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Late Cretaceous (Cenomanian) bakevelliid bivalve, *Pseudoptera acuticarinata* (Nagao, 1932) from the Mikasa Formation, Middle Yezo Group in central Hokkaido, Northeast Japan

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北海道中央部の中部蝦夷層群三笠層から産した後期白亜紀（セノマニアン）の Bakevellia 科二枚貝 *Pseudoptera acuticarinata* (Nagao, 1932)

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Abstract. A Cenomanian bakevelliid bivalve species *Pseudoptera acuticarinata* (Nagao, 1932) that occurred from the lower part of the Mikasa Formation, Middle Yezo Group, Yezo Supergroup in the Ponbetsu River section, is redescribed on the basis of 181 left and 11 right valves newly collected, focussing on ligament structure and right valve morphology. This species is characterized by a strongly inflated, carinated left valve ornamented with fine radial plicae, and a nearly flat and smooth right valve without carina and ornamentation. While the small anterior ear is obtusely demarcated by shallow sulcus, the triangular flat posterior wing is sharply demarcated by dorsal ridge of the main body. Both surfaces are covered by growth lines. Four ligament pits, an oblique cardinal tooth and a posterior lateral tooth are observable on the ligament plate of the left valve. Judging from the shell morphology, mode of fossil occurrence and sedimentary facies, *P. acuticarinata* is presumed to be a kind of twisted recliners, relining on left valve with horizontal commissure, or a gregarious mode of life epibyssately attached to each other or shelly materials with commissure plane oblique to sea bottom, reclining on the nearly flat antero-dorsal surface of left valve.

キーワード：*Pseudoptera acuticarinata*, Bakevelliidae, Bivalvia, Cenomanian, Late Cretaceous, Mikasa Formation

Pseudoptera acuticarinata Nagao, 1932

Pl. 1, Figs. 1-11

1932 *Gervillia* (*Pseudoptera*) *acuticarinata* Nagao, p. 37-38, pl .5, figs. 13-15

Type. — One of the three syntypes described and illustrated by Nagao (1932), is designated as lectotype (fig. 15 on pl. 5; GMH 4561a) in this study. They are reposited in the Department of Earth and Planetary Sciences, Faculty of Science, Hokkaido University in Sapporo.

Material. — As the syntypes are too poorly preserved to observe the detailed morphology except shell outline, the following descriptions are based on about 390 specimens newly collected from the type locality (Ponbetsu River section) and additional two localities. Our collection is composed of 181 left, 11 right valves and other several hundred undifferentiated valves or fragments. Most of them are from the type locality, but a few from the other two. Among them, only seven specimens illustrated here are registered (UMUT MM 27813 to 27819) and reposited in the University Museum, University of Tokyo. Others are kept in the Department of Environmental Sciences, Ibaraki University.

Diagnosis. — Pteriform left valve more inflated, acutely carinated and ornamented by numerous fine radial plicae, with obscurely-demarcated, small semicircular anterior ear and well-separated, medium-sized triangular posterior wing having concentric growth lines and faint radial costae. Right valve flat and smooth.

Description. — Shell small to medium-sized (less than 3.5mm long and 2.5mm high); strongly inequivalved and inequilateral mytiliform with the left valve being much more inflated and finely radial-plicated than the nearly flat right valve; the main body of the left valve is more or less narrow cuneiform with an acutely straight central carina obliquely extending from umbo to postero-ventral extremity and forming a growth axis. Antero-dorsal margin short and inclined with low-angle; antero-ventral margin obliquely descending and broadly arched downward but its posterior end making a right-angled turn to nearly vertical and slightly-rounded postero-ventral margin at the intersection with carina. While the ventral surface below carina round down rather steeply to the ventral margin, the dorsal half nearly flat and gently inclined posterodorsally. Small and narrow semicircular anterior ear gently inflated and obscurely demarcated from the main body by shallow radial sulcus; ventral margin of the sulcus forms shallowly concave byssal sinus; medium-sized and triangular-shaped posterior wing compressed, shallowly concave, and sharply separated by a dorsal ridge of the main body; both surfaces of the ear and wing ornamented with fine growth lines, but with very faint radial striae near the ventral edge of the wing in some specimens; length of posterior wing ranging from one third to two third of shell length, though depending on preservation of specimens. Umbo situated anteriorly at about one sixth of shell length from the anterior extremity, and slightly projected beyond straight hinge line; umbonal angle 50 to 60 in degree. Fine numerous radial plicae extended from umbo to ventral margin straightly and well developed at carina and its nearby, but weakened dorsally above carina. Growth lines well developed on the whole valve surface including anterior ear and posterior wing.

On the other hand, the right valve is nearly flat and smooth without a carina and ornamentation, though based on only 11 small (less than 1 cm long) mold specimens of our collection (Pl. 1, Fig. 7). Anterior ear and posterior wing obscurely demarcated from the main body by shallow sulcus and low ridge respectively.

Multivincular-type hinge structure of left valve having three or four elongated, shallow ligament pits and wider interspaces on hinge plate (Fig. 2; Pl. 1, Figs. 8-10). Posterior pits and interspaces become wider, though the outline of the last pit is indistinct due to preservation; ventral margin of hinge plate grading into an oblique cardinal tooth below umbo and a slightly oblique lateral tooth posteriorly. Probably faint traces of muscle scar observable on inner shell surface below posterior lateral tooth (Fig. 2, Pl. 1, Fig. 10). There is no right valve observable hinge structure.

Though shell materials are too poorly preserved to reconstruct original shell microstructure accurately, outer prismatic calcite and inner homogenous structure composed of granular particles are provisionally observed.

Measurements. — see Fig. 2 for abbreviations of parameters except T (valve thickness)

no.	L	H	T	A	W
UMUT MM 27813	25.2	21.3	3.8	2.6	15.7
UMUT MM 27814	> 20	> 16	2.4	2.2	12.8
UMUT MM 27815	ca21.9	20.8	2.8	2.5	_
UMUT MM 27816	8.2	7.2	ca1	1.1	5.3
UMUT MM 27818	22.6	15	3.5	2.1	11.6

Comparison. — As we could not access the classical monographs and references as Sowerby (1836), Meek and Hayden (1865), Woods (1905) and others, comparisons with the type species, *Pseudoptera anomala* Sowerby (1836) and *P. subtortuosa* (Meek and Hayden, 1865), remains to be studied. As long as we refer to Cox et al. (1969), *P. acuticarinata* differs from the type species in having a rounded central carina, a dorsal ridge of the main body

Introduction

Pseudoptera acuticarinata (Nagao, 1932) is a Cenomanian bakevelliid bivalve species occurring from the lower part of the Mikasa Formation, Middle Yezo Group, Yezo Supergroup, central Hokkaido (Ando, 1987, 1990a, b, 1997). Though this species has been assigned to the Bakevelliidae (Hayami, 1975; Tashiro, 1992) since Nagao (1932), the right valve morphology and ligament structure were not originally described by Nagao (1932). During our paleontological research on the shallow-marine bivalve fauna from the Mikasa Formation distributed around the Ishikari Coal Field area, we found some left valves preserving ligament and shell microstructure and right valves from the type locality in the Ponbetsu River section.

We redescribe *Pseudoptera acuticarinata* on the basis of numerous specimens obtained in our studies, focussing on ligament structure and right valve morphology. Then the paleoecology is discussed from the viewpoints of taphonomy and sedimentary facies in addition to shell morphology. This species is one of the last bakevelliid species in Japan. Bakevelliids were a prolific group in brackish to shallow-marine environments during the Triassic to early Cretaceous time.

Geologic Setting

The Mikasa Formation (Matsumoto, 1951, 1954), the upper half of the Middle Yezo Group, Yezo Supergroup, exposed only in the central western part of the meridional zone of Hokkaido, represents the western marginal facies of the Yezo basin. It is about 300 to 700 m in thickness, and mainly consists of shallow-marine to coastal sandstone, conglomerate and siltstone that yield shallow-marine bivalves more commonly than ammonites. Some well-preserved ammonites and inoceramids obtained from calcareous nodules of various sizes, suggest the formation to be latest Albian to late Turonian in age, though its lower and upper limits are more or less diachronous (Ando, 1990a).

As the Mikasa Formation is distributed along the Sorachi-Ikushunbetsu Anticline and the Manji and Hatonosu Domes, total 40 km in north-south and 10 km in east-west direction, we can trace lateral changes of facies, thickness and also biofacies. Sedimentary facies and their distribution of the Mikasa Formation were described by Ando (1987, 1990a, b) in detail. Due to facies changes, it is difficult to apply lithostratigraphic subdivision into members to the whole area.

The lateral and vertical facies changes show onshore-offshore gradients of the westward-coarsening (shallowing) depositional environments (Ando, 1990b). There had been a north-south running coastline and westerly volcanic hinterland. The abundance of storm deposits represented by hummocky cross-stratified (HCS: Dott and Bourgeois, 1982) sandstone suggests that storm-dominated lower shoreface and sandy upper shelf were widely developed as a delta front. Disarticulated, thick-shelled bivalves (*Pterotrigonia, Apiotrigonia, Yaadia, Glycymeris, Aphrodina* and others) are often concentrated in gravel or shell lags and HCS lamina. The species composition varies depending on the age and depositional environments of the fossil horizons (Ando and Kodama, 1998).

Materials and Stratigraphic Position

About 390 valves and fragments of *Pseudoptera acuticarinata* were obtained from three sections, mostly the Ponbetsu River section (type locality; Fig. 1), and insignificantly the eastern and western limbs of the Ikushunbetsu anticline along the Ikushunbetsu River (E, F, G on fig. 3 in Ando, 1990a). Though Nagao (1932) did not describe the detailed stratigraphic horizon, we confirmed it as the lower part of the Mikasa Formation (middle part of Twa Member in Matsuno et al., 1964) by careful sampling (Fig. 1; Ando, 1987, 1990a, Ando and Kodama, 1998). *P. acuticarinata* occurred from the horizons Po08 to 11 ranging 15 m thick, mainly associated with *Entolium obovatum*, inoceramid, *Pterotrigonia* sp., *Pinna saitoi* and other subordinates. The stratigraphic positions of the other two localities (middle part of Twb and Tb Members, respectively: Matsuno et al., 1964; Ando, 1990a, fig. 3) seem to be approximately the same as the Ponbetsu section. In terms of such the occurrences as an ammonite, *Calycoceras orientale* and an inoceramid, *Birostrina tenuis* from the lower Twa (Matsumoto, 1965 for ammonite and per. comm. with Dr. Asai for inoceramid), the stratigraphic range of *P. acuticarinata* may be the upper Lower to lower Middle Cenomanian at least, according to Matsumoto et al., 1991, Toshimitsu et al., 1995).

Systematic Descriptions

Pterioida Newell, 1965

Pteriina Newell, 1965

Bakevelliidae King, 1850

Pseudoptera Meek, 1873

Type species. — *Pseudoptera anomala* (Sowerby) from Albian, England.

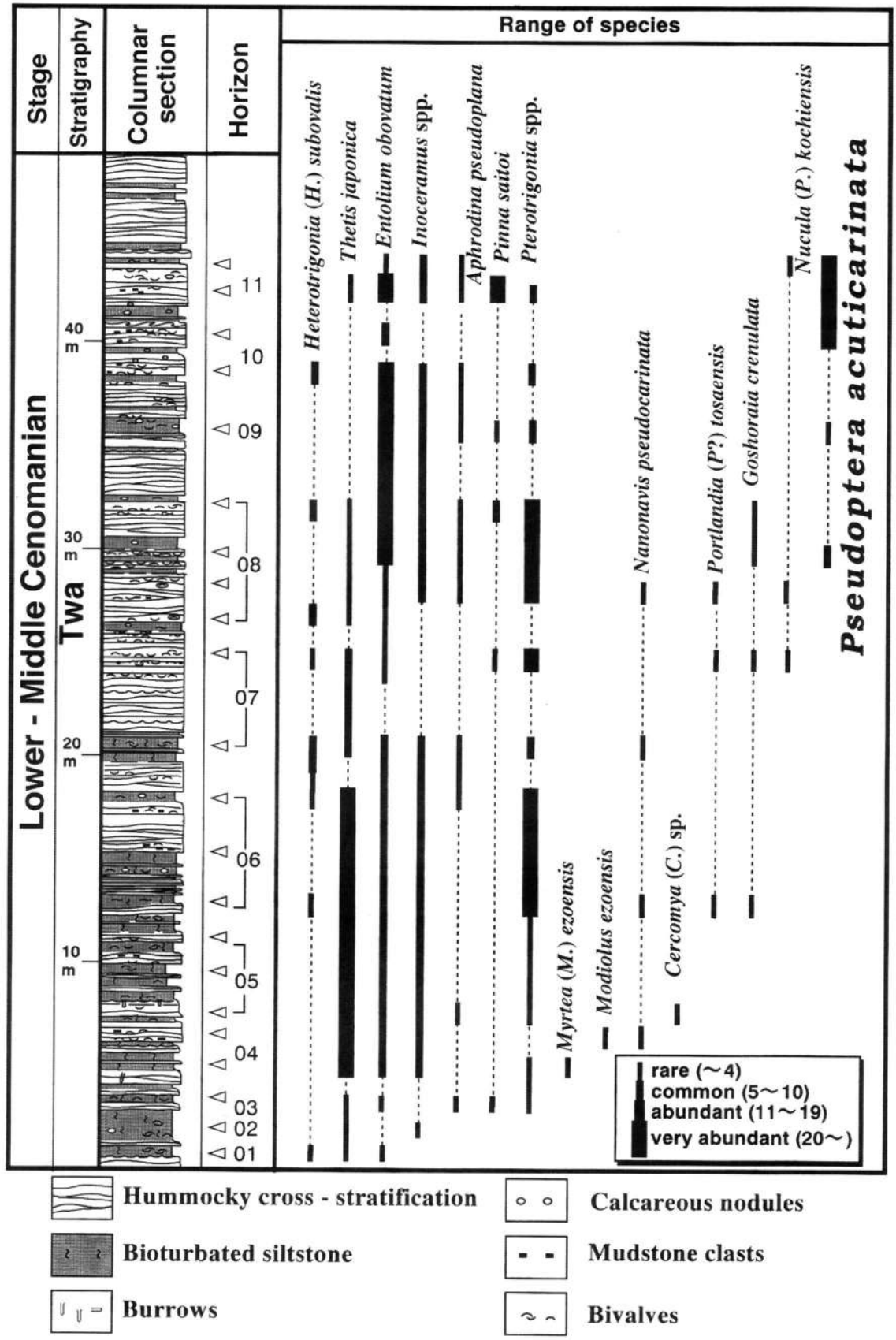

Fig. 1 Stratigraphic ranges of major bivalve species and *Pseudoptera acuticarinata* in the Mikasa Formation along the Ponbetsu River section. Numerals in parentheses in the bottom right inset mean number of occurring individual valves (including right and left valves). After Ando and Kodama (1998).

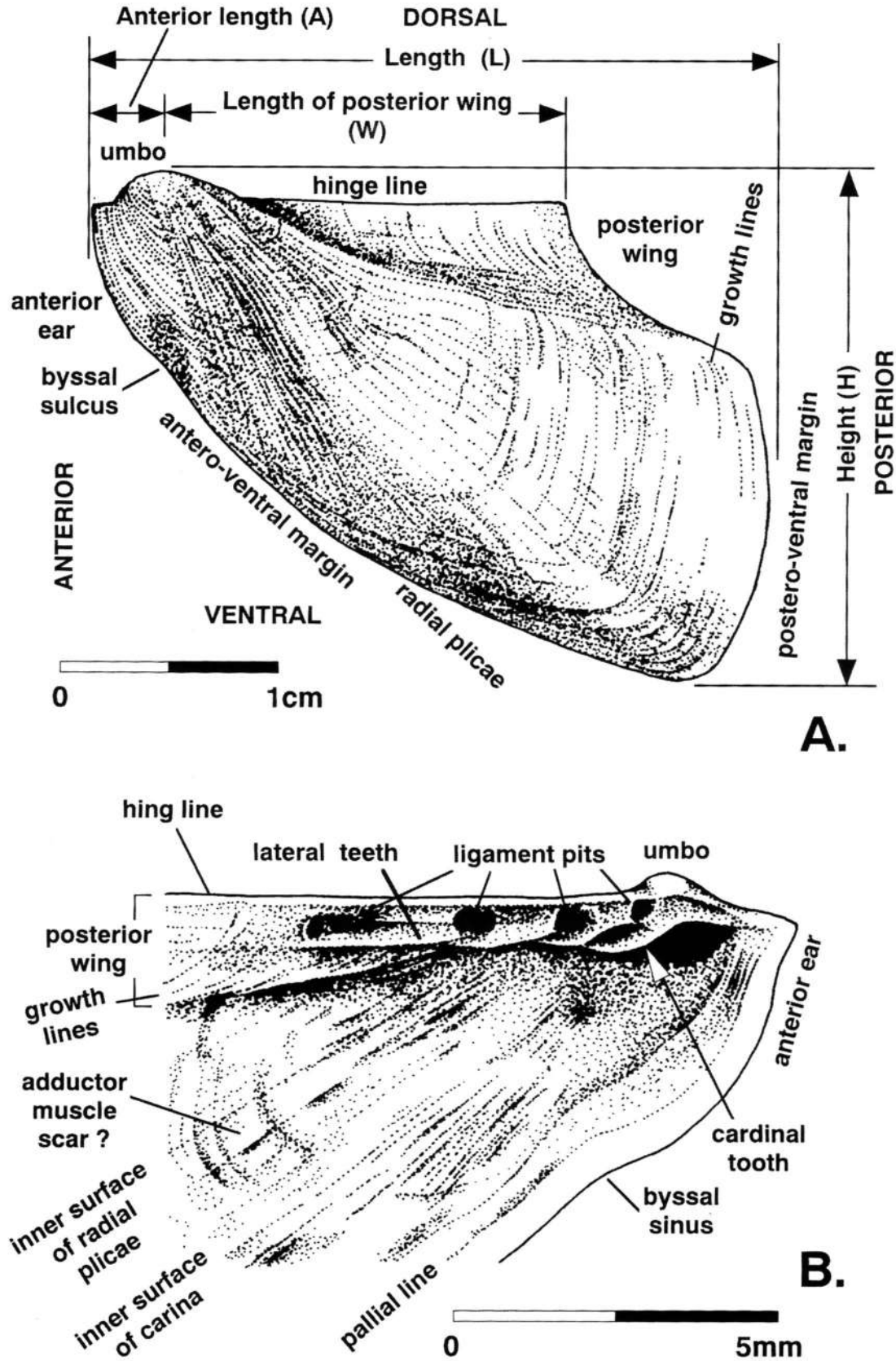

Fig.2 Reconstructed sketch and shell morphology of left valve in *Pseudoptera acuticarinata* . A: lateral view and outline; B: details of inner ligament area and shell surface

and relatively smooth posterior wing.

Stephenson (1952) proposed four Cenomanian *Pseudoptera* species, *P. serrata, hornensis, viana* and *rushana*, in addition to the reproductive illustration of *P. gregaria* (Shumard, 1860) from the Woodbine Formation (Cenomanian), Texas. These are the contemporaneous counterparts in the southern United States, but all of them are different from Japanese *P. acuticarinata* in morphology of shell outline, radial sculptures and posterior wing. *P. serrata* has serrated radial sculptures both on the main body and posterior wing. *P. hornensis* is characterized by gently inflated left valve without carina, ornamented with mainly concentric growth lines on the whole surface and partly corrugated radial sculpture only on the antero-ventral surface. *P. viana* has two distinct angular ridges as a central carina and a dorsal ridge of the main body. According to the quotation of Shumard (1860) in Stephenson (1952), *P. gregaria* has a more inflated right valve than left valve. This feature is different from all other species described until now.

According to Cleevely and Morris (1987), *Pseudoptera coerulescens* (Nilsson) from the upper Campanian in south England, has wide umbonal angle as *Pseudoptera*, posterior wing continuous from the main body and spiny or scaly radial sculpture. Abdel-Gawad (1986) described this species from the uppermost Maastrichtian of eastern Poland. Because the specimens are small and inner molds, an accurate comparison is difficult.

Dhont (1987) redescribed *Pseudoptera raricostata* (Reuss, 1854) from the Santonian of the Gosau Group, Austria. This species is different from *P. acuticarinata*, having only one or two strongly developed beaded radial plicae.

Pseudoptera sp. aff. *P. viana* was described for only an incomplete specimen from the Nekogawa Formation correlative with the lower part (Hauterivian) of the Ofunato Group, north to Ofunato City, Iwate Prefecture, north Honshu (Nakazawa and Murata, 1966). But this is different from *P. acuticarinata* in having radially plicated large posterior wing and more ventral position of carina. Though *P. elongata* (Nakazawa and Murata, 1966) was originally proposed as a species of *Waagenoperna*, it has the further prosocline and narrowly elongate form like *Mytilus* than *P. acuticarinata*.

Stephenson (1952) mentioned the number of ligament pits as 2 or more in *P. rushana*, 3 or more in *P. viana*, 4 to 5 in *P. hornensis* and 3 to 4 in *P. gregaria*. According to Nakazawa and Murata (1966), *P. elongata* has six pits. Therefore, the number depends on species and growth stages.

Occurrence. – Middle part of the Twa Member, the lower part of the Mikasa Formation in the Ponbetsu River section (Fig. 1) and the western limb of Ikushunbetsu anticline along the Ikushunbetsu River, and the middle part of the Tb Member in the eastern limb (Matsuno et al., 1964; Ando, 1987, 1990a, Ando and Kodama, 1998). Upper Lower to lower Middle Cenomanian.

Discussion

Taphonomy: sedimentary facies and mode of fossil occurrence

Sedimentary facies of the horizons 8 to 11 containing *P. acuticarinata* are represented by amalgamated HCS fine sandstone and subordinately intervening bioturbated sandy siltstone (facies 4 and 5 in Ando, 1990a). *P. acuticarinata* and other bivalves are mostly contained within HCS lamina less than one cm thick (Pl. 1, Fig. 11). While thick-shelled infaunal bivalves, *Pterotrigonia* spp. are characteristic of the lower Twa (Po01 - 08), the horizon Po11 is dominated by a thin-shelled epifauna *P. acuticarinata* and a scallop *Entolium obovatum*. The latter also occurs from sandy siltstone deposited within the inner to outer shelf indicating a more offshore sedimentary environment, though no such examples occur in this section. These two species are mostly disarticulated but relatively complete. The third most common are inoceramids. Their prismatic calcite shell fragments in the outer layer are frequently scattered on lamina surfaces. Because the group is generally more frequent in the offshore mudstone facies, the association with *P. acuticarinata* in the HCS sandstone facies of the Mikasa Formation confirm the wide range of habitat substrate for the inoceramids. Other subordinate associates are semi-infaunal or shallow infaunal bivalves such as *Pinna saitoi*, *Thetis japonica*, *Pterotrigonia* spp. and *Nucula kochiensis*.

This bivalve assemblage is characterized by dominant thin-shelled epifauna and subordinate shallow burrowers (infauna). Though the sedimentary facies composed of HCS fine sandstone suggest a high-energy environment of storm-dominated open-marine setting, the abundance of well-preserved, non-abraded complete shells of these species seems to indicate the transportation away from their habitat before burial might be subtle. Therefore, substrate of habitat at the time may correspond to lithofacies of the strata. The assemblage is presumed to reflect a fine-sandy, level-bottom community, on storm-dominated lower shoreface to inner shelf of open sea, which might be somewhat tolerant of physical reworking as waves and storm currents.

In general, *P. acuticarinata* are somewhat exclusively

concentrated on the lamina surface, but do not overlap each other very much (Pl.1, Fig.11). Of all shells distinguishable as right or left valves in our collection, over 90% are disarticulated left valves. On the other hand, right ones are only total 11 and small less than 10mm in length. But there are no articulated valves. About 60% of them are convex-up in position. The rarity of right valves may be due to the weakness of thin and flat valves lack in ornamentation.

Paleoecology

The bakevelliids were ecologically and morphologically a diverse group during the Mesozoic time. Functional morphology and autoecology of several species were considered by Stanley (1972), Savazzi (1984), Seilacher (1984) and Aberhan (1997).

There is no complete equivalent form to *P. acuticarinata* in these studies. But such the general shell morphology as triangular shell outline, strongly inflated left and flat right valves and non-torted flat sagittal plane, probably suggests this species is a twisted reliner somewhat like Triassic to middle Jurassic *Hoernesia*. While *Hoernesia* has neither prominent anterior ear nor byssal sinus, *P. acuticarinata* has both of the two. The presence of shallow byssal sinus below anterior ear surely shows, at least, a byssally attached mode of life for *P. acuticarinata*, though no direct evidence was found for an endobyssate or epibyssate interpretation. Therefore, it is easy to interpret the pleurothetic life position (reclining on left valve) anchored by byssus with horizontal commissure plane on the sea-bottom.

As an another alternative, we presume that *P. acuticarinata* lived epibyssately attached to each other or shelly materials with commissure plane oblique to the sea bottom, reclining on the nearly flat antero-dorsal surface of left valve. On the basis of the gregarious mode of occurrence and high-energy sedimentary environment, it might form patchily distributed small clumps or colonies on fine sandy substrates. Coarser ornamentation in the left valve might be useful to some extent as frictional resistance for physical disturbance by waves or currents.

Acknowledgments

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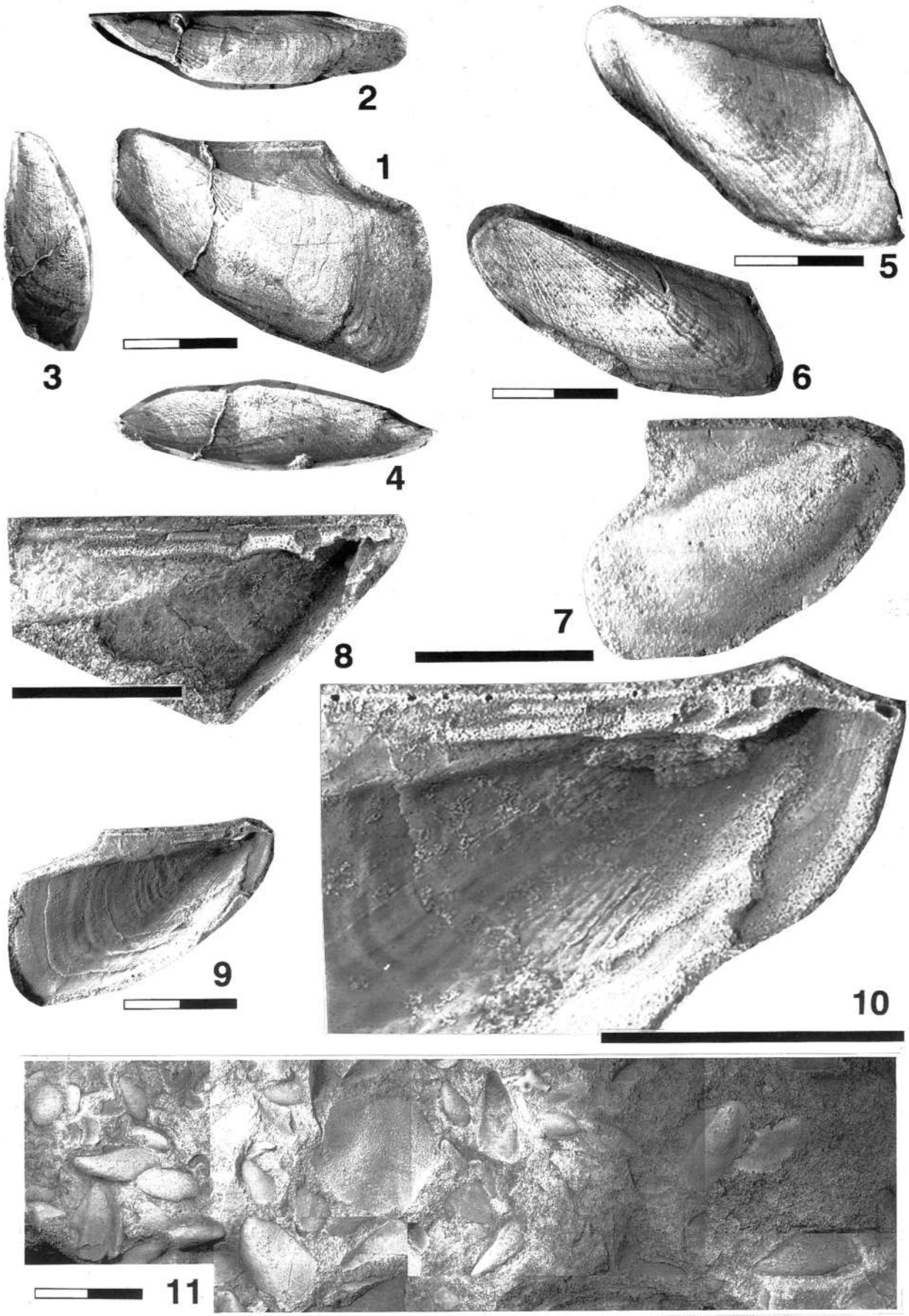
Plate 1 *Pseudoptera acuticarinata* (Nagao, 1932) from the middle part of Twa Member, Mikasa Formation, Middle Yezo Group, Yezo Supergroup in the Ponbetsu River section. Black bar: 5mm; black and white bar: 1cm. 1-6, 9, 10: silicon rubber casts from molds of left valves. The prefix alphabets of the registered numbers mean Mesozoic Mollusca in the University Museum, the University of Tokyo.

Fig. 1: Left valve of lateral external view (UMUT MM 27813)
Fig. 2: Dorsal view of Fig. 1
Fig. 3: Anterior view of Fig.1
Fig. 4: Ventral view of Fig. 1
Fig. 5: Left valve (UMUT MM 27814)
Fig. 6: Left valve (UMUT MM 27815)
Fig. 7: Right valve, lateral view of inner mold (UMUT MM 27816)
Fig. 8: Hinge area of left valve on external cast from inner mold (UMUT MM 27817)
Fig. 9: Inner view of left valve (UMUT MM 27818)
Fig. 10: Enlarged hinge area of Fig. 9
Fig. 11: Concentrated mode of occurrence on hummocky cross-stratified surface of fine sandstone. Most valves are convex-up in position and hardly overlapped each other. The central circular valve is *Entolium obvatum*. All valves of the others are mpsty *Pseudoptera acuticarinata* (UMUT MM 27819).

和文要旨

北海道三笠市の奔別川河床に露出する中部蝦夷層群三笠層下部のセノマニアンから産する，Bakevellia 科二枚貝，*Pseudoptera acuticarinata* (Nagao, 1932) について，新たに採集した左殻 181 個，右殻 11 個に基づき，古生物学的記載を行った．特に本種の靱帯構造と右殻の記載は初めてである．

左殻はよく膨らみ背稜がよく発達し表面が細かな放射肋で覆われるのに対し，右殻は平坦で表面装飾もほとんどない．放射肋がほとんどなく成長線が刻まれる前耳と後翼が発達し，本体とはそれぞれ不明瞭，明瞭に区別される．multivincular 型の靱帯構造が観察され，4 つの靱帯溝と 1 本の主歯，1 本の側歯が確認できた．形態・産状・堆積相から，左殻を海底に横たえた twisted recliner か，もしくは左殻前腹部の平坦部を横たえてお互いに足糸で付着しながら小群体を構成していたものと推定される．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