837. ONTOGENETIC SHELL VARIATION AND STREAMLINING OF SOME CRETACEOUS AMMONITES*

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Abstract. Comparative shell shape analysis of some Cretaceous ammonites has provided significant differences in the ontogenetic pattern and variation of geometric coiling parameters. The differences are especially conspicuous in the distance of venter from coiling axis (D), relative whorl thickness (S) and flank position (F), all of which are key factors for considering hydrodynamic efficiency of the shells. In every species, the ranges of variation of the geometric parameters tend to decrease with age. At the same growth stage, intraspecific variation of parameters S and D is largest in the heavily ornamented morphotypes (Acanthocerataceae) and heteromorphs (Scaphitaceae), intermediate in fine-ribbed platycones (Lytocerataceae), and smallest in the weakly ribbed, highly streamlined involute-compressed morphotypes (*Hypophylloceras*, *Placenticeras* and most Desmocerataceae). This evidence strongly suggests a wide variety of adaptive designs of the shells related to the mode of life of ammonites.

Introduction

The paleoecology of ammonites has long been discussed from various viewpoints. Although opinions on life habits are still divided as to whether ammonites were bottom dwelling or nektoplanktonic, many authors have accepted the idea that most normally coiled ammonites had a certain degree of swimming ability. This interpretation is largely based upon indirect paleontologic evidence such as comparative anatomy (Mutvei, 1964; Mutvei and Reyment, 1973; Jordan, 1968; Stürmer, 1970; Lehmann, 1976) and similarity in fundamental shell morphology to living *Nautilus* (Trueman, 1941). Quantification of hydrodynamic properties of ectocochliate cephalopod shells has been made experimentally using actual specimens (Schmidt, 1930; Kummel and Lloyd, 1955) and scale models (Chamberlain, 1976, 1981; Chamberlain and Westermann, 1976). The experiments demonstrated that the variation in shell geometry caused significant variation in drag coefficients.

Hydrodynamic efficiency of shell shape in fossil ectocochliates has recently been discussed by Ward (1980) and Chamberlain (1981). These papers rely on generic level analysis of certain simple shell shape parameters over various taxonomic groups. Intra- and interspecific variation of shell shape has also been examined extensively in the Upper Paleozoic Agoniatitida and Goniatitida (Kullmann and Kant, 1970, 1972; Kant, 1977; Kant and Scheuch, 1973, 1980; Saunders and Swan, 1984) and Mesozoic Ammonitida (Westermann, 1966; Bayer and McGhee, 1984; Ward, 1980, 1986), but the ontogenetic variation of shell geometry has little investigated in the Cretaceous ammonites. This paper presents quantitative data on the ontogenetic change and variation of shell shape in some late Cretaceous ammonite species, and discusses their adaptive significance for streamlining.

Material and methods

Material—Twenty Cretaceous ammonite species listed in Table 1 were treated in this study. Most species are represented by several individuals which were preserved in single calcareous

Table 1. List of material. Samples with prefix R are from the Cenomanian-Santonian of the Obira area, northwestern Hokkaido (see Tanabe *et al.*, 1977, figs. 4−11 for localities and ages). The localities and ages of the remaining samples are as follows. M135 and PM3007: Upper Turonian of the Manji area, central Hokkaido (see Tanabe *et al.*, 1978, fig. 1 for localities), S2211p and S3006: Lower Campanian at Matsumoto's (1942, pl. 12) loc. T281, middle course of Abeshinai River, Saku area, northern central Hokkaido, Hb-10: from river gravel in the upper course of Nakafutamata River, Haboro area, northwestern Hokkaido (derived from the Coniacian).

Major taxonomy	Species	Sample & locality
Phylloceratina		
Phyllocerataceae	*Hypophylloceras subramosum* (Spath)	R4018 (N= 5), Obira
Lytoceratina		
Lytocerataceae	*Tetragonites glabrus* (Jimbo)	R4020 (N= 6), Obira
	Tetragonites popetensis Yabe	S3006 (N=17), Saku
	Gaudryceras denseplicatum (Jimbo)	R4020 (N= 5), Obira
Ancyloceratina		
Scaphitaceae	*Scaphites planus* (Yabe)	R2110 (N= 4), Obira
	Otoscaphites puerculus (Jimbo)	R2110 (N= 7), Obira
Ammonitina		
Desmocerataceae	*Desmoceras japonicum* (Yabe)	R3013 (N=11), Obira
	Tragodesmoceroides subcostatus Matsumoto	R4001 (N=18), Obira
	Damesites ainuanus Matsumoto	R4582 (N=12), Obira
	Damesites damesi (Jimbo)	R4701p(N=11), Obira
	Damesites semicostatus Matsumoto	R2672 (N=17), Obira
	Damesites sugata (Forbes)	Hb-10 (N= 8), Haboro
	Desmophyllites diphylloides (Forbes)	S2211p(N= 6), Saku
	Neopuzosia ishikawai (Jimbo)	R101p (N= 6), Obira
Acanthocerataceae	*Subprionocyclus bravaisianus* (d'Orbigny)	R4017 (N= 6), Obira
	Subprionocyclus neptuni (Geinitz)	PM3007(N=14), Manji
	Reesidites minimus (Hayasaka & Fukada)	M135 (N=13), Manji
	Yubariceras yubarense Matsumoto, Saito & Fukada	R6020 (N= 1), Obira
	Yubariceras japonicum Matsumoto, Saito & Fukada	R4020 (N= 1), Obira
Hoplitaceae	*Placenticeras intercalare* Meek	USGS loc. no.8036
Nautilida		(N= 1), Montana
Nautilaceae	*Nautilus pompilius* Linné	Off Suva, Fiji Is. (N= 9)

nodules embedded in the Upper Cretaceous deposits of Hokkaido, Japan. The localities and ages of the samples examined are summarized in the explanation of Table 1. Specimens of *Scaphites planus* and *Otoscaphites puerculus* were studied biometrically by Tanabe (1977), and measurements by him are cited in this paper.

In addition to these ammonites, single mature shells of *Placenticeras intercalare, Yubariceras yubarense, Y. japonicum* (see Table 1 for locality records), and nine *Nautilus pompilius* Linné (captured from the Suva area of Fiji; Tanabe, 1985) were used for morphologic comparison. Specimens of the two scaphitids and *N. pompilius* are stored at Kyushu and Kagoshima Universities respectively. All other specimens are kept at University Museum, University of Tokyo with registered numbers beginning UMUT.
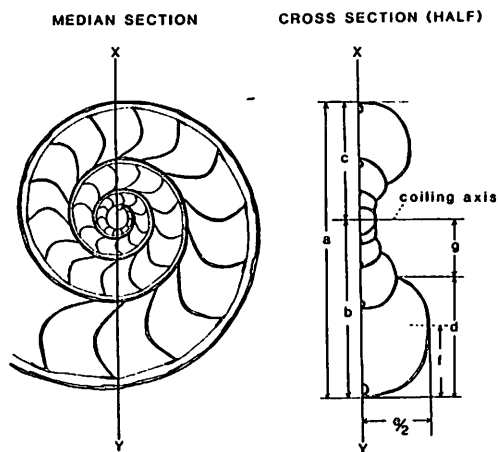
Methods−Most specimens were cut and polished along the median plane, and then cut

perpendicular along the maximum diameter of the protoconch (X-Y plane in Figure 1). The cross sections were etched with 1% acetic acid for ten minutes, and acetate peels were prepared by pressing a sheet of triacetylcellulose film (25 μm in thickness) onto the section flooded with acetone. Shell diameter, radius vector of venter, radius vector of umbilicus, whorl height, whorl breadth and inner whorl height were measured at intervals of one half whorl on the peeled cross section using a profile projector (NIKON V16) attached to a digital micrometer (accuracy 1 μm) (Figure 1). The measurement data were transferred directly to a personal computer through an interface, and the four geometric parameters developed by Raup (1966, 1967) and Chamberlain (1976); *i.e.* the whorl expansion rate (*W*), the distance of venter from coiling axis (*D*), the relative whorl thickness (*S*), and the flank position (*F*) were calculated at intervals of one half whorl for each specimen (Figure 1). Other important aspects of shell morphology,

such as the "strength" and density of external sculpture (ribs, tubercles and a keel) were not analyzed quantitatively, but considered in the morphotypic classification.

Morphotypic variation

Although the Cretaceous ammonites examined vary in coiling, whorl shape, and surface ornament, they possess characteristic features of shell morphology. They are roughly classified into the following morphotypes: (1) narrowly umbilicate and compressed with fine ribs (*Hypophylloceras, Desmoceras, Tragodesmoceroides, Desmophyllites, Placenticeras*) or with fine ribs and a prominent keel (*Damesites*), (2) moderately umbilicate platycone with dense fine ribs (*Tetragonites* and *Gaudryceras*), (3) widely umbilicate and compressed with strong ribs, tubercles (*Yubariceras*) and also with a keel (*Subprionocyclus* and *Reesidites*), and (4) planispirally coiled heteromorph (*Scaphites* and *Otoscaphites*). Selected examples of these ammonites are shown in Figure 2.
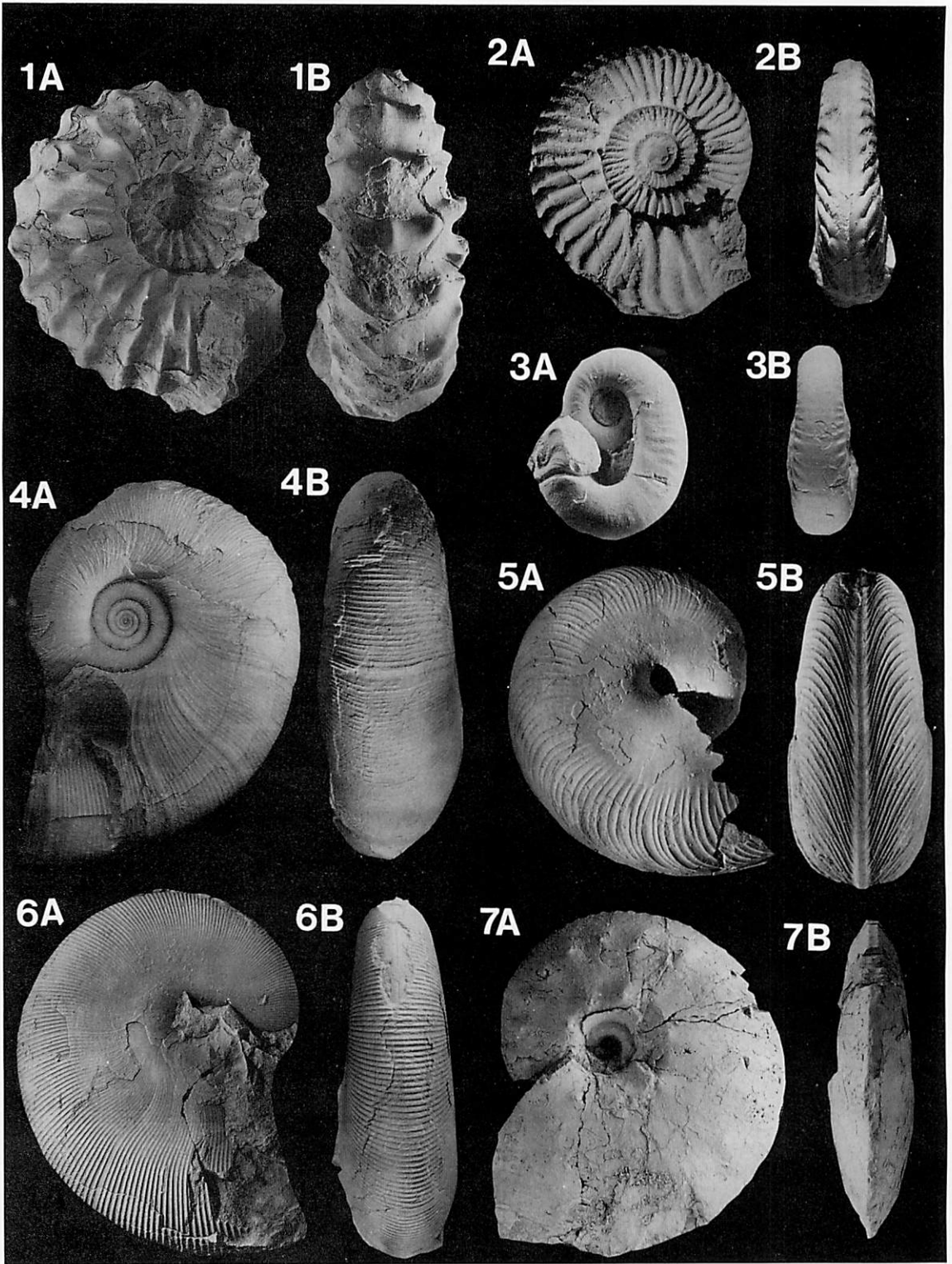
Geometric analysis

Ontogenetic variation—Ontogenetic changes of geometric parameters were examined in seventeen Cretaceous ammonite species. Changes of sample means of parameters *W, D, S* and *F* versus whorl number for each species are shown in Figures 3—6 respectively. In every species, parameter *W* regularly fluctuates between 1.5 and 2.5 at intervals of one whorl in the first three whorls. This is largely due to the abrupt change in allometric growth of whorl radius at the primary constriction near the end of the first whorl. After the third whorl most species have *W* parameters of about 2.0, but in the scaphitids *W* exceeds 3.5 in the loosely coiled adult stage (Figure 3). *D* parameters of *Hypophylloceras subramosum* and most desmoceratids decrease with age in the first three whorls, and after the third whorl remain almost constant (*ca.* 0.1) (Figure 4). In *Neopuzosia ishikawai* (Desmoceratacea) *D* is also small in the second and third

MEDIAN SECTION   CROSS SECTION (HALF)

GEOMETRIC PARAMETERS: $W=(b/c)^2$, $D=g/b$, $S=d/e$, $F=f/a$

Figure 1. Basic morphology and measurements of an ammonite shell in median and cross sections. a, shell diameter; b & c, radius vector of venter; d, whorl height; e, whorl breadth; g, radius vector of umbilicus; f, inner whorl height. Based on these measurements, four geometric parameters, *W* (whorl expansion rate), *D* (distance of venter from coiling axis), *S* (relative whorl thickness), and *F* (flank position) were calculated at intervals of half whorl. Read S = e/d for S = d/e.
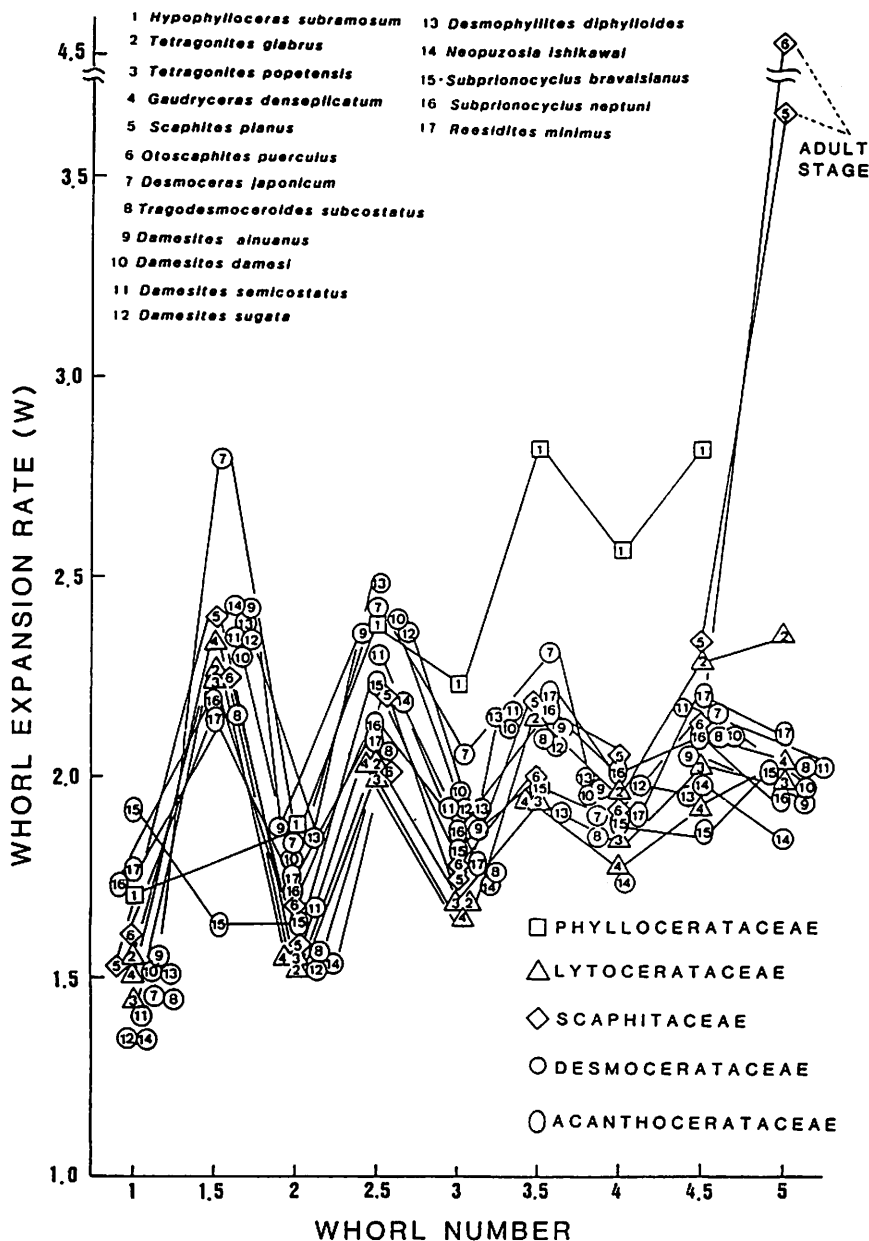
Figure 3. Ontogenetic change of the parameter W in relation to whorl number for seventeen ammonite species. Sample mean at each stage is plotted for every species. The regular fluctuation of W parameters in the first two whorls is due to the abrupt change in growth of whorl diameter at the primary constriction.

← **Figure 2.** Wide variation of shell shape and surface ornament observed in selected Cretaceous ammonites. Lateral (A) and ventral (B) views are shown for each species. For locations see Table 1. 1A–B. *Yubariceras japonicum* Matsumoto, Saito & Fukada (UMUT MM 18213; X0.2). 2A–B. *Subprionocyclus bravaisianus* (d'Orbigny) (UMUT MM 18209; X0.8). 3A–B. *Otoscaphites puerculus* (Jimbo) (Kyushu Univ. specimen, GK. H 5753; X1.6). 4A–B. *Gaudryceras denseplicatum* (Jimbo) (UMUT MM 18200; X0.3). 5A–B. *Damesites semicostatus* Matsumoto (UMUT MM 18205; X0.8). 6A–B. *Hypophylloceras subramosum* (Spath) (UMUT MM 18197; X0.8). 7A–B. *Placenticeras intercalare* Meek (UMUT MM 18214; X0.26).

whorls but then increases abruptly. *D* parameters of other species are almost constant throughout growth (*ca.* 0.3—0.5) and larger than in *Hypophylloceras* and most desmoceratids at the same

growth stage. Two scaphitids possess extremely large *D* parameters in the adult stage. In every species examined, parameter *S* tends to decrease with age (Figure 5). At the same stage, it is
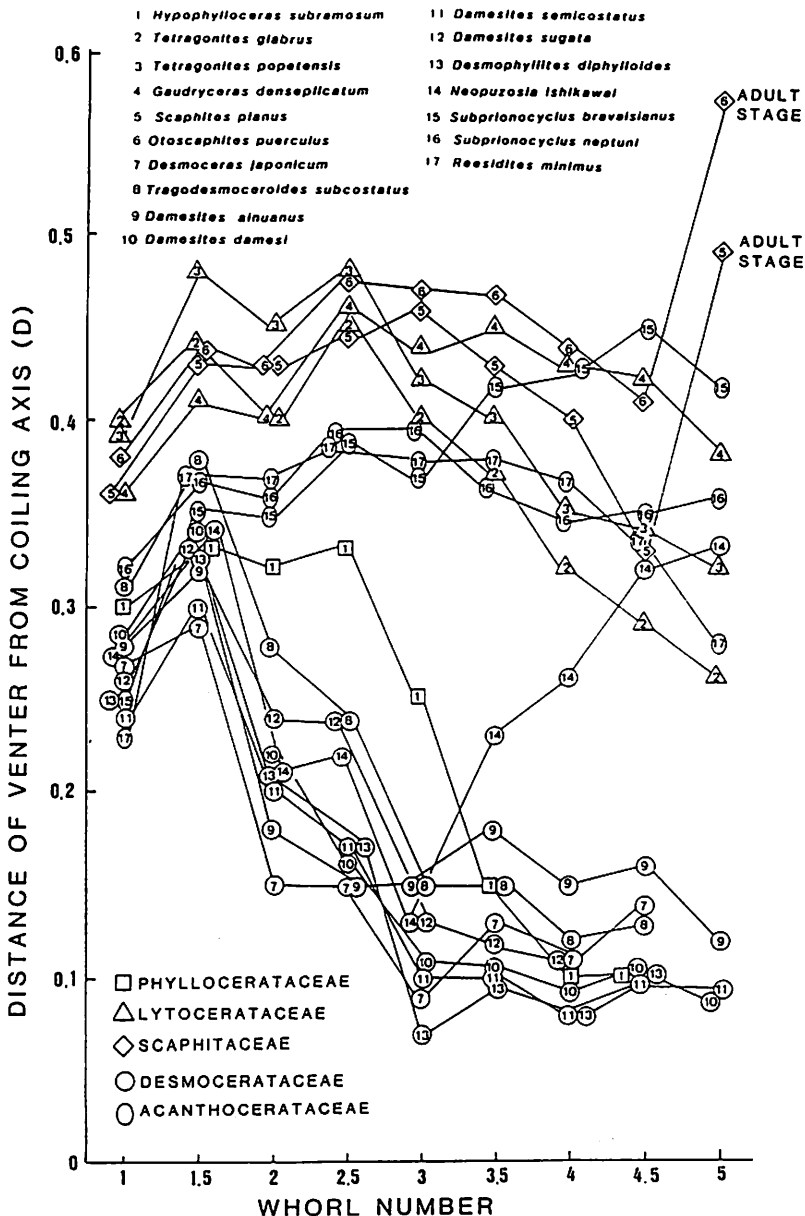

Figure 4.   Ontogenetic change of the parameter *D* in relation to whorl number for seventeen ammonite species. Sample mean at each stage is plotted for every species. In the third to fifth whorls, *D* parameters of the Phyllocerataceae and most Desmocerataceae are much smaller than those of other superfamilies.

smallest in the species of the Phyllocerataceae and the Acanthocerataceae, intermediate in the Desmocerataceae, and largest in the Lytocerataceae and the Scaphitaceae. Ontogenetic change of parameter F also varies greatly among the species examined (Figure 6). It increases rapidly with age in *Hypophylloceras* or slowly in *Tetragonites, Gaudryceras* and *Reesidites*. F parameters of most desmoceratids are relatively large (*ca*. 0.30) and remain almost constant during onto-

1 *Hypophylloceras subramosum*
2 *Tetragonites glabrus*
3 *Tetragonites popetensis*
4 *Gaudryceras densepiicatum*
5 *Scaphites planus*
6 *Otoscaphites puerculus*
7 *Desmoceras japonicum*
8 *Tragodesmoceroides subcostatus*
9 *Damesites sinuanus*
10 *Damesites damesi*
11 *Damesites semicostatus*
12 *Damesites sugata*
13 *Desmophyllites diphylloides*
14 *Neopuzosia ishikawai*
15 *Subprionocyclus bravaisianus*
16 *Subprionocyclus neptuni*
17 *Reesidites minimus*

☐ PHYLLOCERATACEAE
△ LYTOCERATACEAE
◇ SCAPHITACEAE
◯ DESMOCERATACEAE
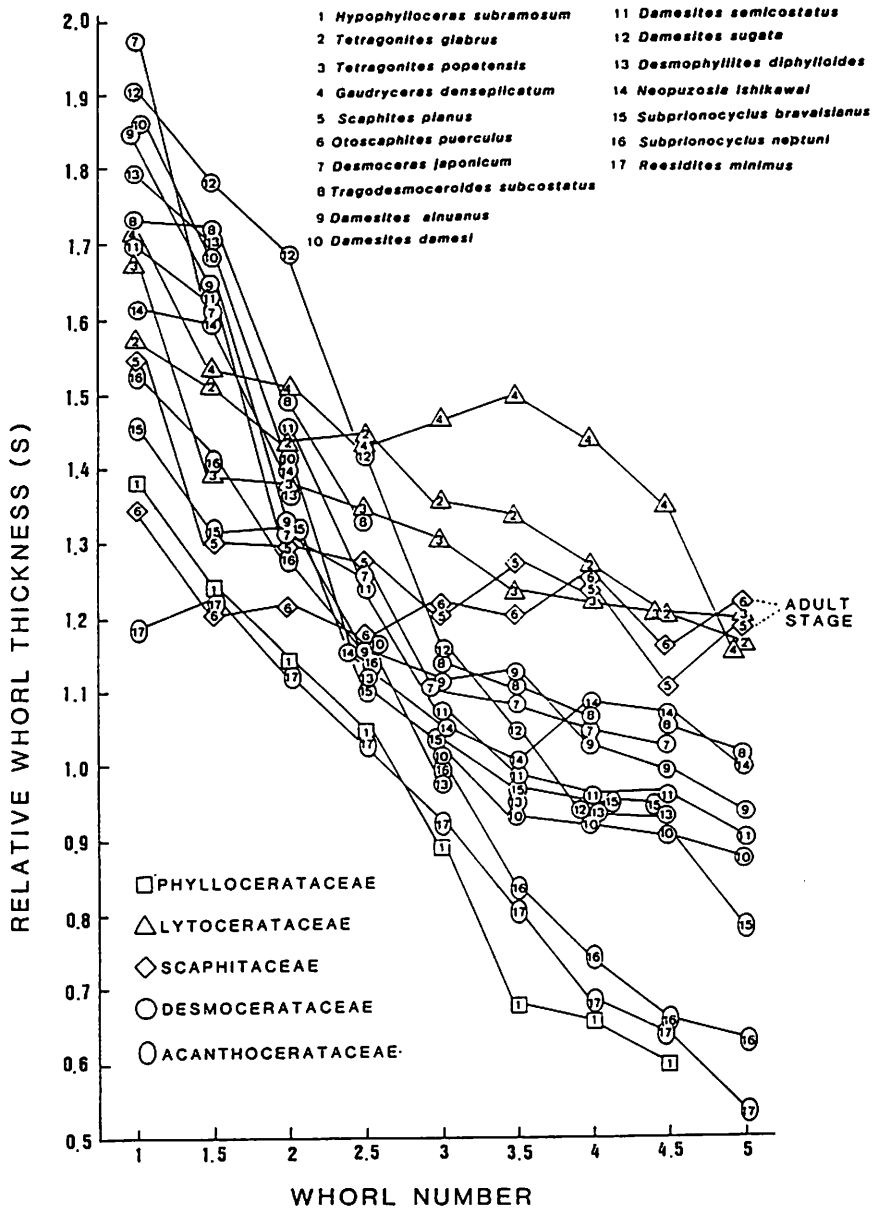◯ ACANTHOCERATACEAE·

Figure 5. Ontogenetic change of the parameter S in relation to whorl number for seventeen ammonite species. Sample mean at each stage is plotted for every species. In every species S decreases with age, but the interspecific variation at the same whorl stage is fairly large.

geny. The only exception is *Neopuzosia ishikawai* with F gradually decreasing.

Intra- and interspecific variation—Shell shape variation in the species examined is summarized in two sets of *S-D* and *W-F* diagrams at different growth stages (Figures 7—8). In every species, intraspecific variation of geometric parameters is larger in the early stage than in the later stage.
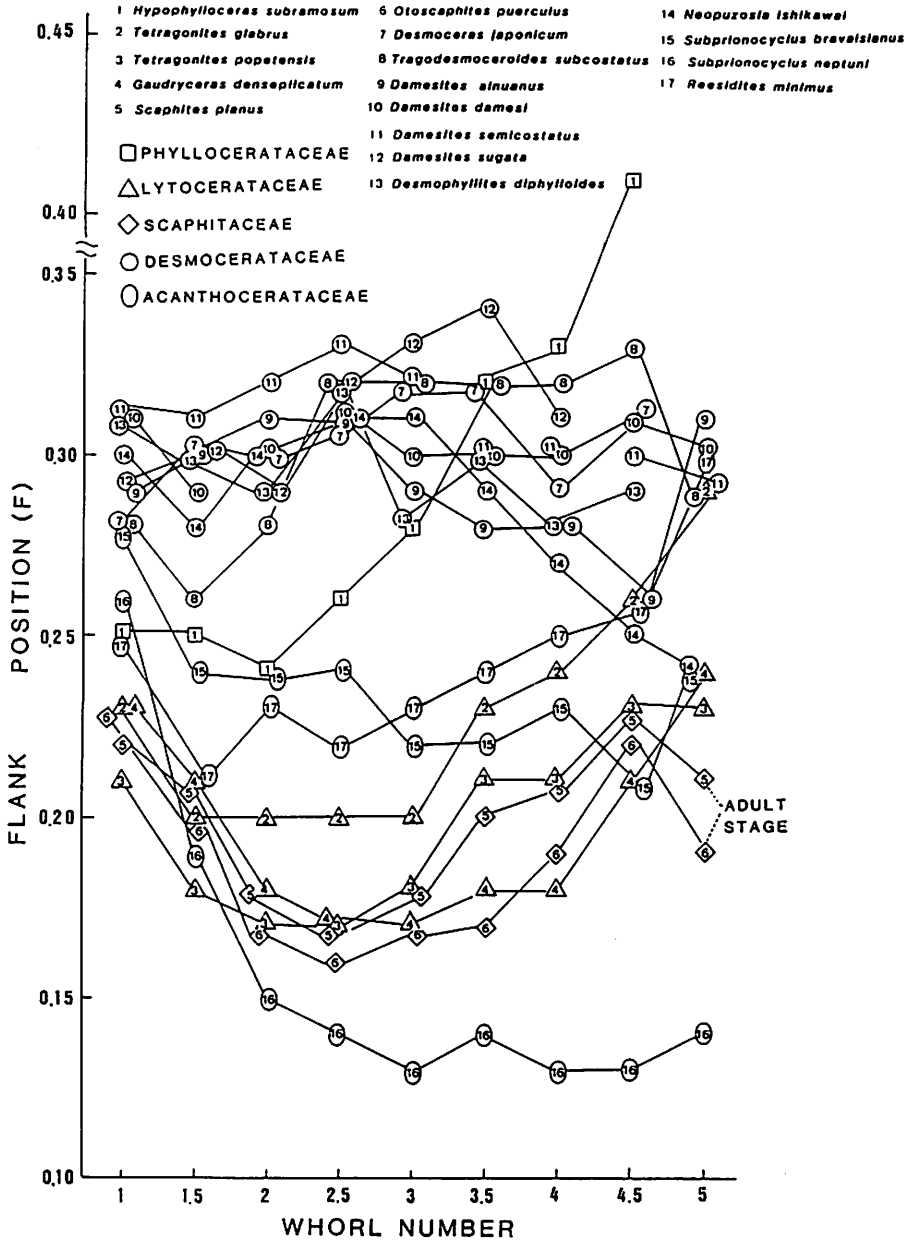

Figure 6. Ontogenetic change of the parameter F in relation to whorl number for seventeen ammonite species. Sample mean at each stage is plotted for every species. Wide interspecific variation can be observed among the species examined at the same whorl stage.
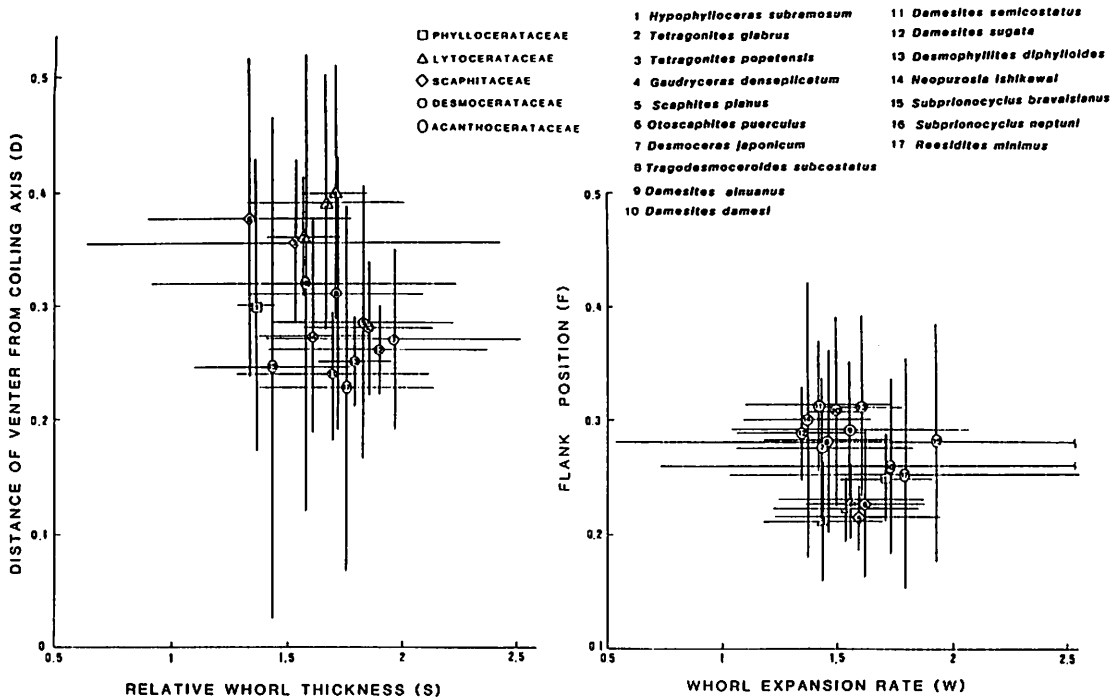
Figure 7. Variation of the geometric parameters at the end of the first whorl in seventeen ammonite species. Sample mean and two standard deviations (horizontal and vertical lines) are indicated for each species. The two figures indicate similarity in juvenile shell morphology among the Cretaceous ammonites.

The species examined do not show significant differences in juvenile shell morphology (Figure 7). In contrast, they show a large interspecific variation in the later growth stage (Figure 8). The coefficients of variation of parameters S and D at the fourth whorl stage are usually largest in the Acanthocerataceae and Scaphitaceae, intermediate in the Lytocerataceae, and smallest in the Phyllocerataceae and Desmocerataceae, at least for the samples examined (Table 2). Geometric parameters of adult *Placenticeras intercalare* and *Hypophylloceras subramosum* are very similar to those of *Nautilus pompilius* (Figure 8).

Discussion

This study demonstrates that the shells of Cretaceous ammonite species examined differ in coiling at all ontogenetic stages. Coefficients of variation of parameters at a given growth

stage also vary greatly among these species (Table 2). Interspecific difference in the sample mean is especially conspicuous for parameters S, D and F. Based on these observations we consider the morphologic adaptations of the high variation in shell geometry. Truly remarkable intraspecific variability has been recognized in many near-shore-type Acanthocerataceae and Hoplitaceae, such as in species of *Acanthoceras* (Kennedy and Hancock, 1970), *Collignoniceras* (Kennedy et al., 1980), *Pseudotissotia* and *Wrightoceras* (Hirano, 1983), and *Neogastroplites* (Reeside and Cobban, 1960). In contrast, shell shape variation is much smaller in the offshore-type ammonites investigated such as *Gaudryceras* (Hirano, 1975, 1978) and *Tetragonites* (Y. Shigeta's unpublished data). Two major adaptive strategies have been considered for the function of ammonite external shell morphology: (1) protective (defensive) in thick-shelled whorls with spines or prominent ribs preventing shell breakage by predators
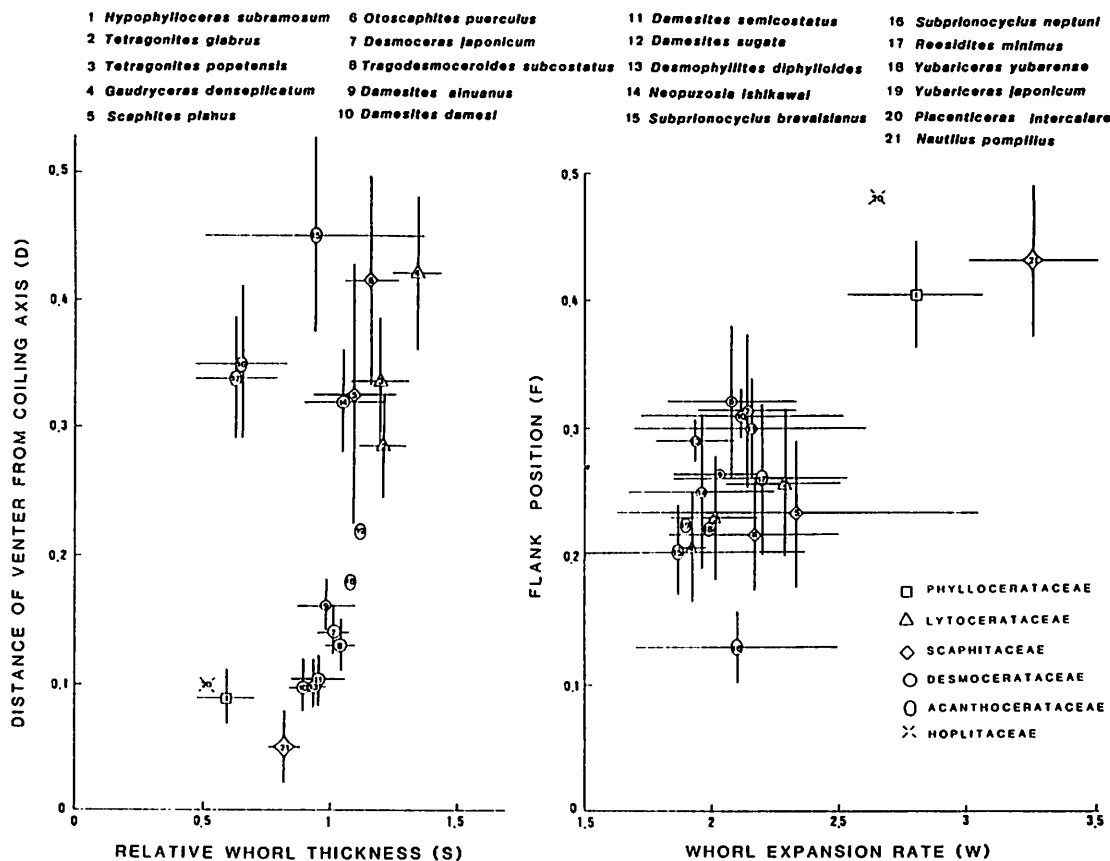
Figure 8. Variation of the geometric parameters at the middle of the fifth whorl in seventeen ammonite species. Data of adult shells of three ammonite species (nos. 18–20) and *Nautilus pompilius* are also indicated for comparison. Sample mean and two standard deviations (horizontal and vertical lines) are indicated for each species. Intraspecific variation of parameters *S* and *D* is especially small in the Phyllocerataceae and the Desmocerataceae. *Hypophylloceras* (no. 1), *Placenticeras* (no. 20) and modern *Nautilus* (no. 21) possess similar geometric parameters.

(Westermann, 1971; Ward, 1980) and (2) hydromechanical for increasing swimming ability (Chamberlain, 1976, 1981; Chamberlain and Westermann, 1976). These two strategies are largely exclusive because hydromecanical efficiency decreases as the external ornament becomes more prominent (Kummel and Lloyd, 1955; Chamberlain and Westermann, 1976; Chamberlain, 1981). Quantitative analysis of the relations between shell geometry and drag coefficients in the ectocochiliate cephalopod shells has been done by Chamberlain (1976, 1981). He used cephalopod scale models with round-whorl sections ($S = 1$) and smooth surfaces, and measured drag coefficients acting on the shells at various water velocities. For aquatic animals the drag force acting on a swimming body can be approximated by the following equation.

$$D_F = 1/2\rho \, V^2 A \, C_D,$$

where D_F is drag force, ρ is fluid density, V is swimming velocity, A is equivalent to a body size (shell size in this case), and C_D is the drag coef-

Table 2. Coefficients of variation of the geometric parameters at the middle of fifth whorl in the seventeen ammonites and *Nautilus pompilius*.

Species	Geometric parameters			
	W	S	D	F
Phyllocerataceae				
Hypophylloceras subramosum	4.79	5.00	7.44	5.19
Lytocerataceae				
Tetragonites glabrus	5.04	4.17	7.10	6.17
Tetragonites popetensis	4.48	5.00	7.37	5.13
Gaudryceras denseplicatum	1.53	3.73	7.33	5.98
Scaphitaceae				
Scaphites planus	15.34	8.18	15.59	12.45
Otoscaphites puerculus	8.03	4.31	9.88	10.14
Desmocerataceae				
Desmoceras japonicum	4.57	2.45	8.21	9.89
Tragodesmoceroides subcostatus	6.20	3.05	7.76	8.68
Damesites ainuanus	4.18	5.98	8.67	8.45
Damesites damesi	9.36	3.57	5.72	4.28
Damesites semicostatus	5.73	3.37	7.18	7.55
Damesites sugata	7.53	6.95	7.62	3.33
Desmophyllites diphylloides	3.65	3.12	4.38	5.94
Neopuzosia ishikawai	3.36	5.42	9.99	6.60
Acanthocerataceae				
Subprionocyclus bravaisianus	13.66	23.40	8.33	8.78
Subprionocyclus neptuni	9.56	13.85	8.68	10.85
Reesidites minimus	7.97	12.31	7.12	11.58
Nautilaceae				
Nautilus pompilius	4.01	3.87	18.62[*]	6.91

* Umblicus is covered by callus.

ficient (Chamberlain, 1976). If we consider that the fluid density of seawater and shell size are constant, the above equation is rewritten as follows.

$$V = \sqrt{2D_F/C_D}$$

Assuming that D_F is constant, V increases as C_D decreases. Thus, C_D is an index of a shell's hydrodynamic efficiency (Chamberlain, 1976).

Chamberlain (1976, 1981) has demonstrated experimentally that at the same shell size C_D varies greatly with geometry. C_D decreases as either W, D or S decrease. S causes the most pronounced changes in C_D, and the degree of shell compression should be a key factor in cephalopod adaptive design. The effect of F on C_D was not demonstrated, but Chamberlain (1980) suggested that within a suite of low S shells, lower drag coefficients will occur when W and D are low, and F is high.

Hydromechanically efficient cephalopod shells are high-shouldered, involute shells (Chamberlain, 1981). Our adult shells of *Hypophylloceras subramosum* (W = 2.8, S = 0.6, D = 0.1, F = 0.4; Figures 2-6A—B) and *Placenticeras intercalare* (W = 2.7, S = 0.5, D = 0.1, F = 0.5; Figures 2-7A—B) are closely allied to this morphotype. The shell shape rather resembles that of *N. pompilius*, whose drag coefficient (in 30° attitude) is 0.48 (Chamberlain, 1976), and a similar or smaller drag coefficient is indicated for the adult stage.

Seven desmoceratines also have relatively low D and high F, but their S parameters are large (ca. 1.0), at least for the fourth and fifth whorls. In the adult stage (six whorls; 100 mm shell diameter) the whorls of Damesites semicostatus are narrowly umblicate and strongly compressed (low S) with a prominent keel (see Figures 2-5A–B). This implies that the shell of this species tends to be well streamlined. Shells of the three lytocerataceans (Figures 2-4A–B) may be compared with the model no. 26 of Chamberlain (1976, table 1). The shells of the three collignoniceratids, Subprionocyclus bravaisianus, S. neptuni and Reesidites minimus, are fairly compressed (S = 0.6–0.7 at fourth to fifth whorls), but D is large. These Turonian collignoniceratids are very closely interrelated, and possibly belong to a single clade (Matsumoto, 1965; Reyment, 1975, 1982; Obata et al., 1979). The oldest species, the middle Turonian Subprionocyclus bravaisianus (Figures 2-2A–B), has larger D and S than the latest, the late Turonian R. minimus. The middle to late Turonian S. neptuni has intermediate values. In correspondence to this, surface ornament (tubercles and ribs) tends to weaken from S. bravaisianus to R. minimus. As Obata et al. (1979) have briefly mentioned, these trends of shell form and ornamentation can be interpreted as adaptation to increasing hydromechanical efficiency. Two species of Yubariceras possess robust depressed shells, with a pair of five rows of tubercles (Figures 2-1A–B). The large S (ca. 1.1) and small F (ca. 0.2) parameters and the coarse ornamentation suggest that both species were poor swimmers. The coiling parameters in the immature stage of scaphitids are similar to those of normally coiled species, but possess extremely large parameters W (ca. 4.0) and D (ca. 0.5) at maturity (Figures 2-3A–B). Their shell type corresponds to Chamberlain's (1976, Table 1) model no. 29, whose drag coefficient is 0.81. These lines of evidence suggest that the scaphitids changed their way of life during ontogeny. In all probability, they abandoned an active mode of life at maturity (Tanabe, 1977).

In conclusion, the results of this study indicate a wide variety of hydromechanical adaptations among Cretaceous ammonites confirming the conclusion of previous authors (e.g. Raup and Chamberlain, 1967; Ward, 1980, 1983; Chamberlain, 1981; Saunders and Swan, 1984) based on W-D analysis of many ammonites and nautiloids. According to Chamberlain's W-D contour maps (1981, figs. 18–19), the range of the morphologic variation of the Ammonoidea is much wider than that of the Nautiloidea. Furthermore, the range of geometric variation in the Mesozoic Ammonoidea is wider than in the Paleozoic, and the main adaptive peak shifts larger D values. In our material, the W and D values of the seven desmoceratines, Hypophylloceras subramosum, and the well-streamlined Placenticeras intercalare all plot near the adaptive peaks of the post-Jurassic Nautilida and the Paleozoic Ammonoidea in the diagrams of Chamberlain (1981, figs. 18–19). W and D data of the other species resemble those of the common Jurassic-Cretaceous ammonites (Ward, 1980, figs. 3–4; Chamberlain, 1981, fig. 19). Coarsely ornamented planispiral ammonites with robust ribs, spines and tubercles became very common in the early Cretaceous, and during the middle to late Cretaceous the number of heteromorph and strongly ornate species comprised more than 50% of the total species (Ward, 1981, 1983, 1986). Most of these morphotypes had larger D and S parameters than streamlined shells (Figure 2; Ward, 1980). Ward (1981) speculated that the increase of coarsely ornamented species in the Cretaceous was a defensive adaptation against shell-crushing predators. In the Upper Cretaceous of Hokkaido, occurrences of coarsely ornated ammonites such as acanthoceratids and collignoniceratids are restricted to the nearshore, coarse-grained lithofacies (Tanabe, 1979). Complete preservation of the aperture and clustered occurrences at a single locality supports the autochthonous origin of these fossil assemblages (Tanabe et al., 1978; Tanabe, 1979). This supports the predation interpretation. We believe that most heavily ornamented ammonites were poor swimmers, and that their possible mode of life was mobile benthic or nektobenthic. Con-

cerning the paleoecology of heteromorphs, opinions remain divided; some believe that they were planktonic (Trueman, 1941; Ward, 1976, 1979; Ward and Westermann, 1977), other that they were benthic (Scott, 1940; Ziegler, 1967; Tanabe *et al.*, 1981). The former interpretation is based mainly on the hydrostatic properties of the shells, and the latter on field occurrence. The mode of coilings and ornamentation in the Cretaceous heteromorphs are, however, quite variable, and a single mode of life may not have applied to all groups. Heteromorphs with weakly ornamented and straight shells (*e.g. Baculites*) probably could swim, while the presence of different coiling modes during ontogeny in some nostoceratids (*e.g. Eubostrychoceras* and *Madagascarites*) suggest the loss of swimming ability, even if they were neutrally buoyant (personal communication with T. Okamoto). Further data on comparative morphology, anatomy and field occurrence are needed to clarify the above problem.

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白亜紀アンモナイト数種の成長に伴う殻形変異と流線効果：北海道産の後期白亜紀アンモナイト17種の集団標本を用いて，成長に伴う殻形パラメータの変化を比較検討した。検討したパラメータは，Raup によって提唱された螺環拡張率 (W)，螺環被覆率 (D)，螺環の高さに対する幅の比 (S)，側面の相対的位置 (F) の4つである。これらのうち，D, S および F は，幼期には種間で大差ないが，成長に伴って大きく異なるようになる。成年期には，表面装飾の乏しいフィロセラス超科やデスモセラス超科の種では S や D は小さく，かつそれらの種内変異値も小さい。逆に，表面装飾の著しいアカントセラス超科や異常巻のスカフィテス科の種では，S, D は大きく，それらの種内変異値は大きい。従来の流体実験の結果では，S, D は流線効果に大きく関与し，それらの小さい平滑型の類は小さい抗力係数を持つことがわかっている。一方強い刺や肋は，流線効果にはマイナスでも捕食者に対する防御として効果的であったと考えられる。以上のことから，白亜紀アンモナイト類に認められる殻形の大きな変異は，多様な生活様式と対応した適応形態を反映していると推察される。　　　　　　　　　　　　　　　　棚部一成・重田康成