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Siphuncular Structure in the Extant *Spirula* and in Other Coleoids (Cephalopoda)

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ABSTRACT

The shell wall in *Spirula* is composed of prismatic layers, whereas the septa consist of lamello-fibrillar nacre. The septal neck is holochranitic and consists of two calcareous layers: the outer lamello-fibrillar nacreous layer that continues from the septum, and the inner pillar layer that covers the inner surface of the septal neck. The pillar layer probably is a structurally modified simple prisma layer that covers the inner surface of the septal neck in *Nautilus*. The pillars have a complicated crystalline structure and contain high amount of chitinous substance. The interspaces between the pillars probably are traversed horizontally by numerous chitinous membranes like in the cuttlebone chambers in *Sepia*. The connecting ring is composed of similar two layers as that in the extant *Nautilus*: the outer spherulitic-prismatic layer and the inner chitinous layer. The spherulitic-prismatic layer takes its origin on the outer surface of the septal neck, whereas the inner chitinous layer is the non-calcified continuation of the lamello-fibrillar nacreous layer of the septal neck. The siphuncular structure in *Spirula* is compared with that in the extant *Nautilus*, fossil nautilusophonate nautilusoids, and five taxa of coleoids.

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Introduction

The connecting ring in cephalopods functions as an osmotic membrane through which the volumes of liquid in the shell chambers are osmotically regulated. The differences in the siphuncular structures indicate different methods of buoyancy regulations, probably caused by different mode of life in different environments.

The siphuncular structure in *Spirula* has been studied by several writers using the light microscope (Branco 1880; Appellöf 1893; Mutvei 1964). However, detailed structural studies were possible first when the scanning electron microscope (SEM) became available (Dauphin 1976; Bandel & Boletzky 1979; Bandel 1990; Doguzhaeva 2000; Mutvei & Donovan 2006). In the latter studies particular attention was paid on the structure of the inner pillar layer of the septal neck. In the present paper, the siphuncular structure in *Spirula* is described and compared with that in the extant *Nautilus* and fossil nautilusophonate nautilusoids (Mutvei 2015a, 2016), ammonoids and ammonoids with partially endocochleate shells (Mutvei 2014; Doguzhaeva & Mutvei 2015), and in four taxa of coleoids: phragmoteuthids (Mutvei & Donovan 2006), bactritid-like coleoids (Doguzhaeva et al. 1999; Mutvei et al. 2012), belemnites (Mutvei 2015b) and extant *Sepia* (Doguzhaeva & Mutvei 2012; Checa et al. 2015). The mode of life of *Spirula* is discussed.

Material and Methods

The material consists of numerous shells of *Spirula spirula* that were collected on the beaches of the Canary Islands. The

siphuncular structure was studied in median sections with a SEM Hitachi S-3400 at the Swedish Museum of Natural History, Stockholm. In order to study the crystalline structure of the siphuncles, the sections were etched with the sodium hypochlorite solution for 2–30 hours. This solution dissolves the chitinous substance between the crystals. The amount and distribution of the chitinous substance were studied by etching the sections of the siphuncles with a solution of 1:1 mixture of 25% glutaraldehyde and 1% of acetic acid, to which alcian blue was added, for 1–60 minutes (Mutvei's solution by Schöne et al. 2005). This solution dissolves the crystals and fixes the chitinous substance between them.

Siphuncular Structure in *Spirula*

Septal Neck

The septal neck is long, holochranitic and extends adapically to the preceding septal neck (Figures 1A, B and 6A, B). Only a narrow interspace is left between the consecutive septal necks. The septa are composed of the lamello-fibrillar nacre (=nacreous type 2 by Mutvei 1970; lamello-fibrillar nacre by Doguzhaeva 2000; lamello-fibrillar structure by Bandel & Boletzky 1979 and Bandel 1990). The septal neck consists of two calcareous layers: the lamello-fibrillar layer that continues from the septal neck and the pillar layer that covers the inner surface of the septal neck. (Figure 6A; =pillar zone by Bandel & Boletzky 1979 and Bandel 1990; semi-prismatic layer by Mutvei 1964 and by Dauphin 1976; prismatic layer by Mutvei & Donovan 2006; spherulitic-prismatic layer by Doguzhaeva 2000). The pillar layer consists of

Figure 1. SEM images. *Spirula*. **A.** Specimen no. Mo. 180825. Median section of the siphuncle to show a long septal neck that is internally coated by a connecting ring of the succeeding siphuncular segment. Untreated. **B.** Specimen no. Mo. 180826. Two consecutive septal necks in higher magnification; the inner chitinous layer of the connecting ring is not preserved. Etched for 2 min with Mutvei's solution. Scale bars: **A** = 200 μ m, **B** = 100 μ m.

numerous calcareous pillars that are separated by interspaces and oriented at right angles to the siphuncular long axis (Figures 1B and 6D). The layer takes its origin on the adoral surface of the septum, close to the septal neck and covers four-fifth of the inner surface of the septal neck (Figure 6A). In the adoral portion of the septal neck, its thickness is about half of that of the septal neck, but in the adapical direction its thickness gradually decreases and the layer wedges out (Figure 6A, B).

Connecting Ring

The connecting ring is composed of two layers: the outer spherulitic-prismatic layer, and the inner chitinous layer (Figure 6A, C). The spherulitic-prismatic layer covers the outer surface of the distal portion of the septal neck and continues into the connecting ring (Figure 1B and 6A). This layer is thick in the septal neck but decreases rapidly in thickness in adapical

direction and becomes very thin (Figures 1B and 6A; see also Dauphin 1976, Figure 14). It is composed of a layer of spherulitic prisms of irregular shapes without preferred orientation (Figure 2B, C). The inner layer of the connecting ring consists of chitinous membranes. This layer is the non-mineralized continuation of the lamello-fibrillar nacreous layer of the septal neck (Figure 6A, C). The chitinous layer is usually only partially preserved in shells collected on the beaches (Figure 1A).

The two layers of the connecting ring, together with the pillar layer of the preceding septal neck, close the narrow interspace between two consecutive septal necks (Figure 6B). The extension of the pillar layer along the inner surface of the septal neck creates a reservoir and a transportation path for the cameral liquid.

Structure of the Pillar Layer

In the most adoral region of the pillar layer the pillars are larger than in the rest of the pillar layer, and they are often attached to each other (Figures 1B and 4E). The growth zones of the pillars are often thick and separated by distinct furrows (“terrace-like annulations” Bandel & Boletzky 1979). The adoral pillars have about 5–15 growth zones (Figures 1B and 4E). As illustrated by Bandel & Boletzky (1979, Figure 7A), chitinous membranes from the growth zones traverse the interspaces between the adoral pillars.

In the rest of the pillar layer the pillars are more or less circular in cross-section (Figures 2A and 4A–D). Together with the adoral pillars, they are arranged into numerous rows parallel to the siphuncular long axis (Mutvei 1997, Figure 8A). The adjacent pillars are usually separated by smaller or larger interspaces, but some pillars in a row are in places in contact with each other (Figure 2A). The proximal portion of each pillar is composed of varying numbers of vertical, crystalline columns, mostly 10–20 µm in diameter (Figures 2A and 3B, C). The crystalline columns are embedded into a chitinous substance, but their outlines are usually more or less clearly recognizable. The surface of the columns is covered by small crystals that protrude from the interior of the columns through the chitinous substance (Figure 2A). The crystals in the columns are arranged into thin growth zones that are oriented at right angles to the length axis of the columns (Figure 4A, C, D). As counted by Bandel & Boletzky (1979, p. 324), each pillar has 50–60 growth zones. The distal portions of the vertical columns are transformed into calcareous prisms of various diameters (Figures 2A, 3B and 4A–D). Most prisms are oriented more or less obliquely towards the siphuncular cavity, giving the distal portion of the pillars a blossom-like or an angle-like shape (Figures 2A, B, 3B, D, and 4A–D). In many pillars numerous additional prisms are added to the distal portion. The shape and arrangement of the calcareous components are best visible in the pillars that are treated with the sodium hypochlorite solution that dissolves the chitinous substance (Figures 3C and 4A–D). In order to study the arrangement and amount of the chitinous substance, the pillars were treated with the Mutvei’s solution (see above) that fixes the chitinous substance and dissolves the calcareous crystals. The pillars contain a large quantity of chitinous substance that is distributed within the calcareous crystal columns and prisms (Figure 5). Not only the pillar layer, but also the entire shell in *Spirula* contains high amount of the chitinous substance. This probably modified the crystalline structure of the shell.

Reconstruction of the Pillar Layer

The *Spirula* shells described here were exposed at different length of time on beaches before they were collected. It is therefore probable that the chitinous membranes in the siphuncles were more or less destroyed by dissolution and bacterial activity. As pointed out above, Bandel & Boletzky (1979) illustrated schematically organic membranes that extend in the interspaces between the most adoral pillars. In the rest of the pillar layer no organic membranes were observed. However, it is reasonable to suppose that also here the organic membranes emerged from the growth zones of the pillars and extended in the interspaces between the pillars. In this case the interspaces were traversed by a great number of organic membranes, and the pillars were formed at the places where the membranes become calcified (Figure 6D).

Also in the extant coleoid *Sepia* numerous, horizontal, chitinous membranes extend between the vertical calcareous pillars in the cuttlebone chambers (Checa et al. 2015). The pillars are formed at the places where the membranes become calcified. In the fossil calciosiphonate nautiloids (Mutvei 2016), the cavities in the calcified perforate layer of the connecting ring probably contained similar chitinous membranes that were destroyed by diagenesis. Also here, the cavity walls probably were formed at places where the membranes became calcified (Mutvei 2016, Figure 9B).

Mode of Life

In the present seas and oceans, the great majority of squids are diurnal vertical migrants. Because the environment in the oceans and seas still is inadequately known, it is often difficult to understand the function of the vertical migration. Also, *Spirula* is a diurnal vertical migrant (Bruun 1943; Clarke 1969, 1970; Warnke et al. 2010; Hoffmann & Warnke 2014). According to Clarke (1969) the entire population lives during daylight at water depths of 600–700 m, but ascends at night to the depths of 100–300 m. Studies of stable isotopes in the shell septa during the ontogeny (Warnke et al. 2010) show that the hatching depth of *Spirula* is about 800 m. The young animal stays at this depth about 10–14 weeks and migrates then upwards to an average depth of 350–400 m where it stays the following half year, then descending to an average depth of 550–600 m. According to Clarke (personal communication), the small size of *Spirula* makes it difficult for the animal to swim against currents. In this case, the animal has to use currents with different directions to maintain its habitat. This was probably also the case with many fossil nautiloids and ammonoids that had inefficient swimming capability.

Comparison with Nautiloids, Ammonoids and Coleoids

Fossil nautilosiphonate nautiloids and extant *Nautilus*

In *Nautilus* and fossil nautilosiphonates (Mutvei 2015a, 2016) the septal neck is composed of two layers: the outer, columnar nacreous layer and the inner, simple prisma layer (Figure 3A). As described above, also the septal neck in *Spirula* is composed of two layers, but the outer layer is the lamello-fibrillar nacreous layer, and the inner layer the pillar layer. The pillars are probably structurally modified prisms, and their interspaces are probably traversed by numerous chitinous membranes (Figure 6D). The

Figure 2. SEM images. *Spirula*. Specimen no. Mo. 180827. **A.** Untreated pillars in the pillar layer; note that pillars consist of numerous crystal columns that are transformed distally into prisms. **B.** Outer surface of the pillar layer; the distal ends of the pillars (right) are covered by a thin spherulitic-prismatic layer (left) of the connecting ring of the succeeding septal neck. **C.** Outer surface of the spherulitic-prismatic layer of the connecting ring in higher magnification. Scale bars: **A** = 5 μ m, **B** = 20 μ m, **C** = 10 μ m.

structure of the connecting ring in *Spirula* shows great similarity to that in *Nautilus* and nautilusiphonate nautiloids in being composed of the outer spherulitic-prismatic layer and the inner chitinous layer (Figure 6C). This type of the connecting ring does not occur in other, hitherto known coleoids.

Phragmoteuthids (Figure 7C, D)

According to Mutvei & Donovan (2006) the septal neck in the Jurassic *Phragmoteuthis* is orthochoanitic, but it is not known whether it consists of the columnar nacre, as in *Nautilus*, or of the lamello-fibrillar nacre, as in belemnites and *Spirula*.

Figure 3. SEM images. *Nautilus pompilius*. **A.** Specimen no. Mo. 180823. Prismatic layer on the inner surface of the septal neck; note that this layer has an uncomplicated structure. Untreated. *Spirula*. **B–D.** Specimen no. Mo. 180828. **B.** Distal portion of a pillar to show crystal columns that are distally transformed into prisms. Untreated. **C.** Pillar layer, treated for 3 h with the sodium hypochlorite solution, to show numerous columns in each pillar and the arrangement of crystals in the columns. **D.** Outer surface of the pillar layer to show radiating prisms. Untreated. Scale bars: **A–C** = 10 μm, **D** = 5 μm.

Characteristic of *Phragmateuthis* is the extremely long, calcareous connecting ring that extends through 5–6 chambers (Figure 7C). The permeable siphuncular wall in each chamber therefore consists of 5–6 consecutive connecting rings (Figure 7D). Each connecting ring consists of a single calcareous

layer that is composed of prismatic or spherulitic crystallites, and that emerges from the distal end of the septal neck, being a structurally modified continuation of the septal neck. The calcified layer contains cavities of irregular sizes and shapes (Figure 7D). It is not possible to confirm whether these cavities correspond

Figure 4. SEM images. *Spirula*. **A–D.** Specimen no. Mo.180829. Longitudinal sections of the pillar layer, treated for 4 h with the sodium hypochlorite solution; note numerous growth layers in the pillars and various arrangements of the distal prisms. **E.** Specimen no. Mo. 190831. Pillar in adoral part of the pillar layer to show thick growth layers (compare with Fig. 1B). Scale bars: **A, C, D, E** = 10 μ m, **B** = 5 μ m.

to those in the calcified perforate layer of the connecting ring in the fossil calciosiphonate nautiloids (Mutvei 2016).

Bacritid-like Coleoids (Figure 6G)

In three taxa designated to Bacritoidea (Mapes 1979, Doguzhaeva et al. 1999; Mutvei et al. 2012) the septa and septal necks consist of the lamello-prismatic layer that differs from the lamello-fibrillar nacre in the belemnites and extant *Spirula* (Doguzhaeva et al. 2003; Mutvei et al. 2012). In the bacritid taxa, the septal

neck is orthochoanitic. The connecting ring is preserved as a single chitinous layer that originates from the lamello-prismatic layer of the septal neck ((Figure 6(G); Doguzhaeva 2000; Mutvei et al. 2012). As in ammonoids and ammonoids with partially endocochleate shells, the connecting ring in the bacritid-like coleoids lacks the outer spherulitic–prismatic layer (Figure 6(G)). In both taxa the chitinous layer of the connecting ring was highly flexible and elastic (Weitschat & Bandel 1991; Mutvei et al. 2012, Figure 12A, C), and resistant against diagenetic destruction. It is not known whether the connecting ring in the bacritid-like

Figure 5. SEM images. *Spirula*. Specimens no. Mo.180832, Mo. 180833, Mo. 180834. **A, B, C.** Longitudinal sections of the pillar layer, treated for 15 min **A**, 30 min **B** and 1 h **C** with the Mutvei's solution; note the high amount of the chitinous substance that is preserved after the dissolution of the calcareous crystals. Scale bars: = 10 μ m.

coleoids contain minute pore canals as that in the ammonoids and ammonoids with partially endocochleate shells.

Ammonoids and Ammonoids with Partially Endocochleate Shells (Figure 6E, F)

It is still unknown how many ammonoids had their shells entirely or partially covered by living tissues. Ammonoids with shells

partially covered by living tissues occurred in Ammonitina and Lytoceratina. This is indicated by: additional layers on the shell surface; abnormal sequence of the shell layers; high amount of the chitinous substance in the shell wall; ultrathin apertural margin (Doguzhaeva & Mutvei 1993, 2015; Mutvei 2014). There are also indications that in some taxa of Goniatina and Anarcestina the shell was covered at least partially by soft tissues (summarized in Doguzhaeva & Mutvei 2015). The connecting ring in the

Figure 6. Schematic presentations. **A–D.** *Spirula* type of the siphuncle. **A.** Structure of the septal neck and connecting ring. **B.** Two consecutive siphuncular segments; note the narrow permeable passage for cameral liquid between the siphuncular segments; **C.** Section of the septal neck and connecting ring. **D.** Section of the pillar layer in higher magnification. **E, F.** Siphuncular type in ammonoids and ammonoids with partially endocochleate shells. **E.** Section of the siphuncular wall. **F.** Connecting ring in higher magnification; note the pore canals. **G.** Bactritid-like coleoid type of the siphuncle. Section of the septal neck and connecting ring.

ammonoids and ammonoids with partially endocochleate shells consists of a single chitinous layer that is traversed by numerous pore canals, ca 0.1 μm in diameter (Figure 6F; Mutvei et al. 2004; Mutvei & Dunca 2007; Doguzhaeva et al. 2010). This layer was

highly flexible (Weitschat & Bandel 1991; Mutvei unpublished observations) and resistant against diagenetic destruction. It agrees in these respects to the single chitinous layer of the connecting ring in the bactritid-like coleoids (Mutvei et al. 2012).

Figure 7. Schematic presentations. **A, B.** Belemnitid type of the siphuncle. **A.** Septal neck and connecting ring. **B.** Connecting ring in higher magnification. **C, D.** Phragmoteuthid type of the siphuncle. **C.** Adoral section of the siphuncular wall to show extremely long connecting rings in the growth zone. **D.** Septal neck and five connecting rings in higher magnification.

Belemnitids (Figure 7A, B)

The siphuncular structure was recently studied in the Jurassic belemnitid *Megateuthis* (Mutvei 2015b). In the belemnitids and in the extant *Spirula*, the septum and the septal neck are composed of the lamello-fibrillar nacre (Mutvei 1972). Instead of the calcareous pillar layer in *Spirula*, the inner surface of the septal neck in the belemnitid *Megateuthis* is covered by an organic tubular layer (Figure 7A). Each tube has a chitinous wall and is divided into three branches that are directed towards the siphuncular cavity (Figure 7B). The tubes probably contained epithelial extensions from the siphuncular cord. The tubular chitinous layer continues into the connecting ring where it becomes the inner

layer. The outer layer of the connecting ring is a chitinous layer that emerges from the distal end of the septal neck. As in the ammonoids and

ammonoids with partially endocochleate shells, and in the bactritid-like coleoids, the spherulitic-prismatic layer of the connecting ring is not developed. The chitinous layer of the connecting ring was highly flexible and elastic and resistant against diagenesis. The connecting ring structure in the belemnitid *Megateuthis* is similar to that in the aulacocerid *Mojsisovicsteuthis* (Mutvei 1971, pl. 5). The unique and complicated siphuncular structure in belemnitids and aulacocerids is different from that in other cephalopods.

Sepia

In the extant *Sepia* the chitinous, strip-like sheets cover the openings to the cuttlebone chambers, being tightly attached to the adoral surfaces of the adjacent septa (Doguzhaeva & Mutvei 2012; Doguzhaeva & Dunca 2015). The sheets are homologues of the connecting rings in other cephalopods. They consist of fibrous chitin and are flexible. Each sheet is probably perforated by numerous micropores (Doguzhaeva & Mutvei 2012, figures 3, 4), similar to those in the chitinous connecting rings in the ammonoids and ammonoids with partially endocochleate shells (Mutvei et al. 2004; Mutvei & Dunca 2007; Doguzhaeva et al., 2010).

Discussion

The extant *Spirula* is the only, hitherto known coleoid in which the connecting ring consists of similar two layers as that in the fossil nautilusiphonate nautiloids and extant *Nautilus*: the inner chitinous layer, and the outer spherulitic–prismatic layer (Mutvei 2015a). This supports the opinion of Engeser & Bandel (1988) that *Spirula* is an ancient species of recent Decabranchia. This is also supported by DNA analysis by Warnke et al. (2003)

In the bactritid-like coleoids, ammonoids and ammonoids with partially endocochleate shells, and belemnites, the siphuncular structure is different from that in the fossil nautilusiphonates and *Nautilus* (Mutvei 2015a): (1) the outer spherulitic–prismatic layer is absent in the septal neck and connecting ring; (2) only the inner chitinous layer of the connecting ring is present, but it differs from that layer in the nautilusiphonates by its resistance against diagenetic destruction, and by its high elasticity and flexibility. In ammonoids and ammonoids with partially endocochleate shells this layer is perforated by numerous, minute pore canals. Also the strip-like, chitinous sheet that covers the opening to the cuttlebone chamber in the extant *Sepia* and corresponds to the chitinous layer in the connecting ring, seems to be perforated by similar, minute pore canals (Doguzhaeva & Mutvei 2012). Thus, during the evolution, the siphuncles in ammonoids and different coleoid taxa underwent considerable changes that resulted in the formation of six different structural types in addition to about six structural types in nautiloids (Mutvei 2015a, 2016). At the present, it is not possible to understand why these structural types appeared, and how they participated in the osmotic pumping of the cameral liquid for buoyancy regulations.

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