Chapter 12
Connecting Ring Ultrastructure in the Jurassic Ammonoid *Quenstedtoceras* with Discussion on Mode of Life of Ammonoids

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1 Introduction

It was generally assumed (e.g., Mutvei, 1967, 1975; Grégoire, 1984; Westermann, 1971, 1982, 1993, 1996; Bandel, 1981; Obata et al., 1980; Tanabe, 1977, 1979; Hewitt et al., 1993; Kulicki, 1994; Hewitt, 1996) that the connecting ring in prosiphonate ammonoids, in which the septal necks are directed adorally, had similar structure and composition as that in the retrosiphonate Recent *Nautilus,* in which the septal necks are directed adapically, and in which the bathymetry is well known. Based on this assumption, Westermann (1971) calculated the mechanical strength of the ammonoid siphuncle against hydrostatic pressure (siphuncular strength index) from the siphuncular wall thickness, multiplied by 100 and divided by the siphuncle inner radius. This index was thought to indicate the maximum water depth where ammonoid shell imploded and, hence, the maximum habitat depth of the animal. In addition,

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the postmortem distribution of ammonoids, and the water depth of the marine sediments where the ammonoid shells accumulated were calculated from this index.

However, as recently demonstrated (Mutvei et al., 2004), the connecting ring structure and composition in two Mesozoic genera, *Aconeceras* and *Grammoceras*, are considerably different from those in Recent *Nautilus*. The connecting ring in these ammonoids is composed of glycoprotein fibers that probably were hardened by phenolic tanning (=sclerotization) in a similar way as reported in crustacean exoskeletons (Dennell, 1960; Florkin, 1960; Passano, 1960; Dalingwater and Mutvei, 1990).

In order to make the connecting ring permeable for cameral liquid, it was traversed by numerous narrow pore canals that probably housed microvillous-like extensions from the siphuncular epithelium (Mutvei et al., 2004). The ammonoid connecting ring is therefore often preserved in fossil environments where the untanned, organic matter in the connecting rings of fossil nautiloids and coleoids is destroyed during diagenesis.

In the present paper, the connecting ring structure is described in the Jurassic ammonoid *Quenstedtoceras* spp. that were recovered from erratic boulders at Luckow, Poland. This structure is compared with that in nautiloid and coleoid cephalopods. The mechanical strength of the connecting ring and the mode of life in ammonoids, particularly swimming by jet propulsion, are discussed.

2 Material and Methods

Shells of *Quenstedtoceras* spp. (Cardioceratidae) were collected by the senior author from calcareous concretions of an erratic boulder at a brick factory near Luckow, eastern Poland (Makowski, 1962). The concretions are of Middle Jurassic, Late Callovian age, and come from the *Quenstedtoceras lamberti* Zone.

Shells of *Aconeceras trautscholdi* were collected by L. A. Doguzhaeva from sideritic concretions in the Lower Cretaceous at the Volga River, near the town Uljnovsk, Russia.

Numerous shells, partially preserved with empty chambers, were mechanically fractured. The exposed siphuncle segments were placed on specimen stubs, gold coated, and studied with a Hitachi S 4300 scanning electron microscope at the Swedish Museum of Natural History, Stockholm. The elemental composition in the connecting ring and shell was analyzed with Energy Dispersive X-Ray Microanalysis (EDAX).

3 Description

3.1 Connecting Ring Structure

Obata et al. (1980), Tanabe et al. (1982), Westermann (1982), and Grégoire (1984) pointed out that the ammonoid connecting ring is composed of glycoprotein fibers that form thin lamellae. These fibers are similar to those in the inner layer of the connecting ring in Recent *Nautilus*, but in ammonoids they seem to have been hardened by tanning and form a compact, semielastic structure that is resistant against diagenesis (Mutvei et al., 2004). The glycoprotein fibers in ammonoids are diagenetically transformed into chain-like aggregates of tiny granules (Fig. 12.1) or globular aggregates (Doguzhaeva and Mutvei, 2003; Mutvei et al., 2004). Structurally similar transformations were observed in muscular fibers of fossil coleoids, and in fibrous organic material of fossil coleoid gladii and arm hooks (Doguzhaeva and Mutvei, 2003).

Two structurally different sublayers can often be distinguished on the vertical fracture planes of the connecting rings in *Quenstedtoceras* (Fig. 12.2E). The outer sublayer differs from the inner sublayer by its more compact structure, probably because the glycoprotein fibers are thinner and more closely packed than those in the inner sublayer (Fig. 12.2E, F). The boundary between the two sublayers is distinct and often forms a narrow interspace. Two structurally similar sublayers occur in the connecting ring of *Grammoceras quadratum* (Fig. 12.2C; Mutvei et al., 2004: Fig. 12.3A). In most connecting rings the glycoprotein fibers in the inner sublayer are diagenetically transformed into chains of large-sized granules, 0.2–0.3 µm in diameter. The fibrous-lamellar structure of the connecting ring is indistinctly visible. Only in well-preserved connecting rings where the glycoprotein fibers consist of smaller granules, about 0.1 µm in diameter or less, is the fibrous-lamellar structure distinctly recognizable (Figs. 12.1B, C, 12.2F, G, 12.3C).

Both sublayers of the connecting ring are traversed by numerous narrow pore canals (Figs. 12.1B, C, 12.2F, G, 12.3C). They can only be observed in the best preserved connecting rings, but even then, the granular structure of the glycoprotein fibers more or less obscures their outlines. The pore canals have a diameter of about 0.1 µm and the distances between adjacent canals are about 1.0 µm. The density of the pore canals in *Quenstedtoceras* (Figs. 12.1B, C, 12.3C) seems to be somewhat higher than that in *Aconeceras* (Figs. 12.2A, B, 12.3A) and *Grammoceras* (Fig. 12.2C, D) in which about 500,000 canals occur per mm^2. The density of the pore canals in *Aconeceras* and *Grammoceras* is much higher than previously estimated by Mutvei et al. (2004).

As previously pointed out (Mutvei et al., 2004: Fig.12.4A, B), the diameter and density of the pore canals in an ammonoid connecting ring roughly correspond to those of the pore canals in arthropod exoskeletons (compare Fig. 12.3A, B). The pore canals in arthropod exoskeletons house microvillous-like epithelial extensions (Mutvei et al., 2004: Fig. 12.4B; Compére and Goffinet, 1987). It is reasonable to conclude that similar pore canals in ammonoid connecting rings also contained epithelial extensions (Mutvei et al., 2004: Fig. 12.4A). These extensions participated in the hardening processes of the connecting ring by tanning and created a considerably enlarged, physiologically active surface of the siphuncular epithelium for efficient removal of cameral liquid.

3.2 Elemental Composition

Energy Dispersive X-Ray Microanalysis (EDAX) showed that the siphonal tube of *Quenstedtoceras* is rich in phosphorus, while the shell and septa are made of

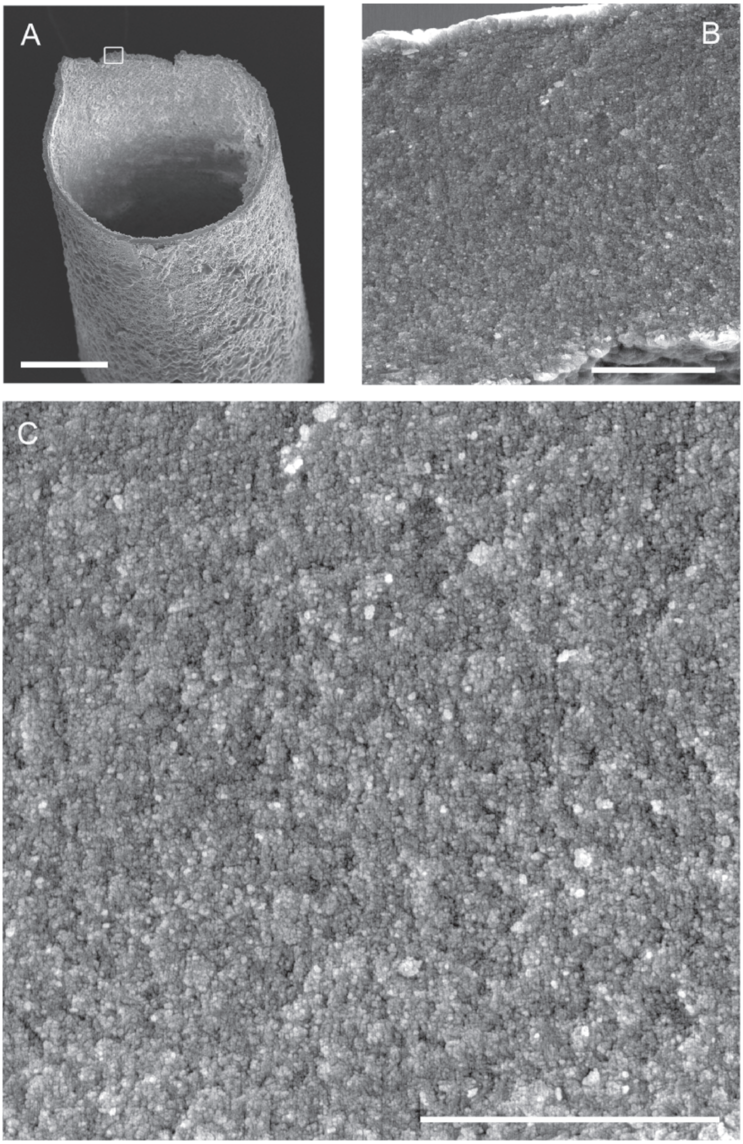

Fig. 12.1 Quenstedtoceras *sp. A – General view of connecting ring. B – Vertical fracture plane of the connecting ring. C – Detail of B in higher magnification to show the granular structure of the glycoprotein fibers and the pore canals. Scale bars: A – 0.1 mm; B, C – 6 μm.*

calcium carbonate. A total of 25 points were analyzed as follows: 8 points on the outer surface of the shell and inner surface of the septa, 16 points on the connecting ring and 1 point on the septal neck. The analysis results are shown in Table 12.1.

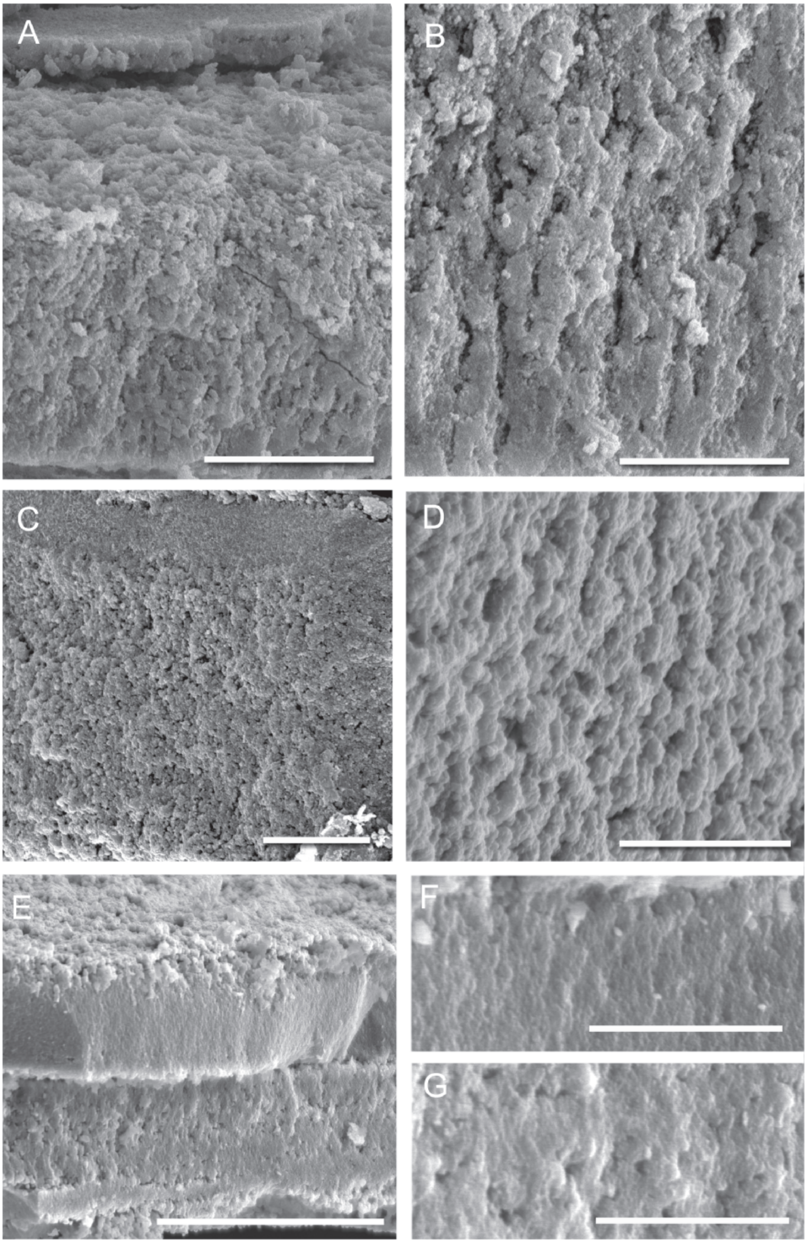

Fig. 12.2 *A, B*. Aconeceras trautscholdi. *A – Vertical fracture plane of connecting ring to show pore canals. B – Detail of A in higher magnification. C, D*. Grammoceras quadratum. *C – Vertical fracture plane of connecting ring to show the outer sublayer with compact structure and the inner sublayer with less compact structure. D – Detail of C in higher magnification to show the pore canals. E–G*. Quenstedtoceras *sp. E – Vertical fracture plane of connecting ring to show the two sublayers. F, G – Outer and inner sublayer, respectively, in higher magnification to show the granular structure of glycoprotein fibers and pore canals. Scale bars: A, C, E – 12 µm; B, D – 6 µm; F, G – 3 µm.*

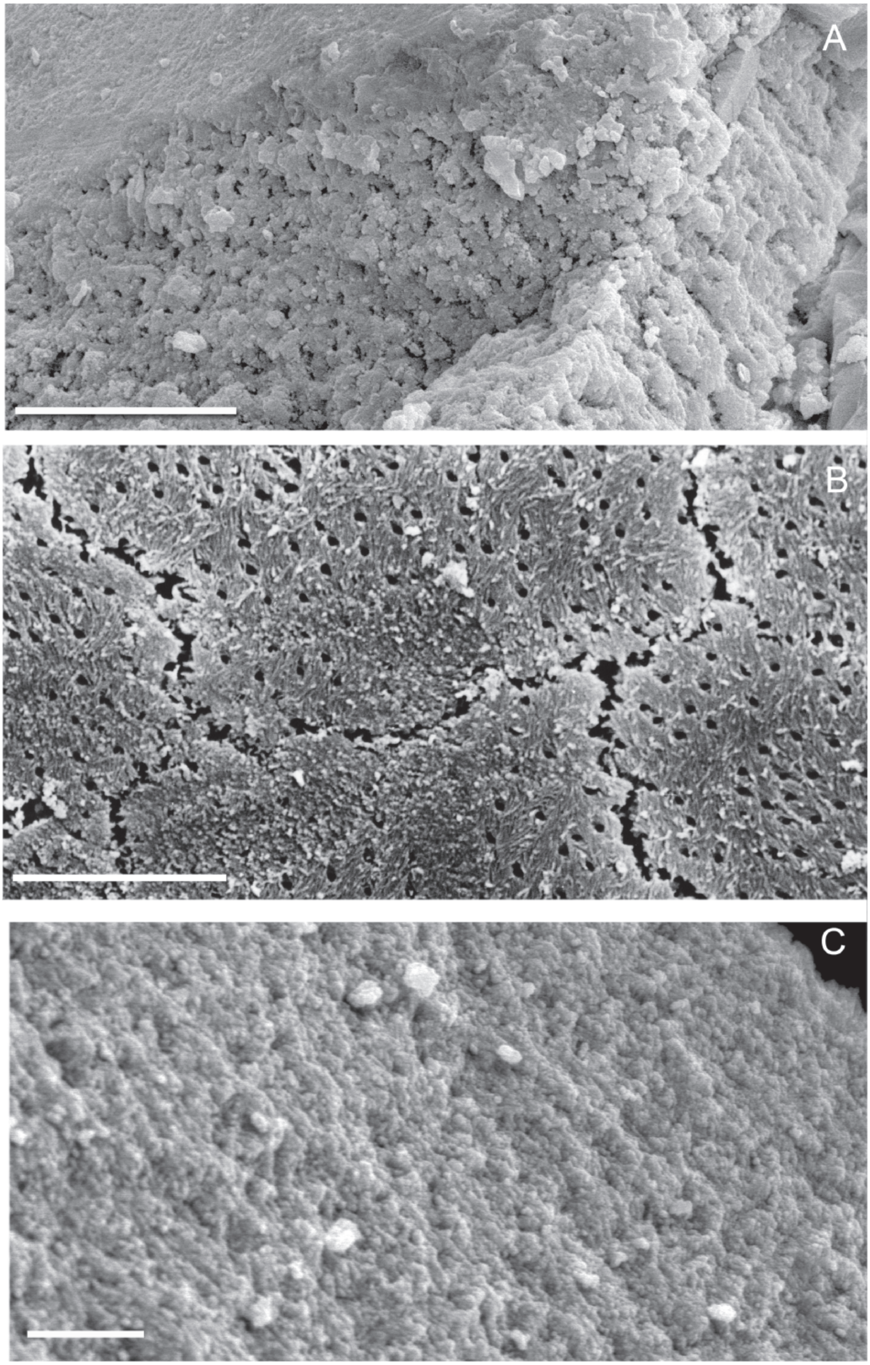

Fig. 12.3 *A*. Aconeceras trautscholdi. *Vertical and horizontal cross sections of a connecting ring to show the pore canals. B*. Carcinus maenas (*Crustacea*). *Horizontal fracture plane of the exoskeleton to show the pore canals and glycoprotein fibers. C*. Quenstedtoceras *sp. Oblique vertical fracture plane of the connecting ring to show granular structure and pore canals. Scale bars: A, B −10 μm; C − 1 μm.*

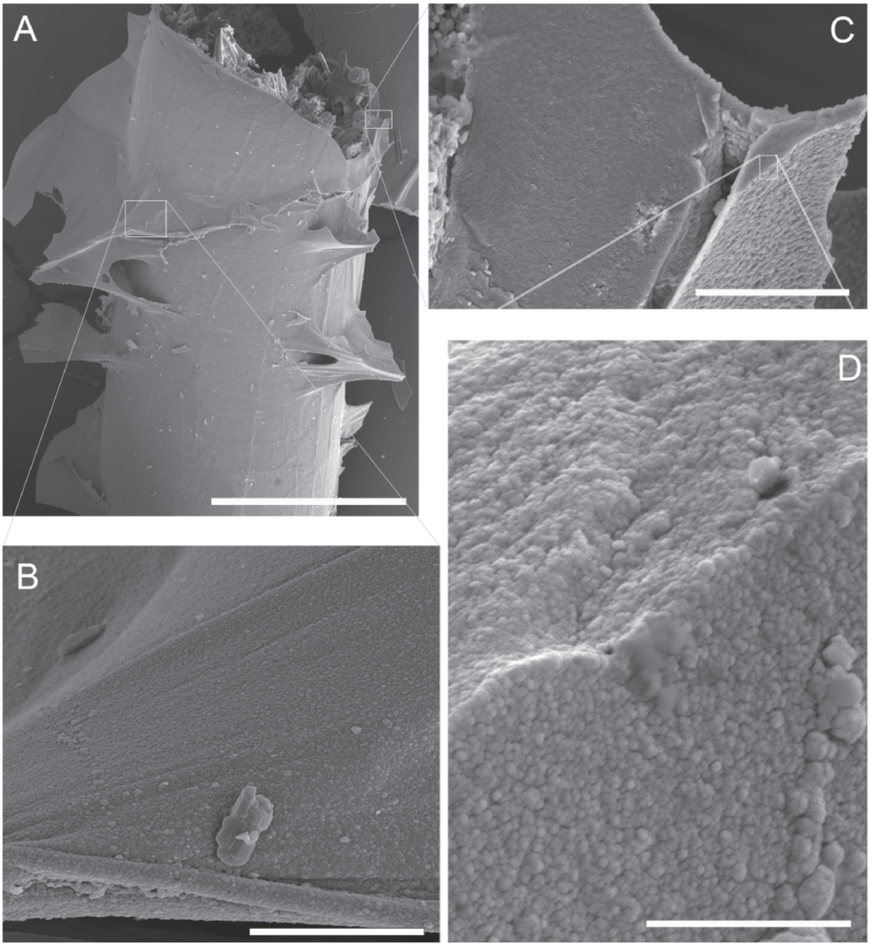

Fig. 12.4 A–D. Quenstedtoceras *sp. A – General view of connecting ring with several siphuncular sheets. B – Granular surface of siphuncular sheet. C – Detail of the vertical fracture plane of the connecting ring and siphuncular sheet. D – Siphuncular sheet in higher magnification. Scale bars: A – 300 µm; B – 30 µm; C – 12 µm; D – 3 µm.*

4 Discussion

4.1 Connecting Ring in Ammonoids

As described in a previous paper (Mutvei et al., 2004) and herein, the connecting rings in three Mesozoic ammonoid taxa *Grammoceras*, *Aconeceras*, and *Quenstedtoceras* form a semisolid, probably tanned layer of glycoprotein (conchiolin)

Table 12.1 *The results (in atomic weight %) of Energy Dispersive X-Ray Microanalysis.*

Points	Calcium	Carbon	Oxygen	Phosphorus	Sulphur
Shell and septa (8)	19–63	16–38	17–63	–	–
Septal neck (1)	18	17	64	1	–
Connecting ring (16)	6–23	19–46	18–63	3–18	1

fibers. In order to make the layer permeable for cameral liquid, it is perforated by numerous, narrow pore canals. The number and diameter of the pore canals in the ammonoid connecting ring roughly match the number and diameter of the pore canals in a crustacean exoskeleton that is composed of tanned glycoprotein fibers (Compére and Goffinet, 1987). In the crustacean exoskeleton the pore canals house thin filaments from the body epithelium representing elongated microvilli. It is probable that the pore canals in ammonoids also housed thin epithelial filaments that participated in the transport of the cameral liquid between the shell chambers and the siphuncular cord (Mutvei et al., 2004: Fig. 12.4A).

4.2 Connecting Ring in Nautiloids

The connecting ring in living *Nautilus* is composed of an inner glycoprotein (conchiolin, horny) layer and an outer, calcified spherulitic-prismatic layer (Mutvei, 1972, 2002a; Grégoire, 1984). The inner layer is an uncalcified and structurally modified continuation of the nacreous layer of the septal neck. It is composed of a thin lamella of glycoprotein fibers similar to those in the connecting ring of ammonoids (Obata et al., 1980; Westermann, 1982; Grégoire, 1984). In contrast to that in ammonoids, this layer is elastic and lacks pore canals. It can stand against hydrostatic pressures of 50–80 atm, but has a low permeability for cameral liquid. The outer, calcified, spherulitic-prismatic layer is a continuation of a structurally similar layer on the outer surface of the septal neck. The latter layer is porous without mechanical strength.

As reported by Mutvei (2002a), the fossil nautiloid taxa Nautilida and Tarphycerida have a similar connecting ring structure to that seen in *Nautilus* and, hence fundamentally different from that in ammonoids. The fibrous, glycoprotein layer of the connecting ring in the Nautilida and Tarphycerida is practically always destroyed during fossilization. However, the direction of the growth lines in the distal end of the septal neck suggests that an inner glycoprotein layer of the connecting ring was present during the animal's lifetime.

In Paleozoic orthoceratid and actinoceratid nautiloids the connecting ring has a different structure. The outer spherulitic-prismatic layer is present but is usually thinner than that in other nautiloids. The inner layer of the connecting ring is calcified and perforated by numerous pore canals, usually about 0.1–0.5 mm in diameter (Fig. 12.5A, B; Mutvei, 1997, 1998, 2002a, b). Thus, the pore canals occur in the connecting rings of actinocerid and orthocerid nautiloids, but they have a considerably larger diameter than those in ammonoids. It is highly probable that the pore canals in orthocerids and actinocerids also housed cellular extensions from the

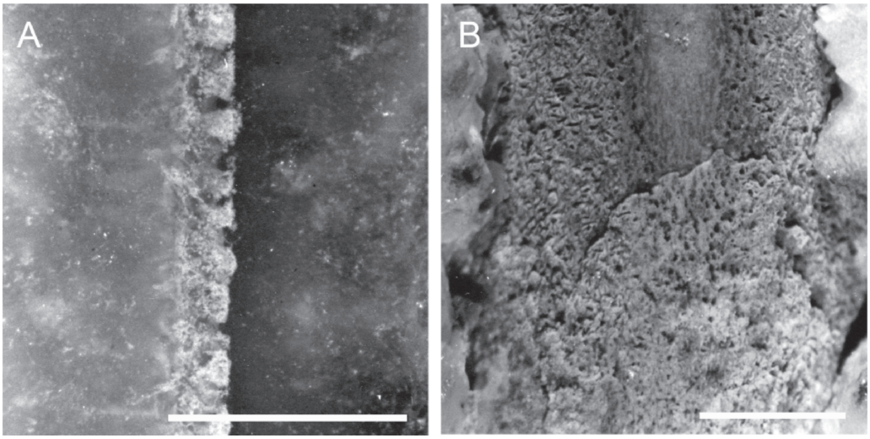

Fig. 12.5 *Connecting rings in Ordovician nautiloids. A –* Orthoceras scabridum. *Longitudinal section of connecting ring to show the calcified layer with pore canals. B –* Lituites *sp. Paramedian section of connecting ring to show the calcified layer with pore canals. Scale bar – 1 mm.*

epithelium of the siphuncular cord, and that these extensions considerably increased the surface of the physiologically active epithelium, thereby increasing the capacity and speed of the "osmotic pumping" function of this epithelium.

4.3 Connecting Ring in Coleoids

Three structural types have been distinguished in coleoids (Mutvei and Donovan, 2006, in press).

In Recent *Spirula* the connecting ring has a structure similar to that in Recent *Nautilus*. It is composed of an outer, calcified, spherulitic-prismatic layer and an inner, fibrous, glycoprotein layer. Because the septal necks are long, the siphuncular wall is mechanically strong to withstand high hydrostatic pressures. The connecting ring is exposed only in a narrow interspace between consecutive necks where the exchange of the cameral liquid takes place. When *Spirula* is in its normal swimming position this liquid is almost completely decoupled from the permeable, exposed region of the connecting ring (Denton et al., 1967; Denton and Gilpin-Brown, 1971). *Spirula* is able to make extensive daily vertical migrations (Clarke, 1969), but the osmotic exchange mechanism to remove cameral liquid is still unknown.

In the Jurassic phragmoteuthid, *Phragmoteuthis huxley*, the connecting ring has a primitive uncomplicated structure, unknown in other cephalopods. Each connecting ring has a calcified, porous, prismatic structure. It is extremely long and extends through 5–6 chambers. The siphuncular wall in each chamber is therefore composed of 5–6 superimposed connecting rings from consecutive septal necks (Mutvei and Donovan, 2006, in press).

The third structural type of connecting ring occurs in the Jurassic belemnoid *Megateuthis gigantea*, and in the aulacocerid *Mojsisovicteuthis* The permeable siphuncular wall in each chamber consists of two superimposed connecting rings from two consecutive septal necks. The connecting ring is composed of calcified lamellae that are perforated by numerous pore canals (Mutvei and Donovan, 2006, in press). Thus, the pore canals in the connecting rings occur not only in belemnoid and aulacocerid coleoids, but also in actinocerid and orthocerid nautiloids, and in ammonoids (Fig. 12.5).

4.4 Ammonoid Paleobathymetry and Paleobiogeography

Westermann (1971) calculated the siphuncular strength index in ammonoids from the siphuncular wall thickness, multiplied by 100 and divided by the inner radius of the siphuncle. This calculation was based on the assumption that the ammonoid connecting ring had the same structure and composition as the inner glycoprotein (cochiolin, horny) layer of the connecting ring in living *Nautilus*. From the siphuncular strength index, Westermann (1971, 1982, 1987) and Hewitt (1996) calculated the habitat limits of several ammonoid taxa. However, as demonstrated in the present paper the siphuncular strength index can only be used as an indicator of relative siphuncular strength between different ammonoid taxa.

The composition and structure of the ammonoid connecting ring is also important for estimations of the postmortem drift of ammonoid shells and hence, for paleobiogeography. Chamberlain et al. (1981) stressed that the postmortem drift in ammonoids was a relatively rare event because “the rate of water influx into the phragmocone due to ambient hydrostatic pressure is sufficiently rapid in most cases to overcome positive buoyancy before the shell reaches the surface” (Chamberlain et al., 1981: 494). The filling of the phragmocone with water is facilitated by postmortem loss of the body and the siphuncular cord. “If the fill rate is rapid compared to the ascent rate, the shell will not reach the surface but will sink back down to the sea floor” (Chamberlain et al., 1981: 497). Consequently, the structure of the connecting ring, its permeability, and the living depth of the animal regulate the postmortem biogeographic distribution of ammonoids (see also Maeda and Seilacher, 1996). As demonstrated here, the permeabilility coefficient of the connecting ring in ammonoids was probably much higher than that in *Nautilus* and this has to be taken into consideration in estimations of the paleobiogeographic distribution of ammonoids.

4.5 Ammonoid Septa

The function of the peripheral folding of ammonoid septa has generally been explained as providing increased mechanical strength for the shell wall from implosion by hydrostatic pressure (e.g., Westermann, 1975). In addition to the mechanical function, the septal folding probably also had a physiological function (Mutvei, 1967;

Kulicki, 1979; Kulicki and Mutvei, 1988). As in living *Nautilus*, the septal surface was covered by a wettable glycoprotein (conchiolin) sheet, but due to the considerably increased septal surface, by septal folding, this sheet attained a considerably larger surface in ammonoids. Also the inner surface of each chamber wall in ammonoids was coated by an organic sheet (Weitschat, 1986; Weitschat and Bandel, 1991). In many ammonoids (summarized in Weitschat and Bandel, 1991), the chambers contained siphuncular sheets that extended from the septal sheets and chamber-wall sheets to the siphuncular surface and became attached to it (Weitschat, 1986; Weitschat and Bandel, 1991; Tanabe and Landman, 1996). The siphuncular sheets created circumsiphonal reservoirs around the siphuncle. Checa (1996) interpreted some of the siphuncular sheets as being formed by desiccation of mucus in cameral liquid, but that interpretation is not supported by our observations. As illustrated in Fig. 12.4A–D, the structure of the siphuncular sheets is identical to that of the connecting ring. Additional sheets, transverse and horizontal, may also occur in the chambers of some ammonoids (Weitschat and Bandel, 1991). As pointed out by the latter writers, all these sheets were interconnected and they facilitated the transport of the cameral liquid through the siphuncular wall (Mapes et al., 1999).

As experimentally demonstrated by Mutvei and Reyment (1973), the amount of cameral liquid in ammonoids was relatively much greater than that in adult *Nautilus* (see also Heptonstall, 1970; Weitschat and Bandel, 1991; Kröger, 2002). Kulicki and Mutvei (1988) showed that spaces between the shell wall and the septal folds in ammonoids were capable of keeping a large volume of cameral liquid by surface tension. The higher amount of cameral liquid seems to have been an adaptive feature for vertical movements. Rapid buoyancy regulation was made possible by the highly porous but mechanically strong connecting ring, and by the epithelial extensions within the pore canals that provided a considerably enlarged surface area for the osmotically pumping, siphuncular epithelium.

4.6 Ammonoid Anatomy

As pointed out by several authors (e.g., Mutvei, 1967; Mutvei and Reyment, 1973; Weitschat and Bandel, 1991; Donovan, 1993; Jacobs and Landman, 1993; Saunders and Ward, 1994; Doguzhaeva and Mutvei, 1996; Richter and Fischer, 2002), the anatomy of the ammonoid body is different from that in living *Nautilus*. (a) In many ammonoid taxa the body was longer than that in *Nautilus* and more or less wormlike in shape; this indicates that the ventral mantle cavity was long and narrow, and contained only a small volume of water, not sufficient for jet-powered swimming (see Mutvei and Reyment, 1973: Text-fig. 12.8B). In Recent *Nautilu*s, an animal that swims by jet propulsion, the volume of the mantle cavity is about one half of the total body volume (Ward, 1987). (b) The ammonoid shell aperture often has a ventral keel instead of a hyponomic sinus. This is in sharp contrast to *Nautilus* and fossil nautiloids. Also living coleoids have a hyponomic sinus in the ventral mantle margin. (c) The mantle-shell attachment in ammonoids was considerably different from that in living *Nautilus* (Crick, 1898; Jordan, 1968; Mutvei, 1967, 1975; Mutvei and Reyment, 1973; Weitschat and Bandel, 1991; Doguzhaeva and Mutvei, 1996; Richter and Fischer, 2002). In *Nautilus* jet propulsion is created by powerful, laterally attached, cephalic muscles that pull the body into the shell, accompanied by simultaneous contractions of the hyponome muscles. The water is thereby forcibly expelled from the mantle cavity through the hyponome. Except in a few taxa, in which the annular area forms a lateral lobe, the lateral muscle attachments are not recognized in ammonoids (Doguzhaeva and Mutvei, 1996; Kennedy et al., 2002; Richter and Fischer, 2002).

The following hypotheses have been generated to explain a possible jet-powered swimming mechanism in ammonoids: (1) The head and a highly muscular hyponome were outside the body chamber and the contractions of the hyponome alone created the jet propulsion for swimming (Doguzhaeva and Mutvei, 1991; Chamberlain, 1993; Saunders and Ward, 1994; Richter and Fischer, 2002). (2) Ammonoids had a muscular, coleoid-like mantle in front of the shell aperture and the contractions of this mantle created the propulsive power (Jacobs and Landman, 1993). However, neither hypothesis can be supported by the morphology and structure of the ammonoid shell.

4.7 Ammonoid Shell Morphology

In Recent *Nautilus*, the intra- and interspecific variations of shell morphology are very small. In fully matured shells the apertural edge is somewhat thickened, the apertural width is slightly contracted, and the ocular sinuses are somewhat deeper. There is also a small change of shell coiling and an increase in the length of the living chamber during growth (Collins and Ward, 1987). Sexual dimorphism differences are also very small and are only expressed by larger shells with somewhat wider shell apertures in males (Saunders and Ward, 1987; Ward, 1987). At early growth stages, before the nepionic constriction, the shell is ornamented by a reticulate pattern that is replaced by fine parallel ridges across the transverse growth lines in some species at later growth stages.

Shells in many ammonoid taxa differ considerably from *Nautilus* shells by their large scale intraspecific variation and more pronounced sexual dimorphism. As summarized by Davis et al. (1996), the late ontogenetic shell modifications comprise: (1) changes in coiling, whorl cross section, and ornamentation, and (2) development of an apertural shell thickening, apertural constriction, and formation of apertural rostrum (keel) or lappets. Sexual dimorphism is expressed in large differences in shell size of dimorphs (micro- and macroconch). At the terminal growth stages, the microconch (probably male) forms a prominent apertural rostrum or lappets whereas the whorls in the macroconch (probably female) become broad and inflated, and the surface of the living chamber becomes smooth (Makowski, 1962; Sarti, 1999).

Makowski (1962) described a considerable range of sexual dimorphism characters in *Quenstedtoceras*. The microconchs and macroconchs are identical up to the 5–5.5 whorls stage. The surface of these shells is ornamented by distinct ribs and the shell is strongly compressed in cross section. During further growth the macroconch attains a large diameter, and the fully grown shell consists of at least 7 whorls. The shell becomes more involute, and after 6–7 whorls, the ribbing gradually disappears, and the shell surface becomes smooth. In cross section the shell becomes broad and inflated. The microconch grows only to 6 whorls and has therefore a much smaller diameter than the macroconch. It maintains a compressed cross section and distinctly ribbed ornamentation. At the terminal growth stage the aperture forms a long ventral keel. The shell surface becomes smooth only immediately behind this keel.

Some taxa show extreme intraspecific variation of shell shape and ornamentation. As reported by Dagys and Weitschat (1993a, b), the adult shells of the Triassic ammonoid *Czekanowskites rieberi* range morphologically from "keeled smooth suboxycones with narrow umbilicus, through feebly ribbed platycones with a little wider umblicus, to subcadicones with relatively wide umbilicus and straight ribs with bullae." Consequently, the "streamlined" oxycones and "subbenthic" cadicones lived together within the same biotope. Based on these observations, Dagys and Weitschat came to the conclusion that "streamlining of shell cannot play any important role among such slow-swimming animals as ammonoids" (Dagys and Weitschat, 1993b: 26). Those writers also pointed out that high intraspecific variation also occurs in several other groups of Triassic ammonoids, and that it has created serious problems in taxonomy.

4.8 Ammonoid Mode of Life

Several authors (e.g., Westermann, 1987, 1996; Jacobs, 1992; Seki et al., 2000; Klug and Korn, 2004) were of the opinion that many ammonoids utilized jet-powered swimming. Westermann (1996) and Jacobs (1992) even calculated the swimming speeds in several ammonoid taxa.

On the other hand, some writers (Mutvei and Reyment, 1973; Mutvei, 1975; Weitschat and Bandel, 1991; Dagys and Weitschat, 1993b) have been more or less critical of the idea of jet-powered swimming in ammonoids. These writers pointed out the great differences between most ammonoids and living *Nautilus* in anatomical design and in intraspecific variation of shell morphology. If ammonoids were jet-powered swimmers, their populations had to have been subdivided into several subpopulations characterized by different shell design and hence, different swimming ability and mode of life. This interpretation is not in agreement with the conditions either in living *Nautilus* or in living coleoid cephalopods. Furthermore, ammonoids do not show any sign of natural selection toward streamlined shell shape during their evolution.

Instead of evolutionary adaptation to jet-powered swimming, most ammonoids show a specialization to vertical, probably diurnal migrations by aid of changes of buoyancy. This is evident from the occurrence of numerous pore canals in the connecting ring that probably contained epithelial extensions from the siphuncular epithelium, and by the complex system of wettable glycoprotein sheets that extended from each chamber to the wall of the connecting ring and functioned for rapid transport of cameral liquid from the chambers.

5 Conclusions

(1) The ammonoid connecting ring was structurally and mechanically different from that in living *Nautilus*: it is composed of glycoprotein (conchiolin) fibers that probably were tanned and formed a semielastic, mechanically strong structure. This made it highly resistant to diagenesis. In order to make the connecting ring permeable for cameral liquid, it was perforated by a great number of very fine pore canals that probably housed microvilli-like epithelial extensions. The epithelium of the siphuncular cord consequently acquired a considerably enlarged surface area for an efficient osmotic pump function.

(2) Connecting rings, perforated by pore canals, occur in Paleozoic orthocerid and actinocerid nautiloids, and in belemnoid and aulacocerid coleoids. This similarity may indicate phylogenetic relationships between these taxa and ammonoids.

(3) The siphuncular strength index in ammonoids cannot be used to estimate implosion depth of the shells and hence the maximum depth habitat, nor can be used to estimate postmortem paleobiogeographic distribution of the shells, and depth of the marine environment where the ammonoid shells were postmortally deposited. However, it can be used to compare the mechanical strength of the connecting ring between different ammonoid taxa.

(4) Ammonoids lack indications that they were jet-powered swimmers. (a) The muscle attachment to the shell differs considerably from that in living *Nautilus*. (b) Contrary to *Nautilus*, many ammonoids had a long, wormlike body that only contained a small, narrow, ventral mantle cavity; the water volume in this cavity was insufficient for jet propulsion. (c) Many ammonoids lack a hyponomic sinus. (d) The shell morphology and ornamentation in many ammonoid taxa show pronounced intraspecific variation, and great differences between juveniles, females, and males. If ammonoids were adapted for swimming by jet propulsion, these variations would indicate that every single population was subdivided into several subpopulations with different modes of life. In contrast, *Nautilus* shows very small intraspecific variation of their shell morphology and ornamentation. This is necessary to maintain a streamlined shell shape for the entire population for jet-powered swimming.

(5) Previously, the idea of vertical, diurnal migrations of ammonoids by means of buoyancy changes was refuted because in living *Nautilus*, the emptying of chambers of cameral liquid is a slow process. However, as shown in the present

paper, the occurrence of a great number of pore canals in the connecting ring indicates that ammonoids were capable of a rapid exchange of cameral liquid and gas between the siphuncle and the chambers. In addition, the physiologically active siphuncular epithelium extended into the pore canals and acquired a larger surface area for osmotic "pumping." Furthermore, the exchange of cameral liquid through the wall of the porous connecting ring was facilitated by a complex system of wettable glycoprotein (conchiolin) sheets that extended from each chamber to the wall of the connecting ring; these sheets were interconnected and facilitated the rapid transport of cameral liquid. All these features strongly indicate that the majority of ammonoids had acquired an efficient adaptation for diurnal vertical migrations by means of buoyancy changes.

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