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Ontogenetic Study of Late Cretaceous *Gaudryceras tenuiliratum*

Hiromichi HIRANO

Abstract

The ontogeny and variation of *Gaudryceras tenuiliratum* were studied on seven samples from the Santonian of Kawakami and Naibuchi of Saghalien and Haboro, Oyubari and Urakawa of Hokkaido.

The growth pattern of the radius length is one of the most important factors which decide the shape of ammonites. The ontogenetic patterns were allometrically analysed on seven samples with reference to the individual and the interpopulational variation. The growth ratio is fairly stable not only intrapopulationally but also interpopulationally. The position of the critical point is also highly stable in each population but geographically shows some variability. The radius length is controlled by the growth ratio and the initial growth index and mostly is not different significantly in three defined growth stages. The growth pattern of the whorl width was analysed in one sample but the possibility of the sexual dimorphism was not detected. The pattern of the umbilical radius length shows the ontogenetic change less delicately in comparison with that of the radius length. The ontogenetic change and the variation of the septal thickness and the complexity of suture were analysed, and the role of these characters is discussed. The periodicity of the appearance of constriction was clarified and is compared with that of some recent mollusks. The quantitative data of the surface ornamentation is shown and its ontogenetic change is described. The individual and the interpopulational variation of the protoconch size was analysed and compared with that of other ammonites. The comprehensive description of *G. tenuiliratum* is given based upon the analyses mentioned above.

Contents

I. Introduction

Gaudryceras is one of the late Cretaceous genera of the Lytoceratina which is nearly world-widely distributed. Its phylogeny has not yet been clarified

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sufficiently, although some authors (e. g., WIEDMANN, 1962) attempted to interpret it. So far as the available works are concerned, this genus seems to be composed of species in which evolutionary rate are comparatively slower than those of the Ammonitina, but the morphological difference between an ancestral species and an assumed descendant seems to be clear.

Among various distributed areas Japan-Saghalien seems to be one of the most suitable area for the study of *Gaudryceras* at the populational level owing to the wide distribution of the fossil beds and good preservation. In fact, a study on the interspecific relation of the *Gaudryceras* from Japan and Saghalien was attempted more than thirty years ago (MATSUMOTO, 1941).

Although it is an indispensable step for the phylogenetic study to clarify the geographic variation age by age, such a work needs much time. Accordingly as the first step I analyse and describe local population samples. The comprehensive consideration on *Gaudryceras* will be given in the other paper after the study of some Japanese and Saghalien species of *Gaudryceras*.

G. tenuiliratum YABE is distributed only in Japan and Saghalien and is regarded as an important key which directly connects with the Campanian and Maastrichtian species of this genus and indirectly a certain genus (personal communication from MATSUMOTO).

The purpose of this article is to clarify the characteristics of *G. tenuiliratum* from the Santonian of Hokkaido and Saghalien at the population level, with special reference to the ontogeny and variation.

Acknowledgements.—This study has been done under the supervision of Professor Tatsuro MATSUMOTO. I am also indebted to Dr. Kametoshi KANMERA, Dr. Itaru HAYAMI, Dr. Tsugio SHUTO and Dr. Ikuwo OBATA who gave me invaluable suggestions on the basic problem of palaeontology as well as every kind of facility. Thanks are extended to Professor Tokio SHIKAMA of the Yokohama National University who introduced me in the study of ammonites, Mr. Masafumi ARITA and Kazushige TANABE for friendly discussion. Professor Tetsuro HANAI generously let me borrow the collection of Professor Tatsuro MATSUMOTO stored in the University Museum of the University of Tokyo. Miss Mutsuko HAYASHIDA helped me in drawing figures and Mrs. Yukiko HIRANO cooperated with me in various kinds of affairs.

II. Growth and variation

A. Material and method.—The materials used in this study were obtained from Kawakami and Naibuchi districts of South Saghalien and Haboro, Oyubari and Urakawa districts of Hokkaido (Fig. 1). Most of these collections are stored in the Type Room of the Kyushu University (prefix; GK) and others are in the

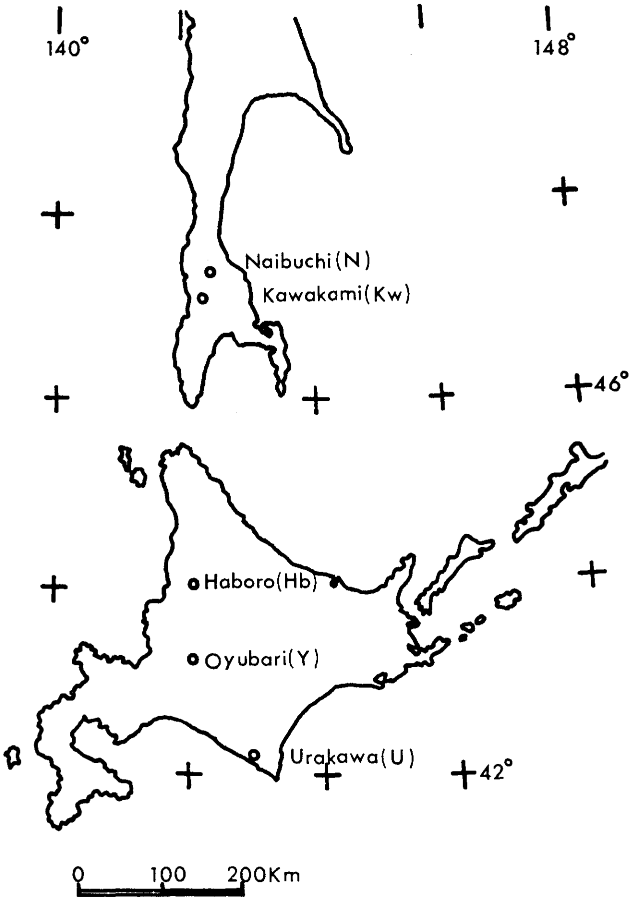


Fig. 1. The sample localities of the fossil populations of *G. tenuiliratum*

University Museum of the University of Tokyo (prefix; UMUT).

The materials occurred in the calcareous concretion (the diameter is from less than 10 cm to more than 100 cm, and 30 cm is most abundant) and are not deformed except the body chamber. It is corroborated by the fact that the coefficient of correlation on the regressed line of the relative growth shows very high value.

The following is the basic information on the samples, including the locality, stratigraphic position, sample size and the collector. The sample number referred to the detailed locality number.

Sample Kw: Kawakami Coal Mine district of Saghalien; Santonian; 13; NAGAOKA.

Sample N22ZB: loc. N22Z of the Naibuchi area, Saghalien (MATSUMOTO, 1942); Zone of Mh6β of MATSUMOTO (1942), Santonian (MATSUMOTO ed., 1954; MATSUMOTO, 1959); 14; T. MATSUMOTO.

Sample N22Z1: loc. N22Z1 of the Naibuchi area (Matsumoto, 1942); the stratigraphic position is the same as above; 3; T. Matsumoto.

Sample N182f: loc. N182f of the Naibuchi area (Matsumoto, 1942); the stratigraphic position is the same as above; 3; T. Matsumoto.

Sample Hb: loc. R417 of the River Sakasa, Haboro district of Hokkaido; base of *I. japonicus* Subzone, Upper Santonian; 3; T. Matsumoto et al.

Sample Y: loc. Y5008 and Y5034 as the pebble fallen from an outcrop in the R. Pankehorokayuparo, Oyubari district; *I. naumanni* Zone, Santonian; 2; T. Matsumoto

Sample U: loc. U600c8 of Urakawa district (Matsumoto, 1942); Santonian (*op. cit.*; Matsumoto, ed., 1954; Matsumoto, 1959); 1; T. Matsumoto.

The growth of whorls was measured along the median plane on a polished section. As shown in the plates the accurate median plane can be recognized by the trace of the siphuncle in every whorl. The basic line of measurement is at first drawn from the aperture of the protoconch to the opposite side where the line is the longest diameter. After setting the first basic line, the second base line is drawn, which perpendicularly crosses the first base line at the middle point (Fig. 2). Measurement is done by using Olympus biocular microscope with Nikon micrometer (the minuteness 1μ), Nakamura manufactory microscope with two dimensional measure (50μ) and Nikon profile projector (1μ). The whorl width is measured by Nihonsokki micrometer (10μ). In all cases measurement is done three times for the same part. The suture line is drawn by using Wild microscope.

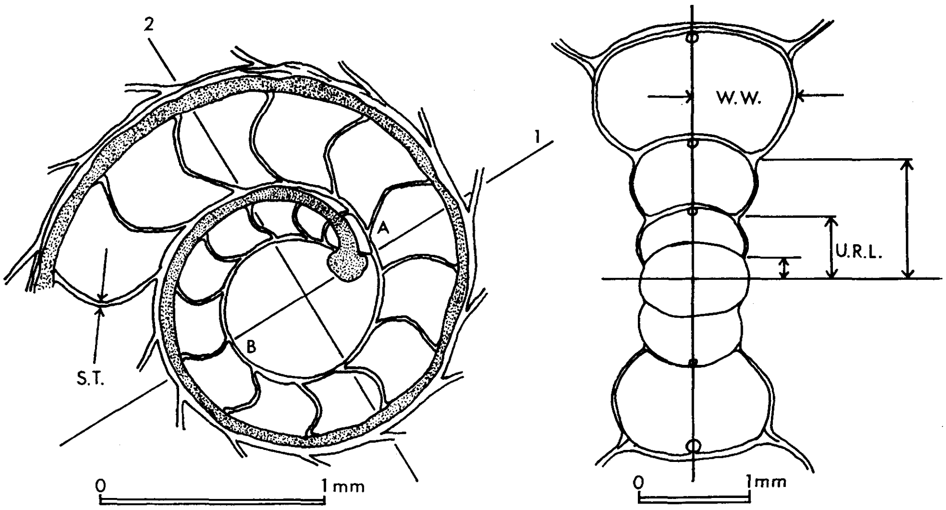


Fig. 2. The diagramatic median section and the cross section showing the base lines for measurement. S. T.: Septal thickness; U. R. L.: Umbilical radius length; W. W.: Half of whorl width.

B. Growth pattern of whorl.—For the morphology and classification of ammonites the growth pattern of whorl is one of the most important characters, because the basic shape of ammonite shell depends on it. Furthermore, this character is also important for the ecological analysis of ammonites, in view of the recent advance in functional morphology.

The whorl is increased by the accretion in the pattern of the logarithmic spiral (Fig. 3) and the form is expressed by a power function ($y=\beta x^{\alpha}$).

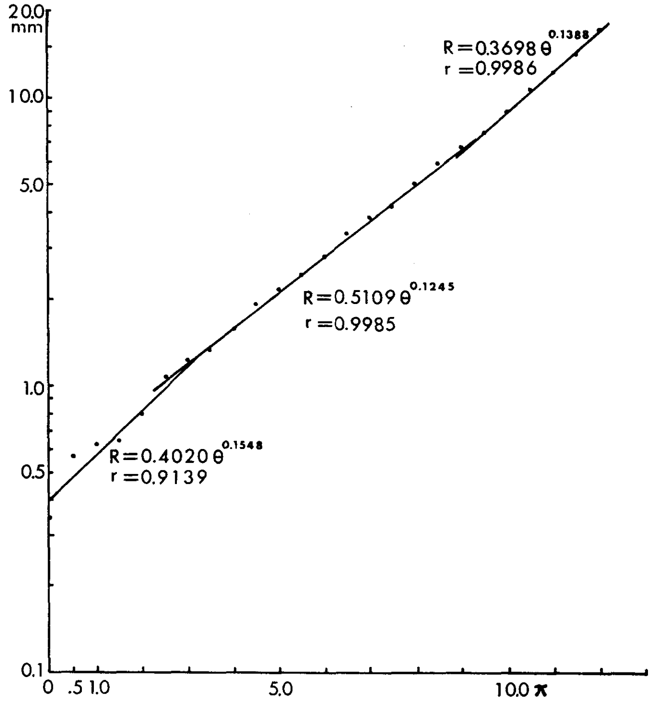


Fig. 3. An example of the growth pattern of the radius length to the spiral. GK. H 5027 of the Sample Kw.

In this section mainly the growth of the radius length as the integral of the whorl height is analysed and additionally that of whorl width and that of umbilical radius length are analysed on each population sample. The individual ontogeny is, at first, analysed on each sample, the variables of a sample are calculated and finally the range of the population mean is stochastically computed.

1. *Radius length.*—The distribution of the growth ratios of the radius length to the spiral is examined for Sample Kw and Sample N22ZB respectively by chi-square test. The results indicate that they are not significantly different from the normal distribution ($P \gg 0.05$). As I will mention in the later sections, this kind of test is done at first on each character in the case when the sample size is sufficiently large

When we draw a relative growth pattern on a logarithmic coordinate, we often find that the slope changes somewhat abruptly in a certain growth point as shown in Fig. 3. When there is such a point called a critical point on a growth pattern, the pattern is not represented by a single power function. As mentioned in the later sections, a change of a growth ratio of a certain character often relates with those of other characters. Therefore in such a polyphasic allometry it is better to analyse the ontogeny stage by stage divided by the critical point. The critical point at first recognized on the graph of the individual growth. Next to that, the propriety of the critical point is reexamined by the coefficient of correlation and the Student's *t*-test on the growth ratios between the growth stage preceding to the critical point and that succeeding to the critical point in each sample, inasmuch as the position of the critical point is little in variation and almost all the specimens in a sample have the critical points at the same growth point (Table 1).

Table 1. The growth ratio and the initial growth index of the radius length to the spiral in the seven samples of *G. tenuiliratum* from Kawakami (Kw) and Naibuchi(N), South Saghalien, and Haboro(Hb), Oyubari(Y) and Urakawa(U), Hokkaido.

Sample	Stage (n)	$\bar{\alpha}$	$\bar{\alpha} \pm t_{005}$ SE	SD	CV	$\bar{\beta}$	$\bar{\beta} \pm t_{005}$ SE	SD	CV
Kw	2.5- 9.5	0.1234	0.1221-0.1247	0.0022	1.8116	0.4969	0.4830-0.5108	0.0231	4.6419
(N=13)	10.0-13.5	0.1356	0.1322-0.1390	0.0057	4.2374	0.3760	0.3561-0.3959	0.0330	8.7678
N22ZB (N=14)	2.5- 4.0	0.1099	0.1028-0.1170	0.0123	11.176	0.5131	0.4773-0.5489	0.0620	12.086
	4.5-10.0	0.1182	0.1165-0.1199	0.0029	2.4893	0.5070	0.4890-0.5250	0.0312	6.1461
	10.5-15.0	0.1347	0.1293-0.1401	0.0094	6.9376	0.3483	0.3039-0.3928	0.0770	22.096
N22Z1 (N=3)	2.5- 4.0	0.1001	0.0874-0.1129	0.0051	5.1237	0.5916	0.5648-0.6185	0.0108	1.8281
	4.5-10.5	0.1185	0.1140-0.1231	0.0018	1.5371	0.5395	0.4562-0.6229	0.0336	6.2192
	11.0-14.0	0.1414	0.1231-0.1596	0.0074	5.1979	0.3122	0.1833-0.4411	0.0519	16.619
N182f (N=3)	2.5- 4.0	0.1001	0.0839-0.1164	0.0065	6.5288	0.5918	0.5427-0.6409	0.0198	3.3411
	4.5-10.0	0.1154	0.1139-0.1168	0.0058	0.5010	0.5592	0.5347-0.5837	0.0099	1.7610
	10.5-13.5	0.1367	0.1334-0.1400	0.0013	0.9747	0.4123	0.1123-0.7123	0.1208	29.293
Hb	2.5- 9.5	0.1208	0.1191-0.1225	0.0007	0.5508	0.5021	0.4813-0.5229	0.0084	1.6662
(N=3)	10.0-13.5	0.1338	0.1082-0.1594	0.0103	7.6962	0.3724	0.1694-0.5753	0.0817	21.945
Y	2.5-10.0	0.1207	0.0991-0.1423	0.0024	2.0289	0.4816	0.0689-0.8942	0.0459	9.5387
(N=2)	10.0-12.5	0.1349	0.1223-0.1475	0.0014	1.0485	0.3480	0.1320-0.5640	0.0240	6.9084
U(N=1)	2.5-10.0	0.1189	-	-	-	0.4850	-	-	-

Explanation of Plate 24

(All in natural size)

Gaudryceras tenuiliratum Yabe

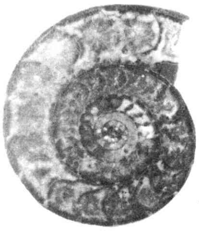
Figs. 1-13: Sample Kw.

1. GK. H. 5037, 2. GK. H. 5023, 3. GK. H. 5038, 4. GK. H. 5039, 5. GK. H. 5029, 6. GK. H. 5019, 7. GK. H. 5031, 8. GK. H. 5035, 9. GK. H. 5019, 10. GK. H. 5027, 11. GK. H. 5032, 12. GK. H. 5020, 13. GK. H. 5021.

Fig. 14: Sample N150a, GK. H. 2258.

Figs. 15-16: Sample R417.

15. GK. H. 5702, 16. GK. H. 5700.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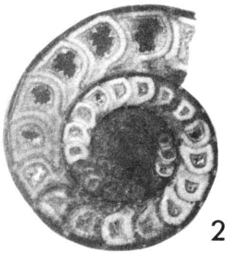
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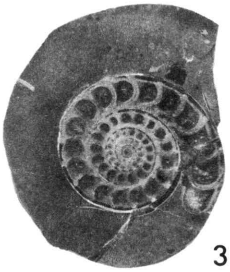
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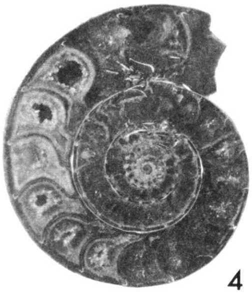
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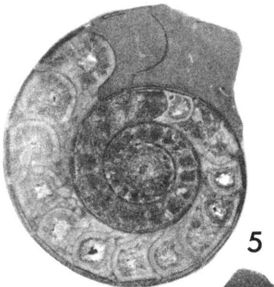
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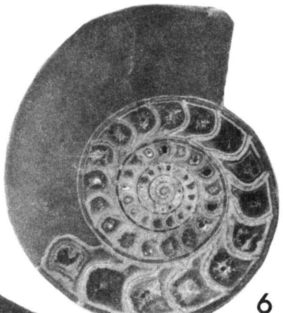
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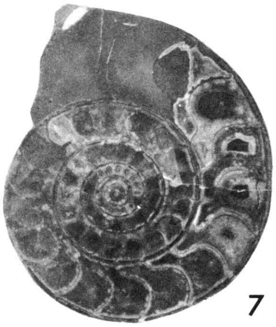
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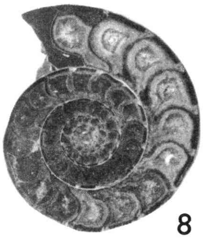
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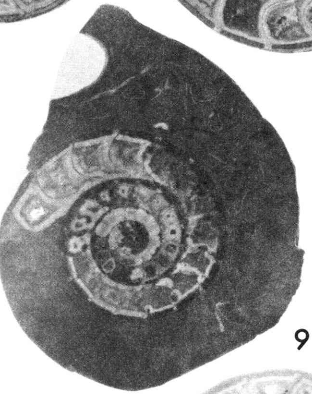
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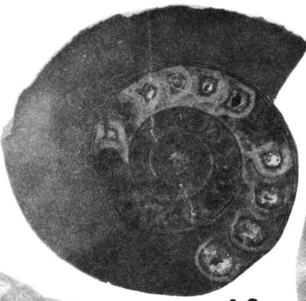
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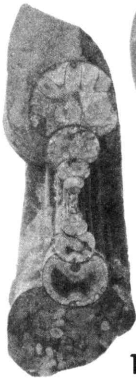
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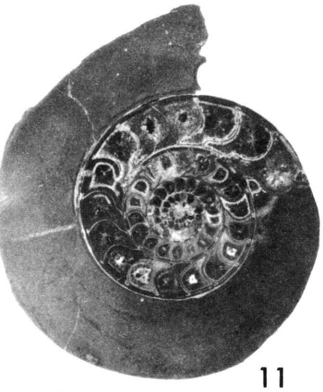
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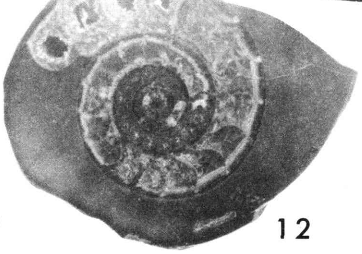
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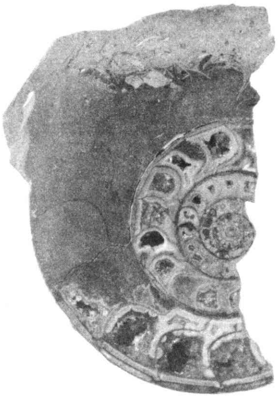
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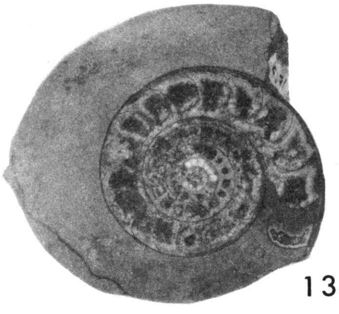
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H. Hirano: *Gaudryceras tenuiliratum*


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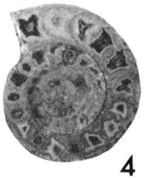
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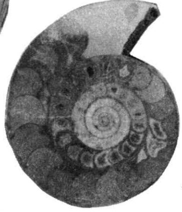
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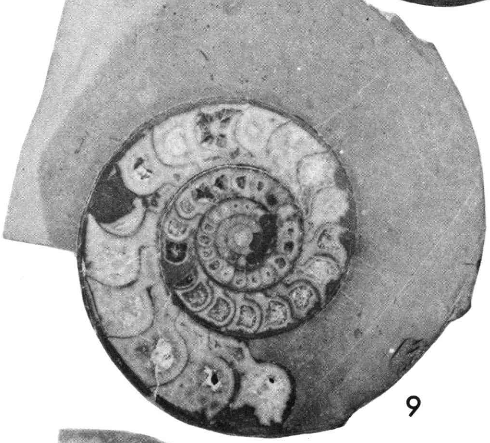
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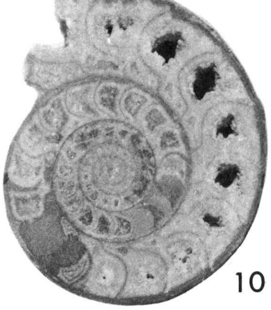
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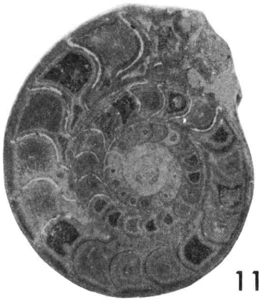
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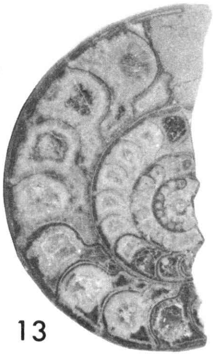
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H. HIRANO: *Gaudryceras tenuiliratum*

As the coefficient of correlation is always significant in the growth stage after the first critical point, the statistical consideration is done on the growth stages after the first critical point. There are two or three critical points in the ontogenetic development of *G. **tenuiliratum***. All the samples clearly show critical points at the growth point somewhere between 2.0π and 2.5π and at the point about 11.0π. In the samples N22ZB, N22Z1 and N 182f one more critical point is shown, although less clearly, at the growth point between 4.0π and 4.5π.

The intrapopulational variation of the growth ratio is fairly small (Table 1). The difference of the growth ratios between two samples is examined stage by stage (Tables 2-4). The results show that the difference is often significant in the early ontogenetic stage (7 combinations in 2.5π-4.0π) and is rarely significant (5 combi., in 4.5π-10.5π) or not significant ($11.0\pi\pm$) in the later stages. The degree of non-overlap of two population curves (MAYR, 1969) is indicated by the

Table 2. *t*-test for the difference of the growth ratio of the radius length to the spiral (2.5-4.0π) and the coefficient of difference.

	Kw	N22Z-B	N22Z-1	N182f	Hb	Y	U
Kw	*	4.0532	7.7778	6.1599	2.3435	1.7770	2.1680
N22Z-B	0.9310	*	1.3307	1.3209	3.3191	1.2075	0.7075
N22Z-1	3.1918	0.5632	*	0.0000	7.0320	5.1718	3.1930
N182f	2.6782	0.5213	0.0000	*	2.8599	2.1562	1.1761
Hb	0.8966	0.8385	3.5690	1.4861	*	0.1090	2.3506
Y	0.5870	0.7347	2.7467	1.1910	0.0323	*	0.6570
U	2.0455	0.7317	3.6863	1.3538	2.7143	0.7500	*

When there is a significant difference between the variances, Welch's method is applied.

Right upper: *t*-test; Significant difference $[0.01<P<0.05]$ is indicated by an underline and very significant difference $[P<0.01]$ is by a dashed underline.

Left lower: Coefficient of difference; Combination of which percent of non-overlap is larger than 90% is indicated by a dashed underline.

Explanation of Plate 25

(All in natural size)

Gaudryceras tenuiliratum YABE

Fig. 1: Sample U, GK. H. 960.
Fig. 2: Sample R417, GK. H. 5701.
Fig. 3: Sample Y, GK. H. 5704.
Figs. 4-13: Sample N22ZB.
4. GK. H. 2209-5, 5. GK. H. 2206-2, 6. GK. H. 2209-2, 7. GK. H. 2209-1, 8. GK. H. 2206, 9. GK. H. 2207-1, 10. GK. H. 2207-2, 11. GK. H. 2206-3, 12. GK. H. 2208-1, 13. GK. H. 2209-6.

Table 3. t-test for the difference of the growth ratio of the radius length to the spiral (4.5-11.0 π), and the coefficient of difference.

	Kw	N22Z-B	N22Z-1	N182f	Hb	Y	U
Kw	*	5.5125	4.4169	2.3790	2.3435	1.7770	2.1680
H22Z-B	1.0196	*	0.1781	1.3272	1.6684	1.2503	0.2390
N22Z-1	1.2250	0.0638	*	0.8949	2.8160	1.3909	0.1998
N182f	1.0000	0.3218	0.4079	*	1.6283	1.2106	0.5277
Hb	0.8966	0.7222	0.9200	0.8308	*	0.1090	2.3506
Y	0.5870	0.4717	0.5238	0.6463	0.0323	*	0.6570
U	2.0455	0.2414	0.2222	0.6034	2.7143	0.7500	*

Table 4. t-test for the difference of the growth ratio of the radius length to the spiral (11.0 π∼), and the coefficient of difference.

	Kw	N22Z-B	N22Z-1	N182f	Hb	Y
Kw	*	0.2991	1.5306	0.3304	0.4336	0.1710
N22Z-B	0.0596	*	1.1560	0.7774	0.1491	0.0293
N22Z-1	0.4427	0.3988	*	1.1078	1.0407	1.1867
N182f	0.1571	0.1869	0.5402	*	0.4856	1.9710
Hb	0.1125	0.0457	0.4294	0.2500	*	0.1429
Y	0.0986	0.0185	0.7386	0.6667	0.0940	*

coefficient of difference and the coefficient is computed stage by stage (Tables 2-4). The degree of non-overlap is often large in the early ontogenetic stage, usually small in the middle stage and always very small in the late stage. The combination which is significant in the difference of α does not always show the large degree of non-overlap of the frequency curve. This may be resulted from the difference of the amount of variation.

Next to that, the differences of the radius length at three points 3.0 π, 7.0 π and 11.0 π, which may represent three different stages divided by critical points, were examined for the estimation of the influence of the growth ratio to the size of a shell (Tables 5-6). In this examination, significant differences are indicated in four combinations at 3.0 π stage, five combinations at 7.0 π stage and three combinations at 11.0 π stage.

From the above examination it follows that a few among the combinations which show the significant differences of the radius length at 3.0 π, 7.0 π and 11.0 π points are significantly different in α. Half or more (two fourth at 3.0 π point and four fifth at 7.0 π point) may have the origin of the significant differences out of α. Conversely, even when the significant differences of α are found in

Table 5. The radius length (mm) at the three defined stages, 3.0 π, 7.0 π and 11.0 π, in descending order.

Sample	N	Mean	SD	CV
Kw	13	1.1717	0.0720	6.1456
N22Z-B	14	1.1129	0.0550	4.9405
N22Z-1	3	1.2007	0.0567	4.7261
N182f	3	1.2052	0.0236	1.9581
Hb	3	1.1856	0.0356	3.0033
Y	2	1.1458	0.0835	7.2881
U	1	1.1131	-	-
Kw	13	3.6631	0.2165	5.9095
N22Z-B	14	3.4366	0.1297	3.7742
N22Z-1	3	3.6617	0.1466	4.0048
N182f	3	3.6318	0.0336	0.9247
Hb	3	3.6068	0.0829	2.2985
Y	2	3.4382	0.1773	5.1578
U	1	3.3099	-	-
Kw	13	11.565	0.9624	8.3216
N22Z-B	12	10.368	0.5755	5.5505
N22Z-1	3	11.180	0.3557	3.1817
N182f	2	10.949	0.0262	0.2393
Hb	3	11.062	0.4270	3.8598
Y	1	10.803	-	-
U	0	-	-	-

Table 6. t-test for the difference of the radius length at the three defined stages, 3.0 π, 7.0 π and 11.0 π (from upper to lower). (Data same as table 5)

	Kw	N22Z-B	N22Z-1	N182f	Hb	Y	U
Kw		S	N	N	N	N	N
N22Z-B			S	S	S	N	N
N22Z-1				N	N	N	N
N182f					N	N	N
Hb						N	N
Y							N
U							
Kw		V	N	N	N	N	N
N22Z-B			S	S	S	N	N
N22Z-1				N	N	N	N
N182f					N	N	S
Hb						N	N
Y							N
U							
Kw		V	N	S	N	N	N
N22Z-B			S	N	N	N	N
N22Z-1				N	N	N	N
N182f					N	N	N
Hb						N	N
Y							N
U							

fairly numerous combinations, only in a few of them the differences of the size are found. For further analyses of this growth mode a method must be devised to separate out the aspect of b value variation due to differences in α as mentioned by Gould (1966).

Summarizing the observation, the following tendencies are concluded:

1) The interpopulational variation of growth ratio decreases with growth and no significant difference is found in the later stage.
2) The difference of α does not always reflect the size.
3) The difference of D (Kw-N22ZB, N22ZB-Hb) does not reflect Y-intercept in the growth stage from 2.5 π to 4.0 π (Tables 7, 15).

Table 7. t-test for the difference of β of the regression formula of the radius length to the spiral ($2.5\pi-4.0\pi$ or 11.0π). (Data same as the table 1)

	Kw	N22ZB	N22Z1	N182f	Hb	Y	U
Kw		N	V	V	N	N	N
N22ZB			S	N	N	N	N
N22Z1				N	V	S	S
N182f					V	S	S
Hb						N	N
Y							N
U							

2. *Umbilical radius length.*—Here the mode of growth of the radius length from the protoconch to the umbilical seam of the outer whorl (Table 8, Fig. 2) is analysed on Sample N22ZB.

Table 8. The growth pattern of the umbilical radius length to the spiral ($4.5\pi-13.0\pi$) in *G. tenuiliratum* (N22ZB) and the difference to that of *G. denseplicatum* (N22ZA).

Sample	N	$\bar{\alpha}$	SD	CV	F	t	$\bar{\beta}$	SD	CV	F	t
N22Z-A	3	0.1208	0.0046	3.7806	1.8182	2.7887	0.3639	0.0082	2.2493	21.136	2.3991
N22Z-B	15	0.1147	0.0034	2.9760			0.4171	0.0374	8.9554		

In the growth of the umbilical radius length the critical point exists at the growth point between 2.0π and 2.5π and this change corresponds to that of the radius length. After this change, the growth ratio of the umbilical radius length continues constantly to the stage 13.0π. It follows that the growth mode is known more precisely in the analysis of the median plane than that of the side view.

3. *Whorl-width.*—In Sample N22ZB and N22Z1 of *G. tenuiliratum* the growth stages from 7.5π to 14.0π are available for the study of the growth of the whorl width (Table 9). There is commonly a critical point somewhere between 11.0π and 12.5π, after which the growth ratio of the whorl width to the spiral becomes

Table 9. The growth ratio and the initial growth index of the whorl-width to the spiral ($7.5\pi-14.0\pi$) in the two samples of *G. tenuiliratum*, from Naibuchi, Saghalien. The variables of one synpatric sample (N22ZA) of *G. denseplicatum* are shown for comparison.

Sample	Stage (π)	N	$\bar{\alpha}$	SD	CV	$\bar{\alpha} \pm t_{005}$ SE	F	t	$\bar{\beta}$	SD	CV	$\bar{\beta} \pm t_{005}$ SE	F	t
N22Z-A	8.0-11.0	3	0.1142	0.0045	3.9159	0.1030-0.1254	9.2388	1.9188	0.2375	0.0526	22.136	0.1069-0.3682	3.6813	1.3236
N22Z-B	8.0-11.0	14	0.1005	0.0120	11.903	0.0936-0.1074			0.3182	0.1009	31.697	0.2600-0.3765		
	11.0-14.0	14	0.1300	0.0307	23.642	0.1123-0.1477			0.2209	0.1795	81.238	0.1173-0.3245		
N22Z-1	7.5-12.0	3	0.1031	0.0116	11.272	0.0743-0.1319			0.2825	0.0621	21.999	0.1281-0.4368		

larger. This change appears 1 π to 2 π later than the change of the radius length. The histogram of the growth ratios during the stages from 8.0 π to 11.0 π of Sample N22ZB are somewhat bimodal. However, the chi-square test does not indicate a significant difference from the normal distribution. The difference is too small for interpreting the bimodality as sexual dimorphism.

C. Growth pattern of septum and suture

1. Septum thickness.—The septum is very thin, being less than 0.020 mm in thickness before the nepionic constriction and less than 0.400 mm at 12 π stage (the sixth whorl). The individual ontogenetic change of the septal thickness in Sample N22ZB is analysed and the mean value at each growth stage is plotted (Fig. 4). The ontogenetic development shows four changes of the growth ratios during the stages from 0 π to 13.5 π. They are at 1.0 π-1.5 π, 3.5 π-4.0 π, 6.5 π-7.0 π and 9.0 π-9.5 π. The growth ratio is smaller in the first stage before the first critical point, becomes larger in the second, decreases in the third and increases

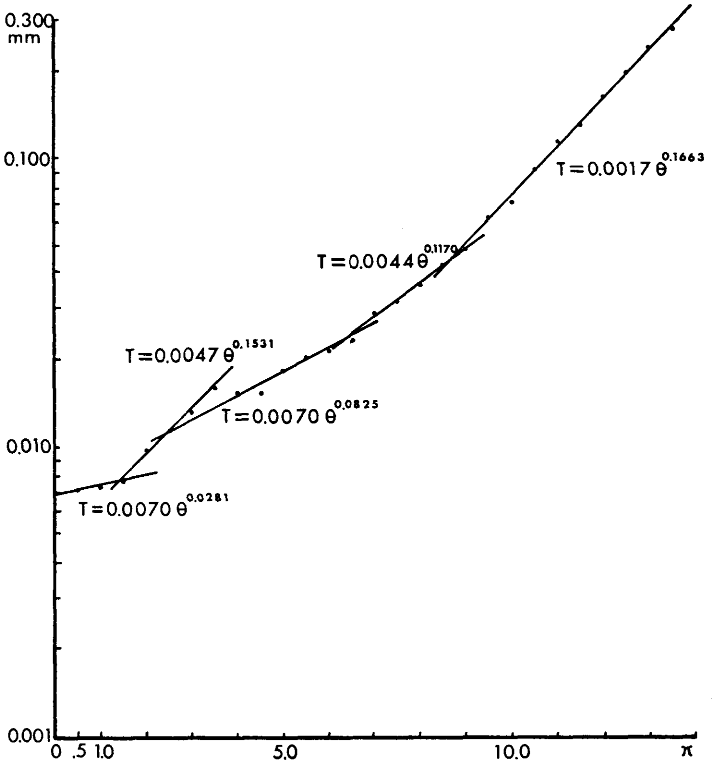


Fig. 4. The growth pattern of the septal thickness to the spiral of the Sample N22ZB (Mean values of the sample are plotted). Although the regression formula of the second growth stage crosses that of the third at the stage 2.5 π, it is not appropriate to regard the cross point 2.5 π as the second critical point for such a phenomenon that the septal thickness decreases after the stage 3.5 π is common in the sample.

Fig. 5. The ontogenetic development and the variation of suture in *G. tenuiliratum*. Those of *G. striatum* are illustrated for comparison.
A–H: UMUT. I. 3842B, *G. tenuiliratum* from loc. N401, Naibuchi. A: the 2nd septum, B: at the end of the 1st whorl, C: the 1st and a half whorl, D: the 2nd whorl, E: the 3rd whorl, F: the 4th whorl, G: the 5th whorl, H: the 6th and a half whorl; I–O: GK. H 5043, *G. tenuiliratum* from Kawakami. I: during the course of the 1st whorl, J: at the end of the 1st whorl, K: the 1st and 100°, L: the 2nd whorl, M: the 3rd whorl, N: the 4th whorl, O: the 5th and 300°; P–T: GK. H 5071, *G. striatum* from Kawakami. P: the $\frac{1}{2}$ whorl, Q: a little before the end of the 1st whorl, R: the 1st whorl, S: the 3rd whorl, T: the 6th whorl. As the surface is dissolved by HCl, the suture is partly simplified in specimen UMUT. I 3842B.

in the fourth and again in the fifth stage.

The ontogenetic change of the septal thickness is fairly well correlated with that of the radius length, the whorl width and the umbilical radius length (Fig. 3). That is, the first critical point of the growth of septal thickness appears a little earlier than that of the radius length. The second critical point of the growth of the septal thickness is correlated with the second critical point of the growth of the radius length and the first critical point of the growth of the umbilical radius length. After this point the growth ratio of the radius length increases and that of the umbilical radius length decreases. Therefore the cross area of the whorl tends to increase but the growth ratio of the septal thickness decreases. At the third critical point of the septal thickness no corresponding change occurs in other characters. The fourth critical point is correlated with the critical point of the radius length and whorl width. After this point the cross area of the whorl increases much more than in the earlier stages. The growth ratio of the septal thickness also tends to increase. From a little earlier stage the suture line becomes more complex. The change of the growth of the radius length is roughly correlated with that of the septal thickness, but they do not precisely coincide each others.

2. *Suture line.*—The suture line is symmetrical between the right and left sides of the whorl, and though the elements of the saddle and lobe become complex and are deepened in response to the growth, the ontogenetic change of each element is traceable when the observation begins from very early stage. The expression method of KULLMANN and WIEDMANN (1970), who followed and revised that of WEDEKIND, is employed, because this method is reasonable and convenient for the expression of the ontogeny. The use of HCl often brings to much simplification of the suture line. Therefore usually the shell is peeled off physically. The variation of the ontogenetic change of the suture line from the first suture is observed on *G. tenuiliratum* (H 5043, I 3842B) and *G. striatum* (H 5071) (Fig. 5). As mentioned by MATSUMOTO (1941), they seem to be phylogenetically related. In *G. tenuiliratum* no differences are shown concerning the basic elements, as mentioned by MATSUMOTO (1941) and more comprehensively by KULLMANN and WIEDMANN (1970). That is, at least in the ontogeny of *G. tenuiliratum* and *G. striatum*, the sutural formula is ELUIs within the growth stage of the first 2π (the first whorl), indicating the characteristics of Lytoceratina in such an early stage, and at about the end of the first 2π the formula becomes $ELU_2\ U_1Is$, which is the characteristics of Gaudryceratinae. After these stages the suture becomes more complex in response to growth and L is divided at about 6π (the third whorl) but the basic elements are constantly $ELU_2U_1(=S)$ Is. The rate of complication is nearly equal in the samples from Naibuchi and Kawakami as shown in the figures. The individual variation of the suture line

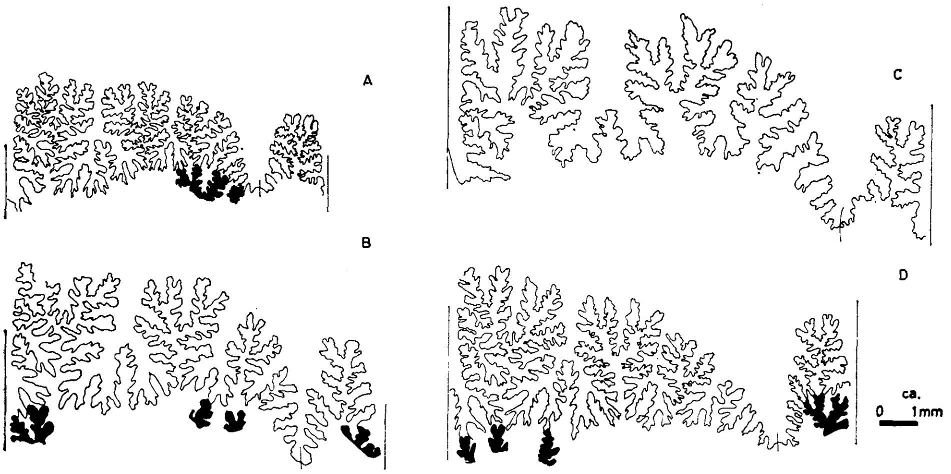


Fig. 6. The variation of suture line of *G. tenuiliratum.* A: H 5022 from Kawakami, B: H5044 from Kawakami, C: H 5043 from Kawakami, D: I 3842B from Naibuchi. All the suture lines are sketched at about the 6th whorl stage.

at a given stage, 12π (a clear suture from the stage 11π to 13π is sketched), is studied on three specimens from Kawakami and one specimen from Naibuchi, Saghalien (Fig. 6). Not only three coexistent specimens from Kawakami but also a specimen from Naibuchi show the same characteristics on the basic elements and the other minute parts. Like this, the variation of the sutural pattern is very slight. Furthermore, the number of the small lobules within $U_1(=S)$ is constantly five in those four specimens. The uniformity of the suture has also been mentioned by Palframann (1966, 1967, 1969) on the Jurassic ammonites.

D. Constriction.—Although it is well known that many ammonites have constrictions, their structures, periodicity and bearing are not well known. In this article the structure and the periodicity are observed and analysed, and the bearing is preliminarily considered in comparison with some other living and fossil molluscs.

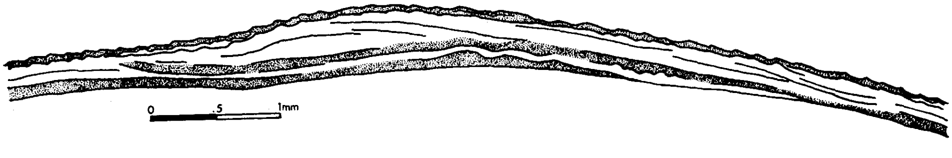


Fig. 7. The shell structure of the constriction at 12π stage of *G. tenuiliratum.* No. GK. H 2206-1 of the Sample N22ZB.

The structure of the constriction of *G. tenuiliratum* (Fig. 7) is the same as that of *Saghalinites wrighti* and *Scaphites* (*Discoscaphites*) sp. (Birkelund, 1967; Birkeluud and Hansen, 1968), although the boundary of the layer are somewhat obscure in my material. It is also the same as that of living *Nautilus pompilius* (Fig. 8) and some gastropods. This structure reveals that the new

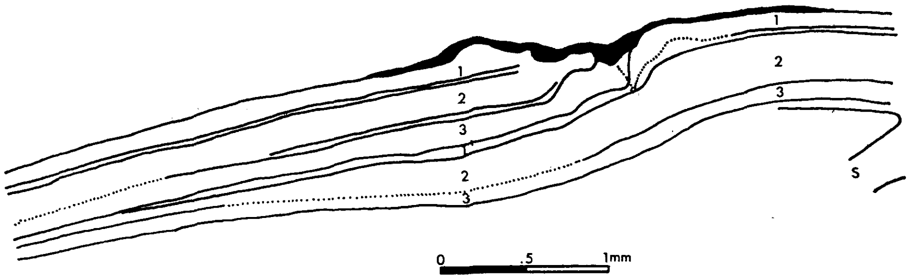


Fig. 8. The shell structure of the nepionic constriction of *Nautilus pompilius* (LINNE) (Specimen No. 7 of PP.). The layers are distinguished and numbered as 1, 2 and 3 from the ventral side. S: Septum. The black part on the ventral margin is the deposits of the organic matter.

layers are secreted, in the order from the outer layer, on the inner side of the shell layer of the preceding stage after the arrest of growth.

The interspace of the constrictions was measured with the result that the peak of the frequency exists in the range from 0.25 π to 0.75 π (Fig. 9). The ontogenetic change of the interspace was analysed, and in two specimens (H 22-02, H 2203) the significant correlation (95 % CL) was found (Fig. 10). In the specimens H 2201, the correlation is significant after the stage 8 π. These phenomena also reveal that the interspace decreases with growth. The number of the subcostae between two constrictions clearly decreases with growth at least after the stage 9 π (Fig. 10). In other words, the number of the subcostae is maximum at the stage 9 π (Table 14).

The first constriction called the nepionic constriction (or the first varix) occurs at a constant position (Table 10). *G. denseplicatum* and even recent *Nautilus pompilius* show the dominant stability on the positon of the nepionic

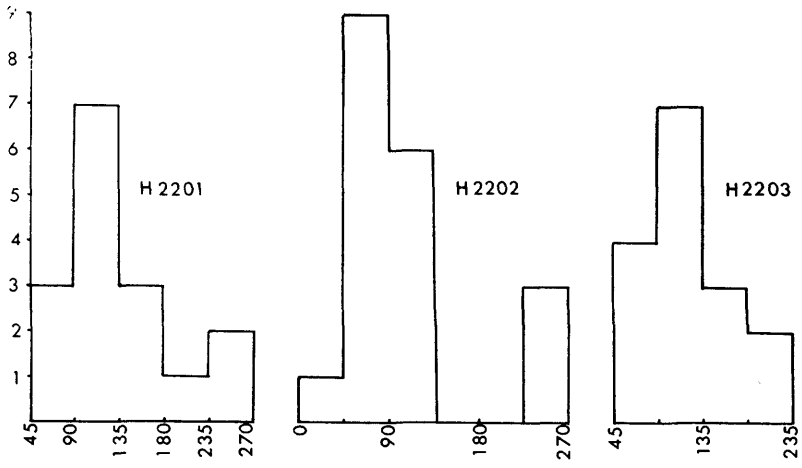


Fig. 9. The histograms of the interval of the constrictions. The abscissa is the degree of interval, and each written numerical value under the abscissa belongs to the left column. Sample N22Z1 of *G. tenuiliratum*.

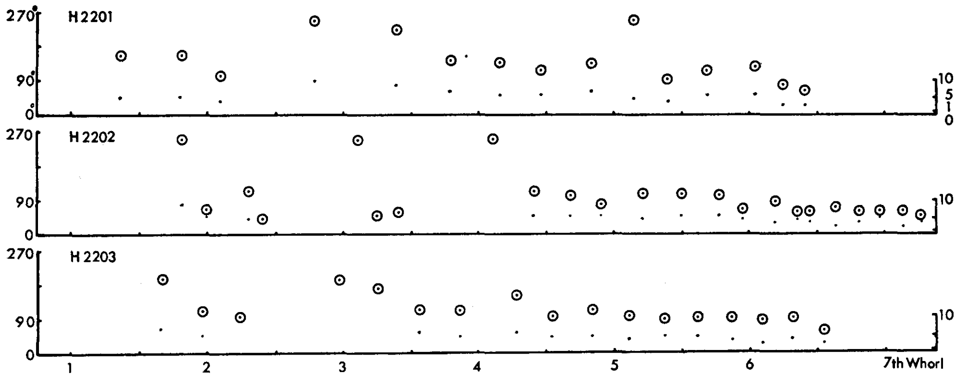


Fig. 10. The ontogenetic change of the appearance of the constrictions. The ordinate (left) is the degree and shows the distance from the preceding constriction. The dot indicates the number of septa between two constrictions and refers to the ordinate at the right side. Sample N22Z1 of *G. tenuiliratum*.

constriction, and the positions are significantly different from one another (Table 10). The bearing of the nepionic constriction of *Nautilus pompilius* was studied by Eichler and Ristedt (1966) but the recent observation by Davis and Mohorter (1973) throws doubt on the explanation of the former.

The palaeotemperature was studied by using the shell of *Staufenia staufensis* (Oppel) and *Quenstedtoceras* (*Eboraciceras*) sp. (Stahl and Jordan, 1969). Their growth rates are respectively eleven septa per year and five septa per year. In

Table 10. The positions of the nepionic constrictions of *G. tenuiliratum*, *G. denseplicatum* (Sample N22ZA) and *Nautilus pompilius* from Puerto Princesa, Palawan, Phillippine.

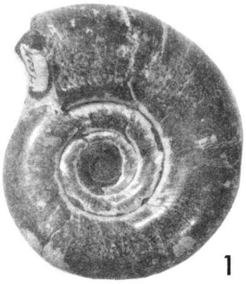
Sample	N	$\bar{\theta}$	CV	SD	F	t
N22Z-A	3	365°63'	4.0108	14°66'	1.0350	9.3181
N22Z-B	14	387°92'	3.7159	14.42'		
P. P.	11	535°45'	8.0159	42°92'		

Explanation of Plate 26

(All in natural size)

Gaudryceras tenuiliratum Yabe

Figs. 1-10: Sample Kw.
1. GK. H. 5039, 2. GK. H. 5023, 3. GK. H. 5032, 4. GK. H. 5038, 5. GK. H. 5035, 6. GK. H. 5027, 7. GK. H. 5029, 8. GK. H. 5037, 9. GK. H. 5031, 10. GK. H. 5019.
Fig. 11: Sample R417, GK. H. 5701.
Fig. 12: Sample Y, GK. H. 5703.
Fig. 13: Sample U, GK. H. 960.
Figs. 14-15: Sample N22ZB.
14. GK. H. 2206, 15. GK. H. 2207-1.



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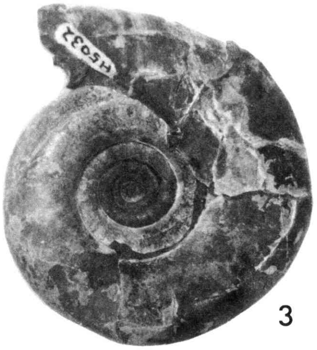

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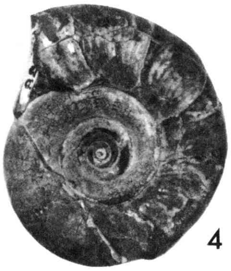

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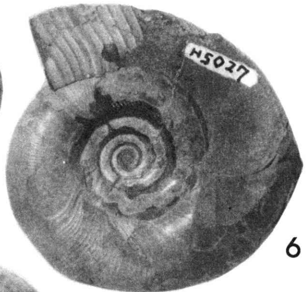

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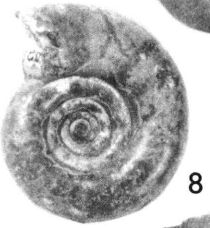

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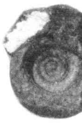

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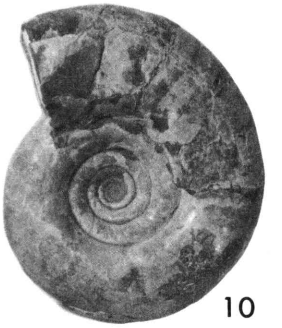

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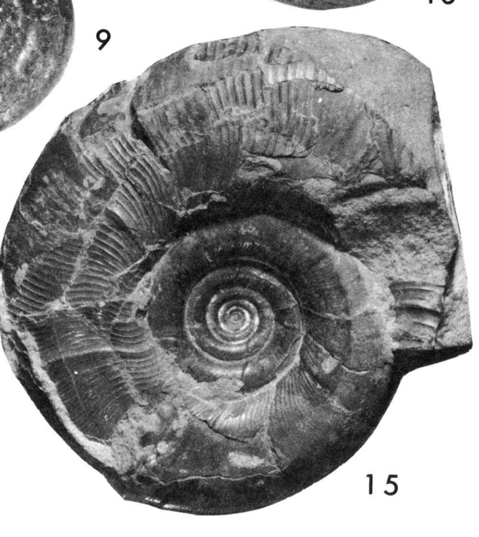

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H. HIRANO: *Gaudryceras tenuiliratum*

G. ***tenuiliratum*** the number of septa in each interval of constrictions is about five. This is not much different from the above figures. This fact might suggest that a constriction could imply an annual growth line. It is recalled here that the constriction of living ***Turbo cornutus*** SOLANDER marks an annual growth line, as has been made clear by UNO (1962). The constriction of ***Kossmatella*** (***Murphyella***) ***enigma*** MATSUMOTO, MURAMOTO and TAKAHASHI (1972), however, is very numerous, and the periodicity of constrictions is not yet clarified in most ammonoids. Furthermore, the bearing of the nepionic constriction and the other three constrictions of *N.* ***pompilius*** are uncertain. Therefore the true bearing of the constriction should be clarified after the physiological study of living *Nautilus* and comparative study of many ammonoids.

E. Ornamentation.—The Lytoceratina are generally different from the Ammonitina in that the surface ornamentation is simple, and ***Gaudryceras*** is not the exception. Not only *G.* ***tenuiliratum*** treated here but also the other species of ***Gaudryceras*** have only three kinds of ornamentations, the costa, the subcosta and the nepionic subcosta, and furthermore their shapes are generally simple. This kind of ornamentation depends structurally on the basic relief of the middle layer, which is covered by the outer layer and then the periostracum. The middle layer is composed of many sublayers partitioned by many organic sheets and the costa and subcosta are formed by the thickening of these sublayers.

In cross section the costa and subcosta have a gentle slope adapically and a steep slope adorally. The same pattern is observed in ***Kossmatella*** (***Murphyella***) ***enigma*** MATSUMOTO, MURAMOTO and TAKAHASHI (1972). It is suggested that the shape is adaptive to decrease the registance of water when it swims.

From the protoconch aperture to the stage 4.0-4.5π (the second whorl-the second and a quarter whorl) the whorl is covered by thin, tall and widely interspaced subcostae (nepionic subcostae). The statistical value on the number of the subcostae is not available on account of the imperfect preservation (the subcosta is very fragile) but a specimen of Sample N22ZB (H 2209-5) shows fourteen subcostae. Another kind of subcosta appears as soon as the nepionic subcostae disappear or in the last interspace of the nepionic subcostae. The newly appeared subcostae are much lower and thinner than the nepionic subcostae in the early stage but quite numerous. While the nepionic subcostae are simple, the newly appeared subcostae show the secondary and tertiary divergence and insertion on the area from the umbilical wall to the lateral side especially on the stages from 6π to 10π, as mentioned by MATSUMOTO (1941).

There are two kinds of subcosta, higher and lower, except the nepionic subcosta mentioned above. *G.* ***denseplicatum*** and *G.* ***intermedium*** have higher subcostae, and on the other hand *G.* ***tenuiliratum*** has lower subcostae (Table 11).

Table 11. The heights of subcostae (mm) at three defined stages in the Sample N22ZB of *Gaudryceras tenuiliratum*. The variables of the coexistent Sample N22ZA of *G. denseplicatum* are listed for comparison. The examination of the difference of the height at each stage is significant between these two synpatric species.

Sample	Stage	N	Mean	SD	CV	$\bar{H} \pm t_{0.05}$ SE
	4th wh.	16	0.0060	0.0010	16.818	0.0055-0.0065
N22ZB	4.5	16	0.0065	0.0010	15.814	0.0060-0.0070
	5	16	0.0071	0.0014	19.734	0.0064-0.0078
	4	3	0.0226	0.0092	40.872	0.0000*-0.0455
N22ZA	4.5	3	0.0343	0.0270	78.770	0.0000*-0.1014
	5	3	0.0457	0.0418	91.362	0.0000*-0.1495

* This sample is composed of only three specimens and the variation is very large. Therefore the smaller end of the range of the population mean at 95% CL is O and is not actual. The detailed characteristics on *G. denseplicatum* are mentioned in another paper (Hirano, 1975, *in preparation*).

Table 12. The ontogenetic change of the number of subcostae in the Sample N22ZB of *G. tenuiliratum*,

Stage	N	Mean	CV	SD
3 3/4 - 4th wh.	12	29.7	14.3	4.25
4 - 4 1/4	14	29.6	14.8	4.38
4 1/4 - 4 1/2	16	30.1	13.9	4.19
4 1/2 - 4 3/4	15	30.5	14.3	4.36
4 3/4 - 5	16	30.0	12.1	3.61
5 - 5 1/4	17	29.2	11.3	3.30
5 1/4 - 5 1/2	11	26.3	14.2	3.72
5 1/2 - 5 3/4	11	26.1	17.4	4.53
5 3/4 - 6	12	26.1	19.2	5.00
6 - 6 1/4	12	27.8	20.9	5.81
6 1/4 - 6 1/2	8	25.5	20.4	5.21
6 1/2 - 6 3/4	4	22.8	11.0	2.50

These are distinguished in appearance but the propriety was statistically examined in the coexistent sample (Table 18). The reason for treating the stages from 8.0π to 10.0π in this examination is that in the stages earlier than 8π measuring is very difficult and that the specimens are often deformed later than stage 10π.

Concerning the number of the subcosta, the ontogenetic change of *G. tenuiliratum* of Sample N22ZB were analysed (Table 12). The number of the subcosta was counted from stage 7.5 π to 13.5 π (from the fourth whorl to the seventh whorl). The number of the subcosta on each 0.5 π spiral seems to attain the maximum value at the stage 9.0 π (the fifth whorl) and decreases gradually after this stage.

The difference of the local population means and the degree of non-overlap are computed in two samples, N22ZB and N182f (Table 13), although this is concerned with the measurements in a certain period of growth stage. The result does not indicate any significant difference. The number of subcostae is not so large in the intrapopulational variation and may be small in the geographic variation.

Table 13. The numbers of the subcostae at two available stages in two samples of *G. tenuiliratum*, and the degree of non-overlap of two local populations (C. D.).

Stage	N22Z-B				N182f				
	N	Mean	SD	CV	N	Mean	SD	CV	CD
5 1/4-5.5	11	26.3	3.72	14.2	2	30.0	2.83	9.43	0.57
5 3/4-6	12	26.1	5.00	19.2	2	29.5	3.54	12.0	0.40

A costa appears much later than the subcosta at about the stage 14 π. The costa of *G. tenuiliratum* is narrow and quadrate in section.

F. Protoconch.—The good observation of the protoconch, apart from the debatable embryologic interpretation, has been reported recently by means of the electron microscope (e. g., Erben et al., 1969). Here the shape is observed by the optical microscope (Fig. 11), and the size is biostatistically analysed (Table 14). The character of the protoconch is very important to consider the early growth mode, the distribution, ecology and evolution of ammonite. In this article the biostatistical analyses are carried on as the first step.

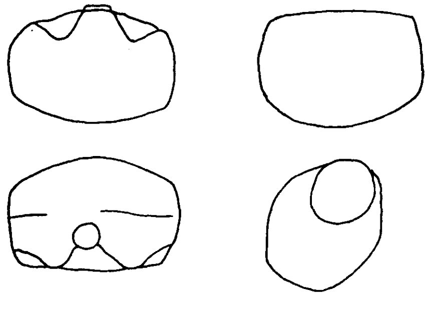

Fig. 11. The microscopic observation of the protoconch. *G. striatum*, GK. H 5071 from Kawakami. Left upper: ventral view; Left lower: antero-ventral view; Right upper: dorsal view; Right lower: dorso-lateral view.

The protoconch was measured along the longest diameter in cross section from the protoconch aperture to the opposite side (A-B direction of Fig. 2)

Table 14. The diameter of the protoconch (1-3 direction) of *G. tenuiliratum.*

Sample	N	$\bar{D}$	$\bar{D} \pm t_{0.05}$ SE	S.D.	C.V.
Kw	12	0.6637	0.6356-0.6918	0.0442	6.6623
N22ZB	14	0.5958	0.5572-0.6344	0.0669	11.233
N22Z1	3	0.6840	0.5245-0.8435	0.0642	9.3943
N182f	3	0.6712	0.6198-0.7226	0.0207	3.0764
Hb	3	0.6829	0.6608-0.7050	0.0089	1.3015
Y	1	0.6848	-	-	-
U	1	0.6302	-	-	-

and the line which is perpendicular to and crosses the middle point of the former (Fig. 2). The intrapopulational variation of the size is never larger than that of the other characters (Table 14), and interpopulational variation is also fairly small (Table 15). Although in the case of *G. denseplicatum* the geographical cline of the protoconch size is found (Hirano, 1975, *in preparation*), in this case no particular trend is found.

Table 15. *t*-test for the difference of the protoconch diameter and the coefficient of difference.

	Kw	N22Z-B	N22Z-1	N182f	Hb	Y	U
Kw	*	2.9960	0.6577	0.2803	0.7292	0.4587	0.7283
N22Z-B	0.6112	*	2.0836	1.8893	4.6827	1.2853	0.4968
N22Z-1	0.1873	0.6728	*	0.3287	0.0294	0.0108	0.7258
N182f	0.1156	0.8607	0.1508	*	0.9009	0.5693	1.7163
Hb	0.3616	1.1491	0.0150	0.3953	*	0.1851	5.1349
Y	0.4774	1.3303	0.0125	0.6570	0.2135	*	0.0000
U	0.7579	0.5142	0.8380	1.9807	5.9213	-	*

Right upper: *t*-test; Significant difference [$0.01<P<0.05$] is indicated by an underline and very significant difference [$P<0.01$] is by a dashed underline.
Left lower: Coefficient of difference; Combination of which percent of non-overlap is larger than 90% is indicated by a dashed underline.

Table 16. The examination of the difference of the protoconch size in two samples of *G. tenuiliratum* (N22ZB) and synpatric *G. denseplicatum* (N22ZA). The longest diameter (A-B direction) is used.

Sample	N	D	SD	CV	F	t
N22Z-A	3	0.6447	0.0420	6.5185	2.5374	1.1985
N22Z-B	14	0.5958	0.0669	11.233		

The protoconch size of *G. tenuiliratum* is not significantly different from that of *G. denseplicatum* in the coexistent samples (Table 16), and the latter is significantly different (*t*-test, $P \gg 0.05$) from those of *Damesites semicostatus* and *Yokoyamaoceras jimboi* in the other coexistent sample (HIRANO, 1975, *in preparation*). This fact suggests the importance of the study of protoconch for the major classification as well as for other palaeobiological aspects of ammonites.

III. Description of examined Santonian samples

The Santonian samples of *G. tenuiliratum* are fairly sufficiently prepared for the ontogenetic research, although they are insufficient for the phylogenetical research. Thereupon I research biostatistically the growth mode and the variation of some characters. As the distribution of *G. tenuiliratum* is restricted to Japan and Saghalien, a picture of the geographic variation in Santonian age can be given by those seven samples. For each value is shown in detail in each table and figure, here I do not repeat it and only indicate the numbers of table and figure.

Suborder Lytoceratina HYATT, 1889
Superfamily Lytocerataceae NEUMAYR, 1875
Family Tetragonitidae HYATT, 1900
Subfamily Gaudryceratinae SPATH, 1927
Genus *Gaudaryceras* GROSSOUVRE, 1894

Type-species.—*Ammonites mitis* HAUER, 1866 (subsequently designated by BOULE, LEMOINE and THEVENIN, 1906).

Gaudryceras tenuiliratum YABE

Pls. 24-26

1890 *Lytoceras Sacya* FORBES; YOKOYAMA, *Palaeontographica*, vol. 36, pp. 177-178, pl. 18, figs. 12-13.
1903 *Gaudryceras tenuiliratum* YABE; YABE, *Jour. Coll. Sci., Imp. Univ. Tokyo*, vol. 18, art. 2, pp. 19-24, pl. 3, figs. 3-4.
1903 *G. tenuiliratum* var. *ornata* YABE; YABE, *op. cit.*, pp. 24-27, pl. 3, figs. 2a-b.
1941 *G. tenuiliratum* YABE; MATSUMOTO, *Jour. Geol. Soc. Japan*, vol. 48, no. 568, pp. 19-24, fig. 2-a.
1941 *G. tenuiliratum* var. *frequence* MATSUMOTO; MATSUMOTO, *op. cit.*, pp. 19-24.
1941 *G. tenuiliratum* var. *substriatum* MATSUMOTO; MATSUMOTO, *op. cit.*, pp. 19-24.
? 1962 *G. navarrense* WIEDMANN; *Palaeontographica*, Bd. 118, Abt. A, pp. 158-159, pl. 9, fig. 3
1963 *G. tenuiliratum* YABE; MATSUMOTO *in* MATSUMOTO ed., *25th Anniversary Vol., Palaeont. Soc. Japan*, p. 29, pl. 44, figs. 12-13.

Types.—YABE (1903) established this species on several syntypes. Subsequently *Lytoceras sacya* FORBES of YOKOYAMA (1890, p. 178, pl. 18, figs. 12-13) was designated as the lectotype of this species by Matsumoto (1963, p. 29, pl. 44, fig. 12).

Material.—Sample N22ZB(N=15), Sample N22Z1(N=3), Sample N182f(N=3), Sample N401g(N=2), Sample N150a(N=1) from Naibuchi and Sample Kw(N=17) from Kawakami Coal Mine, South Saghalien, and Sample Hb(N=3) from Haboro, Sample Y(N=2) from Oyubari and Sample U(N=1) from Urakawa, Hokkaido.

Diagnosis.—A species which has densely interspaced low subcostae in the stages from the young to the adult. The subcostae diverge secondarily and tertiarily on the area from the umbilical wall to the lateral side and insert on the ventral to the ventrolateral area especially in the stages from 6π to 10π. The narrow quadrate costae appear in the adult stage. The first constriction is at the stage 2.16π (mean; see Table 10) and the whorl grows gradually (Table 1, Fig. 3). The variations of the characters are generally small in a local population (Tables 1, 5, 8-9, 11-12, 14).

Description.—Early Stage (Protoconch-2.0π): The shape of the protoconch is like the barrel of beer and the suture of the aperture is EL (cfr. Fig. 5). The median plane of the protoconch is the logarithmic spiral. The intrapopulational and the interpopulational variation of the protoconch size are usually small (Tables 14-15). The difference of the protoconch size does not influence the growth ratio of the radius length and the initial growth index regressed from the stages 2.5-4.0π or 10.0π. The growth pattern of the radius length is not always smooth in comparison with the later stages. The growth ratios of the radius length and the whorl height in the stages from the protoconch to 2.0π are a little larger

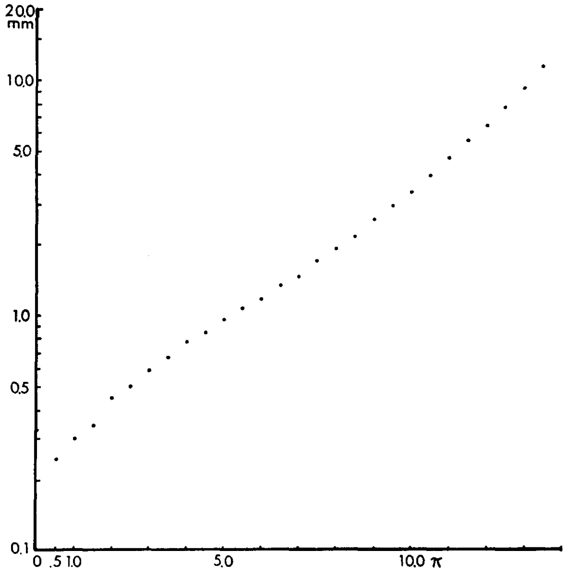

Fig. 12. An example of the growth pattern of the whorl height to the spiral. GK. H 2216-A of the Sample N182f.

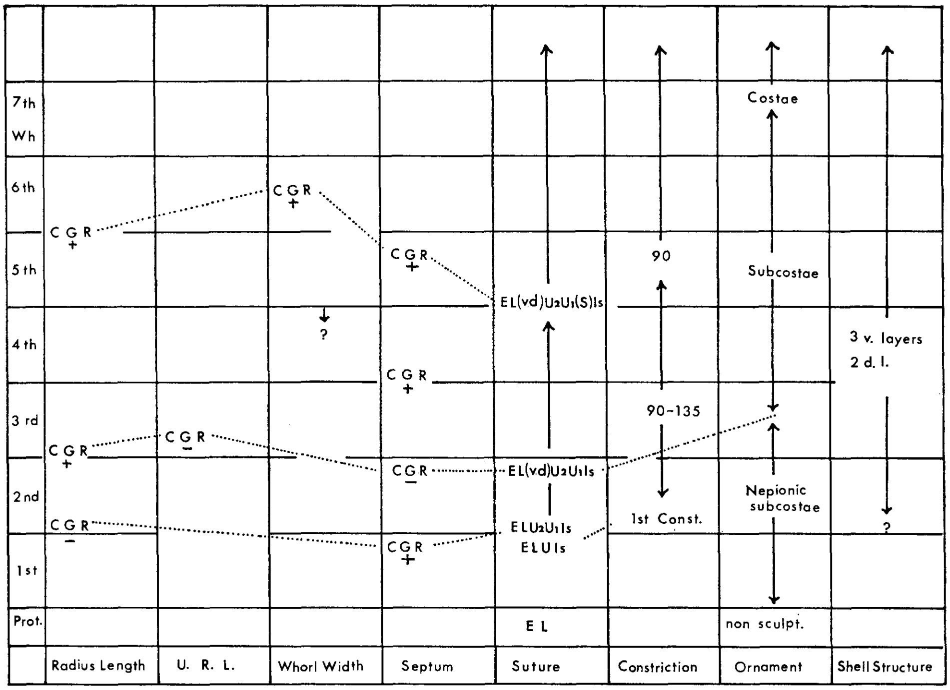

Fig. 13. The ontogenetic changes of selected characters of *G. tenuiliratum*. + : Growth ratio increases after change; − : Growth ratio decreases after change.

than those of the middle stage (Figs. 3, 12-13). The shell surface is covered with a dark brown periostracum and has widely interspaced thin and low radial subcostae which are counted five to six on the first whorl and the second whorl respectively. The subcostae disappear at about the stage 4.5π. No other ornament is discernible on the surface of this stage. The suture increases its complexity from ELUIs to ELU_2U_1Is in the stages from 2π to 3π (Figs. 5, 13). The growth ratio of the septal thickness increases at the stage from 1.5π to 2.0π (Figs. 4, 13). The position of the nepionic constriction is always at the point 2π or slightly more and the intrapopulational variation of the position is very small (Table 10).

Middle Stage (2.5π-9.5π): The growth pattern of the radius length in some samples has the critical point at the point 4π and the growth ratio increases after this change (Table 1, Fig. 3). The position of this critical point is rather constant, showing little variation. The growth pattern of the radius length shows little variation in position and slope and therefore if the value of the radius length is given, the number of the whorl will be answered with an error less than 0.5π in a sample. The growth pattern of the umbilical radius length shows no change from the stage 3π to 12π and the variation of the growth pattern is small (Table 8).

The growth ratio of the septal thickness decreases at the point 4 π but it increases again at the point 7 π.

The suture becomes more complex at the stage 4 π, where the growth ratio of the septal thickness decreases, and is ELU_2U_1Is, showing complementary relationship between the two characters (Figs. 4, 5, 13). The septa number about seventeen per whorl.

The subcosta appears at the stage about 4 π-5 π just after the disappearance of the nepionic subcosta or in the last interspace of the nepionic subcostae and continues through the middle stage to the adult stage. It increases its height with growth (Table 11) and is weakly sigmoidal in lateral view, showing curvature at the ventral shoulder and the umbilical shoulder. The subcosta diverges secondarily and tertiarily on the area from the umbilical wall to the lateral side and inserts on the ventral-ventrolateral area in the stages from 6 π to 10 π. The subcosta crosses the venter without interruption and with a very gentle rounded projection. The number of the subcostae reaches the maximum at the stage 9 π and decreases gradually after that stage (Table 12). The coefficient of variability on the number and the height of the subcostae are both in the order of ten and the finess of the subcosta is generally distinctive.

The external appearance of the constriction is fairly similar to the costa. The interspace decreases usually from 1.5 π to 0.5 π with growth, that is, the frequency is increased (Figs. 9-10).

Adult Stage (10.0 π or 10.5 π-end): The growth ratio of the radius length changes at a certain point between the stages 10.0 π and 11.0 π and increases after that stage (Fig. 3, Table 1). The coefficient of variation of the growth ratio in each sample never attains 7.0 at this stage. The interpopulational difference of the growth ratio is usually not significant, and CD is also small (Tables 2-4). A little after this change, the growth ratio of the whorl-width increases at about the point 13 π, and the whorl becomes larger not only in height but also in width (Tables 1, 9, Figs. 3, 13).

The change of the growth ratio of the septal thickness precedes that of the whorl, although chronologically they may be roughly correlated with each other. It is about the point 11 π (Figs. 4, 13). The suture has all the main elements at the stage 10 π and the complication proceedes with growth (Figs. 5, 13).

Concerning the surface ornamentation, the costa appears at about the stage 14 π. Its pattern is similar to the subcosta and is weakly sigmoidal. It is quadrate in cross section. The width is as three times as wide as the neighbouring subcosta, but the interspace decreases with growth and finally the costae are approximated to each other near the apertural margin.

In the adult stage the interspace of the constrictions is about 0.5 π to 0.3 π spiral inclusive and decreases with growth (Fig. 10).

The shell has three ventral layers and two dorsal layers, and the outer ventral layer wedges out at the umbilical seam. The costa and the subcosta are formed by thickening of the middle ventral layer. The slope of the subcosta is adapically gentle and adorally steep. The outer dorsal layer covers the uneveness of the preceding ventral shell, and the inner surface of the inner dorsal layer is completely smooth.

Comparison.—The present species sometimes occurs with ***G. denseplicatum*** at the same locality. The procedure which I have done for the discrimination of the present species from coexistent ***G. denseplicatum*** is shown at first.

The fifteen specimens (of which fourteen are available) which is regarded as ***G. tenuiliratum*** and three specimens regarded as ***G. denseplicatum*** are obtained from one and the same concretion numbered as N22Z in Naibuchi, Saghalien. The growth pattern of the radius length to the spiral is individually analysed at first, and two patterns are shown. One pattern has three critical points (stages 2.0-2.5 π, 4.0-4.5 π, 9.5-10.0 π) and the other has two points (stages 2.0-2.5 π, 5.5-6.5 π). Then the growth stages are divided into four stages from 2.5 π to 4.0 π, from 4.5 π to 5.5 π, from 6.0 π to 10.5 π and from 10.5 π to the end, and the distribution of the growth ratios of the seventeen specimens is examined in these four stages whether it is significantly different from the normal distribution or not (Table 17). The result indicates the significant difference from the normal distribution in the stage from 6.0 π to 10.5 π ($P \ll 0.05$) and the hypothesis is doubtful that this sample composed of the seventeen specimens is the random sample from one local population.

Table 17. The chi-square test on the growth ratios of the radius length to the spiral in the Collection N22Z (Sample N22ZA + Sample N22ZB).

Stage	N	$\overline{\alpha}$	SD	χ^2	
2.5- 4.0π	17	0.1122	0.0123	3.7733	N. S.
4.5- 6.0	17	0.1187	0.0045	4.6583	N. S.
6.5-10.0	17	0.1216	0.0081	16.309	S.
10.0-	17	0.1352	0.0086	2.8155	N. S.

Next to that examination, the height of the subcosta is examined (Table 18). The chi-square test is carried on three stages of 8 π, 9 π and 10 π of the seventeen specimens. The result indicates significant diffence in all three stages, and these specimens are no longer regarded as the sample from one local population. The height of the subcosta is distinguishable into the two groups, the high and the low ones, on the frequency distirbution and also by the nake eyes, and then the two groups are examined by chi-square test respectively. The result indicates

Table 18. An example of the chi-square test on the height of the subcostae at the stage 4½ whorl in the Collection N22Z (upper) and the Sample N22ZB (lower).

Class	Oi		Ei	
$\bar{x} - 3s \sim \bar{x} - 2s$	0	0	0.3870	2.8332
$\bar{x} - 2s \sim \bar{x} - s$	0		2.4462	
$\bar{x} - s \sim \bar{x}$	16		6.1343	
$\bar{x} \sim \bar{x} + s$	1		6.1343	
$\bar{x} + s \sim \bar{x} + 2s$	0	0	2.4462	2.8332
$\bar{x} + 2s \sim \bar{x} + 3s$	0		0.3870	
	N=17*		17.9532	

$\chi^2 = 25.7867 \gg \chi^2_{0.05(\nu=1)} = 3.8415$, $P \ll 0.05$

Class	Oi		Ei	
$\bar{x} - 3s \sim \bar{x} - 2s$	1	2	0.3440	2.5184
$\bar{x} - 2s \sim \bar{x} - s$	1		2.1744	
$\bar{x} - s \sim \bar{x}$	6		5.4608	
$\bar{x} \sim \bar{x} + s$	6		5.4608	
$\bar{x} + s \sim \bar{x} + 2s$	1	2	2.1744	2.5184
$\bar{x} + 2s \sim \bar{x} + 3s$	1		0.3440	
	N=16		15.9584	

$\chi^2 = 0.3199 \ll \chi^2_{0.05(\nu=1)} = 3.8415$, $P \gg 0.05$

* This collection contains 18 specimens, but one specimen has value out of this range.

no significant difference in this time (Table 18). The distribution of the growth ratios is divided into two groups by the difference of the height of the subcostae and examined by chi-square test. No significant differences are indicated by this test. Therefore it is clear that these seventeen specimens are composed of two forms. One has the high subcostae, two critical points at the points 2.0-2.5 π and 5.5 π-6.5 π and rapid enlarging whorls and the other has the low subcostae, three critical points at the points 2.0-2.5 π, 4.0-4.5 π and 9.5-10.5 π and slowly enalrging whorls. Furthermore by the difference in the geographic distribution and other difference mentioned below the two forms are regarded to be the reflection of the difference at the specific level. As mentioned in the preceding chapter, the position of nepionic constriction is very small in variation, it reflects the characteristics of a local population and concerning this character significant difference exists between the two species (Table 10). The growth patterns of umbilical radius length are also significantly different between the two (Tsble 8). The numbers of the subcostae are significantly different in the stage from 7.5 π

to 11 π. The protoconch size and the growth pattern of the umbilical radius length do not indicate any significant difference between these two species.

JONES (1963) described and illustrated two specimens under the name of *G. tenuiliratum* YABE from the *Pachydiscus kamishakensis* Zone of Southern Alaska. The biostatistical comparison is done between JONES' illustrated specimens and my samples. The position of the critical point of the growth pattern of the umbilical radius length is different from each other but the growth ratios do not show any significant difference ($P \gg 0.05$). As he did not study the specimens biometrically, no more biostatistical examination can be carried on here. The subcosta, however, is larger in JONES' specimens than in my samples. Further the costa and the subcosta are fairly prorsiradiate in the former. He shows a single incomplete suture, but the suture are usually similar in the species of the same genus. In short, there is no evidence to support that JONES' specimens are referable to *G. tenuiliratum*.

G. tenuiliratum is similar to *G. denmanense* WHITEAVES but as it is not at my disposal I cannot mention more than MATSUMOTO (1959).

G. navarrense WIEDMANN (1962) is very similar to the present species in the volution and the ornamentation. Its whorl sections (WIEDMANN, 1962, p. 158, Abb. 16) is much different from ours. The whorl section illustrated by WIEDMANN is unusual for *Gaudryceras* and it may result from secondary deformation. If so, *G. navarrense* could be identified with *G. tenuiliratum*.

Occurrence.—The type locality is Efue, Urakawa, Hidaka Province, Hokkaido (YABE, 1903; MATSUMOTO, 1963). The species is said to be commonly distributed in the stage from Coniacian to Lower Campanian in South Saghalien and Japan (e. g., MATSUMOTO, 1959), and is especially abundant in the Santonian Stage. The examined samples are all from the Santonian.

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