3. A cyclic mode of shell growth and its implications in a Late Cretaceous heteromorph ammonite *Polyptychoceras pseudogaultinum* (Yokoyama)

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Abstract. *Polyptychoceras*, a Cretaceous heteromorph ammonite genus, is characterized by a trombone-like shell called a "hamitoid" shell. In order to clarify the shell-forming mechanism, a large sample, which consists of more than 320 specimens of *P. pseudogaultinum* (Yokoyama) obtained from the Upper Santonian of Hokkaido, was biometrically analyzed. Besides the shell coiling, cyclic changes of growth pattern are recognized by the analyses of the shell ornamentation, the relative growth rate of shell height, and the distance between septa. Intermittent shell growth, which was also deduced from the ontogenetic stage distribution in the population samples, is probably the cause of such peculiar shell coiling. Also, we carried out some computer simulations to reconstruct hydrostatically the ontogenetic change of the living attitude of *P. pseudogaultinum*. It is suggested that the rate of absolute shell growth possibly depends on the living attitude of this ammonite in the water column; the shell grows slowly when the shell aperture faces upward, and grows rapidly when the aperture faces in other directions. It is likely that every individual of this ammonite spent most of its life time with an upward-facing aperture.

Key words: Heteromorph ammonite, mode of growth, mode of life, *Polyptychoceras pseudogaultinum* (Yokoyama), Upper Cretaceous

Introduction

Ammonites, a dominant cephalopod group during Jurassic and Cretaceous times, changed their shell form in various ways in order to adapt themselves to the environment. Heteromorph ammonites were especially diversified and showed various kinds of shell shape in the Late Cretaceous, the last phase of ammonites' prosperity. *Polyptychoceras* Yabe, 1927, belonging to the diplomoceratids, is one of the most conspicuous heteromorph genera and is characterized by a trombone-like "hamitoid" shell; several straight shafts run in parallel, successive shafts being connected with a U-shaped semi-whorl. This genus was probably derived from *Scalarites*, presumably a founder of the Diplomoceratidae, and *Eubostrychoceras*, a nostoceratid, is probably the ancestor of that family (Matsumoto, 1967). The two-dimensional shell coiling as observed in the diplomoceratids generally originated from the three-dimensional shell coiling of nostoceratids in the Late Cretaceous (probably Turonian) (Matsumoto, 1967; Ward, 1976).

Several species of *Polyptychoceras* occur in the Santonian and Campanian of Hokkaido and Sakhalin (Matsumoto, 1984; Verchangin *et al.*, 1965). *Polyptychoceras* and some allied genera of the Diplomoceratidae achieved worldwide distribution, because there are some reliable records of occurrence from other provinces in the Upper Santonian and Lower Campanian, *e.g.* Vancouver Island in Canada (Whiteaves, 1903) and Barra do Dande in Angola (Howarth, 1965). In the Early Santonian and earlier, however, the occurrences of such primitive genera as *Scalarites* and *Rhyoptychoceras* and early species of *Polyptychoceras* are restricted to the Far East province. Early diversification of the Diplomoceratidae is thus suggested from the fossil records in the Far East province. This province is, therefore, important in order to document the evolutionary process of the Diplomoceratidae.

The fossils of *Polyptychoceras* usually occur in fragments in calcareous nodules of the Upper Yezo Group, Hokkaido, Japan. Previous descriptive studies of *Polyptychoceras* have mostly been based on incomplete or fragmentary specimens (Yokoyama, 1890; Jimbo, 1894; Yabe, 1927; Matsumoto, 1984). A peculiar life mode of *Polyptychoceras* was imagined by Matsumoto and Nihongi (1979); they may have lived in schools at the bottom and sometimes in dead shells of large ammonites. In their argument, however, it was not discussed why the peculiar shell form of *Polypty-*

choceras was advantageous.

A hamitoid shell morphology like that of *Polyptychoceras* appeared at least three times in independent clades (i.e. ptychoceratids, hamitids and diplomoceratids). It is, of course, regarded as morphological convergence probably related to a similar mode of life.

The purpose of this study is to clarify the mode of growth of *Polyptychoceras* by analyzing biometrically the ontogenetic change of shell form. The material is *Polyptychoceras pseudogaultinum* (Yokoyama) which occurs abundantly in the Upper Yezo Group. We also attempt recon-

structions of living attitude through growth in the water column, and interpret the mode of life from the relationship between the growth and the reconstructed living attitude. Such an approach would make clear how the hamitoid shell morphology was adaptive to a certain mode of life in the Late Cretaceous seas.

Material and method

The Upper Yezo Group in the reaches of Kotanbetsu River contains numerous fossiliferous calcareous nodules in which
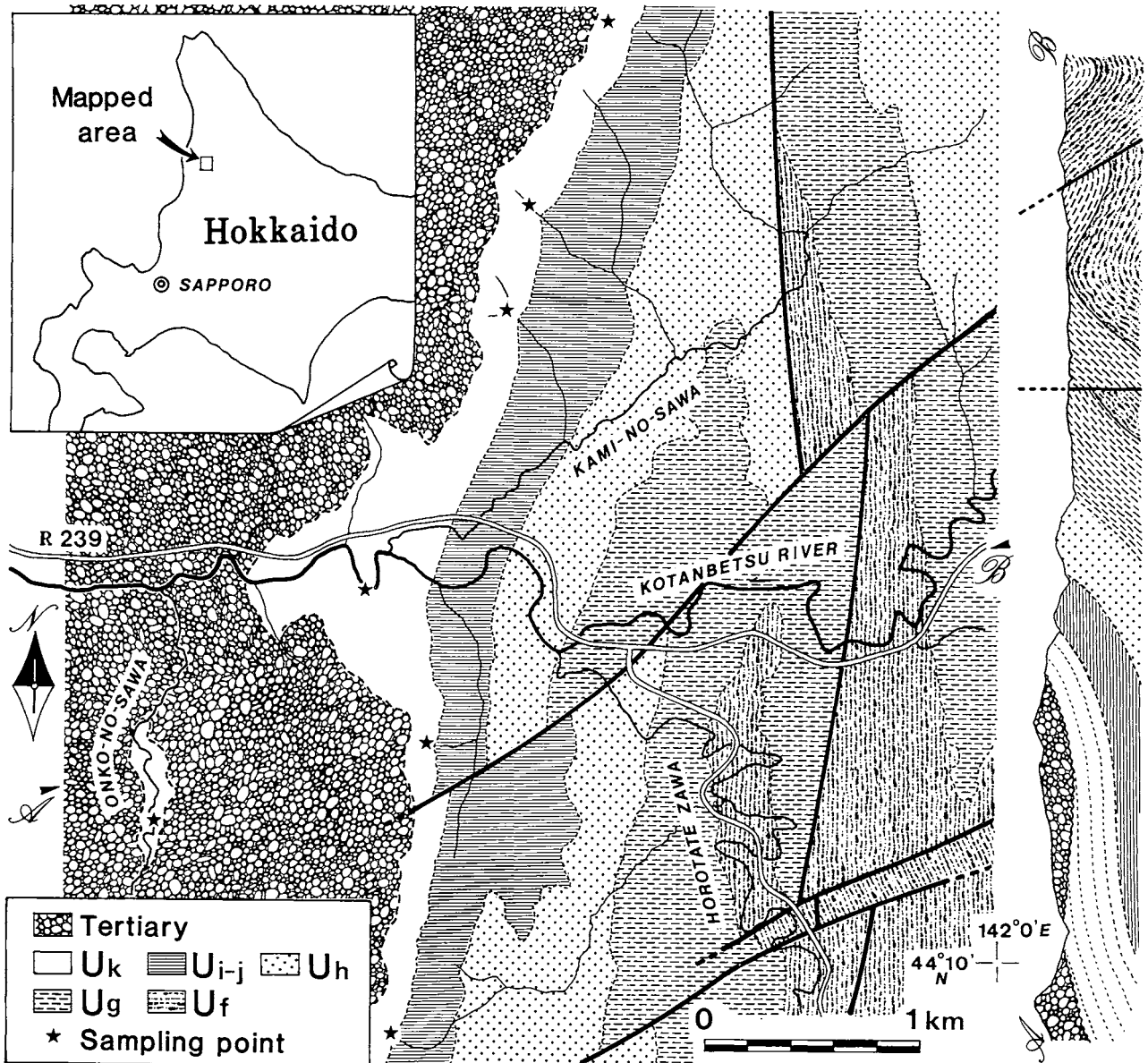

Figure 1. Sampling points shown on geologic map of Kotanbetsu area, Tomamae province, Hokkaido. The Upper Yezo Group in this area was divided into five members, Uf-Uk (Tanaka, 1963). All the localities of *Polyptychoceras pseudogaultinum* (Yokoyama) are in Uk member, Upper Santonian. A useful population sample was obtained from the inlier of this member at Onko-no-sawa.

Polyptychoceras occurs abundantly (Figure 1). In order to collect specimens of *Polyptychoceras* and to clarify their stratigraphic occurrence, we surveyed this area in the field seasons of 1992-1994. Layers of the Upper Yezo Group in this area, generally have north-south strikes and are tilted to the west, though some foldings are recognized in the eastern part. This group is unconformably covered by Tertiary sedimentary rocks in the western part of this area. The Upper Yezo Group is mainly composed of dark gray sandy siltstones and contains many intercalations of tuff and sandstone layers. Tanaka (1963) and Tanabe et al. (1977) defined twelve members (Ua-Ul) in this group, and *Polyptychoceras pseudogaultinum* occurs particularly in Uk, one of the uppermost members. This ammonite is usually contained in a cluster, and sometimes occurs gregariously in calcareous nodules. We treated a total of 323 specimens of *P. pseudogaultinum* in this study. A large population sample of this species was obtained from the Onko-no-sawa valley where the Uk member is locally exposed as an inlier. Several smaller samples were obtained from the main stream of Kotanbetsu River, tributaries of Kami-no-sawa, and a western tributary of Horotate-zawa. All specimens are kept in the University Museum, University of Tokyo with register numbers with the prefix UMUT. MM. We use consecutive specimen numbers with prefix H- or S- throughout this paper, and their correlation with register numbers is shown in the Appendix Table.

Perfectly preserved specimens give us important information concerning the ontogenetic change of shell growth and shell ornamentation. Such specimens of *Polyptychoceras pseudogaultinum* are extremely rare, while fragmentary specimens occur very abundantly in this area. We had to analyze its ontogenetic change by connecting imperfect specimens. An idealized shell form of *Polyptychoceras pseudogaultinum* is reconstructed, and terms for every part are defined as shown in Figure 2. An adult shell is composed of five shafts and four turns connecting two adjacent shafts.

In order to clarify the general shell morphology and its intraspecific variation, we mainly used a slide caliper and a binocular. For observation of the septate phragmocone, several specimens were cut along the median plane. The linear distance between adjacent septa was measured by a profile projector (Nikon, V-12). Some specimens showing early shell morphology were observed and measured by scanning electron microscope (SEM, Jeol JSM-5200). For SEM observation, the polished surface cut along the median plane was etched with 5 percent acetic acid for a half to two minutes. For the computer simulation, programs written in N88-BASIC were run on a personal computer (NEC PC-9801RA) printing to an ink-jet printer (Canon, BJ-130J).
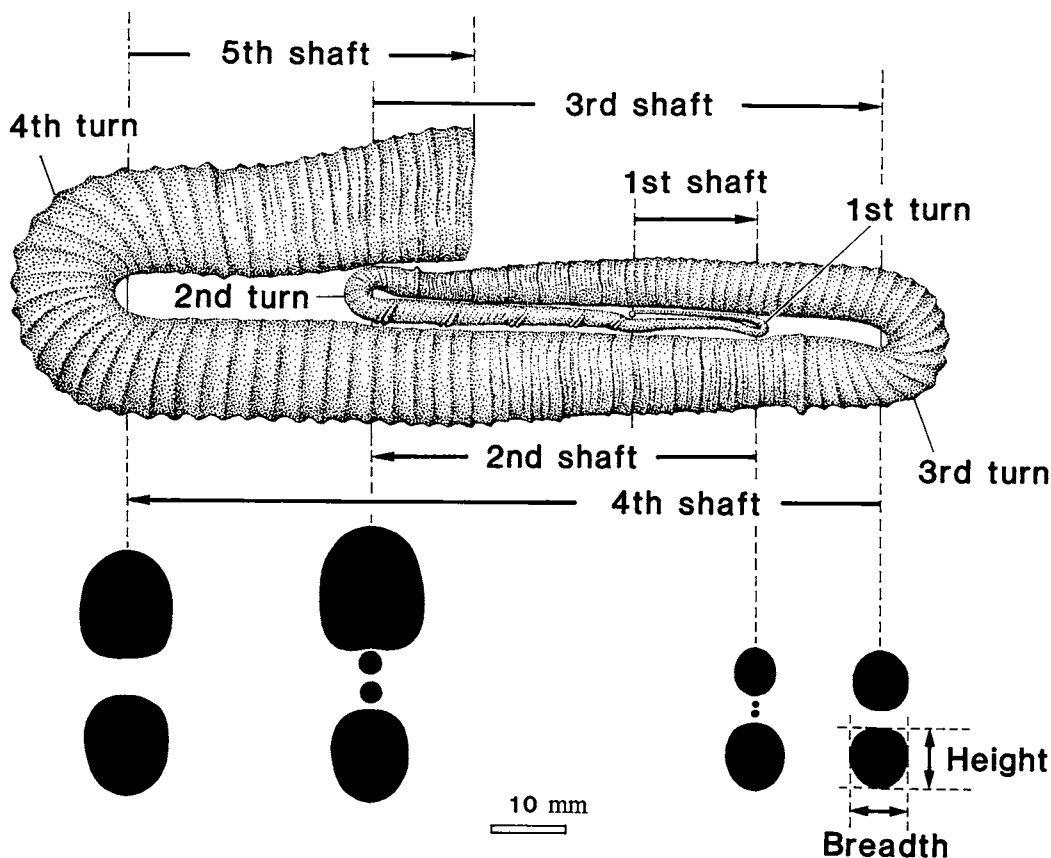

Figure 2. Schematic illustration of *Polyptychoceras pseudogaultinum* (Yokoyama).
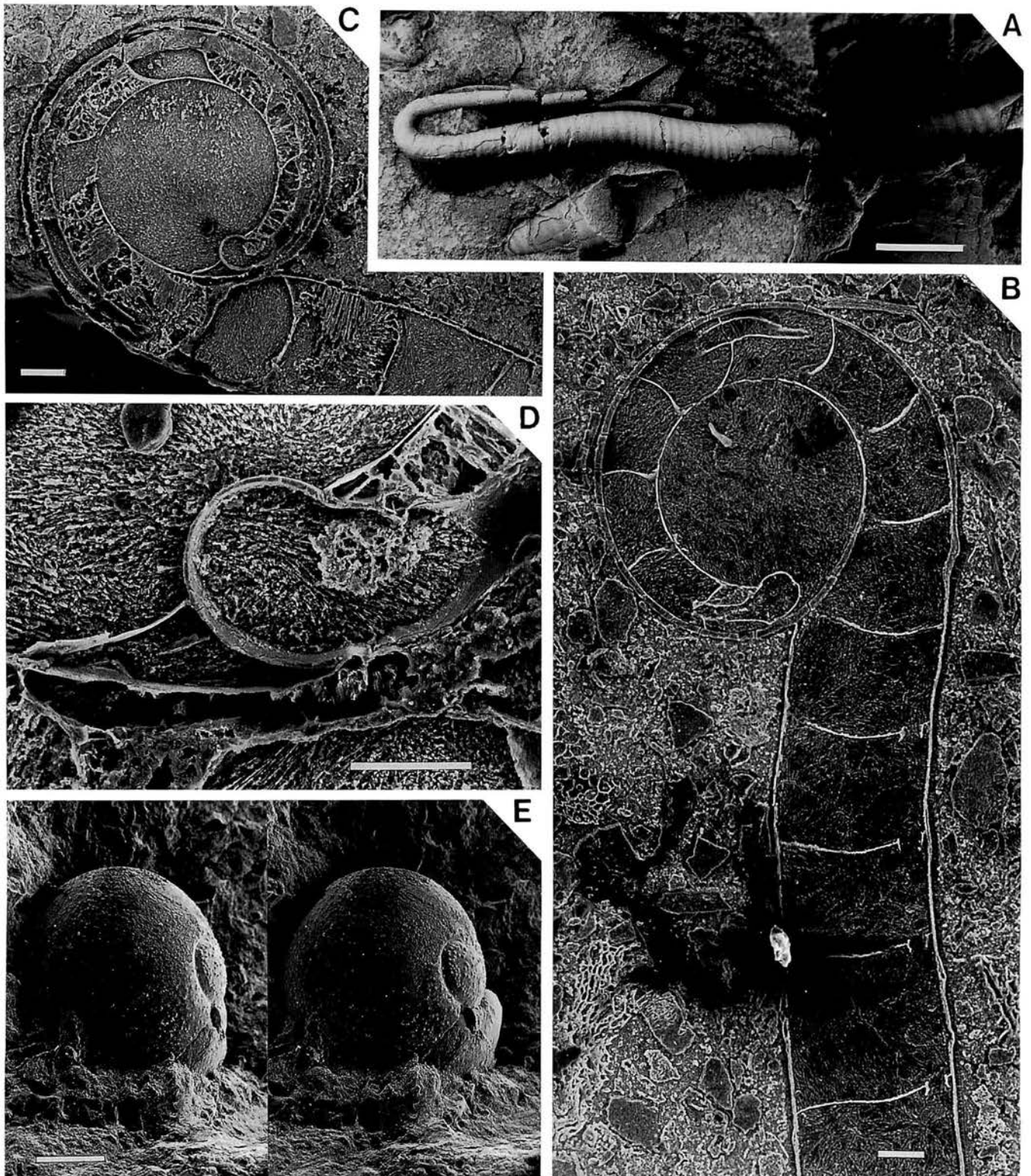
Figure 3.   Early shell morphology of *Polyptychoceras* spp. **A.** Younger shell of *Polyptychoceras* sp. containing an almost complete ammonitella, and following first shaft, S-199. **B-E.** Microstructure of embryonic shell of *P. pseudogaultinum* (Yokoyama), **B** : S-205, **C, D** : S-204, **E** : outer wall of ammonitella, S-203 (stereographic pair). Scale bars : 5 mm for **A**, 100 μm for **B** and **C**, 50 μm for **D**, and 200 μm for **E**.

General morphology and remarks

Protoconch and early shell morphology

Ammonitellas of the Diplomoceratidae are in general rarely preserved. Hayakawa (1988) reported several ammonitellas of *Polyptychoceras* sp. from the Santonian of the Upper Yezo Group. We obtained some early shells of *P. pseudogaultinum* in which the ammonitella is followed by a straight shaft (=first shaft). By SEM observation along the median plane, the main structural elements of the ammonitella such as the primary varix, protoconch, prosiphon, caecum and proseptum were recognized (Figure 3). The microstructure of the embryonic shell of *P. pseudogaultinum* is somewhat similar to that of the Lytoceratina, though the size of the ammonitella is considerably smaller. The ammonitella in this species is about 0.7 mm in diameter, whereas in the Lytoceratina it generally ranges between 1.1 mm to 1.4 mm (Tanabe and Ohtsuka, 1985). It is characterized by a relatively short, arcuate prosiphon and a siphuncular tube rapidly shifting to the ventral margin. The nepionic constriction and accompanying primary varix, by which the ammonitella stage is terminated, appear at about 320 degrees from the beginning of the first whorl, and is followed by the first shaft. The shell height rapidly

increases just after the nepionic constriction (Figure 3).

Tuberculate microornament is observable in some of these specimens. Homologous textures have been described by Bandel *et al.* (1982) and Tanabe (1989) in several other superfamilies of Ammonoidea. According to their arguments, these textures were secreted probably by the interior gland cells of the mantle margin and indicate that the ammonitella was enclosed by the reflected mantle lobe. Namely, the ammonitella stage of these ammonites was endocochliate. The Turrrilitaceae, in which *Polyptychoceras* is included, possibly shared a similar mode of life until the nepionic constriction was formed.

Doguzhaeva and Mutvei (1989, 1993) suggested that *Ptychoceras*, an Early Cretaceous ammonite showing convergent shell form to *Polyptychoceras*, had an internal or semi-internal shell. The grounds of their argument are 1) the mechanical truncation of the phragmocone terminus and 2) the existence of an external coating layer which is secreted probably on the shell surface by an epithelium. In *Polyptychoceras pseudogaultinum*, however, no evidence indicating an endocochliate shell has been obtained throughout the post-embryonic growth stages.
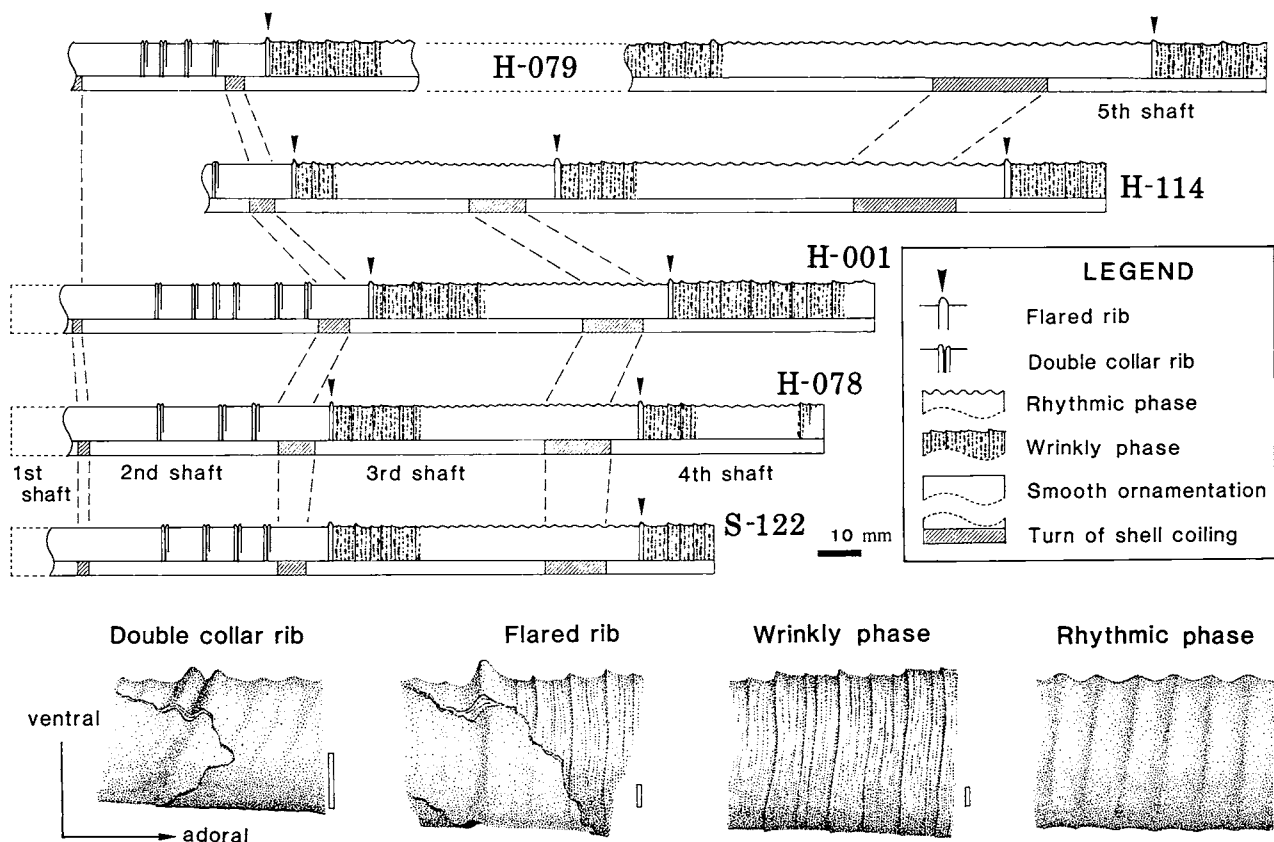

Figure 4. Schematic diagram showing the cyclic change of shell surface ornamentation throughout growth. Two phases of ornamentation appearing alternately are recognized after the second turn. The wrinkly phase which is initiated from a flared rib appearing near the beginning of the new shaft, gradually changes into the rhythmic phase during the earlier half of shaft. Each scale bar (open rectangle) on the right of the illustration indicates 1 mm.

On *Polyptychoceras subquadratum* (Yokoyama)

Polyptychoceras pseudogaultinum (Yokoyama) was established on the basis of some young specimens showing the second to the third shafts, the transverse section of which is nearly circular. In the same paper, Yokoyama (1890) described *Polyptychoceras subquadratum* (Yokoyama) from the same locality of the Urakawa area, southern Hokkaido. The latter species was established on the basis of a single fragmentary specimen showing a nearly adult growth stage having a subquadrate transverse section. In the samples examined, the larger specimens, which are usually fragments, always show the characteristics of *P. subquadratum* (i.e. subquadrate cross section), whereas almost all the younger specimens are clearly identified with *P. pseudogaultinum*. Actually, these larger specimens may look as if they belong to a different species from *P. pseudogaultinum*, because the shell shape is considerably different, and because the sample shows bimodal size distribution. However, a few well-preserved specimens reveal that the difference between the two "species" is only due to ontogenetic change within a single species (Figures 14, 15). We therefore treat *P. subquadratum* as a synonym of *P. pseudogaultinum*, and all the samples examined are regarded as belonging to a single species, *P. pseudogaultinum* (syntypes : *Ptychoceras pseudo-gaultinum* Yokoyama, 1890, *Palaeontographica*, vol. 36, p. 181, pl. 20, figs. 1-3 ; synonymy : *Anisoceras subquadratum* Yokoyama, 1890, *Palaeontographica*, vol. 36, p. 182, pl. 20, fig. 4). Though these two names were established in the same paper, we designate *P. pseudogaultinum* as the name of this species, because *P. pseudogaultinum* has more frequently appeared in literature (e.g. Yabe, 1927 ; Shimizu, 1935 ; and Matsumoto, 1984). Moreover, the type specimens of *Polyptychoceras haradanum* (Yokoyama) and *Polyptychoceras subundulatum* (Yokoyama), both of which were established also in the same paper (Yokoyama, 1890), are possibly includable in the intraspecific variation of *P. pseudogaultinum*.

Ontogenetic change of surface ornamentation

Polyptychoceras shows a periodically changing pattern of surface ornamentation. Since the ammonite shell is formed by accretionary growth, the tempo and mode of growth at every growth stage must be recorded in the commarginal ornamentation on the shell surface.

Polyptychoceras pseudogaultinum has two kinds of characteristic ribs (double collar ribs and single flared rib), which occur periodically at definite stages of the shell growth (Figure 4). The double collar ribs appear at first near the trisecting point of the second shaft at which the adjacent first shaft terminates, and occurs periodically until the end of the second shaft. The number and the position of the double collar ribs are variable among the examined specimens. The flared rib appears just after the shell turning point of every stage except for a point just after the first turn. While the flared rib is relatively clear in the third and fourth shafts, it is not very clear or sometimes unobservable in the fifth shaft. The shell is thickened at these ribs, and the aperture at these stages probably become a little narrower.

The shell growth of *P. pseudogaultinum* is divided into two major stages by the first appearance of the flared rib which is observed just after the beginning of the third shaft (Figure 4). In the earlier stage, several double collar ribs periodically develop and weak striae are observed between them. In the later stage, a cyclic switch of two ornamentation phases corresponds to the shell coiling. The first or wrinkly phase of ornamentation is characterized by slightly notched ribs occurring at irregular intervals and by numerous weak striae between them. This phase usually starts from the flared rib and continues for about one-third of the shaft. The notched ribs gradually change to the simple ribs. The second or rhythmic phase of ornamentation is characterized by the simple ribs occurring at regular intervals. This phase continues to the end of the next turn and is terminated by the next flared rib.

The obliquity of transverse ribs also changes cyclically throughout growth. More or less prorsiradiate ribs are observed through the later half of the second shaft and near the end of each shaft, while rursiradiate or rectiradiate simple ribs are formed during each turn and the early part of the following shaft. The change of rib obliquity is, though, rather obscure in the fourth shaft.

Shell height and shaft length

The shell height at the beginning of every shaft and the shaft length were measured in all the specimens if these values were measurable. The mean values of shell height from the second to fifth shafts are 1.58 mm, 3.78 mm, 8.41 mm, and 16.50 mm, respectively. The standard deviation of
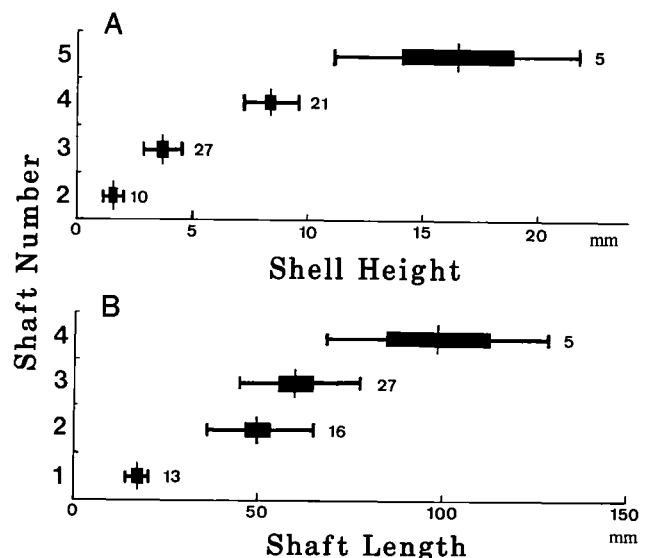

Figure 5. Diagrammatic figures showing the average and intraspecific variation of shell height and shaft length. Shell height is measured at the beginning of every shaft excluding the first shaft. Horizontal bar, solid rectangle and number on the right indicate presumable distribution range of 95% of the population (1.96 times of standard deviation), 95% confidence range of mean value (1.96 times of standard error), and the sample size, respectively.

these measurements are relatively small except for the fifth shaft. The mean values of shaft length from the first shaft to the fourth shaft are 17.86 mm, 51.06 mm, 61.50 mm and 97.87 mm, respectively (Figure 5). The first shaft length is indirectly estimated by the shape of the second shaft as mentioned below, because in no specimen is the first shaft perfect. Unlike the shell height, standard deviation of shaft length is generally large except for the first shaft.

These results indicate that the variation of shell form is fairly wide in the growth stages after the second shaft. The shaft length does not increase proportionally either with the progression of the shaft number or with the shell height. The second shaft is relatively longer than other shafts. This may be a common characteristic feature in the genus *Polyptychoceras*.

Estimation of missing shaft length

P. pseudogaultinum usually grows in parallel with the previous shaft. When the shell passes the origin of the previous shaft, the growth direction temporarily slightly shifts to the dorsal side but soon recovers its original direction. Therefore, the length of earlier shaft can often be estimated by the shape of the later shaft, even if the earlier shaft is missing. The second shaft commonly bends slightly at about 20 mm after the first turning point. This probably means a release from the constraint of the first shaft. Actually, an ammonitella situated just near the bending part of the second shaft is observed in well preserved specimens of a related species (Figure 3A). As to *P. pseudogaultinum*, a relatively long first shaft, which is merely 2.3 mm shorter than the expected first shaft, is preserved in one of our
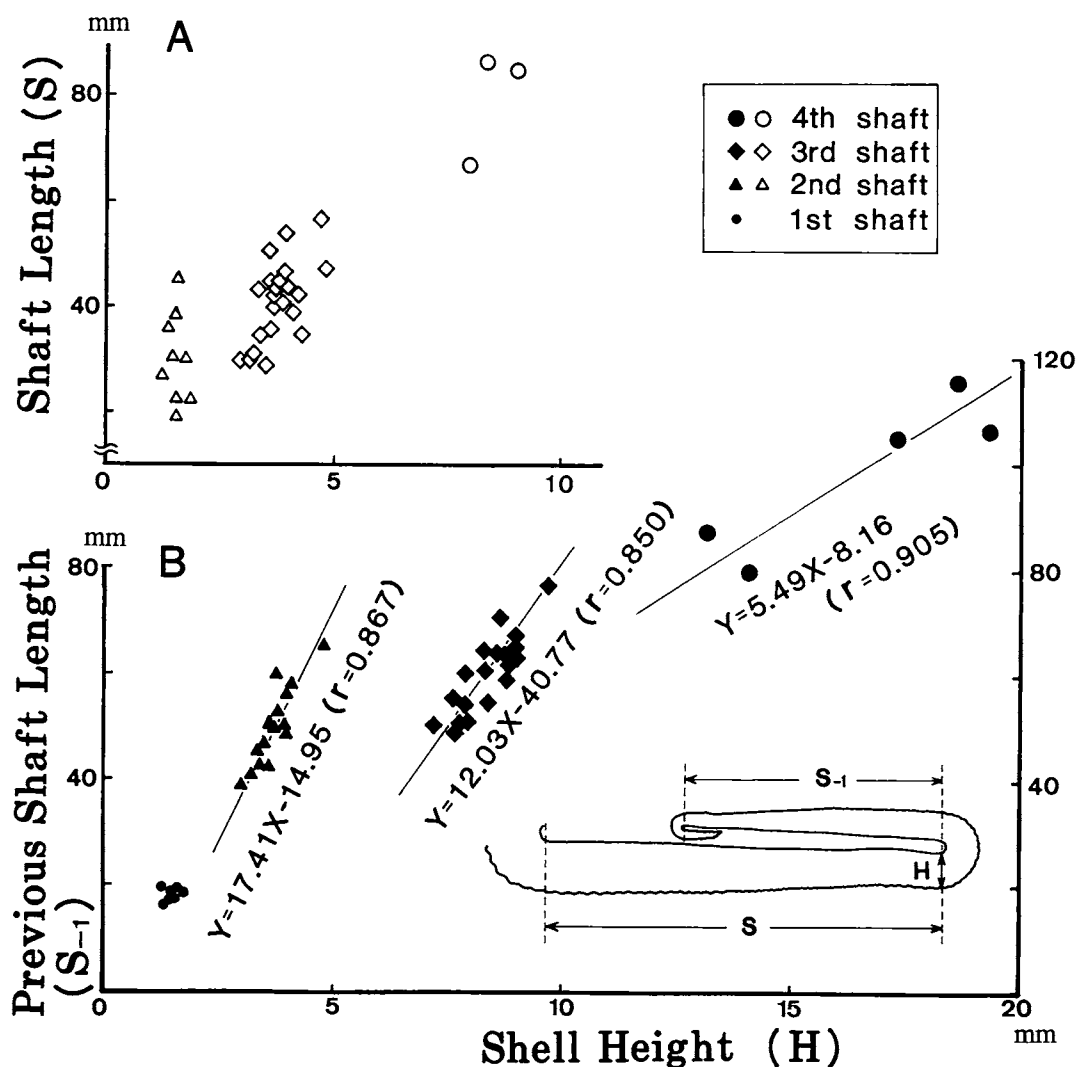
Figure 6. Scatter diagrams showing the relationship of the shaft length versus the shell height measured at the beginning of the shaft. Positive correlation between the shell height and the previous shaft length is significantly recognized (**B**), while the correlation between the shell height and the current shaft length is rather obscure (**A**). Regression line is also shown with the correlation coefficient (r), when the correlation is significant.

specimens (S-194). The shell height at the earliest point of this specimen is 0.32 mm. Since the shell height measured just after the nepionic constriction in this species is generally about 0.31 to 0.35 mm, it is reasonable to consider that the bending point of the second shaft indicates the impression of the protoconch. As a result, the first shaft length can be estimated as the distance between the end of the first turn and the bending point of the second shaft. The intraspecific variation is very small about the first shaft length estimated in this way (Figure 6B).

The shell length would be the most adequate and feasible parameter to compare the same growth stages between specimens. Since every specimen of *P. pseudogaultinum* examined in this study is more or less incomplete, the missing part of the shell must be reconstructed in order to analyze biometric data statistically. The mean values can hardly be employed for the estimation of the missing shaft length because of the large intraspecific variation. So we examined the correlation between the shell height and the shaft length (Figure 6A). No obvious correlation is, however, recognized between the shell height measured at the beginning point of each shaft and corresponding shaft length. The length of the previous shaft is, however, positively correlated to the shell height (Figure 6B). Therefore, the length of the previous shaft can be estimated by the shell height and this relationship, even if the earlier shell is missing.

Further biometric analyses

Relative growth between height and total shell length

Relative shell growth pattern in normally coiled ammonites is usually shown by the shell diameter (or whorl height), breadth and umbilicus measured in various stages along the transverse section. However, this method cannot be applied to heteromorph ammonites at all. The ontogenetic growth of the shell height should be measured relative to the total shell length. The total shell length is defined as the distance from a protoconch to a point of a certain growth stage represented by the track of the apertural center. This definition is also applied to the phragmocone length (from protoconch to the last septum).

The relative growth patterns between the shell height and the shell length in four specimens are shown in Figure 7. Morphology of the earlier shell is observable in two of the four specimens (H-038 and H-078). Relatively advanced growth stages, from the third turn to the early part of the fifth shaft, are observed in the other two specimens (S-108 and H-114). These growth patterns are combined by standardizing the third turn. These four specimens are concordant with each other in the growth pattern, showing cyclic oscillation of whorl height. The height grows slowly at an almost constant rate until the earlier half of the second shaft, but then the rate gradually decreases. Unlike the earlier stage, the height grows rapidly during the earlier halves of the third
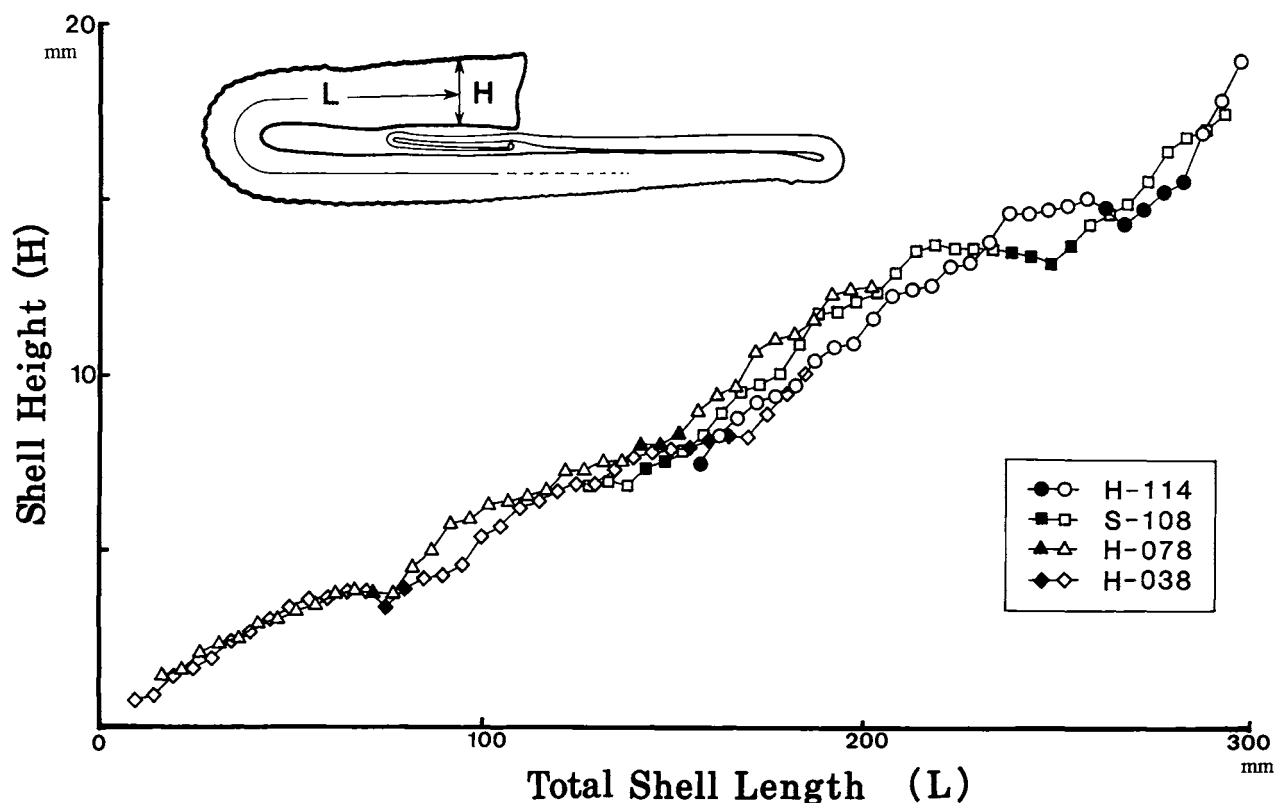

Figure 7. Relative growth between the total shell length and the shell height. Solid symbols indicate the data obtained at the turning part of shell. Shell height rapidly increases during the earlier half of every shaft.

and following shafts. Then the growth rate gradually decreases during the later half of the shafts, and this feature continues until the end of the following turn. Such periodic changes of growth rate are observed until the fifth shaft.

The shape of the transverse section of the shell changes during ontogeny (Figure 2). The section is almost circular until the middle part of the third shaft. It gradually becomes oval during the growth of the third shaft and finally subquadrate in the later stages.

Relative length between phragmocone and total shell

Every ammonite shell consists of a body chamber and a septate phragmocone. The soft part filling in the body chamber advances adorally with growth, and a new septum is formed behind the soft part. The life mode of an ammonite would have been hydrostatically controlled by the total average density of the whole ammonite body. If the density was higher than that of sea water, the ammonite could not stay in the water column without active swimming, because the buoyant force is not enough to cancel the gravity. Conversely, if the density of an ammonite was positively buoyant, the ammonite would be forced to float on the surface. In order to maintain a mode of life suspended in the water column, like extant *Nautilus*, the total average density of the ammonite had to be neutrally buoyant in sea water.

The relative volume of phragmocone to the whole ammonite body must be constant so as to maintain neutral buoyancy, if the ammonite keeps a constant density of phragmocone during growth. The relative volume of phragmocone is roughly expressed by the ratio between the phragmocone length and total shell length (P/T), if the expansion rate of the shell aperture is nearly constant with

growth. The P/T ratio was actually measured in twenty-one specimens showing various growth stages (Figure 8).

The P/T ratio is almost constant throughout various growth stages of the fourth shaft and ranges approximately from 0.57 to 0.61. Younger specimens, however, have relatively short phragmocones. Although relatively little data was obtained for other stages, the ratios are similar to the values measured in the fourth shaft. Consequently, the ratio is roughly 0.6 and is almost invariable throughout growth except for the youngest stage. The value is nearly equivalent to or slightly smaller than the ratios of normally coiled and other heteromorph ammonites (Okamoto, 1996).

In *Polyptychoceras pseudogaultinum,* the expansion rate of the shell aperture is not constant, as shown by the cyclic change of shell height during growth. If the species needs to maintain a total average density so as to achieve neutral buoyancy, for example, the P/T ratio may also change slightly with growth. So we classified the data into two groups by the growth stages; the open circles in Figure 8 indicate that the shell aperture is situated in the later half of the shaft whereas the solid ones indicate that the shell aperture is in the other part. However, no significant difference was detected between the two groups.

Interval of septa throughout growth

The interval between septa becomes rapidly shortened in many ammonites when they reach the fully mature stage. If a stagnation or break of shell growth has occurred during ontogeny, similar shortening of septal distance may appear in the phragmocone. We measured the distance between two adjacent septa together with corresponding phragmocone length.

Because the specimens examined are more or less frag-
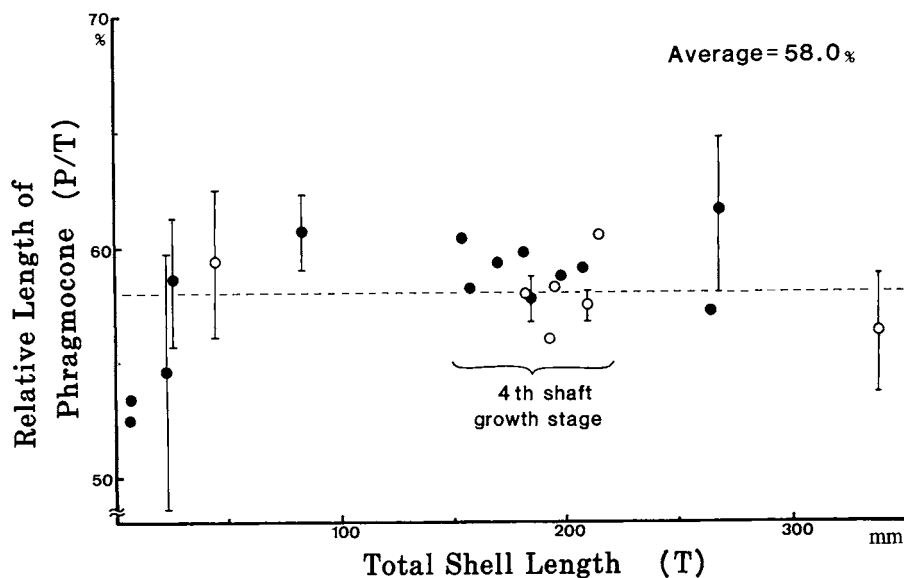
Figure 8. Diagrammatic figure showing the length of phragmocone relative to the total shell length. Vertical bars indicate the presumable range of error owing to the indirect estimation of missing shell length. Solid and open circles stand for specimens with the shell aperture situated in the earlier and later halves of shaft, respectively. The P/T ratio seems to be almost invariable throughout growth except for the two youngest specimens.
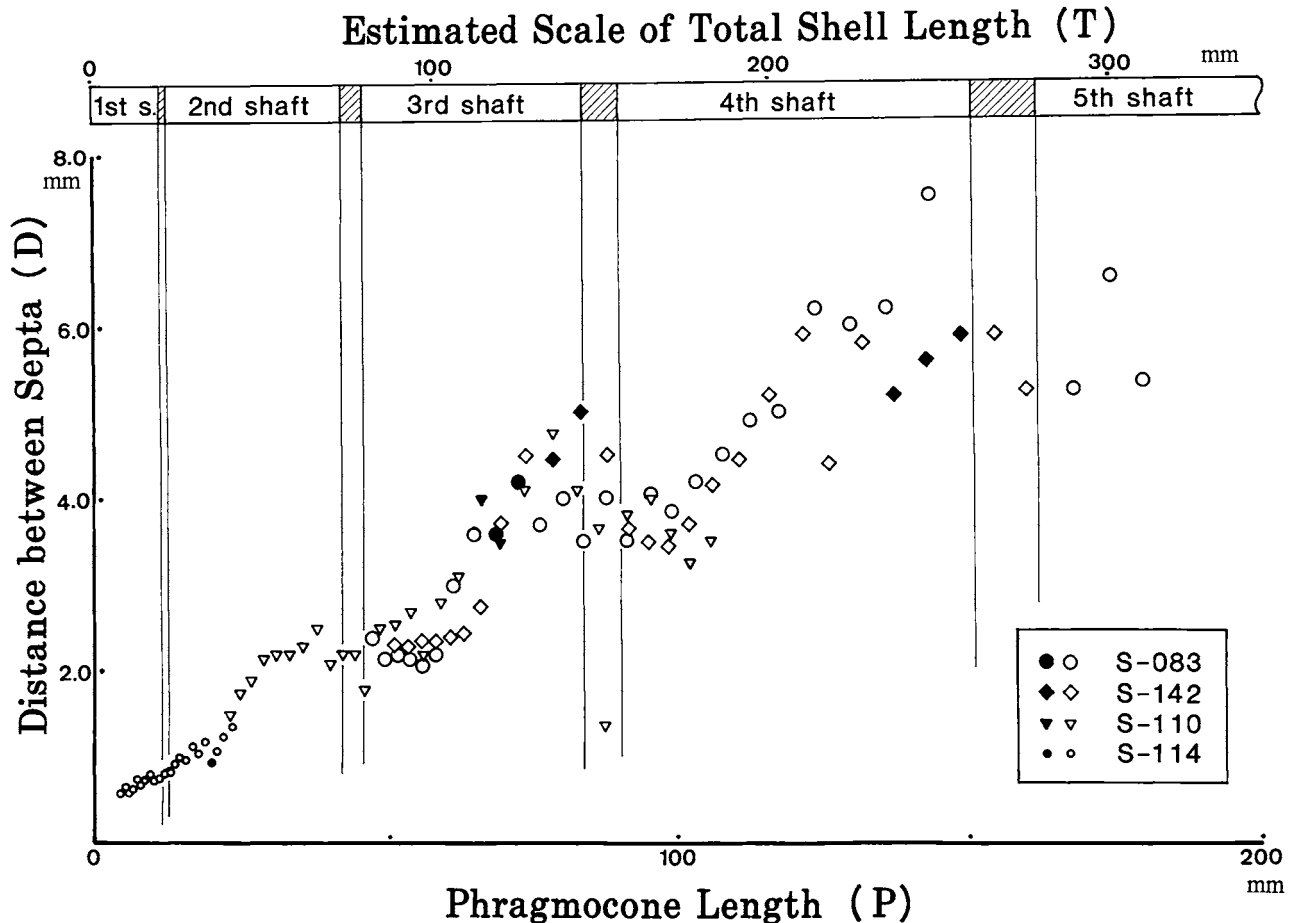
Figure 9. Diagrammatic figure showing the ontogenetic change of distance between septa. Solid symbols indicate the values measured in the turning parts of shell. Estimated length of total shell corresponding to the phragmocone length is also entered on this diagram. The distance between septa rapidly increases when the shell aperture is in the later half of the shaft.

mentary, the developmental change of the septal distance cannot be measured in a single specimen. The septal distance is actually measured on the cross section cut along the median plane. Its ontogenetic change is synthetically shown by connecting four specimens (S-083, S-142, S-110 and S-114) in Figure 9. In this diagram, the lower horizontal axis shows the phragmocone length, and the vertical axis shows the distance between septa. The progressive stages, in which the distance increases more or less rapidly, appears at 20-30 mm, 60-80 mm and 110-140 mm in phragmocone length. These stages are followed by some stagnant stages in which the septal distance is nearly constant. Though this biometric analysis shows that the progressive and stagnant stages alternately appear throughout the ontogeny, the relation to the position of septa is not obvious.

The cyclic change of the septal distance is well demonstrated in relation to the shell aperture. A scale of total shell length estimated from the phragmocone length and P/T ratio is also shown in Figure 9. The progressive stage of the distance between septa corresponds well to the growth stage where the shell aperture is located in the middle part

or later half of every shaft.

Population analysis (Distribution of growth stage)

If the fossils are collected at random, the sample indicates the distribution of growth stages in a fossil population. As to normally coiled ammonites, the growth stage is usually shown by the total revolution angle until the shell aperture. In *Polyptychoceras pseudogaultinum,* however, the growth stage has to be shown by the shaft number and relative position of the shell aperture in the shaft.

A total of 71 specimens with complete apertures was examined, and the frequency distribution is shown in Figure 10B. The intervals of horizontal axis corresponding to every shaft were standardized so as to increase proportionally to the corresponding shell height. Three peaks which appear in the earlier parts of the third to fifth shaft are recognized in this diagram, although the sample size is not sufficient owing to the infrequent preservation of the shell aperture. This method bears some difficulties in requiring randomness of observed sample. For example, full-aperture specimens having only one shaft (without turn and ammonitella) were
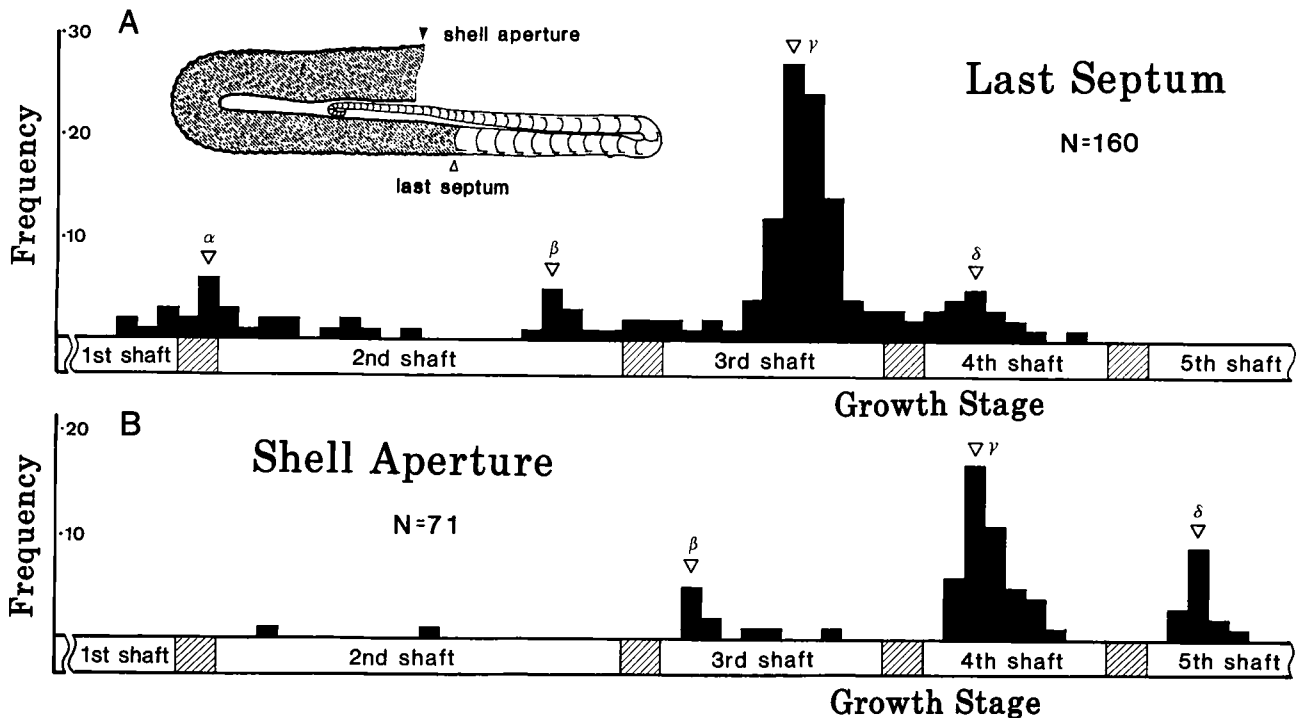
Figure 10. Histograms showing the distribution of the last septum and shell aperture in all the measurable specimens. Horizontal scale for the growth stage is proportionally divided by the corresponding shell height. Obliquely lined rectangle indicates turning part of shell. Three peaks in the histogram 10B for the shell aperture, reffered to *β*, *γ* and *δ*, appear just after every turning point of shell. Three of the four peaks appearing in the histogram 10A for the last septum surely correspond to those for the shell aperture.

not counted, because the growth stage cannot be determined in such specimens ; and such specimens could have originated more frequently from individuals having a long last shaft. The full-aperture specimens being younger than the second turn stage are extremely rare, while such young shells are very common in the samples.

To offset the difficulty mentioned above, we also analyzed the stage distribution of the last septum. In some cases, the shaft length was estimated from the shell height and the relationships shown in Figure 6. A total of 160 specimens with the last septum was examined (Figure 10A). Though the peaks are somewhat broad, three peaks appear between the later half of the second shaft and earlier half of the fourth shaft. They correspond well with the peaks observed in the analysis of full-aperture specimens (Figure 10B). They appear near the end of the second turn, near the midpoint of the third shaft, and near the beginning of the fourth shaft. These data indicate that the effect of the biased sampling is relatively small except for the younger stages. Additionally we detected another peak which appears around the first turn.

While the peaks in the frequency distribution of the shell aperture are quite sharp and occur at a regular interval corresponding to the pattern of shell coiling, the peaks of the last septum are somewhat obscure. The position of the last septum must be related to the position of shell aperture, the P/T ratio, and the length of each shaft. The P/T ratio is

stable among specimens and is also nearly constant throughout the ontogeny (Figure 8), whereas the shaft length is quite variable among specimens (Figures 5, 6). This may be the reason why the position of the last septum is so dispersed in the population sample.

Discussion

Mode of shell growth

If the specimens examined in Figure 10 are regarded as a result of random sampling, the concentration at some definite growth stages is possibly caused by uneven rate of mortality or uneven rate of shell prolongation. The latter cause is more likely, if the data of relative growth and other shell morphologic features are considered.

The mortality rate may change during ontogeny. Though the actual mortality rate of *P. pseudogaultinum* is unknown, a roughly constant mortality rate may be expected within a relatively short growth interval, e.g. within the growth of a single shaft. If this assumption is valid, the uneven and cyclic distribution of growth stages as shown in Figure 10 suggests periodic change of growth rate. It is likely that individuals of *P. pseudogaultinum* temporally ceased or stagnated their shell prolongation at the beginning of every shaft marked by the flared rib (except for the first and second shafts). The shell growth probably gradually accelerated during the earlier half of shaft, and the later half of shaft and

turn must be formed rapidly. Moreover, the truncated distribution of growth stage shown in Figure 10B indicates that an abrupt reduction of growth rate and its gradual recovery occur in the sequence of the cyclic growth.

The aforementioned periodic changes of the enlarging rate of shell height and surface ornamentation also support the cyclic growth mode of *P. pseudogaultinum*. The cyclic oscillation of the increasing rate of the shell height appears to correlate negatively (but significantly) with that of shell prolongation. It is reasonable to consider that the growth of soft parts is proportionate to the increase of the volume of body chamber. The observed rapid increase of shell height may compensate for the slow prolongation of shaft so as to keep an increasing rate of body chamber volume. The cyclic changes of the surface ornamentation may also be influenced by the rate of shell prolongation. The wrinkly phase characterized by the appearance of several irregular, notched ribs and numerous striae in between indicates the stagnation of shell prolongation, whereas the rhythmic phase characterized by the normal transverse ribs occurring at regular intervals is probably accompanied by rapid shell prolongation. The distance between septa also shows a cyclic change during growth. The stages showing wide septal intervals probably correspond to the promotional stages of shell prolongation. Judging from all the observation of specimens and from the result of biometric analyses, the most believable growth pattern of *Polyptychoceras pseudogaultinum* would be summarized as follows.

The first shaft, which directly follows the ammonitella, reaches about 2 cm in length. Then the shell turns back tightly and the second shaft is formed along the existing first shaft in parallel. This shaft bends slightly near the beginning of the first shaft and shows a weak sigmoidal curve just like that protecting the protoconch and ammonitella. Rather rapid and constant shell growth is presumable until this stage. Double collar ribs appear characteristically in the later half of second shaft, suggesting temporal pauses of shell growth. They are prorsiradiate and accompanied by slight narrowing of the shell aperture. The double collar rib seems to have the function of reinforcement of the aperture and protection of the body chamber filled with soft parts. The broad, first peak of the last septum shown in Figure 10A suggests the decline of the rate of shell prolongation during the later half of second shaft. The flared rib is usually formed periodically at definite position. It appears near the beginning of the third and later shafts, and probably shows the beginning of the stagnant interval of shell growth. Unlike the flared rib, the ornamentation of this interval characterized by the notched ribs and fine irregular striae in between does not indicate pauses of shell growth, but means slow shell prolongation. This phase occupies one third or sometimes almost the first half of each shaft. While the rate of shell prolongation is significantly decreased, the soft part may grow constantly during this interval. The rapid enlargement of shell aperture (height) at this phase may resolve the shortage of space for the soft part. The rate of enlargement of the shell aperture becomes lower during the later halves of shafts, while the growth rate of shell prolongation gradually recovers. Toward the end of this phase, the

surface ornamentation composed of the notched ribs and weak striae gradually changes to simple ribs developed at regular intervals. Then the wrinkly phase of surface ornamentation is followed by the rhythmic phase. The sequence of the growth cycle is usually terminated by a flared rib appearing at the beginning of the next shaft.

Specimens showing either the last septum or shell aperture situated in the second shaft are not abundant, and specimens growing until the fifth shaft are also rare. If we ignore possible bias from geologic and diagenetic factors, the stage distribution of the present sample suggests that *P. pseudogaultinum* grows rapidly in the early stage, and that the fifth shaft represents the ultimate growth stage.

A Neutral buoyancy

$$B + G = 0$$

B Negative buoyancy

$$B + G + R = 0$$
$$d_1 G + d_2 B = 0$$
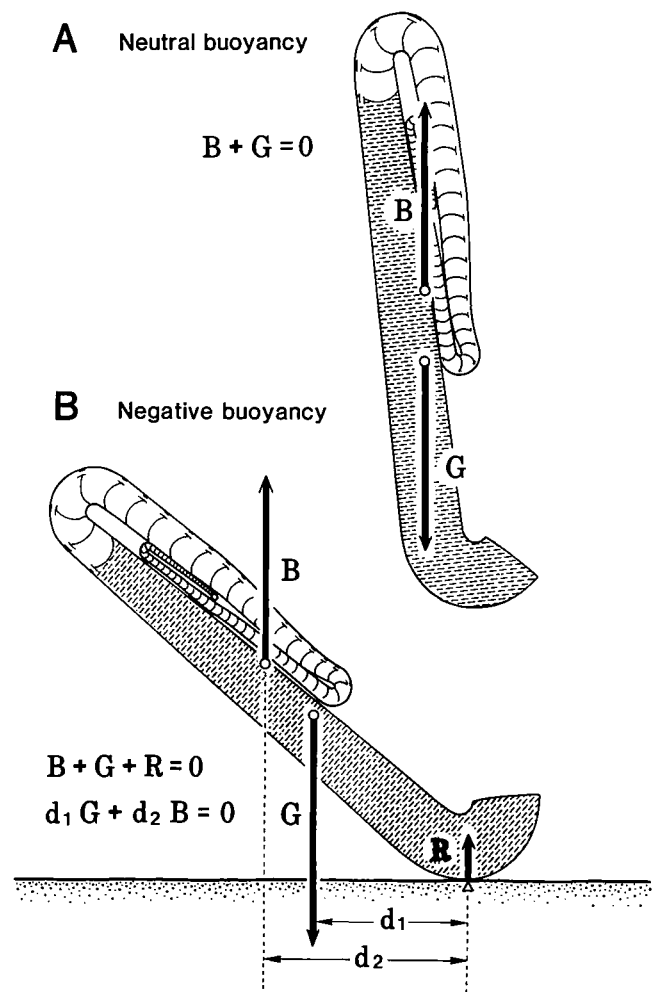
Figure 11. Reconstructions of the living attitude of ammonite. Vectors **B**, **G** and **R** show buoyant force, gravitational force, and resistant force, respectively. Under the condition of neutral buoyancy the center of gravity (the origin of vector **G**) is situated just below the center of buoyancy (the origin of vector **B**). When the ammonite is negatively buoyant, the living attitude is determined so as to keep a balance of moments acting on the circumference of the tangential point (origin of vector **R**).

Suspended in water

Figure 12. Result of computer simulations of living attitude under the assumption of suspended mode life in water column (i.e. the buoyancy is equivalent with gravity). Solid triangle indicates the boundary between the phragmocone and body chamber.

Touching bottom

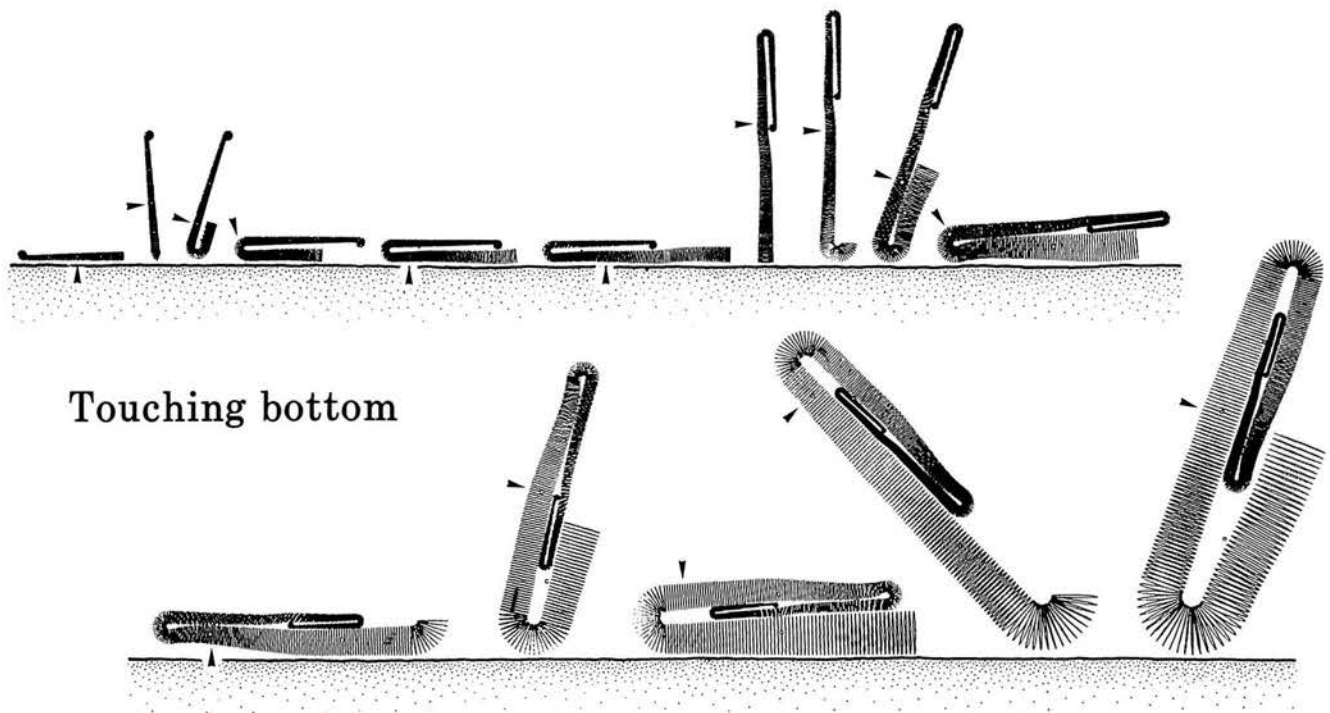**Figure 13.** Result of computer simulations of living attitude on the assumption that the ammonite was lightly touching the bottom (i.e. the gravitational force acting on the ammonite body is 1.1 times larger than the buoyant force, and the density of phragmocone is 0.6 g/cm³). Solid triangle indicates the boundary between the phragmocone and body chamber.

Reconstruction of living attitude

Heteromorph ammonites in general seem to have changed their living attitude during growth according to the aberrant changes of shell coiling. In order to estimate the living attitude of *P. pseudogaultinum* and its ontogenetic change, we carried out computer simulations based on the excellent hydrostatic concept of Trueman (1941). The detailed procedure of this simulation basically follows the method mentioned by Okamoto (1988a, b). The living attitude of ammonites is hydrostatically determined by the distribution of the center of buoyancy and the center of gravity, because the buoyant and gravitational forces act on these centers (Figure 11). Therefore, the living attitude of ammonites is related not only to the shell coiling pattern but also to the share of the phragmocone in the whole ammonite shell. The ratio of the phragmocone length to the total shell length (P/T) is chosen as 0.6 throughout the computer simulation of hypothetical shell growth. The ratio of the gravitational force to the buoyant force (G/B) is also required for the calculation. Since the actual G/B ratio is unknown, two possible cases, i.e. neutral buoyancy and slightly negative buoyancy for the whole ammonite body, are assumed in this study. The two conditions, of course, correspond to nekto-planktic and benthic life modes. The results of simulations are as follows (see also Figures 12, 13).

Neutral buoyancy: The G/B ratio is assumed to be 1.0 throughout this simulation (Figure 12). The gravitational vector must have the direction from the center of buoyancy to the center of gravity. The living attitude is reconstructed so as to situate the center of gravity just below the center of buoyancy (Figure 11A). Under this condition, *P. pseudogaultinum* is suspended in the water column and changes its living attitude in succession. Note that the aperture faces upward when it is situated at the earlier half of each shaft (except for the first shaft), while the direction of the aperture becomes nearly horizontal or downward when it is situated at other part of the shell.

Negative buoyancy: The G/B ratio is hydrostatically chosen as 1.1 throughout this simulation (Figure 13). This assumption means that the total average density is about 1.13 g/cm³. Under this condition, the shell of *P. pseudogaultinum* had to touch the sea bottom lightly. Because many damage scars suggesting attacks by crustaceans are observed on the shells, this species possibly lived near the sea bottom. Since gravity does not balance with buoyancy in this case, the resistant upward force acting at the tangential point between the shell and sea floor must compensate for the surplus weight. The living attitude can be determined so as to keep a balance of moments acting on the circumference of the tangential point. Under this condition, an attitude of stably lying down on the sea bottom is repeatedly reconstructed throughout growth stages. Until the second turn, the shell starts turning when the attitude changes to an upright posture and the aperture faces downward. At the third and the fourth turn, the turning starts slightly before the

stage when the aperture faces downward.

As the result of these simulations, the living attitude shows cyclic changes throughout growth. Though the presumable change of the living attitude is somewhat different between two conditions, the reconstructed living attitude usually shows upward growth direction in the earlier half of every shaft. These stages correspond well with the growth stagnation presumed by the analyses of relative shell growth, shell ornamentation and frequency distribution of growth stages. Consequently, *Polyptychoceras pseudogaultinum* seems to have preferred a living attitude showing an upward growth direction, and to have maintained such a life orientation for most of the time throughout its growth.

Further speculation about shell coiling

One of the authors (T.O.) pointed out that some heteromorph ammonites possibly regulate their shell coiling by referring to some information such as direction of gravity. The meandrous coiling of *Nipponites,* a Late Cretaceous nostoceratid heteromorph, has been explained by the "growth direction regulatory hypothesis", in which *Nipponites* alternately switched three modes of shell coiling so as to maintain its growth direction within a preferable range (Okamoto, 1988c). Some other cases also suggest that the shell coiling of ammonites is *a posteriori* determined (Merkt, 1966; Okamoto, 1992).

Here, we also pointed out that the shell coiling of *Polyptychoceras* was possibly influenced by the change of growth direction. The great variability of shaft length and existence of some aberrant individuals (Figure 15-7, 8) suggest that the shell coiling is not determined rigidly under genetic control. *Polyptychoceras* perhaps had a rather wide range of preferred growth direction which ranges from nearly horizontal to upward vertical. Usually, the shell runs straight while the growth direction is preferable. Shell turning seems to occur when the growth direction becomes downward, so as to recover a more preferable direction of the aperture. The condition in which the ammonite was lightly touching the sea bottom is more likely for interpreting the shell coiling of *Polyptychoceras* by this hypothesis, because the growth direction changes more rapidly to an unfavorable state when the new shaft attains a certain length.

Theoretical approaches by using computer simulations of shell coiling seem to elucidate the process of growth and morphogenesis of this heteromorph ammonite.

Conclusion

In order to interpret the peculiar shell formation of *Polyptychoceras,* more than 320 specimens of *P. pseudogaultinum* were analyzed by various methods of biometry, population analysis and theoretical morphology. It is concluded that the peculiar shell morphology of *P. pseudogaultinum* is related to the intermittent growth pattern and to the cyclic change of living attitude. Namely, the shell grows slowly

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Figure 14. *Polyptychoceras pseudogaultinum* (Yokoyama). All figures natural size. **1-12.** From Onko-no-sawa, **13-15.** From Kami-no-sawa, Kotanbetsu, Tomamae Province, Hokkaido, 1 : H-049, 2 : S- 124, 3 : H-038, 4 : S-148, 5 : H-076, 6 : H-001, 7 : S-146, 8 : H-078, 9 : S-125, 10 : S-065, 11 : S-147, 12 : S-123, 13 : H-114, 14 : T-027, and 15 : T-028.
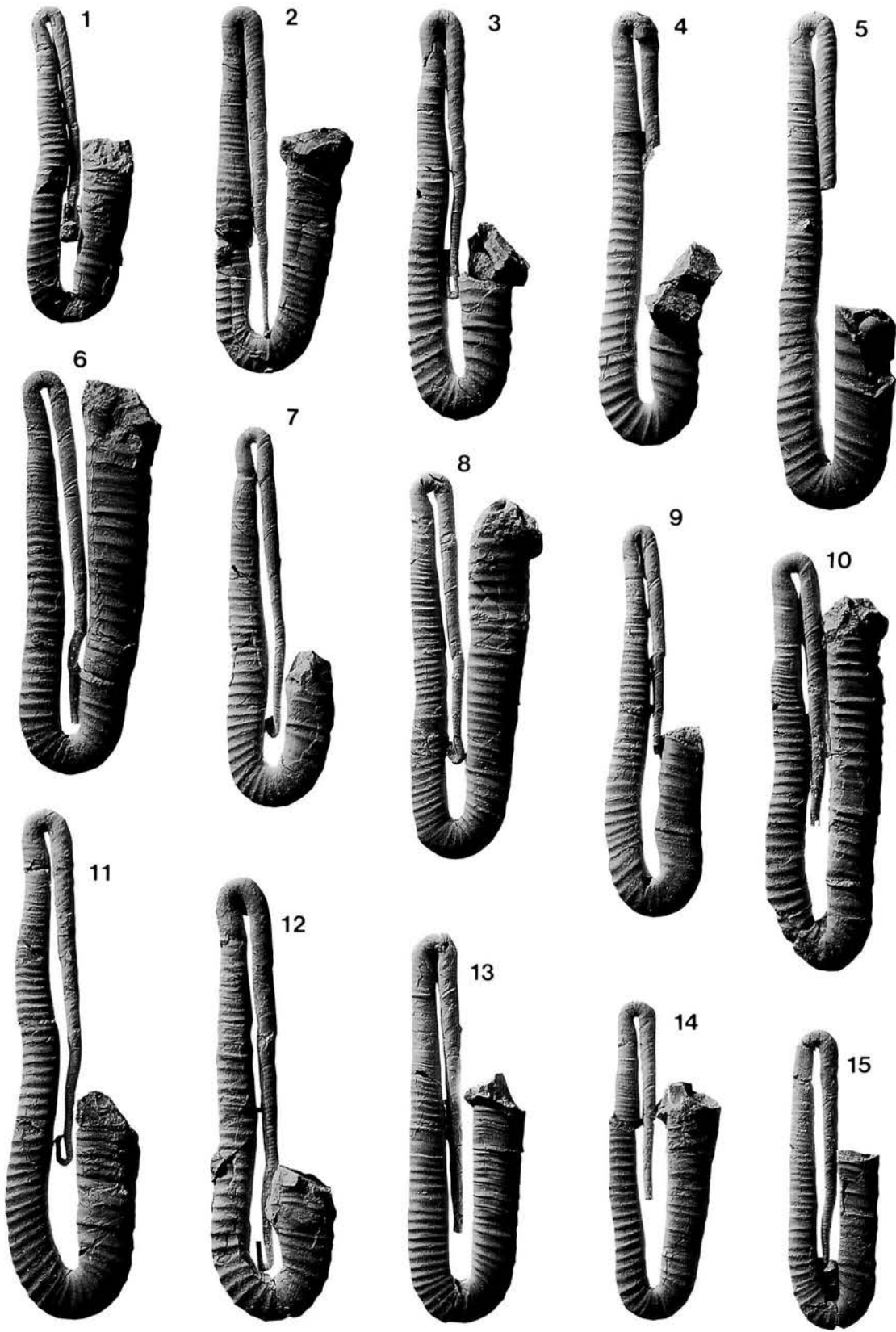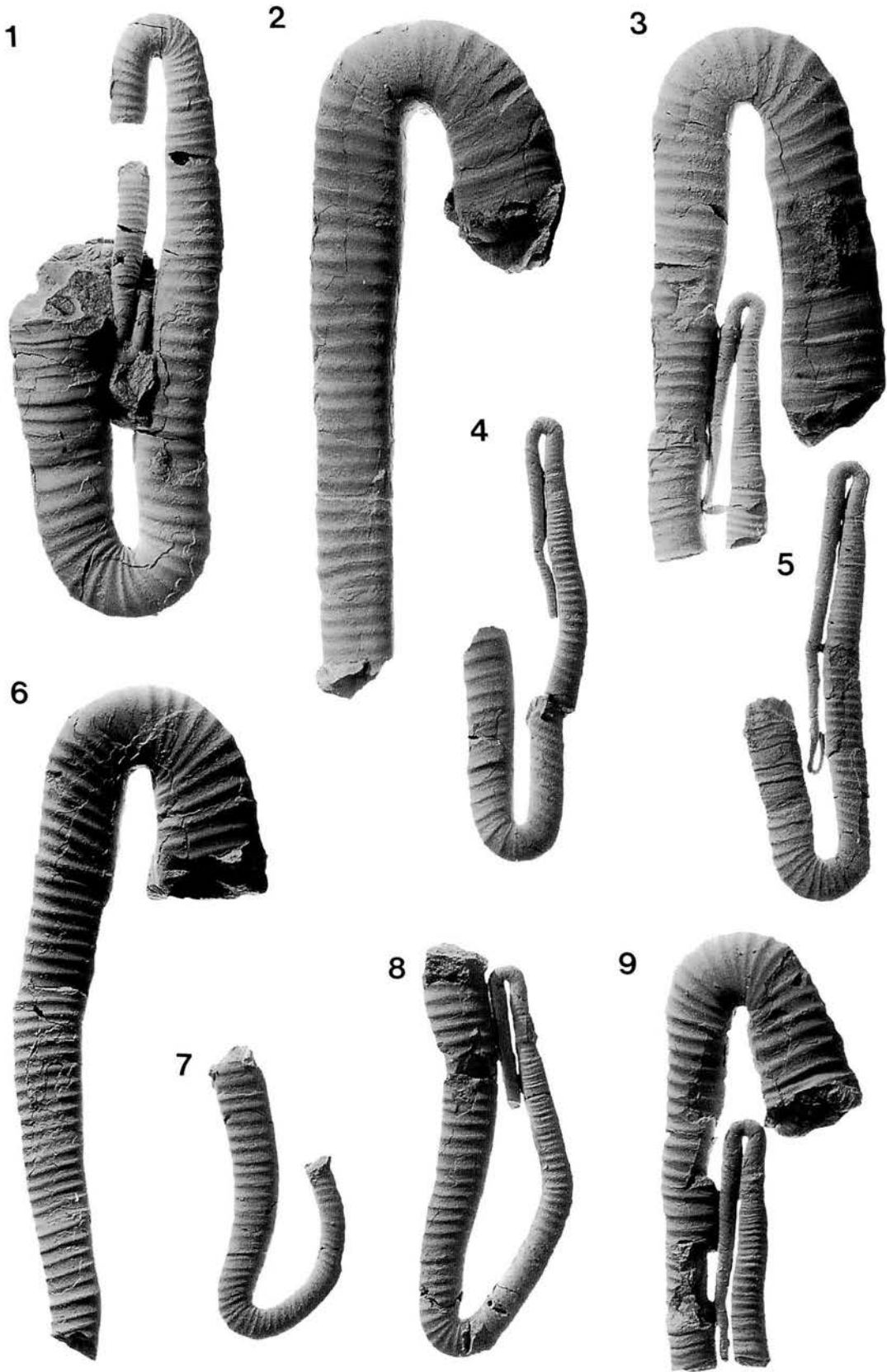
when the aperture faces upward and grows quickly when the aperture faces other directions. Various kinds of cyclic morphologic changes observed during growth can be reasonably interpreted with this hypothesis. The sudden increase of shell height occurs in several stagnant stages of shell prolongation and enables the body to grow continuously. The periodic flared rib occurring near the beginning of every shaft suggests the start of the stagnation interval. The notched ribs characteristically develop during the intervals. Thus, the changes of shell ornamentation reflect the mode of growth, which is related to the change of living attitude.

In this study, we cannot necessarily elucidate the shell-forming mechanism of *P. pseudogaultinum* or the adaptive significance of such an aberrant shell form. We merely have made clear the characteristics of the shell growth of this ammonite which are probably controlled by its life orientation in sea water. The peculiar mode of shell coiling was possibly caused by the cyclic change of growth direction, which must be strongly constrained by the existing shell geometry. The validity of such hypotheses should be checked by a theoretical approach using some computer simulations of shell coiling. The changing process of shell geometry throughout the phylogeny of *Polyptychoceras* and its ancestors is possibly reconstructed by analogous approaches.

Acknowledgments

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Figure 15. *Polyptychoceras pseudogaultinum* (Yokoyama). All figures natural size. **1.** From Kami-no-sawa, **2-9.** from Onko-no-sawa, Kotanbetsu, Tomamae Province, Hokkaido. 1 : H- 114, 2 : H-079, 3 : H-080, 4 : S-126, 5 : S-122, 6 : S-108, 7 : H-007, 8 : H-088, and 9 : S-163.

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Appendix table. Correlation between the consecutive specimen numbers and register numbers.

Register No. [UMUT MM-]	Sample No.	Consecutive specimen No.			
19877 a-c	K1001p-1	H.068-070	19920 a-e	92KT9029g	S.091-095
19878 a-d	K9000p-2	H.049-052	19921 a-b	92KT9029u	S.015, S.202
19879	K9000p-4	H.048	19922	92KT9029v	S.113
19880 a-g	K9000p-6	H.042-047, H.054	19923 a-c	92KT9029w	S.032-033, S.074
19881 a-d	K9000p-7	H.038-041	19924 a-i	92KT9029p-2	S.026-029, S.106,
19882	K9000p-9	S.203			S.110-111, S.119-120
19883	K9000p-17	H.053	19925	92KT9031p-1	H.081
19884	K9000p-21	H.055	19926 a-f	92KT9031p-2	H.096-101
19885 a-b	K9000p-30	H.060-061	19927	92KT9031p-3	S.010
19886 a-c	K9000p-31	H.065-067	19928 a-b	92KT9035a	S.030-031
19887	K9000p-32	H.071	19929 a-d	92KT9035p-1	H.087-090
19888	K9000p-33	H.107	19930 a-i	92KT9035p-2	S.020-025, S.176-178
19889 a-b	K9000p-34	H.110, H.121	19931 a-d	92KT9606p-1	S.076, S.114-116
19890 a-d	K9000p-35	S.197-198, S.204-205	19932 a-b	92KT9611p-1	S.118, S.142
19891	K9009c	H.059	19933 a-e	93KT9019p-1	S.016-019, S.179
19892 a-c	K9011a	H.102-104	19934 a-c	93KT9030b	S.143-145
19893 a-f	K9011b	S.041-046	19935 a-v	93KT9030c	S.012-014, S.037-038,
19894 a-e	K9011d	H.028-032			S.096-097, S.103-105,
19895 a-d	K9011e	H.024-027			S.159-170
19896 a-c	K9011g	H.035-037	19936 a-w	93KT9030d	S.122-141, S.180,
19897	K9011h	H.034			S.188-189
19898	K9011j	H.033	19937 a-g	93KT9030e	S.181-185, S.200-201
19899 a-e	K9011k	H.019-023	19938 a-d	93KT9030f	S.056-059
19900 a-c	K9012b	H.001-003	19939	93KT9030g	S.069
19901 a-d	K9012e	H.004-007	19940 a-b	93KT9030h	S.108-109
19902	K9012g	H.018	19941 a-v	93KT9030k	S.146-158, S.186-187,
19903 a-e	K9012j	H.008-012			S.190-196
19904 a-e	K9012n	H.013-017	19942 a-n	93KT9030l	S.039-040, S.070-072,
19905	K9110a	H.064			S.082-090
19906	K9111b	H.074	19943 a-e	93KT9030n	S.060-064
19907 a-c	K9111d	H.056-058	19944 a-e	93KT9030q	S.051-055
19908	H6101p-3	H.072	19945 a-d	93KT9030r	S.047-050
19909 a-d	92KT1004p-1	H.091-093, H.095	19946	93KT9030u	S.075
19910 a-g	92KT3142p-1	H.113-119	19947 a-d	93KT9030w	S.065-068
19911	92KT3522p-1	H.109	19948	93KT9030x	S.073
19912 a-d	92KT3707p-1	S.009, S.011, S.117, S.121	19949 a-n	93KT9035a	S.001-004, S.034-036,
19913	92KT3713p-1	H.108			S.077-081, S.112, S.175
19914	92KT8563p-1	H.120	19950 a-n	93KT9035b	S.005-008, S.098-102,
19915 a-b	92KT8566p-1	H.111-112			S.107, S.171-174
19916	92KT9008p-1	H.105	19951	95HB4014p-2	S.199
19917	92KT9008p-2	H.106			
19918 a-h	92KT9029c	H.075-080, H.126-127	SKIPPED NUMBERS :		H.062-063, H.073, H.094, H122-125
19919 a-e	92KT9029d	H.082-086			

All specimens are identified with *P. pseudogaultinum* except for S.199.

Hokkaido 北海道, Horotate-zawa 幌立沢, Kami-no-sawa 上の沢, Kotanbetsu 古丹別, Onko-no-sawa オンコの沢, Tomamae 苫前, Urakawa 浦河