[Palaeontology, Vol. 49, Part 3, 2006, pp. 685–691]

SIPHUNCULAR STRUCTURE IN SOME FOSSIL COLEOIDS AND RECENT *SPIRULA*

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Typescript received 12 January 2004; accepted in revised form 16 August 2005

Abstract: In Jurassic *Phragmoteuthis huxleyi* Donovan (Order Phragmoteuthida) the siphuncular wall shows unique structural and morphological features. The septal neck is short, about one-eighth of chamber length, but the connecting ring is extremely long, extending through 5–6 chambers. The permeable siphuncular wall in each chamber is, therefore, unusually thick and consists of 5–6 consecutive connecting rings. Each connecting ring is calcified and has a highly porous structure in being composed of bundles of spicular crystallites, orientated more or less at right angles to the siphuncular wall, and separated by smaller or larger interspaces. A restudy of the belemnoid *Megateuthis gigantea* (Schlotheim) and the aulacoceratid *Mojsisovicsteuthis*? shows that the connecting rings in these taxa are also calcified. Each ring has a length of two chambers and consists of several calcified lamellae that are traversed by minute pores. The permeable siphuncular wall in each chamber therefore consists of two consecutive connecting rings separated by a porous prismatic layer. In Recent *Spirula* the connecting ring is composed of two layers: an outer spherulitic-prismatic layer and an inner glycoprotein layer, of which the latter is not preserved in dry shells. The connecting ring structure is here similar to that in Recent *Nautilus*. Our study shows that at least three different structural types of siphuncular wall occur in coleoids. The phragmoteuthid connecting ring has a primitive structure, unknown in other cephalopods. This indicates that this taxon has no closer relationship with other coleoid taxa. The belemnitid-aulacoceratid connecting ring is calcified and traversed by numerous pore canals. It shows a certain structural similarity to that in fossil actinoceratid and orthoceratid nautiloids. The spirulid connecting ring is structurally similar to that in Recent *Nautilus* and fossil nautilitid and tarphyceratid nautiloids. Thus the connecting ring structure indicates that coleoids include several, phylogenetically clearly separated lineages.

Key words: siphuncular structure, connecting ring, Phragmoteuthida, coleoids.

THE chambered shell in cephalopods is a highly specialized hydrostatic apparatus that regulates the buoyancy of the animal. In order to evacuate the cameral liquid from the newly formed chambers, the siphuncular wall in each chamber consists of a porous connecting ring. This connecting ring is a structurally modified, permeable continuation of the septa and septal necks. In Recent *Nautilus* the septal neck consists of three calcareous layers: a thin, porous, outer spherulitic-prismatic layer, a thick nacreous layer, and a thin, porous, inner prismatic layer (sp.pr, nac, pr; Text-fig. 3A). The connecting ring is composed of an outer spherulitic-prismatic layer directly continuous from that in the septal neck, and an inner, fibrous, glycoprotein (conchiolin) layer that is an uncalcified continuation of the nacreous layer of the septal neck (sp.pr, gp; Text-fig. 3A).

Little attention has previously been paid to the structure of the connecting ring in fossil cephalopods. It was generally assumed that this structure is similar to that in Recent *Nautilus*. However, as shown by Mutvei (1997*b*, 1998, 2002*a*, *b*), only fossil nautilid and tarphyceratid nautiloids have a connecting ring structure similar to that in *Nautilus*, whereas in fossil actinoceratid and orthoceratid nautiloids the connecting ring is wholly calcified and perforated by numerous pore canals. Also in belemnoids and aulacoceratids the connecting ring was found to be structurally different from that in *Nautilus* in that in each chamber it consists of two superimposed rings (Mutvei 1971).

Differences in connecting ring structure indicate differences in hydrostatic function of the shell and, hence, differences in mode of life. In the present paper a hitherto unknown, primitive type of connecting ring is described in the Jurassic *Phragmoteuthis huxleyi* Donovan (2006). The previously described connecting ring structure in Recent *Spirula* (Mutvei 1964, 2002*a*), the belemnoid *Megateuthis gigantea* (Schlothheim) and the aulacoceratid *Mojsisovicsteuthis*? (Mutvei 1971) is restudied and reinterpreted.

MATERIAL AND METHODS

The following coleoids were studied: (1) a median thin section of a phragmocone of *Phragmoteuthis huxleyi* Donovan (2006) collected from bed 85 of Lang and Spath (1926, p. 159), Upper Sinemurian, Obstusum Zone, Stellare Subzone, at Stonebarrow, near Charmouth, Dorset, England, and deposited in the Natural History Museum, London (Holotype no. C46849); (2) median thin sections of two phragmocones of the belemnoid *Megateuthis gigantea* (Schlotheim) previously dealt with by Mutvei (1971, pls 1–2, 4; pl. 3, figs 1–2), from the Dogger, Goslar and Osterfeld, northern Germany; (3) several median sections of dry shells of *Spirula spirula* (L.), collected from beaches on Fuerteventura, Canary Islands.

The shell sections were studied and photographed in incident light with a Leitz Ortoplan microscope equipped with a video camera at magnifications of × 40 and ×80.

SYSTEMATIC PALAEONTOLOGY

Order PHRAGMOTEUTHIDA

Phragmoteuthis huxleyi Donovan 2006
Text-figure 1

Description. Only a median thin section of the phragmocone is present from this coleoid (Text-fig. 1A). The phragmocone is breviconic with an apical angle of about 30 degrees. Most septa on the dorsal side are crushed. The siphuncle is preserved in seven chambers. It is narrow, and in contact with the ventral phragmocone wall. Its diameter is about one-twelfth of the dorsoventral diameter of the phragmocone. The septal necks (sn; Text-fig. 1B) are short, about one-eighth of chamber length. The calcium carbonate in each neck is completely dissolved during diagenesis but the outline of the neck is still clearly recognizable. Each neck passes directly into a single, porous, calcified layer of the connecting ring that has the same thickness as the neck. Contrary to the preservation of the neck, it is structurally well preserved (conn; Text-fig. 1B, D). It consists of bundles of acicular crystallites that are separated by smaller or larger interspaces, and orientated more or less at right angles to the siphuncular wall (Text-fig. 1D). The connecting ring is extremely long, extending through 5–6 chambers (Text-fig. 1C). The permeable siphuncular wall in each chamber is, therefore, unusually thick and composed of 5–6 superimposed connecting rings (1–6; Text-fig. 1D).

Order BELEMNOIDEA

Megateuthis gigantea (Schlotheim)
Text-figure 2

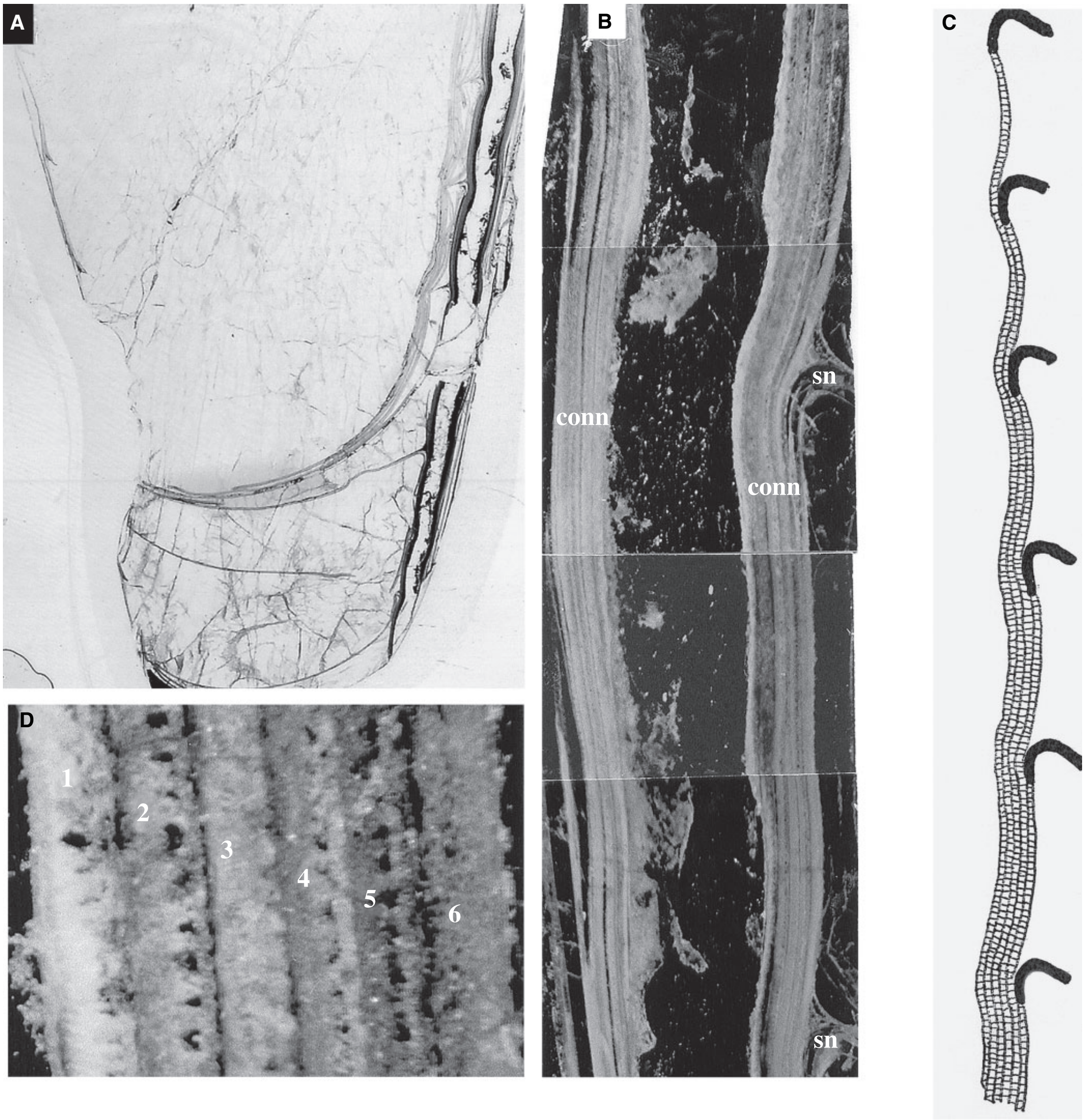
Description. Mutvei (1971) described the structure of the siphuncular wall in three phragmocones of *Megateuthis gigantea* (Schlotheim). This study was carried out on thin sections in transmitted light. The present study is on the same thin sections in reflected light, which shows the structural details more clearly. The septal neck has a length of about one-third of the chamber length (sn; Text-fig. 2A). Two layers can be distinguished in the neck: a nacreous layer and an inner, porous, prismatic layer (sn, sph; Text-fig. 2D). The acicular crystallites in the prisms are orientated at right angles to the inner surface of the neck. The connecting ring consists of (1) a calcified layer (conn1, conn2; Text-fig. 2A–B) that is a direct continuation of the nacreous layer of the neck (sn; Text-fig. 2A–B), but has a different structure in being composed of several thin, calcareous lamellae traversed by very fine pores (conn; Text-fig. 2C), and (2) an inner, porous prismatic layer that is a continuation of that layer in the neck (sph; Text-fig. 2B, D). The connecting ring is long, extending through two chambers (Text-fig. 2A, E). Therefore, the permeable siphuncular wall in each chamber is composed of two superimposed connecting rings (conn1, conn2; Text-fig. 2A–B, E). In a previous report (Mutvei 1971) the calcified outer layer of the connecting ring was erroneously interpreted as being composed of glycoprotein sheets.

Remarks. In the aulacoceratid *Mojsisovicsteuthis*? (Mutvei 1971) the connecting ring structure seems to be identical to that observed in the belemnoid *Megateuthis gigantea*. A similar connecting ring structure was also described by Bandel (1985) in the aulacoceratid *Dictyoconites*.

Order SPIRULIDA

Recent *Spirula spirula* (L.)
Text-figure 3B–E

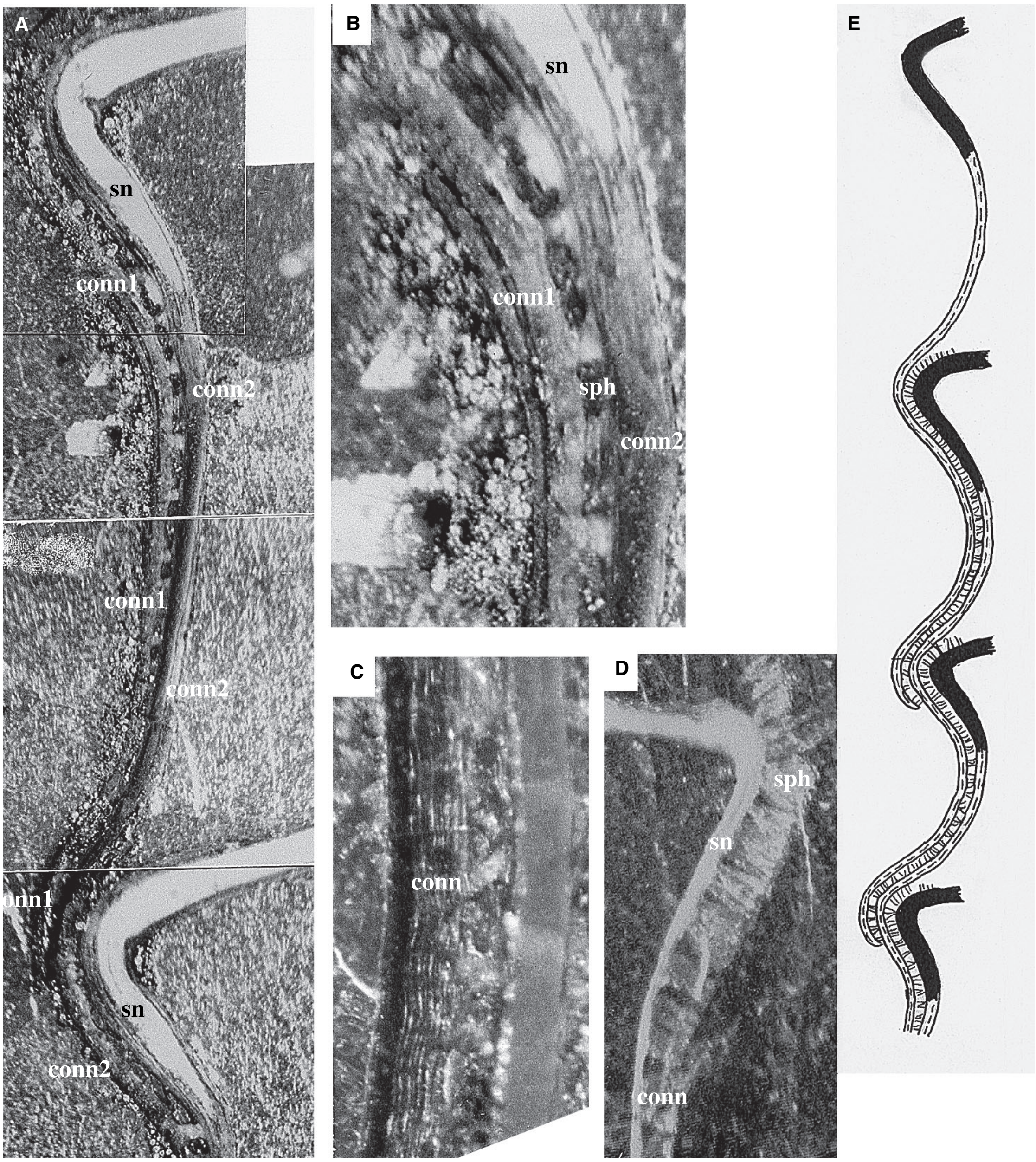
Description. In *Spirula* the siphuncular wall structure has been imperfectly known because only dry shells collected on beaches have hitherto been investigated (Schwarz 1895; Mutvei 1964, 1971, 1997*a*; Dauphin 1976; Bandel and Boletzky 1979; Bandel 1990; Doguzhaeva 2000). The septal neck is long, extending through one shell chamber. Three layers can be distinguished: (1) A thick nacreous layer of structural type 2 (Mutvei 1970) directly continuous with the nacreous layer of the septum (nac; Text-fig. 3B–C). (2) A porous prismatic layer that covers the inner surface of the septal neck, facing the siphuncular cavity; this layer thins out in the distal portion of the neck; it is composed of bundles of acicular crystallites, separated by interspaces, and orientated more or less at right angels to the nacreous layer (pr, Text-fig. 3B). (3) A spherulitic-prismatic layer that can be clearly distinguished only in the outer, distal portion of the septal neck (sp.pr; Text-fig. 3B–C). The latter layer was described by Schwarz (1895, p. 28, fig. 1) as ‘dense shell material just as in the short funnels of the recent *Nautilus*’. In the connecting ring only one layer can be seen in dry *Spirula* shells: the spherulitic-prismatic layer that is a direct continuation of that layer in the septal neck and covers internally the inner prismatic layer of the preceding septal neck (sp.pr; Text-fig. 3C).



TEXT-FIG. 1. A–D, *Phragmoteuthis huxleyi* Donovan. A, median section of phragmocone; × 1·7. B, median section of siphuncle to show thick connecting rings (conn) and septal necks (sn); same specimen as in A; × 10. C, diagrammatic median section of siphuncular wall in six last-formed chambers to show long connecting rings, each extending through 5–6 chambers; note that in the last five chambers the siphuncular wall was incomplete. D, siphuncular wall in higher magnification to show six superimposed connecting rings (1–6); note that each connecting ring is composed of bundles of acicular crystallites arranged more or less at right angles to the siphuncular wall and separated by larger or smaller interspaces; × 65.

The course of the growth lines in the nacreous layer (nac; Text-fig. 3B–C) of the distal end of the septal neck indicates that the connecting ring also has a second layer, the inner glycoprotein layer (gl; Text-fig. 3B), in addition to the outer spherulitic-prismatic layer. The glycoprotein layer is a direct continuation of the nacreous layer of the neck but in dry shells it is not preserved. Thus the connecting ring in *Spirula* is composed of two layers similar to those in *Nautilus*: an outer spherulitic-prismatic layer and an inner glycoprotein (chitin) layer (compare Text-fig. 3A with 3B).

The number of layers in the septal neck and connecting ring has been a matter of disagreement. The prismatic siphuncular layer is here interpreted as the inner layer of the septal neck (see also Schwarz 1895; Mutvei 1964, 1997*a*; Dauphin 1976), but according to Doguzhaeva (2000) this layer ('spherulitic-prismatic' layer) belongs to the subsequent connecting ring. Our study shows that in adult shells this layer is either incompletely developed or absent on the inner surface of the last formed septal neck, but in more juvenile shells, it is often present (pr; Text-fig. 3D). In addition, the prismatic layer extends a short

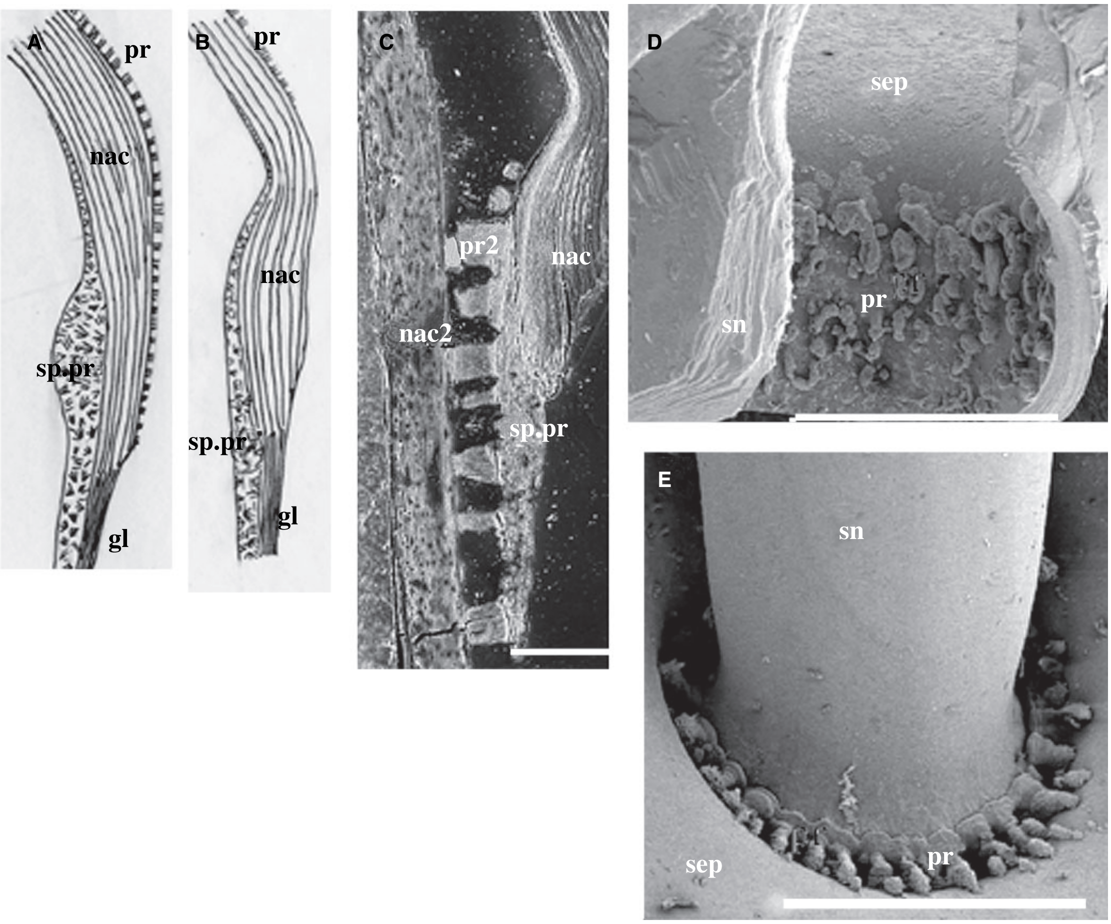


TEXT-FIG. 2. A–E, *Megateuthis gigantea* (Schlotheim). A, median section of two consecutive septal necks (sn) and two superimposed connecting rings (conn1, conn2); × 20. B, close-up of A to show direct continuation of septal neck (sn) into connecting ring (conn2); superimposed connecting rings (conn1, conn2) are separated by a porous prismatic layer (sph); × 40. C, connecting ring (conn) in higher magnification to show its lamellar structure and pores; × 60. D, septal neck (sn), connecting ring (conn) and porous prismatic layer (sph); × 20. E, diagrammatic section of siphuncular wall in three last-formed chambers; note that each connecting ring extends through two chambers and that in the last chamber the siphuncular wall was incomplete.

distance to the septal surface (pr; Text-fig. 3E; see also Schwarz 1895, h, fig. 1; Mutvei 1964, s.pr1, pl. 21, fig. 4) indicating that it belongs to the septum and its septal neck. A similar, porous, prismatic layer in *Nautilus* covers not only the inner surface of the septal neck but also the adoral surface of the septum (pr; Text-fig. 3A). Thus, the septal neck and connecting ring in *Spirula* are composed of layers that are structurally similar to those in recent *Nautilus*.

EVACUATION OF CAMERAL LIQUID

In Recent *Nautilus*, the secretion of a new septal neck and connecting ring is completed when the last septum has only attained half of its final thickness (Ward 1987; Mutvei and Doguzhaeva 1997). The secretory epithelium of the siphonal cord then undergoes histological and functional



TEXT-FIG. 3. A, *Nautilus pompilius* L. Diagrammatic median section of septal neck composed of outer spherulitic-prismatic (sp.pr), nacreous (nac) and inner prismatic (pr) layers, and connecting ring composed of outer spherulitic-prismatic (sp.pr) and inner glycoprotein (gl) (conchiolin) layers. B–E. *Spirula spirula* (L). B, diagrammatic median section of septal neck and connecting ring to show that they consist of layers similar to those in *Nautilus*; inner glycoprotein (gl) layer of connecting ring is not preserved in dry shells. C, median section of septal neck with two layers (sp.pr, nac), and connecting ring with one layer (sp.pr); prismatic layer (pr2) and nacreous layer (nac2) on left-hand side belong to preceding septal neck. D, inner surface of last septum (sep) and its septal neck (sn) with prismatic layer (pr) in still-growing shell. E, oblique view of adoral septal surface (sep) with inner prismatic layer (pr) and next younger septal neck (sn). Scale bars represent 0·1 mm in C and 0·5 mm in D and E.

changes, and begins to remove osmotically the cameral liquid from the last-formed shell chamber (Ward 1987). Consequently, emptying of the last-formed chamber of cameral liquid in *Nautilus*, with the possible exception of the last four chambers at maturity, takes place as soon as possible in order to maintain neutral buoyancy of the animal. In Recent *Spirula spirula* and in the majority of fossil nautiloids the evacuation of the cameral liquid in the last chamber probably took place as in *Nautilus*.

In the belemnitid *Megateuthis gigantea* (Text-fig. 2E), and in the aulacoceratid *Mojsisovicsteuthis*?, the permeable siphuncular wall in each chamber is composed of two superimposed connecting rings from consecutive septa. This means that the evacuation of cameral liquid from the last chamber was delayed and could first take place after the connecting ring of the next septum was completed. The buoyancy of the phragmocone was, therefore, somewhat reduced by temporary retention of cameral liquid. In the phragmoteuthid *Phragmoteuthis huxleyi* (Text-fig. 1C) the permeable siphuncular wall was under construction in the last 5–6 chambers and therefore incomplete. Consequently, these chambers must have been completely filled by cameral liquid and did not contribute to the buoyancy of the phragmocone. The evacuation of cameral liquid could begin first in the sixth or seventh chamber after the siphuncular epithelium changed its function from shell secretion to osmotic evacuation of cameral liquid.

In the case of Belemnitida such as *Megateuthis*, with relatively short chambers, delay in emptying the last-formed chamber was not going to have a serious effect on buoyancy. The case of *Phragmoteuthis huxleyi* is different. With relatively few (30–35?; Donovan 2006) chambers in a breviconic phragmocone, the last five or six chambers constitute more than 50 per cent of the total volume of the phragmocone, so that while they remained liquid-filled, less than half the phragmocone could contribute to buoyancy. Thus the buoyancy system in *P. huxleyi* could be regarded as relatively inefficient. It is possible that, after growth of the phragmocone had ceased, the anterior part of the siphuncle changed its function to withdraw liquid from the last-formed chambers.

COMPARISONS AND DISCUSSION

In Recent *Nautilus*, and in fossil Nautilida and Tarphycerida nautiloids, each connecting ring consists of an outer spherulitic-prismatic layer and an inner, fibrous, glycoprotein (conchiolin) layer, the latter being a structurally modified and uncalcified prolongation of the nacreous layer of the adjacent septal neck. In fossil taxa the inner glycoprotein layer is practically entirely destroyed by diagenesis and its presence is only indicated by the arrangement and direction of the growth lines in the septal neck (Mutvei 2002*b*). In fossil nautiloids Orthocerida and Actinocerida, on the other hand, the inner layer of the connecting ring is wholly calcified and perforated by numerous pore canals (Mutvei 1998, 2002*a*, *b*). The nautiloid taxa with the two different types of connecting rings show distinct differences in number and position of muscle scars indicating differences in anatomy and mode of life.

In most fossil coleoids the structure of the siphuncular wall is still imperfectly known. However, it is justified to assume that differences in connecting ring structure in fossil coleoids are similar in taxonomic importance to those of fossil nautiloids. As shown in this study, three different structural types can be distinguished at present: the phragmoteuthid, spirulid and belemnoid.

1. In the phragmoteuthid *Phragmoteuthis huxleyi* the connecting rings have a primitive, uncomplicated structure, unknown in other cephalopods. The siphuncular wall in each chamber is composed of 5–6 superimposed connecting rings from consecutive septal necks. Because each connecting ring was mechanically weak, several superimposed connecting rings were probably needed to give the siphuncular wall sufficient mechanical strength against hydrostatic pressure. The porous prismatic structure of the connecting ring was permeable for cameral liquid. The primitive connecting ring structure indicates that phragmoteuthids were not closely related to other coleoids.
2. In Recent *Spirula* most of the siphuncular wall is composed of consecutive, solid and long septal necks. In the connecting ring only a mechanically weak spherulitic-prismatic layer was previously distinguished (Mutvei 1964, 1997*a*; Dauphin 1976). However, as shown above, the connecting ring also consists of an inner thin, glycoprotein layer, not preserved in dry shells. Thus the connecting ring structure agrees with that of Recent *Nautilus* in being composed of spherulitic-prismatic and glycoprotein layers. In *Nautilus* the septal neck is short and the connecting ring is long. The inner glycoprotein layer of the connecting ring alone withstands high hydrostatic pressures. The rates of osmotic removal of cameral liquid is low (Ward and Martin 1978; Ward 1987) although higher flow rates of this liquid across the connecting ring have been experimentally demonstrated (Chamberlain and Moor 1982). Consequently, *Nautilus* cannot change the amount of cameral liquid in the chambers for daily vertical migrations (Ward 1979, 1987; Ward and Martin 1978). In *Spirula* the long septal necks can withstand high hydrostatic pressures (Denton and Gilpin-Brown 1971). The connecting ring is exposed only in a narrow interspace between every two consecutive septal necks where the exchange of the cameral liquid takes place. As pointed out by Denton *et al.* (1967, p. 188) 'when *Spirula* is in its normal swimming position, this liquid will be almost completely de-coupled from the permeable region; we have already noted that in *Nautilus* and *Sepia* such a de-coupling probably has an important advantage'(see also Ward 1980). *Spirula* seems to make extensive daily vertical migrations (Clarke 1969) but how the osmotic exchange of cameral liquid across the connecting ring takes place in habitat depths of more than 1000 m is still unknown.

   In the fossil record of spirulids the connecting ring ultrastructure is still unknown. As shown herein, the similarity in the siphuncular structure indicates a relationship between living *Nautilus* and fossil nautilids and tarphyceratids.
3. A different structural type of the connecting rings occurs in the belemnoid *Megateuthis gigantea* and the aulacocerid *Mojsisovicsteuthis*? The permeable siphuncular wall in each chamber consists of two superimposed rings from consecutive septal necks. Each connecting ring is composed of a calcified layer that is a structurally modified continuation of the nacreous layer of the septal neck. It is perforated by numerous pore canals that probably housed epithelial extensions from the siphuncular cord. These extensions may have increased considerably the surface area of the osmotically-active epithelium of the siphuncular cord. Calcified and perforated connecting rings in belemnoids and aulacoceratids show a certain resemblance with the calcified connecting rings in fossil nautiloid orthocerids and actinocerids. This may indicate a phylogenetic relationship between these taxa.

Acknowledgements. This paper has been considerably enhanced by the constructive reviews of P. Doyle and R. H. Mapes.

REFERENCES

BANDEL, K. 1985. Composition and ontogeny of *Dictyoconites* (Aulacocerida, Cephalopoda). *Paläontologisches Zeitschrift*, **59**, 223–244.

—— 1990. Cephalopod shell structure and general mechanism of shell formation. 97–115. *In* CARTER, J. G. (ed.). *Skeletal biomineralization: pattern, processes and evolutionary trends*. Van Nostrand Reinhold, New York, 832 pp.

—— and BOLETZKY, S. VON 1979. A comparative study of the structure, development and morphological relationships of chambered cephalopod shells. *Veliger*, **21**, 313–354.

CHAMBERLAIN, J. and MOORE, W. 1982. Rupture strength and flow rate of *Nautilus* siphuncular tube. *Paleobiology*, **8**, 408–425.

CLARKE, M. R. 1969. Cephalopoda collected on the SOND cruise 1965. *Journal of the Marine Biology Association of the United Kingdom*, **50**, 961–1000.

DAUPHIN, Y. 1976. Microstructure des coquilles de Céphalopodes. I. *Spirula spirula* L. (Dibranchiata, Decapoda). *Bulletin du Muséum National d'Histoire Naturelle, Sciences de la Terre*, **54**, 197–238.

DENTON, E. J. and GILPIN-BROWN, J. B. 1971. Further observations on the buoyancy of *Spirula*. *Journal of the Marine Biology Association of the United Kingdom*, **51**, 363–373.

—— —— and HOWARTH, J. V. 1967. On the buoyancy of *Spirula spirula*. *Journal of the Marine Biology Association of the United Kingdom*, **47**, 181–191.

DOGUZHAEVA, L. A. 2000. The evolutionary morphology of siphonal tube in Spirulida (Cephalopoda, Coleoidea). *Revue de Paléobiologie, Genéve, Volume Spécial*, **8**, 83–94.

DONOVAN, D. T. 2006. Phragmoteuthida (Cephalopoda: Coleoidea) from the Lower Jurassic of Dorset, England. *Palaeontology*, **49**, 673–684.

LANG, W. D. and SPATH, L. F. 1926. The Black Marl of Black Ven and Stonebarrow, in the Lias of the Dorset coast. *Quarterly Journal of the Geological Society of London*, **82**, 144–165.

MUTVEI, H. 1964. On the shells of *Nautilus* and *Spirula* with notes on the shell secretion in non-cephalopod molluscs. *Archiv för Zoologi*, **16**, 221–278.

——1970. Ultrastructure of the mineral and organic components of molluscan nacreous layers. *Biomineralization*, **2**, 48–72.

—— 1971. The siphonal tube in Jurassic Belemnitida and Aulacocerida. *Bulletin of the Geological Institutions of the University of Upsala*, **2**, 27–34.

—— 1997*a*. Siphuncular structure in Ordovician endocerid cephalopods. *Acta Palaeontologica Polonica*, **42**, 375–390.

——1997*b*. Characterization of actinoceratoid cephalopods by their siphuncular structure. *Lethaia*, **29**, 339–348.

——1998. Siphuncular structure in a Silurian narthecoceratid nautiloid cephalopod from the island of Gotland. *GFF (Geologiska Föreningens i Förhandlingar)*, **120**, 375–378.

——2002*a*. Connecting ring structure and its significance for classification of orthoceratid cephalopods. *Acta Palaeontologica Polonica*, **47**, 157–168.

——2002*b*. Nautiloid systematics based on siphuncular structure and position of muscle scars. 379–392. *In* SUMMESBERGER, H., HISTON, K. and DAUER, A. (eds). *Cephalopoda – present and past*. Abhandlungen der Geologischen Bundesanstalt, **57**, 569 pp.

—— and DOGUZHAEVA, L. A. 1997. Shell ultrastructure and ontogenetic growth in *Nautilus pompilius* L. (Mollusca: Cephalopoda). *Palaeontographica A*, **246**, 33–52.

SCHWARZ, E. H. L. 1895. *Spirula peronii*, Lam. *Journal of Marine Zoology and Microscopy*, **2**, 25–30.

WARD, P. D. 1979. Cameral liquid in *Nautilus* and ammonites. *Paleobiology*, **5**, 40–49.

——1980. Restructuring the chambered *Nautilus*. *Paleobiology*, **6**, 247–249.

——1987. *The natural history of* Nautilus. Allen & Unwin, Boston, 267 pp.

—— and MARTIN, A. 1978. On the buoyancy of the Pearly *Nautilus*. *Journal of Experimental Zoology*, **205**, 5–12.