

Post-hatching early life history of Cretaceous Ammonoidea

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Post-hatching early life histories in Cretaceous Ammonoidea are discussed on the basis of density calculations of the shells in 71 species belonging to four separate suborders. The calculation was made under the assumption that a newly hatched ammonoid had a gas-filled chamber and a succeeding body-filled whorl terminating at the primary constriction. The results show that the density of the species examined at the hatching stage is almost constant and is relatively smaller than that of seawater, i.e. the animals are positively buoyant. This fact strongly suggests a planktic mode of life. In all species, the density increases gradually with growth and attains neutral buoyancy at 2.0–2.5 mm in shell diameter. Thus, most ammonoids probably changed their mode of life from planktic to nekto planktic or nekto benthic at this critical point. The rare occurrence of newly hatched specimens (ammonitellas) in many ammonoid assemblages may also support this interpretation. Planktic duration of a newly hatched ammonoid might be regulated by the animal's density at hatching, shell growth pattern, cameral volume (or hatching size), and rate of cameral-liquid removal (or siphuncle diameter). The latter two seem to be very important factors in determining the biogeographical framework of species, as demonstrated in the Tetragonitaceae.

□ Cretaceous, Ammonoidea, density calculation, early life history.

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Every ammonoid possesses a peculiar shell, termed ammonitella, consisting of an initial chamber (protoconch) and approximately one planispiral whorl terminating at the primary constriction. The ammonitellas of Mesozoic ammonoids differ markedly from the subsequent whorls in the micro-structure of the shell wall and the presence of tuberculate micro-ornamentation without growth lines. Most recent workers considered that the ammonitella was formed within an egg-capsule as an embryonic shell, and that the ammonoid hatched directly without a post-hatching larval stage like extant cephalopods (Kulicki 1974, 1975, 1979; Birkelund 1967, 1981; Drushchits *et al.* 1977; Tanabe *et al.* 1980; Bandel *et al.* 1982; Landman 1982).

The mode of life of newly hatched ammonoids has been discussed based on the morphology of the initial chamber and ammonitella. Some workers speculated that the initial chamber would have acted as a float and that the newly hatched ammonoid would have had a planktic mode of life with the aid of a gas-filled, bulbous and relatively large initial chamber (Kulicki 1974, 1979; Birkelund & Hansen 1974; Drushchits *et al.* 1977; Landman 1985). Tanabe *et al.* (1979) and Tanabe & Ohtsuka (1985) found a positive linear relationship between the initial chamber and ammonitella diameters and a negative linear relationship between the total rotation angle and whorl expansion rate of the ammonitella among some Mesozoic

ammonoids. These authors suggested a planktic mode of life in newly hatched ammonoids. But this hypothesis has not been considered from the viewpoint of the density of the early post-hatching shells.

In this paper, I present a detailed scheme of the early life history of Cretaceous ammonoids, relying on the calculation of shell density and morphological analysis in 71 species in which the change of mode of life from planktic to nekto-benthic during the early postembryonic stage is emphasized. This interpretation is further considered with regard to data on the mode of occurrence of fossil assemblages. I also discuss the dispersal property of ammonoids from the paleobiogeographical viewpoint.

Material

A total of 71 species belonging to four Cretaceous suborders (nine superfamilies) were used for buoyancy calculation of the shells and biometrics (Table 1). These species are represented by individual specimens. The specimens utilized were preserved in calcareous nodules embedded in Cretaceous (Barremian–Aptian, Cenomanian–Maastrichtian) rocks of Honshu (Choshi and Miyako areas) and Hokkaido (Soya, Embetsu, Saku, Haboro, Kotanbetsu, Tappu, Soeushinai,

Table 1. List of material. Major taxonomic positions from Wright (1981).

Species	Registered number	Locality	Horizon
Ammonitina			
1 <i>Desmoceras kossmati</i> Matsumoto	MM18916	Soeushinai, R81110	L. Cenomanian
2 <i>Desmoceras japonicum</i> Yabe	MM18917	Ikushumbetsu, Ik1100	L. Cenomanian
3 <i>Desmoceras ezoanum</i> Matsumoto	MM18918	Ikushumbetsu, Ik1100	L. Cenomanian
4 <i>Tragodesmoceroides subcostatus</i> Matsumoto	MM18919	Tappu, R4577	L. Turonian
5 <i>Damesites sugata</i> (Forbes)	MM18920	Haboro, RH2132	Coniacian
6 <i>Damesites semicostatus</i> Matsumoto	MM18921	Tappu, Kawakami	L. Santonian
7 <i>Damesites damesi</i> (Jimbo)	MM18922	Haboro, RH5049	L. Santonian
8 <i>Damesites hetonaiensis</i> Matsumoto	MM18923	Tomiuchi, H12	L. Maastrichtian
9 <i>Desmophyllites diphylloides</i> (Forbes)	MM18924	Soya, W7D	U. Campanian
10 <i>Puzosia orientalis</i> Matsumoto	MM18925	Tappu, R4577	L. Turonian
11 <i>Mesopuzosia pacifica</i> Matsumoto	MM18926	Tappu, R2110	M. Turonian
12 <i>Mesopuzosia yubarensis</i> (Jimbo)	MM18927	Tappu, R6951	Coniacian
13 <i>Kitchinites ishikawai</i> (Jimbo)	MM18928	Saku, T205	U. Santonian
14 <i>Microdesmoceras tetragonum</i> Matsumoto & Muramoto	MM18929	Ikushumbetsu, Ik1100	L. Cenomanian
15 <i>Bhimaites takahashii</i> Matsumoto	MM18930	Oyubari, Isojirou-zawa R.	M. Turonian
16 <i>Hauericeras angustum</i> Yabe	MM18931	Nukibetsu, Nioi-zawa R.	U. Santonian
17 <i>Anapachydiscus yezoensis</i> Matsumoto	MM18932	Kotanbetsu, RK0037	L. Santonian
18 <i>Eupachydiscus haradai</i> (Jimbo)	MM18933	Soya, W4A	L. Campanian
19 <i>Canadoceras kossmati</i> Matsumoto	MM18934	Saku, T313	L. Campanian
20 <i>Canadoceras mysticum</i> Matsumoto	MM18935	Soya, W7C	L. Campanian
21 <i>Teshioites</i> sp.	MM18936	Saku, Nio-gawa R.	L. Campanian
22 <i>Valdedorsella akuschaensis</i> (Anthula)	MM18937	Miyako, Matsushima	U. Aptian
23 <i>Pseudohaploceras nipponicus</i> (Shimizu)	MM18938	Miyako, Matsushima	U. Aptian
24 <i>Eogunnarites unicus</i> (Yabe)	MM18939	Tappu, Kanajiri-zawa R.	M. Cenomanian
25 <i>Marshallites compressus</i> Matsumoto	MM18940	Soeushinai, R81110	L. Cenomanian
26 <i>Yokoyamaoceras jimboi</i> Matsumoto	MM18941	Haboro, Sakasa-gawa R.	L. Santonian
27 <i>Metaplacenticeras subtilistriatum</i> (Jimbo)	MM18942	Soya, W7D	U. Campanian
28 <i>Mantelliceras japonicum</i> Matsumoto, Muramoto & Takahashi	MM18943	Ikushumbetsu, Ik1100	L. Cenomanian
29 <i>Calyoceras orientale</i> Matsumoto, Saito & Fukada	MM18944	Tappu, Kanajiri-zawa R.	M. Cenomanian
30 <i>Subprionocyclus neptuni</i> (Geinitz)	MM18945	Tappu, R4018	M. Turonian
31 <i>Subprionocyclus minimus</i> (Hayasaka & Fukada)	MM18946	Manji, SN2003	U. Turonian
32 <i>Protexanites minimus</i> Matsumoto	MM18947	Kotanbetsu, RK0037	L. Santonian
33 <i>Texanites kawasakii</i> (Kawada)	MM18948	Haboro, RH5049	L. Santonian
Ancyloceratina			
34 <i>Karsteniceras obatai</i> Matsukawa	MM18949	Choshi, Isejigaura	Barremian
35 <i>Hypacanthoplites subcornuerianus</i> (Shimizu)	MM18950	Miyako, Hiraiga	U. Aptian
36 <i>Diadochoceras nodosocostatiforme</i> (Shimizu)	MM18951	Miyako, Matsushima	U. Aptian
37 <i>Scaphites planus</i> (Yabe)	MM18952	Tappu, R4001	M. Turonian
38 <i>Scaphites yonekurai</i> Yabe	MM18953	Kotanbetsu, Horotate-zawa R.	Coniacian
39 <i>Scaphites pseudoequalis</i> Yabe	MM18954	Tappu, T1214	Coniacian
40 <i>Otoscapites puerculus</i> (Jimbo)	MM18955	Tappu, R4001	M. Turonian
41 <i>Otoscapites klamathensis</i> (Anderson)	MM18956	Tappu, T1214	Coniacian
42 <i>Otoscapites matsumotoi</i> Tanabe	MM18957	Tappu, R6951	Coniacian
Lytocerotina			
43 <i>Ga bbioceras michelianum</i> (d'Orbigny)	MM18958	Soeushinai, R81110	L. Cenomanian
44 <i>Parajaubetelle kawakitana</i> Matsumoto	MM18959	Soeushinai, R81110	L. Cenomanian
45 <i>Zelandites inflatus</i> Matsumoto	MM18960	Ikushumbetsu, Ik1100	L. Cenomanian
46 <i>Zelandites mihoensis</i> Matsumoto	MM18961	Haboro, Shirotiune-zawa R.	Coniacian
47 <i>Zelandites kawanoi</i> (Jimbo)	MM18962	Haboro, RH5049	L. Santonian
48 <i>Zelandites varuna</i> (Forbes)	MM18963	Naiba, N115	L. Maastrichtian
49 <i>Anagaudryceras buddha</i> (Forbes)	MM18964	Tappu, Kanajiri-zawa R.	M. Cenomanian
50 <i>Anagaudryceras limatum</i> (Yabe)	MM18965	Tappu, R6951	Coniacian
51 <i>Anagaudryceras yokoyamai</i> (Yabe)	MM18966	Kotanbetsu, RK0030	L. Santonian
52 <i>Anagaudryceras nanum</i> Matsumoto	MM18967	Soya, W7C	L. Campanian
53 <i>Anagaudryceras tetragonum</i> Matsumoto & Kanie	MM18968	Tomiuchi, H12	L. Maastrichtian
54 <i>Anagaudryceras matsumotoi</i> Morozumi	MM18969	Naiba, N110	L. Maastrichtian
55 <i>Eogaudryceras</i> aff. <i>aurarium</i> (Anderson)	MM18970	Soeushinai, R81110	L. Cenomanian
56 <i>Gaudryceras</i> aff. <i>stefaninii</i> Venzo	MM18971	Tappu, Kanajiri-zawa R.	M. Cenomanian
57 <i>Gaudryceras densepicatum</i> (Jimbo)	MM18972	Tappu, R2115	M. Turonian
58 <i>Gaudryceras tenuiliratum</i> Yabe	MM18973	Tappu, Kawakami	L. Santonian
59 <i>Gaudryceras striatum</i> (Jimbo)	MM18974	Embetsu, E42	U. Campanian
60 <i>Gaudryceras tombetsense</i> Matsumoto	MM18975	Furenai, Tonai-zawa R.	L. Maastrichtian
61 <i>Tetragonites</i> aff. <i>kitchini</i> (Krenkel)	MM18976	Tappu, Kanajiri-zawa	M. Cenomanian
62 <i>Tetragonites glabrus</i> (Jimbo)	MM18977	Soya, Higashiura	L. Turonian

Table 1, continued.

Species	Registered number	Locality	Horizon
63 <i>Tetragonites popetensis</i> Yabe	MM18978	Soya, W7C	L. Campanian
64 <i>Tetragonites minimus</i> Shigeta	MM18979	Soya, Higashiura	L. Turonian
65 <i>Pseudophyllites indra</i> (Forbes)	MM18980	Soya, W7D	U. Campanian
66 <i>Saghalinites teshioensis</i> Matsumoto	MM18981	Saku, Abeshinai-gawa R.	U. Campanian
Phylloceratina			
67 <i>Partschiceras japonicum</i> (Matsumoto)	MM18982	Soeushinai, R81110	L. Cenomanian
68 <i>Hypophylloceras velleidae</i> (Michelin)	MM18983	Tappu, Kanajiri-zawa R.	M. Cenomanian
69 <i>Hypophylloceras subramosum</i> (Shimizu)	MM18984	Kotanbetsu, RK0037	L. Santonian
70 <i>Hypophylloceras hetonaiense</i> (Matsumoto)	MM18985	Furenai, Tonai-zawa R.	L. Maastrichtian
71 <i>Phyllopachyceras ezoense</i> (Yokoyama)	MM18986	Haboro, RH5041	U. Santonian

Ikushumbetsu, Manji, Oyubari, Tomiuchi, Furenai and Nukibetsu areas) in Japan and of Sakhalin (Naiba area) in the Republic of Russia (Matsumoto 1942, 1965; Yoshida *et al.* 1959; Tanaka 1960; Matsumoto & Obara 1971; Matsumoto & Inoma 1975; Obata & Futakami 1975; Obata *et al.* 1975; Tanabe *et al.* 1977; Hirano *et al.* 1981; Matsumoto & Miyachi 1984; Sekine *et al.* 1985; Hanai *et al.* 1968; Toshimitsu 1988). I also used 58 specimens of *Tetragonites glabrus* (sample AT2106-2) preserved in a single calcareous nodule from Tappu area (Lower Turonian, Locality R6395 of Tanabe *et al.* 1977) for measurements of the actual volumes. The shell-size distribution was examined for specimens from a calcareous nodule (sample AT2106-1) obtained in Tappu

area (Locality R6395). All specimens are kept in the University Museum, University of Tokyo (UMUT).

Methods

Preparation

Each specimen was first cut and polished along the median plane, and subsequently the half specimen was cut vertically along the base of the proseptum (Fig. 1). The sectioned surface was etched with 5% acetic acid for a few minutes after polishing, and then an acetate peel was prepared by pressing a sheet of triacetylcellulose film (25 μm in thickness) onto the

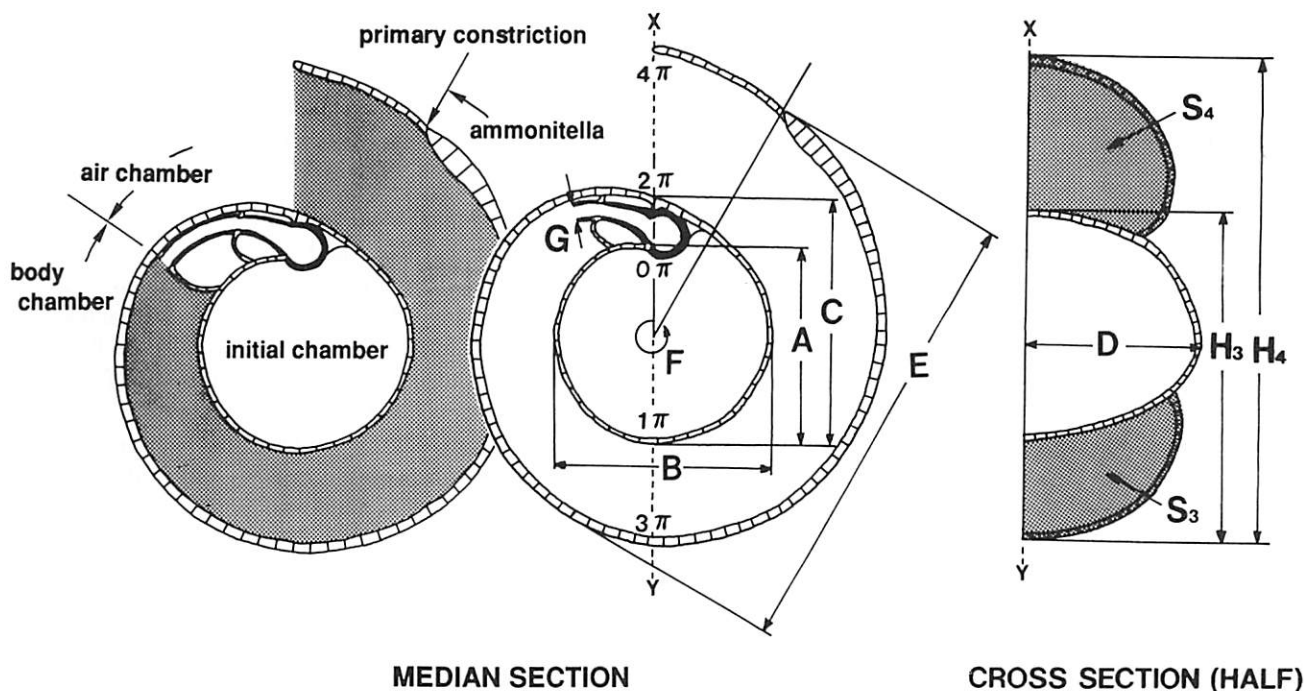


Fig. 1. Diagrams of the internal structure and measurements of the early ammonoid shell in median and cross-sections. □A, minimum initial chamber size; □B, intermediate initial chamber size; □C, maximum initial chamber size; □D, half breadth of initial chamber; □E, ammonitella size; □F, ammonitella angle; □G, siphuncular diameter; H_x , shell diameter at $X\pi$ stage; S_x , half area of whorl cross-section at $X\pi$ stage.

etched surface while it was flooded with acetone. Six parameters within the ammonitella (A–F in Fig. 1), siphuncular diameter at the connecting portion with the first nacreous septum (G), and shell diameters at 3 π and 4 π stages (H_3 , H_4 in Fig. 1) were measured on the peeled cross-section using a digital micrometer (accuracy $\pm 1 \mu\text{m}$) attached to a profile projector (Nikon Model V-16D). The half-shell cross-section (Fig. 1) was enlarged at 100 times on the screen of the profile projector and was traced on a paper. The whorl sectional area at each growth stage was measured by using the planimeter and calibrated to real value.

Buoyancy calculation for embryonic shell

Methods for calculation of shell volume. – Several equations have been developed to calculate the volume of ammonoid shells (e.g. Trueman 1941; Raup & Chamberlain 1967; Heptonstall 1970; Ward & Westermann 1977). All of these equations assume a constant whorl expansion rate (isometric shell growth) and a circular whorl section. As described below, however, the ammonoid shell is composed of a bulbous initial chamber and succeeding planispiral whorls with polyphasic allometric growth patterns. For this reason, a marked difference has been recognized between the volume calculated from these equations and the actual volume in some Mesozoic ammonoids (see Heptonstall 1970). In order to calculate the shell volume more accurately, the ammonoid shell should be divided into many parts throughout the ontogeny. I calculated the volume of the ammonoid shell as the sum of the volume of each of the partitions:

$$V = V_p + \sum V_i (i = 3 \text{ to } j) \quad (1)$$

where V is the total volume, V_p is the volume of the initial chamber, V_i is the volume of the whorl between $i\pi$ and $i-1\pi$ in rotational angle, and j is the total rotation angle of the specimen.

In volumetry, the initial chamber was divided into three parts, 0–1.0 π , 1.0–1.5 π and 1.5–2.0 π in rotation angle, and the volume in each part (V_{p1} , V_{p2} , V_{p3}) was approximated as a part of an ellipsoid (Fig. 1). Three radii of each part are P_1 , P_1 , P_4 for the first one, P_1 , P_2 , P_4 for the second one and P_2 , P_3 , P_4 for the third one, respectively, where $P_1 = A/2$, $P_2 = B - P_1$, $P_3 = C - P_1$ and $P_4 = D$. Thus, the volume of initial chamber (V_p) is given as:

$$V_p = V_{p1} + V_{p2} + V_{p3} \quad (2)$$

As to the succeeding whorls, the increasing rate of the volume (dV) is represented by the following formula.

$$dV = S R d\theta \quad (3)$$

where S is the area of whorl cross-section, R is the radius vector from the coiling center to the whorl center defined as half point of whorl height, θ is the rotational angle and d is the increase of rotational angle. According to Trueman (1941),

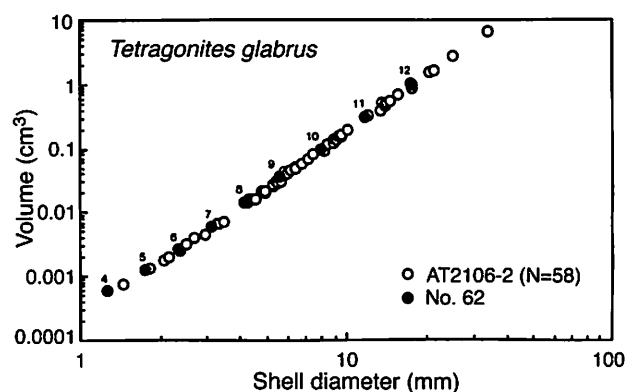


Fig. 2. Scatter plot of mathematically calculated volumes of specimen No. 62 (UMUT MM18977) at different growth stages and of the measured volumes of 58 specimens (AT2106-2 sample, UMUT MM18987) versus shell diameter in *Tetragonites glabrus* from the Lower Turonian of the Tappu area, Hokkaido. The numbers beside each black circle indicate growth stages (π) of specimen No. 62. This diagram shows a close approximation between the volumes obtained by different methods.

the relationship between S and R in many ammonites can be approximated by the following equation.

$$S R = b \exp^{a\theta} \quad (4)$$

where a is defined as the volume expansion rate and b is a constant. Using these relationships (or equations), I calculated the volume of a given half whorl by the following equation:

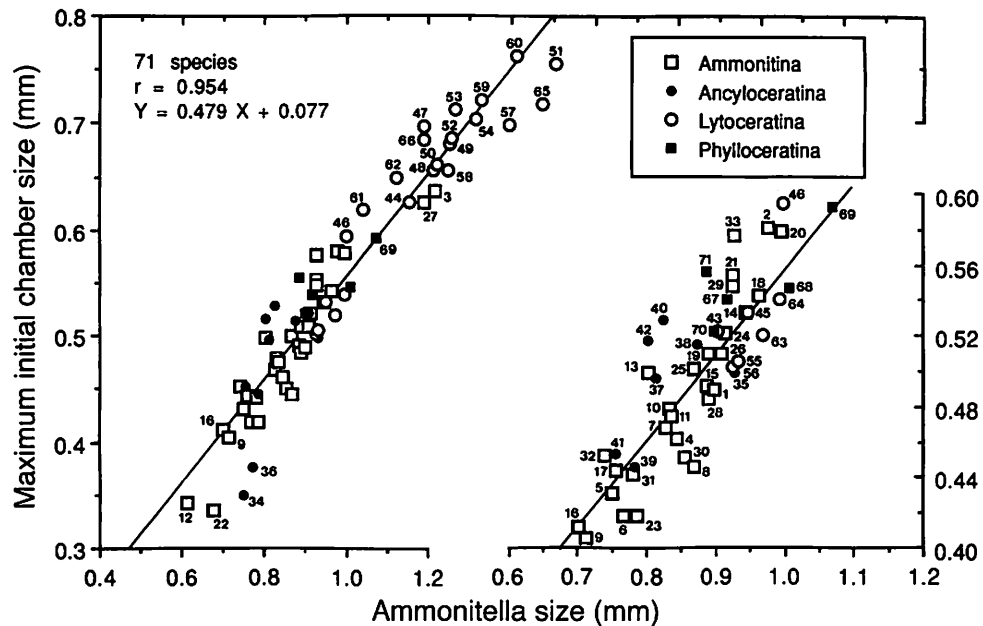
$$V = \int_0^x b \exp^{a\theta} d\theta \quad (0 < X < 1\pi) \quad (5)$$

To test the accuracy of the above equations, I compared the computed volumes of one specimen of *Tetragonites glabrus* at different stages with the actual volumes of many specimens of the same species (Fig. 2). The comparison shows a close approximation between the two.

Volume of shell material. – Volume ratio of shell material to whorl was presumed from the data on biometrics and volume calculation (Eq. 5) in a well preserved specimen of *Tetragonites glabrus* (UMUT MM18977). The volume of the shell material, except for septa, is estimated to be about 8% of the volume of the whorl, because the shell thickness (ST) is about 2% of whorl height (WH) ($ST = 0.020 WH^{1.021}$, $r = 0.998$).

The total rotation angle from the prosepium to the 68th septum (last septum in the specimen) is 1831° and the average interval of septa is 27° in rotation angle. The surface area of a septum is estimated to be three times the area of whorl cross-section, because the length of the simplified suture line that represents a pattern of major fold of septum is about three times the circumference of the whorl. The volume ratio of septum to camera at differential growth stages ranges from 12 to 16%, assuming that the interval of septa is 27° in rotation angle, the surface area of a septum is three times the area of the whorl cross-section, and the thickness of a septum is 2% of

Fig. 3. Plot of maximum initial chamber size versus ammonitella size for the 71 ammonoid species examined. The numbers correspond to those in Table 1. The dense cluster of points is enlarged to the right to make it possible to identify the individual measurements.



whorl height. So, I adopt the average value, 14%, as the volume ratio of septum to camera in all the species examined.

Density of the shell material, tissue and seawater. – A number of different values have been cited for the density of ammonoid shell material. Trueman (1941) and Raup & Chamberlain (1967) used 2.94 g/cm³ for the density of the shell material as pure aragonite. Meanwhile, Reymont (1958) estimated it as 2.62 g/cm³ based on the presence of organic matrix (conchiolin) surrounding the aragonite crystals in the shell nacre as in the shells of Recent *Nautilus* (Stenzel 1964). This value (2.62) has been applied by many authors (Heptonstall 1970; Tanabe 1975, 1977; Ward & Westermann 1977; Saunders & Shapiro 1986; Okamoto 1988), and is also used in this study.

The soft-tissue density of living *Nautilus* was measured as 1.067 g/cm³ for *Nautilus macromphalus* by Denton & Gilpin-Brown (1966), 1.055 g/cm³ for *N. belauensis* and *N. pompilius* by Saunders & Shapiro (1986). I used 1.067 g/cm³ for the soft-tissue density of ammonites according to Denton & Gilpin-Brown (1966). The density of seawater was regarded as 1.026 g/cm³.

Lengths of air chamber and body chambers. – Observations on the preserved ammonitellas (embryonic shells) in *Scaphites* and *Baculites* suggest that ammonoids hatched immediately after the secretion of the first septum, the proseptum (Smith 1901; Drushchits & Khiami 1970; Landman 1982, 1985, 1988). Similar conditions are recognized in ammonitellas of some Paleozoic Goniatitida (K. Tanabe, personal communication). Although minute ammonite shells with several septa have also been reported as embryonic shells (Wetzel 1959; Kulicki 1979; Bandel 1982), they are now regarded as post-hatching specimens with incomplete body chambers (Land-

man 1985). I, therefore, assumed that all species examined had a gas-filled initial chamber and a succeeding body-filled whorl terminating at the primary constriction at the stage of hatching.

In calculating the density of a living ammonoid at the post-hatching stage, I assumed several values of body-chamber length with the range of ammonitella angle plus or minus 0.15 π , because exact measurements of its length were very difficult. Cameral fluid was not taken into consideration in the density calculation at either hatching or post-hatching stages.

Results

Initial chamber and ammonitella size. – In the 71 species examined, the maximum initial chamber size (C in Fig. 1) ranges from 0.336 mm (*Valdedorsella akuschaensis*) to 0.763 mm (*Gaudryceras tombetsensis*) and the ammonitella size (E in Fig. 1) from 0.614 mm (*Mesopuzosia yubarensis*) to 1.512 mm (*Anagaudryceras yokoyamai*). The ammonitella size is generally large (ca. 0.9–1.5 mm) in the Lytoceratina, intermediate (0.8–1.1 mm) in the Phylloceratina, and relatively small (ca. 0.6–1.2 mm) in the Ammonitina and Ancyloceratina, although it is markedly variable among species of the same suborder. There is a statistically significant positive linear relationship between the maximum initial chamber and ammonitella sizes in the species examined (Fig. 3). This suggests that the size ratio of initial chamber to ammonitella is almost constant among many ammonoids. A similar relationship has already been obtained in many Mesozoic ammonoids (Tanabe *et al.* 1979; Tanabe & Ohtsuka 1985; Landman 1987).

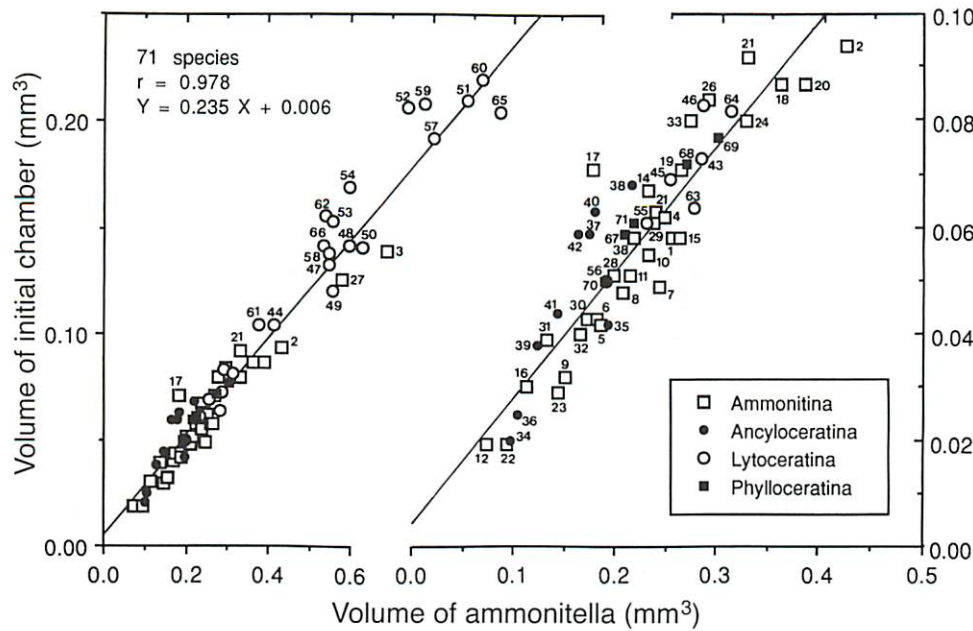


Fig. 4. Plot of volume of initial chamber versus volume of ammonitella for the 71 ammonoid species examined. The numbers correspond to those in Table 1. The dense cluster of points is enlarged to the right to make it possible to identify the individual measurements.

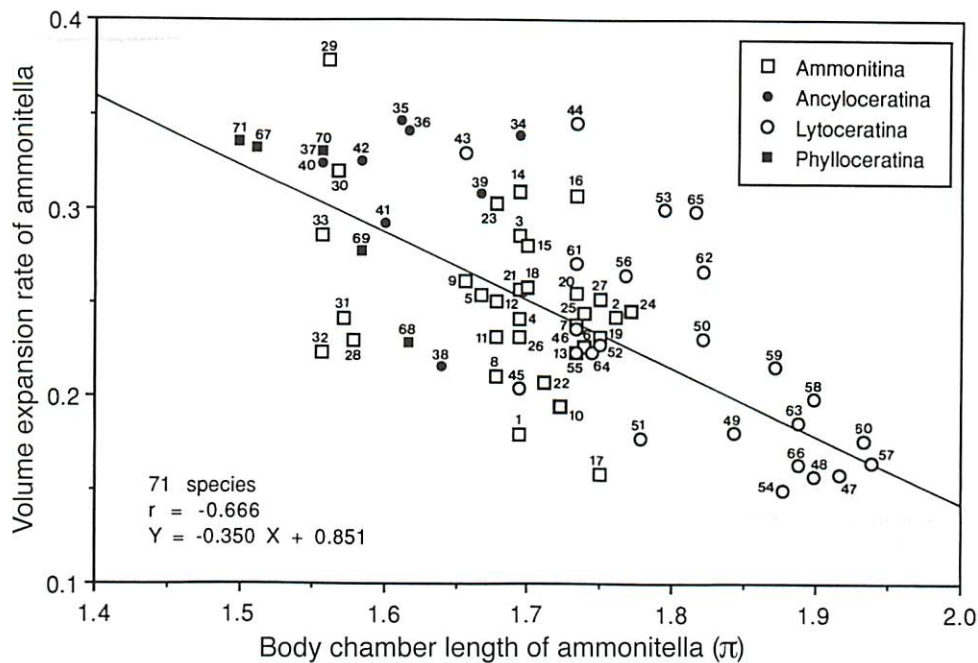


Fig. 5. Plot of volume expansion rate at 3–4 π stage versus body-chamber length of ammonitella for the 71 ammonoid species examined. The numbers correspond to those in Table 1.

Initial chamber and ammonitella volume. – The volume of the initial chamber ranges from 0.019 mm³ (*Mesopuzosia yubarensis*, *Valdedorsella akuschaensis*) to 0.220 mm³ (*Gaudryceras tombetsensis*) and that of ammonitella from 0.074 mm³ (*Mesopuzosia yubarensis*) to 0.962 mm³ (*Pseudophyllites indra*). There is a statistically significant positive linear relationship between the volumes of initial chamber and ammonitella (Fig. 4). This indicates that the volume ratio of initial

chamber to ammonitella is almost constant (≈ 0.24) among the Cretaceous ammonoids.

Body-chamber length of the ammonitella. – The body chamber length of the ammonitella (F in Fig. 1) varies markedly among the species examined, ranging from 1.500 π (*Phyllopacercas ezoense*) to 1.939 π (*Gaudryceras denseplicatum*) in rotation angle. This has a weak negative linear relationship with the

Fig. 6. Plot of body-chamber length of ammonitella versus ammonitella size for the 71 ammonoid species examined. The numbers correspond to those in Table 1.

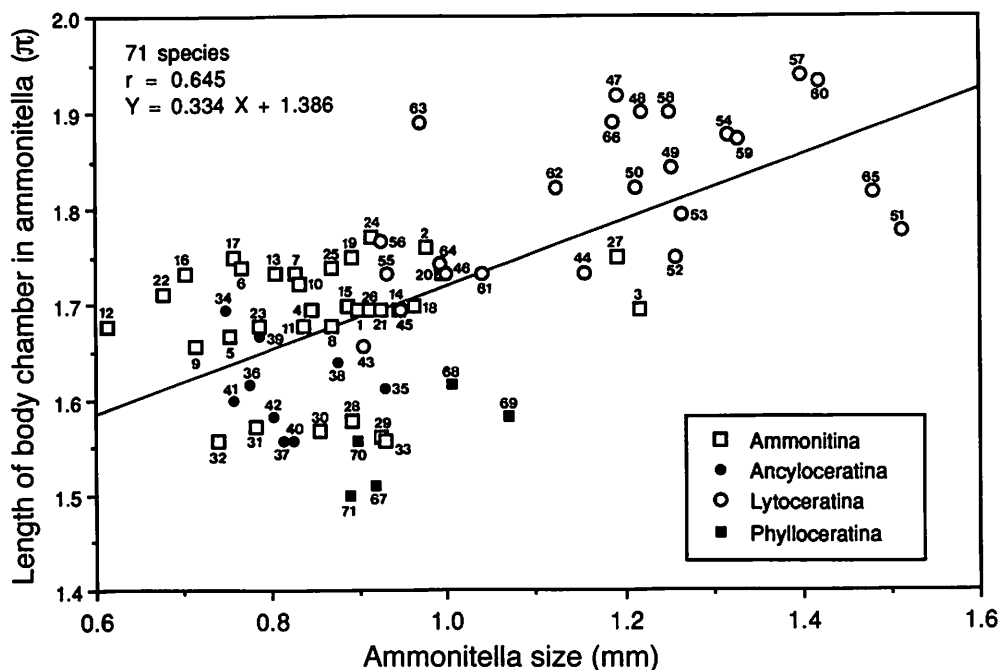
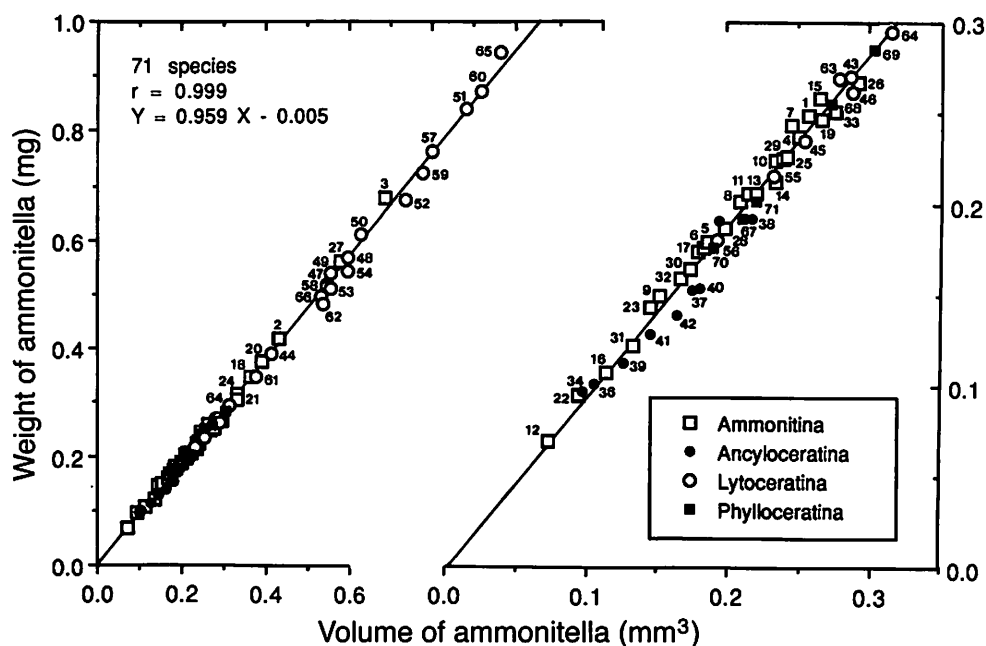


Fig. 7. Plot of total animal weight (shell material plus soft tissue) versus volume at the ammonitella stage for the 71 ammonoid species examined. The numbers correspond to those in Table 1. The dense cluster of points is enlarged to the right to make it possible to identify the individual measurements.



volume expansion rate at the 3–4 π stage (Fig. 5) and a weak positive linear relationship with the ammonitella size (Fig. 6).

Weight and total density of the ammonitella. – Weight of a living ammonoid at the ammonitella stage (= at the hatching stage) is smallest in *Mesopuzosia yubarensis* (0.069 mg) and

largest in *Pseudophyllites indra* (0.944 mg). There is a strong positive linear relationship between the weight and volume of the ammonitella in the species examined (Fig. 7). This indicates that the ratio of weight to volume of a newly hatched animal, that is density, was almost constant among the species examined, with the average density, 0.959 (the slope value of the regression line).

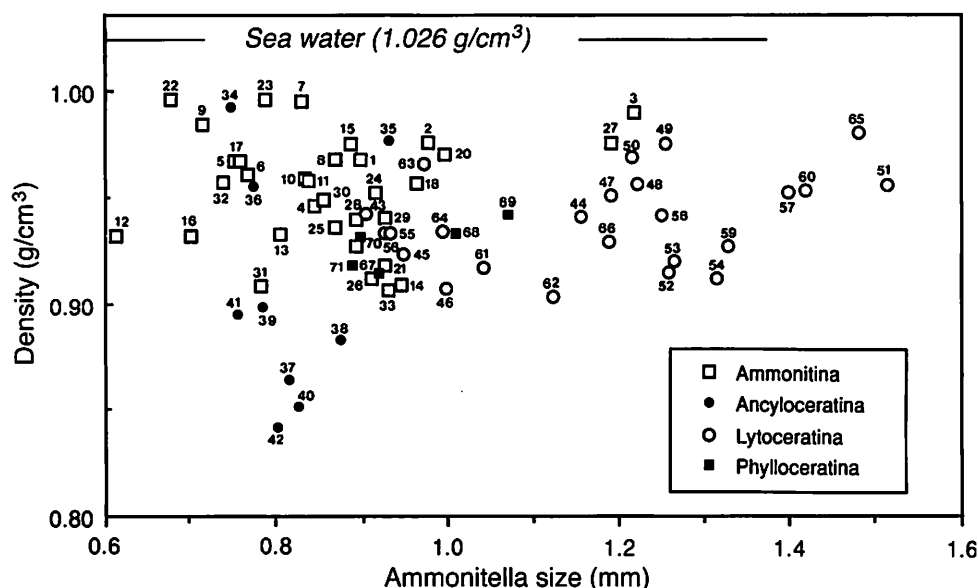


Fig. 8. Plot of total density at the ammonitella stage versus ammonitella size for the 71 ammonoid species examined. The numbers correspond to those in Table 1.

The total density at the hatching stage in the species examined ranges from 0.85 to 1.00 g/cm³, which is lower than the density of seawater (1.026 g/cm³) (Fig. 8). Some species of the Ancyloceratina (*Scaphites planus*, *S. yonekurai*, *S. pseudo-equalis*, *Otoscapites puerculus*, *O. klamathensis* and *O. matsu-motoi*) have relatively small total density (0.85–0.90) as compared with that in the species of other suborders. There is no clear relationship between size and total density at hatching in the species examined (Fig. 8). This suggests that in the Cretaceous ammonites examined the total density of a newly hatched ammonoid was constantly lower than that of seawater, irrespective of their higher-level taxonomy and hatching size.

Ontogenetic change of density. – I examined the ontogenetic change of the total density in three species, *Tetragonites glabrus*, *Tragodesmoceroides subcostatus*, and *Hypophylloceras subramosum*, using immature shells with a shell diameter of 10–20 mm (Fig. 9). In each species, the density gradually increases with shell growth and becomes equal to that of seawater (1.026 g/cm³) at 2.0–2.5 mm in shell diameter. Thereafter the density gradually increases and attains a maximum value (= 1.10 g/cm³) at a diameter of 10–15 mm. Similar ontogenetic changes in total density were observed in other species. These data suggest that many species were positively buoyant at the early post-embryonic stage of less than 2.0–2.5 mm diameter and negatively buoyant at the succeeding stage at least up to 20 mm diameter.

Discussion

Mode of life of newly hatched ammonoids. – Volume calculations show that volume ratio of initial chamber to ammonitella is almost constant among many ammonoids (Fig. 4).

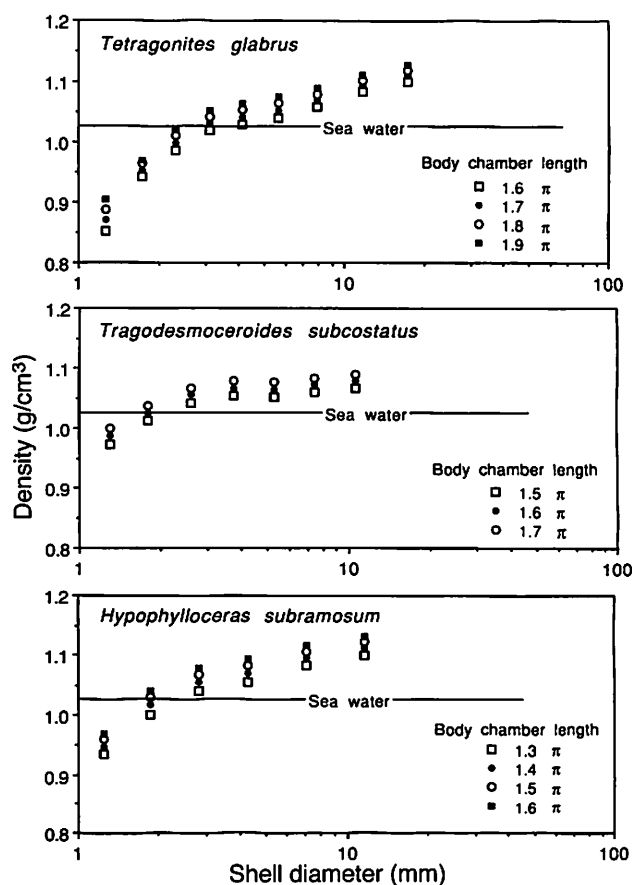


Fig. 9. Ontogenetic changes of total density versus shell diameter for *Tetragonites glabrus* (No. 62, UMUT MM18977), *Tragodesmoceroides subcostatus* (No. 4, UMUT MM18919), and *Hypophylloceras subramosum* (No. 69, UMUT MM18984). The numbers correspond to those in Table 1.

Such a constant volume ratio has been commonly recognized between air and body chambers of many ammonoids (Trueman 1941), and this has been interpreted as indicating a constant and neutral buoyancy of a living ammonite. This evidence is consistent with my assumption that the newly hatched ammonoid had one gas-filled initial chamber and a succeeding body-filled body chamber terminating at the primary constriction. The markedly lower density of the investigated ammonitellas in comparison to seawater (Figs 7, 8) also suggests that most ammonoids had a planktic mode of life during a limited period after hatching. This would be similar to most living molluscs, although unlike many other molluscan classes almost all modern cephalopods develop directly without a post-hatching larval stage. The newly hatched cephalopods are miniatures of the adult form and possess a well-developed mantle system which allows a nektic mode of life (Boletzky 1974, 1977, 1987).

The total density of the Cretaceous ammonoids increased gradually with growth and attained that of seawater (= neutral buoyancy) at a shell diameter of 2.0–2.5 mm (Fig. 9). At this point the ammonoids probably changed their mode of life to nektic or nektobenthic.

Evidence from the analysis of ammonoid assemblages. – The interpretation of early life modes based on density calculations must be tested using other lines of evidence. To investigate the mode of occurrence of ammonoid assemblages in relation to post-mortem dispersal, I crushed hundreds of calcareous nodules and carefully extracted all megafossils (ammonoid, gastropod, bivalve, coral, etc.) from them. The following example (sample AT2106-1) is from the Lower Turonian of the Tappu area, northwest Hokkaido.

The fossil-bearing nodule was spherical, about 20×15×10 cm in longer, intermediate and shorter diameters. As shown in Table 2, the megafossils from the nodule are mostly ammonoids, accounting for 96.2% of total individuals. Many ammonoid species have been reported from the same horizon of the Tappu area (Tanabe *et al.* 1977), but the ammonoid assemblage in this nodule consists of only four species, and most specimens have an almost complete body chamber. This evidence seems to suggest that the ammonoid assemblage is virtually autochthonous.

Table 2. Species composition of the megafossil assemblage ($n = 405$) in the calcareous nodule (Sample AT2106-1) from the Lower Turonian (Loc. R6395) of the Tappu area, Hokkaido.

Fossil	No. of specimens	Percent
<i>Tetragonites glabrus</i>	227	56.0%
<i>Tragodesmoceroideis subcostatus</i>	88	21.7%
<i>Hypophylloceras subramosum</i>	57	14.1%
<i>Sciponoceras orientale</i>	18	4.4%
Bivalves	6	1.5%
Gastropods	5	1.2%
Corals	4	1.0%

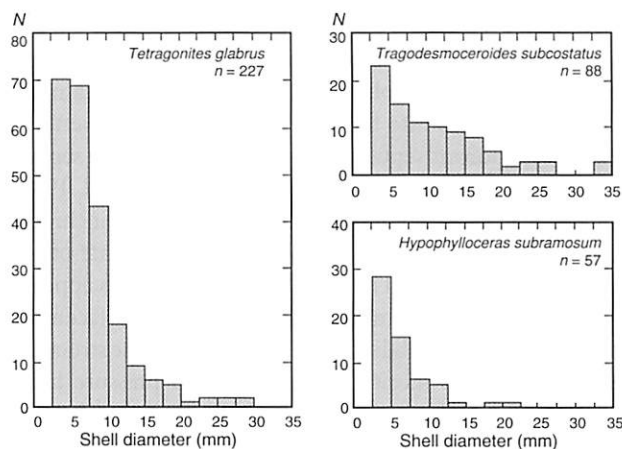


Fig. 10. Size distributions of the three ammonoid species in the calcareous nodule (sample AT2106-1). Left: *Tetragonites glabrus* (UMUT MM18988), upper right: *Tragodesmoceroideis subcostatus* (UMUT MM18989), lower right: *Hypophylloceras subramosum* (UMUT MM18990).

The size-distribution histograms of the specimens of the three species are similar to one another in the absence of juvenile shells less than 2.5 mm diameter, resulting in a left-skewed distribution pattern with the highest peak at about 5 mm diameter (Fig. 10). The absence of juvenile shells was not due to their selective solution during diagenesis, because many adult specimens of the baculitid *Sciponoceras orientale* with an ammonitella and benthic foraminifera are found in the nodule. These lines of evidence strongly suggest that juvenile shells smaller than 2.5 mm in diameter did not accumulate together with the large specimens as a result of differential post-mortem properties of the shell or difference of life habits.

Planktic duration and its regulating factors. – In many benthic gastropods and bivalves, duration of planktic stage is a very important factor controlling the extent of their geographical distribution (Jablonski & Lutz 1980, 1983; Scheltema 1971). A clear tendency is recognizable among Recent marine gastropods that species with a long pelagic larval stage are more widely distributed than those with a short pelagic stage or none at all (Shuto 1974, 1983). Based on the density calculation, I proposed that most Cretaceous ammonites had a short interval of planktic life after hatching.

Following this interpretation, the duration of the planktic stage of ammonoids seems to be controlled by the density of the animal at hatching and the increasing rate of total density during the post-hatching planktic stage. The latter is analyzed from the pattern and rate of shell growth. The shell growth rate and its controlling factors in ammonoids are still unknown. In Recent *Nautilus*, however, the apertural shell growth is related to the timing between new chamber formation and the removal of cameral liquid, because the apertural shell growth is a major factor of buoyancy decrease (Collins *et al.* 1980; Ward *et al.* 1981). So, I assume that the rate of

apertural shell growth in ammonoids was dependent on the rate of cameral-liquid removal, as in *Nautilus*. Previous studies on the ammonoid siphuncular systems show that cameral liquid was drained into the siphuncular code via a wettable pellicle and porous septal prismatic zone within the septal-neck region (Bandel & Boletzky 1979; Obata *et al.* 1980; Tanabe *et al.* 1982, Westermann 1982) or via the conchiolin membranes of the siphuncle (Ward 1982). The rate of removal of cameral liquid in chambered cephalopods appears to be controlled by a number of factors, in which surface area, thickness and permeability of the water-permeable structure within camerae, viscosity of the fluid, and pressure head across the permeable material (= osmotic pressure – hydrostatic pressure) are most important (Chamberlain 1978).

To sum up, the planktic duration of ammonoids may have been affected by a combination of an animal's density at hatching, shell growth pattern, cameral volume, and rate of cameral-liquid removal. If this interpretation is correct, the variation in geographical distribution of ammonoids should be related to the above factors. The Tetragonitaceae will serve to illustrate this problem.

The eighteen species of the Tetragonitaceae examined (see Table 1) fall into three biogeographical groups, Pandemic, North Pacific, and Endemic (Kossmat 1895; Collignon 1956; Anderson 1958; Matsumoto 1959a, b, 1984a, b; Jones 1963, 1967; Murphy 1967a, b, c; Wiedmann 1973; Kennedy & Klinger 1977, 1979; Matsumoto *et al.* 1985; Shigeta 1989).

The Pandemic group, having an almost world-wide distribution (South Africa, Madagascar, southern India, Japan, Alaska, British Columbia, California), includes the following species: *Zelandites varuna* (Forbes) in the early Maastrichtian, *Anagaudryceras buddha* (Forbes) in the early Cenomanian, *Anagaudryceras limatum* (Yabe) in the Coniacian, *Anagaudryceras yokoyamai* (Yabe) in the early Santonian, *Gaudryceras denseplicatum* (Jimbo) in the middle Turonian, *Gaudryceras tenuiliratum* Yabe in the early Santonian, *Gaudryceras striatum* (Jimbo) in the late Campanian, *Pseudophyllites indra* (Forbes) in the late Campanian.

The North Pacific group includes the following species restricted to the region (Japan, Alaska, British Columbia, California): *Gabbioceras michelianum* (d'Orbigny) in the early Cenomanian, *Parajaubetella kawakitana* Matsumoto in the early Cenomanian, *Zelandites inflatus* Matsumoto in the early Cenomanian, *Zelandites mihoensis* Matsumoto in the Coniacian, *Zelandites kawanoi* (Jimbo) in the early Santonian, *Saghalinites teshioensis* Matsumoto in the late Campanian.

The Endemic group includes the following species restricted to the region of Japan and Sakhalin: *Eogaudryceras aff. aurarium* (Anderson) in the early Cenomanian, *Tetragonites aff. kitchini* (Krenkel) in the middle Cenomanian, *Tetragonites glabrus* (Jimbo) in the early Turonian, *Tetragonites minimus* Shigeta in the early Turonian.

There is no significant difference in the total density at hatching in these species (Figs. 7, 8). Also, these species share

similar shell growth patterns and internal shell structures in early ontogeny (Tanabe *et al.* 1979; Drushchits & Doguzhayeva 1981; Tanabe & Ohtsuka 1985; Ohtsuka 1986; Tanabe & Shigeta 1987). Therefore, the variation of geographical distribution in the species of the Tetragonitaceae may be expressed in terms of cameral volume and rate of cameral liquid removal during the post-hatching planktic stage. Cameral volume during the planktic stage seems to correlate with the shell size at a given growth stage, because the shell growth pattern is similar among the species of the Tetragonitaceae. For a given set of pressure, fluid viscosity, and permeability of the permeable material, flow rate roughly increases with increase of siphuncle diameter because the surface area and thickness of the permeable structure within camera increase with siphuncle diameter (Chamberlain 1978). It is, therefore, expected that the ratios of siphuncle diameter to shell size at a given growth stage in the pandemic species should be lower than those of North Pacific species and endemic species.

The relationship between siphuncle diameter (G in Fig. 1) and ammonitella size shows that the three groups can be well distinguished by these characters (Fig. 11). Pandemic species possess smaller ratios of siphuncle diameter to ammonitella size (0.033–0.039) than North Pacific species (0.043–0.050) and endemic species (0.051–0.053). This evidence matches with the above predictions and supports the above interpretation of factors regulating ammonoid planktic duration. Planktic duration could be calculated using assumed values of flow rate, but reasonable such values have not been obtained, and so these calculations must be deferred.

There is an intimate relationship between the embryonic size and developmental types in gastropods and bivalves (Thorson 1950; Ockelmann 1965; Jablonski & Lutz 1980, 1983). Generally, small hatching size is associated with a planktotrophic development, characterized by a long pelagic stage and a high dispersal capability, while large hatching size is found in species with nonplanktotrophic development (Jablonski & Lutz, 1980, 1983). This contrasts with the case in the Tetragonitaceae.

Conclusions

Based on shell density calculations in many species, I have suggested that almost all Cretaceous ammonoids had a planktic mode of life during a limited interval at early post-hatching stage, and that their mode of life changed to nekto planktic or nekto benthic at 2.0 to 2.5 mm shell diameter. This interpretation is also supported by data on the mode of occurrence of fossil assemblages. Planktic duration of a newly hatched ammonoid might be expressed by the density at hatching, shell growth pattern, cameral volume (or hatching size), and flow rate of cameral-liquid removal (or siphuncle diameter). The latter two in particular seem to be very important factors in controlling the biogeographical framework of species, as demonstrated in the Tetragonitaceae.

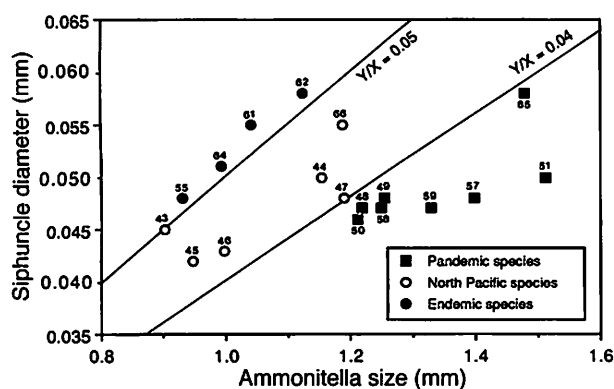


Fig. 11. Double scatter plots of ammonitella size and siphuncle diameter for the 18 species belonging to the Tetragonitacea. Black square: pandemic species. White circle: North Pacific species. Black circle: endemic species. The numbers correspond to those in Table 1.

Most previous paleobiogeographic studies have dealt with distributions of individual taxa or with questions of global or regional provincialism in relation to plate tectonics (e.g., Kennedy & Cobban 1976). The data in these studies have been used as a tool for solving paleogeographical, paleoclimatological, or tectonic problems. However, little was considered about why and how the biogeographic distribution pattern of ammonoids was established? The dispersal property of ammonoids in the early post-embryonic stage may serve as a key for biological control on habitable area and speciation.

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