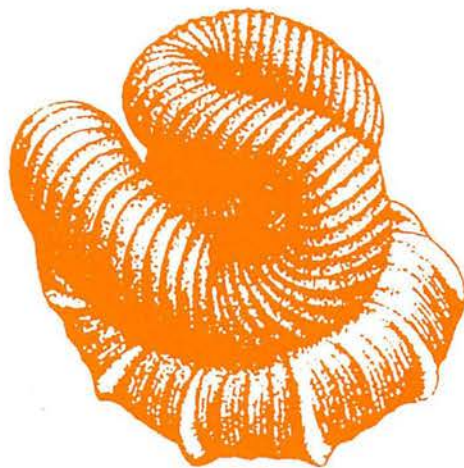


Paleontological Research

ISSN 1342-8144

Formerly
Transactions and Proceedings
of the
Palaeontological Society of Japan



Vol. 2 No. 3
September 1998

The Palaeontological Society of Japan

Co-Editors Kei Mori and Haruyoshi Maeda

Language Editor **Martin Janal** (New York, USA)

Associate Editors

Jan Bergström (Swedish Museum of Natural History, Stockholm, Sweden), Alan G. Beu (Institute of Geological and Nuclear Sciences, Lower Hutt, New Zealand), Kiyotaka Chinzei (Osaka Gakuin University, Japan), Shiro Hasegawa (Hokkaido University, Sapporo, Japan), Hiromichi Hirano (Waseda University, Tokyo, Japan), Wang Hongzhen (China University of Geosciences, Beijing, China), James C. Ingle, Jr. (Stanford University, Stanford, USA), Tomoki Kase (National Science Museum, Tokyo, Japan), Susan M. Kidwell (University of Chicago, Chicago, USA), Kenshiro Ogasawara (University of Tsukuba, Tsukuba, Japan), Andrew B. Smith (Natural History Museum, London, Great Britain), Yoshihiro Tanimura (National Science Museum, Tokyo, Japan), Roger D.K. Thomas, (Franklin and Marshall College, Lancaster, USA), Yukimitsu Tomida (National Science Museum, Tokyo, Japan), Kazuhiko Uemura (National Science Museum, Tokyo, Japan), Akira Yao (Osaka City University, Osaka, Japan)

Officers for 1997-1998

President : Noriyuki Ikeya

Councillors : Kiyotaka Chinzei, Takashi Hamada, Yoshikazu Hasegawa, Itaru Hayami, Hiromichi Hirano, Hisayoshi Igo, Noriyuki Ikeya, Junji Itoigawa, Tomoki Kase, Hiroshi Kitazato, Itaru Koizumi, Haruyoshi Maeda, Ryuichi Majima, Kei Mori, Hiroshi Noda, Ikuo Obata, Kenshiro Ogasawara, Terufumi Ohno, Tatsuo Oji, Tomowo Ozawa, Yukimitsu Tomida, Tsunemasa Saito, Takeshi Setoguchi, Kazushige Tanabe, Akira Yao

Members of Standing Committee : Hiroshi Kitazato (General Affairs), Tatsuo Oji (Liaison Officer), Tomoki Kase (Finance), Kei Mori (Editor in Chief, PR), Haruyoshi Maeda (Co-Editor, PR), Ryuichi Majima (Planning), Hiromichi Hirano (Membership), Kenshiro Ogasawara (Foreign Affairs), Terufumi Ohno (Publicity Officer), Kazushige Tanabe (Editor, "Fossils"), Yukimitsu Tomida (Editor in Chief, Special Papers), Tamiko Ohana (Representative, Friends of Fossils), Itaru Hayami (Representative, Union of Natural History Societies)

Secretaries : Satoshi Chiba, Akihisa Kitamura (General Affairs), Yasunari Shigeta (Finance), Hajime Taru (Planning), Tokuji Mitsugi (Membership), Katsumi Ueno (Foreign Affairs), Rihito Morita (Public Information), Masanori Shimamoto (Editor of PR), Kazuyoshi Endo (Editor of "Fossils"), Naoki Kohno (Editor of Special Papers)

Auditor : Masaki Matsukawa

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).

All communication relating to this journal should be addressed to the
PALAEONTOLOGICAL SOCIETY OF JAPAN
c/o Business Center for Academic Societies,
Honkomagome 5-16-9, Bunkyo-ku, Tokyo 113-8622, Japan

Taxonomy and phylogeny of the genus *Theocorys* (Nassellaria, Radiolaria) from the Eocene and Oligocene sequences in the Antarctic region

ATSUSHI TAKEMURA and HSIN YI LING

Geoscience Institute, Hyogo University of Teacher Education, Yashiro-cho, Kato-gun, Hyogo 673-1494, JAPAN
Department of Geology, Northern Illinois University, DeKalb, IL 60115, USA

Received 10 January 1998; Revised manuscript accepted 13 August 1998

Abstract. Taxonomic and phylogenetic investigations were carried out on the Eocene and Oligocene radiolarians assignable to the genus *Theocorys* from submarine sections of the Southern Indian and Southern Atlantic Oceans. Several well-preserved theoperid species previously described under the genera *Calocyclus*, *Cyrtocapsella* or *Theocorys* are now grouped into *Theocorys*, and their phylogenetic relationships are discussed. Five species are described, of which three are proposed as new. They are: *T. kerguelensis* sp. nov., *T. minuta* sp. nov., *T. saginata* sp. nov., *T. robusta* comb. nov. and *T. semipolita* comb. nov. In addition, another new species, *Calocyclus* (?) *nakasekoi*, is described.

Key words: Antarctic, Eocene, Nassellaria, Oligocene, Radiolaria, taxonomy

Introduction

As with other microfossils, knowledge on Cenozoic radiolarians in the Antarctic Ocean has improved remarkably during the last two decades. The Deep Sea Drilling Project (DSDP) cruises, Legs 28, 29, 35 and 36, clearly established a Neogene radiolarian biostratigraphy, while leaving Paleogene sections untouched. The addition of a Paleogene and Neogene biostratigraphic framework after the cruises of the Ocean Drilling Program (ODP), Legs 113 and 114 in the South Atlantic Ocean, and Legs 119 and 120 in the Southern Indian Ocean, nearly completed the entire Cenozoic sequence (Abelmann, 1990, 1992; Lazarus, 1990, 1992; Caulet, 1991; Takemura, 1992; Takemura and Ling, 1997).

The biostratigraphic framework established from the high-latitude regions is quite different from that of the currently generally accepted one for low-latitude areas (Riedel and Sanfilippo, 1978; Sanfilippo, *et al.*, 1985), because of the nearly complete absence of zonal marker species. In other words, the Antarctic radiolarian biozonation must be proposed based on paleobiogeographically limited endemic species.

Among Paleogene Antarctic radiolarians, species previously assigned to the genera *Calocyclus*, *Cyrtocapsella* or *Theocorys* by several authors (e.g., Petrushevskaya, 1975; Chen, 1975; Abelmann, 1990) are generally observed in submarine sediments. They usually consist of three segments; a small, poreless cephalis, an inflated thorax and a cylindrical abdomen. The pores of the thorax and abdomen

are usually arranged in longitudinal rows. Although some of them were reported from the low-latitude areas, they differ from those of high-latitude areas at the species level.

We investigated the taxonomy and phylogeny of these radiolarians because of their biostratigraphic potential in Antarctic Paleogene sections, and because of the paucity of studies on these taxa until now.

Studied materials and methods of analysis

Deep-sea sediments examined for the present study were collected during ODP cruises, Leg 120 from the Southern Indian and Leg 114 from the South Atlantic Oceans (Figure 1). We used mostly Leg 120 samples for the taxonomic study, and Leg 114 samples to verify the stratigraphic ranges of each species. The biostratigraphic correlation using radiolarians between Paleogene sequences of these two legs was made by Takemura and Ling (1997).

Leg 120 explored the Kerguelen Plateau in the Southern Indian Ocean and drilled five sites, Sites 747 to 751 (Schlich, *et al.*, 1989). Among them, only Sites 748 and 749 from the Southern Kerguelen Plateau yielded well preserved Paleogene radiolarians (Takemura, 1992). We selected samples from Site 748 for the present study because the sedimentation rate at Site 749 was too low in the Upper Eocene to Oligocene section (Schlich, *et al.*, 1989).

Site 748 (58°26.45'S, 78°58.89'E; water depth, 1,290 m) is located on the Southern Kerguelen Plateau in the western Part of the Raggatt Basin, east of the Banzare Bank, approx-

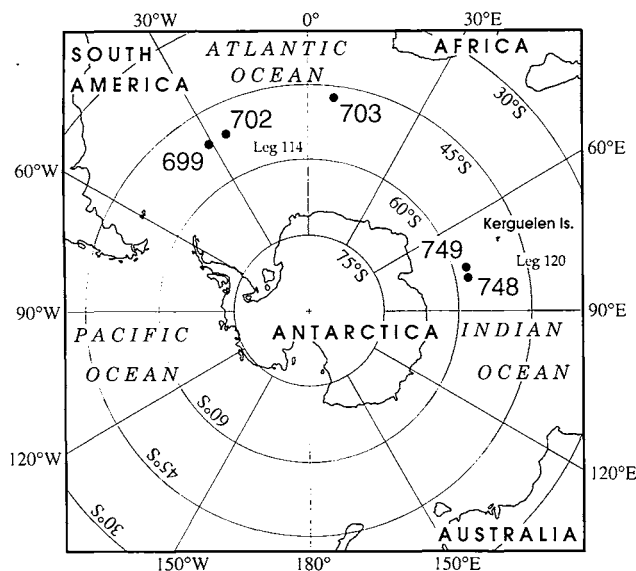


Figure 1. Locality of ODP Sites where the Paleogene radiolarian samples examined in this paper were collected.

imately 900 km south of the present-day Antarctic Convergence (Schlich, *et al.*, 1989). At this site, samples from Cores 9H to 20H (66.6 to 180.6 mbsf = meters below sea floor) of Hole 748B yielded well-preserved Paleogene radiolarians. The sediments are nannofossil ooze (Unit IIA) and are rich in other planktic microfossils, e.g., calcareous nannofossils, foraminifers, diatoms and silicoflagellates. Their biostratigraphic distributions have already been presented (Aubry, 1992; Wei, *et al.*, 1992; Berggren, 1992; Harwood and Maruyama, 1992; McCartney and Harwood, 1992). Based on the results of foraminiferal and magnetostratigraphic analyses (Berggren, 1992; Inokuchi and Heider, 1992), the Oligocene/Miocene boundary, which is correlated with Chron C6CN2, is located between 748B-8H, CC and 748B-9H-1, 40-44 cm, (66.6-67.0 mbsf), while the Eocene/Oligocene boundary is drawn between 748B-14H-5, 40-44 cm and 748B-14H-6, 80-84 cm (120.5-122.4 mbsf). The oldest sediments containing well preserved Cenozoic radiolarians from the hole are Middle Eocene in age. Thus, the age of this interval spans Middle Eocene to Late Oligocene (about 45 Ma to 23.6 Ma, Berggren, *et al.*, 1985).

Takemura (1992) proposed three new radiolarian zones from this Paleogene interval. They are in ascending order the *Eucyridium spinosum*, *Axoprunum* (?) *irregularis*, and *Lychnocanoma conica* Zones, which approximate the Upper Eocene, Lower Oligocene and Upper Oligocene intervals respectively.

During ODP Leg 114, seven sites were drilled from the South Atlantic Ocean (Ciesielski, *et al.*, 1988). Well preserved Eocene to Oligocene radiolarians were observed from Sites 699, 702 and 703. Biostratigraphy for the contained microfossils was presented by Nocchi, *et al.* (1991), Crux (1991), Madile and Monechi (1991), and Ciesielski (1991).

Site 699 is on the northeastern slope of the Northeast Georgia Rise in the western South Atlantic Ocean (51°32.537'

S, 30°40.619'W; water depth, 3,705.5 m). The Oligocene sequence at this site (Hole 699A, Cores 10H to 33X, approx. 90-310 mbsf) is composed of siliceous nannofossil ooze, nannofossil siliceous ooze, nannofossil diatom ooze and mud, in ascending order. Site 702 is located on the central part of the Islas Orcadas Rise in the western South Atlantic Ocean (50°56.786'S, 26°22.117'W; water depth, 3,083.4 m). Middle to late Eocene nannofossil chalk (Hole 702B, Cores 4X to 22X, 32.8-202.45 mbsf) containing radiolarians underlies the Miocene nannofossil ooze with a hiatus. Site 703 is located on the Meteor Rise in the Indo-Atlantic Basin (47°03.042'S, 07°53.679'E; water depth, 1,796 m). At this site, Late Eocene to Late Oligocene sediments (Hole 703A, Cores 5H to 18X, approx. 40-160 mbsf) are composed of calcareous ooze which yielded radiolarians (Ciesielski, *et al.*, 1988).

Treatment methods for extracting radiolarian shells from the samples have been previously described (Takemura, 1992). The samples were processed with HCl (about 3%), followed by H₂O₂ and sodium pyrophosphate (or Calgon). Residues were sieved through a 250-mesh (63 μm) screen, dried and kept in vials. Slides for transmitted light microscope and specimens for SEM (scanning electron microscope) were then made from these residues.

Microslides were prepared by the method described by Sakai (1980) and Takemura (1992). Dried residues were scattered on slides which were coated with thin gum tragacanth. After blowing lightly on each slide, radiolarian shells that did not adhere were allowed to fall off and were removed with a brush. Canada balsam was used as a mounting medium. For observation and photomicrography under SEM, selected specimens were picked with a thin brush from the dried residues under a binocular microscope, mounted on an aluminum stab. We observed both the outer shell structure and the internal cephalic skeletons of the specimens used in this study.

On the generic assignment of "*Calocyclus*" and "*Cyrtocapsella*" group in the Antarctic Paleogene

Several species of theoperids (Riedel, 1967; 1971) of three segments, which were previously assigned to the genus *Theocorys*, *Calocyclus* and *Cyrtocapsella*, occur in Eocene to Oligocene sediments in the Antarctic Ocean. All have an identical cephalic skeletal structure (see Figure 5), small poreless cephalis and nearly cylindrical shell form. The pores on the thorax and abdomen are arranged longitudinally and diagonally, but are often partly irregular. Takemura (1992) described these species under the name *Calocyclus* cf. *semipolita* Clark and Campbell, *Calocyclus* sp. A, *Calocyclus* sp. B, *Calocyclus* sp. C and *Cyrtocapsella robusta* Abelmann. In this paper, we include these species in the genus *Theocorys*.

The genus *Calocyclus* Ehrenberg is a theoperid of three segments, which has a small poreless cephalis and a large inflated thorax. Campbell (1954) designated *Calocyclus turris* Ehrenberg as the type species of the genus. Though Riedel and Sanfilippo (1970) had assigned *C. turris* and *C. hispida* to the genus *Cycladophora*, Foreman (1973) corrected the

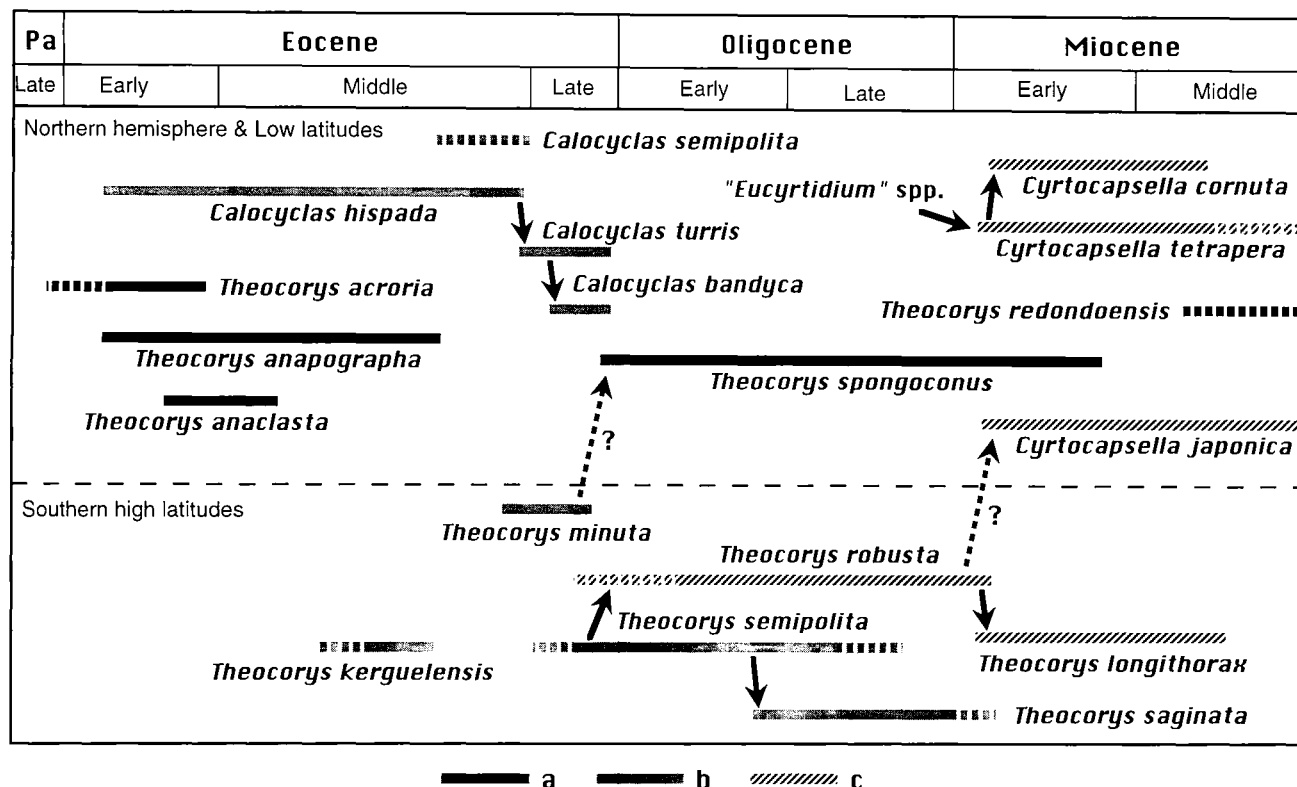


Figure 2. Ranges and phylogeny of the species of the genus *Theocorys*, *Calocyclus* and *Cyrtocapsella*. In addition to our present study, data included are: Abelmann (1990, 92), Blueford (1988), Foreman (1973), Kling (1971, 73), Nigrini and Lombardi (1984), Riedel and Sanfilippo (1971, 1978), Sanfilippo and Riedel (1970) and Sanfilippo, Westberg-Smith and Riedel (1985). a: species described as *Theocorys* in previous studies. b: species described as *Calocyclus* in previous studies. c: species described as *Cyrtocapsella* in previous studies.

generic assignment to this genus. The type species, *Calocyclus turris*, possesses a long apical horn on its cephalis, a large subspherical thorax and a conical abdomen which consists of lamellar feet and bars joining the feet. The thoracic pores are aligned longitudinally and diagonally, whereas the abdominal pores are in both longitudinal and transverse rows. Sanfilippo, *et al.* (1985) stated that this species evolved from *Calocyclus hispida*, which possesses only lamellar feet as abdomen, and left no descendants. On the other hand, Saunders *et al.* (1984) included *Calocyclus bandyca* as a descendant species of *C. turris* (Figure 2).

Although all the species of the "Calocyclus" group in the Antarctic region show a similar structure in both abdominal and thoracic segments, the shell structures of thorax and abdomen are completely different from those of *Calocyclus turris*, *C. hispida* and *C. bandyca*. This fact suggests the evolutionary lineage of this "Calocyclus" group is different from that of *Calocyclus hispida*-*C. turris*-*C. bandyca*.

As for the genus *Cyrtocapsella*, Sanfilippo and Riedel (1970) defined it as follows: "Cenozoic, three- or four-segmented theoperids with a very constricted mouth resembling a large terminal pore surrounded by a differentiated ring. A small apical horn is commonly present, and some specimens have additional, usually more delicate, generally closed conical segment below the constricted one." The geological occur-

rence of the genus *Cyrtocapsella* is mostly within the Miocene and *C. tetrapera*, the oldest species of this genus in low latitudes, evolved from some form of "Eucyrtidium" in the earliest Miocene time. They described four species under the genus, four-segmented *C. tetrapera* Haeckel and *C. cornuta* Haeckel, and three-segmented *C. elongata* (Nakaseko) and *C. japonica* (Nakaseko).

From the southern oceans, Petrushevskaya (1975) described *Theocorys longithorax*, which is the same species as *Cyrtocapsella isopera* described by Chen (1975). Abelmann (1990) reported this species as *Cyrtocapsella longithorax* (Petrushevskaya). She also proposed a new species, *C. robusta*, which is a three-segmented form, and stated that this species was probably the ancestral form of *C. longithorax*. In one of her illustrated Oligocene specimens, the aperture of Oligocene *C. robusta* is neither closed nor constricted. Takemura (1992) also included these forms with the genus *Cyrtocapsella* because he could not differentiate them from the forms with small apertures.

The genus *Cyrtocapsella* becomes a polyphyletic taxon if these Antarctic forms are included. While *Cyrtocapsella tetrapera* evolved from "Eucyrtidium" spp. in low latitudes, it seems reasonable that Antarctic "Cyrtocapsella" *robusta* evolved from "Calocyclus" *semipolita*, as discussed in the next section. Because the evolutionary lineage of the high-

latitude three-segmented "*Calocyclus*" and "*Cyrtocapsella*" group differs from those of *Calocyclus* and *Cyrtocapsella* in low latitudes, in this paper, we include these Antarctic forms under the genus *Theocorys*.

Regarding the genus *Theocorys*, various authors severally designated type species of the genus, e.g., *Eucyrtidium turgidulum* Ehrenberg by Frizzell and Middour, 1951; *Theocorys morchellula* Rüst by Campbell, 1954; *Theocorys veneris* Haeckel by Strelkov and Lipman, 1959. Riedel and Sanfilippo (1970) discussed this problem, and accepted *Theocorys morchellula* Rüst designated by Campbell (1954) as the type species of this genus because it is the first species described under this genus. They (1970) proposed two new species, *T. anaclasta* and *T. anapographa*, for the genus, and stated that this generic assignment was provisional. Indeed, the shell shapes of these two species are quite different from that of the type species, *T. morchellula* (Rüst, 1885, p. 308, pl. 37 (12), fig. 6). Foreman (1973) described *T. acroria*, and considered all three forms, *T. acroria*, *T. anaclasta* and *T. anapographa*, to be related to each other.

All species of *Theocorys* described in this paper share very few similarities in their shell shape to *T. morchellula*. *T. morchellula* has a large, inflated and subspherical thorax with large pores arranged in transverse rows and also diagonally. On the other hand, the shapes of the cephalo-thorax and the abdominal pores of *Theocorys* described in this paper are similar to those of *Theocorys anapographa* or *T. acroria*, indicating some phylogenetic relationship between these two groups. Therefore, we include the Antarctic forms, which were previously classified under the genus *Calocyclus* or *Cyrtocapsella*, in the genus *Theocorys*.

Taxonomy and phylogeny of the genus *Theocorys* in the Antarctic region

From the Antarctic Ocean, Petrushevskaya (1975), Chen (1975), Abelmann (1990), Caulet (1991) and Takemura (1992) reported species belonging to the genus *Theocorys*. Among them *Theocorys semipolita* (Clark and Campbell) is the most common species in Eocene to Oligocene sediments. The species was originally described by Clark and Campbell (1942) from the Eocene in California, and was re-examined by Blueford (1988) recently with photomicrographs from the same region of Clark and Campbell (1942). According to these studies, *Calocyclus semipolita* from California is a moderate-sized form with a relatively long apical horn, and thoracic and abdominal pores arranged longitudinally or irregularly.

In the Antarctic region, although some Eocene forms of this species seem to be identical to those from California, the size and length of the abdomen and thickness of the shell become larger and thicker in the Early Oligocene, and smaller and thinner again in most Late Oligocene specimens (Figures 4-15-21). The maximum length of shell among the Late Eocene and Earliest Oligocene specimens of *T. semipolita* is less than 200 μm , while the largest specimen in Early Oligocene has nearly 300 μm of total length of shell. The distinctive earliest Oligocene cooling event in the Antarctic Ocean (Wei, *et al.*, 1992) probably caused this

inflation of size and thickness of the shell. The Antarctic forms may or may not have a small apical horn. While they vary particularly widely in their forms and sizes overall as well as in the abdominal segment among the specimens, we consider these phenomena as intraspecific variations within a single species because such variation is continuous.

We propose three new species of the genus *Theocorys*. They are *T. saginata* sp. nov. (Figures 4-7-14, Figures 5-9, 10), *T. kerguelensis* sp. nov. (Figures 3-8-15, Figures 5-3, 4) and *T. minuta* sp. nov. (Figures 3-16-21, Figures 5-5, 6). All of these species generally have a large and inflated thorax with basically longitudinally aligned pores, and an abdomen of similar structure, except for *T. minuta*. The detailed biostratigraphic studies on the species of the genus *Theocorys* in the Antarctic region reveal the following geological range and phylogenetic relationships (Figure 2).

Among these species, *Theocorys semipolita* ranges from Middle Eocene through Late Oligocene and shows the largest variations in their shell shapes. The ancestral form from which *T. semipolita* evolved is unknown. The cephalo-thorax of Eocene *T. semipolita* is quite similar to that of *Theocorys anapographa* Riedel and Sanfilippo, although the latter species has not been reported from the Antarctic region yet. *Theocorys kerguelensis* also has some resemblance in shell shape to *T. semipolita*. However, there is a time gap in late Middle Eocene when both *T. kerguelensis* and *T. semipolita* were absent, and we have not observed any intermediate forms between these two species.

T. semipolita shows wider variation in Early Oligocene. Many thick-walled and sometimes large forms have various types of abdomen (Figures 4-19, 20). The shape of the abdominal segments varies: cylindrical or truncate-conical; long or short; with open, closed or fenestrated to tube-like aperture.

Admittedly, the distinction between *T. semipolita* and *T. robusta* is somewhat artificial. The cephalo-thorax of smaller forms of *T. semipolita* (Figures 4-15, 21) and *T. robusta* is very similar in shape and shell structure. These two species can be differentiated based on the facts that *T. robusta* has an abdomen shorter than about twice of thoracic length, a thinner shell wall, and usually a smaller-sized thorax. *T. semipolita*, on the other hand, possesses a longer abdomen, thicker shell wall and/or larger thorax.

Takemura (1992) described two species of the genus *Cyrtocapsella*, *C. robusta* and *C. sp. aff. C. japonica*, based on the length of the abdomen, but also stated that the variation of the length of the abdomen is continuous between the two species. Moreover, the ranges of these two forms are similar, therefore, we combine them into one species as *Theocorys robusta*.

Theocorys robusta (Figures 4-1-6, Figures 5-7, 8) could be the ancestral form of *T. longithorax*, as Abelmann (1990) already discussed. We believe this transition occurred in the Early Miocene through increase of the number of pores at the expense of a reduction in size of the thoracic and abdominal pores.

Caulet (1991) discussed the evolutionary lineage of this group (*op. cit.*, p. 529-530, fig. 4). His observations on this

group are very similar to our conclusion. However, his classification is somewhat different from those of Takemura (1992) or Abelmann (1990). He did not describe the differences or the definition of the species of this group. For example, *Cyrtocapsella longithorax* shown in fig. 4 of Caulet (1991) includes the forms with larger and fewer pores (Specimen 7 of fig. 4). We assign such form to *Theocorys robusta* (Abelmann) following the species concept of Abelmann (1990).

We also observed a transitional form from *Theocorys semipolita* to *T. saginata* in the late Early Oligocene (Figure 4-17). *T. saginata* has a larger thorax, shorter abdomen with open aperture and more distinct lumbar stricture than *T. semipolita*. The intermediate form has a large thorax and distinct lumbar stricture, but has a long abdomen. Therefore, we believe *T. saginata* evolved from *T. semipolita* in the late Early Oligocene at approximately the time of the first appearance of *Lychnocanoma conica* (Takemura, 1992).

The phylogenetic relationship between *Theocorys minuta* and other species of *Theocorys* is unclear, because we have not observed any species which suggests any relationship or similarity in shell shape to *T. minuta* from the Antarctic Eocene sediments. A species which is most similar in shell morphology to *T. minuta* is *T. spongoconus* Kling, although the latter species has a distinct spongy abdomen. The first appearance of *T. spongoconus* occurs the near Eocene-Oligocene boundary in low latitudes (Riedel and Sanfilippo, 1978), while in the Antarctic region *T. minuta* disappeared just before the boundary and after the occurrence of *Theocyrtis tuberosa*. It may be possible that *T. spongoconus* in low-latitudes evolved from *T. minuta*.

Sanfilippo and Riedel (1970) discussed the evolutionary relationships among the species of the genus *Cyrtocapsella*, and considered that *Cyrtocapsella japonica* and *C. elongata* might have originated from *C. tetrapera* by narrowing of the third stricture. However, some forms of *Theocorys robusta* in the Antarctic region possess a short abdomen, and the shell shape is similar to that of *C. japonica*. Although the apertures of these Antarctic forms are usually not constricted, the three-segmented *Cyrtocapsella* species may have evolved from *T. robusta*.

In addition to these species belonging to the genus *Theocorys*, we propose a new species, *Calocyclus* (?) *nakasekoi*, which commonly occurs in Middle Eocene sediments in the Antarctic region. We tentatively have included *C. (?) nakasekoi* in the genus *Calocyclus*, because it has a large inflated thorax with pores aligned longitudinally and diagonally. Furthermore, there is no genus in which this species can be reasonably assigned. This species probably has no phylogenetic relationship with the other species of *Calocyclus* or *Theocorys*. Rather, it may have some relationship with *Lychnocanoma amphitrite* Foreman, because the shell structures of their cephalo-thorax with a long and stout apical horn are somewhat similar, and the three feet of *L. amphitrite* actually have no connection to the cephalic skeletal elements.

Systematic description

The type specimens are deposited in Geoscience Institute, Hyogo University of Teacher Education, Hyogo, Japan (HUTE).

Subclass Radiolaria Müller, 1858

Order Polycystina Ehrenberg, 1838, emend. Riedel, 1967

Suborder Nassellaria Ehrenberg, 1875

Family Theoperidae Haeckel, 1881, emend. Riedel, 1967

Remarks.—All species described below have the same cephalic skeletal structure (Figures 5-2, 4, 6, 8, 10 and 12). They have a median bar (MB), two lateral spines (L) and a vertical spine (V) at the base of the cephalis, and four collar pores. The two lateral spines and a dorsal spine (D) are prolonged onto the inner surface of the thoracic wall. An apical spine (A) arises at the end of MB opposite to V, lying on the inner side of the cephalic wall to the apical horn. This structure is same as the *Arcanica*-type structure of Takemura (1986).

Nishimura (1990) made detailed SEM observations on cephalic skeletal structures of Cenozoic radiolarians including *Cyrtocapsella tetrapera*. She identified some rays or part of rays (= spines of various authors) within the cephalic shell wall of *C. tetrapera*. However, it is difficult to distinguish whether these rays are actually the prolongations of the basic cephalic structure or other accessory elements attached to the main elements. The cephalic structure of *C. (?) nakasekoi* and *Theocorys* described below is regarded as the same as that of *Cyrtocapsella tetrapera*.

We have assigned the genera *Calocyclus* and *Theocorys* to the Family Theoperidae of Riedel (1967) in this paper, because the classification of Nassellaria is still incomplete, and because his classification has been widely accepted for Cenozoic nassellarians.

Genus *Calocyclus* Ehrenberg, 1847

Calocyclus Ehrenberg, 1847b, p. 54; Haeckel, 1887, p. 1381; Campbell, 1954, p. D132; Foreman, 1973, p. 433, 434.

Cycladophora Ehrenberg, 1847a, p. 385; Riedel and Sanfilippo, 1970, p. 529.

Type species.—*Calocyclus turris* Ehrenberg (subsequent designation by Campbell, 1954, p. D132, Foreman, 1973, p. 433)

Remarks.—In this paper, we provisionally assign a new species, *C. (?) nakasekoi*, to this genus because the shape of its cephalo-thorax, and thoracic pore arrangements are somewhat similar to species of the genus. However, the phylogenetic relationship between this new species and *Calocyclus turris*, the type species of this genus, is questionable. Both *Calocyclus taiwanii* described by Bjørklund and Kellogg (1972) and *Calocyclus extensa* described by Clark and Campbell (1942), in which the thoracic pores are arranged in transverse rows, should be excluded from *Calocyclus*.

Calocyclus (?) *nakasekoi* sp. nov.

Figures 3-1-7; 5-1, 2

Sethocyrtis sp. Chen, 1975, p. 459, pl. 1, figs. 4, 5; Takemura, 1992, p. 747, pl. 7, figs. 14, 15; Takemura and Ling, 1997, p. 114, pl. 1, fig. 11.

Description.—Large conical or cylindrical shell with two segments. Cephalis small, subspherical and poreless with a stout and long apical horn, which tapers distally. Collar stricture distinct. Thorax large, usually thick-walled, inflated and barrel- or egg-shaped. Thoracic pores large, mostly uniform in size throughout, and usually arranged longitudinally and diagonally. Twelve to 15 longitudinal rows of thoracic pores visible on one side of the shell. Circular thoracic aperture slightly constricted with distinct peristome.

Measurements.—Length of apical horn, 62–85 μm ; Length and width of cephalis, 37–46 μm ; Length and width of thorax, 138–178 μm , measured in 19 specimens.

Types.—Holotype, HUTE-R-4007, Sample 120-748B-19H-4, 45–47 cm, Middle Eocene. Paratypes, HUTE-R-4008, Sample 120-748B-19H-4, 45–47 cm, Middle Eocene, HUTE-R-4009, Sample 120-748B-19H-4, 45–47 cm, Middle Eocene, HUTE-R-4010, Sample 120-748B-19H-4, 45–47 cm, Middle Eocene.

Remarks.—This species is easily distinguished from other species of the genus by its two-segmented form, large size and characteristic shape of the thorax, and stout, long apical horn. The shell structure of the cephalo-thorax including the apical horn is similar to that of *Lychnocanoma amphitrite* Foreman, although this species has no feet at the base of thorax.

Etymology.—This new species was named after Dr. Kojiro Nakaseko in honor of his significant contributions to Japanese radiolarian research.

Occurrence.—Leg 120, Hole 748B: Sample 120-748B-19H-7 cm (bottom of the examined samples) to Sample 120-748B-17H-7, 45–47 cm. Middle Eocene.

Leg 114, Site 702: Sample 114-702B-11X-1, 60–62 cm to Sample 114-702B-8X-2, 20–22 cm. Middle Eocene.

This species is commonly observed in Middle Eocene sediments in the Antarctic region. Its sporadic occurrence in Oligocene sediments in Hole 748B is considered reworked, based on the poor state of preservation (broken), and the presence of Eocene species of *Lychnocanoma amphitrite*, *Eucyrtidium spinosum* and/or *Lophocyrtis biaurita* in the

same samples.

Genus *Theocorys* Haeckel, 1881

Theocorys Haeckel, 1881, p. 434; Haeckel, 1887, p. 1414, 5; Campbell, 1954, p. D134; Riedel and Sanfilippo, 1970, p. 530; Kling, 1971, p. 1087; Foreman, 1973, p. 439.

Type species.—*Theocorys morchellula* Rüst, 1885, p. 308, pl. 37 (12), fig. 6 (subsequent designation by Campbell, 1954).

Remarks.—We have described five Paleogene species in the Antarctic region, *T. kerguelensis* sp. nov., *T. minuta* sp. nov., *T. robusta* (Abelmann), *T. saginata* sp. nov. and *T. semipolita* (Clark and Campbell), under this genus, because of their possible phylogenetic relationship to such Early to Middle Eocene low latitude species as *Theocorys anaclasta* and *T. anapographa* described by Riedel and Sanfilippo (1970) and *T. acroria* described by Foreman (1973). However, the relationship of all these species to the type species of this genus, *T. morchellula*, is questionable.

Petrushevskaya (1975) described *Theocorys longithorax*, which was later renamed *Cyrtocapsella longithorax* by Abelmann (1990). Petrushevskaya (1975) differentiated *Theocorys* from the genus *Calocyclus* by its smaller shell dimensions, thinner wall and smaller pores, but in some species, the thorax is inflated and large. Herein we assign *T. longithorax* to the genus *Theocorys* because this species evolved from *T. robusta* (Abelmann, 1990).

T. semipolita, *T. saginata*, *T. robusta* and *T. longithorax* must be included in a single genus because of their apparent phylogenetic relationship. However, assignment of two other species, *T. kerguelensis* and *T. minuta*, to this genus is provisional and based only on the similarity of their shell shapes to other *Theocorys*. Among Cenozoic radiolarians from the low latitude Northern Hemisphere, *T. spongoconus* Kling and *T. redondoensis* (Campbell and Clark) are included within this genus. The genus may include *Cyrtocapsella japonica* (Nakaseko) and *C. elongata* (Nakaseko), because these two species may have evolved from *T. robusta*.

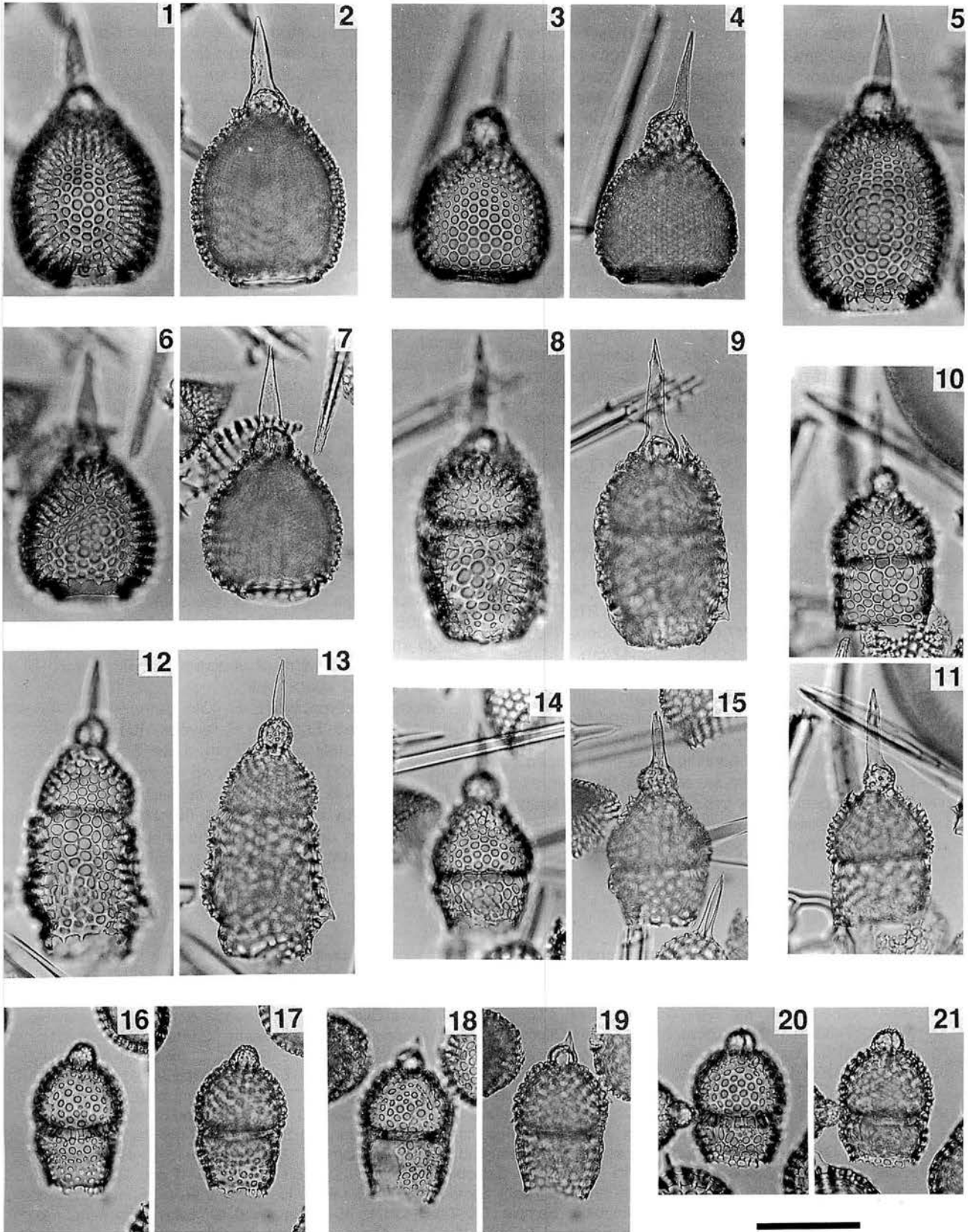
Theocorys kerguelensis sp. nov.

Figures 3-8-15; 5-3, 4

Calocyclus sp. C, Takemura, 1992, p. 745, pl. 7, fig. 3, 4; Takemura and Ling, 1997, p. 111, pl. 1, fig. 17.

Description.—Shell conical to cylindrical with three seg-

Figure 3. Eocene nassellarians from the Antarctic region. **1, 2.** *Calocyclus* (?) *nakasekoi* sp. nov., Holotype, HUTE-R-4007, Sample 120-748B-19H-4, 45–47 cm, Location in slide by England Funder, M41/2. Middle Eocene. **3, 4.** *Calocyclus* (?) *nakasekoi* sp. nov., Paratype, HUTE-R-4008, Sample 120-748B-19H-4, 45–47 cm, X47/0. Middle Eocene. **5.** *Calocyclus* (?) *nakasekoi* sp. nov., Paratype, HUTE-R-4009, Sample 120-748B-19H-4, 45–47 cm, J37/0. Middle Eocene. **6, 7.** *Calocyclus* (?) *nakasekoi* sp. nov., Paratype, HUTE-R-4010, Sample 120-748B-19H-4, 45–47 cm, L22/4. Middle Eocene. **8, 9.** *Theocorys kerguelensis* sp. nov., Holotype, HUTE-R-4011, Sample 120-748B-19H-4, 45–47 cm, Y42/0. Middle Eocene. **10, 11.** *Theocorys kerguelensis* sp. nov., Paratype, HUTE-R-4012, Sample 120-748B-19H-4, 45–47 cm, J20/2. Middle Eocene. **12, 13.** *Theocorys kerguelensis* sp. nov., Paratype, HUTE-R-4013, Sample 120-748B-20H-1, 45–47 cm, P27/1. Middle Eocene. **14, 15.** *Theocorys kerguelensis* sp. nov., Sample 120-748B-19H-4, 45–47 cm, J28/0. Middle Eocene. **16, 17.** *Theocorys minuta* sp. nov., Holotype, HUTE-R-4014, Sample 120-748B-16H-1, 45–47 cm, G29/2. Late Eocene. **18, 19.** *Theocorys minuta* sp. nov., Paratype, HUTE-R-4015, Sample 120-748B-16H-1, 45–47 cm, M29/0. Late Eocene. **20, 21.** *Theocorys minuta* sp. nov., Paratype, HUTE-R-4016, Sample 120-748B-16H-1, 45–47 cm, G45/3. Late Eocene. (scale bar = 100 μm)



ments. Cephalis small, subspherical and poreless, with a long and stout apical horn. Apical horn conical or cylindrical, tapered distally and pointed at its apex, sometimes with some small appendages or thorns on its upper part. Thorax large, inflated and conical to hemispherical, with distinct collar stricture. Thoracic pores spherical or elliptical, nearly equal in size, and aligned diagonally in longitudinal rows or sometimes irregularly distributed. Eight to ten longitudinal rows of pores visible on the thoracic surface. In some specimens, the thoracic and abdominal walls became thick by the secondary growth of the shell wall, and by the upper part of the thoracic wall covering the cephalic wall. Abdomen slightly wider than thorax in general, usually cylindrical, and the length varies from nearly equal to twice that of the thorax. Abdominal pores generally irregular in their shapes, sizes and arrangement, but in some specimens, they are aligned longitudinally and diagonally. Abdominal aperture open without distinct peristome. In some specimens, three short feet or appendages arise from the surface of the abdomen, and the distal part of abdomen approaches a triangle in cross section (Figure 5-4).

Measurements.—Length of the shell excluding the apical horn, 151–222 μm ; Length of apical horn, 52–85 μm ; Length and width of cephalis, 29–36 and 31–40 μm ; Length and width of thorax, 65–78 and 98–123 μm ; Length and width of abdomen, 61–137 and 100–139 μm , measured in 8 specimens.

Types.—Holotype, HUTE-R-4011, Sample 120-748B-19H-4, 45–47 cm, Middle Eocene. Paratypes, HUTE-R-4012, Sample 120-748B-19H-4, 45–47 cm, Middle Eocene, HUTE-R-4013, Sample 120-748B-20H-1, 45–47 cm, Middle Eocene.

Remarks.—*Theocorys kerguelensis*, sp. nov. differs from the other species of *Theocorys* in its stout and long apical horn, and the shape and size of its thorax and abdomen. Although the phylogenetic relationship between this species and other *Theocorys* is not clear, we assigned this species to the present genus because of the similarity of shell shape.

Etymology.—The species, *kerguelensis*, is named after the Kerguelen Plateau, where the samples of ODP Leg 120 were collected.

Occurrence.—Leg 120, Hole 748B: Sample 120-748B-19H-7, 45–47 cm (bottom of the examined samples) to 120-748B-19H-2, 45–47 cm, Middle Eocene.

Leg 114, Site 702: Sample 114-702B-9X-2, 50–52 cm to Sample 114-702B-8X-2, 20–22 cm. Middle Eocene.

***Theocorys minuta* sp. nov.**

Figures 3-16—21; 5-5, 6

Calocyclus sp. B, Takemura 1992, p. 745, pl. 5, fig. 13; Takemura and Ling, 1997, p. 111, pl. 1, fig. 14.

? *Theocyrtis* (*Theocorypha*) *diabloensis* (Clark and Campbell). Chen, 1975, p. 459, pl. 5, figs. 4-7.

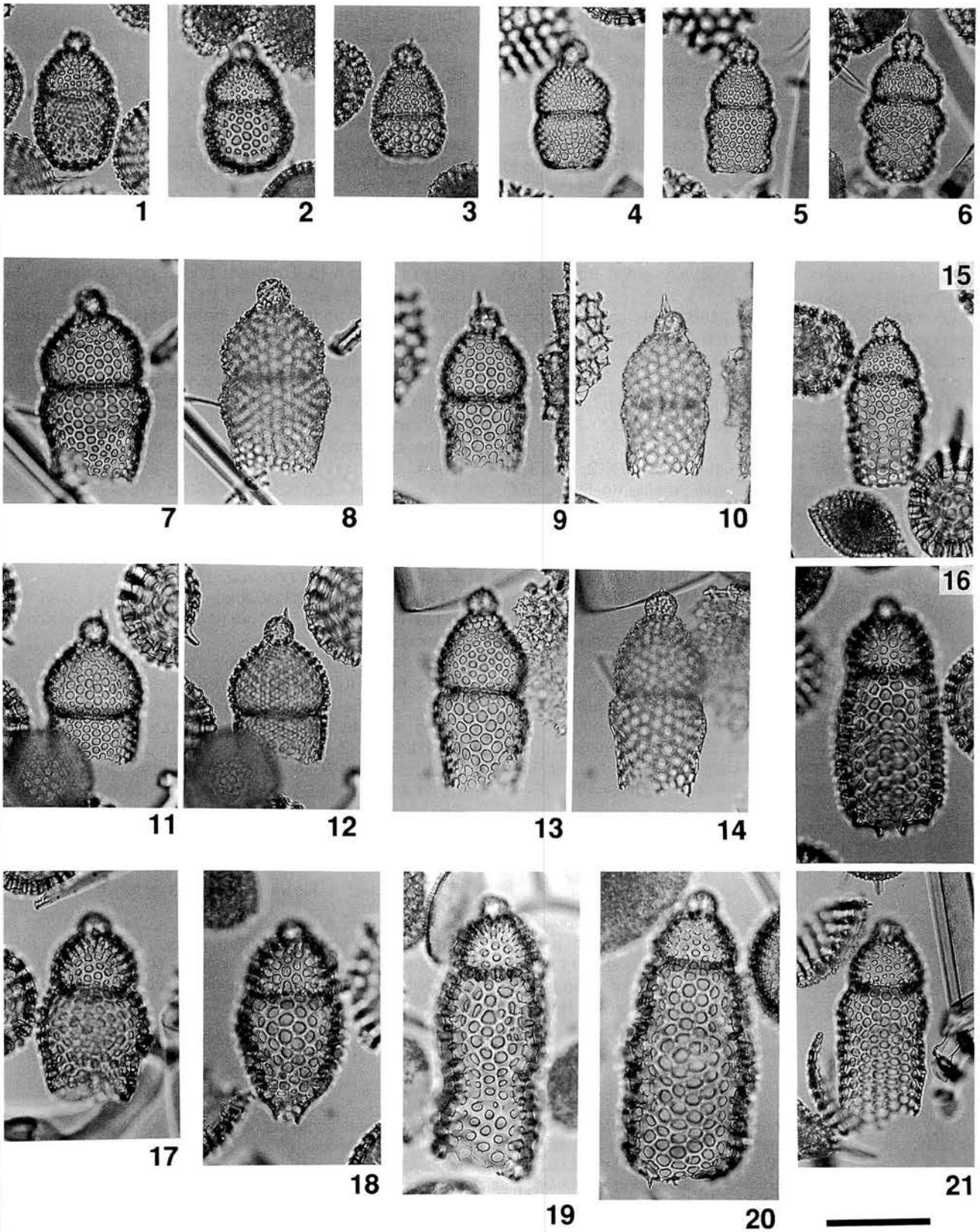
Description.—Shell oval to cylindrical with three segments. Cephalis small, spherical or subspherical and poreless, usually with small and thin apical horn. Thorax inflated, thick-walled and hemispherical to subspherical, with rough surface and distinct collar stricture. Thoracic pores spherical or elliptical and irregularly distributed, but sometimes arranged in longitudinal rows. The size of the thoracic pores is variable within a single specimen. Abdomen cylindrical or barrel-shaped, usually with a thinner shell wall than that of thorax, and tapering distally. Length of abdomen usually shorter than or nearly the same as the length of the thorax. Pores on abdominal surface irregular in both size and arrangement. Abdominal aperture open without peristome or feet. Lumbar stricture visible.

Measurements.—Length of the shell exclusive of apical horn, 105–145 μm ; Length and width of cephalis, 21–30 and 28–35 μm ; Length and width of thorax, 51–80 and 72–101 μm ; Length and width of abdomen, 32–63 and 70–91 μm , measured in 22 specimens.

Types.—Holotype, HUTE-R-4014, Sample 120-748B-16H-1, 45–47 cm, Late Eocene. Paratypes, HUTE-R-4015, Sample 120-748B-16H-1, 45–47 cm, Late Eocene, HUTE-R-4016, Sample 120-748B-16H-1, 45–47 cm, Late Eocene.

Remarks.—This species can be distinguished from the other species by its subspherical thorax usually with irregularly distributed pores, and by the shape of the abdomen, although the distal part of the abdomen is often broken.

Figure 4. *Theocorys* species from Eocene to Oligocene. 1. *Theocorys robusta* (Abelmann), Sample 120-748B-9H-1, 45–47 cm, L27/0. Late Oligocene. 2. *Theocorys robusta* (Abelmann), Sample 120-748B-9H-1, 45–47 cm, M25/0. Late Oligocene. 3. *Theocorys robusta* (Abelmann), Sample 120-748B-9H-2, 45–47 cm, E20/4. Late Oligocene. 4. *Theocorys robusta* (Abelmann), Sample 120-748B-11H-4, 45–47 cm, K54/3. Early Oligocene. 5. *Theocorys robusta* (Abelmann), Sample 120-748B-11H-4, 45–47 cm, K19/1. Early Oligocene. 6. *Theocorys robusta* (Abelmann), Sample 120-748B-12H-1, 45–47 cm, J40/0. Early Oligocene. 7, 8. *Theocorys saginata* sp. nov., Holotype, HUTE-R-4017, Sample 120-748B-9H-1, 45–47 cm, M44/0. Late Oligocene. 9, 10. *Theocorys saginata* sp. nov., Paratype, HUTE-R-4018, Sample 120-748B-9H-4, 45–47 cm, J45/3. Late Oligocene. 11, 12. *Theocorys saginata* sp. nov., Paratype, HUTE-R-4019, Sample 120-748B-10H-1, 45–47 cm, L23/1. Late Oligocene. 13, 14. *Theocorys saginata* sp. nov., Paratype, HUTE-R-4020, Sample 120-748B-10H-4, 45–47 cm, M28/2. Late Oligocene. 15. *Theocorys semipolita* (Clark and Campbell), Sample 120-748B-10H-1, 45–47 cm, H46/3. Late Oligocene. 16. *Theocorys semipolita* (Clark and Campbell), Sample 120-748B-11H-1, 45–47 cm, K24/4. Early Oligocene. 17. *Theocorys semipolita* (Clark and Campbell), Sample 120-748B-11H-4, 45–47 cm, P53/2. Early Oligocene. 18. *Theocorys semipolita* (Clark and Campbell), Sample 120-748B-13H-1, 45–47 cm, L39/4. Early Oligocene. 19. *Theocorys semipolita* (Clark and Campbell), Sample 120-748B-13H-1, 45–47 cm, M21/0. Early Oligocene. 20. *Theocorys semipolita* (Clark and Campbell), Sample 120-748B-14H-1, 45–47 cm, J33/1. Early Oligocene. 21. *Theocorys semipolita* (Clark and Campbell), Sample 120-748B-15H-4, 45–47 cm, J45/2. Late Eocene. (scale bar = 100 μm)



The shape and size of the cephalo-thorax of this species is quite similar to that of *Theocorys spongoconus* Kling. While the abdomen of *T. minuta* is always latticed with irregular pores, that of *T. spongoconus* is an inverted conical shape and spongy. These species might be related phylogenetically as discussed previously.

Although the phylogenetic relationship between the present *T. minuta* and the most other species of *Theocorys* is uncertain, we assigned this species to the genus because of the similarity in shape of the cephalo-thorax to that of the other species in the genus.

Etymology.—The species name, *minuta*, derived from Latin, minutus, refers to the relatively small size of the specimens.

Occurrence.—Leg 120, Hole 748B: This species occurs continuously in samples from 120-748B-17H-7, 45–47 cm (bottom of the examined samples) to 120-748B-15H-7, 45–47 cm, late Middle Eocene to Late Eocene.

Leg 120, Hole 749B: Sample 120-749B-3H-7, 45–47 cm (bottom of the examined samples) to Sample 120-749B-3H-4, 45–47 cm, Late Eocene.

Leg 114, Hole 699A: Sample 114-699A-37X-2, 41–43 cm (bottom of the examined samples) to Sample 114-699A-36X-4, 88–90 cm. Late Eocene.

Leg 114, Site 702: Sample 114-702B-6X-2, 48–50 cm to Sample 114-702A-4H-2, 50–52 cm. Late Eocene.

Leg 114, Hole 703A: Sample 114-703A-18X-3, 50–52 cm to Sample 114-703A-16X-1, 50–52 cm. Late Eocene.

Theocorys robusta (Abelmann) comb. nov.

Figures 4-1–6; 5-7, 8

Cyrtocapsella robusta Abelmann, 1990, p. 696, pl. 5, fig. 11 (not 10); Caulet, 1991, p. 538, Specimens 5(?) and 6 of fig. 4; Takemura, 1992, p. 746, pl. 1, figs. 5, 6; Abelmann, 1992, p. 776, pl. 5, fig. 7; Takemura and Ling, 1997, p. 111, pl. 1, fig. 18.

Cyrtocapsella aff. *japonica* (Nakaseko). Takemura, 1992, p. 746, pl. 1, figs. 11, 12.

Cyrtocapsella longithorax (Petrushevskaya). Caulet, 1991, Specimen 7 of fig. 4.

Theocorys longithorax Petrushevskaya, 1975, pl. 8, fig. 17, pl. 22, fig. 2.

Remarks.—Abelmann (1990) considered *Cyrtocapsella isopera* Chen (1975, p. 460, pl. 11, figs. 7–9) to be a junior synonym of *Theocorys longithorax* Petrushevskaya (1975, p. 580), and described a new species, *Cyrtocapsella robusta*, for the forms which have larger but fewer pores. However, some of Petrushevskaya's specimens (*op. cit.*, pl. 8, fig. 17; pl. 22, fig. 2) apparently have larger but fewer pores on the

thorax than those of *C. isopera* Chen.

Goll and Björklund (1989) described *Cyrtocapsella ampullacea* from Middle Miocene sediments from the Norwegian Sea (p. 732, pl. 5, figs. 10–13, 19, 20). The shell structure and its shape are quite similar to those of *T. robusta*, and it may be possible that those two species are conspecific. However, the geological occurrence of *C. ampullacea* is younger than that of *T. robusta*, (Middle Miocene vs. Latest Eocene to Earliest Miocene), and they were paleobiogeographically separated.

One form of *Cyrtocapsella longithorax* illustrated by Caulet (1991) (Specimen 7 of fig. 4) has larger but fewer pores. We assign this form to *T. robusta* based on Abelmann's (1990) definition of this species.

Further, we differentiate the present species from *T. semipolita* mainly by the abdomen length. *T. semipolita* usually has a longer and wider abdomen, and often a thicker shell wall. However, the distinction between the thin and small forms of *T. semipolita* and *T. robusta* may be difficult. *T. robusta* has a small thorax, thin shell wall, and the length of the abdomen is somewhat less than twice that of its thorax.

Occurrence.—Leg 120, Hole 748B: This species occurs sporadically but continuously in the Eocene samples 120-748B-14H-1, 45–47 cm to Early Oligocene Sample 120-748B-8H-4, 45–47 cm, and to earliest Miocene sediments according to Abelmann (1992).

Leg 120, Hole 749B: Sample 120-749B-2H-5, 45–47 cm to 120-749B-1H-1, 45–47 cm (top of the examined samples). Oligocene.

Leg 114, Hole 699A: Sample 114-699A-35X-4, 50–52 cm to 114-699A-10H-2, 50–52 cm (top of the examined samples). Late Eocene to Late Oligocene.

Leg 114, Site 702: Sample 114-702B-6X-2, 50–52 cm to 114-702B-5X-2, 48–50 cm, Middle to Late Eocene.

Leg 114, Hole 703A: Sample 114-703A-10H-1, 10–12 cm to 114-703A-5H-6, 55–57 cm (top of the examined samples), Early to Late Oligocene.

Theocorys saginata sp. nov.

Figures 4-7–14; 5-9, 10

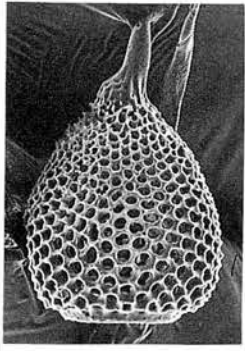
Calocyclus sp. A, Takemura, 1992, p. 745, pl. 1, figs. 3, 4; Takemura and Ling, 1997, p. 111, pl. 1, fig. 15.

Cyrtocapsella robusta (?) Abelmann, 1990, pl. 5, fig. 10.

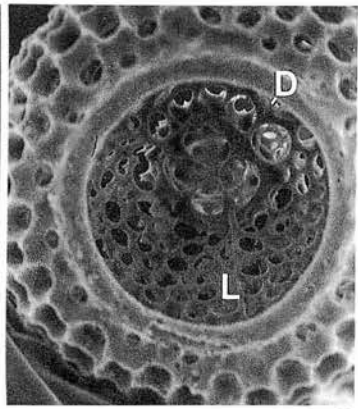
Theocorys robusta (Clark and Campbell). Petrushevskaya, 1975, p. 580, pl. 8, fig. 9, pl. 22, fig. 1.

Description.—Shell cylindrical with three segments.

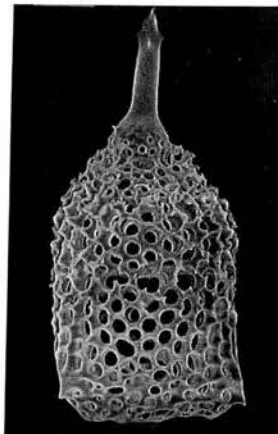
Figure 5. SEM photographs of Antarctic nassellarians. Each pair of these photographs shows both the external shell structure and the internal structure including cephalic skeletons through the aperture, of a single specimen. MB=median bar, V=vertical spine, D=dorsal spine, L=lateral spine. **1, 2.** *Calocyclus* (?) *nakasekoi* sp. nov., Sample 120-748B-19H-4, 45–47 cm, Middle Eocene. **3, 4.** *Theocorys kerguelensis* sp. nov., Sample 120-748B-19H-5, 45–47 cm, Middle Eocene. **5, 6.** *Theocorys minuta* sp. nov., Sample 120-748B-16H-1, 45–47 cm, Late Eocene. **7, 8.** *Theocorys robusta* (Abelmann), Sample 120-748B-9H-4, 45–47 cm, Late Oligocene. **9, 10.** *Theocorys saginata* sp. nov., Sample 120-748B-9H-4, 45–47 cm, Late Oligocene. **11, 12.** *Theocorys semipolita* (Clark and Campbell), Sample 120-748B-13H-4, 45–47 cm, Early Oligocene. (scale bar = 50 μ m)



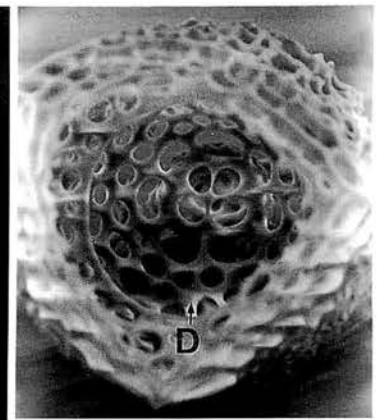
1



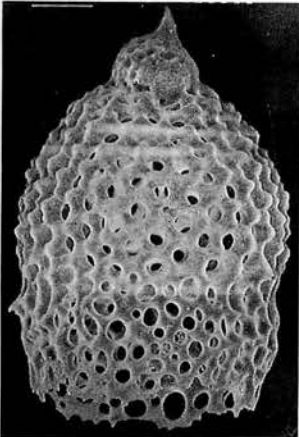
2



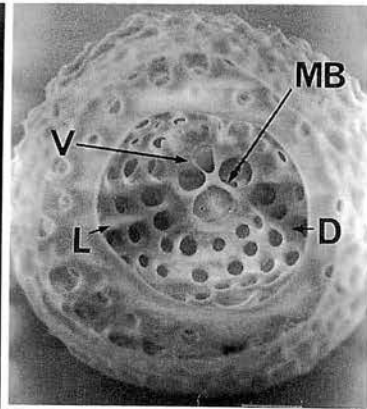
3



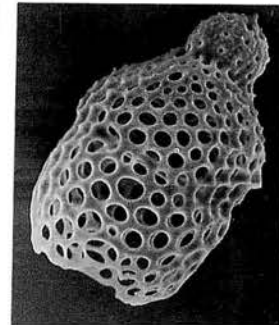
4



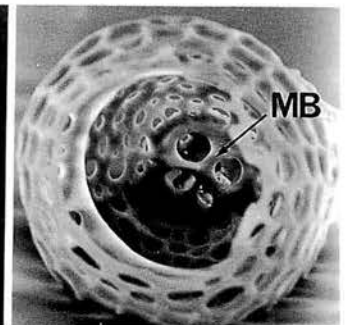
5



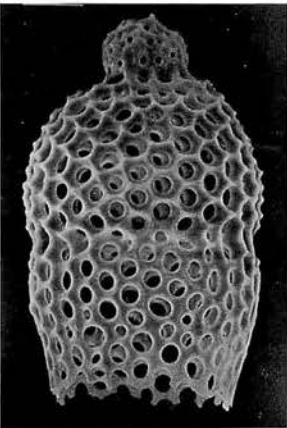
6



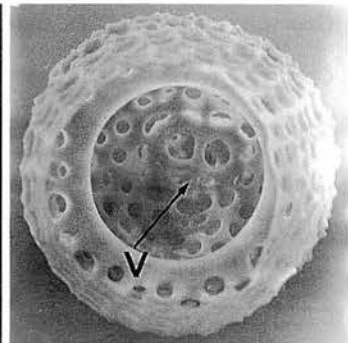
7



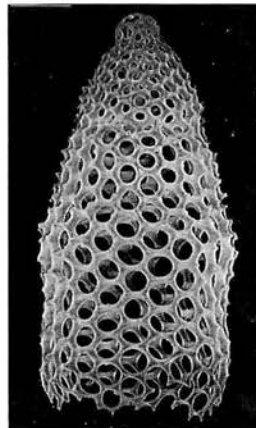
8



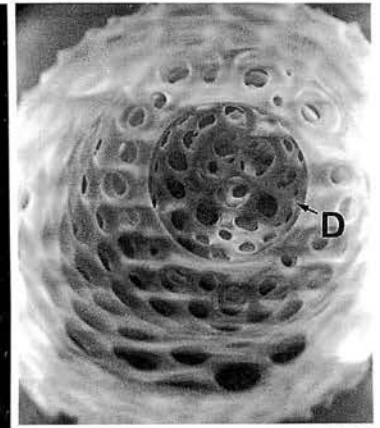
9



10



11



12

Cephalis small, spherical and poreless, with or without apical horn. Apical horn, when present, usually small and conical. Thorax large, inflated and hemispherical or conical, with distinct collar stricture. Thoracic pores usually spherical or elliptical, and generally arranged longitudinally and diagonally, but sometimes irregularly. When they are aligned longitudinally, 8 to 12 rows of pores are visible on the thoracic surface. Abdomen cylindrical or barrel-shaped with distinct lumbar stricture. Abdominal aperture open and large, without peristome or feet. Abdomen shorter than or nearly equal in length to cephalo-thorax. Pores on abdominal surface similar to those on thorax both in size and shape, and usually arranged in longitudinal rows or sometimes irregularly distributed.

Measurements.—Length of the shell exclusive of apical horn, 122–198 μm ; Length and width of cephalis, 22–30 and 26–34 μm ; Length and width of thorax, 58–78 and 85–103 μm ; Length and width of abdomen, 33–100 and 83–104 μm , measured in 23 specimens.

Types.—Holotype, HUTE-R-4017, Sample 120-748B-9H-1, 45–47 cm, Late Oligocene. Paratypes, HUTE-R-4018, Sample 120-748B-9H-4, 45–47 cm, Late Oligocene, HUTE-R-4019, Sample 120-748B-10H-1, 45–47 cm, Late Oligocene, HUTE-R-4020, Sample 120-748B-10H-4, 45–47 cm, Late Oligocene.

Remarks.—*Theocorys saginata* evolved from *T. semipolita* in the Early Oligocene in the Southern Ocean, and can be

differentiated from its ancestor by its larger and more inflated thorax, shorter abdomen and/or more distinct lumbar stricture. The species is also distinguished from *T. robusta* (Abelmann) by the larger overall size. The measurements of the thorax of these two species clearly differentiate them during the Late Oligocene (Figure 6). On the other hand, *Cyrtocapsella robusta* (?) shown by Abelmann (1990, pl. 5, fig. 10 only) has a larger conical thorax and larger shell size than that of her *T. robusta* (Abelmann), and should be included in this new species. While *Theocotyle robusta* (Clark and Campbell) described from the Southeast Pacific by Petrushevskaya (1975) is considered as conspecific with this new species, the California specimens of *Calocyclus semipolita robusta* Clark and Campbell (1942, pl. 8, fig. 21) have a longer apical horn and a more spherical thorax than those of the present species.

Etymology.—The species name, *saginata*, derives from Latin, sagina, fattening, reflecting their overall appearance.

Occurrence.—Leg 120, Hole 748B: Sample 120-748B-12H-3, 45–47 cm to Sample 120-748B-9H-1, 45–47 cm (top of the examined samples). late Early Oligocene to Late Oligocene

Leg 120, Hole 749B: Sample 120-749B-2H-2, 45–47 cm to Sample 120-749B-1H-2, 45–47 cm. Oligocene.

Leg 114, Hole 699A: Sample 114-699A-20H-2, 50–52 cm to Sample 114-699A-10H-2, 50–52 cm (top of the examined samples). late Early Oligocene to Late Oligocene.

Leg 114, Hole 703A: This species sporadically occurs in Sample 114-703A-8H-2, 70–72 cm and Sample 114-703A-6H-4, 60–62 cm. Late Oligocene.

The last occurrence of this species should fall in the Early Miocene.

Theocorys semipolita (Clark and Campbell) comb. nov.

Figures 4-15--21; 5-11, 12

Calocyclus semipolita Clark and Campbell, 1942, p. 83, pl. 8, figs.

12, 14, 17–19, 21–23; Blueford, 1988, p. 246, pl. 2, figs. 4–6

Calocyclus semipolita (?) Clark and Campbell. Chen, 1975, p. 459, pl. 6, figs. 3–6.

Calocyclus semipolita group Clark and Campbell. Caulet, 1991, p. 537, 1 and 2 of fig. 4.

Calocyclus (?) *semipolita* Clark and Campbell group—Petrushevskaya, 1975, p. 580, pl. 8, fig. 8, pl. 41, figs. 6, 7.

Calocyclus cf. *semipolita* Clark and Campbell. Abelmann, 1990, p. 697, pl. 7, fig. 4; Takemura, 1992, p. 745, pl. 4, figs. 5, 6; Takemura and Ling, 1997, p. 111, pl. 1, fig. 16.

Calocyclus asperum (Ehrenberg). Caulet, 1991, p. 537, 3 and 4 of fig. 4.

Calocyclus (?) *fragilis* (Carnevale) group. Petrushevskaya, 1975, p. 580, pl. 8, figs. 6, 7.

? *Theocapsomma* ? sp. Petrushevskaya and Kozlova, 1972, pl. 22, fig. 5.

? Species, similar to Eucyrtidiidae gen. sp. "rocket" Petrushevskaya and Kozlova, 1972, pl. 28, figs. 4, 5.

? Eucyrtidiidae gen. et sp. indet. Petrushevskaya and Kozlova, 1972, pl. 28, fig. 8.

? *Theocorys* ? spp. indet. Petrushevskaya and Kozlova, 1972, pl. 28, figs. 9, 10.

not *Calocyclus* cf. *semipolita* Clark and Campbell. Abelmann,

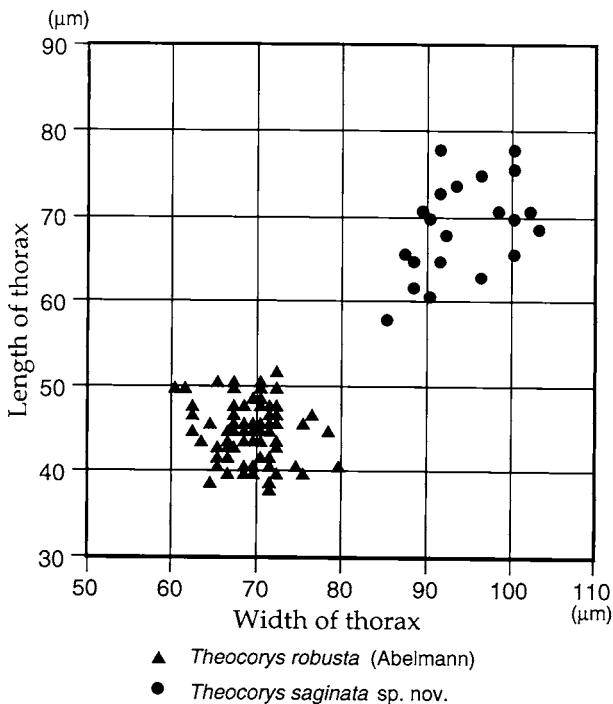


Figure 6. Comparison of thoracic sizes between *T. robusta* and *T. saginata* in the Late Oligocene from Site 748. Samples 120-748B-9H-1, 45–47 cm, 120-748B-9H-4, 45–47 cm, 120-748B-10H-1, 45–47 cm, and 120-748B-10H-4, 45–47 cm are used.

1992, pl. 5, fig. 8.

Remarks.—This species varies widely in its shell shape. In the Eocene, the species have a smaller shell size and often a short apical horn, similar to those described by Clark and Campbell (1942). In the Early Oligocene, most of the specimens have a larger shell size and a variable abdominal shape; abdomen is from very long and cylindrical or truncate-conical to short. The aperture also varies from large (wide open) without peristome to somewhat constricted, or constricted to a small tube. Many Oligocene forms have larger pores on the thorax than those from Eocene sediments, and the shapes and sizes of abdominal pores are quite variable. However, the basic pattern of the arrangement of pores is longitudinal. This species may be divided into two or three species in the future. *T. saginata* evolved from this species in the Early Oligocene. The distinction between *T. semipolita* and *T. robusta* is sometimes difficult, but *T. semipolita* usually has a longer abdomen, thicker shell wall and/or larger thorax.

We include *Calocyclus* (?) *fragilis* (Carnevale) group in the present species. Many forms described by Petrushevskaya and Kozlova (1972) could be related to this species. Caulet (1991) assigned the Oligocene forms of this species to *Calocyclus asperum* (Ehrenberg) (= *Eucyrtidium asperum* Ehrenberg of previous authors). However, according to previous illustrations (Ehrenberg, 1875, pl. 8, fig. 15; Petrushevskaya and Kozlova, 1972, pl. 28, figs. 16–18), *E. asperum* possesses a short, cylindrical abdomen, which is less wide than the thorax. One specimen figured by Abelmann (1992, pl. 5, fig. 8) as *Calocyclus* cf. *semipolita* has thoracic and abdominal pores aligned in diagonal and transverse rows. Because the pores of *T. semipolita* are basically aligned in longitudinal rows, this form is excluded from *T. semipolita*.

Wei *et al.* (1992) proposed a distinct cooling at the earliest Oligocene (upper part of Core 748B–14H, around 115.5 mbsf) in the southern Indian Ocean based on the samples from the same ODP Hole 748B. They based their conclusions on the abrupt increase in abundance of cool-water nannofossil taxa, the occurrence of ice-rafted debris and a distinctive $\delta^{18}\text{O}$ excursion. This cooling event could have brought about the changes in shape, size and thickness of shell wall for this species.

Occurrences.—Leg 120, Hole 748B: Sample 120-748B-17H-4, 45–47 cm Middle Eocene, and Samples 120-748B-16H-5, 45–47 cm to 120-748B-9H-4, 45–47 cm, Late Eocene to Late Oligocene.

Leg 120, Hole 749B: Samples 120-749B-3H-7, 45–47 cm to 120-748B-2H-2, 45–47 cm, Late Eocene and Early Oligocene.

Leg 114, Hole 699A: Sample 114-699A-36X-4, 88–90 cm (almost bottom of the examined samples) to 114-699A-10H-2, 50–52 cm (top of the examined samples). Late Eocene to Late Oligocene.

Leg 114, Site 702: Sample 114-702B-6X-2, 50–52 cm to 114-702B-4H-2, 48–50 cm, Middle to Late Eocene.

Leg 114, Hole 703A: Sample 114-703A-18X-3, 50–52 cm (bottom of the examined samples) to 114-703A-5H-6, 55–57 cm (top of the examined samples), Late Eocene to Late

Oligocene.

Acknowledgments

We express our sincere thanks to Noriko Seki and Kayoko Kishima for their cooperative participation in our study. We thank Akira Tokuyama, Toshiharu Nishimura and Yasuhiro Shibue for their kind understanding and continuous encouragement to this cooperative research. We also thank Stanley A. Kling and Catherine Nigrini for their critical reading of the manuscript. This study was supported in part by Grant-in-Aid for Encouragement of Young Scientists (A, No. 05740325/Takemura) and Grant-in-Aid for Co-operative Research (A, No. 04304009/Yao) by the Ministry of Education, Science and Culture of Japan.

References

- Abelmann, A., 1990: Oligocene to Middle Miocene radiolarian stratigraphy of southern high latitudes from Leg 113, Site 689 and 690, Maud Rise. In, Baker, P.F., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 113, p. 675–708. College Station, TX (Ocean Drilling Program).
- Abelmann, A., 1992: Early to Middle Miocene radiolarian stratigraphy of the Kerguelen Plateau, Leg 120. In, Wise, S.W., Jr., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 120, p. 757–783. College Station, TX (Ocean Drilling Program).
- Aubry, M.-P., 1992: Paleogene calcareous nannofossils from the Kerguelen Plateau, Leg 120. In, Wise, S.W., Jr., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 120, p. 471–491. College Station, TX (Ocean Drilling Program).
- Berggren, W.A., 1992: Paleogene planktonic foraminifer magnetobiostratigraphy of the Southern Kerguelen Plateau (Sites 747–749). In, Wise, S.W., Jr., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 120, p. 551–568. College Station, TX (Ocean Drilling Program).
- Berggren, W.A., Kent, D.V., and Flynn, J.J., 1985: Paleogene geochronology and chronostratigraphy. In, Snelling, N.J. *ed.*, *The Chronology of the Geological Record. Geological Society of London, Memoir*, vol. 10, p. 141–195.
- Bjørklund, K.J. and Kellogg, D.E., 1972: Five new Eocene radiolarian species from the Norwegian Sea. *Micro-paleontology*, vol. 18, p. 386–396.
- Blueford, J., 1988: Radiolarian biostratigraphy of siliceous Eocene deposits in central California. *Micro-paleontology*, vol. 34, p. 236–258.
- Campbell, A.S., 1954: Radiolaria. In, Moore, R.C. *ed.*, *Treatise on Invertebrate Paleontology. Part D, Protista 3*, p. D11–D163. University of Kansas Press and Geological Society of America.
- Caulet, J.-P., 1991: Radiolarians from the Kerguelen Plateau, Leg 119. In, Barron, J., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 119, p. 513–546. College Station, TX (Ocean Drilling Program).
- Chen, P.H., 1975: Antarctic Radiolaria. In, Hayes, D.E., *et al.*, *Initial Reports of the Deep Sea Drilling Project*, vol.

- 28, p. 437-513. Washington (U.S. Government Printing Office).
- Ciesielski, P.F., 1991: Biostratigraphy of diverse silicoflagellate assemblages from the early Paleocene to early Miocene of Holes 698A, 700B, 702B, and 703A: subantarctic South Atlantic. *In*, Ciesielski, P.F., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 114, p. 49-96. College Station, TX (Ocean Drilling Program).
- Ciesielski, P.F., Kristoffersen, Y., Clement, B., Blangy, J.-P., Bourrouilh, R., Crux, J.A., Fenner, J.M., Froelich, P.N., Hailwood, E., Hodell, D., Katz, M.E., Ling, H.Y., Mienert, J., Müller, D., Mwenifumbo, C.J., Nobes, D.C., Nocchi, M., Warnke, D.A. and Westall, F., 1988: *Proceedings of the Ocean Drilling Program, Initial Reports*, vol. 114, 815 p. College Station, TX (Ocean Drilling Program).
- Clark, B.L. and Campbell, A.S., 1942: Eocene radiolarian faunas from the Mt. Diablo area, California. *Geological Society of America, Special Paper* vol. 39, p. 1-112.
- Crux, J.A., 1991: Calcareous nannofossils recovered by Leg 114 in the subantarctic South Atlantic Ocean. *In*, Ciesielski, P.F., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 114, p. 155-177. College Station, TX (Ocean Drilling Program).
- Ehrenberg, C.G., 1838: Über die Bildung der Kreidefelsen und des Kreidemergels durch unsichtbare Organismen. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, Jahre 1838, p. 59-147.
- Ehrenberg, C.G., 1847a: Über eine halibolithische, von Herrn R. Schomburgk entdeckte, vorherrschend aus mikroskopischen Polycystinen gebildete, Gebirgsmasse von Barbados. *Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlichen Preussischen Akademie der Wissenschaften zu Berlin*, Jahre 1846, p. 382-385.
- Ehrenberg, C.G., 1847b: Über die mikroskopischen kiesel-schaligen Polycystinen als mächtige Gebirgsmasse von Barbados und über das Verhältniss der aus mehr als 300 neuen Arten bestehenden ganz eigenthümlichen Formengruppe jener Felsmasse zu den jetzt lebenden Thieren und zur Kreidebildung. Eine neue Anregung zur Erforschung des Erdlebens. *Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlichen Preussischen Akademie der Wissenschaften zu Berlin*, Jahre 1875, p. 40-61.
- Ehrenberg, C.G., 1875: Fortsetzung der mikrogeologischen Studien als Gesamt-Übersicht der mikroskopischen Paläontologie gleichartig analysirter Gebirgsarten der Erde, mit specieller Rücksicht auf Polycystinen-Mergel von Barbados. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, Jahre 1875, p. 1-226.
- Foreman, H.P., 1973: Radiolaria of Leg 10 with systematics and ranges for the families Amphipyndacidae, Artostrobiidae, and Theoperidae. *In*, Worzel, J.L., *et al.*, *Initial Reports of the Deep Sea Drilling Project*, vol. 10, p. 407-474 Washington (U.S. Government Printing Office).
- Frizzell, D.L. and Middour, E.S., 1951: Paleocene Radiolaria from southeastern Missouri. *Bulletin, University of Missouri, School of Mines and Metallurgy*, vol. 77, p. 1-41.
- Goll, R.M. and Bjørklund, K.R., 1989: A new radiolarian biostratigraphy for the Neogene of the Norwegian Sea: ODP Leg 104. *In*, Eldholm, O., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 104, p. 697-737. College Station, TX (Ocean Drilling Program).
- Haeckel, E., 1881: Entwurf eines Radiolarien-Systems auf Grund von Studien der Challenger-Radiolarien. *Jenaische Zeitschrift, Neue Folge* 8, vol. 15, p. 418-472.
- Haeckel, E., 1887: Report on the Radiolaria collected by H.M.S. Challenger during the years 1873-76. *Report on the Scientific Results of the Voyage of H.M.S. Challenger during the Years 1873-76, Zoology*, vol. 18, clxxxviii+1803 p.
- Harwood, D.M. and Maruyama, T., 1992: Middle Eocene to Pleistocene diatom biostratigraphy of Southern Ocean sediments from the Kerguelen Plateau, Leg 120. *In*, Wise, S.W., Jr., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 120, p. 683-733. College Station, TX (Ocean Drilling Program).
- Inokuchi, H. and Heider, F., 1992: Magnetostratigraphy of sediments from Sites 748 and 750, Leg 120. *In*, Wise, S.W., Jr., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 120, p. 247-252. College Station, TX (Ocean Drilling Program).
- Kling, S.A., 1971: Radiolaria: Leg 6 of the Deep Sea Drilling Project. *In*, Fischer, A.G., *et al.*, *Initial Reports of the Deep Sea Drilling Project*, vol. 6, p. 1069-1117. Washington (U.S. Government Printing Office).
- Kling, S.A., 1973: Radiolaria from the eastern North Pacific, Deep Sea Drilling Project, Leg 18. *In*, Kulm, L.D., *et al.*, *Initial Reports of the Deep Sea Drilling Project*, vol. 18, p. 617-671. Washington (U.S. Government Printing Office).
- Lazarus, D., 1990: Middle Miocene to Recent radiolarians from the Weddell Sea, Antarctica, ODP Leg 113. *In*, Baker, P.F., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 113, p. 709-727. College Station, TX (Ocean Drilling Program).
- Lazarus, D., 1992: Antarctic Neogene radiolarians from the Kerguelen Plateau, Legs 119 and 120. *In*, Wise, S.W., Jr., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 120, p. 785-809. College Station, TX (Ocean Drilling Program).
- Madie, M. and Monechi, S., 1991: Late Eocene to early Oligocene calcareous nannofossil assemblages from Sites 699 and 703, Subantarctic South Atlantic Ocean. *In*, Ciesielski, P.F., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 114, p. 179-192. College Station, TX (Ocean Drilling Program).
- McCartney, K., and Harwood, D.M., 1992: Silicoflagellates from Leg 120 on the Kerguelen Plateau. Southeast Indian Ocean. *In*, Wise, S.W., Jr., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 120, p. 811-831. College Station, TX (Ocean Drilling Program).
- Müller, J., 1858: Über die Thalassicollen, Polycystinen und Acanthometren des Mittelmeeres. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, Jahre 1858, p. 1-62.
- Nigrini, C. and Lombardi, G., 1984: *A Guide to Miocene Radiolaria*. Cushman Foundation for Foraminiferal Research, Special Publication, vol. 22, 422 p.
- Nishimura, H., 1990: Taxonomic study on Cenozoic Nassellaria (Radiolaria). *Scientific Reports of the Institute of*

- Geoscience, University of Tsukuba, Section B, Geological Sciences*, vol. 11, p. 69-172.
- Nocchi, M., Amici, E. and Premoli Silva, I., 1991 : Planktonic foraminiferal biostratigraphy and paleoenvironmental interpretation of Paleogene faunas from the Subantarctic transect, Leg 114. In, Ciesielski, P.F., et al., *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 114, p. 233-279. College Station, TX (Ocean Drilling Program).
- Petrushevskaya, M.G., 1975 : Cenozoic radiolarians of the Antarctic, Leg 29, DSDP. In, Kennett, J.P., et al., *Initial Reports of the Deep Sea Drilling Project*, vol. 29, p. 541-675. Washington (U.S. Government Printing Office).
- Petrushevskaya, M.G. and Kozlova, G.E., 1972 : Radiolaria : Leg 14, Deep Sea Drilling Project. In, Hayes, D.E., et al., *Initial Reports of the Deep Sea Drilling Project*, vol. 14, p. 495-648. Washington (U.S. Government Printing Office).
- Riedel, W.R., 1967 : Protozoa (Subclass Radiolaria). In, Harland, W.B., et al., eds., *The Fossil Record*, p. 291-298. The Geological Society of London.
- Riedel, W.R., 1971 : Systematic classification of polycystine Radiolaria. In, Funnell, B.M., and Riedel, W.R. eds., *The Micropaleontology of Oceans*, p. 649-661. Cambridge University Press.
- Riedel, W.R. and Sanfilippo, A., 1970 : Radiolaria, Leg 4, Deep Sea Drilling Project. In, Bader, R.G., et al., *Initial Reports of the Deep Sea Drilling Project*, vol. 4, p. 503-575. Washington (U.S. Government Printing Office).
- Riedel, W.R. and Sanfilippo, A., 1971 : Cenozoic Radiolaria from the western tropical Pacific, Leg 7. In, Winterer, E.L., et al., *Initial Reports of the Deep Sea Drilling Project*, vol. 7, p. 1529-1672. Washington (U.S. Government Printing Office).
- Riedel, W.R. and Sanfilippo, A., 1978 : Stratigraphy and evolution of tropical Cenozoic radiolarians. *Micropaleontology*, vol. 24, p. 61-96.
- Rüst, D., 1885 : Beiträge zur Kenntniss der fossilen Radiolarien aus Gesteinen des Jura. *Palaeontographica*, vol. 31, p. 273-321.
- Sakai, T., 1980 : Radiolarians from Sites 434, 435, and 436, Northwest Pacific, Leg 56, Deep Sea Drilling Project. In, Langseth, M., et al., *Initial Reports of the Deep Sea Drilling Project*, vol. 56, p. 695-733. Washington (U.S. Government Printing Office).
- Sanfilippo, A. and Riedel, W.R., 1970 : Post-Eocene "closed" theoperid radiolarians. *Micropaleontology*, vol. 16, p. 446-462.
- Sanfilippo, A., Westberg-Smith, M.J. and Riedel, W.R., 1985 : Cenozoic Radiolaria. In, Bolli, H.M., et al., eds., *Plankton Stratigraphy*, p. 631-712. Cambridge University Press.
- Saunders, J.B., Bernoulli, D., Müller-Merz, E., Oberhänsli, H., Perch-Nielsen, K., Riedel, W.R., Sanfilippo, A. and Torrini, R., Jr., 1984 : Stratigraphy of the late Middle Eocene to Early Oligocene in the Bath Cliff section, Barbados, West Indies. *Micropaleontology*, vol. 30, p. 390-425.
- Schlich, R., Wise, S.W. Jr., Palmer Julson, A.A., Aubry, M.-P., Berggren, W.A., Bitschene, P.R., Blackburn, N.A., Breza, J., Coffin, M.F., Harwood, D.M., Heider, F., Holmes, M.A., Howard, W.R., Inokuchi, H., Kelts, K., Lazarus, D.B., Mackensen, A., Maruyama, T., Munsch, M., Pratson, E., Quilty, P.G., Rack, F., Salters, V.J.M., Sevigny, J.H., Storey, M., Takemura, A., Watkins, D.K., Whitechurch, H. and Zachos, J., 1989 : *Proceedings of the Ocean Drilling Program, Initial Reports*, vol. 120, 648 p. College Station, TX (Ocean Drilling Program).
- Strelkov, A.A. and Lipman, R. Kh., 1959 : Podklass Radiolaria. Sistematische Chast. In, Orlov, Yu. A. ed., *Osnovy Paleontologii*. Moscow (Izdatelstvo Akad. Nauk SSSR).
- Takemura, A., 1986 : Classification of Jurassic Nassellarians (Radiolaria). *Palaeontographica Abt. A*, vol. 195, p. 29-74.
- Takemura, A., 1992 : Radiolarian Paleogene biostratigraphy in the Southern Indian Ocean, Leg 120. In, Wise, S.W., Jr., et al., *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 120, p. 735-756. College Station, TX (Ocean Drilling Program).
- Takemura, A. and Ling, H.Y., 1997 : Eocene and Oligocene radiolarian biostratigraphy from the Southern Ocean : correlation of ODP Legs 114 (Atlantic Ocean) and 120 (Indian Ocean). *Marine Micropaleontology*, vol. 30, p. 97-116.
- Wei, W., Villa, G. and Wise, S.W., Jr., 1992 : Paleogeographic implications of Eocene-Oligocene calcareous nannofossils from Sites 711 and 748 in the Indian Ocean. In, Wise, S.W., Jr., et al., *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 120, p. 979-999. College Station, TX (Ocean Drilling Program).

Two ammonite species of *Mortoniceras* from the Yubari Mountains (Hokkaido) and their geological implications

(Studies of the Cretaceous ammonites from Hokkaido and Sakhalin-LXXXII)

TATSURO MATSUMOTO¹, FUMIHISA KAWABE² and YOSHITARO KAWASHITA³

¹c/o Kyushu University 33, Fukuoka 812-8581, Japan

²Division of Geology, Graduate School of Science and Engineering, Waseda University, Tokyo 169-8050, Japan

³2-179, Tomatsu Chiyoda, Mikasa 068-2134, Japan

Received 11 February 1998 ; Revised manuscript accepted 23 July 1998

Abstract. Two ammonite species of the genus *Mortoniceras* have been recently obtained from two stratigraphic units, Member Ld of the Lower Yezo Subgroup and Member Mb of the Middle Yezo Subgroup on the Tengu-zawa route of the Yubari Mountains, central Hokkaido. They are identified respectively with *Mortoniceras (Mortoniceras)* cf. *geometricum* Spath and *Mortoniceras (Mortoniceras)* *rostratum* (J. Sowerby). *M. (M.) geometricum*, which is taken here as allied to *M. (M.) pricei* (Spath), probably includes some specimens described as *Pervinguieria arietiformis* by Haas (1942b) from Angola and as *M. (M.) arietiforme* by Renz (1971) from Venezuela. Our study of *Mortoniceras (Mortoniceras)* *rostratum* suggests that *Ammonites rostratus* J. Sowerby should be systematically assigned to *Mortoniceras (Mortoniceras)* rather than to *M. (Subschloenbachia)*. On the evidence of the two ammonite species, Member Ld is correlated with the middle part (probably the *Hysterocheras varicosum* Subzone) of the Upper Albian and Member Mb with the upper part (probably the *M. (M.) rostratum* Subzone) of the same substage. Therefore, no significant time gap exists at the boundary of the Lower and Middle Yezo Subgroups.

Key words : Correlation, *Mortoniceras (Mortoniceras)* *geometricum*, *Mortoniceras (Mortoniceras)* *rostratum*, Upper Albian, Yezo Group, Yubari Mountains

Introduction

The Albian part of the Cretaceous Yezo Group in the forearc basin of Hokkaido and Sakhalin is not so prolific in ammonoids as the same stage in the well studied regions of western Europe. In Europe and adjacent regions of the Boreal Province, the hoplitid ammonites occur abundantly and are very useful for biostratigraphic zonation and correlation (Owen, 1979). For palaeobiogeographic reasons they are almost absent in Japan and adjacent areas. There the acanthocerataceans, including Brancoceratidae (or Mojsisovicziidae by some authors), are found from time to time and helpful for the interregional correlation, for they include worldwide species.

In this paper we report the find of two Albian species of *Mortoniceras* in our recent field work. They are interesting in the systematics of the genus and also useful for a particular stratigraphic problem.

The repositories of the described specimens are abbreviated as follows :

GK : Type Room, Department of Earth and Planetary Sciences, Kyushu University, Fukuoka 812-8581, Japan

GS : Institute of Earth Science, Saga University, Saga 840-8502, Japan

WE : Institute of Earth Science, School of Education, Waseda University, Tokyo 169-8050, Japan

Stratigraphic setting

The specimens described in this paper were obtained from the Cretaceous Yezo Group of the Yubari Mountains in central Hokkaido (see index map in Figure 1).

The Cretaceous stratigraphy in the Yubari Mountains has been investigated by a number of geologists. The paper by Matsumoto (1942) is one of the results and partly cited in this paper. We depend, however, mainly on the recent work by Kawabe *et al.* (1996). Hence, we omit to describe repeatedly the details of the stratigraphy. The important points to be noted for the subject of this paper are as follows :

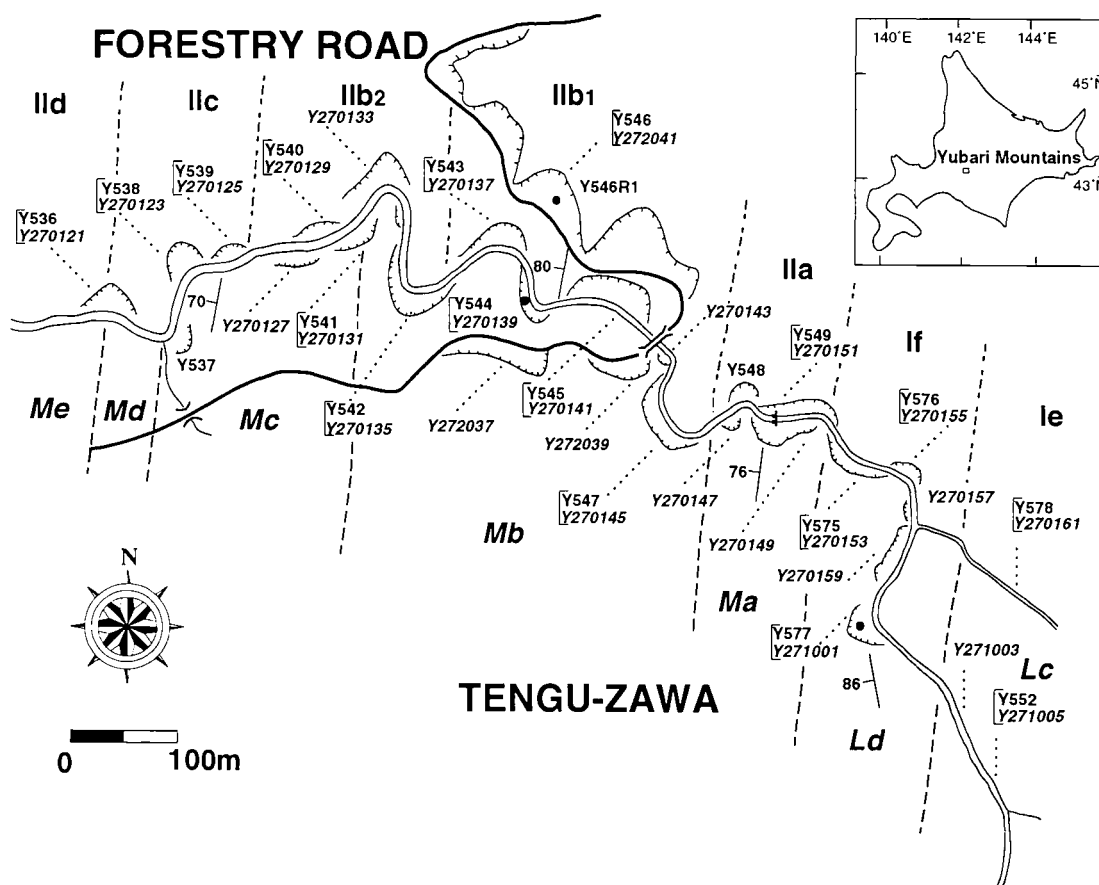


Figure 1. Geological route map along the Tengu-zawa (part) of the Yubari Mountains. Stratigraphic divisions and the number of outcrops by Matsumoto (1942 : above) and Kawabe *et al.* (1996 : below) are shown.

(1) The ammonites described below were obtained from the two units in the continuous outcrops along the upper course of the Tengu-zawa [=Tengu-sawa by some authors], a branch stream of the River Shuparo [=Shuyubari or Siyubari by some authors]. For the general geological map of the Shuparo Valley readers may refer to Kawabe *et al.* (1996, fig. 2) and the columnar sections of the Cretaceous deposits along the selected six routes (including the Tengu-zawa route) are shown in fig. 3 of the same paper.

(2) In this paper we follow Matsumoto (1995, p. 6) and Nishida *et al.* (1996, p. 67, 93) and use the Subgroup category for each of the major lithostratigraphic divisions of the thick deposits of the Yezo Group. Local formational names are omitted for brevity. Members are designated by letters.

(3) Details of the relevant part of the Tengu-zawa route are shown in Figure 1, in which the stratigraphic subdivisions (i.e., Members) and the outcrop numbers of Matsumoto (1942) [above] and also Kawabe *et al.* (1996) [below] are both shown. As to the stratigraphic subdivisions there is discrepancy, though partially, between the two schemes. We now agree to regard the scheme of Kawabe *et al.* (1996) as more reasonable and natural than that of Matsumoto (1942).

(4) The main lithologic constituents and thickness of the successive members are shown in the columnar sections of

Figure 2. The locality numbers and horizons of the two ammonite species are also indicated in the same figure.

(5) The ammonite from the Member Ld was embedded directly in the dark grey mudstone, without forming a nodule.

(6) The ammonites from the dark grey mudstones of the Member Mb were in calcareous nodules. In addition to the described species, *Anagaudryceras sacya* (Forbes), undetermined heteromorph ammonoids and a new kind of inoceramid bivalve have been obtained from the same outcrops. Plant drifts, including fragmentary pieces of wood, are frequently embedded.

(7) Aside from the ammonites from the Members Ld and Mb, the mudstones of the Member Me have yielded more ammonites, such as *Desmoceras* (*Desmoceras*) *kossmati* Matsumoto, *Desmoceras* (*Pseudouhligella*) *japonicum* Yabe *et al.* *Graysonites wooldridgei* Young and *Parajaubertella kawakitana* Matsumoto, among others, indicate that the lower part of the Member Me [=Ild] is referable to the lower Cenomanian.

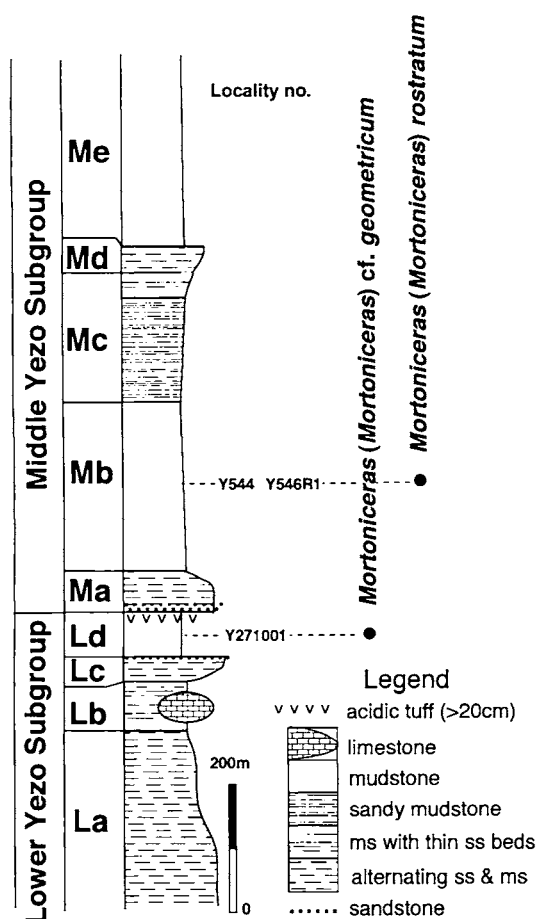


Figure 2. Schematic columnar section along the Tengu-zawa route (part) of the Yubari Mountains.

Palaeontological descriptions

Superfamily Acanthocerataceae Grossouvre, 1894
 Family Brancoceratidae Spath, 1900
 Subfamily Mortoniceratinae H. Douvillé, 1912
 Genus *Mortonicerases* Meek, 1876

Type species.—*Ammonites vespertinus* Morton, 1834, by original designation of Meek (1876, p. 448).

Subgenus *Mortonicerases (Mortonicerases)* Meek, 1876

Remarks.—Subfamily Mortoniceratinae is allocated in the family Mojsisovicziidae Hyatt by Kennedy (*in Gale et al.*, 1996, p. 557), but we follow Wright (1996, p. 134–140) in placing the subfamilies Brancoceratinae, Mojsisovicziinae and Mortoniceratinae in the family Brancoceratidae Spath.

Ammonites vespertinus Morton, 1834 was disregarded by several authors as invalid, but Morton's original specimen (holotype) and other specimens subsequently collected show the diagnostic character, as one of us has described briefly (Matsumoto, 1960, p. 37, fig. 1). As to the definition of the genus *Mortonicerases* we agree with Wright (1996, p. 141).

Classification of the subgenus *Mortonicerases* seems to be somewhat confusing, but we follow Wright (1996) for the time being.

Mortonicerases (Mortonicerases) cf. geometricum

Spath, 1932

Figure 3

Compared.—

Mortonicerases (Pervinquieria) geometricum Spath, 1932, p. 395; Spath, 1933, pl. 44, fig. 1.

Pervinquieria arietiformis (Spath). Haas, 1942b, pl. 19, fig. 2; pl. 20, fig. 4.

Mortonicerases (Mortonicerases) arietiforme (Spath). Renz, 1971, p. 598, pl. 4, fig. 1, text-fig. 5b; Renz, 1982, p. 53, pl. 13, figs. 1a, 1b.

non. Elobicerases arietiforme Spath, 1922, p. 137, pl. 2, figs. 6a, 6b.

Material.—WE.A211Y, obtained by F.K. on 10 September 1993 at loc. Y271001 [= Y577], from the Member Ld along the Tengu-zawa route, Yubari Mountains.

Description.—The specimen is a secondarily distorted and compressed internal mould (Figure 3). It was embedded directly in mudstone without forming a nodule.

The shell is fairly large and loosely coiled. The whorl expands with a low ratio, enlarging rather slowly. Consequently the umbilicus is very wide. The whorl is fairly higher than broad, but the original proportion of B/H cannot be accurately measured.

The keel is moderately high on the inner whorl. On the outer whorl the keel is broken or unpreserved for the most part, but it seems to have been fairly high as can be inferred from its broken base. It may increase its height with growth.

The ornament is characteristic. On the outer whorl, that consists of the adult body chamber and the last part of the phragmocone, ribs are mostly long, single and uniformly disposed. Only a few are slightly shorter, without reaching the umbilical edge. They are mostly rectiradiate and a few ribs on the last portion tend to curve gently forward. This might suggest the presence of a rostrum, which itself is regrettably unpreserved. On the body chamber every rib is swollen at the ventrolateral shoulder and bent there more or less forward. The long rib has a blunt bulla at the umbilical edge. A mid-lateral tubercle is almost imperceptible on the body chamber.

In the preceding stage for a little more than one full whorl, the ribs are alternatingly long and short or sometimes bifurcated (Figure 3). Most of the ribs are roughly rectiradiate, but a few of them are slightly flexiradiate. At this stage the bullate umbilical tubercles at the end of the long ribs are often more distinct than those of the last growth stage. The inner ventrolateral tubercles are likewise more distinct than those of the late stage. Namely, they form distinct tubercles. At least some of these inner ventrolateral tubercles are accompanied by feeble outer ventrolateral clavi. Also at this growth stage lateral tubercles are weakly developed on some ribs.

The ornament of the still earlier part (less than 40 mm in diameter) is not well shown.

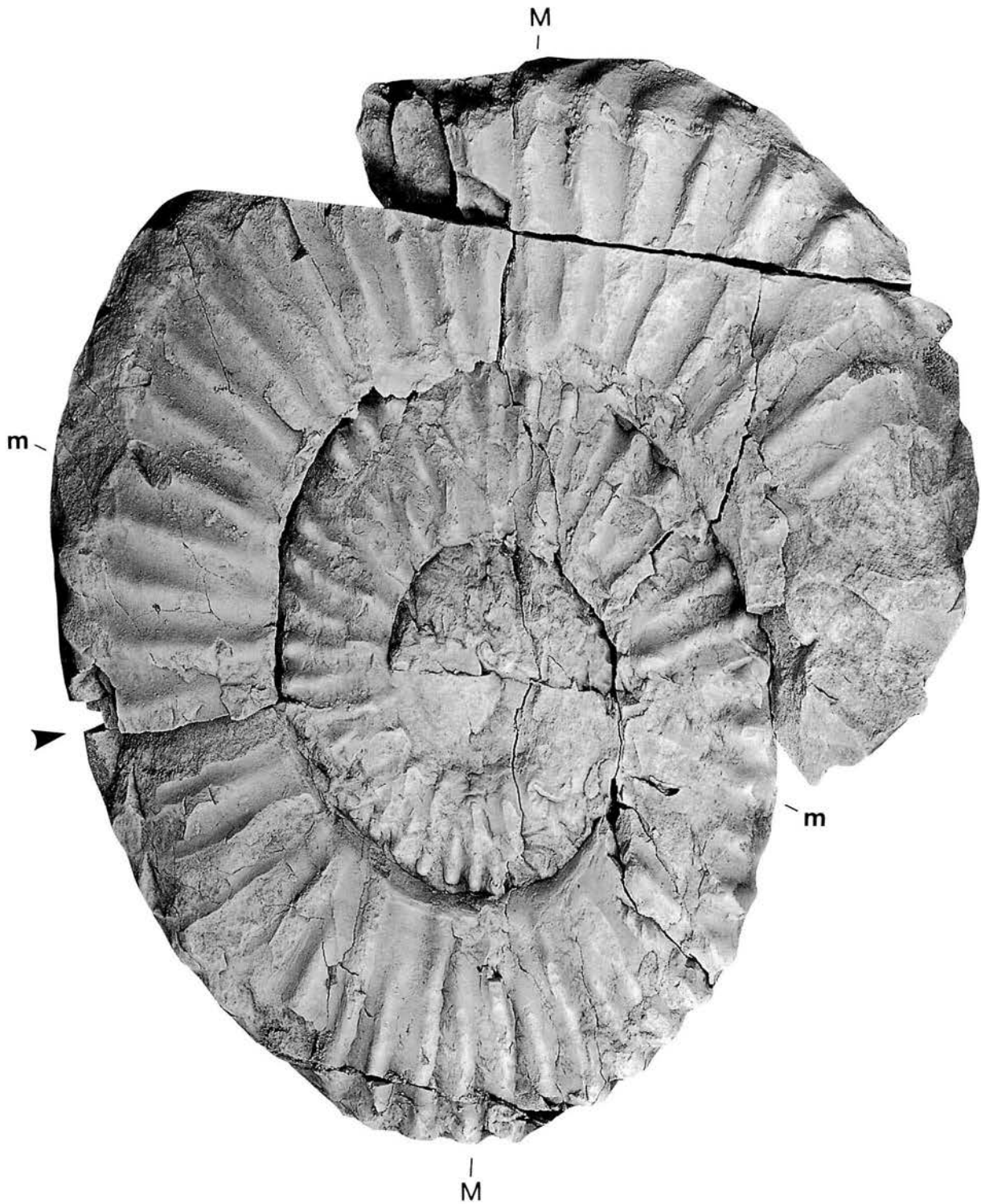


Figure 3. *Mortoniceras (Mortoniceras) cf. geometricum* (Spath). Lateral view of WE. A211Y from Member Ld at loc. Y271001, $\times 1$ (photo by F.K. with whitening). M, m: measured points (see Table 1); arrow: last septum.

As this specimen is an internal mould, the spiral notches are hardly discernible. However, some of them are faintly impressed on several ribs on the outer half of the flank at about the beginning of the body chamber (see Figure 3).

The suture is partly exposed, but it cannot be fully traced. The last septum seems to be located at about the damaged point that is indicated by an arrow mark in Figure 3. The body chamber is hence at least half a whorl.

Dimensions.—See Table 1.

Comparison.—The specimen was indicated, without description, as *Mortonicer* (*Mortonicer*) *cf. inflatum* (Sowerby) by Kawabe *et al.* (1996, p. 448, pl. 2, fig. 6). That tentative identification should be revised. *Mortonicer* (*Mortonicer*) *inflatum* in a correct sense (see Spath, 1931, pl. 35, fig. 9; 1932, p. 384, pl. 37, fig. 1; pl. 39, fig. 2; pl. 42, fig. 6; text-figs. 125–129, 130a, 130b; 1933, pl. 43, fig. 1) has a distinct median row of tubercles on the flank in early to middle growth stages and the umbilical tubercles are strong, whereas in our specimen such distinct flank tubercles are not developed and the ribs are bullate and blunt at the umbilical end. In *Mortonicer* (*Mortonicer*) *inflatum* the bifurcated or alternated ribs persist to later growth stages, but in our specimen single ribs predominate on the late septate whorl to the body chamber.

In many respects the Hokkaido specimen is similar to *Mortonicer* (*Mortonicer*) *geometricum* Spath (1932, p. 395; 1933, pl. 44, fig. 1) from the *varicosum* Subzone (Bed 10) of the Upper Gault. The holotype of that species is somewhat, but not much, larger than the specimen from Hokkaido (see Table 1) and preserves a high keel. In our specimen the keel is destroyed for the major part of the outer whorl. However, a moderately high keel runs continuously on the inner whorl. Because the basal section of the destroyed keel is traced here and there along the abraded mid-venter of the outer whorl (Figure 3), the keel must have existed originally.

Our specimen closely resembles one of the specimens from the Upper Albian of Venezuela illustrated by Renz (1971, pl. 4, fig. 1, text-fig. 5b; also Renz, 1982, p. 53, pl. 13, figs. 1a, 1b). That specimen was described as *Mortonicer* (*Mortonicer*) *arietiforme* (Spath), although Renz (1968a, p. 625) himself once compared it with *Mortonicer* (*Mortonicer*)

geometricum. Likewise, our specimen is quite similar to some of the specimens illustrated by Haas (1942b, pl. 19, fig. 2; pl. 20, fig. 4) under the specific name of *Pervinquieria arietiformis* (Spath).

Occurrence.—As for material.

Discussion.—*Elobicer*, a genus of the Mortoniceratinae in our present knowledge, was established by Spath (1921, p. 306) on the basis of “*Schloenbachia elobiensis* Szajnocha, 1885” as the type species. Spath (1922, p. 137) also designated “*Schloenbachia cf. lenzi* Szajnocha” of Choffat (1888, p. 65, pl. 1, fig. 6) as the holotype of another species of this genus, *Elobicer arietiforme* Spath. That specimen and also the subsequent material of Spath (1922, p. 137, pl. 2, figs. 6a, 6b) are fragmentary segments of body chambers and the whorl section was drawn by Spath diagrammatically. This species is, thus, based on incomplete material, but it has spiral notches on the long ribs like those of other species of *Elobicer*.

In spite of this situation, Haas (1942a, p. 647, pl. 93, fig. 19; 1942b, p. 90–95, pls. 18–20) described a number of specimens from the Upper Albian of Angola as *Pervinquieria arietiformis* (Spath), in which several varieties were included in addition to “*forma typica*”. He did not state a satisfactory reason why he identified the Angola specimens with the insufficiently defined species of Spath. Also the reason why *Elobicer arietiforme* should be transferred to *Pervinquieria* of his sense is not clear. Haas (1942b, p. 99; fig. 18 in p. 40) mentioned, however, that there is “a broad transitional zone” from *Pervinquieria* to *Elobicer* and regarded *Pervinquieria arietiformis* as a species closely approaching *Elobicer*.

Renz (1971, 1982) transferred the generic name from *Pervinquieria* to *Mortonicer* (*Mortonicer*) and reported some examples of *Mortonicer* (*Mortonicer*) *arietiforme* from Venezuela, since he compared them with Haas’ specimens from Angola.

In our view none of the specimens illustrated under the specific name of *Pervinquieria arietiformis* by Haas or *Mortonicer* (*Mortonicer*) *arietiforme* by Renz seems to be identical with the holotype and Spath’s specimens of *Elobicer arietiforme* Spath.

On the other hand, as we have described above (see *Comparison*), the illustrated specimen of Renz’ “*Mortonicer*

Table 1. Measurements of *Mortonicer* (*Mortonicer*) *cf. geometricum* and relevant specimens.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h	Ribs
WE. A211Y (at M)	188	92	0.40	53	0.28	—	—	—	1.23	43
WE. A211Y (at m)	136	65	0.48	42	0.31	—	—	—	1.45	39
Spath (1933, pl. 44, fig. 1)	230	106	0.46	73	0.32	—	—	—	1.43	40
Haas (1942b, pl. 18, fig. 4)	135	51	0.38	45	0.33	30	0.22	0.67	1.15	44
Renz (1971, pl. 4, fig. 1)	185	78	0.42	62	0.34	43	0.23	0.69	1.3	40
Spath (1922, pl. 2, fig. 6)	—	—	—	72	—	44	—	0.61	—	—

The deformed specimen of WE. A211Y is measured as it is; at M along the elongated axis and at m along the shortened axis of the elliptically deformed specimen. Spath (1933, pl. 44, fig. 1): holotype of *Mortonicer* (*Mortonicer*) *geometricum*; Haas (1942b, pl. 18, fig. 4): “*Pervinquieria arietiformis*”; Renz (1971, pl. 4, fig. 1); “*Mortonicer* (*Mortonicer*) *arietiforme*”; Spath (1922, pl. 2, fig. 6): *Elobicer arietiforme*. D=diameter, U=width of umbilicus, H=whorl height, B=whorl breadth, h=whorl height half adapical from H, c=costal, ic=interocstal; Ribs=number of ribs to a whorl. Linear dimensions in mm.

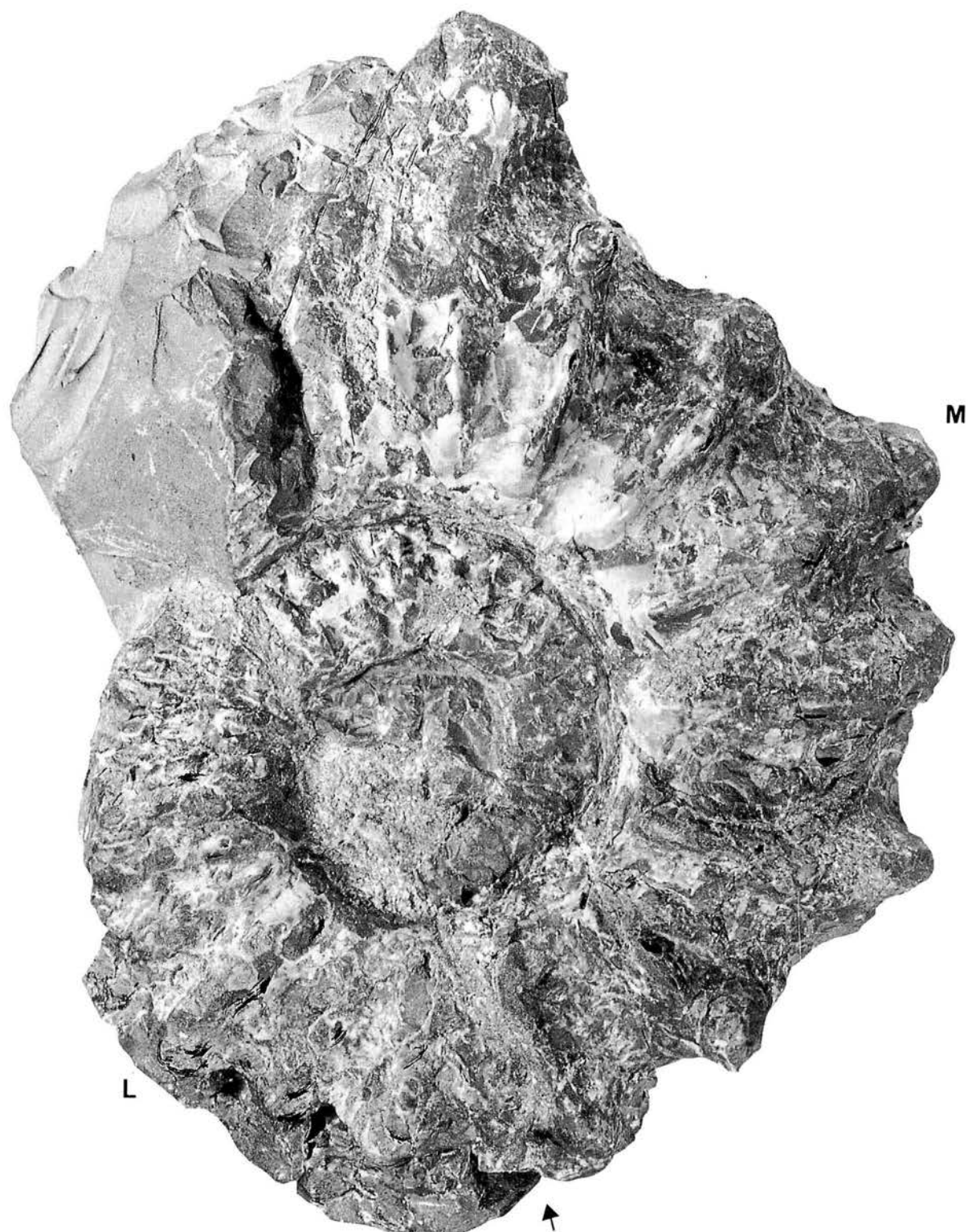


Figure 4. *Mortoniceras (Mortoniceras) rostratum* (J. Sowerby). Lateral view of GK. H8491 from Member Mb at loc. 544, $\times 1$ (photo by N. Egashira without whitening). M: middle part of the adult body chamber; L: late part of the phragmocone; arrow: beginning of the body chamber.

(*Mortoniceras arietiforme*) and also some of Haas' "*Pervinquieria arietiformis*" morphologically resemble the Hokkaido specimen in many respects. These specimens, as well as our specimen, are quite similar to *Mortoniceras (Mortoniceras) geometricum* Spath. Hence, at least provisionally we should call our specimen *Mortoniceras (Mortoniceras) cf. geometricum* Spath.

Spath (1932, p. 395) regarded *Mortoniceras (Mortoniceras) geometricum* as distinct from but more allied to *Mortoniceras (Mortoniceras) pricei* (Spath, 1922) than to *Mortoniceras (Mortoniceras) inflatum*. This is favorable for the systematic allocation of *Mortoniceras (Mortoniceras) geometricum*. In fact Kennedy and Hancock (1978, p. v-9) ranked this species as *Mortoniceras (Mortoniceras) pricei geometricum*, as a member of the *Hysterocheras varicosum* Subzone, although they did not give reasons for the subspecific treatment. So far as the typical forms are concerned, ribs are somewhat flexuous and their alternating long and short feature persists to a later growth stage in *Mortoniceras (Mortoniceras) pricei*, whereas ribs are nearly rectiradial, becoming single and more widely spaced at an earlier growth stage in *Mortoniceras (Mortoniceras) geometricum*.

To sum up, the Hokkaido specimen described above should be called *Mortoniceras (Mortoniceras) cf. geometricum*. This is provisional but taxonomically best.

Mortoniceras (Mortoniceras) rostratum
(Sowerby, 1817)

Figures 4-7

Ammonites rostratus J. Sowerby, 1817, p. 163, pl. 173.

Mortoniceras (Pervinquieria) rostratum (Sowerby). Spath, 1932, p. 400, text-fig. 136.

Pervinquieria (Subschloenbachia) rostrata (Sowerby). Scholz, 1979a, p. 111, pl. 26, figs. 1, 2, pl. 27, figs. 1, 2; Scholz, 1979b, p. 600, pl. 2, figs. 1, 2, pl. 4, fig. 5, pl. 5, fig. 1, text-figs. 2, 3.

Material.—GK.H8491, obtained by Y.K. on 17 August 1994 at loc. Y544 [=Y270139], and GS.G160, also by Y.K. on 26 May 1996 at loc. Y546R1 [=Y272041]; both from Member Mb of the Tengu-zawa route, Yubari Mountains.

Description.—The two specimens are spectacular in showing the adult shell up to the peristome with a recurved rostrum. They are, however, incompletely preserved; namely the first specimen (Figure 4) shows only the right side, with its left side dissolved in the rock matrix to the mid-venter (=half-ammonite preservation: Maeda, 1987). The second specimen (Figures 6, 7) is much distorted, although its venter is partly exposed. Even in side view the younger part less than 40 mm or 30 mm in diameter is not well exposed in both specimens. In spite of these drawbacks, the two specimens exhibit some characteristic features of the species as described below.

The shell is fairly large, about 160 mm in diameter at the point slightly back from the rostrate peristome in the less deformed specimen (Figure 4). This is nearly similar to the restored outline of the holotype (Spath, 1932, text-fig. 136). The distorted specimen (Figures 6, 7) may have been originally somewhat larger than the less deformed one. In both

specimens the shell is rather evolute, with a little overlapping of whorls.

The whorl expands with rather moderate to slightly high ratios. The width of the umbilicus is generally moderate, showing U/D 0.36–0.38. Near the last stage immediately behind the rostrate marginal part the increase of whorl-height is lowered, resulting in a somewhat broadened umbilicus with an increased ratio of U/D (0.41) (Table 2). A similar tendency is observable in the holotype from England.

As the specimens preserve only one side, the proportion of B/H is hardly estimated with precision. The values shown in Table 2 may be affected to some extent by secondary compression. The change of B/H with growth is not correctly known in our material. It is, however, noted that the

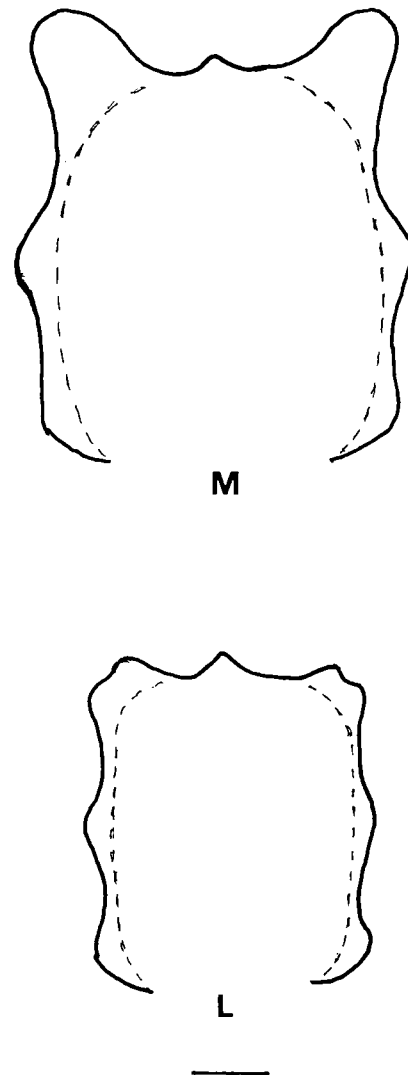


Figure 5. *Mortoniceras (Mortoniceras) rostratum* (J. Sowerby). Restored whorl sections. M: at the middle of the adult body chamber; L: late part of the phragmocone (drawn by T.M. based on the two specimens from Member Mb of the Tengu-zawa route). Bar scale: 10 mm.

inner whorls are rather flat-sided and that the adult body chamber is thickly oval or subelliptical in the intercostal section (Figure 5).

The main part of the body chamber occupies half a whorl (Figure 4). In addition to it there is a marginal part which shows a broadly convex curve along the peristome and extends to a recurved rostrum. Although the apical part of the rostrum was broken away in our specimens, the observable part is similar to that of the holotype (Sowerby, 1817, pl. 173).

The ornament is very characteristic. In the main part of the body chamber there are seven robust ribs which are distantly separated. They are weakly prorsiradiate or very gently concave forward, with or without a slight bending at about the mid-flank. Each rib has a bullate umbilical tubercle, a lateral node, which may have a bullate extension along the rib, and a ventrolateral horn developed from the united inner and outer ventrolateral tubercle of the preceding stage (Figure 5). The median ventral keel is lower than the top of the ventrolateral horns of the most robust ribs in the middle part of the body chamber (Figure 5). There is an additional rib in the basal part of the rostrum. It is narrower and lower than the ribs of the main part and extends to the axial part of the recurved rostrum (Figures 4, 7). Its mid-lateral and ventrolateral tubercles are narrowly bullate, showing a rather sharp summit. In addition to it there are two still narrower and lower riblets on the marginal part.

In the last part of the phragmocone, for about one third of the whorl, the ribs are mostly single, rectiradiate and coarse (Figure 4). Their interspace is somewhat broader than the rib in the late part of the segment and nearly as broad as the rib in the early part. Each rib has a bullate umbilical tubercle, a mid-lateral node and a doubled ventrolateral tubercle, although the ventrolateral part of some ribs is incompletely preserved at this substage. There is an exceptionally short rib at the end of the phragmocone (Figure 4).

The ribs in the earlier part of the septate whorls are denser and narrower than those in the later part. They consist of longer ones and bifurcated or intercalated shorter ones. The umbilical and lateral tubercles are observable; the ventrolateral part is concealed by the overlapping outer whorl.

The external suture is partly exposed on GK.H8491. It shows comparatively broad stems of E/L, L and L/U2 and their minor incisions.

Dimensions.—See Table 2.

Comparison.—The two specimens described above are comparable with the holotype of *Mortoniceras (Mortoniceras) rostratum* (J. Sowerby) (see Spath, 1932, text-fig. 136), from the Upper Albian Malmstone of Oxfordshire (England), and the four adult specimens of the same species illustrated by Scholz (1979a, pl. 26, fig. 1 and pl. 27, fig. 2; 1979b, text-figs. 2, 3), from the "Vraconian" of the Bakony Mountains (West Hungary), the "Upper Vraconian" of France and the "Vraconian" of Germany. As the available specimens are not numerous, we have to compare particular individuals. For example, the ribs on the main part of the adult body chamber are more robust and separated by wider interspaces in the Hokkaido specimens than those of the holotype, but they are nearly similar to those of the French specimen. The lateral tubercles are disposed at about the middle of the flank in our specimens, but they are shifted outward in the five specimens from Europe. This may be merely an intraspecific variation. Even if this difference occurred in many individuals between the two separate provinces, it could be interpreted as suggesting a geographic subspecies.

With respect to the characteristic ornament of the adult body chamber our material appears to resemble *Mortoniceras (Mortoniceras) stoliczkai* (Spath, 1921). The latter is represented by "*Ammonites inflatus* var. I" of Stoliczka (1863, p. 49, pl. 27, fig. 1; pl. 29, fig. 2), from the Utatur Group of southern India, and also by "*Subschloenbachia stoliczka*" of Spath (1922, p. 119, text-figs. c1, c2), from the Albian of Angola. Spath (1932, p. 404) discussed at length the distinction between *Mortoniceras (Mortoniceras) stoliczkai* and *Mortoniceras (Mortoniceras) rostratum*, but such characters as bending of ribs and stage of appearance of simple ribbing are not tenable because of variability. The only criterion is the more depressed whorl of the former than of the latter. In this respect our specimens are not referable to *Mortoniceras (Mortoniceras) stoliczkai*.

Occurrence.—As for material.

Discussion.—Scholz (1979a, b) has upheld the quadrituberculate ornament as the most reliable criterion by which to distinguish *Ammonites rostratus* from the trituberculate *Mortoniceras (Mortoniceras) stoliczkai*. A well-preserved specimen from the Upper Albian of Madagascar illustrated by Collignon (1963, p. 156, pl. 304, fig. 1308) as *Mortoniceras rostratum* has been revised by Scholz to *Mortoniceras (Mor-*

Table 2. Measurements of *Mortoniceras (Mortoniceras) rostratum*.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h	Ribs
Holotype (E-60°, ic)	160	61	0.38	55	0.34	~40	0.25	0.73	1.25	13+10
Holotype (E-90°, ic)	140	50	0.36	52	0.37	~39	0.28	0.75	1.37	11+14
GK. H8491 (E-45°, ic)	147	61	0.41	50	0.34	~36	0.24	0.72	1.39	13+11
GK. H8491 (E-60°, c)	157	60	0.38	56	0.37	~ 8	0.31	0.86	1.37	13+13
GS. G160 (E-45°, ic)	165	63	0.38	56	0.34	~42	0.25	0.75	1.22	14+11
GS. G160 (E-90°, c)	156	59	0.38	55	0.35	~50	0.32	0.91	1.31	13+14

As specimens are all secondarily compressed and distorted, B is estimated from the measured dimension of a less deformed half side. Ribs: number of ribs to a whorl (later single ribs+earlier bifurcating or intercalating ribs). Holotype is measured on a cast. E: preserved end of the whorl, E-60°: at the point 60° adapically from E, ~: approximate. Other abbreviations same as in Table 1.

toniceras stoliczkai [= *Pervinquieria (Pervinquieria) stoliczkai* of Scholz, 1979a, p. 106]. Collignon (1963), however, made mention of the variability of ornament in the Madagascar material. Without examining the actual specimens, we hesitate to comment further. In connection with this question, it is noted that one of the specimens from the Utatur Group described under the name of "*Ammonites inflatus* var. III" by Stoliczka (1863, pl. 29, figs. 4, 4a) shows a double ventrolateral tubercle in his schematic whorl section.

Subgeneric assignment of *Mortoniceras rostratum* is indeed debatable. Spath (1932, p. 400) described this species under *Mortoniceras (Pervinquieria)*, that is *Mortoniceras (Mortoniceras)* of the present nomenclature. Scholz (1979a, b) evaluated *Subschloenbachia* Spath, 1921 [with type species *Ammonites rostratus* J. Sowerby, 1817] as a senior synonym of *Durnovarites* Spath, 1932 [with type species *Subschloenbachia perinflata* Spath, 1921]. Cooper and Kennedy (1979, p. 269) listed a number of species which they refer to the subgenus *Durnovarites* and added *Mortoniceras (Durnovarites) collignoni* Cooper and Kennedy, 1979 (p. 276, figs. 65E-F, 66-67, 68B-D, 69) from Angola. For some reason they did not include *Ammonites rostratus* in the list of *Mortoniceras (Durnovarites)*, but Cooper and Kennedy (1979, p. 280) mentioned that "the ribs of the body chamber of *Mortoniceras rostratum* retain four rows of tubercles almost to the peristome". This is probably a misobservation stemming from the unfavorable preservation. At present Kennedy (in reply to T.M.'s inquiry, 24 April, 1997) believes *Subschloenbachia* and *Durnovarites* to be synonyms and is going to describe, together with co-authors, *Mortoniceras (Subschloenbachia) rostratum* from the Weno Formation (Albian) in northeast Texas.

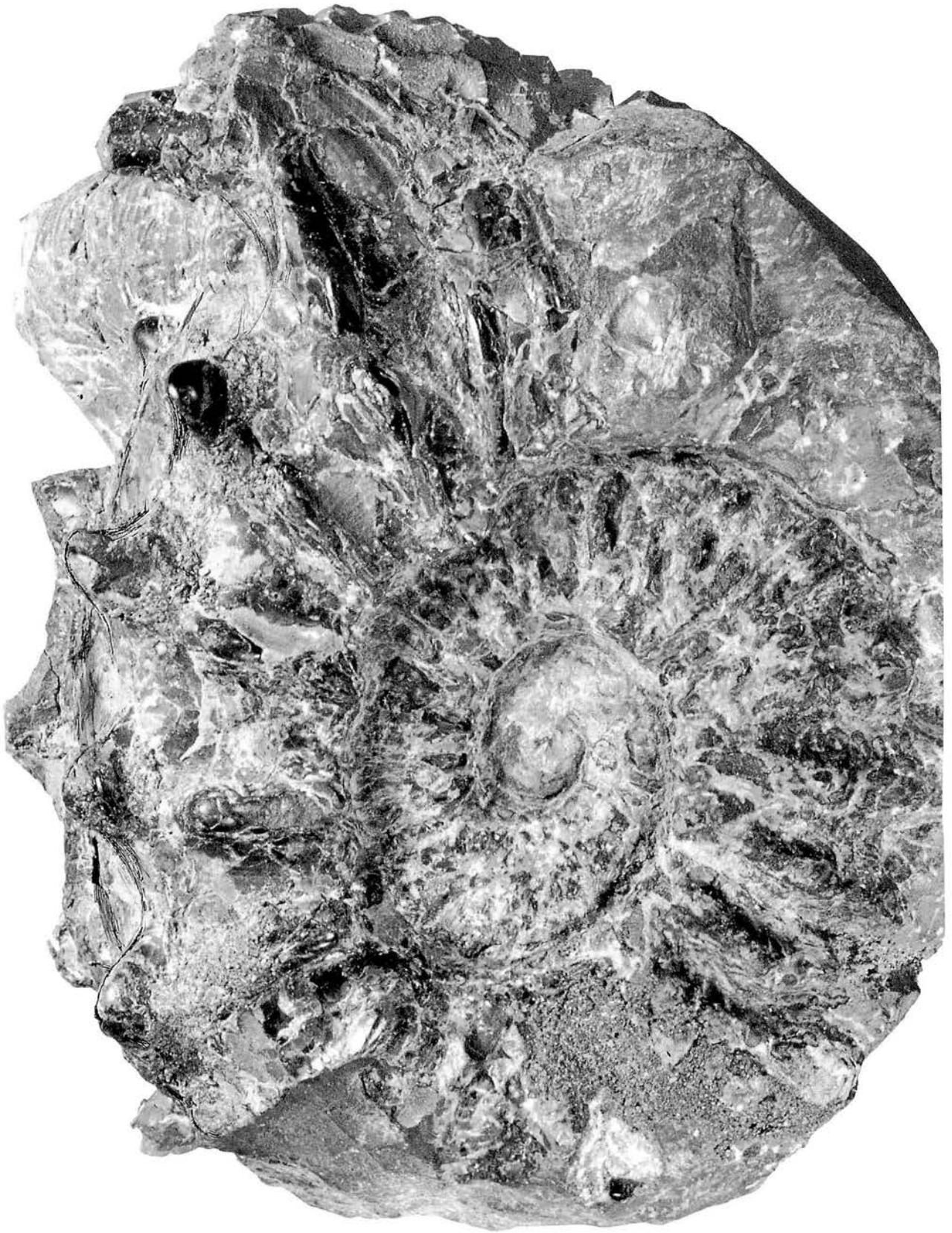
Thanks to W.J. Kennedy, we are now looking at the cast of the holotype of *Ammonites rostratus*. Up to 90 mm or so in diameter (with H=43 mm), the ribs are fairly crowded and the inner and outer ventrolateral tubercles are not well differentiated and covered with spiral striations. This feature is essentially similar to that of middle-aged *Mortoniceras (Mortoniceras) inflatum* (Sowerby), as illustrated by Spath (1931, pl. 35, fig. 9; 1932, text-fig. 127). For about a quarter whorl in the last part of the phragmocone the ribs are thicker and become gradually distant, the inner and outer ventrolateral tubercles are somewhat separated, and thus a quadrituberculate state is manifested. However, the inner node and the outer clavus are never widely separated and seem to rest on a common base of the thickened outer end of a rib. In a little while the two ventrolateral tubercles are closely set and become a double ventrolateral tubercle. Then on the body chamber the paired tubercle is completely united to become a single prominent tubercle. Thus the body chamber is apparently trituberculate (Figure 5). These are essentially similar to the features in the holotype of *Mortoniceras (Mortoniceras) vespertinum* (see Wright, 1996, figs. 109a, b), although the ventrolateral nodes are not horn-like in that holotype.

On the other hand, *Mortoniceras (Durnovarites) perinflatum*



Figure 6. *Mortoniceras (Mortoniceras) rostratum* (J. Sowerby). Ventral view of GS. G160 from Member Mb at loc. Y546R1, $\times 1$ (photo by N. Egashira without whitening).

Figure 7. *Mortoniceras (Mortoniceras) rostratum* (J. Sowerby). Lateral view of GS. G160 from Member Mb at loc. Y546R1, $\times 1$ (photo by N. Egashira, without whitening).



is regarded as quadrituberculate even on the body chamber. In fact, *Mortoniceras (Durnovarites) collignoni* has four rows of tubercles on one side of the body chamber, without forming ventrolateral horns. In *Mortoniceras (Durnovarites) subquadratum* Spath, 1933 (p. 435; 1932, pl. 37, fig. 6; pl. 42, figs. 5, 9; 1933, pl. 43, fig. 7; pl. 44, fig. 6; pl. 47, figs. 2-4; pl. 48, figs. 2, 4) the quadrituberculate state appears earlier than in other species, although the adult body chamber of this species has not been described.

Strictly speaking, the holotype of *Mortoniceras (Durnovarites) perinflatum*, as reillustrated by Renz (1968b, pl. 9, figs. 1a, b), is wholly septate, although its quadrituberculate state is well shown in its preserved last part. A specimen figured by Scholz (1979a, pl. 28, figs. 2a, b), which is explained as "typical example with body chamber" does not seem to preserve completely the adult body chamber. Should this species retain the quadrituberculation up to the last part of the adult body chamber, then *Mortoniceras (Durnovarites)* would not necessarily be regarded as subgenerically identical with *Mortoniceras rostratum*, because the latter is trituberculate throughout the whole stage of the adult body chamber.

In connection with the above question, "*Mortoniceras (Styphloceras) lowrii* McLearn" (1972, p. 72, pl. 30, figs. 1-3; pl. 39, fig. 4), from the Haida Formation of British Columbia, shows a similar mode of tuberculation. Thanks to the late J.A. Jeletzky's kindness, a plaster cast of the holotype of this species is in Kyushu University. It resembles *Mortoniceras rostratum* in important points, namely (1) the quadrituberculate ornament appears for a short while on the last quarter of the septate whorl, (2) the two ventrolateral tubercles in the above substage are paired as was written in detail by McLearn, and (3) the paired tubercles are united into a prominent ventrolateral tubercle and the trituberculate state characterized almost the whorl period of the adult body chamber, although the prominent ventrolateral tubercles are mostly broken in that specimen, with only a few remains without damage. The difference of this species from *Mortoniceras rostratum* is the much depressed shape of the phragmocone with a broadly rounded venter and in the details of the ornament in the adult stage.

Our material, including the Hokkaido specimens described above and also a previously reported one from Kyushu (Matsumoto and Tashiro, 1975, p. 232, pl. 25, fig. 1; text-fig. 2 under *Mortoniceras aff. rostratum*), shows generally the same pattern of ornament as that of the holotypes of *Mortoniceras rostratum* and *Mortoniceras lowrii*. Scholz (1979a, p. 111) mentioned that the quadrituberculate state appears in small immature examples of *Mortoniceras rostratum*. This cannot be examined either in our specimens or in the holotype of *Mortoniceras rostratum* or that of *Mortoniceras lowrii*.

At any rate, the quadrituberculate character which appears in a quite limited substage of ontogeny in the two species (i.e. *Mortoniceras rostratum* and *Mortoniceras lowrii*) can be regarded as incipient, foretelling the more typically quadrituberculate characters of *Mortoniceras (Durnovarites)*. On the other hand, in having widely separated ribs with ventrolateral horns as well as lateral and umbilical tubercles on the body chamber, *Mortoniceras rostratum* resembles *Mortoniceras (Mortoniceras) stoliczkai*. In other words, with

respect to the ornament *Mortoniceras rostratum* is so to speak intermediate between typical *Mortoniceras (Mortoniceras)* and *Mortoniceras (Durnovarites)*. It might be possible to define the subgenus *Mortoniceras (Subschloenbachia)* for such an intermediate subgroup as represented by *Mortoniceras rostratum*. This may be also biostratigraphically convenient. However, our knowledge is still insufficient in various respects and especially in regard to the characters of the full-grown *Mortoniceras perinflatum*. For the time being it is better to follow Wright (1996, p. 141) to use the subgenus *Mortoniceras (Mortoniceras)* even for the subgroup of *Mortoniceras rostratum*, although *Mortoniceras (Mortoniceras)* may be considered as being defined more comprehensively than other subgenera.

Geological implications

Mortoniceras (Mortoniceras) cf. geometricum (Spath) and *Mortoniceras (Mortoniceras) rostratum* (J. Sowerby) described in this paper are the first record of these two species from Hokkaido. This supports the general point that the ammonite species of the Brancoceratidae often show worldwide distribution and that they are useful for interregional correlation irrespective of the provincial difference of the faunas. Furthermore, the described species give a substantial line of evidence for the stratigraphic relationship between the Lower Yezo Subgroup and the Middle Yezo Subgroup in Hokkaido.

Mortoniceras (Mortoniceras) geometricum is an element of the Assemblage Subzone of *Hysterocheras varicosum* in the middle part of the Upper Albian in England. The species identified with *Mortoniceras (Mortoniceras) geometricum* in our definition has been reported to occur, together with *Mortoniceras (Mortoniceras) pricei*, from the correlative of the same subzone in Venezuela (Renz, 1971) and probably in Angola (Haas, 1942b), although it was inadequately called *Mortoniceras (Mortoniceras) arietiformis*.

Although the subgeneric assignment is debatable, what we provisionally call *Mortoniceras (Mortoniceras) rostratum* [= *Mortoniceras (Subschloenbachia) rostratum* by some authors] is a characteristic element of the Assemblage Subzone of *Arrhaphoceras substudei* in the lower part of the tripartite upper part of the Upper Albian in Europe.

In the Tengu-zawa route *Mortoniceras (Mortoniceras) cf. geometricum* occurs in Member Ld and *Mortoniceras (Mortoniceras) rostratum* at the middle horizon of Member Mb. These two stratigraphic levels are quite adequate, provided that the Subzones of the Upper Albian in Europe be correlated with the subdivisions in Japan. It can be also stated that the boundary of the Lower Yezo Subgroup and the Middle Yezo Subgroup is located within the Upper Albian and that the boundary plane does not represent a significant time gap.

It should be noted that Nishida *et al.* (1996, 1997) came recently to a similar conclusion concerning the stratigraphic relationship between the Lower Yezo and Middle Yezo Subgroups in the Soeshinai area of the Teshio Mountains, northwestern Hokkaido. In that area, however, the level of the boundary is between the *Hysterocheras orbinyi* Subzone

and the *Hysterocheras varicosum* Subzone.

Acknowledgements

We thank C.W. Wright (Beaminstor) for a helpful reply to the inquiry from one of us (T.M.), W.J. Kennedy (Oxford) for a gift of a cast together with his opinion and a part of the unpublished manuscript, Hiromichi Hirano (Waseda University) and Tamio Nishida (Saga University) for valuable discussions, and further Seiichi Toshimitsu (GSJ, Tsukuba) and Naoko Egashira (Saga) for kind help in technical aspects.

References cited

- Choffat, P., 1888 : Matériaux pour l'étude stratigraphique et paléontologique de la Province d'Angola. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève*, vol. 30, p. 1-116, pls. 1-8.
- Collignon, M., 1963 : *Atlas des fossiles caractéristiques de Madagascar (Ammonites). Fascicule 10 (Albien)*, 184 p, pls. 241-317. Service Géologique, Tananarive.
- Cooper, M.R. and Kennedy, W.J., 1979 : Upper Albian (*Stoliczkaia dispar* Zone) ammonites from Angola Littoral. *Annals of the South African Museum*, vol. 77, p. 175-308.
- Gale, A.S., Kennedy W.J., Burnett, J.A., Caron, M. and Kidd, B.E., 1996 : The Late Albian to Early Cenomanian succession at Mont Risou near Rosans (Drôme, SE France) : an integrated study (ammonites, inoceramids, planktonic foraminifera, nannofossils, oxygen and carbon isotopes). *Cretaceous Research*, vol. 17, p. 515-606.
- Haas, O., 1942a : Recurrence of morphologic types and evolutionary cycles in Mesozoic ammonites. *Journal of Paleontology*, vol. 16, p. 643-650, pls. 73-74.
- Haas, O., 1942b : The Vernay Collection of Cretaceous (Albian) ammonites from Angola. *Bulletin of the American Museum of Natural History*, vol. 81, p. 1-224, pls. 1-47.
- Kawabe, F., Hirano, H. and Takagi, K., 1996 : Biostratigraphy of the Cretaceous System in the northern Oyubari area, Hokkaido. *Journal of the Geological Society of Japan*, vol. 102, p. 440-459, pls. 1-3. (in Japanese with English abstract)
- Kennedy, W.J. and Hancock, J.M., 1978 : The Mid-Cretaceous of the United Kingdom. *Annales du Museum d'Histoire Naturelle de Nice*, vol. 4 (for 1976), p. v.1-v.72 (including 30 pls.).
- Maeda, H., 1987 : Taphonomy of ammonites from the Cretaceous Yezo Group in the Tappu area, northwestern Hokkaido, Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 148, p. 285-305.
- Matsumoto [Matumoto], T., 1942 : Fundamentals in the Cretaceous stratigraphy of Japan. Part I. *Memoirs of Faculty of Science, Kyushu Imperial University, Series D, Geology*, vol. 1, p. 129-280, pls. 5-20.
- Matsumoto, T., 1960 : On some type ammonites from the Gulf Coast Cretaceous. *Science Reports of the Faculty of Science, Kyushu University, Geology*, vol. 3, p. 36-49. (in Japanese with English abstract)
- Matsumoto, T., 1995 : Notes on gaudryceratid ammonites from Hokkaido and Sakhalin. *Palaeontological Society of Japan, Special Papers*, no. 35, p. i-vi+1-152.
- Matsumoto, T. and Tashiro, M., 1975 : A record of *Mortoniceras* (Cretaceous ammonite) from Goshonoura Island, Kyushu. *Transactions and Proceedings of the Palaeontological Society of Japan, New series*, no. 100, p. 230-238, pl. 25.
- McLearn, F.H., 1972 : Ammonoids of the Lower Cretaceous Sandstone Member of the Haida Formation, Skidegate Inlet, Queen Charlotte Islands, western British Columbia. *Geological Survey of Canada, Bulletin*, vol. 188, p. 1-78, pls. 1-45.
- Meek, F.B., 1876 : A report on the invertebrate Cretaceous and Tertiary fossils of the Upper Missouri Country. *F.V. Hayden, Report of the United States Geological and Geographical Surveys of the Territories*. vol. 9, lxiv+629 p., 84 figs., 45 pls.
- Morton, S.G., 1834 : *Synopsis of the organic remains of the Cretaceous Group of the United States*, 88 p, 19 pls. Key and Biddle, Philadelphia.
- Nishida, T., Matsumoto, T., Kawashita, Y., Egashira, N., Aizawa, J. and Ikuji, Y., 1997 : Biostratigraphy of the middle part of the Cretaceous Yezo Group in the Soeushinai area of Hokkaido — with special reference to the transitional part from Lower to Upper Cretaceous : supplement —. *Journal of the Faculty of Culture and Education, Saga University*, vol. 1, p. 295-337 (including 15 pls.). (in Japanese with English abstract)
- Nishida, T., Matsumoto, T., Yokoi, K., Kawashita, Y., Kyuma, Y., Egashira, N., Aizawa, J., Maiya, S., Ikuji, Y. and Yao, A., 1996 : Biostratigraphy of the Cretaceous Middle Yezo Group in the Soeushinai area of Hokkaido — with special reference to the transitional part from Lower to Upper Cretaceous —. *Journal of the Faculty of Education, Saga University*, vol. 44, p. 65-149 (including 40 pls.). (in Japanese with English abstract)
- Owen, H.G., 1979 : Ammonite zonal stratigraphy in the Albian of North Germany and its setting in the hoplitid faunal province. In, Wiedmann, J. ed., *Aspekte der Kreide Europas*, p. 563-588. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- Renz, O., 1968a : Über die Untergattungen *Venezolicer* Spath und *Laraicer* n. subgen. der Gattung *Oxytropidoceras* Stieler (Ammonoidea) aus den venezolanischen Anden. *Eclogae Geologicae Helvetiae*, vol. 61, p. 615-655, pls. 1-13.
- Renz, O., 1968b : Die Ammonoidea im Stratotyp des Vraconien bei Sainte Croix (Kanton Waadt). *Schweizerische Paläontologische Abhandlungen*, vol. 87, p. 1-97, pls. 1-18.
- Renz, O., 1971 : Die Gattungen *Hysterocheras* Spath und *Mortoniceras* Meek (Ammonoidea) aus den Anden Venezuelas. *Eclogae Geologicae Helvetiae*, vol. 64, p. 569-609, pls. 1-12.
- Renz, O., 1982 : *The Cretaceous ammonites of Venezuela*, 132 p., 40 pls., Maraven, Caracas.
- Scholz, G., 1979a : Die Ammoniten des Vracon (Oberalb, *dispar*-Zone) des Bakony-Gebirges (Westungarn) und eine Revision der wichtigsten Vracon-Arten der West-Mediterranen Faunenprovinz. *Palaeontographica, Abt. A*, vol. 165, p. 1-136, pls. 1-30.
- Scholz, G., 1979b : Vracon-Ammoniten (Oberalb, *dispar*-Zone) aus dem Flammenmergel von Salzgitter. In, Wiedmann, J. ed., *Aspekte der Kreide Europas*, p. 589-

- 606, pls. 1-5. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart.
- Sowerby, J., 1817 : *The Mineral Conchology of Great Britain*, part 30, p. 155-166, pls. 169-174. Meredith, London.
- Spath, L.F., 1921 : On Cretaceous Cephalopoda from Zululand. *Annals of the South African Museum*, vol. 12, p. 217-321, pls. 19-26.
- Spath, L.F., 1922 : On Cretaceous Ammonoidea from Angola, collected by Prof. J.W. Gregory, D.Sc., F.R.S.. *Transactions of the Royal Society of Edinburgh*, vol. 53, p. 91-160, pls. 1-4.
- Spath, L.F., 1931 : A monograph of the Ammonoidea of the Gault, part 8. *Palaeontographical Society, Monograph*, vol. 83, no. 379, p. 313-378, pls. 31-36.
- Spath, L.F., 1932 : A monograph of the Ammonoidea of the Gault, part 9. *Palaeontographical Society, Monograph*, vol. 84, no. 384, p. 379-410, pls. 37-42.
- Spath, L.F., 1933 : A monograph of the Ammonoidea of the Gault, part 10. *Palaeontographical Society, Monograph*, vol. 85, no. 387, p. 411-442, pls. 43-48.
- Stoliczka, F., 1863 : Ammonitidae, with revision of the Nautilidae. In, Blanford, H.F. and Stoliczka, F. eds., *The fossil Cephalopoda of the Cretaceous rocks of southern India. Memoirs of the Geological Survey of India, Palaeontologia Indica, series 3*, vol. 1, p. 41-56, pls. 26-31.
- Szajnocha, L., 1885 : Zur Kenntniss der mittelcretacischen Cephalopoden-Fauna der Inseln Elobi an der Westküste Afrika's. *Denkschriften der Kaiserlichen Akademie der Wissenschaften Wien, Mathematisch-Naturwissenschaftliche Klasse*, vol. 49, p. 231-238, pls. 1-4.
- Wright, C.W., 1996 : Cretaceous Ammonoidea. In, Wright, C.W., Callomon, J.H. and Howarth, M.K., *Treatise on Invertebrate Paleontology, Part L Mollusca 4, revised*, vol. 4, p. 9-362. Geological Society of America, Boulder, and University of Kansas, Lawrence.

Fukuoka 福岡, Hokkaido 北海道, Kyushu 九州, Mikasa 三笠, Oyubari 大夕張, Saga 佐賀, Shuparo シューパロ, Shuyubari [Siyubari] 主夕張, Soeushinai 添牛内, Tengu-zawa 天狗沢, Teshio Mountains 天塩山地, Tokyo 東京, Tomatsu Chiyoda 唐松千代田, Tsukuba つくば, Yubari Mountains 夕張山地

Is the archeopyle of *Tuberculodinium vancampoae* (Rossignol) (Gonyaulacales, Dinophyceae) on the hypocyst ?

KAZUMI MATSUOKA¹, PORNILP PHOLPUNTHIN² and YASUWO FUKUYO³

¹Department of Marine Biology, Faculty of Fisheries, Nagasaki University, 1-14, Bunkyo-machi, Nagasaki 852-8521, Japan.

²Department of Biology, Faculty of Science, Prince of Sognkhla University, Hat-Yai 90112, Thailand.

³Asian Natural Environmental Science Center, University of Tokyo, 1-1-1, Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan.

Received 14 February 1998 ; Revised manuscript accepted 22 June 1998

Abstract. The archeopyle type in modern dinoflagellate cysts is classified into the following saphopylic, theropylic and cryptopylic types. Within the saphopylic type, *Tuberculodinium vancampoae* (=cyst of *Pyrophacus steinii*) is the only species generally accepted as having an archeopyle developed on the hypocyst. However, the archeopyle type of this species has been alternatively explained as being precingular rather than hypocystal. New observations have led us to conclude that the archeopyle of *T. vancampoae* is neither hypocystal nor precingular, but epicystal in type. Specimens of the hypnozygote of *P. steinii* recovered in a plankton sample from Omura Bay, West Japan show archeopyle sutures formed neither on antapical nor precingular sides but on the apical side where they are topologically related to the distribution of large and barrel-shaped processes and remaining thecal plates that overlap the hypnozygote. The hypnozygotes of *P. steinii*, wrapped in their planozygotic thecae, were carefully observed at germination during an incubation experiment. One of the living hypnozygotes was still enveloped by the thecae of the planozygote. Then, several weeks after the encystment, a motile cell germinated from the hypnozygote through one opening (=archeopyle) formed on one flat side. Since the thecae of the planozygote was still attached to the surface of the hypnozygote, the position of the germination site was easily determined with relation to the thecal plates. Above the archeopyle consisting of two paraplates, the apical pore plate with two furrows was observed. It is clear that the archeopyle was formed not on the antapical but on the apical side.

Key words : Archeopyle, dinoflagellate cyst, Dinophyceae, hypnozygote, planozygote, *Pyrophacus*, *Tuberculodinium*

Introduction

For the identification of both modern and fossil dinoflagellate cysts, the archeopyle is one of the important characteristics (e.g., Evitt, 1963, 1985). The archeopyle type in modern dinoflagellate cysts is classified into saphopylic, theropylic and cryptopylic types in the relation to the plate series for the armored group and position for the unarmored group (Matsuoka, 1988). The saphopylic archeopyle type is developed in most gonyaulacoid and protoperidinioid cysts except for an unclear type observed in the cysts of *Alexandrium* species and *Gonyaulax verior*. The other modern cysts in these groups are apical, intercalary, precingular, epicystal or some combinations thereof. Only one example of a hypocystal archeopyle has been generally accepted, this being *Tuberculodinium vancampoae* (Rossignol) (=cyst of *Pyrophacus steinii steinii* and *P. steinii vancampoae*) by Wall and Dale (1971) and followed by Matsuoka (1985).

A hypocystal archeopyle in fossil dinoflagellates has been

proposed in the cyst genus *Caligodinium* by Manum and Williams (1995) based on the careful observation and more rational interpretation of the topological relation of each paraplate. Another example of a hypocystal archeopyle (probably involving loss of postcingular paraplates) archeopyle was introduced for siliceous fossils of some species of *Peridinites* (=a synonym of *Lithoperidinium* according to Lentin and Williams, 1993), *Peridinites oamaruensis* and *P. parvalus*, with semidiagrammatic illustrations by Dale (1978). However, Harding and Lewis (1994) concluded that fossil *Peridinites* is not a cyst but a silicified theca and therefore the opening observed on the hypotheca is not a real germination apparatus (=archeopyle). For the moment, the hypocystal archeopyle seems to be only a hypothetical interpretation for *Peridinites*.

Following Wall and Dale's (1971) proposal for a hypocystal archeopyle in *P. steinii* cysts, there have been no effective and persuasive studies on the hypocystal archeopyle type in modern dinoflagellates. We will prove that the archeopyle

of *T. vancampoae* is not hypocystal but epicystal on the basis of observations for plankton and incubated specimens of *P. steinii*.

**Previous study on the archeopyle type of
*Tuberculodinium vancampoae***

The fossil cyst of *Pyrophacus steinii* (= *Tuberculodinium vancampoae*) was first described from the Pleistocene of Israel as a new species questionably assigned to *Pterosper-*

mopsis, *P. ? vancampoae* by Rossignol (1962). Later this species was transferred to *Tuberculodinium*, then a newly erected dinophycean genus by Wall (1967). In the emended diagnosis for *Tuberculodinium vancampoae*, Wall (1967) mentioned that the archeopyle of this species is a large compound type consisting of precingular and anterior intercalary paraplates. Drugg (1970) also interpreted the archeopyle of fossil *Tuberculodinium* as precingular.

Then in 1971, Wall and Dale concluded that the archeopyle of this cyst is not compound precingular but hypocystal

Table 1.

	Wall (1967)	Drugg (1970)	Wall & Dale (1971)	Stover & Evitt (1978)	Wrenn & Damassa (1989)	This study
Material	fossil cysts	fossil cysts	living hypnozygotes incubated	literature	fossil cysts	living vegetative cells, planozygotes and hypnozygotes
Compression direction in cysts	dorso-ventrally	dorso-ventrally	anterio-posterior	anterio-posterior	dorso-ventral cyst rotated 90 degree within the planozygose	anterio-posterior
Archeopyle type	compound ; precingular + anterior intercalary	precingular	hypocystal	compound ; antapical	precingular	compound ; epicystal
Wall features	not mentioned	not intratabular	not mentioned	intratabular	not mentioned	?

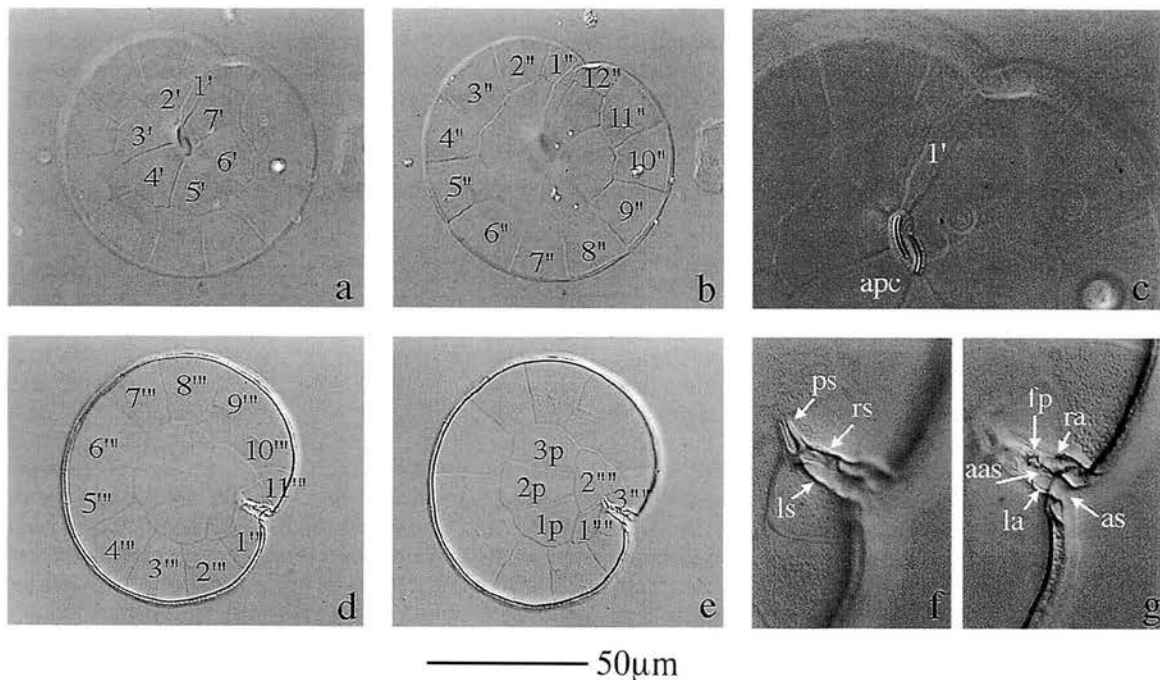


Figure 1. Plate tabulation in vegetative cell. **a** ; apical plate series, **b** ; precingular plate series, **c** ; apical pore complex (apc) and 1', **d** ; postcingular plate series, **e** ; posterior intercalary and antapical plate series, **f** and **g** ; sulcal plates, as : anterior sulcal plate, ra : right accessory sulcal plate, la : left accessory sulcal plate, aas : anterior accessory sulcal plate, rs : right sulcal plate, ls : left sulcal plate, ps : posterior sulcal plate, fp : flagellar pore.

based on the result of cyst incubation experiments on *P. steinii*. This explanation was followed by Matsuoka (1985) based also on the incubation method. Stover and Evitt (1978) suggested that *Tuberculodinium* has an antapical rather than hypocystal archeopyle. However, the possibility that the archeopyle type of *Tuberculodinium* is not hypocystal but precingular was raised by Wrenn and Damassa (1989).

Thus, the archeopyle type of *T. vancampoae* remains unclear and the subject of discussion (see Table 1).

Material and method

A plankton sample was collected with a net haul in June of 1983 from Omura Bay, West Japan, and preserved with 5% formalin. Several specimens of the hypnozygote of *P. steinii*

were picked up with a micropipette and then mounted on a slide glass with glycerine jelly. These hypnozygotes were examined under the interference optics of a Zeiss Axiphoto microscope.

Surface sediments containing living cysts of *P. steinii* were collected from Omura Bay and Tokyo Bay with a TFO gravity corer in 1990. The top 2 cm of the sediments was cut and removed to a refrigerator below 4°C until starting the incubation experiment. The material was sonified and sieved with stainless screens of 120 μm and 20 μm in pore size, and the living cysts of *P. steinii* were picked up to inoculate in a culture dish with SWII medium. The living cysts were cultured under 20°C, about 100 $\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and 12 hours cycle. The culture was continued until one whole life cycle of this species from vegetative cells to planomeiocytes via planozygotes and hypnozygotes, was

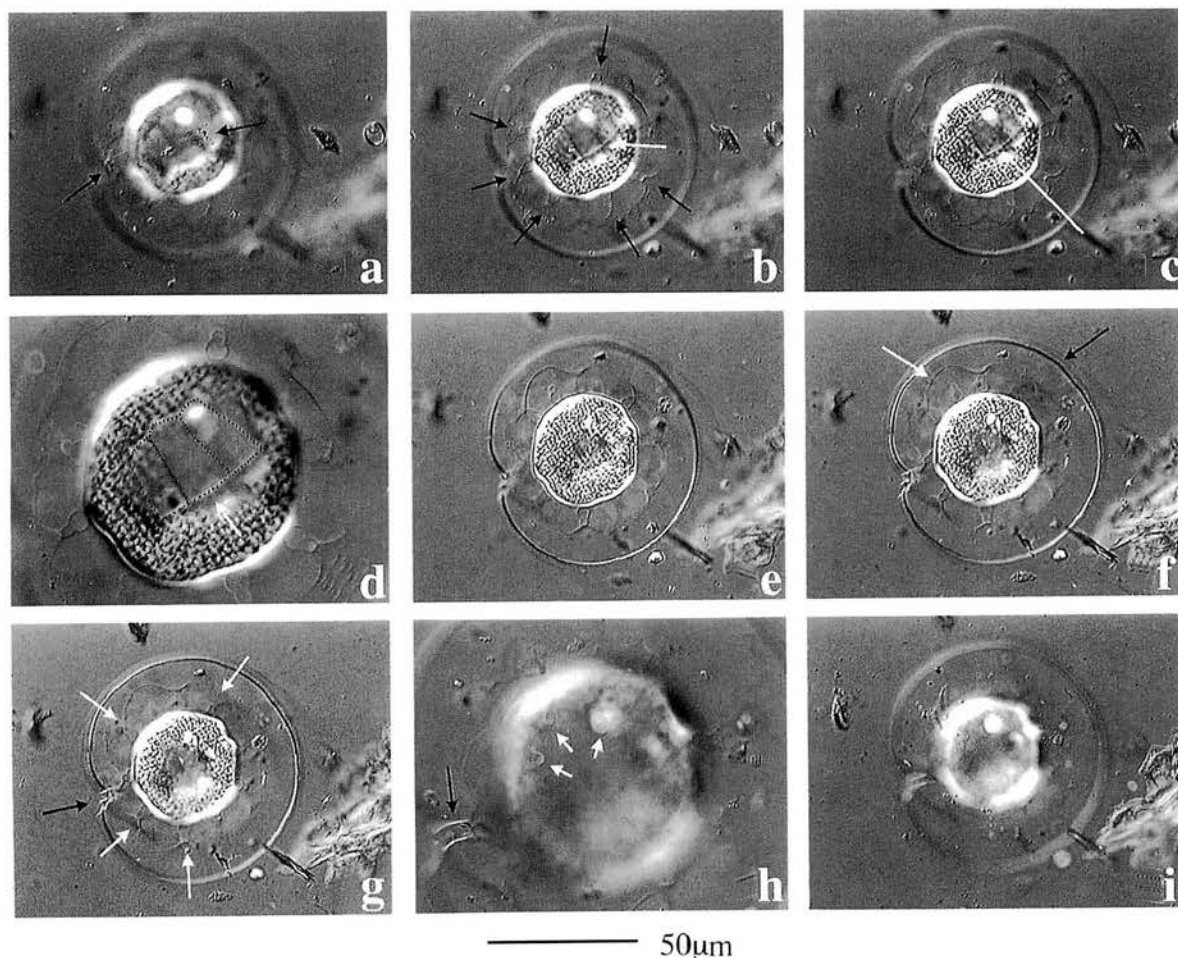


Figure 2. Hypnozygote involved by thecae of planozygote of *Pyrophacus steinii* in plankton sample collected from Omura Bay on June of 1990. A serial photographs from apical surface (a) to antapical surface (i). **a**; apical pore complex (black arrow) and 1' of the planozygote. **b** and **c**; three paraplates (?) corresponding to the archeopyle which has already appeared before germination on the surface of hypnozygote (white arrows), and precingular processes (black arrows). **d**; enlargement of the archeopyle. **e**; optical cross section. **f**; hypotheca of planozygote (black arrow) and ectophragm of hypnozygote. **g**; sulcus of planozygote (black arrow) and postcingular processes of hypnozygote (white arrow). **h**; antapical processes distributing circularly (white arrows) and sulcus of planozygote (black arrow). **i**; antapical surface of planozygote.

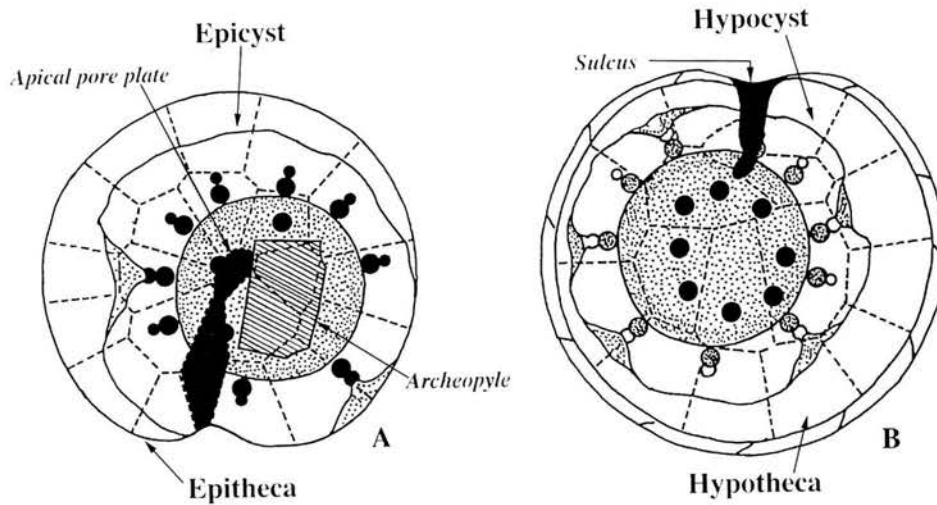


Figure 3. Illustration of a planozygote containing a hypnozygote, collected from Omura Bay, west Japan, June 1990. **A**; Epitheca and epicyst showing archeopyle sutures, **B**; Hypotheca and hypocyst, the same specimen of Figure 2.

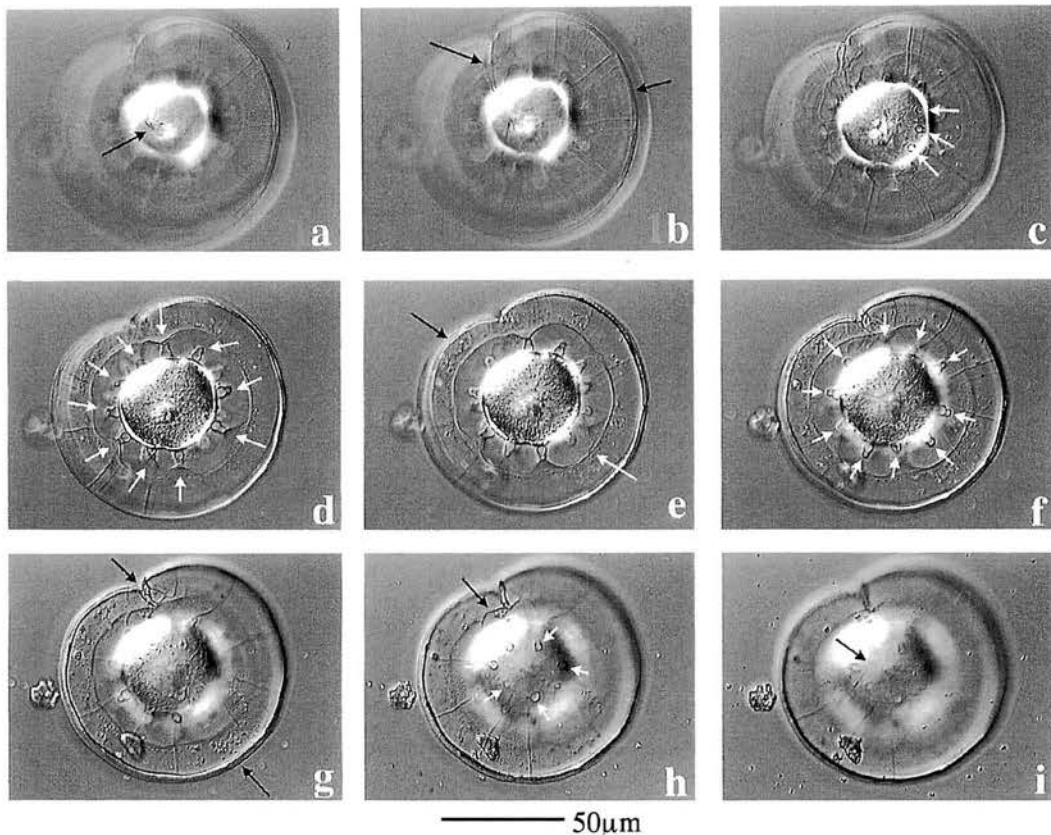


Figure 4. Hypnozygote involved by thecae of planozygote of *Pyrophacus steinii* in plankton sample collected from Omura Bay on June of 1990. Serial photographs from apical surface (a) to antapical surface (i). **a**; apical pore plate (black arrow). **b**; epitheca of planozygote and 1' plate (black arrows). **c**; apical processes with linear distribution (white arrows). **d**; precingular processes (white arrows). **e**; cingular plates of planozygote (black arrow) and ectophragm of hypnozygote (white arrow). **f**; postcingular processes (white arrows). **g**; sulcus of planozygote and hypotheca (black arrows). **h**; 3''' (black arrow) and antapical processes distributing circularly (white arrows). **i**; posterior intercalary of plate planozygote (black arrow).

completely observed. In particular, one specimen which had a well preserved archeopyle structure was carefully examined under interference optics of a Nikon Biophoto microscope.

Since the number of plates in *P. steinii* is (Figure 1) very variable, there have been several different interpretations of its expression. In this paper, we follow the interpretation of Matsuoka (1985).

Results

Plankton specimens of hypnozygotes (Figures 2, 3, 4)

A few immature resting cysts were collected in plankton samples from Omura Bay. These cysts were filled with fresh protoplasm and surrounded the planozygotic theca, clearly demonstrating a morphological relation between the planozygote and resting cyst. It is therefore easy to establish the orientation of the thecal plate and process distribution on the cyst.

The epitheca of the planozygote could easily be confirmed by the presence of the apical pore plate, seven apical, and eleven precingular plates (Figures 2, 3a). Beneath the apical pore plate, three large, barrel-shaped processes and a certain space were noticed on the cyst surface (Figures 2b, d). A polygonal outline similar to some plate boundaries confined this space. One row consisting of ten large and barrel-shaped processes ran along the shoulder (Figures 2b, 4d).

The opposite side of the hypnozygote contained the sulcus, and thirteen postcingular, three posterior intercalary, and three antapical plates were observed (Figures 2f, 3b). Beneath this hypotheca, eleven large barrel-shaped processes were formed on the shoulder of the cyst. Eight large barrel-shaped processes were circularly distributed on this cyst surface (Figures 2g, h).

The plate formula of the planozygote shown in Figure 2 was demonstrated as 7', 11'', 13c, 13''', 3p, 3'''' and 5s, while the process formula on the cyst would be described as 3' + 3@, 10'', 0c, 10''' and 8'''' (@ : paraplates consisting of the operculum).

Observation of empty hypnozygote surrounded by the planozygote (Figures 5, 6)

Some hypnozygotes used for our study on the life cycle remained within the planozygotic theca and its wall even after excystment (Figure 5). Figure 6 shows the morphological features of both planozygote and hypnozygote. The planozygote had one apical pore (Figure 5a), seven apical and eleven precingular plates. On the cyst surface just beneath this epitheca, there was an archeopyle probably corresponding to two paraplates (Figure 5c) and five larger barrel-shaped and three small, simple spherical processes distributed on one shoulder of the peripheral side (Figures 5d, e).

The hypotheca consisted of thirteen postcingular, three posterior intercalary, three antapical, thirteen cingular, and five sulcal plates (Figures 5j, k, l). On the cyst surface of this side, eleven large and barrel-shaped processes were located on the shoulder, and six large and barrel-shaped

processes positioned circularly (Figures 5g, h, i). The plate formula of this planozygote was 7', 11'', 13c, 13''', 4p, 1ap, and 3''', and the process formula of this cyst was 5 (3+2s)' + 2@, 11'', 0c, 10'', and 3'''' + 3s.

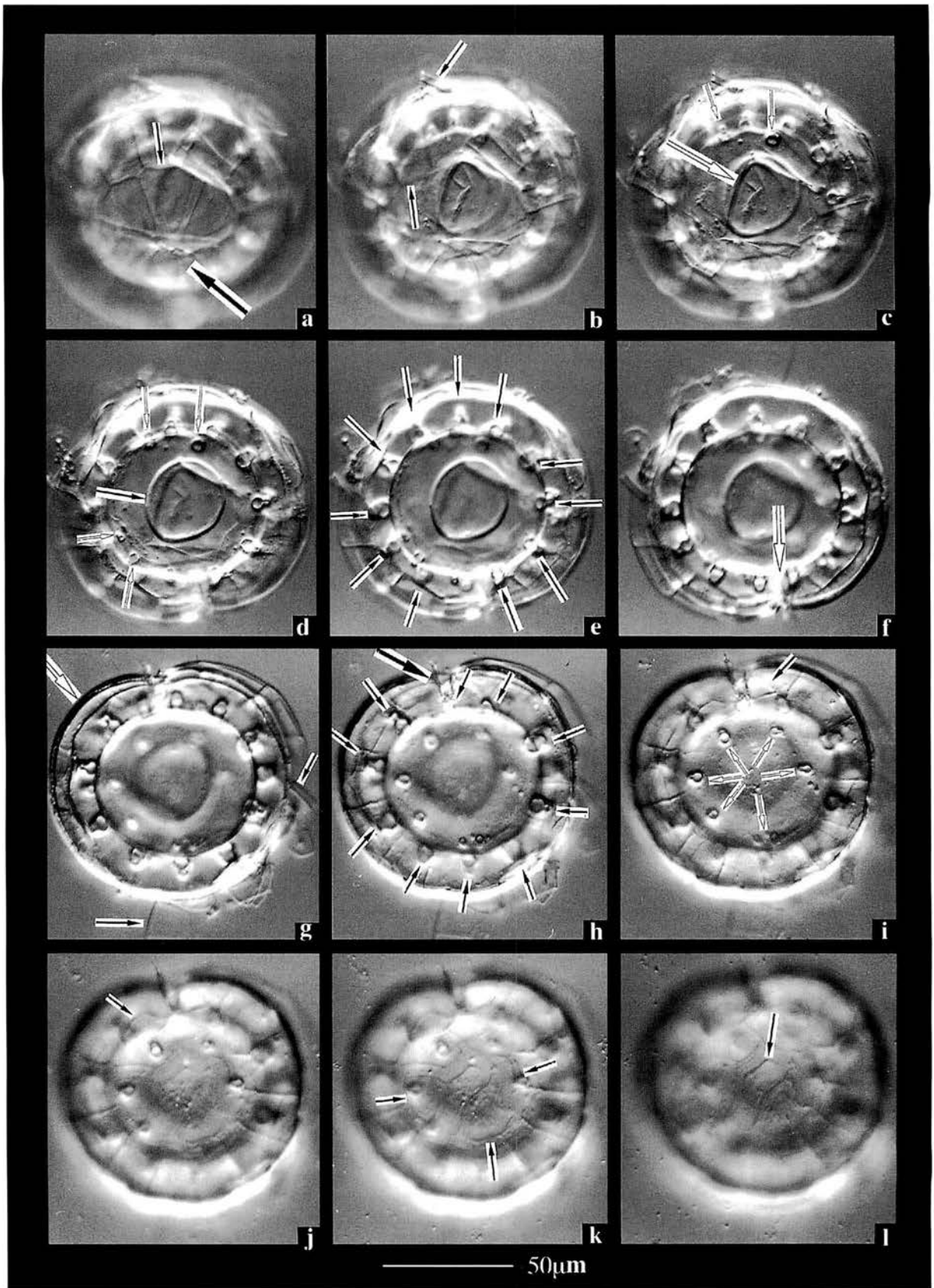
Observation on the transformation from planozygote to hypnozygote during incubation (Figure 7)

Clonal cultures of *P. steinii* were established by a single cell isolation from net-haul samples at Yokohama Umizuri-sambashi in innermost Tokyo Bay on June, 1990. During the clonal culture for this specimen, both sexual and asexual reproduction occurred. Sexual reproduction started to result in small and round thecate cells (male gametes). Female gametes were not morphologically differentiated from normal vegetative cells in plate formula and size. By sexual fusion of male and female gametes, a planozygote was produced and was morphologically similar to vegetative cells except for its larger cell size. After one to two days active swimming, the planozygote stopped moving, and sunk to the bottom of the culture chamber. The hypnozygotes were produced as a result of protoplasm contractions to approximately 1/5 of the original volume. After development of the exospore, many processes were formed between the exospore and the surface of the protoplast (mesospore). These processes were barrel-shaped and identical to those previously observed in fossil forms. This hypnozygote was contained within the theca of the planozygote (Figure 7). Several weeks after the encystment, a motile cell germinated from the hypnozygote through one opening (= archeopyle) formed on one flat side. As the theca of the planozygote was still attached to the surface of the hypnozygote, the position of the germinated side was easily determined with relation to the thecal plates. The archeopyle consisted of two paraplates, and above it, an apical pore plate with two furrows was observed (Figure 5c).

Discussion

Position and type of archeopyle

Wall (1967) established a new genus *Tuberculodinium* after revising *Pterospermopsis? vancampoe* Rossignol and emending the species diagnosis so that the archeopyle corresponds to a combination of precingular and intercalary paraplates. Drugg (1970) also considered the archeopyle of *Tuberculodinium* to be precingular with the number of detached opercular plates being variable in different species. Later, Wall and Dale (1971) observed the cysts of *P. steinii* and *P. vancampoe*, which now Balech (1979) and Matsuoka (1985) consider to be two subspecies of *P. steinii*, and noted that the archeopyle is hypocystal and that the number of paraplates comprising the operculum varies from two to four. However, this conclusion was not based on direct observation of germinated hypnozygotes, but on mostly theoretical grounds. The interpretation given by Wall and Dale (1971) was as follows: Four parallel rows consisting of large and barrel-shaped processes on the cysts were considered to represent apical, precingular, postcingular and antapical plate series of the thecate form respectively. Of these four rows, one contained two to five rectangular to polygonal



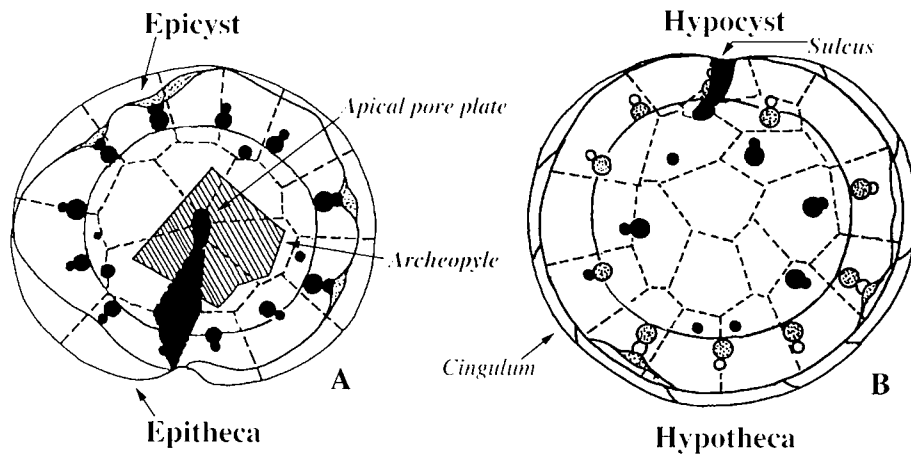


Figure 6. Illustration of a planozygote containing an empty hypnozygote after germination in culture. **A**; Epitheca and epicyst showing archeopyle sutures, **B**; Hypotheca and hypocyst, the same specimen of Figure 4.

paraplates forming the archeopyle which resembled posterior intercalary and sometimes additional posterior plates of the thecate cell. The processes opposite to this row were circularly distributed and apparently similar to the distribution of apical plate series of the vegetative cell. These observations led them to conclude that the cysts of *P. steinii* and *P. vancampoae* have a hypocystal archeopyle.

Matsuoka (1985) found hypnozygotes surrounded by the thecae of planozygotes in a plankton sample collected from Omura Bay. However, as the hypnozygotes were filled with protoplasm, he schematically illustrated the general outline of one specimen of the planozygote and hypnozygote using the same interpretation as Wall and Dale (1971).

Wrenn and Damassa (1989) examined hundreds of fossil specimens of *T. vancampoae* from latest middle Eocene to Holocene in detail, and concluded that the cyst morphology did not correspond to that of the theca; that the cyst was dorso-ventrally compressed and that the archeopyle was precingular rather than hypocystal. In order to rationalize this interpretation, Wrenn and Damassa (1989) proposed that during maturation of the planozygote, the hypnozygote rotated 90° with respect to the planozygote. A full description of this interpretation has yet to be published, and unfortunately we are therefore unable to evaluate their observations in detail. However, we never observed the hypnozygote to rotate from early to matured stage in the planozygote (Figure 7). According to our observations, we can also conclude that this is unlikely as suggested by Manum and Williams

(1995).

The specimens recovered from the net samples of Omura Bay also demonstrated archeopyle formation. These cysts, collected while still floating in surface waters before sinking, showed archeopyle structure on the hypnozygote surface even though these cells were filled with protoplasm. These archeopyles were not yet functional and the opercula were still in place, but the archeopyle suture could nevertheless be traced on the surface. The archeopyle was formed beneath the apical pore and apical plates of the planozygote. According to the outline of the sutures, the opercula seemed to be composed of three or four paraplates. However, none of the paraplates morphologically resembled any apical or precingular plates of the attached planozygote.

The incubated specimens clearly showed the position of an archeopyle, which was also formed beneath the apical pore plate and the apical plate series. In these specimens, although the opercula were completely detached leaving only their outline on the surface, the outline did not resemble either apical or precingular plates of the overlying planozygote. This observation agrees with the plankton specimens from Omura Bay.

Under these circumstances, the archeopyle of *T. vancampoae* (=hypnozygote of *P. steinii*) is formed on the epicyst, but it is very difficult to determine the type exactly. It should be called epicystal and compound rather than hypocystal or antapical.

Figure 5. Theca of planozygote and hypnozygote after germination. Serial photographs from apical view (a) to antapical view (l). **a**: apical pore plate and apical plates (3', 4', and 5'; black arrow). **b**: precingular plates (black arrows), **c**: large apical process (small white arrows) and archeopyle (large white arrow) formed on the surface of hypnozygote. **d**: large apical processes (white arrows) and endospore remaining in the cavity of the hypnozygote (black arrow). **e**: large precingular processes (black arrows). **f**: optical cross section of hypnozygote. **g**: cingular plates. **h**: large postcingular processes. **i**: 1''' (black arrow) and antapical processes distributed circularly (white arrows). **j**: 3''' (black arrow). **k**: posterior intercalary plates (black arrow). **l**: additional posterior intercalary plates (black arrow).

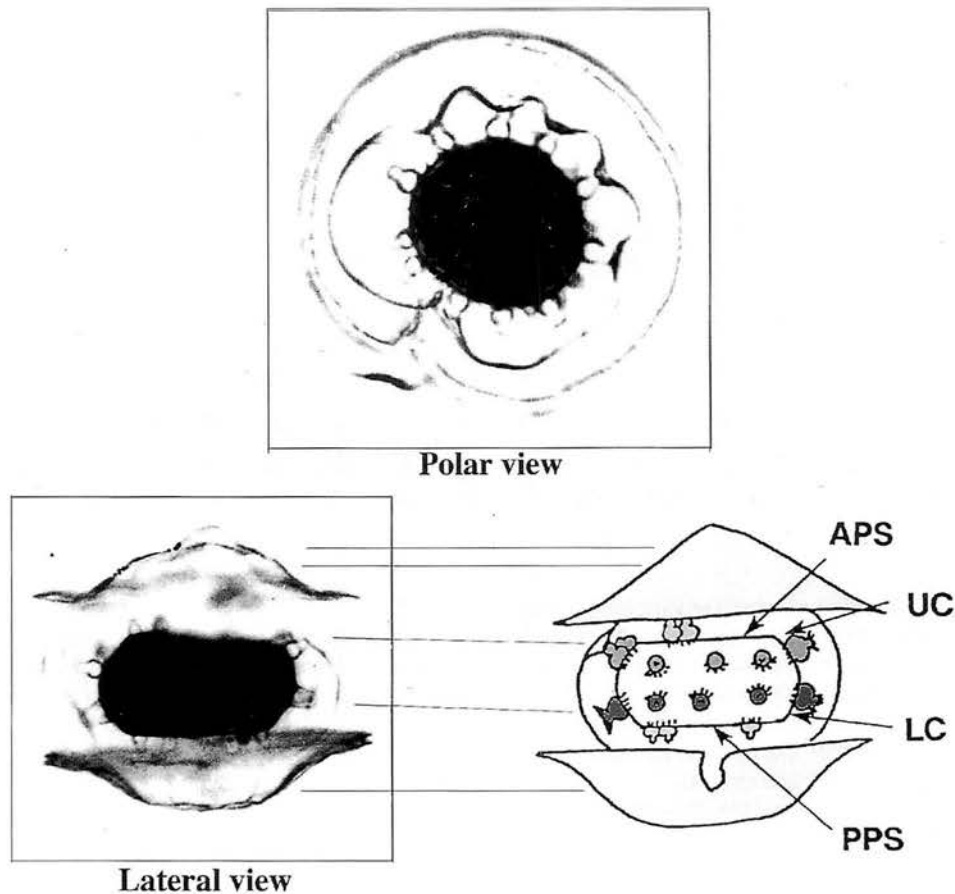


Figure 7. Hypnozygote produced within a planozygote of *Pyrophacus steinii* during the incubation experiment. APS: anterior flattened polar surface, UC: upper corner of flattened polar surface, LC: lower corner of flattened polar surface, PPS: posterior corner of flattened polar surface.

Intratabular structure on the hypnozygote

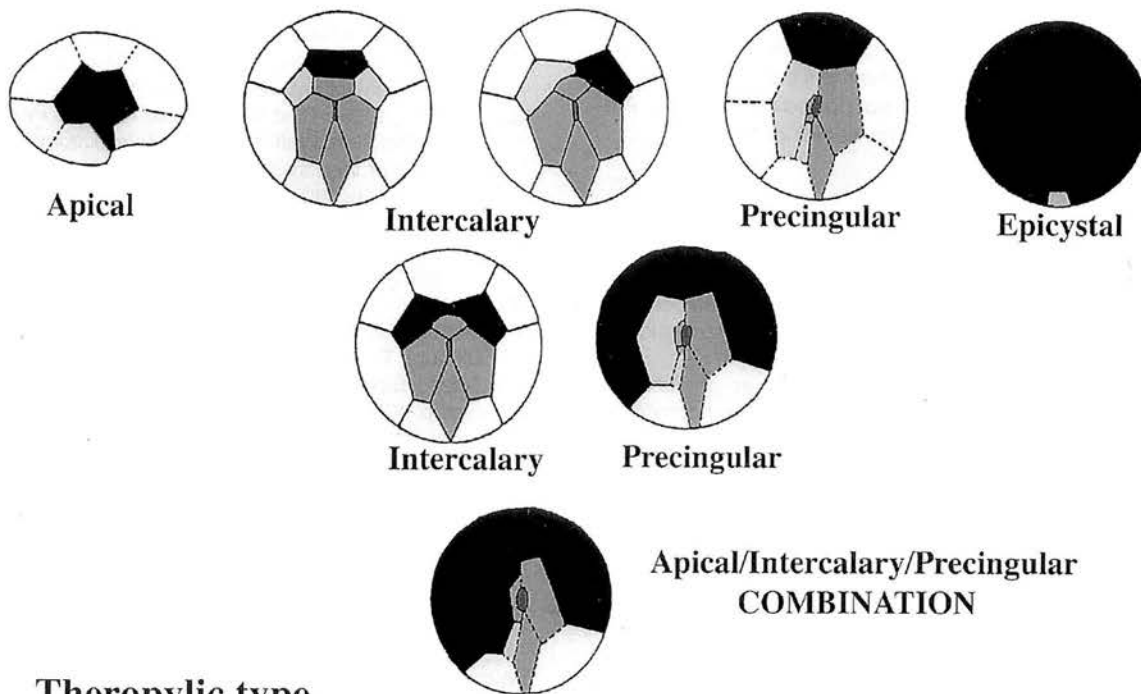
Stover and Evitt (1978) mentioned that intratabular features in *T. vancampoae* are arranged in longitudinal rows of barrel-shaped processes and are absent in the equatorial area. Drugg (1970) considered intratabular features to be absent in two fossil species, *T. vancampoae* and *T. rossignoliae*, and that except for the archeopyle, no parasutural features were observed. However, Wrenn and Damassa (1989) demonstrated an intratabular distribution as suggested by one barrel-shaped, large process placed in the center of one paraplate clearly bounded by parasutural features in fossil *Tuberculodinium vancampoae*. The outline of these paraplates closely resembles each opercular piece.

According to Wall and Dale (1971) and Matsuoka (1985), the modern cysts of *Pyrophacus steinii*, including *P. steinii vancampoae*, do not show any paraplate features like those in fossil specimens. Furthermore, there were no parasutures

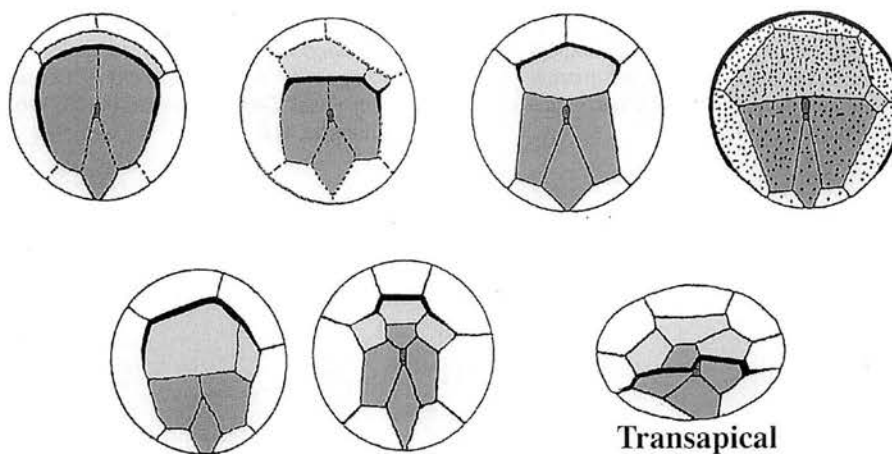
on the cyst and no paraplates except for archeopyle sutures which sometimes showed a polygonal outline. As with other gonyaulacoid cysts, the number of large, barrel-shaped processes is always fewer than that of thecal plates on both vegetative cells and planozygotes. There was no reflection of the cingulum, which was always shown by the space between two rows of large, barrel-shaped processes corresponding to pre- and postcingular plate series. The operculum detached from the cyst does not correspond with any apical and precingular plates of vegetative cells and planozygotes in shape and position.

For clear understanding how the processes are developed during maturation from the planozygote to hypnozygote, this progress should be continuously observed during incubation as was done on *Lingulodinium polyedrum* by Kokinos and Anderson (1995).

Saphopylic type



Theropylic type



Cryptopylic type

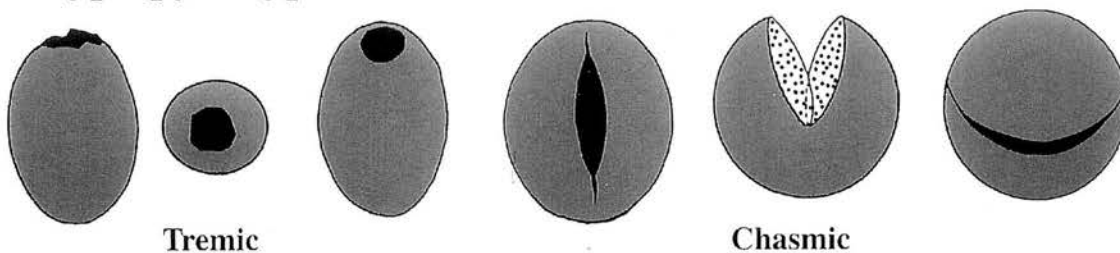


Figure 8. Archeopyle types developed in modern dinoflagellate cysts after modification of Matsuoka *et al.* (1989) based on the new observation.

Acknowledgments

We are indebted to David Wall and John, H. Wrenn for their kind criticism and helpful suggestion on the archeopyle type of *Tuberculodinium vancampoeae* and also to Rex Harland and Martin J. Head for their critical reading of an earlier draft. This paper is partly supported by Grand-in-Aid of Monbusho, No. 08640593 to the senior author.

Reference cited

- Balech, E., 1979: El género *Pyrophacus steinii* Stein (Dinoflagellate). *Physis*, sec. A, 38, p. 27-38.
- Dale, B., 1978: Acritarchous cysts of *Peridinium faeroense* Paulsen: Implications for dinoflagellate systematics. *Palynology*, vol. 2, p. 187-193.
- Drugg, W.S., 1970: Two new Neogene species of *Tuberculodinium* and one of *Xenicodinium* (Pyrrhophyta). *Proceedings of the Biological Society of Washington*, vol. 83, p. 115-122.
- Evitt, W.R., 1963: A discussion and proposals concerning fossil dinoflagellates, hystrichospheres, and acritarchs, I, II. *Proceedings of the Natural Academy of Science*, vol. 49, p. 158-164 and p. 298-302.
- Evitt, W.R., 1985: *Sporopollenin Dinoflagellate Cysts-Their morphology and interpretation*, xv+333 p. American Association of Stratigraphic Palynologists Foundation, Texas.
- Harding, I.C. and Lewis, J., 1994: Siliceous dinoflagellate thecal fossils from the Eocene of Barbados. *Palaeontology*, vol. 37, p. 825-840.
- Kokinos, J.P. and Anderson, D.M., 1995: Morphological development of resting cysts in cultures of the marine dinoflagellate *Lingulodinium polyedrum* (= *L. machaerophorum*). *Palynology*, vol. 19, p. 143-166.
- Lentin, J.K. and Williams, G.L., 1993: *Fossil dinoflagellates: Index to genera and species 1993 edition*. AASP Contribution Series No. 28, viii+856 p. American Association of Stratigraphic Palynologists Foundation.
- Manum, S. and Williams, G.L., 1995: Hypocystal archeopyles in the dinoflagellate cyst genus *Calligodinium* Drugg. *Palynology*, vol. 19, p. 183-190.
- Matsuoka, K., 1985: Cyst and theca forms of *Pyrophacus steinii* (Schiller) Wall et Dale. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, 140, p. 240-262.
- Matsuoka, K., 1988: Cyst-theca relationships in the diplosalid group (Peridinales, Dinophyceae). *Review of Palaeobotany and Palynology*, vol. 56, p. 95-122.
- Matsuoka, K., Fukuyo, Y., and Anderson, D.M., 1989: Methods for modern dinoflagellate cyst studies. In, Okaichi, T., Anderson, D.M., and Nemoto, T. eds., *Red Tides: Biology, Environmental Science, and Toxicology*, p. 461-479. Elsevier, New York.
- Rosignol, M., 1962: Analyse pollinique de sédiments Quaternaires en Israël. I: Sédiments Pleistocènes. *Pollen et Spores*, vol. 4, p. 121-148.
- Stover, L.E. and Evitt, W.R., 1978: *Analyses of Pre-Pleistocene organic-walled dinoflagellates*. Stanford University Publications, Geological Sciences, 25, iii+300 p., Stanford, California.
- Wall, D., 1967: Fossil microplankton in deep-sea cores from the Caribbean Sea. *Palaeontology*, vol. 10, p. 95-123.
- Wall, D. and Dale, B., 1971: A reconsideration of living and fossil *Pyrophacus* Stein, 1883 (Dinophyceae). *Journal of Phycology*, vol. 7, p. 221-235.
- Wrenn, J.H. and Damassa, S.P., 1989: *Tuberculodinium vancampoeae*: A curious reflection of its former self. *Abstract of Fourth International Conference on Modern and Fossil Dinoflagellates*, p. 108, Woods Hole, Massachusetts, U.S.A.

Trogosus-like tillodont (Tillodontia, Mammalia) from the early Middle Eocene of Japan

KAZUNORI MIYATA and YUKIMITSU TOMIDA

Department of Environmental Science, Graduate School of Science and Technology, Kumamoto University, Kurokami-cho 2-39-1, Kumamoto 860-0862, Japan

Department of Geology, National Science Museum, 3-23-1 Hyakunin-cho, Shinjuku-ku, Tokyo 169-0073, Japan

Received 11 March 1998 ; Revised manuscript accepted 27 June 1998

Abstract. A trogosine tillodont, represented by seven fragmentary teeth, is described from the upper part of the Akasaki Formation, early Middle Eocene of Japan. The stratigraphic horizon of the new material is almost the same as that of the holotype of *Higotherium hypsodon*, which is the most recently described tillodont from Japan. In spite of poor preservation, the dental characters of the new specimens are distinguishable from those of the Asian trogosine genera including *Higotherium*, and they may be referable to *Trogosus*, which has been recorded only from the Bridgerian of North America. This *Trogosus*-like tillodont inhabited East Asia together with more advanced *Higotherium* during the early Middle Eocene.

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

Introduction

Recently, several new tillodonts have been found in Asia (e.g., Ting and Zheng, 1989 ; Chow *et al.*, 1996 ; Miyata and Tomida, 1998), and tillodont origin and dispersal have been discussed repeatedly based on various phylogenetic hypotheses (Stucky and Krishtalka, 1983 ; Baudry, 1992 ; Lucas, 1993 ; Chow *et al.*, 1996 ; Miyata and Tomida, 1998). The subfamily Trogosinae Gazin, 1953 is generally believed to be a monophyletic group, and includes five derived genera of Tillodontia: *Trogosus* Leidy, 1871, *Tillodon* Gazin, 1953, *Kuanchuanius* Chow, 1963a, *Chungchienia* Chow, 1963b (see also Chow *et al.*, 1996), and the recently erected genus *Higotherium* (Miyata and Tomida, 1998). Trogosine material from Asia is rare but provides significant records for understanding tillodont diversity during the Middle Eocene. North American trogosines, *Trogosus* and *Tillodon*, have been recorded only from the Bridgerian land mammal age (latest Early to early Middle Eocene ; Prothero, 1995). *Kuanchuanius* and *Higotherium* are known from the early Middle Eocene of China and Japan, respectively, and *Chungchienia* is known from slightly younger Middle Eocene strata of China (Chow *et al.*, 1996). Considering the monophyly of Trogosinae, the appearances of these genera indicate that their divergence had already occurred prior to the Middle Eocene and continued well into the Middle Eocene.

Although our knowledge of Asian trogosines is limited to rare and incomplete material, the three Asian genera mentioned above are easily distinguishable from North American genera in having several derived dental charac-

ters. In comparison with North American taxa, trogosine diversity at the generic level is likely more advanced in Asia, and to date no genus has been recorded from both North America and Asia. *Kuanchuanius shantunensis* Chow, 1963a was regarded as the most closely related taxon to the North American genus *Trogosus* (Stucky and Krishtalka, 1983 ; Lucas, 1993), but this Asian species is distinct in having a peculiar 1/2 morphology (Chow, 1963a ; Miyata and Tomida, 1998).

Seven fragmentary teeth of the tillodont described here were found in the red siltstone belonging to the upper part of the Akasaki Formation, at Iwajima within Ohyanomachi, Kumamoto Prefecture, Japan (Figure 1). The stratigraphic horizon is placed approximately 2 m below the base of the Shiratake Formation, which conformably overlies the Akasaki Formation and bears marine molluscan fossiliferous horizons, namely Lower *Orthaulax* Zone of Nagao (1926), in the basal part. On the basis of our field investigation, the tillodont horizon is almost equal to that of the holotype of *Higotherium hypsodon*, thus the geological age is most likely the early Middle Eocene (see geological setting in Miyata and Tomida, 1998). Although a precise generic assignment of the new tillodont material is difficult because of the poor preservation, it apparently belongs to Trogosinae judging from the dental characters. Moreover, the tooth remains described here closely resemble those of *Trogosus* in morphology, but apparently differ from those of the three Asian genera mentioned above. In this paper, we provide evidence that a *Trogosus*-like tillodont inhabited East Asia during the early Middle Eocene.

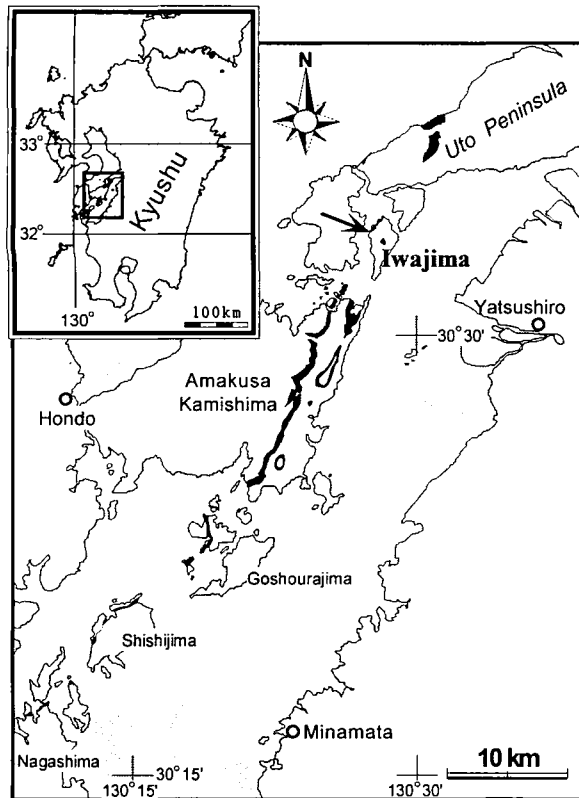


Figure 1. Map showing the fossil locality (allow), Iwajima in Ohyanomachi, western part of Kyushu, Japan, and the distribution of the Akasaki Formation (black area).

The following institutional abbreviations are used in this paper: **AMNH**, American Museum of Natural History, New York, New York, USA; **IVPP**, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, People's Republic of China; **NSM**, Department of Geology, National Science Museum, Shinjuku, Tokyo, Japan; **USNM**, National Museum of Natural History, Washington, D.C., USA; **YPM**, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.

Systematic paleontology

Order Tillodontia Marsh, 1875
 Family Esthonychidae Cope, 1883
 Subfamily Trogosinae Gazin, 1953
 Genus *Trogosus* Leidy, 1871

Type species.—*Trogosus castoridens* Leidy, 1871

Cf. Trogosus sp.

Figures 2, 3

Material.—Seven fragmentary teeth, NSM-PV 20121: partly damaged right I/2 (Figures 2A, B), fragmentary left I/2 (Figure 2C), enamel remains of right and left I2/? (Figures 2D,

E), cracked right P/4 (Figure 2F), trigonid portion of a right lower molar (Figure 2G), and broken talonid portion of right M/3 (Figures 2H–J).

Locality.—Western coast at Iwajima, Ohyanomachi, western part of Kumamoto Prefecture, Japan (Figure 1).

Horizon and Age.—Upper part of the Akasaki Formation, most likely early Middle Eocene (see also Miyata and Tomida, 1998).

Occurrence.—Seven fragmentary teeth (NSM-PV 20121) described below were found in two adjoined concretions from the red siltstone belonging to the Akasaki Formation. The cracked right P/4 and a trigonid portion of a right lower molar (Figures 2F, G) were found from the small concretion (approximately 12 cm in diameter), the other five fragmentary teeth were found from the large concretion (approximately 25 cm in diameter). These teeth are probably of a single individual judging from the massed occurrence.

Description.—All the teeth described below are poorly preserved, and in a few instances all that remains is enamel. However, based on our examination, they are identifiable as fragments of four elongated rootless teeth with enamel bands restricted to the anterior surfaces (second incisors, Figures 2A–E) and three rooted hypsodont teeth with columnar-shaped enamel walls (lower cheek teeth, Figures 2F–J). Illustrations of the reconstructed right I/2, P/4, and M/3 talonid are shown in Figure 3, and measurements of NSM-PV 20121 are presented in Table 1.

Second incisors: The four elongated fragments (Figures 2A–E) are remains of rootless teeth with restricted enamel covering; the enamel layer is distributed on the labial surface and the anterior part of the mesial and distal surfaces. In these fragmentary teeth their mesial and distal sides are distinguishable; the extension of enamel covering on the distal side is greater than on the mesial side, as seen in rodent incisors. Only one tooth (Figures 2A, B; 3A–C) barely retains its natural shape among the four elongated teeth and is certainly identifiable as the right I/2 of a trogosine tillodont. The right I/2 is 85 mm in length from its tip to the proximal end as preserved. It is curved in lateral view, and the tip is chisel-shaped. The labial and distal enamel surfaces of the right I/2 are nearly flattened and are ornamented with weak, longitudinal lines (rugose). Moreover, a growth line-like pattern is observable on the mesial surface of the enamel and is slightly curved toward the tip of the crown (Figure 3C). Both the labiodistal and labiomessial corners of the I/2 are rounded in cross section (Figure 3B). The enamel-free dentine of the right I/2 is partly disintegrated but apparently elongated posteriorly, and its distal side is in the same plane as the enamel covering part. Three other fragments lack dentine (Figures 2C–E) but possess similar enamel features to that of the right I/2. However, the three fragments are too incomplete to permit identification of their position in the jaw. Nevertheless, one of them (Figure 2C) is considered as a fragment of left I/2 because it was found close to the right I/2. The two remaining fragments (Figures 2D, E) were also found in the same concretion but were separated from the lower incisors when collected. These two enamel fragments (Figures 2D, E) are tentatively interpreted as parts of the right and left I2/, respectively, judging

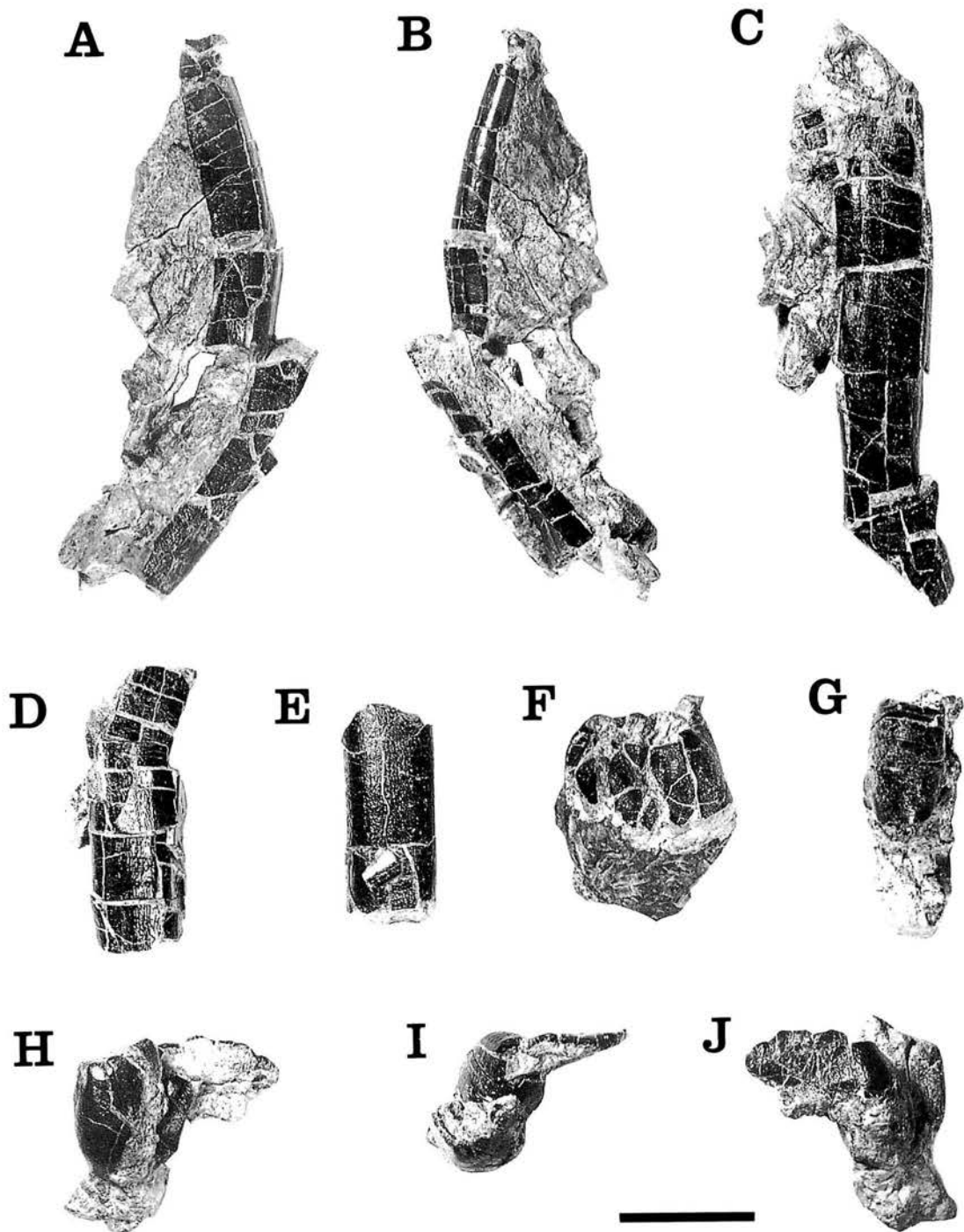


Figure 2. Cf. *Trogosus* sp., NSM-PV 20121. **A-B:** right I/2; A, distal view; B, mesial view. **C:** left I/2, labial view. **D:** right I2/?, labial view. **E:** left I2/?, labial view. **F:** right P/4, buccal view. **G:** trigonid portion of a right lower molar, buccal view. **H-J:** right M/3 talonid; H, buccal view; I, occlusal view; J, lingual view. Scale bar equals 2 cm long.

from the enamel development on the lateral sides and the curvature of the growth line-like pattern in the enamel.

Lower cheek teeth: The lower cheek teeth (Figures 2F-J) of NSM-PV 20121 are also incomplete and damaged, and the

cuspid pattern on the fragmentary teeth is obscured because of heavy wear and poor preservation.

The P/4 of NSM-PV 20121 (Figures 2F, 3D) is incompletely prepared; it is impossible to remove all of the matrix from

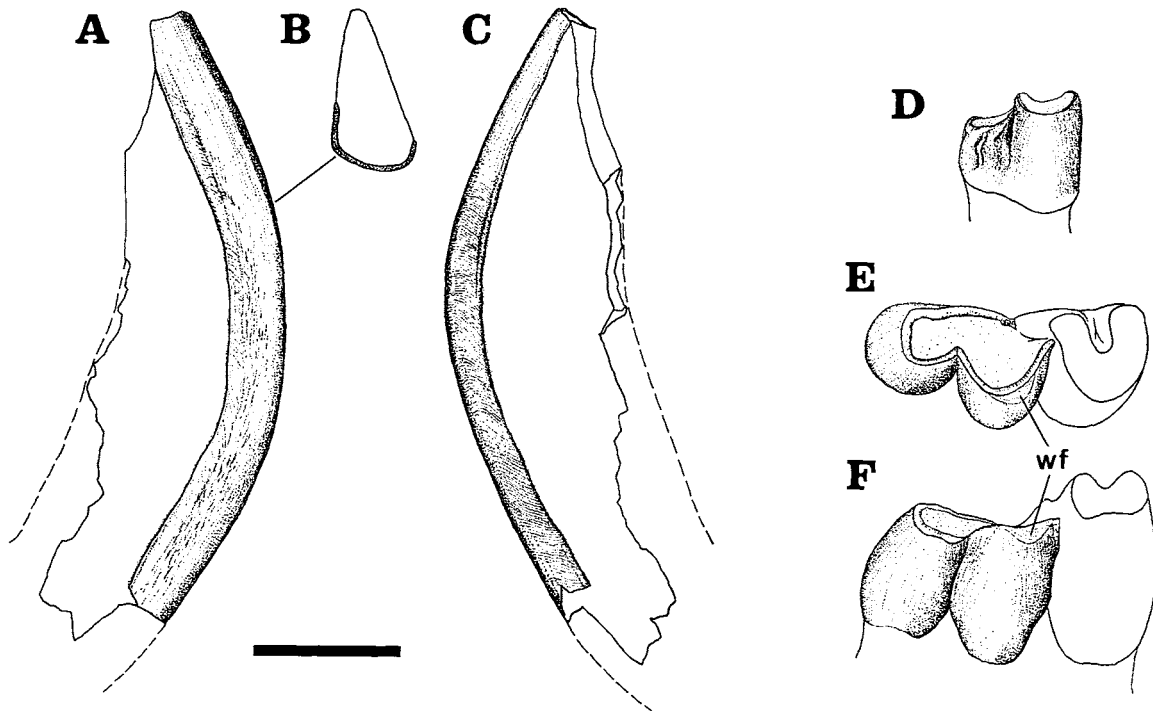


Figure 3. Sketches of reconstructed right I/2, P/4, and M/3 talonid of NSM-PV20121, cf. *Trogosus* sp. **A-C** : right I/2 ; A, distal view ; B, cross section ; C, mesial view. **D** : right P/4, buccal view. **E-F** : right M/3 talonid ; E, occlusal view ; F, buccal view. wf : a crescentic wear facet on the cristid obliqua. Scale bar equals 2 cm long.

Table 1. Measurements (in mm) of NSM-PV 20121, cf. *Trogosus* sp. Asterisks (*) indicate measurements of portions with damage.

Transverse width of right I/2	11.4
Anteroposterior length of right I/2	23.1
Transverse width of left I2/? (enamel portion)	13.3
Transverse width of right P/4 trigonid	15.5*
Transverse width of right M/3 talonid (second lobe)	16.2*
Transverse width of right M/3 third lobe	13.3

this specimen, but most of the crown portion is visible. Although the lingual portion of the tooth and the cristid obliqua are damaged, this tooth is identified as a bilobed hypsodont tooth ; the buccal wall of the trigonid is columnar and is U-shaped in horizontal section. It is difficult to accurately measure the talonid owing to poor preservation, but it is somewhat shorter in width and length than the trigonid portion, judging from the enamel remains. The buccal wall of the hypoconid considerably inclines toward the occlusal surface, and the posterior wall of the talonid is relatively flattened. A small, longitudinal swelling of enamel occurs on the buccal wall anterior to the hypoconid (Figure 3D) ; a similar structure is rarely seen in other trogosine specimens.

The tooth fragment with the buccal enamel wall (Figure 2G) is tentatively considered the trigonid of a right lower molar ; it apparently represents a rooted, hypsodont tooth, although its root and the lingual enamel wall are mostly

missing. The columnar buccal wall is slightly convex in vertical section at the base of the crown.

The talonid portion of a right M/3 (Figures 2H-J) is broken ; the second lobe was displaced posterobuccally relative to the third lobe (Figures 3E, F), and most of the root is also missing. The buccal enamel wall of the talonid is high and double-columnar, whereas the lingual enamel wall, which has a trace of the talonid notch, is low and almost flattened (Figures 2I, J). These enamel features of the M/3 talonid suggest that this tooth is hypsodont on the buccal side, in contrast to the enamel development on the lingual side, as in other trogosine molars. The buccal wall of the second lobe is swollen, V-shaped in horizontal section (Figures 2I, 3E) and is externally convex in vertical section. Although the cristid obliqua is cracked, a crescentic wear facet is present on the cristid obliqua near the occlusal surface (wf in Figures 3E, F) ; this wear facet on the cristid obliqua is also seen on other trogosine molars. The basin-shaped

third lobe is extremely elongated posteriorly, with a wear facet sloping to the buccal side, and the posterior wall of the third lobe is rounded in horizontal section.

Discussion

In spite of poor preservation, NSM-PV 20121 certainly belongs to the subfamily Trogosinae; fragments of rootless, elongated, gliriform teeth and the rooted hypsodont teeth are referable to the second incisors and lower cheek teeth of a trogosine tillodont, respectively. The possession of gliriform I2/2 and an elongated, basin-shaped third lobe of M/3 are diagnostic dental characters of Trogosinae (Gazin, 1953).

Schoch (1986) noted morphological similarities between the second incisors of trogosine tillodonts and the canines of stylinodontid taeniodonts, especially those of *Stylinodon* and *Ectoganus*. Thus, taxonomic assignment for such an isolated gliriform tooth has been confused in some previous studies (Schoch, 1986). However, the gliriform teeth described here are not as laterally compressed as in canines of stylinodontids; and as the right I/2 shows, the distal enamel surface is in the same plane as the posterior dentine (Figure 3B); these characters indicate that NSM-PV 20121 belongs to the Trogosinae. Moreover, lower molars of trogosines are readily distinguished from those of stylinodontid taeniodonts; in stylinodontid molars, trigonids and talonids are anteroposteriorly compressed (trigonid and talonid are no longer divided in lower molars of *Stylinodon*), plus the enamel layer distinctly extends into the alveolus on both buccal and lingual sides, the buccal crowns are not so convex in vertical section as in *Trogosus*, and the third lobe on M/3 is not elongated (Schoch, 1986; Chow *et al.*, 1996). Although the cheek teeth of NSM-PV 20121 are incompletely preserved, they show no features of stylinodontid molars.

In comparison with previously known trogosines, NSM-PV 20121 closely resembles species of *Trogosus* in morphology. The right I/2 is nearly equal in size to those of *Trogosus* species, but its enamel extension on the distal side is relatively wider than that of the holotypes of *Trogosus grangeri* (AMNH 17008) and *Tillodon fodiens* (YPM 11087). The fragmentary lower cheek teeth (Figures 2F-J) are relatively large compared to those of *Trogosus* species; they are similar in size to those of the largest specimen of *T. grangeri* (YPM 16449) examined by Robinson (1966). Moreover, the degree of hypsodonty and the convexity of the buccal walls on the lower molars further are similarities to *Trogosus*. Compared with the best-preserved lower molars of *Tillodon fodiens* (USNM 18164, hypotype), the molars of NSM-PV 20121 are more hypsodont, and their crowns are less tapering upward.

On the other hand, NSM-PV 20121 described here is apparently distinguishable from species of *Kuanchuanius*, *Higotherium*, and *Chungchienia*. All the fragmentary teeth are considerably larger than those of the holotype of *K. shantunensis* (IVPP V 2764), in which the I/2 possesses a longitudinal shallow groove on its labial surface and anteroposteriorly shortened enamel-free dentine; the unique I/2 features of *K. shantunensis* are not seen in either NSM-PV 20121 or other trogosine specimens (Chow, 1963a; Miyata and Tomida, 1998). Incisors of *Higotherium* have been

unknown to date, but NSM-PV 20121 apparently differs from *H. hypsodon* in having much less hypsodont lower molars and posteriorly elongated M/3 third lobe. Undoubtedly, NSM-PV 20121 differs from species of *Chungchienia*, in which all known teeth are far more highly specialized; the lower cheek teeth of *Chungchienia* are extremely hypsodont and rootless, with unilaterally distributed enamel layer (see figure 2 in Chow *et al.*, 1996). Therefore, NSM-PV 20121 is readily distinguishable from the Asian taxa mentioned above, and it may be referable to the North American genus *Trogosus*.

In addition to *K. shantunensis*, Chow (1963a) described two fragmentary but significant I/2 of trogosines from China: "Tillodontia, gen. indet. sp. 1" (IVPP V 2765) and "Tillodontia, gen. indet. sp. 2" (IVPP V 2766). IVPP V 2765 and IVPP V 2766 are recorded from the Heti Formation in Yuanchu Basin and the Lushi Formation in Lushi Basin, respectively (Li and Ting, 1983); both formations are placed within the Middle Eocene (Tong, 1989; Prothero, 1995). The latter specimen (IVPP V 2766) was subsequently referred to "? *Stylinodon* sp." by Chow *et al.* (1973), but later Schoch (1986, p. 121) reidentified the specimen as a fragmentary I/2 of a trogosine tillodont. The right I/2 of NSM-PV 20121 is slightly larger than IVPP V 2765 and is apparently smaller than IVPP V 2766 judging from the illustrations of Chow (1963a). However, except for the size differences, the morphology of these two I/2 from China is basically similar to the North American taxa also. These two Chinese specimens apparently cannot be referred to species of *Chungchienia* in size and morphology, and we have no evidence that IVPP V 2765 and/or IVPP V 2766 are identifiable as I/2 of *Higotherium*. Nevertheless, the two I/2 fragments described by Chow also suggest that other undescribed or uncharacterized trogosines inhabited Asia during the Middle Eocene. The record of NSM-PV 20121 suggests that a *Trogosus*-like tillodont inhabited East Asia together with an advanced form (*Higotherium hypsodon*) during the early Middle Eocene. In addition, this new material strongly indicates the closest affinity with North American trogosines among all known Asian material.

Acknowledgments

We thank Richard H. Tedford and John P. Alexander (AMNH), Mary A. Turner and Christine L. Chandler (YPM), Robert J. Emry and Robert W. Purdy (USNM), and Li Chuan-Kuei (IVPP) for permission and assistance to examine comparative specimens. Our special thanks are due to Everett H. Lindsay (University of Arizona) and Kenneth D. Rose (Johns Hopkins University) for reading the manuscript and making a number of helpful suggestions. Many helpful comments for this research were given by Yasuhide Iwasaki (Kumamoto University, Ph.D. supervisor of K. M.). We also would like to thank Shingo Mogi (Japan Petroleum Exploration Co., Ltd.) who provided information concerning the locality of the described specimen. This research was supported in part by a grant from Fujiwara Natural History Foundation, Tokyo, Japan.

References cited

- Baudry, M., 1992 : Les Tillodontes (Mammalia) de l'Éocène inférieur de France. *Bulletin, Muséum National d'Histoire Naturelle, Paris, section C, série 4*, 14, no. 2, p. 205-243, pls. 1-3.
- Chow, M., 1963a : Tillodont materials from Eocene of Shantung and Honan. *Vertebrata Palasiatica*, vol. 7, no. 2, p. 97-104, pl. 1. (in Chinese with English summary)
- Chow, M., 1963b : A xenarthran-like mammal from the Eocene of Honan. *Scientia Sinica*, vol. 12, no. 12, p. 1889-1893, pl. 1.
- Chow, M., Li, C. and Chang, Y., 1973 : Late Eocene mammalian faunas of Honan and Shansi with notes on some vertebrate fossils collected therefrom. *Vertebrata Palasiatica*, vol. 11, no. 2, p. 165-181. (in Chinese with English summary)
- Chow, M., Wang, J. and Meng, J., 1996 : A new species of *Chungchienia* (Tillodontia, Mammalia) from the Eocene of Lushi, China. *American Museum Novitates*, no. 3171, p. 1-10.
- Gazin, C.L., 1953 : The Tillodontia : an early Tertiary order of mammals. *Smithsonian Miscellaneous Collections*, vol. 121, no. 10, p. 1-110, pls. 1-16.
- Leidy, J., 1871 : Remarks on fossil vertebrates from Wyoming. *Proceedings of the Academy of Natural Sciences of Philadelphia*, vol. 23, no. 2, p. 228-229.
- Li, C. and Ting, S., 1983 : The Paleogene mammals of China. *Bulletin of Carnegie Museum of Natural History*, no. 21, p. 1-93.
- Lucas, S.G., 1993 : Pantodonts, tillodonts, uinatheres, and pyrotheres are not ungulates. In, Szalay, F.S., Novacek, M.J. and McKenna, M.C. eds., *Mammal phylogeny : placentals*, p. 182-194. Springer-Verlag, New York.
- Miyata, K. and Tomida, Y., 1998 : A new tillodont from the early Middle Eocene of Japan and its implication to the subfamily Trogosinae (Tillodontia : Mammalia). *Paleontological Research*, vol. 2, no. 1, p. 53-66.
- Nagao, T., 1926 : The Palaeogene stratigraphy of Kyushu. *Journal of Geography, Tokyo Geographical Society, Japan*, vol. 38, no. 445, p. 115-130. (In Japanese)
- Prothero, D.R., 1995 : Geochronology and magnetostratigraphy of Paleogene North American land mammal "ages" : an update. In, Berggren, W.A. et al. eds., *Geochronology, time scales and global stratigraphic correlation*, p. 305-315. SEPM, Special publication, no. 54, Tulsa.
- Robinson, P., 1966 : Fossil Mammalia of the Huerfano Formation, Eocene, of Colorado. *Peabody Museum of Natural History, Yale University, Bulletin*, no. 21, p. 1-95, pls. 1-10.
- Schoch, R.M., 1986 : Systematics, functional morphology and macroevolution of the extinct mammalian order Taeniodonta. *Peabody Museum of Natural History, Yale University, Bulletin*, no. 42, p. 1-307, pls. 1-65.
- Stucky, R.K. and Krishtalka, L., 1983 : Revision of the Wind River faunas, early Eocene of central Wyoming. Part 4. the Tillodontia. *Annals of Carnegie Museum*, vol. 52, article 17, p. 375-391.
- Ting, S. and Zheng, J., 1989 : The affinities of *Interogale* and *Anchilestes* and the origin of Tillodontia. *Vertebrata Palasiatica*, vol. 27, no. 2, p. 77-86, pl. 1. (in Chinese with English summary)
- Tong, Y., 1989 : A review of Middle and Late Eocene mammalian faunas from China. *Acta Palaeontologica Sinica*, vol. 28, no. 5, p. 663-682. (in Chinese with English summary)

Taxonomy and evolution of the genus *Ocinebrellus* (Gastropoda : Muricidae) in Japan

KAZUTAKA AMANO and GEERAT J. VERMEIJ

Department of Geoscience, Joetsu University of Education, Joetsu, Niigata Prefecture 943-8512, Japan

Department of Geology, University of California, Davis, California 95616, USA

Received 9 May 1998 ; Revised manuscript accepted 24 August 1998

Abstract. We have examined the genus- and species-level taxonomy and distribution of the ocenebrine muricid gastropod genus *Ocinebrellus* Jousseaume, 1880. The genus comprises two stocks. The *O. inornatus* stock includes *O. inornatus* (Recluz, 1851) and *O. lumarius* (Yokoyama, 1926). The *O. aduncus* stock comprises *O. aduncus* (Sowerby, 1834), *O. protoaduncus* (Hatai and Kotaka, 1959) and *O. ogasawarai* sp. nov. Since its first appearance during the middle Miocene, *Ocinebrellus* has been limited to the warm- and cool-temperate shallow seas of northeastern Asia.

Key words : Evolution, Gastropoda, Muricidae, *Ocinebrellus*, Taxonomy

Introduction

The genus *Ocinebrellus* is an endemic ocenebrine muricid group living in shallow warm- to cool-temperate seas in northeastern Asia (Figure 1). It comprises three living species, namely, *Ocinebrellus inornatus* (Recluz), *O. lumarius* (Yokoyama) and *O. aduncus* (Sowerby). Their larvae are non-planktotrophic in development (Amio, 1963).

Among these, *O. inornatus* is a well-known drilling predator of bivalves (Chew and Eisler, 1958) and is the only species in its genus to have been introduced to another part of the world. As reviewed by Carlton (1992), the earliest record of *O. inornatus* on the west coast of North America dates from 1924 in Puget Sound, Washington. Today, the species extends in the northeastern Pacific locally in bays from British Columbia to Morro Bay, California (Carlton, 1992).

Phenotypic variation is so great that the genus- and species-level taxonomy of *Ocinebrellus* has remained confused. This confusion has made it difficult to interpret the fossil record of the group. As a result, no comprehensive account of the living and fossil species of *Ocinebrellus* exists.

Ocinebrellus is one of a number of clades that originated and diversified during the Neogene in warm- to cool-temperate waters of the North Pacific. Whereas the genus has apparently remained confined to the northwestern Pacific, other ocenebrine genera such as *Nucella* have spread throughout the northern hemisphere (Amano *et al.*, 1993; Collins *et al.*, 1996). It would be instructive to know why the same ocenebrines with a similar non-planktotrophic larval stage have achieved such different geographical distributions.

In this paper, we taxonomically revise the species of

Ocinebrellus, and outline the evolutionary and biogeographical history of the group in comparison to other Neogene warm- to cool-temperate clades.

Materials and Methods

As part of this study, some fossil specimens were collected by hand from the following formations: Pliocene, Tentokuji Formation, Akita Prefecture, Locality 3 of Amano *et al.* (1996); Pliocene, Kuwae Formation, Niigata Prefecture, Locality 2 of Amano (1997a); early Pleistocene, Setana Formation, Hokkaido, Locality 2 of Amano (1997b); early Pleistocene, Omma Formation, Ishikawa Prefecture, Locality 5 of Amano *et al.* (1996). These specimens are housed in the Joetsu University of Education (JUE).

In addition, we have examined many fossil and Recent specimens, including types, at the following institutions: American Museum of Natural History (AMNH), Academy of Natural Sciences of Philadelphia (ANSP), Tohoku University (IGPS), Saito Ho-on Kai Museum of Natural History (SHM), Museum of University of Tokyo (UMUT) and National Science Museum (NSMT). Konstantin A. Lutaenko (Institute of Marine Biology, Russian Academy of Sciences) and Anton Oleinik (Purdue University) kindly provided Recent specimens from Korea and Russia.

We have measured or evaluated the following characters: shell height, spire height, length of siphonal canal, number and shape of axial ribs or varices on the last whorl, number of spiral cords on the last whorl, number of denticles on the inner (adaxial) side of outer lip, presence of a labral tooth on the abapical sector of the outer lip, condition (open or sealed) of the siphonal canal (see Figure 2).

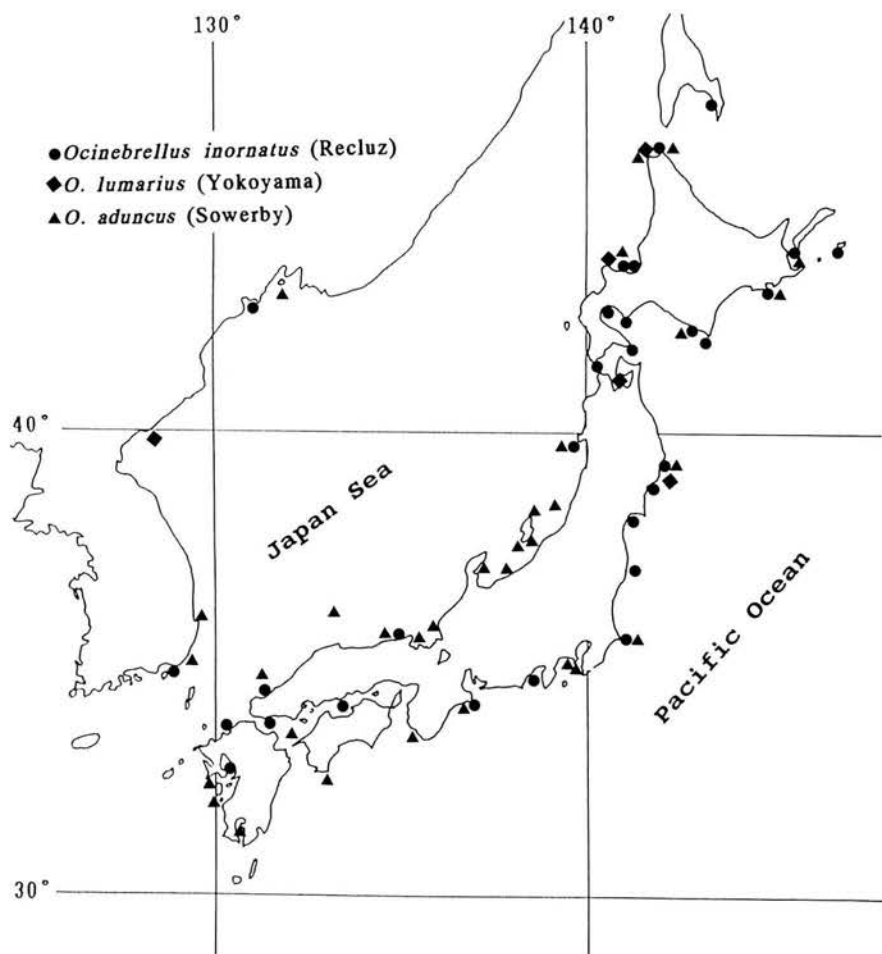


Figure 1. Distribution of the Recent *Ocinebrellus* (mainly after the collection stored in National Science Museum, Tokyo as well as our collections).

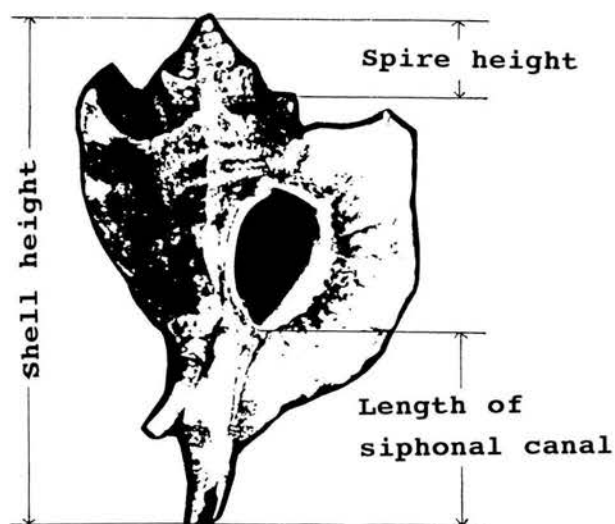


Figure 2. Measurement position.

Systematics

Family Muricidae Rafinesque, 1815
Subfamily Ocenebrinae Cossmann, 1903

Remarks.—The muricid subfamily Ocenebrinae comprises a large number of genera, which are mainly known from the Oligocene to the Recent. One group, which includes *Ocinebrellus*, is characterized by a ventrally (adaperturally) sealed siphonal canal in the adult shell, and by the predominance of axial over spiral sculpture on postnuclear whorls. Vermeij (1998, *in press*) has provided a key to all ocenebrine genera with a sealed siphonal canal.

Genus *Ocinebrellus* Jousseaume, 1880

Type species.—*Murex eurypteron* Reeve, 1845 by original designation, = *Murex aduncus* Sowerby, 1834.

Remarks.—Jousseaume (1880, p. 335) introduced *Ocinebrellus* as a new genus in a list of Purpuridae (= Muricidae). In a later paper (Jousseaume, 1882, p. 331), he provided a

brief diagnosis for the genus, as well as a list of included species. Jousseume (1882) characterized *Ocinebrellus* as having four wing-like varices extending abapically to the middle of the sealed canal. Besides the type species, he included *Murex aduncus* Sowerby, *M. falcatus* Sowerby, and *M. acanthophorous* (A. Adams) in the genus. All these taxa are here considered synonymous of a single species for which the oldest available name is *Murex aduncus* Sowerby, 1834 (see also Fulton, 1917). Curiously, Jousseume (1882) assigned *Murex inornatus* Recluz here included in the genus *Ocinebrellus* and *M. taienwhanensis* Crosse (a synonym of *M. inornatus*) to *Crassilabrum* Jousseume, 1880, a genus otherwise endemic to southwestern South America. Based on our examination of all species in the genus, we offer the following revised diagnosis of *Ocinebrellus*.

Revised diagnosis.—Shell of small to medium size, maximum height approximately 60 mm; protoconch paucispiral, consistent with nonplanktotrophic development; teleoconch whorls strongly shouldered; four to five in number; last whorl basally constricted, large. Axial sculpture of last whorl consisting of three to twelve varices or axial ribs, which are strongly angulated and often spinose at the periphery and which may be adaperturally reflected; spiral sculpture of last whorl usually consisting of four principal cords which form waves or spines on the varices or ribs, and a variable number of intercalated threads. Outer lip is planar, often with five to nine small denticles on its inner (adaxial) side; small labral tooth occasionally present on edge of outer lip below fourth principal spiral cord at upper end of siphonal canal; adapical end of inner lip without parietal tooth or rib; siphonal canal usually ventrally (adaperturally) sealed.

Variability.—Several characters are variably expressed in *Ocinebrellus*. Axial sculpture may consist of simple ribs of uniform size, or it may be differentiated into large varices extending onto the upper end of the siphonal canal and shorter, long ribs. If varices are present, they typically occur on late growth stages of larger shells. Varices are more typical of the *O. aduncus* group than of the *O. inornatus* group (see below). The outer lip of *Ocinebrellus* is characterized abapically by a very short labral tooth in some individuals, especially in larger specimens of *O. aduncus* and *O. inornatus*; but in other specimens there is no trace of the tooth. The adapical sector of the outer lip above the shoulder forms a distinct shallow sinus in *O. inornatus*, but not in *O. aduncus*. Denticles may be present in some individuals of *Ocinebrellus*, but their degree of expression varies considerably, and in many specimens they are absent. Finally, although the siphonal canal is sealed in most individuals, it occasionally remains ventrally open.

Comparison.—*Ocinebrellus* is most similar in shell characters to the genera *Ceratostoma* Herrmannsen, 1846; *Pteropurpura* Jousseume, 1880; *Muregina* Vermeij, 1998 *in press*; and *Pterorytis* Conrad, 1863 (for additional discussion see Vermeij, 1998 *in press*).

Ceratostoma usually has three (rarely four) varices on the last whorl. These are typically blade-like rather than recurved, and lack a spine-like projection at the shoulder as is typical of *Ocinebrellus*. Adjacent varices in *Ceratostoma* are separated by a short axial node. The labral tooth of

Ceratostoma is almost always well developed, and is usually spine-like.

Pteropurpura, like *Ceratostoma*, has three varices on each adult whorl, adjacent ones being separated by a short intervarical node. The varices are usually blade-like, but may be strongly abaperturally reflected, as in *P. festiva* (Hinds). The varices in *Pteropurpura* are not usually spinose at the shoulder or periphery. In *Poropteron* Jousseume, 1880 (South Africa) and *Calcitrapessa* Berry, 1959 (Baja California, Mexico), two genera closely similar to *Pteropurpura*, the varices are adapically extended as adaperturally and adapically pointing spines respectively. There is no labral tooth in *Pteropurpura*, *Poropteron* and *Calcitrapessa*.

The tropical eastern Pacific genus *Muregina* resembles *Ocinebrellus* in having four principal cords on the last whorl and in having a labral tooth. It differs from *Ocinebrellus* by having all axial elements of the same size, and by usually lacking a peripheral angulation on the axial sculpture.

Pterorytis Conrad, 1863 differs from *Ocinebrellus* in having only three instead of four principal cords on the last whorl, of which the upper one forms a strong keel connecting the well-developed, often abaperturally reflected varices. In *Pterorytis*, the varices are not angulated at the periphery as they are in *Ocinebrellus*. A long, spine-like labral tooth is usually present in *Pterorytis* (Vermeij and Vokes, 1997).

Finally, the genus *Ocenebra* Gray, 1847, as restricted by Vermeij and Vokes (1997), is an eastern Atlantic group characterized by eight or more strong principal spiral cords and by the absence of a labral tooth. Axial sculpture of *Ocenebra* is variably developed, sometimes consisting of three varices on the last whorl separated by a narrower intervarical rib, and sometimes consisting of axial ribs of similar size.

***Ocinebrellus inornatus* (Recluz, 1851)**

Figures 3—4, 5, 7-10, 15

Murex inornatus Recluz, 1851, p. 207-209, pl. 6, fig. 8; Sowerby, 1879, fig. 234.

Murex crassus A. Adams, 1853, p. 269.

Murex japonicus Dunker, 1860, p. 4, pl. 1, fig. 14.

Murex taienwhanensis Crosse, 1862, p. 56-57, pl. 1, fig. 9.

Murex endermonis Smith, 1875, p. 420; Sowerby, 1879, fig. 213.

Murex (Ocinebra) inornatus Recluz, Tryon, 1880, p. 126-127, pl. 37, fig. 444.

Murex (Ocinebra) japonicus Dunker. Tryon, 1880, p. 126, pl. 37, figs. 445-448.

Murex (Ocinebra) endermonis Smith. Tryon, 1880, p. 128, pl. 38, fig. 454.

Murex polygonulus Lamarck. Yokoyama, 1931, p. 200-201, pl. 12, figs. 3a, b.

Tritonalia inornata endermonis (Smith). Kinoshita and Isahaya, 1934, pl. 5, fig. 36.

Tritonalia inornata (Recluz). Kuroda, 1931, p. 86, pl. 10, fig. 81; Nomura and Hatai, 1936, p. 140-141, pl. 17, fig. 5; Egorov, 1992, p. 64, fig. 1-E, (*non* figs. 1C, D, F).

Ocenebra japonica endermonis (Smith). Kira, 1959, p. 60, pl. 24, fig. 1.

Ocenebra japonica (Dunker). Kira, 1959, p. 60, pl. 24, fig. 7; Habe, 1958, p. 19-20, pl. 3, figs. 8, 11; Habe, 1961, pl. 4, fig.

10; Habe and Ito, 1965, p. 38, pl. 11, figs. 6, 7; Iwai and Shiobara, 1968, pl. 3, figs. 11a, b; Yoo, 1976, p. 72, pl. 12, figs. 8–10; Akamatsu, 1980, p. 6–7, pl. 1, fig. 10; Akamatsu, 1984, p. 9, pl. 1, fig. 19; Ogasawara *et al.*, 1986, pl. 68, fig. 9; Baba, 1990, p. 154–155, pl. 9, fig. 9; Noda *et al.*, 1993, p. 178, pl. 26, figs. 7a, b, pl. 27, figs. 1a–4b; Amano and Sato, 1995, figs. 5, 6.

Ocenebra endermonis (Smith). Habe and Ito, 1965, p. 39, pl. 11, fig. 8; Iwai and Shiobara, 1968, pl. 3, figs. 12a, b; Ogasawara *et al.*, 1986, pl. 69, fig. 21.

Ceratostoma cf. aduncum (Sowerby). Iwai and Shiobara, 1968, pl. 3, fig. 10.

Ocenebra cf. japonica (Dunker). Iwasaki, 1970, p. 419–420, pl. 5, figs. 10, 11.

Ceratostoma inornatum (Recluz). Radwin and D'Attilio, 1976, p. 113, pl. 18, figs. 10–12.

Tritonalia japonica (Dunker). Golikov and Kusakin, 1978, p. 200–201, fig. 138.

Ceratostoma (Ocenebra) japonica (Dunker). Tsuchida, 1991, p. 3, pl. 1, figs. 7, 8.

Type Locality.—Korea (exact locality is unknown).

Material.—Twenty-eight Recent and fossil specimens.

Remarks.—The shell of *Ocenebrellus inornatus* is medium-sized, maximum height 47.9 mm, fusiform, solid, and with low spire (spire height : shell height = 0.21–0.29). Protoconch whorls are small and smooth. There are five teleoconch whorls. The last whorl is sculptured with four to twelve (commonly eight to nine) axial ribs or varices, which are often slightly adaperturally reflected and which are angulated at periphery or shoulder. Spiral sculpture on the last whorl consists of four to seven cords with a few intercalated threads. Above the first cords, there is a narrow subsutural area, corresponding on the outer lip with shallow adapical sinus. The inner (adaxial) side of outer lip usually bears five small denticles. A short labral tooth occasionally present below the fourth principal cord. Siphonal canal short (canal length : shell height = 0.22–0.31) and may occasionally be open.

Most Japanese authors used the specific name *Ocenebra japonica* (Dunker) for a species known in Japanese by the name ouu-youraku, which lacks a labral tooth; and the name *O. endermonis* for the so-called ezo-youraku, characterized by the presence of a labral tooth. We cannot discern any consistent differences between the *O. japonica* and *O. endermonis* phenotypes other than the presence or absence of the labral tooth. Specimens with and without a labral tooth co-occur at many sites, including Cape Arutori

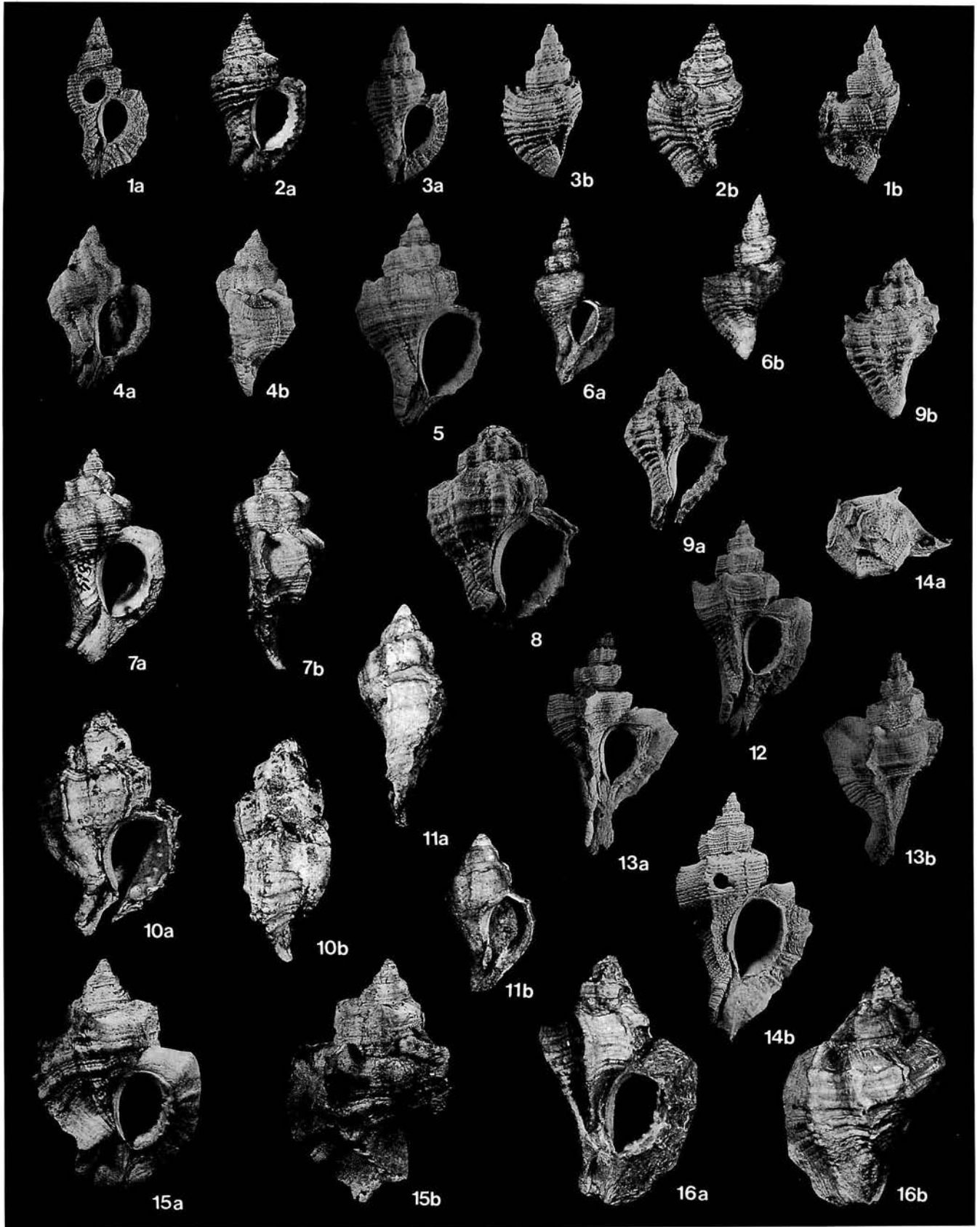
(Hokkaido), Muroran (Hokkaido; type locality for *Murex endermonis*) and Posiet Bay (Primorie). The same phenotypes can be observed in the artificially introduced population in Hood Canal (Washington) (AMNH no. 123802) and Bellingham Bay (Washington) (AMNH no. 140079). Therefore, as already pointed out by Nomura and Hatai (1935a), the *O. japonica* and *O. endermonis* phenotypes belong to the same species, for which the oldest name is *Murex inornatus*.

Radwin and D'Attilio (1976) placed *Ocenebra monoptera* Pilsbry, 1904, in synonymy with *Ocenebrellus inornatus*. The description and illustration of this species (Pilsbry, 1904, p. 17, plate 5, figs. 32, 32a) and our examination of the type material (ANSP 86123) show that *O. monoptera* is not conspecific with *Ocenebrellus inornatus* and that it is, in fact, not even a member of the genus *Ocenebrellus*. This small species (height 12 mm) is characterized by a single very broad, blade-like terminal varix, a strongly erect outer lip whose edge extends distinctly beyond the adapertural face of the varix, and ten to eleven low, sharply rounded axial ribs that on the last whorl extend neither to the suture nor to the strongly constricted base. The subsutural area is smooth. From the rounded shoulder to the tip of the ventrally sealed canal, there are about eleven fine primary spiral cords, of which three are visible on the penultimate whorl. The species appears to belong to the Ocenebrinae, but we do not know to which genus it should be assigned.

Comparisons.—*Ocenebrellus inornatus* is most similar to *O. lumarius* (Yokoyama) in having a short siphonal canal, a similar number of axial ribs on the last whorl (six to eleven), and five or six denticles on the inner side of the outer lip. *O. inornatus* differs from *O. lumarius* by being larger, having a lower spire, and by occasionally having a labral tooth.

Distribution.—Miocene to Recent. Miocene: Kubota Formation, Fukushima Prefecture. Pliocene: Kume Formation, Ibaraki Prefecture; Nadachi Formation, Niigata Prefecture; Takafu and Joshita Formations, Nagano Prefecture. Pleistocene: Shimonoporo and Zaimokuzawa Formations, Hokkaido; Noheji Formation, Amomori Prefecture; Shibikawa Formation, Akita Prefecture; Kiwada and Mandano Formations in Chiba Prefecture. Recent: Busse Lagoon, Sakhalin; off Kunashiri and Shikotan, Kurile Islands; Hokkaido to Kyushu; Korea; Posiet Bay, Primorie; Bohai Bay, China; British Columbia to Morro Bay (artificially introduced).

Figure 3. 1–3, 6: *Ocenebrellus lumarius* (Yokoyama). 1a, b; $\times 1.2$, JUE no. 15640, Setana Formation. 2a, b; $\times 1.2$, NSMT-Mo no. 49546, Asamushi (Recent). 3a, b; $\times 1.5$, UMUT CM no. 23118, Holotype, Sawane Formation. 6a, b; $\times 1.2$, SHM no. 6146, Daishaka Formation. 4–5, 7–10, 15: *Ocenebrellus inornatus* (Recluz). 4a, b; $\times 1$, JUE no. 15641, Cape Erimo (Recent). 5; $\times 1$, JUE no. 15642, Akkeshi (Recent). 7a, b; $\times 1$, IGPS no. 94814, Koje Do Is., Korea (Recent). 8; $\times 1$, UMUT CM no. 9358, "*Ocenebra cf. japonica* (Dunker)" by Iwasaki (1970), Kubota Formation. 9a, b; $\times 1.2$, UMUT CM no. 25896, "*Murex polygonulus Lamarck*" by Yokoyama (1931), Kubota Formation. 10a, b; $\times 1$, SHM no. 2672, "*Tritonalia inornata* (Recluz)" by Nomura and Hatai (1936), Kubota Formation. 15a, b; $\times 1$, NSMT-Mo no. 49538, Toba (Recent). 11a, b: "*Ocenebra katayamai* Matsubara; 11a, $\times 1.5$, 11b, $\times 1$, IGPS no. 102629, Holotype, Yotsuyaku Formation. 12–14: *Ocenebrellus ogasawarai* sp. nov. 12; $\times 1.2$, JUE no. 15643, Kuwae Formation. 13a, b; $\times 1$, JUE no. 15635, Holotype, Omma Formation. 14a, b; $\times 1$, UMUT CM no. 12783, "*Tritonalia (Ocenebrellus) adunca* (Sowerby) subsp. by Otuka (1936), Sasaoka Formation. 16a, b: *Ocenebrellus protoaduncus* (Hatai and Kotaka), $\times 1$, IGPS no. 77798, Holotype, Ginza Formation.



Ocenebrellus lumarius (Yokoyama, 1926)

Figures 3—1-3, 6

- Ocenebra lumaria* Yokoyama, 1926, p. 270, pl. 32, fig. 21.
Tritonalia inornata lumaria (Yokoyama). Kinoshita and Isahaya, 1934, p. 8, pl. 5, fig. 37.
Tritonalia lumaria (Yokoyama). Nomura and Hatai, 1935b, p. 124-125, pl. 13, figs. 1a, b.
Ocenebra lumaria (Yokoyama). Habe and Ito, 1965, p. 38, pl. 11, fig. 2.
Ceratostoma sp., Iwai, 1965, pl. 20, fig. 15.
Ceratostoma (Ocenebra) japonicum (Dunker). Matsuura, 1977, pl. 1, fig. 33.
Ceratostoma (Ocenebra) lumaria Yokoyama. Tsuchida, 1991, p. 3, pl. 1, figs. 5, 6.

Type locality.—Sawane in Sado Island of Niigata Prefecture.

Type specimen.—UMUT CM no. 23118 (Holotype).

Material.—Thirty-three Recent and fossil specimens.

Remarks and comparisons.—This is the smallest species of *Ocenebrellus*, with a maximum shell height of 23.1 mm. The shell is fusiform, slender, and high-spired, with a spire height : shell height ratio of 0.27 to 0.33. Two small, smooth protoconch whorls are followed by six teleoconch whorls. The body whorl is sculptured by six to eleven (usually six to eight) axial ribs or varices, which are pointed at the periphery. These are crossed by twelve to twenty spiral cords. The terminal varix is extended to the most basal portion of the last whorl. A narrow subsutural area above the shoulder is sculptured by one spiral cord. The outer lip usually has five to six small denticles on its inner side; a labral tooth is absent. The siphonal canal is short (canal length : shell height = 0.16 to 0.26) and usually sealed, but is occasionally open.

Kinoshita and Isahaya (1934) considered *O. lumarius* a subspecies of *O. inornatus*, whereas Radwin and D'Attilio (1976) regarded the two taxa as synonyms. Because *O. lumarius* differs consistently from *O. inornatus* and both species have been recorded from Otuchi Bay in Iwate Prefecture (Tsuchida, 1991), we regard the two taxa as separate, distinct species. *O. lumarius* is smaller than *O. inornatus* with the same number of teleoconch whorls. Moreover, *O. lumarius* has a higher spire and more numerous spiral cords (twelve to twenty instead of four to seven) on the last whorl. Habe and Ito (1965) pointed out that *O. lumarius* resembles young individuals of *O. inornatus*. It is therefore probable that *O. lumarius* is phylogenetically derived from the larger *O. inornatus*.

Distribution.—Pleistocene to Recent. Pleistocene : Sawane Formation, Niigata Prefecture; Setana Formation, Hokkaido; Daishaka Formation, Aomori Prefecture; Uji

Shell-bed, Ishikawa Prefecture. Recent : Wakkanai, Oshoro and Takashima, Hokkaido; Asamushi, Aomori Prefecture; Otsuchi Bay, Iwate Prefecture; Shinpo, North Korea.

Ocenebrellus protoaduncus (Hatai and Kotaka, 1959)

Figures 3—16a, b

- Ocenebra adunca protoadunca* Hatai and Kotaka, 1959, p. 10, figs. 1, 3.

Type locality.—Upstream of Okama-zawa, Obanzawa City, Yamagata Prefecture.

Type specimen.—IGPS no. 77798 (Monotype).

Remarks and comparison.—This species is known from a single specimen, characterized by seven varices which are less spinose at the periphery than in most *Ocenebrellus aduncus*. There are four strong spiral cords on the last whorl, and seven denticles on the inner side of the outer lip. The siphonal canal is sealed. A labral tooth is absent. The varices are neither pointed nor reflected, but instead are blade-like, as in *Ceratostoma*. The four cords are stronger than those in *O. aduncus*.

Measurements (in mm).—

Specimen	Height	Spire height	Canal length
IGPS no. 77798 (Holotype)	44.6+	10.1	10.3+

Distribution.—Miocene Ginzan Formation in Yamagata Prefecture.

Ocenebrellus ogasawarai sp. nov.

Figures 3—12-14; 4—1, 4-6, 9, 13

- Tritonalia (Ocenebrellus) adunca* (Sowerby) subsp. Otuka, 1936, p. 733-734, pl. 42, figs. 15a, b (*non* figs. 9, 13).
Ceratostoma (Ocenebra) japonica (Dunker). Kaseno and Matsuura, 1965, pl. 3, figs. 6-8; Matsuura, 1985, pl. 38, fig. 11.
Ocenebra aduncum (Sowerby). Ogasawara, 1977, p. 134-135, pl. 19, figs. 8, 11-13, 15, 17.
Ocenebra japonica (Dunker). Ogasawara *et al.*, 1986, pl. 23, fig. 10.

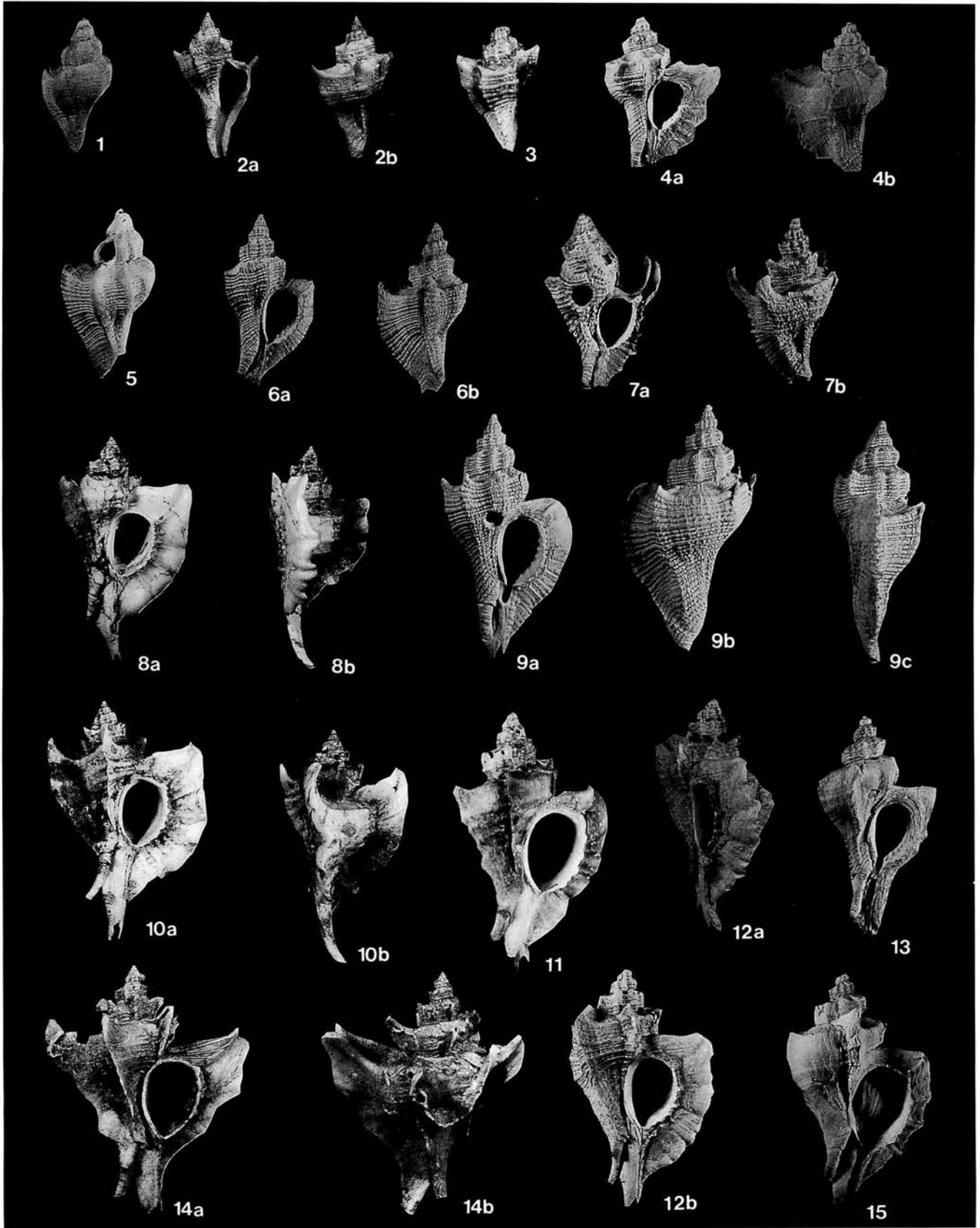
Type Locality.—Bank of Sai River, early Pleistocene Omma Formation.

Type Specimens.—JUE no. 15635 (Holotype), 15636, 15637, 15638 (Paratypes).

Material.—Thirteen fossil specimens.

Diagnosis.—Medium-sized ocenebrine shell characterized by numerous spiral cords (eighteen to forty-four on last whorl), three to ten axial ribs or varices on body whorl,

Figure 4. 1, 4-6, 9, 13 : *Ocenebrellus ogasawarai* sp. nov. 1; ×1.2, JUE no. 15644, Tentokuji Formation. 4a, b; ×1, JUE no. 15639-1, Omma Formation. 5; ×1.2, JUE no. 15639-2, Omma Formation. 6a, b; ×1.25, JUE no. 15637, Paratype, Omma Formation. 9a-c; ×1.5, JUE no. 15636, Paratype, Omma Formation. 13; ×1.5, JUE no. 15638, Paratype, Omma Formation. 2, 3, 7, 8, 10-12, 14, 15 : *Ocenebrellus aduncus* (Sowerby). 2a, b, 8a, b, 10a, b; ×1, NSMT-Mo no. 60254, Oshoro (Recent). 3; ×1, SHM no. 2192, Tatsunokuchi Formation. 7a, b; ×1.5, UMUT CM no. 12784a, Semata Formation. 11; ×1, JUE no. 15645, Pohang, Korea (Recent). 12a, b; ×1, JUE no. 15646, Peter the Great Bay, Russia (Recent). 14a, b; ×1, NSMT-Mo no. 46277, "*Murex eurypteron* Reeve" type, Tosa (Recent). 15; ×1, JUE no. 15647, off Cape Erimo (Recent).



denticulated inner side of outer lip and long sealed siphonal canal.

Description.—Shell of medium size, fusiform, with a low spire; protoconch of two smooth whorls; teleoconch of five whorls. Axial sculpture consisting of six to seven ribs or varices on the penultimate whorl, and three to ten (usually six to seven) ribs or varices on the body whorl; axial elements pointed at periphery; spiral sculpture consisting of two to sixteen cords on the penultimate whorl, and eighteen to forty-four cords on the body whorl; cords mostly of equal size except for a strong keel just above periphery. Suture impressed, distinct; flattened subsutural area above keel ornamented with three spiral cords. Aperture ovate, rather large; inner side of outer lip with five to nine (commonly seven) denticles; labral tooth absent; siphonal canal long, sealed.

Remarks and comparisons.—The new species *Ocinebrellus ogasawarai* is restricted to the Pliocene and early Pleistocene of the Japan Sea borderland. As indicated in the synonymy, *Ocinebrellus ogasawarai* was previously confused with *O. aduncus* (Ogasawara, 1977) and *O. inornatus* (as *O. japonica*) (Kaseno and Matsuura, 1965; Matsuura, 1985; Ogasawara *et al.*, 1986). Otuka (1936) identified it as an unnamed subspecies of *Ocinebrellus aduncus*.

Ocinebrellus ogasawarai resembles *O. aduncus* (Sowerby) in its low spire (spire height : shell height = 0.20 to 0.30), long siphonal canal (canal length : shell height = 0.33 to 0.36), and similar number of axial ribs (three to ten on the body whorl). The presence of denticles on the inner side of the outer lip distinguishes *O. ogasawarai* from *O. aduncus*. A few Recent specimens of *O. aduncus* from off Cape Erimo (Hokkaido) and Peter the Great Bay (Primorie) occasionally have very weak denticles. The new species differs from *O. aduncus* in addition by having more numerous spiral cords on the last whorl (eighteen to forty-four instead of one to twenty), by having the axial ribs usually not reflected, and in the absence of a labral tooth.

O. protoaduncus resembles the new species in having a similar number of axial ribs and in possessing denticles on the inner side of the outer lip, but *O. protoaduncus* has fewer cords and does not have the pointed axial varices.

Measurements (in mm).—

Specimens	Height	Spire height	Canal length
JUE no. 15635 (Holotype)	38.7+	9.7	12.6
JUE no. 15636 (Paratype)	29.4	8.7	10.4
JUE no. 15637 (Paratype)	25.8	6.3	6.4
JUE no. 15638 (Paratype)	33.1	7.1	11.7

Distribution.—Pliocene to early Pleistocene. Pliocene: Tentokuji and Sasaoka Formations, Akita Prefecture; Kuwae Formation, Niigata Prefecture; Zukawa Formation, Toyama Prefecture. Early Pleistocene: Omma Formation, Ishikawa Prefecture.

Etymology.—This species is named after Prof. Kenshiro Ogasawara of the University of Tsukuba, who studied the Omma fauna in detail and suggested that the Omma population possesses a wide range of variation.

Ocinebrellus aduncus (Sowerby, 1834)

Figures 4—2, 3, 7, 8, 10–12, 14, 15

- Murex aduncus* Sowerby, 1834, pl. 62, fig. 35; Sowerby, 1879, p. 45, fig. 216.
Murex falcatus Sowerby, 1834, pl. 62, fig. 31; Sowerby, 1979, p. 44–45, fig. 149; Tokunaga, 1906, p. 4, pl. 1, fig. 1.
Murex eurypteron Reeve, 1845, figs. 176a, b; Sowerby, 1879, p. 25, fig. 106.
Murex speciosus A. Adams, 1855, p. 121.
Murex expansus Sowerby, 1859, p. 428, fig. 5.
Phyllonotus acanthophorous A. Adams, 1862, p. 372.
Murex (Ocinebra) falcatus Sowerby. Tryon, 1880, p. 127, pl. 38, figs. 457–459.
Ocinebra falcata (Sowerby). Yokoyama, 1922, p. 65, pl. 3, fig. 4.
Ocinebra spectata Yokoyama, 1922, p. 65–66, pl. 3, fig. 5.
Tritonalia (Ocinebrellus) adunca (Sowerby). Kinoshita and Isahaya, 1934, p. 8, pl. 5, fig. 39.
Tritonalia (Ocinebrellus) adunca (Sowerby) subsp. Otuka, 1936, pl. 42, figs. 9a, b, 13, 14 (*non* fig. 15).
Tritonalia adunca (Sowerby). Nomura, 1938, p. 269, pl. 34, fig. 19; Kanehara, 1942, pl. 3, figs. 8a–b.
Ocenebra (Ocinebrellus) adunca (Sowerby). Habe, 1958, p. 19, pl. 3, fig. 13, pl. 4, fig. 13; Kira, 1959, p. 60–61, pl. 24, fig. 16.
Ocenebra eurypteron (Adams and Reeve). Kira, 1959, p. 61, pl. 24, fig. 16.
Ceratostoma (Ocinebra) aduncum (Sowerby). Hatai *et al.*, 1961, pl. 3, fig. 6; Tsuchida, 1991, p. 3, pl. 1, figs. 9, 10.
Ocenebra adunca (Sowerby). Habe and Ito, 1965, p. 38, pl. 11, figs. 3, 4; Baba, 1990, p. 154, pl. 9, figs. 8a–b.
Ocinebrellus aduncus (Sowerby). Hall, 1959, p. 432–433, pl. 2, figs. 1–3; Kuroda *et al.*, 1971, p. 147–148, pl. 40, figs. 3–5; Ito *et al.*, 1986, pl. 10, fig. 4; Ito, 1989, pl. 6, fig. 2.
Ocenebrellus falcatus (Sowerby). Yoo, 1976, p. 71, pl. 12, fig. 5.
Ocenebrellus adunca (Sowerby). Yoo, 1976, p. 73, pl. 13, figs. 6, 7.
Pteropurpura adunca (Sowerby). Radwin and D'Attilio, 1976, p. 129, pl. 22, fig. 10.
? *Ocenebra japonica* (Dunker). Nemoto and O'Hara, 1979, pl. 1, fig. 13.
Ceratostoma aduncum (Sowerby). Ogasawara *et al.*, 1986, pl. 68, figs. 7, 12, 16.
Ocinebrellus falcatus eurypteron (Adams and Reeve). Ito *et al.*, 1986, pl. 10, fig. 3.
? *Ocenebrellus* sp., Takahashi, 1986, pl. 14, figs. 15a–b.

Type Locality.—Japan (exact locality is unknown).

Material.—Seventy-five Recent and fossil specimens.

Remarks.—This species is characterized by a large shell (maximum shell height 58.9 mm) with a low spire (spire height : shell height = 0.18 to 0.26) and a long siphonal canal (canal length : shell height = 0.28 to 0.42). The protoconch is small and smooth, and there are six teleoconch whorls. The last whorl is sculptured with three to seven (commonly five) varices, which are usually pointed or spinose at the periphery, and which are frequently adaperturally reflected. Spiral sculpture on the last whorl is highly variable, consisting of one to twenty cords. The flat subsutural area above the first primary cords is smooth. The inner side of the outer lip is usually smooth, but rarely bears very weak denticles. Previous authors have not mentioned a labral tooth, but several Recent populations from Hokkaido and Kyushu have

a very short labral tooth below the basalmost of the four primary cords.

Murex falcatus has sometimes been distinguished from *M. aduncus* by having the spiral sculpture of the last whorl reduced to a single shoulder keel. *Murex eurypteron* was differentiated from *M. aduncus* by having strongly projecting varices. Radwin and D'Attilio (1976) pointed out, however, that the number and expression of spiral and axial sculptural elements vary greatly both within and between populations. The *M. eurypteron* phenotype may be common in deep water (Kira, 1959), but we see no reason to separate either the *M. eurypteron* or the *M. falcatus* phenotypes from *Ocenebrellus aduncus*.

Comparison.—*Ocenebrellus aduncus* closely resembles *O. ogasawarai* sp. nov. (see above), but differs from that fossil species by having fewer spiral cords, usually lacking denticles on the inner side of the outer lip, and occasionally having a short labral tooth. *Ocenebrellus aduncus* differs from *O. inornatus* by its longer siphonal canal, fewer and more distinct varices, usual absence of denticles on the inner side of the outer lip, and absence of a distinct adapical sinus on the outer lip.

Distribution.—Pliocene to Recent. Pliocene: Tatsunokuchi Formation, Miyagi Prefecture; Tomioka Formation, Fukushima Prefecture; ?Kume Formation, Ibaraki Prefecture. Pleistocene: Hamada Formation, Aomori Prefecture; Shibikawa Formation, Akita Prefecture; Higashi-higasa, Nagahama, Mandano, Semata, Narita Formations, Chiba Prefecture; Koshiba Formation, Kanagawa Prefecture. Recent: Hokkaido to Kyushu, Korea, Peter the Great Bay (Primorie), Bohai Bay (China).

Related or Doubtful Species

In addition to the above species of the genus *Ocenebrellus*, there are several Miocene species whose relationship with *Ocenebrellus* remain uncertain. We treat one of these species as "*Ocenebra*" *katayamai* from the early Miocene Yotsuyaku Formation, in detail, and redescribe this form.

In addition, eight species from the Miocene of Kamchatka described by Sinelnikova in Gladenkov and Sinelnikova (1990) are based on poorly preserved material. We treat these eight species collectively, and are unable to resolve their status.

"*Ocenebra*" *katayamai* Matsubara, 1996

Figures 3–11a, b

Type locality.—Upper reaches of the Nesori River about 3 km east of Nosokei, Ichinohe Town, Ninohe County, Iwate Prefecture.

Type specimens.—IGPS no. 102629 (Holotype), 102630, 102631 (Paratypes).

Description.—Shell small, maximum height 29.3 mm; shell thin, fusiform, with a low spire (spire height: shell height = 0.19 to 0.22); protoconch missing, teleoconch consisting four whorls. Last whorl sculptured by seven to eight axial ribs becoming obsolete near aperture; spiral sculpture of

body whorl consisting of six to nine low cords separated by secondary and two tertiary threads; strongest spiral cord located at shoulder. Small labral tooth formed at end of fifth spiral cord counting from suture; inner side of outer lip bearing nine small denticles; siphonal canal short (canal length: shell height = 0.21), open.

Remarks and comparison.—Matsubara (1996) assigned his new species to the genus *Ocenebra* Gray, 1847. The presence of a short labral tooth at the apertural end of a cord, a feature not noted by Matsubara (1996) in his original description, clearly distinguishes "*O.*" *katayamai* from typical members of *Ocenebra*.

"*Ocenebra*" *katayamai* resembles *Ocenebrellus inornatus* in having a short siphonal canal, eight axial ribs on the last whorl, denticles on the inner side of the outer lip, and a small labral tooth. However, the two species differ in the position of the labral tooth. In "*O.*" *katayamai*, the labral tooth is formed at the end of a cord (Figure 3–11a), whereas in *O. inornatus* and *O. aduncus*, it is formed at the end of a shallow groove. There is some resemblance between "*Ocenebra*" *katayamai* and the monotypic late Oligocene genus *Fenolignum* Vermeij and Vokes, 1997, from North Carolina. Both are characterized by a blunt labral tooth at the end of a cord, and by the absence of varices. The siphonal canal of *Fenolignum umbilicatum* Vermeij and Vokes, 1997, however, is sealed instead of open.

From this discussion, it is clear that "*Ocenebra*" *katayamai* does not fit comfortably into any described ocenebrine genus. It may be necessary to establish yet another new ocenebrine genus for this taxon, but we are reluctant to take this step here. We leave "*Ocenebra*" *katayamai* in the genus *Ocenebra* as used in the very broadest sense, but we emphasize that this assignment in no way implies a close relationship to eastern Atlantic members of the genus *Ocenebra*.

Russian species Sinelnikova (in Gladenkov and Sinelnikova, 1990) named eight species of *Tritonalia* from the Miocene of Kamchatka on the basis of poorly preserved material from the Kakert (early middle Miocene) and Etolon (middle Miocene) Formations. The descriptions and illustrations are inadequate for robust taxonomic conclusions to be drawn. Several species, such as *T. chejliensis* from the Kakert Formation, and *T. itelmenica* and *T. palanica* from the Etolon Formation appear to have a much higher spire than any species of *Ocenebrellus*, and therefore probably do not belong to that genus.

Other species have a lower spire and could belong to *Ocenebrellus*. These includes *T. kamtchatica* (Kakert Formation), with high varices and low cords; *T. kavranensis* (Kakert Formation), with sparse varices and low cords; *T. kejscheensis* (Kakert Formation), with six to seven axial blades and obsolete spiral sculpture; *T. ochotika* (Kakert Formation), with thin axial keels and low broad cords; and *T. rekinicus* (Etolon Formation), with more than ten thin wavy axial varices.

From the figures, *Tritonalia kamtchatica*, *T. kavranensis* and *T. ochotika* appears to be shouldered as are species of *Ocenebrellus*, whereas *T. rekinicus* is not. The siphonal

Table 1. Species characters of *Ocinebrellus*.

Species	Characters	Height (mm)	SH/H ¹⁾	CL/H ²⁾	BAN ³⁾	BSN ⁴⁾	LT ⁵⁾	NC ⁶⁾	Living depth ⁷⁾	Geologic range
<i>O. inornatus</i> Stock										
<i>O. inornatus</i> (Recluz)		47.9	0.21-0.29	0.22-0.31	4-12	4-7	+	5	0-20 m	M. Mio.-Rec.
<i>O. lumarius</i> (Yokoyama)		23.1	0.27-0.33	0.16-0.26	6-11	12-20	-	5-6	0-20 m	E. Pleist.-Rec.
<i>O. aduncus</i> Stock										
<i>O. protoaduncus</i> (Hatai and Kotaka)		44.6+	—	—	7	12	-	7	—	M. Mio.
<i>O. ogasawarai</i> sp. nov.		44.3	0.20-0.30	0.33-0.36	3-10	18-44	-	5-9	—	Plio.-E. Pleist.
<i>O. aduncus</i> (Sowerby)		58.9	0.18-0.26	0.28-0.42	3-7	1-20	+	0	0-200 m	Plio.-Rec.

¹⁾SH=spire height ²⁾CL=canal length ³⁾number of axial varices or ribs on body whorl ⁴⁾number of spiral cords on body whorl ⁵⁾existence of labral tooth ⁶⁾number of denticles on the inner side of outer lip ⁷⁾after Higo and Goto (1993)

canal of *T. keijtscheensis* is apparently sealed, whereas that of seven other species is open. None of the eight species has a labral tooth. It is possible that some of these species belong to *Ocinebrellus*. If so, their early middle Miocene appearance in the Kakert Formation would slightly precede the oldest undoubted species of *Ocinebrellus* from the middle Miocene, *O. protoaduncus* from the Ginzan Formation and *O. inornatus* from the Kubota Formation. Definite resolution of the status and assignment of the eight Russian species of *Tritonalia* must await the discovery of better preserved material.

Evolutionary history

Table 1 provides a summary of the morphology and distribution of the species of *Ocinebrellus*. Morphologically, the genus is divisible into two stocks. In the *O. inornatus* stock, the siphonal canal is typically short and occasionally open, the outer lip has five small denticles on its inner side, an adapical sinus on the outer lip is present, and axial varices are often indistinct or absent. It includes the middle Miocene to Recent *O. inornatus* (Recluz) and the early Pleistocene to Recent *O. lumarius* (Yokoyama).

The *O. aduncus* stock is characterized by a long siphonal canal, seven denticles on the inner side of the outer lip (if present), absence of an adapical sinus, and distinctly developed varices. This stock comprises the middle Miocene *O. protoaduncus* (Hatai and Kotaka), the Pliocene to early Pleistocene *O. ogasawarai* sp. nov., and the Pliocene to Recent *O. aduncus* (Sowerby).

The genus *Ocinebrellus* probably originated in the northwestern Pacific, although its precise origins remain obscure. The early Miocene species "*Ocenebra*" *katayamai* Matsubara may lie close to the ancestry of *Ocinebrellus inornatus*, but as discussed above under "*O.*" *katayamai*, the presence of a labral tooth at the end of a cord instead of at the end of a groove together with the open instead of sealed siphonal canal places "*O.*" *katayamai* outside the genus *Ocinebrellus*.

None of the ocenebrine muricids described from the Miocene of the North American side of the Pacific bears a close resemblance to *Ocinebrellus*. Moore (1963) compared her new species *Ocenebra depoensis* from the Astoria Formation (early middle Miocene) of Oregon to *Ocinebrellus lumarius*, but she noted that *O. depoensis* lacks the shoulder

spine characteristic of *Ocinebrellus*. Moreover, the spire of *O. depoensis* is considerably higher. The holotype and only known specimen of *O. depoensis* (USNM no. 563927) has approximately seven denticles on the inner side of the outer lip, approximately seven strong cords on the last whorl, and a high spire. Two of the axial ribs, the one at the outer lip and one ninety degrees back from the aperture, are differentiated as varices. The siphonal canal is sealed. Although the outer lip edge is somewhat damaged, there is no evidence of a labral tooth. This species seems closely related neither to *Ocinebrellus* nor to other North America ocenebrines.

The earliest occurrences of *Ocinebrellus* are in the Miocene strata of northeastern Honshu, which at that time lay in a zone of mild-temperate climate (Ogasawara, 1994). Miocene *Ocinebrellus inornatus* is known from the Kubota Formation in Fukushima Prefecture (Yokoyama, 1931; Nomura and Hatai, 1936; Iwasaki, 1970; Figures 3-8, 9a, b, 10a, b), while *O. protoaduncus* is recorded from the Ginzan Formation of Yamagata Prefecture (Hatai and Kotaka, 1959; Figure 5). During the Pliocene, *Ocinebrellus aduncus* occurred on the Pacific coast of Honshu, whereas *O. ogasawarai* was restricted to, and probably arose in, the Japan Sea, an enclosed basin dominated by a cold-water fauna (see Ogasawara, 1994). *O. ogasawarai* was found in some mixed Pliocene assemblages of warm shallow and cold deep faunas, and persisted until the end of the early Pleistocene.

During the early Pleistocene, *O. lumarius* was differentiated from *O. inornatus* in the northern part of the Japan Sea. Following the extinction of *O. ogasawarai*, *O. aduncus* invaded the Japan Sea, where it colonized relatively deep sublittoral habitats.

Recent work has revealed that many gastropods living in the Pliocene and early Pleistocene of Japan Sea suffered extinction at the end of the early Pleistocene. Ogasawara (1986) listed twenty-three shallow-water gastropods in this category, including *Umbonium akitanum* Suzuki, *Turritella saishuensis* (Yokoyama) group, *Trophonopsis kagaensis* Hatai and Nisiyama, *Lirabuccinum japonica* (Yokoyama), *Fulgoraria masudae* Hayasaka, *Ophiodermella ogurana* (Yokoyama). To this list may be added the teleplanically dispersed ranellid *Fusitriton izumozakiensis* Amano and *Ranella yasumurai* Amano (see Amano, 1997a). Some deep-water buccinids such as the *Ancistrolepis* group, *Neptunea*, were

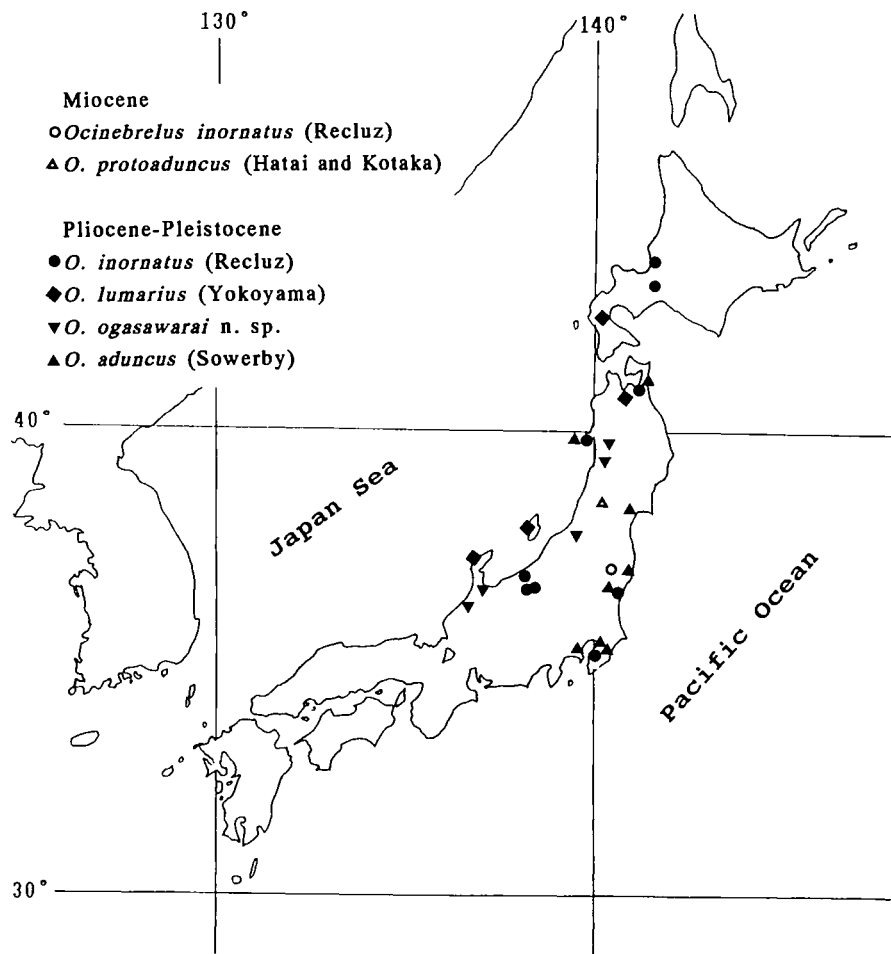


Figure 5. Distribution of fossil *Ocinebrellus*.

also Japan Sea endemics that became extinct at the end of the early Pleistocene (Amano *et al.*, 1996; Amano, 1997b). These extinctions probably resulted from the fact that the deep waters of the Japan Sea became euxinic while surface waters became brackish, which in turn resulted from the enclosed nature of the basin during the middle and late Pleistocene glacial low stands of sea level (see Tada, 1994).

Some evolutionary change in *Ocinebrellus* may be related to predation. *O. aduncus* is unusual among species of *Ocinebrellus* in usually lacking denticles on the inner side of the outer lip. Such denticles often have an anti-predatory function (Vermeij, 1987). The paucity of predators in the deep sublittoral habitat of *O. aduncus* is consistent with the absence of denticles in this species.

From the time of its origin, the genus *Ocinebrellus* has been confined to the northwestern Pacific, except for the introduction of *O. inornatus* by humans to the west coast of North America during the first quarter of the twentieth century. This narrow distribution contrasts with that of *Nucella*, another ocenebrine genus. *Nucella* originated during the early Miocene in the warm-temperate north-eastern Pacific, and had expanded westward to Japan and

Russia by the early middle Miocene (Amano *et al.*, 1993; Collins *et al.*, 1996). In the late Pliocene, at least one lineage penetrated into the North Atlantic. Why *Nucella* but not *Ocinebrellus* adapted to boreal water conditions and spread throughout the North Pacific and North Atlantic remains unclear. It is interesting that intertidal species of *Nucella* can easily colonize newly available habitats. In contrast, introduced populations of *Ocinebrellus inornatus* have spread relatively little from their original sites of introduction in western North America (Carlton, 1992). We do not know what accounts for such differences in dispersability. Future evolutionary and comparative biogeographic research on contemporaneous clades should emphasize the means and extent of dispersal in order to make clear why some clades achieve a wide distribution while others evolving at the same time remain confined to a relatively small region.

Acknowledgments

We thank Konstantin A. Lutaenko (Inst. Marine Biology, Russian Acad. Sci.), Anton Oleinik (Purdue Univ.), Masanori Shimamoto (Tohoku Univ.), Akira Tsukagoshi (Univ. Mus.,

Univ. Tokyo), Sadako Takeuti (Saito Ho-on Kai Mus.), Hiroshi Saito (Nat. Sci. Mus., Tokyo), Toshihiko Yasumura (Shibata Sci. Educ. Center), Tetsuya Tanaka (Kakizaki Junior High School) for their help in examining some fossil and Recent specimens. We also thank Eiji Tsuchida (Ocean Res. Inst., Univ. Tokyo) for his information on the Recent ocenebrines. Finally we thank Janice Cooper and Edith Zipser (Univ. California, Davis) for their technical assistance.

References

- Adams, A., 1853: Descriptions of several new species of *Murex*, *Rissonia*, *Planaxis*, and *Eulima*, from the Cumingian collection. *Proceedings of the Zoological Society of London for 1853*, p. 267-272.
- Adams, A., 1855: Description of two new genera and several new species of Mollusca, from the collection of Hugh Cuming Esq. *Proceedings of the Zoological Society of London for 1855*, p. 119-124.
- Adams, A., 1862: On the species of Muricidae found in Japan. *Proceedings of the Zoological Society of London for 1862*, p. 370-376.
- Akamatsu, M., 1980: On the warmer fauna from the Noppo Hills, neighbouring Sapporo City, Hokkaido. *Annual Report of the Historical Museum of Hokkaido*, no. 8, p. 1-36, pls. 1-8. (in Japanese)
- Akamatsu, M., 1984: On the so-called Shishinai fauna from the Ishikari Hills, Hokkaido. *Annual Report of the Historical Museum of Hokkaido*, no. 12, p. 1-33, pls. 1-5. (in Japanese with English abstract)
- Amano, K., 1997a: Taxonomy and distribution of Cymatiidae (Gastropoda) from the Pliocene and the lower Pleistocene in the Japan Sea borderland. *Venus (Japanese Journal of Malacology)*, vol. 56, no. 2, p. 121-129.
- Amano, K., 1997b: Biogeography of the genus *Neptunea* (Gastropoda: Buccinidae) from the Pliocene and the lower Pleistocene of the Japan Sea borderland. *Paleontological Research*, vol. 1, no. 4, p. 274-284.
- Amano, K. and Sato, H., 1995: Relationship between embayment associations and relict species. — Molluscan fauna from the Pliocene Joshita Formation in the northern part of Nagano Prefecture —. *Fossils*, no. 59, p. 1-13. (in Japanese with English abstract)
- Amano, K., Ukita, M. and Sato, S., 1996: Taxonomy and distribution of the subfamily Ancistrolepidinae (Gastropoda: Buccinidae) from the Plio-Pleistocene of Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 182, p. 467-477.
- Amano, K., Vermeij, G.J. and Narita, K., 1993: Early evolution and distribution of the gastropod genus *Nucella*, with special reference to Miocene species from Japan. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 171, p. 237-248.
- Amio, M., 1963: A comparative embryology of marine gastropods with ecological consideration. *Journal of Shimonoseki College of Fisheries*, vol. 12, nos. 2/3, p. 15-144. (in Japanese with English summary)
- Baba, K., 1990: *Molluscan fossil assemblages of the Kazusa Group, south Kanto, central Japan*, 445 p., 40 pls., Keio Gijuku Yochisha, Tokyo. (in Japanese)
- Berry, S.S., 1959: Notices of new eastern Pacific Mollusca. III. *Leaflets in Malacology*, vol. 1, no. 18, p. 107-114.
- Carlton, J.T., 1992: Introduced marine and estuarine mollusks of North America: an end-of-the twentieth-century perspective. *Journal of Shellfish Research*, vol. 11, no. 2, p. 489-505.
- Chew, K.K. and Eisler, R., 1958: A preliminary study of feeding habits of the Japanese oyster drill, *Ocenebra japonica* (Dunker). *Journal Fisheries Research Board of Canada*, vol. 15, no. 4, p. 529-535.
- Collins, T.M., Frazer, K., Palmer, A.R., Vermeij, G.J. and Brown, W.M., 1996: Evolutionary history of northern Hemisphere *Nucella* (Gastropoda, Muricidae): Molecular, morphological, ecological, and paleontological evidence. *Evolution*, vol. 50, no. 6, p. 2287-2304.
- Conrad, T.A., 1863: Catalogue of the Miocene shells from the Atlantic slope. *Proceedings of Academy of Natural Sciences of Philadelphia*, vol. 14, p. 559-582.
- Cossmann, M., 1903: *Essais de Paléoconchologie Comparée*, vol. 5, 215 p.
- Crosse, H., 1862: Description d'espèces marines recueillies par M.H. Cuming dans le nord de la Chine. *Journal de Conchyliologie*, vol. 10, p. 51-57.
- Dunker, W., 1860: Neue japanische Mollusken. *Malakozoologische Blätter*, vol. 6, p. 221-240.
- Egorov, R.V., 1992: Guide to Recent molluscs of northern Eurasia. 1. Gastropods of the families Muricidae and Thaididae from the seas of Russia. *Ruthenica*, vol. 2, no. 1, p. 63-75.
- Fulton, H.C., 1917: Molluscan notes. III. 10: On the priority of *Murex aduncus*, Sow., over *Murex falcatus*, Sow. *Proceedings of the Malacological Society of London*, vol. 12, p. 238.
- Gladenkov, Yu.B. and Sinelnikova, V.N., 1990: Miocene mollusks and climatic optimum in Kamchatka. *Transactions of Academy of Sciences of the USSR Geological Institute*, vol. 453, p. 1-172. (in Russian)
- Golikov, A.N. and Kusakin, O.G., 1978: Shell-bearing gastropod molluscs from intertidal zone of the USSR seas. *Taxonomic Monographs on the fauna of the USSR*, Sect. 116, p. 1-256, figs. 8-155. (in Russian)
- Gray, 1847: A list of the genera of Recent Mollusca, their synonyma and types. *Proceedings of the Zoological Society of London for 1847*, p. 129-219.
- Habe, T., 1958: The fauna of Akkeshi Bay XXV. Gastropoda. *Publications from the Akkeshi Marine Biological Station, Hokkaido University*, no. 8, p. 1-40, pls. 1-5.
- Habe, T., 1961: Fauna of shell-bearing mollusks of the sea around Shirikishinai, Hokkaido. 2. Gastropoda. *Publications from the Shirikishinai Marine Station for Biological Education, Hokkaido Gakugei University*, no. 8, p. 1-11, pls. 1-5. (in Japanese)
- Habe, T. and Ito, K., 1965: *Shells of the World in colour. vol. 1, the Northern Pacific*, 176 p., 56 pls., Hoikusha, Osaka. (in Japanese)
- Hall, C.A., 1959: The gastropod genus *Ceratostoma*. *Journal of Paleontology*, vol. 33, no. 3, p. 428-434, pls. 61-63.
- Hatai, K. and Kotaka, T., 1959: Some new Miocene gastropods from near the Ginzan hot-spring, Yamagata Prefecture, Northeast Honshu, Japan. *Saito Ho-on Kai Museum, Research Bulletin*, no. 28, p. 6-11.
- Hatai, K., Masuda, K. and Suzuki, Y., 1961: A note on the Pliocene megafossil fauna from the Shimokita Penin-

- sula, Aomori Prefecture, Northeast Honshu, Japan. *Saito Ho-on Kai Museum, Research Bulletin*, no. 30, p. 18-38, pls. 1-4.
- Herrmannsen, A.N., 1846: *Indicis generum Malacozoorum*. vol. 1, 637 p. Casel.
- Higo, S. and Goto, Y., 1993: A systematic list of molluscan shells from the Japanese Islands and the adjacent area, 693 p. Elle Scientific Publications, Osaka. (in Japanese)
- Ito, K., 1989: Distribution of molluscan shells in the coastal areas of Chuetsu, Kaetsu and Sado Island, Niigata Prefecture, Japan. *Bulletin of Japan Sea Regional Fisheries Research Laboratory*, no. 39, p. 37-133. (in Japanese with English abstract)
- Ito, K., Matano, Y., Yamada, Y. and Igarashi, S., 1986: Shell species caught by S/S Rokko-Marui off the coast of Ishikawa Prefecture. *Bulletin of Ishikawa Prefecture Fisheries Experimental Station*, no. 4, p. 1-179. (in Japanese with English abstract)
- Iwai, T., 1965: The geological and paleontological studies in the marginal area of the Tsugaru basin, Aomori Prefecture, Japan. *Bulletin of Educational Faculty of Hirosaki University*, no. 15, p. 1-68, pls. 12-20.
- Iwai, T. and Shiobara, T., 1968: Pleistocene Mollusca from Kamikita-gun, Aomori Prefecture, Japan. *Bulletin of Educational Faculty of Hirosaki University*, no. 20, p. 1-7, pls. 1-3.
- Iwasaki, Y., 1970: The Shiobara-type molluscan fauna. An ecological analysis of fossil molluscs. *Journal of the Faculty of Science, the University of Tokyo, Section 2*, vol. 17, no. 3, p. 351-444, pls. 1-7.
- Jousseume, F., 1880: Division méthodique de la famille des purpurides. *Le Naturaliste*, vol. 2, no. 42, p. 335-336.
- Jousseume, F., 1882: Etudes des Purpuridae et description d'espèces nouvelles. *Revue et Magasin de Zoologie Pure et Appliquée, Sér. 3*, vol. 7, p. 314-348.
- Kanehara, K., 1942: Fossil Mollusca from Tayazawa, Wakomotomura, Katanishi oil field. *The Journal of the Geological Society of Japan*, vol. 49, no. 581, p. 130-133, pl. 3.
- Kaseno, Y. and Matsuura, N., 1965: Pliocene shells from the Omma Formation around Kanazawa City, Japan. *Science Reports of the Kanazawa University*, vol. 10, no. 1, p. 27-62, pls. 1-20.
- Kinoshita, T. and Isahaya, Y., 1934: Catalogue of the shell bearing molluscs from Hokkaido. *Reports of Fisheries Survey, Hokkaido Fisheries Experiment Station*, no. 33, p. 1-9, pls. 1-15. (in Japanese)
- Kira, T., 1959: *Coloured illustrations of the shells of Japan*, 240 p., 71 pls., Hoikusha, Osaka. (in Japanese)
- Kuroda, T., 1931: Mollusca. In, Homma F. ed., *Shinano Chubu Chishitsu-shi (Geology of Central Shinano)*, pt. 4, p. 1-90, pls. 1-13. (in Japanese)
- Kuroda, T., Habe, T. and Oyama, K., 1971: *The sea shells of Sagami Bay*, 741 p. (in Japanese), 489 p. (in English), 121 pls., Maruzen, Tokyo
- Matsubara, T., 1996: Fossil Mollusca of the lower Miocene Yotsuyaku Formation in the Ninohe district, Iwate Prefecture, Northeast Japan. Part 2 (2). Gastropoda. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 181, p. 361-374.
- Matsuura, N., 1977: Molluscan fossils from the late Pleistocene marine terrace deposits of Hokuriku region, Japan Sea side of Central Japan. *Science Reports of the Kanazawa University*, vol. 22, no. 1, p. 117-162, pls. 1-20.
- Matsuura, N., 1985: Successive change of the marine molluscan faunas from the Pliocene to Holocene in Hokuriku Region, Central Japan. *Bulletin of the Mizunami Fossil Museum*, no. 12, p. 71-158, pls. 32-42. (in Japanese with English abstract)
- Moore, E.J., 1963: Miocene marine mollusks from the Astoria Formation in Oregon. *U.S. Geological Survey Professional Paper*, 419, p. 1-109.
- Nemoto, N. and O'Hara, S., 1979: Molluscan fossils from the Tago Group in the vicinity of Futatsu-numa, Hironomachi, Fukushima Prefecture. *Taira Chigaku Doko-kai Kaiho, Special Volume*, p. 52-60. (in Japanese)
- Noda, H., Kikuchi, Y. and Nikaido, A., 1993: Molluscan fossils from the Pliocene Kume Formation in Ibaraki Prefecture, northeastern Kanto, Japan. *Science Reports of the Institute of Geoscience, the University of Tsukuba, Sect. B*, vol. 14, p. 115-204.
- Nomura, S., 1938: Molluscan fossils from the Tatunokuti shell bed exposed at Goroku cliff in the western border of Sendai. *Science Reports of the Tohoku Imperial University, 2nd Series*, vol. 19, no. 2, p. 235-275, pls. 33-36.
- Nomura, S. and Hatai, K., 1935a: Catalogue of the shell-bearing Mollusca collected from the Kesen and Motoyoshi districts, Northeast Honshu, Japan, immediately after the Sanriku Tsunami, March 3, 1933, with the descriptions of five new species. *Saito Ho-on Kai Museum, Research Bulletin*, no. 5, p. 1-47, pls. 1-2.
- Nomura, S. and Hatai, K., 1935b: Pliocene Mollusca from the Daisyaka shell-beds in the vicinity of Daisyaka, Aomori-Ken, Northeast Honshu, Japan. *Saito Ho-on Kai Museum, Research Bulletin*, no. 6, p. 83-142, pls. 9-13.
- Nomura, S. and Hatai, K., 1936: Fossils from the Tanagura beds in the vicinity of the Town Tanagura, Hukusima-Ken, Northeast Honshu, Japan. *Saito Ho-on Kai Museum, Research Bulletin*, no. 10, p. 109-155, pls. 13-17.
- Ogasawara, K., 1977: Paleontological analysis of Omma fauna from Toyama-Ishikawa area, Hokuriku Province, Japan. *Science Reports of the Tohoku University, 2nd Series*, vol. 47, no. 2, 43-156.
- Ogasawara, K., 1986: Note on origin and migration of the Omma-Manganzian fauna, Japan. *Palaeontological Society of Japan, Special Papers*, no. 29, p. 227-244.
- Ogasawara, K., 1994: Neogene paleogeography and marine climate of the Japanese Islands based on shallow marine molluscs. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 108, nos. 3/4, p. 335-351.
- Ogasawara, K., Masuda, K. and Matoba, Y., 1986: *Neogene and Quaternary Molluscs from the Akita Oil-field, Japan*. Commemorative Volume of Prof. Takayasu's Retirement, 310 p., 85 pls. (in Japanese)
- Otuka, Y., 1936: Pliocene Mollusca from Manganzi in Kotomomura, Akita Prefecture, Japan. *Journal of the Geological Society of Japan*, vol. 43, no. 516, p. 726-736, pls. 41-42.
- Pilsbry, H.A., 1904: New Japanese marine Mollusca: Gastropoda. *Proceedings of the Academy of Natural Sci-*

- ences of *Philadelphia*, vol. 56, p. 3-37.
- Radwin, G.E. and D'Attilio, A., 1976: *Murex shells of the world*. 284 p., 32 pls. Stanford University Press, Stanford.
- Rafinesque, C.S., 1815: *Analyse de la nature ou tableau du univers et des corps organisés*. p. 5-6, 136-149, 218-223. Barravechia, Palermo.
- Recluz, M.C., 1851: Description de quelques coquilles nouvelles. *Journal de Conchyliologie*, vol. 2, p. 194-216, pls. 5-6.
- Reeve, L.A., 1845: *Conchologia ichonica, or illustrations of the shells of molluscous animals*. vol. 3, *Murex*. pls. 1-36. Reeve, London.
- Smith, E.A., 1875: A list of the Gastropoda collected by Commander H.C. St. John, R.N. *Annals and Magazine of Natural History, Ser. 4*, vol. 15, p. 414-427.
- Sowerby, G.B., 1834: *The Conchological illustrations, Murex*. pls. 58-67. Sowerby, London.
- Sowerby, G.B., 1859: Descriptions of new shells in the collection of H. Cuming. *Proceedings of the Zoological Society of London for 1859*, p. 428-429.
- Sowerby, G.B., 1879: *Thesaurus Conchyliorum, or Monographs of genera of shells. Monograph of the genus Murex*. 55 p., 24 pls. Sowerby, London.
- Tada, R., 1994: Paleoceanographic evolution of the Japan Sea. *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 108, nos. 3/4, p. 487-508.
- Takahashi, H., 1986: Characteristics of the molluscan assemblages in the Pliocene Kume Formation in the Hitachi-Ota area, Ibaraki Prefecture, central Japan. *Monograph of the Mizunami Fossil Museum*, no. 6, p. 1-103. (in Japanese)
- Tokunaga, S., 1906: Fossils from the environs of Tokyo. *Journal of the College of Science, Imperial University of Tokyo*, vol. 21, art. 2, p. 1-96, pls. 1-6.
- Tryon, G.W., 1880: *Manual of Conchology. Vol. 2, Muricidae Purpuridae*. 289 p., 70 pls. Tryon, Philadelphia.
- Tsuchida, E., 1991: Fauna of marine mollusks of the sea around Otsuchi Bay, Iwate Prefecture. (2) Neogastropoda. *Reports of Otsuchi Marine Research Center*, no. 17, p. 1-27. (in Japanese)
- Vermeij, G.J., 1987: *Evolution and escalation. An ecological history of life*, 527 p., Princeton University Press, Princeton.
- Vermeij, G.J., 1998: New genera of Cenozoic muricid gastropods, with comments on the mode of formation of the labral tooth. *Journal of Paleontology*, vol. 72. (in press)
- Vermeij, G.J. and Vokes, E.H., 1997: Cenozoic Muricidae of the western Atlantic region. Part 12. The subfamily Ocenebrinae (in part). *Tulane Studies in Geology and Paleontology*, vol. 29, no. 3, p. 69-118.
- Yokoyama, M., 1922: Fossils from the Upper Musashino of Kazusa and Shimosa. *Journal of the College of Science, Imperial University of Tokyo*, vol. 44, art. 1, p. 1-200, pls. 1-20.
- Yokoyama, M., 1926: Fossil shells from Sado. *Journal of the Faculty of Science, the Imperial University of Tokyo, Sect. 2*, vol. 1, pt. 8, p. 249-312, pls. 32-37.
- Yokoyama, M., 1931: Tertiary Mollusca from Iwaki. *Journal of the Faculty of Science, the Imperial University of Tokyo, Sect. 2*, vol. 3, pt. 4, p. 197-203, pls. 12-13.
- Yoo, Jong-Saeng, 1976: *Korean shells in colour*, 196 p., 36 pls., Il Ji Sa Publ. Co., Seoul.

The Palaeontological Society of Japan has revitalized its journal. Now entitled **Paleontological Research**, and published preferably in English, its scope and aims have entirely been redefined. The journal now accepts and publishes any international manuscript meeting the Society's scientific and editorial standards. In keeping with the journal's new target audience the Society has established a new category of membership (**Subscribing Membership**) which, hopefully, will be especially attractive to new and existing overseas members. The Society looks forward to receiving your applications. Thank you.

APPLICATION FOR OVERSEAS MEMBERSHIP TO THE PALAEOLOGICAL SOCIETY OF JAPAN

1. NAME : _____

	Title	Last (Surname)	First (Given name)	Middle Initial
--	-------	----------------	--------------------	----------------
2. POSTAL ADDRESS : _____

3. TELEPHONE AND FAX (please include country code if known):
 TEL _____
 FAX _____

	country code	area code	number
--	--------------	-----------	--------
4. E-MAIL : _____
5. MEMBERSHIP CATEGORY (please check one):
 Full Member receives four issues of **Paleontological Research** **8,500 JP Yen**
 and two issues of **Kaseki** (a Japanese language journal of paleontology)
 in a year and all privileges of the Society including voting rights and
 conference programs
 Subscribing Member of PR receives four issues of **6,000 JP Yen**
 Paleontological Research in a year
 Institutional subscription of PR receives four issues of..... **75 US\$**
 Paleontological Research in a year (Current JP Yen is 0.008 U.S. \$)
6. METHOD OF PAYMENT (Please check one box):
 I enclose a bank draft made payable to the PSJ.
 I will remit/have remitted the above amount on _____ JP Yen through my bank to the
 account of JPS, a/c #062-0211501, The Bank of Tokyo-Mitsubishi, Kasuga-cho Branch, Tokyo.
 I agree to pay the amount of _____ JP Yen by my credit card.

<input type="checkbox"/> Master	<input type="checkbox"/> VISA	<input type="checkbox"/> American Express
<input type="checkbox"/> Diners Club	<input type="checkbox"/> Access	<input type="checkbox"/> Euro

 Card Account Number
 Signature (required) _____ Card Expiration _____
7. SIGNATURE _____ DATE _____
8. MAIL TO : Palaeontological Society of Japan
 c/o Business Center for Academic Societies, Japan
 5-16-9 Honkomagome, Bunkyo-ku, Tokyo, 113 Japan

A GUIDE FOR PREPARING MANUSCRIPTS

PALEONTOLOGICAL RESEARCH is dedicated to serving the international community through the dissemination of knowledge in all areas of paleontological research. The journal publishes articles, normally not exceeding 24 pages, and short notes, normally less than 4 pages. Manuscripts submitted are subject to review and editing by reviewers and a language editor. A condition of acceptance for all manuscripts is that they have not been published and will not be submitted nor published elsewhere. Manuscripts accepted for publication will generally be published in order of submission. Authors submit three copies of their manuscript for editorial review. After review, two copies of the revised manuscript are to be returned for copy editing.

Text: Paleontological Research is intended to be read by an international audience, therefore it is particularly critical that language be clear and concise. Though manuscripts in French and German may occasionally be accepted (with abstract and captions for illustrations and tables also provided in English), English is strongly favored as the language of international scientific communication. For manuscripts prepared in English, either British or American usage in style, words and spelling is acceptable. Use SI (Système International d'Unités) units wherever possible.

Text should be typed always in double space on one side of opaque white paper of not less than either 210 × 280 mm (A4 size) or 8 1/2 × 11 inches in the following order.

Cover sheet. Cover sheet should contain (1) full name, address, phone number and fax number of the author taking responsibility for the galley proofs, (2) running title composed of less than 40 characters, and (3) the numbers of tables and figures.

Title page. Title of the paper, names of authors and their professional affiliations with addresses (or residential address, if an author is unaffiliated). Titles are to be brief and simple. Spell out one or more of the authors' first names.

Abstract. Abstract should be a condensation and concentration of the essential qualities of the paper. All the papers, including Short Notes, are to be accompanied by an abstract not exceeding 500 words. New taxonomic or stratigraphic names should be mentioned in the abstract.

Key words. Select keywords (not more than six words or phrases) which identify the most important subjects covered by the paper and arrange them in alphabetical order.

Main text. Use three or fewer levels of heading. No footnotes are to be used. Bibliographical references are to be identified by citing the authors' names, followed, in parentheses, by the date of publication, with a page number if

desired. All citations must have a corresponding entry in the reference list.

The typical format for arrangement of systematic paleontology can be learned from current issues of the Journal. All descriptions of new taxa must include a diagnosis, and, as appropriate, stratigraphic and geographic indications, designation of a type or types, depository information, and specification of illustrations. In synonymies use an abbreviated form of the reference, consisting only of authors of reference, date of publication, and number of pages, plates, figures and text-figures referring to the organism or organisms in question.

References. Heading for the bibliography can be either "References cited" or "References." Entries are to be listed alphabetically. No abbreviations will be used in article and book titles. Journal titles are written out, not abbreviated. Series, volume, and number or part are to be given, with the appropriate word abbreviated in each case ("ser.", "vol.", etc.; see the next page for examples).

Illustrations: All illustrations, including maps, geologic sections, and half-tone illustrations (including "plates") are to be called figures and must be numbered in the same sequence as they are first cited in the text. Citations of illustrations in the text are to be spelled out in full (e.g., Figure 2 or Figure 2.1). Figure captions are to be typed separately. Plan the illustrations so that they take up either the entire width of the printed page (170 mm) or the width of one column (80 mm). Originals should not be smaller than the final intended size for printing. No foldouts will be accepted. Mark all originals clearly with authors' names and figure number. Photographs of all specimens except sections must be illuminated from the upper left side, as is conventional.

Manuscripts on disk: Authors are encouraged to deliver final, revised manuscript copy on disk, but disks should be sent only after the paper has been accepted. 3.5 inch disk with the text in a recent version of Word Perfect or Microsoft Word is acceptable. Be sure to specify, in a covering note, the hardware and the word-processing package used.

Galley proofs and offprints: Galley proofs will be sent to authors about one month before the expected publication date and should be returned to the Editors within 3 days of receipt. The authors are responsible for reading the first galley proof. Minor changes submitted by the author will be permitted while a paper is in galleys, but a charge will be made for substantial alterations.

The authors receive free of charge 50 offprints without covers. Additional copies and covers can be purchased and should be ordered when the proofs are returned.

Charges : If a paper exceeds 24 printed pages, payment of page charges for the extra pages is a prerequisite for acceptance. Illustrations in color can also be published at the authors' expense. For either case, the Editors will provide information about current page charges.

Return of published figures : The manuscripts of the papers published will not be returned to the authors. However, figures will be returned upon request by the authors after the paper has been published.

- Ager, D.V., 1963 : *Principles of Paleocology*, 371 p. McGraw-Hill Co., New York.
- Barron, J.A., 1983 : Latest Oligocene through early Middle Miocene diatom biostratigraphy of the eastern tropical Pacific. *Marine Micropaleontology*, vol. 7, p. 487-515.
- Barron, J.A., 1989 : Lower Miocene to Quaternary diatom biostratigraphy of Leg 57, off northeastern Japan, Deep Sea Drilling Project. In, Scientific Party, *Initial Reports*

- of the Deep Sea Drilling Project*, vols. 56 and 57, p. 641-685. U.S. Govt. Printing Office, Washington, D.C.
- Burckle, L.H., 1978 : Marine diatoms. In, Haq, B.U. and Boersma, A. eds., *Introduction to Marine Micropaleontology*, p. 245-266. Elsevier, New York.
- Fenner, J. and Mikkelsen, N., 1990 : Eocene-Oligocene diatoms in the western Indian Ocean : Taxonomy, stratigraphy, and paleoecology. In, Duncan, R.A., Backman, J., Peterson, L.C., et al., *Proceedings of the Ocean Drilling Program, Scientific Results*, vol. 115, p. 433-463. College Station, TX (Ocean Drilling Program).
- Koizumi, I., 1972 : Marine diatom flora of the Pliocene Tatsunokuchi Formation in Fukushima Prefecture. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 86, p. 340-359.
- Kuramoto, S., 1996 : Geophysical investigation for methane hydrates and the significance of BSR. *Journal of the Geological Society of Japan*, vol. 11, p. 951-958. (in Japanese with English abstract)

Palaeontological Society of Japan (JSP) Standing Committee Actions

During its meeting on September 19, the JSP Standing Committee enacted the following changes to its membership.

New members elected ;		
Jong-Il Fang,	Yoshio Furukawa,	Tomoo Hashimoto,
Myong-Ok Hyon,	Yutaka Tanaka	
Resigned members ;		
Kaname Kanda,	Shinji Kikuchi,	Kagetaka Watanabe,
Win Zaw		
Deceased member ;		
Katsumi Abe,	Shinichi Sato	

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「復元の学科3, 生物事変, 世話人: 海保邦夫, 西 広嗣, 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申し込み締切は1999年3月末日です。
- ◎第149回例会(開催予定時期: 2000年の6月末頃)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。

講演の申し込み先: 〒240-8501 横浜市保土ヶ谷区常盤台 79-2

横浜国立大学教育人間科学部自然環境講座 間嶋隆一 (行事係)

問い合わせ先 間嶋隆一: TEL 045-339-3349 直通 FAX 045-339-3264 学部事務室

E-mail majima@ed.ynu.ac.jp HDA01631@niftyserve.or.jp

樽 創 (行事係幹事):

〒250-0031 小田原市入生田 499

神奈川県立生命の星・地球博物館

TEL 0465-21-1515 FAX 0465-23-8846

E-mail taru@pat-net.or.jp

本誌の発行に要する費用は, 会員の会費以外に, 文部省科学研究費補助金ならびに賛助会員からの会費が当てられています。現在の賛助会員は下記の通りです。

インドネシア石油株式会社	神奈川県立生命の星・地球博物館	北九州市立自然史博物館
石油資源開発株式会社	ダイヤコンサルタント	帝国石油株式会社
兵庫県立人と自然の博物館	ミュージアムパーク茨城県自然博物館	(アイウエオ順)

○文部省科学研究費補助金(研究成果公開促進費)による。

1998年9月27日 印刷	発行者	日本古生物学会
1998年9月30日 発行		〒113-8622 東京都文京区本駒込5-16-9
ISSN 1342-8144		日本学会事務センター内
Paleontological Research	編集者	電話 03-5814-5801
第2巻, 第3号	編集幹事	森 啓・前田晴良
2,500円	印刷者	島本昌憲
		〒984-0011 仙台市若林区六丁の目西町8-45
		笹氣出版印刷株式会社 笹氣 幸緒
		本社 022-288-5555 東京 03-3455-4415

Paleontological Research

Vol. 2 No. 3

September 30, 1998

CONTENTS

Atsushi Takemura and Hsin Yi Ling : Taxonomy and phylogeny of the genus <i>Theocorys</i> (Nassellaria, Radiolaria) from the Eocene and Oligocene sequences in the Antarctic region	155
Tatsuro Matsumoto, Fumihisa Kawabe and Yoshitaro Kawashita : Two ammonite species of <i>Mortonicerias</i> from the Yubari Mountains (Hokkaido) and their geological implications (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin-LXXXII)	170
Kazumi Matsuoka, Pornsilp Pholpunthin and Yasuwo Fukuyo : Is the archeopyle of <i>Tuberculodinium vancampoae</i> (Rossignol) (Gonyaulacales, Dinophyceae) on the hypocyst?	183
Kazunori Miyata and Yukimitsu Tomida : <i>Trogosus</i> -like tillodont (Tillodontia, Mammalia) from the early Middle Eocene of Japan	193
Kazutaka Amano and Geerat J. Vermeij : Taxonomy and evolution of the genus <i>Ocinebrellus</i> (Gastropoda : Muricidae) in Japan	199
PROCEEDINGS	213