SCIENCE REPORT OF THE YOKOSUKA CITY MUSEUM, NO. 21
August, 1975

Some Cretaceous Patelliform Gastropods from the Northern Pacific Region*

Yasumitsu KANIE**

(With 28 text-figures, 2 tables and 20 plates)

北太平洋地域における白亜紀笠型巻貝の研究*

蟹江康光**

Contents

---

* This treatise has been presented to the Kyushu University for Doctor dissertation in 1975.

** Yokosuka City Museum, Yokosuka 238, Japan.
Manuscript received May 3, 1975. Contribution from the Yokosuka City Museum, No. 249.

Abstract

Many species of patelliform gastropods have been reported from the marine Upper Cretaceous deposits of Japan and other parts of the Northern Pacific region. These are one of the groups which enable us to establish Cretaceous biostratigraphic scheme and elucidating evolutionary history of Cretaceous marine faunas. However, our knowledge on them has remained incomplete. In this paper, I present a result of my study on the taxonomy, systematic descriptions and the biostratigraphic succession. I furthermore endeavor to make clear their paleoecology and evolutionary history.

Hitherto the taxonomic allocation of Cretaceous patelliform gastropods has been confusing. The shape of muscle-scars is used in this study to revise the confused state of major taxonomy, because it is one of the important characters of patelliform gastropods. I regard the Cretaceous patelloids under consideration as having a close relationship with the extinct group of the Capulidae in Mesogastropoda. With the respect to the shell structure, the fossil gastropods resemble some species of Mesogastropoda and Archaeogastropoda but differ from Basommatophora.

From the preceding data, a new family Anisomyonidae is proposed to accommodate these patelliform gastropoda. Its type-genus is *Anisomyon* from the Upper Cretaceous of the United States which was erroneously regarded as belonging to the Siphonariidae of Basommatophora. With the establishment of this family, certain species hitherto described under the generic names of *Acmaea* (Acmaeidae); *Helcion, Patella, Scurria* (Patellidae); *Anisomyon, Brunonia, Siphonaria* (Siphonariidae) are reassigned to the Anisomyonidae. The species from the Northern Pacific region are systematically described, with some revision of previous definition and a proposal of new taxa.

The Anisomyonidae appeared in the Aptian and disappeared in the lower Maestrichtian in the Northern Pacific region. Examples of the studied fossils are *Anisomyon annulatus* from the Aptian and Albian, *A. cassidarius* from the Turonian to Santonian, *A. transformis* from the lowest Campanian, *A. giganteus* from the main part of the Campanian and *A. problematicus* from the lower Maestrichtian. The species of this family are useful for the biostratigraphical division of the Upper Cretaceous strata.

In the Northern Pacific region, during the late Cretaceous, the shell became larger and thicker with time, the apex shifted towards the posterior margin and radial ribs appeared on the shell surface. Considering their occurrences in certain rock facies and comparing that with the ecology of recent patelloids, these changes could be regarded as being due to adaptation to the shallowing of the post Campanian sea owing to regression. Their mode of life may have changed from sticking on what other materials in the neritic sea to benthonic life in a shallower sea.

The present fossils occur in neritic deposits with inoceramids and ammonites. Living species of patelliform Archaeogastropoda and Basommatophora fed on seafeeds on rocky surface, whereas patelliform Mesogastropoda snatch planktonic diatoms. The fossil species may have had a similar feeding habit to that of living Mesogastropoda, as judged from their occurrences.

I. Introduction

A. PURPOSE OF THIS STUDY

Certain patelliform gastropods are frequently associated with ammonites and inoceramids in the Upper Cretaceous of Japan, Saghalien, Kamchatka, Alaska, British Columbia and western part of the United States. They have been assigned to such genera as *Acmaea, Anisomyon, Brunonia, Capulus, Helcion, Patella, Scurria* and/or *Siphonaria*. Some of them seem to be valuable as zonal indices, as suggested by Matsumoto (1943) and Kanie (1966). Taxonomically some of the above genera (*Acmaea, Helcion, Patella, Scurria*) were referred to the Archaeogastropoda, some others (*Capulus*) to the Mesogastropoda and still others (*Anisomyon, Brunonia, Siphonaria*) to the Basommatophora. Generally the shape of muscle-scars is most important for the consideration of the major taxonomic position of patelliform gastropods, since it reflects directly the soft part structure. Previous descriptions are mostly insufficient on this point.

In this paper, I present a result of my study to determine the taxonomic position of some Cretaceous patelliform gastropods, give systematic descriptions of the fossils in question, and summarize a knowledge of their, biostratigraphic succession. Furthermore, preliminary considerations of paleoecology and evolutionary history of the described gastropods are given.

For ten years I have engaged in the survey of the Cretaceous deposits of the Urakawa area where I have made a good collection of fossil patelliform gastropods as well as field observation on their occurrences (Fig. 1). They are the main part of the material of the present study. Furthermore I have also studied the specimens from there and other areas of Hokkaido and Saghalien kept at the Universities of Kyushu, Tohoku, Hokkaido and Tokyo. In 1972 I had an oppotunity to examine fossil patelloids from the Cretaceous system of Cali-

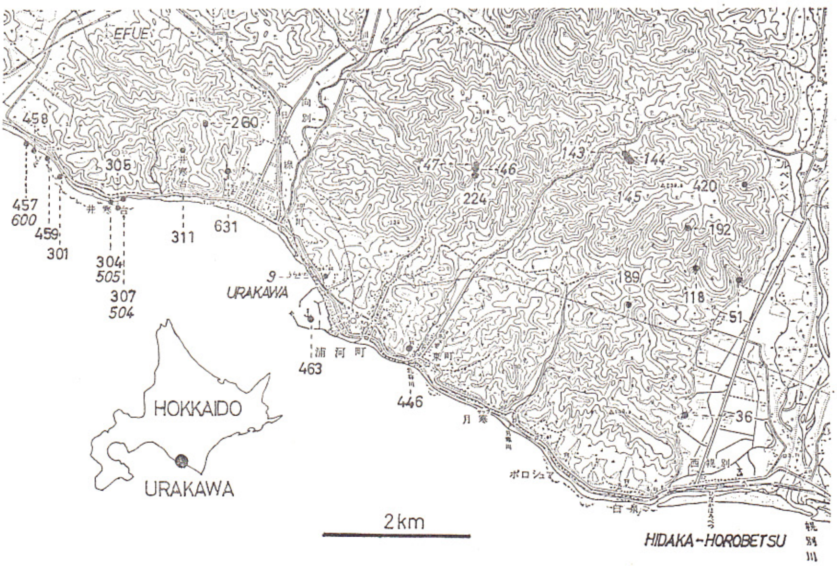


Fig. 1. Fossil localities in the Urakawa district, Hokkaido. e.g. 457: Kanie, 1966; *600*: Matsumoto, 1942.

fornia, Oregon, Washington, Texas, British Columbia and Southern Alaska in the U.S. National Museum, U.S. Geological Survey at Menlo Park, University of California at Los Angeles and California Academy of Sciences.

The repositories of the described specimens are as follows, with abbreviations in blackets:

Yokosuka City Museum, Yokosuka (YCM)
Geological Institute, Yokohama National University, Yokohama (GY)
Department of Geology, Kyushu University, Fukuoka (GK)
Geological Institute, and University Museum, University of Tokyo, Tokyo (GT and UMUT)
Institute of Geology and Paleontology, Tohoku University, Sendai (IGPS)
Institute of Geology and Mineralogy, Hokkaido University, Sapporo (UH)
National Science Museum, Tokyo (NSM)
United States Geological Survey, Menlo Park, California U.S.A. (USGS)
Department of Paleobiology, United States National Museum, Washington, D.C., U.S.A. (USNM)

B. ACKNOWLEDGEMENTS

I express my sincere gratitude to professor Tatsuro MATSUMOTO of the Kyushu University and Norman F. SOHL of the United States Geological Survey, Washington D.C. for their instructive advice and for critical of reading the manuscript, and to Professor Tokio SHIKAMA of the Yokohama National University, at whose suggestion this work was undertaken. I am much indebted to Dr. Ikuwo OBATA of the National Science Museum, Dr. Itaru HAYAMI of the University Museum, University of Tokyo and Professor Tsugio SHUTO of the Kyushu University for helpful criticisms on paleontological problems, to Dr. Tadashige HABE of the National Science Museum and Dr. Masuoki HORIKOSHI of the Ocean Research Institute, University of Tokyo, for providing concerning with the biological and ecological information on the recent patelliform gastropods. Thanks are due to Dr. Yasuhide IWASAKI of the University of Tokyo for the study of the shell structures, to Mr. Masafumi ARITA of the Kyushu University (now in the Geological Survey of Japan) for the mechanical analysis of the sediments, and to Dr. Takashi HAMADA of the University of Tokyo, Dr. F. I. TSUJI of the University of Southern California, Dr. Hiramichi HIRANO and Mr. Kazushige TANABE of the Kyushu University for their helpful discussions on various points. Dr. David L. JONES of the United States Geological Survey, Menlo Park, California, and Dr. W. P. POPENOE, Dr. Takeo SUSUKI and Dr. Louella SAUL of the University of California at Los Angeles, for kindly allowing me to examine certain species stored there. Emeritus Professor Kotora HATAI and Dr. Hiroshi NODA of the Tohoku University, Dr. Makoto KATO of the Hokkaido University, Dr. Naruhiko KASHIMA of the Ehime University and Mr.

Kensaku TAKEI of the Kosei High School, Tokyo and Mr. Masayuki NODA of the Wasada Junior High School, Oita gave me the opportunities to investigate the collections. Messrs. Hiroji TSUDA and Toshiharu MAEHARA assisted me in my field work. Dr. Yata HANEDA, Emeritus Director, Mr. Tatsuaki OHIRA, Director of the Yokosuka City Museum and Kazuko KANIE, gave me constant encouragement and without which the present work could not have been accomplished.

C. HISTORICAL REVIEWS

Most genera of the Cretaceous patelliform gastropods were described before 1880, based mainly on the shape and ornamentation of shell. Examples are *Helcion,* MEEK and HAYDEN, 1860; *Anisomyon,* MEEK and HAYDEN, 1860; *Patella,* GABB, 1864. On the other hand, the classification of extant patelliform gastropods is based commonly on soft part anatomy and shell morphology. Consequently the taxonomic position of fossil patelliform gastropods are often not in harmony with those of the living animals.

MEEK and HAYDEN (1860) redefined *Helcion patelliformis* (MEEK and HAYDEN, 1857) and erected the genus *Anisomyon* on the basis of *A. patelliformis* from the Upper Cretaceous of North America which belonged to the Tecturidae.

GABB (1864) described *Patella traskii, Helcion dichotoma, H.* (?) *circularis* (Archaeogastropoda) and *Anisomyon meekii* (Basommatophora) from the Upper Cretaceous of California.

In the description of many molluscan fossils from the Cretaceous deposits of North Saghalien, SCHMIDT (1873) named a larger-sized patelliform gastropods *Helcion giganteus.* He also distinguished four varieties in accordance with the positions of the shell-apex, e.g. whether marginal or central. They were named *depressa, nasuta, retracta* and *concentricus.*

YOKOYAMA (1890) reported many Cretaceous mollusca from Japan and described two patelliform gastropods, namely *Capulus cassidarius* from Urakawa in Hokkaido, and *C. annulatus* from Sanchu area in the Kanto Mountains.

JIMBO (1894) also recorded the occurrence of *Helcion* cf. *giganteus,* among many other molluscan fossils from the Cretaceous deposits of Hokkaido.

MÜLLER (1898) reported *Brunonia grandis* and *B. irregularis* from the Upper Cretaceous deposits of Germany, suggesting that they were the Siphonariidae on account of a narrow anterior sector in the latter.

WHITEAVES (1903) described two patelliform gastropods, *Capulus corrugatus, Helcion tenuicostatus* and *H. giganteus* var. *vancouverensis,* from the Cretaceous of Vancouver Island, Canada.

ITOH (1932) stduied *Helcion, Capulus* and *Inoceramus* from the Upper Cretaceous deposits of Saghalien. He reached the same conclusion as SCHMIDT about *H. giganteus,* which includes four varieties with respect to the position of the shell-apex. He believed that they had a sedentary life on the rocks and fed on seaweads like, the living species of the Patellidae. He classified *Capulus* into *C. annulatus* and *C. cassidarius,* the latter of which was, in turn, subdivided into ten formae and two varieties.

The Classification of patelliform gastropods was summarized by WENZ (1938) as follows, although his scheme may not be sufficient for some taxa today.

- Subclass PROSOBRANCHIA
  - Order ARCHAEOGASTROPODA
    - Family PATELLIDAE.......*Helcion, Patella, Scurria*
    - Family ACMAEIDAE ....*Acmaea*
  - Order MESOGASTROPODA
    - Family CAPULIDAE........*Capulus*
- Subclass PULMONATA
  - Order BASOMMATOPHORA
    - Family SIPHONARIIDAE...*Anisomyon, Brunonia, Siphonaria*

NAGAO and ÔTATUME (1938) set up *Helcion problematicus* and *Anisomyon ezoensis* in the description of molluscan fossils from the Hakobuchi sandstone group (late Cretaceous) at Tomiuchi [=Hetonail], Hokkaido. The two species are from the zone of *Inoceramus shikotanensis* (lower Maestrichtian) in MATSUMOTO's zonal scheme.

MATSUMOTO (1942–'43, 1959) summarized the biostratigraphy of the Cretaceous deposits in Hokkaido and South Saghalien. He recorded *Patella* (s.l.) *gigantea* from Rayl member of the Ryugase group (upper Campanian) of Naibuchi, South Saghalien, IIIe member of the Upper Yezo group (lower Campanian) of Abeshinai, Hokkaido and Ur2–7 members of the Upper Yezo group (lower-middle Campanian) of Urakawa, Hokkaido. *Scurria cassidaria* from IIIc–d members (Santonian) of Abeshinai and Ur1–2 members (Santonian-lowest Campanian) of Urakawa.

ANDERSON (1958) described the molluscan fossils from the Upper Cretaceous deposits and stratigraphy of the Northern Pacific region. He referred the stratigraphic positions of *Anisomyon meekii* GABB (1964) and *Patella traskii* GABB (1864) to upper Cenomanian and Campanian respectively.

In the classification of Archaeogastropoda KNIGHT *et al.* (1960) removed *Brunonia* from the suborder Pulmonata to the Patellina with a query, because there was no evidence of Pulmonata in the muscle-scars.

The generic name of the *Capulus cassidarius* from Hokkaido was changed to *Brunonia* (?) by MATSUMOTO (1963) in the revision of YOKOYAMA (1890).

In describing well-preserved fossil gastropods from the Upper Cretaceous of the Western Interior and the Atlantic Coast of the North America, SOHL (1960, 1964a, b, 1967) reported *Acmaea galea* and *A.* sp. under Archaeogastropoda and *Capulus monroei, C. corrugatus* and *C. cuthandensis* under Mesogastropoda. He (1964a, 1967) noted the importance of muscle-scars of *Siphonaria wieseri, Anisomyon borealis, A. centrale* and *A. patelliformis,* referring them to the Siphonariidae of the Basommatophora.

In my stratigraphic paper (KANIE, 1966) on the Upper Cretaceous deposits in the Urakawa district, *Brunonia* (?) *cassidaria* was reported to occur in the U1–2 members (Santonian-lowest Campanian), "*B.* (?) *gigantea* (MS)" in the U2 member (lowest Campanian) associated with *Inoceramus orientalis,* and *Helcion* cf. *giganteus* in the U3 member (lower Campanian) associated with *I. schmidti.* At that time I treated them as species of the Patellaceae without palaeontological description.

MACCLINTOCK (1967) studied the shell structure of living and fossil Patellaceae with the microscope and discriminated four types of structure, namely prismatic, foliated crossed and complex crossed layers. Seventeen combinations of such shell structures conformed reasonably well with previously accepted classification on the basis of radula and gill morphology. Two major patelloid families, the Acmaeidae and Patellidae, were distinguished by the different structure. According to MACCLINTOCK further detailed studies on the post-Ordovician patelliform gastropods from various times would clarify more accurately the phylogeny of this group.

When MATSUMOTO (1973) discussed "Dogo-Himezuka fauna (Campanian) from Ehime Prefecture of Southwest-Japan, previously reported by KASHIMA (1972), he noted that the fauna was composed characteristically of big "*Helcion giganteus*" associated with larger sized *Inoceramus schmidti* and *Gaudryceras striatum* etc. This characteristic assemblage of the species has been known from Rayl member of Ryugase group in Naibuchi Valley, South Saghalien, and also the fauna of Alexandrovsk in North Saghalien.

DUNDO and EFREMOVA (1974) described some Cretaceous patelloids along inoceramids from the northern part of the Koryak Highland in Kamchatka. They are *Acmaea barykensis* from the zone of *Inoceramus yokoyamai, Anisomyon transformis* from the zone of *Inoceramus orientalis, Anisomyon koryakensis* from the zone of *Inoceramus kunimiensis, Patella centralis* and *Helcion nasuta* from the zone of *Inoceramus schmidti* (DUNDO *et al.,* 1974).

To sum up, many species of patelliform gastropods have been reported from the Cretaceous deposits of the Northern Pacific region with descriptions of their shell morphology and stratigraphical occurrences. However, significant taxonomic problems have remained unsolved, especially about the evaluation of muscle-scars and shell structure in relation to the classification of the patelloids.

II. Classification

A. TAXONOMIC CHARACTERS

The taxonomic position of Cretaceous patelliform gastropods has varied greatly as reviewed in the preceding chapter. I have attempted to clarify the taxonomic position of the gastropods in question utilizing muscle-scars, shell structure and shell form as significant characters. In addition some ecological consideration has been taken into account (Table 1).

Table 1. Correlation chart of some extant and fossil patelliform gastropods

	Position of shell apex	Shell form	Septum	Muscle-scars toward in oval outline
Acmaeidae Patellidae ARCHAEOGASTROPODA	Anterior or center	Patelloid	Absent	Narrower half
Capulidae MESOGASTROPODA	Posterior	Flattened patelloid	Present	Rounded end
Siphonariidae BASOMMATOPHORA	Near center	Patelloid	Absent	Right side
Anisomyon	Center or posterior	Patelloid to flattened one	Present ?	Rounded end

(a) Muscle-scar

One of the main causes of taxonomic confusion may be attributed to poor preservation of muscle-scars.

In this study I have observed muscle-scars in about 30 individuals of *Anisomyon cassidarius, A. matsumotoi* and *A. giganteus* (Pl. 3, Figs. 2, 3, 5; Pl. 5, Fig. 3). The shell-apex lies on the narrower half of the oval shell form. The muscle-scars are horse-shoe shaped, being gaped toward the rounded broader end of the shell but not in the mid-line. The open side of the muscle-scars is at the anterior part and the shell-apex is at the posterior part (Fig. 2). An inner septum as seen on the living Calyptraeidae and Hipponicidae (Mesogastropoda) is not recognizable even in well preserved specimens of *A. cassidarius*. But some shells of *A. transformis* (e.g. Text-fig. 2–7, 8; Pl. 3, Fig. 7; Pl. 4, Fig. 5) have a narrow channel opening on the anterior side in the posterior part of the apical area of the shell and there is a possibility of the presence of an inner septum of this kind.

The muscle-scars of living patelloids (Fig. 3) are symmetrical in Archaeogastropoda except for the Neritidae, rather symmetrical in most Mesogastropoda and completely assymmetrical in Basommatophora of pulmonates in general.

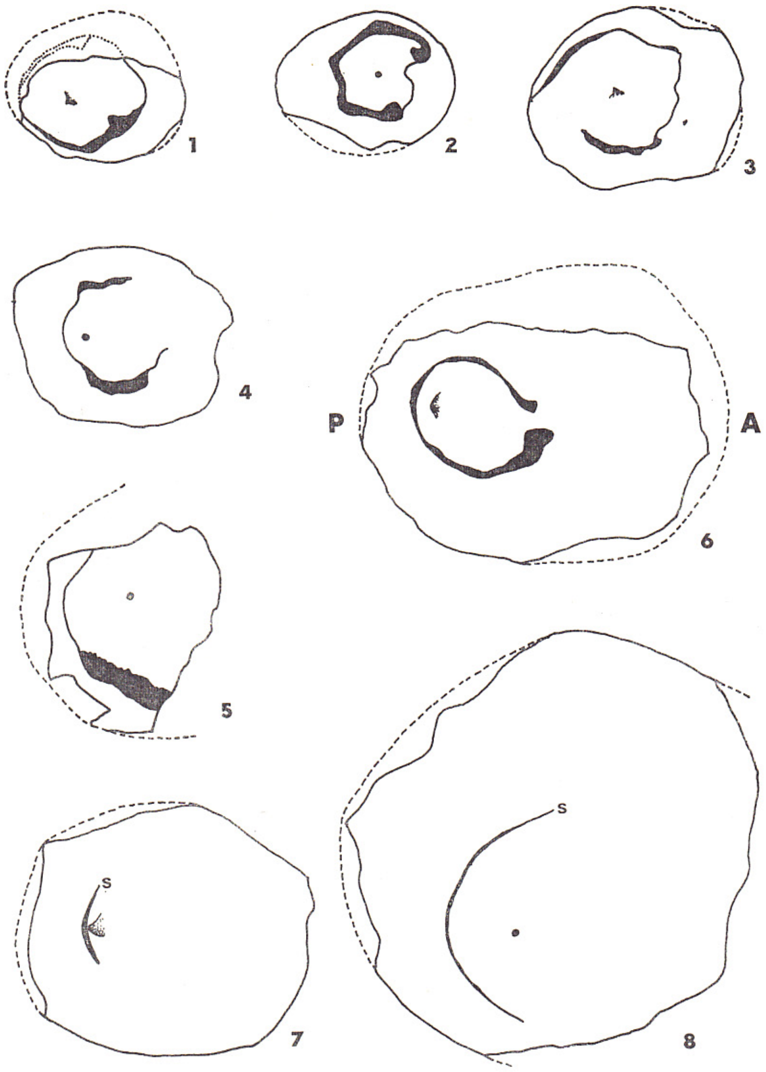


Fig. 2. Shapes of muscle-scars in fossil patelliform gastropods. A: anterior, P: posterior, S: inner septum. 1–5: *Anisomyon cassidarius*; 6–8: *A*: *transformis*. 1: YCM.GP544, Abeshinai, Santonian; 2: YCM.GP.Ur457027–21, Urakawa, Santonian; YCM.GP538, Ikushunbetsu, Santonian ?; 4: YCM.GP534, Abeshinai, lower Campanian; 5: IGPS5324, Abeshinai, lower ? Campanian; 6: IGPS50907, Kawakami, lower ? Campanian; 7: IGPS50907, Kawakami, lower ? Campanian; 8: IGPS50907, Kawakami, lower ? Campanian.

Therefore the muscle-scars of the examined fossil patelliform gastropods are strongly reminiscent of the Mesogastropoda and Pulmonata.

(b) Shell structure

The shell structure of the patelliform gastropods was studied by Bøggild (1930) and MacClintock (1967). Bøggild examined some species of Archaeo-

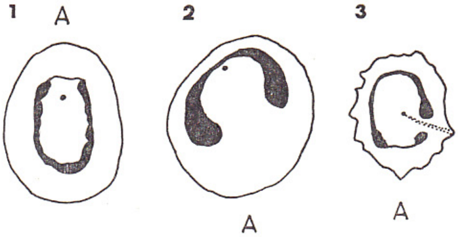


Fig. 3. Shape of muscle-scars in various extant patelliform gastropods. A: anterior. 1: *Cellana nigrolineata* [Patellidae of Archaeogastropoda], 2: *Capulus dilatatus* [Capulidae of Mesogastropoda], 3: *Siphonaria* (*Mastosiphon*) *sirius* [Siphonariidae of Basommatophora].

gastropoda and Mesogastropoda with a polarization-microscope. MACCLINTOCK observed the patelloid and bellerophontoid shells belonging to Archaeogastropoda with an optical microscope. The classification of living patelliform gastropods is mainly based on the radula and gill morphology, whereas the discussion about their classification and phylogeny of fossil patelloids was based on shell structure. MACCLINTOCK examined the shells of 121 patteloid species and recognized four basic types of shell structure in them, i.e. prismatic, foliated, crossed and complex-crossed structures. By the combination of these different structures and myostracum, seventeen groups were distinguished by him. Most of these groups are conformable with the previously accepted taxonomic categories based on the radula and gill morphology. The Acmaeidae have a fibrillar layers in the sequence of layers between the myostracum and the dorsal surface of the shell, whereas the Patellidae with a foliated or cross-foliated layer. These two families are distinguished by these types of shell structure.

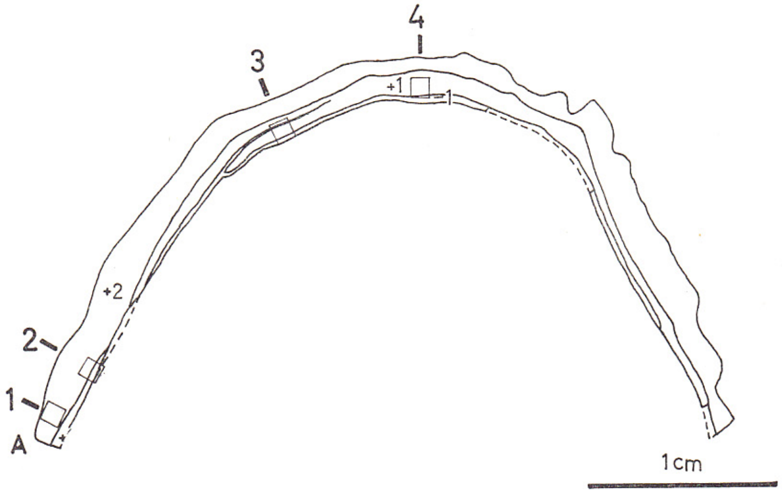
I have examined the longitudinal sections (replica on acethylcellulose film) of two fossil species, i.e. *A. cassidarius* and *A. giganteus* (Text-figs. 4, 5 and Pl. 1), and of species belonging to four extant families, i.e. *Cellana nigrolineata* in the Patellidae, *Notoacmaea concinna* in the Acmaeidae, *Capulus japonicus* in the Capulidae and *Siphonaria sirius* in the Siphonariidae (Text-figs. 6–9 and Pl. 2). Under the optical microscope, the shell is composed of three basic layers, with myostracum at the middle, +1, +2, . . . as the outer layers and −1, −2, . . . as the inner layers. Terms for the shell structures proposed by BØGGILD (1930), KOBAYASHI (1964, 1971) and MACCLINTOCK (1967) are used here.

The followings are the descriptions of shell structures in longitudinal section of the examined species.

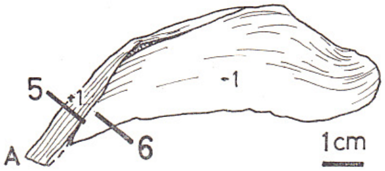
Fossil shell

Anisomyon cassidarius (YOKOYAMA)

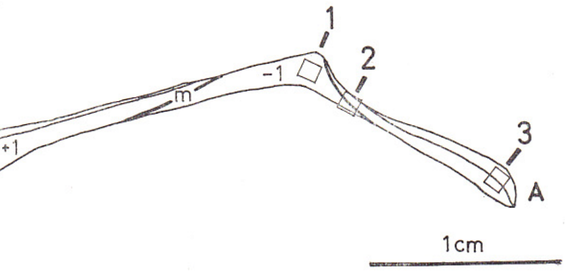
Three structural layers are observed, i.e. the outer layer with prismatic (?)



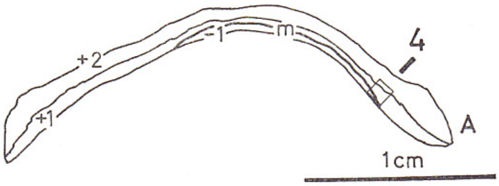
Anisomyon cassidarius
Fig. 4



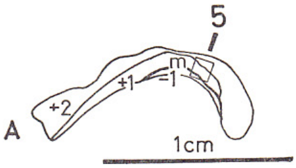
Anisomyon giganteus
Fig. 5



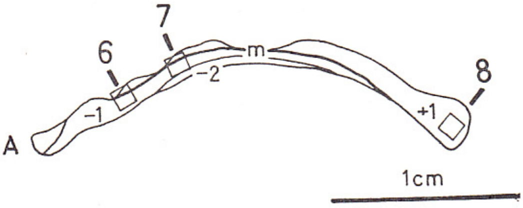
Cellana nigrolineata
Fig. 6



Notoacmaea concinna
Fig. 7



Capulus japonicus
Fig. 8



Siphonaria sirius
Fig. 9

Figs. 4–9. Longitudinal sections of the patelliform gastropods. Numbers in bold letters are on portions of plates 1 and 2. A: anterior part; m: myostracum; +1, +2, ... : outer layers; −1, −2, ... : inner layers.

structure, the middle one with crossed-lamllar structure, and the inner one with radial crossed-lamella or prisms. The myostracum is not preserved (Text-fig. 4 and Pl. 1, Figs. 1–4).

Anisomyon giganteus (SCHMIDT)

Two specimens were examined.

On the one specimen from Naibuchi, South Saghalien, the surface layer is presumed to be composed of crossed-lamellar structure, while a very thick inner layer is of prismatic or radial crossed-lamellar structure though somewhat recrystalized. The uppermost layer might have been exfoliated. The outline of this specimen is incomplete and restored original shell may have been two or more times larger than the preserved portion in view of the extraordinary thick shell (Text-fig. 5 and Pl. 1, Figs. 5–6).

The uppermost layer of the other specimen from above same area is made up of a prismatic layer.

Recent shell

Cellana nigrolineata (REEVE)

(Patellidae of Archaeogastropoda)

The present shell is composed of four basic structural layers, as already described by MACCLINTOCK, i.e. two outer layers, a myostracum in the middle part, and an inner layer. The uppermost layer has a complex prismatic structure and lower half of the outer layer is a finely foliated structure. The inner layer is of crossed-lamellar structure and modified into a complex crossed-lamella at the shell-apex (Text-fig. 6 and Pl. 2, Figs. 1–3).

Notoacmaea concinna (LISCHKE)

(Acmaeidae of Archaeogastropoda)

This shell has four major layers. They are the outer two layers with concentric crossed-lamellar or prismatic structure, the middle layer of myostracum, and the inner layer with radial crossed-lamellar structure (Text-fig. 7 and Pl. 2, Fig. 4)).

Capulus japonicus A. ADAMS

(Capulidae of Mesogastropoda)

The following four structural layers are recognized. The inner layer with a complex crossed-lamellar structure, and a myostracum in the middle. The outer layers of which the lower one with a radial crossed-lamellar structure, which is composed of somewhat regularly spaced lines crossed by fine radiae, and the upper one with a concentric crossed-lamellar structure (Text-fig. 8 and Pl. 2, Fig. 5).

Siphonaria (*Mastosiphon*) *sirius* (PILSBRY)

(Siphonariidae of Basommatophora)

This shell is made up of the following four layers: the outer layer with a concentric crossed-lamellar structure, the middle layer of myostracum and the inner two layers with differently orientated crossed-lamellar structures (Text-fig. 9 and Pl. 2, Figs. 6–8).

Remarks—the shell of the examined fossil and recent patelliform gastropods consists of four major structural layers including a myostracum in the middle. As shown in Fig. 10, two species of *Anisomyon* under consideration are somewhat similar to *Notoacmaea concina* and *Capulus japonicus* respect to the shell structure, but significantly different from *Siphonaria sirius* with respect to the structure of outer and inner layers.

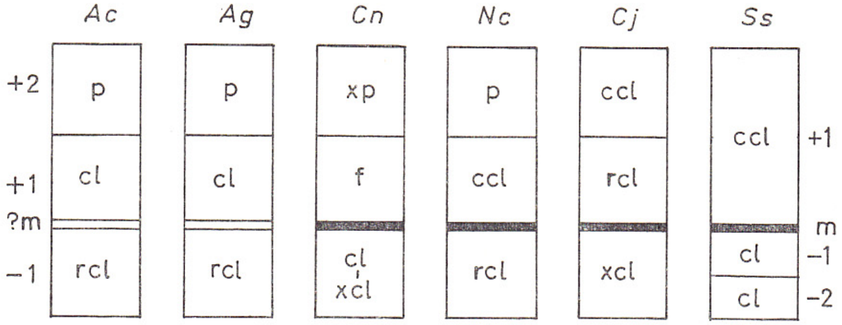


Fig. 10. Generalized columnar sections through patelloid shells. *Ac*: *Anisomyon cassidarius*; *Ag*: *A. giganteus*; *Cn*: *Cellana nigrolineata*; *Nc*: *Notoacmaea concina*; *Cj*: *Capulus japonicus*; *Ss*: *Siphonaria sirius*. m: myostracum; +1, +2, ...: outer layers; −1, −2, ...: inner layers. p: prismatic; xp: complex prismatic; cl: crossed-lamellar; ccl: concentric crossed-lamellar; rcl: radial crossed-lamellar; xcl: complex crossed-lamellar; f: foliated structures.

(c) Shell form

The position of shell-apex of the Cretaceous patelloids (Fig. 11) is generally in the posterior part, which is determinable by muscle-scars position.

The shell-apex of the living patelloids (Fig. 12) of Archaeogastropoda (Acmaeidae and Patellidae) is situated anteriorly, but is unobservable in the adult shell because of the worn state. The Fissurellidae with a fissure on the apex or anterior margin, the Neritidae with thick shell in different outlines and the Cocculinidae is small patelliform shell. The shell-apex of the recent patelloids of Mesogastropoda is located in a posterior part or at the posterior margin and directed posteriorly. The shell of the living Siphonariidae of Pulmonata is oval in outline, and their shell-apex is central, but some of them worn away in the adult shell as in the Archaeogastropoda.

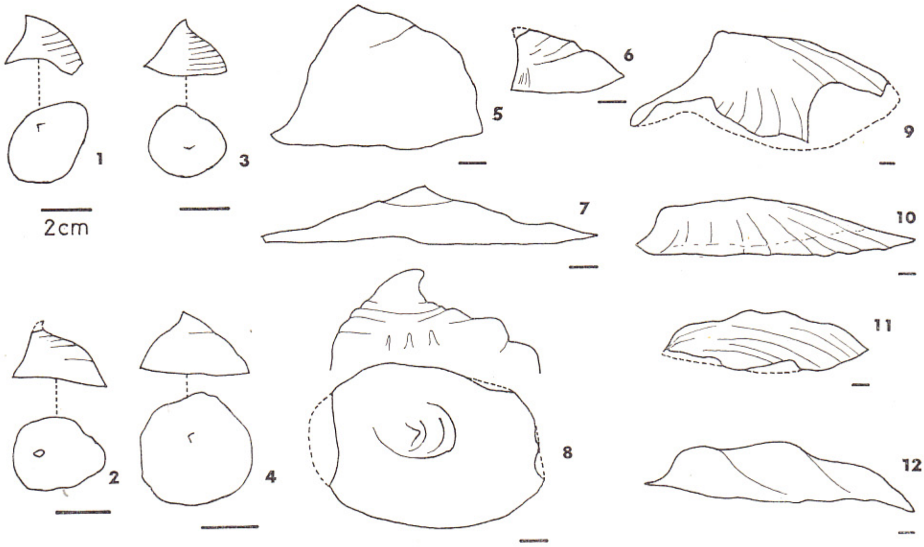


Fig. 11. Position and orientation of shell-apex in *Anisomyon*. 1–3: *Anisomyon cassidarius*. 1: paratype, Urakawa ?, K5β; 2: GK.H10351, R206p6, Kotanbetsu, K5β; 3: GK.H10326, Urakawa, K5β. 4–8: *A. transformis*. 4: YCM. GP.Ur311001 (paratype), Urakawa, K5γ; 5: UMUT.MM7518 (GT.I–142), K5γ; 6: YCM.GP.Ur260012, Urakawa, K5γ; 7: IGPS51067, Kawakami, K5γ; 8: IGPS57879, Kawakami, K5γ. 9–11: *A. giganteus*. 9: IGPS50910, Jon Quiére, K6α; 10: IGPS50919, Jon Quiére, K6α; 11: IGPS, K6α. 12: *A. problematicus*, GK.H10318, Tomiuchi, K6β.

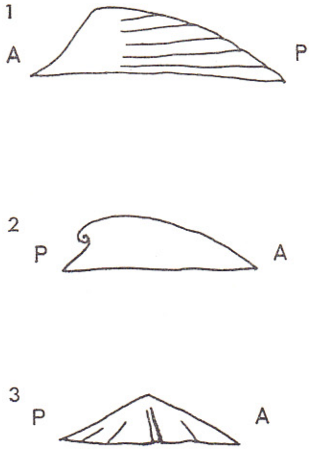


Fig. 12. Position and orientation of shell-apex in the extant patelliform gastropods. A: anterior, P: posterior. 1: *Cellana nigrolineata* [Patellidae], 2: *Capulus dilatatus* [Capulidae], 3: *Siphonaria* (*Mastosiphon*) *sirius* [Siphonariidae].

(d) Ornamentation

Fossil and recent shells of patelloids are ornamented with concentric rings as growth lines. Other ornamental elements differ between each species order, family or genus level.

Fossil shell

Anisomyon cassidarius is ornamented with only growth lines whereas *A. transformis* in addition possesses regularly spaced concentric ribs and often radial ribs on the marginal area of the larger sized shell. *A. giganteus* is characterized by radial ribs. *A. problematicus* is ornamented with broad and rounded concentric ridges (Fig. 26).

Remarks—A similar mode of appearance of radial ribs is known in living pelecypods such as *Anadara subcrenata* (LISCHKE), *A. inflata* (REEVE), *Venerupis* (*Amygdara*) *phillipinarum* (ADAMS and REEVE). The ribs appear subsequent to the prodissconch stage, and after the appearance of these divergent ribs, the molluscs change their habitat from planktonic to benthonic (YOSHIDA, 1935a, b; 1937). The mode of rib appearance is shown in the Upper Cretaceous pelecypoda, i.e. *Inoceramus* (*Sphaenoceramus*) *naumanni* YOKOYAMA by TANABE (1973). According to him the Santonian *I. naumanni naumanni* without divergent ribs turns to Campanian *I. naumanni schmidti* with divergent ribs. Consequently, there may be a good reason to suppose that the appearance of radial ribs in *Anisomyon giganteus* suggests some change in its habitat during growth.

Recent shell

The shell surfaces of Patellidae and Acmaeidae (Archaeogastropoda) range from those having strong radial ribs to rather smooth ornaments. Generally the ribbed forms are found in the powerful surf tidal zone. The patelloids of Mesogastropoda have weak ornaments as a rule. The Siphonariidae (Basommatophora) are ornamented with radial ribs of which one is stronger than others. Under the stronger rib there is a siphon.

B. SYSTEMATIC DESCRIPTION

Subclass PROSOBRANCHIA
Order MESOGASTROPODA
Family ANISOMYONIDAE nov.

Type-genus—*Anisomyon* MEEK and HAYDEN, 1860

Diagnosis—Shell generally thin, but may be very thick in some large species; small to large in size, attaining a large size over 40 cm in longer diameter; patelliform in smaller species but generally flattened in larger species and nearly bilaterally symmetrical; position of shell-apex variable, shifted from the center to the posterior portion; muscle-scars horse-shoe shaped and gaped toward the rounded anterior end of the oval outline. Surface ornamented with regular or irregular concentric lines or folds and some others possess radial ribs.

Occurrence — The Cretaceous of Japan, Saghalien, Kamchatka, North America, Germany, England, South Africa (Zululand) and Antarctica.

Remarks—The Anisomyonidae include two genera, i.e. *Anisomyon* MEEK and HAYDEN, 1860 and *Brunonia* MÜLLER, 1898.

Discussion—The present family is somewhat similar to the extant Calyptoraeidae, and Hipponicidae (Mesogastropoda) in having internal septa. The Anisomyonidae and Capulidae are closely allied to each other in having the same type of muscle-scars except for the lack of anterior connective muscle attachment between the "horse-shoe" of the Capulidae.

WENZ (1938) erected the Symmetrocapulinae under the Patellidae composed of *Symmetrocapulus* DACQUÉ, 1933 (Jurassic, Europe and North America) and *Phyryx* (?) BLASCHKE, 1905 (Triassic, Europe). KNIGHT *et al.* (1960) treated them as a family of the Patellaceae with a query. Unfortunately, little is known about their muscle-scars. The Anisomyonidae is somewhat similar to them in shell form, but I tentatively regard the the two families as unrelated.

As shown in the preceding chapter, the taxonomic criteria of the examined fossil patelliform gastropods such as muscle-scars, shell structures and shell form, together with their ecological conditions, indicate that these fossils have a close relationship with the Capulidae (Mesogastropoda) although there are now no extant genera and species allied to them. They have features of shell outline and ornaments common with the type-genus of the genus *Anisomyon* MEEK and HAYDEN, 1860 from the Upper Cretaceous of the United States of America, and also with *Brunonia* MÜLLER, 1898 from the Upper Cretaceous of Germany. These two genera had been referred to as the Siphonariidae (Basommatophora) by some authors, but they differ from extant species of that family in their muscle-scars.

I consider that these two genera belong to the order Mesogastropoda instead of Basommatophora and that their muscle-scars favour this conclusion.

Since these patelliform gastropods differ from any of the known families of Mesogastropoda, a new family, Anisomyonidae, is proposed herein, taking *Anisomyon* as the type-genus. This family became extinct at the late Cretaceous period like inoceramids and ammonites.

My scheme of classification of Cretaceous patelliform gastropods is as follows.

(Genera treated in this study)

Subclass PROSOBRANCHIA

Order ARCHAEOGASTROPODA
  Family PATELLIDAE ....*Helcion, Patella, Scurria*
  Family ACMAEIDAE ....*Acmaea*
Order MESOGASTROPODA
  Family CAPULIDAE..........*Capulus*
  Family ANISOMYONIDAE....*Anisomyon, Brunonia*
Subclass PULMONATA
Order BASOMMATOPHORA
  Family SIPHONARIIDAE.....*Siphonaria*

Genus ANISOMYON

Type-species—*Anisomyon patelliformis* Meek and Hayden, 1860

Diagnosis—Shell is generally oval in outline, thin to thick; small to large in size; patelliform in small and medium species but flattened patelloid in larger species. Shell-apex shifted from the center to the posterior portion. Muscle-scars are horse-shoe type gaping toward the anterior part but not in the mid-line in the type-species. Shell surface ornamented with concentric lines in addition to them some species with concentric ribs and some others with radial ribs.

Occurrence—Cretaceous of the Northern Pacific region and elsewhere.

Discussion—Genus *Anisomyon* is, above diagnosed, defined by the shape of muscle-scars and shell form. Two species described as *Brunonia,* i.e. *Brunonia grandis* and *B. irregularis* Müller, 1898, have a shell of longer outline and lower cone than those of *Anisomyon.* The latter two species had been recorded only from the lower Senonian of Germany. It is difficult to show that two species of *"Brunonia"* belong to genus *Anisomyon* or not, because its muscle-scars have not been observed. By the previous reasons I tentatively retain the genus *Brunonia.*

Anisomyon cassidarius (Yokoyama)

Pl. 3, Figs. 1–5

1890. *Capulus cassidarius* Yokoyama, p. 177, pl. 18, figs. 10, 11.
1942. *Scurria cassidaria* (Yokoyama), Matsumoto, p. 261, 264 (listed only).
1943. *Scurria cassidaria* (Yokoyama), Matsumoto, p. 125.
1963. *Brunonia* (?) *cassidaria* (Yokoyama), Matsumoto, p.29, pl. 44, figs. 10, 11.
1974. *Acmaea barykensis* Dundo, p. 17–18, pl. 10, fig. 3a, b.

Type—Of the two illustrated syntypes, the larger one (Yokoyama, 1890, pl. 18, fig. 11a, b) is here designated as the lectotype. It was obtained from

Urakawa, Hokkaido, but the precise locality is unknown. The smaller one (pl. 18, fig. 10a, b) from Otaushinai, Tokachi, Hokkaido though this location is believed to be mistake of Urakawa (MATSUMOTO, 1963). These syntypes are preserved in Munich: Bayerische Staatsammlung für Palaeontologie und historische Geologie, München, Deutchland, and their plaster models are in the Geological Survey of Japan and Hiroshima University.

Material—GK. H10345 from Ik2013g2, upper Turonian of the Ikushunbetsu district (MATSUMOTO coll.); GK. H10329, 10330 and 10348–10350 from R2680a, b and R4559p3, R4553p2, R4572p2, respectively, upper Turonian of the Tappu district (MATSUMOTO *et al.* coll.); GK. H10342 from Y132-5, member IIs, upper Turonian of the Yubari district (MATSUMOTO *et al.* coll.); GY526 from U526, uppermost ? Coniacian of the Uwajima district (TANABE coll.); YCM. GP Ur036013–036015, 036058 from U36, 301001 from U301 and 304001 from U304, member U1ß, Santonian of the Urakawa district in KANIE, 1966; GK. H10328 from Ur143, 10326 from 144, 10324 from 145, 10323 from 505, 703 from 600 in MATSUMOTO, 1942; GK. H10333 from IA-1536, Soya district (INOMA coll.).

Diagnosis—Shell is in oval outline, with the rounded anterior margin, small to moderate in size (e.g. 53 mm in maximum length), rather thin, high conical, anteriorly convex and posteriorly concave in lateral view, apex nearly at the center, bending to the posterior or anterior. Shell surface ornamented with numerous concentric growth lines. Muscle-scars are horse-shoe shaped gaping toward anterior part.

Measurements in mm—

Specimen	Length (L)	Breadth (B)	Height (H)
YCM.GP.Ur036013	38.0	33.8	30.3
YCM.GP.Ur457027-19	53.0	45.0	31.7
YCM.GP.Ur457027-21	37.0	30.0	22.1
YCM.GP.Ur457027-23	35.0	29.0	26.0

The following statistics concerning the relation between L and H are obtained from the above measurements: $\alpha=1.2838$, $v=8.16$, $s=0.105$ (Mean reduced major axis: α, coefficient of variability: $v=\frac{100s}{x}$, standard deviation: $s=\sqrt{\frac{\Sigma(xi-\overline{x})^2}{N-1}}$ after HAYAMI, 1969), which are diagramatically illustrated in Fig. 14.

Variation—There are some characters transitional to *Anisomyon transformis* described below which has weak concentric ridges and rather lower cone in some specimens of the upper Santonian.

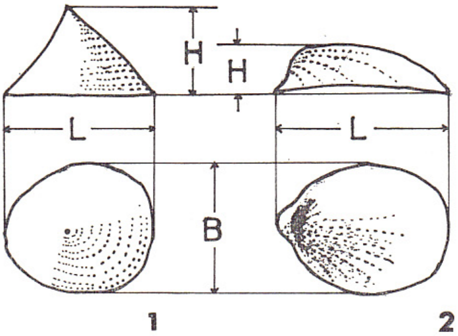


Fig. 13. Measurements of *Anisomyon* shell. L: length, B: breadth, H: height. 1: patelloid, 2: flattened patelloid whose height is from bottom to top of the shell.

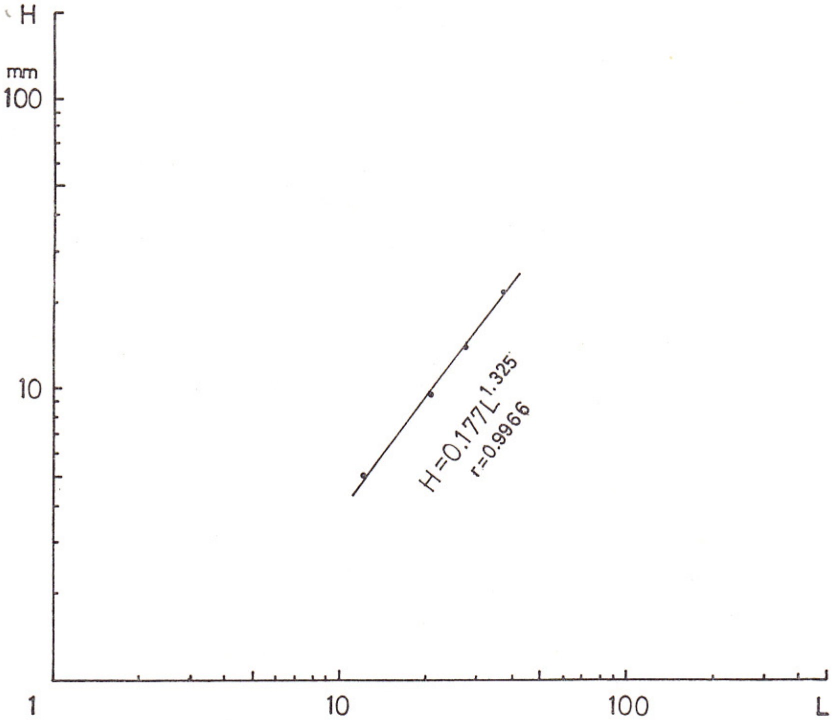


Fig. 14. Diagram showing an example of the relationship between length (L) and height (H) in the shell of *Anisomyon cassidarius* [YCM.GP.Ur457027-21]. r: significant with 95% confidence.

Comparison—The present species differs from *Anisomyon giganteus* (SCHMIDT) described below by the smaller and taller shell and by the absence of radial ribs. *A. patelliformis* MEEK and HAYDEN, from the Senonian of the Western Interior of U.S.A., has on the shell surface concentric growth lines and numerous fine radial striae; *A. borealis* (MORTON), from Wyoming and South

Dakota, has a similar outline but carries a strong carination on the posterior end. *A. ezoensis* NAGAO and ÔTATUME is smaller shell with five radial carinae at the posterior end.

Remarks—SOHL (1967) reported *Anisomyon borealis* from the uppermost Campanian of South Dakota and Wyoming of U.S.A. He thought the carination at the posterior end and the shape of muscle-scars were characteristic of the Siphonariidae. However, I consider that *A. borealis* and *A. patelliformis* should be grouped in the Mesogastropoda in view of the muscle-scars and their paleoecology. Because the interruption of the muscle-scars is symmetry or slightly assymmetry which are seen in the patelliform Archaeogastropoda and Mesogastropoda, and the combination of shell structures differs from *Siphonaria*. Although patelliform Mesogastropoda lacks anterior connective muscle attachment between the horse-shoe and a carinational area places in the symmetry muscle-scar interruption.

Anisomyon transformis DUNDO

Pl. 3, Figs. 6–9; Pl. 4, Figs. 1–5; Pl. 5, Fig. 3

1894. *Helcion* cf. *giganteus* SCHMIDT, JIMBO, p. 41 (87), pl. 9 (25), fig. 4.
1942. *Patella* (s.l.) *gigantea* (SCHMIDT), MATSUMOTO, p. 116 (listed only).
1966. *Brunonia gigantea* KANIE, p. 317, 322–324 (listed only).
1974. *Anisomyon transformis* DUNDO p. 18, pl. 12, fig. 1.

Type—Holotype from the Upper Baruikovskaya formation (zone of *Inoceramus orientalis,* lowest Campanian) in the northeastern part of the Koryak Highland, Kamchatka. Paratypes, YCM. GP. Ur305001, 305002, from loc. Ur305, 311001–311016, 311022, 311037, 311040, 311044–311053, from U311, 051009, from U51, 118005, 118006, from U118, 189005, from U189, 420001, from U420, 446005, from U446, 457001, 457006, 457021, 457023, 457026, 457027, 457030, from U457, 458001, from U458, 459010, 459014, from U459, 463002, 463003, from U463, 631001–631003, from U631, member U2α (lower part of the lowest Campanian), Urakawa district and 260012, 260013, from U260, member U2β (upper part of the lowest Campanian), Urakawa district (KANIE coll.); GK. H10325, 10327, from Ur600 and GK. H708, from Ur144, member U2β in MATSUMOTO, 1942; NSM6367, from loc. 1020, Chisaka district (lowest Campanian) in OBATA *et al.,* 1973 (MAEHARA and TSUDA coll.); UMUT. MM7518 (=GT. I-142), from a left tributary of the Abeshinai district (lower Campanian), in JIMBO, 1894 and YCM. GP531–534, from loc. 3551, 3559, 3575, 3601, Abeshinai district, Campanian (HAYAMI coll.); GK. H10322, from loc. IA-2078 (MATSUMOTO coll.), and YCM. GP539, 543, from the Soya district (MIYAUCHI coll.); IGPS50907, 51067, 57879, from the Kawakami district, South Saghalien (Campanian ?), in ITOH, 1932; UMUT. MM5534 (=GT. Cr695), from the Naibuchi district (Campanian), (KAWADA coll.).

Diagnosis—Shell is oval in outline, with the rounded margin at the anterior end, middle to large sized and rather thick, high conical; apex at the the center, bending to the anterior, convex posteriorly and concave anteriorly in lateral view. Shell surface ornamented with numerous concentric growth lines and rather widely spaced concentric ribs. In later stage, radial ribs appear on the marginal area, and these two types of ribs are combined with each other on the shell surface. There is a narrow, gently curved channel which is estimated to inner septum, opening at the anterior side in the posterior part of the apical area of the shell (Fig. 2–7, 8). Muscle-scars gape toward anteriorly.

Measurements in mm—

Specimen	Length (L)	Breadth (B)	Height (H)
(Without radial rib)			
YCM.GP.Ur311001	46.0	43.4	22.0
YCM.GP.Ur311003	33.1	31.9	13.2
YCM.GP.Ur311004	55.2	45.6	42.0
(With radial ribs)			
YCM.GP.Ur260013	43.0	46.0	20.0
YCM.GP.Ur463002	54.2	52.3	37.4

The following statistics concerning the relation between L and H are obtained from the specimens without radial rib: $\alpha=1.2305$, $v=15.88$, $s=0.195$. The relationships between L and H of above five specimens are diagramatically illustrated in Fig. 15.

Variation—*Anisomyon transformis* is shown with or without radial ribs ornament on the marginal area of the shell surface. In Fig. 16, at the growth stage of less than about 30 mm in shell length the individuals examined are without radial ribs. At the next stage of 30 to 50 mm about half of individuals show radial ribs on the marginal area of the shell. At the stage of about 60 mm in length, two third of the total specimens examined have radial ribs. All specimens at the later growth stage more than 70 mm in length are ornamented with distinct radial ribs.

A. giganteus described below, is decorated by radial ribs throughout every growth stage. Similar order of ribs appearance is also observed in the stratigraphic occurrence of the Urakawa section illustrated in the Fig. 27. All species without radial rib are in the member U1 (*A. cassidarius,* Santonian) and U2α (lower part of the lowest Campanian), some specimens with radial ribs appeared in the member U2β (upper part of the lowest Campanian), and all specimens are ornamented with radial ribs in the member U3 (lower Campanian). *A. trans-*

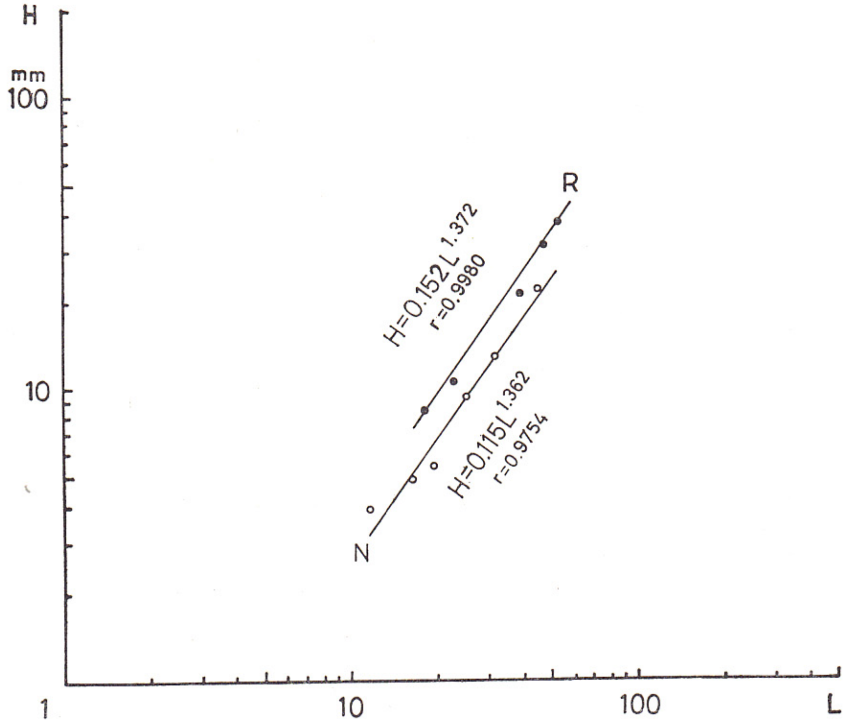


Fig. 15. Diagram showing examples of the relationships between length and height in the shell of *Anisomyon transformis*. R: specimen with radial ribs [YCM.GP.Ur463002]; N: specimen without radial rib [YCM.GP. Ur311001].

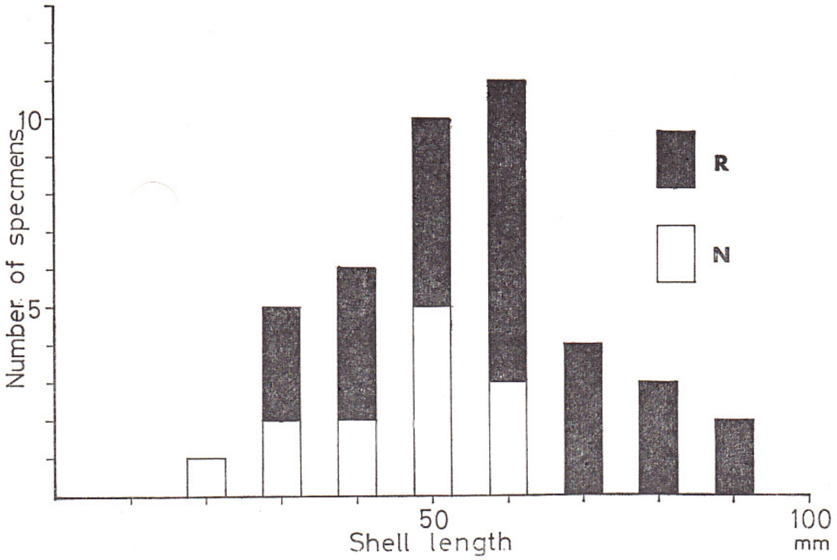


Fig. 16. The relationship between frequency of radial ribs appearance and length in the shell of *Anisomyon transformis*. R: specimen with radial ribs, N: specimen without radial ribs.

formis, thus shows intermediate characters between *A. cassidarius* and *A. giganteus.*

Comparison—The present species differs from *Anisomyon cassidarius* by a larger and taller shell ornamented with concentric ribs. *Brunonia grandis* MÜLLER, from the lower Senonian of Germany, is similar to the present species in the ornamentation of shell surface, but has a more prolonged outline.

Anisomyon giganteus (SCHMIDT)

Pl. 5, Figs. 1, 2; Pl. 6, Figs. 1, 2; Pl. 7, Fig. 1; Pl. 8, Fig. 1; Pl. 9, Fig. 1; Pl. 11, Fig. 1; Pl. 12, Fig. 1; Pl. 13, Fig. 1; Pl. 14, Figs. 1, 2; Pl. 17, Fig. 1; Pl. 18, Fig. 1; Pl. 19, Fig. 5

1873. *Helcion giganteus* SCHMIDT, p. 19–22, pl. 2, figs. 17, 18; pl. 3, figs. 1–10; pl. 8, figs. 2–5.
1894. *Helcion* cf. *giganteus* SCHMIDT, JIMBO, p. 41 (87), pl. 9 (25), fig. 5.
1927. *Helcion giganteus* SCHMIDT, YABE, p. 31, 43, pl. 6, fig. 6.
1942. *Patella* (s.l.) *gigantea* (SCHMIDT), MATSUMOTO, p. 167, 205, 269, 271 (listed only).
1943. *Patella* (s.l.) *gigantea* (SCHMIDT), MATSUMOTO, p. 125.
1963. *Helcion* cf. *giganteus* SCHMIDT, MATSUMOTO, p. 46, pl. 68, fig. 5.
1974. *Helcion nasuta* SCHMIDT, DUNDO, p. 19, pl. 10, fig. 2.
1974. *Petella centralis* SCHMIDT, DUNDO, p. 19, pl. 11, figs. 2, 3.

Type—I designate the specimen illustrated by SCHMIDT (1873, Pl. 2, Fig. 17) as the holotype and other twelve specimens as the paratype. His syntypes are from Alexandrovsk, North Saghalien, and he divided this species into four varieties on the basis of the location of shell-apex, i.e. at the posterior margin (α), at the center (δ), and they are namely var. *α depressa,* var. *β nasuta,* var. *γ retracta* and var. *δ centralis.*

Material—The specimens which I examine in this study are as follows. IGPS50063–50067, 50512, 50910, 50912, 50919, Jon Quiére district, North Saghalien, Campanian ?, in ITOH, 1932; UMUT. MM5533, 5535, Naibuchi district, South Saghalien, Campanian ? (KAWADA coll.); YCM. GP. Ur224003, 457008-1, 2, member U3 (Campanian) of the Urakawa district in KANIE, 1966; GK. H934, 10320, 10321, from loc. U47, 9, 47 respectively, member Ur4β, in MATSUMOTO, 1942; UMUT. MM (GT. I-141), Campanian ? of the Abeshinai district, in JIMBO, 1894; YCM. GP498, Campanian of the same district (KANIE coll.); GK. H10322, loc. IA-2078, Soya district (MATSUMOTO coll.); GK. H10347, loc. So-151, Campanian of the Soya district in MATSUMOTO and OHARA, 1971; NSM. PM6367, the Campanian of the Sarufutsu district, (UEDA coll.); YCM. GP591, from loc. 1009, the Campanian of the Chisaka district, in OBATA *et al.,* 1973; NSM. PM6734–6736 from loc. 1003, 1009, 1019 in same district; the Campanian of the Dogo-Himezuka area, Ehime Prefecture, in KASHIMA, 1972 and MATSUMOTO, 1973; YCM. GP545, 546, from loc. HK101, the Upper Himenoura subgroup (lower Campanian) of the Koshiki-jima, Kagoshima Prefecture, in TASHIRO and NODA, 1973; USGS2840, from the Campanian of the Chichina formation and USGS. M550, 573, 24242, from Matanuska formation, Alaska in JONES, 1963.

Diagnosis—Shell low conical to flattened patelloid, generally large sized with its maximum examples attains 400 mm long and 20 mm thick. The shell-apex is posterior to the center. The shell surface is ornamented with concentric lines and strong radial ribs. Concentric ribs rare or undeveloped. Muscle-scars are horse-shoe shaped, being gaped toward the rounded end of the shell. The ribs are observed only on the outer layer of the shell.

Measurements in mm—

Specimen	Length (L)	Breadth (B)	Height (H)
(Type A)			
YCM.GP498	165	170	90
UMUT.MM5534 (=GT.Cr695)	118	(97)	59
IGPS51067	260	(240)	110
(Type A′)			
IGPS50512	114	131	19
(Type B)			
GK.H10339	300	260	120
IGPS	87	92	(18)
(Type B′)			
IGPS50919	350	—	68
IGPS50919	115	118	15
IGPS51063	225	—	43

The relatiosnhips between L and H of selected three specimens are diagrammatically illustrated in Fig. 17.

Variation—SCHMIDT (1873) divided *"Helcion giganteus"* into four varieties (α, β, γ and δ) by location of shell-apex. ITOH (1932) also recognized SCHMIDT's four varieties using similar method from the specimens of Jon Quiére, North Saghalien. DUNDO and EFREMOVA (1974) erected SCHMIDT's varieties as *Helcion nasuta* and *Patella centralis* with the specimens from Kamchatka. However, I have recognized a certain gradational relationship among these four varieties. Furthermore, shell-apex is mostly at a little posterior and/or at the posterior portion in the Campanian stage. I presume that the shell-apex variation in *A. giganteus* may imply chronological variations, although no stratigraphical evidence is available at present.

A. giganteus has two types (A, B-types in Fig. 26, i.e. the radial ribs of type A is irregular while B is regular, and the relation between them being discontinuous) of surface ornamentation and these occur from the same localities in some areas. The relation of A, B and A′, B′ shows the location of shell-apex, i.e. the former in the center and the latter in the posterior margin. The fre-

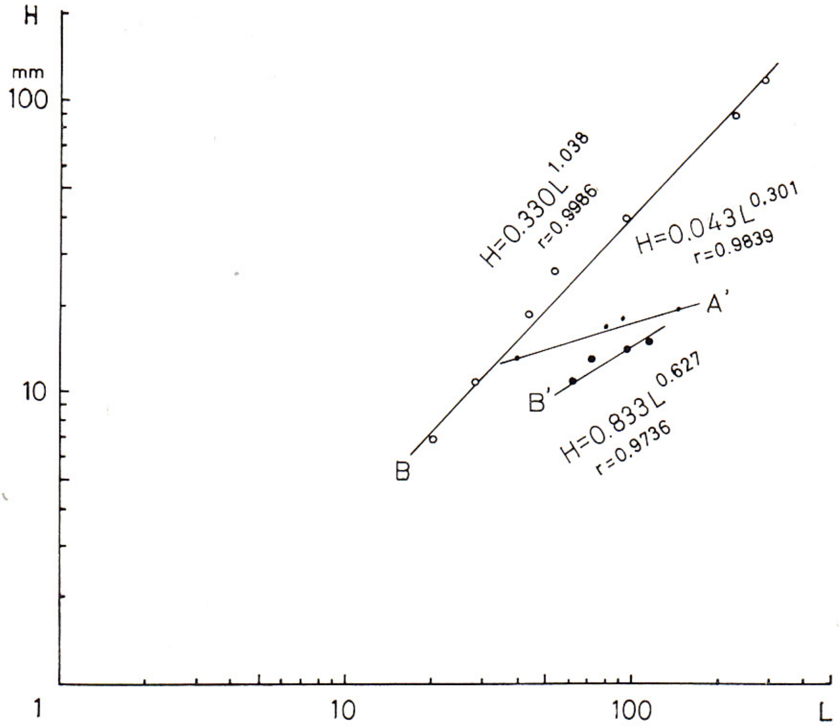


Fig. 17. Diagram showing the relationship between length and height in three specimens of *Anisomyon giganteus* [A′: IGPS50512, B: IGPS10339, B′: IGPS50519].

quency of relation between B+B′ and A+A′ type indicates 41:13 (75.9%) although the numbers of specimens represent total from various localities and ages of Japan and adjacent areas.

Comparison—*Anisomyon giganteus* is clearly distinguished from *A. cassidarius* by the existence of strong radial ribs on the surface, and by its larger and thicker shell. *Capulus monroei* SOHL (1960), from the lower Maestrichtian Ripley formation in Tennessee, U.S.A., is similar to this species in its outline, but the former is too small (L: 15.3, B: 9.4, H: 5.4 in mm) to compare in characteristics between the two species.

Remarks—A living patelloid *Cellana nigrolineata* has two types of surface layer ornamentation, viz, the ribbed type (R) and non ribbed type (N) (Fig. 18). TANABE and I examined the sex and relative abundance of the two types from the tidal zones of some localities in Kanagawa, Chiba and Fukuoka Prefectures. The ratio of R against N in a certain locality varied from 66.7 to 81.4 in % as shown in Table 2. It is quite noteworthy that the ratios have some relationship between male and female. The results do not show sexual dimorphism. They neither show dimorphism as ecoform, for these specimens were collected from

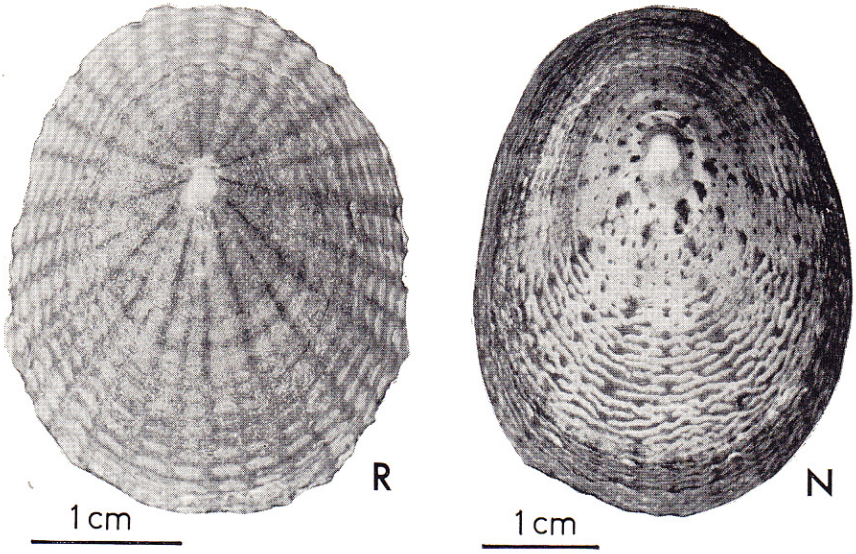


Fig. 18. Two types of surface ornamentation in the living *Cellana nigrolineata*. Locality: Tsuyazaki, Fukuoka Prefecture. R: ribbed type, N: non ribbed type.

Table 2. Relative abundance of two types of surface ornamentations in the living *Cellana nigrolineata*. Collector T: TANABE, K: KANIE

Locality	R	N	$\frac{R}{R+N}\times100$	Coll.
Shirahama, Chiba	15	4	77.9	T
Kominato 1, Chiba	57	23	71.3	T&K
Kominato 2, Chiba	37	9	80.4	T&K
Yokose-jima, Kanagawa	22	5	81.4	T&K
Arasaki 1, Kanagawa	19	9	67.9	T&K
Arasaki 2, Kanagawa	46	17	73.0	T&K
Tenjin-jima, Kanagawa	40	14	74.1	T&K
Koinoura, Fukuoka	56	21	72.7	T
Tsuyazaki, Fukuoka	28	14	66.7	T
Keyanoohto, Fukuoka	60	25	77.9	T

many localities with various environments, non seasonal porymorphism. However, there is a possibility of porymorphism in the surface ornamentation of A and B types of *Anisomyon giganteus* (Fig. 26).

Anisomyon problemaicus (NAGAO and ÔTATUME)

Pl. 19, Figs. 1, 2; Pl. 20, Fg. 1

1936. *Helcion* sp., SASAI, p. 594 (listed only).
1938. *Helcion* (?) *problematicus* NAGAO and ÔTATUME (missprinted as *probloma-ticus* in page 51) p. 51–52, pl. 4, figs. 1, 1a, 2.

1952. *Helcion* (?) *problematicus* NAGAO and ÔTATUME, TANAKA, MATSUMOTO and UEDA, p. 70 (listed only).
1974. *Anisomyon koryakensis* DUNDO, p. 18, pl. 11, fig. 1a, b; pl. 12, fig. 2a, b.

Type—Holotype, UH5992, NAGAO and ÔTATUME, 1936, pl 4, fig. 1, 1a, from Lower Sandy Shale (lower Maestrichtian) in the Tomiuchi [=Hetonai] area, Hokkaido; Paratype, UH5993, pl. 4, fig. 2, from the same member (lower Maestrichtian) at Sososhizawa, Naka-hobetsu area, Hokkaido.

Material—In addition to the above types I have examined GK. H10319, from the Minato Shale of he Izumi group of the Awaji Island, Southwest-Japan (SASAI, 1936); GK. H10318, 10340, 10344, from loc. H122p, the Lower Sandy Siltstone (lower Maestrichitian) of the Tomiuchi district, Hokkaido (MATSUMOTO coll.).

Diagnosis—Shell is oval in outline, in the form of a flattened patelloid. Mouth is gaped anteriorly. Moderately large in size (e.g. 140 mm in shell length). The shell-apex is situated at the posterior margin. On the shell surface, there are broad and rounded regular concentric ridges, becoming somewhat irregular in arrangement and obscure in the adult stage. Test is rather thin. Muscle-scars are not observable.

Measurement in mm—

Specimen	Length (L)	Breadth (B)	Height (H)	H/L
GK.H10318	139.0	95.1	27.1	0.19
	115.1	93.6	26.7	0.23
	44.3	36.5	14.0	0.32
GK.H10340	57.4	38.3	9.2	0.16
	45.7	33.2	9.0	0.20
	37.5	26.0	7.0	0.19
	19.8	14.1	4.4	0.22

The relationships of L and H are diagrammatically illustrated in Fig. 19.

Comparison—*Anisomyon problematicus* can be distinguished from *A. cassidarius* by the excentrally situated shell-apex and by its larger size. It is also different from *A. giganteus* in the absence of radial ribs on the shell surface and thinner shell.

Remarks—The present species should be transferred from *Helcion* to *Anisomyon* in the generic position, for the several reasons mentioned in the preceding chapters (p. 16–17).

Anisomyon annulatus (YOKOYAMA)

Pl. 19, Figs. 3, 4

1890. *Capulus annulatus* YOKOYAMA, p. 200, pl. 25, fig. 17a, b.
1963. *Capulus* (?) *annulatus* YOKOYAMA, TAKEI, p. 136 (listed only).

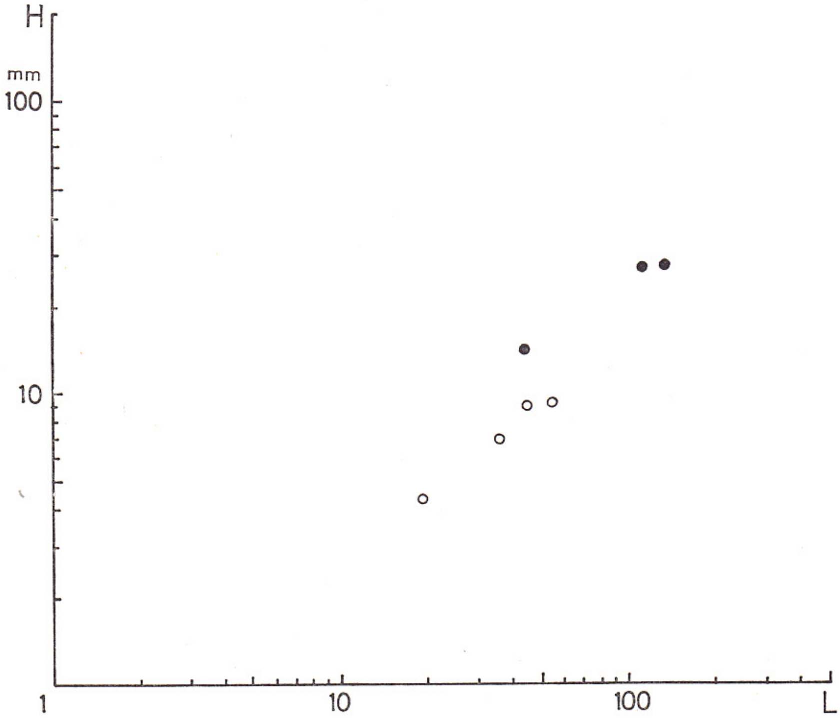


Fig. 19. Diagram showing the relationship between length and height in the shells of *Anisomyon problematicus*.

1963. *Brunonia* (?) *annulata* (YOKOYAMA), MATSUMOTO, p. 32, pl. 51, figs. 17a, b.

Type—Lectotype in YOKOYAMA's specimen (pl. 25, fig. 17a, b) designated by MATSUMOTO (1963) from the upper Neocomian or Aptian Ishido formation, Kagahara, Gunma Prefecture, kept in Munich: Bayerische Staatssammulung für Palaontologie und historische Geologie, München, Deutschland.

Material—In addition to the above type-species, I have examined two specimens from the type area TAKEI coll.).

Diagnosis—Shell is elliptical or subrounded in outline, and lowly conical. Test is rather thin; surface is ornamented with 10–14 concentric ribs and numerous fine concentric striations on the interspaces; shell-apex is almost central or located slightly posteriorly. Adductor-scars have not been observed.

Measurements in mm—

Specimen	Length (L)	Breadth (B)	Height (H)	H/L
Holotype	29.0	—	14.0	0.48
	26.0	26.5	11.0	0.42
	21.5	24.0	9.0	0.42
	10.0	9.0	3.5	0.35

TAKEI's coll.	(60.0)	—	(13.5)	0.23
	31.5	28.9	(9.7)	0.31
	25.9	22.9	(7.7)	0.30
Ditto	27.5	23.6	7.9	0.29
	19.5	15.8	4.3	0.22
	15.0	12.0	3.5	0.23
	12.4	9.9	2.7	0.22

The relationships between L and H are diagramatically illustraed in Fig. 20.

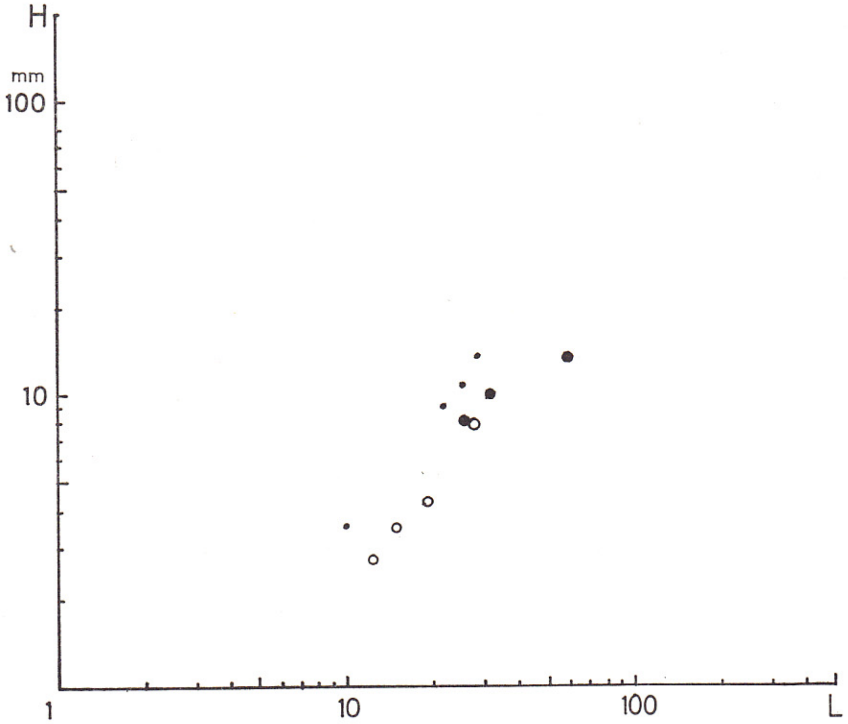


Fig. 20. Diagram showing the relationship between length and height in the shell of *Anisomyon annulatus*.

Comparison—The present species closely resembles no rib stage of *A. transformis* but is distinguished by the lower cone and round outline. *Brunonia grandis* and *B. irregularis* have similar surface ornamentation, but the former has longer outline and the latter a carination from shell-apex to posterior margin.

Remarks—As to shell shape and the surface ornamentation, the present species resembles *Anisomyon transformis* except in possesing a lower cone. Its geological age is late Neocomian or Aptian as indicated by co-existing fossils such as *Pterotrigonia pociliformis* (YOKOYAMA). The present species is represented only by three specimens (lectotype and two specimens collected by TAKEI). *Scurria* sp. from the Albian Yatsushiro formation in Kumamoto Prefecture (p. 115 in MATSUMOTO *ed.*, 1954) resembles to the *Anisomyon annulatus* by personal communication of MATSUMOTO.

III. Biostratigraphic Succession

Species of *Anisomyon* are regarded as good index fossils, as they have a rather short stratigraphical range. They are often associated with certain species of ammonites and inoceramids. They are found abundantly in the Cretaceous neritic sediments.

I collected three species of *Anisomyon* from the continuous stratigraphical section of the Santonian-lower Campanian deposits of the Urakawa district, Hokkaido (Fig. 21). Namely, *A. cassidarius* from the member U1 (Santonian), e.g. loc. U36, claystone, *A. transformis* from the member U2 (lowest Campanian), e.g. loc. U311, fine-grained sandstone and *A. giganteus* from the member U3–5 (lower Campanian), e.g. loc. U224, siltstone in ascending order. The same suc-

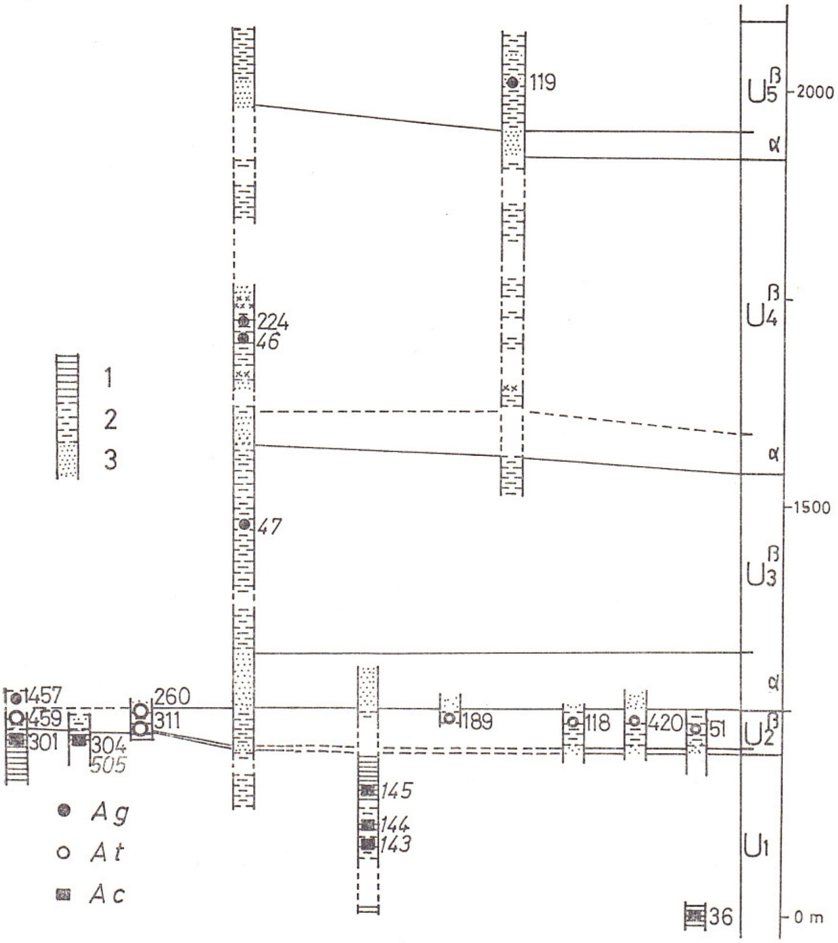


Fig. 21. Occurrences of *Anisomyon cassidarius* [*Ac*], *A*, *transformis* [*At*] and *A. giganteus* [*Ag*] from the Urakawa section. For locality numbers see Fig. 1. 1: claystone, 2: siltstone, 3: sandstone.

cession of biostratigraphic occurrences of the three species has also been found in various other districts in Hokkaido (*A. cassidarius* from Urakawa by YOKOYAMA, 1890; *A. transformis* and *A. giganteus* from Abeshinai by JIMBO, 1894; *A. transformis* from the member U3, lowest Campanian, of the Chisaka district in OBATA *et al.*, 1973), Southwest-Japan (*A. cassidarius* from Uwajima, Coniacian, in TANABE, 1971; *A. giganteus* from Dogo-Himezuka, lower Campanian, in KASHIMA, 1972 and MATSUMOTO, 1973), Northeast-Japan (*A. cassidarius* ?, from Nakaminato, lower Maestrichtian, in SAKAMOTO *et al.*, 1972, p. 22), Saghalien (*A. giganteus* by SCHMIDT, 1873; *A. cassidarius, A. transformis* and *A. giganteus* by ITOH, 1932; *A. giganteus,* from member Ray, lower Campanian, fine-grained sandstone in MATSUMOTO, 1942), Kamchatka (*A. cassidarius,* from the zone of *Inoceramus yokoyamai, A. transformis,* from the zone of *I. orientalis*) and Southern Alaska (*A. giganteus,* JONES, personal communication). But no species of *Anisomyon* has been collected from the upper Campanian (zone of *Metaplacenticeras subtilistriatum* in MATSUMOTO's zonal scheme).

A. problematicus (NAGAO and ÔTATUME) has been found in the lower Maestrichtian of the Tomiuchi district, Hokkaido (NAGAO and ÔTATUME, 1938) and Awaji district, Southwest-Japan (SASAI, 1936; TANAKA *et al.*, 1952).

A. annulatus (YOKOYAMA) has been reported from the upper Neocomian or Aptian (TAKEI, 1963) of the Sanchu areas in the Kanto Mountains and Albian Yatsushiro formation of Kyushu (personal communication of MATSUMOTO; MATSUMOTO *ed.*, 1954, p. 115). The first appearance of the *Anisomyon* species is expected to be older.

Several species of morphollogically somewhat similar to *A. cassidarius* have been reported from the upper Cretaceous of fine-grained sediments in North America. But these fossils are inner mould so it is difficult to compare them with Japanese specimens. They are *A. meekii* from Cenomanian of California (GABB, 1964; ANDERSON, 1958), *A. patelliformis* from Cenomanian of Nebraska (MEEK and HAYDEN, 1857, 1860), *Capulus corrugatus* from Campanian of the British Columbia (WHITEAVES, 1903), *A. centralis* and *A. borealis* from upper Campanian of South Dacota and Wyoming (SOHL, 1960, 1964a, 1964b, 1967). Besides, *Brunonia grandis* and *B. irregularis* have been reported from the lower Senonian deposits of Germany (MÜLLER, 1898).

Five species of *Anisomyon* have been reported through the Lower to Upper Cretaceous of the North Pacific region. Thus, these species seems to be fairly abundant in the vast Pacific region. Further occurrence could be expected in the West Pacific region especially in California.

These species of the Anisomyonidae generally occur abundantly in the muddy sediments, but some are recorded from sandy sediments as shown Campanian of Hokkaido and Saghalien (Figs. 22, 23). The geographical distribution of the

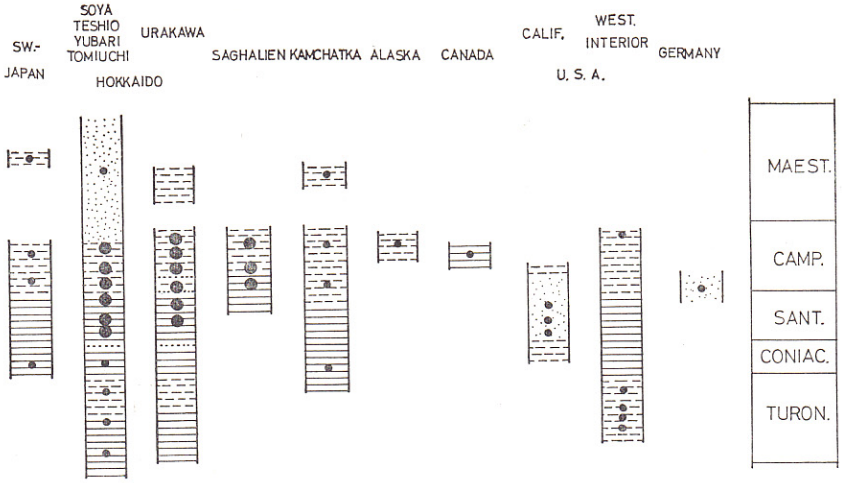


Fig. 22. Occurrence and abundance of the Anisomyonidae species in the Northern Pacific region. ●: abundant, •: less abundant.

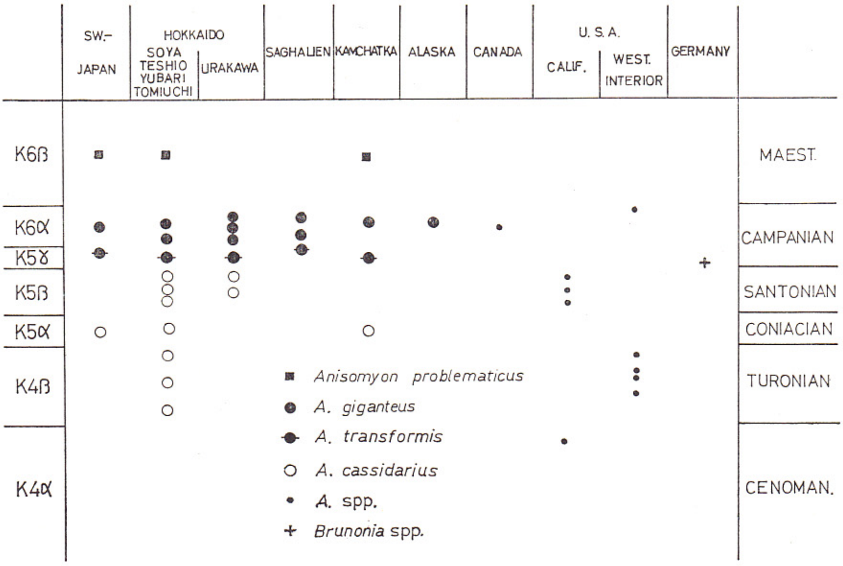


Fig. 23. Distribution of the Anisomyonidae spacies in the Northern Pacific region.

known species of the Anisomyonidae is shown on a world map of Fig. 24. This figure illustrate their occurrences have not been recorded in the area excluding Northern Pacific region, Germany, and England, Zululand and Antarctica (personal communication of SOHL).

Fig. 24. Geographical distribution of the Anisomyonidae.

IV. Further Problems

I have clarified taxonomic position and stratigraphic occurrences of the Cretaceous patelliform gastropods in the previous chapters. But there still remain further problems such as paleoecology and evolutionary history of present gastropods.

A. ECOLOGY

It would be interesting to clarify the mode of these Cretaceous patelliform gastropods. Although strictly autochthonous fossils have not been yet found, the shell characters, the mode of occurrence and nature of host rocks, as well as the ecology of living patelliform gastropods, may be informative for this purpose.

(a) Mode of occurrence

Anisomyon cassidarius (Turonian-Santonian) occurs commonly in calcareous nodules in mudstone or very fine-grained sandstone in association with *Inoceramus*, a less ornate ammonites etc. and the association of inoceramids and *Anisomyon* species are also common in the Western Interior. And these shells of *A. cassidarius* are almostly completely preserved. *A. giganteus* (lower Campanian) occurs sporadically in very fine-grained sandstone or mudstone with *Inoceramus* and ammonites, and their thick shells are not much water-worn.

These occurrences seem to suggest that the fossil patelliform gastropods did not live in the rocky environment like the extant Patellidae and Siphonariidae.

Cretaceous species probably lived in relatively calm condition, and these shells are not considered to have been transported much apart from their habitat.

(b) Lithological facies

The sediments yielding the fossil patelliform gastropods were analyzed mechanically to elucidate their sedimentary facies.

Mechanical analysis

The sediments for the present analysis are calcareous nodule, containing the present gastropods. My experiments show that there is no remarkable difference in the grain-size distribution between the nodules and surrounding mudstone. Namely, it appears that the nodules included in the surrounding mudstones were formed by secondary concentration of calcium carbonate.

Procedure—Crushed fragments of calcareous nodules were dipped in 20 percent hydrochloric acid to dissolve about 50 percent of the carbonate consisting the total weight, washed and neutralized with sodium hydroxide. 34 percent

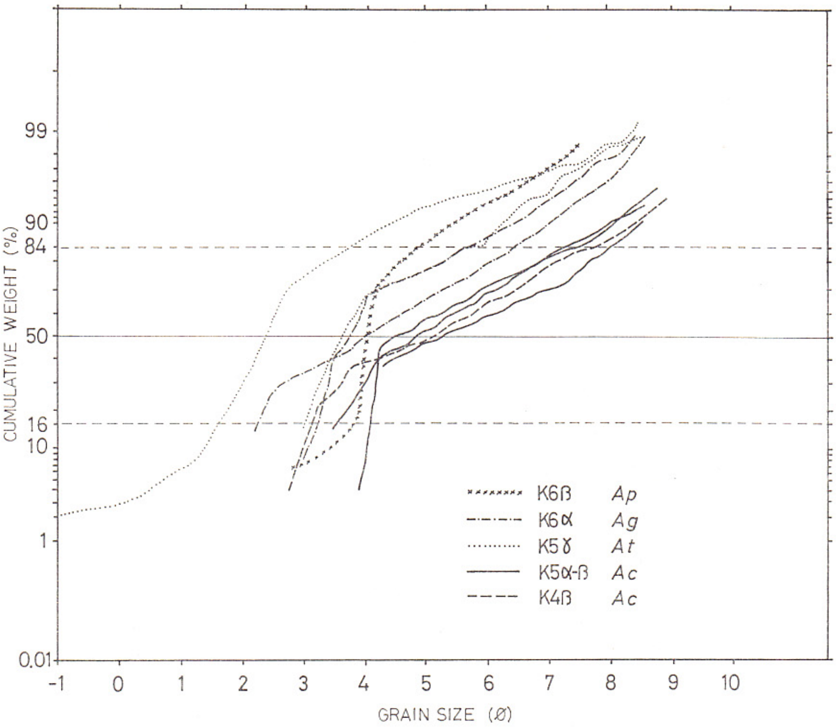


Fig. 25. Size distribution in the Cretaceous sediments yielding patelliform gastropods. *Ap*: *Anisomyon problematicus* from loc.H122, Tomiuchi; *Ag*: *A. giganteus* from loc.U224, Urakawa and 3551, Abenshinai; *At*: *A. transformis* from loc.U260, 458, Urakawa: *Ac*. *A. cassidarius* from loc.U459, 457, Urakawa and R2113, Tappu.

hydrogen peroxide was then added to oxidize the included organic matter. The residual grains were cleaned by ultrasonic vibration in water (29 KHz, 10 minutes). Mechanical analysis were applied to two different materials separated according to sieved grain size, i.e. one with a ϕ value greater than 4 and the other smaller than 4. The former material was analyzed by EMERY's tube method, and the latter by sedimentation method. Sodium hexametaphosphate (0.2%) was added as a dispersant to the solution. Based on the results of these two analysis, the grain size distribution is expressed as cumulative curves in Fig. 25.

Examination—The calcareous nodules from the Upper Cretaceous of the Urakawa and Teshio districts in Hokkaido are divided into two groups in grain size distribution, i.e. those of $K4\beta-K5\beta$ (Turonian-Santonian) and $K5\gamma+K6$ (lower Campanian + lower Maestrichtian). The former are composed mostly of fine grains smaller than 4ϕ, whereas the latter are composed of grains somewhat coarser than the former, and especially those of $K5\gamma$, which contain much organic matters such as wood fragments, etc. The distribution curve is characteristic of material that is composed predominantly of mud (60–20%) and less sandy component. This may be regarded as the sedimentation by suspension (VISHER, 1969). Thus it is assumed that the water energy which formed the sediments was too weak to transport the thick shelled patelliform gastropods. It is, thus, considered that they had probably lived on these bottom sediments and that the shells are mostly autochthonous.

Sedimentation—The sedimentary events represented by grain size distribution are reconstructed as follows. The patelliform gastropods under consideration lived in the calm open sea bottom with little supply of arenaceous sediments from Turonian to Santonian stage. In the lowest Campanian stage, they inhabited the sea with more rapid current, where deposition of sands and drift wood was taking place. The agitated condition continued during the Campanian and Maestrichtian stages. This is conformable with the conclusion by MATSUMOTO and OKADA (1973) that the area was under the "neritic condition of moderate depth", and a shallower neritic condition during the post-Campanian generally regressive sea (MATSUMOTO, 1954).

The sediments containing patelliform gastropods contain glauconite from place to place. The gluconitic beds contain straight-shelled ammonites belonging to *Baculites*. MATSUMOTO and OBATA (1962) explained that the sedimentary environment of the *Baculites* facies was rather calm. A shallow sea probably prevailed off the coast, and the bottom sediments were generally muddy fine sand and occasionally intercalated with calcareous beds. Fossils associaed in the same facies are inoceramids, coiled ammonites and some gastropods. No species characteristic of the tidal zone have been found.

(c) Habitats

The extant patelliform gastropods are classified in three entirely different orders, i.e. Archaeogastropoda, Mesogastropoda and Basommatophora.

Archaeogastropoda

Species of the Patellidae and Acmaeidae are found on rocky surface and feed seaweeds. They are all shallow sea inhabitants of the tidal zone.

Mesogastropoda

According to KOSUGE and HAYASHI (1967), *Capulus dilatatus* of the Capulidae are on the shell surface of the hosts, such as *Pecten albicans* (−20–50 m), *Decatopecten striatus* (−10–20 m), *Amusium japonicum* (−10–100 m), *Propeamusium caducum* (−200–400 m) and *P. puncticulatus* (−40–60 m). They snatch planktonic diatoms on which the host has fed. The *Capulus* species has a peculiar symbiotical life

Basommatophora

The patelliform Siphonariidae are found in the tide pools or on the rocky reef and feed on seaweeds. As they need oxygen from the air, they are by no means benthonic inhabitants of great depth. But some (i.e. *Willamia*) readapted to sublittoral conditions in which lung is filled with water (HUBENDICK, 1945).

So far as I am aware, no extant patelliform gastropod in any of the orders mentioned above inhabits the muddy sea bottom under tranquil circumstances.

B. EVOLUTIONAL CHANGE

The general tendency of successive changes in size, shell form, shell thickness and ornamentation of the studied fossil patelliform gastropods is summarized diagramaically in Fig. 26. During the Upper Cretaceous (Turonian-lower Maestrichtian), the shell of *Anisomyon* became larger. *A. cassidarius* from the member U1 (Santonian) of the Urakawa section is ornamented with fine concentric rings and ribs, in *A. transformis* radial ribs are added in more or less late stage. Examples are shown in Fig. 27. Generally the specimens with radial ribs appeared in the member U2β, but those without radial rib are also found in the same member. This fact seems to suggest that the population of non ribbed form change gradually to that of ribbed form as we ascend the sequence. *A. giganteus* of the member U3–5 (lower Campanian), is decorated with radial ribs throughout growth. The maximum thickness of the shell is less than 1 mm in *A. cassidarius,* 4 mm in *A. transformis* and more than 20 mm in *A. giganteus*. I have also noticed the same order of occurrence in the Chisaka

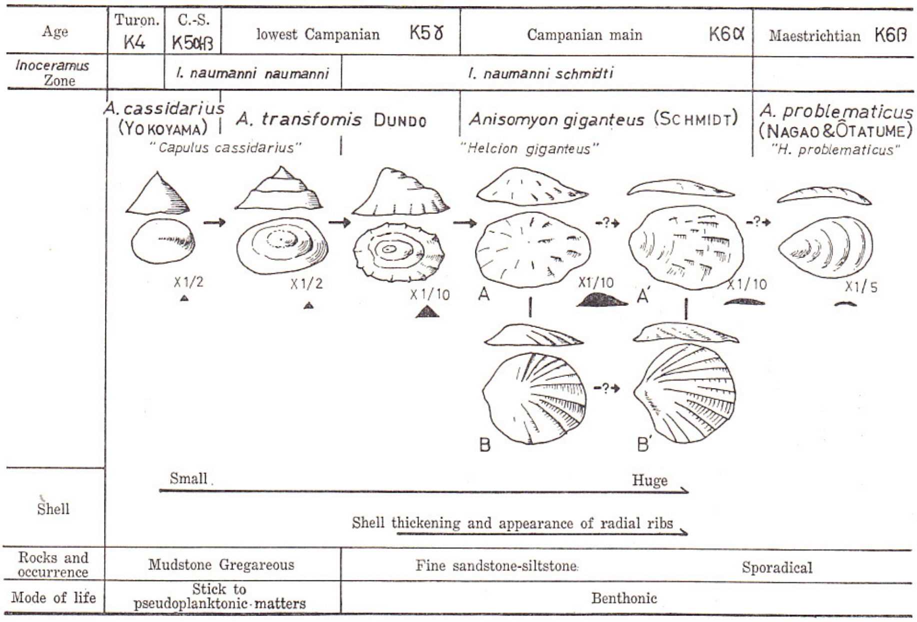


Fig. 26. Evolutional changes of *Anisomyon* species.

district, Hokkaido and other areas. From the above discussion, it can be considered as a possibility that *A. giganteus* evolved from *A. cassidarius* by way of *A. transformis*.

The shell-apex apparently tended to shift posteriorly with time. It can be considered that the animal had a rather highly patelloid shape adapted to sedentary life in the Upper Cretaceous through Santonian, and then changed to a somewhat low or flattened patelloid shape (Fig. 28). This suggests a benthonic life in the post-Campanian times. The random orientation of shell-apex and thin shell in the Santonian and the lowest Campanian species may indicate that they had been planktonic or pseudoplanktonic life and were attached to various places on the host. The posterior orientation of the apex in the lower Campanian and lower Maestrichtian species may be accounted for by a non sedentary life. At that time the radial ribs appeared on the shell surface. Ecologically the genus presumably changed its habitats from a quiet water to a rather stirred shallow sea bottom.

Anisomyon seems to have a close ecological similarity to the group of *Inoceramus* (*Sphaenoceramus*) *naumanni,* since it always occurs in association with the inoceramid species of that group from the Coniacian through Campanian. The appearance of radial ribs and the tendency for shell thickening are seen in both molluscan groups as being adapted to changing circumstances. TANABE (1973) has recently explained that these morphological changes of *I. naumanni* may be the result of an adaptation of their mode of life which had

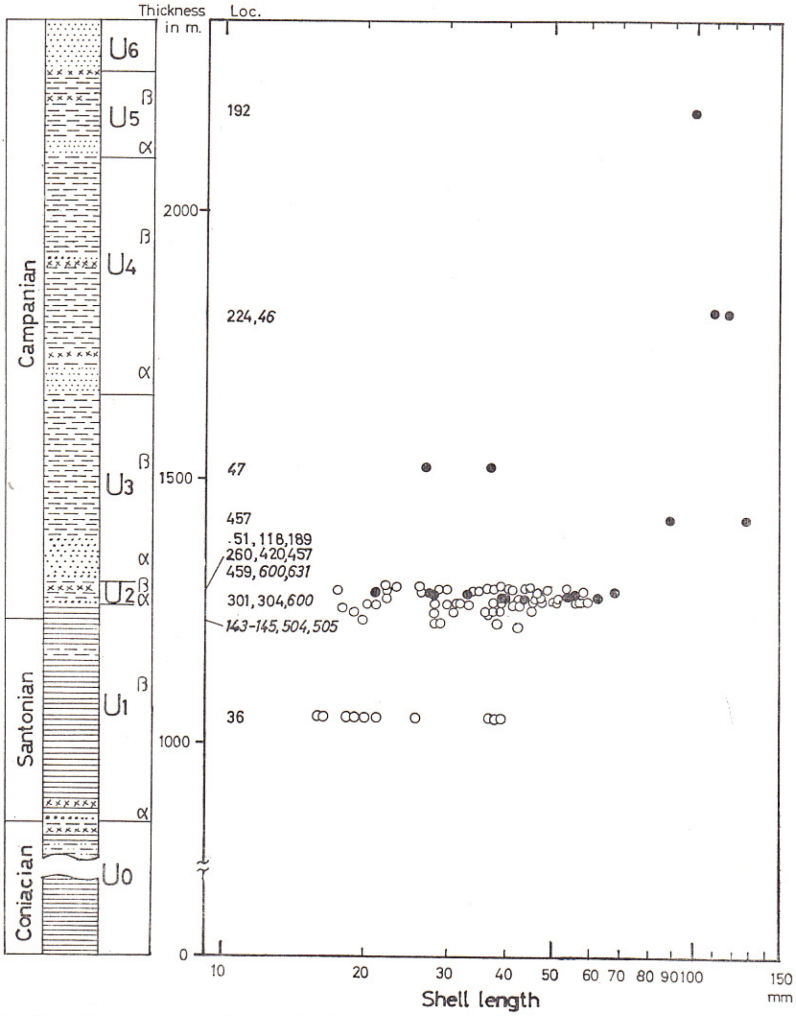


Fig. 27. Occurrence of radial ribs appearance in *Anisomyon transformis* and *A. giganteus* in the geological sequence of the Urakawa district. Localities in Fig. 1. Black and white dots respectively show radial and non radial rib stages of *Anisomyon*.

been changed from pseudoplanktonic to benthonic life.

The change from *A. cassidarius* to *A. giganteus* might represent an ecological adaptation analogous to that shown in the series of *I. naumanni naumanni-I. naumanni schmidti*. Irregular basal outline of the shell of Santonian *A. cassidarius* is regarded as being possibly due to the shell sticking to other shelly material. On the other hand, the Campanian *A. giganteus* is considered to have lived sparsely on sandy bottom, because they became too large to attatch themselves to other shelled animals, although contemporary *I. naumanni schmidti* was extraordinally large. This may indicate that they adapted themselves to the

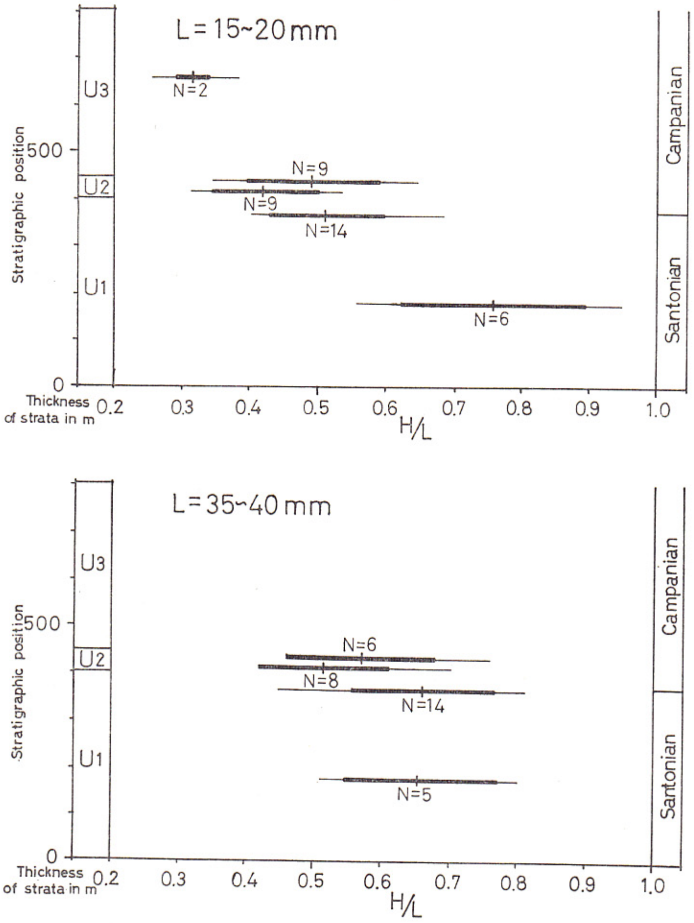


Fig. 28. Diagram showing the ratio $\left(\text{mean: } \bar{x}=\frac{1}{N}\Sigma xi,\right.$ standard deviation: $\left. s=\sqrt{\frac{\Sigma(xi-\bar{x})^2}{N-1}}\right)$ between length and height of the shells of *Anisomyon* in the Urakawa section.

increased roughness of the current during the lower Campanian age when the sea became shallower.

The phylogenetic relationship between lower Campanian *A. giganteus* and lower Maestrichtian *A. problematicus* is uncertain, because there is some break in the record of their successive occurrence. No evidence of gradational change has yet been found there. However, the similarity in shell shape and the orderly stratigraphical occurrence of the two species suggest that the latter could be a descendant of the former.

References

ANDERSON, F. M. (1958). Upper Cretaceous of the Pacific coast. *Geol. Soc. Amer.*, Mem. 71, 378p., 75 pls.

BØGGILD, O. B. (1930). The shell structure of the mollusks. *Kgl. Danske Vidensk. Selsk. Skr., Natur., Ser.* 9, 2: 233–326, pls. 1–15.

DUNDO, O. P., & EFREMOVA, V. I. (1974). Field atlas of the Senonian index fauna in the northeastern part of the Koryak Highland (in Russian), 28p., 12 pls., Sci. Res. Inst. Arct. Geol.

———, KOROTKEVICH, V. D., & BASHILENKO, L. V. (1974). Standard Section of the Senonian. Explanatory note to the field atlas of the Senonian index fauna in the notheastern part of the Koryak Highland (in Russian), 97p., 5 pls., *Ibid.*

GABB, W. M. (1864). Triassic and Cretaceous fossils. *Paleontology*, **2**, 243p., 32 pls., Geol. Surv. Calif.

HAYAMI, I. (1969). Mensuration of fossils and statistics—An example of paleontological exercise—(in Japanese). *Sci. Repts. Dept. Geol. Kyushu Univ.*, **10**(2): 67–90.

HUBENDICK, B. (1945). Phylogenie und Tiergeographie der Siphonariidae. Zur Kenntnis der Phylogenie in der Obdnung Basommatophora und des Ursprungs der Pulmonatengruppe. *Zool. Bidrag Upsala*, **24**, 216p.

ITOH, M. (1932 MS). *Helcion, Capulus* and *Inoceramus. Grad. Thesis Geol. & Paleont., Tohoku Imp. Univ.*, 114p., 18 pls.

JIMBO, K. (1894). Beiträge zur Kentniss der Fauna der Kreideformation von Hokkaido. *Palaeont. Abh., N.F.*, **2**(3): 140–194, Taf. 17–25.

JONES, D. L. (1963). Upper Cretaceous (Campanian and Maestrichtian) ammonites from Southern Alaska. *U.S. Geol. Surv. Prof. Paper*, (432): 1–53, pls. 6–41.

KANIE, Y. (1964 MS). The Cretaceous deposits in the Urakawa district, Hokkaido (in Japanese). *Grad. Thesis Yokohama Nat. Univ.*, 94p., 19 pls.

——— (1966). The Cretaceous deposits in the Urakawa district, Hokkaido (in Japanese). *Jour. Geol. Soc. Japan*, **72**(7): 315–328.

KASHIMA, N. (1972). Fossils from the Dogo-Himezuka, Matsuyama City, no. 2 (in Japanese). *Natures of Ehime (Ehime no shizen)*, **14**(8): 12–15.

KNIGHT, J. B., COX, L. R., KEEN, A. M., BATTEN, B. L., YOCHELSON, E. L., & ROBERTSON, R. (1960): Systematic descriptions, in MOORE, R. C. (*ed.*). *Treat. Invert. Paleont., Part I (Mollusca 1)*: I171–I1310. Geol. Soc. Amer.

KOBAYASHI, I. (1964). Introduction to the shell structure of bivalvian molluscs (in Japanese). *Earth Science*, (73): 1–12, pl. 1.

——— (1971). Internal shell microstructure of recent bivalvian molluscs. *Sci. Repts. Niigata Univ., Ser. E*, (2): 27–50, pls. 1–10 .

KOSUGE, S., & HAYASHI, S. (1967). Notes on the feeding habitats of *Capulus dilatatus* A. ADAMS (in Japanese). *Sci. Rept. Yokosuka City Mus.*, (13): 47–54, pls. 1–2.

MACCLINTOCK, C. (1967): Shell structure of patelloid and bellerophontoid gastropods (mollusca). *Peabody Mus. Nat. Hist., Yale Univ.*, bull. 22, 140p, 32 pls.

MATSUMOTO, T. (1942–'43). Fundamentals in the Cretaceous stratigraphy of Japan. *Mem. Fac. Sci., Kyushu Imp. Univ., Ser. D*, Part I: **1**(3): 129–280, pls. 5–20; Part II & III: **2**(1): 98–237.

——— (1954). The Cretaceous system in the Japanese Island. Japan Soc. Promot. Sci., 324p, 20 pls.

——— (1959). Zonation of the Upper Cretaceous in Japan. *Mem. Fac. Sci., Kyushu Univ., Ser. D*, **9**(2): 55–93, pls. 6–11.

———, & OBATA, I. (1962). On the *Baculites* facies (in Japanese). *Fossils*, (3): 57–63.

——— (1963a). A survey of the fossils from the Japan illustrated in classical monographs, Part 7, YOKOYAMA, M., 1890. Versteinerungen aus der japanischen Kreide. *Palaeontographica*, **36**: 159–202, Taf. 18–25. *Palaeont. Soc. Japan, 25th Anniv. vol.*, : 27–32, pls. 44–51.

——— (1963b). *Ditto,* Part 10, JIMBO, K., 1894. Beiträge zur Kentniss der Fauna der Kreideformation von Hokkaido. *Palaeont. Abh., N.F.,* **2**(3): 140–194, Taf. 17–25. *Ibid.,* 41–48, pls. 60–68.

——— (1965). A monograph of the Collignoniceratidae from Hokkaido, Part I. *Mem. Fac. Sci., Kyushu Univ., Ser. D,* **16**(1): 1–80, pls. 1–18.

———, & OHARA, J. (1971). Relations of Cretaceous and Tertiary strata in the Soya area, Hokkaido (in Japanese). *Sci. Repts., Dept. Geol., Kyushu Univ.,* **11**(1): 17–34.

——— (1973). Further notes on the Dogo-Himezuka fauna (in Japanese). *Jour. Geol. Soc. Japan,* **79**(7): 496.

———, & OKADA, H. (1973). Saku formation of the Yezo geosyncline (in Japanese). *Sci. Repts. Dept. Geol., Kyushu Univ.,* **11**(2): 275–309.

MEEK, F. B., & HAYDEN, F. V. (1857). Description of a new species of gastropoda from the Cretaceous formations of Nebraska Territory. *Philaderphia Acad. Nat. Scis. Proc.* for 1856, **8**: 63–69.

——— (1860). Systematic catalogue with synonymy of Jurassic and Cretaceous, and Tertiary fossils collected in Nebraska. *Ibid.,* **12**: 412–432.

MÜLLER, G. (1898). Die molluskenfauna des Untersenon von Braunschweig und Ilsede. I. Lamellibranchiaten und Glossphoren. *Abh. Preuss. Geol. Landes. N.F.,* **25**: 1–142, Taf. 1–18.

NAGAO, T., & ÔTATUME, K. (1938). Molluscan fossils of the Hakabuchi Sandstone of Hokkaidô. *Jour. Fac. Sci., Hokkaido Imp. Univ., Ser. 4,* **4**(1–2): 31–56, pls. 1–4.

OBATA, I., MAEHARA, T., & TSUDA, H. (1973). Cretaceous stratigraphy of the Hidaka area, Hokkaido (in Japanese). *Mem. Nat. Sci. Mus.,* (6): 131–145.

SAKAMOTO, T., TANAKA, K., SOYA, T., NODA, T., & MATSUNO, K. (1972). Geology of the Nakaminato district (in Japanese). *Quad. Ser.* 1:50,000, Tokyo–8, (11): 94+5p., Geol. Surv. Japan.

SASAI, H. (1936). Izumi-sandstone group in the island of Awaji (in Japanese). *Jour. Geol. Soc. Japan.* **43**: 590–602, pls. 28–29.

SCHMIDT, M. F. (1873). Über die Petrafakten der Kreideformation von Insel Sachalin. *Mem. Acad. Imp. Sci. st-Petersbourg, Ser 7,* **19**(3): 1–33, Taf. 1–8.

SOHL, N. F. (1960). Archaeogastropoda, Mesogastropoda and stratigraphy of the Ripley Owl Creek, and Prairie bluff formations. *U.S. Geol. Surv. Prof. Paper,* (331-A): 1–141, pls. 3–18.

——— (1964a). Neogastropoda, Opisthobranchia and Basommatophora from the Ripley, Owl Creek, and Prairie bluff formations. *Ibid.,* (331-B): 153–335, pls. 19–52.

——— (1964b). Gastropods from the Coffee sand (Upper Cretaceous) of Mississippi. *Ibid.,* (331-C): 345–391, pls. 53–57.

——— (1967). Upper Cretaceous gastropods from the Pierre shale at Red bird, Wyoming. *Ibid.,* (393-B): B1–46, pls. 1–11.

TAKEI, K. (1963). Stratigraphy and geological structure of the Cretaceous system in the eastern part of the Sanchu Graben, Kanto Mountainland (in Japanese). *Jour. Geol. Soc. Japan,* **69**(810): 130–146.

TANABE, K. (1971). Stratigraphy of the Cretaceous formations in the Uwajima district, Ehime Prefecture, Shikoku (in Japanese). *Jour. Geol. Soc. Japan,* **78**(4): 177–190.

——— (1973). Evolution and mode of life of *Inoceramus* (*Sphaenoceramus*) *naumanni* YOKOYAMA emend., an Upper Cretaceous bivalve. *Trans. Proc. Palaeont. Soc. Japan, N.S.,* (92): 163–184, pls. 27–28.

TANAKA, K., MATSUMOTO, T., & MAYEDA, Y. (1952). The Izumi group in the southernmost part of the island of Awaji (in Japanese). *Jour. Geogr.,* **61**(2): 67–72.

TASHIRO, M., & NODA, M. (1973). The geological age of the "Himenoura group", Kyushu, Japan (in Japanese). *Jour. Geol. Soc. Japan,* **79**(7): 465–480, pl. 1.

VISHER, G. S. (1969). Grain size distributions and depositional processes. *Jour. Sed. Petrol.*, **39** (3) : 1074–1106.

WENZ, W. (1938). Gastropoda, Teil I, Allegemeiner Teil und Prosobranchia. 240p, Berlin.

WHITEAVES, J. F. (1903). On some additional fossils from the Vancouver Cretaceous, with a revised list of the species therefrom. *Canada Geol. Surv., Mesozoic fossils.*, **1** (5) : 309–416, pls. 40–51.

YABE, H. (1927). Cretaceous stratigraphy of the Japanese islands. *Sci. Repts. Tohoku Imp. Univ., Ser. 2*, **11** (1) : 27–100, pls. 3–9.

YOKOYAMA, M. (1890). Versteinerungen aus der japanischen Kreide. *Palaeontographica*, **36** (4–6) : 159–202, Taf. 18–25.

YOSHIDA, H. (1935a). On the later pelagic larvae and early benthonic youngs of *Anadara inflata* (REEVE) (in Japanese). *Venus*, **5** (1) : 1–10, pl. 1.

——— (1935b). On the full-grown veligers and early young shell stage of *Venerupis philipinarum* (ADAMS and REEVE) (in Japanese). *Ibid.*, **5**: 264–273, pl. 12.

——— (1937). On the veliger larvae and youngs of *Anadara subcrenata* (LISCHKE) (in Japanese). *Ibid.*, **7** (1) : 5–11, pl. 1.

Locality guide

		East Long.	North Lat.
Abeshinai	安平志内	142°	44°
Arasaki	荒崎	139°36′	35°12′
Awaji	淡路	134°50′	34°19′
Chisaka	千栄	142°33′	42°53′
Dogo-Himezuka	道後姫塚	132°38′	33°50′
Hetonai	辺富内	142°13′	42°47′
Ikushunbetsu	幾春別	142°	43°
Kagahara	神ケ原	138°50′	36° 4′
Kawakami	川上	142°30′	47°20′
Keyanoohto	芥屋大門	130° 1′	33°51′
Koinoura	恋の浦	130°25′	33°58′
Kominato	小湊	140°12′	35° 7′
Koshiki-jima	甑島	129°44′	31°40′
Kotanbetsu	古丹別	141°30′	43°30′
Mukawa	鵡川	142°13′	42°46′
Naibuchi	内淵	142°30′	47°20′
Naka-hobetsu	中穂別	142°13′	42°50′
Nakaminato	那珂湊	140°37′	36° 4′
Otaushinai	オタウシナイ	143°40′	43°17′
Sanchu	山中	138°50′	36° 4′
Sarufutsu	猿払	142° 5′	45° 7′
Shirahama	白浜	139°54′	34°54′
Soya	宗谷	141°56′	45°31′
Tappu	達布	143°	44°
Tenjin-jima	天神島	139°36′	35°13′
Teshio	天塩	142°	44°
Tomiuchi	富内	142°13′	42°17′
Tsuyazaki	津屋崎	130°25′	33°58′
Urakawa	浦河	142°45′	42°11′
Uwajima	宇和島	132°14′	33°30′
Yokose-jima	横瀬島	139°39′	35° 8′
Yubari	夕張	142°	43°

北太平洋地域における白亜紀笠型巻貝の研究

蟹　江　康　光

日本を含む北太平洋沿岸地域に広く発達する海成上部白亜紀層中には，化石笠型巻貝が多産する。これらは白亜紀化石層序の確立および，白亜紀海棲動物群の変遷を解明する上に欠くことのできないグループのひとつである。しかしながら従来それらについての研究は，はなはだ不十分であった。

本論文では，白亜紀笠型巻貝を筋肉痕跡，殼構造，殼の形態，装飾によって分類学的検討を行ない，化石層序学的系列を明らかにしそれらを基礎に，それら巻貝を系統的に位置づけた。さらに堆積物からそのグループの生息していた環境を推定し，類似現生笠型巻貝類の殼形態などから，これらグループの生態を類推することによって，その古生態を解明するように努力し，また，時間とともに環境が変遷していく過程を論じた。

この研究により次の点が明らかにされた。

1)　白亜紀笠型巻貝の従来の分類学的位置は著しく混乱していたが，このたび笠型巻貝にとっては生理学的に最も重要な要素と考えられる筋肉痕跡に注目して分類を行なった。その結果，大部分の白亜紀笠型巻貝はその筋痕から Mesogastropoda の Capulidae に近縁であること，しかし，現生種に相当する科はないこと，また，殼構造から，化石種は Archaeogastropoda と Mesogastropoda の一部の種に似ているが Basommatophora とは異なることが判明した。

2)　上記の事実によって，これら笠型巻貝の分類的位置は従来 Basommatophora の Siphonariidae として記載された北アメリカ上部白亜紀産 *Anisomyon* を模式属とする新科を考えざるを得ない。従ってここに Anisomyonidae を提案する。この科の新設によって，従来 *Acmaea* [Acmaeidae]; *Helcion, Patella, Scurria* [Patellidae]; *Capulus* [Capulidae]; *Anisomyon, Brunonia, Siphonaria* [Siphonariidae] として記載された属中のかなり多くの種は Anisomyonidae に属することになる。

3)　Anisomyonidae は北太平洋沿岸地域で，少なくともアプチアンに出現し，前期マストリヒシアンまで存続する。*Anisomyon annulatus* はアプチアン，アルビアンに *A. cassidarius* はチューロニアンよりサントニアンに，*A. transformas* はカンパニアン最古期に，*A. giganteus* はカンパニアン古期に，*A. problematicus* はマストリヒシアン古期に生存した。*Anisomyon* 各種の生存期間は比較的短期間であるので示準化石として，白亜紀の化石層序学的区分に有効である。

4)　形態の時代的変化の傾向として，殼は白亜紀の時代が新しくなるにつれて大型となり，厚くなる傾向があり，また殼表に放射肋が発達し，殼頂は後部に移動する傾向がある。これらの変化は産状，岩相と現生笠型巻貝類の生態を比較，検討することによって，化石笠型巻貝がチューロニアンからサントニアンにわたる亜深海での付着生活からカンパニアン以降に浅海性細砂底での底生生活に適応した現象と解釈できる。

5)　本化石種は，アンモナイト，*Inoceramus* などといっしょに非潮間帯の海成堆積物

から多産する。現生の Archaeogastropoda と Basommatophora の笠型のものは潮間帯の岩上で海藻を採飼している。いっぽう Mesogastropoda のそれは海中で他物に付着して植物性プランクトンを採飼している。化石種はその産状から Mesogastropoda の笠型のものと似た生態をもっていたと推定される。

Yasumitsu KANIE

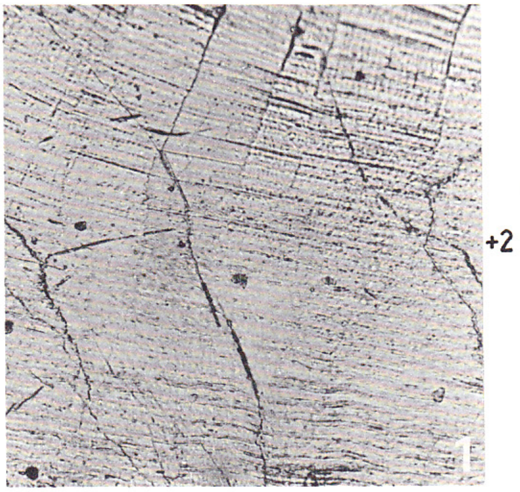
Some Cretaceous Patelliform gastropods from the Northern Pacific region

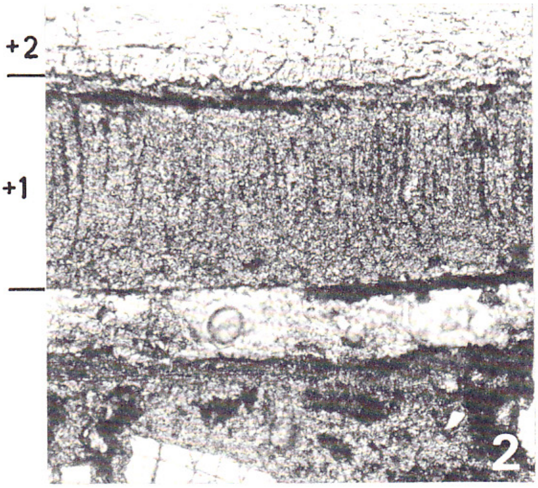
Plates 1–20

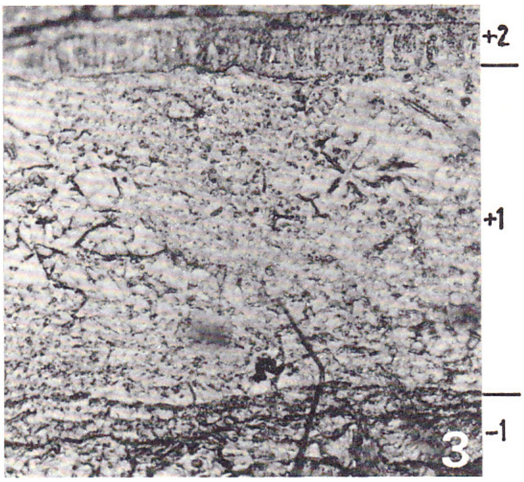
EXPLANATION OF PLATE 1

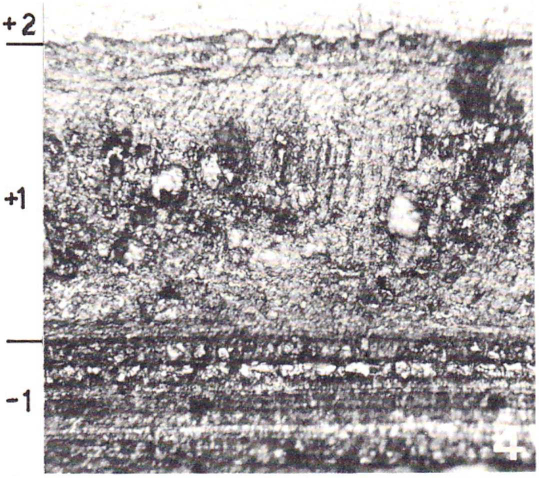
1–4. *Anisomyon cassidarius* (YOKOYAMA) ....page 10, text-fig. 4
Prismatic ? (m+2 ?), crossed-lamellar (m+1 ?) and radial crossed-lamellar (m−1 ?) structures. ×250. Loc. U459, Urakawa area, Hokkaido.

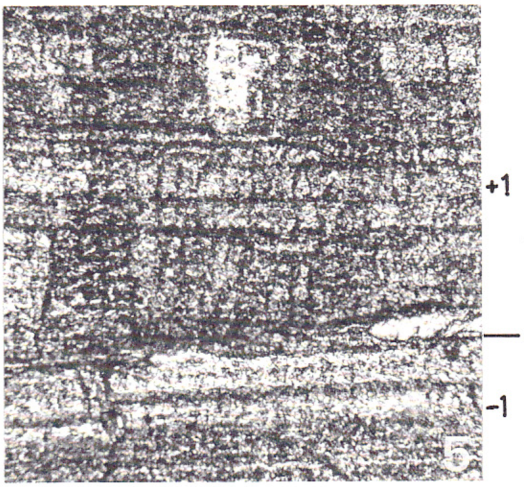
5–6. *A. giganteus* (SCHMIDT) ....page 12, text-fig. 5
Crossed-lamellar ? (m+1 ?) and radial crossed-lamellar or prismatic (m−1 ?) structures. ×250. Loc. Naibuchi, South Saghalien.

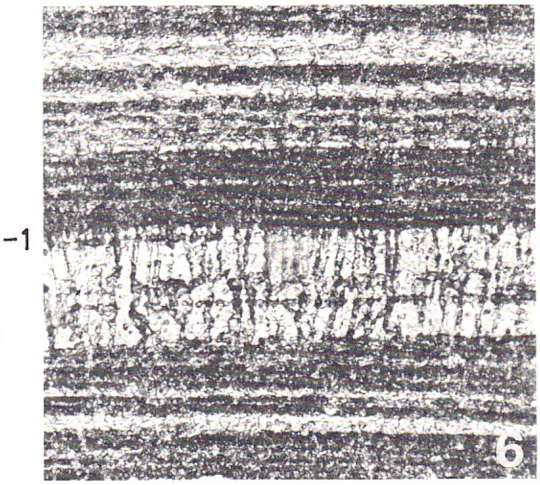

+2
1


+2
+1
2


+2
+1
-1
3


+2
+1
-1
4


+1
-1
5


-1
6

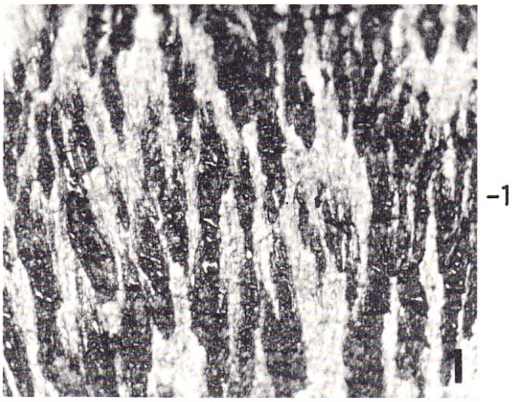
EXPLANATION OF PLATE 2

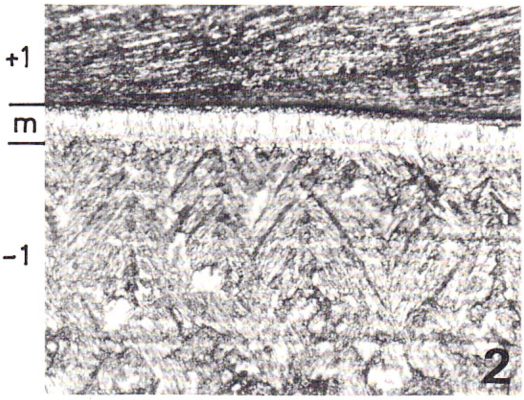
1–3. *Cellana nigrolineata* (REEVE) ....page 12, fig. 6
Complex prismatic (m+2), foliated (m+1), myostracum (m) and crossed-lamellar or complex crossed-lamellar (m—1) structures. ×250.

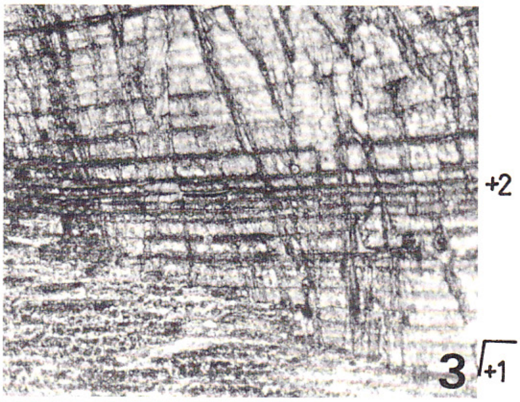
4. *Notoacmaea concina* (LISCHKE) ....page 12, fig. 7
Prismatic ? (m+2), concentric crossed-lamellar (m+1) and radial crossed-lamellar (m—1) structures. ×250.

5. *Capulus japonicus* A. ADAMS ....page 12, fig. 8
Concentric crossed-lamellar (m+2), radial crossed-lamellar (m+1) and complex crossed-lamellar (m—1) structures. ×250.

6–8. *Siphonaria* (*Mastosiphon*) *sirius* (PILSBRY) ....page 13, fig. 9
Concentric crossed-lamellar (m+1), myostracum (m) and crossed-lamellar (m—1, 2) structures. ×250.


-1
1

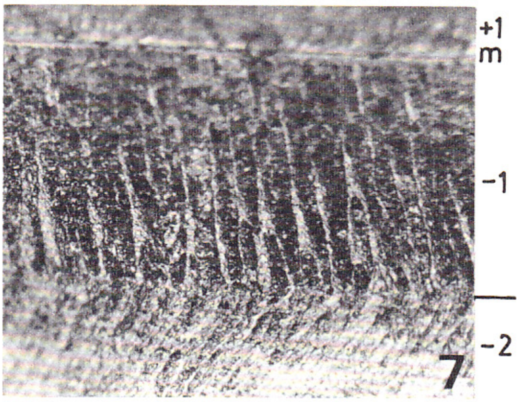

+1
m
-1
2

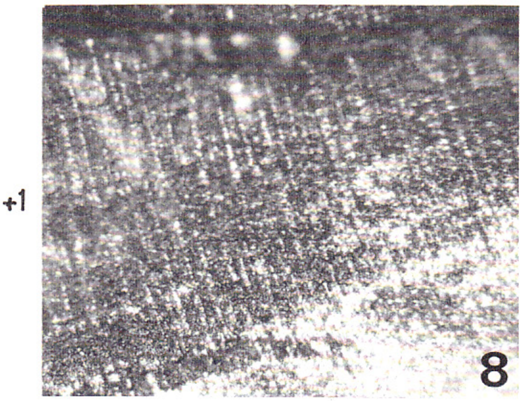

+2
3
+1


+2
+1
-1
4


+2
+1
5
-1


+1
m
-1
6


+1
m
-1
7
-2


+1
8

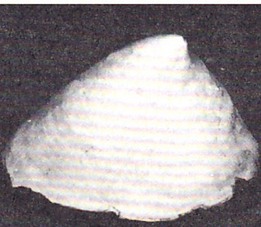
EXPLANATION OF PLATE 3

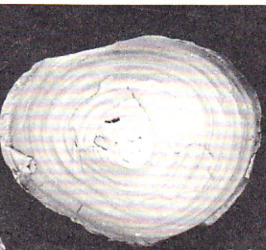
1–5. *Anisomyon cassidarius* (Yokoyama) ....page 17
1. YCM. GP. Ur457001-2, from loc. U457p, Urakawa, the U1β member, Santonian (Kanie coll.) ; 2. YCM. GP544, from Abeshinai, Nigorikawa formation, Santonian (Kanie coll.), muscle-scars observable; 3. YCM. GP. Ur457027-21, from loc. U457p, Urakawa, the U1β member, Santonian (Kanie coll.), muscle-scars observable; 4. YCM. GP538, from loc. Ik1047p, Ikushunbetsu, Santonian ? (Muramoto coll.) ; 5. GK. H703, from loc. U600c, Urakawa, the U2β' member, Santonian (Matsumoto coll.), muscle-scars observable.

6–9. *Anisomyon transformis* Dundo ....page 20
6. YCM. GP. Ur311002, Paratype, from loc. U311, Urakawa, the U2α member, lowest Campanian (Kanie coll.) ; 7. YCM. GP. Ur311001, Paratype, *Ditto*; 8. YCM. GP. Ur311001, *Ditto*; 9. YCM. GP. Ur305002, from loc. U305, Urakawa, the U2α member, lowest Campanian (Kanie coll.).

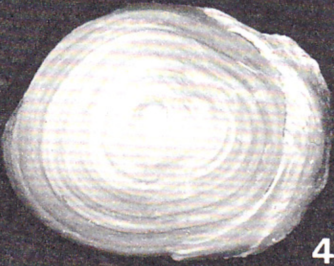
All figures are natural size. Photos with whitening by Kanie (1–4, 6–9) and Hayami (5).

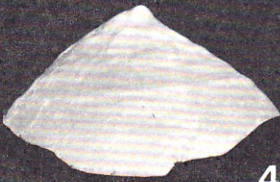

1

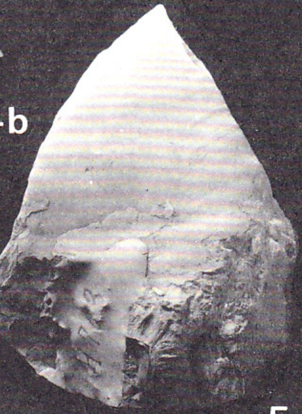

2


3b

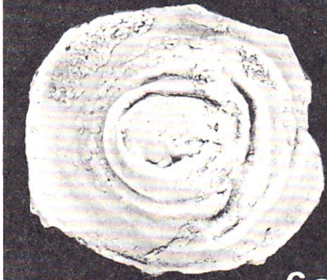

3a


4a


4b

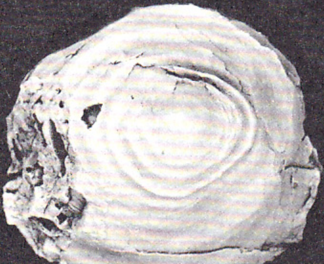

5

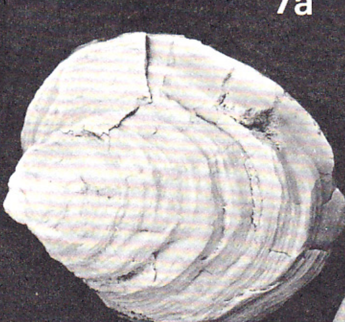

6b

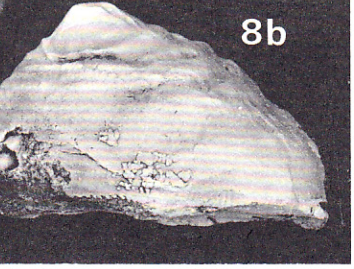

6a


7a


7b


8a


9b

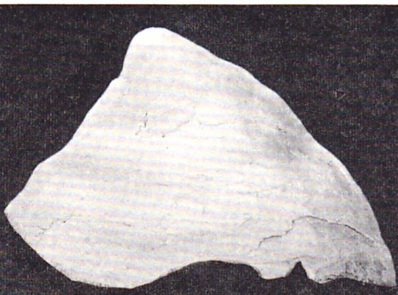

8b

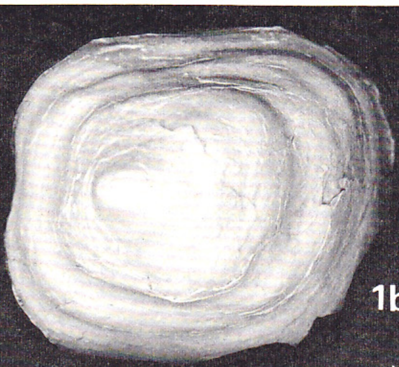

9a

EXPLANATION OF PLATE 4

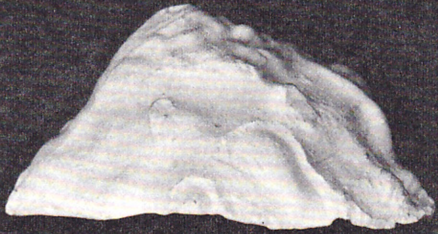
1–5. *Anisomyon transformis* Dundo ....page 20
1. YCM. GP543, from Soya, Campanian (Miyauchi coll.); 2. IGPS50907, from Kawakami, Campanian (Itoh coll.); 3. IGPS50907, *Ditto*; 4. IGPS57879, from Kawakami, Campanian (Itoh coll.); 5. UH12416, from Omagari, Abeshinai, Campanian (Nakajima and Matsushita coll.), scar of inner septa is observable.

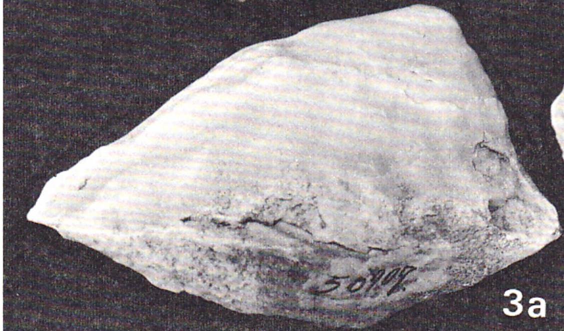
All figures are natural size. Photos with whitening by Kanie (1–3) and Hayami (5), and without whitening by Kanie (4).

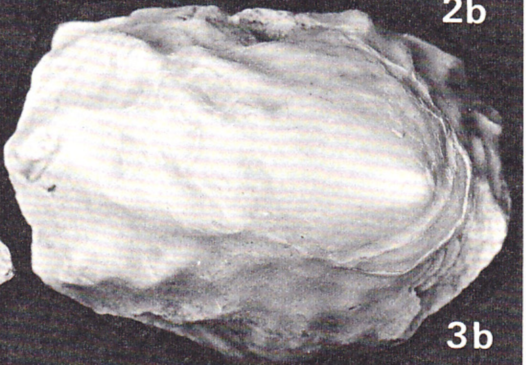

1a


1b

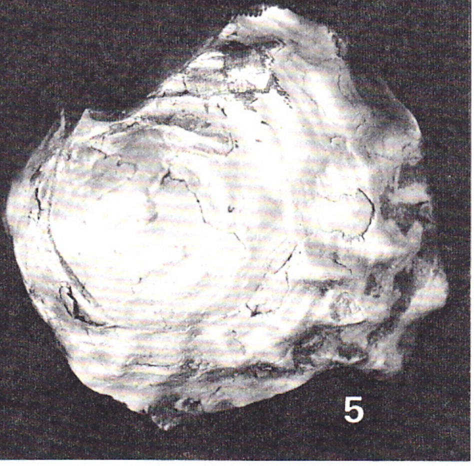

2a


2b


3a


3b


4


5

EXPLANATION OF PLATE 5

1, 2. *Anisomyon giganteus* (SCHMIDT), [Type A] ....page 23

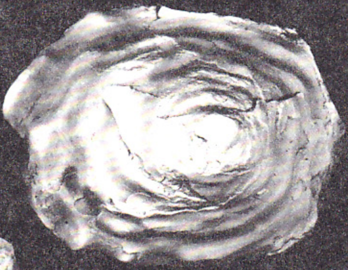
1. USGS. M2840, from loc. 65-AMK33, Alaska, Campanian ? (JONES coll.),
2. GK. H10320, from loc. U9, Urakawa, Ur4 member, Campanian (MATSUMOTO coll.).

3. *Anisomyon transformis* DUNDO ....page 20
YCM. GP534, from loc. 3606p, Abeshinai, Campanian (HAYAMI coll.), muscle-scars observable.

All figures are natural size. Photos with whitening by SAKAMOTO (1), HAYAMI (2) and KANIE (3).

1a

3a



3b

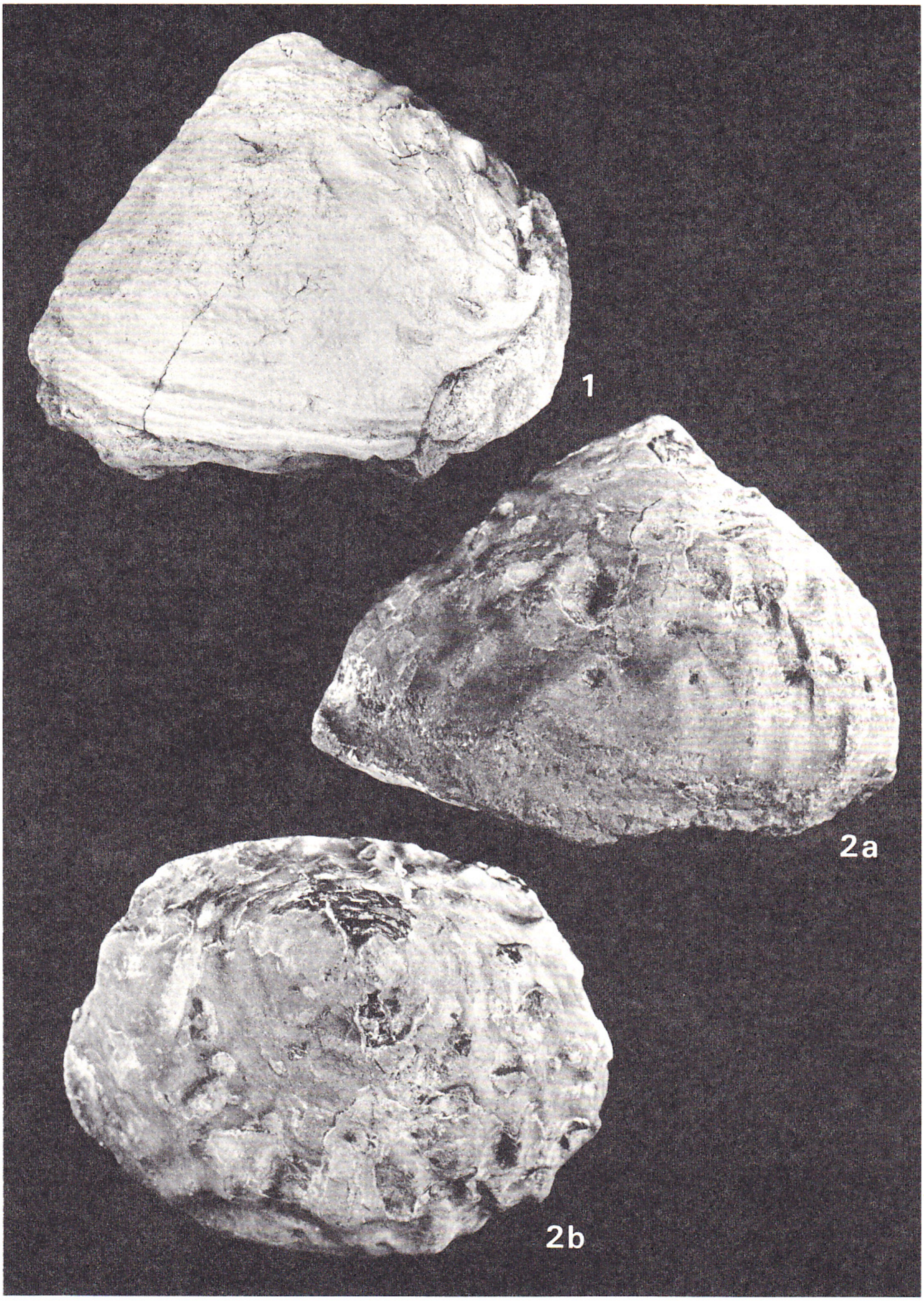
1b

2

EXPLANATION OF PLATE 6

1, 2. *Anisomyon giganteus* (SCHMIDT), [Type A] ....page 23
1. IGPS50907, from Kawakami, Campanian (ITOH coll.). 2. IGPS50907, *Ditto.*

All figures are natural size. Photos with whitening by KANIE (1) and without whitening by KUMAGAI (2).


1
2a
2b

EXPLANATION OF PLATE 7

1. *Anisomyon giganteus* (SCHMIDT), [Type A′] ....page 23
IGPS50512, from Jon Quiére, Campanian (ITOH coll.), ×1.

Photo with whitening by KUMAGAI.


50512

EXPLANATION OF PLATE 8

1. *Anisomyon giganteus* (SCHMIDT), [Type B] ....page 23
IGPS, from Kawakami, Campanian (ITOH coll.), ×1.

Photo with whitening by KUMAGAI.

1a

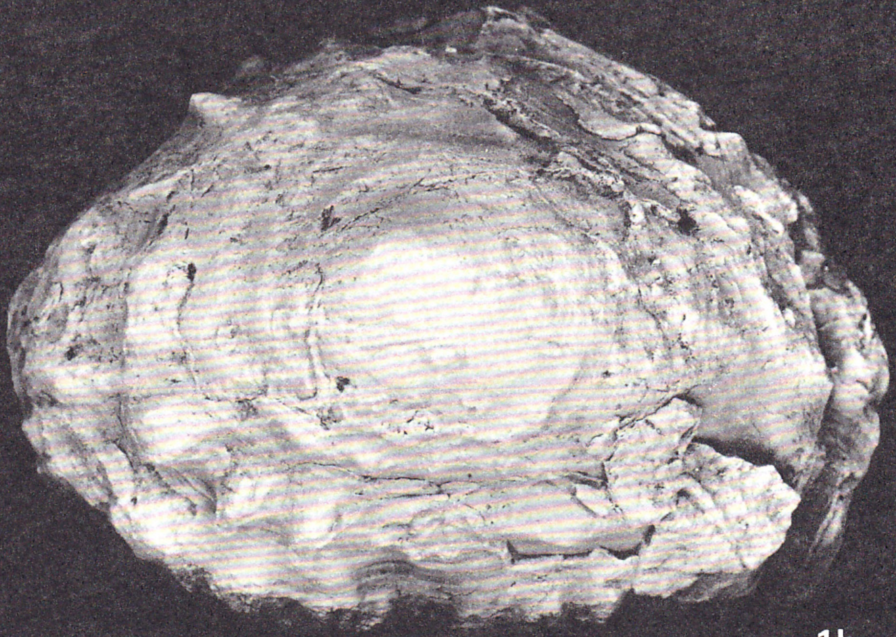
1b

EXPLANATION OF PLATE 9

1. *Anisomyon giganteus* (SCHMIDT), [Type B] ....page 23
UMUT. MM5534 (=GT. Cr695), from Naibuchi, Ryugase group, Campanian (KAWADA coll.), ×1.

Photo with whitening by KANIE.

1a

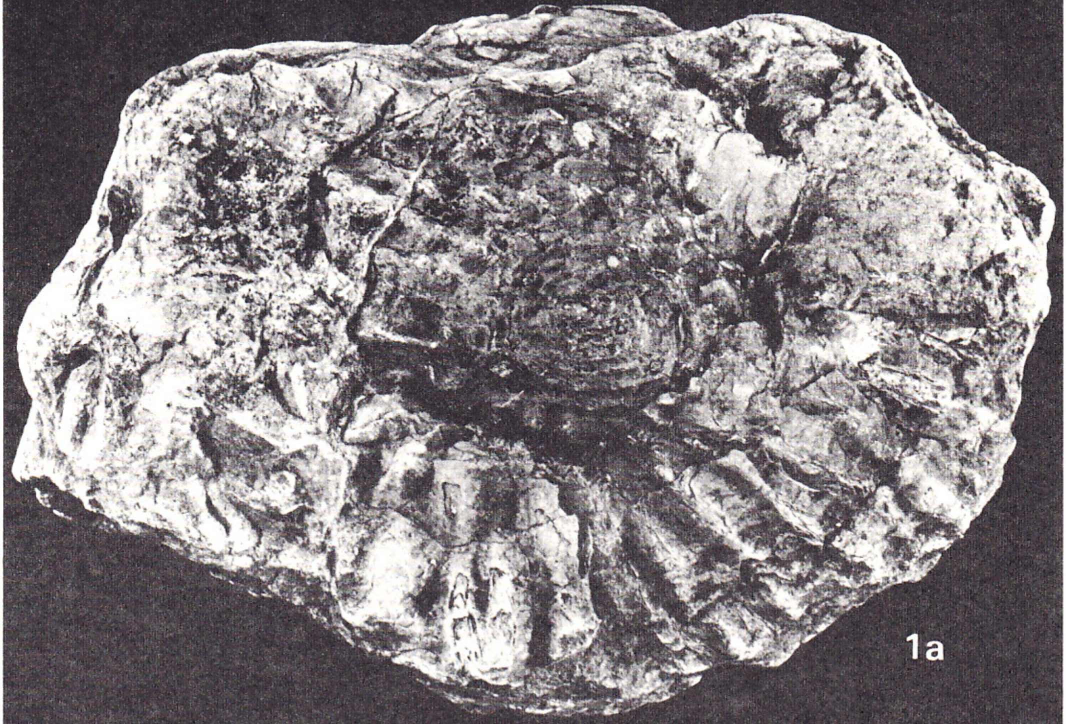


1b

EXPLANATION OF PLATE 10

1. *Anisomyon giganteus* (SCHMIDT), [Type B] ....page 23
IGPS51067, from Kawakami, Campanian (ITOH coll.), ×2/3.

Photo with whitening by KUMAGAI.



1a

1b

EXPLANATION OF PLATE 11

1. *Anisomyon giganteus* (SCHMIDT), [Type B] ....page 23
IGPS51065, from Jon Quiére, Campanian (ITOH coll.), ×3/4.

Photo without whitening by KUMAGAI.

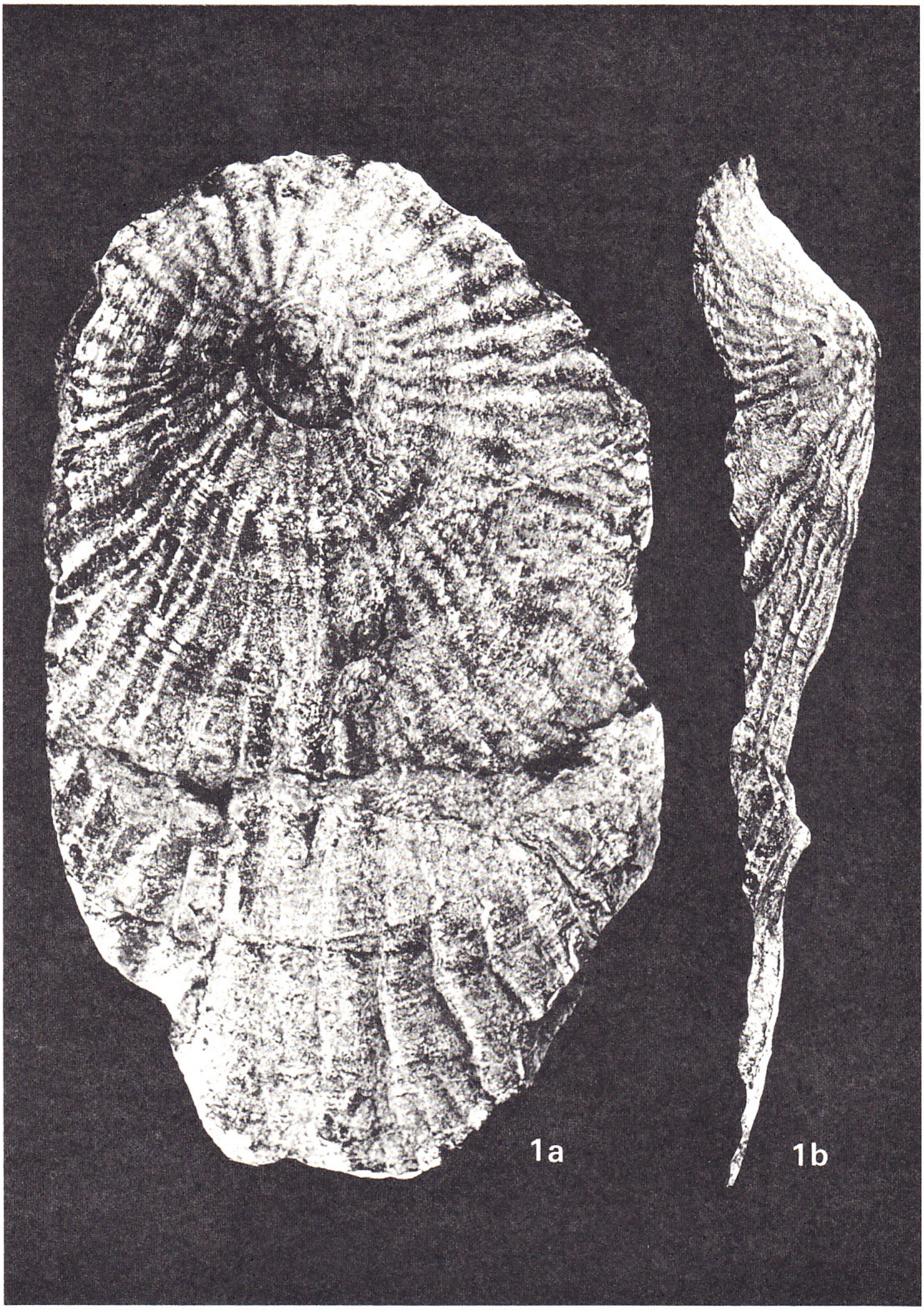
1a

1b

EXPLANATION OF PLATE 12

1. *Anisomyon giganteus* (SCHMIDT), [Type B] ....page 23
IGPS50163, from Jon Quiére, Campanian (ITOH coll.), ×3/4.

Photo without whitening by KUMAGAI.


1a
1b

EXPLANATION OF PLATE 13

1. *Anisomyon giganteus* (SCHMIDT), [Type B] ....page 23
GK. H10339, from South Saghalien ?, Campanian (*Inoceramus schmidti* zone), ×1/2.

Photo with whitening by HAYAMI.

EXPLANATION OF PLATE 14

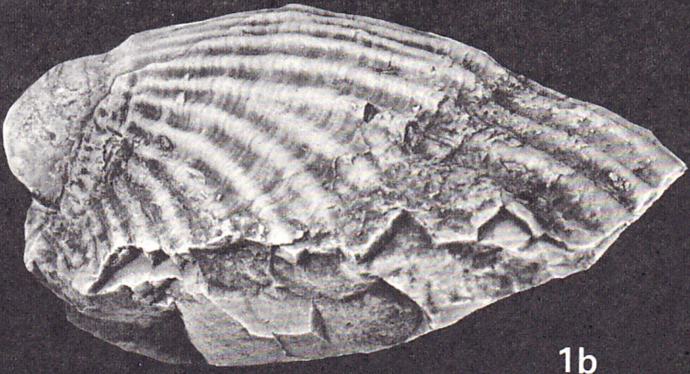
1, 2. *Anisomyon giganteus* (SCHMIDT), [Type B′] .... page 23
1. USGS. M550, from Alaska, Matanuska formation, Campanian (*Inoceramus scmidti* zone) (GRANTZ and JONES coll.) ; 2. USGS24242, from Alaska, Matanuska formation, Campanian (WILLIAMS coll.).

All figures are natural size. Photos with whitening by SAKAMOTO.

1a

2a

2b



1b

EXPLANATION OF PLATE 15

1. *Anisomyon giganteus* (SCHMIDT), [Type B] ....page 23
   IGPS50910, from Jon Quiére, Campanian (*Inoceramus schmidti* zone) (ITOH coll.).

2. *Anisomyon giganteus* (SCHMIDT), [Type B′] ....page 23
   GK. H10347, from loc. So151, Soya, Campanian (MATSUMOTO coll.).

All figures are natural size. Photos with whitening by KANIE (1) and HAYAMI (2).


1a
1b
2

EXPLANATION OF PLATE 16

1, 2. *Anisomyon giganteus* (SCHMIDT), [Type B′] ....page 23
1. IGPS50912, from Jon Quiére, Campanian (ITOH coll.) ; 2. IGPS50919, *Ditto*.

All figures are natural size. Photos with whitening by KANIE (1) and without whitening by KUMAGAI (2).

1

2

EXPLANATION OF PLATE 17

Anisomyon giganteus (SCHMIDT), [Type B′] ....page 23
IGPS, from Jon Quiére, Campanian (ITOH coll.), ×1.

Photo without whitening by KUMAGAI.

EXPLANATION OF PLATE 18

Anisomyon giganteus (SCHMIDT), [Type B′] ....page 23
IGPS51066, from Jon Quiére, Campanian (ITOH coll.), ×1/2.

Photo without whitening by KUMAGAI.

EXPLANATION OF PLATE 19

1, 2. *Anisomyon problematicus* (NAGAO and ÔTATUME) ....page 26
1. GK. H10340, from loc. H122p10, Tomiuchi, Hakobuchi group, lower Maestrichtian (MATSUMOTO coll.); 2. GK. H10319, from Awaji, Izumi group, (lower Maestrichtian) (SASAI coll.).

3, 4. *Anisomyon annulatus* (YOKOYAMA) ....page 27
3. From Kagahara, Gunma Prefecture, Ishido formation, upper Neocomian or Aptian (TAKEI coll.); 4. *Ditto.*

5. *Anisomyon giganteus* (SCHMIDT), [Type B′] ....page 23
From Dogo-Himezuka, Ehime Prefecture, Izumi group, Campanian (KUSUNOKI coll.).

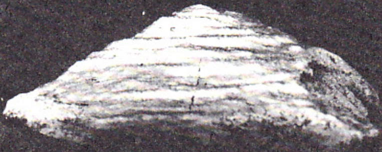
All figures are natural size. Photos with whitening by KANIE (1, 3, 4) and HAYAMI (2), and without whitening by KASHIMA (5).


1


2


3


4a


4b


5

EXPLANATION OF PLATE 20

1. *Anisomyon problematicus* (NAGAO and ÔTATUME) ....page 26
GK. H10318, from loc. H122p, Tomiuchi, Hakobuchi group, lower Maestrichtian (MATSUMOTO coll.), ×1.

Photo with whitening by HAYAMI.