# Importance of transient polymorphism in systematics of ammonoidea*

Hiromichi Hirano

## Abstract

Sexual dimorphism is only one of a number of kinds of polymorphism, but studies on sexual dimorphism of ammonoids are important in that they make us aware of the presence of polymorphism in ancient organisms, as it is universal in living organisms.

Eldredge & Gould (1972) commented that "the history of evolution is not one of stately unfolding, but a story of homeostatic equilibria, disturbed only rarely by rapid and episodic events of speciation", but there seem to exist many taxa in which polymorphism, specially transient polymorphism, has not yet been recognized because of insufficient detailed investigation.

I describe here an example of transient polymorphism in the late Cretaceous ammonite *Gaudryceras denseplicatum*. *G. d.* var. *denseplicatum* and it's dimorph var. *intermedium* appeared in the Turonian and developed rapidly. They were replaced by the early Campanian by *G. d.* var. *tenuiliratum,* which had appeared in the Coniacian, because of the inferior fitness of the former to the latter.

Speciation and evolutionary rate are a function of population size (Ne), genetic variation (V) and fitness (F), Evolution = f (Ne, V, F), and it is fundamentally incorrect to consider the speciation or evolution being as uniformly rapid or gradual.

## Introduction

While systematics is the starting point for study, it is the final result of the study. Therefore, the classification must be changed if the concept on the systematics was developed as well as new recognition was obtained during the course of study for phylogeny or evolution. The recognition which conduces to the change of classification in ammonoidea is polymorphism. In the field of biology, the importance of polymorphism as adaptive strategy is well recognized.

In the field of palaeontology, however, the importance is not always well recognized.

As has been known, Eldredge & Gould (1972) proposed an evolutionary model entitled "Punctuated equilibria" based on their own palaeontological studies and many other works. Those works which they referred to hardly took the recognition of polymorphism (*e. g.*, balanced polymorphism, transient polymorphism) into account. Thereupon, I introduce an example of polymorphism, pointing out the importance of recognition of polymorphism and discuss an evolutionary model.

of Education, Science and Culture (No. 074202 for 1975 ; No. 174269 for 1976 ; Nos. 364286 and 334043 for 1978).

## Phylogeny and polymorphism

As has been known, the shell morphology of the ammonoidea is fairly complicated. SCHOPF et al. (1975) mentioned that descriptive terminologies are most numerous in the Mammalia and Ammonoidea among main animal groups cited in the discussion of evolution, that is, the degree of morphological complexity is the highest in these taxa. For this reason, Ammonoidea has proved to be an excellent tool for biostratigraphy and has been classified exquisitely. Today, the systematics of Ammonoidea is discussed at the specific level, and the palaeoecology produces prolific results. In such a sense, the systematics of Ammonoidea has attained to the stage of beta taxonomy defined by MAYR (1969). In the course of gamma taxonomy, the innegligible concept for the infraspecific discussion is the polymorphism.

*Gaudryceras denseplicatum* (JIMBO) and *G. intermedium* YABE from the Turonian to the early Campanian and *G. tenuiliratum* YABE (Plate I) from the Coniacian to the early Campanian are described as being morphologically serial mutually but distinguished to one another by some clear distinction in MATSUMOTO's (1941) excellent work on the speciation. His concept coincides with the so-called iterative speciation and as an evolutionary model it was a forerunner of "Punctuated equilibria," although the biological background is much different in the two ages. From the viewpoint of biology, specially of population

genetics, however, the former explanation (iterative or punctuated equilibria) on the speciation of these three species cannot fully satisfy us. Thereupon after the detailed biometrical study I studied the historical change of the numerical ratios of the specimens of those three species and the geographic distribution of the related species, and I concluded that *G. denseplicatum* and *G. intermedium* represent balanced dimorphism or sexual dimorphism and *G. tenuiliratum* represents the transient polymorphism (HIRANO, 1978).

Here I discuss the transient polymorphism again in terms of the new absolute age. Because of sexual or balanced dimorphism these two species are expressed as *G. denseplicatum* var. *denseplicatum* and *G. d.* var. *intermedium*.

*G. denseplicatum* distributes in the Turonian of Japan and Sagkalien, in the Coniacian of Japan, Sagkalien and Madagascar and in the Santonian and the early Campanian of Japan and Sagkalien. *G. tenuiliratum* distributes only Japan and Sagkalien from the Coniacian via the Santonian to the early Campanian. Species being similar to but different from *G. tenuiliratum* are known from Coniacian and the Santonian of the Southeast Africa (HOEPEN, 1921) and the Coniacian of the North America (MATSUMOTO, 1959). Both two species under discussion exist until the early Campanian but the usual range is to the end of the Santonian (Table 1). *G. tenuiliratum* might have existed until a little later than *G. denseplicatum* from the field observation.

Next to that, we can obtain the historical change of the relative numerical frequency

**Table 1.** Stratigraphic distribution of *G. denseplicatum* var. *denseplicatum*, var. *intermedium* and var. *tenuiliratum* in Obira, Hokkaido and Naibuchi, Sagkalien.

| Geological age | Zone of Inoceramus | m. y.* | Obira | | Naibuchi | | Local stratigraphic division |
|---|---|---|---|---|---|---|---|
| | | | a | b | a | b | |
| Campanian | orientalis | | 0 | 0 | 0 | 0 | Mh7 |
| | | —82— | | | | | |
| Santonian | japonicus | | 0 | 19 | 36 | 100 | Mh6β |
| | | | | | 17 | 11 | Mh6α–β |
| | amakusensis | | 22 | 19 | 19 | 24 | Mh6α2 |
| | | | | | 9 | 1 | Mh6α1 |
| | | —85— | | | | | |
| Coniacian | mihoensis | | 40 | 3 | 4 | 0 | Mh5 |
| | uwajimensis | | 10 | 1 | 7 | 1 | Mh4 |
| | | —87— | | | | | |
| Turonian | teshioensis | | 35 | 0 | 1 | 0 | Mh3 |
| | hobetsensis | | 60 | 0 | 1 | 0 | Mh2 |
| | labiatus | | 5 | 0 | 1 | 0 | Mh1 |
| | | —96— | | | | | |
| Cenomanian | concentricus | | 0 | 0 | 0 | 0 | Mh0 |

\* Absolute age after OBRADOVICH & COBBAN (1975) and KAUFFMAN (1977).

a : var. *denseplicatum* and var. *intermedium* ; b : var. *tenuiliratum*.
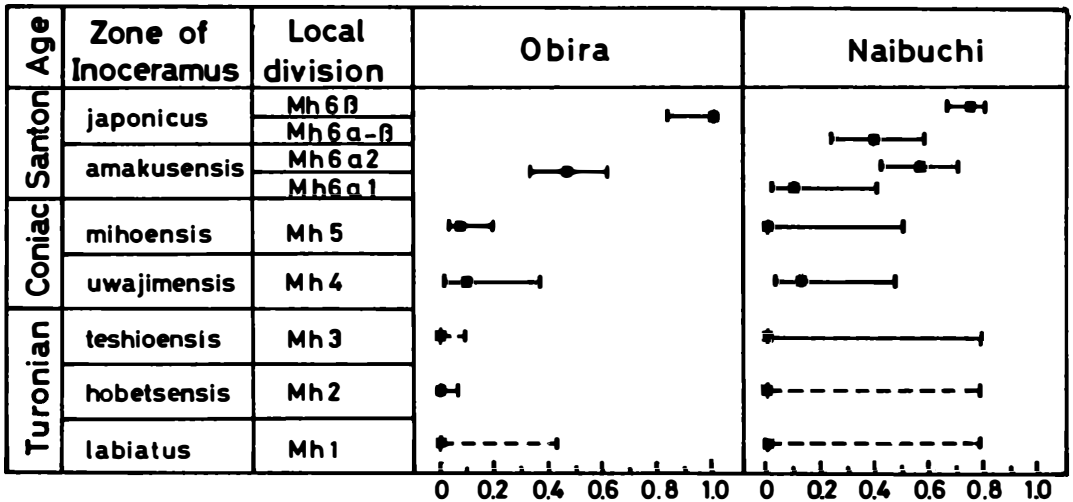


Fig. 1 Historical change of the numerical ratio of var. *tenuiliratum* to the three varieties in the number of specimens (95% confidence interval is shown by a bar or a dashed line).

of the two species from the numerical record of the specimens (Fig. 1). The numbers of the specimens seem to change stratigraphically without any interrelation between Naibuchi and Obira. The pattern of the relative frequency, however, clearly shows that *G. tenuiliratum* replaced *G. denseplicatum*. The numerical ratios of *G. tenuiliratum* to *G. tenuiliratum* plus *G. denseplicatum* are statistically not significantly different at every zone between Naibuchi and Obira. Therefore,

the pattern of the numerical ratio of the two species is not different between these two areas. We can propose three hypothesis which explain the interrelation between these two morphologically similar species.

1). *G. tenuiliratum* had speciated from the species other than *G. denseplicatum,* migrating to around Japan and expelled *G. denseplicatum.*

2). *G. tenuiliratum* had speciated in a peripheral isolate population of *G. denseplicatum* and soon expelled *G. denseplicatum.*

3). *G. tenuiliratum* is the polymorphy of *G. denseplicatum* and replaced *G. denseplicatum* in terms of the higher fitness.

1): Because *G. tenuiliratum* is commonly available from the early Coniacian, the speciation arised during the Turonian. As the Turonian species of *Gaudryceras* only *G. varagurense* is known, except *G. denseplicatum,* from the Southeast Africa and India. Therefore *G. tenuiliratum* speciated from *G. varagurense* in these areas or on the way of the migration to Japan. The evidence that *G. tenuiliratum* is morphologically more similar to *G. varagurense* than *G. denseplicatum* is at least necessary to support this hypothesis. Furthermore, we can expect an intermediate form and the high commonness between the variations of the two species. As a matter of fact, however, there is no evidence that *G. tenuiliratum* is more similar to *G. varagurense* than to *G. denseplicatum.* As HIRANO (1978) showed, *G. tenuiliratum* is morphologically homeostatic, and the morphological variation is not so large in

comparison with some other species. The morphological variation of *G. tenuiliratum* does not seem to overlap with that of *G. varagurense.* For the decisive denial against this hypothesis, *G. varagurense* must be biometrically studied based on the population thinking. Nowadays, however, there is not an actual evidence which supports this hypothesis and therefore it is rejected.

2): A new species arised from the peripheral isolates of the parental species. In this case, as *G. tenuiliratum* distributed Japan and Sagkalien, *G. tenuiliratum* speciated in the peripheral isolated populations around Japan and Sagkalien. *G. denseplicatum* is also homeostatic(HIRANO, 1978) like *G. tenuiliratum.* Some characters are common at some growth stages between the two species but an intermediate forms are not known. Therefore, the speciation proceeded as rapid as an intermediate form was not probabilitically preserved as a fossil. The conditions which enable the rapid speciation are (a): the selection pressure to *G. denseplicatum* is strong in the isolated population, that is, the environmental condition is much different in the peripheral isolate from that in the main area, and the genotype of *G. tenuiliratum* is selected during fairly small number of the generations, (b): the isolated population is small and is easily affected by genetic drift, attaining the speciation. There are problems, however, in both two conditions. One is the fact that *G. tenuiliratum* coexisted with the parental species, *G. denseplicatum,* in the main realm of the parental species for a fairly

long time (=5 m. y.) although one expelled the other. In the case of (a), the optimum conditions of the two species are fairly different and therefore to coexist for so long period as 5 m. y. is not realistic. Although *G. tenuiliratum* prospered and *G. denseplicatum* was replaced by *G. tenuiliratum* in the view of relative frequency, the absolute number of *G. denseplicatum* was not in the trend of the decline (Table 1). Here the condition (a) is decisively denied and (b) is negative. In the case of (b) the genotype of *G. tenuiliratum* should exist within the variation of *G. denseplicatum* from the early time. However there is not such a line of evidence. The genotype of *G. tenuiliratum* might have arisen by gene mutation in the small peripheral populations and the genotype might be survived through genetic drift. The mutation rate, however, is $10^{-5} \sim 10^{-6}/1$ locus (DOBZHANSKY, 1951) and the probability to arise the mutation in the small population is too small. Even if the mutation arised and fixed, it is not real-

istic to form a new species during a short period (less than the longevity of the Turonian) like the case of (a). From the difficulty mentioned above, the hypothesis (2) is rejected.

3): Gene mutation arised in the populations of *G. denseplicatum*. The mutant type was higher in the value of the fitness and the mutant type grandually expelled the wild type. Because the gene mutation rate is $10^{-5} \sim 10^{-6}/1$ locus and the effective population size of *G. denseplicatum* in the main distributional area would be larger than $10^6$, which is assumed from the occurrence, this is a realistic hypothesis. A recessive mutant gene or a dominant mutant gene can supposed. HIRANO (1978) obtained the coefficient of selection ($s$) in the both cases and $s$ is $10^{-6}$ level. In the calculation, the absolute age was from HARLAND et al. (1964). In this time I calculate $s$ based on the new absolute age of OBRADOVICH & COBBAN (1975) and KAUFFMAN (1977), showing $s$ below and the gene frequency in Tables 2, 3 and Fig. 2.

**Table 2.** The change of the gene frequency from Turonian to Santonian observed in Obira samples. The case of dominant and that of recessive are both calculated. p is the frequency of the wild type gene.

| Age | Zone | m. y. | Phenotype | | Wild type | Case of dominant | | Case of recessive | |
|---|---|---|---|---|---|---|---|---|---|
| | | | d | t | All | p | q | p | q |
| | | —82 | | | | | | | |
| Santonian | japonicus | | 0 | 19 | 0.000 | 0.000 | 1.000 | 0.000 | 1.000 |
| | amakusensis | | 22 | 19 | 0.537 | 0.733 | 0.267 | 0.319 | 0.681 |
| | | —85 | | | | | | | |
| Coniacian | mihoensis | | 40 | 3 | 0.930 | 0.964 | 0.036 | 0.736 | 0.264 |
| | uwajimensis | | 10 | 1 | 0.909 | 0.953 | 0.045 | 0.699 | 0.301 |
| | | —87 | | | | | | | |
| Turonian | teshioensis | | 35 | 0 | 1.000 | 1.000 | 0.000 | 1.000 | 0.000 |
| | hobetsensis | | 60 | 0 | 1.000 | 1.000 | 0.000 | 1.000 | 0.000 |
| | labiatus | | 5 | 0 | 1.000 | 1.000 | 0.000 | 1.000 | 0.000 |
| | | —90 | | | | | | | |

**Table 3.** The change of the gene frequency from Mh4 to Mh6β observed in Naibuchi samples. The case of dominant and that of recessive are both calculated. p is the frequency of the wild type gene

| Age | Horizon | m. y. | Phenotype | | Wild type | Case of dominant | | Case of recessive | |
|-----|---------|-------|---|---|---|---|---|---|---|
| | | | d | t | All | p | q | p | q |
| Santonian | | −82 | | | | | | | |
| Santonian | Mh6β | | 36 | 100 | 0.265 | 0.515 | 0.485 | 0.143 | 0.857 |
| Santonian | Mhα−β | | 17 | 11 | 0.607 | 0.779 | 0.221 | 0.373 | 0.627 |
| Santonian | Mh6α2 | | 19 | 34 | 0.358 | 0.598 | 0.402 | 0.199 | 0.801 |
| Santonian | Mh6α1 | | 9 | 1 | 0.900 | 0.949 | 0.051 | 0.684 | 0.316 |
| Coniacian | Mh5 | −85 | 4 | 0 | 1.000 | 1.000 | 0.000 | 1.000 | 0.000 |
| Coniacian | Mh4 | | 7 | 1 | 0.875 | 0.935 | 0.065 | 0.646 | 0.354 |
| Turonian | Mh3 | −87 | 1 | 0 | 1.000 | 1.000 | 0.000 | 1.000 | 0.000 |
| Turonian | Mh2 | | 1 | 0 | 1.000 | 1.000 | 0.000 | 1.000 | 0.000 |
| Turonian | Mh1 | | 1 | 0 | 1.000 | 1.000 | 0.000 | 1.000 | 0.000 |
| | | −90 | | | | | | | |



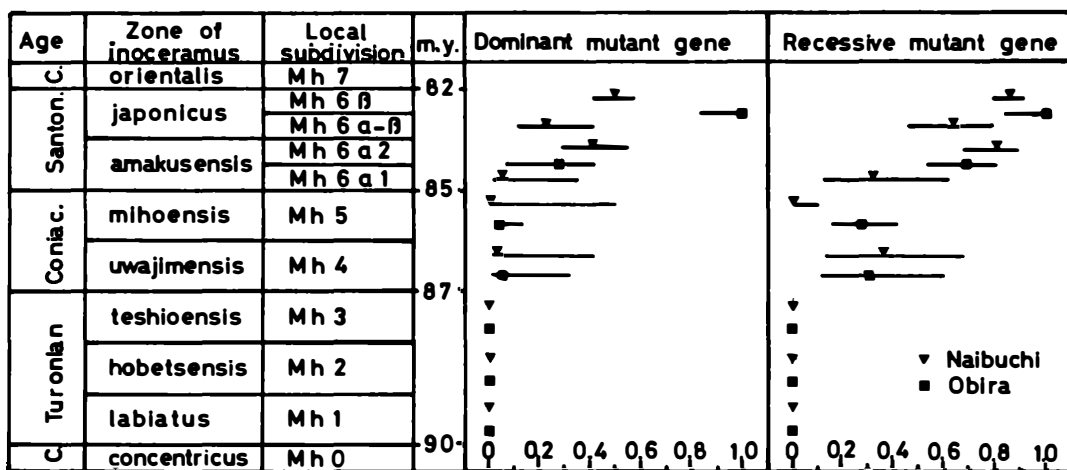**Fig. 2** Historical change of the mutant gene frequency. 95% confidence interval is shown by a bar.

The recessive mutant gene.

Obira: $s = -1.5 \cdot 10^{-5}$

Naibuchi: $s = -9.2 \cdot 10^{-6}$

The dominant mutant gene.

Obira: $s = 1.0 \cdot 10^{-5}$

Naibuchi: $s = 8.2 \cdot 10^{-6}$

Remarks. Obira; From the mid-horizon (86.5 m. y.) of the Uwajimensis Zone to that (84.25 m. y.) of the Amakusensis Zone, the duration is 2.25 m. y., and the number of the generation is $2.25 \cdot 10^5$, i. e., $10^5$ level.

Naibuchi; From the mid-horizon (86.5 m. y.) of the Mh4 to that (82.375 m. y.) of the Mh6ß, the duration is 4.125 m. y., and the number of the generation is $4.125 \cdot 10^5$, i. e., also $10^5$ level.

Thus *G. denseplicatum* and *G. tenuiliratum* represent polymorphism derived from the gene mutation. The mutant type was selectively superior to the wild type and the latter was replaced by the former.

This is transient polymorphism. In this hypothesis the difficulty like the hypotheses (1) and (2) does not arise. Some insoluble problems are that there is not a method to verify this hypothesis and a comparable work with this result is poor.

Furthermore, in the later stage of the duration of *G. denseplicatum* var. *tenuiliratum* (former *G. tenuiliratum* is degraded to a variety of *G. denseplicatum* as is polymorphy) *G. striatum* appeared and existed until the end of the Campanian. Now I am collecting *G. striatum* and preliminarily I point out the possibility that *G. tenuiliratum* and *G. striatum* are in the relation of the transient polymorphism.

## Appendix : Biostratigraphic interest of transient polymorphism

Some biostratigraphers may think that such palaeozoology in the gamma stage contributes nothing to biostratigraphy and only complicates taxonomy. Thereupon I point out that the accuracy of the age determination and the correlation is improved, theoretically in the $10^5$ level, by the detailed analysis of the transient polymorphism. The improvement is due to the following principle. Once transient polymorphism of a certain taxon is analysed, the coefficient of selection ($s$) is obtained. Then a stratigrapher collects many specimens of the taxon from a bed, of which stratigraphic position is uncertain. The relative frequency of the polymorphy is easily obtained and the gene frequency is also obtained based on the Hardy–Weinberg law. Then,

$$Z_t = s \cdot t + Z_0$$

$$Z_0 = \log_e \frac{x}{1-x} + \frac{1}{1-x}$$

$$t = (Z_t - Z_0)/s$$

$t$ : number of generations

$Z_t$ : $Z$ value at $t$-generation

$x$ : gene frequency

Thus the stratigrapher can calculate how many generations passed between the initial generation and his collection.

Supposing the average reproductive age of ammonoidea is 10 years level from Schindewolf (1934), Stahl & Jordan (1969), Jordan & Stahl (1970), Hirano (1975, 1978) and Kennedy & Cobban (1976), he can determine the age of the bed with the accuracy of 10 years level. As the accuracy of the former fossil zone is at $10^5 \sim 10^6$ years level, it follows that the accuracy is improved $10^4 \sim 10^5$ times. Actually the stochastically assumed ratio for the population has a range proportional to the sample size and therefore an error of the range cannot be avoided. In radiolaria, foraminifera and nanno-fossils, which are easy to collect many specimens, the actual accuracy is very high.

## Concluding remarks

1. Polymorphism is well known in biology but in the former ammonite taxonomy it has not been sufficiently analysed. Only sexual dimorphism took attention of many palaeontologists. Balanced and transient polymorphism did not take much attention of palaeontologists and some ammonite palaeontologists seem to ignore them.

2. *Gaudryceras denseplicatum, G. intermedium* and *G. tenuiliratum* are most reasonably explained as sexual or balanced dimorphism and transient polymorphism

respectively. These three are treated as three varieties of *G. denseplicatum.* Concerning the transient polymorphism I calculated the coefficient of selection by using the new absolute age. The coefficient and the replacement rate is sufficiently appropriate from the view of population genetics.

3. These three varieties are morphologically homeostatic during their duration and are contrastive with *Scaphites planus* and *Otoscaphites puerculus* (TANABE, 1975, 1977), which represent phyletic gradualism in the buoyancy evolution. The adaptive strategy is different from each other.

4. As adaptive strategies, there are at least following three ; a) phyletic gradualism, b) polymorphism—balanced polymorphism, transient polymorphism, etc., c) combination of (a) and (b). From the works of HIRANO (1978) and TANABE et al. (1978), I preliminarily suppose that an ammonite lived off shore and stable condition adopted (b) and that lived in shallow sea mainly adopted (a) and (c).

5. Evolutionary rate is decided by the population size (Ne), the amount of genetic variation (V) and the fitness (F), that is, evolutionary rate $=f(Ne, V, F)$. Punctuated equilibria is one of the results of this formula. Taking account of the current level (beta stage) of taxonomy in palaeontology, evolutionary model should be examined after the accumulation of the works of gamma stage. In the forthcoming study, polymorphism should not be ignored.

6. It is often dangerous and biases the result to conclude an evolutionary model or ecology by researching only the fauna of the stable continent. This is exemplified by the work of MUTVEI (1975) that most ammonites were planktic or the work of LEHMANN (1975) that most ammonites were benthic. Some ammonites were planktic, some were benthic and some were nektic. It is documented in the work of TANABE et al. (1978), which was carried out in the field where sediments are preserved from shallow to off shore facies. An evolutionary mode seems to have close relation to the ecology.

7. Attention should be paid to the detailed morphologic analysis, especially to biometric analysis on the growth pattern based on the population thinking, the appropriate introduction of statistics and stochastics and the analysis of the relative frequency of specimens.

8. The introduction of the concept of polymorphism and genetics develops the accuracy of biostratigraphic age determination as well as systematics.

### References

DOBZHANSKY, T., 1951 : *Genetics and the origin of species.* 3rd ed., 364 p., Columbia Univ. Press, N. Y.

ELDREDGE, N. & GOULD, S. J., 1972 : Punctuated equilibria, An alternative to phyletic gradualism. *In* SCHOPF, T. J. ed., *Models in paleobiology.* 82–115 in 250 p., Freeman, Cooper & Co., San Francisco.

HARLAND, W. B., SMITH, A. G. & WILCOCK, B., 1964 : The phanerozoic time-scale. *Q. J. G. S. London., Supplement,* 120 s, 1–458.

HIRANO, H., 1975 : Ontogenetic study of late Cretaceous *Gaudryceras tenuiliratum. Mem. Fac. Sci., Kyushu Univ., Ser. D, Geol.,* 22(2), 165–192.

————, 1978 : Phenotypic substitution of *Gaudryceras* (a Cretaceous ammonite).

Trans. Proc. Palaeont. Soc. Japan, N. S., (109), 235–258.

HOEPEN, V., 1921: Cretaceous cephalopoda from Pondoland. Ann. Transvaal Mus., 8(1), 7.

JORDAN, R. & STAHL, W., 1970: Isotopic Paläotemperatur-Bestimmungen an jurassischen Ammoniten und grundsätzlich Voraussetzungen fur diese Methode. Geol. Jb., 89, 33–62.

KAUFFMAN, E. G., 1977: Evolutionary rates and biostratigraphy. In KAUFFMAN & HAZEL eds., Concepts and methods of biostratigraphy. 109–141 in 658 p., Dowden, Hutchison & Ross Inc., PA. ＇

KENNEDY, W. J. & COBBAN, W. A., 1976: Aspects of ammonite biology, biogeography and biostratigraphy. Spec. Papers Palaeont., (17), 1–94.

LEHMANN, U., 1975: Über Nahrung und Ernahrungsweise von Ammoniten. Paläont. Z., 49, 187–195.

MATSUMOTO, T., 1941: A study on the relation among the different species, with special reference to the duration of a fossil species. Jour. Geol. Soc. Japan, 48 (568), 17–37.

————, 1959: Upper Cretaceous ammonites of California. Pt. II., Mem. Fac. Sci., Kyushu Univ., Ser. D, Geol., Special vol. 1, 1–172.

MAYR, E., 1969: Principles of systematic zoology. 428 p., McGraw-Hill Book Co., N. Y.

MUTVEI, H., 1975: The mode of life in ammonoids. Paläont. Z., 49, 196–202.

OBRADOVICH, J. D. & COBBAN, W. A., 1975: A time-scale for the Late Cretaceous of the Western Interior of North America. Geol. Assn. Canada, Spec. Pap., 13, 31–54.

SCHINDEWOLF, O. H., 1934: Über Epöken auf Cephalopoden-Gehäusen. Paläont. Z., 16(1/2), 15–31.

SCHOPF, T. J. M., RAUP, D. M., GOULD, S. J. & SIMBERLOFF, D. S., 1975: Genomic versus morphologic rates of evelution: influence of morphologic complexity. Paleobiology, 1(1), 63–70.

STAHL, W. & JORDAN, R., 1969: General consideration on isotopic paleotemperature determinations and analyses on Jurassic ammonites. Earth & Planet. Sci. lett., 6, 173–178.

TANABE, K., 1975: Functional morhpology of Otoscaphites puerculus (JIMBO), an Upper Cretaceous ammonite. Trans. Proc. Paleont. Soc. Japan, N. S., (99), 109–132.

————, 1977: Functional evolution of Otoscaphites puerculus(JIMBO)and Scaphites planus (YABE), Upper Cretaceous ammonites. Mem. Fac. Sci., Kyushu Univ., Ser. D, Geol., 23, 367–407.

————, OBATA, I., & FUTAKAMI, M., 1978: Analysis of ammonoid assemblages in the Upper Turonian of the Manji area, central Hokkaido. Bull. Natn. Sci. Mus., C (Geol.), 4, 37–62.
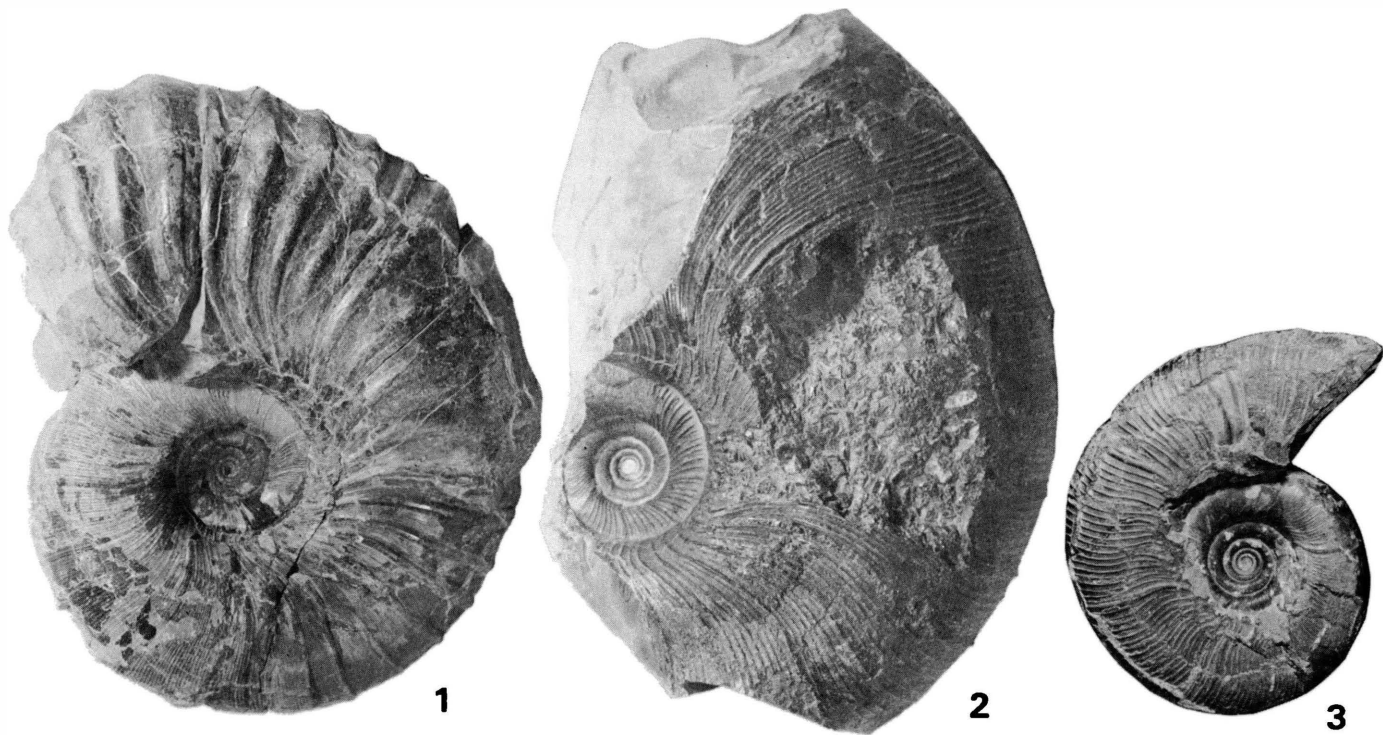
**Fig. 1** *Gaudryceras denseplicatum* var. *denseplicatum* (a fully grown up specimen). R 2113–1, from the Obirashibe River, Obira, Hokkaido. Horizon : *I. hobetsensis* Zone.

**Fig. 2** *G. denseplicatum* var. *intermedium*. N 191 p, from the Santan River, Naibuchi, Sagkalien. Horizon : Mh 6 α.

**Fig. 3** *G. denseplicatum* var. *tenuiliratum*. GK. H. 2206, from the Miho River, Naibuchi, Sagkalien. Horizon : Mh 6 ß.

All figures are ×1/2.0