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

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

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**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 *Calocyclas*, *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. semipollata* comb. nov. In addition, another new species, *Calocyclas (?) 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 (Pliegel and Sanfilippo, 1978; Sanfilippo, et al., 1985), because of the near complete absence of zonal marker species. In other words, the Antarctic radiolarian biozonation must be proposed based on paleoecologically limited endemic species.

Among Paleogene Antarctic radiolarians, species previously assigned to the genera *Calocyclas*, *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 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 (68°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-
The sediments are of graphic distributions have been presented by Nocchi, et al., (1991), Crux thores, which have an identical cephalic skeletal structure (see Figure 5), small poreless cephalids 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 Calocylas cf. sempitopal Clark and Campbell, Calocylas sp. A, Calocylas sp. B, Calocylas sp. C and Cyrtocapsella robusta Abelmann. In this paper, we include these species in the genus Theocorys.

The genus Calocylas Ehrenberg is a theoperid of three segments, which has a small poreless cephalid and a large inflated thorax. Campbell (1954) designated Calocylas 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 insertion of 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 biostatigraphic 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 C6C2N2, is located between 748B-9H, 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 (Ciesieliski, et al., 1988). Well-preserved Eocene to Oligocene radiolarians were observed from Sites 699, 702 and 703. Biostatigraphy for the contained microfossils was presented by Nocchi, et al., (1991), Crux (1991), Madile and Monachi (1991), and Ciesieliski (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°56.718'S, 26°22.117'W; water depth, 3,683.4 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 (Ciesieliski, 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 stub. We observed both the outer shell structure and the internal cephalic skeletons of the specimens used in this study.

On the generic assignment of “Calocylas” 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, Calocylas and Cyrtocapsella, occur in Eocene to Oligocene sediments in the Antarctic Ocean. All have an identical cephalic skeletal structure (see Figure 5), small poreless cephalids 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 Calocylas cf. sempitopal Clark and Campbell, Calocylas sp. A, Calocylas sp. B, Calocylas sp. C and Cyrtocapsella robusta Abelmann. In this paper, we include these species in the genus Theocorys.

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Taxonomy and phylogeny of the genus Theocorys

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Figure 2. Ranges and phylogeny of the species of the genus Theocorys, Calocycias 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 Calocycias in previous studies. c: species described as Cyrtocapsella in previous studies.

generic assignment to this genus. The type species, Calocycias 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 Calocycias hispida, which possesses only lamellar feet as abdomen, and left no descendants. On the other hand, Saunders et al. (1984) included Calocycias bandyca as a descendant species of C. turris (Figure 2).

Although all the species of the "Calocycias" 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 Calocycias turris, C. hispida and C. bandyca. This fact suggests the evolutionary lineage of this "Calocycias" group is different from that of Calocycias hispida-C. turris-C. bandyca.

As for the genus Cyrtocapsella, Sanfilippo and Riedel (1970) defined it as follows: "Cenozoic, three- or four-segmented theopoderis 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 occurrence 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 early 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 (Nekaseko).

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 an 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 "Calocycias" semipolita, as discussed in the next section. Because the evolutionary lineage of the high-
latitude three-segmented “Calocyclas” and “Cyrtocapsella” group differs from those of Calocyclas and Cyrtocapsella in low latitudes, in this paper, we include these Antarctic forms under the genus Theocorys.

Regarding the genus Theocorys, various authors severely designated type species of the genus, e.g., Eucryptidum 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. anapographa 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. acrona, and considered all three forms, T. acrona, T. anapographa 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. acrona, indicating some phylogenetic relationship between these two groups. Therefore, we include the Antarctic forms, which were previously classified under the genus Calocyclas 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, Calocyclas 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 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 abdominal (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 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 longilitorax 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 near the 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 Theocorys 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, Calocyclas (?) nakasekoi, which commonly occurs in Middle Eocene sediments in the Antarctic region. We tentatively have included C. (?) nakasekoi in the genus Calocyclas, 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 Calocyclas 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 Arcaniceps-type structure of Takemura (1966).

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 Calocyclas 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 Calocyclas** Ehrenberg, 1847


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


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 Calocyclas turris, the type species of this genus, is questionable. Both Calocyclas talwani (described by Björklund and Kellogg, 1972) and Calocyclas extensa described by Clark and Campbell (1942), in which the thoracic pores are arranged in transverse rows, should be excluded from Calocyclas.
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, subpelureal and poreless with a stout and long apical horn, which tapers distally. Collar distinct. Thorax large, usually thick-walled, inflated and barrel- or egg-shaped. Thoracic pores large, mostly two segments. Cephalis small, subspherical and poreless with uniform in size throughout, and usually arranged longitudinally thoracic aperture slightly constricted with distinct peristome. Species of the genus by its two-segmented form, large size of cephalis, 37-46 $\mu$m; Length and width of cephalis, 37-46 $\mu$m; Length and width of thorax, 138-178 $\mu$m; 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 of cephalis, 37-46 $\mu$m; Length and width of thorax, 138-178 $\mu$m; measured in 19 specimens.

**Occurrence.**—Leg 120, Hole 74B: 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 74B is considered reworked, based on the poor state of preservation (broken), and the presence of Eocene species of Lynchnocama amphitrite, Eucyrtidium spinosum and/or Lophocystis biaurita in the same samples.

**Genus Theocorys** Haeckel, 1881


**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. acoria 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 Calocycles 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


**Description.**—Shell conical to cylindrical with three seg-
Taxonomy and phylogeny of the genus *Theocorys*
ments. Cephalis small, subshperical 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

Description.—Shell oval to cylindrical with three segments. Cephalis small, spherical or subshperical and poreless, usually with small and thin apical horn. Thorax inflated, thick-walled and hemispherical to subshperical, 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 subshperical thorax usually with irregularly distributed pores, and by the shape of the abdomen, although the distal part of the abdomen is often broken.
Taxonomy and phylogeny of the genus Theocorys
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 B(?) 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.


*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 ampulacea* 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. ampulacea* 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, 48-50 cm to 114-702A-4H-2, 50-52 cm. 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.

*Calocyclas* 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.

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

Description.—Shell cylindrical with three segments.
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, 5 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 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 structure. 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 Theocorys robusta (Clark and Campbell) described from the Southeast Pacific by Petrushevskaya (1975) is considered as conspecific with this new species, the California specimens of Calocyclas 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, late Early Oligocene to Late Oligocene.

Leg 120, Hole 749B: Sample 120-749B-2H-2, 45-47 cm, late Early Oligocene to Late Oligocene.

Leg 114, Hole 699A: Sample 114-699A-20H-2, 50-52 cm, late Early Oligocene to Late Oligocene.

Leg 114, Hole 703A: This species sporadically occurs in Samples 114-703A-6H-2, 70-72 cm and Sample 114-703A-6H-4, 60-82 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

Calocyclas 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

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

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

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

Calocyclas cf. semipolita Clark and Campbell. Abelmann, 1990, p. 897, pl. 7, fig. 4; Takemura, 1992, p. 745, pl. 4, figs. 5, 6; Takemura and Ling, 1997, p. 111, pl. 1, fig. 16.


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


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


not Calocyclas cf. semipolita Clark and Campbell. Abelmann,
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 a larger thorax.

We include Calocyclas (?) fragilis (Carnevale) group in the present species. Many forms described by Petrushhevskaya and Kozlova (1972) could be related to this species. Caulet (1991) assigned the Oligocene forms of this species to Calocyclas asperum (Ehrenberg) (= Eucyrtidium asperum Ehrenberg of previous authors). However, according to previous illustrations (Ehrenberg, 1875, pl. 8, fig. 15; Petrushhevskaya 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 Calocyclas 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 7488Z-14H, around 115.5 mbsf) in the southern Indian Ocean based on the samples from the same ODP Hole 7488B. They based their conclusions on the abrupt increase in abundance of cool-water nannofossil taxa, the occurrence of ice-rafted debris and a distinctive δ18O 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 7488B: Sample 120-7488B-17H-4, 45-47 cm Middle Eocene, and Samples 120-7488B-16H-5, 45-47 cm to 120-7488B-9H-4, 45-47 cm, Late Eocene to Late Oligocene.

Leg 120, Hole 749B: Samples 120-749B-3H-7, 45-47 cm to 120-749B-4H-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, Middie 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.

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Two ammonite species of Mortoniceras from the Yubari Mountains (Hokkaido) and their geological implications
(Studies of the Cretaceous ammonites from Hokkaido and Sakhalin-LXXXII)

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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 Hysteroceras 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 MOSLOVITZIIDAE 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:
Two species of *Mortoniceras* 171

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 ammonoids, such as *Desmoceras* (Desmoceras) *kossmati* Matsumoto, *Desmoceras* (Pseudouhtigella) *japonicum* Yabe etc. *Graysonites wooldridgei* Young and *Parajaubertella kawakitana* Matsumoto, among others, indicate that the lower part of the Member Me [=lid] is referable to the lower Cenomanian.
Type species.—Ammonites vespertinus Morton, 1834, by original designation of Meek (1876, p. 443).

Subgenus Mortoniceras (Mortoniceras) Meek, 1876

Remarks.—Subfamily Mortoniceratinae is allocated in the family Mojsisoviciidae Hyatt by Kennecy (in Gale et al., 1996, p. 557), but we follow Wright (1996, p. 134-140) in placing the subfamilies Brancoceratinae, Mojsisoviciinae 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 Mortoniceras we agree with Wright (1996, p. 141).

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

**Mortoniceras (Mortoniceras) cf. geometricum**

Spath, 1932

![Figure 3](image_url)

**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 bulia 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 bulullate 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.
Two species of Mortoniceras

Figure 3. Mortoniceras (Mortoniceras) cf. geometricum (Spath). Lateral view of WE A211Y from Member Ld at loc. Y271001, ×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 *Mortoniceras (Mortoniceras) cf. inflatum* (Sowerby) by Kawabe et al. (1996, p. 448, pl. 2, fig. 6). That tentative identification should be revised. *Mortoniceras (Mortoniceras) 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. *Mortoniceras (Mortoniceras) geometricum* the bifurcated or alternated ribs persist to later growth stages, but in our specimen single ribs predominate on the late septal whor to the body chamber.

In many respects the Hokkaido specimen is similar to *Mortoniceras (Mortoniceras) 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 Angola illustrated by Renz (1971, pl. 4, fig. 1, text-fig. 5b; also Renz, 1982, p. 63, pl. 13, figs. 1a, 1b). That specimen was described as *Mortoniceras (Mortoniceras) arietiforme* (Spath), although Renz (1968a, p. 625) himself once compared it with *Mortoniceras (Mortoniceras) 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.**—Elobiceras, a genus of the Mortoniceratinae in our present knowledge, was established by Spath (1921, p. 306) on the basis of "Schloenbachia elobiasis Szajnocha, 1885" as the type species. Spath (1922, p. 137) also designated "Schloenbachia lenzi Szajnocha" of Choffat (1888, p. 65, pl. 1, fig. 6) as the holotype of another species of this genus, *Elobiceras 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 *Elobiceras*.

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 *Elobiceras arietiformis* 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 *Elobiceras* and regarded *Pervinquieria arietiformis* as a species closely approaching *Elobiceras*.

Renz (1971, 1982) transferred the generic name from *Pervinquieria* to *Mortoniceras* (Mortoniceras) and reported some examples of *Mortoniceras (Mortoniceras) 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 *Mortoniceras (Mortoniceras) arietiforme* by Renz seems to be identical with the holotype and Spath's specimens of *Elobiceras arietiforme* Spath.

On the other hand, as we have described above (see Comparison), the illustrated specimen of Renz's *Mortoniceras geometricum* is quite different from our specimen. It is an internal mould and has spiral notches on the long ribs. The ribs are bifurcated and the keel is destroyed.

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

<table>
<thead>
<tr>
<th>Specimen</th>
<th>D</th>
<th>U</th>
<th>U/D</th>
<th>H</th>
<th>H/D</th>
<th>B</th>
<th>B/D</th>
<th>B/H</th>
<th>H/h</th>
<th>Ribs</th>
</tr>
</thead>
<tbody>
<tr>
<td>WE. A211Y (at M)</td>
<td>188</td>
<td>92</td>
<td>0.40</td>
<td>53</td>
<td>0.28</td>
<td>—</td>
<td>—</td>
<td>1.00</td>
<td>1.23</td>
<td>43</td>
</tr>
<tr>
<td>WE. A211Y (at m)</td>
<td>136</td>
<td>65</td>
<td>0.48</td>
<td>42</td>
<td>0.31</td>
<td>—</td>
<td>—</td>
<td>1.00</td>
<td>1.45</td>
<td>39</td>
</tr>
<tr>
<td>Spath (1933, pl. 44, fig. 1)</td>
<td>230</td>
<td>106</td>
<td>0.46</td>
<td>73</td>
<td>0.32</td>
<td>—</td>
<td>—</td>
<td>1.00</td>
<td>1.43</td>
<td>40</td>
</tr>
<tr>
<td>Haas (1942b, pl. 18, fig. 4)</td>
<td>136</td>
<td>51</td>
<td>0.38</td>
<td>45</td>
<td>0.33</td>
<td>30</td>
<td>0.22</td>
<td>0.67</td>
<td>1.15</td>
<td>44</td>
</tr>
<tr>
<td>Renz (1971, pl. 4, fig. 1)</td>
<td>185</td>
<td>78</td>
<td>0.42</td>
<td>62</td>
<td>0.34</td>
<td>43</td>
<td>0.23</td>
<td>0.69</td>
<td>1.38</td>
<td>40</td>
</tr>
<tr>
<td>Spath (1922, pl. 2, fig. 6)</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>72</td>
<td>—</td>
<td>44</td>
<td>—</td>
<td>0.61</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

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 *Mortoniceras (Mortoniceras) geometricum*; Haas (1942b, pl. 18, fig. 4); "Pervinquieria arietiformis"; Renz (1971, pl. 4, fig. 1); "Mortoniceras (Mortoniceras) arietiforme"; Spath (1922, pl. 2, fig. 6); *Elobiceras arietiforme*. D = diameter, U = width of umbilicus, H = whorl height, B = whorl breadth, h = whorl height half adapical from H, c = costal, ic = intercostal; Ribs = number of ribs to a whorl. Linear dimensions in mm.
Two species of Mortoniceras

Figure 4. Mortoniceras (Mortoniceras) rostratum (J. Sowerby). Lateral view of GK H8491 from Member Mb at loc. 544, ×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' "Pervinqueria 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. 396) 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 Hysteroceras 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 rectiradiate, 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) 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 (Pervinqueria) rostratum (Sowerby). Spath, 1932, p. 400, text-fig. 136.

Pervinqueria (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 midventer (=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 spits 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.](image-url)
inner whors 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 rhibs 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 stage. There is an exceptionally short rib at the end of the phragmocone (Figure 4).

The ribs in the earlier part of the septate whors 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 stoliczkai" 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-
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. 6.5E-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. 260) 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 quadrituberculate (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 hornlike 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, ×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, ×1 (photo by N. Egashira, without whitening).
Two species of *Mortoniceras*
is regarded as quadrituberculate even on the body chamber. In fact, Mortoniceras (Durnovarites) collignonii has four rows of tubercles on one side of the body chamber, without forming ventrolateral horns. In Mortoniceras (Durnovarites) subquadrum 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” dose 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 tuberculate 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) stoliczkaï. 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 Hysteroceras 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 Anthaphoceras 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 dose 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 Soeushinaï area of the Teshio Mountains, northwestern Hokkaido. In that area, however, the level of the boundary is between the Hysteroceras orbini Subzone and...
and the Hysteroceras varicosum Subzone.

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

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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 armored group and position for the unarmored group and cryptopylic types in the relation to the plate series for the dinoflagellate cysts is classified into saphopylic, theropylic and cryptopylic types. Within the saphopylic type, *Tuberculodinium vancampoae* (= cyst of *Pyrophacus steinii* 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.

A hypnozygote 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

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A hypnozygote 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*.
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 Pterospemopsis, 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.

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<tr>
<td>Compression direction in cysts</td>
<td>dorso-ventrally</td>
<td>dorso-ventrally</td>
<td>antero-posterior</td>
<td>dorso-ventral cyst rotated 90 degree within the planozygote</td>
<td>antero-posterior</td>
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<tr>
<td>Archeopyle type</td>
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<td>hypocystal</td>
<td>compound; antapical</td>
<td>precingular</td>
<td>compound; epicystal</td>
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Figure 1. Plate tabulation in vegetative cell. a: apical plate series; b: precingular plate series; c: apical pore complex (apc) and f; 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, ia: left accessory sulcal plate, aas: anterior accessory sulcal plate, rs: right sulcal plate, ls: left sulcal plate, ps: posterior sulcal plate, fp: flagellar pore.

--- 50μm
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 archoepyle. However, the possibility that the archoepyle type of *Tuberculodinium* is not hypocystal but precingular was raised by Wrenn and Damassa (1989).

Thus, the archoepyle 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 µmol photons·m⁻²·s⁻¹ and 12 hours - 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 (l). a; apical pore complex (black arrow) and t' of the planozygote. b and c; three paraplates (?) corresponding to the archoepyle which has already appeared before germination on the surface of hypnozygote (white arrows), and precingular processes (black arrows). d; enlargement of the archoepyle. 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.](image-url)
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 planozoogotic theca, clearly demonstrating a morphological relation between the planozoogote 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 planozoogote 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 planozoogote 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 planozoogote** (Figures 5, 6)

Some hypnozygotes used for our study on the life cycle remained within the planozoogotic theca and its wall even after exocystment (Figure 5). Figure 6 shows the morphological features of both planozoogote and hypnozygote. The planozoogote 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 planozoogote was 7', 11", 13c, 13"", 4p, 1ap, and 3"", and the process formula of this cyst was 5 (3 + 2s)' + 2 8', 11", 0c, 10"", and 3"" + 3s.

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

Clonal cultures of *P. steinii* were established by a single cell isolation from net-haul samples at Yokohama Umizumashichi 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 planozoogote was produced and was morphologically similar to vegetative cells except for its larger cell size. After one to two days active swimming, the planozoogote 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 (mesosome). These processes were barrel-shaped and identical to those previously observed in fossil forms. This hypnozygote was contained within the theca of the planozoogote (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 planozoogote 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 ? vancampoae.* 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. vancampoae,* which now Balich (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...
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. steini* 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. steini*) 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.
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. rossignolii*, 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

![Images of Saphopylic type with various forms: Apical, Intercalary, Precingular, Epicystal, Intercalary, Precingular, and Apical/Intercalary/Precingular Combination.]

Theropylic type

![Images of Theropylic type with various forms: Precingular, Transapical.]

Cryptopylic type

![Images of Cryptopylic type with various forms: Tremic, Chasmic.]

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 van campae 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.

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

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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 three Asian 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 characters. 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.
York, Beijing, paper: Geology, National Science Japan; Washington, D.C., (Figure 2C), the distribution of the Akasaki Formation in Ohyanomachi, western part of Kyushu, Japan, and 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 1/2 (Figures 2A, B), fragmentary left 1/2 (Figure 2C), enamel remains of right and left 1/2? (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, 1996).

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 1/2, 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 1/2 of a trogosome tillodont. The right 1/2 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 1/2 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 labiomesial corners of the 1/2 are rounded in cross section (Figure 3D). The enamel-free dentine of the right 1/2 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 1/2. 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 1/2 because it was found close to the right 1/2. 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 1/2, respectively, judging

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 cusp 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 1/2, P/4, and M/3 talonid of NSM-PV20121, cf. Trogosus sp. A-C: right 1/2; 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.

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Transverse width of right 1/2</td>
<td>11.4</td>
</tr>
<tr>
<td>Anteroposterior length of right 1/2</td>
<td>23.1</td>
</tr>
<tr>
<td>Transverse width of left 12/? (enamel portion)</td>
<td>13.3</td>
</tr>
<tr>
<td>Transverse width of right P/4 trigonid</td>
<td>15.5*</td>
</tr>
<tr>
<td>Transverse width of right M/3 talonid (second lobe)</td>
<td>16.2*</td>
</tr>
<tr>
<td>Transverse width of right M/3 third lobe</td>
<td>13.3</td>
</tr>
</tbody>
</table>

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 trogogone 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, gilliform teeth and the rooted hypsodont teeth are referable to the second incisors and lower cheek teeth of a trogosine tillodont, respectively. The possession of gilliform l2/2 and an elongated, basin-shaped third lobe of M3/3 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 gilliform tooth has been confused in some previous studies (Schoch, 1986). However, the gilliform teeth described here are not as laterally compressed as in canines of stylinodontid; and as the right l2/2 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 distinguishable 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 alveoli on both buccal and lingual sides, the buccal crowns are not so convex in vertical section as in *Trogosus*, and the third lobe on M3/3 is not elongated (Schoch, 1986; Chow et al., 1999). 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 l2/2 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 *Tilodon 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 18449) 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 *Tildodon 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 *Kuechaunius, Higotherium, and Chungchienia*. All the fragmentary teeth are considerably larger than those of the holotype of *K. shantunensis* (IVPP V 2764), in which the l2/2 possesses a longitudinal shallow groove on its labial surface and anteroposteriorly shortened enamel-free dentine; the unique l2/2 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 M3/3 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 l2/2 of trogosines from China: "Tilodontia, gen. indet. sp. 1" (IVPP V 2765) and "Tilodontia, 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 (1996, p. 121) reidentified the specimen as a fragmentary l2/2 of a trogosine tillodont. The right l2/2 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 l2/2 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 l2/2 of *Higotherium*. Nevertheless, the two l2/2 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.

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

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Abstract. We have examined the genus- and species-level taxonomy and distribution of the ocinebrine 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 ocinebrine 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 ocinebrenine 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 ocinebrenines 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, Tentokujī Formation, Akita Prefecture, Locality 3 of Amano et al. (1996); Pliocene, Kuwae Formation, Niigata Prefecture, Locality 2 of Amano (1993a); 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).

Systematics

Family Muricidae Rafinesque, 1815
Subfamily Ocinebrinae Cossmann, 1903

Remarks.—The muricid subfamily Ocinebrinae 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 (adapturally) 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 ocinebrine 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. Jousseaume (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. acanthophorus_ (A. Adams) in the genus. All these taxa are here considered synonyms of a single species for which the oldest available name is _Murex aduncus_ Sowerby, 1834 (see also Fulton, 1917). Curiously, Jousseaume (1882) assigned _Murex inornatus_ Recluz here included in the genus _Ocinebrellus_ and _M. talienwhanensis_ Crosse (a synonym of _M. inornatus_) to _Crassilabrum_ Jousseaume, 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_ Hermannsen, 1846; _Pteropurpura_ Jousseaume, 1880; _Muregina_ Vermelj, 1996 (in press); and _Pterorytis_ Conrad, 1863 (for additional discussion see Vermelj, 1996 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_ Jousseaume, 1880 (South Africa) and _Calcitrapessa_ Berry, 1959 (Baja California, Mexico), two genera closely similar to _Pteropurpura_, the varices are adaperturally extended as adaperturally and adaperturally pointing spines respectively. There is no labral tooth in _Pteropurpura_, _Poropteron_ and _Calcitrapessa_.

The tropical eastern Pacific genus _Murex_ 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, 1957).

Finally, the genus _Ocenebra_ Gray, 1847, as restricted by Vermeij and Vokes (1957), 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, 1880, p. 4, pl. 1, fig. 14.

_Murex talienwhanensis_ Crosse, 1862, p. 56–57, pl. 1, fig. 9.

_Murex endemonis_ Smith, 1875, p. 420; Sowerby, 1879, fig. 213.

_Murex (Oocenebra) inornatus_ Recluz, Tryon, 1880, p. 126–127, pl. 37, fig. 444.

_Murex (Oocenebra) japonicus_ Dunker. Tryon, 1880, p. 126, pl. 37, figs. 445–448.

_Murex (Oocenebra) endemonis_ Smith. Tryon, 1880, p. 128, pl. 38, fig. 454.

_Murex polygonulus_ Lamarck. Yokoyama, 1931, p. 200–201, pl. 12, figs. 3a, b.

_Tritonalia inornata endemonis_ (Smith). Kinoshita and Ishahaya, 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 endemonis_ (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.
Figure 3. 1-3, 6: Ocinebrina lumarius (Yokoyama). 1a, b; x1.2, JUE no.15640, Setana Formation. 2a, b; x1.2, NSMT-Mo no.49546, Asamushi (Recent). 3a, b; x1.5, UMUT CM no.23118, Holotype, Sawane Formation. 6a, b; x1.2, SHM no.6146, Daishaka Formation. 4-5, 7-10, 15: Ocinebrina inornatus (Recluz). 4a, b; x1, JUE no.15641, Cape Erino (Recent). 5; x1, JUE no.15642, Akkeshi (Recent). 7a, b; x1, IGPS no.94814, Koje Do Is., Korea (Recent). 8; x1, UMUT CM no.9358, "Ocinebra cf. japonica (Dunker)" by Iwasaki (1970), Kubota Formation. 9a, b; x1.2, UMUT CM no.25896, "Murex polygonulus" Lamarck by Yokoyama (1931), Kubota Formation. 10a, b; x1, SHM no.2672, "Tritonalia inornata" (Recluz) by Nomura and Hatai (1936), Kubota Formation. 15a, b; x1, NSMT-Mo no.49538, Toba (Recent). 11a, b: "Ocinebra" katayamai Matsubara; 11a, x1.5, f1b, x1, IGPS no.102829, Holotype, Yotsuyaku Formation. 12-14: Ocinebrina ogasawari sp. nov. 12; x1.2, JUE no.15643, Kwae Formation. 13a, b; x1, JUE no.15635, Holotype, Omma Formation. 14a, b; x1, UMUT CM no.13783, "Tritonalia (Ocinebrinus) aduncus" Sturt, subsp. by Otuka (1936), Sasakawa Formation. 16a, b: Ocinebrinus protoactanucus (Hatai and Kotaka), x1, IGPS no.77798, Holotype, Ginzan Formation.
Taxonomy and evolution of Ocinebrellus
**Ocinebrellus lumarius** (Yokoyama, 1926)

Figures 3—1, 3, 6

Ocinebra lumaria Yokoyama, 1926, p. 270, pl. 32, fig. 21.

Trionalia inornata lumaria (Yokoyama). Kinoshita and Ishaya, 1934, p. 8, pl. 5, fig. 37.

Trionalia lumaria (Yokoyama). Nomura and Hatari, 1935b, p. 124—125, pl. 13, figs. 1a, b.

Ocinebra lumaria (Yokoyama). Habe and Iti, 1965, p. 38, pl. 11, fig. 2.

Ceratostoma sp., Iwai, 1965, pl. 20, fig. 15.

Ceratostoma (Ocinebra) japonicum (Dunker). Matsuura, 1977, pl. 1, fig. 33.

Ceratostoma (Ocinebra) 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 comparison.—This is the smallest species of Ocinebrellus, with a maximum shell height of 233 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 ten (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 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).

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Height</th>
<th>Spire length</th>
<th>Canal length</th>
</tr>
</thead>
<tbody>
<tr>
<td>IGPS no. 77798 (Holotype)</td>
<td>44.6+</td>
<td>10.1</td>
<td>10.3+</td>
</tr>
</tbody>
</table>

Distribution.—Miocene Ginzan Formation in Yamagata Prefecture.

---

**Ocinebrellus aduncus** protoaduncus (Hatai and Kotaka, 1959)

Figures 3—16a, b

Ocinebra aduncus protoaduncus Hatai and Kotaka, 1959, p. 10, figs. 1, 3.

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

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

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 Ocinebrellus 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.

---

**Ocinebrellus ogasawarai** sp. nov.

Figures 3—12—14; 4—1, 4—6, 9, 13

Trionalia (Ocinebrellus) aduncus (Sowerby) subsp. Otuka, 1936, p. 733—734, pl. 42, figs. 15a, b (non figs. 9, 13).

Ceratostoma (Ocinebra) japonica (Dunker). Kaseno and Matsuura, 1965, pl. 3, figs. 6—8; Matsuura, 1965, pl. 38, fig. 11.


Ocinebra japonica (Dunker). Ogasawara et al., 1986, pl. 23, fig. 10.

Type locality.—Bank of Sai River, early Pleistocene Omna Formation.

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

Material.—Thirteen fossil specimens.

Diagnosis.—Medium-sized ocinebrine shell characterized by numerous spiral cords (eighteen to forty-four on last whorl), three to ten axial ribs or varices on body whorl,
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 subterminal 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 0.39), 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 to 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).—

<table>
<thead>
<tr>
<th>Specimens</th>
<th>Height</th>
<th>Spire height</th>
<th>Canal length</th>
</tr>
</thead>
<tbody>
<tr>
<td>JUE no. 15635 (Holotype)</td>
<td>39.7+</td>
<td>9.7</td>
<td>12.6</td>
</tr>
<tr>
<td>JUE no. 15636 (Paratype)</td>
<td>23.4</td>
<td>8.7</td>
<td>10.4</td>
</tr>
<tr>
<td>JUE no. 15637 (Paratype)</td>
<td>25.8</td>
<td>6.3</td>
<td>6.4</td>
</tr>
<tr>
<td>JUE no. 15638 (Paratype)</td>
<td>33.1</td>
<td>7.1</td>
<td>11.7</td>
</tr>
</tbody>
</table>


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, 1879, 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 (Ocinea) falcatus Sowerby. Tryon, 1860, 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) aduncus (Sowerby). Kinoshita and Isahaya, 1934, p. 8, pl. 5, fig. 39.
Tritonalia (Ocinebrellus) aduncus (Sowerby) subsp. Otuka, 1936, pl. 42, figs. 9a, b, 13, 14 (non fig. 15).
Tritonalia aduncus (Sowerby). Nomura, 1938, p. 269, pl. 34, fig. 19.
Kanekihara, 1942, pl. 3, figs. 8a-b.
Ocinebra (Ocinebrellus) aduncus (Sowerby). Habe, 1958, p. 19, pl. 3, fig. 13, pl. 4, fig. 13; Kira, 1959, p. 60-61, pl. 24, fig. 16.
Ocinebra 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.
Ocinebra aduncum (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; Itô et al., 1986, pl. 10, fig. 4; Ito, 1989, pl. 6, fig. 2.
Ocinebrellus aduncus (Sowerby). Yoo, 1976, p. 71, pl. 12, fig. 5.
Ocinebrellus aduncus (Sowerby). Yoo, 1976, p. 73, pl. 13, figs. 6, 7.
Pteropurpa aduncus (Sowerby). Radwin and D'Attilio, 1976, p. 129, pl. 22, fig. 10.
? Ocinebra 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). Itô et al., 1986, pl. 10, fig. 3.

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 subterminal 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’Aittilo (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 *Ocinebrellus* aduncus.

**Comparison.**—*Ocinebrellus* aduncus closely resembles *O. ogasawari* 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. *Ocinebrellus* 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 apical 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, Sennata, 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 *Ocinebrellus*, there are several Miocene species whose relationship with *Ocinebrellus* remain uncertain. We treat one of these species as "*Ocinebra* 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.

"*Ocinebra* katayamai" Matsubara, 1996

**Type locality.**—Upper reaches of the Nesori River about 3 km east of Nosokei, Ichinohe Town, Ninche 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 of 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 *Ocinebra* 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 *Ocinebra*.

"*Ocinebra* katayamai" resembles *Ocinebrellus 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 "*Ocinebra* 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 "*Ocinebra* katayamai" does not fit comfortably into any described *ocinebrine* genus. It may be necessary to establish yet another new ocinebrine genus for this taxon, but we are reluctant to take this step here. We leave "*Ocinebra* katayamai" in the genus *Ocinebra* 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 *Ocinebra*.

**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. chejtschenensis* 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 *Ocinebrellus*, and therefore probably do not belong to that genus.

Other species have a lower spire and could belong to *Ocinebrellus*. These includes *T. kamchtatica* (Kakert Formation), with high varices and low cords; *T. kavanensis* (Kakert Formation), with sparse varices and low cords; *T. kejschenensis* (Kakert Formation), with six to seven axial blades and obsolete spiral sculpture; *T. ochotka* (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 kamchtatica*, *T. kavanensis* and *T. ochotka* appears to be shouldered as are species of *Ocinebrellus*, whereas *T. rekinicus* is not. The siphonal
Table 1. Species characters of Ocinebrellus.

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

1SH=spire height 2CL=canal length 3number of axial varices or ribs on body whorl 4number of denticles on the inner side of outer lip 5number of spiral cords on body whorl 6existence of labral tooth 7category, including

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 adicalip 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 adicalip sinus, and distinctly developed varices. This stock comprises the middle Miocene O. protoaduncus (Hatai and Kotaka), the Pliocene to early Pleistocene O. ogasawari sp. nov., and the Pliocene to Recent O. aduncus (Sowerby).

The genus Ocinebrellus probably originated in the northwestern Pacific, although its precise origin remains 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 ocinebrelline murids 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 ocinebrellines.

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), while O. protoaduncus is recorded 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.
Taxonomy and evolution of *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 ocinebrine genus. *Nucella* originated during the early Miocene in the warm-temperate northeastern 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.,
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**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-II Fang, Myong-Ok Hyon, Yoshio Furukawa, Yutaka Tanaka, Tomoo Hashimoto, Shinji Kikuchi, Kagetaka Watanabe.

Resigned members: Kaname Kanda, Win Zaw, Shinichi Sato.

Deceased member: Katsumi Abe.
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、世言：海保邦夫、西、広戸、大野照文」が行われます。
第148回例会、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、後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、従来とは異なる形式での開催が予定されております。従いまして、第149回例会（2000年6月末に開催予定）までは、従来通り開催の申し込みを受け付けますが、2001年以降の開催申し込みは、しばらくの間見あわせて頂きます。

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