Restudy of some plectronocerid nautiloids (Cephalopoda) from the late Cambrian of China; discussion on nautiloid evolution and origin of the siphuncle

Harry Mutvei

To cite this article: Harry Mutvei (2020) Restudy of some plectronocerid nautiloids (Cephalopoda) from the late Cambrian of China; discussion on nautiloid evolution and origin of the siphuncle, GFF, 142:2, 115-124, DOI: 10.1080/11035897.2020.1739742

To link to this article: https://doi.org/10.1080/11035897.2020.1739742

Published online: 30 Apr 2020.

Submit your article to this journal

Article views: 70

View related articles

View Crossmark data
Restudy of some plectronocerid nautiloids (Cephalopoda) from the late Cambrian of China; discussion on nautiloid evolution and origin of the siphuncle

Harry Mutvei

Department of Paleobiology, Swedish Museum of Natural History, Stockholm, Sweden

ABSTRACT
The sub-class Nautiloidea is divided into two super-orders, Nautilosiphonata and Calciosiphonata, based on different structural types of the connecting rings.

The late Cambrian order Plectronocerida has the calciosiphonate type of connecting ring similar to that in post-Cambrian orthocerids. It is structurally more complex than the nautilosiphonate connecting ring in late Cambrian ellesmerocerid-like nautiloids. The plectronocerid nautiloids, therefore, evolved from the ellesmerocerid-like nautiloids and not vice versa. As indicated by the complex siphuncular structure in plectronocerids, cephalopod evolution began earlier than previously estimated, probably in the early Cambrian. The siphuncle in cephalopods originated from a calcareous septum that became partially non-calcified and formed the connecting ring.

Introduction

The nautiloid cephalopods appeared in the late Cambrian and were most numerous in China where Chen & Teichert (1983) recorded more than 160 species belonging to four orders: Plectronocerida Flower (1964), Protactinocerida Chen and Qi (1979), Yanhecerida Chen & Qi (1979), and Ellesmerocerida Flower (1964). Chen & Teichert (1983) described 40 species, and summarized previous studies on the Cambrian cephalopods. Fang et al. (2018) summarized the palaeogeographic distribution and diversity of cephalopods during the Cambrian–Ordovician transition. Mutvei et al. (2007) established that the siphuncular structure of late Cambrian plectronocerids is of the calciosiphonate type, similar to that of the Ordovician orthocerids. In the present paper, the shell structure in some plectronocerids is restudied. The evolution of nautiloid cephalopods and the origin of the siphuncle are discussed.

Definition of nautiloid super-orders Nautilosiphonata and Calciosiphonata

The siphuncular structure has great importance for classification of shelled cephalopods, and reconstruction of their evolution. Nautiloid cephalopods are divided into two super-orders, Nautilosiphonata and Calciosiphonata, which are characterized by different siphuncular structures (Mutvei 2015, 2016). These super-orders were already established by the late Cambrian (Mutvei et al. 2007).

Nautilosiphonata is characterized by the Nautilus type of connecting ring, composed of two layers: an outer calcareous layer of spherulites and prisms, and an inner conchiolin layer of chitinous membranes (Fig. 1A). Both layers are permeable for water molecules and they function together as an osmotic membrane through which the volumes of cameral liquid in the shell chambers are regulated. In all fossil Nautilosiphonates hitherto studied by the present writer, the chitinous membranes in the inner conchiolin layer are destroyed by diagenesis (Fig. 1B). In the extant Nautilus, the conchiolin layer is semi-elastic and therefore not sufficiently rigid to form expanded connecting rings. This was probably also the case in the fossil Nautilosiphonates that had similar type of connecting rings. The only exception is the nautilosiphonate order Discocerida in which the outer spherulitic-prismatic layer of the connecting ring has a compact, sufficiently strong structure to form expanded connecting rings (Mutvei 2013). The Nautilosiphonate type of the connecting ring has hitherto not been reported in fossil coleoids.

In the ellesmerocerid-like nautiloids from the late Cambrian (see below) the siphuncle is strongly recrystallized and its structure less well preserved than that in the calciosiphonate Plectronoceras. However, as far as can be judged from the illustrations by Chen & Teichert (1983, Pl. 6) the siphuncle strongly resembles to that in the Nautilosiphonates.

ARTICLE HISTORY
Received 16 October 2019
Accepted 29 January 2020

KEYWORDS
Late Cambrian; China; calciosiphonates; plectronocerid nautiloids; ellesmerocerid-like nautiloids; siphuncular structure; cephalopod evolution; origin of siphuncle

Material

The late Cambrian nautiloids, dealt with in the present paper, were described previously by Chen & Teichert (1983) and Mutvei et al. (2007). The material is deposited in the Nanjing Institute of Geology and Palaeontology, China (NIGPAS). The siphuncular structure of plectronocerid nautiloids is compared with that of an Ordovician orthocerid nautiloid Archiogeisonoceras, deposited in the Swedish Museum of Natural History, Stockholm (NRM).

The structure of the shell wall and siphuncle was studied in unetched median and transverse sections that were polished with aluminium oxide. The preparations were studied with a Wild Photomikroskop M 400 at the Swedish Museum of Natural History, Stockholm.
Nautilosiphonata contains seven orders: Ellesmerocerida, Tarphycerida, Discocerida, Ascocerida, Oncocerida, Cyrcocerinida, and Nautilida (Mutvei 2013).

Also in Calciosiphonata the outer layer of the connecting ring consists of spherulites and prisms, but the chitinous membranes in the inner conchiolin layer are in places calcified and form walls (Mutvei 2016). Similar calcification of chitinous membranes gives rise to calcareous pillars in the siphuncles of extant Sepia and Spirula (Checa et al. 2015). The calcareous walls are oriented transversally to the siphuncular length axis and divide the inner layer into numerous cavities. The inner surface of the conchiolin layer, facing the shell

Nautilosiphonates: A, original structure, B, post-mortem structure. Calciosiphonates: C, original structure, D, post-mortem structure. E, F, Different siphuncular sizes in two late Cambrian orders: E, Plectronocerida (modified from Chen & Teichert 1983, Text-fig. 22) and F, Protactinocerida (modified from Chen & Teichert 1983, Pl. 14, Fig. 6).
chamber, is covered by a continuous calcareous wall that is perforated by numerous pores. The calcified-perforate layer was mechanically strong and was able to form expanded connecting rings. Calciosiphonates probably gave rise to a new type of the connecting ring in which the conchiolin layer had changed its chemistry and structure: it became resistant against diagenesis and was perforated by numerous pores. Besides, the outer spherulitic-prismatic layer is absent. This new type occurs in ammonoids (Mutvei et al. 2004; Mutvei & Dunca 2007; Doguzhaeva et al. 2010), in several coleoid taxa (Mutvei et al. 2012; Mutvei & Mapes 2018; Mutvei & Mapes 2019), and in the eoctococlate order Mixosiphonata (Mutvei 2017).

Because the inner conchiolin layer of the connecting ring in plectronocerids contains calcified walls it was mechanically strong and formed highly expanded siphuncular segments (Figs. 2, 5, 6A, B). This increased the length of the connecting ring in each shell chamber, and increased its capacity to participate in buoyancy regulation. Because of its highly complex structure, it is difficult to assume that the plectronocerid connecting ring was primitive and gave rise to the connecting ring in ellesmerocerid-like nautiloids.

According to Chen & Teichert (1983, p.40), *Plectronoceras* has a “very simple” shell structure, and it “closely approximates the reconstruction of the hypothetical “ancestral cephalopod”. Wade et al. (1993, Fig. 12.8E) published a reconstruction of the siphuncular structure in a plectronocerid from the late Cambrian of Australia. This structure is almost identical to that in the Chinese plectronocerids. Also Wade (1988, Fig. 1) and Wade et al. (1993, Fig. 12.2) interpreted plectronocerids as ancestral coleoids.

The super-order Calciosiphonata contains six orders: Plectronocerida, Protactinocerida, Mixosiphonata, Orthocerida, Actinocerida, and Barrandeocerida (Mutvei 2016).

**Differences between the late Cambrian calciosiphonate orders plectronocerida and protactinocerida**

The two orders of the late Cambrian calciosiphonates are: Plectronocerida Flower (1964) and Protactinocerida Chen & Qi (1979) (Chen & Teichert 1983). According to Chen & Teichert (1983, p. 74), Protactinocerida “resembles the Plectronocerida in most features, differing, however, from the latter in its much larger siphuncle with more expanded segments”. However, as shown in numerous illustrations, published by Chen & Teichert (1983), plectronocerids have the same relative siphuncular diameter as most protactinocerids. The siphuncular diameter in both orders varies from 1/5 to 1/7 of the shell diameter (Fig. 1E). Therefore, Mutvei et al. (2007) assigned Protactinocerida to the order Plectronocerida. However, in two species of *Protactinoceras* (Chen & Teichert 1983, pp. 74–75, Plates 3:4; 7:9; 14:4,6), the siphuncle is “very large, having a diameter equivalent to half the diameter of the conch”. Because the longitudinal sections of the shells in the two specimens are paramedian, the median siphuncular diameter may be still larger, probably up to 2/3 of the shell diameter (Fig. 1F). The two species of *Protactinoceras*, characterized by exceptionally broad siphuncles, are, therefore, retained in Protactinocerida whereas the remaining protactinocerid taxa, described by Chen & Teichert (1983), are included in Plectronocerida. Shells with a siphuncular diameter half that of the shell are typical for Palaeozoic actinocerids. The siphuncular diameter is even larger in the Eocene coleoid *Antarcticeras nordenskjoeldi* (Doguzhaeva et al. 2017, Fig. 1F).

**Shell structure in Cambrian calciosiphonate plectronocerids**

As pointed out by Chen & Teichert (1983, pp. 49, 50), all Cambrian cephalopods from China occur in hard limestone from which they cannot be extracted. Because the shells are mostly very small and more or less curved, it is practically impossible to section them medially. The siphuncular structure in different taxa is, therefore, difficult to compare.

**Shell and shell wall**

According to Chen & Teichert (1983), the shell in plectronocerids is mostly conical and endogastrically curved. In most taxa, the shell is very small, from 18–30 mm in length. The shell wall is recrystallized and consists of two layers: a thin outer layer and a thick inner layer. The inner layer incorporates indistinct, narrow sectors, oriented transversely to the shell length axis (Fig. 3C).

**Septa and septal necks**

The septum and the septal neck are much thinner than the shell wall, about 1/4 of the wall thickness (Fig. 5; Chen & Teichert 1983, Plates 5:5; 9:2,7; 13:3,4). In all specimens they are completely recrystallized (Figs. 3A, B, 5). The shell chambers are very narrow (Fig. 4). As noted by Flower (1964), Chen & Teichert (1983) and Wade et al. (1993), the septal neck has a contrasting shape on different siphuncular sides. It is holochonitic on the mid-dorsal side (Figs. 2D, H, 3A). Towards the lateral siphuncular sides its length gradually decreases (Figs. 2C, 3B), and on the lateral and ventral sides it becomes short and cyrtochoanitic (Figs. 2B, E, H, 5).

**Connecting rings**

The connecting ring is very short between the subsequent holochonitic septal necks on the dorsal siphuncular side (Figs. 2D, H, 3A). On the dorsolateral and lateral siphuncular sides, it is strongly expanded (Figs. 2B, C, G, 6A, B) but becomes less expanded on the ventral siphuncular side (Figs. 2E, H, 5).

In contrast to the recrystallized shell wall and septum, in many cases the connecting ring is well preserved structurally and has a brownish colour (Figs. 3B, 5, 6A, B). It is of the calciosiphonate type (see above) and consists of two layers. The inner layer is a direct continuation of the principal layer of the septal neck. As in other calciosiphonates (Fig. 1D), it consists of cavities separated by calcareous walls (Fig. 6A, B). The cavities were originally traversed by chitinous membranes that became destroyed by diagenesis (Fig. 1C). This structure is similar to the calciosiphonate connecting rings in post-Cambrian orthocerids, actinocerids and barrandeocerids (compare Fig. 6B and Fig. 6C;
Figure 2. A-H. Schematic presentation of the shape of the septal neck and connecting ring on different sides of a siphuncular segment.
As in other calciosiphonates, the outer layer of the connecting ring is a porous spherulitic-prismatic layer. It is as thick as the inner layer and consists of numerous, small, calcareous crystals (Fig. 6B).

**Diaphragms**

Calcareous diaphragms seal off the posterior part of the siphuncle (Fig. 4). They are about as thin as the septa (Fig. 5). In some parts of the siphuncle, they are separated by the same intervals as the septa, but in other parts they are crowded or have long intervening intervals (Figs. 4, 5).

**Late Cambrian ellesmerocerid-like nautiloids**

According to Chen and Teichert (1983), ellesmerocerids were numerous in the late Cambrian of China and constituted half of the cephalopod fauna. Most ellesmerocerids have a breviconic to orthoconic, endogastrically curved shell with marginal or submarginal siphuncle. In several taxa, the shell is as small as in electronocerids. The septal necks are orthochoanitic to loxochoanitic, and the connecting rings are cylindrical and of variable thickness. In most taxa, the siphuncle contains diaphragms (Chen & Teichert 1983, p. 55, Pl. 10:2). As judged from the illustrations published by Chen & Teichert (1983, Pl. 6) the siphuncular structure is poorly preserved. As in the nautilisphonate type of siphuncle (see above), only the outer spherulitic-prismatic layer of the connecting ring seems to be partially preserved, but not the inner conchiolin layer.

Cambrian ellesmerocerids are consistent with Ordovician ellesmerocerids in their longitudinal shell shape and marginal, tubular siphuncle. However, the Ordovician ellesmerocerids have numerous features that are not known in Cambrian ellesmerocerids. These are: (a) multiple muscle scars around the base of the body chamber, (b) contracted aperture; and (c) concave connecting rings in many taxa (Kröger 2007; Mutvei 2013). Until their shell structure is better known, the Cambrian ellesmerocerids are assigned to the ellesmerocerid-like nautiloids.

According to Chen & Teichert (1983, p. 47), the late Cambrian cephalopod fauna in China also includes a small order Yanhecerida Chen & Qi (1979). This order differs from the ellesmerocerid-like nautiloids only by “the conical shape of the diaphragms”. However, the main function of the diaphragms was to seal off the posterior part of the siphuncle. They did not participate in the osmotic pumping function of the siphuncle, and have a low taxonomic significance. The order Yanhecerida is, therefore, abolished and included in the ellesmerocerid-like nautiloids.

**Discussion**

**Evolution of nautiloids**

**Previous hypothesis**

Numerous hypothesis have been proposed for the origin of cephalopods. Yochelon et al. (1973) and Webers and Yochelson (1989) were of the opinion that the Middle Cambrian monoplacophorans, represented by *Knightocomas*, were “directly ancestral” to the

![Figure 3. A. Mastoceras qiushugouese. Holochanitic septal necks on mid-dorsal siphuncular side (same specimen as in Chen & Teichert 1983, Pl. 13, Fig. 3), x40. B. Physalactinoceras globosum. Hemichoanitic septal necks on dorso-lateral siphuncular side (same specimen as in Chen & Teichert 1983, Pl. 12, Fig. 7), x40. C. Theskeloceras benxiense. Longitudinal section of ventral shell wall (same specimen as in Chen & Teichert 1983, Pl. 4, Fig. 1, 4), x60.](image_url)
earliest known cephalopod *Plectronoceras* from the late Cambrian. According to Kröger et al. (2011, p. 4) “it can be assumed that the cephalopod ancestral state resembled a benthic monoplacophoran-like mollusc with high conical shell”. Dzik (1981, p. 161) supposed that cephalopods “evolved from planctic monoplacophorans possibly related to the circothecid hyoliths.” However, the hyolithid origin of cephalopods was refuted by Landing and Kröger (2012). Smith and Caron (2010, 2011) and Smith (2019) suggested that cephalopods originated from an early Cambrian soft bodied organism *Nectocaris*. According to Smith (2019), nectocarids are characterized by an axial mantle cavity, anterior funnel, internal gills, eyes, tentacles and lateral fins. Based on these characters nectocarids were classified as coleoids and as ancestral cephalopods (Smith 2019). This interpretation was opposed by Kröger et al. (2011), Runnegar (2011) and Mazurek and Zaton (2011). Instead, Runnegar (2011, p. 373) and Kröger et al. (2011, p. 5) suggested that nectocarids belonged to “some other animal phylum that has convergently developed a mode of life similar to coleoid cephalopods”.

**New theory of origin of cephalopods based on origin of siphuncle**

As pointed out by Mutvei et al. (2007), the two nautiloid super-orders Nautilosiphonata and Calciosiphonata already existed in the late Cambrian. As shown above, the calciosiphonate type of connecting rings in plectronocerids was structurally more complex than the nautilosiphonate type of connecting rings in ellesmerocerid-like nautiloids (compare Fig. 1A, C). Ellesmerocerid-like nautiloids were, therefore, more primitive than plectronocerid nautiloids and gave origin to plectronocerid nautiloids. Most nautiloids from the late Cambrian are considerably smaller than the subsequent Ordovician nautiloids. It is probable that the shell in the oldest nautiloids was still smaller, maybe only a few mm in length and, therefore, difficult to recognize. Because of the structurally advanced connecting rings in the late Cambrian plectronocerids, nautiloid evolution must have begun much earlier than the late Cambrian, probably in the early Cambrian.

The cephalopod shell differs from the shells in all other molluscs by having a siphuncle. Previous hypothesis of origin of cephalopods (see above) were unable to explain the origin of siphuncle. As pointed out by the present writer (Mutvei 1964, p. 377), the connecting ring in the extant *Nautilus* is a non-calcified extension of the septal nacreous layer and consists of chitinous membranes (conchiolin) (see also Mutvei et al. 2010, Fig. 1). The origin of the siphuncle in ancestral nautiloids probably involved the following scenario.

1. The shell was originally small, orthoconic and had a single septum that sealed off the apical part of the shell cavity from the body chamber. A part of the
Figure 5. Same specimen as in Fig. 3C to show the siphuncle and ventral shell wall in higher magnification.
septum was non-calcified and consisted of chitinous membranes that were continuous with similar membranes in the calcified septum. The non-calcified part of the septum was the initial connecting ring. It functioned as an osmotic membrane through which the liquid in the apical chamber was osmotically pumped out, making the animal buoyant (Fig. 7A).

(2) During the course of evolution, the initial connecting ring gradually increased in size and formed a tubular, adapical extension of the septum. This extension was the initial siphuncle. It contained the siphuncular cord that originated from the septal epithelium and contained blood vessels (Fig. 7B). During growth of the shell, the soft body moved forwards in the body chamber and the siphuncular cord grew in length. After an interval, the septal epithelium secreted a new septum and septal neck, and the epithelium on the siphuncular cord secreted simultaneously the connecting ring (Fig. 7C). This made it possible to regulate the volumes of cameral

Figure 6. Structural similarity of the calciosphonate connecting rings in A. late Cambrian pleonocerid Physalactinoceras cf. globosum (same specimen as in Chen & Teichert 1983, Pl. 15, Fig. 2) and B. Ordovician orthocerid Archigeisonoceras folkeslundense (specimen NRM Mo 322304).
liquid in several shell chambers by osmosis, and the cephalopods became efficient vertical migrants.

Thus, the ancestral cephalopod had a single septum from which the siphuncle originated during evolution. This theory does not support previous hypotheses according to which the cephalopods originated from different pre-existing taxa.

Acknowledgments

The author thanks Dr. Xiang Fang, Nanjing Institute of Geology and Palaeontology for valuable contributions, Dr. Steve McLouglin and Dr. Christian Skovsted, Swedish Museum of Natural History, Stockholm, for improvement of the manuscript, and the two reviewers, Dr. Björn Kröger, Finnish Museum of Natural History, Helsinki University, and an anonymous reviewer for valuable suggestions.

Disclosure Statement

No potential conflict of interest was reported by the author.

References


Flower, R.H., 1964: The nautiloid order Ellesmeroceratida (Cephalopoda). *New Mexico Institute of Mining & Technology, Memoire* 12, 164.


Mutvei, H., 2015: Characterization of two new superorders nautilosiphonata and calciosiphonata and a new order cyrtocerinida of the subclass

---

**Figure 7.** Schematic presentation of the origin of cephalopod siphuncle from a single septum.


