

Coniacian collignoniceratid ammonites from Hokkaido
—Stratigraphy and Paleontology of the Cretaceous in the Ishikari province,
central Hokkaido, Part 4—

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Abstract

Four species of the collignoniceratid ammonites from the Coniacian of Hokkaido are described, of which two are new, *viz.* *Prionocycloceras matsumotoi* and *P. obatai*. On this occasion the phylogenetic relationships of some collignoniceratid genera are discussed.

Introduction

In my last paper (Futakami, 1990) I reported a result of my study on the collignoniceratid ammonites from the Turonian of Hokkaido. In this paper I give a part of my study on the ammonites of the same family which I collected from the Coniacian of Hokkaido.

This paper contains paleontological descriptions of four species belonging to *Prionocycloceras* and *Barroisiceras* from the Upper Yezo Group. In addition, I discuss the phylogenetic relationships of some Turonian and Coniacian collignoniceratid ammonites on the basis of available data.

The detailed stratigraphical position and location of the specimens used in this paper are described in Part 1 (Futakami, 1986). All of the described specimens are kept in the National Science Museum, Tokyo.

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Systematic Description

Order Ammonoidea Zittel, 1884
Superfamily Acanthoceraceae de Grossouvre, 1894
Family Collignoniceratidae Wright & Wright, 1951
Subfamily Collignoniceratinae Wright & Wright, 1951
Genus *Prionocycloceras* Spath, 1926

Type species : *Prionocyclus guayabanus* Steinmann, 1897.

Remarks: The genus *Prionocycloceras* was established by Spath (1926, p. 80) as a transitional one between *Prionocyclus* and *Gauthiericeras*. This genus is closely similar in morphological features to *Prionocyclus*. Matsumoto (1965a, p. 39) has described in detail the morphological characters of *Prionocycloceras* and clarified the difference between these two genera. It should be noted, however, that the morphological difference between them does not seem great, but I hesitate to conclude the synonymy in this paper.

One of the differences which should be noticed numerous ribs are crowded on the immature whorls of Turonian *Prionocyclus*, whereas ribs are undeveloped or less crowded on those of Coniacian *Prionocycloceras*. This may imply a change in phylogenetic evolution, since the latter is regarded as a descendant of the former. More material should be examined to confirm this idea. A similar feature is shown in the relationship between ancestral *Collignoniceratid* of the Middle Turonian and descendant *Subprionocyclus* of the Upper Turonian, both of which contain important index species (Futakami, 1990, p. 257).

This genus was included in the subfamily Peroniceratinae by Wright (in Moore, 1957), but I agree with Matsumoto (1965a, p. 40) to ascribe it to the subfamily Collignoniceratinae because of its fine serrations on the top of keel and the close resemblance of shell ornaments to those of *Prionocyclus*.

Prionocycloceras matsumotoi Futakami, sp. nov.

P1. 1, Figs. 1–8; P1. 2, Fig. 5

Material: Holotype, NSM. PM9568 (P1. 1, Fig. 6) was obtained from a rolled nodule on the stream of Kamiichi-no-sawa, a tributary to the Ikushumbetsu. Five paratypes, NSM. PM9569–9573 from the same nodule. NSM. PM9574–9576, at loc. Ki607, the middle stream of the Roku-no-sawa, a branch of the Kamiichi-no-sawa; NSM. PM9577, from loc. Ki313, the middle stream of the Ganseki-zawa (=Hachi-no-sawa), another branch of the Kamiichi-no-sawa, Ikushumbetsu, Hokkaido (Coll. M. Futakami).

Diagnosis: This species is characterized by a somewhat wide umbilicus,

numerous ribs, a distinct keel and relatively weakly spinose ventrolateral tubercles without horn-like ones as in some species of *Prionocycloceras*.

Description: The shell is rather small. The whorl is slightly evolute, moderately umbilicate, higher than broad and subrectangular in cross section, with flatted, nearly parallel flanks. The mid ventral keel is distinct and has finely serrated on the top.

Ribs of holotype (P1. 1, Fig. 6) are mostly simple, prorsiradiate, and rarely intercalated by secondaries on the outer whorl. They are projected somewhat strongly forward on the venter and become extremely weak near the keel. Ribs of NSM. PM9570 (P1. 1, Fig. 4) are numerous and somewhat weak on the body chamber as compared with those of the holotype. On the outer whorl of the adult stage of NSM. PM9576 (P1. 2, Fig. 5), which is a fragment of body chamber, there are distinct striae.

The ribs are bullate at the umbilical margin and somewhat clavate at the ventrolateral shoulder. The ventrolateral tubercles become spinose at the adult stage. On the immature whorl less than 20 mm in diameter, faint clavi-like elevations are sometimes formed irregularly on the ventral ribs between the ventrolateral shoulder and the keel, as shown by NSM. PM9575 (P1. 1, Fig. 1) and NSM. PM9571 (P1. 1, Fig. 8).

The suture is of general *Collignoniceras* pattern: the external lobe (E) is nearly as deep as the lateral lobe (L), and the first lateral saddle is broad and symmetrically bipartite by a shallow lobule (Fig. 1).

Measurements:

Specimen	Diameter	Height	Breadth	B./H.	Umbilicus	U./D.	U.T.	V.T.
NSM. PM9568 (Holotype)	39.5	19.7	12.5	0.63	19.7	0.50	16	—
NSM. PM9569	47.0	18.4	—	—	17.6	0.37	6×2	—
NSM. PM9570	33.3	12.5	9.0	0.72	11.2	0.34	—	—
NSM. PM9571	25.3	8.5	7.3	0.86	10.0	0.40	15	—
NSM. PM9572	14.5	6.0	4.7	0.78	4.6	0.32	—	—
NSM. PM9573	10.1	3.6	3.2	0.89	3.8	0.38	11	11
NSM. PM9574	26.3	10.6	8.5	0.80	9.1	0.35	6×2	11×2
NSM. PM9575	21.5	9.0	—	—	8.0	0.37	11	17
NSM. PM9576	—	35.5	—	—	—	—	—	—
NSM. PM9577	16.8	—	5.5	—	7.2	0.43	6×2	—

U. T.: number of umbilical tubercles per whorl

V. T.: number of ventrolateral tubercles per whorl

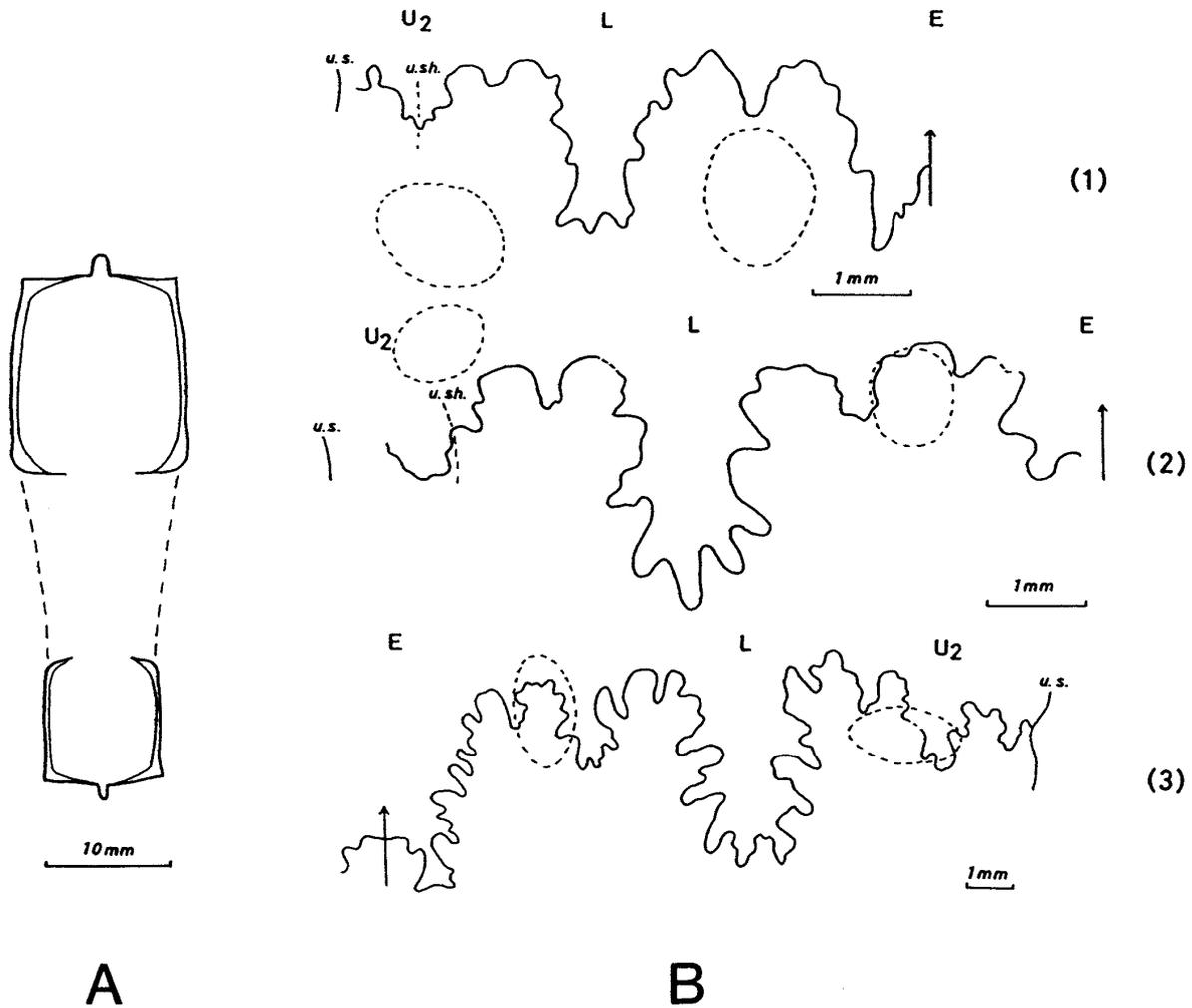


Fig. 1. Whorl section (A) and suture lines (B) of *Prionocycloceras matsumotoi* Futakami sp. nov. A, B(3). NSM. PM9568, Holotype, from loc. Ki504F, the Kamiichi-no-sawa River, Ikushumbetsu. B(1). NSM. PM9575; B(2). NSM. PM9574, from loc. Ki607, the Roku-no-sawa, a tributary of the Kamiichi-no-sawa, Ikushumbetsu, Hokkaido. u. sh.: umbilical shoulder, u. s.: umbilical seam.

Comparison: This species is similar to *Prionocycloceras guayabanum* (Gerhardt, 1897, p. 197, pl. 5, fig. 22a-c) from Colombia in the whorl shape and ornaments, but the former is distinguished from the latter in that the whorl has stronger and more numerous ribs, a weaker ventrolateral tubercle from the middle to the late growth stages and a wider umbilicus. As to the mode of ribbing this species is rather similar to *Prionocycloceras mediotuberculatum* (Gerhardt, 1897, p. 198, pl. 5, fig. 23a-c) from Colombia, but the latter is characterized by the presence of faint mid-lateral elevation on the rib.

Prionocycloceras (?) *recticostatum* (Sornay, 1957, p. 193, pl. 16, fig. 7), the

holotype of which is still immature, is somewhat similar to the present species in the shape of tubercles and ribbing, but the latter can be distinguished from the former in having much wider umbilicus.

Two species from Hokkaido, *Prionocycloceras sigmoidale* (Matsumoto, 1965a, p. 41, pl. 9, fig. 1; pl. 10, fig. 2) and *P. wrighti* (Matsumoto, 1971, p. 134, pl. 22, fig. 2) have been described by Matsumoto on the basis of specimens from the Kamiichi-no-sawa River in the Ikushumbetsu area. The former species is similar to the present one in the umbilical width but differs from the latter in having ventrolateral tubercles of a different type: the spinose-like tubercles as observed in the middle and late growth stages of this species do not appear in the adult stage of *P. sigmoidale*. *P. wrighti* is distinguished from the present species in having a narrower umbilicus, stronger ribs and ventrolateral tubercles and suture lines of a different type, which are characterized by the external lobe (E) being deeper than lateral lobe (L), and the asymmetrically divided first lateral saddle. As above mentioned, in this species E is nearly as deep as L, and the first lateral saddle is broad and symmetrically divided.

Umbilical width and shell ornaments on the outer whorl of the present species is somewhat similar to those of *Prionocyclus cobbani* Matsumoto (1965a, p. 21, pl. 4, fig. 2a-c) and *Prionocyclus aberrans* Matsumoto (1965a, p. 25, pl. 6, fig. 3a-c). But, there are some differences between the two genera: the ribs of *Prionocyclus* are rather irregular in strength, length and arrangement, and are generally denser and more numerous in the immature to adult stage, whereas those of *Prionocycloceras* are faint and widely spaced in the middle and late growth stages.

Occurrence: Locs. Ki313 and Ki607 are included in the lower part of Member U₂, lower part of the Upper Yezo Group (see Futakami, 1986). This stratigraphic position is assigned to the *Inoceramus uwajimensis* Zone. Therefore, the age is probably early to middle (?) Coniacian.

***Prionocycloceras obatai* Futakami, sp. nov.**

Pl. 2, Figs. 3, 4

Material: Holotype, NSM. PM9578 (Pl. 2, Fig. 3) was obtained from a calcareous nodule in the dark grey sandy siltstone, the Upper Yezo Group at loc. Ki607 on the middle stream of the Roku-no-sawa, a tributary of the Kamiichi-no-sawa (Coll. M. Futakami). Paratype, NSM. PM9579 (Pl. 2, Fig. 4) was obtained from a calcareous nodule in a large cliff on the lower stream of the Fukuro-zawa, a tributary of the Kamiichi-no-sawa, Ikushumbetsu, Hokkaido (Coll. M. Futakami). The paratype is imperfect, for it is only a fragmentary body chamber.

Diagnosis: This species is characterized by a compressed whorl, a narrow

umbilicus and sinuous and somewhat sigmoidal ribs which are similar to those of *Subprionocyclus minimus* (Hayasaka et Fukada).

Description: The shell is rather small, being about 30 mm in diameter of the holotype. The whorl is compressed, slightly involute and has more or less narrow umbilicus (U./D.=0.24–0.28) in the adult stage. The cross section of the whorl is subrectangular and higher than broad in the adult shell but is subquadrate and broader than high in the inner shell less than 15 mm in diameter. The umbilical wall is low and perpendicular. The mid ventral keel is distinct, continuous and finely serrate on the top, but not very strong on the body chamber of the holotype. Ribs are flexuous and somewhat sigmoid, intercalated by one or two secondaries between the primaries, and sometimes branched from the umbilical bullae. On the venter these ribs become faint and run forward, crossing the keel with chevrons. On the body chamber growth lines are discernible, there are faint lirae in addition to the ribs.

Bullae on the umbilical margin are not very strong. The inner ventrolateral tubercles are pointed spinose, although they are irregular in strength and arrangement. Namely, the spinose tubercles are, in general, formed remarkably on the primary ribs, but faint or undeveloped on the secondary ribs. It becomes strong on the body chamber and curved backward.

On the suture the external lobe (E) is shallower than the lateral lobe (L), and the first lateral saddle is broad and symmetrically bipartite by a shallow lobule (Fig. 2).

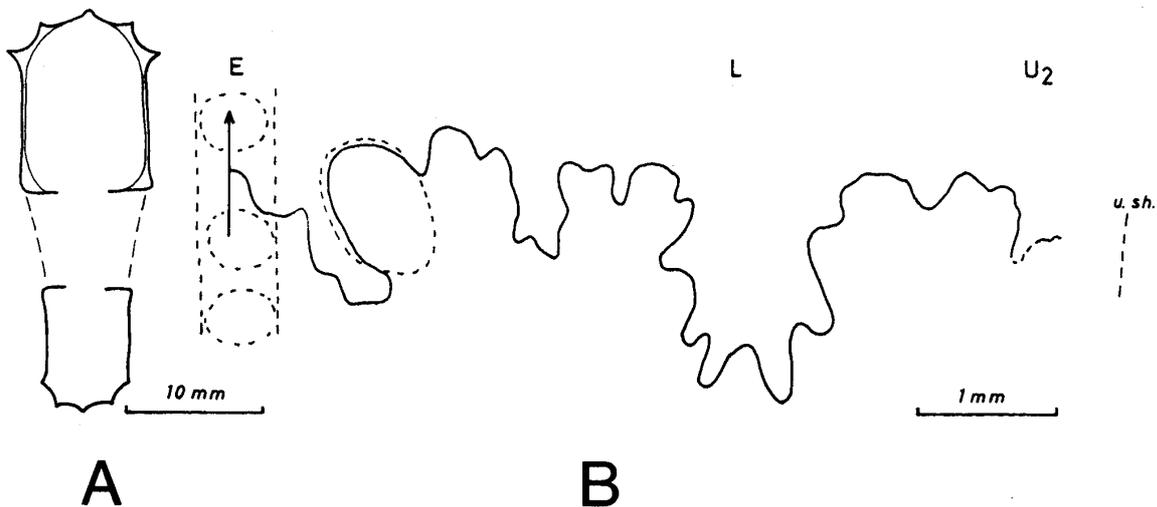


Fig. 2. Whorl section (A) and suture line (B) of *Prionocycloceras obatai* Futakami sp. nov. Holotype, NSM. PM9578, from loc. Ki607, the Roku-no-sawa, a tributary of the Kamiichi-no-sawa, Ikushumbetsu, Hokkaido. u. sh.: umbilical shoulder.

Coniacian collignoniceratid ammonites from Hokkaido

Measurements:

Specimen	Diameter	Height	Breadth	B./H.	Umbilicus	U./D.	U.T.	V.T.
NSM. PM9578 (Holotype)	30.0	12.2	—	—	8.4	0.28	12	32
—90°	22.7	10.8	7.1	0.66	5.4	0.24	—	—
—150°	19.4	9.1	6.6	0.73	5.2	0.27	—	—
NSM. PM9579 (Paratype)	—	7.9	6.0	0.76	—	—	—	—

Comparison: This species is somewhat similar in general features to some species of *Prionocyclus*. Furthermore, in *Prionocyclus* there are fine and numerous ribs on the whorl of the immature stage, whereas they are undeveloped in this species. Therefore, this species is referred to *Prionocycloceras*.

This species is somewhat similar to the immature shell of *P. guayabanum* (Renz, 1982, pl. 35, fig. 13) in that the ribs are flexuous on the flanks. The former, however, is clearly distinguished from the latter in having a more compressed whorl, and stronger, more numerous and more flexuous or sigmoidal ribs. As to the mode of ribbing, this species resembles *Prionocycloceras pseudobravaisi* Collignon (1965, p. 44, pl. 432, figs. 1789–1791) from Madagascar. But, the latter has a wider umbilicus and weaker ventrolateral tubercles on the outer whorl than the former. The similar in these respects to *Subprionocyclus minimus* is a homeomorphy, because of the differences in the serration of keel and the suture.

With respect to the sigmoidal ribs, this species is somewhat similar to *Prionocycloceras sigmoidale* (Matsumoto, 1965a, pl. 10, fig. 1), but the former has finer ribs, a narrower umbilicus and a more compressed whorl than the latter.

Occurrence: Loc. Ki607 in the Roku-no-sawa and loc. Ki404b in the Fukurozawa, the tributaries of the Kamiichi-no-sawa, Ikushumbetsu. These localities correspond to the relatively lower part of the Upper Yezo Group (*I. uwajimensis* Zone). In addition to this species, the above mentioned *P. matsumotoi* sp. nov. occurred from loc. Ki607, and *I. uwajimensis*, *Eubostrioceras saxonicum* and *Damesites damesi intermedium* from loc. Ki404b. Thus this assemblage is assigned to the early to middle (?) Coniacian.

Subfamily Barroisiceratinae Basse, 1947
Genus *Barroisiceras* de Grossouvre, 1894

Type species: *Ammonites haberfellneri* Hauer, 1866.

Remarks: This genus was subdivided into the subgenera *Barroisiceras* and *Texasia* Reeside, 1932 by Wright (1957, p. L432). After that, Matsumoto (1969, p. 300) separated *Texasia* from the genus *Barroisiceras*, because there is a clear

difference between the two in that the type species of *Texasia* develops the ventrolateral nodes on the adult shell. Furthermore, he included the subgenus *Basseoceras* Collignon, 1965, in the genus *Barroisiceras*. Because the morphological features of *Basseoceras* from the early to the middle growth stages are closely similar to those of *Barroisiceras* s.s. Thus, it may be sometimes difficult to judge whether the immature specimens are referred to *Barroisiceras* or *Basseoceras*. Therefore, the genus *Barroisiceras* contains two subgenera, viz. *Barroisiceras* and *Basseoceras*.

***Barroisiceras (Barroisiceras) onilahyense* Basse**

Pl. 2, Figs. 2, 6

Barroisiceras onilahyense Basse, 1947, p. 100, pls. 1–5; pl. 6, figs. 1–4; pl. 7, fig. 1, la; pl. 8, figs. 1, 2.

Barroisiceras onilahyense, Collignon, 1965, p. 68, pl. 444, figs. 1815–1817; pl. 445, fig. 1819.

Barroisiceras (Barroisiceras) onilahyense, Matsumoto *et al.*, 1981, p. 60, pl. 8, figs. 1–3.

Material: The specimens, NSM. PM9580 and 9581, were obtained from a rolled nodule on the middle stream of the Yon-no-sawa, a tributary of the Kamiichi-no-sawa, Ikushumbetsu, Hokkaido (Coll. M. Futakami).

Diagnosis: This species has generally a compressed whorl, a narrow umbilicus and a serrated keel, although the serration becomes clavi-like in the middle and late growth stages. The bullae are formed on the umbilical margin and the clavate tubercles are on the ventrolateral shoulder. There is a considerable extent of variation in the shell ornaments, as Basse (1947) has demonstrated.

Measurements:

Specimen	Diameter	Height	Breadth	B./H.	Umbilicus	U.T.	V.T.
NSM. PM9580	63.7	31.6	19.8	0.63	10.2	5×2	—
NSM. PM9581	—	10.1	8.9	0.85	—	—	—

Descriptive remarks: NSM. PM9580 (Pl. 2, Fig. 6) is of moderate size and preserves a partly destroyed body chamber. There are umbilical bullae, ventrolateral nodes and flexuous ribs on the flanks. The ribs become very faint and replaced by lirae on the last one-fourth of the outer whorl. This specimen closely resembles a weakly ornamented form from Madagascar (Basse, 1947, pl. 6, fig. 2), whereas NSM. PM9581 (Pl. 2, Fig. 2) is quite similar to the specimen from the Obira area, Hokkaido (Matsumoto *et al.*, 1981 pl. 8, fig. 1a-c) in having strong ribs and tubercles.

B. (B.) onilahyense is closely allied to *Barroisiceras (B.) subtuberculatum*

(Gerhardt, 1897, p. 156, pl. 3, fig. 12; Renz, 1982, p. 112, pl. 37, figs. 5–8; pl. 38, figs. 1, 2) from Colombia and Venezuela in the diagnostic features. The both species have the same tendency of variation in the breadth of whorl and the shell ornaments. In fact Renz (1982, p. 112, pl. 37, fig. 4a, b) reported the occurrence of *B. (B.)* aff. *B. onilahyense* from the same area as the latter species. On the average *B. (B.) subtuberculatum* seems to have generally more compressed whorl than that of *B. (B.) onilahyense*.

Occurrence: The specimens were obtained from a rolled nodule which was probably derived from the Member U₂, the lower part of the Upper Yezo Group. In the same nodule *Scaphites pseudoequalis* and *I. cf. uwajimensis* were contained abundantly. Thus, the age is probably early to middle (?) Coniacian. So far this species occurs rarely in Hokkaido.

***Barroisiceras* sp.**

Pl. 2, Fig. 1

Material: A single specimen, NSM. PM5982 from loc. Ki808 (Coll. M. Futakami).

Description: The shell is rather small, and has a very compressed whorl with flattened and nearly parallel flanks. The umbilicus is narrow. On the mid venter a serrated keel is formed, although the serration becomes clavi like on the body chamber. The ribs are fine and flexuous on the flanks, and become the faint bullae like elevations on the umbilical margin. The tubercles develop on the ventrolateral shoulder, but the clavi which are observed in *Subprionocyclus minimus* do not appear.

On the suture the external lobe (E) is shorter than the lateral lobe (L), and L is asymmetrically divided. The first lateral saddle is bipartite at the top and roughly symmetrically divided. The second lateral saddle (between L and U) is broad (Fig. 3). Thus the elements of suture line are similar to that of *Barroisiceras*.

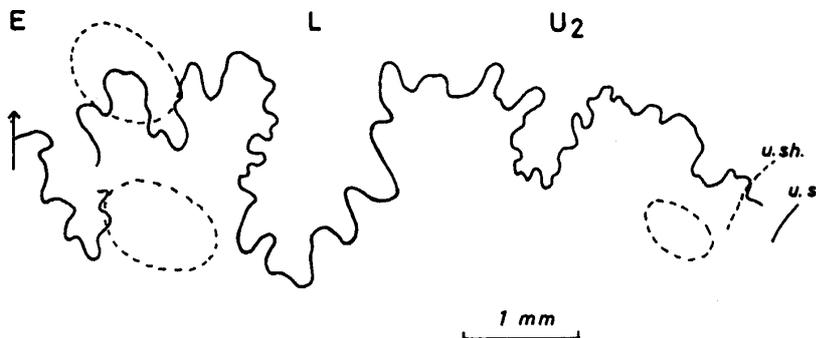


Fig. 3. Suture line of *Barroisiceras* sp. NSM. PM9582, from loc. Ki808, the Ikushumbetsu industrial road, Ikushumbetsu, Hokkaido.
u. sh.: umbilical shoulder, u. s.: umbilical seam.

Measurements:

Specimen	Diameter	Height	Breadth	B./H.	Umbilicus	V.T.
NSM. PM9582	22.6	10.6	—	—	5.0	35
-90°	17.8	8.4	5.0	0.60	4.0	—

Remarks: This species is probably referred to *Barroisiceras* because of its ventral features and the sutural elements as described above. It has more compressed whorls than any other species of *Barroisiceras*. Concerning shell ornaments this species is similar to *Barroisiceras* (*B.*) *onilahyense* (Basse, 1947, pl. 3, fig. 5), but the former has weaker and finer ribs than the latter. It is also similar to *Barroisiceras* aff. *B. subtuberculatus* (Renz, p. 112, pl. 37, fig. 8a, b), but it is distinguished from the latter in having narrower ribs.

As to the mode of ribbing, this specimen is somewhat similar to NHMW1890 of *Forresteria* (*Harleites*) *petrocoriensis* (Coquand) (Kennedy, 1984, pl. 6, fig. 5). But, the latter has distinct tubercles on the ribs at a point one third of the flanks from the umbilical margin.

The present species is closely similar to "*Reesidites*" *minimus* (Matsumoto, 1965a, p. 63, pl. 5, fig. 1) in the compressed whorl and the ribbing, but the latter is distinguished in having the ventrolateral clavi instead of nodes, stronger umbilical bullae, and always a continuous and serrated keel at corresponding growth stages.

In the morphological features this species closely resembles the species described as ? *Solgerites* sp. (Renz, 1982, p. 115, pl. 38, figs. 5a, b, 6a, b, 9a, b), but the former has slightly wider umbilicus.

This specimen could possibly represent a new species, but should be provisionally called *Barroisiceras* sp. in this paper, because the material is only a single "immature" individual.

Occurrence: This specimen is obtained from the siltstone exposed at loc. Ki808 on north side of the Ikushumbetsu industrial road. In addition to this species, *Baculites* sp. is contained abundantly in the same nodule. The stratigraphical position corresponds to the lower part of Member U₂, relatively the lower part of the Upper Yezo Group. Thus, it is probably assigned to the lower part of the Coniacian.

Phylogenetic relationships in some genera of the Collignoniceratidae

I discuss here on the morphological features of some selected genera in Collignoniceratidae. The possession of a keel on the venter is one of the most important morphological characters and is well stabilized in collignoniceratid ammonites. All of the genera in this family, when their ontogeny is examined,

have a continuous keel from the early growth stage. But, in the adult stage the keel shows various features at a subfamily or genus level. Taking this point into account, the collignoniceratid ammonites are divided into two major groups. One of them has a continuous keel through most of its ontogeny, including both types which have a continuous keel with the numerous fine elevations on the top as shown by *Prionocyclus* and *Prionocycloceras* and three entire keels such as *Peroniceras*. The other group fundamentally has the serrated keel in the middle and late growth stages, including a type which becomes the mid-ventral tubercles in the adult stage instead of a serration as shown by *Collignoniceras*, *Barroisiceras*, *Subprionotropis* and *Forresteria*.

As to the shape of the whorl, the family is divided into a group with square or rectangular whorl section and a group with fastigate venter. Most of the former have a continuous keel, whereas the latter has a serrated keel or mid-ventral tubercles.

On the elements of suture-line in the family Collignoniceratidae, I think that one of the important elements is in the mode of the first lateral saddle (between E and L). E/L saddle of the group with square or rectangular whorl section is generally broad and symmetrically divided. But, that of the group with a fastigate venter is rather narrow and not very symmetrically divided. In other words, the mode of E/L saddle seems to be related to the shape of the whorl section.

Collignoniceras, an earliest genus of the family Collignoniceratidae, has the morphological features of both groups mentioned above: the whorl is subrectangular and has a broad and symmetrically divided E/L, a serrated and occasionally continuous keel with fine elevations on the top, in the middle growth stage and mid-ventral tubercle in the late growth stage. As in Fig. 4, the main divergence of the phylogeny in the family Collignoniceratidae seems to be shown in late Turonian, judging from the morphological features such as the mode of keel, whorl shape and suture-line.

Matsumoto (1955, p. 39; 1970, p. 230) pointed out that the origin of *Protexanites* s.l., which is the earliest genus of Texanitinae, is in *Subprionocyclus*, a late Turonian genus, on the ground of the morphological features such as the mode of ribbing and keel and also stratigraphical evidence. On the other hand, Klinger and Kennedy (1980, p. 348) suggested that it would be possible to derive *Protexanites* from "*Fraudatoroceras*", an aberrant genus of the Peroniceratinae on the basis of the South African material.

I consider that the origin of *Protexanites* seems to be rather in the Coniacian *Prionocycloceras*. Because, on the phylogeny of Collignoniceratidae, the nature of keel, shape of whorl and suture-line seem to be stabler characters than the ribbing. The mode of ribbing seems to be extremely variable among the

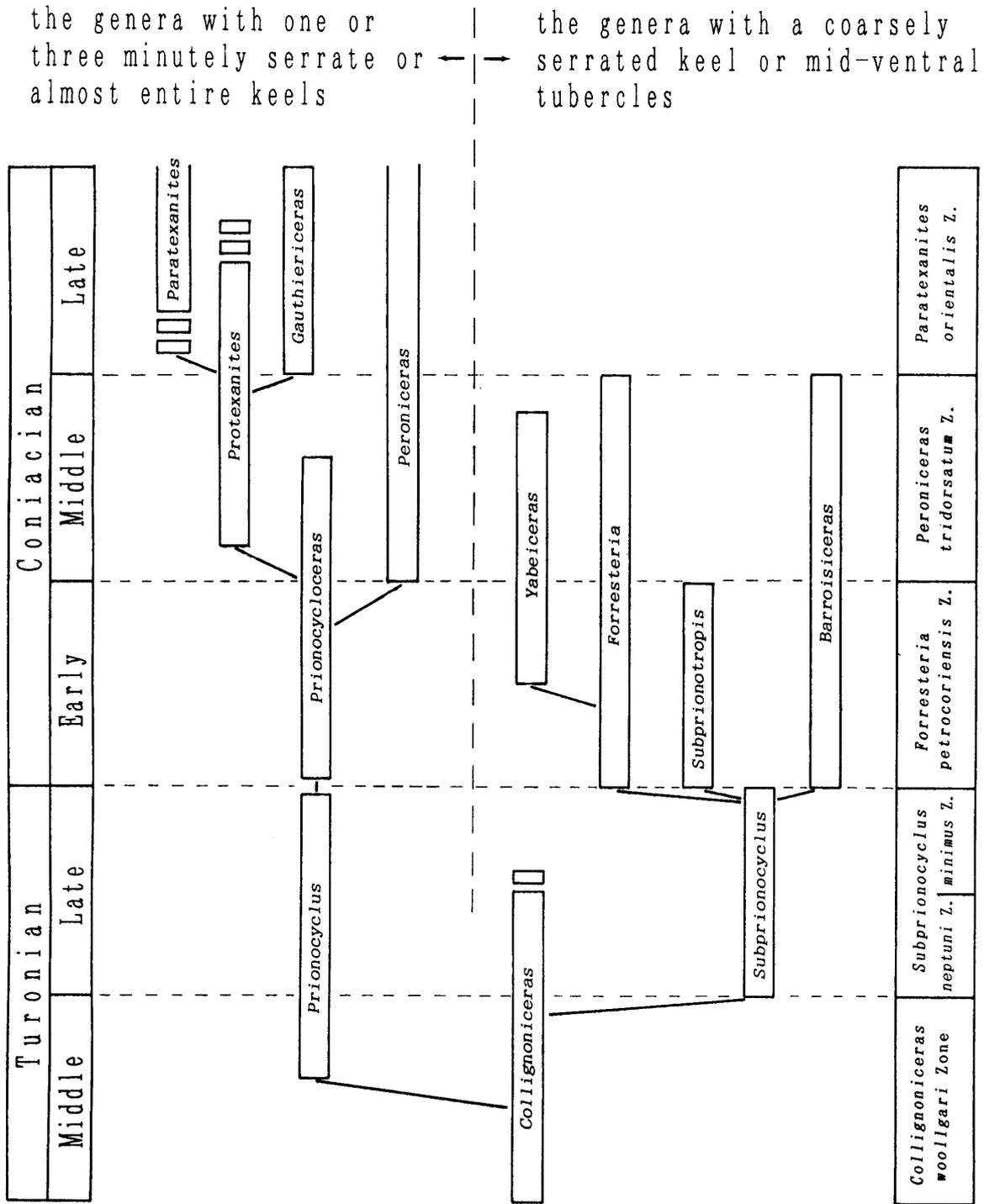


Fig. 4. Phylogenetic relationship of Turonian and Coniacian collignoniceratid genera.

species.

On the other hand, it is possible to derive *Forresteria*, *Barroisiceras* and *Subprionotropis* from *Subprionocyclus*, as suggested by Matsumoto (1969, p. 298), because these Coniacian genera have the ventral clavi of which the serration of keel of *Subprionocyclus* may have been transformed in the middle and late growth stages.

As to the origin of *Peroniceras*, Matsumoto (1965b, p. 213) suggested that it is probably in *Prionocyclus*. I consider that it may be possible to derive *Peroniceras* from the lower to middle Coniacian *Prionocycloceras*, because of the mode of keel.

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