolution.

On the other hand, in many other pectinids periodical growth breaks, if present, are scarcely accompanied by surface swelling. Even in *C. vesiculosus*, Pleistocene fossil populations generally show weaker surface convexity between growth rings than the extant populations. The most plausible explanation in my mind is that the degree of trade-off between the gametogenesis and body growth actually varies among the pectinids species. In other words, the prominent growth rings in the extant populations of *C. vesiculosus* may be the product of more exhaustive trade-off than in many other pectinids and in the fossil populations of this species.

Acknowledgments

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行事予定

◎第148回例会は，1999年6月26日（土)～6月27日（日）に，「兵庫県立人と自然の博物館」で開催されます．一般講演の申し込み締切は5月7日です．6月26日にシンポジウム「日本の陸生哺乳類の起源，世話人：小澤智生・河村善也」が行われる予定です．会期中の宿の確保が難しい可能性があります．早めに宿を確保されることを希望される方は学会ホームページ（http://ammo.kueps.kyoto-u.ac.jp/palaeont）の年次大会のページに宿の一覧が掲載されています．

◎2000年年会・総会は，2000年1月28日（金)～1月30日（日）に「早稲田大学」で開催されます．一般講演の申し込み締め切りは1999年12月3日，シンポジウムの企画申し込み締切は1999年3月末日です．

◎第149回例会（開催予定時期：2000年の6月末頃）には，「群馬県立自然史博物館」から開催申し込みがありました．

◎1999年総会で，2001年からの年会・総会と例会の開催時期の変更が決定されました．年会・総会は6月下旬から7月の初め頃（現在の例会の開催時期），例会は1月下旬から2月の初め頃（現在の年会・総会の開催時期）開催されます．開催を計画されている機関がありましたら，お申し込み下さい．

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