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The fossil on the cover is an adult example (T. TAKAHASHI coll.) of *Mikasaites orbicularis* MATSUMOTO (subfamily Marshallitinae, family Kossmaticeratidae) from the Lower Cenomanian (Cretaceous) of the Mikasa area, central Hokkaido. (photo by M. NODA, natural size)

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A STORY OF THE BELEMNITE—DEVELOPMENTAL APPROACH TO FOSSIL MORPHOLOGY*

(Presidential address, Palaeontological Society of Japan, 1981)

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The addresses that the past presidents of the society have delivered were, in many cases, elegant reviews of taxonomic and phylogenetic studies on a certain taxon, directed toward explaining the relation between their own work and the advancement of knowledge on that taxon. Kobayashi (1960) presented a review of phylogenetic studies on trilobites, and Matsumoto (1975) on ammonites. However, because I am not in position at present to discuss the phylogenetics on any taxon, I would like to reminisce about my ontogenetic studies on a belemnite.

I started my study of paleontology with fossils from the Cretaceous deposits of Miyako district, Iwate Prefecture. Since then, more than 30 years have been passed. Of course, I did not devote all of these years to the studies of this local fauna. Yet, I reflect upon the considerable time that I have spent toward understanding this paleontological problem. The general idea at that time was to make an accurate and precise geological survey and to collect as many fossils as possible. It seems to me that the general trend in thinking at that time was that the more fossils collected, the better the scientific results. Specimens, thus collected during one field season, were too much to cope with in one year of laboratory work and untreated specimens had to be left behind year after year. It was an odd time when research funds tended to be given to those who would remain in the field the longest.

However, I had to describe these specimens in one way or another, and decided to commence my study with the description of belemnites. But I soon noticed that it was an extraordinary, if not impossible task, to describe all of these specimens, which included foraminifers, bivalves, ammonites, gastropods, corals, echinoids, crinoids etc. I was forced to change my approach. Instead of starting the descriptive study, I let my thoughts become confounded about the magnitude of the project and about what type of a product would result from such a descriptive effort. Even if I was lucky enough to find a species that moderately changed its morphology during the time of the depositional sequence, and could trace the chronological variation in that species, I still wondered if we might not be far from elucidation of the paleontological problem. As Makiyama mentioned in his study on the phylogeny of *Umbonium*, boasting about one's phylogenetic tree is similar to boasting of the shape of a tree in his garden, others are at a loss about what to do, except for just praising it (Makiyama, 1935, p. 253).

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* This is the English translation of the presidential address delivered at the Annual Meeting of the Society, held at Tohoku University, Sendai, on 23 January, 1981.

When I look back upon those days, I think that the general belief was that generalizations will surface if enough solid facts are accumulated. It was this approach used by most paleontologists that Kimura ironically criticized. He concluded that they are virtually the same as the person who, when standing at a street corner and looking at the moving car passing by before him, believes he can understand what mechanisms make the car run (Kimura, 1958, p. 124). It was a long time later before I understood that the old inductive philosophy of Francis Bacon, which underlay the thought of paleontology at that time, had led to my problems.

When I was reading Carr's "What is history?", I encountered a situation similar to that of paleontology in the explanation of historical philosophy in 19th century. That was "the belief of fetishism of facts", which might be expressed as "facts speak for themselves (Carr, 1961, p. 16)". He explained that it is this belief "which during the past hundred years has had such devastating effects on the modern historian, producing in Germany, in Great Britain, and in the United States, a vast and growing mass of dry-as-dust factual histories, of minutely specialized monographs of would-be historians knowing more and more about less and less, sunk without trace in an ocean of facts (Carr, 1961, p. 15)". Replacing the words "historians" with paleontologists and "factual histories" with descriptions of species, I was shocked to find the situation quite similar to what I was about to do with belemnites and ostracods. Therefore, in the introduction for the checklist of Japanese ostracods (Hanai, 1977, p. 1), I emphasized the necessity for reflection on that part of Carr's passage quoted above.

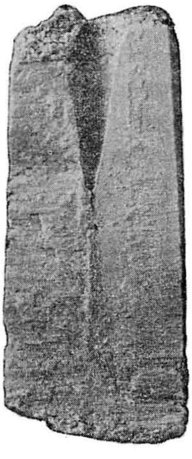
Last year, when Gould (1980, p. 96) discussed the promise of paleobiology as "a nomothetic science based upon evolutionary theory", one of the impediments to paleobiology that he pointed out was overdominance of inductive philosophy in paleontology. Another was easy-going extrapolationism in which biological theory, founded in neontology, is extended rashly into the past to reexemplify the theory utilizing imperfect fossil records, and then conclude that the same rules hold true there. In connection with the latter impediment, I also pointed out that "it is relatively easy to extrapolate biological theories (e.g. the theory of speciation) speculatively into the geological past, but it is difficult, if not impossible, to elucidate with fossil evidence the paleobiologically significant historical events, which may be complicated, but which may interpreted in terms of biological theories (Hanai, 1977, p. 85)". At the same time, I was at a loss as to what approach we should take to find paleobiologically significant events.

Then, I realized that the relation between the facts and the historians explained by Carr is quite similar to that between paleontological facts and paleontologists. On this relation in human history, Carr mentioned that "the historian starts with a provisional interpretation in the light of which selection has been made by others as well as by himself. As he works, both the interpretation and the selection and ordering of facts undergo subtle and perhaps partly unconscious change, through the reciprocal action of one or the other (Carr, 1961, p. 29, 30)", and drew the conclusion on "What is history?" that "it is a continuous process of interaction between the historian and his facts, an unending dialogue between the present and the past (Carr, 1961, p. 30)".

Further, Carr, explaining Croce's "contemporary history", argued that "history consists essentially in seeing the past through the eyes of the present and in the light of its problem, and that the main work of the historian is not to record, but to evaluate; for, if he does not evaluate how can he know what is worth recording? (Carr, 1961, p. 21)". From this argument, it seems clear that an interpretation by a historian stands on the evaluation of the facts using all his knowledge. Therefore, it occurred to me that the task of paleontologists might be started with the interpretation of fossil data through the present eyes of the paleontologist himself. However, my knowledge then did not give me confidence to proceed with this approach.

At first, I took up belemnites for study, but because of their characterless, bullet-shaped morphology, soon the morphological characteristics to describe them were exhausted. Further and fortunately, there was only one species that I could identify with satisfaction. If I had taken up a taxon other than belemnites, which includes many species with variety of morphology, I might have been busily occupied with the description of the species. I completed the description of a species and I gave it a new name, *Neohibolites miyakoensis*. One of the specimens used at that time is shown in Pl. 66, Fig. 1. Its only conspicuous character that can be described is a ventral furrow. How far the furrow extends adapically is considered to be a diagnostic character of species and genus. I felt it rather strange to give a character of unknown biological significance an important taxonomic value without some thought. So, a question, what is the biological meaning of the ventral furrow, occupied my mind. In this case, the need to evaluate the facts became pressing, as I had only anthropocentric knowledge based on my own experience; for example, the electric wires and gas pipes indispensable for our modern life are to be protected in a furrow, an acute spine is suitable for thrusting, and a long time standing at attention is quite uncomfortable ··· etc. Thus, I was satisfied with the restoration of a belemnite by Stevens (1965, p. 48) where he positioned an artery and a vein in the ventral furrow. It was an anthropocentric and unsophisticated interpretation.

However, if that is the case, the furrow alone is sufficient to protect the veins. Yet, when the belemnite is split into two pieces longitudinally along the median plane, a smooth and flat surface is found between the alveolus and ventral furrow, whereas the remaining surface is rough. The presence of the commissure or slit between the planes under the ventral furrow concerned me as I interpreted the biological meaning of the furrow. The commissure was first described by Shvetsov (1913, p. 65) and because it was observable in *Neohibolites* from Miyako, a description was given, leaving aside the question of its biological significance (Text-fig. 1). One can give a description of the specimen in his own way, even if he knows nothing about it.



Text-fig. 1. Slit plane of *Neohibolites miyakoensis* Hanai, 1953. ×3. MM2541

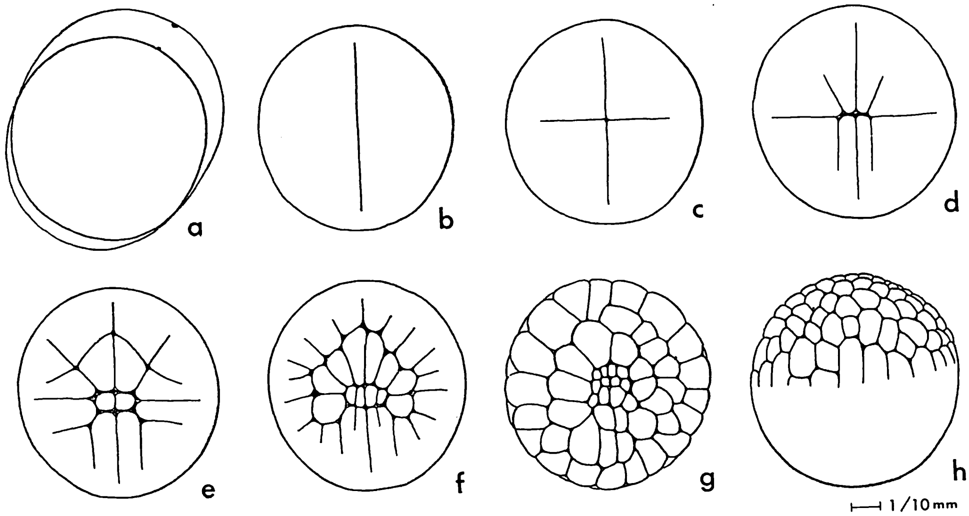
After some effort had been made to overcome Stevens' interpretation, I began to make interpretations based on the knowledge of the living organisms that have a close relationship to the fossils. In other words, it was an effort to have a critical eye for the evaluation of the facts. But, because the neontological knowledge has not always been accumulated for understanding of the ancient organisms, many of the results of neontological studies are little use to paleontologists, or paleontologists are often incapable of utilizing neontological knowledge. Consequently, paleontologists began to make observations and experiment with living organisms, and began to study the neontological literature on pertinent subjects, in order to obtain knowledge and ability applicable to their own purposes. It may be important to emphasize that paleontologists normally have never looked about for fossil characters with an eye to applying or enforcing known neontological theories.

Gustomesov (1975, p. 320), who observed a thin and low ridge running longitudinally on the ventral surface of the squid's mantle, considered it a remnant of a cariniform fin, and further related this knowledge with the facts of the past, that is, the ventral furrow of the belemnite overlying the commissure. The explanation was that the slit between the planes was filled successively as the rostrum grew, and a deposit was secreted by the thin process of the mantle extending into the slit. It has been well established since Naef (1922, p. 213-221) that the lateral furrows of the belemnite are the scars of the attachment or insertion of the muscle of the lateral fins. This interpretation was thus extended into that of the ventral as well as dorsal furrows, the latter of which has also been reported in some belemnites. The restored belemnite has, therefore, a tail which looks something like the posterior half of a dirigible in having horizontal as well as vertical tail planes. Nevertheless, this interpretation did not give us answer to the question of why only the ventral furrow has the commissure and other furrows have no particular structure under them.

In this way, hypotheses are derived from individual experiences, biological knowledge or anything else. The source of the theories is of infinite variety, and it matters not from where we have obtained or as stated by Hempel (1966, p. 15) "invented", the theories. Moreover we "do not believe that we … start with observations and try to derive our theories from them (Popper, 1957, p. 134)". Then the theories must be tested as to whether or not they can explain the results of observations accumulated intentionally. Theories that are falsified are eliminated and among the remaining competing theories, the best-tested one should be preferred. Under the influence of the aforementioned ideas of Popper, Gould (1980, p. 102) explained metaphorically that this method, when applied to paleontology, seems like intelligent fishing in the pool of evolutionary biology. If so, I would like to consider where the fish are.

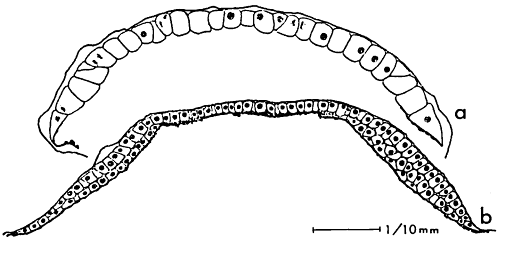
I was not at all satisfied with those hypotheses that had been proposed to explain the morphology of belemnite, because they remain fixed, as if set in concrete. There are some differences among the authors, but since Seilacher's work (1970, p. 393-396), the morphology of fossils has usually been approached in terms of a combination of phylogenetic, adaptational, and architectural aspects. Sophisticated combinations of these approaches are of course useful in morphological studies. The phylogenetic approach is, however, merely an enumeration of the facts following the order of time, unless its explanation is accompanied with genetic and developmental mechanisms. The adaptational approach is also a static comparison between the morphology and the optimal design, because with only this approach we can not make clear the dynamic mechanisms or the genesis of the morphology. The architectural approach may be mechanically dynamic but it is biologically static in itself. In comparison with these static approaches, the developmental approach is the most direct and dynamic way to understand morphology through understanding the mechanisms of its formation. I look upon this approach as the only way, because I hold a belief that every organism has its own unique process of pattern formation. Otherwise it can not attain its existence. However, our present knowledge on pattern formation is still far from sufficient for providing a vehicle for an interpretation of the development of squid.

In the case of belemnites, we fortunately have certain ontogenetic facts in that the early part of the shell growth is preserved, enclosed by the successive growth of the adult shell. In the case of modern squids, their development has been studied intensively; fishery science in Japan provides us with the results of many excellent studies. The first task which I undertook was a study of the ontogeny of belemnites, that is the enumeration of the constituent parts of a belemnite in order of their formation without considering their developmental mechanisms. When I started to describe *Neohibolites* from Miyako, there were only a very few papers on the internal structure that utilized a polished section of the belemnite. But, as the Paleozoic nautiloids were in most cases observed from making polished sections, there seemed to be no reason why the same technical methods were not applicable to the study of belemnites. Then the description of the internal structure of a belemnite was undertaken from observations of both polished and thin sections. A structure, named the intermediate camera was found between the protoconch and the primordial rostrum, and a bowl-in-bowl structure was detected in the primordial rostrum. Further, the commissure seems not to extend into the primordial rostrum. The primordial rostrum has long been thought to be merely a beginning part of the rostrum. Thus the question, which was the earlier construction, protoconch or primordial rostrum, disturbed me in developing a sequential description of the ontogeny of belemnite (Pl. 66, Fig. 2). Finding of new structure, however, changed this view on the primordial rostrum to that it is a construction quite different from the true rostrum. Thus, in my earlier paper (Hanai, 1953, p. 66), I argued that the primordial rostrum was constructed first, according to the view that smaller construction is formed earlier. The bowl-in-bowl structure of primordial rostrum has a smallest bowl in its apex. But in the later papar (Hanai, 1956, p. 1571), I did not designate which construction is the earlier. The only conclusion that can be drawn is that *Neohibolites* experienced two stages. The earlier one is the stage that includes constructions of protoconch, intermediate camera, primordial rostrum and perhaps a few chambers. In the later stage, a slender true rostrum with pointed apex and the rest of the chambers were formed. In applying the methods of microscopic observation of thin sections in petrology, this sequence is determinable from the fact that the true rostrum shaved off the side of the primordial rostrum (cf. Hanai, 1953, pl. 7, figs. 1-4). For a difference of opinion on the details of formation of the primordial rostrum refer to Jeletzky (1966, p. 129, 130; 1972, p. 169, 170) and Barskov (1972, p. 493).

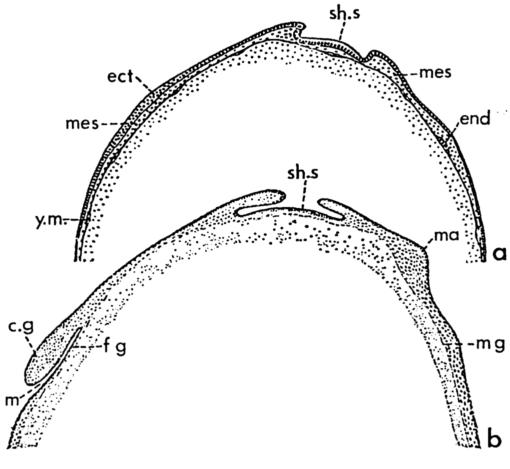


Text-fig. 2. The cleavage of *Todarodes pacificus* Steenstrup, 1888. (After Soeda, 1952.)

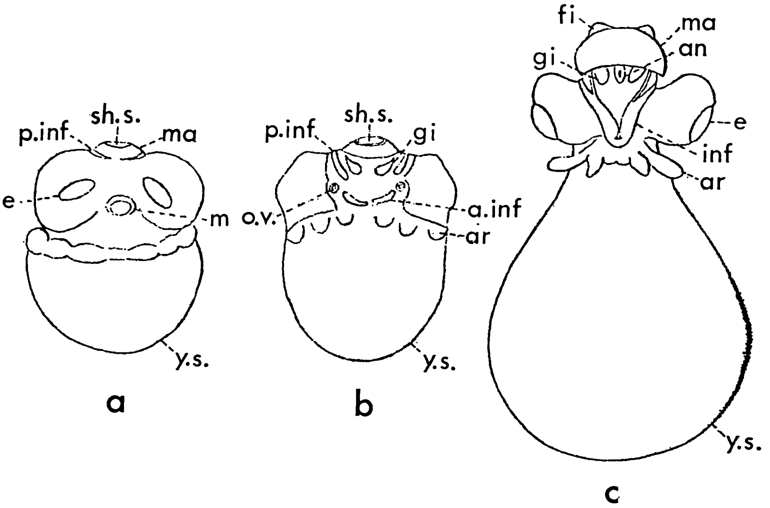
A study on the development of the modern squid was started at the eleventh hour in order to interpret the ontogeny of belemnites in terms of the developmental mechanisms. Text-fig. 2 shows the cleavage of *Todarodes* studied by Soeda (1952, p. 10-15). Fertilized egg and first to fourth cleavage stages are shown in Fig. 2a and Figs. 2b-e, respectively. After the micromere appears in the central area, the blastomere covers the northern hemisphere of the egg and a blastodiscus is formed (Figs. 2f-h). Text-figure 3 shows the median sections of the blastodiscus, where a single layer of blastomer (Fig. 3a) becomes double along the marginal area of the blastodiscus (Fig. 3b). Thus the blastodiscus grows into the blastula. Text-figs. 4 and 5 are the illustrations



Text-fig. 3. Longitudinal sections of an advanced cleavage stage (a) and a blastula stage (b) of *Todarodes pacificus* Steenstrup, 1888. (After Soeda, 1952.)



Text-fig. 4. Longitudinal sections of younger embryos of *Loligo vulgaris* Lamarck, 1799. (After Korschelt, 1892.) c.g. cerebral ganglion; ect. ectoderm; end. endoderm; fg. fore-gut; m. mouth; ma. mantle; mes. mesoderm; mg. mid-gut; sh.s. shell gland; y.m. yolk membrane.

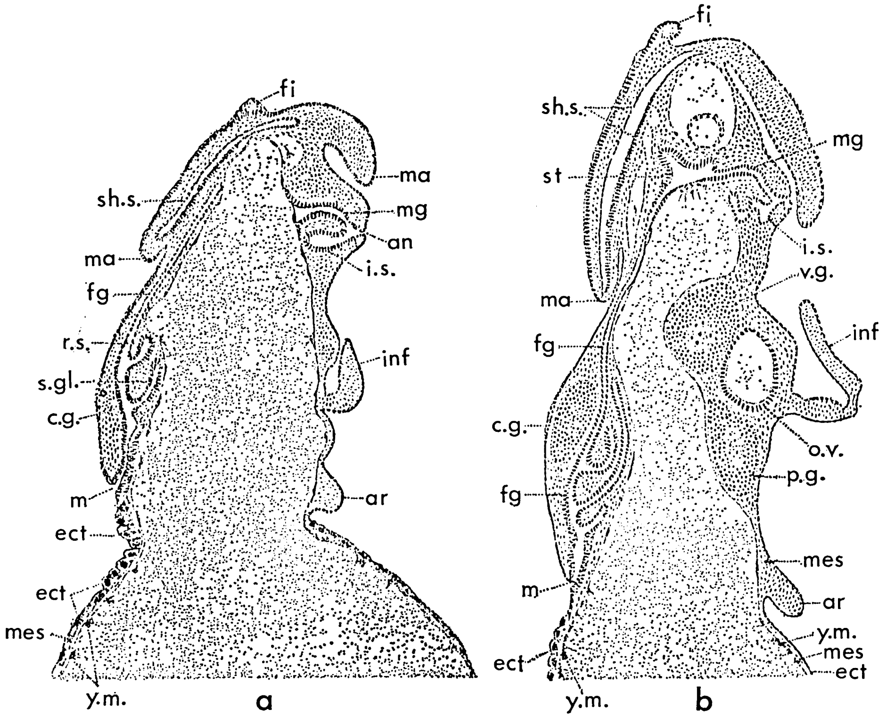


Text-fig. 5. Dorsal (a) and ventral (b, c) views of younger embryos of *Loligo vulgaris* Lamarck, 1799. (After Korschelt, 1892.) a. inf. anterior infundibulum; an. anus; ar. arm; e. eye; fi. fin; gi. gill; inf. infundibulum; m. mouth; ma. mantle; o. v. otolithic vesicle; p. inf. posterior infundibulum; sh. s. shell gland; y. s. yolk sac.

of the development of *Loligo* from Korschelt (1892, p. 349; pl. 36, fig. 2). As the endoderm appears on the inside and the mesoderm in the medial part, the ectoderm in the central area of the blastula subsides to form a shallow invagination, the rudimentary shell gland. Then the rudiment of the mantle extends to close the opening of the invagination in forming the shell sac (Text-fig. 5). According to Korschelt (1892, pl. 37, figs. 23, 24), when the large eyes, rudiments of the fin, connected digestive organs and ganglions are formed, the shell sac is enclosed completely in the dorsal part of the mantle and extends the full length of the mantle (Text-fig. 6). The animal consumes the yolk and takes a shape close to the adult. This is shown in the Text-fig. 7, which is taken from Choe and Oshima (1961, fig. 3•26) who illustrated a young form of *Sepioteuthis* just after hatching by dissolving the shell membrane by using enzymes. These observations on the development of various species of squids are well summarized by Ishikawa (1975, p. 379-381) in Japanese. Recently, the study on the embryonic and post-embryonic development of squids has been advanced very much by Boletzky and Boletzky (1973, p. 141-157) and Bandel and Boletzky (1979, p. 324-335).

Provided that the belemnite shell, including the phragmocone and rostrum, was formed in the shell sac closely similar in function to that of the present day squid, an interpretation that the ventral furrow underlying the commissure corresponds to the concrescence line of the opening of rudimentary shell sac seemed reasonable. Then, it naturally follows that the variously shaped rostra, from slender to sturdy, from sharp and pointed to clavate with a nearly round apical end, and often with many aberrant forms, are all formed in the blind part of the shell sac.

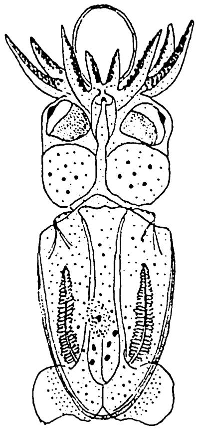
In the second step, an attempt to test this interpretation has been made through



Text-fig. 6. Longitudinal sections of older embryos of *Loligo vulgaris* Lamarck, 1799. (After Korschelt, 1892.) an. anus; ar. arm; c.g. cerebral ganglion; ect. ectoderm; fg. fore-gut; fi. fin; inf. infundibulum; i.s. ink-sac; m. mouth; ma. mantle; mes. mesoderm; mg. mid-gut; o.v. otolithic vesicle; p.g. pedal ganglion; r.s. radula sac; s.gl. salivary gland; sh.s. shell sac; st. stomach; v.g. visceral ganglion; y.m. yolk membrane.

comparative study of the developmental process. The comparison in paleontology consists of two aspects. One is to simplify the complex state by finding out the common aspects between the two objects intended to compare to each other, and to give an explanation to the complexity by minimum interpretation. And the other is to search for the paleobiologically unique historical events through the elimination of the determined common aspects.

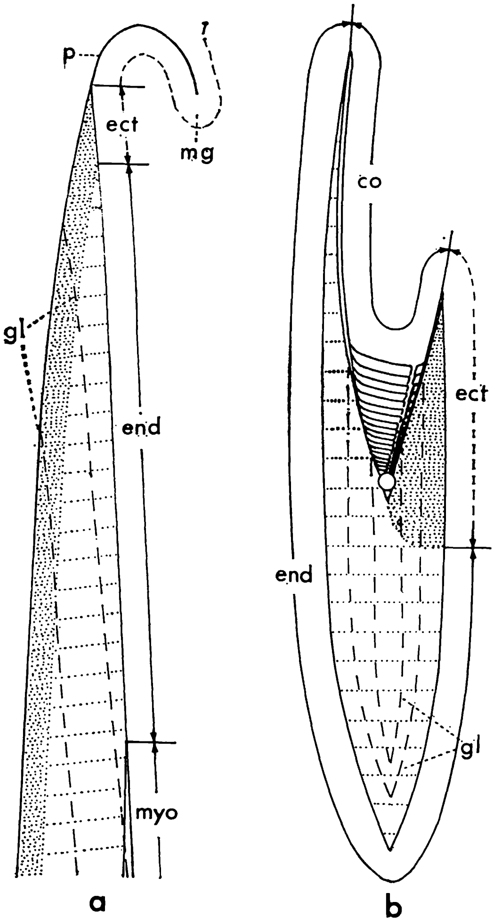
The protoconch of *Neohibolites* is approximately 0.3 mm and opening of shell sac of *Loligo* is approximately 0.2 mm in diameter. The protoconch was probably formed as the outer shell under the relatively protected condition in the egg capsule. It is not necessary to infer that the shell sac was formed by closing its opening at the stage of protoconch formation, but at the stage of the formation of the intermediate camera, the epithelium, which has extended covering the outer face of the protoconch, is perhaps fused to from closed shell sac. The primordial rostrum has a bowl-in-bowl structure of crescent-shaped, solid plates, and its apex has not yet been pointed. Perhaps the animal is still in the egg capsule. The intermediate camera might be filled with fluid, because it does not possess an opening. After hatching, the true rostrum of



Text-fig. 7. A young form of *Sepioteuthis lessoniana* Lesson, 1830, just after hatching. (After Choe and Oshima, 1961.)

the belemnite starts its excessive relative growth, shaving off the side of the primordial rostrum and growing into a pointed and slender rostrum with a length ten times as long as its diameter. Passing this stage, the young rostrum increases its thickness to become a stout adult.

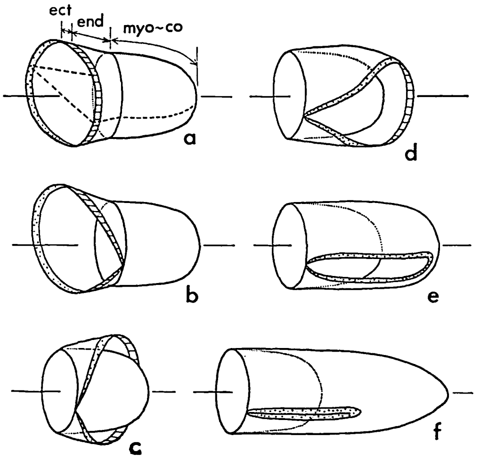
Barskov (1972, p. 493) pointed out that the layer that forms the protoconch is prismatic and the layer, which deposited the adapical side of the protoconch, leaving an intermediate camera between the protoconch and the layer, is nacreous. Spaeth *et al.* (1971, p. 3149) proved that the innermost layer of the rostrum cavum consists at least in part of aragonite. The bowls of the primordial rostrum seem to preserve a structure of perpendicularly disposed acicular crystals presumably of aragonite. Following the pioneer work of Müller-Stoll (1936, p. 172-174), recently Barskov (1970, p. 559), Spaeth (1971, p. 34, 35) and Spaeth *et al.* (1971, p. 3148) clarified that the true rostrum is primarily composed of the alternation of the compact nacreous layer with tabular crystals and a layer of prismatic crystals having the later fillings as a result of diagenesis. This lattice-like construction is somewhat similar to that of the pillar structure observable in *Sepia*. It is a belemnite with a spongy rostrum; it is lighter than that we have supposed. Consequently, Barskov



Text-fig. 8. Scheme of dorsoventral sections of marginal portion of nautiloid shell (a) and an idealized belemnite (b). co. area of mantle epithelium for secretion of conothecal and septal layers; ect. area of mantle epithelium for secretion of ectostracum; end. area of mantle epithelium for secretion of endostracum; gl. growth lines; mg. mantle groove in which periostracum originate at its base; p. periostracum; myo. area of mantle epithelium for secretion of myostracum.

(1972, p. 498, 499; 1973b, p. 292) pointed out correctly that the rostral layers homologously correspond to the nacreous layers or endostracum of *Nautilus*. Where then should the layers corresponding to the periostracum and ectostracum of *Nautilus* be found in belemnite? He concluded that perhaps they were lost. However, it seemed to me that in the process of the development, the layers were pushed away toward the ventral area of the rostrum. The layers correspond to the concrescence zone of the shell sac opening. This opening of the epithelium will have been stretched longitudinally in the process of development as the belemnite grew rapidly towards a direction slightly dorsal to the central axis of the development (Text-fig. 8). The ventral furrow should be expected to be formed in the area where the epithelium for secretion of periostracum and ectostracum extend longitudinally (Text-fig. 9). Certainly, the concept of homology is a driving force and fundamental to comparative biology.

Now, it is clear that if this is the case, then a shell structure different from that of the rest of the rostrum is expected to be found in this area. The cross section of the adapical part of the rostrum is shown in Pl. 66, Fig. 3, where the radial structure with concentric growth lines is found. But the section crossing the ventral furrow shows, in spite of the continuation of growth lines across the commissure, sharp discontinuity of the crystal structure between the calcite which fills the commissure and the calcite which forms the main part of the rostrum (Pl. 66, Fig. 4). Thus the ventral furrow is a structurally weak part of the belemnite body, and the belemnite body coils very loosely as if it held the weak part in its venter. This interpretation may enable us to gain a preferable understanding of the ventral furrow of belemnites.



Text-fig. 9. Explanation of homologous relation of mantle epitherium between nautiloid and belemnite. Idealized mantle epitherium for secretion of nautiloid shell layers (a). Figures for explanation of homologous relation (b-e). Idealized mantle epitherium for secretion of belemnite shell layers (f). ect. area of mantle epitherium for secretion of ectostracum; end. area of mantle epitherium for secretion of endostracum; myo-co. area of mantle epitherium for secretion of either myostracal, conothecal or septal layers. Broken line represents the dorso-ventral plane.

When one studies the paleontological facts, it seems relevant to fish in the pool of the mechanisms by which the organisms build up the facts. Then, I venture to say that the fact of the ventral commissure of belemnites may turn into a paleontologically significant historical event which may have occurred in the rudimentary shell sac in the early stage of the development, and gave rise to the formation of the ventral commissure. The conclusion seems to emerge through giving the developmental explanation to the enumeration of the constituent parts of a belemnite following the order of their formation. The developmental explanation was obtained by comparing this enumeration with the development of the modern organisms closely related to the belemnites. Carr (1961, p. 57) explained the similarity between historians' and scientists' tasks, quoting a modern physicists' statement that what they investigate is not facts but events. What we as paleontologists search for may be the interpretations called events of the past, and we may be satisfied with knowing what was happening in the past.

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(In preparing this English translation of the address, the addition of text-figures 8 and 9 has been made to further explain the contents.)

Explanation of Plate 66

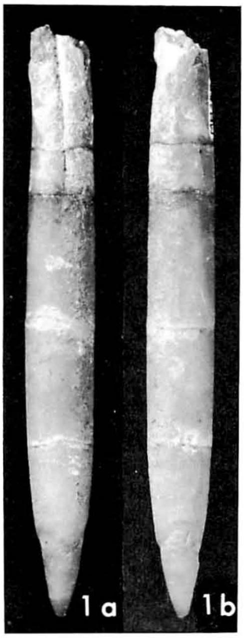
Figs. 1-4. *Neohibolites miyakoensis* Hanai, 1953

1a, b. Ventral and lateral views of rostrum, MM2535, loc. Hn-0220, northern cliff of Hiraiga cove, Tanohata-mura, Tanohata Formation, ×1.

2. Dorso-ventral section of the apex of phragmocone, showing bowl-in-bowl structure of the primordial rostrum, intermediate camera and protoconch, MM6995, loc. Ks-2005, artificial channel east of Ebisudana, Hideshima, Miyako-shi, Tanohata Formation, ×70.

3a, b. Transverse section of adapical region of rostrum, MM6996, loc. Hn-0310, northern cliff of Hiraiga cove, Tanohata-mura, Hiraiga Formation, ×17 (a, transmitted light, b, crossed nicols).

4a, b, c. Transverse section of rostrum cavum, showing sharp discontinuity of crystal structure between commissure and the rest of rostrum, in spite of the continuous nature of the growth lines across the two areas, MM6997, loc. Oj-5549, northern cliff of Raga cove, Tanohata-mura, Hiraiga Formation, *Orbitolina* facies, ×17 (a, transmitted light, b, crossed nicols, c, same as 4b except stage rotated 45°).


1a 1b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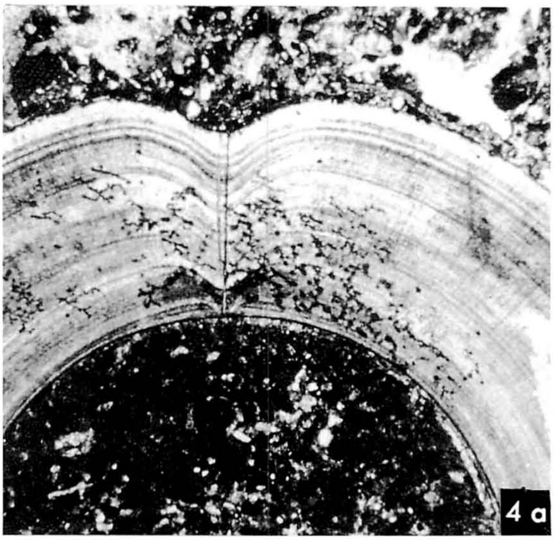
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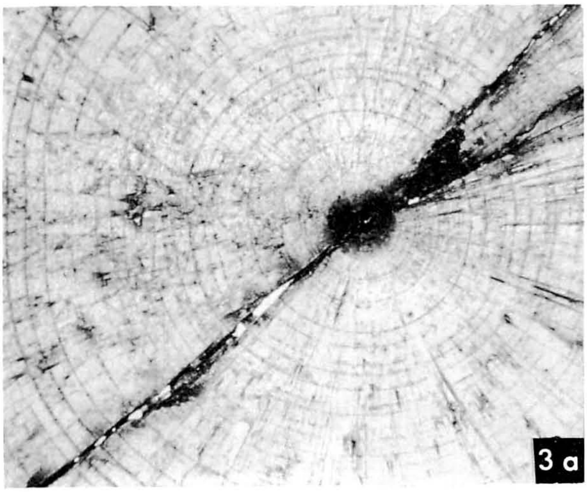
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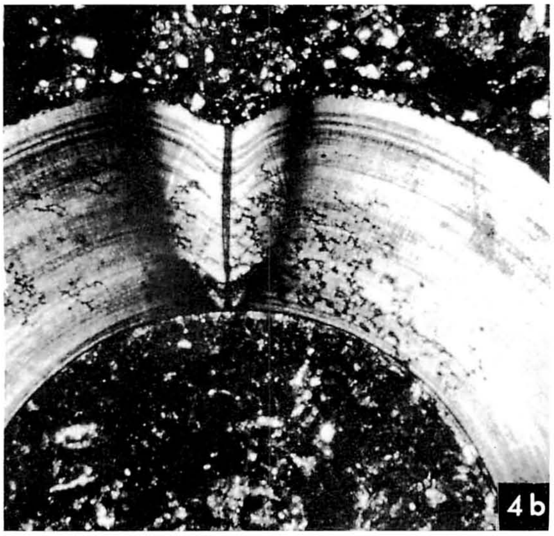
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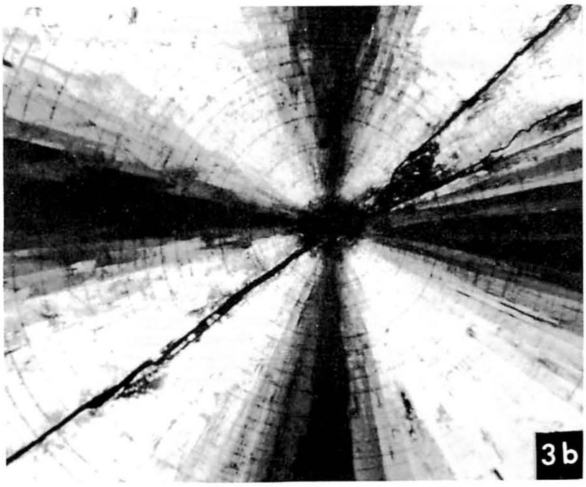
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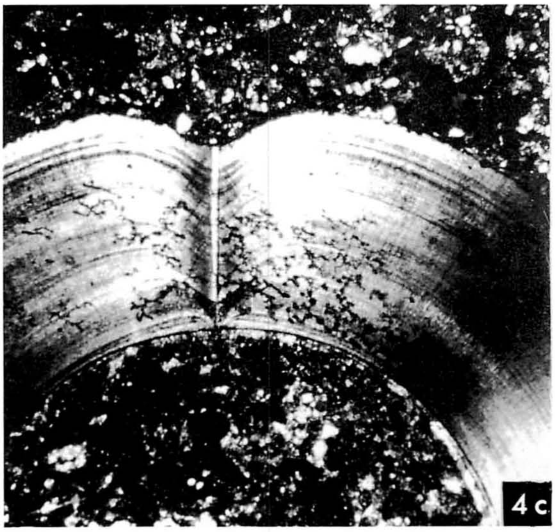
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Trans. Proc. Palaeont. Soc. Japan, N.S., No. 128, pp. 433-443, pl. 67-68, December 30, 1982

753. FORMATION AND FUNCTION OF THE SIPHUNCLE—SEPTAL NECK STRUCTURES IN TWO MESOZOIC AMMONITES*

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Abstract. SEM observation on the siphuncle-septal neck structures in two Mesozoic ammonites, *Eleganticeras elegantulum* and *Reesidites minimus* is described and compared with modern chambered cephalopods. The state of development of the porous and nonporous structures within the chambers of the two ammonites is very similar to that of modern *Nautilus*; and furthermore, a thin conchiolin membrane (pellicle) covers the greater portion of the siphuncle and the inner chamber surface as in *Nautilus*. Based on these observations and the knowledge on modern *Nautilus* biology a model is proposed for a new chamber formation in ammonites. This work also postulates that in ammonites the cameral liquid initially filling up the late-formed chambers was primarily drained into the siphuncular cord osmotically via a wettable pellicle and porous septal prismatic zone within the septal neck region.

Introduction

It is well known that many extinct cephalopods had chambered shells consisting of a shell wall, septa and siphuncle. Among modern cephalopods, chambered shells have been completely lost or reduced to chitinous gladii in most coleoids. Only in three taxonomically different genera, *Nautilus, Sepia* and *Spirula,* have chambered shells preserved in the modern fauna.

Owing much to the works of Denton and Gilpin-Brown (1961a, b, 1966, 1971, 1973) and others (Denton et al. 1961, 1967; Collins and Minton 1967), our knowledge about buoyancy control and shell formation in modern chambered cephalopods has greatly increased: *i.e.* these works demonstrated that (1) living animals possess

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* Received March 12, 1982.

low-pressure gas and various amounts of liquid (cameral liquid) within their chambers in order to approximate their densities to that of seawater, and that (2) they can migrate vertically by pumping cameral liquid osmotically into or out of their chambers through the siphuncle.

The above model for buoyancy control by Denton and Gilpin-Brown has subsequently been applied to many extinct chambered cephalopods including ammonites (e. g. Heptonstall 1970).

Recent advances in modern *Nautilus* functional morphology and physiology (Ward and Martin 1978; Ward et al. 1980; Collins et al. 1980), however, suggest that Denton and Gilpin-Brown's model cannot be entirely accepted for all chambered cephalopods.

In the previous paper (Obata et al. 1980), we have proposed hypothetical models showing possible pathways of cameral liquid removal in ammonites and modern chambered cephalopods. That paper was based mainly upon the comparative ultrastructural observations on the siphuncular membranes and septal prismatic zone within the septal neck region; but little was described for a thin organic membrane covering the siphuncle and inner side of the camera of all modern chambered cephalopods. This membrane, named the pellicle by Denton and Gilpin-Brown (1966), has also been recognized in several exceptionally well-preserved ammonites (Mutvei 1967; Erben and Reid 1971; Bayer 1978; Bandel 1981). Nevertheless, details of its ultrastructure and relations with other fine stuructures such as the de-coupling space and the septal prismatic zone have remain unsolved.

In this paper we describe the ultrastructural relations of these fine stuructures, discussing their possible function for a new chamber formation and cameral liquid removal.

Materials and Methods

Materials: — Specimens of one early Jurassic *Eleganticeras elegantulum* (Young et Bird) and two late Turonian (Cretaceous) *Reesidites minimus* (Hayasaka et Fukada) were examined in this study. The former was found in a derived nodule of late Pleistocene glacial deposits near Hamburg, Germany, and the latter two were collected from a nodule in the sandstone bed (Mikasa Formation) at loc. M 180 in the Sannosawa Valley, Manji area, central Hokkaido (Japan).

Specimens of modern chamberd cephalopods utilized for comparison are: a shell of *Nautilus pompilius* Linnaeus, captured live from off Bindoy, Negros Oriental, the Philippines, a shell of *Spirula spirula* Lamarck stranded on a beach near Nouméa, New Caledonia, and cuttlebones of two *Sepia esculenta* Hoyle captured live from off Tsuyazaki, northern Kyushu (Japan).

Methods:—Ammonite specimens were prepared for SEM observation by sectioning along the median plane. Subsequently the sectioned surface was etched with 4% hydrochloric acid for a few minutes, and thereafter the etched surface was coated with gold using an ion coater. The septal neck region was removed from the shells of Recent species and coated with gold. They were not etched. Our observation was made by means of a SEM (Hitachi Co., H-450 type). All specimens examined are stored in Ehime University without registered number.

Observations

Siphuncular wall: — The siphuncular tubes of *E. elegantulum* and *R. minimus* are both composed of multi-layered, concentric membranes of unporous material (Pl. 67, Figs. 1-3, 5). In the examined two specimens of *R. minimus* decalcified siphuncular membranes, each of which is about 2-3 μm in thickness, retain well-preserved conchiolin, consiting of lace-like, tuberculate fibrils (Pl. 67, Figs. 1-2). The above characteristic features of siphuncular membranes have already described in some other late Cretaceous ammonites by Obata et al. (1980). Obata and others compared the ammonite siphuncular wall with the inner horny layer of modern *Nautilus* siphuncular wall, because of the ultrastructural similarity of conchiolin (*see* TEM photographs of Grégoire, 1962).

Such conchiolinic siphuncular membranes have already found in many Mesozoic ammonites belonging to various taxa (Schindewolf 1967; Erben et al. 1969; Erben and Reid 1971; Westermann 1971; Kulicki 1979; Obata et al. 1980; Bandel 1981). We, therefore, believe that the siphuncular wall in all Mesozoic ammonites was made of conchiolinic material only.

Pellicle:—A thin membrane covering the ammonite siphuncle is clearly distinguished from the siphuncular membranes by its different ultrastructure. As shown on Pl. 67, Figs. 2-3, in *R. minimus* it is formed of unorientated microfibrils of about 0.1 to 0.2 μm in diameter. Ultrastructurally, the membrane is apparently very similar to those of modern *Nautilus* and *Spirula*, which are present on the inner chamber surface (Grégoire 1962, 1973; Denton and Gilpin-Brown 1966, 1973). We, therefore, call this membrane the pellicle. The microfibrils forming the pellicle of *R. minimus* are, however, coarser than those in *Nautilus* (*see* Grégoire, 1962, figs. 43-44, 58, 59-60). Jeunniaux (1963) using a selective enzymatic method, showed that the pellicle of *Nautilus* consists mostly of chitin. From these lines of evidence, the pellicle of ammonites was probably made of chitin.

In *E. elegantulum* the pellicle separates from the siphuncular tube in the anterior portion of a chamber, where it forms a narrow space (here named the de-coupling space), together with the siphuncular tube and septal layer (Pl. 67, Fig. 5). Then it extends to the inner chamber surface (Pl. 67, Fig. 6).

As the presence of a pellicle has already been confirmed in some well-preserved Jurassic and Cretaceous ammonite specimens (Branco 1880; Böhmers 1936; Erben and Reid 1971; Westermann 1971; Bayer 1975, 1978; Bandel 1981), it was probably present in all Mesozoic ammonites. According to the above authors the pellicle covering the greater portion of the siphuncle is fixed to the adapical surface of the septum and ventral shell wall, where it forms a semi-conical space, formerly termed the de-coupling room by Bandel and Boletzky (1979). These previous observations thus correlate well with our data. It should be noted that in both *Nautilus* and ammonites the pellicle covers the greater part of the siphuncular tube in contrast with the absence on the siphucnular surface in *Spirula* (Dauphin 1976; Bandel and Boletzky 1979).

Septal prismatic zone:—In the specimen of *E. elegantulum* a thin, porous ridge-like prismatic zone, is favorably preserved under the nacreous layer within the septal neck region (Pl. 67, Fig. 5). Also it extends to the adapical side of the septa (Pl. 67, Fig. 6). Near the septal neck the prismatic zone is laterally covered with the concentric siphuncular membranes, which are, in part, absent within the prochoanitic septal neck.

The presence of a septal prismatic zone has been ascertained in some Paleozoic and Mesozoic ammonites (Mutvei 1967; Birkelund and Hansen 1968; Erben and Reid 1971; Drushchits et al. 1976; Kulicki 1979; Obata et al. 1980; Bandel 1981).

As compared with the examples of previous reports, the septal prismatic zone in

E. elegantulum is more widely developed.

The septal prismatic zone of ammonites is apparently homologous with those of other modern and extinct chambred cephalopods, as Bandel and Boletzky (1979) and Obata et al. (1980) have already pointed out. The state of development of this zone, however, varies greatly among ammonites and modern chambered cephalopods. Namely, the zone of *Spirula spirula* is characterized by its highly porous structure consisting of pillar-like prisms, which are widely distributed within the long septal neck region (Pl. 68, Figs. 3-4). Such pillar-like prisms are also present within the cuttlebone of *Sepia esculenta* in the early stage (Pl. 68, Fig. 5), but they gradually change to the platy prisms as the cuttlebone grows (Pl. 68, Fig. 6).

In *Nautilus* the septal prismatic zone is restricted to the adoral side of a septum and within the short retrochoanitic septal neck region (Pl. 68, Fig. 1). The zone of *Nautilus* is made of pillar-like prisms, as in *Sepia* and *Spirula*. In the adoral side of the septal neck the prisms are covered with the aggregated spherulitic aragonite needles of the middle chalky layer (Denton and Gilpin-Brown, 1966) of the siphuncular wall (Pl. 68, Fig. 2). Although the chalky layer is completely lost in ammonites, the state of development of the septal prismatic zone in ammonites is, thus, comparable in morphology to that of *Nautilus* in its restriction to the region of the septum.

New Chamber Formation in Ammonites

Mutvei (1967, text-fig. 4) proposed a model showing the successive stages of a new chamber formation in the early Jurassic ammonite, *Promicroceras* sp. According to his model the septal layer is secreted earlier than the conchiolinic siphuncular tube. Mutvei's interpretation is, however, incorrect at least for the formation of a septum and siphuncle. Kulicki (1979, pl. 40, fig. 1) actually figured a median-sectioned specimen of the Jurassic *Holcophylloceras zignodianum*, in which the siphuncular tube in its full length is already present before the secretion of a new septum.

Earlier formation of the siphuncular tube than the septum is also observed in modern *Nautilus* (data from observations of *N. pompilius* specimens captured from the Tañon Strait, Philippines). Recent works on modern *Nautilus* functional morphology have given an important information for a new chamber formation of ammonites. Denton and Gilpin-Brown (1966, 1973), Collins et al. (1980) and Ward et al. (1981) have demonstrated that in modern *Nautilus* and *Spirula* the latest formed chamber is initialy filled with liquid (=cameral liquid). The liquid is subsequently drained into the siphuncular cord after the complete secretion of a new septum. Collins et al. (1980) suggested that during the septum formation the cameral liquid in a living *Nautilus* functions to support an incomplete septum from the hydrostatic pressure. The experiments by Collins and Minton (1967) and Raup and Takahashi (1967) provided another interesting fact that the siphuncular tube of *Nautilus* is imploded more easily than the other parts of the shell. To sum up, an earlier formation of the siphuncular tube than the septum is absolutely necessary for a living *Nautilus* in a deep sea to support this mechanically weak structure from the high hydrostatic pressure. Such situation might present in ammonites.

There are two different views as to the new septum formation in ammonites. One was proposed by Seilacher (1975) and Bayer (1978), who stressed the pellicle was formed before the nacreous septum could form on it. According to their interpretation, the septum of ammonites represents the mineralized elastic membrane of a stretched mantle epithelium (Seilacher's "pull-off" model).

The other opinion is that the pellicle as base for mineral deposits is not present when septum secretion starts (Bandel 1981).

As described before, in the specimen of *E. elegantulum* examined the pellicle covers both the siphuncular tube and inner chamber surafce. Furthermore, in the adapical side of the septum the septal prismatic zone is intercalated between the pellicle and the nacreous septal layer. These observations support Seilacher's "pull-off" model.

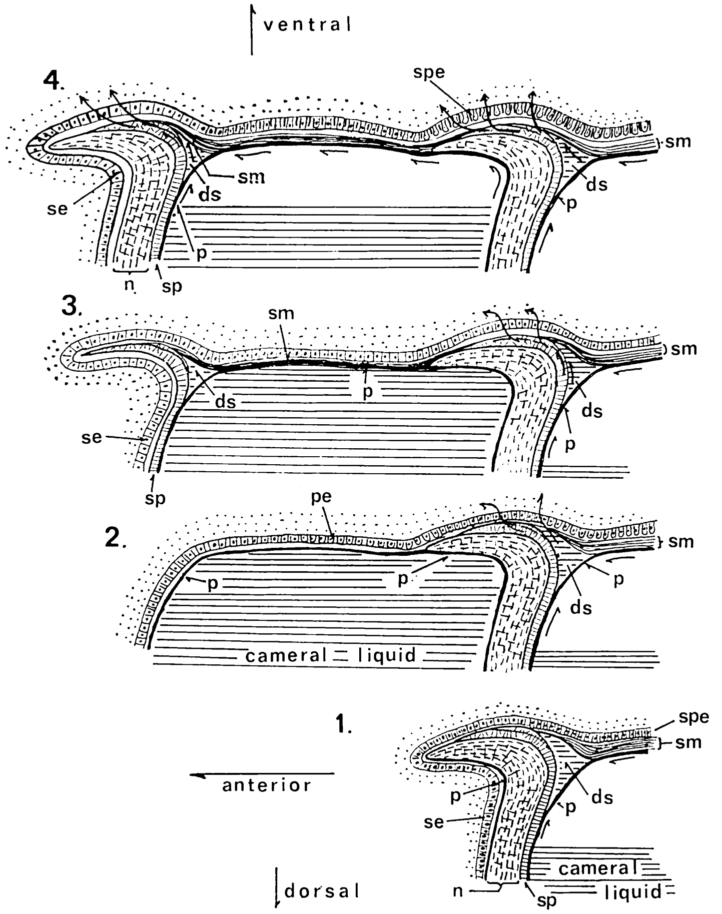
The results of this work and the knowledge on modern *Nautilus* chamber formation may lead the following generalized models for a new chamber formation in ammonites.

1. The primary epithelium of the adorally "withdrawing" mantle first secretes a pellicle (Text-fig. 1-2).
2. In the second stage the adoral end of the epithelial cells secrets the porous septal prismatic zone, and simultaneously concentric siphuncular membranes become thick (Text-fig. 1-3).
3. In the third stage the calcium-secreting cells of the mantle in the adoral side of the septal prismatic zone begin to add the nacreous layers of the septum (Text-fig. 1-3∼4).
4. In the last stage the septum attains to a full thickness, and thereafter the cameral liquid filling up the new chamber is gradually pumped out into the siphuncular cord (Text-fig. 1-4).

Denton and Gilpin-Brown (1973) suggested that in modern chambered cephalopods, cameral liquid removal for a new chamber formation and buoyancy control is caused by the transportation of salt ions and the consequent osmotic flow of the liquid through the liquid permeable siphuncular wall and/or epithelium. Indeed, the siphuncular epithelia of *Nautilus* and *Sepia* are histologically compared with the deep, basal infoldings of proximal renal tubes of advanced animals (Denton and Gilpin-Brown 1961a, 1966, 1973; Bassot and Martoja 1966; Fukuda et al. 1981). Fukuda et al. (1981) also realized that in the almost mature animal of *N. pompilius* the cube, calcium-secreting cells along the adoral side of the last septum are adapically displaced to the high columnar siphuncular epithelial cells with distinct oval cavities. These lines of histological evidence well explain the osmotic removal of cameral liquid under the high hydrostatic pressure.

Judging from the similarities of fundamental internal shell structures to modern *Nautilus*, the above osmotic removal model by Denton and Gilpin-Brown may be applied to the cameral liquid drainage for a new chamber formation in ammonites. If this presumption is correct, the pellicle covering the siphuncular tube and septal surface might have functioned as a transmitting agent of the cameral liquid, if not in direct contact with the siphuncle, out of chamber.

In ammonites the greater portion of the siphuncular tube is made of unporous conchiolinic material, and the porous structure is restricted to the septal prismatic zone within the septal neck region. These structural characteristics support our previous interpretations that most cameral liquid in ammonites was primarily transported through the narrow space of the septal prismatic zone, and that the liquid was not moved directly through the thick, conchiolinic siphuncular membranes (Obata et al. 1980). Furthermore, it is postulated that the de-coupling space in several late-formed chambers was probably filled with liquid for maintaining dampness of the



Text-fig. 1. Model showing the successive stages of a new chamber formation in ammonites. *See* the text for details of this figure. **n**: nacreous layers of septum, **sp**: septal prismatic zone, **p**: pellicle, **ds**: de-coupling space, **sm**: siphuncular membranes, **pe**: primary epithelium of mantle, **se**: calciumsecreting epithelium of mantle, **spe**: siphuncular epithelium. Possible pathways of osmotic cameral liquid drainage are shown by arrows.

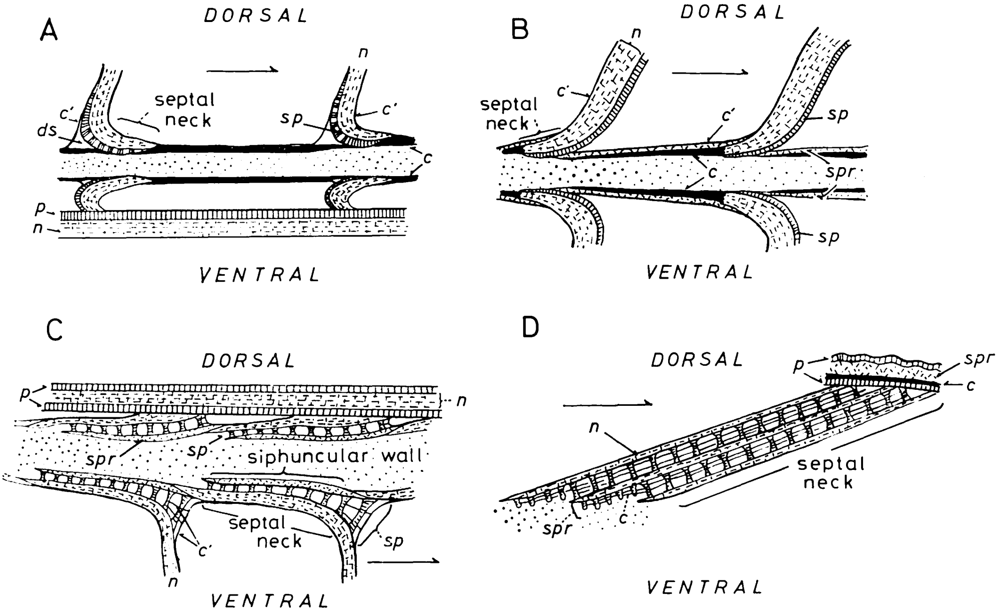
pellicle. This possible case is illustrated in Text-fig. 1.

Remarks on the Mode of Life in Ammonites

We previously showed the diagrams of the siphuncular systems of selected modern and fossil chambered cephalopods including ammonites (Obata et al. 1980, fig. 3). Text-fig. 2 summarizes the revised diagrams of ammonites and modern cephalopods, in which some our own new observations are added. As shown in this figure, the siphuncle-septal neck structures in ammonites and modern species differ considerably from one another in the degree of development of porous and/or nonporous layers. This may be important in estimating the mode of life of ammonites, because the rate of cameral liquid removal is affected by the surface area and the permeability coefficient of the porous layer which contacts the siphuncular epithelium (Heptonstall 1970; Chamberlain 1978).

Obata et al. (1980) and Bandel (1981) emphasized that the conchiolinic siphuncular membranes in ammonites and the inner and horny layer of *Nautilus* siphuncle both seem to be unpermeable to liquid and salts, because of their unporous ultrasturcuture. The conchiolinic membranes are, therefore, regarded as the chief inhibitor of the liquid transport, and causes the liquid permeability coefficient of the *Nautilus* siphuncle to have a low value (ca. 24 microdarcies, Chamberlain 1978; 7 microdarcies, Moore 1981). Recently Ward and Martin (1978) measured a maximum rate of cameral liquid removal of 1.0 ml/day/chamber in four live *N. macromphalus* living at 0 to 25 m in water depth. This pumping capacity of living animals is about 30 times slower than the liquid flow rates through the tube wall (e.g. Collins and Minton 1967; Chamberlain 1978). The osmotic pumping ability of the siphuncular epithelium in living *Nautilus*, accordingly, limits the maximum flow rate to about 1 ml/day/chamber. Collins et al. (1980) showed that the cameral liquid in *Nautilus* is not used for vertical migration but functions as ballast to maintain slight negative buoyancy in the sea. The cameral liquid is, therefore, always pumped out slowly to compensate for both episodic and long-term growth of the shell and tissue.

In contrast to the situation in *Nautilus*, the siphuncular epithelium of *Sepia* and



Text-fig. 2. Diagrams of the siphuncle-septal neck structures in ammonites and modern chambered cephalopods (adapted from Obata et al. 1980, fig. 3). A: ammonites, B: *Nautilus*, C: *Spirula*, D: *Sepia*. *c*: conchiolinic membranes, *c'*: pellicle, *sp*: septal prismatic zone, *ds*: de-coupling space, *spr*: spherulitic prismatic layer, *p*: prismatic layer of shell wall, *n*: nacreous layer. Arrows indicate adoral direction. Siphuncular tissue is dotted.

Spirula is covered with the wide-developed, pillar-like septal prismatic zone and/or the spherulitic prismatic layer of the siphuncular wall, without the intercalation of a conchiolinic layer. *Sepia* undergoes daily vertical migration by changing their weight in the sea with the successive pumping of cameral liquid into or out of siphuncle, and the rate of liquid removal measured in *S. officinalis* is about 4 to 4.5 ml/0.5 day, which is much greater than that measured in *Nautilus* (Denton and Gilpin-Brown 1961a, b).

Although the mode of life in *Spirula* remains uncertain, it lives in mid-water of the deep sea (Clarke 1970; Denton and Gilpin-Brown 1973). Clarke (1970) showed that living *Spirula* is found at depths around 600 to 700 m during the day. Because of the characteristic internal shell structures and the presence of the low-pressure gas within the camerae, it has been generally accepted that *Spirula* can control its buoyancy by pumping cameral liquid osmotically like *Sepia* (Denton et al. 1967; Denton and Gilpin-Brown 1971, 1973). This hypothesis is also supported by the fact that the siphuncular tube wall of *Spirula* is permeable to liquids (Denton et al. 1967).

The septal neck-siphuncle structures of ammonites are apparently very similar to those of modern *Nautilus* in the state of development of porous and unporous layers within the chambers (Text-fig. 2). This fact suggests us an analogy in way of life between the two taxonomically different groups.

Some previous authors emphasized that ammonites, like modern chambered cephalopods, could control their position in the water column via the osmotic flow of cameral liquid through the conchiolinic siphuncular wall (Mutvei 1967; Heptonstall 1970; Mutvei and Reyment 1973; Ward 1979; Ward et al. 1980) or through the septal prismatic zone (Bandel and Boletzky 1979). We, however, do not agree with this interpretation because of the following reason.

As was demonstrated mathematically by Chamberlain (1978), the dimensions of the siphuncle must increase more rapidly than the increase of shell size in order to maintain an uniform fluid transport for a given pressure, fluid viscosity and siphuncle

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Explanation of Plate 67

Figs. 1-6. Siphuncle-septal neck structures in ammonites.

Fig. 1. Ultrastructure of siphuncular wall in *Reesidites minimus* (Hayasaka et Fukada), showing the lace-like coarse fibrils of conchiolin. Specimen A from loc. M 180, Manji area, Hokkaido. K. Tanabe coll.

Fig. 2. Outermost surface of siphuncular tube in *R. minimus*, showing the thin pellicle membrane covering the siphuncular wall. Specimen B from the same locality as that in Fig. 1. K. Tanabe coll.

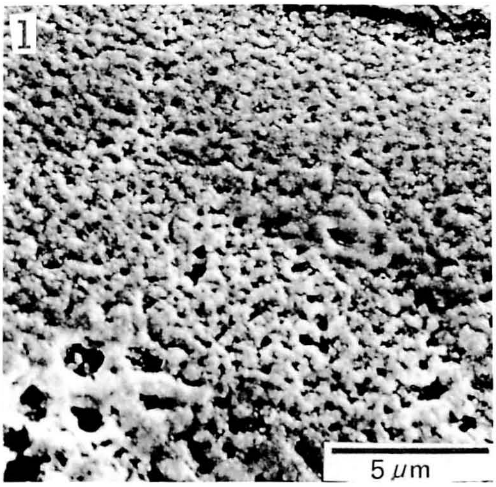
Fig. 3. Part of Fig. 2, showing the unorientated microfibrils of conchiolin.

Fig. 4. Septal neck structure of *Eleganticeras elegantulum* (Young et Bird) in the median section. Arrow indicates adoral direction. Specimen from a derived gravel in the late Quarternary glacial deposits near Hamburg. U. Lehmann coll.

Fig. 5. Part of Fig. 4, showing the de-coupling space (*d*) in the adapical side of the septum. *p*: pellicle, *h*: horny siphuncular membranes.

Fig. 6. Part of Fig. 4, showing the porous septal prismatic zone (*pr*) between the pellicle (*p*) and the nacreous septal layer (*n*).

Photos by Y. Fukuda under 20 KV for an acceleration voltage.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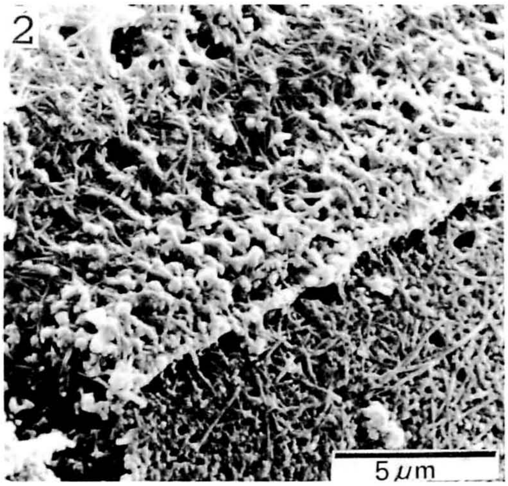
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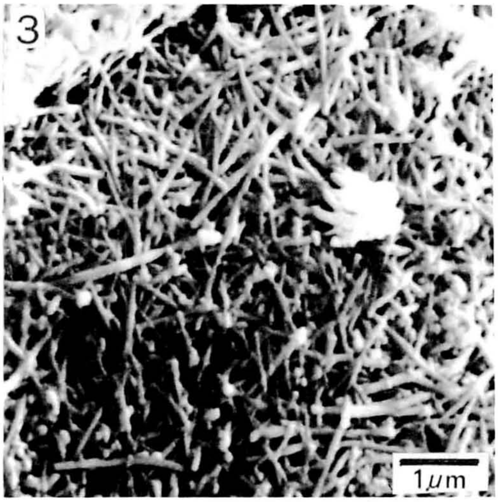
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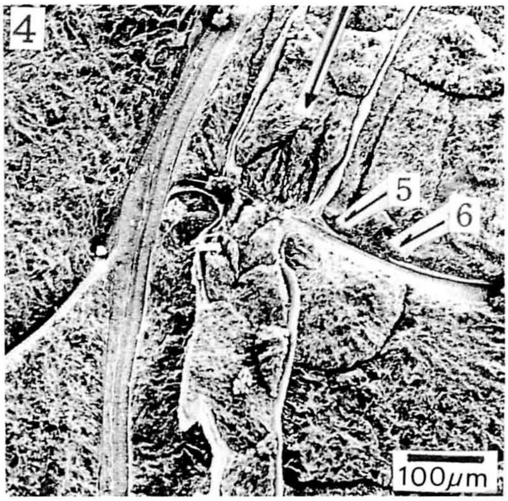
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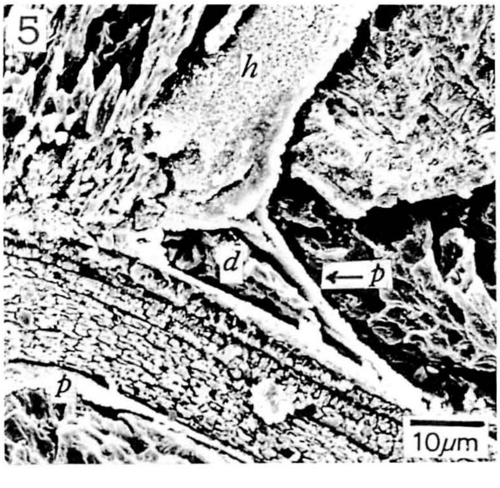
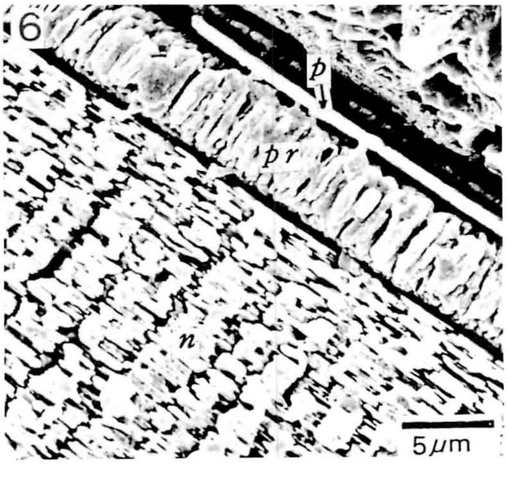
5
6
100 μm


5
h
d
← p
p
10 μm


6
p
pr
n
5 μm

permeability. The growth of siphuncle dimensions (tube diameter and tube wall thickness) versus shell radius in modern *Nautilus* and most ammonites is strongly negatively allometric (Trueman 1941; Westermann 1971; Chamberlain 1978; Tanabe et al. 1979), and this indicates a decrease in the capacity of cameral liquid removal during life, if this is the controlling factor. From these indirect evidence it is suggested that like modern *Nautilus* the cameral liquid removal in ammonites was undoubtedly very slow, at least in the late growth stage. It seems likely that the liquid in adult ammonites was not used for vertical migration as in *Nautilus*.

Acknowledgement

We thank Drs. J.A. Chamberlain Jr. (Brooklyn College of the City University of New York), C.F. Roper (Smithsonian Institution), W.J. Kennedy (University of Oxford) and T. Birkelund (Copenhagen University) for reviewing the earlier darft, and Drs. T. Matsumoto (c/o Kyushu University), U. Lehmann (Hamburg University), C. Grégoire (Liège University) and K. Bandel (Erlangen-Nürnberg University) for their valuable discussions. Studies of modern cephalopods were made possible by facilities of the member of oversea research project in 1981 (leader Dr. S. Hayasaka of Kagoshima University) and the staff of the Marine Biological Station of the Faculty of Agriculture of Kyushu University at Tsuyazaki, Kyushu. U. Lehmann and Dr. S. Mikami also provided specimens of *Eleganticeras* and *Spirula* for this study. This work was supported by the Science Research Fund of the Japanese Ministry of Education, Science and Culture (Tanabe, oversea research and Obata, Tanabe and Fukuda, No. 56340041 for 1981).

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Explanation of Plate 68

Figs. 1-6. Septal neck structures in modern chambered cephalopods.

Fig. 1. Highly porous septal prismatic zone (*pr*) in the adoral side of the septum in *Nautilus pompilius* Linnaeus. *h*, *c*: inner horny (*h*) and middle chalky (*c*) layers of the siphuncular wall, *n*: nacreous septal layer. Specimen from off Bindoy, Negros Oriental, the Philippines. S. Hayasaka and others coll. in 1981.

Fig. 2. Part of Fig. 1, showing the loosely packed, unoridntated aragonite needles of the middle chalky layer, which are adapically replaced to the septal prismatic zone.

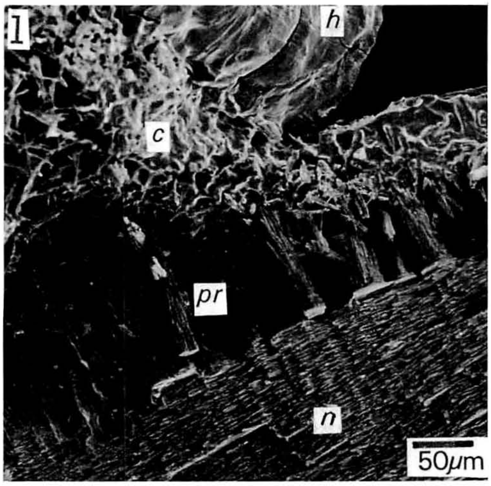
Fig. 3. Septal prismatic zone (*pr*) in *Spirula spirula* Lamarck. *sn*: long septal neck, *s*: adapical surface of the septum. Specimen stranded on a beach near Nouméa, New Caledonia. S. Mikami coll.

Fig. 4. Details of the septal prismatic zone (*pr*) of *S. spirula*, showing the continuous relation with the chalky (=spherulitic prismatic) layer (*c*) of siphunclar tube. Same specimen as that of Fig. 3.

Fig. 5. Pillar-like prisms (*pr*) forming the septal prismatic zone of *Sepia esculenta* Hoyle in the early stage. *sn*: nacreous septal layer. Specimen from off Tsuyazaki, Kyushu.

Fig. 6. Strongly modified platy prisms of the septal prismatic zone in *S. esculenta* in the late-growth stage. Same specimen as that in Fig. 5.

Photos by Y. Fukuda under 20 KV for an acceleration voltage.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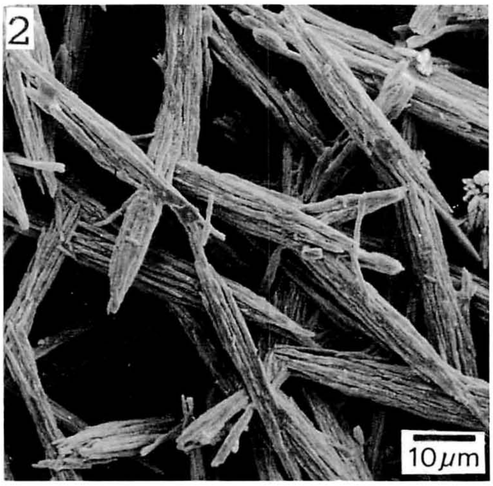
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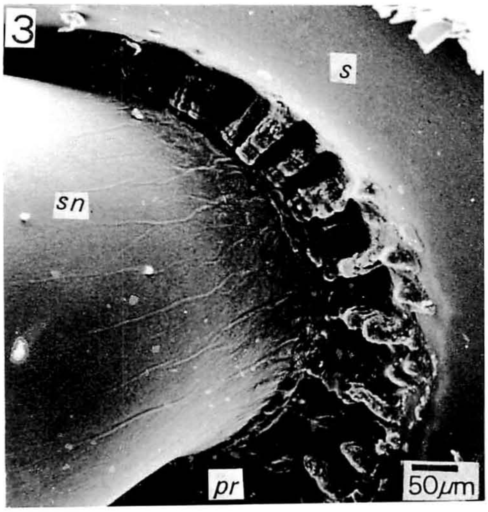
3
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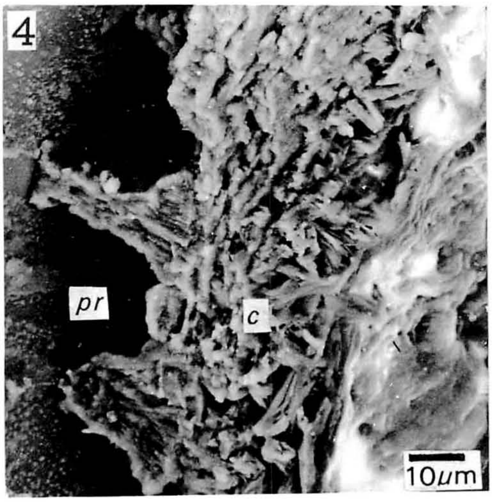
4
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c
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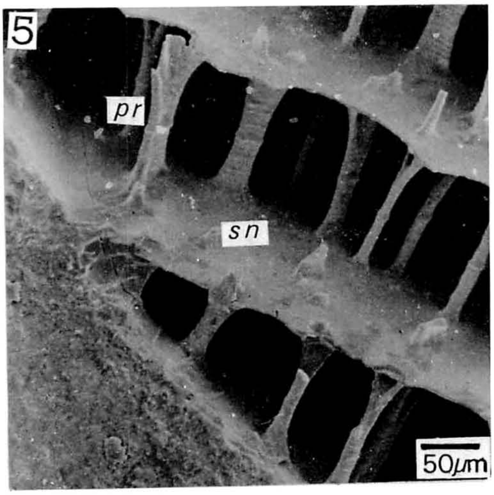
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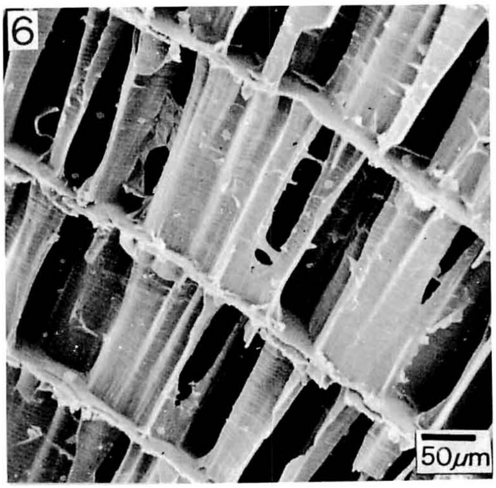
pr
sn
50μm


6
50μm

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中生代アンモナイト類２種の 連室細管—隔壁襟構造の 形成と 機能： ジュラ紀前期 *Eleganticeras elegantulum* および白亜紀後期 *Reesidites minimus* に同定される保存のよい標本（それぞれドイツ，ハンブルグ，および北海道万字地域産）について，殻体内部構造を SEM を用いて検討し，現生有殻頭足類のものと比較した。その結果，上記２種の連室細管—隔壁襟構造はオウムガイのものとよく類似することがわかった。観察結果およびオウムガイの新気室形成に関する研究成果から，“殻皮”の形成に始まり隔壁真珠層の分泌に終わる新気室形成のモデル（第１図）が導かれる。現生オウムガイ類やトグロコウイカでは，形成直後の新気室は血液の成分に似た液体（cameral liquid）によって満たされており，隔壁の完成後その液体は順序に連室細管上皮に排出される。このことから，おそらくアンモナイト類においても新気室は液体で満されていたと推定される。この液体は後に“殻皮”を経由し，隔壁襟付近の多孔質稜柱層を通って気室外へと排出されたであろう。アンモナイト類と似た殻体構造を持つ現生オウムガイの機能形態から考えると，アンモナイト類の気室液体は新隔壁の形成のみに関係し，生体の浮沈には関与しなかったと思われる。 棚部一成・福田芳生・小畠郁生。

Trans. Proc. Palaeont. Soc. Japan, N.S., No. 128, p. 444, December 30, 1980

SHORT NOTES

20. *HAYAMINA*, A NEW NAME FOR *NEUMAYRIA* OHTA 1981, NON DE STEFANI, 1877*

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The name *Neumayria*, recently proposed as a genus of early Cretaceous corbiculids (Ohta, 1981), is a junior homonym of *Neumayria* de Stefani, 1877 (p. 322), a Pliocene gastropod from Italia. I hereby propose the name *Hayamina* to replace *Neumayria* Ohta, 1981 (p. 117).

I am indebted to Emeritus Professor Tatsuro Matsumoto of Kyushu University and Prof. Makoto Kato of Hokkaido University for bringing the homonymy to my attention, and for advice on nomenclature.

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太田 (1981, p. 117) は，日本の下部白亜系から産出する Corbiculids の一部に属名として *Neumayria* を提議したが，この属名はすでに de Stefani (1877, p. 322) により創設されていたので，それに代えるものとして新たに *Hayamina* を提議する。　太田喜久

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* Received September 29, 1982.

Trans. Proc. Palaeont. Soc. Japan, N.S., No. 128, pp. 445-451, pl. 69, December 30, 1982

754. *OLDHAMINA* FROM THE UPPER PERMIAN OF THE KITAKAMI MOUNTAINS, JAPAN AND ITS TETHYAN PROVINCE DISTRIBUTION*

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Abstract. *Oldhamina kitakamiensis* sp. nov. is described from the Upper Permian Toyoma Formation in Kanayashiki, southern Kitakami Mountains, northeast Honshu, Japan. This new species is close to *Oldhamina anshunensis* Huang, 1932 from the Upper Permian Lungtan and Dalong Formations of south China.

The genus *Oldhamina* is now known from the Permian of Armenia, Pakistan, Burma, Thailand, China and Japan, all in the Tethyan Province.

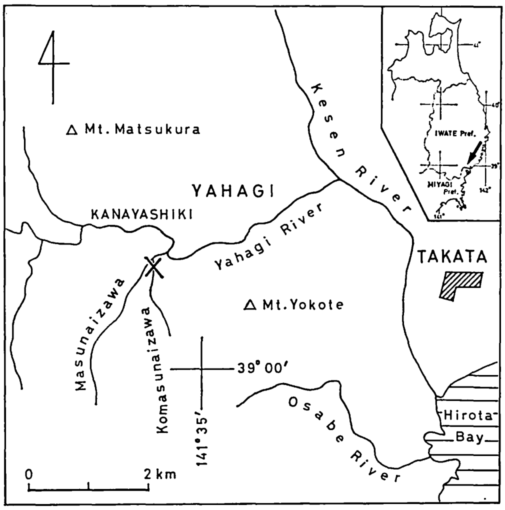
Introduction

The purpose of this paper is to indicate the presence of the aberrant strophomenide *Oldhamina* in the Upper Permian of Japan. The specimen described as *Oldhamina kitakamiensis* sp. nov. was discovered in 1973 by myself and Dr. N. Minoura from sandstone float obtained in the lower stream of Komasunaizawa valley, Kanayashiki, Yahagi-cho, Rikuzentakata City, Iwate Prefecture, northeast Honshu, Japan (Text-fig. 1).

In the Yahagi district sandstone and conglomerate of the Kanayashiki Sandstone Member (60 m thick in Kanayashiki) of the Upper Permian Toyoma Formation are well exposed along the Komasunaizawa valley (Ehiro, 1974, 1977; Murata and Shimoyama, 1979). There is no doubt that the block of grey, coarse-grained sandstone containing the brachiopod fossil was derived from this member.

Murata and his collaborators (Murata, 1969; Working Group on the Permian-Triassic Systems, 1975; Murata and Shimoyama, 1979) assigned the Kanayashiki Sandstone Member to the lower part of the Toyoma Formation (=Abadehian of central Iran, after Murata and Shimoyama, 1979) based mainly on molluscan fossils.

However, I consider that the member belongs to the upper Toyoma Formation



Text-fig. 1. Map showing the fossil locality.

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* Received March 18, 1982.

and is correlated with sandstone beds of the latest Permian Nabekoshian age (=Changxingian of south China, after Tazawa, 1975; Ishii et al., 1975; Minato et al., 1978), which crop out on the southeastern slope of Mt. Nabekoshi, Kesennuma, 10 km south of Kanayashiki. This result is based on the following stratigraphical and paleontological data: (1) the sandstones of both areas are lithologically like each other and they rest on thick shales probably from lower to middle parts of the Toyoma Formation (see Ehiro, 1977, figs. 6, 10; Tazawa, 1976, fig. 1); (2) both sandstones yield *Eolyttonia* cf. *E. nakazawai* Shimizu (Kamada, 1979, p. 738; Tazawa, 1975, p. 637), an element of the uppermost Permian fauna of the Kitakami Mountains; and (3) the sandstone in Kanayashiki carries *Oldhamina kitakamiensis* sp. nov. which is close to *Oldhamina anshunensis* Huang, 1932 from the Upper Permian Lungtan and Dalong Formations of south China; the latter is equivalent to the Changxing Formation (e.g. Zhao, Liang and Zheng, 1978).

Distribution of *Oldhamina*

The genus *Oldhamina* is distributed in the Permian of the Soviet Armenia, west Pakistan, Burma, Thailand, China and Japan. There is no report of this genus outside the Tethyan Province. The following 14 species are known, most of them occur in the Upper Permian Wujaping to Changxing Stages of south China (Table 1):

Oldhamina decipiens (de Koninck, 1863). Middle to Upper Permian (Wargal Limestone and Chhidru Formation) of the Salt Range, west Pakistan (de Koninck, 1863a, 1863b; Waagen, 1883; Noetling, 1904, 1905; Reed, 1944), Upper Permian (Lungtan and Dalong Formations) of Guizhou, south China (Huang, 1932; Wang, 1955; Feng and Jiang, 1978).

Oldhamina cf. *O. decipiens* (de Koninck, 1863). Middle to Upper Permian ("Fusulina Limestone"=Wargal Limestone to Chhidru

Table 1. Distribution of the genus *Oldhamina*.

	Permian			Region
	Lower	Middle	Upper	
O. decipiens		+	+	Pakistan (Salt Range), China (Guizhou)
O. cf. *decipiens*		+	+	Burma (Shan State)
O. aff. *decipiens*	+			Thailand (Thum Nam Maholan)
O. transkaukasica			+	U.S.S.R. (Armenia)
O. squamosa			+	China (Guizhou, Hubei, Sichuan, Fujian)
O. anshunensis			+	China (Guizhou, Sichuan, Guangdong)
O. cf. *ansnunensis*			+	China (Anhui)
O. regularis			+	China (Hubei, Guangdong)
O. grandis			+	China (Guizhou, Guangdong)
O. hoshanensis			+	China (Guangxi)
O. transversa			+	China (Qinghai)
O. jiaozishanensis			+	China (Guizhou)
O. subsquamosa			+	China (Guizhou)
O. kitakamiensis			+	Japan (Kitakami Mountains)

Formation of the Salt Range) of Shan State, east Burma (Diener, 1911).

Oldhamina aff. *O. decipiens* (de Koninck, 1863). Lower Permian (*Pseudoschwagerina* Zone to the lower *Parafusulina* Zone= Sakmarian s. l.) of Thum Nam Maholan, central-north Thailand (Yanagida, 1967).

Oldhamina transkaukasica (Stoyanow, 1916). Upper Permian (Dzhulfian s. s.) of Armenia, U. S. S. R. (Stoyanow, 1916; Ruzhentzev and Sarycheva, 1965).

Oldhamina squamosa Huang, 1932. Upper Permian (Lungtan and Dalong Formations) of Guizhou, Hubei, Sichuan and Fujian, south China (Huang, 1932; Jin, Liao and Fang, 1974; Zhang and Jin, 1976; Yang, Ni, Chang and Zhao, 1977; Tong, 1978; Feng and Jiang, 1978; Liao, 1979, 1980a).

Oldhamina anshunensis Huang, 1932. Upper Permian (Lungtan and Dalong Formations) of Guizhou, Sichuan and Guangdong, south China (Huang, 1932, 1933; Wang, 1955; Zhang and Jin, 1976; Feng and Jiang, 1978; Liao, 1979, 1980a).

Oldhamina cf. *O. anshunensis* Huang, 1932. Upper Permian (Lungtan Formation) of Anhui, south China (Zhang and Jin, 1961).

Oldhamina regularis Huang, 1932. Upper Permian (Lungtan and Dalong Formations) of Hubei and Guangdong, south China (Huang, 1932; Yang, Ni, Chang and Zhao, 1977).

Oldhamina grandis Huang, 1932. Upper Permian (Lungtan and Dalong Formations) of Guizhou and Guangdong, south China (Huang, 1932; Wang, 1955; Yang, Ni, Chang and Zhao, 1977; Feng and Jiang, 1978; Liao, 1980a).

Oldhamina hoshanensis Huang, 1936. Upper Permian (Hoshan Formation) of Guangxi, south China (Huang, 1936).

Oldhamina transversa Jin and Ye, 1979. Upper Permian of Qinghai, northwest China (Jin, Ye, Xu and Sun, 1979).

Oldhamina jiaozishanensis Liao, 1980. Upper Permian (Lungtan Formation) of Guizhou, south China (Liao, 1980a).

Oldhamina subsquamosa Liao, 1980. Upper Permian (Lungtan and Dalong Formations) of Guizhou, south China (Liao, 1979, 1980a, 1980b).

Oldhamina kitakamiensis Tazawa, sp. nov. Upper Permian (Kanayashiki Sandstone Member, upper part of the Toyoma Formation) of the Kitakami Mountains, northeast Honshu, Japan.

Systematic descriptions

Order Strophomenida Öpik, 1934

Suborder Oldhaminidina Williams, 1953

Superfamily Lyttoniacea Waagen, 1883

Family Lyttoniidae Waagen, 1883

Genus *Oldhamina* Waagen, 1883

Type species:—*Bellerophon decipiens* de Koninck, 1863, from the Middle- and Upper Productus Limestone (Wargal Limestone and Chhidru Formation) of the Salt Range (de Koninck, 1863a, p. 8, pl. 3, figs. 1, 1a), by original designation of Waagen (1883, p. 403).

Diagnosis:—Shell medium to large in size. Pedicle valve strongly convex to flattened, with many pairs of lateral septa which are high, sharp and dipping to the front.

Remarks:—The genus *Oldhamina* is characterized by its inward-thinning and forward-dipping lateral septa. This feature was demonstrated by Noetling (1904, fig. 3; 1905, fig. 1) and subsequently pointed to by Huang (1932, p. 73) as the generic diagnosis.

The type species of *Oldhamina* has a very strongly convex pedicle valve and this feature was often regarded as a general character of this genus (e. g. Waagen, 1883; Noetling, 1905; Muir-Wood and Williams, 1965). However, there are some species with weakly inflated or almost flattened pedicle valve, such as *O. anshunensis* Huang, 1932, *O. hoshanensis* Huang, 1936 and *O. jiaozishanensis* Liao, 1980. The new species described herein is a form of the less-convex type.

Oldhamina kitakamiensis sp. nov.

Pl. 69, Figs. 1-6; Text-fig. 2.

Material: — One specimen (Holotype), partial internal cast and mould of a pedicle valve, lacking the anterior and posterior portions, IGPS coll. cat. no. 97715.

Description:—Shell large in size, elongate subtrigonal in outline; length more than 60 mm, width about 70 mm. Pedicle valve slightly convex in lateral and anterior profiles.

Interior of pedicle valve with regularly and symmetrically arranged lateral septa on both sides of median septum. In the present material 13 septa are counted on one side of the pedicle valve. Lateral septa thin, with acute crests, inclined toward the front at angles of 60°-65° near the median septum, almost straight near the lateral margins of the valve and dipping to the front at angles of 40°-50° in lateral profile (see Text-fig. 2; Pl. 69, Fig. 6). The spaces between them 3.5-4.2 mm in width. Median septum low and obscure.

Remarks:—This specimen is safely assigned to the genus *Oldhamina* on the basis of its sharp and forward-dipping lateral septa.

Text-fig. 2. Lateral septa of pedicle valve of *Oldhamina kitakamiensis* sp. nov., longitudinal section.

Oldhamina kitakamiensis seems closest to *Oldhamina anshunensis* Huang, described and figured by Huang (1932, p. 77, pl. 6, figs. 6, 7; pl. 7, figs. 1-4) as *Oldhamina squamosa* var. *anshunensis* from the upper part of the Permian coal-bearing formation (Dalong Formation) of Guizhou, but the lateral septa of the Chinese species are more convex forward than those of the Kitakami species.

Oldhamina hoshanensis Huang from fossiliferous black limestone (Hoshan Formation) of Hoshan, Guangxi (Huang, 1936, p. 491, pl. 1, figs. 2-4; text-fig. 2) resembles *O. kitakamiensis* in having slightly convex pedicle valve, but the former is distinguished from the latter by its lateral septa which are more or less at right angles to the median septum.

Oldhamina jiaozishanensis Liao, described and figured by Liao (1980a, p. 262, pl. 4, fig. 30) from the Lungtan Formation of Guizhou somewhat resembles *O. kitakamiensis* in size, outline and curvature of pedicle valve, but the Chinese species differs from the present form in having 26 lateral septa on each side of the pedicle valve.

Oldhamina decipiens (de Koninck) can be easily distinguished from the present form by its highly inflated pedicle valve.

Ehiro (1974, p. 460; 1977, p. 9) listed *Leptodus richthofeni* Kayser from the Kanayashiki Sandstone Member in the type locality. Ehiro's specimen stored in the Institute of Geology and Paleontology, Tohoku University is represented by a partial internal mould of a pedicle valve. The feature of its lateral septa strongly suggests that the specimen can be assigned to *O. kitakamiensis*.

Acknowledgements

I wish to thank Dr. Nachio Minoura of

Hokkaido University for helpful discussion on stratigraphy of the Yahagi district. I am grateful to Professor Paul Copper of Laurentian University, and Professor Kei Mori of Tohoku University for critical reading of the manuscript, and to Mr. Shohei Otomo of Tohoku University for taking photos.

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Explanation of Plate 69

Oldhamina kitakamiensis sp. nov.

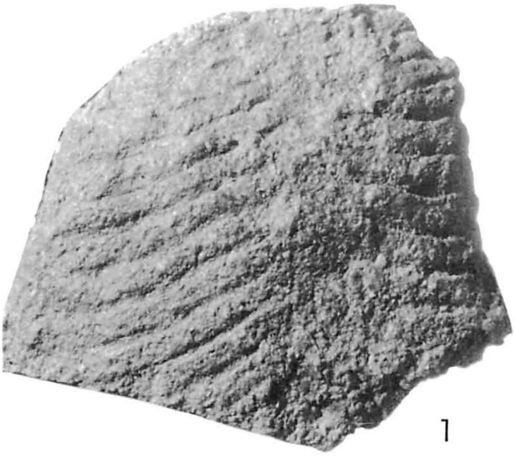
Holotype, from sandstone float of the Kanayashiki Sandstone Member of the Toyoma Formation, lower stream of Komasunaizawa valley, Kanayashiki, Yahagi-cho, Rikuzentakata City, Iwate Prefecture, northeast Honshu, Japan, IGPS coll. cat. no. 97715.

Figs. 1-3. Ventral, side and anterior views of internal mould of pedicle valve (×1).

Fig. 4. Latex cast of pedicle valve interior (×1).

Fig. 5. Natural cast of pedicle valve interior (×1).

Fig. 6. Longitudinal section of the latex cast of pedicle valve interior, showing lateral septa of the valve (×3).



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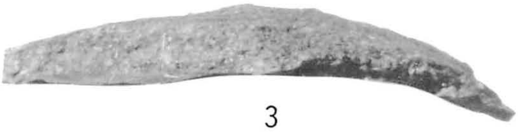

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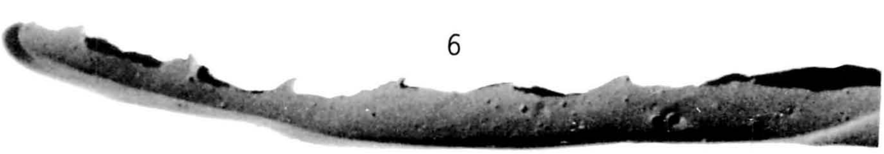

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Iwate 岩手, Kanayashiki 金屋敷, Kesennuma 気仙沼, Kitakami 北上, Komasunaizawa 小桝内沢, Mt. Nabekoshi 鍋越山, Rikuzentakata 陸前高田, Toyoma 登米, Yahagi 矢作

北上山地上部ペルム系産腕足類 *Oldhamina* および同属のテチス地域内分布：南部北上山地，岩手県陸前高田市矢作町金屋敷の小桝内沢において，上部ペルム系金屋敷砂岩部層（登米層上部）に由来する砂岩の転石より，腕足類 *Oldhamina* の化石が1個体発見された。これを *Oldhamina kitakamiensis* と命名し，記載する。本種は中国南部，貴州・四川・広東各省の上部ペルム系，龙潭組および大隆組から報告・記載されている *Oldhamina anshunensis* Huang, 1932 に最もよく似ている。

Oldhamina は従来テチス地域のアルメニア，パキスタン，ビルマ，タイ，中国のペルム系から13種が知られていたが，このたび日本のペルム系から新たに1種が加えられた。

田沢純一

Trans. Proc. Palaeont. Soc. Japan, N.S., No. 128, pp. 452-464, pls. 70-73, December 30, 1982

755. TWO NEW JURASSIC GENERA OF FAMILY PALAEOSCENIDIIDAE (RADIOLARIA)*

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Abstract. Exceedingly well-preserved Jurassic radiolarians have been obtained from manganese ore deposits in the Mino Belt, central Japan. Among them, two species of family Palaeoscenidiidae, *Hilarisirex quadrangularis* n. gen., n. sp. and *Diceratigalea hemisphaera* n. gen., n. sp., which have a median bar, two apical spines and four basal spines, are described. They also belong to Nassellaria, because their tests are composed of cephalis and thorax, and possess cephalic skeletal elements. The new subfamily Hilarisisirecinae has been created for these two new genera. Consequently, taxonomic position of family Palaeoscenidiidae must be re-examinned. This family may be regarded as an ancestor of Nassellaria. Also, it is possible that Nassellaria in the current classification is a polyphyletic taxon. The definition of Nassellaria must be re-examined. A lineage of "Paleozoic Palaeoscenidiids→*Hilarisirex quadrangularis*→*Diceratigalea hemisphaera*" is proposed. If this process of evolution is correct, the most important taxonomic criterion of Nassellaria is the pattern of cephalic skeletal structure.

Introduction

Palaeoscenidiids are primarily Paleozoic spicular forms with two to four apical spines and three to four basal spines, reported from Silurian to Carboniferous (Deflandre, 1953; Foreman, 1963; Riedel, 1967; Holdsworth, 1977).

Holdsworth (1977) proposed systematics of Paleozoic radiolarians, in which he questionably assigned family Palaeoscenidiidae to suborder Spumellaria based on the similarity of skeletons between *Palaeoscenidium* and *Haplentactinia*. Triassic forms of Palaeoscenidiidae were described by Dumitrica (1978). They possess one apical spine and four basal spines within spherical lattice shells. Furutani (1982) carried out a detailed study on Paleozoic palaeoscenidiids and revealed the process of evolution from *Palaeoscenidium* to forms with spherical shells (Genus *Tlecerina* Furutani etc.).

Two forms of Palaeoscenidiidae with

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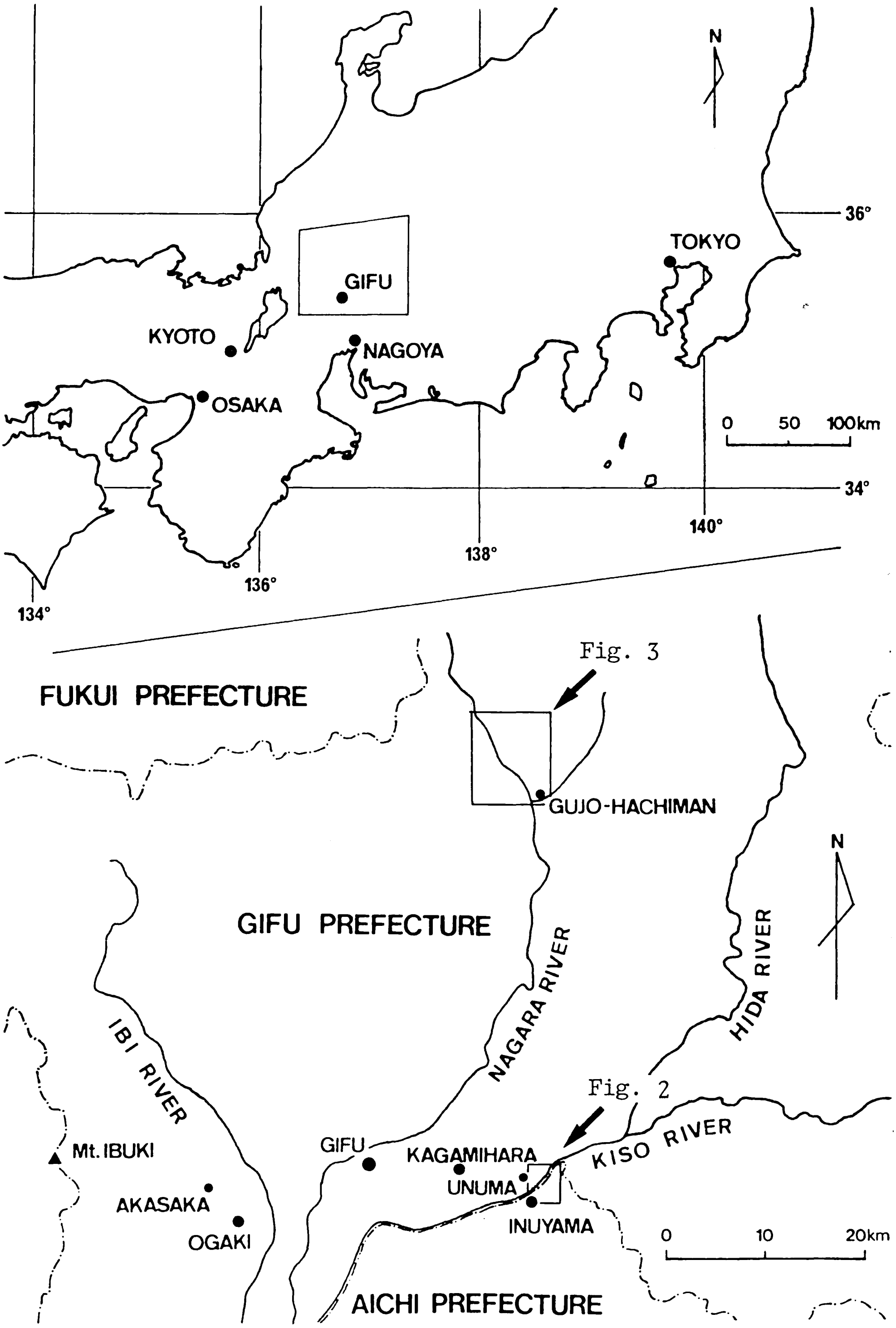
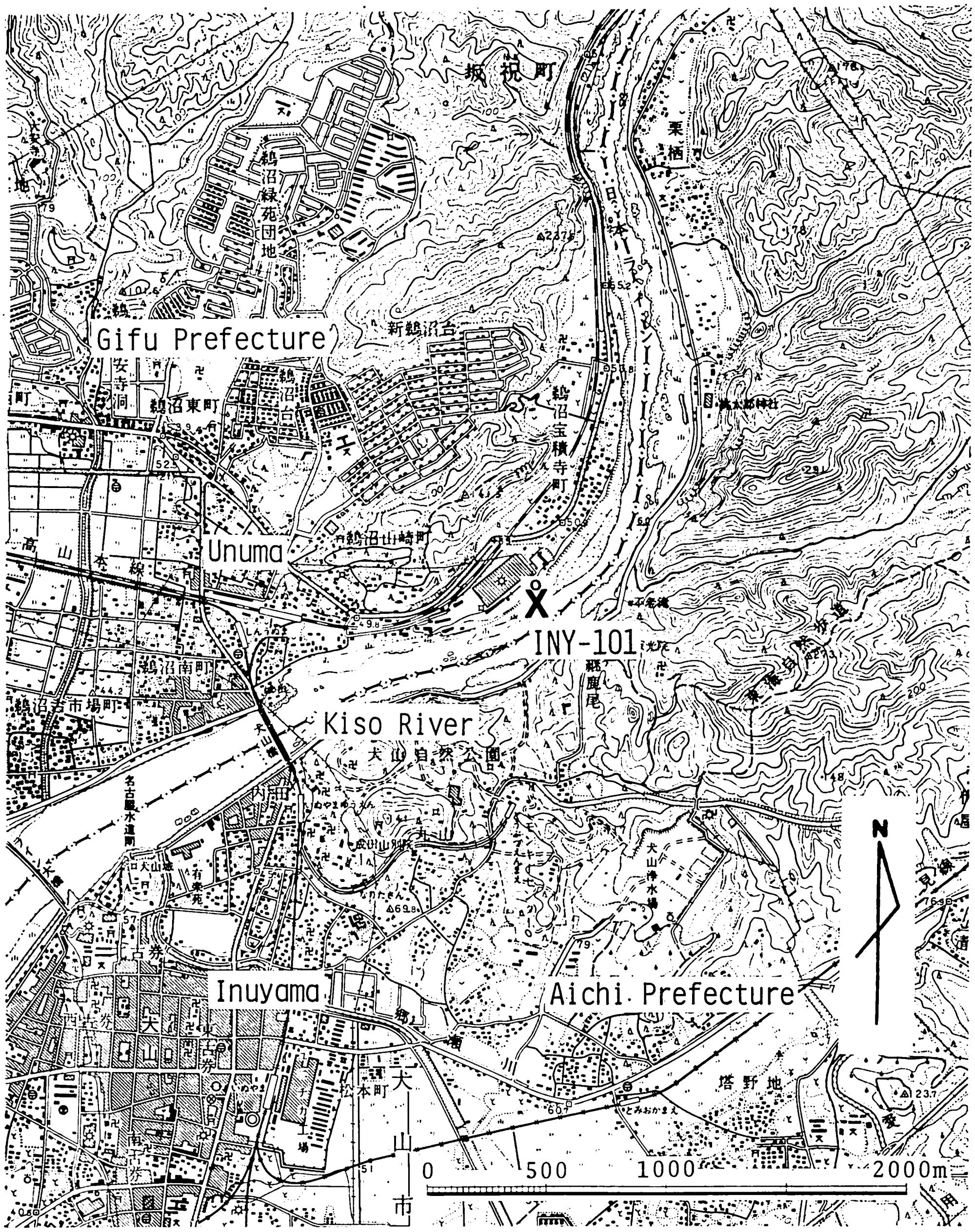
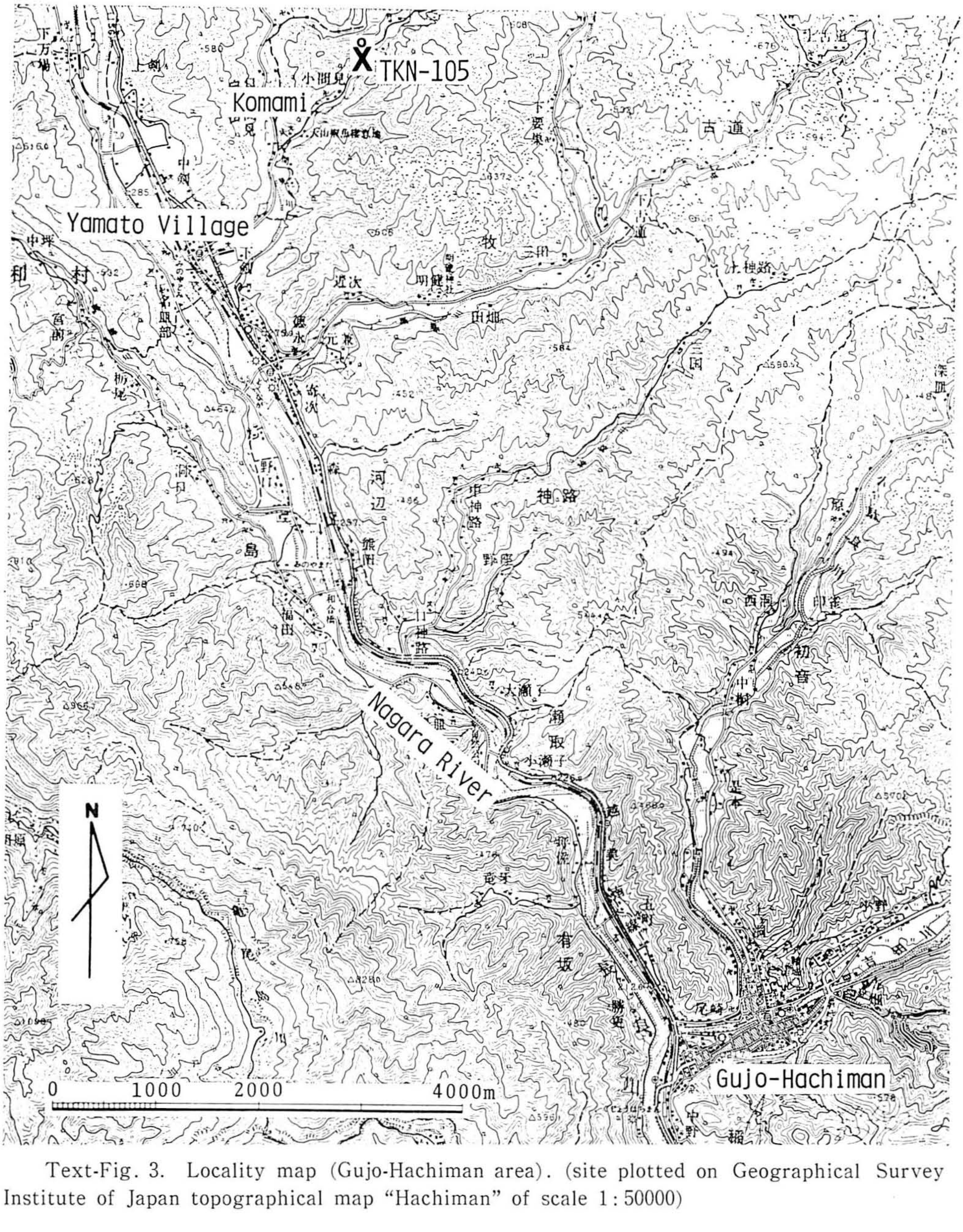
* Received May 20, 1982.



Text-Fig. 1. Index map. Inuyama area (Text-Fig. 2) and Gujo-Hachiman area (Text-Fig. 3)



Text-Fig. 2. Locality map (Inuyama area). (site plotted on Geographical Survey Institute of Japan topogtaphical map "Inuyama" of scale 1 : 25000)



Text-Fig. 3. Locality map (Gujo-Hachiman area). (site plotted on Geographical Survey Institute of Japan topographical map "Hachiman" of scale 1: 50000)

two apical spines and four basal spines occurred in the radiolarian assemblage from manganese ore deposits in the Mino Belt, central Japan (Text-fig. 1-3; Takemura and Nakaseko, 1982a). This assemblage is named as *Unuma echinatus* Assemblage and regarded as middle Jurassic (Yao, Matsuda and Isozaki, 1980; Mizutani *et al.*, 1981).

These two forms also possess cephalis,

thorax and cephalic skeletal elements, same as Nassellaria. We regard them as two new genera, *Hilarisirex* and *Diceratigalea*, of family Palaeoscenidiidae on the basis of the pattern of basic skeletal structure.

We wish to express our sincere thanks to Professor Keiji Nakazawa, Professor Tadao Kamei and Dr. Niichi Nishiwaki of Department of Geology and Mineralogy, Faculty of Science, Kyoto University for their valuable advice. Special thanks are due to Mr. Koji Wakita of Geological Survey of Japan for his guidance in the field.

Problems on phylogeny and classification of Nassellaria and Palaeoscenidiidae

In the present paper, we describe two species, *Hilarisirex quadrangularis* n. gen., n. sp. (Pls. 70-71; Text-fig. 4) and *Diceratigalea hemisphaera* n. gen., n. sp. (Pl. 72; Pl. 73, Fig. 1). These two species belong to the family Palaeoscenidiidae, and at the same time, possess characteristics of Nassellaria. Namely, the pattern of basic skeletal structure accords with that of Palaeoscenidiids (Text-figs. 4-5), and on the other hand, the external shapes of shells, which are composed of cephalis and thorax, are similar to those of nassellarians.

Deflandre (1953) and Foreman (1963) reported spicular form with flat lamellae, named *Palaeoscenidium cladophorum* Deflandre. Holdsworth (1977) illustrated Silurian *Palaeoscenidium* composed of only skeletons. Such various forms with spherical shells as *Pentactinocarpus*, *Pactarentinia*, *Tlecerina* and so on were described by Dumitrica (1978) and Furutani (1982).

In the present paper, we regard *Hilarisirex quadranqularis* and *Diceratigalea hemisphaera* as descendants of Paleozoic *Palaeoscenidium*, based on the accordance of the pattern of their basic skeletons with other Palaeoscenidiids. If not, only relying upon the shell shape, it is very difficult to clarify the phylogeny of other Palaeoscenidiids mentioned above. When the pattern of internal basic skeletal structure is adopted as a criterion, we can easily explain the phylogeny.

Hilarisirex quadrangularis is more similar to Paleozoic *Palaeoscenidium* in shape than *Diceratigalea hemisphaera*. Furthermore, the wall structure and the whole shape of *D. hemisphaera* resemble Mesozoic Nassellaria such as *Napora* (Pl. 73, Fig. 2). Hence, the lineage of "Paleozoic Palaeoscenidiids → *Hilarisirex quadrangularis* → *Diceratigalea hemisphaera*" can be roughly presumed. This lineage may be another one from that of Triassic Pentactinocarpinae.

From these two new genera and this lineage, three problems on phylogeny and classification of Nassellaria and Palaeoscenidiidae have arised. They are 1. on taxonomic position of family Palaeoscenidiidae, 2. on phylogeny of Nassellaria and 3. on taxonomic criteria of Nassellaria.

1. On taxonomic position of family Palaeoscenidiidae

Holdsworth (1977) tentatively assigned family Palaeoscenidiidae to suborder Spumellaria. Dumitrica (1978) and Furutani (1982) support this view because of forms with spherical shells.

However, *Hilarisirex quadrangularis* and *Diceratigalea hemisphaera* possess cephalothorax and cephalic skeletal elements. These two species obviously belong to Nassellaria (Ehrenberg, 1875). Therefore, the assignment of Palaeoscenidiidae to Spumellaria must be re-examined.

2. On phylogeny of Nassellaria

Dumitrica, Kozur and Mostler (1980)

described Anisian or Ladinian (Triassic) radiolarians, which are the oldest identified radiolarians in the Mesozoic Era. This assemblage includes multi-cyrtoids, Pylentonemids and so on, as Nassellaria. De Wever (1981) assigned *Poulpus* and *Saitoum* to Pylentonemidae. But on the other hand, Holdsworth (1977) regarded family Pylentonemidae as Spumellaria.

The origin of Mesozoic multi-cyrtoids is uncertain. Takemura and Nakaseko (1981) described Permian *Neoalbaillella* and pointed out its similarity of internal structures to Mesozoic multi-cyrtoids.

Although *Hilarisirex quadrangularis* and *Diceratigalea hemisphaera* belong to Nassellaria, they are regarded as descendants of Palaeoscenidiids. Therefore, family Palaeoscenidiidae may possibly be an origin of Nassellaria.

But, as mentioned above, there are several possible forerunners of Nassellaria. In this case, Nassellaria is a polyphyletic taxon and the definition of Nassellaria must be changed. Furthermore, all current classification of Nassellaria must be re-examined. In order to solve this problem, detailed studies on internal structures of Paleozoic and Mesozoic radiolarians are required.

3. On taxonomic criteria of Nassellaria

Pessagno actively studied various Mesozoic nassellarians (Pessagno, 1969; 70; 76; 77a; 77b; Pessagno, Finch and Abott, 1979). But he regarded shell structures of post cephalic chambers as a criterion of family-grade classification.

Empson-Morin (1981) described Campanian radiolarians and stated that since cephalic skeletal elements of most di- to multi-cyrtoid Nassellaria show only minor variation, the taxonomic usefulness of it is questionable. She maintained the view that an observational error by "optical illusion" had been made with *Amphipyndax*. Takemura and Nakaseko (1982b), however, showed the existence of Amphipyndacids among Jurassic radiolarians by using SEM.

If the lineage of "Palaeoscenidiids→*H. quadrangularis*→*D. hemisphaera*" is correct, the external shell has been markedly changed through the process of evolution, while the pattern of cephalic structure remained constant. This fact indicates that cephalic skeletal structure is the most important taxonomic criterion of Nassellaria and shell structure is secondary.

Systematic Paleontology

Subclass RADIOLARIA Müller, 1858

Order POLYCYSTINA Ehrenberg, 1838, emend. Riedel, 1967

Family PALAEOSCENIDIIDAE Riedel, 1967, emend. Holdsworth, 1977

Subfamily Hilaricirecinae Takemura and Nakaseko, n. subfam.

Type genus:—*Hilarisirex* Takemura and Nakaseko, n. gen.

Definition:—Palaeoscenidiidae with two apical spines and four basal spines, possessing poreless and spherical cephalis in the apical hemisphere and thorax in the basal hemisphere. Median bar, two apical spines and four basal spines composing cephalic skeletal elements.

Remarks:—Forms of this new subfamily possess characteristics of Nassellaria. But, because of their pattern of basic skeletal structures, it is clear that they belong to family Palaeoscenidiidae. Although forms of this subfamily are regarded as descendants of Paleozoic palaeoscenidiids (see the previous section), they may possibly be on another lineage from Triassic Pentactinocarpinae (Dumitrica, 1978).

Cephalic skeletal elements of this subfamily are composed of seven elements (Text-figs. 4-5). They may correspond to those of Nassellaria; they are median bar (MB), apical spine (A), vertical spine (V), two lateral spines (L) and two secondary lateral spines (1). Dorsal spine (D) do not exist. Four basal spines (two (L) and two (1)) arise primarily laterally from both ends of median bar. This pattern is not reported from other palaeoscenidiids.

This subfamily differs from other palaeoscenidiids in possession of cephalo-thorax, and from other Nassellaria in its pattern of basic skeletal structure.

Genus *Hilarisirex* Takemura and Nakaseko, n. gen.

Type species:—*Hilarisirex quadrangularis* Takemura and Nakaseko, n. sp.

Diagnosis: — Cephalis possessing two equal triradiate apical spines. Thorax, in shape a frustum of a quadrangular pyramid, having thin and irregularly scattered walls between feet. Four triradiate feet according with edges of the thoracic frustum and protruding below aperture.

Remarks:—This genus is distinguished from *Diceratigalea* Takemura and Nakaseko, n. gen. by its shapes of both two apical spines and thorax. The genus name means hilarious king.

Hilarisirex quadrangularis Takemura and Nakaseko, n. sp.

Pl. 70, Figs. 1-2; Pl. 71, Figs. 1-2;
Text-fig. 4

Description:—Test quadrangularly pyramidal with two apical spines and four feet. Cephalis spherical, poreless with uneven surface, from which two strong and triradiate apical spines arise obliquely. Each spine possessing three ridges, of which two are on the apical side and the other one arise from near collar portion. On the lower surface of cephalis, four ridges arising at the terminal point of inner four basal spines, and lying obliquely downward to terminate at four vertices of thoracic frustum. In some specimens, (Pl. 70, Fig. 2a), many cephalic ridges lying on cephalic surface of collar portion.

Thorax in shape a frustum of quadrangular pyramid of which four ridges accord with four feet. At the apical end of thorax, near collar portion, four transverse ridges lying with small nodes at each end, from which four feet arise below. Four feet triradiate, possessing three ridges of which the outer one accords with the edge of thoracic frustum. The other two inner ridges on the inner side of the thoracic wall, are connected with those of adjacent feet in arch-shape at the upper

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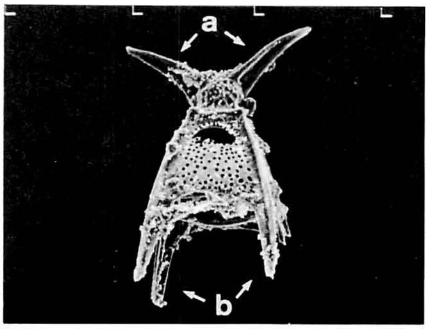
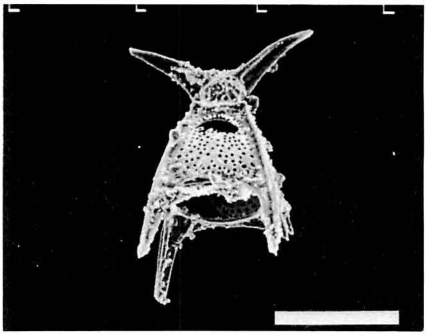
Explanation of Plate 70

(Abbreviations are same as Text-fig. 4.)

Figs. 1-2. *Hilarisirex quadrangulalaris* TAKEMURA and NAKASEKO, n. sp.
  Fig. 1. Holotype, ATJRMN-1101-1, INY-101
    1-a, b. lateral view, stereophotographs (scale = 100 μ)
    1-c, d. basal view, stereographs (scale = 100 μ)
    1-e, f. cephalic skeletal elements, stereophotographs (scale = 10 μ)
  Fig. 2. Paratype, ATJRMN-1103-1, TKN-105
    2-a. lateral view (scale = 100 μ)
    2-b, c. cephalic skeletal elements, stereophotographs (scale = 10 μ)

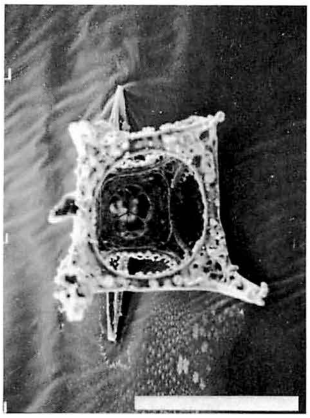
1-a



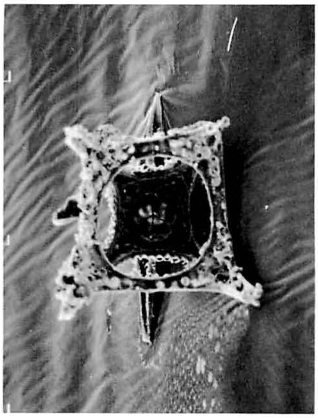


1-b

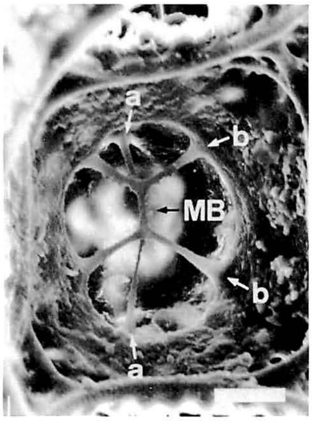
1-c



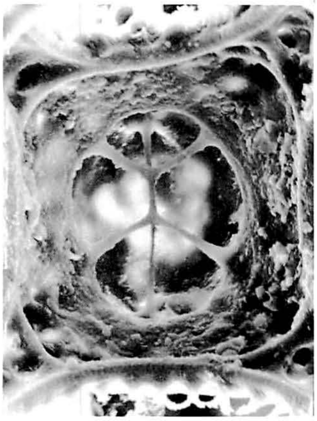
1-d



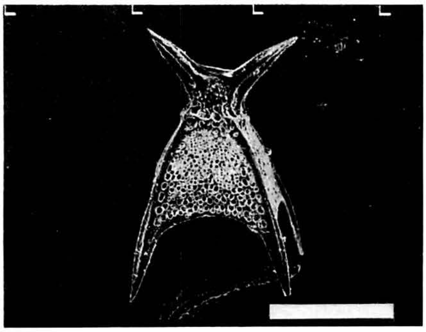
1-e



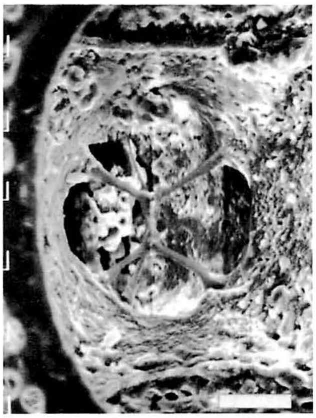
1-f



2-a



2-b



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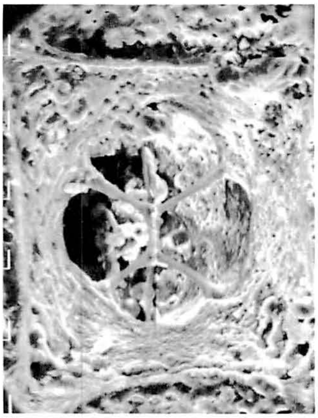
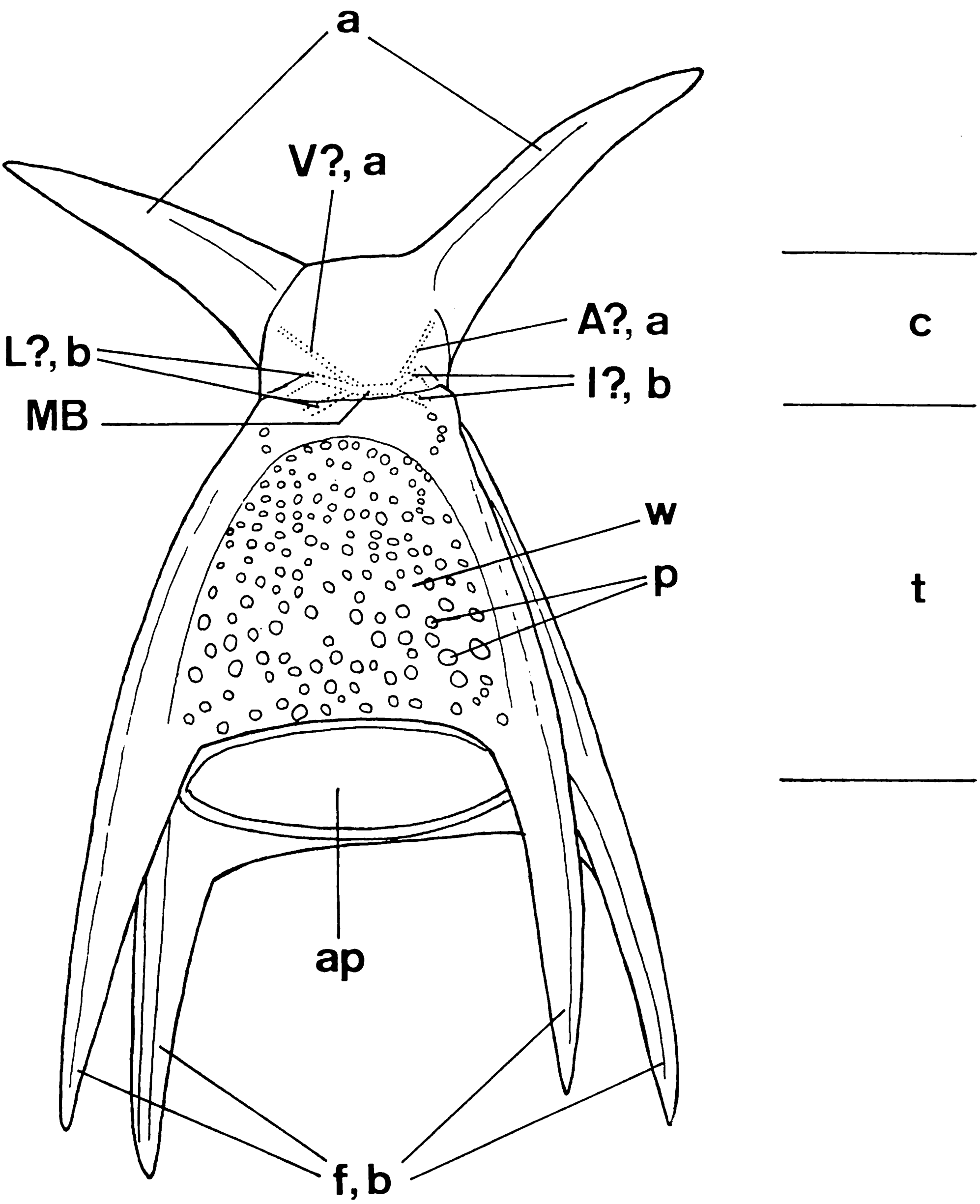
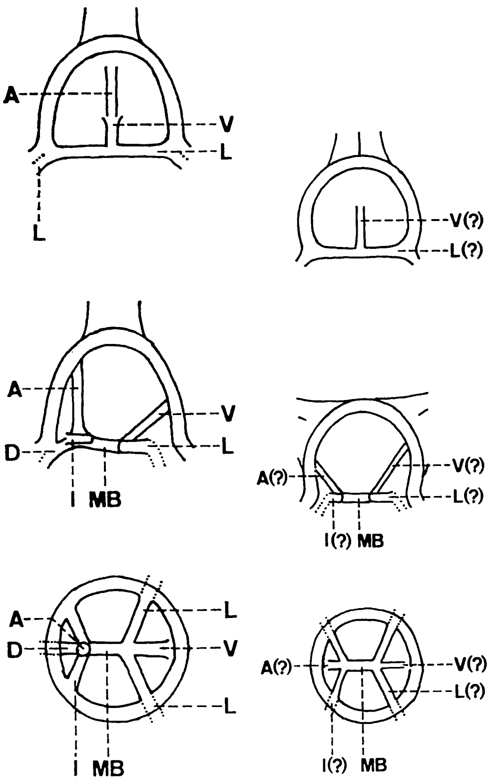




Text-Fig. 4. *Hilarisirex quadrangularis* TAKEMURA and NAKASEKO n. gen., n. sp. a: apical spine of Palaeoscenidiidae, b: basal spine of Palaeoscenidiidae, MB: median bar, A: apical spine of Nassellaria, V: vertical spine, L: lateral spine, l: secondary lateral spine, c: cephalis, t: thorax, w: wall of thorax, p: pore, ap: aperture, f: foot.



Text-fig. 5. Cephalic skeletal structures of *Napora* sp. (left) and *Hilarisirex quadranqularis* TAKEMURA and NAKASEKO n. gen., n. sp. (right)
above: view toward side with vertical spine, middle: side view from position perpendicular to sagittal plane, below: view from apex, D: dorsal spine. (The other abbreviations are same as Text-fig. 4)

part of thorax (Pl. 71, Figs. 2-b, c). At the lowermost part of thorax, inner ridges extend transversely to be connected with the adjacent ridges, forming a square framework in which aperture is enclosed with a circular skeleton. A thin wall scattered with circular pores connects both the square frame and the circular skeleton around aperture.

Four lateral sides of thoracic frustum, where is surrounded by inner ridges of four feet, are covered by generally thin, swelled walls with irregularly distributed, circular or elliptical pores. Four triradiate feet protrude below aperture.

Cephalis possess seven skeletal elements, a median bar two weaker apical spines and four stronger basal spines (Text-fig. 5). The median bar is shifted slightly from the center of collar plate. Two apical spines arise obliquely upward from both ends of median bar, terminating at cephalic wall to be connected with outer triradiate spines of cephalis. Four basal spines run laterally to cephalic wall, jointed with four cephalic ridges on the wall surface and connected with four feet.

Measurements: — Length of shell (exclusive of apical spines and feet), 100-200 μ; maximum width of thorax, 90-110 μ.

Remarks:—Because the median bar is shifted from the center of the collar plate, one of two apical spines of inner cephalic skeletal elements is longer than the other. Longer apical spine may correspond to

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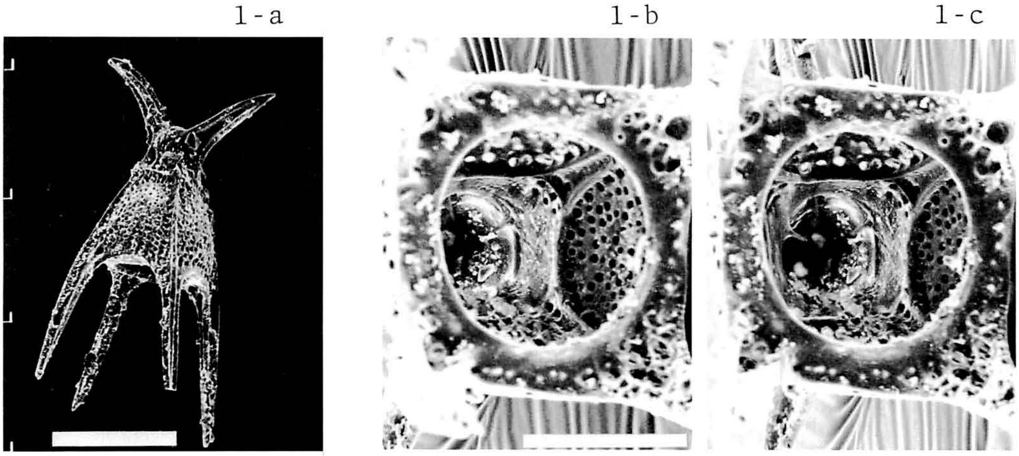
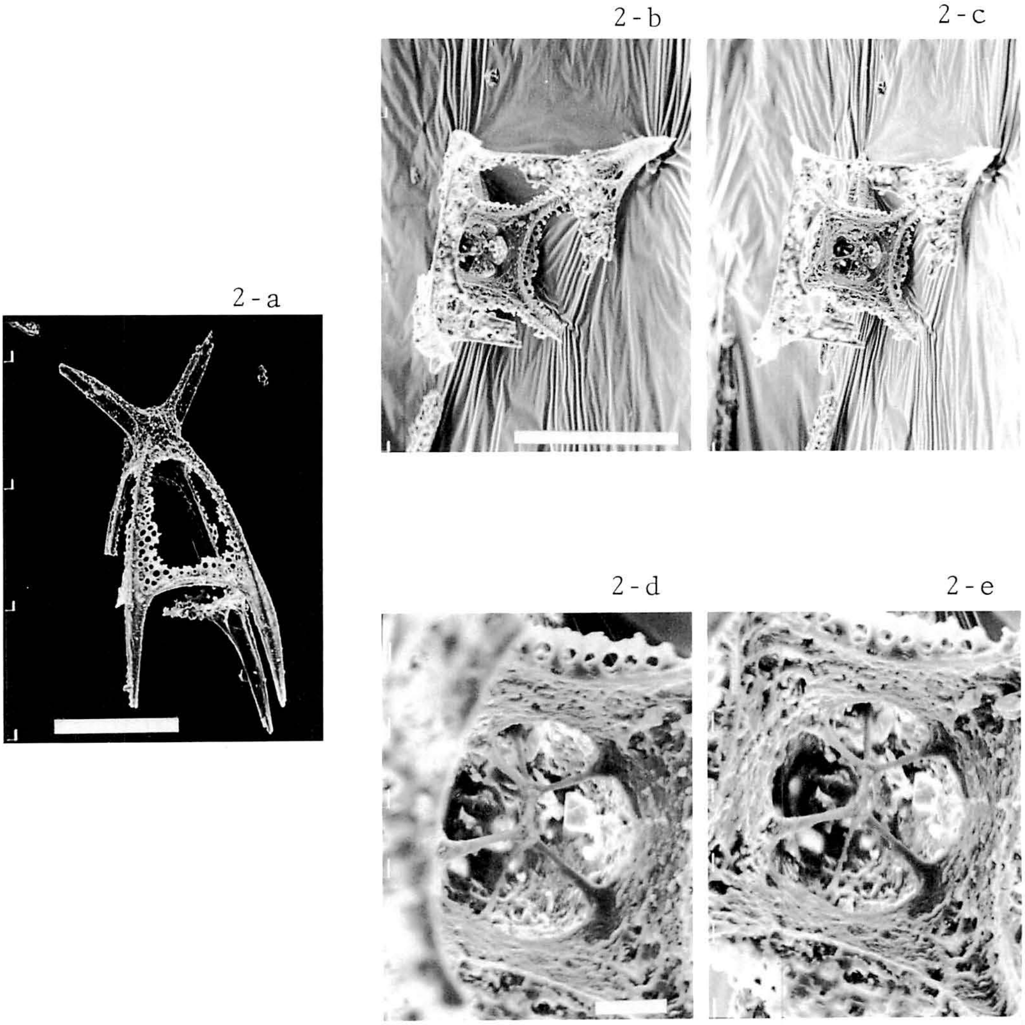
Explanation of Plate 71

Figs. 1-2. *Hilarisirex quadrangularis* TAKEMURA and NAKASEKO, n. sp.
Fig. 1. Paratype, ATJRMN-1102-1, INY-101
1-a. lateral view (scale=100 μ)
1-b, c. basal view, stereophotographs (scale=50 μ)
Fig. 2. Paratype, ATJRMN-1104-1, TKN-105
2-a. lateral view (scale=100 μ)
2-b, c. basal view, stereophotographs (scale=100 μ)
2-d, e. cephalic skeletal elements, stereophotographs (scale=10 μ)


1-a
1-b
1-c


2-a
2-b
2-c
2-d
2-e

vertical spine (V) of Nassellaria, and shorter one to apical spine (A) of Nassellaria. Then, a pair of basal spines on the side of vertical spine (V) are lateral spines (L), and another pair on the opposite side (side of apical spine (A)) are secondary lateral spines (l) (Text-figs. 4-5).

Total shape of this new species is similar to Paleozoic *Palaeoscenidium*. Probably, this new species may have been evolved from Paleozoic spicule-form palaeoscenidiids, by complication of skeletons and formation of cephalo-thorax.

Occurrence: — Jurassic manganese ore deposits in the Mino Belt.

Genus *Diceratigalea* Takemura and Nakaseko, n. gen.

Type species:—*Diceratigalea hemisphaera* Takemura and Nakaseko, n. sp.

Diagnosis: — Cephalis possessing two triradiate apical spines, of which one is weaker. Thorax hemispherical in shape, possessing latticed shell. Four feet triradiate, protruding below from around circular aperture.

Remarks: — This genus differs from *Hilarisirex* Takemura and Nakaseko, n. gen. in possession of both an odd pair of apical spines and hemispherical thorax. The genus name means helmet with two horns.

Diceratigalea hemisphaera Takemura and Nakaseko, n. sp.

Pl. 72, Figs. 1-2; Pl. 73, Fig. 1

Description:—Test hemispherical with two apical spines and four feet. Cephalis spherical, poreless with uneven surface, from which two triradiate apical spines arise. Each spine possessing three ridges, of which two are situated on the apical side. One of two apical spines, strong and long, arising obliquely laterally and curving slightly downward. Another one weak, short and straight, arising more apically.

Thorax hemispherical with thick latticed wall. Pores generally circular or elliptical, of which sizes and disposition are irregular. Aperture at the base of thorax, circular and large. Four feet triradiate and strong, extending obliquely outward. Each foot possessing three ridges, of which one is situated on the outer side. This outer ridges arising from the collar portion, where inner four basal spines terminate, running downward within the thoracic wall and protruding outward at the lower part of thorax to form four feet (Pl. 72, Fig. 2-a). Inner two ridges of four feet arising from around aperture.

Cephalic skeletal elements, of which combination and disposition are same as those of *Hilarisirex quadrangularis* Takemura and Nakaseko, n. sp. (Text-fig. 5), are composed of median bar, two apical spines and four basal spines. Longer apical spine is connected with outer stronger triradiate one, and shorter with outer weaker and straight one. Four basal spines are connected with the outer ridges of four feet at collar portion of cephalic surface.

Measurements: — Length of shell (exclusive of apical spines and feet), 90-100 μ; maximum width of thorax, 90-100 μ.

Remarks:—Correlation of cephalic skeletal elements of this new species with those of Nassellaria is same as that of *Hilarisirex quadrangularis* Takemura and Nakaseko, n. sp. (Text-figs. 4-5).

Although the total shape of this species resembles that of Mesozoic tripod nassellarians such as *Napora*, their skeletal structures are quite different (Text-fig. 5). *Napora* possesses median bar (MB), apical spine (A), vertical spine (V), dorsal spine (D), two lateral spines (L) and two secondary lateral spines (1). In *Napora*, prolongations of dorsal spine (D) and two lateral spines (L) construct three feet. *Diceratigalea hemisphaera* never possesses dorsal spine (D) and prolongations of two lateral spines (L) and two secondary lateral spines (1) construct four feet. One specimen of *Napora* (Pl. 73, Fig. 2) has four feet, of which three are prolongations of dorsal spine (D) and two lateral spines (L). The other one arise from around aperture independently of cephalic skeletal elements.

Total shape of external shell of *Diceratigalea hemisphaera* is more similar to Mesozoic nassellarians than *Hilarisirex quadrangularis*, of which shape resembles Paleozoic *Palaeoscenidium*. Therefore, *Hilarisirex* may be an intermediate form between *Palaeoscenidium* and *Diceratigalea*, and *D. hemisphaera* may have been evolved from *Hilarisirex*.

Occurrence: — Jurassic manganese ore deposits in the Mino Belt.

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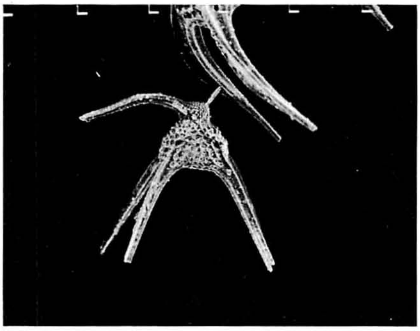
Explanation of Plate 72

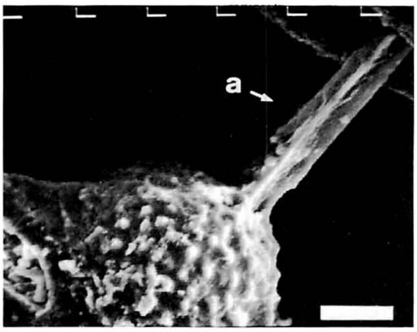
(Abbreviations are same as Text-fig. 4.)

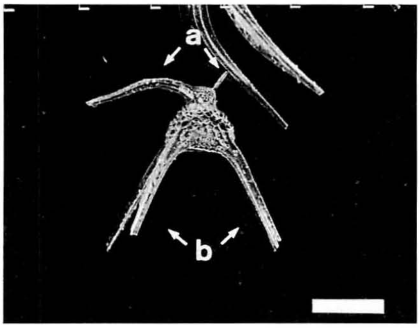
Figs. 1-2. *Diceratigalea hemisphaera* TAKEMURA and NAKASEKO, n. sp.
- Fig. 1. Holotype, ATJRMN-1103-2, TKN-105
  - 1-a, b. lateral view, stereophotographs (scale = 100 μ)
  - 1-c. weaker apical spine (scale = 10 μ)
  - 1-d. basal view (scale = 100 μ)
- Fig. 2. Paratype, ATJRMN-1104-2, TKN-105
  - 2-a. lateral view (scale = 100 μ)
  - 2-b, c. basal view, stereophotographs (scale = 100 μ)
  - 2-d, e. cephalic skeletal elements, stereophotographs (scale = 10 μ)

1-a

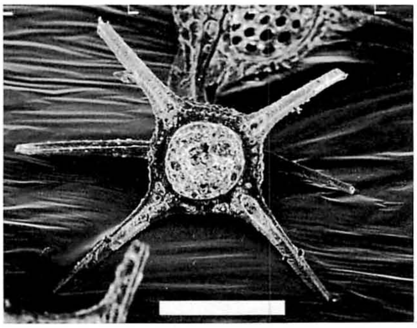


1-c



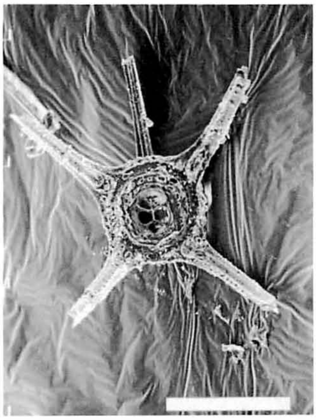


1-b

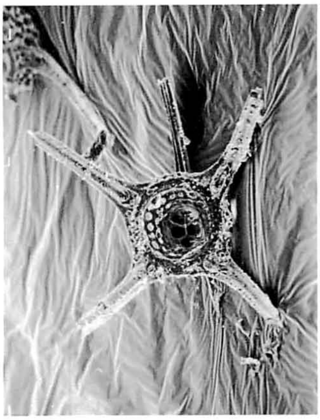


1-d

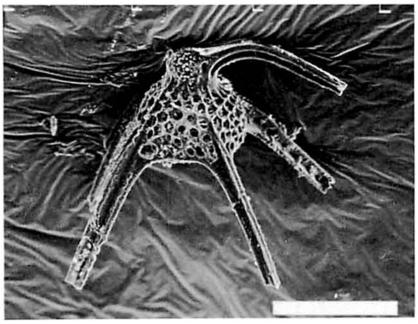
2-b

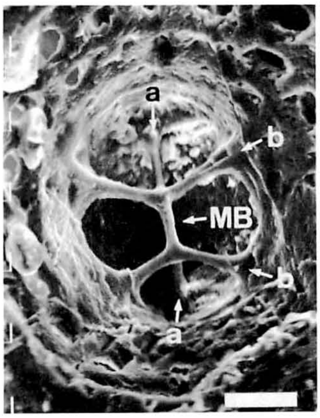


2-c

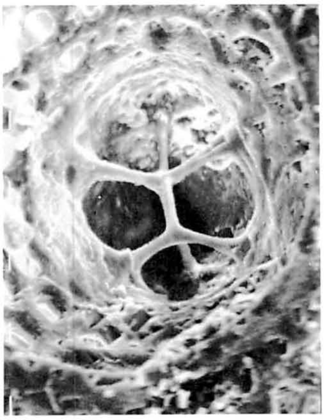


2-a





2-d



2-e

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ジュラ紀 Palaeoscenidiidae 科放散虫の２新属，犬山地域及び郡上八幡地域の美濃帯中・古生層中に分布するマンガン鉱床からは，ジュラ紀中期のものと考えられる，きわめて保存のよい放散虫群集を産出する。その中から，Palaeoscenidiidae 科に属する *Hilarisirex quadrangularis* n. gen., n. sp. ならびに，*Diceratigalea hemisphaera* n. gen., n. sp. の２種を記載した。これら２属は，Nassellaria 亜目の性質をあわせもつため，新亜科 Hilarisirecinae を提唱した。その結果，Palaeoscenidiidae 科の分類的位置及び Nassellaria の定義について再検討する必要が生じた。Nassellaria は多系統である可能性があり，その場合，従来の分類を根本から見直さなければならない。また，これら Palaeoscenidiidae 科の系統発生を考えると，Nassellaria の分類基準としては，cephalis の骨格構造が最も重要であることが示唆される。

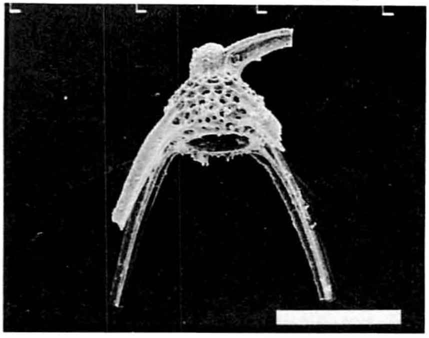
竹村厚司・中世古幸次郎

Explanation of Plate 73

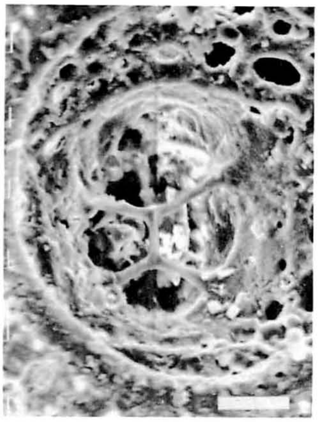
(Abbreviations are same as Text-fig. 5.)

Fig. 1. *Diceratigalea hemisphaera* TAKEMURA and NAKASEKO, n. sp. Paratype, ATJRMN-1104-3, TKN-105
  1-a. lateral view (scale=100 μ)
  1-b, c. cephalic skeletal elements, stereophotographs (scale=10 μ)
  1-d, e. basal view (scale=100 μ)
Fig. 2. *Napora* sp. (possessing four feet) ATJRMN-1104-4, TKN-105
  2-a, b. lateral view, stereophotographs (scale=100 μ)
  2-c, d. cephalic skeletal elements, stereophotogtaphs (scale=10 μ)
  2-e, f. basal view, stereophotographs (scale=50 μ)

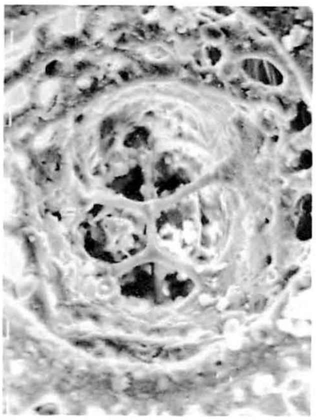
1-a



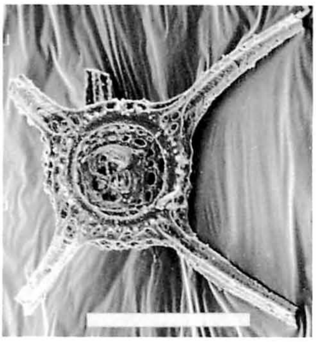
1-b



1-c

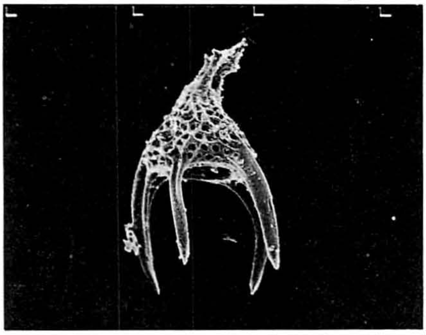


1-d



1-e

2-a



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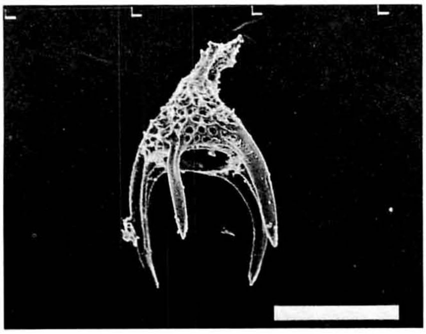

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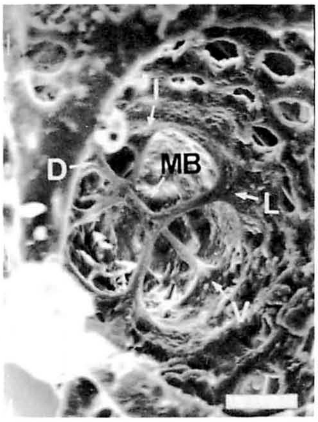
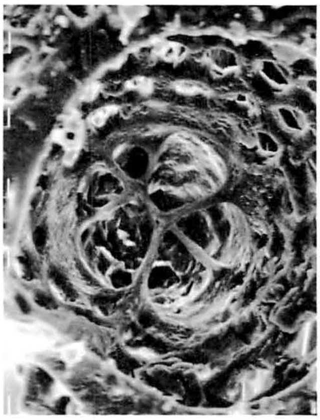
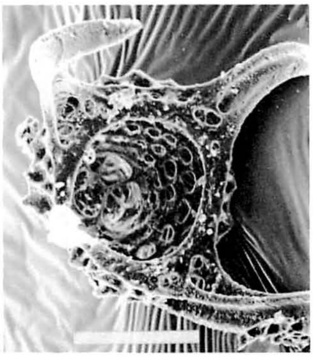


2-d



2-e



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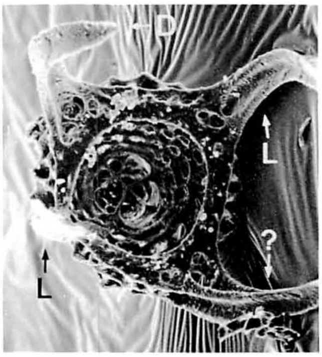

PROCEEDINGS OF THE PALAEONTOLOGICAL SOCIETY OF JAPAN

日本古生物学会第 130 回例会

日本古生物学会第 130 回例会は，1982年10月 17日（日），三重大学教育学部で開催された（参会者80名)。

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日本古生物学会特別号の原稿募集

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- （b） 著者名；論文題目。〔和訳を付記すること〕。
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- （e） 本文の頁数（刷上り見込頁数または原稿で欧文タイプ25行詰の場合の枚数—ただし，パイカーかエリート字体かを添記すること）；また本文中小活字（8ポ組み）に指定すべき部分があるときは，そのおよその内訳（総頁に対するパーセント）；挿図・表の各々の数と刷上り所要頁数；写真図版の枚数。
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- （g） その他参考事項。

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