ISSN 0549-3927

PALAEONTOLOGICAL SOCIETY OF JAPAN
SPECIAL PAPERS
NUMBER 35

NOTES ON GAUDRYCERATID AMMONITES FROM HOKKAIDO AND SAKHALIN

By

Tatsuro MATSUMOTO

PUBLISHED BY THE SOCIETY
December 15, 1995

Palaeontological Society of Japan, Special Papers

*Number 1 (Issued September 25, 1951) Bibliography of Japanese Palaeontology and Related Sciences, 1941–1950 .... Compiled by Riuji ENDO

Number 2 (Issued March 1, 1954) Matajiro YOKOYAMA's Pliocene and Later Faunas from the Kwanto Region .... Revised by Isao TAKI and Katsura ÔYAMA

*Number 3 (Issued August 31, 1957) Matajiro YOKOYAMA's Tertiary Fossils from Various Localities in Japan. Part 1 .... Revised by Jirô MAKIYAMA

*Number 4 (Issued June 30, 1958) Matajiro YOKOYAMA's Tertiary Fossils from Various Localities in Japan. Part 2 .... Revised by Jirô MAKIYAMA

*Number 5 (Issued December 15, 1959) Matajiro YOKOYAMA's Tertiary Fossils from Various Localities in Japan. Part 3 .... Revised by Jirô MAKIYAMA

*Number 6 (Issued July 25, 1960) Matajiro YOKOYAMA's Tertiary Fossils from Various Localities in Japan. Part 4 .... Revised by Jirô MAKIYAMA

*Number 7 (Issued November 30, 1961) Japanese Permian Bryozoa .... Sumio SAKAGAMI

*Number 8 (Issued September 20, 1962) Tertiary Marine Mollusca from the Joban Coal-Field, Japan .... Yasuhiko KAMADA

Number 9 (Issued December 15, 1962) Bibliography of Japanese Palaeontology and Related Sciences, 1951–1960 .... Compiled by Fuyuji TAKAI

*Number 10 (Issued February 20, 1965) Late Tertiary Floras from Northeastern Hokkaido, Japan .... Toshimasa TANAI and Nobuo SUZUKI

Number 11 (Issued February 20, 1966) The Echinoid Fauna from Japan and Adjacent Regions Part I .... Syôzô NISIYAMA

Number 12 (Issued September 20, 1966) Postcranial Skeletons of Japanese Desmostylia .... Tokio SHIKAMA

Number 13 (Issued March 16, 1968) The Echinoid Fauna from Japan and Adjacent Regions Part II .... Syôzô NISIYAMA

*Number 14 (Issued November 25, 1969) Litho- and Bio-Facies of Carbonate Sedimentary Rocks – A Symposium – .... Edited by Tatsuro MATSUMOTO

Number 15 (Issued February 25, 1971) Early Devonian Brachiopods from the Lesser Khingan District of Northeast China .... Takashi HAMADA

Number 16 (Issued December 25, 1971) Tertiary Molluscan Fauna from the Yakataga District and Adjacent Areas of Southern Alaska .... Saburo KANNO

Number 17 (Issued November 30, 1973) Revision of Matajiro YOKOYAMA's Type Mollusca from the Tertiary and Quaternary of the Kanto Area .... Katsura OYAMA

Number 18 (Issued November 30, 1974) Silurian Trilobites of Japan in Comparison with Asian, Pacific and Other Faunas .... Teiichi KOBAYASHI and Takashi HAMADA

Number 19 (Issued February 10, 1976) Bivalve Faunas of the Cretaceous Himenoura Group in Kyushu .... Masayuki TASHIRO

Number 20 (Issued January 31, 1977) Devonian Trilobites of Japan, in Comparison with Asian, Pacific and Other Faunas .... Teiichi KOBAYASHI and Takashi HAMADA

Number 21 (Issued May 10, 1977) Mid-Cretaceous Events – Hokkaido Symposium, 1976 .... Organized by Tatsuro MATSUMOTO

Number 22 (Issued March 30, 1978) Bibliography of Palaeontology in Japan, 1961–1975 .... Edited by Kametoshi KANMERA and Hiroshi UJIIE

Number 23 (Issued December 15, 1980) Carboniferous Trilobites of Japan in Comparison with Asian, Pacific and Other Faunas .... Teiichi KOBAYASHI and Takashi HAMADA

Number 24 (Issued December 15, 1981) Permian Conodont Biostratigraphy of Japan .... Hisaharu IGO

Number 25 (Issued November 15, 1982) Multidisciplinary Research in the Upper Cretaceous of the Monobe Area, Shikoku .... Compiled by Tatsuro MATSUMOTO and Masayuki TASHIRO

Number 26 (Issued December 24, 1984) Permian Trilobites of Japan in Comparison with Asian, Pacific and Other Faunas .... Teiichi KOBAYASHI and Takashi HAMADA

(* Out of Stock)

Continued inside of back cover

PALAEONTOLOGICAL SOCIETY OF JAPAN
SPECIAL PAPERS
NUMBER 35

NOTES ON GAUDRYCERATID AMMONITES FROM HOKKAIDO AND SAKHALIN

By

Tatsuro MATSUMOTO

PUBLISHED BY THE SOCIETY
December 15, 1995

PALAEONTOLOGICAL SOCIETY OF JAPAN
SPECIAL PAPERS
NUMBER 35

This publication is printed by
the GRANT-IN-AID for PUBLICATION of SCIENTIFIC RESEARCH RESULT
of the MINISTRY of EDUCATION, SCIENCE and CULTURE

All Communications relating to this publication should be addressed to
THE SERIES EDITOR
c/o Department of Earth and Planetary Sciences, Faculty of Science,
Kyushu University, Fukuoka 812-81

Frontispiece. *Gaudryceras tenuiliratum* Yabe.

In this nodule (GK. H8467), with dimensions of about 30 cm × 15 cm × 12 cm, at least ten mature shells of *Gaudryceras tenuiliratum* are contained along with a few other species. The nodule was collected by T.M. in August 1937 from Zone Mh6 (Santonian) at loc. N391, mid-valley of the Naibuchi, South Sakhalin. Figure is natural size.

Photo by courtesy of J. Yanagida.

Contents

Abstract

This paper contains mainly the systematic descriptions of selected species of the ammonite family Gaudryceratidae from Hokkaido and South Sakhalin. It is not a comprehensive monograph, as a number of species from the Campanian and Maastrichtian of this region have been recently described and are omitted from this paper, except for necessary remarks on some of them. Also certain other species are not fully described in this paper, as they are being studied by my colleagues of younger generations.

The species which are described in this paper consist of roughly three kinds. The first kind is referred to the species which were established more than 90 years ago. They are *Gaudryceras denseplicatum* (Jimbo), *G. intermedium* Yabe, *G. tenuiliratum* Yabe, *Anagaudryceras limatum* (Yabe), *A. yamashitai* (Yabe) and *A. yokoyamai* (Yabe). They were often misunderstood by previous authors home and abroad. Now they are represented by fairly large collections and are revised in this paper with necessary discussions.

The second kind includes the species which are well known abroad, but have not been sufficiently described on the material from Hokkaido and Sakhalin. Examples are *Anagaudryceras politissimum* (Kossmat), *Gaudryceras stefaninii* Venzo and *G. mite* (Hauer).

The third kind contains rather rare species. Some of them are described now on sufficient material, as exemplified by *Parajaubertella kawakitana* Matsumoto. Some others are based on small collections, but they can be defined clearly. Examples are *Miogaudryceras yokoii* n. gen. and sp., *Anagaudryceras madraspatanum* (Stoliczka), *A. howarthi* n. sp. and *Gaudryceras subcostatum* n. sp. Still others are tentatively named, as shown by *Miogaudryceras* n. sp. (?), *Anagaudryceras* aff. *A. whitneyi* (Gabb), *Gaudryceras* n. sp. (?) and *G.* aff. *G. kayei* (Forbes).

Several species of *Zelandites* are enumerated but not fully described. They may belong to the third kind. *Z. japonicus* Matsumoto is defined on this occasion as distinct from *Z. varuna* (Forbes).

In the concluding chapter, the principal results of the systematics are summarized and the species described in this and recent papers from Japan and S. Sakhalin are listed, showing their stratigraphic occurrences. Remarks on further problems are given concisely as Appendix.

NOTES ON GAUDRYCERATID AMMONITES FROM HOKKAIDO AND SAKHALIN
(Studies of the Cretaceous Ammonites from Hokkaido and Sakhalin-LXXVII)

Tatsuro MATSUMOTO

c/o Department of Earth and Planetary Sciences, Kyushu University 33, Fukuoka 812

Introduction

About 50 years ago, immediately after publication of a short note on the gaudryceratid ammonites from Japan (Matsumoto, 1943), I intended to publish a monograph of them. Actually 25 plates of photographs were prepared but have been left in my private file. For various reasons, however, this work was not published. One of the reasons was the unfavourable situation caused by World War II, but the main reason was that I was not satisfied with the tentative conclusions that could be reached at that date on the systematics of the family Gaudryceratidae.

Meanwhile, systematic descriptions of this family have been published by such eminent palaeontologists as Collignon (1956), Wright (1957), Wiedmann (1962a–c), Murphy (1967a–c), Kennedy & Klinger (1979) and so on. The deficiency of the material from the Lower Cretaceous deposits of Japan is evident, while I have given, often with coauthors, additional descriptions of several Campanian and Maastrichtian species (Matsumoto & Yoshida, 1979; Matsumoto & Morozumi, 1980; Matsumoto & Miyauchi, 1984; Matsumoto, 1984b; Matsumoto *et al.*, 1985), for they show interesting features at the last phase in the evolutionary history of the family. Besides these works several species of *Zelandites* from Hokkaido and South Sakhalin had already been described (Matsumoto, 1938). Also, remarks were given on some guadryceratid species from Alaska and California, including their relations with those from Hokkaido and Sakhalin (Matsumoto, 1959a, b).

In this paper I should like to set forth aspects from the results of my study that have been left unpublished and to point out the problems that still to be worked out.

Currently, palaeontologists of younger generations in Japan endeavour to contribute papers from new research perspectives and they have dealt and will deal with gaudryceratid ammonites as a part of the material for their studies because of the abundance of well-preserved specimens (e.g., Hirano, 1975; 1978). Of course, I have been and will be willing to supply the specimens of my previous collections for them. In this paper, therefore, I refrain from describing several species that could be studied in various ways on such plentiful material.

In this introduction I should like to give general remarks on my own method of study. It has been criticized that too many taxa have been proposed in previous papers of some authors as is shown in the list of species summarized by Collignon (1956) and others. In fact there are quite a number of nominal species that are not well-defined. As to infra-specific taxa many of the named varieties were temporary and may be unnecessary or doubtful, al-

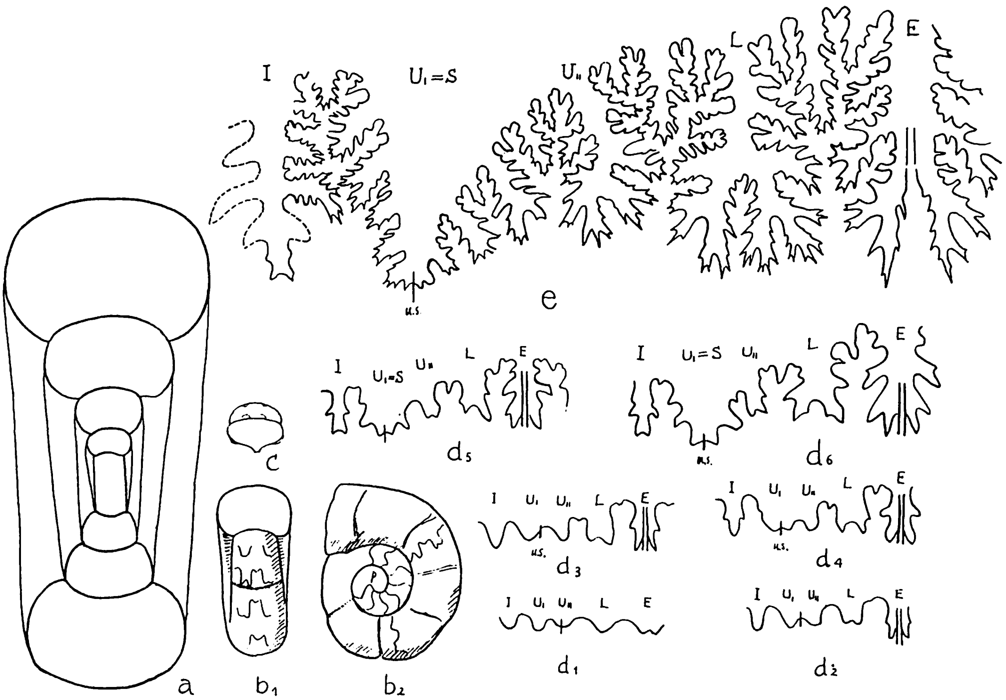


Figure 1. Development of characters in early growth stages of *Gaudryceras tenuiliratum*. (Reproduction of Matsumoto, 1943, fig. 1 in *Proc. Imp. Acad. Tokyo*, vol. 18, no. 10, p. 667 by permission of the Academy of Japan.)

a. Whorl-sections of a young shell (diam. = 13.2 mm).
b. Lateral and apertural views of the primitive stage.
c. Protoconch and a cross-section of the first whorl.
d. Development of suture-line (from d1 = second suture-line to d6 = suture-line at the early substage of the third whorl).
e. Suture-line of the seventh whorl at diam. = 38 mm.

This is based on the successive separation of the whorls of the specimen GK. H2000 from Zone Mh6 of the Naibuchi area, South Sakhalin (T. M. coll.). (T. M. *delin.*)

though a few of them could be evaluated as distinctly independent species.

In principle, a population or populations should be dealt with to recognize a species. In the actual cases of fossil material, however, it is not easy to know an original population from fossil material. This should be emphasized especially, if we consider that post-mortal ammonite shells were buoyant. Even if fossils of gaudryceratid ammonites were obtained abundantly in a layer at one locality, they do not necessarily represent the population of a single species. Remains of two or more species could possibly be intermingled as a result of transportation and sedimentation. Such a possibility should be considered, when the sample consists mostly of septate shells or when accumulations of woody fragments or vegetable material occur together with ammonites of various genera. When a species has a long vertical range, samples should be examined at successive stratigraphic levels.

Despite the occurrence of numerous specimens, completely preserved ones up to the peristome of the adult body chamber are very rare. This may be due partly to the fragile character of the body chamber and partly to the inadequate collection (due to hasty hunting and careless trimming or cleaning) and possibly also to predation. The body chamber of gaudryceratid ammonites is normally longer than that of strongly ornate acanthoceratid ammonites, three fourths of a whorl in the former as compared with half a whorl of the latter. Within a somewhat long adult body chamber, the morphological characters (e.g. B/H ratio, degree of involution, density and flexuosity of the lirae and major ribs) may change. The change of characters with growth from young to middle-aged and then adult shells is significant in many gaudryceratid ammonites.

Every morphological character must have some functional role in the mode of life and should be related to the adaptation to a given environment or a particular ecological factor. It may not be easy to give a satisfactory answer to the character's function, the mode of life, or the relevant environment or ecological factor. I should keep this point in mind, even if I rely upon the morphological characters to recognize or to define a species.

It cannot be always denied to state that in some cases a variability in a character may imply the potential that can give rise to an evolutionary divergence in the next step. The existence of a form which shows intermediate features between species would not always be taken as the evidence to synonymize the two nominal species.

A different difficulty is the problem of preservation. The ammonites of the Gaudryceratide have a fairly thin outer shell layer on which there are more or less fine and dense lirae. Normally the lirae are extremely fine and dense in *Eogaudryceras*, very fine but show minor rhythms in *Anagaudryceras* and often sharply raised or become somewhat coarser in *Gaudryceras*. Some of the coarser lirae can be called subcostae (riblets) if their base is weakly elevated on the inner shell layer. Otherwise the lirae are not observable on the intermediate or inner layer and on the internal mould. When a specimen is abraded or weathered, the liration is hardly discernible or much weakened and it may be misidentified.

I should confess here the attitude that I take in my research work. Field work is, I believe, fundamentally important to let myself commune with nature, where the truth must exist even though not apparent. I love nature deeply and she would open her mind, if I am allowed to write in a personified expression.

At first a keen eye-sight from the depth of ones mind in careful observation would catch what is thought a diagnostic species. Then analytical investigations should follow. In the course of the latter, I may notice an erroneous or doubtful point. Then, I reconsider to avoid such an error and go back to the first step. As I am not clever, I may go on and come back repeatedly, and, if necessary, I should go to the field for reinvestigation. It may, therefore, take much time to reach the final conclusion to my satisfaction.

This way of procedures in my research work is, I believe, analogous to that taken by certain Japanese artists in drawing and painting landscapes or seascapes or animals and plants (still life) in Japanese style. Actually I enjoy to look at the celebrated pictures wrought by such Great Artists as Yokoyama-Taikwan, Takenouchi-Seiho, Higashiyama-Kwaii and so on. I have been much encouraged, though indirectly, by them through their works which suggest me how they had undergone training until they get ability to catch the true beauty in the nature by intuition, and furthermore, how they invent to express that beauty until they eventuually complete the picture of their own originality.

Before going further into the description of the results of my study, I should give the

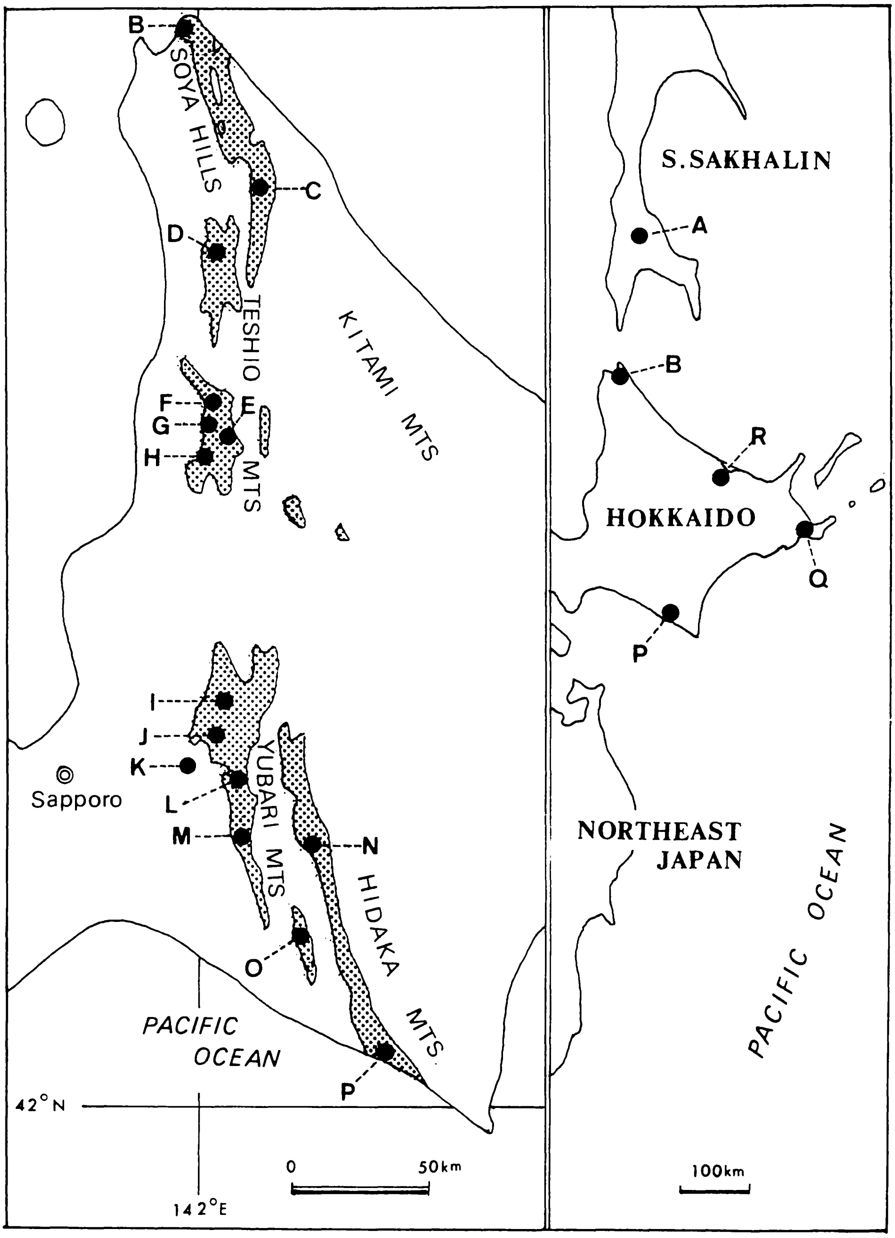


Figure 2. Map of Hokkaido and South Sakhalin, showing the locations of the areas A–R enumerated in the text.

following remarks:

(1) *Material.* – The specimens described in this and previous papers were collected during geological field work in the following Cretaceous areas (from north to south):

A. Naibuchi or Naiba area: Mid-valley of the Naibuchi (= Naiba) River, South Sakhalin

B. Soya area: Cape Soya and the Soya Hills, northern end of Hokkaido

C. Tonbetsu area: Valley of the Tonbetsu River, northern part of the Teshio Mountains

D. Abeshinai-Saku area: Mid-valley of the Teshio River and its tributary the Abeshinai River, central part of the Teshio Mountains. This area may be called by some authors Teshio-Nakagawa. A hilly area of Enbetsu [Wembets] is indicated in Fig. 2 within D, as it is adjacent to the west of the Abeshinai-Saku area

E. Soeushinai area: The so-called Shumarinai-Soeushinai area on the west and east sides of the Uryu River and also the upper reaches of the Kotanbetsu River adjacent to the south-west of Soeushinai. All these parts are included in the Geological Map, scale 1: 50,000, of "Soeushinai".

F. Haboro area: Upper reaches of the Haboro River

G. Kotanbetsu area: Mid-valley of the Kotanbetsu River F and G are adjacent to the west of E; E, F, and G are all in the Teshio Mountains

H. Obira area [= Tappu area of some authors]: Upper reaches of the Obirashibe [Opiraushibets] River, southern part of the Teshio Mountains

I. Ashibetsu area: Upper reaches of the Ashibetsu River. The westery adjacent Bibai area is indicated in Fig. 2 within I.

J. Ikushunbetsu area [= Mikasa area by some authors]: Mid-valley and upper reaches of the Ikushunbetsu [Ikushumbets] River and its tributaries Ponbetsu [Pombets], Kami-ichi, Kumaoi etc.

K. Yubari area: Yubari dome in the western part of Yubari City. Manji dome adjacent to the north of Yubari dome is indicated in Fig. 2 within K.

L. Oyubari-Shuyubari area: Upper reaches of the River Yubari. I, J, K and L are all in the Yubari Mountains, central Hokkaido.

M. Hobetsu district: Previously called Hobets-Hetonai or Hobetsu-Tomiuchi area, south-western part of the Yubari Mountains

N. Shimukappu-Hidaka area: Area of Cretaceous outcrops from the south-eastern part of the Yubari Mountains to the north-western part of the Hidaka Mountains

O. Monbetsu area: Tomihiro and other places in the Monbetsu-Shizunai belt, western part of the Hidaka Mountains

P. Urakawa area: Urakawa and adjacent areas on the south-western side of the Hidaka Mountains

Q. Akkeshi-Hamanaka-Nemuro area: Pacific coast of eastern Hokkaido

R. Saroma area: A potential area near Saroma, Okhotsk Sea coast of eastern Hokkaido. The Saroma Group in the hilly area of Saroma, about 25km north of Kitami, is Campanian-Maastrichtian-Palaeocene age on the evidence of Radiolaria (Nanayama, personal communication) and some bivalves were yielded there (Sakakibara & Tanaka, 1986; Obata *et al.*, 1993). No ammonite has been hitherto reported, but this place is indicated in Fig. 2 as a potential area, in view of the occurrence of gaudryceratids from the almost contemporary Nemuro Group in the east.

Geotectonically, the areas from A to P all belong to the Sorachi-Yezo Belt and the area Q to the Nemuro Belt. The area R (Saroma) is referred to the Tokoro Belt, which is situated adjacent to the west of the Nemuro Belt (see Nanayama *et al.*, 1993).

(2) *Stratigraphy and locality records.* -- Many of the specimens described in this paper are from my own collection made during 1936 to 1939 in the areas A, D, L, M and P of the

above list. The stratigraphy of the Cretaceous System in these areas, with geological maps, route maps, and list of localities, is described by Matsumoto (1942).

The Ikushunbetsu [Mikasa] area (J) in central Hokkaido is one of the classical areas where the reference sequence was established by Yabe (1926, 1927). The results of my biostratigraphic work along the main course of the Ikushunbetsu River and that of the Ponbetsu River were tentatively shown in columnar sections and route maps attached to my paper concerning the Collignoceratidae (Matsumoto, 1965) and more recently are explained in a monograph on the Kossmaticeratidae (Matsumoto *in* Matsumoto compil., 1991). The same area and nearby exposures (I and K) were studied by various persons of which Tanaka (in Shimizu *et al.*, 1953; in Matsuno *et al.*, 1964), Obata & Futakami (1977), Futakami (1982, 1986a, b) and Ando (1990) are important. In addition Matsumoto & Harada (1964) described the stratigraphy of the Yubari dome.

The locality records of the classical papers by Yokoyama (1890), Jimbo (1894) and Yabe (1903) are indicated by local place names in the areas B, C, D, E, H, I, J, K, L, M and P, but they are not pin-pointed and they often depend on transported or fallen nodules.

The Naibuchi area of South Sakhalin was investigated by Kawada (1929), whose localities also were not pin-pointed on a published map, although some of them can be referred to the zones of Matsumoto (1942).

Shimizu (1935b) summarized the results of his cephalopod zonation in a number of Cretaceous areas in South Sakhalin and Japan, but the basic details of stratigraphy, including locality records, were not published. The specimens listed in his 1935b paper are regrettably missing (see Matsumoto, 1988a). Among the ammonites, now held at Tohoku University, from the Naibuchi and other areas in South Sakhalin, there are several gaudryceratids, some of which were described by Matsumoto (1988a).

Coming back to the stratigraphy of the areas in Hokkaido, the results of field work with several colleagues are published in the papers of coauthorship as follows: Matsumoto & Miyauchi (1984) for the Soya area (B); Matsumoto *et al.* (1980 and 1981) for the Tonbetsu area (C); Matsumoto & Okada (1973) for a part of (D), (F), (G), (H), (J), (K) and (M) respectively; Hashimoto *et al.* (1965), Matsumoto & Inoma (1975) and Nishida *et al.* (1992, 1993a) for the Soeushinai area (F), Okada & Matsumoto (1969) and in more detail by Toshimitsu (1988), for the Haboro-Kotanbetsu area (F–G), Tanaka (1963) and Tanabe *et al.* (1977) for the Obira area (H); Hirano *et al.* (1977), Matsumoto *et al.* (1991) and Nishida *et al.* (1993b, 1995) for the Oyubari-Shuyubari area (L); Matsumoto *et al.* (1989; 1994) for the Hobetsu district (M); Matsumoto (1995) for the Urakawa area (P); and Matsumoto & Yoshida (1979) for a part of eastern Hokkaido (Q). Some of the above papers are written in Japanese but contain abstracts and captions of route maps etc. in English. A summary note, with columnar stratigraphic sections of selected areas, given on the occasion of the symposium of IGCP No. 58 (Mid-Cretaceous Events) at Uppsala (Matsumoto *et al.*, 1978) is useful in some respects, but now needs revision.

For the major litho-stratigraphic divisions of the clastic deposits in the meridional (i.e. N-S) belt of Hokkaido, the Lower Yezo Group, Middle Yezo Group, Upper Yezo Group and Hakobuchi Group have been used. The Yezo Group was a nomenclatorial replacement of the Ammonite Beds of Yabe (1903, 1926, 1927), with some revision. That renaming was proposed by Matsumoto (1952) at much earlier date than the accurate definition of the stratigraphic terminology, such as that of Hedberg (1976) or Holland *et al.* (1978).

I write in this paper the above three divisions as the subgroups, e.g. Upper Yezo Subgroup or upper subgroup of the Yezo Group, because of the general conformity and gradual change of lithofacies between them. The base of the Middle Yezo Subgroup was reported as an unconformity by some authors in some areas, but the time-gap does not seem great. This question should be solved by further study.

For a formation, which extends for several quadrangles of geological map (scale 1:50,000), an adequate name has been used, such as the Mikasa Formation (that is a more sandy upper part of the Middle Yezo Subgroup and was called the Trigonia Sandstone by Yabe, 1926). To understand the general configuration and lithological constituents of the major stratigraphic units, a short account given by Matsumoto and Okada (1971, p.61–74) may be useful.

Local formational names or minor subdivisions by lettering (e.g. My1, My2,...or IIa, IIb,...) may be cited, if necessary, from the papers concerned with respective areas.

For the time-stratigraphic units the international stage names (e.g. Cenomanian, Turonian etc.) are used in this paper, although the precise stage-boundaries have yet to be worked out.

(3) *Repositories.* – The specimens from Hokkaido and other areas in Japan and South Sakhalin described in this and referred previous papers are held in the following institutions in the alphabetic order of their abbreviations:

BMNH: British Museum (Natural History)
BSM: Bayerische Staatmuseum für Paläontologie und historische Geologie, München
GK: Type Room, Department of Earth and Planetary Sciences, Kyushu University 33, Hakozaki, Fukuoka 812
GSI: Geological Survey of India, Calcutta, India
GSJ: Geological Museum, Geological Survey of Japan, Tsukuba 305
HMG: Hobetsu Museum, Hobetsu, Hokkaido 054-02
IGPS: Institute of Geology and Palaeontology, Tohoku University, Aoba, Sendai 980
MCM: Mikasa City Museum, Mikasa, Hokkaido 068-21
NSM: National Science Museum, Hyakunin-cho, Tokyo 169
ONHM: Natural History Museum of Osaka, Nagai Park, Osaka 546
TKD: Tokyo Kyoiku Daigaku, now changed to the Institute of Geological Sciences, Tsukuba University, Tsukuba 305 (temporarily kept at GK)
TNHM: Natural History Museum of Toyohashi, 441-31
UMUT [=GT]: University Museum, University of Tokyo, Hongo, Tokyo 113
YCM: Yokosuka City Museum, Fukada-dai, Yokosuka 238

Several specimens belong to private collections indicated as follows, but most of them are shown side by side by MCM number, as they are officially kept there.

MC: The Muramotos' Collection, Yayoi, Mikasa, Hokkaido 068-21
TKC: Tadashi Kawano's Collection, Iwamizawa, Hokkaido 068 (now donated to GK)
TTC: Takemi Takahashi's Collection, Yayoi, Mikasa, Hokkaido 068-21
YKC: Yoshitaro Kawashita's Collection, Tomatsu-Chiyoda, Mikasa, Hokkaido 068-21

(4) *Technical terms.* – The morphological terms in the descriptions follow those used by Matsumoto (1988b, p.4), who generally followed those in the *Treatise* (Arkell *et al.*, 1957, p.L2–L6). In addition to "stria (pl. striae)" which is defined as "minute groove on shell surface, especially on otherwise smooth surface", I use in this paper the term "furrow" for the

minute groove which is impressed on the inner shell-layer or even on the internal mould but is much narrower, weaker and more frequent than the normal groove or constriction.

The abbreviations to explain the sutural elements follow those in my previous papers, which depend on the classical work of Wedekind (1916), as applied by Kullman & Wiedmann (1970). In the drawing of sutures u. s. and u. sh. mean umbilical seam and umbilical shoulder.

The definition of the adjective terms which are often used in the description has been proposed by myself (Matsumoto *in* Matsumoto, compiler, 1954, p. 246). For the persons to whom that book (out of print) may not accessible, I have recently shown it in another paper (Matsumoto *in* Matsumoto (comp.) 1988b, p. 4–5), which is reproduced herein.

Size of shell

- very small = diameter less than 35 mm
- fairly small = diameter from 35 mm to nearly 75 mm
- moderate = diameter from 75 mm to nearly 125 mm
- fairly large = diameter from 125 mm to 250 mm
- very large = diameter more than 250 mm but less than 500 mm
- huge or gigantic = more than 500 mm

Width of umbilicus (in proportion to the entire shell diameter)

- very narrow = less than 8%
- narrow = 8% to nearly 17%
- fairly narrow = from 17% to nearly 30%
- moderate = from 30% to nearly 40%
- fairly wide = from 40% to nearly 50%
- wide = from 50% to 65%
- very wide = more than 65%

Compression of whorl

- defined by the proportion of whorl-breadth to whorl-height (B/H)
- compressed or higher than broad { much compressed = $B/H<2/3$; fairly compressed = $1>B/H>2/3$ }
- as high as broad = $B/H = 1$
- depressed or broader than high { fairly depressed = $3/2>B/H>1$; much depressed = $B/H>3/2$ }

Involution of whorl

- overlapped part of the next inner whorl, measured in whorl-height
- evolute............ { very evolute = less than one third; fairly evolute = about one third }
- moderate......... about a half
- involute........... { fairly involute = nearly two thirds; very involute = more than two thirds }

The measurements of linear dimensions are in mm. The following abbreviations are used in the table of dimensions:

D = diameter, U = width of umbilicus, H = whorl-height, W = whorl-breadth, h = whorl-height at half a whorl (i.e. 180°) adaptical from H; HT: holotype, LT: lectotype, PL: paralectotype, PT: paratype; E: preserved end, E-90° = at a point 90° (a quarter whorl) adaptical from E, LS = last suture (i.e. at the end of the phragmocone, or at the beginning of the body chamber, *c.* = approximate or inferred

(5) *Remarks on figures* – In the captions of Figures the specific name, specimen number or other indication, category of type(s) and rate of magnification or reduction are written. The locality records, including the locality number, place name, general area or region, stratigraphic position and collector(s), are omitted for brevity. They are described under "Material" in the text.

The minor figure number(s) is(are) not used but the same specimen in the same rate of magnification in different views (lateral, frontal, back etc.) are connected by dotted lines. If a figure contains two or more specimens or a specimen of different rate of magnification, they are indicated as A, B, C...etc. and they are explained in the caption. The position of the last suture (LS) may be indicated by a mark of small arrow. Scale bar is 10 mm in most cases; otherwise the length of the bar is explained in the caption.

The photographs have been taken mostly by courtesy of Masayuki Noda unless otherwise stated. Some are by the late Mr. Chuzaburo Ueki who worked for years in the Department of Geology, University of Tokyo. Some of MCM specimens are by courtesy of Katsumi Shinohara and Kikuo Muramoto. Drawings of specimens and sutures are by myself.

SYSTEMATIC DESCRIPTIONS

Order Ammonoidea
Family Gaudryceratidae Spath, 1927
Genus *Parajaubertella* Matsumoto, 1943

Type species. – *Parajaubertella kawakitana* Matsumoto, 1943, by the original designation (Matsumoto, 1943, p. 666).

Diagnosis. – Mature shell large or medium-sized and fairly involute, showing subrounded to suboval whorl-section with abruptly rounded umbilical edge and high wall. The ornament of the adult body chamber similar to that of *Anagaudryceras sacya* (Forbes).

Umbilicus of the young growth stage narrow, deep and stepped, showing subangular edges and nearly vertical or very steeply inclined, high walls. The whorl-section at the corresponding growth stages lunate to semi-circular but never carinate on sides, forming broad dome-like outline from the umbilical edges to the venter, and much broader than high. The surface of the shell in these younger stages is marked by very fine and dense, radial lirae as on that of young *Anagaudryceras*; crowding of the lirae and faint striation may occur periodically, suggesting rhythms in growth. At a certain growth stage on the middle-aged shell, a constriction, accompanied by a collar behind, appears, which is prorsiradiate around the umbilicus and nearly rectiradiate on the main part of flank, crossing the venter without or with a gentle projection.

Whorl of the very early stage similar to that of normal gaudryceratids, reniform in section and ornamented with flanges on surface.

Suture fundamentally similar to that of *Eogaudryceras* and *Gaudryceras*, except for somewhat broadened stem and enlarged two folioles of the apparent "third saddle" (called here for convenience) at the umbilical edge of a certain juvenile stage, say at D=28mm in the type species.

Discussion. – *Parajaubertella* was regarded by Wiedmann (1962c, p. 9) as a synonym of *Gabbioceras* Hyatt, 1900. He referred it, however, to the subgroup of *Gabbioceras hertleini* Wiedmann in the subfamily Gabbioceratinae Breistroffer, 1953. *G. hertleini* is actually a member of *Eogaudryceras* Spath (see Murphy, 1967b, p. 9) and should be excluded from the Gabbioceratinae.

Based on the study of a number of specimens stored in Europe (mainly France) as well as in the United States, Murphy (1967a) has given a comprehensive account of the Gabbioceratinae, including a result of his discussion with Wiedmann. This is still useful and I owe much to Murphy's (1967a–c) three papers for the sound understanding of *Gabbioceras*. The type species is *Gabbioceras angulatum* Anderson, 1902 (p. 87, pl. 6, fig. 139), from the Upper Aptian *Eotetragonites wintunius* Zone of California. The diagnosis of the genus *Gabbioceras* has been given by Murphy (1967c, p. 597) and is not repeated here.

Murphy furthermore described all the species of *Gabbioceras* and *Jauberticeras*. The description of *G. angulatum* by Murphy (1967c, p. 597, pl. 64, figs. 1, 2, 8, 9; 1967b, p. 27, pl. 3, figs. 1–3; text-figs. 20, 21) conforms with my observation on several examples of this species from California. Incidentally specimens of "*Ammonites batesi* Trask" (angulated variety) of Gabb (1869, in part), which should be stored in the Academy of Natural Science, Philadelphia, were not located there (in October 1957). I examined, however, three specimens, though without clear locality records on the labels, in the Museum of Comparative Zoology, Harvard.

They include a beautifully preserved young shell and an adult (D=68mm), whose body chamber is somewhat displaced. My observation conforms generally with Murphy's.

All the hitherto described species of *Gabbioceras* have globose young shells characterized by a funnel shaped umbilicus with angulation on the flank and a broadly arched venter. This gives an apparent similarity of *Gabbioceras* to *Parajaubertella* in youth. It is too bad that many of these species of *Gabbioceras* are represented only by immature specimens. Fortunately, however, characters of the mature stage are known in the type species. *G. angulatum* is rather small; its adult outer whorl, less than 100 mm in diameter; is rounded to suboval in section and marked by lirae and fairly frequent constrictions but devoid of ornament of the adult *sacya* type.

As to the pattern of suture the two genera can be said fundamentally similar but are not quite identical. In *Parajaubertella* the umbilical edge is located at the site of the "third saddle" on the umbilical side of U2 and that saddle is modified to have a broad stem on which the two folioles are going to be but not completely independent (see Fig. 3d). In *Gabbioceras* the angulation is located originally in the midst of U2 and this gave rise to broadening of U2 and development of additional saddle and lobes in later species (see Murphy, 1967c, text-fig. 1).

The above difference corresponds to the difference in the site of angulation in the ontogeny. The angulation occurs at the middle of the flank in *Gabbioceras*, whereas in *Parajaubertella* the umbilical edge is angular or subangular. In other words, the similarity in the shell form of immature stage between the two genera is homeomorphic.

To sum up, I agree with Murphy (1967c, p. 596) in regarding *Parajaubertella* as an offshoot from the main stock of *Eogaudryceras-Anagaudryceras*. More specimens from successive stratigraphic levels should be searched for to trace precisely the presumed line of descent. At any rate *Parajaubertella* is not a member of the subfamily Gabbioceratinae.

Occurrence. – So far *Parajaubertella* is known in the Lower Cenomanian strata of the northern Pacific region. Its true geographical and stratigraphical ranges should be determined by further investigations.

Parajaubertella kawakitana Matsumoto, 1943

Figures 3–13

Parajaubertella kawakitana Matsumoto, 1943, p. 667, fig. 2a–d; Matsumoto, 1959a, p. 70, pl. 23, fig. 1a–d; text-fig. 11; Murphy, 1967b, p. 26.
Parajaubertella imlayi Matsumoto, 1959a, p. 71, pl. 21, figs. 1a–d, 2; text-figs. 12, 13; Murphy, 1967b, p. 26.
Gabbioceras kawakitanum (Matsumoto); Wiedmann, 1962c, p. 19, fig. 1b.
Gabbioceras imlayi (Matsumoto); Wiedmann, 1962c, p. 20.
Parajaubertella imlayi Matsumoto; McLearn, 1972, p. 40, pl. 21, fig. 1.

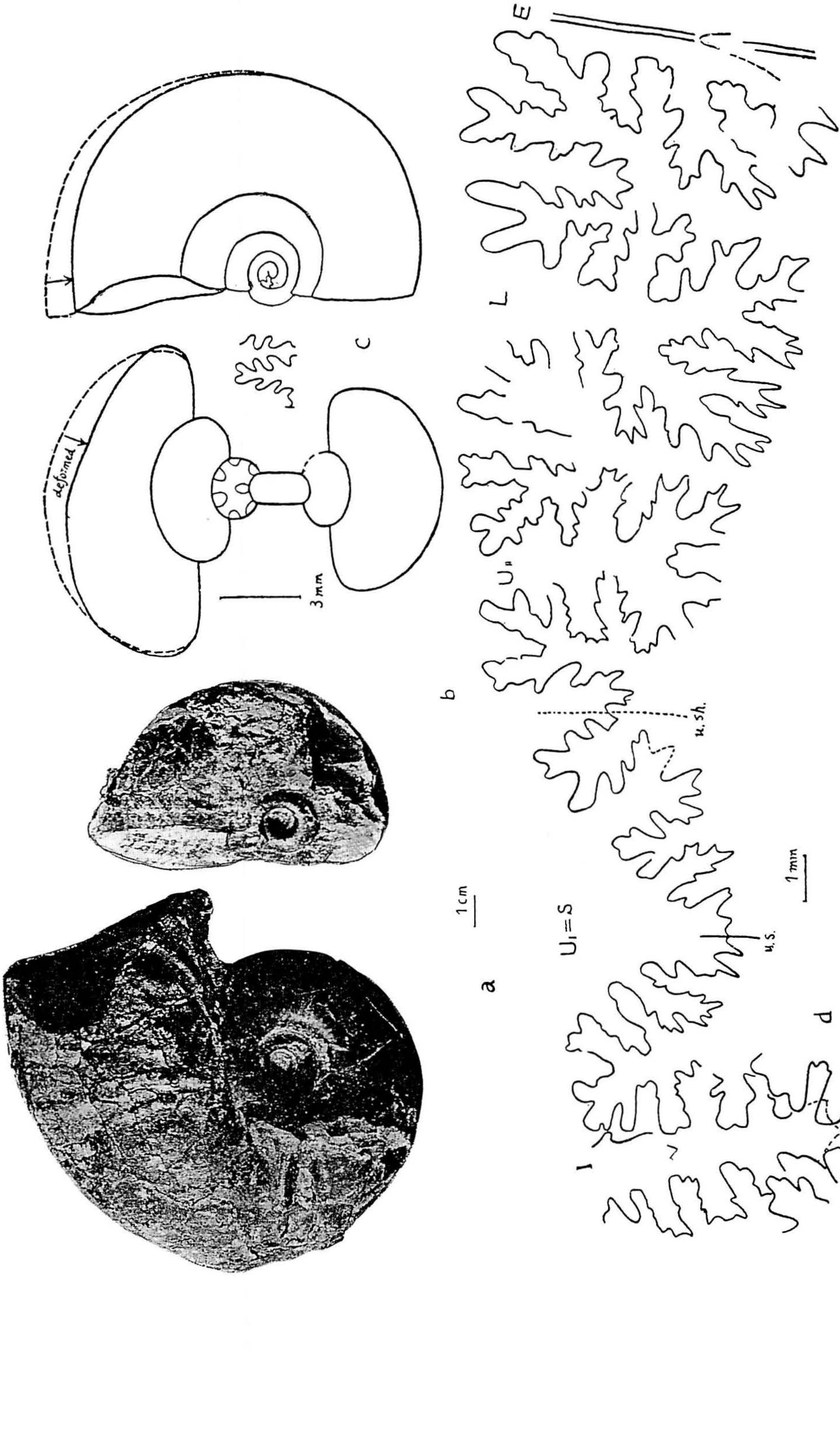
Holotype. – UMUT. MM19698 [= I-3716] (Fig. 4) collected by T. M. (in 1937) from a nodule in mudstone of Member Ky of the Kawakita Group at locality N94b. on the Yuno-sawa, a short eastern branch of the River Naibuchi [= Naiba], South Sakhalin.

Material. – In addition to the holotype, the following specimens (paratypes) of T.M.'s collection were used when this species was established: UMUT. MM19699 [= I-3717] (Fig. 7C) (original of Matsumoto, 1943, fig. 2d, reproduced in this paper as Fig. 3d) from a nodule in mudstone of Member Kx of the Kawakita Group at loc. N97p, Yuno-sawa of the Naibuchi area; UMUT MM19700 [= I-3266] (Fig. 7B) from the upper part of Member IIa, middle part of the Yezo Group at loc. T596 on the left bank of the River Abeshinai, tributary of the River Teshio, northwestern Hokkaido; GK. H1136 (Fig. 7A) from Member IId, middle subgroup of the Yezo Group, at loc. Y536a, Tengu-zawa, a tributary of the River Shuparo [= Shiyubari or Siyubari, i.e. the main stream in the upper reaches of the River Yubari] (This is the original specimen of Matsumoto, 1943, fig. 2c, whose nuclear part is separated from that figured part to examine the protoconch and succeeding whorls; the latter is drawn as Figs. 5, 6 of this paper.) GK. H1137 from Member IIe at loc. Y533 on the Tengu-zawa.

When I established this species, there were more specimens (which should be part of paratypes) collected by T.M. from the Naibuchi area of South Sakhalin. Their registes numbers in UMUT are unknown but their localities and stratigraphic levels are recorded as follows (Matsumoto, 1942, p. 149–150): locs. N99d on the Yuno-sawa and N56d on the Kamo-gawa, another short eastern branch of the River Naibuchi, in parallel to the Yuno-sawa, Member Kx; loc. N95 of the Yuno-sawa, Member Ky. Now they seem to be missing.

The following specimens of the subsequent collections by several friends and myself are added as a part of the material for this revised study: TKD 30049 (Figs. 9, 10) obtained by S. Kanno from a transported nodule at loc. 80614 of A. Inoma (for the location see Matsumoto & Inoma, 1975, fig. 2) in the River Sounnai; TKD 30037 (Figs. 8A, B) from a floated nodule at loc. 81012 of Inoma in the Suribachi-zawa a tributary of the River Sounnai; GK. H8443 (Fig. 3D) in a nodule at loc. R733p2, together with *Desmoceras* cf. *kossmati*, in the Oku-futamata-zawa, a tributary of the River Kotanbetsu (see Nishida *et al.*, 1993, fig. 1 for the location); GK. H8444 (Fig. 11) in a much transported nodule collected by K. Sanada at loc. R654p from the Oku-futamata-zawa (see Nishida *et al.*, 1992, fig. 1 for the location) on July 7, 1991 in the geological field work with S. Uchida, M. Noda and T.M.; GK. H8456 (Fig. 13) collected by Y. Kawashita as a block (YKC.060607) derived from Member My3 in the Suribachi-zawa and GK. H8457 collected by Y. Kawashita from the lower part of My4 at loc. R590 on the right side of the upper course of the Sounnai River, both in the Soeushinai area. These GK specimens were donated to Kyushu University. MCM. A113-2 (Fig. 12) collected by Takashi Sasaki from the lower part of the middle subgroup of the Yezo Group in the upper reaches of the Shuparo River.

Figure 3. *Parajaubertella kawakitana* Matsumoto. →
(Reproduction of Matsumoto, 1943, fig. 2 in *Proc. Imp. Acad. Tokyo*, vol. 18, no. 10, p. 668 by permission of the Academy of Japan.)
a, b. Holotype (see Fig. 4 for a better illustration). c. Outline of the natural cross-section and lateral view of an immature shell (see Fig. 6 for another sketch of the same specimen, GK. H1136) and its internal suture-line. d. Suture-line of a young shell (GT. I-3717) at D = 27.5 mm.


a
b
c
d
1cm
3mm
1mm
deformed
E
L
U1=S
u.s.
u.sh.

Description. – As the morphologic characters of this species change remarkably with growth, description is given here in accordance with the ontogenic stages which can be divided as follows:

(1) Early whorls, up to 5 mm in diameter (Fig. 5) are evolute, at first crescent-shaped in cross-section, with very low H and comparatively elongated B, although B is shorter than the axis of a barrel-shaped protoconch. Soon the whorl-section becomes reniform and broader than high. The whorl expands with a low rate, keeping the evolute coiling. The first constriction appears in the last part of the first whorl (of the examined specimen, i.e. GK. H1136). The suture consists of E, L, U2, U1 and I, of which U1 is located on the internal side and U2 is shallow and located at the umbilical seam.

The above characters are generally the same as those of the very early stage of normal gaudryceratid species, as represented by *Gaudryceras tenuiliratum* Yabe. (For the ontogeny of *G. tenuiliratum* readers may refer to Matsumoto, 1943, fig. 1 which is reproduced in Fig. 1 of this paper).

(2) Typical immature shell, with diameters over 5 mm to 40 mm (see Figs. 6, 7). The shell of this growth stage shows the following diagnostic features: the whorl is involute, overlapping more than half in H of the preceding one, and itself is much broader than high, with B/H 2.0 to 1.2 (generally decreasing with growth), roughly lunate (half-moon-shaped) in cross-section, showing a steeply inclined or nearly vertical, high umbilical wall, angular to subangular umbilical edge and a semicircular outline formed by gradual transition from the inflated flanks to the more or less broadly rounded venter. The umbilicus is fairly narrow, deep, roughly conical but stepped. The shell form is thus globose or subspherical.

The surface of the outer shell layer is ornamented with very fine lirae, which show minor rhythms in density with associated occurrence of "striae" or very shallow and narrow furrows. These features are observable only if the preservation is favourable. Also, they are not particular to this species nor to this growth stage, but occur commonly on the shell surface of *Anagaudryceras, Eogaudryceras, Gabbioceras* and *Zelandites*. The course of the lirae is similar to that on the shell surface of the next growth stage. The lirae do not show branching and intercalation on the outer part of the whorl, passing across the broadly rounded venter with a very gentle adorally, convex curve.

The suture of this stage is important, because it shows clearly the difference from that of similarly globose immature stage in a number of *Gabbioceras* species (see the discussion in the genus *Parajaubertella*). It consists of E, L, U2, U1 = S and I as in normal gaudryceratid species. The suture illustrated in Fig. 3d is at D = 27.5 (or H = 13, B = 20) of GT. I-3717. It shows that the first (E/L) and the second (L/U2) lateral saddles as well as the lobes E, L and U2 are on the rounded or dome-like main or outer part of the whorl, that the "third lateral saddle" is laid across the umbilical shoulder and that the stem of the third lateral saddle at the angular umbilical edge is broader and the lobule and two folioles in the adoral part of the same saddle are somewhat larger in comparison with those of the normal case. A similar configuration of the sutural elements seems to have appeared at somewhat earlier

Figure 4. *Parajaubertella kawakitana* Matsumoto. →
Holotype, UMUT MM19698 [= I-3716]. Left side view shows the phragmocone and the affixed main part of the body chamber. Right side view shows the phragmocone and the posterior portion of the body chamber; the main part of the body chamber is taken out to show clearly the inner whorls and the last part of the phragmocone. Figures are natural size. Scale bar: 10 mm. Photos by C. Ueki†.

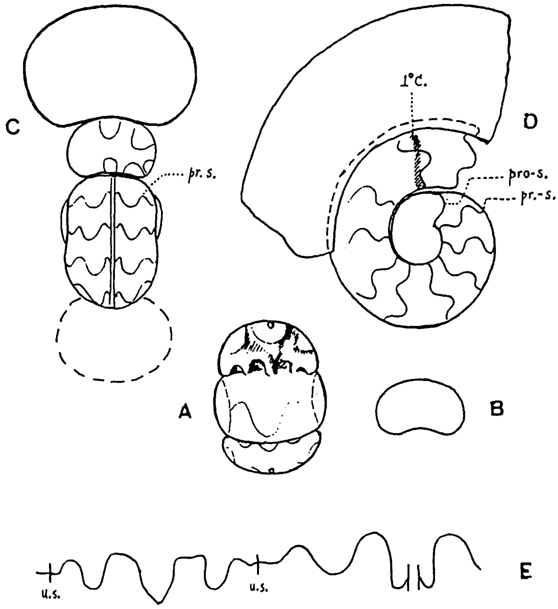


Figure 5. *Parajaubertella kawakitana* Matsumoto.
Morphological characters of a very young shell, based on GK. H1136. A: Protoconch and sectional views of the first whorl at the 3rd septum (below) and the 7th (above). B: Section at three quarters of the first whorl. C: Ventral view of the early part of the first whorl (internal mould) and the cross-section at the end of the first and the second whorls. D: Lateral view at the same stage as C. A–D, ×10. E: The 7th suture.

substage of this "typical immature" stage, whereas in its later substage, e.g. from the next suture at D = 28.5 (or H = 13.6, B = 20.6) in the same specimen [GT. I-3717], the stem and the folioles of the third lateral saddle begin to be narrowed in accordance with the increasing and deepening incision. While the outer foliole of the third lateral saddle is nearly vertical to the radius of a whorl, the lobule between the two folioles and the inner foliole are somewhat oblique, forming a part of the descending auxiliaries (i.e. outer part of U1 = S).

(3) Middle-aged shell, with diameters from 40 mm to about 130 mm. This corresponds to the main part of the phragmocone of the full-grown shell. It is merely for convenience's sake to define the latest limit of the middle-age at the last septum (i.e. the beginning of the body chamber) of the full-grown shell. I do not know when the true adult stage (i.e. having ability of sexual mating) begins in this ammonite species, but the above defined growth stage of middle age is fit very well for describing the change of morphological characters with growth. It consists of one full whorl plus less than a quarter of the preceding one.

The whorl is moderately involute, overlapping about half in H of the inner one. The umbilicus is fairly narrow, keeping the ratio U/D at 0.26 or 0.27 as in the typical immature stage. The whorl-section is subcordate to subrounded, somewhat broader than high in earlier part and nearly às high as broad or slightly higher than broad later, showing gradual increase of H in proportion to B with growth. The venter is broadly arched earlier and modrately so

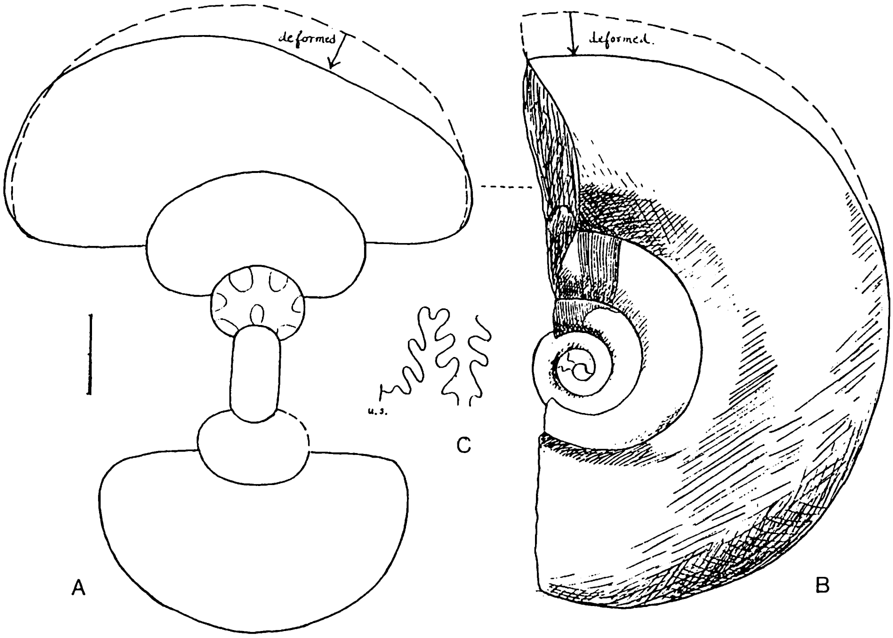


Figure 6. *Parajaubertella kawakitana* Matsumoto.
Sketch of a typical immature shell represented by GK. H1136. A: Sectional view. B: Lateral view. C: Internal suture. Scale bar: 2 mm.

later, passing to a rather gently convex flank, which in turn is abruptly rounded at the umbilical edge, descending very steeply or almost vertically to form a fairly high wall. The maximum breadth (i.e. B) in whorl-section is between the inner flanks at about one third of H.

The ornament of this stage is diagnostic. The segments having a set of four (or 3 to 5) narrow grooves in each of them occur periodically. A groove is associated with a narrow rib behind it. Each grooved segment extends for about 30° in the angle of volution and the ribless interval is generally wider than the ribbed segment, although its width may vary to some extent. The periodicity is, thus, from 70° to 120° in the angle of volution. In other words, there are four or five grooved segments per whorl.

The grooves and ribs are weak and narrow in earlier parts of this stage, becoming more distinct later. On account of the slight asymmetry in the depth of grooves and height of ribs the ornament may look scale-like. There is also some variation in the width and intensity of grooves or ribs between individuals and even within one and the same segment. Also the grooves or ribs are generally more distinct on the inner flank than their extensions on the outer part of the whorl. On the interspece between the grooved segments very weak and fine furrows may be discernible on the inner flank, fading away outward.

Very fine lirae are discernible on the well-preserved surface of the outer shell-layer, showing minor rhythmic changes in density. They are gently concave on the umbilical wall, curved forward on the abruptly rounded umbilical shoulder, forming an asymmetric convexity on the inner flank, nearly radial or slightly prorsiradiate on the main part of flank, passing over the

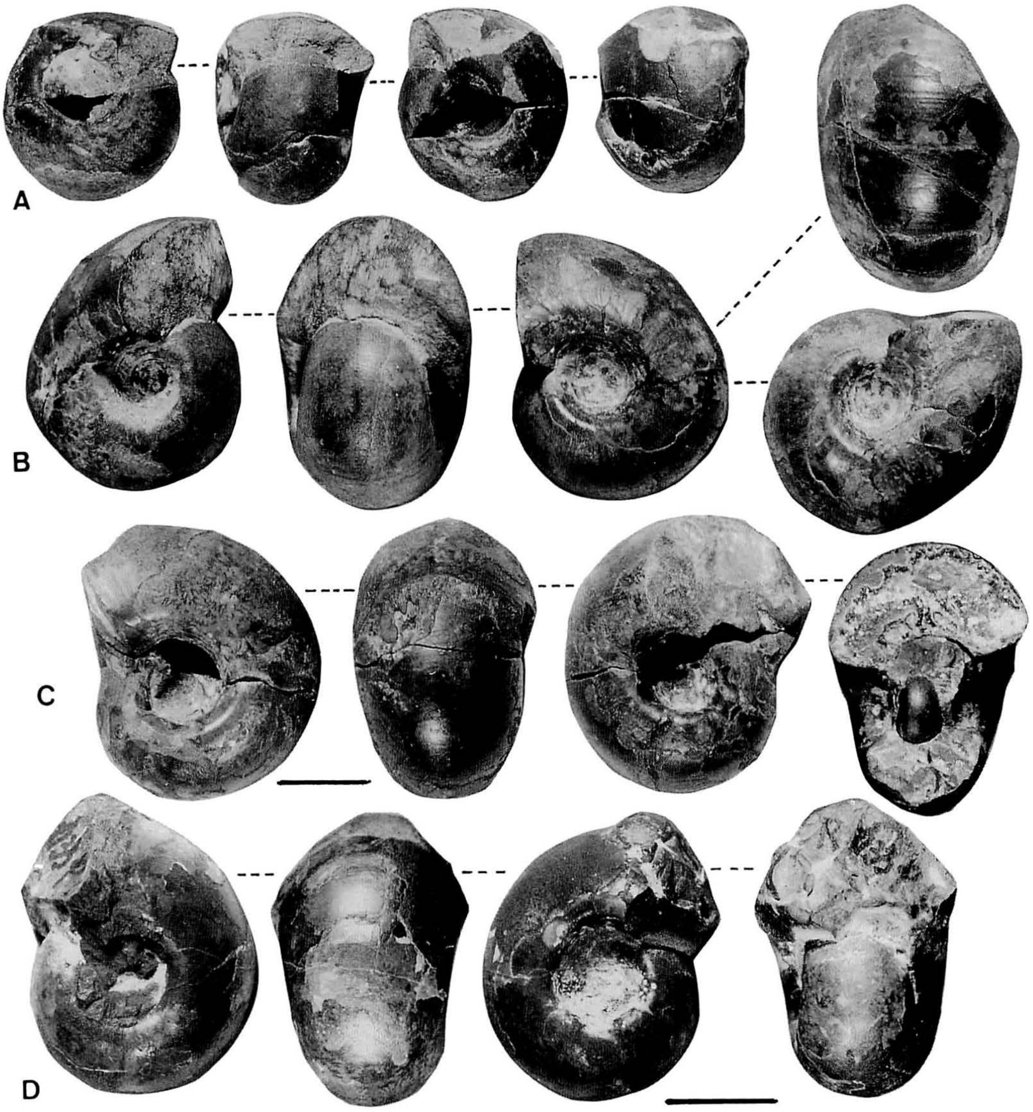


Figure 7. *Parajaubertella kawakitana* Matsumoto.
Examples of typical immature shells. A; GK. H1136, ×1.5. B: GT. I-3266, ×1.5. C: UMUT. MM19699 [GT. I-3717], ×1.2. D: GK. H8443, ×1.5. GK. H1136 was used for inspecting the early ontogeny as shown in Figs. 5, 6; GT. I-3717 for illustrating the suture (Fig. 3d). Scale bar: 10 mm (longer one is ×1.5; shorter one ×1.2).

rounded venter with a very gentle convexity. The grooves and narrow ribs run in parallel to the lirae on the surface. They are impressed on the internal shell-layers and some of them may be impressed even on the internal mould.

The suture of this stage is finely and deeply incised, leaving increasingly narrowed stems of the lobes, saddles and their subdivisions with growth. In the later part, the third lateral saddle is somewhat shifted outward, with the inner foliole located at the umbilical shoulder.

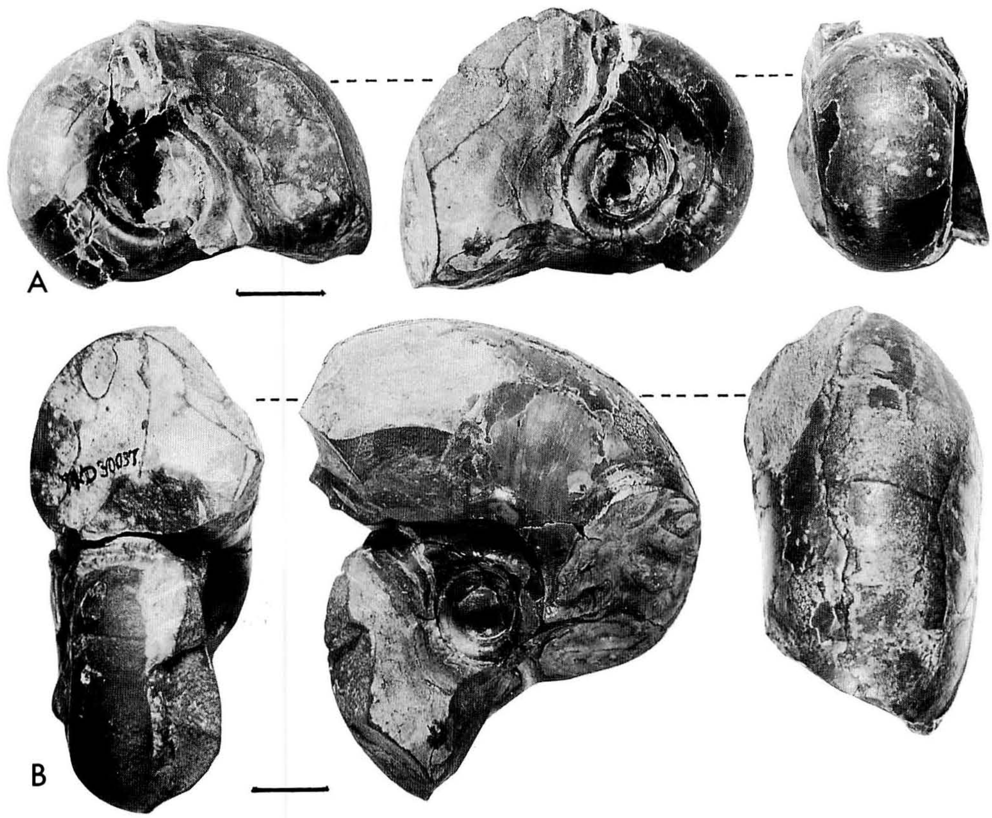
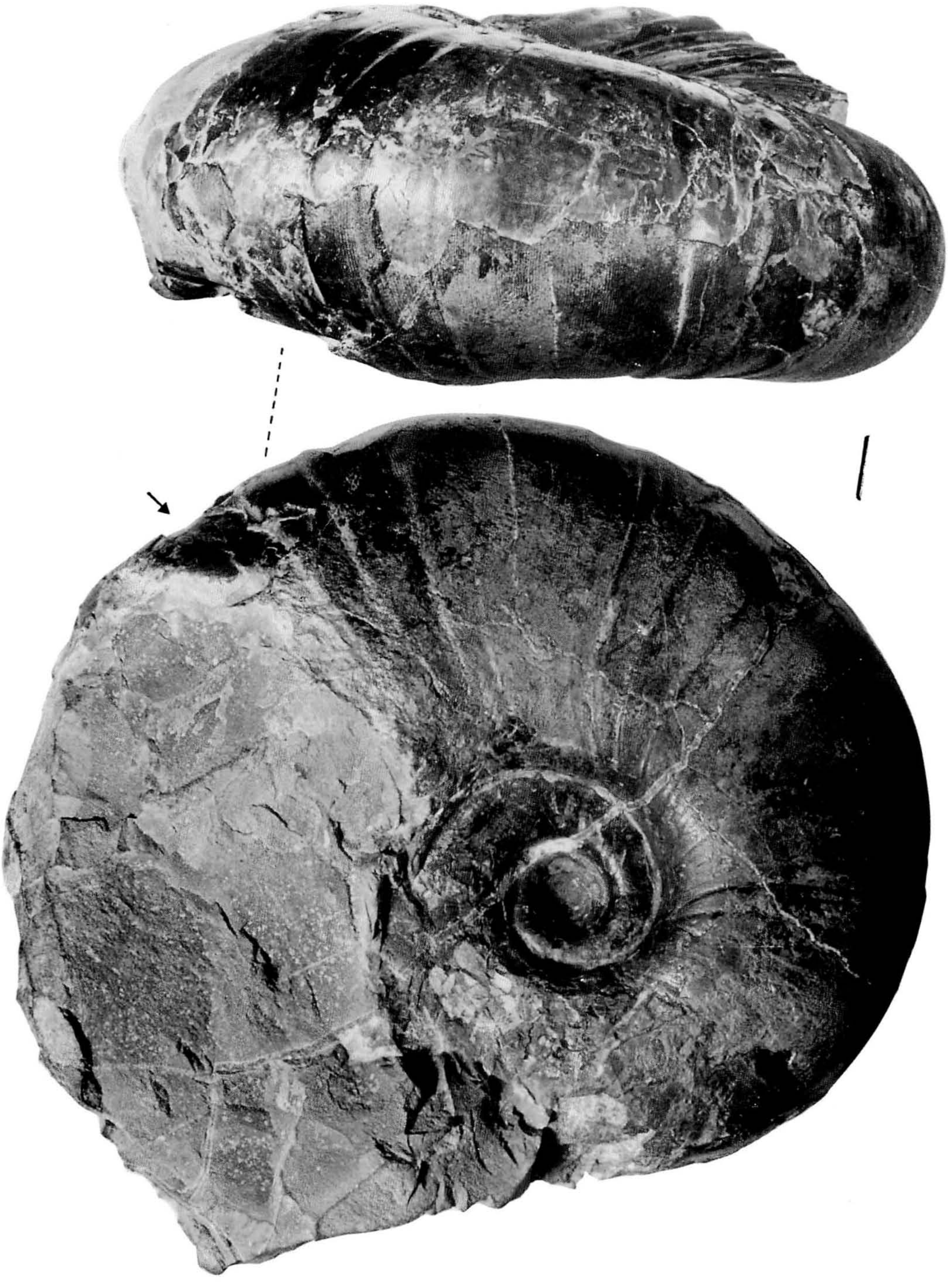


Figure 8. *Parajaubertella kawakitana* Matsumoto.
TKD 30037, an example which shows the last part of the typical immature stage by the inner whorl (A) and the beginning of the middle-aged stage by the outer whorl (B). Scale bar: 10 mm.

That foliole is disposed obliquely as a part of the descending auxiliaries on the umbilical wall.

(4) Body chamber of the full-grown adult shell, with diameters from 130 mm to about 240 mm.–This stage is observable incompletely in the available material. It is characterized by the type of ornament that is well-developed in the adult body chamber of *Anagaudryceras sacya*. On the inner part of the flank the ribs are strong, asymmetric fold form in section, with adorally steep and adapically gentle slopes, and separated by fairly deep interspaces. They are curved there with an asymmetric convexity, passing gradually to the subradial and broader ribs on the main part of the flank. On the outer part of the flank and the venter the ribs are broad-band-like or scale-like or low fold-shaped and separated by narrow but fairly deep grooves. The ribs may vary somewhat irregularly in their breadth. When the preservation is favourable the fine lirae on the shell surface are discernible as in those of the preceding stage.

The size of the full-grown adult shell is not known from the direct evidence. There is, however, a trace of the umbilical seam of the outer whorl weakly impressed on the late part of the phragmocone, suggesting that the body chamber was about three quarters of the entire one whorl. The width of the umbilicus at the terminal point of that trace is 65 mm. On the



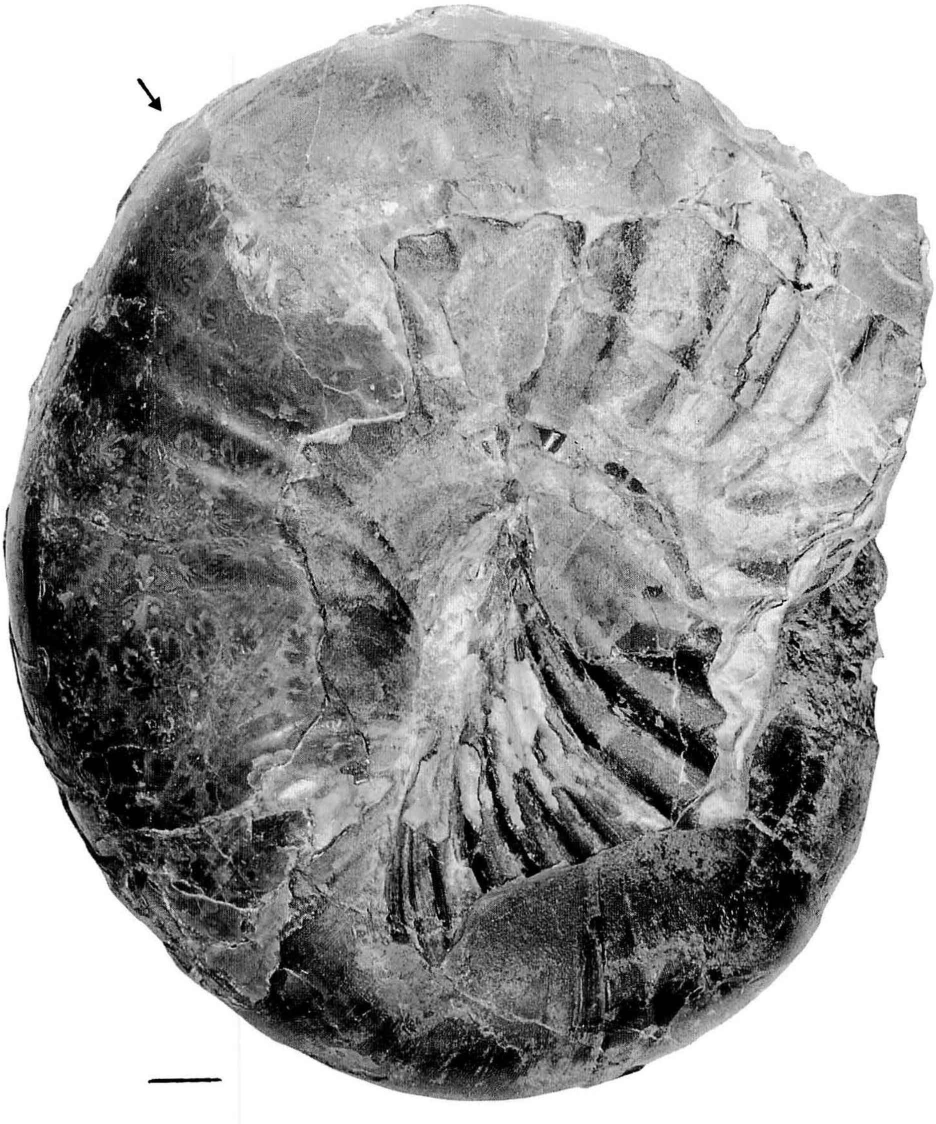


Figure 10. *Parajaubertella kawakitana* Matsumoto.
TKD 30049, left side of the same specimen as Fig. 9, showing the abraded posterior part and much displaced fragment of the body chamber. Scale bar: 10 mm.

←Figure 9. *Parajaubertella kawakitana* Matsumoto.
TKD 30049, an example in which the characters of the middle growth stage are well shown. Scale bar: 10 mm.

assumption that the ratio U/D is 0.27 as that of the preceding stage, the diameter of the full-grown adult shell is estimated as 240mm. GK. H8456 (Fig. 13) exemplifies such a large body chamber, although it is incomplete. It shows the apertual margin where a few narrow ribs are crowded.

As the body chamber is distorted or crushed, the original outline of the whorl-section is not observable directly. A less deformed portion suggests a nearly vertical wall and an abruptly rounded edge around the umbilicus. An apparently gradual slope in this part of some specimens is evidently the product of secondary deformation. As the whorl height grows with a somewhat greater ratio in comparison with the whorl breadth already in the preceding growth stage, the adult body chamber must be higher than broad in cross-section. This is also shown, though incompletely by GK. H8456 mentioned above.

Dimensions. – See Table 1.

Discussion. – The two specimens, GK. H8444 and TKD 30049, obtained at separated localities in the Soeushinai area, show a notable conformity in the size of the phragmocone (i.e. D at LS), the ratios between measured dimensions, the characteristic ornament. They certainly represent the middle-aged stage defined above. Between the ribbed segment in the last part of the middle-aged stage and the continuously ribbed body chamber of full-grown adult stage there is a weakly ribbed or almost rib-less interval for a short duration in these two specimens.

Table 1. Dimensions of *Parajaubertella kawakitana*.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H
P. kawakitana, HT (LS)	73.0	19.7	.27	33.6	.46	36.0	.49	1.07
" (LS – 270°)	35.0	9.0	.26	16.5	.47	23.5	.67	1.42
P. imlayi, HT (E)	95.0	26.0	.27	44.0	.46	47.0	.49	1.07
" (E – 90°)	75.0	20.2	.27	35.0	.46	37.6	.50	1.07
GK. H8444 (LS + 60°)	150.0	39.0	.26	69.0	.46	63.0	.42	0.91
" (LS) [restored]	[131]	34.0	.26	[60]	.46	57.5	.44	0.96
" (LS – 120°)	91.0	25.0	.27	42.0	.46	44.0	.48	1.05
TKD 30049 (LS)	132.0	34.5	.26	62.0	.47	60.0	.45	0.97
MCM. A113-2 (LS)	122.0	31.0	.25	57.0	.47	54.0	.44	0.95
TKD 30037*	62.0	17.0	.27	27.0	.44	30.0	.48	1.11
GT. I-3717 (E)	28.5	7.8	.27	13.6	.48	20.6	.72	1.51
" (S)	27.5	7.2	.26	13.0	.47	20.0	.73	1.54
" (E – 90°)	23.6	5.6	.24	11.0	.47	18.0	.76	1.64
GK. H8443	23.5	6.5	.28	9.5	.40	17.0	.72	1.71
GT. I-3266*	18.0	4.8	.25	9.0	.47	15.0	.79	1.67
GK. H1136*	15.5	4.0	.26	6.0	.39	12.0	.77	2.00

S: measured at illustrated suture; *: at less deformed earlier part.

←Figure 11. *Parajaubertella kawakitana* Matsumoto.
GK. H8444, an eroded but less deformed specimen. Only a posterior portion of the body chamber is preserved.

Figure 12. *Parajaubertella kawakitana* Matsumoto.
MCM. A113-2, hypotype, phragmocone and the beginning of the body chamber, ×0.6.

The holotype of *P. kawakitana* has the last suture at D = 73.0 mm, which corresponds to the middle substage of the above defined middle-aged shell. In fact, the ornament characterized by periodic segments of ribbing separated by smooth interspaces persists up to the approximately restored D = 130 mm and then the stronger ribs of adult *sacya* type appear in the preserved terminal part. In other words, this specimen was not the full-grown adult shell as described above. Moreover, the dimensions at D =131 mm conform surprisingly with those of TKD 30049 on one hand and also those at D = 73 mm with those of the holotype of *P. imlayi* on the other. The difference in the angularity at the umbilical edge of the inner whorls was taken as one of the criteria to distinguish *P. imlayi* from *P. kawakitana* (see Matsumoto, 1959a, p. 71), but this is not reliable, because it is often modified by the condition of preservation. In fact the holotype of *P. imlayi* is somewhat weathered. There is, thus, no difference that merits the specific distinction. Thus, *P. imlayi* Matsumoto, 1959 should be suppressed as a junior synonym of *P. kawakitana* Matsumoto, 1943.

Occurrence. – This species occurs fairly commonly in Members Kx and Ky of the Kawakita Group (i.e. approximate extension of the lower part of the middle subgroup of the Yezo Group in Hokkaido) in the Naibuchi [= Naiba] area of South Sakhalin. As no acanthoceratacean ammonite has been obtained, the geological ages of the two members are not precisely determined, but *Inoceramus* aff. *reachensis* Etheridge from Ky and upper part of Kx suggests the early Cenomanian age of the main part of the range of *P. kawakitana* in S. Sakhalin.

The occurrence of this species in the upper part of Member IIa in the Abeshinai area of northern Hokkaido suggests also the same age, because the overlying Member IIb contains Middle Cenomanian species, such as *Turrilites costatus* Lamarck (which begins to occur in the *Mantelliceras japonicum* Zone in Hokkaido), *T. acutus* Passy, *Calycoceras* (*Newboldiceras*) *spinosum* (Kossmat) etc.

In the Soeushinai area a number of specimens of various growth-stages have been obtained, but they are mostly found in transported nodules. The mode of preservation (including the colour of the fossils) and associated ammonites suggest their derivation from the Zone of *Graysonites adkinsi-Desmoceras kossmati* of Member My3, the basal Cenomanian in the Japanese scale. A specimen from loc. R590 is from the lower part of Member My4. It is on the extension of loc. R81, where *Neostlingoceras* cf. *carcitanense* (Sharpe) was obtained, and is within the Lower Cenomanian. (Note that *N. carcitanense* occurs also in the Zone of *Mantelliceras japonicum* of the Ikushunbetsu area.)

In the Oyubari-Shiyubari area *P. kawakitana* occurs fairly commonly in Member IId and occasionally in Member IIe of the middle subgroup of the Yezo Group. IId is early Cenomanian age because of the occurrence of *Sounnaites alaskaensis* (Matsumoto) and *Graysonites* cf. *wooldridgei* Young. Whether a small specimen (GK. H1135) from Member IIb (loc.Y540) is *Parajaubertella* or *Gabbioceras* has not yet determined. Member IIb is late Albian age as evidenced by *Mortoniceras* (*Cantabrigites*) sp.

A peculiar occurrence of *P. kawakitana* in a nodule at loc.H5021a in the Lower Turonian bed of the Hobetsu district is interpreted as a derived fossil (see Matsumoto *et al.*, 1994).

I once saw a medium-sized (D = 90 mm), probale example of this species, from Chienaibo, eastern coast of Cape Soya, which was erroneously identified as *Anagaudryceras* cf. *sacya* by Osanai *et al.* (1957, pl. 11, fig. 7) and also another larger specimen in the collection of T.

Yoshida from a locality near Hirotomi of the Monbetsu area. They came from mudstone formations, which were tentatively referred to the Lower Cenomanian.

Genus ***Miogaudryceras*** nov.

Type species. – *Miogaudryceras yokoii* sp. nov. (described below).

Diagnosis. – Adult shell small to medium-sized. Phragmocone virtually similar to a young shell of *Anagaudryceras* Shimizu, 1934 in the general shape and the ornamentation, showing rounded whorls with reniform to subcircular sections and dense and very fine lirae with little or no flexuosity on its surface and periodic constrictions accompanied by collars behind.

Adult body chamber higher than broad with progressively increasing height and suboval or subrectangular in section. On more or less later parts of the body chamber the lirae are not so dense and fine as those on the earlier parts, being sharply raised and similar to those in some species of *Gaudryceras*. In addition to them, weak and narrow subcostae occur, but stronger or broader major ribs like those in the late growth stage of the typical species group of *Anagaudryceras* and that of *Gaudryceras* do not develop. The lirae are almost straight or slightly flexuous on the main part of the body chamber except for a shallow sinus around the umbilicus.

Suture as for that of *Gaudryceras, Anagaudryceras* and *Eogaudryceras*.

Discussion. – The adult body chamber of *Miogaudryceras* is somewhat similar to that of *Mesogaudryceras* Spath, 1927 in the compressed shape with suboval section and the ornament of raised lirae, but the lirae in the latter are sinuous and strongly projected on the venter. The phragmocone of *Miogaudryceras* resembles that of *Anagaudryceras*, whereas that of *Mesogaudryceras* is compressed and has coarser and more interspaced lirae (see Wright and Kennedy, 1984, text-fig. 3A–M).

Eogaudryceras has a trapezoidal to rounded whorl-section and almost smooth surface with only fine striae or growth-lines and periodic constrictions and associated collars. It is hence somewhat similar to young shells of *Anagaudryceras*. The smooth surface with very fine striation is thought to persist to the adult stage in *Eogaudryceras*. Actually the adult body chamber seems to be scarcely preserved in the hitherto described species of *Eogaudryceras*. As to *E. numidum* (Coquand), the type species, a full-grown adult shell has not been illustrated in any published paper.

The better preserved specimens of *E. aurarium* (Anderson) (1938, p. 151, pl. 20, fig. 1; Murphy, 1967b, p. 13, pl. 1, fig. 7), from the Lower Albian strata of California, show almost smooth surface of the outer whorl, except for periodic collars and associated constrictions. They are about 85 mm in diameter. According to Murphy's information (in lit. May 6, 1993), there are larger specimens (about 120 mm in diameter) of *E. hertleini* (Wiedmann), from the Upper Aptian strata of California, that show the same ornament as that of *E. aurarium* on the body chamber.

←Figure 13. *Parajaubertella kawakitana* Matsumoto.
GK. H8456, hypotype, late part of the body chamber, with the apertural margin at the left end of the figure, ×0.8. Scale bar: 20 mm.

As these specimens certainly represent the adult stage of *Eogaudryceras*, *Miogaudryceras* can be discriminated by the ornament of its adult body chamber that consists of sharply raised lirae developed from the fine but clearly perceptible lirae on its young whorls and also some narrow and weak ribs or riblets.

Furthermore, it is interesting to note that there is a fairly well-preserved example, from the Albian of Madagascar, which is interpreted by Murphy (1967b, pl. 5, fig. 9) as showing intermediate features between *Eogaudryceras* and *Gaudryceras*. That specimen is similar to, if not identical with, the phragmocone of the type species described below.

On the ground of the above discussions and also from the characters of the type species and another species to be described below, *Miogaudryceras* may have evolved as an offshoot from somewhere near the point where *Anagaudryceras* and then *Gaudryceras* were going to diverge from some species of *Eogaudryceras* (see Murphy, 1967b, text-fig. 4c). Likewise *Mesogaudryceras* may be another offshoot, although its direct origin is uncertain. Anyhow, it is noticeable that a phylogenetic divergence or branching seems to have occurred at about the age of the Albian-Cenomanian transition.

Occurrence. – This new genus has been found so far rarely in the Cenomanian strata of the Soeushinai area, northwestern Hokkaido. Its true vertical range and geographic distribution should be investigated further.

Miogaudryceras yokoii sp. nov.

Figures 14–16

Material. – Holotype, GK. H8411 (Figs. 14, 15), is nearly complete but for the squashed adapical part of the body chamber. It was collected by Katsujo Yokoi (1987.8.2) at loc.KY740 as a fall from Member My3 in the main gully of the upper reaches of the Suribachi-zawa. The rocks exposed at KY740 and upstream in the gully are sandy siltstones from which *Graysonites adkinsi* Young and *Sounnaites alaskaensis* (Matsumoto) were obtained in situ.

Paratype (1), GK. H8412 (Fig. 16B) is a well-preserved phragmocone, except for an eroded portion of its venter. It was collected by K. Yokoi at loc. KY800 in the lower course of the Suribachi-zawa, about 450 m NW from the confluence with the Sounnai River.

Paratype (2), GK. H8413 (Fig. 16A) is a tiny juvenile which matches the inner whorls of the above two specimens. It was collected by K. Yokoi at loc.KY541 as a transported nodule in the Shumarinai River.

Diagnosis. – In general as for generic diagnosis. Adult body chamber compressed and suboval in section, with narrowly arched venter.

Description. – The adult shell represented by the holotype is 75 mm in diameter at the peristome and 40 mm or so at the beginning of the body chamber, which occupies slightly over half a whorl. It is considerably involute and narrowly umbilicate.

Young whorls are rather evolute and reniform in section, changing gradually to become moderately involute and subcircular in section at the late septate stage. The adult body chamber is higher than broad and suboval in section with a narrowly arched venter, showing a marked increase of whorl height. The outline of its peristome is simple, with only a shallow ocular sinus.

When the outer shell layer is preserved, the surface of the septate whorls is ornamented with very fine and dense thread-like lirae and periodic flares or collars. The flares are very densely striated on their surface. They are normally four per whorl and accompanied by constrictions on the internal mould. On a few very young whorls sharply raised flanges (see Murphy, 1967, fig. 1) occur more frequently, whereas the last half of the septate whorl is free from flares and constrictions.

On the adult body chamber the lirae are at first very fine and dense, becoming gradually less dense and coarser and are raised to sharp-crested lirae or riblets. Moreover, narrow and weak ribs occur at intervals.

The lirae, riblets and flares show a forward swing around the umbilicus and they run nearly straight on the main part of the flank and also across the venter without notable projection. Shorter lirae may be intercalated on the flank but the break up of the lirae at the ventrolateral shoulder into extremely fine striae in *Vertebrites*-like fashion is not found in any of the three examined specimens of dissimilar growth stages.

The pattern of suture observable through semi-transparent inner shell layer is essentially similar to that of the well-known species of *Gaudryceras* (see Matsumoto, 1943, fig. 1).

Dimensions. – See Table 2.

Specific name. – This species is dedicated to Katsujo Yokoi of Kenbuchi town, Hokkaido, who has contributed much for palaeontologically interesting collection.

Discussion. – See the generic diagnosis and discussion in the foregoing pages and also a comparison with the unnamed species below.

Anagaudryceras matsumotoi Morozumi (1985, p. 29, pl. 9, fig. 1a–d) (also Matsumoto *in* Matsumoto *et al*., 1985, p. 27, pl. 4, figs. 1–10), is small even in the adult stage. Its phragmocone is quite similar to *A. yokoyamai* (Yabe, 1903), showing a subcircular section in its late part of the septate whorl. Its adult body chamber is progressively higher than broad and egg-shaped in section. It is hence similar to *Miogaudryceras yokoii* in the shell form and small size. Its adult body chamber has broad band-type or scale-like ribs separated by subradial furrows and never shows sharply raised lirae or riblets. The two species are thus clearly discriminated by the difference in the ornament of the adult body chamber. Moreover *A. matsumotoi* is a Maastrichtian species and much separated in age from the early Cenomanian

Table 2. Dimensions of *Miogaudryceras yokoii*.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
HT (E)*	73.0	18.0	.25	38.0	.52	24.5	.34	.64	2.24
" (LS)	c. 37.5	11.0	.29	17.5	–	17.5	–	1.00	1.94
GK. H8412 (LS)	43.0	13.0	.30	19.5	.45	19.5	.45	1.00	1.86
GK. H8413 (E-270°)	15.7	6.5	.41	5.3	.34	6.5	.41	1.23	1.36

*The specimen is measured as it is, although its body chamber is secondarily compressed.

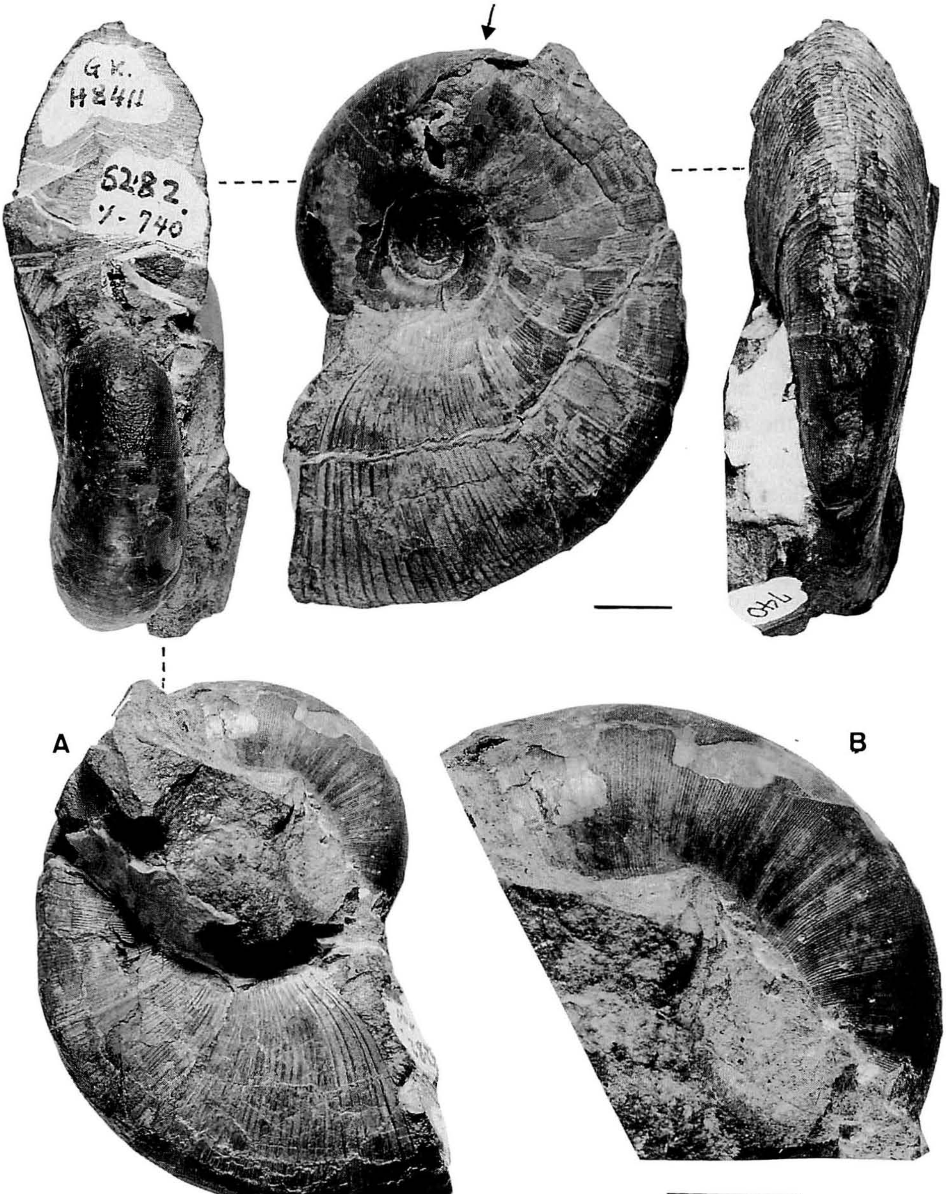
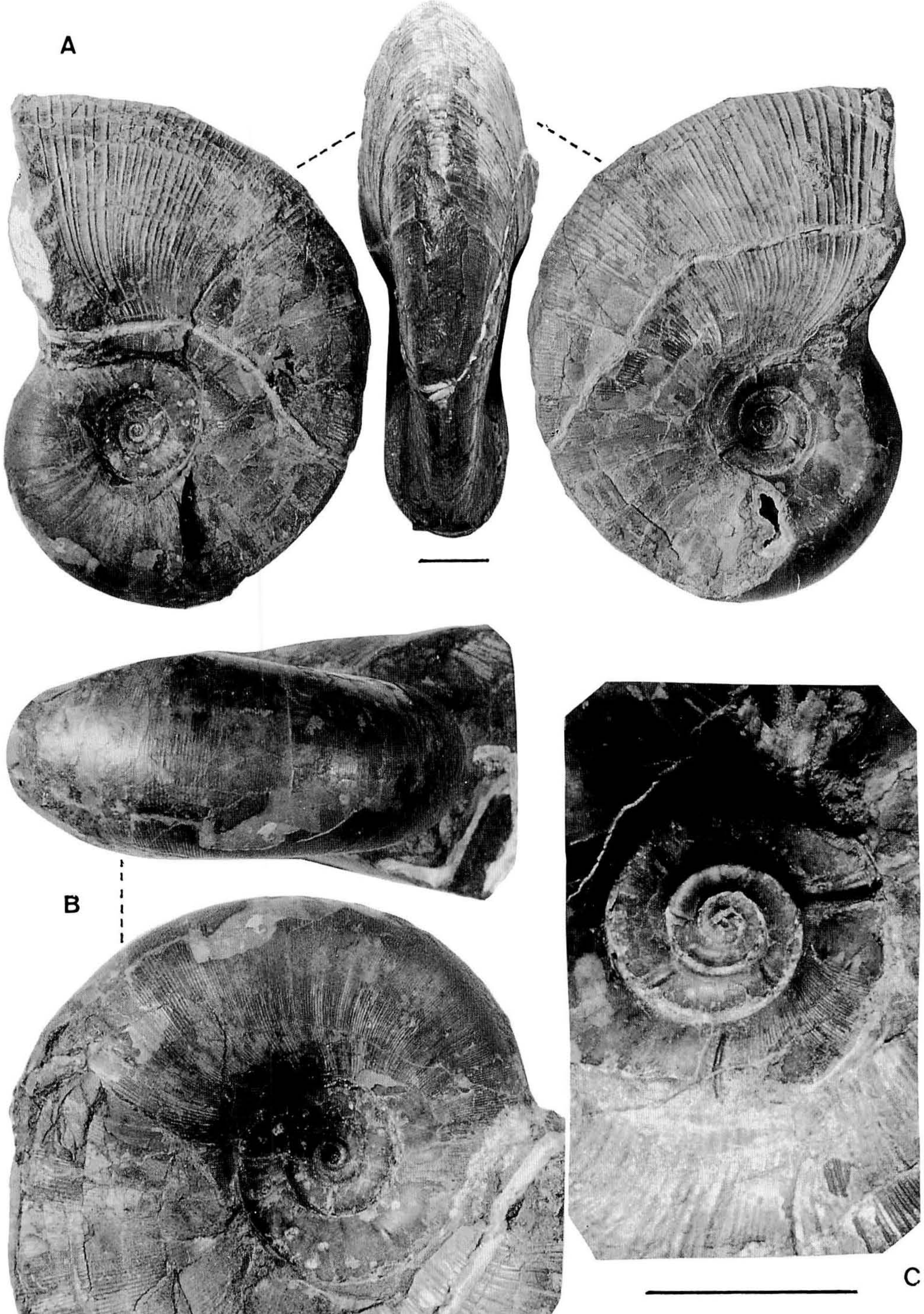


Figure 14. *Miogaudryceras yokoii* gen. et sp. nov.
Holotype, GK. H8411, with a piece of rock matrix attached to its right side. A: Four views in natural size. B: Enlarged last part of the phragmocone, showing minute ornament on the surface of shell, ×7/4. Scale bar: 10 mm.

Figure 15. *Miogaudryceras yokoii* gen. et sp. nov. →
Holotype, now cleaned by removal of the attached rock matrix. A: Three views in natural size. B: Enlarged phragmocone, ×7/4. C: Enlarged umbilicus to show the details of the inner whorls, ×3. Scale bar: 10 mm.


A
B
C

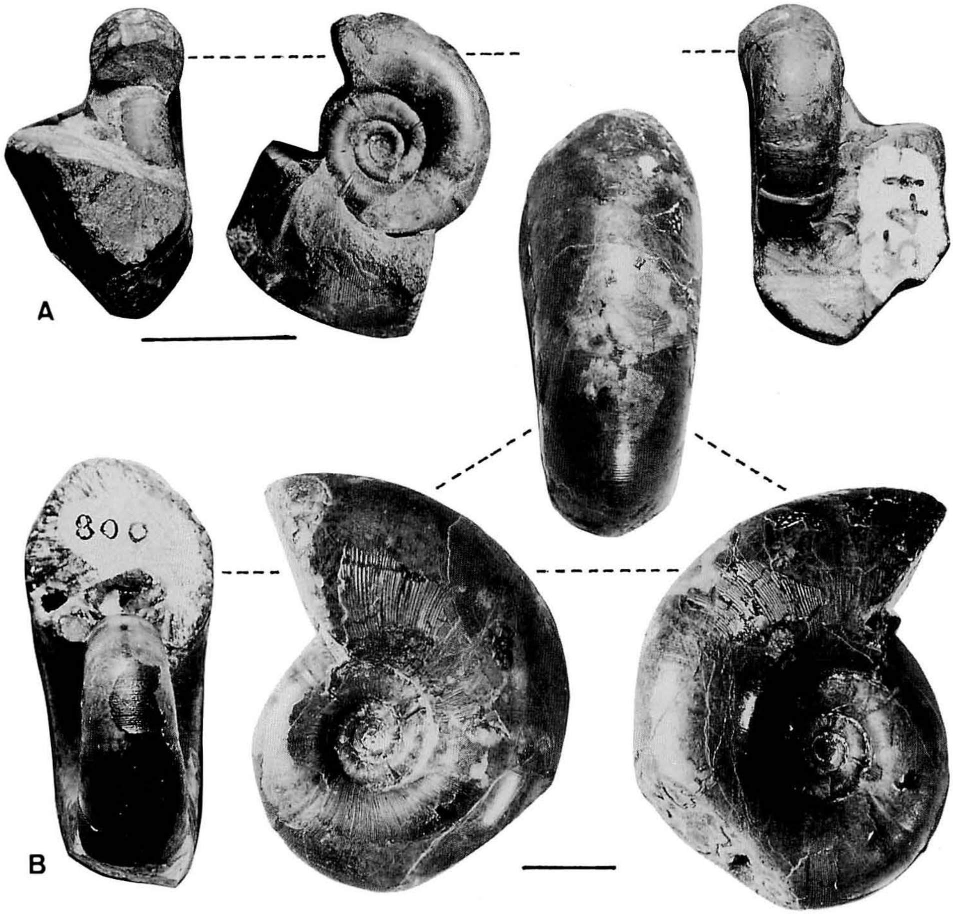


Figure 16. *Miogaudryceras yokoii* gen. et sp. nov.
Paratypes. A: GK. H8413, juvenile, ×2. B: GK. H8412, phragmocone, ×1.25. Scale bar: 10 mm.

Miogaudryceras yokoii. The similarity in shell form is merely homeomorphic.

It should be noted that the late septate whorl of *M. yokoii* resembles *Anagaudryceras madraspatanum* (Stoliczka) (described below) of corresponding diameters in the somewhat coarsening lirae and subcircular cross-section. They are, however, distinguished in the shape and ornament of adult body chamber and well-marked radial constrictions and associated collars in the main part of phragmocone of *M. yokoii*.

Occurrence. – As for Material.

Miogaudryceras sp. nov. (?)

Figure 17

Material. – GK. H8395 (Fig. 17A) and GK. H8396 (Fig. 17B) in one and the same nodule in the sandy siltstone exposed at loc. R715 of the Oku-futamata-zawa, a tributary in the upper reaches of the River Kotanbetsu (collected by T. Nishida & T.M.). An isolated specimen, GK. H8389 (Fig. 17C, D), taken from a transported nodule at loc. R653p in the lower course of the Oku-futamata-zawa (collected by Yuko Kyuma).

Description. – GK. H8396 is a fragmentary body chamber, with height greater than breadth. It is subrounded-subrectangular in cross-section, with a gently arched venter, although the original shape may have been somewhat modified by secondary deformation. It is ornamented with lirae which run radially on the flank with little flexuosity, curve gently forward on the ventrolateral part and pass across the venter almost vertically. The lirae are mostly single but irregular in the density and coarseness. Many of them are dense and fine on the inner flank and more or less coarsen outward. Some of them are less dense and coarser than others and can be called riblets or subcostae.

GK. H8395 is small but well-preserved. It represents certainly a juvenile stage. The shell is rather evolute, expanding with a low ratio and has a wide umbilicus. Its outer whorl is subrounded-subquadrate in section and somewhat broader than high (B/H = 1.15). The increase of the whorl breadth is of low ratio and the shell is rather parallel-sided in back (or ventral) view. The surface of the shell is marked densely by very fine lirae and intervening striae which are subradial or weakly prorsiradiate on the main part of the flank and gradually curved forward on the ventrolateral part, passing across the venter almost vertically (i.e. with a slight convexity). The periodic flares are well-marked, three or four per whorl, running in parallel to the fine lirae. The suture is similar to that of young *Gaudryceras*.

GK. H8389 is also a juvenile and shows quite similar characters as those of GK. H8395. The external mould of this specimen (Fig. 17D) shows very clearly frequent flanges on its earlier part for at least two whorls.

Dimensions. – See Table 3.

Discussion. – GK. H8375 and GK. H8376 are different in size but can be regarded as a juvenile and an adult body chamber of the same species, because they occur in one and the same rock and because they have common characters such as the course of the lirae and subrounded-subquadrate to subrounded-subrectangular outline of the whorl-section. I failed to search for a specimen of intermediate size. Should a middle-aged specimen which could connect the described two specimens be obtained, the specific characters would become more confirmative than the above interpreted ones. Anyhow, the presumed species is certainly referable to *Miogaudryceras* and can be clearly discriminated from *M. yokoii*. However, as the present material is insufficient, I merely describe it without giving a new specific name.

Occurrence. – The rock exposed at loc. R715 contains *Birostrina nipponica* (Nagao & Matsumoto) and *Inoceramus pictus minus* Matsumoto. It is hence late Cenomanian in age

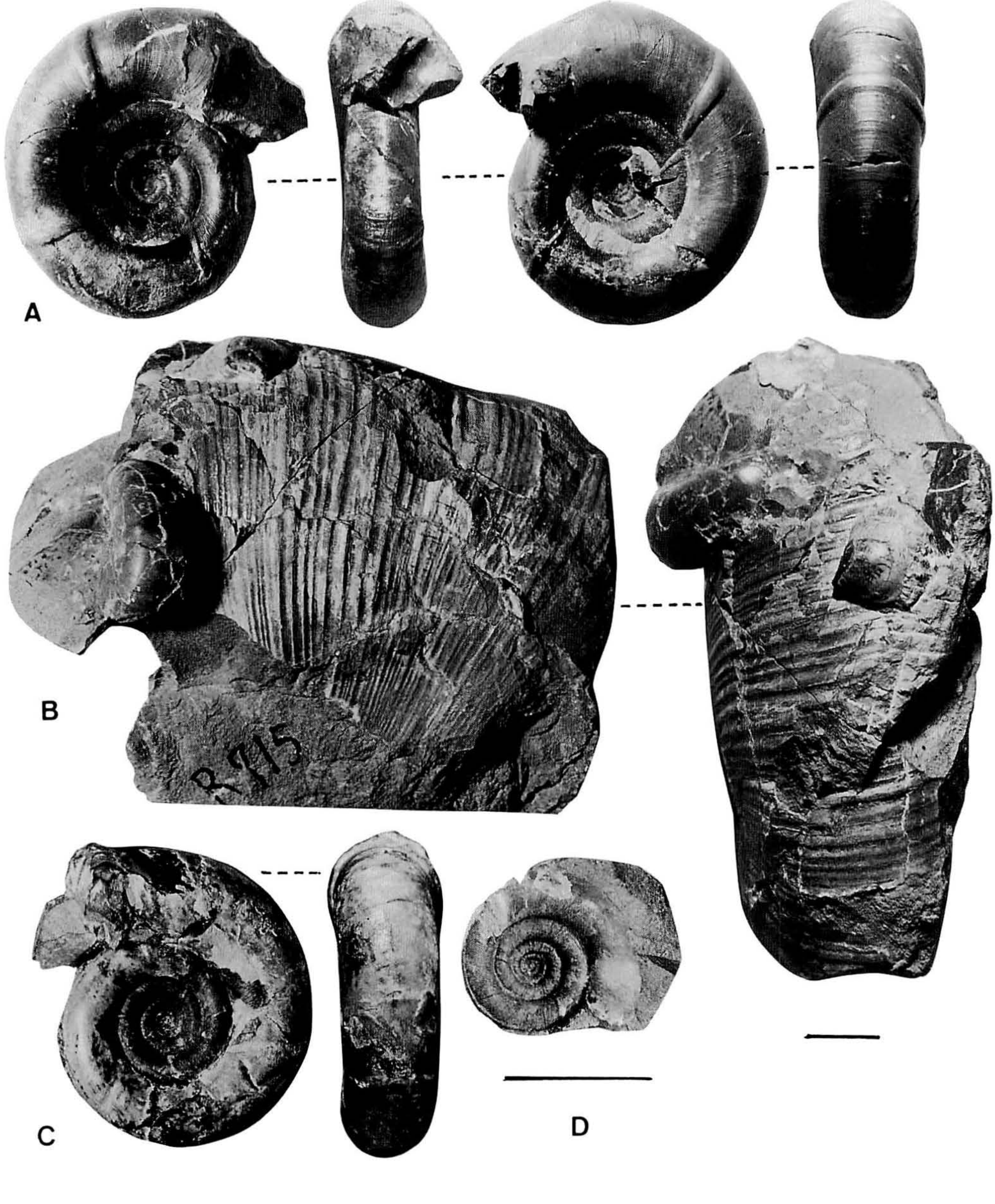


Figure 17. *Miogaudryceras* sp. nov. (?)
A: GK. H8395, juvenile, ×2. B: GK. H8396, fragmentary body chamber, ×1. Associated with it there are *Tetragonites* cf. *kiliani* and *Inoceramus nodai*. C: GK. H8389, juvenile, ×2. D: Ditto, external mould of the umbilicus, ×2. Scale bar: 10 mm.

Table 3. Dimensions of *Miogaudryceras* sp. nov. (?)

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
GK. H8395	21.0	9.5	.45	6.5	.31	7.5	.36	1.15	1.30
GK. H8396	–	–	–	c.60	–	c.30	–	c.0.5	–
GK. H8389	20.0	9.0	.45	6.4	.32	7.4	.37	1.16	1.39

(see Nishida *et al.*, 1993a, p. 100). The small specimens which are associated with GK. H8396 are *Inoceramus nodai* Matsumoto & Tanaka (juvenile) and *Tetragonites* cf. *kiliani* (Krenkel).

The outcropping strata at loc. R653 are of early Turonian age because of the occurrence of *Mytiloides* cf. *columbianus* (Heinz) (see Nishida *et al.*, 1992), but the fossils are embedded in situ in the tuffaceous mudstone. The nodule of R653p which contains GK. H8389 was probably transported from somewhere upstream where Upper Cenomanian strata are exposed.

Genus ***Anagaudryceras*** Shimizu, 1934

Type species. – *Ammonites sacya* Forbes, 1846 by the original designation of Shimizu (1934, p. 67).

Diagnosis. – See Wright & Kennedy, 1984, p. 49–50.

Description. – The shell is normally medium-sized, but may be small or fairly large in some particular species. It is more or less polygyral and moderately to weakly involute. The umbilicus is moderately wide to fairly narrow, depending on species and changing with growth. The whorl-section is reniform in very young shells; more or less evenly rounded and subcircular in young to middle aged shells, but may be compressed suboval or flat-sided already at these growth-stages in some species; finally subrounded to suboval in the typical mature shells.

On the whorl(s) of very young shells, the flanges (as defined by Murphy, 1967b) occur more or less frequently, as in other genera of the Gaudryceratidae. The external surface of the whorl all through from young to adult stages is ornamented with extremely fine or very fine lirae, which show a shallow sinus on the umbilical wall, curve backward on inner flank and run radially or with a gentle flexuosity on the main part of the flank, crossing the venter nearly vertically or with a weakly forward convex curve. A strong flexuosity on the flank or a marked projection of the lirae on the venter does not occur in this genus, except for a few cases.

A minor rhythm in the details of density and distinctness of the lirae and also weak furrows are discernible. These minor periodic furrows or shallow grooves may be impressed faintly even on the inner shell layer, suggesting minor rhythmic arrests of growth. Besides these faint furrows, periodic constrictions are marked more clearly in many if not all of the species. Each constriction is normally preceded by a collar.

In more or less later growth-stage, normally on the adult body chamber but sometimes from the late part of the phragmocone onward, the rhythmic furrows or very shallow grooves become clearer to be called narrow but distinct grooves and the intergrooves are elevated relatively to form wide, band-like or low, fold-like major ribs, which sometimes show an asymmetric scale-like cross-sectional shape with adorally steep and adapically gentle inclinations. These grooves are not necessarily the approximated constrictions, but may result from minor rhythmic arrests of growth, of which some are periodic constrictions. This type of major rib is well exhibited by the holotype (BMNH. C22673) of *Ammonites buddha* Forbes, 1846. It was called by Kennedy & Klinger (1979) *buddha*-type or *buddha*-like fashion. However, the name of the type species is *A. sacya* instead of *A. buddha*, as is explained in p. 37. To avoid confusion, I use in this paper a terminology "the ribs of adult *sacya*-type". Anyhow, on the shell surface, the major ornament is superposed by fine lirae.

In various species of *Anagaudryceras*, the major ribs on the body chamber are not necessarily of adult *sacya*-type. In some cases they are narrowly elevated ribs separated by wider interspaces, whereas in others they are strong fold ribs separated by concave interspaces nearly as broad as the ribs, that may be called normal ribbing.

The suture is of the same pattern as that of *Gaudryceras*.

Discussion. – A number of genera or subgenera proposed by Shimizu (1934, 1935a, b) in the Gaudryceratidae were sorted by Wright & Matsumoto (1954, p. 111–113). Since then *Anagaudryceras* Shimizu, 1934 (*in* Shimizu & Obata, p. 67) has been settled to correspond to what Yabe (1903, p. 17) called the group of *Gaudryceras sacya* (Forbes). The generic diagnosis given by Wright (1957, *Treatise on Invertebrate Paleontology* L, p. L200) and more recently by Wright & Kennedy (1984, p. 49–50) is adequate.

Kennedy & Klinger (1979, p. 146) have set up two groups in the genus, namely the group of *A. sacya* [=*A. buddha* in their paper] and that of *A. involvulum*, showing several species to be included in each of them.

The group of *A. involvulum* is criticized in this paper. *Ammonites involvulus* Stoliczka, 1865 itself is very ambiguous. *Anag. yamashitai* (Yabe) was cited as a representative of the group. Its phragmocone is indeed similar to the much smaller holotype of *A. involvulum*, but the presence of unmistakable major ribs on the adult body chamber of *A. yamashitai* is shown in this paper. *A. yamashitai*, thus emended, occurs in the upper subgroup (mainly Coniacian-Santonian and possibly extending to earliest Campanian age) of the Yezo Group.

A. yokoyamai (Yabe), whose septate whorls are thicker and more rounded than those of *A. yamashitai*, have narrow but elevated major ribs on its adult body chamber. *A. politissimum* (Kossmat) has more compressed whorls than those of *A. yokoyamai* and was cited as another member of the *A. involvulum* group, but the major ribs on its adult body chamber are fairly similar to those of the latter, as some examples from Hokkaido and South Sakhalin show clearly. I have already described an example of *A. mikobokense* Collignon, from the probable Maastrichtian strata of California, which shows the *A. yokoyamai*-type major ribs on its fairly large adult body chamber (Matsumoto, 1959b, p. 139, pl. 38, fig. 1a–c).

A. matsumotoi Morozumi, 1985 resembles *A. yokoyamai* in its septate whorls, but it is smaller and peculiar in having a *Zelandites*-like body chamber (see Matsumoto *in* Matsumoto *et al.*, 1985, p. 29).

To sum up the above discussion, there is no reason to maintain the group of *A. involvulum* in the sense of Kennedy & Klinger (1979, p. 146). It may be perceivable that the band-like broad ribs separated by narrow grooves on the adult body chamber occur in the earlier species of *Anagaudryceras*, such as *A. whitenyi, A. sacya* and a new species (*A. howarthi*) established below, from mid-Albian to mid-Turonian ages, whereas the *yokoyamai*-type narrow and strong ribs separated by wide interspaces predominate in the later species of the same genus (such as *A. yamashitai, A. yokoyamai* and *A. politissimum*) from Coniacian to Maastrichtian ages. *A. limatum* of intermediate age (late Turonian-Coniacian) has strong fold ribs separated by wide to moderate interspaces on the main part of the adult body chamber, although the ribs may become somewhat broader on the last part. This seems to show a general evolutionary change with age. If we consider more details in the ornament and also the shell form and/or shell size, the actual evolution may have been diverse. Also the above species of later ages should be separated from early Cretaceous *Eogaudryceras*.

A. madraspatanum (Stoliczka) of late Albian-Cenomanian age somewhat deviates from the contemporary *A. sacya* and other *A.* species in showing somewhat coarser lirae in late growth stages and also weaker major ribs on body chamber, as is described below.

Distribution. – Well-known species of *Anagaudryceras* occur in wide regions of the world but certain particular species have been reported from particular provincès. In general, the genus occurs more commonly in the Indo-Pacific realms and its stratigraphic range is from Albian to Maastrichtian. The stratigraphic range of individual species is rather long, extending for two or more stages. Certain species are known to occur abundantly in a stratigraphically restricted part, as exemplified by *A. limatum* which ranges from the Upper Turonian to Coniacian strata in Hokkaido and South Sakhalin.

Anagaudryceras sacya (Forbes)

Figure 18

Ammonites buddha Forbes, 1846, p. 112, pl. 14, fig. 9.
Ammonites sacya Forbes, 1846, p. 113, pl. 14, fig. 10.
Ammonites sacya Forbes; Stoliczka, 1865, p. 154, pl. 75, figs. 5, 6; pl. 76, fig. 2.
Anagaudryceras buddha (Forbes); Kennedy & Klinger, 1979, p. 146 (with synonymy list).

Type and specific name. – The holotype of *Amm. sacya* by monotypy, is BMNH. C51067 and that of *Amm. buddha* by monotypy, is BMNH. C22673. For the reasons of my observation below, I regard them as conspecific. Kennedy & Klinger (1979) also regarded them as synonymy and proposed to call this species *A. buddha* because of page priority. However, Stoliczka (1865) had already chosen *Amm. sacya* for the united two species of Forbes. In accordance to ICZN Article 24, I should follow Stoliczka's choice. As to the same problem readers may refer to Wright & Kennedy, 1984 (p. 50).

Observation. – I examined the two specimens mentioned above three times (in 1954, 1965 and 1979) in BMNH and also Stoliczka's specimens (in 1964) in GSI. All of them came from the Ootatoor [Utatur] Group of South India.

BMNH. C51067 (Kennedy & Klinger, 1979, pl. 8, fig. 3) is small (D = 33 mm), wholly septate and certainly juvenile. Although it is incompletely preserved, it does show important characters; namely, a low ratio of the whorl increase (H/h = 1.24), moderately wide umbilicus (U/D = 0.37), rounded whorl-section with B/H = 1.1 at the preserved end, frequent flanges on the very early whorl, gently flexuous to subradial, fine lirae on the shell surface, showing

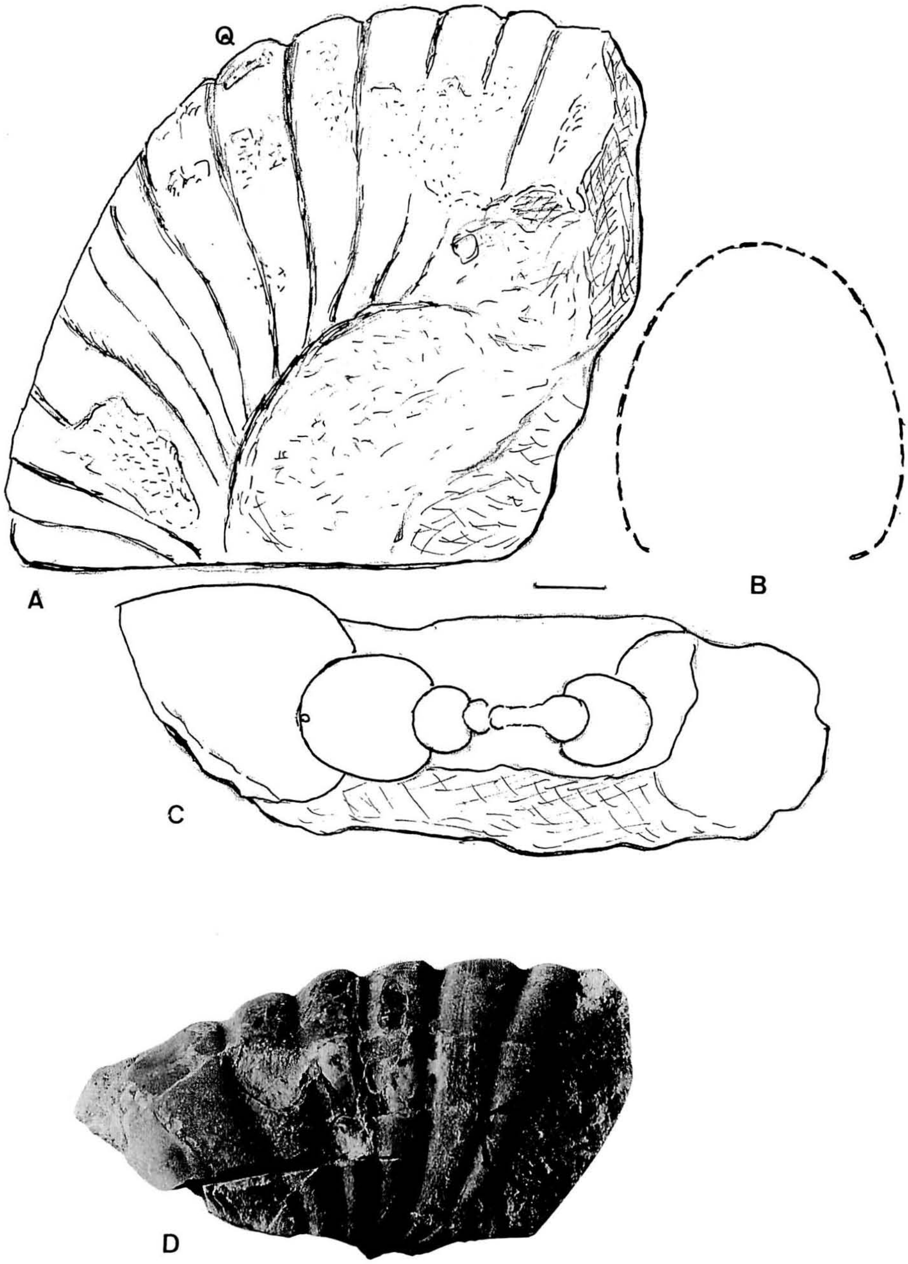


Figure 18. *Anagaudryceras sacya* (Forbes).

A–C: BMNH. C22673, holotype of *Ammonites buddha* Forbes (drawn by T. M.). A: Lateral view of incomplete body chamber, whose posterior part is planed by erosion. B: Whorl section at Q in A. C: Natural cross-section of the inner whorls. D: UMUT. MM19773 [I-3729], fragmentary body chamber from South Sakhalin, which is similar to A. Scale bar: 10 mm.

sometimes intercalation on the flank, and the periodic collars covered by very fine lirae on their surface.

BMNH. C22673 (Kennedy & Klinger, 1979, pl. 8, fig. 2; also Fig. 18A, B in this paper) is a fragmentary body chamber which has more or less broad, low ribs separated by narrow grooves as shown in the illustration. Where a shell layer is preserved, fine lirae are discernible in parallel with the ribs. The cross-section of this body chamber is suboval (B/H = 0.95) with its maximum breadth in the lower part at about one fourth of H. This specimen contains its inner whorls as indicated by the slightly oblique cross-section (see Fig. 18C). The young part of this holotype of *Amm. buddha* is close to the holotype of *Amm. sacya*, showing a rounded whorl-section and modrately wide umbilicus. The whorl changes in cross-section from subcircular to suboval with growth. The two nominal species are thus regarded as conspecific. The specimens of subsequent collections from South India (e.g. Stoliczka, 1865, pl. 75, figs. 5–7; *non* pl. 76, figs. 2, 3) and other regions support this conclusion.

Remarks. – A number of specimens from the Upper Albian and Cenomanian of Hokkaido and South Sakhalin are referable to *A. sacya*, but their full description is reserved until a study with coworkers is completed. Only a specimen, which is fragentary but closely resembles BMNH. C22673, is illustrated in Fig. 18D. It is GT. I-3729 [= UMUT. MM19773] from loc. N312a, horizon Kz-Mh (mid-Cenomanian) of the Naibuchi area, South Sakhalin. Better preserved examples have been illustrated, with brief remarks, by Obata *et al.* (1981, pl. 4, fig. 1) from the Upper Albian of the Shizunai area and also by Futakami (1982, pl. 1, fig. 7) from the Upper Albian of the Yubari dome, Hokkaido.

Kennedy & Klinger (1979) interpreted *A. sacya* as extremely variable and listed such species as *A. whitneyi* (Gabb, 1869), *A. coagmentum* (Collignon, 1963), *A. limatum* (Yabe, 1903) and *Kossmatella* (*Murphyella*) *enigma* Matsumoto, Muramoto & Takahashi, 1972 as synonyms. In this paper remarks are given on the first two species in connection with the allied species from Hokkaido; *A. limatum* is resurrected with a revised description. The last one was erroneously referred to *Kossmatella.* It is indeed a species of *Anagaudryceras*, but needs reinvestigation and is not discussed here.

Anagaudryceras aff. *A. whitneyi* (Gabb, 1869)

Figure 19

Material. – MCM. A250 (Fig. 19C) collected by Shigehiro Uchida from the shale exposed at his loc. MK67 [= T.M.'s loc. Ik1091] on the Ikushunbetsu River near the confluence with a rivulet called Yu-no-sawa. Smaller specimens, GK. H8414 (Fig. 19B) from loc. KY801 and GK. H8415 (Fig. 19A) from loc. KY808, both obtained by Katsujo Yokoi from transported nodules at the above two provisionally numbered localities of the Suribachi-zawa in the Soeushinai area. They are donated to Kyushu University.

Description. – MCM. A250 is fairly large, for its body chamber begins at 114 mm diameter and seems to reach at least 200 to 215 mm, if the lost part (about 120° to 150°) is restored. Its outer whorl is subelliptical in section, broadest at a point somewhat outside of the umbilical shoulder, with the height increasing with growth in proportion to the breadth.

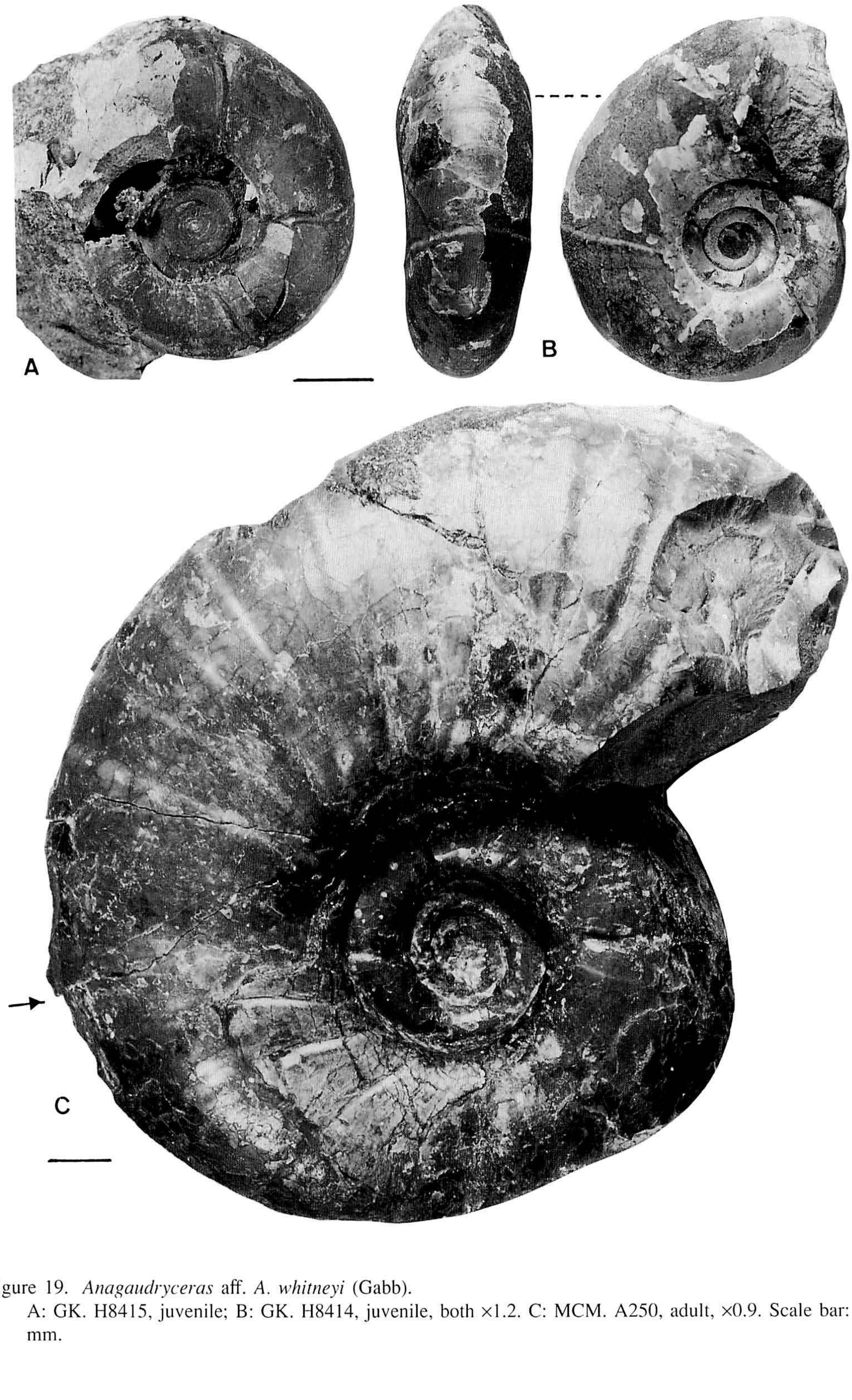


Figure 19. *Anagaudryceras* aff. *A. whitneyi* (Gabb).
A: GK. H8415, juvenile; B: GK. H8414, juvenile, both ×1.2. C: MCM. A250, adult, ×0.9. Scale bar: 10 mm.

The flanks are gently convex, although the right side is dissolved in rock matrix. The umbilicus is of moderate width, and the umbilical proportion (U/D) decreases gradually with growth. The umbilical shoulder is rounded.

The ornament is unusual, as has already been noticed by Uchida (personal communication). The constrictions on immature whorls are deep, prorsiradiate on the flank, showing a gentle flexuosity around the umbilicus; 5 to 6 per whorl. On the last part of the septate whorl and also on the earlier half (about 120°) of the body chamber, there are narrow but distinctly elevated major ribs with associated narrow and shallow grooves in front of them. In general, the narrow ribs look predominant over the groove. Only in the preserved last portion, a few low, band-like ribs of the adult *sacya*-type appear, but the narrowly elevated ribs still persist behind the depressed adapical portion of the bands of scale-like cross-section. The ribs and grooves are flexuous around the umbilicus as in other species of *Anagaudryceras* and weakly prorsiradiate or subradial on the main part of the flank.

Where the outer shell layer is preserved, very fine lirae and minor rhythmic furrows are discernible on surface.

The smaller specimens of K. Yokoi's collection are undeformed phragmocones, with a crushed adapical portion of the body chamber. They probably represent young shells. They show moderate ratios in the degree of involution, expansion of whorl and width of umbilicus. The preserved outer whorl is subrounded in section and somewhat higher than broad, with the maximum breadth between inner flanks somewhat outside the rounded umbilical shoulders. The most diagnostic is the clearly prorsiradiate constrictions each of which is preceded by a collar. The constrictions and collars are projected on the venter. The surface of the shell looks smooth, but very fine lirae are discernible where preservation is favourable.

Dimensions. – See Table 4.

Discussion. – The described specimens in young stages closely resemble the inner whorls of *A. whitneyi* (Gabb, 1869) as represented typically by SOC Collection K173/1 from the Ono Quadrangle, California, which was illustrated by Murphy (1976b, pl. 2, fig. 6). As the latter has a part of the body chamber (*op. cit.*, pl. 2, fig. 5), its generic identification is undoubted.

I appreciate Murphy's (*op. cit.*, p. 15) suggestion that the specimen which I illustrated as *A. sacya* from Alaska (Matsumoto, 1959a, pl. 22, fig. 4) is more like *A. whitneyi.*

Kennedy & Klinger (1979, p. 148) regarded *A. whitneyi* as a synonym of *A. sacya* [= *A. buddha* in their paper], without mentioning particular reasons. I would evaluate, at least in this case, the diagnostic character, which appears consistently in the immature shell as more

Table 4. Dimensions of *Anagaudryceras* aff. *A. whitneyi.*

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
MCM. A250 (LS+120°)	153.0	43.0	.28	66.0	.44	*c*.56	.35	.85	–
MCM. A250 (LS+30°)	122.0	36.0	.30	54.0	.44	*c*.48	.39	.89	1.69
GK. H8414	37.5	12.3	.33	16.4	.44	16.0	.43	.98	1.86
GK. H8415	40.0	15.2	.38	15.7	.39	14.8	.37	.94	1.73

important for taxonomic purposes than the apparently variable ornament of more or less similar type in later stages.

Even in the ornament of later growth stages there are some distinctions. Numerous specimens that have been collected from the Albian to Cenomanian sequence in Hokkaido were called *A. sacya* mainly on account of the adult *sacya*-type ornament in the late stages, but they should be reexamined. MCM. A250 is one of such examples and I appreciate Uchida's notice given to me.

The ornament of MCM. A250 (collected by Uchida) is not quite identical to that of the holotype of *A. whitneyi* (Gabb, 1869, p. 134, pl. 22, figs. 14, 14a, 14b) from California. As I failed to restudy the latter in Philadelphia, I depend on photographic illustration of Murphy (1967b, pl. 2, fig. 3). In the middle-aged whorl of Gabb's specimen, thre are deep and frequent grooves for about a quarter whorl. This ornament is peculiar but it may be a result of the approximation of the prorsiradiate, deep constrictions, which are particular to that species. The narrow major ribs that occur for fairly long span of outer whorl in MCM. A250 seem to develop for nearly half a whorl in Gabb's holotype. A similar ornament occurs in some specimens of *A. sacya*, but shortly the broad ribs of the adult *sacya*-type become predominant. The broad ribs separated by narrow grooves seem to occur in the last part of the outer whorl in Gabb's holotype, but the ribs are very low and scale-like in cross-section. This is also shown by SOC Collection K173/1 (Murphy, 1967c, pl. 2, fig. 5) and in the preserved last part of MCM. A250.

In conclusion, our form is not identical with *A. whitneyi*, but it is closer to that species than to *A. sacya*.

Incidentally, *A. coagmentum* (Collignon) (1963, p. 20, pl. 249, fig. 1064), from the Albian of Madagascar, is described as being characterized by narrow ribs behind frequent constrictions, but its holotype is too incomplete for accurate comparison.

Occurrence. – MCM. A250 was collected from the shale exposed at loc. Ik1091 [= MK67 of Uchida], which is assigned to the lower part of the middle subgroup of the Yezo Group, above the predominant sandstones at the base of the subgroup. *Oxytropidoceras* (*Adkinsites*) sp. (see Matsumoto, 1977, sheet 294, fig. 2) was collected by Tatsuo Muramoto at the same locality and *Dipoloceras pseudaon* Spath (see Matsumoto, comp., 1988b, fig. 78A) was found by Takemi Takahashi in the corresponding shale on the west side of the Ikushunbetsu anticline. This member is correlated to the lower part of the tripartite upper Albian substage.

GK. H8414 and H8415 are presumed to be derived from somewhere in the Upper Albian-Lower Cenomanian of the Soeushinai area.

Anagaudryceras madraspatanum (Stoliczka, 1865)

Figure 20

Ammonites madraspatanus Blanford, 1862 (*nom. nud.*); Stoliczka, 1865, p. 151, pl. 75, figs. 2, 2a–c (with. indication of synonymy).

Lytoceras (*Gaudryceras*) *madraspatanus* (Blanford); Kossmat, 1895, p. 128.

Gaudryceras aff. *madraspatanum* (Blanford) Stoliczka; Spath, 1923, p. 22, pl. 1, figs. 4a, b; text-fig. 5.

Anagaudryceras madraspatanum (Stoliczka); Matsumoto, 1942, p. 193; Collignon, 1956, p. 68; Howarth, 1965,

p. 358; Kennedy & Klinger, 1979, p. 146.

Lectotype. – Stoliczka (1865) based this species on several specimens of which the figured one, GSI. 307, is here designated as the **lectotype.** It came from the Ootatoor Group in the neighbourhood of Odium.

Material. – Three figured specimens, UMUT. MM19774 [= I-3273a] (Fig. 20A, B), MM19775 [= I-3273b] (Fig. 20C) and MM19776 [= I-3281] (Fig. 20D, E, F) collected by T.M. in the Abeshinai-Saku area. The first two came from the mudstone of Member IIa exposed at loc. T863 and another, unfigured specimen (GT. I-3273c) was contained in the same nodule. I-3281 was in a transported nodule at loc. T35p in the Saku-gakko-no-sawa, derived probably from sandy mudstone of Member IIb or IIa, middle subgroup of the Yezo Group.

K. Sanada collected another specimen from loc. Ik1100, a famous lower Cenomanian outcrop of Ikushunbetsu.

Description. – The largest one (Fig. 20A, B) of the three specimens is the best preserved. It is almost wholly septate and 62 mm diameter at the last septum. A fraction of the body chamber at its preserved last portion is secondarily compressed and looks smooth, except for a narrow major rib. The second, smaller specimen (Fig. 20C) is likewise well-preserved. The third one (Fig. 20D–F) is similar to the above two in the septate part (D = 53 mm) and has a displaced fragment of its body chamber (Fig. 20D).

The whorl enlarges at fairly high rate, and is subcircular in section for the major part, with a very slow increase of H in proportion to B. The whorl cross-section in a very young stage is broader and reniform. The change with growth is observable on a natural cross-section along a fracture and also on separable inner whorls.

The involution is moderate (about 2/5 earlier and 1/2 later), the umbilical ratio (U/D) is also moderate, decreasing gradually with growth; *viz* from 36 to 29 percent in the measured range. The umbilical shoulder is well-rounded.

The shell is virtually smooth. The periodic constrictions are not recognized clearly, except for the weak one on the internal mould of an inner whorl, as shown in Fig. 20B. The surface of the test is ornamented with numerous lirae, which are comparatively coarse for the genus and run continuously across the flank, except for a gentle convexity at about the umbilical shoulder. Bifurcation and intercalation of the lirae are present but not common. If one scrutinizes carefully, some lirae are somewhat coarser and slightly more elevated than others and narrow bands covered with finer lirae and bounded by those elevated lirae are discernible where preservation is favourable. The feature is probably a kind of minor rhythm during growth. A very early whorl shows frequent flanges as in other species.

Sutures are shown finely on GT. I-3281 and also here and there on GT. I-3273a, b. They are the typical gaudryceratid pattern.

Dimensions. – See Table 5.

Discussion. – *Ammonites madraspatanus* has been thought as ill-defined, because it was established on small juveniles. In this species, however, some diagnostic characters appear

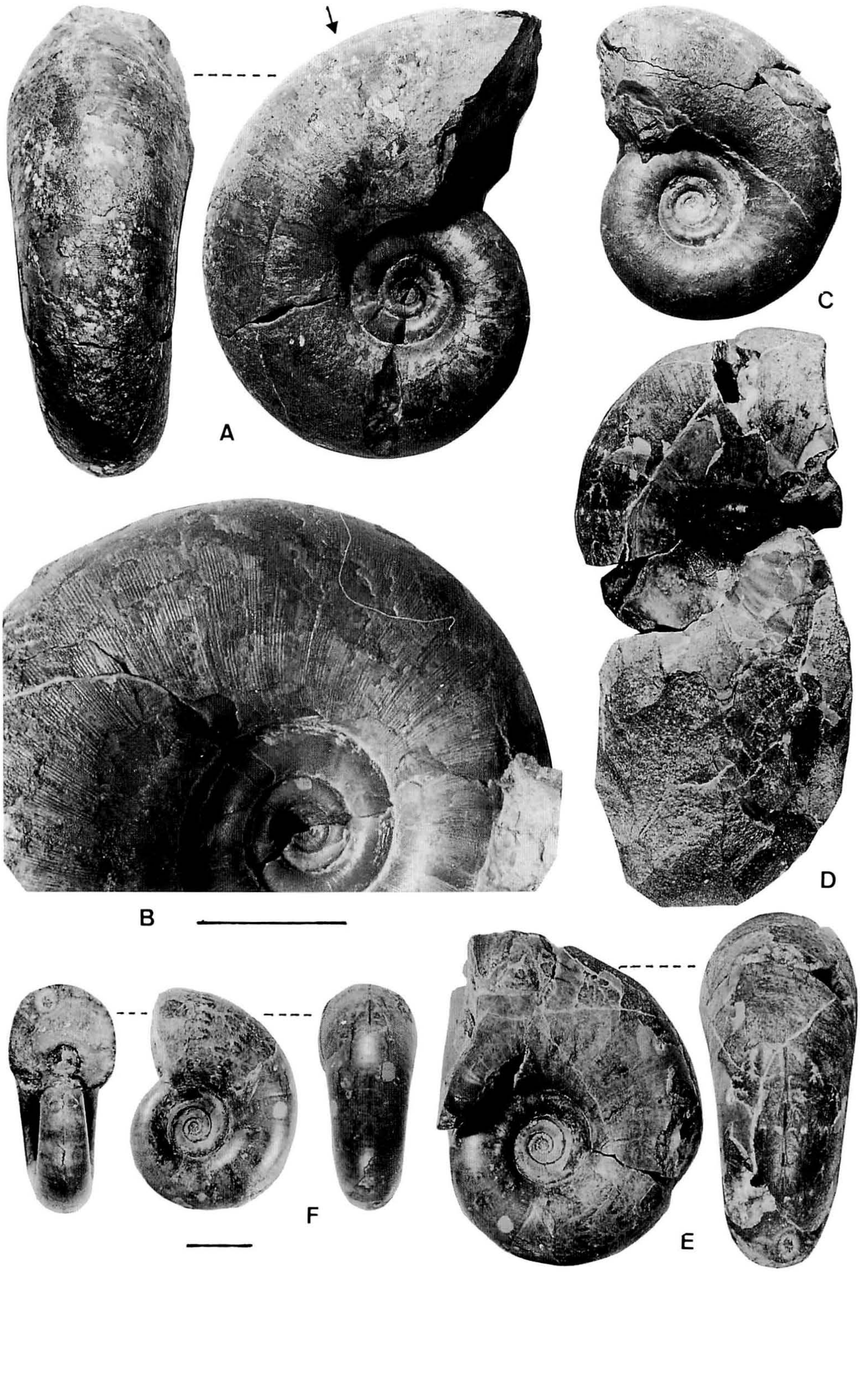

A
B
C
D
E
F

Table 5. Dimensions of *Anagaudryceras madraspatanum.*

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
LT	32.0	11.5	.36	12.7	.40	13.5	.43	1.06	1.74
GT. I-3273a (LS)	62.3	18.3	.29	27.5	.44	26.6	.43	.97	1.67
" I-3273a (LS-150°)	43.5	14.2	.33	18.2	.42	18.4	.42	1.01	1.64
GT. I-3273b (E-120°)	38.2	12.8	.34	16.4	.43	15.6	.41	.95	1.82
GT. I-3281 (LS-30°)	53.0	15.4	.29	24.0	.45	24.0	.45	1.00	1.76
" I-3281 (LS-180°)	34.2	11.2	.33	14.4	.42	15.8	.46	1.10	1.67
Spath, 1923	28.0	10.0	.36	11.8	.42	11.8	.42	1.00	–
For comparison: "*A. utaturense*".									
GSI. 317	129.0	41.0	.32	56.0	.43	48.0	.37	.86	1.75

already in younger shells.

The described specimens from Hokkaido are somewhat larger than the lectotype and at least one of them can be regarded as representing the late growth stage. This species is, thus, characterized by a high ratio of whorl expansion, moderate involution and subcircular whorl-section with a rounded umbilical shoulder. This enables us to distinguish it from *A. involvulum* (Stoliczka) which is characterized by an oblong-ovoid whorl-section already in youth and from immature shells of *A. sacya* which show a lower ratio of whorl expansion, somewhat wider umbilicus at corresponding size, and well-marked constrictions.

Now a question remains as to the character of the adult body chamber. The preserved last part of GT. I-3273 is the beginning of the body chamber where a narrow major rib appears. Furthermore, a fragmentary body chamber of GT. I-3281 shows low and broad ribs, suggesting the appearance of the adult *sacya*-type ornament. On the assumption that the body chamber occupies three quarters of the outer whorl and the umbilical ratio is kept at 29%, the entire shell diameter would be slightly over 100 mm. This is comparable with the size of such species as *A. sacya* and *A. whitneyi.* The above consideration and the described characters of young to middle-aged shells suggest that this species is referable to *Anagaudryceras.* This would be confirmed by a find of an unmistakable adult shell at loc. T863 or from a correlated bed.

On the other hand, I should examine the specimens from the Ootatoor Group. One of them, illustrated by Stoliczka (1865, pl. 75, figs. 1, 1a, 1b), is taken here for discussion. It was named as *Anagaudryceras utaturense* by Shimizu (1935b, p. 176) and thought by Howarth (1965, p. 220) to be an example of *A. involvulum* at a later growth stage. I examined this specimen, GSI. 317, in Calcutta and considered that it could be rather a middle-aged shell of *Ammonites madraspatanus.* Its fine but clearly perceptible lirae on the shell surface and also very weak and less frequent constrictions and collars are fairly similar to those of *A. madraspatanum* described above. Its shell form is also similar to that of the latter, if the

←Figure 20. *Anagaudryceras madraspatanum* (Stoliczka).
A: UMUT. MM19774 (I-3273a], phragmocone and the beginning of body chamber; B: ditto, part of the right side, enlarged (×2.15) to show ornamentation. C: UMUT. MM19775 [I-3273b], middle-aged example. D: UMUT. MM19776 [I-3281], with a displaced fragment of body chamber; E: ditto (fragmentary body chamber removed); F: ditto, younger part, A, C–F are natural size. Scale bar: 10 mm.

change with growth (decrease of U/D, B/D, B/H and increase of H/D) is considered (see Table 5). It should be noticed, however, that the shell size is much different between GSI. 317 and our specimens. The former is still septate at D = 129 mm. Nobody knows what kind of ornament would appear on the lost body chamber of GSI. 317. Despite Shimizu's proposal of a new name, that species cannot be said well-defined. It could be an *Eogaudryceras*. A search for an adult specimen in the neighbourhood of Odium is needed.

Occurrence. – The Hokkaido specimens described above came from the lower part of the Cenomanian (see *Material*). The specimens described by Stoliczka are from the yellow earthy limestone, west and north of Odium and described as neighbourhood of Odium, Ootatoor Group (Stoliczka, 1865, p. 152 and explanation of pl. 75). This locaity is assigned to the lower part of the group, commonly called the Lower Utatur Group (Kossmat, 1895, p. 128), and should be late Albian in age. A British specimen from the Cambridge Greensand (Spath, 1923, p. 25) is of late Albian age.

Anagaudryceras cf. *A. madraspatanum* (Stoliczka)

Figure 21

Material. – GK. H1146A (Fig. 21), and associated H1146B, C, collected by T. M. at loc. Y667 from Member IIb (upper Albian) of the Hikage-zawa, Oyubari-Shuyubari area.

Description. – GK. H1146A is distorted, but attains 85 mm diameter and probably is mature. Weak ribs and associated grooves of *A. sacya*-type are discernible in oblique lighting. The lirae on the partly preserved test are less flexuous, weak and fairly fine, but not very fine (Fig. 21B). The ornament is, thus, quite similar to that of *A. madraspatanum* described above.

GK. H1146B is small (D = 10 mm). It shows a broadly rounded whorl section and a gaudryceratid suture. It is probably a juvenile of the same species. GK. H1146C is of intermediate size, but a fragmentary whorl with a subcircular section.

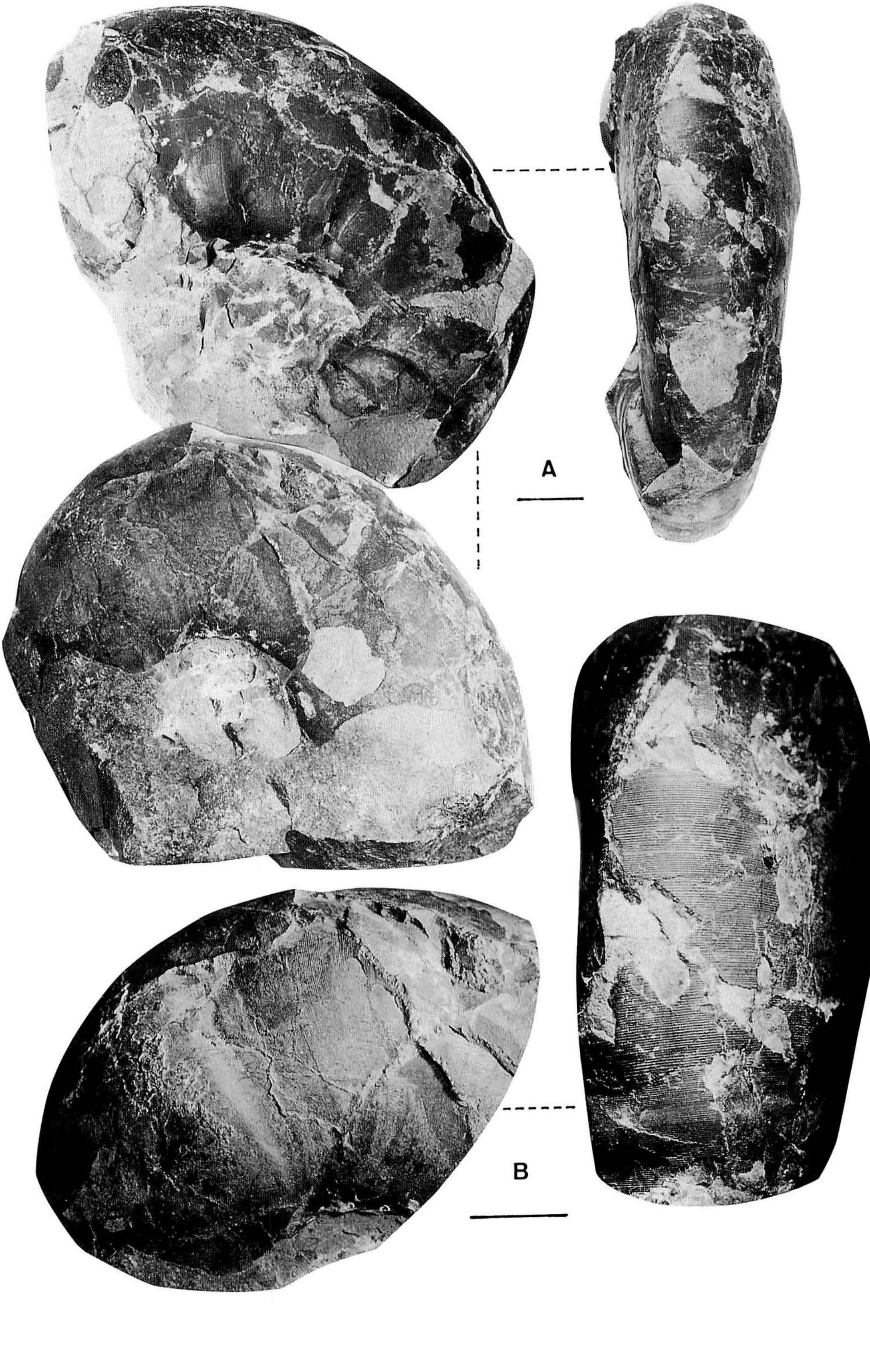
Occurrence. – As for material.

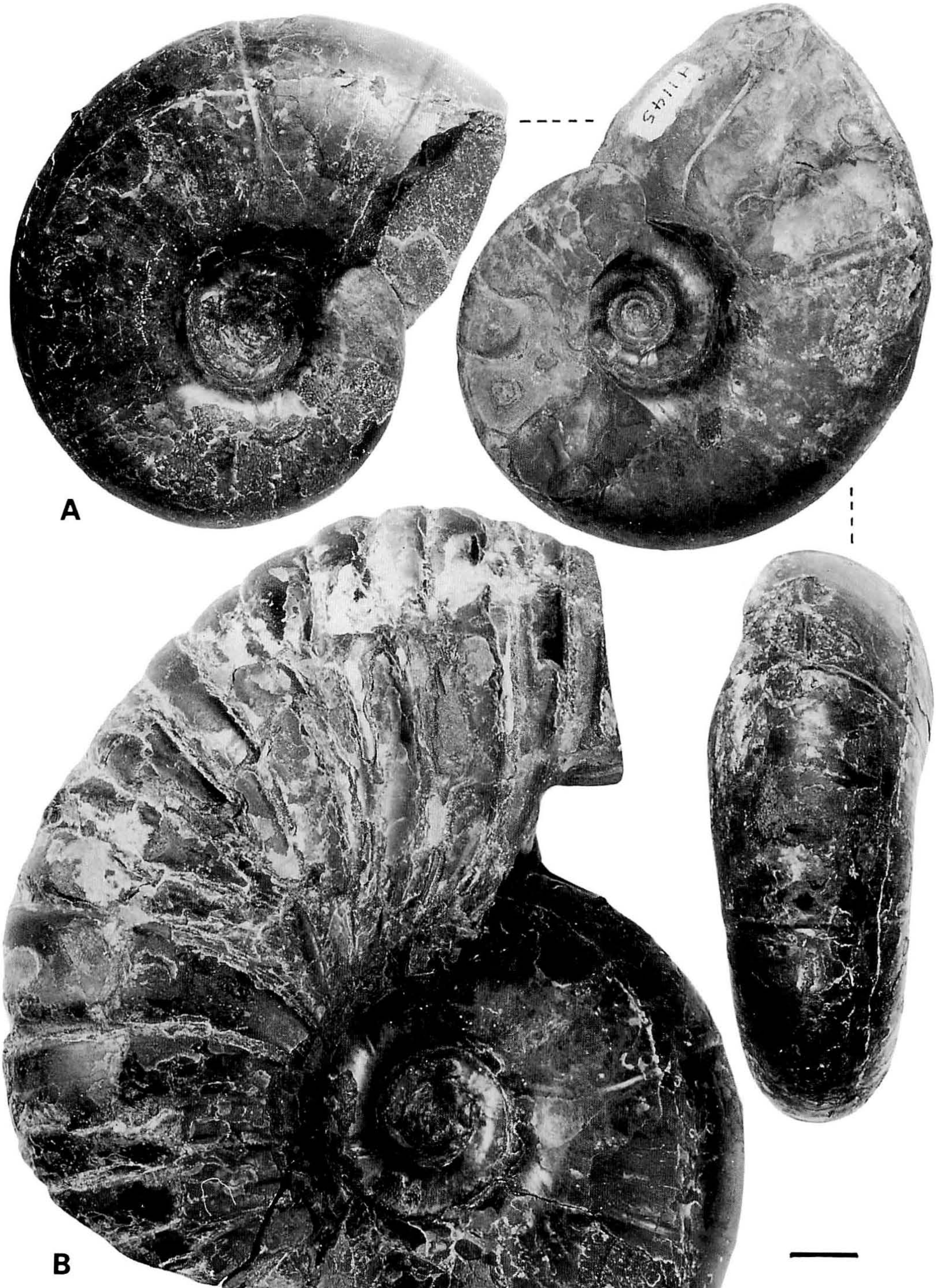
Anagaudryceras howarthi sp. nov.

Figures 22, 23, 24

Anagaudryceras involvulum (Stoliczka); Howarth, 1966, p. 219, pl. 1, figs. 1, 2.

Figure 21. *Anagaudryceras* cf. *A. madraspatanum* (Stoliczka). →
GK. H1146A, distorted and incomplete, adult example. A: Two lateral and ventral views, showing the whole aspects of the specimen, ×1. Right side view is in an oblique light to exaggerate the weakly developed *sacya* type ornament. B: Enlarged (×1.5) views of a part of the flank and venter, showing the details of the ornamentation. Scale bar: 10 mm.


A
B


A
B

Material. – Holotype, GK. H1145 (Fig. 22), collected by T.M. at loc. Y213p of the Shuparo River, in a transported nodule, which is inferred to have been derived from Member IIq (more fossiliferous) or IIp (less so), mid-Turonian part of the Saku Formation in the Oyubari-Shuyubari area.

Paratypes, GK. H1151 (Fig. 24A), collected by T.M. at loc. Y129p4 of the Shuparo River, in a transported nodule from the Saku Formation; GT. I-3280 (now missing in UMUT) and GK. H8448 (Fig. 23), both collected by T.M. at loc. T542p (nodule derived from either Unit IIc or IId) and loc. T1078 (sandstone of IId, i.e. Saku Formation), respectively, in the Saku-gakko-no-sawa, Abeshinai-Saku area; TNHM. 9501 (Fig. 24B) collected by Ryoichi Sato from a layer of mid-Turonian mudstone in a rivulet called Raunenai-zawa to the east of the Shuparo Lake.

Diagnosis. – Fairly involute shell of medium to fairly large size. Whorls of late stages subelliptical in section, with gently convex flanks and moderately arched venter, showing high ratio of height increase. Weak to moderately elevated, narrow ribs occur for some extent from the last part of phragmocone to the beginning of body chamber; major ribs of body chamber at first low, band- or scale-like and later more distinctly folded and crowded.

Description. – The available five specimens are deficient in some respects, but they are complementary in showing the diagnosis. In the holotype the phragmocone is well preserved (Fig. 22A), but the body chamber lacks its last portion and the outer part of its early part; also its surface is abraded (Fig. 22B).

GT. I-3280 looks fine in lateral view, but is secondarily compressed and the adoral part (about one third) of its body chamber is destroyed out. GK. H8448 (Fig. 23) is still more incomplete in lacking later half of its body chamber. These two specimens may be nearly of the same size as the holotype, if the destroyed parts were restored. The entire diameter of the holotype would be about 140 mm that exceeds the defined limit (125 mm) of the moderate size. GK. H1151 and TNHM.9501 have almost complete length of body chamber but are secondarily distorted (see Fig. 24). Their original diameters may have been about 120 mm, that can be said moderate in size.

The whorl expands with a high ratio and is fairly involute (3/5 to 2/3 in H). It is nearly as high as broad at an immature stage (with D = 35–40 mm) and subcircular in section. The last part of the phragmocone is higher than broad and suboval in section, with a round umbilical shoulder and gently convex flanks which gradually converge to a moderately arched venter. The umbilicus at this stage is fairly narrow and its wall is steeply inclined. The adult body chamber is somewhat higher than broad and suboval to subelliptical in section. It occupies at least two thirds (240°) of the last whorl.

The ornament is very weak on the surface of the phragmocone, except for very fine lirae which show rhythmic arrests of growth by very narrow furrows. Periodic constrictions, with a collar behind each of them, are more or less distinct but narrow. The lirae and constrictions are prorsiradiate around the umbilicus, showing a shallow, asymmetric sinus on the wall,

←Figure 22. *Anagaudryceras howarthi* sp. nov.
GK. H1145, holotype. A: Phragmocone. B: Whole part of the specimen, including the body chamber, ×1. Scale bar: 10 mm.

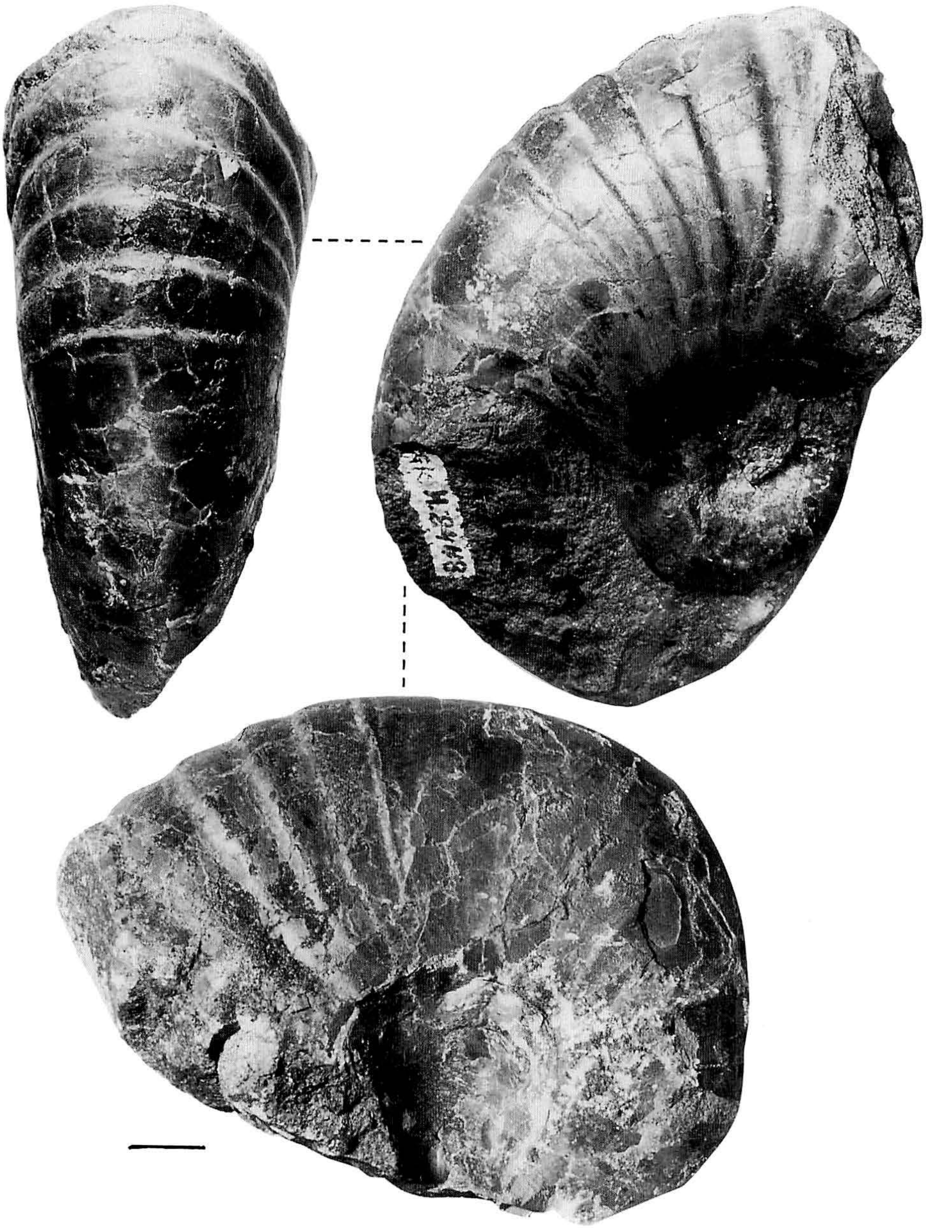
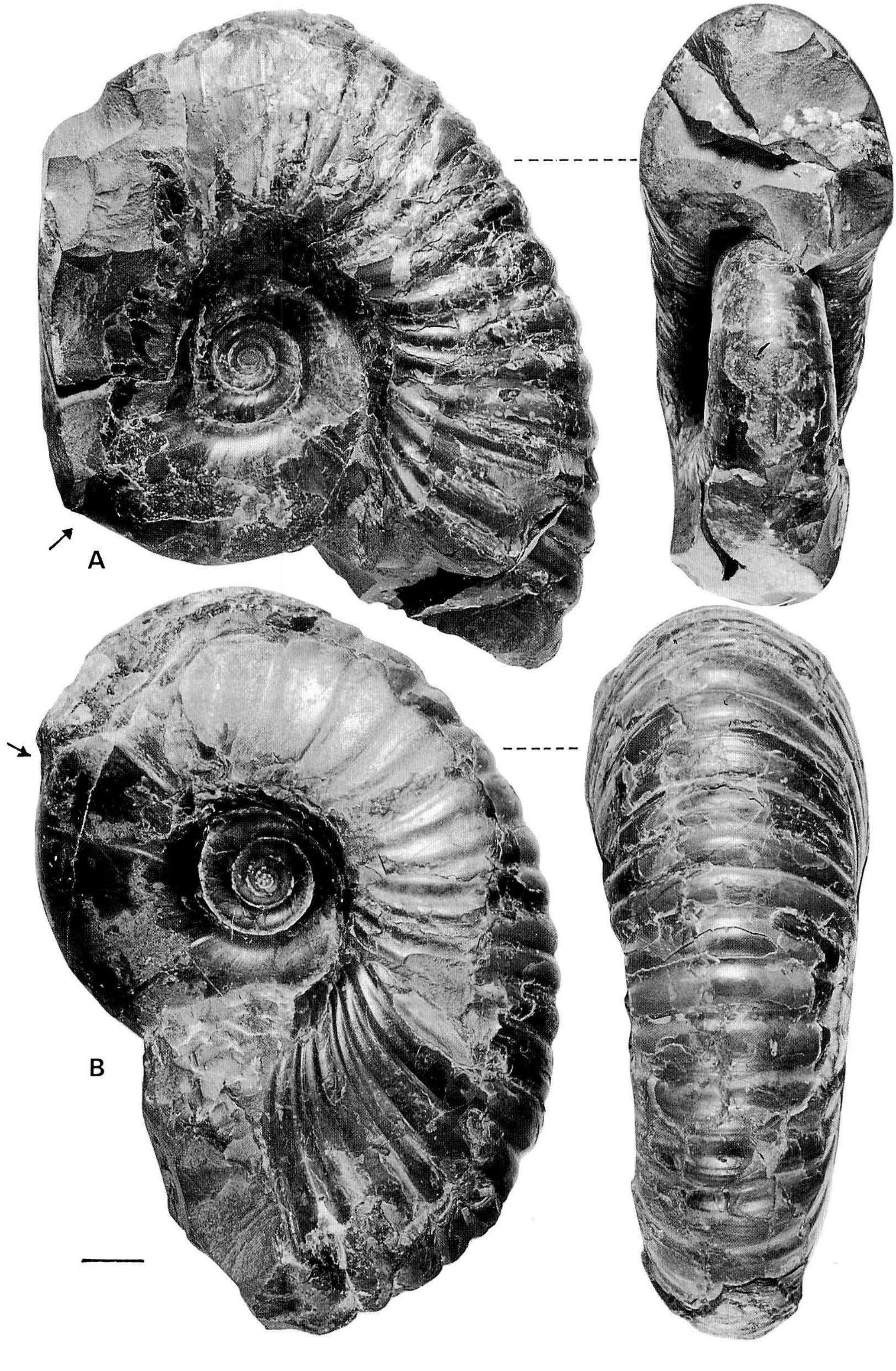


Figure 23. *Anagaudryceras howarthi* sp. nov.
GK. H8448, one of paratypes, but incomplete in lacking later part of body chamber; septate part is also poorly preserved. Scale bar: 10 mm.

Figure 24. *Anagaudryceras howarthi* sp. nov. →
A: GK. H1151, paratype; B: TNHM. 9501, paratype. In both specimens the body chamber is secondarily distorted and the frontal cross-section of A is much depressed from the original subelliptical outline. Figures ×0.9. Scale bar: 10 mm.


A
B

swing back slightly on inner flank, and run almost straight subradially outward, passing across the venter with or without a slight convexity.

For a variable extent from the last part of the phragmocone to the beginning of the body chamber, there are narrow ribs of weak to moderate intensity. They may look approximated collars. They are succeeded by low, band- or scale-like major ribs and intervening shallow grooves on the early part of body chamber. On the rest late part of body chamber, the major ribs are more elevated, rounded on their crests, separated by deeper grooves and fairly crowded. The surface of the outer shell layer has fine lirae, but at this last stage some of them may be coarser than those of the normal cases.

Dimensions. – See Table 6.

Specific name. – In honour of Dr. M.K. Howarth of the British Natural History Museum, who has made valuable contributions to the palaeontology of Jurassic and Cretaceous ammonites.

Discussion. – An example of "*A. involvulum*" described by Howarth (1966, p. 219, pl. 1, figs. 1–2), from the mid-Turonian of Angola, closely resembles the phragmocone of this species. The holotype of *Ammonites involvulus* Stoliczka, 1865 (p. 150, pl. 75, fig. 1, 1a, 1b), GSI. No. 306, from the Ootatoor Group of Odium, southern India, is not so involute as generally thought, but the increase of H with growth is very high in despite of its small size. The whorl-section at its preserved end (at D = 44mm) was described as prolonged ovate, but its weakly converging flanks are flattened and not so convex as the immature shell of *A. howarthi.* Its "constrictions" are very feeble furrows and Stoliczka reported that they were absent. In view of the above observations, I am inclined to regard the Angola specimen mentioned above as probably conspecific with *A. howarthi.*

This species could be misidentified with *A. sacya* (of the preceding age), if incomplete specimens alone were dealt with. It is discriminated by its more distinctly plicate and more crowded major ribs on the late part of the body chamber. This ornament may foretell the development of typical fold ribs separated by wider interspaces in *A. limatum* (Yabe) of the

Table 6. Dimensions of *Anagaudryceras howarthi.*

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
HT (LS+180°)	125	32	.26	57	.46	49	.39	.86	1.58
" (LS)	85	22	.26	39	.46	34	.40	.87	1.62
" (LS-90°)	68	19	.28	32	.47	29	.43	.91	–
GK. H1151 (LS+150°)*	92	27	.29	42	.46	37	.41	.88	1.8
TNHM. 9501 (E)*	122	32	.26	54	.44	49	.40	.91	1.5
" (LS)*	73	20	.27	33	.45	30	.41	.91	1.65
GK. H8448 (E)*	100	25	.25	48	.48	40	.40	.83	1.78
Howarth, 1966	74	20.5	.28	34.5	.47	29	.39	.84	1.81

*: restored.

For comparison: Holotype of *Ammonites involvulus.*

Stoliczka, 1865	44	13	.30	19	.43	16	.36	.84	1.58

succeeding age.

Occurrence. – As for material. So far, this species is represented by rather a small number of specimens, but its occurrences in the mid-Turonian strata of both Japan and Angola suggest its wide distribution.

Anagaudryceras limatum (Yabe, 1903)

Figures 25–31

Gaudryceras limatum Yabe, 1903, p. 34, pl. 4, fig. 2; pl. 5, fig. 2; pl. 6, figs. 3a, b; 1927, pl. 8, fig. 1.
Gaudryceras limatum var. *obscura* Yabe, 1903, p. 36.
Gaudryceras limatum Yabe var. *iwakiensis* Tokunaga & Shimizu, 1926, p. 190, pl. 22, figs. 1a, b; pl. 25, figs. 1, 2a, b, 3a, b.
Gaudryceras (*Paragaudryceras*) *limatum* (Yabe); Shimizu, 1935b, p. 177.
Paragaudryceras limatum (Yabe); Shimizu, 1934 *in* Shimizu & Obata, p. 67, fig. 41; Collignon, 1956, p. 66.
Anagaudryceras limatum (Yabe); Matsumoto, 1941, p. 20, fig. 1b; Matsumoto, 1943, p. 666; Wright & Matsumoto, 1954, p. 113.
Anagaudryceras sacya (Forbes); Howarth, 1965, p. 358 (pars).
Anagaudryceras buddha (Forbes); Kennedy & Klinger, 1979, p. 146 (*pars*).

Material. – The holotype is UMUT. MM7465 [= GT. I-193] (Yabe, 1903, pl. 6, fig. 3a, b), (Fig. 25) from the "Upper Ammonite-beds" (i.e. upper subgroup of the Yezo Group) of the Yoshiashi-zawa, a tributary in the upper reaches of the Ikushunbetsu River. This part of the "upper Ammonite-beds" is referred to the Zone of *Inoceramus uwajimensis* and of Coniacian age (confirmed by T.M.'s field work).

One of the paratypes is UMUT. MM7466 [GT. I-194] (Yabe, 1903, pl. 4, fig. 2; pl. 5, fig. 2) (Fig. 26) from the "upper Ammonite-beds" of the Yubarigawa [= Shiyubari or Shuparo River]. It may be an example of a variety called *obscura* (Yabe, 1903, p. 36), although it was not designated particularly.

There are numerous specimens in the subsequent collections, but they are often distorted, as are Yabe's type specimens, or septate whorls and body chambers are embedded separately. The following specimens are selected among others: GK. H1156 (Figs. 27, 28) from Member IIIa, lower part of the upper subgroup of the Yezo Group at loc. Y122a (collected by T.M.); GK. H8450 from the Nishichirashinai Formation (IIIa) of the Yezo Group at loc. IA 2051, hilly part on the east side of the Abeshinai River, collected by A. Inoma and donated to Kyushu University; GK. H8451 from the same formation at loc. T592dp2, close to the above locality (collected by T.M.); GK. H8463 (Fig. 29) and H8464 (Fig. 30) from Member IIIa, left side of the Masago-zawa, Oyubari area (collected by Masatoshi Kera in a field work with T.M.); GK. H8465 (Fig. 31A) and GK. H8466 (Fig. 31B) from Member IIIa, Komaki-zawa, Oyubari area (collected by Yasuji Kera); the last four specimens were donated to Kyushu University.

Description. – The size of the shell is moderate in many of the available specimens. When the adult shell is completely preserved upto the peristome of the body chamber, as represented by GK. H8463, the diameter is about 132 mm, exceeding the arbitary limit of the term moderate size (from 75 mm to 125 mm) in the definition proposed by me (Matsumoto,

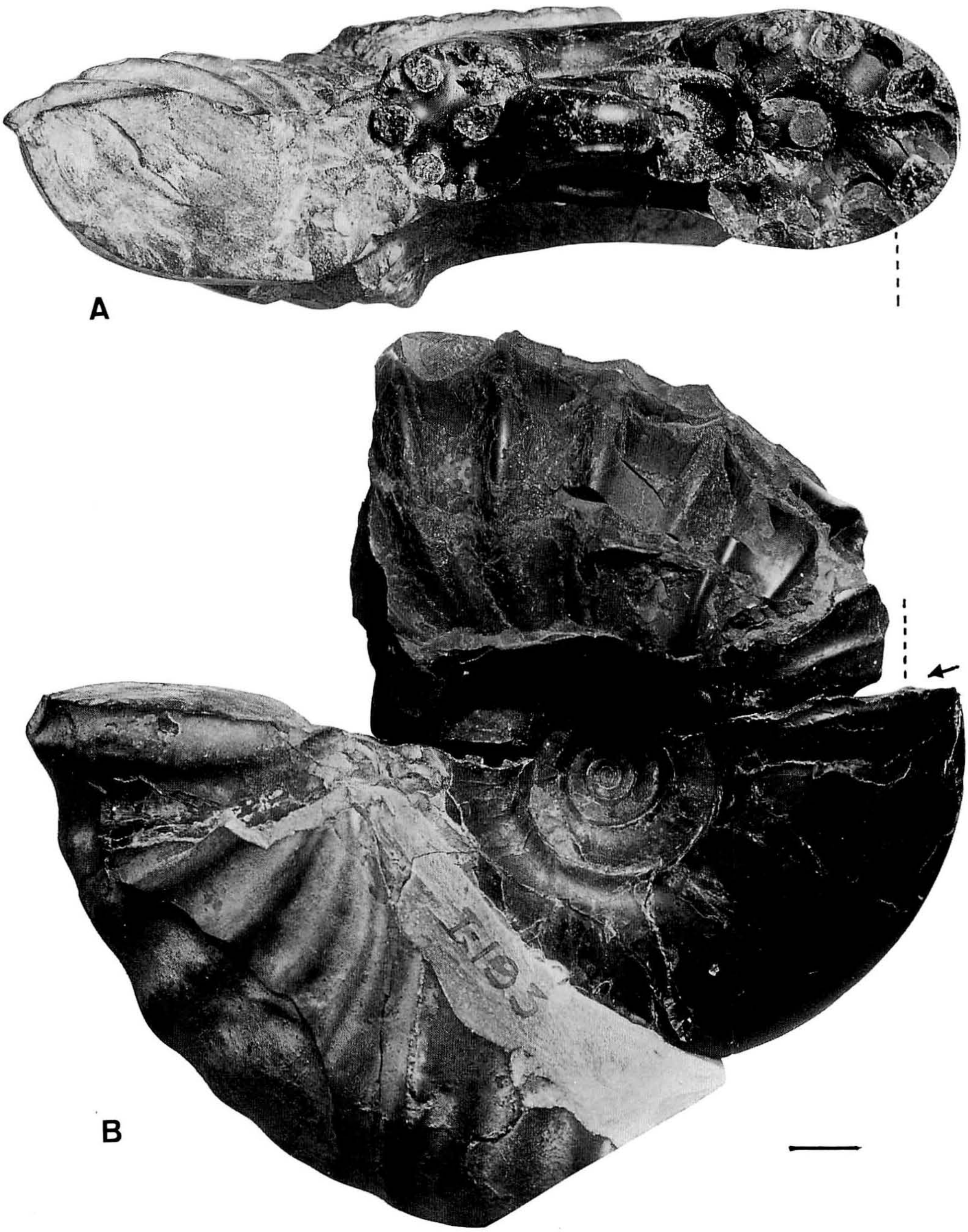


Figure 25. *Anagaudryceras limatum* (Yabe).
UMUT. MM7465, holotype. A: Sectional view along the natural fissure, as observed when the early part of the body chamber is taken out. B: Right lateral view.

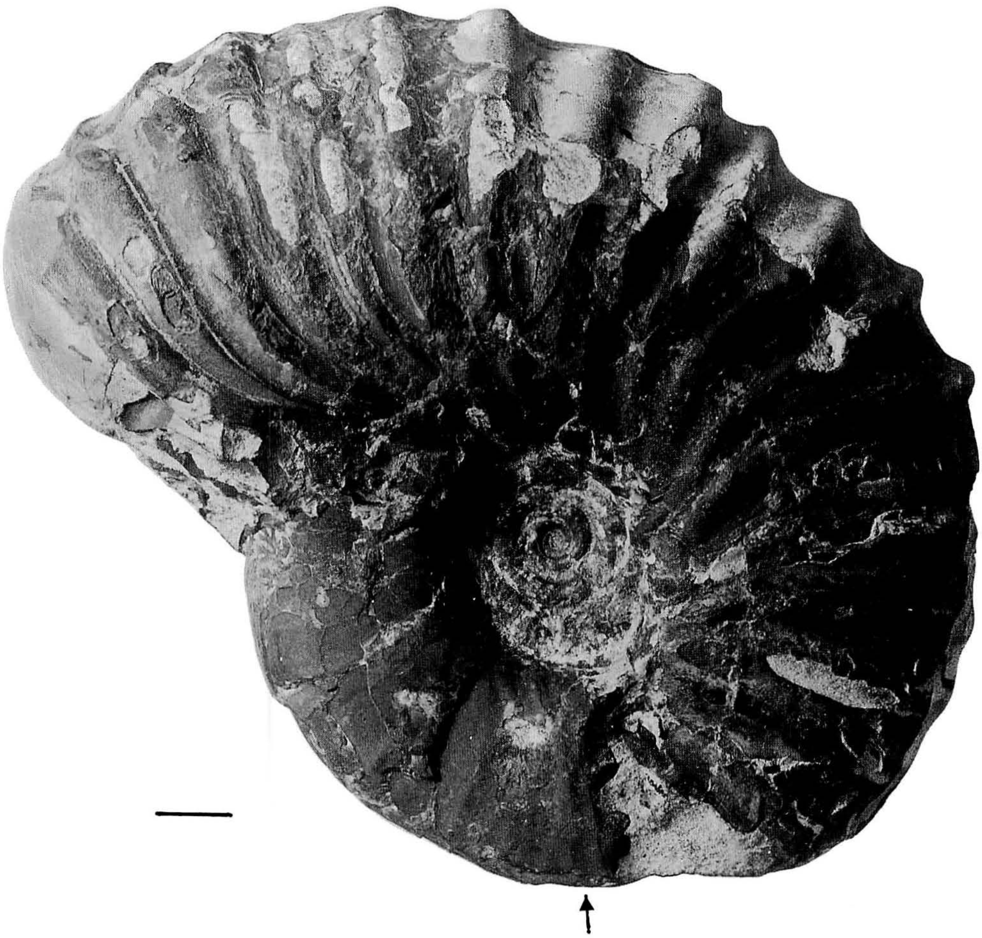


Figure 26. *Anagaudryceras limatum* (Yabe).
UMUT. MM7466, a paratype, which is secondarily deformed, but preserves almost the whole length of the body chamber. Scale bar: 10 mm.

1954, p. 246; see also Introduction). The adult ammonite, when it was alive, must have been fairly large. A number of adult specimens, collected by Y. Kera from the Coniacian mudstones in a limited part of the Oyubari area, range from 120 mm to 150 mm in diameter.

The phragmocone is normally moderate in size at its last septum. The whorl in its middle to later part is nearly as high as broad to slightly higher than broad, becoming gradually higher as the shell grows. It is subcircular to suboval in cross-section, with an evenly rounded venter, moderately to gently convex flanks, narrowly rounded umbilical shoulders and low, but steep or nearly vertical umbilical walls. The ratio of the whorl expansion is moderate and the degree of involution of the whorl is about 2/5. The umbilicus is rather shallow and moderately wide.

The surface of the main part of the phragmocone looks nearly smooth, except for the very fine lirae or intervening striae on the well-preserved outer shell layer. The lirae show

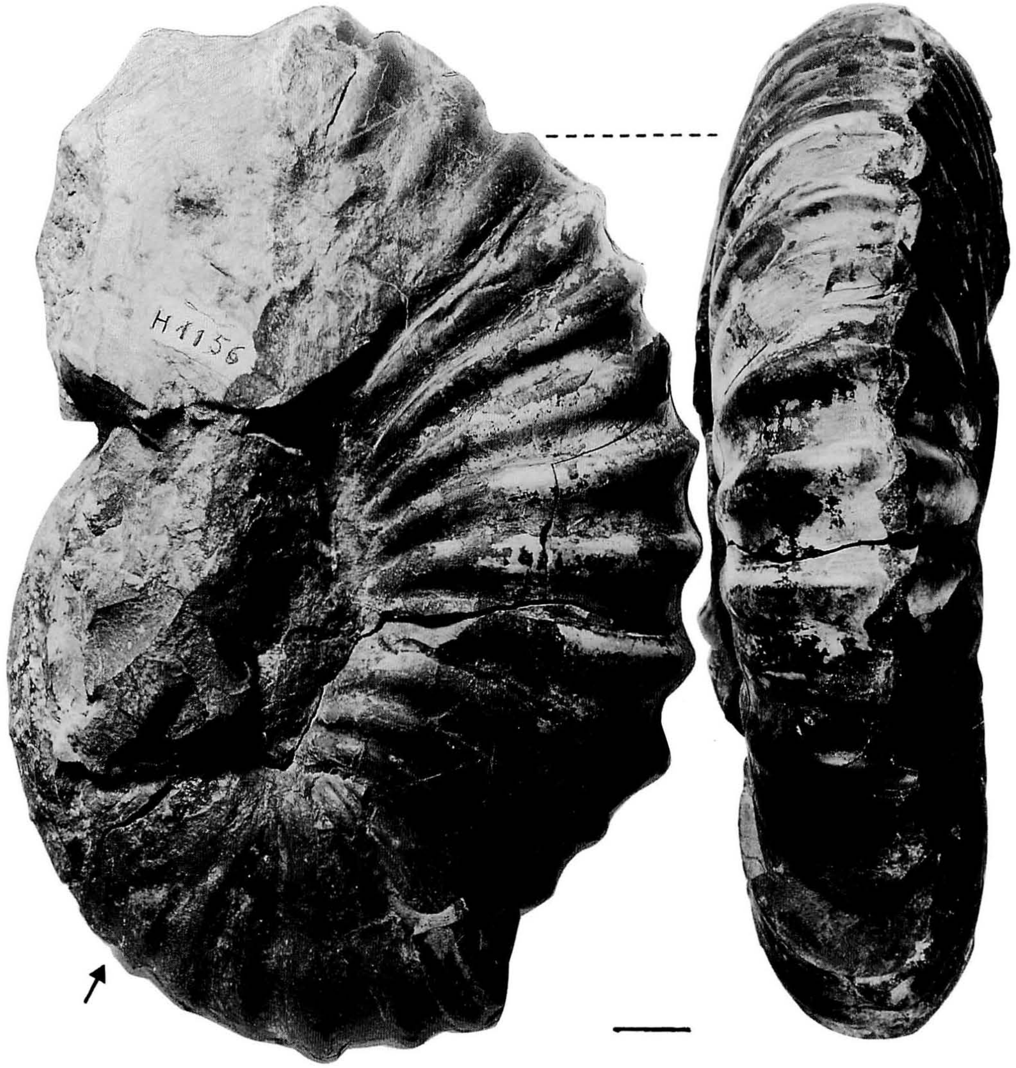


Figure 27. *Anagaudryceras limatum* (Yabe).
GK. H1156, a hypotype, showing the mode of ribbing on the body chamber. Scale bar: 10 mm.

rhythms in their density and sharpness and there are weak furrows corresponding to these rhythms. The furrows may imply minor rhythmic arrests of growth and are often impressed faintly or shallowly on the internal shell layer or occasionally on the internal mold. Besides them, normal constrictions accompanied by narrow collars occur periodically.

On the last part of the septate whorl in some specimens, the furrows mentioned above may become more distinct and are accompanied by narrow ribs. The interspace between these narrow ribs corresponds to the rhythmic interval of the preceding stage.

The ribs become increasingly strong on the main part of the adult body chamber. They are fold ribs without accompanied grooves. On the last portion of phragmocone and the

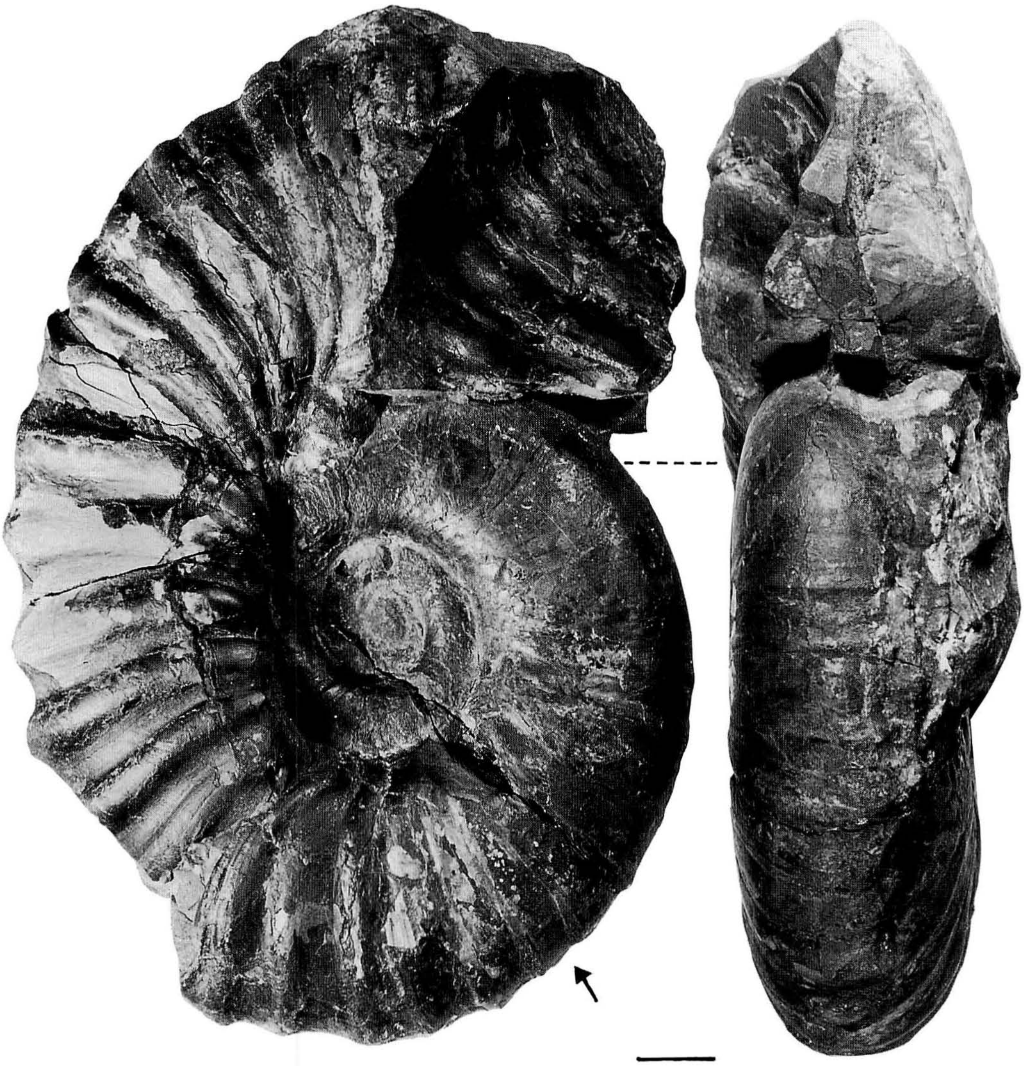


Figure 28. *Anagaudryceras limatum* (Yabe).
GK. H1156, the same specimen as in Fig. 27. The body chamber is so much distorted on its left side that the mode of ribbing is apparently modified. The phragmocone is better shown in Fig. 28. Note a facing body chamber, though fragmentary, of another individual. Scale bar: 10 mm.

adapical part of the body chamber, they are rather narrow but markedly raised and separated by flat and wider interspaces. Then on the middle part of the body chamber they strengthen to typical fold ribs separated by concave interspaces which are more or less wider or nearly as narrow as the ribs. On the adoral part of the body chamber the fold ribs tend to be broadened and lowered, whereas the interspaces are often narrower than the ribs. On the last portion of the body chamber, that is regarded as the apertural margin of the shell, several minor ribs or subcostae and striae superpose on a few lowered major ribs.

The courses of the fine lirae, striae, minor rhythmic furrows and major ribs are essen-

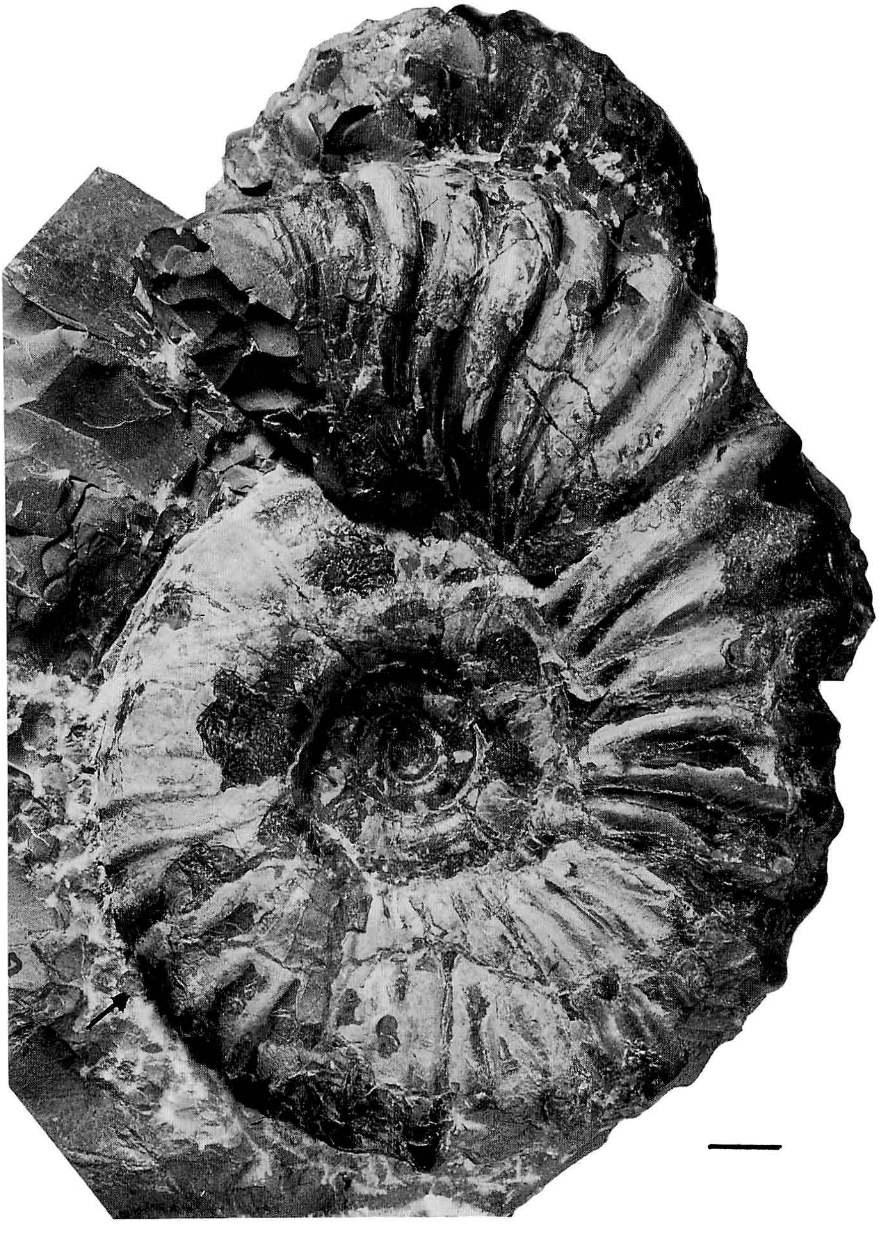


Figure 29. *Anagaudryceras limatum* (Yabe).
GK. H8463, a hypotype, which preserves the full length of the body chamber. Scale-bar: 10 mm.

tially parallel. They show a shallow, asymmetric sinus followed by a forward inclination around the umbilicus, a gently convex curve on the inner part of the flank passing to nearly straight radial course on the outer part of the flank, with or without a very gentle projection on the venter.

The suture is of *Gaudryceras* pattern, with very fine and deep incisions on the later part of the phragmocone (see Yabe, 1903, pl. 4, fig. 2).

Figure 30. *Anagaudryceras limatum* (Yabe).
GK. H8464, a hypotype, an exceptionally small specimen embedded side by side with GK. H8463. Scale-bar: 10 mm.

Dimensions. – See Table 7.

Discussion. – As far as the main part of the septate stage is concerned, there is no significant difference between *A. limatum* and *A. sacya*. Due to the secondary deformation and destruction of the body chamber, it is often difficult to reconstruct the original shell form and size in the adult stage. If a certain extent of variation is allowed, the difference between the two species in these points is hardly noticeable.

A. limatum (Yabe, 1903) was considered by some authors (Howarth, 1965; Kennedy & Klinger, 1979) as a synonym of *A. sacya* (Forbes, 1846). In my view, however, the two

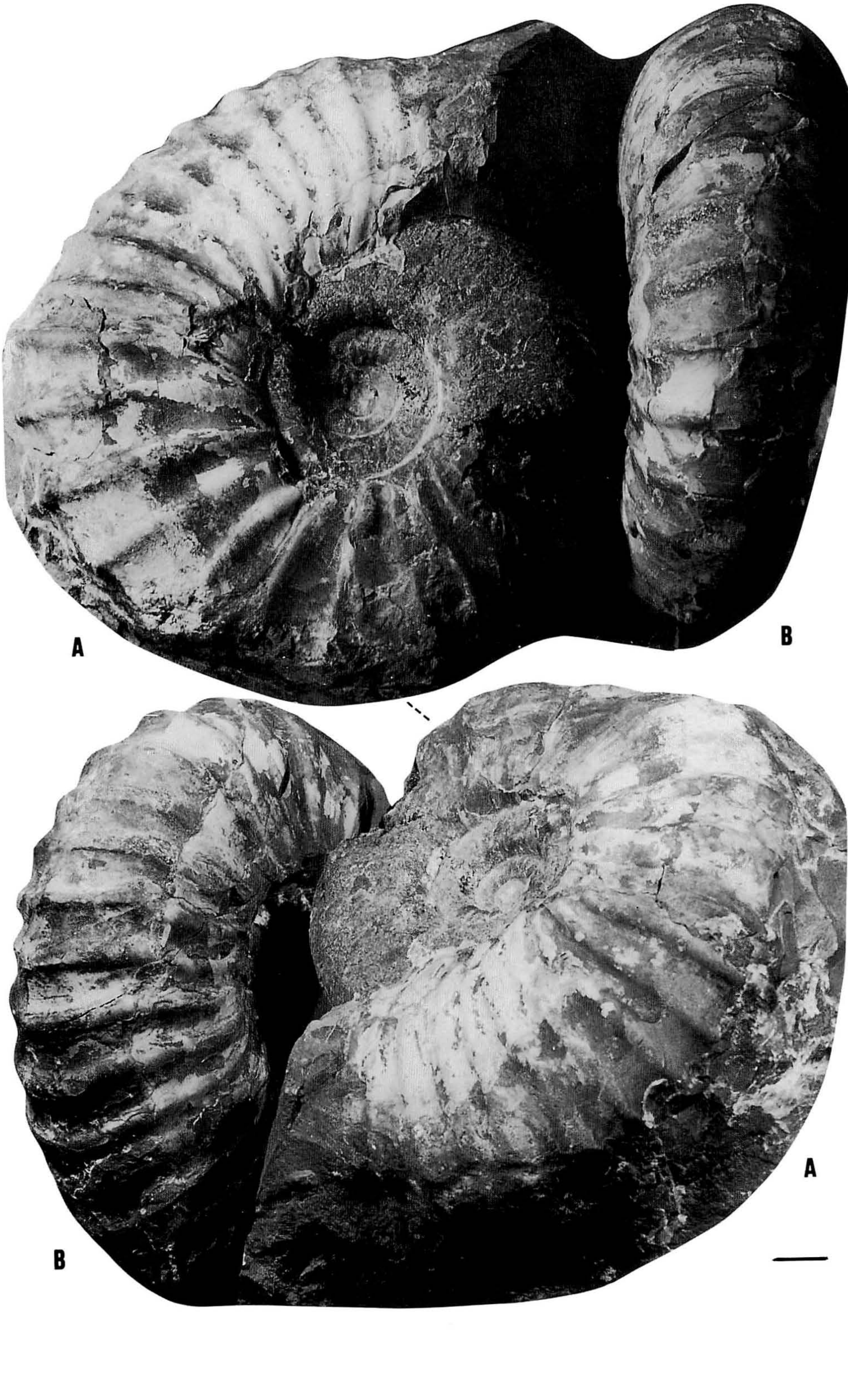

A
B
B
A

Table 7. Dimensions of *Anagaudryceras limatum*.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
HT (LS)	82.0	26.0	.32	34.5	.42	32.5	.40	.94	1.60
PT (E-360°)	77.0	26.0	.34	30.0	.39	27.0	.35	.90	1.43
GK. H1156 (LS)	96.0	30.0	.31	40.0	.42	35.0	.36	.85	1.54
GK. H8450 (LS)	86.0	26.5	.31	35.0	.41	33.5	.39	.96	1.43
GK. H8451A	57.5	17.5	.29	25.0	.42	25.0	.42	1.00	1.47
GK. H8463 (E)*	132.0	48.0	.36	48.0	.36	30	–	–	1.33
" (LS)	80.0	25.0	.31	33.0	.41	–	–	–	1.50
GK. H8464 (E)*	103.0	34.0	.33	42.0	.41	30	–	–	1.55

In HT, PT and GK. H1156 the much deformed body chambers are excluded from the measurements, whereas the specimens marked with * are measured at their preserved end, although the body chambers are somewhat deformed.

species are closely allied, but should be distinguished. The diagnostic difference is recognized in the ornament of the adult stage. As is described above, the major ornament of adult *sacya*-type does not appear on the main part of the body chamber in *A. limatum*. The strong fold ribs predominate without accompanied narrow grooves on the adult body chamber of this species. The interspaces of the ribs are concave and more or less wider than or nearly as wide as the ribs. Only occasionally, especially in the last part of the adult body chamber, the major ribs may be separated by narrower interspaces. This may give a similarity to the ornament of *A. sacya*. In fact, in many cases of ammonite stocks, the ancestral characters apparently reappear at the last growth stage of descendants.

An apparent, instead of essential, similarity sometimes occurs as a result of deformation. An example is shown by an extremely deformed body chamber of GK. H1156 (see Figs. 27–28). On the less deformed right side of its main part of the body chamber, the ribbing is shown in a rather normal state, but on the much compressed left side the extension of the same ribs are so flattened or broadened and the interspaces are so narrowed that they give rise to an apparent *sacya*-like ribbing. Also an inadequate drawing in a paper of older publication (Yabe, 1903, pl. 5, fig. 2) may have caused a misunderstanding for some palaeontologists who had little opportunity to examine the actual specimens from Japan.

In addition to the difference in morphological characters, there is a break in the stratigraphic occurrences of *A. sacya* and *A. limatum* in Hokkaido and South Sakhalin. I have seen no examples of *A. limatum* from the Cenomanian and Lower Turonian strata of the region mentioned above as well as other areas in Japan. Even from the Middle Turonian Zone of *Inoceramus hobetsensis-Romaniceras deverianum* I have not obtained an unmistakable example of *A. sacya*, but there is a form, which I refer to *A. howarthi* n. sp. The widely separated, narrow ribs, which occur in the last part of phragmocone and the adapical part of body chamber, are weak in *A. howarthi*, but much stronger in *A. limatum*. The major ribs on the later part of the body chamber are of moderate strength, round crested, and crowded in *A. howarthi*, but they are more stoutly elevated and broader, fold ribs in *A. limatum*.

←Figure 31. *Anagaudryceras limatum* (Yabe).
Example of paired individuals in two views, ×0.8. A: GK. H8465 and B: GK. H8466.

The unusually smaller size of GK. H8464 which occurs side by side together with GK. H8463 of normal size may give a problem of dimorphism. I interpret it as a malformation, because another nodule, which I obtained in the Saku-Abeshinai area, contained the two adult specimens of the same size with their apertures facing each other. Furthermore Y. Kera has recently showed me over 20 nodules in each of which paired specimens of almost the same size are included. One of them, kindly given to me, is illustrated in Figure 31. These specimens came from his collection from the Coniacian rocks of a restricted area (i.e. Masago-zawa, the Shuparo and Komaki-zawa) (about 6 km × 4 km).

Occurrence. – *A. limatum* has been found commonly from the Upper Turonian Zone of *Subprionocyclus neptuni-Inoceramus teshioensis* and from the Coniacian Zone of *Kossmaticeras theobaldianum-Inoceramus uwajimensis* in Hokkaido.

Anagaudryceras yamashitai (Yabe, 1903)

Figures 32–34

Gaudryceras yamahsitai Yabe, 1903, p. 38, pl. 4, fig. 7.
Anagaudryceras yamashitai (Yabe); Matsumoto, 1943, p. 666; 1959b, p. 138, pl. 37, fig. 1a–d.

Material. – The holotype is UMUT. MM7462 [= I-201] (Yabe, 1903, pl. 4, fig. 7) by original designation. It is recorded to have been obtained from the upper subgroup [= "Upper Ammonite-beds"] of the Yezo Group in the Sanushibe (explanation of plate) or the Makaushippe (tributary of the Sanushibe) (in the text), a major tributary of the Popets [= the Hobetsu River], Hobetsu district, south-central Hokkaido. The paratype from the same subgroup of the Ikushunbetsu, measured by Yabe (1903) as D = 88 mm, U = 22(.25), H = 44(.50), B = 33(.37), B/H = 0.75 is missing now.

Among T.M.'s subsequent collections, adult shells are represented by GK. H8424 (Figs. 32, 33) in a transported nodule at loc. T1091p, derived from Member IIId (Santonian-Lowest Campanian) of the upper subgroup of the Yezo Group, Saku-gakko-no-sawa, Abeshinai-Saku area and GK. H3102B (Fig. 34C) frm Ur2β' at loc. U600c3, Ikandai of the Urakawa district. Phragmocones, some with the beginning of the body chamber preserved, are represented by GK. H3102A (Fig. 34B), which was included in the same nodule as H3102B; GK. H3104 from Ur2β' at loc. U513, the Ikandai rivulet; GK. H3105 and GK. H3113 from Ur2α at los. U150p14 and U153p4, respectively, of the Shakin-zawa, a branch in the upper reaches of the Chinomi-gawa of the Urakawa district; GK. H8446 (Fig. 34A) obtained by T. Katahira (JAPEX) at loc. KH 11, Nioi-zawa of Monbetsu area; and GK. H8447 by H. Kido (JAPEX) at loc. Fn 372, Furenai, both of which were from the Santonian part of the same group and donated to Kyushu University.

Description. – The specimens listed above, including the holotype, are more or less deformed, but they exhibit the diagnostic features of the septate stage, as does an undeformed phragmocone of the specimen GK. H8424 (Figs. 32, 33B) of the Abeshinai-Saku area.

The whorl of the middle growth stage (about 40 to 80 mm in D) shows a high ratio of increase in height, with H greater than B, and suboval section, which has a slightly convex to nearly flat sides, moderately to rather narrowly arched venter and abruptly rounded umbilical shoulder, passing to a steep wall. The umbilicus is fairly narrow (normally 26–27% of D), although the involution is moderate (1/2 or slightly less than 1/2).

The body chamber is crushed in these specimens, but it seems to maintain the relative increase of height and must have been originally high-oval in section. It occupies about three quarters of the outer whorl.

The surface of the phragmocone looks nearly smooth and the young shell up to about 60 mm diameter has neither periodic collars nor constrictions. When the preservation is favourable, very fine lirae and striae are discernible as in other species of *Anagaudryceras*. They show minor rhythms, which may be impressed as rhythmic faint furrows, instead of clear constrictions, even on the internal layer of the test.

These rhythmic furrows on the phragmocone are developed into clear, narrow grooves on the adult body chamber. Each of the grooves is accompanied behind by a narrow rib, which is more distinct where the test is preserved, but may sometimes look as if an elevated frontal margin of a scale-like broad elevation that may be regarded as a kind of the adult *sacya*-type ornament. The major ribs tend to be approximated on the last part of the body chamber.

The lirae and striae on the phragmocone and the grooves and ribs as well as the lirae on the body chamber are parallel, showing a shallow and asymmetric sinus on the umbilical wall, a gently convex curve on the inner flank, and then nearly straight radial course on the outer flank and finally cross the venter with or without a slight projection. The curvature may be modified in various ways by secondary deformation.

The suture is of *Gaudryceras* pattern and deeply and finely incised in later part of the whorl.

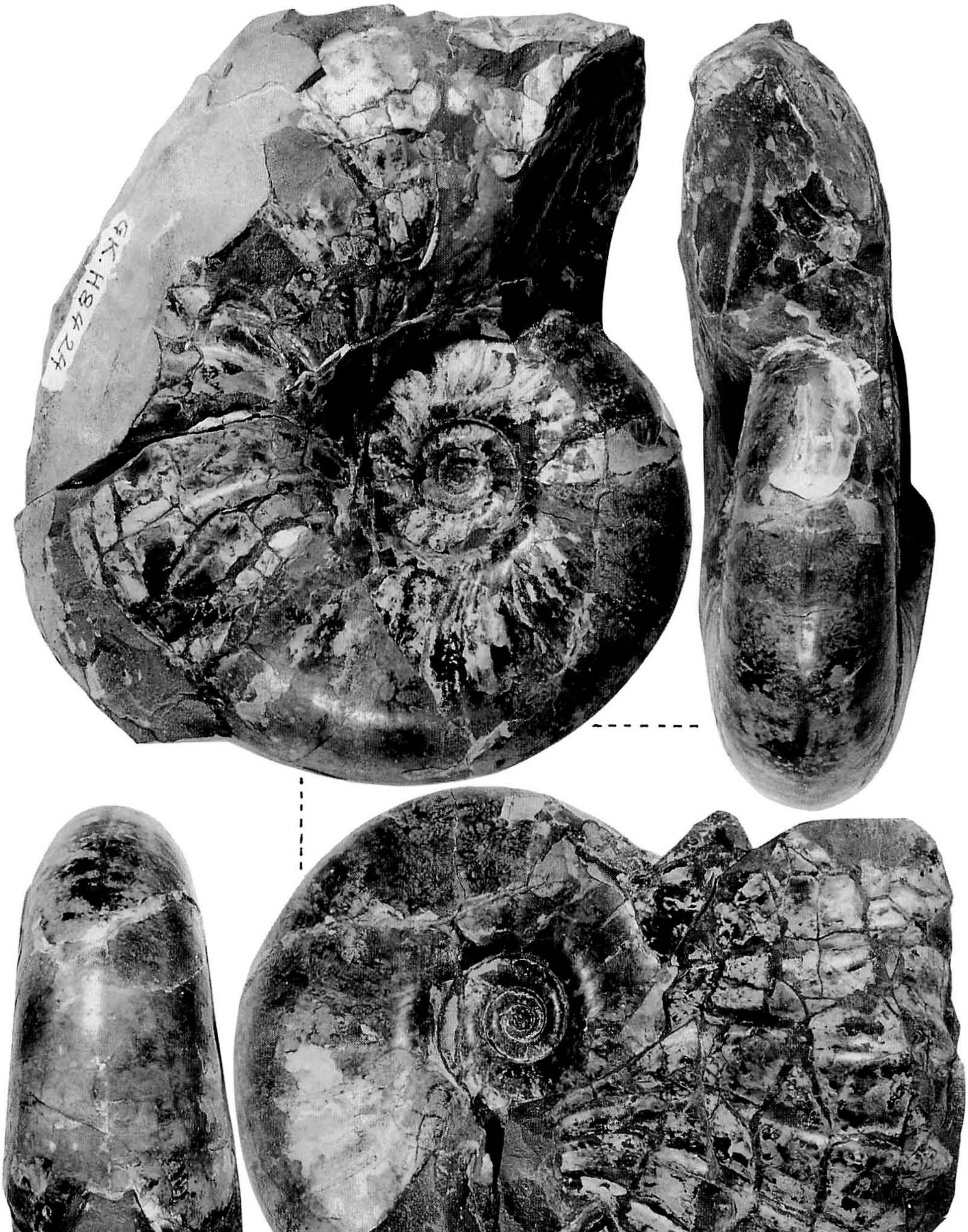
Dimensions. – See Table 8.

Discussion. – As has been previously pointed out by Howarth (1965, p. 220) and Kennedy & Klinger (1979, p. 146), *A. yamashitai* resembles *Ammonites involvulus* during early growth in shell form and smooth-looking ornament without clearly defined periodic constrictions and

Table 8. Dimensions of *Anagaudryceras yamashitai*.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
HT (E)	63.0	17.0	.27	28.8	.46	22.4	.36	.82	1.67
" (E-90°)	45.0	12.0	.27	22.0	.49	18.0	.40	.82	–
GK. PT (E) [Yabe, 1903]	88.0	22.0	.25	44.0	.50	33.0	.37	.75	–
GK. H3102A (LS)	–	–	–	32.0	–	28.0	–	.87	–
GK. H3104 (E-90°)	54.0	14.0	.26	26.0	.48	23.0	.43	.88	–
GK. H3106	53.0	14.4	.27	24.4	.46	21.2	.40	.87	–
GK. H8424 (LS)	77.0	20.0	.26	36.0	.47	31.0	.40	.86	1.71
" (LS+240°)*	150.0	40.0	.27	75.0	.50	–	–	–	–
GK. H8446 (LS)	71.0	18.0	.25	33.0	.46	28.0	.39	.85	1.65

*The body chamber of GK. H8424 is secondarily distorted and its approximate dimensions are on a restored outline.


GK.H8424

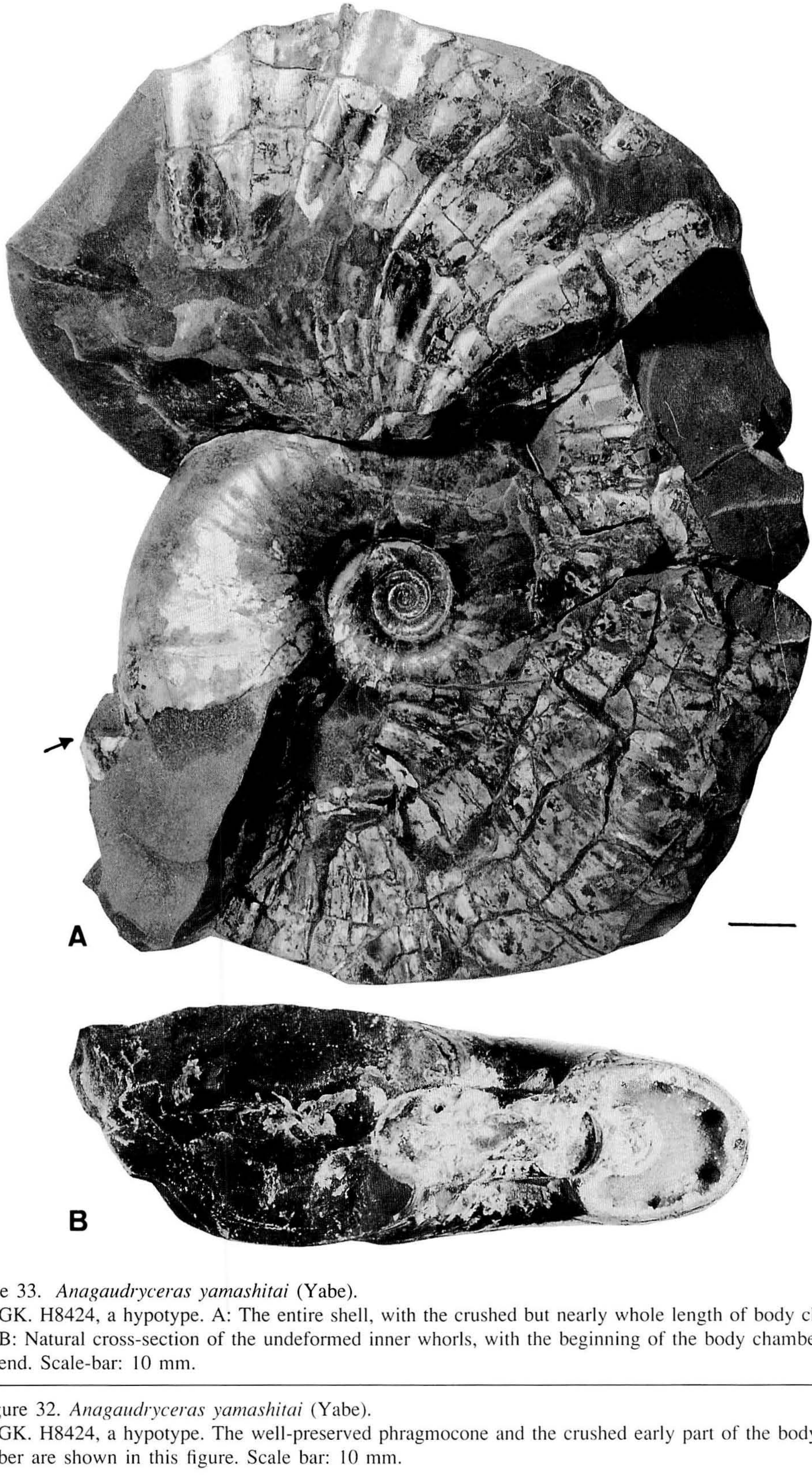
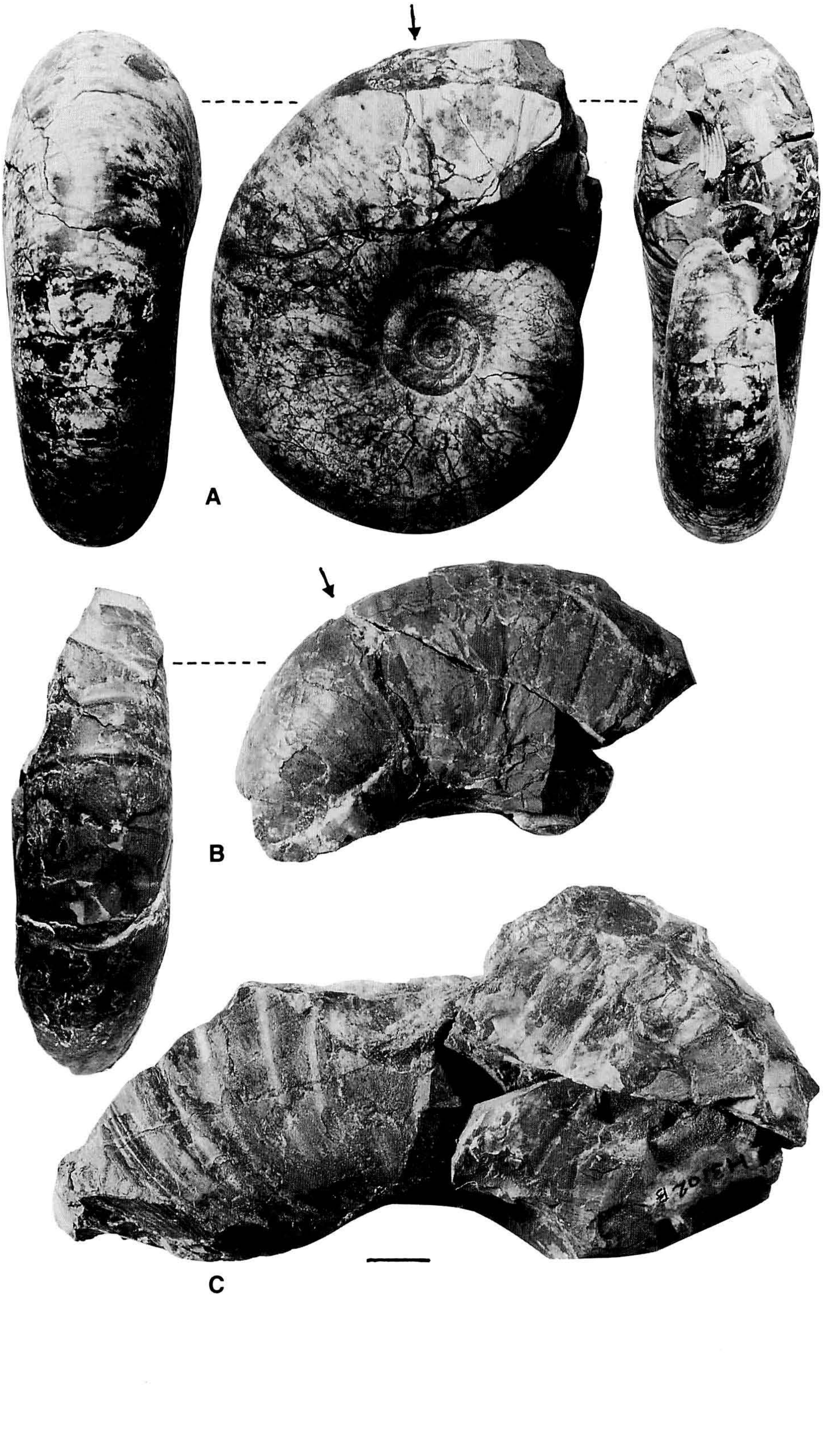


Figure 33. *Anagaudryceras yamashitai* (Yabe).
GK. H8424, a hypotype. A: The entire shell, with the crushed but nearly whole length of body chamber. B: Natural cross-section of the undeformed inner whorls, with the beginning of the body chamber at the end. Scale-bar: 10 mm.

←Figure 32. *Anagaudryceras yamashitai* (Yabe).
GK. H8424, a hypotype. The well-preserved phragmocone and the crushed early part of the body chamber are shown in this figure. Scale bar: 10 mm.


A
B
C

collars. The former has now proved to possess clearly defined major ribs on its adult body chamber.

A. yamashitai resembles *A. howarthi* sp. nov., but is devoid of periodic collars and accompanied constrictions on the inner whorls. The early part of the outer whorl is ornamented with narrow, major ribs, with or without accompanied narrow grooves, in both species. On the late part of the outer whorl, that is the main part of body chamber, the narrowly raised ribs persist and may sometime form scale-like appearance in *A. yamashitai*, whereas at first the adult *sacya*-type broad ribs and then round-crested, crowded ribs characterize *A. howarthi.*

Occurrence. – The locality records of this species by Yabe (1903) referred only to the Upper Ammonite-beds (i.e. the upper subgroup of the Yezo Group) in the Hobetsu and Ikushunbetsu areas. This suggests somewhere in the sequence from Coniacian to lowest Campanian. The age of member IIId of the same subgroup in the Abeshinai-Saku area is mainly Santonian. The horizons indicated as Ur2α and Ur2β' of the Urakawa Cretaceous area may be in the transitional part from Santonian to Campanian. The specimens of Katahira and Kido are Santonian in age. More records in various areas of Hokkaido and the precise range of this species should be investigated further.

An example from the bed with *Baculites capensis* Woods in the Upper Marlife Shale of the Panoche Group in California is assigned to the Santonian (Matsumoto, 1960, p. 43).

Anagaudryceras yokoyamai (Yabe, 1903)

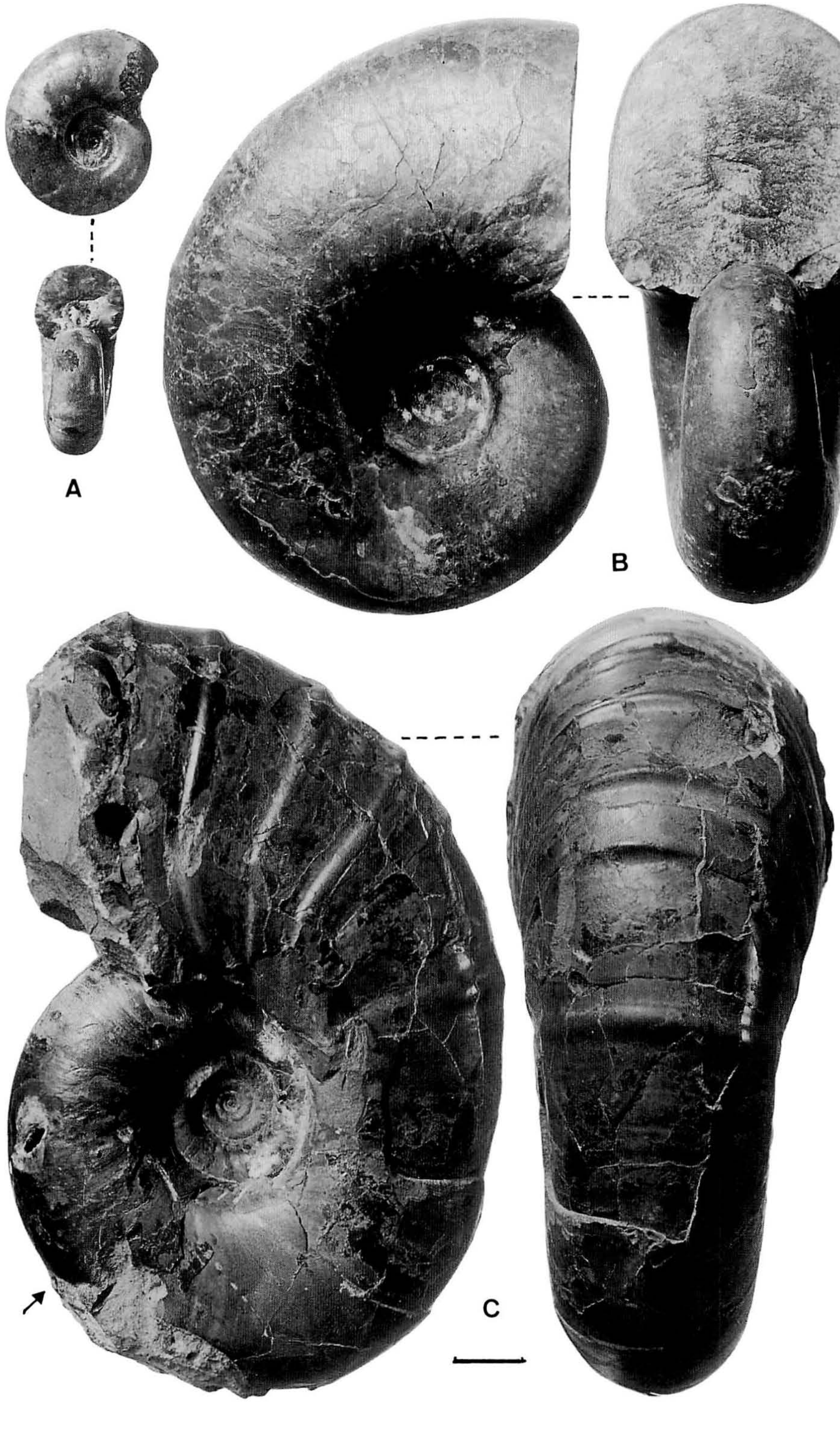
Figure 35

Gaudryceras yokoyamai Yabe, 1903, p. 36, pl. 6, figs. 1a, b, 2a, b; pl. 7, fig. 6'.
Anagaudryceras yokoyamai (Yabe); Matsumoto, 1941, p. 20, fig. 1c; 1943, p. 666; 1988a, p. 182, pl. 50, fig. 6.

Material. – The holotype by original designation is UMUT. MM7464 [= GT. I-197] (Yabe, 1903, pl. 6, fig. 1a, b) (Fig. 35B in this paper). Regrettably, two localities were given for the holotype, "the Ikushumbets" [= Ikushunbetsu River of Mikasa district] in the text (p. 36) and "the Yubarigawa" [the Shiyubari or Shuparo River of the Oyubari area] in the explanation of plate. In either case, it was found in a transported nodule from the upper subgroup [= Upper Ammonite-beds of Yabe] of the Yezo Group.

One of the paratypes illustrated by Yabe (1903, pl. 6, fig. 2a, b and pl. 7, fig. 6'), UMUT. MM7463 [= GT. I-208], and the other of the paratypes, UMUT. MM19777 [GT. I-199] (without fig. in Yabe, 1903) (Fig. 35A of this paper), from the same subgroup of the Yubarigawa; GK. H3106 collected by T.M. from Member Ur2α at loc. U 150p14 of the Shakin-zawa, a branch in the upper reaches of the Chinomi-gawa, Urakawa area; GK. H2132 from Zone Mh6 (mainly Santonian but possibly extending upto the lowest Campanian), collected by T.M. at loc. N145p of the Santan-gawa, and UMUT. MM 19792 [GT. I-475] collected by M.

← Figure 34. *Anagaudryceras yamashitai* (Yabe).
A: GK. H8446, a hypotype, well-preserved phragmocone with the beginning of the body chamber. B: GK. H3102A, a fragmentary whorl which shows the last part of the phragmocone and the early part of the body chamber. C: GK. H3102B, a broken body chamber, showing a part of the apertural margin at the left end of the figure. Scale bar: 10 mm.


A
B
C

Kawada, both from the Naibuchi area; also GK. H5098 of Nagaoka's collection and IGPS. 58087a, b from somewhere in South Sakhalin, all these represent younger shells.

The adult shells that preserve the body chamber at least partly are represented by UMUT. MM19778 [GT. I-470] (Fig. 35C) collected by M. Kawada from Zone Mh6 (of T.M.) of the Santan-gawa, a tributary of the Naibuchi River, South Sakhalin, and also GK. H3101 from Ur2β at loc. U150p20 of the Shakin-zawa, Urakawa area.

Description. – The young shells as represented by the smaller paratype (Fig. 35A) and other specimens listed above (less than 40 mm in diameter) have more or less broad whorls that are reniform to broadly rounded in cross-section. The degree of involution is less than 1/2 and the umbilicus is of moderate width (30% of D). Periodic constrictions are indefinite and infrequent, except for the flanges on the very early whorl.

The holotype represents a middle-aged shell and is not adult as originally described (Yabe, 1903, p. 37), although the latest part of its outer whorl may be the beginning of the body chamber. The whorl increases with high ratios in height and breadth both and is fairly involute, about 3/5. The umbilicus is hence fairly narrow (25% of D in HT). The whorl at this stage is nearly as high as broad or slightly higher than broad and subcircular in cross-section, with an evenly rounded venter, moderately convex flanks that are bent rapidly to the steeply inclined or nearly vertical umbilical wall of moderate height. The maximum breadth of the whorl is between the inner flanks immediately outside of the well-rounded umbilical shoulders.

The whorls of the early to middle-aged stages do not show distinct, periodic constrictions and look smooth. The external surface of the test is marked by very fine lirae or striae with the rhythms manifested by shallow and fine furrows, which may be impressed on inner shell layer. The intervals of the furrows are from 3 mm to 5 mm measured on the outer flank of the whorl with diameters from 50 mm to 85 mm. The course of the lirae and furrows are similar to that described in *A. yamashitai.*

The adult shell is medium-sized (D = ca. 110 mm) and its body chamber occupies at least two thirds of the outer whorl. It is somewhat higher than broad, increasing with a high ratio in height, and is suboval in cross-section, although the available specimens are actually more or less deformed.

The outer whorl of the adult stage is ornamented with narrow, major ribs that occur at wide intervals. On its early part, that extends from the last portion of the phragmocone to the adapical part of the body chamber, the ribs are weak and sometimes accompanied in front by shallow grooves. On the later half, i.e. the main part of the body chamber, the ribs become stronger; especially on the outer flank and on the venter, they are definitely elevated and almost free from grooves. The course of the rib is similar to that of *A. yamashitai.*

Dimensions. – See Table 9.

Discussion. – *A. yokoyamai* resembles the nearly contemporary *A. yamashitai* in orna-

←Figure 35. *Anagaudryceras yokoyamai* (Yabe).
A: UMUT. MM19777 [I-199], a paratype, a juvenile example. B: UMUT. MM7464 [I-197], holotype, middle aged. C: UMUT. MM19778 [GT. I-470], a hypotype, adult shell. Scale bar: 10 mm.

Table 9. Dimensions of *Anagaudryceras yokoyamai*.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
HT (E)	86.0	21.5	.25	42.0	.49	40.0	.46	.95	1.87
GT. I-199 (E)	26.0	7.8	.30	10.8	.42	12.4	.48	1.15	1.38
GT. I-475 (E)	27.0	8.0	.30	11.0	.41	12.8	.47	1.16	1.38
GT. I-208	44.0	12.7	.29	19.0	.43	18.0	.41	.95	1.54
GT. I-470 (E)*	107.0	27.0	.25	51.0	.48	46.0	.43	.90	1.70
GK. H3101A	32.2	9.5	.29	14.5	.45	14.5	.45	1.00	–
IGPS. 58087a	35.0	11.0	.31	15.0	.43	14.0	.40	.93	1.67

*Body chamber is somewhat distorted.

ment and shell size. The distinction is in the shell form of the septate stage, namely, the whorl of the former is subcircular in section with an evenly rounded venter and fairly convex flanks and becomes more involute with growth, whereas that of the latter is suboval in section with a rather narrowly arched venter and slightly convex or nearly flat flanks. The narrow but fairly strong ribs seem to be more predominant in *A. yokoyamai* than in *A. yamashitai*, but there may be variation in this respect and the available specimens are not numerous enough to assess the variability.

Occurrence. – The stratigraphic occurrence of *A. yokoyamai* is similar to that of *A. yamashitai.* It occurs mainly in the Santonian part of the upper subgroup of the Yezo Group of Hokkaido and South Sakhalin, although it may extend upward to the lower Campanian, depending on the definition of the Santonian-Campanian boundary. Further investigation is required to determine precisely the geological time-range and geographical distribution of this species.

Anagaudryceras politissimum (Kossmat, 1895)

Figures 36 and 37

Lytoceras (*Gaudryceras*) *politissimum* Kossmat, 1895, p. 128, pl. 15, figs. 7a–c.
Anagaudryceras politissimum (Kossmat); Collignon, 1956, p. 58, pl. 8, fig. 2, 2a, 2b; Collignon, 1971, p. 4, pl. 641, fig. 2364 (?); Kennedy & Klinger, 1979, p. 154, pl. 5, fig. 3; Henderson & McNamara, 1985, p. 46, pl. 1, figs. 9–10; text-fig. 4d; Matsumoto *in* Matsumoto *et al.*, 1985, p. 23, pl. 3, figs. 1–6; pl. 5, figs. 5–8; Matsumoto, 1988a, p. 182, pl. 50, fig. 7.

Holotype. – The holotype, by monotypy, is the specimen, described and illustrated by Kossmat (1895, *supra*), from the upper part of the Trichinopoly Group of Varagur, southern India.

Material. – UMUT. MM19779 [I-3798] (Fig. 36) from Member Rdy 1 (dark colored, fine-sandy siltstone) in the upper part of the Ryugase Group, collected by T.M. at loc. N112d4 on the left bank of the Miho River of the Naibuchi area, South Sakhalin; GK. H8445 (Fig. 37) obtained by T.M. at loc. Ik 10011 r7, a fallen block of sandstone in front of a high cliff on the left side of the Ganseki-zawa (i.e. the 8th branch) of the Kami-ichi-no-sawa, a tribu-

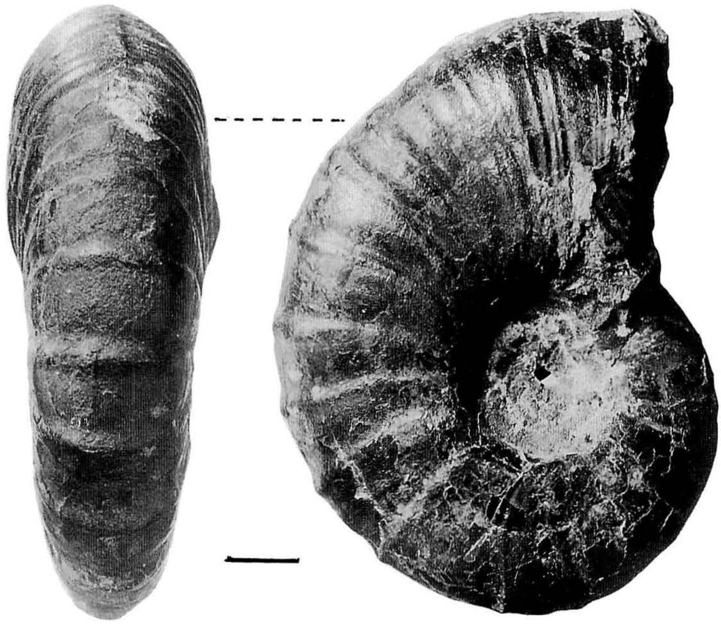


Figure 36. *Anagaudryceras politissimum* (Kossmat).
UMUT. MM19799 [GT. I-3798], a hypotype, adult. Scale bar: 10 mm.

tary of the Ikushumbetsu River, central Hokkaido. It probably came from the sandstone in the basal part of the Coniacian (as defined by Matsumoto, 1984a). See also the specimens described by Matsumoto *in* Matsumoto *et al.*, 1985 and Matsumoto, 1988a.

Description. – The two specimens illustrated in this paper are larger than the specimens previously described from Hokkaido and South Sakhalin and have the clearly ribbed body chamber.

Their ratio of whorl-expansion is moderate to fairly high. The involution is moderate. The whorl is higher than broad in later growth stages, with only gently convex or nearly flat flanks, an arched venter, rounded umbilical shoulders and steep walls. The umbilicus is shallow and moderately wide, becoming somewhat narrower in the last part of the full-grown shell as represented by GT. I-3798. The body chamber occupies about two thirds of the outer whorl.

The phragmocone has very fine and dense lirae or striae on the external surface of the test. Constrictions with associated collars occur periodically and they are more or less prorsiradiate. The body chamber is ornamented with narrow, *yokoyamai*-like fold ribs. At first a few, narrow and weak ribs with associated faint furrows occur at wide intervals. The ribs on the main part of the body chamber are strong and fold type but comparatively narrow, being separated by wider interspaces. Some ribs have shallow, indistinct grooves in front of them, especially on the internal mould. In the last part of the body whorl ribs tend to be approximated and finally near the peristrome there are crowded narrow ribs, subcostae and fine lirae.

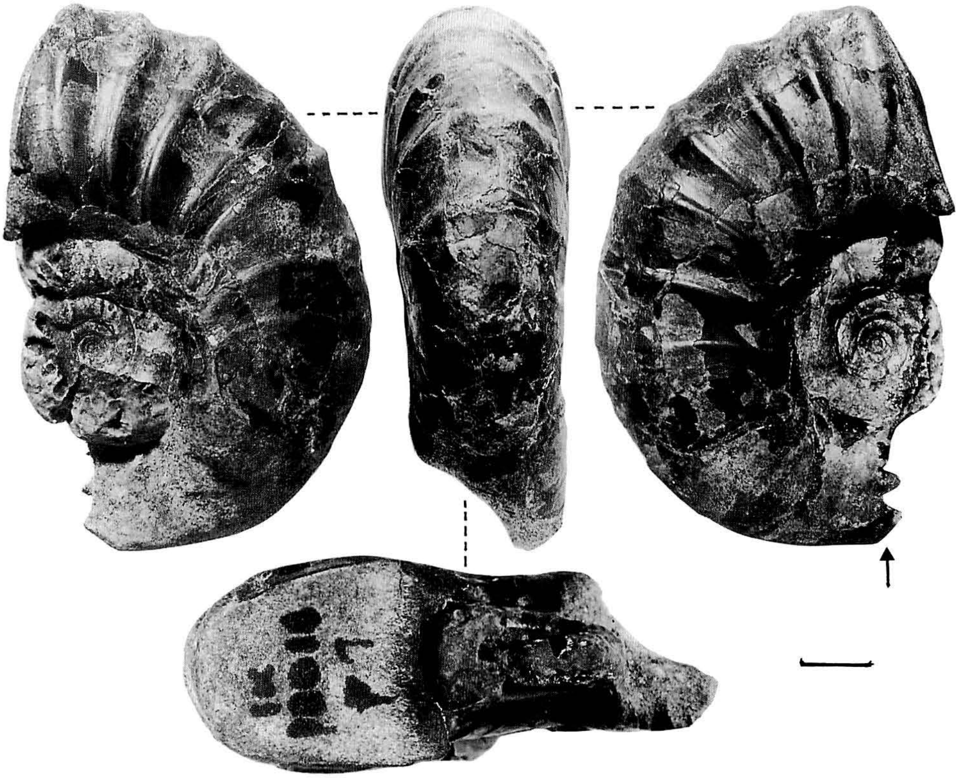


Figure 37. *Anagaudryceras politissimum* (Kossmat).
GK. H8445, a hypotype, adult. Scale bar: 10 mm.

The ribs run parallel to the lirae on the external surface. They show an indistinct sinus on the umbilical wall and then a forward inclination on passing across the umbilical shoulder, followed by a convex curve on the inner flank to take a subradial orientation on the main part of the flank. There is or is not a slight forwad inclination of the ribs from the ventrolateral shoulder to the mid-venter. Thus the ribs are gently flexuous in GK. H8445, whereas they run subradially in GT. I-3798.

Dimensions. – See Table 10.

Discussion. – This is, so far as I know, the first description of the adult characters of *A. politissimum*, for the specimens that have been described or illustrated in previous papers are all mainly phragmocones without or with a posterior fraction of the body chamber. Now this species has proved to have *yokoyamai*-like ribs on the main part of the adult body chamber.

A question remains as to the size of the shell. Examples from Japan and South Sakhalin are smaller than those from South India, West Australia, Madagascar and South Africa, which surrounded the opening Indian Ocean in the late Cretaceous time. In the characters other than the shell size, there is no significant difference for separating species, provided that the body chamber would be similarly *yokoyamai*-like in the material from the circum-Indian Ocean

Tasble 10. Dimensions of *Anagaudryceras politissimum*.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
HT (E)*	89.0	34.0	.38	33.0	.38	28.0	.31	.85	1.50
GT. I-3798 (E)	80.0	23.5	.29	36.0	.45	27.5	.34	.76	1.75
" (E-90°)	61.0	20.0	.33	26.0	.43	21.0	.34	.81	1.73
GK. H8445 (E)	71.0	23.0	.32	30.0	.42	25.5	.36	.85	1.67
GK. H2302 (E)	27.6	10.2	.37	11.2	.40	10.4	.38	.93	1.80
GK. H3823 (LS)	41.3	13.3	.32	17.5	.42	15.0	.36	.86	1.67

*After Kossmat (1895); see also Matsumoto *in* Matsumoto *et al.* (1985, p. 24) and Matsumoto (1988a, p. 182).

region. The collections from the northwestern Pacific region (including Japan and Sakhalin) and those from the Indian Ocean region are not large enough even for subspecific separation. I hereby propose merely a problem that the small form of the northwestern Pacific region could possibly be a geographic subspecies, leaving the final conclusion for further investigations.

Occurrence. – As for Material. The range of this species is from Coniacian to Maastrichtian from the available evidence in both northwestern Pacific and circum-Indian Ocean regions. More material from the Santonian and Campanian strata is wanted in both regions.

Genus *Gaudryceras* de Grossouvre, 1894

Type species. – *Ammonites mitis* Hauer, 1866 by the subsequent designation of Boule, Lemoine & Thévenin (1906, p. 183).

Diagnosis. – See Wright & Kennedy, 1984, p. 51.

Description. – The adult shell is medium-sized or large or even huge, depending on species. It is more or less polygyral. The whorls of younger stages are rather evolute and depressed reniform to round in section, expanding slowly; those of later stages tend to be more or less involute and variably higher than broad, expanding comparatively rapidly. The umbilicus is, consequently, moderately wide to fairly narrow.

The very young whorls which follow the primary constriction have flanges as in other genera of this family. The external surface of the shell from young to adult stages is normally ornamented with fine but sharply raised lirae which are more or less flexuous in lateral view and projected on the venter in many species as typified by *G. mite*, but in some cases the flexuosity in the outer part of the whorl is less pronounced or very slight. A minor, shallowly concave, asymmetric sinus may be discernible on the umbilical wall. In addition to the periodic collars, which may occur on the inner whorls in association with the constrictions, major ribs develop in more or less later whorls. They run generally in parallel to the lirae. The lirae are coarse and may have weakly elevated bases on the intermediate shell layer, forming fine riblets. They are often bifurcated and/or intercalated and may be bundled around the umbilicus to form ill-defined or partial major ribs. Still other kinds of modification of the lirae may occur (see Discussion).

The lateral lobes, L and U2, and also the lateral saddles, E/L and L/U2, are bifid; the suspensive lobe, U1 [= S], is strongly retracted; the internal suture consists of I and U1 [= S (internal side)]. Thus, the suture of this genus typifies that of the Gaudryceratidae (Fig. 1), although certain kinds of modification to the typical pattern occur in *Gabbioceras, Zelandites*, and *Vertebrites*, respectively. The sutures of later growth stages are very finely and deeply incised.

Discussion. – The phylogenetic origin of *Gaudryceras* is not known precisely. Murphy (1967c) suggested an interesting view on the basis of a certain form from the Albian of Madagascar that *Anagaudryceras* and then *Gaudryceras* may have diverged successively from *Eogaudryceras* in late Albian time. In *Anagaudryceras madraspatanum* (Stoliczka) and *A.* sp. cf. *A. madraspatanum*, the lirae are well shown (see Figs. 20B, 21B). They are dense, fairly fine and less flexuous, but they are somewhat coarser and have sharper crests than those of typical species of *Anagaudryceras* and *Eogaudryceras*. This feature suggests an ancestral character towards more distinct lirae of *Gaudryceras*.

The lirae of Cenomanian *G. subcostatum* n. sp. (described below) are finer than in those of other species of *Gaudryceras*, but they are more sharply crested than those of *Anagaudryceras*.

It should be noted, furthermore, that the earlier species of *Gaudryceras*, such as *G. stefaninii* Venzo of late Albian to late Cenomanian age and *G.* sp. nov. (?) (describe below) of early Turonian age, show little flexuosity of the lirae on the outer part of the whorl. This can be regarded as a morphological similarity between early species of *Gaudryceras* and Albian to Cenomanian species of *Anagaudryceras*. The flexuosity of the lirae and ribs may be, however, related to the mode of life. The less flexuous ribs and lirae reappear on the gerontic last part of some typical, later species of *Gaudryceras* that are characterized by flexuous ornament throughout the main growth stages (see Figs. 44, 59).

It is true that too many specific names have been proposed under the genus *Gaudryceras*, as Kennedy & Klinger (1979, p. 129) complained. However, if one observe carefully well-characterized species, they show respectively their own diagnostic features in size, shell form and ornament. It is important to follow after the change of characters with growth. Specific diagnosis should be given with respect to both the immature and adult stages. Even in the adult body chamber the characters may change with growth. One should indicate, as far as possible, the position of the last suture, i.e. the beginning of the body chamber. This has been neglected or sometimes misplaced in previous papers. Also the original length of the body chamber should be observed carefully to estimate properly the original diameter of shell. Of course, I should consider variation which would occur in every character.

I endeavour in this paper to give revised descriptions, through the investigations along the above lines, to the three old established species, which have been interpreted in various ways by authors. In addition to them, I introduce five species, which are new or little known in Hokkaido and S. Sakhalin, although each of them are based on a small collection from this province. Furthermore, six species from the Campanian and Maastrichtian of Japan have been recently described by Matsumoto & Yoshida (1979), Matsumoto & Morozumi (1980), Matsumoto & Miyauchi (1984), Matsumoto (1984b), Matsumoto *et al.* (1985) and Matsumoto

& Toshimitsu (1995). They are not repeated in this paper, except for the indication in a list of species in the conclusion and short remarks on some of them in the discussion. Another Campanian species, *G. striatum* (Jimbo), is reserved for a restudy. At any rate, *Gaudryceras* includes fairly numerous species, which suggest diverse evolutionary lines. Yet, it is too early to propose a scheme of subgeneric classification.

Occurrence. – A concise summary by Wright & Kennedy (1984, p. 51) is quite adequate and cited here: "Upper Albian to Maastrichtian, typically Tethyan and Indo-Pacific in distribution but occurring rarely to both north and south."

Gaudryceras subcostatum sp. nov.

Figure 38

Material. – Holotype, UMUT. MM19693 [= GT. I-3268a] (Fig. 38A–C) and paratype, UMUT. MM19694 [I-3268b] (Fig. 38D, E), both collected by T.M. in 1938 from a nodule in the sandy siltstone of Member IIb, middle subgroup of the Yezo Group, at loc. T881b, Shibunnai, in the upper reaches of the River Abeshinai, which is a tributary of the River Teshio, Teshio Mountains, northern Hokkaido.

Diagnosis. – Shell small and evolute; whorl-section reniform to subrounded in septate stages and that of adult stage somewhat broader than high, with moderately arched venter and parallel flanks. Ornament consists of periodic constrictions with associated collars and fine but sharp crested lirae throughout growth, and additional subcostae (i.e. fine ribs) in the adult. These are all prorsiradiate on the flank and projected on the venter.

Description. – The shell is small, about 50 mm in diameter even at the adult stage. It is polygyral (8 whorls in this small size), and evolute, with a wide and shallow umbilicus. Whorls enlarge slowly, reniform to subrounded in section and more or less broader than high in the phragmocone. The adult body chamber occupies three quarters of the outer whorl and is flat-sided, subcircular in section and broader than high.

The early whorls have frequent flanges. Then, there are prorsiradiate, distinct collars with associated constrictions, three to four per whorl in the main part of the phragmocone, becoming more frequent on the body chamber. They are projected on the venter.

Fine lirae of two kinds are developed on the surface of the outer shell layer, running parallel to the collars. Very fine ones are perceptible by naked eye only with suitable lighting. They are on the interspaces of coarser but sharp-crested ones and also superposed on the latter as well as on the periodic collars. Where they are discernible, the liration looks very dense and also rhythmical on account of the combination of the two kinds. The internal mould of the main part of the phragmocone is smooth, except for periodic constrictions.

The body chamber has additionally weak riblets (i.e. subcostae), which are separated by the interspaces as narrow as or slightly narrower than the riblets. They are prorsiradiate on the flank, parallel to the more elevated periodic flares, and show a forward convex curve on the venter. Where the outer shell layer is preserved, fine lirae cover the riblets and the flares.

The suture is of *Gaudryceras* pattern and deeply and finely incised in the last part of the

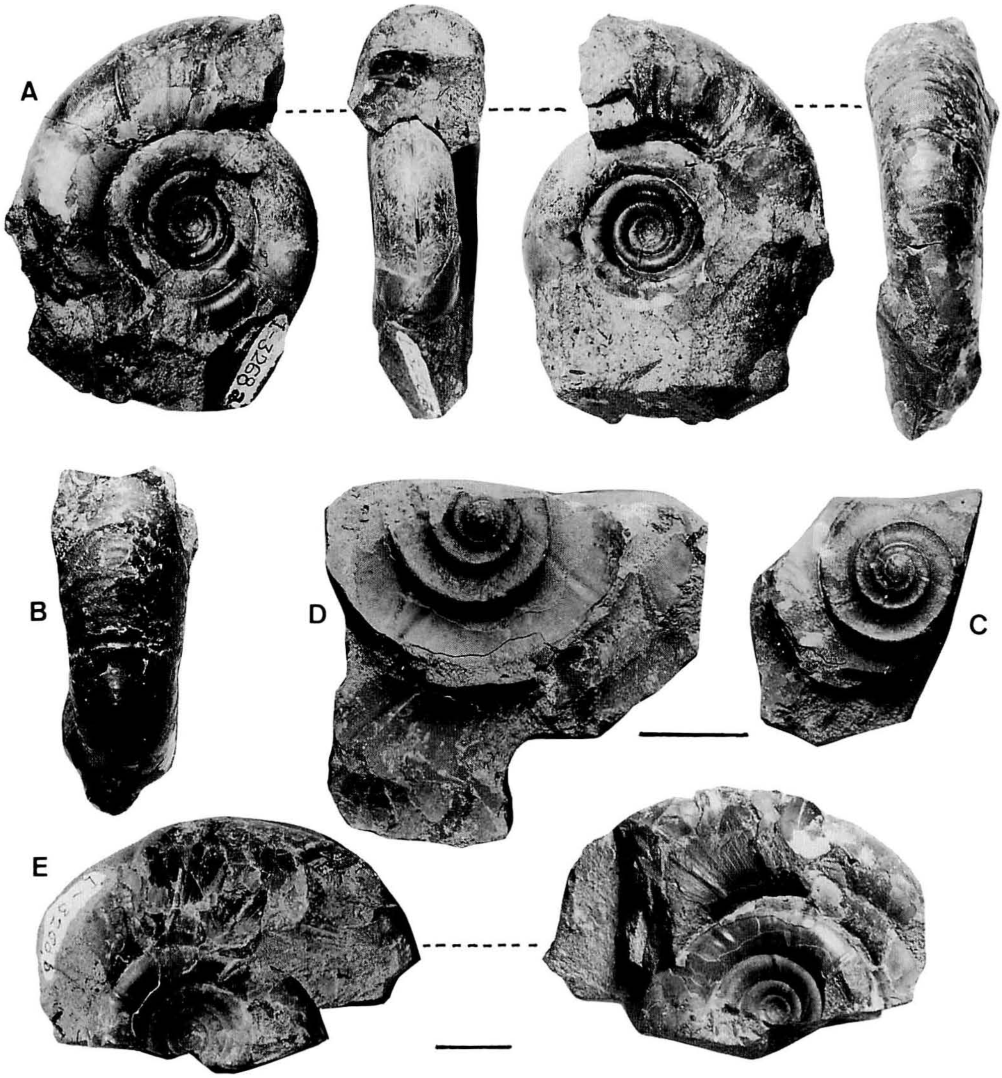


Figure 38. *Gaudryceras subcostatum* sp. nov.
A: UMUT. MM19693 [I-3268a], holotype; B: ditto, ventral view of the last quarter whorl; C: ditto, external mould of inner whorls. D: External mould of paratype (i.e., E); E: UMUT. MM19694, [I-3268b], paratype. A, B, E are natural size; C, D are enlarged (×1.5). Scale bar: 10 mm.

fairly small phragmocone.

Dimensions. – See Table 11.

Discussion. – This species was listed as *Gaudryceras subcostatum* by Matsumoto (1942, p. 194; 1943, p. 666), although it was *nom. nud.* Because of its peculiar characters, I have hesitated to decide its generic assignment. Now it is described as a species of *Gaudryceras* on account of its wide umbilicus, existence of sharp-crested lirae and development of fine

Table 11. Dimensions of *Gaudryceras subcostatum*.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H
HT.	50.0	23.0	.46	15.0	.34	17.0	.30	1.13
For comparsion: *G. multiplexum*.								
HT.	50.0	22.0	.44	15.0	.30	15.5	.33	1.03

ribs on the body chamber.

The lirae of this species are much weaker and less flexuous than those of such typical species of *Gaudryceras* as *G. mite* (Hauer) and *G. denseplicatum* (Jimbo), but they are more distinctly sharp-crested than those of *Anagaudryceras*. The evolute shell form of this species is similar to that of juveniles of various *Gaudryceras* species.

Ammonites sacya var. *multiplex* Stoliczka (1865, p. 155, pl. 76, fig. 1) is a small specimen with D = 50 mm, characterized by polygyral and evolute shell and a wide umbilicus. It is, thus, distinct from the young form of *A. sacya*. It has prorsiradiate, weak constrictions. *G. multiplexum* (Stoliczka) (*non* Kossmat, 1895) is, therefore, fairly similar to *G. subcostatum*, but is distinct in having a somewhat more compressed whorl with convergent flat flanks without such subcostae as in the latter.

GK. H8397 (Nishida *et al.*, 1993a, pl. 1, fig. 6), a small and secondarily much compressed specimen from a layer of sandy siltstone at loc. R739 of the Oku-futamata-zawa in the upper reaches of the River Kotanbetsu (coll. T.M.), southern part of the Teshio Mountains, may be referable to this species as *G.* cf. *G. subcostatum*, although it was erroneously indicated as *Mesogaudryceras* (?) sp. nov.

Mesogaudryceras leptonema (Sharpe) (see Wright & Kennedy, 1984, p. 51, pl. 2, fig. 3; text-figs. 3A–M) is rather involute and has compressed whorls from an early stage, showing a high egg-shaped section in the adult. Its lirae which develop from an early stage are very coarse and become finer and more flexuous in the adult.

Occurrence. – The bed that yielded the holotype and paratype belongs to Member IIb of the Abeshinai area, which is of mid-Cenomanian age, because *Calycoceras* (*Newboldiceras*) *orientale* and *C.* (*N.*) *spinosum* occur in the middle and upper parts and *Turrilites costatus* from the lower and middle parts of the same member.

G. cf. *subcostatum* mentioned above is of late Early Cenomanian age (see Nishida *et al.*, 1993a, text-fig. 1, p. 102).

Gaudryceras stefaninii Venzo

Figure 39

Lytoceras (*Gaudryceras*) *stefaninii* Venzo, 1936, p. 79(21), pl. 6(2), figs. 3, 4.
Gaudryceras stefaninii Venzo; Collignon, 1963, pl. 247, fig. 1057; Collignon, 1964, pl. 318, fig. 1352; Kennedy & Klinger, 1979, p. 130, pl. 1, figs. 2, 5, 8; pl. 2, fig. 1; Matsumoto, 1988a, p. 181, pl. 50, fig. 8.
Gaudryceras sp. aff. *G. varagurense* (Kossmat); Matsumoto & Kawano, 1975, pl. 1, fig. 3.

Types. – Venzo's syntypes in Pisa seem to have been destroyed during World-War II, but because of the uncertain situation Kennedy & Klinger (1979) refrained from designating a lectotype or making a neotype proposal. This procedure is followed here.

Material. – A small, probably juvenile specimen, GK. H5618 (Fig. 39A) collected and donated to GK by Tatsuo Muramoto; medium-sized specimen, GK. H8477 (Fig. 39B) collected and donated to GK by Tadashi Kawano; another medium-sized specimen with a broken body chamber, TTC 380331A (Fig. 39D), and another juvenile, TTC 380331B (Fig. 39C), in Takemi Takahashi's collection.

Description. – The shell characters change with growth. Two stages are distinguished in our material. The young shell less than 30 mm diameter and the shell of the later stage with diameter from 30 mm to 85 mm.

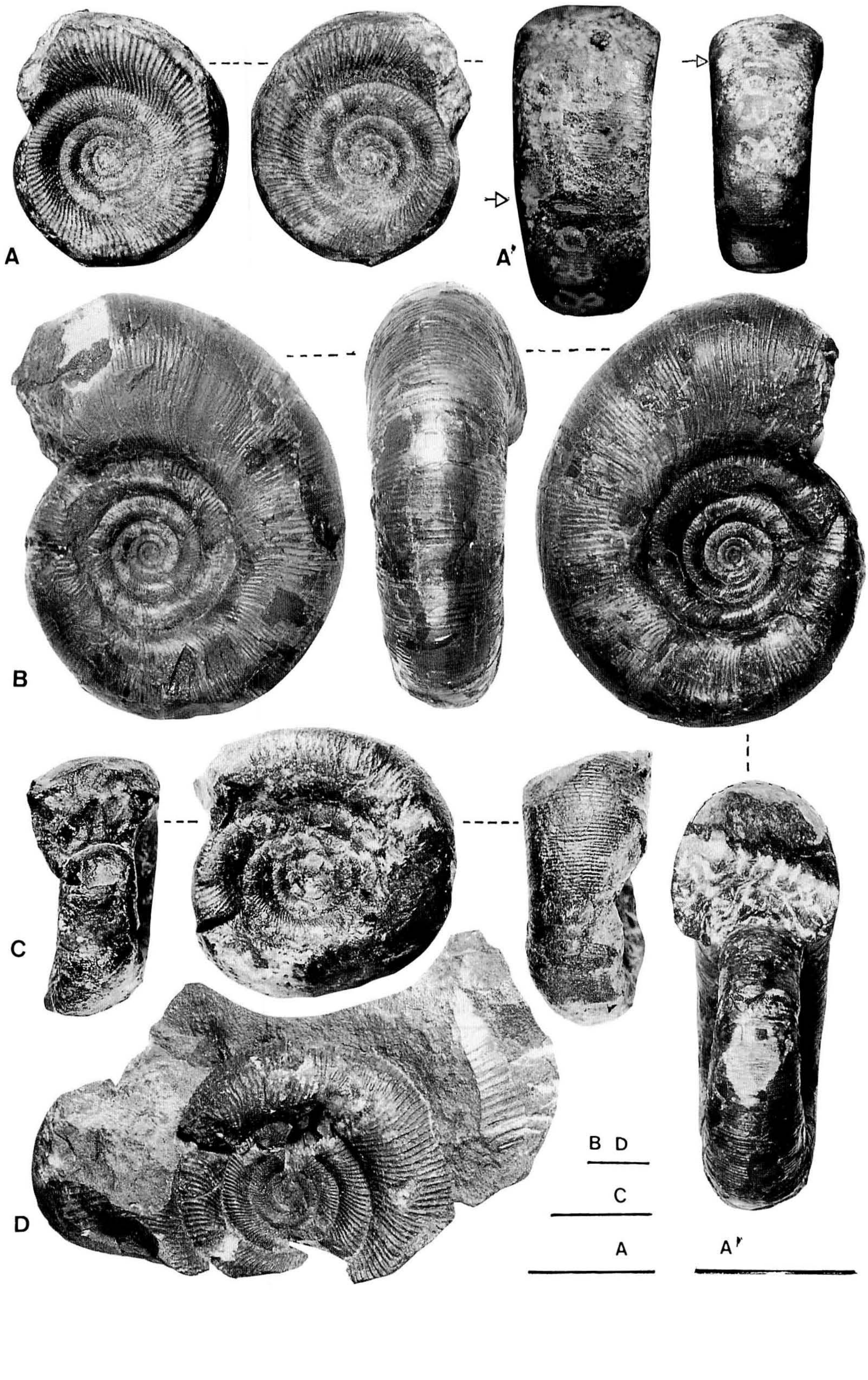
The young shell consists of several, slowly expanding, rather evolute and much depressed whorls. Its umbilicus is wide. In this stage the venter is broadly arched and flattened; the flank is gently convex and demarcated by more or less abrupt, ventrolateral and umbilical edges; the umbilical wall is steeply inclined. The lirae from the umbilical seam to the ventrolateral shoulder are dense and rather coarse for this small and young stage. They are somewhat prorsiradiate with a slight concavity on the umbilical wall, gradually bent at about the umbilical edge and run weakly forward on the flank. They are mostly single, but bifurcation or intercalation may occur. Constrictions with associated collars are infrequent and weak. In contrast to the rather coarse lirae on sides, the lirae are extremely fine and numerous on the venter of this young stage, showing branching and intercalation at the ventrolateral shoulder (see Fig. 39A, A', C). They run almost straight across the venter. The ornament of the very young stage less than 3 mm diameter is not clearly observable in the available material. The suture is gaudryceratid, with L at the ventrolateral shoulder, U2 immediately outside the umbilical edge and descending auxiliaries on the umbilical wall.

The shell of the late stage is represented by the two illustrated specimens, Fig. 39B (D = 68 mm at the preserved end) and Fig. 39D (D = about 85 mm at the end of destroyed outer whorl). They have body chamber, the last suture is presumably at about 55 mm diameter, although it is not clearly shown on account of unfavourable preservation. Whether these specimens are middle-aged or adult is hardly decided. Such a large example as illustrated by Kennedy & Klinger (1979, pl. 2) from South Africa does not exist in the available material from Hokkaido.

The whorl later than 30 mm diameter shows an increase of the expansion rate and a consequent decrease of the umbilical ratio U/D. In the septate part, the whorl is more or less broader than high and rounded in section. The early part of the better preserved body chamber (Fig. 39B) is slightly higher than broad and broadest between inner flanks, showing a thickly suboval section. Its venter is moderately arched, sloping gradually to the gently con-

Figure 39. *Gaudryceras stefaninii* Venzo. →

A: GK. H5618, a hypotype, juvenile. The left one (A') of the two ventral views is the later half and the right one the middle part of the outer whorl, ×2; A' ×2.5. B: GK. H8477, a hypotype, middle growth stage, nearly ×1. C: TTC 380331B, a hypotype, juvenile, ×1.6. D: TTC 380331A, a hypotype, middle growth stage, ×1. Scale bars: all 10 mm.


A
A'
B
C
D
B D
C
A
A'

vex flank, which in turn passes the rounded umbilical shoulder to the moderately high umbilical wall.

The surface of the shell in the late stage described above is ornamented by sharp-crested lirae that may have bluntly elevated bases on the intermediate shell layer. They may be bifurcated or intercalated around the umbilicus and also on the flank, but the extremely fine and dense lirae which characterize the young shell do not persist to this stage. The lirae run forward on the umbilical wall with a weakly concave sinus, swing back over the umbilical shoulder to the inner portion of the flank and then run nearly radially with a slightly forward inclination on the main part of the flank, passing across the venter almost straight or with a very gentle convexity. Shallow constrictions associated with weak flares occur infrequently.

Dimensions. – See Table 12.

Discussion. – The morphological characters of the young specimens described above conform closely to those of *Gaudryceras stefaninii* originally described by Venzo (1936) from South Africa, then by Collignon (1956, 1963, 1964) from Madagascar, and more recently by Kennedy & Klinger (1979) from South Africa, and also a small specimen from South Sakhalin (Matsumoto, 1988a).

Kennedy & Klinger (1979, p. 130, pl. 1, figs. 2, 5, 8; pl. 2) described the ontogenetic change of characters of three stages, early, middle-aged and late. The two medium-sized specimens from Hokkaido correspond approximately to the middle-aged stage, although they have body chambers in their preserved outer whorls which exceed 60 mm in diameter. As Kennedy & Klinger have noticed, the largest of their 8 specimens is about 120 mm in diameter but still septate, and bears traces of a further septate half whorls. When it was complete, it must have been very large and its outer whorl may have been more compressed, but its style of ornament is unknown. If the two specimens from Hokkaido were mature, variation in size could be considered. They are geologically younger than the South African specimens.

Kawano's specimen was once illustrated under *G.* aff. *varagurense* (Kossmat) (see Matsumoto & Kawano, 1975, pl. 1, fig. 3), but the typical form of *G. varagurense* is now regarded as conspecific with *G. mite* (Hauer) and has more flexuous lirae that show distinct ventral projection.

Table 12. Dimensions of *Gaudryceras stefaninii.*

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
GK. H5618	20.4	10.2	.50	5.2	.25	8.3	.41	1.60	1.27
IGPS 58085	15.0	7.4	.49	4.5	.30	6.8	.45	1.51	1.45
GK. H8477	68.0	28.0	.41	25.5	.37	25.0	.37	0.98	1.76
TTC 380331 A	46.0	23.0	.50	14.0	.30	18.0	.39	1.29	–
TTC 380331 B	26.2	13.2	.50	6.8	.26	10.0	.38	1.47	–
Syntype*	29.0	15.0	.51	9.0	.31	12.0	.41	1.33	–
SAS A834*	34.5	17.2	.50	9.5	.28	14.6	.42	1.53	–
SAS A1086*	*c.* 120.0	43.0	.36	52.8	.44	50.3	.41	0.95	–

*For comparison cited from Kennedy & Klinger, 1979, p. 133.

Occurrence. – The described specimens occur in the Zone of *Euomphaloceras septemseriatum*, which is currently referred to the middle Upper Cenomanian substage (Wright & Kennedy, 1984, p. 6; Kennedy & Cobban, 1991, fig. 15). An immature specimen is recorded from somewhere in the Upper Albian-Lower Cenomanian transitional part on the south bank of the River Naibuchi, South Sakhalin (Matsumoto, 1988a).

G. stefaninii has been reported to occur in the Lower and Middle Cenomanian of South Africa and Albian and Lower Cenomanian of Madagascar. On the basis of the occurrences reported here, its stratigraphic range goes up to the Upper Cenomanian and its geographic distribution extends to the northwestern Pacific region.

Gaudryceras sp. nov. (?)

Figures 40, 41

Material. – Two specimens of different size are concerned here. The larger one is MCM. A245 [YKC. 610605] (Figs. 40, 41A) collected by Yoshitaro Kawashita on a rivulet called the Satoh-no-sawa, a branch of the Kami-Kinenbetsu-zawa in the Obirashibe Valley from the *Fagesia*-bearing mudstone (Member Mj of Tanaka, 1963) in the middle subgroup of the Yezo Group. The smaller one is MCM. A248 [YKC.060718] (Fig. 41B) collected by Yoshitaro Kawashita from the mudstone exposed on the cliff of the Shuparo [Shuyubari] River at about 500 m upstream from the confluence with the Kita-no-sawa. The locality corresponds to Y230a or a part of Y229 (Matsumoto, 1942) and consequently the mudstone is Member IIm' or IIn, i.e. mainly Lower Turonian (possibly including the uppermost part of Cenomanian) in the middle subgroup of the Yezo Group.

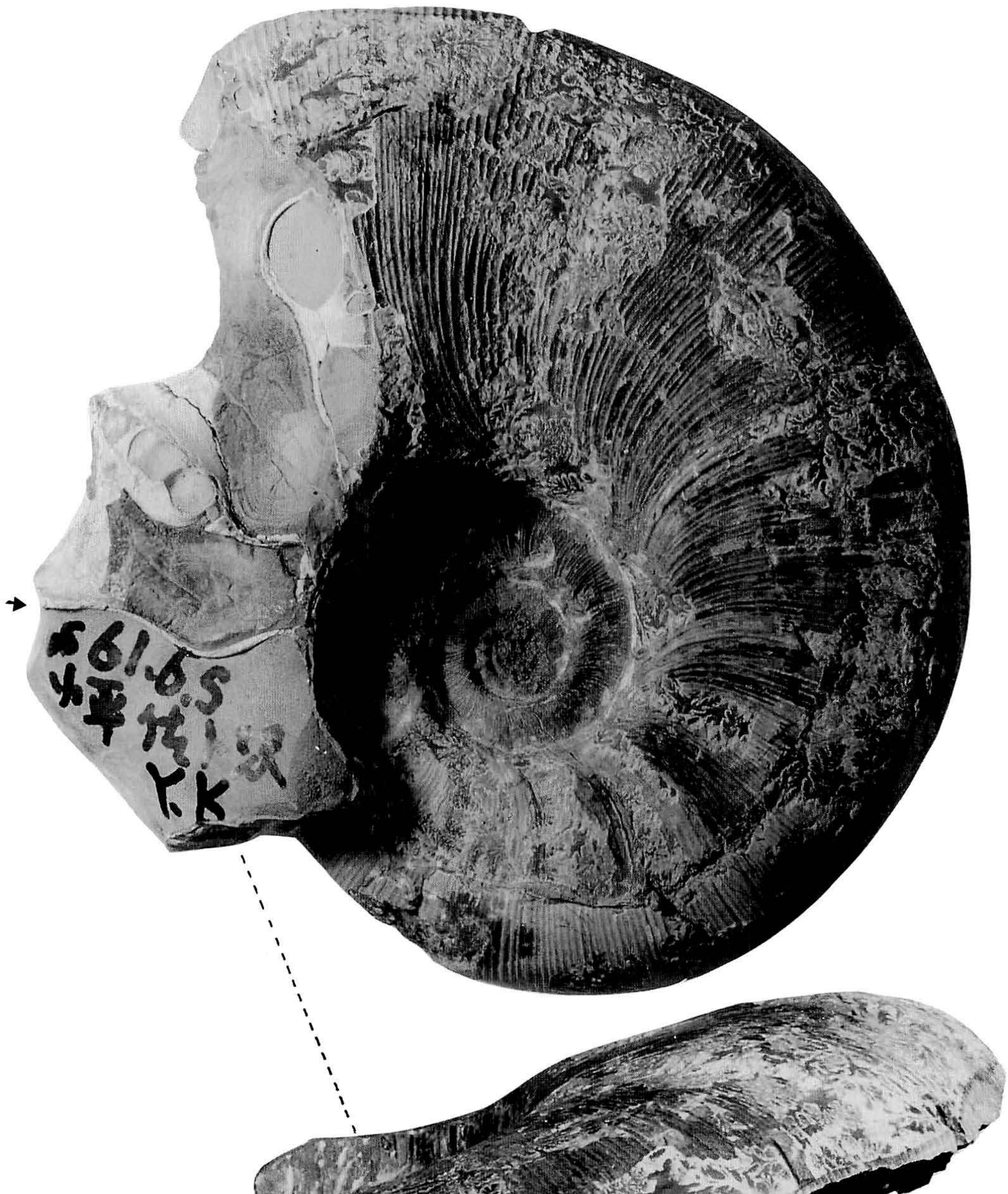
Description. – The shell of the larger specimen is fairly well-preserved up to 60° adapically from the last septum, although its last half is eroded on the left side. It is very large. Its diameter at the end of well preserved part is 200 mm. On the preserved last whorl, there is a trace of the umbilical seam impressed by the body chamber, which occupied about three quarters of the outer whorl. The umbilicus of the full-grown shell was about 145 m in width, the degree of involution was from 0.3 to 3/8 (=0.375) and the whorl-height increased greatly. Hence the entire shell must have been originally very large (*c.* 50 cm) for *Gaudryceras.*

The whorl of the main part of the phragmocone is much compressed and suboval in section, with a narrowly arched venter, gently convex to nearly flat flanks, abruptly bent umbilical shoulder and low but nearly vertical umbilical wall.

The surface of the shell is ornamented with numerous, fine but sharply raised lirae which show branching (mostly bifurcation) and intercalation at or near the umbilical shoulder and also on the flank. At rhythmic intervals bunched lirae tend to form narrow and slightly elevated major ribs around the umbilicus, but the ribs fade away outward. The lirae show a shallow, asymmetric sinus on the umbilical wall, run forward on crossing the umbilical shoulder, and then form a convex curve on the inner flank and are almost subradial on the main part of the flank. They show a slight forward curve on the ventrolateral part, passing across the venter at right angles with the siphonal line.

A similar ornamentation is shown on the observable part of the inner whorls.

The suture of the *Gaudryceras* pattern is very finely and deeply incised on the internal



mould of the last whorl of the phragmocone.

The second specimen is much smaller than the first and immature. In despite of its small size, the coiling is moderately involute (*c.* 50%) and the whorl expands with a high ratio. The preserved last whorl is subrounded, broader than high in its main part but in the last part it is nearly as high as broad, showing a rapid increase of whorl-height and a tendency towards gently convex flanks.

Besides the frequent flanges on very early part, the whorl is ornamented with numerous lirae, which are rather coarse for this small young shell. Around the umbilicus the lirae are coarse enough to be called subcostae. They become finer and denser on the outer part of the whorl owing to bifurcation and intercalation at about the umbilical edge and also on the flank. They are flexuous around the umbilicus, subradial on the main part of flank, and show a slight projection across the venter.

The periodic constrictions are very shallow and the associated collars are very weak.

On the preserved last portion of the outer whorl the lirae are abnormally rursiradiate especially on the left side. This is probably caused by injury and in fact there is a trace of injury immediately in front of the measured point (D = 28.8).

The sutures are observable through the semitransparent inner shell-layer as well as on the internal mould. They are similar to those of *G. tenuiliratum* (Fig. 1).

Dimensions. – See Table 13.

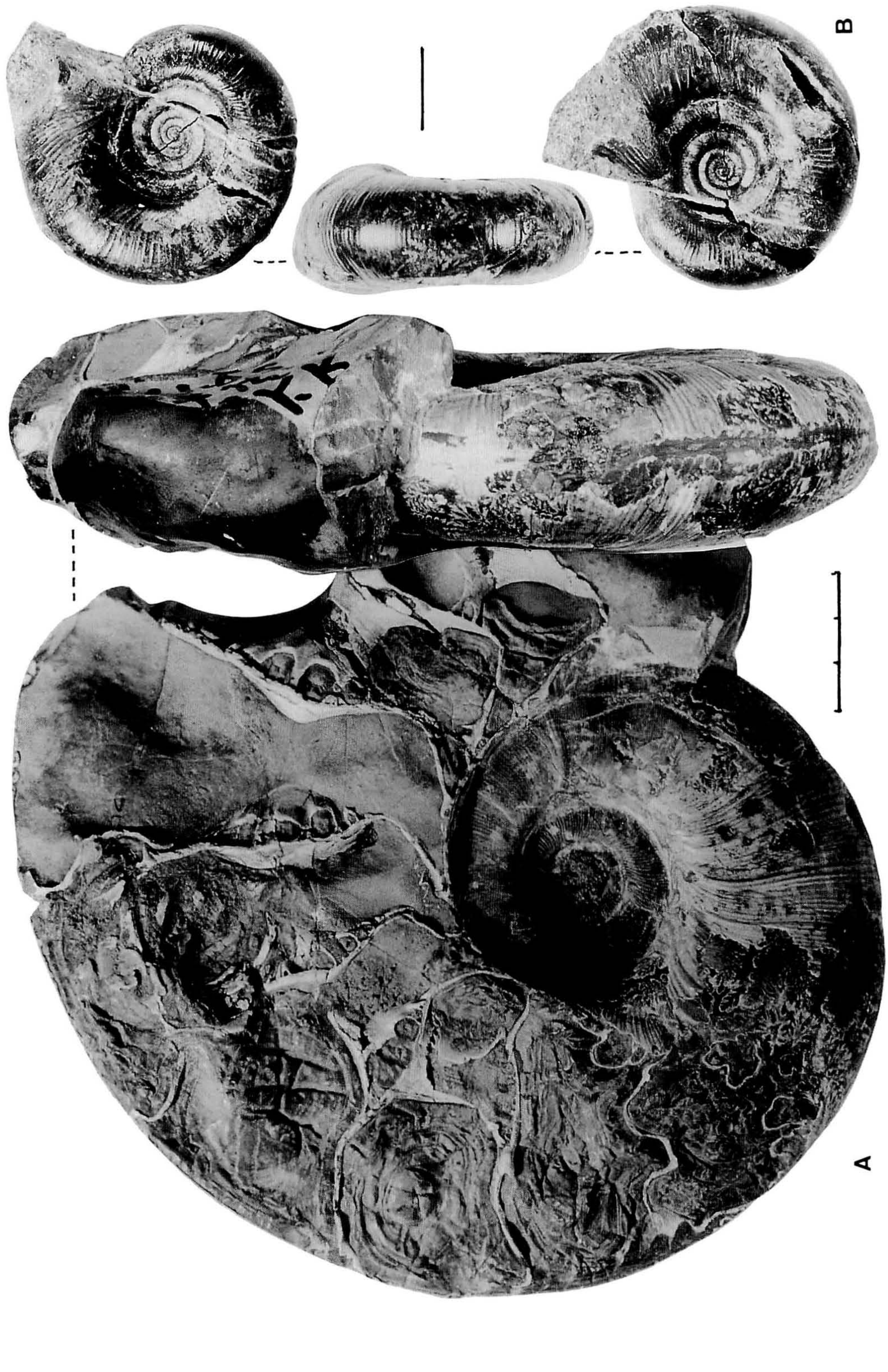
Discussion. – The smaller specimen resembles in lateral view the inner young whorls of the larger one. The former shows several features that can develop to the characteristic features of the latter. Moreover, the two specimens are not much different in geological age. Despite the great difference in size, I am, therefore, inclined to identify them as the same species. They represent probably a new species for their particular characters described above. I hesitate, however, to propose a new specific name until the above interpretation is confirmed by more specimens including an example of intermediate size.

G. stefaninii of Cenomanian age seems to attain a very large size at the adult stage (see Kennedy & Klinger, 1979), but the species described here shows a higher ratio of whorl expansion and its lirae in later growth stages are finer and bifurcated more frequently. The small, young shell from Shuyubari is less depressed and does not show extremely fine, *Vertebrites*-like lirae on the venter. Thus, the two species are not allied to each other, al-

Table 13. Dimensions of *Gaudryceras* sp. nov. (?)

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
MCM. A245 (last 3rd septum)	200.0	52.0	.26	98.0	.49	68.0	.34	.70	1.96
" (ditto – 180°)	–	34.0	–	50.0	–	36.5	–	.73	–
MCM. A248 (undeformed part)	28.8	11.6	.40	11.2	.39	11.0	.38	.99	1.87
" (ditto – 90°)	24.3	10.5	.43	8.3	.34	9.6	.39	1.16	1.51

← Figure 40. *Gaudryceras* sp. nov. (?)
MCM. A245 [YKC 510605], mainly phragmocone, with the beginning of the body chamber at the preserved end, ×0.7. Scale bar: 30 mm.


B
A

though they seem to occur successively in the stratigraphic sequence.

Occurrence. – As for Material. The true range and geographical distribution should be worked out further.

Gaudryceras mite (Hauer, 1866)

Figures 42, 43A

Ammonites mitis Hauer, 1866, p. 305, pl. 2, figs. 3–4; Redtenbacher, 1873, p. 119, pl. 27, fig. 4.
Gaudryceras mite (Hauer); de Grossouvre, 1894, p. 227, pl. 26, fig. 4; pl. 39; Kennedy & Summesberger, 1979, p. 74, pl. 1, fig. 1A–D; pl. 2, figs. 1A–C, 2A–B; text-fig. 1 (with full synonymy list).

Type. – The original specimen of von Hauer (1866, pl. 2, figs. 3–4), from the Gosau Beds of Strobl, Austria, is the holotype by monotypy. For its photographic illustration see Kennedy & Summesberger (1979, pl. 1, fig. 1A–D, which is not in natural size as indicated in the explanation but enlarged to nearly ×1.2). Its external suture was drawn by Redtenbacher (1873, pl. 27, fig. 4).

Material. – The following two specimens represent *G. mite* from Hokkaido.
(1) YKC 440715 (Fig. 42) is from a calcareous nodule derived probably from the Coniacian mudstone in the lower course of the Go-no-sawa (fifth branch) of the Kami-ichi-no-sawa, a tributary of the River Ikushumbetsu, collected by Y. Kawashita and now kept in the Mikasa City Museum, MCM. A247.
(2) GK. H8415 (Fig. 43A) is from the *Polyptychoceras*-bearing mudstone of the transitional part from Coniacian to Santonian exposed at the entrance of the Kikume-zawa, a tributary of the River Ikushumbetsu, collected and donated by Kenji Sanada to Kyushu University.

Description. – The first specimen is wholly septate at D = 135 mm. It probably represents a middle-aged shell. The second specimen shows characters of younger stages, but its last preserved part can be regarded as a passage to the middle growth-stage.

In young stages, with diameters less than 60 mm, the shell is comparatively polygyral, consisting of 7 whorls at D = 60 mm, with a low ratio of expansion and slight involution. Its umbilicus is fairly wide and shallow, with a rather low wall and abruptly rounded edge. The whorl section is at first depressed, becoming subcircular at D = 60 (±10) mm.

Later in the middle stage of growth, the whorl becomes moderately involute and grows with progressively higher expansion ratios. It is subcircular to oval in section, becoming somewhat higher than broad. The umbilicus is of moderate width and depth, having a steep to nearly vertical wall and a rounded edge. The flanks are gently convex, passing to a moderately arched venter.

For about one whorl after the first constriction there are frequent flares (i.e. what Murphy,

←Figure 41. *Gaudryceras* sp. nov. (?)
A: MCM. A245 [YKC 510605], two other views of the same specimen as Fig. 40, ×0.7. B: MCM. A248 [YKC 060718], juvenile; probably the same species as A, ×1.2. Scale bar: 30 mm for A; 10 mm for B.

1967b called flanges), at least 18, which run obliquely forward on inner flank in the nuclear part of the umbilicus. On the succeeding whorls that constitute the main part of the shell, the surface is ornamented densely with flexuous lirae, which are prorsiradiate on the umbilical wall, curved backward on the umbilical edge and inner flank to form a gently sigmoid subradial line on the main part of the flank and then curved forward at about the ventrolateral shoulder, passing across the venter with a weakly to moderately convex curve. The lirae may branch to or may be intercalated by shorter ones at various points between the umbilical seam and the outer flank. They are sharp headed and distinct on the surface of the outer shell layer, rather bluntly impressed on the next intermediate layer, but scarcely discernible on the inner shell layer. The internal mould is smooth.

Narrow and low major ribs or subcostae occur at rather irregular intervals and sometimes faintly. They may develop from bundles of a few raised lirae around the umbilicus and extend outward, as in the smaller specimen or may so much weaken on the outer flank that they are discernible merely as extensions of the bundled lirae, as in the outer whorl of the larger specimen. Whorls of younger stages have periodic constrictions, which are accompanied by the major ribs mentioned above. In such a case, the major rib can be called a collar.

The external suture is exposed on several parts of the two specimens. It shows a typical pattern of *Gaudryceras* and is very finely incised in later growth-stages.

Dimensions. – See Table 14.

Discussion. – As the holotype of *Amrnonites mitis* was so poorly preserved, nobody had dared to point out the synonymous relationship between *G. mite* (Hauer, 1866) and *G varagurense* (Kossmat, 1895) until the issue of the paper by Kennedy & Summesberger (1979). It is now difficult to deny their proposal of the synonymy. I should like rather to support them in connection with the Hokkaido specimens described above and the comparable ones from the regions outside Japan.

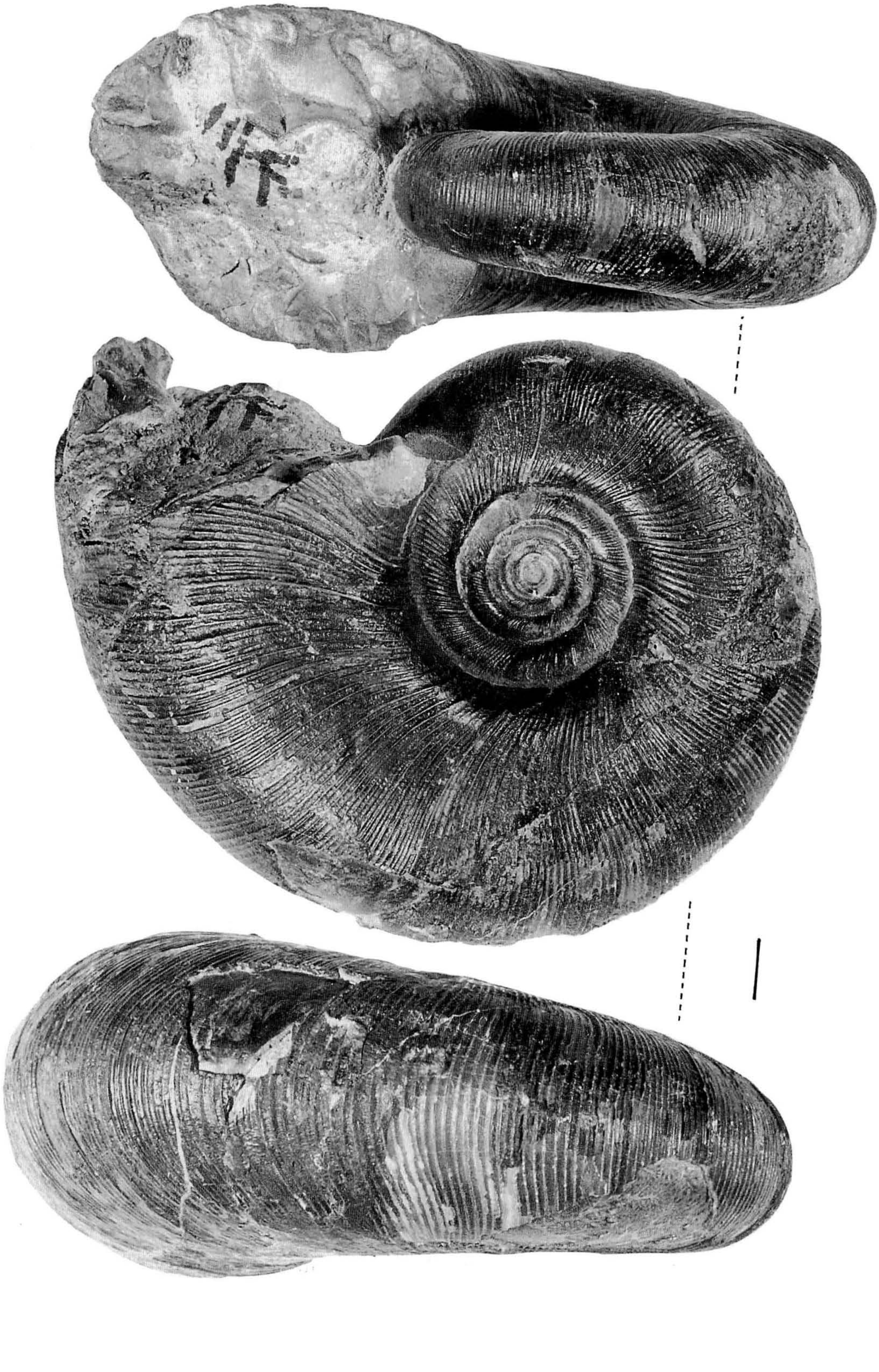
MCM. A247 is wholly septate and measured as 135 mm in diameter at its preserved end. Normally the body chamber of *Gaudryceras* species occupies at least two thirds of a volution and may reach as long as three quarters. If that specimen is assumed as a complete phragmocone and the lost body chamber is recovered, the entire shell must have been con-

Table 14. Dimensions of *Gaudryceras mite*.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
MCM. A247	125.0	36.0	.29	56.0	.45	52.0	.42	0.93	1.70
Ditto (–1/3 vol.)	90.0	30.7	.34	36.0	.40	34.3	.38	0.95	1.55
GK. H8415	68.0	28.0	.41	25.0	.37	26.0	.38	1.04	1.67
Gr. 1894, pl. 39*	187.0	47.0	.25	92.0	.49	73.0	.39	0.79	1.92
" *	125.0	37.0	.30	55.0	.44	52.0	.42	0.95	1.67

*Approximate dimensions measured on photographs. Gr. 1894 = Grossouvre, 1894.

Figure 42. *Gaudryceras mite* (Hauer). →
MCM. A247, phragmocone, approximately ×0.9. Scale bar: 10 mm.



siderably larger, being comparable in size with the large specimen of *G. mite* described from the Santonian of France by Grossouvre (1894, pl. 39). As he did not show measured dimensions and as I have not examined the actual specimen (now msising as Kennedy has written to me), the approximate dimensions are measured on the photographs and shown in Table 14. A remarkable similarity in the dimensions and proportins between the two specimens is noticed. Moreover, they are quite similar in the mode of ornamentation, which is characterized by dense and flexuous lirae often with branching and intercalation and also by less pronounced appearance of major ribs formed by the periodic bundles of somewhat coarser lirae elevated around the umbilicus but lowering outward.

The specimen of Grossouvre mentioned above is large and described as adult, but the position of the last suture was not indicated. Its body chamber does not seem complete and, strictly speaking, it is a presumption that the same kind of ornament as that described above would continue to the aperture.

Kossmat (1895) established *G. varagurense* on two fragmentary specimens. One of them illustrated with restored outline (*op. cit.*, pl. 18, figs. 2a, b), which was called the holotype by Howarth (1965, p. 362), should be the **lectotype**. The proportions of MCM. A247 at D = 90 mm (shown in Table 14) compare closely with those of the lectotype at D = 101 mm (shown in Table 15). The ornament in the successive whorls of the lectotype is essentially similar to that of the Hokkaido specimen.

Subsequent to Kossmat (1895) a considerable number of specimens have been described as *G. varagurense* (e.g. Basse, 1931; Collignon, 1931; 1956; 1965a, b; 1966; Howarth, 1965, 1966; Kennedy & Klinger, 1979) from Madagascar, South Africa, Angola etc. Their diagnostic characters are quite similar to those of the specimens from Hokkaido and also to those of *G. mite* from Austria and France. Their dimensions cited from the original papers or measured on photographs, are shown in Table 15 for comparison with those in Table 14. Generally a good conformity is recognized between the two tables, provided the change of ratios (U/D, B/H, etc.) with growth is properly considered.

The specimen described by Howarth (1966, p. 4, pl. 1, figs. 6, 7), from the mid-Tronian of Angola, is especially interesting in showing a considerable similarity to the larger Hokkaido

Table 15. Dimensions of *Gaudryceras varagurense*.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
Lectotype	101	35	.35	40	.40	38	.38	0.95	1.54
Howarth, 1966, 1–6, 7	85	32.3	.38	33.4	.39	29.5	.35	0.88	1.73
Ditto, (–1/4 vol.)	68	27.6	.41	23.7	.35	21.5	.32	0.91	1.42
Howarth, 1965, 4–5*	51	21.7	.42	17.6	.34	17.6	.34	1.0	1.50
Ditto, 5-1*	65	27	.42	22	.34	22	.34	1.0	1.4
Ditto, 5-2*	52	21	.40	18.3	.35	17.6	.34	0.96	1.44
Collig., 1965a, 1635	109	37	.34	46	.42	44	.40	0.96	1.77
Collig., 1965b, 1712	68	23	.34	27	.40	27	.40	1.0	1.5
Collig., 1966, 1852	36	15	.41	11	.31	11	.31	1.0	1.1
Ken. & Kl., 1979, 1-7	33.8*	15.6	.46	10.8	.32	11.6	.34	1.07	1.46

*measured on photographs; 31.8 in Kennedy & Klinger (1979) is probably a misprint of 33.8. 1-7 means pl. 1, fig. 7.

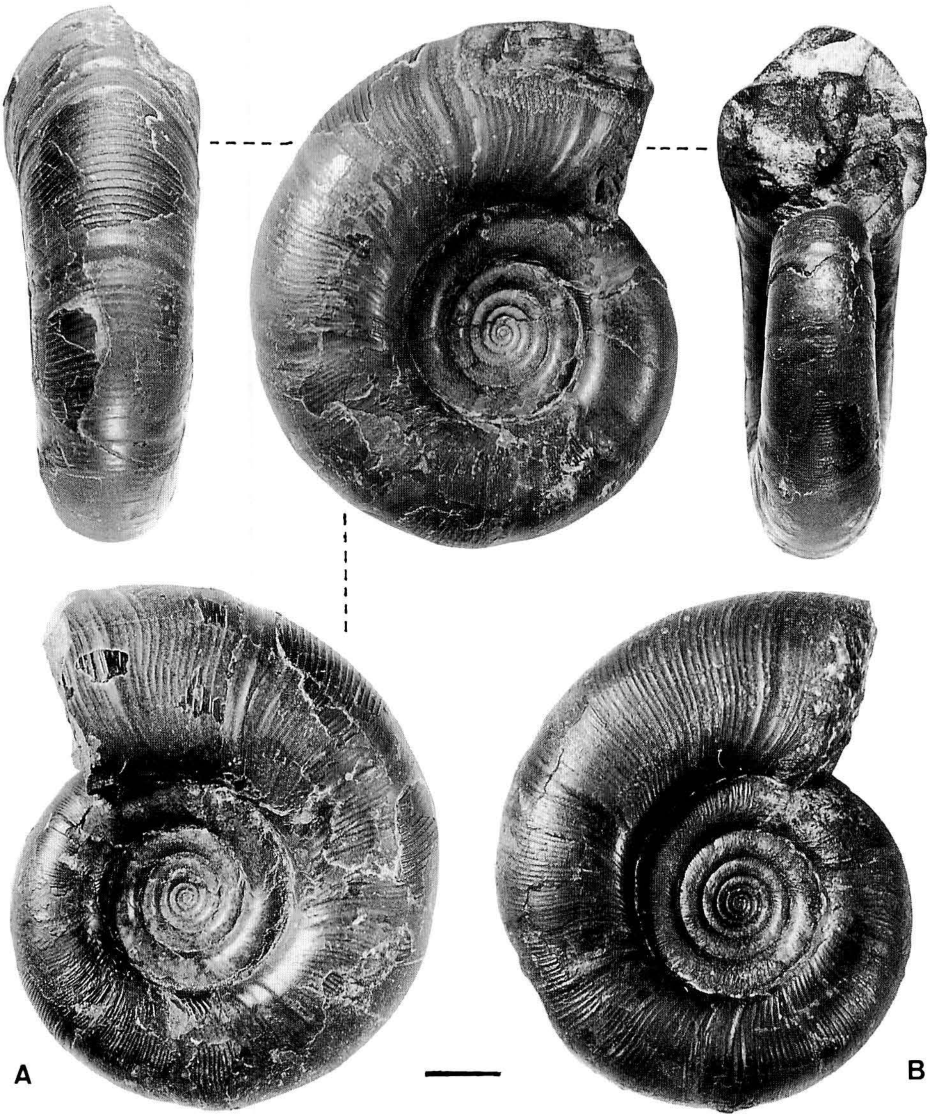


Figure 43. *Gaudryceras mite* (Hauer) and *G.* aff. *G. kayei (*Forbes*)*.
A: *G. mite*, GK. H8415, immature, ×1. B; *G.* aff. *G. kayei* (Forbes), showing affinity with *G. mite*. GK. H8414 (see Fig. 68B for other views), ×1. Scale bar: 10 mm.

specimen (MCM. A247) at a corresponding growth stage. It is still septate at D = 90 mm, has a trace of the umbilical seam of the outer whorl for about 5/6 of the last preserved volution. Its original shell must have been fairly large.

An example from the Turonian of Madagascar illustrated by Collignon (1965a, pl. 376, fig. 1635) under *G. varagurense* gives still closer resemblance to the Hokkaido specimen in dimensions and proportions as well as in ornamentation. Thus the two specimens mentioned above are essentially similar to the larger specimen of Grossouvre's *G. mite*.

The specimens from the Campanian of Angola described by Howarth (1965, p. 361, pl. 4, fig. 5; pl. 5, figs. 1, 2) are rather small and the small specimen from the Coniacian-Santonian transition of Hokkaido are quite similar to them in size and ornament. I agree with Howarth (1966, p. 5) in regarding the slight difference in the details of major ribs as a variation within the species.

There is a specimen, GK. H8414 (Fig. 43B), which resembles GK. H8415 (Fig. 43A) in lateral view. It has, however, a compressed outer whorl and a narrowly arched venter. It suggests a relationship of *G. mite* with *G. kayei* (Forbes). (See *G.* aff. *G. kayei* in p. 128.)

Summarizing the above comparison and discussion, I support Kennedy & Summesberger in regarding *G. varagurense* (Kossmat, 1895) as a junior synonym of *G. mite* (Hauer, 1866).

A question remains as to the difference in size. The specimen described as adult by Grossouvre (1894, pl. 39), the restored originals of Collignon's (1965a) and Howarth's (1966) specimens and that of Hokkaido specimen (MCM. A247) exemplify a large form with diameter of about 20 cm or more. The holotype of *G. mite* is highly deformed but its original size can be reckoned as the order of about 10 cm in diameter. According to Kennedy & Summesberger (1979), its outer whorl consists of a septate part and partly body chamber. In view of the change of ornament from the dense and fine lirae in earlier half to the less dense ones with fairly pronounced bundles of branching coarse lirae around the umbilicus in later half, it could represent an adult stage. Should this tentative interpretation be warranted, there might be dimorphs in this species; the larger form is macroconch and the smaller form microconch.

The smaller specimen from the Santonian of France described by Grossouvre (1894, p. 227, pl. 25, fig. 4) under *G. mite* is fairly similar to the holotype in size, shell-form and ornament. It was, however, regarded by Grossouvre as immature and, in fact, it is wholly septate (Kennedy in lit. Feb. 1994).

There is a specimen (NSM. PM-6039) labeled and listed as *Gaudryceras* cf. *mite* by Obata *et al.* (1973, table 1). It was obtained by H. Tsuda at loc. 1637F-1 (misprinted in the table as 1631) as a float specimen from the Turonian mudstone exposed in a stream called Penke-ushap-zawa of the Hidaka district, south-central Hokkaido. It is as large as and looks similar to MCM. A247, but the crushed later half of its outer whorl is not septate and, hence, in the size of the restored original shell, the two ammonites are dissimilar. On the body chamber of the Hidaka specimen narrow major ribs occur frequently, although some of them are suppressed secondarily. This may suggest an example of *Gaudryceras denseplicatum* with narrow major ribs appearing irregularly in the late part of the phragmocone, as exemplified by such specimens as GK. H1166A (Fig. 46), from Member IIs [Upper Turonian] of the Oyubari-Shiyubari area, and UMUT MM19703 [= I-3736] from loc. N319a3, Zone Mh2 [Middle Turonian] of the Naibuchi area, South Sakhalin.

G. mite of later growth stages looks indeed similar to certain examples of *G. denseplicatum* in the late septate stage. It shows the involute shell form with a high ratio of whorl expansion and the ornament with flexuous lirae, but *G. denseplicatum* has distinctly stronger and broader major ribs on the adult body chamber. Moreover, in early growth stages *G. mite* has a more evolute shell with a wider umbilicus.

The holotype of *G. beantalyense* Collignon (1956, p. 53, pl. 5, fig. 3), is wholly septate and probably middle-aged. It is very similar to examples of *G. mite* at the corresponding growth stage.

There are a number of smaller specimens (less than 10 cm in diameter) which were described as *G. varagurense* in previous papers, but many of them seem to be merely immature and it is difficult to regard them as microconchs. To sum up, further careful examination on adequate material is required to reach the final conclusion on the problem of dimorphism in *G. mite*.

Occurrence. – See Material. As *G. mite* includes *G. varagurense* as its synonym, its geographical distribution is world-wide and the geological range becomes very long from early Turonian to late Campanian.

Gaudryceras denseplicatum (Jimbo)

Figures 44–52, 53A, 67E, F

Lytoceras denseplicatum Jimbo, 1894, p. 182, pl. 23, fig. 1, 1a.
Gaudryceras denseplicatum (Jimbo); Yabe, 1903, p. 27 (pars.); Matsumoto, 1941, p. 20, fig. 2a; Matsumoto, 1943, p. 666; Matsumoto, 1959b, p. 142 (pars.); Verechagin, 1965, p. 49, pl. 52, figs. 1, 2; ?Szász & Lacatusu, 1974, p. 206, pl. 1, pl. 2, fig. 1; Kennedy & Klinger, 1979, p. 140, pl. 6, fig. 2; pl. 7, fig. 1; ?Szász & Ion, 1988, pl. 5, fig. 4.
Gaudryceras denseplicatum var. *kawadai* Matsumoto, 1943, p. 666 (*nom. nud.*).
Gaudryceras (*Epigaudryceras*) *denseplicatum* (Jimbo); Shimizu, 1935b, p. 194.
Neogaudryceras denseplicatum (Jimbo); Collignon, 1956, p. 60, pl. 9, fig. 1; Collignon, 1965b, p. 6, pl. 416–417, fig. 1719.
Gaudryceras denseplicatum var. *denseplicatum* (Jimbo); Hirano, 1978, p. 240, pl. 33, fig. 1; pl. 34, fig. 1.
Gaudryceras tenuiliratum var. *infrequens* Yabe, 1903, p. 28, pl. 4, fig. 3; Verechagin, 1965, p. 49, pl. 51, pl. 51, figs. 2–4.

Material. – In addition to the holotype, the following specimens among many others are selected as showing wholly or partly the diagnostic characters of *G. denseplicatum*:

MCM. A118-1 (MCM, 1988, Atlas, fig. 82) (Fig. 44) and MCM. A118-2 (Fig. 45) collected by Kanichi Fujiwara from the Coniacian part of the Yezo Group on the Hidarimata-zawa [= Samata-zawa], and the Yoshiyachi-zawa, respectively, tributaries in the upper reaches of the Ikushunbetsu River, Mikasa district. They represent nearly full-grown adult shells and are comparable with a large specimen from the Coniacian of Madagascar (Collignon, 1965b, pl. 46–47, fig. 1719).

MCM. A560825-1 collected by Y. Kawashita (YKC. 560517) from the Komaki-zawa (probably Coniacian-Upper Turonian part of the Yezo Group) of the Oyubari area. This specimen preserves the major part of the adult body chamber as well as the phragmocone, although it is not figured here.

GK H8453 (Hirano, 1978, pl. 34, fig. 1) (Fig. 48) collected by K. Tanabe and H. Hirano from the basal part of Member Mm-n in the middle part of the Turonian at loc. R2113 on the main course of the Obirashibe River. This specimen is comparable with and better preserved than the holotype but partly compressed secondarily. It is also comparable with another specimen illustrated by Collignon (1956, pl. 9, fig. 1, 1a). GT. I-3849 [UMUT. MM19787] (Fig. 53A) collected by T.M. from loc. N332b, Zone Mh6 of the Naibuchi area. It is distorted, but similar to GK. H8453.

UMUT. MM19786 [= GT. I-471] (Hirano, 1978, pl. 33, fig. 1a, b) (Fig. 52) collected by M. Kawada from the Miho Group (precise horizon unrecorded, but indicated as Mh3 by

Figure 44. *Gaudryceras denseplicatum* (Jimbo).
MCM. A118-1, a fairly large adult specimen, showing typical ornament of this species, approximately ×0.7. Scale bar: 20 mm. Photo by courtesy of K. Muramoto.

Figure 45. *Gaudryceras denseplicatum* (Jimbo).
MCM. A118-2, one of the largest examples of this species, ×0.58. Scale bar: 20 mm. Photo by courtesy of K. Muramoto.

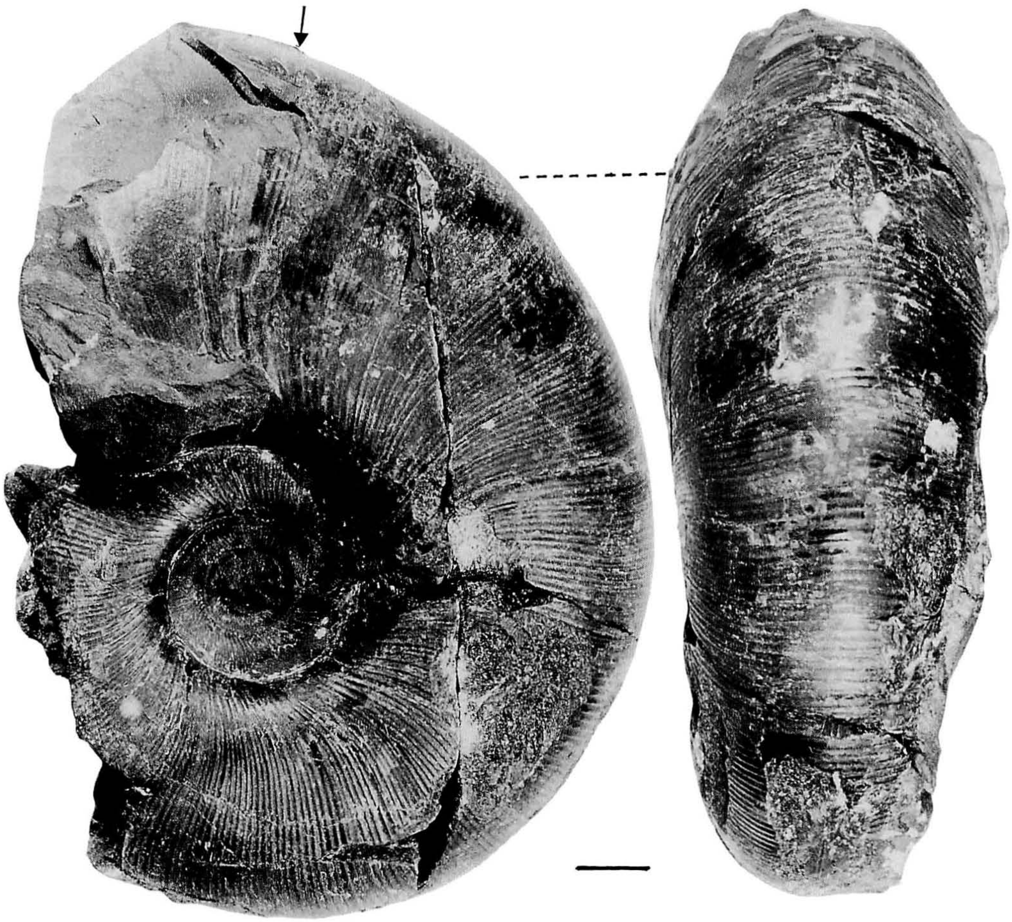


Figure 46. *Gaudryceras denseplicatum* (Jimbo).
GK. H1166A, phragmocone of a fairly large individual, whose body chamber was taken away, ×1. Scale bar: 10 mm.

Hirano) in the Miho River of the Naibuchi [Naiba] area; UMUT. MM19780 [= GT. I-468] (Fig. 49A) collected by M. Kawada from the Miho Group (precise horizon unrecorded) of the Naibuchi area. GK. H3131 (Fig. 50E) collected by T.M. at loc. U505, Horizon Ur1β of the Urakawa area.

GK. H1166A (Fig. 46) obtained by T.M. from Member IIs (upper Turonian) of the Saku Formation at loc. Y132 of the Shuparo River, Oyubari area; MCM. A249 (Fig. 47) collected by K. Kato from the Turonian of the Isojiro-zawa, Oyubari area; GK. H8452A and B (Fig. 67F, E) collected by T.M. from the Saku Formation (middle Turonian) at loc. T1022p7 in the Saku-gakko-no-sawa of the Abeshinai-Saku area; GK. H2171 (Fig. 50B) obtained by T.M. from Zone Mh6β of the Naibuchi area; GT. I-4020 [UMUT. MM19783] from the Obira area (H. Yabe coll.) (Fig. 50C); all of these are examples, among many others, of middle and young growth-stages.

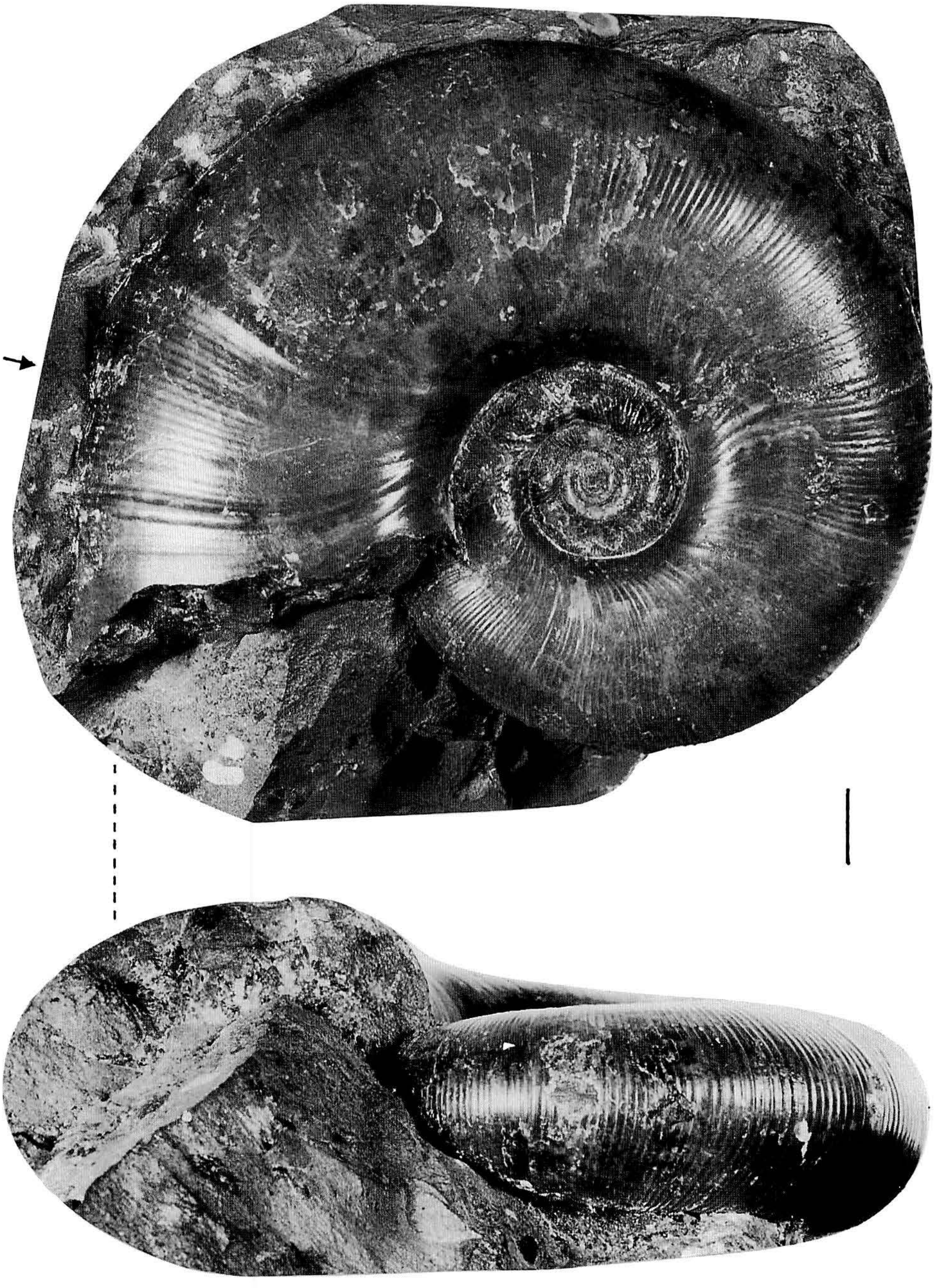


Figure 47. *Gaudryceras denseplicatum* (Jimbo).
MCM. A249 [Kikue Kato's 560831], phragmocone of a large adult individual. The umbilical seam of the lost body chamber is tracable for about three quarters of a whorl, ×1. Scale bar: 10 mm.

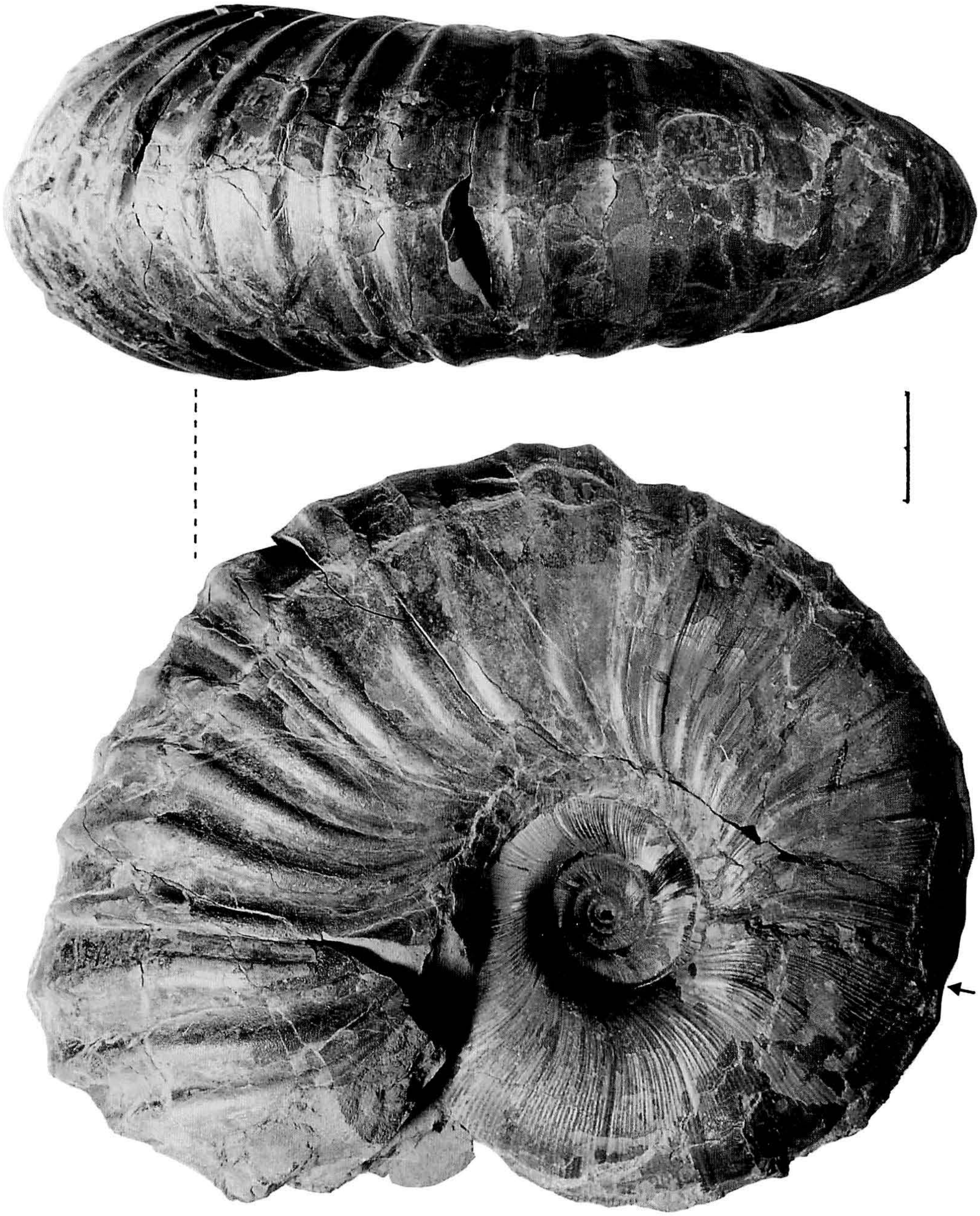


Figure 48. *Gaudryceras denseplicatum* (Jimbo).
GK. H8453, an adult example of a moderate size for this species, ×0.75. Scale bar: 20 mm.

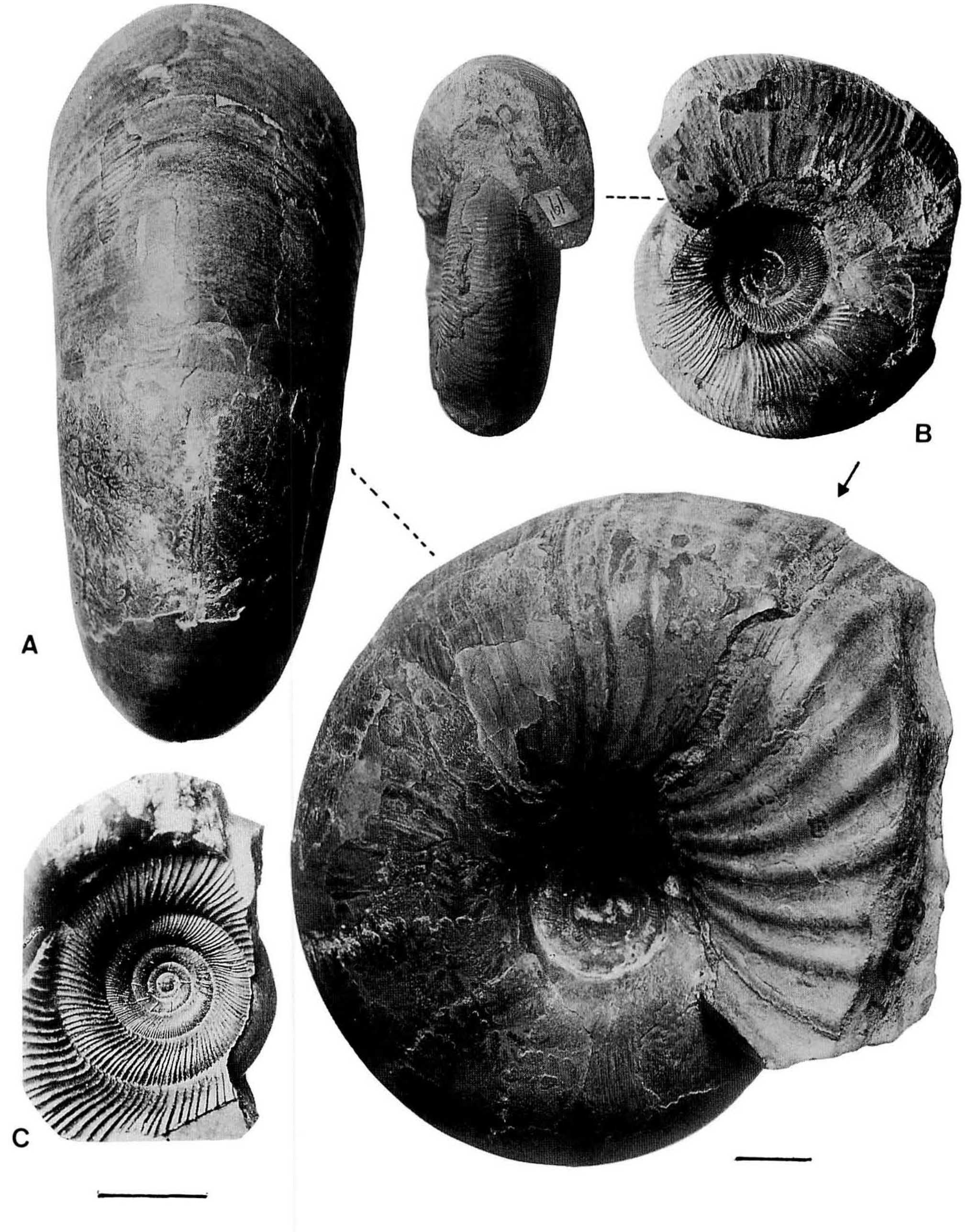


Figure 49. *Gaudryceras denseplicatum* (Jimbo).
A: UMUT. MM19780 [GT. I-468], a narrowly umbilicate example, which was temporarily called var. *kawadai* (*nom. nud.*); its outer shell-layer is not preserved for the most part, ×1. B: UMUT. MM7470 [GT. I-187], an early middle-aged example of *G. denseplicatum*, ×1. This was named *G. tenuiliratum* var. *infrequens* Yabe. C: UMUT. MM19781 [GT. I-3744b], inner whorls of a young specimen, ×3. Scale bar: 10 mm for A and B; 5 mm for C.

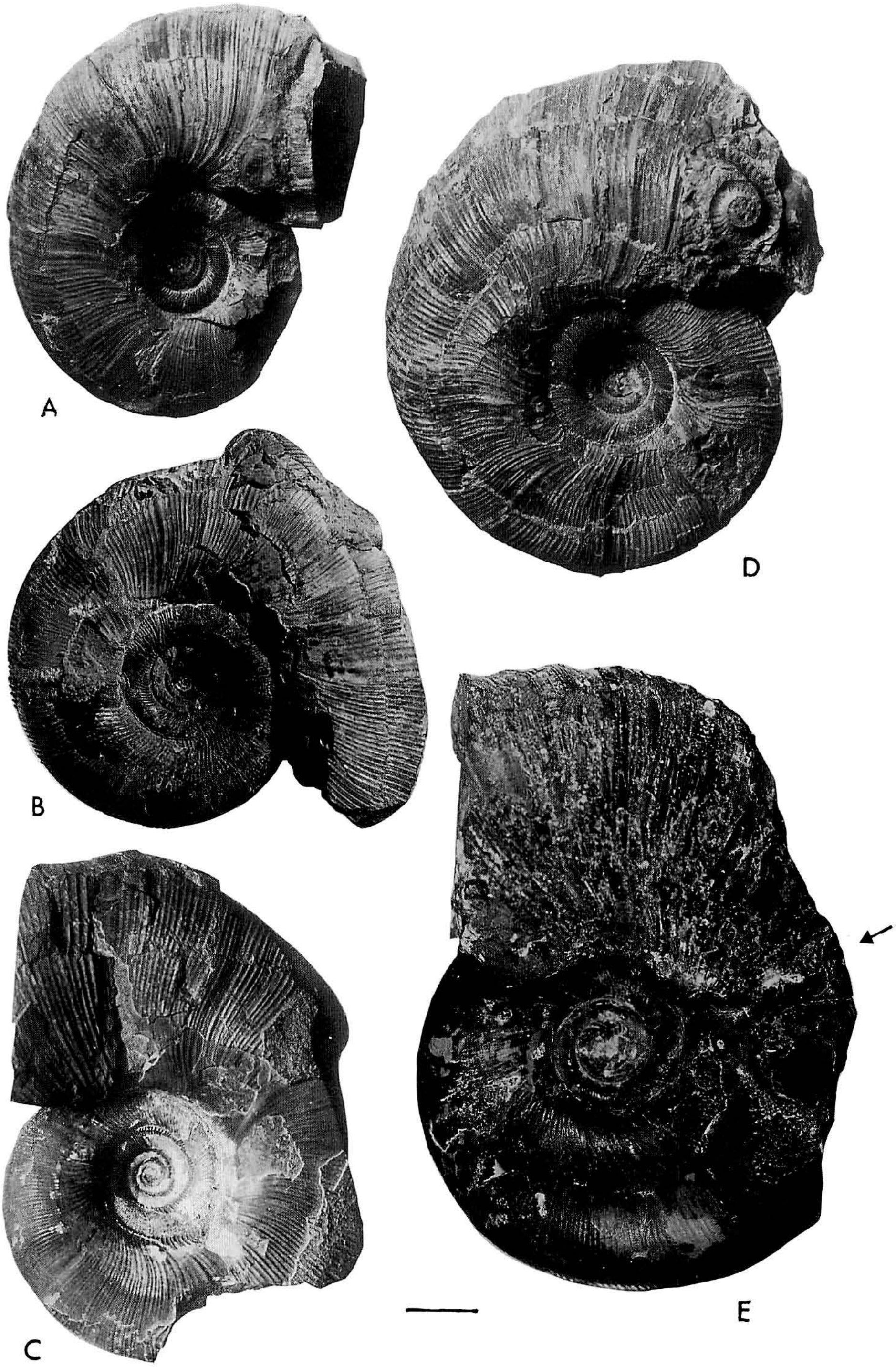


Figure 50. *Gaudryceras denseplicatum* (Jimbo).
A: UMUT. MM19782 [GT. I-3742]. B: GK. H2171. C: UMUT. MM19783 [GT. I-4020]. D: UMUT. MM19784 [GT. I-3768]. E: GK. H3131. All ×1. Scale bar: 10 mm. This figure is referred to the discussion in p. 103.

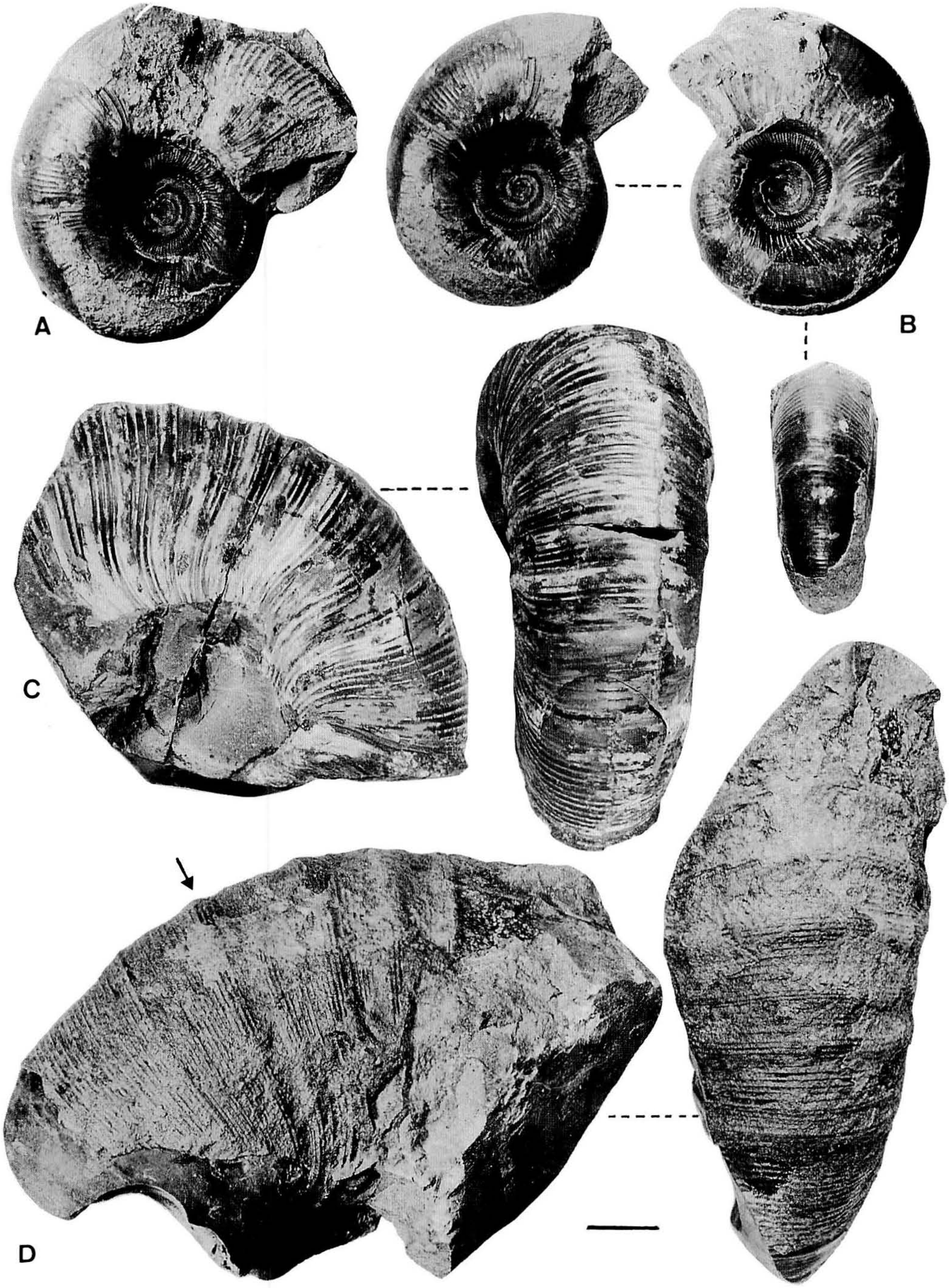
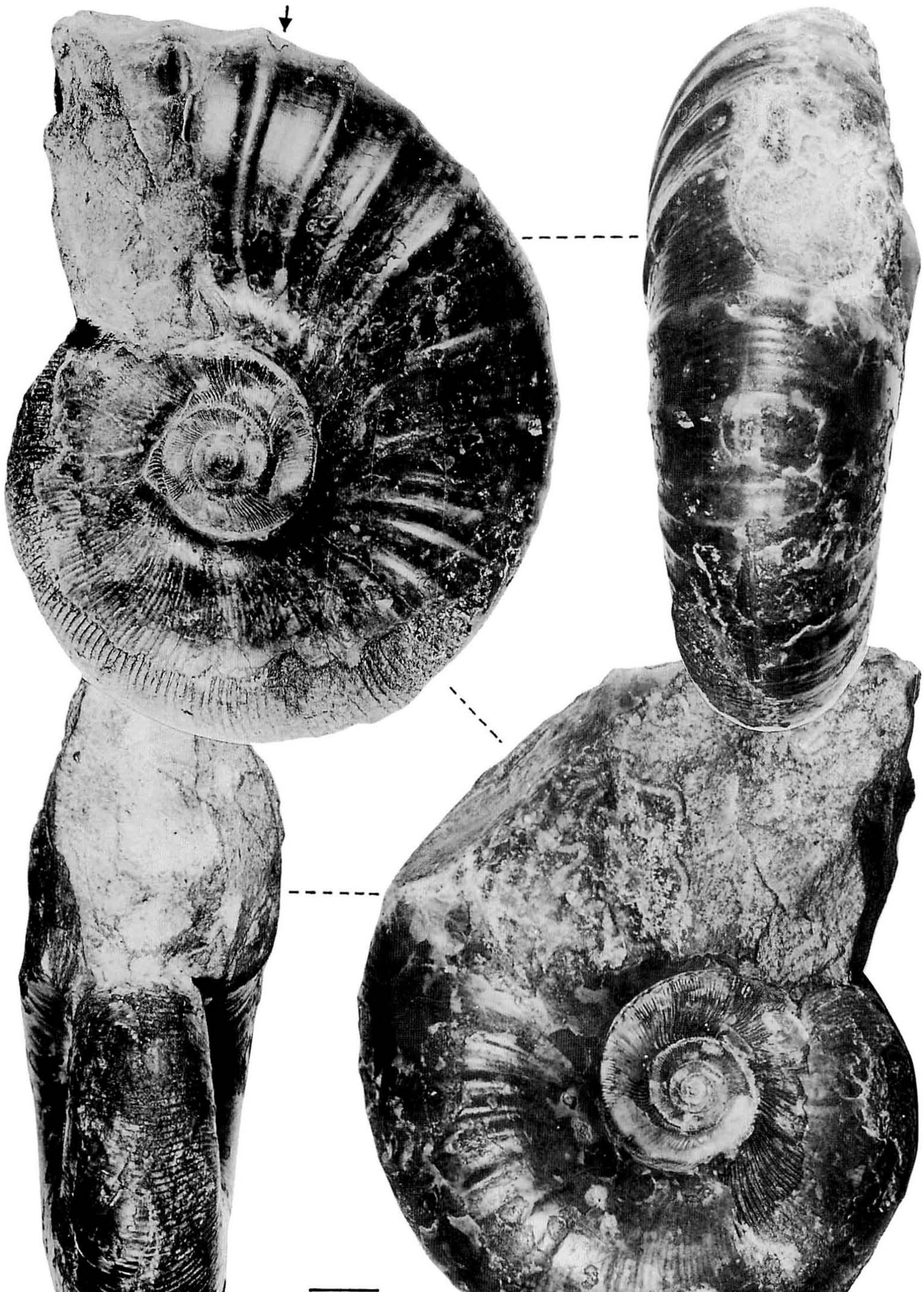


Figure 51. *Gaudryceras denseplicatum* (Jimbo).
A; B: UMUT. MM19785 [GT. I-3746], immature example, of which A includes the distorted portion of the body chamber. C: GK. H8460. D: GK. H8453. All ×1. Scale bar: 10 mm. This figure is also referred to the discussion in p. 103.



Description. – The adult shell is fairly large. The known largest example from Hokkaido is MCM. A118-2 (Fig. 45), with D = 280 mm at the peristome, and the next is MCM. A118-1 (Fig. 44), whose diameter is 110 mm at the last septum, 215 mm at the preserved end, (i.e. LS + 240°), and nearly 240 mm at the restored end of the body chamber. Its preserved part of the body chamber occupies two thirds of the outer whorl but the trace of the umbilical seam indicates that the entire body chamber is about three quarters (270°) of the outer whorl.

The young shells, as exemplified by GK. H8452B (Fig. 66E) GT. I-3744 a–f (Fig. 49C for I-3744b [UMUT MM19781]) and GK. H1166B with D less than 35 mm, are moderate in the degree of involution, rate of whorl expansion and umbilical ratio (U/D).

In the middle-aged and adult shells the coiling is fairly involute and the whorl expands with a high ratio. The umbilicus is consequently fairly narrow, showing the range of umbilical ratio (U/D) from 30 to 22 percent in measured examples.

The whorl section is broadly reniform in youth and becomes gradually subcircular later. In the shells of late growth stages, including the adult body chamber, the whorl height is slightly or somewhat greater than the whorl breadth, showing the range of B/H from 0.98 to 0.80 in the measured specimens, with general decrease with growth and also some variation between individuals. The whorl is broadest between inner flanks. The venter is well rounded, passing to the gently convex flanks. The umbilical shoulder is also well rounded and passes gradually (sometimes rather abruptly) to steep wall. In the adult shell the umbilical wall is fairly high.

Diagnostic features are shown in the ornament. The multiple branching into very fine and dense ventral lirae at the ventrolateral shoulder like that observable in young whorls of *G. tenuiliratum* never occur in *G. denseplicatum* (see Fig. 67). Apart from the earliest whorl with frequent flanges, the external surface of the test is ornamented with numerous lirae of moderate intensity, which are flexuous throughout all growth substages of the phragmocone, with a shallow sinus on the umbilical wall, prorsiradiate and gently convex on the inner flank, nearly rectiradiate on the middle of flank, passing gradually to another forward curve on the ventrolateral part and continue to a gentle or moderate projection on the venter. The flexuosity on the inner flank is more pronounced than that of the outer part. The lirae are less numerous and somewhat coarser around the umbilicus and become finer outward by bifurcation and intercalation at various points between the umbilial seam and the mid-flank.

The periodic constrictions with associated collars occur rather infrequently in the immature shell. In addition, narrow major ribs without constrictions but covered with a few lirae may occur on the phragmocone. They may be rare or weak or limited to a portion of the shell. The development of the major ribs is, thus, incomplete and irregular on the phragmocone.

The ornament of the adult body chamber is more constant and characteristic. It consists of the major fold ribs and distinct lirae in combination. The major ribs are at first narrow and separated regularly by the interspaces, which are wider than the ribs on the outer flank, but nearly as narrow as the ribs around the umbilicus. They may appear on the last part of the phragmocone, but sooner or later they are strengthened and on the main part of the body chamber the major ribs are moderately thick (i.e. wide and elevated). They are rounded on

←Figure 52. *Gaudryceras denseplicatum* (Jimbo).
UMUT. MM19786 [GT. I-471], with major ribs developing in the last part (1/3 whorl) of phragmocone, ×1. Scale bar: 10 mm.

top and occur at regular intervals; the interspaces are concave and nearly as wide as or somewhat wider than the ribs on the outer flank and also on the venter. Thus, the typical fold ribs characterize the main part of the adult body chamber.

The major ribs and interspaces are superimposed by the lirae, normally several lirae for each of them. If the test was subject to abrasion or taken off, the lirae remain as faint traces or the smooth internal mould is exposed. The fold ribs and lirae are generally parallel. In the early part of the body chamber, they are as flexuous as the lirae on the phragmocone, but on the rest main part of the adult body chamber their flexuosity weakens gradually and especially their ventrolateral to ventral projection is much reduced. (This seems, in my view, to suggest the decrease of active swimming and longer time of bottom stay with occasional up and down locomotion in the late adult substage in the life history of this species.) In the preserved last portion (but at some distance from the true peristome) of the body chamber the major ribs are lowered and the lirae tend to be finer and denser. This may suggest the coming of old age.

The suture is of the same pattern as that of *G. tenuiliratum* and looks much intricate in the late growth stage.

Dimensions. – See Table 16.

Discussion. – Kennedy & Summesberger (1979, p. 77) concluded that *Lytoceras denseplicatum* Jimbo, 1894 is a synonym of *Ammonites glaneggensis* Redtenbacher, 1873. This is based on their comparison of the holotypes, which are more or less incompletely preserved. This could remain as a possible interpretation. I hesitate, however, to follow that

Table 16. Dimensions of *Gaudryceras denseplicatum.*

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
HT (LS+210°)	159	38	.24	67	.42	57	.36	.85	–
MCM. A118-1 (E)	220	50	.23	104	.47	–	–	–	–
" (LS+180°)	195	45	.23	95	.49	89	.46	.94	1.73
MCM. A118-2 (E)	280	65	.23	140	.50	132	.49	.94	1.87
MCM. A560825 (LS+180°)	175	48	.25	79	.45	65	.37	.82	1.65
GK. H8453 (E)	177	44	.25	82	.46	65	.37	.79	1.61
" (E-90°)	140	36	.26	64	.46	53	.38	.83	1.60
MCM. A249 (E = LS)	121	32	.26	55	.45	52	.43	.94	1.62
GK. H1166A (E)	114	30	.26	54.5	.48	48.5	.42	.89	1.84
GT. I-468 (LS)	98	21.5	.22	48	.49	45	.46	.94	1.75
GT. I-471 (LS-80°)	86	23	.27	39	.45	36	.42	.92	1.63
GK. H8452A	63	18	.29	28	.44	28	.44	1.00	1.65
GT. I-187 (E)	54.0	16.3	.30	23.5	.44	25.0	.46	1.11	1.62
GK. H8452B	33.8	11.6	.34	13.3	.39	13.6	.40	1.02	1.43
GK. H1166C	20.0	7.6	.38	7.4	.37	8.1	.41	1.09	1.48
Coll. '65 (E)	221	58	.26	98	.44	78	.35	.80	–
Coll. '56 (LS+90°)	150	38	.25	73	.49	65	.44	.89	1.82
" (LS)*	123	36	.29	56	.46	55	.45	.98	1.81
K. & K. '79 (E)*	140	38	.27	66	.47	58	.41	.88	1.83

Coll. '65; '56: cited from Collignon, 1965b; 1956. K. & K. '79: SAS P7/1 of Kennedy & Klinger, 1979. *: measured on photos.

conclusion at this moment.

The holotype of *G. denseplicatum* is partly destroyed, but on its left side the last second suture is exposed and the last septum is located at H = 45 mm. The major part of the body chamber is preserved, showing the characteristic ornament as described above. The abnormally rursiradiate courses of the rib and a few lirae in the middle part of the body chamber are evidently a secondary features caused by an injury on the venter. On the unillustrated left side of the late septate whorl, fairly dense and somewhat flexuous lirae are shown and a single narrow major rib is recognized at some distance back from the last septum.

Based on the holotype and subsequently collected numerous specimens from Japan and Sakhalin, *G. denseplicatum* is now recognized as a distinct species. The specimens from Madagascar and South Africa as described by Collignon (1956, 1965b) and Kennedy & Klinger (1979) are referable to *G. denseplicatum* without hesitation. On the other hand, there is too little collection from the Gosau Beds to give a clear specific diagnosis of *G. glaneggense*.

G. denseplicatum is closely allied to but can be distinguished from *G. mite* (Hauer), as I have written in the foregoing pages. Its relationship with *G. intermedium* will be discussed under that species.

The distinction of *G. denseplicatum* from *G. tenuiliratum* is discussed in the description of the latter species. My former view (e.g. Matsumoto, 1941) of the intimate relationship between the two species was incorrect.

G. denseplicatum var. *nonstriata* Yehara (1924, p. 35, pl. 2, fig. 1) from the Uwajima district of Shikoku, is most probably an example of *Anagaudryceras limatum* (Yabe).

UMUT. MM7470 [= GT. I-187], described and illustrated by Yabe (1903, p. 28, pl. 4, fig. 3a, b) (Fig. 49B), from the "*Scaphites*-beds of the Opiraushibets" (somewhere in the Turonian-Coniacian sequence of the Obira area), was named *G. tenuiliratum* var. *infrequens* Yabe. This is designated here as the **lectotype** of the named taxon. It is, however, interpreted as an early middle-aged shell of *G. denseplicatum*.. The dimensions of that taxon listed by Yabe may be probably on another syntype which is missing in the UMUT.

UMUT. MM19780 [= GT. I-468] (Fig. 49A) collected by M. Kawada from the Miho Group (horizon uncertain) of the Naibuchi area, was listed by Matsumoto (1943, p. 666) as *G. denseplicatum* var. *kawadai* Matsumoto MS., *nomen nudum* because of no description or indication. It is here regarded as a more involute and narrowly umbilicate form within the variation of *G. denseplicatum*. It consists of the undeformed phragmocone and a fraction of the adult body chamber, but the outer shell layer is taken out for a considerable part.

Lastly with respect to the size of the shell, there is a questionable small form. There are, of course, fossils of small immature shells, as exemplified by GT. I-187 (Fig. 49B), GT. I-3746 (Fig. 51A–B), GK. H2171 (Fig. 50B), GT. I-4020 (Fig. 50C), etc. in which the *ornament of the adult type* does not appear on the body chamber. For the above terminology written in italic, I mean the frequent development of the major ribs of appreciable breadth with superposed lirae. The ornament is similar to, if not quite identical with, that of the undoubted adult body chamber in the typical or normal form.

Selected small specimens, which exemplify the appearance of such ornament on the early part of the body chamber and sometimes also on the last part of the phragmocone, are as follows:

GT. I-3742 [UMUT. MM19782] (Fig. 50A) from Zone Mh2 at loc. N320b;

GT. I-3768 [UMUT. Mm19784] (Fig. 50D) from Zone Mh1 at loc. N315d, both in the

Naibuchi area;

GK. H8452A (Fig. 67F) and GK. H8459 from the Saku Formation at loc. T1022 p7 and T1022 p3 in the Saku-Abeshinai area;

GK. H8460 (Fig. 51C) from Member IIn (Lower Turonian) at loc. Y5109 in the Oyubari area; all collected by T.M.

As the body chamber is incomplete, it is appropriate to state the dimension of whorl height at the point where the adult-type ornament begins to develop. Namely, H = 24 to 30 mm in the above five specimens.

On the other hand, in the holotype and GK. H8453 (Fig. 51D) the body chamber begins at H = 45 and 48 mm respectively and is ornamented by major fold ribs and numerous lirae. In still larger specimens, such as MCM. A118-1 and MCM. A118-2 the adult body chamber begins at H = 55 mm and 61 mm respectively.

The two extreme forms mentioned above are not separated in geological time. Although the above five small specimens were found from the Turonian, there are some examples of the large form found in the Turonian, e.g. GK. H1166A (Fig. 46) and MCM. A249 (Fig. 47).

Furthermore, in GK. H3131 (Fig. 50E), the major ribs of body chamber begin at H = 35 mm; in UMUT. MM19786 [GT. I-471] (Fig. 52), the frequent, but narrow ribs begin to develop at H = 33 mm and they strengthen gradually on the last 90° of the phragmocone, whereas the last septum is located at H = 46 mm (D = 103 mm). There are, thus, gradation and also variation in aspects of the development of the adult type ornament. I include, hence, the questionable small form at least tentatively in *G. denseplicatum*, although it could be regarded morphologically as an ancestral form.

Occurrence. – Based on the material from my field work, sometimes aided by several friends, *G. denseplicatum* in the revised definition ranges from the Turonian to Santonian sequence, but possibly to lowest Campanian, depending on the definition of the stage boundary. It is common in the Turonian and Coniacian strata of Hokkaido and South Sakhalin. The occurrences in Madagascar and South Africa are within the above mentioned stratigraphic range (mostly in the Turonian and Contacian).

Gaudryceras intermedium Yabe, 1903

Figures 53B, 54–60

Lytoceras sacya Jimbo, 1894 (non Forbes, 1846), p. 34 [190], pl. 6 [22], fig. 1–1a.
Gaudryceras tenuiliratum var. *intermedia* Yabe, 1903, p. 27, pl. 3, fig. 1a–b.
Gaudryceras tenuiliratum Yabe, 1903 (pars), pl. 3, fig. 3 (only); 1927, pl. 7, fig. 5.
Gaudryceras (Pseudogaudryceras) intermedium Yabe; Shimizu, 1935b, p. 172.
Gaudryceras denseplicatum var. *intermedia* Yabe; Matsumoto, 1943, p. 666.
Gaudryceras denseplicatum intermedium Yabe; Matsumoto, 1959b, p. 143.
Gaudryceras denseplicatum var. *intermedium* Yabe; Hirano, 1978, p. 235, pl. 33, fig. 1; pl. 34, fig. 2; pl. 35, fig. 1.
Gaudryceras denseplicatum var. *tenuiliratum* Yabe (pars); Hirano, 1978, p. 240, pl. 3, fig. 2.

Lectotype. – One of Yabe's syntypes described as *G. tenuiliratum* var. *intermedia* (1903, p. 27, pl. 3, fig. 1a–b) was designated by Matsumoto (1959b, p. 143) as the lectotype of *G. intermedium*. It is registered as UMUT. MM7471 [= GT. I-185] and illustrated in this paper

(Fig. 54). Its original locality was not pin-pointed in a map but is recorded as "from the Upper Ammonite-beds" [= upper subgroup of the Yezo Group] of the Makaushippe, a branch rivulet of the Sanushibe, a tributary of the Popets [= Hobetsu River], Hobetsu district.

Material. – In addition to the lectotype, selected specimens that show wholly or partly the diagnostic characters of *G. intermedium* are as follows:

UMUT. MM7473, fairly large, fragmentary septate whorl whose suture is illustrated (Yabe, 1903, pl. 3, fig. 3) at B = 110 mm as that of "*G. tenuiliratum* normal type". It is recorded to have come from the "*Pachydiscus* beds" (= a zone containing *Anapachydiscus sutneri* (Yokoyama) and *A. deccanensis yezoensis* Matsumoto of Santonian-lowest Campanian age) exposed in the Ban-no-sawa, a tributary of the Ikushunbetsu River.

UMUT. MM19788 [= GT. I-177] (Fig. 53B) (collected by H. Yabe) is from the Urakawa area (precise locality and horizon unrecorded). Also YCM GP. Ur 736001 (Kanie, 1971, cover-fig.), collected by Y. Kanie from the Urakawa Formation of Nishihorobetsu, Urakawa area.

UMUT. MM7495 [= GT. I-109] (Jimbo, 1894, pl. 6, fig. 1–1a) is a juvenile from the Shuparo River above the Hakobuchi gorge, probably upper part (Santonian and possibly extending up to lower Campanian) of the Yezo Group. It is regarded here as a juvenile of this species.

GT. I-3496A, B [UMUT. MM19789, 19790] (Fig. 55A, B) are a large but incomplete main part of a shell and a detached last part of its body chamber, collected by T.M. from Member IIId (mainly upper Santonian-possibly ranging up to lower Campanian) at loc. T281p of the Abeshinai-Saku area.

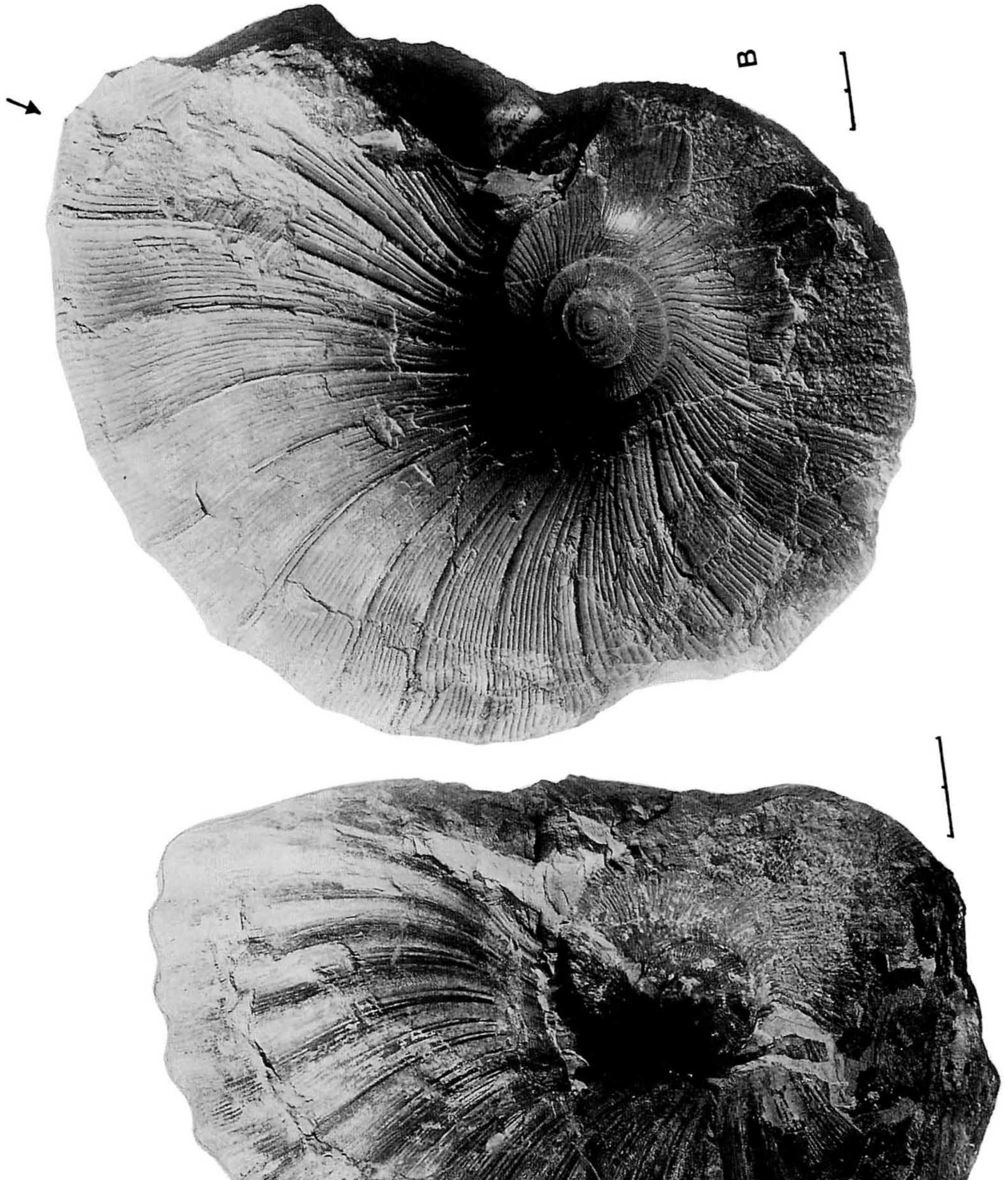
MCM. A29-11 [YKC. 510900] (MCM, 1988, Atlas, fig. 97) is a large full-grown, but distorted, specimen collected by Y. Kawashita from the upper reaches of the Hobetsu River in the Yubari Mountains.

MCM. A183 (Fig. 56) collected by Mamoru Shimomura from the upper subgroup of the Yezo Group in the upper reaches of the Ikushunbetsu River and MCM. A310-14 (MCM, 1988, Atlas, fig. 94) collected by Yuriko Mitsunaga from the same subgroup of the same area, both are mostly septate, although a posterior fraction of the body chamber is preserved in the former.

MCM. A143 (Fig. 57) collected by K. Muramoto from the upper part (Santonian-possibly lower Campanian) of the Yezo Group, Wakka-wenbetsu creek, a branch of the Abeshinai River. It is a well-preserved phragmocone, with a trace of the umbilical seam of the lost body chamber.

MC. R.-K. X. P1 of the Muramotos' Collection, a very large specimen obtained by K. Muramoto from a huge nodule washed out from the Santonian (*Texanites*-bearing) sandy siltstone (Member Ug of Tanaka, 1963) of the upper subgroup of the Yezo Group in the upper course of the Yamaguchi-zawa, a tributary of the Kotanbetsu River, northeastern part of the Tappu Quadrangle (Tsushima *et al.*, 1958).

Two very large specimens in the Katsujo Yokoi's Collection no. 299A and B, occurring side by side in a huge nodule in mudstone of the upper subgroup of the Yezo Group exposed on the Onnebetsu River, eastern hilly area of the Teshio Mountains, east of Soeushinai; YKC. 581009 [= MCM. A243], a very large specimen (Figs. 59–60) collected by Y. Kawashita from the upper subgroup (Santonian-Lower Campanian) of the Yezo Group exposed in the upper reaches of the Enbetsu [=Wembets] River, western hilly area adjacent to the Saku-


B
A

Abeshinai area.

GK. H8454 (Hirano, 1978, pl. 35, fig. 1) collected by T.M. from Zone Mh6 of the Miho Group at loc. N191-p on the Santan-gawa, a tributary of the Naibuchi [Naiba] River, South Sakhalin. This specimen is wholly septate and incomplete. It was longitudinally cut by Hirano who prepared a plaster cast (GK. H8455) before that cutting. GT. I-4034 [= UMUT. MM19702] (Fig. 58) collected by M. Kawada as a pebble from the Miho Group (horizon uncertain) in the Juhachi-rinpan-ni-no-sawa, Naibuchi area. It was labelled as *G. tenuiliratum* var. *infrequens* Yabe by Kawada (without description) and regarded as an example of *G. denseplicatum* var. *tenuiliratum* by Hirano (1978, pl. 33, fig. 2) (named incorrectly in both cases; horizon inadequately recorded by Hirano). Actually it is a middle-aged part of a very large specimen, which is comparable with MC. R-K.XP1 of Muramoto.

Description. – The full-grown adult shell is very large. This is exemplified by a number of specimens as follows: (1) The specimen MC. R-K.XP1, which shows the ornament of a gerontic substage at its end, is 436 mm diameter; (2) MCM. A143 is estimated as 450 mm diameter from the trace of the umbilical seam of the outer whorl; (3) MCM. A183 preserves only a fraction of its body chamber, but from the trace of the umbilical seam of the rest main part of the body chamber, it is estimated as originally exceeding 50 cm diameter; (4) MCM. A29-11 is distorted but preserves the crushed body chamber nearly to the apertural margin and about 480 mm in a restored outline (5, 6). The somewhat deformed two specimens (no. 299A and B) of K. Yokoi's Collection are likewise very large, about 44 cm and 40 cm respectively (7). Kanie's (1971) estimation of a very large specimen from Urakawa is recorded as roughly 40 cm. There is naturally some variation in size. For example, a completely preserved specimen, YKC. 581009 [= MCM. A243], from Enbetsu is 342 mm at the preserved end (i.e. nearly peristome) of the adult body chamber. It is exceptionally smaller than the above mentioned very large specimens but exceeds undoubtedly the known largest example of *G. denseplicatum*.

The body chamber occupies at least two thirds and probably three quarters of the outer whorl. Generally in more or less later growth stages the coiling is fairly involute and the whorl expands with a high ratio; the umbilicus is consequently fairly narrow, showing 0.25 to 0.20 in U/D in the representative specimens. The whorl is subcircular in section but slightly higher than broad.

In more or less younger whorls the coiling is moderate and the umbilicus is also of moderate width. Even in these stages the whorl expands with a fairly high ratio, is subcircular in cross-section and nearly as broad as high or somewhat broader than high. Ontogenetic changes of shell shape occur at various diameters. For instance, GT. I-4034 (Fig. 58) shows the youthful shell form at D = 105 mm, whereas the lectotype shows a more mature form at D = 80 mm onward. They are both wholly septate and it should be noted that the former resembles the inner whorls of the very large specimen of MC. R-K. X P1 and the latter is similar to the phragmocones of such larger specimens as MCM. A183, MC. A310-14, MCM. A29-11 and YCM-GP. Ur036001. So far as the available material is concerned, a shell form

←Figure 53. Two species of *Gaudryceras* in comparison.
A: *G. denseplicatum* (Jimbo), UMUT. MM19787 [GT. I-3849], ×2/3. B: *G. intermedium* Yabe, UMUT. MM19788 [GT. I-177], ×1/2. Scale bar: 20 mm. Photos by C. Ueki+.

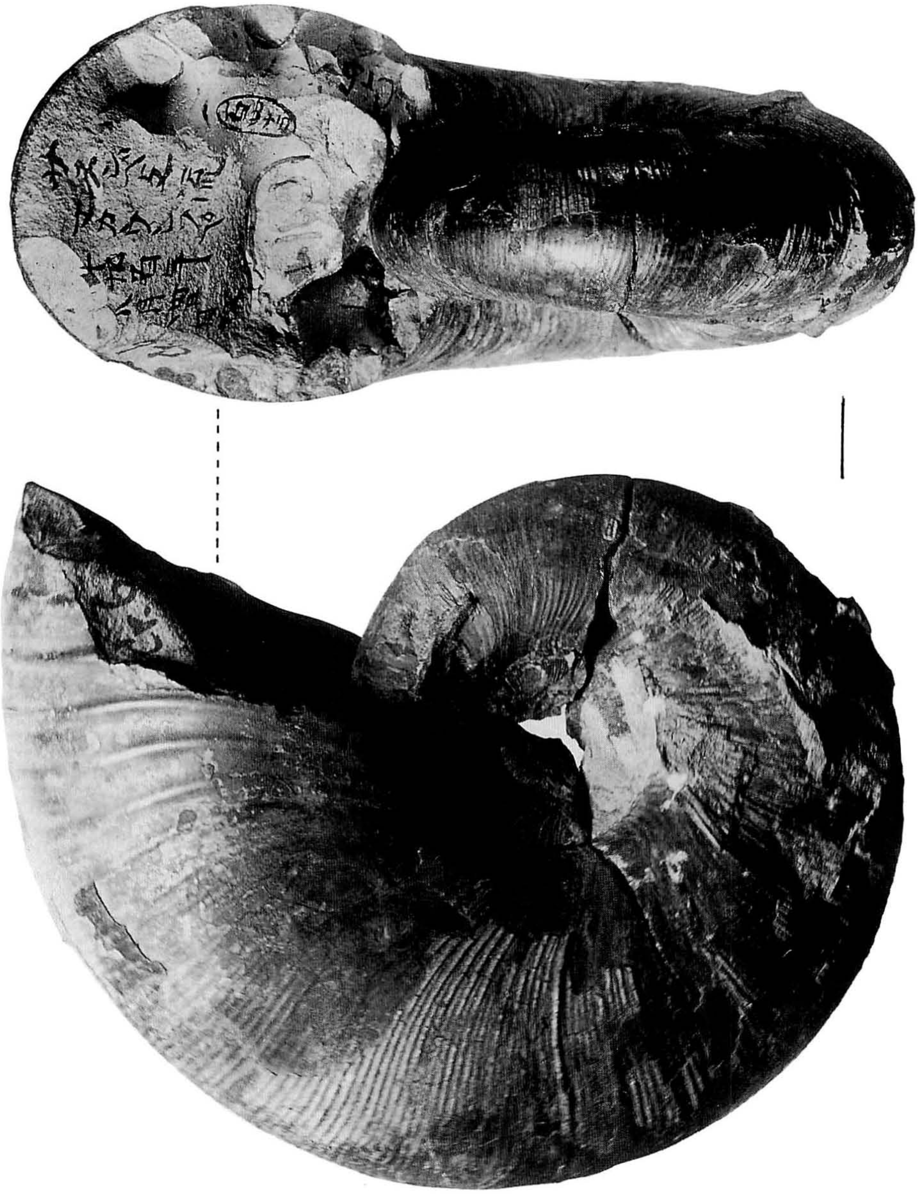
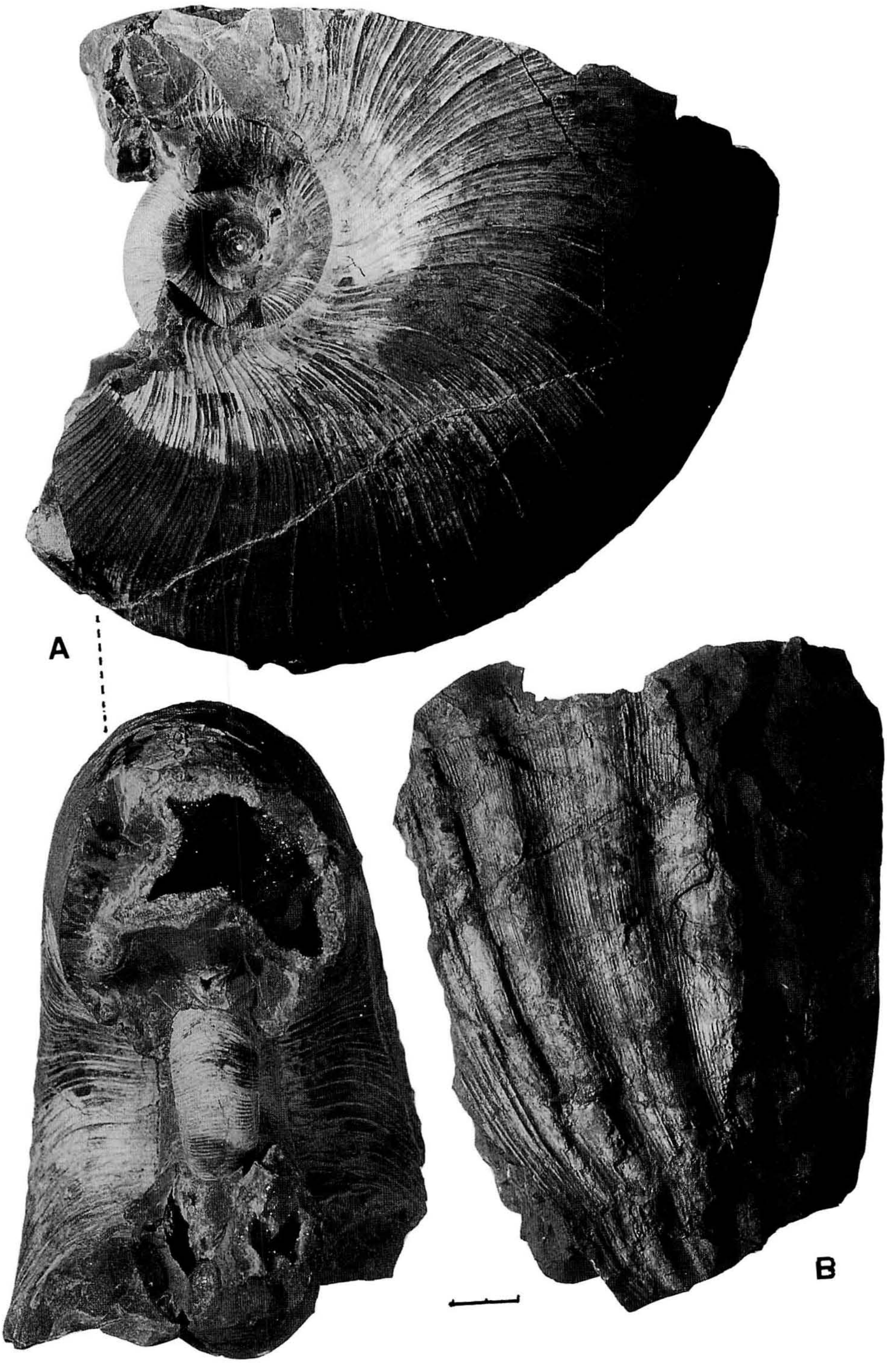


Figure 54. *Gaudryceras intermedium* Yabe.
UMUT. Mm7471 [GT. I-185], lectotype, wholly septate, ×1. Scale bar: 10 mm. Photos by C. Ueki+.

Figure 55. *Gaudryceras intermedium* Yabe. →
A: UMUT. MM19789 [GT. I-3496A], undeformed but partly broken, ×1/2. B: UMUT. MM19790 [GT. I-3496B], last portion of body-chamber (side-view), ×1/2. A and B probably belong to one and the same individual. Scale bar: 20 mm. Photos by C. Ueki+.


A
B

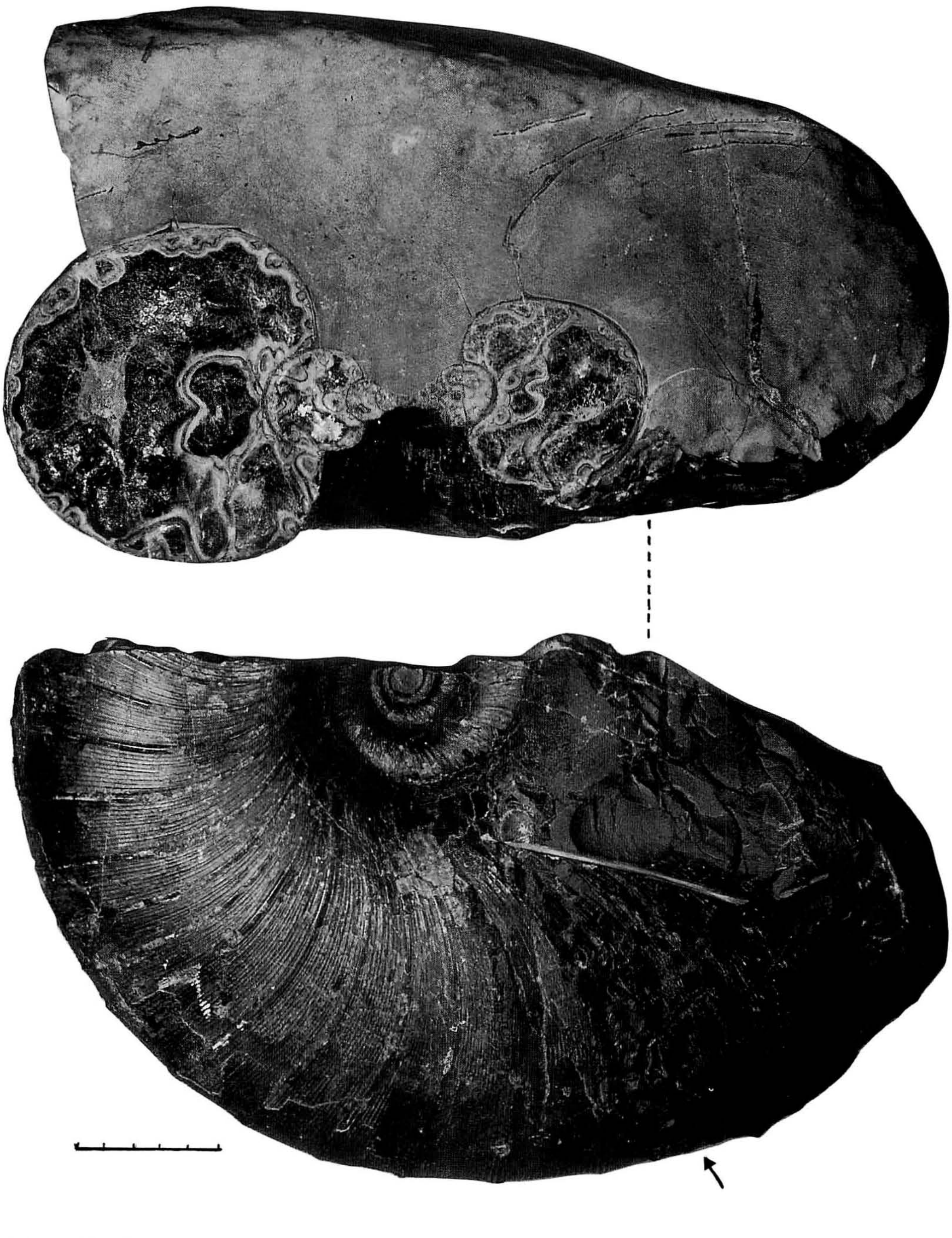


Figure 56. *Gaudryceras intermedium* Yabe.
MCM. A183, right side and cross-section of a half-cut specimen, ×0.42. Scale bar: 50 mm. Photos by courtesy of K. Shinohara.

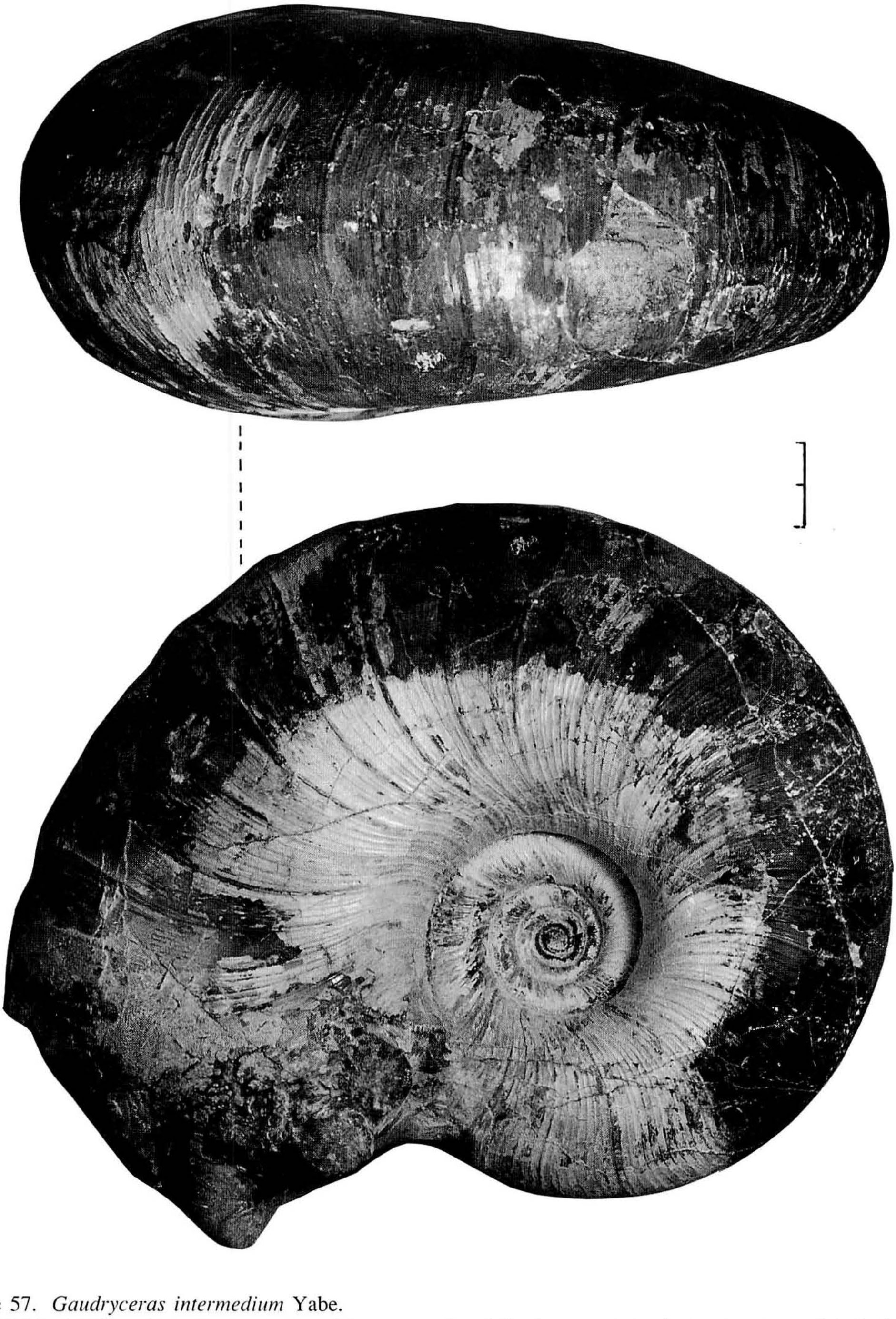


Figure 57. *Gaudryceras intermedium* Yabe.
MCM. A143, mainly phragmocone, with a trace of umbilical seam of the body chamber, ×0.575. Scale bar: 20 mm. Photos by courtesy of K. Shinohara.

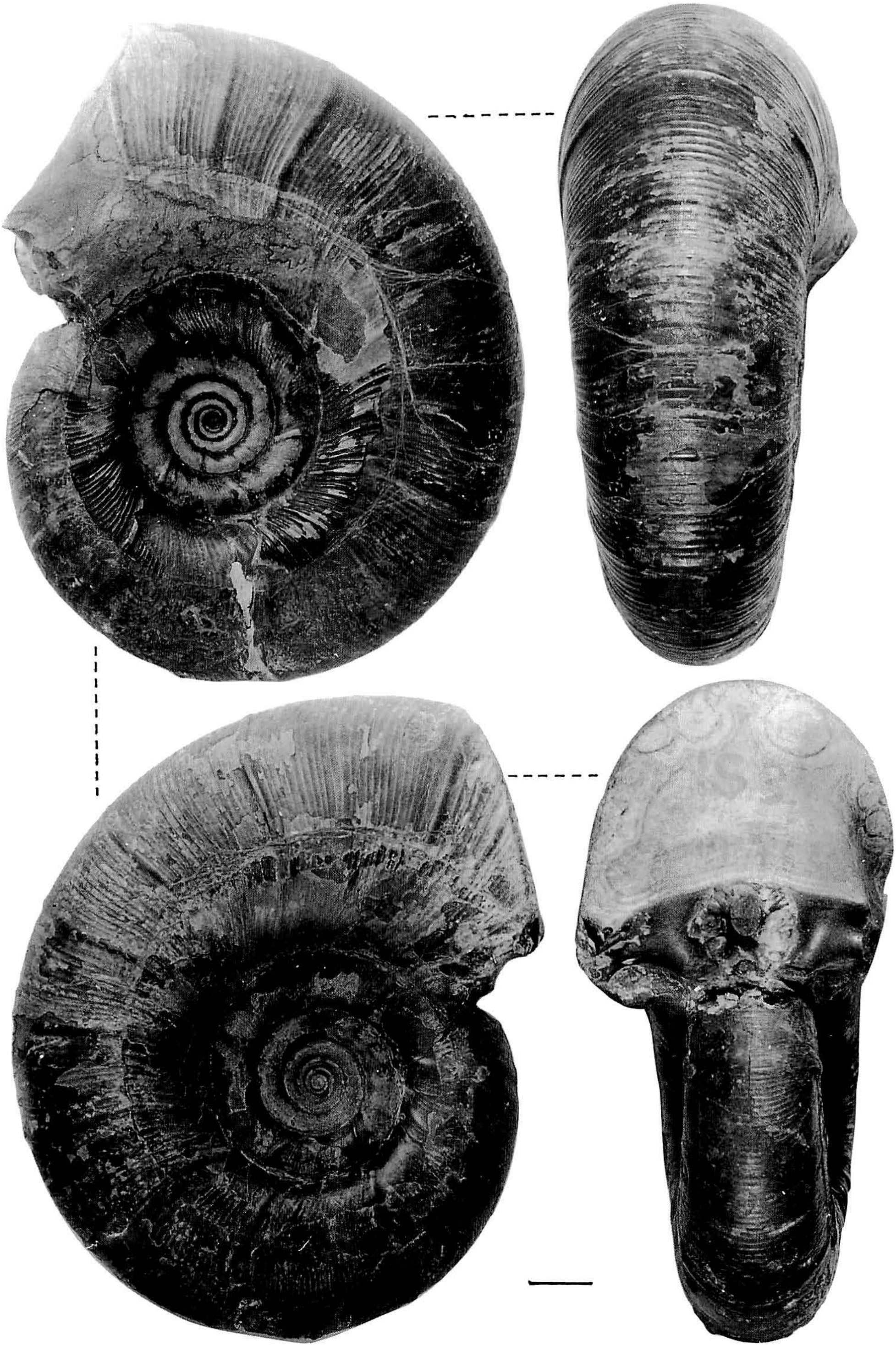


Figure 58. *Gaudryceras intermedium* Yabe.
UMUT. MM19702 [GT. I-434], inner whorls of a very large specimen, ×0.9. Scale bar: 10 mm.

like that of the lectotype is more common, but it is unnatural to separate the form like GT. I-4034, because of the gradation in the character as well as the same type of ornament. MCM. A243 is an example in which the whorl expansion is somewhat lowered in the last part of the adult body chamber, suggesting a gerontic substage.

The ornament characteristic of this species consists of regularly arranged, narrow major ribs in both inner (or younger) and outer (or later) whorls and the fine, but sharp-crested lirae on the surface of the test.

At first, the major ribs appear as collars associated with 5 to 7 periodic constrictions per whorl, increasing their frequency with growth. Sooner or later, the constrictions become indistinct or obsolete and the narrow major ribs continue to develop, increasing their number from 12 to 15 per whorl in some middle-aged shells. On the late part of the septate whorl and on the main part of the body chamber, the narrow major ribs continue to develop at nearly regular intervals. In a number of mature specimens examined, there are 20 ribs per half a whorl. The lirae on a rib are one or two. Those on each interspace number 7 to 11 on the venter, but are less numerous and coarser around the umbilicus. Bifurcation and/or intercalation occur between the umbilical seam and the mid-flank. The bundled lirae around the umbilicus may be called the subcostae.

The flexuous lirae on the phragmocone are similar to those of *G. denseplicatum*. On the body chamber the flexuosity is weakened peripherally, with slight variation between individuals.

On the last part of the body chamber, the lirae become extremely fine and dense and the major ribs are weakened. In some cases, (e.g., MCM. A243 and UMUT. MM19790) a few major ribs are slightly broadened but weakened and approximated. These feature may suggest a gerontic substage.

The sutures are the typical pattern of *Gaudryceras* and are very intricate in the later part of a large shell.

Dimensions. – See Table 17.

Table 17. Dimensions of *Gaudryceras intermedium*.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
LT (E)	120	30	.25	58	.48	52	.43	.90	1.81
MC. R-K. X. PI (E)	436	106	.24	216	.50	–	–	–	1.89
" (E-180°)	268	84	.31	112	.42	112	.42	1.0	1.56
KY. 199B (E)	400	95	.24	–	–	–	–	–	–
" (LS)	–	–	–	122	–	104	–	.85	–
MCM. A243 (E)	342	76	.22	155	.45	142	.42	.92	1.40
" (E-170°)	227	49	.22	115	.51	106	.47	.92	1.82
UMUT. MM7473	300	55	.18	160	.53	165	.55	1.03	1.88
GT. I-177 (E)	236	51.5	.22	118	.50	108	.46	.92	1.77
MCM. A183 (LS)	–	–	–	155	–	150	–	.97	–
" (LS-100°)	220	50	.23	111	.50	111	.50	1.00	1.80
MCM. A143 (E-30°)	208	50	.24	102	.49	100	.48	.98	1.82
MCM. A310 (E)	204	54	.24	96	.48	96	.48	1.00	1.78
GT. I-434	105	36	.34	44	.41	45	.43	1.05	1.65
UMUT. MM7475	35	11	.31	15	.43	16.5	.47	1.10	1.67

Figure 59–60. *Gaudryceras intermedium* Yabe.
MCM. A243 [YKC. 581009], completely preserved shell up to the peristome, ×0.42. Scale bar: 50 mm.

Discussion. – The taxonomic name *intermedia* or *intermedium* has been used in different ways. Yabe (1903) interpreted it as a variety of *G. tenuiliratum* with a narrower umbilicus and coarser ribs. Shimizu (1935b) seems to have interpreted *G. intermedium* as a species independent of *G. tenuiliratum* and *G. denseplicatum*, for he listed the three species under different subgenera: *G.* (*Pseudogaudryceras*), *G.* (*Neogaudryceras*) and *G.* (*Epigaudryceras*) respectively. He did not give a clear subgeneric diagnosis or specific diagnosis in that paper. Moreover, Shimizu (1934 *in* Shimizu & Obata, p. 67) proposed *Pseudogaudryceras* and some other subgenera differently than in his papers of 1935a, b. Anyhow, Wright & Matsumoto

(1954) sorted out these doubtful taxa of generic level. Shimizu (1935b) listed *G. intermedium* frequently occurring in several "zones" of various areas, but *G. denseplicatum* at only one point (i.e. Jimbo's original locality of the Ishikari Coalfield).

Since 1943, I have transferred *G., tenuiliratum* var. *intermedia* to *G. denseplicatum* var. *intermedia* in the lists of several papers and explained the reason in my California paper (1959b, p. 143). In that paper, it was treated as a subspecies, *G. denseplicatum intermedium* Yabe. This "subspecies" was not a geographical subspecies, but a morphologically defined taxon (phenotype) implying an evolutionary step towards *G. tenuiliratum*. However, such an evolutionary interpretation was tentative and speculative. The idea was further developed by Hirano (1978) to explain the appearance of *G. tenuiliratum* as transient polymorphism. This would be hardly maintained in the light of up-dated knowledge on *G. tenuiliratum* (see a revised description of *G. tenuiliratum* in this paper).

In the same paper Hirano interpreted *G. denseplicatum* and *G. intermedium* as a sexual dimorphic pair. This remains a tenable hypothesis, although his nomenclature of the dimorphic pair as *G. denseplicatum* var. *denseplicatum* and *G. denseplicatum* var. *intermedium* is unacceptable. As Hirano has noted, the difference in the size and ornament of the adult stage is distinct between *G. denseplicatum* and *G. intermedium*. In fact, the characters of the immature stages are fairly similar to each other between the two forms.

In my observations on *G. intermedium*, however, the narrow major ribs at regular intervals like those of the adult body chamber begin to develop from a fairly early growth stage (variable in terms of the shell diameter, but from a young substage as small as D = 25 mm in some examples), whereas the major ribs are faint or develop irregularly in small or immature shells of *G. denseplicatum*.

Based on field experience and museum collection, *G. denseplicatum* is common in the Turonian and Coniacian strata, whereas *G. intermedium* occurs frequently in the Santonian and possibly also lower Campanian parts of the Yezo Group.

On the grounds of my observations mentioned above and on my revised description, I regard *G. intermedium* as a distinct species. It is indeed allied to *G. denseplicatum*, but is distinguishable from the latter. Present data permit the interpretation that *G. intermedium* a macroconch of *G. denseplicatum*, but the available evidence is yet insufficient to be sure.

G. intermedium Yabe, 1903 may be a junior synonym of *G. glaneggense* (Redtenbacher, 1873). However, until the latter is sufficiently described ontogenetically and also on larger collection, this problem cannot be resolved. Yabe suggested it as being intermediate between *G. denseplicatum* and *G. intermedium*. This may be supported by some examples from Romania (Szász, 1976, pl. 6) and Spain (Wiedmann, 1962b, pl. 9, figs. 2 and 6 under *G. vascogoticum*). It could be an ancestor of *G. intermedium*.

Incidentally, Yabe (1909, fig. 1) illustrated a fairly large specimen as an example of *Gaudryceras striatum* (Jimbo). It came from Dui [Due], North Sakhalin and was held at Naturhistorische Museum zu Berlin. Jimbo (1894, p. 183) did not identify it to his *G. striatum* and gave his observations in detail as a species which is allied to, but different from *G. denseplicatum*. I would suggest that it could be *G. intermedium*, but without examining the actual specimen, I hesitate to give a definite conclusion.

Occurrence. – Common in the Santonian and possibly also lower Campanian parts of the Yezo Group in Hokkaido and the corresponding parts in South Sakhalin. The true range of this species and the occurrences in other areas of Japan (e.g. in Kyushu and Shikoku) should be examined further.

Gaudryceras tenuiliratum Yabe, 1903

Frontispiece; Figures 1; 61–66; 67A–D

Ltyoceras sacya Forbes; Yokoyama, 1890, p. 178, pl. 18, figs. 12a, b and 13a, b (*non*. Forbes, 1846, pl. 14,

fig. 10).
Gaudryceras tenuiliratum Yabe, 1903, p. 19, pl. 3, fig. 4 (?); Matsumoto, 1941, p. 22, fig. 3b; 1943, p. 667, fig. 1; 1963, p. 29, pl. 44, figs. 12a–b; 13a–b; Hirano, 1975, p. 185, pls. 24–26; Matsumoto & Miyauchi, 1984, text-fig. 8; Matsumoto, 1995, fig. 2A.

Lectotype. – Yabe (1903, p. 19) established this species on several syntypes, of which the one illustrated by Yokoyama (1890, pl. 18, figs. 12a, b) (Fig. 61B, C) was designated as lectotype independently by Matsumoto (1963, p. 29) and Jones (1963, p. 28). It is indicated as Nr. 1889. IX. 16 of BSP [Bayer Staatssammlung für Paläontologie und historische Geologie, München]. It came from Efue [= Ibui] of the Urakawa district, south-central Hokkaido.

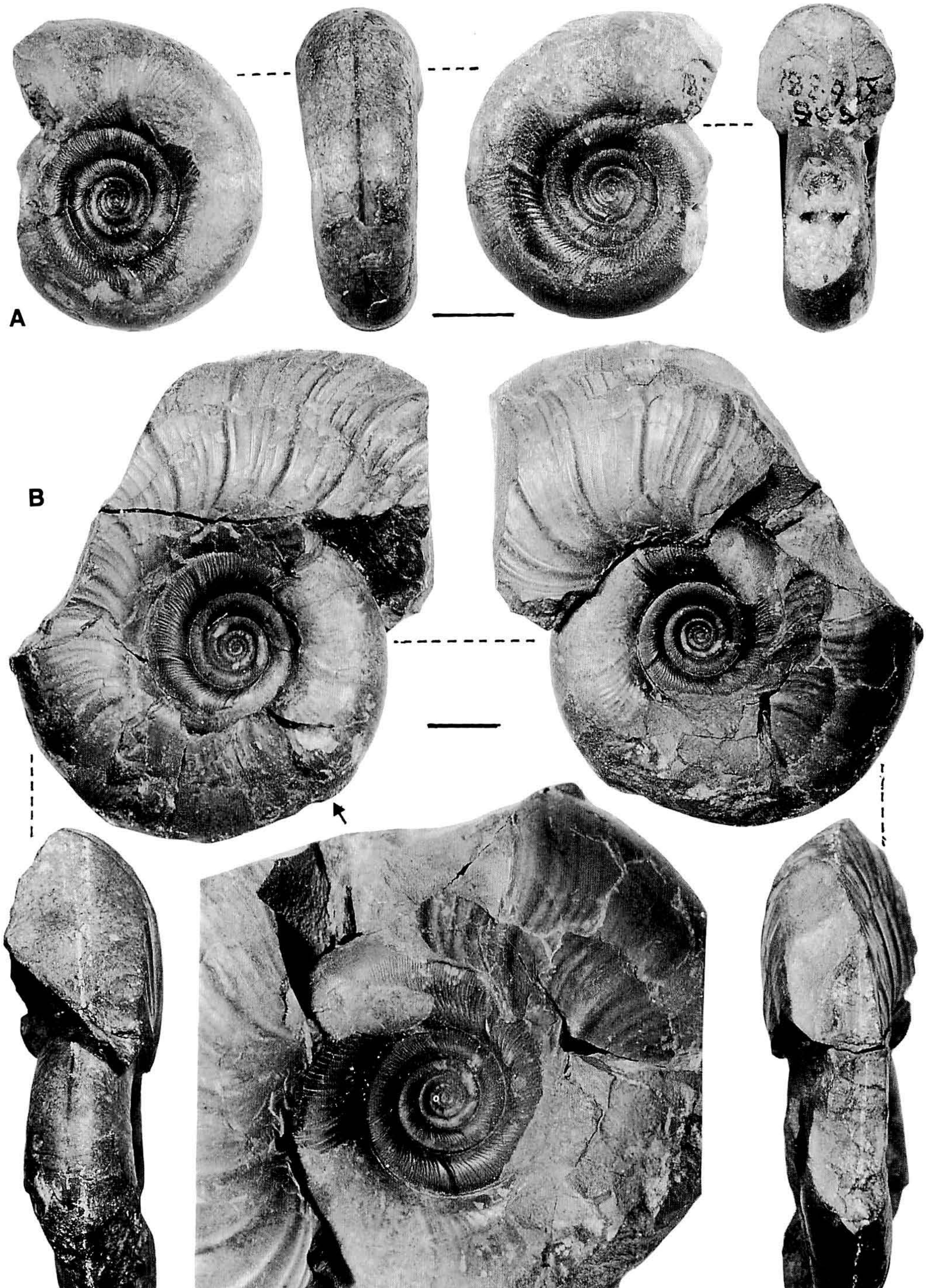
Material. – In addition to the lectotype there are a number of well-preserved adult specimens, which agree with the lectotype in diagnostic characters. Examples are, among others, GK. H3171 (Fig. 65A, B) collected by T.M. from Unit Ur1β at loc. U141p2, upper reaches of the River Chinomi (Tinomi), Urakawa area; GK. H8421 (Fig. 63A, B) collected by T. Takahashi and T.M. from the Santonian Zone of *Inoceramus amakusensis* at loc. Ik 8010, right bank of the Kikume-zawa, tributary of the River Ikushunbetsu (for the location see Matsumoto *et al.*, 1988, text-fig. 1); GK. H2206 (Hirano, 1975, pl. 25, fig. 8; pl. 26, fig. 14) collected by T.M. from Zone Mh6β at loc. N22z, on the River Miho, i.e. the 2nd major tributary of the River Naibuchi, South Sakhalin; GK. H2215 (Fig. 62) collect by T.M. from Zone Mh6β at loc. N182f, lower course of the River Santan, a tributary of the River Naibuchi; UMUT. MM19697 [= I-433] (Fig. 64) collected by M. Kawada from Zone Mh6, upper reaches of Juhachi-rinpan-ni-no-sawa, a tributary of the River Naibuchi, South Sakhalin.

Selected examples of the septate shells which show diagnostic immature characters are the smaller one illustrated by Yokoyama (1890, pl. 18, fig. 13a, b) and this paper (Fig. 61A) from Efue and IGPS. 102530 (Matsumoto, 1995, fig. 2A) collected by K. Wada from his loc. Mk-92201 Mukobetsu, both in the Urakawa area; UMUT. MM19695 [= I-3397a, b] (Fig. 66A–C) and MM19696 [= I-3397c] collected by T.M. from the Santonian mudstone at loc. T731p, Nio-no-sawa of the Saku area; UMUT. MM19701 [= I-452] (Fig. 67A–D) collected by M. Kawada from Zone Mh6 of the River Santan, Naibuchi area; many other specimens dealt with by Hirano (1975, pls. 25, 26) for the ontogenic study are not listed here.

Description. – The mature shell is medium sized. The body chamber occupies at least three quarters of the outer whorl and the umbilicus is of moderate width (32 to 36 percent of the diameter). The whorl section is broadly reniform in youth, subcircular in late septate stage and subelliptical in the adult, showing progressive increase of height and degree of involution with growth.

The outer shell layer is ornamented by sharp-crested lirae that are flexuous in lateral view; at first prorsiradiate on the umbilical wall, pass with asymmetrical convexity across the rounded umbilical edge and swing back weakly on the main part of the flank and then project forward from the ventrolateral shoulder to the venter. The lirae are scarcely impressed on the inner shell layers and on the quite smooth internal mould. Bifurcation and intercalation of the lirae occur normally at the umbilical margin, but also on the flank.

The presence of extremely fine and dense lirae (or a great number of intervening striae) on the venter of whorls with diameters less than 30 mm caused by multiple branching and


A
B
C

intercalation of the normal flank lirae is one of the most diagnostic features. The shell of this ventral part is also very thin. Still earlier nuclear part of the whorl has frequent flanges as noticed generally in the gaudryceratids by Murphy (1967b, fig. 1).

Periodic collars, with accompanied constrictions in front or on internal mould, occur clearly on the main part of the phragmocone with moderate frequency (4 or 5 per whorl). On the adult body chamber narrowly raised major ribs are developed frequently, as if they substitute for the collars on the phragmocone, but do not accompany the constriction. They become generally more frequent adorally. The lirae on the interspaces of the major ribs become less crowded and sharper, but not necessarily coarser. The major ribs run in parallel to the flexuous lirae and each of them is superposed by a few lirae.

The sutures show the typical gaudryceratid pattern (see Fig. 1, reproduced from Matsumoto, 1943, fig. 1 by permission).

Dimensions. – See Table 18.

Discussion. – The definition of *G. tenuiliratum* Yabe, 1903 (p. 19) was much confused from the beginning, because *G. intermedium* and some immature specimens of *G. denseplicatum* (Jimbo) were included in the syntypes. To clear up this confusion the specimen illustrated by Yokoyama (1890, pl. 18, figs. 12a, b) was designated as the lectotye (Matsumoto, 1963, p. 29), but a revised description was postponed. In the same year Jones (1963, p. 28) designated the same specimen as the lectotype and described the specimens from the *Pachydiscus kamishakensis* Zone (of Campanian-Maastrichtian transitional age) of

Table 18. Dimensions of *Gaudryceras tenuiliratum*.

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
LT (E)	75.0	25.0	.33	31.0	.41	–	–	–	1.63
" (E-270°)	40.8	16.4	.40	14.4	.35	15.6	.38	1.08	1.44
PL * (E)	37.0	15.5	.42	13.0	.35	15.0	.41	1.15	1.53
GK. H2215 (E)	97.0	32.0	.33	41.0	.42	36.0	.37	0.88	1.63
" (LS)	55.0	21.0	.38	19.5	.35	19.5	.35	1.00	1.34
" (E-270°)	–	–	–	18.3	–	19.3	–	1.05	–
GK. H3171 (LS+270°)	91.0	28.0	.31	37.0	.41	–	–	–	–
" (LS+170°)	68.0	23.0	.34	29.0	.43	27.0	.40	0.93	–
GT. I-433	84.0	30.0	.36	34.0	.40	32.0	.38	0.94	1.70
GK. H8421 (E)	82.0	26.0	.32	35.0	.43	30.0	.37	0.86	1.67
" (E-270°)	–	–	–	16.8	–	17.4	–	1.04	–
GT. I-3397a (LS)	51.0	18.0	.35	21.0	.41	21.6	.42	1.03	1.75
GT. I-452 (LS)	47.0	19.0	.40	16.0	.34	17.5	.37	1.09	1.33
GT. I-3397c (E)	11.5	5.5	.48	3.4	.30	4.8	.42	1.41	1.31

*PL (paralectotype): Smaller specimen of Yokoyama (1890, pl. 18, fig. 13).

←Figure 61. *Gaudryceras tenuiliratum* Yabe.
A: BSP. 1889-IX-505, immature (= "*Lytoceras sacya*" of Yokoyama, 1890, pl. 18, fig. 13), ×5/4. B: BSP. 1889-IX-16, lectotype (= "*L. sacya*" of Yokoyama, 1890, pl. 18, fig. 12), ×1. C: Ditto, right side, enlarged to show details of inner whorls, ×1.6. Scale bar: 10 mm for each. Photos by courtesy of K. Takenouchi and K. Miyakita.

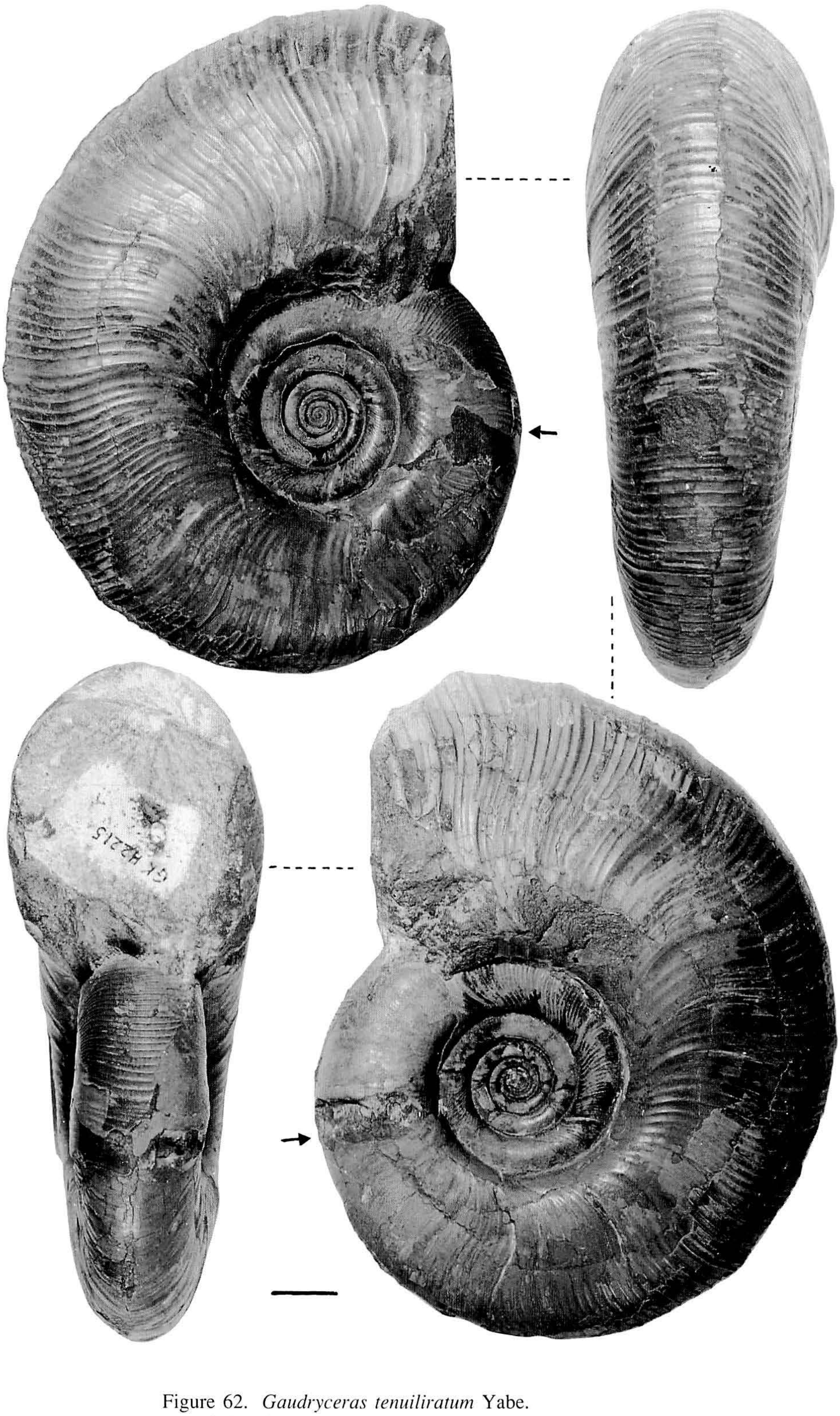


Figure 62. *Gaudryceras tenuiliratum* Yabe.
GK. H2215, typical adult shell, ×1. Scale bar: 10 mm.

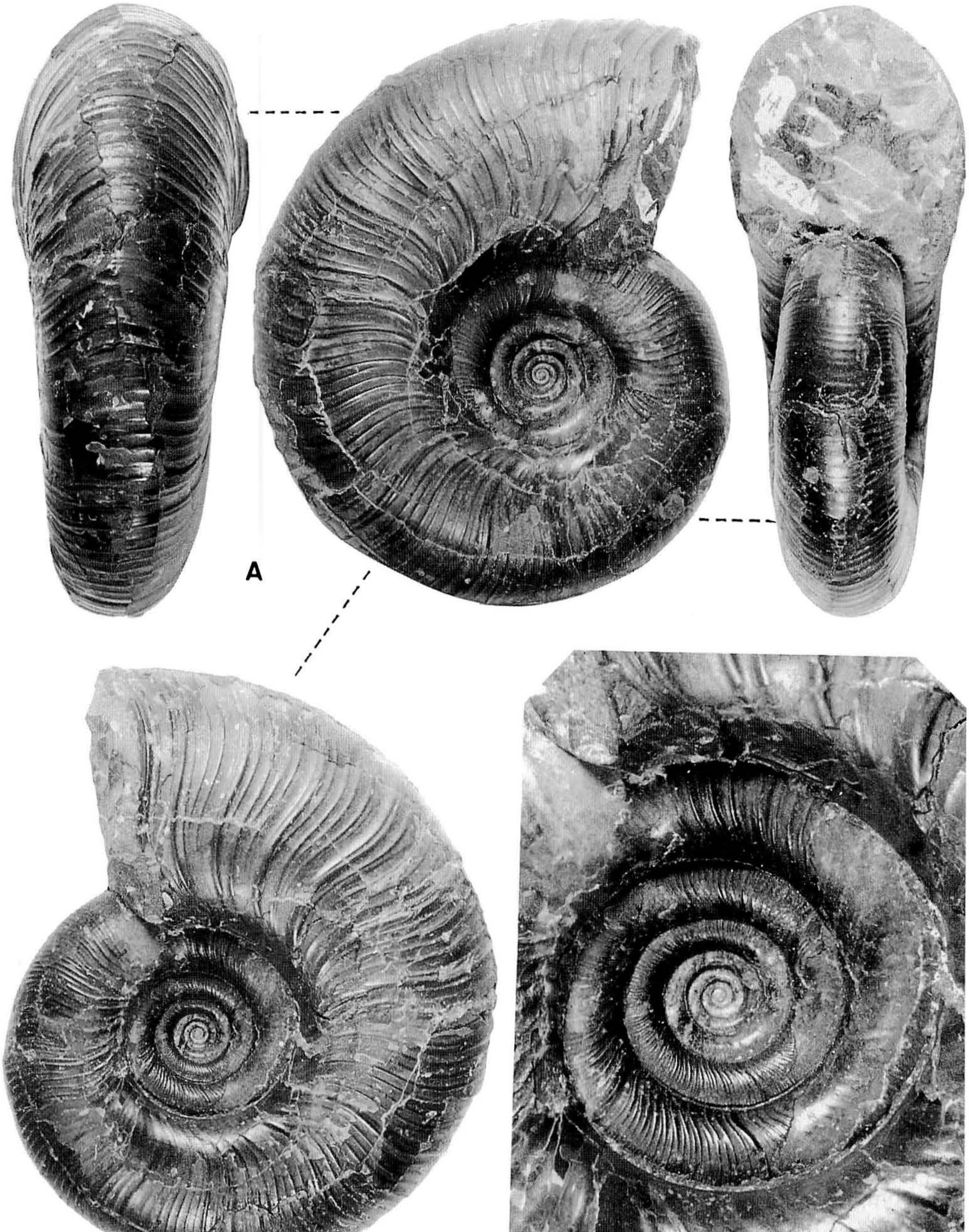


Figure 63. *Gaudryceras tenuiliratum* Yabe.
GK. H8421, adult but rather small example. A: Four views in natural size. B: Umbilical part of the right side; enlarged to show the details of inner whorls, ×2.2. Scale bar: 10 mm.

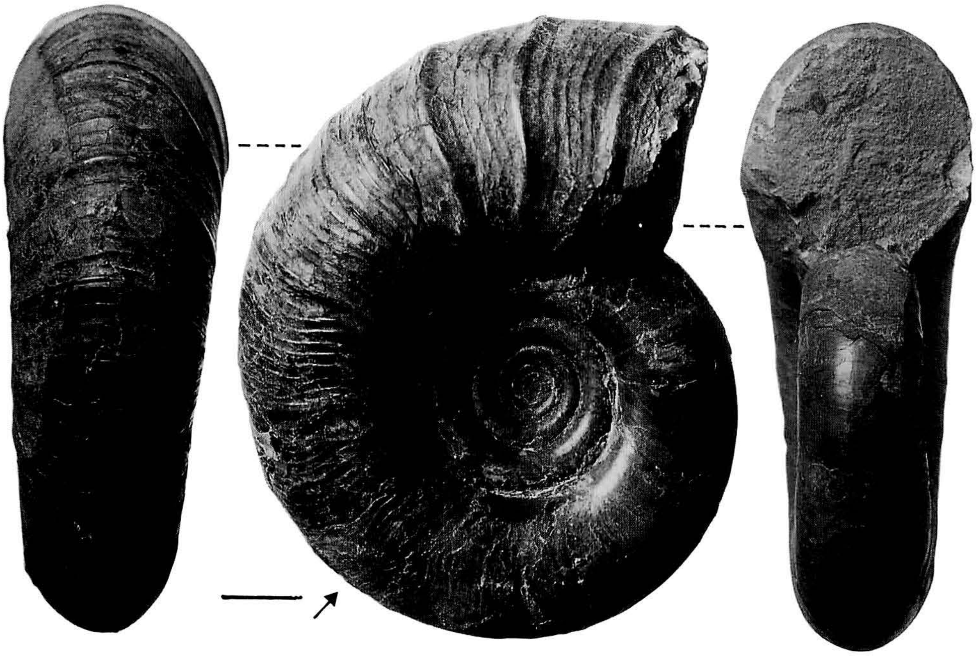


Figure 64. *Gaudryceras tenuiliratum* Yabe.
UMUT. MM19697 [GT. I-433], ×1. Scale bar: 10 mm. Photos by C. Ueki+.

Alaska under *G. tenuiliratum* (Jones, 1963, p. 26, pl. 9, figs. 1–3; pl. 10, figs. 1–3). Kennedy & Klinger (1979, p. 138) cited Jones' paper but overlooked Matsumoto's (1963, p. 20) proposal and Hirano's (1975) excellent paper on *G. tenuiliratum* and, thus, have given another misinterpretation of *G. tenuiliratum*. Although comments were given on Jones' *G. tenuiliratum* in connection with the descriptions of *Gaudryceras hamanakense* Matsumoto & Yoshida (1979, p. 71), *G. izumiense* Matsumoto & Morozumi (1980, p. 14), and *G. mamiyai* Matsumoto & Miyauchi (1984, p. 58), I have reserved the full description of *G. tenuiliratum* itself until this paper.

By courtesy of the authorities of the Bayer Staatssammlung für Paläontologie und historische Geologie, in November 1993, I was able to examine the lectotype of *G. tenuiliratum* on loan at the Fossa Magna Museum of the City of Itoigawa. The lectotype may be regarded as incomplete, because its body chamber is crushed. It does, however, show the diagnostic characters of this species. It was described as immature by Yabe (1903, p. 20), but actually it represents the adult shell. I have examined a number of specimens which conform with this lectotype in the essential characters (see Frontispiece and Figs. 61–65). By chance the diagnostic feature on the ventral part of the inner whorl is observable through the opening of the destroyed right side of the outer whorl of the lectotype (see Fig. 61C).

The smaller specimen of Yokoyama (1890, pl. 18, figs. 13a, b) (Fig. 61A of this paper) is fairly well-preserved, showing characters of the immature stage, although the outer shell layer is partly abraded. To supplement this specimen two examples of the septate stage in the subsequent collections are selected. One of them UMUT. MM19695 (Figs. 66A–C) shows

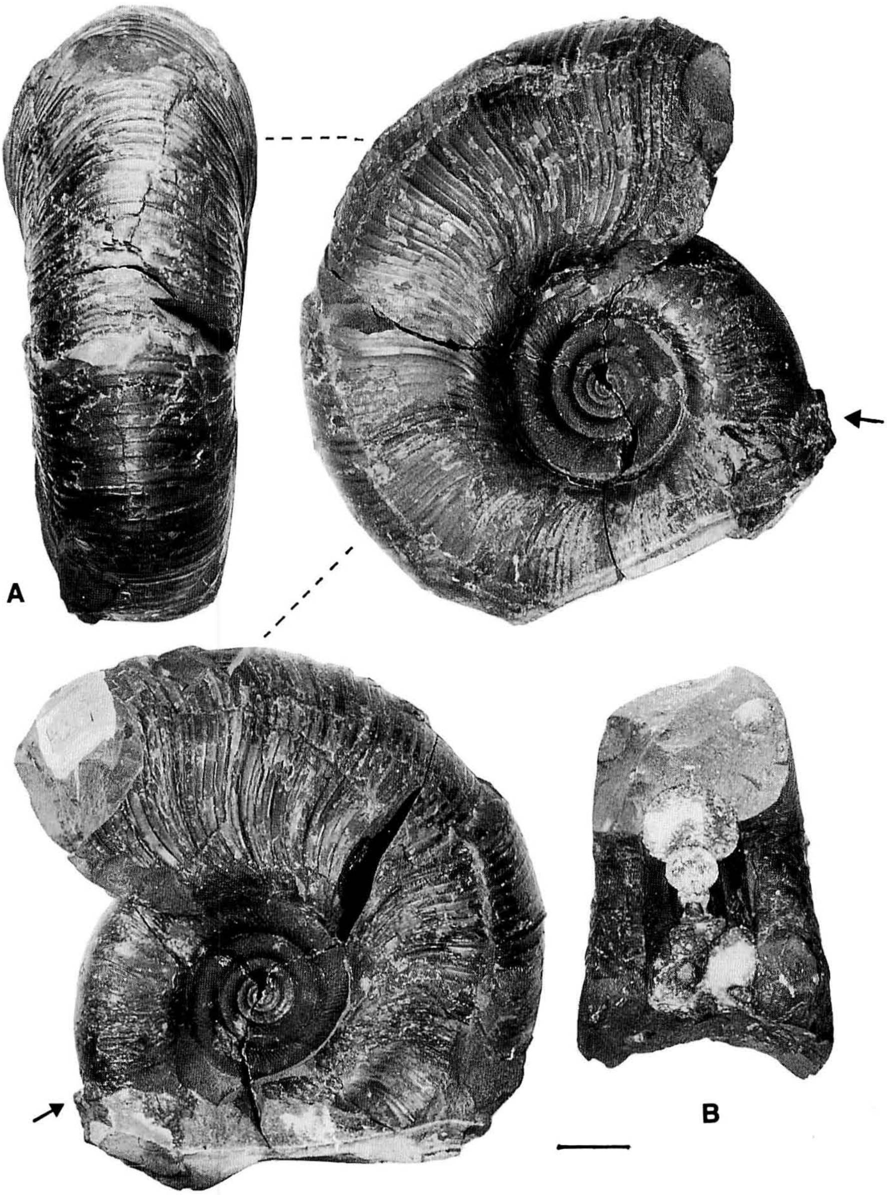


Figure 65. *Gaudryceras tenuiliratum* Yabe.
A, B: GK. H3171, ×1. A: Adult shell, whose body chamber is somewhat secondarily depressed. B: Cross-section along a zigzag crack. Scale bar: 10 mm.

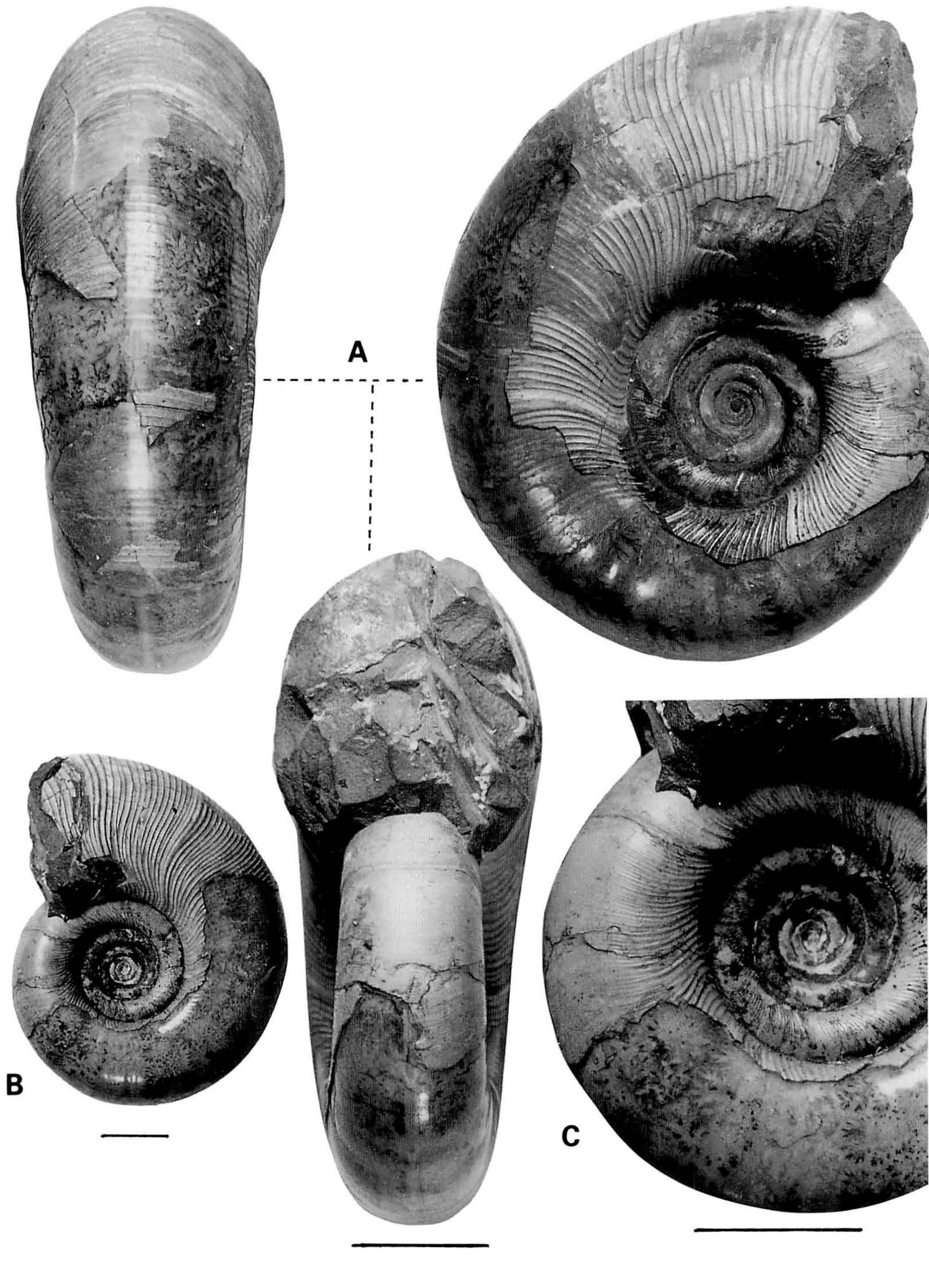


Figure 66. *Gaudryceras tenuiliratum* Yabe.
UMUT. MM19695 [GT. I-3397a], well preserved phragmocone. A: ×2; B: ×1; C: ×2.5. A and C are magnified to show the details. The characteristic ornament of the young shell is observable in C. Scale bar: 10 mm for each.

the extremely fine ventral lirae on the early part of the preserved outer whorl. The other, UMUT. MM19701 (Figs. 67A–D), is an injured phragmocone (with a part of crushed body chamber attached). Probably because of the recovery from the injury the multiple branching and intercalation of lateral lirae into very fine lirae (or intervening striae) on the venter persist to the last part of the phragmocone and, thus, this particular feature is well shown. For comparison young or small examples of *G. denseplicatum* (Jimbo), which do not show such a character, are illustrated (Figs. 67E, F).

A similar particular feature has been reported on young shells of *G. varicostatum* van Hoepen, 1921 (p. 7, pl. 2, figs. 10–12) from the late Santonian to early Campanian Umzamba Formation of South Africa, although that species evidently differs from *G. tenuiliratum* in the characters of adult shells (see Kennedy & Klinger, 1979, p. 133, pl. 3, figs. 1–3).

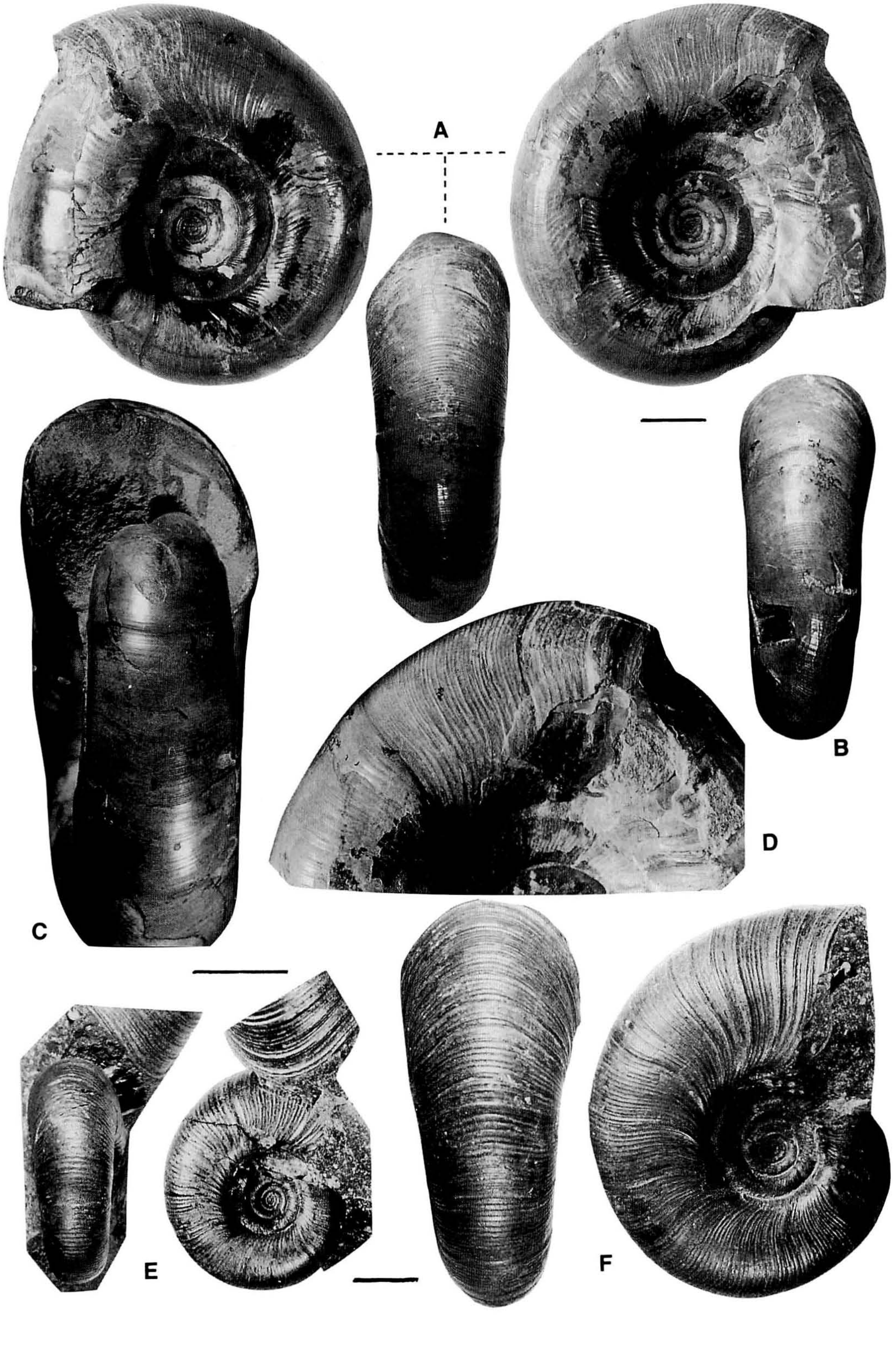
The phylogenetic origin of *G. tenuiliratum* is not known. *G. mite*, emended above, appeared earlier than *G. tenuiliratum*. In the young stage they are fairly similar to each other in shell shape, but the former does not show the very fine and dense lirae on the venter like those of the latter (see Kennedy & Klinger, 1979, pl. 1, fig. 7). They differ undoubtedly in shell size and ornament of later growth stages.

The extremely fine ventral lirae occur in a small, young shell of *G. stefaninii*, but they are formed by sudden break up of coarser flank lirae at the abruptly rounded ventrolateral shoulder of a broadly subquadrate whorl (Figs. 39A, C; also Kennedy & Klinger, 1979, pl. 1, figs. 2a–e). In the young stage of *G. tenuiliratum*, the braching and intercalation of the lirae occur gradually at various positions from the inner flank to the gently rounded ventrolateral shoulder, and, thus, resulting in very fine and dense lirae (or intervening striae) on the venter (Figs. 61C, 66, 67A–D). In the characters of later growth stages, *G. stefaninii* is much different from *G. tenuiliratum*. Moreover, it ranges from late Albian to late Cenomanian, and there is no species which could link the two species.

On the other hand, in later geological times there are several species that have affinities with *G. tenuiliratum*. *G. striatum* (Jimbo, 1894), from the Campanian of Hokkaido and Sakhalin is one of them. Its holotype, by monotypy, is UMUT. MM7493 [= I-116], which was described under *Lytoceras striatum* (Jimbo) (1894, p. 181 [35], pl. 22 [6], figs. 6, 6a, 6b). Its locality is recorded as Abeshinai-Rubeshibe. In fact this species occurs commonly in Member IIIe (Campanian Zone of *Canadoceras kossmati*) of the Abeshinai-Saku area (Matsumoto, 1942, p. 204). One of the specimen described by Yabe (1903, p. 31, pl. 4, fig. 5) (UMUT. MM7468 [= I-191]) supplements the holotype in some respects. These specimens and some of subsequent collection show that *G. striatum* closely resembles *G. tenuiliratum* in size, shell shape, and general configuration of ornament, but is distinguished by its finer and more numerous lirae on both septate whorls and adult body chamber. The extremely fine and dense ventral lirae occur also in the young shell of *G. striatum*.

I reported preliminarily results of a study of the relationship between *G. tenuiliratum* and *G. striatum* in Japanese (Matsumoto, 1941, p. 23), but I have not completed the work. *G. tenuiliratum* var. *substriata* and *G. striatum* var. *paucistriata* were named in that paper as morphologically intermediate forms between typical forms of the two species. They may not be *nom. nud.*, because their characteristics were written concisely, though in Japanese, and their representative specimens were illustrated. At any rate, the relationships should be restudied more precisely on samples from successive stratigraphic levels. This is left for future work.

G. crassicostatum (Jimbo. 1894) (p. 182 [36], pl. 22 [6], figs. 7, 7a; also Yabe, 1903, p.


A
B
C
D
E
F

29, pl. 4, fig. 4; Matsumoto, 1984b, p. 6, pl. 4, figs. 1–3; pl. 5, figs. 1–2; Matsumoto & Miyauchi, *in* Matsumoto *et al.*, 1985, p. 20, pl. 1, figs. 1–3; pl. 2, figs. 1–4; pl. 3, figs. 7–10), from the Campanian of Hokkaido and South Sakhalin (common in the Subzone of *Schlueterella kawadai* of the type Soya area), resembles *G. tenuiliratum* in shell shape and general aspects of ornament, but is larger (130–150 mm diameter); its very fine lirae persist to the last of phragmocone (at D = 65 mm) and its major ribs are broader and stronger on the main part of body chamber.

G. venustum Matsumoto (1984b, p. 5, pl. 3, figs. 1–2) (recently restudied by Matsumoto & Toshimitsu, 1995, p. 2, pls. 1–8), from the upper part of lower Maastrichtian of Hokkaido, is similar to *G. tenuiliratum* and *G. crassicostatum* in the mode of coiling and general configuration of ornament, but is much larger (220–240 mm diameter); its extremely fine ventral lirae persist to the end of larger phragmocone (at D = 130 mm), and the main part of its adult body chamber has weaker, less flexuous major ribs and shows a peculiar (dorsally subtrapezoidal and ventrally semi-oval) cross-section.

G. hamanakense Matsumoto & Yoshida (1979, p. 68, pl. 10, figs. 1–3; pl. 11, figs. 1–2; text-fig. 2), from the Akkeshi Formation (s. str., i.e. in Kiminami's sense as indicated *op. cit.*, table 1) (upper part of Maastrichtian) of eastern Hokkaido, resembles *G. tenuiliratum* in the average size of adult shells and in having narrow but distinct, flexuous major ribs on the body chamber. It also has flexuous, periodic flares with accompanied constrictions and numerous lirae on the septate whorls. The lirae are moderately coarse on the umbilical margin and become finer and more numerous outward. The outstanding differences are the lower ratio of whorl expansion and the consequent wider umbilicus in *G. hamanakense* as compared with *G. tenuiliratum* and in the persistent development of the extremely fine ventral lirae up to the adult body chamber in the former.

To sum up, the character of the multipartite, very fine lirae on the venter developed progressively with geological age from *G. tenuiliratum* to *G. hamanakense*, but in other characters the five species discussed above show their own particular features, respectively. At any rate, these species are allied to one another and can be regarded as forming a subgroup in *Gaudryceras*. As *Neogaudryceras* was proposed by Shimizu (1934), with *G. tenuiliratum* as the type species, it could be used as a subgenus for this subgroup. There are, however, several species whose relationships with the above subgroup are still ambiguous. Moreover, the difference between *G. tenuiliratum* and *G. mite* does not seem to be significant. At the moment, I think it too hasty to resurrect *Neogaudryceras*. The idea suggested above should be examined further.

Occurrence. – *G. tenuiliratum* ranges from Coniacian to lower part of Campanian, as far as the reliable stratigraphical records are concerned. It occurs fairly commonly in Japan and Sakhalin. Often a considerable number of individuals are contained in a nodule embedded in sediments of muddy facies (see frontispiece).

←Figure 67. *Gaudryceras tenuiliratum* Yabe and *G. denseplicatum* (Jimbo).
A–D: UMUT. MM19701 [= GT. I-452], injured young shell of *G. tenuiliratum*. A: Phragmocone plus a displaced portion of body chamber, ×1. B: Another ventral view, showing an injured part, ×1. C, D: A part of phragmocone, magnified to show the characteristic ornament on the ventral part, ×1.5. E: GK. H8452B, young shell of *G. denseplicatum*, ×1. F: GK. H8452A, small form of *G. denseplicatum*, ×1. Scale bar: 10 mm.

Gaudryceras aff. *G. kayei* (Forbes, 1846)

Figures 68–69

Lectotype of G. kayei. – BMNH C51050 (the original of Forbes, 1846, pl. 8, fig. 3), from the Valudayur Formation of Pondicherry. South India, designated by Matsumoto & Yoshida (1979, p. 70).

Material. – Four specimens from the Coniacian strata of the Ikushumbetsu area: GK. H8461 (Fig. 68A) collected by K. Sanada from the Zone with *Forresteria alluaudi* in the Ponbetsu-go-no-sawa; GK. H8414 (Figs. 68B, D) collected by T. Takahashi from the *Kossmaticeras* bearing bed in the left branch of the Oku-futamata-zawa, a branch of the Kumaoi-zawa; GK. H8462 (Figs. 68C and 69A) collected by T.M. at loc. Ik1381p4 of the Kumaoi-zawa; MCM. A246 [YKC 050511] (Fig. 69B) collected by Y. Kawashita, from the left branch of the Horomui-zawa, upper-most reaches of the Ikushumbetsu River, associated with *Inoceramus uwajimensis* Yehara.

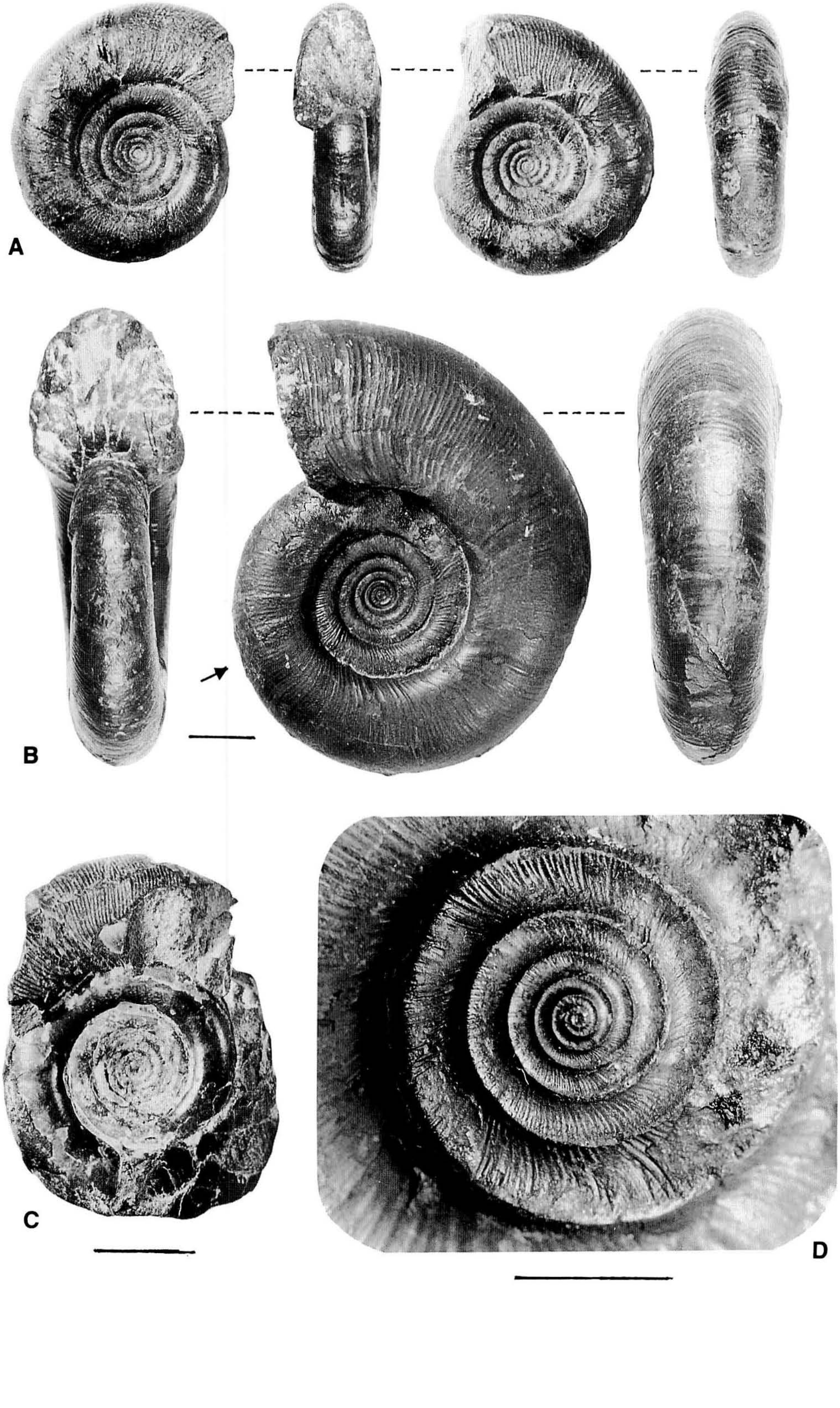
Description. – The shell is rather small, but the full grown shell, as represented by MCM. A246, reaches D = 80 mm. GK. H8414, with D = 70 mm, is also nearly complete. In these specimens the body chamber occupies three quarters of the outer whorl and the last suture is located at about D = 50 mm and 45 mm respectively.

The shell is fairly polygyral. It consists of the protoconch plus 7.5 whorls, as is observable in well-preserved examples (e.g. GK. H8414). The coiling is rather evolute in youth, becoming moderate later. The ratio of increase in whorl height (as indicated by H/h) is low at first, moderate in the middle growth stage and becomes fairly high later. The umbilicus is, consequently very wide in youth, with U = about 50 (±2) percent of D, but becoming less so, indicating finally U = 40 or 39 percent of D at the end.

The whorl is subrounded in section, depressed (H<W) in youth, showing a more or less broadly arched venter. Sooner or later in the middle growth stage, it becomes nearly as high as broad. In maturity it is somewhat compressed, showing a rather narrowly arched venter. The flanks are rather gently convex or even nearly flat, except for a very young stage. The maximum whorl breadth is immediately outside the abruptly bent umbilical shoulder. The umbilical wall is very low to rather low, but it is steeply inclined and sometimes almost vertical.

The first whorl up to the first constriction is smooth, the second whorl is marked frequently by flanges as in other species of *Gaudryceras*. The periodic constrictions, 5 or 6 per whorl, on the main part of phragmocone, are prorsiradiate and projected on the venter. They are accompanied by collars on the shell. The shell layer is preserved in GK. H8461 and GK. H8414 and also in a part of GK. H8462. On its external surface fine lirae run roughly in parallel to the periodic collars and are gently sigmoidal in lateral view. They show bifurca-

Figure 68. *Gaudryceras* aff. *G. kayei* (Forbes). →
A: GK. H8461, young shell, ×1. B: GK. H8414, ×1. C: GK. H8462, lateral view of an imperfect young shell (see Fig. 69A for other views), ×1.5. D: Inner whorls of GK. H8414, magnified to show the details, ×2.4. Scale bar: 10 mm.


A
B
C
D

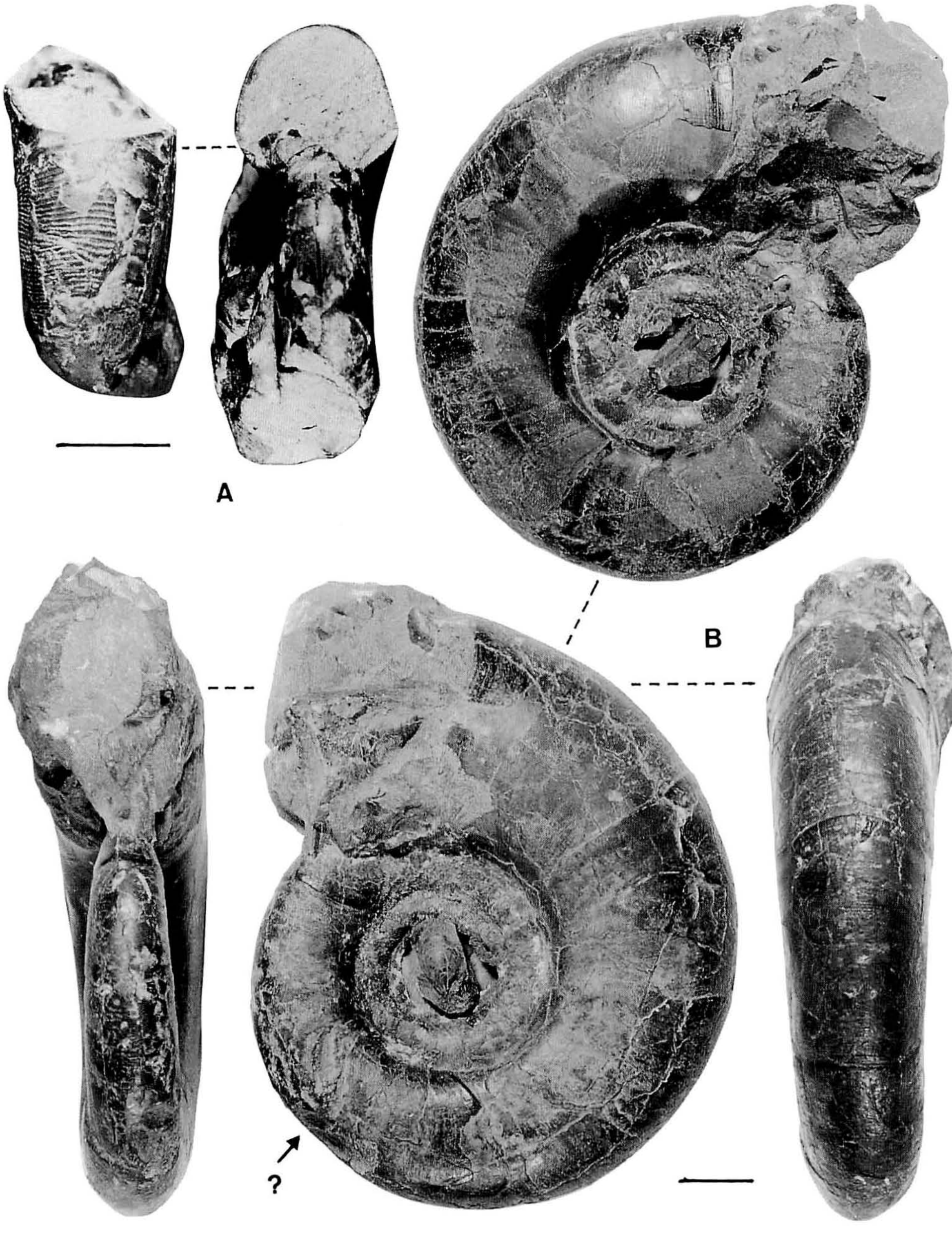


Figure 69. *Gaudryceras* aff. *kayei* (Forbes).
A: GK. H8462, venter of outer whorl and end-on view of the same specimen as Fig. 67C, ×1.5. B: MCM. A246 [YKC. 050511], adult, ×1. Young shells of *Inoceramus uwajimensis* Yehara are contained in the rock matrix. Scale bar: 10 mm.

tion and intercalation on the flank and are weakly or moderately projected on the venter. They never show multiple branching as in *Vertebrites*. The ornament on the body chamber is similar to that on the phragmocone, but the constrictions become fainter and the periodic collars can be called narrow major ribs. Their frequency is similar to that on the phragmocone. The lirae are also similar to those on the phragmocone, although their density varies to some extent from place to place. On the well-preserved surface they are fine and sharp crested and are separated by slightly wider interspaces.

The suture is similar to that of other *Gaudryceras* species at the corresponding size.

Dimensions. – See Table 19.

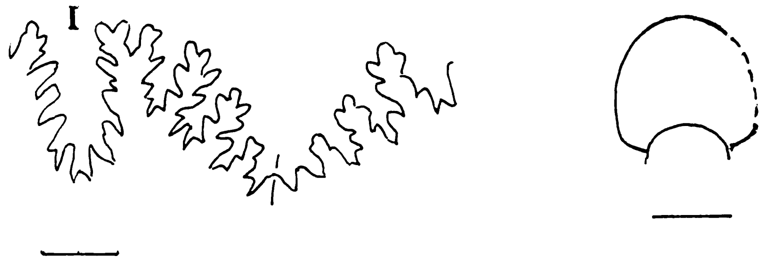
Discussion. – The specimens from Hokkaido described above represent a species that is closely allied to *G. kayei* (Forbes), which was redescribed by Henderson & McNamara (1985) from western Australia, Stinnisbeck (1986) from Chile and Kennedy & Henderson (1992) from the type area in South India.

In this paper, however, I do not identify our form with that species, because I notice some differences and because there are still ambiguities in previous papers. The details are as follows: (1) The shell form of the younger stages is very similar between the two species. As to the shells of later growth stages, with diameters over 70 mm, the present form has somewhat narrower umbilicus and higher ratio of whorl expansion as compared with the form from South India and West Australia. (2) The number of coiling whorls is not recorded from the specimens from Australia and India. Stinnesbeck (1986, p. 198) reported 8 or 9 for the specimens from Chile with diameters over 25 mm. I counted 9.5 for an example (BMNH C51049) from South India. On the other hand, GK. H8414 from Hokkaido, which has a slightly larger diameter than that specimen, consists of 7.5 whorls around the protoconch. (3) The difference in the fineness or density of lirae is not clear on account of poor preservation of the test on the specimens illustrated by previous authors. BMNH C51049 shows a portion of the test on which lirae look very fine and dense as illustrated by Kossmat (1895, pl. 17,

Table 19. Dimensions of *Gaudryceras* aff. *kayei.*

Specimen	D	U	U/D	H	H/D	B	B/D	B/H	H/h
GK. H8461 (E)	40.0	19.2	.48	13.0	.33	12.0	.30	.92	1.67
" (E-120°)	32.2	16.2	.50	9.7	.30	10.8	.34	1.11	1.54
GK. H8462*	25.6	13.4	.52	7.1	.28	8.6	.34	1.21	1.39
GK. H8414 (E)	70.0	28.0	.40	26.8	.38	24.0	.34	.89	1.76
" (E-160°)	50.0	22.4	.45	17.0	.33	16.6	.33	.98	1.60
YKC. 050511 (E)	80.0	31.0	.39	31.0	.39	24.0	.30	.77	1.72
G. kayei from India for comparison (T.M.'s measurements)									
LT	32.0	16.5	.52	9.6	.30	11.4	.36	1.19	1.63
BMNH C51049	62.0	29.8	.48	19.4	.31	18.7	.30	.96	1.52
" "	56.4	26.6	.47	17.0	.30	19.0	.34	1.12	1.33

*Measurements of GK. H8462 are on the inner whorl at about 270° back from the preserved end. H [= Wh] of LT was indicated as 7.2 by Henderson & McNamara (1985) and also by Kennedy & Henderson (1992), but this is evidently a misprint.



A B

Figure 70. *Gaudryceras kayei* (Forbes).
A: Internal suture of the lectotype, BMNH C51050 at H = 5.5 mm, ×2. B: Whorl-section of BMNH C51049 at D = 56.4 mm, ×1. Scale bar: 2 mm for A; 10 mm for B. (T. M. *delin.*)

fig. 2a) and Kennedy & Henderson (1992, pl. 5, figs. 40–41). The latter authors (*op. cit.*, p. 404) indicated the number of lirae about 80 per half whorl, but did not show the place of counting or size of the whorl. In GK. H8414, for example, about 80 lirae are counted immediately outside of the umbilical edge per half whorl at D = 68 mm and more than 120 at about the ventrolateral shoulder in the same span of the shell. (4) The difference in geologic age should be considered.

It should be noted that there is some resemblance between the species described above and *G. mite* (Hauer), especially when specimens of a similar size are compared (see Fig. 43). The latter has, however, more rounded whorl, with a more evenly rounded venter, more convex flanks and well-rounded umbilical edges. The present species may have diverged from some form of *G. mite* and may be ancestral to *G. kayei.*

I previously wrote (Matsumoto, 1959b, p. 146–147) that *Lytoceras* (*Gaudryceras*) *coalingense* Anderson (1958, p. 184, pl. 68, fig. 1) and *L.* (*G.*) *birkhauseri* Anderson (1958, p. 185, pl. 68, fig. 4, 4a), from the Maastrichtian of California, could be synonyms of *Gaudryceras* (*Vertebrites*) *kayei* (Forbes). Besides the difference in whorl shape, which I mentioned, the holotypes of the Anderson's species are still septate at diameter of about 70 mm and must have been originally much larger than the hitherto known examples of *G. kayei*. Moreover, their lirae and constrictions do not show ventral projection and are not sigmoidal in lateral view. For these reasons I am now inclined to consider them outside the variation exhibited by *G. kayei* and also that of *G.* aff. *kayei* described above.

Genus *Zelandites* Marshall, 1926

Type species. – *Zelandites kaiparaensis* Marshall, 1926.

Remarks. – Wright and Kennedy (1984, p. 52) have given adequate comments on this genus. The species of *Zelandites* from Japan and South Sakhalin were described by Matsumoto (1938). Although additional specimens are available, the material is not sufficient to warrant revised descriptions. The following is a list of species and their occurrences, with a concise note on the last species:

Zelandites cf. *odiensis* (Kossmat, 1895): Upper Albian of the Soeushinai area (Hashimoto *et al.*, 1965) and Lower Cenomanian of the Abeshinai-Saku and Shiyubari areas (Matsumoto, 1942).

Z. inflatus Matsumoto: (1959a, p. 74, pl. 23, figs. 2–5; pl. 20, fig. 1; text-fig. 14): Lower Cenomanian of the Ikushunbetsu Valley; fairly common in the Zone of *Mantelliceras japonicum* (see Matsumoto *et al.*, 1969, p. 287; MCM, 1988, figs. 91–92).

Z. europae Wright & Kennedy, 1984: Lower Cenomanian of the Ikushunbetsu Valley; found rarely in the *Acompsoceras*-bearing bed above the zone of *Mantelliceras japonicum* (see Matsumoto & Takahashi, 1992, p. 1145).

Z. mihoensis Matsumoto, 1938: Turonian of the Naibuchi, Abeshinai-Saku and Oyubari areas.

Z. kawanoi (Jimbo, 1894): Santonian and Campanian of the Urakawa, Ikushunbetsu, Abeshinai-Saku areas and South Sakhalin.

Z. japonicus Matsumoto, 1938: Maastrichtian of South Sakhalin and eastern Hokkaido. This species was proposed as a variety of *Z. varuna* (Forbes) by Matsumoto (1938, p. 140) but regarded as a synonym of *Z. varuna* by Macellari (1986, p. 14). I appreciate the observation of Kennedy and Henderson (1992, p. 405) to distinguish it from *Z. varuna*. GT. I-2502 [= UMUT. MM9123] (Matsumoto, 1938, pl. 14, fig. 5a, b), an adult specimen, is here designated as the **lectotype** of *Z. japonicus*. This species has frequent constrictions or grooves which are prorsiradiate from the umbilical seam to about the mid-flank and bent there, running radially on the outer flank onto the venter. Depending on the conditions of preservation, the grooves may look faint or absent, but actually they do exist even in the young to middle growth stages. Taking into consideration of the above diagnosis, *Z.* cf. *varuna* from the Maastrichtian of Southwest Japan (Morozumi, 1985, p. 32, pl. 9, fig. 2; text-fig. 8) should be reexamined. Incidentally, BMNH C51059 was designated as the lectotype of *Ammonites varuna* Forbes, 1846 by Matsumoto (1988a, p. 184) prior to the designation by Kennedy and Henderson (1992, p. 404).

CONCLUDING REMARKS

The principal results obtained through this study are summarized in this chapter.

1. Results on the systematics

(1) As no species of undoubted *Eogaudryceras* is at my disposal, I am unable to discuss the phylogenetic origin of the family Gaudryceratidae. In almost all the examined genera, the whorl of early growth stage, that succeeds the first constriction, shows a number of flanges with fairly high or moderate frequency. This may give some suggestion to the problem of origin, but I hesitate to discuss further.

(2) The pattern of sutures, as typically manifested in this paper by *Gaudryceras tenuiliratum* (Fig. 1), is fundamentally maintained in *Eogaudryceras, Anagaudryceras* and *Gaudryceras*. These three genera, which contain a number of species and are widely distributed, can be regarded as forming the main stock of the family. In certain other genera, such as *Zelandites* and *Vertebrites*, the fundamental suture pattern is somewhat, but never greatly modified. The modification is considerable in *Gabbioceras* and *Jauberticeras*, as discussed by Murphy (1967c). No species of these two genera is, however, described in this paper.

(3) *Parajaubertella* is defined precisely in this paper. It is closely related to and derived from the main stock of *Eogaudryceras-Anagaudryceras*. The similarity in the shape of shell between *Parajaubertella* and *Gabbioceras* with angular shoulders in the juvenile stages is homeomorphy.

(4) *Miogaudryceras* is proposed as an offshoot from the main stock near the diverging point of *Anagaudryceras* and *Gaudryceras*. Its type species is *M. yokoii* n. sp. from the Lower Cenomanian of Hokkaido. Another unnamed, probably new species is reported frm higher horizons of the Cenomanian.

It is noted that the lirae of *Anagaudryceras madraspatanum* and those of the septate whorls of *Miogaudryceras* are somewhat coarser than those of the majority of *Anagaudryceras* species. This feature may foretell the development towards sharper lirae of *Gaudryceras*.

(5) The so-called *A. involvulum* group is criticized as mesleading. Various species of *Anagaudryceras* should not be so simply classified. They show divergence in various ways. Almost all the species of *Anagaudryceras* that I have studied have major ribs in maturity. The major ribs can be described as adult *sacya*-type in such "typical" species as *A. sacya* (Forbes) and some others, but they are developed or modified in other ways in some other species. The characters of the immature or septate stage also vary between species.

Thus, *A. howarthi* n. sp. may be regarded as the so-called *involvulum* type in its septate stage, but its adult body chamber has low and broad *sacya*-type major ribs in the adapical part and more crowded and round-crested ones in the adoral part. It is based on mid-Turonian specimens.

Again, *A. yamashitai* (Yabe) has been referred to the "*involvulum* group" with respect to the characters of septate stage (Howarth, 1966; Kennedy & Klinger, 1979), but its adult body chamber has narrower major ribs which seem to have developed from the adoral margin of the broad, but low, scale-like elevations.

(6) *A. limatum* (Yabe) of late Turonian to Coniacian age resembles *A. sacya* in septate stage,

but the main part of its adult body chamber is characterized by strongly folded major ribs. For some extent from the last part of the phragmocone to the beginning of body chamber, the ribs may be narrower than those of the main part of body chamber, but they are considerably raised.

Narrow but fairly strong major ribs like those mentioned above persist for a longer period and characterize the main part of the body chamber in *A. yokoyamai* (Yabe) and *A. politissimum* (Kossmat) of later ages. The ornament of these species is apparently similar to that of certain species of early Cretaceous *Eogaudryceras.* This may imply general affinities of the two genera, but no direct relationship could be presumed between the species of much separated geological age. *A. yokoyamai* and *A. politissimum* are intimately related with such species as *A. limatum* and *A. yamashitai*, and thus, in my opinion they should be assigned to *Anagaudryceras.*

The ornament of a large adult body chamber of *A. seymouriense* Macellari, 1986 has yet to be made clear. *A. nanum* Matsumoto, 1985 and *A. matsumotoi* Morozumi, 1985 are small species which have their own peculiar features (Matsumoto *et al.*, 1985). They show some aspects of diversity in *Anagaudryceras.*

(7) *Gaudryceras* includes many species, some of which are closely allied to each other. Through careful studies, however, the described species from Japan and related regions are distinguished by their own diagnostic characters. They reveal varieties of divergence in the genus, but any attempt at grouping them into subgenera would not be successful in the present state of knowledge.

(8) It should be noted that the *Gaudryceras* species of earlier geological ages, such as *G. stefaninii* Venzo of Albian and Cenomanian ages and *G.* n. sp. (?) (in this paper) of early Turonian age, have lirae with little or almost no ventrolateral flexuosity. Their very large size is rather peculiar and *G.* n. sp. (?) has unusually compressed whorls, showing already a kind of specialization. *G. subcostatum* n. sp., from the Cenomanian of Hokkaido, shows another aspect of specialization in its small size and less flexuous, but prorsiradiate lirae and riblets.

(9) *G. mite* (Hauer) has typically flexuous ornament and is intermediate in shell shape within the genus. It attains to fairly large size, but its major ribs are not well developed and there is some variation in their appearance. *G. denseplicatum* (Jimbo) is allied to and nearly contemporary with *G. mite*, but has well-developed, major ribs in maturity. *G. intermedium* Yabe is defined as distinct from *G. denseplicatum* in having narrow but sharply raised major ribs from fairly young to very large adult stage. The two species are closely allied, but *G. denseplicatum* occurs frequently in the Turonian and Coniacian strata, whereas *G. intermedium* predominates in the Santonian and Lower Campanian.

G. kayei (Forbes) was thought to be an ally of *Vertebrites murdochi* Murshall, because of the resemblance in the evolute coiling. It is suggested in this paper that *G. kayei* of Santonian to Maastrichtian age is more likely to have descended from *G. mite*, on account of the find of a Coniacian species, which is described tentatively under *G.* aff. *G. kayei.*

(10) *G. tenuiliratum* Yabe has been confused or misunderstood since 1903, but is now characterized by a large number of specimens in addition to the lectotype. It is rather small to medium sized; in young stage the flexuous lirae on the flanks are branched and also with some intercalation into extremely fine and dense lirae on the venter; later the lirae are normal and on the adult body chamber the periodic collars are replaced by frequent major ribs and the lirae become more prominent and less dense;, evolute young shells become more involute

in maturity.

The ornament of multipartite, very fine lirae on the venter in the young stage of *G. tenuiliratum* developed progressively with geological age to that in the adult stage of *G. hamanakense* Matsumoto & Yoshida, by way of *G. crassicostatum* (Jimbo) and *G. venustum* Matsumoto, but in other respects these species have their own particular characters. In these and other species of Campanian and Maastrichtian ages, divergence in various ways are shown. This has already been concluded on the grounds of the systematic descriptions (Matsumoto, 1984; Matsumoto *et al.*, 1985; Matsumoto & Toshimitsu, 1995).

2. Geological occurrences

The geological occurrences of the investigated species are summarized in tabular form. In the list below: the species with two asterisks are based on a large collection from various areas in Japan and South Sakhalin; the species with one asterisk do not occur so abundantly in Japan and S. Sakhalin, but distributed extensively outside of this region; the species without an asterisk are defined on a small collection from a limited span of stratigraphic sequence of a few areas within the region.

Parajaubertella kawakitana Matsumoto**: Lower Cenomanian
Miogaudryceras yokoii n. sp.: Lower Cenomanian
M. n. sp. (?): Cenomanian
Angaudryceras sacya (Forbes)**: Albian-Cenomanian
A. aff. *A. whitneyi* (Gabb): Upper Albian
A. madraspatanum (Stoliczka): Upper Albian-Cenomanian
A. howarthi n. sp.: Turonian
A. limatum (Yabe)**: Upper Turonian-Coniacian
*A. yamashitai*** (Yabe): Coniacian-Santonian and possibly lower part of Campanian
A. yokoyamai (Yabe)**: mainly Santonian and possibly lower part of Campanian
A. politissimum (Kossmat)*: Coniacian-Maastrichtian
A. matsumotoi Morozumi: Maastrichtian
A. nanum Matsumoto: Campanian
A. tetragonum Matsumoto & Kanie: Maastrichtian
A. cf. *A. seymouriense* Macellari: Maastrichtian
Gaudryceras subcostatum n. sp.: Cenomanian
G. stefaninii Venzo*: Upper Albian-Cenomanian
G. n. sp. (?): Lower Turonian
G. mite (Hauer)*: Turonian-Campanian
G. denseplicatum (Jimbo)**: Turonian-Santonian and possibly lower part of Campanian
G. intermedium (Yabe)**: Coniacian (?), Santonian and possibly lower part of Campanian
G. aff. *G. kayei* (Forbes): Coniacian
G. tenuiliratum Yabe**: Coniacian-lower part of Campanian
G. striatum (Jimbo)**: Campanian
G. crassicostatum (Jimbo)**: Campanian
G. venustum Matsumoto: Lower Maastrichtian
G. hamanakense Matsumoto & Yoshida: Upper Maastrichtian
G. mamiyai Matsumoto & Miyauchi: Campanian

G. izumiense Matsumoto & Morozumi: Maastrichtian
G. tombetsense Matsumoto: Maastrichtian
Zelandites spp.: See p. 132–133.

APPENDIX

Further problems

Various morphological characters that are used in the systematic descriptions are interesting in their functional implications and, thus, must be concerned with ecological aspects of the described species. These problems exceed the main purpose of this paper and need further analytical investigations. I give here, however, short and preliminary remarks on them as an Appendix.

(1) The lirae on the surface of the outer primsatic shell layer are interesting among other morphological features of gaudryceratid ammonites. Their fineness, density, sharpness and mode of branching or intercalation are important criteria for generic and specific distinction. Also they may have evolved phylogenetically.

Some of the well-preserved specimens of *Gaudryceras* have been already used to examine the structural features of shell wall. The wall structure was discussed with respect to the phylogenetic relationship between certain coleoid and ammonoid cephalopoda (Doguzhaeva & Mutvei, 1993). Details of ornamentation should be studied in connection with the wall structure, as suggested by Hirano (1975), Drushchitz *et al.* (1978) and Doguzhaeva (1981).

In the late growth stage of some species the lirae on the outer prismatic layer become coarser and have weakly elevated bases on the underlying nacreous layer; hence, they can be called riblets or subcostae. In addition to the periodic collars which are associated behind the constrictions on septate whorls, major ribs are normally developed in more or less late growth stages and are combined with the lirae. The degree of their development, their strength, sharpness or roundness, style of plication, and also their flexuosity are used as significant criteria in taxonomy. The features may change with growth and also seem to have evolved phylogenetically.

All the characters mentioned above are comprehensively called ornament, but their functional implications must be more than mere decoration. It could be presumed, for instance, that the flexuosity of lirae and ribs may be a factor of streaming, whereas the thick major ribs of adult body chamber may be favorable for steady repose on bottom sediments. The sharply raised, narrower major ribs may act as protection against predators. This sort of hypothetical idea should be confirmed by various lines of evidence.

How was the difference in the mode of life between *Anagaudryceras* with very fine and weak lirae and *Gaudryceras* with sharp crested lirae? What was the merit of the extremely fine, multipartite lirae on the venter of a certain species of *Gaudryceras*? These are examples of the problems about the functional implications of certain morphological characters. They are here pointed out for further studies.

A periostracum is suggested to exist in a certain species of *Gaudryceras*. To inspect the same structure in more gaudryceratid species is a problem which is concerned with their mode of life and ecological aspects.

(2) The shell size of gaudryceratid species varies to a great extent; namely from about 25 or 30 mm in diameters of adult shells (e.g., *Zelandites kawanoi, Anagaudryceras nanum*, etc.) to nearly 450 or even 500 mm (e.g. *Gaudryceras intermedium*). In some cases variation in

size may occur within a species. There may be merits of particular size for respective species, although it is often difficult to give a reasonable explanation.

The problem of sexual dimorphism in shell size has been discussed on *G. denseplicatum* and *G. intermedium*. I am rather inclined to deny a marked difference in size between male and female shells in the above two species and also in *Anagaudryceras limatum*. Is this interpretation maintained in other species of the Gaudryceratidae?

(3) The shell shape is also important for taxonomy and ecology. It is made up of several morphological factors, such as size and shape of ammonitella, number and mode of coiling, degree of involution, ratio of whorl expansion, umbilical ratio (U/D), breadth-height ratio (B/H) of a whorl, outline of whorl cross-section, length of body chamber and features of the peristome. In general the shell shape changes with growth; for example in many species of *Anagaudryceras* and *Gaudryceras*, young whorls are comparatively evolute and broad reniform or broadly rounded in cross-section; in the middle growth stage whorls become more of less involute, with an intermediate ratio of U/D, and subcircular in cross-section; in the late stages, including the adult body chamber, the shell is comparatively involute with smaller ratios of U/D and B/H, and suboval or subelliptical in cross-section. The details of the ontogenetic change are dissimilar between species and may vary within a species. The change with growth in shell shape and also in ornamentation must have intimate relationship to the life history of a species, although it is difficult to state precisely how the mode of life changed with growth in respective species.

Zelandies is particular in its small size and progressive involution and compression of whorls with growth. It is rather similar to certain desmoceratid species in shell shape and septal fluting, but what kind of adaptation was taken by *Zelandites* is not known in detail.

Parajaubertella and also homeomorphic *Gabbioceras* are interesting in having globular juvenile shells with angular or subangular umbilical or ventrolateral edges. What was the merit for these ammonites in having such special shape in their young stage?

(4) The body chamber of the examined species of the Gaudryceratidae is moderately long. Namely, it occupies about three quarters (270°) of the last whorl. This is longer than that in most cases of the Acanthoceratidae, i.e. half a whorl. Speaking generally, the main soft body was long and subcircular to subelliptical in cross-section in the former in contrast to short and thick, roughly subquadrate one of the latter. In this connection, the phragmocone is more polygyral and longer in the former as compared with the latter. The apertural margin of the shell is simple in both groups, as far as the examined examples are concerned. The aptychi, or anaptychi, and radula are contained in the buccal mass which could protrude from the shell. In fact jaw apparati of *Tetragonites, Gaudryceras* and *Zelandites* from Hokkaido were reported in several papers (e.g. Lehmann *et al.*, 1980; Tanabe *et al.*, 1982; Kanie, 1982), although this kind of organs is omitted from the present description.

(5) In addition to the characters mentioned above, the type and complexity of septal sutures, shape and frequency of septa, and features of septal neck and siphuncle, as expressed by "Septal Strength Index" and "Siphuncle Strength Index", are altogether important for studies of buoyancy and locomotion in or under sea-waters and habitats of various kinds of ammonites. Westermann (1990) has recently presented an interesting paper on habitats of overall Jurassic-Cretaceous ammonoids from analysis of morphological characters, stratigraphy and taphonomy. *Lytoceras*, as a representative of Lytoceratidae, is interpreted as an oceanic, nektobenthic dweller of fairly deep sea bottom, with ability of nekto-pelagic, vertical migration.

This interpretation may be applied generally to gaudryceratid ammonites, but varieties at generic and specific ranks should be worked out in more detail by precise analytical investigations. The abundance of the gaudryceratid ammonites around the oceanic regions and their scarcity in shallow epicontinental sea would be explained by their original habitats.

ACKNOWLEDGMENTS

I started to study the gaudryceratid ammonites when I was a graduate student of the University of Tokyo, although the work was preliminary. I should like to express my sincere thanks to the late Professor Hisakatsu Yabe, the late Professor Takeo Kato and Professor Emeritus Teiichi Kobayashi for their warm encouragements to me during the period of that study.

At Prof. T. Kobayashi's suggestion, I catalogued there the specimens of Cretaceous ammonites and some others described by Jimbo (1894) and Yabe (1903, 1904) and also listed by M. Kawada (1929) and those which I collected during the term 1935–1938 under GT. I-numbers. These specimens were stored in the Geological Institute, University of Tokyo, except for temporary removal to countryside during World War II. When the University Museum, University of Tokyo was opened in 1966, they were transferred there and the described specimens of them have been catalogued under UMUT. MM-numbers [MM are Mesozoic Mollusca]. I frequently visited there from Fukuoka and for the study of the gaudryceratids and I owed much to Professors Itaru Hayami and Kazushige Tanabe and especially to Mr. Takeo Ichikawa for every facility which they offered to me.

During my study abroad I examined several gaudriceratid specimens. I should record here my debt of gratitude to Mr. D. Phillips and Dr. M. K. Howarth (BMNH), Drs. C. W. Wright (Beaminster), J. M. Hancock (London), W. J. Kennedy (Oxford), the late Professors Hubert G. Schenck (Stanford), Bernhard Kummel (Harvard) and also the late Dr. L. G. Hertlein (California Academy of Sciences) for their help in various ways.

I wish to thank also a number of colleagues who kindly helped me in my study at the University of Kyushu. For a fairly long period I was engaged in the study of the Desmocerataceae, Acanthocerataceae and some heteromorpha, but from time to time gaudryceratids were dealt with. I should especially express my gratitude to Drs. Ikuwo Obata, Yoshiro Ueda, I. Hayami, Hakuyu Okada, Hiromichi Hirano, K. Tanabe and Seiichi Toshimitsu for their joyful cooperation as members of Kyushu University. In addition to them, a number of kind persons assisted me in my previous and recent field works in Hokkaido, of whom the late Mr. Tatsuo Muramoto, Messrs Kikuo Muramoto, Takemi Takahashi, Kenji Sanada, Yoshitaro Kawashita, Toshio Shimanuki, Masatoshi Kera, Yasuji Kera and Shigehiro Uchida, also Professor Tamio Nishida (Saga University), Ms. Yuko Kyuma and Ms. Kikue Kato, would incur my gratitude. All of them and also Dr. Akitoshi Inoma, Messrs. Katsujo Yokoi, Masashi Kawano†, Kanichi Fujiwara, Takashi Sasaki, Mamoru Shimomura, Ryoichi Sato, Takayuki Yokoi and Hiroji Tsuda and also Ms. Yuriko Matsunaga and Ms. Toku Koiso showed me valuable specimens for this study. Some of them were donated to Kyushu University. My thanks are extended to the above persons and also Drs. Yasumitsu Kanie, Masaki Matsukawa, Masao Futakami and again Dr. A. Inoma for their kindness in giving me necessary information.

To study the gaudryceratid specimens I visited the Mikasa City Museum, where Mr. Kikuo Muramoto and Mr. Koji Hasegawa helped me, and by courtesy of Dr. Morio Akamatsu I had an opportunity to inspect several specimens on display at the Historical Museum of Hokkaido (Sapporo). I also examined some of the specimens held at Tohoku University (Sendai), where the late Professor Kotora Hatai and Professor Tamio Kotaka generously gave facilities to my study. The specimens treated by Dr. Edmund Naumann and described by Yokoyama (1890) are held in the "Bayer Staatssammlung für Paläontologie und historische Geologie, München" and by chance I was able to study some of them (including the gaudryceratids) at the Fossa Magna Museum (Itoigawa), where they were exhibited for a short while on loan from Munich. For this affair I owe much to the authorities of the two Museums and also Dr. Hiroshi Miyajima, Mr. Koh Takenouchi and Mr. Kenichi Miyakita who kindly helped me in my work at Itoigawa and took photographs of the specimens.

My thanks are extended to the late Professor Jost Wiedmann (Tübingen), who offered valuable suggestions to me during his stay (August, 1991) in Fukuoka, and also to Professor H. Hirano (Waseda University) for suggestive discussions, although we are not always of the same opinion.

I am especially indebted to Professor Emeritus Michael A. Murphy of the University of California (Davis), and Dr. Ikuwo Obata of the Institute of Natural History (Tokyo) for their kindness in reading critically the lengthy first draft of this paper, giving me constructive comments and suggestions.

I should like to record here my special appreciation to Dr. Masayuki Noda for his friendly help in taking the majority of the photographs in this paper. Likewise, I am much obliged to the late Mr. Chuzaburo Ueki, the former photographer in the University of Tokyo, and Messrs Katsumi Shinohara and again Kikuwo Muramoto, who kindly took photographs of some other specimens in UMUT. and MCM. The colour photograph of the frontispiece was kindly taken by Dr. J. Yanagida.

I wish to thank Professor Hakuyu Okada who kindly offered me necessary facility to complete this work in the Department of Earth and Planetary Sciences, Kyushu University. My thanks are extended to Miss Akiko Murakami and Miss Kazuko Mori, who both assisted me joyfully in preparing the typescript.

Finally, I owe much to Professor Juichi Yanagida, the Series Editor, and also Miss Seiko Hayakawa, secretary, in setting forth the final manuscript as Special Paper No. 35 of the Palaeontological Society of Japan, and should like to record here the debt of gratitude to the Ministry of Education, Science and Culture (Monbusho) for the subsidy which facilitated this publication.

Japanese Place Names

Abeshinai アベシナイ［安川］, Akkeshi 厚岸, Anoro アノロ, Ban-no-sawa 盤の沢, Bibai 美唄, Chienaibo チエナイボ, Chinomi［Tinomi］乳呑, Chiraibetsu 知来別, Efue［Ibui］絵笛, Ekimoanruru［Ekimonaanoro］エキモアンルル, Enbetsu［Wembets］遠別, Furenai 振内, Ganseki-zawa 岩石沢, Go-no-sawa 五の沢, Haboro 羽幌, Hakobuchi 函淵, Hamanaka 浜中, Hatonosu 鳩の巣, Hetonai 辺富内［ヘトナイ］, Hidaka 日高, Hidarimata-zawa 左股沢, Higure-zawa 日暮沢, Hikage-zawa 日蔭沢, Hirotomi 広富, Hobetsu［Popets］穂別, Hokkaido 北海道, Horomui-zawa 幌向沢, Ikushunbetsu［Ikushumbets］幾春別, Ikandai 井寒台, Isojiro-zawa 磯次郎沢, Itoigawa 糸魚川, Iwamizawa 岩見沢, Juhachi-rinpan-ichi-no-sawa 十八林班一の沢, Juhachi-rinpan-ni-no-sawa 十八林班二の沢, Kami-ichi-no-sawa 上一の沢, Kami-kinenbetsu-zawa 上記念別沢, Kawakita 川北, Kikume-zawa 菊面沢, Kitami 北見, Kita-no-sawa 北の沢, Komaki-zawa 小巻沢, Kotanbetsu 古丹別, Kuma-no-sawa 熊の沢, Kumaoi-zawa 熊追沢, Kyushu 九州, Makaushuppe マカウシュッペ, Manji 万字, Masago-zawa 真砂沢, Miho 美保, Mikasa 三笠, Monbetsu 門別, Mukobetsu 向別, Naibuchi［Naiba］内淵, Nakagawa 中川, Nemuro 根室, Nioi-zawa ニオイ沢, Nishichirashinai 西知良志内, Nishihorobetsu 西幌別, Obira 小平, Obirashibe［Opiraushibets］小平蘂, Oku-futamata-zawa 奥二股沢, Onnebetsu 温根別, Oyubari 大夕張, Penke-moyuparo ペンケモユーパロ,［Taki-no-sawa］, Penke-ushap-zawa ペンケウシャップ沢, Ponbetsu-go-no-sawa 奔別五の沢, Popets ポベツ［Hobetsu］, Raunenai-zawa ラウネナイ沢, Rubeshibe-goe-no-sawa ルベシベ越の沢, Saku 佐久, Saku-gakko-no-sawa 佐久学校の沢, Samata-zawa 左股沢, Santan-gawa 三丹川, Sanushibe［Sanushuppe］サヌシベ, Saroma 佐呂間, Satoh-no-sawa 佐藤の沢, Sendai 仙台, Shakin-zawa 砂金沢, Shibunnai 志文内, Shikoku 四国, Shimukappu 占冠, Shizunai 静内, Shumarinai 朱鞠内, Shuyubari [Shiyubari] 主夕張, Shuparo シューパロ, Soeushinai 添牛内, Sorachi 空知, Sounnai 早雲内, Soya 宗谷, Suribachi-zawa スリバチ沢［摺鉢沢］, Taki-no-sawa 滝の沢, Tappu 達布, Tengu-zawa 天狗沢, Teshio 天塩, Tokoro 常呂, Tomiuchi 富内, Tonbetsu 頓別, Urakawa 浦河, Uryu 雨竜, Uwajima 宇和島, Wakka-wembetsu ワッカウェンベツ, Yamaguchi-zawa 山口沢, Yezo 蝦夷（イェゾ, エゾ）Yoshiyachi-zawa ヨシヤチ沢［Yoshiashi-zawa ヨシアシ沢］, Yubari 夕張, Yu-no-sawa 湯の沢

References Cited

Anderson, F. M. (1902: Cretaceous deposits of the Pacific Coast. *Proc. Calif. Acad. Sci.* [3], **2** (1), 1–154, pls. 1–11.

——— (1938): Lower Cretaceous deposits in California and Oregon. *Geol. Soc. Amer. Spec. Pap.*, **16**, 339 pp., 84 pls.

——— (1958): Upper Cretaceous of the Pacific Coast. *Geol. Soc. Amer. Mem.* **71**, 378 pp., 75 pls.

Ando, H. (1990): Stratigraphy and shallow marine sedimentary facies of the Mikasa Formation, Middle Yezo Group (Upper Cretaceous). *Jour. Geol. Soc. Japan*, **96**, 279–295 (in Japanese with English abstract).

Arkell, W. J., Kummel, B., Miller, A. K. and Wright, C. W. (1957): Morphological terms applied to Ammonoidea. *In* Moore, R. C. (ed.): *Treatise on Invertebrate Paleontology*, Part L, Mollusca 4, Cephalopoda, Ammonoidea, L2–L6. Geol. Soc. Amer. & Univ. Kansas Press, N. York & Lawrence.

Basse, E. (1931): *Monographie paléontologique de Crétacé de la province de Maintirano (Madagascar).* Serv. Min., Gouv. General Madagascar et Dependances, Tananarive, 86pp., 13 pls.

Blanford, H. F. (1862): On the Cretaceous and other rocks of the South Arcot and Trichinopoly districts, Madras. *Mem. Geol. Serv. India*, **4**, 1–200.

Boule, M., Lemoine, P. & Thévenin, A. (1906): Paléontologie de Madagascar, III. Céphalopodes crétacés des environs de Diego-Suarez. *Ann. Paléont.*, **1**, 173–192 (1-20), pls. 14–20 (1–7).

Collignon, M. (1931): Faunes senoniennes du nord et de l'ouest de Madagascar. *Ann. Géol. Serv. Min. Madagascar*, **1**, 7–64, pls. 1–9.

——— (1956): Ammonites néocretacées du Menabe (Madagascar). IV – Les Phylloceratidae; V – Les Gaudryceratidae; VI – Les Tetragonitidae. *Ann. Serv. Géol. Min. Madagascar*, **23**, 1–106, pls. 1–11.

——— (1963): *Atlas des fossiles caracteristiques de Madagascar (Ammonites)*, **10** (Albien), i–xv, 1–184, pls. 241–317. Serv. Géol. Repub. Malag., Tananarive.

——— (1964): *Ditto*, **11** (Cenomanien), i–xi, 1–152, pls. 318–375. Serv. Géol. Repub. Malag., Tananarive.

——— (1965a): *Ditto*, **12** (Turonian), i–iv, 1–82, pls. 376–413. Serv. Géol. Repub. Malag., Tananarive.

——— (1965b): *Ditto*, **13** (Coniacian), i–vii, 1–88, pls. 414–454. Serv. Géol. Repub. Malag., Tananarive.

——— (1966): *Ditto*, **14** (Santonien), i–x, 1–134, pls. 455–513. Serv. Géol. Repub. Malag., Tananarive.

——— (1971): *Ditto*, **17** (Maastrichtien), , 1–44, pls. 640–658. Serv. Géol. Repub. Malag., Tananarive.

Crick, G. C. (1907): Cretaceous fossils of Natal. *In* Anderson, W.: *Third and final report of the Geological Survey of Natal and Zululand*, 161–250, pls. 10–15.

Doguzhaeva, L. (1981): Wrinkle layer of shell wall structure in ammonoids. *Paleontol. Zhurnal*, 1981 (2), 38–48 (in Russian).

——— and Mutvei, H. (1993): Structural features in Cretaceous ammonoids indicative of semi-internal or internal shells. In House, M. R. (ed.): The Ammonoidea-Environments, Ecology and Evolutionary Change. *The Systematic Association Special Vol.*, **47**, 99–114, Clarendon Press, Oxford.

Drushchitz, v. v., Doguzhaeva, L. and Mikhailova, I. A. (1978): Unusual coating layers in ammonoids. *Paleontol. Zhurnal*, 1978 (2), 36–44 (in Russian).

Forbes, E. (1846): Report on the Cretaceous fossil invertebrates from southern India, collected by Mr. Kaye and Mr. Cunliffe. *Trans. Geol. Soc. London*, [2nd ser.], **7**, 97–174, ps. 7–19.

Futakami, M. (1982): Cretaceous stratigraphy and ammonite assemblages of the Hatonosu area, central Hokkaido. *Jour. Geol. Soc. Japan*, **88**, 101–120, pls. 1–2 (in Japanese with English abstract).

——— (1986a): Stratigraphy and paleontology of the Cretaceous in the Ishikari province, central Hokkaido. Part 1. Stratigraphy of the Cretaceous in the southern areas. *Bull. Natn. Sci. Mus.*, ser. C, **12**, 7–34, 2 pls.

——— (1986b): Ditto. Part 2. Stratigraphy of the Cretaceous in the northern areas. *Bull. Natn. Sci. Mus.*, ser. C, **12**, 91–120.

Gabb, W. M. (1869): *Paleontology of California*, **2**, 299 pp., 36 pls. Geol. Surv. Calif.

Grossouvre, A. de (1894): Recherches sur la craie supérieure. 2. Paléontologie – Les ammonites de la craie supérieure. *Mém. Serv. Carte Géol. Det. France*, ii + 264 pp., 39 pls.

Hashimoto, W., Nagao, S. and Kanno, S. (1965): Soeushinai. *Expl. Text Geol. Map Japan, scale 1: 50,000*, 1–73 (in Japanese), 75–92 (in English), quadrangle map.

Hauer, E. F.. von (1866): Neue Cephalopoden aus dem Gosaugebilden der Alpen. *Sitz. ber. Akad. Wiss. Wien*, **53**, 300–308, pls. 1–2.

Henderson, R. A. (1970): Ammonoidea from the Mata Series (Santonian-Maastrichtian) of New Zealand. *Spec. Pap. Palaeont.*, London, **6**, 81 pp., 15 pls.

——— and McNamara, K. J. (1985): Maastrichtian non-heteromorph ammonites from the Miria Formation, Western Australia. *Palaeontology*, **28**, 35–88 (includ. 9 pls.).

Hirano, H. (1975): Ontogenetic study of late Cretaceous *Gaudryceras tenuiliratum*. *Mem. Fac. Sci. Kyushu Univ.*, [D] Geol., **22** (2), 165–192, pls. 24–26.

——— (1978): Phenotypic substitution of *Gaudryceras* (a Cretaceous ammonite). *Trans. Proc. Palaeont. Soc. Japan* [N.S.], (109), 235–258, pls. 33–35.

———, Matsumoto, T. and Tanabe, K. (1977): Mid-Cretaceous stratigraphy of the Oyubari area, central Hokkaido. *Palaeont. Soc. Japan Spec. Pap.*, **21**, 1–10.

Hoepen, E. C. N. van (1921): Cretaceous Cephalopoda from Pondoland. *Ann. Transv. Mus.*, **8**, 1–48, pls. 1–11.

Howarth, M. K. (1965): Cretaceous ammonites and nautiloides from Angola. *Bull. Brit. Mus. (Nat. Hist.)* [Geol.], **10** (10), 337–412, pls. 1–13.

——— (1966): A mid-Turonian ammonite fauna from the Mocamedes desert, Angola. *Garcia de Orta (Lisboa)*, **14** (2), 217–228, pls. 1–3.

Ichikawa, T. and Hayami, I. (1978): Catalogue of the type and illustrated specimens in the Department of Historical Geology and Palaeontology of the University Museum, University of Tokyo. Part 1. Paleozoic and Mesozoic Fossils. *Univ. Mus., Univ. Tokyo, Material Rept.*, **2**, x + 396 pp.

Jimbo, K. (1894): Beiträge zur Kenntniss der Fauna der Kreideformation von Hokkaido. *Palaeont. Abhandl.* [N.F.], **2** (3), 147–194 (1–48), pls. 17–25 (1–9).

Jones, D. L. (1963): Upper Cretaceous (Campanian and Maestrichtian) ammonites from southern Alaska. *U.S. Geol. Surv. Prof. Pap.*, **432**, i–iv, 1–53, pls. 1–41.

——— (1967): Cretaceous ammonites from the lower part of the Matanuska Formation, southern Alaska. *U.S. Geol. Surv. Prof. Pap.*, **547**, i–iv, 1–49, pls. 1–9.

Kanie, Y. (1971): Ammonite. *Chishitsu News*, (202), cover sheet, Geol. Surv. Japan (in Japanese).

——— (1982): Cretaceous tetragonitid ammonite jaws: A comparison with modern *Nautilus* jaws. *Trans. Proc. Palaeont. Soc. Japan*, [N.S.], (125), 239–258, pls. 39, 40.

Kawada, M. (1929): On the Cretaceous formations of the Naibuchi district, South Sakhalin. *Jour. Geol. Soc. Tokyo*, **36** (1), 1–11 (in Japanese).

Kennedy, W. J. and Cobban, W. A. (1991): Stratigraphy and international correlation of the Cenomanian-Turonian transition in the Western Interior of the United States near Pueblo, Colorado, a potential boundary stratotype for the base of the Turonian stage. *Newsl. Stratigr.*, **24**, 1–33.

——— and Henderson, R. A. (1992): Non-heteromorph ammonites from the Upper Maastrichtian of Pondicherry, South India. *Palaeontology*, **35** (2), 381–442 (includ. 18 pls.).

——— and Klinger, H. C. (1979): Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Gaudryceratidae. *Bull. Brit. Mus. (Nat. Hist.)* [Geol.], **31** (2), 121–174 (incl. 14 pls.).

——— & Summesberger, H. (1979): A revision of *Ammonites mitis* Hauer and *Ammonites glaneggensis* Redtenbacher from the Gosau Beds (Upper Cretaceous) of Austria. *Beitr. Paläont. Österr.*, (6), 71–87, pls. 1–4.

Kossmat, F. (1895): Untersuchungen über die südindische Kreideformation. I. *Beitr. Paläont. Geol. Österr.-Ung. Orients*, **9** (for 1894), 197–203 (1–107), pls. 15–25 (1–11).

Kullman, J. and Wiedmann, J. (1970): Significance of sutures in phylogeny of Ammonoidea. *Palaeontological Contributions, Univ. Kansas*, **44**, 1–32.

Lehmann, U., Tanabe, K., Kanie, Y. and Fukuda, Y. (1980): Über die Kiefer apparat der Lytoceratacea (Ammonoidea). *Paläont. Zeitsch.*, **54**, 319–329.

Macellari, C. E. (1986): Late Campanian-Maastrichtian ammonite fauna from Seymour Island (Antarctic Peninsula). *Jour. Paleont.*, **60**, Suppl. to (2), *Pal. Soc. Mem.* **18**, 1–55, incl. 41 figs.

McLearn, F. H. (1972): Ammonoids of the Lower Cretaceous Sandstone Member of the Haida Formation, Skidegate Inlet, Queen Charlotte Islands, western British Columbia. *Geol. Surv. Canada, Bull.* **188,** 1–78, pls. 1–45.

Marshall, P. (1926): The Upper Cretaceous ammonites of New Zealand. *Trans. New Zeal. Inst.*, **56**, 129–210, pls. 19–47.

Matsumoto [Matumoto], T. (1938): *Zelandites*, a genus of Cretaceous ammonites. *Japan. Jour. Geol. Geogr.*, **15**, 137–148, pl. 14.

——— (1941): A study of the relationship between different species, with special reference to the problem on the range of a fossil species. *Jour. Geol. Soc. Japan*, **48**, 17–37 (in Japanese).

——— (1942): Fundamentals in the Cretaceous stratigraphy of Japan. Part I. *Mem. Fac. Sci. Kyushu Univ.* [D] Geol., **1** (3), 129–280, pls. 5–20.

——— (1943): A note on the Japanese ammonites belonging to the Gaudryceratidae. *Proc. Imp. Acad., Tokyo*,

18 (10), 666–670.
——— (1954): Selected Cretaceous leading ammonites in Hokkaido and Saghalien. *In* Matsumoto, T. (comp.): *The Cretaceous System in the Japanese Islands*, Appendix, 243–313, pls. 17–36 (1–20), Japan Soc. Prom. Sci. Res., Tokyo (for 1953).
——— (1959a): Cretaceous ammonites from the upper Chitina valley, Alaska. *Mem. Fac. Sci. Kyushu Univ.* [D] Geol., **8** (3), 49–90, pls. 12–29.
——— (1959b): Upper Cretaceous ammonites of California. Part II. *Mem. Fac. Sci. Kyushu Univ.*, [D] Geol., *Spec. Vol.* **1**, 1–172, pls. 1–41.
——— (1960): Ditto. Part III. *Mem. Fac. Sci. Kyushu Univ.* [D] Geol., *Spec. Vol.* **2**, 1–204.
——— (1963): *A Survey of the Fossils from Japan Illustrated in Classical Monographs.* Part X, 41–48, pls. 60–68, Palaeont. Soc. Japan, Spec. Publication.
——— (1965): A monograph of the Collignoniceratidae from Hokkaido. Part I. *Mem. Fac. Sci. Kyushu Univ.* [D] Geol., **16** (1), 1–80, pls. 1–18.
——— (1977): Lower Cretaceous ammonites, 5–6. *In* Matsumoto, T. (ed.): *Atlas of Japanese Fossils*, **49**, Sheet Cr 41–42. Tsukiji Shokan, Tokyo (in Japanese).
——— (1984a): The so-called Turonian-Coniacian boundary in Japan. *Bull. Geol. Soc. Denmark*, **33**, 171–181.
——— (1984b): Some gaudryceratid ammonites from the Campanian and Maastrichtian of Hokkaido. Part I. *Sci. Rept. Yokosuka City Mus.*, (32), 1–10, pls. 1–5.
——— (1988a): Notes on some Cretaceous ammonites from South Sakhalin held at Tohoku University, Sendai. *Sci. Rept. Tohoku Univ.* [2] Geol., **59** (2), 177–190, pls. 50–53.
——— (comp.) (1988b): A monograph of the Puzosiidae (Ammonoidea) from the Cretaceous of Hokkaido. *Palaeont. Soc. Japan Spec. Pap.*, **30**, 179 pp. (includ. 88 figs.).
——— (comp.) (1991): The Mid-Cretaceous ammonites of the Family Kossmaticeratidae from Japan. *Palaeont. Soc. Japan Spec. Pap.*, **33**, 143 pp. (includ. 31 pls.).
——— (1995): Selected five species from the Cretaceous rocks of the Urakawa area, Hokkaido, with special reference to the age correlation. *Sci. Rept. Yokosuka City Mus.*, (43), in press (in Japanese with English abstract).
——— and Harada, M. (1964): Cretaceous stratigraphy of the Yubari dome, Hokkaido. *Mem. Fac. Sci., Kyushu Univ.*, [D] Geol., **15** (1), 79–115, pls. 9–11.
———, Hayami, I. and Asano, K. (1963): *A Survey of Fossils from Japan illustrated in Classical Monographs.* Part VII, Paraeont. Soc. Japan, Spec. Publication.
——— and Inoma, A. (1975): Mid-Cretaceous ammonites from the Shumarinai-Soeushinai area, Hokkaido. Part I. *Mem. Fac. Sci. Kyushu Univ.* [D] Geol., **23** (2), 263–293, pls. 38–42.
——— and Kawano, T. (1975): A find of *Pseudocalycoceras* from Hokkaido. *Trans. Proc. Palaeont. Soc. Japan* [N.S.], (97), 7–21, pl. 1.
———, Kinoshita, K., Inoma, A., Kido, H., Nishijima, S. and Kato, S. (1980): Stratigraphy of the Upper Cretaceous of the Tombetsu Valley, Hokkaido. *Sci. Rept. Dept. Geol. Kyushu Univ.*, **13** (2), 265–275 (in Japanese with English abstract).
———, Maiya, S., Inoue, Y., Noda, M. and Kaiho, K. (1981): Coordinated mega- and micro-biostratigraphy of the Upper Cretaceous in the Tombetsu Valley, Hokkaido. *Jour. Japan. Assoc. Petrol. Techn.*, **46** (5), 301–313 (in Japanese with English abstract).
———, Maiya, S. and Noda, M. (1988): Inoceramids and foraminifera correlation in the Upper Cretaceous of Kikume-zawa, Hokkaido. *Fossils* (Palaeont. Soc. Japan) (44), 25–32 (in Japanese with English abstract).
——— and Miyauchi, T. (1984): Some ammonites from the Campanian (Upper Cretaceous) of northern Hokkaido. Part II. Some Campanian ammonites from the Soya area. *Palaeont. Soc. Japan Spec. Pap.*, **27**, 13–76, pls. 10–31.
———, Miyauchi, T. and Kanie, Y. (1985): Some gaudryceratid ammonites from the Campanian and Maastrichtian of Hokkaido. Part II. *Sci. Rept. Yokosuka City Mus.* (33), 19–36, pls. 1–5.
——— and Morozumi, Y. (1980): Late Cretaceous ammonites from the Izumi Mountains, Southwester Japan. *Bull. Osaka Mus. Nat. Hist.*, (33), 1–31, pls. 1–16.
———, Muramoto, T. and Takahashi, T. (1969): Selected acanthoceratids from Hokkaido. *Mem. Fac. Sci. Kyushu Univ.* [D] Geol., **19** (2), 251–296, pls. 25–38.
———, Noda, M., Kanie, Y., Yoshikawa, S., Toshimitsu, S., Maiya, S. and Hanagata, S. (1994): Stratigraphy of the Cenomanian-Turonian transition in the Hobetsu district, Hokkaido. *Bull. Hobetsu Museum*, (10), 1–25 (includ. 10 pls.) (in Japanese with English abstract).
———, ——— and Maiya, S. (1991): Towards an integrated ammonoid-, inoceramid- and foraminiferal

biostratigraphy of the Cenomanian and Turonian (Cretaceous) in Hokkaido. *Jour. Geogr.* (Tokyo), **100** (3), 378–398 (in Japanese with English abstract).

———, ——— and Toshimitsu, S. (1989): Gigantic ammonite held in the Hobetsu Museum – Its record of occurrence and its stratigraphic position. *Bull. Hobetsu Museum*, (5), 13–25, pls. 1–2 (in Japanese with English abstract).

——— and Okada, H. (1971): Clastic sediments of the Cretaceous Yezo geosyncline. *Mem. Geol. Soc. Japan*, (6), 61–74, pl. 1.

———, ——— (1973): Saku Formation of the Yezo geosyncline. *Sci. Rept. Dept. Geol. Kyushu Univ.*, **11** (2), 275–309 (in Japanese with English abstract).

———, ———, Hirano, H., Tanabe, K., Okamura, M., Takayanagi, Y., Obata, I., Noda, M. and Tamura, M. (1978): Mid-Cretaceous zonation in Japan. *In* Reyment, R. A. and Thomel, G. (eds.): Mid-Cretaceous Events, Uppsala 1975–Nice 1976. *Ann. Mus. d'Hist. Nat. Nice*, **4** (for 1976), (33) 1–23.

——— and Takahashi, T. (1992): Ammonites of the genus *Acompsoceras* and some other acanthoceratid species from the Ikushunbetsu valley, central Hokkaido. *Trans. Proc. Palaeont. Soc. Japan*, [N. S.], (166), 1144–1156 (incl. 7 figs.).

——— and Toshimitsu, S. (1995): Restudy of *Gaudryceras venustum* Matsumoto from the Hobetsu district, Hokkaido. *Bull. Hobetsu Mus.*, (11), p. 1–16 (includ. 8 pls)

——— and Yoshida, S. (1979): A new gaudryceratid ammonite from eastern Hokkaido. *Trans. Proc. Palaeont. Soc. Japan* [N.S.], (114), 65–76, pls. 1–11.

Matsuno, K., Tanaka, K., Mizuno, A. and Ishida, M. (1964): Iwamizawa. *Expl. Text Geol. Map Japan, scale 1:50,000* 1–168 (in Japanese), 1–11 (English abstract), quandrangle map.

MCM (Mikasa City Museum) (1988): *Atlas of Ammonites*, 61 pp. (includ. 221 figs.) (in Japanese).

Morozumi, Y. (1985): Late Cretaceous (Campanian and Maastrichtian) ammonites from Awaji Island, Southwest Japan. *Bull. Osaka Mus. Nat. Hist.*, (39), 1–58, pls. 1–18.

Murphy, M. A. (1967a): The Aptian-Cenomanian members of the ammonite genus *Tetragonites*. *Univ. Calif. Publ. Geol. Sci.*, **69**, 1–78, pls. 1–7.

——— (1967b): Aptian and Albian Tetragonitidae (Ammonoidea) from northern California. *Univ. Calif. Publ. Geol. Sci.*, **70**, 1–32, pls. 1–5.

——— (1967c): The ammonoid subfamily Gabbioceratinae Breistroffer. *Jour. Paleont.*, **41**, 595–607, pl. 64.

Nagao, S. (1962): Teshio-Nakagawa. *Expl. Text Geol. Map Japan, scale 1:50,000*, 1–39 (in Japanese with English résumé), quadrangle map. Geol. Surv. Hokkaido, Sapporo.

Nanayama, F., Kanamatsu, T. and Fujiwara, Y. (1993): Sedimentary petrology and paleotectonic analysis of the arc-arc junction: the Paleocene Nakanogawa Group in the Hidaka Belt, central Hokkaido, Japan. *Palaegeogr., Palaeclimatol., Palaeoecol.*, (105), 53–60.

Nishida, T., Matsumoto, T., Kyuma, Y. and Maiya, S. (1992): Integrated inoceramid- and foraminiferal biostratigraphy of the Cenomanian and Turonian (Cretaceous) in the Kotanbetsu Valley, Hokkaido. *Jour. Fac. Educ. Saga Univ.*, **39** (2) [II], 21–59 (includ. 11 pls.) (in Japanese with English abstract).

———, ———, Yao, A. and Maiya, S. (1993a): Towards an integrated mega- and micro-biostratigraphy on the Cenomanian (Cretaceous) sequence in the Kotanbetsu Valley, Hokkaido, including the C-T boundary problem. *Jour. Fac. Educ. Saga Univ.*, **40** (3), 95–137 (includ. 7 pls.) (in Japanese with English abstract).

———, ———, Maiya, S., Hanagata, S., Yao, A. and Kyuma, Y. (1993b): Integrated mega- and micro-biostratigraphy of the Cenomanian Stage in the Oyubari area, Hokkaido – with special reference to its upper and lower limits. Part 1. *Jour. Fac. Educ. Saga Univ.*, **41** (1) [II], 11–57 (includ. 11 pls.) (in Japanese with English abstract).

———, ———, ———, Yao, A., Uematsu, K., Kawashita, Y. and Kyuma, Y. (1995): Ditto, Part 2. *Jour. Fac. Educ. Saga Univ.*, **42** (2), 179–199 (includ. 5 pls.) (in Japanese with English abstract).

Obata, I. and Futakami, M. (1975): Cretaceous stratigraphy of the Manji area, Hokkaido. *Bull. Natn. Sci. Mus., Tokyo* [C] **1** (3), 93–110, pls. 1–2 (in Japanese with English summary).

———, ——— (1977): Cretaceous sequence of the Manji dome, Hokkaido. *Palaeont. Soc. Japan Spec. Pap.*, **21**, 23–30.

———, ———, Tanabe, K., Kawashita, Y., Saito, N. and Tanaka, M. (1981): Cretaceous strata exposed along the Shizunai-gawa River, Hokkaido. *Bull. Natn. Sci. Mus., Tokyo* [C], **7** (1), 15–26, pls. 1–8 (in Japanese with English summary).

———, Hayami, I., Matsukawa, M., Teraoka, Y. and Taketani, Y. (1993): A problematic bivalve from the Saroma Group of northeastern Hokkaido and its geological significance. *Mem. Natn. Sci. Mus.*, (26), 31–37.

———, Maehara, T. and Tsuda, H. (1973): Cretaceous stratigraphy of the Hidaka area, Hokkaido. *Mem. Natn.*

Sci. Mus., (6), 131–145 (in Japanese with English summary).

Okada, H. and Matsumoto, T. (1969): Cyclic sedimentation in a part of the Cretaceous sequence of the Yezo geosyncline, Hokkaido. *Jour. Geol. Soc. Japan*, **75**, 311–328 (in Japanese with English abstract).

Osanai, H., Mitani, K. and Ishiyama, S. (1957): Chiraibetsu. *Expl. Text Geol. Map Japan, scale 1:50,000*, 44 p., pls. 1–11, quadrangle map (in Japanese with English abstract). Geol. Surv. Hokkaido.

Pervinquière, L. (1907): Études de paléontologie tunisienne. 1. Céphalopodes des terrains secondaires. *Carte Géol. Tunisie.* De Rudeval, Paris. v + 438 pp., 27 pls.

Redtenbacher, A. (1873): Die Cephalopoden fauna der Gosauschichten in der nordöstlichen Alpen. *Abh. K.-K. Geol. Reichsanst*, **5**, 91–140.

Sakakibara, M. and Tanaka, K. (1986): Discovery of *Inoceramus* from the Saroma Group, Tokoro Belt, northeastern Hokkaido. *Chikyu Kagaku* [Earth Sci.], **40**, 205–206, pl. 1 (in Japanese).

Shimizu, I., Tanaka, K. and Imai, I. (1953): Kami-Ashibetsu. *Expl. Text Geol. Map Japan, scale 1:50,000*, 1–78 (in Japanese), 1–21 (résumé in English), folded tables 1–2, folded figs. 1–6, route maps 1–8, quadrangle map. Geol. Surv. Japan.

Shimizu, S. (1934): [Classification of the Gaudryceratidae]. *in* Shimizu, S. and Obata, T. [Cephalopoda, Chapter 6]. [*Iwanami's Lecture Series of Geology and Palaeontology*], p. 65–73. Tokyo (in Japanese).

—— (1935a): Remarks on *Gaudryceras aeolum* (d'Orbigny) and *Gaudryceras aeoliforme* Fallot from the Albian of France. *Jour. Shanghai Sci. Inst.*, [II], **2**, 155–159.

—— (1935b): The Upper Cretaceous Cephalopoda of Japan, Part 1. *Jour. Shanghai Sci. Inst.*, [II], **2**, 159–226.

Spath, L. F. (1923): A monograph of the Ammonoidea of the Gault. Part 1. *Monogr. Palaeontogr. Soc.* London for 1921, 1–72, pls. 1–4.

—— (1927): Revision of the Jurassic Cephalopoda fauna of Kachh (Cutch). *Mem. Geol. Surv. India, Palaeont. Indica* [N.S.], **9**, mem. no. 2, pt. 1, 1–71, pls. 1–7.

Stinnesbeck, W. (1986): Zu den faunistischen und palökologischen Verhältnissen in der Quiriquina Formation (Maastrichtium), Zentral-Chiles, *Palaeontographica Abt. A*, **194**, 99–237, pls. 1–16.

Stoliczka, F. (1865): The fossil Cephalopoda of the Cretaceous rocks of southern India. *Mem. Geol. Surv. India, Palaeont. Indica*, [3] (6–9), 107–166, pls. 55–80.

Szász, L. (1976): Biostratigrafia si paleontologia cretacicului superior din Bazinul Brezoi (Carpatii meridionali). *Dari de Seama ale Sedintelor*, **62** [4] Stratigrafie., 189–220, pls. 1–21.

—— and Ion, J. (1988): Cretace superieur du Bassin de Baradag (Roumanie). Biostratigraphie integree (Ammonites, Inocerames, Foraminiferes planctoniques). *Mem. Inst. Geol. Geophys. Bucaresti*, **33**, 91–149, pls. 1–30.

—— & Lacatusu, A. (1974): Contributii studiul amonitilor din neocretacicul Bazinului Babadag (Dobrogea de Nord). *Dari de Seama ale Sedintelor*, **60** [3] Paleont., 206–215, pls. 1–7.

Tanabe, K., Fukuda, Y., Kanie, Y. and Lehmann, U. (1982): Rhyncholites and conchorhynchs as calcified jaw-elements in some late Cretaceous ammonites. *Lethaia*, **13**, 157–168.

——, Hirano, H., Matsumoto, T. and Miyata, Y. (1977): Stratigraphy of the Upper Cretaceous deposits in the Obira area, northwestern Hokkaido. *Sci. Rept. Dept. Geol., Kyushu Univ.*, **12** (3), 181–202 (in Japanese with English abstract).

Tanaka, K. (1963): A study of the Cretaceous sedimentation in Hokkaido, Japan. *Rept. Geol. Surv. Japan*, **197**, 122 pp., 3 pls., 2 maps.

Tokunaga, S. and Shimizu, S. (1926): The Cretaceous formation of Futaba in Iwaki and its fossils. *Jour. Fac. Sci. Imp. Univ. Tokyo* [II], **1** (6), 183–212, pls. 21–27.

Toshimitsu, S. (1988): Biostratigraphy of the Upper Cretaceous Santonian Stage in northwestern Hokkaido. *Mem. Fac. Sci. Kyushu Univ.* [D] Geol., **26** (2), 125–192, pls. 23–29.

Tsushima, K., Tanaka, K., Matsuno, K. and Yamaguchi, S. (1958): Tappu. *Expl. Text Geol. Map Japan, scale 1:50,000*, 1–66 (in Japanese), 1–8 (English abstract), quadrangle map. Geol. Surv. Japan.

Venzo, S. (1936): Cephalopodi del Cretacea medio-superiore dello Zululand. *Palaeontogr. Ital.*, **36**, 59–133 (1–7), pls. 5–12 (1–8).

Verechagin, V. V. (1965): *In* Verechagin, V. V., Kinasov, V. P., Parakechov, K. V. and Terechova, G. P.: [*Field Atlas of the Cretaceous Faunas from Northeast Soviet Russia Socialist Republic.*] 215 pp. includ. 74 pls.), Magaden (in Russian).

Wedekind, R. (1916): Über Lobus, Suturallobus und Inzision. *Zentbl. Miner. Geol. Palaont.*, [B], (1916), (8), 185–195.

Westerman, G. E. G. (1989): New developments in ecology of Jurassic-Cretaceous ammonoids. *Proc. II Pergola Symposium*, 1987, 1–21.

Wiedmann, J. (1962a): Unterkreide-Ammoniten von Mallorca. I, Lytoceratina, Aptychi. *Abh. Math.-Kl. Akad.*

Wiss. Mainz, (1962), (1), 1–148, 10 pls.
——— (1962b): Ammoniten aus der Vascogotischen Kreide (Nordspanien). 1, Phylloceratina, Lytoceratina. *Palaeontographica*, **A118**, 119–237, pls. 11–21.
——— (1962c): Die Gabbioceratinae Breistroffer. *Neues Jahrbuch Geol. Palaeont., Abh.*, 115, 1–43, pl. 2.
Wright, C. W. (1957): *In* Moore, R. C. (ed.): *Treatise on Invertebrate Paleontology*. Part L, Mollusca 4, Cephalopoda, Ammonoidea, [mainly Cretaceous ammonites] L92–L232; L362–437, Geol. Soc. Amer. & Univ. Kanasa Press, N. York & Lawrence.
——— and Kennedy, W. J. (1984): The Ammonoidea of the Lower Chalk. Part 1. *Monogr. Palaeontogr. Soc.*, London, 1–126, pls. 1–40 (Publ. No. 567, part of vol. 137 for 1983).
——— and Matsumoto, T. (1954): Some doubtful Cretaceous ammonite genera from Japan and Saghalien. *Mem. Fac. Sci. Kyushu Univ.* [D] Geol., **4** (2), 107–134, pls. 7, 8.
Yabe, H. (1903): Cretaceous Cephalopoda from the Hokkaido. Part 1. *Jour. Coll. Sci. Imp. Univ. Tokyo*, **18** (2), 1–55, pls. 1–7.
——— (1904): Ditto. Part 2. *Jour. Coll. Sci. Imp. Univ. Tokyo*, **20** (2), 1–45, pls. 1–6.
——— (1909): Zur Stratigraphie und Paläontologie der oberen Kreide von Hokkaido und Sachalin. *Zeitsch. Deutsh. Geol. Gesellsch.*, 61, 402–404.
——— (1926): A new scheme of the stratigraphical subdivision of the Cretaceous deposits of Hokkaido. *Proc. Imp. Acad. Japan*, **5** (2), 214–218.
——— (1927): Cretaceous stratigraphy of the Japanese Islands. *Sci. Rept. Tohoku Imp. Univ.*, [2nd ser.], **11** (1), 27–100, pls. 3–9.
Yehara, S. (1924): On the Izumi Sandstone Group in the Onogawa Basin, Province of Bungo, and the same group in the Uwajima. Province of Iyo. *Japan. Jour. Geol. Geogr.*, **3**, 27–39, pls. 2–4.
Yokoyama, M. (1890): Versteinerungen aus der japanischen Kreide. *Palaeontographica*, **35**, 159–202, pls. 18–25.

Taxa Index

Names of genera, subgenera, species, subspecies and "varieties" are indicated in alphabetic order, with page(s) where they are described (by bold) or discussed or listed. F. means Figures. New taxa are bold-faced.

K

L

M

N

O

P

S

T

U

V

W

Y

Z

Number 27 (Issued November 24, 1984) Some Ammonites from the Campanian (Upper Cretaceous) of Northern Hokkaido ....Part I and III by T. MATSUMOTO, Part II by T. MATSUMOTO and T. MIYAUCHI

Number 28 (Issued November 24, 1985) Bibliography of Palaeontology in Japan 1976–1980 ....Tomoki KASE and Kazuo ASAMA

Number 29 (Issued November 25, 1986) Japanese Cenozoic Molluscs – Their Origin and Migration ....Edited by Tamio KOTAKA

Number 30 (Issued December 15, 1988) A Monograph of the Puzosiidae (Amnonoidea) from the Cretaceous of Hokkaido ....Tatsuro MATSUMOTO

Number 31 (Issued October 30, 1990) Bibliography of Palaeontology in Japan, 1981–1985 ....Kunihiro ISHIZAKI and Kei MORI

Number 32 (Issued November 20, 1991) Fusuline Biostratigraphy of the Upper Carboniferous and Lower Permian of Japan, with Special Reference to the Carboniferous-Permian Boundary ....Kozo WATANABE

Number 33 (Issued December 10, 1991) The Mid-Cretaceous Ammonites of the Family Kossmaticeratidae from Japan ....Compiled by Tatsuro MATSUMOTO

Number 34 (Issued October 30, 1993) Bibliography of Palaeontology in Japan, 1986–1990 ....Hisayoshi IGO, Hiroshi NODA and Harumi NISHIMURA

Special Publications, Palaeontological Society of Japan

*Twenty-Fifth Anniversary Volume (Issued February 15, 1961) Catalogue of Type-Specimens of Fossils in Japan ....Compiled by Shoshiro HANZAWA, Kiyoshi ASANO and Fuyuji TAKAI

*Twenty-Fifth Anniversary Volume (Issued September 16, 1963) A Survey of the Fossils from Japan Illustrated in Classical Monographs (Primarily a Nomenclatorial Revision) ....Edited by Tatsuro MATSUMOTO

Palaeontological Society of Japan, Special Papers No. 35

Notes on Gaudryceratid Ammonites from Hokkaido and Sakhalin

1995年12月12日 印刷
1995年12月15日 発行

定価 5,500円

編 集 者 柳 田 寿 一
発 行 者 日 本 古 生 物 学 会
東京都文京区本駒込5-16-9
日本学会事務センター内
印 刷 者 学術図書印刷株式会社
富 田 潔
東京都練馬区豊玉北2ノ13ノ1