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Estimation of allometric shell growth by fragmentary specimens of *Baculites tanakae* Matsumoto and Obata (a Late Cretaceous heteromorph ammonoid)

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Abstract. We introduce a new biometric method to reconstruct ontogenetic shell development of *Baculites* species. In order to estimate original total shaft length from fragmentary specimens and to clarify their shell growth patterns, a large number of samples *of Baculites tanakae* Matsumoto and Obata, collected from the Upper Cretaceous deposits in Hokkaido, Japan, were examined. Biometric analysis revealed a characteristic allometric shell growth pattern of *B. tanakae* expressed by the formula $L = 3.03H^{1.50}$, where L and H are original total shaft length and whorl height, respectively. The analysis gives a quantitative diagnosis of the morphology of this species and enables us to estimate L including the missing apical part. Reconstruction of the total shaft length reveals that the shell ornament of *B. tanakae* shifts ontogenetically from a smooth phase to a tuberculate phase via a ribbed phase. It also demonstrates wide intraspecific variation on switching timing of the shell ornament phases. The ontogenetic change and the intraspecific variation can be clearly discriminated from each other by our method.

Key words: allometry, *Baculites tanakae*, fragmentary specimen, intraspecific variation, shell ontogeny, straight shell

Introduction

A heteromorph ammonoid genus *Baculites* (Lamarck, 1799 in Wright, 1957, 1996) has a peculiar shell characterized by a long straight shaft following the initial coiled conch. The genus stratigraphically ranges within the Upper Cretaceous (Upper Turonian to Maastrichtian), and is distributed almost worldwide (Wright, 1957, 1996).

Its wide distribution and rapid rate of morphological evolution make the genus one of the most important groups among the Upper Cretaceous ammonoids for interregional biostratigraphic correlation. Many species of *Baculites* are known from Japan (Tokunaga and Shimizu, 1926; Matsumoto and Obata, 1963; Matsumoto *et al*, 1980; Matsumoto and Miyauchi, 1984). In particular, several species of *Baculites* occur abundantly in the Upper Cretaceous deposits (Coniacian-Maastrichtian) of Hokkaido and Sakhalin.

However, since shells of *Baculites* consist of an open straight shaft, they occur mostly as fragments, unlike normally coiled ammonoids. Therefore, previous descriptive studies of *Baculites* have largely been based on small numbers of fragmentary specimens. As a result, previous studies have found it difficult to evaluate its ontogeny and intraspecific variation. Although there are several ontogenetic studies of normally coiled ammonoids (Obata, 1965; Hirano, 1975; Tanabe and Shigeta, 1987; Maeda, 1993) and also of a few heteromorph ammonoids (Tanabe, 1975, 1977; Okamoto, 1988a, 1988b; Okamoto and Shibata, 1997) based on well-preserved Japanese materials, no ontogenetic study of *Baculites* has been done previously. It is desirable to develop a method to reconstruct the ontogenetic growth pattern of *Baculites* using fragmentary specimens, which will allow us to confirm or revise their classification within the framework of the population concept.

For this purpose, we obtained many well-preserved specimens of *Baculites tanakae* Matsumoto and Obata, 1963 from the Upper Yezo Group in the Kotanbetsu and adjacent areas (Figures 1, 2). In this paper, we first introduce a new method for calculating the allometry of *Baculites tanakae* and estimating the original total shaft length of the individual from fragmentary specimens.

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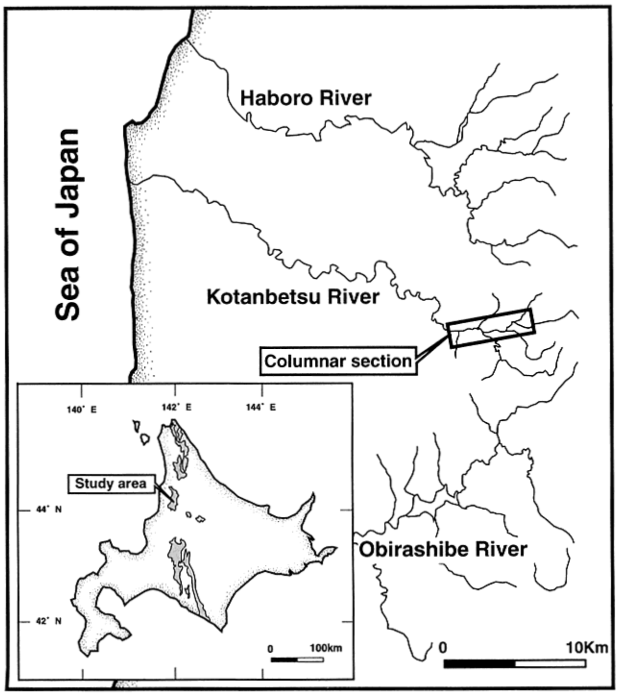

Figure 1. Index map showing the distribution of the Cretaceous Yezo Supergroup in Hokkaido and the location of the study area. The rectangle shows the route-mapped area (Figure 2).

Secondly, we discuss the ontogeny and intraspecific variation of *B. tanakae*, in relation to other *Baculites* species.

Materials

The Upper Yezo Group in the central zone of Hokkaido (Figure 1) contains numerous fossiliferous calcareous nodules both in fine mudstone and in sandy mudstone. *Baculites* tends to occur most abundantly from sandy mudstone facies bearing very fine to medium-grained sands, which was once called the "*Baculites* Facies" by Matsumoto and Obata (1962). In this study, we surveyed the Kotanbetsu and adjacent areas, in which the "*Baculites* Facies" is typically developed in the Coniacian to lowermost Campanian sequence (Figures 2, 3). Figure 3 shows the typical stratigraphic occurrence of *Baculites* species from the Coniacian to the lowermost Campanian sequence in the Kotanbetsu and adjacent areas. The Cretaceous strata exposed in the areas are divided into twelve lithostratigraphic units (Ua-Ul) by Tsushima *et al.* (1958) and Tanaka (1963). Three different species, *B. yokoyamai*, *B. uedae* and *B. tanakae* occur abundantly from the Ub-c unit, the Ug-h unit and the Uk unit representing the typical "*Baculites* Facies," respectively (Figure 3).

Baculites species usually dominate the fossil assemblages. For example, *B. tanakae* accounts for 73% of the total faunal content in a calcareous concretion of about 200 mm in diameter (Figure 4). Other heteromorph ammonoids, inoceramids and other bivalves occur as associate species of *B. tanakae*. Most *Baculites* specimens obtained from the calcareous concretion are incomplete fragments of various sizes (Figure 5.1–5.15). However, their shell tests are very well preserved owing to the chemical conditions. Some of them show aragonite preservation and there is no sign of abrasion.

In this study, we observed more than 400 specimens of *B. tanakae* and 100 specimens of *B. uedae* for comparison. Thirty-five *B. tanakae* and 23 *B. uedae* specimens of various sizes, all of which were free from compactional deformation, were selected for biometric analysis. All population samples of *B. tanakae* were obtained from the Uk unit along the Onkono-sawa Valley (particularly locs. KT2028, KT2028a, KT2029). Population samples of *B. uedae* were obtained from the Uh-g unit along the Kotanbetsu River, Kamino-sawa Valley, Chimei-sawa Valley and Detofutamata River.

Repository of specimens.—All the specimens utilized in this study are housed in the Tokushima Prefectural Museum with prefix of TKPM.GFI except for the holotype of *B. tanakae* (GK.H4288) and *B. uedae* (GK.H4794) in Kyushu University. Material utilized here is listed in Table 1.

Method

In order to clarify shell growth patterns of *Baculites*, biometric analyses were carried out. The following abbreviations are used in this study for the metric characters. L: original total shaft length, l: actual shaft length, H: whorl height.

As all fragmentary specimens of *Baculites* have part of the original shell growth pattern, we can construct the total original shell growth pattern by integrating local shell growth patterns with population samples. According to the general theory of allometry (Nomura, 1926; Huxley and Teissier, 1936; Hayami, 1969; Raup and Stanley, 1971), the relationship between H and L is expected to be represented by the equation $L = \beta H^{\alpha}$ if it represents a single phase of allometry. Here, α and β are constants. Differentiating this equation gives $dH/dL = H^{\alpha-1}/\alpha\beta$. Since it is impractical to calculate dH/dL, H is measured and $\Delta H/\Delta L$ substituted. The values of α and β are found from regressing the data between H and $\Delta H/\Delta L$ with exponential curve of $\Delta H/\Delta L \approx H^{\alpha-1}/\alpha\beta$. Consequently, the allometric equation of α and β, substituting the values of α and β, is defined as the shell growth pattern of *Baculites*. Furthermore, the original shaft length is estimated by $L = \beta H^{\alpha}$, substituting the actual measured values of H. In the case that two variables, X and

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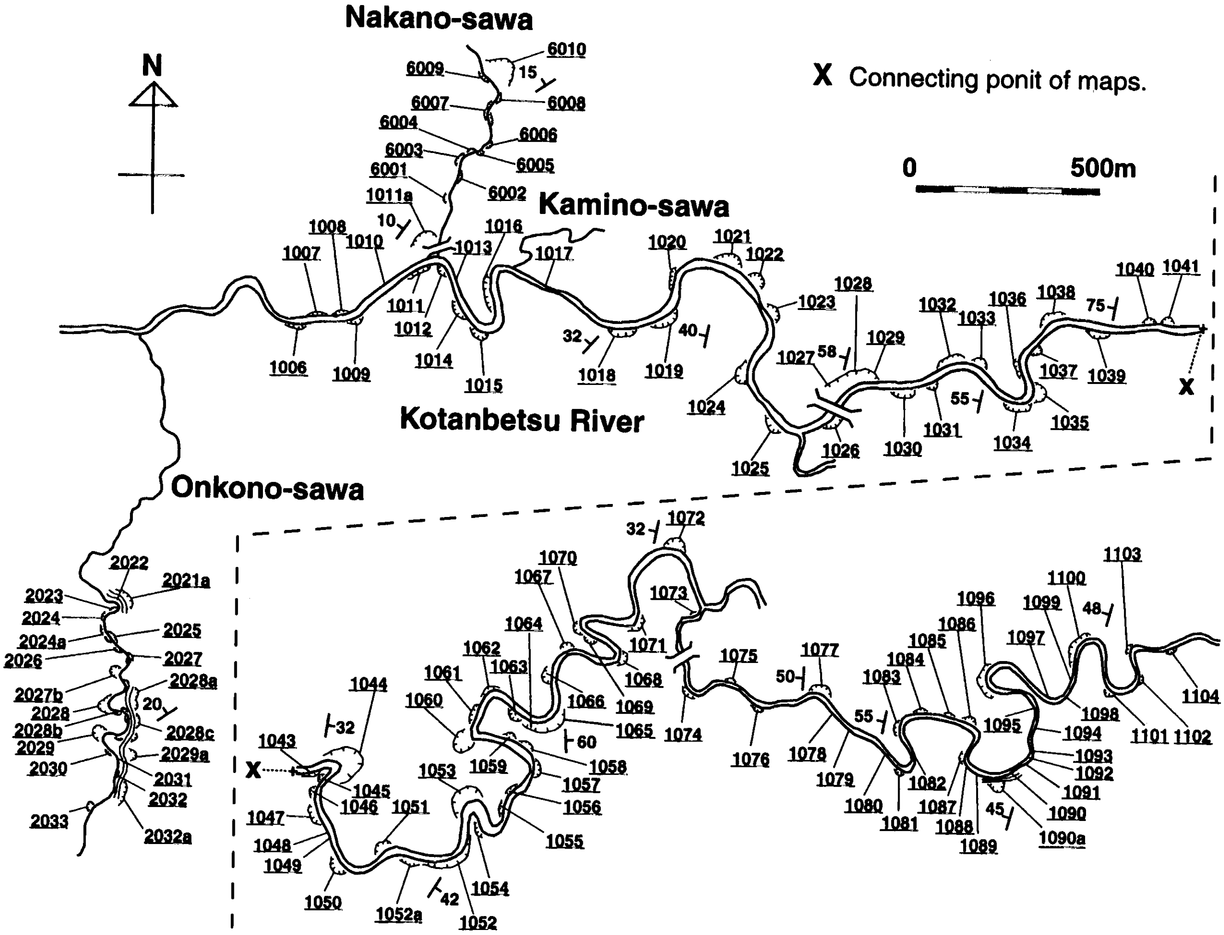

Figure 2. Route map along the Kotanbetsu River, the Nanano-sawa and the Onkono-sawa. Prefix: KT- is abbreviated in the locality numbers.

Y, are equivalent, the regression line is calculated using the reduced major axis method. However, if Y is dependent on X, the least squares method is used (Imbrie, 1956; Hayami and Matsukuma, 1971).

Whorl heights of all specimens of *Baculites* were measured at intervals of 5 mm along the longitudinal axis of the broken shell from each apical posterior end by using a digital micrometer attached to profile projector (Nikon, V-12B, accuracy ± 1 μm) (Figure 6). A local growth rate of *Baculites* shell is assumed for every 25 mm of shaft length, which is measured at 6 points at intervals of 5 mm. For example, the *B. tanakae* shell illustrated in Figure 6 is subdivided into two local growth parts, which range from 0 mm to 25 mm and from 25 mm to 50 mm, respectively. The excess at the adapertual end, from 50 mm to 60 mm, is less than the minimum requirement of 25 mm shaft length, and therefore is not involved in the calculation. In order to maintain accuracy, we rejected specimens less than 25 mm long (fewer than five measuring points: Figure 5.9, 5.11, 5.12, 5.13, 5.15) and specimens deformed by compaction (Figure 5.10, 5.14).

Result

Shell growth rate

According to the allometric formula $L = \beta H^{\alpha}$, the original total shaft length (L) of a *Baculites* shell can be estimated from the relationship between whorl height and actual shaft length of various fragmentary specimens (Figure 5). In order to estimate the shell growth pattern of *Baculites*, a bivariate analysis of whorl height (H) and actual shaft length (l) was performed. Figure 7 shows the relationship between whorl height and actual shaft length within a single fragmentary specimen of *B. tanakae* (TKPM.GFI5108; l = 110.76 mm). A total of 21 plots of H against l at intervals of 5 mm (H_0-H_{20}) within the specimen are shown in

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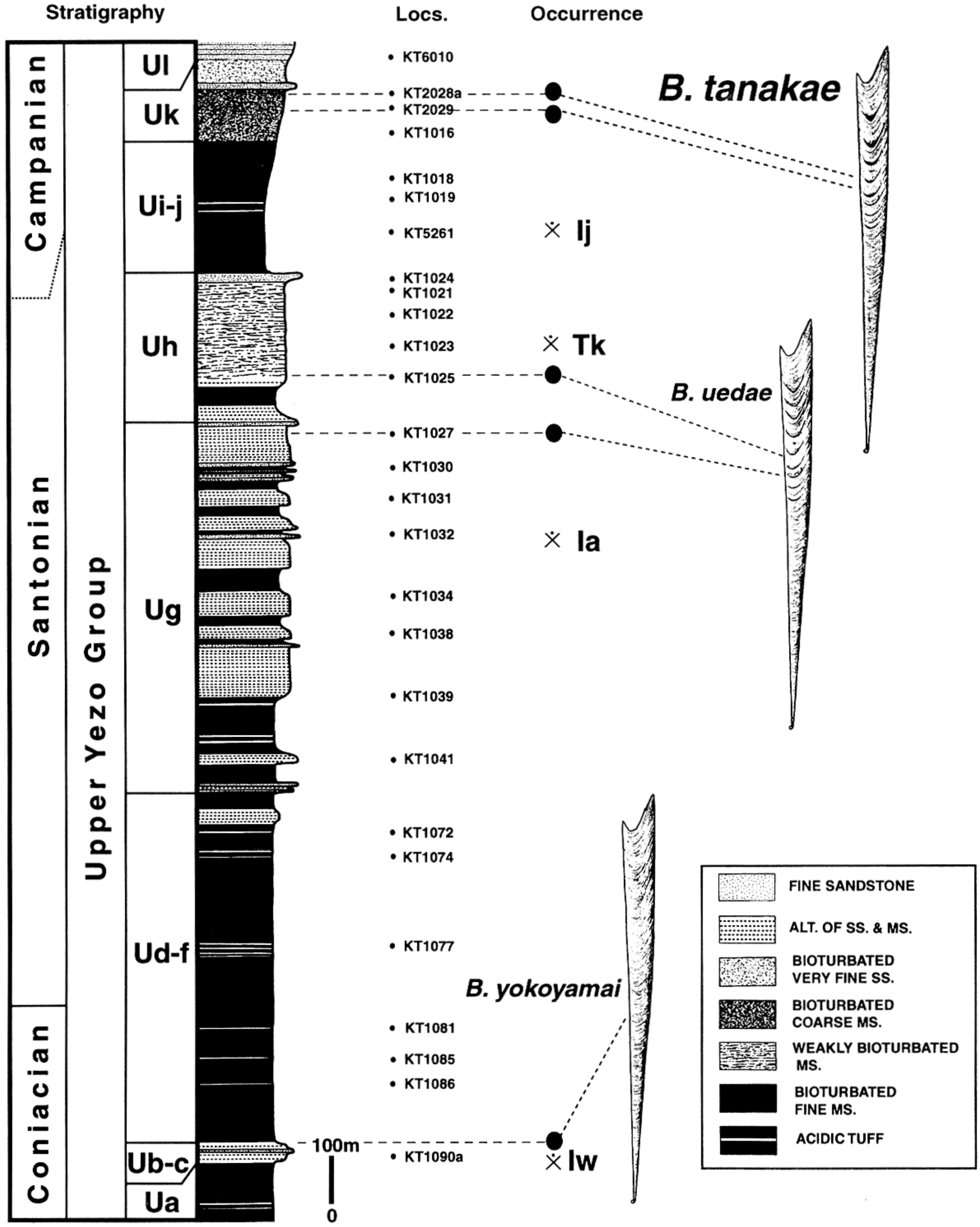

Figure 3. Generalized columnar section of the Upper Cretaceous System in the Kotanbetsu area showing stratigraphic occurrence of *Baculites* species. Solid circle: occurrence of *Baculites* species; a X̂: occurrence of stage diagnostic fossils. Ij: *Inoceramus* (*Platyceramus*) *japonicus*; Tk: *Texanites* (*Plesiotexanites*) *kawasakii*; Ia: *Inoceramus* (*Inoceramus*) *amakusensis*; Iw: *Inoceramus* (*Inoceramus*) *uwajimensis*; SS.: sandstone; MS.: mudstone.

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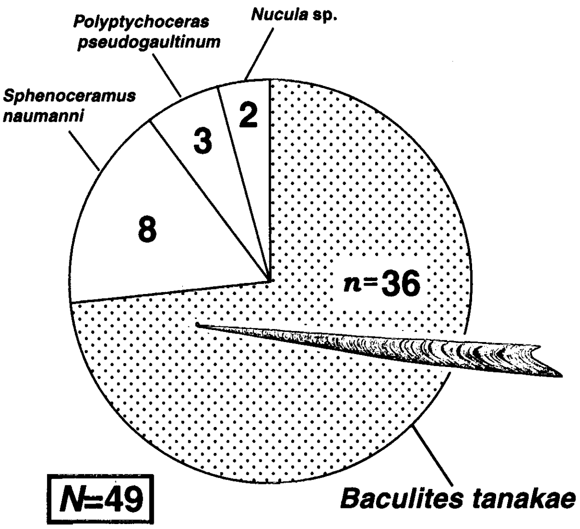

Figure 4. Species composition of a molluscan assemblage from a calcareous nodule of 200 mm diameter, obtained from Loc. KT2029 (Uk unit, lowermost Campanian) along the Onkono-sawa; *n*: individual number; *N*: total number. *Baculites tanakae* accounts for more than 70% of the faunal contents of a calcareous nodule.

Figure 7. The specimen TKPM.GFI5108, plotted with 21 points in Figure 7, has four local growth rates, one for each stretch of 25 mm length. The linear regression line of H on l using the least squares method (Imbrie, 1956; Hayami and Matsukuma, 1971) gives the four formulas shown in Figure 7.

If we assume the linear relationship between whorl height and actual shaft length, the relative growth rate can be represented by the slope of the regression. Local growth rates of all the specimens examined, *Baculites tanakae* and *Baculites uedae*, were calculated in the same way as for TKPM.GFI5108.

Expansion rate

If H is expressed by a linear function of l, namely $H = \mathbf{a}l+\mathbf{b}$, **a** represents the slope of the regression line shown in Figure 7. Then, the rate of the whorl expansion defined as $\Delta H/\Delta L$ is given as follows:

$$\Delta H/\Delta L \approx dH/dL = \mathbf{a}$$

In this case, **a** represents an average value of $\Delta H/\Delta L$

Table 1. List of material. All the specimens used obtained from the Santonian to lowermost Campanian of the Kotanbetsu and its adjacent areas, northwestern Hokkaido. Sampling localities with prefix KT see Figure 2, and with prefix RH see Toshimitsu (1988). Remaining samples are as follows: HB1000P, from river gravel in Detofutamata River, KT1000P, from river gravel in Kotanbetsu River, KT2000P, from river gravel in Onkono-sawa valley, KT3000P, from river gravel in Kamino-sawa valley. Specimens TKPM.GFI5108-5149 and TKPM.GFI5150-5172 are assigned to *B. tanakae* and *B. uedae*, respectively.

Register No.	Locality	Horizon	Register No.	Locality	Horizon
TKPM.GFI5108	KT2028a	L. Campanian	TKPM.GFI5144	KT2029	L. Campanian
TKPM.GFI5109	KT2028a	L. Campanian	TKPM.GFI5145	KT2029	L. Campanian
TKPM.GFI5110	KT2028a	L. Campanian	TKPM.GFI5146	KT2029	L. Campanian
TKPM.GFI5112	KT2028a	L. Campanian	TKPM.GFI5147	KT2029	L. Campanian
TKPM.GFI5113	KT2029	L. Campanian	TKPM.GFI5148	KT2029	L. Campanian
TKPM.GFI5114	KT2029	L. Campanian	TKPM.GFI5149	KT2029	L. Campanian
TKPM.GFI5115	KT2029	L. Campanian	TKPM.GFI5150	KT3000P	U. Santonian
TKPM.GFI5116	KT2029	L. Campanian	TKPM.GFI5151	KT3000P	U. Santonian
TKPM.GFI5117	KT2029	L. Campanian	TKPM.GFI5152	KT3000P	U. Santonian
TKPM.GFI5118	KT2029	L. Campanian	TKPM.GFI5153	KT3000P	U. Santonian
TKPM.GFI5119	KT2029	L. Campanian	TKPM.GFI5154	KT3000P	U. Santonian
TKPM.GFI5120	KT2029	L. Campanian	TKPM.GFI5155	KT3000P	U. Santonian
TKPM.GFI5121	KT2029	L. Campanian	TKPM.GFI5156	KT3000P	U. Santonian
TKPM.GFI5122	KT2029	L. Campanian	TKPM.GFI5157	KT3000P	U. Santonian
TKPM.GFI5123	KT2029	L. Campanian	TKPM.GFI5158	RH5050	U. Santonian
TKPM.GFI5124	KT2029	L. Campanian	TKPM.GFI5159	RH5050	U. Santonian
TKPM.GFI5127	KT2000P	L. Campanian	TKPM.GFI5160	KT3000P	U. Santonian
TKPM.GFI5128	KT2000P	L. Campanian	TKPM.GFI5161	KT1000P	U. Santonian
TKPM.GFI5129	KT2000P	L. Campanian	TKPM.GFI5162	KT3000P	U. Santonian
TKPM.GFI5132	KT2028a	L. Campanian	TKPM.GFI5163	KT3000P	U. Santonian
TKPM.GFI5133	KT2028a	L. Campanian	TKPM.GFI5164	KT3000P	U. Santonian
TKPM.GFI5134	KT2028a	L. Campanian	TKPM.GFI5165	KT1000P	U. Santonian
TKPM.GFI5135	KT2028	L. Campanian	TKPM.GFI5166	KT1000P	U. Santonian
TKPM.GFI5136	KT2028	L. Campanian	TKPM.GFI5167	KT1000P	U. Santonian
TKPM.GFI5137	KT2000P	L. Campanian	TKPM.GFI5168	KT1000P	U. Santonian
TKPM.GFI5139	KT2000P	L. Campanian	TKPM.GFI5169	KT1000P	U. Santonian
TKPM.GFI5140	KT2000P	L. Campanian	TKPM.GFI5170	HB1000P	U. Santonian
TKPM.GFI5142	KT2028a	L. Campanian	TKPM.GFI5171	HB1000P	U. Santonian
TKPM.GFI5143	KT2029	L. Campanian	TKPM.GFI5172	HB1000P	U. Santonian

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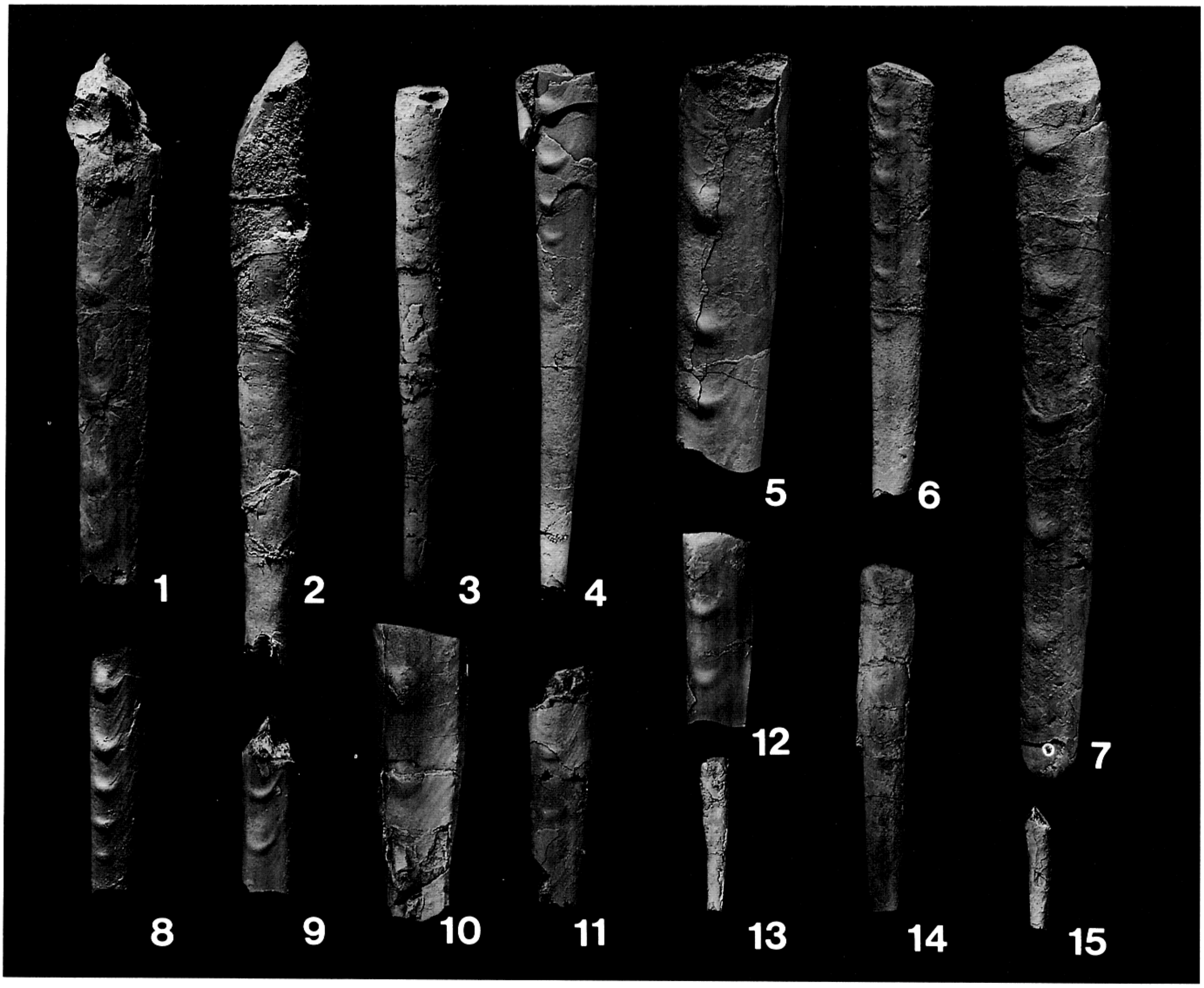

Figure 5. Fragmentary specimens of *Baculites tanakae* Matsumoto and Obata (**1**, **4**–**15**) and *Baculites uedae* Matsumoto and Obata (**2**, **3**). All figures are right lateral views of natural size. **1**. Holotype, GK.H4288, from the lowermost Campanian of the main stream of the Haboro (same specimen as in Matsumoto and Obata, 1963, pl. 17, figs. 2a–d). **2**. Holotype, GK.H4794, from the Santonian of the main stream of the Detofutamata River (same specimen as in Matsumoto and Obata, 1963, pl. 20, figs. 6a–d). **3**. TKPM.GFI5155, Loc. KT3000P from the Santonian of the Kaminosawa Valley. **4**. TKPM.GFI5118, Loc. KT2029 from the lowermost Campanian of the Onkono-sawa Valley (same as in 5–15). **5**. TKPM.GFI5117, Loc. KT2029. **6**. TKPM.GFI5115, Loc. KT2029. **7**. TKPM.GFI5133, Loc. KT2028a. **8**. TKPM.GFI5114, Loc. KT2029. **9**. TKPM.GFI5130, Loc. KT2028b. **10**. TKPM.GFI5141, Loc. KT2000P. **11**. TKPM.GFI5125, Loc. KT2028a. **12**. TKPM.GFI5131, Loc. KT2029. **13**. TKPM.GFI5126, Loc. KT2028a. **14**. TKPM.GFI5138, Loc. KT2028a. **15**. TKPM.GFI5111, Loc. KT2028a.

($\overline{\Delta H/\Delta L}$) within the actual shaft length of each specimen. Consequently, the whorl expansion rate at each of the four growth phases of TKPM.GFI5108 is estimated as follows:

(1) $\overline{\Delta H/\Delta L} = 0.090$
(2) $\overline{\Delta H/\Delta L} = 0.069$
(3) $\overline{\Delta H/\Delta L} = 0.057$
(4) $\overline{\Delta H/\Delta L} = 0.056$

Figure 8 shows the relationship between $\overline{H}$ and $\overline{\Delta H/\Delta L}$ in 53 sections of 35 specimens of *Baculites tanakae*. When a specimen involves two or more local rates (l = 50 mm), plural rates are plotted independently. Mean H value ($\overline{H}$) of 6 measurements is plotted on the graph. The values of $\overline{\Delta H/\Delta L}$ were concentrated around 0.05 to 0.1 (Figure 8). The regression line was obtained by the reduced major axis method, resulting in the following equation (Figure 8):

$$\Delta H/\Delta L = 0.220H^{-0.502} \ (r = -0.639)$$

Figure 9 shows the relationship between $\overline{H}$ and $\overline{\Delta H/\Delta L}$ in 34 sections of 23 specimens of *Baculites uedae*, which oc-

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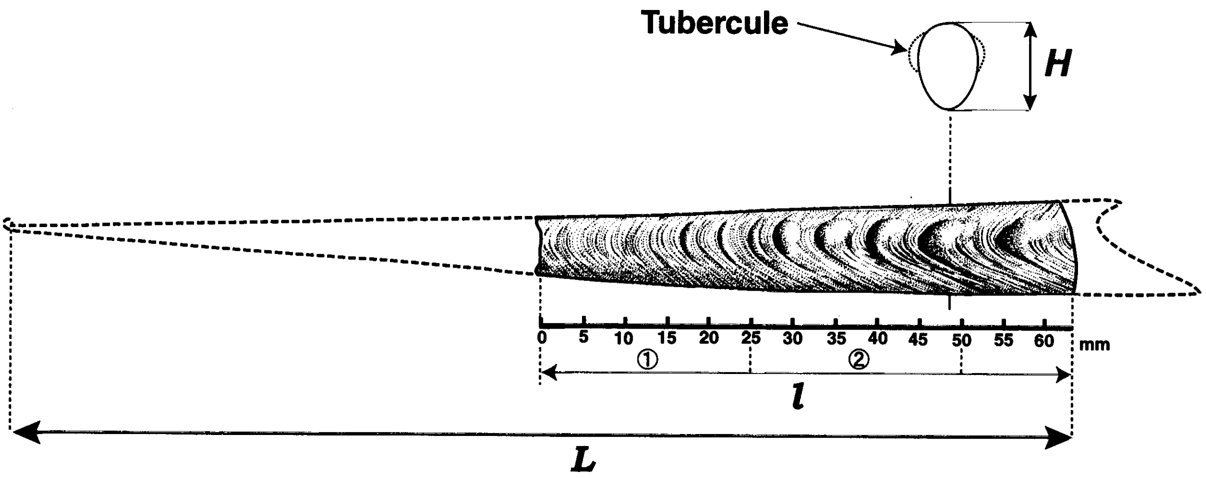

Figure 6. Morphology of *Baculites tanakae* Matsumoto and Obata and biometric dimensions. Actual shell length (l), shell height (H) are biometrically measured. Within a fragmentary specimen, H was measured at intervals of 5 mm along the shaft length from the apical end. L: Estimated total shaft length.

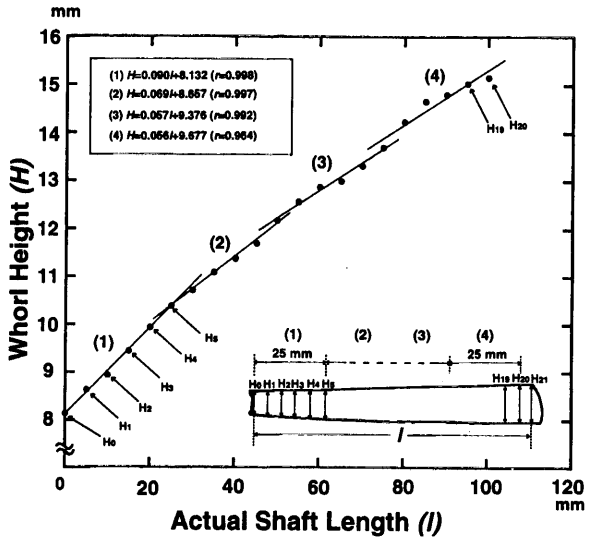

Figure 7. Relation of shell height (H) versus actual shell length (l) for a fragmentary specimen of *B. tanakae* (TKPM.GFI5108; actual shell length: 110.763 mm). Plots consists of 21 measurements of shell height (H_0-H_{20}) at intervals of 5 mm in shell length (l). Relationship between H and l is approximated by a linear function. A long shaft is subdivided into four parts of 25 mm length (1)–(4). Four straight lines are formulated as shown at the left upper side. The regression line is obtained using the least squares method of H on l (Imbrie, 1956; Hayami and Matsukuma, 1971).

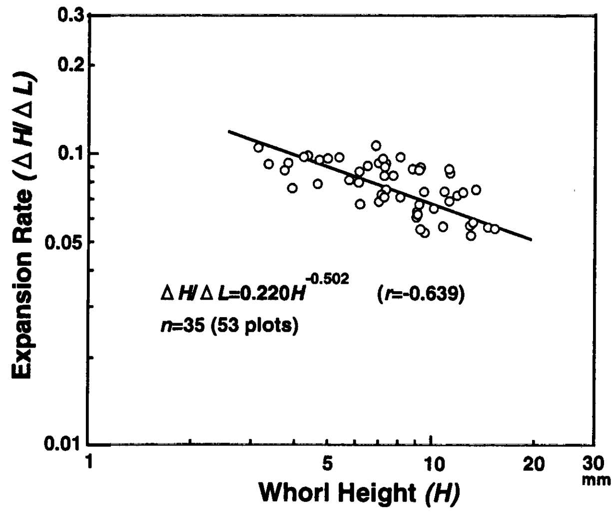

Figure 8. Diagram showing shell enlarging rates (= growth rates) of various sizes of *Baculites tanakae*. Values of enlarging rate ($\Delta H/\Delta L$) against whorl height (H) in 53 sections of 35 specimens are plotted. Mean H value of 6 points measured within a local part of 25 mm long is plotted. The regression line with the reduced major axis is shown in this figure.

curs from the underlying Ug-h unit (Santonian) in the Upper Yezo Group. The regression line using the major axis method gives the following equation (Figure 9):

$$\Delta H/\Delta L = 0.254H^{-0.681} \ (r = -0.741)$$

The shell growth pattern of *B. uedae* is clearly distinguishable from that of *B. tanakae* by its much steeply inclined line. The difference between their growth patterns is particularly clear in the late growth stage.

In order to identify or to discriminate the two species statistically, we carried out a significance test for the difference of allometric slopes between the two species (Imbrie, 1956). The slope of allometry in a log-log plot is given as:

$$\alpha = S_y/S_x,$$

where S_x and S_y are the standard deviations of x and y, respectively. The standard errors of the slopes are given as:

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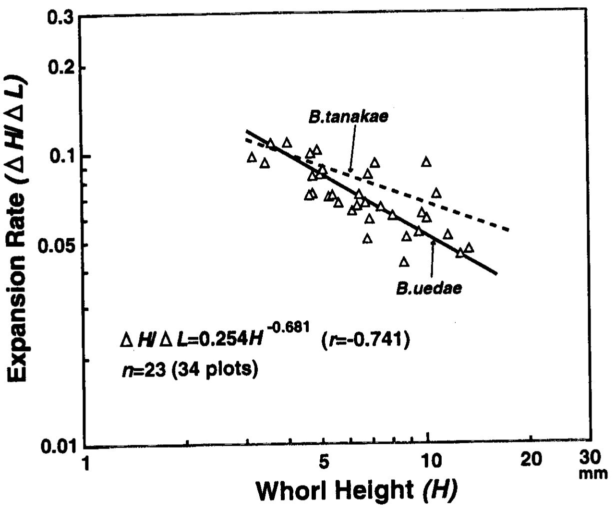

Figure 9. Diagram showing shell enlarging rates of various sizes of *Baculites uedae*. Values of enlarging rate ($\Delta H/\Delta L$) against whorl height (H) in 34 sections of 23 specimens are plotted. Mean H value of 6 points measured within a local part of 25 mm long is plotted. The regression line (solid line) with the reduced major axis is given in the figure. A broken line shows shell enlarging rates of *Baculites tanakae* ($\Delta H/\Delta L$ = $0.220H^{-0.502}$), which is statistically discriminated from that of *B. uedae* at 95% reliability.

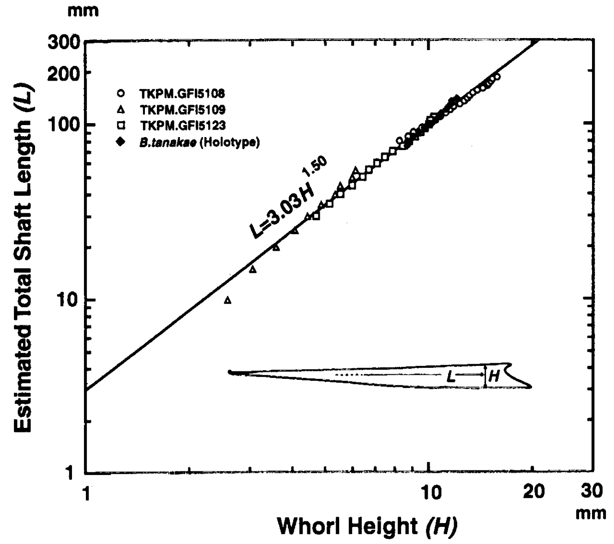

Figure 10. Diagram showing the allometry of total shell length (L) with respect to the shell height (H) obtained from integration of the regression curve of $\Delta H/\Delta L$ (Figure 8). The measurements of shell height (H) of fragmentary specimens (TKPM.GFI5108, 5109 and 5123) and the holotype of *Baculites tanakae* (GK.H4288) are well fitted along the regression line. For plotting the representative value of H is selected from the median part of each shaft. For example, TKPM.GFI5109 involves 10 measurements (H), and the fifth measurement from the apical end is adopted for plotting. Likewise, TKPM.GFI5123 involves 17 measurements (H), and the eighth measurement from the apical end is adopted for plotting.

$$\sigma_{\alpha_1} = \alpha_1\sqrt{(1-r_1^2/P_1)}$$

$$\sigma_{\alpha_2} = \alpha_2\sqrt{(1-r_2^2/P_2)},$$

where α_1 and α_2 are the slopes of the reduced major axes of two species, r_1 and r_2 and the correlation coefficients between two variables and P_1 and P_2 are the numbers of intervals of individuals measured in respective samples (Kermack and Haldane, 1950). We can test the statistical significance of the difference in slopes by the following equation:

$$K = \alpha_1 - \alpha_2/\sqrt{(\sigma_{\alpha_1}^2 + \sigma_{\alpha_2}^2)},$$

where K has a normal distribution.

Discrimination between slopes of two reduced major axes is arbitrarily defined at the confidence level of 95% (Hayami and Matsukuma, 1971). In slopes of the two species examined, the value of $|K|$ exceeds 1.96. Therefore, the difference of the reduced major axes on double logarithmic scatter diagrams is significant at the 95% confidence level, and two samples can be discriminated by the difference of their specific growth patterns.

Estimation of allometric shell growth pattern

The relationship between H and L is expected to be represented by the equation $L=\beta H^{\alpha}$, where α and β are constants. Consequently, integrating a regression curve of $\Delta H/\Delta L=0.220H^{-0.502}$ obtained from measurements on variable specimens of *Baculites tanakae*, we get as an estimate of the allometric formula of *B. tanakae*:

$$L = 3.03H^{1.50} \text{ (Figure 10).}$$

The raw data of H in specimens TKPM.GFI5108, 5109, 5123 and the holotype (GK.H4288) are plotted along the curve $L = 3.03H^{1.50}$ (Figure 10). For plotting, the representative value of H that is substituted in the formula is taken from the median part of each shaft. The results show the reasonability of using this curve to represent the shell growth pattern of *B. tanakae*, at least after the early growth stage (H > 2.5 mm). Thus, we can infer the original total shaft length of fragmentary specimens including the missing shaft length.

Observation of sculptural pattern

Five specimens (TKPM.GFI5108, 5109, 5123, 5124 and 5127) of *Baculites tanakae* of various shell sizes are arranged in order of shell size based on the estimated original total shaft length (L) (Figure 11). The arranged photographs clearly illustrate the ontogenetic change of shell ornament. The shell ornament of *B. tanakae* consists of three successive phases: 1) smooth phase with fine growth lines, 2) phase of crescent ribs, and 3) tuberculate phase.

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In general, the ribs and tubercles become prominent with increasing shaft length. For example, in the specimen TKPM.GFI5127, the boundary between the smooth phase and the ribbed phase is expected to be situated at the distance of 41 mm from the lost apex, and the ribbed phase grades into the tuberculate phase at 51 mm in *L* (Figure 11.2). This successive change of shell ornament is observed in most individuals of *B. tanakae*.

The interval of the ribbed phase is considerably short than the other phases. In some specimens, the smooth phase changes directly to the tuberculate phase without the ribbed phase (e.g., TKPM.GFI5124: Figure 11.4). However, the order of the phase expression seems to be fixed during ontogeny.

Figure 11 also demonstrates that the timing of switching the phase of shell ornament is fairly variable among individuals of *Baculites tanakae*. For example, the ribbed phase starts at 24 mm in shaft length in the smallest specimen TKPM.GFI5109 (Figure 11.1), while in the largest specimen TKPM.GFI5108 it appears at 107 mm in shaft length (Figure 11.5).

Discussion

The newly introduced biometric analysis of *Baculites* is particularly advantageous in the following aspects: (1) quantification of allometric growth pattern, (2) documentation of change of shell ornament with ontogeny, and (3) evaluation of intraspecific variation of shell ornament. All of them are well applicable to taxonomic paleontology.

In previous taxonomic studies, the shell expansion rate (= growth rate) has been used as one of the important taxonomic characters of *Baculites* species (Tokunaga and Shimizu, 1926; Matsumoto and Obata, 1963; Matsumoto *et al*, 1980; Matsumoto and Miyauchi, 1984). For example, *Baculites tanakae* examined in this study was originally described as a species in which "the shell is rather small, expanding moderately or rapidly in the early growth-stage but slowly in the late" (Matsumoto and Obata, 1963, p. 51, lines 37–38). Likewise, *Baculites uedae* was described as a species whose "shell is comparatively small and tapers rapidly or moderately" (Matsumoto and Obata, 1963, p. 41, lines 1–2). However, the previous taxonomic definitions of these species were based on qualitative observations of small samples, and they were often confused. In contrast, our result in Figure 9 indicates that the specific difference of growth pattern between the two species can be revealed and defined quantitatively.

Second, ontogenetic change of shell morphology can be documented based on estimated total shaft length (*L*). Figure 11 clearly illustrates the ontogenetic change of shell ornament in *Baculites tanakae*, i.e., 1) smooth, 2) crescent rib and 3) tuberclate phase.

Third, evaluation for intraspecific variation of shell morphology is possible by our method. Matsumoto and Obata (1963, p. 51, lines 42–43; p. 52, lines 1–2) described the shell of *B. tanakae* as "ornamented with a dorsolateral row of tubercles, which are typically, but not always, strong, widely spaced and asymmetrically crescent or elongated obliquely or parallel to the long axis of the shell". Matsumoto and Obata (1963, p. 52, lines 41–43) also described a few doubtful fragmentary specimens which lack the diagnostic intense tubercles, and assigned them to a variant of *B. tanakae*. However, it is possible that several specimens lacking typical tubercles merely represent the smooth or crescent-rib phase. Ontogenetic change and intraspecific variation have been sometimes confused by previous studies. In contrast, they are clearly distinguishable by our method (Figure 11).

The present biometric analysis can serve to revise the diagnostic character of *B. tanakae* given by Matsumoto and Obata (1963: see above) from the viewpoint of the population concept. It is also applicable to taxonomic and paleobiologic studies of other *Baculites* species.

Concluding remarks and perspective

In this paper, we have introduced a method that reconstructs the lost ontogenetic trajectory of a fragmentary shell of *Baculites*. The reconstructed growth pattern throughout the whole ontogeny provides a quantitative diagnosis of the morphology of *Baculites*, and allows us to estimate the missing shaft length of fragmentary specimens. By using the estimated total shaft length, we detect ontogenetic change of shell ornament of *Baculites tanakae*, which grades from 1) smooth to 3) tubercle via 2) crescent rib, and its wide intraspecific variation separately. We believe that our method is useful for solution of taxonomic problem of *Baculites*.

In the Coniacian to lowermost Campanian sequence of the Upper Yezo Group, the successive occurrence of possibly closely allied *Baculites* species, i.e., *B. yokoyamai* to *B. tanakae* via *B. uedae* has been recognized (Figure 3). These species have been distinguished by differences in the ontogenetic change of surface ornament; namely, *B. yokoyamai* with a smooth surface throughout ontogeny, *B. uedae* with smooth and crescent-rib phases, and *B. tanakae* with smooth, ribbed, and tuberculated phases. Hereafter, the evolution of these *Baculites* species will be revealed by investigating ontogeny and intraspecific variation in shell ornament in deal.

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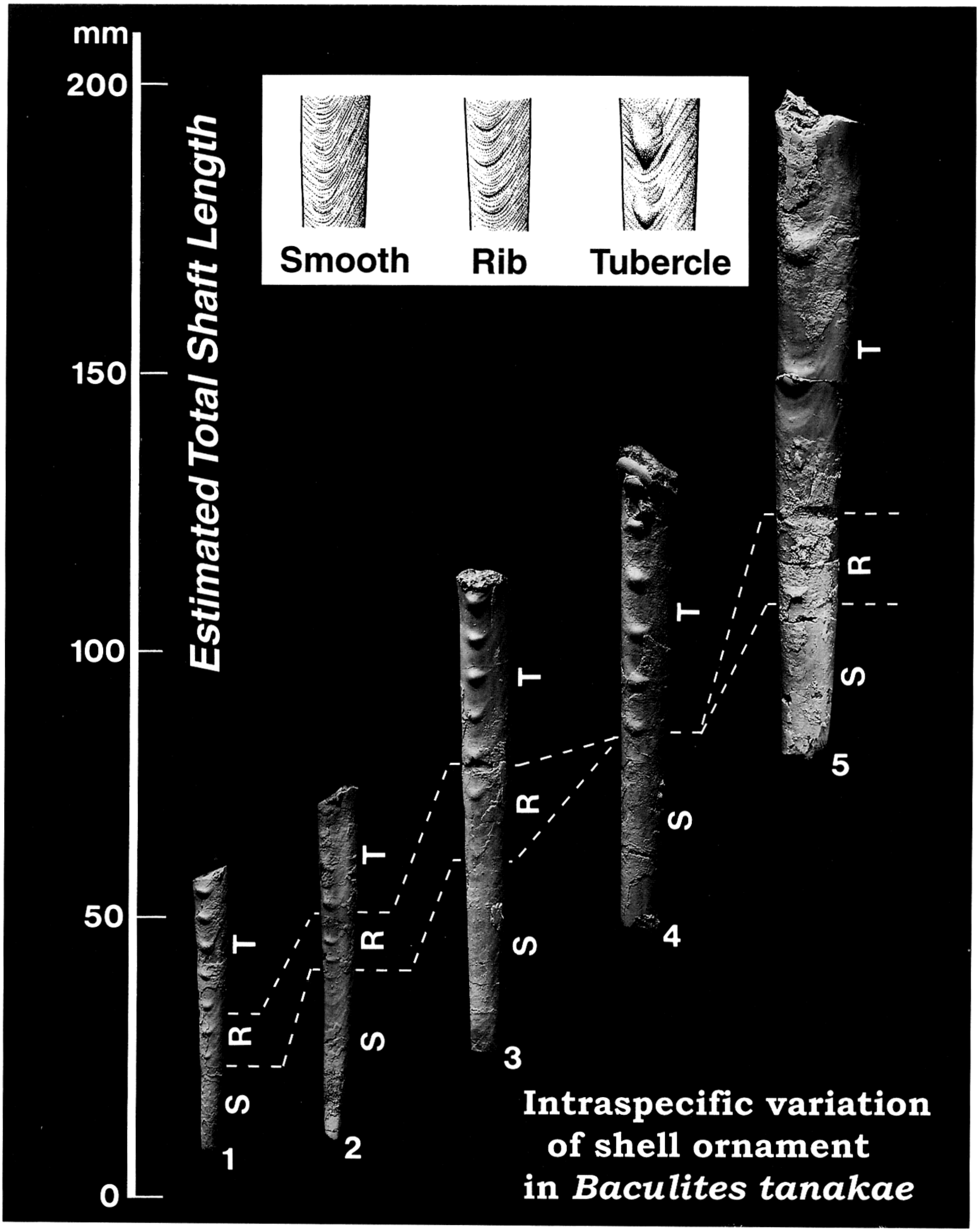

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← **Figure 11.** *Baculites tanakae* Matsumoto and Obata. All figures are right lateral views of natural size and from the lowermost Campanian of the Onkono-sawa Valley. 1. TKPM.GFI5109, Loc. KT2028a. 2. TKPM.GFI5127, Loc. KT2000P. 3. TKPM.GFI5123, Loc. KT2029. 4. TKPM.GFI5124, Loc. KT2029. 5. TKPM.GFI5108, Loc. KT2028a. S: smooth phase R: ribbed phase T: tuberculate phase

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