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STRUCTURES AND PHYLOGENY OF ACTINOCEROID CEPHALOPODS.

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INTRODUCTION.

The following pages are mainly devoted to a résumé of the results of former studies of the present writer, which recently have been published in German (1933). These results were reached by observations on North American and Canadian actinoceroid cephalopods. Still more recently (1934) additional facts have been uncovered by a study of actinoceroids from North Greenland. The chapter on phylogeny, however, is original.

NOMENCLATURE.

Part of the nomenclature pertaining to the Actinoceroids has been compiled and redefined by Foerste and Teichert in 1930. As the study of the actinoceroid structures advanced it became necessary to introduce a number of new terms designating so far unknown, insufficiently known, or disregarded facts and features of the representatives of this group.

Already Foerste and Teichert proposed to call the outwardly curved part of the septal neck the *brim*. The area of contact between the lower surface of the connecting ring and the immediately underlying septum was called the *adnation area*, whereas the part of the connecting ring which is free from contact with the upper as well as with the lower septum was called the *free part of the connecting ring*. Below are listed terms designating new features which have been discovered or extensively described by the present writer, in his detailed study of the actinoceroid structures. For further explanation the reader is referred to the following pages and still more to the original paper (1933).

Contact layer (Kontaktschicht): a deposit, occasionally formed between the connecting ring and the septum, preventing an immediate contact of both.

False contact of the connecting ring is present, if there is a contact layer between the connecting ring and the septum.

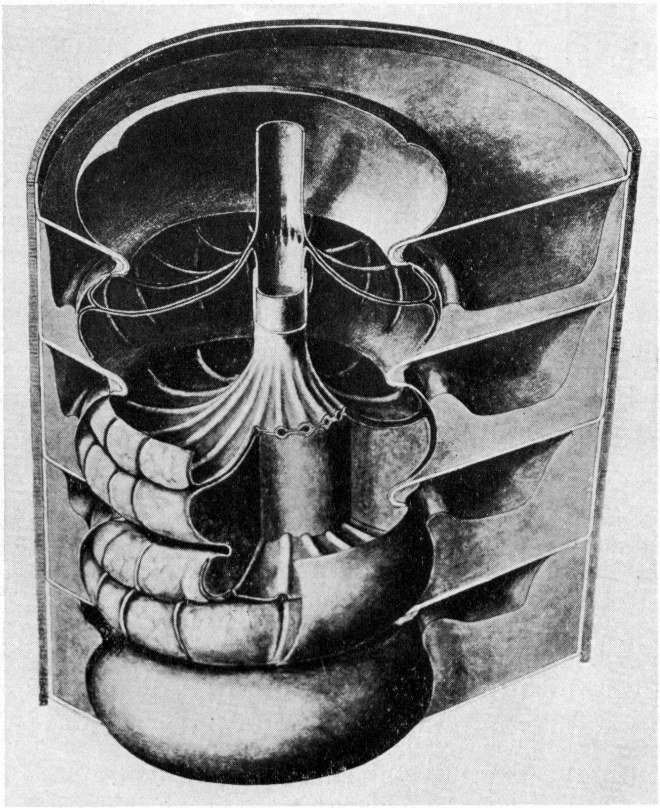

Fig. 1. Reconstruction of an Actinoceratoid shell of the type of *Actinoceras ruedemanni.*

Central obstruction deposits, mostly called "obstruction rings": solid deposits within the siphuncle (with the exception of the perispatial deposits).

Centrifugal type of obstruction rings: deposits first tending to fill out the marginal parts of the siphuncular segments.

Centripetal type of obstruction rings: developing first concentrically around the septal neck and rapidly constricting the septal foramen.

Endosiphuncular tissue: hypothetical organic tissue, by calcification of which the so-called obstruction rings are supposed to have originated.

Maximal stage of growth of the obstruction deposits: the stage of growth beyond which no further development of obstruction deposits is possible, because all of the endosiphuncular tissue is calcified.

Pseudoendocone: the space which is left free between the obstruction deposits of the centrifugal type in the upper part of the siphuncle; without significance for the explanation of the organic structures of the endosiphuncle.

Perispatium: free space between central obstruction deposits (or endosiphuncular tissue) and connecting ring.

Perispatial deposits: deposits in the upper and lower end of the perispatium, developing when the entire space of the perispatium is no longer needed.

Mural part of the septum: that part of the septum which is attached to the inner side of the shell.

Intracameral deposits: deposits of solid material within the air chambers, "*primary*" when developed during the life of the animal by organic action, "*secondary*" when built afterwards by inorganic infiltration.

Episeptal deposits: primary deposits on the upper side of the septum and along the mural part of it.

Circumsiphuncular ridge (Zirkumsiphonale Leiste): thickening of episeptal deposits in the immediate neighborhood of the connecting ring.

Hyposeptal deposits: primary deposits on the lower side of the septum.

Supporting ring (Stützring): primary deposit on the concave outer side of the septal neck.

The diagrammatic sketch on Fig. 2 shows as many of these essential features as possible.

CLASSIFICATION.

A provisional classification of the Actinoceroids was first undertaken by Hyatt in 1900, who divided them into *Loxoceratidae*, *Uranoceratidae*, and *Actinoceratidae*. After the establishment in recent years of a number of new genera as

Armenoceras, *Elrodoceras* and others by Foerste, Troedsson pointed out the peculiarity of the entire armenoceroid group, characterized by short septal necks, proposing tentatively a new family *Armenoceratidae*.

This was adopted by Foerste and Teichert in 1930, who furthermore rearranged the then known genera in a new classificatory attempt.

Results of more recent studies made necessary a few additions and changes. A closer study of specimens assigned to *Discosorus* and allied genera (Teichert, 1931) forced the present writer to remove this group from the Actinoceroids. They were regarded as a distinct family, consisting of *Discosorus* Hall, *Stokesoceras* Foerste, and *Endosicosorus* Teichert, with doubtful affinities, but certainly not belonging to the Actinoceroids.

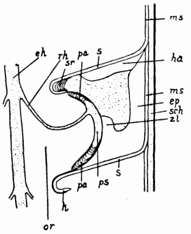

Fig. 2. Diagrammatic sketch, showing the most important features of the siphuncle and air chamber of an actinoceroid. ek, endosiphuncular tube; rk, radial canal, or obstruction ring; ps, perispatium; pa, perispatial deposits; s, septum; k, brim; ms, mural part of the septum; sch, shell; ep, episeptal deposits; zl, circumsiphuncular ridge; ha, hyposeptal deposits; sr, supporting ring.

In 1933 the present writer regarded *Westonoceras* as a type of a new family then being the only genus of it. Since then another genus closely related to *Westonoceras* and belonging to the same family has been described by Foerste as *Teichertoceras*. At the same time *Maruyamaceras*, a new genus of the *Actinoceratidae*, has been established by Kobayashi and *Cyrtonybyoceras*, a new armenoceroid, by the present writer. Furthermore, study of the type material of *Calhounoceras* Troedsson has convinced the writer that this genus was rightly placed by Troedsson among the Actinoceroids. Its more exact position, however, is uncertain. The scheme given below follows essentially the arrangement published in 1933 with the necessary additions according to our increased knowledge:

Actinoceratidae Hyatt
  Actinoceras Bronn
  Kochoceras Troedsson
  Maruyamaceras Kobayashi
  Paractinoceras Hyatt
  Rayonnoceras Croneis
  Saffordoceras Foerste and Teichert
  Troostoceras Foerste and Teichert
Armenoceratidae Troedsson
  Armenoceras Foerste
  Cyrtonybyoceras Teichert
  Elrodoceras Foerste
  Megadiscosorus Foerste
  Nybyoceras Troedsson
  Selkirkoceras Foerste
Huroniidae Foerste and Teichert
  Huronia Bigsby
  Huroniella Foerste
  Discoactinoceras Kobayashi
Gonioceratidae Foerste and Teichert
  Gonioceras Hall
  Lambeoceras Foerste
Sactoceratidae Troedsson
  Cyrtactonoceras Hyatt
  Deiroceras Hyatt
  Ormoceras Stokes
  Sactoceras Hyatt
Westonoceratidae Teichert
  Westonoceras Foerste
  Teichertoceras Foerste
  Calhounoceras Troedsson (of doubtful position)

This classification is certainly not to be regarded as final, but it is based on our present knowledge and may moreover contribute towards an understanding of the phylogeny of the Actinoceroids. Particularly the family *Sactoceratidae* needs further research, as also the family *Huroniidae* does.

SHELL MORPHOLOGY.

THE SIPHUNCLE.

a. *The Connecting Ring.*

As is well known the ectosiphuncle of ellipochoanitic cephalopods consists of the septal necks and of the connecting rings between the septal necks. The connecting ring attaches itself at the end of the brim and approaches the next following septum in a varying distance from the septal neck, sometimes in contact with the septum around the septal foramen along an adnation surface as defined by Foerste and Teichert in 1930. It follows the entire septal neck, gradually thinning out towards the outer edge of the brim, where the new connecting ring begins. With regard to the nature of the connecting ring two features are of importance: 1, the connecting ring is in most cases considerably thinner than the septum, 2. the connecting ring is made up of a material different from that of the septum. It is reasonable to assume that the connecting ring of the actinoceroids consisted of a material similar to that of the connecting ring of the living *Nautilus.*

We may speak of an *upper adnation surface* and a *lower adnation surface,* when the septum is in contact with the upper or the lower septum respectively. In some cases a dense layer is intercalated between the connecting ring and the septum along the adnation surface, which has been called the "*adnation layer,*" causing a "*false adnation surface.*"

On account of its delicate nature the connecting ring is frequently destroyed during or after the deposition of the shell into the sediment,[1] or during the process of weathering. The sometimes poor state of preservation is mainly responsible for the opinion maintained by a number of authors that the connecting ring should be perforated by foramina, serving the exchange of gas or fluids between the siphuncle and the air chambers. A careful examination of well-preserved specimens, however, always results in the observation that such foramina do not exist. It can be shown that under favorable conditions of imbedding and fossilization no trace of foramina in the connecting rings can be discovered, and the supposed existence of foramina in certain specimens is due to some formerly unknown peculiarities of the so-called obstruction rings which will be discussed on the following pages.

b. *The "Obstruction Rings."*

The deposits within the siphuncle which are long known as obstruction rings, exhibit a considerable variability in appearance. In many cases they appear as evenly shaped ring-like

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[1] It can, therefore, be questioned whether the absence of connecting rings in specimens of the Upper Cambrian genus *Plectronoceras* really has to be regarded as a primitive feature (Ulrich and Foerste, 1933) or rather is due to the mode of preservation.

deposits around the septal neck, but the expression obstruction "rings" is hardly justified in the great number of cases, where those deposits are rather irregular in shape and sometimes, especially in the older segments of the siphuncle, arranged in an extremely complicated manner.

It has been the prevailing opinion that these obstruction rings began to develop in the "open space" of the siphuncle as the animal grew older and that more or less incidentally they did not happen to occupy finally the entire interior of the siphuncle, leaving free certain parts known as the endosiphuncular tube and the radial canals or diverticula. The latter were sometimes thought to stand in connection with the supposed openings in the connecting rings, the absence of which has just been mentioned. A closer examination of the shape of the endosiphuncular tube and particularly of the arrangement of the radial canals and related features leads to an entirely different view upon the subject.

A most important peculiarity of the obstruction ring deposits is that they never touch the inner side of the connecting rings in any considerable extent, except on those parts of the connecting rings which are adnate to the septum. The free part of the connecting ring remains free from contact with deposits situated within the siphuncle. The open space left between the obstruction rings and the connecting ring has been called *perispatium* and is regarded as a very important feature in connection with the explanation of the endosiphuncular structures of the actinoceroids.

A comparative study of different genera of actinoceroids reveals that the perispatium is represented in every specimen where, according to the prevailing conditions of preservation, it can be reasonably expected to be preserved. Naturally, where the connecting ring is removed by invading matrix, the perispatium cannot be preserved.

It can clearly be shown that the possibilities of growth of the endosiphuncular deposits (obstruction rings) are limited to a certain space beyond which no further enlargement is possible. This is the entire space not occupied by the endosiphuncular vascular system and the perispatia. This fact, of course, can best be seen in the lower part of the siphuncle where the obstruction rings have reached their maximal stage of growth. The upper part of the siphuncle, where the obstruction rings are still in the early stage of their development, furnishes no complete information pertaining to the structural details of the interior of the siphuncle. In the upper part of the siphuncle a more or less wide open space, later on filled with matrix, is left open by the not fully developed obstruction rings. While the obstruction deposits are enlarging from one segment to the other, this central space becomes narrower and in many cases its outer appearance is that of the endocone of the endoceroids. However, since the shape of this cone has no bearing upon the explanation of the anatomy of the siphuncle, I introduced the name *pseudoendocone* for it. The obstruction rings are of a "centrifugal type," when they first tend to fill out the marginal part of the siphuncle, they are "centripetal" when developing around the septal neck, thus first constricting the septal foramen. Only really ring-like deposits of this kind deserve the name "obstruction rings."

Another type of endosiphuncular deposits develops without any connection to the obstruction rings just discussed. These are deposits frequently to be found within the perispatium and they may conveniently be called *perispatial deposits.* Usually they develop during later stages after the obstruction deposits are more or less completed, though sometimes they can be found to grow at earlier stages of growth, when the deposition of obstruction-ring material is not yet entirely completed and the obstruction rings have not yet reached their maximal stage of growth. Perispatial deposits are always found in distinct layers indicating a progressive growth, when the open space of the perispatium, at least in its entire original extent, was not needed any longer.

c. *The Endosiphuncular Vascular System.*

When an investigation of the arrangement of the endosiphuncular deposits or rather of the arrangement and structure of the "open spaces" between these deposits is made, a system of canals and tubes reveals itself which is arranged in such a systematic manner that it is difficult to explain otherwise than by regarding it as something that originally must have been a system of vascular tubes.

These investigations started from a collection of actinoceroids, mainly consisting of species of *Elrodoceras*, from the Silurian Racine dolomite. These fossils were dolomitized in such a way that all parts, which were solid at the life-time of the animal, had been dissolved, at the present state of preservation, presenting open spaces, whereas all those parts, which were formerly open and became filled with matrix after the deposition of the shell into the sediment, were dolomitized and are now solid. Thus, within the siphuncle of these specimens we obtain a natural cast of the entire space, which has not been occupied by endosiphuncular or obstruction deposits. Though the process of dolomitization, of course, has destroyed many of the more delicate structures, those specimens give an excellent idea of the arrangement of the canals and tubes in the interior of the siphuncle. Studying these structures it at once becomes evident, that they are arranged in a conspicuously systematic manner.

In general it was possible to distinguish between several kinds of structural arrangement of the endosiphuncular tubes.

The simplest type is represented by *Actinoceras ruedemanni* Foerste and Teichert and related forms. At the passage of the endosiphuncular tube through the septal foramen or a little above, about 20 radial tubes diverge from the central tube and approach the perispatium evenly curved. To this type belong most species of *Actinoceras*, a larger group of *Armenoceras*, the members of the family *Huroniidae* and the genera *Kochoceras* and *Lambeoceras*.

Of a more complicated character is the endosiphuncular structure of *Nybyoceras* and others. In specimens of the *Nybyoceras* type the radial tubes present themselves in a system of arcs, sometimes arranged in a rather intricate manner. In some genera these arcs branch into several tubes when approaching the perispatium. Of the *Nybyoceras* type are the siphuncles of *Nybyoceras*, *Cyrtonybyoceras*, *Selkirkoceras*, of some species of *Armenoceras* and most probably of *Gonioceras*, though the latter is often simpler in structure.

The endosiphuncular structure of *Elrodoceras* has been regarded as a third type, which occupies an intermediate position between the two formerly mentioned. The radial tubes in *Elrodoceras* are distinctly arc-like, but they are in closer contact with the central tube than in *Nybyoceras* and similar forms.

Another type is represented by *Deiroceras* and a group of *Ormoceras*, showing a rather wide endosiphuncular canal and simple, straight, thin radial tubes which branch off from the central tube about in the middle plain of the segments.

In a number of genera as *Cyrtactinoceras*, *Paractinoceras*, *Megadiscosorus*, *Discoactinoceras* and others the structure of the siphuncle is too insufficiently known to permit any definite conclusions.

It is quite evident that these endosiphuncular structures cannot be regarded as mere openings within the siphuncle, left free in a more or less incidental way by the growing obstruction deposits. These systems of canals or tubes are so complicated, that it must be assumed, that they existed already long before the obstruction deposits were formed and that their origin is quite independent from the formation of the latter. Therefore, we arrive at the conclusion that the system of tubes within the siphuncle was once a *system of organic vascular tubes* during the life of the animal. The hypothesis is put forward, that this vascular system has been embedded in some kind of *organic tissue*, by calcification of which the so-called "obstruction rings" were formed and the organic tubes could be preserved in their original arrangement (Fig. 3).

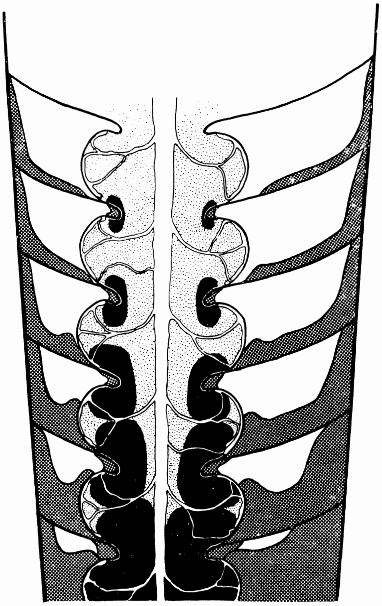


Fig. 3. Diagrammatic sketch, showing the development of "obstruction rings" by calcification of the endosiphuncular organic tissue. (White: endosiphuncular vascular system and free space within the air chambers. Stippled: endosiphuncular tissue. Black: calcified parts of the endosiphuncular tissue. Crossed: intracameral deposits.)

Both the vascular system and the organic tissue surrounding the latter must have had important organic functions, the nature of which we can only guess. It was necessary to transport solid material in a dissolved state through the porous walls of the segments into the air chambers in order to build intracameral deposits above and below the septa. Since the connecting rings do not possess foramina which could serve this purpose, the open space of the perispatium must have been of some importance for the transportation of fluids. In this way these could be evenly distributed all around the siphuncular segment and could continuously be pressed through the segmental wall.

According to the progressive growth of the animal the endosiphuncular tissue of the earlier segments became superfluous and gradually was calcified.

In the upper part of the siphuncle the calcification of the endosiphuncular tissue was not yet completed—the "obstruction rings" have not yet reached their maximal stage of growth. The tapering cone-like space in the upper part of the siphuncle, the pseudoendocone, which can be met within a number of actinoceroids, results from the incompleteness of the calcification of the endosiphuncular tissue in this part of the siphuncle. Here the vascular system cannot be found preserved in fossil state.

It is of importance that in some cases it has been observed that the structure of the "obstruction rings" is that of concentric lamellae (Teichert, 1934). This is a conspicuous analogy to the development of endosiphuncular sheaths in endoceroids. However, whereas the sheaths in endoceroids run parallel to the endocone and the latter originates by the cone-shaped form of the sheaths, the pseudoendocone of the actinoceroids results from an increase in number of lamellae in an apical direction, the form of the lamellae being approximately cylindrical.

The Intracameral Deposits (organic deposits, stereoplasma).

Only gradually first the presence, then the importance, of solid deposits within the air chambers has been realized. We know now that these deposits can be found within the shell of various groups of shell-bearing cephalopods, in Nautiloidea as well as in Ammonoidea, though seldom observed in the latter. In connection with the organic deposit of the septa the question of the nature of the "pseudoseptum" must be considered, the latter being an intermediate lining between two real septa, which frequently has been regarded as being of a similar nature as the true septa.

The question of the intracameral deposits and of the "pseudoseptum" has been given attention in earlier days by Woodward, Dewitz, Remelé, Mascke, Noetling, Blake, Holm, Meek and Worthen, Mojsisowicz and particularly by Barrande, later on by Hyatt and Pompeckj and more recently by Grabau, Croneis, Endo, Kobayashi and the present writer. Foerste and Teichert in 1930 doubted the validity of the "pseudoseptum" and the intracameral deposits in the use of classification. The latter view probably is still right. Kobayashi, when regarding the presence of intracameral deposits as an important feature of the actinoceroids, is quite right as far as the actinoceroids of Eastern Asia are concerned. This feature, however, loses much of its importance, when we turn to the actinoceroids of North America and Europe and no satisfactory explanation exists for the almost constant presence and regularity of the intercameral deposits among the Asiatic actinoceroids. Moreover, considerably large groups of decidedly non-actinoceroid cephalopods exhibit beautifully developed intracameral deposits as has been particularly well shown by the investigations of Barrande.

Considering the most important features of the intercameral deposits we can easily distinguish between three different kinds of them. The first one is deposited on the upper side of the septa and the term *episeptal deposits* has been proposed for them. Another kind is deposited on the lower surface of the septa and has been called *hyposeptal deposits*. Hyposeptal in its nature, but mostly independently developed, is a deposit along the outside of the septal necks, filling the concavity caused by the outward curvature of the septum. This layer is comparatively rare. When present, it usually does not stand in connection with the hyposeptal deposits. It has been given the name *supporting ring* ("Stützring"), because it is thought to strengthen the constriction of the siphuncle at the septal neck.

The episeptal deposits may occur alone or in connection with either the hyposeptal deposits or the supporting ring or both, but never do hyposeptal deposits develop alone. They do not even begin to form earlier than the episeptal deposits in case of both kinds of deposits being present. If both types of deposits develop, they either begin simultaneously or the episeptal deposits start earlier.

In many cases the episeptal deposits show a particularly remarkable growth along the outer side of the connecting ring, forming a distinct "*circumsiphuncular ridge*" around the segment of the siphuncle, elevated above the surface of the episeptal deposits in the rest of the camera. It is not known what the cause of this peculiar growth of the episeptal deposits in the vicinity of the siphuncle may be. But since the material, by which the deposits are built up, must be supplied from the interior of the siphuncle through the porous wall, it may be assumed that an especially large part of the material thus transported was precipitated in the immediate neighborhood of the siphuncle.

To understand the shape of the episeptal deposits it is necessary to investigate the shape and extension of the septa. Tracing these towards the wall of the conch one will find them to continue upward along the inner side of the wall of the conch for the entire length of the camera. This forward directed part of the septum has been called its *mural part.* It is quite evident that, if episeptal deposits are developed, they are to be expected to be found, not only upon the septa dividing the different camerae, but also along the side walls of the camerae, as deposited on the mural parts of the septa.

Speaking of intracameral deposits in general, one should be well aware of the fact that deposits within the air chambers can originate also by infiltration of inorganic matter after the deposition of the shell into the sediment. Deposits of such kind may be called *secondary deposits.* Their appearance is fundamentally different from that of the primary deposits. If the connecting ring is preserved, we may expect the secondary deposits to precipitate also along the latter, or, if the connecting ring is destroyed, the secondary deposits usually follow the entire septum around the septal neck. Of course, nothing of this kind could happen while the animal was still alive. Under normal circumstances there will be no trouble in distinguishing both kinds of deposits.

Shape and development of the primary intracameral deposits can be very different. In many cases they are but slightly developed in the lower part of the conch, increasing in thickness towards the middle part and again decreasing and sometimes disappearing in the uppermost camerae. Sometimes, however, we find the entire lower part of the conch filled out with solid deposits, gradually decreasing in size towards the upper end of the specimen. This is true for some Actinoceroids, but especially for a great number of Bohemian Orthoceroids as described by Barrande. The biologic purpose of the intracameral deposits must have been to balance the buoyancy of the air chambers. It still remains to be considered, why intracameral deposits, as it appears, are not a feature common to the majority of shell-bearing cephalopods.

Fig. 4 gives an idea of the variability in appearance of the intracameral deposits.

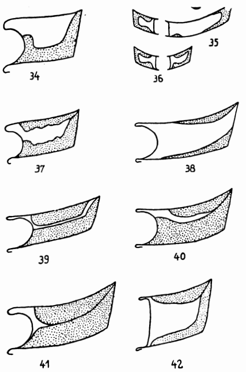


Fig. 4. Diagrammatic sketches of several types of intracameral deposits. 34. Episeptal deposits with circumsiphuncular ridge. 35. Intracameral deposits of *Westonoceras* in dorso-ventral section. 36. Intracameral deposits of *Westonoceras* in lateral section. 37. Episeptal and hyposeptal deposits with irregular surface. 38. Slightly developed episeptal and hyposeptal deposits. 39. Strongly developed episeptal and hyposeptal deposits as in some species of *Stereoplasmoceras* Grabau. 40. Strongly developed episeptal and slightly developed hyposeptal deposits as in some species of *Stereoplasmoceras* Grabau. 41. Chamber nearly completely filled with intracameral deposits and formation of a "pseudoseptum" as in *Rayonnoceras* Croneis. 42. Evenly distributed episeptal and hyposeptal deposits with beginning of a pseudoseptum.

Mode of Life.

A discussion of the mode of life of the Actinoceroids cannot be based on very safe conclusions. It is, however, reasonable to assume, that forms with very large and heavy siphuncles, forms which are known to have strongly developed intracameral deposits, and finally forms with a distinctly flattened ventral side show a decided adaptation to benthonic life. To this group we may assign the following genera:

Kochoceras and *Selkirkoceras*, large siphuncle, distinctly flattened ventral side.

Rayonnoceras, *camerae* and siphuncle almost entirely filled out by solid deposits.

Several species of *Actinoceras* and *Armenoceras* with wide siphuncles or abundant intracameral deposits.

A second group may have been capable of swimming, but perhaps mainly inclined to a benthonic life. Most species of *Actinoceras* and *Armenoceras*, *Nybyoceras*, the *Huroniidae*, *Gonioceratidae* and possibly *Saffordoceras*.

The curved Actinoceroids, all of them conspicuously lacking a distinct flatness of the ventral side, may have been mainly swimming: *Troostoceras*, *Elrodoceras*, *Megadiscosorus*, *Cyrtonybyoceras*, *Cyrtactinoceras*.

None of these develop intracameral deposits of any considerable extent, which also indicates a swimming mode of life. The same may be concluded for *Ormoceras*, *Deiroceras* and *Sactoceras*, on account of their usually small size, their rounded cross-section and their lack of intracameral deposits.

To the swimming forms certainly the *Westonoceratidae* must be added.

This tabulation shows that among the *Actinoceratidae* as well as among the *Armenoceratidae* both swimming and benthonic forms are represented. Phylogenetically the benthonic adaptation is very likely to be the primary one, whereas the swimming forms represent later branches, the development of which stands in close connection with degenerative processes of the siphuncle within certain groups of the Actinoceroids.

The benthonic forms, however, were the more or less persistent ones. The last representation of the Actinoceroids is the genus *Rayonnoceras* in the Mississippian of Oklahoma and the Lower Carboniferous of England. It is by far the largest Actinoceroid we know of and at the same time its endosiphuncular and intracameral deposits show such a hypertrophical development, that a benthonic life of that animal can be assumed with certainty.

Ontogeny.

An investigation of specimens of the genus *Kochoceras* from North Greenland brought to light a number of facts which disclose some of the main aspects of the ontogeny of the actinoceroids (Teichert, 1934). It is characteristic of actinoceroids that they do not taper to a point as the Endoceratidae and apparently many other straight forms do, but end bluntly.

The last segment of the siphuncle is of about the same size as the following segments. In some instances it is inconsiderably smaller, but in other cases it is somewhat larger than the next-following one. This first segment occupies the greater part of the initial chamber. The rate of enlargement of the diameter of the conch is comparatively little.

It follows, that the actinoceroid animal possessed a rather large size when it began to secrete a solid conch. Its body was certainly considerably larger than that of orthoceroids and particularly of nautiloids at the same stage of their development. At the same time with the formation of the first septum the creation of the first siphuncular segment took place, which was very large in comparison with that part of the body, which at that time occupied the living chamber. The further development of the growth of the animal is mainly characterized by the growth of the siphuncular substance, whereas the body occupying the living chamber enlarges in a smaller rate. This is contrary to the conditions in orthoceroids and nautiloids, where the growth of the body is more rapid and the increase in siphuncular organic substance inconsiderable.

Within the last segment almost always an increase in diameter of the endosiphuncular tube can be observed. It seems that an apical aperture of the conch exists, where the endosiphuncular tube ends, but it is still undecided whether such an aperture was held open during the life of the animal.

Development of the Actinoceroids.

Though our knowledge of the distribution and development of the Actinoceroids is far from being complete, a point is reached where it seems to be advisable to sum up the data at hand. During recent years considerable progress has been made in the study not only of the actinoceroids, but also of other groups of nautiloids in a broader sense. Still the problem as to the origin of the cephalopods remains unsolved. I shall not endeavor to enter into many speculations of that kind, but mainly restrict myself to actinoceroids proper.

Since Hyatt's time the shape and size of the septal neck (septal funnel) have played the most important rôle in the classification of the nautiloids. Quite recently newly revealed facts have led the present writer to doubt the usefulness of basing the classification on this feature instead of on others possibly more important. The same doubts have been independently expressed by Kobayashi in a recent publication. We know now, that in the same specimen the character of the septal neck may change from holochoanitic to cyrtochoanitic or orthochoanitic, from orthochoanitic to cyrtochoanitic, or from an actinoceroid to an armenoceroid type, either continually or irregularly. Serious doubts as to the systematic position of such specimens may arise, when the shape of the septal neck alone is taken as a criterion. Realizing the fact that, when the cephalopods are arranged under the present system of classification, we will find very different siphuncular structures among the different members of each group, Troedsson (1932) spoke of endoceroid, orthoceroid, and actinoceroid structures of the siphuncle, all of which could be found to develop within siphuncles of genera of each of the three larger groups of cephalopods. Recognizing, however, that the siphuncle is part of the body of the animal and its form and structure, therefore, reflects the organization of a part of the living animal, it at once becomes evident, that it is an impossibility to maintain classificatory principles by which animals with widely divaricating organization of the body are placed in the same systematic group.

It seems safer and at the same time more in accordance with biologic principles to pay more attention to the interior structure of the siphuncle as exhibited by those deposits which can be preserved. This still leaves us in a doubtful position with regard to the character of siphuncles lacking interior deposits, but nevertheless recent investigations seem to show that we are on safer ground when taking the structure and organization of the siphuncle as our basis of classification.

Therefore, the present writer proposed to abandon Holochoanoidea, Orthochoanoidea, and Cyrtochoanoidea as classificatory terms, though they may still conveniently be used in explaining the structures of the septal necks in individual groups. The length and the shape of the septal necks and in consequence the expressions holo-, ortho-, cyrtochoanitic may be used in the delineation of families and even genera or species. A similarity of the endosiphuncular structures counts heavier in favor of the kinship of various forms than a congruency of the septal necks, the bearing of which on systematics doubtlessly has been overestimated.

To replace the former terms the present writer proposed the names: *Endoceroidea* (largely identical with, but not entirely covering the former Holochoanites), mainly comprising forms with comparatively wide siphuncles containing a great variety of sheath-like deposits and horizontal diaphragms. The latter group, however, for which recently Hyatt's term "Diphragmida" has been successfully revived by Ulrich and Foerste, might eventually prove to be quite independent.

Actinoceroidea (largely identical with, but not entirely covering the annulosiphonate group of the Cyrtochoanites), comprising forms with mostly wide nummuloidal siphuncles and a distinctly developed endosiphuncular vascular system.

Cyrtoceroidea (identical with that part of the Actinosiphonate group of the Cyrtochoanites which actually shows radial lamellae within the siphuncle as true *Cyrtoceras* does). Very little is as yet known about the organization of this group.

"*Gomphoceroidea*," a group with mostly wide siphuncles of unknown interior structure. The name is provisional. The group may comprehend a variety of incoherent types of animals.

Nautiloidea sensu stricto, a term which should only be applied to the stenosiphonate, orthochoanitic forms with a siphuncle either degenerated or serving other purposes than that of the foregoing groups.

The Ammonoidea and the Nautiloidea, the latter in the sense here applied, have been linked closer together by recent investigations of Schindewolf. It may, therefore, become possible to divide the entire group of shell-bearing cephalopods in the two large sub-orders of the *Stenosiphonata* (Nautiloidea, Ammonoidea) and the *Eurysiphonata* (Endoveroidea, Actinoceroidea, Cyrtoceroidea, "Gomphoceroidea").

At present no really successful attempt could be made to link these two large groups together. Among the groups, however, belonging to the eurysiphonate branch of the cephalopoda we may be able to trace a few connections and point out some possibilities.

Several attempts have been made to derive the actinoceroids, or rather that entire extremely heterogenous group which has been called Cyrtochoanites, from the Orthochoanites or Nautiloidea s. str.

It must, however, be borne in mind, that the first known actinoceroids are forms with considerably wide siphuncles, such as *Maruyamaceras* from the Chazyan of Manchuria and *Nybyoceras* from the same formation in Manchuria and Oklahoma. On account of its age as well as on account of its structural features *Maruyamaceras* may well be regarded as an ancestral type of the actinoceroids or at least to be very near to it. From a *Maruyamaceras*-like type straight lines of development can be traced in almost every direction to the different branches of the actinoceroid groups. By preservation of the septal neck and a decrease in width of the siphuncle true actinoceratid forms may develop which can be traced upward until the Carboniferous to its last representative *Rayonnoceras.*

A side branch of this group may be the family of *Sactoceratidae* with greatly decreased siphuncle. From this point of view the *Sactoceratidae* represent a remarkably degenerated group of the actinoceroids.

Another large group which may have arisen from the ancestral *Maruyamaceras*-like type is represented by the *Armenoceratidae*, which resulted from an advancing shortage of the septal neck. Whether *Armenoceras* or *Nybyoceras* is the older type is difficult to decide. *Nybyoceras* makes its first occurrence in older beds than *Armenoceras*, but yet the *Armenoceras*-type has a more primitive significance. The decidedly excentric siphuncle as in *Nybyoceras* is usually regarded as a feature of more advanced specialization.

Apparently a direct offspring from *Armenoceras* or *Nybyoceras* is a group of curved animals, beginning with *Cyrtonybyoceras* and developing into *Megadiscosorus* and *Elrodoceras* in Silurian time. A descendant of *Nybyoceras* is *Selkirkoceras* with its flattened ventral side and with a siphuncle attached to the latter, a parallel to the *Kochoceras* branch of the *Actinoceratidae.*

A separate branch of the *Armenoceratidae* is represented by the *Huroniidae* and also by the *Gonioceratidae.* Both families have many features in common with the *Armenoceratidae,* but are both specialized in different directions.

Regarding the general tendencies of development the trend is rather to diminish the diameter of the siphuncle than to enlarge it, as it is usually assumed. It is the earliest forms of the actinoceroids that are characterized by large siphuncles. Among the younger representatives, in the Upper Ordovician as well as in the Silurian, the number of species with smaller siphuncles increases considerably, in fact, in the Silurian, actinoceroids with very wide siphuncles are rather uncommon.

With these facts in mind the suggestion lies quite near to derive the actinoceroids from other eurysiphonate forms rather than from stenosiphonate ones. It seems that in actinoceroids a wide siphuncle, not a narrow one, is a primitive feature.

Therefore, in my opinion, all attempts that have been made to connect genetically the Actinoceroids with the Orthochoanoidea (or Nautiloidea s. str., as I would prefer to call them) are likely to fail. It is true that Nautiloidea may be able to develop features of the siphuncle which in a certain degree can resemble those known in Actinoceroids. A slight inflation of the segments can be observed, rings of solid material around the septal necks may be built. But these features may very well be regarded as occasional convergencies, as they are frequently a hindrance for the delineation of true phylogenetical connections. In the same way intracameral deposits are common among the Nautiloidea which certainly does not impose the necessity of phylogenetic relationships to the actinoceroids, where they are more common.

It does not seem unlikely to suppose that the Actinoceroids branched off from some group of the Endoceroidea. As we now know, not all Endoceroidea are holochoanitic. In some very peculiar forms especially of Asiatic Endoceroidea the septal funnel does not reach the next septum. Between the end of the funnel and the next septum an outwardly curved connecting ring is intercalated, reminding strongly of actinoceroid structures of segmental walls. In these cases the outer appearance of the siphuncle is rather that of an actinoceroid, whereas the endosiphuncular structures, though not very well preserved, still seem to be that of an endoceroid. Forms of this kind have been described by Kobayashi as *Multicameroceras* and *Sinoeremoceras* from the Canadian of Manchuria.

Like the actinoceroids, these endoceroids are characterized by the presence of an endosiphuncular tube. In both cases the siphuncle is wide and must be regarded as having contained some important parts of the body of the animal. The endosiphuncular tube, the most important part of the siphuncle organ, was imbedded in the endosiphuncular tissue, which in most cases became calcified. The radial canals, radiating from the endosiphuncular tube and so characteristic for the Actinoceroids must represent a later stage of development, following the inflation of the siphuncular segments which already took place during the endoceroid stage of development.

A difficulty still represents itself in the fact that *Multicameroceras* and *Sinoeremoceras*, the two genera mentioned above, show marginal siphuncles. It is the general assumption that in all lines of cephalopod development the marginal position of the siphuncle indicates a later and more specialized stage. If this is true, *Multicameroceras* and *Sinoeremoceras* could not be supposed to be the immediate forerunners of the actinoceroids, but we would have to look for related types with the siphuncle situated in some distance from the wall of the conch.

In my opinion the cephalopods with narrow siphuncles as best known in *Orthoceras*, *Nautilus* and others, in other words the group to which I should like to restrict the name Nautiloidea, represent an entirely independent line of development. The unity and the monophyletic descent of the so-called shell-bearing cephalopoda may be seriously doubted.

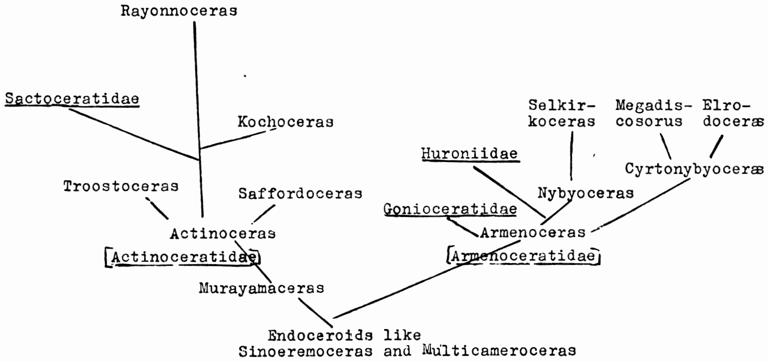
The so far known Cambrian cephalopods furnish too little evidence to settle the question. Schindewolf regarded *Volborthella* as orthochoanitic. An examination of the same material led Dr. Kobayashi and the present writer to the suspicion that this genus is more likely to show holochoanitic features. Moreover, we think that the septa are extremely close together. The writer counted about 20 of them to a millimeter.

This figure would fit with observations made on specimens of *Salterella* as given by T. H. Clark and Chr. Poulsen. However, the study of slides made from a number of *Salterella* specimens in the U. S. National Museum left the writer in a very doubtful position. These slides revealed structures essentially similar to those described by Clark and Poulsen. On the other hand it was impossible to the writer to find really conclusive evidence as to the cephalopod nature of this genus. It is doubtlessly not congeneric with *Volborthella*, which unquestionably is a cephalopod. In the specimens of *Salterella*, however, which I had the opportunity to investigate, no wall of the conch could be discovered. The nature of the "septal necks" was doubtful and even the very existence of a siphuncle was open to question. It appears that L. F. Spath (1933) is referring to similar observations, when speaking of transverse striation "more like that of certain rugose corals than of molluscan shells." However, to clear up the true nature of Salterella, further investigation is still needed.

In the accompanying table a scheme for the development of actinoceroids is proposed, which seems to be in accordance with the facts known at present. The basic principle is, that the actinoceroids are derived from eurysiphonate ancestors which may be similar to or identical with some known representatives of endoceroids. In these deductions the character of the septal neck is left out of consideration.

It was not the purpose of these lines to enter into a discussion of the phyletic relationships of other groups of cephalopods, but it may be added that even an apparently holochoanitic structure in Volborthella would not necessarily exclude the latter from the possibility of being ancestral to the so-called Orthochoanoidea.

Evolution of the Actinoceroids.



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