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VARIABLE GROWTH MODES IN LATE CRETACEOUS AMMONOIDS: IMPLICATIONS FOR DIVERSE EARLY LIFE HISTORIES

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ABSTRACT—Examination of ontogenetic changes in the septal angle of Late Cretaceous ammonoids (ten species representing seven superfamilies and four suborders) reveals four patterns: 1) a single abrupt change in septal angle; 2) two abrupt changes in septal angle; 3) cyclic fluctuations in septal angle throughout ontogeny; and 4) an almost constant septal angle throughout ontogeny. These various septal-angle patterns in Late Cretaceous ammonoids are in contrast with modern and fossil nautiloids, which have the common pattern displaying a single abrupt change in septal angles. Although the abrupt change of septal angles in nautiloids corresponds with the hatching event from the egg, change of septal angles in the examined ammonoids is hypothesized to correspond not to hatching but to the change from a planktic to a nektobenthic habit demarcated by the post-embryonic stage. Therefore, the variable patterns of septal angles within ammonoids suggest a diverse set of early life histories.

INTRODUCTION

ECTOCOCHLEATE CEPHALOPODS (ammonoids and nautiloids) retain the record of growth in their shells, which consist of a septate phragmocone as well as a body chamber. Through analyses of the septate phragmocones (e.g., the angles between succeeding septa), many studies have attempted to determine their growth modes (for Modern nautiloids Landman et al., 1983; Collins and Ward, 1987; Tanabe and Tsukahara, 1987; Landman, 1988; Klug, 2004; Chirat et al., 2008; Klug et al., 2008; for fossil nautiloids Ruzhencev and Shimansky, 1954; Davis and Mohorter, 1973; Landman et al., 1983; Landman, 1988; Chirat and Rioult, 1998; Chirat, 2001; Wani and Ayyasami, 2009; Wani and Mapes, 2010; and for ammonoids Kulicki, 1974; Doguzhaeva, 1982; Checa, 1987; Landman, 1987; Dommergues, 1988; Bucher et al., 1996; Okamoto and Shibata, 1997; Korn and Titus, 2006; Ebbighausen and Korn, 2007; Kraft et al., 2008). Based on morphologic changes seen in ammonoid shells (i.e., changes in coiling, umbilicus, ornamentation, and septal angle), the ammonoid growth has subdivided into four intervals: the embryonic, neanic, juvenile, and mature stages (Westermann, 1958; Bucher et al., 1996; Klug, 2001; and references therein). Each stage generally has the following septal-angle patterns: 1) the embryonic ammonoid, termed the ammonitella (Druschits and Khiami, 1970), consists of the protoconch (initial chamber) and approximately one planispiral whorl initiating at the caecum and terminating at the primary constriction with the proseptum (Tanabe et al., 1993; Landman et al., 1996); 2) the neanic stage generally has widely spaced septal angles (Landman, 1987; Bucher et al., 1996); 3) juvenile ammonoids have almost uniform septal angles (Bucher et al., 1996); and 4) mature ammonoids initially display increased angles followed by decreased angles over the last few septa (Callomon, 1963; Crick, 1978; Landman and Waage, 1993; Davis et al., 1996; Klug, 2004; Klug et al., 2007).

In this paper, the septal angles of several Late Cretaceous ammonoids species were examined in detail and were compared with those of Modern and fossil nautiloids. Furthermore, their implications relative to life habits, especially for the early life histories (from the embryonic to neanic stages), in ammonoids were discussed on the basis of the patterns of ontogenetic change in septal angles.

MATERIAL

All ammonoid shells used in this study were collected from calcareous concretions as float in the Kotanbetsu and Tappu areas, northwestern Hokkaido, Japan (Fig. 1), which show no irregular growth of shells (e.g., injuries) and are preserved without shell deformation during diagenesis. In this study, 23 specimens belonging to ten species of Late Cretaceous ammonoids (*Hypophylloceras subramosum* [Shimizu, 1934]; *Phyllopachyceras ezoense* [Yokoyama, 1890]; *Anagaudryceras yokoyamai* [Yabe, 1903]; *Gaudryceras tenuiliratum* Yabe, 1903; *Tetragonites glabrus* [Jimbo, 1894]; *Damesites sugata* [Forbes, 1845]; *Yokoyamaoceras ishikawai* [Jimbo, 1894]; *Haboroceras haboroense* Toshimitsu, 1988; *Protexanites minimus* Matsumoto, 1970; and *Scaphites planus* [Yabe, 1910]) were examined and utilized for determining septal angle (Table 1; Fig. 2). The geological age of the examined specimens is Turonian–lowest Campanian, based on previous reports (Tanaka, 1963; Tanabe et al., 1977; Toshimitsu, 1988; Wani, 2003; Takashima et al., 2004), although the detailed horizons of the specimens are unknown. All specimens are housed in the collections of the Mikasa City Museum, Hokkaido.

METHODS

Each specimen was polished along the median plane using silicon carbide powders. The septal angle between succeeding septa, which is defined as the rotational angle of two succeeding septa (i.e., septum numbers N and N-1) at the positions of attachment between the septa and the shell whorl (Fig. 3.1), were measured using a digital optical microscope. The center of the rotational angles was approximated as the center of the logarithmic shell spiral denoting the shell whorls (Fig. 3.2). To determine the position of the spiral's center, the points of intersection between parallel tangential lines and the logarithmic spiral were constructed, and then straight lines were drawn connecting these points (Fig. 3.2; see also Wani and Mapes, 2010). The intersection of point of two straight lines was used to denote the position of the coiling axis, because a single intersection can be defined in a logarithmic spiral based on any pair of tangential lines (Fig. 3.2). Tangential lines at the position up to ~140° in rotational angle from the primary constriction were not considered as the shape up to this position approximates a true circle rather than a logarithm spiral (Kulicki, 1974). The total rotational septal

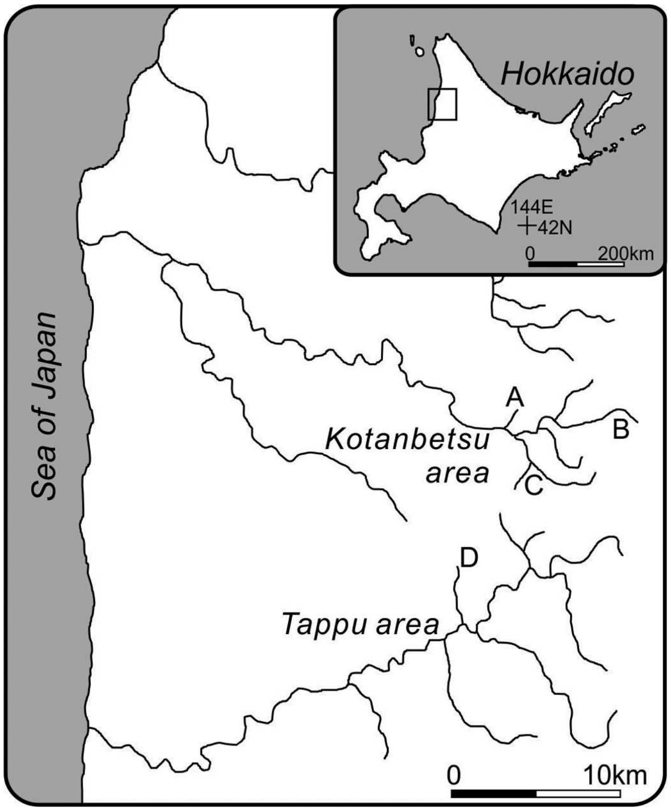

FIGURE *1*—Index map of Kotanbetsu (*A–C*) and Tappu (*D*) areas, northwestern Hokkaido, Japan. *A*, Kamino-sawa Creek; *B*, Kotanbetsu Creek; *C*, Horotate-sawa Creek; *D*, Gakko-no-sawa Creek. For detailed geological information, see Tanaka (1963), Tanabe et al. (1977), Wani (2003), and Takashima et al. (2004).

angles were measured from the line through proseptum and the center of the coiling axis (Fig. 3.1). The measured septal angles are shown in pairs of scatter diagrams and display: 1) the total rotational angle at each septum versus the septal number through ontogeny; and 2) the septal angle between two adjacent septa versus the septal number through ontogeny (Figs. 4–6). Based on these scatter diagrams, the patterns of the ontogenetic change of the septal angle were examined and compared in the ten species.

RESULTS

The measurements of the septal angles of ten species are summarized in Table 2 and Figures 4–6 (for raw data, see Appendix 1 in the Supplemental Data Archive). The septal angles through ontogeny change in some specimens, which were recognized as critical points on the reduced major axes in the scatter diagrams.

Hypophylloceras subramosum.—The ontogenetic patterns display two types (Types 1 and 2). Type 1 (Hs3 and 5) is characterized by relatively large septal angles early in ontogeny, followed by one critical point on the reduced major axis and then virtually constant septal angle (Table 2). Type 2 (Hs1–2, 4, and 6) has almost constant septal angles throughout the whole ontogeny and lack a critical point. All specimens, regardless of whether they are Type 1 or 2 show a similar pattern later in ontogeny (Fig. 4.1–4.4). The difference between Types 1 and 2 is recognized only in the early ontogenetic stage (rotational angle less than ~900°).

Phyllopachyceras ezoense.—The ontogenetic patterns display two critical points early in ontogeny (Fig. 4.5, 4.6; Table 2). The septal angles gradually decrease between the first and second critical points. After the second critical point, the septal angles gradually increase toward the later ontogenetic stage without any critical point.

Anagaudryceras yokoyamai (Fig. 4.7, 4.8; Table 2), *Tetragonites glabrus* (Fig. 5.3, 5.4; Table 2), *Damesites sugata* (Fig. 5.5, 5.6; Table 2), and *Yokoyamaoceras ishikawai* (Fig. 5.7, 5.8; Table 2).—The ontogenetic patterns display one critical point early in ontogeny. The septal angles after the critical point are almost constant.

Gaudryceras tenuiliratum.—The ontogenetic patterns display one critical point early in ontogeny (Fig. 5.1, 5.2; Table 2). The septal angles after the critical point show an initial decrease, followed by almost constant septal angle.

Haboroceras haboroense (Fig. 6.1, 6.2; Table 2) and *Protexanites minimus* (Fig. 6.3, 6.4; Table 2).—The ontogenetic patterns display cyclic fluctuations through ontogeny lacking a critical point. The fluctuations are composed of alternations of larger and smaller septal angles, with almost constant amplitudes of fluctuations.

Scaphites planus.—The ontogenetic patterns display two critical points (Fig. 6.5, 6.6; Table 2). The septal angles between the first and second critical points are almost constant. The last few septa demonstrate the second critical point. This septal crowding of the final few septa, together with the apertural modification, and the changes in conch geometry and coiling, indicates that this specimen had attained sexual maturity (e.g., Davis et al., 1996; Klug, 2004).

VARIATION OF SEPTAL ANGLE

The Late Cretaceous ammonoids examined in this study reveal that the ontogenetic patterns of septal angles are classified into four groups characterized by: 1) a single critical point in early ontogeny (Type 1 of *H. subramosum*, *A. yokoyamai*, *G. tenuiliratum*, *T. glabrus*, *D. sugata*, and *Y. ishikawai*); 2) two critical points in early and/or later ontogeny (*P. ezoense* and *S. planus*); 3) cyclic fluctuations through ontogeny lacking a critical point (*H. haboroense* and *P. minimus*); and 4) an almost constant

TABLE *1*—Late Cretaceous ammonoid species used in this study. Taxonomy follows Wright (1996).

Order	Suborder	Superfamily	Family	Subfamily	Species	Number of specimens
Ammonoidea	Phylloceratina	Phylloceratoidea	Phylloceratidae	Phylloceratinae	*Hypophylloceras subramosum*	6
					Phyllopachyceras ezoense	1
	Lytoceratina	Tetragonitoidea	Gaudryceratidae		*Anagaudryceras yokoyamai*	2
					Gaudryceras tenuiliratum	2
			Tetragonitidae	Tetragonitinae	*Tetragonites glabrus*	3
	Ammonitina	Desmoceratoidea	Desmoceratidae	Desmoceratinae	*Damesites sugata*	3
			Kossmaticeratidae	Kossmaticeratinae	*Yokoyamaoceras ishikawai*	2
		Acanthoceratoidea	Collignoniceratidae	Texanitinae	*Haboroceras haboroense*	2
					Protexanites minimus	1
	Ancyloceratina	Scaphitoidea	Scaphitidae	Scaphitinae	*Scaphites planus*	1

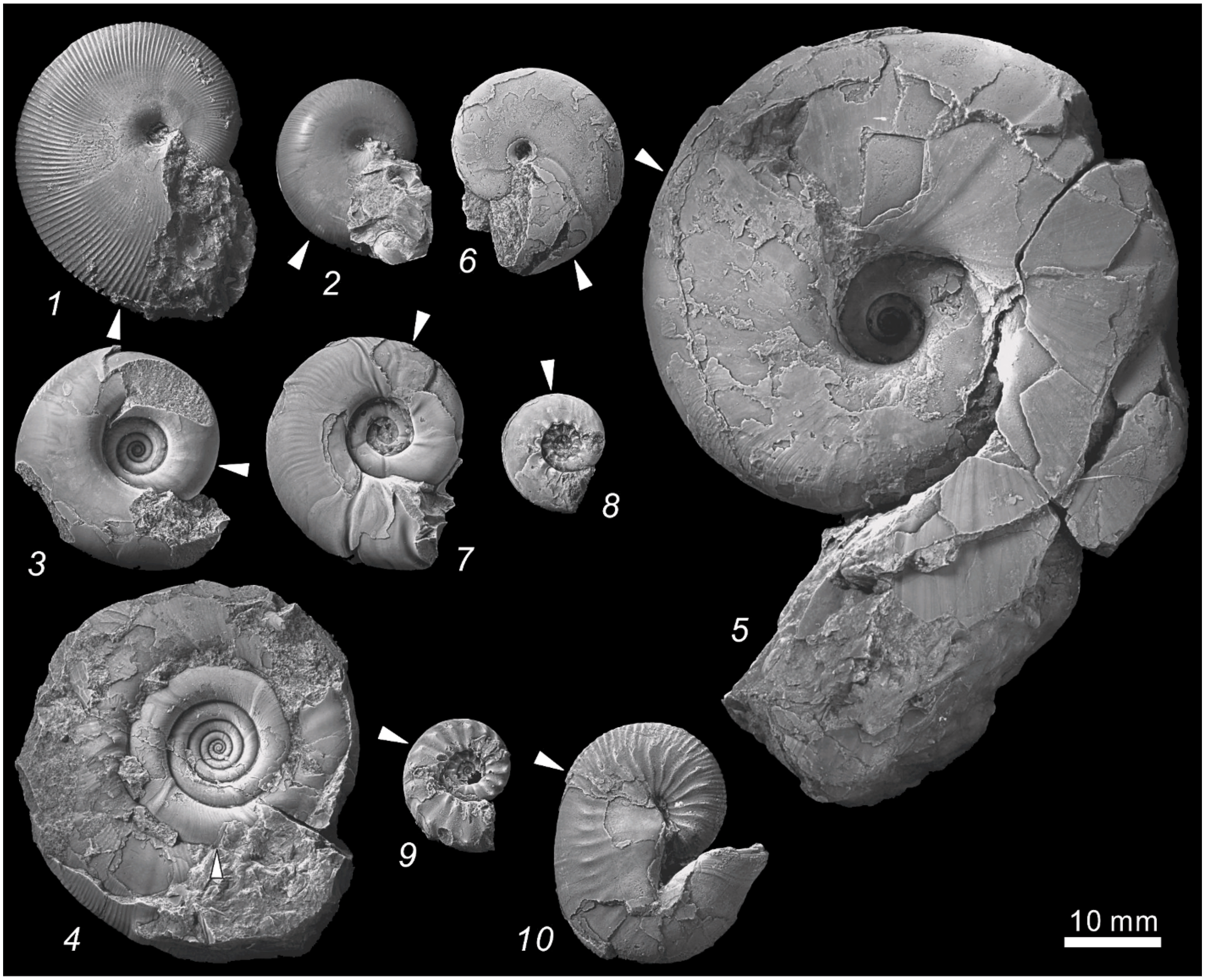

FIGURE 2—Photographs of specimens from the Kotanbetsu and Tappu areas, northwestern Hokkaido, Japan. *1*, *Hypophylloceras subramosum* (Hs5); *2*, *Phyllopachyceras ezoense* (Pe1); *3*, *Anagaudryceras yokoyamai* (Ay2); *4*, *Gaudryceras tenuiliratum* (Gt2); *5*, *Tetragonites glabrus* (Tg2); 6, *Damesites sugata* (Ds3); *7*, *Yokoyamaoceras ishikawai* (Yi2); *8*, *Haboroceras haboroense* (Hh1); *9*, *Protexanites minimus* (Pm1); *10*, *Scaphites planus* (Sp1). Triangles indicate the last preserved septum.

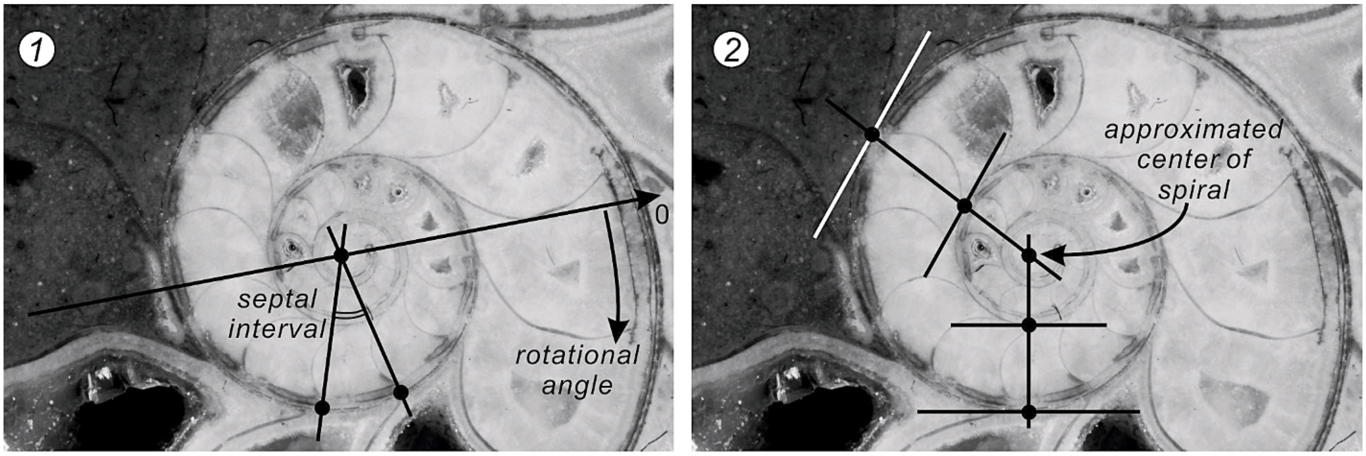

FIGURE 3—Measurement of septal angle. *1*, septal angle and the base of measurement through proseptum and the center of the logarithm spiral; *2*, approximated center of spiral.

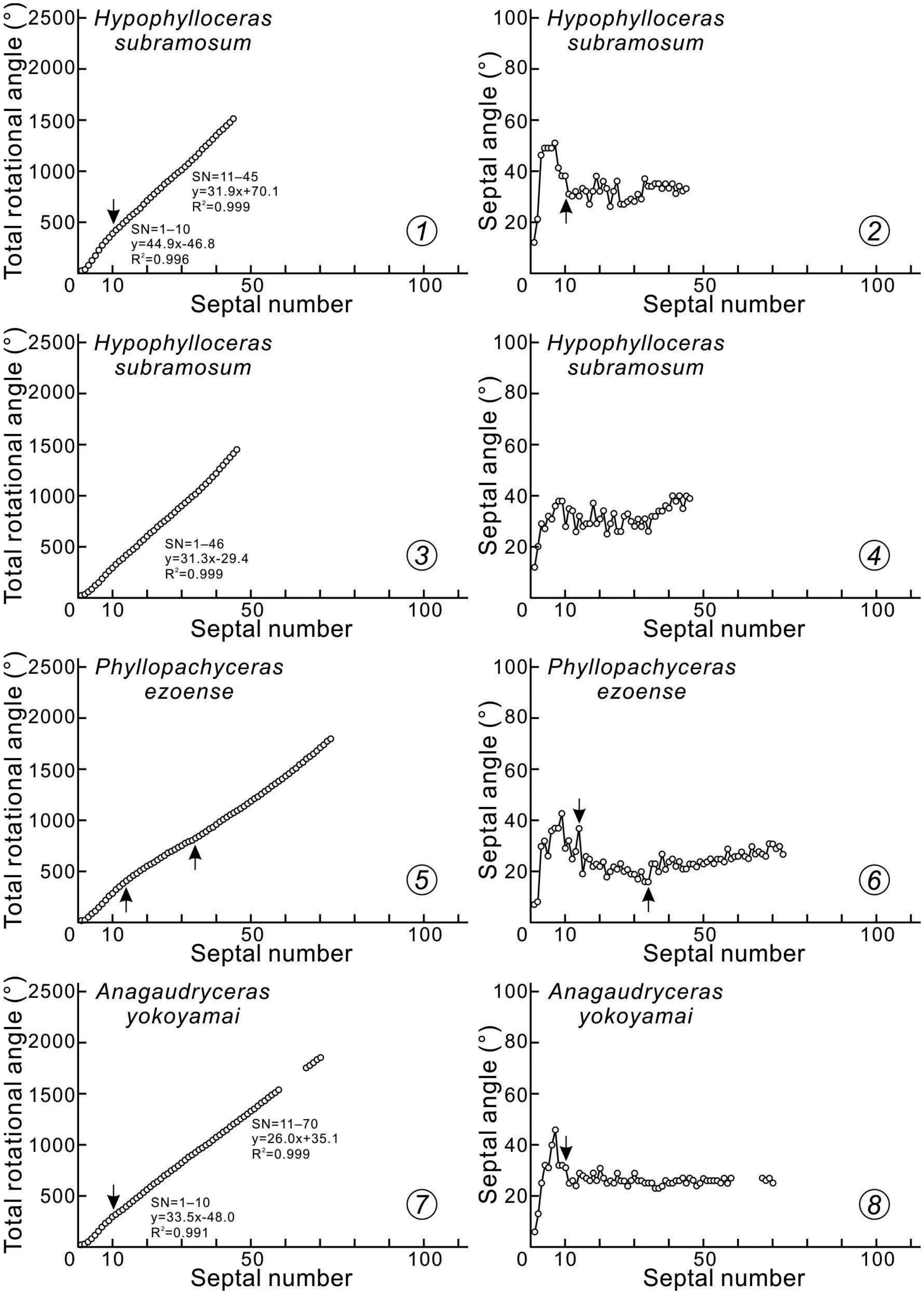

FIGURE 4—Scatter diagrams of septal angles through ontogeny. *1, 2*, *Hypophylloceras subramosum* (Hs5); *3, 4*, *Hypophylloceras subramosum* (Hs1); *5, 6*, *Phyllopachyceras ezoense* (Pe1); *7, 8*, *Anagaudryceras yokoyamai* (Ay1). Arrows indicate the critical points on the reduced major axes. The regression equation is shown in intervals with a constant septal angle. SN=septal number.

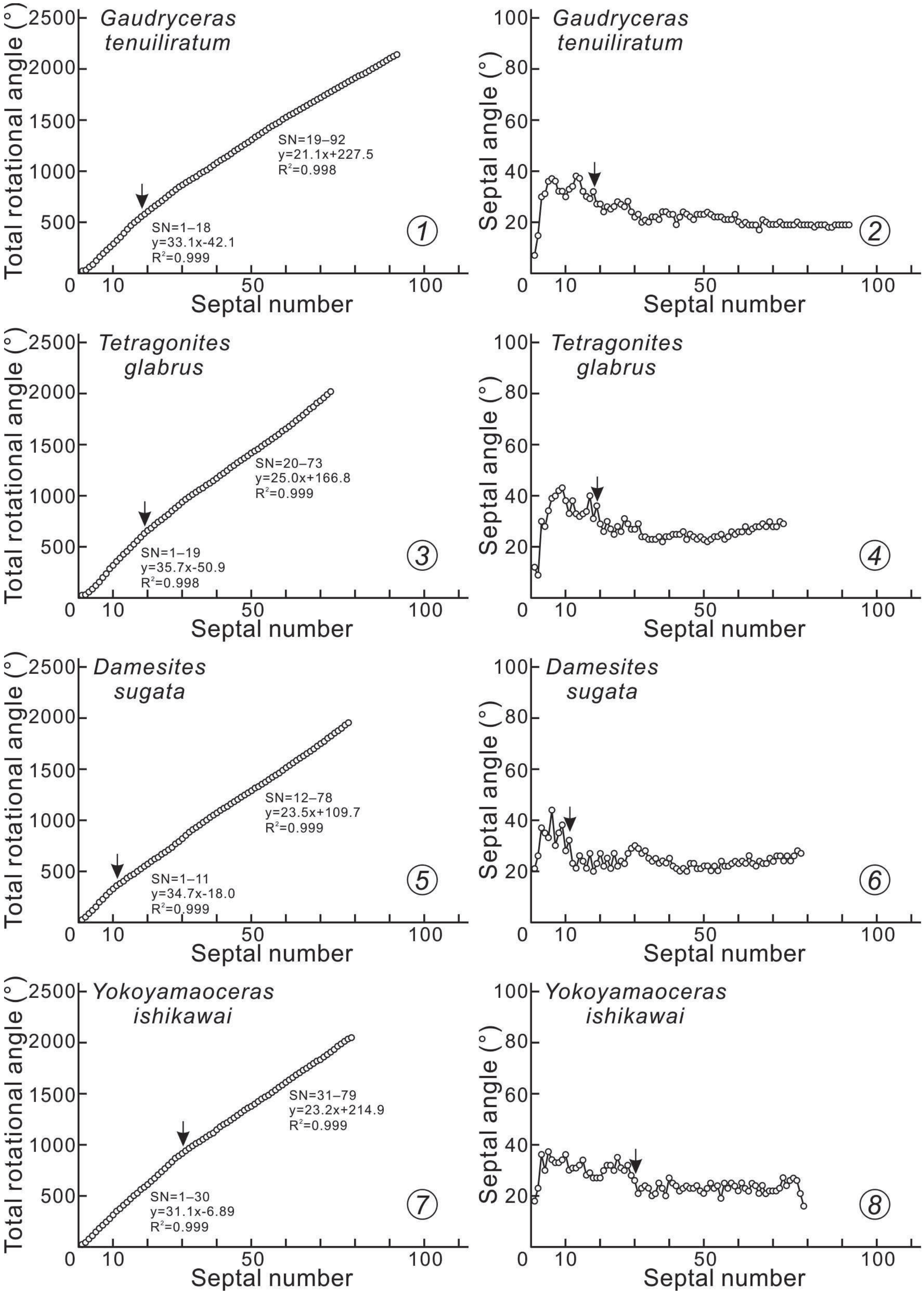

FIGURE 5—Scatter diagrams of septal angles through ontogeny. *1, 2*, *Gaudryceras tenuiliratum* (Gt2); *3, 4*, *Tetragonites glabrus* (Tg1); *5, 6*, *Damesites sugata* (Ds3); *7, 8*, *Yokoyamaoceras ishikawai* (Yi2). Arrows indicate the critical points on the reduced major axes. The regression equation is shown in intervals with a constant septal angle. SN=septal number.

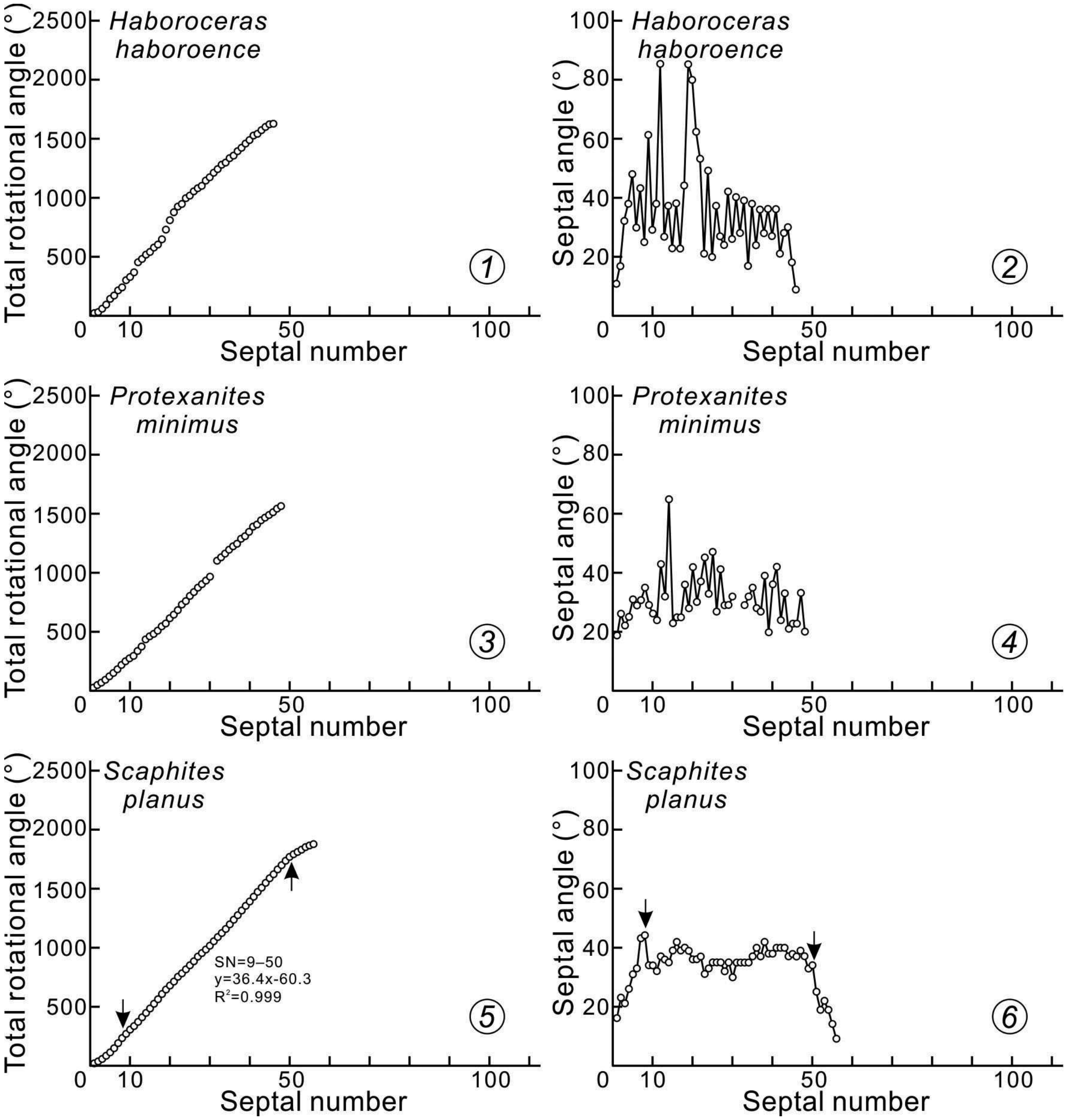

FIGURE 6—Scatter diagrams of septal angles through ontogeny. *1, 2*, *Haboroceras haboroense* (Hh2); *3, 4*, *Protexanites minimus* (Pm1); *5, 6*, *Scaphites planus* (Sp1). Arrows indicate the critical points on the reduced major axes. The regression equation is shown in intervals with a constant septal angle. SN=septal number.

septal angle throughout ontogeny and lacking a critical point (Type 2 of *H. subramosum*).

In all modern and fossil nautiloids examined (for Modern nautili, e.g., Tanabe and Tsukahara, 1987; Arnold et al., 1987; and for fossil nautiloids, e.g., Landman et al., 1983; Chirat and Rioult, 1998; Wani and Mapes, 2010), the septal angles through ontogeny reveal a single critical point in early ontogeny as seen in Group 1 in this study, although the critical points are generally more obvious in nautiloids than in ammonoids. This conservatism of septal angles in nautiloids clearly contrasts with those in ammonoids where at least four variations were revealed in this study.

The septal-angle patterns in the examined Late Cretaceous ammonoids tend to conform to the higher taxonomy. The septal-angle patterns are rather uniform within each superfamily except in the Phylloceratoidea (Table 2; Figs. 4–6). The Tetragonitoidea (*A. yokoyamai*, *G. tenuiliratum*, and *T. glabrus*) and Desmoceratoidea (*D. sugata* and *Y. ishikawai*) display a single critical point early in the ontogeny, whereas the Acanthoceratoidea (*H. haboroense* and *P. minimus*) display a cyclically fluctuating pattern through ontogeny lacking a critical point (compare Korn and Titus, 2006; Ebbighausen and Korn, 2007; Kraft et al., 2008).

IMPLICATIONS FOR EARLY LIFE HISTORY

The critical points within the ontogenetic variability of septal angles in nautiloids correspond to a constriction on the early whorls, and are related to hatching (Davis and Mohorter, 1973; Landman et al., 1983; Landman, 1988; Chirat and Rioult, 1998; Chirat, 2001; Wani and Ayyasami, 2009; Wani and Mapes, 2010). This causal relationship between hatching and changes in shell morphology (critical points in septal angles, and constriction on the early whorls) has been confirmed in Recent nautili mainly based on oxygen and carbon isotopic analyses (Eichler and Ristedt, 1966; Cochran et al., 1981; Taylor and Ward, 1983; Arnold et al., 1987; Oba et al., 1992; Landman et al., 1994).

TABLE 2—Summarized information of septal angle. D (mm)=the maximum diameter at the last preserved septum; SN=total number of septa; TA (degree)=total rotational angle; AA (degree)=the average septal angle of all septa; maxA (degree)=the maximum septal angle; minA (degree)=the minimum septal angle; SD (degree)=standard deviation; "-"=immeasurable due to poor preservation.

Species	Specimen no.	Locality	D (mm)	SN	TA (°)	AA (°)	maxA (°)	minA (°)	SD (°)	Septal no. of 1st critical point	Shell diameter with 1st critical point	Septal no. of 2nd critical point	Shell diameter with 2nd critical point	Ammonitella diameter (mm)	Protoconch diameter (mm)	Ammonitella angle from proseptum (°)
Hypophylloceras subramosum	Hs1	Horotate-sawa C., Kotanbetsu	18.5	46	1,448	31.5	40	12	5.411					1.06	0.63	283
	Hs2	Kamino-sawa C., Kotanbetsu	10.5	55	1,412	25.7	39	10	4.895					0.78	0.47	243
	Hs3	Kamino-sawa C., Kotanbetsu	30.5	53	1,732	32.7	51	12	6.633	14	2.37			0.78	0.44	255
	Hs4	Kamino-sawa C., Kotanbetsu	50.0	67	1,810	27.0	38	13	5.591					1.08	0.62	268
	Hs5	Kamino-sawa C., Kotanbetsu	14.4	45	1,514	33.6	51	12	7.221	10	1.81			0.78	0.46	265
	Hs6	Horotate-sawa C., Kotanbetsu	20.4	42	1,356	32.3	42	9	5.645					1.23	0.69	279
Phyllopachyceras ezoense	Pe1	Horotate-sawa C., Kotanbetsu	17.8	73	1,803	24.7	43	7	5.859	14	1.99	33	3.81	0.96	0.59	266
Anagaudryceras yokoyamai	Ay1	Horotate-sawa C., Kotanbetsu	—	70	1,641	26.2	46	6	4.844	10	2.51			1.40	0.68	345
	Ay2	Kamino-sawa C., Kotanbetsu	16.6	56	1,477	26.4	34	7	3.735	21	4.86			1.50	0.72	359
Gaudryceras tenuiliratum	Gt1	Horotate-sawa C., Kotanbetsu	28.9	105	2,352	22.4	39	16	4.986	16	3.17			1.33	0.66	344
	Gt2	Kamino-sawa C., Kotanbetsu	23.3	92	2,132	23.2	38	7	5.540	18	2.85			1.37	0.68	348
Tetragonites glabrus	Tg1	Gakko-no-sawa C., Tappu	43.6	73	2,020	27.7	43	9	5.812	19	3.72			1.21	0.63	334
	Tg2	Gakko-no-sawa C., Tappu	45.7	74	2,028	27.4	39	7	4.655	17	3.19			1.24	0.64	342
	Tg3	Gakko-no-sawa C., Tappu	44.2	74	2,044	27.6	40	14	4.511	17	3.31			1.21	—	339
Damesites sugata	Ds1	Horotate-sawa C., Kotanbetsu	13.9	70	1,700	24.3	43	19	4.562	10	1.65			0.87	0.46	318
	Ds2	Kamino-sawa C., Kotanbetsu	10.4	65	1,580	24.3	39	17	4.253	17	1.98			0.80	0.44	305
	Ds3	Kamino-sawa C., Kotanbetsu	21.7	78	1,954	25.1	44	20	4.449	11	1.62			0.79	0.43	319
Yokoyamaoceras ishikawai	Yi1	Horotate-sawa C., Kotanbetsu	14.6	75	1,906	26.0	42	11	4.547	28	3.41			0.85	—	310
	Yi2	Kamino-sawa C., Kotanbetsu	16.7	79	2,048	25.9	37	16	4.684	30	4.22			0.91	0.53	331
Haboroceras haboroense	Hh1	Kamino-sawa C., Kotanbetsu	9.6	57	1,552	27.2	41	10	5.919					0.82	—	278
	Hh2	Horotate-sawa C., Kotanbetsu	12.0	46	1,630	35.4	85	9	17.220					—	—	310
Protexanites minimus	Pm1	Kamino-sawa C., Kotanbetsu	11.8	48	1,568	32.7	65	19	8.662					0.87	0.48	285
Scaphites planus	Sp1	Kotanbetsu C., Kotanbetsu	17.5	56	1,874	32.9	44	9	7.541	8	1.23	50	26.97	0.88	0.55	277

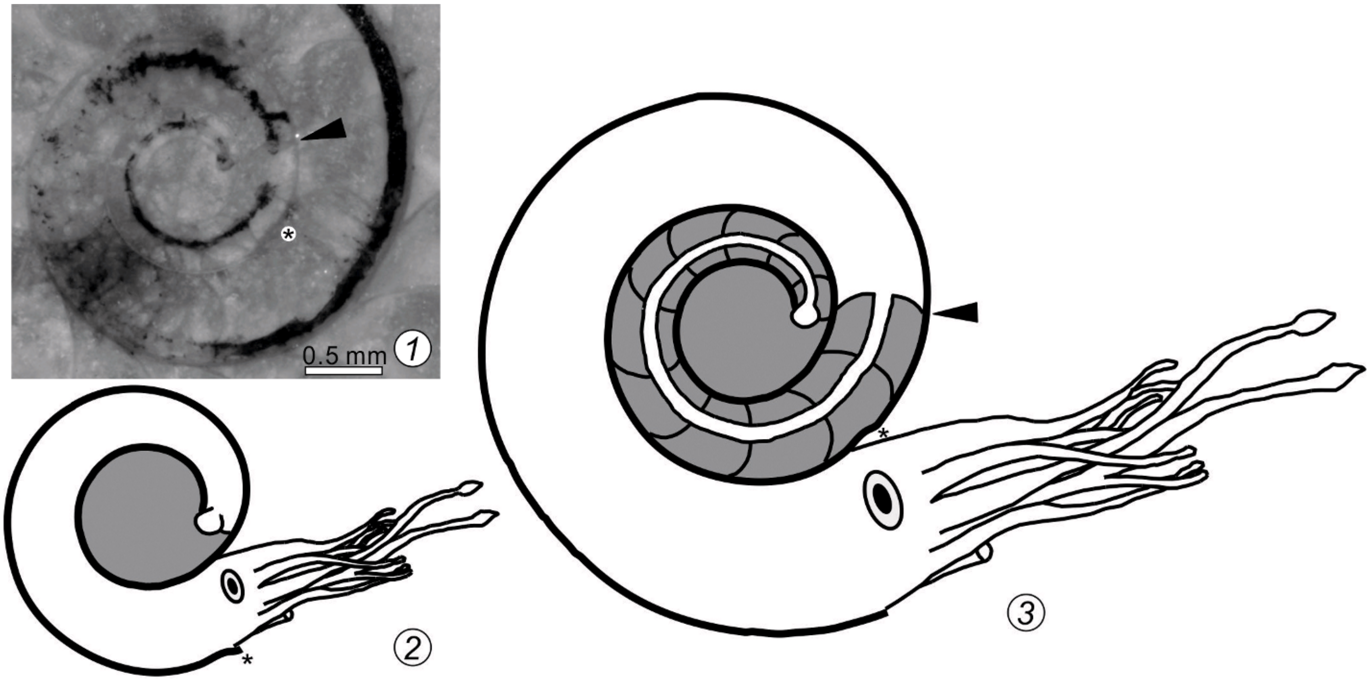

FIGURE 7—Photograph of *Damesites sugata* (Ds3; *1*) and schematic drawings of ammonoid ammonitella (*2*) and of the ammonoid with the critical point in septal angle (*3*). Asterisks=the nepionic constriction; triangle=the septum with the critical point. Note that the critical point is situated adorally from the nepionic constriction. The rotational angle of the body chamber with critical point of septal angle (*3*) is postulated to be same as those in ammonoid ammonitella (*2*).

Some ammonoids examined in this study (Groups 1 and 2) have critical point(s) early in ontogeny, similar to those in nautiloids. However, these critical points do not correspond with hatching from eggs. This is because the septa associated with the critical points (8th to 21st; Table 2) in most ammonoid specimens are situated adorally of the primary constriction, which formed at hatching (Landman et al., 1996; Klofak et al., 2007; and references therein). In some specimens, however, the critical points are situated adapically from the primary constriction. The actual shell diameters at the time of the critical points were reconstructed in this study as the sum of shell diameter at the critical point and the estimated body chamber length that is approximated to the angle between the primary constriction and proseptum (Fig. 7; Table 2). This suggestion that the septa had not formed until hatching is concordant with previous studies (e.g., Smith, 1901; Drushchits and Khiami, 1970; Landman, 1982, 1985, 1988; Tanabe et al., 1993). The reconstructed shell diameters with the first critical points range between 1.23–4.86 mm, which are larger than their ammonitella diameters (0.78–1.50 mm; Table 2).

Alternatively, the changes of septal angles with these calculated shell diameters were possibly related to the change of their life habits early in ontogeny (e.g., from a planktic habit at the neanic stage to nektobenthic habit at the juvenile stage). Shigeta (1993) has theoretically calculated total density in Cretaceous ammonoid ammonitellas and also examined in detail the ontogenetic changes of the total density of *Hypophylloceras subramosum* and *Tetragonites glabrus*. He concluded that *H. subramosum* and *T. glabrus* became negatively buoyant and changed from a planktic to nektoplanktic or nektobenthic habits at shell diameters of 2.0–2.5 and 2.0–4.0 mm, respectively. The reconstructed shell diameters with the first critical points of *H. subramosum* and *T. glabrus*, in this study, are 1.81–2.37 and 3.19–3.72 mm, respectively (Table 2). The similarity of these shell diameters reconstructed by different methodologies suggests that the critical points of septal angles were related to the change from a planktic to a nektoplanktic or nektobenthic habits. Furthermore, the habitats of Late Cretaceous ammonoids from Hokkaido were analyzed using oxygen isotopic data and suggested that ammonoids, including *H. subramosum*, *P. ezoense*, *G. tenuiliratum*, *T. glabrus*, and *Y. ishikawai*, lived nektobenthically (Moriya et al., 2003). Most ammonoid hatchlings have been hypothesized to have a planktic habit (Kulicki, 1974, 1979, 1996; Druschits et al., 1977; Tanabe et al., 1980, 2001, 2003; Landman, 1985; Tanabe and Ohtsuka, 1985; Landman et al., 1996; Westermann, 1996; Rouget and Neige, 2001; Mapes and Nützel, 2009; Tajika and Wani, 2011). These facts and assumptions suggest that the critical points of septal angles in all the examined species were related to the change from a planktic habit at the neanic stage to a nektobenthic habit afterwards. If this hypothesis holds then, the shell diameters at the transition from a planktic to a nektobenthic habits varies between 1.23 and 4.86 mm for the examined ammonoids (Table 2). This suggests that there are various early life histories associated with different shell diameters at the end of the planktic dispersal post-embryonic stage (relatively larger in *G. tenuiliratum*, *T. glabrus*, and *Y. ishikawai*; Table 2), which might affect their geographic dispersal and evolutionary history.

It is still unclear whether or not the septal angle patterns of Groups 3 and 4, which lack critical points, were related to the change of their life habits, and, if so, what that relationship is. The ammonoids of Groups 3 and 4 might have lived without any change in their life habits throughout their ontogeny; or they had different septal-angle patterns that did not record their change of life habits, although they potentially changed their habit (e.g., from planktic to nektobenthic).

CONCLUSION

The ontogenetic changes of the septal angle in Late Cretaceous ammonoids (ten species representing seven superfamilies and four suborders) from Hokkaido, Japan, were examined in this study. The ontogenetic changes display four patterns: 1) a single abrupt change in septal angle; 2) two abrupt changes in septal angle; 3) cyclic fluctuations in septal angle throughout ontogeny; and 4) an almost constant septal angle throughout ontogeny. These various septal-angle patterns tend to conform to the higher taxonomy and are rather uniform within each superfamily except in the Phylloceratoidea. The tendency between the higher taxonomy and septal-angle patterns should be examined in various species to further test this tendency. The various septal-angle patterns in Late Cretaceous ammonoids are in contrast with modern and fossil nautiloids which have the common pattern displaying a single abrupt change in septal angles. Although the abrupt change of septal angles in nautiloids corresponds with the hatching event from the egg, change of septal angles in the examined ammonoids is hypothesized to correspond not to hatching but to the change from a planktic to a nektobenthic habit demarcated by the post-embryonic stage. Therefore, the variable patterns of septal angles within ammonoids suggest a diverse set of early life histories.

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