from Recent Progress of Natural Sciences
, vol.6 (1981), pp.100-106. Sci. Council of Japan

II. Recent Progress of Ammonite Paleobiology in Japan

Ikuwo OBATA*, Kazushige TANABE**, Hiromichi HIRANO***
and Yoshio FUKUDA****

The recent advances in modern cephalopod biological study (e.g. *see* Hamada et al. in this volume for *Nautilus* studies) have greatly influenced researches on ammonites as a living animal. Some of the significant, early works on functional morphology and early ontogency of ammonites by foreign authors published between 1960 and 1970 was introduced by Matsumoto (1974) in a Japanese textbook of paleontology. In the last 10 years, however, ammonite paleobiology has been advanced further with the development of biological paleontology (paleobiology or geobiology) throughout the world. In addition to this, a brisk international exchange of knowledge has taken place. For example, a world newsletter for cephalopod workers, entitled "Cephalopod Newsletter", has been published since 1977,and in August of 1979 a Systematics Association symposium on the Ammonoidea was held at the University of York, at which occasion 57 workers from 12 countries (including 7 Japanese contributors) were assembled. Abstracts of the papers delivered at the symposium were published by the association in 1981 with House and Senior being its editors.

In accordance with the rapid progress of ammonite paleobiology in the world, some noteworthy contributions have recently been made from Japan. They treat such a wide range of subjects as ammonite ecology, functional morphology, taxonomy, evolution, and biogeography. This article attempts to give a concise summary of these recent works as a basis for further advancement in this field.

1. Paleoecology

New light has been shed on significant aspects of ammonite paleoecology in Japan through detailed examination of the Cretaceous ammonites from Hokkaido both points of view from auto- and assemblage-paleoecology. Kanie *et al.* (1978), Tanabe, Hirano and Kanie (1980), and Tanabe, Fukuda, Kanie and Lehmann (1980) studied the jaw apparatuses of certain ammonites genera in comparison with the modern Cephalopoda. Tanabe and others (1980) concluded that species of *Gaudryceras, Tetragonites* and *Neophylloceras* may have had a carnivorous feeding habit using their well-developed jaws bearing rhyncholites and conchorhynchs (anterior calcified deposits) to bite and cut up prey, as in modern *Nautilus.* A biological reconstruction of the jaw apparatus and functions of it in feeding in a late Cretaceous hetermorph *Scalarites mihoensis* was attempted and discussed by Tanabe, Hirano and Kanie (1980), who suggested a carnivorous mode of life for the ammonite similar to that of modern coleoids. Lehmann *et al.* (1980) further considered the morphological variation of the jaw apparatus of the Mesozoic Ammonoidea with special reference to major taxonomic categories and their paleoecology.

* Department of Paleontology, National Science Museum, Tokyo 160, Japan
** Department of Earth Sciences, Ehime University, Matsuyama 790, Japan
*** Institute of Earth Science, School of Education, Waseda University, Tokyo 160, Japan
**** Chiba Prefectural Institute of Public Health, Chiba 280, Japan

The mode of life of ammonites has long been a subject of argument by many ammonitologists. Some previous authors interpreted it as being planktonic, whereas others stressed a benthic mode of life. As a result of recent studies of functional morphology (Tanabe 1977) and paleoecology (Matsumoto 1977; Matsumoto and Nihongi, 1979; Tanabe, 1979; Tanabe *et al.* 1978), it was postulated that the mode of life of the Cretaceous ammonites might be quite variable ranging from benthic to nektonic and that some heteromorphs were actually benthic at least in their adult stage.

It has been recognized empirically that the faunal composition of ammonite assemblages in the marine Cretaceous basin of Hokkaido shows a considerable geographic variation in relation to bio- and lithio-facies (Matsumoto 1965); and several characteristic ammonite biofacies (e.g. the *Baculites* facies by Matsumoto and Obata 1962) have been recognized in selected areas and/or horizons. Tanabe (1979) and Tanabe *et al.* (1978) have analyzed the ammonite assemblages in the Turonian shallow water and intermediate facies of Hokkaido to determine approximately bathymetric and habitat distributions and the effect of postmortem drift. On the basis of quantitative data on the distribution, mode of occurrence and the state of preservation of many species as well as the examination of relative siphuncular strength in selected specimens, they concluded that such groups as tetragonitids, phylloceratids and desmoceratids might have inhabited environments deeper than those of the heteromorphs and collignoniceratids. The role of ammonites as facies fossils was further examined by Futakami *et al.* (1980).

2. Functional morphology

The functional morphology is one of the most important approaches to ammonite paleobiology. Tanabe (1975, 1977) analysed ontogenetic allometries of various shell characters in successively collected samples of *Scaphites* and *Otoscaphites* from Hokkaido and Sakhalin, discussing them in connection with their evolution of the mode of life. As is well known, all kinds of modern and fossil chambered cephalopods have a siphuncular system in their phragmocone. Recent physiological studies on the modern chambered cephalopods have demonstrated that the siphuncular membranes or epithelium or both have an important function to control the buoyancy of living animals. Utilizing such modern techniques as a scanning electron microscope and energy dispersion X-ray microanalyzer, Obata *et al.* (1980) examined the ultrastructure and mineralogical composition of the siphuncular wall membranes (conchiolin) and septal necks in several well-preserved specimens of the Cretaceous ammonites from Hokkaido. They also compared the siphuncular structure of ammonites with those of other modern and fossil cephalopods, proposing an interesting model (here cited in Fig. 1) for possible pathways of cameral liquid removal. Their comparative morphologic research on cephalopod siphuncles is now extending to histology of siphuncular cords of modern *Nautilus* and *Sepia*, but the result has not been published yet. It is expected that their future work will contribute much to an understanding not only of the osmotic mechanism of cameral liquid removal in these living animals but also of the evolutionary history of the Cephalopoda in the sense of adaptive strategy.

Beside the above-mentioned works, colour marking which were fortuitously preserved in

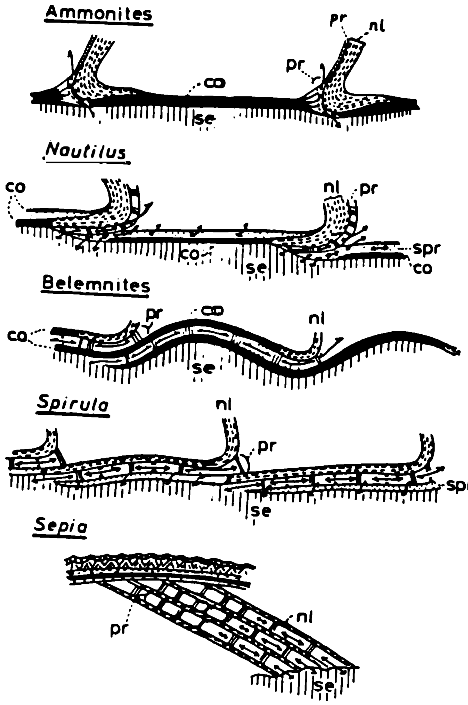

Fig. 1 Hypothetical models showing the pathways (arrows) of cameral liquid removal through siphuncle in selected chambered cephalopods (modified from Obata *et al.* 1980). nl: nacreous layer, pr: porous prismatic layer or zone, co: unpermeable conchiolin membranes of siphuncular wall, spr: spherulitic prismatic layer of siphuncular wall, se: siphuncular epithelium.

some Cretaceous ammonites from Hokkaido were described by Matsumoto and Hirano (1976) and Tanabe and Kanie (1978) with a brief note on their meaning as camouflage. Furthermore, Obata *et al.* (1978) considered a functional significance of apertural features (lappets and rostrum) in some Cretaceous ammonites in relation to their effect for swimming.

3. Analysis of ontogeny and variation

As reviewed by Matsumoto (1975) and Obata (1976), the first successful application of a biological concept, such as allometry to the ammonite study was made by Obata (1959, 1960, 1965, 1966). He demonstrated that the spiral growth of whorls in many ammonites can be approximated as a function of polar coordinates with high degrees of correlation. He also showed that the growth of two continuous characters in an ammonite is expressed as an allometric equation, $Y = bX^{\alpha}$. Thus, a series of Obata's works might have given a guide for analysing the relations between ontogeny and phylogeny not only in ammonites but also in other molluscan fossils. Indeed, they have been followed and advanced further by several paleobiologists (e.g. Hayami, I.) who introduced a population concept in the biometric analysis. An attempt to combine both population concept and relative growth analysis in studies of the ontogenetic and interspecific variation of some Cretaceous ammonites has been made by Hirano (1975, 1979), Tanabe (1977), Obata *et al.* (1979) and Obata and Matsukawa (1980).

Concerning the early ontogeny, growth patterns of shell wall, septa and sutures in *Gaudryceras* were demonstrated by Hirano (1975). The internal structural characteristics of nepionic shells of many Cretaceous ammonite species, and their implications to major taxonomy and phylogeny were made clear by Tanabe *et al.* (1979). Subsequently, an interesting model emphasizing the direct development of the Ammonoidea (here cited in Fig. 2) was proposed by Tanabe *et al.* (1979), based on their analysis of microstructure and chemical composition in selected, well-preserved Cretaceous ammonite specimens from Hokkaido in comparison with the data on the early ontogeny of modern cephalopods.

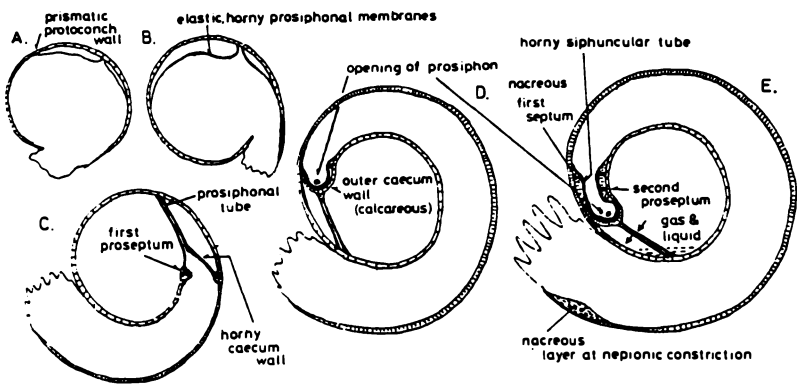

Fig. 2 Diagrammatic model showing the successive stages in the early ontogenetic development of the Ammonoidea (after Tanabe, Fukuda and Obata 1980). A-d: 1st to 4th substages, E: transitional phase from 5th substage (embryonic stage) to post-embryonic stage.

4. Evolutionary research

As Matsumoto (1964) mentioned earlier, the mode of chronological shift of shell morphology in ammonites greatly varies among various groups in the superfamily level. In taking Cretaceous ammonites as examples, the Acanthocerataceae with ornate shells had evolved rapidly, in contrast to the slow morphological transformation in the Phyllocerataceae and the normally-coiled Lytocerataceae. This generalized idea for the chronological change of Cretaceous ammonite morphology has been confirmed from quantitative biometric studies of fossil populations of *Gaudryceras* (Hirano 1978), *Scaphites* and *Otoscaphites* (Tanabe 1977), and *Subprionocyclus* (Obata *et al.* 1979).

Concerning the relation between the ranges of two related species, Matsumoto (1941) showed several different examples based on his careful field observation of startigraphic occurrences of Cretaceous ammonites in Hokkaido and Sakhalin. Recently, Hayami and Ozawa (1975) considered continuous and discontinuous variations in ammonite evolution relying on modern genetic theories and using Matsumoto's (1941) data as one of the examples for discussion. In this work, Hayami and Ozawa concluded that some of the seemingly discontinuous relations between two, or more than three ancestral-descendant "species" observed in the fossil record can be explained by the non-sex-associated genetic variation (polymorphism) within a single evolutionary species. Their interesting conceptual model has subsequently been confirmed by an evolutionary analysis of the *Gaudryceras denseplicatum* lineage by Hirano (1978), who explained partly coexistent relations among three related typological species to be a transient and sexual dimorphisum within a single evolutionary species (Fig. 3). He (1980) further discussed the implication of transient polymorphism in the systematics of the Ammonoidea. Hirano's works (1978, 1980) seem to be very important and innovative, because ammonites, although they are one of the most suitable materials for evolutionary analysis, have not yet been fully studied from a standpoint of paleogenetics.

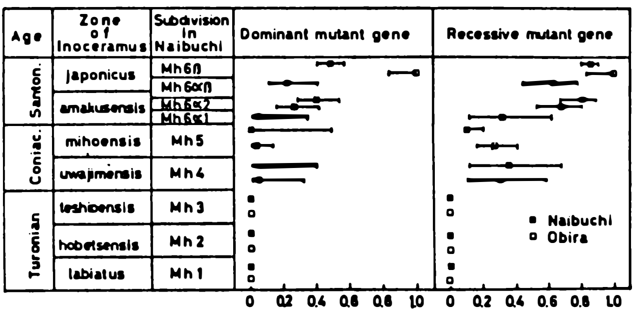

Fig. 3 Historical change of the mutant gene frequency in the lineage of late Cretaceous Gaudryceras denseplicatum (after Hirano 1978). 95% confidence interval is shown by a bar.

A great number of taxonomic results on Paleozoic and Mesozoic ammonites have recently been published by Japanese authors. We do not intend to review these works here, because most of them have already been summarized by Matsumoto (1975) and Obata (1976).

5. Paleobiogeography

Two interesting papers focussing on faunal provinces, migration and evolution of the Mesozoic Ammonoidea were summarized by Matsumoto (1973) and Bando (1980).

Matsumoto showed the geographic distribution of many late Cretaceous genera each stage by stage using the present-day world maps in which continents and oceans are paleogeographically reconstructed. On the basis of these maps he also commented climate and sea level changes, the existense of possible barriers between different faunal provinces and ecology of ammonites, all of which might have affected migration patterns and evolution.

Bando (1980) discussed the Permo-Triassic otoceratacean ammonite evolution above the generic level, showing migrational pathways from the Permian Araxoceratidae and Otoceratidae in the western part of central Tethys to the early Triassic Otoceratidae (*Otoceras*, *Ophiceras* and others) in the eastern central Tethys on a reconstructed paleocontinent-ocean world map.

References

Bando, Y., 1980. On the otoceratacean ammonoids in he central Teths, with a note on their evolution and migration, Mem. Fac. Educ., Kagawa Univ. Pt. 2, 30, 23-44.

Futakami, M., Tanabe, K., Obata, I. 1980. Characteristics of the megafossil assemblages in the Upper Turonian (Cretaceous) of the Pombets area, central Hokkaido. Bull, Kitakyushu Mus. Nat. Hist. (2), 1–13 (in Japanese with English abstract).

Hayami, I., Ozawa, T. 1975. Evolutionary models of lineage zones, Lethaia 8, 1–14.

House, M.R., Senior, J.R., eds. 1981. The Ammonoidea: The Evolution, Classification, Mode of Life and Geological Usefulness of a Major Fossil Group. The System. Assoc. Spec. Vol., No. 18, 594 p. Academic Press, London.

Hirano, H. 1975. Ontognetic study of late Cretaceous *Gaudryceras tenuiliratum*. Mem. Fac. Sci, Kyushu Univ., Ser. D, Geol. 22, 165–192.

Hirano, H., 1978. Phenotypic substitution of *Gaudryceras* (a Cretaceous ammonite). Trans. Proc. Palaeont, Soc. Japan, N.S. (109), 235-258.

Hirano, H., 1979. Importance of transient polymorphism in systematics of Ammonoidea. Gakujutsu-kenkyu, school of Educ., Waseda Univ. (28), 35–43.

Kanie, Y., Tanabe, K., Fukuda, Y., Hirano, H., Obata, I. 1978. Preliminary study of jaw apparatus in some late Cretaceous ammonites from Japan and Sakhalin. Jour. Geol. Soc. Japan 84, 629–631 (in Japanese).

Lehmann, U., Tanabe, K., Kanie, Y., Fukuda, Y. 1980. Über den Kieferapparat der Lytoceratacea (Ammonoidea). Paläont. Z. 54, 319–329.

Matsumoto, T., 1941. A study on the relation between different species, with special reference to the problems on the range of fossil species. Jour. Geol. Soc. Japan 48, 17–37 (in Japanese).

Matsumoto, T. 1964. Ontogeny and evolution in some Cretaceous ammonites. Fossils (8), 67–76 (in Japanese).

Matsumoto, T. 1965. Faunal changes in Cretaceous cepahlopods. Fossils (9), 24–29 (in Japanese).

Matsumoto, T. 1973. Late Cretaceous Ammonoidea. In Hallam, A. (ed.): Atlas of Palaeobiogeography. 421–429. Elsevier.

Matsumoto, T. 1974. Ammonoidea. In Matsumoto, T. (ed.): Paleontology, 2: 94–148. Asakura Book Co. (in Japanese).

Matsumoto, T. 1975. Ammonitology in Japan – A historical review. Trans. Proc. Palaeont. Soc. Japan, N. S. (97), 1–6.

Matsumoto, T. 1977. Some heteromorph ammonites from the Cretaceous of Hokkaido. Mem. Fac. Sci., Kyushu Univ., Ser. D, Geol. 23, 303–366.

Matsumoto, T., Hirano, H. 1976. Colour markings in some Cretaceous ammonites from Hokkaido. Trans. Proc. Palaeont. Soc. Japan, N. S. (102), 334–342.

Matsumoto, T., Nihongi, M. 1979. An interesting mode of occurrence of *Polyptychoceras* (Cretaceous heteromorph ammonoid). Proc. Japan Acad. 55, Ser. B, 115–119.

Matsumoto, T., Obata, I. 1962. On the *Baculites* facies. Fossils (3), 57–63 (in Japanese).

Obata, I. 1959. Croissance relative sur quelques Espèces des Desmoceratidae. Mem. Fac. Sci., Kyushu Univ., Ser. D, Geol. 9, 33–45.

Obata, I. 1960. Spirale de quelques Ammonites. Mem. Fac. Sci., Kyushu Univ., Ser. D, Geol. 9, 151–163.

Obata, I. 1965. Allometry of *Reesidites minimus*, a Cretaceous ammonite species. Trans. Proc. Palaeont. Soc. Japan, N. S. (58), 39–63.

Obata, I. 1966. Paleontology and relative growth. Biol. Sci., Monthly 18(1), 23–32 (in Japanese).

Obata, I. 1976. Cephalopods. In Matsumoto, T. et al. (eds.): A concise history of palaeontology in Japan. Trans. Proc. Palaeont. Soc. Japan, N. S. (100s), 33–37.

Obata, I., Futakami, M., Kawashita, Y., Takahashi, T. 1978. Apertural features in some Cretaceous ammonites from Hokkaido. Bull. Natn. Sci. Mus., Tokyo, Ser. D (Geol.), 6, 61–74.

Obata, I., Matsukawa, M. 1980. Ontogeny and variation in *Hypacanthoplites subcornuerianus*, a Lower Cretaceous hoplitid ammonite. Prof. S. Kanno Mem. Vol. 185–211.

Obata, I., Tanabe, K., Fukuda, Y. 1980. The ammonite shiphncular wall: its microstructure and functional significance. Bull. Natn. Sci. Mus., Tokyo, Ser. C (Geol.), 6, 61–74.

Obata, I., Tanabe, K., Futakami, M. 1979. Ontogeny and variation in *Subprionocyclus neptuni*, an Upper Cretaceous collignoniceratid ammonite. Bull. Natn. Sci. Mus., Tokyo, Ser. C (Geol.), 5, 51–88.

Tanabe, K. 1975. Functional morphology of *Otoscaphites puerculus* (Jimbo), an Upper Cretaceous ammonite. Trans. Proc. Palaeont. Soc. Japan, N. S. (99), 109–132.

Tanabe, K. 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.

Tanabe, K. 1979. Palaeoecological analysis of ammonoid assemblages in the Turonian Scaphites facies of Hokkaido, Japan. Palaeontology 22, 609–630.

Tanabe, K., Fukuda, Y., Obata, I. 1980. Ontogenetic development and functional morphology in the early growth-stages of three Cretaceous ammonites. Bull. Natn. Sci. Mus., Tokyo, Ser. C (Geol.), 6 9–26.

Tanabe, K., Fukuda, Y., Kanie, Y., Lehmann, U. 1980. Rhyncholites and conchorhynchs as calcified jaw elements in some late Cretaceous ammonites. Lethaia 13, 155–166.

Tanabe, K., Hirano, H., Kanie, Y. 1980. The jaw apparatus of *Scalarites mihoensis*, a late Cretaceous ammonite. Prof. S. Kanno Mem. Vol. 159–165.

Tanabe, K., Kanie, Y. 1978. Colour markings in two species of tetragonitid ammonites from the Upper Cretaceous of Hokkaido, Japan. Sci. Rep. Yokosuka City Mus. (25), 1–6.

Tanabe, K., Obata, I., Fukuda, Y., Futakami, M. 1979. Early shell growth in some Upper Cretaceous ammonites and its implications to major taxonomy. Bull. Natn. Sci. Mus., Tokyo, Ser. C (Geol.), 5, 153–176.

Tanabe, K., Obata, I., Futakami, M. 1978. Analysis of ammonoid assemblages in the Upper Turonian of the Manji area, central Hokkaido. Bull. Natn. Sci. Mus., Tokyo, Ser. C (Geol.), 4, 37–62.