SPECIAL ARTICLES

THE EARLIEST KNOWN CEPHALOPODS

FORMERLY the Holochoanites, including the endoceroids and piloceroids, were regarded as the most primitive cephalopods. Later discoveries, however, showed that they are by no means the earliest cephalopods, and that their structure is not simple. While in the Holochoanites the lower part of the siphuncle is occupied by a close succession of funnel-shaped endocones, the corresponding part of the earliest known cephalopods is free from deposits of any kind.

The oldest genus referable to the cephalopods is *Volborthella* from the lower Cambrian of the Baltic areas of Europe. In this genus the conch is straight, the siphuncle is central in location, and Schindewolf[1] has shown that the septal necks are short and relatively straight.

Next in age are several species of *Plectronoceras,*[2] occurring in the Upper Cambrian of northeastern China and Manchuria. In this genus the conch is curved lengthwise, the siphuncle is located close to the concave side of the conch, and Kobayashi[3] has shown that the septal necks are short with their lower margins curved strongly outward, as in the Cyrtochoanites.

In *Plectronoceras,* no connecting rings are present in the intervals between the successive septal necks, and no deposits are found in the interior of the siphuncle. Apparently the absence of these features is to be regarded as primitive, the introduction of connecting rings and of deposits within the interior of the siphuncle taking place at later stages of development.

Cephalopods with lamellae or tabulae crossing the interior of the siphuncle in a transverse direction make their appearance first in the Middle Ozarkian and become relatively abundant in the Upper Ozarkian. Among genera already described are *Levisoceras, Burenoceras, Dakeoceras, Ectenoceras* and *Clarkoceras.* They belong to the group of Diphragmida, proposed by Hyatt for his genus *Diphragmoceras,* and now known to include about ten other genera. In all but one of these genera the conch is curved lengthwise, the siphuncle is located close to the concave side of the conch, and the tabulae occur in series along the lower part of the siphuncle at distinct intervals from each other. The tenth genus, *Robsonoceras,* is founded by Ulrich and Foerste on the species *Ellesmereoceras robsonense* Walcott. It presents a similar series of tabulae, but the conch is straight, and the siphuncle is located close to the side regarded as ventral.

In these Diphragmida the concavity of the tabulae usually is small or at least moderate. In some cases they are sufficiently deep to suggest blunt endocones. In no case, however, are these endocones so closely crowded as to form an apparently continuous series, nor are their central parts ever narrowed downward into a relatively acute point, nor connected by a narrow, vertical, continuous tube, corresponding to the endosiphotube of the Endoceratidae. In this sense the Diphragmida may be regarded as more primitive than the Holochoanites, though making their appearance subsequent to forms in which deposits within the interior of the siphuncle are entirely absent.

In the Upper Ozarkian, the Diphragmida are accompanied by various Endoceratidae, one of the chief divisions of the Holochoanites. In these, the conch is straight, the siphuncle is large and marginal, and the lower part of the siphuncle is occupied by numerous funnel-shaped endocones crowded so closely together as to suggest a continuous deposit, though on close examination the individual endocones often can be distinguished readily. The lower pointed ends of these funnel-shaped endocones are connected together by a continuous, narrow, central, vertical endosiphotube extending as far downward as the apical end of the siphuncle.

Similar funnel-shaped endocones occur in the Piloceratidae, which differ from the Endoceratidae chiefly in the lengthwise curvature of their relatively short conchs and in the location of their siphuncles close to the concave side of the conch. Endosiphotubes may be present, but their existence has not yet been established in an altogether satisfactory manner. Their distribution is Upper Canadian.

A peculiar type of structure occurs within the siphuncles of *Protocycloceras,* also of Canadian age. In this genus the siphuncle is more central in location, though usually not located in the exact center of the conch. The lower part of the siphuncle is occupied, as in the Holochoanites, by a close succession of transverse lamellae, but these lamellae are not funnel-shaped. In a dorsoventral direction, they slope downward at a very steep angle from the ventral toward the dorsal side of the siphuncle. Parallel to their length these lamellae are straight, but in a lateral direction they arch more or less distinctly upward along their median parts.

Another peculiar type of structure is that presented by *Buttsoceras,*[4] a genus proposed by Ulrich and Foerste, and founded on *Orthoceras adamsi* Butts,

[1] O. H. Schindewolf. *Paläontologische Zeitschrift,* Vol. 10, pp. 68–89, 1928.

[2] Genus proposed by Ulrich and Foerste and based on *Cyrtoceras cambria* Walcott, described in "Research in China," Carnegie Institution of Washington, Vol. 3, p. 98, 1913.

[3] Teichii Kobayashi. Personal communication, still unpublished.

[4] Charles Butts, "Geology of Alabama," pl. 18, figs. 22, 23, 1926.

from the uppermost Upper Canadian. In this genus the conchs are straight, the location of the siphuncle is central, the septal necks are short, connecting rings are present, all in conformity with the structure of the Orthochoanites, but in several specimens the center of the siphuncle is occupied by a long central tube, slowly tapering downward. This tapering of the central tube is in such close conformity with the tapering of the walls of the enclosing siphuncle, remaining equidistant from the latter on all sides, so as to preclude any possibility of the tube being merely some extraneous body accidentally washed into the open end of the siphuncle in its original condition after the death of the animal. Unfortunately, the homology of this tube remains uncertain, since in no specimen has its upper end been observed in contact with the inner walls of the siphuncle.

The Holochoanites include those conchs in which the septal necks extend downward at least for the length of one camera, their lower ends invaginating into the top of the neck immediately beneath. In this suborder Hyatt included not only the endoceroids and piloceroids but also the Diphragmida. However, two occurrences among the Diphragmida suggest that their structure may have been not holochoanoidal but ellipochoanoidal, the latter term having been introduced by Hyatt for siphuncles in which the septal necks are short and must be supplemented by connecting rings in order to produce a continuous siphuncle. For instance, several specimens from the central mineral area of Texas, apparently referable to *Levisoceras,* not only show the transverse tabulae within the siphuncle but also segments of the siphuncle which are composed of short septal necks and intermediate connecting rings. Both surfaces of the septal necks are sharply defined from the adjacent matrix, but those of the connecting rings apparently diffuse rapidly into the latter so that no sharp line exists between the rings and the matrix. Moreover, the substance of the connecting rings is slightly lighter in color than that of the septal necks. In that case the Diphragmida could originate from forms similar to those occurring in the Cambrian which have no connecting rings by the addition of connecting rings and tabulae.

A similar occurrence of short septal necks with intermediate connecting rings occurs in the orthoconic genus *Robsonoceras,* another member of the Diphragmida.

In the Texan Diphragmida here described the septa curve downward only slightly on approaching contact with the siphuncle, this downward curvature being too slight to merit the name of *neck.* They certainly are not orthochoanitic and the term aneuchoanitic (without neck) here is proposed for structures of this type.

The structure of the siphuncle of the Holochoanites may have originated by the prolongation of septal necks originally short until their lower margins invaginated into the necks immediately beneath. Since connecting rings are formed subsequent to the formation of the septal necks a holochoanitic structure could originate either from forms with or without such rings. However, the origin of the endocones of the Holochoanites could be explained more readily if ascribed to derivation from the transverse tabulae of the Diphragmida by a deepening in the concavity of these tabulae, and an enormous increase in the number of the latter, resulting in their crowding into a continuous mass. In that case the continuous vertical endosiphotube connecting the apexes of the endocones is an added feature.

Protocycloceras was referred by Hyatt to the Orthochoanites, a group of ellipochoanoidal conchs with relatively straight septal necks and connecting rings which are not expanded conspicuously. Such a reference may have been suggested by the subcentral location of its siphuncle, but is nullified by the presence of a continuous series of strongly oblique transverse lamellae or tabulae within the interior of the latter, this structure being more suggestive of the Holochoanites, though here the location of the siphuncle usually is marginal or nearly so.

In *Buttsoceras* the siphuncle is central in location and its structure also is ellipochoanoidal as in the Orthochoanites. There are short septal necks and intermediate connecting rings. But the much elongated central tube is an anomalous feature which might be an aberrant form of endocone but whose true nature at present remains unknown.

Cyrtoceroids and nautiloids with siphuncles located on the convex side of the conch made their first appearance in the Upper Canadian. Those in which the siphuncle is located on the concave side of the conch at mature stages of growth show a more ventral location at the apical end of the conch, suggesting that they are derivatives from forms in which the location of the siphuncle was on the convex side.

Although *Volborthella* in the central location of its siphuncle suggests relationship with the Orthochoanites, true Orthochoanites are not known until the Chazyan. In a similar manner, although the form of the septal necks of *Plectronoceras* suggests relationship with the Cyrtochoanites, true Cyrtochoanites also do not make their appearance until the Chazyan. The derivation of the Orthochoanites and Cyrtochoanites undoubtedly invites speculation, but at present few facts are known to serve as a basis for such speculation.

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