TERMS FOR THE SHELL-ELEMENTS IN THE HOLOCHOANITES.

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In 1918, at the meeting of the Palæontological Society of America, I first advanced the proposition that the shell of the Holochoanites (*Proterocameroceras*, *Cameroceras*, *Endoceras*, *Vaginoceras* etc) was not the homologue of the shell of the Orthochoanites (*Orthoceras* etc) but that it was only the so-called siphuncle of the former that was to be compared with the shell of the Orthoceran. The so-called endosiphosheaths were held to be the homologues of the Orthoceran septa, and the endosiphuncle or endosiphotube, the homologue of the Orthoceran siphon. A summary together with discussions (chiefly unfavorable) was published in the proceedings of that meeting in 1919.[1] This thesis was elaborated and dealt with somewhat at length in my paper on Ordovician Fossils from North China published April 28, 1922, in a section dealing with the Phylogenetic significance of the "Siphuncle" of the Holochoanites.[2] Meanwhile in 1921 Dacqué[3] independently advanced the same idea, and as I had done, derived the Orthochoanites and the Holochoanites independently from the Cambrian genus Volborthella, which Dr. Shimer and I had proposed to place in the order Protochoanites.[4] Dacqué however ranked that genus with the Orthochoanites.

Troedsson in 1926[5] reviewed these interpretations and came to the conclusion that the geologically younger *Orthoceras* group (not found according to Foerste below the Chazy) is a specialized derivative from the older Holochoanites. *Orthoceras* he says "is nothing but a life form well adapted for swimming. The structure of its septal necks indicates a close relationship with the whole Ordovician—Silurian group of nautiloids, while it is more difficult to trace its affinity to the Cambrian genus *Volborthella*, in which septal

1. A. W. Grabau. Relation of the Holochoanites and the Orthochoanites to the Protochoanites and the significance of the Bactritidae. Bull. Geol. Soc. America Vol. 30, 1919, pp. 148-149.
2. Palæontologia Sinica Ser. B. Vol. I, Fascicle 1, especially pp. 53-63.
3. E. Dacqué: Vergleichende biologische Formenkunde der fossilen niederen Tiere, Berlin 1921.
4. A. W. Grabau and H. W. Shimer North American Index Fossils Vol. II, 1910. p. 39
5. Gustaf T. Troedsson; On the Middle and Upper Ordovician Faunas of Northern Greenland, I. cephalopods. Jubilaeumsekspeditionen Nord om Grönland, 1920-23, No. 1, Kopenhagen. See especially pp. 14-24.

foramina are not known with certainty". In this latter respect he follows Schuchert, who in the discussion of my earlier paper questioned the existence of siphuncular foramina in the septa of *Volborthella*, a question, which as we snall see, has since been settled in the affirmative by Schindewolf. Troedsson concludes.

"For these reasons I cannot agree with Dacqué or Grabau in claiming that *Orthoceras* is a direct descendant of *Volborthella*, and that the siphuncle of *Orthoceras* is homologically different from that of *Endoceras*. On the other hand, they are certainly right in recognizing the *Volborthella* conch structure in the siphuncle of the Endoceratidæ."

That *Volborthella* is really an Orthoceroid type was shown in 1928 by Schindewolf[6] from the study of some hundreds of individuals and 30 thin sections made from selected specimens, although hardly a dozen of these proved available for detailed study. Nevertheless he was able to demonstrate that in this typical species from the Lower Cambrian Eophyton sandstone of Esthonia, the snell is a normal orthoceran with inverted, broadly conical, rather than concave septa, and with a median siphuncle, the septa being prolonged into short siphonal necks.

The total length of these minute organisms is not over 10 mm, of which the camerated part occupies about 7 mm. The greatest diameter measured was 2 mm and the rate of tapering 1 mm in 4 mm. The septa are conical and regularly divide the shell into cameræ. These average 0.5 mm in depth where the diameter is 1 mm, increasing slightly with the increase in diameter and becoming slightly less where the diameter decreases. In section it is seen that the septa make angles of 55 to 60 degrees with the conch walls.

The siphon is centrally situated, and short straight collar-form siphonal funnels project from the under side of the septa around the foramen. Where the diameter of the shell is 1 mm, the siphonal foramen has a diameter of 0.15 mm; at 1.4 mm it is 0.2 mm and at 2 mm shell diameter it is 0.3 mm. Thus the siphuncle occupies usually about 1/7th of the shell diameter. In addition to the siponal funnels, there appears in some cases to be a connecting membrane, this being indicated when the siphuncle is filled with an apparently independent reddish brown or brownish black mass.

There can then be no further doubt that *Volborthella* represents a true Orthochoanite cephalopod, characteristic of the Cambrian, and the Order Pro-

6. O. H. Schindewolf: Ueber *Volborthella tenuis* Schm. und die Stammesgeschichte der ältesten Cephalopoden. Palaeontologische Zeitschrift, Band 10, Heft 1, 1928, pp. 68-86. With discussions pp. 87-89.

tochoanites, based primarily on the supposed absence of siphonal funnels and the simple piercing of the septa by a foramen, must be abandoned for those organisms, though it might still be retained for a hypothetical type with such neckless septa, should such a form be found one day.

Schindewolf rejects our suggestion of the homologies of the Orthoceran shell with the "Gross-sipho" of the Holochanite but discusses at some length the question of derivation of the Endoceran "sipho" (Endoconch see below) from *Volborthella*, the conical septa of which suggest the conical "endosiphosheaths" (endo-septa see below) of the Endoceran. He, however, points out that the cameræ of the "siphuncle" of the Holochoanites are never so regular as are those of *Volborthella*, being sometimes distant at others crowded together. Nor are they usually symmetric and centran as are the conical septa of *Volborthella*. Furthermore the cones of the Holochoanites are much steeper and longer than the conical septa of *Volborthella*, making angles from 5 to 10 degrees with the wall of the "Siphuncle" (endotheca) whereas the septa of *Volborthella* make angles of 55 to 60 degrees with the shell wall. Corresponding to this the apical angle of the cones in the Holochoanites does not exceed 20°, whereas in *Volborthella* it averages 120°. Again the filling by stereoplasm of the spaces between the cones (endocameræ) so common in the Holochoanites is not found in the cameræ of *Volborthella*. Finally the siphonal funnels of *Volborthella* have no parallel in the "siphuncle" (endoconch) of the Holochoanites, although the continuous siphonal tube of the former recalls the endosiphotube of the latter.

Schindewolf concludes that for the reasons enumerated even the *Volborthella* shell can not be regarded as the homologue of the Holochoanite "Gross-sipho" (endoconch) but that, like the *Orthoceras* shell it is the homologue of the entire shell of the Holochoanite. Thus we have returned to our original starting point, and the argument has to begin all over again. For it appears that both Troedsson and Schindewolf, like others before them, have failed to give due consideration to the important subject of the ontogeny of the primitive Holochoanites. However, I am ready to eliminate *Volborthella* from the direct ancestry of the Holochoanites since it has now been shown that it is a true Orthochoanite. I do not have such difficulty as Schindewolf finds in deriving the longer conical endosepta of the Holochoanites from the shorter broader cones, the septa of *Volborthella*, which in another direction may become reduced to the concave septa of the Orthoceran shell. Nor do I see an nsurmountable obstacle in the presence of the stereoplasmic filling, for it should be obvious that in any case a stereoplasmic filling is a secondary feature indicating a further specialization.

As well might we assert that orthoceran forms with the cameræ filled by streoplasm such as *Stereoplasmoceras* and others, could not have been derived from Orthoceran types with empty cameræ. But I do find a serious difficulty in deriving the endosiphuncle (endosiphotube) of the Holochoanites from the siphuncle of Volborthella because of the septal funnels in the latter. These indicate a specialization not reached by the endosiphuncle, unless we consider that in the latter the funnels have been prolonged to form a continuous tube. I am ready to accept *Volborthella* as a true Orthoceran, especially in view of the fact that *Salterella* of the Lower Cambrian has proved to be another one (see below). This merely removes the common ancestor of the two orders (if common ancestor there was) to an earlier, still undiscovered simpler type, which we may continue to designate as the now hypothetical Protochoanite.

Before taking up the discussion again, I desire to present a more precise terminology for the different structural units of the Holochoanite shell one that does not prejudge the case by assuming homologies which may or may not exist. I believe this terminology is also simpler and less cumbersome than the one hitherto in use. These terms are as follows:

1. *Ectoconch* The outer shell with its air-chambers (*ectocameræ*) and septa which is usually homologized with the shell of *Othoceras*, but which I consider to be a new structure built around the original shell which thus becomes the Endoconch.
2. *Endoconch.* The inner shell with its septa and siphuncle generally spoken of as the large siphuncle and commonly homologized with the siphuncle of *Othoceras*, but which I consider the homologue of the entire shell of *Othoceras*. In primitive forms such as *Proterocameroceras* it is alone present in the young stage and has generally been spoken of as the pre-septal cone.
3. *Ectotheca.* The wall or shell, in the restricted sense, of the ectoconch, exclusive of the septa or other internal structures.
4. *Endotheca.* The wall or shell proper of the Endoconch. The so-called endosipholining of authors. It is present in primitive forms but becomes lost in specialized types.
5. *Ectosepta.* The septa of the ectoconch.
6. *Endosepta.* The more or less funnel-shaped septa of the endoconch. The endo-siphosheaths of authors. These I consider to be the homologues of the septa of *Orthoceras*.

7. *Tubus*. (Plural *tubi*) The tube-like prolongations of the ectosepta which surround the endoconch and in the specialized types replace the endotheca. These have generally, though as I believe, erroneously been homologized with the siphonal funnels of *Othoceras*. These tubi may be of various lengths and we may distinguish the two following types.
   a. *Tubus continuous*. When the tube extends to the preceding septum ex: *Endoceras*.
   b. *Tubus invado*. When the tube extends to a greater or less distance within the preceding tubus. ex: *Vaginoceras*.
   c. A Third type *Tubus discontinuous*, in which the tubes do not reach the preceding ectoseptum may or may not exist. At present it is unknown.
8. *Endosiphuncle*. The median siphuncle of the endoconch, comparable to, and in my view homologous with, the siphuncle of *Othoceras*, though of a more primitive character.
9. *Endocone*. The terminal conical living chamber of the endoconch. Formed by the last endo-septum. The endosiphocone of authors.
10. *Endocylinder*. The cylindrical tube which in some specialized forms continues from the lip of the endocone to the terminal ectoseptum. It is usually lined by the tubi only, and is due to the more rapid growth of the ectonch, which leaves the endoconch behind.
11. *Endocameræ*. The chambers limited by the endosepta of the endoconch. Generally they are filled in solidly with stereoplasm.

In the discussion of the relationships of the Orthochoanites and the Holochoanites, a fundamental point has been commonly left out of consideration, namely the ontogeny of the latter. Both those who would derive the Holochoanites from an Orthoceran ancestor by the enlargement and specialization of the siphuncle, and those who would consider *Orthoceras* as derived from an Endoceran or similar Holochoanite by the simplification of the siphuncle, have entirely neglected to take into consideration the stages in development of the primitive Holochoanite, and the light which they throw upon the evolution of these forms.

Proterocameroceras of the Lower Ordovician of North America and China represents one of the most primitive of the Holochoanites known. It begins with the so-called "pre-septal cone", which may become six inches in length before the ectoconch makes its appearance. The preseptal cone is the endoconch appearing by itself, and only after it has reached a certain length does it become enclosed within the newly built ectoconch. In other words, in these primitive Holochoanites the endoconch appears first and for a certain period of time is the only shell in existence. In the language of the older terminology, there is at first only a siphuncle surrounded by a definite shell-wall of its own (our endotheca) and at a later stage the cameræ, septa, and shell-wall, develop around it. This much is well understood and has previously been described. I am merely expressing it in a different set of terms thus: *Proterocameroceras* when young, is purely an endoconch, with a wall or endotheca of its own and presumably with the conical endosepta, for we can hardly assume that the primitive shell will be a hollow tube six inches long and that the filling by endosepta and stereoplasm is a later addition, after the outer shell or ectoconch has appeared.

When the ectoconch makes its appearance it encloses the endoconch, but not medially, the latter remains rather close to one side. The ectoconch has its own shell or ectotheca, while in these primitive forms the endoconch retains its shell (endotheca) even after it is enclosed by the ectoconch. But in this later stage the endotheca does not remain free; it is closely surrounded by the successive tubi, which connect the septa (ectosepta) of the outer shell or ectoconch.

In the next more specialized genus *Cameroceras* the free part of the endoconch is very short, the ectoconch appearing almost from the beginning and enclosing it. Nevertheless, the endoconch retains its own shell (endotheca, endosipholining of authors), but in still later, more specialized genera such as *Endoceras*, this endotheca becomes suppressed, at least in the later stages. Whether it is present or not in the young *Endoceras* has I believe never been ascertained, but one might assume that in the least specialized species of *Endoceras*, this inner wall might still be present in the young stage. In the adult, however, the tubi, entirely replace it, the endoconch remaining without a wall of its own.

If, as we firmly believe, ontogeny is a guide to phylogeny, then we cannot escape the conclusion that the free portion of the young *Proterocameroceras*, the most primitive of the Holochoanites, represents the characteristics of the adult ancestral form, or in the older terminology: it is the 'preseptal cone" which gives us the characteristics of the ancestral shell, and an adult shell entirely comparable to this preseptal cone (or free endoconch) should occur in Cambrian strata.

Such a shell should consist, as does the free endoconch (preseptal cone), of a distinct shell (endotheca) enclosing conical endocameræ limited by conical endo-septa and pierced by a median endo-siphuncle. In other words this ancestor should have a shell which is neither an Orthoceran nor an Endoceran type, differing from the former in its deeply conical septa and absence of septal funnels, and from the latter in the absence of the outer septated ectoconch. Whether or not such a primitive shell has its cameræ (endocameræ) filled with stereoplasm, is of little moment, for the ability to produce such a filling may be, and probably was, a subsequent acquisition. Types in which the cameræ were empty might well have lead a floating or swimming existence. But when, perhaps because of an excess of secretion of lime, stereoplasm was deposited upon the septum and continued to form until the time arrived for the building of the new septum, then the cameræ became solid. The resulting weight of the entire shell would force the animal to lead a benthonic and probably a sedentary life. It is this which, in the struggle for existence, favoured those individuals which had acquired the habit of building a new enlarged shell with air chambers, around the solid heavy endoconch. For such individuals would be less likely to be submerged by their own weight in the mud of the sea bottom. The new conch would be built principally around the sides and top, for the contact of the ventral side with the sea bottom would prevent the development of the shell there, to any marked degree. This would account for the position of the endoconch on the ventral side of the ectoconch, a position so characteristic of nearly all the Holochoanites.

Returning to the primitive ancestral form of the Holochoanites for which, though it has not yet been discovered with certainty, I have coined the generic name *Teilhardoceras*[7], we may give it the following characteristics.

Slender, conical shells, divided into chambers by steeply conical septa, the apices of which are incomplete, thus forming a median tube without however, prolongations, comparable to the septal funnels of the Orthochoanites. Terminal living chamber formed by the last conical septum and the prolongation of the shell beyond it.

Such shells would certainly not be ancestral to *Orthoceras*, nor would an Orthoceran be likely to be derived from a shell of this type. As long as we believed *Volborthella* to have its conical septa merely pierced at the apex, it

7. This name has been provisionally applied to certain Cambrian shells found by Pere Teilhard de Chardin in Shansi, which suggest such a structure as here postulated for the primitive Holochoanites. However the material is not complete enough to make the diagnosis a definite one.

seemed that it satisfied the requirements of such an ancestral shell, even though the septa were less conical than we now postulate for the hypothetical *Teilhardoceras*. But now that *Volborthella* is known to have septal necks, it must be referred to the Orthochoanites as a primitive and probably ancestral type of Orthoceran. That such types are common in the Cambrian, even in the Lower Cambrian, is indicated by the recent discoveries by Thomas H. Clark[8] of the fact that typical *Salterella* of the Lower Cambrian rocks of Labrador shows the characteristic Orthoceran structures.

Foerste[9] has expressed the opinion, that so far no true Orthochoanites or Cyrtochoanites are known from rocks older than the Chazy i. e. the Middle Ordovician, the older Ordovician rocks containing only Holochoanites. Now that both *Volborthella* and *Salterella* of the Cambrian rocks are recognized Orthoceran types, this statement no longer holds. Moreover Dr. Y.C. Sun of the Chinese Geological Survey has discovered in the uppermost Cambrian beds of Shantung, a layer filled with large Orthoceracones and Cyrtoceracones. Though strongly compressed, they show typical Orthoceran characteristics and in the few cases in which the siphuncle is exposed, it is a narrow tube, totally different from those found in the Holochoanites. These specimens have not yet been studied in detail, but there can be little doubt that they are representatives of the Orthochoanites. Indeed, they probably belong to the genus *Orthoceras*, with which the form and size of the shell and the character of the septa agree.

If the Holochoanites and the Orthochoanites have a common ancestor, that ancestral type probably lived in pre-Cambrian time. If it had a shell, this probably had moderately conical septa without septal necks. The septa perhaps had a form intermediate between those of *Volborthella* and of *Teilhardoceras*. By decrease in the chonicity and the development of septal necks *Volborthella*, the probable ancestral *Orthochoanite* would be produced. By increase in chonicity of the septa, without development of septal necks, *Teilhardoceras* would be produced which in time would give rise to the specialized group of Holochoanites.

It is quite possible that the development of the two groups proceeded in geographically independent centers. If the present distribution is a clue to the centers of radiation the Holochoanites may have developed in the Indian Ocean for they are extremely abundant in the Ordovician of South China and

8. Bulletins of American Palæontology, Vol. X, No. 41, 1924.

9. Quoted by Troedsson p. 19.

may be traced along the Ordovician geosynclines to Europe on the one hand, and through the Cathaysian geosynclines to the Boreal region, and thence to North America, on the other.

The center of distribution of the Orthochoanites may have been the Boreal Sea, for both *Volborthella* and *Salterella* are characteristic, the former of the Atlantic and the latter of the Boreal early Cambrian. The presence of the Orthoceran shells in the Upper Cambrian of Shantung is not out of harmony with this interpretation, for these shells are associated with Boreal types of Cambrian organism.

These statements, however, must be taken as mere suggestions and guides to future study which may or may not substantiate their validity.