

## The Ammonite Siphuncular Wall: Its Microstructure and Functional Significance

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### Introduction

As is well known, all kinds of modern and fossil chambered cephalopods have a siphuncular system in their phragmocone. Recent works on the floatation mechanism in modern chambered cephalopods (*Nautilus*, *Sepia* and *Spirula*) have demonstrated that the siphuncle functions to control the buoyancy of living animals (DENTON & GILPIN-BROWN, 1961a, b, 1966, 1971, 1973; DENTON *et al.*, 1961, 1967; COLLINS & MINTON, 1967; GILPIN-BROWN, 1972; WARD & MARTIN, 1978). Namely, the internal (*Sepia* and *Spirula*) and external (*Nautilus*) septate shells of these animals contain some gas at markedly lower than the atmospheric pressure, and a living animal can control its buoyancy by changing the total gas-space within chambers with the successive pumping of liquid through the fluid-permeable siphuncular membranes and/or epithelium. Because of the fundamental similarity of internal shell structures among modern and fossil chambered cephalopods, it has been assumed that the hydrostatic buoyancy control given by the low pressure gas-space in the chambered shells has been achieved in the earliest cephalopods (DONOVAN, 1964), and that the mechanism had remained the same in many forms over the history of the Cephalopoda (DENTON & GILPIN-BROWN, 1973).

The study of siphuncular systems, therefore, will much contribute for understanding the evolutionary history of the Cephalopoda in the sense of adaptive strategy.

In the case of the Ammonoidea, the gross morphology and structure of siphuncle have been described in detail by many authors (e.g. GRANDJEAN, 1910; TRUEMAN,

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1920; SHIMIZU, 1929; MUTVEI, 1967; BIRKELUND & HANSEN, 1968; ERBEN *et al.*, 1969; ERBEN & REID, 1971; WESTERMANN, 1971, 1979). The microstructural characteristics and their exact comparison with those of other cephalopods, however, have not yet been fully described.

This paper deals with the microstructure and ultimate composition of siphuncular wall in four late Cretaceous ammonite species. It is based on the scanning electron microscopic (SEM) and the energy dispersion X-ray microanalytical (EDX) examinations on several well-preserved specimens from Hokkaido. The results obtained are compared with the previous publications and our own unpublished data on the siphuncular systems of some other cephalopods, and are discussed with special reference to the buoyancy control.

### Material and Method

*Material:* The following five specimens of four late Cretaceous (Turonian to Campanian) species have been used in this study.

*Damesites semicostatus* MATSUMOTO . . . . 2 specimens (GK. H 8039, 8085)

*Eupachydiscus haradai* (JIMBO) . . . . . 1 specimen (GK. H 8024)

*Mesopuzosia yubarensis* (JIMBO) . . . . . 1 specimen (GK. H 8038)

*Scalarites scalaris* (YABE) . . . . . 1 specimen (GK. H 8042)

They are preserved at Kyushu University with the registered numbers shown in parentheses. The locations and horizons of GK. H 8085, 8039, 8038 and 8024 have already noted elsewhere by TANABE *et al.* (1979, 1980). GK. H 8042 was collected from a nodule embedded in the Middle Turonian mudstone at loc. R6733a, northern branch of the Sannosawa, the tributary of the Shimokinembets River, Obira area, north-western Hokkaido by Y. MIYATA, together with several specimens of *Inoceramus hobetsensis* NAGAO *et al.* MATSUMOTO.

*Method:* The specimens examined except for GK. H 8042 (*S. scalaris*) were first cut or polished along the median plane. Subsequently, the sectioned surface was etched with 4% hydrochloric acid for about three minutes, and thereafter the surface was washed with pure water for several times. As to GK. H 8042, a part of the siphuncular tube was carefully separated from the phragmocone. The siphuncular portion in each specimen was coated with gold (for GK. H 8039, 8024, 8038) or carbon (H 8085, 8042) using ioncoaters (Eiko Engineering Co., IB-3 type for gold coating and JEOL, JEE-4X type for carbon). The siphuncular wall microstructure was observed with an aid of a scanning electron microscope (Hitachi Co., H-450 type) under 20KV for an acceleration voltage. The semi-quantitative ultimate composition of siphuncular wall was also analyzed on GK. H 8042 by means of an energy dispersion X-ray microanalyzer (Kevex Co., 7000 type) attached to the SEM.

The comparison with the siphuncular structures of other cephalopods is mostly based on our own unpublished data (FUKUDA *et al.*, *in press*; TANABE *et al.*, *in prep.*), but some previous works are also cited in this paper.

### Microstructure

The internal shell structures including the siphuncular tube are very well preserved in the specimens examined, because of favorable post-depositional conditions in calcareous nodules. The siphuncular tube wall in the specimens examined is formed of multi-layered concentric membranes of closely packed, homogeneous material (Pls. 1–2); in *D. semicostatus* and *M. yubarensis* each membrane has a thickness of about 1 to 2  $\mu\text{m}$  (Pl. 1, Figs. 1–2, 4). This observation seems to coincide with those of previous works of MUTVEI (1967), ERBEN *et al.* (1969) and ERBEN & REID (1971). GRANDJEAN (1910) reported transverse growth lines on the outer surface of siphuncular tube in some ammonites, but such a surface ornament has not been ascertained in the specimens examined under the SEM (Pl. 1, Fig. 3; Pl. 2, Fig. 3).

As TANABE *et al.* (1980) have already described, in GK. H 8085 (*D. semicostatus*) the outer shell wall, septa and siphuncular tube had been replaced to silica-rich material during diagenesis. Nevertheless, the ultrastructure of siphuncular wall membranes is partly very well preserved in the specimen. Fig. 6 on Pl. 1 and Fig. 7 on Pl. 3 are the enlarged electron micrographs of siphuncular membranes in the middle part of a chamber and the septal neck area respectively. They show that each membrane is made of reticulate, lace-like microfibrils with many irregular tubercles on their surface. The microfibrils, about 0.3 to 0.4  $\mu\text{m}$  in diameter, are densely arranged in perpendicular to the longitudinal axis of the siphuncular tube. On the surface of a membrane many elongate pores are regularly distributed with their largest axis in parallel to the microfibrils. In Fig. 6 on Pl. 1 most of the pores are covered by exotic material, but the details of membrane ultrastructure are clearly represented in Fig. 7 on Pl. 3.

FLORKIN (1966) showed some electron micrographs of the conchiolin membranes within the nacreous layer of modern and fossil molluscan shells. The membranes in his micrographs are all composed of closely packed, reticulate, lace-like microfibrils with round to elongate pores. Based on forms, densities and dimensions of microfibrils and pores, FLORKIN (1966) classified the molluscan conchiolin membranes into the three structural types, namely the Cephalopoda, Gastropoda and Bivalve types. According to him, the Cephalopoda type structure is characterized by much thicker tuberculate microfibrils (about 0.2  $\mu\text{m}$  in diameter) and more elongate, larger pores (about 0.2 to 0.4  $\mu\text{m}$  in maximum diameter) than those of the other two types. Such a characteristic Cephalopoda type conchiolin ultrastructure has been reported within the nacreous layers of several well-preserved Carboniferous and Eocene nautiloids (GRÉGOIRE, 1959; FLORKIN *et al.*, 1961). Although the microfibrils in GK. H 8085 are thicker than those of the previously known cephalopod shells, the fundamental ultrastructure of siphuncular membranes of the former is undoubtedly comparable with those of conchiolin membranes of the latter.

### Ultimate Composition

The mineralogical composition of ammonoid siphuncular wall has long been

regarded as calcium phosphate (GRANDJEAN, 1910; SHIMIZU, 1929) or calcareous material with a prismatic structure (HYATT, 1875; BIRKELUND & HANSEN, 1968). Most recent authors (e.g. SCHINDEWOLF, 1967; MUTVEI, 1967; ERBEN *et al.*, 1969; ERBEN & REID, 1971; WESTERMANN, 1971, 1979; KULICKI, 1979), however, regard the original composition as organic material only. Thus, calcareous material described by BIRKELUND & HANSEN (*op. cit.*) and others is believed to be a product of diagenetic, secondary calcification (ERBEN & REID, 1971). ERBEN & REID (*op. cit.*) have also mentioned that in a specimen of the Kimmeridgian ammonite, *Pavlovia* sp., the dark-coloured, horny or conchiolineous siphuncular membranes do not show any structural pattern under the SEM. Most previous interpretations on the composition of ammonoid siphuncular wall are, however, based on the homogeneous structure under the SEM or light microscope, and nobody has given the concrete mineralogical and biochemical data on this problem.

As a result of our SEM examination, it has been made clear that the ultrastructure of siphuncular wall membranes in the specimens examined (especially in GK. H 8085 of *D. semicostatus*) is closely similar to those of conchiolin membranes of molluscan shells. This fact suggests us that the siphuncular wall of the Ammonoidea is founded up mostly of non-calcareous, organic material. The term conchiolin was defined by FRÉMY (1855) for the residual substances in the decalcified molluscan shells. According to FLORKIN (1966), conchiolin within molluscan shells is constituted of mucopolysaccharide. It is rich in such intermediate amino-acids as alanine, glycine, serine and aspartic acid, and chitin. Such amino-acids have been detected in the shell organic matrix of some well-preserved fossil nautiloids and ammonoid (*Baculites inornatus*) (FLORKIN *et al.*, 1961; WEINER *et al.*, 1979). The total amount of chitin or protein within the organic skeleton elements of the invertebrates is not large. In the case of molluscan shells the organic layers and matrix contain isolate chitin of about 25 to 68% of the total volume (FLORKIN, 1966). Therefore, the rest is occupied by non-organic substances such as calcium carbonate, silicon dioxide, apatite etc. These non-organic materials have been regarded as the important components to produce the hardness of organic structures (GRANDJEAN *et al.*, 1964).

To determine the amounts of these non-organic components in the siphuncular membranes, we made the semi-quantitative analysis of ultimate composition for GK. H 8042 of *S. scalaris* using the EDX. We note that the detective range of EDX is restricted to elements between  $N_{11}$  and  $U_{92}$ . Figs. 1–4 on Pl. 2 summarize the results of the analysis. For comparison EDX spectra for the middle chalky (=porous spherulitic prismatic layer of MUTVEI, 1967) and the inner conchiolin layers of the siphuncular tube in *Nautilus pompilius* LINNAEUS are reproduced in Figs. 1A–B on the basis of the original data of FUKUDA *et al.* (*in press*).

The EDX spectra in GK. H 8042 show the existence of the large amounts of calcium and phosphate, with lesser amounts of sulphur, silica, potassium and magnesium. Furthermore, the characteristic X-ray image and line spectrum of phosphate indicate that a fairly large amount of this element is uniformly distributed on the si-

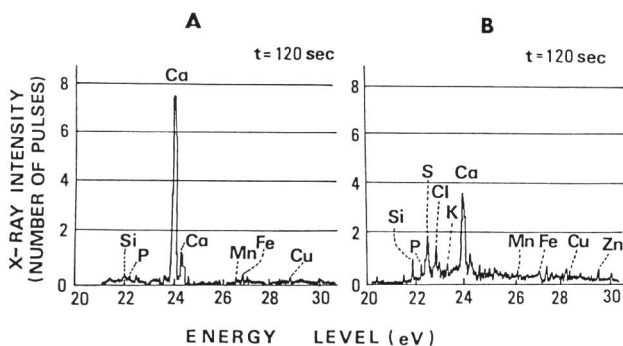


Fig. 1. Energy dispersion X-ray intensity spectra for the siphuncular wall of *Nautilus pompilius* LINNAEUS (redrawn from FUKUDA *et al.*, *in press*). Kyushu University unregistered specimen from off Panglao Island, Philippines. **A**, middle chalky (=spherulitic prismatic) layer, **B**, inner conchiolin layer, *t*; integral time. The amounts of elements detected are proportional to the X-ray intensities.

phuncular wall surface (see Pl. 2, Figs. 1–2). In *N. pompilius* the EDX spectral pattern of the middle layer is characterized by a high peak of calcium, while that of the inner layer shows low peaks of calcium, sulphur, silica, phosphate and magnesium. Therefore, the pattern of the inner (Fig. 1B) suggests the existence of a considerable amount of organic components. With respect to the presence of small amounts of sulphur, silica and magnesium, the EDX pattern of the ammonite siphuncular wall analyzed somewhat resembles that of the inner, conchiolin layer of *N. pompilius*. From these lines of evidence it is postulated that some amounts of calcium and phosphate in the specimen examined had been secondarily brought during diagenesis.

### Structural Relationship with Septal Necks

Several recent workers have reported a thin calcareous layer at the connecting part of the siphuncular membranes and the septal necks in many ammonites (MUTVEI, 1967; ERBEN *et al.*, 1969; ERBEN & REID, 1971; DRUSHCHITS *et al.*, 1976; KULICKI, 1979). According to them, the layer covers a wide area of a septal neck and is laterally replaced to siphuncular membranes. We have previously described the septal neck structures of many late Cretaceous ammonite specimens from Hokkaido under the light microscope with magnification, X20 (TANABE *et al.*, 1979). In that study we were unable to ascertain the existense of such a calcareous layer in the specimens examined. After having reexamined the same material on this occasion, we have newly discriminated a thin calcareous layer near the septal neck area of the specimens of *D. semicostatus* and *E. haradai* under the SEM. The calcareous layer around the septal necks has been termed as annular calcareous deposits (MUTVEI, 1967), calcareous deposits (BIRKELUND & HANSEN, 1968), a “cuff” (DRUSHCHITS *et al.*, 1976) and a porous prismatic zone with a de-coupling room (BANDEL & BOLETZKY, 1979). MUTVEI

(1967) and KULICKI (1979) have briefly described that the layer has a porous, annular, ridge-like structure.

To clarify the microstructural characteristics of this layer, we observed the connecting part of siphuncular membranes and septal necks in details on GK. H 8085 of *D. semicostatus* by means of the SEM. The micrographs of the portion at a young and a middle growth-stages are given in Pl. 3. They show that the layer is divided into the two parts, namely the inner, porous, prismatic layer and the outer or marginal, more or less massive calcareous zone (Pl. 3, Fig. 4). The inner prismatic layer covers almost the whole area of septal necks and is partly covered by the conchiolin membranes of the siphuncular wall on both (adoral and adapical) sides of the necks (Pl. 3, Figs. 1, 5). In contrast, the outer massive calcareous zone is restricted in the adoral

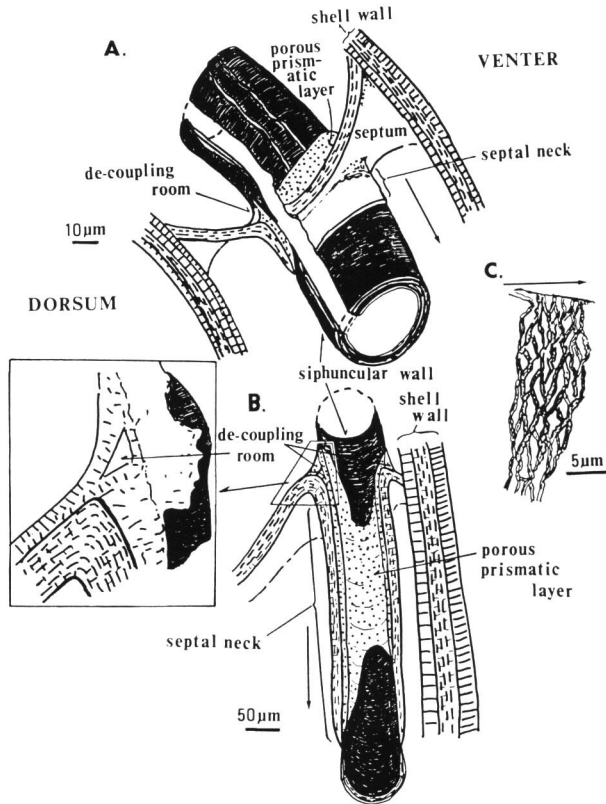


Fig. 2. Diagrams showing the structural relationship between conchiolineous siphuncular membranes and septal neck at the young and middle growth-stages in *Damesites semicostatus* based on the SEM observation on GK. H 8085. A.  $2.5\pi$  stage, B.  $7\pi$  stage, C. part of B showing the microstructure of a conchiolin membrane (consisting of reticulate, lace-like microfibrils and elongate pores) within the septal neck area. Arrows in A-C mean the adoral direction.

margin of the necks (Pl. 3, Figs. 3–4). It should be emphasized that the degree of development of this calcareous layer gradually changes in the specimen examined as the shell grows. In the early stage the layer covers the whole area of the necks, which occupy the central to subcentral position in the whorl section (Pl. 3, Figs. 1–2). In accordance with the gradual approximation of the siphuncular tube toward the ventral side with growth, the development of this layer begins to be restricted to the dorsal side for a limited distance within the long septal neck area (Pl. 3, Figs. 3–5).

The inner prismatic layer and the outer massive zone distinguished in GK. H 8085 may respectively correspond to the inner, porous prismatic zone and the outer, decoupling room in the hypothetical diagram of BANDEL & BOLETZKY (1979, figure 26) for the adult ammonite septal neck structure. The structural relationship between siphuncular membranes and septal necks in the early and middle growth-stages in *D. semicostatus* is diagrammatically illustrated in Fig. 2.

### Comparison with other Cephalopod Siphuncles

The structural characteristics of the siphuncular systems of modern and fossil chambered cephalopods (*Nautilus*, *Sepia*, *Spirula*, *Pseudorthoceras*, belemnoids and ammonoids) have already been summarized by some authors (APPELLÖF, 1893; NAEF, 1922; GRÉGOIRE, 1962; MUTVEI, 1964, 1971, 1972; DENTON & GILPIN-BROWN, 1966; ERBEN *et al.*, 1969; BANDEL & BOLETZKY, 1979). In addition, we are going to discuss the functional significance of the siphuncular systems of the selected modern and fossil chambered cephalopods in two other papers (FUKUDA *et al.*, *in press*; TANABE *et al.*, *in prep.*).

Based on our own unpublished data in addition to the previous references, let us compare the siphuncle of ammonites examined with those of other chambered cephalopods. The generalized internal structures of siphuncle and septal necks of ammonoids, belemnoids, *Nautilus*, *Spirula* and *Sepia* in the median dorsoventral section are diagrammatically shown in Fig. 3A–E. The similarities and dissimilarities among these groups may be summarized as follows: (1) chitinous or conchiolineous siphuncular membranes are restricted in the ammonoids, nautiloids and belemnoids, (2) the siphuncular tube wall of *Spirula* is made up of calcareous material only, (3) in *Sepia* the siphuncular epithelium directly contacts with the calcareous “chambers” (cuttlebone) without a siphuncular wall. The most remarkable difference between ammonoids and other groups is the difference in the relationship between siphuncle and septal necks. As described in the preceding pages, in ammonoids the siphuncular wall membranes are discontinuous with the septal layer, in contrast to the continuous relationship in nautiloids, belemnoids and *Spirula*. MUTVEI (1967, text-figs. 3–4) explained the difference between ammonoids and nautiloids as follows: thus, in ammonoids the secretion of siphuncular membranes was prolonged after the completion of the nacreous septal layer, as against the earlier secretion of the membranes in nautiloids.

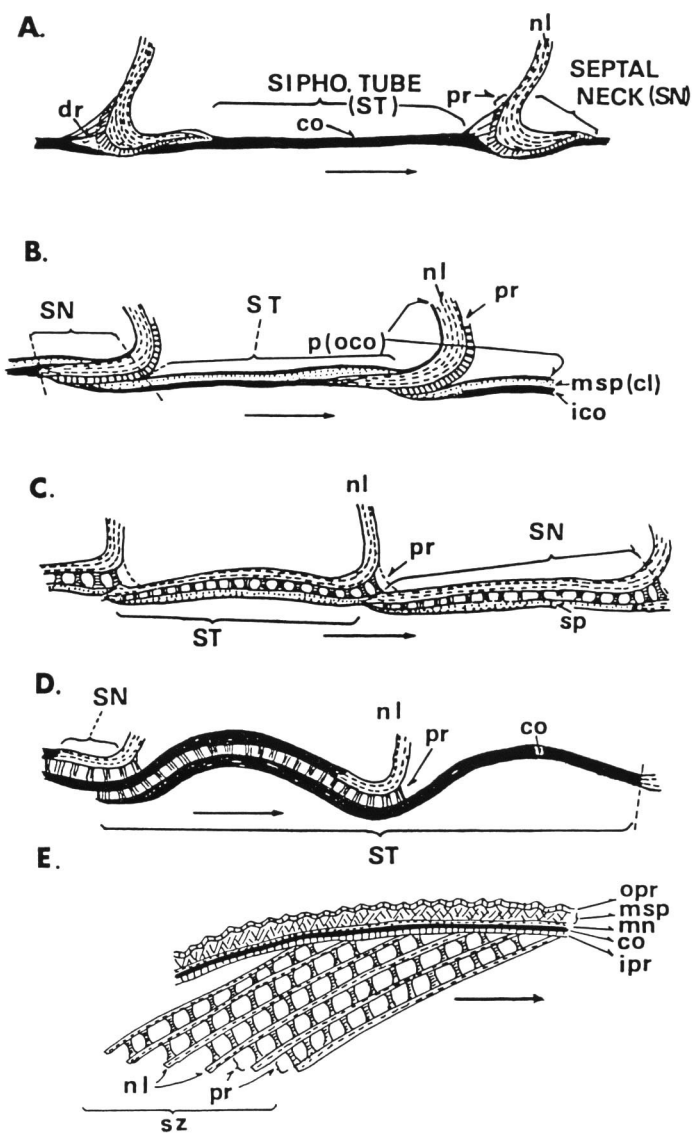


Fig. 3. Diagrams of the siphuncular systems of selected modern and fossil cephalopods (median sections). **A.** ammonoids, **B.** *Nautilus* (redrawn from MUTVEI, 1972), **C.** *Spirula* (modified from BANDEL & BOLETZKY, 1979), **D.** belemnoids (based on our own observation on the specimens of *Acrocoelites* sp.), **E.** *Sepia* (based on our unpublished data). **co**: conchiolin membranes or layer, **Pr**: porous prismatic layer, **sp**: spherulitic prismatic layer, **nl**: naucleous layer, **dr**: de-coupling room, **ico**: inner conchiolin layer, **msp(cl)**: middle spherulitic prismatic layer (=chalky layer), **p(oco)**: pellicle (=outer thin conchiolin membrane), **ipr**: inner prismatic layer, **opr**: outer prismatic layer, **mn**: middle naucleous layer, **sz**: siphuncular zone. Arrow in each diagram shows the adoral direction. Terminologies are partly cited from MUTVEI (1967, 1971, 1972), DENTON & GILPIN-BROWN (1966) and BANDEL & BOLETZKY (1979).



The porous, prismatic layer similar to that within the septal neck area of ammonoids also exists in belemnoids, *Nautilus*, *Sepia* and *Spirula* (see **ipr** and **pr** in Fig. 3B–E). BANDEL & BOLETZKY (1969) interpreted this layer as a homologous character in the chambered cephalopods. In the cuttlebone of *Sepia* it is specialized as the porous zone consisting of annular-like calcareous pillars (BANDEL & BOLETZKY, 1979 & our own unpublished data). If the interpretation of BANDEL & BOLETZKY is correct, numerous “chambers” in the cuttlebone anatomically correspond to the alternating septal necks.

### Discussion

As reviewed in the beginning of the text, recent works on the buoyancy mechanism of *Nautilus*, *Sepia* and *Spirula* have demonstrated that living animals can change their levels in the sea by controlling the low-pressure gas-space within the chambers. The works of DENTON & GILPIN-BROWN (1961a, b) and DENTON *et al.* (1961) have shown that in *Sepia* the change of gas-space is caused by altering the balance between the hydrostatic pressure of the sea and the osmotic force derived from the withdrawal of salt ions ( $\text{Na}^+$  and  $\text{Cl}^-$ ) in the fluid immediately in contact with the siphuncular epithelium. Furthermore, the experiments of DENTON & GILPIN-BROWN (1966), COLLINS & MINTON (1967) and WARD & MARTIN (1978) have made clear that the siphuncular wall of *Nautilus* is more or less permeable for fluid.

According to WARD & MARTIN, cameral liquid and salt removal rates are very slow (average 0.7 to 1.0 cm<sup>3</sup> per day) as to the four live specimens of *N. macromphalus* SOWERBY in the aqualium (water depth ranges from 0 to 25 m). This fact seems to coincide precisely with the data of permeability of CHAMBERLAIN (1978). The permeability coefficient of *Nautilus* siphuncular wall calculated by him (ca. 2.4 microdarcys) is very low as compared with those of porous, consolidated materials ( $10^2$  to  $10^6$  microdarcys). The works of CHAMBERLAIN (1978) and WARD & MARTIN (1978) may also give an important basis to assume the rate of fluid removal through the ammonoid siphuncular wall. As shown in Fig. 3B, the siphuncular wall of *Nautilus* is made up of three different layers, namely the very thin outer (conchiolin), middle (chalky) and inner (conchiolin) layers. The middle layer seems to be more permeable for fluid than the inner one, because the internal structure consisting of spherulitic prisms is more porous than that of closely packed, homogeneous membranes of the inner (DENTON & GILPIN-BROWN, 1966; MUTVEI, 1972; BLIND, 1976; FUKUDA *et al.*, *in press*). As is evident from the foregoing description, the conchiolineous siphuncular membranes in the four Cretaceous ammonites is undoubtedly comparable with the inner conchiolin layer of the *Nautilus* siphuncular wall in the ultrastructure. This fact suggests a low permeability of the former.

It is very important that in the modern chambered cephalopods the degrees of development of the porous prismatic zone or layer are related to the rates of cameral liquid removal. The porous zone is very well developed in the shells of *Spirula* and

*Sepia* (BANDEL & BOLETZKY, 1979; TANABE *et al.*, *in prep.*; see Fig. 3C & E). *Spirula spirula* LAMARCK has a planktonic mode of life in the pelagic sea with a daily migration from about 100 to 1100 m depth (DENTON & GILPIN-BROWN, 1973). Such a daily migration has also been confirmed in the coastal squids, *Sepia*, by DENTON & GILPIN-BROWN (1961a, b; 1973). From these facts it is certain that animals of *Sepia* and *Spirula* can remove cameral liquid efficiently through the widely developed porous prismatic zone. Conversely, nektobenthonic *Nautilus* species have a restricted,

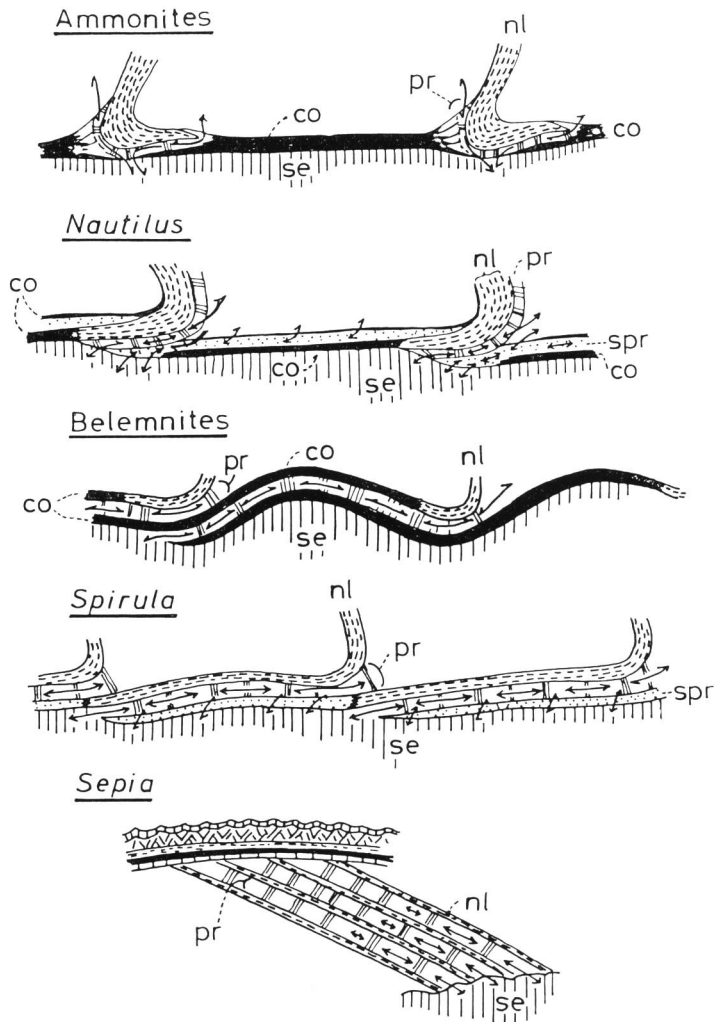


Fig. 4. Hypothetical models showing the cameral liquid removal through siphuncle in selected chambered cephalopods. Pathways of liquid removal are shown by arrows. **nl**: nacreous layer, **pr**: porous prismatic layer or zone, **co**: conchiolin membranes of siphuncular wall, **spr**: spherulitic prismatic layer of siphuncular wall, **se**: siphuncular epithelium.

narrow, porous prismatic zone in their phragmocone (Fig. 3B). This fact is well explained from the very slow cameral liquid removal and the low permeability coefficient of the siphuncular wall. Taking the microstructural similarity with the inner layer of modern *Nautilus* siphuncle into account, it is postulated that the cameral liquid removal in ammonoids was very slow as in *Nautilus*; and furthermore, from the above comparative study it may be suggested that in ammonoids the liquid was primarily transferred through the prismatic layer which is limitedly developed around the septal necks (Fig. 4).

We have previously shown that offshore type Cretaceous ammonites such as *Neophylloceras*, *Gaudryceras*, *Tetragonites* and *Damesites*, although they are different from one another in their major taxonomic positions, have very long septal necks (about 30 to 50% of a chamber length) in the middle to the latter growth-stages (TANABE *et al.*, 1979). If they have a porous prismatic layer covering almost the whole area of the long septal necks, it can be assumed that they could remove the cameral liquid more efficiently through the widely developed porous layer than the other groups with short septal necks (e.g. collignoniceratids and heteromorphs). However, further microstructural study of the septal necks in many species is needed to substantiate the above-mentioned hypothesis.

### Conclusions

1. The siphuncular walls of the four late Cretaceous ammonite species examined (*Damesites semicostatus*, *Eupachydiscus haradai*, *Mesopuzosia yubarensis* and *Scalarites scalaris*) are composed of layered, concentric conchiolineous membranes. The membrane ultrastructure of the specimen of *D. semicostatus* (Pl. 1, Fig. 6; Pl. 3, Fig. 7), which is characterized by the reticulate, lace-like microfibrils with some irregular tubercles and elongate pores, is comparable with those of conchiolin within the nacreous layer of modern and fossil molluscan shells.

2. The specimen of *S. scalaris* (GK. H 8042) contains a large amount of non-organic components such as calcium, phosphate, sulphur, silica, potassium and magnesium in the siphuncular wall. Small amounts of the same elements also exist in the inner conchiolin layer of the modern *Nautilus* siphuncular wall. This fact implies that some of the non-organic elements in the ammonite may have been secondarily derived during diagenesis.

3. The comparison of the siphuncular wall structure between ammonites and some modern and fossil chambered cephalopods show that the ammonite siphuncular wall is similar to the inner conchiolin layer of the modern *Nautilus* siphuncular wall. The well-developed unporous siphuncular membranes and the restricted distribution of the porous prismatic layer around the septal necks may suggest that the rate of cameral liquid removal in ammonoids was very slow as in *Nautilus*.

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## Explanation of Plates

All photos, by FUKUDA

### Plate 1

- Figs. 1–6. Scanning electron micrographs showing the conchiolineous siphuncular wall microstructure in *Damesites semicostatus* (1–2, 5–6), *Eupachydiscus haradai* (3) and *Mesopuzosia yubarensis* (4). U under a bar in each figure means  $\mu\text{m}$ .
- Fig. 1. Layered concentric membranes of siphuncular wall in the longitudinal section. GK. H 8039.  $8\pi$  stage.  $\times 800$ .
- Fig. 2. Part of Fig. 1, showing the closely packed siphuncular membrane microstructure (cm).  $\times 4700$ .
- Fig. 3. Siphuncular wall with smooth inner surface and its relationship with septal neck. GK. H 8024.  $3\pi$  stage.  $\times 700$ .
- Fig. 4. Outermost surface of siphuncular wall, showing the homogeneous membrane microstructure. GK. H 8038.  $3.5\pi$  stage.  $\times 4200$ . cm: conchiolineous membrane.
- Fig. 5. Etched outer surface of siphuncular tube, showing the microstructure of layered, concentric conchiolin membranes. GK. H 8085.  $3\pi$  stage.  $\times 1800$ .
- Fig. 6. Part of Fig. 5, showing the ultrastructure of conchiolin membrane consisting of reticulate, lace-like microfibrils (m) with irregular tubercles and small, elongate pores (p).  $\times 10000$ .

### Plate 2

- Figs. 1–4. Results of scanning electron microscope (1, 3) and energy dispersion X-ray (1–2, 4) examinations of siphuncular wall in *Scalarites scalaris*. GK. H 8042.
- Figs. 1–2. Characteristic X-ray line spectrum (1) and image (2; white dots) of phosphate on siphuncular wall surface, showing the uniform concentration of this element on the surface. Bars indicate  $500 \mu\text{m}$  ( $\times 64$ ).
- Fig. 3. Part of Fig. 1, showing the outermost surface of siphuncular wall without any trace of ornamentation. Bar indicates  $50 \mu\text{m}$  ( $\times 620$ ).
- Fig. 4. Energy dispersion X-ray intensity spectra on Fig. 1, showing the semi-quantitative ultimate composition of siphuncular wall. The amounts of elements detected are proportional to the X-ray intensities. The operation was performed under the conditions: 20 to 46 KeV for an acceleration voltage, 60 seconds for an integral time and 20 eV for an energy level per channel. Analysed by FUKUDA.

### Plate 3

- Figs. 1–7. Scanning electron micrographs of GK. H 8085 of *Damesites semicostatus*, showing the structural relationship between siphuncular wall and septal necks. co: conchiolin membranes of siphuncular wall, s: septum, sn: septal neck, pr: porous prismatic layer, dr: de-coupling room, vw: ventral shell wall, m & p: microfibrils (m) and pores (p) constituting a conchiolin membrane of siphuncular wall. Arrows in Figs. 1–3 and 5 show the adoral direction. (U means  $\mu\text{m}$ ).
- Fig. 1. Discontinuity of siphuncular wall in septal neck area at  $3\pi$  stage.  $\times 650$ .
- Fig. 2. Short prochoanitic septal neck at  $2.5\pi$  stage, showing the uniformly developed porous prismatic layer in the adapical part.  $\times 450$ .
- Fig. 3. Long prochoanitic septal neck at  $7\pi$  stage, showing the widely distributed porous prismatic layer in the dorsal side.  $\times 160$ .
- Fig. 4. Part of Fig. 3 (adapical margin of septal neck), showing the distribution of porous prismatic layer, de-coupling room and conchiolineous siphuncular membranes.  $\times 1000$ .
- Fig. 5. Long prochoanitic septal neck at  $6\pi$  stage, showing the distribution of conchiolineous siphuncular membranes and porous prismatic layer within the neck area.  $\times 170$ .
- Fig. 6. Part of Fig. 5, showing the microstructure of porous prismatic layer.  $\times 900$ .
- Fig. 7. Part of Fig. 5, showing the microstructure of a conchiolin membrane consisting of reticulate, lace-like microfibrils and elongate pores.  $\times 2200$ .

