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Turonian collignoniceratid ammonites from Hokkaido, Japan —Stratigraphy and Paleontology of the Cretaceous in the Ishikari province, central Hokkaido, Part 3—

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Abstract

In this paper five species belonging to the two genera of the Turonian collignoniceratid ammonites from Hokkaido are described, *viz. Collignoniceras woollgari* (Mantell), *C. bravaisianum* (d'Orbigny), *Subprionocyclus neptuni* (Geinitz), *S. minimus* (Hayasaka et Fukada) and *S.* (?) sp.

Subprionocyclus bravaisianus is reasonably referred to the genus *Collignoniceras* and independent of *S. neptuni*. *"Reesidites minimus"* and *"Subprionocyclus normalis"* cannot be maintained as separate species. Furthermore, the relation between the Japanese *"R. minimus"* and *"S. normalis"* and the North American *"S. normalis"* [=*Oregoniceras condoni, O. jacksonense* and *O. argonautarum*] is examined, with a suggestion that they may represent geographical subspecies.

A dimorphism represented by macroconchs and microconchs probably existed in the Turonian collignoniceratids.

An evolutional change of the Turonian collignoniceratids as shown by a series of *C. woollgari, S. neptuni* and *S. minimus* shows a paedomorphosis, and probably is a case of the neoteny. This change is interpreted as an evolutional adaptation for the decrease in the resistance of water. In other words, the phylogenetic evolution of these Turonian collignoniceratids seems to suggest a trend of shell adaptation for more successful swimmer.

Introduction

The Cretaceous System in Hokkaido has been highly studied in various fields of geological sciences and paleontology (e.g. Matsumoto, 1942–43, 1965). Most of them have occupied an important position for the biostratigraphy of Japanese Cretaceous, and have offered many significant data for the interregional correlation and ammonite taxonomy.

However, as to the precise stratigraphical and geographical ranges of some species of ammonites, our knowledge has not been always satisfactory. Therefore, I carried out the geological investigation of the Cretaceous rocks in the

Ishikari province, Hokkaido, where there are significant type-sections of biostratigraphy for the Cretaceous System in Japan. I intend to make clear the mode of occurrence and distribution of selected species of the Turonian collignoniceratid genera such as *Collignoniceras*, *Subprionocyclus* and "*Reesidites*". In addition, through this investigation I intend to get important data for the discussion of the phyletic evolution of these species.

This paper is Part 3 of *Stratigraphy and Paleontology of the Cretaceous in the Ishikari province, central Hokkaido,* and contains primarily the paleontological description on the Turonian collignoniceratid ammonites from the Ishikari province and some others.

The detailed stratigraphical position and location of the used specimens in this paper are described in Parts 1 and 2 which are already published (Futakami, 1986a, b). The described specimens are kept in the National Science Museum, Tokyo.

Acknowledgements

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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 ***Collignoniceras*** Breistroffer, 1947

Type species: *Ammonites woollgari* Mantell, 1822 (designated by Meek, 1876)

Remarks: The genus *Collignoniceras* has been highly studied on its morphological features (e.g. Matsumoto, 1965; Kennedy *et al.*, 1980), because it includes cosmopolitan and important indices of the Middle Turonian. The species which have been hitherto referred to this genus are, in addition to *C. woollgari, C. boreale* (Warren, 1930), *C. papale* (d'Orbigny, 1841), *C. carolinum* (d'Orbigny, 1841), *C. canthus* (Sornay, 1951) and *C. turoniense* (Sornay, 1951) (see Kennedy *et al.*, 1980).

The morphological characteristics of this genus are in having the serrated siphonal keel in the early to middle growth stage, the clavi on the venter instead of the keel in the late growth stage and the radial or flexuous ribs with umbilical bullae, inner and outer ventrolateral tubercles. These features are similar to those of the genera *Prionocyclus* and *Subprionocyclus* of the Collignoniceratinae. Among them, *Prionocyclus* distinctly differs from *Collignoniceras* in that the former has a continuous keel with the numerous fine elevations on the top through most of its ontogeny. The morphological differences between *Subprionocyclus* and *Collignoniceras* have been discussed by Matsumoto (1959, p. 109) and Kennedy *et al.* (1980, p. 559). However, it is somewhat difficult to distinguish these two genera, because, there are some species which show intermediate morphological features between these two genera, *viz. C. carolinum, C. woollgari bakeri* (Anderson), *S. bravaisianus* and *S. branneri* (Anderson).

To solve this problem it is necessary to examine the ontogeny and variation of every species which has been referred to *Collignoniceras* and *Subprionocyclus*. For this procedure, I provisionally distinguish *Collignoniceras* from *Subprionocyclus* in that the former has, generally, simpler sutural lines in early to middle growth stage, prorsiradiate ribs and siphonal clavi on the outer whorl in comparison with paired or alternated long and short sigmoidal ribs and a continuous and persistent keel in the latter.

Collignoniceras woollgari (Mantell)

Pl. 1, Figs. 1–3, 6

Synonymy: See Kennedy *et al.*, 1980, p. 560.

Material: The specimens have been obtained from a calcareous nodule at loc. Y61, a cliff on the Kaneobetsu forestry road along the Kaneobetsu River, Oyubari, Hokkaido (coll. Y. Kawashita). The plaster casts of these specimens are registered in National Science Museum, Tokyo: NSM. PM7624–7626.

Measurements:

Specimen	Diameter	Height	Breadth	B./H.	Umbilicus	U.T.	V.T.
KC. 620524	79.0	29.2	13.6×2	0.93	31.0	12	—
(cast: NSM. PM7626)							
NSM. PM7624	21.0	8.4	6.2	0.74	8.0	—	19×2
NSM. PM7625	15.1	5.0	—	—	6.2	—	—
−180°	12.8	4.0	4.5	1.13	5.4	—	—

U. T.: number of umbilical tubercles per whorl

V. T.: number of ventrolateral tubercles per whorl

Descriptive remarks: This species has a high morphological variation (Matsu-

moto, 1965, p. 12). The examined specimens have a moderate umbilicus, subrectangular whorl section and normally prorsiradiate single ribs on the flanks. There are, however, rarely branched ribs arising from the umbilical bullae on the inner whorl, and all the ribs become coarse and are much widely spaced on the outer whorl. KC. 620524 (Pl. 1, Fig. 1), a specimen of moderate size, closely resembles the specimen of Muramoto Museum Collection, 68. 10. 14 from loc. Y5206 of T. M., Hakkin-zawa, Oyubari (Matsumoto, 1971, pl. 21, fig. 4) in ornaments and whorl shape. In these specimens the presence or absence of horn like tubercles cannot be determined owing to the unfavourable preservation. In the typical form *Collignoniceras woollgari,* the inner ventrolateral tubercles may develop into distinctive conical horns in the late part of a larger outer whorl (Kennedy *et al.,* 1980, p. 562, pl. 62).

NSM. PM7624 and NSM. PM7625 are immature shells and comparable well with some specimens from Wyoming (Matsumoto, 1965, pl. 1, figs. 2, 4) in having prorsiradiate ribs.

A large specimen with the horn like tubercles on the ventrolateral shoulders has not been obtained yet from the Japanese Cretaceous.

Occurrence : The stratigraphic position is probably equivalent to relatively the lower part of *Inoceramus hobetsensis* Zone. This species occurs rarely in Hokkaido.

Collignoniceras bravaisianum (d'Orbigny)

Pl. 1, Figs. 4–5, 7; Pl. 2, Figs. 1–14; Pl. 3, Fig. 1; Pl. 4, Figs. 2, 4–5

Ammonites bravaisianus d'Orbigny, 1841, p. 308, pl. 91, figs. 3, 4;
Fritsch and Schloenbach, 1872, p. 29, pl. 8, fig. 5; pl. 16, fig. 4.
Ammonites percarinatus Hall and Meek, 1856, p. 396, pl. 4, fig. 2a, b.
Schloenbachia bakeri Anderson, 1902, p. 121, pl. 2, figs. 26–33.
Prionotropis bravaisianus, Roman and Mazeran, 1913, p. 22, pl. 1, figs. 13–17.
Prionotropis teshioensis Yabe and Shimizu, 1925, p. 134, pl. 21, fig. 10; pl. 33, figs. 6–10.
Collignoniceras woollgari bakeri, Matsumoto, 1965, p. 16, pl. 3, figs. 3, 4.
Subprionocyclus branneri, Matsumoto, 1965, p. 50, pl. 13, fig. 2a, b.
Subprionocyclus bravaisianus, Matsumoto and Noda, 1966, p. 359, pl. 40, figs. 1–8; Thomel, 1969, p. 117, pl. F, figs. 4–6; Matsumoto, 1971, p. 137, pl. 21, fig. 3; Tanabe and Shigeta, 1987, p. 168, fig. 2a, b.
Subprionocyclus percarinatus, Cobban, 1983, p. 18, pl. 5, figs. 26–37; pl. 15, figs. 5, 6.

Material: KC. 560419 (coll. Y. Kawashita), NSM. PM9538 (coll. M. Futakami) were obtained from locs. Y410 and Y411F (see Futakami, 1986a), the lower stream of the Kaneobetsu River, the Oyubari area, Hokkaido. NSM.

PM7451, 7457, 7460–7463 (coll. I. Obata), S. C. 3738A (plaster cast: NSM. PM7630), S. C. 3738B (plaster cast: NSM. PM7631), S. C. 41 (plaster cast: NSM. PM7633) (coll. T. Shimanuki) from loc. Ob1, near the entrance of the Nanbu-no-sawa, the Obira area, Hokkaido. S. C. 1813 (plaster cast: NSM. PM7628), S. C. 3326A (plaster cast: NSM. PM7629), S. C. 3326B (plaster cast: NSM. PM7632) from a cliff of the Kamikinenbetsu River near the Shigeru-no-sawa, the Obira area, Hokkaido (coll. T. Shimanuki). NSM. PM9516–9519, 9521, 9523, 9525, 9537 from loc. Y200F, a rolled nodule on the middle stream of the Shuparo River, the Oyubari area, Hokkaido (coll. M. Futakami).

Diagnosis: This species is characterized by a compressed whorl, a wide umbilicus, persistency of the crowded and numerous ribs and siphonal clavi at the late growth stage.

Description: The shell of KC. 560419 is about 100 mm in diameter and regarded as a full grown shell of the species. It is the largest specimen that has been studied on this species. The ornamentation on the exposed part of the inner whorl is similar to that of the type specimen of *Collignoniceras bravaisianum* (d'Orbigny, 1841, pl. 91, figs. 3–4), and also to that of No. 1 and No. 4 specimens which have been redescribed by Matsumoto and Noda (1966, pl. 40, figs. 2, 4). The whorl of KC. 560419 is fairly compressed, roughly subrectangular in cross section, moderately involute and umbilicate. The keel of mid-venter is continuous, distinct and serrate. On the venter of body whorl its serration gradually strengthens, and develops into clavate tubercles.

Ribs on the septate whorls are mostly simple, prorsiradiate, and sometimes intercalated, but in the late part of body chamber they are flexuous. Occasionally the inner whorl has some branching ribs from the umbilical bullae. Each rib has distinct inner and outer ventrolateral clavi. Inner one, however, becomes faintly by degrees on the body chamber, and it is indistinct at diameters over 87 mm.

The suture is rather massive. The external lobe (E) is nearly as deep as the lateral lobe (L). The first lateral saddle (between E and L) is broad and rather symmetrically divided (Figs. 1, 2). These elements show the sutural pattern of a genus *Collignoniceras*.

Measurements:

Specimen	Diameter	Height	Breadth	B./H.	Umbilicus	U.T.	V.T.
KC. 560419	100.0	39.5	23.9	0.61	29.5	24	44
NSM. PM7451	32.9	10.7	8.3	0.78	15.0	30	32
NSM. PM7457	20.3	7.1	—	—	9.2	24	34
NSM. PM7460	17.4	5.9	5.0	0.85	7.8	—	—
NSM. PM7461	19.2	5.6	—	—	9.6	36	36

NSM. PM7463	21.0	5.8	5.5	0.95	10.2	13×2	22×2
NSM. PM9516	22.4	9.2	6.0	0.65	8.1	—	41
NSM. PM9517	28.0	9.8	—	—	11.0	—	25×2
NSM. PM9518	24.0	8.6	—	—	9.0	—	33
NSM. PM9519	20.8	6.9	—	—	8.5	—	48
−180°	14.5	5.1	3.7	0.73	5.8	—	—
NSM. PM9521	19.2	6.7	5.6	0.81	7.8	—	20×2
NSM. PM9523	15.4	5.9	4.5	0.76	5.6	—	43
NSM. PM9525	12.8	4.4	3.1	0.70	5.0	—	40
NSM. PM9537	24.1	9.3	6.2	0.67	8.8	—	49
NSM. PM9538	45.2	18.4	11.8	0.64	16.4	—	—
S.C. 1813	25.7	8.2	6.1	0.76	11.2	—	54
S.C. 3326A	31.7	11.5	—	—	11.7	—	49
S.C. 3326B	38.4	15.3	—	—	12.7	19	33
S.C. 3738A	40.1	15.4	10.4	0.68	13.6	—	—
S.C. 3738B	41.1	15.2	—	—	14.4	—	—
S.C. 41	47.7	17.0	—	—	18.4	13×2	14×2

Remrks: This species was established as *Ammonites bravaisianus* by d'Orbigny, 1841. After that Matsumoto and Noda (1966) have rescrutinized on its specific characters and variation. They pointed out that *bravaisianus* is referred to *Subprionocyclus*, and is closely allied to *Subprionocyclus neptuni* in various respects but is distinguished between these two species by its less involute and more widely umbilicate whorl.

On the other hand, Hancock *et al.* (1977, p. 165) and Wright (1979, p. 320) have regarded *S. bravaisianus* as a synonym of *S. neptuni* because the range of variation in *S. neptuni* is greater than the difference between *bravaisianus* and *neptuni*.

The different opinions on the taxonomic position of this species may be due to the situation that previous authors discussed on the basis of immature shells alone.

I consider that this species has an intermediate feature between *Collignoniceras woollgari* and *Subprionocyclus neptuni* in ornamentation of the shell. Namely, ribs are sometimes paired or alternately long and short. This is similar to those of *Subprionocyclus*, but most of the syntypes of this species (Matsumoto and noda, 1966) are immature shells, and such ribbing is also observable on some species belonging to *Collignoniceras* in some growth stages (*C. woollgari*: Matsumoto, 1965, p. 13, fig. 6; *C. carolinum:* Kennedy *et al.*, 1980, pl. 68, fig. 10; Wright and Kennedy, 1981, pl. 30, fig. 5). Some syntypes of *bravaisianus* occasionally show gently sigmoidal ribs which are often formed on the flanks in

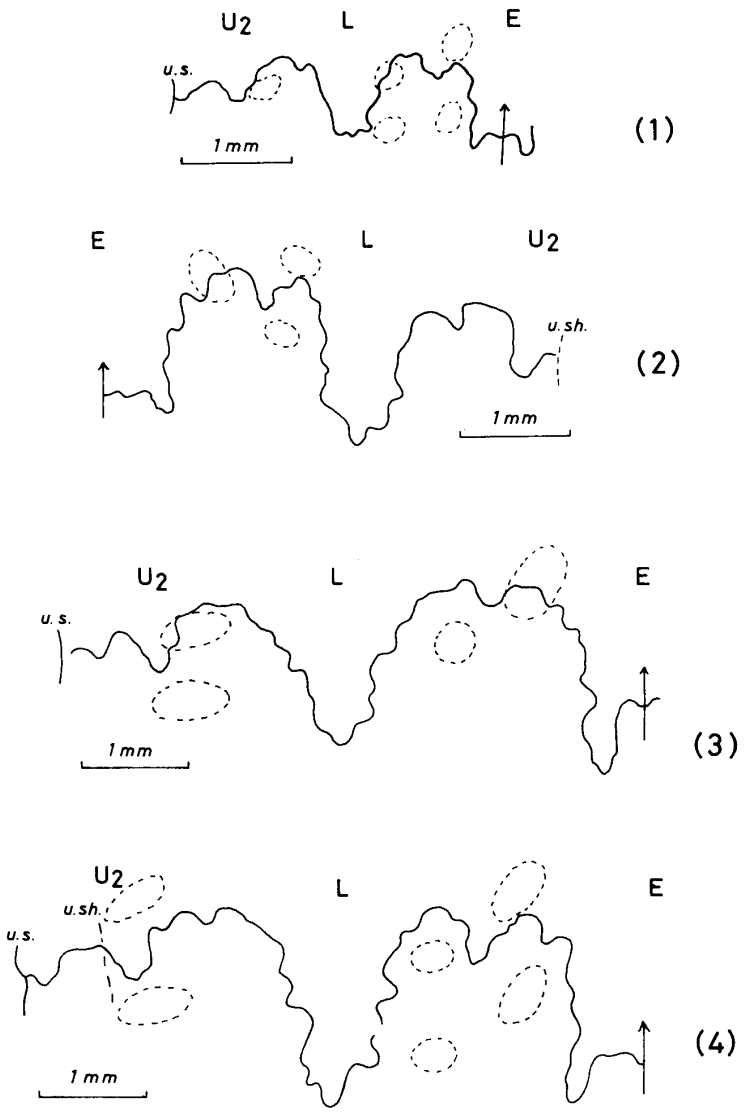

Fig. 1 Suture of *Collignoniceras bravaisianum* (d'Orbigny). NSM. PM9525 (1), NSM. PM9584 (2), NSM. PM9524 (3), NSM. PM9519 (4), from loc. Y200F, the Shuparo River in the Oyubari area, Yubari. u. sh.: umbilical shoulder, u. s.: umbilical seam

Subprionocyclus. Ribs in most of the Hokkaido material seem to be rather simple and prorsiradiate in the middle growth stage as in *Collignoniceras woollgari* (Pl. 2, Figs. 3–13). The mid-ventral keel in this species is continuous, distinct, broad and serrate in early to middle growth stage (e.g. Roman and Mazeran, 1913, pl. 1, figs. 13, 14; Matsumoto and Noda, 1966, pl. 40, figs. 1, 2), but it turns into the siphonal clavi in the full grown shell as shown by a Hokkaido specimen, KC. 560419 (Pl. 3, Fig. 1c). It also seems to be similar to that of *Collignoniceras woollgari*. Shape of keel of *S. neptuni* in the same growth stage,

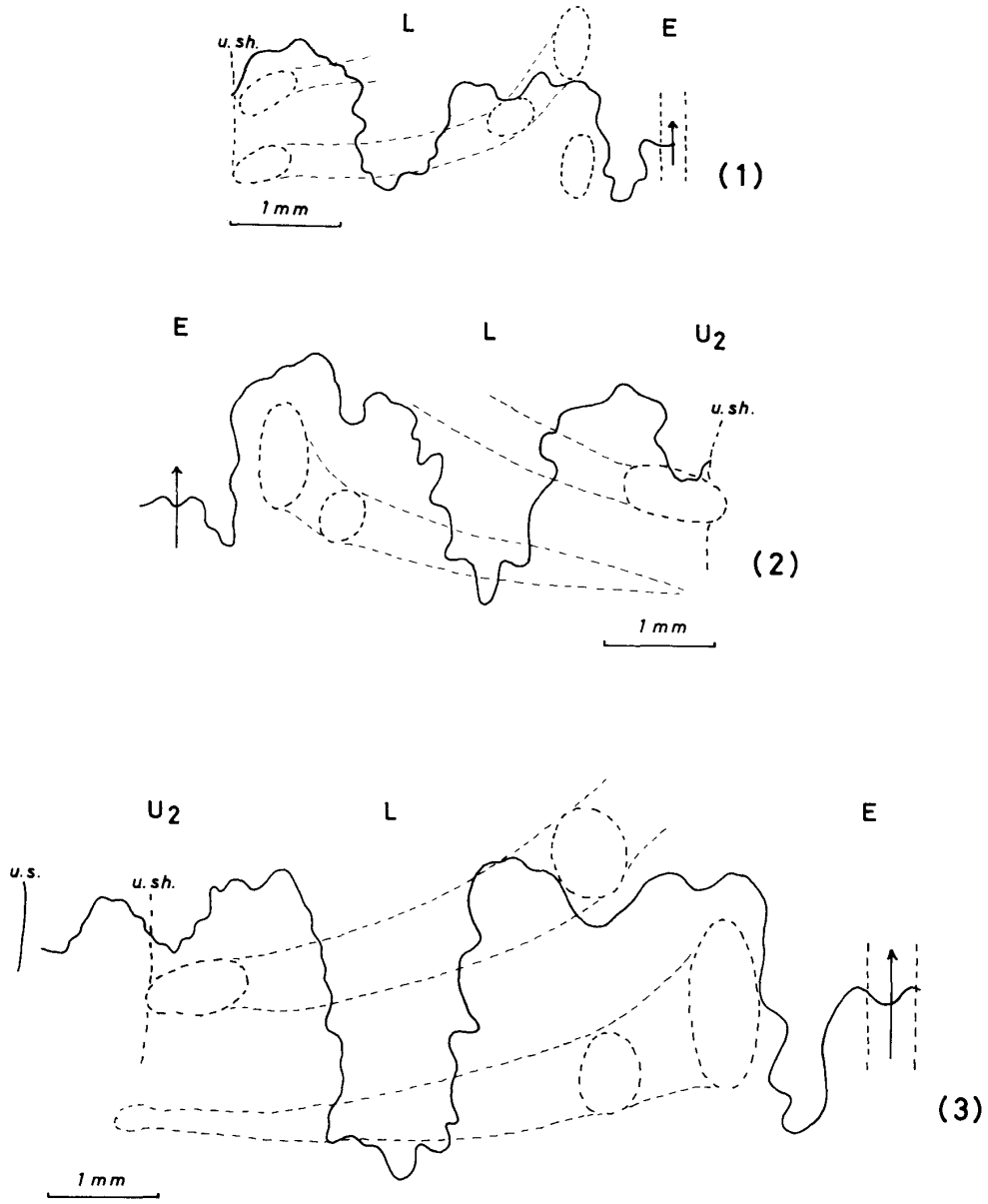

Fig. 2 Suture of *Collignoniceras bravaisianum* (d'Orbigny).
NSM. PM7462 (1), NSM. PM7458 (2), NSM. PM7451 (3), from loc. Ob. 1, the Nanbu-no-sawa in the Obira area. u. sh.: umbilical shoulder, u. s.: umbilical seam

however, differs from that of this species: less distinct and narrower (Obata *et al.*, 1979, pl. 1, figs. 1–5; pl. 3, figs. 1, 4). The inner ventrolateral tubercles are weaker than the outer ones. This character is similar to *Subprionocyclus neptuni.* The suture is rather massive, and the first lateral saddle is broad and symmetrically divided as in *Collignoniceras woollgari.* In *Subprionocyclus neptuni* it is more complicated, and the first lateral saddle asymmetrically divided.

As mentioned above, *Am. bravaisianus* has some intermediate morphological features between the two genera. But I am inclined to conclude that this species is better placed in the genus *Collignoniceras* because of the general similarity in features of keel, ribbing and sutural elements to *C. woollgari* rather than to *S. neptuni.*

In short, this species is distinguishable from *S. neptuni* in having sharper and more numerous ribs with fewer sigmoid ones, a wider umbilicus, sutural elements of the *Collignoniceras woollgari* type and siphonal clavi on the venter in late growth stage on the basis of the available material.

The morphological character of this species closely resembles that of *Ammonites percarinatus* by Hall and Meek (1856) in the ornamentation and whorl shape. Cobban (1983) has assigned *Am. percarinatus* to the genus *Subprionocyclus,* because he has considered that the morphological features of *A. percarinatus* seem to be more similar to those of *Subprionocyclus* which have been described by Wright and Matsumoto (1954, p. 129) and Matsumoto (1959, p. 108–9). But, he has also described that a specimen in this collection suggests a link to *Collignoniceras* in the tuberculation on the ventral shoulder.

On the other hand, *C. bravaisianum* is also closely similar to *Schloenbachia bakeri* Anderson, 1902 (=*Collignoniceras woollgari bakeri* by Matsumoto, 1965) in having the compressed whorl with crowded and numerous ribs and relatively wide umbilicus. In fact it seems to be difficult to distinguish the lectotype of *Am. bravaisianus* (Matsumoto and Noda, 1966, pl. 40, fig. 1) from the holotype of *S. bakeri* Anderson (1958, pl. 38, fig. 3). Thus *S. bakeri* seems to be a synonym of this species. But, there is an interesting specimen (Anderson, 1958, pl. 38, fig. 2) which resembles the inner whorl of *C. woollgari* in having the coarse and strong ribs with growth. The fact suggests a link of this species to *C. woollgari* as in the case of *Ammonites percarinatus* mentioned above.

Wright and Kennedy (1981) has regarded *S. bakeri* as a synonym of *C. woollgari.* Certainly the ornamentation of immature shells of *S. bakeri* closely resembles that of a specimen of type D in the young stages of *C. woollgari* which has been shown by Matsumoto (1965, p. 13, fig. 6), and that of *C. woollgari regularis* by Haas (1946, pl. 16, figs. 1–17). But, in the adult stage of *C. woollgari,* the ribs become coarse, and each rib is commonly provided with a ventrolateral horn like tubercle which developed from the inner ventrolateral one.

An adult specimen of this species, KC. 560419 (Pl. 3, Fig. 1), has the faint inner ventrolateral tubercles and the dense and numerous ribs on the body chamber. In these respects, this species is similar to *C. carolinum* from the Middle Chalk of England (Kennedy *et al.*, 1980, p. 574, pl. 68) in which the ribs are fine and dense, the inner ventrolateral tubercles of the adult shell are

not so enlarged as horn like ones, and the bullae on the umbilical margin are week. Especially the immature shell of *C. bravaisianum* is similar to that of *C. carolinum* which has been shown by Kennedy *et al.* (1980, pl. 68, fig. 10). But, this species is distinguished from the latter species in that the outer whorl is slender, and the rib is weaker and more numerous in the adult stage.

KC. 560419, a Hokkaido specimen, is similar to the specimen of *Subprionocyclus hitchinensis,* which is shown by Wright (1979, pl. 5, fig. 13), in the ornamentation. *S. hitchinensis,* however, differs from this species in having more compressed whorls, the "*S. normalis*"-like ventrolateral tubercles and the continuous keel throughout its ontogeny.

A dimorphism is recognized in this species. Microconchs as represented by Pl. 1, Figs. 5, 7 and Pl. 4, Fig. 2 have a weaker ornamentation on the outer whorl than macroconchs (Pl. 2, Fig. 14; Pl. 3, Fig. 1; Pl. 4, Figs. 4, 5): on the body chamber of the former the inner and outer ventrolateral tubercles are faint or disappear, and flexuous ribs are crowded and numerous (Pl. 1, Fig. 7). In the adult stage macroconchs are up to 100 mm in diameter, while microconchs are only 40–45 mm in diameter at most.

Occurrence: The fossiliferous beds are assigned to the upper part of the *I. hobetsensis* Zone. Its stratigraphical position is correlated with the upper Middle Turonian to lower Upper Turonian. This species is common in Hokkaido.

Genus ***Subprionocyclus*** Shimizu, 1932

Type species: Prionocyclus hitchinensis Billinghurst, 1927

Remarks: The genus *Subprionocyclus* was established by Shimizu (1932) with *P. hitchinensis* from the Upper Turonian Chalk Rock of England as the type species. This genus is distinguished from *Collignoniceras* from the Middle Turonian and *Prionocyclus* from the Middle to Upper Turonian in that it has weaker ribs, a distinct serration of keel, suture lines of a different type, which are characterized by the external lobe (E) being much shorter than the first lateral lobe (L) and the asymmetrically divided first lateral saddle. The diagnostic features of the genus have been described in detail by Matsumoto (1959, p. 108).

Subprionocyclus neptuni (Geinitz)

Pl. 5, Figs. 1–2; Pl. 6, Fig. 1

Ammonites neptuni Geinitz, 1850, p. 114, pl. 3, fig. 3.

Schloenbachia oregonensis Anderson, 1902, p. 122, pl. 2, figs. 48–57; pl. 6, fig. 144; pl. 7, figs. 149–150.

Subprionocyclus neptuni, Matsumoto, 1959, p. 112, pl. 29, figs. 2, 3; pl. 30, figs. 1, 2.

Subprionocyclus neptuni, Matsumoto, 1965, p. 52, pl. 3, fig. 5; pl. 13, figs. 1, 4.
Subprionocyclus neptuni, Collignon, 1965, p. 67, figs. 1691, 1692.
Subprionocyclus neptuni, Matsumoto, 1971, p. 136, pl. 22, fig. 3.
Subprionocyclus neptuni, Wright, 1979, p. 319, pl. 5, figs. 2, 3.
Subprionocyclus neptuni, Obata *et al.,* 1979, p. 51, pl. 1, figs. 1–5; pl. 2, figs. 1–5; pl. 3, figs. 1–7; pl. 4, figs. 1–3.

Material: KC. 56102501, 56102502 (coll. Y. Kawashita) have been obtained from loc. Ki318, the Ganseki-zawa, a tributary of the Kamiichi-no-sawa, Ikushumbetsu. NSM. PM9539 (coll. M. Futakami), from loc. Ki607F, the Roku-no-sawa, a tributary of the Kamiichi-no-sawa, Ikushumbetsu. NSM. PM9583 (coll. M. Futakami), from loc. Ni311, the Kita-no-sawa, a tributary of the Naie River, Naie, Hokkaido.

Measurements:

Specimen	Diameter	Height	Breadth	B./H.	Umbilicus	U.T.	V.T.
KC. 56102501	48.7	19.7	13.9	0.71	15.0	12	28
KC. 56102502	33.2	13.7	10.4	0.76	9.8	12	29
NSM. PM9539	43.6	18.4	12.0	0.65	12.6	12	24
NSM. PM9583	22.5	11.0	8.3	0.75	4.9	—	—

Remarks: The diagnostic feature of this species was described in detail by Matsumoto (1959, p. 112). The morphologic feature of *S. neptuni* is similar to that of *S. branneri* Anderson (1902, pl. 1, figs. 11–16), but the latter has coarser ornaments and broader whorls. Obata *et al.* (1979) pointed out that this species shows a considerable extent of variation in every growth stage and they distinguished three types: A, B and C. It is very interesting that the specimens of type C in the variation (p. 74, pl. 3, figs. 3, 5a, b; pl. 4, fig. 1a-d) is similar to those of *S. branneri* in the whorl section and ornaments. All the described specimens in this paper closely resemble those of type A of Obata *et al.* (1979, p. 71, pl. 3, fig. la, b; pl. 4, fig. 2a-c).

Holotype of *Oregoniceras oregonense* (Anderson, 1958, pl. 24, fig. 4) conforms well with NSM. PM7336 (Obata *et al.,* 1979, pl. 3, fig. 7; text-fig. 11–5), which was assigned to type B in the morphological variation, in ribbing and tuberculation on the outer whorl. Thus, *O. oregonense* is probably a synonym of this species.

On the other hand, the ornamentations such as ventrolateral tubercles, ribs and keel of type B are weaker than the types A and C in the late growth stage, and its shell is smaller. This probably suggests the dimorphism: type B represents the microconch and types A and C the macroconch.

S. neptuni shows the world wide distribution, and it serves an important

role in the biostratigraphy. Furthermore this species exemplifies the phyletic evolution in a series of collignoniceratids.

Occurrence: This species occurs in the Upper Turonian and fairly commonly in Hokkaido.

Subprionocyclus minimus (Hayasaka et Fukada)

Pl. 4, Figs. 1, 3; Pl. 5, Fig. 3; Pl. 6, Figs. 2–3; Pl. 7, Figs. 1–8; Pl. 8, Figs. 1–10; Pl. 9, Fig. 1

Barroisiceras minimum Hayasaka and Fukada, 1951, p. 325, pl. 1, figs. 1–4; pl. 2, figs. 1–7.
Reesidites minimus, Wright and Matsumoto, 1954, p. 130.
Subprionocyclus normalis, Matsumoto, 1965, p. 55, pl. 12, figs. 1–5; pl. 13, fig. 3.
Reesidites minimus, Matsumoto, 1965, p. 63, pl. 14, fig. 1; pl. 15, figs. 1–3.
Reesidites minimus, Obata, 1965, p. 39, pl. 4, figs. 1–13; pl. 5, figs. 1–6.
Reesidites elegans Matsumoto and Inoma, 1971, p. 139, pl. 23, figs. 1–3.
Reesidites minimus, Tanabe *et al.*, 1978, pl. 1, figs. 1–2.
Reesidites minimus, Futakami, 1982, pl. 1, figs. 1–3.
Subprionocyclus normalis, Futakami, 1982, pl. 1, figs. 5–6.
Reesidites minimus, Matsumoto and Obata, 1982, p. 80, pl. 5, fig. 2; pl. 6, fig. 1.

Material: NSM. PM7635–36, 7642, 7649, 9540–9559 (coll. M. Futakami) have been obtained at loc. Ht304F, from the rolled nodules on the Ichi-no-sawa and the Pomporokabetsu River, Hatonosu (=Yubari), NSM. PM9560 (coll. M. F.), from loc. Ki406, the Fukuro-zawa, a tributary of the Kamiichi-no-sawa River, Ikushumbetsu, NSM. PM9561 (coll. M. F.), from a rolled nodule on the Kumami-zawa, a tributary of the Ashibetsu River, Ashibetsu, NSM. PM6991, from loc. SN2F01, NSM. PM7181, from loc. SN2003, the San-no-sawa, a tributary of the Poromui River, Manji, NSM. PM6961, 6970 (coll. M. F.), NSM. PM9254 (coll. T. Takahashi), from the rolled nodules on the Ponnebetsu River, NSM. PM7111 (coll. M. F.), from loc. RN8001, a cliff on the Ponnebetsu forestry road along the Ponnebetsu River, Manji, NSM. PM7627, 9562 (coll. M. F.), from a rolled nodule on the Pomporomui River, Manji, Hokkaido.

Measurements:

Specimen	Diameter	Height	Breadth	B./H.	Umbilicus	U.T.	V.T.
NSM. PM6961	50.4	24.0	12.4	0.52	10.5	10	—
NSM. PM6970	57.9	27.4	—	—	9.9	12	—
NSM. PM6991	57.0	28.3	13.4	0.47	10.6	11	36
NSM. PM7111	42.1	22.1	9.2	0.42	4.3	9	45
NSM. PM7181	43.2	22.1	—	—	5.9	11	—
NSM. PM7627	86.9	41.8	18.7	0.45	16.0	9	27

NSM. PM7635*	29.4	12.9	6.4	0.50	7.6	11	30
NSM. PM7636	28.6	14.7	7.1	0.48	4.9	10	35
NSM. PM7642	20.5	8.3	5.0	0.60	7.2	13	—
NSM. PM7649	—	7.0	5.2	0.74	—	—	—
NSM. PM9253	62.0	32.7	13.5	0.41	8.0	8	35
NSM. PM9254	109.3	52.8	21.9	0.41	15.4	16	—
NSM. PM9540*	63.0	31.5	—	—	10.4	8	32
−180°	41.6	20.8	8.9	0.43	7.2	—	—
NSM. PM9541*	34.5	17.4	—	—	6.7	10	36
NSM. PM9542*	29.0	12.3	6.5	0.53	8.8	13	27
−120°	22.0	8.4	6.0	0.71	8.1	—	—
NSM. PM9543*	26.5	12.4	6.2	0.50	6.2	12	35
NSM. PM9544*	28.4	14.5	7.0	0.48	5.1	10	—
NSM. PM9545*	25.0	10.5	6.1	0.58	8.0	12	32
NSM. PM9546*	29.0	12.8	6.2	0.48	8.5	12	30
NSM. PM9547*	21.9	10.3	5.1	0.50	7.0	10	29
NSM. PM9548*	26.1	10.8	6.0	0.56	6.9	6×2	15×2
NSM. PM9549*	24.3	11.8	—	—	6.2	—	—
NSM. PM9550*	23.5	10.2	7.3	0.72	7.1	—	—
NSM. PM9551*	19.9	8.4	4.9	0.58	6.0	11	30
NSM. PM9552*	19.2	8.2	4.9	0.60	5.8	12	26
NSM. PM9553*	19.1	8.0	5.0	0.63	6.1	6×2	16×2
NSM. PM9554*	25.3	8.7	7.0	0.80	7.7	11	32
NSM. PM9555*	27.0	13.1	7.0	0.53	5.9	11	43
NSM. PM9556*	20.0	9.7	5.5	0.57	5.6	12	34
NSM. PM9557*	27.9	13.1	—	—	—	—	—
NSM. PM9558*	24.8	12.0	6.4	0.53	5.1	12	40
NSM. PM9559*	21.6	9.7	5.6	0.58	5.9	6×2	16×2
NSM. PM9560*	26.3	11.8	5.9	0.50	6.8	—	—
NSM. PM9561*	64.8	29.3	16.7	0.57	16.2	11	—
NSM. PM9562	—	47.0	23.9	0.51	—	—	—

*: the specimens which have inner and outer ventrolateral tubercles on the ventrolateral shoulders

Discussion: The genus *Reesidites* has been established by Wright and Matsumoto (1954, p. 130) because of the absence of an inner ventrolateral tubercle at any stage in comparision with that of *Subprionocyclus*.

But, there are some different opinions for the systematic position of the genus *Reesidites*. Wright and Matsumoto (1954) have classified the genus *Reesidites* into Collignoniceratinae, while Kennedy *et al.* (1980, 1983), into the Sub-

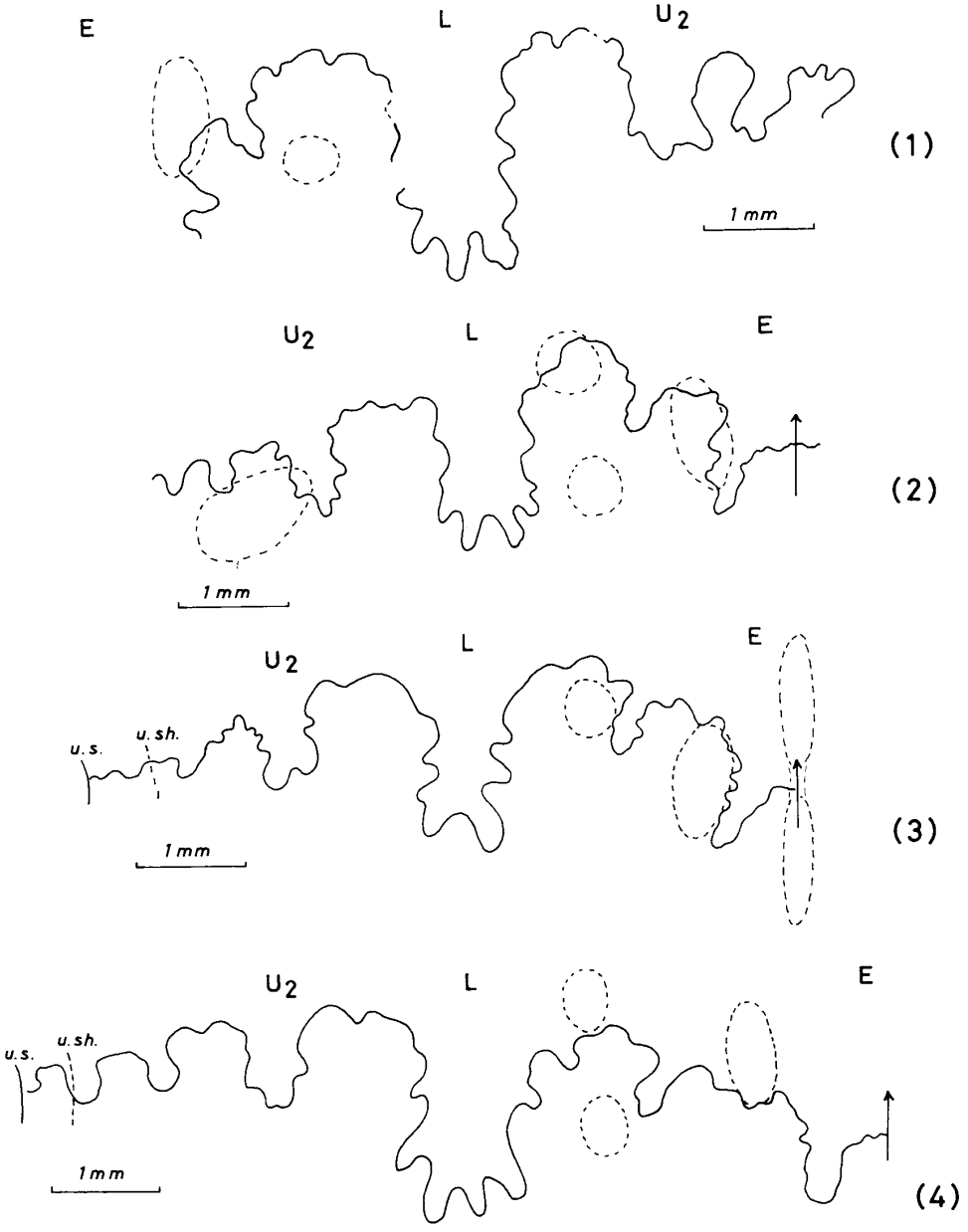

Fig. 3 Suture of *Subprionocyclus minimus* (Hayasaka et Fukada).
NSM. PM9560 (1) from loc. Ki406, the Fukuro-zawa in the Kamiichi-no-sawa area, Ikushumbetsu. NSM. PM9545 (2) from loc. Ht304F, NSM. PM9556 (3), NSM. PM9555 (4), from loc. Ht102F, the Hatonosu area, Yubari. u. sh.: umbilical shoulder, u. s.: umbilical seam

family Barroisiceratinae, because the ornamentation of *Reesidites minimus* differs only little from that of *Barroisiceras haberfellneri*. On the other hand, Reyment (1982) investigated the relationships between size and tuberculation density and between size and tridimentional shape of *R. minimus*. As the result, he recog-

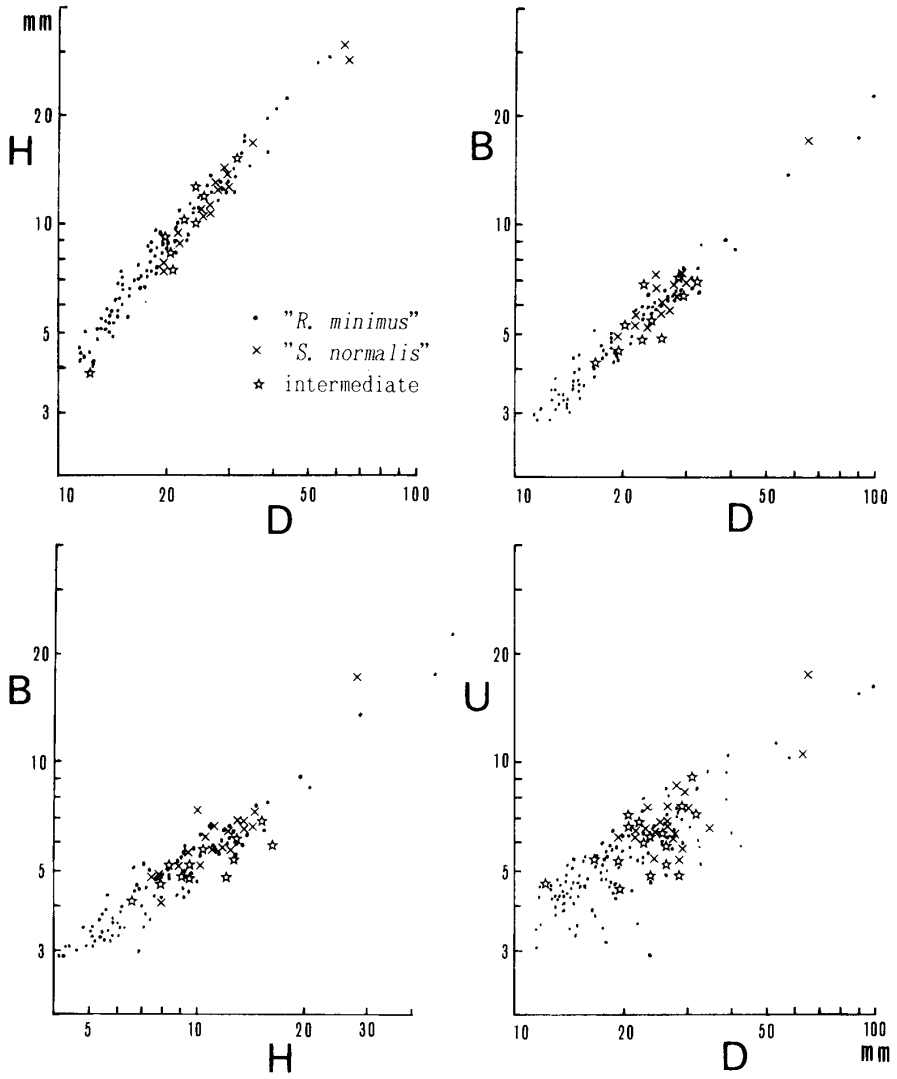

Fig. 4 Average relative growth on the shell-diameter (D), the whorl-height (H), the whorl-breadth (B) and the umbilical diameter (U) of "*Subprionocyclus normalis*", "*Reesidites minimus*" and intermediate form of the two nominal species.

nized that this species differs from *S. neptui* and *S. normalis* in the morphological character, but he regarded *Reesidites* as a subgenus of *Subprionocyclus* for the reason that their difference seems to be rather small and insufficient to justify a generic separation.

Reesidites minimus is very similar to *Subprionocyclus normalis* in the morphological features. The most important morphological distinction between them is the number of row of tubercle at the ventrolateral shoulders: the former has one row of tubercle at each shoulder, whereas the latter has two rows in a

limited period of the middle growth stage. But, there is a great extent of variation in the stage of first appearance, that of disappearance, range of the existing period and the strength of the inner ventrolateral tubercles.

This is the result of my reexamination of more than a thousand individuals of the so-called *Reesidites minimus* and *Subprionocylus normalis* from Hokkaido, as well as their stratigraphical occurrences. Actually the typical specimens of *Subprionocyclus normalis* not only occur together with many *Reesidites minimus* but also the specimens with intermediate character between the two

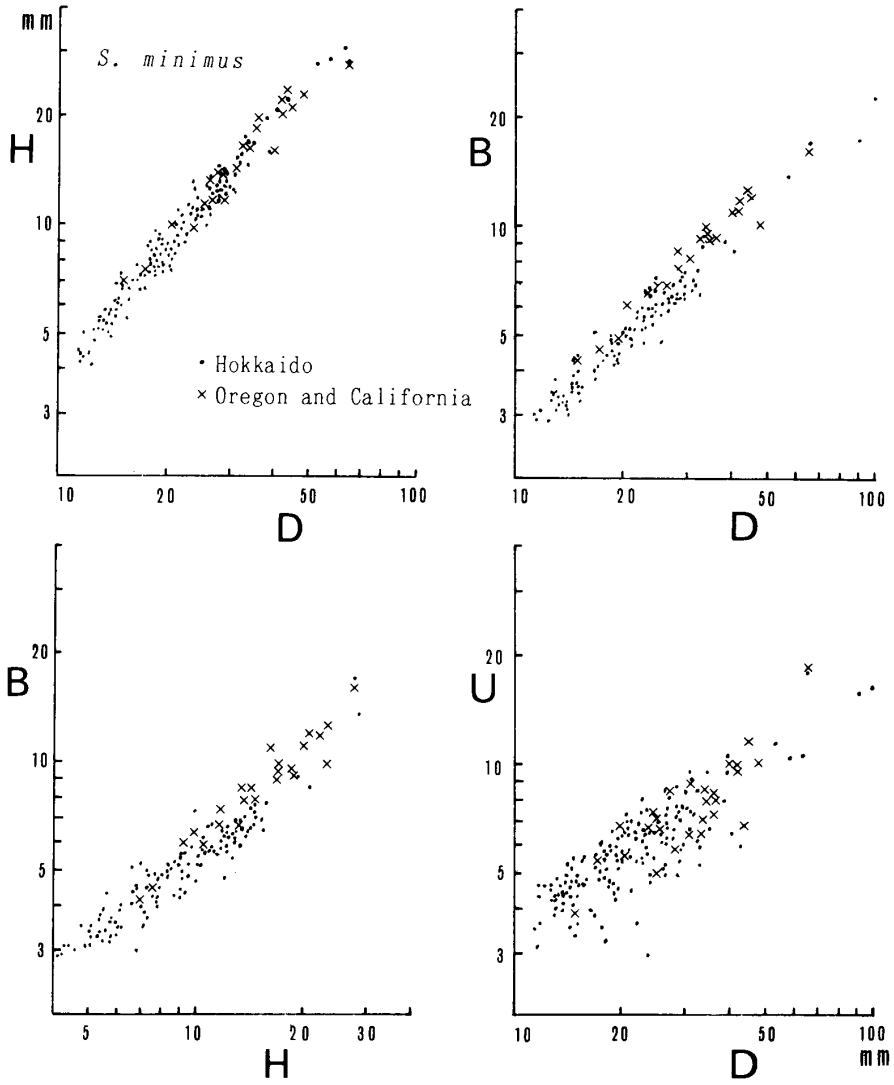

Fig. 5 Average relative growth on the shell-diameter (D), the whorl-height (H), the whorl-breadth (B) and the umbilical diameter (U) of *Subprionocyclus minimus* (Hayasaka et Fukada) from Hokkaido and from Oregon and California.

nominal species occur in the same nodules with typical examples of either of them.

In other words, the development of inner ventrolateral tubercles in the middle growth stage which has been thought as a distinctive characteristic of *S. normalis* is extremely variable by individuals. The inner ventrolateral tubercles generally begin to appear at a shell diameter of about 12 to 15 mm and disappear at about 20 to 30 mm, although disappearance is at 40.7 mm in an exceptional case (NSM. PM9540: Pl. 6, Fig. 2). NSM. PM9542 (Pl. 8, Fig. 5) has the inner ventrolateral tubercle on only three ribs and is an example of the shortest existing period of that tubercle. Furthermore, as to the strength of the inner ventrolateral tubercle, there are not a few specimens which have the very faint elevations and angulations instead of the tubercles at the ventrolateral shoulders. NSM. PM7649 (Pl. 8, Fig. 1), which is rather peculiar in morphological features, has distinct inner ventrolateral tubercles on the left side of shell, but is perfectly devoid of them on the right side.

On the ground of above observations, I believe that the two forms which have been called *Reesidites minimus* and *Subprionocyclus normalis* in Hokkaido are in the range of variation in one and the same species.

On the other hand, *Oregoniceras condoni, O. jacksonense* and *O. argonautarum* from Oregon, the Pacific Coast of North America, which were described by Anderson (1958), conform well with "*Reesidites minimus*" from Hokkaido in both the absence of inner ventrolateral tubercle and mode of ribbing. In addition, "*Subprionocyclus normalis*" occurs also from the same area with them. Therefore, these four nominal species from Oregon may be merely variants of one and the same species as in the case of Hokkaido mentioned above. From California a large number of specimens of "*Subprionocyclus normalis*" have been described by Matsumoto (1959). But, the Oregon and Californian specimens are somewhat different from the Japanese ones in having both a coarser ornamentation and a relatively wider whorl breadth as is shown by Fig. 5.

I interpret the above differences as a geographical variation. I propose here that the form which has been called *Reesidites minimus* and *Subprionocyclus normalis* from Japan should be called *Subprionocyclus minimus minimus* (Hayasaka et Fukada) and the one from Oregon and California which has been called *Subprionocyclus normalis, Oregoniceras condoni, O. jacksonense* and *O. argonautarum* should be called *S. minimus normalis* (Anderson). In case of the geographical subspecies, the prior name is *condoni* but the name has not been used at all since this species was proposed in 1958, whereas *normalis* is regularly and widely used.

"*S. normalis*" which occurs from the Chalk Rock of England may be similar to *S. minimus normalis* from the Pacific Coast of North America in both a whorl

proportion and an ornamentation as compared with the Japanese subspecies (e. g. Wright, 1979, pl. 5, fig. 12a, b; pl. 7, fig. 2).

Recently, *Reesidites minimus* has been reported by Cobban and Kennedy (1988) from New Mexico, the Western Interior of North America. It seems to be somewhat different from the Japanese one in the ornamentations. Namely, the specimens of New Mexico have a prorsiradiate rib on the flanks and a strong siphonal clavi on the venter, whereas the Japanese specimens have sinuous ribs and a serrated distinct keel instead of a siphonal clavi at the same growth stage as USNM414511 (Cobban and Kennedy, 1988, fig. 1). The New Mexican specimens are out of the range of variation in *Subprionocyclus minimus* from Japan redefined in this paper. They represent another species which is rather referable to *Barroisiceras s.s.*

Reesidites latus Matsumoto and Obata (1982), which was obtained from the Upper Turonian "*Reesidites minimus*" Zone in Hokkaido, is similar to *Subprionocyclus minimus* in the ornamentation. The former, however, is distinguishable from the latter in having more evolute whorls, much wider umbilicus and a larger proportion of B/H. In these respects, *R. latus* is closer to *Reesidites lornae* (van Hoepen) from the Coniacian of Zululand as redescribed by Kennedy *et al.* (1983). These two species may be better referred to the genus *Barroisiceras* in view of the absence of inner ventrolateral tubercles. Alternatively, a new genus might be required to accomodate these "*Reesidites*" like species with a wide umbilicus. On this problem, I hesitate to give a conclusion at this moment because I have not enough material of populations.

Schloenbachia subtuberculatus Gerhardt (1897) from the Coniacian of Colombia and Venezuela, South America was described under the genus *Reesidites* by Reyment (1958, p. 10). I agree with Renz (1982, p. 112) in his assignment of this species to *Barroisiceras*, because it has siphonal clavi from the early growth stage onward and straighter ribs.

In most species of the genus *Subprionocyclus*, the ornaments on the adult body chamber such as the tubercles, ribs and keel tend to become faint. On the basis of that ornamentation the dimorphism is recognized in this species. Namely, a microconch of *S. minimus* has a narrower whorl breadth, and its ornamentation on the body chamber becomes faint in earlier growth stage than a macroconch, showing a continuous low keel without or with only indistinct serration, lirae or striae instead of ribs and obsolete ventrolateral tubercles. Its shell diameter is less than 60 mm (NSM. PM9540: Pl. 6, Fig. 2; NSM. PM6961: Pl. 8, Fig. 10). As compared with a microconch, a macroconch has, generally, a coaser ornamentation and a wider whorl breadth, and attains more than 120 mm in shell diameter (NSM. PM9254; Pl. 9, Fig. 1). Unfortunately, the completely preserved specimen upto the peristome has not yet been found.

Occurrence: This species occurs fairly commonly in the middle to upper Upper Turonian in Hokkaido.

Subprionocyclus (?) sp.

Pl. 10, Figs. 1–5

Material: The specimens here described, NSM. PM9563–9567 (coll. M. Futakami) were obtained from a calcareous nodule in the massive, fine-grained sandstone at loc. Ki323, the middle stream of the Ganseki-zawa, a tributary of the Kamiichi-no-sawa River, Ikushumbetsu.

Diagnosis: The shell ornaments of this species are similar to those of *S. neptuni*, but the inner ventrolateral tubercles do not appear on the shoulders in any growth stage.

Description: The shell is rather small. The whorl is moderately involute with a moderate width of umbilicus, ranging from 28 to 40 percent of shell diameter by individuals, and its cross section is roughly subrectangular and higher than broad. The umbilical wall is low and nearly perpendicular. The flanks are nearly parallel or slightly convergent to the venter. The ventral keel is distinct and serrate. The ribs are flexuous on the flank and projected somewhat strongly forward on the venter. They spring in twos or threes from the umbilical bullae, and one or two shorter ribs are rarely intercalated. The clavus is formed at the outer ventrolateral shoulder of every rib and the bulla at the umbilical edge, but the inner ventrolateral tubercle does not appear in any growth stage.

The suture is rather simple in the small shells. The lateral lobe (L) is deeper than the external one (E), trifid at the bottom; E/L saddle broad and not very asymmetrically divided (Fig. 6).

Measurements:

Specimen	Diameter	Height	Breadth	B./H.	Umbilicus	U.T.	V.T.
NSM. PM9563	30.0	12.7	8.0	0.63	8.8	18	39
−90°	25.2	10.5	6.0	0.57	7.6	—	—
NSM. PM9564	35.0	15.8	—	—	9.8	16	35
−240°	19.6	7.2	4.9	0.68	5.4	—	—
NSM. PM9565	23.9	9.0	6.5	0.72	7.8	11×2	21×2
−180°	19.5	7.9	5.0	0.63	7.1	—	—
NSM. PM9566	21.1	8.4	5.4	0.64	8.0	20	42
−90°	16.8	6.3	4.5	0.71	6.2	—	—
NSM. PM9567	32.5	13.1	—	—	9.2	9×2	26×2

Remarks: In all the five specimens examined here the inner ventrolateral

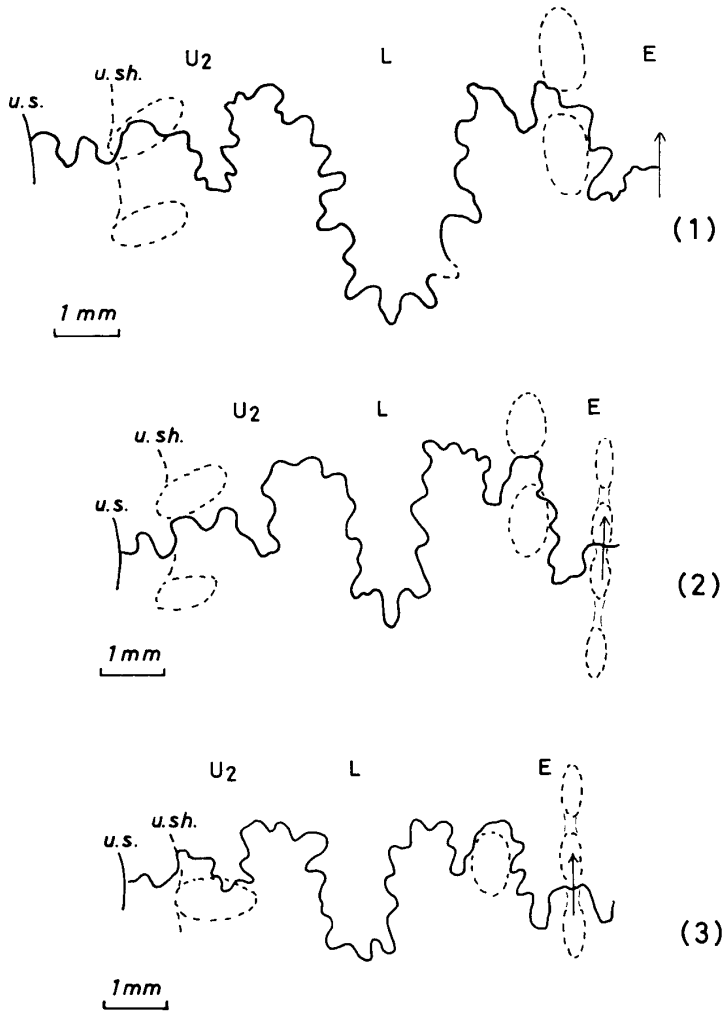

Fig. 6 Suture of *Subprionocyclus* (?) sp.
NSM. PM9563 (1), NSM. PM9564 (2), NSM. PM9565 (3), from loc. Ki323, the Ganseki-zawa in the Kamiichi-no-sawa area, Ikushumbetsu. u. sh.: umbilical shoulder, u. s.: umbilical seam

tubercle never appears on each rib. Accordingly, these specimens seem to be assigned to the genus "*Reesidites*" in the morphological characters. But, there are many morphological features in which this species is similar to *Subprionocyclus neptuni*. Namely, these specimens show roughly subrectangular outline in cross section of the whorl with somewhat broad distance between ventral shoulders, rather a wide umbilicus and simple sutures with the broad first lateral saddle (between E and L) which is often symmetrically divided. The general morphological features of these specimens are especially similar to those of the specimens of similar size described by Obata *et al.* in the ontogeny and varia-

tion of *S. neptuni* (1979, pl. 2, figs. 1, 3–5), except for the presence of the inner ventrolateral tubercles in the latter. Considering the morphological characters and the geological occurrence, this species may be regarded as a transitional form between *S. neptuni* and *S. minimus*.

Atabekian and Akobian (1972) described four specimens of *R. minimus* from Armenia, U.S.S.R. But those specimens are distinguished from the Japanese specimens in that the whorl has a wider umbilicus as compared with the typical specimen of "*R.*" *minimus*, and in that the Armenian specimens have the subconical nodes instead of clavate tubercles on the ventrolateral shoulders. Moreover, they occur in the Coniacian.

Subprionocyclus casterasi from Madagascar (Collignon, 1965, figs. 1693–1695) is somewhat similar to the present species in having a single ventrolateral clavi. *S. casterasi* is, however, distinguished from this species in that the umbilicus is narrower and the ribs are coarser. On the other hand, *S. casterasi* closely resembles *S. neptuni* from Madagascar (Collignon, 1965, figs. 1691, 1692), but is distinguished from the latter having in a single ventrolateral tubercle on each rib. It is noted that *S. casterasi* seems to have double ventrolateral tubercles at least at some growth stage as far as the illustrated holotype and paratype (figs. 1693, 1694) are concerned.

The inner ventrolateral tubercles are not always stable as a diagnostic character of the species and even of the genus, I have fully discussed in the preceding species. For this reason I am describing provisionally these specimens as *Subprionocyclus* (?) sp.

This species may be included in a range of variation of *Subprionocyclus minimus*, but its stratigraphical position is lower than the *S. minimus* Zone, *viz.* in the upper part of *C. woollgari* Zone or *S. neptuni* Zone.

Occurrence: The stratigraphical position of this species is probably assigned to the lower Upper Turonian.

The specimens which are probably referred to the same species occurred abundantly at loc. Y412F in the upper part of the *I. hobetsensis* Zone, the lower stream of the Kaneobetsu River, Oyubari, although they are not always well preserved.

Evolutional change of Turonian collignoniceratids

Subprionocyclus neptuni, "*S. normalis*" and "*Reesidites minimus*" had been regarded to constitute a single phylogenetic line in the sense of phyletic gradualism of Moore *et al.* (1952), on the basis of the mode of successive occurrence, the ontogeny and the variation (Matsumoto, 1965; Obata, 1965). Reyment (1975) carried out a principal component analysis of the morphological charac-

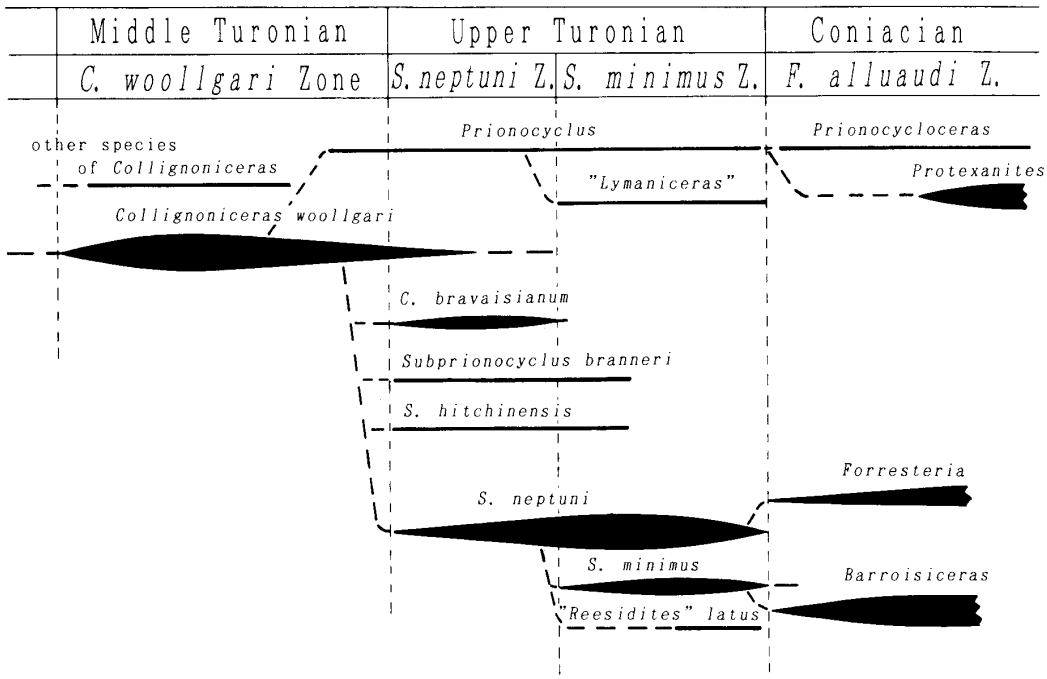

Fig. 7 An attempt to illustrate diagrammatically phylogenetic lineage of some Turonian species belonging to the Collignoniceratinae.

ters by using the Japanese specimens by Matsumoto (1965) and Obata (1965), and he found out that evolutional change in that lineage seems to fit the concept of punctuated equilibria of Eldrege and Gould (1972). Gingerich (1977) stratigraphically discussed on the change of eigenvector coefficients in principal component analysis on the size, shape and ornamentation of their three species. He concluded whether this change is an example of the gradualism or the punctuated equilibria can not be judged.

As mentioned above, the Upper Turonian collignoniceratids have been internationally noticed and discussed on the phylogeny and the evolution by the morphological analysis. Furthermore, all the usable data for analysis were based on the publications by some Japanese authors such as Matsumoto, 1965; Obata, 1965; Obata *et al.*, 1979. Yet a definite conclusion has not been led. To solve this problem it is neccessary to analyse from both the paleontological and biostratigraphical sides. For the latter approach I have examined the mode of occurrence and distribution of these Turonian collignoniceratids in the Ishikari province, central Hokkaido and sorted precisely the fundamental data into Fig. 7 (see also Futakami, 1986b).

Obata (1964) has inferred that *Subprionocyclus* may have been inhabited in shallower sea than "*Reesidites*". Obata *et al.*(1979) have indicated that the phylogenetic line from *Collignoniceras woollgari* to "*Reesidites*" *minimus* via *Subprionocy-*

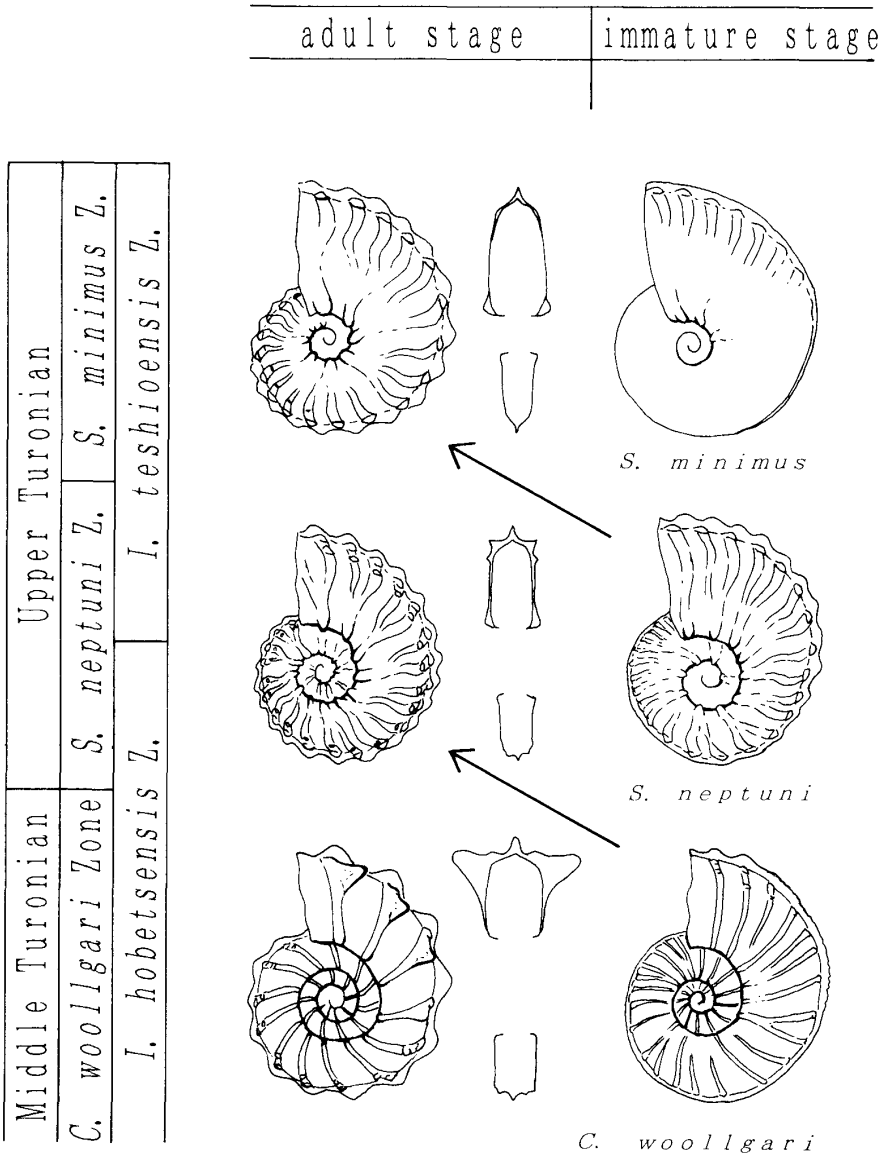

Fig. 8 Morphologic change in Turonian collignoniceratids.

clus neptuni probably represents adaptation to shallower sea environments. Based on my preliminary investigation, the phylogenetic evolution of these Turonian collignoniceratids suggests a trend of shell adaptation for more successful swimmer, *viz.* from ancestral *Collignoniceras woollgari* to descendant *Subprionocyclus neptuni* and further to *S. minimus*, the serial change in morphology is represented by the development toward more flexuous and weaker ribs, weaker and decreasing rows of the ventrolateral tubercles, narrower umbilicus, more compressed whorls and more complicated sutures. Taking the flow patterns of cephalopod shells (Chamberlain, 1976) into consideration, the above

noted morphologic change is probably interpreted as an evolutional adaptation for the decrease in the resistance of water.

Another aspect of phylogeny as exemplified by the series of *Collignoniceras woollgari, Subprionocyclus neptuni* and *S. minimus* is manifested by that the morphological features in the early immature stage of an ancestral species appear in the late immature or middle stage of the next descendant species, and the latter in turn characterizes the adult stage of further descendant species. Besides, the descendants generally show a tendency to have somewhat smaller shell than the ancestor. The evolutional change noted above is a case of the neoteny.

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