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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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The fine structures of some living *Spyrida* (*Nassellaria*, *Radiolaria*) and their implications for nassellarian classification

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Abstract. Cytological structures of the two sphyrids *Acanthodesmia vinculata* (Müller) and *Lithocircus reticulatus* (Ehrenberg) were examined. The cytological features of the two species are obviously different. *A. vinculata* has a pear-shaped central capsule containing an eccentrically situated nucleus and juxtannuclear axoplast. The fusules are concentrated around the base of the central capsule in a pore field (porocora), which is the most diagnostic feature of nassellarian cytology. In contrast, *L. reticulatus* possesses a globular central capsule containing a large centrally located nucleus. Of particular interest, fusules of *L. reticulatus* are distributed radially, all around the central capsule, which previously has been described as a typical feature of spumellarians, not nassellarians. In addition, there are some minor differences in ultrastructure of the capsular wall and fusules between the two sphyrids. This evidence indicates that these two species should be separated above the generic level. Beyond these fine structural differences, the two sphyrids have some common features of the capsular wall and fusule structure. Their capsular wall is considerably thicker (0.3-0.5 μm thick) and multilayered compared to that of the cyrtid capsular wall that is composed of a single osmiophilic layer (0.03-0.05 μm thick). Moreover, the sphyrid fusules lack an inner osmiophilic zone that is characteristic of the cyrtid fusules. The general shape of the fusules is also different between the sphyrids and cyrtids. These features are sufficiently different to validate the suborders *Spyrida* and *Cyrtida* as the highest hierarchical division among the nassellarians, and do not support assigning sphyrids to a family taxon such as *Acanthodesmiidae* or *Trissocyclidae* as previously suggested by some workers. The *Spyrida* and *Cyrtida* include respectively two and four types of nucleus-axoplast relationships, which appear to be useful for considering family classification. Among them, one relationship named *Acanthodesmia*-type is recognized both in the *Spyrida* and *Cyrtida*. This clearly suggests that convergence occurs frequently in radiolarian evolution. Hence, it is necessary to synthesize cytological, morphological and stratigraphic information to construct a consistent classification scheme of nassellarians.

Key words : Classification, fine structures, *Nassellaria*, *Radiolaria*, *Spyrida*

Introduction

Cenozoic nassellarians can be classified into suborders *Spyrida* and *Cyrtida* based on the presence or absence of a sagittal ring in their skeleton (Petrushevskaya, 1971). In contrast to recent progress in classificatory and phylogenetic studies of *Cyrtida*, which lack a sagittal ring (e.g., Funakawa, 1995), less is known about the *Spyrida*, which do have sagittal ring. According to Petrushevskaya (1971), the *Spyrida* can be divided into two families *Acanthodesmiidae* and *Triospyridae* based mainly on the development of primary lateral rays that are elements of the nassellarian internal skeleton. However, Sanfilippo *et al.* (1985) and Sanfilippo

(1988) did not classify the *Spyrida* into any family categories due to their poorly understood taxonomy. On the other hand, Nishimura (1990) and Takahashi (1991) classified those nassellarians with sagittal rings into the family *Acanthodesmiidae* as previously recommended by Riedel (1967), whereas Lazarus and Pallant (1989) and Abelmann (1990) placed them in the family *Trissocyclidae* defined by Goll (1968, 1969). This confusion clearly needs to be resolved if we are to progress toward a better understanding of nassellarian taxonomy. Moreover, taxonomic confusion limits potential use of the sphyrids as a paleoceanographic tool, although they are widely distributed and common constituents of radiolarian communities in all oceans.

One of the first tasks needed to resolve this troubling problem is to confirm whether the Spyrida and Cyrtida are taxonomically valid groups. Fine structural information on living organisms can provide substantial evidence toward resolving major outstanding issues of natural affinities. We report fine structural features of some spyrids collected during studies of living radiolaria collected from surface seawater off Barbados, West Indies. Although extensive studies are needed to fully describe this highly diverse group, we have obtained some significant comparative microanatomical data on *Acanthodesmia vinculata* (Müller, 1856) and *Lithocircus reticulatus* (Ehrenberg, 1872) that holds promise of clarifying taxonomic issues among the spyrids. This paper describes observations of living individuals and some important ultrastructural attributes that may contribute to a better understanding of nassellarian suprageneric classification.

For information on research methods see Sugiyama and Anderson (1997a, b, in press). Daily observations, using a Nikon Diaphot inverted light microscope, were made of 10 living *Acanthodesmia vinculata* and 10 *Lithocircus reticulatus*, that were cultured in non-toxic, plastic tissue culture dishes containing ambient seawater from the sampling site. For the ultrastructural study, two specimens of each species were fixed in electron microscopic grade glutaraldehyde (2% in cacodylate buffer, pH=7.8) post-stained in 2% osmium tetroxide in the same buffer, dehydrated in an aqueous acetone series, embedded in epon resin, sectioned with a Porter-Blum ultramicrotome fitted with a diamond knife, and observed with a transmission electron microscope.

Living features of *Acanthodesmia vinculata* and *Lithocircus reticulatus*

***Acanthodesmia vinculata*.**—The subglobular transparent extracapsular cytoplasm, containing yellow to orange symbiotic algae (SA, 5–7 μm in diameter), encloses a crown-shaped skeleton and surrounds a centrally-located apparently spherical (but pear-shaped in electron microscopic view), lucid central capsule (CC, ca. 50 μm in diameter) (Figures 1-1, 1-2).

The distribution and number of the symbiotic algae are variable. In some cases a small number of symbionts (<10) are concentrated around the basal region of the central capsule; in other cases they are numerous and scattered all around the skeleton. The central capsule is surrounded by the sagittal ring. Numerous fine axopodia radiate outward around the central capsule (Figure 1-1). As shown in Figures 1-1, 1-2, some individuals matured in culture and increased their skeletal thickness.

***Lithocircus reticulatus*.**—The cytoplasm of *L. reticulatus* is also subglobular and transparent, and contains a cage-shaped skeleton, yellow to orange symbiotic algae (SA, 15–20 μm in diameter) and a spherical, lucid centrally located central capsule (CC) ca. 50 μm in diameter (Figures 1-3, 1-4).

The symbiotic algae, usually more than 30 in number, are obviously much larger than those of *A. vinculata*, and densely distributed within a space between the shell and central capsule. No symbionts were observed outside the shell.

Axopodia are evident around the skeleton, but they are not as distinct as those of *A. vinculata*.

Description of characteristic ultrastructural features

***Acanthodesmia vinculata*.**—*A. vinculata* has a somewhat pear-shaped central capsule that contains mitochondria with tubular cristae, Golgi bodies, large reserve bodies (R), electron-opaque pigment granules and other organelles (Figure 2-1). The nucleus (N) is eccentrically located and indented at one side. The indented surface is oriented inward toward the center of the central capsule (large arrow in Figure 2-1). Bundles of microtubules (B) extend downward from a region near the nuclear indentation, where the axoplast appears to be located. The bundles penetrate the capsular wall (CW, 0.3–0.5 μm in thickness) forming fusules (F, ca. 1 μm in diameter) that emerge as a concentrated group around the base of the central capsule and form a particular pore field called a porochora (Pr, Figure 2-2).

High-magnification views (Figures 3-2, 3-3) clearly exhibit that the capsular wall consists of four electron-dense layers (i.e., SL, DO, DM and DI) and three electron-lucent layers (i.e., LO, LO' and LI) as schematically shown in Figure 4. The outermost electron-dense layer SL has numerous, relatively small, spherical and subspherical ornaments. Layer DO is ca. 0.01 μm thick and slightly thicker than SL. Layer DM is the main constituent of the capsular wall. Layer DI is the most electron-dense, lying immediately adjacent to the peripheral electron-lucent zone (PELZ) of the intracapsular cytoplasm (IC). The electron-lucent layers LO and LO' are thin, approximately as thick as DO. However, layer LI is much thicker than LO and LO' (Figure 4-1), but is sometimes less distinct as shown in Figure 3-3. The capsular wall, especially layer DI, increases its thickness around the fusules (Figure 3-1). The schematic illustration of the fusule structures is shown in Figure 5. The diameter of the fusules is less than 1.0 μm . Each fusule always has an outward-directed, funnel-like appendage (FA) at the tip, from which bundles of the microtubules extend into extracapsular cytoplasm (EC) to form a barrel-shaped outer osmiophilic zone (OOZ) comprising an outer osmiophilic tube (OOT, Figure 3-1). Unlike cyrtid nassellarians, however, the inner osmiophilic zone (IOZ) and inner osmiophilic tube (IOT) are not recognizable (Sugiyama and Anderson, 1997b). Instead of an inner osmiophilic tube, the inner electron-lucent tube (IELT) occurs at the distal part of the fusules.

Symbionts are densely stained as shown in Figure 6. They appear to be subspherical based on their outline in ultrathin sections, and are closely or loosely enclosed by the perialgal envelope (PE) produced from the host (Figures 6-1a, 2 and 3). The margin of the symbionts is usually not smooth but irregularly rugged. The centrally located nucleus (N), bordered by the nuclear envelope membranes (NM), has numerous puffy, coiled chromosomes (Ch) characteristic of some dinoflagellates. The peripheral region of the cytoplasm contains a relatively massive chloroplast (Cl) having triple-thylakoid lamellae, opaque reserve bodies (R) and other organelles such as mitochondria and Golgi bodies.

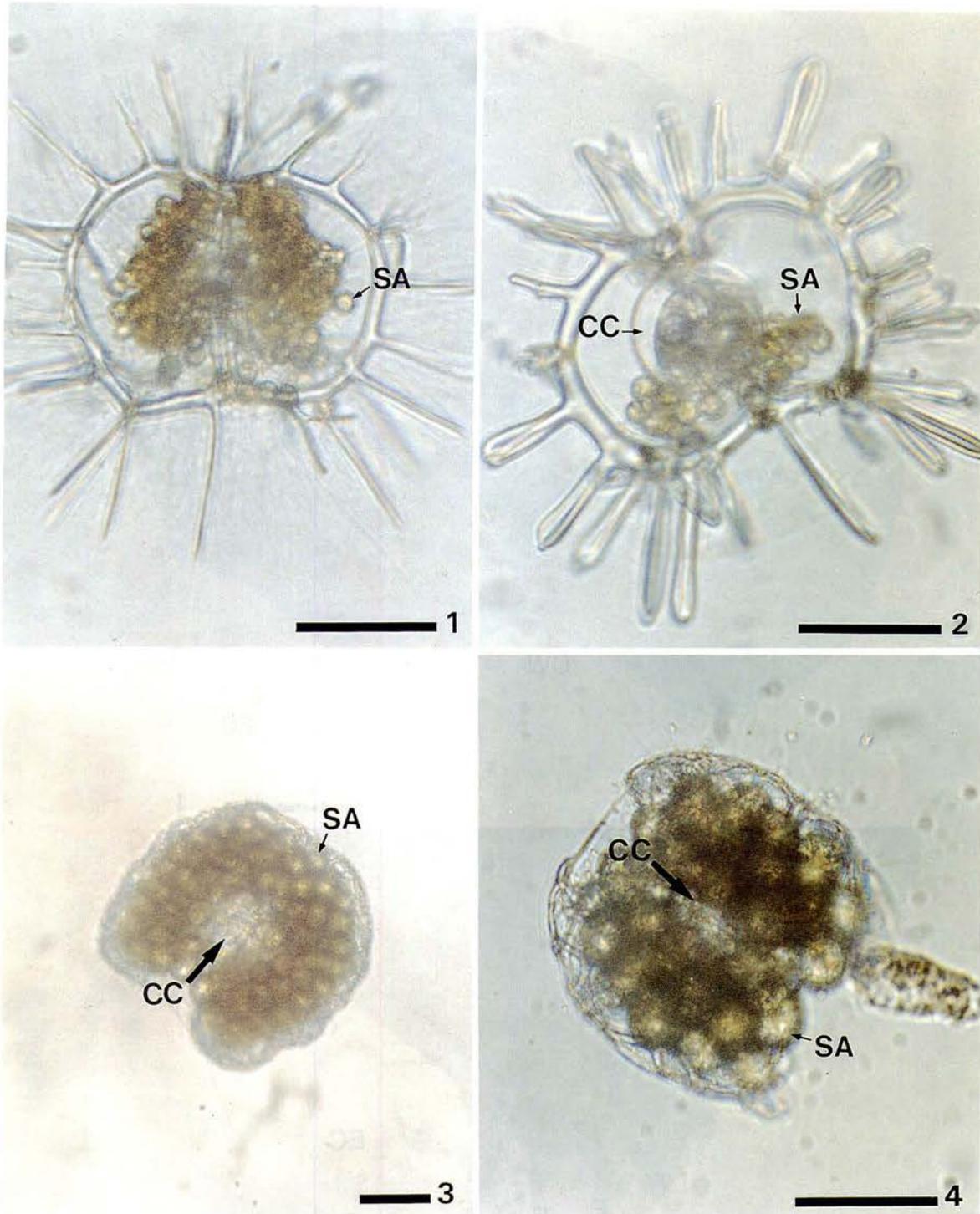


Figure 1. Light micrographs of living *Acanthodesmia vinculata* (Müller) and *Lithocircus reticulatus* (Ehrenberg). **1, 2.** *Acanthodesmia vinculata*. **1:** Healthy individual, Day 0 (captured day). Symbiotic algae (SA) are dense all around the central capsule. **2:** Same individual, Day 8, showing skeletal growth, mainly increase in skeletal thickness, during culture. Number of symbiotic algae (SA) are decreased, and they are concentrated around the base of the central capsule (CC). **3, 4.** *Lithocircus reticulatus* (Ehrenberg). **3:** Healthy individual, Day 0. Numerous symbiotic algae (SA) are dense around the centered, transparent central capsule (CC). **4:** Healthy individual, Day 4. In this individual, symbiotic algae (SA) are also dense around the central capsule (CC). Scale bars are 50 μm .

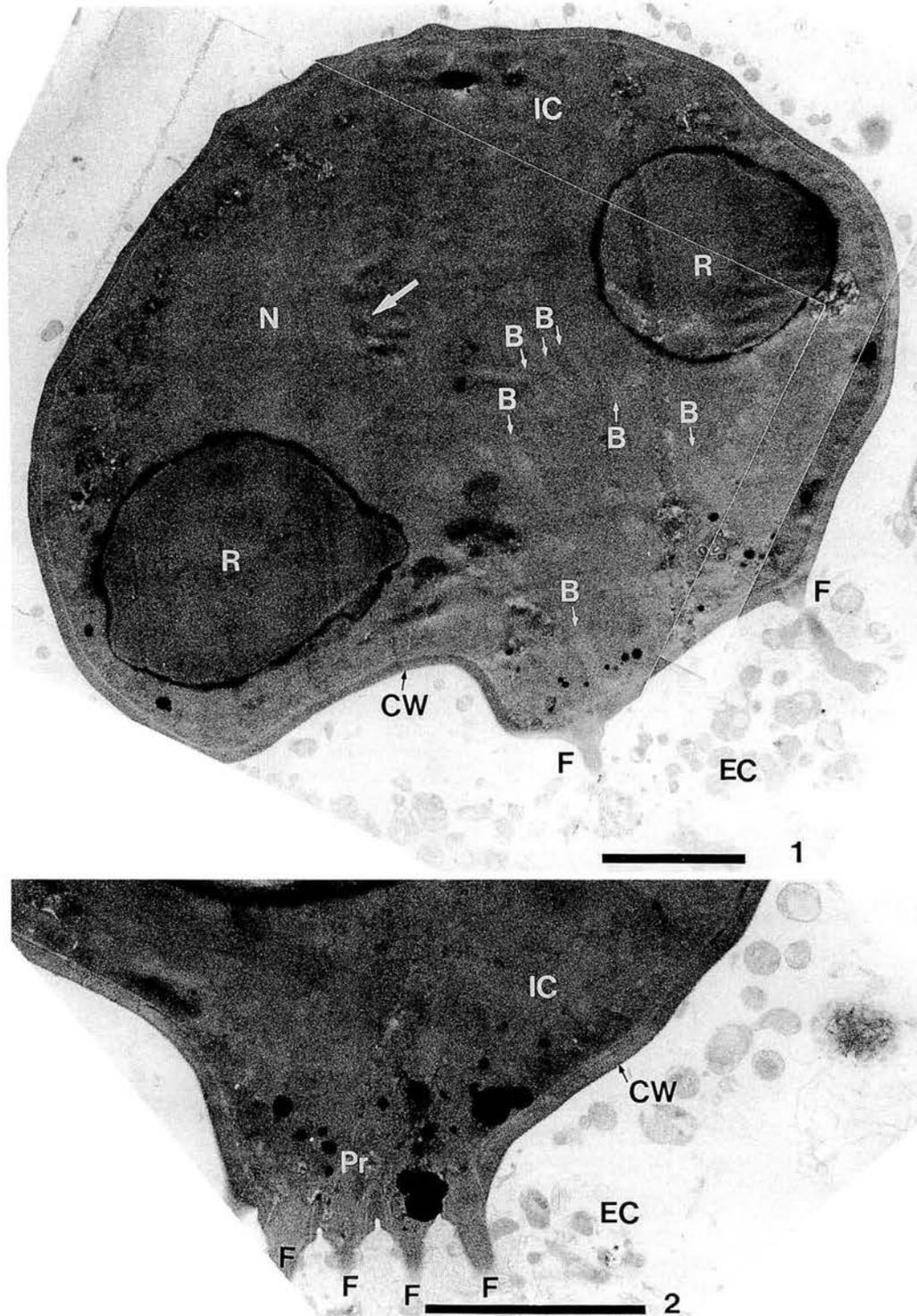


Figure 2. Transmission electron micrographs of the central capsule in *Acanthodesmia vinculata*. **1.** A composite micrograph showing the gross structure. A thick capsular wall (CW) encloses intracapsular cytoplasm (IC) in which large reserve bodies (R) and eccentrically situated nucleus can be seen. The nuclear indentation is shown by a thick arrow. Bundles of microtubules (B) extend downward from the center of the central capsule, and penetrate the capsular wall at the base to form fusules (F). **2.** A longitudinal section showing concentration of fusules (F) to form a porochora at the base of the central capsule. Thick capsular wall (CW) separates intracapsular cytoplasm (IC) and extracapsular cytoplasm (EC). Scale bars indicate 5 μm .

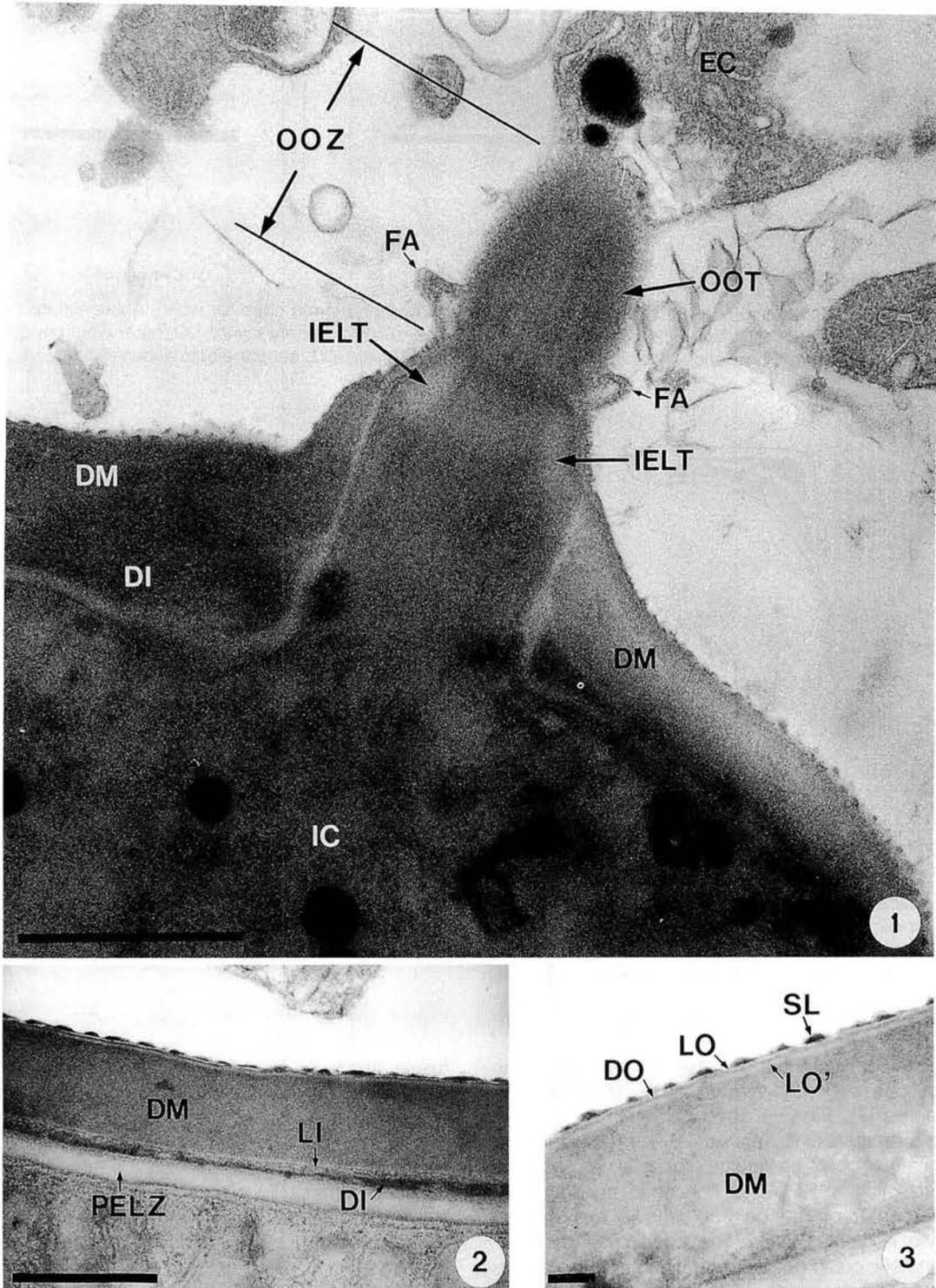


Figure 3. Transmission electron micrographs of fusule and capsular wall in *Acanthodesmia vinculata*. **1.** A high-magnification view of fusule showing the detailed structure of a fusule containing microtubules that extend from the intracapsular cytoplasm (IC) to extracapsular cytoplasm (EC). Inner electron-lucent tube (IELT) and funnel-shaped appendage (FA) are clearly visible. The capsular wall, surrounding the fusule, increases in thickness, and the inner, electron-dense layer (DI) is as thick as the main electron-dense layer (DM). Scale bar is 1 μm . **2, 3.** High-magnification views of the capsular wall. Note that the inner electron-dense layer (DI), recognized in 2, is not visible in 3. Other abbreviations are explained in Figure 4. Scale bars are 0.5 μm and 0.1 μm , respectively.

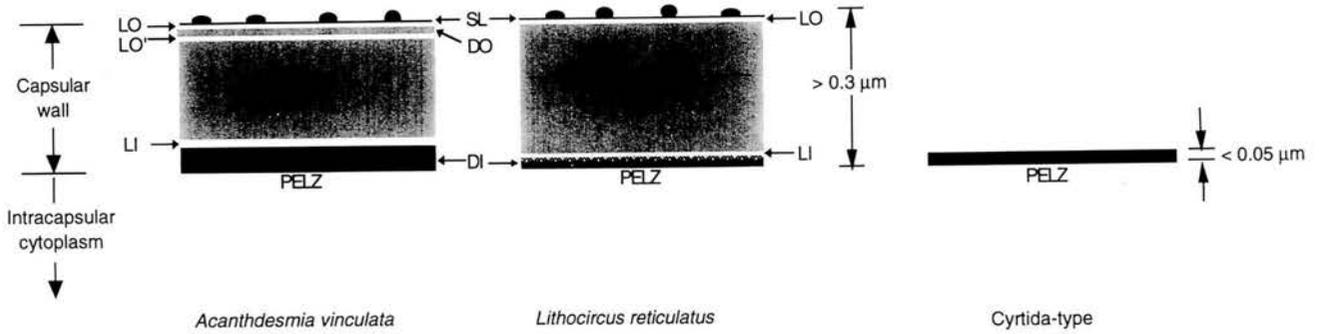


Figure 4. Schematic illustration showing the details of sphyrid and cyrtid capsular wall. Abbreviations: SL, surface layer; LO and LO', outer electron-lucent layer; LI, inner electron-lucent layer; DO, outer electron-dense layer; DM, main electron-dense layer; DI, inner electron-lucent layer; DC, central electron-dense layer.

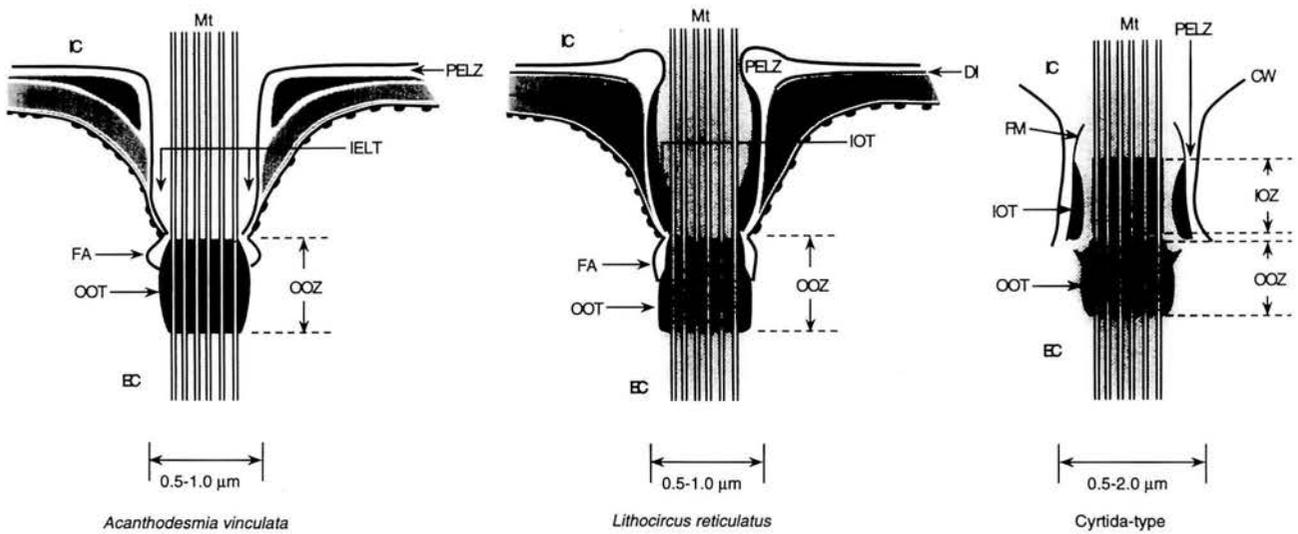


Figure 5. Schematic illustration showing longitudinal sections of sphyrid and cyrtid fusules. Abbreviations: IC, intracapsular cytoplasm; EC, extracapsular cytoplasm; CW, capsular wall; FM, fusule membrane; IOZ, inner osmiophilic zone; IELT, inner electron-lucent tube; IOT, inner osmiophilic tube; FA, funneled appendage; OOT, outer osmiophilic tube; PELZ, peripheral electron-lucent zone; DM and DI, electron-dense layers of sphyrid capsular wall.

There is a prominent pyrenoid (Py) that is attached to the chloroplast by one stalk and penetrated by three double-thylakoid lamellae (TL, Figure 6-1b).

***Lithocircus reticulatus*.**—*L. reticulatus* has a subglobular central capsule that contains various organelles as observed in *A. vinculata* (Figure 7). The spherical nucleus (N) occupies the center of the central capsule and has an electron-dense nucleolus (Nu). The position of the axoplasm, unfortunately, could not be determined in these preparations. Fusules (F) are distributed radially around the capsular wall. The thick capsular wall, which is 0.3–0.5 μm thick, consists of three electron-dense layers (i.e., SL, DM and DI) and two electron-lucent layers (i.e., LO and LI) as shown in Figures 4 and 8. Layers SL and LO are similar to those of *A. vinculata*. Layer DM is the thickest, and often has a central more electron-dense layer (DC, Figure 8-2). Layers DI and LI are thinner than those of *A. vinculata*. The

fusule structures are schematically shown in Figure 5. The diameter of the fusules is 0.5–1.0 μm . Each fusule always possesses a funnel-shaped, outward-directed appendage (FA) at the tip as observed in *A. vinculata*. Bundles of the microtubules (B) passing through the fusules are shielded by an outer osmiophilic tube (OOT) outside the capsular wall. Inside the capsular wall, no structures corresponding to the electron-lucent tube observed in *A. vinculata* were observed in this species. Instead, an inner osmiophilic tube (IOT) shields the bundles of microtubules (B). An inner osmiophilic zone (IOZ), identified in some cyrtid nassellarians, is not present in this species as well as *A. vinculata*.

Symbionts are in general ellipsoidal and closely or loosely enclosed within the perialgal envelope (PE) of the host, which is further entirely or partly surrounded by a perforated and finely wrinkled external wrap (EW, Figures 9-1–4). Some perialgal envelopes possess one or more pores with margins

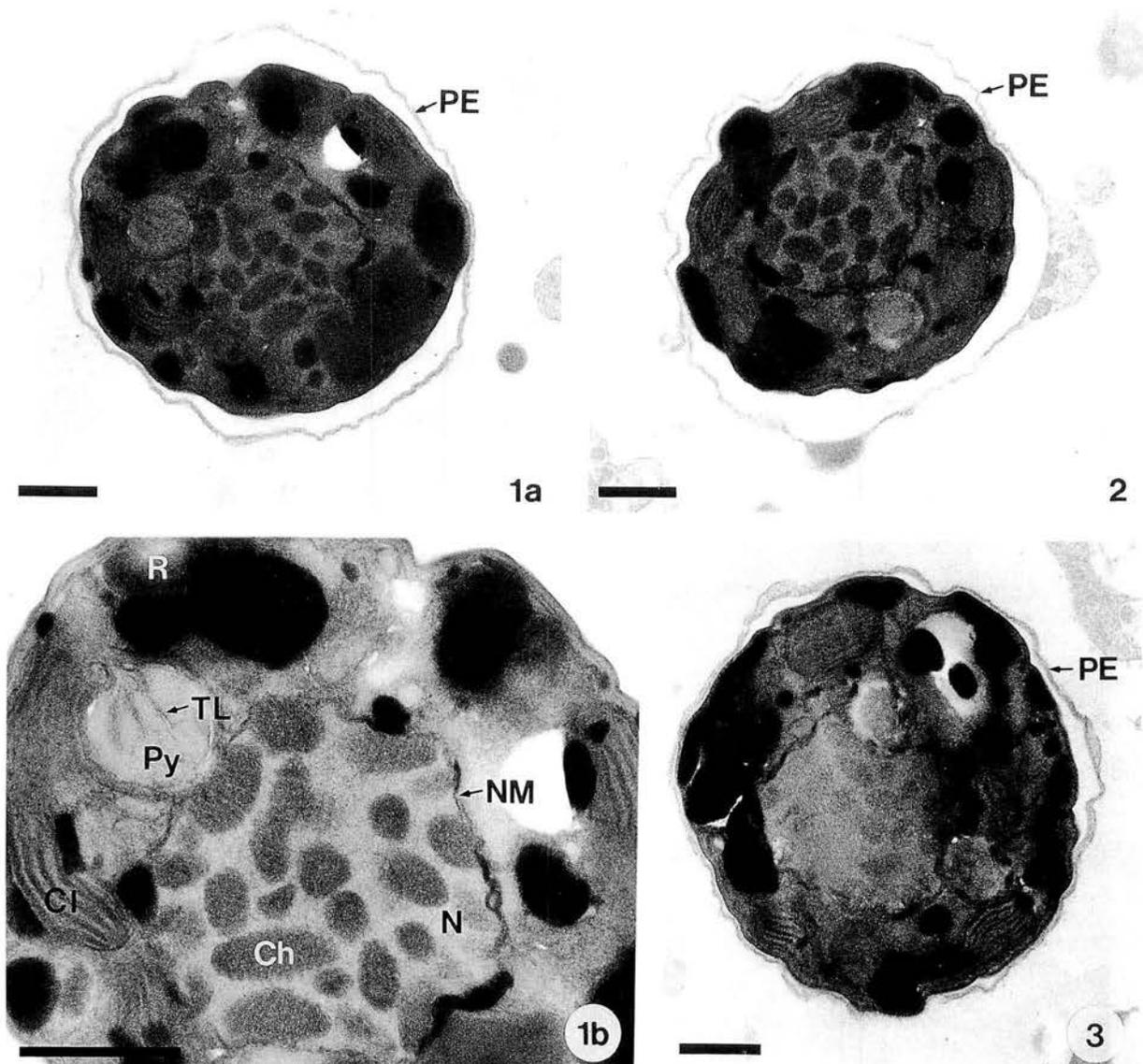


Figure 6. Transmission electron micrographs of symbiotic algae (dinoflagellates) in *Acanthodesmia vinculata*. **1a, 2 and 3.** Symbionts have irregularly rugged outline. They are enclosed by a perialgal envelope of the pseudopodial system produced from the host. **1b.** Enlargement of 1a showing the details of symbiont fine structures. Abbreviations: Ch, chromosome; Cl, chloroplast; N, nucleus; NM, nuclear membrane; Py, pyrenoid; R, reserve body; TL, thylakoid lamella.

that are approximately reflexed inward (large arrow, Figure 9-3). The symbionts are enclosed in a well developed organic wall (OW, $0.5\ \mu\text{m}$ thick at the maximum, Figure 9-4). The nucleus (N), $5-7\ \mu\text{m}$ in diameter, is centrally located, and contains numerous puffy, coiled chromosomes (Ch) characteristic of some dinoflagellates (Figure 9-1). The coiling of the chromosomes is considerably finer than that of the symbionts in *A. vinculata*. The cytoplasmic region, containing mitochondria (Mt) and Golgi bodies, immediately surrounds the nucleus (N, Figures 9-1, 9-2). The peripheral chloroplasts (Cl) having triple-thylakoid lamellae are relatively narrow (ca. $0.5\ \mu\text{m}$ wide) and partially reticulated especially

around the pyrenoids (Figure 9-1). The pyrenoids (Py) are more than one, usually two, next to the nucleus. Each pyrenoid (Py) is penetrated by numerous double-thylakoid lamellae and attached to the chloroplasts (Cl) by two stalks (Figure 9-4). Between the chloroplasts and the nucleus is a remarkably developed feature, organic reserve substances (ORS=food storage material) in which there are numerous starch grains (St) derived from photosynthesis and darker matter that is probably lipid (Figures 9-1, 9-2).

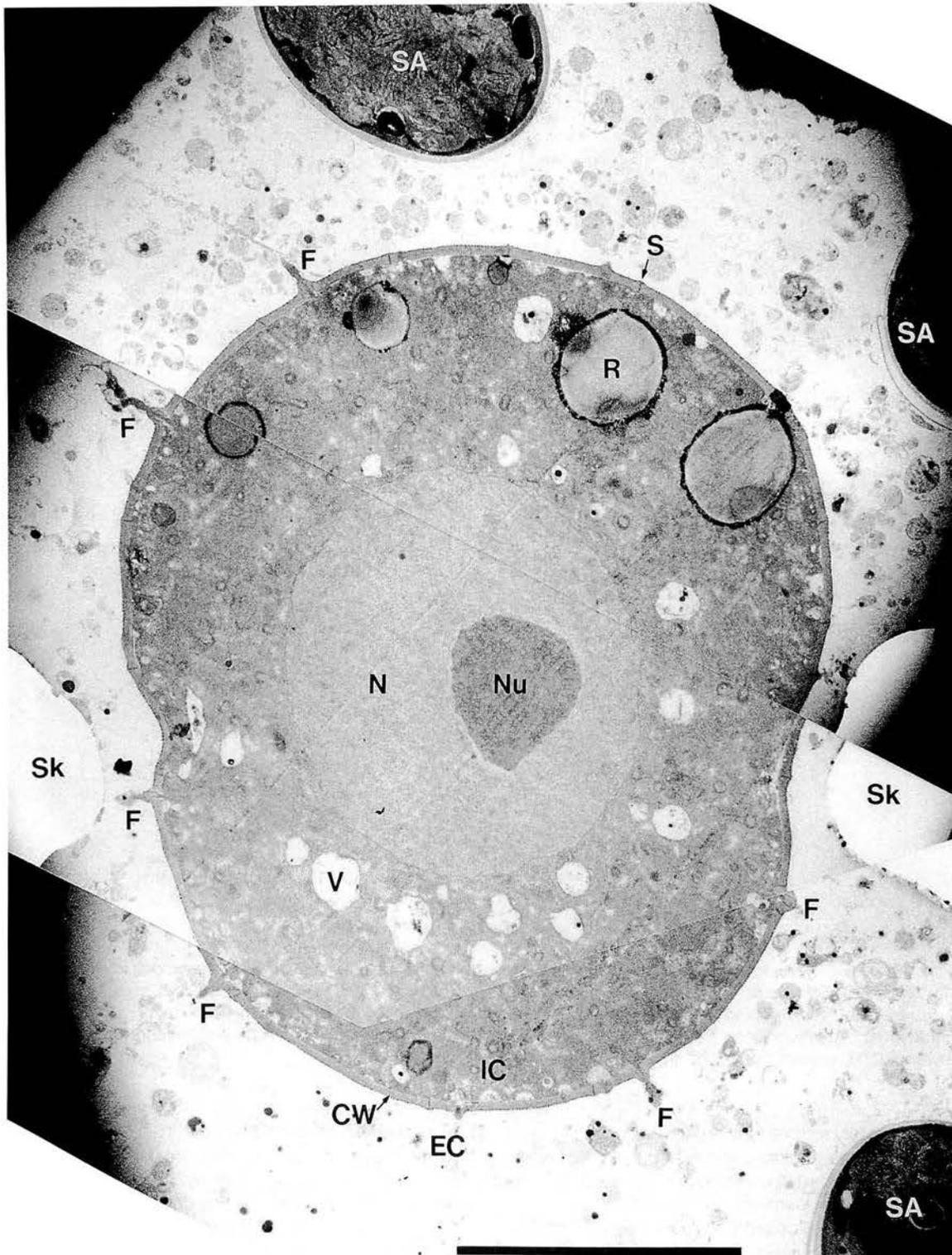


Figure 7. A composite transmission electron micrograph of the central capsule in *Lithocircus reticulatus* which is held by siliceous skeleton (Sk). Thick capsular wall (CW) encloses intracapsular cytoplasm (IC) at the center of which there is a large, spherical nucleus (N) comprising much electron-dense nucleolus (Nu). Relatively large reserve bodies (R) are distributed near the capsular wall, whereas inner region of intracapsular cytoplasm is rich in electron-lucent vacuoles (V). Fusules (F) and minor slits (S) penetrate all parts of the capsular wall. In extracapsular cytoplasm (EC), there are symbiotic algae (SA). Scale bar indicates 10 μm .

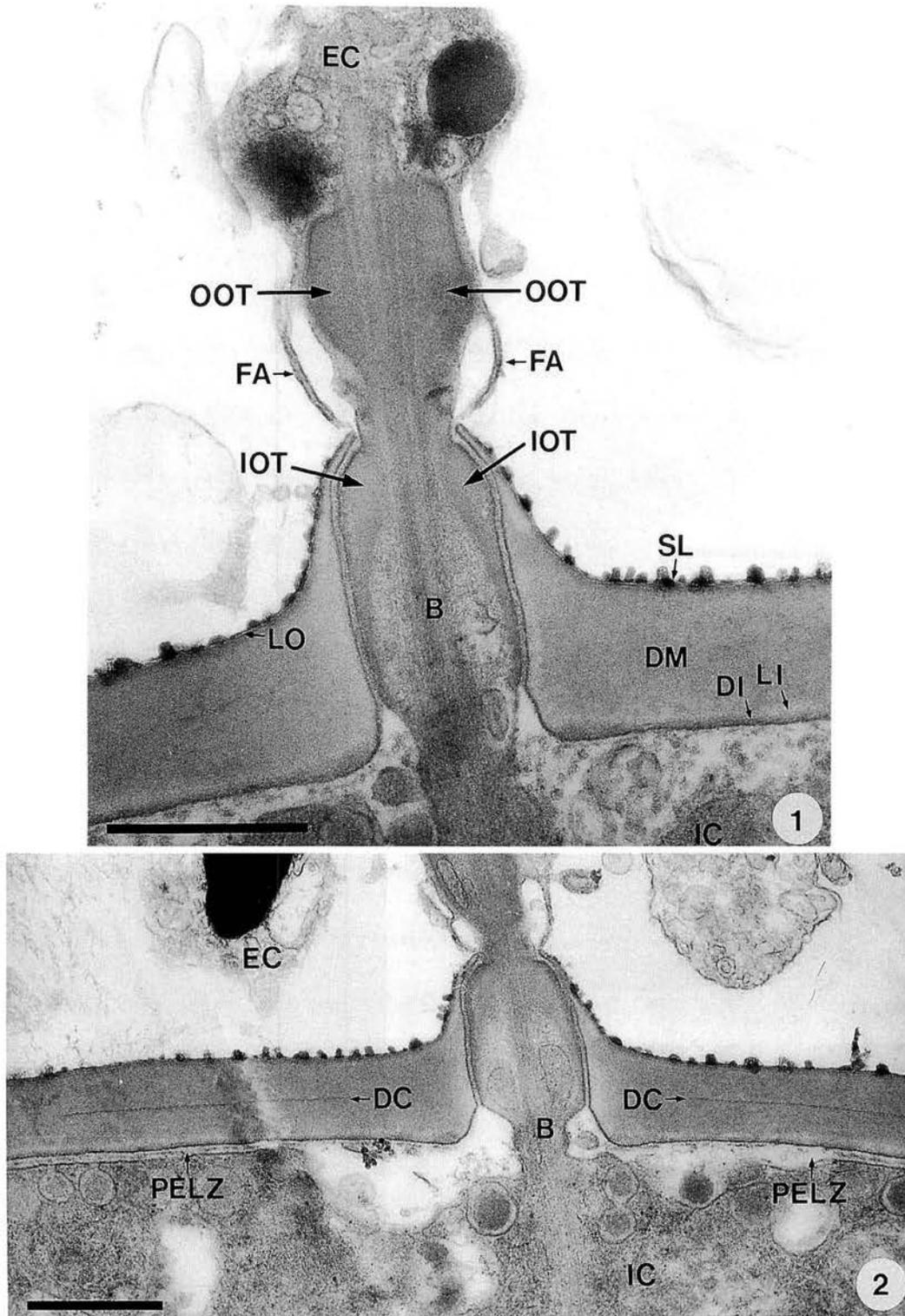
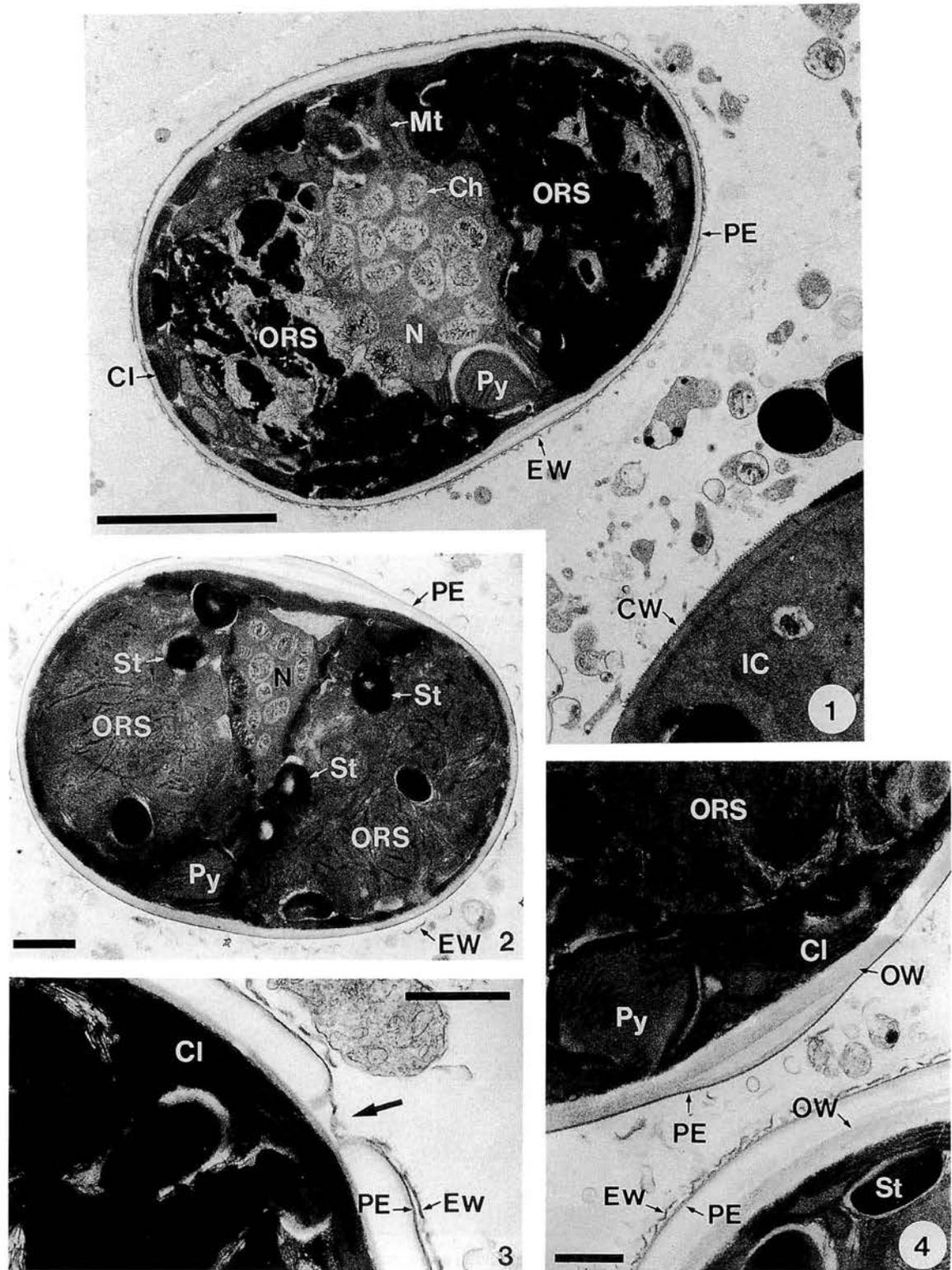


Figure 8. Transmission electron micrographs of fusule and capsular wall in *Lithocircus reticulatus*. **1.** Bundle of microtubules (B) extending from intracapsular cytoplasm (IC) to extracapsular cytoplasm (EC) is sheathed by inner osmiophilic tube (IOT) and outer osmiophilic tube (OOT). Funneled appendage (FA) further encloses the proximal part of outer osmiophilic tube. Abbreviations of capsular wall are explained in Figure 4. Scale bar indicates 0.5 μm . **2.** Thick capsular wall lying on peripheral electron lucent zone (PELZ) has central electron-dense layer (DC) at the middle. Scale bar indicates 0.5 μm .



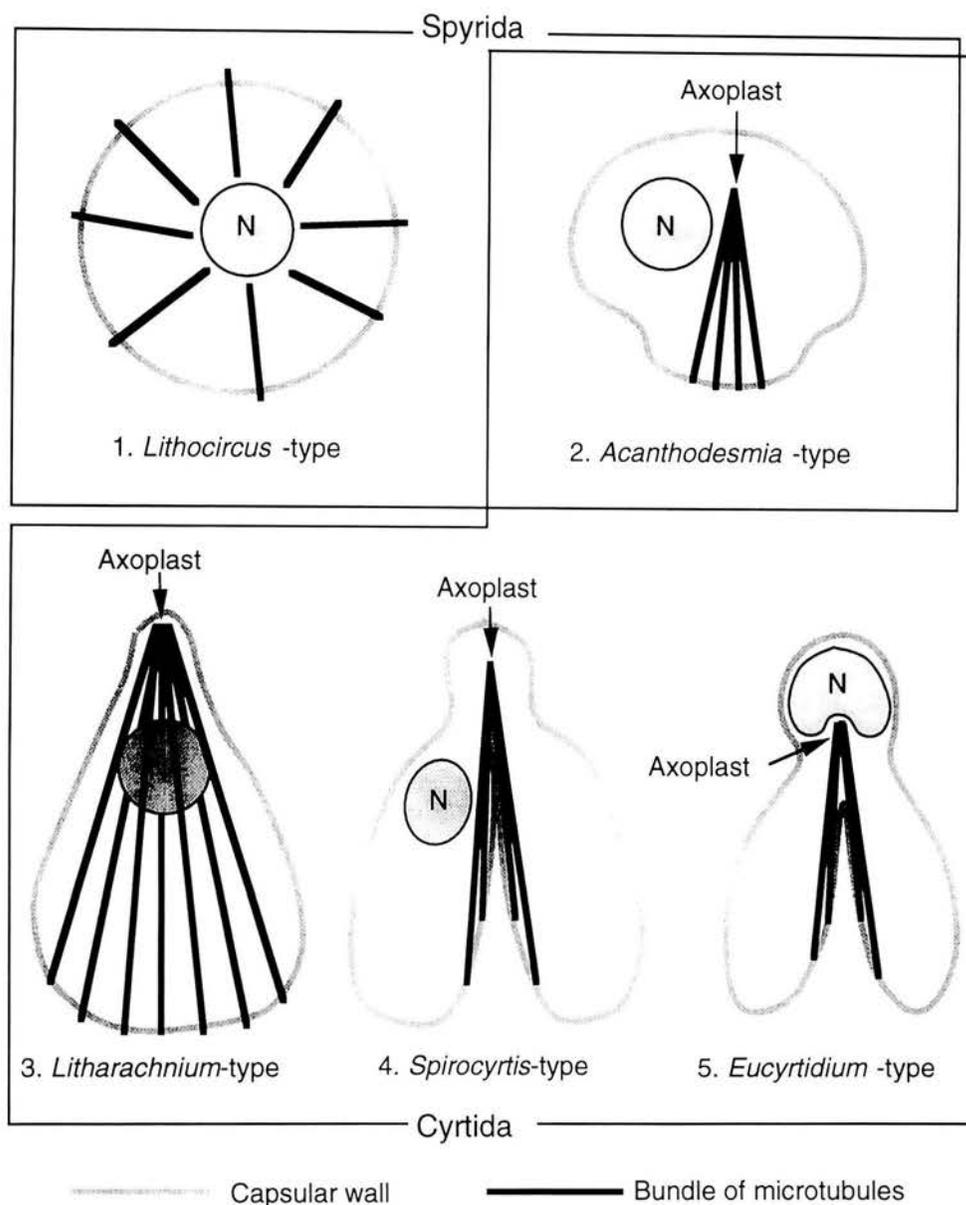


Figure 10. Schematic illustration showing types of the nucleus-axoplast relationships hitherto recognized in the Sphyrida and Cyrtida.

Figure 9. Transmission electron micrographs of symbiotic algae (dinoflagellates) in *Lithocircus reticulatus*. **1.** Symbiont is ellipsoidal in outline and sequestered in a perialgal envelope (PE) which is further enclosed by wrinkled extra wrap (EW). Nucleus (N) containing puffy chromosomes (Ch) is located at the center. Peripheral chloroplast (Cl) is narrow and partially reticulated around the juxtannuclear pyrenoid (Py) and other organelles such as mitochondria (Mt). The most conspicuous feature is the organic reserve substances (ORS) widely distributed between the nucleus and chloroplast. Intracapsular cytoplasm (IC) of the host bounded by a thick capsular wall (CW) is visible near the symbiont. Scale bar indicates 5 μm . **2.** Within well developed organic reserve substances (ORS), there are numerous starch grains (St). Scale bar indicates 2 μm . **3.** Arrow points to a pore where perialgal envelope (PE) is reflexed inward. Scale bar indicates 1 μm . **4.** Two symbionts are closely located. The outermost part of both symbionts is relatively thick organic wall (OW). Perialgal envelope (PE) from host directly or indirectly encloses the symbiont. The details of pyrenoid (Py) are also shown. It is attached to chloroplast (Cl) by two stalks and penetrated by numerous, thin thylakoid lamellae. Scale bar indicates 1 μm .

Discussion

1. Comparison of cytoplasmic features between *Acanthodesmia vinculata* and *Lithocircus reticulatus*

As described above, the two sphyrids have some differentiating fine structural features. The most conspicuous is the arrangement of the fusules in the central capsular wall. *A. vinculata* has a typical nassellarian fusule arrangement, forming a porochora at the base of the central capsule. However, worthy of special attention is that the fusule arrangement of *L. reticulatus* is more representative of Spumellaria than Nassellaria; namely the fusules of *L. reticulatus* are disposed radially around the periphery of the central capsule. In addition, there are several minor differences in the capsular wall and fusule structures as schematically shown in Figures 4 and 5. The capsular wall of *L. reticulatus* has only two electron-lucent layers (i.e., LO and LI) as compared to three of *A. vinculata* (i.e., LO, LO' and LI). In *A. vinculata*, the inner electron-lucent tubes ensheath the microtubules where they pass through the fusules, whereas *L. reticulatus* has inner osmiophilic tubes instead of inner electron-lucent tubes. The organization of the inner electron-dense layer (DI) relative to the overall organization of the capsular wall and the shape of FA at the tip of the fusules are also different between the two species.

Based on these major fine structural features of the cytoplasm, particularly the arrangement of the fusules in the central capsular wall, it seems quite reasonable that the two species should be separated at or above the family level, in spite of the similarities of the skeletal elements. Cytoplasmic features are more likely to be conservative and more compelling evidence for making phyletic affinities than the skeleton which can be highly variable and in some cases may represent convergent lines of adaptation (e.g., Swanberg *et al.*, 1990). As mentioned in the introduction, Petrushevskaya (1971) defined two families Acanthodesmiidae and Triosphyridae based on the skeletal structures. *A. vinculata* is the type species of the genus *Acanthodesmia* and the type genus of the family Acanthodesmiidae. The genus *Lithocircus*, including *L. reticulatus*, also belongs to this family according to Petrushevskaya (1971). However, the fine structural evidence obtained in the present study strongly suggests that Petrushevskaya's (1971) classification of the sphyrids does not reflect a natural monophyletic taxon. To establish a consistent sphyrid classification, further cytoplasmic studies are necessary for other members of the Sphyrida.

The results of this study clearly indicate that the Sphyrida can be subdivided into at least two families or superfamilies based on the arrangement of the fusules. Moreover, the atypical arrangement of the fusules in *L. reticulatus*, observed in both sectioned specimens, provides some compelling evidence that one of the established characteristics of Nassellaria since Haeckel (1887), namely, that the most distinctive cytoplasmic feature of the Nassellaria is possession of a porochora at one pole of the central capsule, is not indicative of all the members.

2. Comparison of cytoplasmic features between the Sphyrida and Cyrtida

Some major cytoplasmic similarities of *A. vinculata* and *L. reticulatus*, distinctively different from cyrtid cytoplasmic features, are presented as a means of clarifying natural boundaries between the Sphyrida and Cyrtida. As shown in Figure 4, the capsular wall of the two sphyrid species exhibits a thick, multilayered profile consisting of alternating electronlucent and dense layers. Although there are some minor differences in wall structure between the two sphyrids as mentioned above, this common feature is quite different from hitherto known cyrtid capsular walls that are much thinner (0.03–0.05 μm thick) and composed only of a single osmiophilic layer (e. g., Cachon and Cachon, 1971; Anderson, 1983; Sugiyama and Anderson, 1997b).

This indicates, based on current evidence, that sphyrid cytoplasmic organization is fundamentally different from that of cyrtids and validates separating Sphyrida and Cyrtida as formal higher-order taxa. In other words, the magnitude of the differences in fine structural organization between the two suggests that it is not suitable to regard the Sphyrida as a family taxon such as Riedel's (1967) Acanthodesmiidae or Goll's (1968) Trissocyclidae. Capsular wall structure, including fusule organization, appears to be a very useful criterion to cytologically distinguish Sphyrida and Cyrtida.

Moreover, we can see that the general morphology of the sphyrid fusules is also quite different from those of the cyrtids (Figure 5). In the cyrtid fusules, there are two osmiophilic zones named inner and outer osmiophilic zones (IOZ and OZ), respectively. However, we have not seen the former zone in the sphyrid fusules. The sphyrid fusules are relatively narrow (0.5–1.0 μm in diameter) and distally convergent, while the cyrtid fusules, commonly 0.5–2.0 μm in diameter, are distally divergent (Sugiyama and Anderson, 1997b). This observation also supports separating Sphyrida and Cyrtida as a first-order classification of the Nassellaria.

3. Implications for nassellarian classification

Riedel (1967) and Petrushevskaya (1971) pioneered modern schemes of nassellarian classification based on cephalic skeletal structures. Subsequent investigators have performed further detailed studies aiming at establishing a more natural classification system of the Nassellaria using scanning electron microscopy (e.g., Sugiyama, 1993, 1994; Funakawa, 1995; O'Connor, 1997). However, it appears that none of these approaches, based solely on skeletal structures, so far have produced decisive evidence for a consistent classification. Consequently, emendations of the family and generic diagnoses have appeared repeatedly in papers treating nassellarian taxonomy. To evaluate the significance of a particular skeletal feature, it is necessary to broaden the base of evidence and discuss the problem using other features with useful phylogenetic information. Cytological and fine-structural evidence combined with more traditional sources of evidence can yield quite fruitful results as already demonstrated by Sugiyama and Anderson (1997b) for some cyrtids.

As discussed above, capsular wall and fusule structures are useful for the first-order classification of the Nassellaria.

For the second order, corresponding to the family category (i.e., superfamily, family and subfamily), the nucleus-axoplast relationship seems to be important since it may be related to the basic physiology and ontogenesis of organisms, especially as it may regulate cell shape and the deposition of primary skeletal structures, although we do not know the details of this mechanism. Until now, five types of nucleus-axoplast relationships are known as shown in Figure 10. They are tentatively named *Lithocircus*-, *Acanthodesmia*-, *Litharachnium*-, *Spirocyrtis*-, and *Eucyrtidium*-types. The first *Lithocircus*-type is known exclusively in the Spyrida, whereas the latter three types are restricted only in the Cyrtida. The second *Acanthodesmia*-type occurs both in the Spyrida and Cyrtida.

The *Lithocircus*-type (Figure 10-1) discovered by the present study represents one of variations in the Spyrida. This type exhibits a typical spumellarian feature that lacks a porochora as described above. The *Acanthodesmia*-type (Figure 10-2) was first reported by Cachon and Cachon (1971) as a gross cytological structure found in *Eucoronis challengerii* Haeckel that is a junior objective synonym of *Acanthodesmia vinculata*. In this type, the nucleus is not located on the axis of the central capsule. However, the juxtannuclear axoplast and tip of the podoconus, which are located at the same level above the base of the capsule as the nucleus, are approximately on the axis. It is noteworthy that this type of nucleus-axoplast relationship is known from a cyrtid species illustrated by Anderson (1977, 1983).

The *Litharachnium*-type (Figure 10-3) confirmed also by Cachon and Cachon (1971) has a nucleus that is below the axoplast and surrounded by numerous bundles of microtubules extending downward from the axoplast. The *Spirocyrtis*-type (Figure 19-4) discovered by Sugiyama and Anderson (1997b) has a somewhat similar structure to the *Acanthodesmia*-type since both the types do not have the nucleus on the axis of the central capsule. However, the former is easily distinguished from the latter, since the axoplast is far from the nucleus. The axoplast and subjacent conical podoconus in *Spirocyrtis scalaris*, the type species of the genus, are situated at the cephalothorax that is the center of the lobated central capsule. The nucleus is situated in one of the branched lobes below the thorax.

The *Eucyrtidium*-type (Figure 10-5) is characterized by having an axoplast immediately below the nucleus whose base is often concave. Both the axoplast and nucleus are within the cephalis. This type, including theoperids, pterocorythids and most lophophaenids, was first illustrated by Cachon and Cachon (1971) in their study of the cytoplasmic organization of *Spongomelissa* sp. and "*Eucyrtidium cienkowskii*" (misidentification of *Pterocorys* species, probably *P. zancleus*). Cachon and Cachon (1971) also presented some significant gross cytoplasmic structures of *Paracystidium spiculolum* and *Pseudocubus obeliscus* (Cachon and Cachon, 1971, figs. 1a, c). These two species do not have a lobated central capsule, but the nucleus-axoplast relationship is quite homologous to that of *Spongomelissa* sp. and "*Eucyrtidium cienkowskii*." Because lobation of the central capsule seems to be related probably to multisegmentation of the shell, the feature is minor and not so important for

considering taxonomic problems of suprageneric categories. Therefore, the cytoplasmic organizations of *Spongomelissa* sp., "*Eucyrtidium cienkowskii*", *Paracystidium spiculolum* and *Pseudocubus obeliscus* shown by Cachon and Cachon (1971) can be united into one group as the *Eucyrtidium*-type.

4. Conclusion

Based on the fusule and capsular wall structures of living *Acanthodesmia vinculata* and *Lithocircus reticulatus*, it seems quite reasonable that they should be separated from the Cyrtida and classified with the Spyrida, which indicates that it is not appropriate to treat the latter as a family-level taxon such as Acanthodesmiidae and Trissocyclidae. The Spyrida can be subdivided into more than two families or superfamilies based on the arrangement of the fusules. We must pay attention for the fusule arrangement of *L. reticulatus* that is not typical for nassellarians, which suggests that the traditional diagnosis of nassellarians needs redefinition.

In the nucleus-axoplast relationship that seems to be useful for second-order classification of nassellarians, we can recognize two types in the Spyrida (e.g., *Lithocircus*- and *Acanthodesmia*-types) and four types in the Cyrtida (*Acanthodesmia*-, *Litharachnium*-, *Spirocyrtis*- and *Eucyrtidium*-types) at the present. The number of the types will likely be increased by subsequent examinations, and further extensive studies are necessary to clarify the detailed relationship between cytological and skeletal structures. Here, the most important thing we need to consider now is the existence of the same type of nucleus-axoplast relationship (i.e., *Acanthodesmia*-type) in both the Spyrida and Cyrtida as mentioned above. This means that the same pattern of nucleus-axoplast relationship can occur even in phylogenetically independent lineages separated at the level of the family category. This indicates further how convergence can occur, possibly many times over, during the long evolutionary history of radiolarians. Therefore, we have to be very cautious about accepting one line of evidence as authoritative, and need to synthesize all available information, based on cytology, skeletal morphology and stratigraphic data from continuous fossil records, in order to check for convergent evolution and thereby construct a consistent and natural classification of nassellarians.

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Two ammonite species of the genus *Sharpeiceras* from the Cretaceous of Hokkaido

(Studies of Cretaceous ammonites from Hokkaido and Sakhalin–LXXXI)

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Abstract. *Sharpeiceras mexicanum* (Böse, 1928) has been recently found in a mudstone unit of Hirotomi in the Monbetsu Valley, south-central Hokkaido. It possesses the adult body chamber, which has not been well shown in the hitherto described specimens of this species. *Sharpeiceras kikuae* Matsumoto and Kawashita, 1995 is redescribed in this paper, since it was established as an appendix to a stratigraphic paper written in Japanese and seems to have been little noticed. It came from a mudstone member in the lower part of the Middle Yezo Subgroup in the Oyubari area, central Hokkaido. It is somewhat similar to *S. florencae* Spath but has a wider umbilicus, less crowded ribs on the septate whorls and more distinctly separated two lateral tubercles. In these respects it seems to resemble *S. mocambiquense* (Choffat), but the available material is insufficient for exact comparison. The two species described indicate an early Cenomanian age for the fossiliferous mudstone.

Key words: Adult body chamber, Cenomanian, Hokkaido, *Sharpeiceras kikuae*, *Sharpeiceras mexicanum*.

Introduction

In this paper two ammonite species of the genus *Sharpeiceras* recently acquired by one of us (Y.K.) are described. They were found independently from two separate areas in Hokkaido, but they are valuable for taxonomy and for biostratigraphic correlation.

Repository.—The specimens from Hokkaido described in this paper are housed in the following institution or collection, with abbreviation at the heading;

MCM: Mikasa City Museum, Mikasa 068-2111

YKC: Yoshitaro Kawashita Collection, temporarily in his residence (Tomatsu-Chiyoda, Mikasa 068-2134), but eventually to be transferred to some institutions. The numbering of YKC refers to the date of acquisition, e.g., 060625=25 June 1994 [the first two digits refer to the Japanese era year, Heisei 6].

Palaeontological description

Family Acanthoceratidae Grossouvre, 1894

Subfamily Mantelliceratinae Hyatt, 1903

Genus *Sharpeiceras* Hyatt, 1903

Type species.—*Ammonites laticlavium* Sharpe, 1855.

Remarks.—General accounts of this genus have been

given by several authors, e.g., Matsumoto *et al.* (1969), Wright and Kennedy (1984), Howarth (1985) and Wright (1996). The genus occurs in the Lower Cenomanian, but its accurate relationships with other genera have yet to be worked out. In some of the hitherto described species, the characters of the adult body chamber are not sufficiently known.

Sharpeiceras mexicanum (Böse, 1928)

Figures 1 and 2

Mantelliceras laticlavium (Sharpe) var. *mexicanum* Böse, 1928, p. 253, pl. 10, fig. 6; pl. 11, fig. 1.

Sharpeiceras mexicanum (Böse), Young and Powell, 1976, p. 19, pl. 7, figs 1, 3; Mancini, 1982, p. 254, fig. 6e; Howarth, 1985, p. 88, figs 20, 23.

'*Sharpeiceras laticlavium* var. *mexicanum*' (Böse, 1928), Wright and Kennedy, 1987, p. 128, text-fig. 31.

Holotype.—A specimen described by Böse, 1928 (see above) from the Buda Limestone of Mexico, by monotypy.

Material.—MCM T260 [=previous YKC 080416A] (Figure 1) and another incomplete specimen [YKC 060625] from the Chennai-zawa, southern branch of the Monbetsu River near Hirotomi. For the location readers may refer to Matsumoto *et al.* (1997, fig. 1).

Description.—MCM T260 is large and preserves the body

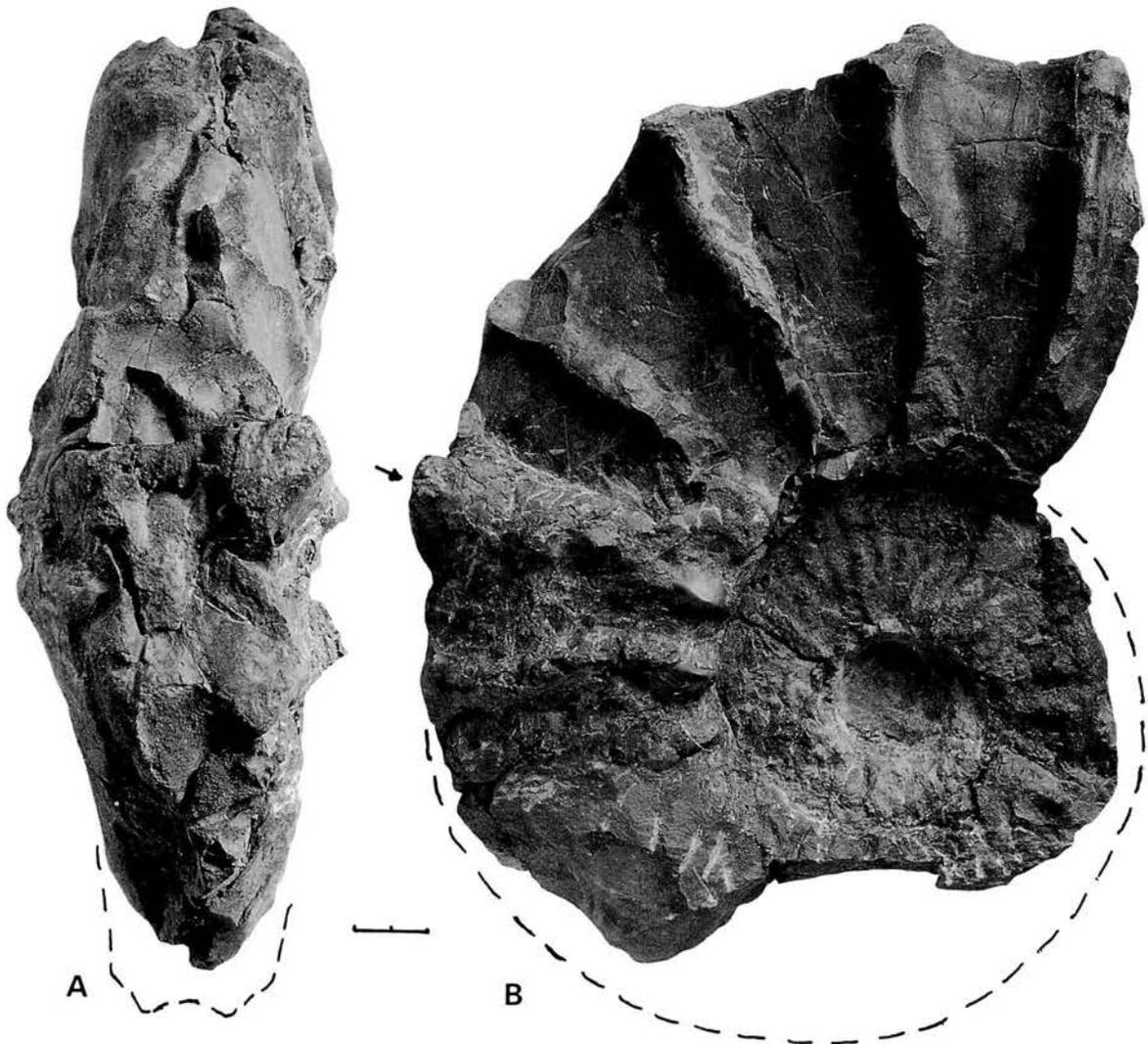


Figure 1. *Sharpeiceras mexicanum* (Böse). MCM T260 [=previous YKC 080416A] from the Chennai-zawa, a branch of the Monbetsu River. Back (A) and left side (B) views, $\times 0.5$. Arrow mark indicates the beginning of body chamber. Bar scale: 20 mm. Photos by K. Shinohara.

chamber for more than a quarter whorl, but its right side and its ventral part is more or less eroded and partly destroyed. In spite of the incomplete preservation, it shows to some extent important characters of the species.

Should the body chamber be assumed as half a whorl as in other well preserved specimens of *Sharpeiceras*, the entire shell diameter would be more than 300 mm, i.e. nearly as large as *S. kongo* Matsumoto, Muramoto and Takahashi, 1969 (p. 261, pl. 29, fig. 1; pl. 30, fig. 1).

The shell is rather evolute, but the rate of whorl expansion is fairly high. The umbilical ratio (U/D) is moderate at maturity (0.36-0.37) but is low in earlier stages (≤ 0.30 ; Table 1). Whorl section is subrectangular, higher than broad and roughly parallel-sided, with an abruptly bent umbilical shoulder and a low but nearly vertical umbilical wall (Figure 2).

On the inner whorl ribs are numerous and dense, with frequent bifurcation at the umbilical tubercle or with intercalation at variable distance from the umbilical edge (Figure 1). Each rib has also mid-lateral, outer and inner ventrolateral tubercles. Many ribs are gently flexuous or weakly bent at the tubercle, but some are weakly prosirradiate or nearly rectiradiate. In the late part of the septate stage, for about half a whorl, the ribs become single and gradually separated. On the adult body chamber the ribs are strong, thick and distantly spaced, but some of them continue to be weakly flexuous; the tubercles also strengthen. The umbilical tubercles on the main part of the body chamber are spinose and upright, as is observable on YKC 060625 (Figure 2). The lateral tubercles are bullate; the rounded inner and clavate outer ventrolateral tubercles tend to share a common base, but are not completely united

Table 1. Measurements of *Sharpeiceras mexicanum* (above) and *S. laticlavium* (below).

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
MCM T260 (E)	~270	96.0	.36	117.0	.43	88.0	.33	.75	1.75
MCM T260 (LS, ic)	~212	78.0	.37	86.0	.41	~64	.30	.74	~1.79
HT (Böse)	119.8	36.3	.30	54.8	.46	~38	.32	.69	—
Howarth, fig. 20	127.0	34.0	.27	55.4	.44	38.2	.30	.69	1.47
Mancini	—	—	—	46.5	—	34.1	—	.73	—
HT (E, c)*	130	34	.26	59	.45	50	.38	.85	1.45

D=diameter, U=width of umbilicus, H=whorl height, B=whorl breadth, h=whorl height at half a whorl back from measured H, HT=holotype, E=preserved end, LS=last septum, c=costal, ic=intercostal, ~≈approximate, Linear dimensions in mm. * Measured by T.M.

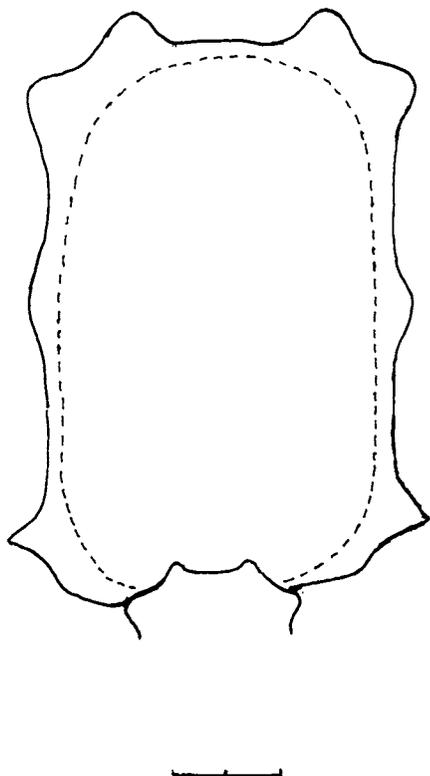


Figure 2. *Sharpeiceras mexicanum* (Böse). Restored cross-section of the adult body chamber, based on MCM T260 and YKC 060625. Bar scale: 20 mm.

and not horned.

The suture is partly observable.

Dimensions.—See Table 1.

Comparison and discussion.—The characters of the inner whorl of the specimens described above are well comparable with those of the holotype and other examples of *Sharpeiceras mexicanum* from Mexico (Böse, 1928), Texas (Young and Powell, 1976; Mancini, 1982) and Angola (Howarth, 1985). In these hitherto reported specimens the characters of the adult body chamber were not well shown. Mancini's specimen shows the change in the mode of ribbing from the dense and bifurcated or intercalated state on the younger whorl to the single, gradually separated state,

but it lacks the body chamber. In our specimen a similar change of ornament is observable in the late part of the phragmocone, and on the adult body chamber the ribs strengthen and become widely spaced.

The holotype of *Sharpeiceras laticlavium* (Sharpe, 1855, p. 31, pl. 14, fig. 1) (refigured by Wright and Kennedy, 1987, pl. 41, fig. 4), which one of us (T.M.) examined in London, is a wholly septate internal mould and 130 mm in diameter. One of the figured specimens of *S. mexicanum* from Angola (Howarth, 1985, fig. 20) is similar to that holotype in lateral view of the shell shape and the rib density. The holotype of *S. mexicanum*, as illustrated by Wright and Kennedy (1987, text-fig. 31), seems to have somewhat more crowded ribs. Thus, Böse may have been reasonable in regarding the specimen from Mexico as a variety of Sharpe's species. There is, however, a considerable difference in the proportion of B/H; namely, 0.69 in the specimens of Böse and Howarth as compared with 0.84 in Sharpe's holotype (See Table 1). Furthermore, the ribs in the early growth stages are frequently bifurcated at the umbilical bullae or have intercalated ones and are often gently sinuous in *S. mexicanum*. In contrast they are mostly, if not exclusively, single and straight in *S. laticlavium*. In these respects of the ribbing in earlier growth stages our specimen from Hokkaido is certainly identical with *S. mexicanum*.

The ratio of B/H in the measured parts of Mancini's and Hokkaido specimens is somewhat higher (0.71-0.75) than that of Böse's holotype (0.69), but this is for the whorl of later growth stages. It is undoubtedly lower than B/H value at the last part of the holotype of *S. laticlavium*.

We do not know the ornament on the adult body chamber of Sharpe's holotype. Hyatt's specimen illustrated by Wright and Kennedy (1987, text-fig. 30) shows a near-adult phragmocone plus the beginning of the body chamber of *S. laticlavium*. More recently Marcinowski *et al.* (1996, pl. 13, fig. 1) have illustrated a fine specimen of *S. laticlavium* from the Lower Cenomanian of Kazakhstan, in which the adult body chamber is fully preserved. In these two examples of late growth stage the ribs very gradually become coarser and are separated by interspaces slightly wider than the ribs. In our specimen of *S. mexicanum* the ribs are much stronger and more distantly spaced at the corresponding growth stage.

Strictly speaking, the available material from a particular stratigraphic unit of a given area is not sufficient for forming

an adequate concept of a species. Tentatively, *S. mexicanum* is regarded as allied to but distinct from *S. laticlavium*.

S. mexicanum is undoubtedly more compressed and shows a higher rate of whorl expansion than *S. florencae* Spath, 1925 (p. 198, p. 37) (see also Howarth, 1985). The latter has more rigid ribs and stronger tubercles; of which the ventrolateral ones on the adult body chamber may become horn-like.

Occurrence.—As for material. The Upper Cretaceous sequence in the Hirotsu area of the Monbetsu Valley is provisionally subdivided into Members A1, A2, B, C1, C2, and D by A. Inoma (personal information), as indicated by Matsumoto *et al.* (1997, fig. 1). The specimen described above came from Member A1 (mudstone) in the Chennai-zawa, a short branch rivulet of the Monbetsu River, southern-central Hokkaido. *Desmoceras* (*Pseudouhligella*) *japonicum* Yabe, *Parajaubertella kawakitana* Matsumoto and *Gabbioceras*

yezoense Shigeta are among the main associates. Member A1 is, hence, most probably assignable to the Lower Cenomanian.

Outside Japan, *S. mexicanum* has been recorded from the Lower Cenomanian of Mexico (Buda Limestone), Texas (Buda Limestone and Grayson Formation) and Angola.

***Sharpeiceras kikuae* Matsumoto and Kawashita, 1995**

Figures 3 and 4

Sharpeiceras kikuae Matsumoto and Kawashita, *In* Nishida *et al.*, 1995, Appendix, p. 186, pl. 5, figs. 1a, b.

Remarks.—This species was established in an appendix to a stratigraphic paper of Nishida *et al.* (1995) written in Japanese. Although the palaeontologic description was in English, it seems to have been little noticed. For this reason

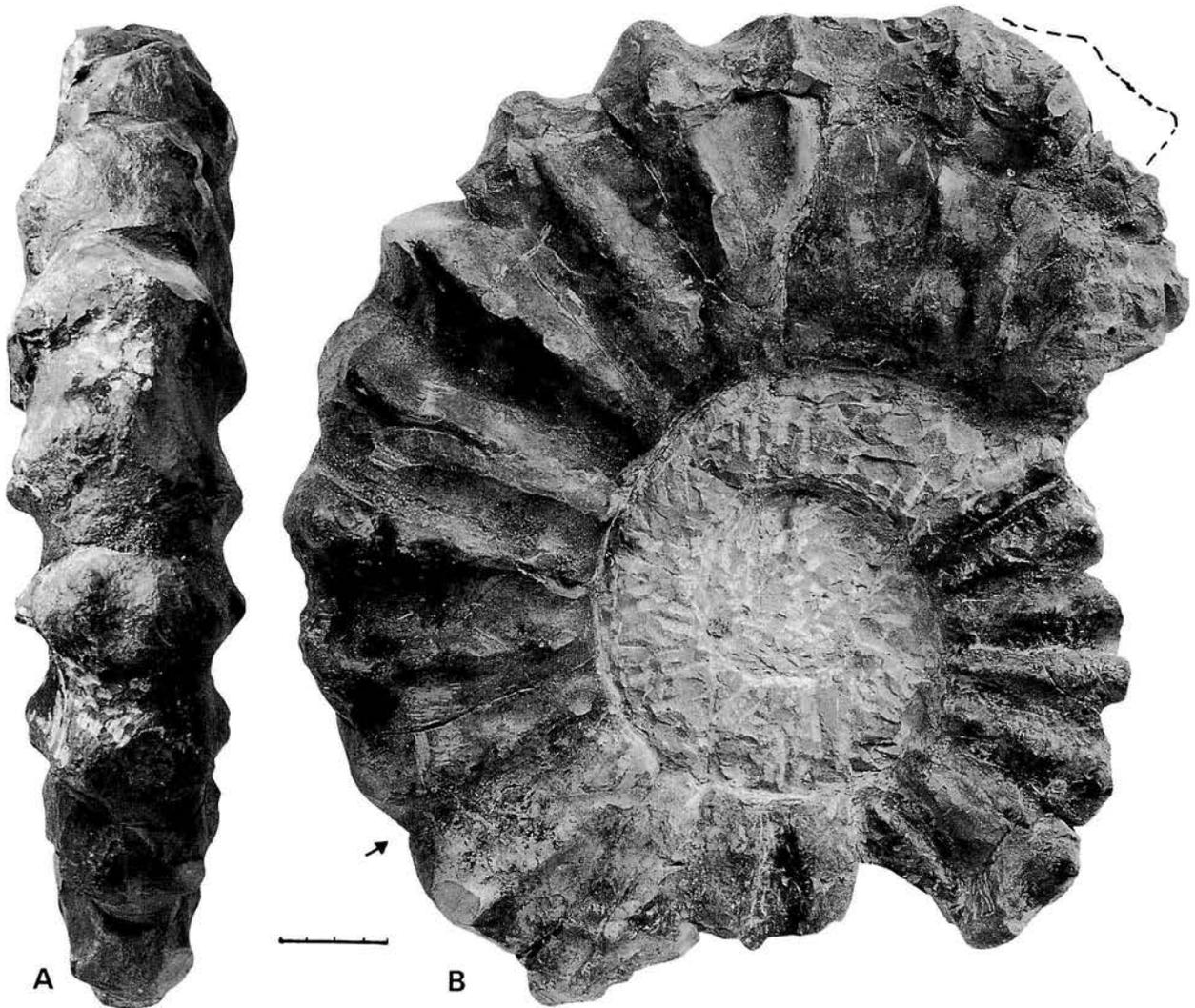


Figure 3. *Sharpeiceras kikuae* Matsumoto and Kawashita. Holotype, MCM T244 [=previous YKC 060628] from loc. Y5091, Oyubari area. Back (A) and left side (B) views, $\times 0.375$. Arrow mark same as in Fig. 1. Bar scale: 40 mm. Photos by K. Shinohara.

this species is redescribed and supplemented herein, in agreement with the Editor and the senior author (T. Nishida) of the original paper.

Material.—Holotype is MCM T244 [=previous YKC 060628] (Figures 3 and 4A) obtained at loc. Y5091 on the right side of the Shirakin River of the Oyubari area, central Hokkaido. It was embedded in a stratum of mudstone at about the middle (horizon Y5091B) of the outcrop as long as 70 m. Also two other fragmentary pieces of a large body chamber [YKC 090523] (Figure 4B) are in the subsequent acquisition by Y.K. at loc. S901, left side of the same river, about 700 m upstream from loc. Y5091. The above two localities are indicated in a paper by Nishida *et al.* (1993, figs. 1, 4). The Shirakin River is called the synonymous Hakkinzawa in that paper.

Diagnosis.—Shell very large, rather evolute and ornamented by moderately to fairly widely spaced, strong, rectiradiate ribs on the outer whorl; each rib provided with two lateral tubercles. The main part of the adult body chamber suboval in section, with somewhat convex flanks and sloping umbilical wall; septate whorl subrectangular in section.

Description.—The shell is very large, showing a fairly wide umbilicus, evolute coiling and a rather moderate rate of whorl expansion (Figure 3). The septate whorl is subrectangular in section, somewhat higher than broad: the body chamber, which occupies half a whorl, is ovate in intercostal section with somewhat convex flanks and sloping umbilical wall (Figure 4A, B).

The ribs on the late part of the phragmocone and the adult body chamber are mostly single, strong, rectiradiate and moderately to fairly widely separated. The umbilical bulla is pointed at the umbilical edge; the two lateral tubercles are bullate, with the normal one at about the mid-flank and the smaller one on the outer flank; the inner ventrolateral tubercle is the most prominent and the outer one is clavate; they are somewhat thickened and on the body chamber tend to have a common base (Figure 4B). The ribs and tubercles are strongest in the middle part of the body chamber. A few ribs on the adoral part of the body chamber are narrower and less strong (Figure 3).

The ornamentation of the inner whorl is not well shown because of the poor preservation. The ribs seem to be somewhat denser and narrower.

The sutures are exposed here and there and follow the general pattern of *Sharpeiceras*.

Dimensions.—See Table 2.

Comparison and discussion.—In the stout ornament and the general outline of the whorl section this species is similar to *Sharpeiceras florencae* Spath (1925, p. 198, pl. 37), from Mozambique, Angola and other regions (see Howarth, 1985, p. 88), but it has a distinctly wider umbilicus. Its adult body chamber is oval in section instead of the thickly rectangular one of *S. florencae*. The two lateral tubercles are very clear in *S. kikuae*, in contrast to one lateral tubercle in the holotype of *S. florencae*. An example illustrated by Howarth (1985, fig. 17) seems to show a tendency to the doubling of a lateral tubercle, but that is by no means distinct.

On the grounds of the above comparison, we have regarded the described specimen as a species which is allied to but distinct from *S. florencae*.

S. kikuae may be allied to *S. mocambiquense* [= *Acanthoceras laticlavium* var. *mocambiquense* Choffat, 1903, p. 25, pl. 4, fig. 3; pl. 7, fig. 2] in the large size and the two lateral tubercles. The specimen from Mozambique is flat-sided, whereas our specimen has somewhat convex sides and coarser and stronger ornament from a late septate stage onward. With respect to the measured proportions of U/D (Table 2) *S. mocambiquense* is more similar to *S. florencae* than to *S. kikuae*, but the former seems to be allied to *S. schlueteri* Hyatt (see Wright and Kennedy, 1987, p. 130). At any rate the available material is insufficient for a definite conclusion.

Occurrence.—As for material. Loc. Y5091 is an outcrop of steeply inclined dark gray mudstone with some intercalated thin layers of sandstone for a distance of 70 m on the right side of the Shirakin River. The exposed part is assigned to the lower part of the Middle Yezo Subgroup. *Desmoceras* (*Pseudouhligella*) cf. *japonicum* occurs commonly there. In the eastern part of the outcrop *Inoceramus* aff. *reachensis* Etheridge (see Nishida *et al.*, 1993, pl. 6, fig. 1) occurs commonly. The exposed part is, thus, probably the Lower Cenomanian. Loc. S901 on the eastern limb of an anticline is nearly at the same stratigraphic level as loc. Y5091 and "*Sharpeiceras* aff. *vohipalense* Collignon" was reported to occur there (Matsumoto and Suekane, 1987, p. 3, pl. 1, figs. 1-3); also *Inoceramus* aff. *reachensis* [= "*I. virgatus* Schlüter"

Table 2. Measurements of *Sharpeiceras kikuae* (above) and three other species. I: *S. florencae*, II: *S. schlueteri*, and III: *S. mocambiquense*.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h	R
MCM T244 (M, c)	~348	140	.40	128	.37	~96	.28	.75	1.60	12
I. HT (E, c)*	220	69	.31	86	.39	—	—	—	1.32	9
I. HT (LS, ic)*	~165	56	.34	63	.38	54	.33	.86	1.37	13
Howarth, fig. 15	—	—	—	79	—	63.5	—	.80	—	>9
II. LT (~)	348	135	.39	123	.35	102	.29	.83	1.37	13
III. HT (E-150°, ic)	350	100	.29	132	.38	96	.27	.73	1.38	12

M=at the middle of the adult body chamber; LT=lectotype, R=number of ribs per half a whorl. Other abbreviations same as in Table 1.

* Measurements on the illustration of Spath (1925, pl. 37). They are not quite conformable with his indication (*op. cit.*, p. 198) of relative proportions.

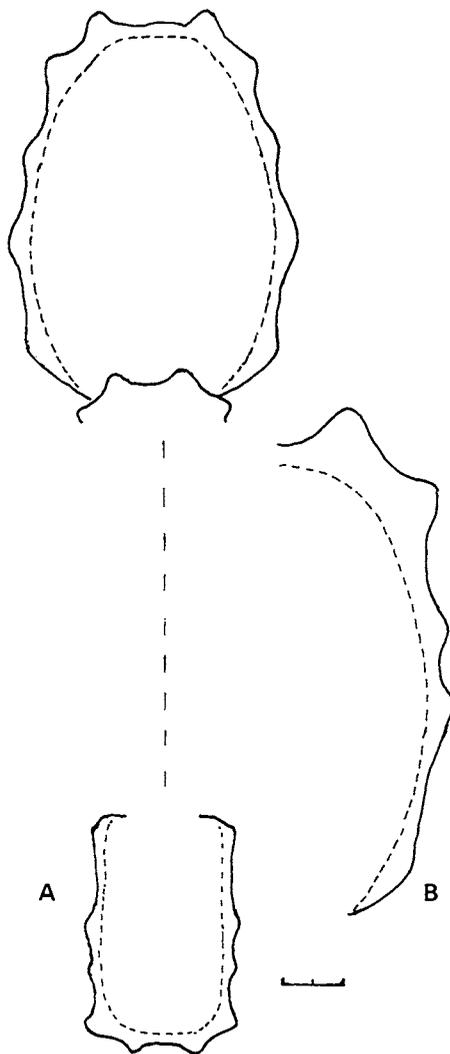


Figure 4. *Sharpeiceras kikuae* Matsumoto and Kawashita. **A:** Diagrammatic section of the holotype across the middle part of the adult body chamber (above) and that of the septate part half a whorl adaptically from it. **B:** Sectional view (sketch) of a fragmentary piece (left half) of a large body chamber [YKC 090523] from loc. S901, showing the convex flank and the disposition of the tubercles. Bar scale: 20 mm.

of Matsumoto *et al.* (1987, fig. 8-2 only)] was found at a nearby locality.

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Early to Middle Devonian Ceratoikiscidae (Radiolaria) from the Yokokurayama Group in the Kurosegawa Terrane, Southwest Japan

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Abstract. This paper focuses on ceratoikiscid radiolarians from the Devonian Nakahata Formation of the Yokokurayama Group in the Kurosegawa Terrane. The fauna is assigned to the Emsian to Eifelian (late Early to early Middle Devonian). There are 13 species of radiolarians, including 4 new species, which belong to the genera *Ceratoikiscum*, *Glanta*, *Protoholoeciscus*, *Circulaforma* and *Helenifore*. The morphology and stratigraphic distribution of the genera suggest that *Protoholoeciscus* evolved from *Ceratoikiscum* via *Glanta* with the process of acquisition of shell.

Key words : Ceratoikiscidae, Early to Middle Devonian, Kurosegawa Terrane, Radiolaria, Yokokurayama Group

Introduction

Ceratoikiscidae characterized by triangular skeletal framework is one of the guide taxa for Middle Paleozoic radiolarian biostratigraphy. In recent years, many species of Late Devonian Ceratoikiscidae have been described from various localities of the world and keen interest has been focused on setting up the Upper Devonian radiolarian zones (Cheng, 1986; Schwartzapfel and Holdsworth, 1996). From the Lower to Middle Devonian, reports of occurrences of Radiolaria have quite recently been accumulating (Wakamatsu *et al.*, 1990; Umeda, 1996, in press b; Stratford and Aitchison, 1997). Four Lower to Middle Devonian radiolarian zones are proposed from the Kurosegawa Terrane (Umeda, in press a). However, paleontological research of Early to Middle Devonian Ceratoikiscidae is still insufficient.

Many species of Ceratoikiscidae, belonging to the genera *Ceratoikiscum*, *Glanta*, *Protoholoeciscus*, *Circulaforma* and *Helenifore*, were found from the Lower to Middle Devonian Nakahata Formation of the Yokokurayama Group in the Kurosegawa Terrane. The radiolarians are described and phylogenetic significances of these species are discussed in this paper.

Well-preserved radiolarians were obtained from some horizons of the sections examined in this study (Figures 5, 7, 8). The studied radiolarians are listed in Table 1. The collected rock samples were put into a bowl with 5% HF solution for 24 hours. The residues were gathered on a 200 mesh sieve. Radiolarians were picked with a very fine

brush under a binocular microscope, and observed with a scanning electron microscope. Type and figured specimens are registered and deposited in the Department of Geosciences, Osaka City University.

Geologic setting

The Kurosegawa Terrane of the Outer Zone of Southwest Japan is situated as a klippe upon the Jurassic accretionary complex of the Chichibu Belt (Figure 1-A). Paleozoic unmetamorphosed sedimentary strata are widely distributed in the Kurosegawa Terrane. Siluro-Devonian strata have been known from the Yokokurayama area (Figure 1-B) and were named as the Yokokurayama Group (Hirata, 1966).

The Yokokurayama Group is subdivided into six formations, namely the Gomi, Fukata, Ichiyama, Joryu, Nakahata and Ochi formations in ascending order (Umeda, 1998). The Nakahata Formation consists of acidic tuff, mudstone, tuffaceous sandstone and conglomerate. Rock samples for radiolarian research were collected from the acidic tuff and mudstone layers of Sections A, B and C in the Nakahata Formation (Figures 2, 3).

Estimated thickness of Section A is about 23 m. Section A consists of acidic tuff layers and tuffaceous sandstone layers (Figures 3, 4). The acidic tuff layers are composed of vitric tuff layers of 3 to 7 cm thickness, and are rhythmically interbedded with tuffaceous mudstone layers. Color of the tuff is green, dark green, gray and red. A single tuffaceous mudstone layer ranges from several millimeters to several

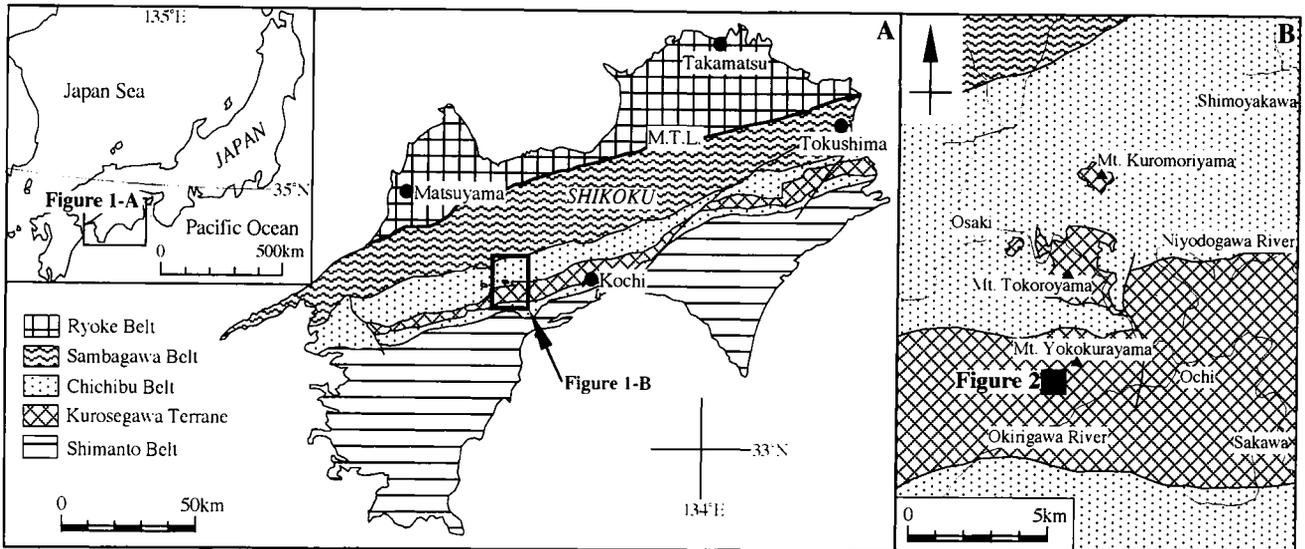


Figure 1. Index map showing the study area.

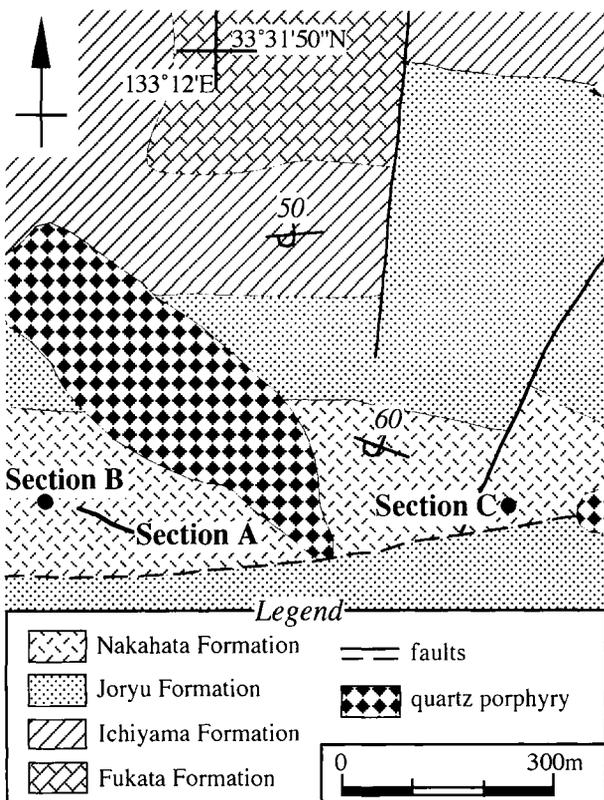


Figure 2. Geologic map and distribution of the examined sections.

centimeters thick and the color is white, yellow, light red and dark red. The tuffaceous sandstone is light green and fine- to medium-grained. Section B, about 4 m thick, is composed of dark red mudstone layers and green to red vitric tuff layers. Estimated thickness of Section C is about 6 m. Rocks of Section C consist of light green vitric acidic tuff

layers and tuffaceous sandstone layers. A bed of the tuff is 5 to 20 cm in thickness. Parallel laminations are commonly observed in acidic tuff and tuffaceous sandstone layers. The acidic tuff and mudstone include many radiolarian remains and sponge spicules. The reddish vitric tuff comprises volcanic glasses in abundance.

Radiolarian zones and age

Four Early to Middle Devonian radiolarian zones, namely the *Futobari solidus*, *Trilonche* (?) sp. A, *Glanta fragilis* and *Protoholoeciscus hindea* zones in ascending order, have been proposed recently (Umeda, in press a). The lower part of Section A (2F to 3A) and the lower to middle part of Section B (37C and 37D) are assigned to the *G. fragilis* Zone. The upper part of Section A (3B to 3N) and the upper part of Section B (37E) are assigned to the *Pr. hindea* Zone. *Protoholoeciscus triangularis* (Wakamatsu, Sugiyama and Furutani) and *Glanta yokokurayamaensis* sp. nov. in Section C possess bladed rods, while the rods of *Glanta* and *Protoholoeciscus* in Sections A and B are circular in cross section. Bladed rods can be regarded as a rather evolved feature (Nazarov and Ormiston, 1985). This evidence suggests that Section C is situated at a higher stratigraphic level than the *Pr. hindea* Zone. The *G. fragilis* Zone is assigned to the Emsian to Eifelian (late Early Devonian-early Middle Devonian) and the *Pr. hindea* Zone to the Eifelian.

Systematic paleontology

Subclass Radiolaria Müller, 1858

Order Polycystina Ehrenberg, 1838, emend. Riedel, 1967

Suborder Albaillellaria Deflandre, 1953, emend. Holdsworth, 1969

Family Ceratoliscidae Holdsworth, 1969

Genus *Ceratoliscum* Deflandre, 1953

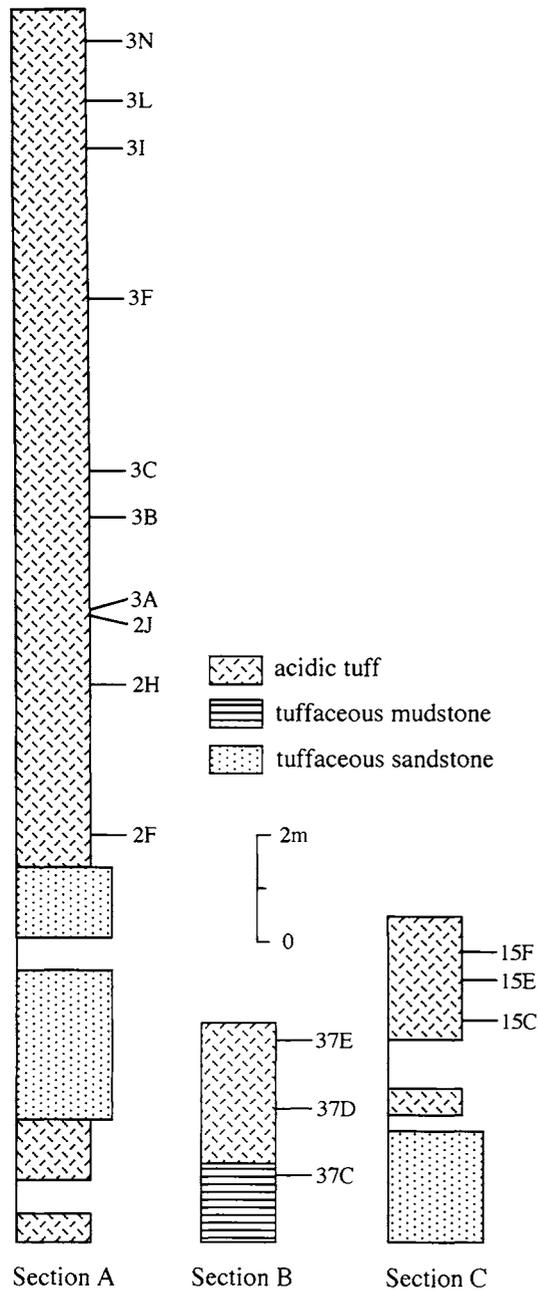


Figure 3. Columnar sections of the examined sections showing lithologic and sampling horizons.

Ceratoikiscum lyratum Ishiga, 1988

Figures 5-1—3

Ceratoikiscum lyratum Ishiga, 1988, p. 74, pl. 1, figs. 4-5; Ishiga, 1992, p. 392-395, fig. 9, 1-6; Aitchison, Hada, Ireland and Yoshikura, 1996, p. 59, pl. 1-3, 4; 3-4, 5; Umeda, 1997, p. 21, pl. 1, figs. 15-18, pl. 3, figs. 10-13.

Ceratoikiscum vimineum Wakamatsu, Sugiyama and Furutani, 1990, p. 179-180, pl. 1, figs. 1-5; Furutani, 1996, fig. 7, 6.

Ceratoikiscum sp. Aitchison, Hada and Yoshikura, 1991, fig. 3,

A-B.

Material.—Ten specimens from 2F, 3A, 3I, 3N in Section A, 37C and 37D in Section B and 15E in Section C.

Remarks.—This species possesses a developed patagium and long and slender extratriangular rods.

Range and occurrence.—Late Silurian to Middle Devonian time. The Upper Silurian and Lower Devonian in the Konomori area, central Kochi (Ishiga, 1988, 1992; Aitchison *et al.*, 1991, 1996; Umeda, 1997) and the Nakahata Formation in the Yokokurayama area (Wakamatsu *et al.*, 1990; Furutani, 1996), both in the Kurosegawa Terrane, Southwest Japan.

Ceratoikiscum turgidum sp. nov.

Figures 5-4, 5

Diagnosis.—This species is characterized by a well-developed lamellar patagium with a porous swell around the junction of a- and i-rods.

Description.—A distinctive swell is thick and spongy. Pores on the swell are circular to oval. Lamellar patagium is perforated and developed in horizontal plane. A.t., b.t. and i.t. (see Figure 6) rim the interior sides of the lamellar patagium. Central opening is subtriangular to suboval. Patagial tissue is weakly developed around the junction of b- and i-rods. A- and b-rods are curved and i-rod is much straighter. A.a. and b.d. are sturdy and long. B.v. and i.v. are short and rather conical. All rods are circular in cross section. Caveal ribs remain uncertain.

Measurements.—Measured features are shown in Figure 6-a.

Length of w.c.: 109-126, average 118, based on 4 specimens, in μm .

Material.—Four specimens from 37C in Section B and 15E in Section C.

Comparison.—This species differs from other species of *Ceratoikiscum* in having a thick swell around the junction of a- and i-rods. This species bears resemblance to *C. kochiense* Umeda in possessing developed lamellar patagium. This also is similar to *Glanta fragilis* Wakamatsu, Sugiyama and Furutani in having developed lamellar patagium, sturdy a.a., short b.v. and i.v., but it differs from *Glanta* in lacking a shell.

Range and occurrence.—Possible Emsian age (late Early Devonian time) to Eifelian age (early Middle Devonian time). Nakahata Formation of the Yokokurayama Group.

Etymology.—This name is derived from the Latin adjective *turgidus*, meaning inflated.

Type specimen.—Holotype OCU PR 0137 (Figure 5-4) from 37C.

Genus ***Glanta*** Wakamatsu, Sugiyama and Furutani, 1990; emend. herein

Type species.—*Glanta fragilis* Wakamatsu, Sugiyama and Furutani, 1990, p. 180-181, pl. 12.

Emended diagnosis.—Triangular skeletal framework with bilaterally symmetric porous shell which is situated between

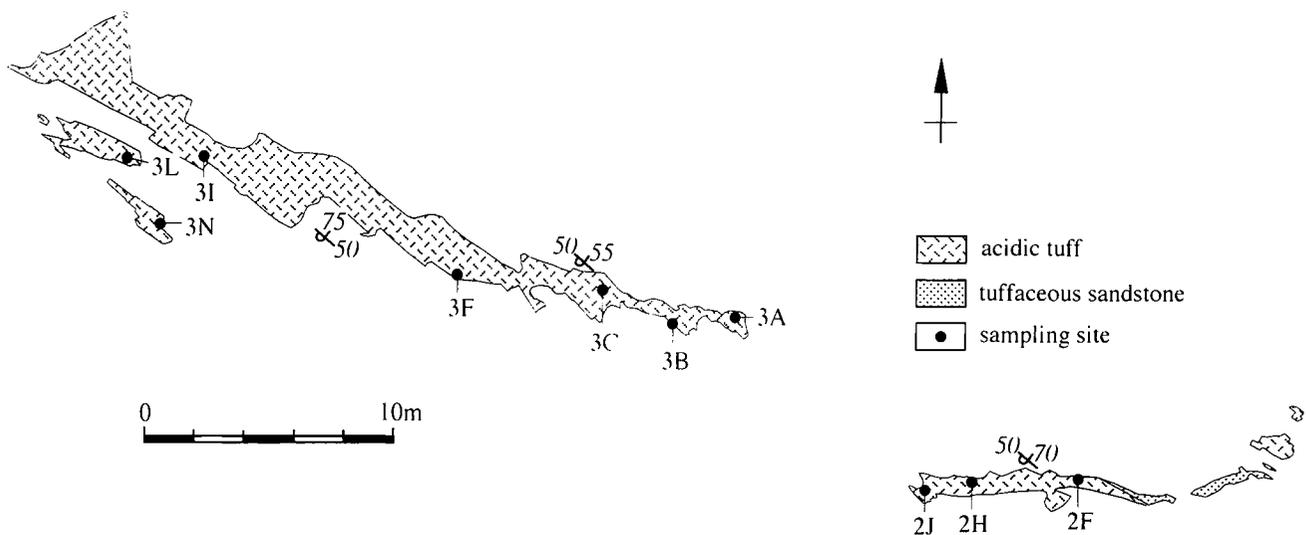


Figure 4. Route map of the Section A showing sampling sites.

Table 1. List of studied radiolarian fossils from the Nakahata Formation in the Yokokurayama Group.

RADIOLARIA \ SAMPLE NO.	Section A									Section B			Section C			
	2F	2H	2J	3A	3B	3C	3F	3I	3L	3N	37C	37DF	37E	15C	15E	15F
<i>Ceratoikiscum lyratum</i> Ishiga	+			+				+		+	+	+			+	
<i>C. turgidum</i> sp. nov.											+				+	
<i>Glanta fragilis</i> Wakamatsu, Furutani and Sugiyama	+	+	+	+							+	+	+			
<i>G.</i> sp.											+					
<i>G. yokokurayamaensis</i> sp. nov.														+	+	+
<i>Circulaforma</i> (?) sp. aff. <i>C.</i> sp. A														+	+	+
<i>Helenifora</i> sp. A Stratford and Aitchison								+	+	+				+	+	+
<i>He.</i> sp. B											+					
<i>Protoholoeciscus</i> sp.													+		+	
<i>Pr. hindea</i> Aitchison						+	+	+	+	+			+			
<i>Pr. spinosus</i> sp. nov.						+	+		+	+						
<i>Pr. ochiensis</i> sp. nov.														+	+	+
<i>Pr. triangularis</i> (Wakamatsu, Furutani and Sugiyama)														+	+	+

b.d. and i.d. or i.t.

Remarks.—Wakamatsu *et al.* (1990) described the new genus *Glanta* which has a porous or lamellar shell. Central framework is triangular with five to six extratriangular rods. A.t. and the dorsal portion of i.t. are covered by the shell (Wakamatsu *et al.*, 1990). Later, Aitchison (1993) separated a species with lamellar shell from *Glanta* as a new genus *Protoholoeciscus*. Stratford and Aitchison (1997) suggested that the species of *Glanta* described by Wakamatsu *et al.* (1990) might be best placed within *Protoholoeciscus*, which can be differentiated from *Glanta* on the basis of its having an imperforate shell.

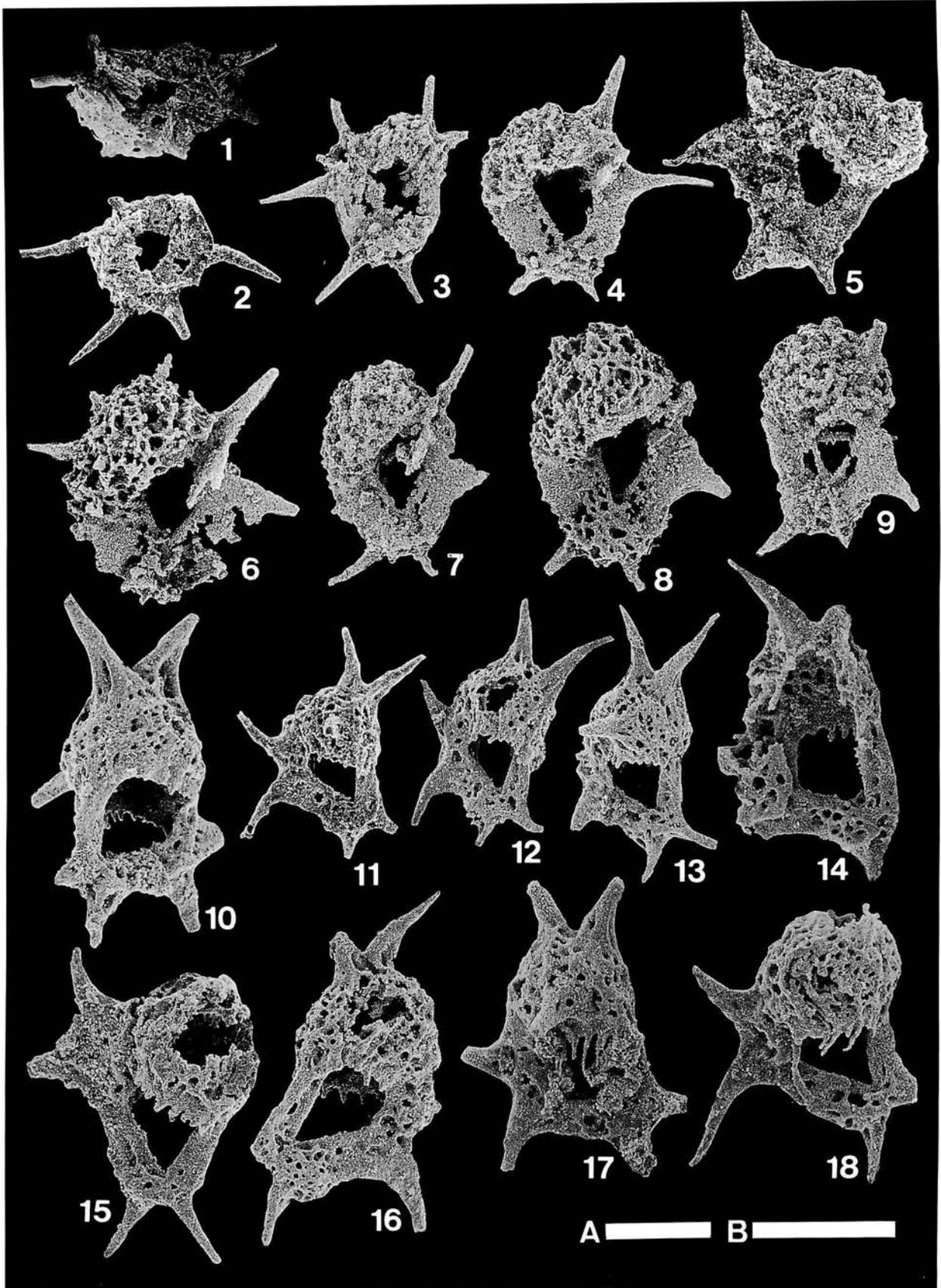
Glanta fragilis Wakamatsu, Sugiyama and Furutani, 1990

Figures 5–6—8

Glanta fragilis Wakamatsu, Sugiyama and Furutani, 1990, p. 180–181, pl. 12; Furutani, 1996, fig. 7–10, 11; Furutani, 1997, pl. 1, fig. 11.

Glanta sp. A Furutani, 1996, p. 76, fig. 7–8, 9.

Description.—Shell is suboval in anterior view and subtrapezoidal in lateral view. Subcircular basal aperture of the ventral portion of the shell faces a subtriangular to suboval central opening. A.t. and the dorsal part of i.t. are covered with the shell. A.a. is long, flat and tapered distally. B.d. is longer and thicker than i.d.. B.t. and i.t. rim the interior side of the lamellar patagium which is well-developed, wide and



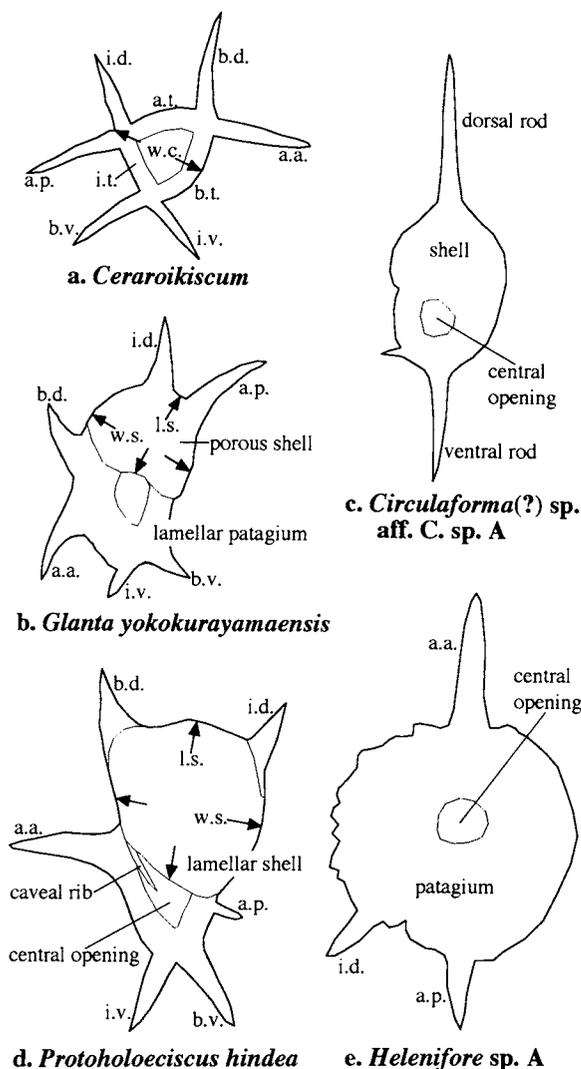


Figure 6. Terminology of skeletal structures of Devonian Ceratoikiscidae. a.a.: a-rod, anterior portion, a.p.: a-rod, posterior portion, a.t.: a-rod, triangle-forming portion, b.d.: b-rod, dorsal portion, b.v.: b-rod, ventral portion, b.t.: b-rod, triangle-forming portion, i.d.: i-rod, dorsal portion, i.v.: i-rod, ventral portion, i.t.: i-rod, triangle-forming portion, l.s.: length of shell, w.s.: width of shell.

flat. The junction of b- and i-rods is ornamented with patagial tissue. Pores on the shell and patagial tissue are circular to oval in shape and variable in size. A pair of caveal ribs extends from the junction of a- and b-rods.

Material.—26 specimens from 2F to 3A of Section A and from 37C to 37E in Section B.

Range and occurrence.—Possible Emsian to Eifelian age. Nakahata Formation in the Yokokurayama Group.

***Glanta* sp.**

Figures 5-9

Description.—Porous shell develops at the dorsal side of a.t. The shell is suboval in anterior view and trapezoidal to suboval in lateral view. B.d. and i.d. connect with the shell and are enveloped in the lateral margin of the shell. The junction of b- and i-rods is ornamented with patagial tissue. Pores on the shell and the patagial tissue are circular to subcircular in shape and variable in size. A.t., b.t. and i.t. form an equilateral triangle in the central opening. Basal aperture faces to the central opening. The lamellar patagium is well developed and flat. A.a. is sturdy, rather flat and long. B.v. and i.v. are short and rather conical. B.d. is longer and thicker than i.d.. Caveal ribs remain uncertain.

Material.—Two specimens from 37C in Section B.

Remarks.—This species is similar to *G. fragilis* Wakamatsu, Sugiyama and Furutani in having porous shell, but it differs by having a.t. in the central opening.

Range and occurrence.—Possible Emsian to Eifelian age. Nakahata Formation in the Yokokurayama Group.

***Glanta yokokurayamaensis* sp. nov.**

Figures 5-10—18

Diagnosis.—Porous shell covers a.t. and dorsal part of i.t. I.d., a.p. and a pair of spines extending from the shell are robust and their bases are bladed.

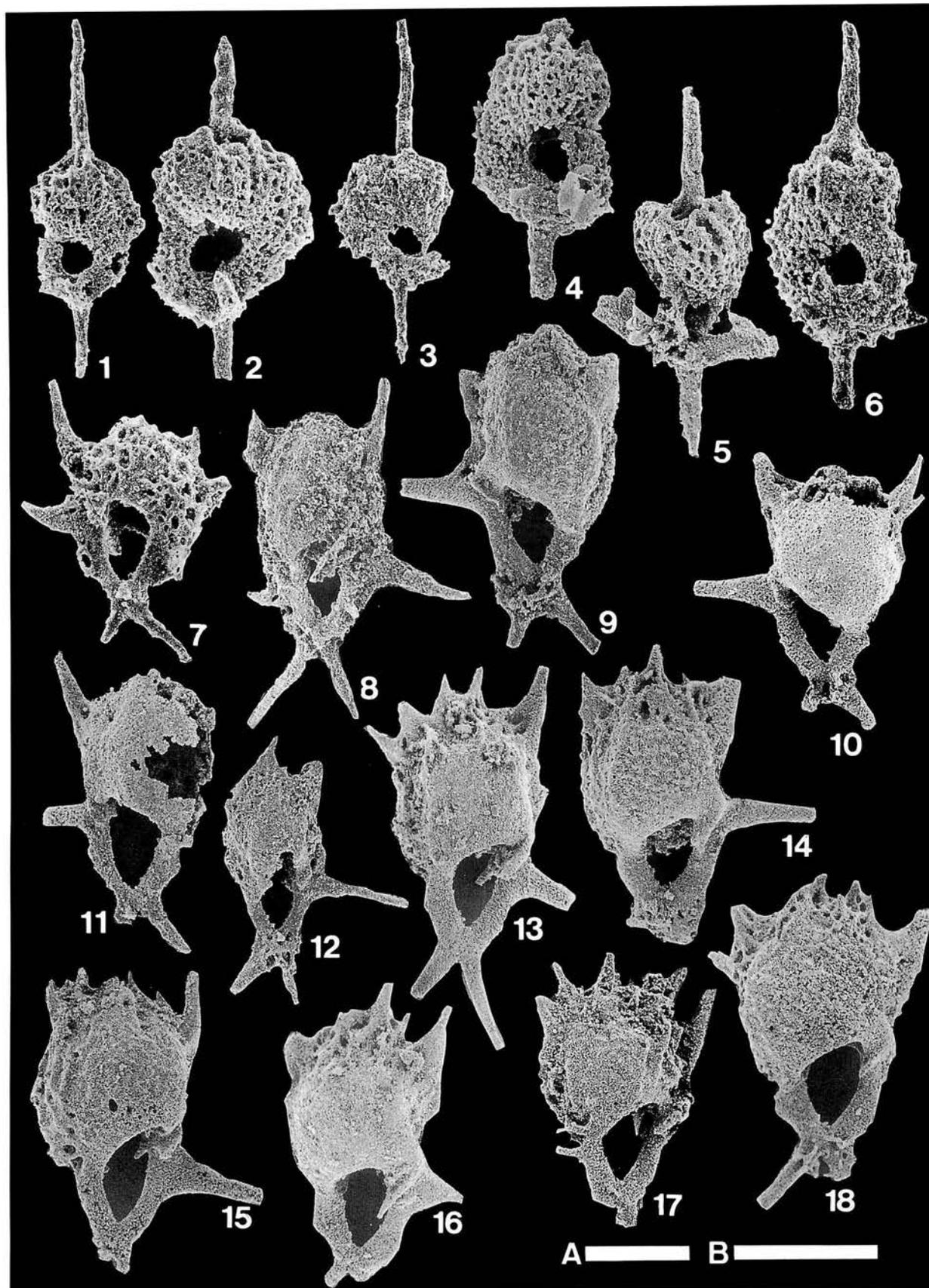
Description.—Shell is oval in anterior view and trapezoidal form in lateral view. The ventral margin of the shell is serrated. Several pairs of caveal ribs are traceable along the surface of the shell. Pores on the shell are circular to subcircular in form and irregular in size. Subcircular basal aperture faces central opening. B.t. and i.t. connect with the interior sides of lamellar patagium. The lamellar patagium with several pores is well developed and flat. Patagial tissue is often developed around the junction of b- and i-rods. Extratriangular rods are sturdy. A pair of spines, extending from the central part of the shell bilaterally symmetrically in an almost vertical plane, is thick and long. The spines and the extratriangular rods are tapered distally. I.d., a.p. and the spines are bladed at the base.

Measurements.—Measured features are shown in Figure 6-b.

Length of shell: 65-88, average 74, based on 25 specimens, in μm .

Width of shell: 85-100, average 92.

Figure 5. 1-3. *Ceratoikiscum lyratum* Ishiga, 1: OCU PR 0134, 3N, 2: OCU PR 0135, 15E, 3: OCU PR 0136, 37C. 4, 5. *Ceratoikiscum turgidum* sp. nov., 4: OCU PR 0137, 37C, holotype, 5: OCU PR 0138, 15E. 6-8. *Glanta fragilis* Wakamatsu, Furutani and Sugiyama, 6: OCU PR 0139, 2J, 7: OCU PR 0140, 37C, 8: OCU PR 0141, 3A. 9. *Glanta* sp., OCU PR 0142, 37C. 10-18. *Glanta yokokurayamaensis* sp. nov., 10: OCU PR 0143, 15C, holotype, 11: OCU PR 0144, 15E, 12-18: OCU PR 0145-51, 15C. Scale bar is 100 μm , A: 1-3, 11-13, B: 4-10, 14-18.



Material.—27 specimens from 15C, 15E and 15F in Section C.

Comparison.—This species differs from other species of *Glanta* in having robust and bladed i.d., a.p. and spines extending from the shell.

Range and occurrence.—Possible Eifelian age. Nakahata Formation of the Yokokurayama Group.

Etymology.—From the name of Mt. Yokokurayama, the study area.

Type specimen.—Holotype OCU PR 0143 (Figure 5-10) from 15C.

Genus *Circulaforma* Cheng, 1986

Circulaforma sp. aff. *C.* sp. A Stratford and Aitchison, 1997

Figures 7-1—6

Description.—Specimens possess elongate ring-like shell with three rods. The dorsal portion of the shell is large and oval in posterior and lateral view. Subcircular basal aperture faces to oval central opening. Pores on the shell are circular to subcircular in shape and irregular in size. The internal structure of the shell is not observed. Ventral and dorsal rods are prominent, opposite, long, sturdy, mostly straight and blunt at end. The ventral rod is longer than the dorsal rod. The third subsidiary rod is thin, delicate and short. All rods are circular in cross section. A pair of spines extends from the junction of the shell and basal rod bilaterally symmetrically in an almost vertical plane.

Measurements.—Measured features are shown in Figure 6-c.

Axial diameter of shell : 115-160, average 136, based on 10 specimens, in μm .

Axial diameter of central opening : 25-35, average 30.

Length of dorsal rod : 115-140, average 127.

Length of ventral rod : 60-80, average 72.

Material.—Ten specimens from 15C, 15E and 15F in Section C.

Comparison.—This form is similar to *Circulaforma* sp. A Stratford and Aitchison in having two opposite long rods and a ring-like fabric, but differs in the presence of developed shell at the dorsal portion. The assignment of this species to the genus *Ceratoikiscum* is difficult.

Range and occurrence.—Possible Eifelian age. Nakahata Formation in the Yokokurayama Group.

Genus *Protoholoeciscus* Aitchison, 1993

Description.—Triangular skeletal framework with bilaterally symmetric lamellar shell which is located between b.d. and i.d..

Comparison.—The disposition of rods of *Protoholoeciscus*

is similar to that of *Glanta*, but it is distinguished by the presence of a lamellar shell. It differs from *Holoeciscus* in having a rather equilateral triangular framework (Aitchison, 1993).

Protoholoeciscus sp.

Figure 7-7

Description.—Small lamellar shell is clothed with a delicate and thin perforate sheet. Pores on the spongy layer are circular to subcircular in shape and irregular in size. Subcircular basal aperture faces a subtriangular to suboval central opening. Patagial tissue is weakly developed around the junction of b- and i-rods. A.t. is covered with the shell. B. d. is longer and thicker than i.d.. A.a. and b.d. are robust. A.p. and i.d. are short and delicate. All rods are circular in cross section. Caveal ribs remain uncertain.

Material.—One specimens from 37E in Section B and two specimens from 15E in Section C.

Remarks.—This species differs from other species of *Protoholoeciscus* in having a small shell with a perforate sheet which is regarded as the primitive feature of *Protoholoeciscus* as discussed later.

Range and occurrence.—Possible Emsian to Eifelian age. Nakahata Formation in the Yokokurayama Group.

Protoholoeciscus hindea Aitchison, 1993

Figures 7-8—12

Albaillellaria gen. indet. sp. Aitchison, Flood and Spiller, 1992, fig. 6, O-S.

Protoholoeciscus hindea Aitchison, 1993, p. 362, pl. 1, fig. 3; Stratford and Aitchison, 1997, pl. IV, A-B.

Glanta sp. B Furutani, 1996, p. 76, fig. 7, 12-13.

Glanta sp. Furutani, 1997, pl. 1, fig. 12.

Description.—Large lamellar shell is rectangular to trap-ezoidal in lateral view. A.a., b.d., b.v. and i.v. are robust. A. p. and i.d. are short and delicate. All rods are circular in cross section. Patagial tissue weakly developed around the junction of b- and i-rods. A pair of caveal ribs extends from the junction of a- and b rods. Subcircular basal aperture faces subtriangular to suboval central opening.

Material.—44 specimens from 3B to 3N in Section A and 37E in Section B.

Range and occurrence.—Possible Eifelian age. Nakahata Formation in the Yokokurayama Group; Gamilaroi Terrane (Stratford and Aitchison, 1997) and Djungati Terrane (Aitchison *et al.*, 1992; Aitchison, 1993), N.S.W., Australia.

Figure 7. 1-6. *Circulaforma* sp. aff. *C.* sp. A Stratford and Aitchison, 1: OCU PR 0152, 15E, 2: OCU PR 0153, 15E, 3: OCU PR 0154, 15F, 4, 5: OCU PR 0155-156, 15C, 6: OCU PR 0157, 15E. 7. *Protoholoeciscus* sp., OCU PR 0158, 15E. 8-12. *Protoholoeciscus hindea* Aitchison, 8: OCU PR 0159, 3N, 9: OCU PR 0160, 3B, 10: OCU PR 0161, 3I, 11, 12: OCU PR 0162-163, 3L. 13-18. *Protoholoeciscus spinosus* sp. nov., 13: OCU PR 0164, 3B, holotype, 14: OCU PR 0165, 3N, 15-17: OCU PR 0166-168, 3B, 18: OCU PR 0169, 3B. Scale bar is 100 μm , A: 1, 3, 12, B: 2, 4-11, 13-18.

***Protoholoeciscus spinosus* sp. nov.**

Figures 7-13-18

Diagnosis.—Several projections extend from the dorsal part of a large lamellar shell.

Description.—Large lamellar shell is trapezoidal to rectangular in lateral view and oval in anterior view. The internal structure of the shell is not observed. Several irregularly arranged pores on the shell are circular to subcircular. Several projections are short, delicate, tapered distally, arise from the dorsal part of the shell and trend in a dorsal direction. A.a., b.d., b.v. and i.v. are long and robust. A pair of caveal ribs extends from the junction of a- and b rods. All rods, caveal ribs and projections are circular in cross section. Patagial tissue is often ornamented around the junction of b- and i-rods. Subcircular basal aperture faces the central opening, which is subtriangular to suboval.

Measurements.—Measured features are shown in Figure 6-d.

Length of shell : 70-105, average 90, based on 15 specimens, in μm .

Width of shell : 75-105, average 91.

Material.—15 specimens from 3B, 3C and 3I to 3N in Section A.

Comparison.—This species is distinguished from other species of *Protoholoeciscus* in possessing several projections from the dorsal part of the shell.

Range and occurrence.—Possible Eifelian age. Nakahata Formation of the Yokokurayama Group.

Etymology.—This name is derived from the Latin adjective *spinosus*, meaning thorny.

Type specimens.—Holotype OCU PR 0164 (Figure 7-13); Paratype OCU PR 0165 (Figure 7-14). Both from 3B.

***Protoholoeciscus ochiensis* sp. nov.**

Figures 8-1-6

Diagnosis.—This species is characterized by an equilateral triangular shape with long b.d. and slender b.v. and i.v.. All rods are circular in cross section.

Description.—Large lamellar shell is subtrapezoidal in lateral view. Pores on the shell are circular to subcircular. A. a. is weakly developed and a.p. is absent. A.t. remains uncertain. B.d. is longer and thicker than i.d.. B.v. and i.v. are thin and slender. Patagial tissue is weakly developed around the junction of b- and i-rods. A pair of spines is short, delicate and extends bilaterally symmetrically from the junction in the vertical plane. A pair of caveal ribs extends from the junction of a- and b rods. Ovate basal aperture faces central opening, which is subtriangular to oval.

Measurements.—Measured features are shown in Figure 6-d.

Length of shell : 70-115, average 97, based on 19 specimens, in μm .

Width of shell : 95-135, average 115.

Material.—19 specimens from 15C, 15E and 15F in Section C.

Comparison.—This species differs from *Protoholoeciscus hindea* Aitchison and *Pr. spinosus* sp. nov. in having an equilateral triangular shape with slender b.v. and i.v. This species is distinguished from *Pr. triangularis* (Wakamatsu, Sugiyama and Furutani) in having rod-like b.d.

Range and occurrence.—Possible Eifelian age. Nakahata Formation of the Yokokurayama Group.

Etymology.—From the town of Ochi, where the study area is situated.

Type specimen.—Holotype OCU PR 0170 (Figure 8-1) from 15F.

***Protoholoeciscus triangularis* (Wakamatsu, Sugiyama and Furutani, 1990)**

Figures 8-7-9

Glanta triangularis Wakamatsu, Sugiyama and Furutani, 1990, p. 182, pl. 13, figs. 1-7; Furutani, 1996, fig. 7, 15.

Description.—Large lamellar shell is subtrapezoidal in lateral view. A.a., b.d., b.v. and i.v. are robust. B.d. is thickest and deeply grooved. Patagial tissue is weakly ornamented around the junction of b- and i-rods. A pair of spines extends bilaterally symmetrically from the junction in the vertical plane. A pair of caveal ribs extends from the junction of a- and b rods. Pores on lamellar shell are circular to subcircular. Subcircular basal aperture faces subtriangular to ovate central opening.

Material.—Eight specimens from 15C, 15E and 15F in Section C.

Remarks.—Although this species was assigned to genus *Glanta* in previous work (Wakamatsu *et al.*, 1990), it belongs to *Protoholoeciscus* based on the presence of a lamellar shell (Stratford and Aitchison, 1997). This species differs from other species of *Protoholoeciscus* in having deeply grooved b.d..

Range and occurrence.—Possible Eifelian age. Nakahata Formation of the Yokokurayama Group.

Genus ***Helenifore*** Nazarov and Ormiston, 1983

***Helenifore* sp. A** Stratford and Aitchison, 1997

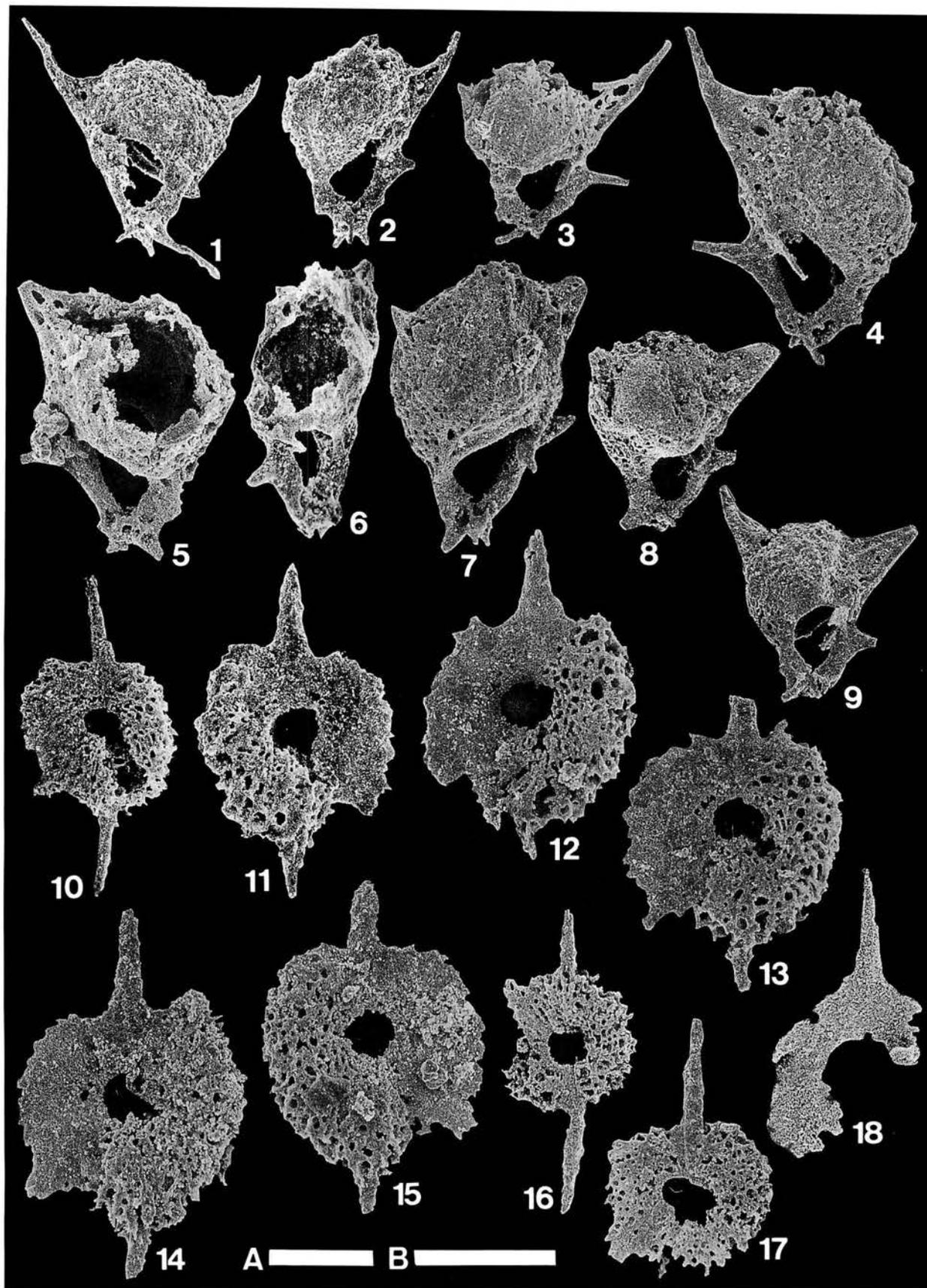
Figures 8-10-17

Helenifore sp. Aitchison, Flood and Spiller, 1992, fig. 6C.

Helenifore sp. A Stratford and Aitchison, 1997, pl. III, A-D.

Description.—This species is characterized by large disk-

Figure 8. 1-6. *Protoholoeciscus ochiensis* sp. nov., 1 : OCU PR 0170, 15E, holotype, 2 : OCU PR 0171, 15E, 3-5 : OCU PR 0172-174, 15C, 6 : OCU PR 0175, 15E. 7-9. *Protoholoeciscus triangularis* (Wakamatsu, Sugiyama and Furutani, 1990), OCU PR 0176-178, 15C. 10-17. *Helenifore* sp. A Stratford and Aitchison, 10 : OCU PR 0179, 15F, 11 : OCU PR 0180, 15E, 12-16 : OCU PR 0181-185, 15C, 17 : OCU PR 0186, 15E. 18. *Helenifore* sp. B, OCU PR 0186, 37C. Scale bar is 100 μm , A : 1-3, 8-10, 16-18, B : 4-7, 11-15.



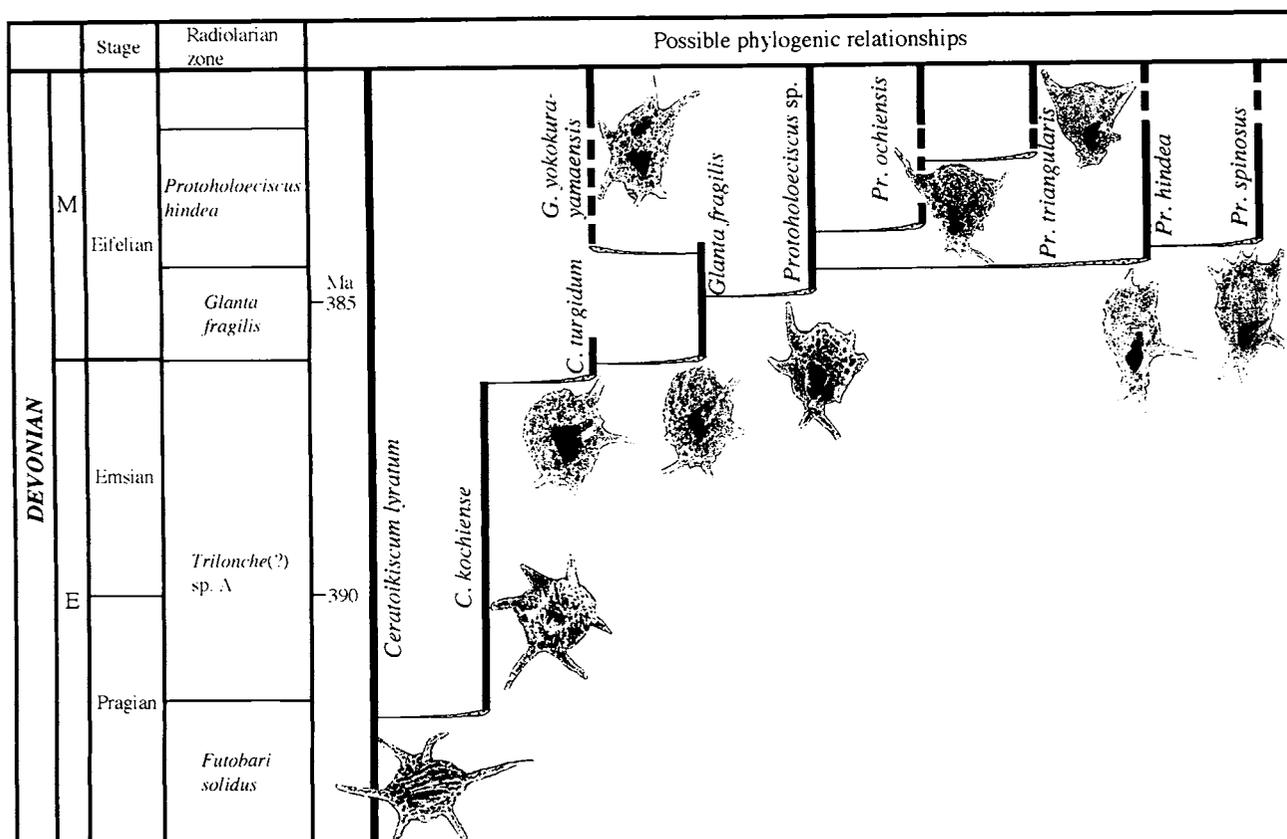


Figure 9. Possible phylogenetic relationships among *Ceratoikiscum*, *Glanta* and *Protoholoeciscus*.

like shape with two prominent rods which extend in opposite directions in the horizontal plane (Figure 6-e). Developed patagium is porous, large, extensive and circular to subcircular. Pores on the patagium are circular to oval in shape and irregular in size. Central opening is circular to oval. Opposite a.a. and a.p. are sturdy, acute, slightly curved, blunt at end and variable in length. l.d. is rather short. All rods are circular in cross section.

Material.—33 specimens from 3I, 3L and 3N in Section A and 15C, 15E and 15F in Section C.

Comparison.—This species is distinguished from *Helenifore planus* Umeda (1997) in having a large patagium and rather short rods and in absence of b.d. and b.v..

Remarks.—Stratford and Aitchison (1997) described the *Helenifore* sp. A Assemblage from eastern Australia and assumed the age to be Eifelian.

Range and occurrence.—Possible Emsian to Eifelian age. Djungati Terrane (Aitchison *et al.*, 1992) and Gamilaroi Terrane (Stratford and Aitchison, 1997) in the New England Fold Belt, eastern Australia; Nakahata Formation of the Yokokurayama Group.

Discussion

Five genera and twelve species of Ceratoikiscidae from three sections are described in this paper. *Ceratoikiscum* and *Helenifore* are known from the Silurian to Carboniferous,

whereas *Glanta* and *Protoholoeciscus* are restricted to the Devonian. Furutani (1996) examined the evolution of Devonian Ceratoikiscidae based on materials from the Nakahata Formation and recognized morphologic similarities in well-developed patagium between *Ceratoikiscum* and *Glanta*. Emsian (late Early Devonian) species of *Ceratoikiscum* (*C. kochiense* Umeda) from the Konomori area in the Kurosegawa Terrane possesses developed lamellar patagium and robust rods (Umeda, 1997). This species seems to have arisen from *C. lyratum* Ishiga with the addition of developed patagium (Umeda, 1997). *C. kochiense* is similar to *C. sp.* in this paper and *Glanta fragilis* Wakamatsu, Sugiyama and Furutani in having developed lamellar patagium, rather sturdy a.a. and short and rather conical b.v. and i.v. The shape of the inflated swell of *C. sp.* is similar to the porous shell of *G. fragilis*. Accordingly *G. fragilis* seems to have arisen from *C. sp.* which seems in turn to have evolved from *C. kochiense*. *G. fragilis* appears to be the primitive form among *Glanta* species and gave rise to *G. yokokurayamaensis* sp. nov. The perforate shell of *Glanta* changed to a lamellar shell in successive stratigraphic sections (Furutani, 1996). *Glanta* morphologically resembles *Protoholoeciscus* in its framework. The perforate sheet on small lamellar shell of *Protoholoeciscus* sp. in this paper is similar to the porous shell of *Glanta*; this feature is regarded as transitional between *Glanta* and *Protoholoeciscus*. *Pr. sp.* seems to have evolved from *G. fragilis* with the change of

shell from porous to lamellar type. *Pr.* sp. is similar to *Pr. ochiensis* sp. nov. in having an equilateral triangular framework and subtrapezoidal shell. *Pr.* sp. gave rise to *Pr. ochiensis* and *Pr. hindea* Aitchison, in which the perforate sheet on the shell is lost. *Pr. triangularis* (Wakamatsu, Sugiyama and Furutani) possesses an equilateral triangular framework with bladed rods. *Pr. triangularis* seems to have arisen from *Pr. ochiensis* with the change of rods from circular to bladed in cross section. *Pr. hindea* and *Pr. spinosus* sp. nov. possess a large trapezoidal to rectangular shell. *Pr. spinosus* seems to have arisen from *Pr. hindea*.

Aitchison (1993) considered that *Protoholoeciscus* is the transitional form between *Ceratoikiscum* and *Holoeciscus*. Based on the above-mentioned morphologies and biostratigraphic distributions, it is supposed that *Protoholoeciscus* evolved from *Ceratoikiscum* via *Glanta* (Figure 9). *Protoholoeciscus* is regarded as the ancestor of *Holoeciscus*. Acquisitions of shell of Ceratoikiscidae show drastic and significant evolutionary change in short time, namely Emsian to Eifelian age.

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***Bennetticarpus yezoites* sp. nov. (Bennettitales)** **from the Upper Cretaceous of Hokkaido, Japan**

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Abstract. Recently many plant taxa have been described from the marine Upper Yezo Group (Coniacian–Santonian). These plant fossils are preserved as permineralized debris in calcareous nodules together with various marine animals. A single bennettitalean specimen was collected from the Upper Yezo Group. It consists of a receptacle, with numerous fertile (seminiferous) and sterile (interseminal) scales. Although the specimen is fragmented, its anatomical features are well preserved. This paper provides a description of a new reproductive organ belonging to Bennettitales. As its affinity to Williamsoniaceae or Cycadeoidaceae and their allies is uncertain, we provisionally place our specimen in the form-genus *Bennetticarpus* and describe *B. yezoites* sp. nov. Comparison of *Bennetticarpus yezoites* with known bennettitalean taxa in other regions is given briefly.

Key words: *Bennetticarpus*, Bennettitales, Hokkaido (Japan), Late Cretaceous, Upper Yezo Group.

Introduction

Since the classical study on the Late Cretaceous permineralized plants from Hokkaido, Japan, by Stopes and Fujii (1910), many papers have been published on the fossil plants collected from the Upper Yezo Group (Coniacian–Santonian) of marine origin. The Upper Yezo Group yields abundant fossil plants, and anatomically studied bennettitaleans are not rare, including, for example, *Cycadeoidea petiolata* Ogura (Ogura, 1930), *Cycadeoidella japonica* Ogura (Ogura, 1930; Nishida, H., 1991), *Otozamites kerae* Ohana and Kimura (Ohana and Kimura, 1991), *O. takahashii* Ohana and Kimura (Ohana and Kimura, 1991).

Many other taxa known by early 1991 were listed by H. Nishida (1991, p. 256–261). Recently several permineralized conifer taxa were described (e.g., Ohana and Kimura, 1993, 1995; Ohsawa *et al.*, 1991, 1992, 1993, 1995; Nishida, H. *et al.* 1991; Nishida, M. *et al.*, 1991, 1992; Saiki, 1992; Saiki and Kimura, 1993; Stockey *et al.*, 1993, 1994).

Recently a bennettitalean reproductive organ collected by Yasuji Kera from the Upper Yezo Group in the Yubari area, Hokkaido, Japan, was given to us for the present investigation.

Although the specimen is fragmentary, its unique anatomical structure is well preserved.

It differs from other known bennettitalean taxa, so we place it in the form-genus *Bennetticarpus* following Harris (1932, 1969).

Description

Order Bennettitales

Form-genus *Bennetticarpus* Harris, 1932

This form-genus was established by Harris (1932) based on material derived from the Upper Triassic and Lower Jurassic plant-sites in Scoresby Sound, East Greenland. Some authors have used the name of gynoecium or gynoecia for bennettitalean seminiferous scales or both seminiferous and interseminal scales (e.g. Harris, 1932). This form-genus was designated for “all gynoecia which show definitely bennettitalean characters, but which are not fully enough known either to be included in or definitely separated from the existing genera” (Harris, 1932).

Subsequently *Bennetticarpus* has been used by Hsü (1948), Kräusel (1949), Harris (1969) and Watson and Sincock (1992).

Bennetticarpus yezoites sp. nov.

Figures 1–6

Material.—INH-005 (Holotype). Collected by Yasuji Kera. Stored in the Institute of Natural History, Tokyo.

Locality and horizon.—Kaneobetsu Valley (roughly 142°33′ 02″E, 42°28′52″N), a branch of the Hakkinzawa Valley, Kashima, Yubari City, Hokkaido, Japan (reference map was shown in Ohana and Kimura, 1993; figure 1B). Upper Yezo Group of marine origin (Coniacian–Santonian).

Etymology.—Named after Yezo, older name of Hokkaido.

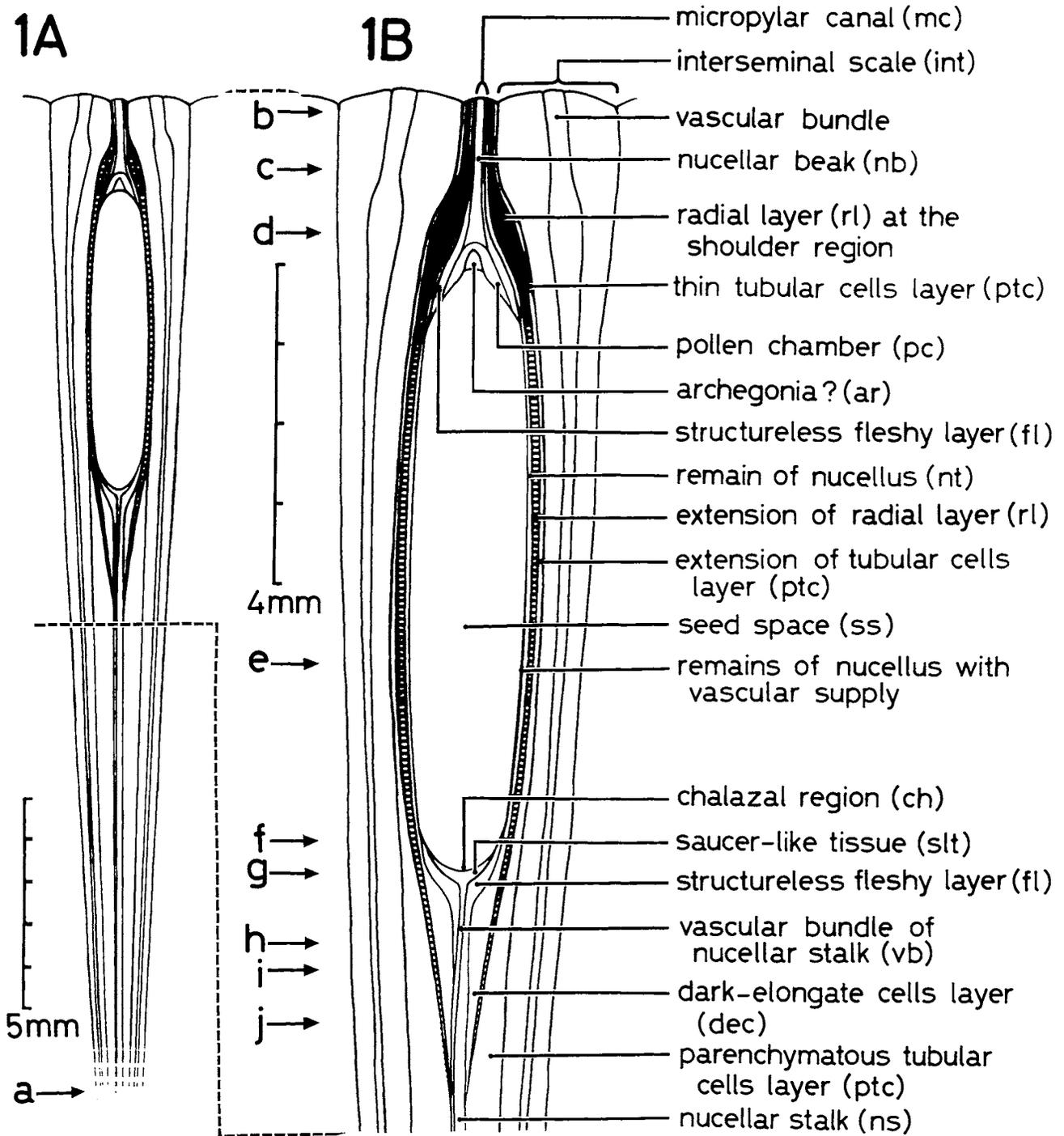


Figure 1. *Bennetticarpus yezoites* sp. nov., **1A**: Radial longitudinal section, showing the whole structure of seminiferous and interseminal scales, except for their basal disintegrated parts (at level a in Figure 1A). **1B**: Distal half of radial longitudinal section of scales, enlarged from Figure 1A. The terminology of tissues is shown on the right side with their abbreviations. Main transversely cut planes are indicated on the left side.

Specific diagnosis.—Large-sized bennettitalean female reproductive organ ('gynoecium'), consisting of a semispherical receptacle covered by densely spaced seminiferous (fertile) and interseminal (sterile) scales, both about 25 mm long.

Seminiferous scale consisting of an orthotropous ovule born on a long, slender stalk with a median bundle consisting of scalariform tracheids. Stalk expanding to saucer-like structure, at the basal part of the seed-space, where vascular bundle diverging laterally and entering the thin nucellus

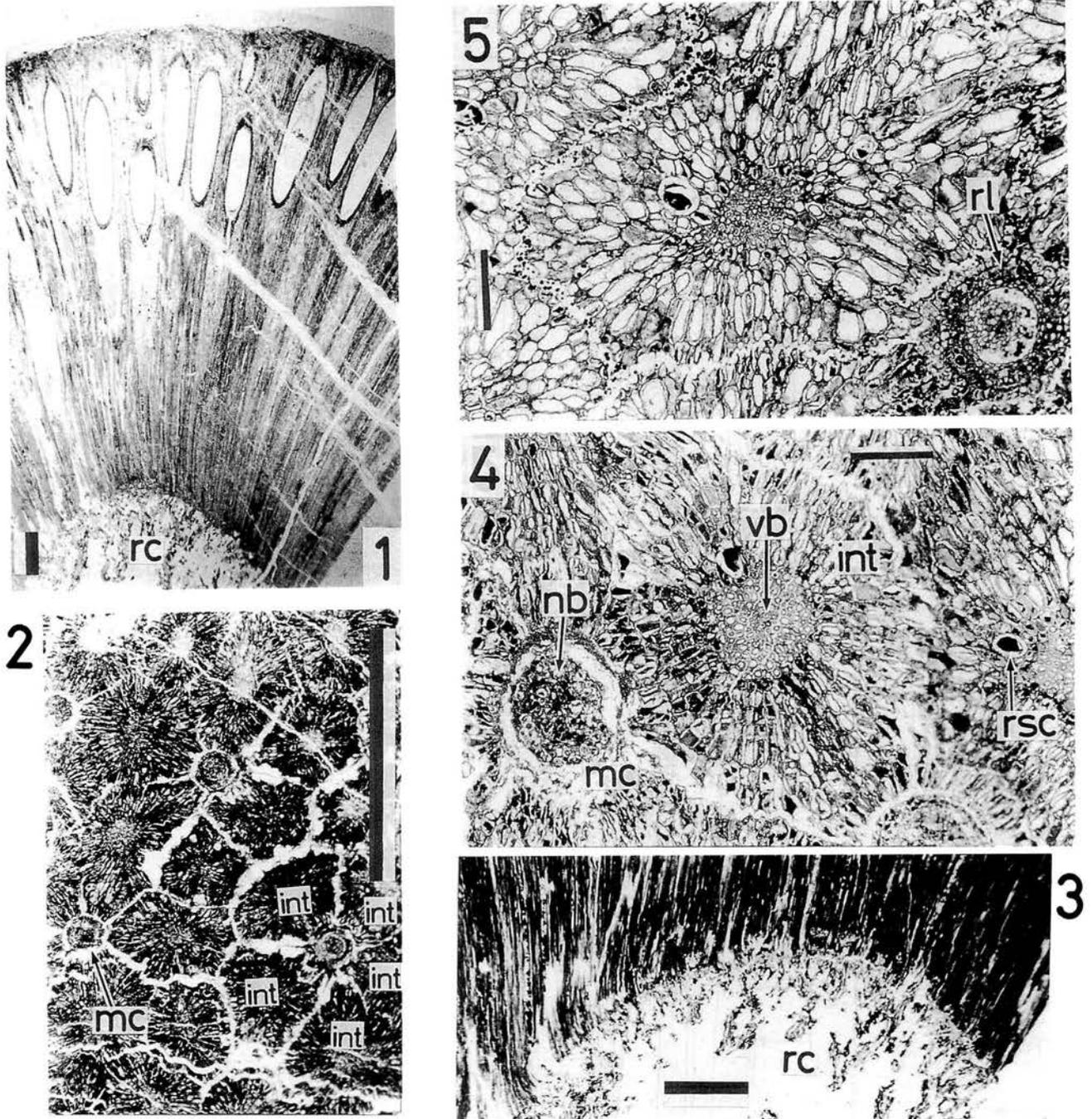


Figure 2. *Bennetticarpus yezoites* sp. nov. All sections were made from INH-005. Thick and thin scale-bars indicate 2 mm and 200 μ m respectively. **1:** Radial longitudinal section of a gynoecium with partly preserved hemispherical receptacle (rc; 15 mm in diameter and 9 mm high), and closely covered seminiferous and interseminal scales (about 25 mm long). **2:** Peripheral view of seminiferous and interseminal (int) scales. A micropyle (mc; small circular tissue) is surrounded by five polygonal interseminal scale heads. Note that the presence of thickly cutinized papillae around the margins of the interseminal scale heads. **3:** Longitudinal section of receptacle (rc) and basal part of the scales. Unfortunately cellular structures of receptacle are disintegrated, and the base of the scale are unclear (at level a in Figure 1A). **4:** Transverse section slightly below the periphery (at level b in Figure 1B), showing the micropylar canals (mc) at left and right corners and interseminal scales (int). The micropylar canals are filled by nucellar beaks (nb). An interseminal scale at the center is composed of a medial vascular bundle (vb) and radially disposed parenchymatous cells. **5:** Transverse section slightly below the former section (at level c in Figure 1B), showing the micropylar canal surrounded by thick walled radial cells layer (rl). Large resinous cells with dark contents (rsc) are scattered in the interseminal scales.

layer. Micropylar canal longer and circular in cross section, surrounded by five interseminal scales. Semiferous scale having an inner layer of darkish, elongate cells, a middle layer of radial cells, and an outer layer of tubular cells. Tubular cell layer being thick below the chalazal region, otherwise thin. Radial cell layer thickened in the region above the pollen chamber where the cross section being pentagonal.

Interseminal scales thick at the peripheral region and deformed towards the base. Cells rectangular in the apical region while tubular near the base. A thick median vascular bundle present.

Description.—The single specimen obtained is permineralized with calcium carbonate. It consists of a fragmentary semiferous and interseminal scales and a receptacle. About one-third of the original gynoecium and receptacle is preserved as a fan-shaped form. Radius of the gynoecium including interseminal scales is about 3 cm in its transverse section and the original gynoecium is estimated to be about 9.4 cm in diameter. The receptacle (rc), is hemispherical, about 15 mm in diameter and 9 mm high, covered by numerous semiferous (fertile) and interseminal (sterile) scales (Figure 2-1). Internal structure of the receptacle is disintegrated. We prepared numerous longitudinal and transverse peel sections from the specimen. Figures 1A and 1B are drawn on the basis of our observations of these sections. The main transversely cut planes are indicated by levels a-j (Figures 1A and 1B).

(1) Semiferous scale (Figures 1A and 1B): The ovule (seed) is borne on a long nucellar stalk and has a micropylar canal (mc), pollen chamber (pc), archegonia? (ar), orthotropous seed space (ss), saucer-like structure (slt), chalazal region (ch) and long nucellar stalk (ns) with a vascular bundle (vb). Unfortunately details of basal disintegrated parts (level a in Figure 1A) of the scales are indistinct.

These tissues are surrounded by a layer of parenchymatous tubular cells (ptc) outside, robust radial layer (rl), and a layer of dark elongate cells (dec) inside. Remains of the nucellar tissue (nt) are present along the outer margin of seed space (ss).

In addition, structureless fleshy layers (fl) are present below the micropylar canal and below the saucer-like tissue.

1) Micropylar canal (Figures 2-2, 4, 3-3): This canal is slightly projected out of the general surface of the interseminal scale heads, and is circular in transverse section, 320 μm in diameter. The canal is 900 μm long, and is filled by longitudinally elongated parenchymatous cells, forming a nucellar beak (or plug) (nb).

2) Pollen chamber (Figure 3-1) is present below the nucellar beak, but pollen grains were not observed. Archegonium-like tissue (ar) is seen below the pollen chamber.

3) Seed space (Figure 5-1) is elongately elliptical, 7.25 mm long and up to 1.85 mm wide, circular or oblong in transverse section (Figure 5-2). No structure is seen inside the seed space except for the remains of the nucellar tissue (nt).

4) Nucellar stalk (ns): This stalk develops from the base of the semiferous scale, 14.5 mm long and 0.5 mm wide (Figure 1A), running to the base of the saucer-like tissue (slt). The vascular bundle in the nucellar stalk (ns) consists of

scalariform tracheids (Figures 4-2, 4, 5-3, 4). The bundle diverges into the saucer-like tissue as fibrous strands. These fibrous strands join the thin remains of nucellar tissue, 2-3 cells thick, located along the outer wall of the seed space (Figure 4-1, 4).

The saucer-like tissue consists of nearly isodiametric small cells each with scalariform ornamentation on the cell walls (Figure 4-2, 3).

5) Radial layer (rl): The cells of the radial layer are thick-walled and cube-like. This layer originates from the part of the micropylar canal as a single row, laterally expanding at the shoulder area in two rows, running downward as a single row, and then thinning out at the upper part of the nucellar stalk. Longitudinally, this looks like a brick-shaped layer.

The thickest part of the radial layer, cut at the shoulder region, shows a pentagonal outline in transverse section and is constructed by two radial rows of cells (level d in Figure 1B). Cellular details just around the pentagonal tissue are indistinct (Figure 3-2, 3).

6) Layer of dark elongate cells (dec): This layer originates from the part of the micropylar canal, running downward along the outer margin of the seed space, broadening at the chalazal region and upper part of the nucellar stalk, then thinning out (Figure 4-1, 4).

7) Layer of tubular cells: This parenchymatous layer (ptc) is the outermost coat of the semiferous scale. It originates from the micropylar region running downward as a very thin coat.

Thickness of this layer increases from the lower part of the seed space to the nucellar stalk region. Consequently the basal half of the semiferous scale (below level j in Figure 1B) is occupied by nucellar stalk (ns) surrounded by a layer of thick parenchymatous tubular cells.

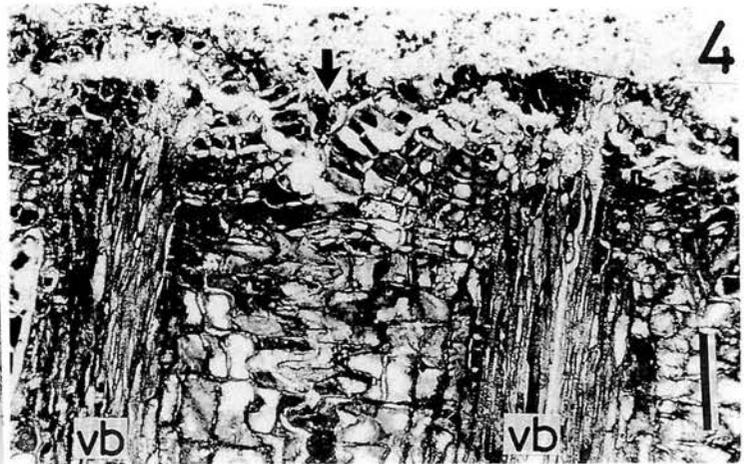
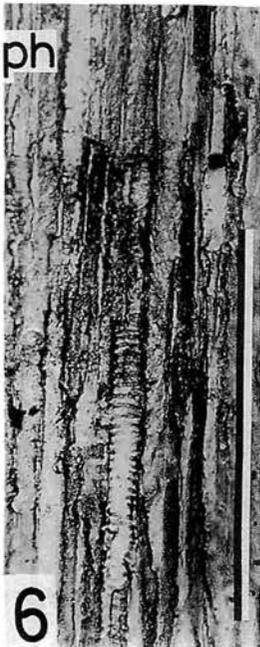
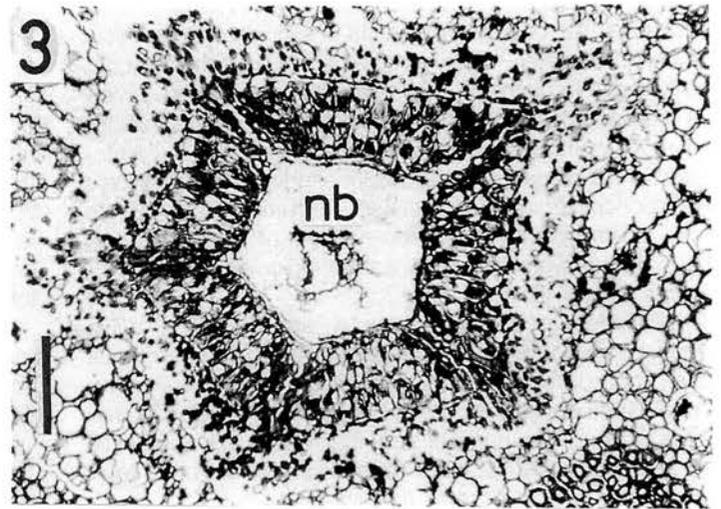
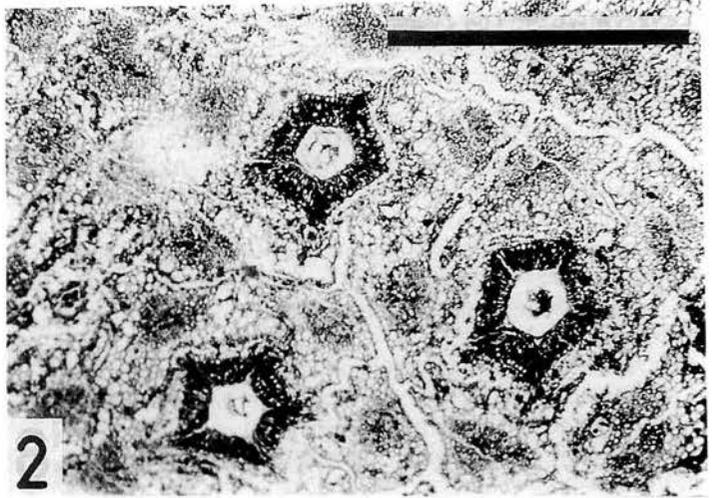
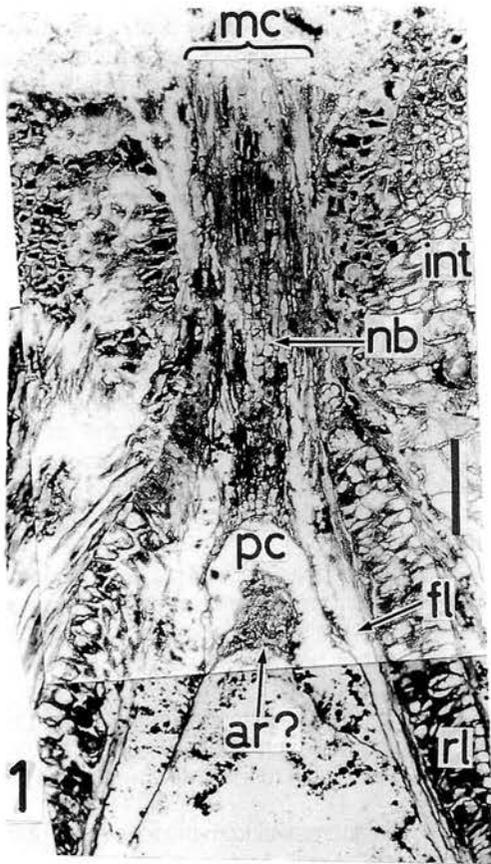
The tubular cells, as shown in Figures 4-1, 5-5, 6 (ptc), are elongate in longitudinal section, typically 1056 μm long, fusiform, pointed at both ends. Their walls are thin and smooth, and septum (or end wall) is not present. In transverse section [Figure 6-1—6 (ptc)], the tubular cells appear circular or oval, 55 μm in diameter. They are loosely arranged with many scattered intercellular spaces.

8) Integument: It is difficult to identify integument in the present semiferous scales. However, the layers of tubular cells, radial cells and dark elongate cells might belong to the integument. It is noted that the above three layers do not receive any vascular supply.

9) Nucellar stalk: The lower half of the semiferous scale consists of concentrically arranged cell layers. At the level f of the transverse section as shown in Figure 6-1, the layer of tubular cells is the outermost, followed, from outside to inside, by radial (rl), dark elongate (dec), fleshy (fl), saucer-like tissue (slt) and the base of seed space. The fleshy layer is an empty space (Figures 1B, 3-1, 4-1, 4).

The center of the nucellar stalk is almost without structure, and in transverse section the vascular bundle is located centrally (Figure 5-4) or often laterally, and is pinned against the margin of a fleshy circular cylinder (Figures 5-3, 6-3, 4, 5, 6).

Surrounding cells in transverse section are normally oval-shaped (Figure 6-4).



(2) Interseminal scale: This scale is sterile, club-shaped, and its distal part is expanded transversely with a median vascular bundle throughout. In surface view, interseminal scale heads are polygonal, and five scale heads surround the small circular micropyle.

The heads are dark due to the heavily cutinized and thick-walled cells which are radially elongated. Thickly cutinized papillae are present on the margins of the interseminal scale heads (Figure 2-2).

Under the peripheral surface (at level b in Figure 1B), most cells are light-colored, because of the absence of thick-walled and heavily cutinized cells. The center of the interseminal scale is occupied by a thick median vascular bundle (Figure 2-4, 5). Large-sized resin cells with dark contents are present. In the longitudinal section, thick epidermal and hypodermal cell layers are present (Figure 3-4). Under the hypodermis, cells are cubic or rectangular and stacked like bricks (Figure 3-4). Vascular bundle consists of tracheids with scalariform thickening (Figure 3-5, 6).

The lower half of the interseminal scale is markedly deformed and its cells are small-sized, parenchymatous and loosely arranged. These cells correspond to the tubular cells of the seminiferous scales. Layer of these small-sized cells surrounds the tubular cell layer of the seminiferous scale (Figure 6-6, 7, 8). Large-sized resin cells with dark contents are also present. Such resin cells are not found in the seminiferous scale.

The so-called 'boss', arising on the center of an interseminal scale head (Harris, 1932) is not observed, and so also stomata said to be located around the boss are not observed in our interseminal scale head. Our scale heads are slightly convex as seen in the longitudinal section (Figure 3-4).

Discussion and comparison

The specimen described here is a fragment of a permineralized gynoecium, consisting of a receptacle bearing numerous interseminal and seminiferous scales. Except for the receptacle, the fossil is well preserved, allowing the preparation of numerous serial peel sections along longitudinal and transverse surfaces. Figure 1A shows the entire structure of seminiferous and interseminal scales and Figure 1B shows the enlarged upper half of the scales mainly on the basis of longitudinally cut section.

The terminology for the tissues in bennettitalean gynoecium varies according to the authors, except for the micropylar canal, nucellar beak and pollen chamber, because the function of other tissues is still uncertain.

The present structure is characterized by its rather large-sized scales (24 mm long and up to 1.5 mm in diameter) similar to those of *Cycadeoidea morierei* (Saporta and Marion) Seward (30-45 mm long and up to 1.5 mm in diameter) (e.g. Seward, 1917). Another characteristic feature of the present gynoecium described here is the presence of a thick radial cell layer at the shoulder region above the seed space (Figure 3-1, 2, 3), similar to those recorded for *Cycadeoidea dartoni* Wieland (Wieland, 1916, fig. 46), *C. dacotensis* (MacBride) Ward (Wieland, 1916, fig. 47), *C. morierei* (Saporta and Marion) Seward (in Seward, 1917) and *C. wielandi* Ward (Wieland, 1906, fig. 63-1).

This tissue was called prismatic layer for *Cycadeoidea morierei* (Wieland, 1906), radial and tubular layers (Seward, 1917), and a slightly palisaded layer of heavily walled cells for *C. wielandi* (Wieland, 1906). A thick radial layer appears to be restricted to some *Cycadeoidea* species and has not yet been found in *Williamsonia* species and its allies.

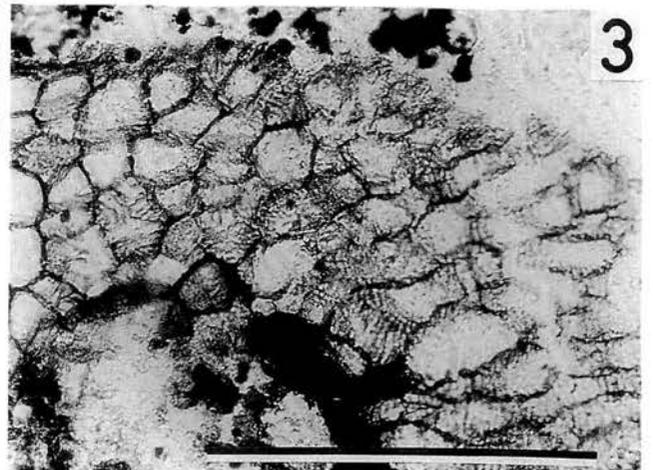
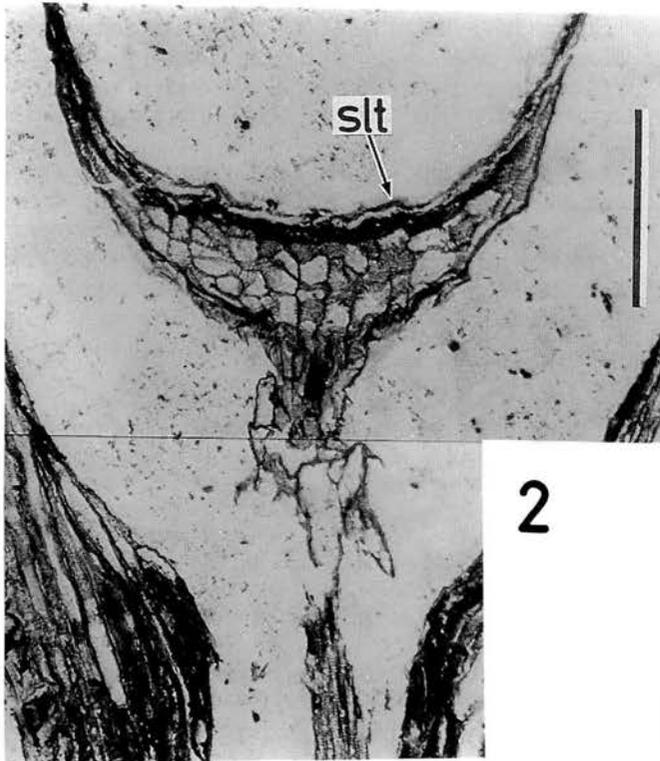
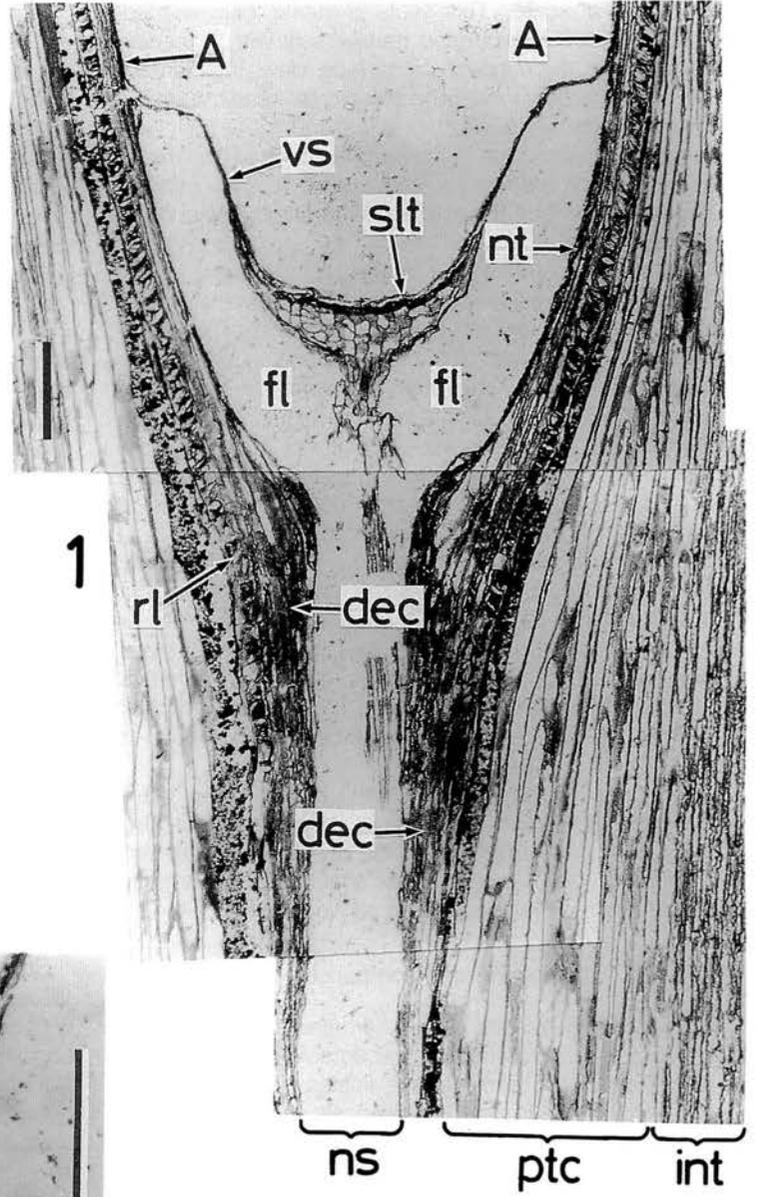
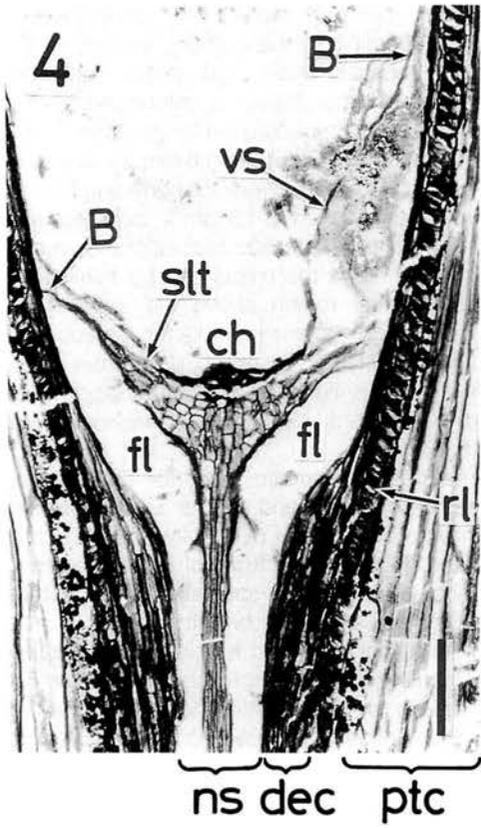
However, as said earlier regarding terminology of tissues, in *Cycadeoidea morierei*, the parenchymatous tubular cell layer is called tubular envelope (Wieland, 1906; Seward, 1917) and in *C. wielandi*, this layer is said to be the continuation of the heavy-walled tubular cells (Wieland, 1906).

According to Stewart and Rothwell (1993), the integument of *Cycadeoidea morierei* corresponds to the fibrous layer, an extension of the nucellar stalk. This layer may correspond to our layer of dark elongate cells. However, we believe that the radial layer is real integument, because it envelopes the internal tissues throughout.

Sharma (1977, 1990) made some ontogenic studies on the *Williamsonia* ovules and mentioned that ovule development was basipetal. But in our gynoecium, such a trend is not observed. The developmental stage of our gynoecium is still uncertain.

Nishida (1994) redescribed *Cycadeoidella japonica* Ogura from the Turonian Middle Yezo Group, Hokkaido. In this species the vascular bundle does not enter the outer margin of nucellar remains. In his interseminal scale head, cells appear to be not radially arranged and nearly isodiametric. These features are different from those of our interseminal

Figure 3. *Bennetticarpus yezoites* sp. nov. Thick and thin scale-bars indicate 2 mm and 200 μ m respectively. **1:** Radial longitudinal section of an upper part of the ovule, composed of micropylar canal filled by nucellar beak (nb), pollen chamber (pc), archegonium? (ar), and outer radial layer (rl) in two rows at the shoulder region. Along the micropylar region, swollen interseminal scales are close to the micropylar canal. Thin structureless fleshy layer (fl) is present inside the radial layer. **2:** At the shoulder region cut at level d (Figure 1B), pentagonal radial layers are present, composed of two rows of thick walled cells radially arranged. Each angle is separated by narrow wing-like tissue. In other part, the radial layer is a single row. **3:** Pentagonal radial layer enlarged from Figure 3-2. Broken nucellar beak (nb) is seen. **4:** Radial longitudinal section of distal part of two interseminal scales. An arrow shows the position of boundary between two scales. Each scale is penetrated by a rather thick median vascular bundle (vb). The scale head is slightly convex and is composed of heavily cutinized epidermal and thick-walled hypodermal cell layers. The ground tissue is composed of rectangular cells and looks like a stack of bricks. **5:** Vascular bundle in longitudinal section of an interseminal scale, and the presence of intercellular spaces (is). **6:** Longitudinal section of scalariform tracheids at the proximal portion of an interseminal scale. Note that the surrounding cells are longitudinally elongated, instead of rectangular cells at the apical portion of scale. Some elongate cells are thought to be phloem elements (ph).



scales. Further, he showed outer structureless membranes which respectively did envelope the seminiferous and the interseminal scales throughout. However, such a membranous structure is not observed in our gynoecium.

The structure of the bennettitalean scales at the base has been illustrated in various ways as, for example, in *Williamsonia* sp. (Sharma, 1970, 1974), *W. sewardiana* Sahni (Sahni, 1932), *W. scotica* Seward (Seward, 1912) and *Cycadeoidea* sp. (Crepet, 1974). Unfortunately, the basal details of our scales are not clear (Figure 2-1, 3).

At present, it is difficult to establish the generic affinity of our gynoecium, which is represented only by a receptacle and a thick layer of seminiferous and interseminal scales.

Nevertheless, it is clear that the present gynoecium is bennettitalean. Numerous permineralized bennettitalean reproductive organs have been recorded from Mesozoic plant sites, but the internal features of their gynoecia are different from the present specimen. Under the circumstances we assign the specimen to the bennettitalean form-genus *Bennetticarpus* with the specific name *Bennetticarpus yezoites* until additional information is available.

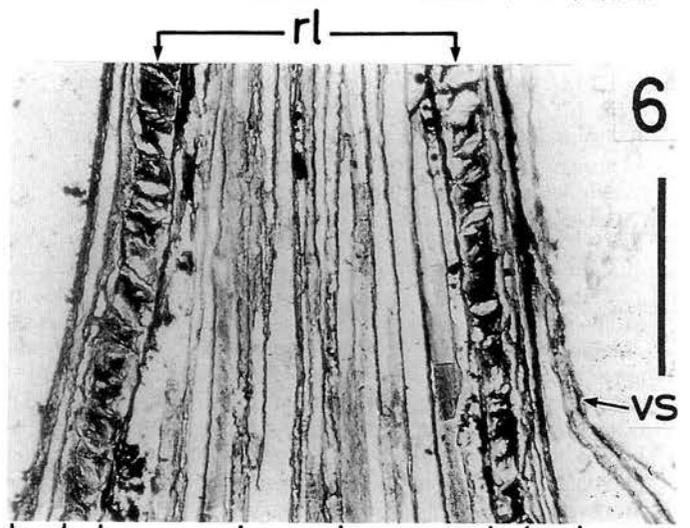
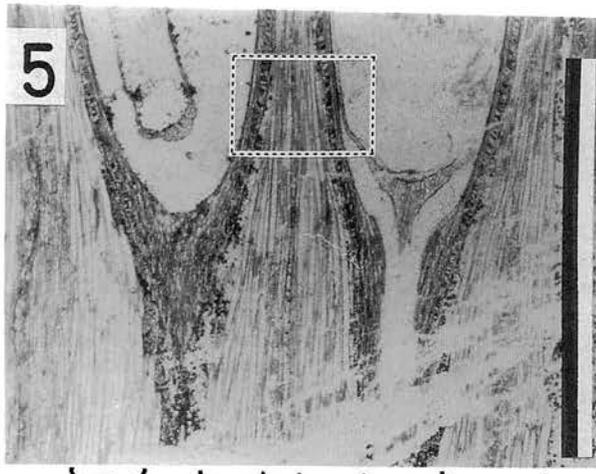
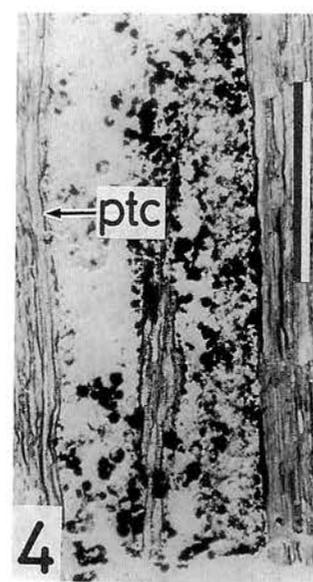
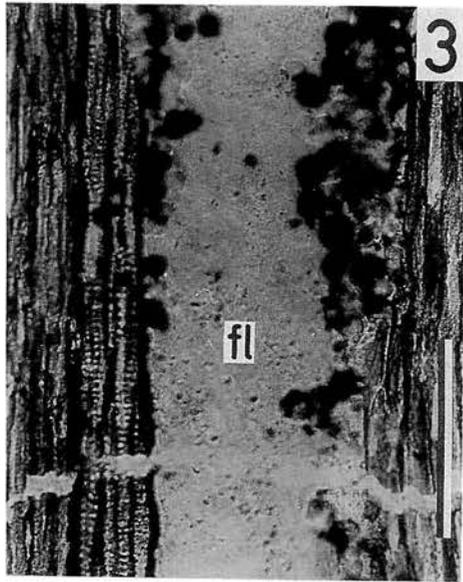
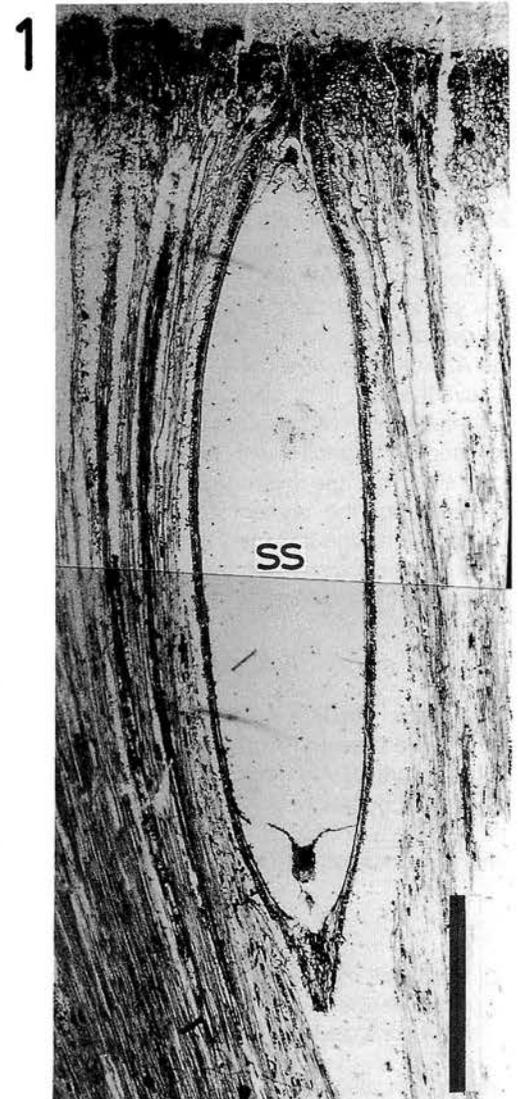
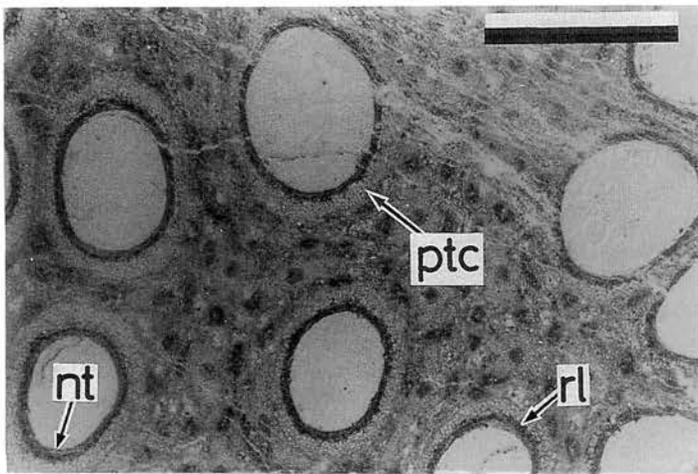
Acknowledgments

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Figure 4. *Bennetticarpus yezoites* sp. nov. Thin scale-bar indicates 200 μ m. **1:** Radial longitudinal section of the middle portion of a seminiferous scale. Nucellar stalk (ns) is slender consisting of scalariform tracheids, running upward and diverging in the saucer-like tissue (slt) as fibrous vascular strands (vs). This strand merges into the thin layer of nucellus remains at the outer marginal part of the seed space (Arrow A). Dark elongate cell layer (dec) is thickest just above the level h in Figure 1B, thinning out upward and downward. At level f (Figure 1B), this layer merges into the remains of nucellus (nt). Outside the radial layer (rl), this layer is enveloped by long and thin walled tubular cell layers (ptc), and is in contact with more narrow tubular cell layers of neighboring interseminal scales (int). Note that this figure was made by adjoining two photographs, consequently there is a small offset where they meet. **2:** Saucer-like tissue (slt) enlarged from Figure 4-1. **3:** Transverse section of the saucer-like tissue (at g-level in Figure 1B). Cells are nearly isodiametric and their cell walls are ornamented by scalariform pattern. **4:** Radial longitudinal section of the nucellar stalk. The fibrous vascular strand (vs) is about to enter and merge into the remains of the nucellus (Arrow B). Structureless fleshy layer (fl) is seen around the nucellar stalk and saucer-like tissue.



ptc ptc ptc

nt ptc ptc nt

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Figure 5. *Bennetticarpus yezoites* sp. nov. Thick and thin scale-bars indicate 2 mm and 200 μ m respectively. **1:** Nearly radial longitudinal section of an orthotropous ovule. Neighboring interseminal scales are curved as a result of the corpulence of the seed space. Peripheral layers are darkish because of thick-walled and heavily cutinized cells. **2:** Transverse section of seed spaces. Each space is surrounded, from inside to outside, by remains of nucellus (nt), dark elongate cells, radial and parenchymatous tubular cell layers, cut at level e (Figure 1B). Both dark elongate cells and radial cell layers are darkish. Among these seed spaces many interseminal scales are seen. Dark dots show the transverse section of the vascular bundles. **3:** Longitudinal section of scalariform tracheids in nucellar stalk. They are often pinned against the wall of fleshy cylinder (cf. Figure 6-5, 6). **4:** Longitudinal section of poorly preserved tracheids in the nucellar stalk. **5:** Longitudinal section of two ovules. Both nucellar stalks are surrounded by radial layers inside and parenchymatous tubular cell layers (ptc) outside. **6:** Enlarged from the boxed area in Figure 5-5. A fibrous vascular strand (vs) enters into and merges with remains of the nucellar tissue (nt).

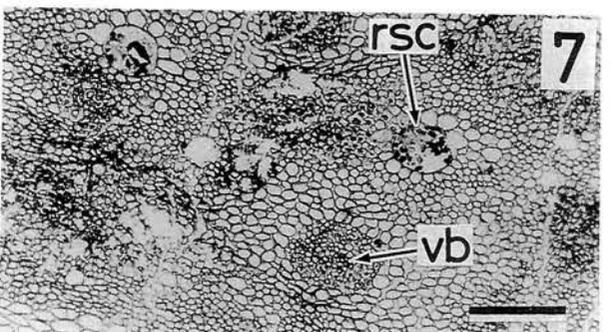
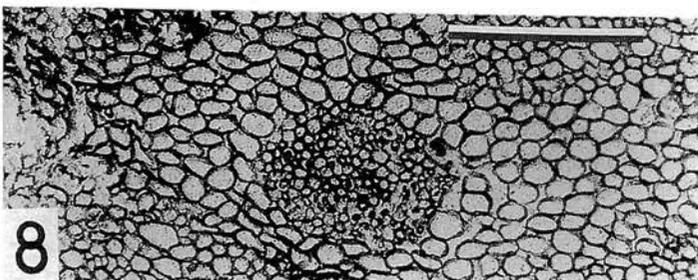
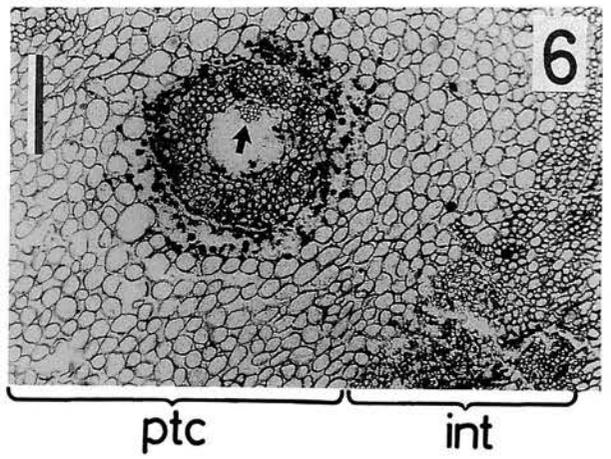
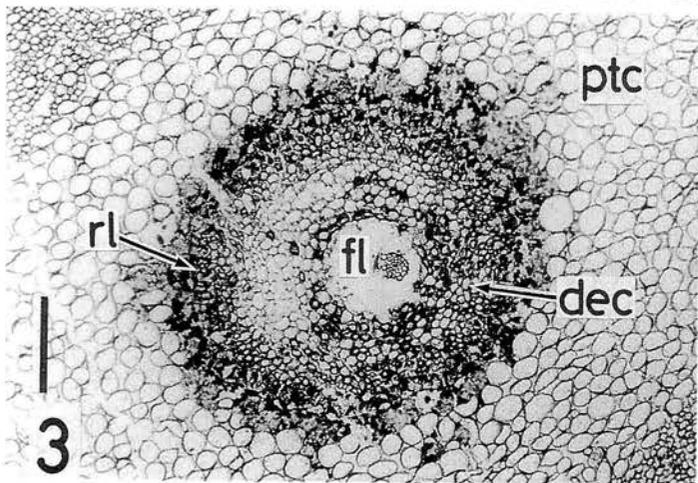
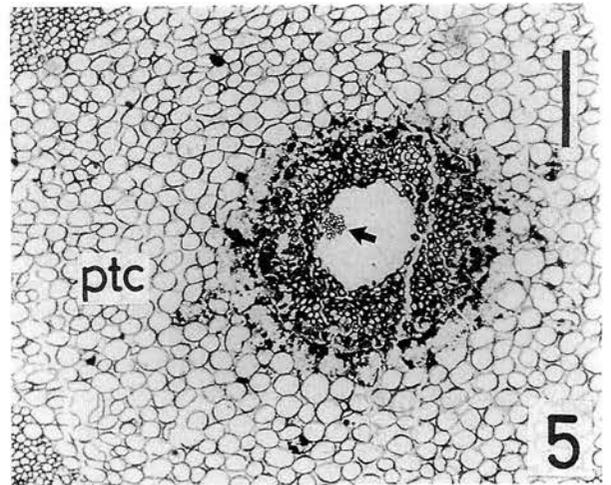
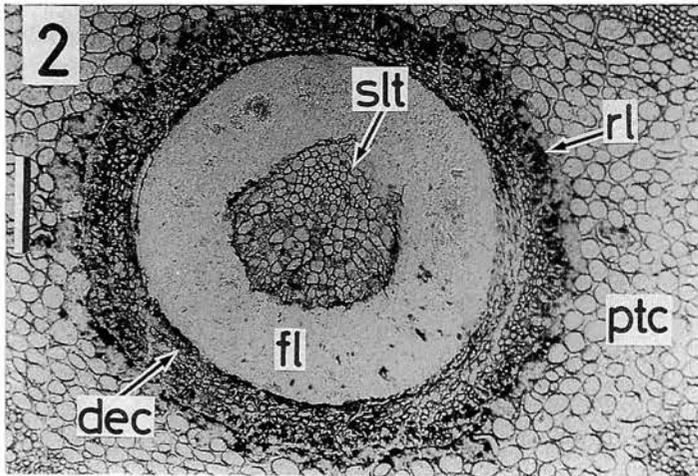
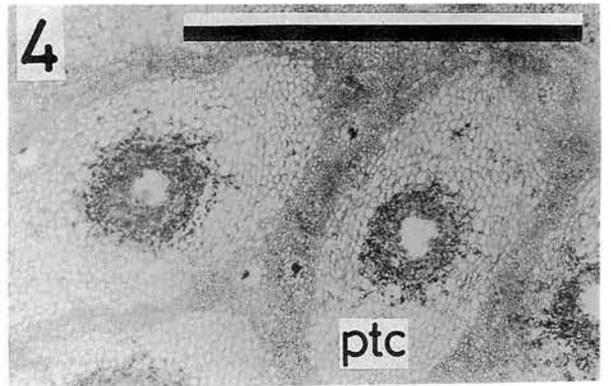
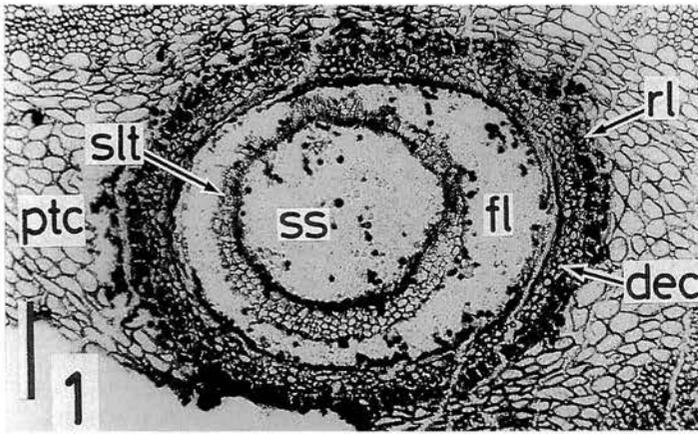


Figure 6. *Bennetticarpus yezoites* sp. nov. Thick and thin scale-bars indicate 2 mm and 200 μm respectively. **1:** Transverse section cut at level f (Figure 1B). Concentric tissues, from outside to inside, are: darkish radial layer (one cell thick and single row) (rl), layer of dark elongate cells (dec), structureless fleshy layer (fl), saucer-like tissue (slt) and bottom of the seed space (ss). These tissues (or layers) are enveloped by parenchymatous tubular cells layer (ptc). Layers of small cells seen at three corners belong to the neighboring interseminal scales. **2:** Transverse section cut at level g (Figure 1B). Concentric tissues, from outside to inside, are: radial layer (one cell thick) (rl), layer of dark elongate cells (dec), structureless fleshy layer (fl) and saucer-like tissue (slt). They are enveloped by a layer of parenchymatous tubular cells (ptc). **3:** Transverse section cut at level h (Figure 1B). Three concentric tissues are seen; they are in turn, radial layer (one cell thick) (rl), dark elongate cells layer (dec) and structureless fleshy layer (fl). Vascular bundle is seen in the fleshy cylinder. **4:** Transverse section cut at level i (Figure 1B). Darkish ring consists of thin radial layer and dark elongate cells layer. Parenchymatous tubular cells layer (ptc) is usually oval-shaped. **5:** One-sided location of the vascular bundle (arrow) in the fleshy cylinder. **6:** The same. Small-sized cells belong to the neighboring interseminal scales (int). **7:** Transverse section of deformed interseminal scales cut at level j (Figure 1B), showing vascular bundle (vb) and many scattered resin cells (rsc). **8:** A vascular bundle enlarged from Figure 6-7. It is difficult to distinguish the phloem elements.

Triassic coniform conodont genera *Aduncodina* and *Neostrachanognathus*

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Abstract. Lower Triassic coniform conodonts *Aduncodina unicosta* Ding and *Neostrachanognathus tahoensis* gen. et sp. nov. from the pelagic limestone of the Taho Formation in Ehime Prefecture, Southwest Japan are newly reconstructed as quadrimembrate apparatuses with the M, Sa, Sb, and Sc elements. *A. unicosta* Ding, originally described as a form species, is the Sb element of the skeletal apparatus of *A. unicosta*, newly conceived. Furthermore, the form species *Cornudina anterodentata* Ding and *C. angularis* Wang and Cao are referable to the Sa and Sc elements of *A. unicosta*, respectively. The elements of *A. unicosta* and *N. tahoensis* are all coniform types. The M elements of the two species are adenticulated and the Sa, Sb, and Sc elements are denticulated with one to four denticles on the anterobasal margin of the base. The morphologic similarity between Triassic *A. unicosta* and *N. tahoensis* and the Early to Middle Paleozoic coniform-type conodonts probably represents an adaptive convergence of the feeding apparatuses. *A. unicosta* and *N. tahoensis* indicate the early Spathian.

Key words : *Aduncodina unicosta* Ding, coniform conodonts, *Neostrachanognathus tahoensis* gen. et sp. nov., quadrimembrate apparatus, Taho Formation, Triassic.

Introduction

A form species of conodont, *Aduncodina unicosta* Ding, was recovered by Ding (1983) from the Lower Triassic Helongshan Formation of Mt. Majiashan of Chaoxian, Anhui Province, South China. This species is a coniform element characterized by a nongeniculate, slender, and suberect cusp and the presence of one to three hook-like denticles on the anterobasal margin of the base.

This uniquely shaped conodont also occurs abundantly in the pelagic limestone of the Triassic Taho Formation exposed at Tahokamigumi, Shirokawa-cho, Higashiuwagun, Ehime Prefecture, Southwest Japan (Figure 1). As a result of statistical analysis of the conodont fauna, including the form species *A. unicosta*, it has been made clear that this form species is one of the elements of a quadrimembrate skeletal apparatus composed of the M, Sa, Sb, and Sc elements. The M element is an adenticulated and the Sa, Sb, and Sc elements are denticulated nongeniculate coniform types with one to four denticles on the anterobasal margin of the base. The form species *A. unicosta* of Ding (1983) is the Sb element of the apparatus. Furthermore, the form species *Cornudina anterodentata* Ding and *C. cf. oezdemirae* Gedik described by Ding (1983) from the same sample yielding *A. unicosta* can be regarded as the Sa and Sc elements of the apparatus, respectively. The form species *C. angularis* Wang and Cao (1993) from the Upper

Chinglung Formation of the Early Triassic at Jiangning in Nanjing can be also referred to the Sc element of the skeletal apparatus.

I propose herein *Aduncodina unicosta* Ding for this quadrimembrate skeletal apparatus composed of four coniform type elements. *Aduncodina unicosta* is an index of the early Spathian.

In the Taho Formation there occurs another quadrimembrate coniform species. The elements are basically common in morphology with those of *A. unicosta*. The M element is an adenticulated and the Sa, Sb, and Sc elements are denticulated nongeniculate coniform types with one denticle on the anterobasal margin of the base.

I also propose herein *Neostrachanognathus tahoensis* gen. et sp. nov. for the quadrimembrate conodont species. *Cratognathodus* sp. reported by Buryi (1989) from the Spathian in the Dalnegorsk region, Sikhote-Alin is the Sb element of this new species. *Neostrachanognathus tahoensis* indicates the early Spathian.

Coniform elements are considerably dominant components in apparatuses of conodonts diversified during the Late Cambrian to Devonian but quite rare or almost absent in the post-Devonian Paleozoic. The reconstruction of coniform conodont apparatuses is, therefore, very important for the study of evolution of the Conodonta. I describe the skeletal apparatuses of *A. unicosta* and *N. tahoensis* and consider the phylogeny of these genera comparing with

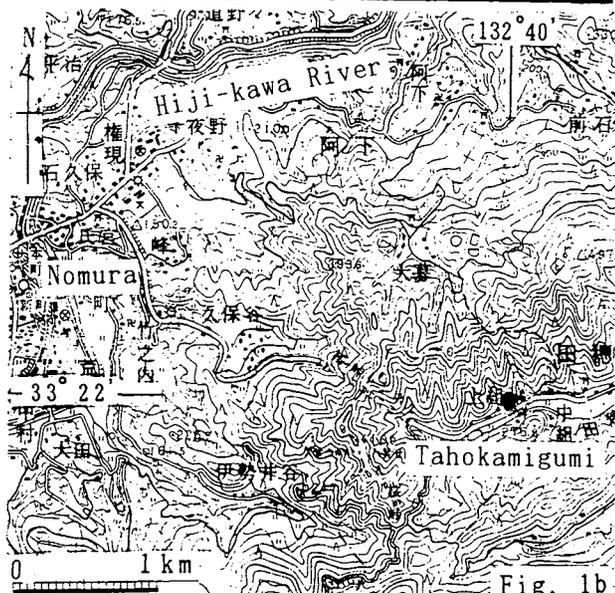
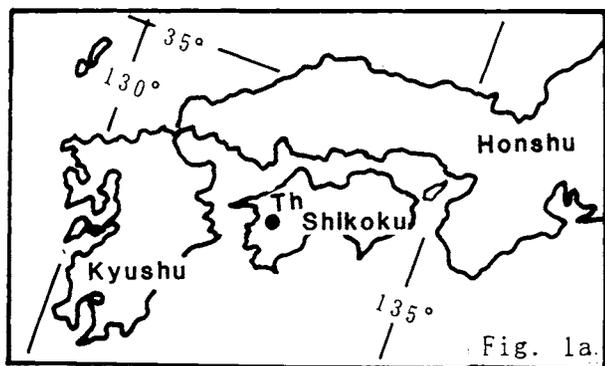


Figure 1. Index map showing the location of the study section. 1a. Index map. Th: Tahokamigumi. 1b. Solid circle shows the outcrop section of Taho Formation at Tahokamigumi, Shirokawa-cho, Higashi-ura-gun, Ehime Prefecture, Southwest Japan.

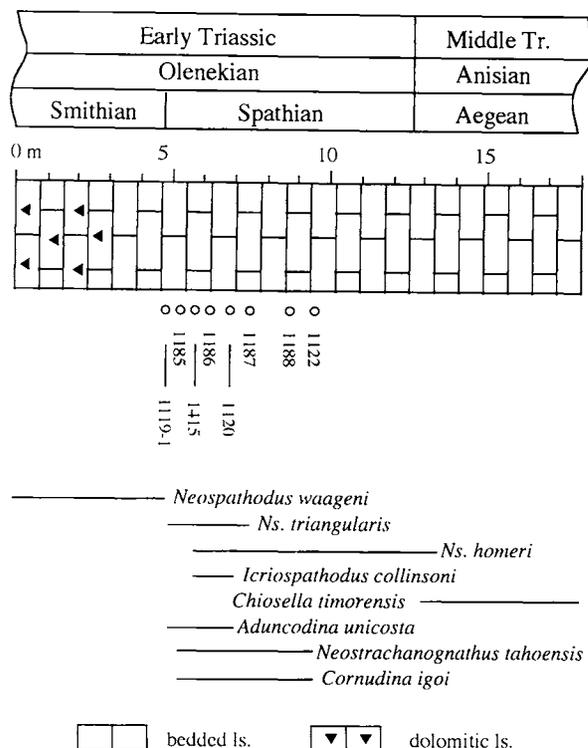


Figure 2. Stratigraphic section and vertical distribution of *Aduncodina unicosta* Ding, *Neostrachanognathus tahoensis* gen. et sp. nov., and important pectiniform conodonts.

Cornudina in the Triassic and some coniform apparatuses in the Paleozoic.

All of the described specimens are kept in the Department of Science Education, Faculty of Education and Human Sciences, Yokohama National University.

Biostratigraphic setting

Aduncodina unicosta and *N. tahoensis* are restricted respectively within the basal 2 and 4 m of the Spathian *Neospathodus triangularis*-*N. homeri* Zone (8 m thick) in the Triassic Taho Formation (Figure 2). The Spathian limestone is composed of dark gray, thin- to medium-bedded biomicrite including abundant thin-shelled bivalves and radiolarians and subordinate echinoderm crusts, small gastropods, and foraminifers. This lithologic feature indicates that the limestone is pelagic in origin. An estimated sedimentation rate is about 0.5-0.8 g/cm²/1,000 yr (Koike, 1994).

In the Taho Formation, *A. unicosta* and *N. tahoensis* occur

with *Neospathodus triangularis* (Bender), *N. homeri* (Bender), *Icriospathodus collinsoni* (Solien), *Cornudina igoi* Koike, *Elisonia triassica* Müller, *E. dinodoides* (Tatge), and many unidentified coniform and ramiform elements. Among them, the first four species are restricted to the Spathian.

The form species *A. unicosta* proposed by Ding (1983) for the Sb element of the *A. unicosta* apparatus is associated with *N. triangularis*, *N. homeri*, and *I. collinsoni* in the Helongshan Formation in Anhui Province, South China. The form species *Cornudina angularis* proposed by Wang and Cao (1993) for the Sc element of the *A. unicosta* apparatus occurs in the Upper Chinglung Formation in Nanjing which yields *N. triangularis* and *N. homeri*. Consequently, the occurrence of the *A. unicosta* apparatus in South China well accords with that of Japan in age.

Cratognathodus sp., described by Buryi (1989) from the Spathian of Sikhote-Alin can be assigned to the Sb element of the *N. tahoensis* apparatus. The biostratigraphic range of *N. tahoensis* also accords with that established in Japan.

The apparatus of *Aduncodina unicosta* Ding

Aduncodina unicosta is reconstructed as a quadrimembrate skeletal apparatus in this study (Figure 3). The elements are composed of an adenticulated, a denticulated bilaterally subsymmetric, and two denticulated asymmetric nongeniculate coniform types. The denticulated coniform elements carry one to four anterobasal denticles. I assign

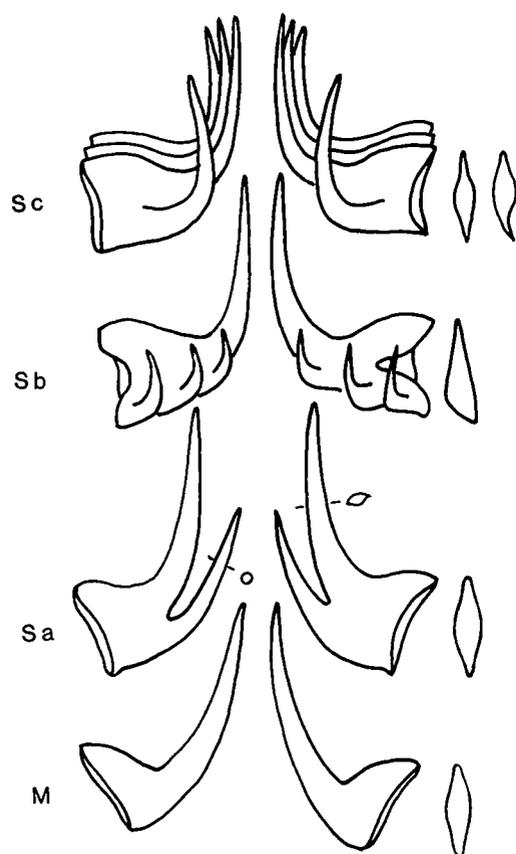


Figure 3. A hypothetically reconstructed apparatus of *Aduncodina unicosta* Ding. All elements are arranged in symmetric pairs.

the adenticulated subsymmetric coniform element to the M, the denticulated subsymmetric one to the Sa, and the asymmetric denticulated ones to the Sb and Sc positions, respectively.

The frequency of the M, Sa, Sb, and Sc elements in four samples is 20, 84, 58, and 181 and an approximate ratio of the elements is 0.3 : 1.5 : 1 : 3.1, respectively (Table 1). Triassic *Ellisonia dinodoides* (Tatge) statistically reconstructed by Koike (1994) comprises the M (breviform digyrate), Sa (bilaterally symmetric alate), Sb (extensiform digyrate), Sc (bipennate) elements whose inferred ratio is 2 : 1 : 2 : 4 or 6. Paleozoic ozarkodinid apparatuses reconstructed based on natural assemblages are composed of the M (breviform digyrate), Sa (alate), Sb₁ (bipennate), Sb₂ (bipennate), Sc₁ (bipennate), Sc₂ (bipennate), Pa (carminiscaphate), and Pb (angulate) elements, the ratio among which is 2 : 1 : 2 : 2 : 2 : 2 : 2 : 2 (Purnell and Donoghue, 1998, etc.). The composition of the apparatus of the Pennsylvanian prioniodinid *Gondolella* is almost the same as for the ozarkodinids (von Bitter and Merrill, 1998). *Aduncodina unicosta* has, therefore, relatively rare M elements and abundant Sa elements compared with those previously confirmed multielement apparatuses with ramiform (M and S series) and pectiniform (P series) elements.

According to Dzik and Drygant (1986), the Sa (tr) element

Table 1. Occurrence of M, Sa, Sb, and Sc elements of *Aduncodina unicosta* Ding obtained from 5 to 10 kg of limestone.

Loc.	M	Sa	Sb	Sc
1119-1	2	3	4	19
1185	1	9	2	15
1415	16	63	45	111
1186	1	9	7	36
total	20	84	58	181
ratio	0.3	: 1.5	: 1	: 3.1

is bilaterally subsymmetric and considered to be paired in most coniform apparatuses in the Ordovician. The relative abundance of the Sa element in the *A. unicosta* apparatus may be comparable to the above-mentioned feature of the Ordovician coniform apparatuses.

It is, however, difficult to explain why the occurrence of the M element is rare compared with that of the Sa and Sb elements in the *A. unicosta* apparatus. Further study is necessary to confirm the positions and proportions of the elements in *A. unicosta* based on more abundant specimens.

The four elements considered to be of the *A. unicosta* apparatus have common morphologic characteristics such as thin wall, suberect cusp, moderately deep basal cavity, and hook-like anterobasal denticles in the S series. The morphologic characteristics of each element are as follows.

The M element is a bilaterally subsymmetric adenticulated coniform type.

The Sa element is a bilaterally subsymmetric coniform type with one proclined denticle on the anterobasal margin.

The Sb element is a bilaterally asymmetric coniform type with the triangular basal margin and one to three laterally curved hook-like anterobasal denticles.

The Sc element is a bilaterally asymmetric coniform type with the lenticular basal margin and one to four laterally curved hook-like anterobasal denticles.

The apparatus of *Neostrachanognathus tahoensis* gen. et sp. nov.

The skeletal apparatus of *N. tahoensis* is quadrimembrate and consists of an adenticulated, a denticulated subsymmetric, and two denticulated asymmetric nongeniculate coniform elements (Figure 4). The denticulated asymmetric elements bear one or two anterobasal denticles. I regard the subsymmetric adenticulated element as the M, the subsymmetric denticulated one as in the Sa, and the asymmetric denticulated ones as in the Sb and Sc positions, respectively.

The total number of the M, Sa, Sb, and Sc elements from six samples is 18, 39, 41, and 85 and an approximate ratio of the elements is 0.4 : 1 : 1 : 2, respectively (Table 2). The relative small number of the M and large number of the Sa elements in this skeletal apparatus show the same tendency with the *A. unicosta* apparatus.

The four elements possess common characteristics such as thick wall, suberect to proclined and tapering cusp,

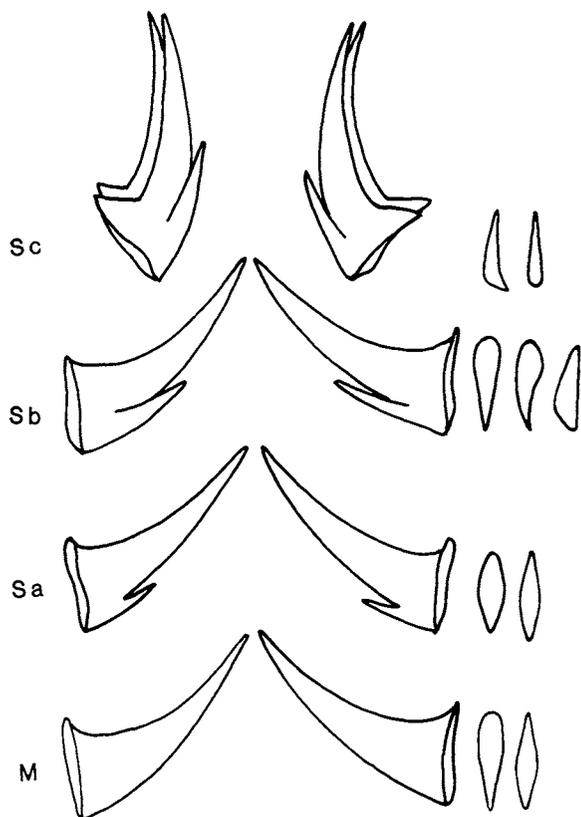


Figure 4. A hypothetically reconstructed apparatus of *Neostrachanognathus tahoensis* gen. et sp. nov. All elements are arranged in symmetric pairs.

Table 2. Occurrence of M, Sa, Sb, and Sc elements of *Neostrachanognathus tahoensis* gen. et sp. nov. obtained from 3 to 5 kg of limestone.

Loc.	M	Sa	Sb	Sc
1185	1	3	4	8
1415	3	6	7	8
1120	9	29	28	67
1186	3	1	1	1
1188	1	0	1	0
1122	1	0	0	1
total	18	39	41	85
ratio	0.4	: 1	: 1	: 2

shallow basal cavity, and one or two small to large antero-basal denticles in the S series. The morphologic characteristics of each element are as follows.

The M element is a bilaterally subsymmetric adenticulated coniform type.

The Sa element is a bilaterally subsymmetric coniform type with one denticle on the antero-basal margin.

The Sb element is a bilaterally asymmetric coniform type with one or two antero-basal denticles bending inwardly.

The Sc element is a bilaterally asymmetric coniform type with the posteriorly extending base and one or two antero-basal denticles bending inwardly. A small denticle may be present on the posterior portion of the base.

Coniform conodonts in the Triassic

As mentioned above, coniform elements are dominant components in the apparatuses of most conodont genera and species in the Late Cambrian to Devonian but are quite rare or almost absent in the Carboniferous and Permian. In the Triassic, coniform conodont elements are also rare but more common than in the Carboniferous and Permian.

In addition to *A. unicosta*, *Zieglericonus rhaeticus* Kozur and Mock was previously proposed as a coniform type and some coniform conodonts were assigned to *Cornudina* or allocated as an unidentified genus.

Zieglericonus rhaeticus proposed by Kozur and Mock (1991) for the coniform element occurred in the upper Rhaetian of Hungary. This species is characterized by a proclined to erect cusp with fine striations and a deeply excavated basal cavity.

Genus A reported by Hatleberg and Clark (1984) from the upper Spathian of Nepal consists of three nongeniculate coniform elements of the alate (Sa), digyrate (M or Sb), and bipennate (Sc) types. They did not describe whether the three elements are of one or more apparatuses. It is probable that the alate type (Pl. 4, fig. 14 of Hatleberg and Clark, 1984) is of a multielement species, the digyrate (Pl. 4, fig. 15) and bipennate (Pl. 4, figs. 11, 12) types are of another multielement species judging from the same type elements occurring in the Spathian of the Taho Formation.

The form genus *Cornudina* was recently reconstructed as a unimembrate or bimembrate apparatus on the basis of samples from the Taho Formation and two species were proposed for the *Cornudina* apparatuses by Koike (1996).

The bimembrate *Cornudina* apparatus, *C. breviamulis* (Tatge) is the type species of *Cornudina* and consists of the segminate pectiniform Pa and angulate pectiniform Pb elements. The Pa element is composed of a long cusp and short anteroposterior processes with one to four denticles. The Pb element consists of a large cusp, a short anterior process with one to five denticles, and a relatively long twisted posterior process with four to seven denticles (Figure 5).

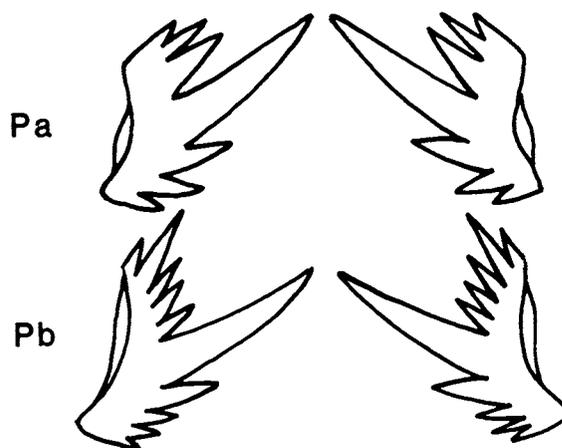


Figure 5. A reconstructed apparatus of *Cornudina breviamulis* (Tatge).

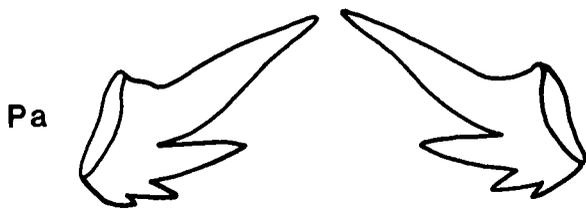


Figure 6. A reconstructed apparatus of *Cornudina igoi* Koike.

The pectiniform Pa and Pb elements of *C. breviramulis* reveal evolutionary trends of decrease in size of the processes and in number of denticles on the processes during Early to Late Triassic times and some of the Pa elements in the Middle and Late Triassic appear to be coniform.

The unimembrate *Cornudina* apparatus, *C. igoi* enacted by Koike (1996), is composed of the segminate pectiniform Pa elements with a long cusp and a very short anterior process carrying one to three denticles (Figure 6). *Cornudina igoi* is restricted within the early Spathian. The elements of *C. igoi* with one anterior denticle look like a coniform type and fairly resemble the Sa element of *N. tahoensis*.

Cornudina was allocated to the genus *Chirodella* of the family Xaniognathidae by Sweet (1981). Koike (1996) separated *Cornudina* from *Chirodella* because the elements of their apparatuses are completely different. It is very difficult to determine the phylogenetic position of *C. breviramulis* and *C. igoi* in the family-group category because both species are different in combination and morphology of apparatus elements from the previously proposed conodont groups in the Triassic. I regard *Cornudina*, however, as belonging to the family Gondolellidae because the segminate Pa elements of *C. breviramulis* and *C. igoi* and the angulate Pb elements of *C. breviramulis* indicate some morphologic similarities with the Pa and Pb elements of the family Gondolellidae proposed by Sweet (1988), respectively.

Early Anisian *Cornudina oezdemirae* proposed by Geidik (1975) and late Anisian *C. unidentata* proposed by Kozur and Mostler (1972) are coniform types whose generic names should be reexamined.

The Tahoe Formation yields more than eight types of coniform elements besides those in *A. unicosta* and *N. tahoensis*. I have not reconstructed yet any apparatuses based on the elements because they are not abundant in number. They are, however, referable to 3 or 4 multielement species judging from their occurrence in the strata. More than five coniform multielement species are, therefore, present in the Tahoe Formation.

Phylogeny of *Aduncodina* and *Neostrachanognathus*

Most Early Triassic conodonts previously described belong to the family Sweetgnathidae and Spathognathodontidae of the order Ozarkodinida, the family Ellisoniidae and Gondolellidae of the order Prioniodinida (Sweet, 1988). The apparatuses of these families in the late Paleozoic are composed of six to eight types of elements with the pectiniform P

elements in the P position and ramiform elements in the M and S positions but some lineages lost elements in the Triassic, becoming quinquimembrate with ramiform elements in the M and S positions or unimembrate with a pectiniform element in the Pa position (Sweet, 1988, etc.). Skeletal apparatuses with coniform elements are uncommon in the Ozarkodinida and Prioniodinida which ranged from the Early or Middle Ordovician through the Triassic.

On the other hand, the Early to Middle Paleozoic conodont orders (e.g., Belodellida, Protopanderodontida, and Prioniodontida) include many species and genera with multimembrate apparatuses composed of coniform elements (Sweet, 1988; Dzik, 1989, 1991, etc.).

Among the species and genera in these orders, Ordovician *Strachanognathus parvus* enacted by Rhodes (1955) is closely similar to *Neostrachanognathus tahoensis* proposed herein, being composed of nongeniculate coniform elements with a distinct anterobasal denticle. *Strachanognathus parvus* was identified as a unimembrate apparatus by Bergström (1981). Dzik (1989) distinguished, however, six types of coniform elements with an anterobasal denticle in the *S. parvus* apparatus.

The S elements of *Dapsilodus* and *Walliserodus* of the Belodellida are similar to the elements of *Aduncodina unicosta* in shape of the base and cusp, although they have no anterobasal denticles. The Belodellida became extinct by the end of the Devonian.

The Icriodontidae of the Prioniodontida is one of the youngest families including coniform elements in the M and S positions of the apparatuses. The coniform elements in the S positions of *Pelekysgnathus* of the Icriodontidae somewhat resemble *N. tahoensis*, although they do not possess any anterobasal denticles. The family is regarded to disappear by the end of the Devonian.

The coniform elements from the Carboniferous are quite rare. Among less than five coniform type species described (Cooper, 1939, etc.), Pennsylvanian *Neoprioniodus? expandofundus* Webster reported by Rabe (1977) from the Eastern Andes of Colombia is somewhat similar to the Sa element of *N. tahoensis*. I am unaware of any reports of Permian or Early Triassic Induan coniform conodonts.

It is quite interesting that more than five coniform multielement species including *A. unicosta* and *N. tahoensis* appeared in the Spathian 120 to 50 million years after the extinction of Devonian or Carboniferous coniform conodonts. I consider that the Triassic coniform types evolved from the ramiform types and the morphologic similarity (homeomorphy) between the Triassic coniform types and the Early to Middle Paleozoic ones may be a result of adaptive convergence of the elements as the feeding apparatuses. It is difficult to show in detail the differences in function between coniform and ramiform types and those among coniform elements in an apparatus. It is thought, however, that conodont animals were predators and coniform and ramiform types functioned in grasping and/or cutting food (Jeppsson, 1979; Dzik, 1991; Purnell, 1995).

A probable evolution from ramiform to coniform elements in the Early Triassic may represent the divergence of feeding mechanisms in the conodont apparatuses. The Triassic

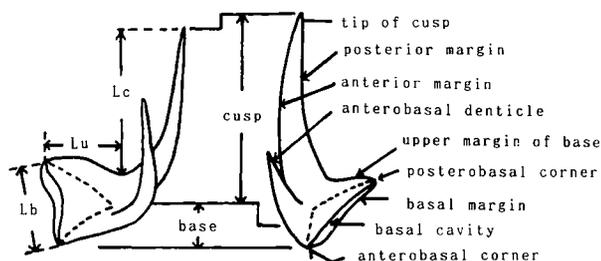


Figure 7. The morphology of the Sc elements of *Aduncodina unicosta* Ding (left) and *Neostrachanognathus tahoensis* gen. et sp. nov. (right). Lc: length of cusp, Lu: length of upper margin of base, Lb: length of basal margin

coniform elements probably evolved from the lineage of the Gondolellidae or Ellisonidae, which survived the Permian and diversified in the Early Triassic. Much more paleontological information on the Early Triassic conodont apparatuses is necessary to discuss this problem in more detail.

Systematic paleontology

Genus *Aduncodina* Ding, 1983

Type species.—*Aduncodina unicosta* Ding, 1983

Diagnosis.—*Aduncodina* a quadrimembrate apparatus composed of an adenticulated and three denticulated non-geniculate coniform elements. Base of coniform unit relatively large and long. Basal cavity moderately deep. Cusp suberect. Denticles of denticulated elements situated at the anterobasal portion and relatively long, proclined or curved inwardly (Figures 7, 8). Quadrimembrate elements are of the M, Sa, Sb, and Sc positions. M element bilaterally subsymmetric and adenticulated. Sa element bilaterally subsymmetric and denticulated with a proclined denticle. Sb element characterized by a conspicuous outward basal expansion and one to three hook-like anterobasal denticles curved inwardly. Sc element has lenticular basal margin and carries one to four hook-like anterobasal denticles curved inwardly.

Aduncodina unicosta Ding, 1983

Figure 8

Sa element

Cornudina anterodentata Ding, 1983. p. 41, pl. 6, figs. 18 (?)–19, 23–24.

Sb element

Aduncodina unicosta Ding, 1983. p. 41, pl. 6, figs. 10–14, 20 (?)–21.

Sc element

Cornudina cf. *oezdemirae* (Gedik), Ding, 1983. p. 42, pl. 7, figs. 25–26.

Cornudina angularis Wang and Cao, 1993. p. 249, pl. 60, figs. 2, 15.

Description.— M, Sa, Sb, and Sc elements have common morphologic characteristics such as small unit, thin wall, relatively large and long base, suberect slender cusp with

subcircular cross section, and moderately deep basal cavity.

M element bilaterally subsymmetric adenticulated coniform. Base lenticular in cross section (Figure 3). Basal margin very weakly convex toward anterior and 180 to 240 μm in diameter. Upper margin of base 140 to 180 μm in length. Cusp attains 230 to 400 μm in length.

Sa element bilaterally subsymmetric denticulated coniform. Base lenticular in cross section. Basal margin weakly convex toward anterior and 110 to 210 μm in diameter. Upper margin of base 100 to 180 μm in length. Cusp attains 150 to 300 μm in length. Anterobasal margin carries one proclined denticle, about one third to one half of length of cusp, and subcircular in cross section. Apex of basal cavity extends near junction of cusp and anterobasal denticle.

Sb element bilaterally asymmetric denticulated coniform. Base conspicuously expands outwardly and triangular in cross section. Basal margin weakly to strongly convex anteriorly and 130 to 200 μm in diameter. Upper margin of base 100 to 200 μm in length. Cusp attains 130 to 300 μm in length. Anterobasal margin carries one to three hook-like denticles, which are discrete, subequal in size and about one fifth of length of cusp, and extended inwardly and curved upwardly. Apex of basal cavity situated near junction of cusp and anteriormost denticle.

Sc element bilaterally asymmetric denticulated coniform. Base lenticular in cross section. Basal margin weakly to strongly convex anteriorly and 110 to 180 μm in diameter. Upper margin of base 110 to 200 μm in length. Cusp attains 140 to 280 μm . Anterobasal margin bears one to four hook-like denticles, which exhibit the same features as those of Sb element. Basal cavity also shows the same characteristics as that of Sb element.

Remarks.—The form species *Cornudina anterodentata* proposed by Ding (1983) is bilaterally subsymmetric non-geniculate coniform with one or two proclined denticles on the anterobasal margin. The morphologic characteristics of the form species well accord with those of the Sa element of the *A. unicosta* apparatus. The Sa element from the Taho Formation, however, does not have two anterobasal denticles but only one denticle as far as observed.

The form species *Cornudina angularis* proposed by Wang and Cao (1993) and *Cornudina* cf. *oezdemirae* (Gedik) described by Ding (1983) are identical with the Sc element of *A. unicosta* in having lenticular cross section of the basal margin and carrying one inwardly flexing anterobasal denticle.

The Sa, Sb, and Sc elements of the *A. unicosta* and *N. tahoensis* apparatuses are common in arrangement of the anterobasal denticles, respectively. They are different, however, in outline of the unit, relative size of the base, shape of the basal cavity, cross section of the basal margin, and shape of the cusp and anterobasal denticles.

Repository.—YNUC15832–15857.

Genus *Neostrachanognathus* gen. nov.

Type species.—*Neostrachanognathus tahoensis* sp. nov.

Diagnosis.—Diagnosis of *Neostrachanognathus* newly

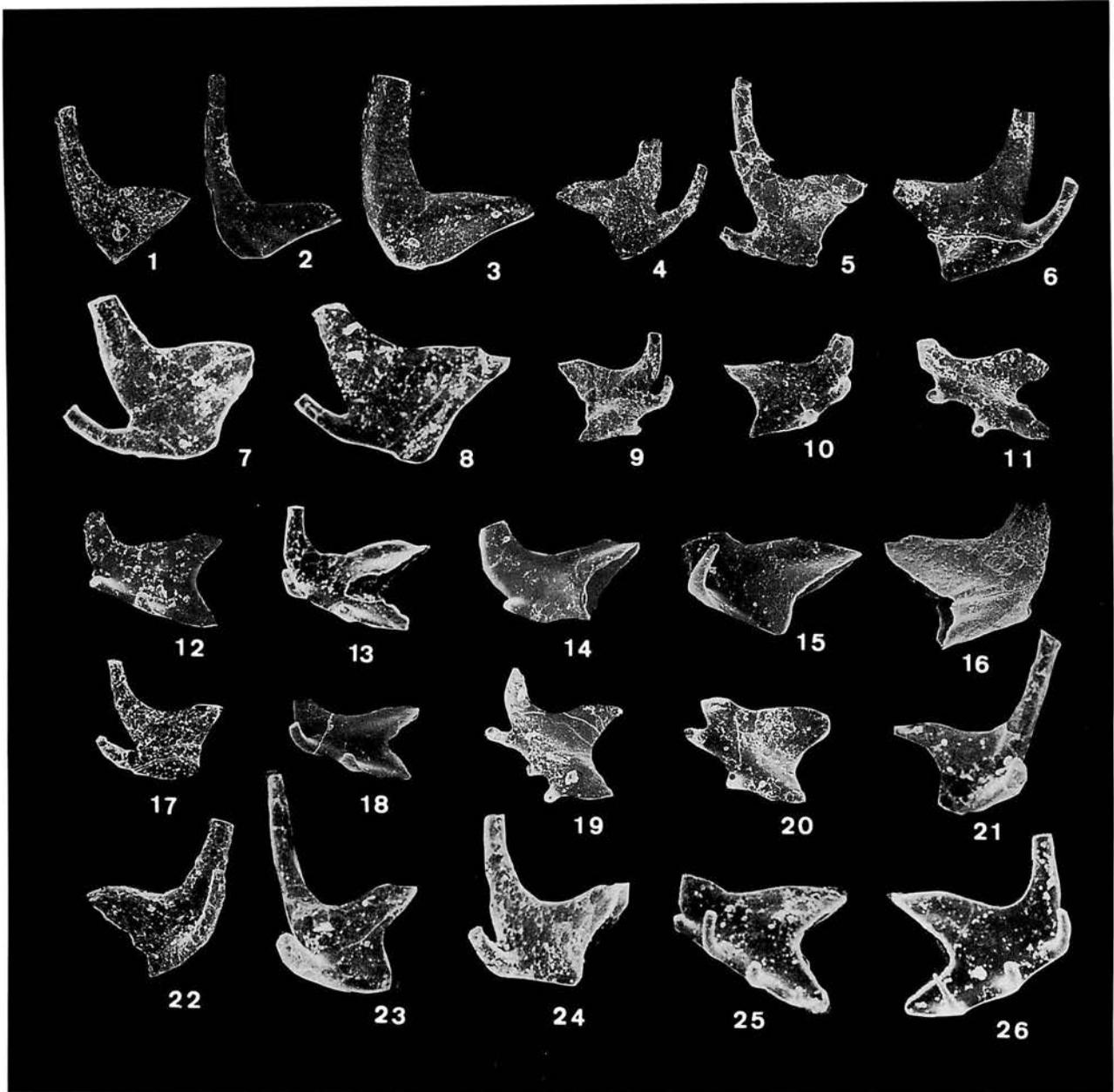


Figure 8. Elements of *Aduncodina unicosta* Ding from the Taho Formation, all $\times 100$. 1-3. M elements, YNUC15832-15834 from Loc. 1415. 4-8. Sa elements, 4: YNUC 15835 from Loc. 1415, 5: YNUC 15836 from Loc. 1119-1, 6: YNUC 15837 from Loc. 1415, 7-8: YNUC15838-15839 from Loc. 1185. 9-16. Sb elements, 9: outer lateral view, YNUC15840 from Loc. 1415, 10-12: inner lateral views, YNUC15841-15843 from Loc. 1415, 13: outer lateral view, YNUC15844 from Loc. 1186, 14-15: inner lateral views, YNUC15845-15846 from Loc. 1415, 16: outer lateral view, YNUC15847. 17-26. Inner lateral views of Sc elements, 17-20: YNUC15848-15851 from Loc. 1415, 21-24: YNUC15852-15855 from Loc. 1119-1, 25-26: YNUC15856-15857 from Loc. 1185.

proposed is based on *N. tahoensis* sp. nov. *Neostrachanognathus* is characterized by a quadrimembrate apparatus composed of an adenticulated and three denticulated nongeniculate coniform elements. Base of elements relatively small and short and the basal cavity shallow. Cusp proclined and tapered. Denticles of denticulated elements situated at anterobasal portion (Figures 7, 9).

elements referable to M, Sa, Sb, and Sc. M element bilaterally subsymmetric adenticulated coniform. Sa element bilaterally subsymmetric denticulated coniform and carries one small proclined anterobasal denticle. Sb element has inwardly bending one or two small to large anterobasal denticles. Sc element possesses long upper basal margin and carries inwardly flexing one or two small to large

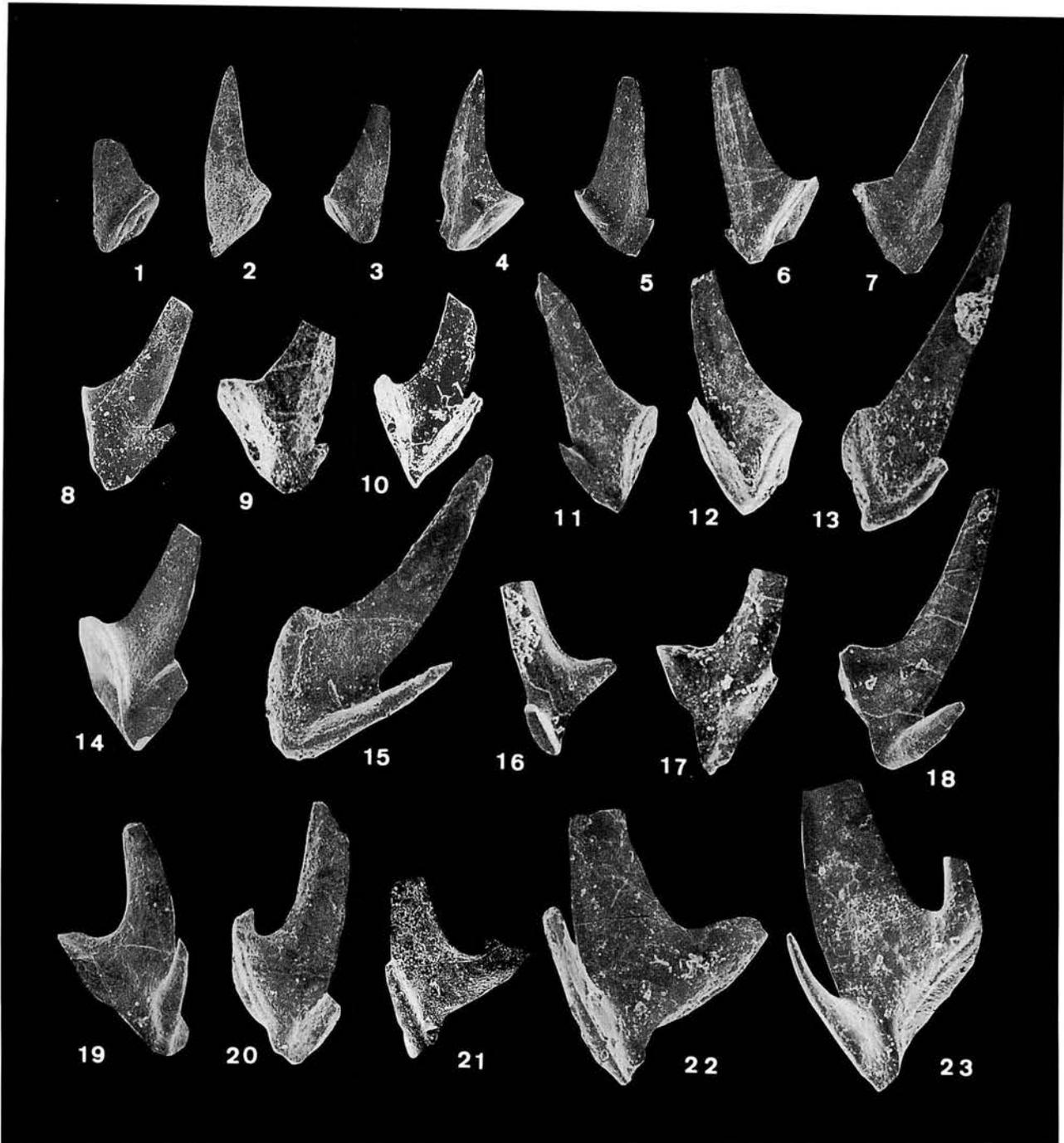


Figure 9. Elements of *Neostrachanognathus tahoensis* gen. et sp. nov., all $\times 100$. 1-4. M elements, YNUC15858-15861 from Loc 1120. 5-9. Sa elements, 5-8: YNUC15862-15865 from Loc. 1120, 9: YNUC15866 from Loc. 1185. 10-15. Inner lateral views of Sb elements, YNUC15867-15872 from Loc. 1120. 16-23. Inner lateral views of Sc elements, 16-17: YNUC15873-15874 from Loc. 1185, 18: YNUC15875 from Loc. 1120, 19: holotype, YNUC15876 from Loc. 1120, 20-23: YNUC15877-15880 from Loc. 1120.

anterobasal denticles. One posterior denticle may be present on the base.

Neostrachanognathus tahoensis sp. nov.

Figure 9

Sb element
Cratognathodus sp. Buryi, 1989, pl. 2, fig. 6.

Holotype.—Sc element YNUC 15876; Figure 9–19; Taho Limestone, Tahokamigumi, Shirokawa-cho, Ehime Prefecture.

Description.—Four elements of this apparatus exhibit common characteristics such as thick wall, relatively small and short base, and proclined and tapered cusp.

M element bilaterally subsymmetric adenticulated coniform. Lower view of basal margin lenticular shape with broadly or narrowly rounded posterobasal corner and bluntly pointed anterobasal corner. Basal margin 150 to 230 μm in diameter and upper margin of base 50 to 100 μm in length. Cusp stout, ellipsoidal in cross section, and 250 to 300 μm in length.

Sa element bilaterally subsymmetric denticulated coniform. Basal margin lenticular in shape, rounded and bluntly pointed at posterobasal and anterobasal corners, respectively in cross section, and 150 to 200 μm in diameter. Upper margin of base 30 to 80 μm in length. Cusp attains 240 to 300 μm in length. Anterobasal margin carries one short proclined denticle, which ranges from 20 to 50 μm in length and is ellipsoidal to subcircular in cross section.

Sb element bilaterally asymmetric denticulated coniform. Lower view of basal margin lenticular in shape with broadly rounded or bluntly pointed posterobasal corner and bluntly or sharply pointed anterobasal corner. Basal margin 180 to 230 μm in diameter and upper margin of base 40 to 80 μm in length. Cusp 250 to 350 μm in length. Anterobasal margin possesses inwardly bending one or two denticles. Longer denticle 50 to 150 μm in length.

Sc element bilaterally asymmetric denticulated coniform. Basal outer surface expanded and basal margin shows laterally compressed triangular shape in cross section. Basal margin 180 to 340 μm in length. Upper margin of base long and 80 to 140 μm in length. Cusp proclined to suberect and 270 to 500 μm in length. Anterobasal margin carries one or two inwardly flexing denticles. Longer denticle 80 to 250 μm in length.

Remarks.—The form species *Cornudina oezdemirae* proposed by Gedik (1975) was based on 16 specimens from the lower Anisian of the Kocaeli Peninsula, Turkey and its morphologic characteristics correspond to the subsymmetric Sa element of *N. tahoensis*. The holotype of *C. oezdemirae* illustrated by Gedik (Pl. 7, Fig. 24), however, lacks the anterobasal part. In that case, it is difficult to compare the specimen with *N. tahoensis* because incomplete specimens of *Cornudina igoi* lacking anterior denticles are also quite similar to *N. tahoensis*. There is a possibility that *N. tahoensis* or *C. igoi* is a synonym of *C. oezdemirae*. The information about *C. oezdemirae* by Gedik (1975), however, is insufficient to clearly distinguish it from these Japanese species.

The Sa element of *N. tahoensis* with a relatively large denticle is quite similar to *C. igoi* carrying only one anterior denticle, and *N. tahoensis* occurs together with *C. igoi*. Hence, there is a probability that *C. igoi* represents the Pa element of the *N. tahoensis* apparatus. The occurrence of *C. igoi*, however, is very common compared with that of *N. tahoensis*. For example, the frequency of the M, Sa, Sb, and Sc elements in *N. tahoensis* is 9, 29, 28, and 67, respectively but the specimens referable to *C. igoi* attain 318 in the

sample from the locality number 1120 in which both *N. tahoensis* and *C. igoi* occur abundantly. Thus, *Cornudina igoi* occurs more than ten times more commonly than the Sa and Sb elements of *N. tahoensis*, although robustness of the elements is almost the same. I regard here that *C. igoi* should not be considered the Pa element of *N. tahoensis*.

Buryi (1989) illustrated one specimen of the form species *Cratognathodus* sp. but did not offer any description. It is probably referable to the Sb element of the *N. tahoensis* apparatus, judging from the arrangement of the anterobasal denticles.

Repository.—YNUC15858–15880.

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Muscle attachment scars in a Carboniferous goniatite

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Abstract. A row of oval unpaired, ventral body attachment scars, accompanied by pseudosutures and drag bands, is preserved on surfaces of steinkerns of a lower Chesterian (Mississippian) goniatitid ammonoid, *Goniatites multiliratus*, from Oklahoma. Many smaller oval and crescentic attachment scars are present in the interspaces between these ventral attachment scars and between pseudosutures. Comparison with the muscle scars of other extant and fossil shelled cephalopods suggests that the unpaired ventral scars of this species represent the attachment sites of the muscle or ligament at the posterior end of the body. The smaller oval and crescentic scars on the ventral and lateral sides of each chamber appear to indicate weaker and less permanent attachments of muscular tissue to the shell wall. These are presumed to have been formed during gradual forward movement of the body.

Key words: Ammonoidea, Carboniferous, goniatites, mantle growth, muscle scar

Introduction

Various kinds of body attachment scars and impressions have been recognized on the inside shell surfaces and steinkerns of ammonoids (see Doguzhaeva and Mutvei, 1996, for a recent review). Two of the most common are: 1) suture-like impressions ("Pseudoloben" or pseudosutures) usually associated with spiral traces ("Schleppstreifen" or drag bands) (John, 1909; Bayer, 1977; Zaborski, 1986; Hewitt *et al.*, 1991; Lominadze *et al.*, 1993; Checa and Garcia-Ruiz, 1996); and 2) unpaired attachment scars on the mid-venter at the base of the body chamber (Crick, 1898; Jordan, 1968; Sarikadze *et al.*, 1990; Weitschat and Bandel, 1991; Doguzhaeva and Mutvei, 1996). Pseudosutures and drag bands are currently interpreted as impressions made by the rear part of the mantle as it gradually moved forward (Hewitt *et al.*, 1991; Checa and Garcia-Ruiz, 1996), while the mid-ventral attachment scar was probably the attachment site of the muscle or ligament that supported the circumsciphonal invagination at the poste-

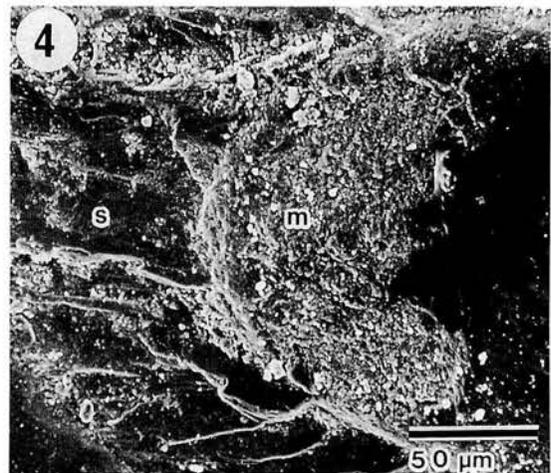
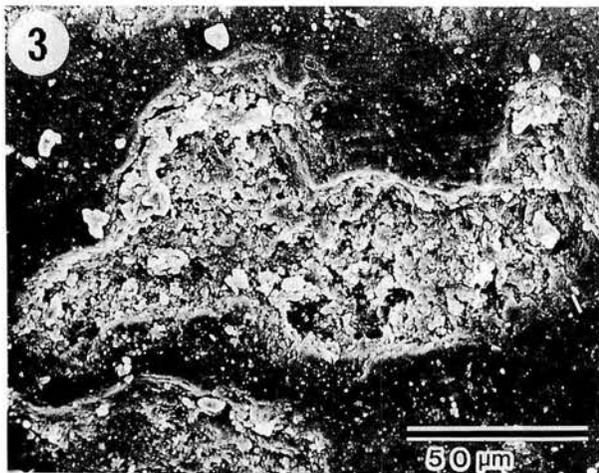
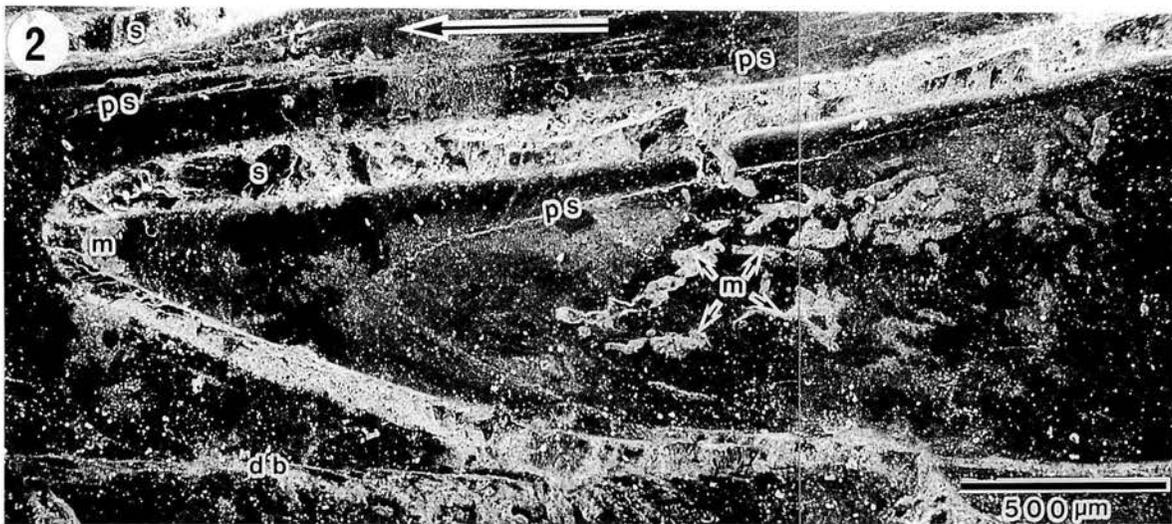
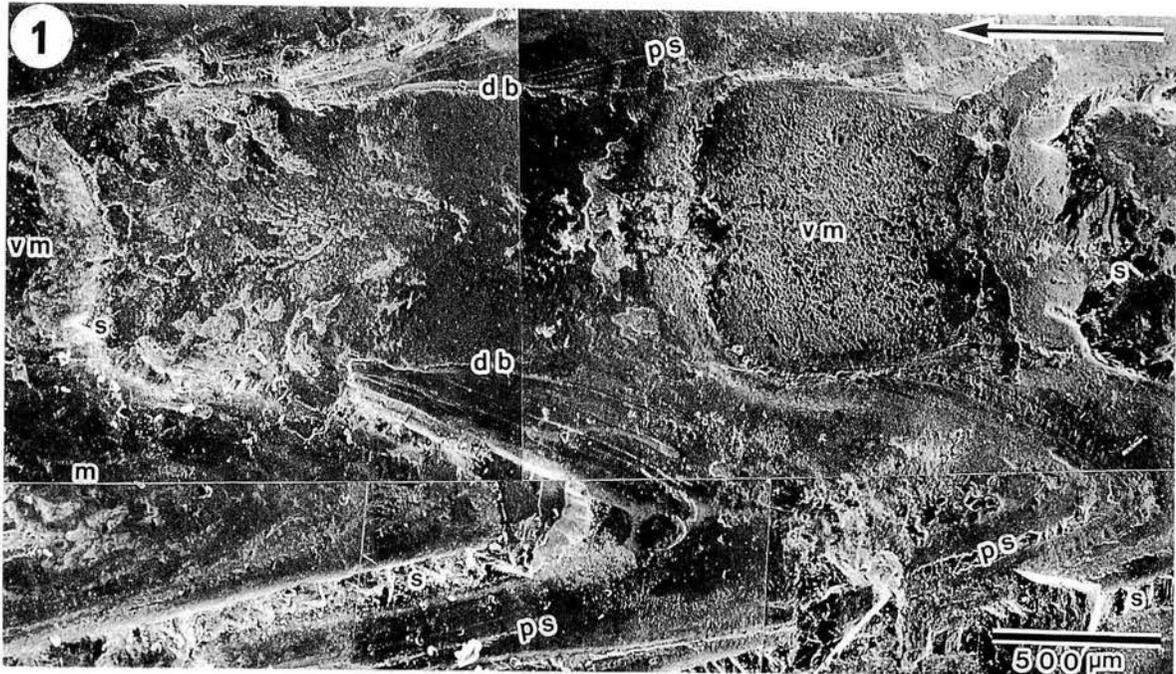
rior end of the body (Jordan, 1968; Doguzhaeva and Mutvei, 1996). These closely related types of scars and impressions are important in understanding the development of the growing mantle. However, they rarely co-occur in a single specimen, so previous studies of the growth of the ammonoid body in relation to new chamber formation have been based mainly on observations of pseudosutures and drag bands.

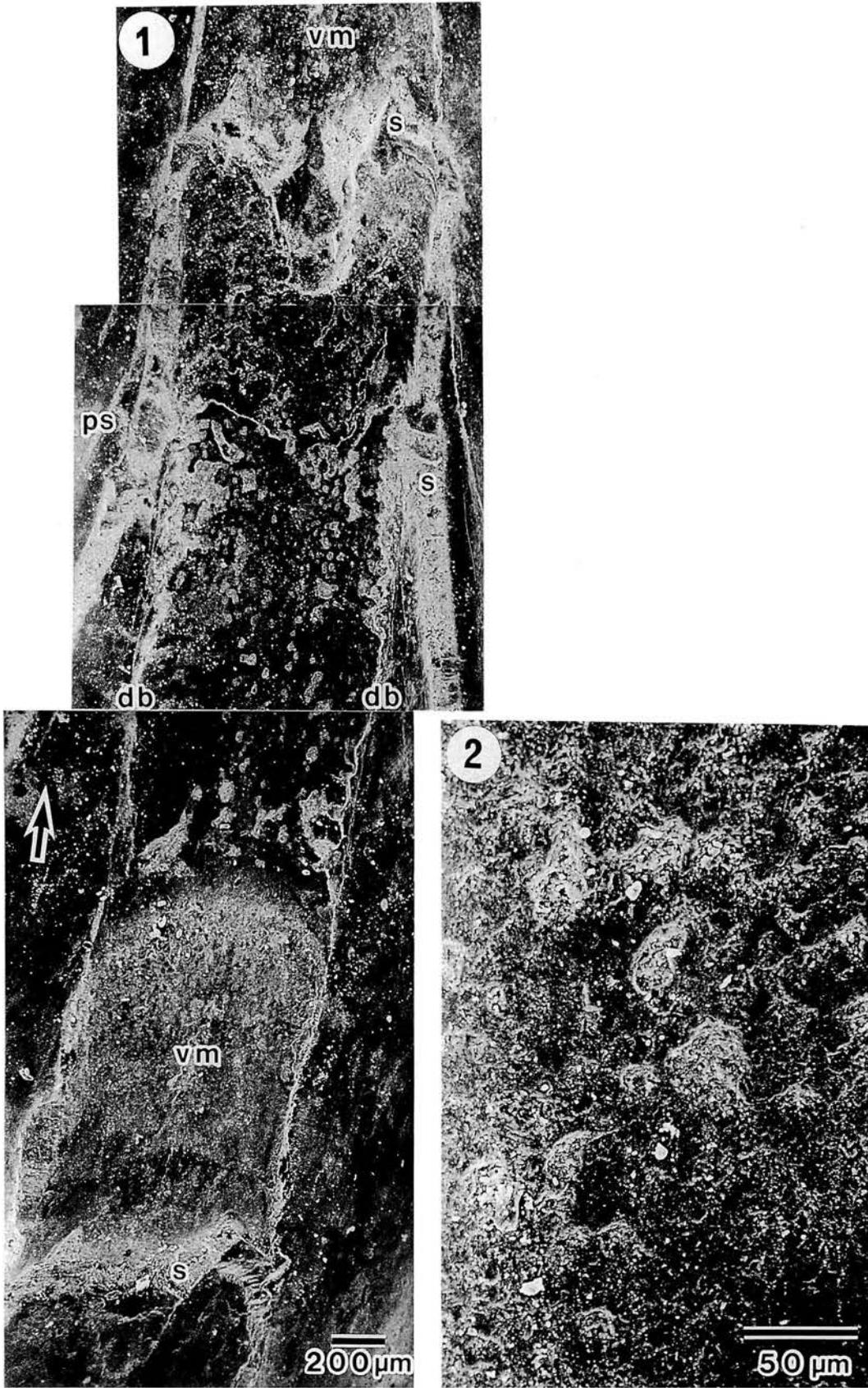
Here, two specimens of a Carboniferous goniatite in which both types of body attachment scars occur are described and their paleobiological implications are discussed.

Material and methods

Two immature specimens of *Goniatites multiliratus* Gordon (Goniatitina: Goniatitidae), both about 15 mm diameter, were examined. They were discovered in a calcareous concretion from the lower Chesterian (Mississippian) Caney Shale, exposed in Jack Fork Creek, Pontotoc County, Oklahoma (=Loc. M-1 of Mapes, 1979, fig. 2). We have previously

Figure 1. SEM micrographs showing muscle attachment scars and impressions on a specimen of the Mississippian ammonoid *Goniatites multiliratus* Gordon (UMUT, PM 19020-3). Arrows in 1 and 2 indicate the adoral direction. **1.** Unpaired ventral attachment scars (vm) on the adoral side of each mineralized septum (s). A pair of longitudinal drag bands (db) runs along the lateral margins of these scars. A sequence of pseudosutures (ps) and a cluster of small irregularly shaped attachment scars (m) are visible just adoral of the ventral lobe on the left side. **2.** Close-up of the adapical side of the first lateral saddle showing a cluster of small irregularly shaped attachment scars (m). **3.** Close-up of 2, showing a small irregularly shaped attachment scar adapical of the lateral saddle. **4.** Small attachment scar (m) just adapical of the first lateral saddle.





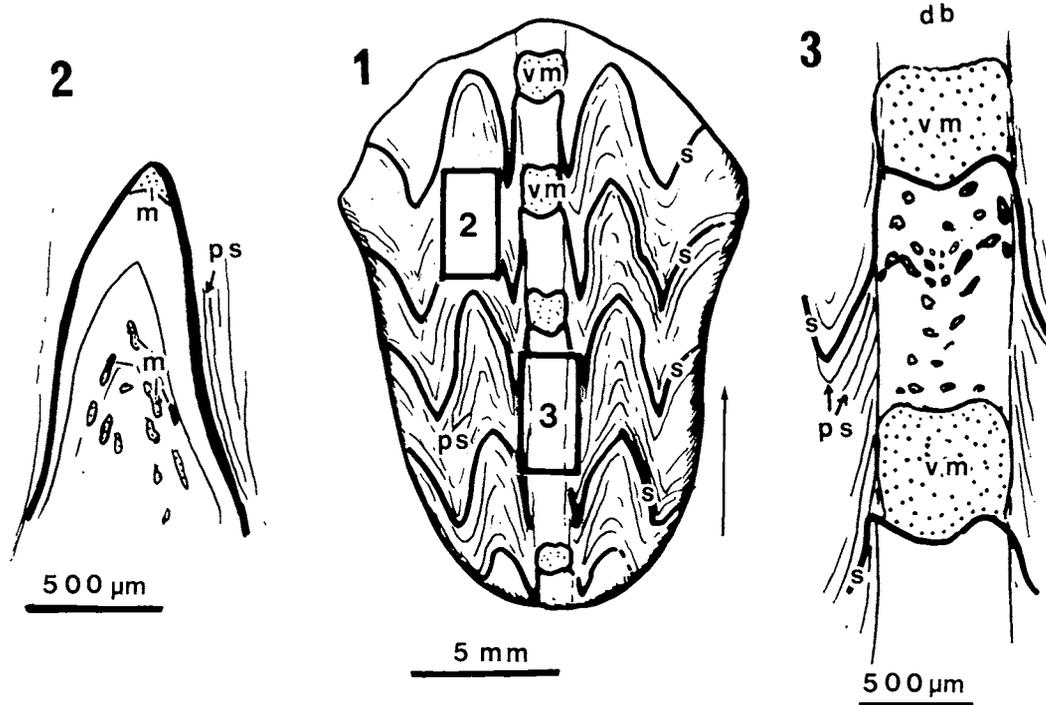


Figure 3. Diagrammatic drawing of a specimen of *Goniatices multiliratus* (UMUT. PM 19020-3), with unpaired ventral muscle attachment scars (vm) on the adoral side of each mineralized septum (s), that are accompanied by pseudosutures (ps) and drag bands (db). 1. Frontal view. 2. Close-up of the first lateral saddle portion, showing many smaller oval and crescentic attachment scars (m) in the interspaces between pseudosutures. 3. Close-up of the mid-venter, showing the unpaired ventral muscle attachment scars (vm) and associated smaller attachment scars on the adoral side of each mineralized septum (s). The arrow indicate the adoral direction.

reported several specimens of the same species with pseudosutures and drag bands from this locality (Landman *et al.*, 1993). The two specimens were coated with platinum and then observed with a Hitachi Model S 2,400 scanning electron microscope.

For comparison, SEM observations were also made on the following extant and extinct cephalopods: 1) a specimen of *Spirula spirula* (Linnaeus) (Coleoidea: Spirulidae), with unpaired ventral attachment scars, which was caught alive in the waters off Surinam (810 m depth); 2) a specimen of the Callovian (Middle Jurassic) ammonite *Quenstedtoceras* sp. from Luków, Poland; 3) a specimen of the Desmoinesian (Pennsylvanian) orthocerid *Pseudorthoceras knoxense* (McChesney) from the Buckhorn Asphalt, Arbuckle Mountains, Oklahoma; and 4) a specimen of an indeterminate Late Mississippian member of the Aulacocerida from Durham, Arkansas. The specimens observed are housed in the American Museum of Natural History (AMNH) (aulacocerid specimen), Institut für Paläontologie, Universität Bonn (GPIBo) (orthocerid specimen), and the University Museum, University

of Tokyo (UMUT) (remaining specimens).

Observations

In both specimens of *Goniatices multiliratus* examined, the body attachment scars, pseudosutures, and drag bands are preserved on the surfaces of the steinkerns. The attachment scars on the mid-venter are represented by a row of oval swellings on the adoral side of each ventral saddle (vm, Figures 1-1, 2-1, 3). In close-up, these scars are characterized by many small, round depressions with flat bottoms, each about 20-30 μm in diameter (Figure 2-2). This implies the presence of many small mounds on the surfaces of scars on the external shell (not preserved).

A pair of linear drag bands (db, Figures 1-1, 2-1, 3) runs longitudinally along the lateral margins of each scar. Rounded, oval, or more commonly irregularly shaped smaller attachment scars are visible in the interspace between paired drag bands, extending from the adoral side of one mid-ventral scar to the adapical side of the next (Figures 1-

Figure 2. 1. SEM micrographs of unpaired ventral muscle attachment scars (vm) on a specimen of *Goniatices multiliratus* (UMUT. PM 19018-4); the lateral margins are marked by a pair of drag bands (db). The large oval scar just adoral of each mineralized septum (s) indicates a firm attachment of the muscle to the shell, while the cluster of smaller scars within each chamber suggests weaker and less permanent muscular attachment. The arrow indicates the adoral direction. db=drag band, s=septum, ps=pseudosuture. 2. Close-up of the unpaired ventral muscle attachment scar, showing many small, round depressions with flat bottoms.

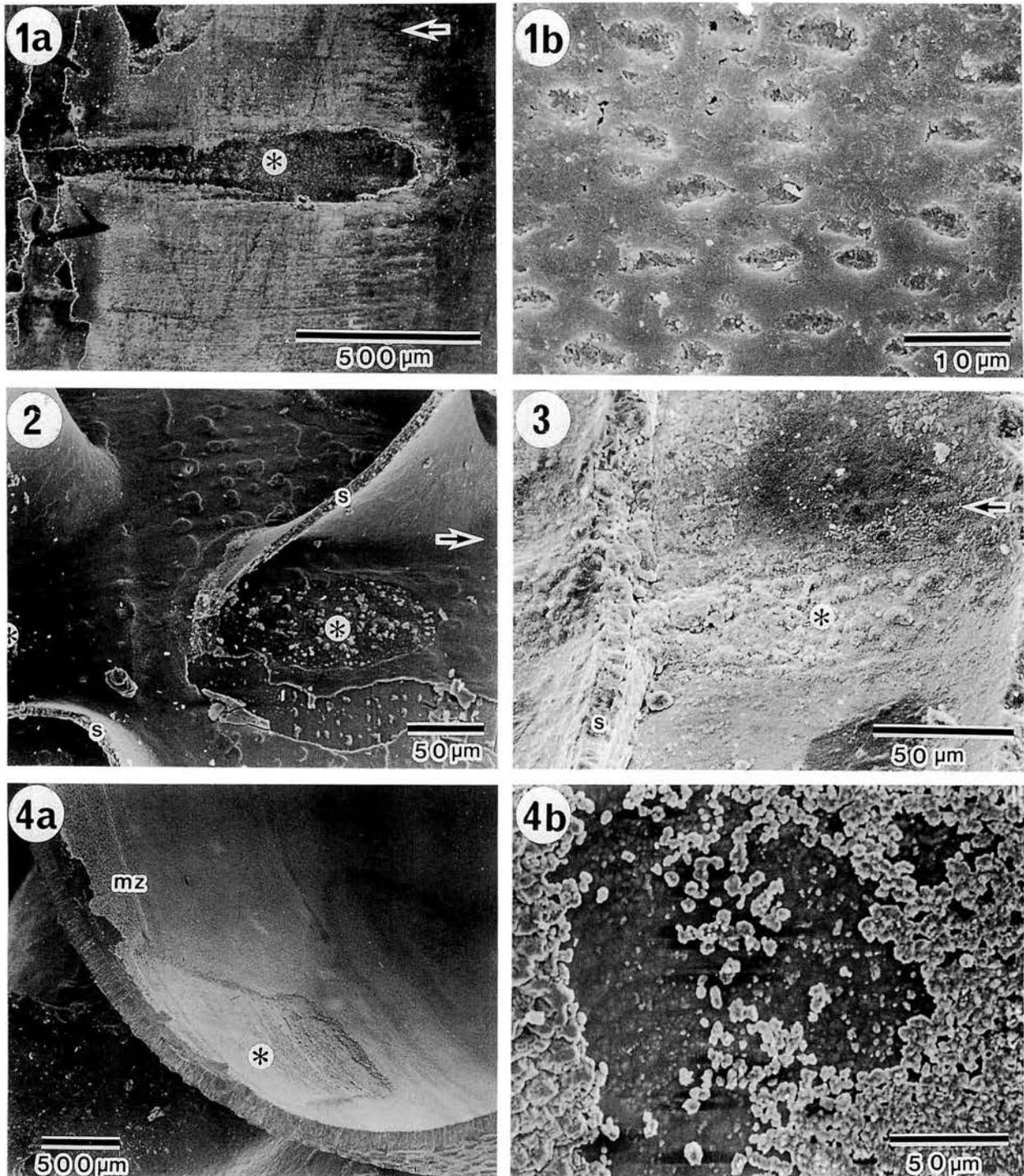


Figure 4. SEM micrographs of muscle attachment scars (asterisk) in selected shelled cephalopods. The arrows indicate the adoral direction. s: septum. **1a, b.** Unpaired ventral muscle scar and close-up on a steinkern of *Pseudorthoceras knoxense* (McChesney) (Orthocerida). GPIBo-Ri 90 from the Desmoinesian (Pennsylvanian) Buckhorn Asphalt, Arbuckle Mountains, Oklahoma (same specimen as that figured by Ristedt, 1971, pl. 34, fig. 2). **2.** Unpaired dorsal muscle scars on the inside shell surface of a specimen of *Qenstedtoceras* sp. (Ammonoidea: Ammonitina). UMUT. MM 19876 from the Callovian of Luków, Poland. **3.** Unpaired ventral muscle scar on the inside shell surface of a member of the Aulacocerida, gen. et sp. indet. (Coleoidea: Aulacocerida). AMNH 45338 from the middle Chesterian (Upper Mississippian), White River, Durham, Arkansas. **4a, b.** Unpaired ventral muscle scar on the inside shell surface of *Spirula spirula* (Linnaeus) (Coleoidea: Spirulidae). UMUT. RM 19874, Surinam (810 m depth).

1,2-1,3). A small attachment scar also occurs on the adapical side of the first lateral saddle in one of the two figured specimens (Figure 1-4). Many similar small oval and crescentic scars are present in the interspaces between pseudosutures (Figures 1-2, 1-3). All these attachment scars were originally expressed as shallow depressions or pores on the inside surface of the shell wall. There are no traces of organic remains (cameral membranes and/or gels) around the oval and crescentic scars.

Comparison and discussion

Preservation of muscle attachment scars is extremely rare in the Goniatitina and has only been documented in *Goniatites* and *Muensteroceras* (Crick, 1898; Jordan, 1968). The muscle scars of the two genera described by these authors differ from the unpaired ventral attachment scars of *Goniatites multiliratus* described herein and are both represented by dorsal paired attachment scars that occur on the anterolateral side of the steinkerns of the body chambers. In their shape and mid-ventral position within each chamber, the unpaired ventral attachment scars of *G. multiliratus* are comparable to those known from various Mesozoic ammonites (Crick, 1898; Jordan, 1968; Sarikadze *et al.*, 1990; see also Doguzhaeva and Mutvei, 1996, table 1 for a complete list of genera with this kind of attachment scar), members of the Orthocerida (Ristedt, 1971; Figure 4-1a, b) and Aulacocerida (Figure 4-3), and *Spirula* (Figure 4-4a, b). In extant *Nautilus*, the attachment site for the paired retractor muscles is located in the posterior region of the body chamber, where it is demarcated by the conspicuous ridge of the myo adhesive epithelial zone. Mutvei and Doguzhaeva (1997) demonstrated that the myo adhesive epithelium secretes a thick prismatic myostracal layer, consisting of bundles of vertically oriented acicular crystallites, at the attachment site to which the muscle is firmly attached. In *Spirula*, the myo adhesive epithelial zone is situated near the shell aperture (mz, Figure 4-4a). The myostracal layer at its muscle attachment site likewise consists of bundles of crystallites (Figure 4-4b). Bundles of crystallites are also observed on the unpaired ventral muscle scar in the aulacocerid specimen from Arkansas (Figure 4-3). Although the prismatic myostracal layer is not preserved in the two goniatite specimens examined here, the small, round depressions on the mid-ventral scars were presumably sites for attachment of bundles of crystallites secreted by the myo adhesive epithelium, as in *Nautilus*, *Spirula* and the Aulacocerida.

The unpaired mid-ventral muscle scars of *Goniatites multiliratus* (Figures 1, 2) are remarkably similar in their overall shape to unpaired dorsal attachment scars known from some Mesozoic Ceratitina (e.g. *Amphipopanoceras*, Lehmann, 1990, fig. 4.38) and Ammonitina (e.g. *Quenstedtoceras* and *Kosmoceras*, Bandel, 1982, pl. 13, figs. 3-5; *Euhoplites*, Landman and Bandel, 1985, fig. 31). In close-up, many small mounds of crystallites are developed on the inner surface of the dorsal scars in these genera (Figure 4-2).

Our observations strongly suggest that in *Goniatites multiliratus*, the unpaired ventral muscle was attached to the

shell wall at the base of the body chamber for some time before formation of the next chamber. A similar condition is postulated for the unpaired dorsal muscle in some Mesozoic ammonites. In contrast, the round, oval, or irregularly shaped smaller pits observed on the ventral and lateral sides of each chamber (m, Figures 1-1, 1-2, 1-4) appear to indicate a weaker and less permanent attachment of muscular or ligamental tissue to the shell wall. These latter scars were presumably formed during the slow and stepwise forward movement of the body during growth.

As our data indicate, there are still many questions regarding the attachment of the soft body to the shell. A variety of models have been proposed to explain septal morphogenesis and the forward movement of the body (e.g., Checa and Garcia-Ruiz, 1996), but most of them lack comparative anatomical background. Are all the pseudosutures we observed related to pseudosepta and/or to the presence of so-called cameral gel? Are the small oval and crescentic scars between pseudosutures present in other ammonoids? How do all these different kinds of attachment scars fit in with the tie point model of septal formation (e.g. Seilacher, 1988) and with the more recent model of the "Cartesian Diver" (Seilacher and LaBarbera, 1995)? Future studies of well-preserved material and comparison with the anatomy of extant cephalopods may yield solutions to these problems.

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Ophiura sarsii sarsii (Echinodermata, Ophiuroidea) from the Late Pliocene Hachioji Formation in Niigata Prefecture, Central Japan

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Abstract. Specimens of the Recent species *Ophiura sarsii sarsii* Lütken, collected from the Late Pliocene Hachioji Formation in Kashiwazaki City, Niigata Prefecture, central Japan, represent the first record of this species from the Pliocene, although this species has been found from the Middle-Late Miocene. The fossil specimens have been compared and contrasted with related species using morphometric characteristics of the disk, basal arm portions and radial shields.

Key words: Hachioji Formation, Late Pliocene, *Ophiura sarsii sarsii*, Ophiuroidea

Introduction

Ophiura sarsii sarsii is an extant, circumpolar species in the Northern Hemisphere, occurring in high-density populations in the upper bathyal zone surrounding northern Japan (Fujita and Ohta, 1989). Fossil ophiuroids assigned to *Ophiura s. sarsii* have been found in the Pleistocene from off northern Norway (Jensen and Thomsen, 1987), from southern Norway (Bjørlykke, 1998), from the Middle Pleistocene Ichijuku Formation (Kazusa Group) in Chiba Prefecture (Ishida and Inoue, 1993, 1995), from the Plio-Pleistocene Hijikata Formation in Shizuoka Prefecture (Ishida *et al.*, 1996), from the Late Miocene Ogawa Formation in Nagano Prefecture (Ishida, Kurita *et al.*, 1997; Ishida *et al.*, 1998), from the Late Miocene Hongo Formation in Yamagata Prefecture (Ishida, Tokairin *et al.*, 1997), and from the Middle-Late Miocene Wakkanai Formation in Hokkaido (Ishida and Fujita, 1998).

We have recently discovered fossil ophiuroids in the Late Pliocene Hachioji Formation, Kashiwazaki City (Ishida, Kurita *et al.*, 1997), which proved to be assignable to *Ophiura s. sarsii*, based on a detailed morphological analysis. This paper describes *Ophiura s. sarsii* from the Pliocene in detail and discusses the comparison of the fossils with related species, which are important for its identification.

Locality and age

Thirty-five individuals were collected from a cliff outcrop of the Hachikoku Oil Field, about two kilometers southeast of Nagatori Station on the Japan Railways Shin-etsu Line in the district of Kashiwazaki City, Niigata Prefecture in May 1995

(Figure 1). The Pliocene and Pleistocene in this area comprise, in ascending order, the Hododaira Formation, the Hachikokusan Formation, the Suganuma Formation, the Hachioji Formation and the Uonuma Formation (Yasui *et al.*, 1983; Kobayashi *et al.*, 1989). The strata in this cliff are

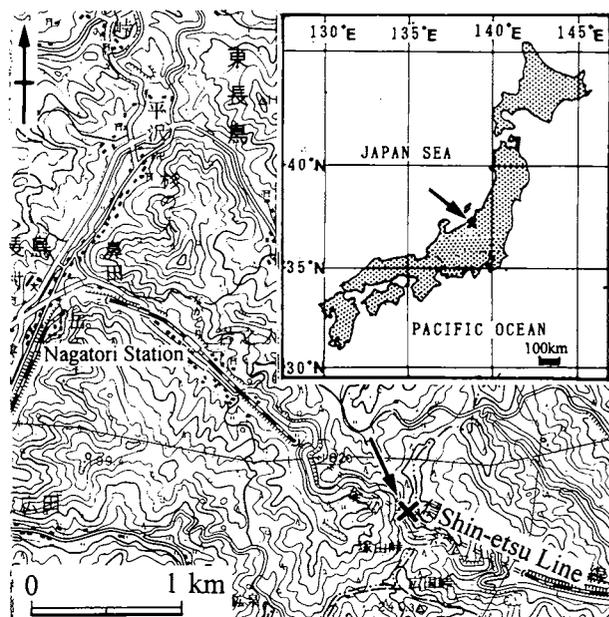


Figure 1. Sampling locality in the Hachikoku Oil Field. Part of the "Kashiwazaki" 1:50,000 topographic map by the Geographical Survey Institute. ×: Sampling locality.

composed of massive sandy siltstone assigned to the middle part of the Hachioji Formation (Yasui *et al.*, 1983; Kobayashi *et al.*, 1989).

The age of the Hachioji Formation is inferred to be Late Pliocene from the following studies. The formation was correlated with the Pliocene Nishiyama Formation of the standard succession in the Niigata area on the basis of tephra-stratigraphy and foraminiferal biostratigraphical data (Kobayashi *et al.*, 1989). From an analysis of the stratigraphic sequence of the Niigata sedimentary basin, the Hachioji Formation falls into the Late Pliocene (Arato, 1997). The Hachioji Formation was correlated lithologically with the Asojima Formation in the Yoneyama area (Kobayashi *et al.*, 1989). Fission track ages of 3.24 and 2.91 Ma have been obtained for the Asojima Formation (Unpublished data of Muramatsu, in Kobayashi *et al.*, 1989).

Fossil specimens of *Ophiura s. sarsii* have been described from the Middle Pleistocene, the Plio-Pleistocene boundary and the Late Miocene (Ishida and Inoue, 1993; Ishida *et al.*,

1996, 1998), and also from the Middle-Late Miocene (Ishida and Fujita, 1998), but this is the first report of the species from the Pliocene.

Systematic description

Family Ophiuridae Lyman, 1865
Subfamily Ophiurinae Lyman, 1865
Genus *Ophiura* Lamarck, 1816

Ophiura sarsii sarsii Lütken, 1855

Figures 2, 3

Ophiura sarsii Lütken, 1855, p. 101; Clark, 1911, p. 37; Matsumoto, 1917, p. 272, fig. 74; Mortensen, 1927, p. 238, figs. 128-1, 2; Berry, 1934, p. 98, pls. 5, 6; D'yakonov, 1954, p. 98, fig. 35; Irimura, 1990, p. 98; Ishida and Inoue, 1993, p. 104, pls. 1-3; Ishida *et al.*, 1996, p. 67-69, fig. 3; Ishida *et al.*,

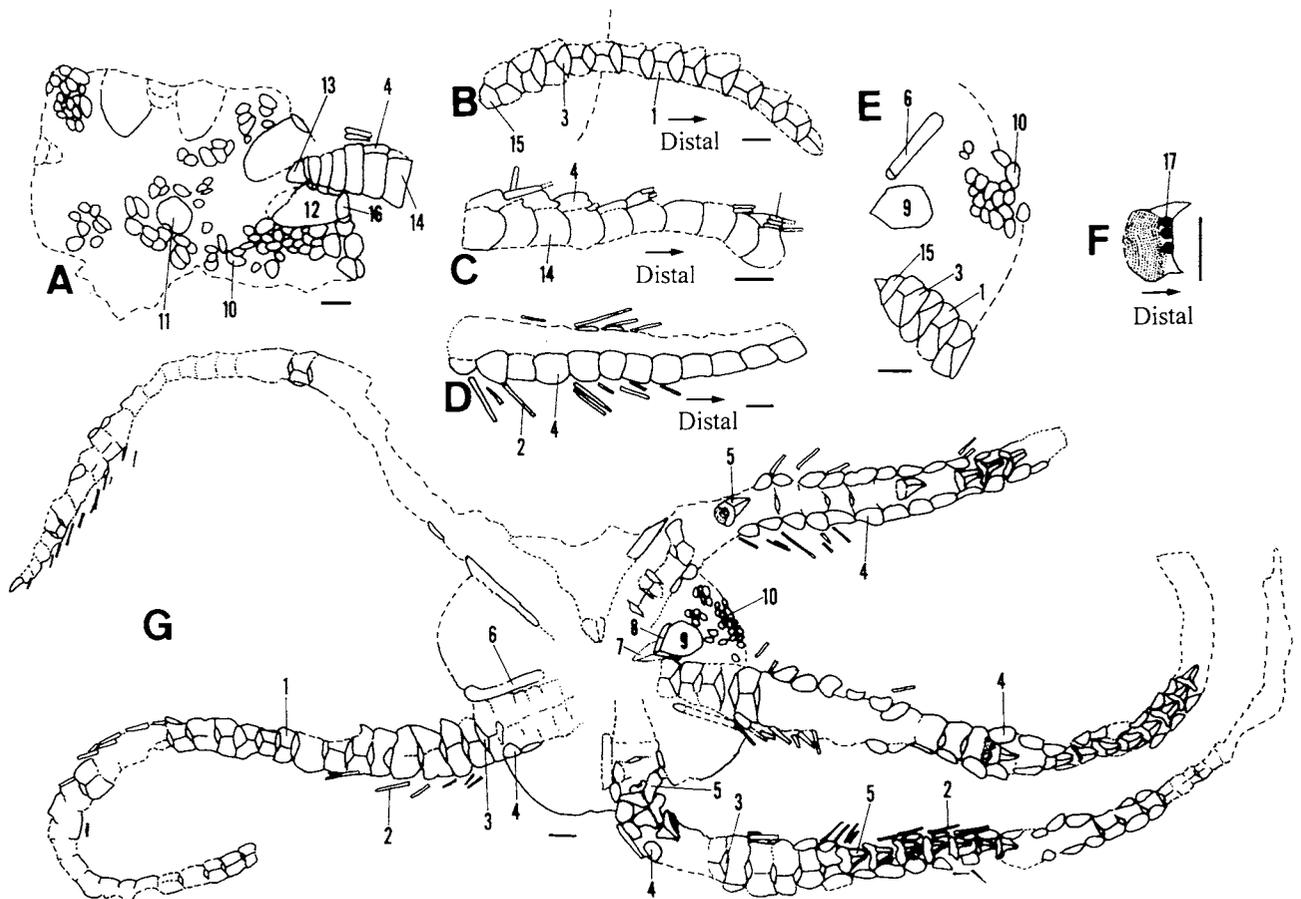


Figure 2. Camera lucida drawings of the figured specimens of *Ophiura sarsii sarsii* Lütken, 1855 from the Hachioji Formation. **A.** Dorsal view of disk and proximal arm; **B.** Ventral view, proximal to mid arm; **C.** Dorsal view, proximal to mid arm; **D.** Latero-ventral view, proximal to mid arm; **E.** Partial ventral view of disk; **F.** Lateral view of lateral arm plate (inside); **G.** Entire animal, showing ventral side (vertebral ossicles showing dorsal side). Abbreviation: 1, Lateral arm plate (ventral view); 2, Arm spine; 3, Ventral arm plate; 4, Lateral arm plate (lateral side); 5, Vertebral ossicle (dorsal side); 6, A part of genital plate; 7, Oral plate; 8, Adoral plate; 9, Oral shield; 10, Disk scale; 11, Primary scale; 12, Radial shield; 13, First dorsal arm plate; 14, Dorsal arm plate; 15, First ventral arm plate; 16, Arm comb plate; 17, Socket of arm spine. Scale bars equal 1 mm.

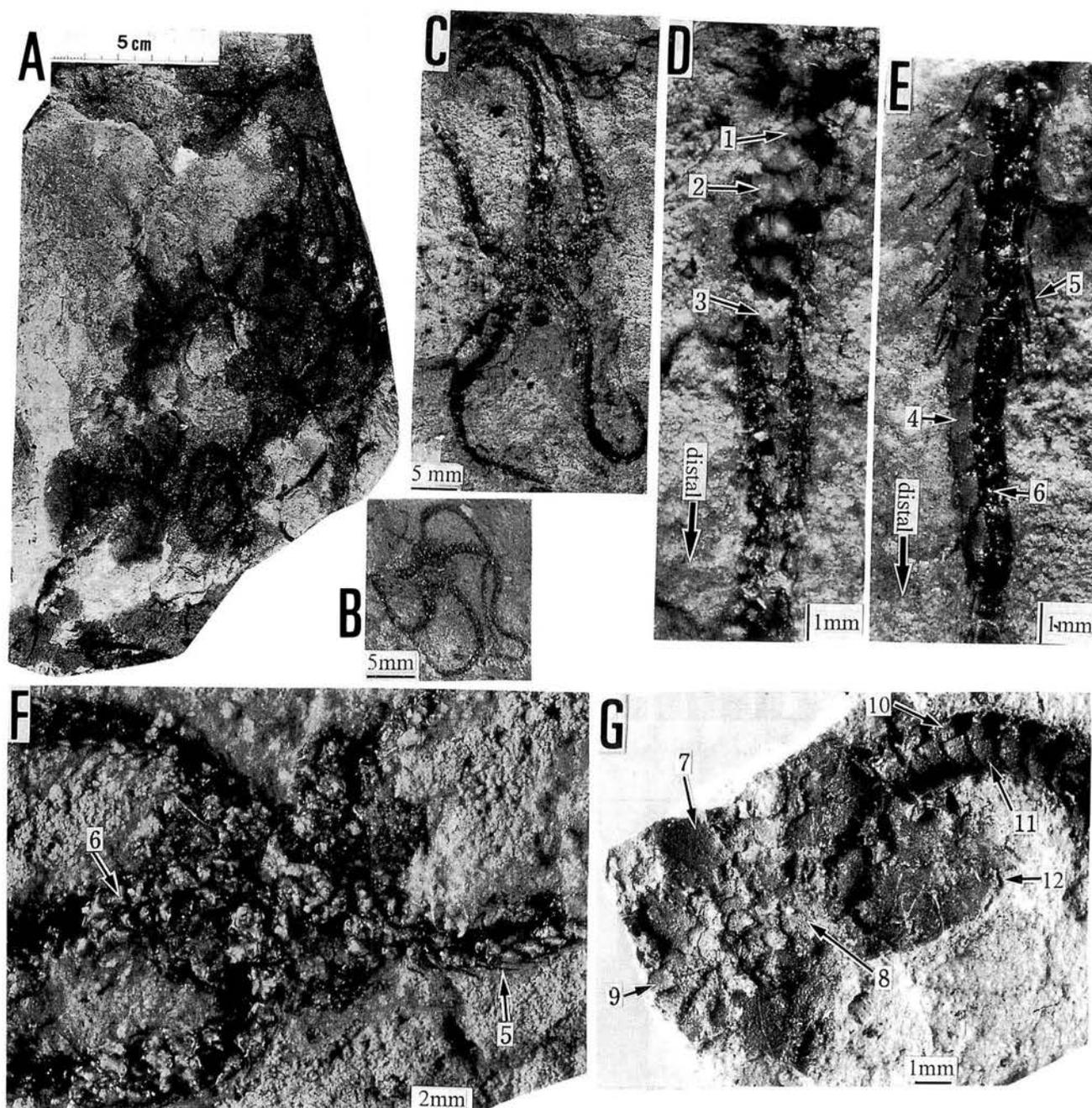


Figure 3. Fossil *Ophiura sarsii sarsii* Lütken, 1855 from the Hachioji Formation. **A.** Dense occurrence of fossils; **B.** Small individuals; **C.** Dorsal view of a complete specimen; **D.** Free arm, proximal part showing inside of ventral arm plates and lateral arm plates, distal part showing dorsal side of vertebral ossicles; **E.** Free arm, latero-ventral view; **F.** Ventral view of disk and proximal arms; **G.** Dorsal view of disk and proximal arm. Morphological explanation: 1, Inside of ventral arm plate; 2, Inner ventral side of lateral arm plate; 3, Dorsal view of vertebral ossicle; 4, Lateral side of lateral arm plate; 5, Arm spine; 6, Ventral view of vertebral ossicle; 7, A part of radial shield; 8, Central plate; 9, Scale; 10, Lateral side of lateral arm plate; 11, Dorsal arm plate; 12, Disk margin.

1998, p. 10-12, figs. 3, 4.

Materials.—Thirty-five specimens from the Hachioji Formation, three of which are illustrated here, are housed at the Municipal Nagaoka Science Museum, Niigata Prefecture

(Gf8-10).

Measurements.—Measurements are based on 31 specimens; disk diameter ranges from 6.0-14.1 mm; mean, 9.7 mm; median, 9.9 mm.

Description.—Disk circular in outline, low and flat, covered with small, flat and imbricated scales. Primary scales fairly large and circular. Radial shields oval, about twice as long as wide, separated from each other and about half as long as disk radius. Comb plates elliptical. Oral shields about one third of disk radius, pentagonal with rounded distal borders, with a pointed corner proximally and slightly longer than wide. Adoral plates slender, rectangular, in contact with each other at adoral margin. Oral plates fairly long, rectangular with a pointed corner proximally, in contact with each other at adoral side. Genital plates slender and long. First 4 or 5 arm segments insert laterally into disk. Arms

bent gradually on bedding plane, more than three times as long as disk diameter. Arms flattened, much wider than high, rather wide at base, tapering gradually. Dorsal arm plates well developed, rectangular, wider than long, with median keel, successive plates broadly in contact. First dorsal arm plates triangular. Ventral arm plates triangular, about 2-3 times as wide as long. First ventral arm plates trapezoidal. Lateral arm plates well developed, separated by dorsal arm plates, but in contact ventrally. Arm spines long and tapering, about twice as long as arm segment proximally and almost equal to length of arm segment at mid-arm, three in number, adpressed or often somewhat

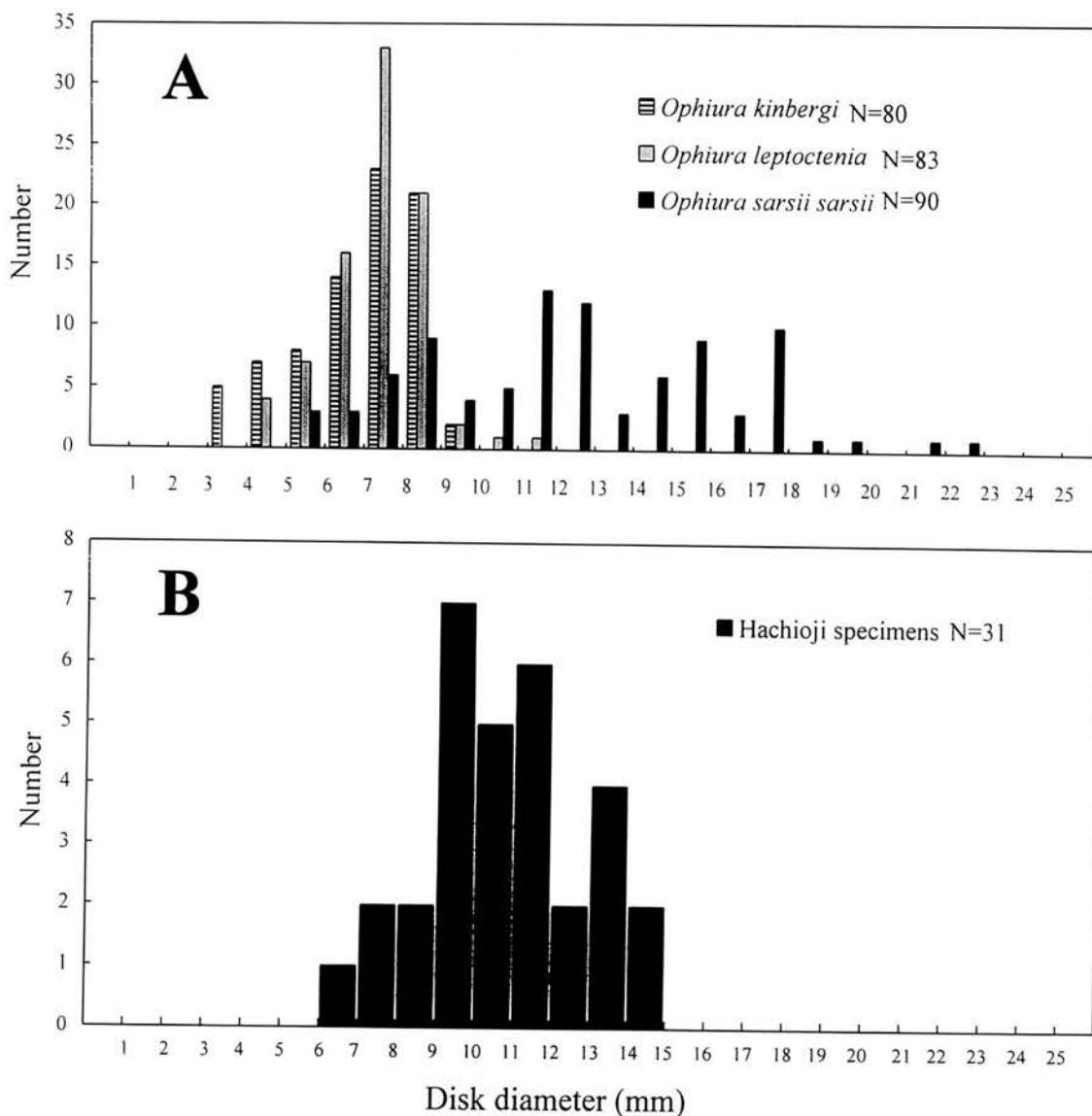


Figure 4. Size frequency distribution of Recent *Ophiura sarsii sarsii*, *Ophiura leptoctenia*, *Ophiura kinbergi* (A) and fossil *Ophiura sarsii sarsii* from the Hachioji Formation (B). Data for these Recent specimens are from the specimens stored at the National Science Museum, Tokyo (*Ophiura s. sarsii*, NSMT-E 1608, Wakasa Bay, Fukui Prefecture, 270 m depth; 1414, Toyama Bay, Toyama Prefecture, ca. 200 m depth; *Ophiura leptoctenia*, NSMT-E 1987, Off Otsuchi, Iwate Prefecture, 1,038-1,055 m depth; *Ophiura kinbergi*, NSMT-E 0670, Amakusa Isls., Kumamoto Prefecture, ca. 30 m depth).

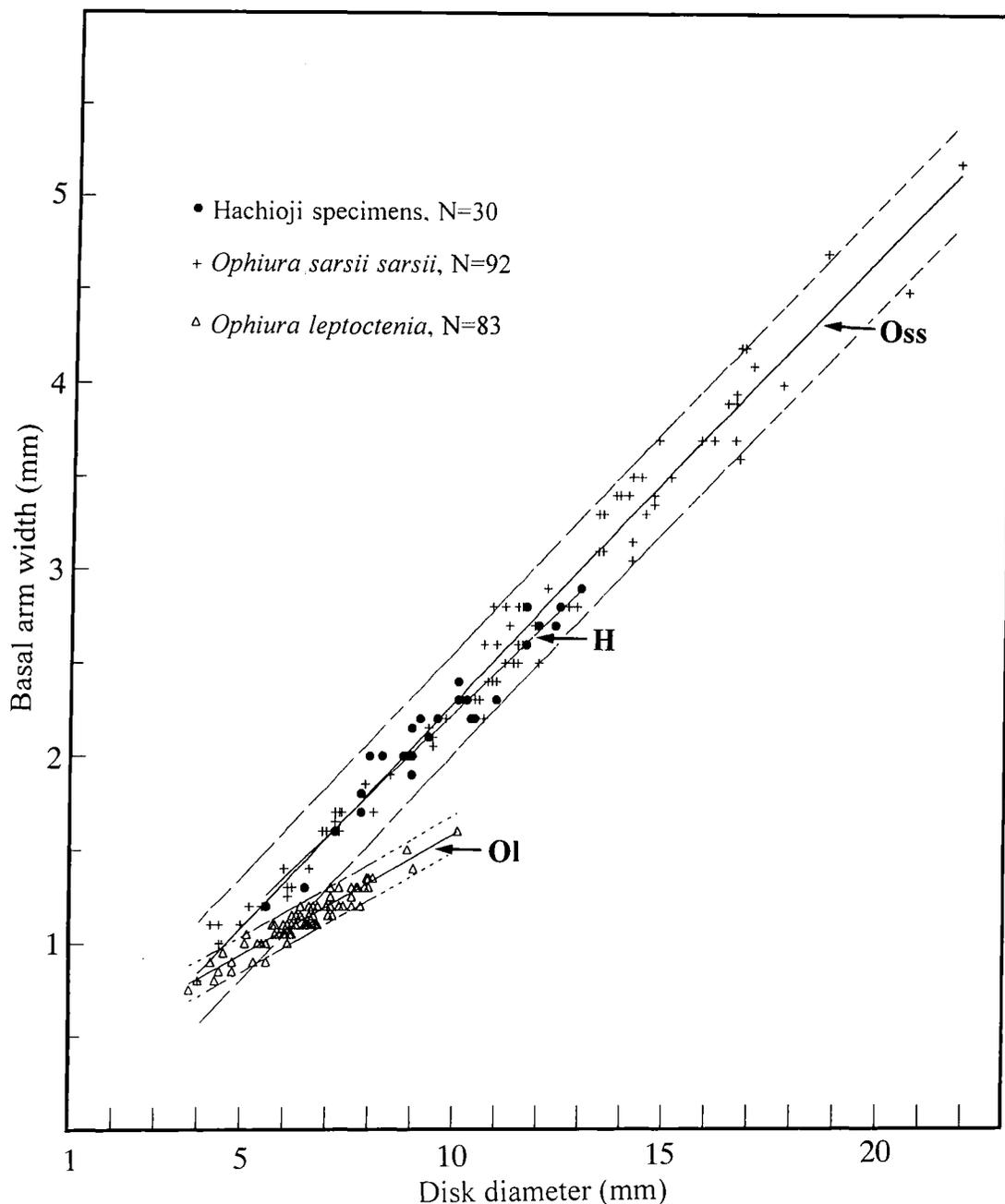


Figure 5. The relationship between disk diameter and basal arm width of Recent *Ophiura sarsii sarsii*, *Ophiura leptoctenia* and fossil *Ophiura sarsii sarsii* from the Hachioji Formation. Solid lines show linear regression and broken lines show 95% confidence limits. Each regression line is statistically significant ($r=0.99$, $p<0.05$ for living *O. s. sarsii* (Oss), $r=0.95$, $p<0.05$ for *O. leptoctenia* (Ol) and $r=0.97$, $p<0.05$ for fossil specimens of *O. s. sarsii* from the Hachioji Formation (H)). There is a statistically significant difference on intercept ($p<0.05$) and regression coefficient ($p<0.05$) between the two regression lines (Oss, Ol). The fossil specimens safely fall into the confidence interval of Recent *O. s. sarsii*, but not into that of *O. leptoctenia*. Data for Recent *O. s. sarsii* and *O. leptoctenia* are from specimens stored at the National Science Museum, Tokyo (*O. s. sarsii* NSMT-E 0568, Wakasa Bay, 275 m depth; 1414, 1608, 1609, Wakasa Bay, 240 m depth; *O. leptoctenia* NSMT-E 1987).

detached. Vertebral ossicles, triangular dorsally, with a pointed distal corner.

Remarks.—Morphologically the Hachioji specimens have much in common with Recent *O. s. sarsii*, which is related to *Ophiura s. vadicola*, *Ophiura kinbergi* and *Ophiura leptoctenia*. These four (sub)species can be distinguished mainly on the basis of the shape of arm comb papillae. Although the arm comb papillae were not discernible in the Hachioji fossils, they have been identified as *Ophiura s. sarsii* for the following reasons. Recent *O. s. sarsii* is larger than *O. kinbergi*, while the Hachioji specimens are similar to *O. s. sarsii* in size (Figure 4). Recent *O. s. sarsii* has a larger ratio of basal arm

width to disk diameter than has *O. leptoctenia*, while the Hachioji specimens are close to *O. s. sarsii* in this ratio: the values are 0.24 for *O. s. sarsii*, 0.12 for *O. leptoctenia* and 0.22 for the Hachioji specimens (Figure 5). Recent specimens of *O. s. sarsii* possess a smaller width to length ratio for radial shields than *O. s. vadicola* (the ratio is 0.75 for *O. s. vadicola* and 0.54 for *O. s. sarsii*), while the Hachioji specimens are similar to *O. s. sarsii* (the ratio is 0.58) (Figure 6). Recent *O. s. sarsii* has longer radial shields than those of Recent *O. s. vadicola* (the length is 0.5 times disk radius in *O. s. sarsii*, and 0.4 times disk radius in *O. s. vadicola* based on the same samples as Figure 6), while the Hachioji specimens are similar to *O. s. sarsii*. The body size of the Hachioji specimens is similar to that of specimens from the Lower Pleistocene Ichijuku Formation (mean disk diameter 9.6 mm) (Ishida and Inoue, 1993), but is larger than that of specimens from the Plio-Pleistocene Hijikata Formation (mean disk diameter 8.2 mm) (Ishida *et al.*, 1996).

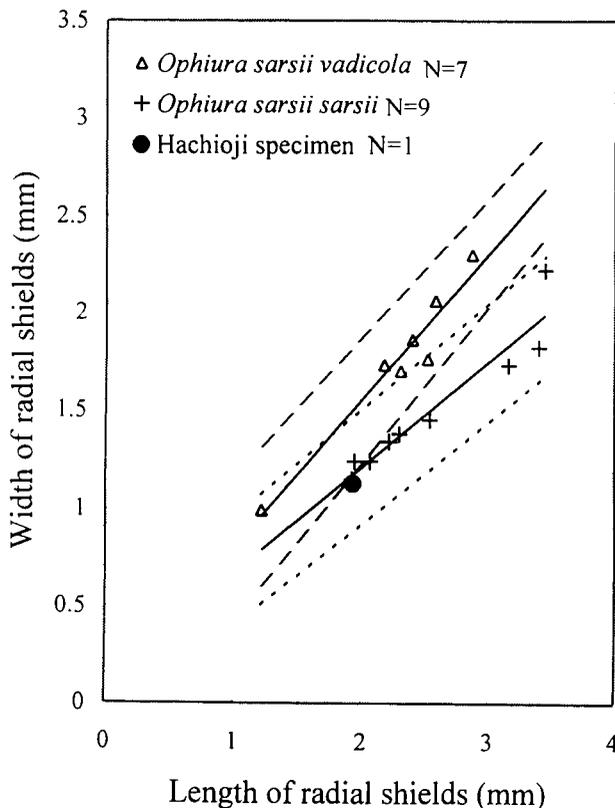


Figure 6. The relationship between width and length of radial shields in Recent *Ophiura sarsii vadicola*, *Ophiura sarsii sarsii* and a fossil specimen from the Hachioji Formation. The value at each point for *O. s. vadicola* and *O. s. sarsii* indicates the mean value measured from five radial shields in the specimen. The value for the fossil specimen indicates the mean value measured from three radial shields in the specimen. Solid lines show linear regression and broken lines show 95% confidence limits. Each regression line is statistically significant ($r=0.97$, $p<0.05$ for living *O. s. vadicola*, $r=0.95$, $p<0.05$ for *O. s. sarsii*). There is a statistically significant difference on intercept ($p<0.05$) and regression coefficient ($p<0.05$) between the two regression lines. The fossil specimen safely falls into the confidence interval of Recent *O. s. sarsii*, but not into that of *O. s. vadicola*. Data for Recent specimens of *O. s. vadicola* and *O. s. sarsii* are from the specimens stored at the National Science Museum, Tokyo (*O. s. vadicola* NSMT-E1821, *O. s. sarsii* NSMT-E1609, 0568).

Mode of occurrence and paleoenvironment

Dense aggregations of fossilized ophiuroids were found in sandy siltstone layers. Many of their arms and disks are still attached, and most individuals (85%) lie dorsal side up on the bedding plane (Figure 7). This suggests the assemblage is

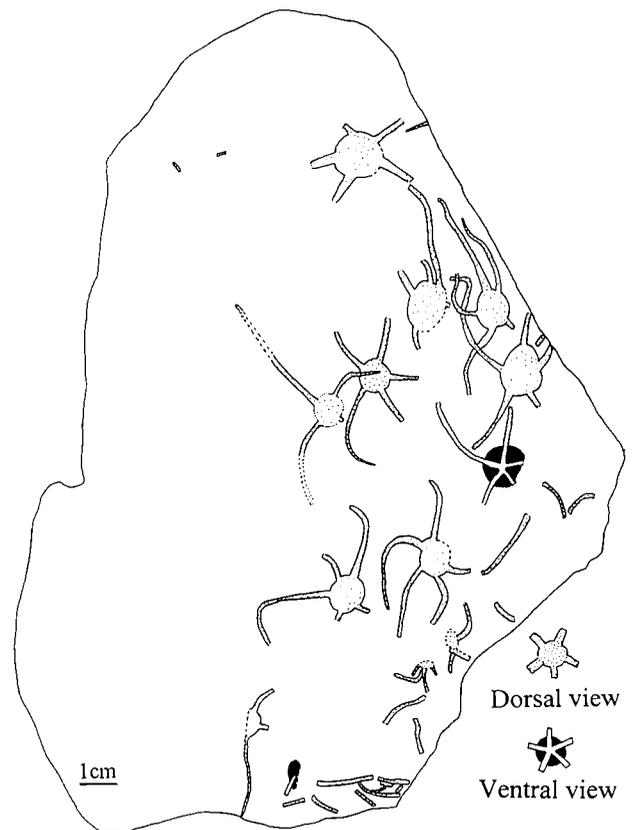


Figure 7. Sketch illustrating the dense occurrence of fossil *Ophiura sarsii sarsii* in sandy siltstone matrix from the Hachioji Formation.

Table 1. List of molluscan fossils associated with fossil ophiuroids. N; Numbers. For Recent species, depth and latitudinal range are given, according to Habe (1977), Higo (1973) and Kuroda and Habe (1952).

Species	N	Depth (m)	Latitude (°N)
Pelecypoda			
<i>Saccula confusa</i> (Hanley)	4	10-60	-35
<i>Nuculana (Thestyleda) yokoyamai</i> (Kuroda)	3	50-450	32-43
<i>Acila</i> sp.	1		
<i>Yoldia (Cnesterium) notabilis</i> Yokoyama	4	50-100	32-48
<i>Portlandia (Megayoldia) thraciaeformis</i> (Storer)	5	25-550	37-70
<i>Limopsis (Empleconia) cumingi</i> A. Adams	4	30-300	31-36
<i>Anadara (Scapharca) ommaensis</i> Otuka	3		
<i>Clementia vatheleti</i> Mebille	5	0-140	33-41
<i>Solamen spectabilis</i> (A. Adams)	3	30-300	30?-42
<i>Nemocardium (Keenaea) cf. samarangae</i> (Makiyama)	3	50-300	30-42
<i>Felaniella usta</i> (Gould)	5	10-150	33-45
<i>Megacardia ferruginosa</i> (A. Adams and Reeve)	4	10-120	31-42
<i>Macoma calcarea</i> (Gmelin)	2	0-1000	33-72
<i>Thracia cf. kakumana</i> Yokoyama	1		
Gastropoda			
<i>Turritella (Neohaustator) saishuensis</i> Yokoyama	44		
<i>Neverita (Glassaulax) reiniana</i> (Dunker)	1	10-50	31-37
<i>Cryptonatica janthostomoides</i> (Kuroda and Habe)	10	20-300	31-43
<i>Siphonalia cf. fusoides</i> (Reeve)	1	10-100	32-41
<i>Fusinus perplexus</i> (A. Adams)	1	10-100	31-42
<i>Mitra</i> sp.	1		
<i>Fulgoraria cf. masudae</i> Hayasaka	1		
<i>Turbonilla</i> sp.	4		
Scaphopoda			
<i>Dentalium (Antalis) weinkauffi</i> (Dunker)	25	15-550	30-42

autochthonous or semiautochthonous. The number of specimens observed on the surface area of the block illustrated in Figure 7 is 13/222 cm², which is equivalent to a density of 585 ind./m². This value is nearly the same as that reported for Recent faunas (Fujita, 1992).

Together with ophiuroids, we found 23 molluscan species at this locality (Table 1). Species typical mainly of the lower sublittoral zone, such as *Limopsis (Empleconia) cumingi* and *Cryptonatica janthostomoides*, are common in the Hachioji Formation. The mode of occurrence of ophiuroids and molluscs suggests that the ophiuroids lived on a lower sublittoral, sandy silt bottom. Recent *O. s. sarsii* is distributed mainly on the uppermost continental slope around Japan (Fujita and Ohta, 1990). The Hachioji specimens lived in a slightly shallower setting than their extant counterparts. Some molluscs, e.g. *Anadara (Scapharca) ommaensis*, *Yoldia (Cnesterium) notabilis* and *Turritella (Neohaustator) saishuensis* have been recognized as typical of the Omma-Manganji fauna (Ogasawara, 1994), which suggests the sedimentary environment of the Hachioji Formation to have been one of a mild to cool temperate marine climate.

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SHORT NOTES

First discosorid cephalopod from Japan

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Abstract. *Ukhtoceras hidense* sp. nov. is described from the Lochkovian (Early Devonian) shale of the Fukuji Formation, Gifu Prefecture as the first find of a discosorid cephalopod in Japan. This species also extends the geographic range of the ukhtoceratids into East Asia.

Key words: Discosorid cephalopod, Fukuji Formation, Gifu, Lochkovian, *Ukhtoceras hidense*

A new species of ukhtoceratid discosorid cephalopod, *Ukhtoceras hidense*, is described from the Early Devonian (Lochkovian) calcareous shale of the Fukuji Formation. This species occurs at locality FH-1 of Niko (1996) in the Fukuji area of Kamitakara Village, Yoshiki-gun, Gifu Prefecture, Central Japan. Although locality FH-1 is exceptionally prolific for cephalopods among Paleozoic strata in Japan, only a single and somewhat deformed specimen of this species is usable for study, despite intensive collecting efforts during 1985-1991. This discovery provides new information on the distribution of ukhtoceratid cephalopods. UMUT stands for the University Museum of the University of Tokyo.

Systematic paleontology

Order Discosorida Flower in Flower and Kummel, 1950
Family Ukhtoceratidae Zhuravleva, 1972
Genus *Ukhtoceras* Zhuravleva, 1972

Type species.—*Gomphoceras uchtense* Holzapfel, 1899.

Ukhtoceras hidense sp. nov.

Diagnosis.—Relatively small, dorsoventrally depressed shell with aperture weakly constricted by shell thickening; sutures form shallow lateral lobes; siphuncle close to ventral margin, adoral siphuncle in contact with ventral shell wall; septal necks loxochoanitic ventrally, cyrtochoanitic to suborthochoanitic dorsally; connecting rings corpulent, differentiated, subtrapezoidal profile.

Description.—Shell relatively small for ukhtoceratid, nearly orthoconic longicone with slightly curved exogastric juvenile portion, apical angle approximately 8°; shell cross section dorsoventrally depressed; holotype (only known specimen) 70 mm in length, of which adoral 28 mm represents body chamber; apertural modification not observed in external shell, but shell thickening forms a weak constriction at

aperture; approximately 18 mm in lateral diameter and 14 mm (slightly deformed) in dorsoventral diameter at adoral end; sutures transverse with shallow but broad lateral lobes; camerae short, its reconstructed ratio (diameter/length) in dorsoventral plane approximately 5-7; siphuncular position close to ventral margin, but apical siphuncle only short distance from ventral shell wall, adoral siphuncle in contact with ventral shell wall; septal neck attains 0.25 mm in length at lateral shell diameter of approximately 14 mm, loxochoanitic ventral septal necks and cyrtochoanitic dorsal septal necks in apical shell shifting into loxochoanitic ventral septal necks and suborthochoanitic dorsal septal necks, respectively, with shell growth; connecting rings corpulent, with subtrapezoidal profile in dorsoventral section; structural differentiation of ventral wall of connecting rings obscure, but weak banded condition partly present; dorsal wall of connecting rings composed of inner thin, dense layer and outer thick, more transparent layer, in addition to partly preserved vinculum-like structure.

Discussion.—The shell shape of the nearly orthoconic longicone and the differentiated connecting rings of this material are undoubtedly those of an ukhtoceratid discosorid, and this species may belong to the genus *Ukhtoceras*. However, the aperture is not well preserved, and it cannot be determined whether this species has the trilobate peristome that is a diagnostic feature of *Ukhtoceras*. Therefore generic assignment of the species is tentative at present. Among the known species of *Ukhtoceras*, this species is most similar in outer shell morphology to *U. angustiangulare* Zhuravleva (1972, pl. 10, figs. 4, 5) and *U. quietum* Zhuravleva (1972, pl. 10, figs. 6, 7) from the Upper Devonian of southern Timan, but is easily distinguished from both Upper Devonian species by its smaller shell and the siphuncular shifting to contact with the ventral margin in the adoral shell.

The oncocerid? cephalopod *Shuranoceras dolmatovi* Barskov (1959, pl. 5, figs. 4a, b; monotype of the genus) from the Middle Silurian of southern Ferghana, Kazakhstan, at first glance looks similar to *Ukhtoceras hidense*. It differs from

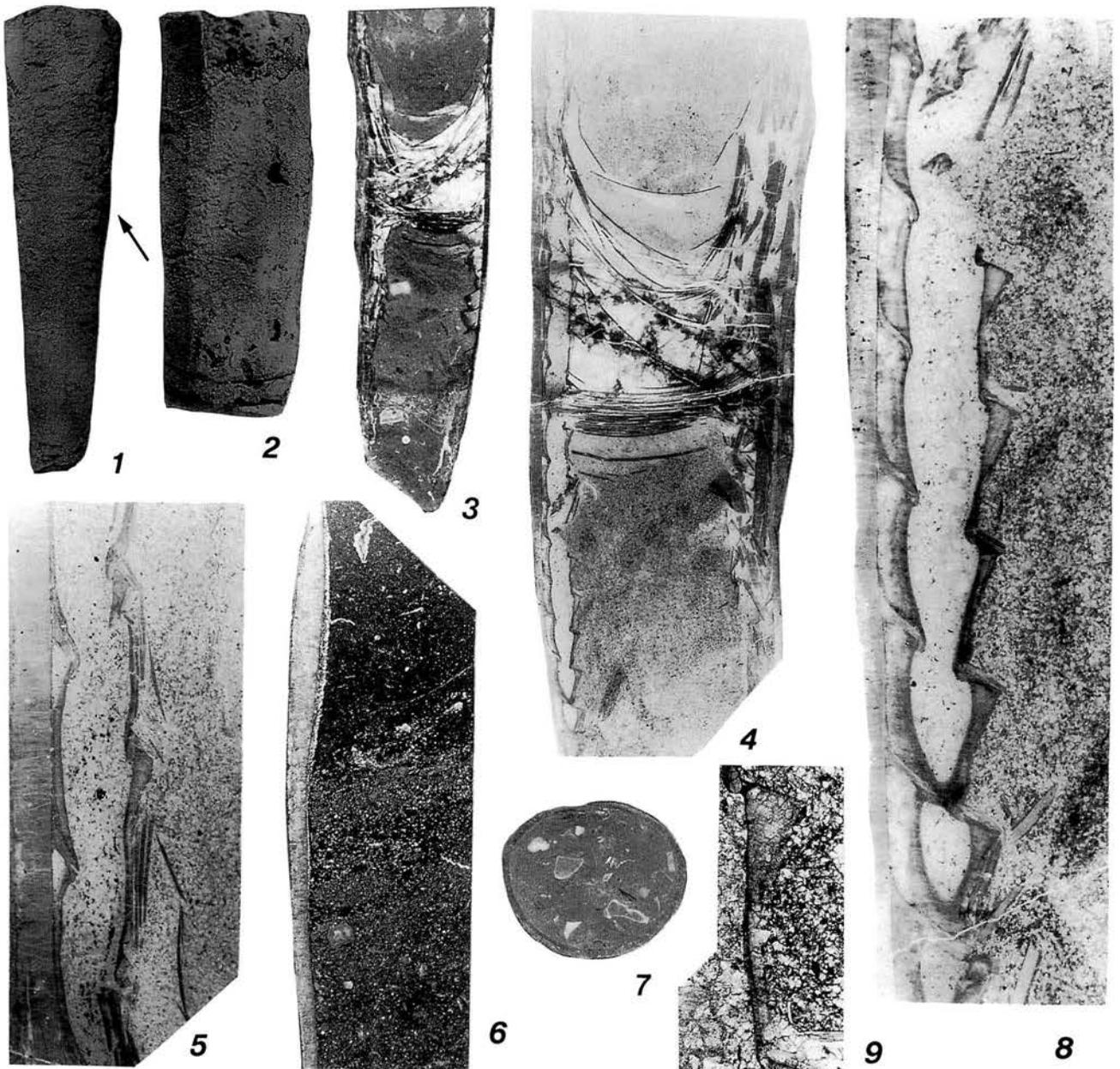


Figure 1. *Ukhtoceras hidense* sp. nov., holotype, UMUT PM 27325 from the Fukuji Formation. 1. ventral view, arrow indicates position of cross section given in 7, $\times 1$. 2. lateral view of internal mold of body chamber and last two camerae, venter on right, shell dissolved with hydrochloric acid, showing sutures, $\times 2$. 3. dorsoventral polished section, slightly apart from siphuncle, venter on right, note exogastric curvature of juvenile shell, $\times 2$. 4. dorsoventral thin section, venter on left, $\times 4$. 5. dorsoventral thin section, showing details of adoral siphuncular structure, $\times 15$. 6. dorsoventral thin section, showing shell thickening at aperture, $\times 5$. 7. cross polished section, venter down, dorsal shell slightly deformed, $\times 2$. 8. dorsoventral thin section, details of siphuncular structure of apical shell, $\times 15$. 9. dorsoventral thin section, showing differentiated nature of dorsal wall of connecting rings, $\times 30$. 1, 2, coated with ammonium chloride.

U. hidense in having a laterally compressed shell and a ventral lobe in the suture line. There is a possibility that *Shuranoceras* is referable to the Discosorida rather than to the Oncocerida, based on its siphuncular structure.

This species extends the geographic distribution of the

ukhtoceratids into East Asia, and represents the first discosorid cephalopod from Japan.

Etymology.—The specific name is derived from Hida, which is the medieval provincial name of the type locality.

Material.—UMUT PM 27325.

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Fukuji 福地, Kamitakara 上宝, Yoshiki-gun 吉城郡

SHORT NOTES

Haplophragmoides yoshidai, a new name for a homonym of a Japanese foraminiferal species

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Abstract. *Haplophragmoides yoshidai* Hanagata nom. nov. is proposed as a replacement for *Haplophragmoides kushiroensis* Yoshida, 1963.

Key words : Foraminifera, *Haplophragmoides yoshidai*, homonym

Introduction

The species name *Haplophragmoides kushiroensis* Yoshida, 1963, is preoccupied by *H. kushiroensis* Asano, 1962 (Asano, 1962, p. 30, pl. 1, figs. 8a, b, 9a, b). Both *H. kushiroensis* Yoshida and *H. kushiroensis* Asano have an agglutinated planispiral involute test with interiomarginal aperture. Therefore, according to Loeblich and Tappan (1987) and Jones *et al.* (1993), both of them belong to the genus "*Haplophragmoides*." However, at the species level, they are differ in character of periphery, umbilical area, sutures and test size as shown in Table 1.

Systematic taxonomy

For suprageneric classification, Loeblich and Tappan (1987, 1992) is applied.

Class Foraminifera Lee, 1990
Order Lituolida Lankester, 1885
Superfamily Lituolacea de Blainville, 1827
Family Haplophragmoididae Maync, 1952

Genus *Haplophragmoides* Cushman, 1910

Haplophragmoides kushiroensis Asano

Haplophragmoides kushiroensis Asano, 1962, p. 30, pl. 1, figs. 8a, b, 9a, b.

Remarks : This species is described from the Charo Forma-

tion distributed in eastern Hokkaido. The geologic age of the Charo Formation is Oligocene (Okada and Kaiho, 1992).

Haplophragmoides yoshidai nom. nov.

Haplophragmoides kushiroensis Yoshida, 1963, p. 220, pl. II, figs. 1a, b, c, 2a, b, c.

Remarks : This species is a junior homonym of *H. kushiroensis* Asano. *Haplophragmoides kushiroensis* Yoshida was described from the Nemuro Group distributed in eastern Hokkaido, Japan. This species occurs throughout the Nemuro Group. According to the systematic description, the holotype was obtained from the Semposhi Formation, whose geologic age is late Maastrichtian (Okada *et al.*, 1987). However, Yoshida writes in the plate explanation that the holotype is from the Akkeshi Formation, Nemuro Group, whose geologic age is Paleocene (Okada *et al.*, 1987). It has not been clarified which is the true holotype. Comparison of this species with similar ones is shown in Table 1. No other species is identical to *H. kushiroensis* Yoshida. Yasuda (1986) assigned the paratype (sic) of *H. kushiroensis* Yoshida (Yoshida, 1963, pl. II, figs. 1a, b, c, not 2a, b, c) to *H. obesus* Takayanagi (Takayanagi, 1960, p. 63, pl. 2, figs. 5a-6b). However, the paratype and holotype of *H. kushiroensis* Yoshida are obviously the same species, and as described by Yoshida (1963) himself, the species "... differs from *H. obesus* Takayanagi in having a greater number of chambers." Consequently, *H. obesus* Takayanagi is morphologically different from the "paratype" and "holotype" of *H. kushiroensis* Yoshida.

Table 1. Comparison of *Haplophragmoides yoshidai* nom. nov. with similar species based on original diagnosis.

	general shape	umbilicus	periphery	final whorl chambers	camber	suture	aperture	wall	Level
<i>H. kushiroensis</i> Asano, 1962	compressed	somewhat umbilicate	subacute	6-7	indistinct	indistinct	indistinct	medium to coarse-textured	Oligocene
<i>H. yoshidai</i> nom. nov. (<i>H. Kushiroensis</i> Yoshida, 1963)	nautiloid, globular	umbilicate	broadly rounded	6-8		depressed, sometimes obscured, almost straight	low arch opening at the base of the apertural face	roughly cemented	Maastrichtian to Paleocene
<i>H. tanaii</i> Kaiho, 1984	compressed	biumbilicate	subacute to somewhat rounded	6-7	slightly inflated	straight radial	interiomarginal equatorial arch	coarsely agglutinated	Eocene
<i>H. obesus</i> Takayanagi, 1960	subglobular, coarsely coiled	(completely involute)	very broadly rounded	5 (figured specimen)	inflated	not usually distinct, radial, slightly curved, very slightly depressed	low slit at base of apertural face	rather coarsely arenaceous	Lower to Upper Cretaceous
<i>Cribrostomoides cretacea</i> Cushman and Goudkoff, 1944	subglobular	involute, with a distinctly depressed umbilical region	broadly rounded	8-10	very slightly if at all inflated	fairly distinct, little if at all depressed	in adult with several pores along the base of the apertural face	very finely arenaceous	Coniacian to Maastrichtian
<i>H. renzi</i> Asano, 1950	compressed	involute	rounded but somewhat lobulate	7-8	slightly inflated	nearly radial, often indistinct	curved slit at the base of the apertural face	thick with much cement	Miocene to Pliocene
<i>H. subamakusaensis</i> Fukuta, 1962	wide	somewhat opened	broadly rounded	10-12	slightly inflated	fairly distinct	at base of apertural face	finely arenaceous	Eocene

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Palaeontological Society of Japan (JSP) Standing Committee Actions

During its meeting on April 25, the JSP Standing Committee enacted the following changes to its membership.

New members elected ;

Atsushi Chiyoda,
Toyoho Ishimura,
Kwang-Nam Kim,
Kentaro Toda,
Katsura Yamada,

Masayuki Fujikawa,
Chika Ito,
Tomohiro Sekiguchi,
Takanobu Tsuihiji,
Taizo Yokoyama

Yohsuke Ibaraki,
Hiroshi Iwaoka,
Masamichi Takahashi,
Kozin Wada,

Subscribing member elected ;

David I. Holloway

Membership changed from Oversea members to Subscribing members ;

Wilbert R. Danner,

Charles Scott King,

Georg Waldmann

Resigned members ;

Vladimir I. Davydov,
Goro Jitsuzaki,
Yuri Sato,
Shigemoto Tokunaga,

Kosho Hanazawa,
Takashi Matsunaga,
Hiroshi Sugano,
Stone Museum Inc

Isamu Hashimoto,
Saneatsu Saito.
Masayuki Tagawa,

Deceased Member ;

Osamu Koseki

During its meeting on 26 June, the JSP Standing Committee enacted the following changes to its membership.

New members elected ;

Natsuko Adachi,
Yoshihiro Katsura,
Kosuke Nakada,
Chisato Suzuki,

Koji Hase,
Kazuto Koarai,
Kazuhiko Sakurai,
Yumi Yasuhara,

Harumasa Kano,
Gerard J. McGowan,
Satoshi Shinohara,

Subscribing member elected;

Tak-Cheung Lau,

Royal H. Mapes

Resigned members ;

Hsin Yi Ling

行事予定

- ◎1999年年会は1999年1月29日(金)～1月31日(日)に、「東北大学」で開催されます。一般講演の申し込み締切は12月3日です。シンポジウムとして1月29日に「生物事変：復元の科学 3 世話人：海保邦夫，西 弘嗣，大野照文」が行われます。
- ◎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」で行なわれます。一般講演の申し込み締切は5月7日です。シンポジウムの企画をお持ちの方は，1998年12月末までに行事係までお申し込み下さい。
- ◎2000年年会・総会には現在の所「早稲田大学」から開催の申し込みがありました。(決定ではありません)。シンポジウム企画の締切は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)は，今の所開催申し込みがありません。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。
- ◎現在，常務委員会は2001年からの学会行事の変更を検討しております。2001年からは，従来とは異なった時期や開催形式で年会，例会，総会が開催される可能性があります。従いまして，第149回例会(2000年6月末に開催予定)までは，従来通り開催の申し込みを受け付けますが，2001年以降の開催申し込みは，しばらくの間見あわせて頂きます。

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